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THE CRUSTACEAN ZOOPLANKTON OF LOCH LEVEN, KINROSS.

by

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The work presented in this thesis is the result of my own investigations. It has not been, nor will be, submitted for any other degree.

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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.

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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.

[illegible]

The thesis is somewhat biased in favour 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 $3^{\circ}30'$W, latitude $56^{\circ}10'$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 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.

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(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	–	■	■	■	○	○	■	■	■
D. longispina O.F. Müller	■	–	–	–	○	○	○	○	○
D. pulex (De Geer)	■	–	–	–	○	○	○	○	○
Diaphanosoma brachyurum Lievin	■	–	–	–	○	○	○	○	○
Bosmina longirostris (O.F. Müller)	■	■	–	–	○	○	○	○	○
B. coregoni var. longispina (Leydig)	–	■	–	–	○	○	○	○	○
B. coregoni var. obtusirostris (Sars)	–	■	–	■	○	○	○	○	○
Bythotrephes longimanus Leydig	■	■	■	■	■	■	■	■	■
Leptodora kindti (Focke)	■	■	–	–	■	○	■	■	■
Polyphemus pediculus (L.)	■	–	–	–	○	○	○	○	○
COPEPODA									
Diaptomus gracilis Sars	■	■	■	■	■	■	■	■	■
Cyclops strenuus (Fischer)	■	■	–	■	○	○	○	○	○
C. strenuus abyssorum Sars	–	–	–	–	■	■	■	■	■
C. albidus (Jurine)	■	■	–	–	○	■	○	○	○
C. macrurus (Sars)	–	■	–	–	○	○	○	○	○
C. agilis (Koch, Sars)	■	■	■	–	○	○	○	○	○

■ Present. ○ 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 mesh-work is used (Langford 1952), it is extremely versatile and can be used to good effect in large, deep water-bodies 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.

7. Production studies

Production (and biomass) studies are of particular significance to freshwater ecology in providing the basis for detailed quantitative comparisons of populations from different waters and for assessing the role of a given population within its ecosystem. The production of a specific population for a given period of time is defined as the sum of all the growth increments of all the specimens of that population. Although production can be estimated for any given time interval (week, month, season, year), annual production is the most useful for comparative purposes, together with the maximum short-term rate.

Various methods of estimating secondary production have been devised and are extensively reviewed by Edmondson and Winberg (1971). Those usually applicable to zooplankton populations are either based on the concept of turnover-time *or* on the finite rate of growth of individuals.

Among the methods based on turnover-time are methods by Elster (1954, 1955) for copepod species and Stross *et al*. (1961), Hall (1964), Wright (1965) and George and Edwards (1974) all for *Daphnia* spp. Using the method of Heinle (1966), George and Edwards (1974) estimated the production of *Daphnia hyalina* var. *lacustris* from Eglwys Nynydd, South Wales, using quantitative field data and experimentally determined egg duration times. Having derived the turnover-time for each sampling date from a sequence of calculations (see Results Section page 60) involving estimations of finite and instantaneous birth and death rates, the authors then multiplied the daily percentage turnover by the standing crop biomass to obtain a series of daily production rates. However, estimations of production calculated along these lines can only be considered as approximations, since the estimates of birth rate only hold true for populations with a stable age structure - a situation which is unlikely to occur in natural systems. Furthermore, the death rate determinations do not take into account age-specific mortalities.

Examples of production estimates based upon the finite growth of individuals are provided by Pechen and Shushkina (1964), Greze and Baldina (1964) and Winberg *et al*. (1965) for copepod species. Apart from field population data, these methods require knowledge of the weight increments of individuals throughout their life-span, from hatching to death. This necessarily involves growth-rate studies under specifically controlled laboratory conditions. In the method of Winberg *et al*. (1965) the production of a given developmental stage is obtained by multiplying the numbers of that stage present on a given sampling date by its daily weight increment. Edmondson and Winberg (1971) considered that these methods were likely to provide more accurate production estimates than those based upon potential population changes. The main source of error would be with the experimentally determined growth-rates and longevities which may not truly represent the situation encountered in natural systems. However, these methods appear to be the best so far devised for continuously reproducing zooplankton populations and have been adopted in the present study for estimating the production of *Daphnia hyalina* var. *lacustris* and *Cyclops strenuus abyssorum* from Loch Leven.

SECTION B MATERIALS AND METHODS

1. Zooplankton sampling and sample analysis

(a) Sampling procedure

The zooplankton of Loch Leven was quantitatively sampled from late September 1971 until January 1974, thus giving data for two full years, 1972 and 1973. The sampling programmes were designed to provide population data representative of the entire loch.

The sampling device used was a 5-litre Friedinger water-bottle (Plate 1, A and B) as modified by Mr. H.C. Gilson of the F.B.A., Windermere and manufactured in the Stirling University workshops. The mode of operation is described elsewhere (Section A, part 6 and legend of Plate 1).

The zooplankton were filtered from the collected water sample through a detachable tap-filter (Plate 1,c), which incorporates a stainless-steel micromesh of 119 microns aperture size, and retained in a collecting funnel-basin which is drained by means of a tap. The animals were then emptied into numbered polythene specimen tubes containing 2 ml of 40 per cent formalin with lignin pink (or chlorazyl black) added for staining. The filter was washed three times using a wash-bottle containing filtered loch water - the preservative being consequently diluted to approximately 4 per cent.

Plate 1 (Opposite)

The Friedinger 5-litre water-bottle sampler and tap-filter.

- A. The sampler with lids closed
- B. The sampler with lids open
- C. The tap-filter incorporating micromesh of 119μ aperture size.

Mode of operation :

The top end of the sampler is attached by means of a braided nylon line, marked at metre intervals, to a davit and winch assembly. The latter is mounted in a boat and allows the Friedinger to be raised and lowered in the water.

To collect a water sample, the two lids, situated at the top and bottom of the transparent perspex cylinder, are opened (B). The top lid is held open by means of a catch, the bottom lid by means of spring tension created only when the top lid is open. Once the sampler has been lowered to the required depth, a heavy brass "messenger" weight is promptly sent down the line. This weight releases the catch holding the top lid and causes both lids to snap shut. The sampler is closed as quickly as possible on reaching its sampling destination to minimise loss of catch by avoidance reactions (Smyly 1968b). In practise, it was possible to close the sampler within five seconds at all sites and sampling depths except at the deep site E, where at 10, 15 and 20 metres closing took marginally longer, less than ten seconds.

On board the boat, the tap-filter (C) is screwed into the bottom lid and by means of a push-button valve (shown clearly in A) the water sample is drained through the filter. The concentrated zooplankton sample, which is retained in the funnel basin of the tap-filter, is then emptied into a numbered specimen tube, containing preservative and dye, via the outlet tap.

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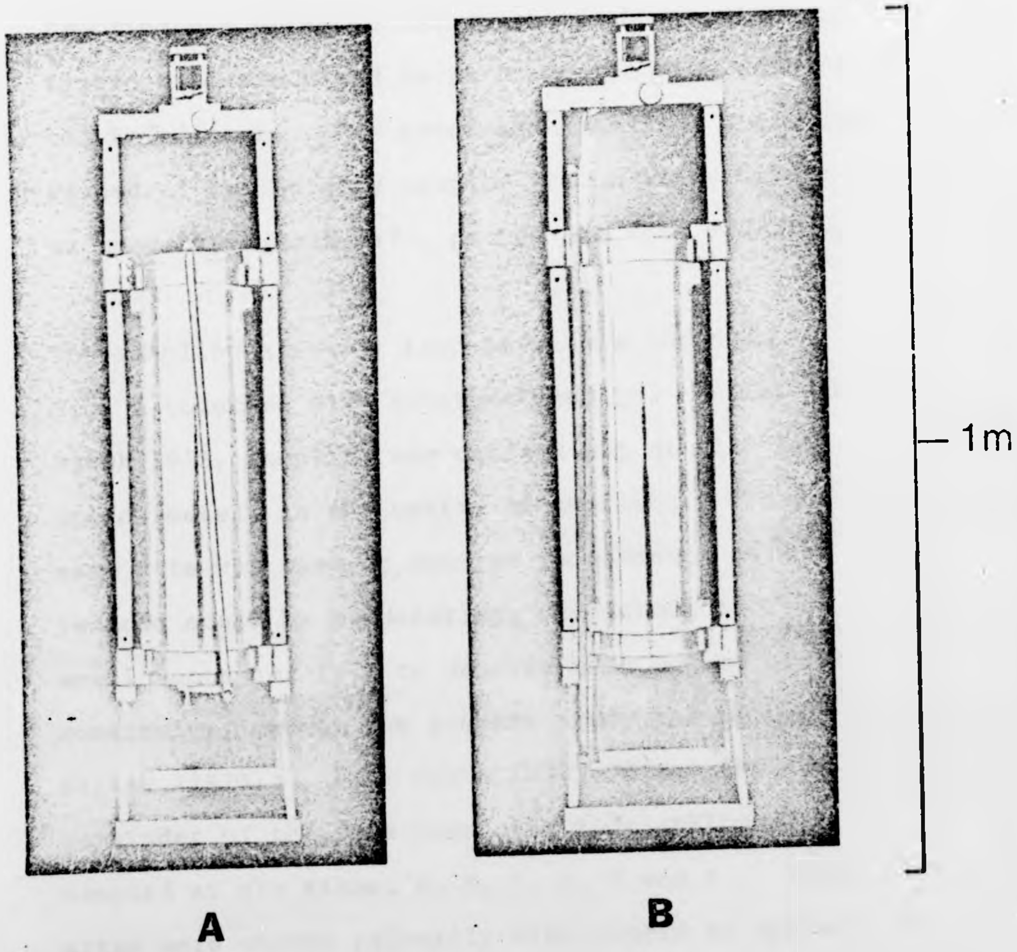

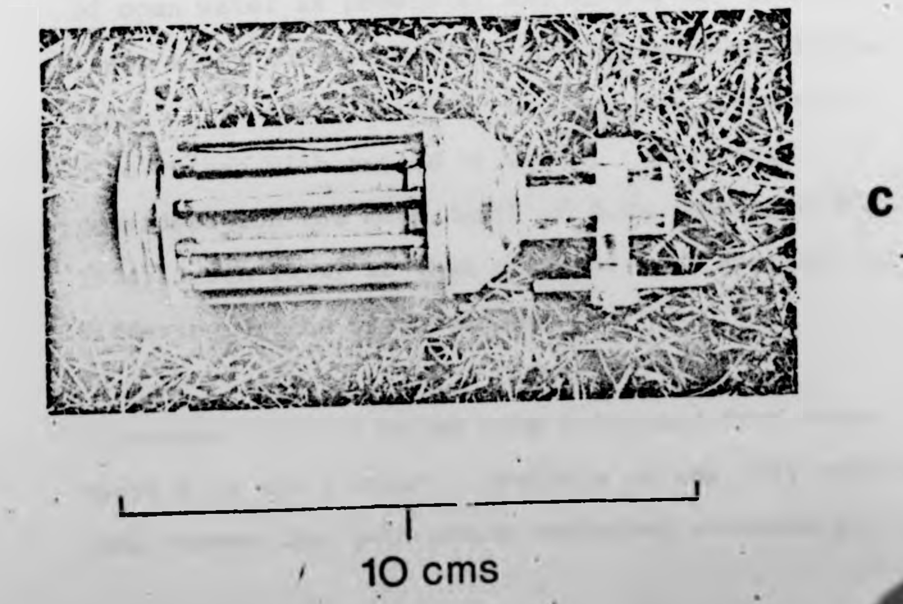

Sampling was effected using various boats with fitted hand-winch and davit assemblies for operating the Friedinger. For speed and handling, a 12-foot cathedral-hulled dory coupled with a 20 HP outboard, as used throughout 1973, proved the most effective.

The sampling sites at Loch Leven are shown in Fig. 1 together with relevant details. Prior to March 1972, sampling was carried out at site 4 approximately in the centre of the loch. This same site was used to monitor zooplankton on a reduced scale by A. Mcfarlane throughout 1970 until September 1971 to provide some degree of continuity between the present study and that of Walker (1970). From March 1972 and for the remainder of the same year, the zooplankton were sampled at six sites, A, B, C, D, E and F. These sites were chosen primarily with regard to their positions in the loch, covering as wide an area of open water as possible, and giving two transect lines along north-south and north-east — south-west axes, with three sites on each. The sites were also chosen with regard to depth, taking into consideration the mean depth of 3.9m (Morgan 1970, 1974; Smith 1974) so that sites of both similar and differing depths were sampled.

Throughout 1973, samples were collected from three sites A, D and E only. Analysis of the 1972 sampling data showed that population estimates obtained by

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 samples. Throughout 1973, however, three sites, A,D and E were sampled, collecting twenty-eight samples.

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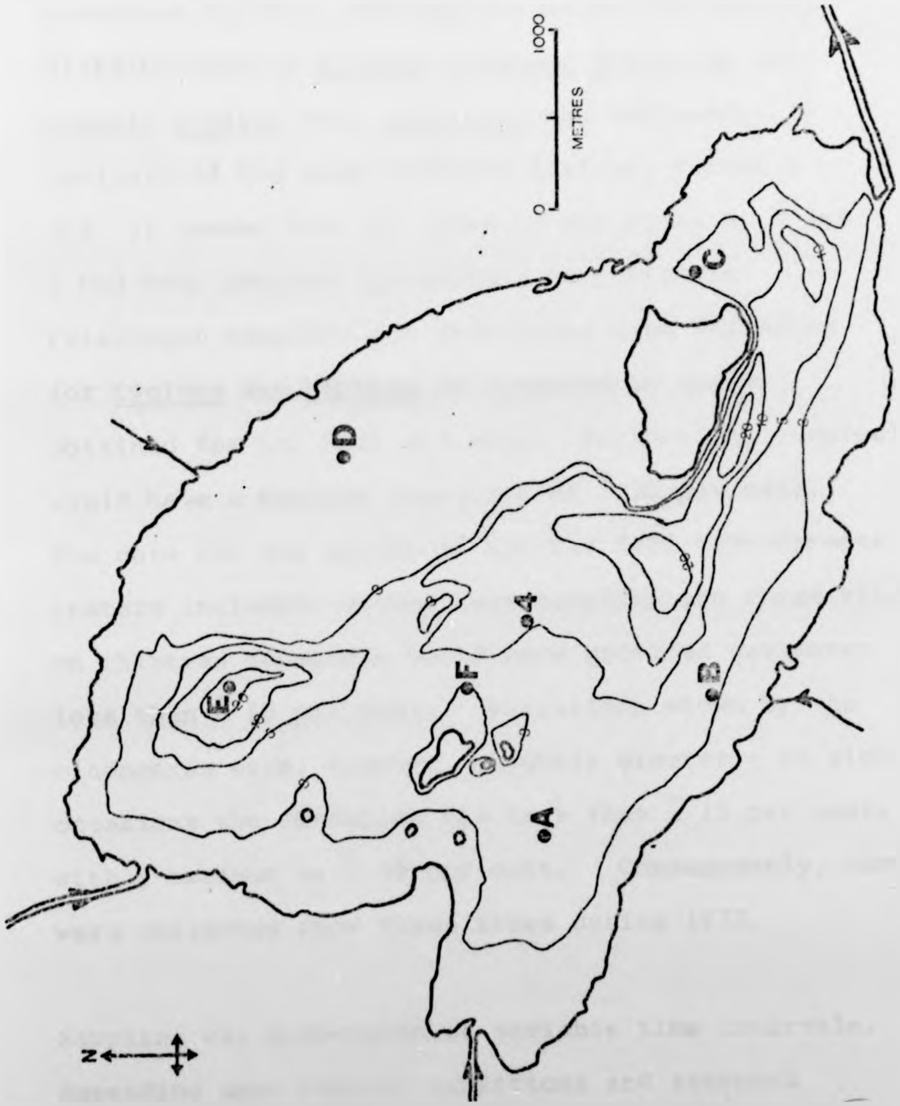

sampling these three sites would provide similar estimates to those obtained from the six sites. Having collected a considerable volume of data by sampling the full six sites on seventeen occasions in 1972, information on the horizontal distributions of Cyclops strenuus abyssorum and Daphnia hyalina 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	Size	
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).

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* 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 round-headed using an imaginery line (shallow arc) between the brow in front of the crest and the slope at the back of the head and measuring accordingly.

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 flask, the contents being shaken, and sub-samples of 5 ml 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.

2. Laboratory growth studies

The method of estimating production, adopted for the present study for populations undergoing continuous reproduction, is based upon the finite growth of individuals. This requires the knowledge of the weight increments of the individual thoughout its life-span, from hatching to death, and consequently laboratory growth-rate determinations under certain constant conditions are necessary.

Laboratory growth studies of Cyclops strenuus abyssorum from Loch Leven were attempted but because of complications resulting in the deaths of animals beyond copepodid stage 1 and because of overwhelming bacterial contamination of the copepod food cultures (Euglena gracilis), these experiments were discontinued. However, the same species has been reared in laboratory conditions by Lewis et al. (1971) and their growth-rate data has been used for the purposes of estimating production in the present study.

Daphnia hyalina var. lacustris from Loch Leven were successfully cultured in the laboratory on an excess Chlorella pyrenoidosa diet at three temperatures 15°, 10° and 5°C with a 12-hour photoperiod. The materials and methods were as follows :

(a) Algal cultures

In order to obtain reliable and abundant supplies of food-algae throughout the duration of Daphnia growth experiments, a number of algal species were obtained and cultures attempted. Pure sub-cultures of the following species : Oocystis solitaria, Chlamydomonas reinhardii, Chlorella pyrenoidosa and Cyclotella pseudostelligera were obtained from the Culture Centre of Algae and Protozoa, Cambridge, together with recommendations on culture procedures and nutrient mediums. The algae were chosen with regard to their size, cell-wall thickness, nutrient value and growth capabilities. In addition, the species of diatom, Cyclotella, was chosen because of its regular appearance in the phytoplankton of Loch Leven and consequent presence in gut contents of D. h. var. lacustris. Oocystis solitaria was selected because D. hyalina Leydig had been previously reared on Oocystis spp. (Duncan pers. comm.).

However, the only consistently successful and easily maintained uni-algal culture was that of the green alga, Chlorella pyrenoidosa, which grew exceptionally well in laboratory conditions. Pilot experiments showed that this was an acceptable food alga for D. hyalina var lacustris as Chlorella cells were readily ingested. Furthermore, preliminary growth trials showed that adult Daphnia fed on excess Chlorella produced relatively large brood sizes - up to nineteen eggs. Food supply directly influences clutch size in all Cladocera

(Hutchinson 1967), so this success indicated that *Chlorella* cultures were suitable for rearing *D*. *h*. var. *lacustris* from Loch Leven. Previous workers have used *Chlorella* spp. as a cladoceran food source. Lefevre (1942) observed good development of *Daphnia magna* and *D*. *pulex* on *Chlorella vulgaris* and *C*. *pyrenoidosa*. Similarly,Pratt (1943) reared *D*. *magna* on *Chlorella pyrenoidosa*. In addition, species of *Chlorella* have been used for cladoceran filter-feeding experiments (Ryther 1954; Shushtchenia 1958; Rigler 1961; McMahon and Rigler 1963).

Chlorella culture techniques have been fully described elsewhere (Culture Collection of Algae and Protozoa, 1971). However, essential details of mediums and procedures used in the present study are as follows. The culture medium was prepared with the following constituents : 10 per cent soil extract, 0.002 per cent di-potassium hydrogen phosphate, 0.002 per cent magnesium sulphate and 0.02 per cent potassium nitrate, made up with de-ionised water. The solution was autoclaved. Using sterile techniques, the *Chlorella* sample, fresh from the suppliers, was introduced into the medium. Subsequent sub-cultures were similarly prepared and maintained, under laboratory room and light conditions, in 1 litre conical flasks sealed with cotton wool. Magnetic stirrers and aerators, incorporating 0.3μ aperture MS 681 bacterial pipeline filters, kept the algae in suspension, the aeration also providing carbon dioxide.

To prepare the algal suspension given to the growing Daphnia, the Chlorella culture was allowed to settle on the bottom of the holding flask where quantities of algae were extracted using a clean pipette. The algae were then injected into Loch Leven water, which had been filtered, using a 0.45μ aperture membrane filter (Triacetate metricel type GA-6), and autoclaved. The sterilised water had been previously stored at experimental temperatures (i.e. 15°, 10° and 5°C). Before being given to the Daphnia, the algal suspensions were aerated (aerators incorporating pipeline filters). The algal concentrations required to give suspensions of excess food were initially determined photometrically, using a nephelometer. In practice, concentrations could easily be estimated visually.

The Chlorella cultures and derived food suspensions contained variable quantities of bacteria. Bacteria were certainly abundant on bacterial plates when the various mediums were tested - some of these were presumably inherent on the algal cells. In effect, the Daphnia food source was a uni-algal, bacterially contaminated suspension.

Sterile techniques were employed for the various culture preparations in an attempt to limit excessive bacterial contamination. Bacteria are known to contribute a significant role in the nutrition of zooplankton (Gliwicz 1968). However, stocks of nutrient solution and filtered Loch Leven water were necessarily maintained in a sterile condition during storage.

Attempts were made to culture algae from Loch Leven, but these were generally unsuccessful resulting in mixed, fluctuating populations which were eventually dominated by blue-green algae, *Oscillatoria* (*planktonica* ?) or *Anabaena* spp. (*flos-aquae* ?). However, a species of *Scenedesmus* (*S*. *obliquus* or *falcatus* ?) became dominant in one case and subsequent sub-cultures proved to be very fast-growing although minor contamination by *Chlamydomonas* spp. was evident. For comparative reasons, *Daphnia hyalina* var. *lacustris* were also cultured using excess *Scenedesmus* but at 15°C only.

(b) Growth-rate determinations

Populations of round-headed (Fig. 13) female *Daphnia hyalina* var. *lacustris* from Loch Leven were reared and maintained on a *Chlorella pyrenoidosa* diet in several partially-covered plastic aquariums which were situated in constant temperature rooms (set at 15°, 10° and 5°C). The aquarium water, which had been obtained from Loch Leven, had been previously filtered using a 0.45μ aperture membrane filter and was constantly aerated. The animals were subjected to dim reflected light from a fluorescent lamp for a 12-hour photoperiod and fed by periodic inoculations of Chlorella suspension into the aquarium water, the algae being circulated by turbulence from the aerator.

The growth studies were carried out using isolated individuals whose parents had been reared for at least one generation in the previously mentioned circumstances. Gravid females, carrying well developed embryos, were removed from the aquarium and isolated into petri-dishes with abundant food and closely observed until the embryos were released from the brood-pouch.

Selected juveniles were removed and placed individually into glass vials containing the algal suspension. Initially the animals were reared in 15 ml of suspension in 20 ml vials until the onset of maturity - the mature individuals being subsequently kept in 30 ml of suspension in 35 ml vials. These vials had relatively high internal volume to surface area ratios, providing a living-space of sufficient depth to decrease the probabilities of individuals becoming trapped on the surface film. The vials were retained in holding-crates suspended within water-baths, the latter being covered and kept in the various constant temperature rooms. This ensured that temperatures would be kept constant ± 1°C in 5°c C.T. room, ± 0.5°C in 10° and 15°C C.T. rooms.

The <u>Daphnia</u> were examined and placed into clean vials containing fresh algal suspension every day. Daily observations involved measuring the animals and inspection of their mediums for moulted carapace casts or newly-released juveniles where applicable. Measurements were taken of the length from the base of the tail spine to the middle of the insertion of the locomotory antenna and to the top of the head using apparatus previously described (page 29). The animals were manipulated using a wide-mouth pipette or a camel-hair brush. Occasionally, exceptionally lively individuals were anaethetised using carbon dioxide from a soda-siphon.

Using the above methods, ten individual <u>Daphnia hyalina</u> var. <u>lacustris</u>, including one male, were reared at 15°C on a <u>Chlorella</u> diet, with three individuals persisting for approximately sixty days and producing twelve successive broods each. The male lived for fifty-five days. At 10°C, five individuals were reared for up to sixty days -

the growth studies being subsequently discontinued for convenience. Because of the slow development and extended longevity expectable at low temperatures, the 5°C experiments mainly involved the assessment of egg durations using mature individuals with developing broods.

Six *Daphnia* were reared on a *Scenedesmus* diet at 15°C. The methods used were essentially similar to those used for rearing animals on the *Chlorella* diet.

3. Dry-weight determinations

In order to calculate the biomass and production (in the manner previously specified on page 31) of a given species population, information on the weights of the various developmental or size components of that population is required. Representative weight data can be obtained from body-length measurements by extrapolation from previously established linear relationships between length and weight.

In order to obtain sufficient data to compute a linear length-weight regression for *Daphnia hyalina* var *lacustris*, approximately two hundred round-headed *Daphnia*, covering the entire size spectrum (from newly released juveniles to old mature females) were measured and weighed. The methods and apparatus used are as follows:

The required samples of D. h. var. lacustris were obtained from laboratory aquarium populations (page35) and placed in petri-dishes of membrane-filtered Loch Leven water. Selected animals were subsequently removed, briefly washed and narcotised in carbonated distilled water (carbon dioxide added using a soda-siphon) and arranged individually onto marked portions on microscope slides. The slides had been suitably marked out into several numbered divisions so that individuals could be indexed. Each individual was measured from the base of the tail spine to the middle of the insertion of the locomotory antenna and to the top of the head. Mature Daphnia carrying broods were then placed under the binocular microscope, the eggs/embryos being carefully removed using tungsten needles. When dealing with the very small newly-released juveniles, groups of five to ten individuals were measured individually, but placed together on a cavity slide for the purposes of drying and weighing.

The animals were initially allowed to dehydrate in laboratory atmospheric conditions so that they could be periodically rolled or turned over - this eliminated any tendency for the animals to adhere closely to the slide. They were then dried in an oven at 60°C for forty-eight hours (Edmondson and Winberg 1971). After drying, the Daphnia on their slides were placed in a calcium chloride dessicator for at least one hour prior to weighing (Lovegrove 1966).

Using tungsten needles with hooked points, the Daphnia were placed individually into the scale-pan of a Beckman LM500 electrobalance (sensitivity 0.5 ug; precision 0.05 per cent of the scale range). Any damaged animals were discarded. After one weight reading had been taken, the balance was not returned to zero but a second individual was added to the loaded scale-pan and the new weight recorded. This procedure was repeated until five sets of cumulated weighings had been taken (Doohan and Rainbow 1971).

Egg weights were determined by removing eggs {up to stage two of embryonic development as classified by Green (1956)} from several brood-pouches under the binocular microscope and placing batches of fifty eggs onto individual Daphnia which had been previously weighed. The above drying and weighing procedures were carried out and the weight of the egg mass was calculated by difference.

The weight data used for the biomass and production estimates of Cyclops strenuus abyssorum in Loch Leven was obtained by extrapolation from the length-weight equation of Klekowski and Shushkina (1966). This allowed the calculated estimates to be directly comparable with those of Walker (1970).

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

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.

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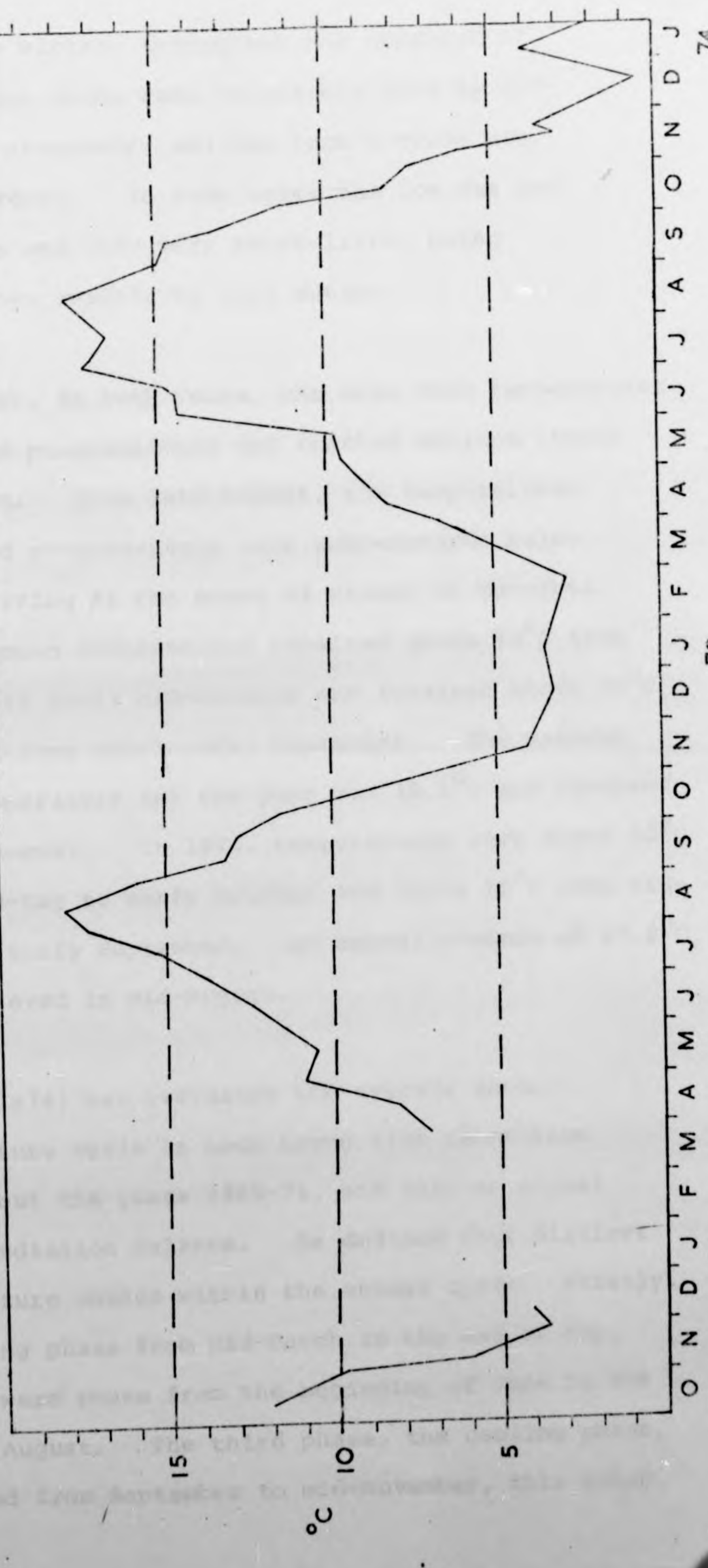
ure in ^{o}C.



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°C occurring at the onset of winter in November. In 1972 mean temperatures remained above 10°C from late April until mid-October and remained above 15°C from mid-June until early September. The maximum mean temperature for the year was 18.1°C and occurred in mid-August. In 1973, temperatures were above 10°C from mid-May to early October and above 15°C from mid-June to early September. An annual maximum of 17.8°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 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.

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 °C.

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

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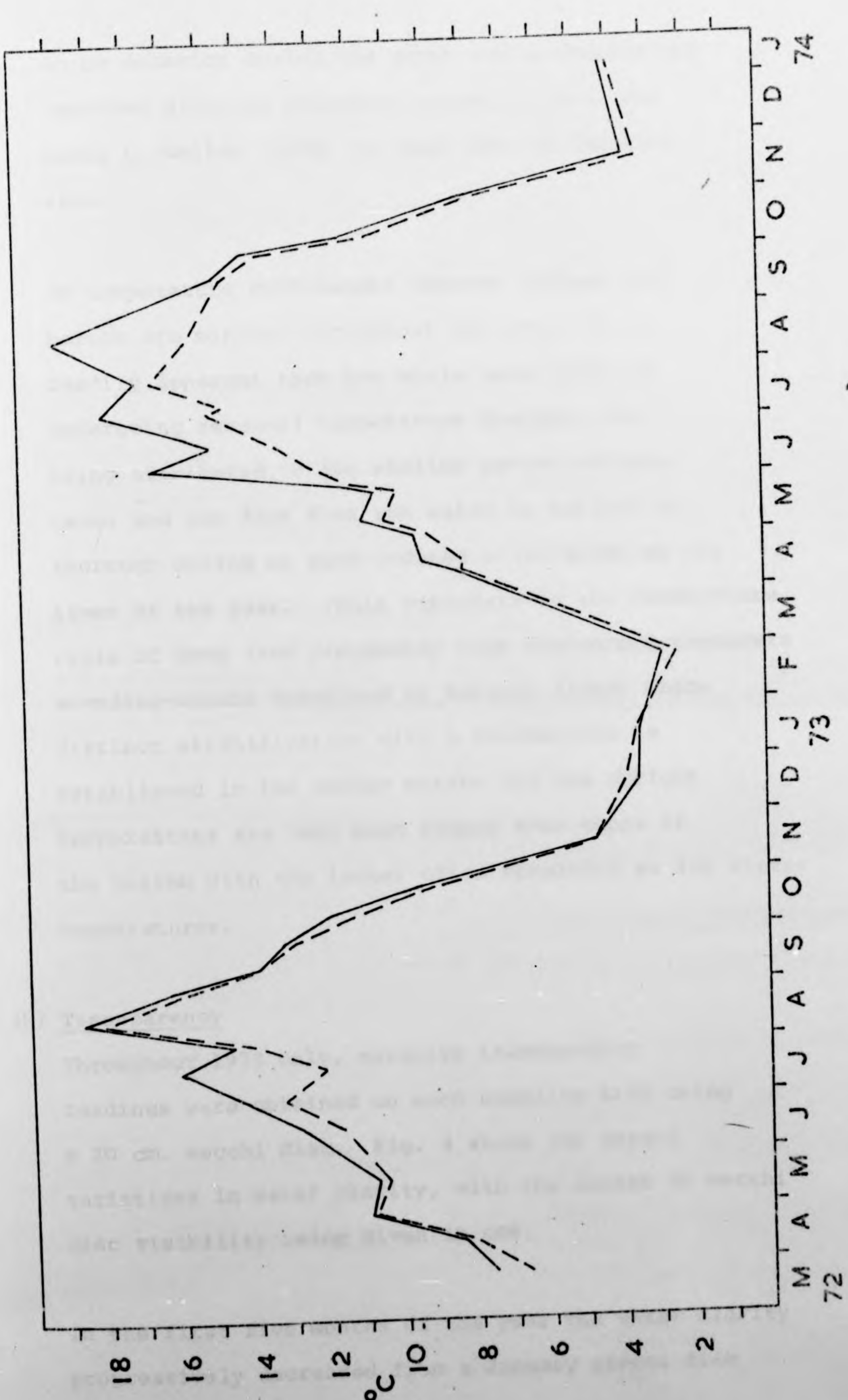

On no occasion during the study was a thermocline recorded although temporary stratification was noted by Walker (1970) in June 1969 at the same site.

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 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.

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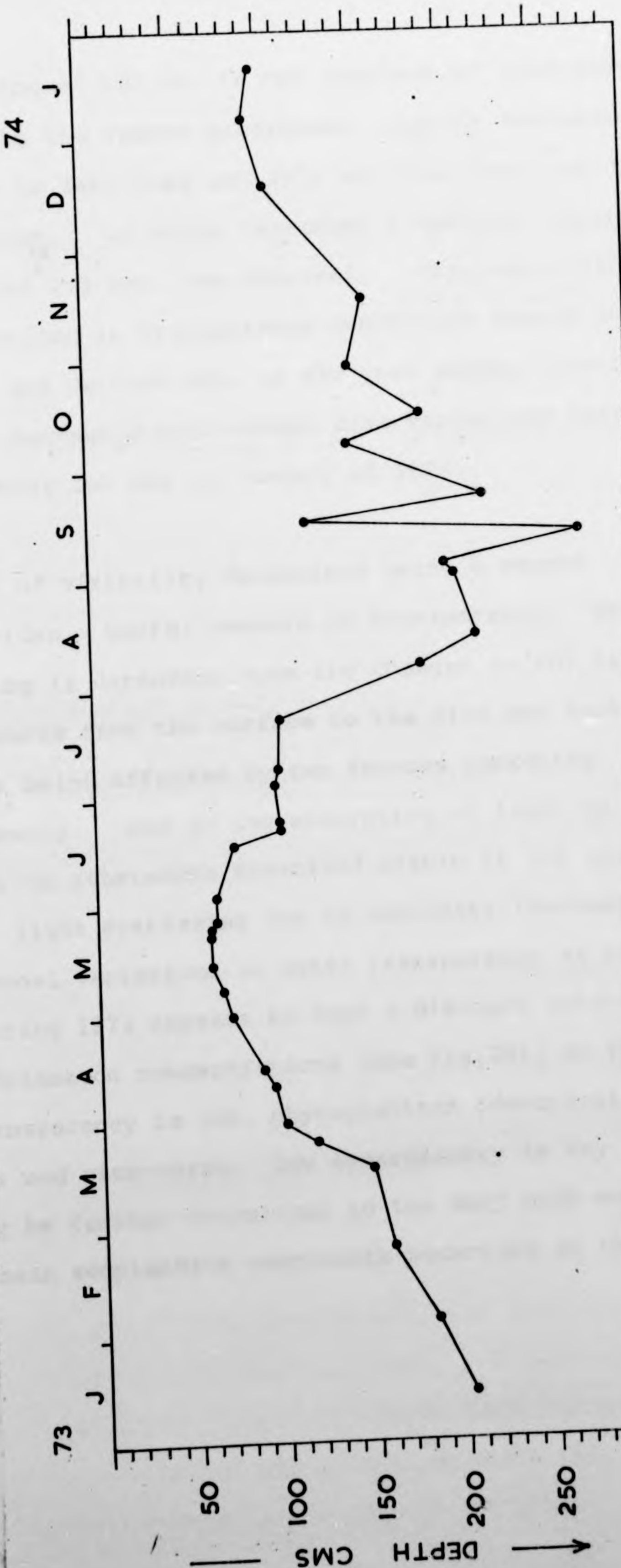
Fig. 4



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*.

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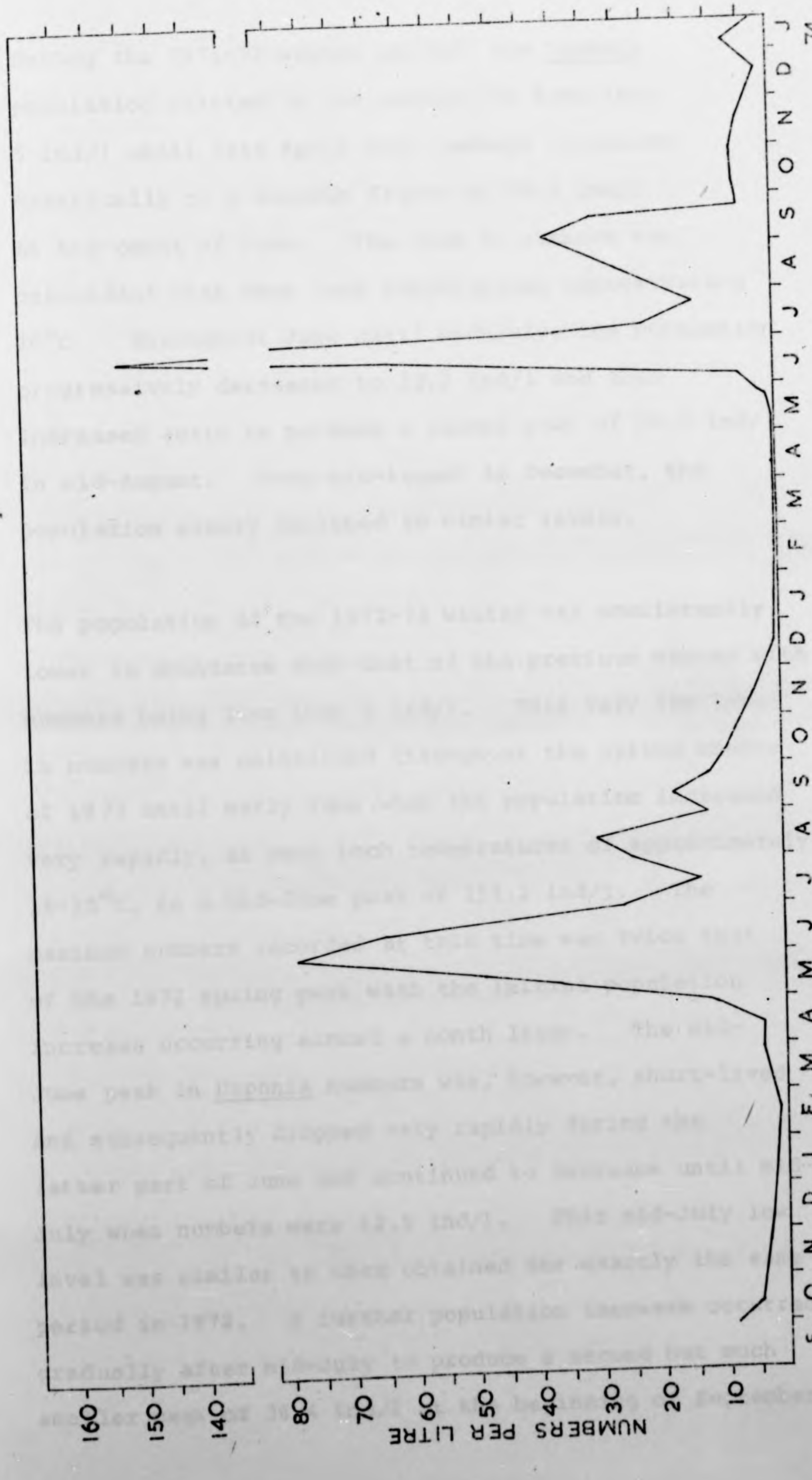


During the 1971-72 winter period, the Daphnia population existed in low numbers of less than 5 ind/l until late April when numbers increased drastically to a maximum figure of 78.2 ind/l at the onset of June. The rise in numbers was coincident with mean loch temperatures approximating 10°C. Throughout 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

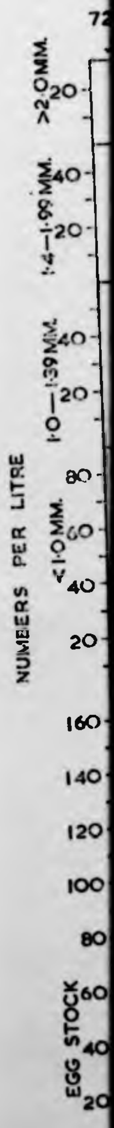
Figure 6 (opposite)

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.



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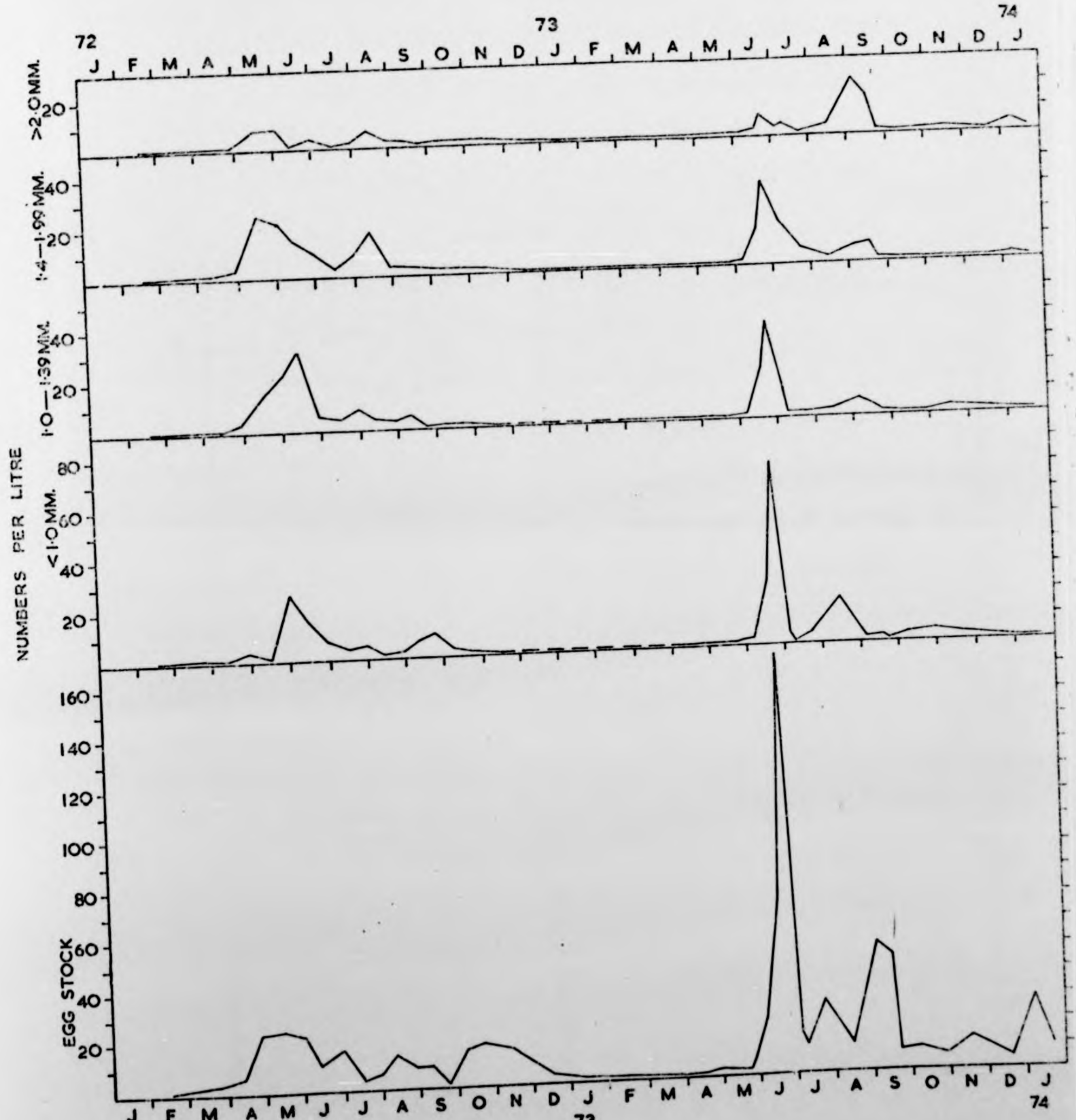

Figure 7 (opposite)

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.

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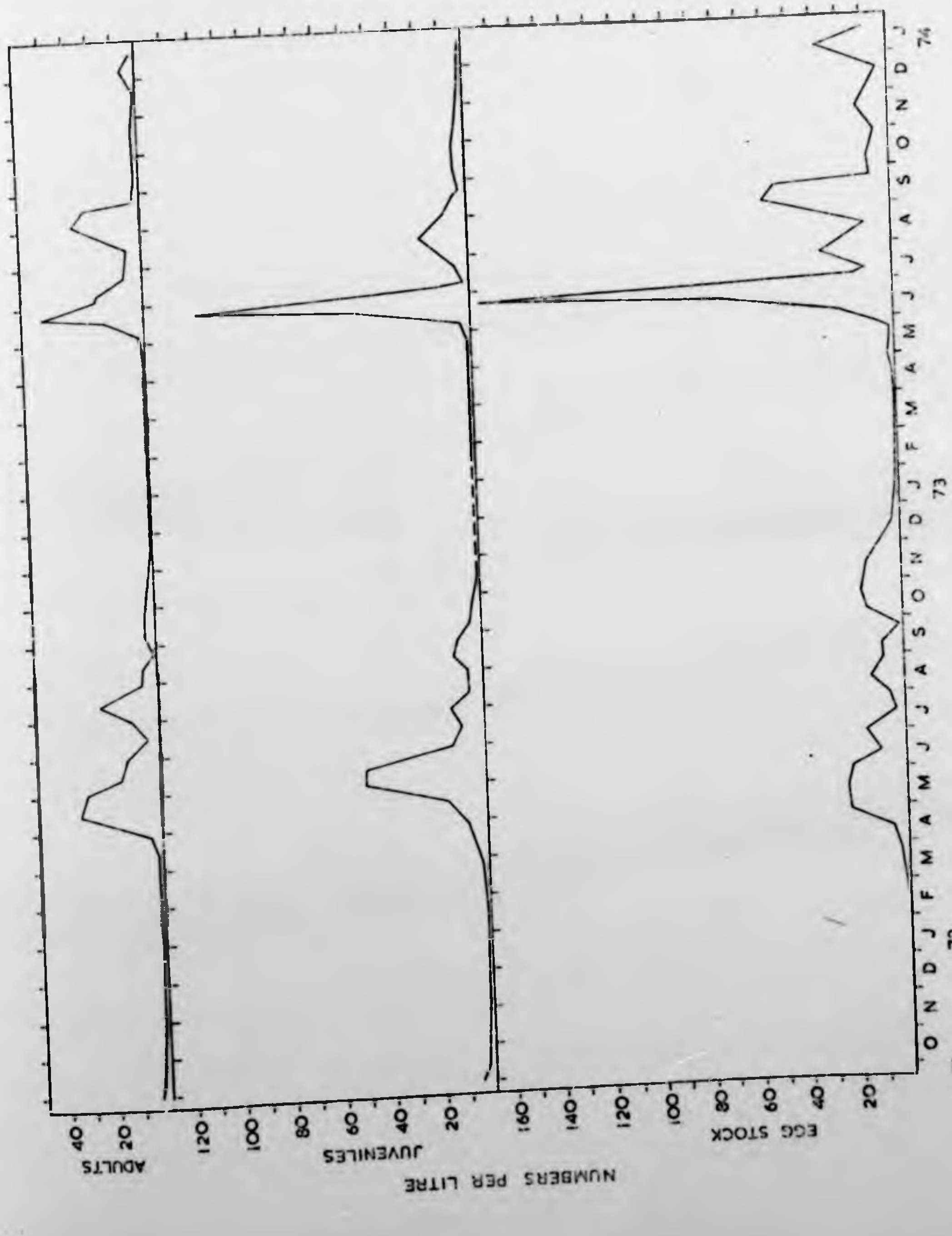

Figure 8 (opposite)

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.

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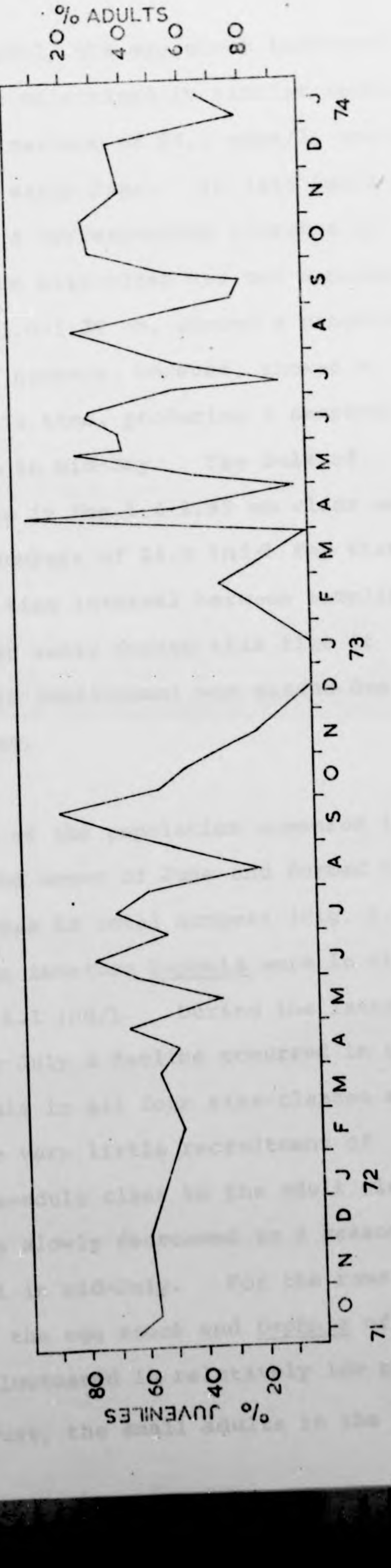
Fig. 8



under $5^{\circ}C$. 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 although in mid-August, the small adults in the 1.4 - 1.99 mm 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 with clearly defined rises in egg stock, to a mid-June 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

Figure 9 (opposite)

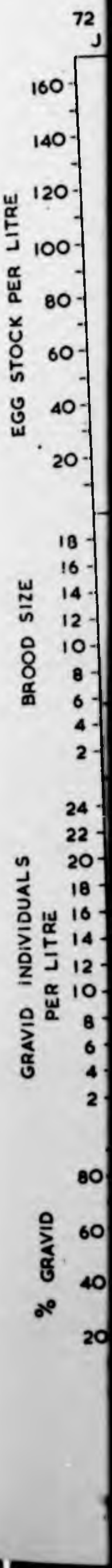
The breeding parameters of the D. hyalina var lacustris population of Loch Leven during 1972-73.

Abcissa - the study period

Ordinates - the percentage of gravid (parthenogenetic) females making up the adult (size >1.4mm) Daphnia population.

- the mean numbers per litre of gravid females.
- the mean brood-size.
- 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 number of gravid females per litre for each sampling date.



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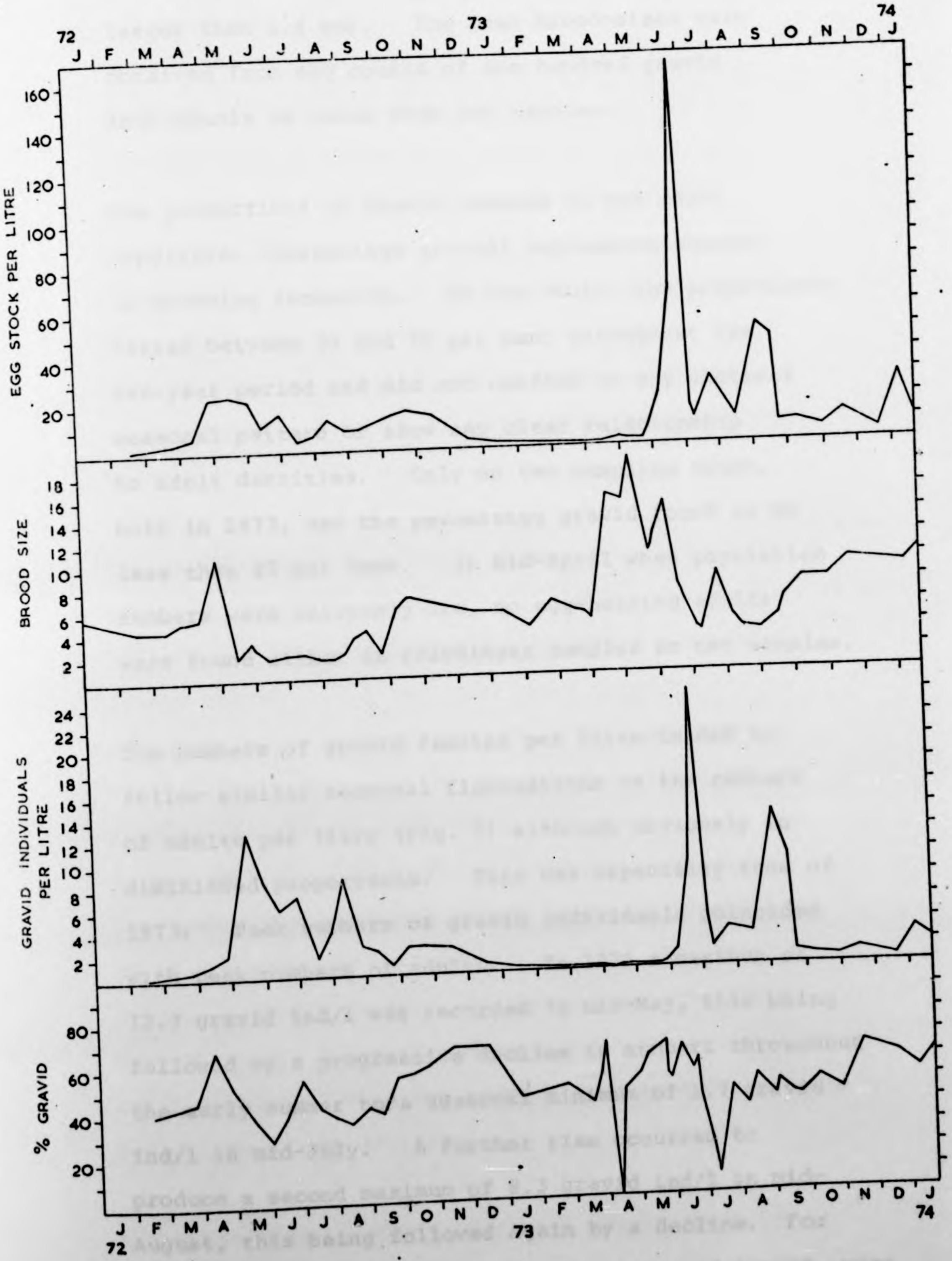

being acertained from the proportion of gravid females in the adult population (i.e. individuals larger than 1.4 mm). The mean brood-sizes were obtained from egg counts of one hundred gravid individuals as taken from net samples.

The proportions of gravid females in the adult population (percentage gravid) represents changes in breeding intensity. On the whole, the proportions varied between 30 and 70 per cent throughout the two-year period and did not conform to any distinct seasonal pattern or show any clear relationship to adult densities. Only on two sampling dates, both in 1973, was the percentage gravid found to be less than 25 per cent. In mid-April when population numbers were extremely low, no egg-bearing adults were found either in Friedinger samples or net samples.

The numbers of gravid females per litre tended to follow similar seasonal fluctuations as the numbers of adults per litre (Fig. 7) although obviously in diminished proportions. This was especially true of 1973. Peak numbers of gravid individuals coincided with peak numbers of adults. In 1972 a maximum of 12.7 gravid ind/l was recorded in mid-May, this being followed by a progressive decline in numbers throughout the early summer to a seasonal minimum of 1.7 gravid ind/l in mid-July. A further rise occurred to produce a second maximum of 8.3 gravid ind/l in mid-August, this being followed again by a decline. For only three months during 1972, May, June and August, were the numbers of gravid individuals consistently above 4 ind/l.

During 1973, however, a mid-June maximum of 24.3 gravid ind/l was obtained, this being followed by a sudden drop in early July caused by a lack of egg production in the adult population (only 8 per cent gravid). Low numbers of gravid individuals, less than 4 ind/l persisted until late August when a further rise to produce a second peak of 13.5 gravid ind/l was recorded at the onset of September. Numbers of egg-bearing adults dropped sharply towards the end of September.

The variations in mean brood-size showed a distinct seasonal pattern in both years. During the winters 1971-72 and 1972-73, the mean brood-size remained fairly stable at 4-6 eggs per brood (eggs/brood) although in the early winter of 1973-74 egg numbers were slightly higher 8-10 eggs/brood. The most notable changes occurred during the early spring and summer periods. In 1972, egg numbers increased very rapidly from winter levels to an annual maximum of 10.7 eggs/brood in late April. The egg numbers then dropped markedly in May and subsequently remained at approximately 2 eggs/brood throughout the entire summer until September, when the numbers increased again quite rapidly to winter levels.

A similar annual pattern of events was apparent in 1973 although brood-sizes were generally much larger. The egg numbers drastically increased from winter levels to 15.1 eggs/brood in mid-April and were maintained at high levels, reaching a mean maximum of 18.9 eggs/brood in early May, until brood-sizes declined in June. Despite an apparent rise in egg numbers to 8.7 eggs/brood in late July, brood-sizes were generally low during the summer, particularly in August when numbers were approximately 4 eggs/brood. From mid-September onwards, brood-sizes steadily increased to winter levels.

The mean brood-sizes during 1972 and 1973 are again shown in Fig. 10 with the inclusion of the range (maximum and minimum) and 95 per cent confidence limits (standard error x t) for each of the data points. On most sampling dates, females with just one egg in their brood-pouches were encountered, this being the obvious lowest limit. In 1972 there was one exception. In late April a minimum brood-size of 4 eggs was noted, this being concurrent with the annual mean maximum brood-size of 10.7 eggs/brood. However, in 1973 during April and for most of May, the minimum limit was between 3-6 eggs/brood. Maximum brood-sizes were consistently higher in 1973 than in 1972 with the largest brood of the two years, 39 eggs/brood being recorded in early May 1973. Only on two sampling dates in 1972 were broods larger than 20 eggs recorded whereas in 1973, broods of over 20 eggs were noted on ten occasions.

Figure 10 (opposite)

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

Abcissa - the study period

Ordinates - the mean adult body length in mm.

- the mean brood-size.

Key

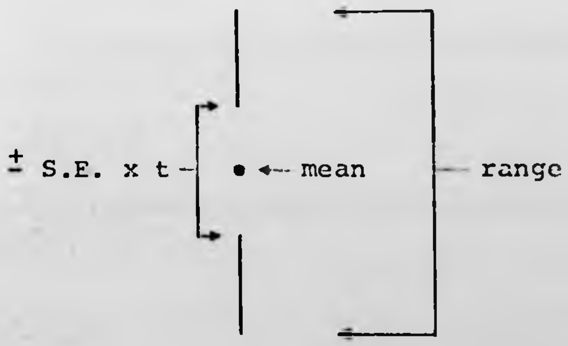

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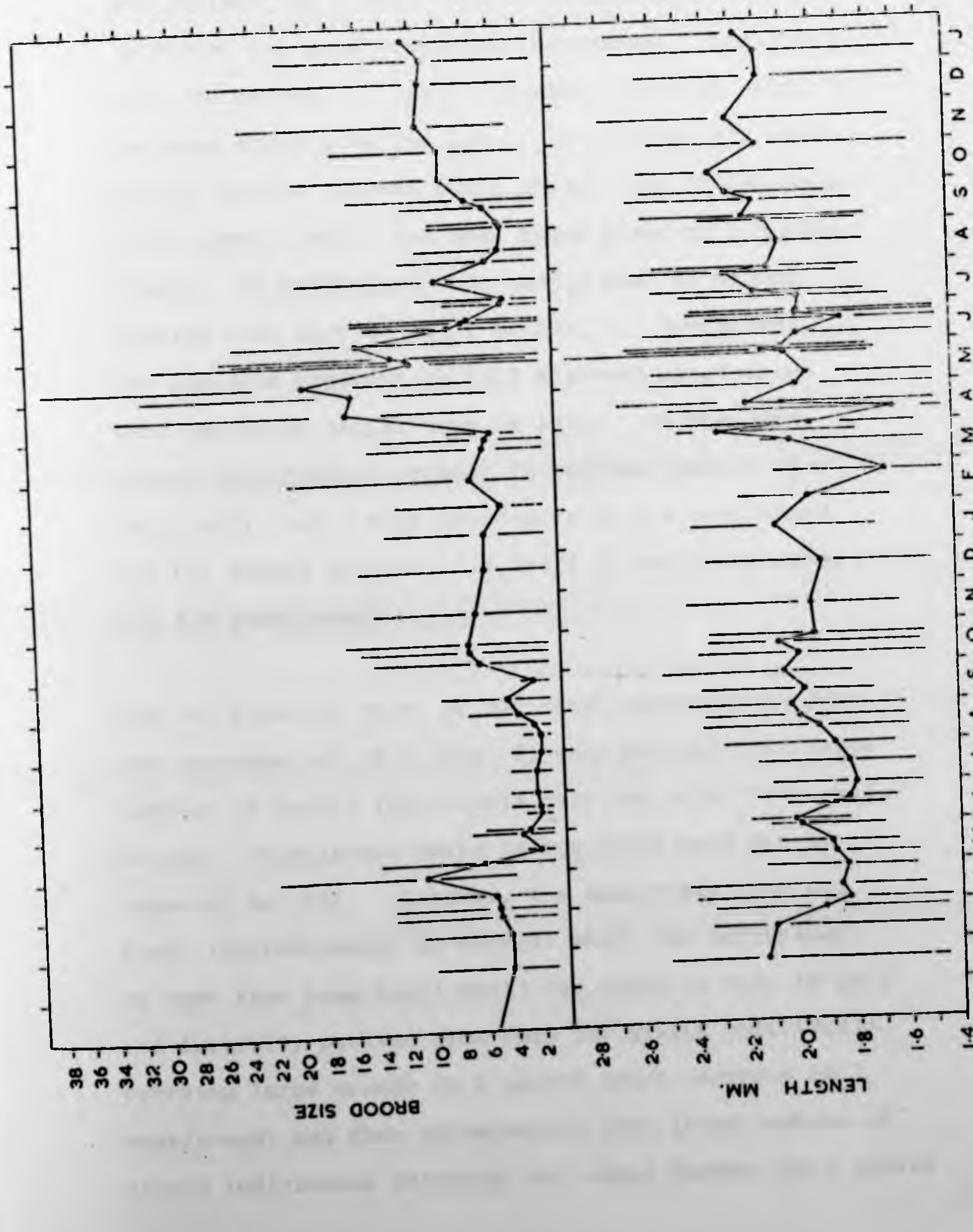
Fig. 10



With reference to Fig. 5, it is apparent that in the spring of 1972 and in the spring and early summer of 1973 the maximum mean brood-sizes were achieved at very low Daphnia population densities, particularly in 1973. When the population numbers increased the mean brood-size decreased. Similarly when the numbers of gravid females were high (Fig. 9) the mean brood-size was low. In mid-May 1972 when gravid females reached their annual peak of abundance (12.7 gravid ind/l) the mean brood size was 1.9 eggs/brood. In mid-August, the second peak of gravid females also carried small broods, 1.7 eggs/brood. The same was apparent in 1973 although brood-sizes were generally larger than in 1972. In mid-June, gravid individuals, present in maximum numbers of 24.3 ind/l, had a mean brood-size of 6.8 eggs/brood and the second peak of 13.5 ind/l in early September had 3.8 eggs/brood.

The two distinct peaks in egg stock occurring in June and September of 1973 (Fig. 9) were derived from large numbers of gravid individuals carrying relatively small broods. Comparable peaks in egg stock were not so apparent in 1972. However, the moderately high egg stock (approximately 23 eggs/l) which was maintained as such from late April until the onset of June in 1972 was initially derived from very few gravid individuals carrying large broods (2.2 gravid ind/l carrying 10.7 eggs/brood) and then subsequently from large numbers of gravid individuals carrying very small broods (12.7 gravid ind/l carrying 1.9 eggs/brood in mid-May and 8.5 gravid ind/l carrying 2.6 eggs/brood in the beginning of June).

iii. Variations in mean adult body-size

Fig. 10 shows the variations in mean adult body-size during 1972 and 1973. The length data was initially derived from carapace measurements, according to Burns (1969), of one hundred gravid female individuals per sampling visit but, so that the data depicted total length from the base of the tail spine to the top of the head as for a round-headed individual, each of the means was multiplied by a factor of 1.385. Total length for a round-headed Daphnia hyalina var. lacustris adult was found to be 138.5 per cent of the carapace length. The graph also gives the range (maximum and minimum) and 95 per cent confidence limits (S.E. x t) similarly modified to total length for each of the means. Note that all the adults under consideration carried eggs and were measured prior to brood-size assessments. (Materials and Methods, page 29). The mean length data and mean brood-size data are presented together in Fig. 10.

The variations in mean adult length, unlike those of the mean brood-size did not show a clear seasonal pattern in either year. In 1972, the mean length fluctuated from 1.79 mm to 2.13 mm and in 1973 from 1.62 mm to 2.29 mm. However, the mean sizes of adult females in 1973 were generally larger than in 1972. On eight sampling dates in 1972 the mean sizes were above 2.0 mm as compared to nineteen occasions in 1973. Similarly, mean sizes were above 2.1 mm only on two occasions in 1972 as compared to eleven occasions in 1973.

Maximum individual size ranges were consistently higher in 1973 also. For most of 1973 the maximum female size range was above 2.5mm. This contrasts to the situation in 1972 when on only two occasions were maximum range sizes above 2.5 mm. The largest individual encountered during the entire study was 2.85 mm in length and appeared in late May 1973. The mean maximum size, obtained as the average of all the largest females on each sampling date during the entire study, was 2.4 mm.

The lower limit of the size ranges showed distinct variations in both years. In 1972 the minimum egg-bearing size varied from 1.44-1.82 mm. From February until early April, the minimum size was low, between 1.4-1.5 mm, but for the rest of the year it was consistently higher and remained above 1.5 mm.

In the latter half of May and in June and September the minimum was greater than 1.6 mm. In 1973 the lower limit varied from 1.44-1.89mm. During the first six months the minimum size remained low within 1.4-1.5mm., but from July to October it remained consistently above 1.7mm.

Egg-bearing females less than 1.6mm were, however, found in samples from late October until January of 1974.

iv. Population birth and death rates

Various population parameters can be derived from a knowledge of egg numbers, egg development-times and standing crop numbers. These include population birth and death rates and have been applied to cladoceran populations by Hall (1964), Edmondson — [illegible] (1964), Wright (1965) and George and Edwards (1975).

If the number of eggs in a population (E) is known, and the duration of development of the eggs (D) determined, then given the initial population size (N_o), the finite birth rate or number of newborn per individual per day (B) may be calculated thus :

$$B = \frac{E}{D, N_o}$$

Once B has been determined, an estimate of the instantaneous birth rate (b) may be calculated :

$$b = \log_e \ (1+B)$$

Although this holds rigorously for a population with a stable age structure, it can be applied to non-steady-state population as an approximation.

A measure of the actual or net rate of population growth, the coefficient of population growth (r) can be calculated from successive pairs of population density values. If N_o is the initial population size and N_t the population after time t, then on the basis of the instantaneous growth equation:

$$N_t = N_o e^{rt}$$

and thus $$r = \frac{\log_e N_t - \log_e N_o}{t}$$

Once b and r have been obtained, the instantaneous death rate (d) can be calculated :

$$d = b - r^{*}$$

The population parameters b, r and d have been calculated for the Loch Leven Daphnia population, throughout the two year sampling period and are presented in Fig. 11. Egg durations used for the assessments of b are given on page 73. The values of b relate to specific points in time (i.e. sampling

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* Further calculations can provide estimates of turnover time and eventually production as outlined in the Review Section, pages 19 and 20. The instantaneous death rate can be converted to finite death rate (D) by the equation :

$$D = 1 - e^{-d}$$

and from this the turnover time in days can be derived thus :

$$T = \frac{1}{D}$$

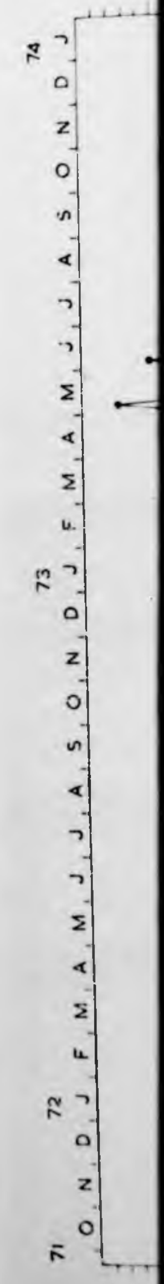
with the percentage turnover per day being $\frac{1}{T} \times 100$.
An estimate of production can then be acertained by multiplying the daily percentage turnover by the standing crop biomass.

Figure 11 (opposite)

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

Abcissa - the study period.

Ordinates - the population parameters :-
Observed (r) and estimated (b) instantaneous rates of population increase and estimated death rates (d).



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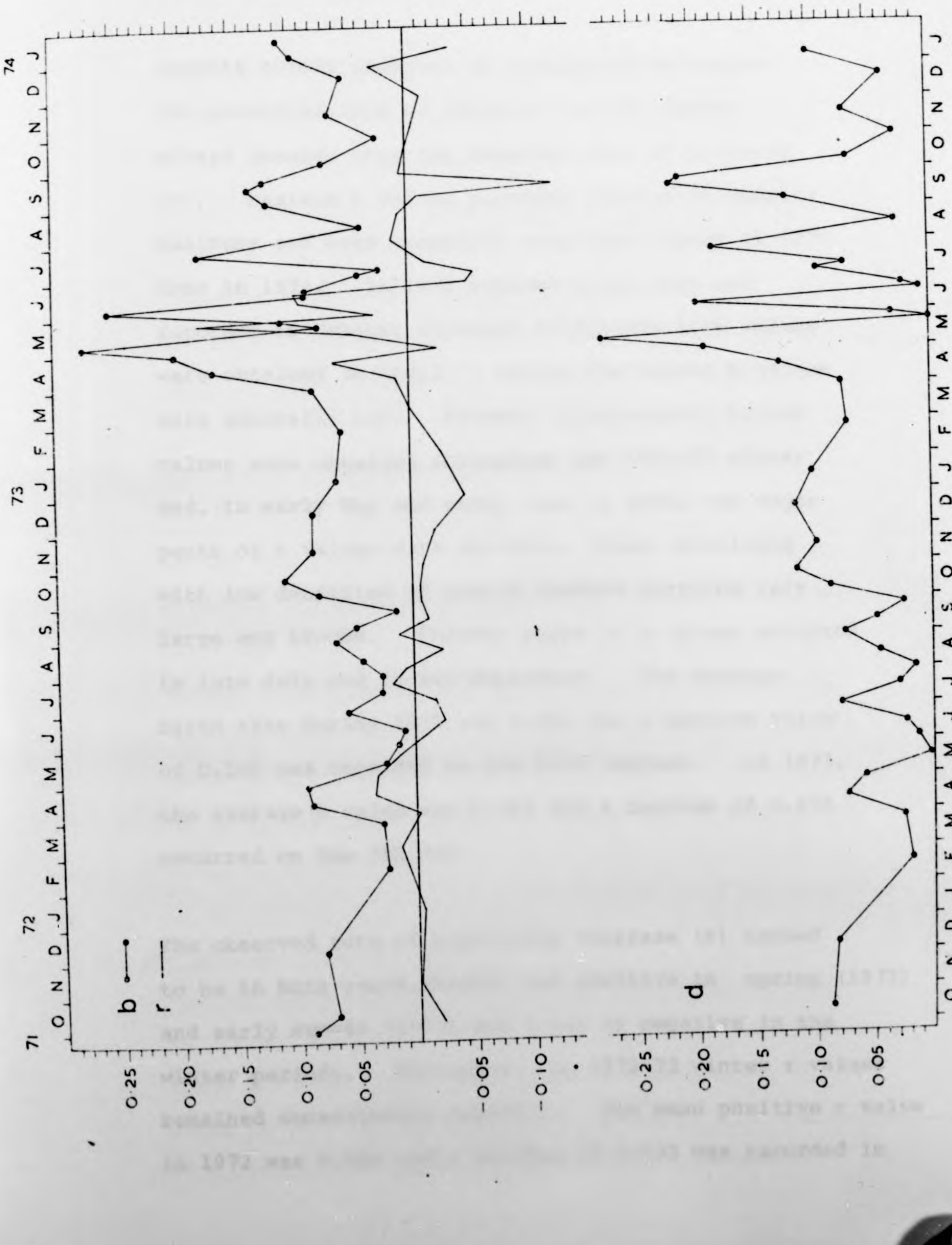

dates) whereas the values of r represent an average for a given period and have thus been plotted on the mid-point of each period.

Despite errors inherent in population estimates, the potential rate of increase (b) was nearly always greater than the observed rate of increase (r). Maximum b values preceded population density maximums and were generally very much higher in 1973 than in 1972. In 1972 maximum birth rate was recorded in October although relatively high values were obtained in April. During the summer b values were generally low. However, consistently higher values were obtained throughout the 1972-73 winter and, in early May and early June of 1973, two major peaks of b values were obtained, these coinciding with low densities of gravid females carrying very large egg broods. Further peaks of b values occurred in late July and in mid-September. The average birth rate during 1972 was 0.052 and a maximum value of 0.109 was recorded on the 21st October. In 1973, the average b value was 0.106 and a maximum of 0.278 occurred on the 7th May.

The observed rate of population increase (r) tended to be in both years, higher and positive in spring (1972) and early summer (1973) and lower or negative in the winter periods. Throughout the 1972-73 winter r values remained consistently negative. The mean positive r value in 1972 was 0.019 and a maximum of 0.035 was recorded in 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 <u>Daphnia</u> <u>hyalina</u> var <u>lacustris</u> (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 lm 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 of sites. Sites A, D and E were sampled in 1973.

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.

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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 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

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

sexual forms of

Leven.

parthenogenetic

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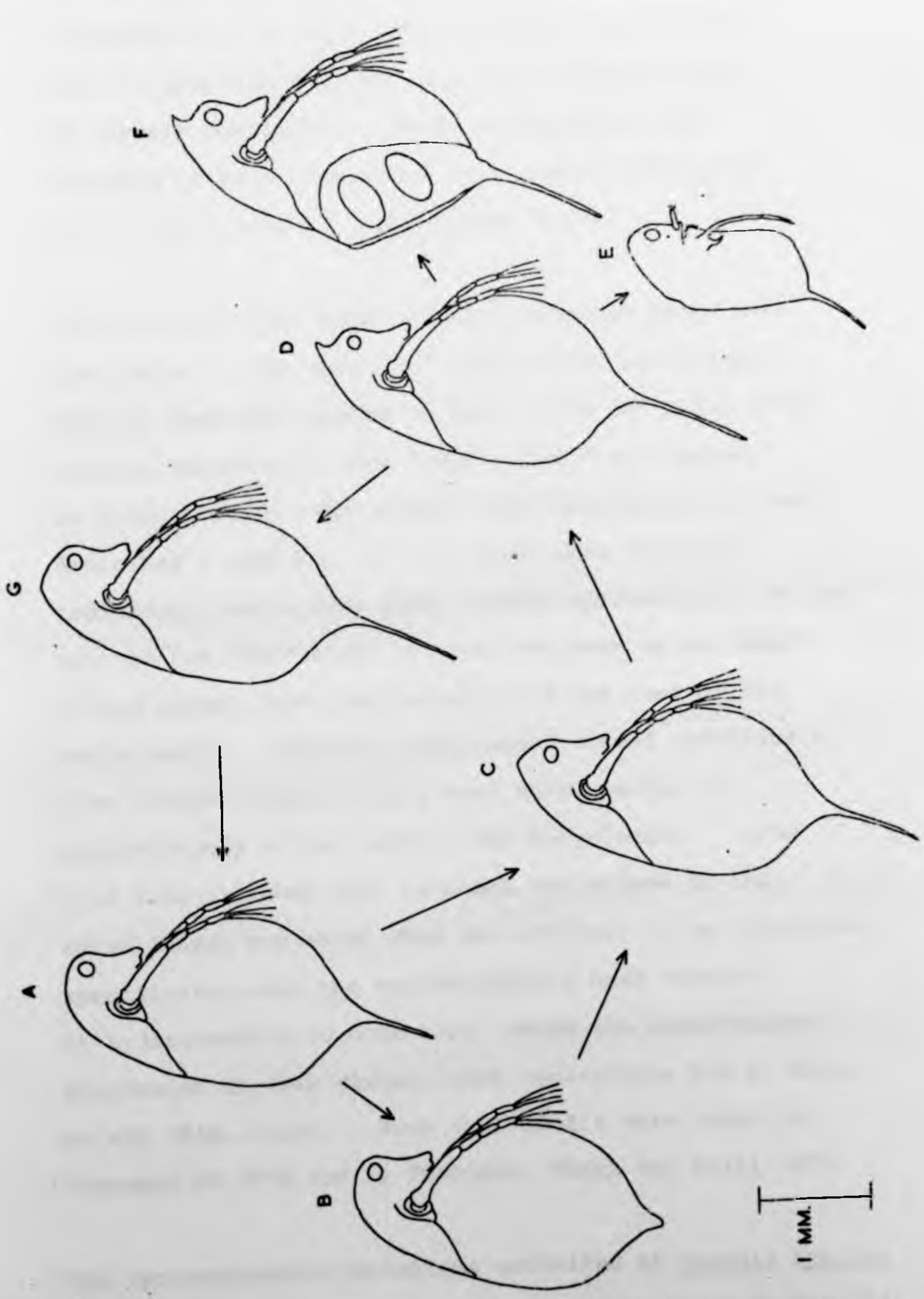
Fig. 13



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. The data applies to egg-bearing females only and was derived

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).

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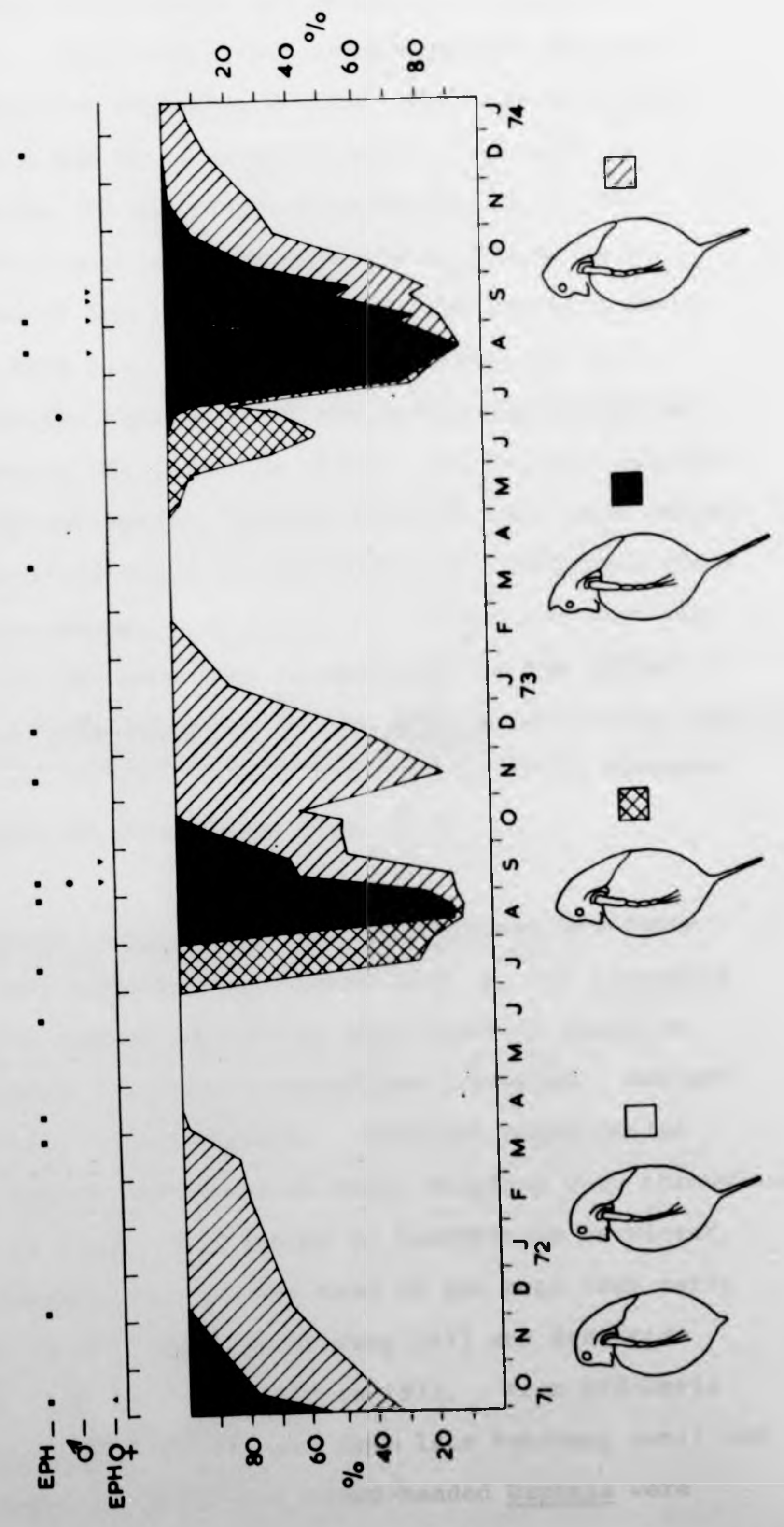
Fig. 14



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 encountered during net-sample analysis.

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.

i. The growth-rates of individuals and egg durations

On a diet of excess *Chlorella pyrenoidosa* at 15°C, nine female individuals and one male were successfully reared. The growth-rates of the nine females showed considerable variation despite being reared in apparently identical conditions. This is best illustrated using the body-size (total length) and date at the onset of the first brood as a comparative index. Body-length at maturity varied from 1.47-1.74 mm and the mean length derived as the average of all nine individuals was 1.59mm. The number of juvenile moults (estimated from evidence of carapace casts) varied from four to five, with five out of the nine individuals moulting four times. The number of days required to reach maturity varied from 8-13 days with the mean for the nine females being 11.2 days.

Once maturity had been attained, each individual produced broods of eggs in succession, with ecdysis and consequential size increases being coincident with the release of fully developed embryos. One of the nine individuals produced only three successive broods before it died from accidental mishandling, the other eight produced at least seven broods each with three individuals producing a maximum of twelve broods each. The duration of egg development, defined here as the number of days from the appearance of egg batches in the brood pouch to the release of the young, varied from

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3-7 days. A mean egg duration based on seventy-seven such observations at 15°C was calculated to be 4.42 days.

The longevity, or to be more exact, the occurrence of death in the obvious absence of accidental mishandling, was ascertained from eight individuals and varied from 39-71 days. For the purposes of assessing longevity it seemed appropriate to use the data from the three individuals which had produced twelve broods each. The mean life-span of these at 15°C was 65 days and the mean size at death was 2.42mm.

At 10°C, on a Chlorella diet, five females were reared. One of these individuals died due to mishandling after forty-one days, the other four were maintained for a maximum of sixty-eight days, the experiment being subsequently discontinued. The growth-rates of these females were also subject to variation. The number of juvenile moults and the body-sizes at maturity varied in a similar manner to the 15°C experiments. The times required for maturity to be reached were longer because of the lower temperature, varying from 15-22 days with a mean for the five individuals being 18.8 days. From forty-five observations of egg development, a mean egg duration of 8.23 days was calculated and the range was 7-9 days.

Because of the slow development-rates and the extended longevities with Daphnia individuals at low temperatures, the 5°C experiments mainly involved the assessment of egg durations using mature individuals with developing broods. From four such observations a mean egg duration of 15.52 days was established with a range of 14-17 days.

Mean growth curves were calculated for Daphnia females at 15°C and 10°C and are shown in Fig. 15. The mean growth curves were derived as the average growth rates of nine individuals at 15°C and five individuals at 10°c and were calculated from the sizes anddates of comparable moult-stages, using the size and date at maturity as the common reference point. In Fig. 15 each data point indicates a moult-stage and the arrows point to the onset of maturity. The 10°C curve has no end-point as a mean longevity was not established.

Two important points arise from Fig. 15 which need mention. Firstly, the body-lengths of young juveniles, newly-released from the parent brood pouch, were consistently found to be either 0.57mm or 0.58mm. Secondly, having established a mean growth curve at 15°C complete with a mean longevity, it can be said that a female D. h. var lacustris reared in such laboratory conditions is likely to have a maximum of seventeen moult-stages during its life-span, five as a juvenile and twelve as an adult.

One male individual was reared on an excess Chlorella diet at 15°C and the actual growth-rate depicting size

Figure 15 (opposite)

Mean growth curves for female D. hyalina var lacustris reared in laboratory conditions at 15°C and 10°C.

Abcissa - the mean age in days

Ordinate - the mean length in mm.

Note that each data point indicates a mean moult-stage and that the arrows depict the onset of the first brood of eggs (i.e. maturity). Note also that the 10°C curve has no end-point because a mean longevity at 10°C was not established.

Although growth in *Daphnia* spp. is discontinuous, with body-size increases occurring only during and immediately following ecdysis, the mean moult-stages in the graph are joined together simply by straight lines to emphasise that the graphs represent *mean* growth curves (of nine individuals at 15°C and five individuals at 10°C).

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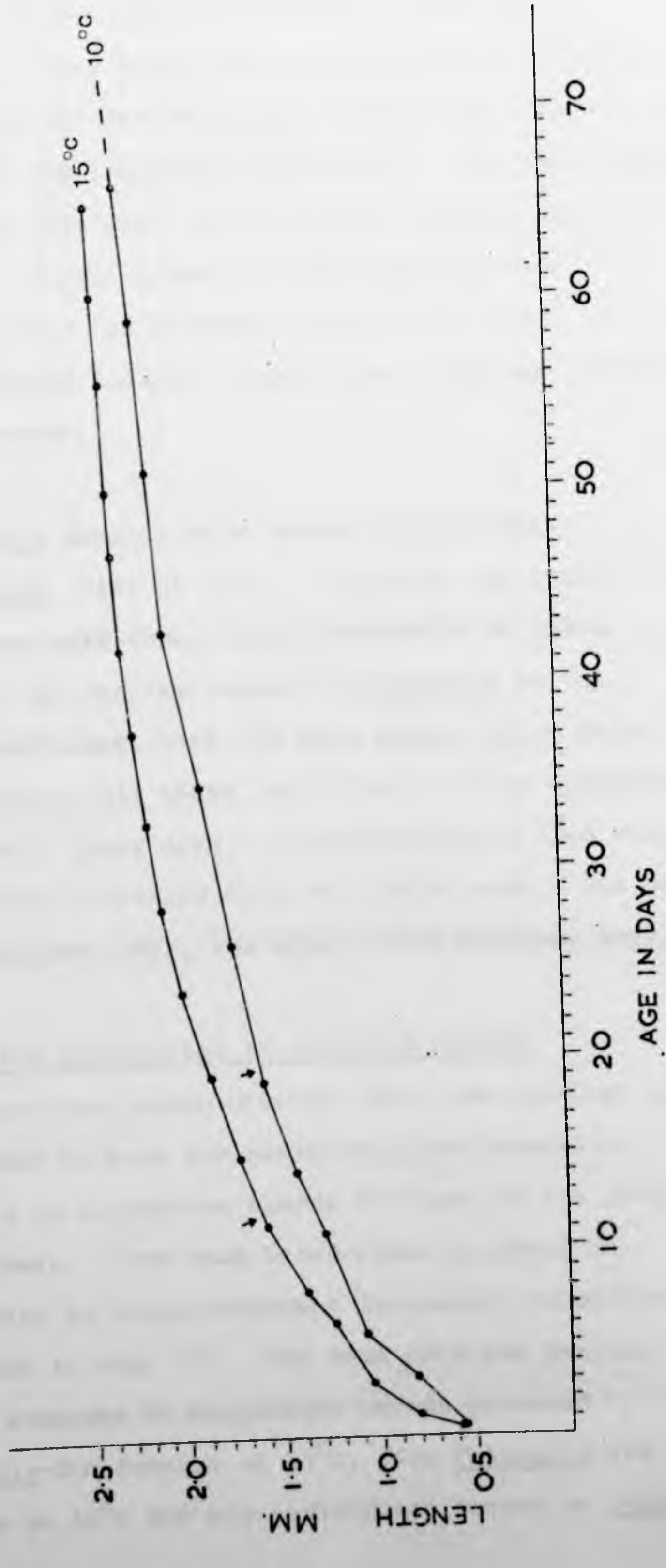
Fig. 15



increments at successive moults is shown in Fig. 16. This individual was approximately round-headed and was derived from a round-headed female parent reared in the laboratory aquariums. The male lived for fifty-five days and attained a maximum size of 1.55mm. Testes appeared after thirteen days. Although only ten carapace moults were found, the animal showed eleven distinct size increases throughout its life-span.

Six Daphnia females were reared on an excess Scenedesmus diet at 15°C. Although the growth-rate variations were found to be comparable to those obtained for females reared on Chlorella at the same temperature, with the mean growth curve being very similar, all these individuals fed on Scenedesmus died within forty days. Two individuals died very early after producing only two broods each - one died after eighteen days, the other after nineteen days.

ii. Successive brood-sizes of cultured females

Throughout the growth studies, data was obtained on the number of eggs (or newly-released juveniles) produced in successive broods for each of the female individuals. The mean brood-sizes produced in succession in three different laboratory conditions are shown in Fig. 17. The mean data was derived as the averages of successive broods produced by nine Chlorella-fed females at 15°C, five Chlorella-fed females at 10°C and six individuals reared on Scenedesmus

Figure 16 (opposite)

The growth-rate of an individual male *D. hyalina* var *lacustris* reared in laboratory conditions at 15°C.

Abcissa - the age of the male in days

Ordinate - the length of the male in mm.

Note that the graph depicts size-increments at successive moults in a step-wise fashion.

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Fig. 16

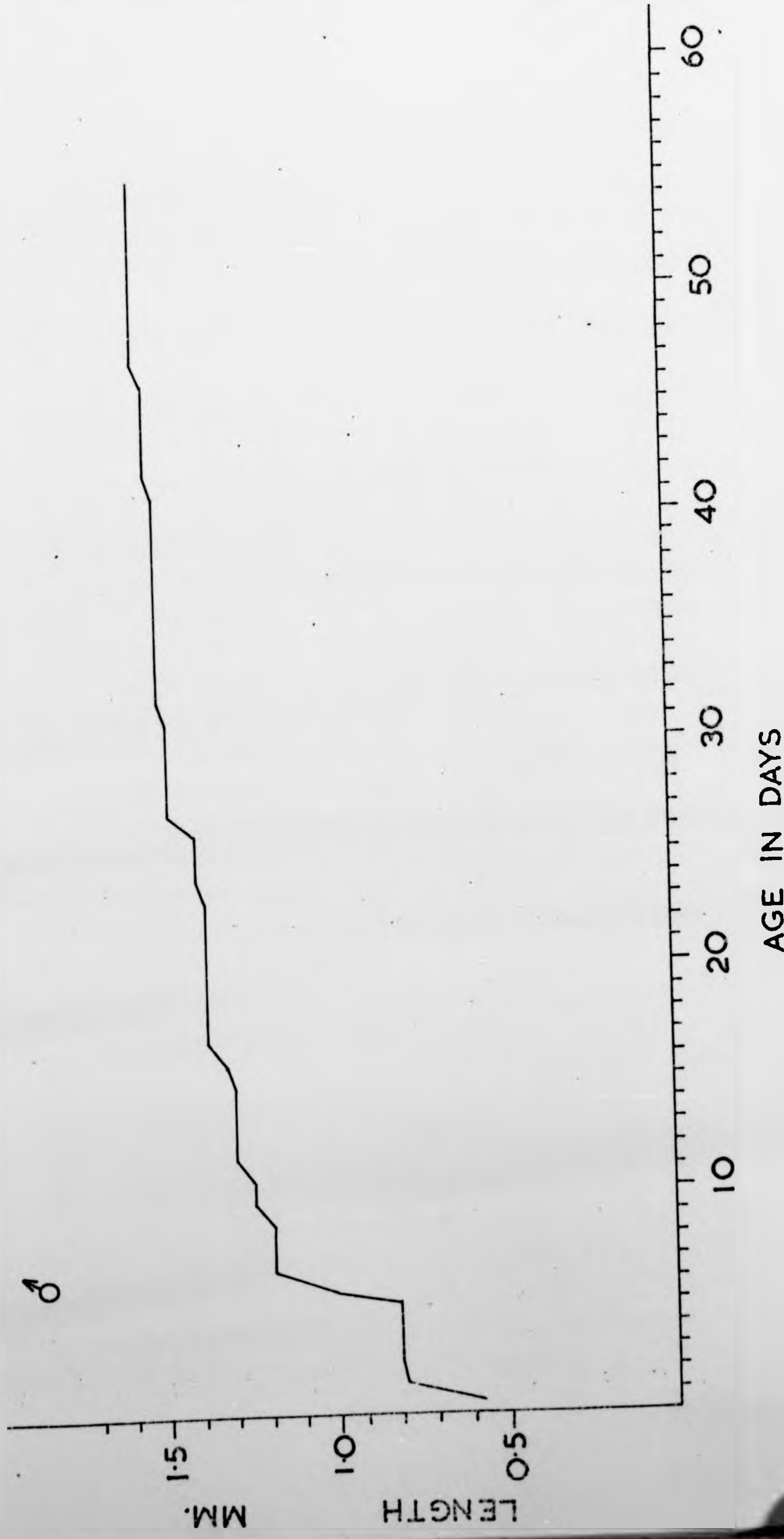

Figure 17 (opposite)

The mean brood-sizes produced in succession by *D. hyalina* var *lacustris* females reared in three different laboratory conditions.

Abcissa - successive broods 1st, 2nd, 3rd .... etc.

Ordinate - the mean brood-size of *Daphnia* fed on *Chlorella* at 15°C and 10°C and *Daphnia* fed on *Scenedesmus* at 15°C.

Note that the data for *Chlorella*-fed *Daphnia* at 10°C and *Scenedesmus*-fed *Daphnia* at 15°C extends to seven successive broods only. The limitation to seven broods for the *Chlorella*-fed 10°C data is due to the curtailment of the growth experiments (pages 37-38) whereas that for the *Scenedesmus*-fed 15°C data is due to mortality of all individuals reared.

Note also that because of variable longevities of individuals, the mean data points were derived from fewer females as successive brood numbers progressed (see Appendix (xiii)).

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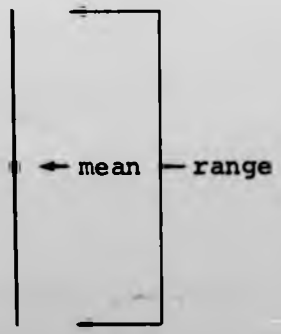

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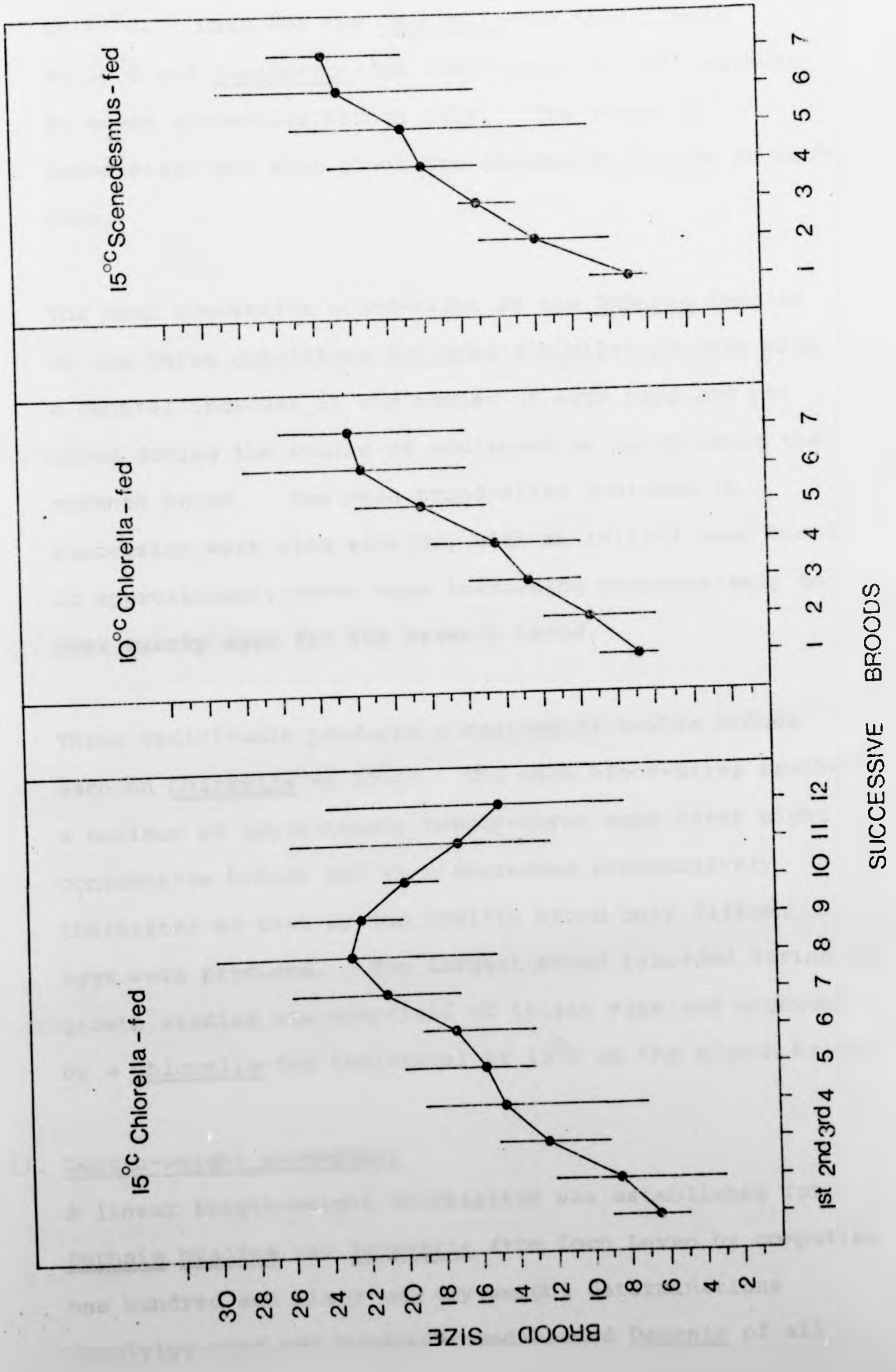
Fig. 17



at 15°C. Data for the Chlorella-fed individuals at 10°C and Scendesmus-fed individuals at 15°C extends to seven successive broods only. The range of brood-sizes are also given for successive broods in each case.

The mean successive brood-sizes of the Daphnia females in the three conditions followed a similar pattern with a general increase in the number of eggs produced per brood during the course of adulthood up to at least the seventh brood. The mean brood-sizes achieved in succession were also similar, with an initial mean brood of approximately seven eggs increasing progressively to over twenty eggs for the seventh brood.

Three individuals produced a maximum of twelve broods each on Chlorella at 15°C. The mean brood-sizes reached a maximum of approximtely twenty-three eggs after eight consecutive broods and then decreased progressively thereafter so that by the twelfth brood only fifteen eggs were produced. The largest brood recorded during the growth studies was comprised of thirty eggs and produced by a Chlorella-fed individual at 15°C as the eighth brood.

iii. Length-weight assessment

A linear length-weight correlation was established for Daphnia hyalina var lacustris from Loch Leven by computing one hundred and sixty-two dry-weight determinations involving over two hundred round-headed Daphnia of all sizes. The relationship between length and weight was found to be :

$$W = 6.28L^{2.81}$$

Where W = dry-weight in µg and L = length in mm. The length-weight regression is shown in Fig. 18.

The mean weight of an egg, obtained from separate dry-weight estimations of eight batches of fifty eggs each, was found to be 1.83µg with a range of mean values 1.32-2.80µg.

(e) Biomass and production estimates

i. Biomass

The numerical standing crop data obtained for Daphnia hyalina var lacustris was converted to biomass as follows. Using the length-weight equation, the mean weight of an individual in each of the four size-classes was calculated. These are given in Table 3 below.

Table 3. The calculated mean weights of Daphnia individuals in the four size-classes.

	1	2	3	4
Size-class mm	<1.00	1.00-1.39	1.40-2.00	>2.00
Length-range mm	0.58-1.00	1.00-1.39	1.40-2.00	2.00-2.40
Mean length mm	0.79	1.20	1.70	2.20
Mean weight µg	3.33	10.50	27.96	57.78

The minimum length of an individual in the <1.00mm size-classes was taken to be 0.58mm as derived from the growth studies.

Figure 18 (opposite)

The linear length-weight correlation for D. hyalina var lacustris from Loch Leven.

Abcissa - length in mm. on a logarithmic scale.

Ordinate - dry-weight in µg on a logarithmic scale.

The relationship between length and weight was found to be :

$$W = 6.28 L^{2.81}$$

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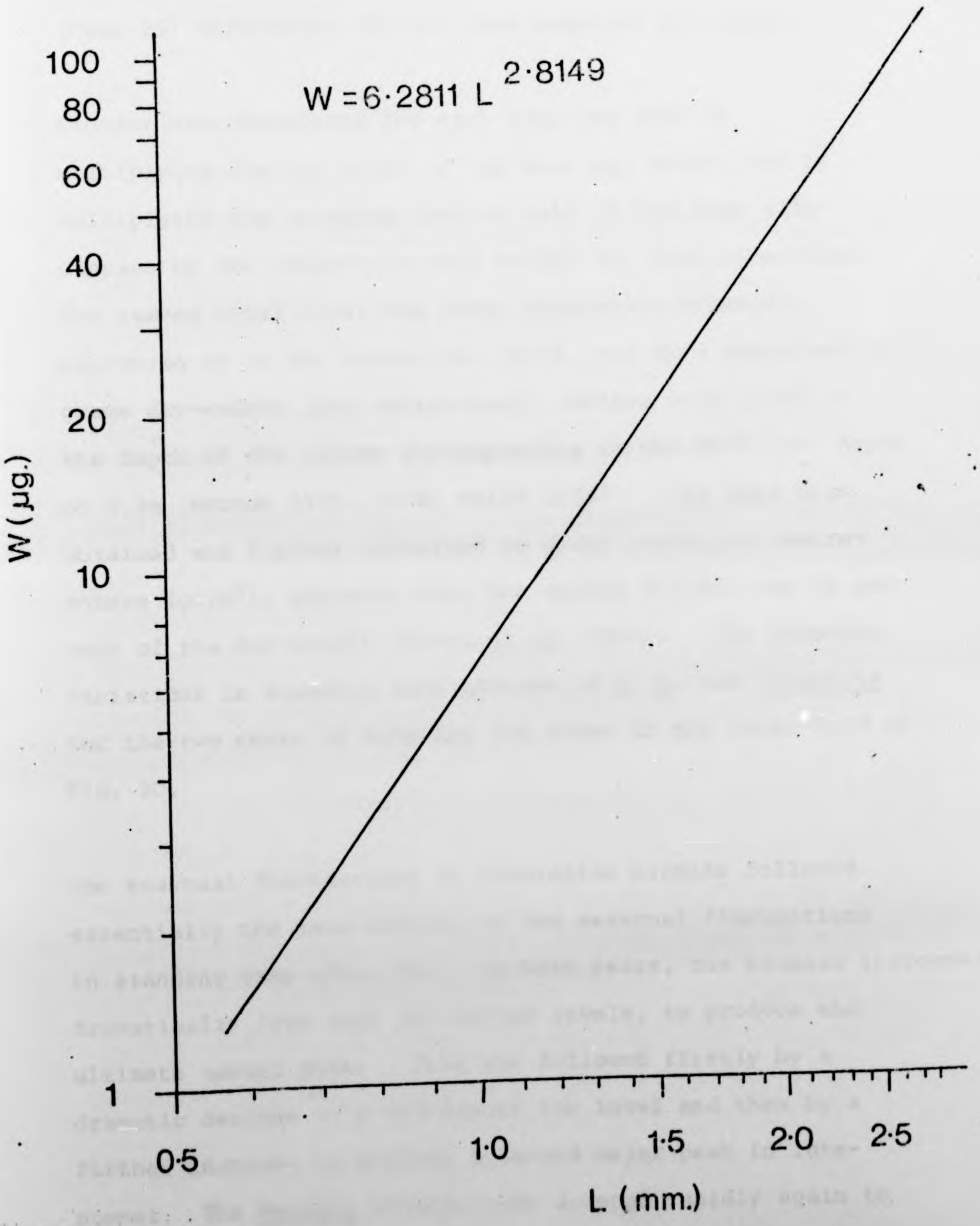
Fig. 18



The maximum size of an adult in the >2.00 mm size-class was taken to be 2.40mm, this being the mean of all the largest gravid females found in the body-length assessments (Page 58) throughout the two year sampling programme.

Biomass was calculated for each sampling date by multiplying the egg stock by the mean egg weight and by multiplying the standing crop of each of the four size-classes by the respective mean weight for each size-class. The summed total (i.e. the total population biomass), expressed as µg dry weight/per litre, was then converted to grams dry-weight /per metre-square surface area (g/m^2) - the depth of the column corresponding to the mean loch depth of 3.9m (Morgan 1970, 1974; Smith 1974). The data thus obtained was further converted to grams carbon/per metre-square (gC/m^2), assuming that the carbon content was 44 per cent of the dry-weight (Steel *et al*. 1972). The seasonal variations in standing crop biomass of *D*. *h*. var *lacustris* for the two years of sampling are shown in the lower half of Fig. 20.

The seasonal fluctuations in population biomass followed essentially the same pattern as the seasonal fluctuations in standing crop (Fig. 5). In both years, the biomass increased dramatically from very low winter levels, to produce the ultimate annual peak. This was followed firstly by a dramatic decline to a mid-summer low level and then by a further increase to produce a second major peak in late-summer. The *Daphnia* biomass then dropped rapidly again to low winter levels.

For most of the winter months during the sampling period, the population biomass levels remained consistently below 0.25 gC/m^2. In late April 1972, the biomass increased very drastically from low winter levels to a high value of 2.31 gC/m^2 in mid-May. This high level was maintained throughout the remainder of May with a further marginal increase giving rise to the annual maximum of 2.43 gC/m^2 at the onset of June. The biomass subsequently decreased steadily throughout June and in early July to give a mid-summer low level of 0.36 gC/m^2 in mid-July. Thereafter the biomass increased again to reach a second maximum value of 1.61 gC/m^2 in mid-August, this being followed firstly by a sharp decline in the latter half of August and then by a more gradual decline as the year ended.

From mid-December 1972 until late May 1973, the Daphnia biomass was exceptionally low, remaining consistently below 0.10 gC/m^2. In early June the population biomass rose very sharply to produce the ultimate annual maximum of 4.00 gC/m^2 in mid-June. This was followed by a rapid decline to a mid-July low level of 0.52 gC/m^2. The low level was similarly maintained until mid-August when the biomass once again increased very rapidly to achieve a second maximum of 2.72 gC/m^2 at the beginning of September. During the latter part of September the biomass level promptly dropped to winter levels.

There are two points concerning the biomass data which require mention at this stage. Firstly, the spring and autumn biomass peaks of both sampling years coincided exactly with the respective peaks of total population numbers as seen in Fig. 5. Secondly, the biomass on any given sampling date is dependent not only on the numbers of individuals but also on the sizes, and therefore weights, of the individuals present. For example, in terms of population numbers, the spring peak of 1972 (78.2 ind/l at the onset of June) is two-fold that of the autumn peak of 1973 (36.4 ind/l in early September), yet, in terms of biomass, the autumn peak of 1973 (2.72 gC/m^2) is marginally greater than that of the spring peak of 1972 (2.43 gC/m^2). This point emphasises the value of biomass (as opposed to simply numerical data) to evaluate the same population from the same water at different times and also to compare similar populations from different waters. It should be emphasised that the population biomass, as presented here, also includes the egg stock.

ii. Production

The method of estimating production adopted in the present study has been discussed in the Review Section (Page 20). Apart from field population and temperature data, the method requires information on the durations at different temperatures and the weight increments of all the various developmental components of the population. The formula used to calculate the production of the Daphnia hyalina var lacustris population for each sampling date is as follows:

$$P = \frac{Ne.We}{De} + N_1 \frac{(W_1\text{max}-We)}{D_1} + N_2 \frac{(W_2\text{max}-W_1\text{max})}{D_2} + N_3 \frac{(W_3\text{max}-W_2\text{max})}{D_3} + N_4 \frac{(W_4\text{max}-W_3\text{max})}{D_4}$$

Where P = production in µg per litre per day (µg/l/day)

N = number per litre

W = dry-weight in µg ($W_?\text{max}$ = maximum dry-weight in µg).

D = duration of life stage in days

e = eggs

1 = size-class <1.0mm

2 = " " 1.0 - 1.39 mm

3 = " " 1.4 - 1.99 mm

4 = " " >2.0mm

Using the length-weight formula (Fig. 18) the weight increments of each of the four size-classes were obtained by subtracting the maximum weight of one size-class from the maximum weight of the following size-class. The derivation of this data is summarised in Table 4 below.

Table 4. The weight increments of the four size-classes of *D. hyalina* var *lacustris*.

	1	2	3	4
Size-class mm	<1.00	1.00-1.39	1.40-1.99	>2.00
Maximum size mm	1.00	1.39	1.99	2.40
Maximum weight µg	6.28	16.19	44.19	73.82
Weight increment µg	$W_1\text{max}-We$	$W_2\text{max}-W_1\text{max}$	$W_3\text{max}-W_2\text{max}$	$W_4\text{max}-W_3\text{max}$
=	6.28-1.83	16.19-6.28	44.19-16.19	73.82-44.19
=	4.45	9.91	28.0	29.63

Assuming that the initial weight of an egg approximates to zero, the value W_e (i.e. 1.83 µg) equals the final weight of an egg. The maximum weight of an individual in the >2.0mm size-class was accepted as being the weight of an individual with a body-length of 2.40 mm, this being the mean of all the largest gravid females found in the body-length assessments (page 58).

The durations of each of the four size-classes at three different temperatures were obtained by extrapolation from the constructed *Daphnia* growth curves at 15°, 10° and 5°C shown in Fig. 19 (a full explanation of Fig. 19 is given in the appropriate legend). The durations to the nearest 0.25 day are summarised in Table 5.

Table 5. The durations of the four size-classes of *D. hyalina* var *lacustris* at 15°C, 10°C and 5°C.

	1	2	3	4
Size-class mm	< 1.00	1.00 - 1.39	1.40 - 1.99	> 2.00
length range mm	0.58 - 0.99	1.00 - 1.39	1.40 - 1.99	2.00 - 2.40
duration in days, 15°C	2.75	3.75	16.50	35.25
duration in days, 10°C	4.25	8.25	27.00	68.25
duration in days, 5°C	6.25	14.25	49.75	129.75

Egg durations are given on page 73. In order to relate the variations in *Daphnia* growth-rates at 15°, 10° and 5°C to the field temperature for each sampling date, the graph of mean loch temperatures (Fig. 2) was divided into three temperature regimes with the growth-rate data being applied as follows :

Temperature regime	
<7.5°C	applicable to 5°C growth-rates
7.5°-12.5°C	" " 10°C " "
>12.5°C	" " 15°C " "

Figure 19 (opposite)

Constructed growth curves for *D. hyalina* var *lacustris* at 15°, 10° and 5°C.

Abcissa - the mean age in days

Ordinate - the mean length in mm.

Each data point indicates a moult-stage.

The durations of each of the four *Daphnia* size-classes at different temperatures were obtained by extrapolation from the constructed growth curves at 15°, 10° and 5°C shown opposite. The growth curves at 15° and 10°C are essentially the same as those shown in Fig. 15 except that the 10°C curve was extended to seventeen moult-stages, using appropriate mean body-length data from the 15°C curve and assuming that adult instar durations corresponded to the 10°C egg development time of 8.23 days.

The 5°C curve was constructed using the mean body-length data from the completed 10°C curve and the egg development time of 15.52 days as the adult instar duration. Juvenile development time at 5°C was calculated by proportion, using the ratio of juvenile development time to egg development time from the 10°C growth data and applying it to the egg development time at 5°C.

Although the 5°C curve was not based on actual growth-rates of individuals, it was accepted as being adequate for the purposes of estimating production, knowing that its application would be restricted to the very slow-growing winter populations comprised of very low mean densities at mean loch temperatures of below 7.5°C. Furthermore, it has already been pointed out (page 20) that the main source of error associated with methods of estimating production based on the finite growth of individuals lies with the experimentally determined growth-rates which are unlikely to duplicate the field rates.

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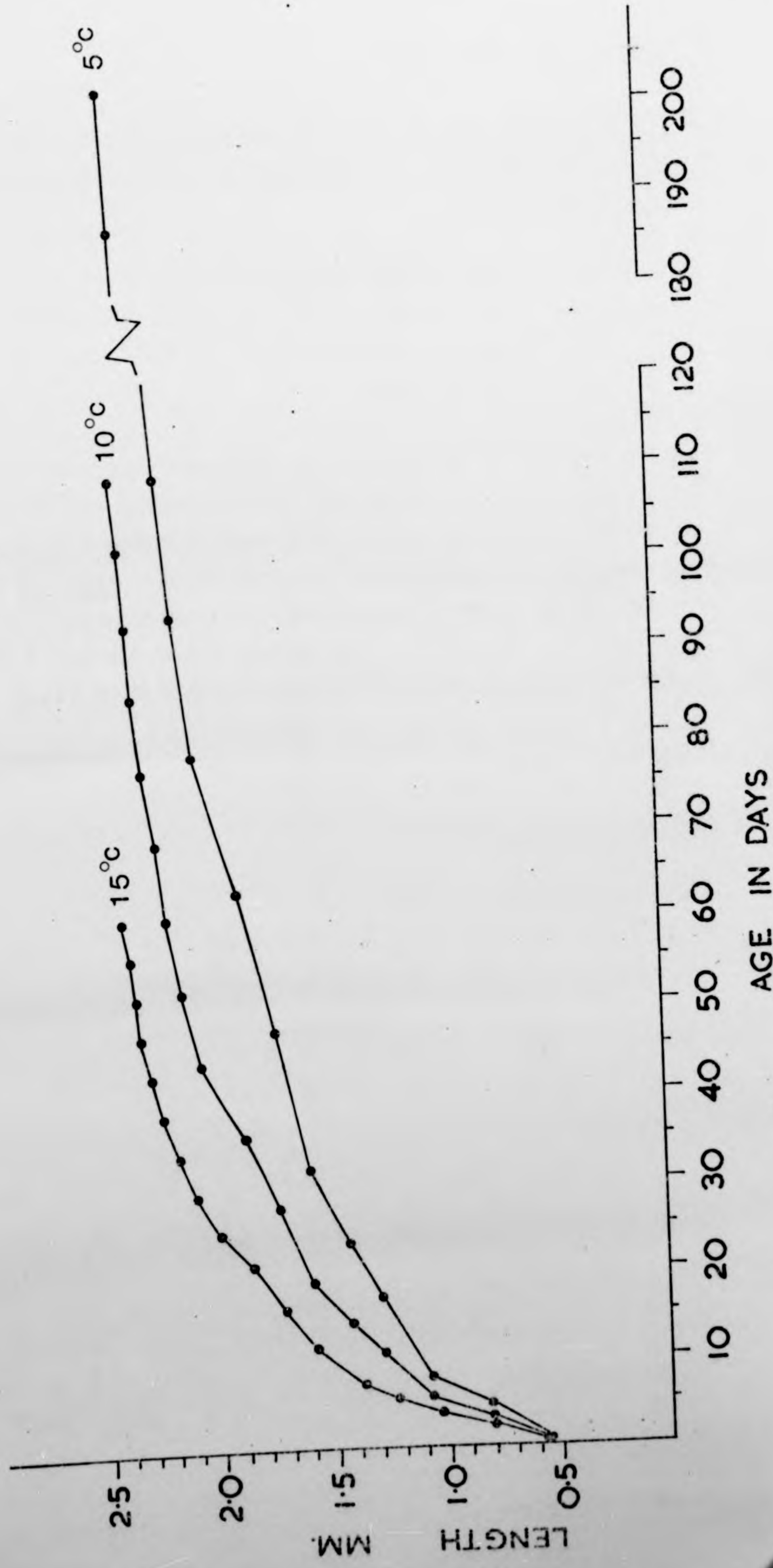

Figure 20 (opposite)

The seasonal variations in biomass and production of the D. hyalina var lacustris population during 1972-73.

Abcissa - the study period
Ordinates - the biomass (B) in g/m^2 and gC/m^2.
- the production (P) in g/m^2/day and gC/m^2/day.

An estimate of biomass was obtained for mid-June 1973 by weighing directly the combined Friedinger samples (dried at 60°C) for each of the six sampling sites, having initially separated the Daphnia from other planktonic components using the method of Straskraba (1964). The value obtained was 6.1 g/m^2 and is denoted in the biomass graph as a black dot.

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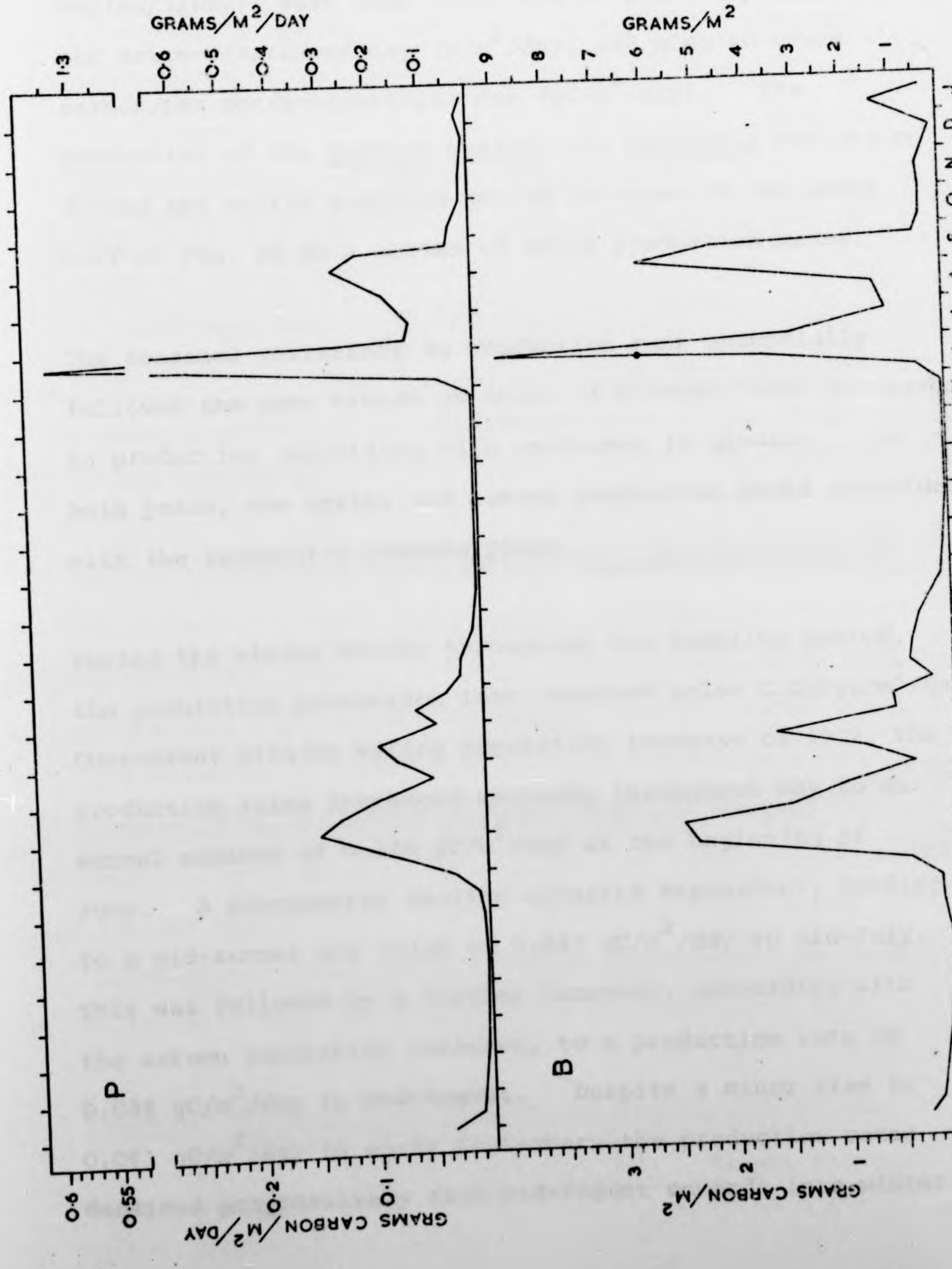


The population production estimates for each sampling date, initially expressed as µg dry-weight/per litre/per day(µg/l/day), were then converted to grams dry-weight/ per metre-square/per day ($g/m^2/day$) and also to grams carbon/per metre-square/per day ($gC/m^2/day$). The production of the Daphnia hyalina var lacustris population during the entire sampling period is shown in the upper half of Fig. 20 as a series of daily production rates.

The seasonal variations in production rate essentially followed the same trends as those of biomass, with increases in production coinciding with increases in biomass. In both years, the spring and autumn production peaks coincided with the respective biomass peaks.

During the winter months throughout the sampling period, the population production rate remained below $0.010gC/m^2/day$. Concurrent with the spring population increase of 1972, the production rates increased markedly throughout May to an annual maximum of 0.146 $gC/m^2/day$ at the beginning of June. A progressive decline occurred thereafter, leading to a mid-summer low value of 0.047 $gC/m^2/day$ in mid-July. This was followed by a further increase, coinciding with the autumn population increase, to a production rate of 0.088 $gC/m^2/day$ in mid-August. Despite a minor rise to 0.061 $gC/m^2/day$ in early September, the production rates declined progressively from mid-August onwards into winter.

In 1973, exceptionally low production rates of less than 0.001 $gC/m^2/day$ were maintained from January to mid-April with marginal increases occurring progressively in late April and throughout May. However, in early June, a dramatic increase occurred giving rise to the annual peak rate of 0.597 gC/m^2/day - the maximum short-term rate recorded during the entire study period. This was followed firstly by a sudden drop to a lower rate of below 0.060 gC/m^2/day in July and then by a gradual increase resulting in a second maximum of 0.122 gC/m^2/day in early September. In the latter half of September the production rate dropped sharply to 0.021 gC/m^2/day and from then onwards declined progressively to winter levels as the year ended.

The production of a population is dependent not only on the numbers of individuals present, but also on the sizes of these individuals. If the weight increments of each of the four size-classes of *Daphnia* are divided by the respective durations at a given temperature, say, for example 15°C, it becomes apparent that the fastest growth-rates (i.e. weight increase per unit of time) are associated with the smaller individuals, especially those in the 1.0-1.39mm size-class. This point is demonstrated in Table 6 below using data previously given in Table 4 and 5.

Table 6. The weight increments per day at 15°C of the four size-classes of *D. hyalina* var *lacustris*.

Size - class mm		Weight increment (μg) / duration at 15°C (days)		Weight increment (μg) per day at 15°C.
1	<1.00	$\frac{4.45}{2.75}$	=	1.62
2	1.00-1.39	$\frac{9.91}{3.75}$	=	2.64
3	1.40-1.99	$\frac{28.00}{16.50}$	=	1.70
4	>2.00	$\frac{29.63}{35.25}$	=	0.84

The weight increment per day of an individual in the 1.0-1.39 mm size-class is three times that of an individual in the >2.0 mm size-class. Although, for a hypothetical population consisting of equal numbers of Daphnia of all four size-classes, it would be expected that the individuals in the 1.0-1.39 mm size-class would provide the greatest contribution to the total population production, it must not be forgotten that the adult components provide the egg production.

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 (Cl-V) and adults (CVl). 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 adults, with a few individuals of each of the

Figure 21 (opposite)

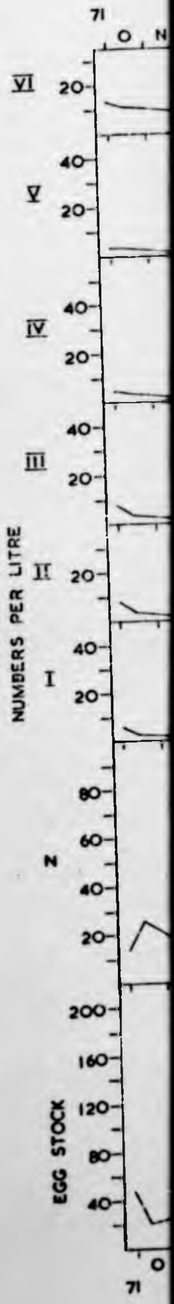
Seasonal variations in the mean egg stock and in the mean standing crop of all the developmental stages of Cyclops strenuus abyssorum from Loch Leven during 1972-73.

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.



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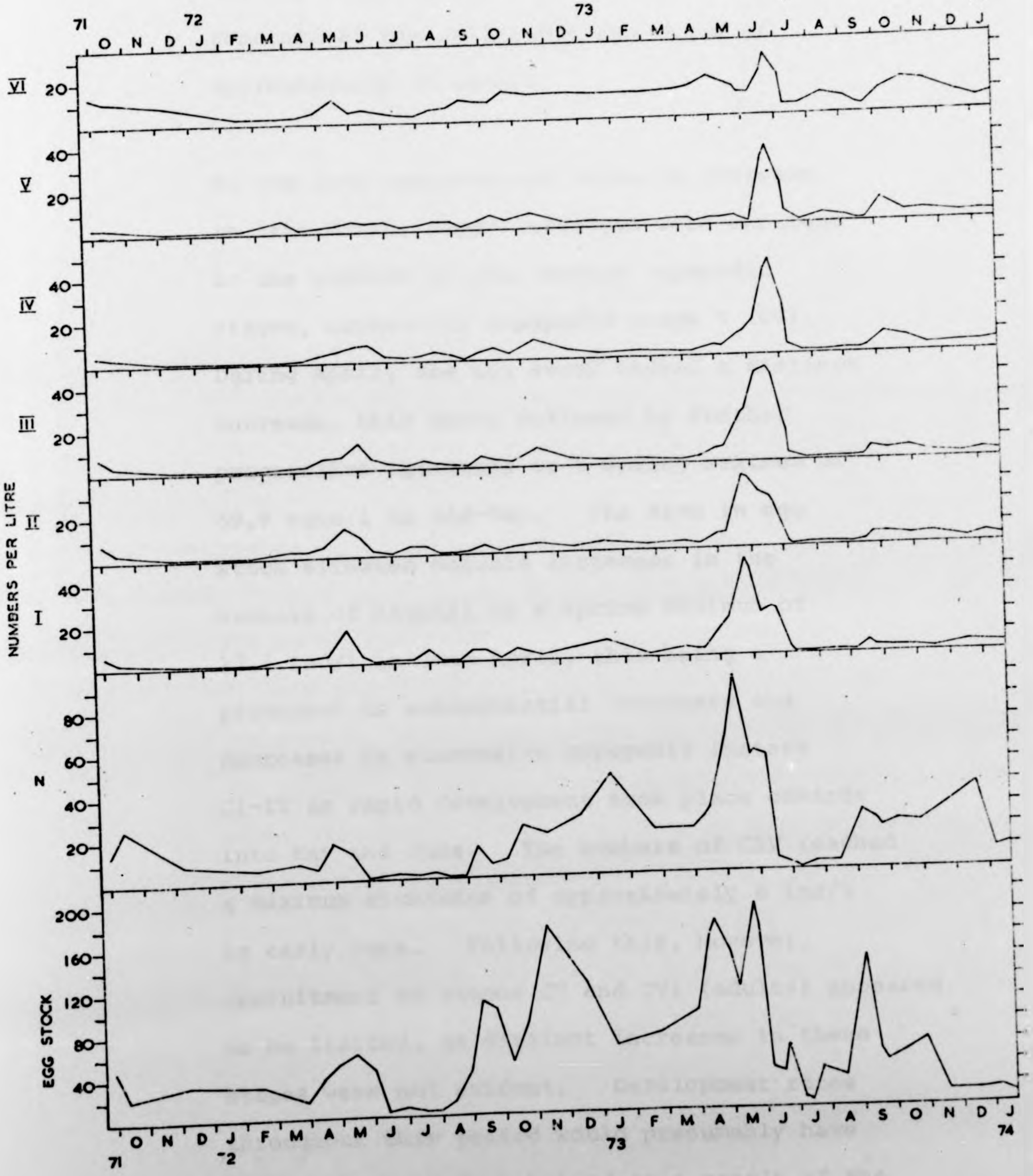

developmental instars. Total population numbers amounted to less than 20 ind/l. The egg stock at this time consistently remained at the relatively low value of approximately 30 eggs/l.

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).

The most notable increase in the adult fraction 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 up to stage Cll. 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.

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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/l 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 of Loch Leven, information was collected on the 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 per cent were more frequent in 1973, these were

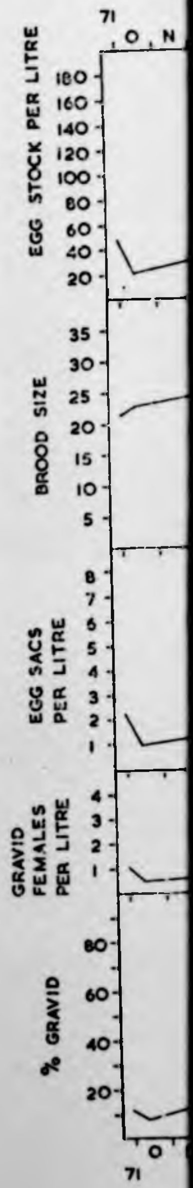
Figure 22 (opposite)

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.



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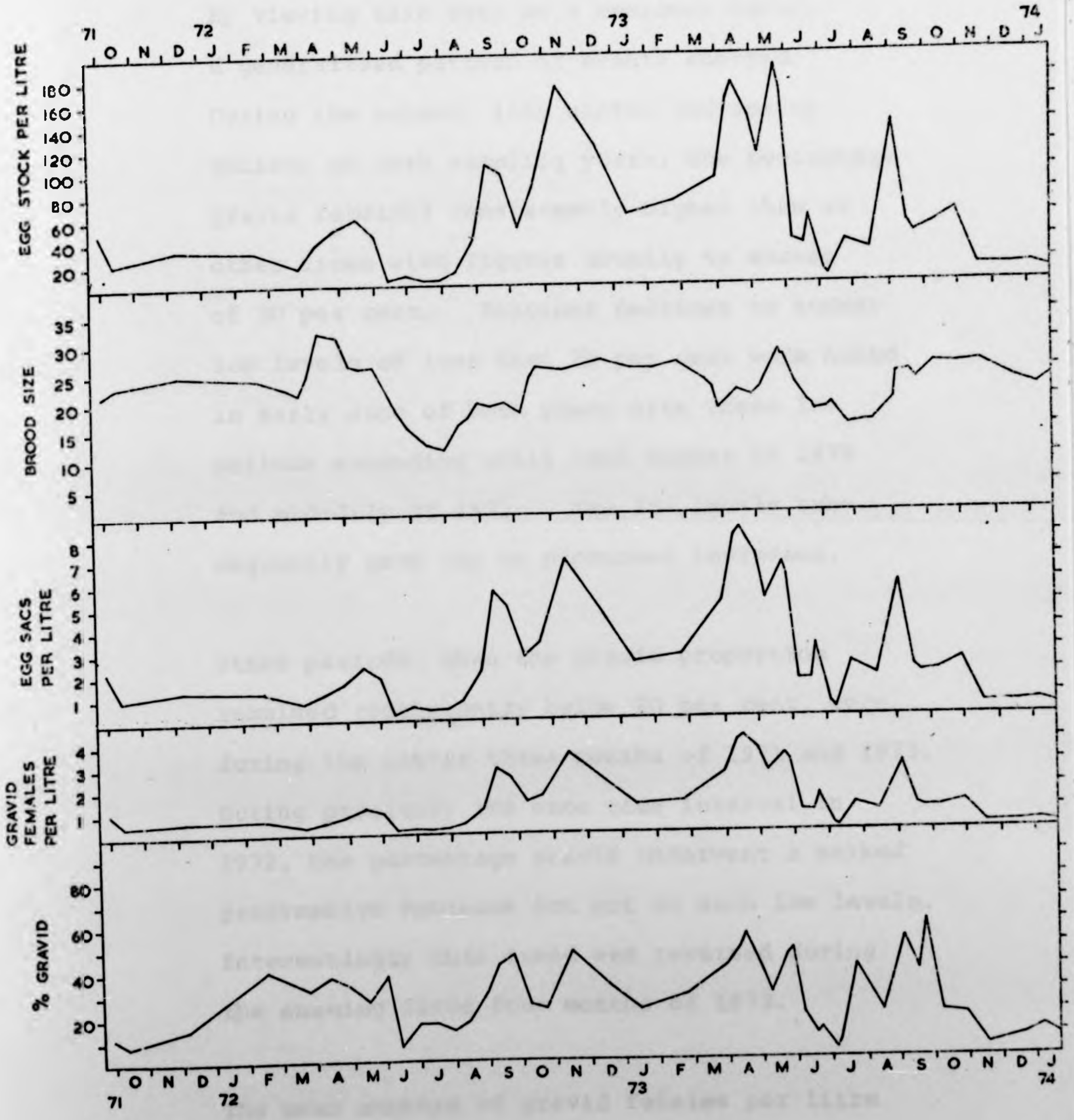

periodic and short-lived and only on three occasions did they exceed 50 per cent.

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 $\overset{4\ 11}{3.9}$ 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.

— not number of eggs per female ∴ 2 × broodsize

During the months of winter or more precisely from November to the end of March throughout the 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.

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— not number of eggs per female 2 × broodsize

During the months of winter or more precisely from November to the end of March throughout the 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/1 and each female carried two egg-sacs comprised of twenty-five eggs each, then the egg stock would be 50 eggs/1. A doubling of the gravid female number to 2 ind/1, which in itself seems a minor increase, boosts the egg stock to 100 eggs/1.

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

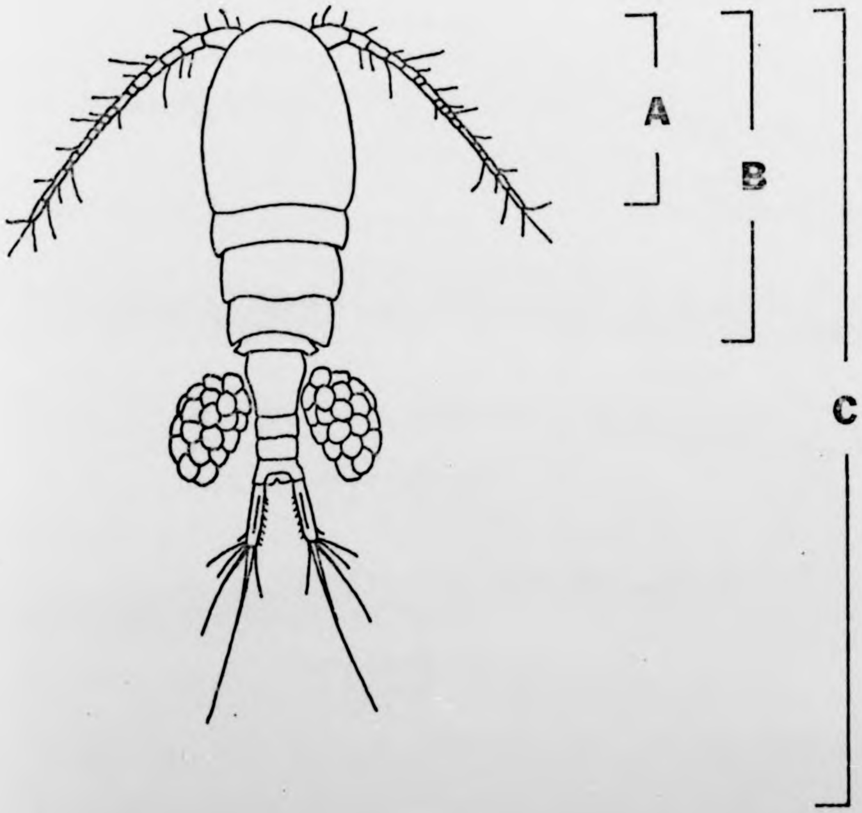


Figure 24 (opposite)

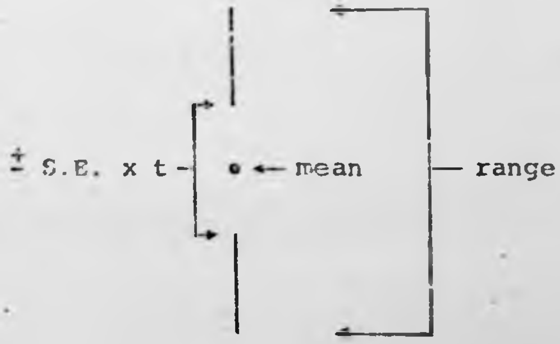
Seasonal changes in mean brood-size and in mean metasomal length of adult female C. strenuus abyssorum from Loch Leven during 1972-73.

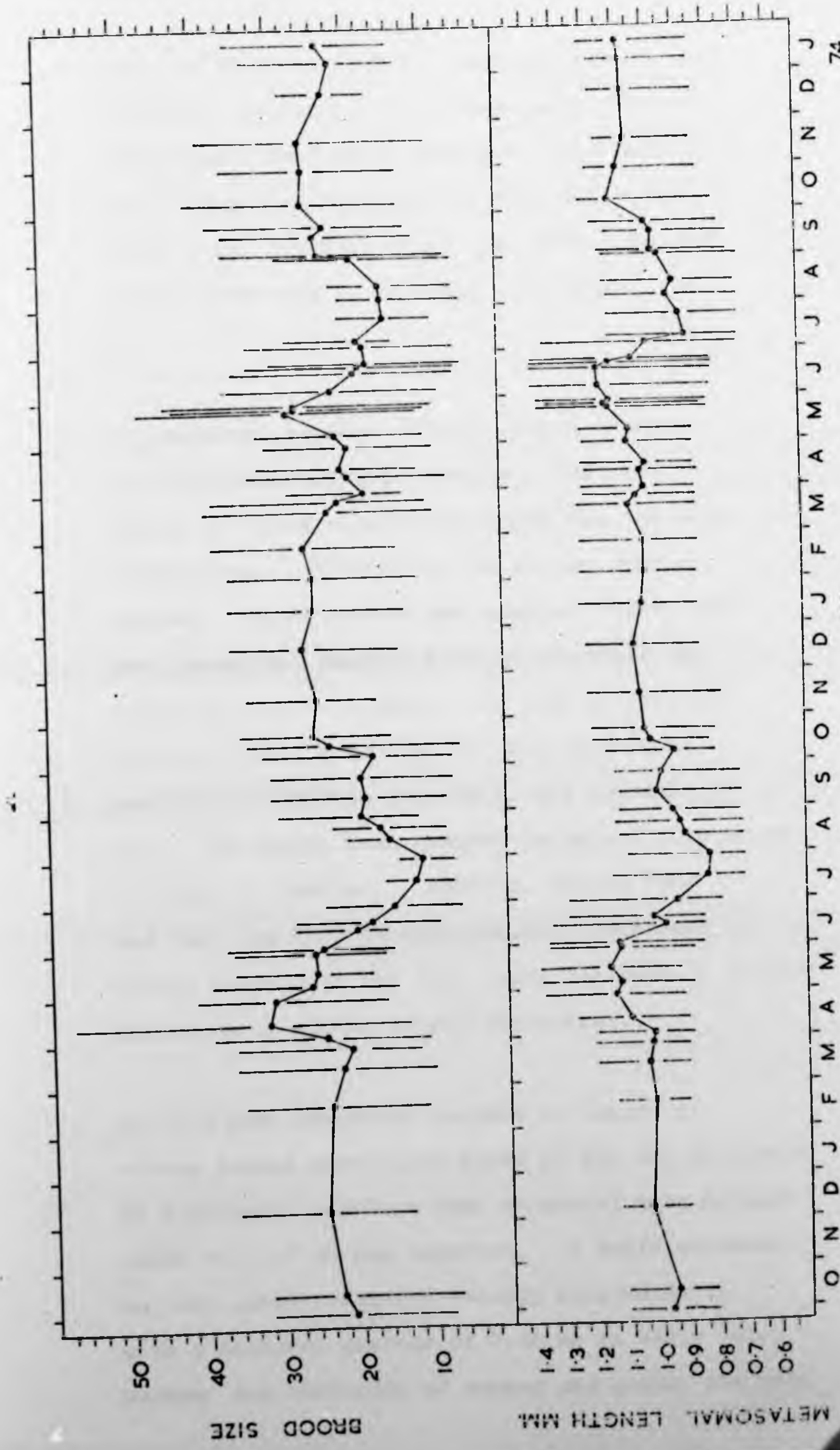
Abcissa - the study period.

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

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

Key

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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. During the remainder of summer and autumn the mean 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 CVl (adults). Fig. 25 shows the seasonal variations

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.

C. strenuus

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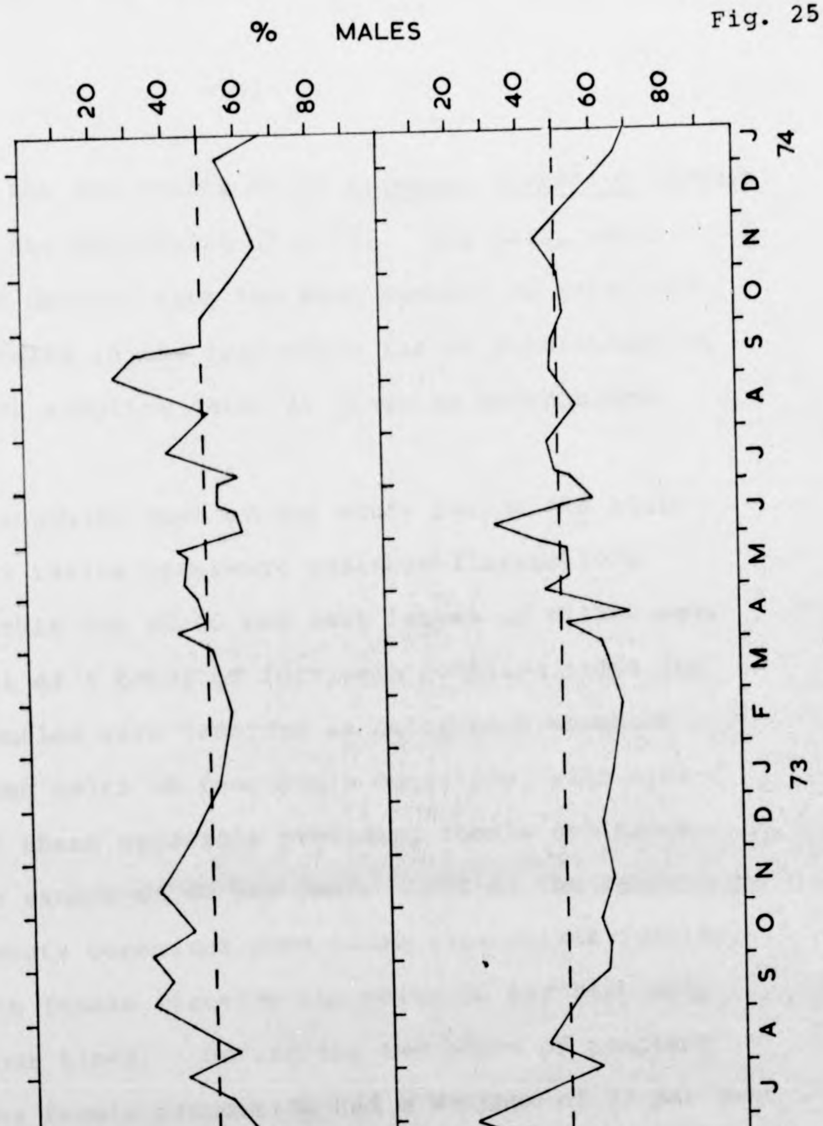
Fig. 25



in the sex ratios of C. strenuus abyssorum instars CV and CV1 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	97.3	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.

(c) Biomass and production estimates

i. Biomass

The numerical standing crop data obtained for *Cyclops strenuus abyssorum* was converted to biomass using exactly the same method as that adopted by Walker (1970). The formula employed to convert copepod length data into weight units was that of Klekowski and Shushkina (1966):

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

Where W = Wet-weight in mg.

L = length in mm.

It has already been demonstrated earlier in the Results Section that successively maturing adult females of the *C. strenuus abyssorum* population were of variable lengths throughout the yearly cycles. It therefore seems likely that the various developmental stages also varied in length accordingly. In order to compensate for this, length data for all of the copepod developmental instars (nauplii and copepodids 1-V) and also adult males were calculated for each sampling trip using previously determined proportionate length-relationships between these instars and the adult females. These proportions, given as percentages, are shown in Table 8 below and were derived from Walker (1970).

Table 8/contd.

Table 8. The lengths of *C. strenuus abyssorum* developmental stages as proportions of the adult female length. (from Walker 1970)

The proportions relate to total length (minus furcal setae) as explained in Fig. 23.

Instar	N	C1	C11	C111	C1V	CV♂	CV♀	CV1♂	CV1♀
% of adult female length	15	38	48	61	73	78	94	87	100

The calculated lengths of the stages of *C. s. abyssorum* throughout the yearly cycles were then converted into wet-weight using the conversion formula given above, and the wet-weights of the individual instars were multiplied by the respective mean numbers of these stages present on each sampling date during the two-year period to obtain the biomass of nauplii, copepodids and adults.

The density of a *C. s. abyssorum* egg was assumed to be little different from water. Therefore, the mean diameter of a sample of eggs was used to calculate the volume and consequently the weight of an egg. The value obtained was 0.00126 mg. The numerical standing stocks of eggs were then multiplied by this figure and the resultant egg stock weights were then added to the biomass estimates of the other stages.

The total population biomass estimates for each sampling date, initially expressed as mg wet-weight/

per litre, were then coverted to grams dry-weight/ per metre-square surface area (g/m^2) assuming that dry-weight was equivalent to 10 per cent* of the wet-weight (Walker 1970; Burgis and Walker 1972). The depth of the column corresponded to the mean loch depth of 3.9 m (Morgan 1970, 1974; Smith 1974). The data thus obtained was further converted to grams carbon/per metre-square (gC/m^2), assuming that the carbon content was 44 per cent of the dry-weight (Burgis 1971). The seasonal variations in standing crop biomass of the Cyclops strenuus abyssorum population for the two years of sampling are shown in the lower half of Fig. 26.

During the 1971-72 winter the population biomass remained at low levels of below 0.40 gC/m^2 until April of 1972 when the biomass increased steadily to produce an annual maximum of 1.08 gC/m^2 in mid-May. This was followed firstly by a progressive decline to an annual minimum of 0.13 gC/m^2 in mid-July and then by a further but more gradual increase throughout late summer and autumn to eventually give rise to a second peak of 1.06 gC/m^2 in mid-November. As the year ended the biomass level showed an initial decrease and then stabilised at around 0.60 gC/m^2 until April 1973.

* According to Duncan (pers. comm.) the dry-weight as a proportion of wet-weight may vary in copepods from 10-20 per cent. Although it might have been appropriate to have used a factor of 15 per cent, it seemed more useful to use 10 per cent in order to provide direct comparison with the dry-weight biomass estimates of Walker (1970).

Figure 26 (opposite)

The seasonal variations in biomass and production of the C. strenuus abyssorum population during 1972-73.

Abcissa - the study period

Ordinates - the biomass (B) in gm/m^2 and gmC/m^2

- the production (P) in gm/m^2/ day and gmC/m^2/day.

• An estimate of biomass was obtained for mid-June 1973 by weighing directly the combined Friedinger samples (dried at 60°C) for each of the six sampling sites, having initially separated the Daphnia from the copepod fraction using the method of Straskraba (1964). The value obtained was $2.5 gm/m^2$ and is denoted in the biomass graph as a black dot. It appears that this estimate is a considerable underestimate, perhaps due to errors associated with the separation and weighing of the smaller Cyclops.

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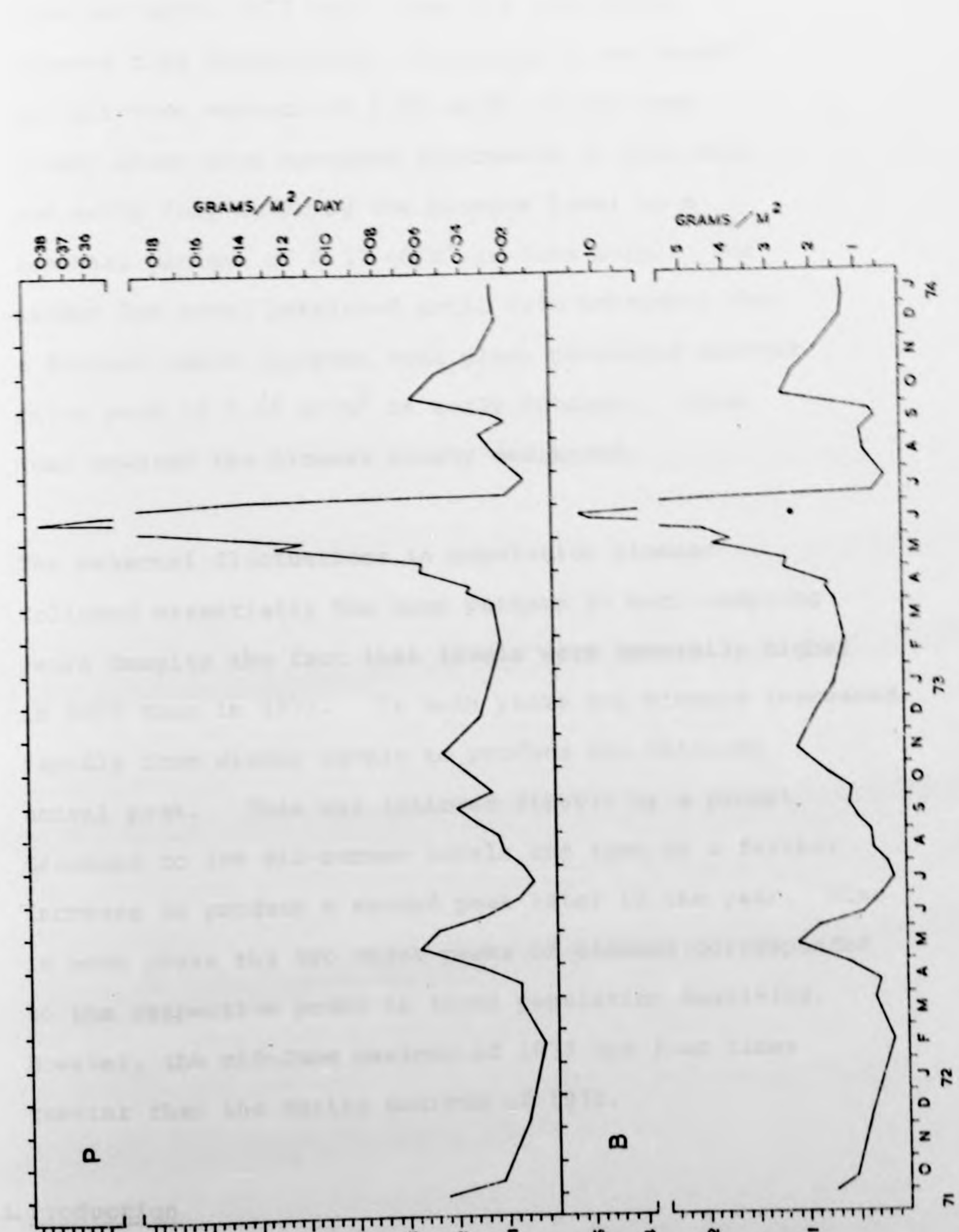

From mid-April 1973 until June the population biomass rose dramatically, resulting in an annual and all-time maximum of 4.56 gC/m^2 in mid-June. A very sharp drop occurred afterwards in late June and early July reducing the biomass level to a seasonal minimum of 0.17 gC/m^2 in late July. The summer low level persisted until late September when a further rapid increase took place producing another major peak of 1.19 gC/m^2 in early October. From then onwards the biomass slowly decreased.

The seasonal fluctuations in population biomass followed essentially the same pattern in both sampling years despite the fact that levels were generally higher in 1973 than in 1972. In both years the biomass increased rapidly from winter levels to produce the ultimate annual peak. This was followed firstly by a prompt decrease to low mid-summer levels and then by a further increase to produce a second peak later in the year. Also in both years the two major peaks of biomass corresponded to the respective peaks in total population densities. However, the mid-June maximum of 1973 was four times greater than the spring maximum of 1972.

ii. Production

The method used to estimate the production of Cyclops strenuus abyssorum was based on exactly the same principles as that described for Daphnia hyalina var lacustris (pages 80-83). The generalised production formula given below was applied to the copepod population to produce a series of daily production rates spanning the entire sampling period.

$$P=\frac{Ne.We}{De} + Nn\frac{(Wn-We)}{Dn} + NC1\frac{(WC1-Wn)}{DC1} \cdots\cdots\cdots\cdots \quad NCV1\text{♀}\frac{(WCV1\text{♀}-WCV\text{♀})}{DCV1\text{♀}}$$

Where P = production in mg per litre per day (mg/l/day)

N = number per litre

W = wet-weight in mg.

D = duration of life-stage in days

e = eggs

n = nauplii

C1....CV1♀= copepodid stages C1, C11, C111, CV1, CV♂, CV♀, CV1♂ and CV1♀ treated independently.

The weight data of all the life-stages for each sampling date was obtained from that derived during the process of calculating biomass, thus compensating for the previously mentioned seasonal variations in body length (page 98). The initial weight of any given stage was taken to be the final weight of the preceeding stage. Concerning the egg weight, the initial weight of an egg was presumed to be zero thus the value We (i.e. 0.00126 mg) equals the final weight of an egg.

The durations of each of the life-stages at the three temperatures 15°, 10° and 5°C were extrapolated from appropriate growth-rate data obtained by Lewis (1971) for _Cyclops abyssorum_ Sars from Lake Trawsfynydd. These are given in Table 9 below.

Table 9. The durations of C. strenuus abyssorum life-stages at 15°, 10° and 5°C. (from Lewis 1971)

The durations are given in days.

Life-stage	Temperature °C		
	15°	10°	5°
Eggs	5	9	18
Nauplii	25	35	57
Cl	10	14	16
Cll	10	14	16
Clll	10	14	16
ClV	10	14	16
CV	10	14	16
CVl	10	14	16

Although at a given temperature the rates of growth of the separate copepodid instars Cl-CV are likely to vary from one another, it was considered adequate, for the purposes here, simply to ascertain the time of development from the Cl stage to the adult stage and divide this time by five thus giving each copepodid instar a similar duration. As the longevity of the adult stages were not determined it was assumed that the adults persisted only for the standard duration time at each temperature.

The variations in copepod growth-rates at 15°, 10° and 5°C were applied to the field temperatures for each sampling date using the field temperature regimes given on page 82 and relating them accordingly.

The population production estimates for each sampling date, initially expressed as mg wet-weight/ per litre/per day, were then converted to grams dry-weight/per metre-square/per day (g/m^2/day) and also to grams carbon/per metre-square/per day (gC/m^2/day). The production of the C. strenuus abyssorum population during the entire sampling period is shown in the upper half of Fig. 26 as a series of daily production rates.

During the 1971-72 winter production rates remained low, at levels usually below 0.005 gC/m^2/day, until April 1972 when the rates steadily increased to give an annual maximum of 0.028 gC/m^2/day in mid-May. During June a progressive decline occurred resulting in an annual minimum of 0.004 gC/m^2/day in mid-July. This was followed by staggered increases in late summer and autumn which produced further peaks of 0.020 gC/m^2/day and 0.023 gC/m^2/day in late September and mid-November respectively. Towards the end of the year the production rates underwent an initial decrease and then levelled off at approximately 0.012 gC/m^2/day until April 1973.

During the period mid-April 1973 to June the production rates increased dramatically to produce an annual maximum rate of 0.169 gC/m^2/day - the ultimate short-term rate of the entire study. However, a decline promptly followed to give an annual minimum of 0.005 gC/m^2/day in late July. Low levels below 0.014gC/m^2/day persisted until late September when a further rapid increase occurred resulting in a second maximum value of 0.028 gC/m^2/day in early October. As the year ended, production rates decreased slowly.

The seasonal variations in C. s. abyssorum production rate parallelled the variations in biomass with major peaks and troughs coinciding exactly. In fact the patterns of the two graphs shown in Fig. 26 were very similar in most respects. As with the biomass levels, the production rates were generally higher in 1973 than in 1972 especially during the first six months of the year. The mid-June production maximum of 1973 was six times greater than the spring maximum of 1972.

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) are considered to be characteristically planktonic in their 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.

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.

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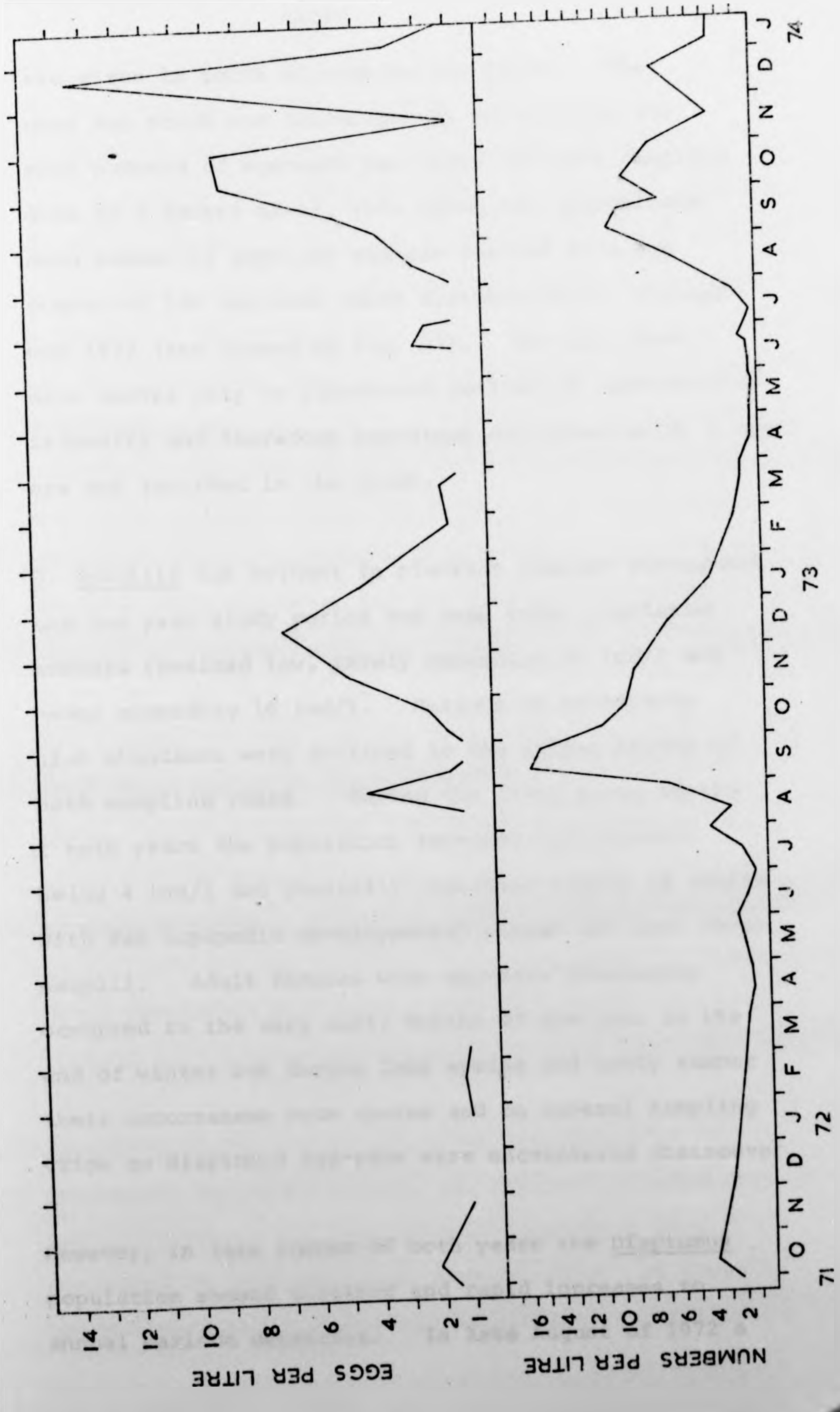
Fig. 27



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

d abundance

trephes longimanus

ring 1972-73.

mbers per sampling

ous species in net

are denoted by

iedinger samples

Chydorus sphaericus
44
35
9
2
3

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 (Table 12). 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 the bottom sediments within the region of site C is much greater than in areas where other sites were situated.

SECTION D DISCUSSION

1. Preliminary discussion

(a) Sampling strategy

It was stated earlier (page 21) that the sampling scheme of the present study was designed to provide zooplankton population data representative of Loch Leven as a whole. In considering such a scheme, based on the use of a bottle-sampler, two important details needed to be taken into account - firstly, the number of sites to be visited and consequently the number of samples to be taken per trip and secondly the frequency of sampling visits. In practise these two aspects become related and provide a third consideration regarding the number of samples which could be efficiently analysed within the allocated interval between sampling trips. It is important to avoid a back-log of samples not analysed in a long-term sampling project as these inevitably accumulate progressively as time passes.

The basis of the present sampling scheme was derived from Walker (1970) who worked a system of 'major' and 'minor' visits to Loch Leven in 1969 when *Cyclops strenuus abyssorum* dominated the zooplankton. On a major visit eight sites were sampled and sixty-eight Friedinger samples were collected and on a minor visit two sites were sampled and twenty-two samples were collected. The major programme was undertaken at approximately monthly intervals with minor visits being carried out intermittently, usually fortnightly between major visits. Walker showed that in the majority of cases a minor visit was likely to provide similar data to a major visit within a variation of ± 10 per cent and noted a maximum variation of ± 35 per cent. He concluded that, because of the wind-swept and therefore well-mixed shallow water of Loch Leven, the horizontal distribution of the zooplankton was likely to be less problematic as regards sampling than a more sheltered water.

Although Walker's data provided a background on which to base the present sampling scheme, it was anticipated at the out-set that the horizontal distribution of the zooplankton might be more variable because of the renewed presence of _Daphnia hyalina_ var _lacustris_. _Daphnia_ spp. are known to exhibit patchiness in a horizontal plane (Hutchinson, 1967) and this phenomenon was noted at Loch Leven by Morgan (pers. comm.). In view of this, a sampling system involving major and minor visits such as that of Walker was rejected on the grounds that minor sampling might render inadequacies regarding horizontal distribution. It was also apparent that, for safety reasons, sampling could only be undertaken in relatively calm conditions when it was presumed that patchiness in distribution might occur.

In the preparatory stages of this study (October 1971), pilot sampling programmes to assess horizontal distribution* were prevented because of complications arising from the available boating facilities as well as mechanical faults with the Friedinger sampler. Daphnia were unlikely to have been present in sufficient quantity anyway because of the time of year. Therefore, in order to ensure adequate sampling for the forthcoming year (1972) it was decided to take as many Friedinger samples on every trip as was feasible to examine in the periods between sampling trips. Within limits, a policy of oversampling is better than undersampling.

In 1969 Walker effectively collected and analysed approximately ninety Friedinger samples per month, this being acknowledged by Walker (pers. comm.) as being an appropriate number of samples to analyse within that time period. With this in mind, the sampling scheme of 1972 was established with visits to the loch at least twice monthly at all times except winter, collecting forty-eight samples per trip and consequently providing an average of ninety-six samples to analyse per month.

In the light of practical experience, the sampling scheme was reduced to twenty-eight samples per trip for 1973, with a view to increasing the sampling frequency especially during the spring production period. The proposed plan for weekly visits gave

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* A 4m water-core sampler, based on Pennak (1962) was designed and built in the University workshops during 1972 for the explicit purpose of estimating horizontal variability at Loch Leven but regrettably this sampler was badly damaged before being put to good use.

rise to problems arising from transport and boating facilities as well as unpredictable adverse wind conditions. However, sampling was more frequent in 1973 than 1972 and cancelled Friedinger sampling trips throughout were usually substituted by collection of net samples.

From the evidence given in Table 2 and 7 on horizontal distribution and in view of the problematic nature of zooplankton sampling, it was assumed that the sampling programmes of both years provided acceptably reliable quantitative data representative of the whole loch.

One further point deserves mention. In retrospect it would have been advantageous to have been able to efficiently sample the first few centimetres above the bottom substrate at several sites during certain times of the year. It is possible that Daphnia may resort to the bottom if, for example, food was limited in the open water. The Daphnia in culture (pages 35 and 36) were seen to feed actively on the bottom in the laboratory aquariums and in growth-vials when much of the algal-food suspension had settled. Although this may in part have been due to the lack of turbulence in the vials, this was probably not the case in the aquarium conditions where circulation was effected by air-pumps. Utilisation of the bottom substrate by the Cyclops strenuus abyssorum population also deserves consideration as some cyclopoids undergo quiescence in the benthic mud (Elgmork, 1967). It was noted in laboratory tanks that the older copepodid stages and adult females of C. s. abyssorum spent relatively long periods on the mud surface of the bottom or clinging to the glass sides. Clearly relationships between zooplankton and the benthic surface are of potential interest and deserve investigation.

As regards sampling devices, the Friedinger does not allow sampling of this nature because of the space required for closure of the bottom lid (Plate 1). However, the core sampler used by Bryant and Laybourn (1974) or the Jenkins sampler (Edmondson and Winberg, 1971) might have accomplished this task, although only where the bottom deposits were soft.

(b) Aspects of the data collected

In view of the abundance of data collected during the course of the present study it was considered appropriate within the context of this thesis to include the majority of this data presented in a direct manner thereby providing an overall picture of the zooplankton of Loch Leven during 1972-73. In accordance with the aims and purposes outlined in the Introduction (Page 1), the task undertaken in the Discussion section is essentially an evaluation of the more important details on population parameters, with an attempt to place the zooplankton in the context of the Loch Leven ecosystem and a final summary of biomass and production.

A criticism of the form and presentation of the data in the Results section necessarily precedes its interpretation and is as follows.

By differentiating, for example, the Daphnia hyalina var lacustris population, into convenient size-classes (page 27) it may be possible to determine successional changes in the population. However, the standing crop data is essentially a measure of the number of animals present at an instantaneous moment in time and does not provide direct information on the turnover or rate of change within the population. The number of animals present within a particular size-class at any given moment is dependent upon the duration time of that size-class so that the standing crop of a size-class which takes a relatively long time to pass through will be consistently greater than that of a size-class which is undergone more rapidly. If the population has an extensive breeding period or breeds continually (as with both D. h. var lacustris and Cyclops strenuus abyssorum from Loch Leven) it may be impossible to follow the progress of the individual cohorts as they develop through successive size-classes using standing crop data in isolation. If Daphnia within the 1.00-1.39mm pre-adult class increase in size after successive moults and recruit the 1.40-1.99mm size-class one would expect that numbers in the smaller size-class would decrease and those in the larger size-class would increase. However, growth of individuals from the <1.00mm class to the 1.00-1.39mm class and growth of individuals from the 1.40-1.99mm class into the largest >2.00mm size class would considerably obscure the developmental flow of animals through the population. This of course equally applies to the copepod population of the present study which was differentiated more extensively on an instar age-basis.

A greater frequency of field sampling enhances the clarity of standing crop data especially during warm phases when development is rapid. The inadequate fortnightly sampling frequency during the spring of 1972 unfortunately precluded a fuller evaluation of developmental changes in the Daphnia population (Fig. 6) and as noted on page 49 the early juvenile phase of development (<1.00mm class) was apparently missed during late April and May. However, because of the very short durations of the immature classes as opposed to the adult classes, especially at higher temperatures (Table 5), the same situation may have arisen even with a weekly sampling interval, although the likelihood would have been considerably less. The same problem also manifested itself with Cyclops strenuus abyssorum population data although not so acutely as the durations of the various copepod life-stages are generally much longer (Table 9). However, the quoted duration times relate to laboratory culture and not necessarily to field conditions which may enhance or retard the rates of growth.

One further point about standing crop data concerns the use of *mean* data, supposedly representative of the whole loch, as derived from variable numbers of samples - in this case either forty-eight (1972) or twenty-eight (1973) Friedinger samples. Although a detailed statistical analysis of variation might have been suggested, with confidence intervals for each data point being depicted on the appropriate population graphs, it was regarded as unnecessary for the purposes here on the grounds that the primary considerations revolved around major population changes (i.e. notable increases or decreases) and consistent trends. Even so, if confidence limits were presented as a simple statistic of all samples collected on any given sampling date, these would have been exaggerated because of the inclusion of variation in both horizontal and vertical planes. Similarly problems would have arisen from statistics derived from site-to-site variations as the chosen sites were of variable depths which invalidates comparability of this nature*. In addition, the situation would have been further complicated when the populations

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* Relating back to sampling strategy, analysis of site-to-site variations (i.e. variations between columns of water) would have been more readily accomplished had the sampling programme of 1972 involved six sites of equal depth say 4m, approximating to the mean loch depth of 3.9m (Morgan 1970, 1974; Smith, 1974), thus providing the accepted forty-eight samples per trip.

concerned were sub-divided into size components (Fig. 6) or age-groups (Fig. 21). The fact that sampling three sites provided similar population data to that obtained from sampling six sites (Table 2 and 7) suggested that the mean data provided acceptably realistic assessments of population numbers in the majority of cases anyway. Finally, in connection with population data variation, it should be noted that the variation between replicate samples (page 24) never deviated beyond ± 5 per cent of the mean when the summed totals of "first" and "second" samples for any given sampling date were used independently to derive mean population data for either *Daphnia* or *Cyclops*.

The mean data on body-size and egg numbers as presented for *Daphnia* in Fig. 10 and *Cyclops* in Fig. 24 requires brief criticism, especially if the two sets of related data are to be correlated on this basis. For any given set of data with a normal distribution, the mean and its statistical derivatives provide useful information but if the distribution is bimodal the mean is in fact unrepresentative of the raw data. Although no clear-cut instances of bimodal distributions were noted with the *Cyclops* data, several cases of this phenomenon arose with the *Daphnia* data. Fuller assessment of such situations would require preparation of distribution histograms for each set of data and probably an increase in the sample number. As regards the present thesis, this factor has been taken into account when interpreting the described data.

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/l) 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 main shoreline and around islands as well as near 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 noted at Site D 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 and possibly water movements. As regards temperature, 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 Mesocyclops leuckarti 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.), carbon dioxide, pH 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 existence of a strong positive correlation between 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 somewhat retarded, being in June as opposed to May as 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 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 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).

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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.

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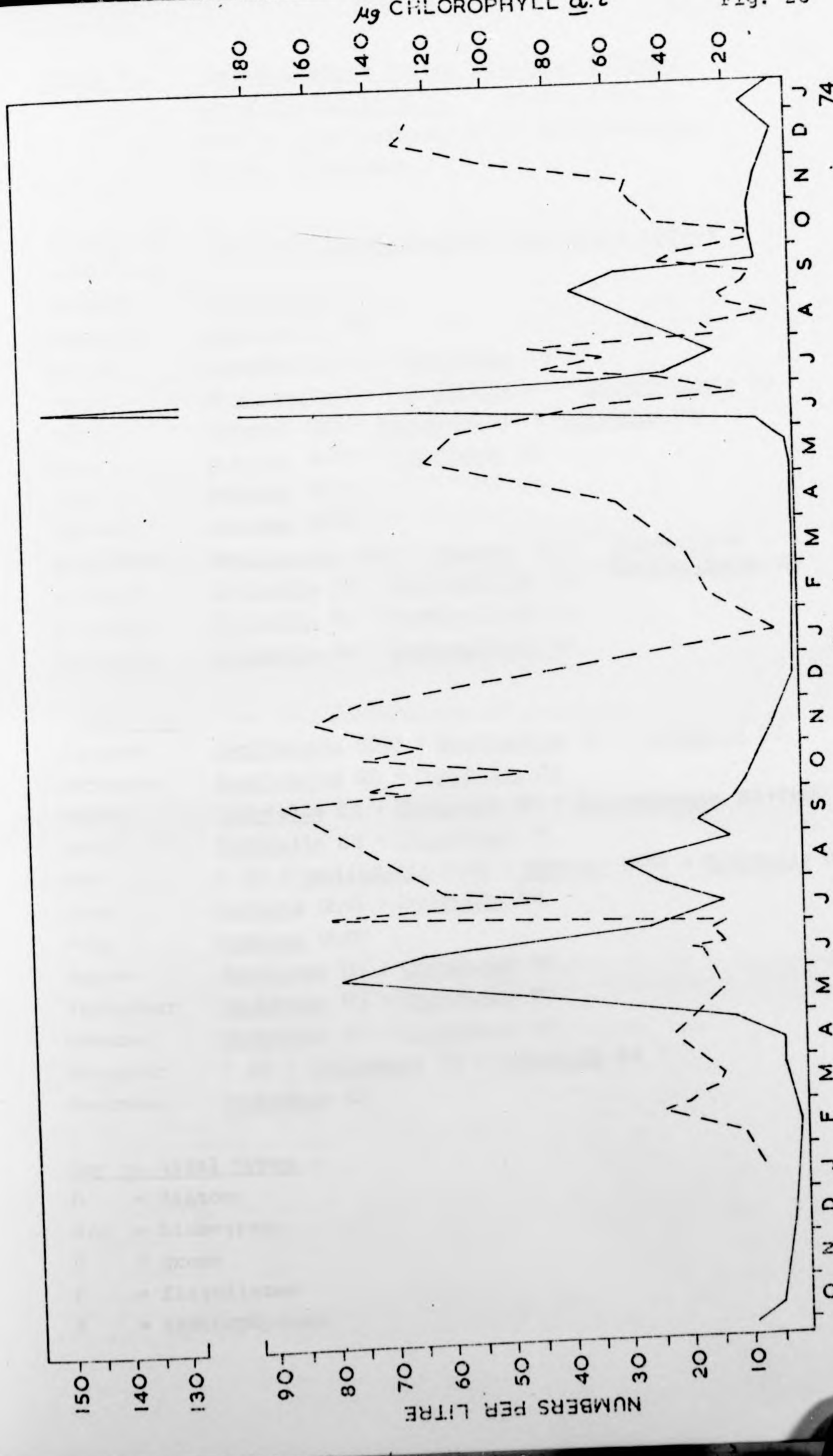
Fig. 28



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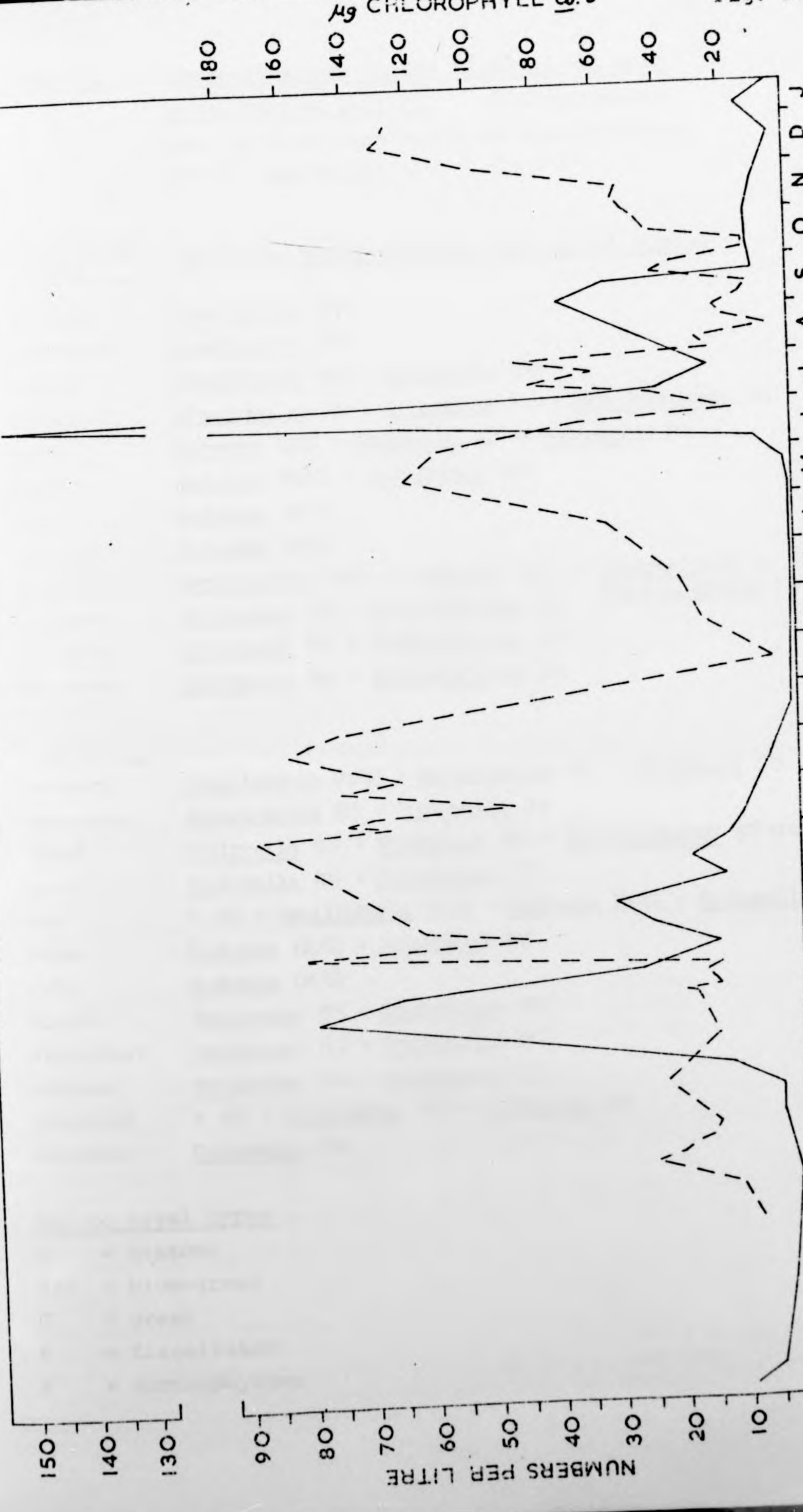

Table 12. Dominant algae in the plankton of Loch Leven during 1972-73. (Phytoplankton data by kind permission of Bailey-Watts, I.T.E., Edinburgh.)

Year/Month	Dominant algal species (and algal types)
1972	
January	*Asterionella* (D)
February	*Asterionella* (D)
March	*Asterionella* (D) + *Cyclotella* (D)
April	*Asterionella* (D) + *Cyclotella* (D) + *Akanthochloris* (X)
May	*Anabaena* (B/G) + *Rhodomonas* (F) + *Pediastrum* (G)
June	*Anabaena* (B/G) + *Cryptomonas* (F)
July	*Anabaena* (B/G)
August	*Anabaena* (B/G)
September	*Oscillatoria* (B/G) + *Anabaena* (B/G) + *Cyclotella* (D) + *Stephanodiscus* (D)
October	*Cyclotella* (D) + *Stephanodiscus* (D)
November	*Cyclotella* (D) + *Stephanodiscus* (D)
December	*Cyclotella* (D) + *Stephanodiscus* (D)
1973	
January	*Oscillatoria* (B/G) + *Asterionella* (D) + *Cyclotella* (D)
February	*Asterionella* (D) + *Cyclotella* (D)
March	*Cyclotella* (D) + *Rhodomonas* (F) + *Ankistrodesmus* (G)+?(G)
April	*Cyclotella* (D) + *Cryptomonas* (F)
May	? (G) + *Oscillatoria* (B/G) + *Anabaena* (B/G) + *Cyclotella* (D)
June	*Anabaena* (B/G) + *Cyclotella* (D)
July	*Anabaena* (B/G)
August	*Rhodomonas* (F) + *Cryptomonas* (F)
September	*Rhodomonas* (F) + *Cryptomonas* (F)
October	*RhodoMonas* (F) + *Cryptomonas* (F)
November	? (G) + *Cryptomonas* (F) + *Cyclotella* (D)
December	*Cyclotella* (D)

Key to algal types :

D = diatoms
B/G = blue-green
G = green
F = flagellates
X = xanthophycean

NOTES TO TABLE 12

The dominant algal species at Loch Leven during 1972-73 reviewed as potential cladoceran food sources.

Approximate cell-sizes and cell volumes are from Nadin-Hurley and Duncan (1976) unless otherwise stated. Although several of the algal species in Table 12 may be of acceptable size and/or shape for ingestion their susceptibility to digestion may be affected by the physical and chemical properties of the cell wall and their investments. Indeed, certain species may be rejected on chemical grounds prior to ingestion and these species may not be consumed as live cells but rather as preliminary detritus.

Green Algae

Green algae probably represented good food sources. For example, *Ankistrodesmus* sp. was used to feed *D. hyalina* var *lacustris* in culture by George and Edwards (1974) and Schindler (1971) noted an assimilation rate of 0.72 μg/h and an assimilation efficiency of *100* per cent for *D. longispina* fed on this alga.

Chlorella sp. and *Scenedesmus* sp. were used as laboratory foods and were not important species present in Loch Leven. *Chlorella*, with a cell diameter of 3.3μm (Gliwicz, 1970), is of suitable size and shape for ingestion and its thin cell wall (Saunders, 1969) permits easy digestion. Schindler (1967) fed *D. magna* with a high calorie diet of *Chlorella* (5.2 cal/mg, Richman 1958) and calculated that assimilation amounted to 67 per cent of the body-weight per day.

Scenedesmus (cell diameter 6μm and cell volume $423\mu m^3$) has been criticized as a cladoceran food by Saunders (1969) who considered the alga as difficult to digest on account of the thick, heavy cell wall. Similarly, Lefevre (1942) noted that *Scenedesmus* spp. were "mediocre" foods for *D. magna* and *D. pulex* and Wagler (1925) inferred that the spinous nature of the cell wall of the species may prove injurous to *Daphnia* during assimilation. Even so, this alga was fed to cultured copepod nauplii (Smyly, 1970, 1973a) and *Ceriodaphnia quadrangula* (Smyly & Collins, 1975).

Although the algal food sources fed to cultured *D. hyalina* var *lacustris* were probably highly nutritious (judging by the large broods produced, Fig. 17) the contribution of bacteria to the diet may have been important. Interestingly, Smyly and Collins (1975) found that the microbes associated with *Scenedesmus* and not the alga per se seemed to be utilised by cultured *C. quadrangula*.

Diatoms

Diatoms are solid, hard-walled structures enveloped by siliceous skeletons which may partly inhibit their exploitation by Daphnia (Fryer, 1957a). Nadin-Hurley and Duncan (1976) noted that diatoms were always found intact in Daphnia guts, suggesting that the cell walls were not crushed by the powerful mandibles and that enzymes had to penetrate through the wall to effect digestion. These authors also noted that the small centric diatoms, Cyclotella sp. and Stephanodiscus sp. (with cell diameters of 10 and 37μm respectively), were numerically important algal species in the Lower Thames Valley reservoirs, yet their presence was never detected in Daphnia guts. However, Nadin-Hurley and Duncan found that the larger diatoms, such as the colonial Asterionella sp. (cell diameter 5μm and cell volume 425μm^3), were ingested. Schindler (1971) measured an assimilation rate of 0.68 μg/h and an assimilation efficiency of 38.7 per cent for D. longispina fed on Asterionella.

Flagellates

Pacaud (1939) and Lefevre (1942) considered phytoflagellates as good food for cladocera as they are small, have fragile cell membranes and a means of remaining in suspension. Saunders (1969) noted that both Rhodomonas sp. (cell diameter 5 μm and cell volume 77 μm^3) and Cryptomonas sp. (cell diameter 10μm and cell volume 724μm^3) were highly digestible because the naked cell wall ensured accessibility to digestive enzymes and Schindler (1971) recorded a very high assimilation efficiency of 91.6 per cent for D. longispina fed on Cryptomonas. Nadin-Hurley and Duncan (1976) did not find these flagellate species in the guts of Daphnia in the reservoirs studied (perhaps because they were readily broken down) yet they found that in cultures D. magna fed on Cryptomonas produced broods of 20-30 eggs, these being much greater than in reservoir conditions. Pacaud (1939) made similar observations.

Blue-green Algae

In general blue-green algae may be considered as a poor food source for Daphnia as noted by George and Edwards (1974). Anabaena sp. is a colonial filamentous alga with an approximate cell diameter of 4μm and cell volume of 33μm^3. Despite the small cell-size and the fact that Daphnia can cope with filamentous algae (e.g. Tribonema) Anabaena was not ingested by the Loch Leven Daphnia or by Daphnia spp. in Lower Thames Valley reservoirs (Nadin-Hurley and Duncan, 1976), even though this alga was highly abundant in these waters. However, Gliwicz (1969a) and Monakov (1972) pointed out that blue-green colonies were more ingestible as small fragments rather than complete filaments. Both Burns (1966) and Saunders (1969) noted sharp reductions in Daphnia filtering rates in association with Anabaena blooms and suggested that this alga may have suppressed feeding either mechanically or by chemical secretions. The chemical unacceptability of blue-greens to cladocera has also been noted by Monakov and Sorokin (1961) and Hrbacek (1964). The poor food value of blue-greens is further demonstrated by Schindler (1971) who established an assimilation rate of 0.07μg/h and an assimilation efficiency of 17.9 per cent for _D. longispina_ fed on _Microcystis_; these figures being substantially lower than those quoted for other algal types. As regards _Oscillatoria_ sp., with a cell diameter of 7.5μm, this species is also filamentous with chain lengths of 20-400μm (Gibson, 1976). Its size and chemical properties may prevent its utilisation by _Daphnia_.

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 ($<20\mu g/l^{-1}$). 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

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.

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ion to algal chlorophyll

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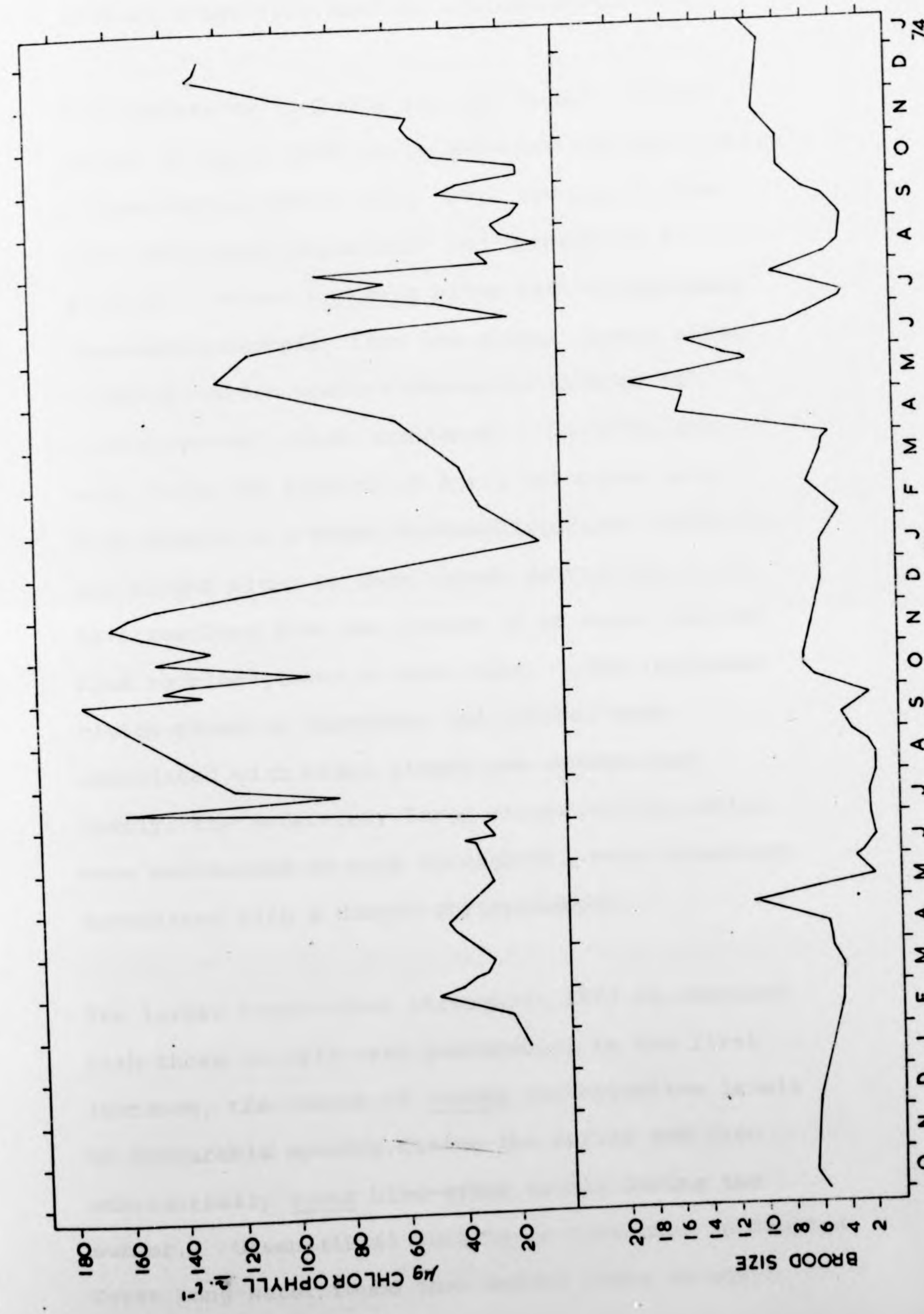
_a_ concentrations as

Fig. 29



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 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 Eglwys Nynydd, found that mean adult lengths underwent 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°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 O+ 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.

(i) Growth rates and development

The laboratory studies showed that considerable variation existed in individual growth rates of D. hyalina var lacustris despite being reared in apparently identical conditions and the presumed similar genetic or clonal history of all the animals used. All the Daphnia from laboratory aquaria were roundheaded and originated from selected individuals obtained from Loch Leven during August 1973. Perhaps the growth rates would have been subject to even greater variations had peaked or intermediate forms been used as well, or if the roundheaded Daphnia had been obtained from the loch at other times of year.

By using the onset of the first brood as a common reference point, growth variability amongst individuals was clearly demonstrated (Page 72). Growth in Daphnia spp. is discontinuous with body-size increases occurring only during and immediately following ecdysis; thus growth variability relates to the ages and sizes of comparable moult-stages. The size at maturity depends upon the number of pre-adult instars and this has repercussions on the timing of maturity. D. hyalina var lacustris in culture exhibited either four or five pre-reproductive instars and it was noted that individuals which underwent only four juvenile moults matured earlier and at a smaller size than those which underwent five. In comparison, an individual D. hyalina Leydig as depicted in Duncan et al. (1970), exhibited four juvenile moults and the same number was described as normal (but not absolute) for D. carinata (Hutchinson, 1967), for D. laevis (Wood et al. 1939) and also for D. galeata mendotae (Hall, 1962). However, considerable variation in this respect is possible as four to eight pre-adult instars were recorded for D. magna by Anderson and Jenkins (1942).

The occurrence of maturity appears to be in part genetically controlled. Green (1956) noted that D. magna individuals which were large in the first instar usually matured earlier, in the fifth rather than sixth instar, and Green (1954) found that the young derived from the third parent brood were generally the largest and thus matured earliest. However, it appeared that in the case of the Loch Leven Daphnia the young individuals from cultures were of a consistent size when released from the brood pouch and so a correlation between large neonates and early breeding is unlikely. Perhaps the factor determining the number of pre-adult instars in the cultured D. hyalina var lacustris relates to the differential utilisation of the food source in the very early independent stages.

According to Hutchinson (1967) the rate of growth both absolute and per instar under fixed conditions increases to a maximum and then decreases and, in general, reproductive maturity approximately coincides with the inflection point of the growth curve. Although this was partly true of the cultured D. hyalina var lacustris (the latter effect being somewhat dampened in Figs. 15 and 19 by virtue of average as opposed to individual growth curves), the maximum growth was usually associated with the early immature stages, a phenomenon previously recorded for D. magna by Green (1956). Hall (1964) found that food level affected the amount of growth per instar but noted that the adult stages were more affected by different food levels than were juvenile stages. Since food level strongly affects both brood-size and body-size, it might be implied from the very large broods produced by D. hyalina var lacustris in culture that the food sources used promoted high, if not maximum, growth rates throughout life, especially in adult stages. Further aspects of the laboratory diets are mentioned in Discussion, Part 4(a). The negative growth which, according to Hutchinson (1967), may be manifest in Cladocera of extreme old age, was not apparent in the present cultures. However, the three longest-living individuals reared on Chlorella (Page 73) showed little or no increases in body-size during moults in late adulthood.

It was always observed in the laboratory cultures that female Daphnia produced broods in continual succession and the release of young always occurred within the same 24 hour period as the adult moults. In D. magna the parthenogenetic egg is laid half-an-hour after moulting and the developed young in the brood pouch are usually liberated just before moulting (Green 1956) so that the time interval between successive broods is very short. The implications of this on the percentage gravid data must be acknowledged (Page 164). According to Hall (1962) the duration of egg development and that of the adult instar are strictly temperature dependent so that for a given temperature the two durations are essentially equivalent. However, Green (1956)observed that in D. magna, the length of the adult instar increased progressively with age and that whilst the embryonic development period was totally temperature dependent and fixed, the retention time (when the young are in the brood pouch) may be much greater. This factor may have repercussions on the number of juvenile moults of neonates, suggesting that neonates which were retained for longer periods in the parent brood pouch matured earlier. Although variations in adult instar durations were observed in the D. hyalina var lacustris cultures (at 15°C the range was 3-7 days) these showed no significant relation to the age of individuals.

Leading on from this, the egg durations quoted for three temperatures on Pages 73 and 74 effectively represent the average times at three temperatures from the onset of a brood to the time shortly after the release of the independent young. In fact these denoted the mean adult instar durations. Such a method of egg duration assessment with timing being measured on a 24 hour basis was considered adequate in view of the large numbers of recordings from which the means were obtained. Nevertheless, the egg durations obtained bear close similarity to those of George and Edwards (1974) for D. hyalina var lacustris from Eglwys Nynydd, these authors having timed and characterised egg-development very specifically using similar embryonic stages to those described by Green (1956). In addition, the Loch Leven egg durations are very similar to those ascertained by Hall (1964) for D. galeata mendotae.

The mean life span based on the three maximum longevities of cultured D. hyalina var lacustris females amounted to sixty-five days at 15°C.

However, as the life expectancies varied between 39-71 days (averaging fifty-two days) for eight individuals reared at this temperature, longevity is undoubtedly subject to wide variation and it might be expected that even greater variations would occur in the highly changeable field conditions. In comparison Hall (1964) quoted a median life-span of 60-80 days for cultured *D. galeata mendotae* at 20°C; Duncan *et al.* (1970) showed that an individual *D. hyalina* Leydig persisted for about twenty-five days at the same temperature and MacArthur and Baillie (1929) established a mean longevity of forty-five days for *D. magna* females at 18°C.

Hall (1964) showed that life expectancy decreased as temperature increased and noted that the number of instars during life was marginally increased at lower temperatures. Although in the present study, temperature effects on longevity were not fully realised, there is evidence to parallel the findings of Hall. The majority of individuals kept at 10°C were certainly active after sixty-eight days (when the experiments were stopped) and assuming that they would have experienced seventeen moults per life span (as at 15°C) their expected longevities would have been around 110 days (Fig. 19). Hall (1964) quoted 150 days for D. galeata mendotae kept at 11°C. On the same basis, individuals of D. hyalina var lacustris kept at 5°C could have lived for over 200 days (Fig. 19).

Hutchinson (1967) stated that the total number of instars per life span could extend to well over twenty in cultured Daphnia spp. This might certainly be the case with D. hyalina var lacustris in Loch Leven, for although under optimum growth conditions the cultured Daphnia females exhibited seventeen moults with the attainment of a final size of 2.4mm, larger individuals were regularly encountered in field samples (Fig. 10, maximum size ranges). Periods of low temperature in the loch might certainly increase the maximum sizes as demonstrated by Hall (1964) and Green (1956). However, although Hall (1964) showed that food level exerted no influence on longevity (within his experimental limits), Ingle et al. (1937) demonstrated that longevity was increased under near starvation conditions. The latter authors showed that when D. laevis females which had been previously kept in a poor nutrient medium were tranferred to a very rich medium, their life expectancy was considerably enhanced over well fed or poorly fed animals and the longer the period of partial starvation the greater the effect. Wide variations in food availability in the natural conditions of Loch Leven might therefore have given rise to extended longevities (i.e. more moults per life span) and hence larger final sizes of D. hyalina var lacustris than those encountered in culture conditions at 15°C.

The Daphnia females reared on Scenedesmus at 15°C persisted for much shorter periods than those fed on Chlorella at the same temperature. The mean longevity for the six individuals was thirty days and the range 18-39 days. The reason for this is uncertain; although it is possible that bacterial contamination of the cultured food suspensions became excessive leading to bacterial slime which could seriously inconvenience the animals (Pratt, 1943) and/or that the algal food had deteriorated and cell breakdown products proved adverse.

The male individual reared on Chlorella at 15°C reached a final size (1.55mm) which was much smaller than that of females; showed fewer moults per lifespan (eleven as opposed to a possible seventeen) but lived for a comparable time (fifty-five days) to most females, although this was less than the mean maximum longevity. According to Hutchinson (1967) males of Daphnia spp. are smaller than the females but are not in any way ephemeral creatures. MacArthur and Baillie (1929) showed that the life expectancies of male *D. magna* were similar to those of females at low temperature but markedly shorter at high temperatures. The generalisations of Hutchinson (1967) regarding cladoceran growth (Page 178) certainly appeared to apply to the male growth curve (Fig. 16). However, adult moults occurred at very irregular time intervals which disputes the findings of Hall (1964) that adult instar durations are strictly temperature dependent. Lastly, it might be inferred that the food requirements of male *Daphnia* is much less than that of females since food is not needed for egg production and male growth is consistently less, resulting in the reduced adult body-size. Perhaps this has important implications regarding survival, allowing the males to function efficiently under poor food conditions. The reduced size may also offset their likelihood of predation by fish.

(ii) Variations in clutch-size

The factors which influence egg production in *Daphnia* spp. were detailed earlier (Page 159). The fecundities of the individual *Daphnia hyalina* var *lacustris* females in culture conditions were generally high (Fig. 17), much higher in fact than those generally experienced in the field conditions at comparable temperatures.

The effects of temperature on egg production (Page 159) could not be fully ascertained in the laboratory since temperatures were necessarily restricted to 10° and 15°C only. However, the fact that mean broods produced in succession by Chlorella-fed individuals (Fig. 17) were very similar at 10° and 15°C implies a further indication that the optimum temperature range for the species is around 10°-15°C (Page 160). Although in the field conditions the highest egg production was generally associated more with 10°C than 15°C it now seems conclusive that other factors, mainly density related food limitations, operated to reduce egg production at the higher end of this temperature range. The adverse effects of higher temperatures much above 15°C might be suggested by the low egg production (maximum of ten eggs per clutch) of an individual D. hyalina Leydig reared on excess Oocystis sp. at 20°C by Duncan et al. (1970) - although species variations and diet differences must be acknowledged.

Under the optimum temperature conditions, the clutch-size of the cultured females should have been primarily determined by food quantity (Ingle et al., 1939). As food was always given in excess of daily requirements, food quantity cannot have been limiting and it may be inferred from the high egg production that food quality was good. This applies to the Scenedesmus as well as Chlorella food sources. Having established that both temperature and food provided no apparent limitation on egg production but acted purely to enhance it, the intrinsic factors which affect fecundity, such as age, size and genetic constitution of the parent, may be considered more or less in isolation.

The general pattern with age is a rise to and a fall from a maximum in fecundity during the course of adulthood (De Kerherve, 1927; Anderson and Jenkins, 1942; Hutchinson, 1967). The initial rise in fecundity to an optimum capacity appears to be reasonable since the size of the ovaries and the capacity of the brood pouch increase progressively as the individual increases in overall size - a small body-size would thus naturally restrict the egg-laying capability (Green, 1954, 1956). This pattern of events certainly applied to the cultured D. hyalina var lacustris females in the three laboratory conditions (Fig. 17). In the case of the Chlorella-fed females at 15°C, where fecundity was measured throughout total life, the mean maximum brood-size of 22.8 eggs (as obtained from six individuals) was achieved in the eighth adult instar. In comparison, De Kerherve

(1927) working on D. magna found a maximum in the seventh reproductive instar; Anderson and Jenkins (1942) working on the same species found a maximum in the fifth instar; and Wood et al. (1939) found that D. laevis showed a maximum in the fifth or sixth instar. With the Loch Leven form, the maximum was reached on an individual basis in the seventh to eleventh instars (Appendix xiii) so that variation clearly exists in this respect.

However, with the mean successive broods thereafter, the egg numbers gradually declined (Fig. 17), despite the absence of body-size restrictions. The fall-back in egg production coincided with minimal growth increments during moults and presumably indicated the onset of a scenescent phase in life. Interestingly, one of the three longest-living Daphnia did not exhibit reductions in fecundity during old age (Appendix xiii) and this had the effect of increasing the mean brood numbers in instars eleven and twelve (Fig. 17). Scenescence was very marked in the two other individuals with a minimum final brood of only eight eggs being recorded. Egg production decline in old age was distinctly exhibited by D. magna (De Kerherve, 1927) and D. laevis (Wood et al, 1939).

From the above information it is clear that a good correlation would exist between Daphnia body-size and brood-size up to the body-size (age) of maximum brood-size; beyond this point the relationship would be obscured. This age factor may additionally preclude the association between large body-size and large brood-size in the field data of Fig. 10. In late May 1973, when mean broods were high, it was noted that several of the larger females carried small broods tending to suggest their old age.

Total egg production throughout life of a single D. hyalina var lacustris could amount to 200 eggs (Appendix xiii). This may seem large and act to emphasise the highly fecund nature of Daphnia spp. as a whole, but De Kerherve (1929) quoted that an individual D. magna produced a total of 1072 eggs, with a maximum brood of 105 eggs, so this surely must serve as the extreme if not supreme example!

The clonal or genetic effects on egg production (Green, 1956) were not assessed since all the Daphnia used were of similar origin. It would certainly have been interesting to have reared "peaked" and "intermediate" forms and assessed fecundity for comparison, but this was outside the scope of the present study. However, the culture animals were derived from roundheaded stock obtained from August 1973 field samples, when egg numbers in Loch Leven were generally at mid-summer low levels. The progeny of these individuals (several generations removed) were used for the growth studies and had they been left in field, their presence would have coincided with the autumnal increases in mean brood-size. Their clonal background may have partly determined the extent of their high egg production. Maximum brood-sizes of cultured Daphnia corresponded well to the maximum achieved by their roundheaded counterparts in the field during the latter three months of 1973. Despite the optimum laboratory growth conditions, these maxima were less than those produced by wild Daphnia of separate clonal history during the spring of 1973 when numbers in excess of thirty eggs per clutch were recorded several times.

(iii) The length-weight relationship

There are three points concerning the length-weight relationship (Fig. 18) which deserve mention. Firstly, the mean weights of Daphnia hyalina var lacustris, as derived from the regression line, and the mean egg weight correspond well to those for D. hyalina Leydig as obtained by Baudouin and Ravera (1972). Secondly, the mean dry-weight of a fully-developed embryo (2.8μg) was more than that of an egg (1.8μg). This is surprising since

Green (1956), working on *D. magna*, found that 16-25 per cent of the dry matter was *lost* during egg development and Hutchinson (1967) stated that in most Cladocera no additional nutrients are supplied by the parent to the embryoes in the brood pouch. However, the alternative method of egg weight assessment, by calculation* as opposed to direct weighing, produced a precisely similar figure to that given above, so it appears that the egg weight value was not a considerable under-estimate as might be implied.

Lastly, although the weight assessments were based on individuals of uniform standards - all were roundheaded, derived from similar parentage and reared in identical conditions - adult individuals of a given size varied markedly in weight, particularly individuals larger than 2.0mm (Appendix xiv). For example, an individual of 2.5mm might weigh as little as 60µg or as much as 110µg dry weight. Presumably such weight variation related either to the condition of the ovaries (spent or gravid) or to the stage of moulting of the individual such that an individual just about to moult would effectively be carrying

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* By using the mean radius of an egg (0.13mm) the weight was calculated from the volume of a sphere $(4/3\ \Pi r^3)$, assuming that the density of an egg is equal to that of water and that dry weight is equal to 20 percent of wet weight.

a double layer of cuticle. Since egg production and moulting are virtually concurrent in the adult, both factors may manifest themselves simultaneously, thus explaining the wide extent of the weight variation. An individual which had just introduced a batch of eggs into its brood chamber would be light because it would have a spent ovary and would have moulted previously. An individual which was just about to liberate its well-developed young would be heavy because it would have a gravid ovary (in preparation for the next brood) and a double carapace layer prior to the forthcoming moult. The contribution of gut-contents to overall individual weights was not considered important but assumed to be consistently proportional to the sizes of the individuals. Incidentally, attempts to starve *Daphnia* individuals and thus clear their gut-contents, by placing them in filtered loch water, proved ineffective over a two-day period because under such conditions defaecation was apparently inhibited. The prolonged retention of gut contents in poor nutrient media may be of adaptive advantage in allowing *Daphnia* to utilise limited food sources as effectively as possible.

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.

Walker presumed, however, that these beneficial 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.

Nevertheless, there are reasonable grounds for 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.

The seasonal events within the *Cyclops* annual 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 annual increases in *Diaptomus gracilis* (Figs. 27

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 a peak 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 *C. s. abyssorum* population changes of 1976 were

* See Text-Fig 2 in Johnson & Walker (1974) -attached at back of thesis.

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 be prolonged in active planktonic animals if 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 <u>Cyclops</u> <u>leuckarti</u> and Elbourn (1966a) noted a 60-80 per cent success rate for <u>C</u>. <u>strenuus</u> <u>strenuus</u>, 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 adult longevity of at least six months seems 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

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* 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 egg to adult, the duration of the CV stage at each temperature was assumed to be equal to that of the CIV stage.

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 cases, however, the major parameter governing 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.

Seasonal changes in body-size similar to those in Loch Leven have been frequently observed in other copepod populations and are thought to be primarily associated with the annual temperature cycle although food availability during larval development may also be influential (Coker, 1933; Deevey, 1960; McLaren, 1963; Smyly, 1968c, 1975; George, 1976). Smyly (1975), working on *C. s. abyssorum*, demonstrated that the body-size for a given copepodid instar was not subject to notable variation up to instar CIV, but in the last two instars of the female large differences in size could become apparent. In the process of calculating the biomass and production of the *C.s. abyssorum* population, the body-sizes of each of the developmental instars for each sampling date were adjusted in accordance with the seasonal variations in adult female body-size (Page 104). This procedure was unnecessary for nauplii and copepodid stages CI-IV since Smyly (1975) implied that seasonal body-size variations only manifest themselves from the CV stage. Although the biomass and production estimates could be recalculated to take this into account, the data as it stands is directly comparable to that of Walker (1970). It appears, therefore, that temperature and food conditions experienced during the CV stage determine the ultimate adult female size.

Several authors have recognised an inverse relationship between body-size and temperature (Coker, 1933; Elgmork, 1959; Elbourn, 1966). However, Deevey (1960) found that the relative effects of temperature and food on the seasonal changes in body-size depended on the extent of the annual temperature range. She discovered that when the annual mean temperature range was 14°C or less, food exerted the prime influence on development. When the mean range exceeded 14°C, she found significant negative correlations between body-length and temperature at the time of sampling. Moreover, each species from every locality investigated gave significant negative correlations between body-length and the mean temperature of the previous month. Thus, in Loch Leven which undergoes a temperature range in excess of 14°C, one might expect that temperature would be the major factor governing body-size changes. Negative correlations would be expected between the loch temperature during larval development (i.e. during the CV stage) of the adults and their size at sampling, while it might also be expected that similar correlations would be found between water temperatures at the time of sampling and adult body-size. By comparing the graph of mean water temperature (Fig. 2) with that of adult female body-length changes

(Fig. 24) it seems that the latter conclusion is not feasible with regard to the Loch Leven results since, for example, the largest females were not encountered in the coolest temperatures. Nevertheless, a relationship between temperature during development and body-size at maturity may be suggested since the largest females, which appeared in spring, developed during the cold winter months while the smallest females of the year developed during the warmest periods.

Although, as Walker (1970) deduced, such a relationship held true throughout 1969, it was noted that in 1972-73 the smallest females of the year appeared in July rather than later, say, in August when the maximum annual temperatures prevailed (Fig. 2). Perhaps food limitations during development could account for this discrepancy since these individuals were derived from the main spring population and their appearances as adults were concurrent with notable reductions in the over-all population (thus suggesting adverse conditions). Since body-size changes manifest themselves during the CV instar and the duration of the CV instar is highly variable (Smyly 1973a), it might also be suggested that short or prolonged development during this stage has differing effects on the final adult size.

It was previously stated (Page 12) that the body-sizes of C. s. abyssorum from Loch Leven varied from 1.20-2.35 mm (total length minus furcal setae) and that the maximum range was significantly larger than that described as typical for the species by Harding and Smith (1960). The apparently larger "race" of C. s. abyssorum in Loch Leven may have evolved as a result of the highly eutrophic status of the loch coupled with the fact that the copepod existed in virtual monoculture for several years. Smyly (1968C) compared the body-sizes of Diaptomus gracilis from various localities in the English Lake District and generally concluded that larger sizes were related to better food conditions.

Finally, as regards the seasonal changes in copepod body-length, it might be suggested that the smaller body-sizes observed in summer tend to offset predation by fish (Discussion, Part 6) and, as such, indirectly serve the same purpose as cyclomorphotic changes in Daphnia spp. (Discussion, Part 2(d)).

(d) Variations in clutch-size in relation to body-size, food and temperature

It was noted earlier (Page 96) that in 1972-73 the mean numbers of eggs per egg-sac showed distinct seasonal patterns of variation repeated in each year and that a close correlation existed between the mean egg numbers and the mean adult sizes (Fig. 24). Precisely similar phenomena were noted in 1969 (Walker 1970) indicating perhaps that these parameters were not subject to notable modification as a result of the contrasting circumstances between these years. However, although the spring mean maximum and summer mean minimum egg numbers were approximately similar in all three years (these being 37 eggs per sac and 9 eggs per sac respectively in 1969), the mean winter levels in 1969 (around 15 eggs per sac) were much lower than those recorded during the winters within the 1971-74 period, this being perhaps due to the colder conditions in 1969. Nevertheless, the timing of events was somewhat different in 1969. Although in all three years the maximum mean egg numbers were recorded in either April or May, the minimum mean egg numbers in 1969 prevailed from August to October, as opposed to July-early August as in 1972-73, and thus corresponded with the minimum mean body-sizes (Page 215). Perhaps the later appearance of the small adults with small broods in 1969 was due to the later start and prolonged development of the spring <u>Cyclops</u> population.

As regards C. s. abyssorum populations from the four Lake District waters, Smyly (1973a) noted that clutch-sizes varied markedly from one lake to another. In Estwaite Water mean clutch-sizes exceeded 40 eggs per female on most sampling occasions, whereas in Rydal Water and Grasmere mean clutch-sizes outside the limits of 15-30 eggs per female were rare and in Buttermere mean clutches were usually less than 15 eggs per female. However, he noted that in all lakes the egg numbers rose to a peak in May and then declined. In Buttermere breeding discontinued after this period but in Rydal Water breeding continued, although clutch-sizes remained at low levels; and in Estwaite Water further peaks in clutch-size comparable to those of spring occurred in October. Smyly (1973b) found that mean body-sizes (thoracic volume) in Estwaite Water were considerably larger than those in the other three lakes and suggested that this accounted for the larger overall clutch-sizes in this lake.

The seasonal changes in mean clutch-size of C. s. abyssorum in Loch Leven (during 1969 as well as 1972-73) were comparable to those in the Lake District Waters, particularly those in Estwaite Water. However, clutch-sizes in Loch Leven were generally larger than in all the lakes studied by Smyly and perhaps this is related to the exceptionally large sizes of spring C. s.

abyssorum females in the loch.

It is well established that the number of eggs carried by a copepod is mainly dependent upon its food supply (Marshall and Orr, 1952, 1955; Hutchinson, 1967), whilst the actual number of egg-sacs produced in a unit of time is primarily dependent upon temperature (Corkett and McLaren, 1969), although food supply may also affect this (McLaren , 1963, 1965; Edmondson, 1964). Smyly (1970) has shown that the type of food available to carnivorous copepods affects the numbers of eggs produced per egg-sac and that in general fecundity declines with age. Relationships between body-size (or metasomal volume) and egg number (or total yolk volume) have also been postulated (Ravera and Tonolli, 1956; Burgis and Walker, 1972; Smyly, 1973b), and it certainly seems reasonable that body-size would limit the maximum clutch-size (i.e. a small body with correspondingly small ovaries would restrict the egg-laying capacity). Although previous studies have indicated that brood-sizes vary inversely with temperature (Elgmork, 1959; Elbourn, 1966), the additional fact that body-sizes of adult females also vary inversely with temperature suggests that brood-size is only related to temperature indirectly through the effect of temperature on size.

From the evidence given in Fig. 24 and from Walker's data for 1969, it appears that the brood-sizes of C. strenuus abyssorum in Loch Leven are primarily governed by the seasonal changes in body-size. However, in all years the maximum brood-sizes were not coincident with the maximum body-sizes suggesting that other factors were operating, perhaps food supply.

Walker(1970) found that in 1969 the seasonal changes in mean brood-sizes (and/or mean body-sizes) followed very similar trends to the seasonal changes in phytoplankton standing crop (chlorophyll a), although he realised that adult female C. s. abyssorum did not necessarily feed directly on algae. Fig. 30 compares the mean numbers of eggs per egg-sac of C. s. abyssorum, as in Fig. 22, with phytoplantkon chlorophyll a concentrations during 1972-73 (the algal species which dominated during these years are given in Table 12). It is immediately apparent that the phenomenon noted by Walker for 1969 did not apply during these later years. Perhaps the expected relationship between brood-sizes and phytoplankton biomass was obscured by the grazing effects of Daphnia hyalina var lacustris. Even so, it is perhaps significant that the seasonal changes in Cyclops brood-sizes show

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.

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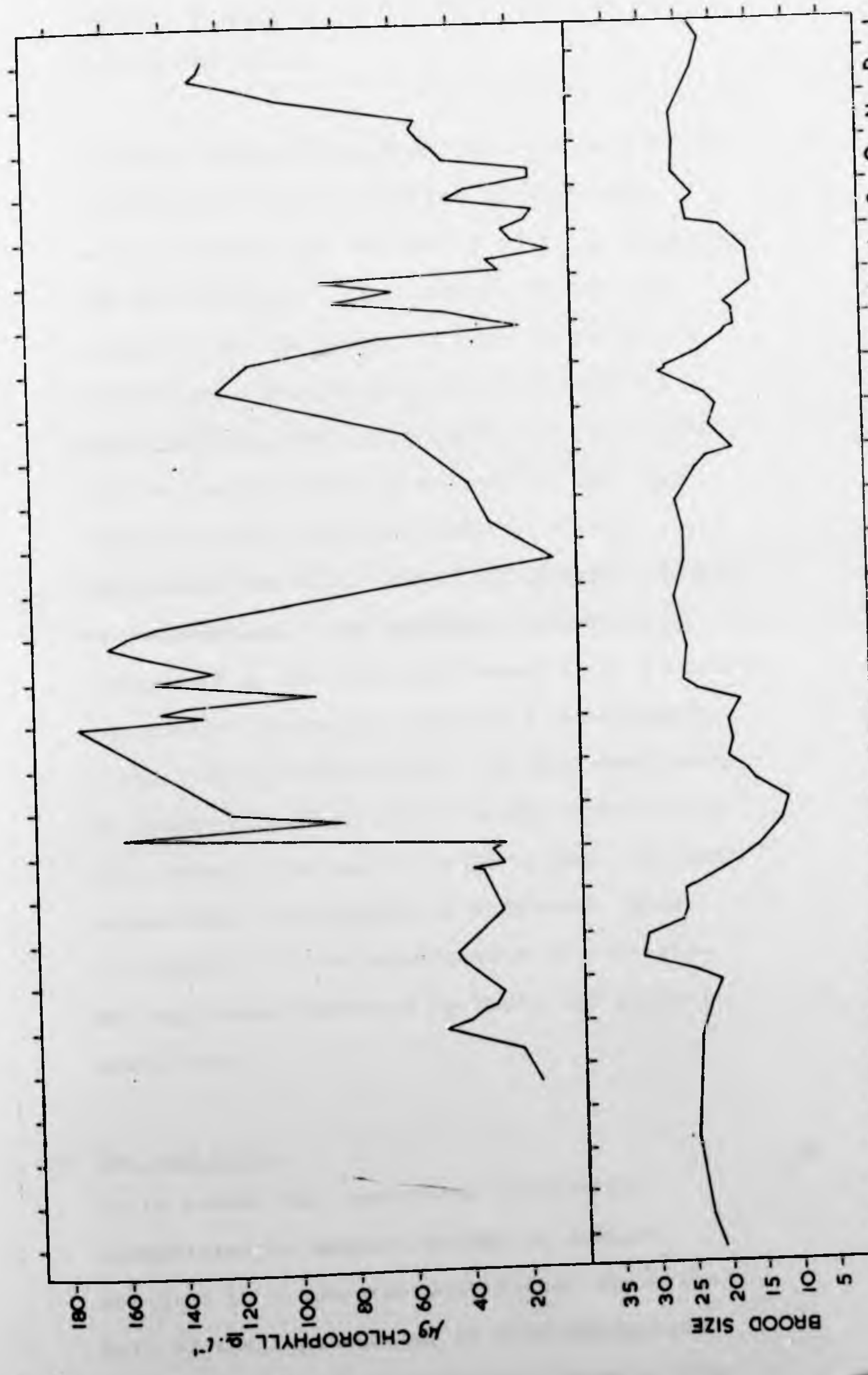
Fig. 30



superficial resemblence to the seasonal changes in Daphnia brood-sizes (Fig. 29 and Discussion, 2(b)).

It would appear, therefore that the mechanisms influencing seasonal changes in body-size and egg numbers of the adults of C. s. abyssorum are very complex. In summary, it may be deduced that the number of eggs which can be carried by a female is directly related to her body-size, while the number of eggs which she can produce must be related to her food supply and the energetic demands of her metabolic rate which itself is directly related to temperature. In addition, body-size is influenced by the food and temperature conditions experienced during the pre-adult developmental stages, while superimposed on this complexity of inter-related variables is the possibility that longer-term genetic effects have "moulded" populations of copepods in different lakes in response to the requirements of body-size and egg number governed by their own special conditions.

(e) The sex ratio

It is common for crustacean zooplankton communities to consist mainly of females, not just in cladoceran populations where the bulk of the reproduction is parthenogenetic, but also in copepod populations (Ravera 1955;

Elgmork, 1957; Smyly, 1961; Hutchinson, 1967; Chapman, 1969). The usual explanation for a preponderance of copepod females is that the smaller males are shorter-lived. The males supply the females with spermatophores (sperm-sacs) during copulation and the stored sperms then fertilise successive egg broods (Corkett and McLaren, 1969). After copulation the males then represent an unnecessary burden on the food supply of the population, as Smyly (1970) noted. If they copulated with more than one female then undoubtedly fewer males would be required.

It is not surprising therefore that in Loch Leven during 1972-73 adult female Cyclops strenuus abyssorum generally outnumbered the males on most sampling occasions. (Fig. 25.) In total contrast, Walker (1970) found that on most sampling dates in 1969 male C. s. abyssorum were numerically superior to females (i.e. on twenty-seven out of thirty visits). On twenty-two occasions during 1969 the males represented more than 60 per cent of the adult fraction and on eleven occasions more than 70 per cent, so that the male dominance was indeed very marked. Walker attributed this unusual situation to differential size-selective predation on females by fish (Discussion, Part 6).

Assuming that at birth the genetic constitution of the population is not biased towards either sex, then the following several factors may account for the fluctuations in sex ratios of CV and adult C. s. abyssorum as illustrated in Fig. 25. Firstly, the sample number (Page 126). Secondly, variable rates of development between males and females. In general the males develop faster than the females from CV onwards (Smyly 1961; George 1976). George (1976) noted that with C. vicinus in Eglwys Nynydd phase differences in the appearance of adult males and females occurred. In each generation adult males tended to precede the adult female peaks and this implied that in field conditions the females took longer to reach maturity. The fact that in Loch Leven the sex ratios remained fairly stable when temperatures were low in winter and yet fluctuated markedly during warm periods, implied that growth accounted for much of the variation, although pulses of either sex were not clearly linked to population development in the way George inferred. It was noted earlier (Page 102) that the graph of CV sex-ratios was often a mirror-image to that of the CVIs (Fig. 25). This can be explained as follows. If, for example, a batch of males moulted from CV to CVI, they would reduce the number of males in the CV instar and increase the number of males in the CVI instar. This would cause a decrease in the proportions of males to females in the CVs with a concurrent increase in the proportions of CVI males to females. Similarly, an increase in the percentage of CV males at the same time as a drop in the percentage of CVI males implied that a number of females had moulted to the adult stage. If this hypothesis is correct, then the entry into adulthood of the males and females was not usually concurrent. With continuous recruitment, resulting from continuous reproduction, this effect is perhaps unexpected. However, it seems that the bulk of the males may have matured at different times to the females during most of the year. Interestingly, this mirror-image effect was a notable feature of the sex-ratio data of 1969 (Walker, 1970).

Lastly, variations in sex-ratio can be caused by behavioural differences between males and females. Several workers have shown that with the cyclopoid copepods which undergo diapause in the late copepodid instars, the proportions of males involved in dormancy is far greater than that of females (Smyly, 1961; George, 1976). George (1976) found that the major factor inducing shifts in the sex ratios of _C_. _vicinus_, in Eglwys Nynydd was related to the effects of diapause in the life-cycle. Copepodids underwent diapause at CIV and 70-80 per cent were males. Thus, during the course of a year, the male/female ratios reached a high level in the spring at the time of emergence from dormancy and fell markedly to low levels when animals entered diapause in mid-summer. It may be implied, however, by the absence of such clearly defined changes, that C. strenuus abyssorum in Loch Leven did not in fact undergo diapause. Nevertheless, it is possible that at times males or females showed a marked preference for a more benthic rather than planktonic existence and were therefore less likely to be sampled. This might perhaps explain the consistent paucity of female CV stages during the 1972-73 winter.

Ravera (1955) emphasised that the adult sex ratios of Mesocyclops leuckarti and Cyclops strenuus Fischer in Lake Maggiore did not vary at random but showed characteristic seasonal variations. In general the males predominated in spring, the females predominated at the beginning of summer and at the end of this season the sex-ratios almost approached unity. He pointed out, however, that males predominated in the periods of high density, whereas the females were most numerous in periods of low density and he interpreted this phenomenon by suggesting that the females outlived the males during the numerical depression of the population thus guaranteeing a certain number of births in the low periods.

Additionally, Ravera observed approximate relationships between the sex ratio and the number of eggs, in that the egg stock densities increased when the sex ratios shifted in favour of females.

In Loch Leven during 1972-73 (and in 1969) clear-cut seasonal patterns of variation in adult sex ratios were not apparent, nor were there any distinct correlations between sex ratios and population densites or egg stock. However, in September and November in 1972 and in September of 1973, sex ratios which were strongly biased towards females were coincident with high egg stock, but this phenomenon was not apparent at other times. Similarly, George (1976) working on C. vicinus did not find a clear relationship between sex ratios and periods of egg production.

4. The food sources of the zooplankton populations of 1972-73.

It is of interest in ecological studies to ascertain where each of the populations concerned derive their energy, this information being basic to the understanding of the trophic dynamics within the ecosystem. The crustacean zooplankton community of Loch Leven collectively constitutes at least two trophic consumer levels, the herbivores (primary consumers) and the carnivores (secondary and possibly tertiary consumers). On the basis of feeding mechanisms the five principal species can be suitably divided into either filter-feeders, which graze upon minute particles suspended in the water, or seizers, which grasp individual particles. Using these classifications, Daphnia hyalina var lacustris and Diaptomus gracilis can be conveniently described as herbivorous filter-feeders; Cyclops strenuus abyssorum as essentially an omnivorous seizer; and Leptodora kindti and Bythotrephes longimanus both as carnivorous seizers.

(a) The herbivorous filter-feeders

It is widely acknowledged that Daphnia spp. are filter-feeders which depend for their nutrition on a wide variety of fine particles suspended in the surrounding medium such as algae, detritus, bacteria and possibly protozoa and fungi. The intricate details of the cladoceran feeding mechanism have been described by Cannon (1933). These organisms utilise particles within a fairly restricted size spectrum of 1<20µm (Brooks 1969; Nadin-Hurley and Duncan 1976) and their filtering mechanisms function most effectively with particle sizes of about 2-4µm (Gliwicz 1969c, 1970). Nadin-Hurley and Duncan (1976) evaluated the gut contents of three species of Daphnia (including D. hyalina Leydig) which occurred in two Thames Valley reservoirs and found no apparent variation in the nature or sizes of particles ingested by the different species. They found that in general the most frequent size of ingested particle was between 1-2µm and up to 60 per cent of all animals examined contained particles which were smaller than 20µm. They also concluded that the limiting factor for ingestion was the width rather than the length of the particle so that long, narrow and pliant algal filaments could be utilised.

Gut samples analyses of D. hyalina var lacustris from Loch Leven during 1972 (page 30) revealed that unicellular and colonial algae were the major components ingested during the spring and early summer periods (May-June) but in mid- to late summer the guts mostly contained amorphous detrital material 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 ponds, studied the effects of different sizes of 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, whereas in lakes of lesser productivity, zooplankton 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 the adults are voracious predators.

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. The predators initially subject their prey to 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/51 Friedinger sample

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).

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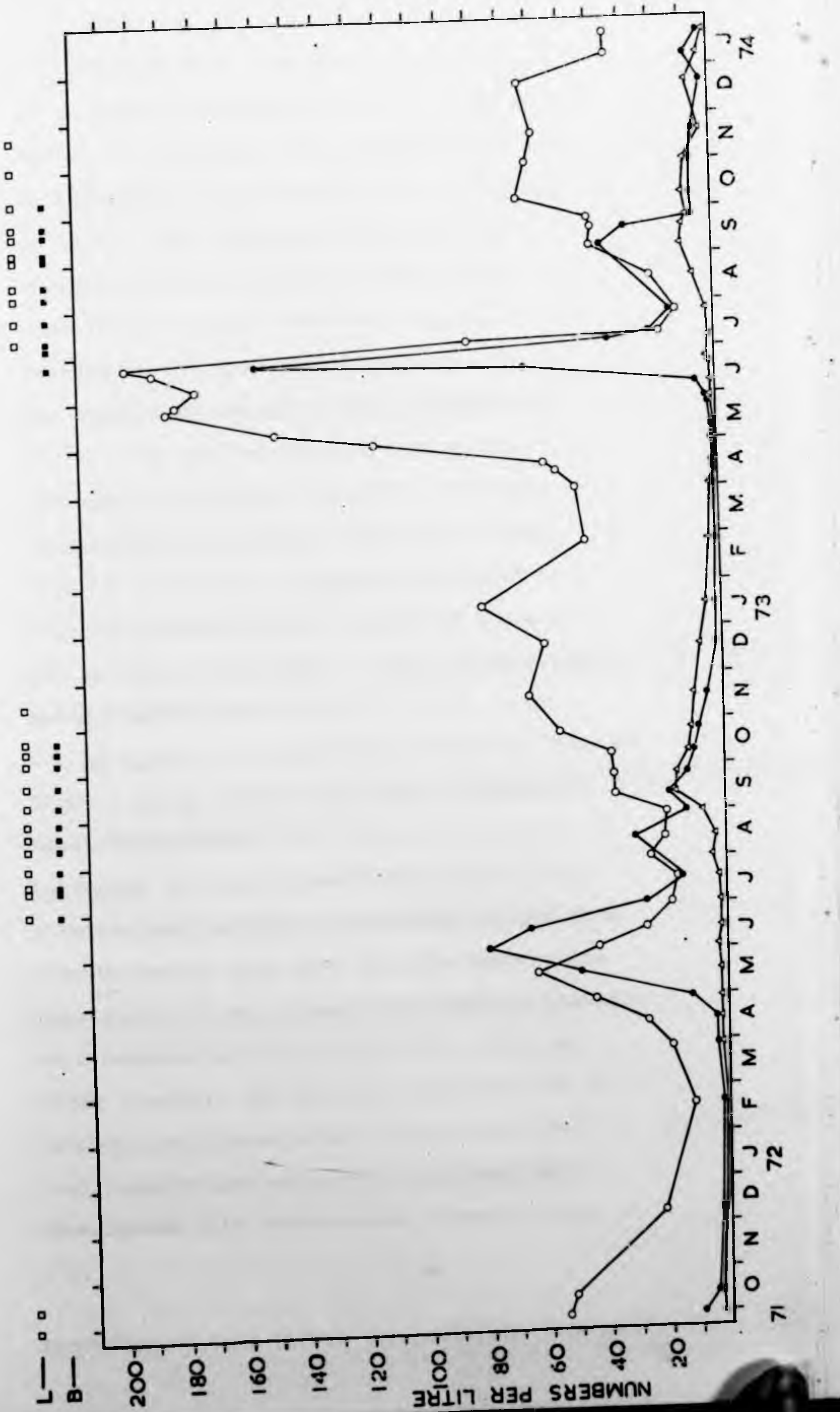
Fig. 31



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/5l) 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 September 1973 (Table 11B) could have been 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 copepodids IV-VI (adults) amounted to 107 ind/l

(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 their own nauplii (together with 30 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)).

Fig. 32 compares the seasonal variations in D. hyalina var lacustris densities (as in Fig. 5) 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.

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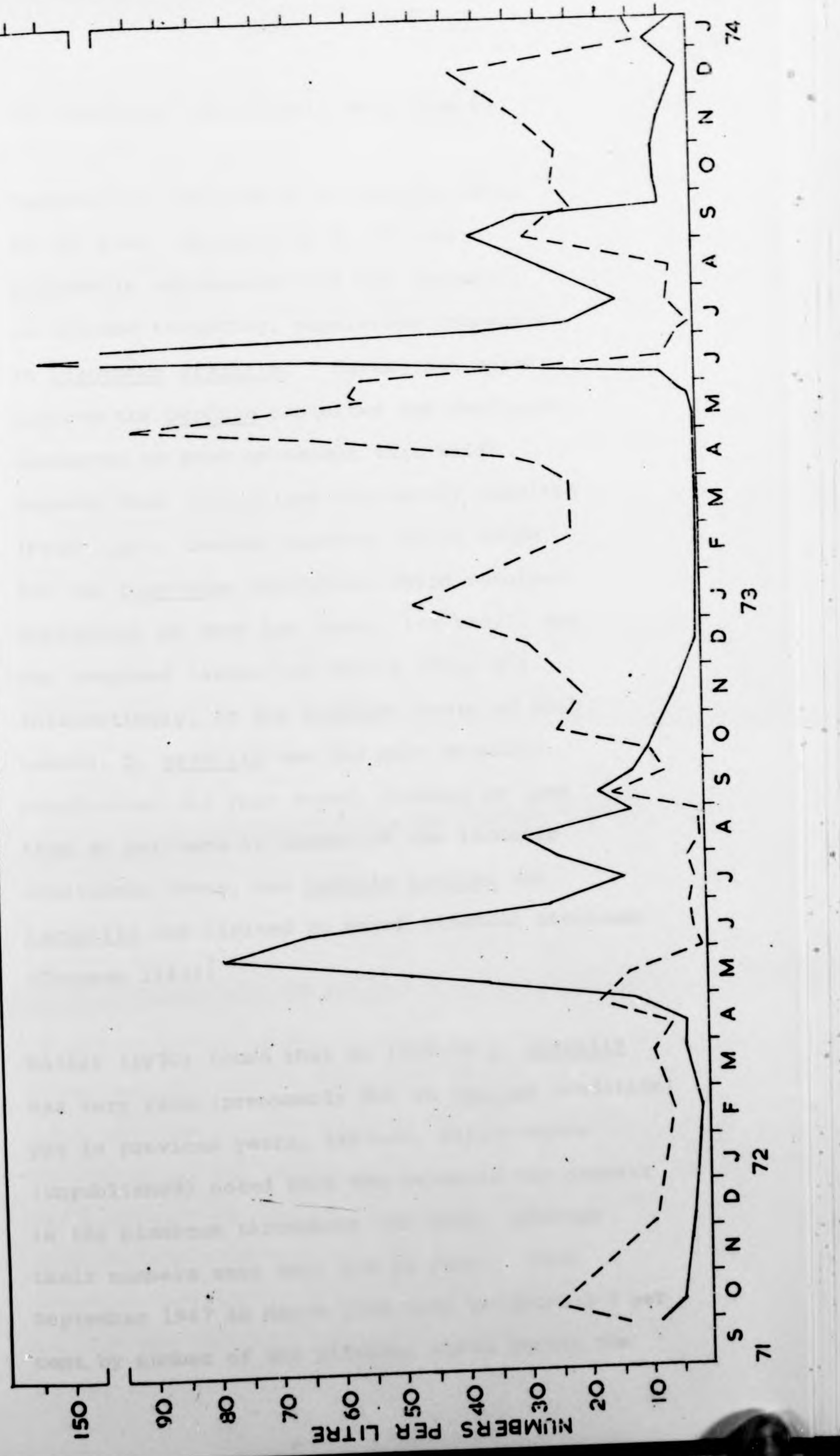

the necessary nutritional requirements.

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 O+ 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/5l 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 acute 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 to the relative paucity of adult females in early 1973 (Fig. 25).

7. A summary of biomass and production

(a) *Daphnia hyalina* var *lacustris*

Monthly and annual production measured by planimetry of curves of daily production against time are summarised for *Daphnia hyalina* var *lacustris* in Table 15, together with mean biomass estimates and P/B coefficients. The mean monthly biomass is additionally presented as histograms in Fig. 33.

The maximum mean monthly and the annual mean biomasses supported in Loch Leven in 1972 were 1.98gC/m^2 (May) and 0.57gC/m^2 respectively; and in 1973 1.72 gC/m^2 (June) and 0.57 gC/m^2 (Table 15). From Fig. 20 the maximum biomass value was 2.43 gC/m^2 in 1972 and 4.0 gC/m^2 in 1973. These data compare very favourably with those obtained by George and Edwards (1974) for *D. hyalina* var *lacustris* in Eglwys Nynydd (mean depth 3.5m). On the same basis these authors recorded maximum mean monthly and annual mean biomasses of 2.11 gC/m^2 (April) and 0.88 gC/m^2 in 1970; and 1.35 gC/m^2 (May) and 0.49 gC/m^2 in 1971. Their data on maximum biomass values were 3.66 gC/m^2 in 1970 and 2.58 gC/m^2 in 1971. In addition, Steel *et al.*(1972) recorded that in the 12m deep Queen Mary Reservoir, *D. hyalina* Leydig biomass values ranged from less than 1gC/m^2 to 5 gC/m^2 and Winberg *et al.*(1972) quoted average annual biomass estimates of 0.12 gC/m^2 to 0.32 gC/m^2

Table 15. Monthly and annual biomass and productivity data for D. hyalina var lacustris from Loch Leven during 1972-73.

	Mean Biomass (B) g^C/m^2		Production (P) g^C/m^2		P/B coefficient	
	1972	1973	1972	1973	1972	1973
Jan	0.08	0.05	0.08	0.02	1.00	0.40
Feb	0.06	0.01	0.05	0.005	0.83	0.50
Mar	0.11	0.002	0.09	0.002	0.82	1.00
Apr	0.26	0.01	0.48	0.02	1.85	2.00
May	1.98	0.05	2.88	0.13	1.45	2.60
Jun	1.54	1.72	3.61	7.34	2.34	4.27
Jul	0.62	0.94	2.04	2.43	3.29	2.59
Aug	1.06	1.07	2.13	2.63	2.01	2.46
Sep	0.39	1.60	1.37	2.31	3.51	1.44
Oct	0.36	0.19	0.64	0.36	1.78	1.89
Nov	0.27	0.20	0.23	0.22	0.85	1.10
Dec	0.11	0.17	0.08	0.17	0.73	1.00
Annual	0.57	0.50	13.68	15.64	24.00	31.28

Figure 33 (opposite)

Mean monthly biomass histograms for *D. hyalina* var *lacustris* during 1972-73.

Abcissa - the study period

Ordinate - the mean monthly biomass in g/m^2 and gC/m^2.

The broken line denotes the mean annual biomass.

Note that the histograms serve to illustrate the mean monthly biomass values given in Table 15.

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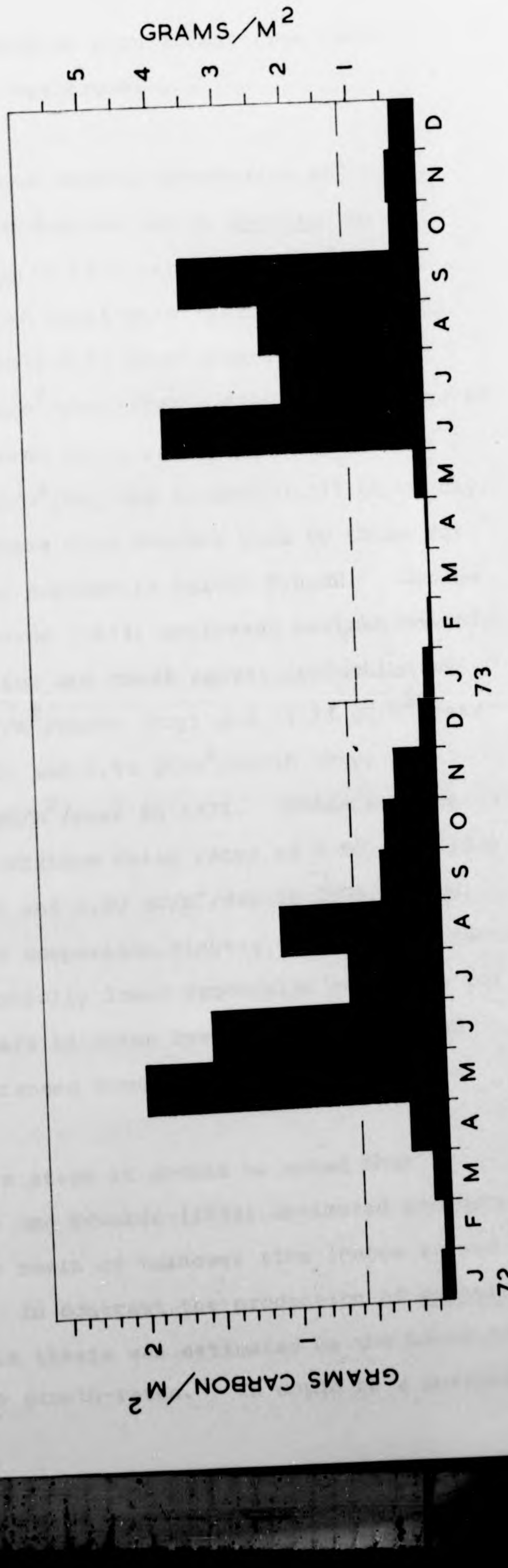

for cladoceran populations from three lakes in Byelorussia.

The maximum monthly production and total annual production for D. hyalina var lacustris in 1972 were 3.61 gC/m^2/month (June) and 13.68 gC/m^2/year respectively; and in 1973 7.34 gC/m^2/month (June) and 15.64 gC/m^2/year (Table 15). From Fig. 20 the maximum daily production in 1972 was 0.146 gC/m^2/day and in 1973 0.597 gC/m^2/day. Again these data compare well to those for the same species in Eglwys Nynydd. George and Edwards (1974) estimated maximum monthly production and total annual production of 6.61 gC/m^2/month (May) and 18.25 gC/m^2/year in 1970; and 5.44 gC/m^2/month (May) and 12.78 gC/m^2/year in 1971. These authors quoted maximum daily rates of 0.60 gC/m^2/day in 1970 and 0.50 gC/m^2/day in 1971. For further comparison Winberg et al. (1972) quoted substantially lower production estimates for cladocera in three Byelorussian lakes and these ranged from 1.88 to 6.97 gC/m^2/year.

At this stage it should be noted that George and Edwards (1974) estimated production on the basis of turnover time (Pages 19 and 60). In contrast the production of Daphnia in this thesis was estimated on the basis of finite growth-rates. In would be a worthwhile future pursuit to calculate production from the present data using the concept of turnover time as well, in order to compare and contrast the information produced by the two methods. If notable differences occurred, it would be beneficial to compare the production data of similar populations from different waters using data derived from the compatable method. However, it must not be forgotten that several permutations of both methods exist (Edmondson and Winberg, 1971) and these may provide additional complications.

The monthly P/B coefficients for Loch Leven Daphnia ranged from 0.73 to 3.51 in 1972 and from 0.40 to 4.27 in 1973. The annual P/B coefficients were 24.0 in 1972 and 31.3 in 1973. Yet again these were similar to those obtained by George and Edwards (1974) who recorded monthly coefficients ranging from 0.61 to 3.90 in 1970 and 0.75 to 4.01 in 1971. The annual P/B coefficients for D. hyalina var lacustris in Eglwys Nynydd were 20.8 in 1970 and 25.9 in 1971. Winberg et al. (1972) noted that annual P/B coefficients for cladocera in the three Byelorussian lakes varied from 13.1 to 17.1. There is a tendency for the P/B coefficients (for all groups of zooplankton including carnivorous copepods) to increase in proportion to the productivity of a lake (Winberg et al. 1965; Patalas, 1970). Winberg et al. (1965) calculated P/B coefficients for cladocera, during a five month period which constituted the growth season, in several lakes of variable trophic status, from mesotrophic to eutrophic. Their results respective to each lake in order of increasing eutrophic conditions were 9.0 for L. Naroch (mesotrophic), 11.3 for L. Myastro and 26.8 for L. Batorin (eutrophic). Loch Leven is certainly eutrophic (Morgan 1970, 1972, 1974) and the high Daphnia P/B coefficients obtained no doubt bear reflection of this.

The biomass histograms in Fig. 33 clearly illustrate that the Daphnia population of Loch Leven was present in appreciable quantities (above 0.5 gC/m^2 or above the mean annual biomass level) for only four months of each year; from May to August inclusive in 1972 and from June to September in 1973. Despite the notable differences between the two years as regards Daphnia population attributes (the timing of major population events, absolute numbers achieved, population size components, brood-sizes, etc.) and the more favourable food conditions of 1973, the overall outcome in terms of Daphnia biomass and production for the entire annual cycle was similar in both years. The similarity between the summarised annual biomass and production data for Loch

Leven (Table 15), and that for D. hyalina var lacustris from Eglwys Nynydd (George and Edwards, 1974) certainly implies that, since its re-establishment in 1970, the Loch Leven Daphnia population has maintained itself as well as might be expected in a typical shallow eutrophic lake ecosystem. The summarised data for 1972 in Loch Leven bears a particularly close resemblance to that for 1971 in Eglwys Nynydd. The similar biomass data for both waters is particularly significant since the annual cycles of the two Daphnia populations were different. In Eglwys Nynydd, Daphnia were present in substantial numbers from at least April until October in each year (page 146) whereas in Loch Leven the annual cycle was distinctly bimodal with major population events being restricted to a four-month period. However, as a reflection of population size-composition, the mean adult sizes in Eglwys Nynydd were considerably and consistently smaller than in Loch Leven. As a suggestion for future work, it would be worthwhile to undertake a more detailed comparison of the D. hyalina var lacustris populations from the two waters with an emphasis on the inter-relationships within the respective ecosystems. It would also be of interest to incorporate the Daphnia data for 1976 (George in prep.) to the present pool of knowledge concerning Loch Leven zooplankton.

(b) Cyclops strenuus abyssorum

Monthly and annual production derived from planimetric integration of daily production against time are given for Cyclops strenuus abyssorum in Table 16, together with mean biomass estimates and P/B coefficients. In addition, the monthly biomass is presented as histograms in Fig. 34. For comparative purposes, some data is quoted as mg dry wt/l in the following text.

The maximum mean monthly and the annual mean biomasses of C. strenuus abyssorum in Loch Leven in 1972 were 0.93 gC/m^2 (May) and 0.50 gC/m^2 (0.30 mg dry wt/l) respectively; and in 1973 3.29 gC/m^2 (June) and 0.95 gC/m^2 (0.55 mg dry wt/l) - Table 16. From Fig. 26 the maximum biomass value recorded in 1972 was 1.08 gC/m^2 (mid-May) and in 1973 4.56 gC/m^2 (mid-June). In 1969 when C. strenuus abyssorum exclusively dominated the Loch Leven zooplankton, the annual mean biomass was estimated at 0.62 gC/m^2 (0.35 mg dry wt/l); the maximum mean monthly biomass was 1.76 gC/m^2 (July) and the maximum biomass value was 2.55 gC/m^2 (early July) - (Walker 1970; Johnson and Walker 1974). As regards other waters, mean biomass estimates given by Smyly (1973) for C. strenuus abyssorum in four lakes in the Lake District ranged

Table16. Monthly and annual biomass and productivity data for C. strenuus abyssorum from Loch Leven during 1972-73.

	Mean Biomass (B) g^C/m^2		Production (P) g^C/m^2		P/B coefficient	
	1972	1973	1972	1973	1972	1973
Jan	0.25	0.70	0.13	0.40	0.52	0.57
Feb	0.18	0.62	0.09	0.31	0.50	0.50
Mar	0.28	0.64	0.18	0.35	0.64	0.55
Apr	0.39	0.85	0.30	0.56	0.77	0.66
May	0.93	1.52	0.74	1.29	0.79	0.85
Jun	0.48	3.29	0.44	3.59	0.92	1.09
Jul	0.18	0.55	0.18	0.60	1.00	1.09
Aug	0.31	0.32	0.31	0.33	1.00	1.03
Sep	0.50	0.38	0.49	0.39	0.98	1.02
Oct	0.68	1.09	0.48	0.78	0.70	0.71
Nov	1.00	0.88	0.63	0.49	0.63	0.57
Dec	0.88	0.62	0.48	0.36	0.54	0.58
Annual	0.50	0.95	4.45	9.45	8.90	9.95

Figure 34 (opposite)

Mean monthly biomass histograms for *C. strenuus abyssorum* during 1972-73.

Abcissa - the study period

Ordinate - the mean monthly biomass in g/m^2 and gC/m^2.

The broken line denotes the mean annual biomass.

Note that the histograms serve to illustrate the mean monthly biomass values given in Table 16.

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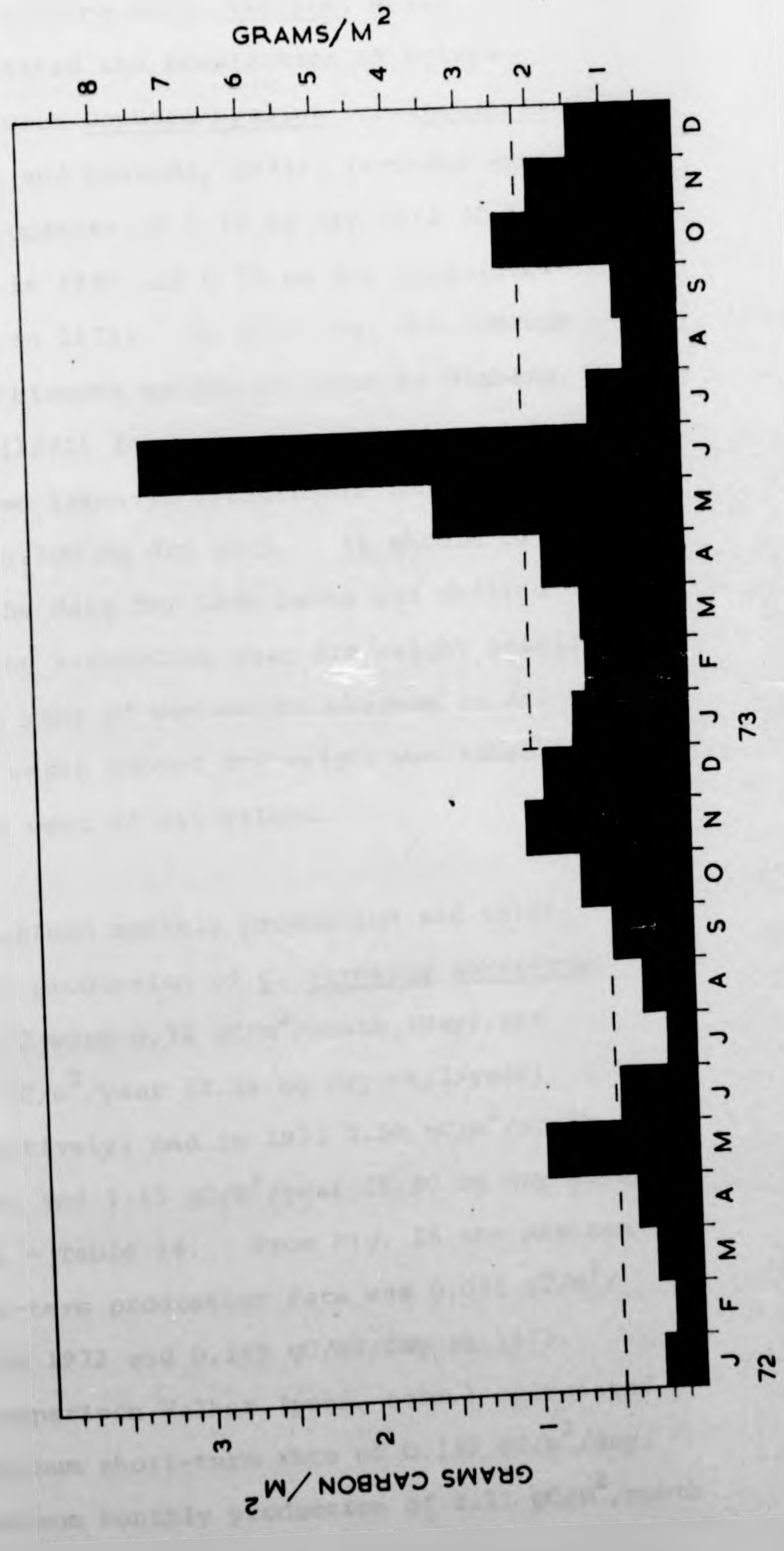
Fig. 34



from 0.004 to 0.008 mg dry wt/l. George (1976) working on C. vicinus, which co-dominated the zooplankton of Eglwys Nynydd with Daphnia hyalina var lacustris (George and Edwards, 1974), recorded annual mean biomasses of 0.12 mg dry wt/l (0.18 gC/m^2) in 1970 and 0.16 mg dry wt/l (0.24 gC/m^2) in 1971. In addition, the average annual biomass estimates given by Winberg et al. (1972) for predatory Cyclops populations of three lakes in Byelorussia ranged from 0.006-0.100 mg dry wt/l. It should be noted that the data for Loch Leven was derived with the assumption that dry weight equalled 10 per cent of wet weight whereas in all the other works quoted dry weight was taken as 20 per cent of wet weight.

The maximum monthly production and total annual production of C. strenuus abyssorum in 1972 were 0.74 gC/m^2/month (May) and 4.45 gC/m^2/year (2.59 mg dry wt/l/year) respectively; and in 1973 3.59 gC/m^2/month (June) and 9.45 gC/m^2/year (5.50 mg dry wt/l/year) - Table 16. From Fig. 26 the maximum short-term production rate was 0.028 gC/m^2/day in 1972 and 0.169 gC/m2/day in 1973. In comparison Walker (pers. comm.) calculated a maximum short-term rate of 0.132 gC/m^2/day, a maximum monthly production of 2.11 gC/m^2/month

(June) and a total annual production of 7.92 gC/m^2/year (4.61 mg dry wt/l/year) for *C. strenuus abyssorum* during 1969. For further comparison Smyly(1973) estimated the production of *C. strenuus abyssorum* by two different methods and obtained values of annual production ranging from 0.04 to 0.25 mg dry wt/l/year. George (1976) estimated annual production for *C. vicinus* in Eglwys Nynydd and obtained figures of 4.2 gC/m^2/year (2.71 mg dry wt/l/year) for 1970 and 4.8 gC/m^2/year (3.10 mg dry wt/l/year) for 1971. The annual production estimates givenby Winberg *et al.*(1972) for predatory *Cyclops* spp. populations ranged from 0.12-1.30 mg dry wt/l/year.

The monthly P/B coefficients for Loch Leven *Cyclops* ranged from 0.50-1.00 in 1972 and from 0.50 to 1.09 in 1973. The annual P/B coefficients were 8.90 in 1972 and 9.95 in 1973. In 1969 monthly values higher than those obtained during 1972-73 were recorded for June (1.60) and July (1.15) and the annual P/B value was 12.80 (Walker pers. comm.). Winberg *et al.*(1965) estimated P/B coefficients for cyclopoids in three lakes of varying trophic status and noted values for a five-month period for each lake in order of increasing eutrophic conditions thus : 7.7 for L. Naroch (mesotrophic), 10.2 for L. Myastro and 10.2 for L. Batorin (eutrophic). George (1976) calculated P/B coefficients of 22.5 in 1970 and 19.4 in 1971 for C. vicinus in the eutrophic Eglwys Nynydd.

From Fig. 34 and Table 16 it is evident that both the mean annual biomass and the total annual production of Cyclops in Loch Leven were approximately two-fold greater in 1973 than in 1972. The corresponding data for 1969 (Johnson and Walker 1974) represents an intermediate situation, being greater than in 1972 yet much less than in 1973. Biomass and production of Cyclops in Loch Leven was generally much higher than in other waters quoted. However, the annual P/B coefficients for the years 1972 and 1973 were similar, yet both were lower than that for 1969. In 1969 the bulk biomass of the Cyclops population was concentrated in the summer months from June to August inclusive so that the higher production per unit biomass (P/B) was associated with high temperatures. During 1972 and 1973, the bulk biomass of Cyclops was generally confined to the spring, autumn and winter periods (Fig. 34) when loch temperatures were comparatively low. In both years, the months of July and August represented periods of very low biomass (Fig. 34). Incidentally, in all years the important variations in biomass were due to copepodid stages; nauplii contributed little to the overall biomass.

Using the summarised biomass and production data for Cyclops, it would be difficult to state categorically that the changes in the open water system at Loch Leven as a result of the renewed presence of Daphnia in 1970 have acted either to the benefit or to the detriment of the Cyclops population as a whole. However, the contrast between the monthly biomass distributions of 1969 (Walker, 1970) and those of 1972-73 (Fig. 34) might suggest that in the latter years the presence of Daphnia restricted the fuller expression of the copepod population during the summer months, July and August, perhaps by limiting the food sources available to the young copepodid stages.

Nevertheless, in 1972 and 1973 this was compensated for by increased population development during the mild winter periods. Development of the copepod population during the winters associated with 1969 were presumably inhibited by the severity of conditions as noted by Smith (1974).

(c) Summary

Fig. 35 provides a summary of relationships in the food chains at Loch Leven for the year

1971 (revised from Morgan and McLusky, 1974). All values are given as KJ/m^2/year and appropriate conversion factors used to calculate the energy equivalents of mean annual biomass and total annual production for both Daphnia hyalina var lacustris and Cyclops strenuus abyssorum are given in the legend to Fig. 35, together with other relevant information.

The mean annual biomass and total annual production of Daphnia in 1972 were 23.9 KJ/m^2 and 552 KJ/m^2/ year respectively; and in 1973 21.0 KJ/m^2 and 654 KJ/m^2/year. For Cyclops these were 231.1 KJ/m^2 and 204 KJ/m^2/year in 1972 and 43.6 KJ/m^2 and 432 KJ/m^2/year in 1973. Expressed as averages for the two years, the mean standing crop and annual production of Daphnia were 22.4 KJ/m^2 and 603 KJ/m^2/year respectively; and for Cyclops 33.3 KJ/m^2 and 318 KJ/m^2/year (Fig. 35). In 1969 the mean standing crop of Cyclops was 28.3 KJ/m^2 (Morgan and McLusky 1974) and the annual production was 361 KJ/m^2/year (Walker pers. comm.)

The biomass and production of Cyclops in 1969 was almost the same as the averaged data for 1972-73; yet in the latter years the additional presence of Daphnia accounted for a total annual production which was approximately two-fold greater than that of Cyclops. This surely

Figure 35 (opposite)

Flow diagram summarising relationships in the food chains at Loch Leven for the year 1971. (from Morgan and McLusky 1974.)

Note that the energy circuit language symbols of Odum (as in Jansson 1972) have been used in the diagram as explained in the insert key. All values given are expressed as $KJ/m^2/year$. Known feeding relationships are shown by a solid arrow, and hyperthetical ones by a hatched arrow. Data for years other than 1971 are shown in italics - this includes zooplankton (1972-73), macrophytes and nematodes (1972) and tufted duck (1970).

The mean annual biomass and total annual production estimates for both Daphnia and Cyclops (from Tables 15 and 16) were converted to $KJ/m^2/year$ using appropriate conversion factors. Daphnia data was converted to K cal using the formula 1 gram dry weight = 4.4 K cal (Richman 1958; Prus 1970) and Cyclops data was converted to K cal using 1 gram dry weight = 4.8 K cal (Wierzbicka 1967; Prus 1970). All data was then converted to K Joules assuming that 1 K cal = 4.184 KJ (Phillipson 1970; McLusky and McFarlane 1974). The figures inserted into the diagram opposite represent averages for the two years 1972 and 1973.

Although the energy flow diagram relates to the year 1971, the inclusion of mean annual biomass and total annual production of Daphnia and Cyclops for 1972-73 was considered appropriate as Daphnia were present at Loch Leven throughout 1971 and the limited numerical standing crop data available for that year (Johnson and Walker 1974) suggested that these zooplankers were present in comparable quantities as in 1972-73.

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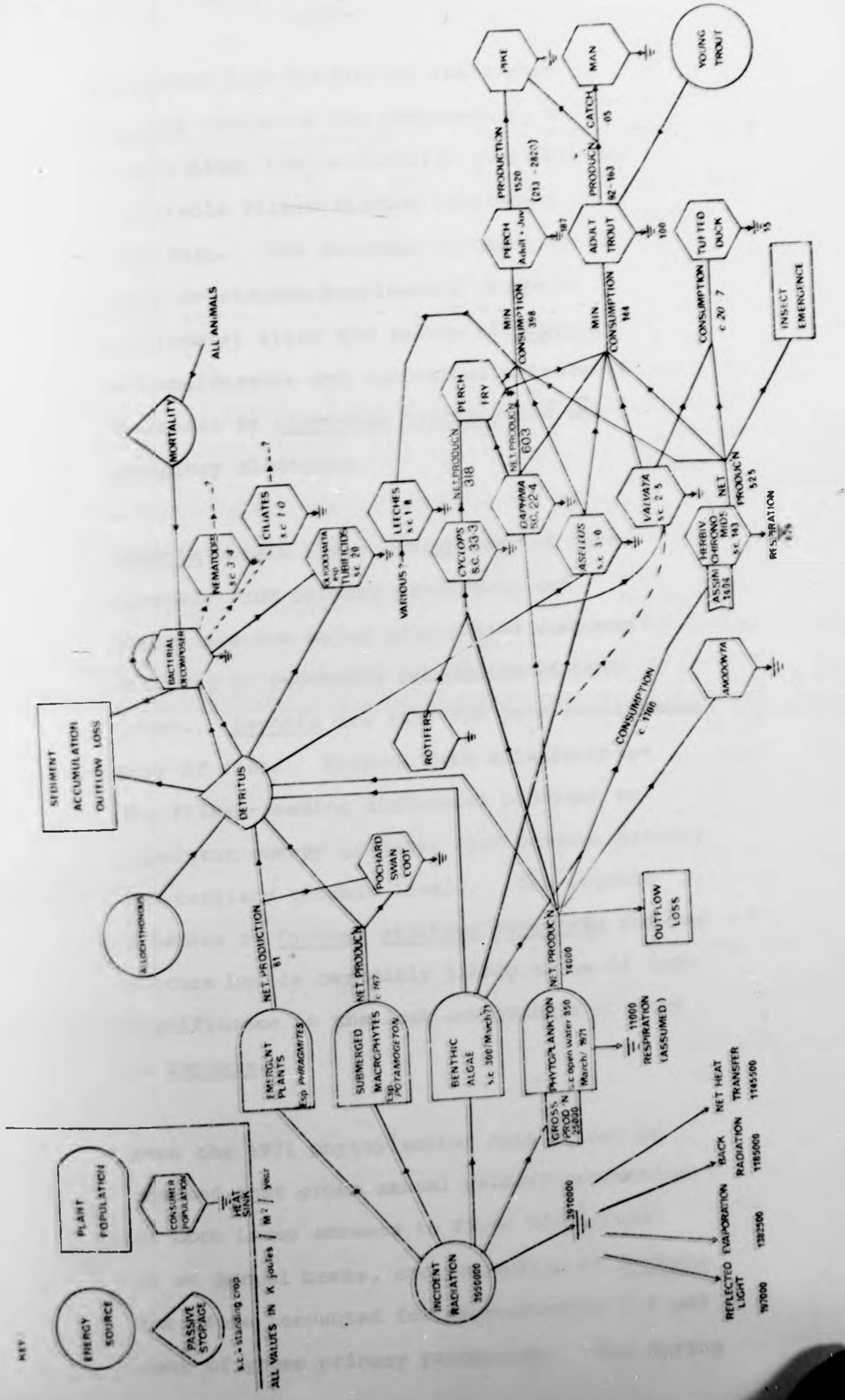

indicates that during the years when Cyclops dominated the zooplankton, a vacant niche was potentially available to a suitable filter-feeding crustacean herbivore. The increase in quantity of total crustacean zooplankton (numbers or biomass) since the return of Daphnia is considerable and additionally includes increases in Diaptomus gracilis and the predatory cladocera.

Daphnia obtain their energy more or less directly from primary production and constitute the major zooplankton component involved in secondary production at Loch Leven. Daphnia are also the main zooplankton prey of fish. Through such relationships the filter-feeding cladoceran provides an important energy transfer link between primary and tertiary trophic levels. The trophic dynamics of Cyclops strenuus abyssorum remains obscure but is certainly likely to be of less significance to the loch ecosystem than that of Daphnia.

From the 1971 phytoplankton data it can be assumed that gross annual primary production at Loch Leven amounts to 25000 KJ/m^2/year. On an annual basis, the production of Daphnia therefore accounted for approximately 2.4 per cent of gross primary production. The spring

Daphnia production maximum of May 1972 (monthly total 66.4 $KJ/m^2/month$) and that of June 1973 (135.1 $KJ/m^2/month$) are equivalent to only about 3.2 and 6.5 per cent respectively of gross monthly production. According to George and Edwards (1974) the production of D. hyalina var lacustris in Eglwys Nynydd was less than 2 per cent of gross primary production for most months of the year and the maximum monthly production was equivalent only to about 9 per cent. Wright (1965) found that in Canyon Ferry Reservoir, D. schodleri, the most important component of the zooplankton, accounted for 9.2 per cent of gross primary production.

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 <u>alone</u>. 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.

However, after the unusual disturbances in Loch

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.

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Appendix (i) - data for Figure 2.

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

Note that only the overall mean loch temperatures are presented graphically in Figure 2.

	Temperature °C		
Sampling 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 (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.

Sampling Dates	Temperature °C	
	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	17.18
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.

Sampling Dates	% of total numbers in water column at site E								
	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 (xi) - data for Figure 15

Mean growth curves for female D. hyalina var lacustris reared in laboratory conditions at 15°C and 10°C.

Data for 15°C growth curve

Mean Age at Moult-stages (days)	Mean Body-length (mm)
1st day	0.58
2.11	0.80
3.78	1.04
6.00	1.24
7.71	1.39
11.22 1st brood of eggs	1.59
14.78	1.73
19.11	1.86
23.63	2.00
28.00	2.10
32.50	2.17
37.25	2.24
41.67	2.29
46.67	2.33
50.00	2.35
55.67	2.37
60.33	2.40
65.00 Longevity	2.42

Data for 10° growth curve (up to seven adult moults)

Mean Age at Moult-stages (days)	Mean Body-length (mm)
1st day	0.57
3.06	0.81
5.40	1.08
10.60	1.29
14.00	1.43
18.80 1st brood of eggs	1.60
26.00	1.74
34.40	1.88
42.50	2.06
51.00	2.14
59.00	2.20
66.00	2.27

Note that Fig. 19 was derived from the above data (see legend of Fig. 19.).

Appendix (xii) - data for Figure 16

The growth-rate of an individual male D. hyalina var lacustris reared in laboratory conditions at 15°C.

Age (days)	Body-length (mm)	Occurrence of carapace casts
1st Day	0.58	
2	0.82	-
3	0.84	-
6	1.00	moult
7	1.18	-
10	1.24	moult
12	1.29	moult
16	1.32 Testes	moult
17	1.37	-
24	1.39	moult
27	1.47	moult
31	1.50	moult
42	1.53	moult
47	1.55	moult
54	1.55	moult
56 Longevity		

Appendix (xiii) - data for Figure 17

The mean brood-sizes produced in succession by *D. hyalina* var *lacustris* females reared in three different laboratory conditions.

Data for 15°C Chlorella-fed

	SUCCESSIVE BROOD-SIZES												Total
Female	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	Eggs
1	6	6	13	17	13	13	21	21	20	21	26	24	201
2	7	10	13	16	13	16	20	26	26	18	13	12	190
3	5	3	9	14	18	18	20	29	21	21	12	8	178
4	8	8	15	7	15	19	26	30					128
5	6	10	11	15	16	19	21	15					113
6	5	11	14	19	16	18	22	16					121
7	5	9	10	15	20	16	21						96
8	9	12	15	15	15	19	17						102
9	7	8	2										27
Mean Brood-size	6.44	8.56	12.44	14.75	15.75	17.25	21.00	22.83	22.33	20.00	17.00	14.67	

Data for 10°C Chlorella-fed (up to seventh brood)

	SUCCESSIVE BROOD-SIZES							
Female	1st	2nd	3rd	4th	5th	6th	7th	Total eggs
10	9	12	16	10	19	22	16	104
11	6	9	11	16	18	21	23	104
12	7	10	13	18	22	28	26	124
13	6	6	14	14	15	16		71
14	6	10	10					26
Mean Brood-size	6.80	9.40	12.80	14.50	18.50	21.75	22.33	

Data for 15°C Scenedesmus-fed

	SUCCESSIVE BROOD-SIZES							
Female	1st	2nd	3rd	4th	5th	6th	7th	Total Eggs
15	6	12	16	18	25	27	26	130
16	9	15	16	23	25	29	25	142
17	6	12	16	16	17	15	19	101
18	6	8	13	15	9	19		70
19	7	12	14					33
20	7	12						19
Mean Brood-size	6.83	11.83	15.00	18.00	19.00	22.50	23.33	

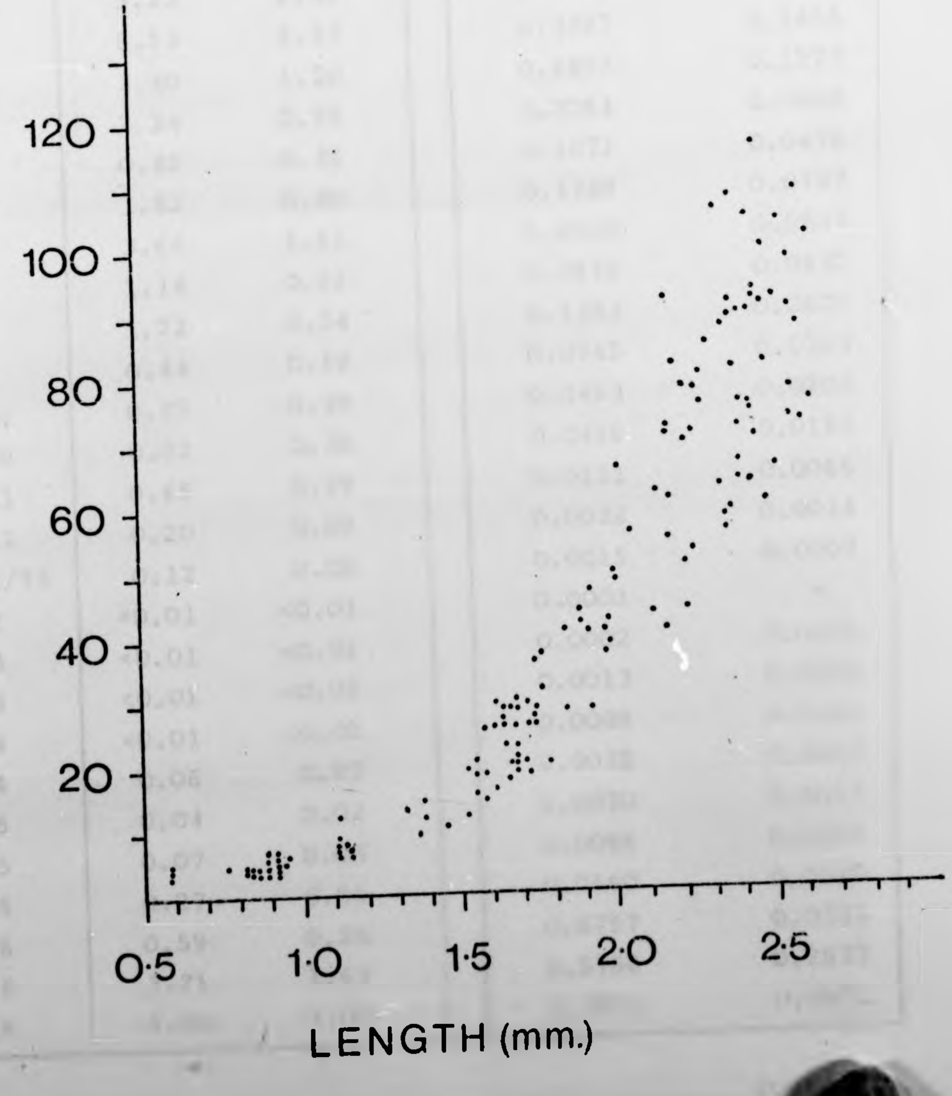
Appendix (xiv) - data for Figure 18

The linear length-weight correlation for D. hyalina var lacustris from Loch Leven.

The data used for obtaining the length-weight regression line of Fig. 18 is given in the graph below as a series of data points.

Abcissa - length in mm.

Ordinate - dry-weight in μg.



Appendix (xv) - data for Figure 20

The seasonal variations in biomass and production of the *D. hyalina* var *lacustris* population during 1972-73.

Sampling Dates	BIOMASS g/m^2	BIOMASS g^c/m^2	PRODUCTION g/m^2/day	PRODUCTION g^c/m^2/day
29/9/71	0.69	0.30	0.0793	0.0349
12/10	0.43	0.19	0.0231	0.0102
07/12	0.25	0.11	0.0091	0.0040
17/2/72	0.11	0.05	0.0030	0.0013
25/3	0.32	0.14	0.0106	0.0047
12/4	0.35	0.15	0.0193	0.0085
27/4	0.92	0.40	0.0685	0.0301
15/5	5.25	2.31	0.2068	0.0910
01/6	5.53	2.43	0.3327	0.1464
13/6	3.40	1.50	0.2893	0.1273
29/6	2.24	0.99	0.2064	0.0908
15/7	0.82	0.36	0.1072	0.0472
29/7	1.82	0.80	0.1789	0.0787
12/8	3.66	1.61	0.2010	0.0884
28/8	1.18	0.52	0.0978	0.0430
10/9	1.22	0.54	0.1383	0.0609
23/9	0.44	0.19	0.0745	0.0328
07/10	0.89	0.39	0.0463	0.0204
21/10	0.82	0.36	0.0416	0.0183
14/11	0.65	0.29	0.0151	0.0066
16/12	0.20	0.09	0.0032	0.0014
13/1/73	0.12	0.05	0.0015	0.0007
24/2	<0.01	<0.01	0.0001	-
29/3	<0.01	<0.01	0.0002	0.0001
10/4	<0.01	<0.01	0.0013	0.0006
15/4	<0.01	<0.01	0.0009	0.0004
29/4	0.06	0.03	0.0038	0.0017
07/5	0.04	0.02	0.0030	0.0013
22/5	0.07	0.03	0.0066	0.0029
26/5	0.27	0.01	0.0160	0.0070
06/6	0.59	0.26	0.0757	0.0333
17/6	3.71	1.63	0.5766	0.2537
21/6	9.08	4.00	1.3571	0.5971

contd./

Appendix (xv) - contd.

Sampling Dates	BIOMASS g/m^2	BIOMASS g^c/m^2	PRODUCTION $g/m^2/day$	PRODUCTION $g^c/m^2/day$
04/7/73	3.14	1.38	0.2803	0.1233
08/7	2.71	1.19	0.1348	0.0593
22/7	1.19	0.52	0.1285	0.0565
14/8	1.41	0.62	0.1766	0.0777
04/9	6.19	2.72	0.2764	0.1216
16/9	4.69	2.06	0.2258	0.0994
22/9	0.58	0.26	0.0472	0.0208
07/10	0.44	0.19	0.0315	0.0139
28/10	0.40	0.18	0.0182	0.0080
17/11	0.50	0.22	0.0172	0.0076
18/12	0.17	0.07	0.0088	0.0039
06/1/74	1.39	0.61	0.0247	0.0109
20/1	0.37	0.16	0.0081	0.0036

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	Cl	Cll	Clll	ClV	CV	CVl
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
26/5	55.42	40.14	32.58	24.45	10.52	3.15	10.90
6/6	53.64	19.36	25.46	41.04	15.20	1.69	10.43
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

Contd/...

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

Appendix (xviii) - data for Fig. 24

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

* Mean obtained from 50 samples unless stated otherwise.

Mean brood-size is the mean numbers of eggs per egg-sac.

Mean metasomal length in mm.

Sampling Dates	Mean Brood-size	Mean metasomal length	Sample No. *
29/9/71	21.36	0.972	
12/10	22.62	0.951	25
7/12	24.49	1.037	
17/2/72	23.98	1.020	
12/3	22.32	1.035	
25/3	21.15	1.027	25
2/4	24.46	1.012	
12/4	31.80	1.095	
27/4	31.22	1.143	
7/5	26.24	1.125	
15/5	25.60	1.163	25
28/5	25.84	1.123	
1/6	24.60	1.133	
13/6	20.10	0.975	25
18/6	18.13	1.012	25
29/6	15.10	0.937	25
15/7	12.05	0.833	25
29/7	11.35	0.827	25
12/8	15.75	0.905	25
20/8	16.93	0.922	
28/8	19.34	0.947	
10/9	18.88	1.001	
23/9	19.46	0.983	
7/10	17.74	0.933	
15/10	23.63	1.015	

contd/...

Appendix (xviii) - contd.

* Mean obtained from 50 samples unless stated otherwise.

Mean metasomal lengths in mm.

Sampling Dates	Mean Brood-size	Mean metasomal length	Sample No. *
21/10/72	25.58	1.037	
14/11	25.00	1.049	
16/12	26.72	1.068	
13/1/73	25.23	1.034	
4/2	25.12	1.027	
24/2/73	26.16	1.025	
17/3	23.03	1.073	
24/3	21.77	1.059	
29/3	18.00	1.027	25
10/4	20.39	1.037	
15/4	21.22	1.019	
29/4	20.42	1.076	
7/5	21.89	1.069	
22/5	28.21	1.133	
24/5	27.12	1.147	
26/5	27.32	1.122	
6/6	22.40	1.169	
17/6	19.20	1.175	
21/6	18.70	1.134	
23/6	17.47	1.053	
4/7	17.93	1.008	25
8/7	18.98	0.878	25
22/7	15.12	0.893	
6/8	15.49	0.904	
14/8	15.60	0.913	25
1/9	19.55	0.962	
4/9	23.72	0.989	
16/9	24.20	0.982	
22/9	22.81	1.005	
7/10	25.75	1.124	
28/10	25.44	1.097	
17/11	25.84	1.067	
18/12	22.79	1.071	12
6/1/74	21.70	1.076	
20/1	23.36	1.084	

Appendix (xix) - data for Fig. 25

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

	Percentage of Females (% males = 100 - % females)	
Sampling Dates	Stage V	Stage Vl(adults)
29/9/71	52.2	73.3
12/10	41.4	54.9
7/12	39.6	52.4
17/2/72	40.2	68.4
25/3	52.8	50.0
12/4	54.0	54.5
27/4	40.1	49.6
15/5	53.8	41.8
1/6	44.0	54.4
13/6	52.7	41.0
29/6	75.5	39.2
15/7	56.2	45.2
29/7	40.3	58.7
12/8	55.5	43.1
28/8	50.4	57.2
10/9	46.1	67.2
23/9	38.4	62.0
7/10	37.1	67.0
21/10	39.9	55.9
14/11	35.9	65.5
16/12	38.6	54.8
13/1/73	36.4	47.3
24/2	32.5	43.7
29/3	38.2	48.3
10/4	48.4	58.7
15/4	30.3	50.2
29/4	54.3	52.7
7/5	47.3	56.2
22/5	47.6	55.2
26/5	53.7	58.3
6/6	67.5	39.9

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Appendix (xix) - contd.

Sampling Dates	Percentage of Females (% males = 100 - % females)	
	Stage V	Stage Vl (adults)
17/6/73	49.4	41.1
21/6	40.0	46.8
4/7	46.1	46.8
8/7	50.3	40.9
22/7	52.1	60.9
14/8	44.0	48.2
4/9	50.5	74.3
16/9	50.9	68.1
22/9	50.0	50.3
7/10	47.6	50.3
28/10	49.4	41.9
17/11	55.4	34.8
18/12	40.6	40.1
6/1/74	31.5	45.2
20/1	29.4	32.4

Appendix (xx) - data for Fig. 26

The seasonal variations in biomass and production of the C. strenuus abyssorum population during 1972-73.

	BIOMASS		PRODUCTION	
Sampling Dates	g/m^2	gC/m^2	$g/m^2/day$	$gC/m^2/day$
29/9/71	1.69	0.74	0.0501	0.0220
12/10	1.22	0.54	0.0252	0.0110
7/12	0.86	0.38	0.0137	0.0060
17/2/72	0.33	0.15	0.0062	0.0027
24/3	0.74	0.33	0.0162	0.0071
12/4	0.61	0.27	0.0161	0.0071
27/4	1.29	0.57	0.0337	0.0148
15/5	2.45	1.08	0.0628	0.0276
1/6	1.96	0.86	0.0543	0.0239
13/6	1.00	0.44	0.0330	0.0145
29/6	0.59	0.26	0.0179	0.0079
15/7	0.29	0.13	0.0101	0.0044
29/7	0.40	0.18	0.0152	0.0067
12/8	0.72	0.32	0.0231	0.0102
28/8	0.80	0.35	0.0260	0.0114
10/9	1.09	0.48	0.0358	0.0158
23/9	1.26	0.55	0.0446	0.0196
7/10	1.23	0.54	0.0290	0.0128
21/10	1.71	0.75	0.0374	0.0165
14/11	2.41	1.06	0.0515	0.0227
16/12	2.00	0.88	0.0334	0.0147
13/1/73	1.57	0.69	0.0298	0.0131
24/2	1.35	0.59	0.0238	0.0105
29/3	1.50	0.66	0.0267	0.0117
10/4	1.73	0.76	0.0387	0.0170
15/4	1.67	0.73	0.0373	0.0164
29/4	2.68	1.18	0.0603	0.0265
7/5	2.60	1.14	0.0599	0.0264
22/5	4.29	1.89	0.1263	0.0556
26/5	3.90	1.72	0.1145	0.0504
6/6	4.51	1.98	0.1792	0.0788
17/6	10.12	4.45	0.3844	0.1691

contd/...

Appendix (xx) - contd.

Sampling Dates	BIOMASS		PRODUCTION	
	g/m^2	gC/m^2	$g/m^2/day$	$gC/m^2/day$
21/6/73	10.36	4.56	0.3556	0.1565
4/7	4.32	1.90	0.1377	0.0606
8/7	0.63	0.28	0.0206	0.0091
22/7	0.39	0.17	0.0122	0.0054
14/8	0.83	0.37	0.0245	0.0108
4/9	0.90	0.40	0.0321	0.0141
16/9	0.59	0.26	0.0208	0.0092
22/9	0.67	0.29	0.0269	0.0118
7/10	2.70	1.19	0.0637	0.0280
28/10	2.44	1.07	0.0524	0.0231
17/11	1.92	0.84	0.0330	0.0145
18/12	1.31	0.58	0.0246	0.0108
6/1/74	1.26	0.55	0.0266	0.0117
20/1	1.30	0.57	0.0265	0.0117

Appendix (xxi) - data for Fig. 27

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

Sampling Dates	Total numbers of *D. gracilis* per litre	Egg stock per litre
29/9/71	2.32	1.50
12/10	3.88	2.25
7/12	2.78	0.75
17/2/72	1.88	1.14
25/3	1.46	0.81
12/4	1.10	0.39
27/4	1.34	0.18
15/5	1.76	-
1/6	2.08	0.12
13/6	1.44	0.06
29/6	0.86	0.24
15/7	1.66	0.12
29/7	3.68	-
12/8	2.38	0.63
28/8	6.32	4.14
10/9	15.52	1.44
23/9	14.80	0.51
7/10	10.68	1.50
21/10	9.10	2.07
14/11	8.56	4.68
16/12	6.06	6.87
13/1/73	3.38	4.29
24/2	1.66	1.29
29/3	1.18	1.50
10/4	0.74	0.75
15/4	0.48	0.12
29/4	0.54	-
7/5	0.52	-
22/5	0.36	0.12
26/5	0.48	-
6/6	0.52	-
17/6	0.76	-

contd/

Appendix (xxi) - contd.

Sampling Dates	Total numbers of *D. gracilis* per litre	Egg stock per litre
21/6/73	1.05	2.25
4/7	0.47	1.83
8/7	0.36	0.21
22/7	1.44	-
14/8	5.38	2.25
4/9	9.54	3.90
16/9	8.92	4.83
22/9	6.05	6.00
7/10	8.52	8.58
28/10	6.80	8.79
17/11	2.80	0.75
18/12	6.56	13.50
6/1/74	2.70	3.00
20/1	2.69	1.29