# THE CRUSTACEAN ZOOPLANKTON OF LOCH LEVEN, KINROSS.

*by*

MICHEL DONALD ANDREW JOHNSON B.Sc.

Thesis submitted for the degree of Doctor of Philosophy

DEPARTMENT OF BIOLOGY
UNIVERSITY OF STIRLING
JULY 1977

# ABSTRACT

The general biology and production ecology of the crustacean zooplankton of Loch Leven, Kinross, has been studied as a contribution to a major International Biological Programme - Freshwater Productivity study. The zooplankton populations were sampled on a routine basis throughout the period September 1971 - January 1974 and data was collected on all the major population parameters of the two co-dominant species, Daphnia hyalina var lacustris Sars and Cyclops strenuus abyssorum Sars, including changes in numerical densities of the various age and/or size groups, brood-sizes, body-sizes, horizontal and vertical distributions, cyclomorphotic changes in Daphnia and gut-contents analyses. The numerically subordinate species, Diaptomus gracilis Sars, Leptodora kindti (Focke) and Bythotrephes longimanus Leydig, were monitored solely in terms of numerical densities. Field observations were also made on water temperatures and water transparency; and additional laboratory work involved the assessment of growth-rates at various temperatures and the evaluation of a length-weight relationship for Daphnia, the resultant information being used in conjunction with appropriate population data to calculate biomass and production using a method based on the concept of finite growth-rates.

The work somewhat emphasised Daphnia due to its important role in secondary production and because this species had never before been studied in detail at Loch Leven. Cyclops strenuus abyssorum, which exclusively dominated the loch plankton within the years 1966-69, had been previously studied during 1969.

The seasonal changes in the above parameters are discussed and compared and contrasted with similar populations from other waters and also with the earlier work at Loch Leven. The annual mean biomass and total annual production for Daphnia were found to be 0.57 $gC/m^2$ and 13.68 $gC/m^2/year$ respectively in 1972; and 0.50 $gC/m^2$ and 15.64 $gC/m^2/year$ in 1973. For Cyclops these were 0.50 $gC/m^2$ and 4.45 $gC/m^2/year$ in 1972; and 0.95 $gC/m^2$ and 9.45 $gC/m^2/year$ in 1973. The zooplankton was assessed within the context of the Loch Leven ecosystem, with special emphasis on trophic interactions, and a detailed discussion of the peculiar post-war zooplankton species changes which had occurred at Loch Leven is presented.

# CONTENTS

SECTION A REVIEW

SECTION B MATERIALS AND METHODS

SECTION C RESULTS

CONTENTS/contd.

SECTION C RESULTS

SECTION D DISCUSSION

## CONTENTS/contd.

SECTION D DISCUSSION

2. *Daphnia hyalina* var *lacustris*

3. *Cyclops strenuus abyssorum*

CONTENTS/contd.

SECTION D DISCUSSION

BIBLIOGRAPHY

APPENDIX

# INTRODUCTION

In May 1966 an International Biological Programme, Freshwater Productivity study was initiated at Loch Leven, Kinross, as a combined research project between the Nature Conservancy, Edinburgh, the Freshwater Fisheries Laboratory, Pitlochry, and the Wildfowl Trust, Slimbridge. Shortly afterwards these organisations were joined by workers from the Universities of Stirling, Edinburgh, Dundee and St. Andrews. When the project reached its peak in October 1970, forty-one full or part-time workers were involved.

The basis of this study was to assess production at various trophic levels in Loch Leven and to define the flow of energy in the food chains ultimately relating to the fish population and the diving ducks.

The first detailed research programme on Loch Leven zooplankton was undertaken in 1969-70 by A.F. Walker at Stirling University. This work was designed to assess the quality and quantity of the zooplankton, at that time dominated by a copepod species *Cyclops strenuus abyssorum* Sars, its temporal and spatial variation and importance in the food web. The completed work formed the basis for an M.Sc. thesis (Walker 1970). Continuation in this line of research was considered to be of utmost importance, firstly because of the very significant role of zooplankton communities within the lake ecosystem and secondly because of drastic qualitative changes which had occurred in the Loch Leven zooplankton during 1970.

The aims and purposes of the present study, which began in September 1971, are to assess the quality and quantity of the crustacean zooplankton, its temporal and spatial variation, with a detailed emphasis on the biomass and production of the two dominant species, Daphnia hyalina var. lacustris Sars and Cyclops strenuus abyssorum Sars.

The thesis is somewhat biased [illegible] towards D firstly because this animal has never been studied in detail at LL and secondly because of its important trophic status in the loch ecosystem.

## SECTION A REVIEW

### 1. The study area

The morphology and history of the study area have been described extensively by Morgan (1970, 1972, 1974) and also by Kirby (1974). A brief summary is as follows:

Loch Leven lies within a wedge of hills in the fertile plain of Kinross (National Grid Ref. NO 145015) between Perth and Edinburgh and is positioned at longitude 3°30'W, latitude 56°10'N, at an altitude of 107m above sea-level. It covers an area of 13.3km$^2$ within a catchment extending to 145km$^2$, of which 70 per cent is rich agricultural farmland and 30 per cent is upland grassland and heath. The loch was formed at the end of the last glaciation from kettle-holes left in the glacial drift by retreating ice, and overlies substrata of Old Red Sandstone and Carboniferous bedrocks.

Loch Leven is relatively shallow, about 42 per cent being less than 3m deep, and has a mean depth of 3.9m with maximum depths occurring in the two main kettle-holes, the north and south deeps, which are 23.2m and 25.5m deep respectively (see map, Fig. 1). The bottom sediments consist mainly of sand and gravel in areas less than 3m deep, whereas in the deeper waters they are essentially organic muds except for a small zone of exposed glacial drift and gravel in the south deeps.

There are three main inflows to the loch, the North and South Queichs and the Gairney Water, which enter from the west draining the Ochil and Cleish Hills. Lying to the east is the River Leven, the main outflow, which controls the loch level by means of sluice-gates and eventually flows into the sea.

Loch Leven is widely exposed to wind, especially from the east and west, and this combined with its shallowness ensures that the water-body is mixed regularly and thoroughly. This situation rarely allows the establishment of thermally stratified layers.

The loch has gained world-wide recognition as a brown trout fishery and has been regarded as the most important inland water-body in Scotland for wildfowl. In 1964, it was declared a National Nature Reserve.

## 2. Important biological changes at Loch Leven

A detailed account of the biological history of the loch has been presented elsewhere (Morgan 1970, 1972, 1974). An outline of important changes is as follows :

In 1830, the water-level at Loch Leven was permanently lowered by 1.4m after an artificial channel was constructed for the outflowing River Leven in order to drain and thus reclaim land for agricultural purposes. This effected a reduction of the loch area by $4km^2$ and allowed the new water-level to fluctuate down a further 1.4m by means of sluices. The latter prevented the passage of migratory fish, salmon and sea-trout, into the loch. By 1837, the Charr had also ceased to inhabit the water.

Isolated scientific studies of Loch Leven at the turn of the century provided evidence of a water-body with an overwhelming abundance and diversity of submerged and emergent vegetation, with a rich invertebrate fauna and a crustacean zooplankton community primarily dominated by cladoceran filter-feeders. The loch had at least a moderately rich nutrient level typical of lowland-type lakes.

A similarly extensive vegetation, although apparently reduced, was noted shortly after the last war and, in the early 1950's, cladoceran filter-feeders were still evident.

However, by 1966 the loch had undergone serious biological changes. The macrophyte population and its associated fauna had drastically declined in quality and quantity, so too had many species of benthic invertebrates. Prolonged diatom and blue-green algal blooms occurred regularly and the number of species of green algae had decreased. The cladoceran filter-feeders of the loch had apparently disappeared leaving a crustacean zooplankton totally dominated by a cyclopoid copepod species

(Cyclops strenuus abyssorum Sars). Furthermore, fewer wildfowl frequented the loch to moult and the quality of the brown trout fishing was notably poorer.

Further changes have occurred since. In the summer of 1970, a former member of the Loch Leven zooplankton, the cladoceran Daphnia hyalina var. lacustris Sars, reappeared. This was coincident with changes in the phytoplankton from one essentially dominated by small species to one composed mainly of large species (Bailey-Watts 1974). Similarly, the submerged macrophytes increased in abundance (Jupp et al. 1974) and the brown trout fishing showed a considerable improvement with bigger, better-conditioned fish being caught.

Although numerous changes in the lake biota are commonplace in the normal course of eutrophication, such changes as exhibited by Loch Leven in recent years are as unusual as they are drastic.

## 3. Eutrophication at Loch Leven

Although Loch Leven is a naturally nutrient-rich water, man has considerably increased the rate of eutrophication - especially since the last war. The extensive use of nitrogenous fertilisers by agricultural farmers and the recent establishment of poultry units within the catchment have increasingly contributed nitrogen to the loch via leaching through the substrata or, more directly, via run-offs to feeder-streams (Morgan 1974). The local townships of Kinross and Milnathort provide a regular discharge of domestic sewage into the water and a nearby woollen mill has increased the phosphate input by releasing detergent effluents (Walker 1970; Morgan 1974). The woollen industry has also been responsible for contaminating the loch with dieldrin, a chlorinated hydrocarbon pesticide, until the use of this chemical was abandoned in 1964 (Holden 1966).

The sources and quantities of nutrients discharged into Loch Leven have been assessed by Holden and Caines (1974).

## 4. Qualitative changes in the zooplankton

The zooplankton of Loch Leven has undergone considerable qualitative changes during the present century. Periodic species lists form a framework to illustrate these changes (Table 1).

Investigations by Scott (1891, 1898) at the turn of the century revealed a rich crustacean population comprising of twenty-one species of Cladocera and eighteen species of Copepoda. In open water tow-net samples, he recorded at least three species of *Daphnia*, three species of *Bosmina*, two species of predatory Cladocera and six species of Copepoda. Amongst the most numerous were *Daphnia lacustris* Sars (*D. hyalina* var. *lacustris* Sars), *Cyclops strenuus* (Fischer) (presumed to be *C. strenuus abyssorum* Sars, Johnson and Walker 1974) and also *Diaptomus gracilis* Sars.

# Changes in the Loch Leven Zooplankton

| | 1890 | 1897-98 | 1952 | 1954 | 1966-68 | 1969 | 1970 | 1971 | 1972-73 |
|---|---|---|---|---|---|---|---|---|---|
| CLADOCERA | | | | | | | | | |
| *Daphnia hyalina* var. *lacustris* Sars | — | ■ | ■ | ■ | O | O | ■ | ■ | ■ |
| *D. longispina* O.F. Müller | ■ | — | — | — | O | O | O | O | O |
| *D. pulex* (De Geer) | ■ | — | — | — | O | O | O | O | O |
| *Diaphanosoma brachyurum* Lievin | ■ | — | — | — | O | O | O | O | O |
| *Bosmina longirostris* (O.F. Müller) | ■ | ■ | — | — | O | O | O | O | O |
| *B. coregoni* var. *longispina* (Leydig) | — | ■ | — | — | O | O | O | O | O |
| *B. coregoni* var. *obtusirostris* (Sars) | — | ■ | — | ■ | O | O | O | O | O |
| *Bythotrephes longimanus* Leydig | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Leptodora kindti* (Focke) | ■ | ■ | — | — | ■ | O | ■ | ■ | ■ |
| *Polyphemus pediculus* (L.) | ■ | — | — | — | O | O | O | O | O |
| COPEPODA | | | | | | | | | |
| *Diaptomus gracilis* Sars | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Cyclops strenuus* (Fischer) | ■ | ■ | — | ■ | O | O | O | O | O |
| *C. strenuus abyssorum* Sars | — | — | — | — | ■ | ■ | ■ | ■ | ■ |
| *C. albidus* (Jurine) | ■ | ■ | — | — | O | ■ | O | O | O |
| *C. macrurus* (Sars) | — | ■ | — | — | O | O | O | O | O |
| *C. agilis* (Koch, Sars) | ■ | ■ | ■ | — | O | O | O | O | O |

■ Present. O Absent — Not found, limited samples.

Note : 1. The first seven Cladocera are filter-feeders — the last three are predatory.

2. *Cyclops strenuus* (Fischer) can be presumed synonymous with *C. strenuus abyssorum*.

Table 1 lists the Copepoda and Cladocera of Loch Leven which, according to Harding and Smith (1960) and Scourfield and Harding (1958), are essentially planktonic. Those associated with with macrophytes and the benthos are listed elsewhere (Maitland and Hudspith 1974).

In 1954 Woodward took three pump samples from Kinross pier and noted the presence of *D. hyalina* var. *lacustris*, *Bosmina coregoni* var. *obtusirostris* (Sars), *Chydorus sphaericus* (O.F. Müller), *Bythotrephes longimanus* Leydig, together with *Cyclops strenuus* (again presumed to be *C. strenuus abyssorum*) and *Diaptomus gracilis*. In 1952 and 1954 *Daphnia* spp. were taken from trout stomach contents (Balmain and Shearer 1953; Morgan 1970).

However, by 1966 the filter-feeding Cladocera had disappeared so that from at least 1966 until the summer of 1970, the crustacean zooplankton of Loch Leven was consistently dominated by the cyclopoid copepod *C. s. abyssorum* with *D. gracilis* forming no more than 5 per cent by number and with the predatory cladocerans *Leptodora kindti* (Focke) and *B. longimanus* present in small numbers each autumn (Walker 1970; Bailey-Watts unpublished). It is very unusual for a zooplankton community to be dominated by a non-filter-feeder.

Late in 1970, the filter-feeding *D. hyalina* var. *lacustris* reappeared and has since maintained an important co-dominant position in the zooplankton of Loch Leven.

## 5. The principal planktonic crustacea encountered at Loch Leven during the present study

### (a) Cladocera

The taxonomy of this group have been described by Birge (1918), Brooks (1966) and also by Scourfield and Harding (1966). According to the work of the latter authors, the Cladocera form an order within the sub-class Branchiopoda and are further separated on the basis of feeding mechanisms into two divisions, the Calyptomera and the Gymnomera. The Calyptomera is comprised of four families and includes all the filter-feeding forms and surface raspers. The Gymnomera consist of two families of active predators.

The most important cladoceran present at Loch Leven is *Daphnia hyalina* var. *lacustris* Sars, classified within the family Daphniidae, division Calyptomera. The identification of this species at the loch by Walker (1970) has been criticised by Hrbacek (pers. comm.) who is of the opinion that the daphnid is *D. hyalina* var. *galeata* Sars. The present author, having compared samples of *D. hyalina* var. *galeata* from Lake Windermere with the Loch Leven form suggests that the original identification holds true as it conforms with the diagnostic characteristics depicted in Scourfield and Harding (1966) - the ventral margin of the head is distinctly concave and the head crest of the summer form is less pronounced and less pointed than that of the Windermere species. Cyclomorphotic changes as exhibited by these species may provide confusion in identification especially when this relates to the head shape (see Fig. 13).

The general morphology and biology of *Daphnia* spp. is well known and extensively documented. *Daphnia* spp. are found in all types of standing water in Britain and are small in size - less than 5 mm in length. Their populations are typically composed of parthenogenetic females which commonly undergo seasonal cyclomorphotic changes. Males usually appear in autumn or at the onset of adverse conditions to engage in sexual reproduction, thereby giving rise to resistant resting-eggs known as ephippia. Feeding is effected by filtration of microscopic algae and fine detritus from the surrounding medium. By feeding upon primary producers and in turn being consumed by tertiary producers such as fish fry, Daphnia provide an important contribution to the general energy flow of standing waters.

Varieties of Daphnia hyalina have been recorded in many of the Lake District waters (Smyly 1968 a), in Queen Mary Reservoir near London ( Steel et al. 1972) and in Lough Neagh, Northern Ireland (Graham 1970). The Loch Leven form D. hyalina var. lacustris has been found in three Lake District waters (Scourfield and Harding 1966) and in Eglwys Nynydd, South Wales (George and Edwards 1974). In Scotland this species has been found in Loch Lomond (Chapman 1965) and in four lochs within a twenty-five mile radius of Loch Leven (Walker 1970).

Two other planktonic cladocerans occur regularly at Loch Leven. These are the predatory species Leptodora kindti (Focke) and Bythotrephes longimanus Leydig belonging respectively to the families Leptodoridae and Polyphemidae within the division Gymnomera (Scourfield and Harding 1966).

*Leptodora kindti* is a large, extremely transparent cladoceran with adult females attaining the size of 18 mm (Brooks 1966). It is widespread but very scarce in the Lake District (Smyly 1968a) and has a consistent seasonal presence from May to October in the Windermere plankton (Scourfield and Harding 1966). A significant feature of its life history is that its winter eggs hatch into nauplii (or metanauplii) as distinct from other Cladocera which develop directly from parthenogenetic and fertilised eggs (Brooks 1966). *Leptodora* is an active predator, seizing large particles with its prehensile legs. Investigations by Cummins *et al*. (1969) have shown that the adults are fluid-feeders relying primarily on *Daphnia* and *Cyclops* as prey - the immature individuals probably feeding upon algae, bacteria and organic detritus.

*Bythotrephes longimanus* has a relatively small body, females reaching 2-3mm in length, with a long posterior spine greater than two times the body length. Like *Leptodora*, it is colourless, transparent and actively predatory. It also has a comparable distribution in the Lake District with a similar seasonal presence in the plankton of Windermere. Smyly (1968a) found the two species co-existing in eleven Lake District waters.

### (b) Copepoda

The taxonomy of British freshwater Copepoda has been described by Gurney (1931-33) and reassessed by Harding and Smith (1960). The Order Copepoda is divided into three sub-orders, the Cyclopoida, Calanoida and

Harpacticoida. Members of the first two sub-orders commonly inhabit benthic, littoral and limnetic zones of standing waters, the Harpacticoida are typically benthic and littoral forms (Wilson and Yeatman 1959).

The principal copepod of the Loch Leven plankton is a species of *Cyclops strenuus*, belonging to the sub-order Cyclopoida, genus Cyclops and sub-genus Cyclops. According to Harding and Smith (1960), two forms of *C. strenuus* are found in Britain, *C. s.* (*s. str.*) (Fischer) and *C.s. abyssorum* Sars, differing essentially in body size, with *C.s.* (*s. str.*) being the larger of the two, and also in the structural components of legs IV and V. Although species of *C. strenuus* are known to be very variable (Gurney 1933; Kozminski 1927, 1932) with their taxonomy being somewhat ambiguous, the Loch Leven form complies in every respect except size to the description of *C. s. abyssorum*. Harding and Smith (1960) specify a size range of 1.20 - 1.47 mm (minus furcal setae) for adult females of the species in contrast to the range 1.20 - 2.35 mm established for the Loch Leven form during the present study.

According to Harding and Smith (1960) *C. strenuus* (*s. str.*) commonly occurs in small ponds and ditches throughout England, has been recorded in Wales and Ireland, but is rare in Scotland. Its presence in the Lake District is uncertain. *C.s. abyssorum* is widespread in Scotland

and in the Lake District. Smyly (1968a) observed that C.s. abyssorum and Mesocyclops leuckarti (Claus) were the common limnetic species of the Lake District and co-existed in three lakes where their competition was restricted by differing seasonal cycles and depth distributions. C.s. abyssorum was found alone in eleven of the lakes. The two species were also found together in Loch Lomond, Scotland (Chapman 1965) and C.s. abyssorum has been recorded in five lochs within a twenty-five mile radius of Loch Leven (Walker 1970).

The annual cycle of C.s. abyssorum seems to be variable, being monocyclic in some waters and polycyclic, with continuous reproduction, in others. Gurney (1933) suggested that the species is monocyclic and breeds in late summer and autumn. The Loch Lomond species is certainly monocyclic but breeds from June until early autumn (Chapman 1965). In contrast, Walker (1970) found that the Loch Leven form was polycyclic.

Several members of the Cyclopoida undergo periods of quiescence during unfavourable conditions. The subject of diapause has been reviewed by Elgmork (1967) whose literature survey lists eighteen species of Cyclopoida exhibiting this phenomenon. Diapause is prevalent in late copepodid stages (often stage IV) and adults and may involve encystment. Usually only one stage is capable of dormancy although as many as four have been known for *Cyclops scutifer* (Elgmork 1962; 1965). Wierzbicka (1962) observed that adults of *Cyclops abyssorum* (*C.s. abyssorum*) burrowed down into the bottom mud and remained there for long periods and Chapman (1965) deduced that the same species in Loch Lomond overwintered as resting eggs. However, the Loch Leven form has not been known to undergo dormancy (Walker 1970).

Some species of *Cyclops* are known to be carnivorous. Fryer (1957a, b) studied the predatory behaviour of several Cyclopoida and noted that *C. strenuus abyssorum* was an active planktonic predator, primarily feeding upon the calanoid copepod *Diaptomus* sp. and assumed that, if this prey species was not available, Cladocera and rotifers would be suitable food items. Canabalism among cyclopoids has also been noted. McQueen (1969) working on *C. bicuspidatus thomasi* demonstrated that adults and pre-adult stages IV and V consumed 31 per cent of their own nauplii standing crop. Having mentioned nauplii, it is important to note that the nauplii of *Cyclops* spp. are phytophagus and possess a primitive mechanism for catching nannoplankton (Ruttner 1968).

Laboratory culture techniques and growth-rates of *C. strenuus abyssorum* have been studied by Lewis *et al.* (1971) and Whitehouse and Lewis (1973) - see Results Section.

The only other copepod which features regularly in the plankton of Loch Leven is *Diaptomus gracilis*

Sars, belonging to the sub-order Calanoida, genus Diaptomus. It is essentially a planktonic filter-feeder relying on nannoplankton for its nutrition (Ruttner 1968). Its distribution is widespread in Scotland and Ireland, and in the Lake District and Norfolk Broads in England (Harding and Smith 1960). D. gracilis is the dominant zooplankter in Loch Lomond where it rarely forms less than 40 per cent by number of the limnetic crustaceans (Chapman 1965).

## 6. Zooplankton sampling techniques

Zooplankton sampling techniques are discussed in comprehensive surveys by Fraser (1968) and Edmondson and Winberg (1971). Numerous methods are available for quantitative work, each having advantages and disadvantages, the choice being dictated by the specific requirements of the task undertaken and the characteristics of the water to be sampled (Elster 1958). As a rule, zooplankton are not distributed at random but tend to be patchy, thus presenting the main problem of zooplankton sampling.

Vertical hauls using tow-nets are frequently used for quantitative work by virtue of their simplicity but, unfortunately, give rise to many problems (Elster 1958). The main difficulty involves the progressive clogging and consequent decrease in filtering efficiency of the meshwork during tows. This can be partially overcome by restricting the tows to short distances only, increasing the mesh aperture-size or increasing the ratio of filtering surface to mouth area. However, nets are suitable for qualitative work.

The Clarke-Bumpus sampler (Clarke and Bumpus 1950) is a highly sophisticated tow-net incorporating a flow-meter, a truncated entrance and an opening and closing device. Despite having the usual disadvantages of a net and being notably inefficient when fine meshwork is used (Langford 1952), it is extremely versatile and can be used to good effect in large, deep waterbodies where substantial volumes of water can be filtered in both vertical and horizontal planes.

The plankton trap is another sampler incorporating a net. It consists of a metal box of ten litres capacity with hinged (or sliding) top and bottom lids, the net being in a fixed position at the lower end (Juday 1916; Clarke 1942). Once the apparatus is lowered to the required depth with its two lids open, a messenger device triggers the lids shut. The box is filtered as it is lifted out of the water.

Water-bottle samplers work in essentially the same way as the plankton traps but do not possess a net - the water sample being lifted to the surface and filtered through a detachable gauge cylinder fitted to the lower lid. These samplers are usually of five litres capacity in order to make them convenient for lifting. Examples of these samplers are the Friedinger (Walker 1970), Rodhe (1946), Bernatowicz (1953) and Patalas (1954) types.

The trap and bottle samplers are particularly advantageous for quantitative studies because they collect a precise volume of water from a known depth and their efficiency is unlikely to alter between samples. They are also relatively simple to use. However, they have two distinct disadvantages. Firstly, the volume of water collected is small, so that numerous samples are needed to provide representative quantitative information for the entire lake. This is especially true with the smaller water-bottles. Secondly, certain zooplankters, notably the more mobile ones, are likely to show avoidance reactions. Smyly (1968b) showed that, unless the sampler was closed at or immediately after it reached the sampling depth, the animals within would escape progressively; and also that the effects of avoidance could be reduced by building the walls of the sampler from transparent material such as perspex, instead of metal.

The "water-core" or tube sampler is a useful instrument when information on vertical distribution is not important. It is essentially a tube of selected diameter and length with a closing mechanism and weight at one end. Usually the tube is rubber or plastic with thin flexible walls which can maintain an even circular cross-section. Its operation is simple. Having lowered the tube, weighted end first, to the desired depth, it is then closed. For short cores up to 4m, a straight, stiff plastic tube (i.e. a household drain-pipe) can be used. Pennak (1962) has used this method for sampling free-swimming organisms amongst vegetation.

Various battery-operated and hand-turned pumps, attached to rubber tubes up to 30m long, have been used for sampling zooplankton and allow the uptake of large volumes of water as well as facilitating continual sampling. However, the main draw-backs with these devices is that they are extremely bulky requiring a sizeable boat for transportation and, more important, the intake currents incite avoidance reactions by zooplankton (Fleminger and Clutter 1965; Szlauer 1968).

Walker (1970) deduced that Loch Leven could be effectively sampled quantitatively using a water-bottle sampler, having considered the characteristics of the water, the type of information to be collected and following recommendations given by Edmondson and Winberg (I.B.P. manual - published 1971). He used a 5-litre Friedinger type (modified by Gilson of the Freshwater Biological Association) incorporating a rigid perspex tube and closing lids designed so as not to impede the flow of water through the tube as the sampler descended to its sampling destination. In order to provide directly comparable data to that of Walker (1970) and because the water-bottle samplers are reliable and accurate sampling devices, the Friedinger sampler was chosen for the task undertaken in the present study.

Figure 1 (opposite)

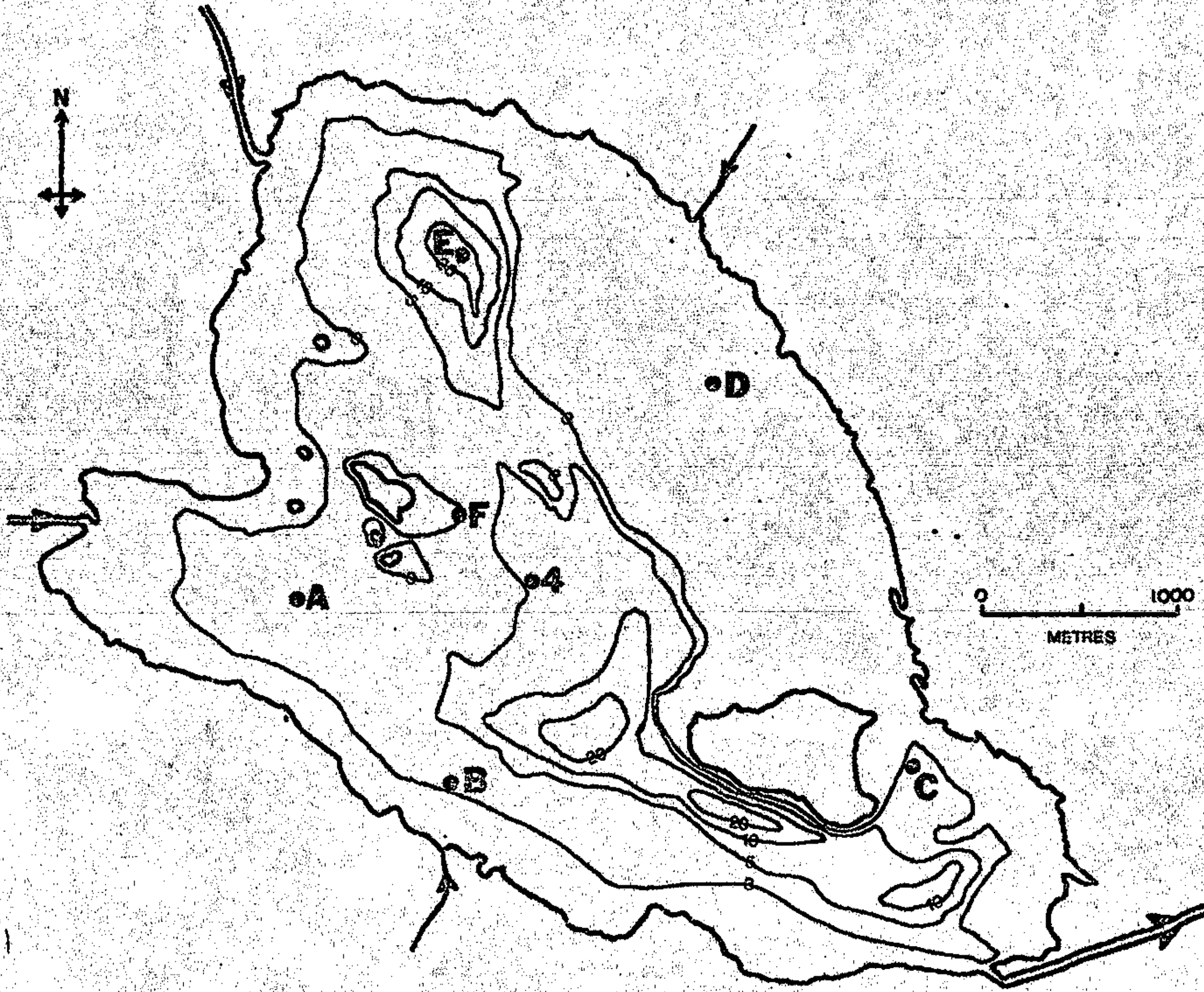
Sampling sites at Loch Leven, Kinross.

The sampling sites are shown by capital letters A, B, C, D, E and F and also by the Number 4. Relevent details about these sites are given in the table below. Depth contours in metres are shown by the thin lines and islands are bounded by thick lines. The inflow streams in clockwork rotation from the base of the map are the Gairney water, the South Queich, the North Queich and the Pow Burn. The outflow, controlled by means of a sluice, is into the River Leven. The boat-house is situated beside the inflowing South Queich.

| Site | Minimum Depth m. | Number of Friedinger samples collected including replicates | Bottom substrate (Smith 1974) |
|---|---|---|---|
| A | 3 | 6 | mud |
| B | 3 | 6 | mud |
| C | 3 | 6 | mud |
| D | 2 | 4 | sand |
| E | 20+ | 18 | mud |
| F | 4 | 8 | mud |
| 4 | 5 | 10 | mud |

From September 1971 to March 1972 sampling was carried out at Site 4 only. For the remainder of 1972, the full six sites were sampled, collecting forty-eight Throughout 1973, however, three sites, A,D and

Fig. 1



sampling these three sites would provide similar estimates to those obtained from the six sites. Having collected a considerable volume of data by sampling the full six sites on seventeen occasions in 1972, information on the horizontal distributions of Cyclops strenuus abyssorum and Daphnia hyalina var. lacustris was reviewed. Analysis of the data (Results Section, Tables 2 and 7) showed that if three of the sites A, D and E had been sampled (collecting twenty-eight Friedinger samples) the calculated mean estimates for Cyclops and Daphnia as compared to those obtained for the full six sites (forty-eight samples) would have a maximum variation of ± 35 per cent. The data for the cyclopoid species (all developmental instars included) showed that sampling the three sites on thirteen occasions would have provided estimates less than ± 10 per cent. Variations shown by the cladoceran were, however, slightly greater - on eight occasions the variation was less than ± 15 per cent, with a maximum at ± 35 per cent. Consequently, samples were collected from three sites during 1973.

Sampling was undertaken at 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. As a rule, sampling took place at monthly intervals during the spring, summer and autumn periods.

The sites were visited in alphabetical order and sampling was timed so that the deep site, E, was dealt with at approximately mid-day (12 noon - 2.00 p.m.) thus attempting to regularise temporal changes in zooplankton distribution. The location of the sites was simplified by use of land-marks and depth-finders and, in the case of site E, by means of a marker-bouy.

At each site replicate Friedinger samples were collected from each metre depth, from the surface to the bottom, except at the deep site E where this procedure was maintained down to 5 metres and thereafter at 5-metre intervals.

Water temperature readings were obtained from each sampling depth at each site using a thermistor. This device was regularly calibrated to ensure accuracy. Throughout 1973, a 20 cm diameter all-white secchi disc was used to estimate transparency - usually at the north deeps.

On each visit qualitative vertical, oblique and horizontal tow-net samples were collected, usually from the north deeps, using standard coarse (23.6 mesh per cm) and fine (70.8 mesh per cm) nylon plankton nets as supplied by the F.B.A. When quantitative trips were abandoned, mainly because of strong wind conditions, tow-net samples were collected from the west bay near the boat-house. The bulk of these samples was preserved in dilute formalin, 4 per cent, in 300 ml bottles, whilst the remainder was kept fresh in order to examine the gut contents of Daphnia and Cyclops and to note the presence of rotifers.

On occasions when Perch (Perca fluviatilis L.) fry shoals accumulated in the boat-house bay, samples were captured with nets in order to examine gut contents for the presence of zooplankton.

## (b) Sample analysis

### i. Analysis of Friedinger samples

Individual tubed samples were pipetted into a revolving counting-trough adapted from Ward (1955) and Warren (1958) and constructed in the Stirling University workshops. The counting trough consists of a perspex disc, incorporating a circular channel (7 mm wide and 5 mm deep) where the sample contents are placed, and is mounted by means of a ball-bearing race on an adjustable perspex stage. The apparatus was set under a binocular microscope - the extent of the microscope field being marginally greater than the width of the channel. By slow manual rotation of the disc, the zooplankton sample, whose limits are fixed by a block in the channel, can be fully enumerated.

All samples were counted in their entirety, all organisms other than the rotifers being identified and counted. In practise, the main organisms encountered were the crustaceans, Cyclops strenuus abyssorum, Daphnia hyalina var. lacustris and Diaptomus gracilis with seasonal appearances of Bythotrephes longimanus and Leptodora kindti. 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 and nematodes were not identified further. After examination, the samples were replaced into their respective specimen tubes using a pipette.

Knowledge of the age or size structure of a species population is necessary to analyse its population changes fully. The two principal Crustacea, C.s. abyssorum and D.h. var lacustris were thus analysed on a developmental instar basis and size basis respectively.

Individuals of C.s. abyssorum were identified as nauplii (all five instars grouped) and as separate copepodid instars I - VI. Sexes were differentiated at instars V and VI (adults). Adult females were recorded as ovigerous or non-ovigerous and all egg sacs were counted, attached or loose.

Unlike copepods, Daphnia do not exhibit identifiable age specific characteristics, thus making it more difficult to describe the age structure of the population. It is, therefore, necessary to adopt appropriate size-class limits. By means of a calibrated microscope eye-piece grid, the D. h. var. lacustris individuals were sub-divided into four size-classes:

| | | |
|---|---|---|
| Class 1 | <1.00 mm | Immature |
| 2 | 1.00 - 1.39 mm | |
| 3 | 1.40 - 1.99 mm | Mature |
| 4 | >2.00 mm | |

The animals are measured from the base of the tail spine to the top of the head* - the measurement corresponding to the "total length" of Anderson (1932) and "length" of Edmondson (1955). The lower limit of the third class was found to correspond to the carapace length at the onset of reproduction - no animals below 1.40 mm carried eggs. As the sample was being analysed, all egg-bearing Daphnia were counted together with any loose eggs if they occurred. The above size-class limits have been adopted for D. hyalina Leydig by Steel et al. (1972) and for D. hyalina var. lacustris by George and Edwards (1974).

---

* For most of the year, round-headed and approximately round-headed Daphnia prevail but in late summer and autumn, peaked headed individuals appear (Fig. 13 and 14). The crest is relatively small (approximately 6 per cent of the length) and cyclomorphotic distortion of the head is slight. To overcome this discrepancy when measuring, it is possible to discount the crest by visualising the individual as being

When samples consisted of excessively large numbers of either C. s. abyssorum or D. h. var lacustris, part of the sample, one quarter or more usually one half was used for Cyclops instar analysis or Daphnia size-class analysis. The sub-sampling did not, however, include copepod nauplii, egg-bearing females or loose egg sacs - these were always fully enumerated. Occasionally the sub-sampling technique was checked by doing total instar or size counts after sub-sampling and the accuracy was found to be consistently high.

A series of mechanical tap-counters was used to record the various animals as they passed through the microscope field. Tungsten needles (0.2 mm or 35 S.W.G., sharpened in fused sodium nitrite) mounted in glass rods were used to manipulate the animals where necessary and the adjustable "zoom" magnification of the microscope (x28 - x120) was used when greater detail was required for copepod instar analysis.

## II. Analysis of net samples

Preserved samples taken with coarse nets on each visit to Loch Leven were used for assessment of Daphnia egg/embryo numbers, adult body size and cyclomorphotic variations and for Cyclops adult female body size and egg numbers per egg sac. When ovigerous females of Diaptomus gracilis were present in appreciable numbers, the egg numbers per egg sac were estimated.

The net samples were placed in a 500 ml round-bottomed were withdrawn using a stempel-type pipette. The sub-samples were placed into a petri-dish marked with grid-partitions and examined under the binocular microscope. This was maintained until a total of one hundred egg bearing Daphnia had been collected and removed to a separate petri-dish. Groups of individuals were systematically placed on a slide and measured under a microscope, with a calibrated eye-piece, to an accuracy of 0.026 mm. To avoid complications caused by cyclomorphotic variations of the helmet and because greater accuracy was required than that used for placing individuals into size-classes, Daphnia body sizes were measured according to Burns (1969) - from the base of the tail to the middle of the insertion of the locomotory antenna. The cyclomorphotic variation, separated essentially into four categories (Fig. 13), was noted for each individual. Once a group of individuals had been measured, the slide was placed under the binocular microscope and the number of eggs (or embryos) per brood pouch was determined by teasing the eggs from the carapace using tungsten needles.

When Daphnia were low in abundance, such as during winter, it was necessary to search the entire net sample on a systematic basis (dispensing with the use of the stempel pipette) until sufficient animals had been obtained. The net samples were similarly searched for ovigerous Cyclops strenuus abyssorum females, because of their relative scarcity. Usually fifty such individuals were thus collected although on occasions it was necessary to lower the target number to twenty-five. The metasomal and total body lengths (Fig.23) were measured and egg sacs were teased apart to acertain egg numbers - the apparatus and methods being similar to that used for Daphnia hyalina var. lacustris. Where less than the specified numbers of Daphnia or Cyclops individuals were collected for the above purposes, details are given in the appendix data sheets relating to appropriate graphical figures.

Fresh samples, collected using the fine net, were used for superficial examination of the rotifer populations and to obtain live samples of Cyclops strenuus abyssorum and Daphnia hyalina var. lacustris for assessment of gut contents. Cyclops and Daphnia individuals were washed in tap-water, placed on a clean slide and dissected under the binocular microscope using tungsten needles in order to remove the digestive tract. The latter was placed on a separate clean slide with a cover-slip added and examined under high-power (and oil-emersion) lens of a standard microscope. When necessary, the gut contents could be extruded by slight pressure applied to the cover-slip. On the whole, gut-contents analysis was not undertaken on a regular basis. The gut contents of Daphnia from Loch Leven have been studied in detail by Bailey-Watts (pers. comm.).

When Perch fry had been netted from the boat-house bay, the stomach contents of several individuals were examined for the presence of zooplankton.

## SECTION C RESULTS

### 1. Physical parameters

#### (a) Temperature

As water temperature is an important environmental variable influencing the growth-rates of planktonic Crustacea, recordings of temperature were obtained on every sampling trip to Loch Leven. The mean temperatures, as will be seen later, have a fundamental role in the production estimates of *Daphnia hyalina* var. *lacustris* and *Cyclops strenuus abyssorum*.

The mean water temperatures for the entire sampling period are shown in Fig. 2. The mean data was obtained from the average of all temperature readings at every sampling site and depth on each quantitative (Friedinger) sampling visit to the loch. Also included is the mean temperature obtained from the average of surface and bottom readings taken at one site only, in the west bay near site A, on net sampling visits.

The annual mean temperature cycles of 1972 and 1973 were essentially similar. During the winter months or, more specifically, from at least mid-November until early March of the following year as in the 1972-73 winter, mean loch temperatures remained below 5°C, fluctuating at 3-4°C approximately maximum density. Only on one sampling trip (18th December 1973) was the loch found to be covered by ice. The winters throughout the duration of the present study were relatively mild by mid-Scotland standards, and the loch surface was rarely frozen. In such cases the ice was not extensive and only very short-lived, being broken down readily by wind action.

From March, in both years, the mean loch temperatures increased progressively and reached maximum limits in August. From late August, the temperatures decreased progressively with temperatures below $5^{o}C$ occurring at the onset of winter in November. In 1972 mean temperatures remained above $10^{o}C$ from late April until mid-October and remained above $15^{o}C$ from mid-June until early September. The maximum mean temperature for the year was $18.1^{o}C$ and occurred in mid-August. In 1973, temperatures were above $10^{o}C$ from mid-May to early October and above $15^{o}C$ from mid-June to early September. An annual maximum of $17.8^{o}C$ was achieved in mid-August.

Smith (1974) has evaluated the average annual temperature cycle at Loch Leven from recordings throughout the years 1968-71, and also an annual total radiation balance. He defined four distinct temperature phases within the annual cycle. Firstly, a heating phase from mid-March to the end of May, then a warm phase from the beginning of June to the end of August. The third phase, the cooling phase, occurred from September to mid-November, this being

Figure 2 (opposite)

Seasonal changes in mean water temperature at Loch Leven during 1972-73.

Abcissa - the study period

Ordinate - the mean water temperature in $^{o}$C.

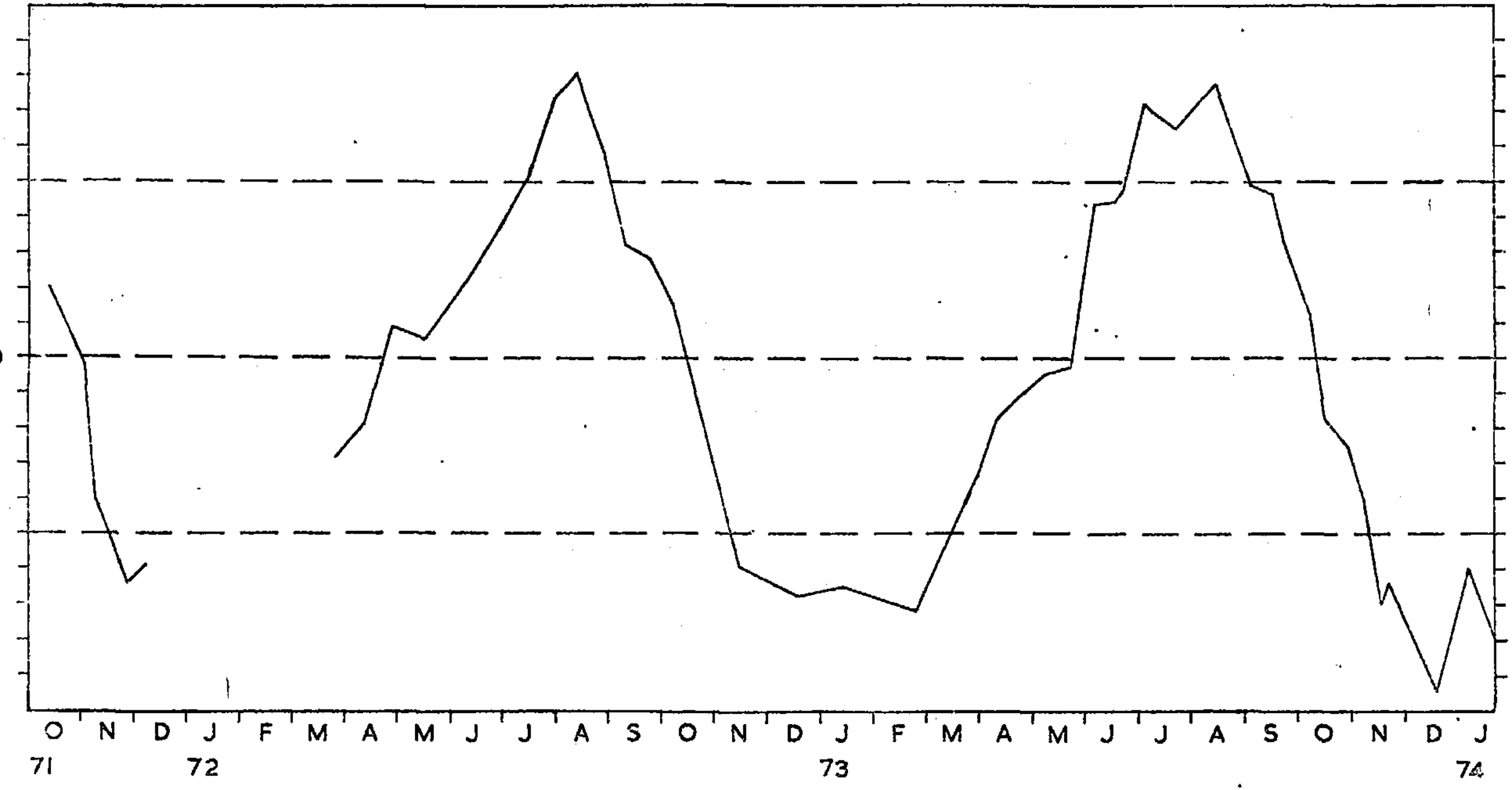


Fig. 2

followed by the winter cold phase. The mean temperature data collected for 1972 and 1973 during the present study conforms in all essentials to the typical annual Loch Leven pattern described by Smith 1974.

The appendix sheet to Fig. 2 (appendix {i}) gives the mean surface and mean bottom temperatures from all six sampling sites in 1972 and from three sites in 1973, together with the surface and bottom temperatures obtained at a 3m site on net sampling visits. The data shows that throughout the year, in both years, the mean surface and bottom temperatures were very similar with variations rarely exceeding 1°C. A maximum difference in excess of 1°C was, however, recorded in mid-August 1973 - the difference being 3°C.

Fig. 3 shows the surface and bottom temperatures as obtained at Site E, the north deeps, on quantitative visits during 1972 and 1973. The bottom temperature refers to a depth of 20m. For most of the year, in both years, the surface and bottom temperatures were similar although generally the surface temperatures were marginally higher - less than 1°C. However, during the summer months, especially during 1973, the surface temperature was noticeably higher than that of the bottom. The maximum temperature difference recorded was 4°C occurring in early June 1973.

On no occasion during the study was a thermocline recorded although temporary stratification was noted by Walker (1970) in June 1969 at the same site.

As temperature differences between surface and bottom are minimal throughout the year, it is readily apparent that the whole water body is undergoing seasonal temperature changes, this being attributed to the shallow nature of Loch Leven and the fact that the water is subject to thorough mixing by wind-induced circulation at all times of the year. This contrasts to the temperature cycle of deep (and presumably more sheltered) temperate standing-waters described by Ruttner (1968) where distinct stratification with a thermocline is established in the summer months and the surface temperatures are very much higher than those of the bottom with the latter often remaining at low winter temperatures.

### (b) Transparency

Throughout 1973 only, relative transparency readings were obtained on each sampling trip using a 20 cm. secchi disc. Fig. 4 shows the annual variations in water clarity, with the depths of secchi disc visibility being given in cms.

In the first five months of the year the water clarity progressively decreased from a January secchi disc

Figure 3 (opposite)

Seasonal changes in water temperature at the surface and at the bottom of the north deeps (Site E) of Loch Leven during 1972-73.

Abcissa - the study period

Ordinate - the water temperature in $^{o}C$.

The solid line designates surface temperature and the broken line designates bottom temperature.

Fig. 3

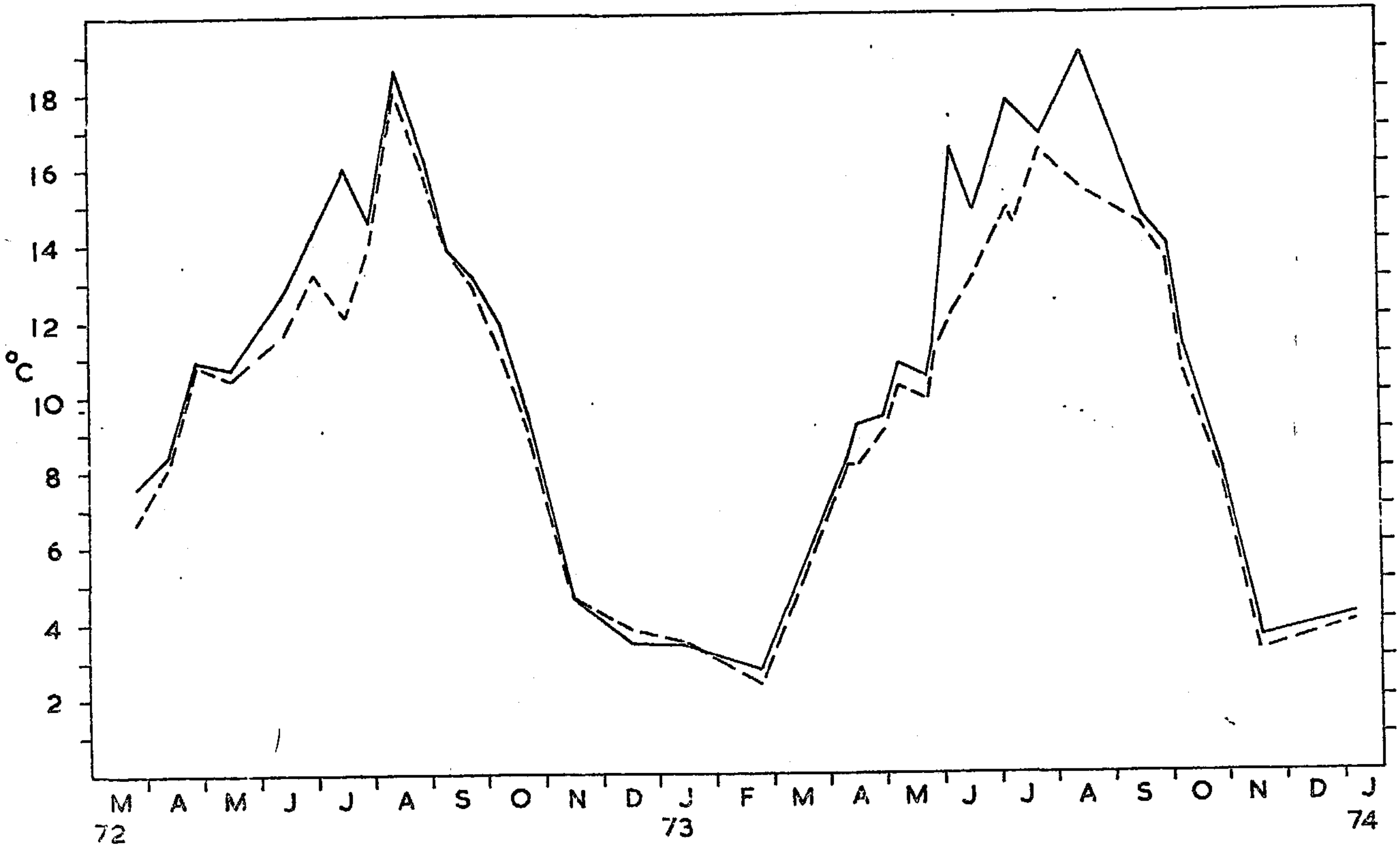


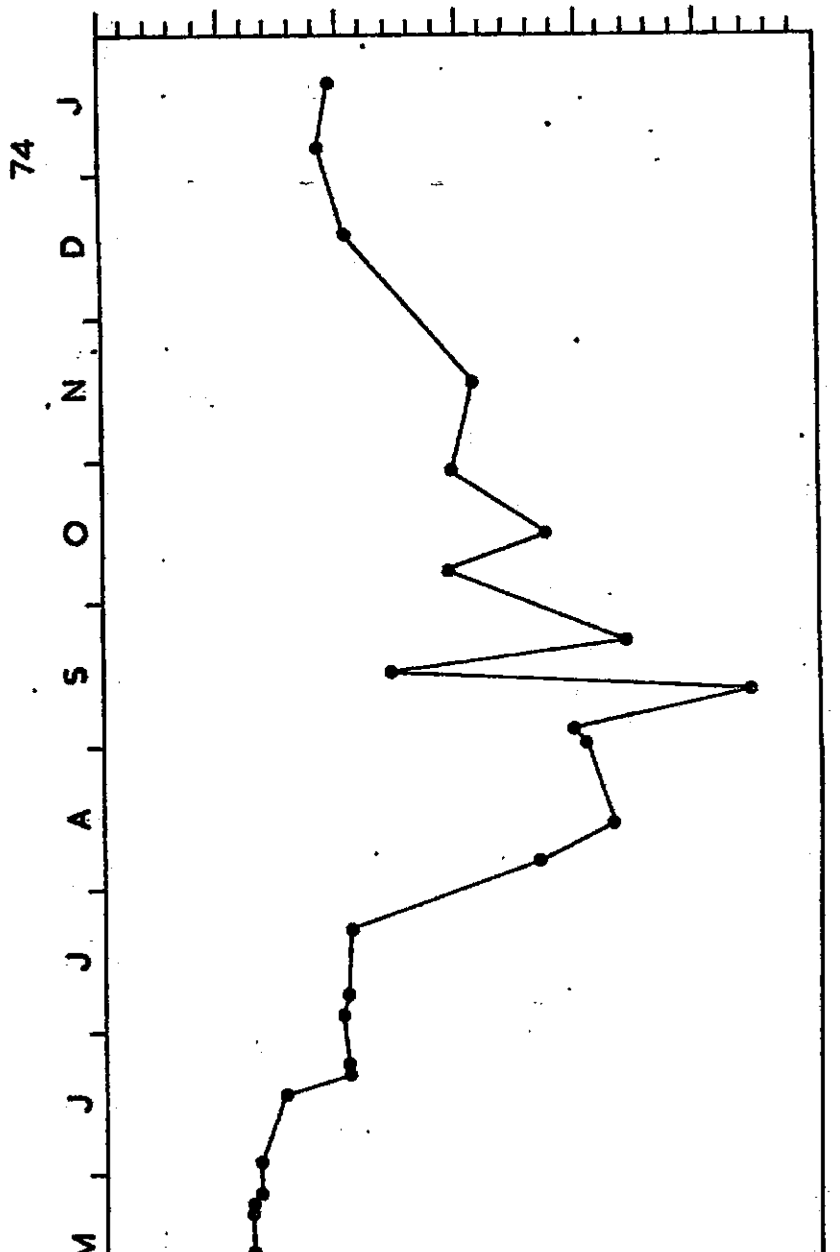
Figure 4 (opposite)

Seasonal variations in water transparency at Loch Leven during 1973.

Abcissa - the study period

Ordinate - the depth of secchi disc visibility in cms.

Fig. 4



depth-reading of 200 cm. to May readings of approximately 60 cms. As the summer progressed, clarity increased marginally in late June and July and then very rapidly during August. In early September a maximum transparency recording of 273 cms. was obtained. This was followed by fluctuations in transparency conditions during late September and October and, as the year ended, clarity generally decreased with secchi disc visibility being approximately 100 cms in January of 1974.

The depth of visibility determined using a secchi disc provides a useful measure of transparency. However, the reading is dependent upon the changes in the light on its course from the surface to the disc and back to the eye, this being affected by two factors operating independently. One is the absorption of light by the water or substances dissolved within it and the other is light scattering due to turbidity (Ruttner 1968). The seasonal variations in water transparency at Loch Leven during 1973 appears to show a distinct relationship to phytoplankton concentrations (See Fig.28), so that when transparency is low, phytoplankton concentrations are high and vice-versa. Low transparency in May and June may be further correlated to the very high numbers of the main zooplankton components occurring at this time.

## 2. Daphnia hyalina var lacustris

### (a) The annual cycles

### i. Quantitative changes in standing crop

Changes in the numerical standing crop of *Daphnia hyalina* var. *lacustris* from Loch Leven throughout the entire sampling period are shown in Fig. 5. The arithmetic mean densities derived from total counts of forty-eight or twenty-eight samples are expressed as numbers per litre.

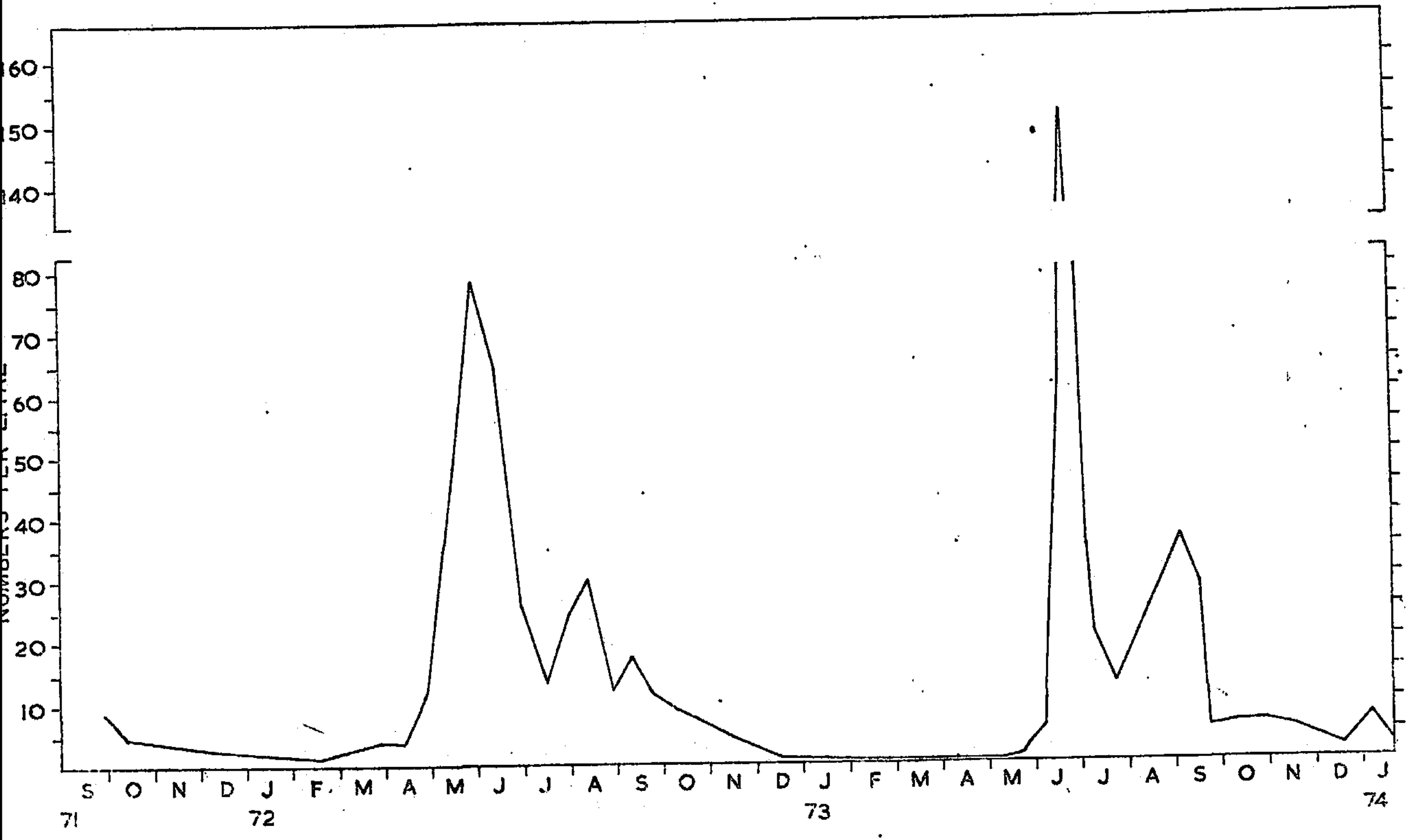
The *Daphnia* population remained consistently planktonic throughout the two years and was essentially composed of female individuals, with adults undergoing continual reproduction by parthenogenesis. The seasonal changes in abundance followed a similar pattern in both years. From low winter levels an initial spring or early summer population bloom developed producing the ultimate annual peak in numbers. This was followed firstly by a rapid decline to low mid-summer levels and then by a subsequent increase to produce a late summer peak of moderately high numbers. From then onwards, the population declined again to the very low winter levels. The major population changes, when numbers were over and above ten individuals per litre (ind/l), occurred from the beginning of May to the end of September in 1972 and from early June to mid-September in 1973.

Figure 5 (opposite)

Seasonal changes in the numerical standing crop of *Daphnia hyalina* var *lacustris* from Loch Leven during 1972-73.

Abcissa - the study period

Ordinate - the mean numbers per litre of *D. hyalina* var *lacustris*.


160
150
140
80
70
60
50
40
30
20
10
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J
71
72
73
74

During the 1971-72 winter period, the Daphnia population existed in low numbers of less than 5 ind/l until late April when numbers increased drastically to a maximum figure of 78.2 ind/l at the onset of June. The rise in numbers was coincident with mean loch temperatures approximating 10°C. Throughout June until mid-July, the population progressively decreased to 13.2 ind/l and then increased again to produce a second peak of 29.5 ind/l in mid-August. From mid-August to December, the population slowly declined to winter levels.

The population of the 1972-73 winter was consistently lower in abundance than that of the previous winter with numbers being less than 1 ind/l. This very low level in numbers was maintained throughout the spring months of 1973 until early June when the population increased very rapidly, at mean loch temperatures of approximately 14-15°C, to a mid-June peak of 151.2 ind/l. The maximum numbers recorded at this time was twice that of the 1972 spring peak with the initial population increase occurring almost a month later. The mid-June peak in Daphnia numbers was, however, short-lived and subsequently dropped very rapidly during the latter part of June and continued to decrease until mid-July when numbers were 12.5 ind/l. This mid-July low level was similar to that obtained for exactly the same period in 1972. A further population increase occurred gradually after mid-July to produce a second but much smaller peak of 36.4 ind/l at the beginning of September.

The population subsequently decreased quickly during September to winter levels.

The seasonal fluctuations in standing crop of the Daphnia population can be evaluated more clearly when the total population numbers are separated into the four convenient size-classes (page 27). Fig. 6 shows the seasonal changes in mean standing crop of individuals in the four size categories and also the changes in mean egg stock. The mean egg stock was obtained by multiplying the mean brood-size by the mean number of gravid females per litre for each sampling date. The same data given in Fig. 6 has been condensed to show the variations in mean standing crop of adults (size >1.4mm) and juveniles (size <1.39mm) in Fig. 7. The arithmetic mean densities are given as numbers per litre. In addition, the seasonal variations in proportions of adults and juveniles making up the Daphnia population are depicted as percentages in Fig. 8.

The overwintering Daphnia population of the 1971-72 winter was comprised of very low numbers of animals in each size-class with relatively stable proportions of adults and juveniles, the juveniles being marginally more abundant than the adults. The egg stock in early 1972 was low, less than 10 eggs per litre (eggs/l). Development rates at this time were likely to have been at their slowest with mean loch temperatures being

Figure 6 (opposite)

Seasonal changes in the mean egg stock and in the mean standing crop of the four size-classes of *D. hyalina* var *lacustris* from Loch Leven during 1972-73.

Abcissa - the study period

Ordinates - the mean egg stock per litre

- the mean numbers per litre of *D. hyalina* var *lacustris* individuals in the four size-classes : <1.0mm, 1.0-1.39mm, 1.4-1.99mm. and >2.0mm.

Fig. 6

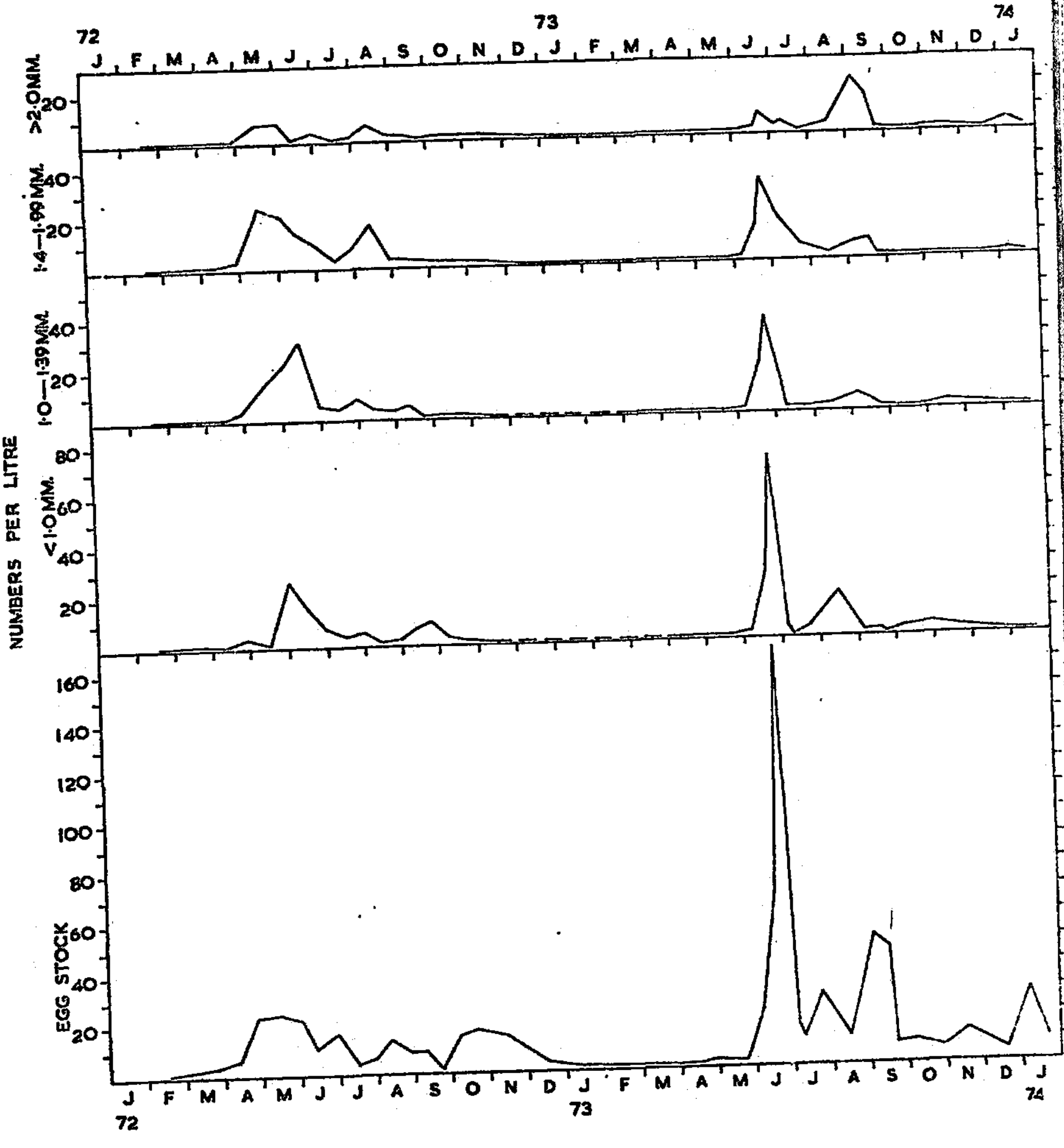

72
73
74
J F M A M J J A S O N D J F M A M J J A S O N D J
>2·0MM.
20
1·4—1·99MM.
40
20
1·0—1·39MM.
40
20
NUMBERS PER LITRE
<1·0MM.
80
60
40
20
EGG STOCK
160
140
120
100
80
60
40
20
J F M A M J J A S O N D J F M A M J J A S O N D J
72
73
74

Figure 7 (opposite)

Seasonal changes in the mean egg stock and in the mean standing crop of adults and juveniles comprising the *D. hyalina* var *lacustris* population from Loch Leven during 1972-73.

Abcissa - the study period

Ordinates - the mean egg stock per litre

- the mean numbers per litre of *Daphnia* adults (size >1.4mm) and juveniles (size <1.39mm).

Note that the data for egg stock commenced in February 1972.

Fig. 7

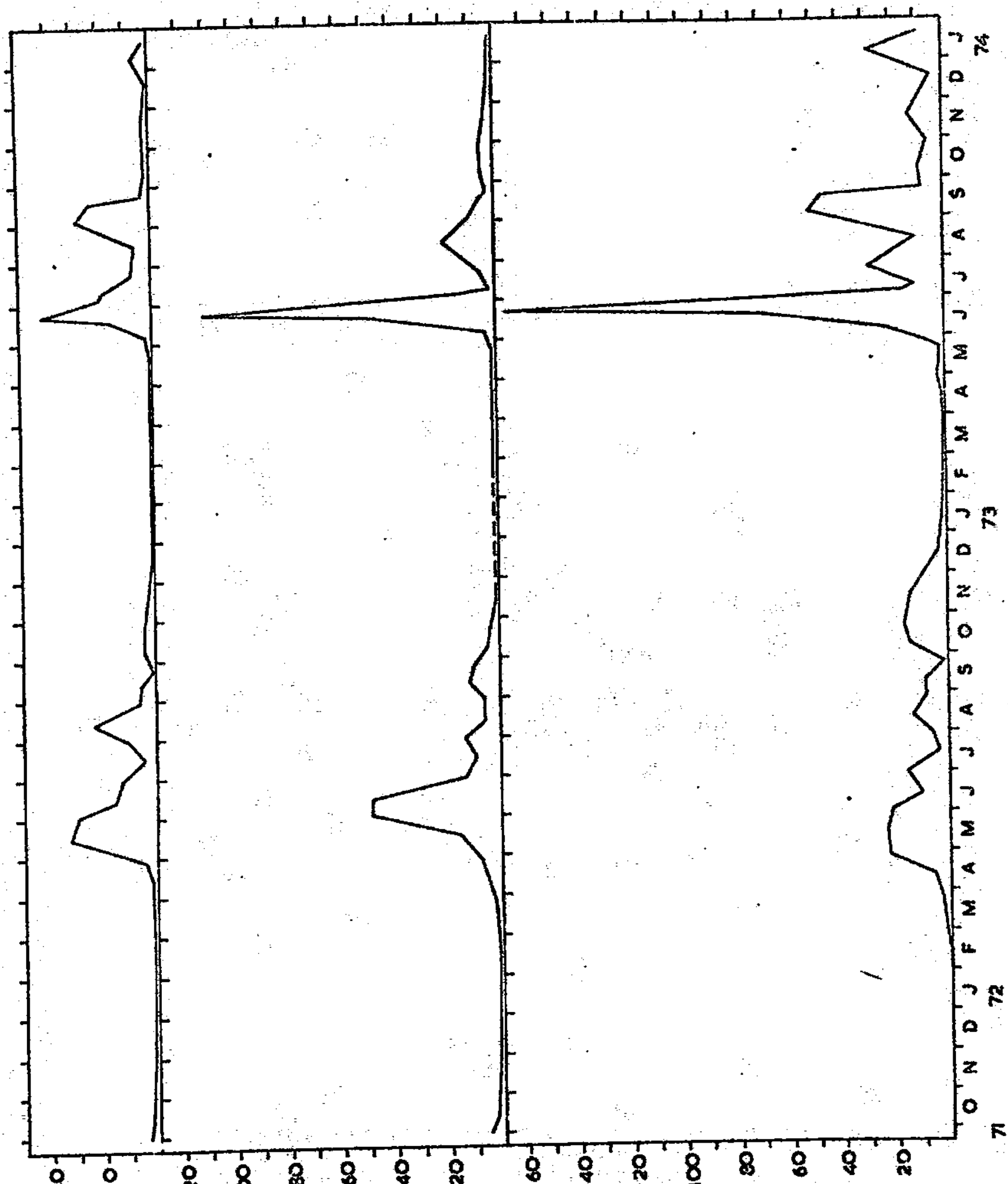

ADULTS
40
20
JUVENILES
120
100
80
60
40
20
EGG STOCK
160
140
120
100
80
60
40
20
NUMBERS PER LITRE
71
O
N
D
J
72
F
M
A
M
J
J
A
S
O
N
D
J
73
F
M
A
M
J
J
A
S
O
N
D
J
74

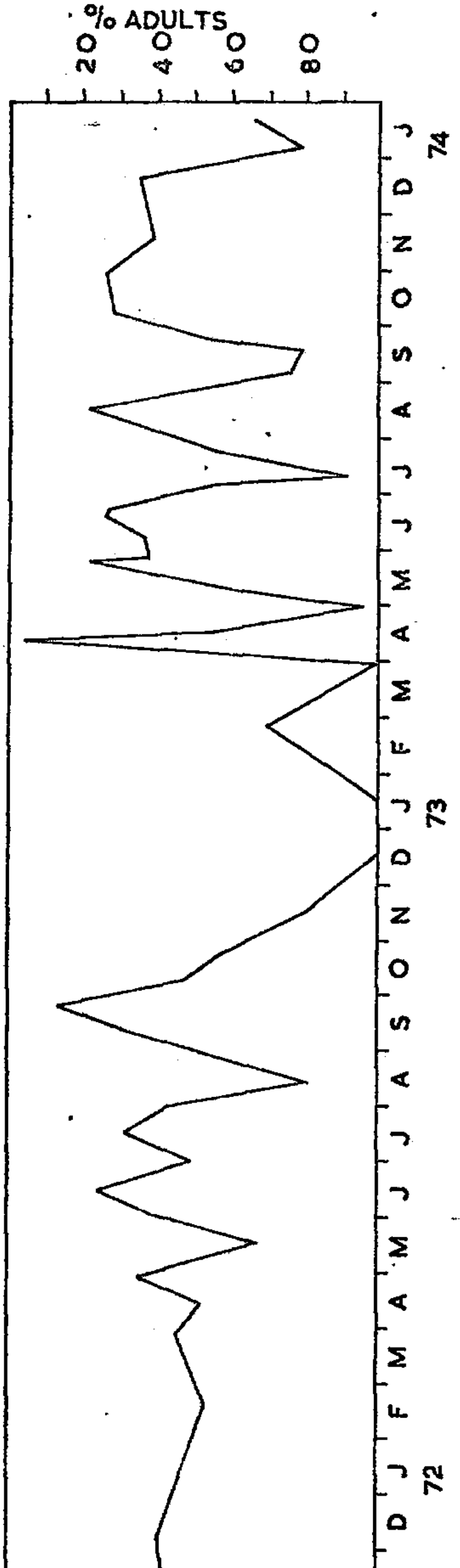
Figure 8 (opposite)

Seasonal variations in the proportions of adults and juveniles comprising the *D. hyalina* var *lacustris* population of Loch Leven during 1972-73.

Abcissa - the study period

Ordinate - the percentage juveniles or the percentage adults making up the *Daphnia* population.

Fig. 8



% ADULTS
20
40
60
80
71
O
N
D
J
72
F
M
A
M
J
J
A
S
O
N
D
J
73
F
M
A
M
J
J
A
S
O
N
D
J
74

under 5°C. In mid-April, the egg stock increased to 23.2 eggs/l and was maintained in similar numbers, with a mid-May annual maximum of 24.1 eggs/l, until a decline occurred in early June. In late April and during early May, a corresponding increase in juveniles in the <1.0mm size-class was not apparent although pre-adults, 1.0-1.39 mm, showed a progressive increase. The adult numbers, however, showed a marked increase at this time, producing a seasonal maximum of 32.7 ind/l in mid-May. The bulk of these individuals were in the 1.4-1.99 mm class and gave rise to maximum numbers of 24.9 ind/l for that class. Because the time interval between sampling visits amounted to two weeks during this time it is possible that juvenile development was missed due to inadequate sampling.

The juvenile members of the population appeared in maximum numbers at the onset of June and formed 62.6 per cent of the spring peak in total numbers (Fig. 5.). The majority of these immature <u>Daphnia</u> were in the <1.0 mm class and totalled 26.1 ind/l. During the latter half of June and in early July a decline occurred in the numbers of individuals in all four size-classes and there appeared to be very little recruitment of animals from the pre-adult class to the adult classes - the adult numbers slowly decreased to a seasonal minimum of 4.1 ind/l in mid-July. For the remainder of the 1972 summer, the egg stock and <u>Daphnia</u> of all four size-classes fluctuated in relatively low numbers class reached an abundance of 17.0 ind/l. These were presumably derived by progressive recruitment from juvenile size-classes, although substantial increases in the juvenile components and in the egg stock were not apparent prior to the adult increase. The mid-August peak in total numbers (Fig. 5) was composed mainly of adults, 80.5 per cent.

From late September onwards, the *Daphnia* population became progressively dominated by adult individuals, as shown in Fig. 8, and during December and January juveniles were not detected in samples despite the fact that the adults were producing parthenogenetic eggs. This contrasts with the *Daphnia* population of the previous winter when juveniles were marginally more abundant than adults. From February 1973 until June, the population existed in low numbers and was comprised of animals in all size groups. The egg stock was consistently low and did not exceed 2.3 eggs/l. Despite low numbers of individuals, the proportions of adults and juveniles in the populations showed distinct fluctuations (Fig. 8). There was a marked increase in proportions of juveniles during early and mid-April, this situations being reversed in favour of adults at the end of April. Throughout May and June, however, the bulk of the population, over 60 per cent, was composed of juveniles.

In June, the *Daphnia* population increased dramatically maximum of 166.2 eggs/l, and corresponding increases in the numbers of individuals in successive size-classes. Although growth was very rapid with adults appearing in the latter half of June to a seasonal maximum of 41.1 ind/l, recruitment to the >2.0mm class was poor. Because of the very high egg numbers, it seems reasonable to assume that the population increases had been affected by parthenogenetic birth as opposed to ephippial emergence. The drastic decline of the population in late June and early July was effected by a loss of individuals in all size-classes, although with the small adults, in the 1.4-1.99 mm. class, the decline was more gradual. The reduced population of early July was composed predominantly of adults with only 8.7 per cent juveniles. During this time, the egg stock was also severely reduced - to 5.2 eggs/l.

As the summer progressed into August, minor fluctuations were apparent in the egg stock and standing crop of successive size groups. The egg stock increased to 28.2 eggs/l in the latter half of July and declined again in mid-August when juvenile numbers had progressively built up to 19.8 ind/l. Adult numbers began to rise in late August and, at the onset of September, a late summer maximum of 27.8 ind/l was recorded with these adults being predominantly in the >2.0mm class. At the same time the egg stock rose sharply to 50.9 eggs/l but this was not followed by a corresponding rise in juvenile numbers. During the latter part of September, the

Daphnia population declined with a notable loss of large adults in the >2.0 mm class and a substantial reduction in egg stock. The low population which persisted into winter was mainly composed of juveniles approximately 60 per cent and bears resemblence to the population encountered during the same months at the end of 1971.

### ii. The breeding parameters

For most of the year populations of Daphnia spp. are typically composed only of female individuals which reproduce asexually by parthenogenesis. Eggs are extruded from the ovaries and retained for initial development in the brood pouch of the parent. Observations relating to the number of adult females carrying eggs in the population and to the number of eggs being carried by each female provide a measure of the reproductive state of the population on any given sampling date. These breeding parameters were estimated for the Daphnia hyalina var. lacustris population at Loch Leven throughout the two-year sampling period.

Fig. 9 shows the derivation of the mean egg stock from the percentage and mean numbers per litre of gravid females present in the population and the mean numbers of eggs carried per female. The mean numbers of gravid adults per litre were obtained by analysis of Friedinger samples with the percentage gravid mid-April. In 1973 the mean positive r value was 0.048 and a maximum value of 0.178 was recorded at the end of May.

Estimates of the instantaneous death rate (d) were derived by subtracting the interpolated values of r from b on each sampling date. It should be noted that d is the least reliable statistic associated with the egg ratio method of estimating population parameters since it depends on the difference between two quantities already calculated with error (Edmondson 1960). Since the values of d have been calculated from the egg stage, they include pre-natal as well as post-natal mortality.

On the whole the seasonal fluctuations in death rate parallel the changes in birth rate although remaining somewhat out of phase. As a consequence death rate values in 1973 were consistently higher than in 1972. The mean death rate for 1972 was 0.041 with a maximum value of 0.117 in late October and also mid-December. In 1973, the mean d value was 0.105 with a maximum of 0.278 in early May.

## (b) The spatial distribution

### i. The horizontal distribution and sampling variability

As already explained in the Materials and Methods section (page 22) sampling at Loch Leven was undertaken at six sites in 1972 and at three sites in 1973. An evaluation of horizontal distribution essentially involves a comparison of standing crop data obtained at each site on any given sampling date. This is best done using the data for the six sites as obtained in 1972.

Table 2 shows the variability between mean counts of total Daphnia hyalina var lacustris (i.e. all size-classes grouped) as obtained from each of the six sites on seventeen separate sampling occasions in 1972. The data is given as numbers per five litres as derived from Friedinger sample counts. It is clear from the data that several large discrepancies do occur between mean counts at different sites on the same date but it is very difficult to assess whether this variability is real or merely a function of the small variable numbers of samples which were taken at each site. In fact the only readily comparable samples common to all six sites were the replicates taken at Om (surface) and 1m depths. These are unlikely, however, to provide sufficient information for a full assessment of horizontal variations on any given date.

In practise errors due to insufficient numbers of samples are likely to have been reduced as the overall standing crops which were used to elucidate the annual cycles were derived from the combined sample counts, divided by the total number of samples taken. It is apparent that when standing crops were calculated from sampling visits which were only a few days apart there was either a close similarity or a reasonable

Table 2 The horizontal variations in the *Daphnia hyalina* var *lacustris* population from zooplankton samples taken at six sites on seventeen visits to Loch Leven in 1972.

The data is given as numbers per five litres

| Date | SITES | | | | | | Overall mean (48) | Mean for A, D &E (28) | Mean for A, D & E as % of overall mean | % difference |
|---|---|---|---|---|---|---|---|---|---|---|
| | A (6) | B (6) | C (6) | D (4) | E (18) | F (8) | | | | |
| 25/3 | 7.2 | 55.5 | 14.2 | 22.0 | 15.9 | 7.7 | 18.7 | 14.9 | 79.7 | -20.3 |
| 12/4 | 20.2 | 18.3 | 15.2 | 10.0 | 19.8 | 13.2 | 17.2 | 18.5 | 107.6 | + 7.6 |
| 27/4 | 63.0 | 60.0 | 76.5 | 44.2 | 58.2 | 51.4 | 59.0 | 57.2 | 96.9 | - 3.1 |
| 15/5 | 336.2 | 240.7 | 260.7 | 46.2 | 287.4 | 147.7 | 240.9 | 263.4 | 109.3 | + 9.3 |
| 01/6 | 323.2 | 563.7 | 385.2 | 335.2 | 379.6 | 371.1 | 391.1 | 361.2 | 92.3 | - 7.7 |
| 13/6 | 197.0 | 671.7 | 139.7 | 84.5 | 299.6 | 460.2 | 322.0 | 246.7 | 76.6 | -23.4 |
| 29/6 | 134.5 | 47.8 | 128.7 | 112.2 | 199.7 | 38.6 | 129.5 | 173.2 | 133.7 | +33.7 |
| 15/7 | 28.2 | 138.8 | 49.2 | 165.7 | 42.8 | 56.0 | 66.2 | 57.2 | 86.4 | -13.6 |
| 29/7 | 231.0 | 223.8 | 59.0 | 38.5 | 116.8 | 50.2 | 118.9 | 130.1 | 109.4 | + 9.4 |
| 12/8 | 73.7 | 95.0 | 273.0 | 139.7 | 165.5 | 113.1 | 147.0 | 140.3 | 95.4 | - 4.6 |
| 28/8 | 98.2 | 48.5 | 79.7 | 71.2 | 32.7 | 78.3 | 59.7 | 53.0 | 88.8 | -11.2 |
| 10/9 | 24.2 | 39.3 | 165.7 | 140.5 | 104.4 | 38.4 | 85.9 | 92.4 | 107.6 | + 7.6 |
| 23/9 | 34.3 | 137.2 | 57.3 | 104.7 | 27.3 | 58.5 | 57.3 | 39.9 | 69.6 | -30.4 |
| 07/10 | 50.4 | 69.6 | 32.2 | 56.3 | 42.1 | 31.2 | 44.9 | 45.9 | 102.2 | + 2.2 |
| 21/10 | 37.7 | 38.3 | 35.5 | 30.7 | 30.3 | 47.6 | 36.0 | 32.1 | 89.2 | -10.8 |
| 14/11 | 12.5 | 18.2 | 17.5 | 30.0 | 27.2 | 16.4 | 21.2 | 24.2 | 114.1 | +14.1 |
| 16/12 | 1.0 | 3.0 | 1.2 | 9.2 | 8.2 | 3.7 | 4.9 | 6.6 | 134.7 | +34.7 |

The table shows the variability between mean counts of total numbers of *D. h.* var *lacustris* taken from different sites on the same date and compares the mean derived from sites A,D and E with the overall mean derived from all six sites. The numbers of samples per site on each visit are shown in brackets. See. Fig. 1 for explanation continuation in trend, thus suggesting that the sampling means were not unreasonable (see Appendix sheet appropriate to Fig. 5).

As mentioned in the Materials and Methods, the 1972 data on horizontal distribution was analysed with a view to reducing the number of samples collected per sampling trip during 1973. Table 2 compares the mean standing crop derived from three sites A, D and E (mean of twenty-eight Friedinger samples) with the overall mean derived from all six sites (mean of forty-eight samples) for each of the seventeen sampling visits in 1972. The differences are expressed as percentages.

It was found that if the three sites had been sampled, the calculated mean estimates for Daphnia hyalina var lacustris as compared to those for the full six sites would have a maximum variation of ± 35 per cent. On eight occasions the variation was less than ± 10 per cent and on twelve occasions out of a total of seventeen it was less than ± 15 per cent. On the basis of these evaluations it was fair to assume that sampling three sites in 1973 would provide reliable quantitative estimates of the Daphnia population. When one considers the problems associated with zooplankton sampling, variations in the order of 30 per cent do not appear unreasonable, and according to Cushing (1951) these are not excessive.

### ii. The vertical distribution

Depth histograms of the seasonal vertical distribution of *Daphnia hyalina* var *lacustris*, representing sampling at site E in the north deeps on thirteen dates in 1972 and on twelve dates in 1973, are presented in Fig. 12. On each sampling date the mean numbers of *Daphnia* taken at each sampling depth are expressed as a percentage of the total numbers of *Daphnia* taken in the water column. The dates only apply to sampling visits when *Daphnia* numerical mean loch densities were above 5 ind/l. Ideally, it would have been desirable to have provided information on the vertical distribution throughout the entire water column but this would have resulted in more samples than it was feasible to examine. However, the sampling programme selected, with replicate samples collected from each of the surface five metres and at 10, 15 and 20 metres (totalling eighteen Friedinger samples) provided a reasonable compromise. On each sampling visit, site E was sampled at approximately mid-day, 12 noon to 2.00 p.m. as an attempt to regularise temporal changes in zooplankton distribution.

*Daphnia* individuals were encountered at every sampling depth in the water column on every sampling visit except for two, both in 1973. On the 6th June and 8th July no individuals were found at 15 or 20m. Generally the maximum concentrations occurred within the upper-most five metres and often (especially in 1973) only relatively

Figure 12 (opposite)

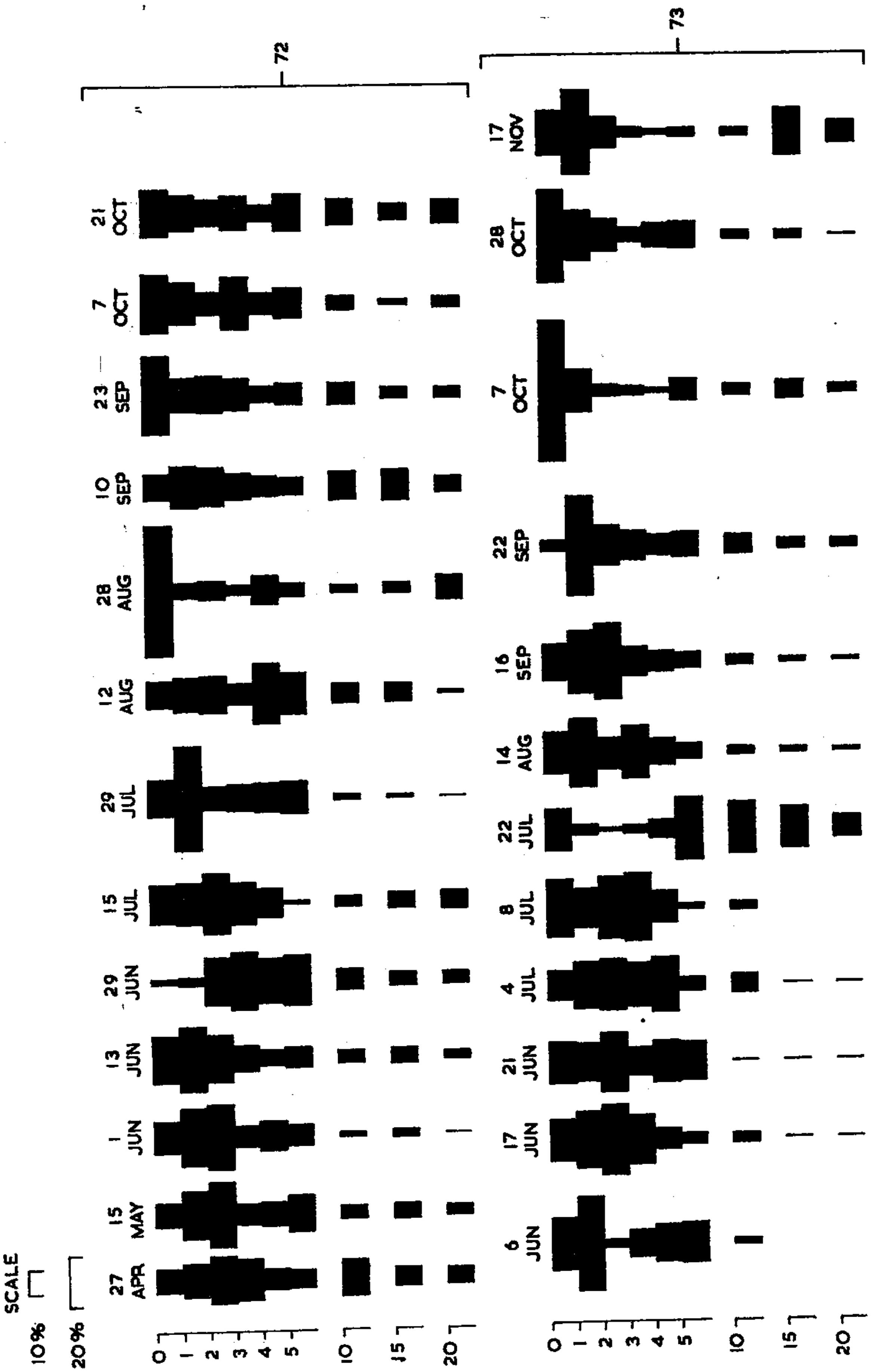
Seasonal vertical distributions of the *D. hyalina* var *lacustris* population at Loch Leven during 1972-73.

Abcissae - the study period represented by thirteen sampling dates in 1972 and twelve sampling dates in 1973.

Ordinates - the loch depth in metres (from the surface almost to the loch bed) at site E.

For each sampling date the mean numbers of *Daphnia* taken at each sampling depth are expressed as a percentage of the total numbers of *Daphnia* taken in the water column at site E. Note that the blank spaces in the histograms indicate the discontinuity in the sampling of the water column from 6-10m, 11-15m and 16-20m and are not in scale. Also note that the dates apply only to sampling visits when *Daphnia* mean loch densities were above 5 ind/l.

Fig. 12


SCALE
10%
20%
72
27 APR
15 MAY
1 JUN
13 JUN
29 JUN
15 JUL
29 JUL
12 AUG
28 AUG
10 SEP
23 SEP
7 OCT
21 OCT
73
6 JUN
17 JUN
21 JUN
4 JUL
8 JUL
22 JUL
14 AUG
16 SEP
22 SEP
7 OCT
28 OCT
17 NOV
0
1
2
3
4
5
10
15
20

minor aggregations were recorded from the deeper sampling depths. Distinctly even distributions throughout the water column were however noted on several occasions in 1972 - examples being 27th April, 10th September and 21st October.

On two sampling occasions, 28th October 1972 and 7th October 1973, over 50 per cent of the Daphnia population congregated just below the surface (surface samples down to 1m) with the rest of the population showing a relatively even distribution throughout the rest of the column. In total contrast, on the 29th June 1972, the bulk of the population was seen to accumulate in depths below 2m, leaving the surface two metres of water with only very sparce Daphnia proportions totalling only 5 per cent. This coincided with dense surface accumulations of blue-green algae (Anabaena sp.) in very still water conditions. An interesting vertical distribution pattern occurred on the 22nd July 1973 when the bulk of the population accumulated in surface water down to 1m and in the deeper water below 5m, leaving the upper layers between 1m down to 5m depths with only sparse aggregations.

### (c) Cyclomorphosis and sexual reproduction

The subject of cyclomorphosis in Cladocera has been extensively reviewed by Hutchinson (1967). The phenomenon in the genus Daphnia consists essentially of

Figure 13 (opposite)

The cyclomorphotic variations and sexual forms of *D. hyalina* var *lacustris* from Loch Leven.

Cyclomorphotic variations of adult parthenogenetic females

A - Round-headed form
B - Round-headed with vestigial posterior spine
C - Spring-intermediate form
D - Crested or peaked form
G - Autumn-intermediate form

Cyclomorphosis as exhibited by *Daphnia* from Loch Leven relates mainly to seasonal changes in the shape of the head. Although seasonal variations in the length of the posterior spine were noted and are included in the diagrams, these variations may be totally unrelated to seasonal head changes. The flow of arrows indicates the suggested parental origin of each form.

Sexual forms of *D. hyalina* var *lacustris*

F - Adult crested female bearing ephippial eggs
E - Adult male

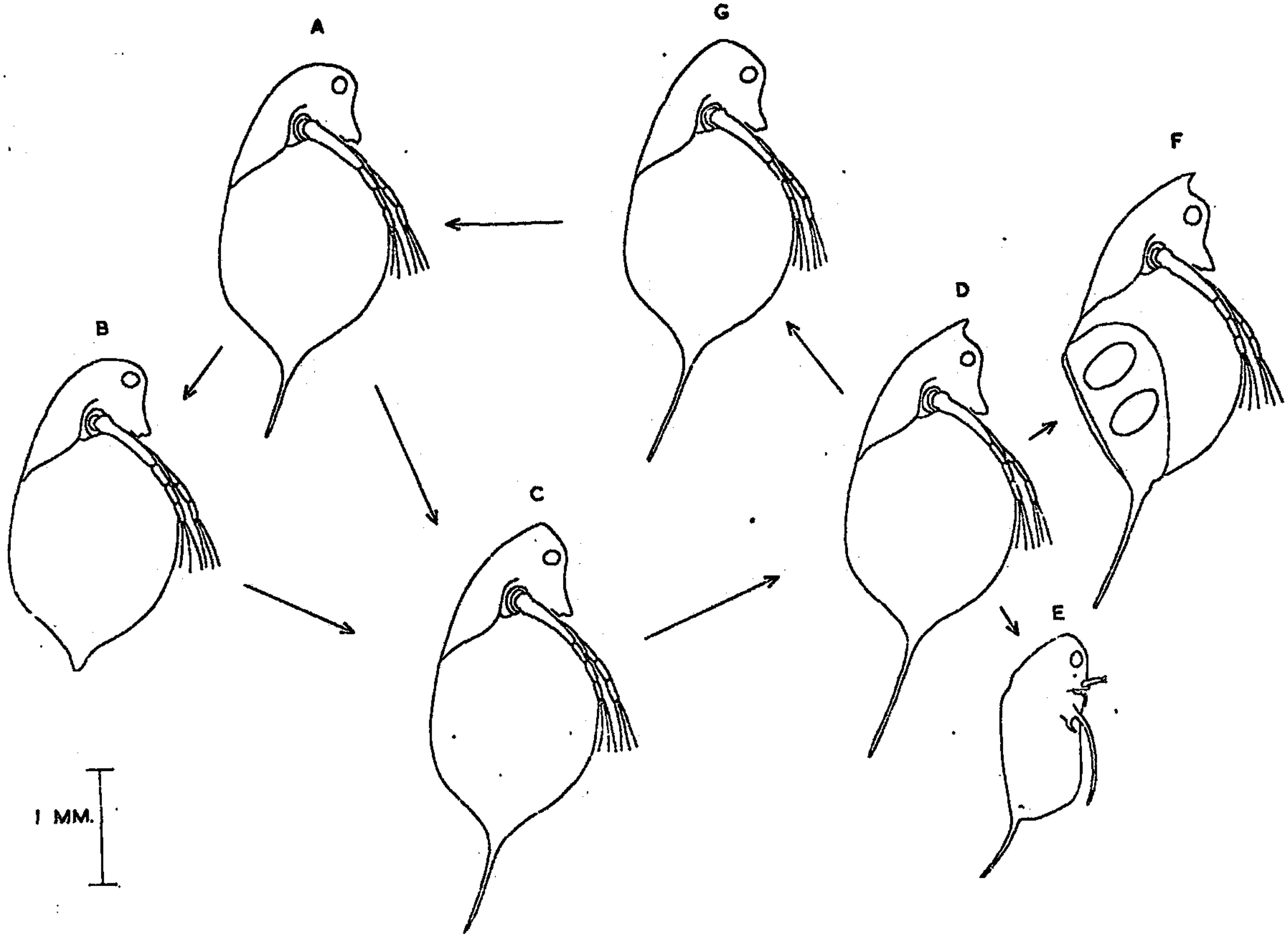


Fig. 13

a seasonal variation of the helmet or crest of the head although changes in the shape of the ventral margin of the head and rostrum have also been noted. The posterior spine is also subject to variations in length but these are not fully understood and may be totally unrelated to seasonal head changes.

Species of Daphnia hyalina are known to undergo seasonal changes in head shape (Hutchinson 1967) with D. h. var galeata from Lake Windermere being a prime example (Scourfield and Harding 1966). During the present study D. h. var lacustris from Loch Leven exhibited distinct seasonal variations in helmet shape - these are outlined in diagrams of adult individuals in Fig. 13. The flow of arrows indicates the suggested parental origin of each form.

The contour of the top of the head varied from a distinctly round shape (Fig. 13, A and B) to a shape incorporating a ventrally-orientated peak or crest (D and F). This crest was relatively small and rarely exceeded 6 per cent of the body-length. Two intermediate forms (C and G) could also be distinguished. One form (C) had a head contour deformation approximating a wide inverted 'v' shape with the apex being positioned distinctly ventral to the body-line between the insertion of the locomotary antenna and the base of the tail spine. Individuals showing this characteristic were named 'spring-intermediates' and were presumed to have derived from round-headed forms and in turn were presumed to have given rise to the crested forms. The other intermediate type described here as the 'autumn-intermediate' (G) had a characteristic 'protrusion' more or less directly in line with the body-line previously mentioned. These individuals were presumed to have originated from crested forms and in turn gave rise to round-headed forms.

Variations in the length of the posterior spine were also noted. The spines of fifty adult round-headed Daphnia from net samples in April 1972 and fifty adult crested individuals from August 1972 were measured in proportion to body-length using apparatus previously described ( page 29). It was found that the April individuals had a mean spine length approximating 36 per cent of the body-length whereas the mean spine length of the August forms approximated 48 per cent of the body-length. However, fifty round-headed individuals from October samples had a mean spine length of approximately 44 per cent of the body-length. From this data it seems that although variations in the spine length may occur they are unlikely to be associated specifically with the cyclomorphotic head changes. It is interesting to note that, among the round-headed population in late winter, some individuals had no spine at all (Fig. 13,B). Such individuals were found in February of 1972 and in February, March and April 1973.

The cyclomorphotic variations exhibited by Daphnia hyalina var lacustris are shown on a quantitative basis in Fig. 14.

Figure 14 (opposite)

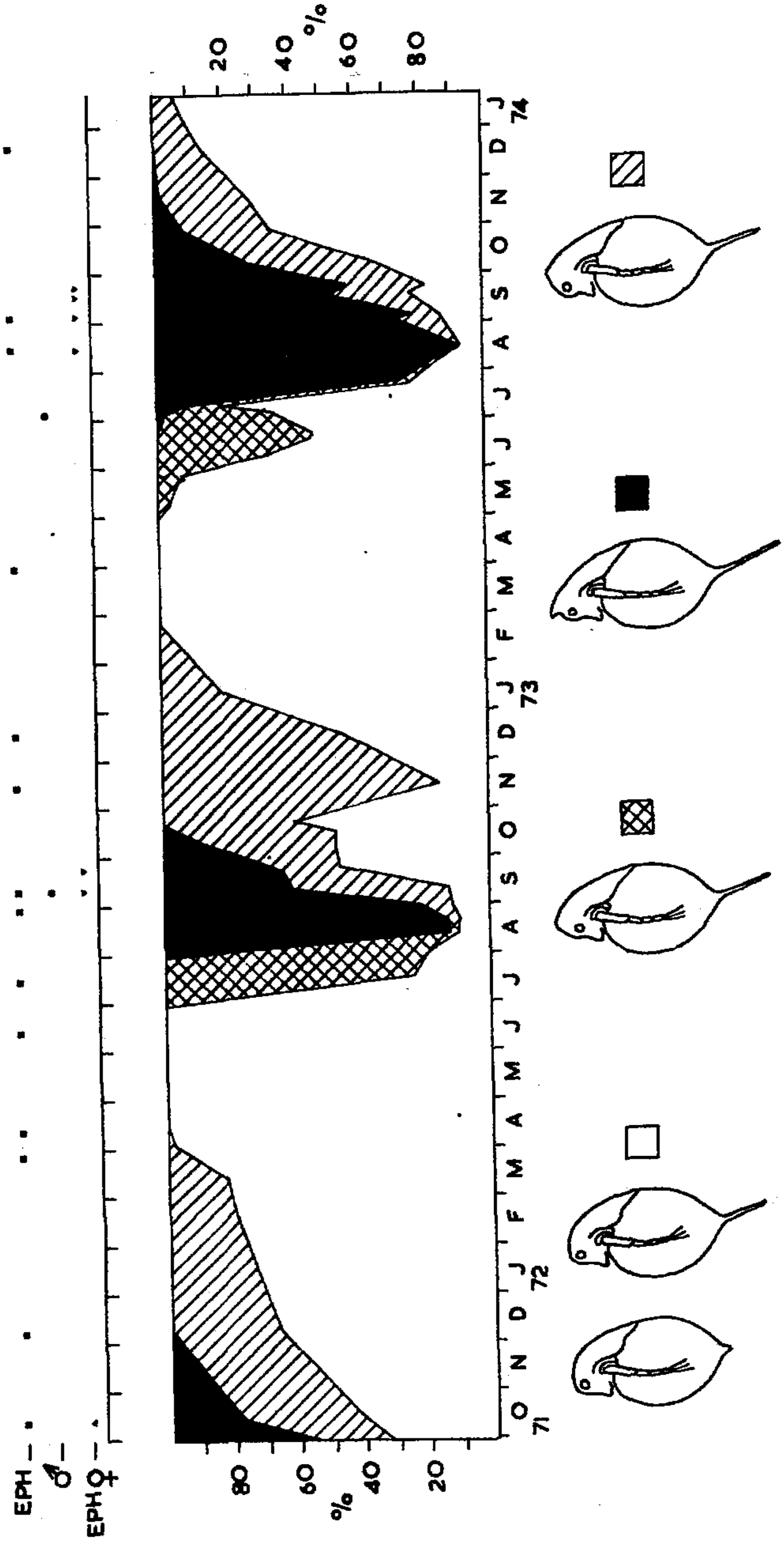
Seasonal succession and quantitative assessment of four characteristic cyclomorphotic forms of D. hyalina var lacustris from Loch Leven during 1972-73.

Abcissa - the study period
Ordinate - the percentage abundance of the four cyclomorphotic forms :
round-headed □
Spring-intermediate ▩
peaked ■
Autumn-intermediate ▧

Note that the quantitative data applies to egg-bearing females only and was derived during adult body-length and brood-size assessment (page 29).

Information on the seasonal occurrence of sexual reproduction is presented above the graph in the form of data on the presence of males (♂), ephippial females (EPH♀) and loose ephippia (EPH).

Fig. 14


EPH
♂
EPH♀
%
80
60
40
20
%
20
40
60
80
O
71
N
D
J
72
F
M
A
M
J
J
A
S
O
N
D
J
73
F
M
A
M
J
J
A
S
O
N
D
J
74
▨
■
▩
□

during adult body-length and brood-size assessment (page 29). Individuals were separated into one of four categories depending on head shape: round-headed (Fig. 13, A and B), crested (D and F), spring-intermediate (C) and autumn-intermediate (G). The abundance of each of these types is expressed as a percentage of the total adults for each sampling date. It would have been desirable to have analysed the cyclomorphotic variations of the entire population but unfortunately the juveniles showed considerable variation and it was not certain whether some of their head shapes characteristics would be maintained into adulthood after successive moults. It should be pointed out that the intentions here have been to characterise the cyclomorphatic forms exhibited by the Daphnia population (Fig. 13) and are now to provide some information on the seasonal appearances of these forms (Fig. 14).

The sequence of appearance and successional abundance of the four cyclomorphotic forms of D. h. var lacustris followed a similar pattern in both years of sampling : round-headed → spring-intermediate → crested → autumn-intermediate → round-headed. Although round-headed Daphnia adults were found on every sampling date throughout the entire study, they tended to predominate in winter. Their abundance was greater than 50 per cent from early November in 1971 until early July 1972 and from mid-December 1972 until mid-July in 1973. From mid-April until early June in 1972 and from late February until the end of April in 1973, only round-headed Daphnia were

In 1972, the spring-intermediate forms appeared and predominated in July. In the following month, however, the crested forms appeared and reached a proportionate maximum of 80 per cent in mid-August. The crested individuals progressively declined in relative abundance during September and October giving way to an adult population composed of autumn-intermediates and round-headed Daphnia.

Comparable events occurred in 1973 although spring-intermediate and crested individuals appeared earlier in the year - in May and in July respectively. The crested Daphnia again reached maximum proportions (93 per cent) in mid-August but persisted until mid-November.

Although Daphnia spp. populations consist mainly of female individuals undergoing reproduction by parthenogenesis, at certain times of the year, usually autumn, males may appear in order to allow sexual reproduction to take place. Sexual reproduction results in the production of ephippial resting eggs. Fig. 14 provides information on the presence of males, ephippial females and loose ephippia as recorded during analysis of Friedinger and net-samples during the entire sampling period. The data is qualitative.

Male D. h. var lacustris were only found on two sampling occasions during the present study. In early September of 1972 one male was found in a Friedinger sample and two were found in net-samples, and in early July of 1973 one male was found in net-samples. All of these males were within the size range 1.3-1.5 mm. total length (see Fig. 13, E).

Females bearing ephippial eggs were encountered on two sampling visits in 1972, both in September and on four visits in 1973, one in August and three in September. All these females were crested individuals (Fig. 13, F). In Friedinger samples ephippial females were never very abundant, remaining less than 1 ind/l in all cases except in mid-September 1973 when a maximum abundance of 1.7 ind/l was recorded, which accounted for approximately 7.5 per cent of the adult population at that time.

Loose ephippia were found in samples at various times of year on fourteen visits to Loch Leven. As ephippial production took place, for the most part, in September of both years, it is likely that the presence of ephippia at other times of year was effected by strong wind-induced water turbulence which brought them into the water-body from the bottom sediments.

### (d) The laboratory growth studies and length-weight assessment

The laboratory growth studies of round-headed *Daphnia hyalina* var *lacustris* from Loch Leven proved to be successful with the resultant data providing an abundance of information on growth-rates, moult-stages, longevities, brood-sizes and egg durations.

## 3. Cyclops strenuus abyssorum

### (a) The annual cycles

### i. Quantitative changes in standing crop

Throughout the entire sampling period the *Cyclops strenuus abyssorum* population at Loch Leven remained essentially planktonic with adults and all developmental stages being represented on every sampling date. Adult females with egg-sacs were always encountered so that reproduction was continuous throughout the yearly cycle. However, the annual cycles of 1972 and 1973 showed considerable variation particularly in terms of numerical abundance. Fig. 21 shows the seasonal changes in mean standing crop of the entire population, separated into nauplii (all five instars grouped), five copepodid stages (C1-V) and adults (CV1). The arithmetic mean densities derived from total counts of forty-eight or twenty-eight Friedinger samples are expressed as numbers per litre. The graph also includes the seasonal variations in mean egg stock, calculated for each sampling date by multiplying the mean number of egg-sacs per litre by the mean number of eggs per egg-sac (brood-size).

During the winter of 1971-72 the copepod population was comprised mainly of nauplii and

Figure 21 (opposite)

Seasonal variations in the mean egg stock and in the mean standing crop of all the developmental stages of *Cyclops strenuus abyssorum* from Loch Leven during 1972-73.

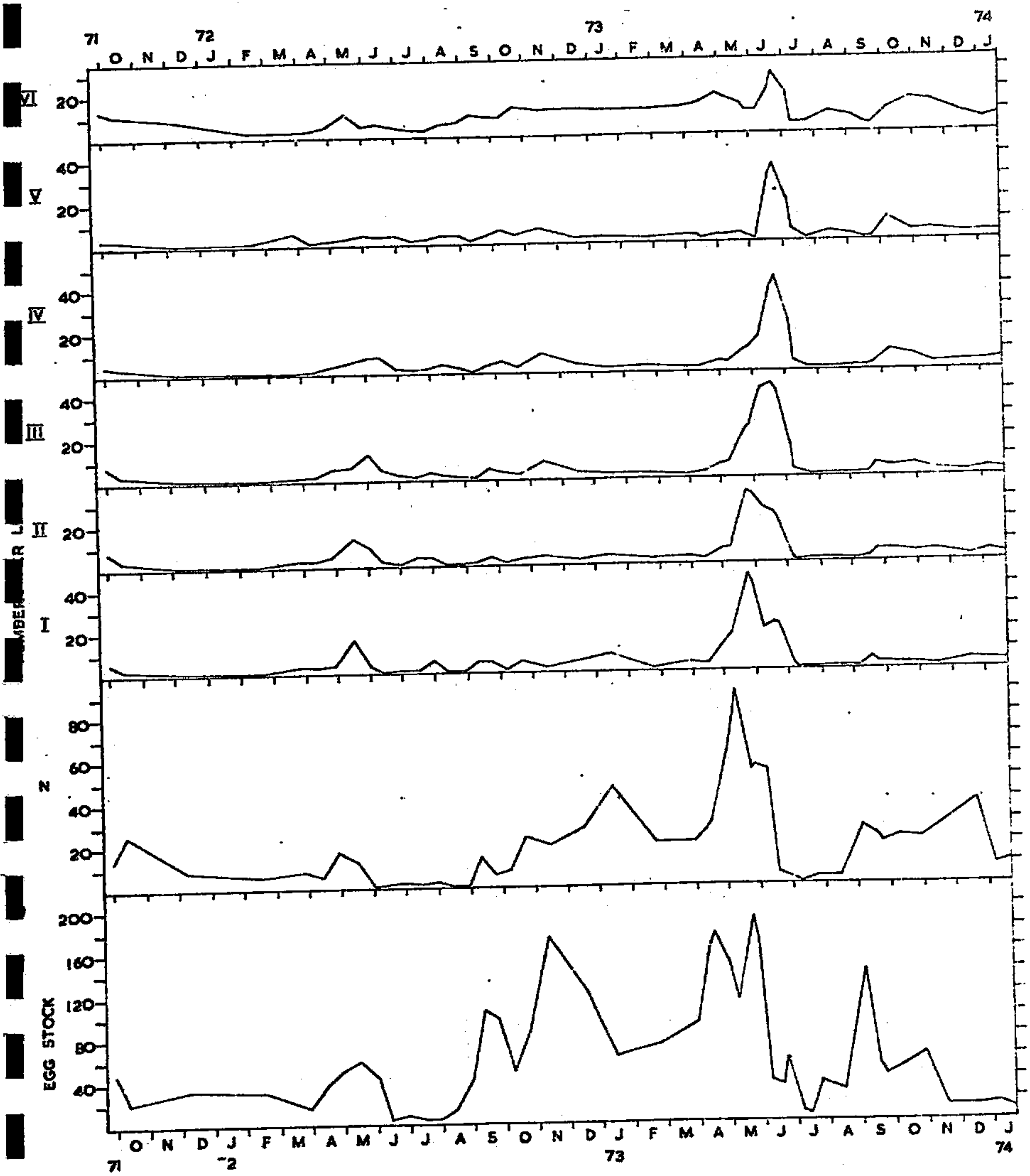
Abcissa - the study period

Ordinates - the mean egg stock per litre.

- the mean numbers per litre of *C. strenuus abyssorum* nauplii and successive copepodid stages 1 - VI.

Note that the data for egg stock is on a different scale to that of the nauplii and successive copepodid stages.

Fig. 21


71
72
73
74
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
VI
20
V
40
20
IV
40
20
III
40
20
II
20
I
40
20
N
80
60
40
20
EGG STOCK
200
160
120
80
40
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
71
72
73
74

developmental instars. Total population numbers amounted to less than 20 ind/l. The egg stock at this time consistently remained at the relatively low value of approximately 30 eggs/l.

As the loch temperatures began to increase in late March, minor increases were apparent in the numbers of the various copepodid stages, especially copepodid stage V (CV). During April, the egg stock showed a distinct increase, this being followed by further progressive increases to a spring maximum of 59.9 eggs/l in mid-May. The rise in egg stock effected notable increases in the numbers of nauplii to a spring maximum of 17.4 ind/l in late April, this being a precursor to consequential increases and decreases in successive copepodid instars C1-1V as rapid development took place onwards into May and June. The numbers of C1V reached a maximum abundance of approximately 8 ind/l in early June. Following this, however, recruitment to stages CV and CV1 (adults) appeared to be limited, as distinct increases in these stages were not evident. Development rates throughout this period would presumably have been progressively enhanced as a result of the steadily increasing loch temperatures (Fig. 2).

of the population had in fact occurred earlier - during May when a mid-May maximum of 10.4 ind/l was recorded. These adults, which presumably had arisen by development from the CV stages evident in late March, provided the high egg stock of mid-May. At precisely this time the total population numbers of C. s. abyssorum reached a spring climax of 62.9 ind/l (see Fig. 31 in the Discussion section) consisting mostly of nauplii and early copepodid stages Cl and Cll, with adults representing 15 per cent by number.

The June population consisted essentially of late copepodid instars and adults with very few nauplii and stages Cl and Cll. As the summer progressed into July and early August, minor fluctuations were apparent in each of the various developmental stages although the egg stock and nauplii numbers remained consistently at their seasonal lowest, <10 eggs/l and <3 ind/l respectively. From late June until late August, the total population numbers remained consistently low, fluctuating around 20 ind/l with adults amounting to approximately 20 per cent by proportion.

In the latter half of August, adult numbers started to increase presumably by recruitment from late copepodid stages and accumulation because of survival of existing adults. In early September, these individuals gave rise to a high egg stock of over 100 eggs/l and at the same time increases in nauplii numbers were apparent. In October, minor increases were detectable in successive copepodid stages and in late October the adult fraction was once again incremented to give an annual mean maximum adult abundance of 13.1 ind/l. Similar numbers of adults (above 10 ind/l) were also recorded in late September and early October of 1971. The C. s. abyssorum population attained a second peak of numerical abundance in mid-November. A mean of 63.2 ind/l was recorded, this being very similar to the maximum achieved in mid-May. The egg stock also reached an annual maximum of 173.2 eggs/l in mid-November. As the year ended, the egg stock showed a distinct drop, this being concurrent with progressive increases in nauplii numbers into the new year.

The copepod population which persisted throughout the 1972-73 winter was consistently comprised of high numbers of adults and nauplii, with relatively few individuals in each of the developmental copepodid instars. Although the nauplii numbers were subject to fluctuations, the adult numbers remained consistently stable at approximately

12 ind/l. Total population numbers were consistently higher than that of the 1971-72 winter with a difference of at least two-fold being maintained throughout. A high egg stock of over and above 60 eggs/l was constantly maintained by the adult population, this being much greater than that recorded during the previous winter and marginally greater than that of the spring maximum. This high egg stock was thus maintained until early April of 1973.

In April, concurrent with a minor increase in the adult numbers from overwintering levels to over 15 ind/l, the egg stock rose sharply to over 170 eggs/l. Development of this egg stock gave rise to peak numbers of nauplii, 90.4 ind/l, in early May. This was then followed by very drastic increases in successive copepodid instars throughout May and early June until the adult population was once again incremented in June. Although the bulk egg stock of April provided the major increases in subsequent developmental stages during this period, the developing population was further boosted by a second increase in egg stock to 189.0 eggs/l in late May. Cohorts originating from this secondary influx of eggs could be clearly traced up to stage C11. The total population built up during May and early June to a maximum standing crop for the entire sampling period of over 190 ind/l in mid-June. Although the adults attained an ultimate peak of 27.4 ind/l at this time, they did not produce further substantial increases in egg stock - the latter being limited to comparatively low levels of less than 60 eggs/l.

However, in late June and early July the C. s. abyssorum population showed a catastrophic decline to a seasonal minimum of 12.3 ind/l. The loss was effected in all copepodid developmental instars and also in the adult stage. Notable decreases in nauplii (and egg stock) had occurred much earlier during June presumably by recruitment to further developmental phases. It appeared that the relatively high numbers of stage CV (up to 35.9 ind/l) in late June and at the onset of July did not manifest themselves as adults in July. In addition, a further reduction in egg stock to less than 10 eggs/l was coincident with the main population decrease.

For the remainder of July and into early August the egg stock and the various population components remained at their seasonal lowest. Adults increased marginally during August and, at the onset of September, produced a substantial increase in egg stock to 139.0 eggs/l. Subsequent increases in nauplii and successive copepodid instars ensured into early October and eventually incremented the adult population towards the end of the same month and into November.

As the year ended and loch temperatures declined, the population consisted mainly of high numbers of nauplii and relatively low numbers of each of the copepodid instars. The adults and egg stock generally declined in abundance as time progressed thereafter.

Although the *C. s. abyssorum* populations of 1972 and 1973 showed considerable variation as regards numerical abundance, there appeared to be certain points of similarity in the seasonal cycle of events. The overwintering populations of the 1971-72 and 1972-73 winters consisted more or less of similar proportions of the various life-stages. In early spring, as loch temperatures began to increase, development of late copepodid instars gave rise to increases in the adult numbers. The spring adults then gave rise to an increase in egg stock which in turn produced the spring or early summer population maximums. The population maximum was followed by a drastic decrease to a seasonal minimum in July. In both years, the egg stock and nauplii numbers remained consistently at their seasonal lowest throughout June, July and for most of August. A further population increase then occurred in the autumn, this being effected by a sharp rise in egg stock in early September of both years.

However, the most distinct difference between the copepod populations of both sampling years relates to the numerical densities of the spring and early summer maximums. With reference to Fig. 31 (in the Discussion section) it can be seen that in 1973, the population maintained an abundance of over 180 ind/1 from mid-May until late June. This was approximately three times greater than the short-lived mid-May maximum of 1972.

### ii. The breeding parameters

Unlike *Daphnia* spp. which reproduce asexually by parthenogenesis and also by sexual means, copepods reproduce only sexually. Gravid adult female members of the sub-order Cyclopoida characteristically carry paired egg-sacs making them distinct from the Harpacticoida and Calanoida which only carry one egg-sac. In order to assess the variations in the breeding capacity of the *Cyclops strenuus abyssorum* population numbers of adult egg-bearing females in the population and the numbers of eggs per egg-sac for each sampling date during the two year study period.

Fig. 22 shows the derivation of the mean egg stock from the percentage and mean numbers per litre of gravid females present in the adult population, the mean numbers per litre of egg-sacs and also the mean numbers of eggs per egg-sac (brood size). The mean numbers of gravid females per litre were obtained during Friedinger sample analysis with the percentage gravid being then calculated as a proportion of the adult female population bearing egg-sacs. The mean numbers of egg-sacs per litre were ascertained by simply doubling the mean numbers of gravid females per litre and the mean brood-sizes were obtained from egg counts of individual egg-sacs taken from fifty, or in certain cases twenty-five, gravid females obtained from net samples.

The percentage of gravid females in the adult population was subject to considerable fluctuation and varied from 3-60 per cent during the two-year period. In 1972 the percentage gravid rarely rose above 40 per cent and on no occasion achieved 50 per cent. Although values above 40

Figure 22 (opposite)

The breeding parameters of the *C. strenuus abyssorum* population of Loch Leven during 1972-73.

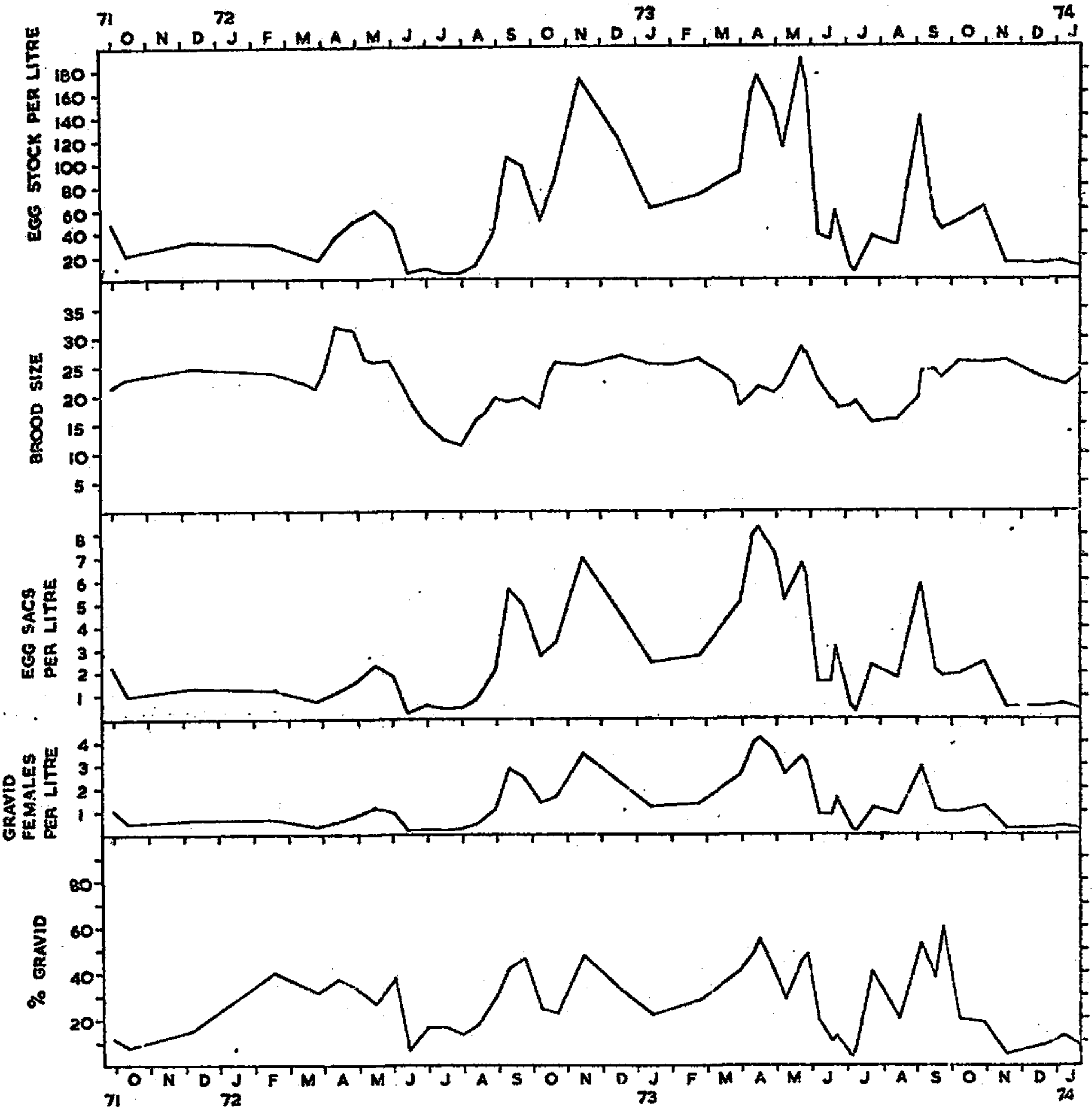
Abcissa - the study period

Ordinates - the percentage of gravid females making up the adult female population.

- the mean numbers per litre of gravid females.
- the mean numbers of egg sacs per litre (i.e. 2 x the mean numbers per litre of gravid females).
- the mean brood-size (i.e. numbers of eggs per egg sac).
- the mean egg stock per litre.

Note that the mean egg stock per litre was obtained by multiplying the mean brood-size by the mean numbers of egg sacs per litre for each sampling date.

Fig. 22


71
72
73
74
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
EGG STOCK PER LITRE
20
40
60
80
100
120
140
160
180
BROOD SIZE
5
10
15
20
25
30
35
EGG SACS PER LITRE
1
2
3
4
5
6
7
8
GRAVID FEMALES PER LITRE
1
2
3
4
% GRAVID
20
40
60
80
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
71
72
73
74

periodic and short-lived and only on three occasions did they exceed 50 per cent.

By viewing this data on a seasonal basis, a generalised pattern of events emerged. During the autumn, late winter and spring periods of both sampling years, the percentage gravid remained consistently higher than at other times with figures usually in excess of 30 per cent. Distinct declines to summer low levels of less than 20 per cent were noted in early June of both years with these low periods extending until late August in 1972 and mid-July of 1973. The low levels subsequently gave way to prominent increases.

Other periods, when the gravid proportion remained consistently below 20 per cent, were during the latter three months of 1971 and 1973. During precisely the same time interval in 1972, the percentage gravid underwent a marked progressive decrease but not to such low levels. Interestingly this trend was reversed during the ensuing first four months of 1973.

The mean numbers of gravid females per litre varied from extremely low levels of well below 1 ind/l to an all-time maximum of 4 || 3.9 ind/l. During 1972 densities of 1 ind/l were recorded on only two occasions prior to a sharp increase to 2.8 ind/l in September. For the remaining months of that year, the numbers generally remained high and reached an annual peak of 3.5 ind/l in mid-November. In 1973 gravid females persisted in considerably high numbers during the spring to give an annual mean maximum of 3.9 ind/l in mid-April. In June the numbers dropped to low summer densities of approximately 1 ind/l and apart from a short-lived increase to 2.9 ind/l in early September, remained at this level or below during the rest of the year. The numbers of egg-sacs per litre obviously followed the same trends but as double the numbers quoted for the gravid females per litre.

The variations in the mean numbers of eggs per egg-sac followed a well defined seasonal pattern in both sampling years. From steady winter levels the mean brood-size underwent a minor decrease in early spring. This was followed firstly by a distinct spring rise to an annual maximum value and then by a gradual decrease to summer minimum levels. During late summer and autumn the mean brood-sizes slowly increased to winter levels once again.

During the months of winter or more precisely study perid, the mean brood-size remained at a constant level of approximately 25 eggs per sac. In 1972 the egg number increased sharply to a spring peak of 31.8 eggs per sac in April and from May to July progressively declined to mid-summer low levels of under 15 eggs per sac. In 1973, however, a spring maximum of 28.2 eggs per sac was attained in late May, this being followed by decreases to minimum levels marginally above 15 eggs per sac. It is interesting to note that in 1972 the spring maximum was higher and the summer minimum lower (11.3 eggs per sac) than those of 1973. Note also that the spring maximum of 1973 is only slightly higher than the typical winter levels.

The mean brood-sizes during 1972 and 1973 are again shown in Fig. 24 with the inclusion of the range (maximum and minimum) and 95 per cent confidence limits for each of the data points. Concerning the range of brood-sizes it leaves only to say that the largest brood encountered during the period of study was 57 eggs per sac and the smallest, 5 eggs per sac.

In relating the above parameters to the derivation of the mean egg stock, two main points arise. Firstly, periods of high mean egg stock are associated with higher percentages of gravid females, higher mean numerical densities of gravid females (or egg-sacs) and usually higher mean brood-sizes. Conversely, periods of low mean egg stock are associated with low levels of the forementioned factors, this being amply demonstrated by the mid-summer depressions of both sampling years. Secondly, the most important parameter governing the egg stock quantity of C. strenuus abyssorum from Loch Leven was the actual numbers of gravid females (or egg-sacs) present in the population and not the brood-sizes. Furthermore, apparently minor increases in the numbers of gravid individuals manifested themselves as prominent increases in egg stock. For example, if the gravid component of a given population was 1 ind/l and each female carried two egg-sacs comprised of twenty-five eggs each, then the egg stock would be 50 eggs/l. A doubling of the gravid female number to 2 ind/l, which in itself seems a minor increase, boosts the egg stock to 100 eggs/l.

### iii. Variations in mean adult female metasomal length

Fig. 24 shows the variations in mean body length of adult female C. strenuus abyssorum from Loch Leven during 1972 and 1973. The mean length

Figure 23 (opposite)

Diagram of a gravid adult female *C. strenuus abyssorum*.

Key

A - cephalothorax
B - metasome
C - total length minus furcal setae

Fig. 23

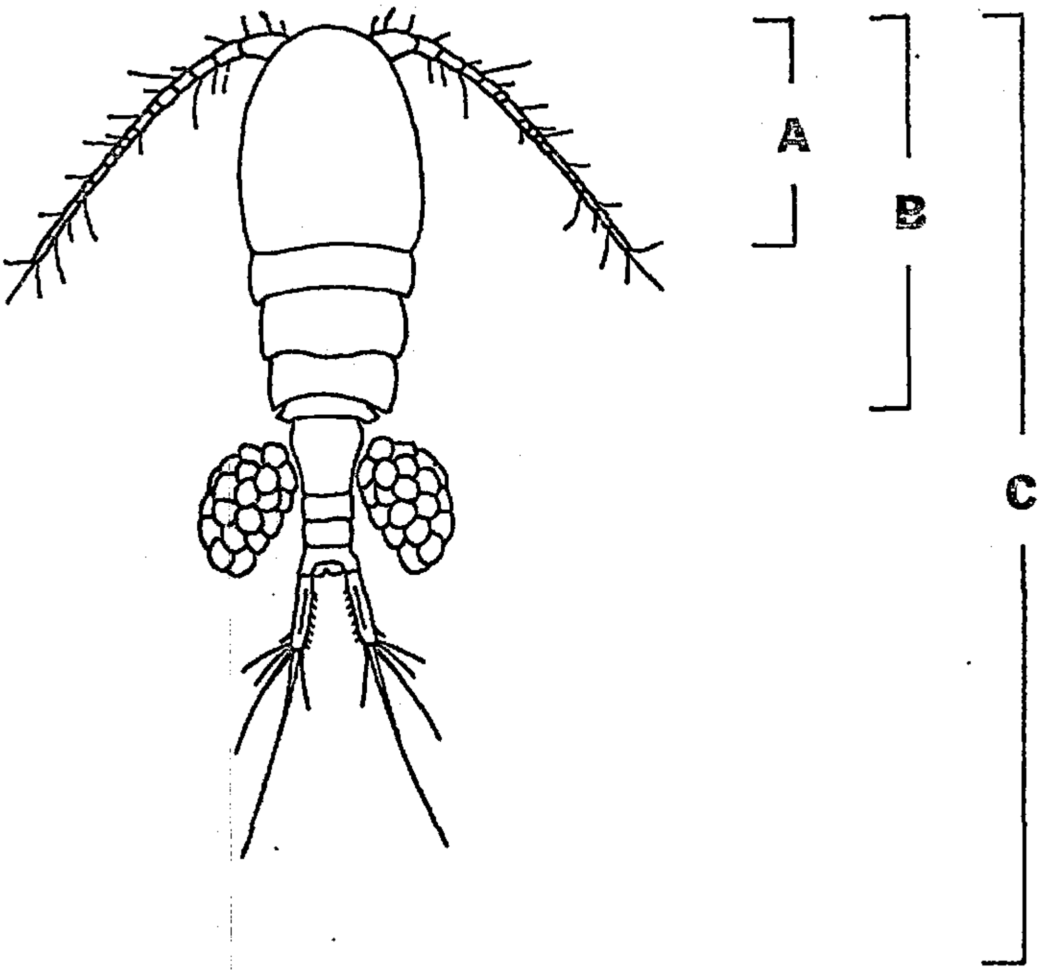


Figure 24 (opposite)

Seasonal changes in mean brood-size and in mean metasomal length of adult female *C. strenuus abyssorum* from Loch Leven during 1972-73.

Abcissa - the study period.

Ordinates - the mean metasomal length in mm. of gravid adult females.

- the mean brood-size (i.e. numbers of eggs per egg sac).

Key

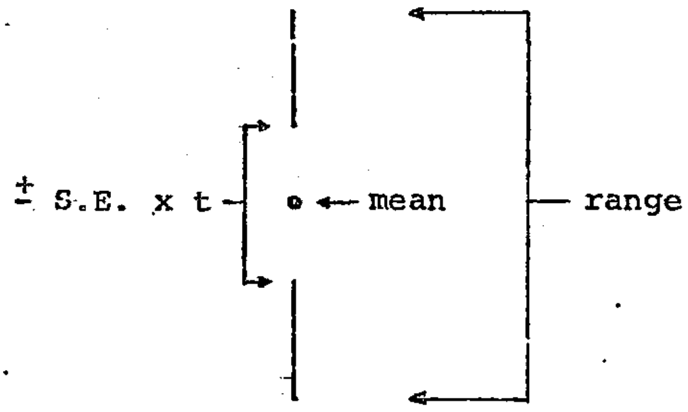
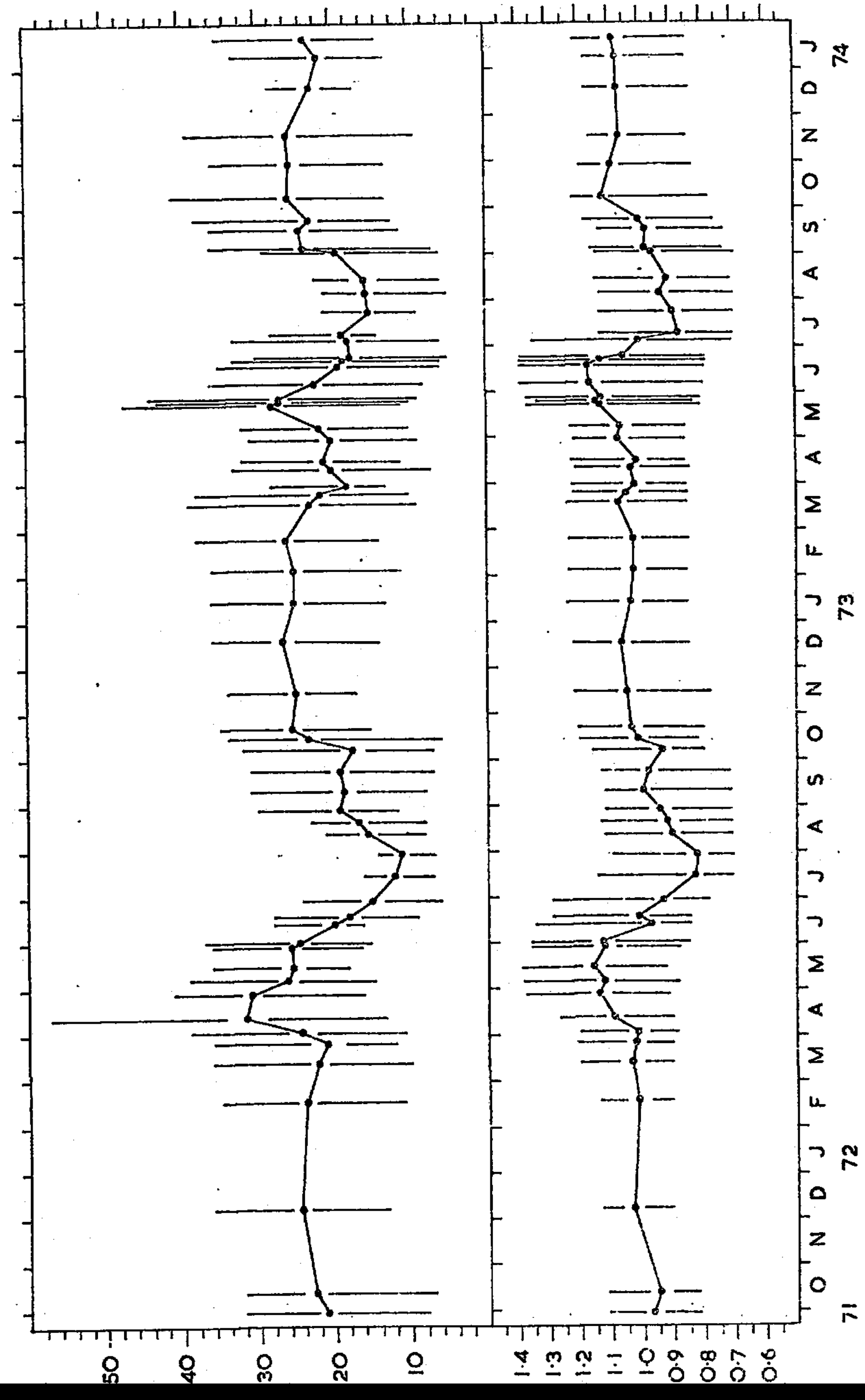


Fig. 24


50
40
30
20
10
1·4
1·3
1·2
1·1
1·0
0·9
0·8
0·7
0·6
71
O
N
D
J
72
F
M
A
M
J
J
A
S
O
N
D
J
73
F
M
A
M
J
J
A
S
O
N
D
J
74

body length increased progressively once again to winter levels.

It is apparent from Fig. 24 that a clear relationship exists between the adult female body length and the brood-size as both sets of data undergo comparable seasonal changes. Although, in general, larger females carry larger broods (and vice-versa), the _largest_ females did not carry the _largest_ broods, as the spring peaks of both parameters do not coincide with one another in either year.

Regarding the maximum and minimum ranges of metasomal lengths encountered during the study period, the largest was 1.38 mm and the smallest was 0.70 mm. It was estimated during the routine measurements that the metasomal length of an adult female corresponded to approximately 58.5 per cent of the total length (minus furcal setae) as depicted in Fig. 23. Thus, in terms of total length, the largest female recorded during the entire study was 2.35 mm and the smallest was 1.20 mm.

### iv. The sex ratio

In the process of analysing the copepod population from Friedinger samples, sexes were differentiated at instars CV and CVI (adults). Fig. 25 shows the seasonal variations data was derived from the measurements of metasomes of fifty, or in some cases twenty-five, individual adult females. The metasomal length is explained in Fig. 23. The graph (Fig. 24) also gives the range (maximum and minimum) and 95 per cent confidence limits (S.E. x t.).

The seasonal pattern of body length changes in both years followed precisely the same trends as those already described for the mean brood-sizes. Throughout the winter months October - March during the sampling years, the mean metasomal lengths fluctuated within the limits of 1.00 - 1.10mm. In 1972 an increase in early April gave rise to mean lengths of over 1.10 mm during late April and throughout May. An annual mean maximum length of 1.16 mm was recorded in mid-May. However, during June and July the body lengths steadily decreased to levels below 0.85 mm, this being followed by gradual increases to winter levels thereafter.

In 1973 mean metasomal lengths in excess of winter levels were first noted in May and persisted as such until mid-June when an annual mean maximum value of 1.17 mm was recorded. A rapid decrease in body length occurred shortly afterwards to give a seasonal minimum of 0.88 mm in early July.

Figure 25 (opposite)

Seasonal variations in the sex ratios of *C. strenuus abyssorum* instars V and VI (adults) during 1972-73.

Abcissa - the study period

Ordinate - the percentage females *or* the percentage males making up the stage V and stage VI (adult) populations.

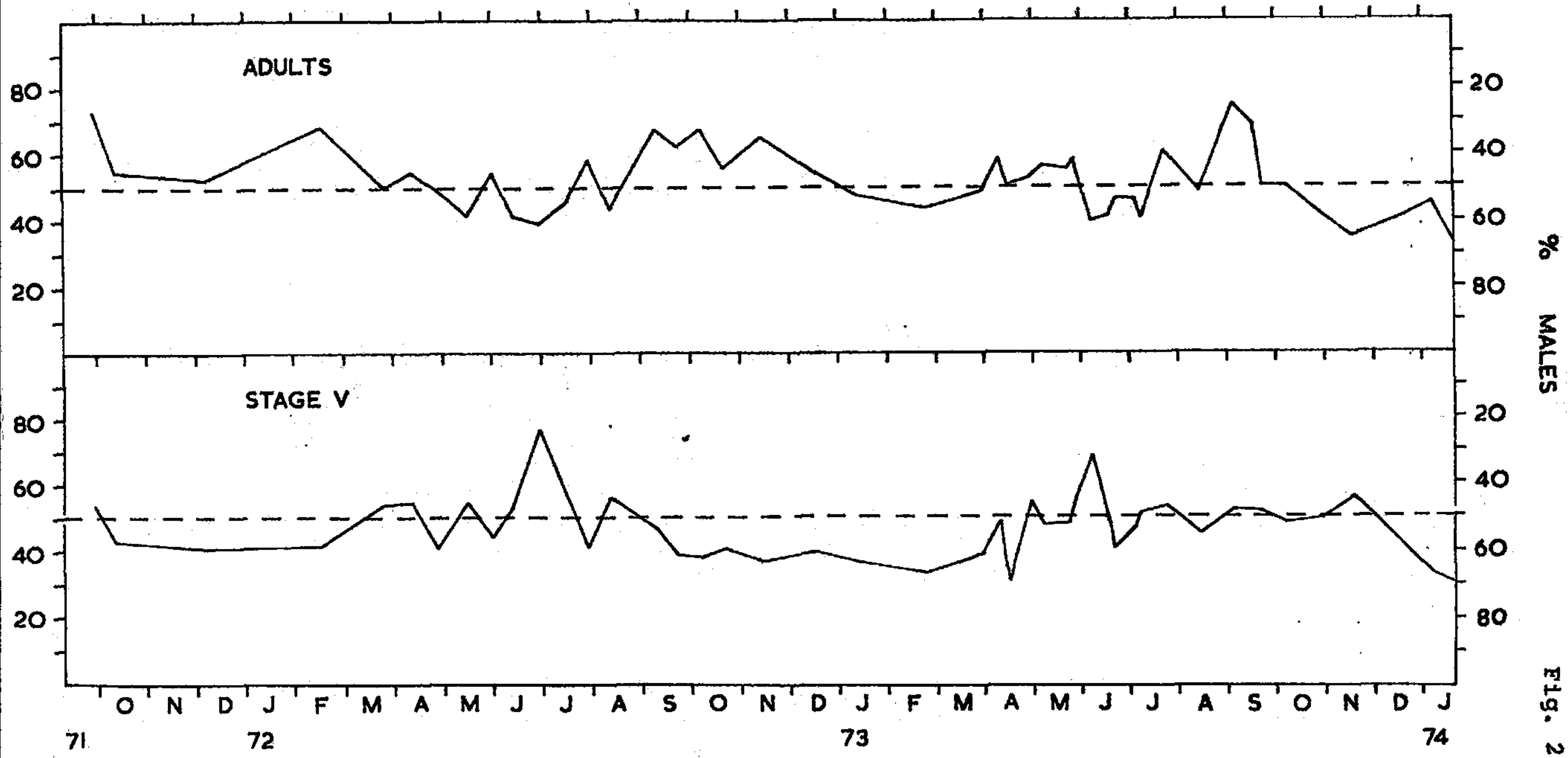

ADULTS
STAGE V
80
60
40
20
20
40
60
80
% MALES
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
71
72
73
74

Fig. 25

in the sex ratios of C. strenuus abyssorum instars CV and CVl during 1972-73. The data, which was derived from the mean numbers of males and females in the respective instar populations on each sampling date, is given as percentages.

Throughout most of the study period the adult sex ratios underwent variable fluctuations within the 40-60 per cent ranges of either sex. Out of a total of forty-six sampling trips the females were recorded as being more abundant than males on twenty-six occasions, with nine of these occasions providing female dominance in excess of 60 per cent. Out of the remaining twenty occasions when males outnumbered females, the female fraction was below 40 per cent only four times. During the two years of sampling the female proportion had a maximum of 73 per cent and a minimum of 32 per cent.

The proportions of males and females in CV developmental component of the copepod population varied within a similar range to that of the adults. The female fraction also had a similar maximum and minimum for the entire sampling period; 75 per cent and 29 per cent respectively. However, out of forty-six sampling trips the females were numerically superior on only eighteen occasions. Interestingly the graph of CV sex ratios often reflected a mirror image to that of the adults. Thus, an increase or decrease in one was mirrored by the opposite effect in the other. This phenomenon is well demonstrated during the spring and summer months of 1972.

The sex ratios of both the CV and CVl instars appeared to show greater stability during the winter months than at other times. During the period September 1972 to March 1973 the males constantly dominated the CV population, suppressing the female proportions to a steady level of approximately 40 per cent. In the adult population, however, the opposite situation prevailed with females dominating during this period until January when the sex ratio gradually reversed in favour of the males.

### (b) The horizontal distribution and sampling variability

Using the sampling data obtained during 1972, the horizontal distribution of the *Cyclops strenuus abyssorum* population was evaluated on exactly the same basis as that of *Daphnia hyalina* var *lacustris* which has already been dealt with in detail (pages 62-64). Table 7 shows the variability between mean counts of total *C. strenuus abyssorum* (all life-stages grouped) as obtained from each of the six sites on seventeen separate sampling visits to Loch Leven during 1972. Regarding this data, it suffices only

Table 7 The horizontal variations in the Cyclops strenuus abyssorum population from zooplankton samples taken at six sites on seventeen visits to Loch Leven In 1972.

The data is given as numbers per five litres.

| Date | SITES | | | | | | Overall mean (48) | Mean for A, D & E (28) | Mean for A, D & E as % of overall mean | % difference |
|---|---|---|---|---|---|---|---|---|---|---|
| | A (6) | B (6) | C (6) | D (4) | E (18) | F (8) | | | | |
| 25/3 | 93.1 | 117.7 | 79.0 | 109.0 | 89.6 | 81.2 | 92.5 | 93.1 | 100.6 | +0.6 |
| 12/4 | 151.0 | 110.7 | 154.5 | 65.7 | 151.7 | 100.5 | 131.1 | 139.3 | 106.2 | +6.2 |
| 27/4 | 224.3 | 242.8 | 222.8 | 150.2 | 226.2 | 201.5 | 217.2 | 214.9 | 98.9 | -1.1 |
| 15/5 | 228.0 | 171.0 | 389.0 | 155.0 | 389.8 | 342.0 | 314.6 | 321.6 | 102.2 | +2.2 |
| 1/6 | 148.3 | 254.2 | 217.7 | 188.7 | 208.3 | 227.1 | 209.2 | 192.6 | 92.1 | -7.9 |
| 13/6 | 114.3 | 143.7 | 143.5 | 104.0 | 139.4 | 122.0 | 131.4 | 128.9 | 98.1 | -1.9 |
| 29/6 | 92.2 | 66.7 | 109.7 | 76.2 | 69.8 | 132.7 | 88.2 | 75.5 | 85.6 | -14.4 |
| 15/7 | 37.2 | 66.3 | 45.8 | 43.5 | 94.0 | 120.1 | 77.6 | 74.6 | 96.1 | -3.9 |
| 29/7 | 30.2 | 50.0 | 406.8 | 62.7 | 139.7 | 33.7 | 124.1 | 105.2 | 84.8 | -15.2 |
| 12/8 | 91.2 | 73.8 | 123.8 | 72.5 | 61.7 | 181.4 | 97.0 | 70.1 | 72.3 | -27.7 |
| 28/8 | 49.8 | 60.0 | 78.2 | 59.0 | 120.1 | 114.9 | 91.5 | 95.4 | 104.3 | +4.3 |
| 10/9 | 145.3 | 262.3 | 132.7 | 227.2 | 174.9 | 161.4 | 179.0 | 176.0 | 98.3 | -1.7 |
| 23/9 | 166.5 | 224.7 | 95.5 | 353.7 | 177.2 | 136.9 | 179.6 | 200.1 | 111.4 | +11.4 |
| 7/10 | 211.2 | 273.2 | 97.8 | 158.3 | 192.0 | 148.4 | 181.9 | 191.8 | 105.4 | +5.4 |
| 21/10 | 298.2 | 284.2 | 149.5 | 194.7 | 290.8 | 299.0 | 265.5 | 277.7 | 104.6 | +4.6 |
| 14/11 | 344.3 | 275.3 | 238.5 | 202.5 | 376.7 | 320.5 | 316.1 | 342.5 | 108.3 | +8.3 |
| 16/12 | 202.2 | 253.8 | 251.8 | 398.0 | 318.5 | 299.6 | 288.9 | 303.3 | 105.0 | +5.0 |

The table shows the variability between mean counts of total numbers of C.s. abyssorum taken from different sites on the same date and compares the mean derived from sites A, D and E with the overall mean derived from all six sites. The numbers of samples per site on each visit are shown in brackets. See Fig. 1 for explanation of sites. Sites A, D and E were sampled in 1973.

to say that all the main points previously mentioned concerning the horizontal distribution of *D. hyalina* var *lacustris* also apply to the copepod species.

As explained in the Materials and Methods section, the 1972 data on horizontal distribution was analysed in order to assess the feasibility of reducing the numbers of Friedinger samples taken per sampling visit during 1973. Table 7 compares the mean standing crop derived from three sites A, D and E (mean of twenty-eight Friedinger samples) with the overall mean derived from all six sites (mean of forty-eight samples) for each of the seventeen sampling trips in 1972. The differences are expressed as percentages.

The data shows that if the three sites had been sampled, the calculated mean estimates for *C. s. abyssorum* as compared to those for the full six sites would have a maximum variation of ± 28 per cent. On thirteen occasions the variation was less than ± 10 per cent and on fifteen occasions out of a total of seventeen it was less than ± 15 per cent. On the basis of these assessments it was reasonable to suppose that sampling three sites in 1973 would provide reliable quantitative estimates of the *Cyclops* population.

### 4. Other crustacean species occurring in Loch Leven plankton samples during 1972-73.

Although the present study was primarily concerned with the two co-dominant species *Daphnia hyalina* var *lacustris* and *Cyclops strenuus abyssorum*, the populations of the numerically subordinate crustacean species were monitored throughout the entire sampling period. Table 10 lists all the crustacean species encountered in plankton samples at Loch Leven in order of numerical importance.

Table 10. Species list of crustaceans taken from plankton samples at Loch Leven during 1972-73.

In order of numerical abundance

| Cladocera | Copepoda |
|---|---|
| *Daphnia hyalina* var *lacustris* Sars | *Cyclops strenuus abyssorum* Sars |
| *Leptodora kindti* (Focke) | *Diaptomus gracilis* Sars |
| *Bythotrephes longimanus* Leydig | *Cyclops affinis* Sars |
| *Chydorus sphaericus* (O.F. Müller) | *Cyclops fimbriatus* (s.str.) (Fischer) |
| *Alona affinis* Leydig | |

All of the above species, except *D. hyalina* var *lacustris* and *Leptodora kindti*, were also recorded in plankton samples during 1969 (Walker 1970).

Apart from *D. hyalina* var *lacustris* and *C. strenuus abyssorum*, only *Diaptomus gracilis*, *Leptodora kindti* and *Bythotrephes longimanus* occurred regularly and in quantity and, according to Scourfield and Harding (1966) and Harding and Smith (1960) life-styles. The remaining four species were noted by these authors to be essentially littoral or benthic forms. Observations relating to the copepods *Cyclops affinis* and *C. fimbriatus* and the cladoceran *Alona affinis* amounted to less than ten individuals in each case being recorded within the two years and thus their appearance in plankton samples suggested only brief excursions into the open water. However, the bottom-dwelling cladoceran *Chydorus sphaericus* occurred more often and at certain times in relatively large numbers (see Table 11 and accompanying notes).

### (a) *Diaptomus gracilis*

In the process of routine Friedinger sample analysis the *Diaptomus gracilis* population was differentiated simply into nauplii and copepodids (all instars grouped including adults) with all egg-sacs, loose or attached, being counted. Periodically the population was examined more fully, mainly to assess the proportions of adults amongst the copepodid stages. It was considered adequate to treat the species on a superficial level because of the relatively low numerical densities maintained moreor less throughout the year.

Fig. 27 shows the seasonal variations in mean standing crop of the entire *D. gracilis* population (all life-stages grouped) together with the variations in mean egg stock during 1972-73. Both sets of data

Figure 27 (opposite)

Seasonal variations in mean egg stock and in the mean standing crop of the *Diaptomus gracilis* population of Loch Leven during 1972-73.

Abcissa - the study period

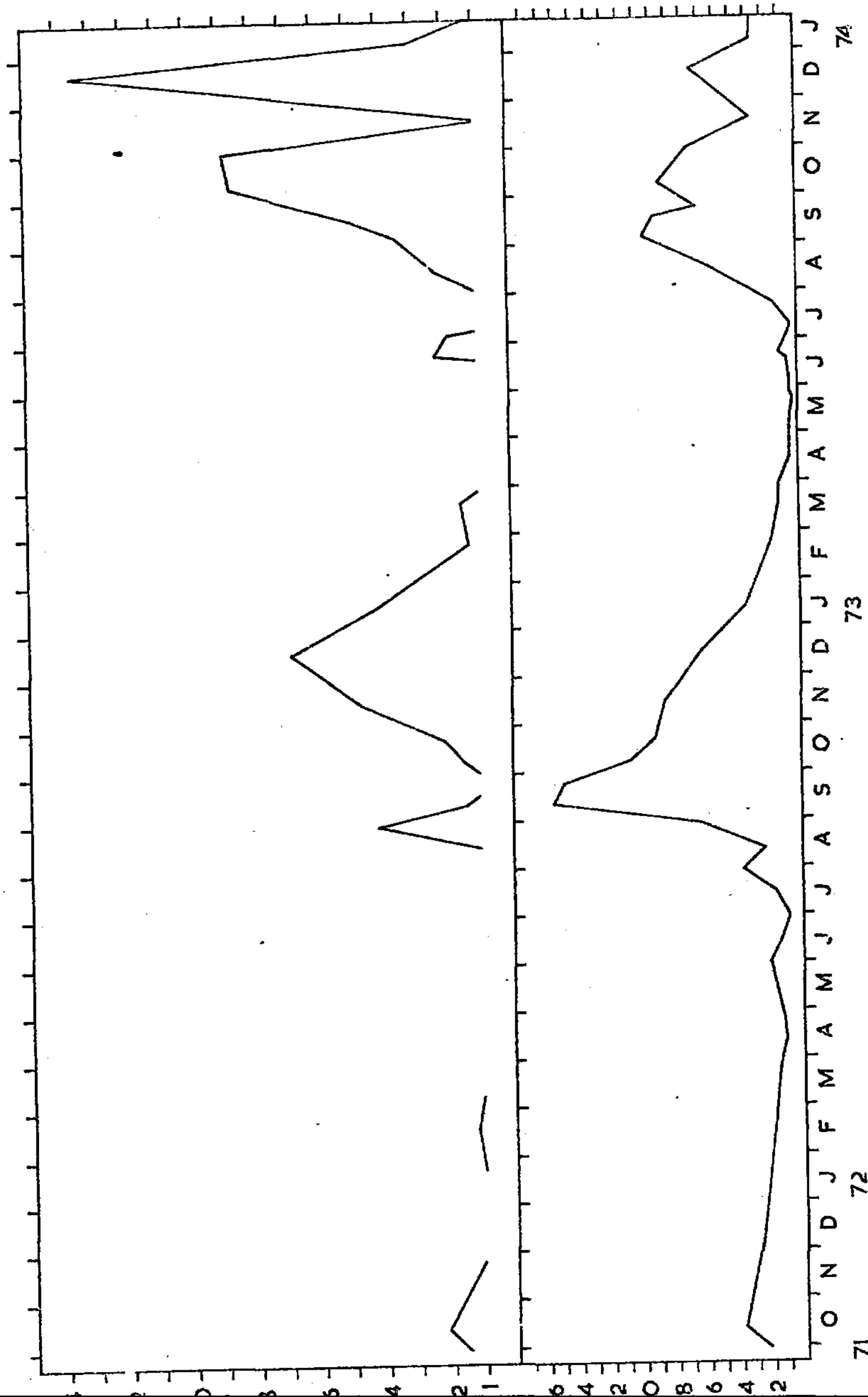
Ordinates - the mean numbers per litre of *Diaptomus gracilis*

- the mean egg stock per litre

Note that the two sets of data are presented on different scales.

The mean egg stock data was calculated by multiplying the mean number of egg-sacs per litre for each sampling trip by a factor of 15 - the *approximate* mean number of eggs per egg-sac. This figure was derived as the average egg count of 120 egg-sacs, the egg-sacs being systematically taken from net samples in the form of ten egg-sacs per month throughout the year 1973. The mean obtained, 15.04 eggs per egg-sac, had a range of 4-24. A higher degree of quantitative accuracy was considered to be unnecessary in the evaluation of *Diaptomus* egg-stock as this data serves only to illustrate peaks of reproductive intensity. Note also that because of this, egg-stock estimates below 1 egg/l are not included in the graph.

Fig. 27



are given in terms of numbers per litre. The mean egg stock was calculated by multiplying the mean numbers of egg-sacs per litre for each sampling date by a factor of 15, this being the approximate mean number of eggs per egg-sac derived from egg counts of 120 egg-sacs taken systematically throughout 1973 (see legend of Fig. 27). The egg stock data serves only to illustrate periods of reproductive intensity and therefore egg-stock estimates below 1 egg/l are not included in the graph.

D. gracilis was evident in plankton samples throughout the two year study period but mean total population numbers remained low, rarely exceeding 10 ind/l and never exceeding 16 ind/l. Periods of relatively high abundance were confined to the latter halves of both sampling years. During the first seven months of both years the population remained consistently below 4 ind/l and generally consisted mainly of adults with few copepodid developmental stages and even fewer nauplii. Adult females with egg-sacs frequently occurred in the very early months of the year at the end of winter but during late spring and early summer their occurrences were sparse and on several sampling trips no diaptomid egg-sacs were encountered whatsoever.

However, in late summer of both years the Diaptomus population showed distinct and rapid increases to annual maximum densities. In late August of 1972 a prominent rise in egg stock to 4.1 eggs/l was noted, this being the precursor to the peak population numbers of 15.5 ind/l in mid-September - the maximum density recorded during the entire sampling period. Throughout September the bulk of these animals were nauplii and early developmental copepodid stages with adults making up less than 20 per cent by proportion. As the year ended, the population progressively declined with late copepodid instars and adults being numerically dominant. The egg stock was comparatively high during this period remaining above 4 eggs/l and reached an annual maximum abundance of 6.9 eggs/l in mid-December. However, this egg stock did not manifest itself as nauplii in samples taken thereafter.

The pattern of events in the latter half of 1973 were very similar to those of the same period in 1972. Maximum numerical densities were somewhat lower with an annual peak of 9.5 ind/l being achieved in mid-September. Unlike in 1972, a notable rise in nauplii numbers was recorded at the end of 1973, this being coincident with an all-time maximum in egg stock to 13.5 eggs/l in mid-December.

(b) Leptodora kindti and Bythotrephes longimanus.

Throughout the study period, the predatory cladocerans Leptodora kindti and Bythotrephes longimanus were monitored in terms of total numbers only. As these animals were never present in substantial quantities, attempts at assessing further aspects of their populations were considered unnecessary and inappropriate to the main context of this thesis. Table 11 presents information on the seasonal appearances and abundance of *L. kindti* and *B. longimanus* (as well as *Chydorus sphaericus*) during 1972-73. Because of the low population densities the quantitative data is given as total numbers per sampling visit or more precisely as numbers per forty-eight Friedinger samples during 1972 (Table 11A) and numbers per twenty-eight samples during 1973 (Table 11B). The occurrences of these species in net samples but not in Friedinger samples are denoted by a '+' sign.

The predatory cladocerans showed a distinct seasonal presence in the plankton of Loch Leven and were only found in samples from June to November in both sampling years. In 1972 the two species just appeared in samples towards the end of June and in both cases reached annual maximum abundance in mid-August with their respective populations declining thereafter. Neither species was found in December samples. In 1973 *L. kindti* initially occurred in early July, achieved a numerical maximum in late September and persisted in open water until mid-November. *B. longimanus* was first encountered in mid-June samples, attained peaks of abundance from late July until mid-August and then declined to total absence in November.

Table 11 The seasonal appearances and abundance of *Leptodora kindti*, *Bythotrephes longimanus* and *Chydorus sphaericus* during 1972-73.

Quantitative data is given as total numbers per sampling visit and the occurrences of the various species in net samples but not in Friedinger samples are denoted by '+' signs.

Table 11A Numbers per forty-eight Friedinger samples in 1972.

| Sampling Dates | *Leptodora kindti* | *Bythotrephes longimanus* | *Chydorus sphaericus* |
|---|---|---|---|
| 17/2/72 | | | |
| 25/3 | | | |
| 12/4 | | | |
| 27/4 | | | |
| 15/5 | | | |
| 1/6 | | | |
| 13/6 | | + | |
| 29/6 * | 5 | 1 | |
| 15/7 | 2 | 5 | 44 |
| 29/7 | 15 | 19 | |
| 12/8 | 109 | 72 | |
| 28/8 | 55 | 10 | 35 |
| 10/9 | 44 | 21 | 9 |
| 23/9 | 39 | 10 | 2 |
| 7/10 | 32 | 5 | |
| 21/10 | 26 | 3 | |
| 14/11 | 12 | + | 3 |
| 16/12 | | | |

* 50 samples

Table 11B Numbers per twenty-eight Friedinger samples in 1973.

| Sampling Dates | Leptodora kindti | Bythotrephes longimanus | Chydorus sphaericus |
|---|---|---|---|
| 13/1/73 | | | |
| 24/2 | | | |
| 29/3 ** | | | |
| 10/4 | | | |
| 15/4 | | | |
| 29/4 | | | |
| 7/5 | | | 2 |
| 22/5 | | | 2 |
| 26/5 | | | 1 |
| 6/6 | | | |
| 17/6 | | | |
| 21/6 | | 5 | |
| 4/7 | | + | |
| 8/7 | 1 | 16 | |
| 22/7 | 9 | 68 | |
| 14/8 | 31 | 70 | |
| 4/9 *** | 41 | 28 | 1 |
| 16/9 | 37 | 11 | |
| 22/9 | 82 | 6 | |
| 7/10 | 7 | 3 | |
| 28/10 | 11 | + | |
| 17/11 | 1 | | |
| 18/12**** | | | |

** 18 samples *** 6 samples **** 6 samples

Chydorus sphaericus appeared in sufficient quantity to deserve mention. Its appearance in the Loch Leven plankton was spasmodic, generally occurring in the summer months and seemed to coincide with dense accumulations of blue-green algae (Table12). According to Hutchinson (1966) the species is generally acknowledged to be perennial in the littoral zones but may appear in quantity in the open water only during the summer - usually July and August (Birge 1898; Wesenburg-Lund 1904; Patalas 1954). Berg and Nygaard (1929) showed that C. sphaericus reached a peak of abundance in August during an Anacystis bloom in the Frederiksborg Slotsø, this being thought to be associated with an increase in the back-scattering of light from open water in which much seston was suspended. Similarly C. sphaericus in Lake Mendota became planktonic during blue-green algal blooms (Apstein, 1896; Birge, 1898).

The fact that the Loch Leven species was recorded more often and in greater abundance during 1972 than 1973 is largely because approximately 67 per cent of the animals taken during 1972 were located at site C and this site was not sampled during 1973. Presumably the population existing

In Tables 2 and 7 and in Figures 8,9,12,14,22 and 25 data were presented as proportions of a total and expressed as percentages. The reliability of such information is dependent upon the numerical extent of the total such that the greater the total (sample number) the greater the reliability. Apparently minor proportions obtained from small totals manifest themselves as considerable percentages. For example, when evaluating the feasibility of using three sampling sites instead of six (*Daphnia* horizontal distribution Table 2) the greatest percentage difference (+34.7) was encountered with the lowest population density (<1 ind/1) implying in this case a discrepancy with data quantity as opposed to the proposed sampling scheme. However, with most of the other data presented as percentages, the totals involved are generally adequately large to provide reasonable reliability.

### (c) Zooplankton distribution

Loch Leven is a large body of water and has a complicated structure incorporating six islands (Fig. 1). Its form has been likened to that of a dish (Smith 1974), having a very shallow rim and a central area of deeper water which includes two deep kettle-holes (page 3). The zooplankton within such an irregular loch might not be expected to exhibit a uniform horizontal distribution. Similarly, within the limited areas of deep water (to a maximum of 25 m) the scope for variation in a vertical plane is considerable.

### (i) Horizontal distribution

A full evaluation of the horizontal distribution of zooplankton in Loch Leven would be difficult with the data at hand. Although it would be possible to assess site-to-site variations for the full six sites in 1972, comparable data would be limited to 0m and 1m depths (page 63) which is probably insufficient. Such an analysis might suggest departures from random distributions (i.e. super-dispersions or infra-dispersions) within the described water layers but even so it would be difficult to ascertain causal phenomena. Furthermore, when Walker (1970) analysed within-site variance from mean copepod population data obtained from sampling one site on six occasions within a twenty-four hour period, he found that substantial variations existed and concluded that there was little difference in variability between means calculated from groups of samples taken during an extended period at a single site with that obtained between means of groups of samples taken from several sites at approximately the same time. Thus, real differences existing between sites, and hence peculiarities in horizontal distribution, would be difficult to elucidate.

Because of the nature and purposes of the present sampling scheme, sampling stations were confined to deeper (2m+) open water sites. Areas close to the water inlet and outlet sources were avoided to off-set the possibilities of collecting erroneous data for inclusion in overall population estimates. Areas around the perimeter of the loch would have been too shallow for effective use of the Friedinger sampler anyway.

In the literature, conflicting results have been obtained regarding horizontal distribution of zooplankton. Needham and Lloyd (1937) stated that planktonic organisms are uniformly distributed in a horizontal direction. Similarly, randomness has been described by Ricker (1937) and Langford (1938). However, Welch (1935) observed substantial horizontal irregularities which were not correlated with any physical or chemical parameters nor with phytoplankton densities. Plankton patchiness has been reported by Dumont (1967) and this phenomenon was recorded for Daphnia spp. by Ragotzkie and Bryson (1953) in the upper-most water layers of Lake Mendota. Primary factors which have been linked with horizontal variability are peculiarities of the shoreline, inflowing and outflowing water, wind action, predation by planktonic predators, swarming of the species and indirect results of diurnal migration (Hutchinson, 1967; Patalas, 1969; Hodgkiss and Chan, 1976).

Zooplankton populations are known to avoid the shore especially where this is shallow (Hutchinson, 1967). Burckhardt (1910) recorded an almost complete absence of Cladocera and a considerable reduction in copepod numbers near the shores of the eastern arm of Lago Lugano. Although mechanisms involved are uncertain it has been suggested that depth limitation of downward movement may be important and that animals intent on descending follow the bottom on a downward trend and eventually arrive at greater depths (Hutchinson, 1967). It is also possible that such littoral zones possess adverse optical properties influenced by reflection of light from the bottom sediments, although this would not apply at night.

Although this aspect was not tested at Loch Leven, the phenomenon of littoral avoidance might apply within the very extensive sandy-bottomed shallows around the north-east shoreline, around the shallow stony regions of the north-west margin and around island boundaries. If,because of certain circumstances, the zooplankton showed a preferential vertical zonation well below the surface, say below two metres, this might preclude their abundance in the proximity of the main shoreline and around islands. It should be added that the artificially controlled seasonal variations in water level (Smith, 1974), which obviously affect water depth (up to 1m, Smith pers. comm.) in the shallow regions, may be influential as regards plankton dispersion. However, at no time during the present study was a prominent paucity in zooplankton

which was only two metres deep and

situated in the north-east shallows (Fig. 1).

Avoidance of littoral vegetation by zooplankton, which according to Hasler and Jones (1949) relates more to planktonic rotifers than crustaceans, would not apply to Loch Leven under the present circumstances of sparse vegetation although the phenomenon may have arisen in pre-war conditions when vegetation was very dense (Morgan, 1970, 1974) and possibly in the future as macrophytes are progressively re-establishing themselves (Jupp *et al*, 1974).

Loch Leven has four inlets and one artificially controlled outlet. In some cases planktonic organisms appear to avoid outlets of lakes (or more precisely show avoidance of currents) as noted by Hutchinson (1967). Clear evidence of this has been shown by Chandler (1939) at Base Line Lake, Michigan and Brook and Woodward (1956) at Loch Kinardochy although Hall (1962) found no such avoidance by *Daphnia galeata mendotae* at Base Line Lake and likewise Brook and Woodward (1956) for *D. hyalina* in a small lochan. As regards Loch Leven, no sampling was undertaken where such water flow existed although Walker (1970) sampled near the exist point of the outlet sluice and judging by his data no distinct or consistent scarcity of *Cyclops strenuus abyssorum* was recorded.

Wind-induced water movements appear to be a major factor giving rise to plankton patchiness as recorded for Daphnia spp. in Lake Mendota by Ragotzkie and Bryson (1953) and McNaught and Hasler (1961). The hydrodynamic properties of Langmuir spirals may produce plankton streaks (Hutchinson, 1967; George and Edwards,1973) which would appear as clumps or aggregates if sampled in transverse section. In fact, Ragotzkie and Bryson concluded that plankton accumulations might be predictable using appropriate data on water movments. With the available detailed information on water movments obtained by Smith (1974) the assumption of Ragotzkie and Bryson could be applied and tested at Loch Leven. However, Hodgkiss and Chan (1976) concluded that wind action (even tycoon winds!) had no apparent effect on the horizontal distribution of zooplankton in Plover Cove Reservoir, Hong Kong.

Relating the previous information to sampling strategy, a question might be raised as to whether to sample zooplankton in calm or windy conditions? During the present study, sampling at Loch Leven could only be entertained in moderate wind conditions and it was noted on several occasions that wind varied very much in strength and even direction during the course of one day. The question, therefore, has a practical as well as a possible theoretical answer.

Loch Leven is generally well-mixed due to persistent wind action, therefore it may be assumed that passive, less mobile or small particles are likely to be horizontally uniform most of the time. On this basis Bailey-Watts (1974) effectively sampled the phytoplankton at Loch Leven using only one site and noted that uniformity in algal distribution did not necessarily demand high wind speeds. Similarly, uniform distributions might apply to small or less mobile zooplankters such as rotifers, possibly copepod nauplii and early copepodid stages and even immature Daphnia. By relating Table 7 to Appendix (XVI), it can be seen that at times of high nauplii densities or when nauplii and small copepodid stages predominated in the copepod population (27/4, 15/5, 10/9, 21/10, 14/11 and 16/12 all dates in 1972) the percentage difference in mean data obtained from three sites as opposed to six, usually remained below 5 per cent thus implying a fairly even horizontal distribution.

However, wind action of moderate intensity may effect highly variable horizontal distributions of certain algae and probably zooplankton as implicated by the following example. On the 29th June 1972, very still conditions initially gave rise to a widespread surface accumulation of the bouyant blue-green algae Anabaena sp. until a mild easterly breeze ensued in the early afternoon and promoted a surface water shift. This drift eventually gave rise to vast accumulations of Anabaena in the Western bay towards the boat-house making the water thereabouts appear like "pea-soup" and, in the opposite eastern regions of the loch, the water was virtually "gin clear". The effects of this presumably lasted for several days (possibly longer as anticyclonic conditions prevailed) and may have consequently established very prominent differential horizontal distributions of the zooplankton. Blue-green algae, notably Anabaena, occurred frequently and abundantly at Loch Leven within the study period especially during the summer months (Table 12) and such dense accumulations as just described might provide adverse conditions for zooplankton by, for example, restricting or depleting dissolved oxygen and increasing the carbon dioxide content (especially at night) or by producing toxic metabolic or cell-breakdown products. In Table 2, a large percentage difference (+33.7) in mean data obtained from three sites as opposed to six was recorded for 29th June thus suggesting possible irregularities in Daphnia horizontal distribution.

The horizontal distribution of zooplankton might show variations as a direct result of actual population numbers as well as the size, age or sex of the various population components. Rapidly expanding populations might for example spread out horizontally tending to establish more even distributions thus enabling them to exploit the full potential of open water. Behavioural aspects of each species and interaction between different species probably needs to be taken into account also. If adults and late copepodid instars of C. strenuus abyssorum exhibited aggregate behaviour and were known to feed on their own nauplii, a paucity of nauplii might be noted where the older instars gathered. However, in order to evaluate distributions of individual stages as opposed to total populations (this would be advisable for C. s. abyssorum as behavioural as well as size differences exist between the various life stages) large numbers of samples would be required to effectively demonstrate departures from randomness (Comita and Comita, 1957).

The distribution of planktonic predators, notably perch fry at Loch Leven, is likely to have pronounced implications on zooplankton distribution especially with preferred prey species. Young perch (up to 5cm) usually congregate in vast numbers around prominent features of the shoreline, such as the boat-house bay, outlet sluice, mouth of the South Quiech and the pier in the western bay, during the autumn and most of winter. A series of four Friedinger samples taken in the boat-house bay in early October of 1972 revealed very few Cyclops or Diaptomus gracilis and no Daphnia whereas in open water samples, all three species were accounted for in substantial numbers. Predation pressure by fish probably has an influence on vertical as well as horizontal distribution of zooplankton at other times of year when these predators are presumably scattered off-shore in deeper waters. As regards other plankton predators, Tonolli (1958) demonstrated that the whereabouts of the predatory cladocerans, Bythotrephes longimanus and Leptodora kindti taken together, were significantly correlated with the total numbers of other planktonic crustacea on which they fed.

Clearly the possibilities of variable horizontal distributions of zooplankton at Loch Leven are considerable and random or non-random dispersions may be invoked by a wide variety of prevailing circumstances.

### ii. Vertical distribution

According to several authors it is generally acknowledged that freshwater planktonic crustacea may exhibit distinctly uneven distributions in a vertical plane and such variations may arise by multiple causation involving physical and chemical factors, which usually manifest themselves as gradients throughout the depths and may vary diurnally, seasonally or in accordance with prevailing weather conditions, and also biotic factors, which relate to particular attributes of the species population concerned and also to interaction phenomena with other animal or plant species (Hutchinson, 1967; Ruttner, 1968; Cushing, 1951). The structural configuration of the lake may also be important especially if depth is limiting (Hutchinson 1967).

The primary physical factors are temperature, light the most striking vertical distributions of zooplankton are observed in deep lakes where extensive thermal stratification develops in summer - the populations in the hypolimnion often differ markedly to those of the epilimnion (Welch, 1935; Hutchinson, 1967). Smyly (1961) found that early in the year <u>Mesocyclops</u> <u>leuckarti</u> were scattered at all depths in Estwaite Water, while from May until September, when the lake was thermally stratified, they were found almost entirely above 6m depth. However, light appears to be of paramount importance in influencing zooplankton depth positioning and variations in illumination associated with the diurnal light cycle are known to govern the diurnal vertical migratory rhythms of zooplankton (Cushing 1951; Krishnamoorthi and Visweswara, 1965; Hutchinson, 1967; Rudjakov, 1970). Typical migratory behaviour of animal plankton is either an upward movement at night (nocturnal migration) or at dawn and dusk (twilight migration) and such migrations are often accentuated in the more transparent lakes (Hutchinson, 1967). In any event the quality and quantity of light passing through the water and the consequential depth of light penetration may be considerably modified by the optical properties of the water - dissolved substances and suspended particles which may absorb or reflect light.

Chemical gradients relating to oxygen (B.O.D.),

and possibly metabolic waste products

may affect vertical distribution of plankton (Krishnamoorthi and Visweswara, 1965). For example, seasonal changes in migratory patterns may depend on, or be modified by, the decline of oxygen and increase in carbon dioxide in the deeper layers of stratified lakes during summer (Hutchinson, 1967). Tash and Armitage (1960) found that *Daphnia galeata mendotae* was limited for a time to the upper six metres of Leavenworth County Lake by an oxygen deficiency in the hypolimnion.

As regards biotic factors, not only are the inherent responses by the particular organism to the above parameters important, but also attributes of the population components, such as size, age and sex, give rise to variable vertical distributions. Furthermore, the presence of competing populations, planktonic predators and the distribution of phytoplankton may be involved. In the Lake of Lucerne, Worthington (1931) found that by day *Daphnia longispina* adults lived at higher levels than the young and noted that the copepod populations (two species of Calanoida and three species of Cyclopoida) inhabited different water layers so that similar species did not compete. Walker (1970) evaluated the vertical distribution of *C. strenuus abyssorum* in the north deeps at Loch Leven during 1969 and showed that although well-mixed distributions were commonplace, there were several instances of clear, vertical aggregations and that age and sex-specific demarcations between these aggregations were displayed.

Clearly the causal phenomenon responsible for vertical distributions of zooplankton are both varied and complex, although as an isolated factor light appears to be crucial, and thus any attempts to explain the observed vertical distributions of Daphnia hyalina var lacustris in Fig. 12 are likely to be incomplete with only data on temperature (Fig. 3), secchi-disc readings (Fig. 4) and weather conditions being available for comparison. Data is also limiting because of the discontinuous sampling of the water column at Site E (pages 24 and 65). In addition, sampling was always undertaken in daylight with Site E being sampled at approximately mid-day, so that diurnal variations cannot be taken into account.

Although a differentiation of the Daphnia population into size or age groups (e.g. adults and juveniles) and reproductive state of adults (e.g. gravid and non-gravid) could have been incorporated in the distribution profiles at Site E (Fig. 12), such a detailed analysis was not considered appropriate for the present purposes. Similarly, a full description of the vertical distributions of C. strenuus abyssorum would have been desirable but this would have necessarily entailed age-specific (and thereby behavioural) differentiation for meaningful results as demonstrated by Walker (1970). Hopefully this will be accomplished at a later date. However, Cyclops were noted in samples throughout the water column at Site E at all times in both sampling years.

Although very deep regions in Loch Leven are limited in area and according to Smith (1974) the volume and lake bed area below 10m are small in comparison to the total (10.3 per cent and 6.2 per cent respectively), there is probably sufficient depth in many areas to allow for distinct vertical separation of zooplankton populations to occur (Fig. 1).

As Loch Leven is generally well-mixed by regular wind action, the establishment of gradients through the depths, relating to temperature (Fig. 3) or the fore-mentioned chemical factors, are unlikely to manifest themselves and, should they arise, are likely to be minimal and short lived as prolonged periods of absolute calm are very rare and little opportunity exists for the formation of separate water masses. Walker (1970) deduced that uniform vertical distributions of C. strenuus abyssorum in 1969 were promoted by the well-mixed conditions of Loch Leven.

It should be noted, however, that data available for the north deeps (Site E) may not reflect plankton distribution in other regions of deep water such as the south deeps and the channel south of St. Serf's Island (Fig. 1) as the latter deeps are exposed to greater water current velocities than the north deeps (Smith, 1974).

In Loch Leven both *Daphnia hyalina* var *lacustris* and *Cyclops strenuus abyssorum* are not affected by similar species acting as competitors so that zonal separation of similar species, as noted by Worthington (1931) in the Lake of Lucerne, could not arise.

It would appear therefore by tentative elimination of some of the above causal phenomena that the factors operating or excerting considerable influence on zooplankton vertical distribution in Loch Leven are light, water movements, peculiarities of the species and population components, the distribution of fish which are planktonic predators (perch and trout) and possibly minor temperature differences. The possible effects of light (and associated diurnal migrations) could have been more pronounced in 1972-73 than in 1969 as greater water transparency has been associated with the re-establishment of *D. hyalina* var *lacustris* (Morgan, 1970, 1974). During the years when *C. strenuus abyssorum* dominated (at least 1966 to 1970) Loch Leven was subjected to such prolonged and severe phytoplankton blooms that 99 per cent of the visible light was extinguished within the first metre depth during most of the year (Walker, 1970). Even so, Walker noted irregular age-specific groupings in deeper water, well beyond possible light penetration and attributed this to intra-specific predation. In 1973, secchi-disc readings of up to 2.5m were noted (Fig. 4).

The most significant features shown by the Daphnia distribution profiles in Fig. 12 is that on most sampling dates the population occupied the entire water column down to 20m (the same applies to the copepod population) and that the greatest concentrations often appeared to be within the uppermost five metres during daylight. The optimum level of occurrence does not appear to vary markedly with seasonal events although in cooler conditions a tendency towards more even distributions might be enhanced as suggested by profiles for 27th April and 21st October 1972. A comparable situation was reported for six species of zooplankton (four species of Cladocera and two species of Copepoda) in Plover Cove Reservoir by Hodgkiss and Chan (1976).

More or less uniform distribution profiles probably reflect a uniformity of water conditions at all depths, relating to all factors except light, as induced by wind action. A scarcity of Daphnia in the deeper waters (below 5m) was noted much more often in 1973 (especially in June and July) than in 1972. This might be associated with the minor temperature differences (up to 4°C) between top and bottom water layers which were greater and more consistent in 1973 than 1972 (Fig. 3). Dumont (1968) revealed the water temperature and plankton migration. The apparent absence of Daphnia in water layers below 10m on the 6th June and 8th July 1973 coincided with surface-bottom temperature differences of 4.3° and 3.1°C respectively, with the most significant drop in temperature occurring between 10 and 15m depths. However, copepods were present in the deeper water. In 1969 Walker (1970) found no C. strenuus abyssorum below 10m when a 6°C thermal difference prevailed between top and bottom water.

As regards minor variations in distribution profiles of Fig. 12, these were presumably attributable to causal phenomena which apply to Loch Leven as discussed earlier. No obvious and consistent connections could be established between these variations and transparency readings (Fig. 4) or with prevailing weather conditions. The notable paucity of Daphnia in the upper two metres on the 29th June 1972 was probably due to avoidance of adverse conditions provided by surface accumulations of Anabaena ( see page 133) or possible reduced light effects. Finally, it might be added that possible reactions to the vibrations and shadow case by the boat overlying the upper layers may have disrupted plankton distribution within the vicinity as plankton are known to avoid sampling devices (Smyly, 1968b).

## 2. Daphnia hyalina var lacustris

Fluctuations in zooplankton population densities over a period of time are essentially determined by the interaction between rates of multiplication and depletion. Both are subject to a wide variety of intricately inter-related biotic and abiotic environmental variables which constitute the basis for temporal succession. Some of the influencing factors have been mentioned in respect to zooplankton distribution. Amongst the more important variables applied to the population aspects now under consideration are food supply, temperature and predation.

### (a) The population changes

*Daphnia hyalina* var *lacustris* was the only species of *Daphnia* recorded during the study at Loch Leven and was the dominant filter-feeding zooplankter. It was perennial and overwintered in the free-swimming stage with winter adults reproducing parthenogenetically. A comparable situation was noted for the same species in Eglwys Nynydd by George and Edwards (1974). Although the winters during this study were mild (page 42) the population persisted throughout at very low densities especially during the 1972-73 winter (Fig. 5.). It is probable, therefore, that under more severe conditions the ephippial resting eggs produced in September of each year are required to maintain the population through future winters.

The annual population cycles of D. hyalina var lacustris during 1972 and 1973 were basically similar, exhibiting a pronounced bimodal pattern, with the initial spring peak in late May or June being at least two-fold greater in numerical densities than the second August or September peak (Fig. 5). Although this pattern contrasts with the limited data for 1971 (Johnson and Walker 1974) when a single major peak in late June - early July to 74 ind/l was recorded, the likelihood of the bimodal annual cycle emerging in future years is considerable. In fact George (pers. comm.) has demonstrated a distinct bimodal pattern of population densities for the Loch Leven Daphnia in 1976 with seasonal phases occurring as in 1973, but with a spring maximum of approximately 80 ind/l as in 1972. The abundance of Daphnia and the yearly regularity in population cycle both suggest that, since its reappearance in 1970 (page 6), this filter-feeding cladoceran has become firmly established in Loch Leven and has fully integrated its position in the zooplankton. Furthermore, the stability of its annual cycle may indicate and possibly promote stability in other biotic faculties of what was formerly (pre-1972) considered an unstable ecosystem where irregular seasonal cycles of major components, notably phytoplankton, were common-place (Morgan and McLusky 1974).

The seasonal density fluctuations of the Loch Leven Daphnia are not unusual. Hall (1964) recalls that the bimodal annual curve is "typical" of many zooplankton populations and has in the past been generally interpreted (although over-simplified) as being a reflection of a food-limited ecosystem dependent upon spring and autumn phytoplankton fluxes. Similar annual events to those in Loch Leven have been described for D. hyalina Leydig in Queen Mary Reservoir (Steel et al, 1972), for D. galeata mendotae in Base Line Lake (Hall, 1964) and for D. hyalina in Chew Valley Lake during 1971 (Maxwell, 1975; Wilson et al., 1975). In the latter case a spring peak of approximately 120 ind/l was recorded with a subsequent late summer peak of around 60 ind/l. As regards peak densities in other waters, Duncan et al. (1970) and George and Edwards (1974), who both prepared similar size-class distributions to those given in Fig. 6 for species of D. hyalina in Q.M.R. and Eglwys Nynydd respectively, recorded lower spring densities for all four size classes (separated and totalled) than those obtained in Loch Leven during the 1973 spring climax. Perhaps the overall peak numbers (150 ind/l) in Loch Leven at this time were exceptional by most standards. However, at other times in 1973 and during 1972 (and also 1971 and 1976) maximum densities achieved in Loch Leven were comparable to or well within the limits of those attained by similar species of Daphnia in other waters.

However, totally different seasonal cycles have been shown by species of D. hyalina. George and Edwards (1974) demonstrated that during 1970 and 1971 D. hyalina var lacustris from Eglwys Nynydd underwent continual population fluctuations, for most of the year except winter, at densities around 50-60 ind/l (range approximately 30-120 ind/l), thus producing a series of ossillations in densities derived from successions of discrete generations likened to those in Daphnia spp. cultures described by Pratt (1943) and Slobodkin (1954). Examples of somewhat irregular annual cycles or those with an apparent trimodal nature are provided by D. hyalina from Blagdon Lake and the same species in Chew Valley during 1972 (Maxwell 1975; Wilson et al, 1975). Interestingly, where population data is available for two or more years, Chew and Blagdon Lakes, Eglwys Nynydd and Loch Leven, only the D. hyalina from the last two waters had a similar annual cycle repeated in each year. In the other waters the presence of other Daphnia species may in part account for year-to-year variations.

According to Ruttner (1968) planktonic organisms undeniably exhibit a consistent preference for a certain temperature range. Although mean temperatures in Loch Leven were not extreme at either end of the scale with winter and summer conditions being neither excessively cold ($3^oC$) nor excessively warm ($18^oC$) respectively, it may be assumed that D. hyalina var lacustris in Loch Leven is most productive above $10^oC$.

This statement will be qualified later (Page160) leading to the conclusion that the optimum - operative or "preferred" range is 10-15°C for the species. The spring increases of both years occurred with temperature increases within this range and the late summer increases occurred at temperatures around 15°C or greater. Bimodal population events are not necessarily related to the temperate temperature cycle as the population phases do not coincide with particular temperature regimes provided during spring temperature increases and autumn temperature decreases.

The fast-breeding attributes of all-female parthenogenetic _Daphnia_ spp. populations and the fact that newly-released juveniles are fast growing and structurally identical to the adult forms allows them an adaptive advantage to rapidly respond to and exploit potentially favourable conditions. The spring _Daphnia_ _hyalina_ var _lacustris_ population increases of both years were accountable for by an increase in birth rate (Fig. 11) associated with a high average brood-size and accelerated development-rates due to increasing temperature within the fore-mentioned range. At these times, environmental conditions, particularly food type and abundance, were presumably very favourable - perhaps more so in 1973 than in 1972 - and survival rates were generally high. The fact that the spring increase in 1973 was in 1972, may in part have been due to the very low initial densities (Fig. 5). The possibility of recruitment by ephippial emergence cannot be discounted on the grounds of considerable and regular ephippial production in previous autumns, despite the fact that parthenogenetic birth rate (b) accounted for population increase (r) at these times.

Although the spring population explosion of 1973 appeared surprisingly fast - being the maximum for the two-year period - comparable rates of increase (r) were noted by Hall (1964), Wright (1965) and George and Edwards (1974). In terms of birth rate (b) the maxima recorded during the 1973 spring were very similar to those of *D. hyalina* var *lacustris* in Eglwys Nynydd which were 0.298 in 1970 and 0.230 in 1971 (George and Edwards, 1974). However, these are considerably less (approximately half) than the maximum values computed by Hall (1964) for *D. galeata mendotae* (0.61) and by Wright (1965) for *D. schodleri* (0.59). The yearly averages and maxima of the population parameters b,r and assumed d, as quoted on pages 61 and 62 are considerably greater in 1973 than 1972. The 1972 data are generally much lower than those depicted by all the above authors. In fact 1973 was in many respects a more productive year than 1972, with higher mean densities, mean brood-sizes and mean adult sizes, but not altogether exceptional for *Daphnia* populations as a whole.

However, in both years, as the populations were attaining ultimate spring densities, further population increases were checked by considerable reductions in birth rate, the populations subsequently declined markedly with notable mass mortality in the latter half of June. The declines were seemingly associated with a loss of all independent life-stages. In 1973, however, when the decrease was very rapid, there appeared to have been a distinct loss of eggs and/or immature individuals as the proportion of adults remaining after the crash was exceptionally high (Fig. 8). In fact a similar loss of young stages appeared to prevent the 1973 population from increasing earlier in the spring (Fig. 8 and 11). The reasons for these losses are suggested later (page 252).

The spring declines of both years were manifested by multiple circumstances. In both cases the progressively increasing populations were concurrent with reductions in average brood-size - the two parameters essentially showing an inverse correlation at these times - and in 1972 with a reduction in percentage gravid (Fig. 5 compared with Fig. 9). Comparable phenomena were recorded for *D. hyalina* var *lacustris* in Eglwys Nynydd (George and Edwards, 1974). Although in the first instance the reductions in brood-size as the population increased resulted in more females carrying fewer eggs, giving rise to comparable recruitment to the previous situation of few females with large broods, the eventual outcome was an overall reduction in birth rate. It is probable that the populations of both spring periods were reaching and then overwhelming the "holding capacity" of the prevailing environmental conditions and that food limitation both in quality and quantity was progressively imposed, to the detriment of each individual acting competitively in the situation, and consequently to the point of exhaustion. Michael (1962) concluded that the major population crashes of *Ceriodaphnia cornuta* in "fish-ponds" in India were instigated by a depletion of food sources, notably flagellates and ciliates; but, according to Bhajan and Hynes (1971) the observed crashes of *Bosmina* sp. in cultures were not related to food shortage (nor incidently to accumulation of metabolites) but that a deficiency of an essential dietary component was probably responsible. Interestingly, in the latter case, the *Bosmina* declines were experienced by the second generations which in essence is comparable to the Loch Leven situation.

Rapid utilisation of food resources, however, may not necessarily have involved mass mortality for although *complete* starvation is rapidly fatal to *Daphnia* spp. as shown by von Dehn (1930), these animals can persist under conditions of partial starvation as experienced in the field, despite reductions in growth and reproduction (Hutchinson, 1967). The adults surviving after the 1973 crash certainly produced few eggs, with the percentage gravid and mean brood-sizes being at minimum annual levels. The adaptive significance of such survival presumably relates to the opportunistic nature of population growth and the rapid variations likely to occur in planktonic food systems.

However, crowding beyond optimum densities coupled with higher temperatures may have invoked a prominent reduction in longevity resulting in mass physiological death. In Cladocera longevity generally decreases as temperature increases (Hall, 1964); thus rapidly increasing temperatures during spring progressively increase metabolic rate and reduce life-span. It is perhaps significant that in 1972, 1973 _and_ 1976 the spring _Daphnia_ crashes occurred at the same time of year and phase of the temperature cycle - late June at around 15°C. It was shown, however, that _D. hyalina_ var _lacustris_ reared in laboratory conditions persisted for about sixty days at 15°C whereas in Loch Leven during the spring bloom of 1973 the survival times amounted to less than thirty days.

Nevertheless, MacArthur and Baillie (1929) working on cultures of _D. magna_ in the _absence_ of food limitations noted that high densities reduced longevity. Similar observations were made by Pratt (1943). Although the reasons are obscure, the accumulation of metabolic waste products such as ammonia and carbon dioxide could have proved deleterious or, as a further suggestion, certain substances externally secreted by the *Daphnia* (as pheromones described by Wilson, 1963) may have induced alterations in physiological activity of other individuals. As regards toxic substances, Dollar (      ) noted that the major ions, potassium and nitrate, proved highly adverse to *Daphnia* in culture.

Certainly such effects of crowding would have been particularly acute to the very high densities of the 1973 bloom when *Daphnia* peak numbers were two-fold greater than in 1972, amounting to 150 ind/l, and were coincident with maximum densities of all *Cyclops strenuus abyssorum* life-stages (190 ind/l) except nauplii, with the crustacean zooplankton totalling 340 ind/l. Notably, the *Cyclops* population crash accompanied that of the *Daphnia* (Discussion part 5, Fig. 31). The rapidity of the 1973 crash, as compared to that in 1972, and the exceptionally high numbers previous to it might suggest that *very* adverse conditions prevailed and that differences in causal phenomena existed between the 1972 and 1973 spring declines. Other separate factors may have been peculiar to each year. For example, in 1972 the foremost reduction in peak standing crop of Daphnia in late June was concurrent with widespread surface accumulations of Anabaena - the possible effects have been mentioned (pages 132-133.).

The contribution of predation to the spring Daphnia declines was likely to have been minimal. During the spring and early summer, the predatory cladocera were either absent or present in what may be assumed as insignificant numbers and the Loch Leven fish populations (adult perch and trout) were preoccupied with other food stuffs —Asellus or chironomid larvae and pupae (Thorpe, 1974). However, the peak numbers of adult copepods of mid-June 1973 may have played a minor role in the losses of small Daphnia.

In both years the mid-summer low density periods which followed the spring population crashes were sustained by reduced birth rates. Although tendencies toward further population increase in late July were indicated by prominent rises in the percentage gravid component(to 50 per cent) these were retarded by low average brood-sizes and low numbers of gravid females. In addition the death rate in 1973 was high in late July and appeared to be due to losses of adults (Figs. 8 and 11).

The second late summer peaks of both years, although indicating a recovery of better conditions as noted by Hall (1964), were considerably less than the respective spring climaxes, despite the maximum growth-rates associated with the high temperatures at such times. As will be apparent later (Discussion 5(a) and 6) the effects of predation exerted considerable influence on the *Daphnia* populations by suppressing growth potential and thereby peak numbers achieved, *after* the spring declines and for the remainder of the summer, with fish limiting the survival of larger individuals and predatory cladocera cropping small individuals. In addition, *Daphnia* longevities in high summer were presumably further reduced as a factor of maximum annual temperatures (Hall 1964).

A comparison of Figs. 7, 8 and 11, suggests that the high death rates following the second annual density peaks were mainly derived from adult losses in 1972. In 1973, however, the mortalities were attributable to all life-stages. It must be noted that apparent "losses" of juveniles, as derived from data relating to Fig. 8, may manifest themselves also by recruitment of young stages to adulthood and not always by death.

The populations which survived the late summer peak declines of both years were subsequently exposed to rapidly cooling loch temperatures as winter approached, which acted to reduce growth by progressively retarding all metabolic functions to the absolute annual minimum. Further population losses at the onset of winter corresponded to the final decline of the species in the loch and the establishment of the small overwintering population which would remain as such until the following spring. Comparable winter declines were exhibited by the same species in Eglwys Nynydd (George and Edwards,1974).

The complete winter data of 1972-73 showed that although birth rates (b) were high (certainly by overall 1972 standards), population growth (r) was negative (Fig. 11) and that the very reduced population was increasingly dominated by adult individuals (Fig. 8.). Presumably the survivial of young stages throughout was very limited for reasons given later (Page 252) and this accounted for the exceptionally low numbers of Daphnia during this winter as opposed to other winter periods covered by the sampling programme.

The densities of cladoceran populations are primarily determined by food supply (Slobodkin, 1954; Borecky, 1956; Michael, 1962). As the food of filter-feeding cladocera consists mainly of algae (Discussion 4(a)), a comparison of seasonal D. hyalina var lacustris densities with respective phytoplankton abundance is justified. Populations of zooplankton ultimately depend on primary production for nutritional sources anyway. It must be noted that a temperature dependent "time-lag" necessarily exists between the occurrence of favourable food conditions and the response, through increased egg production and eventually increased densities, of the prevailing *Daphnia* populations.

Fig. 28 compares the *D. hyalina* var *lacustris* densities as given in Fig. 5 with phytoplankton chlorophyll *a* concentrations over the two-year study period at Loch Leven. The major species of algae contributing to the chlorophyll components are given on a monthly basis in Table 12. Although the chlorophyll data represents food quantity and not food quality, it may be assumed for simplicity that all algal species are acceptable to the *Daphnia* with the likely exceptions of the blue-green algae, *Anabaena* sp. and *Oscillatoria* sp., which may be regarded as poor food sources.

The most significant feature of the chlorophyll data in Fig. 28 is the totally different seasonal variations in phytoplankton quantity of the two years. This contrasts with the regular bimodal annual curve of the *Daphnia* population. The spring increases of *D. hyalina* var *lacustris* in 1972 and 1973 occurred at markedly different initial phytoplankton levels, with chlorophyll *a* being consistent at approximately $30\mu g/l^{-1}$ in 1972 and over $100\mu g/l^{-1}$ in 1973. These differences in food level may have accounted for the higher spring densities achieved in 1973 as compared to 1972. In 1972, the May *Daphnia* increase presumably restricted phytoplankton increases due to grazing. It was noted that the chlorophyll component rose dramatically to over $140\mu g/l^{-1}$

Figure 28 (opposite)

The seasonal changes in numerical standing crop of *D. hyalina* var *lacustris* in relation to algal chlorophyll *a* concentrations during 1972-73.

(Phytoplankton data by kind permission of Bailey-Watts, I.T.E., Edinburgh)

Abcissa - the study period

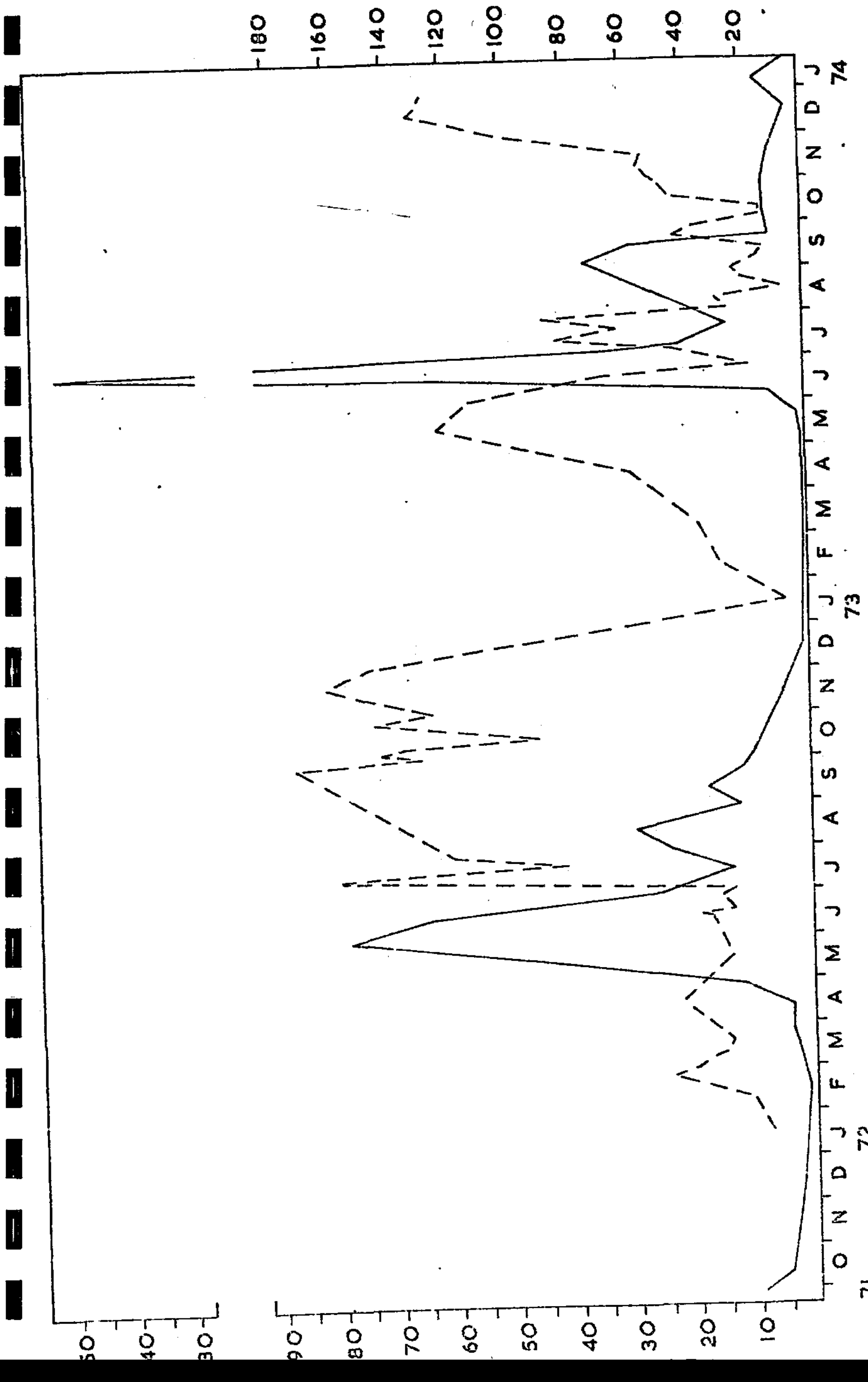
Ordinates:-

Left - the mean numbers per litre of *D. hyalina* var *lacustris*.

Right - the algal chlorophyll *a* concentrations as µg per litre.

The solid line designates *Daphnia* numbers and the broken line designates chlorophyll concentrations.

Fig. 28


µg CHLOROPHYLL a/L
180
160
140
120
100
80
60
40
20
10
20
30
40
50
60
70
80
90
30
40
50
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
71
72
73
74

after the Daphnia decline, this being affected by Anabaena sp., and remained at such levels for the remainder of the year with an October species change to diatoms (Table 12). The high summer levels of blue-green algae may have suppressed the development of more favourable algal food species for the filterfeeders as well as being adverse in themselves.

Despite high phytoplankton levels in April and May of 1973, the main Daphnia increase occurred in June. It may be inferred that the high blue-green component of May (Table 12) inhibited earlier development of the Daphnia population. In any event, the Daphnia increase coincided with an acute decline in chlorophyll level, the peak Daphnia densities being concurrent with very low algal abundance (<20μg/l$^{-1}$). Although the algal losses may have resulted from Daphnia grazing, necessarily suggesting that the filter-feeders were consuming the blue-green component, a more likely implication is that the algal populations were deteriorating anyway (perhaps due to nutrient limitation) and that the Daphnia were utilising the resultant algal detritus rich in bacteria. Manuilova (1962) has observed similar increases in zooplankton after blue-green population declines. In fact George (pers. comm.) observed that the spring increase of D. hyalina var lacustris in Loch Leven during 1976 subsequently followed a notable decline of Oscillatoria sp. As in 1972, the species of alga which bloomed after the

1973 Daphnia decline was Anabaena. The second increase of Daphnia in late summer 1973 was initially preceded by a decline of Anabaena and, as the cladoceran population declined in September the phytoplankton again increased, this being effected by flagellate species.

With the exception of the 1972 late summer maximum, high numerical densities of Daphnia were invariably associated with very low chlorophyll a. In 1973, high algal concentrations preceded the major Daphnia increases. These facts suggest that the grazing effects of D. hyalina var lacustris caused prominent reductions in the abundance of favourable phytoplanktonic food sources and that food limitation played a fundamental role in the Daphnia declines in Loch Leven. Comparable phytoplankton/zooplankton fluxes have been demonstrated by Steel et al. (1972) and George and Edwards (1974).

## (b) The breeding parameters

A discussion on breeding parameters (Fig. 9) necessarily relates basically to variations in mean brood-size. The seasonal changes in mean brood-size of Daphnia hyalina var lacustris from Loch Leven followed a similar pattern in both sampling years (Fig. 9 and 10). Precisely the same annual patterns of clutch-size variations were exhibited by D. hyalina var lacustris from Eglwys Nynydd during a two-year period (George and Edwards, 1974). It is probable that factors causing these fluctuations were essentially similar in both waters despite the fact that the Loch Leven mean broods were generally larger all round.

The number of eggs produced by a female Daphnia sp. is highly variable and is known to be influenced by various factors both intrinsic, such as the age, size and clonal characteristics of the individual, and environmental, such as the available food and temperature (Green, 1956). Some aspects of the intrinsic factors are described elsewhere (Pages 186-189 ).

Studies of temperature effects on egg production have shown that beyond the optimum range characteristic of each species, both high and low temperatures can restrict egg production (Berge, 1931; Hutchinson, 1967). By comparing the annual temperature cycles in Fig. 2 with mean brood-sizes in Fig. 10, an approximate relationship can be extracted. During spring and autumn when temperatures varied around 10°C (10°-15°C in Spring 1973), the mean brood-sizes were generally at annual maximum values although spring values were well in excess of autumn values. Clearly, however, at summer temperatures above 15°C, the average broods (and maximum ranges) were maintained at seasonal minimum levels suggesting the limiting effects of high temperatures; and during the cold phases below 5°C the mean brood-sizes remained consistently at levels between spring and summer levels. It may be tentatively concluded that the optimum functional range (Ruttner, 1968) for *D. hyalina* var *lacustris* in Loch Leven was 10°-15°C (Page 147). As regards the adverse effects of high temperature on egg production, Gophen (1976) explained that in these conditions filter-feeding zooplankton compensated for the increased metabolic rates and related energy maintenance demands by *reductions* in egg production (and/or reductions in body-size). Furthermore, it is probably advantageous for a parent *Daphnia* to carry fewer eggs in warmer conditions to offset the tendency to sink or to reduce the excess weight or drag factor in locomotion even though the density of an egg approximates to that of water. The apparent disadvantage to potential population increase of lower fecundity at higher temperatures is partially cancelled by shorter development times and the enhanced rapidity in production of successive broods. However, the fact that mean brood-sizes were generally larger throughout 1973 than 1972 certainly indicates the influence of other factors besides temperature.

Food supply has a direct influence on egg production in all cladocera (Hutchinson, 1967). Ingle *et al.* (1937) established that, within an optimum temperature range, the clutch-sizes of *D. longispina* in culture were proportional to the available food quantity. Fig. 29 compares the mean broods of D. hyalina var lacustris, with phytoplankton chlorophyll a concentrations over the two sampling years at Loch Leven. Important considerations relating to the chlorophyll data were given previously (Page 156). However, although the chlorophyll estimates relate to food quantity, the amount of food available per individual is a function of population density. Strictly speaking, the absolute food levels should be correlated with egg numbers. Nevertheless, as noted from Fig. 28, an apparent inverse relationship was evident between Daphnia densities and chlorophyll quantity, especially during 1973. Moreover, by comparing Daphnia densities (Fig. 5) with mean brood-sizes (Fig. 10) it can be seen that when Daphnia densities were high, brood-sizes were low - an approximate inverse relationship being detectable, this being again most prominent in 1973. This phenomenon is equally apparent if the mean brood-sizes are compared with the mean numbers of gravid females per litre as in Fig. 9. High densities of D. hyalina var lacustris in Loch Leven were generally associated with low chlorphyll and low mean brood-sizes and vice-versa; this situation being comparable to that of Eglwys Nynydd (George and Edwards, 1974). This explains why the graphs depicting chlorophyll concentrations and mean brood-sizes should be approximately complementary, and more so in 1973 than in 1972 (Fig. 29). The additional introduction of appropriate lag factors (Page 155) must be acknowledged.

With reference to Table 12, the highest spring broods of April 1972 coincided with a predominantly diatom phytoplankton (Fig. 29), low brood-sizes were maintained thereafter and throughout a prominent summer <u>Anabaena</u> bloom with brood-sizes increasing markedly from low summer levels after a phytoplankton species change to diatoms of correspondingly high abundance. In 1973, the very large egg numbers of April coincided with high levels of a mixed diatom/flagellate community. The slight slump in mean broods during May could have resulted from the advent of an algal species flux to blue-greens at that time. The increased clutch-sizes of September and October were associated with mixed flagellate communities. Lastly, the moderately large winter broods, which were maintained as such throughout, were invariably associated with a diatom phytoplankton.

The larger brood-sizes throughout 1973 as compared with those in 1972 were presumably, in the first instance, the result of <u>higher</u> phytoplankton levels of favourable species during the spring and then substantially <u>lower</u> blue-green levels during the summer. Green (1956) working on Cladocera in Hampton Court Long Water found that spring peaks in egg

Figure 29 (opposite)

The seasonal variations in mean brood-size of *D. hyalina* var *lacustris* in relation to algal chlorophyll *a* concentrations during 1972-73.

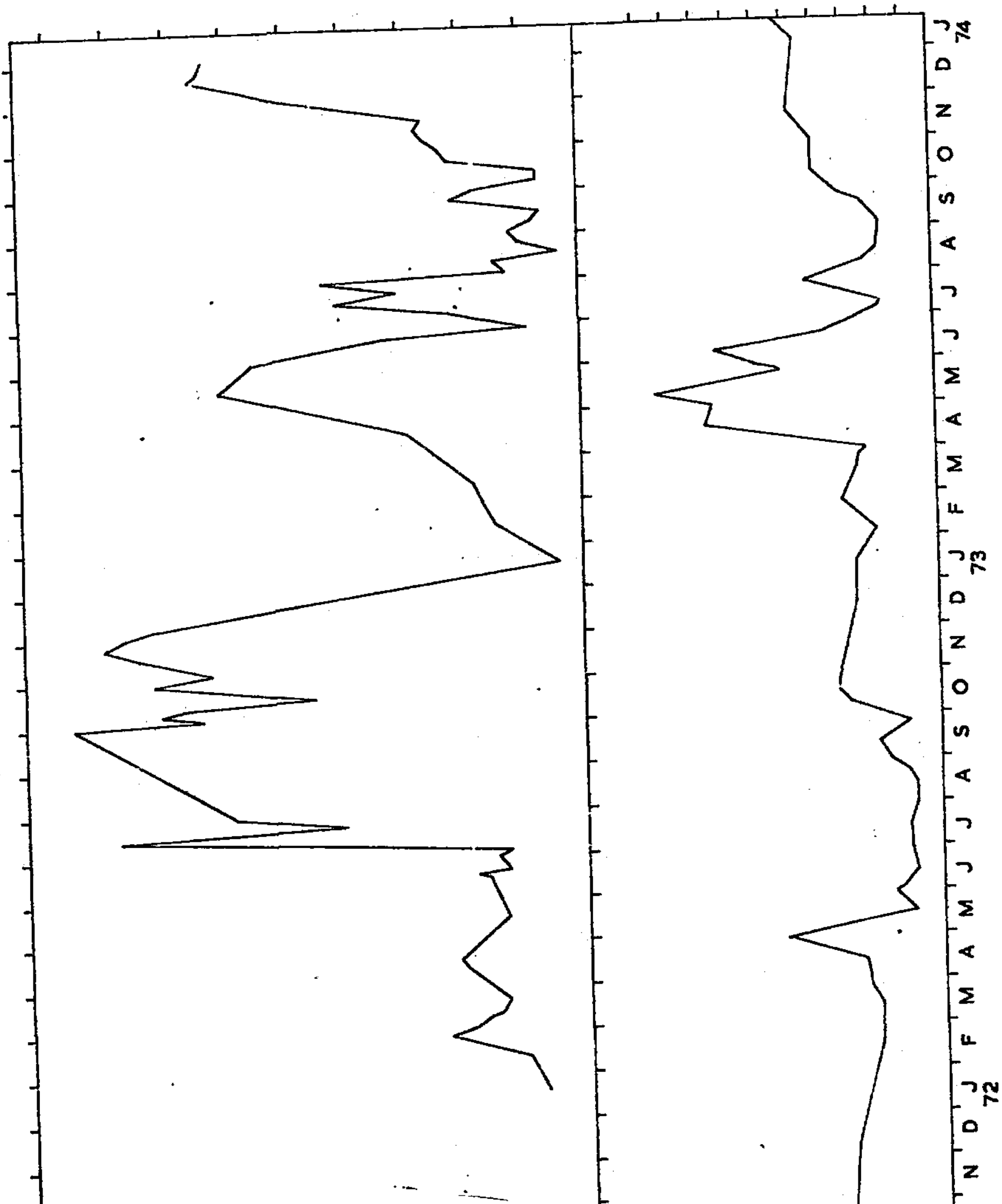
(Phytoplankton data by kind permission of Bailey-Watts, I.T.E., Edinburgh)

Abcissa - the study period

Ordinates - the mean brood-size.

- the algal chlorophyll *a* concentrations as µg per litre.

Fig. 29


μg CHLOROPHYLL a. l⁻¹
180
160
140
120
100
80
60
40
20
BROOD SIZE
20
18
16
14
12
10
8
6
4
2
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
71
72
73
74

production coincided with peaks in chlorophyll content of the water; while George and Edwards (1974) working on D. hyalina var lacustris in Eglwys Nynydd noted that in spring and autumn, when diatoms and green algae dominated the phytoplankton, brood-sizes tended to increase with increasing food levels. The latter authors also found that when blue-greens dominated, the brood-sizes remained low despite increases in algal biomass and that under such conditions larger broods were carried at lower blue-green densities.

It seems apparent that the variations in clutch-size experienced by the Loch Leven D. hyalina var lacustris populations over the course of two annual cycles were caused by both temperature and food/population density effects. Although the additional influence of body-size variations (Page 186) may provide a further variable, the mean brood-sizes showed no significant correlation with mean body-sizes of adults (Fig. 10). This is perhaps surprising since conditions which favour egg production would also favour growth and it might therefore be expected for adult length and brood-size to fluctuate together as demonstrated by George and Edwards (1974). However, the mean body-sizes like the mean brood sizes were generally much larger in 1973 than in 1972 and this again tends to reflect the better food-related growth conditions of 1973 as a whole. As a final note regarding mean brood-sizes, it is suggested that the larger broods generally produced by _D_. _hyalina_ var _lacustris_ from Loch Leven as compared to those produced by its counterpart in Eglwys Nynydd (George and Edwards, 1974) were the result of higher overall levels of favourable food algae and also larger adult body-sizes associated with the loch.

In the favourable laboratory culture conditions it was observed that broods were produced by _D_. _hyalina_ var _lacustris_ in continual succession (Page 72) and, although the retention of young was dependent upon the duration of adult instars, since the young were released at times proximate to the adult moults, this corresponded more or less to the egg duration times (Page 179). Once a brood of young juveniles had been released a further brood was rapidly introduced into the brood pouch, the time lag being short. As regards the percentage gravid data (Fig. 9), which were derived from large sample numbers, it might reasonably have been assumed that on any given sampling date the proportion of females carrying eggs in the population would correspond to the overall retention time of the developing young as a proportion of the time interval between the onset of successive broods. This assumption accepts that the gravid population as a whole were always carrying an even distribution of eggs of all developmental stages. Since the time lag between the release of one brood and the appearance of the following brood was short (Page 179 ), the percentage gravid would inevitably be high, say above 80 per cent. This was clearly not the case, the percentage gravid in Loch Leven fluctuating between 30-70 per cent (Fig. 9, page 53).

Two independent factors may account for the lower percentage gravid components (a third consideration relating to data credibility is explained on Page 167). In the first instance, the gravid population may at certain times have been carrying a disproportionate number of eggs/young of a given developmental stage and when these were simultaneously released the gravid component would naturally drop substantially. This effect would occur as a result of adult cohorts derived from distinct generations. The data on gravid proportions of D. hyalina var lacustris in Eglwys Nynydd (George and Edwards, 1974) exhibited considerable and continual fluctuations, much more so than in Loch Leven, this presumably being effected by the sequences of discrete generations which manifested the series of population ossillations. In the second case, a lower percentage gravid could have resulted from a considerable increase in the time lag between the release of one brood and the occurrence of the next. Such a delay in egg production would presumably have arisen through food limitation and have been concurrent with periods of low mean brood-sizes. This factor may for example have depressed the percentage gravid component during the summer of 1972. However, both forementioned phenomena probably gave rise to the very low percentage gravid recorded in early July 1973.

### (c) Variations in mean adult body-size

The variations in mean adult length of Daphnia hyalina var lacustris in Loch Leven during 1972-73 (Fig. 10) did not conform to any distinct or repeated seasonal trends or show a clear correlation with other measured parameters. The body length at maturity (minimum adult range) underwent marked fluctuations (1.44-1.89 mm), tending to parallel the changes in mean length. This precludes the assumption that periods of high average body-size simply reflected increased survival and continued moulting in the adult. Nevertheless, the overall consistently greater sizes in 1973 compared with those in 1972 may be an indication of the more favourable food conditions outlined earlier (Page 156), or even of reduced predation by fish at certain times (Discussion, part 6).

In total contrast, George and Edwards (1974), who prepared comparable data for the same species in substantial seasonal variations, tending to be larger in winter than in summer and largest in spring; these changes being similar to the respective fluctuations in mean clutch-size. These authors suggested, with reference to the finding of Green (1956), that in cooler conditions the female Daphnia were likely to grow more slowly but reach a larger final size than their counterparts in warmer conditions. The overall mean body-sizes in Eglwys Nynydd were generally much smaller than those encountered in Loch Leven, with summer individuals varying around 1.6mm and the largest spring individuals be <2.0mm. Perhaps most significant of all, the body length at maturity (1.4 mm) in Eglwys Nynydd remained much the same throughout the year. George and Edwards implied that predation on Daphnia in Eglwys Nynydd was minimal because comparisons of Daphnia death rates with suspected planktonic predators produced no obvious interaction, not even at trout stocking times. However, at Loch Leven the effects of predation on Daphnia may be profound (Discussion, 5(a) and 6) and have notable influence on the mean adult length data, tending to obscure the possible correlations with other population parameters.

As regards the minimum size at maturity, the cultured specimens from Loch Leven had a minimum egg-bearing size within the range 1.47-1.74mm., this being primarily determined by the number of preadult instars (either four or five) and assumed as normal for the species under the favourable laboratory conditions. However, under field conditions the limit was extended to 1.89 mm, suggesting a further moult to a possible six pre-reproductive instars. Although this may imply a delay in maturation, perhaps due to food limitation (Hutchinson, 1967), it might equally signify better growth in juvenile stages. Nevertheless, the occurrence of retarded maturity, outside the "normal" limit, was rare, being mainly restricted to September of 1972 and September and early October of 1973. This may have been a function of the clonal peculiarities of individuals at such times.

The variable nature of the minimum egg-bearing size inevitably casts a doubt on the data based on the assumption that all individuals larger than 1.4mm were adults. The problem is manifested in Fig. 6 which depicts adult and juvenile numbers; Fig. 7 which gives adult/juvenile proportions and also Fig. 9 which gives the percentage gravid. The data in the first two graphs was predominantly biased towards adults with a corresponding under-estimate of juveniles and, in the third, the proportions of gravid females were generally under-estimated. Such discrepancies could be rectified by deducting a calculated proportion of individuals, based on the minimum adult-size, from the 1.40-1.99mm group for each sampling date and adding this to the respective 1.00-1.39mm size-class. Even so, the data as it stands is not strictly speaking incorrect since the 1.4mm demarcation refers to an absolute limit - no individual below this size can bear eggs and all animals above can be considered as potential egg-bearers. Furthermore, as the D. hyalina var lacustris from Eglwys Nynydd showed little variation in this respect (George and Edwards 1974), although ecological differences with the same species in Loch Leven must be acknowledged, exaustive searching of net samples from each sampling date might have eventually produced female egg-bearers of the smallest size.

### (d) Cyclomorphosis and sexual reproduction

The cyclomorphotic changes relating to head shape (Fig. 13) of Daphnia hyalina var lacustris from Loch Leven were similar in both sampling years and were manifested through successive generations during the course of the annual cycles (Fig. 14). Such events are commonplace in Daphnia spp. from temperate zones and numerous examples, which essentially parallel those in Loch Leven, are quoted by Hutchinson (1967), these including several species allied to D. hyalina. Seasonal polymorphism is not confined to Cladocera, the phenomenon being also associated with freshwater copepoda, rotifers and even algae. That more than one polymorphic form of Daphnia could occur at any time, for example during late summer when peaked, intermediate and roundheaded forms co-existed, is not unusual, similar events have been observed elsewhere (Hutchinson, 1967). Additionally the variations in tail-spine length, which tended to be short or absent in winter and long in summer in Loch Leven Daphnia, have been parallelled by other Daphnia species, notably D. pulex (Berg, 1931). However, George (pers. comm.) observed that D. hyalina var lacustris from Eglwys Nynydd exhibited only minimal seasonal changes in body form, certainly not as marked as those in Loch Leven.

The factors which induce and set the timing of morphological changes and the selective advantages of such changes have been the subject of considerable controversy. It is now accepted that both increased temperature and turbulence act to stimulate helmet formation in Daphnia spp. (Hutchinson, 1967; Ruttner, 1968; Kerfoot, 1975) and the evidence from Loch Leven lends added support. In the loch, increased helmet height was concurrent with increasing loch temperatures (above $10^{o}$C) and peaked individuals with extended tail spines were associated with August annual maximum temperatures in both years (Fig. 14). Conversely, decreases in helmet height were concurrent with decreasing loch temperatures in autumn. In addition, Loch Leven is undoubtedly turbulent all year round. Presumably these factors also influence the extension of the tail spine, even in the roundheaded Daphnia which persist in this form during the summer months (page 68).

According to Hutchinson (1967), helmet formation in Daphnia spp. as an end-point to cyclomorphosis, was originally viewed solely as an aid to suspension in warmer water conditions (Wesenberg-Lund and Ostwald Bouyance Theory) or as a mechanism to guide and stabilise the swimming functions of the animals (Woltereck's work). However, recent findings strongly indicate that the prime function of helmet development is to offset predation by certain planktivores, notably fish (Kerfoot, 1975). The transparent helmet may reduce conspicuousness (Brooks, 1965) and, together with the extension of the tail-spine, may increase the absolute length of the Daphnia making it more difficult for an individual of a given body-size (Burns, 1969) to be engulfed. In Loch Leven, the risk of predation on D. hyalina var lacustris by fish certainly seemed to be associated with the warmer months (Discussion, Part 6) when fully-peaked Daphnia prevailed. Perhaps a good correlation might be obtained between the increasing body length (including helmet and spine) of Loch Leven Daphnia and the increasing mouth-gape of developing perch fry in the 0+ year group during the course of the summer. Nevertheless, it could be argued that, whilst cyclomorphotic changes in *Daphnia* would deter predation from small fry, these could not prevent predation by larger fish (or even carnivorous cladocera, Discussion, Part 4 (c)). Cummins *et al.* (1969) observed that in Sanctuary Lake, Pennsylvania, certain fish species selectively consumed *Leptodora* sp. despite its extremely transparent and inconspicuous nature; and Thorpe (1974) found that Trout and Perch in Loch Leven consumed *Bythotrephes longimanus* despite its exceptionally long body spine.

Seasonal polymorphism in *Daphnia* provides convenient, although limited, biological "tagging", enabling changes in populations to be traced when numerical densities are not undergoing marked fluctuations. Despite being restricted to gravid adults, the data in Fig. 14 suggests that in 1972 the spring intermediates persisted for less than six weeks and the peaked forms for less than ten weeks. In both years, the autumn population crashes corresponded to a loss of peaked adults and the early winter declines to a gradual phase-out of autumn intermediate forms. A comparison of Figs. 5 and 14 showed that the *Daphnia* spring peak of 1972 was composed entirely of roundheaded individuals whereas in 1973, the spring peak was composed of roundheaded and spring intermediate forms in approximately equal proportions. The late summer maximum of August 1972, like that of early September 1973, was made up of over 80 per cent peaked headed adults.

Considerable physiological differences, in for example growth rate, egg production and longevity, might perhaps exist between Daphnia of differing cyclomorphotic form, irrespective of environmental conditions. In Loch Leven, round-headed forms were generally associated with the highest egg production and the peaked variety were exclusively associated with ephippia formation and low parthenogenetic egg production. The formation of a Daphnia sp. ephippium requires only two eggs (Hutchinson, 1967), so that ephippial production would likely coincide with periods of low egg production. (Alternatively, this might be purely a function of specific individual types with genetically regulated low ovary output.) The roundheadedness of all the three males from field samples (Pages 70 and 71) suggests derivation from roundheaded parents and not from peaked forms which were otherwise functional in sexual reproduction.

Sexual reproduction in D. hyalina var lacustris took place each year during August and September when males were present and ephippial production occurred. In contrast George and Edwards (1974) noted that D. hyalina var lacustris in Eglwys Nynydd produced ephippia in spring and autumn of one year (1970) but not at all in another year (1971).

According to Hutchinson (1967) sexual reproduction in Daphnia spp. is not simply a predetermined event which strictly occurs after a fixed number of parthenogenetic generations, but is influenced by several environmental stimuli. This author noted that the stimuli involved in male production and in the formation of the ephippial eggs are different, although they usually succeed one another in nature:- Male production usually occurs as a result of high population density, under conditions of good nutrition and high average temperature. Ephippial production, on the other hand, appears to be induced primarily by rapid reductions in food supply. In the field circumstances, high Daphnia densities inevitably cause reductions in food quantity so that male production is likely to synchronise with ephippial production.

However, the association of sexual reproduction in Daphnia with autumn indicates that a photoperiodic factor is also involved in the production of both males and ephippia. Hutchinson (1967) noted that in high density cultures, D. pulex produced ephippia most readily when subjected to a 12 hour photoperiod; a situation which would occur in nature during September at the time of the equinox.

The conditions inducing Daphnia sexual reproduction were apparently present in Loch Leven. The timing of events in both years was associated with high loch temperatures and suitable photoperiodic requirements. In 1973, the ephippial production in August and September was concurrent with high population numbers and notable reductions in chlorophyll (Fig. 28). However, the latter conditions were not so apparent in September 1972. By coincidence, the male in laboratory culture (Page 74) was produced (by a roundheaded female) under aquarium conditions of crowding, good nutrition and a 12-hour photoperiod.

In both years, ephippial production was fairly extensive yet male sightings in samples were rare. The single male recorded in July of 1973 (Fig. 14) was out of phase with the main sexual activity of August and September. This suggests either that males were overlooked during sample analysis (an adult male of 1.5mm could easily be mistaken for an immature female of that size) or that male production was poor and ephippia were produced asexually. "Pseudosexual" resting eggs produced parthenogenetically have been recorded for D. pulex (Edmondson, 1955) and for Ceriodaphnia cornuta (Michael, 1962).

The contribution of ephippial eggs to population recruitment remains uncertain with regard to timing of emergence and numbers involved. Hutchinson (1967) noted that ephippia of Daphnia spp. may develop directly and immediately after production *or* after a latent period of freezing or drying and that the factors promoting hatching were variable; low osmotic pressure, replenishment of nutrients, aeration and illumination being amongst those quoted. The finding of loose ephippia at times far removed from the autumn production period (Fig. 14) suggests that a latent period is certainly involved.

### (e) Laboratory growth studies and length-weight relationship

Although the laboratory growth work was mainly relevant to the production estimates, interesting details arose concerning the life-history of *Daphnia hyalina* var *lacustris* some of which have implications on the general field data. The laboratory conditions, unlike those of the field, were standardised allowing particular factors which regulate growth to be evaluated more specifically. In the literature, the information available on growth rates of related *D. hyalina* species is limited to studies on *D. hyalina* Leydig reared on excess *Oocystis* sp. (Duncan *et al*. 1970), egg-duration assessments on *D. hyalina* var *lacustris* (George and Edwards 1974) and possibly growth work on *D. galeata mendotae* (presumed *D. hyalina* var *galeata*) by Hall (1964).

(i) Growth rates and development/contd.

## 3. Cyclops strenuus abyssorum

### (a) The population changes

The most significant features of the annual cycles of Cyclops strenuus abyssorum in Loch Leven during 1972-73 were that the population was represented in the plankton by all life-stages all year round, breeding was continuous and there did not appear to be well-defined instances of quiescence (although the possibilities of a dormancy period are discussed below). These features also occurred during the annual cycles of 1969 (Walker 1970) and 1976 (George pers. comm.).

The annual cycles of freshwater cyclopoid copepods appear to by highly variable. According to Kurenkov (1973) they may be designated as either monocyclic, with a single period of reproduction, or as polycyclic, with several periods or continuous reproduction. Additionally, at certain times, population development may (or may not) be interrupted by the occurrence of diapause which may by-pass either the summer or winter periods or both (Elgmork, 1967). Most interestingly, however, the annual cycles of a given species may vary markedly from one water to another and this appears to be true of C. strenuus abyssorum (Page 13). This species has been observed to be both monocyclic (Gurney, 1923, 1933; Chapman, 1965; Smyly, 1973a) and polycyclic (Colebrook, 1956; Walker 1970; Smyly, 1973a) and resting phases, when present, have been recorded in the egg stage (Chapman, 1965), in copepodid stages CIV and particularly CV (Smyly, 1973a) and also in the adult instar (Wierzbicka, 1962).

It has often been stated that the *Cyclops strenuus* "group" is very variable from a taxonomic point of view (Gurney, 1933; Kozminski, 1927, 1932; Fryer, 1954), with distinct, although perhaps inconspicuous, differences in, for example, the length and/or breadth of the spines on the swimming legs, and it could be assumed that such differences are a function of geographic isolation of populations. Likewise, variations in the annual cycle may have arisen as direct responses to differences in environmental conditions. The physical peculiarities of the lake may be important, but major factors such as temperature, food supply and competition, which not only vary from one lake to another but also seasonally, must each exert a profound effect on the dynamics of a limnetic population, influencing for example the rates of growth and thereby the number of generations per year. Furthermore, it is possible that due to changing circumstances the annual cycle may show year-to-year variations in any one lake.

Walker (1970) inferred that in 1969 growth conditions for C. s. abyssorum in Loch Leven were more or less ideal all year round. The population at that time existed in virtual monoculture, so that the total absence of competitive interactions with other crustacean zooplankters enabled the copepod to monopolize all the available resources;
the highly enriched status of Loch Leven ensured consistently abundant and diverse food sources (according to Bailey-Watts (Walker, 1970) the standing crop of phytoplankton found in Loch Leven during winter was generally greater than the highest summer levels attained in many lakes and presumably this promoted equal success to protozoa and rotifers, etc. which probably constituted major components of the copepod diet (Page 239 )); and the shallow and well-mixed waters of Loch Leven prevented the formation of thermally stratified layers and the accompanying de-oxygenation of the hypolimnion in summer, thus allowing the copepod free-range throughout the entire water column at all times.

growth conditions alleviated the "necessity" for a quiescent period and that this in turn led to the Cyclops population becoming polycyclic. Although this may seem reasonable, George (1973) found that C. vicinus in Eglwys Nynydd was polycyclic and yet this species exhibited diapause, with notable proportions of CIVs undergoing dormancy from mid-summer of one year to the following spring of the next, thus demonstrating that continuous reproduction and quiescence can occur together within the same annual cycle. It may be suggested that continuous reproduction was a more useful indicator of the consistently favourable growth conditions rather than the absence of diapause. In any event, the continual recruitment which resulted from continuous reproduction ensured that the population could respond fairly rapidly to potentially favourable circumstances and, in addition, tended to prevent the upsurge of possible competitive species.

Nevertheless, the ability to undergo dormancy undoubtedly has adaptive significance in overcoming adverse conditions, as Elgmork (1967) pointed out (and may incidentally have evolved from copepod populations living in temporary pools), but it may also work to advantage during favourable conditions if part (but not all) of the population is involved in dormancy - the latent population potentially guarantees the success of the species at a future date whilst the existing population, operating at reduced densities, persist with less likelihood of self-imposed food limitation. In view of the highly unpredictable nature of still-water ecosystems and the fact that copepods have a long and complex developmental history from the egg to the reproductive adult instar, which tends to retard rapid population build-up in suitable conditions, it may also be of considerable benefit for the population to be recruited by a sudden emergence of latent adult or pre-adult stages when conditions allow it.

Although it was previously stated that the *C. strenuus abyssorum* population of 1972-73 did not appear to undergo quiescence, there is still considerable doubt as to the fate of most of the dense accumulations of late copepodid stages of late June 1973 which suddenly disappeared from open water (Fig. 21). The apparently poor recruitment to instars CV and CVI during the early summer of 1972 also needs to be accounted for. Did these individuals die out or did they undergo dormancy? If dormancy in older copepodid instars is facultative, as Elgmork (1967) implied, then this seems to be the most satisfactory explanation. Factors which induce dormancy are not clearly understood but Elgmork (1967), who reviewed the ecological aspects of copepod diapause, stated that although changes in temperature and lack of food were probably involved, changes in photoperiodicity (day-length) were of paramount importance.

Since the reappearance of *Daphnia hyalina* var *lacustris* in 1970, growth conditions for *C. s. abyssorum* in Loch Leven may have changed considerably (Pages 242 and 255) and this relates particularly to food and illumination. As regards illumination, it may be tentatively suggested that the very pronounced increases in water clarity associated with the renewed presence of the cladocerans (Page 232) may have greatly exposed the copepods to the effects of light at certain times, thus allowing the influence of photoperiodicity to induce diapause (note the high water transparency readings during the summer of 1973 in Fig. 4). Moreover, it was noted earlier (Page 150) that the main reason for the major collapse of the spring *Daphnia* populations in 1973 was food limitation and that this population downfall was more or less coincident with that of *C. s. abyssorum* (Fig. 31). Several authors have suggested the possible link between lack of food and the onset of arrested development in late copepodid instars (Coker, 1933; Ravera, 1954; Smyly, 1961), so it appears that food limitation may have been a precursor to the observed mass "losses" of copepodid instars at Loch Leven in 1973. Some of the individuals may initially have resorted to the bottom sediments in search of food and then eventually burrowed deep into the muddy deposits of selected areas of the loch bed for the purposes of dormancy.

However, their reappearance in open water was not detected in samples thereafter, but, as with _C_. _vicinus_ in Eglwys Nynydd (George 1973), they may have returned to the plankton during the following spring (i.e. sometime in early 1974 which unfortunately was outside the limits of the two year sampling programme). This hypothesis may be further substantiated by several examples of quiescence in late copepodid instars of _C_. _s_. _abyssorum_ in the Lake District (quoted below). According to Elgmork (1959) revival after dormancy appears to be influenced by internal physiological changes which pre-set the duration of latency (i.e. "biological clock"), although environmental changes involving temperature and oxygen may also promote this effect.

suggesting that the lack of dormancy in 1969 was attributable firstly to the reduced effects of photoperiodicity due to the very poor light penetration (the copepods at that time existed in virtual darkness compared to the conditions in 1972-73) and secondly to an absence of distinct periods of food shortage.

Finally, as regards dormancy, it might be added that since winter conditions in mid-Scotland may be particularly severe and prolonged, overwintering resting stages may be important in maintaining the *C. s. abyssorum* population in years to come. Chapman (1965) deduced that *C. s. abyssorum* in Loch Lomond overwintered as resting eggs, since the adult population died out in the autumn and the planktonic population consisted of young copepodids in the following spring. Interestingly, 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 temperatures reached in Loch Leven during 1972-73 were less than 20°C but perhaps a resting phase would be necessarily induced if summer conditions were warmer.

cycles of 1972 and 1973 had several points in common as given on Page 92 but perhaps most important was the fact that the major population developments occurred in spring and autumn and that these were separated by distinct mid-summer low periods. In this respect, the copepod population changes were reminiscent of the bimodal annual cycles of *Daphnia hyalina* var *lacustris* (comparisons can be made in Fig. 31) and again suggest, as previously noted from Hall (1964), a food-limited ecosystem. It would appear, therefore that certain factors which favoured and disfavoured *Daphnia* population growth had corresponding effects on the *Cyclops* population, although the complex inter-actions between the two species, particularly relating to trophic aspects, must be acknowldged (Discussion, Part 5). The mid-summer depression in the copepod annual cycles may, for example, have been a function of food depletion caused directly or indirectly by *Daphnia* grazing (Page 254). However, George (1973) found that in Eglwys Nynydd a marked positive correlation existed between birth rates of *Cyclops vicinus* and *Daphnia hyalina* var *lacustris*, and it seems reasonable to suppose that comparable relationships existed in Loch Leven. In addition, the autumnal increases in *C. s. abyssorum* appeared to correspond with the and 31). Presumably, the conditions which suit the nauplii and young copepodids of both species are similar, especially as regards food sources.

The population changes of C. s. abyssorum during 1969 provide interesting comparisons with the previously described events of 1972-73 (Pages 86-93). Walker (1970) found that early in the year the very small overwintering population consisted mainly of adults (only 2 ind/l) and a few of each of the developmental instars. Subsequent to an extended period of ice-cover which lasted throughout February and into early March, minor population increases were effected from eggs laid by the winter adults and the resultant offspring reached the adult stage by mid-April. The egg stock rose steadily thereafter to a maximum of about 120 eggs/l in late May before declining, thus effecting substantial increases firstly in nauplii and then in each of the successive copepodid instars in turn. The population built up to a grand maximum of 292 ind/l in June and was comprised mainly of young copepodid instars. In July, however, there was a notable accummulation of individuals in the CIV and CV stages, implying a temporary delay in maturation, but these eventually matured in August giving of 45 adults/l. These adults then gave rise to a vast egg stock of 220 eggs/l which arose and declined in August providing autumnal increases in the older life-stages. The population subsequently declined to its previous winter proportions.

Several important differences were apparent between the seasonal events of 1969 and 1972-73. Firstly, the overwintering C.s. abyssorum populations of 1969 were very much smaller in terms of numerical densities than in 1972-73 and these differences were probably related to contrasting climatic conditions. Whereas the winters within the period late 1971 to early 1974 were very mild, the winters surrounding 1969 were notably harsh. Smith(1974) made observations on winter conditions at Loch Leven and recorded that during the winters of 1968-69 and 1969-70, the loch was subjected to more than 50 per cent ice-cover for forty-two days and thirty-five days respectively. In the 1971-72 winter, days with more than 50 per cent ice-cover were nil and in the 1972-73 winter only five days were recorded. The colder conditions of early 1969 also retarded the major spring increases of Cyclops densities to May as opposed to April (as in 1972-73). Walker (1970) noted that mean loch temperatures below 5°C were maintained until early April in 1969, whereas in 1972-73 temperatures during comparable months were well above 5°C (Fig. 2).

Secondly, and most significantly, the major spring population development of 1969 ensued well into mid-summer. Although the duration of development at the CV stage was apparently extended during July (possibly due to temporary food shortage), there was no indication of a mid-summer population recession. In fact, total population numerical densities in 1969 were maintained at high levels of over 60 ind/l from late May until late October*. Maximum population numbers and peak egg-stock recorded for 1969 were also significantly greater than their respective equivalents in either 1972 or 1973.

Thirdly, the spring increases of *Cyclops* in 1969 ultimately resulted in far greater recruitment to the adult population than in 1972-73 and therefore the possibilities of dormancy having occurred in the late copepodid stages during that year were distinctly remote. From mid-June to November adult numbers generally remained above 10 ind/l; and throughout August, well above 15 ind/l.

It was noted earlier (Page 144) that the annual cycle of *Daphnia hyalina* var *lacustris* in Loch Leven during 1976 (George pers. comm.) was very similar to the events in 1972 and 1973. To complement this, George also found that the almost identical, in terms of numerical densities, to those of 1972. The re-establishment of stability in the limnetic ecosystem at Loch Leven is again suggested.

For additional comparison, further examples of annual cycles of _C_. _s_. _abyssorum_ are provided by Smyly (1973 a) who worked on populations in four lakes of the English Lake District, Esthwaite Water, Rydal Water, Grasmere and Buttermere. He found that in each of those lakes there was only one effective generation in each year and that in each case individuals of this generation were derived from eggs laid in spring. In Buttermere (the deepest and least productive of all four lakes) these individuals attained adulthood by early winter, overwintered in open water and began reproducing early in the following year. (Apparently Smyly (1973b) demonstrated that scarcity of food and not low temperature during winter delayed the breeding in this lake.) In contrast, _most_ of the individuals derived from the spring generations in the other three lakes reached CV by mid-summer and then spent the following eight months or so in the profundal zone. In February or March of the following year, they reappeared in the plankton, moulted to adults and then started reproducing. However, in July of each year, a small percentage of the spring population matured in open water and initiated a second minor generation in the autumn. Interestingly, Smyly (1973a) correlated the appearance of older copepodids (predominantly CV but also CIV) in the profundal zone with oxygen depletion in the hypolimnion - a phenomenon which perhaps could never occur at Loch Leven. The copepod annual cycles in the Lake District waters (Buttermere excepted) bear closer resemblence to the events in Loch Leven during 1972-73 rather than 1969. However, in all cases quoted, the main population developments were centred in spring.

Before discussing the seasonal events of 1972-73 any further, certain aspects of copepod growth deserve mention. In laboratory experiments, inverse relationships between temperature and development rates have been clearly demonstrated (Smyly 1961, 1973a; Lewis 1971); although according to Lewis (1971) drastic changes in temperature during development (as perhaps in the field) may have more complex effects on growth. Both Lewis (1971) and Smyly (1973a) determined the growth-rate of *Cyclops strenuus abyssorum* in cultures and their results for egg duration and at lower temperatures agree, but they differ markedly at higher temperatures. For example, Smyly found that at 4°C and 16°C development from the newly-hatched nauplius to the CV stage took 132 days and 30 days respectively; as compared to Lewis who found that at temperatures of 5°C and 15°C such development took approximately 138 days and 76 days respectively. Interestingly, the duration obtained by Lewis at 25°C was about 44 days and this was much slower than the 16°C rate determined by Smyly.

Although the development time of copepod eggs is 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 all other developmental stages, particularly the later copepodid instars (Smyly, 1970). However, the time spent in each instar, under standardised conditions, is important. Smyly (1961) found that at 16-18°C *Mesocyclops leuckarti* took 12 days to develop from hatching egg to CI, whereas development from CI to the adult instar took a further 20 days, half of which was spent in Stages CIV and CV. As regards *C. strenuus abyssorum*, Smyly (1973a) pointed out that the time spent in these last two instars was extremely variable ranging from a few weeks to several months. Although diapause may interrupt development in the pre-adult phases, the duration of these stages may food shortage occurs (Ravera, 1954; Smyly, 1961).

Apparently copepods do not moult in the adult instar (Smyly, 1973a). This is particularly significant because several authors have noted that adult body-lengths undergo changes which follow a seasonal pattern, probably related to temperature modified by food availability during development (Coker, 1933; Deevey, 1960; McLaren, 1963; Smyly, 1968c), as successive adults mature into the existing population and this "biological tagging" has been used as a means of elucidating the adult turnover (Tonolli, 1964; Chapman, 1969).

For the purposes of assessing population events during the annual cycle, the data for 1973 is preferable to that of 1972 since the sampling during the critical spring period was more frequent and population changes were more clearly defined. The major differences between the two years related to the numerical densities achieved during spring, these being very much greater in 1973 than in 1972 (Page 92). The exceptionally high population densities attained in spring 1973 were primarily the results of the very high egg stock provided in March, April and May by the consistently high numbers of surviving winter adults.

The consistently abundant overwintering adult population during the 1972-73 winter appeared to remain stable as denoted by unchanging numerical densities (Fig. 21) and mean adult body-lengths (Fig. 24). Even so, minor changes were detectable by variations in sex-ratio (Fig. 25) at the beginning of 1973 (Fig. 25), implying an influx of males and a loss of females. The nauplii numbers, on the other hand, fluctuated markedly during this winter and since corresponding changes in the numbers of the younger copepodid stages were not apparent, it is fair to assume that the "losses" of nauplii represented mortalities (perhaps due to adult predation, Page 252 ). Although survival at the egg stage appears to be very high in copepods, since Smyly (1961) recorded a success rate of hatching at 80-90 per cent for _Cyclops leuckarti_ and Elbourn (1966a) noted a 60-80 per cent success rate for _C. strenuus strenuus_, nauplii survival rates may be very poor (Monakov, 1958; McQueen, 1969).

Nevertheless, the overwintering adults probably survived at least until May in 1973 and since their appearances as adults probably took place in October or November of the previous year, an possible. The copepodid stages which persisted during the winter appeared to recruit the adult population in April and May and contributed to the very high egg stock of these months Although it is possible that latent copepodids (CIV or CV) from the spring generation in 1972 arose from dormancy during this time (assuming, of course, that arrested development took place), such events would be difficult to demonstrate with the data at hand. Using the *C. s. abyssorum* growth rates of Lewis (1971), eggs laid in January could have resulted in an influx of adults in May (or, using the growth rates of Smyly (1973a) such adults could have appeared in late April-early May). It certainly seems likely, therefore, that overwintering copepodid stages, which eventually matured, accounted for the observed adult increments in April.

However, the high egg stocks of April and May were precursors to an exceptionally large population explosion; and rapid development in conditions of increasing water temperatures enabled some of these offspring to mature in June, implying a total growth period of about two months.

The majority of the resultant adults did not appear to survive for long, although the drastic losses of adults in early July (Fig. 21) appeared to be mostly associated with mortalities of winter and spring adults, since notable reductions in mean adult body-length were concurrent with these losses (Fig. 24.).

Although total population numbers remained low and did not undergo marked fluctuations during July and August (Figs. 21 and 31), variations in the mean adult body-length indicated that changes in the adult population occurred, with the small summer individuals being eventually phases out in September and October (Fig. 24). Increases in egg stock in late August-early September promoted a second major upsurge of _C_. _s_. _abyssorum_, with the resultant offspring boosting the adult fraction in October and November and thus providing the future over-wintering stock.

An influx or loss of adults can be demonstrated using body-length data when the standing crop data does not show density changes, although usually it is difficult to define exactly when specific animals entered or left the population since changes in mean body-length are generally gradual with recruitment of newly-matured individuals overlapping the existing adult population. It must be emphasised that standing crop data does not necessarily record changes within the population as the gain of young individuals may be exactly counter-balanced by the loss of older animals due to moulting or mortality.

Although, because of continual reproduction and continual recruitment, there was considerable overlap between successive cohorts and discrete generations were difficult to discern, it is possible to calculate the maximum number of generations per year using the C. s. abyssorum growth-rate data of Lewis (1971) and Smyly (1973a) in conjunction with the graph of mean water temperatures during the year (Fig. 2). Using the growth data of Lewis (1971), three generations were possible :

| | |
|---|---|
| 1st | January - end of May |
| 2nd | end of May - end of August |
| 3rd | end of August - mid-December |

However, using the growth-rates of Smyly (1973a)*, a more likely maximum of five generations were possible :

| | |
|---|---|
| 1st | January - early May |
| 2nd | early May - end of June |
| 3rd | end of June - early August |
| 4th | early August - early September |
| 5th | early September - mid-November |

Walker (1970) estimated a possible total of six generations during 1969 but his calculations of

---

* Smyly (1973a) did not quote durations for the CV stage (presumably because these were highly variable) so, for the purposes of estimating total development times from

growth-rate, which were based on field observations, appeared to differ markedly to those obtained in laboratory cultures by Lewis (1971) and Smyly (1973a), being in general very much faster. Interestingly, Smyly noted that growth-rates of _C_. _s_. _abyssorum_ in laboratory cultures were _faster_ than the observed rates in the field conditions of several lakes of the Lake District and he attributed this to the consistently better foods supplied to the cultured animals. Finally, George (1976) deduced from standing crop data that _C_. _vicinus_ populations in Eglwys Nynydd underwent four distinct generations in one year and five generations in another.

### (b) The breeding parameters

Although the reproduction of the _Cyclops strenuus abyssorum_ population during 1972-73 was continuous, breeding, as reflected by egg stock, was most intensive during the spring and autumn periods (April-May and September respectively) and also during the mild winter months (especially during the 1972-73 winter). The summer months of June, July and August generally represented periods of very low reproduction (Fig. 22). In contrast, the main phases of reproductive activity in 1969 occurred in May - early June and also in August (Walker, 1970). In all egg stock quantity was the actual number of gravid females present in the population (Page 98), the mean brood-size being of much lesser significance. This is understandable since female copepods usually carry very large numbers of eggs. During the two-year study period, the minimum mean clutch-size was 22 eggs per female (i.e. 11.3 eggs per sac) and the maximum mean clutch-size was 64 eggs per female (31.8 eggs per sac), with the absolute range for individuals being 10 eggs per female and 114 eggs per female.

The high fecundity of copepod females may be of considerable importance, not only to offset the potentially high naupliar mortalities noted earlier (Page 208 ), but also to compensate for the fact that, at any given time, only a minor proportion of the population is actively reproductive. For example on the 21st June 1973 when adult numbers reached an all-time maximum of 27 ind/l and total population numbers amounted to 193 ind/l (all copepodids), the number of gravid females was less than 2 ind/l! Even when the numbers of gravid females reached the all-time maximum of 4 ind/l in mid-April 1973, they only represented 8 per cent of the total population.

The drastic fall-back in egg production during the mid-summer periods of both sampling years was caused by a notable paucity of gravid females coupled with low average brood-sizes (Fig. 22). Most significantly, however, the proportions of gravid females remained very low (<20 per cent) during these periods and the initial drop in the percentage gravid was coincident with maximum population build-up. Several factors may cause reductions in the percentage gravid as noted for Daphnia hyalina var lacustris (Pages 163 - 165 ) but in the case of Cyclops it seems that this was due most likely to an increase in the time interval between successive broods, probably as a result of food restrictions. In 1969, Walker (1970) found that the percentage gravid fluctuated from about 10 per cent to over 80 per cent, but during September and October values remained consistently below 20 per cent. Interestingly, these low proportions coincided with notable reductions in adult densities, perhaps suggesting unfavourable conditions or selective predation on gravid females by fish (Page 265 ).

As regards C. s. abyssorum populations in the Lake District, Smyly (1973a) found that the egg stocks in all four lakes (Page 204) were greatest in March, April and May and were coincident with large stocks of adults. At all other times egg stocks were low due to scarcity of adults, irrespective of clutch-sizes.

However, before discussing the seasonal variations in mean brood-size (Figs. 22 and 24), the seasonal changes in mean body-length must be mentioned first since body-size influences brood-size.

## (c) Variations in mean adult female metasomal length

It was mentioned earlier (Page 99) that in 1972-73 the mean metasomal lengths of adult female *Cyclops strenuus abyssorum* varied according to a distinct seasonal pattern in each year (Fig. 24). Walker (1970) observed similar events in 1969, although the maximum mean sizes of spring females in May 1969 were much greater than those recorded in the later years, being about 1.3 mm as opposed to 1.16-1.17 mm. However, maximum *ranges* during the spring periods in 1972-73 were similar to those in 1969, implying that the actual sizes of the largest individuals were about the same in all years. Minimum mean sizes (and ranges) were similar in all three years but in 1969 these occurred later in the summer, August - October rather than during July.

which varied in colour from dark green to variable shades of brown to almost black. Unfortunately the algal types were not reliably identified to species but these certainly included diatoms (such as _Asterionella_ sp.) and possibly green algae and flagellates. The blue-green species _Anabaena flos-aquae_ (Lyngb.) Breb. which was highly abundant from July to September (Fig. 28; Table 12) was _not_ identified in gut samples (either as fragments or as distinct cells) suggesting that it did not contribute to the _Daphnia_ diet as live cells.

Since its re-establishment in 1970, _D. hyalina_ var _lacustris_ has exerted a profound influence on the abundance and diversity of open water particulate material in Loch Leven, especially during the spring and summer periods of subsequent years when this filter-feeder was most numerous The effects of _Daphnia_ grazing have generally acted to reduce the overall abundance of phytoplankton (Fig. 28) and other suspended particles in the 1-20μm size-class; and this has ultimately resulted in increased water clarity (Fig. 4). As an example, Bailey-Watts (1974) recalled that in the summer of 1971 when _Daphnia_ first became abundant (60 ind/l), algal densities and Secchi-disc readings were respectively the lowest ($3\mu g/l^{-1}$) and highest (4.75m) since the start of the IBP investigations. The grazing activities of _Daphnia_ have also invoked important changes in the size and species composition of the Loch Leven phytoplankton (Bailey-Watts, 1973; Morgan, 1974) tending to suppress the developments of smaller edible "nannoplankton" species and, in so doing, enhancing the success of larger inedible "net-phytoplankton" species (i.e. the large-celled or colonial forms), especially of the blue-green variety. During the period of Cyclops domination (at least 1966 to 1970) the phytoplankton of Loch Leven was exclusively dominated by small species, whereas now (post 1970) larger species generally predominate (Morgan, 1974). The relationships between algal sizes and Daphnia abundance in Loch Leven during 1972 have been assessed by Duncan and Bailey-Watts (pers. comm. - publication in press). From May to September when Daphnia were abundant (Fig. 5) algal sizes were generally above 40μm (cell-diameter), whereas at all other times algal sizes were below 12μm. Brooks (1969) noted that in highly enriched waters, the extensive utilisation of minute algae by cladocera tended to encourage the development of blue-green species; and it might therefore be suggested that in Loch Leven during 1972, the abundance of D. hyalina var lacustris in the spring and early summer indirectly promoted the upsurge of Anabaena sp. in high summer (Fig. 28; Table 12). Hrbacek et al. (1961), working on several Czechoslovakian dominant planktonic grazers (small *Bosmina* sp. contrasted with large *Daphnia* sp.) on algal size-composition and water clarity and their results provide a close parallel to the recent findings in Loch Leven.

In order to provide some details on the nutrition of the *D. hyalina* var *lacustris* population during 1972-73, the algal species which dominated the phytoplankton during these years are briefly reviewed in relation to their acceptability as cladoceran food sources (see notes accompanying Table 12). The algal species, *Chlorella* sp. and *Scenedesmus* sp., which were used to feed the laboratory *Daphnia* cultures are also mentioned. However, it must be noted that the algal list in Table 12 does not account for the numerically subordinate species at Loch Leven which may have been important in the diet of *D. hyalina* var *lacustris*. Similarly, the dietary roles of detritus and bacteria remain obscure.

The term "detritus" collectively describes a complex array of non-living organic substrate which may vary considerably in its origin, its state of decomposition (by bacteria) and consequently its food value. Saunders (1969) noted that in highly productive lakes the correspondingly high levels of detritus provided an important food source to filter-feeders and occupied a dominant role in zooplankton feeding along with phytoplankton. He pointed out, however, that although low-calorie detritus in large amounts would maintain a zooplankton population during periods subsequent to a catastrophic decline in phytoplankton abundance, the detritus could also act as a diluent which would "dampen" the assimilation of high quality algae when these were abundant. This dampening effect would generally tend to suppress cladoceran population growth at such times and thus allow the phytoplankton to adjust to higher grazing rates. In effect, Saunders deduced that detritus acted to buffer the dynamics and energetics of the phytoplankton - zooplankton feeding system. Additionally, Steel (1972) demonstrated that detritus was notably important in maintaining large overwintering *Daphnia* populations.

Several authors have emphasised the importance of bacteria as a food for zooplankton (Saunders, 1969; Gliwicz, 1969 a,b,c; Smyly , 1975). The review by Gliwicz (1969b) demonstrated how capable *Daphnia* spp. are of filtering, ingesting and assimilating single bacterial cells in liquid medium. In fact Gliwicz (1969c) was of the opinion that zooplankton production in eutrophic lakes was essentially dependent upon bacteria, plankton were more dependent upon phytoplankton. The high levels of detritus and soluble organic nutrients associated with enriched lakes would certainly be expected to encourage extensive bacterial growth. Saunders observed that in Frains Lake, Michigan, the summer developments of blue-green algae gave rise to sharp increases in dissolved carbohydrates which in turn promoted ten-fold increases in bacteria. These bacteria consequently provided the major cladoceran food component during blue-green algal blooms.

The highly eutrophic status of Loch Leven definitely suggests that both detritus and bacteria play significant roles in the nutrition of *D. hyalina* var *lacustris*; but clearly more information is needed regarding these aspects. It may be tentatively concluded that during the spring and early summer periods phytoplankton dominated the zooplankton feeding, whereas in mid- to late summer detritus and bacteria became increasingly important.

Lastly, the nutrition of *Diaptomus gracilis* deserves brief mention. Calanoid copepods feed on essentially the same food items as *Daphnia*, although according to Hutchinson (1967) they are generally regarded to be *coarse* rather than fine suspension feeders. Gliwicz (1969c, 1970) established that the filtering mechanism of Eudiaptomus graciloides functioned most effectively with particle sizes of 5-10µm. However, D. gracilis was rarely abundant at Loch Leven (except perhaps in autumn when nauplii and young copepodids predominated) so that the population food demand and the consequent effects on phytoplanton were likely to have been minimal at most times.

(b) The omnivorous seizer

The most significant feature concerning the feeding of Cyclops strenuus abyssorum is the apparent differences in diet between the younger and older life stages. Cyclops nauplii bear primitive mechanisms for collecting minute particles (unlike the copepodid stages) and are essentially phytophagus (Ruttner, 1968), relying upon algae, protozoa and possibly bacteria for their nutrition (Walker, 1970). Phytoplankton was also considered by Elgmork (1959) to be important in the diet of younger copepodid stages of C. strenuus strenuus, whilst the older stages were thought to be predatory. The adults of C. strenuus abyssorum are certainly predaceous (Fryer,1957b) and the transition from an essentially herbivorous diet to a predominantly carnivorous diet appears to be associated with copepodid stage III (CIII). Lewis et al. (1971)

reared *C. s. abyssorum* in laboratory cultures and found that CIII to adult stages readily accepted *Artemia* nauplii as food but the copepodid instars prior to CIII could not manage even the smallest *Artemia* nauplii and were consequently fed an alternative diet of *Euglena gracilis*, an organism which possesses both "algal" and "protozoan" characteristics. Similarly, Smyly (1970) observed that large *Daphnia obtusa* could only be utilised by *Acanthocyclops viridis* at stage CIII and deduced that since the development time to this instar was relatively short, any advantage derived from changing to an animal diet at CI was probably minimal. Furthermore, McQueen (1969) noted that copepodids IV, V and adults of *Cyclops bicuspidatus thomasi*, a planktonic copepod similar in size to *C. s. abyssorum*, did *not* feed upon seven different species of algae which were offered to them in the laboratory. As these algae were representative of the flora of Marion Lake (British Columbia), from which the copepods were taken, he concluded that it was unlikely that the later copepodid stages were herbivorous.

Fryer (1957a,b) evaluated the feeding mechanism and dietary components of adult cyclopoid copepods and noted that some species, especially the larger forms, were markedly carnivorous, eating animals both larger and smaller than themselves and with prey items including other copepods, cladocerans, rotifers, protozoa, oligochaetes, chironomid larvae and even fish fry. His observations showed that chance encounter played a fundamental role in food-finding and that once the prey was firmly clasped (by means of the maxillules, and when possible by the additional use of the maxillae and maxillipeds in the form of an "embrace") the vulnerable parts of the prey were then torn apart by the intermittent action of the mandibles. Most important, however, the mandibles do not usually macerate the food but act rather to cram chunks of material into the oesophagus, thus allowing smaller prey items to be swallowed whole. Fryer (1957a) noted that small copepods were frequently swallowed intact by large adults and on one occasion a chironomid larva of 600µm in length was found in the stomach of a specimen of Macrocyclops albidus!

Fryer (1957b) found that C. strenuus abyssorum from Windermere and Coniston Water in the Lake District and from Loch Lomond fed principally 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 may have been derived from the guts of 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.

Walker (1970) evaluated the gut contents of *C. s. abyssorum* from Loch Leven during 1969 and found large quantities of algae (diatoms in spring and colonial green algae in autumn) together with loricas and trophi of *Keratella cochlearis* and occasionally small chironomid larvae. Bailey-Watts (1974) identified cells of *Diatoma elongatum* and *Dictyosphaerium pulchellum* in the guts of adult *Cyclops* from Loch Leven and concluded that the larger copepodid stages would graze to a limited extent upon the *larger* algal species which they could grasp and the younger stages would exploit the very small algae (<5μm) such as phytoflagellates.

Gut contents analyses of adult female *C. s. abyssorum* undertaken periodically throughout 1972 (Page 30) revealed comparable results to those of Walker (1970), except that identifiable remains of *Daphnia hyalina* var *lacustris*, *Diaptomus gracilis*, other rotifer species (*K. quadrata*, *Asplanchna* ?, Synchaeta ?), oligochaetes and C. s. abyssorum nauplii and other stages were also found. During routine Friedinger sample analyses, over sixty instances were noted of adult and late copepodid stages grasping Daphnia individuals of various sizes. In several cases copepods were actually seen inside Daphnia brood-pouches and presumably such behaviour was directed towards feeding on cladoceran eggs. Twelve instances of predatory interaction between Cyclops and Diaptomus gracilis were also observed.

Canabalism amongst carnivorous copepods is a recognised phenomenon (Fryer, 1957 a,b; McQueen, 1969; Walker, 1970), with adults and older copepodids feeding upon the nauplii and younger copepodids. In preserved samples during 1972-1973, fifty instances of canabalism were observed and these are presented in Table 13. Walker (1970) made similar observations and emphasised the importance of canabalism by C. s. abyssorum during 1969. Although all the above cases of predatory interaction from preserved samples appear to be conclusive evidence of Cyclops feeding, it is possible that such behaviour may be incited prior to death by the effects of the preservative. However, in laboratory cultures, adult female C. s. abyssorum were seen to devour juvenile Daphnia, Diaptomus gracilis, their own nauplii and even Artemia nauplii, so that there is no doubt that

Table 13

Table 13 Observations of canabalism in Cyclops strenuus abyssorum. The data is given as numbers of observations of predator-prey interaction and was obtained during routine Friedinger sample analysis.

| | Prey | | | | |
|---|---|---|---|---|---|
| Predator | Nauplii | C1 | C11 | C111 | CIV |
| C1V | 3 | | | | |
| CV | 16 | 3 | 1 | | |
| CV1 | 10 | 2 | 7 | 5 | 3 |

Nevertheless, most of the above information relates to the feeding of adult copepods. Little is known about the diet of the younger stages which were always numerically more important than the adults at Loch Leven. Since 1970, the food sources of the copepod population may have undergone fundamental changes. The renewed presence of *Daphnia* and the increases in *Diaptomus gracilis* would certainly have boosted the prey items available to the older copepodid instars; but the extensive removal of small edible particles by the filtrators may have adversely affected the younger stages. Additionally, the utilisation of particulate material by *Daphnia* may have drastically altered the balance of other small zooplankters such as rotifers and protozoa (which rely on similar foods to *Daphnia*) and these organisms may have featured prominently in the copepod diet. The extent of bottom-feeding by *C. s. abyssorum* (on benthic algae, chironomid larvae, oligochaetes and nematodes) during periods of food shortage in open water is again unknown. These aspects deserve future investigation.

### (c) The carnivorous seizers

According to Mordukhai-Boltovskaia (1958) the carnivorous cladocerans *Leptodora kindti* and *Bythotrephes longimanus* feed in a similar manner.

physical damage using the mandibles and then suck up the available liquid food substances into the gut. Such fluid-feeding results in the ingestion of amorphous material which precludes recognition of prey organisms from gut contents analyses. *Leptodora* is considerably larger than *Bythotrophes* (Pages 10-11), is highly mobile and has a reduced carapace, the limbs being free and thus able to efficiently grasp particulate objects (Hutchinson, 1967). It might, therefore, be expected that *Leptodora* is the more effective predator of the two species.

Conflicting results have been obtained regarding acceptable and preferred prey items of predatory cladocera and the onset of predatory feeding in the life history of *Leptodora*. Studies on *L. kindti* by Cummins *et al.* (1969) indicated that only the larger size group (>6 mm) are predaceous whereas the smaller counterparts (2-5mm) probably rely on algae, bacteria and detritus (also protozoa ?) and that initial predatory activity may be restricted to naupliar copepods and possibly rotifers. These authors noted that young stages of *Leptodora* would effectively feed on yeast in laboratory circumstances. Further work showed that larger *Leptodora* in culture fed upon a wide variety of prey even including *Artemia* (the brine shrimp) and that predatory feeding in field conditions was opportunistic with *Leptodora* cropping the most readily available prey which was usually, but not always, the most abundant prey species. In the Santuary Lake, Pennsylvania, *Daphnia* and *Cyclops* appeared to be the most important prey organisms, although species of *Ceriodaphnia*, *Bosmina*, *Chydorus*, *Diaptomus* and some rotifers may have been subjected to periodic predation pressure.

However, the laboratory experiments of Mordukhai-Boltovskaia (1958) showed that both *Leptodora* and *Bythotrephes* preferred small prey, crustaceans up to 0.7 mm, especially those brightly coloured such as the conspicuous brown *Polyphemus pediculus*, and noted that large *Daphnia*,(presumably *above* 0.7mm), the hard-shelled Chydoridae and copepods were not favoured as a food source. This author inferred that the haphazard "dashing" movements typical of copepods offset their predation by carnivorous cladocera and that both *Leptodora* and *Bythotrephes* do *not* eat adult carnivorous copepods such as *Cyclops* spp. Interestingly, his work demonstrated that the predatory cladocera became victims themselves to such copepods and that an adult *Macrocyclops albidus* could eat up to five *Leptodora* (4-6mm in size) per day. Other results of Mordukhai-Boltovskaia suggested that predatory feeding of Leptodora began very early in life - this conflicting strongly with Cummins et al.(1969). Within the first 24 hours of life an individual (1.3mm) could consume up to five small water-fleas (Polyphemus pediculus); individuals up to 3mm could eat twelve per day and individuals up to 6mm could eat thirty per day. One might ask how many water-fleas an 18mm Leptodora (Page 11, Brooks (1966)) would devour? In addition, Mordukhai-Boltovskaia noted canabalism with both Leptodora and Bythotrephes and apparently concluded that Bythotrephes is more voracious than Leptodora and has a higher feeding rate despite its small size.

As a compromise between the somewhat contradictory information provided by Cummins et al.(1969) and Mordukhai-Boltovskaia, it may be assumed that, within the context of the Loch Leven plankton, the carnivorous cladocera are likely to feed primarily upon Daphnia, probably favouring smaller immature individuals, and to a lesser degree upon young Cyclops and also Diaptomus. The immature predators may initially rely on phyto- and bacterio-plankton, rotifers and protozoa.

## 5. Inter-specific zooplankton relationships

The inter-specific relationships now under consideration relate to the trophic interactions between the various crustacean zooplankton at Loch Leven and are conveniently separated into two categories, predation and competition. The degree of interaction between any two or several species is essentially dependent upon the abundance of individuals in the respective populations. Indeed the seasonal occurrence and timing of major population events of a given species may be considerably influenced by the existence of such interaction. A predator population which is primarily reliant upon a specific prey will be most productive when the prey is available and plentiful; and an animal which is competitively suppressed by a more successful counterpart can only prosper when the conflicting species is absent or limited in abundance. Fig. 31 shows the seasonal variations in numerical standing crop of the principal crustacean zooplankton at Loch Leven during 1972-73, together with notations on the seasonal occurrences of the predatory cladocera. Densities are expressed as numbers per litre.

### (a) Predation

The predatory cladocera, *Leptodora kindti* and *Bythotrephes longimanus* were only present in the Loch Leven plankton from late June to November in each year and showed high abundances (1-2 ind/5l Friedinger sample

Figure 30 (opposite)

The seasonal variations in mean brood-size of *C. strenuus abyssorum* in relation to algal chlorophyll *a* concentrations during 1972-73.

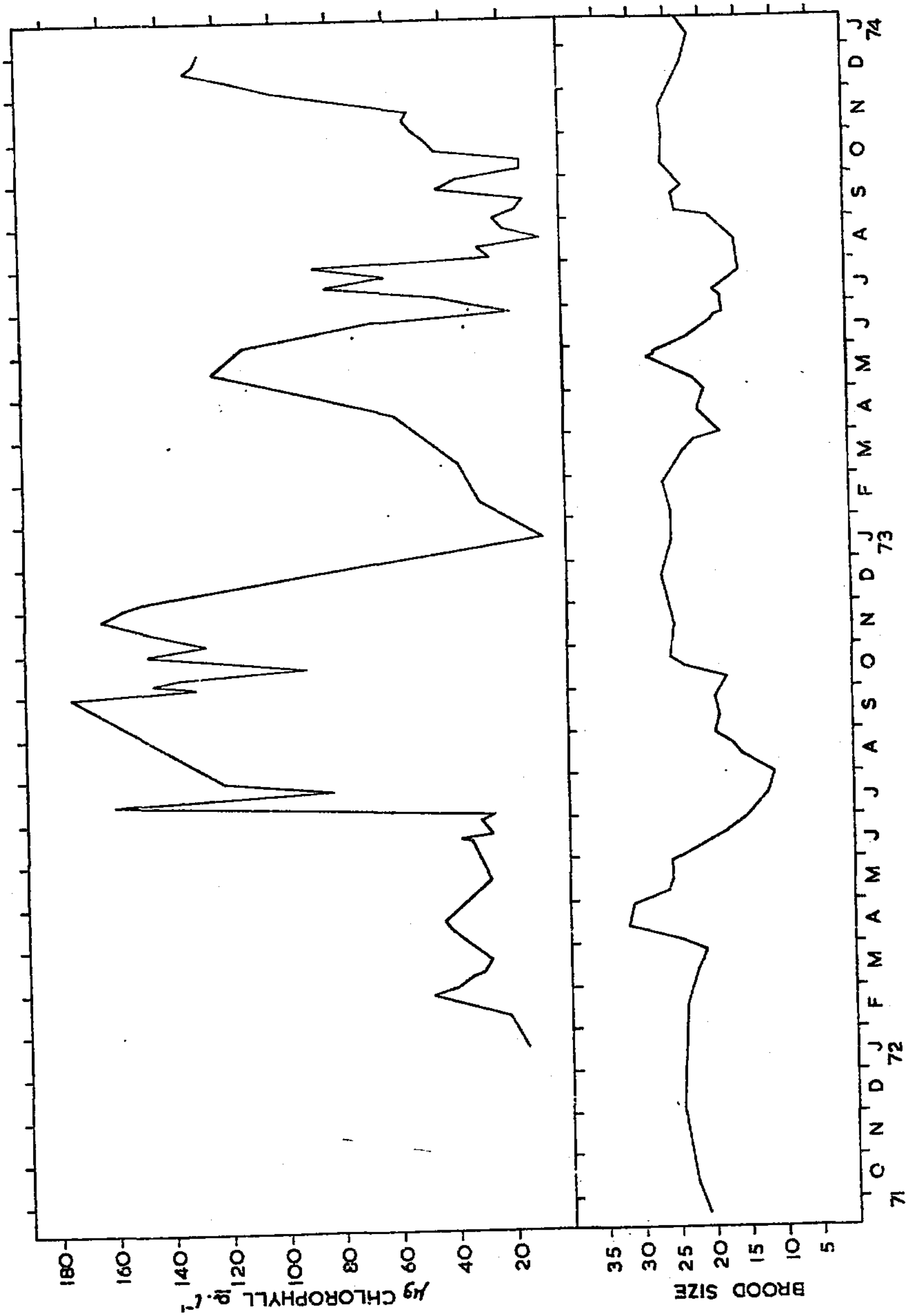
(Phytoplankton data by kind permission of Bailey-Watts, I.T.E., Edinburgh)

Abcissa - the study period

Ordinates - the mean brood-size (i.e. numbers of eggs per egg-sac).

- the algal chlorophyll *a* concentrations as µg per litre.

Fig. 30



μg CHLOROPHYLL a.l⁻¹
180
160
140
120
100
80
60
40
20
BROOD SIZE
35
30
25
20
15
10
5
71
O
N
D
J
72
F
M
A
M
J
J
A
S
O
N
D
J
73
F
M
A
M
J
J
A
S
O
N
D
J
74

Figure 31 (opposite)

The seasonal variations in the numerical standing crop of the principal crustacean zooplankton at Loch Leven during 1972-73.

Abcissa - the study period.

Ordinate - total population numbers per litre of :

●——● *D. hyalina* var *lacustris*

○——○ *C. strenuus abyssorum*

△——△ *Diaptomus gracilis*

Information on the seasonal occurrence of the predatory cladocerans is presented above the graph in the form of data on the presence of *Leptodora kindti* (L) and *Bythotrephes longimanus* (B).

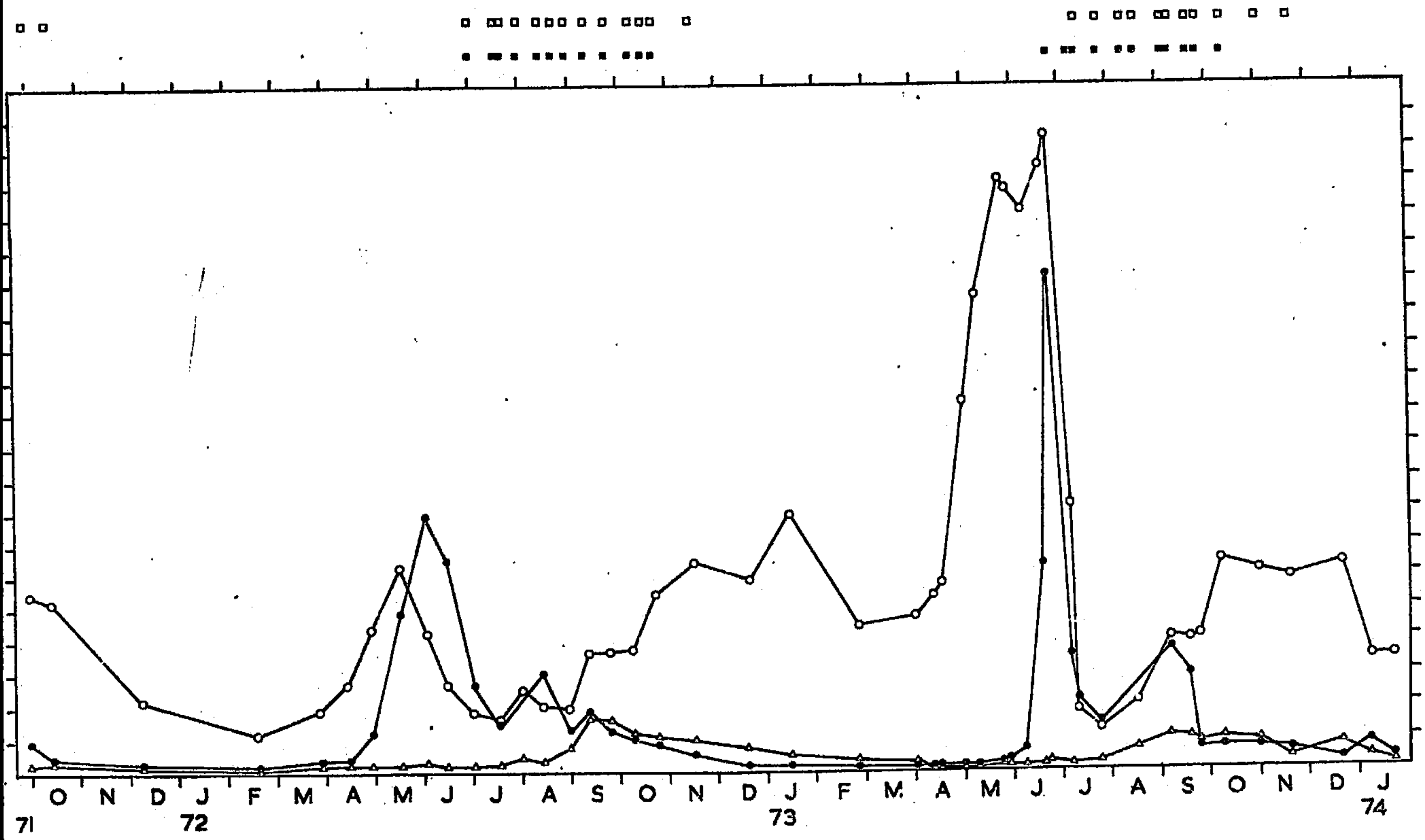


Fig. 31

for each species) from about late July to the end of September (Fig. 31, Table 11A and B). In general the densities attained by both species were greater in 1973 than in 1972. The predatory cladocera are characteristically aestival (Wesenburg-Lund 1904; Patalas, 1954) and typically feature in the open water community during the summer and autumn months (Hutchinson, 1967). In Lake Windermere both species occupied the plankton from May to October (Scourfield and Harding 1966) and in Base Line Lake, Michigan, Leptodora appeared in June and reached maximum densities (<1 ind/51) in July (Hall, 1964), these latter findings being exactly parallelled by Wright (1965) for Leptodora in Canyon Ferry Reservoir, Montana. Cummins et al. (1969) found that in Sanctuary Lake, Pennsylvania, the seasonal appearance of Leptodora followed a consistent pattern over a three-year period; the predator emerged from over-wintering eggs when the lake temperature rose above 9°C and disappeared from the plankton when temperatures fell below 9°C. In Loch Leven, however, the initial appearances of the carnivorous cladocera were associated with loch temperatures above 15°C and their disappearances with temperatures dropping below 5°C.

According to Hall (1964) the predatory effects of *Leptodora* may play a significant role in regulating the seasonal occurrences of other planktonic species; and Mordukhai-Boltovskaia (1958) suggested that losses of zooplankton due to the combined activities of *Leptodora* and *Bythotrephes* could be of the same magnitude as those losses attributed to fish. Substantial losses of young *Daphnia* due to *Leptodora* were thought to have caused the mid-summer population declines of *D. galeata mendotae* in Base Line Lake (Hall, 1964) and *D. schodleri* in Canyon Ferry Reservoir (Wright, 1965). In fact Hall inferred that *Leptodora* was the most likely causal agent responsible for the mid-summer minimum in the bimodal annual cycle of *D. galeata mendotae*.

In Loch Leven an important predator-prey relationship between the predatory cladocera and young *Daphnia hyalina* var *lacustris* may certainly have been established during the mid- to late summer periods of both years. *Leptodora* was marginally more abundant in the loch than in the other named waters (above) so that, with the *additional* presence of *Bythotrephes* in similar numbers, the losses of *Daphnia* attributable to the predatory cladocera may have been considerable. Combined numbers of *Leptodora* and *Bythotrephes* at any time during August or September in either year could have amounted to about 3 ind/5l (Table 11A and B), and assuming that each individual could devour thirty small *Daphnia* per day (as for a 6mm *Leptodora*, Page 245 ) the daily demand for young *Daphnia* could have been about 18 ind/l/day. This might explain the relatively low numerical densities of immature *D. hyalina* var *lacustris* during the latter half of summer in both years (Fig. 7). If juvenile *Daphnia* were limited in abundance, the size selective predation could then have accounted for losses of *small* adults and this would have acted to *increase* the minimum adult sizes (Page 167 ) and also the mean adult sizes (Fig. 10) during this time.

In both years maximum numbers of *Leptodora* were exactly coincident with the maximum densities of *D. hyalina* var *lacustris* in the second phase of the bimodal annual cycle. Prior to these maxima, the predatory cladocera presumably acted to depress the rate of *Daphnia* population increase, thereby reducing the overall peak numbers achieved. Thereafter the predators probably contributed to the decline of the *Daphnia* populations. Peak numbers of both species of predator in mid-August 1972 (Table 11A) most likely accounted for the relative paucity of juvenile *Daphnia* at that time (Fig. 8). Similarly, maximum numbers of *Leptodora* in responsible for the high juvenile mortality of mid-September (Figs. 8 and 11). It is noteworthy that in Eglwys Nynydd predatory cladocera were not recorded (George and Edwards, 1974; George, 1976). Perhaps the very marked differences between the annual cycle of _D. hyalina_ var _lacustris_ in Loch Leven and that in Eglwys Nynydd (Page 146 ) may be partly due to the influence of predatory cladocera in the loch.

Cummins _et al._ (1969) deduced that predator-prey relationships involving _Leptodora_ were "quite complex" since, at any given time, _Leptodora_ populations were usually dependent upon at least _two_ species of prey. This being the case, the most likely subsidiary species sought by the predatory cladocera at Loch Leven would have been _Diaptomus gracilis_ and _Cyclops strenuus abyssorum_ (young instars). However, the notable late summer increases in both _Diaptomus_ and _Cyclops_ tended to imply that such predation was minimal. Additionally, canabalism and mutual predation between _Leptodora_ and _Bythotrephes_ (and also older _Cyclops_ instars) may have occurred, but this would again have been minimal because alternative (or preferred) food species were always sufficiently available.

Walker (1970) recalled that in 1969, Bythotrephes was the only predatory cladoceran found in Loch Leven, although Leptodora was recorded in small numbers during August to October in 1967-68. Most significantly, the predatory cladocera were considerably less abundant during these years than in 1972-73. Walker counted a total of only thirty-eight Bythotrephes from all Friedinger samples taken during August to November in 1969. It appears, therefore, that during the years prior to 1970, the sparcity of predatory cladocera was due to the total absence of the most suitable prey species (i.e. D. hyalina var lacustris) and/or excessive predation by the high summer abundances of older Cyclops instars. (Page 203 ).

C. strenuus abyssorum may also have predated upon Daphnia during 1972-73, although generally this predator-prey relationship would not have overlapped with periods when the carnivorous cladocera exploited Daphnia (Fig. 31). The effects of Cyclops predation would have been greatest when adult and advanced copepodid stages were particularly abundant. For instance, in mid-June 1973 when the combined numbers of

(Fig. 21) the daily demand for young Daphnia could have been around 100-300 ind/l/day, assuming that each copepodid consumed 1-3 young Daphnia per day (as for an adult Acanthocyclops viridis, Smyly (1970)). Although Cyclops undoubtedly contributed to the high losses of young Daphnia in late June, (Page 153 ) the figures quoted are probably considerable over-estimates since the copepods are essentially catholic in their food requirements and may equally have exploited the alternative prey items, such as rotifers (Keratella cochlearis var tecta, K. quadrata, Asplanchna (priodonta ?) and Conochilus unicornis) and chironomid pupae, which were extremely abundant at that time. Throughout the mild winter of 1972-73 the consistently high levels of adult C. strenuus abyssorum (about 12 ind/l) probably restricted the recruitment of young Daphnia to an already diminished overwintering Daphnia population. Such predation may have led to the progressive dominance of adults in the Daphnia population as time ensued (Fig. 8). It may be further implied that the continued effects of this predation into early 1973 ultimately acted to retard the spring development of the Daphnia population from May (as in 1972) to June. High juvenile death-rates in late April - early May (Figs 8 and 11) could be attributed to

*Cyclops* predation.

*Diaptomus gracilis*, being a preferred prey species (Fryer 1957b) would certainly have suffered losses due to *C. strenuus abyssorum*. The gradual early winter declines of *Diaptomus* in both years (Fig. 27) could well be attributed to predation, although this effect would have been partly buffered by the correspondingly high abundances of young stages of *C. strenuus abyssorum* which would also have been consumed. Since chance encounter mainly determines prey selectivity the predation would be indiscriminate at such times; thus the predation pressure exerted on a given species (or on any particular developmental phase of a species) would be directly related to the abundance of that species (or developmental phase) as a proportion of the total abundance of all zooplankton prey. The abundance of the predators must also be taken into account.

Canabalism may therefore have been important at certain times, with older copepodids feeding on younger instars, especially nauplii (Table 13). This may explain the high nauplii mortalities during the 1972-73 winter (Page 208). McQueen (1969) found that in Marion Lake, British Columbia, instars IV, V and adults of *C.* bicuspidatus thomasi consumed 31 per cent of the available diaptomid nauplii). Walker (1970) considered that canabalism played a significant role in Loch Leven during 1969 when *C. strenuus abyssorum* existed in virtual monoculture. However, in the present circumstances (1972-73), the presence of *Daphnia* may have alleviated the necessity for canabalism at certain times, thus favouring the survival of young instars. The increased autumnal abundances of *Diaptomus gracilis* in recent years may be partly due to the "dampening" effect of *Daphnia*, or more likely to the overall reduced abundances of *Cyclops* adults (Page 203).

(b) Competition

The co-dominant crustacean zooplankters at Loch Leven, *Daphnia hyalina* var *lacustris* and *Cyclops strenuus abyssorum*, were not affected by similar species which could have acted in direct competition. Because of this both species were allowed to reach the high densities acknowledged earlier. However, *D. hyalina* var *lacustris*, young stages of *C. strenuus abyssorum* (particularly nauplii) and *Diaptomus gracilis* (all life-stages) all feed on essentially similar food items within the size spectrum 1-20 µm. Of these species, *Daphnia* are the largest and most effective collectors of fine particles by virtue of their highly efficient filter-feeding mechanisms.

Not only can they utilise smaller particles (1-5µm) more rapidly but they can also take in the larger particles which the smaller zooplanters cannot manage. Brooks (1969) noted that, because larger Cladocera filter more effectively than do their smaller relatives (the filtering rates of cladocera at low algal concentrations increases with at least the square and sometimes the cube of the body length (Burns and Rigler, 1967)) this often led to the competitive suppression or elimination of the smaller species. It may be expected, therefore, that *D. hyalina* var *lacustris* would competitively suppress the developments of the other populations at Loch Leven. Parker (1960, 1961) studied aspects of competition between Cladocera and Copepoda in laboratory situations and found that when cultures were fed on *Chlamydomonas* sp. the cladocerans invariably suppressed the copepods without any apparent effect of the latter upon the former. In one experiment (Parker 1961) *Daphnia pulex* over-ruled *Cyclops agilis* (an essentially vegetation species, Fryer (1957b)); and in another (Parker 1960) *Simocephalus vetulus* suppressed *Cyclops viridis* (a notably carnivorous form, Fryer (1957b)).

with those of C. strenuus abyssorum nauplii (from Fig. 21) during 1972-73. It is generally apparent that high abundances of nauplii did not conflict with high abundances of Daphnia. However, in early May 1972 the spring influxes of Cyclops nauplii were coincident with rapid increases in the cladoceran population. Perhaps the speedy utilisation of small particles by Daphnia adversely affected the success of nauplii at this time, resulting in the poor recruitment of eggs to nauplii and nauplii to young copepodids (Fig. 21). Similarly, the survival of existing copepodids 1-111 may have been impaired by this effect since their maximum numbers directly coincided with peak numbers of Daphnia (Fig. 5 and 21). Most likely, however, these copepodids resorted to alternative food sources such as rotifers and protozoa. In direct contrast, the exceptionally high spring increases of nauplii in 1973 occurred at least one month before the major Daphnia pulse (Fig. 32) and subsequent development of the Cyclops population was particularly successful (Fig. 21). Nevertheless autumnal increases in Cyclops nauplii (and diaptomid nauplii) in both years conflicted with notable abundances of Daphnia, although the latter were not so numerous as in Spring (Fig. 32). Presumably the higher detrital content of the water expectable at such times provided

Figure 32 (opposite)

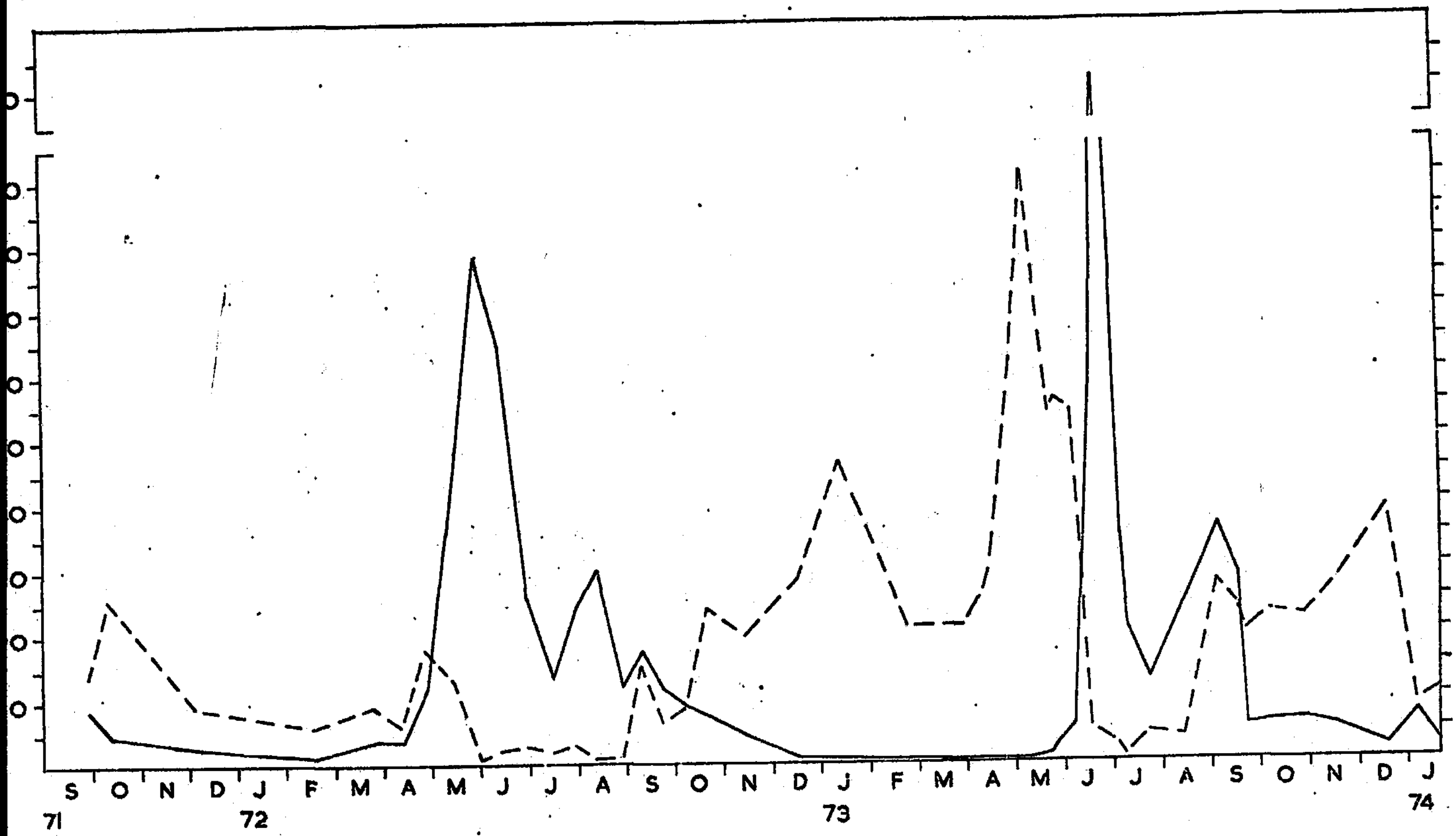
The seasonal changes in numerical standing crop of *D. hyalina* var *lacustris* in relation to densities of *C. strenuus abyssorum* nauplii during 1972-73.

Abcissa - the study period

Ordinate - the mean numbers per litre of *D. hyalina* var *lacustris* (total population numbers) or *C. strenuus abyssorum* nauplii.

The solid line designates *Daphnia* numbers and the broken line designates *Cyclops* nauplii numbers.

Fig. 32



the necessary nutritional requirements.

Competitive suppression by Daphnia early in the year, appeared to be the most reasonable explanation for the autumnal, as opposed to spring, population increases in Diaptomus gracilis. During the spring periods the Daphnia exploited the available resources to such an extent that self-imposed food limitations ultimately resulted (Page 150), thereby leaving little scope for the Diaptomus population which remained throughout at very low levels (<4 ind/l) and was composed largely of adults (Fig. 27). Interestingly, in the southern basin of Loch Lomond, D. gracilis was the most abundant zooplankter all year round, forming no less than 40 per cent by number of the limnetic crustacean fauna, and Daphnia hyalina var lacustris was limited to brief autumnal increases (Chapman 1969)!

Walker (1970) found that in 1969-70 D. gracilis was very rare (presumably due to Cyclops predation) yet in previous years, 1967-68, Bailey-Watts (unpublished) noted that the calanoid was present in the plankton throughout the year, although their numbers were very low in July. From September 1967 to March 1968 they occupied 3-7 per cent by number of the plankton while during the remaining period, they constituted less than 3 per cent. As in 1972-73, the *Diaptomus* population was composed mainly of copepodids during the winter period. In contrast Chapman (1969) found that in Loch Lomond *D. gracilis* overwintered solely as adults.

As in the cladocera, egg production in *Diaptomus* spp. is influenced by phytoplankton abundance (Edmondson, 1964). Walker (1970) revealed that *D. gracilis* fecundity in 1969 could have been as much as 50 eggs per sac due to the totally unexploited abundance of small algae; whereas in 1972-73, when *Daphnia* was present, *Diaptomus* egg numbers ranged from 1-24 eggs per sac. For comparison Chapman (1969) found a range of 2-25 eggs per sac for *D. gracilis* in Loch Lomond.

Further aspects of competition are possible at Loch Leven. In accordance with the findings of Brooks (1969) mentioned above, it could be suggested that during the summer months at the loch, the dominant presence of *Daphnia hyalina* var *lacustris* may totally preclude the re-establishment of species of *Bosmina* (these being much smaller cladoceran filter-feeders which formerly featured in the Loch Leven zooplankton in 1954 and 1890-98, Table 1). Additionally, it may be inferred that when the *Daphnia* population was comprised of large numbers of _large_ adult individuals, these may have offset the survival of their own young when food was limited. This factor might explain the preponderance of adults after the catastrophic 1973 spring crash (Figs. 5 and 8). Lastly, competitive relationships between _Leptodora kindti_ and _Bythotrephes longimanus_ for preferred prey items (i.e. young _Daphnia_) are possible, but since competition can only truly occur when the resource which is being competed for is _low_ in abundance, such relationships are unlikely to be important.

## 6. The zooplankton in relation to the fish populations of Loch Leven

The fish fauna of Loch Leven is comprised of seven species (Thorpe, 1974) of which only two, brown trout (*Salmo trutta fario*) and perch (*Perca fluviatilis* L), are likely to have significant predatory effects on the loch zooplankton in view of their abundance and feeding attributes. The dietary components of *adult* trout and perch populations at Loch Leven have been studied by Thorpe (1974). His work has shown that when these fish species fed upon zooplankton, they selectively predated *Daphnia hyalina* var *lacustris* and *Bythotrephes longimanus*. The copepods *Cyclops strenuus abyssorum* and *Diaptomus gracilis* appeared to be insignificant to the diets. Additionally, *Daphnia* spp. (?) were recorded in the gut contents of Loch Leven trout in years prior to the main IBP studies (Balmain and Shearer 1953; Morgan, 1970).

Previous studies on zooplankton as a fish food have shown that fish frequently select the largest species of zooplankton and also the largest individuals of a single species (Wong and Ward, 1972). In general, cladocera are preferred as prey to calanoid copepods of the same visual size and cyclopoid copepods are an intermediate choice (Brooks, 1969). *Daphnia* being larger, more conspicuous and having more predictable swimming movements than the copepods would certainly be the most vulnerable zooplankton prey at Loch Leven. Although being present in consistently lower numbers than Daphnia, Bythotrephes are also likely candidates for predation since their adult sizes are similar, if not larger, than those of Daphnia. Scourfield and Harding (1966) quoted a body-size of 2-3 mm for adult female B. longimanus.

Adult trout and perch are facultative planktivores and consume zooplankton only when large crustacean zooplankters are plentiful or when other preferred food sources are restricted. In Table 14 the consumption of D. hyalina var lacustris and B. longimanus by both trout and perch are given for the summer months of 1971. The values are expressed as percentages of the daily food ration for each month, June to September inclusive, and were derived from Thorpe (1974). Throughout the summer months of 1971, Daphnia were exploited as a food source by mature specimens of both species. However, trout fed on Daphnia most intensely during September when consumption of this item amounted to 35.5 per cent of the daily ration (Table 14A). Perch consumed Daphnia most prominently during August (26.3 per cent) but high consumptions (say above 10 per cent) were also recorded for July and September (Table 14B). Bythotrephes did not appear in the diet of either fish species during June, presumably because it was unavailable in the plankton (as in 1972-73, Table 11A and B), yet in July this clado-

Table 14 The consumption of zooplankton by trout and perch at Loch Leven during the summer months of 1971. (From Thorpe 1974).
Daily consumption of *Daphnia* and *Bythotrephes* by trout and perch during June-September of 1971. Data is given as percentage of total food ration.

Table 14A Trout

| Food | June | July | August | September |
|---|---|---|---|---|
| *Daphnia* | 7.3 | 3.5 | 6.6 | 35.5 |
| *Bythotrephes* | - | 6.2 | 3.7 | 0.2 |

Table 14B Perch

| Food | June | July | August | September |
|---|---|---|---|---|
| *Daphnia* | 3.4 | 13.8 | 26.3 | 19.5 |
| *Bythotrephes* | - | 0.4 | 10.2 | 0.5 |

ceran formed 6.2 per cent of the trout diet and in August 10.2 per cent of the perch diet. Compared with the respective consumptions of *Daphnia*, the values for *Bythotrephes* appeared to be high especially since *Daphnia* are always far more abundant in the plankton than *Bythotrephes* (ratio of 20:1). The data may therefore indicate that *Bythotrephes* is preferred to *Daphnia*.

However, in terms of numbers and probably total biomass the immature trout and perch at Loch Leven are likely to be considerably more abundant than their respective adult members. At present little is known about the population dynamics and trophic status of the young perch in the loch, but it is highly probable that they are very abundant and exert considerable predation pressure on the zooplankton. Most fish species inhabiting standing waters subsist on zooplankton when they commence feeding as young fry shortly after hatching from the egg stage (Brooks, 1969). Wong and Ward (1972) studied the yellow perch fry in West Blue Lake, Manitoba, and reported that the fry of this species occupied the epilimnion of the deep lake in early and mid-summer in order to feed on zooplankton. Their observations indicated that the food size-selectivity of young fry was related to the mouth gape and that in the initial stages of development during early summer these fish sought the *smaller* components of the zooplankton. These authors quoted, for example, that prior to mid-July yellow perch fry of body-size <18mm were unable to engulf *Daphnia pulicaria* longer than 1.3mm. In late summer the fry were of sufficient size to then utilise the largest zooplankton available. Even so, Wong and Ward noted that the predation was always specific to *Daphnia* and not to the equally abundant copepods which would have represented the smallest prey in early summer.

At Loch Leven perch fry were regularly observed in considerable quantities around distinct features of the shoreline, such as the boathouse bay, during the autumn to spring months (Page 134). On various occasions in late 1972 and early 1973 samples of fry were captured near the boathouse for gut contents analyses (Page 25). The little perch were all in the 0+ year group and ranged in size from 4-7cms although the vast majority were under 5cms. On examination, most of the stomachs on each occasion (usually above 90 per cent) were found to be empty; rarely were any of the guts full, but in several cases the recognisable remains of planktonic crustacea were evident. In general the zooplankters which featured most regularly in gut samples were adult and pre-adult stages of *Cyclops strenuus abyssorum* and to a much lesser extent large *Daphnia* and *Diaptomus gracilis*. However, these limited samples only bear reflection of periods when loch temperatures were low and when perch fry exhibited highly localised distributions; such conditions would likely contribute to minimal feeding. The zooplankton at these times was predominantly composed of copepods, with Daphnia being particularly scarce (Fig. 31), so that the preponderance of Cyclops in gut contents is accountable. The situation is likely to be totally different during the summer months when feeding is enhanced by the warmer conditions. Presumably the developing fry are well dispersed in the open water of the loch in order to feed specifically on zooplankton (as in West Blue Lake) and the main prey is D. hyalina var lacustris which is plentiful at such times. Clearly the feeding attributes of young perch in Loch Leven deserve fuller investigation especially during summer. As regards juvenile trout at Loch Leven, Arowomo (pers. comm.) has noted the presence of both Daphnia and Cyclops in stomach contents.

In summary, predation by fish on zooplankton at Loch Leven is essentially restricted to the summer months and mainly concerns D. hyalina var lacustris. In early to mid-summer, small perch fry may effect losses of juvenile and possibly young adult Daphnia (this provides a tentative explanation for such mortalities in late June 1973, page 149 ) but in late summer (August and September) predation is likely to be greatest, with the combined planktivorous activity of adult trout and perch as well as perch fry effecting losses of large *Daphnia* and also *Bythotrephes*. Assuming that the data for 1971 in Table 14 (Thorpe, 1974) is also representative of zooplankton predation in 1972 and 1973, the heaviest predation on *Daphnia* by adult fish would coincide with maximum abundance of peaked headed forms (Fig. 14) and would tend to suppress *Daphnia* population development during the second phase of the bimodal annual cycle (Fig. 5). Maximum predation on *Bythotrephes* would be concurrent with maximum seasonal abundance (about 2 ind/51 Friedinger sample) of this predatory cladoceran (Table 11A and B). In the cooler months when *Daphnia* are scarse, the perch fry may resort to the larger copepod instars for food, in particular adult female *Cyclops strenuus abyssorum*.

During a period of intense predation, the high demand for large *Daphnia* would be expected to cause a notable lowering of the *mean* adult *Daphnia* sizes (Fig. 10) especially as time progressed. It is perhaps surprising, therefore, that during August and September of both sampling years the mean adult sizes of *Daphnia* were generally high, being consistently above 2.0mm (Fig. 10). Although other factors certainly influence the mean body-sizes (Discussion, part 2(c)), this suggests that the effects of predation by adult fish may not be as

as might be anticipated. Indeed the degree of predation at Loch Leven may vary markedly from year to year by virtue of the opportunistic nature of trout and perch feeding. In any event, to ascertain the full extent of planktivorous feeding in 1971 the data in Table 14 (Thorpe, 1974) would most certainly need to be related both to Daphnia and adult fish densities.

During the years 1966 to 1970 D. hyalina var lacustris were absent from the Loch Leven plankton so that the only zooplankton prey available to fish was Cyclops strenuus abyssorum. Walker (1970) observed that in 1969 adult female copepods were consistently less abundant than the smaller adult males and attributed this phenomenon to size-selective predation by fish, since adult female Cyclops (especially those with egg-sacs) would be the obvious prey. Walker's assumption seems reasonable because in 1972-73, when Daphnia were plentiful and thus available as the preferred prey of fish, the sex ratios of adult C. strenuus abyssorum were generally in favour of females (Fig. 25). In these latter years the presence of Daphnia relieved the predation pressure on Cyclops females and thus enhanced the reproduction potential of the copepod population. Lastly, it is suggested that during the mild winter of 1972-73 when Daphnia were notably scarce, selective predation on Cyclops females by perch fry gave rise

## 8. The zooplankton of Loch Leven, past, present and future.

Loch Leven has undergone important biological changes since the last war (Pages 4-8) and these relate particularly to zooplankton (Table 1), most notably the disappearance of *Daphnia hyalina* var *lacustris* within the years 1954-1966 and its reappearance in 1970. Such qualitative changes in the zooplankton are extremely unusual because the species composition of lake zooplankton generally remains stable over considerable periods of time. Baldi (1951) noted that the species make-up of Lake Maggiore, Italy, remained constant over a period of forty years and Tappa (1965) observed the same zooplankton species in Aziscoos Lake, Maine (U.S.A.)., as had been found twenty-five years previously. Long-term stability in plankton populations was also observed by Smyly (1968a) who recorded similar planktonic crustaceans in the lakes of the English Lake District to those found by Gurney in 1923.

Crustacean zooplankton play a fundamental role in the energy flow systems of standing waters, especially the filter-feeding herbivorous cladocera which constitute one of the chief trophic links between algae (and bacteria) and the fish that dominate the higher trophic levels (Brooks 1969). Pennak (1957) stated that, at any given time, most limnetic habitats include 2-4 species of

Cladocera and 1-3 species of Copepoda; and the Nature Conservancy, surveying twenty-one eutrophic lakes in Britain noted an average of three species of filter-feeders (Cladocera and Calanoida) and one non-filtering copepod (Walker 1970). The present zooplankton of Loch Leven (post 1970) would approximately conform to the above findings, being comprised of three species of Cladocera and two species of Copepoda, or alternatively two species of filter-feeder, two species of carnivore and one non-filtering copepod (omnivore). However, during at least 1966 to 1970 the Loch Leven zooplankton was totally devoid of all filter-feeding Cladocera resulting in the loss of a major energy transfer link. The cyclopoid dominated plankton of this latter period remains seemingly unparalled, with the possible exception of Lake Hemfjärden in Central Sweden which, according to Pejler (1965), was "remarkably poor in species, dominated by cyclopoids and *Keratella cochlearis*". This lake was heavily polluted by the city of Orebro and, when visited by Pejler, was "green and thick as spinach soup with water-blooming algae (transparency only 18 cms!)".

The extensive IBP investigations, which began in 1966, indicated that the loch was a highly unstable ecosystem exhibiting marked year-to-year variability in both the quality and quantity of its flora and fauna (Morgan and McLusky, 1974). These problematic circumstances were generally attributed to the high rate of enrichment (Morgan and McLusky, 1974), the causal linkage being that the high levels of available plant nutrients led to an overwhelming excess of phytoplankton production over *loss* (Bindloss, 1974). Studies on phytoplankton (Bailey-Watts, 1974) showed that up until 1971 (although *D. hyalina* var *lacustris* reappeared in August 1970 (Walker 1970), it was never sufficiently abundant until 1971 to have any widespread effects on the size-composition of the phytoplankton), algal grazing was rarely important, thus favouring the success of small species (this feature being generally atypical of eutrophic lakes) which were allowed to develop unimpeded into *very* dense crops. Although the effects of algal grazing in open water by *Cyclops strenuus abyssorum*, protozoa and rotifers appeared to have been minimal, the losses of phytoplankton due to chironomid larvae and duck mussels (*Anodonta anatina* (L)), operating on the benthic substrate, may have been considerable (Fig. 35). Nevertheless, by restricting light penetration during the growth season, the dense algal blooms tended to offset the developments of submerged macrophytes and benthic algae, this having further adverse repercussions on the plant-associated fauna. Furthermore, Johnson *et al.* (1974)

emphasised the problems of extracting potable water from Loch Leven for urban usage due to the super-abundance of very small algae which were difficult to remove using conventional water-treatment methods.

However, the return of Daphnia hyalina var lacustris in 1970 and with it the re-establishment of the all important trophic link (Page 277 ), were precursors to widespread improvements in the loch (Page 6), these being generally associated with changes in the size-composition of the algae (to larger species), reductions in overall phytoplankton standing crops and enhanced water clarity. Nevertheless, certain fundamental questions remain unanswered. Firstly, what factors resulted in the elimination of all cladoceran filter-feeders from the loch? Were these factors associated with the rapid rate of cultural eutrophication or perhaps with toxic pollutants or even with a fluke combination of purely natural circumstances? Secondly, what factors led to the re-establishment of D. hyalina var lacustris? At present the solutions are left entirely to speculation.

The gradual process of nutrient enrichment (or natural lake maturation) generally results in increased species diversity which in turn enhances the complexity of food webs within the ecosystem, but most prominently the effects relate to increased phytoplankton productivity. Although corresponding increases in crustacean zooplankton are to be expected these do not necessarily occur since, as Brooks (1969) pointed out, such increases may be counteracted by fish predation. Walker (1970) was curious to know whether a possible link existed between persistent phytoplankton blooms and limited numbers of individuals and species of crustacean filter-feeders. He therefore undertook several sampling trips to five lochs local to Loch Leven where eutrophication was particularly enhanced and where algal blooms were troublesome; but in all cases he found no shortage of cladoceran filter-feeders. Indeed the same observations were made by the Nature Conservancy in their surveys of twenty-one eutrophic lakes (above). Loch Leven was a highly enriched water at the turn of the century (Morgan, 1970) and as such had a long-term record of persistent phytoplankton blooms usually due to blue-green algae (Rosenberg 1937; Brook 1965; Morgan 1970); yet the filter-feeding cladocera persisted at least until 1954 (Table 1).

Brooks (1969) reviewed the effects of enrichment upon zooplankton and stated that the species composition of lake zooplankton was rarely subject to drastic modifications by eutrophication alone. Minor changes directly associated with eutrophication have nevertheless been noted, such as the substitution of *Bosmina coregoni* var *longispina* (Leydig) by the rather smaller *B. longirostris* (O.F. Müller) (Minder 1938; Deevey 1942); and it is noteworthy that comparable shifts in *Bosmina* species have apparently occurred at Loch Leven (Table 1). Brooks concluded, however, that the long-term effects of both artificial enrichment and natural maturation led to changes in the populations of planktivorous fish (from salmonids and possibly coregonids to greater abundances of cyprinids) and that this caused increases in the degree of predation upon zooplankton, leading ultimately to changes in the *size-composition* of the zooplankters. In Loch Leven the species of fish have not changed markedly (if at all) since the last war, although variations in the abundances of different age groups of both trout and perch are certainly likely to have occurred. If the decline in macrophytes and the possibly associated decline in littoral and benthic invertebrate diversity took place at Loch Leven relatively recently (i.e. within the years 1954-1966, and by all accounts this is likely (Morgan 1970, 1972, 1974)), then the fish population may have resorted primarily to zooplankton for their nutrition due to the lack of alternatives. White (pers. comm.) showed that in the totally *featureless* (i.e. no macrophytes, etc.) lagoons of Rye Mead Sewage Plant, Roydon, the coarse fish populations fed exclusively on zooplankton.

Brooks (1968, 1969) showed that when predation on zooplankton was excessive, the largest cladoceran prey species would be so severely cropped that few, if any, individuals were allowed to reach the size of maturity, resulting in the elimination of the species. Similar observations were recorded by Galbraith (1966). However, in all cases, the loss (and where predation was not so intense, the suppression) of the large cladocerans then permitted the much smaller cladoceran filter-feeders, such as *Bosmina* spp., to assume dominance in the zooplankton. It is therefore unlikely that predation alone caused the decline of the filter-feeding cladocerans at Loch Leven because the species of *Bosmina* which was last recorded in 1954 (Table 1) would have been expected to replace *D. hyalina* var *lacustris* and this was clearly not the case.

A further possibility for the changes in zooplankton composition is the undetermined effect on the loch biota of the organochlorine pesticide Dieldrin which was discharged into Loch Leven from the woollen mill at Kinross during the period 1958-64 (Page 7). Morgan and McLusky (1974) considered that this may have caused a decline in fecundity of *Daphnia* but acknowledged the fact that Dieldrin levels were probably too low to kill off the *Daphnia* directly. Walker (1970) further noted that, in the literature on toxicity, trout were known to be more susceptible to the poison than were Daphnia spp. However, 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 temperature. The complexity of the effects of the poison therefore leaves little ground on which to discount the possibility that Dieldrin caused the elimination of filter-feeders at Loch Leven. The long and short-term effects of very low concentrations of this pesticide in natural ecosystems are unknown. If, for example, the pesticide was absorbed by certain types of algae or bacteria which were favourable food species, the filter-feeding cladocera by virtue of their feeding mechanisms would inadvertently accumulate highly concentrated doses very quickly. Such an effect would have adverse repercussions on all life-stages of both Daphnia and Bosmina; but the copepod, C. strenuus abyssorum, would not be affected in the same way and would therefore be expected to persist.

In Chew Valley Lake, 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 Dieldrin was thought to be responsible for 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.

As an alternative suggestion, Loch Leven may have suffered the ill-effects of other pollutants as yet undiscovered in the loch, such as heavy metals or detergents. However, it is perhaps most significant that in cases of recognised poisoning of still-waters or where the habitat concerned has undergone drastic changes which are not clearly understood (as in Lake Hemfjärden, Chew Valley Lake and Loch Leven), the filter-feeding cladocera tend to succumb to the effects and the cyclopoid copepods tend to withstand them. A further noteworthy example is provided by Woodward (Walker 1970) who was concerned with the eradication of unwanted pike in Loch Kinardochy, Perthshire, by application of rotenone (derris root extract). He recalled that after a virtual elimination of the crustacean zooplankton following the poisoning, there was a bloom of rotifers together with Cyclops strenuus.

Daphnia reappeared much later and after about four years the zooplankton resumed its former state, with Diaptomus and Bosmina occurring in large numbers and with Cyclops and Daphnia in lesser numbers. Woodward was certain that C. strenuus dominated the plankton in the years immediately following the poisoning.

However, certain adverse but none-the-less natural events at Loch Leven may have led to the paucity of filter-feeders. For example, the overwintering open-water populations of both Daphnia and Bosmina may not have survived the exceptionally severe winter of 1962-63. Even if these species had persisted in the loch by means of latent ephippial eggs, they may not have been able to maintain themselves thereafter due to apparently unfavourable food conditions which prevailed throughout 1963. Morgan (1970) recalled that after the extended period of ice-cover in 1963, a notable bloom of blue-green algae occurred (17,000 filaments per ml)and persisted as such for fourteen months. Interestingly, the loch continued to suffer prolonged blue-green algal blooms in the years immediately following (Morgan 1970), suggesting that the years 1962-63 were important landmarks in the biological history of Loch Leven. Indeed, the changes in zooplankton species composition may be a by-product of the other peculiar manifestations at Loch Leven.

Kinardochy, Chew Valley Lake and also Loch Leven, the zooplankton eventually returned to "normality" with filter-feeders being once again abundant. How *Daphnia hyalina* var *lacustris* effected its re-establishment in Loch Leven is again a mystery. Walker (pers. comm.) noted the existence of a small lochan containing *D. hyalina* var *lacustris* which was linked to Loch Leven via the North Quiech (Fig. 1) and suggested that under severe flood conditions, overspill from this body of water could have provided sufficient *Daphnia* to propagate a viable population. Alternatively, recolonisation could have been implemented by wind-blown ephippia from say GartMorn Dam, a reservoir about ten miles away from the loch which also contains *D. hyalina* var *lacustris*. Winds are strong and persistent in Central Scotland so that this mode of dispersal is plausible. As a further possibility, migrating water-fowl could have transported ephippia from other local waters on their bodies or by depositing them through their faeces. Even so, it is surprising that recolonisation by *Daphnia* did not occur earlier because the above conditions surely must have occurred before 1970. Walker (1970) maintained laboratory cultures of *Daphnia* sp. using water obtained from Loch Leven during 1969 and this implies that water quality could not have been detrimental to *Daphnia* survival at that time. Walker in fact suggested that artificial introduction of several species of Daphnia from other nearby lochs should be attempted; but unfortunately this was not done. Small scale experiments along these lines using stock-ponds would certainly be worth attempting for future reference. It remains to be seen, however, whether species of Bosmina (or indeed other species of Daphnia) will naturally re-establish themselves in Loch Leven.

Fuller investigations into the causal agents responsible for all the unusual biological changes at Loch Leven are certainly to be recommended. The resultant information could prove very beneficial to the future management of still-waters, especially those which are exploited for urban tap-water supplies. Further research on the zooplankton of Loch Leven could also be recommended: As yet little is known about the rotifer populations or the food requirements and trophic importance of Cyclops strenuus abyssorum. It should be emphasised, however, that the data presented in this thesis is potentially open to fuller exploitation and that certain aspects require future desk-analysis. For example, correlation coefficients could be computed for all possible inter-actions between recorded population parameters and a selected range of environmental variables (as in George and Edwards 1974); energy budgets could be derived for the two co-dominant species (e.g. Richman, 1958); or the role of zooplankton in nutrient cycles could be evaluated using appropriate conversion data as quoted in Baudouin and Ravera (1972) and Vijverberg and Frank (1976). Future application of this data would certainly be desirable not only to provide co-ordination with the wealth of related information already collected during the IBP investigations but also because the biotic peculiarities of Loch Leven has rendered a unique and valuable opportunity to study the ecological role of zooplankton with (the present study) and without (Walker 1970) the presence of a dominant filter-feeding cladoceran.

Baudouin, M.F. & Ravera, O. (1972). Weight, size and chemical composition of some freshwater zooplankters : Daphnia hyalina Leydig. Limnol. Oceanogr. 4, 645-649.

Bays, L.R. (1969). Pesticide pollution and the effects on the biota of Chew Valley Lake. Wat. Treat. Exam., 18, 295-326

Berg, K. (1931). Studies on the genus Daphnia O.F. Muller with especial reference to the mode of reproduction. Vidensk. Meddr. dansk Naturh. Foren., 92, 1-222.

Berg, K. & Nygaard, G. (1929). Studies on the plankton in the lake of Frederiksborg Castle. Mem. de l'Acad. Roy. des Sci. et des Lett. de Danemark, Sec. des Sci., ser. 91, 223-316. In : Hutchinson, 1967.

Bernatowicz, S. (1953). Czerapacz do ilosciowego polowu planktonu. Wszechswiat 127-128. In : Edmondson and Winberg, 1971.

Bhajan, W.R. & Hynes, H.B.N. (1972). Experimental study on the ecology of Bosmina longirostris (O.F. Muller) (Cladocera). Crustaceana, 23, 133-140.

Bindloss, M.E. (1974). Phytoplankton production at Loch Leven, Kinross. Proc. Roy. Soc. Edinb., B, 74, 157-181.

Birge, E.A. (1898). Plankton studies on Lake Mendota. II. The crustacea of the plankton from July 1894 to December 1896. Trans. Wis. Acad. Sci. Arts. Lett., 11, 274-451. In : Hutchinson, 1967.

——— (1918) Water-fleas (Cladocera) In : Ward and Whipple "Freshwater Biology " New York.

Borecky, C.W. (1956). Population density of the limnetic Cladocera of Pymatuning Reservoir. Ecology, 37, 719-727.

Brook, A.J. (1965). Planktonic algae as indicators of lake types with special reference to the Desmidiaceae. Limnol. Oceanogr., 10, 403-411.

Brook, A.J. & Woodward, W.B. (1956). Some observations on the effects of water inflow and outflow on the plankton of small lakes. J. Anim. Ecol., 25, 22-35.

Brooks, J.L. (1965). Predation and relative helmet size in cyclomorphic Daphnia. Proc. Natl. Acad. Sci., 53, 119-126.

——— (1966). Cladocera . In : W.T. Edmondson (Ed.) "Freshwater Biology" 1248 pages John Wiley & sons. New York, London.

——— (1968). The effects of prey size selection by lake planktivores. Syst. Zool., 17, 3, 272-291.

Brooks, J.L. (1969). Eutrophication and changes in the composition of the zooplankton. In :"Eutrophication, causes, consequences, correctives." National Academy of Sciences. Washington, D.C.

Bryant, V.M.T. & Laybourn, J.E.M. (1974). The vertical distribution of Ciliophora and Nematoda in the sediments of Loch Leven, Kinross. Proc. Roy. Soc. Edinb., B, 74, 265-273.

Burckhardt, G. (1910). Hypothesen und Beobachtungen uber die Bedeutung der vertikalen Planktonwandrung. Int. Revue ges Hydrobiol. Hydrogr., 3, 156-172, 335-338.

Burgis, M.J. (1971). The ecology and production of copepods, particularly Thermocyclops hyalinus in the tropical Lake George, Uganda. Freshwat. Biol., 1, 169-192.

Burgis, M.J. & Walker, A.F. (1972). A preliminary comparison of the zooplankton in a tropical and a temperate lake (Lake George, Uganda and Loch Leven, Scotland). Verh. Int. Verein. Theor. Angew. Limnol., 18, 647-655.

Burns, C.W. (1969). Particle size and sedimentation in the feeding behaviour of two species of Daphnia. Limnol. Oceanogr. 14, 392-402.

Burns, C.W. & Rigler, F.H. (1967). Comparisons of filtering rates of Daphnia in lakewater and in suspensions of yeast. Limnol. Oceanogr. 12, 492-502.

Cannon, H.G. (1933). On the feeding mechanism of the Branchiopoda. Phil. Trans. R. Soc., 222B: 267-352.

Chandler, D.C. (1939). Plankton entering the Huron River from Portage and Base Line Lake, Michigan. Trans. Am. microsc. Soc., 58, 24-41.

Chapman, M.A. (1965). Ecological studies on the zooplankton of Loch Lomond. Ph.D. thesis, Univ. Glasgow.

——— (1969). The bionomics of Diaptomus gracilis Sars (Copepoda, Calanoida) in Loch Lomond, Scotland. J. Anim. Ecol. 38, 257-284.

Clarke, E.B. (1942). A modification of the Juday plankton trap. Spec. Publ. No. 8, Limnol. Soc. Amer. (4 pages).

Clarke, G.L. & Bumpus, D.F. (1950). The plankton sampler - an instrument for quantitative plankton investigations. Spec. Publ. Amer. Soc. Limn. Oceanogr. Revised 1950, 8 pages.

reference to the vertical migration of the zooplankton. Hydrobiologia, 32, 97-130.

Duncan, A., *et al.* (1970). The measurements of respiratory rates under field and laboratory conditions during an ecological study on zooplankton. Pol. Arch. Hydrobiol., 17, 149-160.

Edmondson, W.T. (1955). Seasonal life-history of *Daphnia* in an Arctic Lake. Ecology, 36, 439-455.

——— (1960). Reproductive rates of rotifers in natural populations. Mem. 1st.ital. Idrobiol., 12, 21-77.

——— (1964). The rate of egg production by rotifers and copepods as controlled by food and temperature. Verh. Int. Verein. Limnol., 15, 673-675.

Edmondson, W.T. & Winberg, G.G. (1971). A manual on methods for the assessment of secondary productivity in freshwaters. IBP Handbook no. 17, Blackwell Scientific Publications, Oxford and Edinburgh.

Elbourn, C.A. (1966a) The life-cycle of *Cyclops strenuus strenuus* Fischer in a small pond. J. Anim. Ecol., 35, 333-347.

Verein. Limnol., 13, 2, 961-973.

Fleminger, A. & Clutter, R.I. (1965). Avoidance of towed nets by zooplankton. Limnol. Oceanogr., 10, 96-104.

Fraser, J.H. (1968). The history of plankton sampling. In : "Zooplankton Sampling". Monographs of Oceanographic Methodology, No. 2, Unesco, 174 pages.

Fryer, G. (1954). Contributions to our knowledge of the biology and systematics of the freshwater Copepoda. Schweiz. Z. Hydrol., 16, 64-77.

——— (1957a). The feeding mechanisms of some freshwater cyclopoid copepods. Proc. zool. Soc. Lond., 129, 1, 1-25.

——— (1957b). The food of some freshwater cyclopoid copepods and its ecological significance. J. Anim. Ecol., 26, 263-286.

Galbraith, M.G. (1966). Size-selective predation on Daphnia by rainbow trout and yellow perch. Trans. Amer. Fish Soc., 96, 1-10.

George, D.G. (1973). Diapause in Cyclops vicinus. Oikos, 24, 136-142.

George, D.G. (1976). Life cycle and production of *Cyclops vicinus* in a shallow eutrophic reservoir. Oikos, 27, 101-110.

George, D.G. & Edwards, R.W. (1973). *Daphnia* distribution within Langmuir circulations. Limnol. Oceanogr., 18, 5, 798-800.

——— (1974). Population dynamics and production of *Daphnia hyalina* in a eutrophic reservoir. Freshwat. Biol., 2, 107-130.

Gliwicz, Z.M. (1969a). Studies on the feeding of pelagic zooplankton in lakes with varying trophy. Ekol. Pol. A, 17, 663-708.

——— (1969b). The food sources of lake zooplankton. Ekol. Pol. B, 15, 205- 223.

——— (1969c). The share of algae, bacteria and trypton in the food of the pelagic zooplankton of lakes with various trophic characteristics. Bull. Acad. Pol. Sci., Ser. Sci biol., 17, 159-165.

——— (1970). Calculation of food ration of zooplankton community as an example of using laboratory data for field conditions. Pol. Arch. Hydrobiol., 17, 169-175.

Gophen, M. (1976). Temperature dependence of food intake, ammonia excretion and respiration in *Ceriodaphnia* *reticulata* (Jurine) (Lake Kinneret, Israel). Freshwat. Biol., *6*, 451-455.

Graham, T.R. (1970). The zooplankton of Lough Neagh, 1968-69. The Irish Naturalists' Journal, *16*, 9, 265-271.

Green, J. (1954). Size and reproduction in *Daphnia magna.* Proc. zool. Soc. Lond., *124*, 535-545.

——— (1956). Growth, size and reproduction in *Daphnia*. Proc. zool. Soc. Lond., *126*, 173-204.

——— (1966). Seasonal variation in egg production by Cladocera. J. Anim. Ecol., *35*, 77-104.

Greze, V.V. & Baldina, E.P. (1964). Dinamika populacii i godovaya produktsiya *Acartia clausi* Giesbr. i. *Centropages kroyeri* Giesbr. v neriticheskoy zone Chernogo Morya. Tr. Sevastop. Biol. Stancii., *17*, 249-261. In : Edmondson and Winberg (1971).

Gurney, R. (1923). The crustacean plankton of the English Lake District, J. Linn. Soc., *35*, 411-447.

——— (1931-33). British Freshwater Copepoda. Vols. I-III, Ray. Soc. Lond.

Hall, D.J. (1962). An experimental approach to the dynamics of a natural population of *Daphnia galeata*

Kurenkov, I.I. (1973). The biological cycles of pelagic copepods in the lakes of Kamchatka. Hydrobiologia, 43, 39-44.

Langford, R.R. (1938). Diurnal and seasonal changes in the distribution of limnetic crustacea of Lake Nipissing, Ontario. Univ. Toronto Stud. biol., ser. No. 45 (Publs Ontario Fish. Lab. 56), 1-42.

——— (1952). Methods of plankton collection and a description of a new sampler. J. Fish Res. Bd. Can., 10, 238-252.

Lefevre, M. (1942). L'ulitisation des algues d'eau douce par les Cladoceres. Bull. biol. Fr. Belg., 76, 250-276.

Lewis, B.G. (1971). Copepod development. Laboratory observations on Cyclops abyssorum Sars. C.E.R.L. RD/L/M 312 187-191.

Lewis, B.G. et al. (1971). Laboratory culture of Cyclops abyssorum. Crustaceana, 21, 2, 176-182.

Lovegrove, T. (1966). In : Some contemporary studies in marine science (ed. H. Barnes), 429 pages. George Allen and Unwin Ltd.

MacArthur, J.W. & Baillie, W.H.T. (1929). Metabolic activity and duration of life. i. influence of temperature

10, 528-538.

McLusky, D.S. & McFarlane, A. (1974). The energy requirements of certain larval chironomic populations in Loch Leven, Kinross. Proc. Roy. Soc. Edinb., B, 74, 259-264.

McMahon, J.W. & Rigler, F.H. (1963). Mechanisms regulating the feeding rate of Daphnia magna Straus. Can. J. Zool., 41, 321-332.

McNaught, D.C. & Hasler, A.D. (1961). Surface schooling and feeding behaviour in the White Bass Roccus chrysops (Rafinesque), in Lake Mendota. Limnol. Oceanogr., 6, 53-60.

McQueen, D.J. (1969). Reductions of zooplankton standing stocks by predaceous Cyclops bicuspidatus thomasi in Marion Lake, British Columbia. J. Fish Res. Bd Can., 26, 1605-1618.

Michael, R.G. (1962). Seasonal events in a natural population of the cladoceran Ceriodaphnia cornuta Sars and observations on its life cycle. J. Zool. Soc. India., 14, 211-218.

Minder, L. (1938). Der Zurichsee als Eutrophierungsphanomen. Geol. Meere Binnengewasser, 2, 284-299.

Monakov, A.V. (1958). The life-cycle of Mesocyclops leuckartii Claus (Copepoda, Cyclopoida). C.R. Acad. Sci., U.R.S.S., 120, 419-421.

in Lake Mendota. J. mar. Res. 12, 157-172.

Ravera, O. (1954). La struttura demografica dei Copepodi del Lago Maggiore. Mem. Ist ital. Idrobiol. de Marchi, 5, 255-279.

——— (1955). Seasonal variation of the reproductive rate in pelagic copepods of Lake Maggiore. Verh. int. Ver. theor. angew. Limnol., 12, 436-446.

Ravera, O. & Tonolli, V. (1956). Body size and number of eggs in diaptomids, as related to water renewal in mountain lakes. Limnol. Oceanogr., 1, 118-122.

Richman, S. (1958). The transformation of energy by *Daphnia pulex*. Ecol. Monogr., 28, 275-291.

Ricker, W.G. (1937). Statistical treatment of sampling processes useful in the enumeration of plankton organisms. Arch. Hydrobiol., 31, 68-84.

Rigler, F.H. (1961). The relation between concentration of food and feeding rate of *Daphnia magna* Straus. Can. J. Zool., 39, 857-868.

Rodhe, W. (1941). Zur Verbesserung der Quantitativen Planktometodik nebst profilen des

Scott, T. (1898). The invertebrate fauna of the inland waters of Scotland, a report on special investigation. 17th Rep. Fishery Bd Scotl. III, 161-165.

Scourfield, D.J. & Harding, J.P. (1958). A key to the British species of freshwater cladocera with notes on their ecology. 2nd edn. Scient. Publs. Freshwat. Biol. Ass., 5.

Slobodkin, L.B. (1954). Population dynamics in Daphnia obtusa Kutz. Ecol. Monogr., 24, 69-88.

Smith, I.R. (1974). The structure and physical environment of Loch Leven, Scotland. Proc. Roy. Soc. Edinb., B, 74, 81-100.

Smyly, W.J.P. (1961). The life-cycle of the freshwater copepod Cyclops leuckarti Claus in Esthwaite Water. J. Anim. Ecol., 30, 153-171.

——— (1968a). Observations on the planktonic and profundal crustacea of the lakes of the English Lake District. J. Anim. Ecol., 37, 693-708.

——— (1968b). Some observations on the effect of sampling technique under different conditions on numbers of some freshwater planktonic Entomostraca and Rotifera caught by a water-bottle. J. nat. Hist., 2, 569-575.

Smyly, W.J.P. (1968c). Number of eggs and body-size in the freshwater copepod Diaptomus gracilis Sars in the English Lake District. Oikos, 2, 323-338.

——— (1970). Observations on rate of development, longevity and fecundity of Acanthocyclops viridis (Jurine). (Copepoda, Cyclopoida) in relation to type of prey. Crustaceana, 18, 21-36.

——— (1973a). Bionomics of Cyclops strenuus abyssorum Sar. (Copepoda, Cyclopoida). Oecologia (Berl.), 11, 163-186.

——— (1973b). Clutch-size in the freshwater cyclopoid copepod Cyclops strenuus abyssorum Sars in relation to thoracic volume and food. J. nat. Hist., 7, 545-549.

——— (1975). Changes in body-length, and in shape of the furcal ramus, of a freshwater cyclopoid copepod. Zool. J. Linn. Soc., 54, 137-144.

Smyly, W.J.P. & Collins, V.G. (1975). The influence of microbial food sources and aeration on the growth of Ceriodaphnia quadrangula (O.F. Muller)(Crustacea, Cladocera) under experimental conditions. Freshwat. Biol., 5, 251-256.

Wright, J.C. (1965). The population dynamics and production of *Daphnia* in Canyon Ferry reservoir, Montana. Limnol. Oceanogr., *10*, 583-590.

Wong, B. & Ward, F.J. (1972). Size selection of *Daphnia pulicaria* by Yellow Perch (*Perca flavescens*) fry in the West Blue Lake, Manitoba. J. Fish. Bd. Can., *29*, 1761-1764.

Wood, T.R. *et al.* (1939). Growth and reproductive characteristics of *Daphnia longispina*. Carnegie Inst. Washington, Pub. 513, Paper No. 39, Dept. Genetics, 182-200.

Worthington, E.B. (1931). Vertical movements of freshwater macroplankton. Int. Rev. ges. Hydrobiol. Hydrogr., *25*, 394-436.

# Appendix (i) - data for Figure 2.

asonal changes in mean water temperature at Loch Leven
ring 1972-73.

te that only the overall mean loch temperatures are
esented graphically in Figure 2.

| | Temperature °C | | |
|---|---|---|---|
| mpling Dates | Overall Mean | Mean Surface | Mean Bottom |
| 12/10/71 | 12.0 | 12.2 | 11.9 |
| 2/11 | 9.8 | 9.8 | 9.8 |
| 9/11 | 5.9 | 5.9 | 5.9 |
| 26/11 | 3.5 | 3.6 | 3.5 |
| 7/12 | 4.1 | 4.2 | 4.1 |
| 25/3/72 | 7.2 | 7.4 | 7.0 |
| 12/4 | 8.1 | 8.3 | 8.0 |
| 27/4 | 10.8 | 10.9 | 10.8 |
| 15/5 | 10.5 | 10.6 | 10.5 |
| 13/6 | 12.5 | 12.6 | 12.4 |
| 29/6 | 13.8 | 14.1 | 13.5 |
| 15/7 | 15.2 | 15.9 | 14.4 |
| 29/7 | 17.3 | 17.3 | 17.4 |
| 12/8 | 18.1 | 18.3 | 17.9 |
| 28/8 | 15.7 | 15.8 | 15.6 |
| 10/9 | 13.2 | 13.2 | 13.2 |
| 23/9 | 12.8 | 13.0 | 12.6 |
| 7/10 | 11.5 | 11.7 | 11.4 |
| 21/10 | 8.6 | 8.6 | 8.6 |
| 14/11 | 4.0 | 4.0 | 4.1 |
| 16/12 | 3.3 | 3.2 | 3.4 |
| 13/1/73 | 3.5 | 3.5 | 3.5 |
| 24/2 | 2.8 | 3.0 | 2.7 |

contd./...

Appendix (i) - contd.

| | Temperature °C | | |
|---|---|---|---|
| Sampling Dates | Overall Mean | Mean Surface | Mean Bottom |
| 29/3/73 | 6.7 | 6.7 | 6.7 |
| 10/4 | 8.2 | 8.2 | 8.1 |
| 15/4 | 8.5 | 8.4 | 8.7 |
| 29/4 | 9.1 | 9.2 | 9.0 |
| 7/5 | 9.6 | 9.7 | 9.4 |
| 22/5 | 9.8 | 9.7 | 9.8 |
| 26/5 | 11.2 | 11.4 | 11.1 |
| 6/6 | 14.3 | 14.6 | 14.0 |
| 17/6 | 14.5 | 14.8 | 14.2 |
| 21/6 | 14.7 | 15.0 | 14.5 |
| 4/7 | 17.2 | 17.6 | 16.8 |
| 8/7 | 17.0 | 17.4 | 16.6 |
| 22/7 | 16.5 | 16.8 | 16.2 |
| 14/8 | 17.9 | 19.2 | 16.3 |
| 4/9 | 14.9 | 14.9 | 14.9 |
| 16/9 | 14.6 | 14.7 | 14.6 |
| 22/9 | 13.3 | 13.4 | 13.2 |
| 7/10 | 11.2 | 11.3 | 11.0 |
| 15/10 | 8.3 | 8.4 | 8.2 |
| 28/10 | 7.4 | 7.5 | 7.4 |
| 7/11 | 5.9 | 5.9 | 5.9 |
| 17/11 | 3.0 | 3.1 | 3.0 |
| 21/11 | 3.6 | 3.6 | 3.6 |
| 18/12 | 0.5 | 0.3 | 0.8 |
| 6/1/74 | 4.0 | 4.1 | 3.9 |
| 20/1 | 2.0 | 2.1 | 2.0 |

## Appendix (ii) - data for Figure 3

Seasonal changes in water temperature at the surface and at the bottom of the north deeps (site E) of Loch Leven during 1972-73.

| | Temperature °C | |
|---|---|---|
| Sampling Dates | Surface | Bottom (20m) |
| 25/3/72 | 7.6 | 6.6 |
| 12/4 | 8.4 | 8.1 |
| 27/4 | 10.9 | 10.8 |
| 15/5 | 10.7 | 10.4 |
| 13/6 | 12.8 | 11.6 |
| 29/6 | 14.4 | 13.2 |
| 15/7 | 16.0 | 12.0 |
| 29/7 | 14.7 | 14.0 |
| 12/8 | 18.6 | 18.0 |
| 28/8 | 16.2 | 15.8 |
| 10/9 | 13.8 | 13.8 |
| 23/9 | 13.1 | 12.8 |
| 07/10 | 11.9 | 11.1 |
| 21/10 | 9.3 | 9.1 |
| 14/11 | 4.6 | 4.6 |
| 16/12 | 3.4 | 3.8 |
| 13/1/73 | 3.4 | 3.5 |
| 24/2 | 2.7 | 2.4 |
| 10/4 | 8.3 | 8.1 |
| 15/4 | 9.2 | 8.1 |
| 29/4 | 9.4 | 9.0 |
| 07/5 | 10.8 | 10.2 |
| 22/5 | 10.4 | 9.8 |
| 26/5 | 11.4 | 11.1 |
| 06/6 | 16.5 | 12.2 |
| 17/6 | 14.8 | 13.1 |
| 21/6 | 15.5 | 13.6 |
| 04/7 | 17.7 | 14.9 |
| 08/7 | 17.5 | 14.4 |
| 22/7 | 16.8 | 16.4 |
| 14/8 | 19.0 | 15.4 |
| 16/9 | 14.6 | 14.4 |
| 22/9 | 13.9 | 13.5 |
| 07/10 | 11.2 | 10.6 |
| 28/10 | 7.9 | 7.6 |
| 17/11 | 3.5 | 3.2 |
| 06/1/74 | 4.1 | 3.9 |

## Appendix (iii) - data for Figure 4

Seasonal variations in water transparency at Loch Leven during 1973.

| Sampling dates | Depth of Secchi disc visibility cms. |
|---|---|
| 13/1/73 | 204 |
| 04/2 | 184 |
| 24/2 | 164 |
| 17/3 | 149 |
| 24/3 | 119 |
| 29/3 | 101 |
| 10/4 | 96 |
| 15/4 | 90 |
| 29/4 | 72 |
| 07/5 | 68 |
| 14/5 | 62 |
| 22/5 | 61 |
| 24/5 | 62 |
| 26/5 | 65 |
| 06/6 | 65 |
| 17/6 | 75 |
| 21/6 | 103 |
| 23/6 | 102 |
| 04/7 | 99 |
| 08/7 | 102 |
| 22/7 | 103 |
| 06/8 | 183 |
| 14/8 | 215 |
| 01/9 | 203 |
| 04/9 | 197 |
| 12/9 | 273 |
| 16/9 | 120 |
| 22/9 | 220 |
| 07/10 | 145 |
| 15/10 | 187 |
| 28/10 | 147 |
| 17/11 | 156 |
| 18/12 | 103 |
| 06/1/74 | 92 |
| 20/1 | 97 |

## Appendix (iv) - data for Figures 5 and 6

Figure 5 : Seasonal changes in the numerical standing crop of *Daphnia hyalina* var *lacustris* from Loch Leven during 1972-73. (See column marked total numbers per litre.)

Figure 6 : Seasonal changes in the mean egg stock and in the mean standing crop of the four size-classes of *D. hyalina* var *lacustris* from Loch Leven during 1972-73. (For mean egg stock per litre see Appendix (vi).)

Also included is the number of sites visited and the number of Friedinger samples collected on each sampling date.

| | | Numbers per litre | | | | |
|---|---|---|---|---|---|---|
| Sampling Dates | No.of sites/ No. of samples | <1.0mm | 1.0-1.39mm | 1.4-1.99m | <2.0mm | Total |
| 29/9/71 | 1/10 | - | - | - | - | 9.10 |
| 12/10 | 1/10 | - | - | - | - | 4.83 |
| 07/12 | 1/10 | - | - | - | - | 2.62 |
| 17/2/72 | 1/10 | 0.27 | 0.27 | 0.4 | 0.21 | 1.15 |
| 25/3 | 6/48 | 1.02 | 1.02 | 1.28 | 0.42 | 3.74 |
| 12/4 | 6/48 | 1.03 | 0.64 | 1.34 | 0.53 | 3.54 |
| 27/4 | 6/48 | 3.81 | 3.83 | 3.33 | 0.84 | 11.80 |
| 15/5 | 6/48 | 1.03 | 14.47 | 24.89 | 7.80 | 48.18 |
| 01/6 | 6/48 | 26.15 | 22.79 | 21.46 | 7.79 | 78.2 |
| 13/6 | 6/48 | 16.67 | 32.08 | 14.93 | 0.72 | 64.4 |
| 29/6 | 6/50 | 7.11 | 5.89 | 9.63 | 3.28 | 25.91 |
| 15/7 | 6/48 | 4.36 | 4.73 | 3.38 | 0.77 | 13.24 |
| 29/7 | 6/48 | 5.19 | 8.24 | 8.21 | 2.10 | 23.74 |
| 12/8 | 6/48 | 1.60 | 4.15 | 17.02 | 6.73 | 29.50 |
| 28/8 | 6/48 | 2.28 | 3.56 | 3.76 | 2.35 | 11.94 |
| 10/9 | 6/48 | 6.37 | 5.23 | 3.41 | 2.16 | 17.16 |
| 23/9 | 6/48 | 9.37 | 0.57 | 0.55 | 0.98 | 11.46 |
| 07/10 | 6/48 | 3.04 | 1.65 | 2.53 | 1.77 | 8.99 |
| 21/10 | 6/48 | 1.55 | 1.49 | 2.80 | 1.37 | 7.21 |
| 14/11 | 6/48 | 0.55 | 0.28 | 2.03 | 1.38 | 4.24 |
| 16/12 | 6/48 | - | - | 0.45 | 0.54 | 0.99 |
| 13/1/73 | 3/28 | - | - | 0.22 | 0.38 | 0.60 |
| 24/2 | 3/28 | - | 0.01 | 0.01 | 0.01 | 0.03 |
| 29/3 | 3/18 | - | - | 0.04 | - | 0.04 |
| 10/4 | 3/28 | 0.03 | 0.02 | - | 0.01 | 0.06 |
| 15/4 | 3/28 | 0.01 | 0.01 | 0.01 | 0.02 | 0.05 |
| 29/4 | 3/28 | 0.08 | 0.11 | 0.21 | 0.07 | 0.47 |

contd./....

Appendix (iv) - contd.

| Sampling Dates | No. of sites/ No. of Samples | Numbers per litre | | | | |
|---|---|---|---|---|---|---|
| | | <1.0mm | 1.0-1.39mm | 1.4-1.99m | <2.0mm | Total |
| 07/5/73 | 3/28 | 0.10 | 0.01 | 0.14 | 0.05 | 0.30 |
| 22/5 | 3/28 | 0.71 | 0.24 | 0.18 | 0.10 | 1.23 |
| 26/5 | 3/28 | 1.11 | 0.61 | 0.50 | 0.57 | 2.79 |
| 06/6 | 3/28 | 2.06 | 1.67 | 1.29 | 0.90 | 5.92 |
| 17/6 | 3/28 | 25.47 | 19.82 | 14.21 | 2.37 | 61.87 |
| 21/6 | 3/28 | 72.79 | 37.32 | 32.97 | 8.09 | 151.17 |
| 04/7 | 3/28 | 4.33 | 10.34 | 16.72 | 3.23 | 34.62 |
| 08/7 | 3/28 | 0.36 | 1.45 | 14.15 | 4.72 | 20.68 |
| 22/7 | 3/28 | 4.24 | 1.25 | 6.07 | 1.00 | 12.56 |
| 14/8 | 3/28 | 17.42 | 2.35 | 2.08 | 3.46 | 25.31 |
| 04/9 | 1/6 | 1.73 | 6.85 | 6.42 | 21.40 | 36.40 |
| 16/9 | 3/28 | 2.51 | 3.46 | 7.81 | 14.80 | 28.58 |
| 22/9 | 3/28 | 0.86 | 1.50 | 1.55 | 1.25 | 5.16 |
| 07/10 | 3/28 | 3.40 | 0.98 | 0.92 | 0.85 | 6.15 |
| 28/10 | 3/28 | 4.21 | 0.44 | 0.81 | 0.89 | 6.35 |
| 17/11 | 3/28 | 2.79 | 0.26 | 0.83 | 1.19 | 5.07 |
| 18/12 | 1/6 | 1.35 | - | 0.38 | 0.37 | 2.10 |
| 06/1/74 | 3/28 | 0.99 | 0.56 | 1.54 | 4.34 | 7.43 |
| 20/1 | 3/28 | 0.73 | - | 0.30 | 1.15 | 2.18 |

When total population numbers were exceptionally low, i.e. <1 ind/l during the period 16/12/72 to 7/5/73, the size-class frequency analysis was carried out using net samples as opposed to Friedinger samples, the data being then calculated to appropriate population numbers as obtained from Friedinger sample analysis.

## Appendix (v) - data for Figures 7 and 8.

Figure 7 : Seasonal changes in the mean egg stock and in the mean standing crop of adults and juveniles comprising the D. hyalina var lacustris population from Loch Leven during 1972-73.

For mean egg stock per litre see Appendix (vi).

Note that the numbers of adults and juveniles were calculated from Appendix (iv) :

Adults (size >1.4mm) = 1.4 - 1.99mm + >2.0mm
Juveniles (size <1.39mm) = <1.0mm + 1.0 - 1.39mm

Figure 8 : Seasonal variations in the proportions of adults and juveniles comprising the D. hyalina var lacustris population of Loch Leven during 1972-73. (% adults = 100 - % juveniles)

| | Numbers per litre | | |
|---|---|---|---|
| Sampling Dates | Adults | Juveniles | % Juveniles |
| 29/9/71 | 3.26 | 5.85 | 64.3 |
| 12/10 | 2.12 | 2.70 | 56.0 |
| 07/12 | 1.07 | 1.55 | 59.2 |
| 17/2/72 | 0.61 | 0.54 | 47.0 |
| 25/3 | 1.70 | 2.04 | 54.5 |
| 12/4 | 1.87 | 1.67 | 47.2 |
| 27/4 | 4.17 | 7.64 | 64.7 |
| 15/5 | 32.69 | 15.5 | 32.2 |
| 01/6 | 29.25 | 48.94 | 62.6 |
| 13/6 | 15.65 | 48.75 | 75.7 |
| 29/6 | 12.91 | 13.00 | 50.2 |
| 15/7 | 4.15 | 9.09 | 68.7 |
| 29/7 | 10.31 | 13.43 | 56.6 |
| 12/8 | 23.75 | 5.75 | 19.5 |
| 28/8 | 6.11 | 5.84 | 48.9 |
| 10/9 | 5.57 | 11.60 | 67.5 |
| 23/9 | 1.53 | 9.94 | 86.7 |
| 07/10 | 4.30 | 4.69 | 52.2 |
| 21/10 | 4.17 | 3.04 | 42.2 |
| 14/11 | 3.41 | 0.83 | 19.6 |
| 16/12 | 0.99 | - | 0 |
| 13/1/73 | 0.60 | - | 0 |
| 24/2 | 0.03 | 0.01 | 30.0 |
| 29/3 | 0.04 | - | 0 |

contd./....

## Appendix (v) - contd.

| | Numbers per litre | | |
|---|---|---|---|
| Sampling Dates | Adults | Juveniles | % Juveniles |
| 10/4/73 | 0.01 | 0.06 | 95.3 |
| 15/4 | 0.03 | 0.03 | 45.8 |
| 29/4 | 0.28 | 0.02 | 4.1 |
| 07/5/73 | 0.19 | 0.11 | 36.7 |
| 22/5 | 0.28 | 0.95 | 77.2 |
| 26/5 | 1.07 | 1.72 | 61.6 |
| 06/6 | 2.19 | 3.73 | 63.0 |
| 17/6 | 16.58 | 45.29 | 73.2 |
| 21/6 | 41.06 | 110.11 | 72.8 |
| 04/7 | 19.95 | 14.67 | 43.4 |
| 08/7 | 18.87 | 1.81 | 8.7 |
| 22/7 | 7.07 | 5.49 | 43.7 |
| 14/8 | 5.54 | 19.77 | 78.1 |
| 04/9 | 27.82 | 8.58 | 23.6 |
| 16/9 | 22.61 | 5.97 | 20.9 |
| 22/9 | 2.80 | 2.36 | 45.7 |
| 07/10 | 1.77 | 4.38 | 71.2 |
| 28/10 | 1.70 | 4.65 | 73.2 |
| 17/11 | 2.02 | 3.05 | 60.2 |
| 18/12 | 0.75 | 1.35 | 64.3 |
| 06/1/74 | 5.88 | 1.55 | 20.9 |
| 20/1 | 1.45 | 0.73 | 33.5 |

*Daphnia* collected in Friedinger samples prior to 17/2/72 were only size-analysed into adults (size >1.4mm) and juveniles (size >1.39mm) and not into the four size classes.

# Appendix (vi) - data for Figure 9

The breeding parameters of the D. hyalina var lacustris population of Loch Leven during 1972-73.

For mean brood-size data see Appendix (vii).

| Sampling Dates | % gravid | gravid individuals numbers per litre | egg stock per litre |
|---|---|---|---|
| 17/2/72 | 41 | 0.25 | 1.08 |
| 25/3 | 46 | 0.78 | 3.99 |
| 12/4 | 68 | 1.27 | 6.67 |
| 27/4 | 52 | 2.17 | 23.24 |
| 15/5 | 39 | 12.75 | 24.10 |
| 01/6 | 29 | 8.48 | 22.13 |
| 13/6 | 38 | 5.95 | 10.71 |
| 29/6 | 55 | 7.10 | 16.33 |
| 15/7 | 42 | 1.74 | 3.79 |
| 29/7 | 38 | 3.92 | 6.70 |
| 12/8 | 35 | 8.31 | 13.88 |
| 28/8 | 42 | 2.55 | 8.72 |
| 10/9 | 39 | 2.18 | 9.00 |
| 23/9 | 54 | 0.83 | 1.66 |
| 07/10 | 56 | 2.42 | 14.96 |
| 21/10 | 59 | 2.48 | 16.89 |
| 14/11 | 67 | 2.27 | 14.28 |
| 16/12 | 67 | 0.66 | 3.65 |
| 13/1/73 | 44 | 0.27 | 1.48 |
| 24/2 | 49 | 0.01 | 0.09 |
| 29/3 | 67 | 0.03 | 0.13 |
| 15/4 | 46 | 0.01 | 0.23 |
| 29/4 | 53 | 0.15 | 2.26 |
| 07/5 | 61 | 0.11 | 2.21 |
| 22/5 | 67 | 0.19 | 1.96 |
| 26/5 | 50 | 0.54 | 6.49 |
| 06/6 | 65 | 1.42 | 21.04 |
| 17/6 | 54 | 8.95 | 68.02 |
| 21/6 | 59 | 24.26 | 166.18 |
| 04/7 | 21 | 4.19 | 15.59 |
| 08/7 | 8 | 1.48 | 5.24 |

contd./...

Appendix (vi) - contd.

| Sampling Dates | % gravid | gravid individuals numbers per litre | egg stock per litre |
|---|---|---|---|
| 22/7/73 | 46 | 3.24 | 28.16 |
| 14/8 | 51 | 2.83 | 10.73 |
| 04/9 | 48 | 13.51 | 50.93 |
| 16/9/73 | 43 | 9.72 | 45.88 |
| 22/9 | 42 | 1.18 | 7.39 |
| 07/10 | 50 | 0.88 | 9.02 |
| 28/10 | 44 | 0.74 | 5.92 |
| 17/11 | 65 | 1.31 | 12.65 |
| 18/12 | 60 | 0.45 | 4.18 |
| 06/1/74 | 53 | 3.13 | 28.76 |
| 20/1 | 62 | 0.91 | 9.58 |

% gravid as obtained from analysis of net samples only.

| Sampling Dates | % gravid |
|---|---|
| 17/3/73 | 41 |
| 24/3 | 54 |
| 24/5 | 52 |
| 23/6 | 43 |
| 06/8 | 38 |
| 01/9 | 42 |

Note that on the 10/4/73 no gravid Daphnia were found in either Friedinger or net samples.

## Appendix (vii) - data for Figure 10

Seasonal changes in mean body-size and in mean brood-size of adult *D. hyalina* var *lacustris* from Loch Leven during 1972-73.

*Mean obtained from 100 samples unless stated otherwise.

Mean body-size in mm.

| Sampling Dates | Mean Brood-size | Mean Body-size | Sample No.* |
|---|---|---|---|
| 29/9/71 | 5.62 | - | 50 |
| 12/10 | 6.54 | - | 50 |
| 07/12 | 6.14 | - | 50 |
| 17/2/72 | 4.30 | 2.13 | |
| 12/3 | 4.23 | 2.10 | |
| 25/3 | 5.11 | 1.92 | |
| 02/4 | 5.02 | 1.82 | |
| 12/4 | 5.25 | 1.86 | |
| 27/4 | 10.71 | 1.83 | |
| 07/5 | 6.05 | 1.88 | |
| 15/5 | 1.89 | 1.89 | |
| 28/5 | 3.24 | 2.00 | |
| 01/6 | 2.61 | 2.02 | |
| 13/6 | 1.80 | 1.87 | |
| 18/6 | 1.93 | 1.82 | |
| 29/6 | 2.30 | 1.79 | |
| 15/7 | 2.18 | 1.82 | |
| 29/7 | 1.71 | 1.87 | |
| 12/8 | 1.67 | 1.93 | |
| 20/8 | 2.10 | 2.00 | |
| 28/8 | 3.42 | 2.03 | |
| 10/9 | 4.13 | 1.97 | |
| 23/9 | 2.00 | 2.05 | |
| 07/10 | 6.18 | 1.99 | |
| 15/10 | 6.86 | 2.07 | |
| 21/10 | 6.81 | 1.93 | |
| 14/11 | 6.29 | 1.95 | |
| 16/12 | 5.53 | 1.91 | |
| 13/1/73 | 5.56 | 2.07 | 50 |
| 04/2 | 4.07 | 1.95 | 50 |
| 24/2 | 6.44 | 1.65 | 64 |

contd./....

Appendix (vii) - contd.

* Mean obtained from 100 samples unless stated otherwise.
Mean body-size in mm.

| Sampling Dates | Mean Brood-size | Mean Body-size | Sample No.* |
|---|---|---|---|
| 17/3/73 | 5.38 | 2.01 | 50 |
| 24/3 | 5.23 | 2.28 | 50 |
| 29/3 | 4.75 | 1.94 | 28 |
| 10/4 | - | 1.62 | 50 |
| 15/4 | 15.60 | 2.17 | 50 |
| 29/4 | 15.06 | 1.98 | 50 |
| 07/5 | 18.88 | 1.94 | 50 |
| 22/5 | 10.51 | 2.02 | |
| 24/5 | 10.98 | 2.11 | |
| 26/5 | 12.02 | 2.03 | |
| 06/6 | 14.85 | 1.97 | |
| 17/6 | 7.60 | 1.81 | |
| 21/6 | 6.85 | 1.98 | |
| 23/6 | 6.14 | 1.97 | |
| 04/7 | 3.72 | 1.96 | |
| 08/7 | 3.54 | 2.13 | |
| 22/7 | 8.69 | 2.24 | |
| 06/8 | 4.72 | 2.07 | |
| 14/8 | 3.79 | 2.03 | |
| 01/9 | 3.51 | 2.08 | |
| 04/9 | 3.77 | 2.17 | |
| 16/9 | 4.72 | 2.12 | |
| 22/9 | 6.26 | 2.23 | |
| 07/10 | 8.14 | 2.29 | |
| 28/10 | 8.00 | 2.10 | |
| 17/11 | 9.66 | 2.22 | |
| 18/12 | 9.29 | 2.09 | |
| 06/1/74 | 9.19 | 2.10 | |
| 20/1 | 10.53 | 2.18 | |

## Appendix (viii) - data for Figure 11

### Population parameters of D. hyalina var lacustris from Loch Leven during 1972-73.

Values of b, d, and r. The values of b and d relate to specific sampling dates whereas the values of r represent an average for a given period and have thus been plotted on dates mid-way between two sampling dates.

| Sampling Dates | b | d |
|---|---|---|
| 29/9/71 | 0.0891 | - |
| 12/10 | 0.0697 | 0.0880 |
| 07/12 | 0.0783 | 0.0831 |
| 17/2/72 | 0.0255 | 0.0197 |
| 25/3 | 0.0290 | 0.0256 |
| 12/4 | 0.0895 | 0.0750 |
| 27/4 | 0.0930 | 0.0586 |
| 15/5 | 0.0256 | 0.0014 |
| 01/6 | 0.0147 | 0.0136 |
| 13/6 | 0.0086 | 0.0232 |
| 29/6 | 0.0579 | 0.0793 |
| 15/7 | 0.0274 | 0.0286 |
| 29/7 | 0.0270 | 0.0146 |
| 12/8 | 0.0438 | 0.0448 |
| 28/8 | 0.0664 | 0.0752 |
| 10/9 | 0.0485 | 0.0482 |
| 23/9 | 0.0140 | 0.0242 |
| 07/10 | 0.0799 | 0.0871 |
| 21/10 | 0.1089 | 0.1168 |
| 14/11 | 0.0852 | 0.0986 |
| 16/12 | 0.0848 | 0.1169 |
| 13/1/73 | 0.0640 | 0.1022 |
| 24/2 | 0.0588 | 0.0713 |
| 29/3 | 0.0823 | 0.0759 |
| 15/4 | 0.1661 | 0.1288 |
| 29/4 | 0.1981 | 0.1907 |
| 07/5 | 0.2777 | 0.2784 |
| 22/5 | 0.0770 | 0.0720 |
| 26/5 | 0.1082 | 0.0326 |
| 06/6 | 0.2562 | 0.1979 |

| Dates | r |
|---|---|
| 06/10/71 | -0.0212 |
| 09/11 | -0.0047 |
| 12/1/72 | -0.0050 |
| 05/3 | +0.0138 |
| 03/4 | -0.0013 |
| 19/4 | +0.0349 |
| 06/5 | +0.0339 |
| 23/5 | +0.0132 |
| 07/6 | -0.0070 |
| 21/6 | -0.0247 |
| 07/7 | -0.0182 |
| 22/7 | +0.0181 |
| 05/8 | +0.0067 |
| 20/8 | +0.0246 |
| 03/9 | +0.0122 |
| 16/9 | +0.0135 |
| 30/9 | -0.0075 |
| 14/10 | -0.0069 |
| 02/11 | -0.0096 |
| 01/12 | -0.0184 |
| 30/12 | -0.0450 |
| 03/2/73 | -0.0280 |
| 13/3 | 0.0000 |
| 08/4 | +0.0104 |
| 22/4 | +0.0642 |
| 03/5 | -0.0250 |
| 15/5 | +0.0478 |
| 24/5 | +0.1779 |
| 01/6 | +0.0297 |
| 12/6 | +0.0927 |

contd./....

## Appendix (viii) - contd.

| Sampling Dates | b | d |
|---|---|---|
| 17/6/73 | 0.0880 | 0.0078 |
| 21/6/ | 0.0880 | 0.0235 |
| 04/7 | 0.0422 | 0.0965 |
| 08/7 | 0.0242 | 0.0712 |
| 22/7 | 0.1781 | 0.1830 |
| 14/8 | 0.0399 | 0.0296 |
| 04/9 | 0.1194 | 0.1221 |
| 16/9 | 0.1345 | 0.2200 |
| 22/9 | 0.1219 | 0.2106 |
| 07/10 | 0.0712 | 0.0678 |
| 28/10 | 0.0253 | 0.0274 |
| 17/11 | 0.0648 | 0.0724 |
| 18/12 | 0.0523 | 0.0399 |
| 06/1/74 | 0.0965 | 0.1052 |
| 20/1 | 0.1083 | - |

| Dates | r |
|---|---|
| 19/6/73 | +0.0970 |
| 28/6 | -0.0492 |
| 06/7 | -0.0560 |
| 15/7 | -0.0155 |
| 03/8 | +0.0132 |
| 25/8 | +0.0075 |
| 10/9 | -0.0088 |
| 19/9 | -0.1239 |
| 30/9 | +0.0051 |
| 18/10 | +0.0007 |
| 07/11 | -0.0049 |
| 03/12 | -0.0123 |
| 28/12 | +0.0289 |
| 13/1/74 | -0.0380 |

## Appendix (ix) - data for Figure 12

Seasonal vertical distributions of the *D. hyalina* var *lacustris* population at Loch Leven during 1972-73.

| | % of total numbers in water column at site E | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sampling Dates | 0m | 1m | 2m | 3m | 4m | 5m | 10m | 15m | 20m |
| 27/4/72 | 9.5 | 13.3 | 18.2 | 15.8 | 8.4 | 7.9 | 14.3 | 6.7 | 5.9 |
| 15/5 | 8.7 | 18.4 | 25.3 | 8.3 | 9.4 | 13.7 | 5.4 | 6.5 | 4.3 |
| 01/6 | 12.0 | 22.0 | 25.0 | 16.0 | 11.0 | 8.0 | 2.0 | 3.0 | <1 |
| 13/6 | 17.8 | 25.0 | 18.3 | 10.3 | 6.5 | 7.9 | 5.2 | 5.8 | 3.2 |
| 29/6 | 2.3 | 2.7 | 18.4 | 21.8 | 16.6 | 19.4 | 8.5 | 5.3 | 4.9 |
| 15/7 | 15.4 | 16.2 | 22.6 | 16.5 | 10.9 | 1.5 | 3.7 | 5.6 | 7.5 |
| 29/7 | 14.5 | 40.4 | 8.9 | 9.6 | 11.2 | 12.3 | 1.8 | 1.0 | <1 |
| 12/8 | 10.5 | 12.9 | 14.2 | 7.9 | 23.0 | 16.2 | 6.8 | 6.9 | 1.4 |
| 28/8 | 50.5 | 6.0 | 6.6 | 4.4 | 11.3 | 5.1 | 2.5 | 4.0 | 9.4 |
| 10/9 | 10.4 | 16.8 | 17.9 | 10.2 | 7.9 | 7.4 | 11.1 | 12.1 | 6.4 |
| 23/9 | 30.7 | 13.4 | 14.5 | 11.8 | 5.9 | 7.5 | 7.9 | 4.1 | 4.1 |
| 07/10 | 22.4 | 16.4 | 8.8 | 20.1 | 7.6 | 11.1 | 5.2 | 1.7 | 4.7 |
| 21/10 | 18.8 | 14.0 | 9.9 | 12.9 | 6.1 | 13.8 | 9.5 | 6.1 | 8.9 |
| | | | | | | | | | |
| 06/6/73 | 19.6 | 35.7 | 3.6 | 10.7 | 14.3 | 14.3 | 1.8 | - | - |
| 17/6 | 16.0 | 22.0 | 27.0 | 19.0 | 8.0 | 4.0 | 4.0 | <1 | <1 |
| 21/6 | 16.3 | 17.6 | 23.0 | 11.0 | 15.6 | 15.0 | <1 | <1 | 1.0 |
| 04/7 | 11.0 | 18.0 | 19.0 | 17.0 | 21.0 | 5.0 | 7.0 | <1 | <1 |
| 08/7 | 21.6 | 14.5 | 23.5 | 23.4 | 11.7 | 2.1 | 3.2 | - | - |
| 22/7 | 15.6 | 3.3 | 1.3 | 2.8 | 7.6 | 23.5 | 20.9 | 15.3 | 9.7 |
| 14/8 | 17.2 | 27.1 | 13.2 | 20.0 | 10.9 | 5.2 | 3.3 | 1.9 | 1.1 |
| 16/9 | 14.0 | 24.0 | 29.0 | 11.0 | 8.0 | 6.0 | 4.0 | 3.0 | 1.0 |
| 22/9 | 4.4 | 38.2 | 15.1 | 11.3 | 8.3 | 8.9 | 7.2 | 3.7 | 2.8 |
| 07/10 | 54.2 | 16.2 | 3.7 | 2.9 | 1.5 | 8.1 | 3.7 | 7.0 | 2.9 |
| 28/10 | 36.7 | 19.0 | 12.2 | 4.9 | 9.2 | 10.4 | 3.4 | 3.7 | <1 |
| 17/11 | 17.3 | 33.3 | 11.9 | 3.2 | 2.4 | 3.2 | 3.6 | 18.2 | 7.9 |

## Appendix (x) - data for Figure 14.

Seasonal succession and quantitative assessment of four characteristic cyclomorphotic forms of *D. hyalina* var *lacustris* from Loch Leven during 1972-73.

| Sampling Dates | Cyclomorphotic types % Composition | | | |
|---|---|---|---|---|
| | Round-headed | Spring-intermediate | Peaked | Autumn-intermediate |
| 29/9/71 | 32 | | 47 | 21 |
| 12/10 | 41 | | 21.5 | 37.5 |
| 07/12 | 66 | | | 34 |
| 17/2/72 | 79 | | | 21 |
| 12/3 | 82 | | | 18 |
| 25/3 | 95 | | | 5 |
| 02/4 | 98 | | | 2 |
| 12/4 | 100 | | | |
| 27/4 | 100 | | | |
| 07/5 | 100 | | | |
| 15/5 | 100 | | | |
| 28/5 | 100 | | | |
| 01/6 | 100 | | | |
| 13/6 | 100 | | | |
| 18/6 | 100 | | | |
| 29/6 | 100 | | | |
| 15/7 | 24 | 76 | | |
| 29/7 | 20 | 80 | | |
| 12/8 | 9.5 | 3 | 87.5 | |
| 20/8 | 9.5 | 3.5 | 87 | |
| 28/8 | 11.5 | | 79.5 | 9 |
| 10/9 | 13 | | 40 | 47 |
| 23/9 | 4.6 | | 36 | 18 |
| 07/10 | 47.5 | | 15.5 | 37 |
| 15/10 | 47 | | 6 | 47 |
| 21/10 | 60.5 | | | 39.5 |
| 14/11 | 15 | | | 85 |
| 16/12 | 45.5 | | | 54.5 |
| 13/1/73 | 82 | | | 18 |
| 04/2 | 91 | | | 9 |

contd./....

Appendix (x) - contd.

| Sampling Dates | Cyclomorphotic types % Composition | | | |
|---|---|---|---|---|
| | Round-headed | Spring-intermediate | Peaked | Autumn-intermediate |
| 24/2/73 | 100 | | | |
| 17/3 | 100 | | | |
| 24/3 | 100 | | | |
| 29/3 | 100 | | | |
| 10/4 | 100 | | | |
| 15/4 | 100 | | | |
| 29/4 | 100 | | | |
| 07/5 | 97 | 3 | | |
| 22/5 | 94 | 6 | | |
| 24/5 | 92 | 8 | | |
| 26/5 | 93 | 7 | | |
| 06/6 | 69 | 31 | | |
| 17/6 | 54 | 46 | | |
| 21/6 | 53 | 47 | | |
| 23/6 | 54.5 | 45.5 | | |
| 04/7 | 65 | 33 | 2 | |
| 08/7 | 81 | 11.5 | 7.5 | |
| 22/7 | 23 | 4 | 73 | |
| 06/8 | 13 | 2.5 | 84.5 | |
| 14/8 | 7 | | 93 | |
| 01/9 | 12.5 | | 72.5 | 15 |
| 04/9 | 14 | | 78 | 8 |
| 16/9 | 22.5 | | 53 | 24.5 |
| 22/9 | 17.5 | | 58 | 24.5 |
| 07/10 | 34 | | 27.5 | 38.5 |
| 28/10 | 65.5 | | 7.5 | 27 |
| 17/11 | 72 | | 1 | 27 |
| 18/12 | 86 | | | 14 |
| 06/1/74 | 91.5 | | | 8.5 |
| 20/1 | 94 | | | 6 |

## Appendix (xvi) - data for Fig. 21

Seasonal variations in the mean egg stock and in the mean standing crop of all the developmental stages of *Cyclops strenuus abyssorum* from Loch Leven during 1972-73.

For mean egg stock per litre see Appendix (xvii)

| Sampling Dates | Numbers per litre | | | | | | |
|---|---|---|---|---|---|---|---|
| | N | Cl | Cll | Clll | CIV | CV | CVI |
| 29/9/71 | 13.43 | 5.75 | 7.44 | 7.36 | 4.12 | 3.10 | 13.30 |
| 12/10 | 25.44 | 2.19 | 3.30 | 3.26 | 3.82 | 3.21 | 11.16 |
| 7/12 | 8.70 | 1.65 | 0.76 | 0.75 | 0.98 | 0.91 | 8.11 |
| 17/2/72 | 5.65 | 0.92 | 0.75 | 0.43 | 0.24 | 1.14 | 2.28 |
| 25/3 | 8.61 | 3.75 | 3.65 | 1.75 | 0.45 | 5.80 | 2.50 |
| 12/4 | 5.86 | 3.75 | 3.25 | 2.50 | 1.35 | 1.00 | 2.86 |
| 27/4 | 17.42 | 4.98 | 5.53 | 5.98 | 3.38 | 1.92 | 4.78 |
| 15/5 | 12.26 | 16.40 | 13.35 | 6.85 | 5.30 | 2.90 | 10.37 |
| 1/6 | 0.31 | 3.71 | 9.36 | 12.32 | 7.55 | 4.80 | 4.36 |
| 13/6 | 1.74 | 0.43 | 2.09 | 5.21 | 7.80 | 3.40 | 5.41 |
| 29/6 | 2.31 | 1.87 | 0.81 | 2.28 | 2.17 | 4.13 | 4.41 |
| 15/7 | 1.64 | 1.94 | 4.36 | 1.82 | 1.50 | 1,46 | 2.90 |
| 29/7 | 2.82 | 6.11 | 4.01 | 3.90 | 2.63 | 2.38 | 2.83 |
| 12/8 | 0.70 | 0.44 | 1.00 | 2.84 | 4.45 | 4.07 | 5.91 |
| 28/8 | 0.77 | 0.43 | 0.77 | 1.57 | 2.70 | 4.31 | 6.07 |
| 10/9 | 14.95 | 5.81 | 1.85 | 0.95 | 0.75 | 1.78 | 9.72 |
| 23/9 | 6.00 | 5.13 | 4.52 | 5.02 | 3.30 | 3.39 | 8.69 |
| 7/10 | 8.32 | 1.55 | 1.61 | 3.28 | 5.27 | 6.74 | 8.37 |
| 21/10 | 23.51 | 5.58 | 3.12 | 2.32 | 2.06 | 4.09 | 13.06 |
| 14/11 | 19.01 | 2.76 | 4.92 | 8.88 | 8.43 | 7.77 | 11.11 |
| 16/12 | 27.72 | 5.82 | 2.37 | 3.09 | 3.46 | 2.85 | 12.47 |
| 13/1/73 | 46.15 | 8.42 | 4.29 | 2.44 | 1.99 | 3.49 | 11.64 |
| 24/2 | 20.56 | 1.91 | 2.24 | 2.94 | 2.59 | 2.49 | 11.09 |
| 29/3 | 20.91 | 4.07 | 3.41 | 1.13 | 1.16 | 3.17 | 12.85 |
| 10/4 | 25.43 | 3.60 | 2.80 | 2.30 | 1.70 | 3.20 | 13.90 |
| 15/4 | 29.84 | 3.14 | 2.10 | 2.78 | 2.20 | 1.19 | 14.99 |
| 29/4 | 62.31 | 12.31 | 6.49 | 6.35 | 4.47 | 3.46 | 17.58 |

Contd/...

## Appendix (xvi) - contd.

| Sampling Dates | Numbers per litre |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  | N | CI | CII | CIII | CIV | CV | CVI |  |
| 7/5/73 | 90.40 | 17.03 | 7.76 | 7.08 | 3.99 | 3.28 | 16.36 |  |
| 22/5 | 53.20 | 44.27 | 33.41 | 22.42 | 9.69 | 4.03 | 13.45 | 127.27 |
| 26/5 | 55.42 | 40.14 | 32.58 | 24.45 | 10.52 | 3.15 | 10.90 | 12[illegible].[illegible]74 |
| 6/6 | 53.64 | 19.36 | 25.46 | 41.04 | 15.20 | 1.69 | 10.43 | 113.39 |
| 17/6 | 5.17 | 22.44 | 22.75 | 43.68 | 39.34 | 31.43 | 19.89 |  |
| 21/6 | 4.62 | 21.37 | 19.90 | 40.60 | 43.33 | 35.92 | 27.43 |  |
| 4/7 | 2.15 | 2.94 | 2.34 | 14.29 | 22.32 | 18.99 | 18.12 |  |
| 8/7 | 0.36 | 0.06 | 0.82 | 3.02 | 3.90 | 5.17 | 4.60 |  |
| 22/7 | 4.03 | 0.28 | 1.16 | 0.27 | 0.59 | 1.21 | 4.78 |  |
| 14/8 | 3.29 | 1.08 | 1.80 | 0.36 | 0.35 | 4.50 | 9.29 |  |
| 4/9 | 27.2 | 1.04 | 0.52 | 0.44 | 1.06 | 2.18 | 7.54 |  |
| 16/9 | 23.45 | 5.59 | 2.12 | 1.92 | 1.20 | 1.06 | 4.14 |  |
| 22/9 | 19.31 | 3.04 | 5.92 | 5.41 | 2.54 | 1.02 | 3.04 |  |
| 7/10 | 22.30 | 2.70 | 5.94 | 4.32 | 8.10 | 10.22 | 10.07 |  |
| 28/10 | 21.83 | 2.86 | 4.49 | 5.30 | 6.12 | 4.13 | 15.67 |  |
| 17/11 | 27.12 | 1.85 | 5.02 | 2.90 | 2.38 | 4.77 | 14.69 |  |
| 18/12 | 38.30 | 4.81 | 2.76 | 1.83 | 3.12 | 3.03 | 8.38 |  |
| 6/1/74 | 8.22 | 3.53 | 5.00 | 3.23 | 3.82 | 3.87 | 5.89 |  |
| 20/1 | 10.20 | 3.20 | 3.20 | 2.20 | 4.20 | 3.40 | 7.40 |  |

# Appendix (xvii) - data for Fig. 22

The breeding parameters of the C. strenuus abyssorum population of Loch Leven during 1972-73.

For mean brood-size data see Appendix (xviii)

Note that the mean numbers per litre of egg-sacs equals twice the mean numbers per litre of gravid females.

| Sampling Dates | % gravid | gravid individuals numbers per litre | Egg stock per litre |
|---|---|---|---|
| 29/9/71 | 11.6 | 1.13 | 48.27 |
| 12/10 | 7.8 | 0.48 | 21.72 |
| 7/12 | 15.5 | 0.66 | 32.33 |
| 17/2/72 | 40.4 | 0.63 | 30.21 |
| 25/3 | 31.2 | 0.39 | 16.29 |
| 12/4 | 37.2 | 0.58 | 36.89 |
| 27/4 | 33.8 | 0.80 | 49.95 |
| 15/5 | 26.9 | 1.17 | 59.90 |
| 1/6 | 38.4 | 0.91 | 44.53 |
| 13/6 | 6.3 | 0.14 | 5.63 |
| 29/6 | 16.8 | 0.29 | 8.76 |
| 15/7 | 16.8 | 0.22 | 5.30 |
| 29/7 | 13.9 | 0.23 | 5.22 |
| 12/8 | 17.2 | 0.44 | 13.70 |
| 28/8 | 30.3 | 1.05 | 40.42 |
| 10/9 | 42.9 | 2.80 | 105.73 |
| 23/9 | 46.2 | 2.49 | 96.91 |
| 7/10 | 24.4 | 1.37 | 48.43 |
| 21/10 | 22.7 | 1.66 | 84.67 |
| 14/11 | 47.7 | 3.47 | 173.25 |
| 16/12 | 32.9 | 2.25 | 120.24 |
| 13/1/73 | 21.9 | 1.21 | 60.80 |
| 24/2 | 28.2 | 1.37 | 71.68 |
| 29/3 | 40.6 | 2.52 | 90.54 |
| 10/4 | 48.4 | 3.95 | 161.08 |
| 15/4 | 54.6 | 4.11 | 174.43 |
| 29/4 | 38.1 | 3.53 | 143.96 |
| 7/5 | 28.0 | 2.58 | 112.73 |
| 22/5 | 45.1 | 3.35 | 189.01 |
| 26/5 | 48.2 | 3.06 | 166.93 |
| 6/6 | 19.5 | 0.81 | 36.06 |
| 17/6 | 10.3 | 0.84 | 32.06 |

Appendix (xvii) - contd.

| Sampling Dates | % gravid | gravid individuals numbers per litre | egg stock per litre |
|---|---|---|---|
| 21/6/73 | 12.1 | 1.56 | 58.34 |
| 4/7 | 3.1 | 0.26 | 9.14 |
| 8/7 | 7.4 | 0.14 | 5.12 |
| 22/7 | 40.2 | 1.17 | 35.23 |
| 14/8 | 19.9 | 0.89 | 27.77 |
| 4/9 | 52.3 | 2.93 | 139.00 |
| 16/9 | 37.6 | 1.06 | 51.03 |
| 22/9 | 59.5 | 0.91 | 41.29 |
| 7/10 | 19.1 | 0.97 | 49.70 |
| 28/10 | 18.8 | 1.22 | 61.82 |
| 17/11 | 4.9 | 0.25 | 12.92 |
| 18/12 | 8.0 | 0.27 | 12.07 |
| 6/1/74 | 12.8 | 0.34 | 14.54 |
| 20/1 | 8.3 | 0.20 | 9.34 |