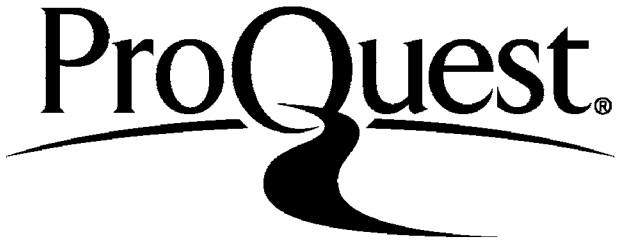
THE PRODUCTION AND RESPIRATION ECOLOGY OF RESERVOIR POPULATIONS OF ZOOPLANKTON, WITH SPECIAL REFERENCE TO DAPHNIDS.

Thesis submitted for the degree of Ph.D. to the University of London (Royal Holloway College).

by T. E. Andrew

July 1976.



D E C L A R A T I O N

I declare that the material presented in this thesis is my own unaided work except where otherwise acknowledged. Furthermore, I declare that no part of this work has been previously submitted in fulfilment of the requirements for a higher degree.

SIGNED Tony E Andrew

DATE 29/7/76

CONTENTS

these pages in fact carry rather different headings

1. ABSTRACT.

Field measurements of standing crop biomass and population numbers at weekly intervals and respiration rates of zooplankton at fortnightly intervals were determined in a London storage reservoir between January 1968 and June 1969. Biomass estimates fell within a range of 0.38 - 4.56 g dry weight.m^{-2} for cladocerans and 0.08 - 2.66g.dry weight.m^{-2} for copepods. Daphnia hyalina population numbers were highest in the spring, 601.35 x 10^3.m^{-2} in 1968 and 761.71 x 10^3.m^{-2} in 1969. Daily production rates were calculated to be between 0.0022 and 0.225gC.m^{-2}.day^{-1} and the annual production for 1968 was estimated at 12.70gC.m^{-2} the main contribution coming from D. hyalina. Population respiration rates were between 2.35 and 27.28µgO_2.mg.dry $weight^{-1}$. $hr.^{-1}$ with the highest rates occurring in spring and autumn.

A length weight relationship, growth rates of eggs and stages of life and respiration rates of D. hyalina were determined in the laboratory. These culture experiments at 10°C gave an egg duration rate of 7-10 days. Respiration determinations, measured by the Cartesian diver technique, were lower than the field measurements.

2. ACKNOWLEDGEMENTS

My sincere thanks are due to my supervisor Dr. A. Duncan for her kindness, help and friendly criticism during the course of this work. I am most grateful to Dr. E. Windle Taylor, C.B.E., Director of Water Examination of the Metropolitan Water Board, for permission to sample in the reservoirs and for the generous help of his staff, especially Dr. J. Ridley, Mr. J.A.P. Steel and the boat crew. I would also like to thank Professor P. Butler of Royal Holloway College for the use of the facilities in the Zoology Department. Finally I gratefully acknowledge the studentship from the Natural Environmental Research Council for this study.

3. INTRODUCTION

The study of zooplankton in freshwater ecosystems has attracted much attention which has been directed largely towards explaining and analysing population fluctuations and more recently to estimate secondary production. Recently the International Biological Programme gave a new impetus to these studies. The publication of methodological handbooks, particularly I.B.P. Handbook No. 17 (EDMONDSON AND WINBERG 1971), the publication of various international symposia and the encouragement to translate valuable texts such as that of WINBERG (1971) has extended the range of ideas, literature and techniques, particularly those of Eastern Europe, to researchers in this field.

Most of the interest in secondary production has been directed towards the evaluation of the role of a single constituent of the animal population present in the ecosystem. HALL (1964) has drawn attention to the fact that most zooplankton populations have been studied in the laboratory under controlled conditions or in their natural habitat where variables are uncontrolled and he concludes that, although these studies provide valuable information, a more useful approach is to combine a laboratory-experimental approach with a field description to prevent gross mis-estimations of population rate processes and production. His approach has been further usefully modified to include the measurement of rates other than population change, such as laboratory studies of feeding and respiration for interpolation into field studies and this has been attempted by several investigators including SCHINDLER (1968), KIRBY (1969) and

CUMMINS ET AL. (1969). The logical extension of this approach is to measure these variables in field situations, but this is, unfortunately, beyond the resource of most investigations, although some attempts to measure processes, such as respiration, under field conditions have been made (STRAŠKRABA 1967, CREMER AND DUNCAN 1969, GANF AND BLAŽKA 1974). Attempts to relate field and laboratory measurements of the same process provides useful information and indicates areas of large discrepancy when extrapolating results from the laboratory to the field situation (DUNCAN ET AL. 1970). A further, and possibly more rewarding, stage is to integrate studies of this sort with detailed studies at other trophic levels. This may be done by correlation (WRIGHT 1965) or simultaneous studies integrated by the use of common and comparable units such as carbon or energy (STEEL ET AL. 1972).

The purpose of the present study was to examine, both in the field and the laboratory, selected characteristics of the zooplankton of freshwaters, to determine probable influences on other parts of the ecosystem. Research was concentrated on the principle herbivore (Daphnia sp.) and the characteristics studied included growth, production and respiration which, it was hoped, might indirectly reveal information on the trophic relationships of the natural populations - a notoriously difficult area to study directly.

3.1. THE FIELD STUDY AREA

Two Metropolitan Water Board[1,2] reservoirs, the Queen

---

[1] Now the Thames Water Authority, Metropolitan Division.

[2] For the sake of brevity in the text, the Queen Mary Reservoir will be referred to as Q.M., Queen Elizabeth II as Q.E.II, and the Metropolitan Water Board as M.W.B.

Mary[2] and the Queen Elizabeth II[2] were used to obtain field samples. These are two of several reservoirs situated in the Lower Thames Valley which form part of the London water supply storage system. A map, showing the location of these reservoirs, can be seen in figure 3.1(a). These reservoirs are man-made and consist of a basin excavated from the London clay and surrounded by an embankment of the spoil with a clay core keyed into the lower clay and lined with concrete blocks. Both reservoirs have flat bottoms, a simple outline shape, are in exposed situations and are filled with water from the River Thames. Table 3.1(a) gives their dimensions

Table 3.1(a)

	Q.M.	Q.E.II
Area	290 ha	130 ha
Depth	12 m	17.5 m
Volume	$30 \times 10^6 m^3$	$19.3 \times 10^6 m^3$

[From RIDLEY (1964)]

The River Thames is an enriched calcareous river with the following nutrient levels: NH_3-N ... 0.1-1.2 mg/L, NO_3-N ... 5 mg/L, orthophosphate ... 1-2 mg/L, SiO_2 ... 15-20 mg/L and $CaCO_3$ ... 250 mg/L (WINDLE-TAYLOR 1967).

The Q.M. is roughly circular with a baffle wall delimiting the outlet area to approximately one-third of the whole (fig. 3.1(b)). Water enters the basin through pipes with submerged orifices and impinges on a small wall which absorbs most of the momentum and restricts mixing to the space between the

---

[2]See footnote on page 7.

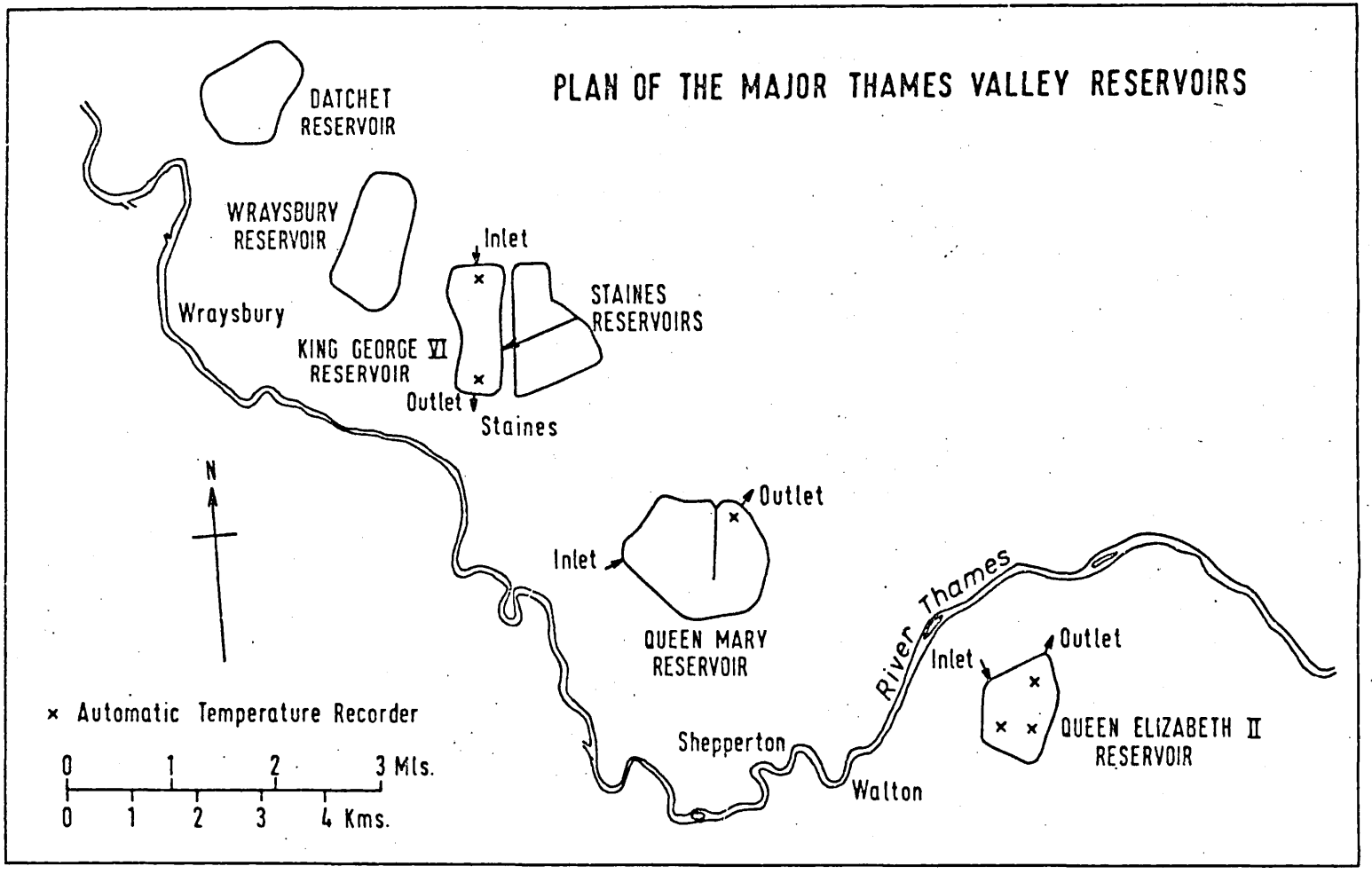

PLAN OF THE MAJOR THAMES VALLEY RESERVOIRS
DATCHET RESERVOIR
WRAYSBURY RESERVOIR
Wraysbury
KING GEORGE VI RESERVOIR
Inlet
Outlet
Staines
STAINES RESERVOIRS
N
Outlet
Inlet
QUEEN MARY RESERVOIR
River Thames
Inlet
Outlet
QUEEN ELIZABETH II RESERVOIR
Shepperton
Walton
× Automatic Temperature Recorder
0 1 2 3 Mls.
0 1 2 3 4 Kms.

Fig. 3.1(a).

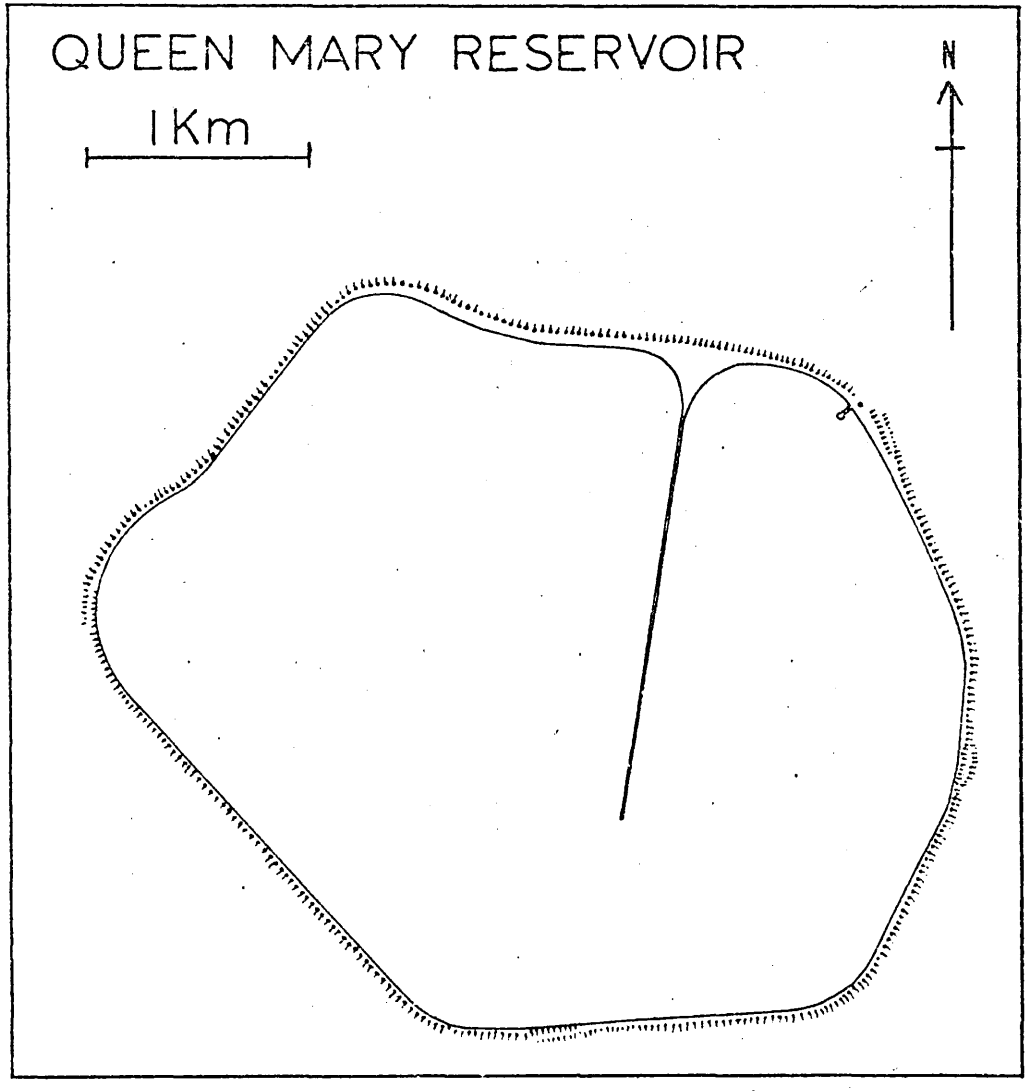
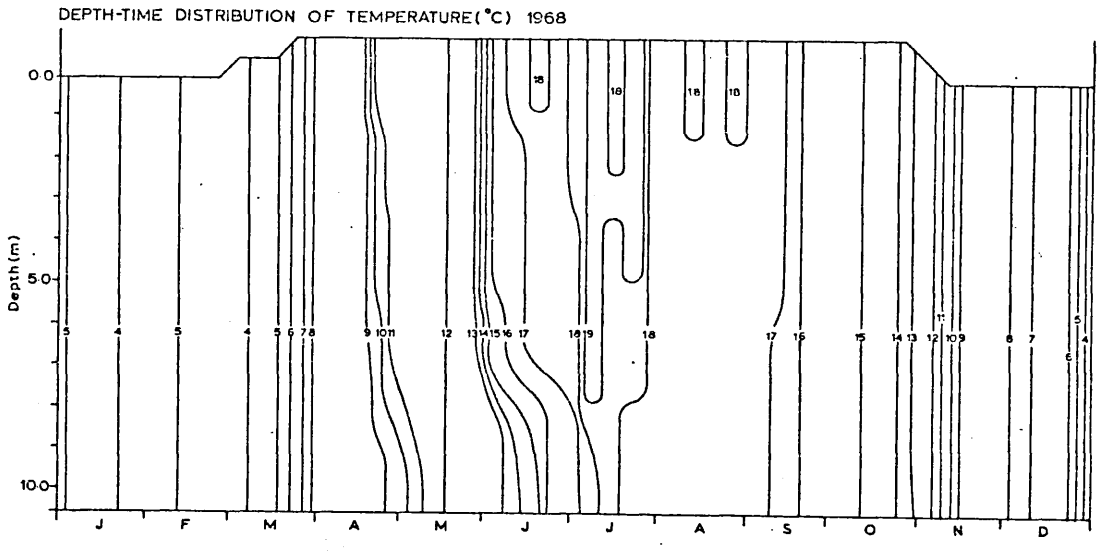


Fig. 3.1(b).

pipes and the wall. Normally between one and two per cent of the volume of water is abstracted from the reservoir daily. The large area, shallowness, the exposed situation and volume of the water transported each day normally ensures that the reservoir is isothermal for most of the year. However, when periods of intense radiation coincide with relative stillness, some degree of stratification occurs but this usually only involves the bottom metre of the reservoir where chemical deterioration takes place. Such conditions do not usually persist for very long periods and the reservoir then de-stratifies. The period of stratification is not usually long enough for gross deterioration of the bottom waters and overturns do not significantly affect the quality of the main water mass although such overturns may, of course, affect biological production. The Q.M. is therefore characterised by intermittent stratification with, perhaps, three mixings per year (WINDLE-TAYLOR 1967). The depth-time distribution of temperature can be seen in figure 3.1(c) and can be seen to be very much the same for the different years of the study. Similarly the depth time distribution of oxygen in the Q.M. can be seen in figure 3.1(d). The fluctuations in the surface levels during the study represent the normal winter lowering of the water level. Algalogical data will be introduced in the main body of the text where pertinent.

The Q.E.II is also roughly circular but has no baffle (figure 3.1(e)) and has a complex inlet jet arrangement to facilitate the artificial mixing of the water mass when stratification occurs. The function of these jets and a fuller description of the reservoir can be found in RIDLEY (1964) and RIDLEY ET AL. (1966). Normally two per cent of the water passes through the reservoir daily. Depth-time



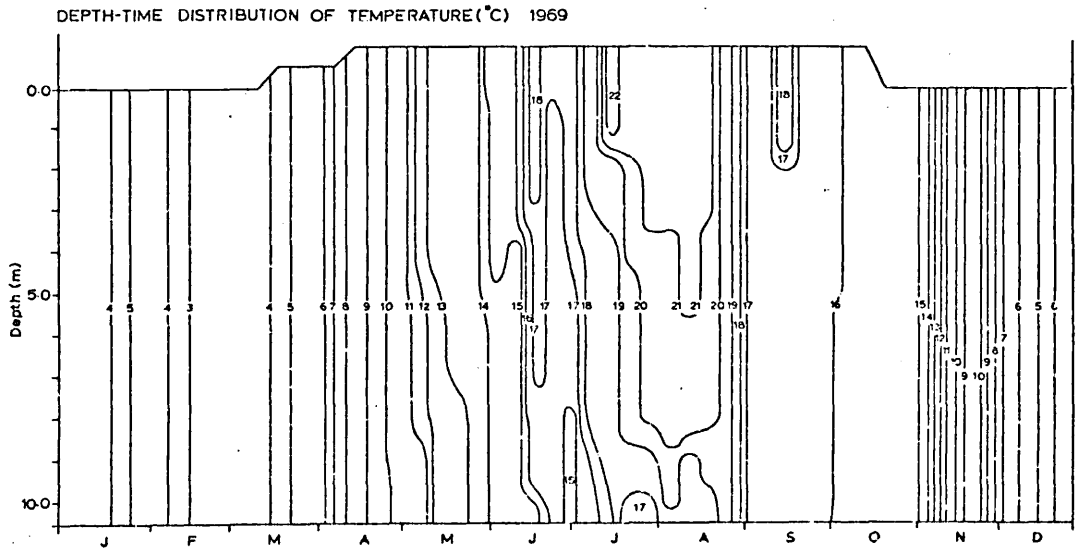
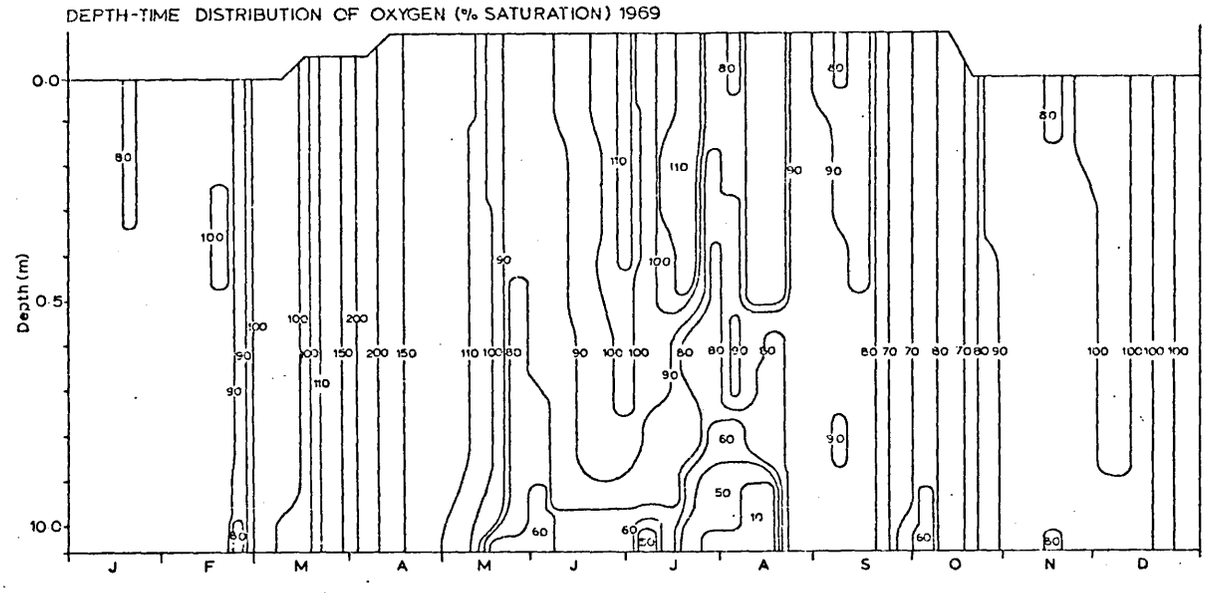


Fig. 3.1(c). (from Steel unpubl.)



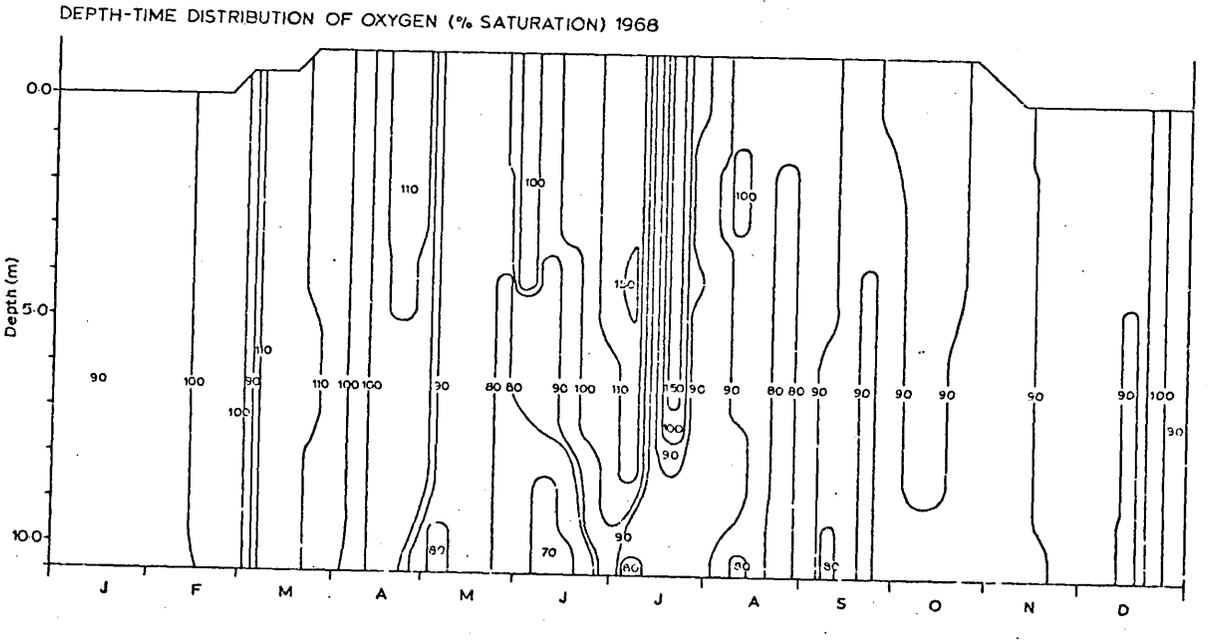


Fig. 3.1(d). (from Steel unpubl.)

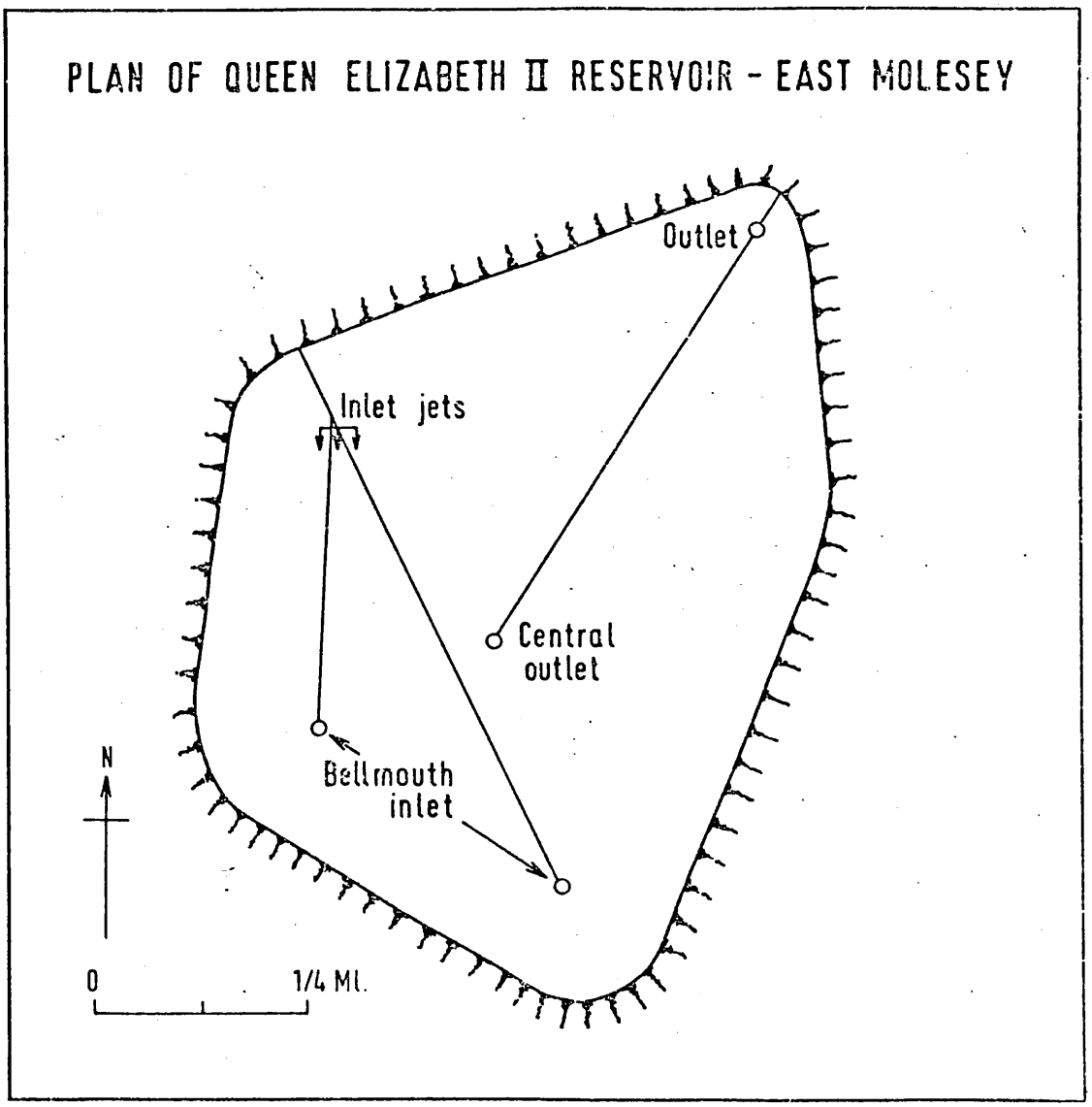

PLAN OF QUEEN ELIZABETH II RESERVOIR - EAST MOLESEY
Outlet
Inlet jets
Central outlet
Bellmouth inlet
N
0
1/4 Ml.

Fig. 3.1(e).

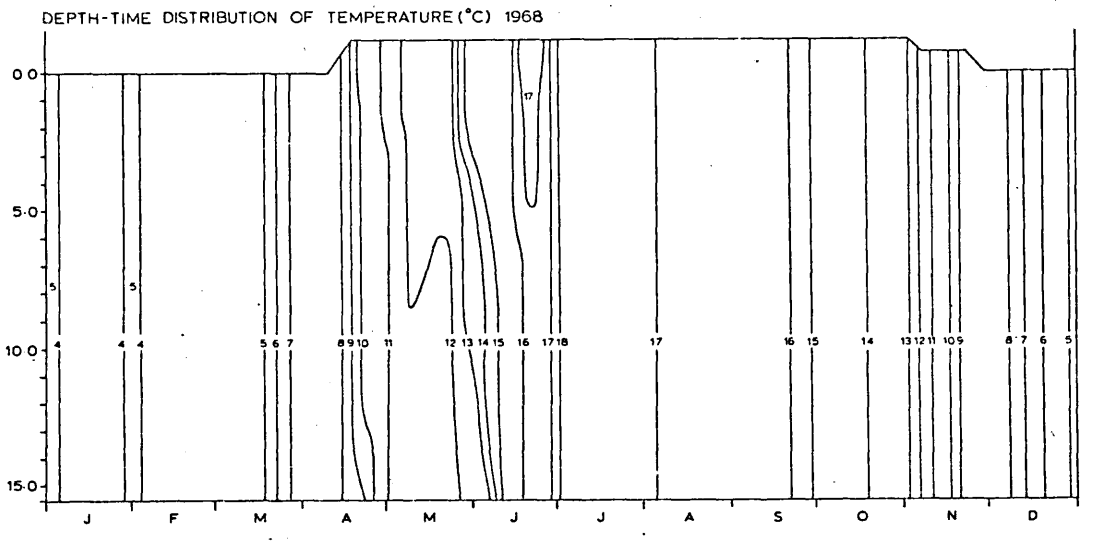
distribution of temperature and oxygen saturation can be seen in figures 3.1(f) and 3.1(g), respectively.

This study was concentrated principally on the Q.M.

There were several advantages in working on the M.W.B. reservoirs. Several biological and physico-chemical studies pre-dated this study and continuing work is being carried out by the M.W.B. biological section and other institutions. Earlier studies of particular relevance to this work include those of TURNBULL (unpublished), ANGOLD (1968), LANGHELT (1968) and CREMER (unpublished) who worked on various aspects of the zooplankton of reservoirs. The study of KIBBY (1969) on Diaptomus gracilis in the Q.E. II and King George VI reservoir, the subsequent work of BURGIS (1975 in prep.) on cyclopoid populations in the Q.E.II and that of DOOHAN (1973) who worked on rotifer populations particularly in the Q.E.II and the continuing interest of DUNCAN (1975(a),(b)), DUNCAN ET AL. (1970) and NADIN-HURLEY AND DUNCAN (1976) have extended the understanding of the zooplankton. Algal studies have been carried out by BELLINGER (1967) and McGILL (1969) and EVANS and McGILL (1970) and a large body of information has been gathered by Mr. J. A. P. Steel, Assistant Biologist of the M.W.B. who has carried out a study of the primary production of both reservoirs simultaneously with the present study. He has generously made available a large body of basic limnological and algal data used in this work (STEEL 1972, STEEL 1973, STEEL 1975 and STEEL ET AL. 1972).

3.2 Daphnia sp.

Daphnids were the principal herbivores in the two reservoirs studied and much has been reported about the biology of Daphnia spp. which is extremely useful to field and laboratory studies of this nature. Daphnia spp. have



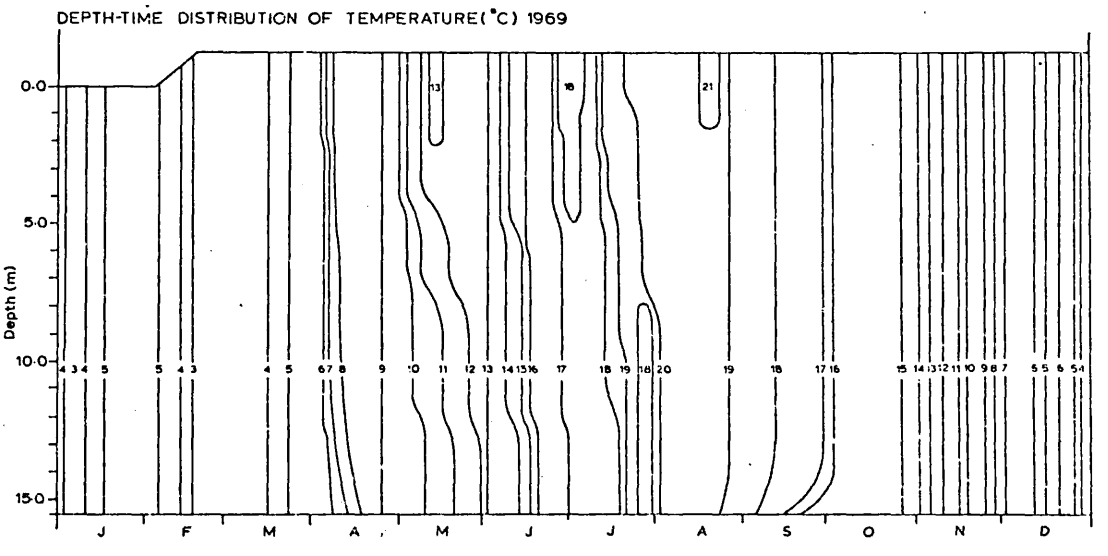
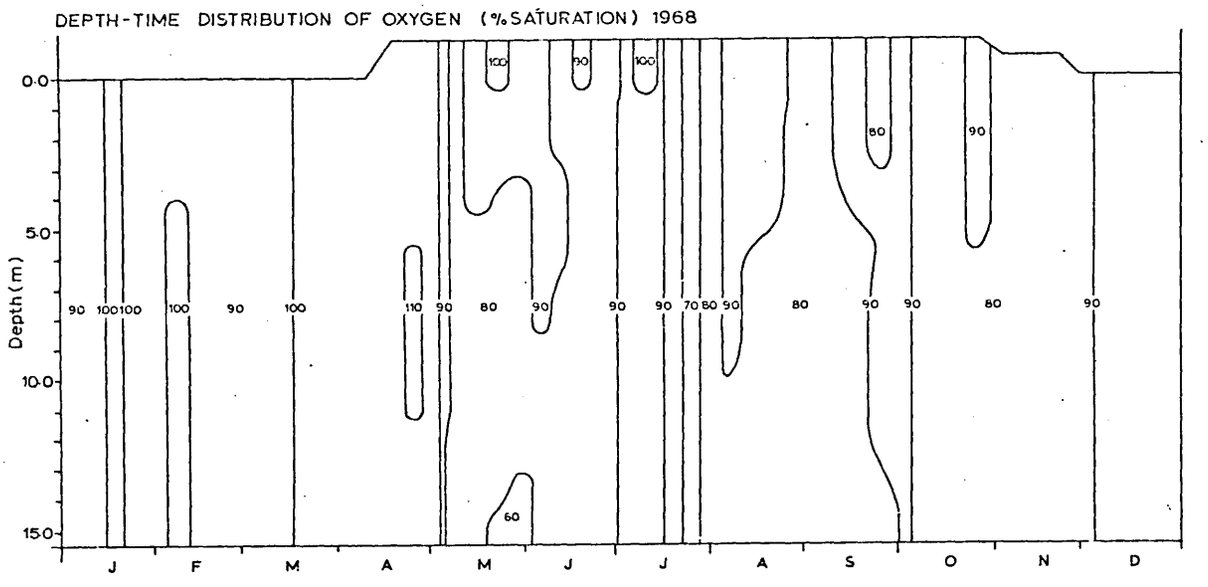


Fig. 3.1(f). (from Steel unpubl.)



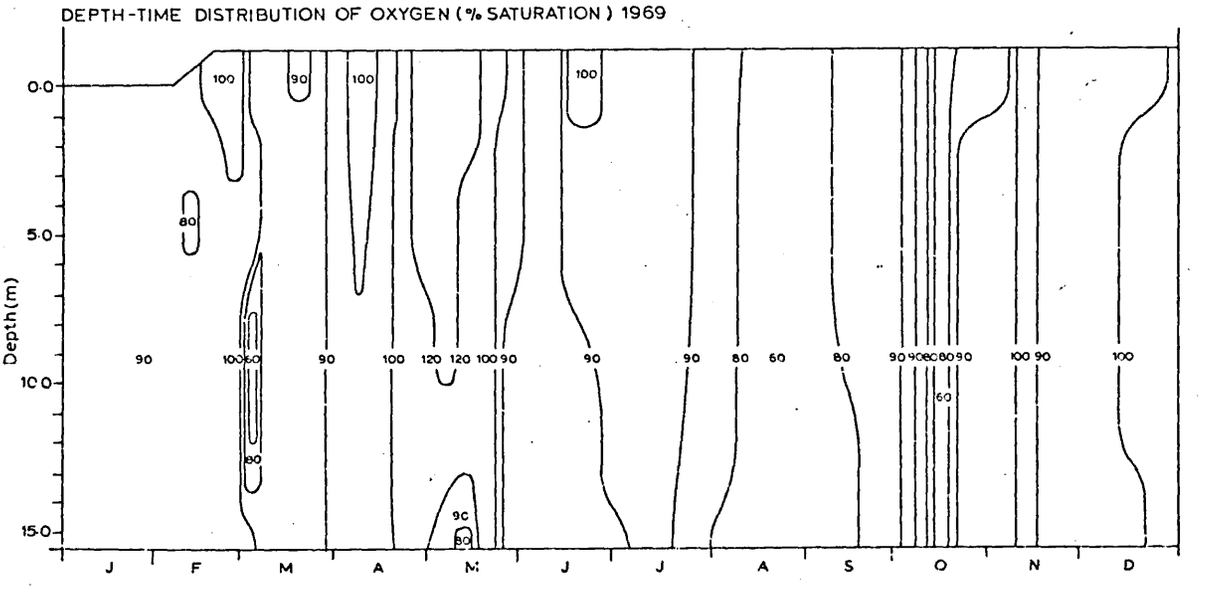


Fig. 3.1(g). (from Steel unpubl.)

been studied frequently in the laboratory because of their ease of culture and parthenogenetic mode of reproduction in normal conditions. BANTA ET AL. (1939), in their monograph, record much information on the growth, genetics and physiology of the genus and this to a large extent represents a synthesis of their earlier work. BERG (1931, 1936) studied reproduction in Daphnia and ANDERSON (1932), ANDERSON AND JENKINS (1932) and ANDERSON ET AL. (1937) describe the events in the life span and growth characteristics of D. magna and D. pulex. MACARTHUR AND BAILLIE (1929(a)) describe the effect of temperature on the duration of life of D. magna. Later studies of growth in culture include those of GREEN (1954, 1956) who defines the reproductive development of D. magna, and HALL (1964) and HRBAČKOVA-ESSLOVA (1966) who define growth rates and reproductive rates of Daphnia spp. at different temperatures.

Metabolic laboratory studies include those of MACARTHUR AND BAILLIE (1929(b)) who measured the respiration rate of D. magna and SCHERBAKOFF (1935) with D. longispina. More recent respiration studies include those of: RICHMAN (1958) - D. pulex, ZEISS (1963) - D. magna, SCHINDLER (1968) - D. magna and CREMER AND DUNCAN (1969) - D. hyalina. PLAŽKA (1966) published an interesting paper on the metabolism of Daphnia spp. related to secondary production.

Feeding studies in the laboratory have been made by several workers, early studies including those of SMITH (1936), DUNHAM (1938), PACAUD (1939), COKER AND HAYES (1940), RYTHER (1954), SUSHTCHENIA (1958) and NAUWERCK (1959). More quantitative studies have been undertaken by RIGLER (1961(a),(b)), McMAHON AND RIGLER (1963, 1965), McMAHON (1965), BURNS AND RIGLER (1967), BURNS (1968, 1969). These

studies have been concerned with the mechanisms of feeding and the relationships between filtering rates and food concentrations, food types, body size and temperature. RICHMAN (1958) and SCHINDLER (1968) examine food uptake, by D. magna and D. pulex respectively, as part of their investigations. Some authors cast doubts on the suitability of certain food organisms for laboratory culture of Daphnia sp. (SCHINDLER 1968, OTSUKI AND TAKAHISHA 1969) but although these may be justified it is difficult to draw conclusions about the diet of daphnids as only recently have we seen clear information on the diet in natural conditions (NADIN-HURLEY AND DUNCAN 1976).

RICHMAN , influenced by the classic work of LINDEMAN (1942) on community dynamics and MACFADYEN's (1948) discussion of the meaning of production in biological systems, produced his important laboratory study of the transformation of energy by D. pulex in 1958. This was the first attempt to produce a complete laboratory energy budget for Daphnia sp. by measuring growth, respiration and feeding of the animals in the laboratory at 20°C. This has influenced many other studies since - not only those concerned with the Cladocera.

There have been many studies of field populations of Daphnia and extensive discussion can be found in HUTCHINSON (1967).

Among these studies, PATALAS (1954, 1956) and WIKTOR (1961) describe the seasonal occurrence of D. hyalina in Polish lakes and both authors describe a perennial species comparable with that found in the O.M. by the present author and CREMER (pers. comm.), BAUDOUIN AND RAVERA (1972) and by GEORGE AND EDWARDS (1974) and GEORGE (1973) in a Welsh reservoir.

Studies important to the development of the understanding of population fluctuations and the concept of turnover time as a method of estimating field production include that of EDMONDSON (1960) on rotifer populations which influenced the work of STROSS ET AL. (1961), HALL (1964), WRIGHT (1965), and most subsequent workers with daphnid populations. The population dynamics of Daphnia are described from an estimate of the population size and a knowledge of the eggs-to-female ratio which gives a reproductive index and together with the egg developmental times at different temperatures enables a prediction of the rate of increase of the population to be made. First described for zooplankton by ELSTER (1954) for the calanoid copepod, Eudiaptomus gracilis and later used by EDMONDSON (1960) for a population of rotifers, the method is set out clearly, as used for the Cladocera, by CUMMINS ET AL. (1969).

It has been widely recognised that estimations of production in populations that have continuous reproduction present special problems and this is the case with perennial populations of daphnids where cohorts cannot be easily distinguished. PETROVICH ET AL. (1964) reported in WINBERG (1971) estimate the production of copepods using mean individual weights of developmental stages, the numbers and duration of these stages. KONSTANTINOVA (1961) described in WINBERG (1971) with various species of Cladocera and LEBEDEVA (1964) for D. longispina use the same technique applied to field recognised size classes for the estimation of production and a similar method has been used by STEEL ET AL. (1972).

Another problem encountered in estimating production is the effect of predators on daphnid populations and these might include invertebrate predators such as adult Cyclops sp. and Leptodora kindtii (described by CUMMINS ET AL. (1969)) or vertebrate predation by young fish. These are difficult to

relate unless direct measurements of predation have been made but recently it has been shown that estimations of the instantaneous death rate, using the birth rate model given by EDMONDSON (1960) can be used to pinpoint periods of intense predation (DUNCAN 1975) a. Knowing the size classes being predated it becomes possible to guess whether the predator is fish or invertebrate.

STEEL ET AL. (1972) show how combined studies at different trophic levels may be used to estimate the demand of herbivore populations on primary production. This approach is not easily within the compass of an individual worker. This paper raises the interesting question of what source of carbon supports daphnid populations when algal populations are insufficient. STEEL (1972) discusses this further and it appears that the other food sources might be detrital carbon or bacteria and that these sources might be more important than hitherto expected. NADIN-HURLEY AND DUNCAN (1976) have looked more directly at this problem.

4. METHODS

4.1. FIELD SAMPLING

Zooplankton samples were collected using two different sampling techniques. F.B.A. plankton nets were used to take vertical hauls through the water column and a 5L Patalas volume sampler (PATALAS, 1954) was used to take samples at set depths through the water column. These two methods provide data for comparison of the techniques and both are shown to have their advantages. Net hauls are simple and quick to take-an advantage when weather conditions are extreme - and they give large numbers of animals for estimates especially of animals present in small numbers such as egg bearing adult daphnids, adult copepods etc. The principal difficulty is that large corrections have to be made to give absolute numbers. Patalas samples provide more accurate volume estimates of zooplankton which may be used to show the depth distribution of the animals and larger numbers were always caught than with the net samples, but the labour involved to obtain large numbers is greater than with the net samples. Patalas samples were used to calculate the net factors.

Samples were used for estimating population numbers and biomass. These were, in turn, used for population analysis. Samples were also used for collecting animals for field and laboratory experiments for respiration and growth.

4.1.1 Collection of net samples.

Two grades of F.B.A. plankton net were used, a coarse and a fine net. The coarse mesh net (23.6 meshes per cm) had a measured pore size of 0.188mm and was used to collect the larger zooplankton. The fine mesh net (70.9 meshes per cm) with a measured pore size of 0.050mm was suitable for collection of the smaller zooplankton. The fine mesh net retained some phytoplankton and during periods when large quantities of

algae were present tended to clog, reducing, it is suspected, the efficiency of sampling.

Net samples were taken through the vertical column of the water (vertical net haul, V.N.H.), the nets being fitted with copper buckets and heavy weights. The net was lowered into the water until the weight was felt to touch the bottom and then pulled back through the water at as constant a rate as possible. The length between the net mouth and tip of the weight was one metre, thus all net samples were taken from one metre above the bottom.

The contents of the nets were run off into screw topped bottles and the nets were washed by dipping the net, to its mouth, in the water and concentrating the sample in the bucket. This washing was added to the sample and then repeated. The net was further scoured of plankton using a plastic wash bottle filled with distilled water.

Samples to be counted were preserved in situ by the addition of formalin, to a concentration of 5%, from a wash bottle. This method proved satisfactory for keeping samples until they could be counted.

4.1.2. Collection of Patalas samples.

Patalas samples were taken at 2m intervals through the water column at the depths 1m, 3m, 5m, 7m and 9m. The procedure that was used is shown diagramatically in fig. 4.1.2(a). The sampler described by PATALAS (1954) was lowered to the appropriate depth and 'jerked' shut. The sampler was then lifted from the water and its contents filtered through a coarse mesh filter (with a pore size of 0.188mm) using a large plastic funnel fitted with the perspex filtering unit shown in fig. 4.1.2.(a). The zooplankton trapped was washed into storage jars using a wash bottle containing distilled water and the netting filter was then removed and washed separately into the container. This ensured that losses of zooplankton in the

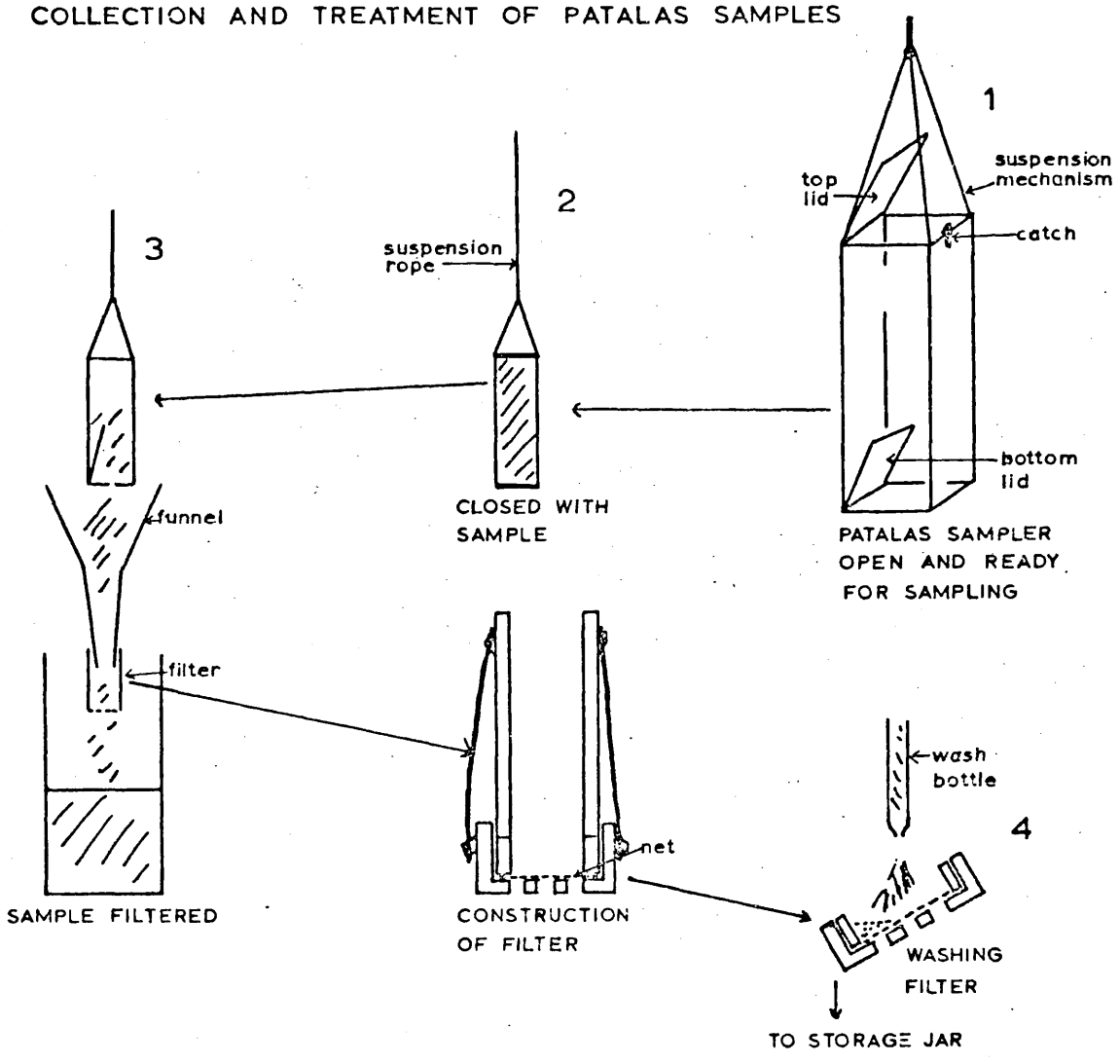

COLLECTION AND TREATMENT OF PATALAS SAMPLES
1
top lid
suspension mechanism
catch
bottom lid
PATALAS SAMPLER OPEN AND READY FOR SAMPLING
2
suspension rope
CLOSED WITH SAMPLE
3
funnel
filter
SAMPLE FILTERED
net
CONSTRUCTION OF FILTER
wash bottle
4
WASHING FILTER
TO STORAGE JAR

Fig. 4.1.2(a).

filter were minimal. Samples required for counts were fixed with formalin in the same way as for the net samples.

The depth of Patalas samples was monitored by metre markings of the suspension rope which was calibrated allowing for the length of the sampler. A Kern--Mantel type rope was used to suspend the sampler as this has less stretch than the more common 'Hawser wound' rope. The weight of the sampler ensured a vertical descent if it was lowered carefully into the water. If the sampler, was allowed to descend under its own weight it tended to 'plane' sideways in the water, but as the catch mechanism was fairly sensitive to jerks, care was taken in lowering the sampler and this reduced the sideways drift. If the drift had been 30° then samples of '9'm would have been taken at 8m, - less error towards the surface. With the exception of very extreme weather conditions it is thought that samples were taken from the correct depth.

4.1.3. Sampling frequency.

Samples were taken from October 1967 to June 1969 from both Q.M. and Q.E.II. The samples were taken at weekly intervals from Q.M. but these were increased at some periods of the year. Samples were taken at fortnightly intervals from Q.E.II., again with some more frequent samples in some periods. In the event of unfavourable conditions samples were taken from the outlet pier of the reservoir and samples were repeated at the earliest possible day afterwards. Samples were taken in the mornings between 8 am and 11am.

The frequency of sampling was based on the experience gained from previous studies of the reservoir (CREMER, in prep.). It was thought that monthly sampling left too large a gap between samples for major changes in zooplankton and algal populations to register but that shorter sampling times than one week normally involved too much labour for the results obtained.

4.1.4. Sampling stations.

Samples were normally taken from single stations on both reservoirs. The representativeness of this procedure has been discussed in earlier work (STEEL, in prep.) (CREMER, in prep.).

A small sampling programme, designed to test the validity of single station sampling of the Q.M., was carried out during the late spring of 1970 (5/6/70). Samples were taken from different stations over the reservoir and were examined in terms of biomass per vertical net haul. The results of 35 samples taken are shown in fig. 4.1.4(a). For the whole reservoir a mean dry weight of 232mg $\pm$ 64 (S.D.) was obtained. This is equivalent to 232mg $\pm$ 27.6% (S.D.). If samples of a weight between 100 and 300mg are considered they represent an area of approximately 80% of the reservoir and include the sampling station A. The result of 24 midwater samples gives a mean dry weight of 187mg $\pm$ 49 equivalent to 187 $\pm$ 26.2%.

Figure 4.1.4(a) shows the areas of high concentration of zooplankton to be limited to an area around the inlet of the reservoir. This may reflect a local concentration of zooplankton where River Thames water is flowing, via an aqueduct, into the reservoir. The areas of low concentration of zooplankton are found close to the baffle that divides the reservoir and this might affect the local populations here. More samples may have amplified the picture obtained but it seems that an accuracy of about $\pm$ 26% can be obtained from one sampling station if samples are not taken from close to the reservoir edge or in close proximity of the inlet pier. LANGHELDT (1968) sampled for a year from the tip of the baffle and at the outlet and this work is in general agreement with these findings.

The earlier procedure of STEEL ET AL (in prep.) of taking samples from three stations and mixing them to obtain a meaned sample for the reservoir, has little advantage over

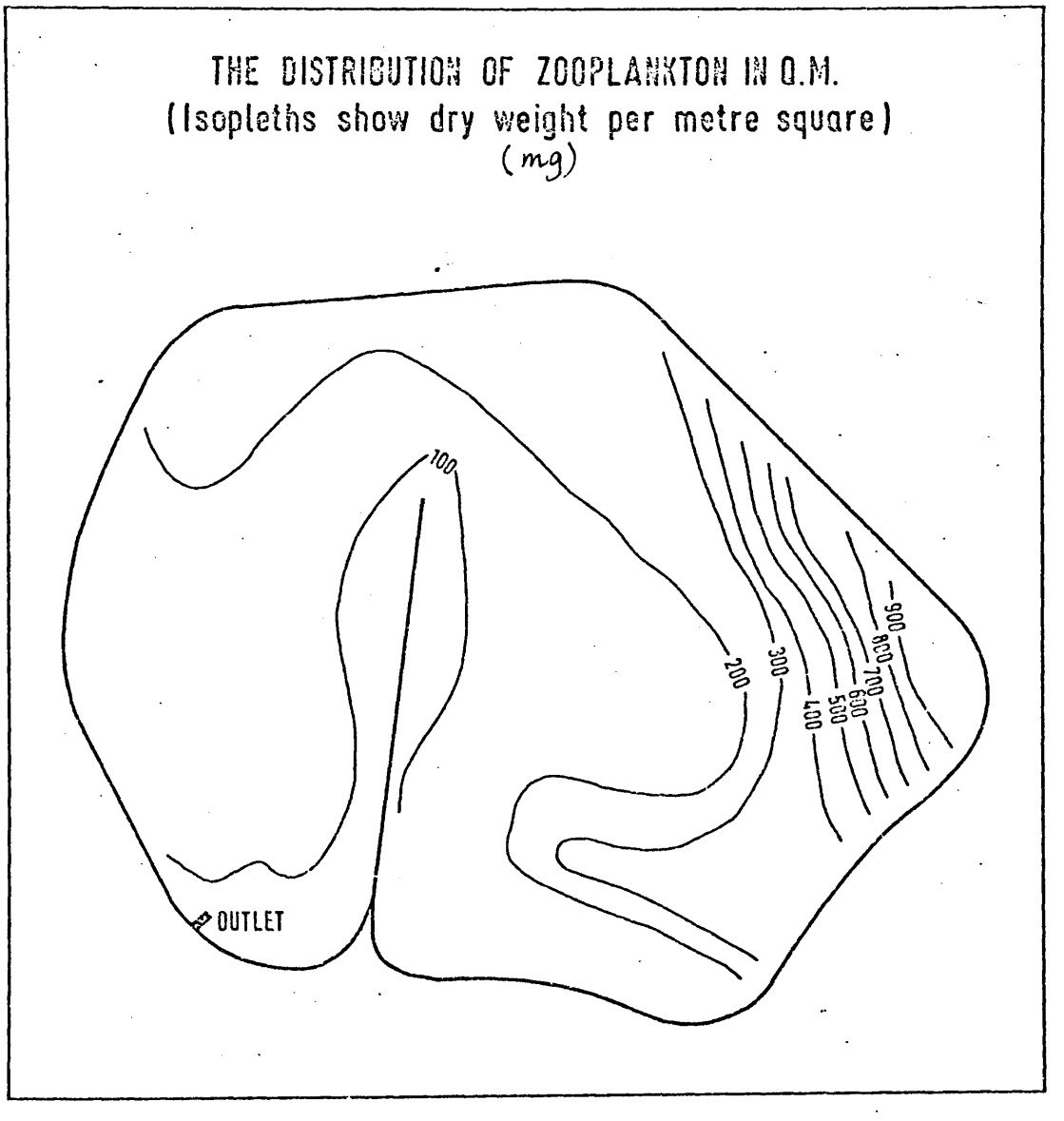

THE DISTRIBUTION OF ZOOPLANKTON IN O.M.
(Isopleths show dry weight per metre square)
(mg)
100
200
300
400
500
600
700
800
900
OUTLET

Fig. 4.1.4(a).

a single station. This method, of lumping samples, was later abandoned by STEEL in favour of a single station sampling programme for phytoplankton samples.

Similar programmes for QEII have been carried out by DUNCAN (pers. comm.) and these show a similar situation to exist in this reservoir.

4.1.5. Sampling reproducibility.

Net Sampling.

For vertical net hauls, in ideal conditions, the volume of water sampled should be the product of the area of the net mouth and the height of the water column sampled.

$V = \pi r^2 z$ where V = volume of water sampled
r = radius of net mouth
z = height of water column.

Theoretically all animals in the path of the net should be included in the sample. In practice, a smaller volume of water is filtered by the net because several different factors act to reduce the efficiency of capture of the net. These factors include water resistance to the net and net avoidance by the animals being sampled. Discussion of these factors has been given by other authors and major contributions have been made by WINSOR AND CLARKE (1940), SZLAUER (1964, 1965, 1968), ELSTER (1958) and McNAUGHT (1971). CREMER (in prep.) examined the effect of hauling speed on capture and concluded that a constant hauling speed reduced the variation in sampling error. Using vertical net hauls, CREMER (in prep.) measured the biomass of the hauls at varying hauling speeds and the results for replicate samples taken from the QEII are presented in table 4.1.5(a).

Table 4.1.5(a)

	Composition of sample (VNH)	No. of samples N	dry weight B mg	SD mg	SD/x/%
Duncan 9/8/67	Daphnids + copepods	4	81.5	±7.0	± 8.6
Cremer* 24/8/67	Daphnids + copepods	6	30.9	±5.8	±18.6
	Daphnids	6	15.3	±4.9	±31.9
	Copepods	6	15.7	±2.6	±16.6

* Twice the amount of zooplankton was left behind in the cylinder than in the experiment of the 9/8/67.

Samples were examined, using information from several sources, to discover how much reliability can be placed on individual samples.

Specific experiments, designed to test the reproducibility of samples in terms of numbers of animals and biomass per vertical net haul, were performed on 19/6/70 and 19/8/70 respectively. In both experiments ten net hauls were taken sequentially from the same place and the subsequent treatment was as for normal field samples.

Biomass. Ten samples taken from the raft had a mean dry weight of 74.96mg ± 13.49SD (range 61.47-88.45mg), which is equivalent to 74.96mg ± 18% (SE 5.7%). These results are comparable with results presented in table 4.1.5(a).

Counts. Ten samples taken from the raft were counted exhaustively using the Stempel pipette subsampling technique. The results of this experiment are presented in table 4.1.5(b).

Table 4.1.5(b)

	Mean	S.D.	SD%$\bar{x}$	Range
Daphnia without eggs	954	±114.7	*12%	339-1069
Daphnia with eggs	9.2	± 3.5	38%	5.7-12.7
Daphnid eggs	782	± 35	4.5%	747- 817
Bosmina sp	419	± 43	*10%	376- 462
Asplanchna sp	226	± 55	*24%	171- 462
Cyclops adult	13.8	± 2.5	18%	11.3-16.3
Cyclops copepodid	207	± 29	*14%	178- 236
Diaptomus adult	11.4	± 3.3	29%	8.1-14.7
Diaptomus copepodid	6.8	± 3.0	44%	3.8-9.8
Total animals	1923	± 143	7%	1780-2066

* These figures show a greater deviation than expected from the mean count than is expected for a Poisson distribution (S.D. $=\sqrt{\bar{x}}$) and this suggests clumping within the samples.

The results show that the variation for the whole sample (all animals present), 1923 ± 7% animals, is less than most of the individual components of the sample. When the numbers in a component of the sample are small the error may tend towards ± 50% and this error may be critical in any field samples containing, say, low egg numbers.

Net samples were always taken in pairs. Samples for counting were mixed and counted as a single sample. Samples for biomass measurements were treated individually and these results (from the field sampling programme) have been treated to examine differences in pairs of samples. Biomass samples were separated into two fractions - a daphnid fraction and a copepod fraction - which are comparable individually or as a total sample. Samples were identified in the order taken from the reservoir and results are presented in fig. 4.1.5(a). That biomass samples normally are ±5mg means little as samples vary considerably in size at different times of the year.

Most samples collected, during this study, were less than 25mg weight and figure 4.1.5(a), although a useful indicator; is better expressed as difference in weight as a percentage of the mean weight of the sample pairs. Results treated in this way show the samples to be $\pm$17.7% of the mean (N = 172) for the fractions of the sample.

Patalas sampling.

In ideal conditions the Patalas sampler should trap five litres of water and the organisms contained in it. These should be filtered from the water. Little experimentation was carried out on the reproducibility of samples. From biomass data available the Patalas sample variation obtained was $\pm$10.94% (N = 46) which compares favourably with net haul data. Results are presented in figure 4.1.5(b). The symmetry of the histogram is the result of each pair of samples giving rise to its mean, one will be positive and one negative in relation to that mean. The results were obtained from duplicate Patalas samples taken during the course of field respiration experiments.

Reproducibility of numbers was tested in a small experiment performed on 5/6/70. Ten samples taken from the raft area of the reservoir from a depth of three metres were treated as normal field samples. The results are presented in table 4.1.5(c).

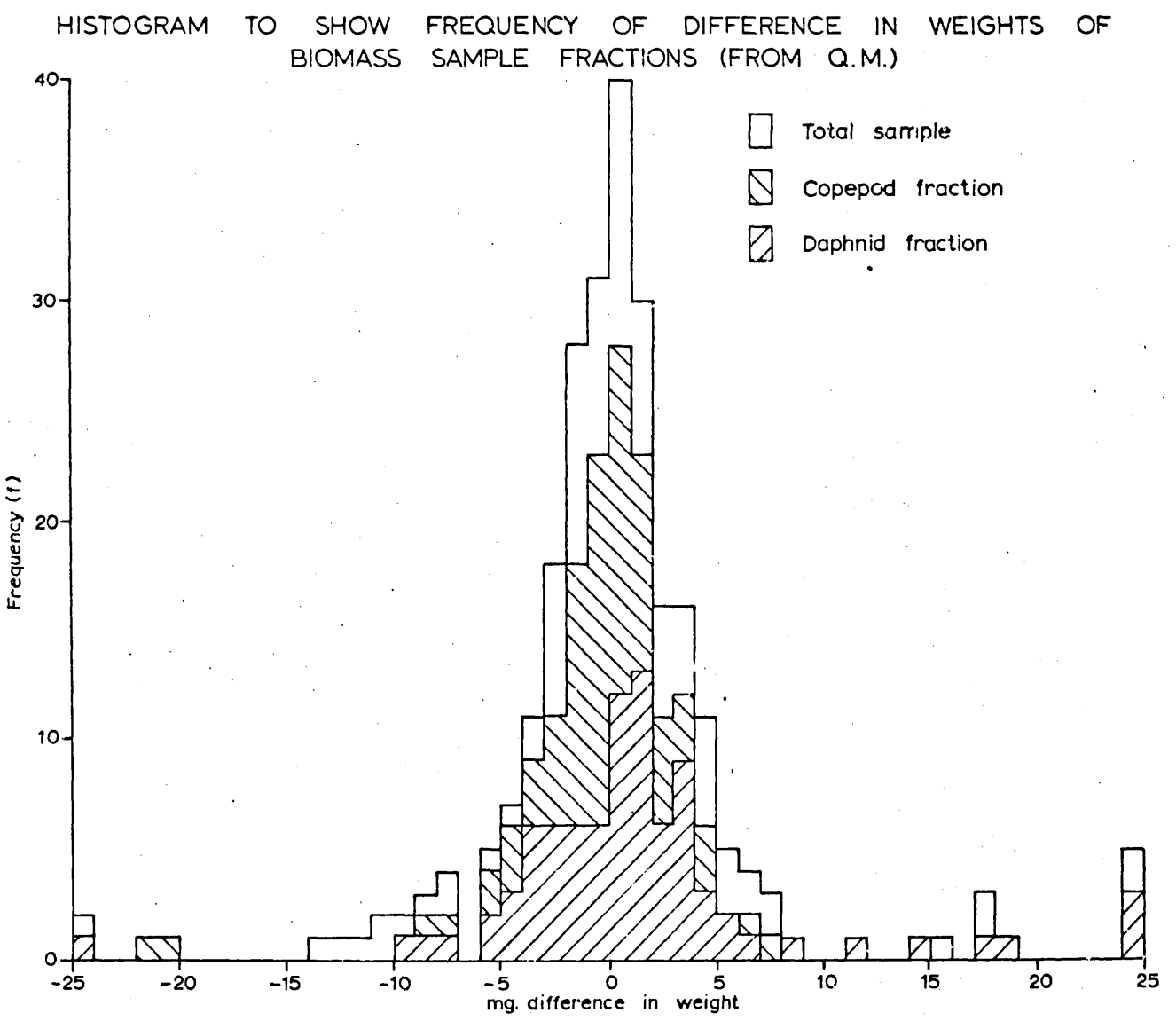

HISTOGRAM TO SHOW FREQUENCY OF DIFFERENCE IN WEIGHTS OF BIOMASS SAMPLE FRACTIONS (FROM Q.M.)
Total sample
Copepod fraction
Daphnid fraction
Frequency (f)
40
30
20
10
0
-25
-20
-15
-10
-5
0
5
10
15
20
25
mg. difference in weight

Fig. 4.1.5(a).

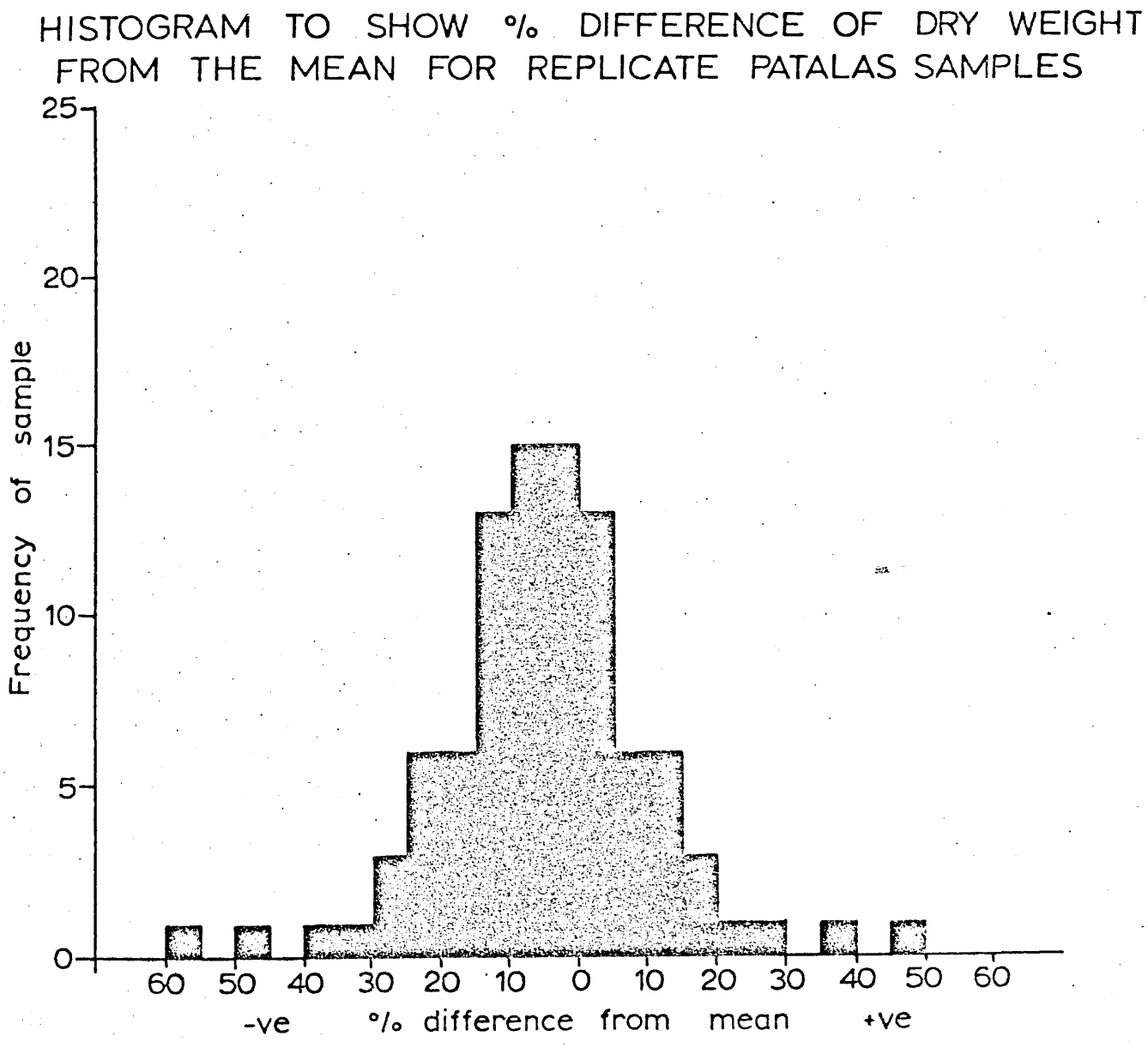

HISTOGRAM TO SHOW % DIFFERENCE OF DRY WEIGHT FROM THE MEAN FOR REPLICATE PATALAS SAMPLES
Frequency of sample
25
20
15
10
5
0
60 50 40 30 20 10 0 10 20 30 40 50 60
-ve % difference from mean +ve

Fig. 4.1.5(b).

Table 4.1.5(c)

	Mean no per patalas	SD	SD%$\bar{x}$	Range
Daphnia >2.0mm	0.5	0.49	98	0.1- 9.9
Daphnia 1.40-1.99mm	18.2	3.6	20	14.6- 21.8
Daphnia 1.00-1.39mm	12.6	5.3	41	7.3- 17.9
Daphnia <1.00mm	135.1	12.1	9	123.0-147.2
Daphnia eggs	5.4	4.2*	77	1.2- 6.6
Cyclops adult	1.1	1.1	99	0- 2.2
Cyclops copepodite	0.8	0.4	57	0.4- 1.2
Diaptomus adult	2.0	1.5	74	0.5- 3.5
Diaptomus copepodite	0.8	0.3	33	0.5- 1.1
Bosmina sp.	13.2	2.7	20	10.5- 15.9
Nauplii	0.9	1.7*	184	0- 2.8
Asplanchna sp.	1.4	1.6	112	0- 3.0
Total animals	192	±9.7	5%	194.3-201.7

* Samples deviating from expected S.D. This suggests clumping which is actually the case for the eggs. This occurs in three samples from ten.

This figure is comparable with table 4.1.5(b) and the same comments apply. The total variation is low 192±5%, and where numbers are high, in excess of 100 individuals, variation is less than ±10%. This is in agreement with the recommendation of LUND ET AL. (1958) to count 100 organisms or more.

Comparison of coarse and fine nets.

Two grades of plankton net, a coarse (60 mesh) and fine (180 mesh), were used for vertical net samples throughout this study (4.1). The results of the field sampling programme provide a comparison of the two types of plankton nets.

Five groups of animals caught in the nets were compared numerically using size-class data from sample counting. Results show that Daphnia hyalina of a size range 0.4-1.0mm in length were, except in three samples, always present in larger numbers in the coarse nets. Daphnia hyalina egg numbers were higher in the coarse nets. Bosmina sp. numbers were higher in the fine net samples as were Asplanchna sp., copepod nauplii and the smaller rotifers. The results are presented in table 4.1.5(d).

For Daphnia, ($\leq$1.00mm), the fine net catch was 49.6% that of the coarse net. Bosmina numbers were 136.9% of the coarse net catch. The probable explanation of the figures presented in table 4.1.5(d) is that the numbers captured are related to the pore size of the nets used. Daphnids cannot escape through the mesh of either net whereas Bosmina and Asplanchna, the smaller rotifers and the nauplii can probably be washed through the coarse mesh net. The eggs of daphnids are held in the brood pouch of the adult females and as these are normally greater than 1.4mm in length, the numbers of eggs are related to the efficiency of capture of this size group.

Less of the larger animals are caught in the fine nets because the smaller pore size increases pressure in the net mouth and also increases clogging of the net filtering surface. These factors effectively reduce the volume of water column filtered. The effects of clogging are difficult to assess as clogging can occur under a variety of conditions and may be caused either by phytoplankton or the zooplankton itself as the net gets full. This may result in an apparently greater efficiency of capture of the smaller zooplankton by coarse nets.

Table 4.1.5(d)

	Daphnia <1.0		Eggs		Bosmina		Asplanchna	
	F	C	F	C	F	C	F	C
8/1/68	350	560	100	175	0	0	200	-
22/1	1950	1890	575	1200	0	0	50	-
29/1	270	1069	10	163	0	0	140	-
12/2	840	1630	830	740	220	90	0	-
19/2	560	700	520	305	0	0	10	-
26/2	780	895	650	260	10	0	110	-
4/3	580	810	50	180	10	0	140	-
11/3	470	670	100	250	0	0	50	-
25/3	120	395	10	45	10	5	40	-
1/4	150	136	110	26	10	2	50	-
29/4	7950	13675	650	600	150	20	850	-
6/5	6600	10200	100	0	50	25	1050	-
13/5	2950	6525	0	25	125	100	575	-
20/5	1175	3090	0	50	100	113	0	-
27/5	1350	1490	33	30	383	70	33	-
5/6	75	664	0	35	150	83	350	-
10/6	110	90	0	0	90	60	20	-
22/7	4300	3225	0	0	350	125	7200	-
12/8	500	1160	0	0	525	370	800	-
19/8	775	1848	550	170	175	233	2675	+
26/8	325	325	250	450	25	0	25	-
3/9	1775	3375	25	50	0	0	175	-
9/9	850	1510	0	0	0	0	0	-
7/10	850	1710	100	0	0	0	0	-
14/10	875	940	25	150	0	0	250	-
21/10	90	120	0	0	20	40	410	-
17/3/69	400	1240	900	850	40	20	180	
24/3	340	900	240	1070	40	10	180	0
8/4	80	190	120	180	20	20	100	? 20
14/4	200	630	575	1510	50	50	300	90

Table 4.1.5(d) cont.

21/4	100	216	0	25	0	100	625	100
28/4	875	4800	1575	1940	200	40	1625	550
5/5	2100	10050	200	1400	100	375	4700	7225
12/5	3250	7575	200	2000	750	725	17150	14850
19/5	7000	15920	150	250	550	350	3500	4075
27/5	2800	7900	260	625	310	400	830	375
2/6	1880	4020	100	100	500	210	410	230
9/6	410	890	0	10	180	90	150	50
Total	56055	113033	8908	14874	5143	3756	29750	27565
N	38	38	38	38	38	38	12	12
$\%^{f}/_{c}$	49.59		59.89		136.93		107.93	
$\%^{c}/_{f}$	201.60		166.90		73.00		92.60	

Comparison numbers caught by fine net and coarse net using the comparable field data available.

0 = zero

- = not recorded.

	Bosmina	Asplanchna	Daphnia
Fine net	100	4700	2100
Coarse net	375	7225	10,050

As plankton nets age with use the mesh size changes gradually. With a new 180 mesh per inch net the pore size was measured initially as 0.050mm and after use for eight months this became reduced to 0.047mm. Similarly, for a 60 mesh per inch net pore sizes decreasing from 0.188mm to 0.183mm are observed. The sizes are further decreased by teasing of the fibres caused by wear. The nets in use in this study were employed for 21 months and the effect was probably further increased. This may partially explain the fact that during the first year of the study Asplanchna was not caught in the coarse net at all whereas they were caught in large numbers during the spring of 1969. This effect was probably increased as Asplanchna numbers were higher in the second year during the spring period (1968 max. 1050/fine net haul, max. 1969 14,850/fine net haul).

Coarse and fine nets were compared for catching characteristics by regression analysis. Different components of the catch, Daphnia <1.0mm, daphnid eggs, Bosmina sp and Asplanchna sp were compared for the two types of net for catches per vertical haul. Results are presented in table 4.1.5(e).

Table 4.1.5(e)

x= coarse net y=fine net haul	Correlation coefficient (r)	Regression equation y=bx+c	Standard deviation Sres at $\bar{x}$
Daphnia < 1.0mm	0.559, $p<0.001$	y=0.33x+51.3	265 at 297.5
Daphnid eggs	0.174, $p<0.1$	No significant correlation	
Bosmina sp.	0.596, $p<0.001$	y=123x+5.5	26.3 at 9.88
Asplanchna sp.	0.974, $p<0.001$	y=1.041x+8.8	103 at 229.7

Although there is a very highly significant correlation, except for the daphnid eggs, where there is no correlation, the standard deviations of the regression analyses are extremely high. Examination of the results for Asplanchna sp. catches in both nets (table 4.1.5(d) sheds some light on this discrepancy. Where numbers are low, the fine nets are superior in catching Asplanchna sp. Where numbers are high, the coarse net catches the same numbers or more, probably due to the filtering surface of the net becoming clogged with animals and reducing the relative filtering area of the net surface. The same may apply to other organisms. Normally the smaller animals (Bosmina sp and Asplanchna sp) are caught better in the fine nets than the larger animals (daphnids and adult copepods). The non-correlation of the egg numbers is probably related to the low numbers of egg carrying adult Daphnia appearing in the fine net hauls i.e. not enough eggs were sampled.

A comparison of net and Patalas samples.

Coarse net samples and Patalas samples were taken simultaneously throughout the sampling programme and both samples were filtered through 60 mesh per inch plankton net. The data obtained provide a basis on which to compare the properties of the two sampling techniques.

The Patalas sampler took 5L samples from a column and

the column average was treated as an "integrated" column sample. The net haul samples through the column and in a sense represents an integrated column sample. If the catching efficiencies of the two methods were the same, results should be identical. In practice this is not the case.

The net has a mouth size of 0.30m and in the Q.M. sampled through a depth of 11m which should sample $0.7776m^3$. This is equal to 777.6L. The five Patalas samples are equal to 25L of the column. These results are comparable and if there were a 100% capture in both techniques the net haul should contain 31.10 times the number of animals in the net. The proportions of the components of the nets and Patalas samples should remain the same.

Numbers caught by the two methods were compared by regression analysis and the results are presented in table 4.1.5(f). All Daphnia, daphnid egg numbers and all animals captured are compared. The daphnid egg numbers include those eggs shaken loose from the brood pouches of the adult females.

table 4.1.5(f) y=Patalas nos. =net haul nos.	Regression equation y=bx+c	Standard deviation Sres at $\bar{x}$	Correlation coefficient r (p).
All animals	y=0.075x+12.96	27.58 at 442.0	0.827($p<.001$)
All Daphnia	y=0.078x+ 9.57	21.50 at 283.0	0.828($p<.001$)
Total Daphnia egg nos.	y=0.122x+ 1.20	7.49 at 34.0	o.614($p<.001$)

These results are presented graphically in figs. 4.1.5(c), (d) and (e). The results show a very significant correlation coefficient and the regression equations and deviations for all animals and all Daphnia are very similar and show that the net hauls contain 33% the expected numbers of animals if the Patalas samples have a 100% efficiency of capture.

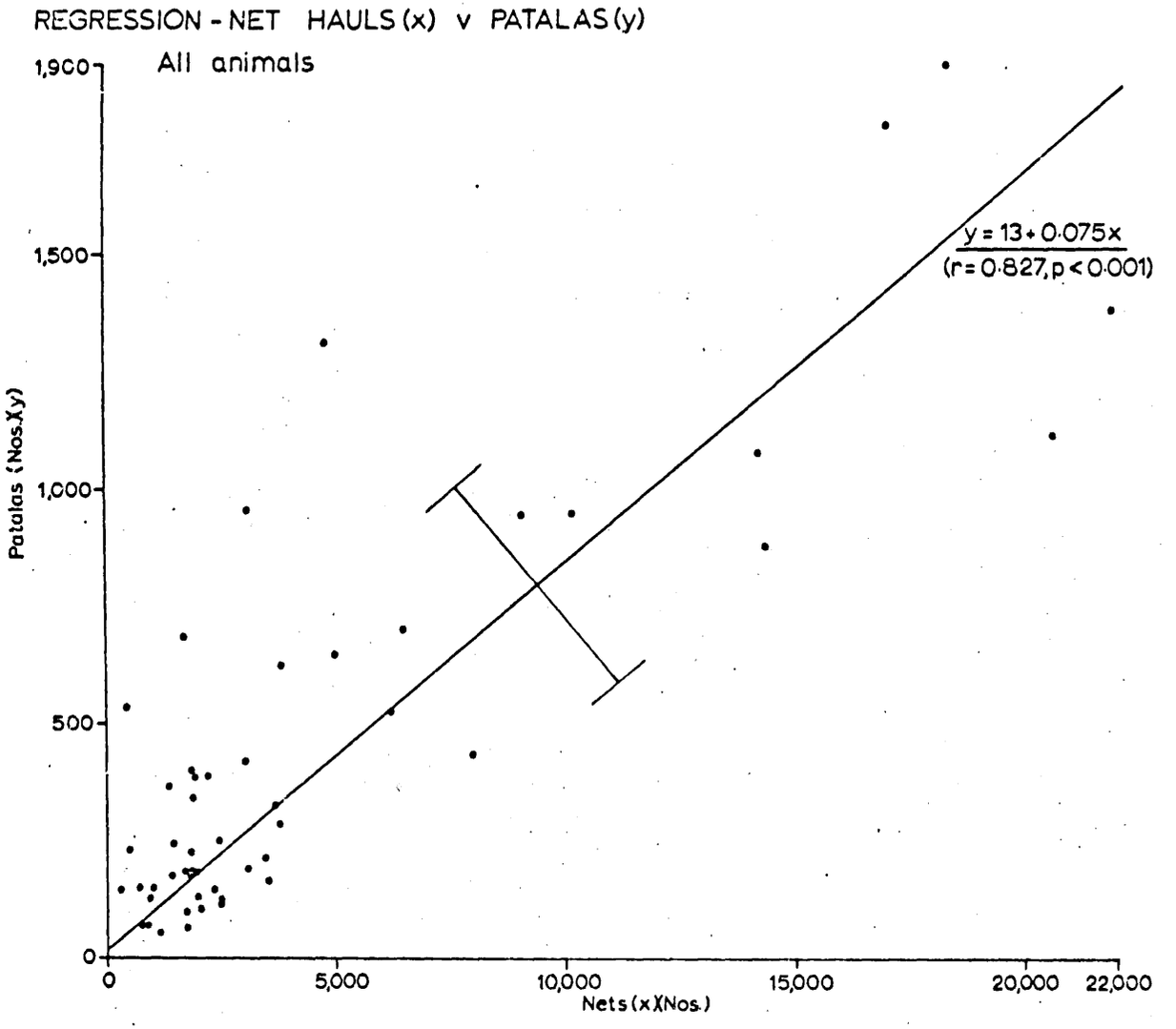

REGRESSION - NET HAULS (x) v PATALAS (y)
All animals
1,900
1,500
1,000
500
0
Patalas (Nos.X y)
y = 13 + 0·075x
(r = 0·827, p < 0·001)
0
5,000
10,000
15,000
20,000
22,000
Nets (x X Nos.)

Fig. 4.1.5(c).

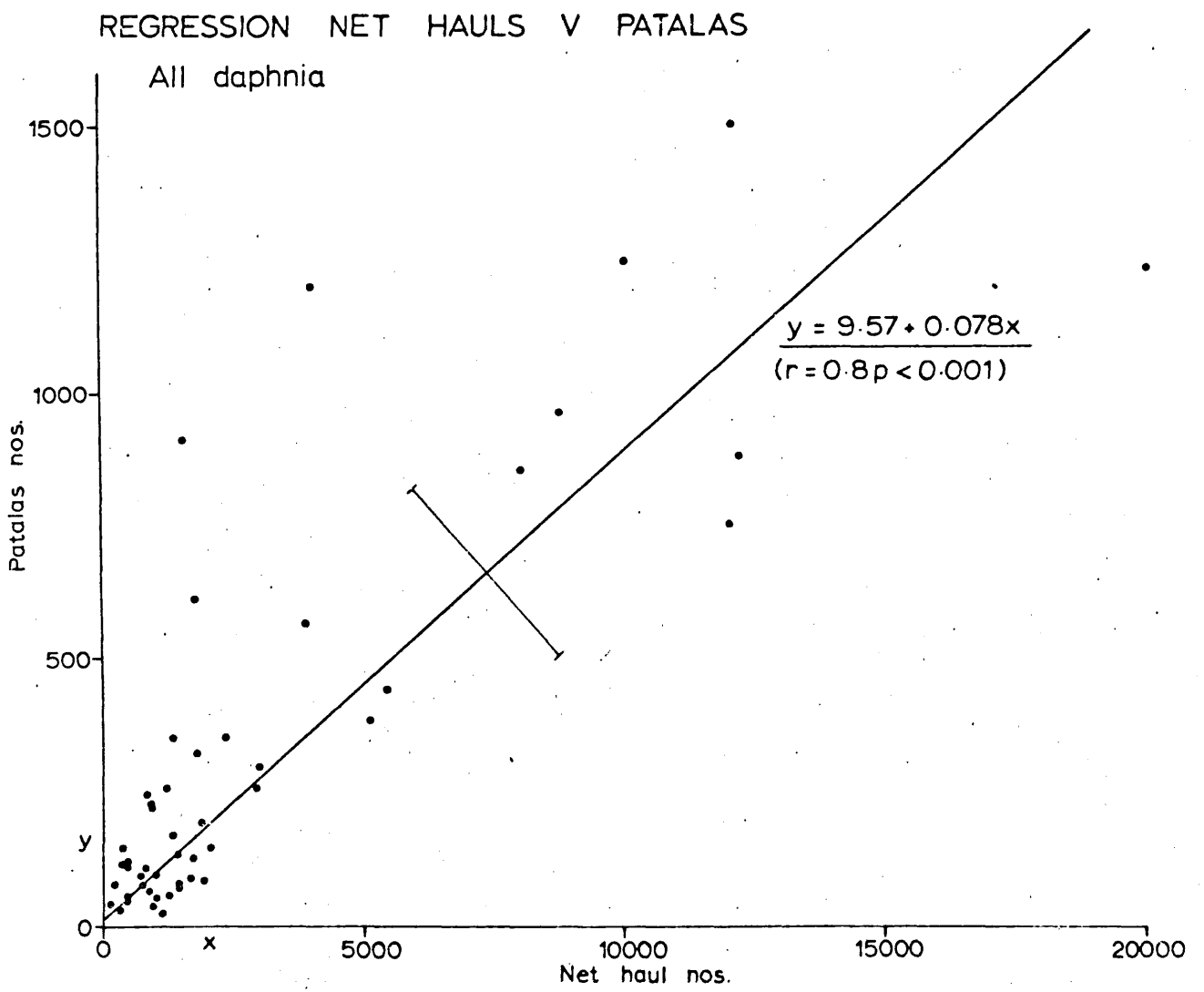

REGRESSION NET HAULS V PATALAS
All daphnia
1500
1000
500
0
Patalas nos.
y
x
0
5000
10000
15000
20000
Net haul nos.
y = 9·57 + 0·078x
(r = 0·8 p < 0·001)

Fig. 4.1.5(d).

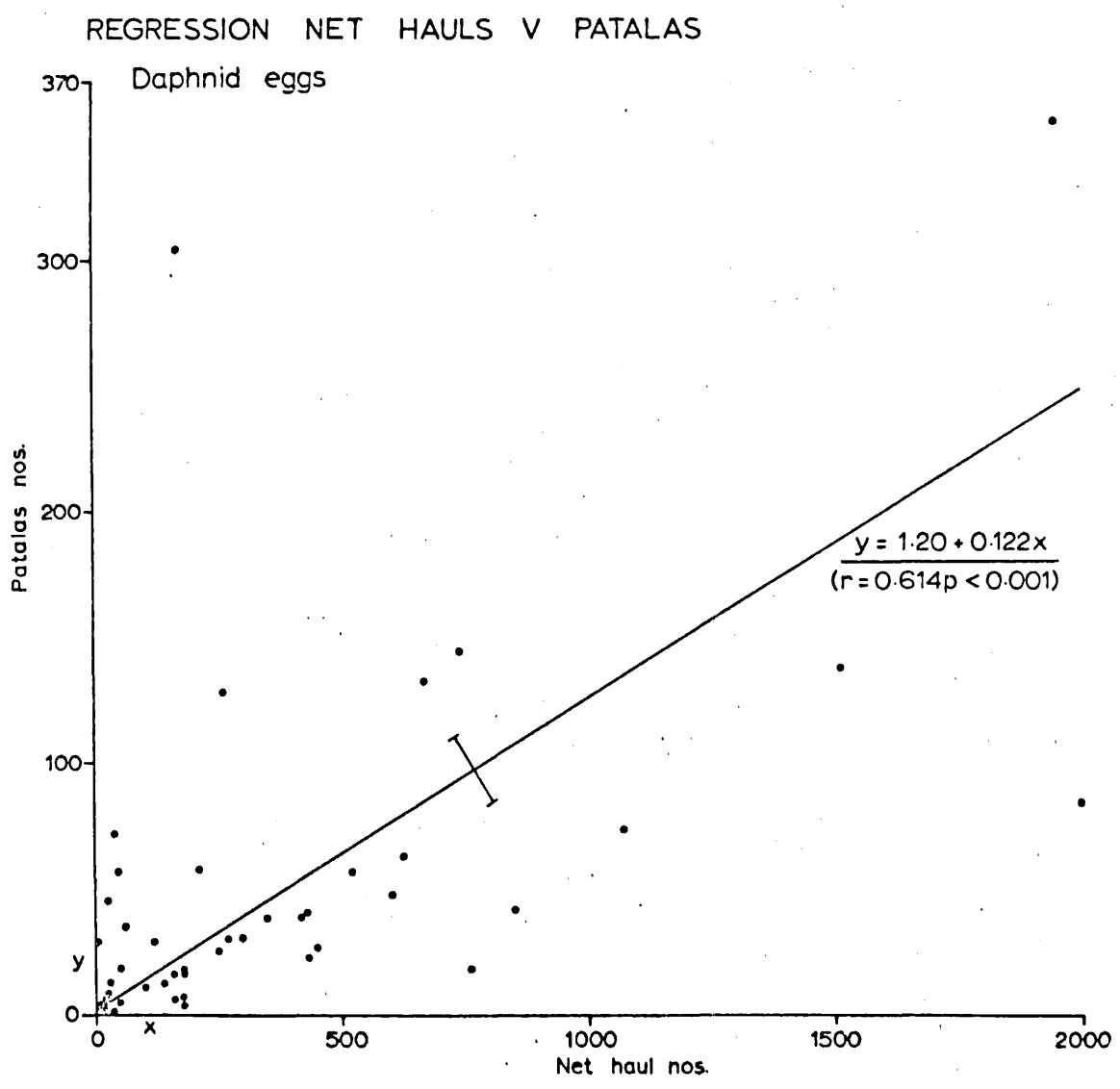

REGRESSION NET HAULS V PATALAS
Daphnid eggs
370
300
200
100
0
Patalas nos.
y
x
0
500
1000
1500
2000
Net haul nos.
y = 1·20 + 0·122x
(r = 0·614 p < 0·001)

Fig. 4.1.5(e).

A similar result can be obtained by comparing the fractions of net hauls that the Patalas samples represent on comparable sampling days. These data are conveniently treated as the fraction of a net haul, that each Patalas sample represents expressed as a percentage of the net haul ($\frac{25bP}{VNH} \times 100$). The negative binomial distribution obtained is satisfactorily treated by a log transformation (ELLIOT 1971). Results for all daphnids are presented as a histogram in fig. 4.1.5(f). The arithmetic mean (14.1%) is different from the mode (10.7%) but the mode is a better estimate of the relationship between net hauls and Patalas samples. This result shows that, if the Patalas sampler has a 100% efficiency of capture, then the net hauls capture 34% the expected number of animals.

Nets and Patalas samples were compared, by adjusting graphical scales, over the season where comparable samples had been taken. The results are presented in figs. 4.1.5(g)$_i$ and (g)$_{ii}$. The same trends are seen in both sampling techniques, all major peaks of numbers being present. This picture could only have been improved by more frequent sampling.

The relationship between the composition of net and Patalas samples has been examined by regression analysis. The results analysed for size classes of Daphnia are presented in table 4.1.5(g). Results are presented graphically in fig. 4.1.5(h). These results show that the composition of net and Patalas samples are very similar and have a high correlation coefficient. The larger size classes of daphnids are less well correlated, probably due to the low numbers representing this fraction.

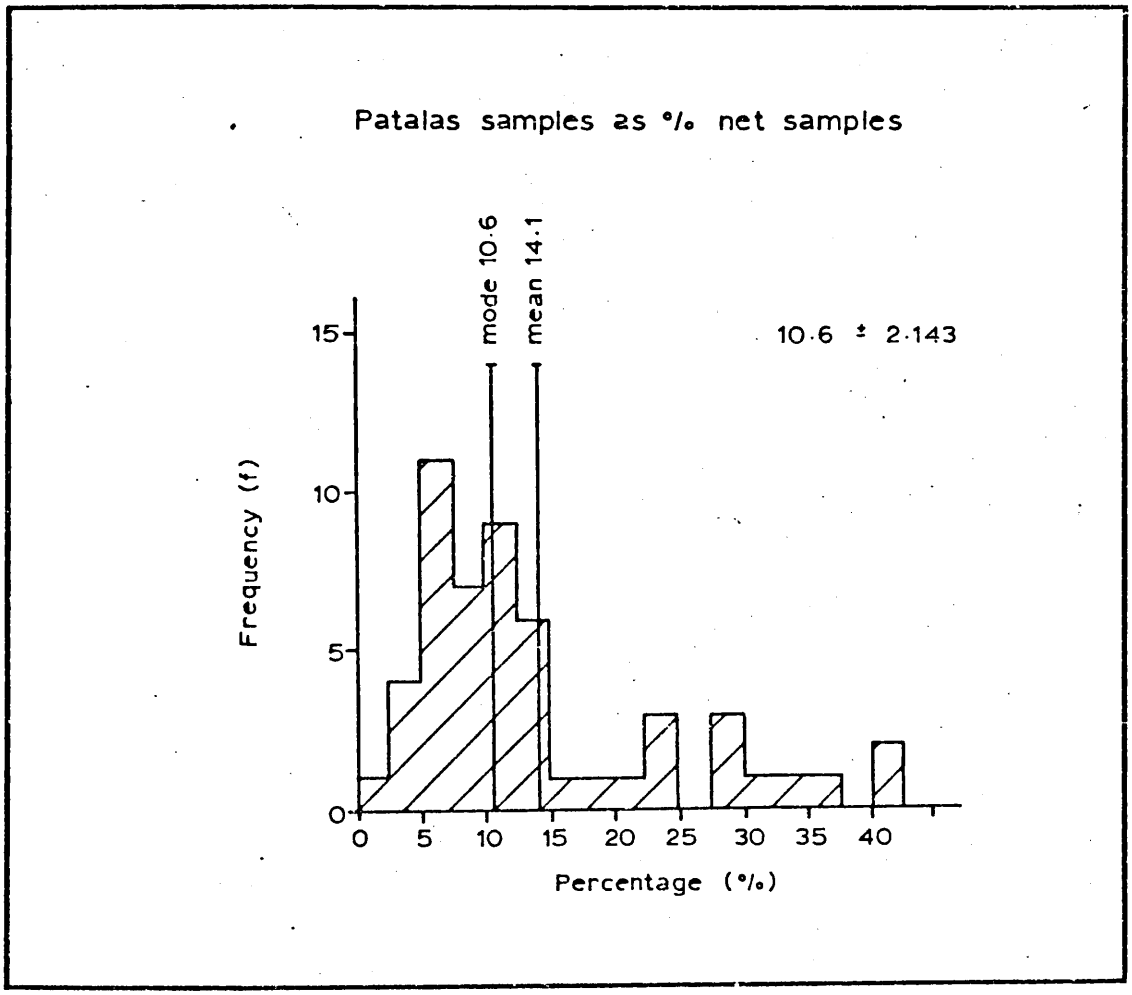

Patalas samples as °/₀ net samples
mode 10·6
mean 14·1
10·6 ± 2·143
Frequency (f)
15
10
5
0
0 5 10 15 20 25 30 35 40
Percentage (°/₀)

Fig. 4.1.5(f).

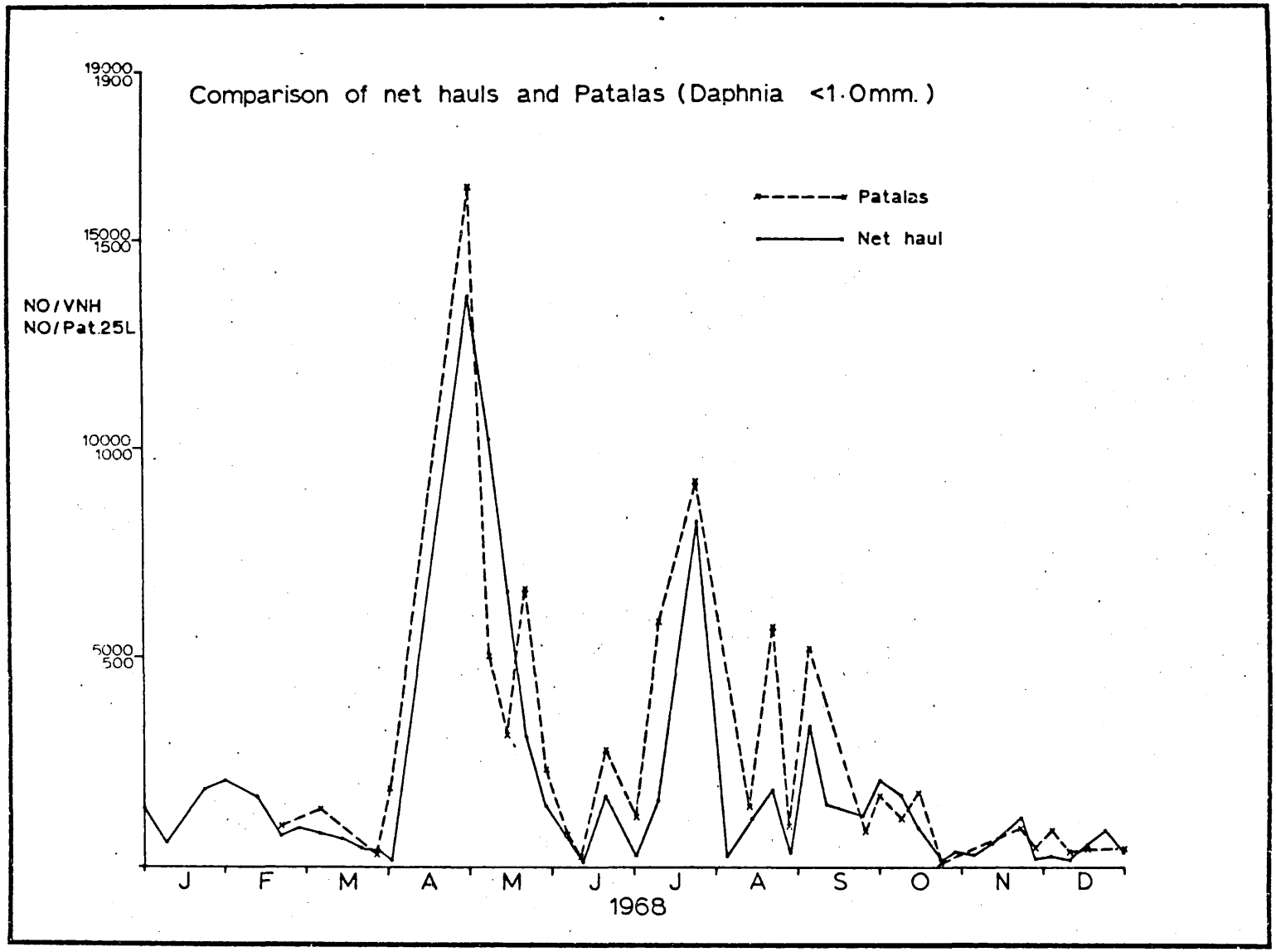

Comparison of net hauls and Patalas (Daphnia <1·0mm.)
Patalas
Net haul
NO/VNH
NO/Pat.25L
19000
1900
15000
1500
10000
1000
5000
500
J
F
M
A
M
J
J
A
S
O
N
D
1968

Fig. 4.1.5(g)(i).

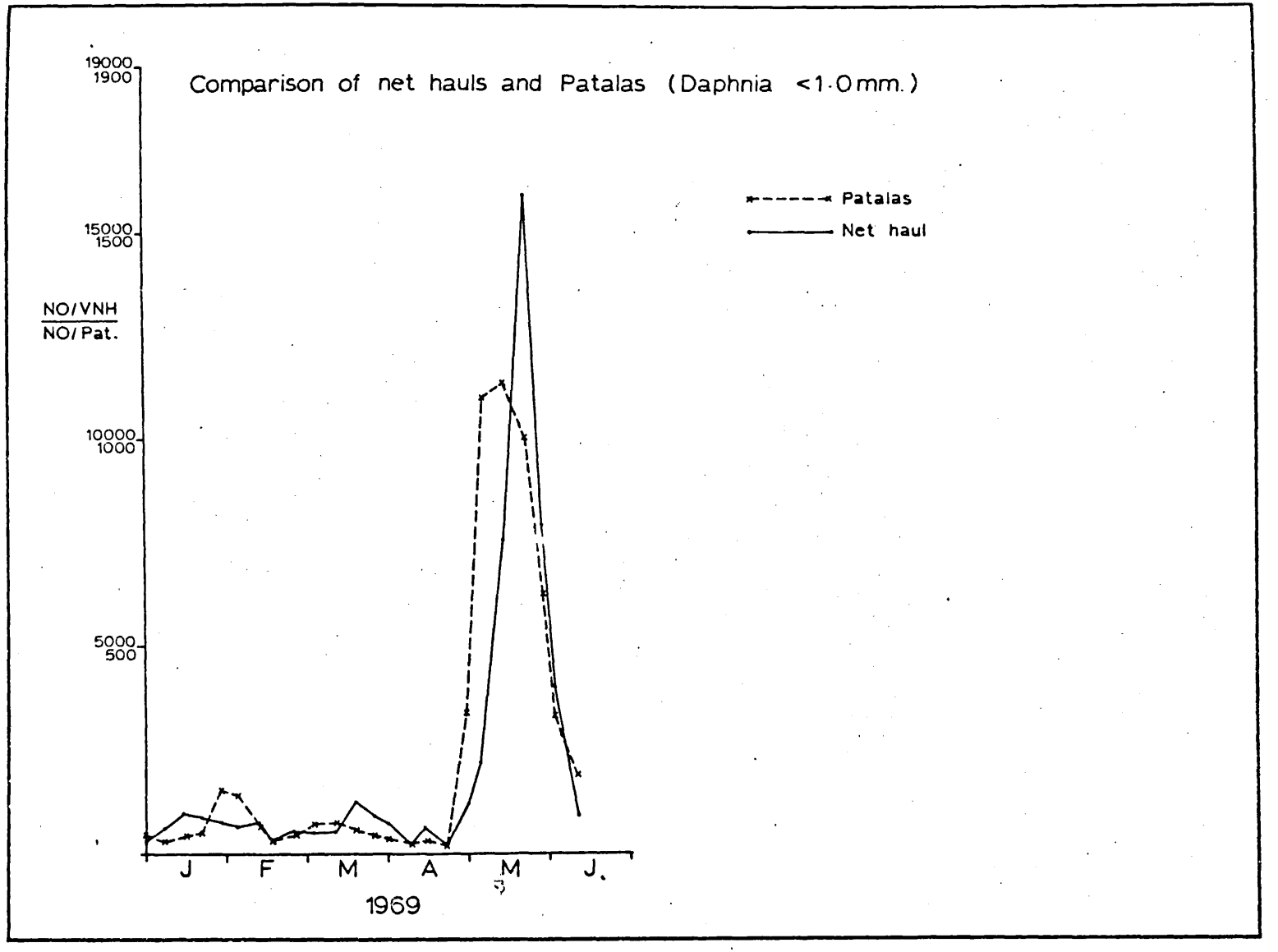

Comparison of net hauls and Patalas (Daphnia <1·0mm.)
19000
1900
15000
1500
10000
1000
5000
500
NO/VNH
NO/Pat.
Patalas
Net haul
J
F
M
A
M
J.
1969

Fig. 4.1.5(g)(ii).

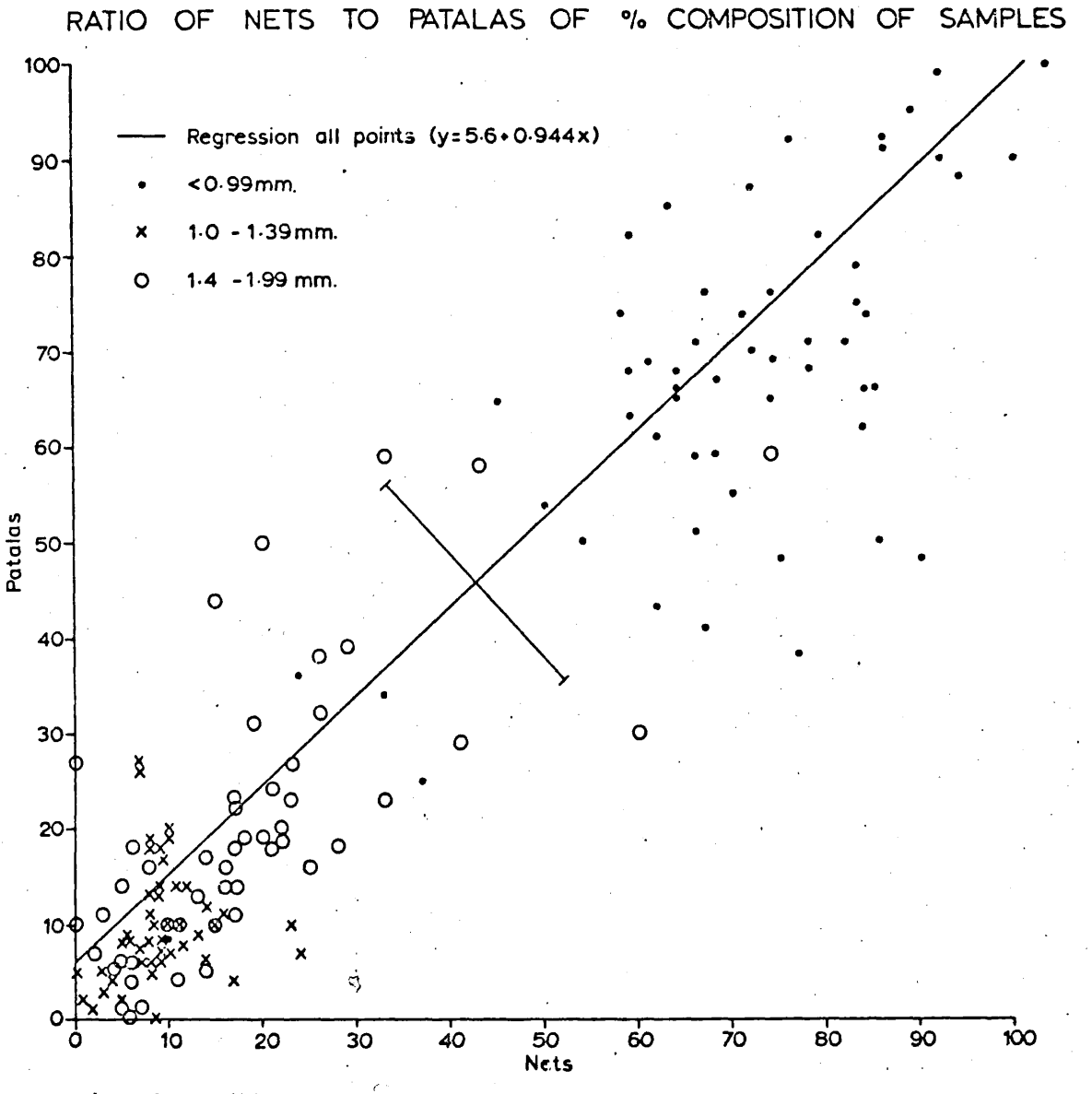

RATIO OF NETS TO PATALAS OF % COMPOSITION OF SAMPLES
Regression all points (y=5·6+0·944x)
<0·99mm.
1·0 - 1·39mm.
1·4 - 1·99 mm.
Patalas
Nets
0
10
20
30
40
50
60
70
80
90
100

Fig. 4.1.5(h).

Table 4.1.5(g)

	Regression equation	Standard deviation	Correlation coefficient
Daphnid size class	y=bx+c	Sres at $\bar{x}$	r(p)
<1.0mm	y=0.69x+18.9	12.36 at 71.0	0.629(p<0.001)
1.0-1.39mm	y=0.418x+6.1	6.09 at 9.0	0.824(p<0.001)
1.4-1.99mm	y=0.712x+6.4	10.40 at 17.9	0.712(p<0.001)
>2.0mm	y=0.328x+1.5	3.08 at 1.9	0.423(p<0.001)
Total Daphnia	y=0.944x+5.6	28.29 at 100	0.944(p<0.001)

Biomass - number relationship.

The data available from net samples were examined to discover whether a relationship existed between numbers of animals caught and the dry weight of animal samples captured by the same method. A regression analysis of weight on numbers of daphnids shows a high correlation coefficient ($r = 0.870$ $p<0.001$) and gives the regression equation (fig. 4.1.5(i))

$$y = 0.0059x + 0.759$$

y = sample dry weight per vertical net haul (mg)

x = numbers of daphnids per vertical net haul

The biomass results obtained from the dry weight of net samples were also compared with the biomass calculated from numbers obtained in the field samples and from laboratory measurements of individual dry weights (section 5.2.1). The size classes measured from field samples were given a mean dry weight for the class and these figures were used to compute the calculated dry weight. The calculated dry weight is given by the formula

$$Bcalc = (Nc.\bar{w}e + N_1.\bar{w}_1 + N_2.\bar{w}_2 + N_3.\bar{w}_3 + N_4.\bar{w}_4)$$

The values of $\bar{w}$ used are presented in table 4.1.5(h)

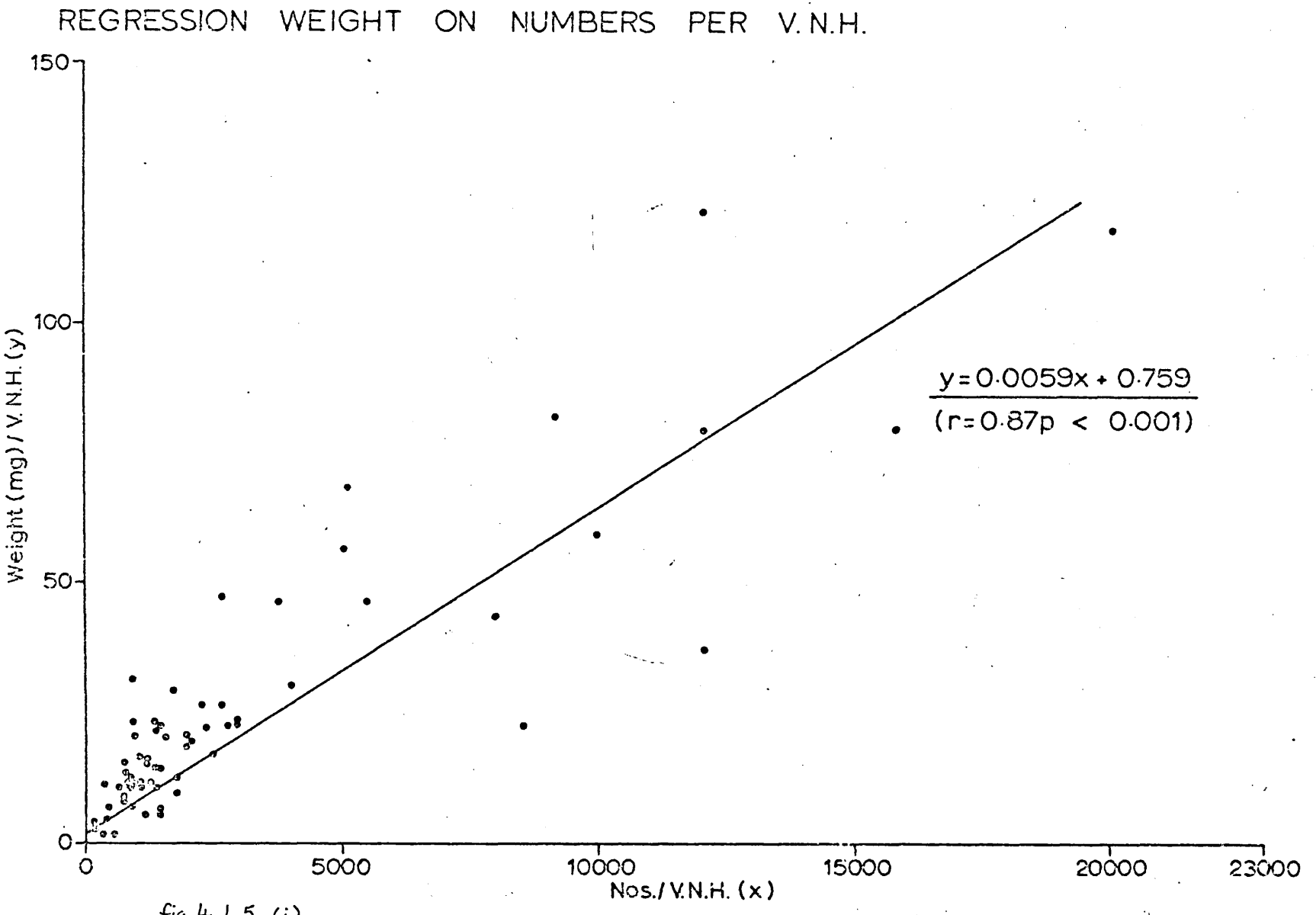

REGRESSION WEIGHT ON NUMBERS PER V.N.H.
150
100
50
0
Weight (mg) / V.N.H. (y)
0
5000
10000
15000
20000
23000
Nos./V.N.H. (x)
y = 0·0059x + 0·759
(r = 0·87 p < 0·001)

fig 4.1.5.(i)

Table 4.1.5(h)

Size class		mean individual dry weight (mg)
Eggs	($\bar{w}_e$)	0.0018
<1.0mm	($\bar{w}_1$)	0.0044
1.0 - 1.39mm	($\bar{w}_2$)	0.0088
1.4 - 1.99mm	($\bar{w}_3$)	0.0242
>2.0mm	($\bar{w}_4$)	0.0532

Results were analysed by regression analysis and the results for 71 samples are presented in figure 4.1.5(j). There is a very high correlation coefficient ($r = 0.449$ $p<0.001$) and the value of b in the regression equation approaches 1.0.

$$y = 0.96x - 0.75$$

y = calculated dry weight (mg)

x = measured dry weight (mg)

Variation seen in these results depends on two principle errors. Firstly, the sampling error of the numbers and field biomasses and secondly the choice of mean individual dry weights for the different size classes. The latter error varies from sample to sample as animals may be nearer to one end of a size group than another on different sampling dates. As an approximation the values chosen seem to be adequate.

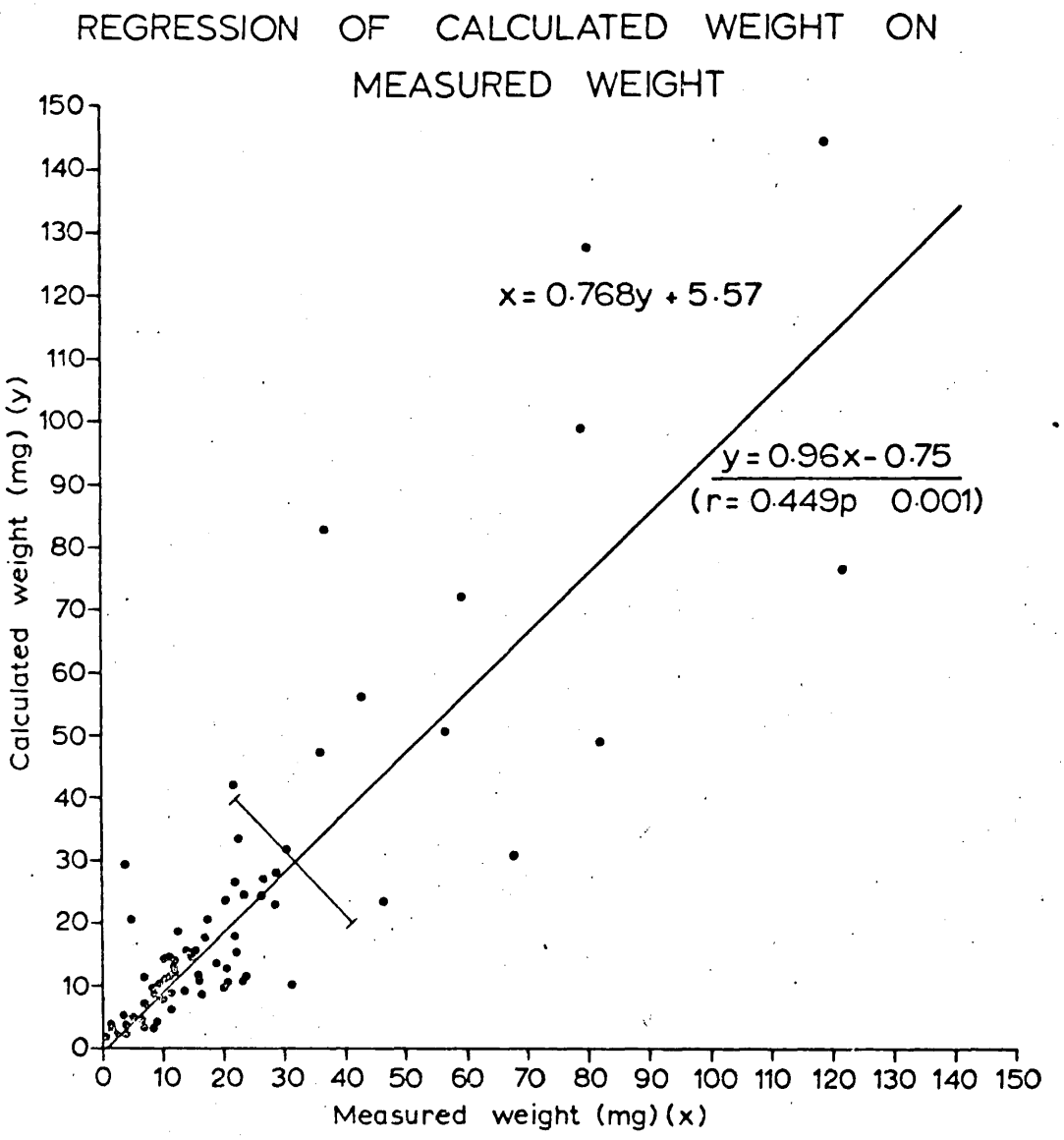

REGRESSION OF CALCULATED WEIGHT ON MEASURED WEIGHT
x = 0·768y + 5·57
y = 0·96x - 0·75
(r = 0·449p 0·001)
Calculated weight (mg) (y)
Measured weight (mg) (x)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150

Fig. 4.1.5(j).

4.2. FIELD SAMPLE TREATMENT

Samples collected in the field using the methods described (section 4.1.) were used in one of four ways: either for laboratory experimentation, field experimentation, estimation of field standing crops in terms of biomass or for population data analysis (5 1.3).

4.2.1 Counting of samples.

Samples required for counting were preserved in 5% formalin solution. These samples were fixed immediately after collection, normally within ten minutes and never more than one hour later. Several authors (WRIGHT 1965, CUMMINS ET AL 1969) criticise the use of formalin as a preservative for zooplankton, WRIGHT recommends the use of 95% ethanol to prevent the ballooning of carapaces and the subsequent loss of eggs, whereas CUMMINS suggests that no preservatives are suitable. ARMSTRONG & WICKSTEAD (1962) recommend the use of 4 or 5% formalin as a simple effective method of preservation and the evidence of the present study agrees with this conclusion.

All samples were examined in a specially constructed clear perspex dish. This dish (fig. 4.2.1(a)) was of perspex plate excavated to create a trough fitted with a baffle in order to prevent currents moving animals in the sample. The trough sides were angled to prevent plankton adhering to the sides. The bottom of the trough was divided into three equal sections of one mm by machine scoring.

The examination of samples was by means of a Watson binocular microscope fitted with an ocular micrometer. The microscope had a magnification range of 12.5 - 140 X which proved adequate for all but the most critical examination.

Characteristics of zooplankton examined.

Species were identified for the Cladocera. Cyclopoid copepods were grouped as were diaptomid copepods and all

Diagram of counting chamber.
(to scale)

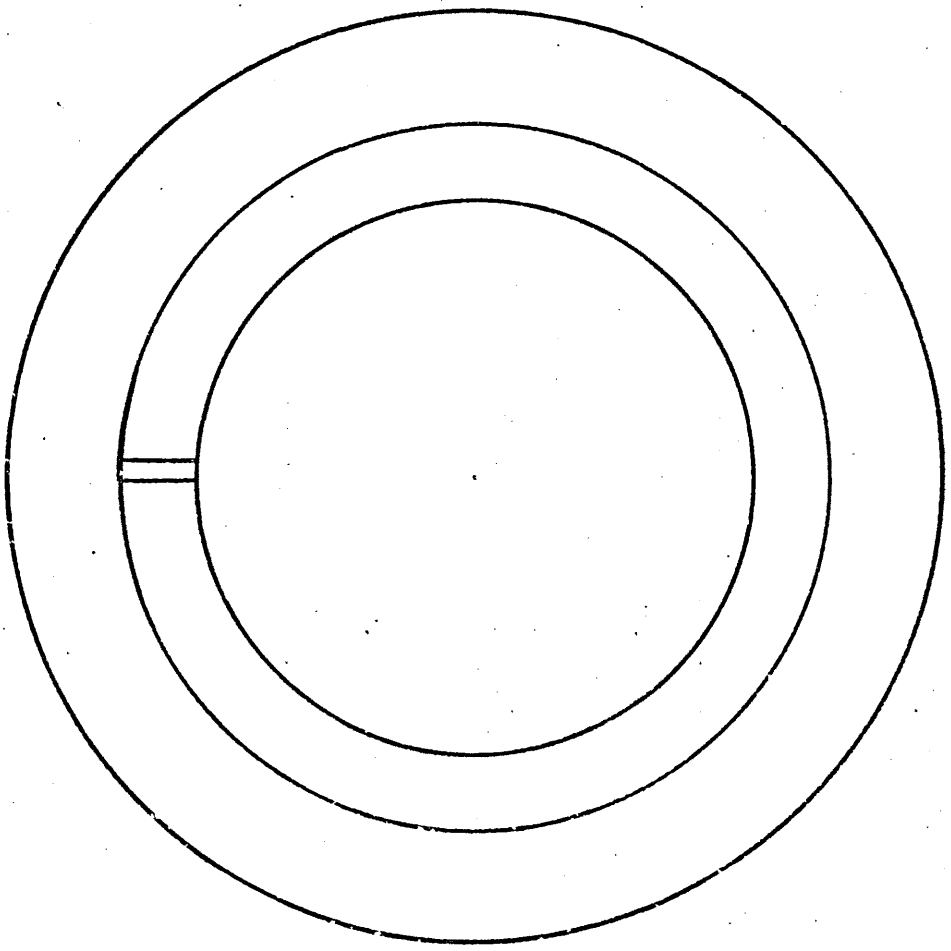


fig. 4.2.1(a)

nauplii were grouped irrespective of species. Asplanchna was identified but other rotifers were grouped together. Other animals that were captured were identified as far as was quickly possible.

Cyclopoid and diaptomid copepodites were distinguished and these were sexed where possible.

Daphnia hyalina was identified as one of the following categories:-

Daphnia hyalina	< 1.0mm	(a)
	1.0 - 1.39mm	(b)
	1.4 - 1.99mm without eggs	(c)
	1.4 - 1.99mm with eggs (Nos)	(c)
	> 2.0mm without eggs	(d)
	> 2.0mm with eggs (Nos)	(d)

This breakdown of D. hyalina into categories that represent stages of biological significance is based on laboratory studies of the animal.

(a) early instars

(b) includes primiparous instars

(c) egg carrying instars

(d) adults of more than 10 instars.

Eggs found loose in samples were rare but these were easily recognisable and were counted. Stages of egg development - whether or not the egg was recognised as an embryo - were also recorded.

Individual animal sizes were not recorded except as in the categories already described but accuracy and reproducibility of measurement is discussed in section 4.4.2.

Subsampling.

Patalas samples were completely counted irrespective of the numbers of plankton present.

FATE OF FIELD COLLECTIONS

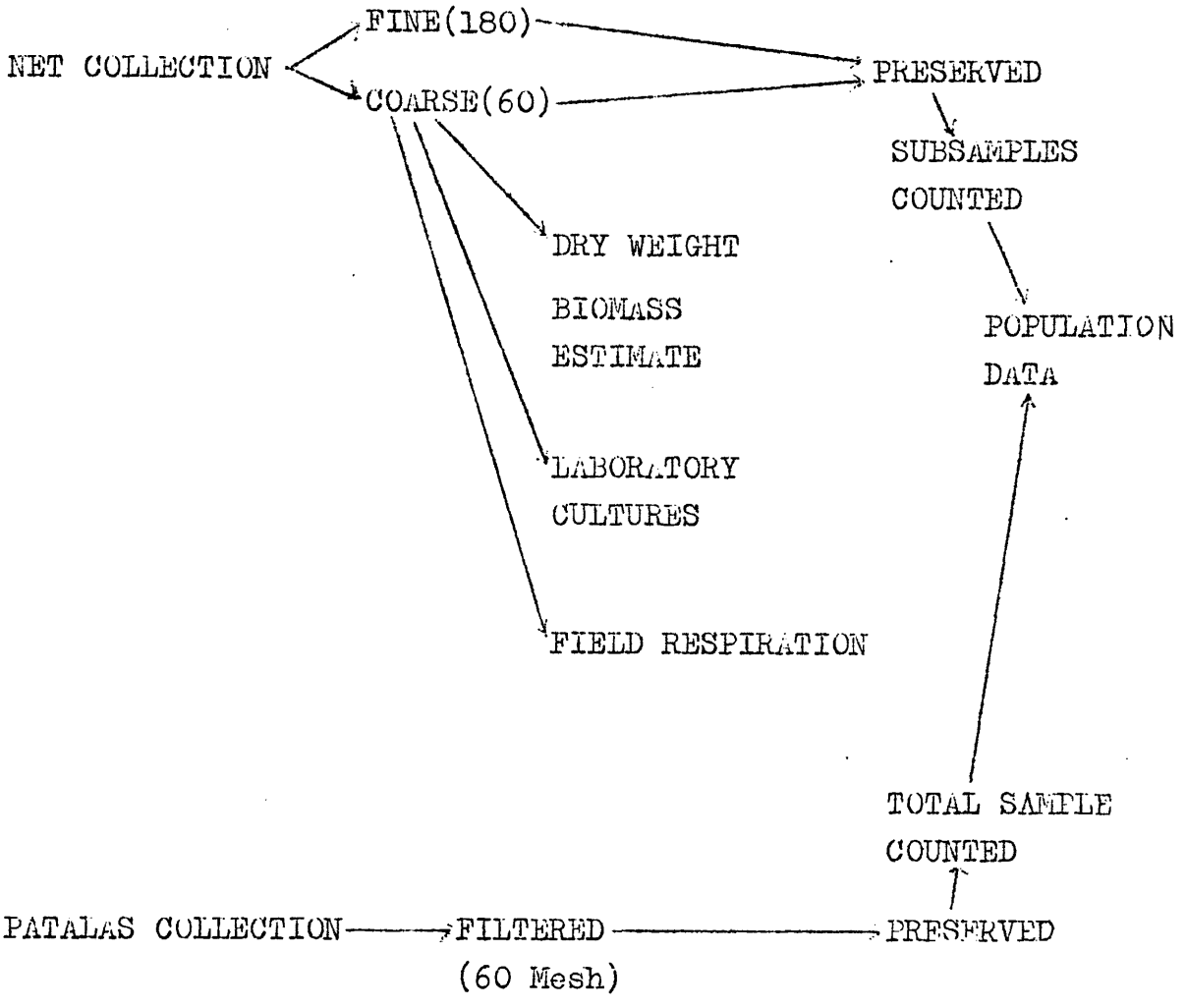


Fig. 4.2(a)

Net hauls were subsampled using a Stempel pipette. The complete sample was made up to a volume of 250 ml and subsamples of 2.5ml were abstracted. Each subsample, therefore, represented 1/100th of the total sample. A minimum of 100 daphnids was counted giving an error of $\pm$ 20% $p < 0.05$. In practice between 5 and 10 subsamples were counted (minimum 3 subsamples) and if more than 10 subsamples were required the whole sample was counted. Non-daphnid species counted and egg numbers had a greater error when their numbers were less than 100.

The mean of the subsamples was used to estimate the total sample number. Fifteen subsamples of one sample were counted to estimate the degree of error using this technique. The results are presented in Table 4.2.1(a). Different groups of animals were examined to see the effect of numbers present in the sample on the reliability of the estimate. The results show that the variation of the total sample number is $\pm$6.1% and for a large part of the sample, for example daphnids without eggs, the deviation is $\pm$ 9%. This compared favourably with errors encountered by GRAHAM (1970) of $\pm$13%. For small parts of the sample errors of the order of $\pm$65% are important especially in the estimation of egg numbers in the sample for production estimates.

Table 4.2.1(a)

	Mean No	Standard deviation	SD%$\bar{x}$
Daphnids without eggs	183.1	16.7	8.9
Daphnids with eggs	1.4	0.9	65.0
Daphnid eggs	10.8	6.2	67.6
Bosmina sp.	84.0	10.1	12.0
Cyclops adults	2.7	1.5	57.8
Total Sample (N = 15)	373.9	22.7	6.1

4.2.2. Field biomass measurement.

Zooplankton standing crop measurements, in terms of biomass, were determined from coarse vertical net hauls. The samples were transferred to the laboratory in clean glass jars and treated rapidly, a process which occurred within one hour after collection.

Separation.

Samples were separated into two fractions (copepods and daphnids) using the technique of STRAŠKRABA (1967). This mechanical separation technique involves narcotising the zooplankton with a 90% ethanol-10% chloroform mixture for a few minutes in a separating funnel and following this with vigorous shaking during which air trapped under the carapaces of the daphnids causes them to float. The copepod fraction sinks to the bottom and was run off separately from the daphnid fraction.

When samples were too large to be accommodated in the flask, they were reduced by use of a net and perspex filter arrangement.

Whenever large algal population affected net samples significantly, the animals were separated from the algae using a simple device employing the response of zooplankton to red light of low intensity. Horizontal illumination with this light causes a horizontal swimming response towards the red light (BAYLOR AND SMITH 1953). The diagram of the apparatus is shown in figure 4.2.2 (a). The animals were introduced into the reflux tube, the tap was opened and then left overnight in a cold room at 10°C. The technique was used previously by CREMER AND DUNCAN (1969) who found the separation to be satisfactory.

Filtering and drying.

Samples were filtered, using a Sartorius, stainless steel, filtering unit and collecting the filtrate on 4.2cm

Separation apparatus.

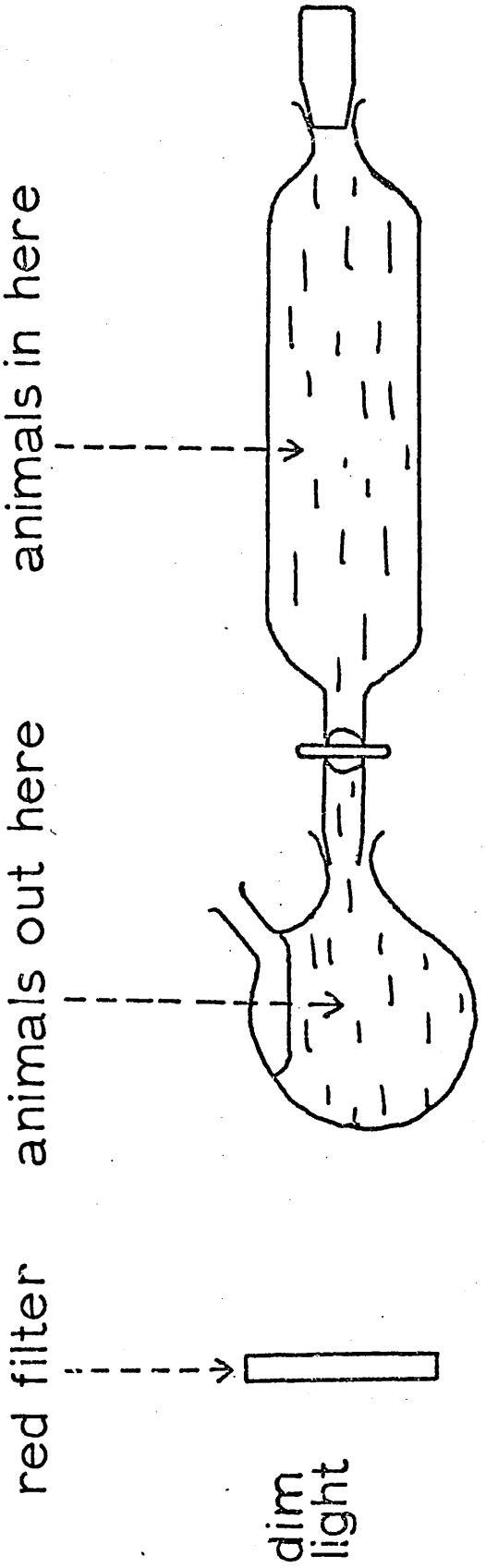


fig. 4.2.2(a)

Whatman GF/C filter papers. These glass fibre filter papers were previously oven dried at 60°C and preweighed. The pore size of the filter was sufficiently small to retain all zooplankton. Samples were filtered under vacuum and animals adhering to the filter unit were added to the sample with a camel hair brush or fine forceps.

Samples were dried at 60°C in a Pickstone oven. The temperature of 60°C was chosen to ensure no loss of lipid material which is reported to occur by evaporation above this temperature (SOUTHWOOD (1966), GROVE ET AL (1961)). Samples were dried for at least 24 hours before weighing to constant weight. Samples were transferred to the balance in a desiccator containing silica gel to prevent loss of material or the hygroscopic collection of water from the atmosphere and also to allow the samples to cool.

Weighing

Samples were weighed on an Oertling beam balance (Model 146) with a sensitivity of 0.01mg. This, applied to a minimum sample weight of approximately 1.0mg, has an accuracy of 1% which compares favourably with the work of TRANTER(1962) who claims an accuracy of 1.8 - 9.4% with zooplankton wet weights.

4.2.3. Individual biomass measurements.

Dry weights for measured individuals of D. hyalina were obtained in order to construct a length-weight relationship for this species. Two different, but comparable, methods were used. The first method was the same as that of RICHMAN (1958) and EDMONDSON (1955) who measured groups of animals of the same size category with an ocular micrometer, dried them on cover slips at 60°C and found the mean dry weight of the size group. The second method, using a Cahn Gram Electrobalance, involved the weighing of a measured individual daphnid.

Collection and sorting

Daphnids were collected from the Q.M. during the two weeks of 16/9/69 with coarse net hauls and kept alive in 2L Dewar flasks for examination in the laboratory. The animals were sorted according to sexual condition and measured with an ocular micrometer, fitted to a Watson binocular microscope, while still living. Length measurements had a consistent reproducibility (0.16% standard error expressed as a percentage of the mean - see section 4.4.2).

Samples were oven dried at 60°C for 24 hours before weighing and carried to the balance in a desiccator containing silica gel.

Oertling balance mean dry weights.

Groups of animals of the same size group and reproductive condition were selected and measured. These were dried on a preweighed 2.5cm Whatman GF/C glass fibre filter paper and weighed to constant weight on an Oertling beam balance. The mean individual dry weight was obtained by dividing the weight by the number of animals. Between 13 and 60 animals, depending on size and reproductive condition, of each size group were weighed the balance had a sensitivity of 0.02mg and the minimum sample size was 0.45mg which shows an accuracy of about 4% but the reproducibility of the experiment was always better than 10% of the animal weights. Size groupings were predetermined arbitrarily as 0.10mm groupings e.g. 0.50 - 0.59mm, 0.60 - 0.69mm. This practice could lead to bias if all animals had occurred at one end of a size range but in practice this error was found to be self cancelling. 35 length - weight points were determined by this method.

Individual dry weights.

Individual dry weights were measured directly using the Cahn Gram Electrobalance which, it is stated, can measure

10^{-7}g (0.1μg) but actually has a sensitivity of 0.2μg which is 0.05% of the scale range. Animals were measured while living and dried on glass coverslips. The animals were removed from the coverslips with a fine tungsten needle and weighed complete on the balance. The weighing chamber of the balance had a dish of colour sensitive silica gel to maintain a dry atmosphere during weighing. The smallest animals measured had a weight of 3.5μg which had an accuracy of about 6%. 450 measurements of individual dry weights were made.

The Oertling method preceded and was replaced by the Cahn individual method which gave more results for the same measuring and sorting effort and provided more information in terms of reproductive and size categories. Results were analysed graphically and by simple regression analysis by the method of least squares.

4.3 FIELD RESPIRATION

An attempt was made to measure respiratory rates of zooplankton populations in the field. A simple technique, essential for the type of field conditions encountered, was developed. It was essentially the closed bottle technique used by several workers in the laboratory (RICHMAN 1958, MARSHALL ET AL 1935, etc.) with minor modifications to suit field conditions. Oxygen was determined using the Winkler method (WINKLER 1888) and the technique evolved from an earlier study by CREMER AND DUNCAN (1969) and DUNCAN ET AL (1970).

4.3.1. Apparatus and procedure

Apparatus used had to be simple and robust to cope with variable weather conditions encountered in the reservoir throughout the year. Bottles used were 300ml "Quickfit" flasks fitted with hollow, ground-glass stoppers.

The bottles were suspended by putting them in a length of excavated "Nalgene" tube (Jencons) which had been cut to accommodate five bottles. This arrangement is shown in figure 4.3.1 (a). When loaded, the bottles were wrapped in black polythene sheeting secured firmly by elastic bands. This darkening prevented light affecting results by preventing photosynthetic activity within the bottles. The bottles fitted tightly in the tubes and the ends of the tubes were secured with a continuous chain which also served to suspend the unit. These units could then be easily suspended at set depths on a chain fitted with carbine clips which made removal simple and fast.

Animal samples were taken from the field and filtered through a coarse net (60 meshes) filter before

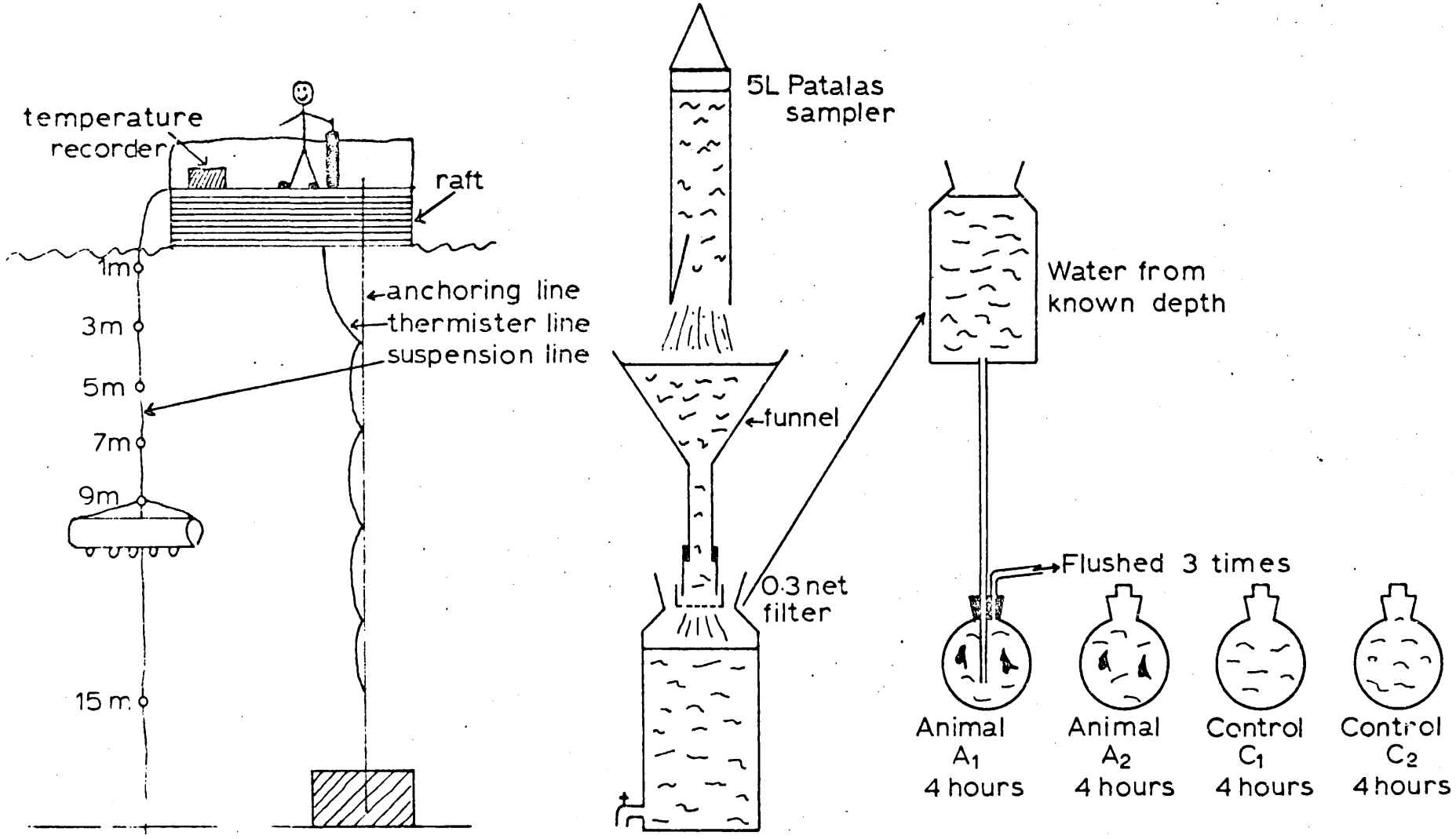


Diagram showing the collection, handling and suspension of samples for field respirations.

Fig. 4.3.1(a).

being put into the experimental bottles. The unit of animals for the experiment was normally one 5L Patalas sample per bottle, but when animal numbers were estimated to be too small to obtain a result for a 4 hour exposure, a fraction of one vertical net haul was used.

While concentrating animal samples, the excess water was collected in a 13.6L plastic container (Geeco). This water was used to fill control and animal bottles and also came from the same depth as the animal samples. This process had the advantage that the water was at the same reservoir temperature and food concentration that the animals were taken from but the animals were concentrated to about 17 times their original concentration. Bottles were filled with a siphon and flushed through with at least three times their own volume of water. The animal samples were then added to the top of the bottles and allowed to sink into the water before the stoppers were inserted.

Duplicate bottles were used for each sample at each depth. One control bottle was fixed immediately with Winkler's reagents and the bottles were then suspended in the reservoir, at the fixed depth that the animals were taken from, for approximately four hours. The actual time of exposure was measured exactly. After exposure, the bottles were removed from the water, fixed immediately with animals present, with Winkler's reagents, and then carried to the laboratory for titration.

When conditions allowed, a complete depth profile of the reservoir was made at 1,3,5,7 and 9 metres. As conditions worsened samples were progressively removed from the bottom strata or vertical net hauls were taken as the sample unit.

The Winkler's technique used was that described in Standard Methods (A.P.H.A 1965) with minor modifications. Reagents were made up and put under a small vacuum to remove excess air. (Reagents are described in Appendix 4.3.). Winkler's reagents I and II were added in the field and the bottles were stored in this condition. Bottles were moved from field to laboratory in plastic dustbins filled with reservoir water. This helped to maintain field temperatures and to prevent air diffusion through the ground glass joint.

Samples were acidified immediately prior to titration and 50ml samples were titrated against N/80 sodium thiosulphate solution using soluble starch with urea as an indicator. Bottles were kept in the dark until titration which was carried out as quickly as possible after removal from the reservoir. Titration was usually carried out on the same day.

Initially an N.P.L grade 'A' 5 ml burette was used but later it was found more convenient to use a Smith's free piston burette in conjunction with a magnetic stirrer. 50 ml grade 'A' pipettes were used for taking samples from the bottles and animals were left in the bottles while subsampling. The sample was then filtered through Whatman g/f filter papers and dried to constant weight. The procedure was the same as for field biomass dry weights (see section 4.2.2).

To measure the respiration of the animals, the animals were placed in water of known oxygen concentration and left for a known time with the bottle closed. The oxygen consumption is the difference between the initial oxygen concentration and the final oxygen concentration of the water. In the field, the situation is more complex because of the presence of other oxygen consuming organisms in the water

and the difference between initial and final oxygen concentrations may be an overestimate of the oxygen consumption. A better estimate can be obtained by using a final control of water left for the same time period as the animal experiments.

The oxygen consumption was calculated in the following way

Oxygen consumption per bottle C_b = If - Af mgO_2

Zooplankton Respiration C_z = Cb/w/t mgO_2/mg/hour

Where Cb = oxygen consumption per bottle (mgO_2)

I_f = oxygen concentration of final control(mgO_2)

Af = oxygen concentration of animal bottle(mgO_2)

W = dry weight of zooplankton (mg)

t = time of exposure (hrs.)

4.3.2 Errors associated with using the Winkler's method for the determination of oxygen consumption of animals in closed bottles.

Discussion may be found in standard texts concerning volumetric titration errors (VOGEL 1954, CONWAY 1962) and will only be considered briefly here. These errors apply equally and are valid here, but normally concern titrations carried out in solutions not containing living organisms. When the Winkler's method is applied to respiratory measurements various new errors are introduced. The oxygen consumption is normally measured as the difference between two samples and errors should be applied to the level of oxygen consumption by the animals and not the total oxygen content of the samples. The type of errors considered include those associated with fixation and titration of samples containing animals, the measurement of lowered oxygen concentrations, the flushing of respirometer bottles, the storage and transport of samples

in various conditions of light, temperature and time and the relationship of the normality of the sodium thiosulphate used with accuracy of the burette as well as the size of sub-sample and level of oxygen consumption.

The whole procedure was examined to discover sources of error and how these might be rectified or reduced in relation to the total error involved in the experimental design.

Effects of filtration of animals

The effect on the metabolism of the animals of being filtered out of the samples has not been examined directly, but is almost certainly related to the 'disturbed period' respiration accounted for later. Losses of animals to the filter are very small and are unlikely to affect the results significantly as results are computed as O_2 consumption/mg dry weight/hour and the dry weight of animals is the weight of animals in the respirometer bottle. Any losses to the filter will not reach the bottle.

A second effect of filtering will be on the oxygen tension of the water used for filtering the sample bottles. This oxygen concentration is only likely to be seriously affected if the water is grossly supersaturated. When the water is undersaturated, the filtering process is such that it will tend to saturate the water. At supersaturations the oxygen will tend to bubble out. These effects will both be heightened by any increase in temperature occuring while samples are out of the reservoir. Except during periods of high supersaturation, the effect of filtering is to raise the oxygen concentration by 38% ±9.7. This comparison was made between initial control samples

and the oxygen concentration found in the field and the correlation coefficient for this test is very high ($r = 0.725$ $p < .001$). Where supersaturation occurred there was a 15% drop in oxygen concentration but this only occurred once during an experiment when the oxygen tension in the reservoir was 205%

These results, however, are unlikely to affect the respiration values obtained very seriously. The oxygen saturation of the bottles will decrease as the animals respire and final levels reached would be close to field concentrations but they may affect the respiration rate of the animals and this would 'show up' in the 'disturbed period' respiration.

Effects of bottle treatment

Respiration bottles were fixed with zooplankton still in the sample. Direct fixation in the presence of the animals is the simplest procedure and of advantage in field situations. This procedure does not appear to affect the precision of the titration if carried out quickly after the experiment ($\pm$ 0.026 ml 0.0125 N thiosulphate for a 50 ml sample) but it does alter the accuracy. The error, which is 0.013 ml 0.0125 N thiosulphate per mg dry weight of animal, is due to the loss of iodine either because the manganic hydroxide is trapped in or on the carapaces and is not all dissolved on acidification or because it 'stains' the animal bodies and is isolated from the titration.

An alternative procedure would be to siphon samples from the respirometer with a filtering siphon but this would incorporate the error associated with filtering of incressing the oxygen content of the sample and the flushing error - a much more serious error at this stage.

Animal errors.

Animal errors are most likely to be the result of concentrating animals to obtain a measurable respiration rate and the effect of 'handling' animals upon their metabolic activity. ZEISS (1963) discusses the effect of population density on zooplankton respiration rate and records that adult D. magna confined to a space of 0.24 or 0.12 ml per individual had an oxygen consumption 2 to 2.5 times those animals with 12 ml or more at 19-21°C. He criticises respirometers where crowding occurs on this basis. During field experiments only three samples (from 95) came within the 0.24 - 0.12 ml/individual that he discusses. These occurred during winter months when net hauls were employed as the sampling unit. With Patalas samples only seven samples show individuals with less than I ml/individual, made up largely of small individuals of D.hyalina, Bosmina sp. and copepods.

A second effect of concentrating animals is to increase the concentration of metabolic wastes. These are carbon dioxide and nitrogenous waste. The nitrogenous waste of zooplankton is largely in the form of ammonium ions (BLAŽKA 1966) and these might be oxidised to nitrite ions. REBSDORF (1966) concludes that if nitrites are suspected to be present in the water, the Pomeroy-Kirschman azide modification of the Winkler technique removes the error due to nitrites. As nitrite is frequently present in the field situation, this practice was employed. The effect of metabolic waste was not considered further except in that it was recognised that high concentrations of ammonia might affect

the metabolism of the animals. However, the time of exposure of the experiment was relatively short (4 hours) and this effect was considered to be small.

The third effect of 'handling' has been discussed by several other authors working with different animals. MARSHALL et al (1935) studying the marine copepod, Calanus finmarchius, suggest that there is a period of disturbed respiration of up to ten hours after capture. They suggest that this is due to 'handling' and confinement. KAMLER (1969), working with Isoperla buresi and comparing closed bottle and other respirometer measurements, records a disturbed period of up to five hours.

In the field experiments the effects due to handling are incorporated in the results but several experiments were carried out to assess the extent of this disturbance and its duration. Bottles were filled and exposed in the same way as field samples except that bottles were removed at hourly intervals,

The results of this experiment are presented in figures 4.3.2.(a) and (b). Each result represents a cumulated mean respiration result at the particular hour. After three to four hours exposure the respiration rate appears to slow down to a steady level but the levels are high because the first hours of disturbed respiration affect the final result. The results are the same between three and eight hours and, although too high, the four hour exposure period is a reasonable compromise if a correction factor of about 0.6 the final value is used. The measurement of respiration at one or two hours is also very variable due not only to disturbed

RESPIRATION RATE OF ZOOPLANKTON IN RESPIROMETER BOTTLES AGAINST TIME AFTER LOADING

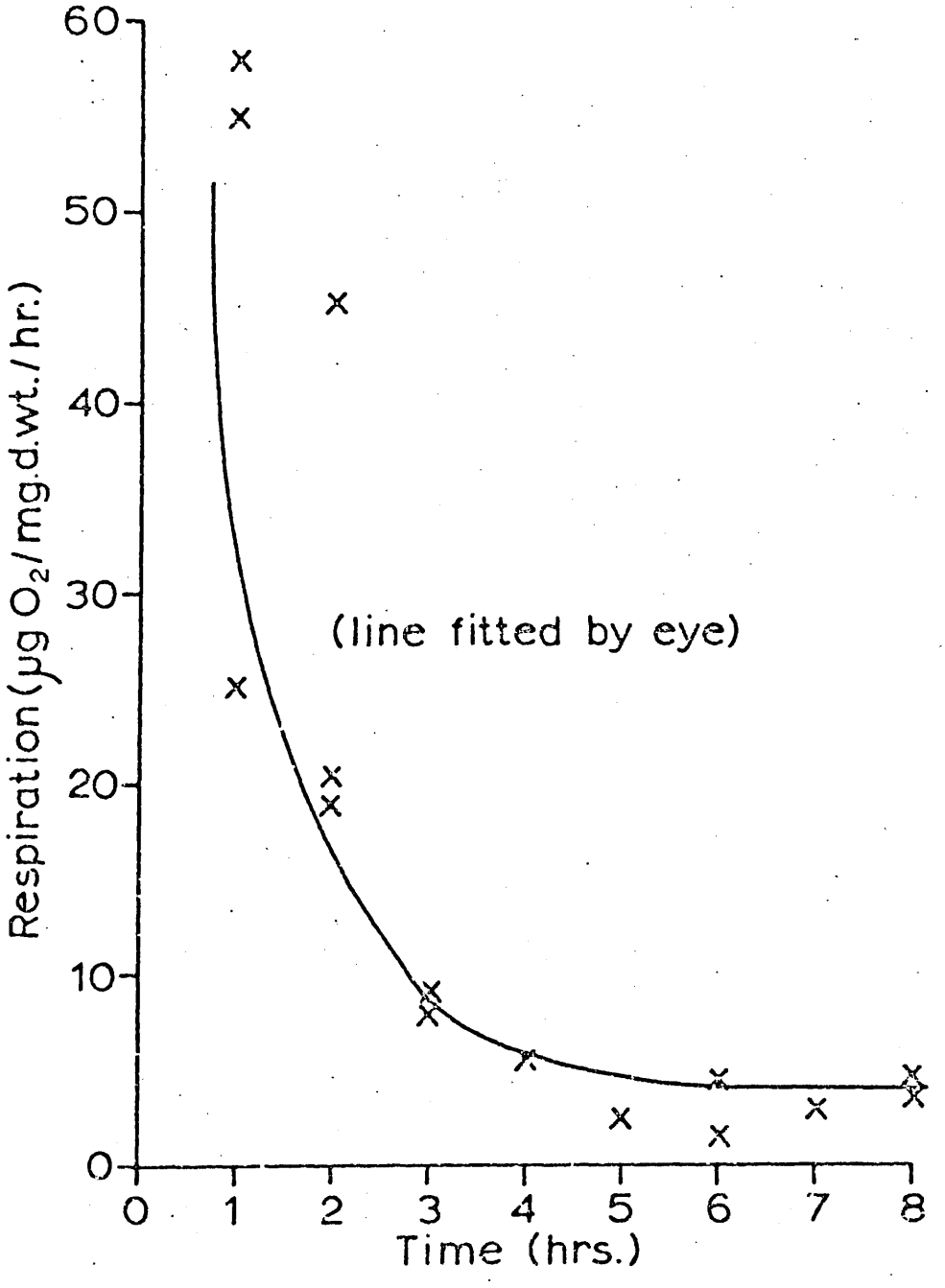


Fig. 4.3.2(a).

RESPIRATION RATE OF ZOOPLANKTON IN RESPIROMETER BOTTLES AGAINST TIME AFTER LOADING

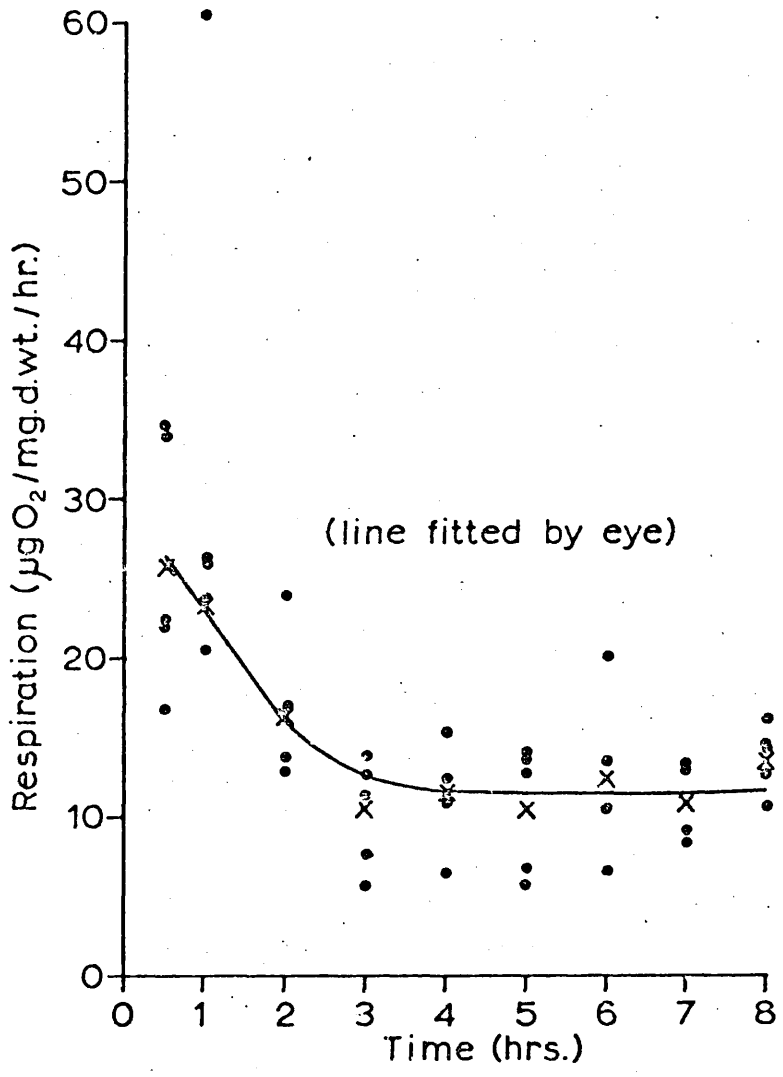


Fig. 4.3.2(b).

period respiration but also because in this region the oxygen differences are of the same order of magnitude as the oxygen consumed by the animals and the limits of sensitivity of the technique are being approached.

The effect of a change in concentration of the food of the animals on their respiration is not known but is not as large as it would have been if all food was removed. The exposure time is relatively short compared with change of food concentration and this error will also be incorporated in the results of the experiments described above.

Winkler's errors

Delay of titration:

The results of a series of experiments to test the effects of delaying titration of samples in various conditions are presented in table 4.3.2(a). The results show that the precision of the titration varies very little but the accuracy alters significantly if the titration is delayed for 24 hours. There is very little difference between samples kept in the light or dark. The results presented here apply to 50 ml subsamples taken from the respiration bottles and it can be seen that if the samples are left overnight, the error can be greater than the total differences of a respiration measurement. For this study, no results are given where this error has been exceeded.

Table 4.3.2(a)

	Mean titration $Na_2S_2O_4$ (mls)	Standard deviation	SD% mean	N.
Immediate titration	4.439	0.035	0.79	24
Stored for 24 hrs. (in dark)	4.509	0.026	0.58	24
Stored for 24 hrs. (in dark)	4.512	0.029	0.64	24

Chemical errors were minimal if the solutions were freshly made up and well stirred before titrations were carried out. Any oxygen taken up by Winkler's Reagents is self cancelling as it appears unchanged in both experimental and control samples. Sodium thiosuphate solution was made from commercially produced stock ampoules and diluted to the required strength. When standardised against Potassium iodate solution of known normality, this was found to be less than 0.5% different from the required strength. 'Analar' reagents, low in impurities, were used throughout. Initially difficulty was experienced with starch indicators but the use of 'starch-soluble-urea' proved satisfactory as its colorimetric endpoint was clearly visible. The chemical error was estimated as a coefficient of variation of 0.789% , which is largely due to the photochemical reaction of iodine.

KAMLER (1969) draws attention to the error associated with insufficient bottle flushing which partially saturates samples with oxygen from the bottles. KAMLER'S results show that flushing at least three times is necessary. MARSHALL ET AL (1935) circumvented this problem by flushing the bottles with nine times their own volume of the water used. KAMLER obtains an error of 0.196% $\pm$ 0.0066 mg/L, a standard error of 3.4% of the mean. RICHMAN (1958) obtains a standard error of 10% of the mean. These figures are related to the oxygen difference rather than the total oxygen concentration of the samples.

Experiments were performed to test the effect of measuring oxygen tensions near saturation and with lowered oxygen tensions which related to control and final experimental bottles. Results obtained showed that with concentrations at 100% and 30% oxygen

saturations, the standard deviations were low (table 4.3.2(b)) but if bottle flushing was not carried out these deviations increase two to four times.

Table 4.3.2(b)

	Mean $Na_2S_2O_4$	Standard deviation	SD as % mean	N.
Air saturated water (flushed 3x)	4.082 (mls)	.0036	.08%	20
O_2 reduced water (flushed 3x)	1.290 (mls)	.0054	.42%	20
Air saturated water (not flushed)	4.815 (mls)	.015	.31%	10
O_2 reduced water (not flushed)	2.793 (mls)	.012	.43%	10

These results also show that errors increase as oxygen saturation gets lower. During the experimental work saturations fell below 80% of the total saturation on only two occasions.

Glass Errors.

CONWAY (1962) suggests that the glass error is best expressed as the coefficient of variation of the individual glass errors (Cg).

$$Cg = \sqrt{(Cp^2 + Cb^2 + Cm^2)}$$

where Cp = coefficient of variation of pipette

Cb = " " " " burette

Cm = " " " " manipulation

The coefficient of variation of the pipette varies with the drop size and its precision on how much it delivers. The coefficient of variation of the burette is dependent on drop size and the coefficient of variation of manipulation on how well the burette may be read.

The total coefficient of variation (Cg) was found to be 0.062%, which is very small compared with other errors discussed.

A second glass error is associated with the volume of the respirometer bottles. These volumes were determined by weighing with and without water. For the experiments, it was assumed that the bottles had a volume of 300 mls but in practice it was higher than this at 308.94 ± 7.98 (2.6%) which respresents an underestimate of 2.9% in bottle size. This is not significant in the estimation of a respiration rate.

Other Errors.

Other errors that occurred include interference by other living organisms. Algal photosynthetic production was ignored as the bottles were blackened with polythene sheet and the effects of respiration and as a trap for iodine were ignored as quantities of algae were small. Bacteria may act as a consumer of oxygen but the exposure time of the experiment was kept short (4-5 hours) and bacterial action was minimal at this period of exposure.

Combined Errors.

The total combined error, C, may be estimated by

$$C = \sqrt{(Cg^2 + Cw^2 + Ct^2 + Ca^2)}$$

where Cg = glass variation Cw = Winkler variation

Ct = treatment variation Ca = Animal variation

The largest errors occur as parts of Cw and Ca where Ca is in the order of 10%. The total error has been estimated as 10.57%.

In addition a correction of plus 0.013ml N/80 thiosulphate has to be made for each mg dry wt of animal in the samples and the final result reduced to 0.6 of its level to account for disturbed period respiration.

4.4 BUDGET WORK

Individuals of D. hyalina were cultured in the laboratory, to measure growth, development and respiration rates, at the constant temperature of 10°C. This was designed to complement previous studies from the same laboratory, by DUNCAN AND CREMER, carried out at 20°C. The temperatures chosen reflected critical periods in the field situation where 10°C was the modal temperature of the spring zooplankton peak and 20°C was the maximum summer temperature.

4.4.1. Culture of animals

Animals were collected from the R.M. with coarse net hauls on 9/4/69 when the water temperature was 7°C and the reservoir was isothermal. These were transported to the laboratory in 2L Dewar flasks and sorted for culturing. Large, >2.0mm, females, with eggs in the brood pouch, were selected for culturing.

Large glass aquaria, maintained at a constant temperature of 10°C, were used to contain the culture vessels. Temperature control, better than ± 0.1°C, was maintained by using blackened 40W, light bulbs connected, via a Sunvic relay, to a Beckmann mercury contact thermometer, as a heat source and copper cooling coils containing refrigerant as a heat sink. The tanks were insulated with expanded polystyrene foam jackets and the arrangement is shown diagrammatically in figure 4.4.1.(a). The water contained the algicide, Phenoxytol, to prevent troublesome growths.

Animals were cultured individually in labelled 25ml open topped dishes which floated in the aquaria. Dishes were cleaned carefully with chromic acid mixture and thoroughly rinsed with distilled water each time the culture medium was changed. The culture medium

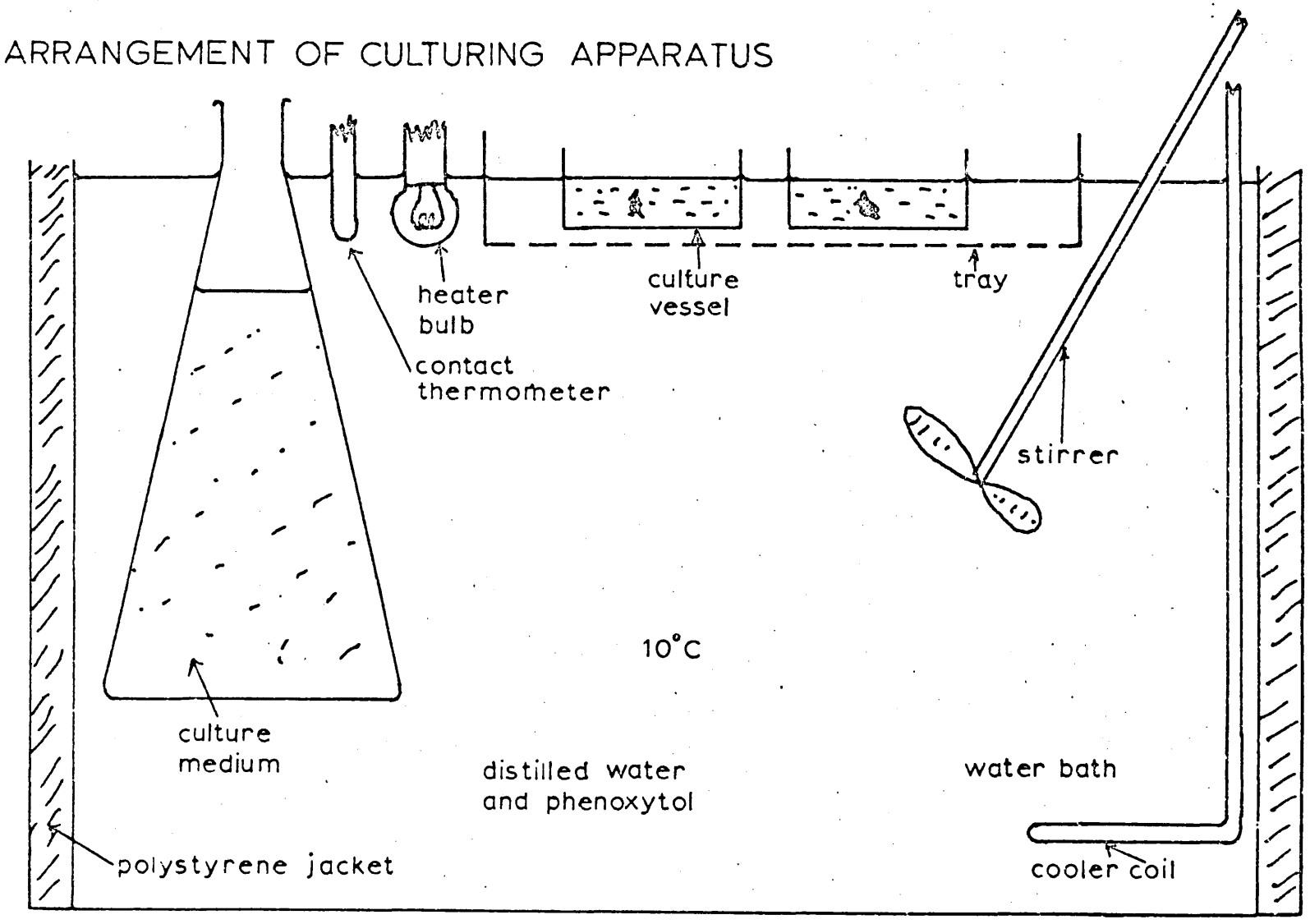

ARRANGEMENT OF CULTURING APPARATUS
heater bulb
contact thermometer
culture vessel
tray
stirrer
10°C
culture medium
distilled water and phenoxytol
water bath
polystyrene jacket
cooler coil

Fig. 4.4.1(a).

was filtered reservoir water taken freshly from the Q.M. It was filtered through Whatman GFC filter papers to remove algae and detritus, and kept in large (2L) conical flasks at 10°C. Reservoir water was collected twice weekly in 20L polythene containers.

Animals were fed from a culture of Oocystis solitaria (Withr.) obtained from the M.W.B. which had been isolated from reservoir populations and had been maintained in bottle cultures since 1967. Oocystis cultures were maintained in the exponential growth phase by subculturing and cultures showing a tendency to become sessile were discarded. Cell numbers were estimated by taking one ml subsamples, diluting to 100 ml and counting further one ml subsamples, in a haemocytometer. Cell concentrations were maintained at approximately 2.5×10^4 cells/ml in the animal cultures.

4.4.2. Measurement of animals.

Animals were measured daily and records were kept by means of sketches and notes of other relevant features of their development.

Several different measurements of each animal were recorded and these correspond with measurements made by ANDERSON (1932). The physical dimensions measured are presented in figure 4.4.2(a). For these measurements animals were gently transferred to a glass slide in a drop of water and the water was reduced until the animal was restricted by the boundary of the water drop. Measurement took less than a minute and animals were then returned to their culture dish. This handling of animals proved to be inexpensive in terms of animal deaths although it placed an obvious strain upon them.

Reproducibility of measurements was examined by remeasuring the same living animal. Three dimensions: length, width and body length were measured ten times

DIMENSIONS OF DAPHNIA RECORDED

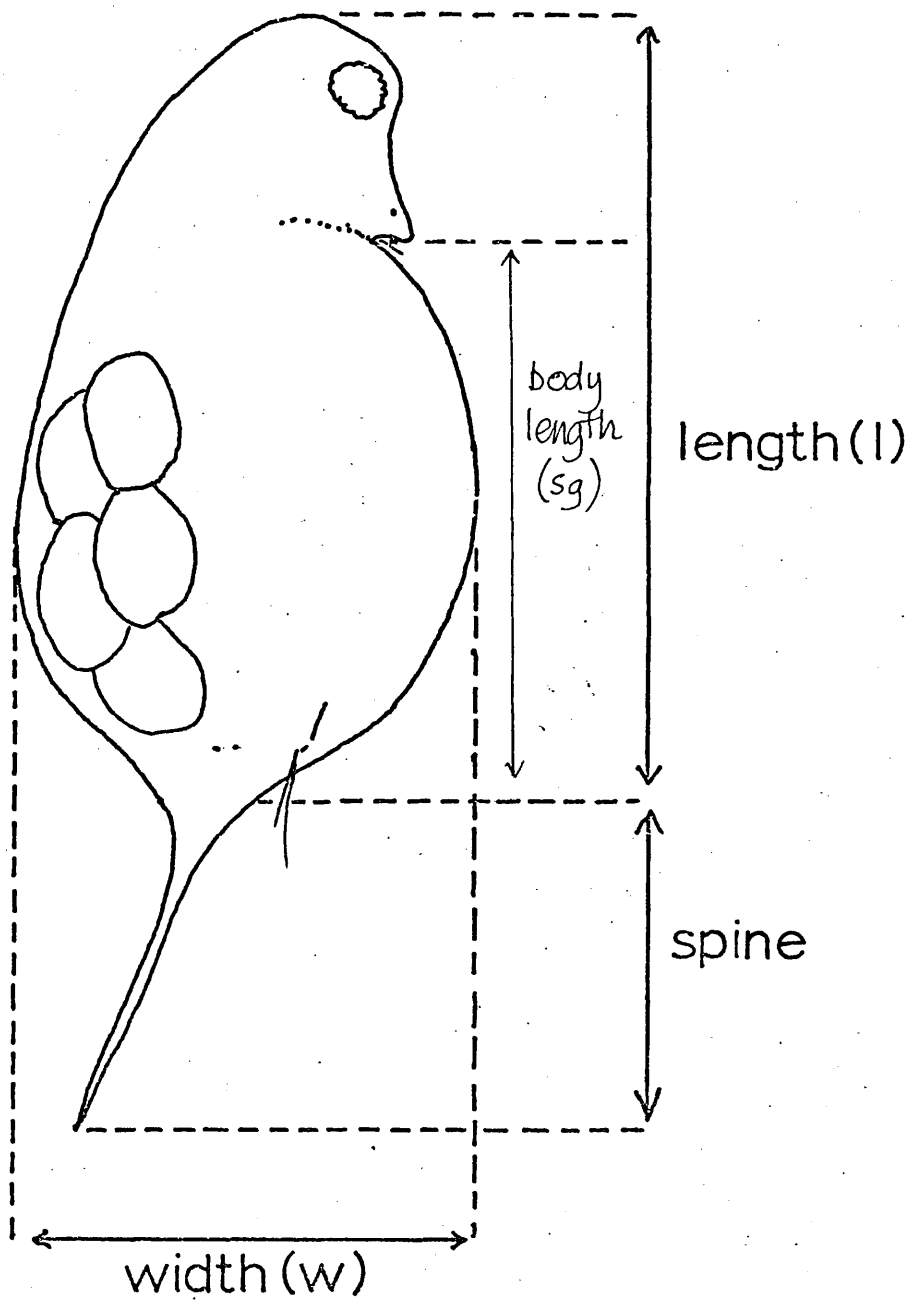


fig. 4.4.2.(a)

using the normal Watson binocular microscope with micrometer eyepiece. Results are presented in table

Table 4.2.4(a)

	length (mm)	width (mm)	body length (mm)
N=10 mean	2.241	1.415	1.880
S.D.	0.011	0.013	0.012
S.E.	0.16%	0.28%	0.17%

Stages of growth were also recognised. At each daily measurement, or more frequently if the animal was used for respiration experiments, the presence or absence of a carapace was noted and this indicated whether the animal had changed instar. By this means a map of instar-time development was created.

Adult daphnids were recognised by the first development of an ovary which marked the onset of sexual maturity. An attempt was made to quantify this for the construction of energy budgets and life tables. The production of offspring by the Cladocera may be conveniently divided into two stages which occur in adjacent instars. The first stage is seen as ovary development and the second stage as the shedding of the eggs into the brood pouch and their subsequent development until release. CREMER AND DUNCAN (1969) describe ovary growth in semi- quantitative terms - small, large etc., but in this study the length of the ovary was measured and used as an index of its growth and in later stages the numbers of developing eggs were ascertained.

Stages of egg development in the brood pouch were also recognised and these were recorded together with numbers of young and length measurements. The stages of egg development recognised corresponded with those observed by GREEN (1954) for D.magna and those observed by

CUMMINS ET AL (1969) for *Leptodora kindtii*. This information was used to illuminate length measurements. The stages of egg development recognised were:

1. Undifferentiated eggs
2. Differentiated eggs
3. Antennae forming
4. Two red eyes present
5. One black eye present
6. Heart beating, limbs moving

During these experiments some of the animals developed ephippia (resting eggs). Measurements were made of ephippial development as far as possible and postephippial animals were distinguished.

Limited observations of the nutritional state of the animals were made. Food concentrations were monitored and the state of the guts (full, empty, colour) were recorded with the presence of food reserves such as oil droplets in the body tissues.

Other observations such as heart beat rate and spine damage were recorded if they were thought to be of significance.

Measurements and observations were made at least once a day, normally early in the morning, and more frequently if the animals were in the process of moulting. Other observations were made at the times when animals were used for respiration work. Overall the culturing experiments lasted 108 days until the death of the last animal.

4.4.3. LABORATORY RESPIRATION

The Cartesian diver micro-respirometer was used to measure respiration rates of D. hyalina in the laboratory. These were measured at 10°C and the results used for the construction of an energy budget. This work was carried out jointly with Dr. A. Duncan and followed a similar study from the same laboratory by A. Duncan and G. Cremer at 20°C.

The Cartesian diver technique, origi nally described by LINDSTRØM-LANG (1937, 1943) and HOLTER (1943), was modified by ZEUTHEN (1943, 1950) who provides a basic description of 'stoppered divers' which were used in this study. The method used is that of KLEKOWSKI (1968, 1971).

It is not proposed to give a detailed discussion of the principles and practice of the Cartesian diver here since the subject is adequately covered by LINDERSTRØM-LANG (1943), HOLTER (1943) and in relation to aquatic animals by KLEKOWSKI (1968).

The Cartesian diver respirometer is a constant volume variable pressure system and the stoppered diver encloses a gas bubble which makes it slightly buoyant in its flotation medium (0.1NNaOH). The flotation vessels are fixed in a constant temperature tank (± 0.01°C) and are connected to a manometer filled with Brodie's fluid (UMBREIT ET AL 1949). The manometer was read against a mm scale of 150 cm. The internal pressure of the system is controlled by means of coarse and fine screw adjustments attached to the manometer, changes in pressure in the flo tation medium being transmitted through the fluid filled space between the diver chamber and stopper to the gas bubble inside the diver. Increased pressure decreases the gas volume and the diver sinks and vice versa. This

happens because each diver has a constant volume which maintains neutral bouyancy at an arbitrary level which can be maintained by pressure adjustment of the manometer. The manometer, flotation vessels and temperature bath arrangement are presented diagramatically in figure 4.4.3(a) and the diver construction is shown in figure 4.4.3(b).

The apparatus used was built with eight flotation vessels and maintained in a cool, dimily lit basement. During experimentation, the divers were observed with a microscope modified to 'travel' vertically which had a built-in low intensity light source.

Divers of various sizes were constructed from thin walled 'Pyrex' glass capillary tubing with a specific gravity of 2.55 and these were washed in concentrated sulphuric acid and rinsed in distilled water before use. Braking and loading pipettes were constructed from similar capillary tubing. After use in experiments, divers were again washed in sulphuric acid and rinsed carefully with distilled water and stored in cotton wool in small Petri dishes.

Before experiments were performed the flotation medium was air saturated by bubbling washed air through the medium.

The experimental animals were transferred to the loading dish which contained filtered reservoir water at 10°C. The diver was also transferred to this dish, filled with this water and then the animal was 'persuaded' to enter the diver. Difficulty was experienced with small individuals which tended to adhere to the diver walls and these were gently pushed in with a loading pipette. The diver (with animal) was then transferred to O.I.N NaOH solution which was introduced into the lower neck of the diver and the stopper was then inserted.

SCHEMATIC DRAWING OF CARTESIAN DIVER ASSEMBLY

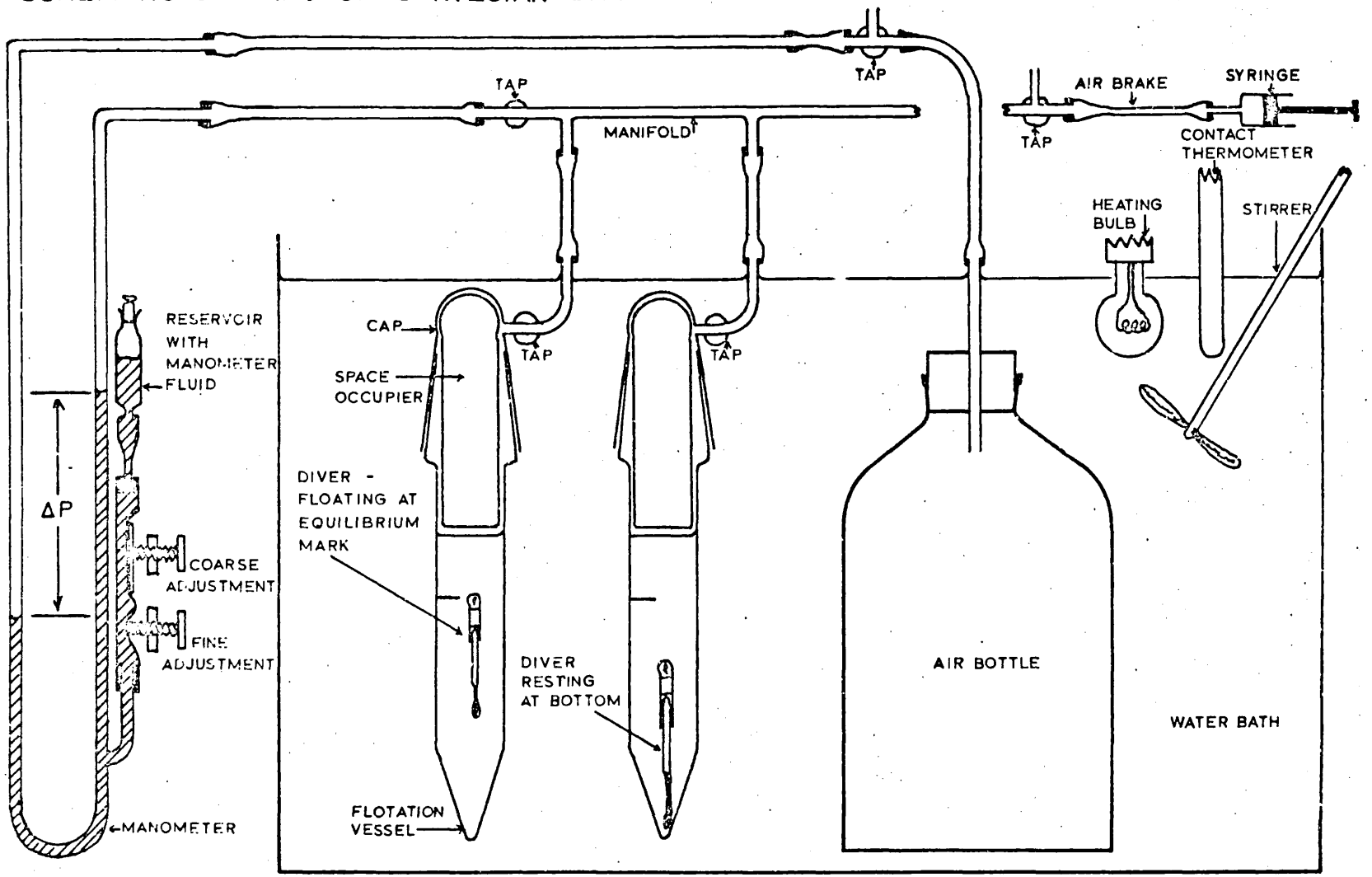


Fig. 4.4.3(a).

LOADED CARTESIAN DIVER

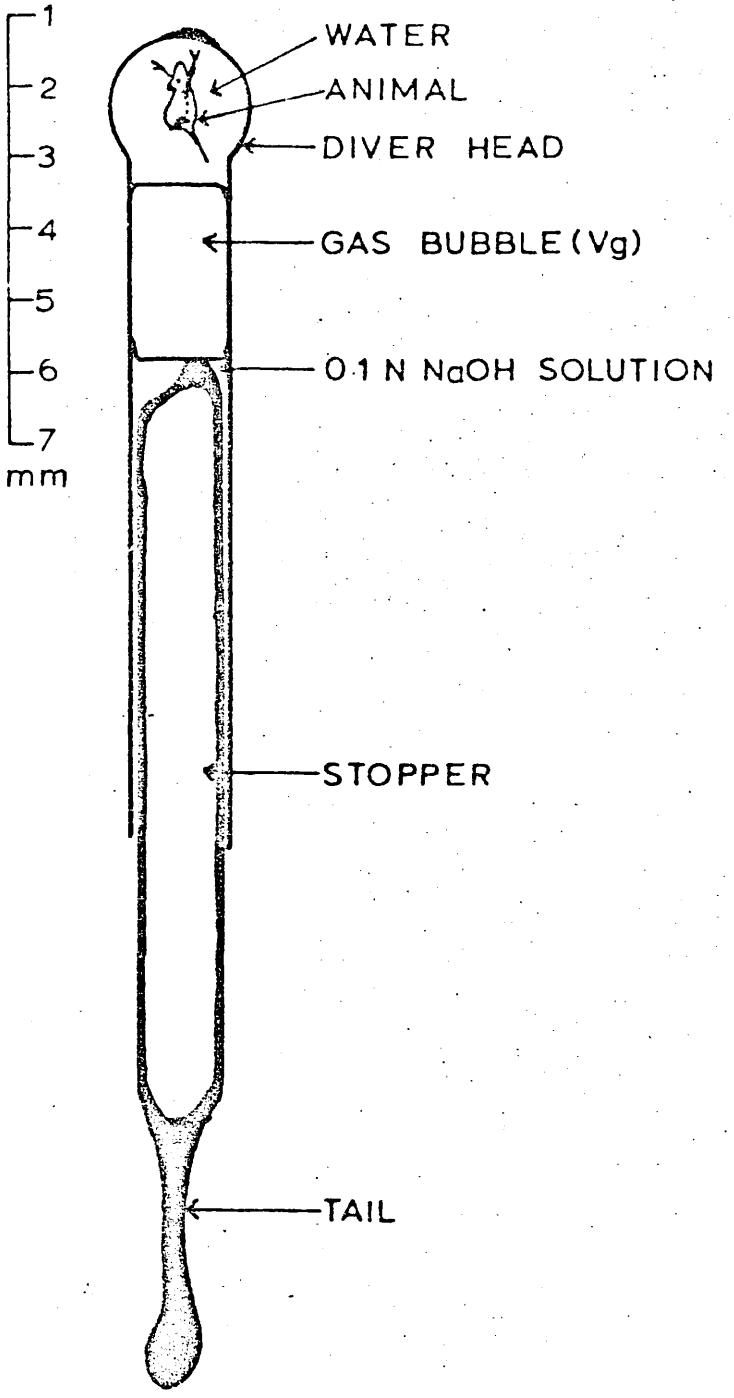


Fig. 4.4.3(b).

The diver was then transferred to the flotation vessel.

Manometer readings were commenced immediately and recorded at 15-20 minute intervals until a 'straight line' respiration rate was obtained and the manometer was read to 0.5mm of Brodie's fluid. A specimen graph of the rate of change of equilibrium pressure is shown in fig. 4.4.3(c) and the rate of oxygen consumption was calculated using the procedure outlined by KLEKOWSKI (1968)

After experimentation, divers were removed, dismantled and the animals returned to their culture vessels.

DIVER EXPERIMENT

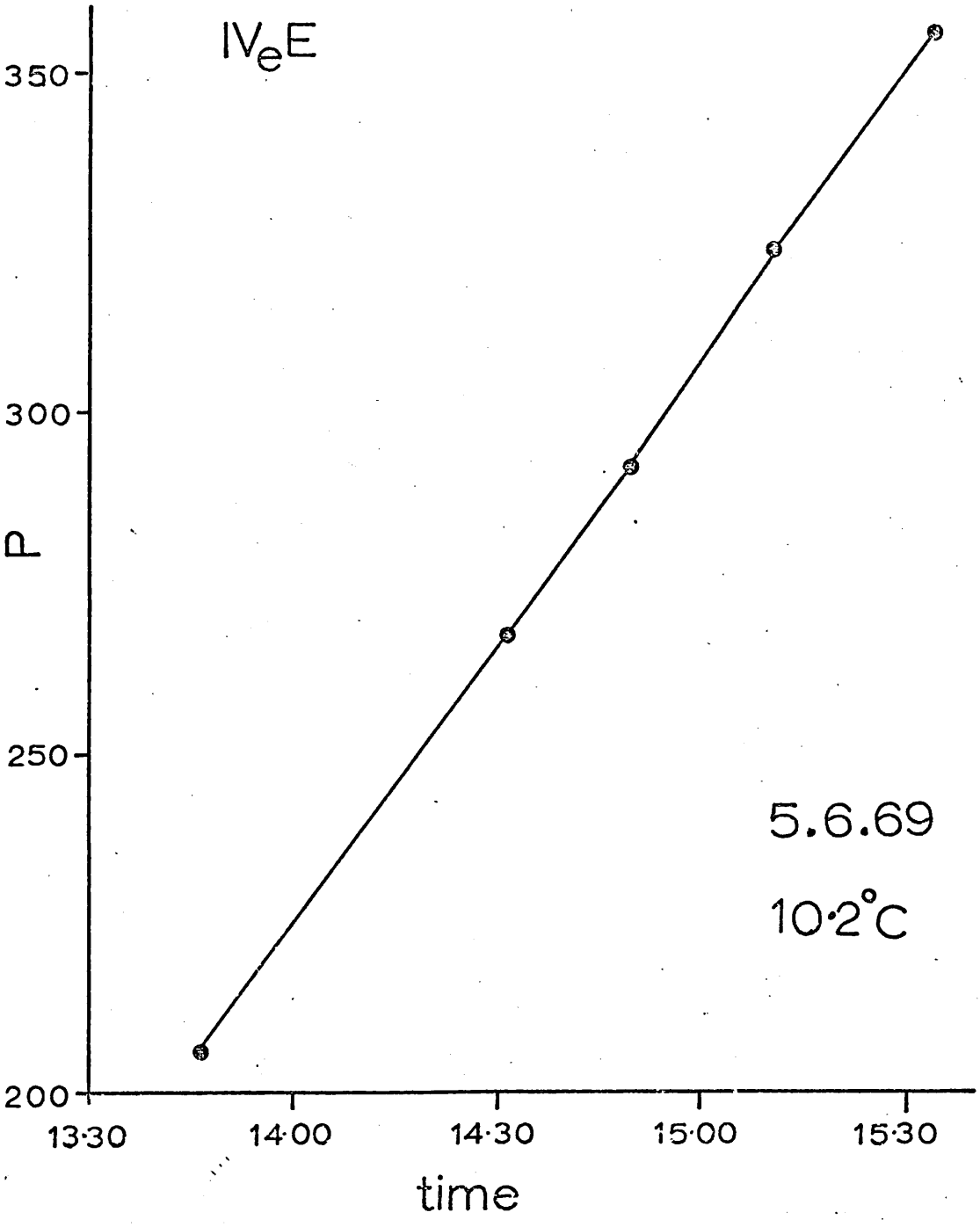


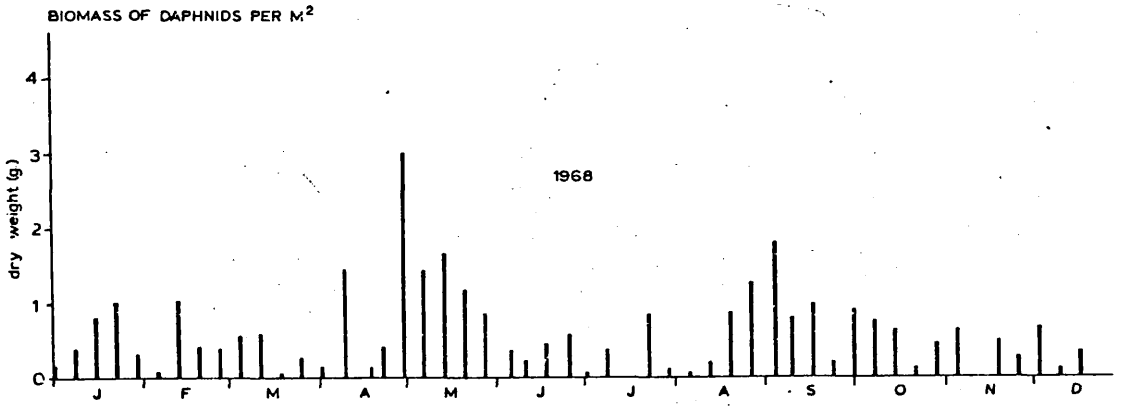
fig. 4.4.3(c)

5.1. FIELD RESULTS.

All results presented in this section are calculated from vertical net haul samples using Patalas samples only to amplify results or when no vertical net hauls were taken. Samples have been converted to the best corrected estimate using the relationship found in section 4.1.5. All figures where relevant are presented on a scale for an area under a metre ^{2} surface of the reservoirs.

5.1.1. STANDING CROP (WEIGHT)

The standing crop measured directly of daphnids in Q.M. for the period of this study can be seen in figure 5.1.1.(a). The sequence of the seasonal cycle is normal for a temperate lake with standing crop maxima occuring in the spring (April/May) and autumn (August/September) for the years of the study. This sequence is widely recognised (reviewed in HUTCHINSON 1967) and similar to previous studies of these reservoirs (CREMER AND DUNCAN 1969, ANGOLD 1968, LANGHELT 1968). It can also be seen that the winter levels are quite high (normally 380 to 1140mg/m^2) which are approximately the same in both years of the study. The spring maxima, however, are considerably different in 1968 and 1969. The 1968 spring maximum reached a level of about 3040mg/m^2 and in 1969 this reached about 4560mg/m^2 this will be discussed more fully in a later section (section 5.1.4.). The autumn maximum in 1968 reached a level of about 1900mg/m^2 which probably compares with the late autumn value of about 1520mg/m^2 in 1967. In both 1968 and 1969 the spring maximum is preceded by very low standing crop in mid April and this in turn is preceded by a smaller peak in early April. The significance of this event will be discussed in the


BIOMASS OF DAPHNIDS PER M²
dry weight (g)
0
1
2
3
4
1968
J
F
M
A
M
J
J
A
S
O
N
D

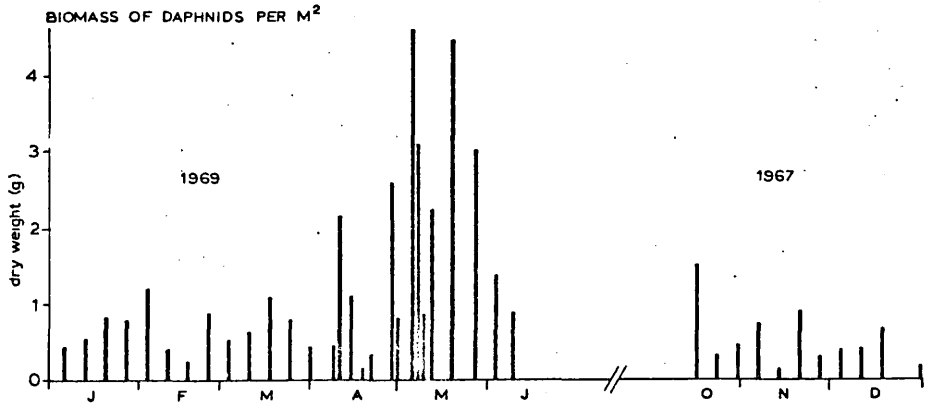
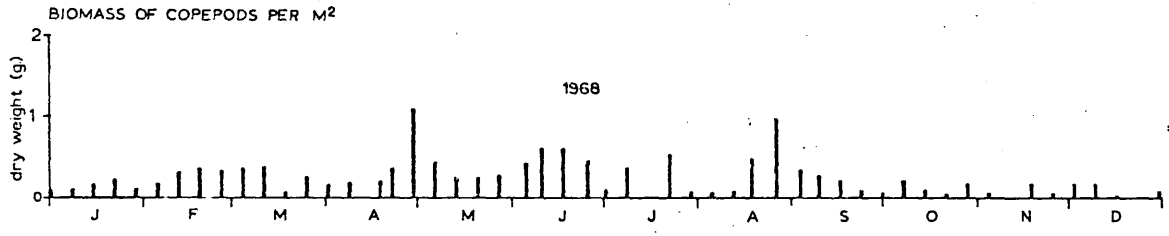

BIOMASS OF DAPHNIDS PER M²
dry weight (g)
0
1
2
3
4
1969
1967
J
F
M
A
M
J
O
N
D

Fig. 5.1.1(a).

section relating to population dynamics (5.1.3). During the whole course of the year the standing crop fluctuates in a fairly regular fashion a peak being followed by a low followed by a peak which in the winter months at least probably represents regular changes in the population structure (section 5.1.3).

Figure 5.1.1(b) shows the standing crop of copepods (Cyclops sp and Diaptomus sp) throughout the year. The technique used to separate the Copepoda from the Cladocera does not separate cyclopoid from calanoid copepods and the numerical analysis must be used to distinguish specific accession. The 1968 data show that the standing crop reaches a peak in late April, followed by a high summer level and a subsequent peak in late August. The spring peak is also seen in 1969 but is a much higher level (~2660mg/m^2) which correlates with the higher daphnid standing crop in that year. The raw data for the biomass figures are presented in Appendix 5.1.1.

Figure 5.1.1(c) shows the mean individual dry weight for Cladocera in field samples calculated from the dry weight per V.N.H. and the numbers per V.N.H. (Section 5.1.2.) and this provides a crude idea of the population structure at different periods of the year. When thefigure is high it indicates that the population is composed mainly of large old individuals and when low it is mainly small (young) individuals. It can be seen from the figure that during the winter the population is composed of large old females whereas during the spring peak (late April and early May) the population is of small animals. Towards the end of the spring outburst the age structure changes and there are fewer but larger animals in the population (see fig.5.1.2(a) showing percentage age structure of populations).


BIOMASS OF COPEPODS PER M²
dry weight (g)
2
1
0
1968
J
F
M
A
M
J
J
A
S
O
N
D

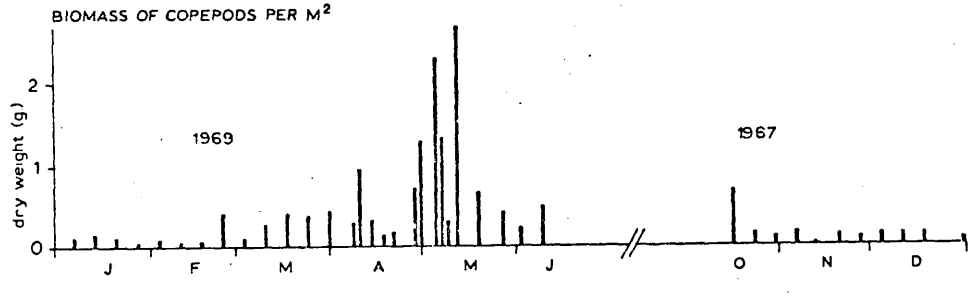

BIOMASS OF COPEPODS PER M²
dry weight (g)
2
1
0
1969
1967
J
F
M
A
M
J
O
N
D

Fig. 5.1.1(b).

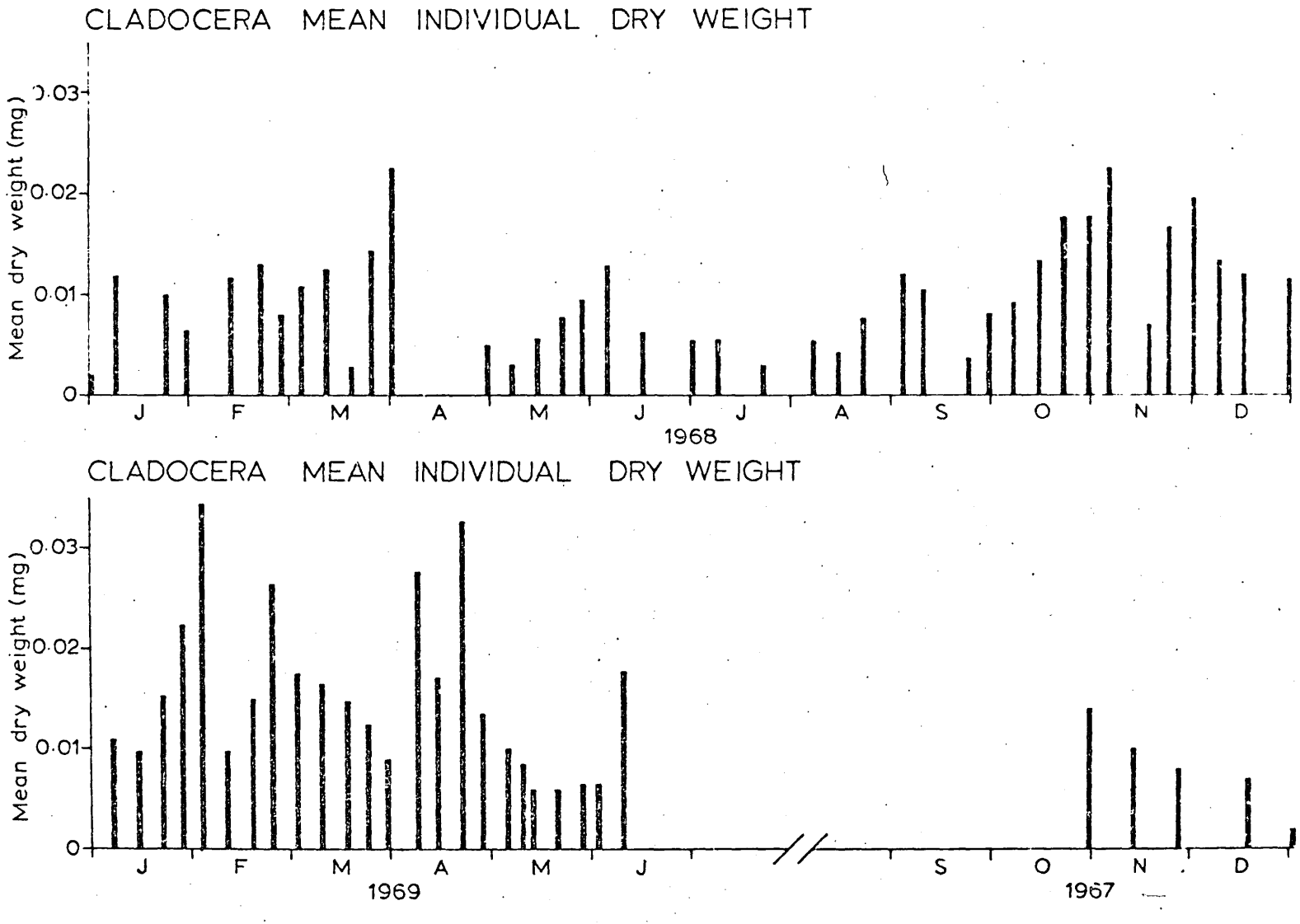

CLADOCERA MEAN INDIVIDUAL DRY WEIGHT
Mean dry weight (mg)
0·03
0·02
0·01
0
J F M A M J J A S O N D
1968
CLADOCERA MEAN INDIVIDUAL DRY WEIGHT
Mean dry weight (mg)
0·03
0·02
0·01
0
J F M A M J
1969
S O N D
1967

Fig. 5.1.1(c).

Figure 5.1.1(d) shows a similar approach to the copepod populations and the same pattern in each year can be seen.

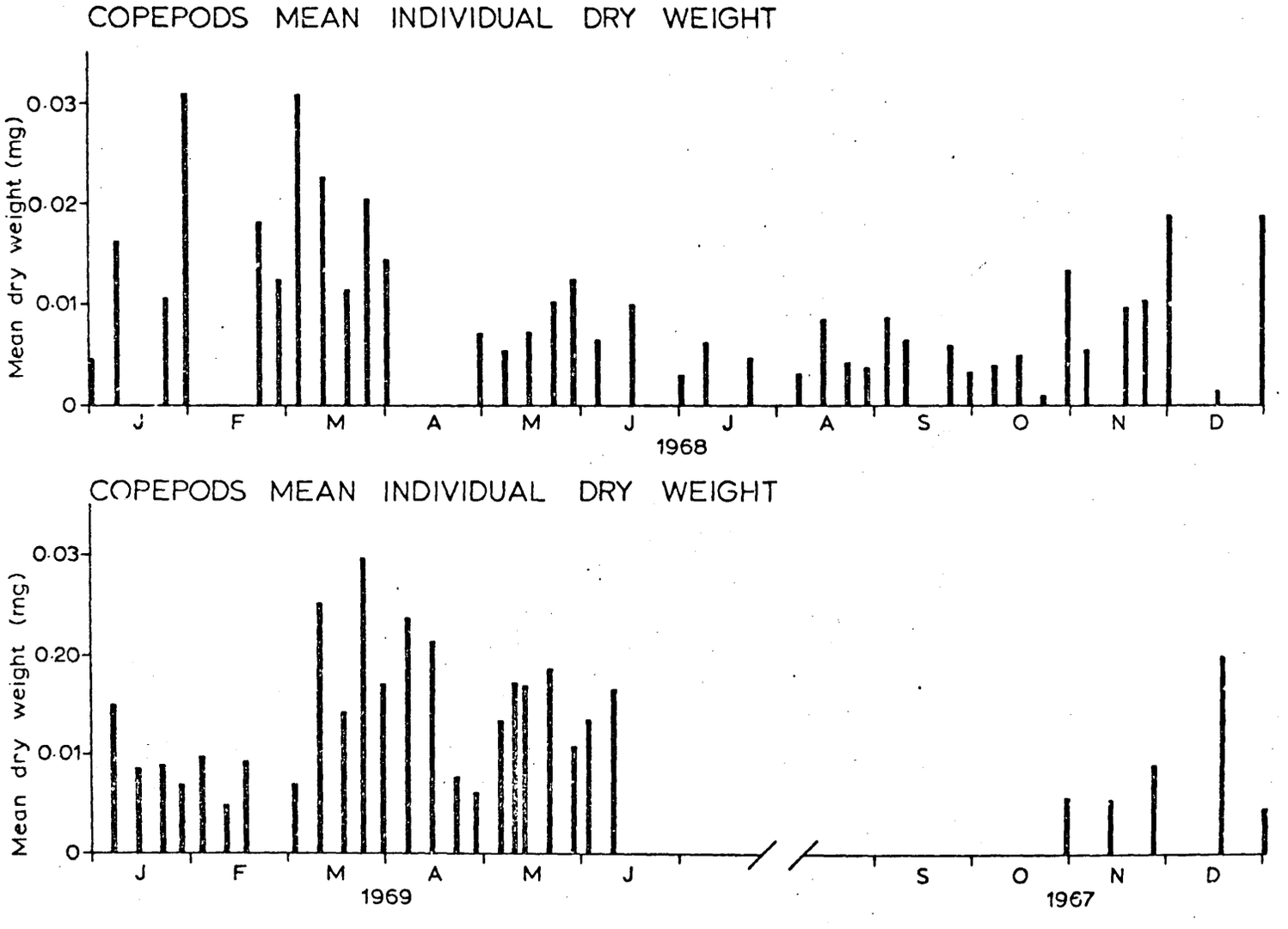
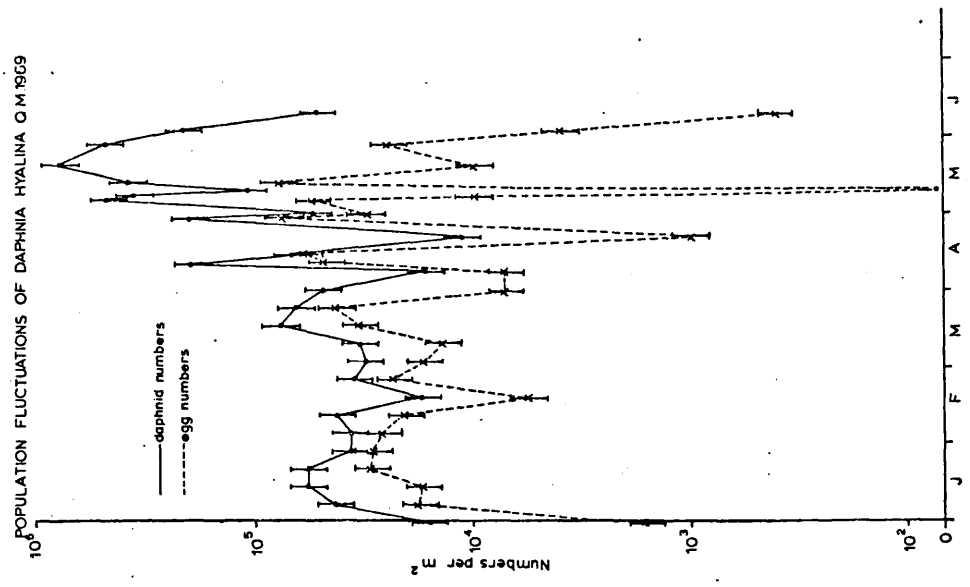

COPEPODS MEAN INDIVIDUAL DRY WEIGHT
Mean dry weight (mg)
0·03
0·02
0·01
0
J F M A M J J A S O N D
1968
COPEPODS MEAN INDIVIDUAL DRY WEIGHT
Mean dry weight (mg)
0·03
0·20
0·01
0
J F M A M J
1969
S O N D
1967

Fig. 5.1.1(d).

5.1.2. STANDING CROP (NUMBERS)

Population sizes are normally presented as numbers e.g. EDMONDSON (1955), HALL (1964), WRIGHT (1965) and standing crops in terms of weight calculated from these and a knowledge of the population structure. Figure 5.1.2(a)(i) and 5.1.2(a)(ii) shows the population size of D. hyalina throughout the period of this study. The numbers are shown on a logarithmic scale and egg numbers are also shown. The population size of D. hyalina varies throughout the course of the year in 1968, the spring population maximum occurring in late April (601350 /m^2) followed by a second maximum in July (32580 /m^2) and the autumn maximum in early September (147744 /m^2). The winter levels are fairly high compared with the low numbers immediately preceding the spring period of population increase. The same pattern can be seen in 1969 except that the maximum spring population size is higher (76710 /m^2). In 1969 more samples were taken preceding the spring peak and an earlier prepeak maximum can be seen in early April (190000/m^2). This situation can be seen in 1968 if the Patalas data are examined (section 5.1.8) where samples were taken during April, and this appears to be a normal pattern associated with egg production before the spring maximum.

Egg numbers can also be seen in figure 5.1.2(a) and the obvious feature is that the winter levels are consistently high (7600 – 456000/m^2) whereas the summer levels are very low. The 1969 data show high egg numbers occurring during March and April before the spring maximum. Again in 1969 the winter egg levels are consistently high. These egg numbers are more understandable when the internal structure of the population is considered in conjunction with the egg numbers.



(a)ii

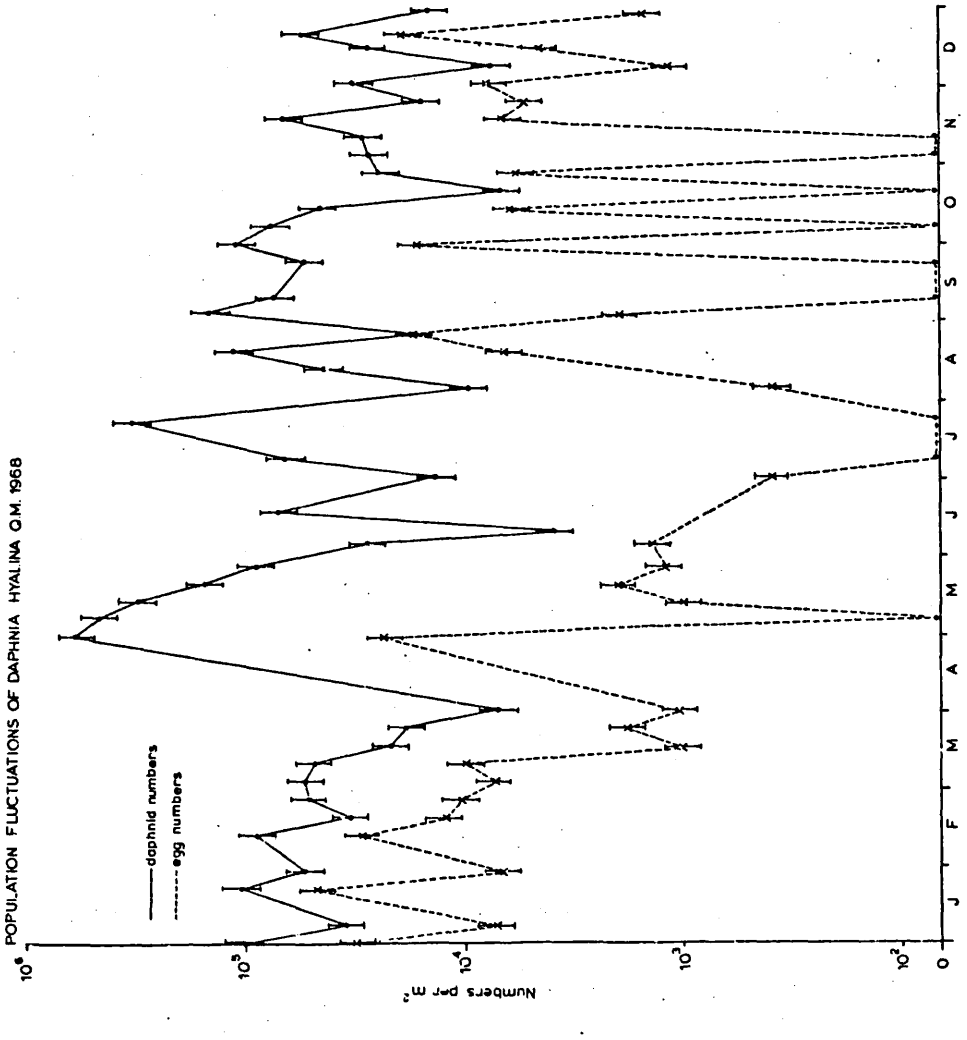
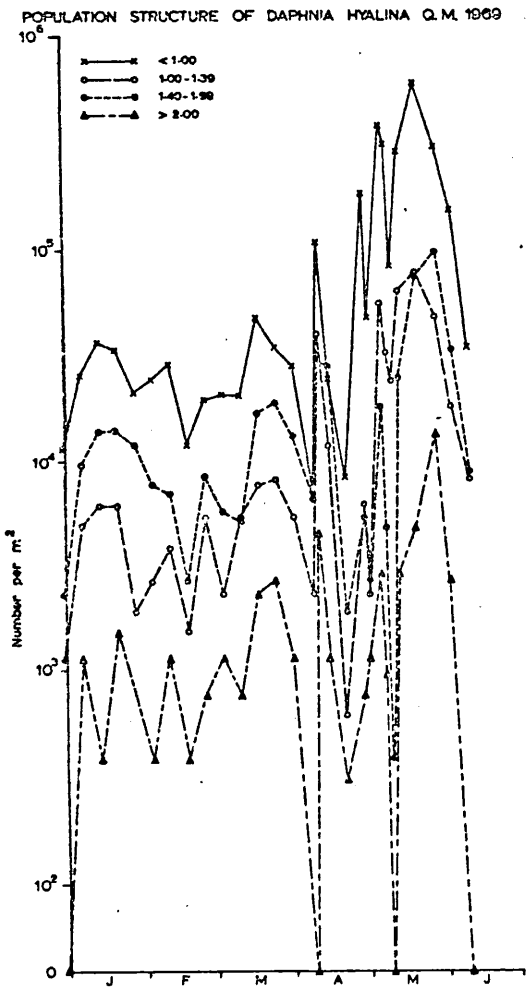


Fig. 5.1.2(a)i.

Figure 5.1.2(b) shows the size structure of the D.hyalina population throughout the course of the study. Numbers are plotted on a logarithmic scale for convenience and the overall pattern is the same as the total numbers seen in figure 5.1.2(a). Except during October and November 1968, the smallest size class (<1.00mm length) exceeds all the other size classes in absolute numbers for the whole year and with rare exceptions the largest size class (>2.00mm) is always lower in numbers than the other size classes. The size class 1.40 - 1.99mm follows a very similar pattern to the 1.00 - 1.39mm size class but often exceeds the latter which is a function of the relative duration of these size classes as a size group.

The relative proportions of sexually mature to immature animals can be seen more clearly in figure 5.1.2(c)$^{(i)\&(ii)}_{A}$ where mature animals (>1.40mm length) are compared with sexually immature animals (<1.40mm length) The situation is the same in each year of the study. Late winter and early spring populations have a high percentage of mature animals which reach a maximum of 60-80% during early April and precede the spring population maximum, and correspomds with the minor premaximum peak that can be seen in fig. 5.1.1.(a). During the spring, summer and autumn peaks the proportion of older, larger animals decreases and slowly increases again as the population numbers decline. The major population peaks, which coincide with the high biomass figures, are composed largely of small animals.

The mean maximal brood size (eggs per female with eggs) can be seen in figure 5.1.2(d)$_{(i)\&(ii)}$. It can be seen that the pre-spring values are high and rise to a maximum before the spring peak and each subsequent peak. The brood size falls throughout the spring peak and reaches a low level throughout the summer months. GREEN (1956) indicates that the egg number per female is related to size of adult and food and


POPULATION STRUCTURE OF DAPHNIA HYALINA Q.M. 1969
< 1·00
1·00 - 1·39
1·40 - 1·99
> 2·00
Number per m²
J
F
M
A
M
J

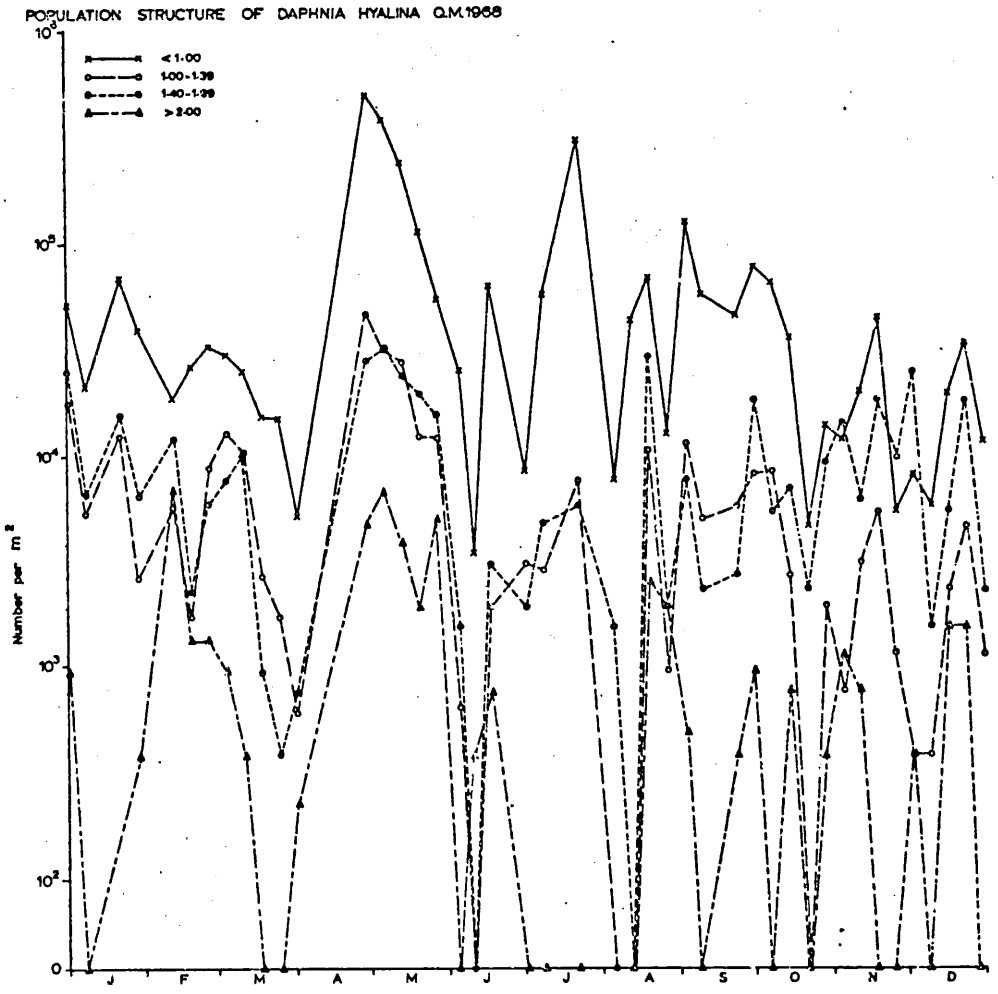

POPULATION STRUCTURE OF DAPHNIA HYALINA Q.M.1968
< 1·00
1·00 - 1·39
1·40 - 1·99
> 2·00
Number per m²
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.2(b)

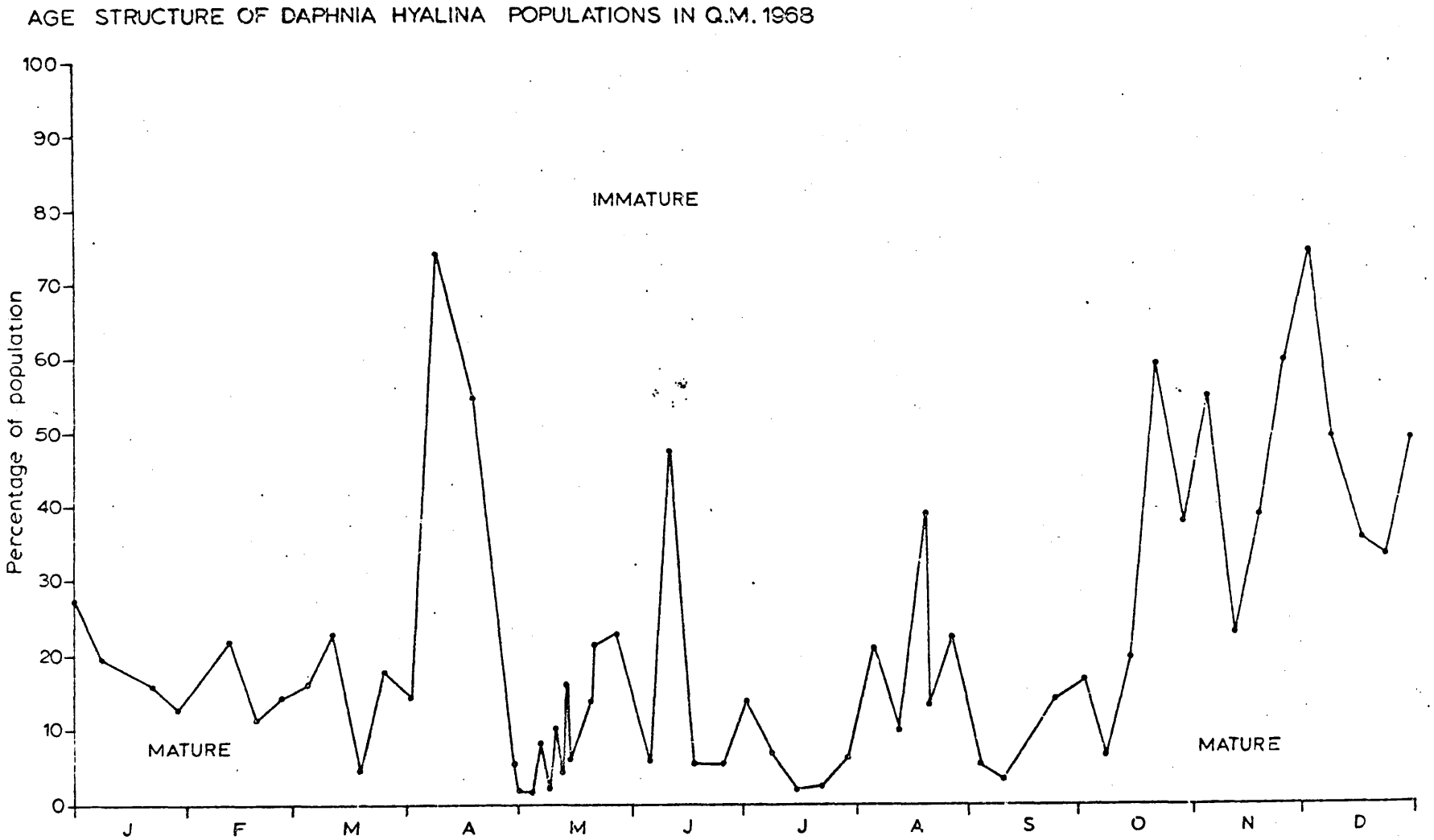

AGE STRUCTURE OF DAPHNIA HYALINA POPULATIONS IN Q.M. 1968
Percentage of population
100
90
80
70
60
50
40
30
20
10
0
IMMATURE
MATURE
MATURE
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.2(c)i.

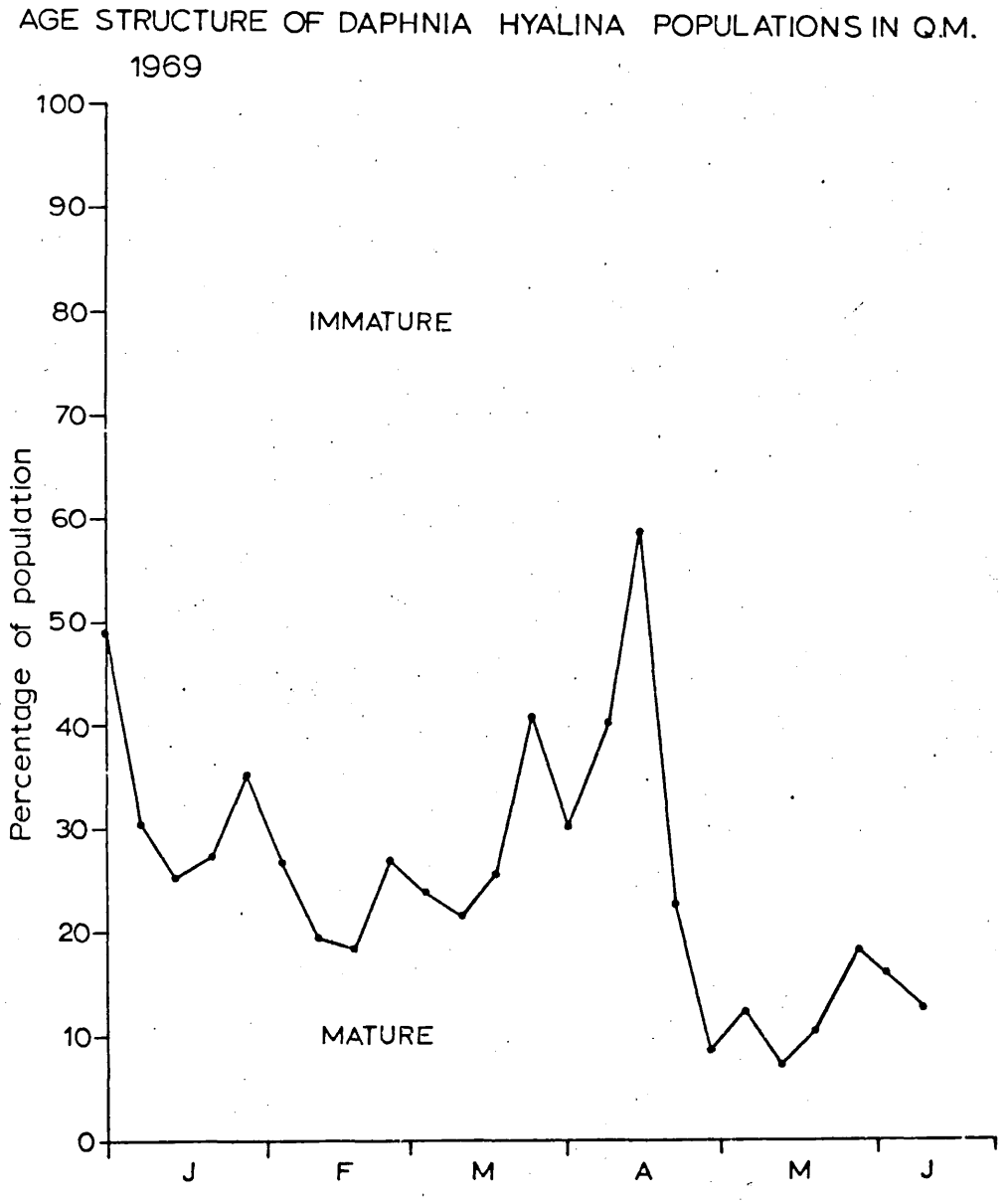

AGE STRUCTURE OF DAPHNIA HYALINA POPULATIONS IN Q.M.
1969
Percentage of population
100
90
80
70
60
50
40
30
20
10
0
IMMATURE
MATURE
J
F
M
A
M
J

Fig. 5.1.2(c)ii.

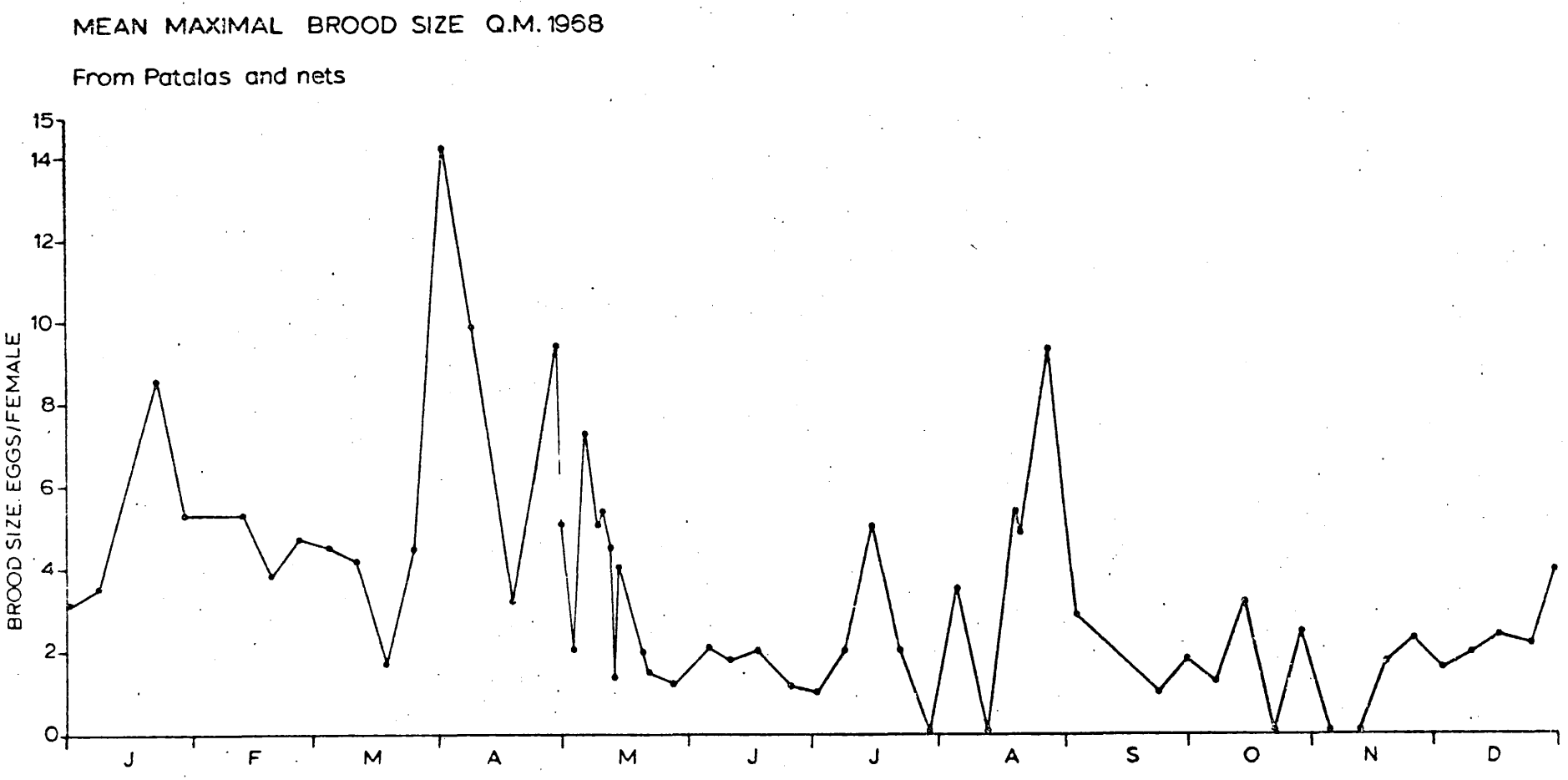

MEAN MAXIMAL BROOD SIZE Q.M. 1968
From Patalas and nets
BROOD SIZE. EGGS/FEMALE
0
2
4
6
8
10
12
14
15
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.2(d)i.

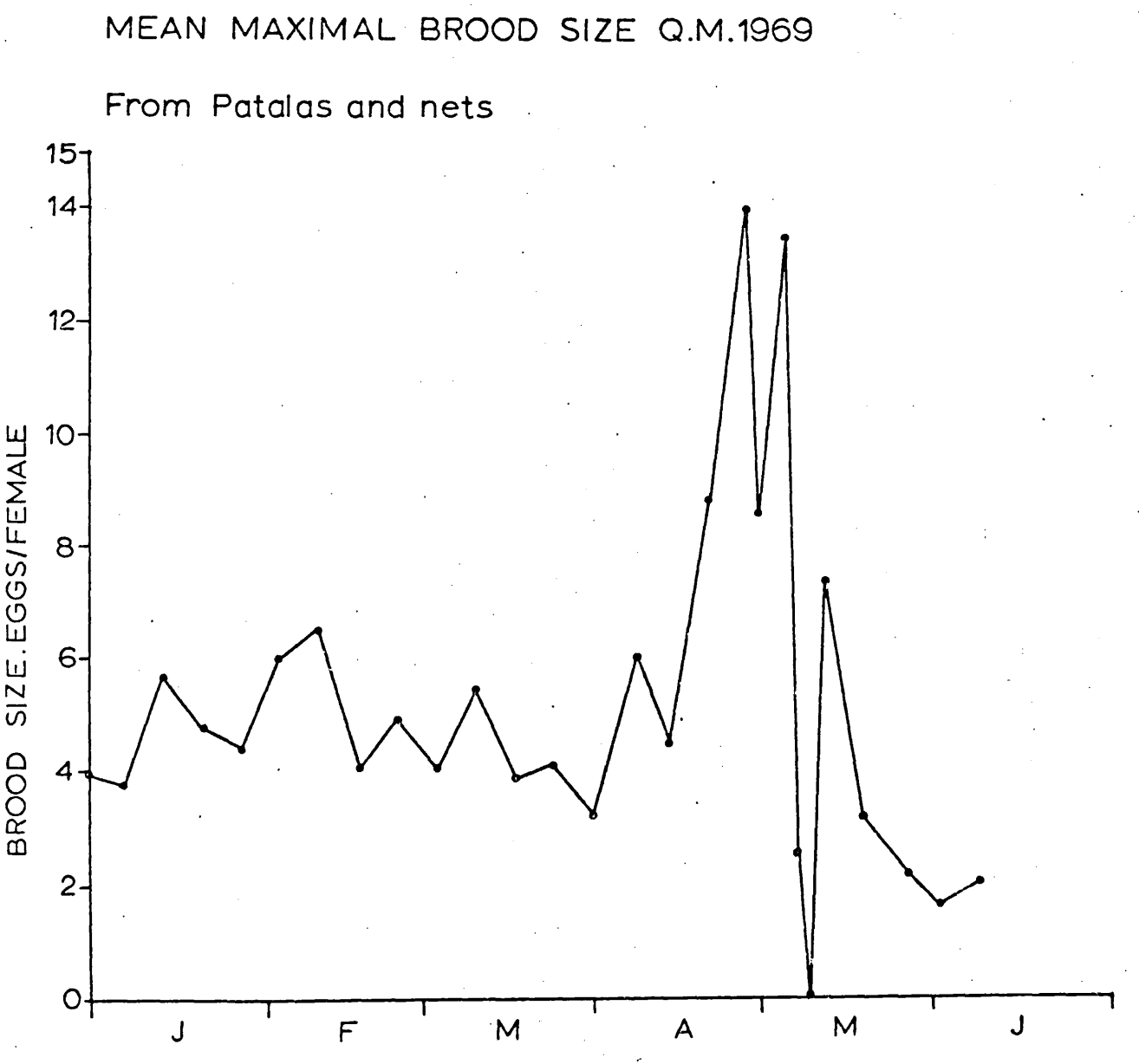

MEAN MAXIMAL BROOD SIZE Q.M.1969
From Patalas and nets
BROOD SIZE. EGGS/FEMALE
15
14
12
10
8
6
4
2
0
J
F
M
A
M
J

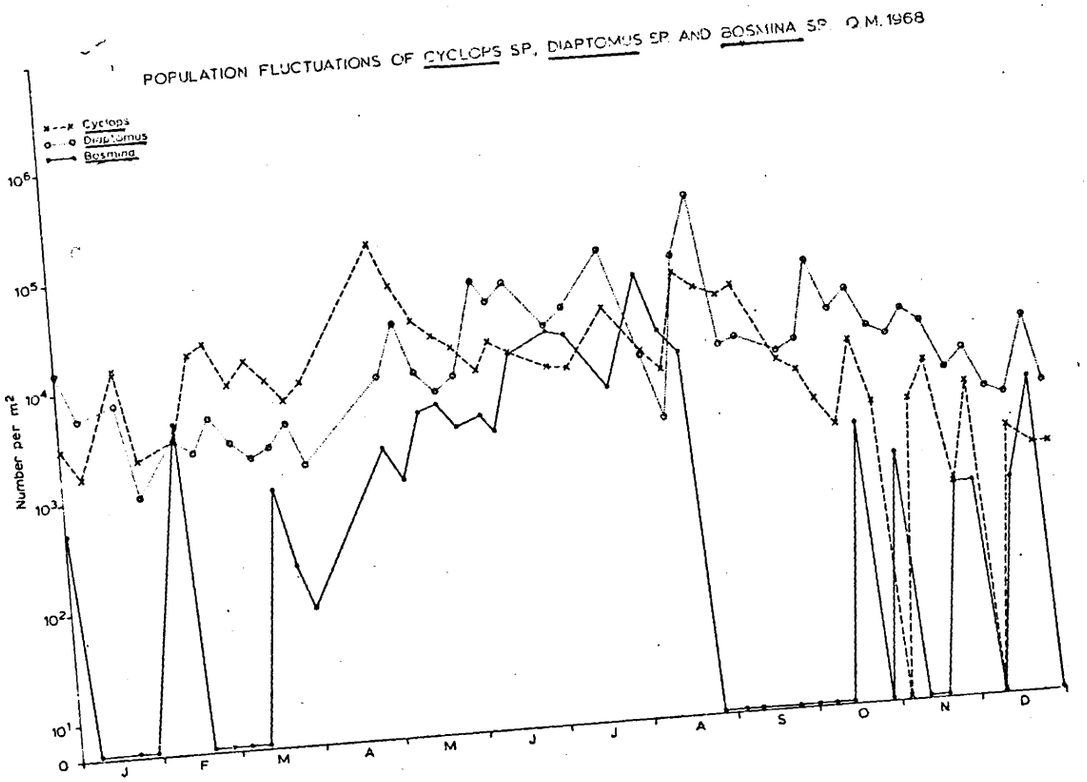
Fig. 5.1.2(d)(ii).

the winter months the mean size is high but food quality is probably poor (STEEL *et al* 1972). As a result of this mean egg numbers are high but not as high as pre-peak conditions when food and size conditions are suitable.

The occurrence and numbers of other species of macro-zooplankton identified can be seen in figure 5.1.2(e). Results are on a logarithmic scale and the total numbers are presented. The cyclopoids have a low population density during the winter and a spring peak in late April which coincides with the daphnid population peak. Summer cyclopoid populations are high and there is a second peak in late summer (late August) and the population falls to the winter level. The pattern was repeated in spring 1969 although the population maximum was higher in this year (1968 - 139.65 x $10^3.m^{-2}$, 1969 - 157.70 x $10^3.m^{-2}$). There is a suggestion from the work of CREMER (pers. comm.) that two species of Cyclops exist in the reservoir and that one is a spring population and the other a late summer population but taxonomic separation of these was not made and no further comment can be offered here.

The diaptomid populations are low in the winter, high throughout the summer and reach a population maximum in late August (229.0 x $10^3.m^2$) then fall to low numbers during the winter. This pattern is essentially the same as described for Diaptomus gracilis in the Q.E.II by KIBBY (1969). The population structure of cyclopoids and diaptomids as juveniles and adults are shown in figures 5.1.2(f) and 5.1.2(g) respectively.

+ Information taken from both net and Patalas samples.


POPULATION FLUCTUATIONS OF CYCLOPS SP, DIAPTOMUS SP AND BOSMINA SP O.M. 1968
Cyclops
Diaptomus
Bosmina
Number per m²
10⁶
10⁵
10⁴
10³
10²
10¹
0
J
F
M
A
M
J
J
A
S
O
N
D

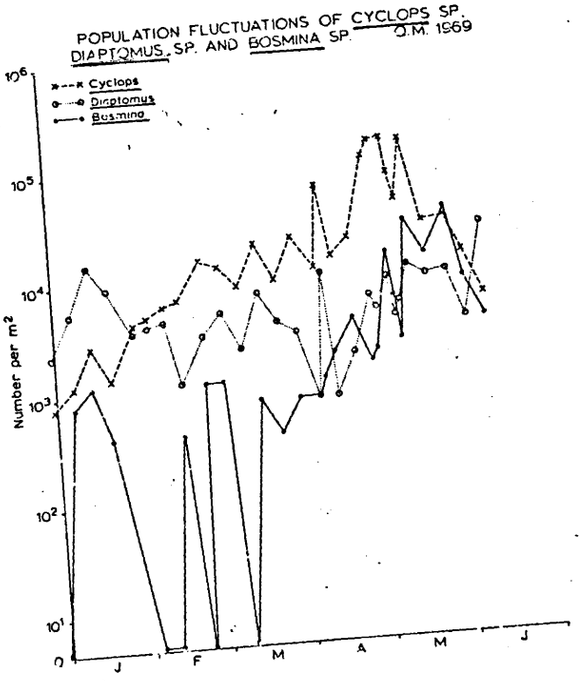
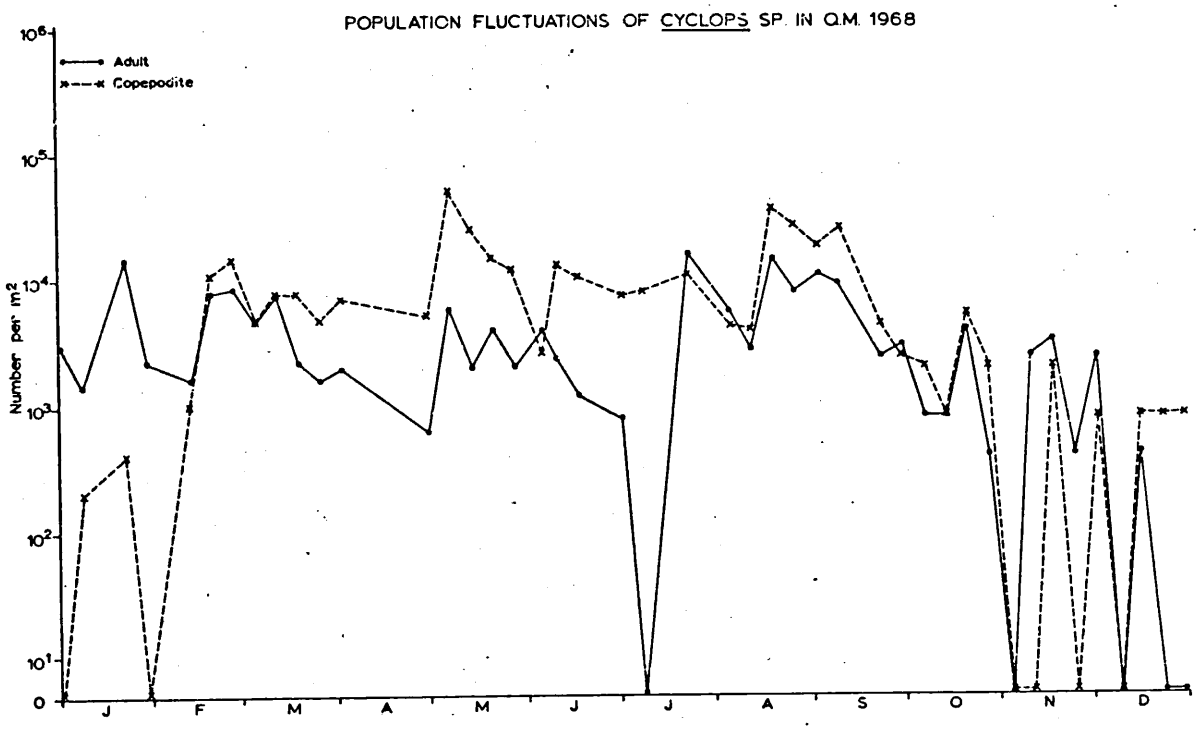

POPULATION FLUCTUATIONS OF CYCLOPS SP. DIAPTOMUS SP. AND BOSMINA SP. O.M. 1969
Cyclops
Diaptomus
Bosmina
Number per m²
10⁶
10⁵
10⁴
10³
10²
10¹
0
J
F
M
A
M
J

Fig. 5.1.2(e).


POPULATION FLUCTUATIONS OF CYCLOPS SP. IN O.M. 1968
Adult
Copepodite
Number per m²
10⁶
10⁵
10⁴
10³
10²
10¹
0
J
F
M
A
M
J
J
A
S
O
N
D

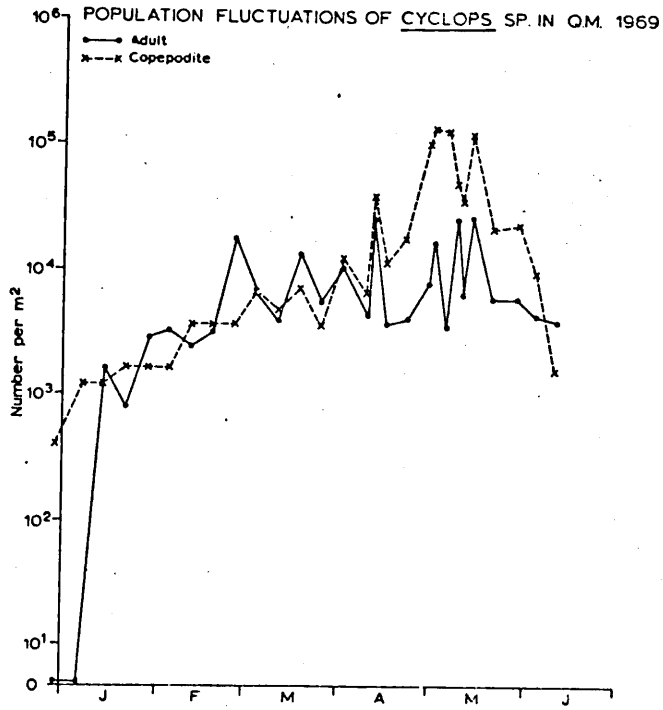
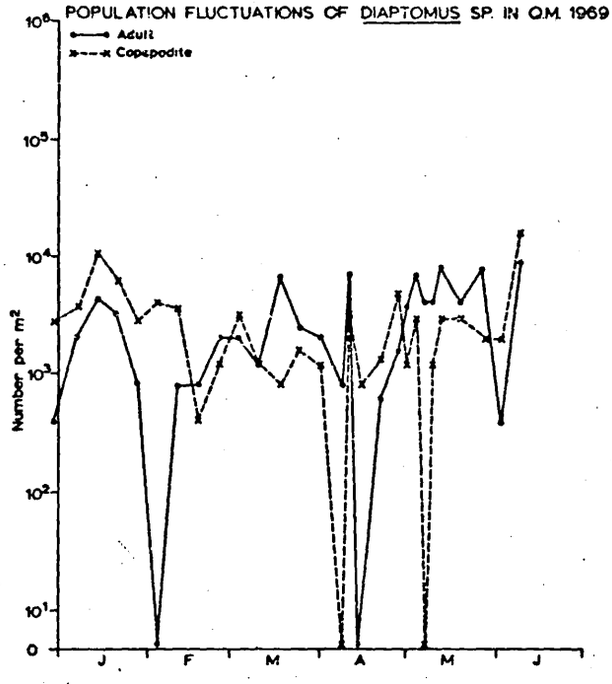

POPULATION FLUCTUATIONS OF CYCLOPS SP. IN O.M. 1969
Adult
Copepodite
Number per m²
10⁶
10⁵
10⁴
10³
10²
10¹
0
J
F
M
A
M
J

Fig. 5.1.2(f).


POPULATION FLUCTUATIONS OF DIAPTOMUS SP. IN O.M. 1969
Adult
Copepodite
Number per m²
J
F
M
A
M
J

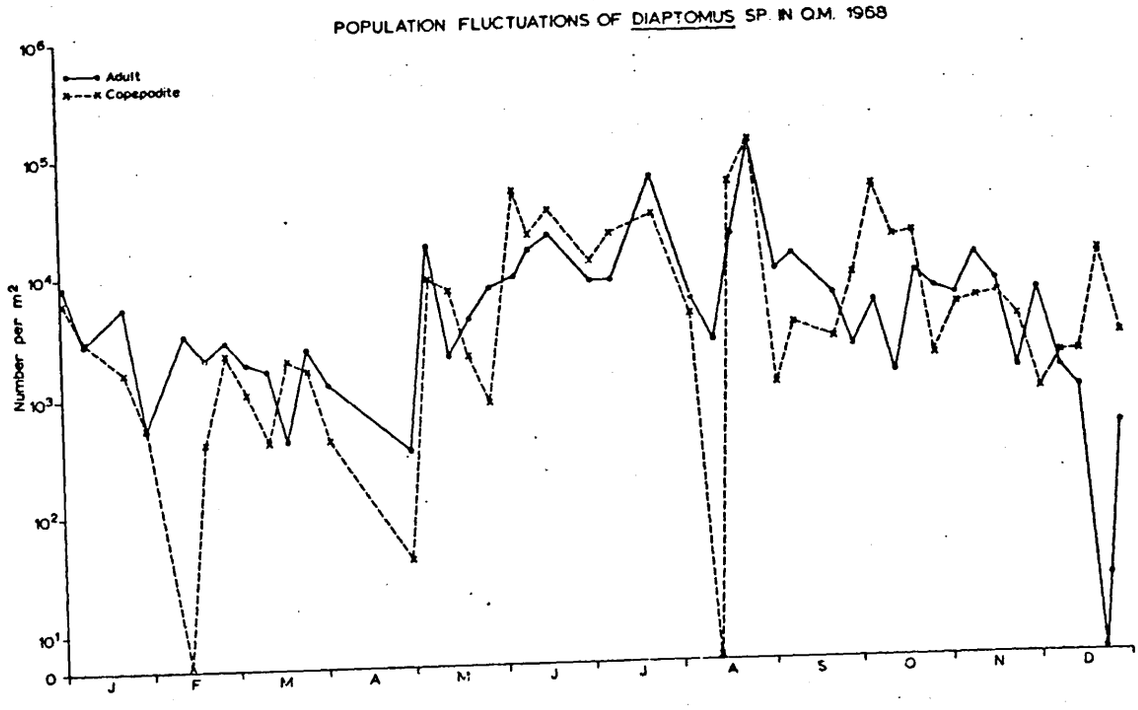

POPULATION FLUCTUATIONS OF DIAPTOMUS SP. IN O.M. 1968
Adult
Copepodite
Number per m²
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.2(g).

Bosmina sp. are largely absent throughout the winter from September to March appearing sporadically in very low numbers. The population begins to increase in March of each year and in 1968 reaches a population maximum in early August ($45.98 \times 10^3.m^{-2}$) although the spring levels were higher in 1969.

The only other species that appeared in significant numbers in the macrozooplankton was Asplanchna sp. - a large carnivorous rotifer. The only records in 1968 were in July when populations reached $60.8 \times 10^3.m^{-2}$ but during spring 1969 the Asplanchna populations reached very high levels and crashed over a period of two months. The maximum values recorded were $564.3 \times 10^3.m^{-2}$ on May 12 when they were by far the most numerically abundant catch in the coarse net. The population rise can be seen in figure 5.1.2(h) for this period. The reasons for the appearance of Asplanchna in the coarse nets are obscure except that they were larger individuals in 1969. It is possible that they were predating on small daphnids; both Bosmina sp. and small D. hyalina were present at this time but no direct evidence of this is available.

Other species found in the macrozooplankton were rare in numbers and occurrence but included:

Eurycercus sp.	(11 occasions)
Cypris sp.	(once)
Leptodora kindtii	(once)
Chironomid larvae	(once).

Of these Eurycercus is a littoral form and like Cypris may have been washed in from the river or the edges of the reservoir. Chironomids are benthic and Leptodora kindtii is a truly planktonic cladoceran carnivore associated with late summer.

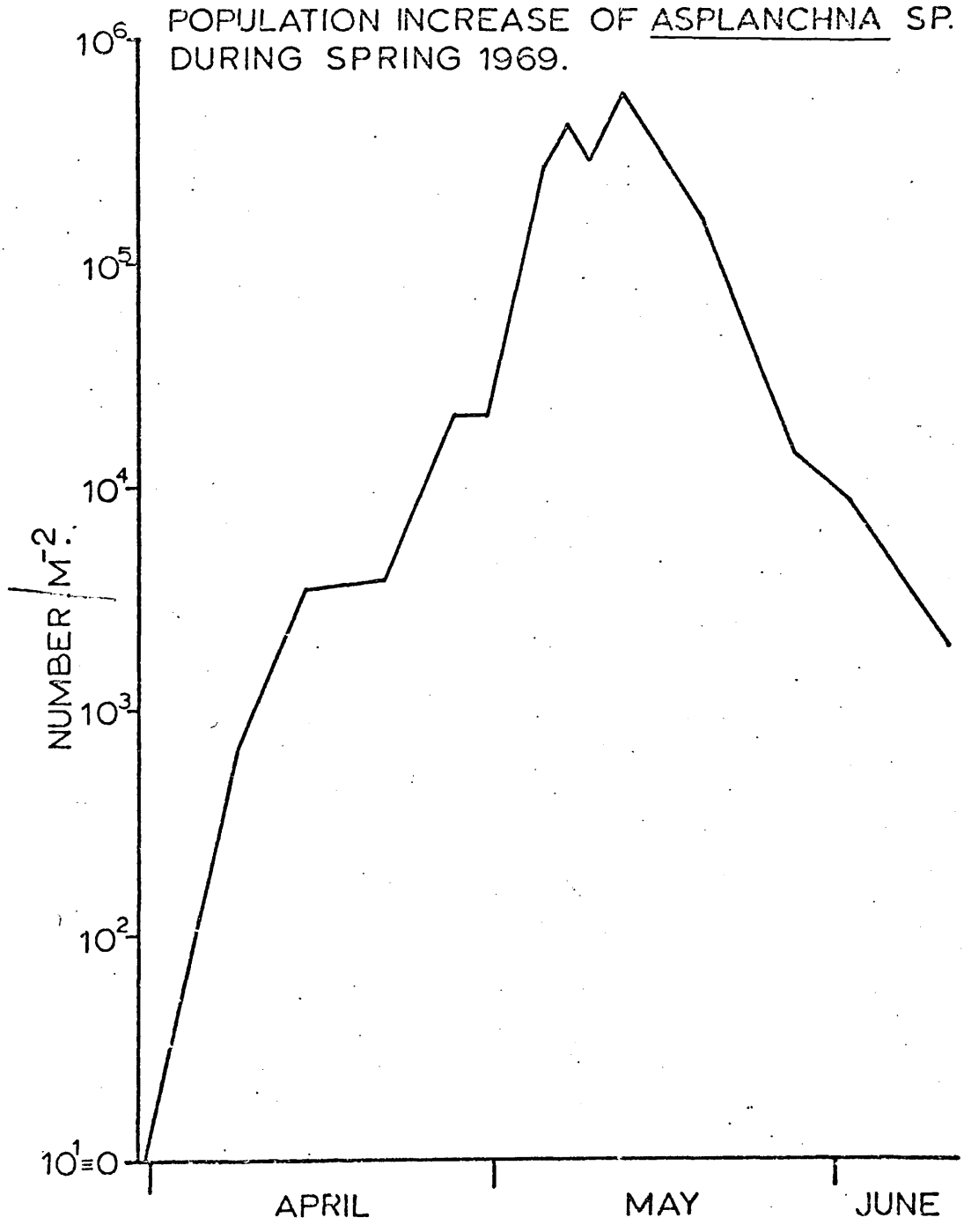

POPULATION INCREASE OF ASPLANCHNA SP.
DURING SPRING 1969.
NUMBER M-2.
10^6
10^5
10^4
10^3
10^2
10^1≡0
APRIL
MAY
JUNE

Fig. 5.1.2(h).

5.1.3. POPULATION CHARACTERISTICS

Population size changes, in terms of numbers and biomass, have been described in section 5.1.2 and 5.1.1. Some characteristics and attributes of the population structure of D. hyalina are examined in this section, especially those that have been used by other workers for analysis of population dynamics of daphnids.

It was seen in figure 5.1.2(a) that the occurrence of a high proportion of adults in the population corresponded with high egg numbers. This occurs during the early months of the year and precedes population maxima. However, the maximum number of eggs per adult (brood size) is not synchronous with highest proportion of adults in the population. Figure 5.1.3(a) shows the mean brood size (the mean number of eggs in adults with eggs) and the number of eggs per adult in the population. (HALL (1964) refers to this as the average brood size). Egg counts of field samples identified eggs and developing embryos and for each embryo recognised, 1.92 eggs were seen. This result is at variance with the result presented by HALL (1964) and is curious rather than of consequence. The figure shows that during the winter, when the population has a high proportion of adults, the mean brood size is 4-6 eggs per female. During the pre-spring peak situation this rises to about 14 eggs per brood. Although egg numbers become very high during pre-spring peaks, not enough eggs are found to account for the observed, subsequent daphnid populations. This anomaly may be explained in one of three ways:(a) that egg sampling is inefficient and not all the eggs in the population are trapped (b) that juveniles are imported

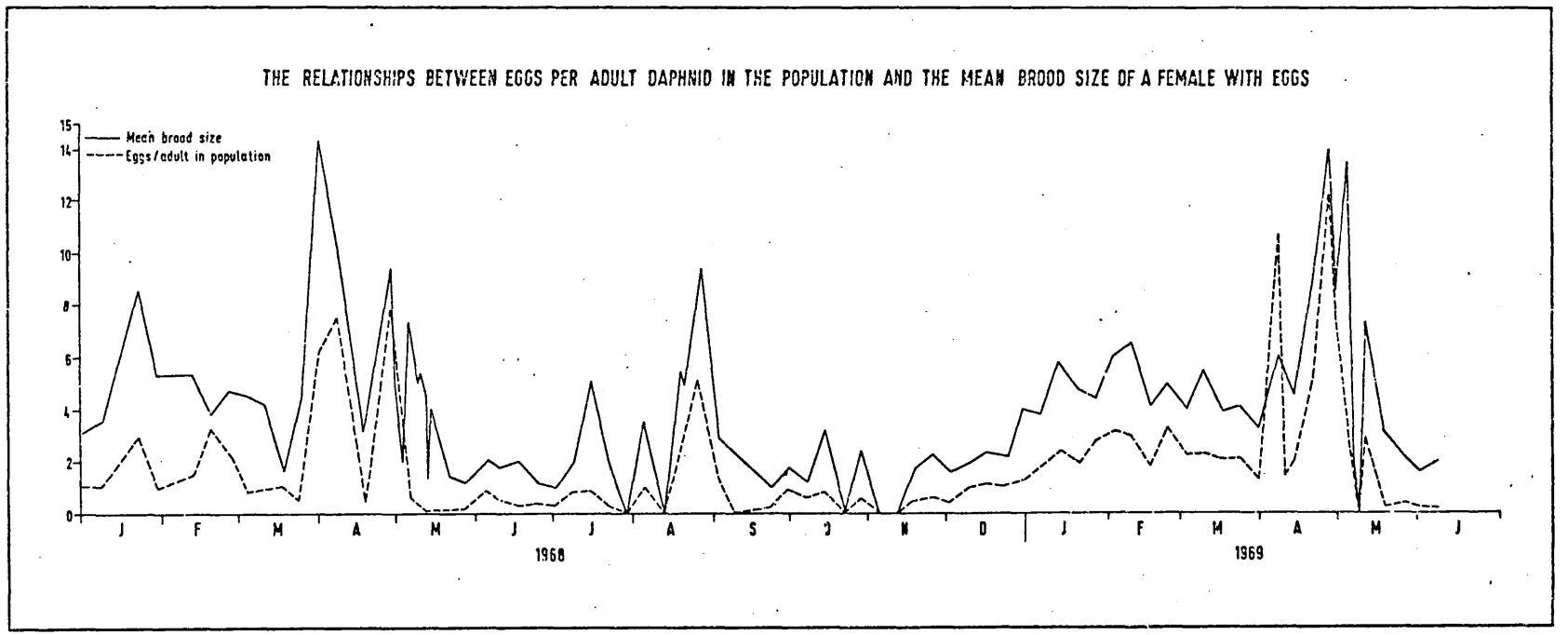

THE RELATIONSHIPS BETWEEN EGGS PER ADULT DAPHNID IN THE POPULATION AND THE MEAN BROOD SIZE OF A FEMALE WITH EGGS
Mean brood size
Eggs/adult in population
15
14
12
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J
1968
1969

Fig. 5.1.3(a).

from the river source and (c) that ephippial hatching occurs from the bottom of the reservoir. Recent work by DUNCAN (pers. comm.) suggests that ephippial hatching may account for this discrepancy. No degenerating eggs were seen in field samples, some were seen in the laboratory cultures, although these have been widely reported (HALL 1964, WRIGHT 1965 and GREEN 1956).

The factors controlling the number of eggs produced by daphnids may be affected by intrinsic factors such as age, size and clonal characteristics or environmental characteristics such as food or temperature (GREEN 1956). Most studies of these factors have been laboratory based. GREEN (1954, 1956) demonstrated that the mean number of eggs increases with the size of the adult female but ANDERSON AND JENKINS (1942) showed that egg production decreases in successive generations -a clonal defect. BERG (1931) showed that extreme temperatures can be deleterious to egg production and INGLE ET AL (1937) described the optimal temperatures for egg production. SCHINDLER (1971) examined the quality of the food and suggests that blue-green algae provide poor dietary material. GREEN (1966), in Hampton Court Long Water, found that the egg peaks coincided with the highest chlorophyll a levels. Other workers in field situations have tacitly assumed a relationship between chlorophyll $\underline{a}$ peaks and egg production although it is more often necessary to introduce a lag period between chlorophyll $\underline{a}$ peak and egg production (HALL 1964, WRIGHT 1965). GEORGE AND EDWARDS (1974) also make this assumption and further define the importance of the quality of the diet.

In this study it has been found difficult to detect

these direct influences on egg production. Attempts to relate egg production to temperature are inconclusive as there is an obvious seasonal variation which may well be controlled by diet. Analysis shows no easily definable relationship between egg numbers and chlorophyll *a* peaks even when lag factors based on developmental times are introduced. Attempts to discover a relationship between mean brood size and chlorophyll *a* per individual have also proved negative. (The availability of chlorophyll *a* in the Q.M. appears to be two orders of magnitude higher than that in Eglwys Nynydd Reservoir reported by GEORGE AND EDWARDS (1974).) Undoubtedly there is a relationship between the algae and the daphnid egg production but it has proved difficult to find a satisfactory relationship here. The seasonal variation in the chlorophyll *a* concentration is presented in figure 5.1.3(b) with an indication of the specific composition of the predominant components of the algae.

The Cladocera provide a special problem when analysing population fluctuations because they have continuous reproduction and mortality. This means that birth rates and death rates cannot be determined by counting alone. However, the egg ratio method of estimating production modified from ELSTER (1954) and used by EDMONDSON (1960) for rotifers has been applied by HALL (1964), WRIGHT (1965) and GEORGE AND EDWARDS (1974) to populations of daphnids and CUMMINS *et al* 1969 for a variety of Cladocera.

Knowing the number of eggs (E), the duration of development (De) and the initial population size (No) the finite birth rate (B) can be calculated from,

$$(i) \quad B = \frac{E}{D_e N_o}$$

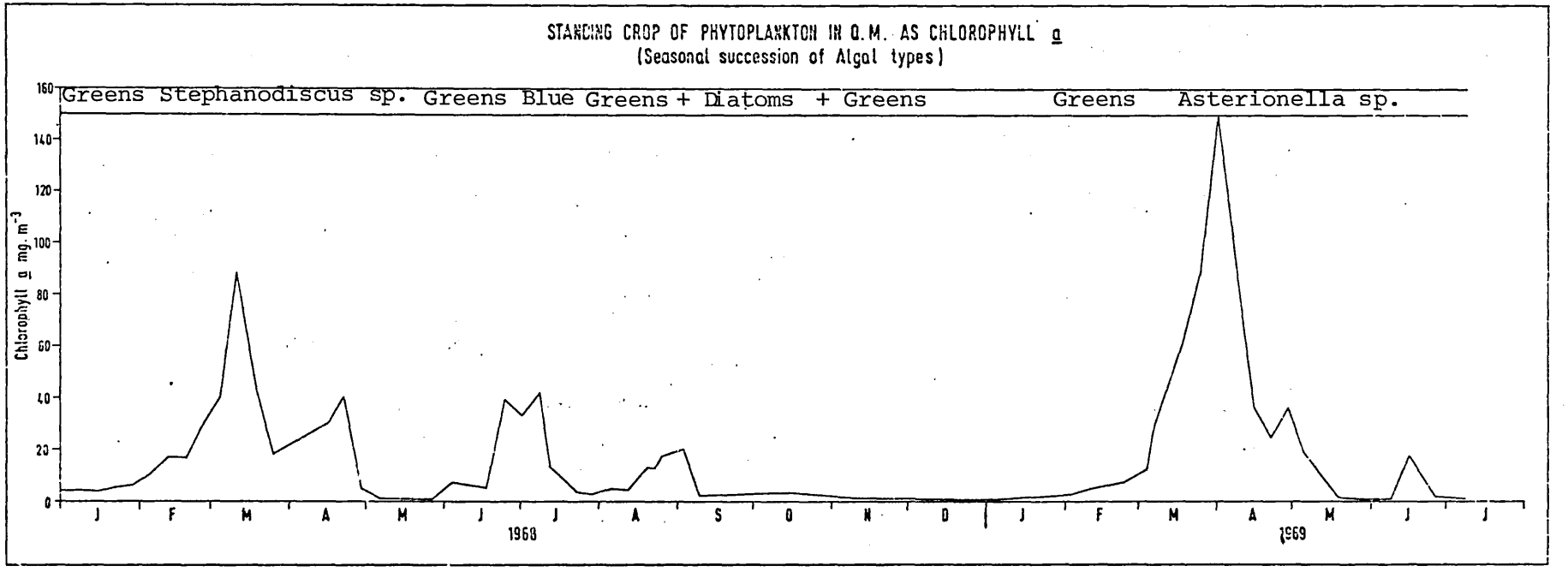


Fig. 5.1.3(b). (after Steel unpubl.)

From B, the instantaneous birth rate (b') can be calculated where,

(ii) $b' = \ln (1+B)$

Although this only operates rigorously for a population with a stable age distribution, it can be applied to populations with an unstable age distribution if there is a short sampling interval.

The coefficient of population growth (r'), a measure of the actual population change, can be calculated from sequential estimates of population numbers. If No is the initial population size and Nt is the population size after time t, then,

(iii) $N_t = N_o e^{r't}$

or (iv) $r' = \frac{\ln Nt - \ln No}{t}$

The prime sign is conventionally used to indicate that r' and b' have been calculated from counts (EDMONDSON 1960). Knowing b' and r' the instantaneous death rate can be calculated from,

(v) $d' = b' - r'$

The finite death rate (D) may be calculated from d' the equation;

(vi) $D = I - e^{-d'}$

In this study two independent population estimates were available for the calculation of these population parameters (b', r' and d') as counts of the zooplankton were made from both net hauls and Patalas samples. The numbers obtained for b', r', d' and D can be seen in Appendix 5.1.3.

Figure 5.1.3(c) shows the instantaneous birth rate, instantaneous rate of change and instantaneous death rate during the course of this study for D. hyalina. The values have been calculated from the net haul counts except

when no information is available, when Patalas data are used. Theoretically both sets of data should give the same values for b', r' and d' as they are dimensionless numbers. In general they do reveal the same trends but differ in some details. The values of r', which are calculated from successive pairs of population numbers are plotted at the midpoint of each period.

In a stable population, values of b' should exceed the values of r' if the egg production is to account for the observed changes in population size. When the population density is low, for example during the winter, the total egg estimations may be unsatisfactory and may account for variation from this pattern. But during this study the values of r' frequently exceeded b' during most periods of the year which indicates that the estimate of egg production of the population existing in the reservoir does not entirely account for the subsequent changes.

The winter situation is very similar both in 1968 and 1969 with consistent b' values, which were slightly higher in 1969 than 1968, and r' values generally lower but occasionally exceeding b' values. During the spring of 1968 the changes in population size may be accounted for by the egg production in the reservoir but this is not so in 1969 when r' values far exceed b' values. There is evidence from the Patalas samples during April 1969 that the net haul b' values are too low but not sufficiently low to account for this discrepancy. The situation becomes very confused in the mid summer when large population peaks in June, July and early August cannot be sustained by the eggs produced in the reservoir. The explanation of these discrepancies is either in the poor quality of

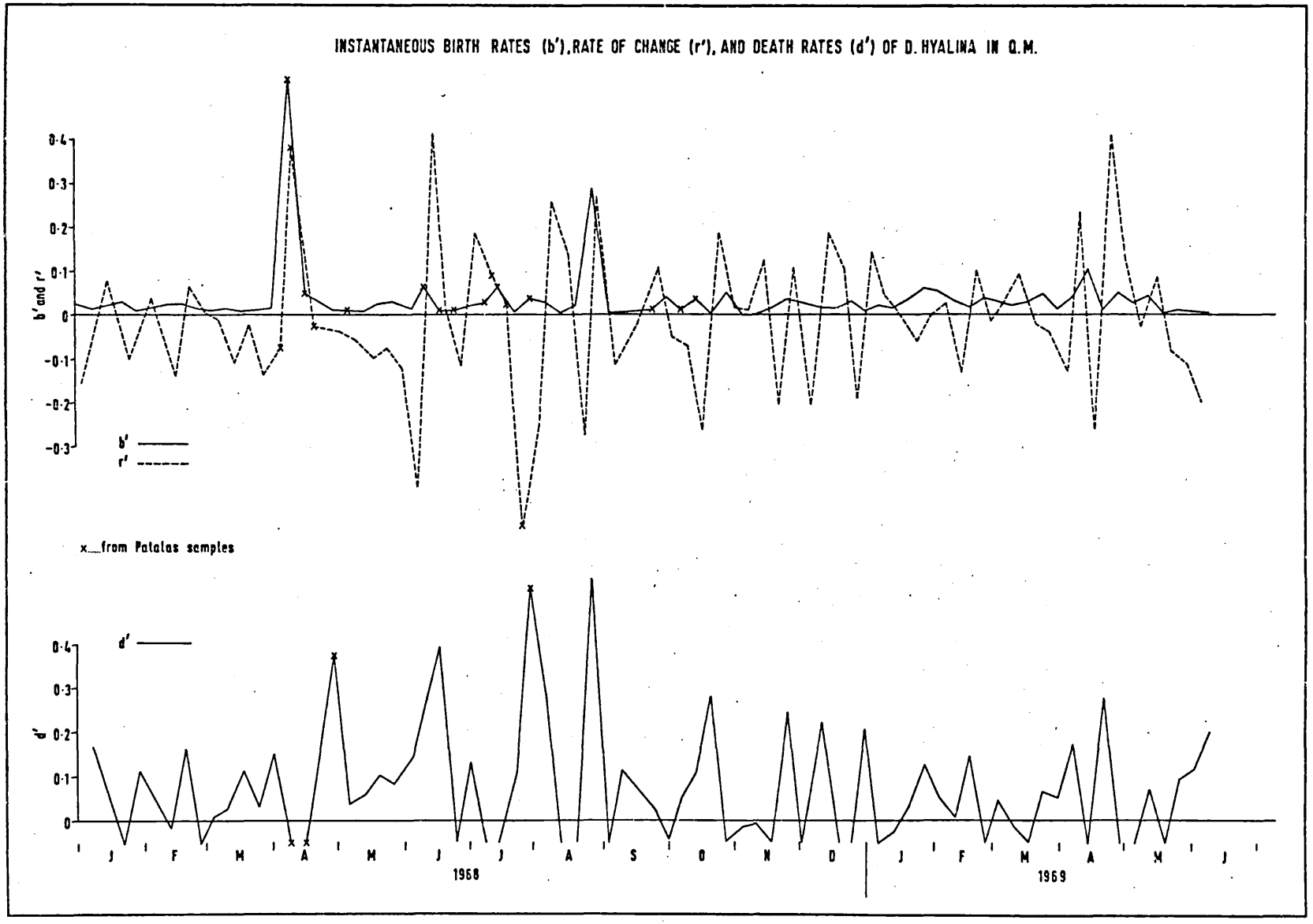

INSTANTANEOUS BIRTH RATES (b'), RATE OF CHANGE (r'), AND DEATH RATES (d') OF D. HYALINA IN Q.M.
b' and r'
0·4
0·3
0·2
0·1
0
-0·1
-0·2
-0·3
b'
r'
x.....from Patalas samples
d'
d'
0·4
0·3
0·2
0·1
0
J F M A M J J A S O N D J F M A M J
1968
1969

Fig. 5.1.3(c).

the egg estimates or that alternative sources of young animals exist. The methods used to collect samples were comparable with other workers (HALL 1964, WRIGHT 1965 and GEORGE AND EDWARDS 1974) who only occasionally had r' values exceeding b' values and it would appear more likely that either ephippial production and direct import from the river would account for the differences. Never-the-less, the figures presented cast doubt on the validity of using these data for other purposes such as production esimations.

The instantaneous death rate, d', indicates the mortality of the population, also on a seasonal basis. Periods of negative mortality, shown below the base line, indicate where population growth is not supported by egg production. The negative mortality is not shown to scale. The periods of highest death rates occur during population crashes, as might be expected, but the real value of this estimate, as a means of calculating finite death rates (D) is lessened if it is accepted that there is some import of animals from other sources. It would be logical to assume that the death of some of the population occurs continuously however small this may be, and negative mortality rates point to a deficiency in the model for use in this particular situation.

Table 5.1.3(a) shows the mean instantaneous birth rate and positive rate of increase of population for each year of the study and compares this with results given by other authors. The mean instantaneous birth rate is similar to although lower than that of GEORGE AND EDWARDS (1974) which in turn is lower than the value given by WRIGHT (1965). However the maximum birth rate

Table 5.1.3(a)	Mean b'	Maximum b'	Mean −+ ve r'	Maximum +ve r'
Q.M. 1968	.033	.534	.133	.418
1969	.030	.101	.130	.420
HALL(1964)	–	.610	–	.150
WRIGHT(1965)	. 15	.590	–	.140
GEORGE & 1970	.049	.298	.028	.132
EDWARDS 1971	.053	.230	.040	.124
(1974)				

Taken from Patalas results.

approaches the higher values given in the literature. The instantaneous rate of change is about threefold that previously reported. If the mean values of b' and r' are used to satisfy equation (v) and then (vi) on an annual basis the average value for the finite death rate (d') obtained for both years of the study is 0.0952 which is equivalent to a 9.5% loss of individuals to the population each day. This compares with values given by GEORGE AND EDWARDS (1974) of between 4.7 and 6.5%.

5.1.4. PRODUCTION

Several alternative methods are available for calculating production from zooplankton field data. Each has advantages and disadvantages and instead of selecting one method, several have been tried in this study.

A. WINBERG (1971) examines the problems associated with production estimations for populations that reproduce continuously and have cohorts that cannot easily be distinguished. Most approaches to these populations are based on the finite growth rate of individuals from egg to death. This requires a knowledge of the duration of stages of the life of the individuals and the weight increment of and numbers of these stages. Using this method, Winberg proposes the following generalised formula for estimating production per unit area or unit volume per unit time. The units of production may be any convenient unit such as dry weight or unit carbon.

$$\text{(i) Production (P)} = \frac{N_e . w_e}{D_e} + \frac{N_i . \Delta w_i}{D_i} + \ldots\ldots \frac{N_n . \Delta w_n}{D_n}$$

where N_e, N_i....N_n = the number of individuals in stage e, i, ...n.

Δw_e, Δw_i,.... Δw_n = the weight increment of that stage.

D_e, D_i,.....D_n = the duration of that stage at the field temperature, usually in days.

This method of estimating production has been used by several authors including PECHEN AND SHUSHKINA (1964),

GREZE AND BALDINA (1964), WINBERG ET AL (1965) and STEEL ET AL (1972). This method involves analysing the population within arbitrary size classes, the durations of which are known, and making these corresponding to the elements of equation (i). The duration rates were determined in the laboratory study of growth (figure 5.2.2(h).) and the weight increments in the length-weight determinations (section 5.2.1). Population biomasses were estimated as the product of the numerical population analysis and the length-weight determinations indicated in figure 5.2.1.(a).

Results of this estimate of production can be seen in figure 5.1.4(a) and the data are presented as production of dry weight of D. hyalina in milligrammes per metre square per day. The pattern of production is similar for each year of the study although the levels of production achieved differ. The winter production is low, 25–60 mg.m^{-2}.day^{-1}, but during the spring this rises to the maximum level (1968 662 mg. $m^{-2}.day^{-1}$ 1969 1064 mg. $m^{-2}.day^{-1}$.) Production falls during June, reaches high levels in July (641 mg. $m^{-2}.day^{-1}$) and during the autumn period (up to 300 m. $m^{-2}.day^{-1}$

An estimate of annual production is obtained by integrating the area under the daily production curve and is found to be 50.60 g. $m^{-2}.yr.^{-1}$. which is equal to about 4.22 g. $m^{-3}.yr^{-1}$. (It is only possible to speculate the m^3 value as the level of the water is altered at different times of the year. A 12m depth is assumed. Production was also estimated for the

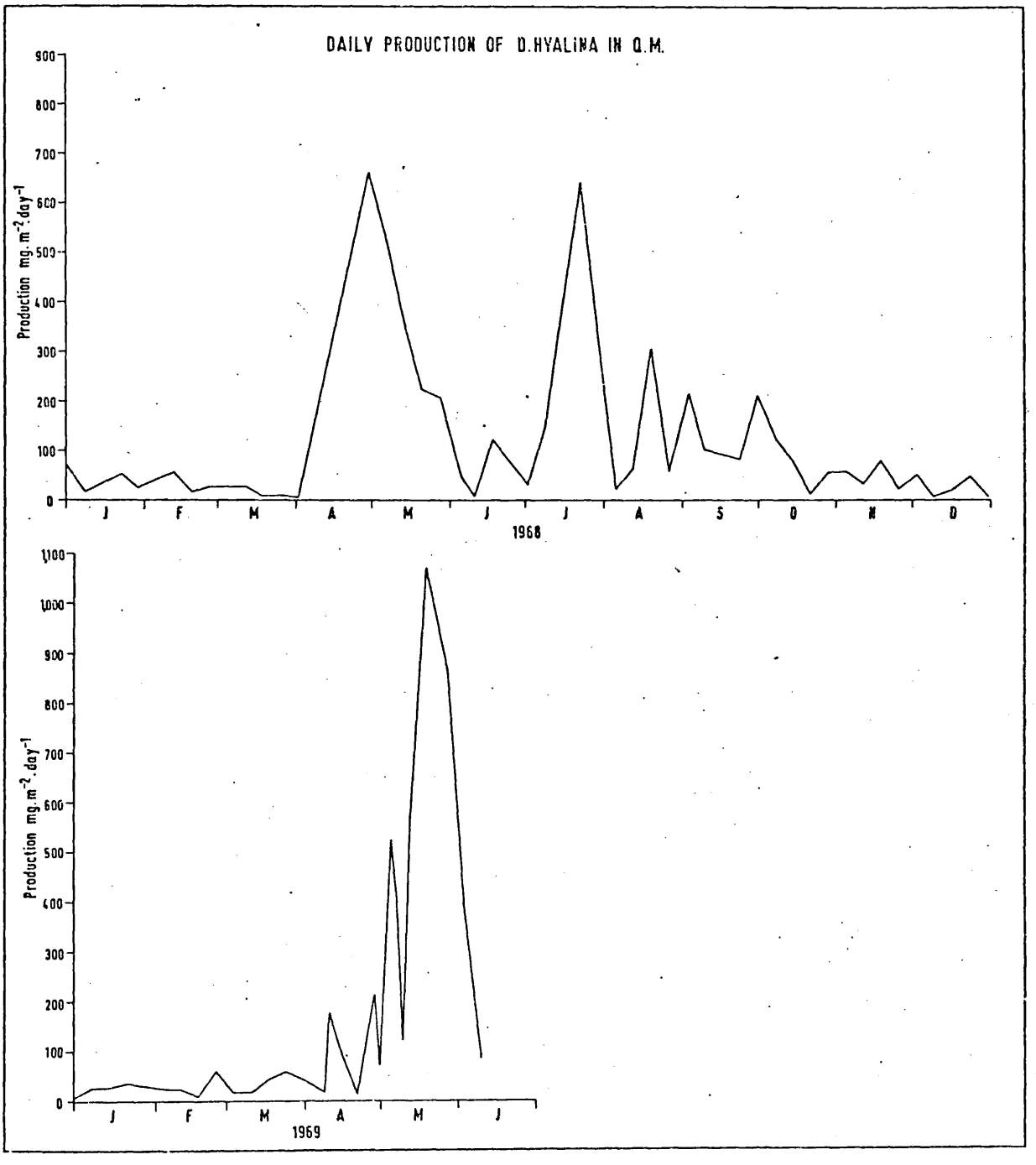

DAILY PRODUCTION OF D.HYALINA IN Q.M.
Production mg.m-2.day-1
900
800
700
600
500
400
300
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D
1968
1100
1000
900
800
700
600
500
400
300
200
100
0
J
F
M
A
M
J
1969

Fig. 5.1.4(a).

period until the end of the spring period for each year.

1968 to 10.6.68 24.95 $g.m^{-2}$. 2.08 $g.m^{-3}$

1969 to 10.6.68 27.92 $g.m^{-2}$. 2.33 $g.m^{-3}$

These results are compared with the results given by a few other workers in Table 5.1.4(a)

Meshkova (1952) in Winberg(1971)*	D.longispina sevanica eulimnctica	2.153$g.m^{-3}.yr^{-1}$
Petrovich et al (1961)*	D.galeata mendotae	5.82$g.m^{-3}.yr^{-1}$
Wright(1965)*	D.galeata mendotae	41.50$g.m^{-3}yr^{-1}$
Wright (1965)*	D.schodleri	82.86$g.m.^{-3}.yr^{-1}$
George & Edwards (1974)	D.hyalina	11.68$g.m.^{-3}.yr^{-1}$

*These results were not complete years sampling.

The percentage contribution to the daily production of eggs, juveniles and adults is shown in figure 5.1.4(b). The same pattern can be seen in both years of the study. Egg production accounts for a relatively small proportion of the total production (max. 30% in August 1968) and is normally highest in the winter (10–20%) although this level was sustained into late March in 1969. Adult production is high in the winter, normally 30–50% of the total but occasionally exceeding 80%. The proportion of adult production increases rapidly immediately before and after production maxima. The juvenile production is the largest proportion of the total (40–80% for most of the time) and accounts for the largest proportion of production peaks. During the summer the juvenile production remains high.

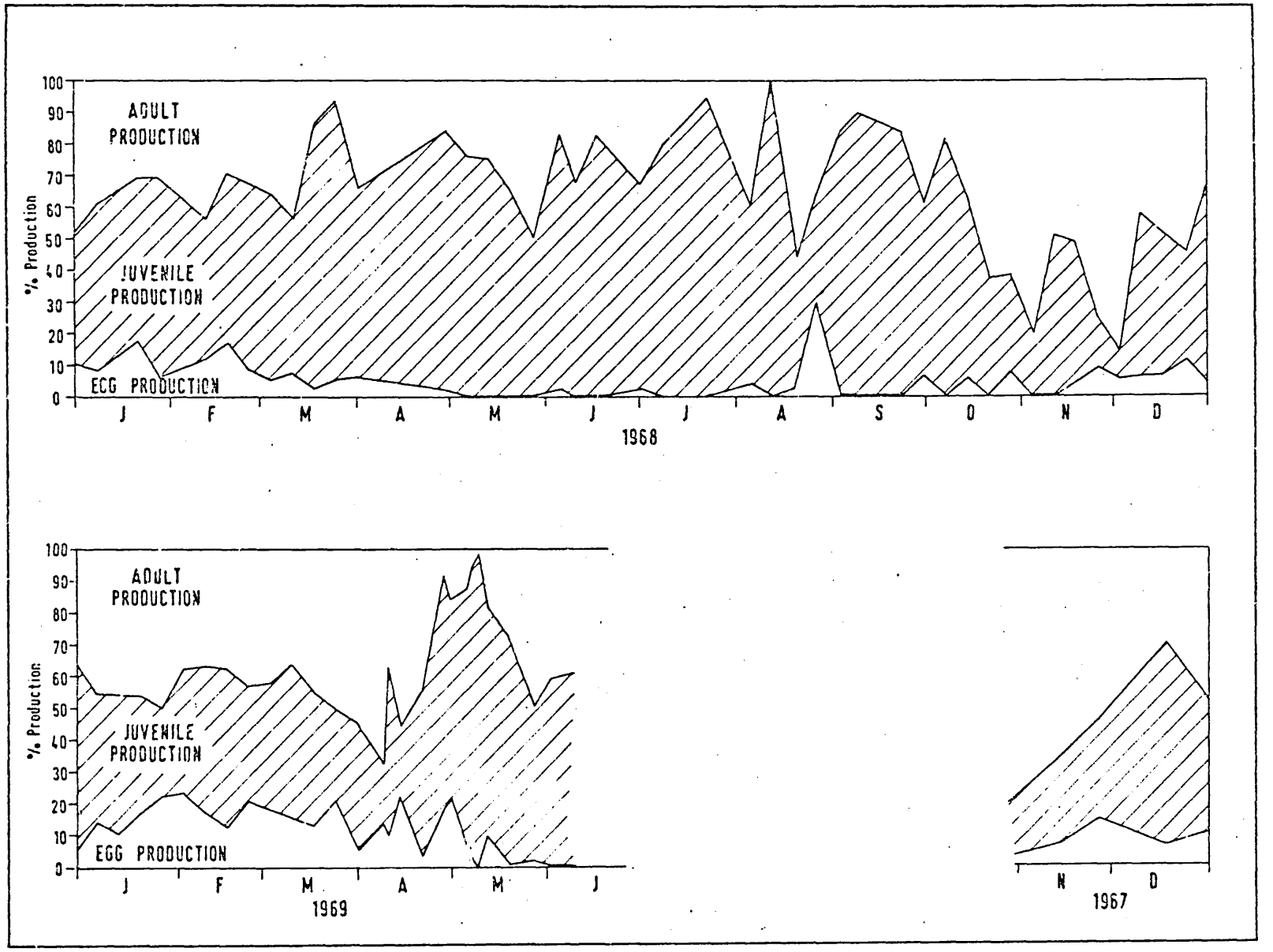

ADULT PRODUCTION
JUVENILE PRODUCTION
EGG PRODUCTION
% Production
100
90
80
70
60
50
40
30
20
10
0
J F M A M J J A S O N D
1968
ADULT PRODUCTION
JUVENILE PRODUCTION
EGG PRODUCTION
% Production
J F M A M J
1969
N D
1967

Fig. 5.1.4(b).

The daily production to biomass (P/B) ratios are shown in figure 5.1.4(c). The biomass in the value calculated from the product of the number and weight of each stage summed for all stages. The minimum value (0.027) occurs in the winter and the maximum value (0.224) occurs in the mid summer and values are very much the same during the different years of the study. The annual P/B ratio in the Q.M. for D. hyalina was found to be 38.62 and this is compared with values reported in the literature in table 5.1.4(b).

The annual P/B ratios are high compared with other workers but not the highest reported in the literature, for WINBERG et al (1972) report an annual P/B ratio in Rybinsk Reservoir of 50.0 GEORGE AND EDWARDS (1974) working with the same species, D. hyalina, in the very shallow Elgws Nynydd reservoir give daily P/B ratios between 0.003 and 0.263 and an annual P/B ratio of 20.8 in 1970 and 25.9 in 1971.

It can be seen in figure 5.1.4(c) where the seasonal temperature curve is shown, that there is a strong correlation between temperature and P/B ratio. This relationship is examined further in figure 5.1.4(d) where the daily P/B ratio is plotted against temperature. Although the correlation is strong, no further statistical analysis has been performed on the data because production (P) has already been estimated partly as a function of the field temperature (equation (i) element D in this section) and such analysis becomes statistically fatuous. The data of SCHINDLER (1972) also show this correlation and although his P/B values are lower the average temperatures are lower and for the same temperature the P/B values correspond.

Table 5.1.4(b)

ZOOPLANKTON TYPE	ANNUAL P/B	DAILY P/B	LAKE	SOURCE
Herbivore		.105	Mikolajskie	Kajak et al (1972)
"		.098	Taltowisko	"
"		.160	Flosek	"
"		.067	Sniardwy	"
Crustacean	14.334	0.011-0.096	Arctic Lake	Schindler (1972)
Herbivore	12.6		L. Krugloe	Winberg (1972)
"	13.0		L. Krivoe	"
"	22.1		L. Krasnoe	"
"	50.0		Rybinsk Res.	"
"	24.7		L. Drivyati	"
"	16.3		L. Naroch	"
"	13.9		L. Myastro	"
"	18.4		L. Batorin	"
"	26.2		Kiev Res.	"
D. hyalina	38.622	0.027-0.224	Q.M.	Present Study
"	20.8		Eglwys Nynydd	George & Edwards (1974)
"	25.9			

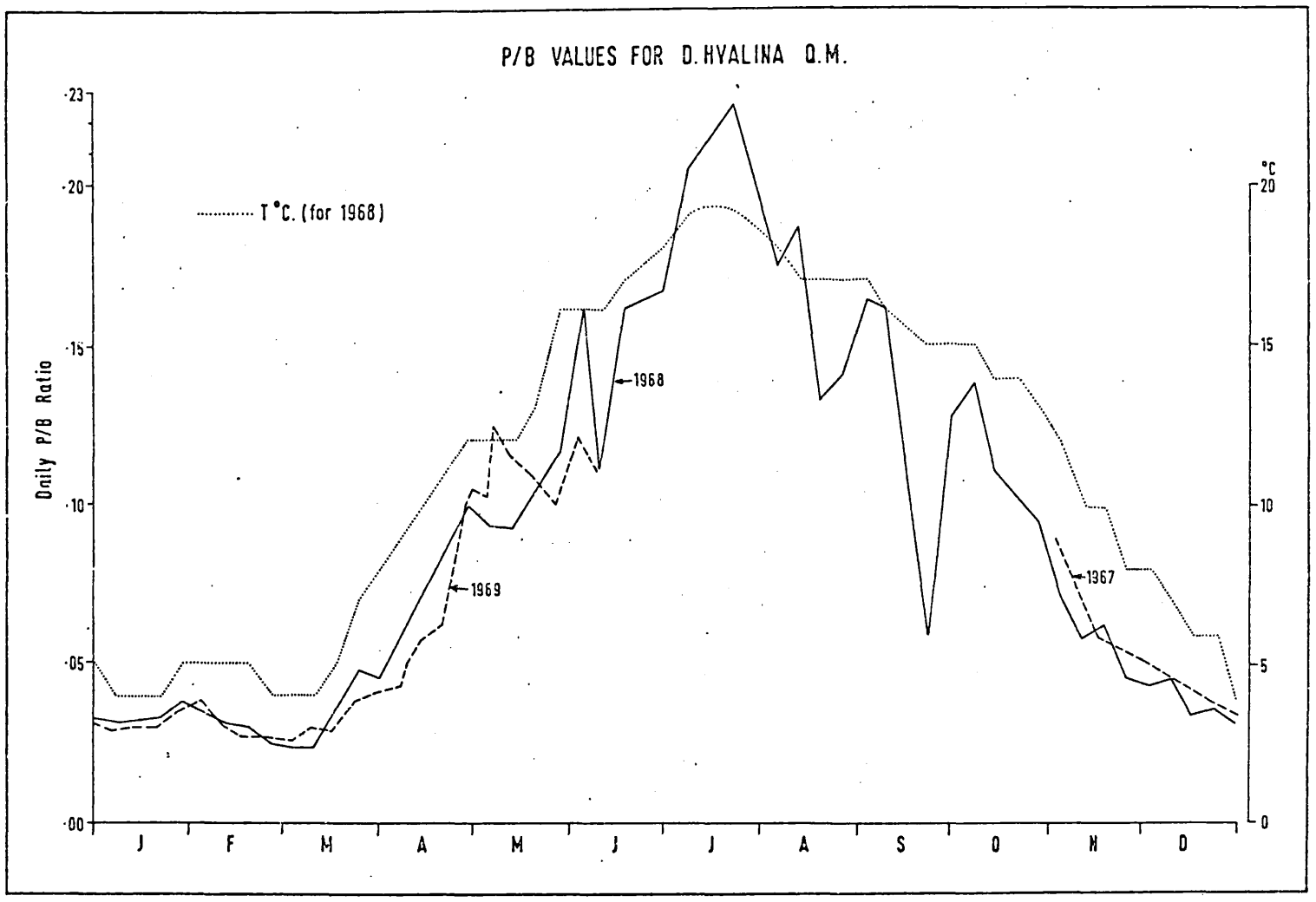

P/B VALUES FOR D.HYALINA Q.M.
T °C. (for 1968)
Daily P/B Ratio
°C
1968
1969
1967
·23
·20
·15
·10
·05
·00
20
15
10
5
0
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.4(c).

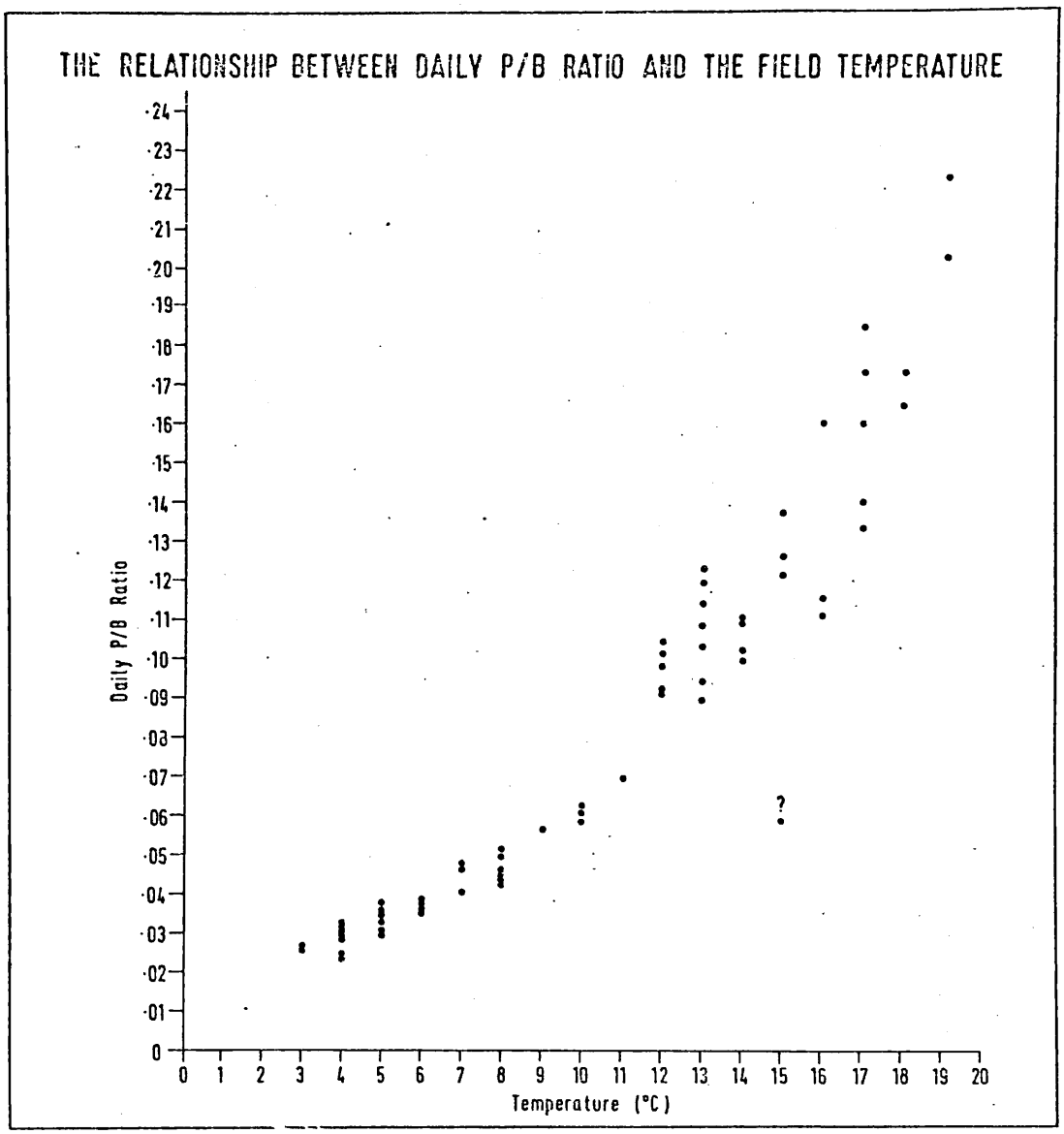

THE RELATIONSHIP BETWEEN DAILY P/B RATIO AND THE FIELD TEMPERATURE
Daily P/B Ratio
·24
·23
·22
·21
·20
·19
·18
·17
·16
·15
·14
·13
·12
·11
·10
·09
·08
·07
·06
·05
·04
·03
·02
·01
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Temperature (°C)
?

Fig. 5.1.4(d).

Using the P/B values as derived above, the production may be calculated using the directly measured field biomass. Results for D. hyalina in the Q.M. can be seen in figure 5.1.4(e). The pattern is similar to the calculated production (figure 5.1.4(a)) but values obtained are lower, especially at peak production periods. The peaks occur at the same time and through the winter values are very similar but in the spring and summer peaks values are about 50% less in each year. The annual production estimate by this method is 45% of the calculated method and was calculated to be 23.04 g.dry weight $m.^{-2}y.^{-1}$ for 1968. The first six months production of 1969 was calculated to be 15.66 g.dry weight.m^{-2}. The difference may be ascribed to the value of the weight increment used for juvenile daphnids, due to the fact that many of this size class do not reach full size and account for thelargest numbers in the population especially during population maxima.

B. A second method of estimating population production may be based on a knowledge of the instantaneous growth rates of the individuals in that population knowing the instantaneous growth rate (g.) in a particular stage, the growth, or production, of the individual (P_s) in one day may be calculated from

(ii) $Ps = gs.\ ws.$

where ws is the weight of the individual stage. (see equation (iii) section 5.2.2.). Knowing the weight contribution of the different stages to the total

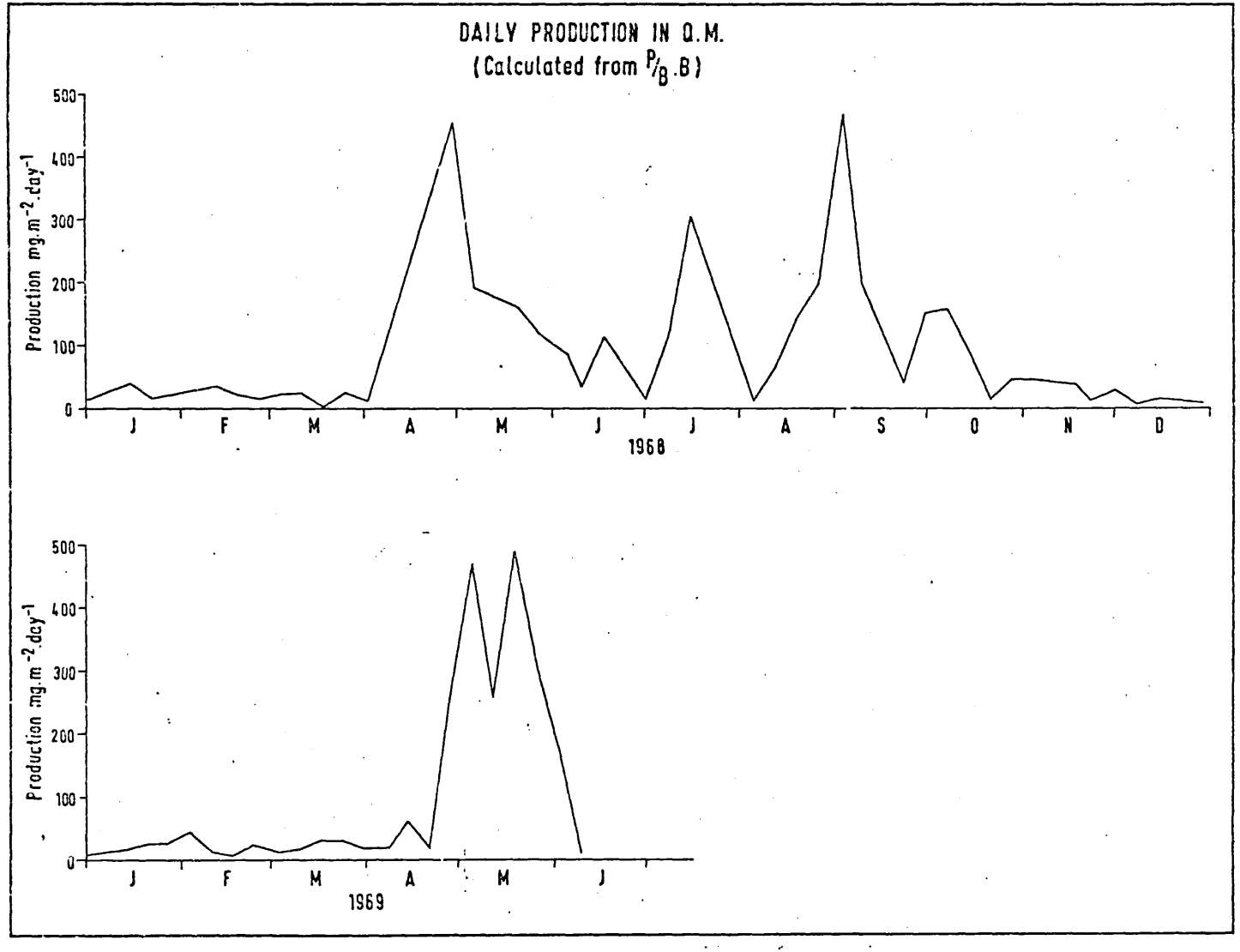

DAILY PRODUCTION IN Q.M.
(Calculated from P/B.B)
Production mg.m-2.day-1
500
400
300
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D
1968
Production mg.m-2.day-1
500
400
300
200
100
0
J
F
M
A
M
J
1969

Fig. 5.1.4(e).

population biomass and the instantaneous growth rate of the different stages, daily population production may be calculated. In a sense this is similar to the application of P/B ratios to biomass measurements because $g.B \equiv \frac{P}{B} . B.$. The stages recognised in field samples were eggs, animals >1.0mm (1), between 1.0 and 1.4 mm (2), between 1.4 and 2.0mm(3) and animals >2.0mm. From the body-length relationship shown in figure 5.2.1.(a) an approximate relative weight has been assumed for egg, (1), (2), (3) and (4) of 0.324: 1.0: 1.5: 5:10 and using this ratio, the numbers in the stages of the population counts and the directly measured population biomass (B), the weights of these stages contributing to the biomass was calculated from

$$\text{(iii)} \quad B_e = \frac{0.324.Ne}{0.324.N_e+1.n_1+1.5N_2+5.N_3+10N_4} . B \text{ mg.m}^{-2}$$

and similarly for B_1, B_2, B_3 and B_4.

The instantaneous growth rate (g) was taken from the values given in table 5.2.2(c) and the egg duration rate (1/D) was that shown in table 5.2.2(h). Instantaneous growth rates were corrected to existing field temperature relationship shown for egg development. Population production was then estimated from

$$\text{(iv)} \quad P = \frac{1}{} . B_e + g_1.B_1 + g_2.B_2 + g_3.B_3 + g_4.B_4 . \text{mg.m}^{-2}.$$

Daily production rates calculated by this method can be seen in figure 5.1.4(f). The pattern of results obtained is very similar to those calculated for figure 5.1.4(a) but the values are generally lower except in early September 1968 when a maximum of 422 mg.m^{-2} was recorded. During the early part of the

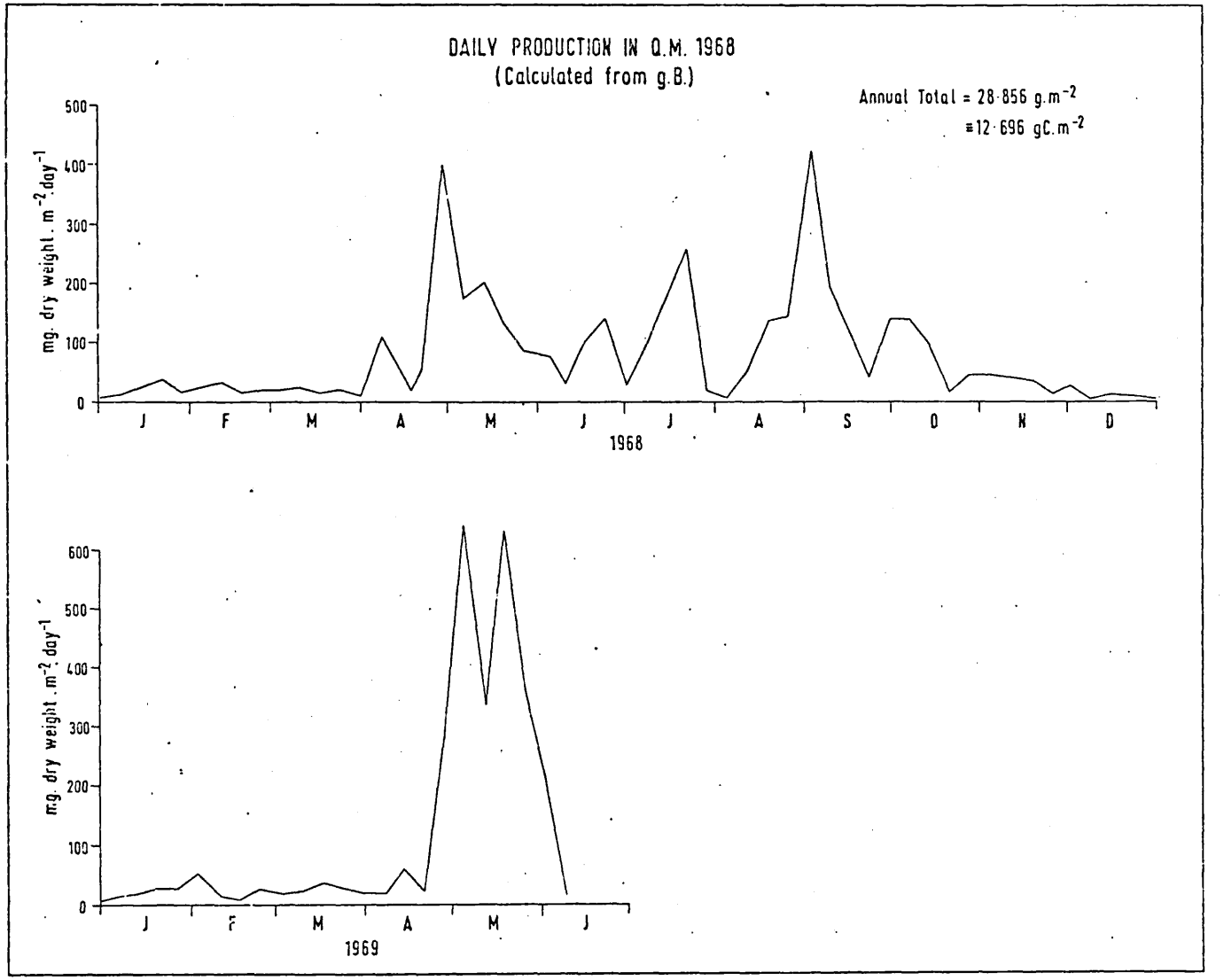

DAILY PRODUCTION IN Q.M. 1968
(Calculated from g.B.)
Annual Total = 28·856 g.m⁻²
≡12·696 gC.m⁻²
mg. dry weight. m⁻². day⁻¹
500
400
300
200
100
0
J F M A M J J A S O N D
1968
mg. dry weight. m⁻². day⁻¹
600
500
400
300
200
100
0
J F M A M J
1969

Fig. 5.1.4(f).

spring peak in 1968, biomass data were more complete than numerical estimates of population size and 5.1.4(f) probably more nearly reflects the true situation. The annual production for this method was calculated to be 28.856g.m^{-2}. which is 57% of the first method. The similarities between figure 5.1.4(f) and (e) are very striking.

C. The third alternative method of calculating production, developed by EDMONDSON (1960) for use with rotifer populations from the earlier work of ELSTER (1954) and applied by a variety of workers to Cladocera, is based on the concept of turnover time, T, Turnover time in days, defined as the time required for a population of steady size to replace itself in numbers is derived from

(v) $T = \frac{1}{B}$ where B is the finite birth rate (used by HALL (1964), WRIGHT (1965)

or(vi) $T^1 = \frac{1}{D}$ where D is the finite death rate derived in section 5.1.3 equation (vi) used by GEORGE AND EDWARDS (1974)

The percentage turnover per day,

(vii) $\frac{1}{T}(1) \cdot 100$

may be applied to the standing crop biomass to obtain a figure for the daily production. The disadvantages of using this method for calculating production in this particular situation are the incorporation of the inadequecies of using b', d' and r' to describe the population dynamics in the Q.M. However, production estimates for production values from equations (v) and (vi) are presented in figure 5.1.4.(g). The results

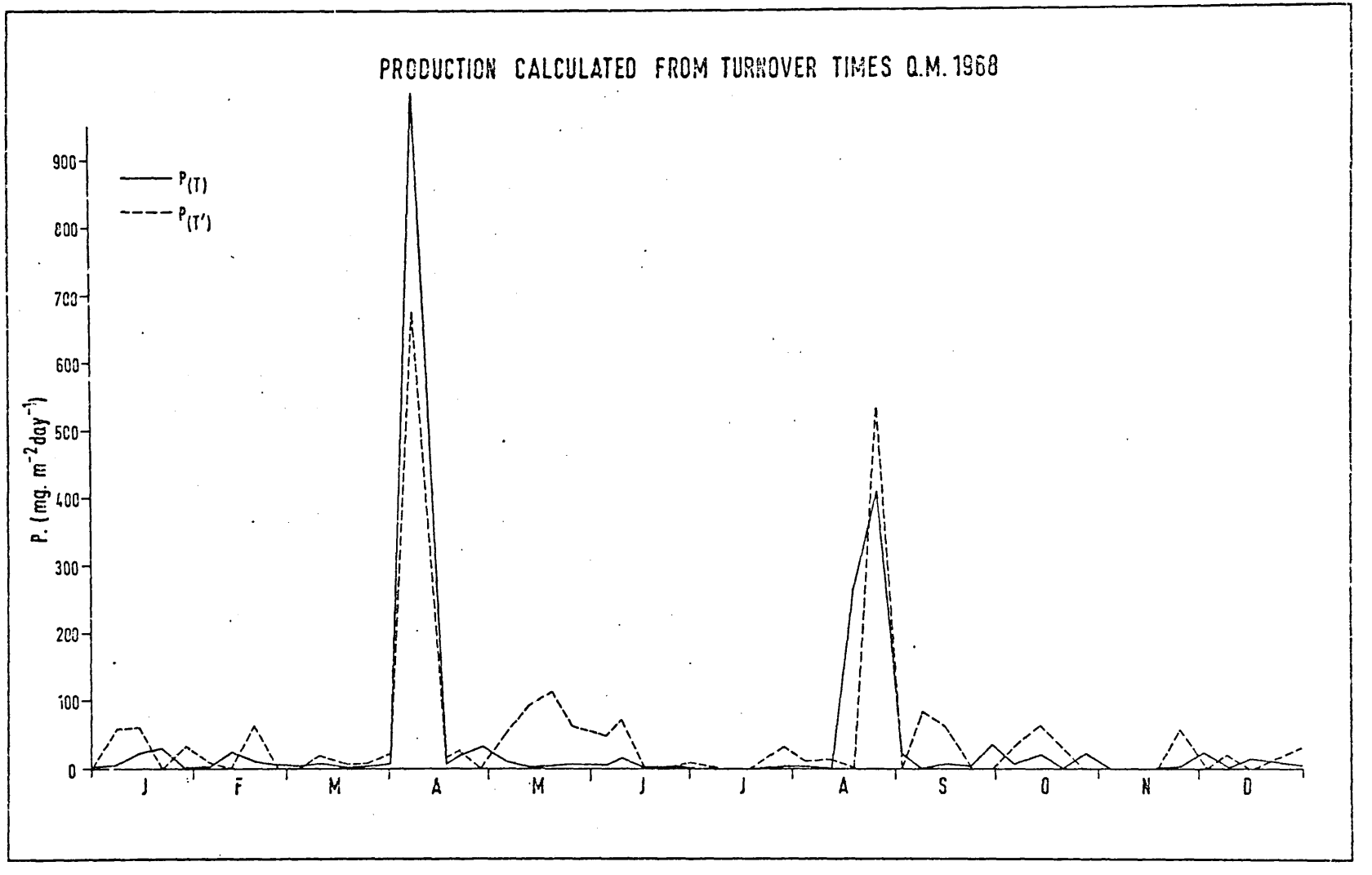

PRODUCTION CALCULATED FROM TURNOVER TIMES Q.M. 1968
P(T)
P(T')
P. (mg. m-2day-1)
900
800
700
600
500
400
300
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.4(g).

do not compare satisfactorily with results presented in figures 5.1.4(e) and (f) although this calculation is also based on the directly measured field biomass. Production peaks occur in both spring periods although the amount of production is considerably less than that measured by the other methods. The amplitude of the peak in 1968 is considerably higher than other figures but this is recorded at the begining of April, the others fall at the end of the month. The annual production for 1968 is calculated to be 12.944g.m^{-2} (25.6% of that calculated by the first method).

The different methods of calculating production used in this section produce very different results and care must be taken in selecting the set of results that reflect the actual situation. The first method used probably over-estimates the actual production as it relies heavily on laboratory measured biomass estimates. The last method is unsatisfactory because the population parameters derived are insufficient to describe the situation and also take no account of the time it takes daphnids to develop from hatching to reproducing adult. The best methods to use here are probably those applying a measure of P/B, derived from the first method or from g.B. and applied to the measured population biomass. There is, in practice, very little difference between these two techniques in the result achieved. In subsequent sections, production estimations, where referred to, will be based on the results shown in figure 5.1.4(f) and the actual values used are presented in Appendix 5.1.4.

Length-weight relationships and the growth rates of the stages of Diaptomus sp. and Cyclops sp. were not determined in this study. However values of these are available in the literature. Growth rates of stages of Cyclops sp. and, or, Diaptomus sp. have been reported by several workers including CUMMINS et al.. (1969), BURGIS (1970), WINBERG (1971) and MUNRO (1974). Length-weight relationships have been reported by WINBERG (1971) and KIBBY (1969) among others.

Population densities of the copepods in the Q.M. were estimated by counting and direct measurements of the biomass (section 4.2.2.). The numerical analysis subdivided the diaptomid and cyclopoid copepods into adults and juveniles. From these data, together with developmental rates and length-weight data taken from the literature, estimates were made of the daily production of the copepods. Using established relationships for the effect of temperature on developmental rates (MUNRO 1974) and the numerical population analysis, calculated production values for diaptomids and cyclopoids were derived from equation 5.1.4(i) for the adult and copepodite fraction of the population. Biomass was calculated from the product of the number of the stage and the average weight of the stage. From these values of production and biomass, P/B ratios were established for the different copepod populations and these can be seen in figure 5.1.4(h). Also shown in the figure is a general line for the total copepod production to total copepod biomass ratio on a daily basis. The daily P/B ratios exhibit the same general features of the daphnid line shown in figure 5.1.4(c) except that the correlation with temperature is not quite so marked in the mid summer.

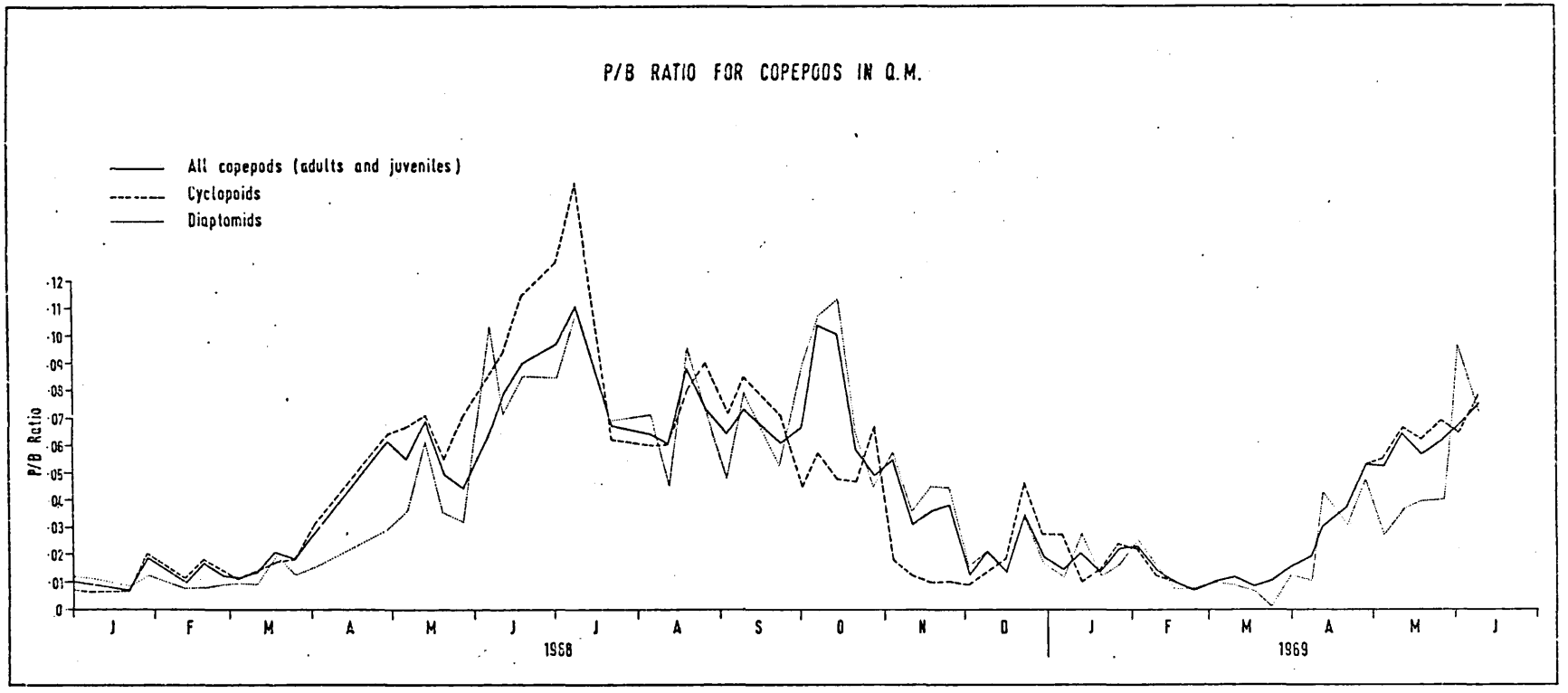

P/B RATIO FOR COPEPODS IN Q.M.
All copepods (adults and juveniles)
Cyclopoids
Diaptomids
P/B Ratio
·12
·11
·10
·09
·08
·07
·06
·05
·04
·03
·02
·01
0
J F M A M J J A S O N D J F M A M J
1968
1969

Fig. 5.1.4(h).

The best value of production of copepods was determined by the product of these daily P/B ratios and the directly measured biomass (see section 5.1.1, figure 5.1.1.(b)) of the copepods and the values obtained are presented in figure 5.1.4(i). The annual production of the copepod fraction of the zooplankton calculated by this method was found to be 5.286 $g.m^{-2}$, which is equal in each year although the production levels during the spring of 1969 are nearly three times as high as spring 1968. The winter levels are low and rise steadily to the spring maximum which is largely produced by the Cyclops sp. populations (Figure 5.1.4(j) shows the percentage contribution of cyclopoids and diaptomids to the daily production rate.of the copepods). The summer levels of production are high, peaks occurring in June (max. 55 $mg.m^{-2}.day^{-1}$) and July and August (max. 71 $mg.m^{-2}.day^{-1}$) when the highest production peak occurs. This peak is again cyclopoid-dominated whereas the June and July peaks are produced mainly by Diaptomus sp. The highest production rate occurred in 1969 during the spring when the, mainly cyclopoid, population achieved a rate of 172 $mg.m^{-2}.day^{-1}$.

This method of estimating production, although admittedly open to criticism, provides what appears to be a reasonable estimate of the production of the copepod population. The P/B ratios tend to be lower than those for daphnids (figure 5.1.4(c)) but this may well be an underestimate as no account is taken of naupliar production and might be expected for animals with a longer developmental time attaining a smaller final size. One interesting feature of the copepod production is the fact that the cyclopoids dominate the spring and autumn production peaks while the diaptomids are the main producers in the mid summer.

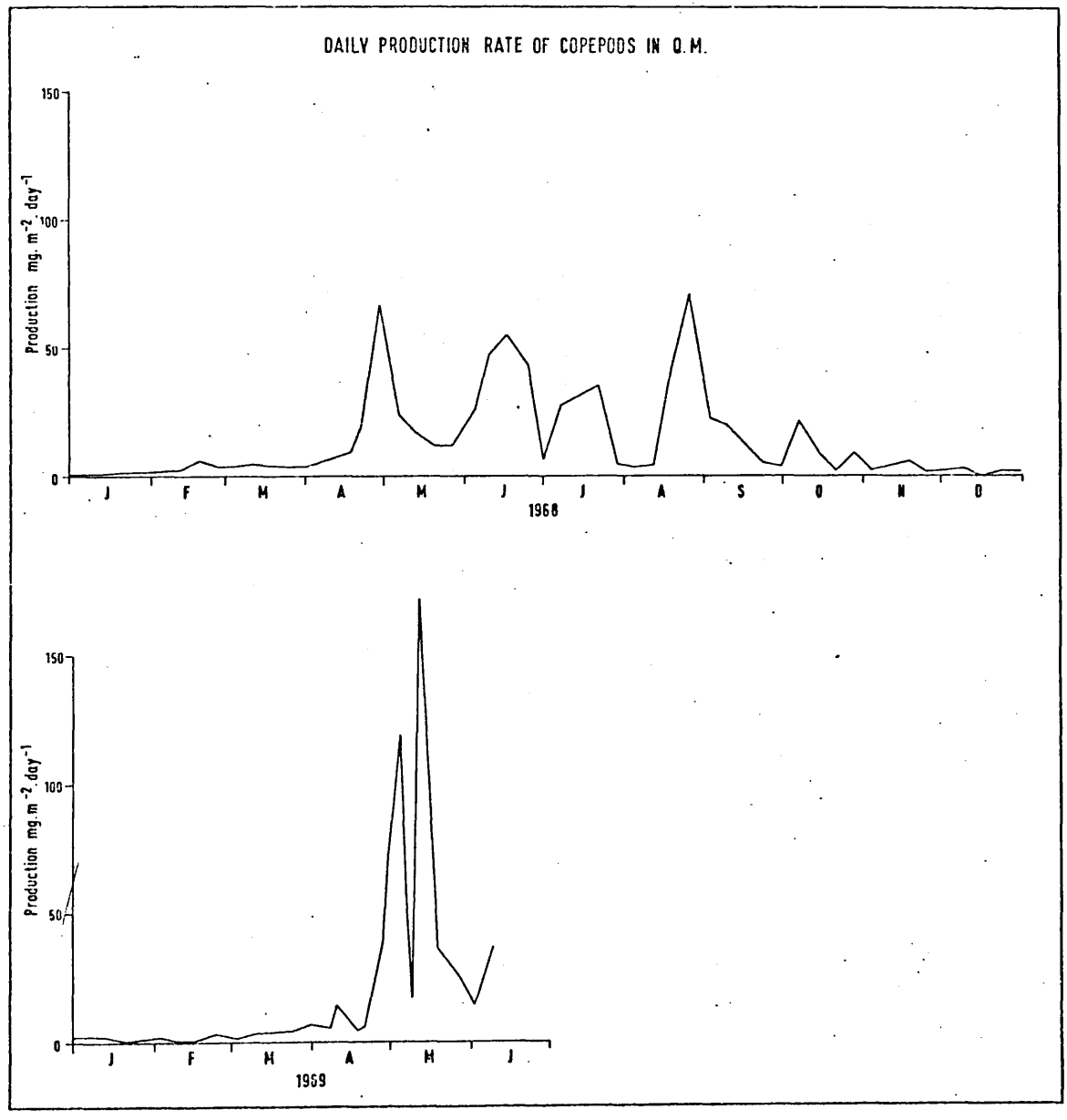

DAILY PRODUCTION RATE OF COPEPODS IN Q.M.
Production mg. m-2 day-1
150
100
50
0
J F M A M J J A S O N D
1968
Production mg. m-2 day-1
150
100
50
0
J F M A M J
1969

Fig. 5.1.4(i).

5.1.5. FIELD RESPIRATION

It is well known that the metabolic rate of animals can be affected by a range of environmental factors such as food concentration and quality, temperature, stage and state of development and the body size of the particular species (see section 5.2.3). BLAŽKA (1966) suggests that three types of metabolic regulation may occur in field conditions. Firstly that respiration rates may be lowered in low seston conditions (insufficient food) for food reserves to last. The return to normal or heightened respiration rates may be delayed for several generations when food becomes sufficient. This response may occur in the change from winter to spring conditions. Secondly he suggests that the respiration rate may vary with the percentage utilisation of protein for different types of diet (quality of diet). His third suggestion is that daphnids show a seasonality of respiration rates and that field animals show a more marked acclimation to temperature than laboratory cultured animals.

It is difficult to simulate field food conditions, either quality or concentration, in the laboratory and impossible to simulate the life histories of previous field generations. For these reasons, an attempt has been made, in this study, to measure oxygen consumption of the zooplankton in as near field conditions as possible to detect gross variations that might occur from laboratory measurements of oxygen consumption. The technique used was the simple closed bottle technique described in section 4.3. Other studies of this nature have been attempted by MARSHALL ET AL (1935), STRAŠKRABA (1967)

and CREMER AND DUNCAN (1969). BISHOP (1968) and GANF AND BLAŽKA (1974) measured oxygen consumption by the bottle method in the laboratory. The results of this study are presented here and subsequently compared with laboratory results interpolated into field population estimates. Part of this work has been published separately with additional material by DUNCAN et al. (1970).

Figure 5.1.5. (a) shows the seasonal change in oxygen consumption per milligram dry weight per hour for the macrozooplankton during 1968 and 1969 at approximately fortnightly intervals. The vertical bars represent the range of results obtained. It can be seen that there is a period of intense metabolism occurring in the spring of both years, and to a lesser extent in the summer. It is not easy to define a causal relationship of this seasonal fluctuation in metabolic rate and several different factors probably contribute to the differences that can be seen. The spring period of high metabolism, that can be seen in both years but which is higher in 1969, coincides with a period of intense parthenogenetic reproduction by D. hyalina resulting in very large standing crops of young, small animals - a category that has a high weight-specific respiratory rate. An indication of the size structure of the population is given by the mean individual dry weight, estimated by dividing the field standing crop biomass by the field standing crop numbers (see section 5.1.1. figure 5.1.1(c)) The field estimations of respiration rate have been plotted against the mean

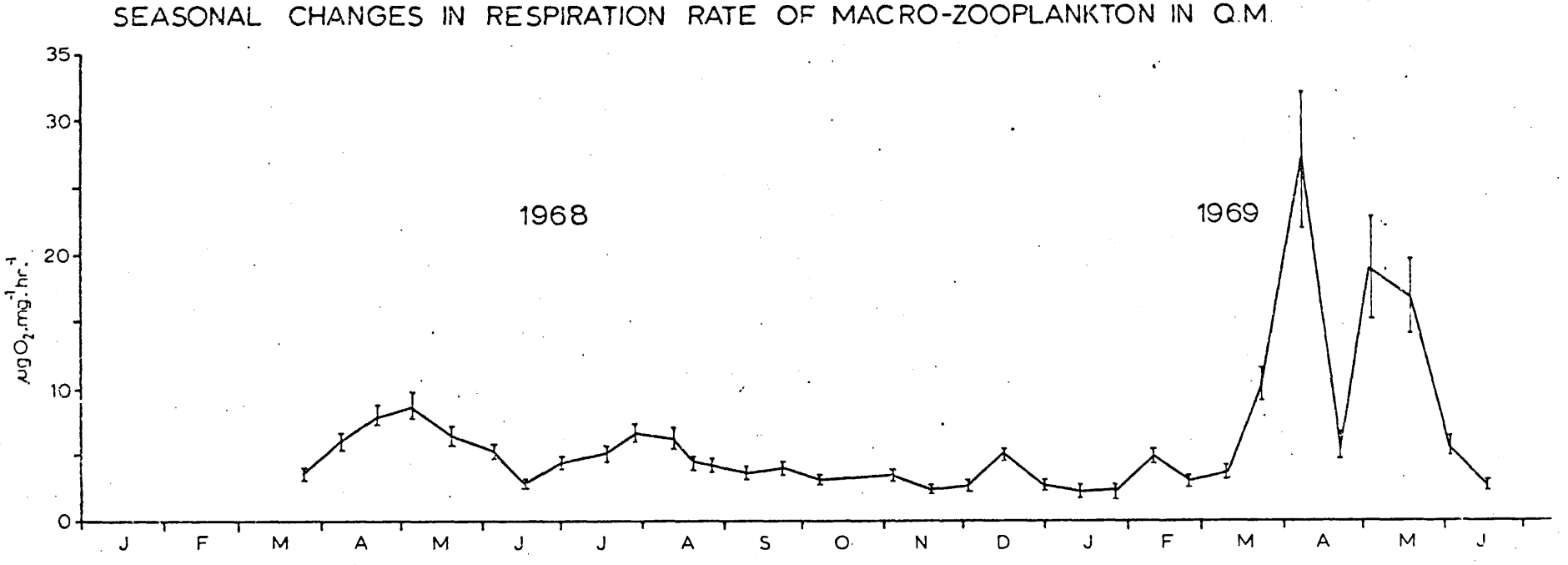

SEASONAL CHANGES IN RESPIRATION RATE OF MACRO-ZOOPLANKTON IN Q.M.
35
30
20
10
0
1968
1969
J F M A M J J A S O N D J F M A M J

Fig. 5.1.5(a).

individual dry weight and the results can be seen in figure 5.1.5(b). The relationship, although mean individual dry weight is a crude index of population structure, is analogous to other respiration rate per unit weight relationships (see fig 5.2.3.(b)). Regression analysis of the results, excluding measurements made during the spring period of each year, produce a highly correlated relationship when plotted as a doubly logarithmic function. ($y = 5.53\, x^{-1.168}$, $r^2 = 0.8727$ $p < 0.001$ $n = 22$). This relationship has been used to estimate expected respiration rates knowing the mean individual dry weights. Results are presented in figure 5.1.5.(c) and it is possible, from this figure, to identify periods when respiration rates are impressed more than might be expected from size structure attributes of the population. The specific composition of the zooplankton, with high numbers of Cyclops sp in the spring population, may also enhance field estimations of metabolic rate but not enough even to approach the levels recorded. The summer rate, during July and August 1968, which is marginally higher than the line estimated from mean individual dry weights is most likely to be explained by the presence of relatively large numbers of Bosmina longirostris and gravid female Diaptomus gracilis. During the winter months, when respiration rates are fairly steady, the zooplankton population structure remains predominantly cladoceran, with a higher proportion of old individuals than in the spring and late summer (section 5.1.3.)

Food quantity and quality probably exert the effects on the metabolic rate in the way that BLAŽKA (1966)

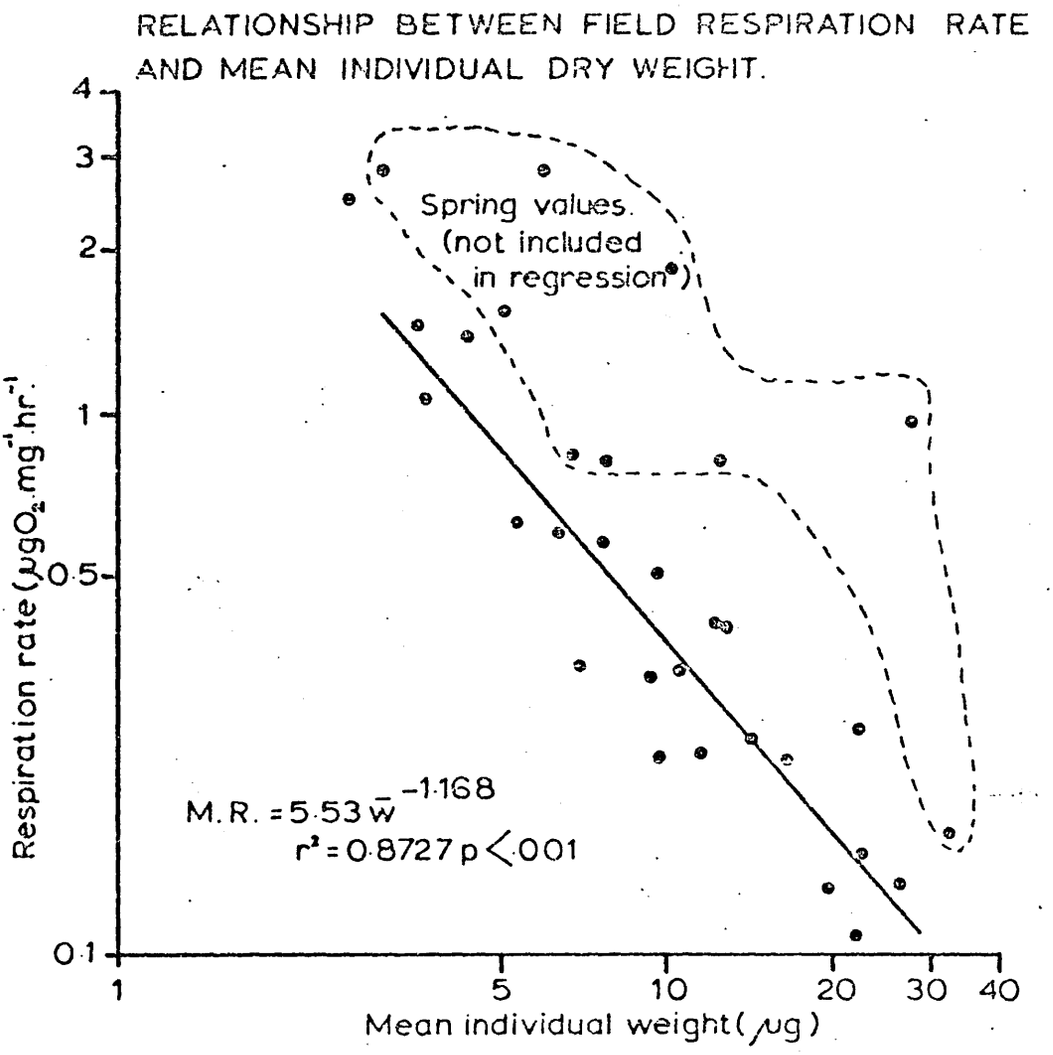

RELATIONSHIP BETWEEN FIELD RESPIRATION RATE AND MEAN INDIVIDUAL DRY WEIGHT.
Spring values. (not included in regression)
M.R. = 5·53 $\bar{w}^{-1·168}$
r^2 = 0·8727 p < 001
Respiration rate ($\mu gO_2 . mg^{-1} . hr^{-1}$)
Mean individual weight (μg)
4
3
2
1
0·5
0·1
1
5
10
20
30
40

Fig. 5.1.5(b).

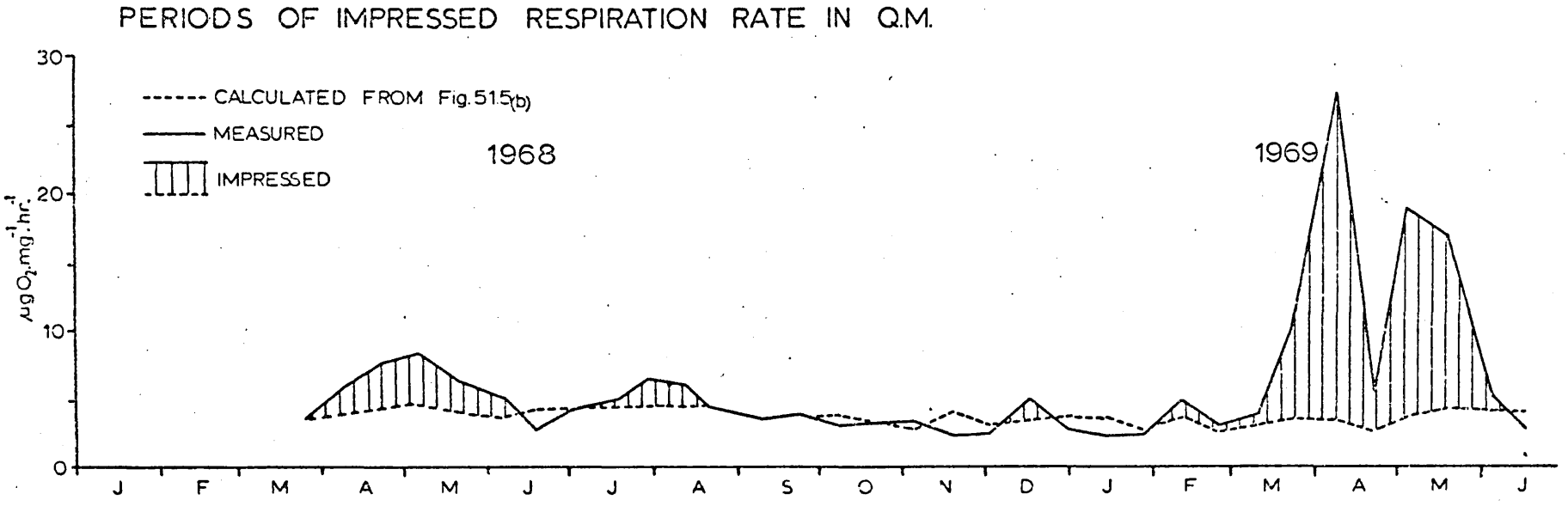

PERIODS OF IMPRESSED RESPIRATION RATE IN Q.M.
------ CALCULATED FROM Fig. 5.1.5(b)
—— MEASURED
IMPRESSED
1968
1969
μg O2.mg-1.hr-1
30
20
10
0
J F M A M J J A S O N D J F M A M J

Fig. 5.1.5(c).

suggests although no direct evidence of this is presented here as measurements of ingestion and assimilation were not made. DUNCAN (1975)$_a$ suggests that the filtering rate nay be depressed below its maximum due to the high concentration of detritus present in the water, although the critical limiting concentration suggested by RIGLER (1961 (a)) is lower than the algal plus detrital biomass present at the time. During the winter the sest-on has a larger proportion of detrital material present and overall lower concentrationsthan other periods of the year. This low quality, low quantity food source might, if BLAŻKA'S hypothesis is correct, depress the metabolic rate slightly during the winter months and cause a heightened period of metabolism in the spring when food becomes abundant. DUNCAN ET AL (1970) indicate that seston levels can decline dramatically during mid-summer and possibly cause corresponding dips in the zooplankton metabolic activity as occurs during late June 1968.

No obvious temperature effect can be seen on the respiratory rates of the zooplankton and regression analysis of respiration rate per unit weight against temperature shows no correlation even at the 20% level ($r = -0.1140$). However, the impressed rates of respiration that are seen in the spring occur at the time of year when the most rapid rate of rise in temperature occurs. At this time of the year the zooplankton, particularly the cladoceran fraction, may not be fully acclimated to the changing temperature in relation to its generation time. In spring this might cause the increase in thelevel of metabolic

activity that is observed in the field measurements. Figure 5.1.5(d) shows the mean respiration rate per unit weight from the field measurements plotted against the rate of change of temperature of the reservoir. The broken lineis highly speculative and fitted by eye but appears to demonstrate that with a positive increase in the rate of change of temperature there is a heightened metabolic rate. Increased negative rates cause a raised, but less easily distinguished, metabolic rate. Many more field measurements would be required to test the validity of this line but non-acclimatisation of the population metabolism might be a large contributory factor in the enhanced metabolic rate found in spring. A corresponding fall in metabolic rate in the autumn is less detectable as the rise in rate is less dramatic and, as with all these measurements, can be disguised by other factors such as population structure and food conditions.

Interpolation of laboratory respiration measurements into field population data gives an equally confused picture. Results obtained from laboratory experiments, described in section 5.2.3, are presented in figure 5.1.5.(e) together with a composite field line taken from the two years of the study. The dotted line ~~with the open circles~~ represents the respiration rate, calculated from the actual laboratory rates obtained applied without any temperature correction. This assumes that the field populations are fully acclimated to the field temperature. As can be seen, this derived line is consistently higher than the field measured line except during the spring period of 1969 when the measured field line is two to three times higher. Except during

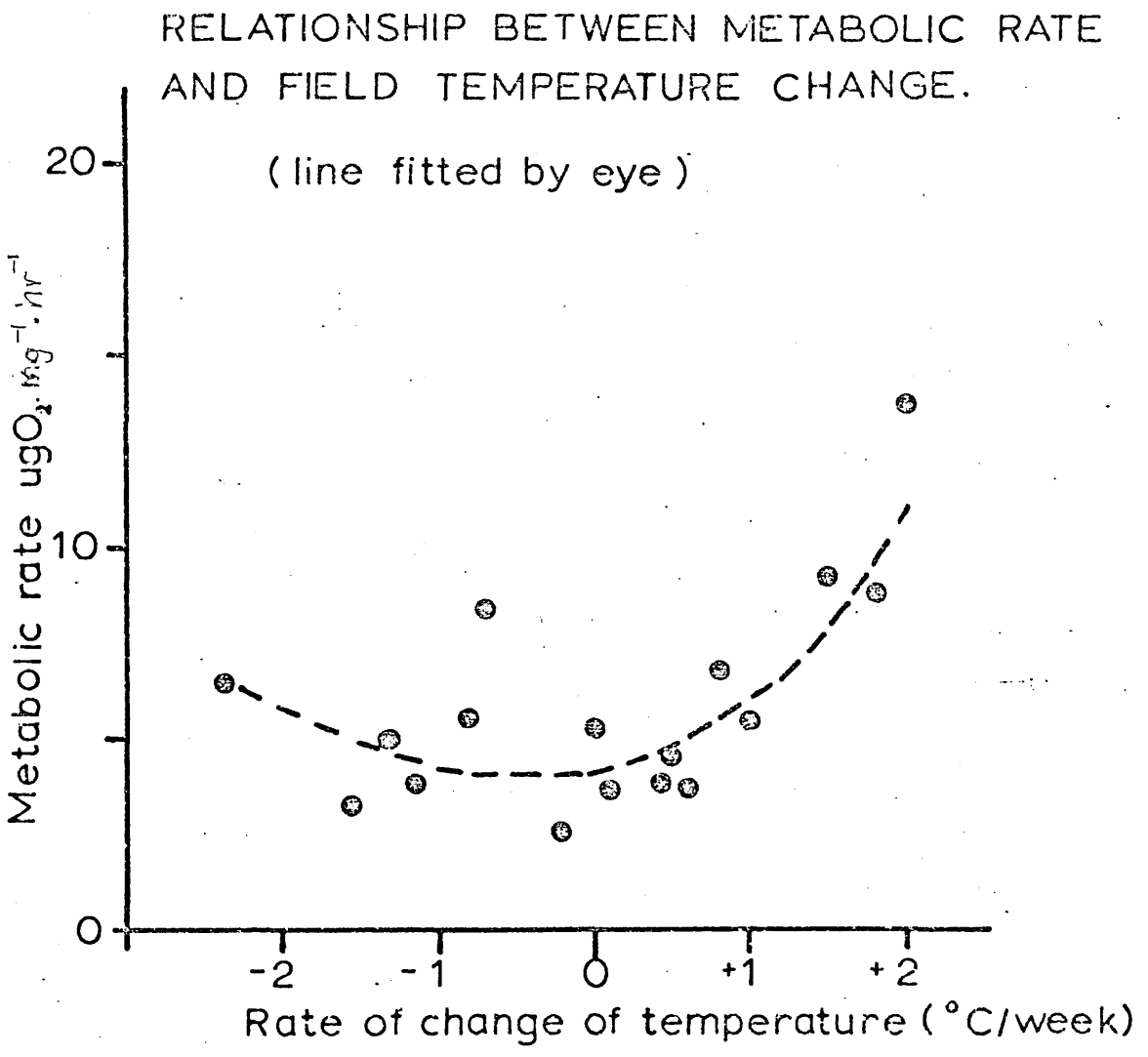

RELATIONSHIP BETWEEN METABOLIC RATE AND FIELD TEMPERATURE CHANGE.
(line fitted by eye)
20
10
0
Metabolic rate ugO2.mg-1.hr-1
-2
-1
0
+1
+2
Rate of change of temperature (°C/week)

Fig. 5.1.5(d).

CALCULATED RESPIRATION RATE OF ZOOPLANKTON IN Q.M.

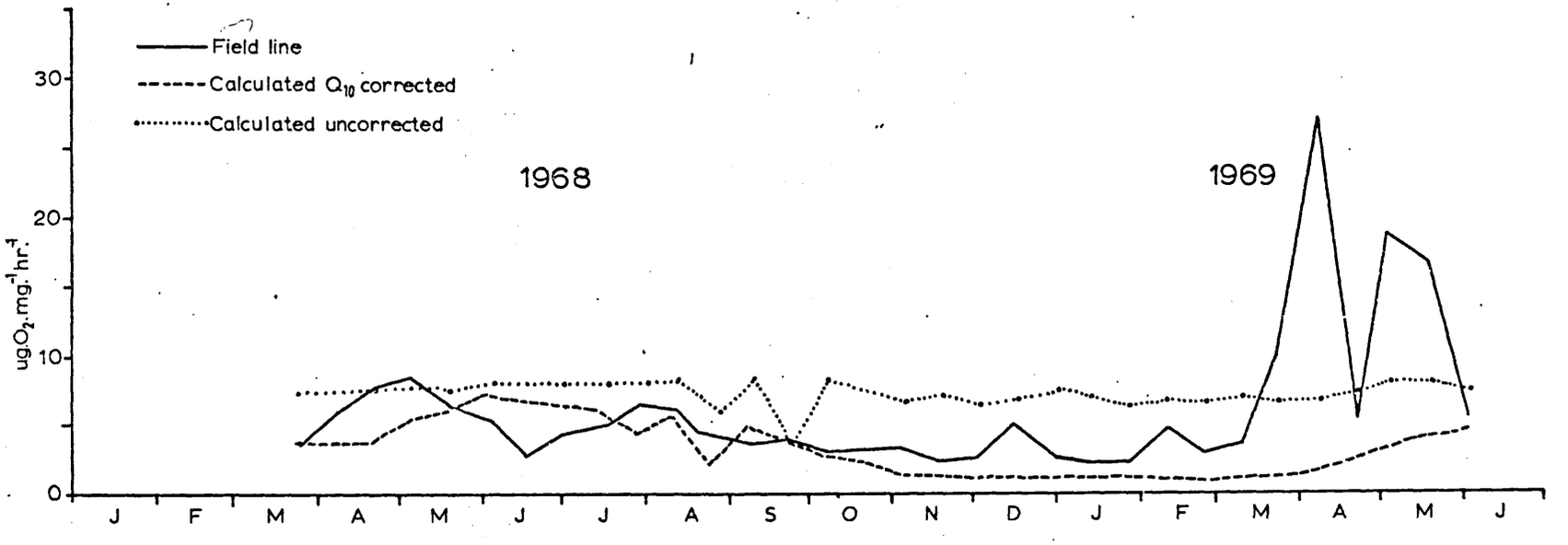


fig. 5.1.5(e)

one period in late September, and where the spring lines cross, the respiration rates from these laboratory calculations are one and a half to two times the field measurements.

The Q_{10} corrected line, which is calculated on the assumption that the laboratory measurements at 20°C were most satisfactory, as the nutritional state may have been better, gives a fair degree of agreement from August to the end of November but underestimates the respiration rate during the winter and spring and overestimates it during the early summer. Using the 10°C line, Q_{10} corrected, the same pattern is observed except that the correspondence occurs with the winter respiration rates. As might be expected, the Q_{10} corrected line shows a direct correlation with the observed field temperature.

Neither the fully acclimated laboratory line or the Q_{10} corrected laboratory lines give a satisfactory approximation to the field measured lines except at occasional times of the year. The explanation of this difference is obscure.

The work of CREMER AND DUNCAN (1969) provides the only directly comparable study of field metabolic rate measurements in zooplankton populations. Their results appear to show a temperature–metabolic relationship during the summer but not during the winter or spring where the calculated values are twice the measured rate. They also look for explanations other than a simple temperature function and explain discrepancies in terms of diet and population structure for spring and autumn. The seasonal pattern they show is slightly different

from that of the present study but differences may be due to differences of sampling interval and the differences found in zooplankton populations found from year to year. The values for the metabolic rates they show are in the same order of magnitude as results found in this study. BISHOP (1968) and GANF AND BLAŽKA (1974) report a temperature dependent metabolic relationship with their experiments but these were laboratory based and involved rapid acclimation to the new temperatures.

The conclusions to be drawn from the field results are tentative and much more field and laboratory work needs to be undertaken to verify these. Results obtained are obviously different from laboratory measurements interpolated into field population data. The seasonal pattern of events appears to be as follows: during the winter and summer, when the ambient temperature is stable for longish periods, the zooplankton metabolic rates are temperature adapted. These may be depressed during the winter by poor quality or insufficient food resources. During the spring the metabolic rate is raised by two to three times its expected level caused by a combination of the following factors: (a) a rapid rise in the rate of temperature change leading to unacclimatised animal populations (b) improvement in the quality and quantity of the food and (c) a change in the weight-specific metabolic rate caused by changes in the population structure. Summer levels are normally enhanced by the presence of significant numbers of other, smaller, species such as Diaptomus gracilis and Bosmina longirostris. The autumn rates are raised , but this is less obvious than the spring changes, by the rapid fall in environmental temperature which leads to unacclimatised populations.

5.1.6. FIELD ASSIMILATION

It is widely accepted that assimilation is equal to the sum of the production and respiration of an individual animal (MACFADYEN 1963 and PETRUSEWICZ AND MACFADYEN 1970) and that this may be applied to populations (MACFADYEN 1963 and EDMONDSON AND WINBERG 1971), thus

(i) $A = P + R.$

For this study the daily production rate for the zooplankton was estimated from the sum of the daily production rates of the daphnids and copepods described in section 5.1.4 calculated from the product of the respective P/B ratio and standing crop biomass.

(ii) $P_{total} = P_{daphnids} + P_{copepods}.$

The population respiration was calculated from the product of the hourly field respiration rate (section 5.1.5) and the standing crop biomass multiplied up for a daily value.

(iii) $R_{daily} = R.B.24.$

No account has been taken of any possible diurnal fluctuation of respiration rate. At sample periods where no respiration rate was measured, values have been estimated from the adja cent values and the early period of 1968 from measured 1969 values at the same period and appropriate temperature. All results except where otherwise stated are on a daily basis. In this section different elements of the study are compared and a common unit is used and that is taken to be unit carbon per metre square ($g.C.m^{-2}$) following the practice of STEEL ET AL (1972). This approach has been used by other workers studying the zooplankton (GEORGE AND EDWARDS 1974) but is more frequently found in algalogical studies (e.g. STEEL 1972). To

facilitate this approach it has been assumed that:

gC = g.dryweight.0.44. (as a measure of P)

gC = gO_2.0.375 (assuming an R.Q. = 1.0). (as a measure of R assuming carbohydrate metabolism)

g.C = g chlorophyll a.30.

The daily assimilation rate of the zooplankton population for the course of the study is shown in figure 5.1.6(a) and this is drawn on a logarithmic scale. The figure also shows the standing crop of the algal population. The contributions of daphnid and copepod production and the respiration of the population to the total assimilation are distinguished. It can be seen that the standing crop of algal carbon is usually an order of magnitude higher than the zooplankton assimilation except towards the end of the spring algal peak when assimilation approaches the total available algal carbon (in 1969 this is exceeded). The zooplankton assimilation peaks can be seen to follow the algal peaks and tend to be proportional to the available algae. STEEL ET AL (1972) draw attention to the fact that assimilation efficiences of the Cladocera are normally less than 50% (RICHMAN 1958) and therefore the actual carbon demand may well be more than twice the assimilation levels shown here. At certain times of the year, particularly during the winter, detrital carbon may provide another significant source of food and this is found in quantities between 4.0 and 600 mg $C.m^{-3}$ (STEEL pers. comm.). However, there is evidence that although this provides a food source at certain times of the year it is likely to provide a poor quality diet. It is more rewarding to relate zooplankton assimilation to other daily "gains" and "losses" of carbon in the system as attempted by STEEL ET AL. (1972) - see paper attached in Appendix 5.3 - but as the algal primary

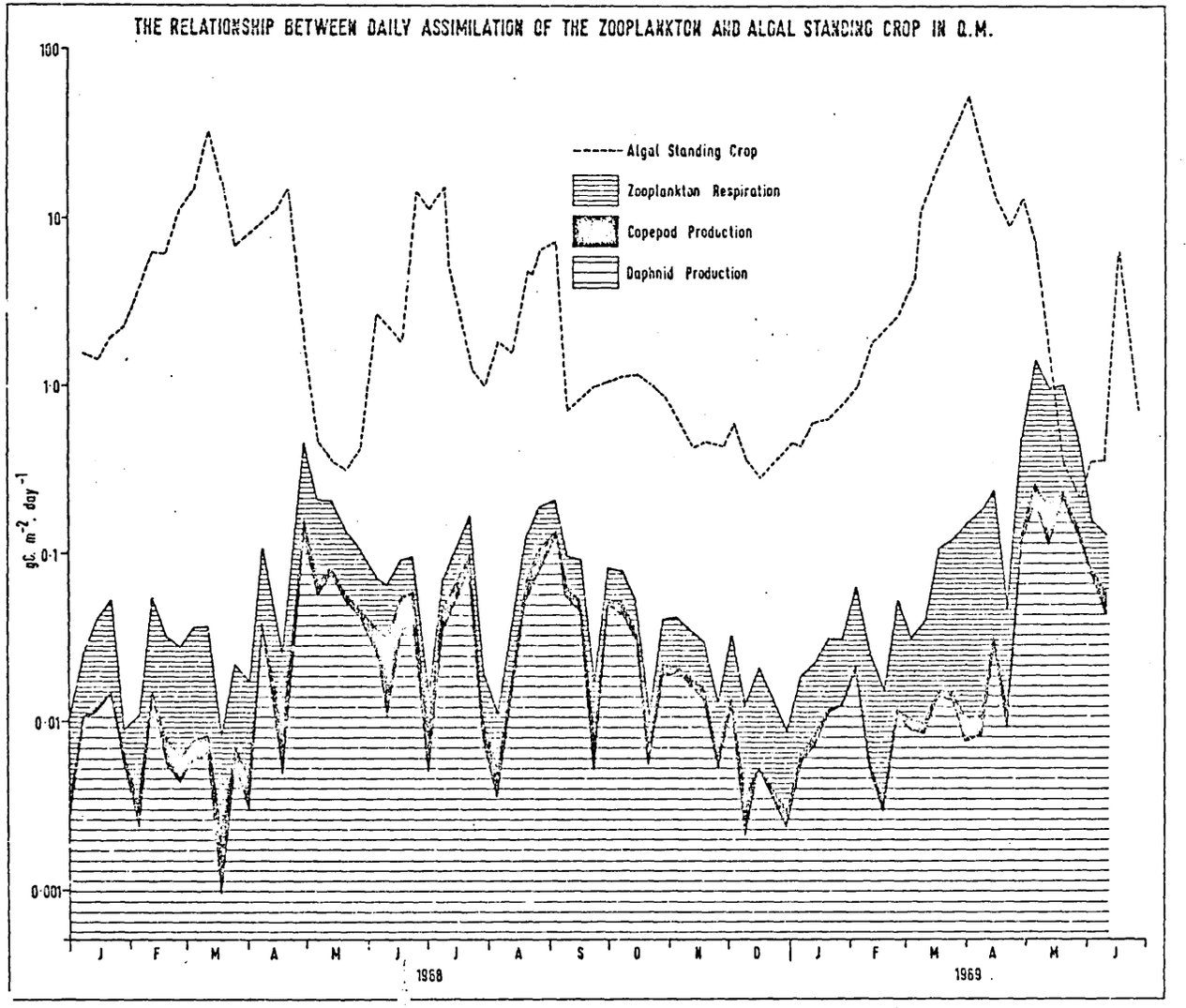

THE RELATIONSHIP BETWEEN DAILY ASSIMILATION OF THE ZOOPLANKTON AND ALGAL STANDING CROP IN Q.M.
Algal Standing Crop
Zooplankton Respiration
Copepod Production
Daphnid Production
gC. m⁻². day⁻¹
100
10
1·0
0·1
0·01
0·001
J F M A M J J A S O N D J F M A M J
1968
1969

Fig. 5.1.6(a).

production rates and much other necessary information were not determined as part of this study it has been deemed inappropriate here.

The figure also reveals the extent of the daphnid contribution to the total production rate which is the main component of the zooplankton and the tacit assumption is that the zooplankton is herbivorous. This is certainly not true of all adult copepods, some adult Cyclops spp. being carnivorous but Diaptomus copepodites and adults are phytoplankton feeders (KIBBY 1969) and there is evidence that Daphnia spp. are more omnivorous than the literature shows (NADIN-HURLEY AND DUNCAN, 1976).

The respiration component of the zooplankton assimilation varies at different times of the year, being high in the winter and during spring peaks and low in the summer. The total amount of energy needed for respiratory maintenance occurs just before and during the spring peaks of zooplankton production. The ratio of production to assimilation (K_2) more effectively describes this situation where

$$\text{(iv)} \quad K_2 = \frac{P}{A} = \frac{P}{P+R}$$

which is analagous to the K_2 values described in section 5.2.4. The daily K_2 values are shown in figure 5.1.6(b) together with the existing field temperature. There is a very strong correlation between K_2 and temperature but this might be expected as production and respiration to some degree have been shown to be functions of temperature (see Sections 5.1.4 and 5.1.5). What is interesting is that for over half the year the respiration element of the assimilation exceeds the

RATIO OF PRODUCTION TO ASSIMILATION (K_2) FOR FIELD ZOOPLANKTON POPULATIONS. Q.M.

fig. 5.1.6.(b)

production and most of the available energy is used for maintenance of the population although this period includes the highest period of production. The heightened spring and autumn metabolism creates a higher demand on the available carbon than the summer levels. K_2 values will be affected not only by temperature but by quality and quantity of available food as well as the specific composition of the plankton but it must be repeated that these K_2 values demonstrate a remarkable sensitivity to even relatively small changes in field temperature.

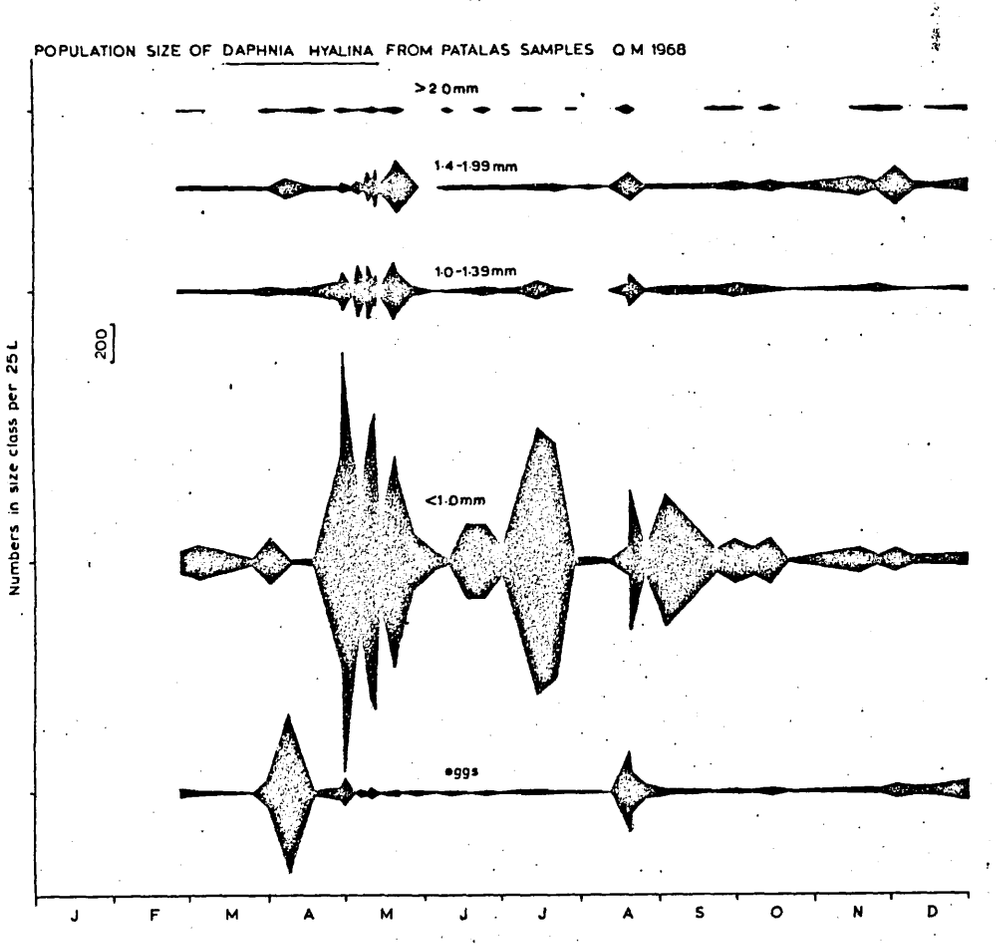
Footnote

The assimilation values for zooplankton given above are very similar to the values shown by STEEL ET AL. (1972) but the values used to satisfy equation (i) were obtained by different methods. The laboratory respiration estimates probably underestimate this demand while the calculated production (as in section 5.1.4, method A) probably overestimates this fraction.

5.1.7. PATALAS SAMPLING

Patalas samples were taken from February 1968 until the end of the study. These samples were used principally to check and calibrate the net sampling procedure as described in section 4.1.2. They were also used to provide the five litre sampling unit for the field respiration measurements (section 4.3.1). However they also provide a body of information on the seasonal depth distribution of the zooplankton and as this has not been recorded in the literature before, these data have been presented here. Most depth-distribution descriptions have been limited to a short period of time such as one or two days and describe the diurnal vertical migrations of the zooplankton (see HUTCHINSON 1967 for review and ANGOLD 1968 for work on M.W.B. reservoirs).

Population fluctuations from Patalas samples for the Q.M. are shown in figure 5.1.7.(a) for D. hyalina field size classes as kite diagrams. The figures presented represent an averaged value for each sampling date in a 25L sample. It can be clearly seen in the figure how peak egg numbers precede peak numbers in the immature size classes except before the June and July peak of 1968. During these peak periods, the egg numbers are not sufficient to account for the subsequent population changes and this may be due either to unsatisfactory egg estimates (insufficient females with eggs counted) or to another source of immature animals. Subsequent work of DUNCAN (pers. comm.) suggests that ephippial hatching may account for this difference in numbers but import of juveniles from the


POPULATION SIZE OF DAPHNIA HYALINA FROM PATALAS SAMPLES Q M 1968
>2·0mm
1·4-1·99mm
1·0-1·39mm
200
<1·0mm
eggs
Numbers in size class per 25L
J F M A M J J A S O N D

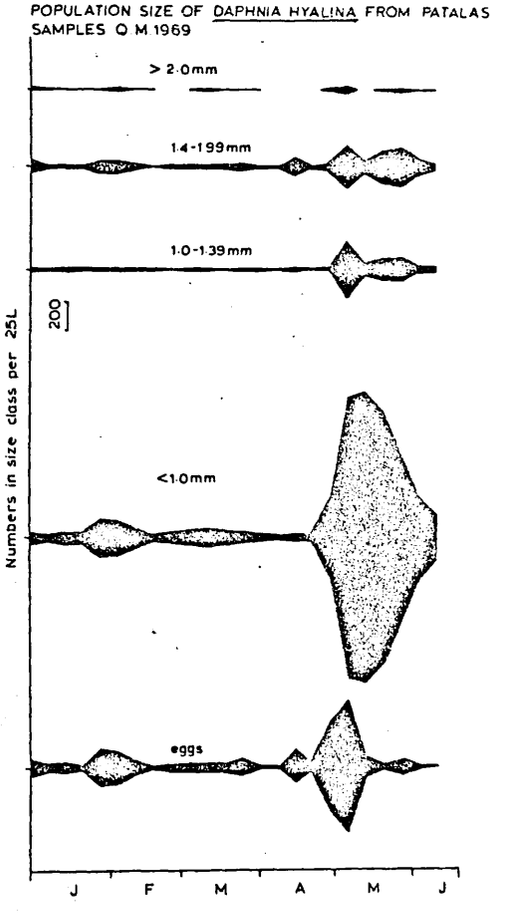
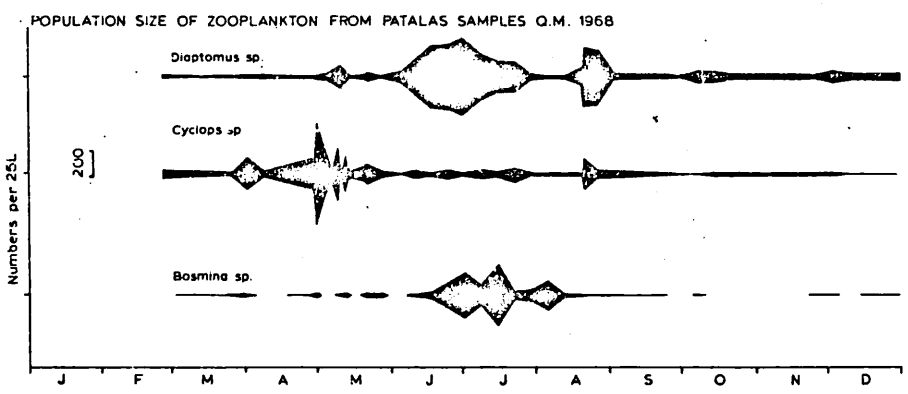

POPULATION SIZE OF DAPHNIA HYALINA FROM PATALAS SAMPLES Q M 1969
> 2·0mm
1·4-1·99mm
1·0-1·39mm
200
<1·0mm
eggs
Numbers in size class per 25L
J F M A M J

Fig. 5.1.7(a).

river may also contribute part of the population. The winter numbers of November 1968 to March 1969 show that egg and immature stage numbers are very similar which suggests that the population structure remains fairly stable during this period. A more sophisticated comparison may be made by comparing the relationship between numbers and duration rates for eggs and immature stages and this confirms the above observation, Ne/De : Nimm/Dimm. The rapid fluctuations of the population during the spring of 1968 is probably an artefact of close interval sampling and does not occur in 1969 when samples were taken at weekly intervals. In other respects the samples showed the same characteristics as the net samples (see section 5.1.2.).

Figure 5.1.7.(b) shows Patalas samples for the other principal zooplankton as averaged 25L samples. This figure shows that Bosmina sp. is found intermittently throughout the year and reaches a population maximum in late June and July. Cyclopoid copepods occur mainly in the spring reaching peak numbers in late April and May of both years studied. Diaptomid copepods follow the cyclopoids and peak in June and July with a second peak in late August. Winter populations of Cyclops sp and Diaptomus sp. are consistently low.

The time depth distribution of the zooplankton is shown in figures 5.1.7.(c), (d), (e), (f), and (g),. As samples were normally taken during the morning no observations are possible about diurnal depth fluctuations although these might be considerable (M^{c}CLAREN 1963). It is very difficult to determine a simple pattern of time-depth distribution but it seems


POPULATION SIZE OF ZOOPLANKTON FROM PATALAS SAMPLES Q.M. 1968
Diaptomus sp.
Cyclops sp
Bosmina sp.
200
Numbers per 25L
J
F
M
A
M
J
J
A
S
O
N
D

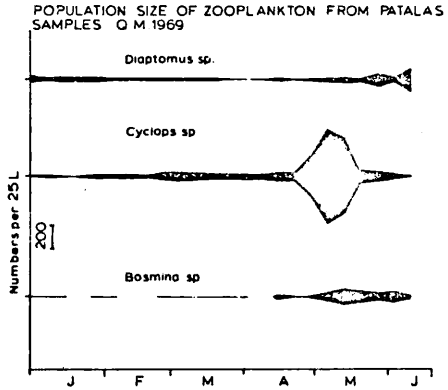
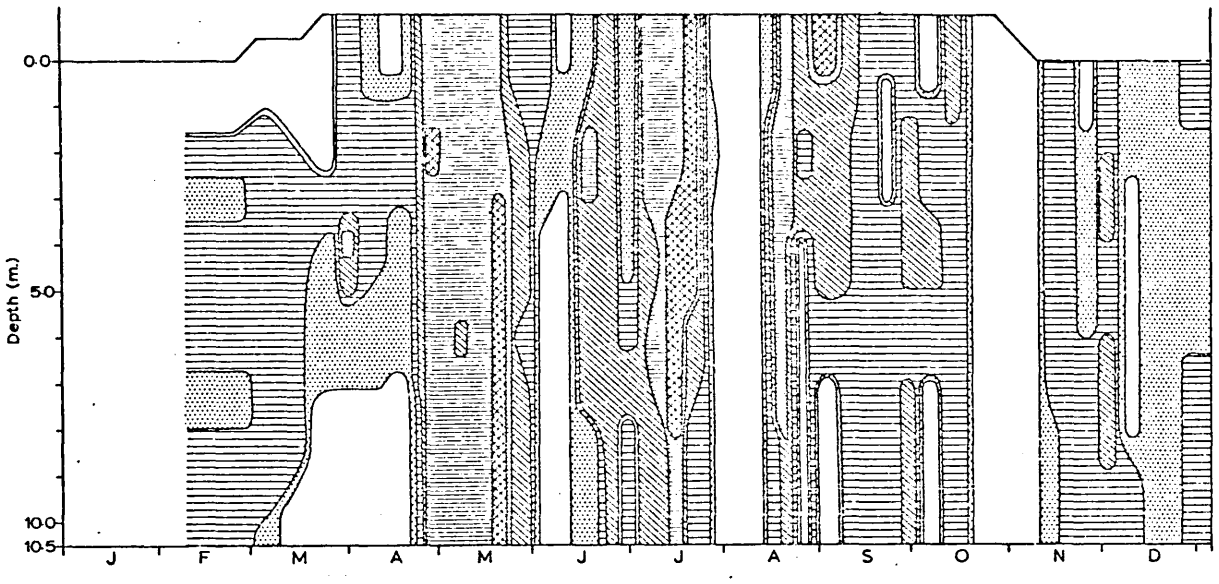

POPULATION SIZE OF ZOOPLANKTON FROM PATALAS SAMPLES Q M 1969
Diaptomus sp.
Cyclops sp
Bosmina sp
200
Numbers per 25L
J
F
M
A
M
J

Fig. 5.1.7(b).

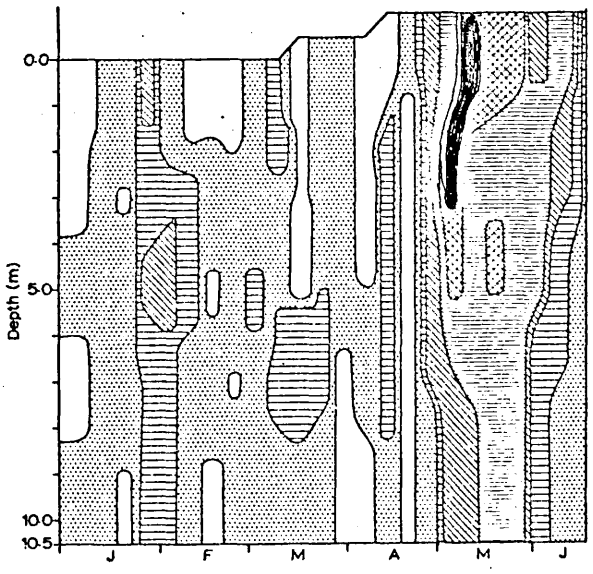
QUEEN MARY RESERVOIR 1968

TIME-DEPTH DISTRIBUTION OF DAPHNIA POPULATION (NOS./5L PATALAS SAMPLE)



QUEEN MARY RESERVOIR 1969

TIME-DEPTH DISTRIBUTION OF DAPHNIA POPULATION (NOS./5L PATALAS SAMPLE)



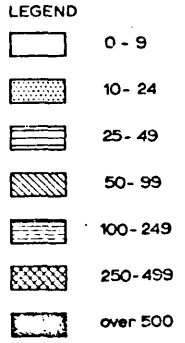


Fig. 5.1.7(c).

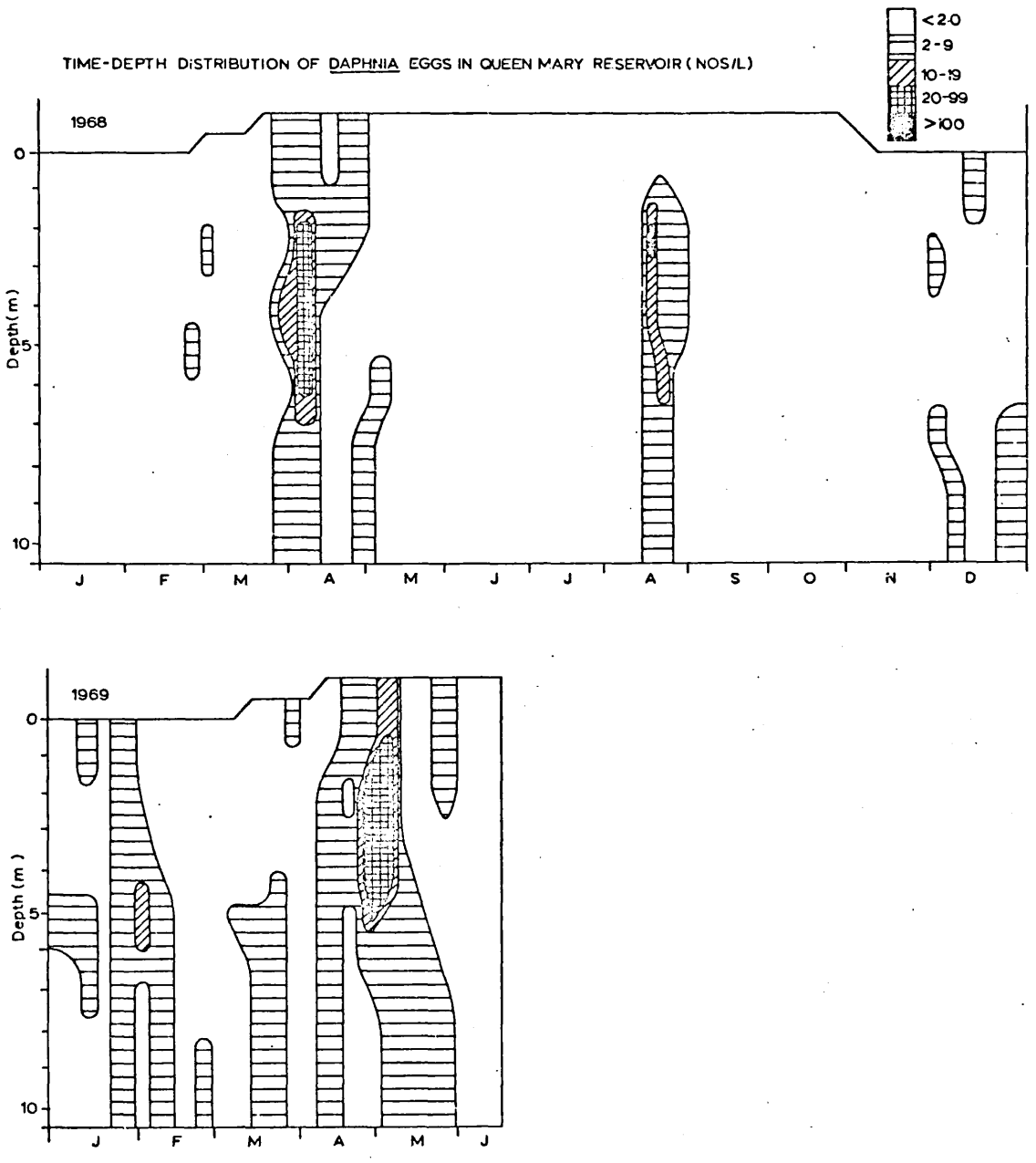

TIME-DEPTH DISTRIBUTION OF DAPHNIA EGGS IN QUEEN MARY RESERVOIR (NOS/L)
<2·0
2-9
10-19
20-99
>100
1968
Depth (m)
0
5
10
J
F
M
A
M
J
J
A
S
O
N
D
1969
Depth (m)
0
5
10
J
F
M
A
M
J

Fig. 5.1.7(d).

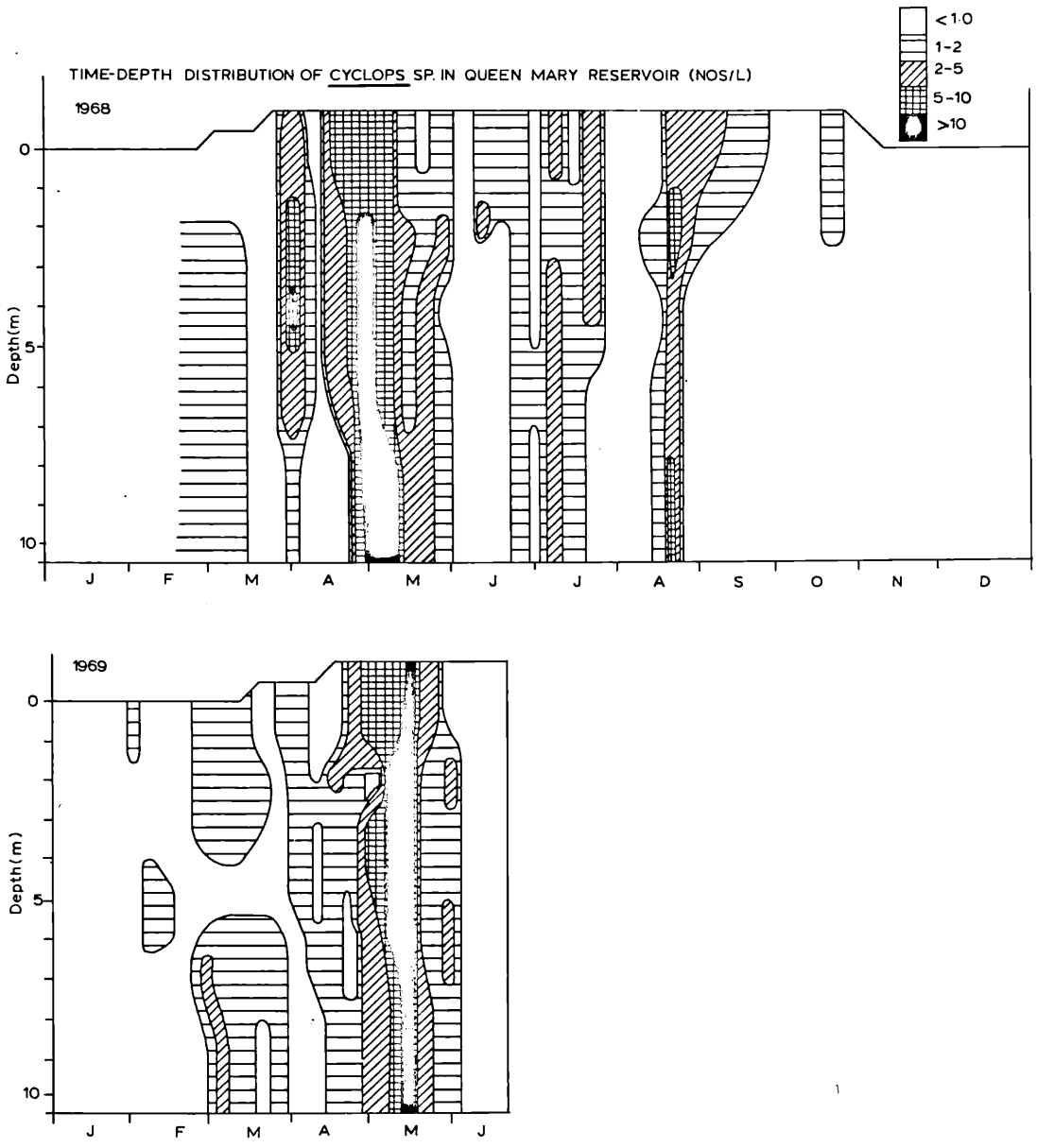

TIME-DEPTH DISTRIBUTION OF CYCLOPS SP. IN QUEEN MARY RESERVOIR (NOS/L)
<1·0
1-2
2-5
5-10
>10
1968
Depth(m)
0
5
10
J
F
M
A
M
J
J
A
S
O
N
D
1969
Depth(m)
0
5
10
J
F
M
A
M
J

Fig. 5.1.7(e).

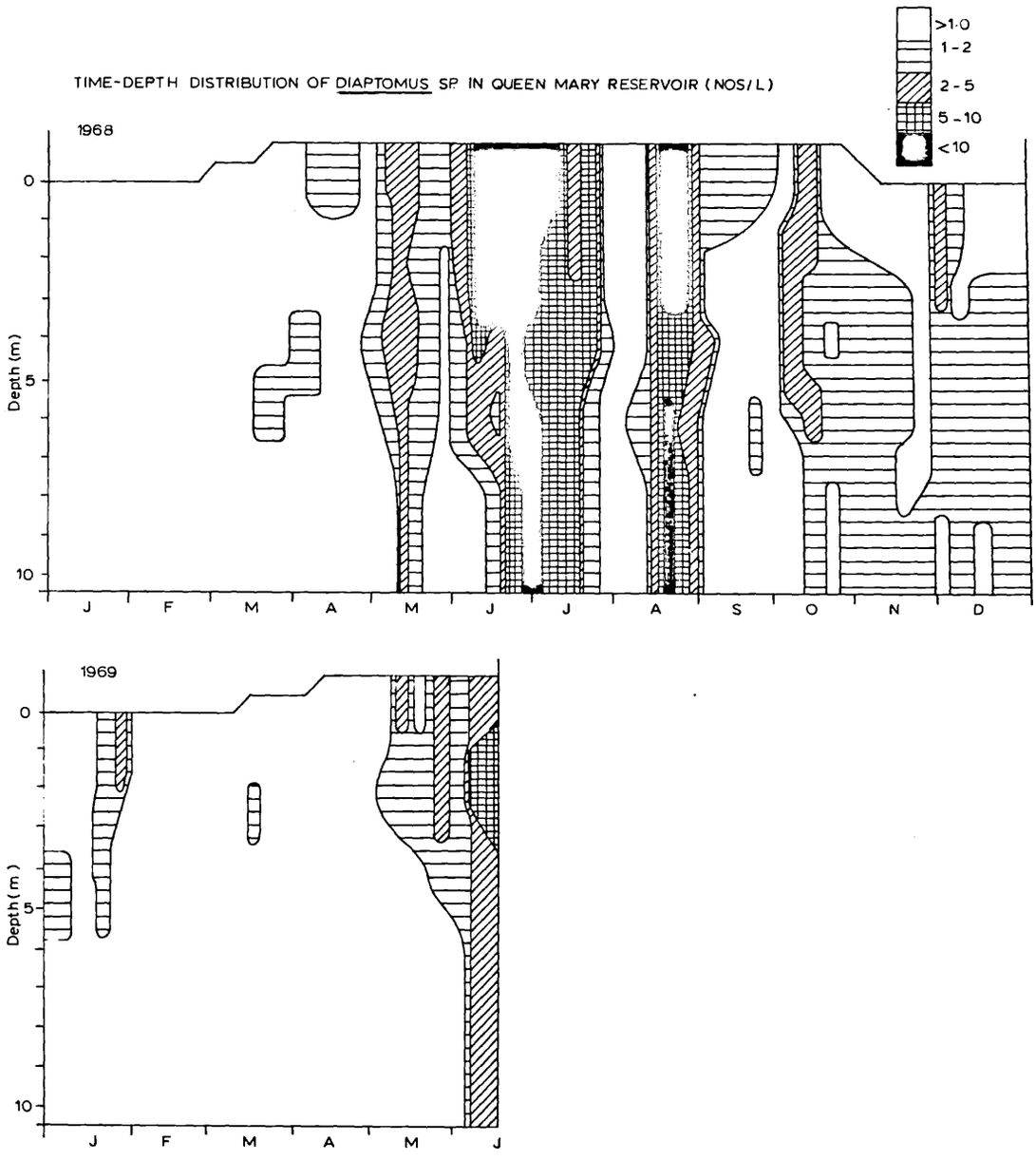

TIME-DEPTH DISTRIBUTION OF DIAPTOMUS SP. IN QUEEN MARY RESERVOIR (NOS/L)
>1·0
1-2
2-5
5-10
<10
1968
Depth (m)
0
5
10
J
F
M
A
M
J
J
A
S
O
N
D
1969
Depth (m)
0
5
10
J
F
M
A
M
J

Fig. 5.1.7(f).

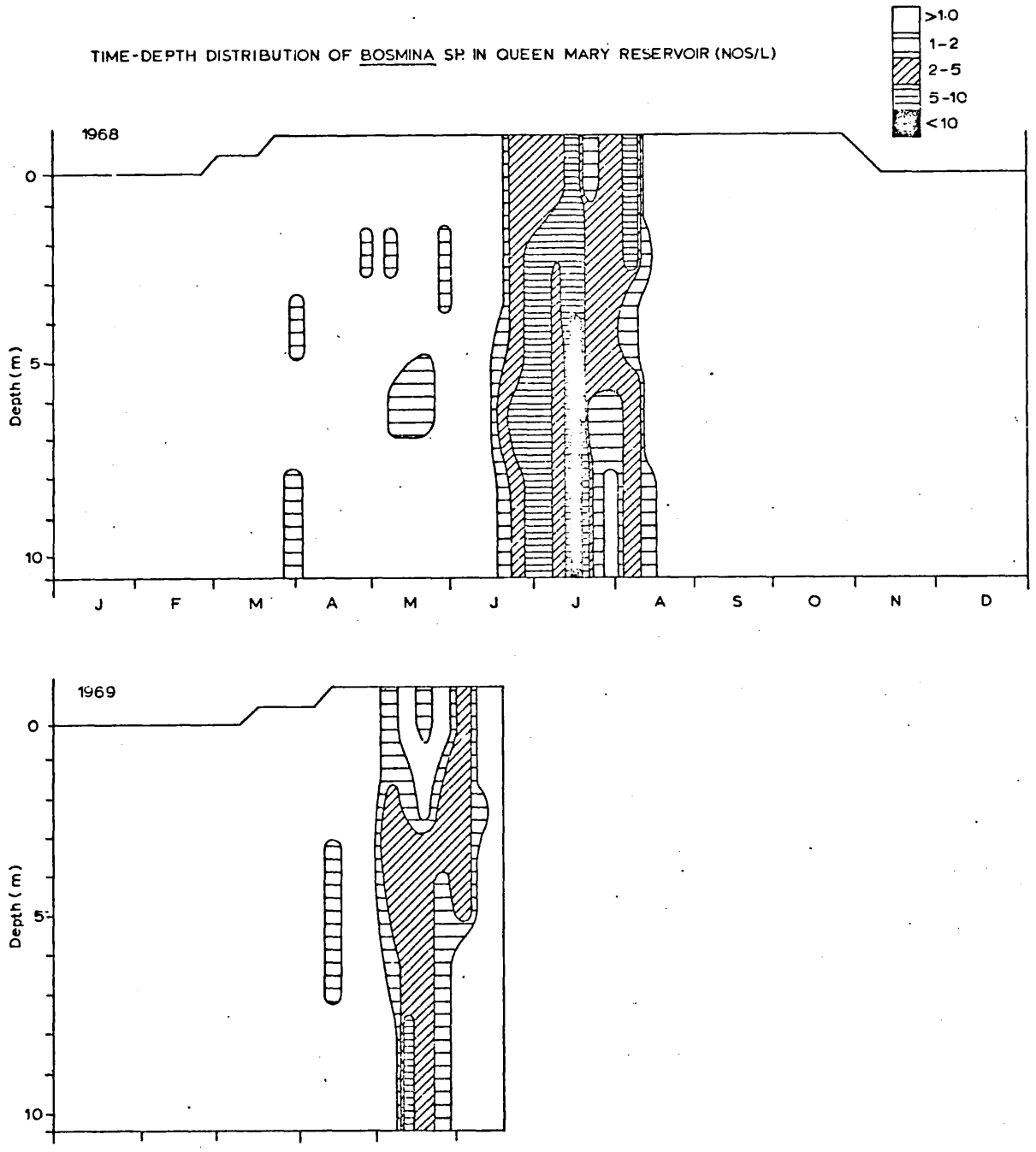

TIME-DEPTH DISTRIBUTION OF BOSMINA SP. IN QUEEN MARY RESERVOIR (NOS/L)
>1·0
1-2
2-5
5-10
<10
1968
1969
Depth (m)
0
5
10
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 5.1.7(g).

likely that the distributions seen are the result of three different factors. The classical description of vertical migration includes a dawn and evening rise for the zooplankton and a gentle sinking during the night and day. As samples were taken in the morning after dawn, they are likely to be in the sinking portion of the migration. . HARRIS (1953) suggests that zooplankton vertical migrations are an adaptive response to be in the regions of most satisfactory food conditions. If this simple view is accepted then the zooplankton will predominate in the deeper waters during the winter when detrital carbon is likely to be most important and the situation is reversed in other parts of the year when the diet is mainly algal and optimum conditions occur in the upper few metres of the water. A second factor that might affect distribution might be thermal stratification which does occur transiently during spring, summer and autumn and may be responsible for localised concentrations of zooplankton during these periods. The third factor is the extent of the duirnal migration itself, which may be masked by the first two factors mentioned. There is experimental evidence (see HUTCHINSON 1967) that vertical migration in daphnids is controlled by different wavelengths of light but the size of the animals might also affect the distance of the migration and there are indications that sexual differences in copepods may contribute behavioural differences (HART AND ALLANSON, 1976). ANGOLD (1968) examined the duirnal distribution of zooplankton in an M.W.B. reservoir (King George VI, Staines) during one 48 hour period but her results are difficult to generalise from as they covered the period of an overturn of the water mass.

Figure 5.1.7.(c) shows the distribution of D. hyalina to be fairly uniform throughout the depths except that winter concentrations, when they occur, tend to be in the mid and lower waters (5 to 10.5m) whereas spring and summer concentrations are normally seen above five metres. This may best be seen as a food related response and the situation is the same for both years of the study. Egg distribution, which is related to the distribution of (normally) large gravid females, show eggs to be concentrated between three and seven metres during the spring and autumn egg peaks and below five metres during the winter; at other times of the year they are fairly evenly distributed (figure 5.1.7.(d).

The cyclopoid copepods (figure 5.1.7(e) show a confusing distribution. Winter concentrations are found towards the bottom and at other times of the year in the middle water, three to seven metres, except during May 1968 when the biggest concentrations were at nine metres. During the autumn the cyclopoid populations are concentrated near the surface. The cyclopoid distribution is probably a predominantly food related response. The diaptomids aggregate near the bottom during the winter and towards the surface during peak periods (June/July and late August). This can be seen in figure 5.1.7.(f).

Bosmina sp. (figure 5.1.7.(g) appeared earlier in 1969 than 1968 and during the spring of 1969 were found mainly below three metres with the biggest concentrations at the bottom. In 1968 the animals were

found mainly below three metres with biggest concentrations below five metres except that immediately before the population crashed the greatest densities were found near the surface.

5.1.8. QUEEN ELIZABETH II RESERVOIR

The sampling programme for the Q.E.II. was restricted to taking direct biomass measurements by vertical net hauls at approximately fortnightly intervals. During this part of the study KIBBY (1969) took samples at weekly intervals to examine the Diaptomus gracilis populations and he has also reported mean numbers of Bosmina sp., Daphnia sp and Cyclops sp in addition to the fluctuations in the calanoid copepod population. Three species of Daphnia coexist in the Q.E.II although not throughout the full season, D. hyalina, D. pulex and D. magna, D. magna is normally associated with shallower bodies of water and its appearance in the Q.E.II is curious and probably related to the management of the reservoir.

The standing crop of the zooplankton is seen in figure 5.1.8(a) for the course of the study. The same pattern for the daphnids, as was seen for the Q.M., is exhibited with the highest crops occurring in the spring (mid May 1968 and early June 1969) when the crops reached 8.471 $g.m^{-2}$ dry weight in 1968 and 6.515 $g.m^{-2}$ dry weight in 1969. These values are about twice those recorded in the Q.M. but in fact the largest crops were recorded in different years. The winter levels were low, between 0.135 $g.m^{-2}$ and 2.234 $g.m^{-2}$ 1967/68 and considerably lower in 1968/69. The spring peak in 1969 occurs later in the year and this may be related to the fact that the temperature rise occurred later in this year. The summer levels remain fairly high and there are indications that there was an autumnal peak in late September and October although the sampling frequency

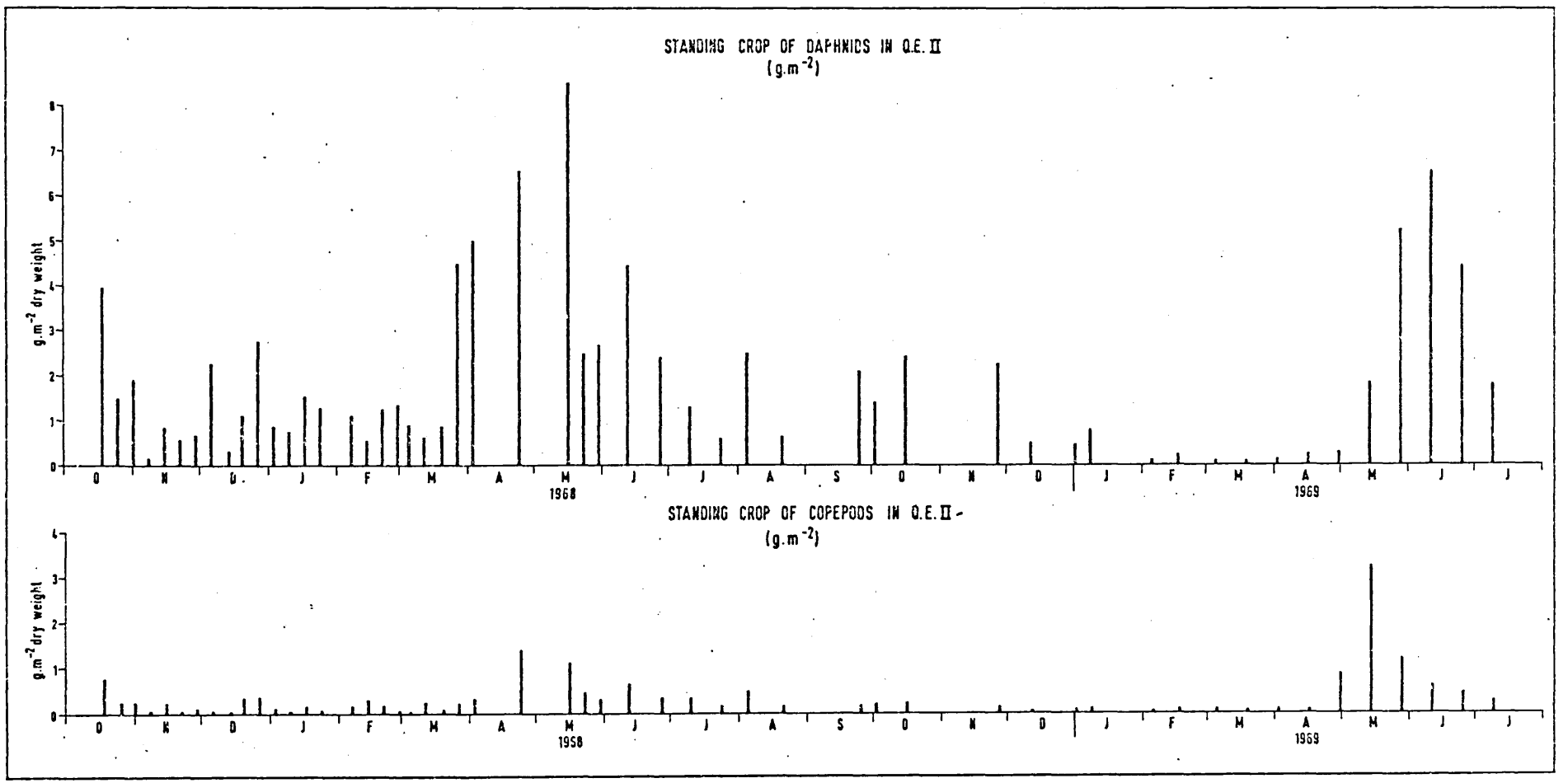

STANDING CROP OF DAPHNIDS IN Q.E. II
(g.m⁻²)
g.m⁻² dry weight
0 1 2 3 4 5 6 7 8
O N D J F M A M J J A S O N D J F M A M J J
1968
1969
STANDING CROP OF COPEPODS IN Q.E.II -
(g.m⁻²)
g.m⁻² dry weight
0 1 2 3 4
O N D J F M A M J J A S O N D J F M A M J J
1968
1969

Fig. 5.1.8(a).

was poor at this time making observations speculative. The average daily standing crop during 1968 was 2.365 $g.m^{-2}$ which is equal to 0.138 $g.m^{-3}$ (comparable results for Q.M. are 0.645 $g.m^{-2}$ and 0.0537 $g.m^{-3}$).

The standing crop of the copepods during the course of the study can also be seen in figure 5.1.8(a) and here not only the levels but also the measured values of the copepod standing crop are similar in the Q.M. Peaks occur in both spring periods slightly before the main daphnid peaks and the maximum standing crop of each year occurred at this time (1.391 $g.m^{-2}$ 1968 3.275 $g.m^{-2}$ 1969). The autumn peak seen in the Q.M. is not revealed here, again probably because of the infrequent sampling at this time. The average daily standing crop during 1968 was 0.299 $g.m^{-2}$ (0.018 $g.m^{-3}$), the corresponding figures for the Q.M. are 0.253 $g.m^{-2}$ (0.021 $g.m^{-3}$)

It is not possible to estimate production directly in the Q.E.II as no data are available from population counts to satisfy the equations to calculate this. However an approximate estimate may be obtained by using the P/B values obtained for the Q.M. (section 5.1.4) and applying these to the population standing crop of daphnids. This suffers from the obvious criticism that three different species of daphnids were present and each of these may have different growth characteristics and this is especially true of D. magna which is a much larger species (specimens of over 6 mm in length carrying more than 400 eggs were caught in samples during March 1968). But the P/B values obtained for the Q.M. fall well within the range given by other workers

(see table 5.1.4(b)) and SCHINDLER (1972) finds similar P/B values for the same temperature with D. magna . Therefore an estimate of production using this method is presented in figure 5.1.8(b) with reservations about the values presented. The P/B values used have been applied on the basis of the same field temperature at the same period of the year.

The daily production rates for the Q.E.II are higher than the Q.M. as would be expected as the standing crop is larger. The maximum rate, 0.780 $g.m^{-2}.$ day^{-1} occurs in late May 1968 and the levels remain consistently high through the summer although large fluctuations do occur. The lowest levels of daily production are recorded in March 1969, 0.002 $g.m^{-2}.$ day^{-1} and during this pre-spring period the production rate was consistently low but rises steadily to the high values in late June. The annual production of the Q.E.II was calculated to be 82.185 $g.m^{-2}$ which is equivalent to 4.834 $g.m^{-3}.yr.^{-1}$ The annual P/B ratio for the reservoir may therefore be calculated as 34.75 which is high but in the same order of magnitude as other workers. The spring production peak in 1969 came more than a month after the 1968 peak, the production up until the same time in early July being 35.33 $g.m^{-2}$ in 1969 and 48.34 $g.m^{-2}$ in the corresponding period in 1968. This may be due principally to two factors. Firstly the spring rise in temperature of the water body was delayed by cold weather (see temperature lines in figure 3.1. (f) and secondly that the overwintering population is very much smaller in 1969 thus not giving the population the good growing start it

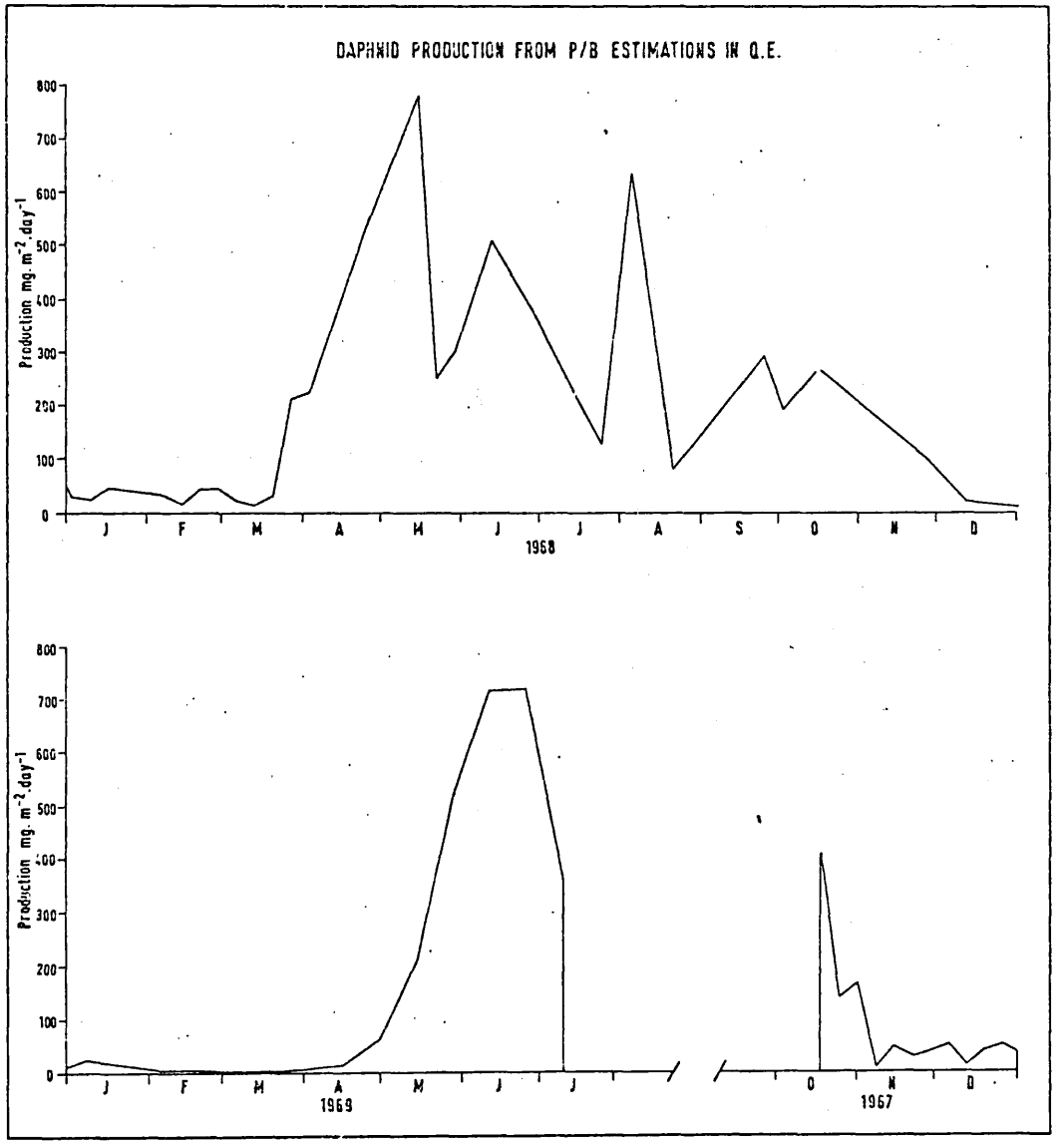

DAPHNID PRODUCTION FROM P/B ESTIMATIONS IN Q.E.
Production mg.m-2.day-1
800
700
600
500
400
300
200
100
0
J F M A M J J A S O N D
1968
Production mg.m-2.day-1
800
700
600
500
400
300
200
100
0
J F M A M J J
1969
O N D
1967

Fig. 5.1.8(b).

had in 1968.

The daily production rates for the copepod populations in the Q.E.II are shown in figure 5.1.8(c). These also have been obtained by multiplying the P/B ratio obtained in the Q.M. for the copepod populations by the standing crop. The criticisms of the method are the same as for its rise in the Q.M, in addition to the (unknown) differences in population structure prevailing in the Q.E.II. However, examination of the data of KIBBY (1969) shows that the population structure of the copepod populations is very similar in both reservoirs and this treatment provides at least an approximate estimate of copepod production.

The values for daily production fall within the range 0.39 to 210.65 mg dry weight.m^{-2}. day which is very similar to the Q.M. The maximum value was achieved in May 1969 but a comparable value may well have been reached in May 1968 when sampling was less frequent the rates of production are high in the spring and autumn but the winter levels fall extremely low in both years of the study. The annual production of copepods in the Q.E.II is calculated to be 6.334 $g.m^{-2}$. for 1968 which is the equivalent to 0.373 $g.m^{-2}$. The metre square column value is higher than the Q.M. (5.286 $g.m^{-2}$) but the metre cube value is lower (Q.M. = 0.440 $g.m^{-3}$.). The total production until the end of June in 1969 was higher than in 1968 (4.553 $g.m^{-2}$ and 6.488 $g.m^{-2}$ respectively) but, as has been indicated, these values may be distorted by inadequate sampling.

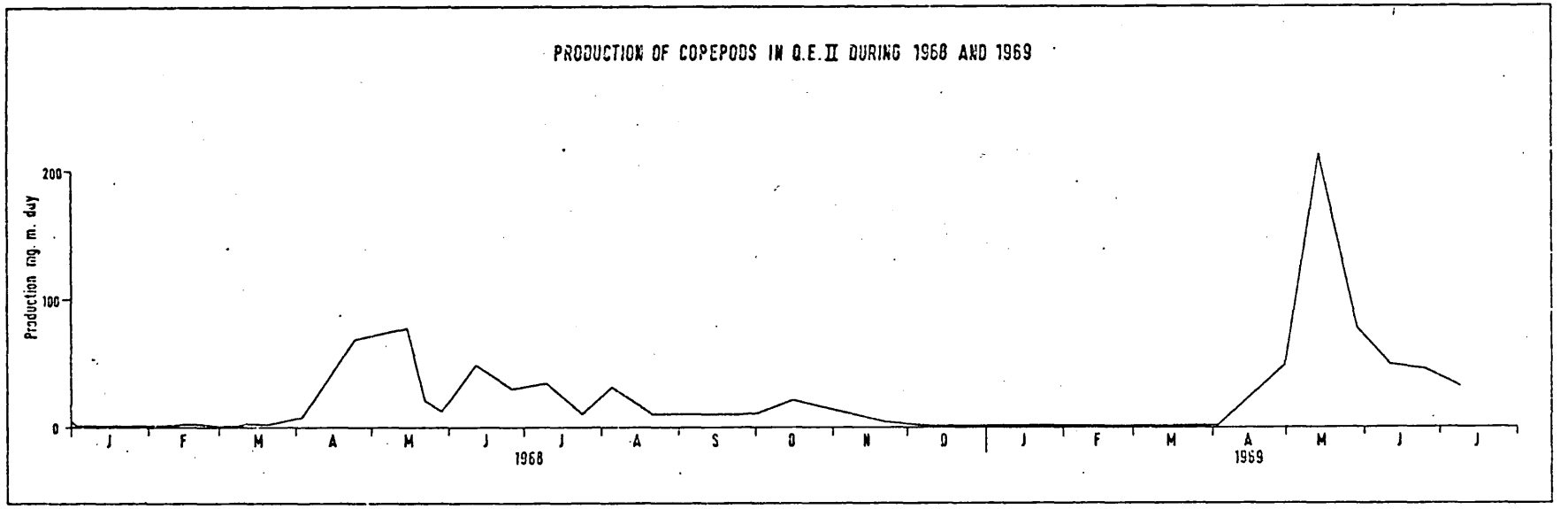

PRODUCTION OF COPEPODS IN O.E.II DURING 1968 AND 1969
Production mg. m. day
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D
1968
J
F
M
A
M
J
J
1969

Fig. 5.1.8(c).

Figure 5.1.8(d) shows the annual variation in the algal standing crop in terms of chlorophyll a as well as an indication of the succession of algal species throughout the study. It is interesting to note that although the zooplankton standing crop and production is higher in the Q.E.II than the Q.M. the algal standing crop is lower in the Q.E.II than the Q.M.

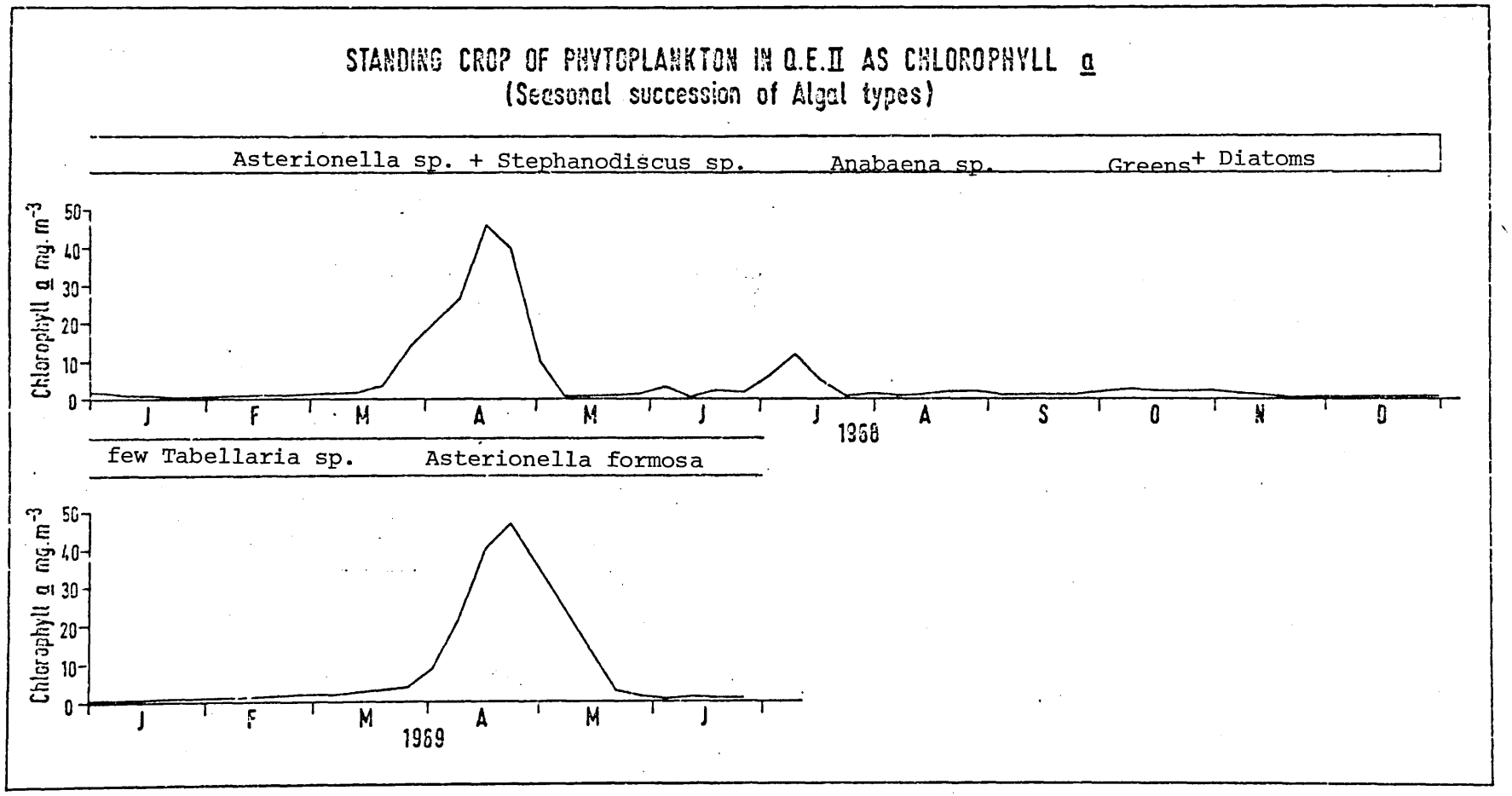


Fig. 5.1.8(d). (after Steel unpubl.)

5.2. LABORATORY RESULTS

5.2.1 BODY LENGTH-BODY WEIGHT RELATIONSHIPS IN DAPHNIA

Length measurements provide the most commonly used indication of body size in the Cladocera (WINBERG, 1971 RICHMAN 1958, LE SEUR 1960 , EDMONDSON 1955, KLEKOWSKI AND IVANOVA unpubl., BURNS 1968). A length-weight relationship may be used to convert length measurements to weight measurements and the weight is most conveniently expressed as dry weight. This relationship may be measured empirically or by assuming a mathematical relationship and fitting the results obtained to this equation by regression analysis.

In this study two methods were used to determine the length-weight relationship for D. hyalina. A Cahn balance was used to obtain individual dry weights and an Oertling balance to obtain mean dry weights for different size classes of animals. Results obtained are presented in figure 5.2.1(a) plotted in an arithmetic fashion and approximate to a power equation.

$$W = aL^b$$

This becomes more apparent when redrawn on double logarithmic paper where a straight line is seen (fig. 5.2.1.(b). A regression analysis, using the method of least squares, produces the following equations for all the animals measured.

Oertling means $W_{(\mu g)} = 8.47L^{3.22}(mm)$

Cahn individual $W_{(\mu g)} = 11.78L^{2.52}(mm)$.

A closer examination of fig. 5.2.1.(a) shows that it may be more satisfactory to analyse the curve into more specific areas which represent stages of development of the animal either in size or reproductive terms. Figure 5.2.1.(c) presents the results of regression analyses breaking down the curve in different ways.

Figure 5.2.1(a) shows there to be a break in the curve at 0.9mm and regression analysis for animals above and below this length shows that the value of "b" is different.

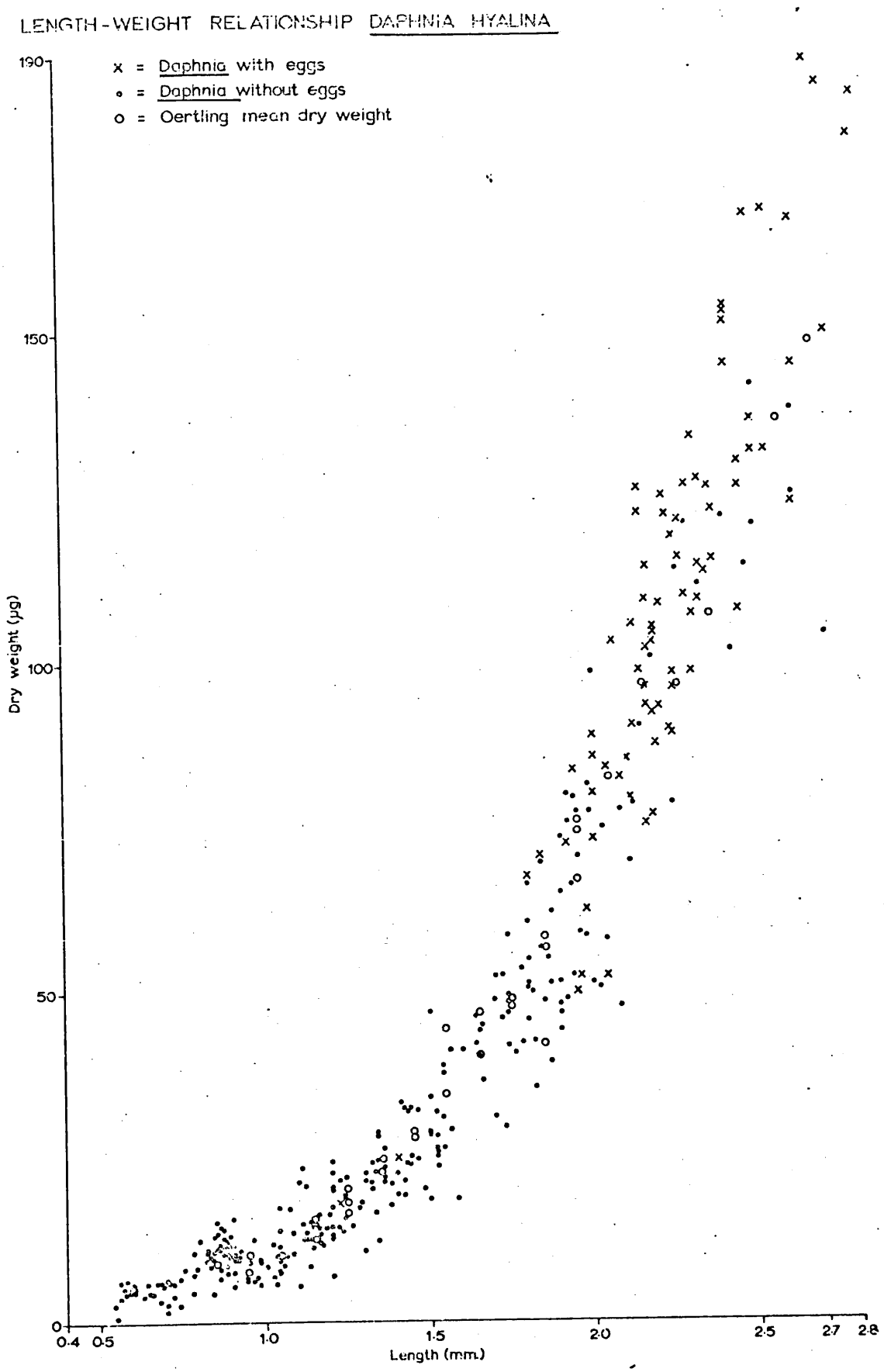

LENGTH-WEIGHT RELATIONSHIP DAPHNIA HYALINA
x = Daphnia with eggs
• = Daphnia without eggs
o = Oertling mean dry weight
Dry weight (µg)
190
150
100
50
0
0·4
0·5
1·0
1·5
2·0
2·5
2·7
2·8
Length (mm.)

Fig. 5.2.1(a).

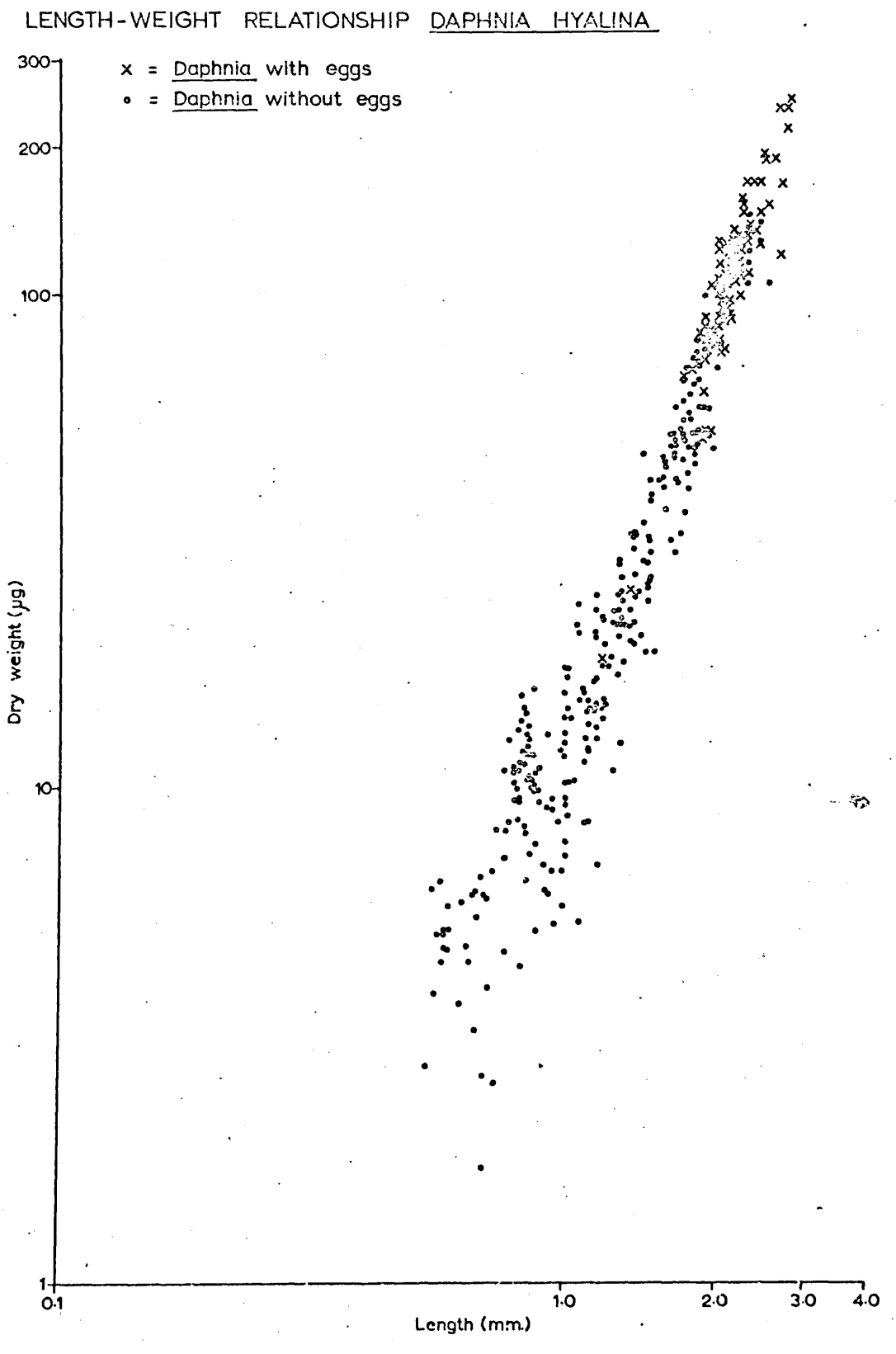

LENGTH-WEIGHT RELATIONSHIP DAPHNIA HYALINA
x = Daphnia with eggs
o = Daphnia without eggs
300
200
100
10
1
Dry weight (µg)
0·1
1·0
2·0
3·0
4·0
Length (m.m.)

Fig. 5.2.1(b).

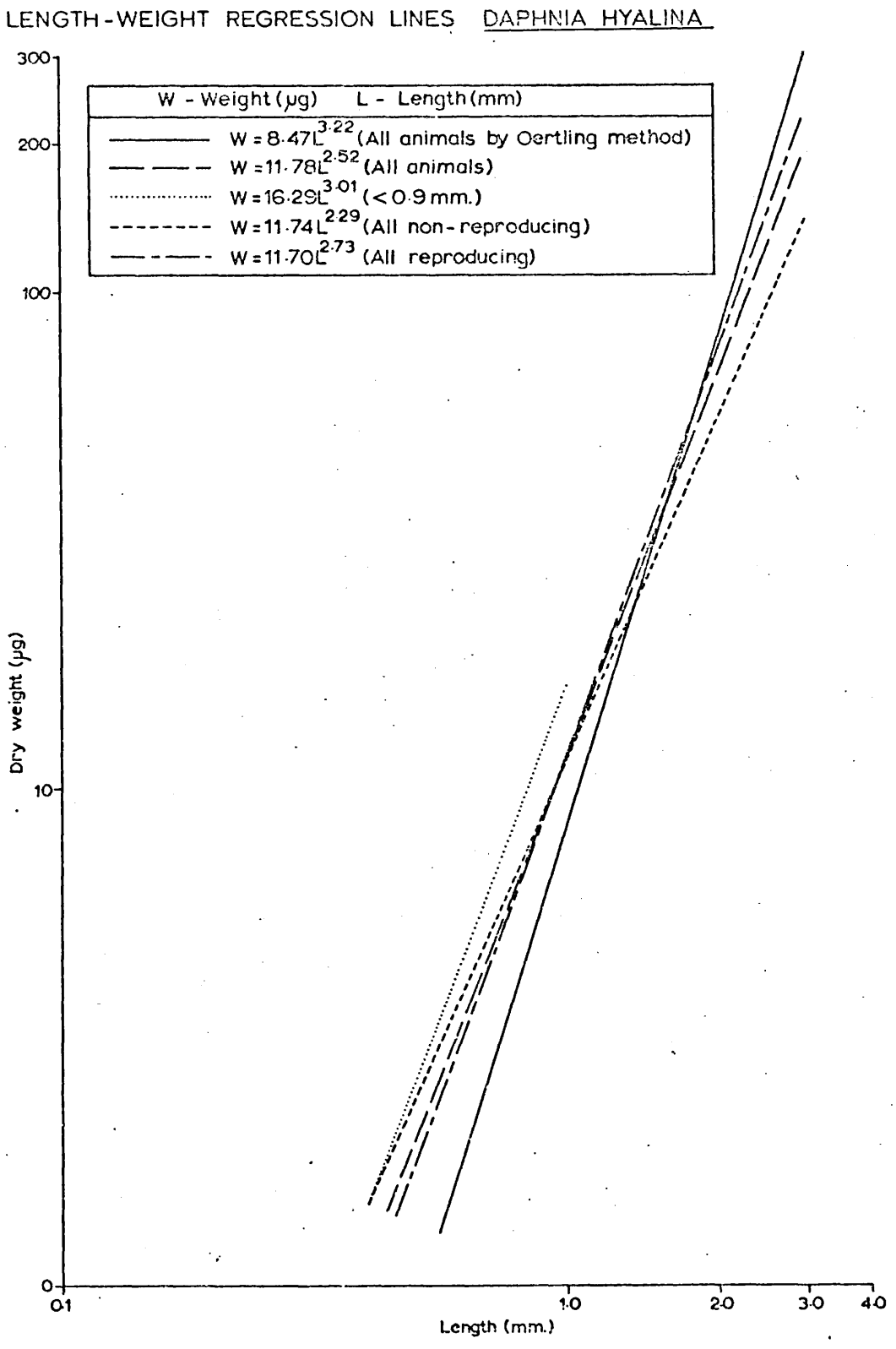

LENGTH-WEIGHT REGRESSION LINES DAPHNIA HYALINA
W - Weight (µg) L - Length (mm)
W = 8·47L^3·22 (All animals by Oertling method)
W = 11·78L^2·52 (All animals)
W = 16·29L^3·01 (< 0·9 mm.)
W = 11·74L^2·29 (All non-reproducing)
W = 11·70L^2·73 (All reproducing)
Dry weight (µg)
300
200
100
10
0
0·1
1·0
2·0
3·0
4·0
Length (mm.)

Fig. 5.2.1(c).

For animals less than 0.9mm length b $\simeq$ 3 which suggests that growth is geometric, i.e. there is a constant relationship between linear dimensions during growth. The full regression equation is

$$<0.9\text{mm} \quad W = 16.29L^{3.01}$$

For animals above 0.9mm b $\simeq$ 3, indicating that the relationship is nearly geometric.

$$>0.9\text{mm} \quad W = 11.74L^{2.29}$$

The reason for this change in growth pattern is discussed more fully later in this section but the body length 0.9mm is significant in the growth of D. hyalina as this is the normal size before the primiparous instar and the value of "b" may be affected by the onset of sexual maturity.

A difference is also seen with animals seen to be in a reproductive state with ovaries, eggs or embryos.

$$\text{Reproductive animals} > 0.9\text{mm} \quad W = 11.70L^{2.73}$$

This figure shows that b is approaching 3 and the conclusion is that animals with eggs etc., approach the more geometric form of growth.

During the course of this study the mean dry egg weight for D. hyalina was determined as 3.24μg per egg. Also the mean dry weight of the cast ephippium was found to be 20μg per ephippium.

The results obtained for length-weight relationships are consistent with, and in the range obtained by, other workers. The results obtained for all animals are presented with those of other workers for different species in figure 5.2.1(d) and the numerical values of their regression lines are presented in table 5.2.1.(a)

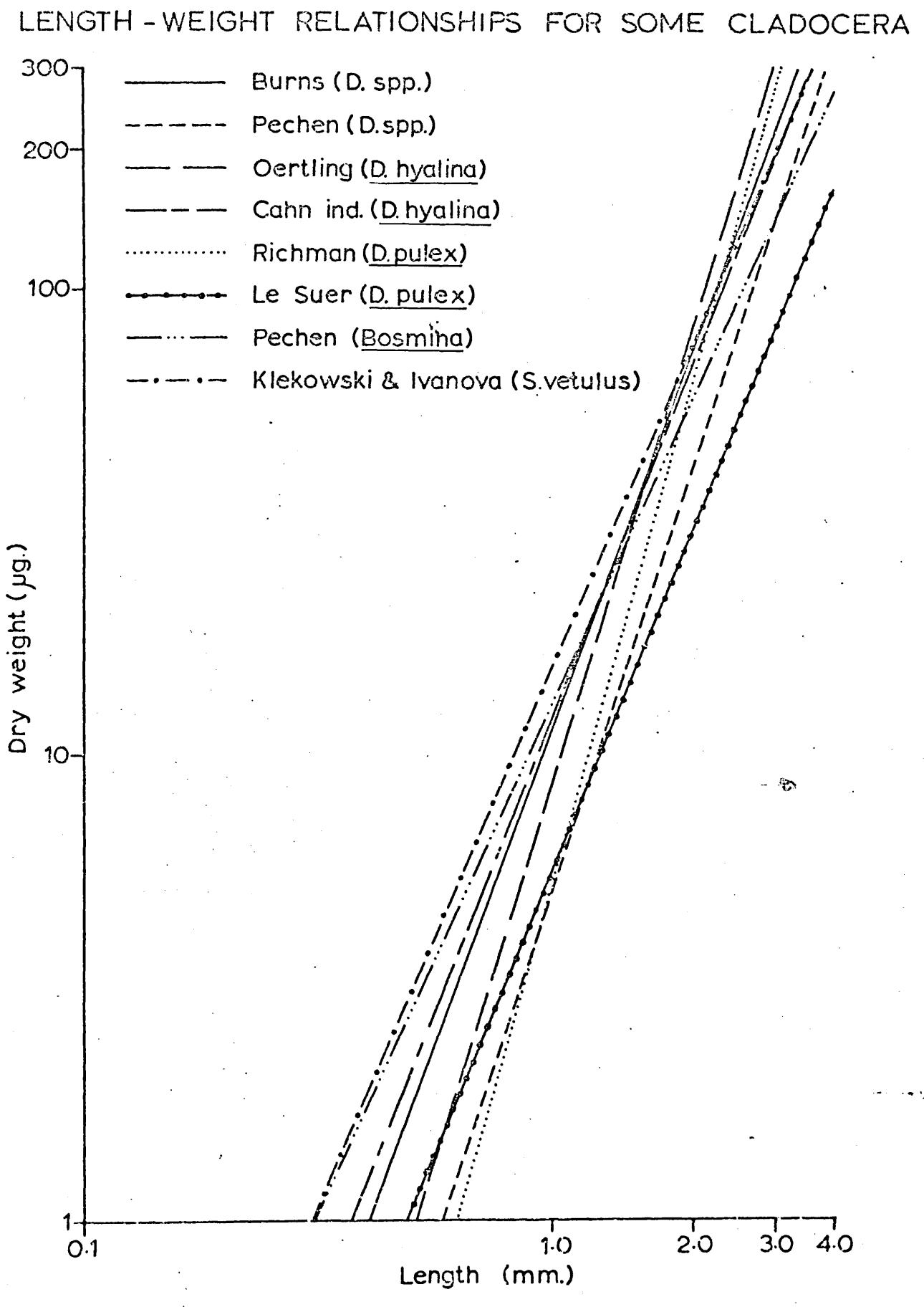

LENGTH - WEIGHT RELATIONSHIPS FOR SOME CLADOCERA
Burns (D. spp.)
Pechen (D.spp.)
Oertling (D. hyalina)
Cahn ind. (D. hyalina)
Richman (D.pulex)
Le Suer (D. pulex)
Pechen (Bosmina)
Klekowski & Ivanova (S.vetulus)
Dry weight (µg.)
300
200
100
10
1
0·1
1·0
2·0
3·0
4·0
Length (mm.)

Fig. 5.2.1(d).

Table 5.2.1.(a)

Species	W g = aL^b(mm)	Author	Comment
Daphnia spp.	$W = 5.2L^{3.00}$	Pechen (1965)	
Bosmina sp.	$W = 12.4L^{2.20}$	Pechen (1965)	
Daphnia pulex	$W = 5.4L^{3.45}$	Richman(1958)	Recalculated
Daphnia pulex	$W = 5.5L^{2.43}$	LeSeur (1960)	Recalculated
Daphnia spp.	$W = 11.6L^{2.61}$	Burns (1964)	
Simocephalus vetulus	$W = 15.0L^{2.33}$	Klekowski and Ivanova(unpub.)	

Variations of "b" values from 2.2 to 3.45 are found within these results. The values of b = 3.22 for the Oertling means and b = 2.52 for the Cahn individual measurements fall well within this range.

The results presented here, with those of the other workers, assume that there is a mathematical relationship between weight and length. An inherent danger in this procedure is that the wrong mathematical relationship may be assumed and as direct measurement of the weight of most Cladocera is not easy, small errors in weight determination may lead to large discrepancies when interconverting for values such as calorific determinations.

Early workers assumed there to be a direct relationship between weight and the cube of the body length when interpreting metabolic experiments with Cladocera (OBRESHKOVE 1930, OBRESHKOVE & FRAZER (1940). These authors use the following expression

$$W = a\ L^3 \qquad \text{(i)}$$

WINBERG(1971) draws attention to the fact that the implication of this equation is that geometic proportions of the body do not change throughout the growth of the animal if b = 3.

WINBERG(1971) uses the more general formula

$W = a L^{b}$ (ii)

and concludes that "if the body form changes during growth of the animal so that the ratio of linear measurement to weight decreases then $b > 3$ or in the opposite case $b < 3$."

Most modern workers use the assumptions of WINBERG (1971) and assume that there is a straight line relationship for the equation

(iii) $\log_{10} W = b \log_{10} L + \log_{10} a$

which is the same as equation (ii). Equation (i) is a special case of this.

Some other workers make their data fit other equations such as

(iv) $W = bL - a$ (Richman 1958, Le Seur 1960)

(v) $\log_{10} W = bL + a$

but these only seem to fit when data are either insufficient or discontinuous.

Several studies involving the measurement of the linear dimensions of Cladocera have been reported, and those working with Daphnia pulex and Daphnia magna (ANDERSON 1932, ANDERSON et al 1937). indicate that linear dimensions appear to be constant. KONSTANTINOVA (1961) measured length (l), height (h) and thickness (t) for a small range of immature animals (up to l = 1.32mm) and found that the ratios of l:t:h were constant.

Relationships are further complicated, however, by the fact that cyclomorphosis is common in some species of Cladocera and the usefulness of total length measurement may be impaired under environmental or genetic conditions which cause variation in helmet length (BROOKS 1946, 1957, GREEN 1954, HRBÁČEK 1962,).

In the present study, animals from culture experiments were measured for length (l), body length (sg) and width (b) to see of the relationships were geometric.

Results for all animals (D.hyalina) are presented in figures 5.2.1.(e), (f) and (g) and are summarised in table 5.2.1.(b).

Table 5.2.1.(b)

Relationship	Regression equation	Standard deviation (S_{res})	Correlation coefficient(r)
length / width	l=.735b−.153	0.0707	0.987p<0.001
length body/length	l=.8445g−.059	0.0361	0.997p<0.001
body length/width	Sg=.880y−.081	0.0894	0.980p<0.001

The results show a very high correlation coefficient and a very low standard deviation and the relationship between linear dimensions appears to be geometric throughout the life of the animals.

Results for the length–width relationship for individual animals are presented in figure 5.2.1.(h) and these show very little difference from the general figures.

A further assumption implied when assuming a length–weight relationship corresponding to equation (ii) is that the density of the animal remains constant throughout the life cycle of the animal (This was noted by BRODY(1945) who worked with domestic animals). GLIWICZ (1968) has pointed out that, in practice, the density of the animal may vary throughout its life although the linear proportions remain constant. He observed that the fat content of D. cucculata, D. longispina and other Cladocera varies seasonally and that it might be affected by food conditions prevailing. Observations of the condition of individuals during this study indicate that oil droplets are most often present in newly released juveniles and ovigerous adults and this could affect the density at these stages. The presence of eggs and ovaries could also affect the density of the animals and this may explain the "kinks" in the curves.

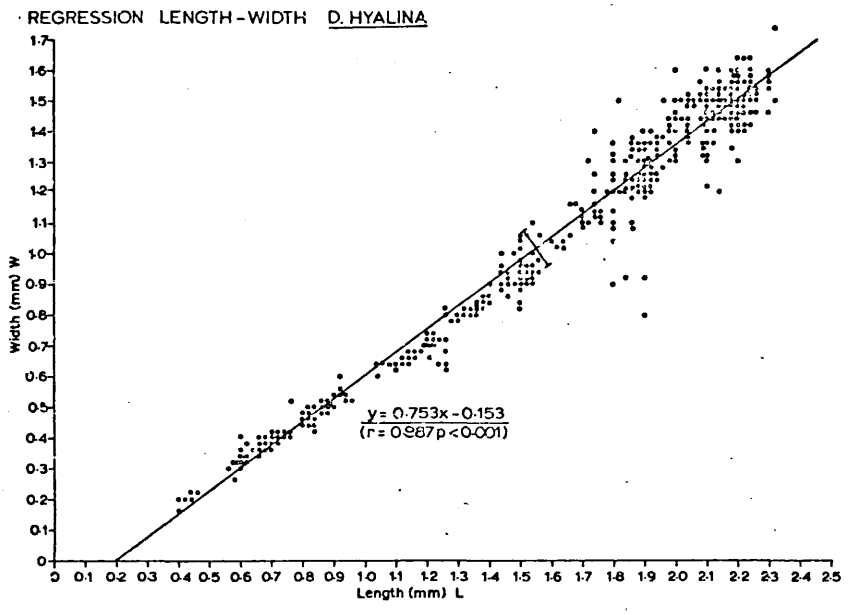


Fig. 5.2.1(e).

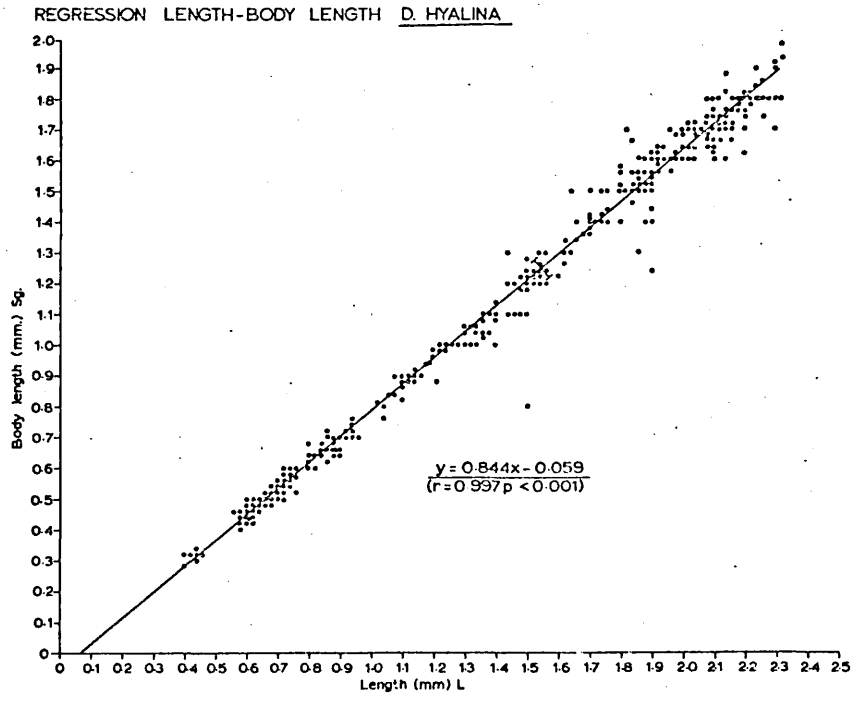


Fig. 5.2.1(f).

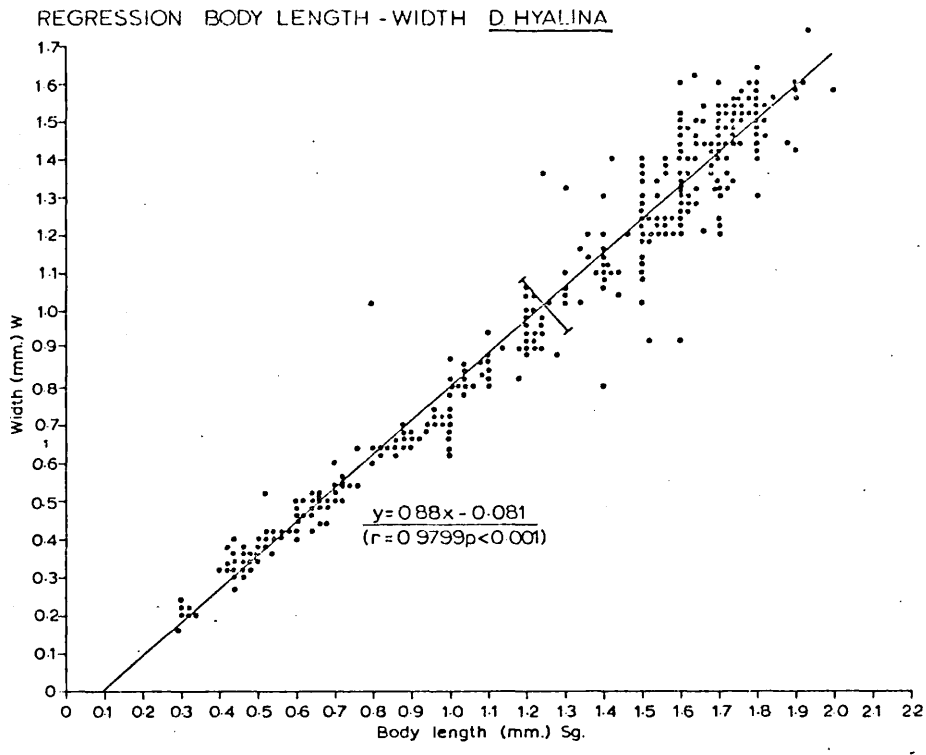


Fig. 5.2.1(g).

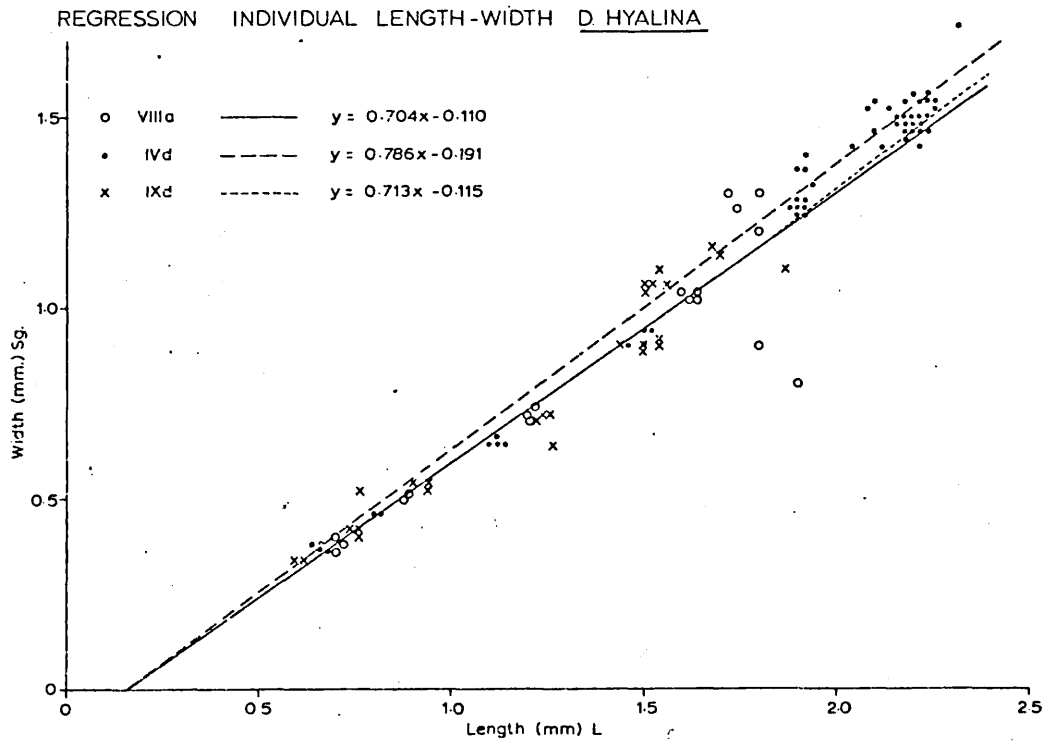


Fig. 5.2.1(h).

5.2.2. GROWTH OF DAPHNIA IN CULTURE

Culture of D. hyalina in the laboratory at 10°C provided information for developmental rates at different stages of the life history, growth characteristics and a source of animals for laboratory respiration studies. This study followed similar work by DUNCAN AND CREMER (unpubl.) at 20°C and some of their unpublished results are presented here for comparison.

Increase in length

Daphnids, like other Crustacea, grow in discrete stages or instars. The end of each instar is marked by the animal shedding its carapace and rapidly increasing in size before the new carapace becomes toughened.

Results of observations of the growth of D. hyalina as body length measurements are presented in figure 5.2.2(a) for all animals cultured except line XIII. (Line XIII is discussed separately). These results show that the length of the animal normally increases at each instar but that the rate of increase in length decreases as the animal gets older. Each instar is usually characterised by an immediate increase to the maximum length for the instar followed by a slight contraction to the final length for the instar. The increase in length in the pre-adult instar is 20–40% and this decreases to about 5 to 10%by the sixth instar and the increase in length per instar is fairly constant to death. Variation in length for the same instars in different animals of the same line may be considerable and the variation tends to be much greater in the adult instars. This sequence of events appears to be normal for daphnids and compares with results reported by HALL (1964) and CREMER AND DUNCAN (1969).

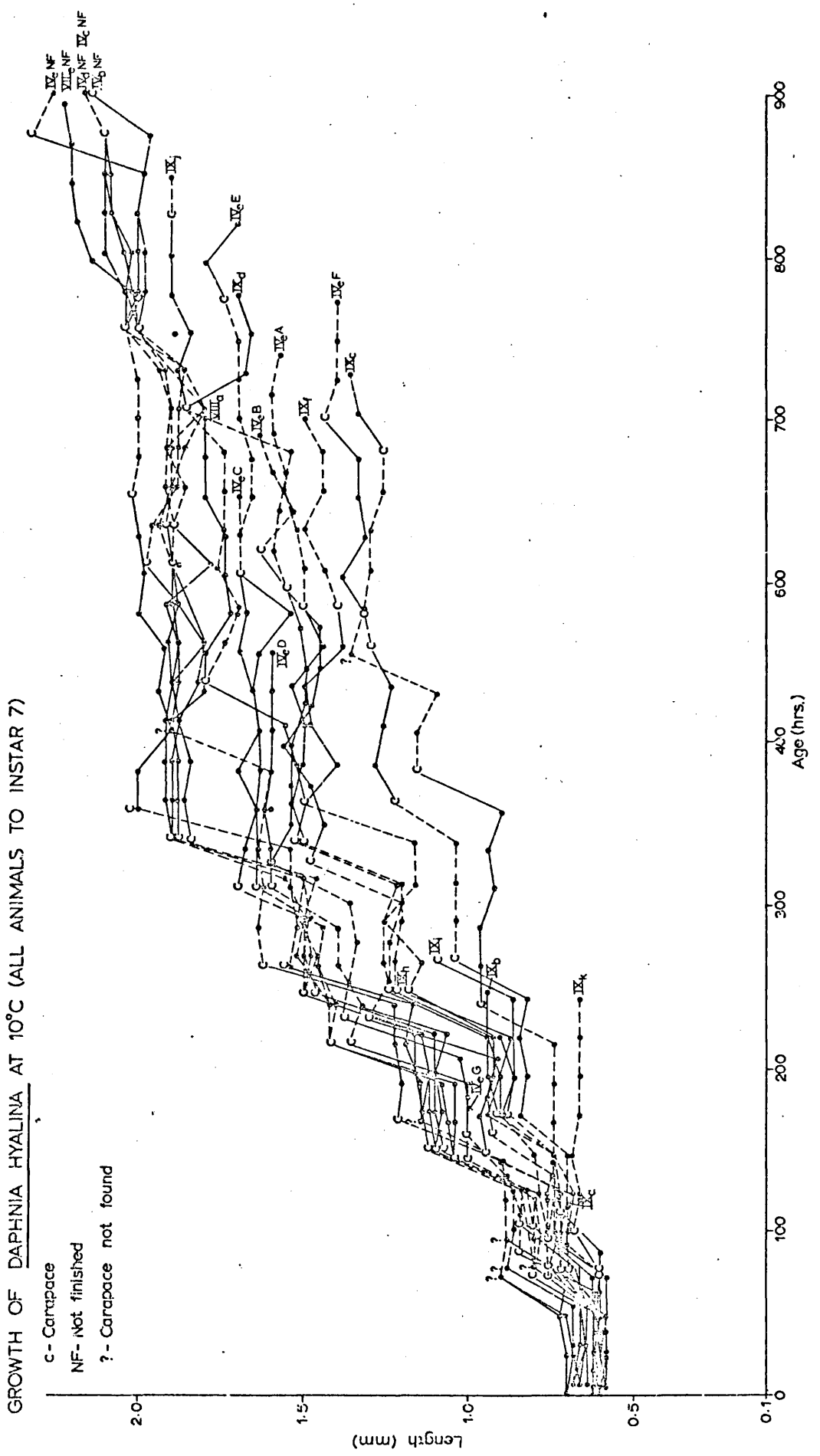

GROWTH OF DAPHNIA HYALINA AT 10°C (ALL ANIMALS TO INSTAR 7)
c - Carapace
NF - Not finished
? - Carapace not found
Length (mm)
Age (hrs.)
2.0
1.5
1.0
0.5
0.1
0
100
200
300
400
600
700
800
900

Fig. 5.2.2(a).

Table 5.2.2(a)

$10^{o}C$ All animals except line XIII

STAGE (instar)	LENGTH (mm)				DURATION (hrs)				AGE (hrs)			
	N	Mean	S.E.%	Range	N	Mean	S.E.%	Range	N	Mean	S.E.%	Range
		0.21	3.5	0.12-0.28								
EGG	21	0.43	3.1	0.30-0.52	16	167	1.8	144-192	16	167	1.8	144-192
1	22	0.61	14	0.56-0.68	21	81	3.4	72-110	B I R T H = 0			
2	21	0.76	4.8	0.68-0.88	20	88	8.1	48-168	21	86	3.5	72-110
3	19	0.99	6.4	0.84-1.12	17	95	7.5	72-168	20	169	10.8	144-268
4	16	1.34	6.7	1.04-1.52	15	106	6.9	72-192	17	265	4.3	216-384
5	15	1.64	10.6	1.22-1.90	13	159	3.8	96-199	15	373	5.0	312-484
6	14	1.68	11.5	1.24-1.90	7	139	4.0	120-168	13	527	3.0	436-604.5
7	7	1.95	6.7	1.74-2.04	5	130	4.7	120-146	7	646	7.7	604.5-672
8	5	2.11	7.9	1.90-2.32	4	181	12.7	146-242	5	769	13.1	724.5-800
9	4	2.12	2.8	2.10-2.18	4	186	20	120-288	4	962	2.6	920-1016
10	4	2.15	4.9	2.06-2.20	4	174	3.4	168-192	4	1148	3.1	1064-1208
11	4	2.22	1.7	2.18-2.24	3	228	17.3	168-302	4	1422	3.0	1232-1400
12	3	2.21	1.8	2.20-2.24					3	1533	5.8	1400-1702

A summary of the measurements for all animals except line XIII is presented in table 5.2.2(a). These figures are means for the animals (mean length, mean age etc.) for each instar until the end of the experiment.

Increase in weight.

A more useful measure of the growth is the increase in terms of weight. (see WINBERG 1971 and PETRUSEWICZ AND MACFADYEN 1970). Length measurements were converted to weight using the relationships derived in section 5.2.1. The length-weight relationships used for this conversion were:

for animals <0.9mm, $W = 16.29L^{3.01}$ g

for animals >0.9mm, $W = 11.74L^{2.29}$ g

The results are presented in table 5.2.2(b) and graphically in figure 5.2.2(b).

The line in figure 5.2.2(b) was fitted by inspection and this compares with examples given in PETRUSEWICZ AND MACFADYEN (1970) for other animals. The size categories recognised in field classes are also shown. The figures obtained may be used to calculate the finite growth rate of the animals (G) using the expression.

$$G = \frac{W_2 - W_1}{t_2 - t_1} = \frac{W}{t} \text{ g/ind./day}$$

The growth rate per unit weight may be calculated by dividing the finite growth rate (G) by the average weight of the individual where

$$G = \frac{W}{t\bar{W}}$$

Table 5.2.2(b)

Instar	Age (hrs)	Length (mm)	Weight (g)
Egg	-167	0.43	3.24
1	0	0.61	3.68
2	86	0.76	6.97
3	169	0.99	15.81
4	265	1.34	22.95
5	373	1.64	36.34
6	527	1.68	48.49
7	646	1.95	54.18
8	769	2.11	64.91
9	962	2.12	65.60
10	1148	2.15	67.75
11	1422	2.22	72.93
12	1533	2.21	72.18

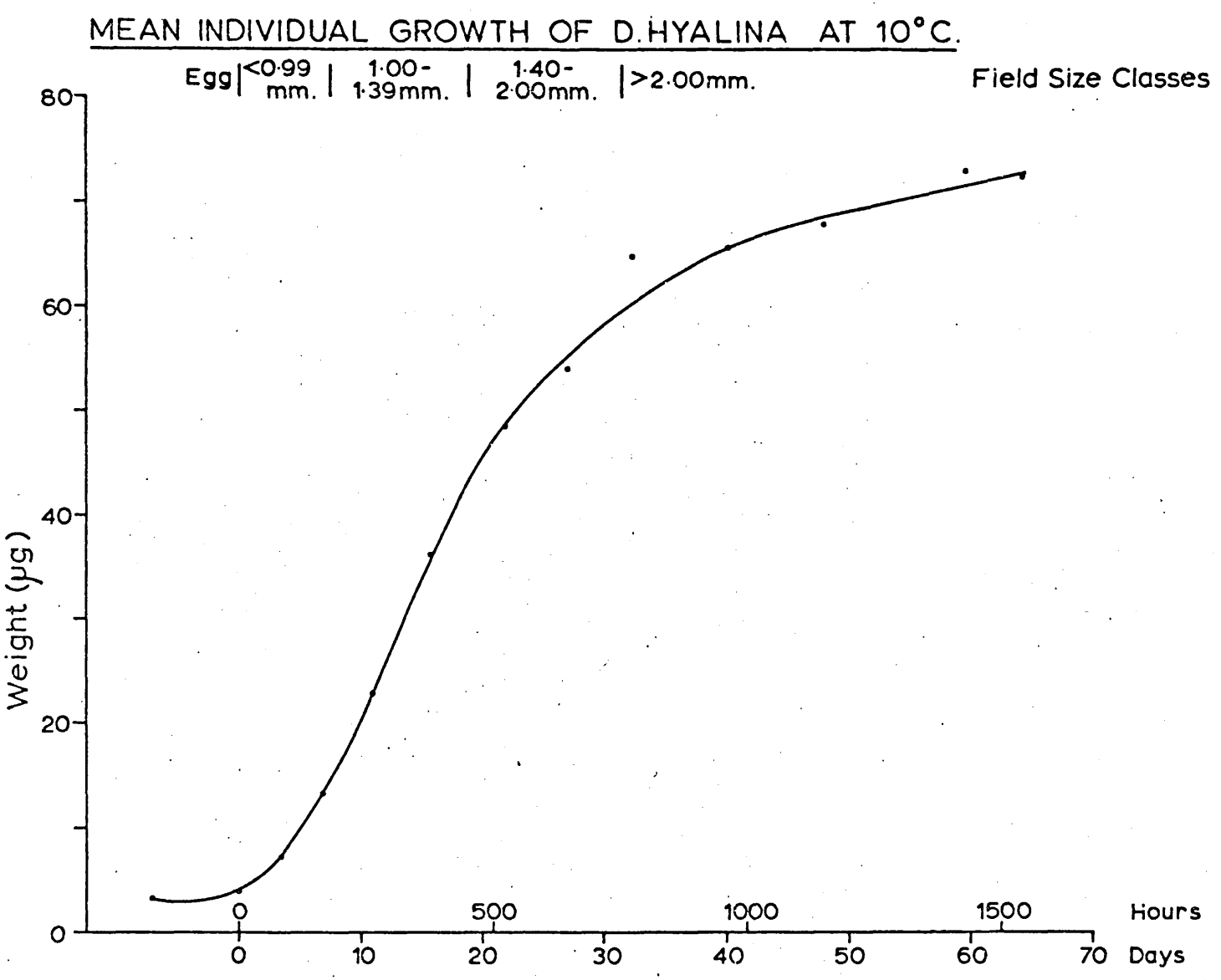

MEAN INDIVIDUAL GROWTH OF D.HYALINA AT 10°C.
Egg
<0·99 mm.
1·00-1·39mm.
1·40-2·00mm.
>2·00mm.
Field Size Classes
Weight (µg)
80
60
40
20
0
0
500
1000
1500
Hours
0
10
20
30
40
50
60
70
Days

Fig. 5.2.2(b)

A more useful measure of growth is defined by the instantaneous growth rate, g, of the animals where:

$$g = \frac{\ln Wt_2 - \ln Wt_1}{t_2 - t_1}$$

which represents the daily growth as a percentage of the previous days body weight. Results of the calculation of g are presented in table 5.2.2(c).

Table 5.2.2(c)

Instar	Weight (μg)	Daily Instantaneous growth rate, g.		Field size class (mm)	
Egg	3.24	daily	hourly	during	
1	3.68	.0355	.0075		
2	6.97	.1600	.0067	.1177	<0.99
3	15.81	.1575	.0065		
4	22.95	.1022	.0046	.1022	1.00–1.39
5	36.34	.0715	.0030		
6	48.49	.0581	.0024	.0504	1.40–1.99
7	54.18	.0216	.0009		
8	64.91	.0221	.0009		
9	65.60	.0014	.0001		
10	67.75	.0028	.0001	.0716	>2.00
11	72.93	.0203	.0008		
12	72.18	–	–		

These results have been calculated from a smoothed semi-logarithmic plot of the data which probably gives a better estimate as the result for instar 3 appears to be too high.

These figures are used in section 5.1.4 for the calculation of the production in the field populations.

Reproductive development

Parthenogenetic development is normal in the Cladocera and most of the animals used in this study developed their first ovary during the fourth instar (N = 13), but some during the fifth or sixth instar. This variability appears to be normal and has been recorded by other workers including BANTA ET AL (1939), ANDERSON (1932), HRBACKOVA-ESSLOVA (1966) and MURUGAN AND SIVARAAKRISHNA (1973). The first instar in which the ovary develops is known as the primiparous instar and the ovary appears early in, and develops during the rest of, the instar. In the later stages of ovary development eggs can often be distinguished and enumerated.

The eggs are shed into the brood pouch of the female at the end of each instar when the animal has shed its carapace. The eggs develop in the brood pouch for the rest of the instar and the young are released just before the carapace has been shed at the following moult. This sequence of events has been recognised by other workers with other species and is described fully by GREEN (1956), working with D. magna, who also described different stages of the egg development (section 4.2.2).

Results of observations of the reproductive history of all animals, except line XIII, are presented as a summary in table 5.2.2.(d).

Table 5.2.2(d)

INSTAR	SIZE (mm)	AGE (hrs)	FIRST (N)	PARTHENOGENETIC BROODS		NO. OF FEMALES WITH EPHIPPIA
				N	Mean egg No.	
1	0.61	-	-	-	-	-
2	0.76	86	-	-	-	-
3	0.99	169	-	-	-	-
4	1.44	265	13	-	-	-
5	1.74	340	3	11	7.8	2
6	1.80	436	-	1	7.0	12
7	1.95	646	-	0	-	1
8	2.11	769	-	3	17	2
9	2.12	962	-	0	-	3
10	2.15	11·8	-	0	-	-
11	2.22	1422	-	1	6	1

The table shows instar, mean size, mean age for the primiparous and reproductive instars, mean egg numbers (brood size) and the occurrence and numbers of ephippial broods. The brood size varied considerably (maximum 18, minimum 1 egg) but during this study were maximal in the fifth and eigth instars for all animals. Figure 5.2.2.(c) shows the numbers of eggs per instar for all except line XIII and it can be seen that egg numbers increase with instar number until instar II and then decrease with age (as do ephippial broods). This sequence may be related to food quantity or quality but is also seen in other studies such as those reported by BANTA ET AL (1939).

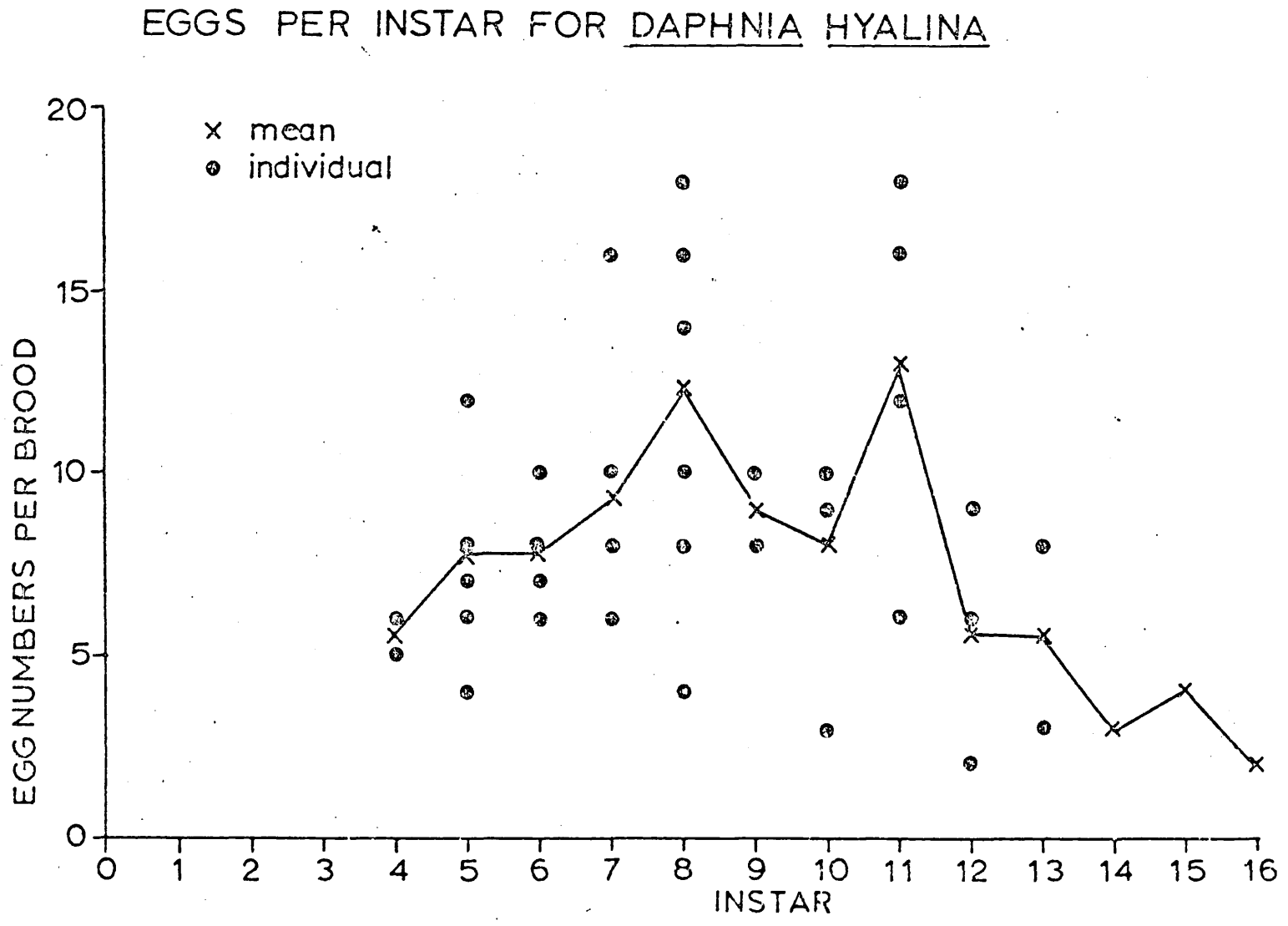

EGGS PER INSTAR FOR DAPHNIA HYALINA
× mean
individual
EGG NUMBERS PER BROOD
0
5
10
15
20
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
INSTAR

Fig. 5.2.2(c).

During this study normal parthenogenetic reproduction was interrupted in all lines, except line XIII, by ephippial reproduction. It is generally thought that ephippial production is generated by unsuitable environmental conditions such as low temperature or insufficient or poor quality food (BANTA AND BROWN 1939, BROOKS 1946) and this is marked by the production of males and the distinctive resting eggs. Although ephippial production in cultures has been observed before (BANTA ET AL 1939), and ephippia have been used to start cultures (GREEN 1956), no satisfactory explanation of their occurrence has been given. In this study no male daphnids appeared and all cultures were of individual animals isolated from each other in glass culture dishes. BANTA (1926) and SCHRADER (1926) reported the production of "pseudosexual" eggs (ephippia) without the presence of males for laboratory cultures of D. pulex. Developing ephippia were first seen as a thickening and change in shape of the carapace and as these developed, eggs were laid into them. The development of an ephippium spanned two normal instars and the ephippium was then cast with the carapace. After casting the carapace with the ephippium, the female D. hyalina then either developed another ephippium or produced a normal parthenogenetic brood. Animals that had cast an ephippium were left with a characteristic shape to the dorsal side of the carapace which remained with the animal during its future development. In one instance a parthenogenetic brood that was developing degenerated before the ephippium developed.

The results presented in table 5.2.2(d) show that ephippial development occurred in all instars, after the animal became sexually mature, except instar ten. Very few of the cultured animals survived to instar ten. Ephippial broods only occurred in the first reproductive instar in two cases, most ephippial broods occurring in instar six (N = 12).

The reasons for the appearance of the ephippial reproductive phase of D. hyalina, in these cultures, are not clear and are especially difficult to understand as no males developed. Cast ephippia were kept isolated in the same culture conditions and these did not develop during the course of the experiment but this may be due to the fact that they were not fertilised. The ephippial production seemed to occur in similar instars but these were not at all synchronised and the animals also consisted of groups from different generations. The effect of low temperature ($10^{o}C$) may have triggered ephippial production but a much more likely cause is the quality of the food. TAUB AND DOLLAR (1968) suggest that food quality is of importance to the growth and reproduction of daphnids and feeding on a monoculture of Oocystis may not have been satisfactory (15.3×10^{3} cells/ml $\pm$ 0.9) and falls into the limits discussed by BURNS AND RIGLER (1967) who suggest that up to 25×10^{3} cells per ml D. rosea, which is of comparable size to D. hyalina, is filtering maximally with yeast as a food. This situation is likely to be common in field populations but again BURNS AND RIGLER (1967) suggest that field filtering rates may be lower than those measured in the laboratory. One difficulty in accepting the suggestion that food quality may have caused ephippial production

is that line XIII, although cultured in identical conditions and at the same time, produced no ephippia. This might suggest that control of ephippial production may be in part genetic but may be triggered by environmental conditions (although this appears to be very rare in the reservoir populations).

Line XIII

Line XIII was cultured from an adult D. hyalina (XIII) taken from the original field sample and was normal in all respects except that it was a dwarf line. BANTA (1939) recognises the existence of dwarf lines in daphnids.

Results are presented in figure 5.2.2(d) and table 5.2.2(e) and these show that the embryos were smaller, before release from the brood pouch, than the mean length for embryos of other lines (0.38 and 0.43mm respectively), but that they fall within the size range for all embryos (0.30-0.52mm). The length at instar one and subsequent instars can be seen to be smaller than all other animals and the instar lengths do not fall into the normal range. The rate of increase in length of the animals appears to be different from the other lines in instars one, two and three but not in subsequent instars. The mean maximum length reached at maturity (instar 12) was 1.71mm (maximum 1.88mm) compared with 2.22mm for other lines. Line XIII was much longer lived than other lines and the maximum age was reached in instar 19 as opposed to instar 14 in other lines.

Line XIII reached its primiparous instar (instar four) at a mean length of 0.94mm compared with 1.34mm for other lines. Reproductively line XIII was different

Table 5.2.2(e)

10°C Line XIII

Stage (instar)	LENGTH (mm)				DURATION (hrs)				AGE (hrs)			
	N	mean	SE%x	Range	N	mean	SE%x	Range	N	mean	SE%x	Range
Egg	1	0.14 0.38	-	-	1	157	-	-	1	157	-	-
1	12	0.44	0.7	0.40-0.46	7	140	13.5	78-150	BIRTH = 0			
2	6	0.61	4.1	0.54-0.70	6	76	5.3	72-96	7	140	13.5	78-150
3	6	0.76	4.1	0.70-0.90	6	112	13.4	96-168	6	214	6.3	150-246
4	6	0.94	4.9	0.84-1.14	5	82.4	24.2	24-124	6	318	8.5	222-414
5	5	1.08	4.6	1.00-1.24	5	114	19.6	72-168	5	414	7.1	318-462
6	5	1.25	3.1	1.18-1.38	5	163	10.8	96-192	5	548	5.7	486-630
7	5	1.33	2.2	1.28-1.42	4	168	0	168	5	707	6.5	582-822
8	5	1.41	1.5	1.34-1.44	4	180	3.8	168-192	4	875	5.3	750-990
9	4	1.48	3.3	1.40-1.60	4	186	3.2	168-192	4	1026	4.6	918-1110
10	4	1.54	3.2	1.44 1.64	3	160	16.2	120-192	4	1212	3.8	1110-1302
11	3	1.63	0.2	1.58-1.17	3	168	12.5	144-192	3	1366	2.6	1302-1422
12	3	1.71	3.1	1.62-1.76	3	185	19.9	144-244	3	1534	3.6	1446-1590
13	3	1.71	6.3	1.60-1.88	1	144	-	-	3	1686	2.7	1614-1734
14	1	1.60	-	-	1	192	-	-	1	1758	-	-
15	1	1.60	-	-	1	120	-	-	1	1950	-	-
16	1	1.60	-	-	1	196	-	-	1	2070	-	-
17	1	1.60	-	-	1	72	-	-	1	2166	-	-
18	1	1.70	-	-	1	24	-	-	1	2238	-	-
19	1	1.60	-	-	-	-	-	-	1	2254	-	-

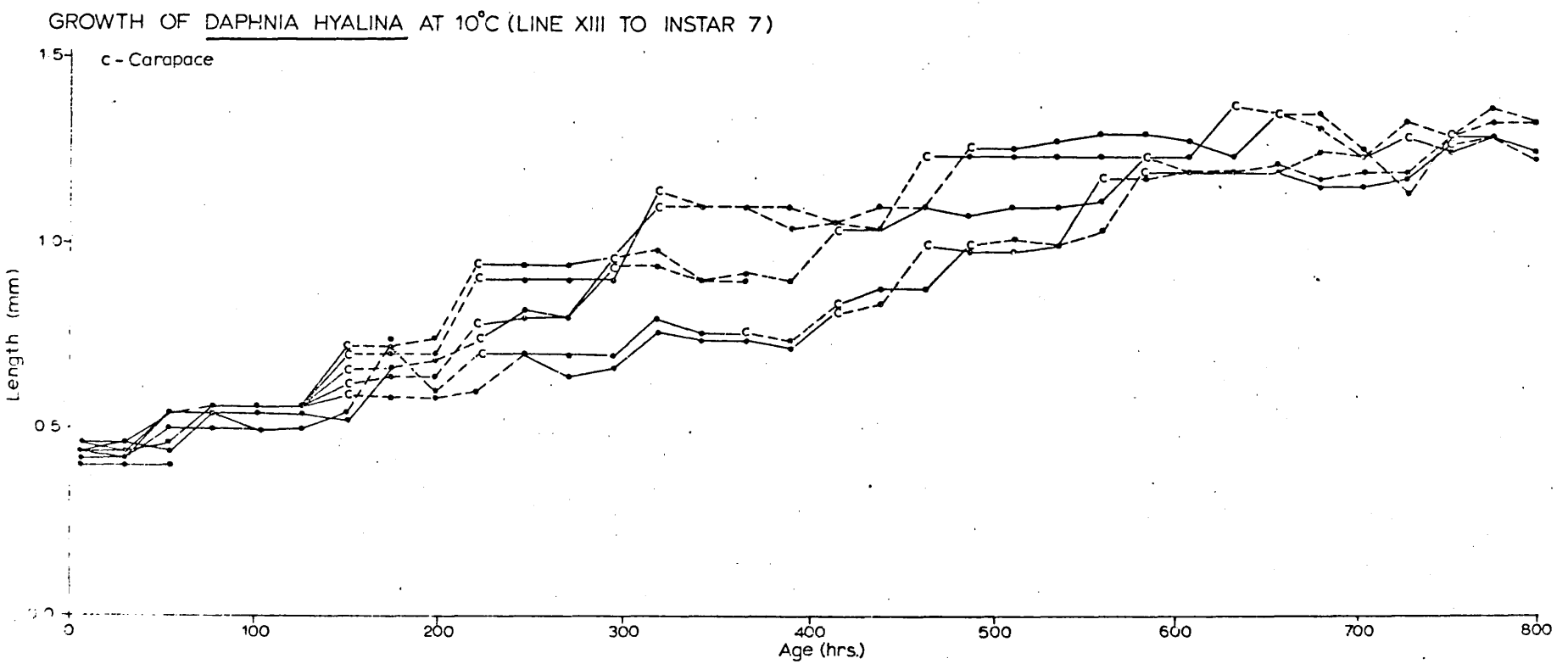

GROWTH OF DAPHNIA HYALINA AT 10°C (LINE XIII TO INSTAR 7)
c - Carapace
Length (mm)
1.5
1.0
0.5
0.0
0
100
200
300
400
500
600
700
800
Age (hrs.)

Fig. 5.2.2(d).

from other lines in that no ephippial broods were produced and mean egg numbers per brood were much higher than other lines. Two animals reached their primiparous instar at instar three and the rest in instar four but, as only five animals survived to instar four, little more can be inferred from this. Results of the reproductive observations are presented in table 5.2.2(f). In all other respects the development of line XIII was similar to other lines.

Table 5.2.2(f)

INSTAR	SIZE (mm)	AGE (hrs)	FIRST OVARY (N)	PARTHENOGENETIC BROODS	
				N	Mean Egg No.
1	0.44	-	-	-	-
2	0.61	140	-	-	-
3	0.76	214	2	-	-
4	0.94	318	3	2	5.5
5	1.08	414	-	2	7.5
6	1.25	548	-	3	8.0
7	1.33	707	-	5	9.2
8	1.41	875	-	4	9.0
9	1.48	1026	-	4	9.0
10	1.54	1212	-	4	8.0
11	1.63	1366	-	3	15.3
12	1.71	1534	-	2	8.5
13	1.71	1686	-	2	5.5
14	1.60	1758	-	1	3
15	1.60	1950	-	1	4
16	1.60	2070	-	1	2

The occurrence of the dwarf line XIII is difficult to explain but was probably genetic rather than environmentally controlled. The fact that the line developed

from an otherwise normal adult collected from the field (1.36mm when collected) and identified as D. hyalina indicates that this was not another species. It is not known how frequently dwarf lines occur in the field situation but if this is high it might bias production estimates.

Duration of stages

Results of the experiments to determine the duration of stages of development for all lines are presented in the tables 5.2.2(a) and 5.2.2(e) for animals cultured at 10°C. The duration of egg development corresponds with the duration of the instar that the egg develops in and can be seen to be 167 hours (range 144–192 hrs) which is about six days. Line XIII is very similar at 157 hours. The results for the duration of instars are presented graphically in figure 5.2.2(e) for all lines and although there is variation from line to line, there is a general trend for the duration of the instar to increase with the age of the animal up to instar eight when it becomes relatively constant until instar 12. After this instar duration fluctuates and then decreases as the animal becomes more senile. From the eighth to the 13th instar the duration is around 170–180 hours and this corresponds with the mean egg development time of 167 hours for parthenogenetic broods.

The variation between lines for duration of instars is quite considerable in both early and late instars (up to 144 hrs) but at the primiparous instar (three to six) the variation is low and it appears that the mean duration time of the lines becomes synchronised at the onset of sexual maturity.

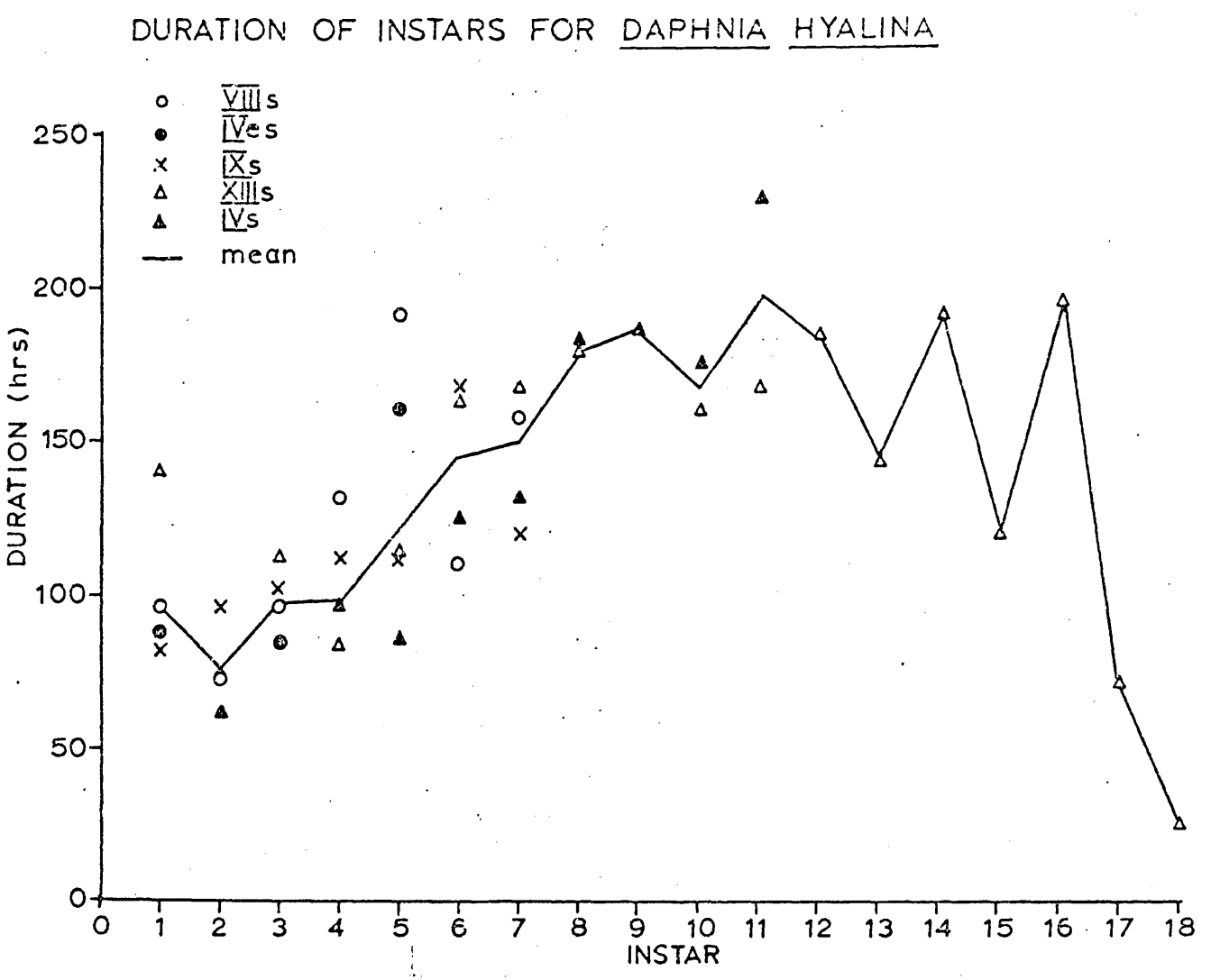

DURATION OF INSTARS FOR DAPHNIA HYALINA
VIIIs
IVes
IXs
XIIIs
IVs
mean
DURATION (hrs)
250
200
150
100
50
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
INSTAR

Fig. 5.2.2(e).

Similarly, the ages of the animals may be compared at the same instars and it is apparent that most animals reach the same instar at the same time. The standard error, expressed as a percentage of the mean age for each instar for all lines, is 13% but this is less than 5% at most instars.

Growth at 20°C (Duncan and Cremer)

Results of a similar experiment by DUNCAN AND CREMER (in prep.) are presented in table 5.2.2(g). These results are directly comparable with the results shown in table 5.2.2(a) and similar inferences may be drawn except that the experiment was performed at 20°C. During the course of this work only parthenogenetic reproduction occurred but development time for eggs, not egg production, is considered here. These data is presented to enable conclusions to be drawn about the effect of temperature on the rate of development.

Relationship between temperature and development for D. hyalina

The rate of development of the animal is the time it takes for a stage of the life history to be reached. The rate of egg development in D. hyalina, for example, is the time the egg takes to develop from its release from the ovary until it is released from the brood pouch of the adult: the rate of development of a juvenile daphnid is the time from hatching until it reaches sexual maturity or death. The relationship between temperature and development rate for different stages of the life history of the animal must be known accurately for production calculations from field data.

Table 5.2.2(g) 20°C All animals (from G. Cremer)

STAGE (instar)	LENGTH (mm)				DURATION (hrs)				AGE (hrs)			
	N	Mean	S.E.%	Range	N	Mean	S.E.%	Range	N	Mean	S.E.%	Range
		0.19-		0.14-0.24								
EGG	16	0.43		0.32-0.53	2	53	11.2	40-66	2	53	11.2	40-66
1	8	0.50	6.2	0.46-0.52	5	33	14	14-38	B I R T H = 0			
2	5	0.90	2.8	0.84-0.98	7	49	23	24-71	5	47		36-85
3	7	1.09	3.1	0.97-1.24	9	38	11	22-47	7	73		58-107
4	9	1.31	2.1	1.19-1.45	11	37	12	25-53	9	105		86-132
5	11	1.50	2.4	1.40-1.70	10	54	8	25-72	11	146		127-176
6	10	1.62	1.5	1.49-1.72	8	60	8	46-75	10	211		174-248
7	8	1.68	0.8	1.63-1.75	6	71	5	64-85	8	268		250-198
8	6	1.78	1.8	1.70-1.91	4	70	10	47-84	6	344		314-372
9	3	1.81	1.5	1.74-1.86	4	78	44	74-86	4	413		392-450
10	3	1.93	3.0	1.86-2.05	2	66			4	491		466-496
11	2	2.02		1.95-2.08					2	575		562-589
12	1	2.13							1	636		
13									1	766		
14	1	2.32							1	789		

The stages chosen may relate to a period of biological significance in the life of the animal, such as the time taken from hatching to sexual maturity, or it may relate to an arbitrary measurement of the animal such as size. In either case the value chosen must be recognisable in field samples for satisfactory estimates of production to be made. This point is discussed further by EDMONDSON AND WINBERG (1971) and PETRUSEWICZ AND MACFADYEN (1970).

Using the developmental rates obtained for animals cultured at 10°C and 20°C, developmental periods for other temperatures were calculated on the basis of Krogh's normal curve as used by WINBERG (1971). The rate of egg development is presented in figure 5.2.2(f). Calculated results, falling within the range of field temperatures, are presented in table 5.2.2(h). The line obtained from these results is compared with a similar line given by BURGIS (1970) and SCHINDLER (1972) for other planktonic crustacea. SCHINDLER (1972) using results cited by other workers, derives the equation relating the duration of egg development and temperature (°C) where

$$1/D = 0.0426 + 0.0008T^2$$

which can be seen to be slightly different from the values obtained for the duration of egg development for D. hyalina.

The results obtained for the duration of egg development from laboratory culturing were:

10°C D = 170 $\pm$ 30 hours S.E.% $\bar{D}$ = 6.29% (N=8)

20°C D = 56.5 $\pm$ 9.3hours S.E.% $\bar{D}$ = 6.23% (N=7)

RELATIONSHIP BETWEEN TEMPERATURE AND DEVELOPMENTAL TIME ($^1/_D$)

FOR DAPHNIA HYALINA

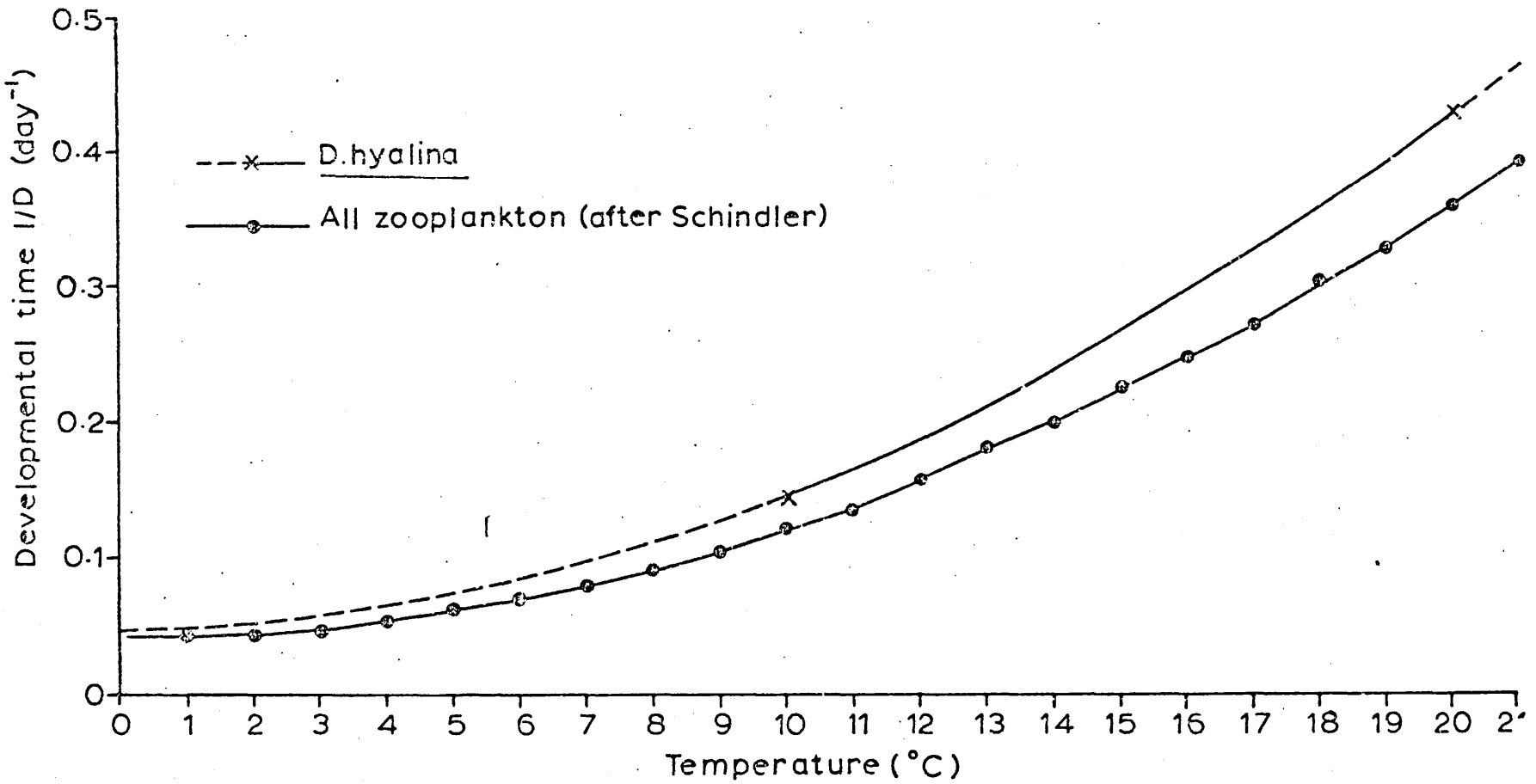


Fig. 5.2.2(f).

For line XIII at 10°C the value can be seen to be very similar:

20°C D = 164.1 ± 27.5 hours S.E.% = 4.34% (N=13)

Table 5.2.2(h)

T°C	$^1/D$ (day^{-1})	D (days)	D (hrs)
1	0.0475	21.05	505
2	0.0500	20.00	448
3	0.0575	17.39	417
4	0.0650	15.38	369
5	0.0750	13.33	310
6	0.0850	11.76	282
7	0.0975	10.26	246
8	0.1125	8.89	213
9	0.1275	7.84	188
10	0.1408	7.10	170.5
11	0.1675	5.97	143
12	0.1925	5.19	125
13	0.2200	4.55	109
14	0.2400	4.17	100
15	0.2700	3.70	89
16	0.2975	3.36	81
17	0.3275	3.05	73
18	0.3575	2.80	67
19	0.3900	2.56	62
20	0.4284	2.35	56.5

Figure 5.2.2(g) shows that the extrapolation of results, using Krogh's normal curve, produces a line comparable with other published results. BOTTRELL (1975), as with M^{c}CLAREN (1963), questions the validity of assuming a relationship such as Krogh's curve or the van't Hoff-Arrhenius function to describe developmental rates

of epiphytic cladocerans and copepods. Although his criticism is probably justifiable, and he suggests several curvilinear functions of a quadratic form that may give slightly better statistical fits to the published figures, it is difficult to select a particular function for a single species. To use Krogh's approximation, when few measurements are available, was thought to be the best compromise. The resulting errors in production estimations are, in practice, very small as the greatest deviation from the assumed line occurs at extremely low temperatures when production is low because developmental rates are very slow and population sizes are very small.

These results were checked with results obtained using the approximate method of WRIGHT (1965) who estimated the duration of egg development from field data. WRIGHT describes the method as "determining the average time required for dominanant cohorts to pass through each of a succession of adult sizeclasses at different times throughout the study". In this study the interval between successive and distinct population peaks of the smallest size class was assumed to be an estimate of the duration of egg development at the known field temperature. This technique is certainly subject to sampling errors and the errors of interval sampling as well as subjective errors about the distinctiveness of a peak, and also the assumption that successive peaks represent distinct cohorts, but the results, with a range represented by vertical bars, proved to be in fairly good agreement with and to complement the calculated values. These results can be seen in figure 5.2.2(g) and table 5.2.2(i).

RELATIONSHIP BETWEEN TEMPERATURE AND DEVELOPMENTAL TIME(D) FOR DAPHNIA HYALINA

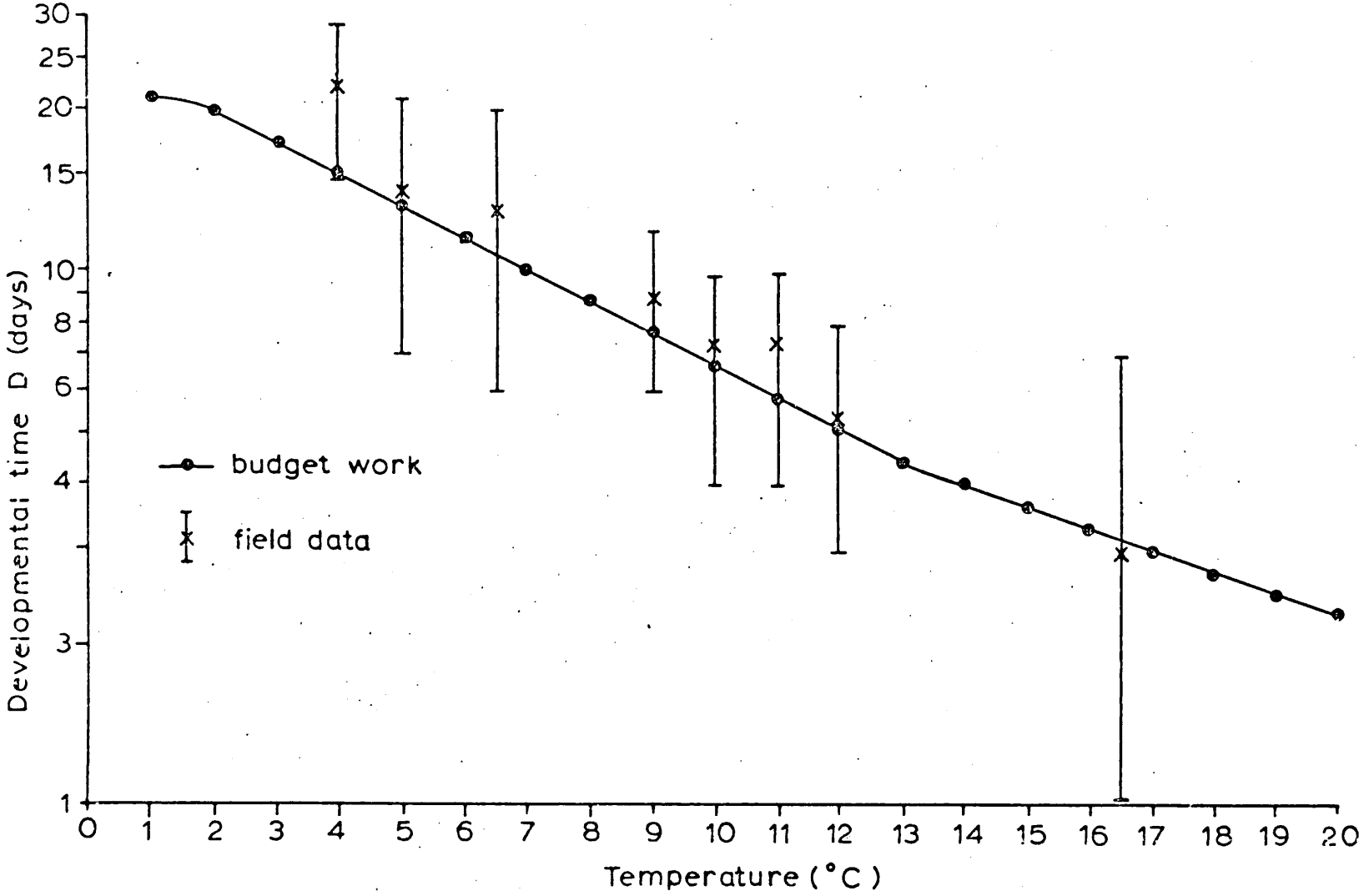


Fig. 5.2.2(g).

Table 5.2.2(i)

Field temperature (°C)	Mean duration of eggs (days)	Range (days)	N
4	22.0	15–29	2
5	14.5	7–22	2
6	13.0	6–20	2
9	9.0	6–12	2
10	7.5	4–10	3
11	7.5	4–10	3
12	5.5	3–8	2
16.5	3.0	1–7	3

The results for the developmental time of stages identified in the field samples, calculated from laboratory budget figures are presented in table 5.2.2(j)

Table 5.2.2.(j)

		10°C		20°C		
Stage	Instar	hours	days	hours	days	Q10
Egg		170.5	7.10	56.5	2.35	3.02
1.00	1 and 2	169	7.04	82	3.42	2.06
1.00–1.39	3 and 4	201	8.38	75	3.13	2.63
1.40–1.99	5,6 and 7*	428	17.38	185	7.71	2.32

*at 20°C instars 8, 9 and 10 were also less than 2.00mm.

Q10 is the frequently accepted relationship between a metabolic function and temperature and has been used here to estimate developmental rates, using the reciprocal of duration of a stage, for the calculation of field production estimates. (see section 5.1.4)

5.2.3. LABORATORY RESPIRATION

There have been few published studies of the respiration of daphnids in the laboratory and these include the work of MACARTHUR AND BAILLIE (1929)$_b$, ZEISS (1963) and SCHINDLER (1968) working with D. magna.

Other relevant studies include the field respiration experiments of BLAŽKA (1966), STRAŠKRABA (1967) and CREMER AND DUNCAN (1969) as well as the comparison of field and laboratory results by DUNCAN ET AL (1970). Laboratory studies of respiration with other Cladocera include those of OBRESHKOVE AND BANTA (1930) and OBRESHKOVE (1930) with Simocephalus expinosus, OBRESHKOVE AND KING (1932) and IVANOVA AND KLEKOWSKI (1972) with S. vetulus and MOSHIRI ET AL (1969) working with the carnivorous cladoceran Leptodora kindtii.

It is widely recognised that respiration may be used as a measure of the metabolism of an animal and that this may be affected by a wide range of physiological and environmental factors. Physiological factors include body size, age, reproductive state, nutritional state and stress. Environmental factors include temperature, oxygen tension and the degree of crowding or confinement of the animal.

Metablic rate is proportional to a power of the body weight (WEYMOUTH ET AL 1944, ZEUTHEN 1947, 1953 and HEMINGSEN 1950, 1960);

$$R = aW^b.$$

Theoretical values such as b=0.75 (HEMMINGSEN 1960) have been suggested, but values within the range b=0.7 and 0.9 have been reported for microcrustacea. RICHMAN (1958) gives a figure of $b = 0.88$ for D. pulex and

SCHINDLER (1968) hints at a similar value for D.magna. ZEUTHEN(1953) suggests that the 'b' value changes with ontogenetic increase in body size. The study by ZEISS (1963) is concerned with the effect of space and crowding on D. magna which he finds can affect the metabolic rate significantly at levels not found in nature but that may become important in laboratory studies. SCHINDLER (1968) studied the effects of crowding, reproductive state, body weight and temperature on metabolic weight and found that only body weight and temperature have a significant effect on the respiration rate of D. magna.

In this study, respiration rates were measured for animals with a known life history at times throughout their development. (The respiration work was completed in conjunction with and on the same animals used for developmental studies and described in section 5.2.2. The bulk of the respiratory determinations were made by Dr. A. Duncan with the close assistance of the author and results are presented here with her permission and the author's own interpretation). This had the advantage that the effects of body size, age and reproductive state on respiratory activity could be examined for individual animals. The effect of nutritional state, stress and activity have been discussed in an earlier section (4.4.3.).

The relationship between respiration rate and body size in terms of weight for D. hyalina at 10°C are presented in figure 5.2.3(a). The line, which is for all animals, can be seen to have a satisfactory double

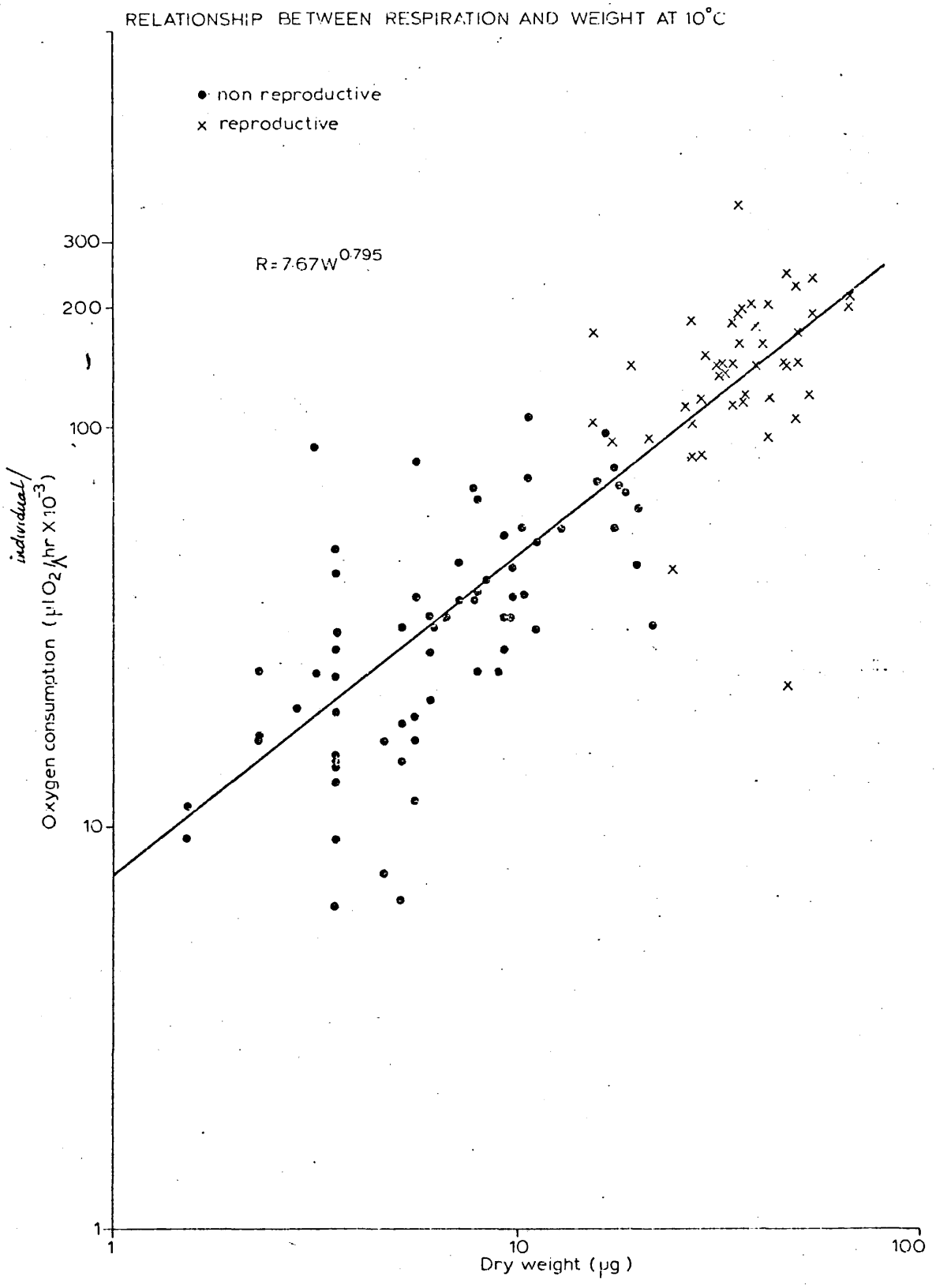

RELATIONSHIP BETWEEN RESPIRATION AND WEIGHT AT 10°C
• non reproductive
x reproductive
R = 7.67W^0.795
300
200
100
10
1
1
10
100
Dry weight (µg)
Oxygen consumption (µl O2/individual/hr X 10^-3)

Fig. 5.2.3(a).

logarithmic relationship (i.e. $R = aW^b$ see table 5.2.3(a) below) and the weights were calculated from measured lengths and the length-weight relationship obtained in section 5.2.1. The results were analysed by regression analysis producing satisfactory regression lines for all animals and immature animals and these results can be seen in table 5.2.3(a).

Table 5.2.3(a)

	$R=aW^b$ $\mu l O_2/x10^{-3}$	Standard Error (Syx)	Residual Variance (S^2)	N	Regression Coefficient (b)
All animals	$7.67W^{0.795}$	0.2891	0.3024	116	0.8502p< 0.001
Immature	$9.06W^{0.677}$	0.9215	0.3340	70	0.6483p< 0.001

It can be seen from the table that the regression coefficient is highly significant in each case. The regression equation for reproductive animals does not provide a satisfactory line because the weight range of the adult animals used for these experiments was too

small and the vertical spread of results is too wide. The variation obtained may appear to be high when compared with other workers' results (e.g. RICHMAN 1958), but the measurement of respiration rates of daphnids using the Cartesian diver technique reveals individual variations whereas the respiration of many animals in a closed bottle technique disguises individual variation and only produces an average value.

The results are also shown as respiration rate per unit weight against weight in figure 5.2.3.(b) and it can be seen that this relationship has a negative exponential form. Of the results of regression analyses, the line of best fit is given by

$$R/W = 7.67W^{-0.205} \ \mu l O_2 \ .hr^{-1} \times 10^{-3} \quad .(b=0.3845 p<0.001)$$

Figure 5.2.3(c) shows an arithmetic plot of individual respiration rate against length for all animals at 10°C. This figure shows the respiration rate of reproductive animals falling between sizes 1.10mm and 2.00mm length the upper limit of which is an artefact of the culturing technique. Animals frequently exceed 2.00mm in the field situation. The stages and types of reproductive development are distinguished in this figure and ovigerous animals, animals with eggs and developing ovaries and those with an ephippium have been distinguished from those without any obvious sexual attribute. It is apparent that the same sized individuals with both eggs and ovaries have a higher respiration rate than those with only eggs or than those with ephippia.

Oxygen consumption is compared with age and instar in figures 5.2.3.(d) and 5.2.3.(e) (lines IVe and IX

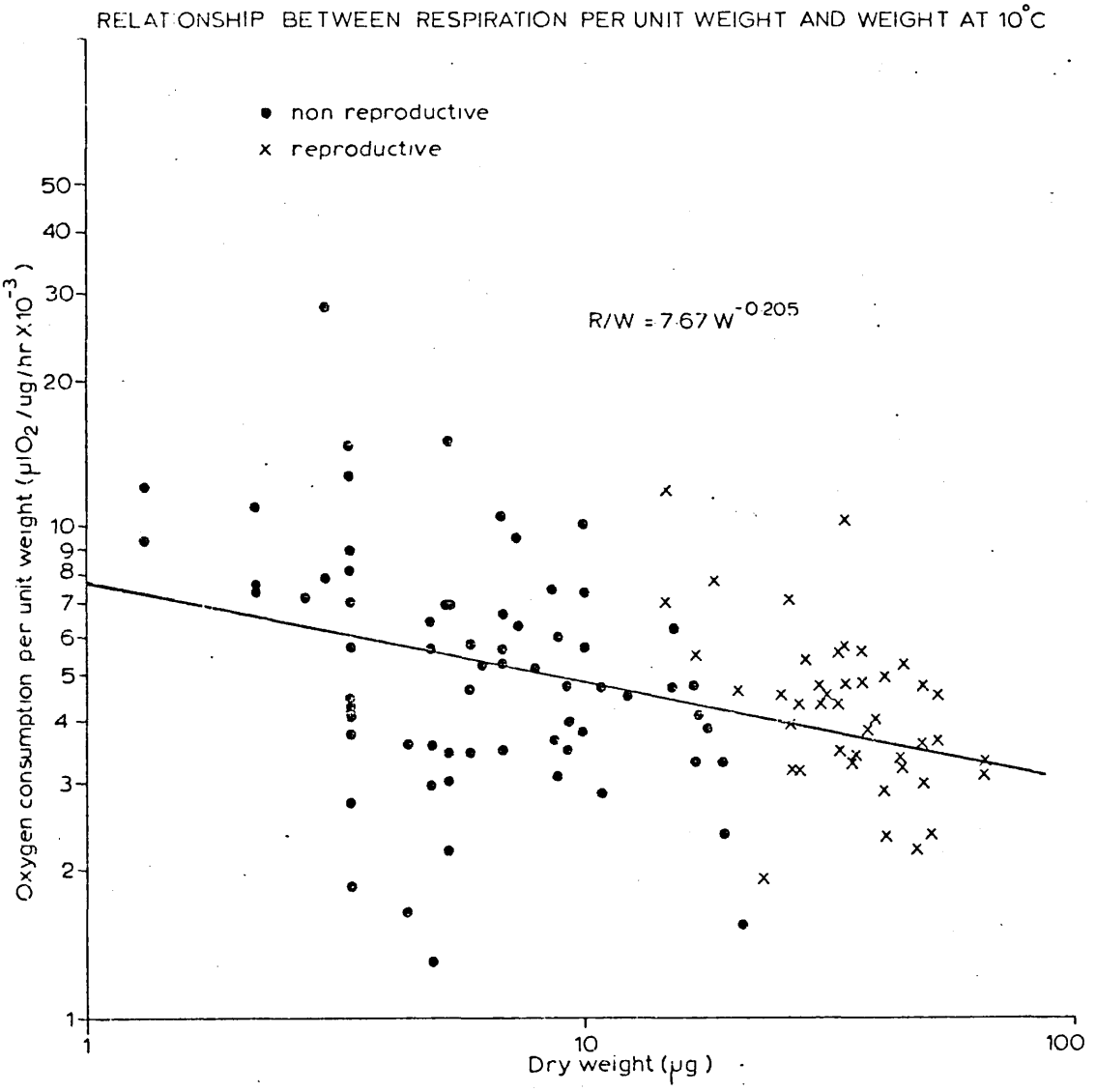

RELATIONSHIP BETWEEN RESPIRATION PER UNIT WEIGHT AND WEIGHT AT 10°C
non reproductive
reproductive
R/W = 7.67 W^-0.205
Oxygen consumption per unit weight (µlO2/ug/hr X10^-3)
50
40
30
20
10
9
8
7
6
5
4
3
2
1
1
10
100
Dry weight (µg)

Fig. 5.2.3(b).

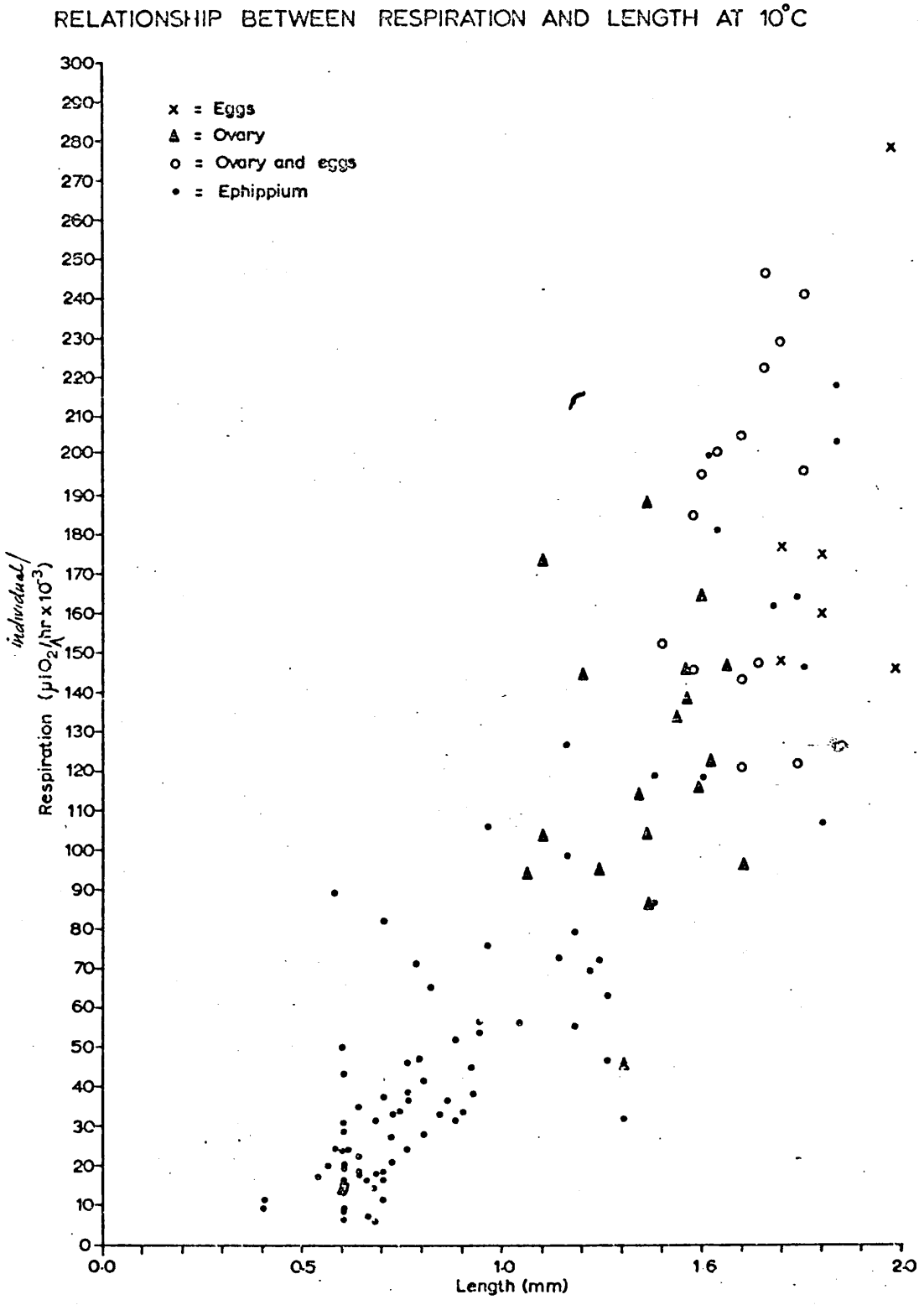

RELATIONSHIP BETWEEN RESPIRATION AND LENGTH AT 10°C
x = Eggs
▲ = Ovary
o = Ovary and eggs
• = Ephippium
Respiration (µlO2/individual/hr x 10-3)
Length (mm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
300
0·0
0·5
1·0
1·6
2·0

Fig. 5.2.3(c).

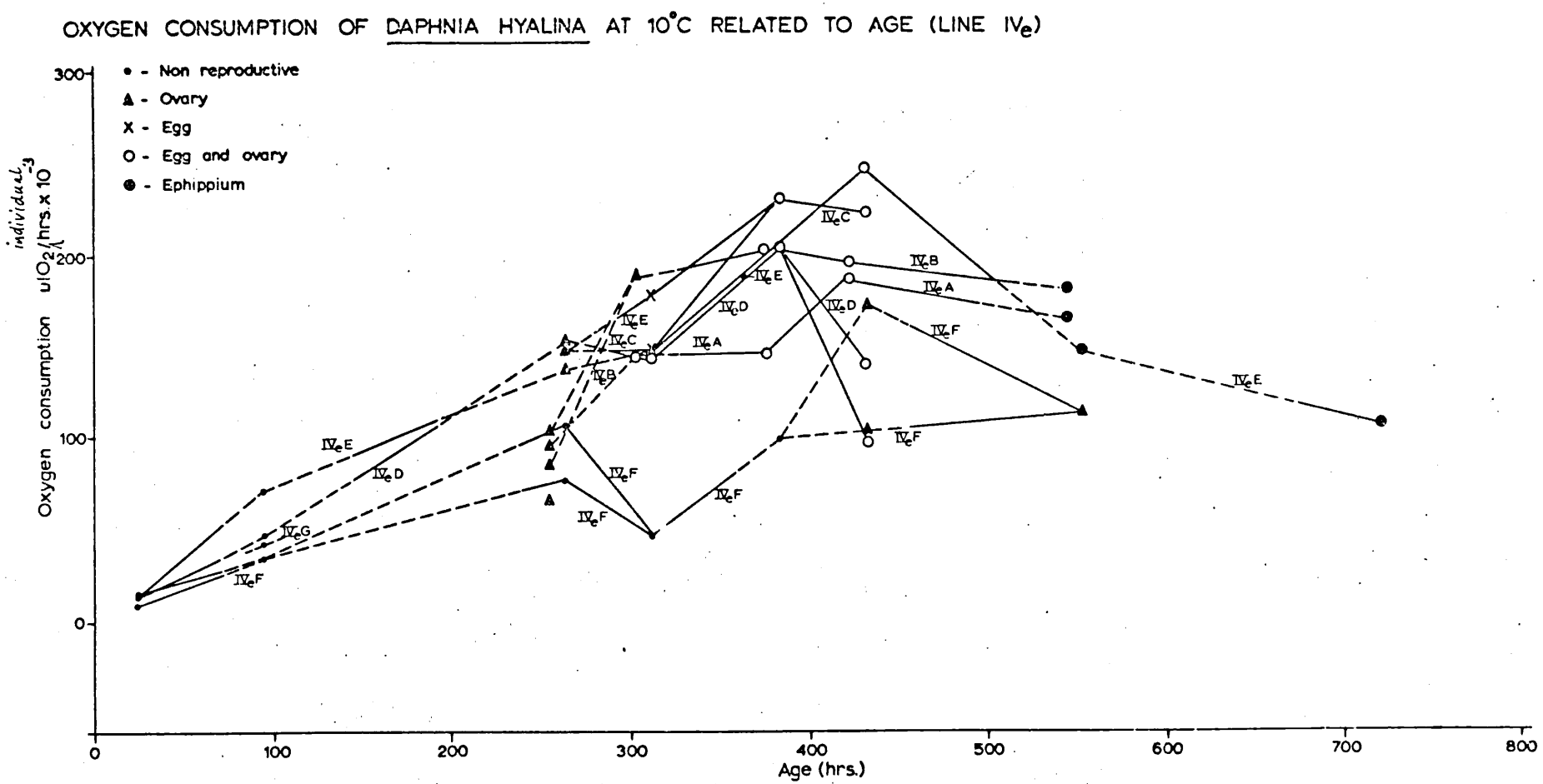

OXYGEN CONSUMPTION OF DAPHNIA HYALINA AT 10°C RELATED TO AGE (LINE IVe)
• - Non reproductive
▲ - Ovary
X - Egg
O - Egg and ovary
◉ - Ephippium
Oxygen consumption ul O2/individual-1/hrs. x 10
Age (hrs.)
0
100
200
300
400
500
600
700
800
IVeA
IVeB
IVeC
IVeD
IVeE
IVeF
IVeG

Fig. 5.2.3(d).

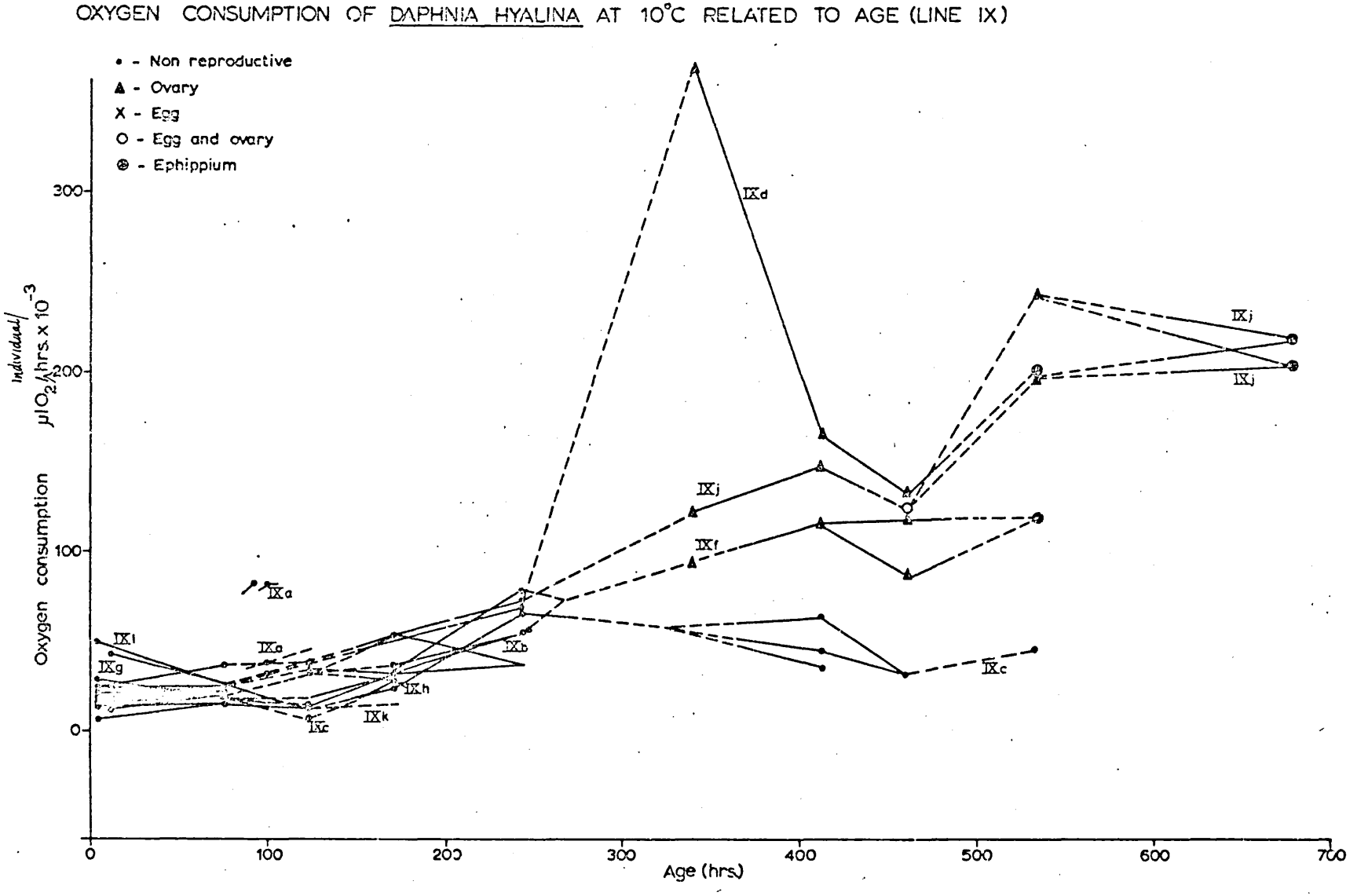

OXYGEN CONSUMPTION OF DAPHNIA HYALINA AT 10°C RELATED TO AGE (LINE IX)
• - Non reproductive
▲ - Ovary
X - Egg
O - Egg and ovary
⊕ - Ephippium
Oxygen consumption µl O2/individual/hrs. x 10-3
Age (hrs)
0
100
200
300
400
500
600
700
IXa
IXb
IXc
IXd
IXe
IXf
IXg
IXh
IXi
IXj
IXk

Fig. 5.2.3(e).

respectively) for individual animals throughout their life history. It can be seen that the respiration rate is fairly uniform for the first three instars but the variation becomes large in the primiparous instar, individuals such as 1Xd, showing up to a three-fold increase in the respiration rate. Other measurements are consistent with the results discussed although it seems that the production of ephippia, by adult females, coincides with a depressed respiration rate. This reduction in respiration rate may reflect either a reduced food intake or a poor quality food and that it is these semistarved animals that produce ephippia. When an animal fails to reach sexual maturity at the normal stage, it also exhibits a depressed respiration rate in the adult (see individual IXj). Where two respiration rates for the same individual occur at the same time of measurement it represents two actual rates measured consecutively during the same experiment. The difference may be related to a difference in activity of, or conditions imposed upon, the animal during the experiment. The lower measurements in these cases have a profound effect on the errors of the regression analyses but have been included as there is no reason to doubt their validity.

The relationship between respiration rate and temperature

Although no specific experiment was designed to study the effect of temperature on the respiration rate of D. hyalina, the experimental temperature of 10°C was chosen to complement the earlier unpublished work of DUNCAN AND CREMER at 20°C. using the same species and techniques. Their results are used here in summary, with their full approval, to discuss and interpret this relationship. The interpretation is solely the responsibility of the present author.

The relationship between temperature and metabolic processes is a complex and controversial issue and useful reviews of this topic can be found in ANDREWARTHA AND BIRCH (1954), TETIENS-NIELSEN AND EVANS (1960), M^{c}CLAREN (1963), WIGGLESWORTH (1966) and HEGARTY (1973).

One of the most frequently accepted relationships is expressed by the empirical Q10 formula which is generally used in the following form:

(i) $Q\ 10 = \frac{V_1}{V2}^{\frac{10}{t_1 - t_2}}$

This theoretic relationship, and the very similar Law of Arrhenius,

(ii) $V_2 = V_1 \, e^{\frac{1 - 1}{t2 - t1}}$

where V_1 = velocity of reaction at temperature t1

V_2 = velocity of reaction at temperature t2

e = base of natural logarithms

= reaction constant

were derived for application to specific chemical reactions taking place under defined laboratory conditions. Although much use has been made of these formulae in biology, it is debatable as to whether they have any predictive significance in animal metabolic studies although it may be argued that they may be useful describing different rate- temperature reactions. KROGH (1914) in KROGH 1916 from measurements of the rates of respiration of a series of poikilotherms at different temperatures produced a graph of respiration rate against temperature where maximum rates coincided on a simple curve described by van't Hoff's rule (where V_{t+10} = VtQ10). Since them many studies have been used to confirm this result. WINBERG (1971) analysed Krogh's normal curve at different temperatures and has constructed

a table of temperature corrections (q values) for converting respiratory rates measured at one temperature to respiratory rates at another known temperature where

$$Rt_2 = Rt_1 \cdot \frac{q2}{q1}$$

Rt_1 = respiration rate at temperature t_1

Rt_2 = respiration rate at temperature t_2

q_1 = 'q value' rate at temperature t_1

q_2 = q value rate at temperature t_2

Initially it was proposed to use respiratory data obtained at 10°C and 20°C together with Winbergs 'quick' method to produce a respiration temperature relationship.

Regression analyses, calculated from the original data of DUNCAN AND CREMER (unpubl.), for respiration – weight curves can be seen in table 5.2.3.(b) and these are comparable with results for the 'all animal' lines from the 10°C work as seen in tables 5.2.3.(b) and the text.

Table 5.2.3..(b)

All D.hyalina at 20°C	Standard error (s.y.x.)	Residual variance (S^2)	N	Regression coefficient(b)
$R = 8.602\ W^{-0.73}$	0.3002	0.2451	191	$0.7437 p < 0.001$
$R/W = 8.602\ W^{-0.27}$	0.3002	0.2451	191	$-0.3801 p < 0.001$

Using Winbergs 'quick' method where, q10 = 2.67 and q20 = 1.00, and $R_{10} = 7.67\ \mu l O_2 . hr^{-1} x 10^{-3}$, for an animal of unit weight, substitution in the formula

$$R_{t20} = Rt_{10} \cdot \frac{q20}{q10} \text{ gives } 20.47 \mu l O_2 . hr^{-1} x 10^{-3}.$$

The actual result obtained by measurement (see table 5.2.3 (b)) is:

$$Rt_{20} = 8.602 \mu l O_2 . hr^{-1} x 10^{-3}.$$

Either R_{20} is lower than would be expected according to Krogh's curve or R_{10} is higher than expected. The use of this method assumes that the response of respiration to temperature follows Krogh's curve. Few studies of cladoceran metabolism have been undertaken at different temperatures and SCHINDLER (1968) gives no indication that his experiments at 10°C and 20°C with D.magna did other than obey Krogh's surve. MOSHIRI etal (1969) also report results consistent with Krogh's curve for Leptodora kindtii. M^{c}CLAREN (1963), reviewing a wide range of temperature functions in marine zooplankton, suggests theoretical curves that give a better degree of fit than Krogh's curve but he still finds differences in rates at different temperatures.

The results obtained at 10°C and 20°C are plotted together in figure 5.2.3.(f) and regression analysis produces the relationship

$$R = 8.305W^{0.748} \quad O_2.\mu l^{-1}x10^{-3} (syx. = 0.1946, S^2 = 0.2598,$$

$$b = 0.8285 \; p < 0.001)$$

The 'a' values at 10°C, 20°C and as the same regression line are very similar (7.67, 8.60 and 8.30 respectively) but the values are significantly different as is seen by analysis of variance (table 5.2.3.(c)). The correlation coefficients are extremely high and the standard error very low for these analyses and the analysis shows the slopes of the lines ('b' values) to be the same.

RELATIONSHIP BETWEEN RESPIRATION AND WEIGHT FOR ALL ANIMALS AT 10°C AND 20°C

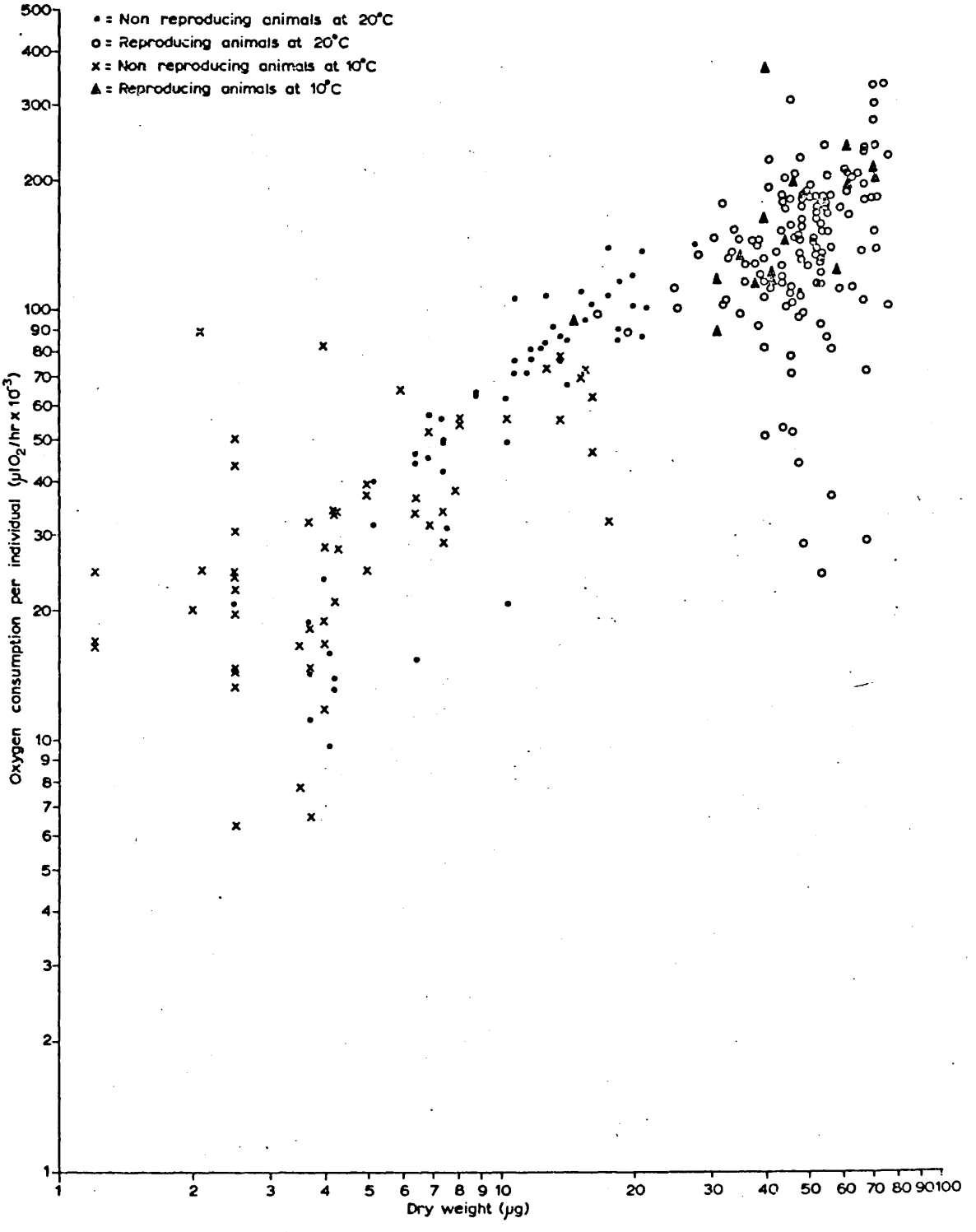


Fig. 5.2.3(f).

Table 5.2.3(c) Analysis of variance of regression lines at 10°C and 20°C.

Source of variation	d.f.	S.S.	M.S.	V.Ratio	$F_{.05}$
Explained by parallel Reg.	1	23.36210	23.36210	551.3800	3.87
Improve. due to indiv. slopes	1	0.04076	0.04076	0.9621	3.87
Difference in intercepts	1	5.05099	5.05099	119.2110	3.87
Devns. from indiv. slopes	303	12.83820	0.04237		
Total	306	41.29200			

The results seen here suggest that D. hyalina has acclimated its respiration rate to the experimental temperature to a much greater extent than expected. Acclimation of respiration rate to temperature in this way has not previously been reported in the literature for daphnids and although complete acclimation has not occurred the rate measured is only 5% of the expected value. MUNRO (1974) reports a degree of acclimation of developmental rate to temperature for Cyclops sp but does not indicate whether this applies to other metabolic processes.

Adaptation of respiratory rates to different temperatures in geographically separated races of poikilotherms has been recognised for a long time (see VERNBERG AND VERNBERG 1970). RAO AND BULLOCK (1954), PRECHT ETAL (1955), PRECHT (1958), PROSSER AND BROWN (1961), PROSSER (1962) and NEWELL (1971) review the occurrence of acclimation of metabolic rate functions to temperature in poikilotherms. These authors suggest that respiratory acclimation may occur if the animal is kept at the new temperature for many days'. PRECHT (1958) proposes a classification scheme of response

patterns to temperature change which includes completely adapted types. NEWELL (1971) points out that acclimation is a complex phenomenon and depends on factors other than time, such as activity and nutritional state.

In the present study, daphnids used in the respiration experiments had been collected from the field when the environmental temperature was low (between 7°C and 10°C) and transferred to the experimental temperature. The offspring of these animals and subsequent generations were used for respiration experiments. All the animals used for respiration determinations had been at the experimental temperature for the whole of their life. In other words the animals had generation rather than many days' to acclimate to their new temperature. The degree of temperature change (10°C) for the 20°C experiment was large even compared with the annual range of field temperatures (from 4°C to 20°C), although no individual animal would survive long enough to be subject to this temperature range, and yet the animals still acclimated. The nutritional state and activity were, as far as was observed, the same in both experiments. The conclusion to be drawn from these two experiments is that temperature acclimation of respiration rate occurred. It is felt, by the author, that the period of acclimation, which covered generations, in relation to the change in temperature, was sufficient for almost complete acclimation to have occurred. BUFFINGTON (1969) finds a similar phenomenon with the dipteran, Culex pipiens pipiens where complete respiratory acclimation occurred during the culture of individuals at the experimental temperature for the whole life cycle. Acclimation of this sort may be a more widespread occurrence than has been previously reported. FRALEIGH AND WIEGERT (pers. comm.) find the same function

in blue-green algae in hot springs. No explanation of the kinetic changes that must occur can be offered on the basis of the results presented here and there is very little indication from the literature about this (see NEWELL 1971). The ecological occurrence of this phenomenon is also discussed in section 5.1.5 describing field respiration measurements.

5.2.4 LABORATORY BUDGET

Since RICHMAN (1958) produced his laboratory energy budget for *D. pulex*, there have been no published energy budgets for daphnids. It has not been widely recognised that energy budgets can be most revealing in the strategy of a species by compartmentalising its available energy and this can be useful for interpreting field data. This method has been pioneered by KLEKOWSKI AND SHUSHKINA (1966) working with *Macrocyclops albidus* and some information is available from work on *Simocephalus vetulus* (KLEKOWSKI AND IVANOVA 1972).

Using the data obtained from growth and respiration experimentation, described in sections 5.2.2 and 5.2.3, it was possible to produce a partial energy budget for *D. hyalina* at 10°C. Using the results of DUNCAN and CREMER (in prep.) at 20°C, the effect of temperature on the energy budget was examined. RICHMAN (1958) uses two generally accepted equations for the theoretical basis of his energy budget, that of IVLEV (1939, 1945), later modified by RICKER (1946) where:

$$\text{Input} = \text{Growth} + \text{Respiration} + \text{Egestion} \quad \ldots\ldots(1)$$

and that of LINDEMANN (1942) where:

$$\text{Assimilation} = \text{Growth} + \text{Respiration} \quad \ldots\ldots\ldots(2)$$

Neither input nor egestion rates were measured in the present study but assimilation was estimated from equation (2) using respiration and growth data. The results obtained are presented below.

Figure 5.2.4(a) shows the growth and respiration of an individual *D. hyalina* ($\overline{IX}_j$) from the 10°C experiment. Individual $\overline{IX}_j$ was chosen as a good representative of line $\overline{IX}$, in that the primiparous instar was the fifth and it also produced an ephippial as well as the more normal parthenogentic broods. Results for

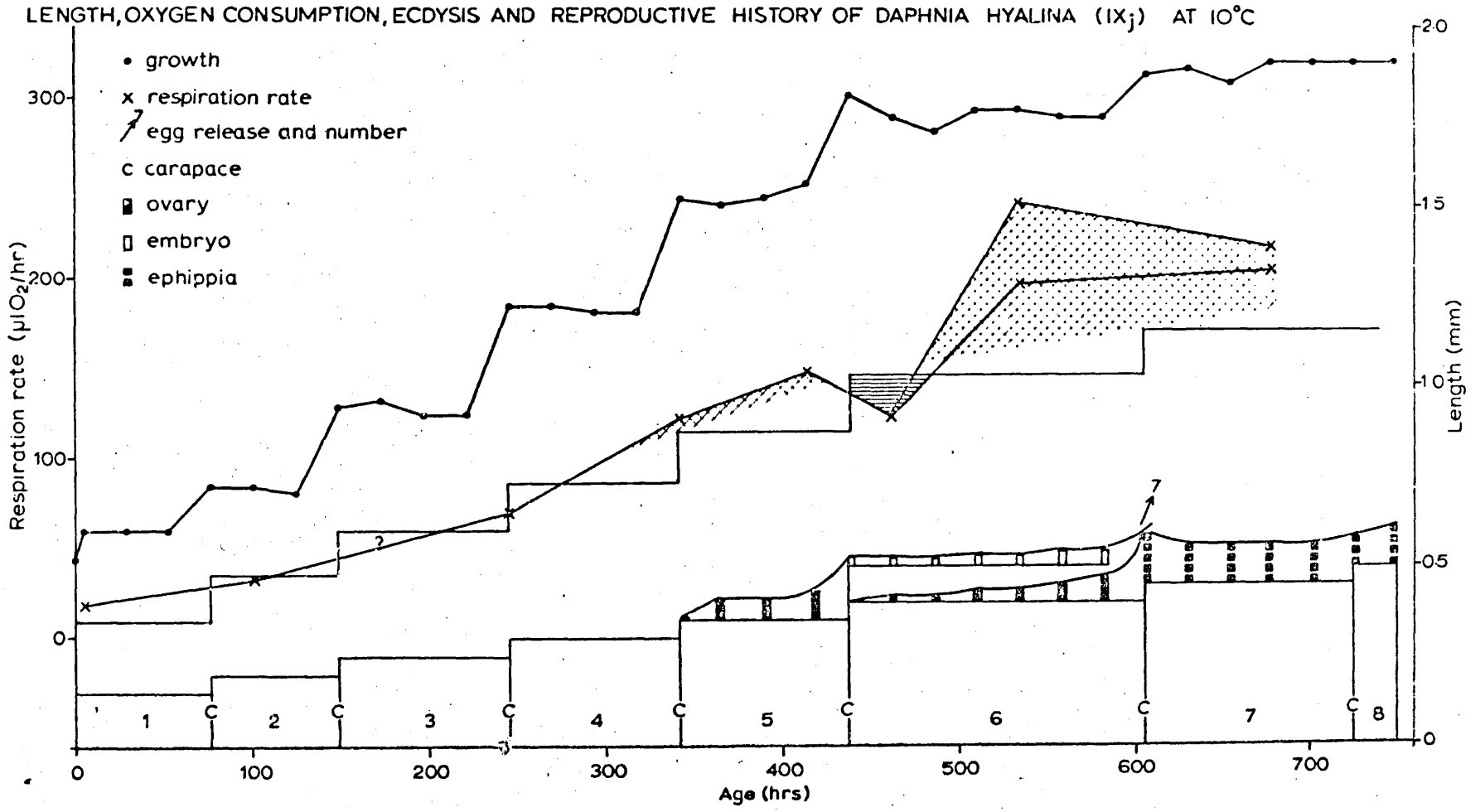

LENGTH, OXYGEN CONSUMPTION, ECDYSIS AND REPRODUCTIVE HISTORY OF DAPHNIA HYALINA (IXj) AT 10°C
• growth
x respiration rate
egg release and number
c carapace
ovary
embryo
ephippia
Respiration rate (µlO2/hr)
Length (mm)
Age (hrs)
0
100
200
300
400
500
600
700
1
2
3
4
5
6
7
8
C

Fig. 5.2.4(a).

other individuals of lines IXd and IVeE are shown in Appendix figs. 5.2.4(a) & (b) (pp. 294 & 295) and these show the same general features.

Using the information shown in figure 5.2.4(a) an instantaneous and cumulative energy budget has been constructed and is shown in figure 5.2.4(b) for the individual IXj. To construct this budget, length was converted to weight using the relationships obtained in section 5.2.4 and this weight was then converted to a common energy unit (calories) using the calorific values obtained by RICHMAN (1958), where:

	calorific value
newborn animals	4059 cal/g ash free
last pre-adult instar	4124 cal/g " "
actively reproducing animals	5075 cal/g " "

Egg production was calculated from the number of eggs and the calorific value of the eggs was assumed to be the same as that of a newborn individual. Ephippia were assumed to be equal in value to two parthenogenetic eggs as the normal number of eggs per ephippium in the Cladocera (BANTA ET AL 1939). The oxycalorific value of oxygen was taken to be 3.57 calories per mg. (MACFADYEN 1963). The final assumption made was that animals had an R.Q. =1, which assumes that carbohydrate metabolism was occurring (MACFADYEN 1963). The cumulated energy budget in figure 5.2.4(b_1), calculated in this way, shows, for individual IXj at 10°C, that by the end of its life, during the eighth instar, growth and respiration (assimilation) had totalled 0.87 calories of which 0.38 calories were growth in terms of body and egg growth. It can be seen that when the animal becomes sexually mature the rate of increase in body growth falls but the growth rate is continued as egg production. Figure 5.2.4(b_2) shows the instantaneous budget for individual IXj for body growth and reproduction and also for the

CUMULATED ENERGY OF PRODUCTION AND RESPIRATION FOR INDIVIDUAL D.HYALINA IX$_J$ AT 10°C

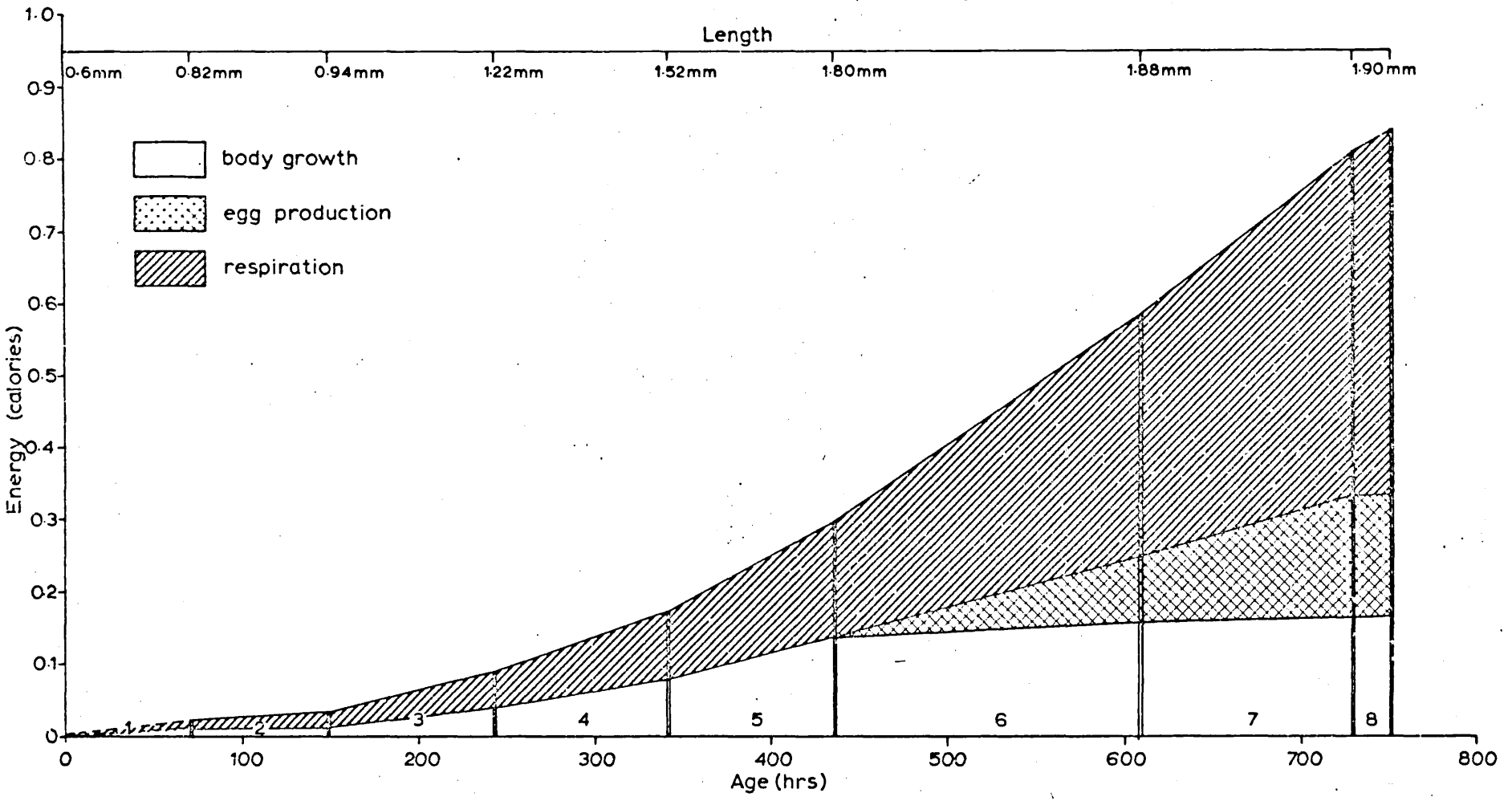


Fig. 4.2.4(b)1

INSTANTANEOUS ENERGY BUDGET FOR D.HYALINA AT 10°C. (INDIVIDUAL IXj)

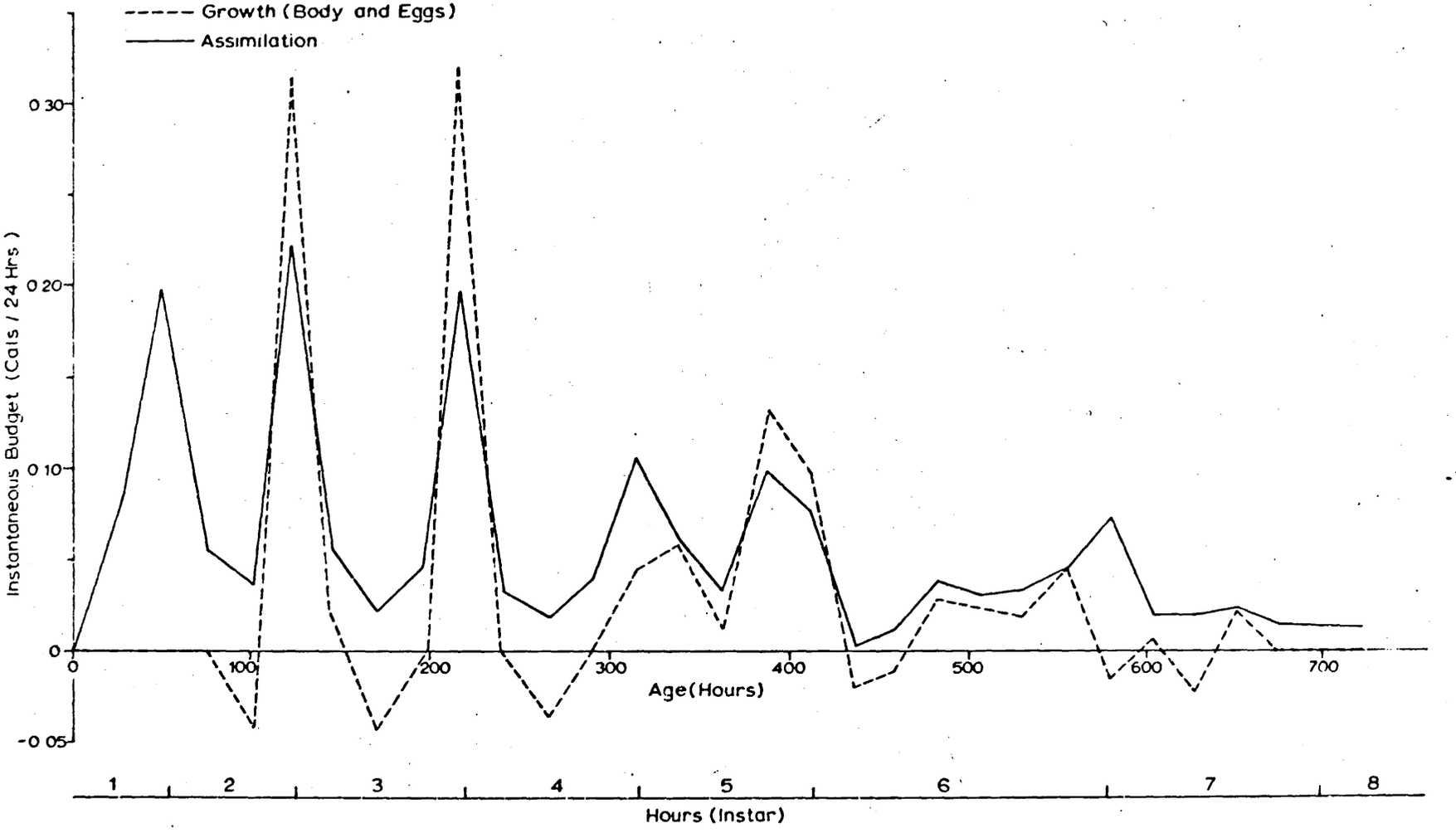


Fig. 5.2.4(b)$_2$

assimilated energy. The highest rates can be seen at the start of an instar when an abrupt change occurs for growth and there is a decrease as the animal gets older. The assimilation line is a reflection of the growth line as respiration is a function of size.

The results of the cumulated budget for all animals at 10°C are presented in table 5.2.4(a) and shown graphically in figure 5.2.4(c). The budget is shown to instar 12 at 10°C and the relationship between egg production and body growth can be seen much more clearly although mean egg numbers, not maximal egg numbers, are used for the calculation. It appears that the ratio of cumulated egg to body growth becomes fairly constant during active adult growth whereas in the juvenile period active growth is manifested as rapid body growth. This observation relates to the growth rate of animals which is discussed in section 5.2.2 and is seen as a decrease of the growth rate (G) in mature animals. The index of growth to assimilation (K_2) seen in table 5.2.4(a), which includes egg growth (Ge) as well as body growth (Gb) changes slightly throughout life. Initially at a low level, it reaches a maximum of 0.63 (63%) during the first reproductive instar and slowly falls throughout the rest of the animals life. The change in the value of K_2 can be seen in figure 5.2.4(d) and the values obtained compare well with the results given by RICHMAN (1958) where:

juvenile K_2	=	55 – 59%	(at 20°C)
adult of K2 40 days old	=	56 – 73%	

and the results of IVANOVA AND KLEKOWSKI (1972) for

Table 5.2.4(a)

	Instar	Age (hr)	Length (mm)	Weight (µg)	Eggs	Respiration µl/hr	Cumulated growth (cal.) body G_b	Cumulated growth (cal.) eggs G_e	Cumulated growth (cal.) G_e+G_b	Cumulated respiration (cal.)	Assimilation (cal.) $A=G_b+G_e+R$	$K_2=\frac{G_b+G_e}{A}$
	Egg	-167	-	3.24	-	20.0	0.0132	-	0.0132	0.0169	0.0301	0.439
1.00- 1.39 < 1.00mm	1	0	0.61	3.68	-	22.0	0.0149	-	0.0149	0.0259	0.0398	0.374
	2	86	0.76	6.97	-	35.5	0.0283	-	0.0283	0.0417	0.0700	0.547
	3	169	0.99	15.81	0vary	65.5	0.0652	-	0.0652	0.0731	0.1383	0.471
	4	265	1.34	22.95	5.6	86.5	0.1165	0.739	0.1904	0.1194	0.3098	0.615
< 2.00	5	373	1.64	36.34	7.8	122.0	0.1844	0.1769	0.3613	0.2174	0.5787	0.624
	6	527	1.68	48.49	7.8	151.4	0.2461	0.2799	0.5260	0.3237	0.8497	0.619
	7	646	1.95	54.18	9.0	164.4	0.2750	0.3987	0.6737	0.4316	1.1053	0.610
> 2.00	8	769	2.11	64.91	12.3	188.3	0.3294	0.5611	0.8905	0.6037	1.4942	0.596
	9	962	2.12	65.60	9.0	189.8	0.3329	0.6799	1.0128	0.7820	1.7948	0.564
	10	1148	2.15	67.75	8.0	194.5	0.3438	0.7855	1.1293	0.9529	2.0822	0.542
	11	1422	2.22	72.93	13.0	205.4	0.3701	0.9571	1.3272	1.1894	2.5166	0.517
	12	1533	2.21	72.18	5.6	203.9	0.3663	1.0310	1.3973	1.3037	2.7010	0.517

Table shows cumulated energy budget for D. hyalina at 10°C.

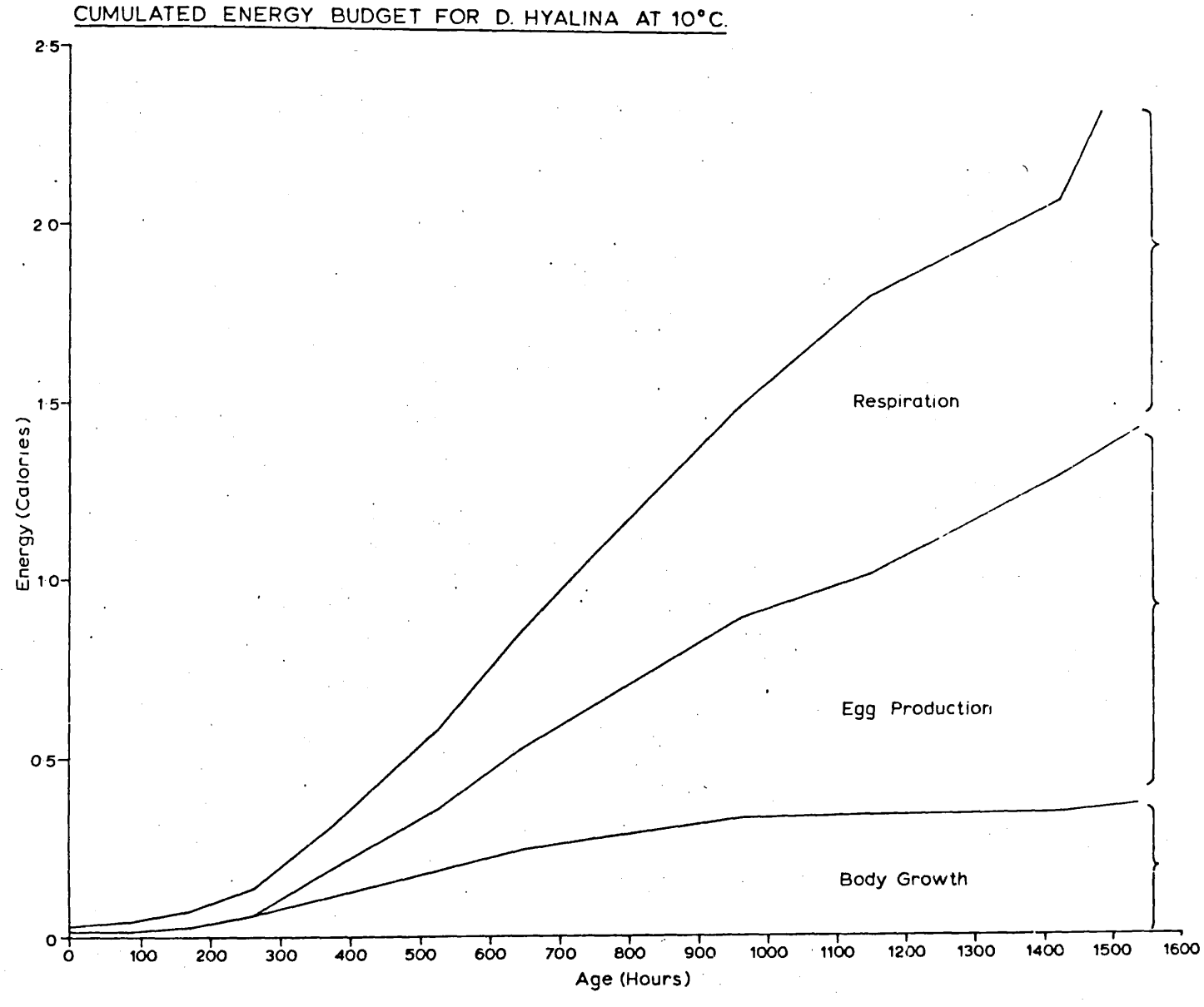

CUMULATED ENERGY BUDGET FOR D. HYALINA AT 10°C.
Energy (Calories)
2·5
2·0
1·5
1·0
0·5
0
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
Age (Hours)
Respiration
Egg Production
Body Growth

Fig. 5.2.4(c).

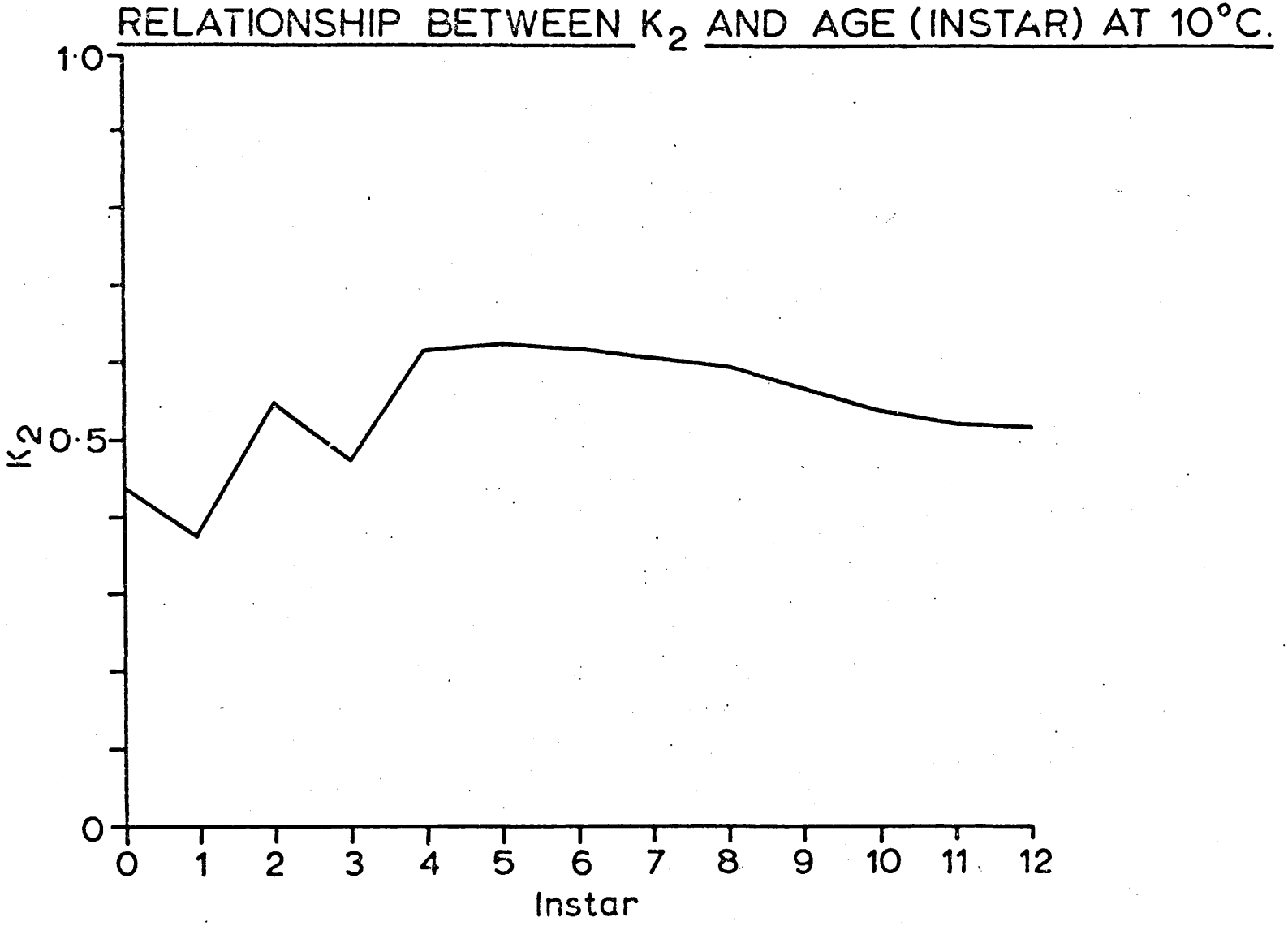

RELATIONSHIP BETWEEN K_2 AND AGE (INSTAR) AT 10°C.
1·0
0·5
0
K_2
0 1 2 3 4 5 6 7 8 9 10 11 12
Instar

Fig. 5.2.4(d).

Simocephalus vetulus where:

juvenile	K_2	=	71.3%	at (22°C)
preadult	K_2	=	73.1%	
adult	K_2	=	64.7%	

Comparing K_2 values at 10°C and 20°C the results of which can be seen in Table 5.2.4(b) and are calculated by the same methods (plotted graphically in figure 5.2.4(f) it can be seen that the shape of the curves are the same but the values at 20°C are slightly higher. The ratio of K_2 values ($K_{2.20}/K_{2.10}$) is fairly constant at 1.26.

Table 5.2.4(b) shows a summary of the budget results for D. hyalina obtained by DUNCAN AND CREMER (unpubl.) calculated by the same methods used to obtain table 5.2.4(a). The results can be seen graphically in figure 5.2.4(e) which shows the same features as figure 5.2.4(c) except that the time to reach a given instar is much shorter. A comparison of the two figures shows that the respiration demand to reach a given instar is smaller at 20°C than 10°C.

Figure 5.2.4(g) compares the cumulated budgets of 20°C and 10°C animals using the same instar scale instead of the same time scale. This figure shows that for the same stage of growth the energy of body growth is the same in both cases. The energy of egg growth is very similar but differences are apparent and due to a different rate of egg production (number per instar). This difference is probably the result of using sparse data for the egg production at 20°C and relates to the one individual (IIc). The 10°C figures are based on the mean egg numbers per instar for all animals cultured. GREEN (1956) and HALL (1964) demonstrate clearly that the rate of egg development in Daphnia, and not the actual egg numbers produced, is a function of temperature

Table 5.2.4(b)

Instar	Age (hrs)	Length (mm)	Weight (µg)	Eggs	Respiration µl/hr	Cumulated growth (cal.)			Cumulated resp. (cal.)	Assimilation (cal.)(A)	$K_2=\frac{G_b+G_e}{A}$
						Body G_b	Eggs G_e	G_e+G_b			
Egg	-53	-	3.24	-	20	0.0132	-	0.0132	0.0054	0.0186	0.710
1	0	0.50	2.46	-	16.6	0.0100	-	0.0100	0.0082	0.0182	0.549
2	47	0.90	11.86	-	52.8	0.0481	-	0.0481	0.0213	0.0694	0.693
3	73	1.09	14.63	-	61.8	0.0594	-	0.0594	0.0332	0.0926	0.641
4	105	1.31	23.27	Ovary	87.5	0.0960	-	0.0960	0.0495	0.1455	0.660
5	146	1.50	32.73	5(i)	112,9	0.1661	0.0660	0.2321	0.0803	0.3124	0.743
6	212	1.62	39.73	7.8(ii)	130.5	0.2016	0.1690	0.3706	0.1198	0.4904	0.756
7	268	1.68	48.49	5(i)	151.4	0.2461	0.2350	0.4811	0.1741	0.6552	0.734
8	344	1.78	50.37	4(i)	156.2	0.2556	0.2878	0.5434	0.2293	0.7727	0.703
9	413	1.81	52.55	4(i)	160.8	0.2667	0.3406	0.6073	0.2926	0.8999	0.675
10	491	1.93	61.79	10(i)	181.6	0.3136	0.4726	0.7862	0.3531	1.1393	0.690
11	575	2.02	68,44	13(ii)	196.0	0.3473	0.6442	0.9915	0.4283	1.4198	0.698
12	636	2.13	79.21	5.6(ii)	218.6	0.4020	0.7181	1.1201	0.4956	1.6157	0.693
13	766	2.22	87.92	5.6(ii)	236.3	0.4462	0.7920	1.2382	0.6507	1.8889	0.656
14	789	2.32	98.74	5.6(ii)	256.8	0.4986	0.8659	1.3645	0.6795	2.0440	0.668

(i) from animal II_c.

(ii) from 10°C numbers.

Cumulated energy budget for *D. hyalina* at 20°C (using the data of Cremer and Duncan unpubl.).

CUMULATED ENERGY BUDGET FOR D.HYALINA AT 20°C.

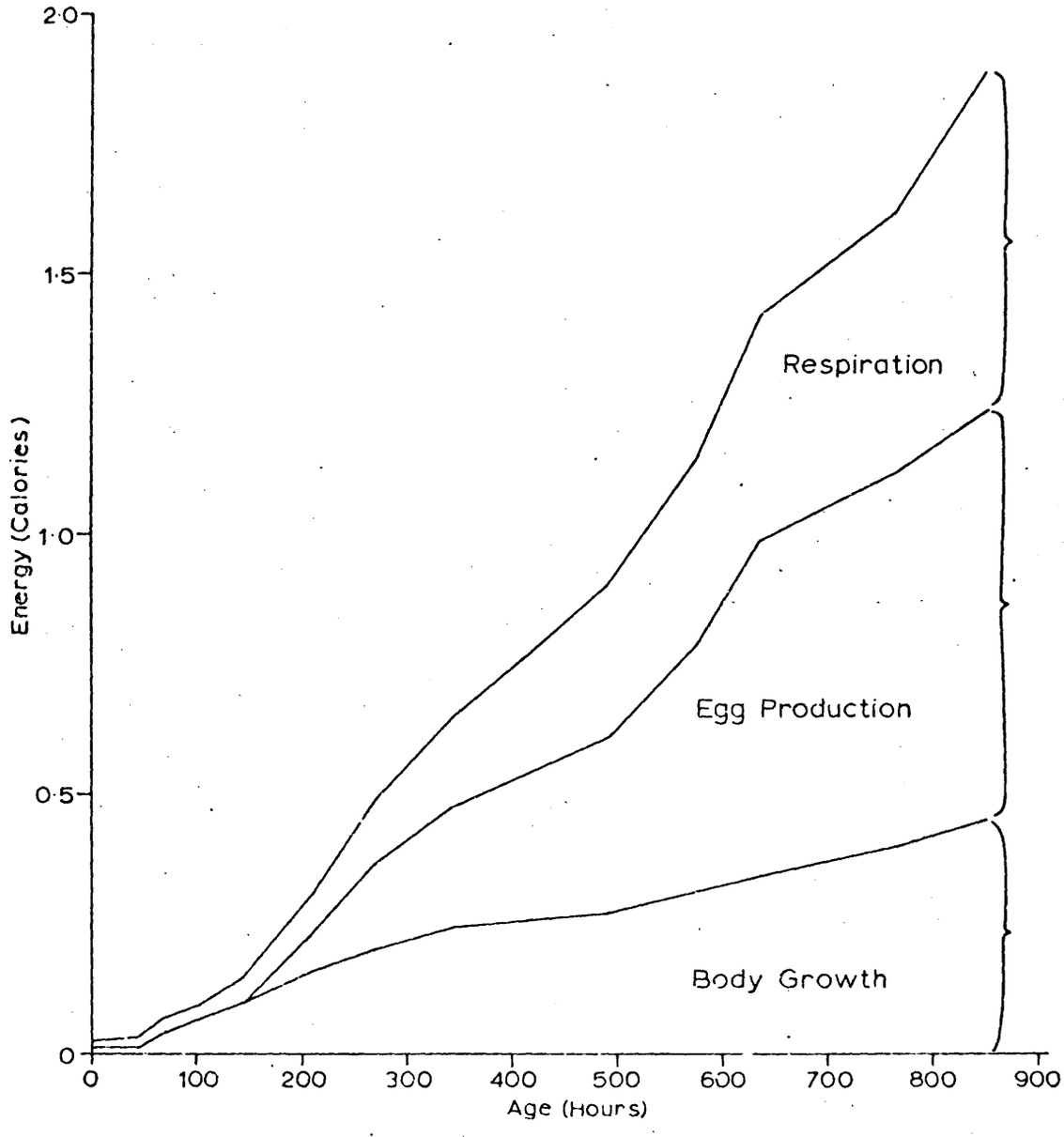


Fig. 5.2.4(e).

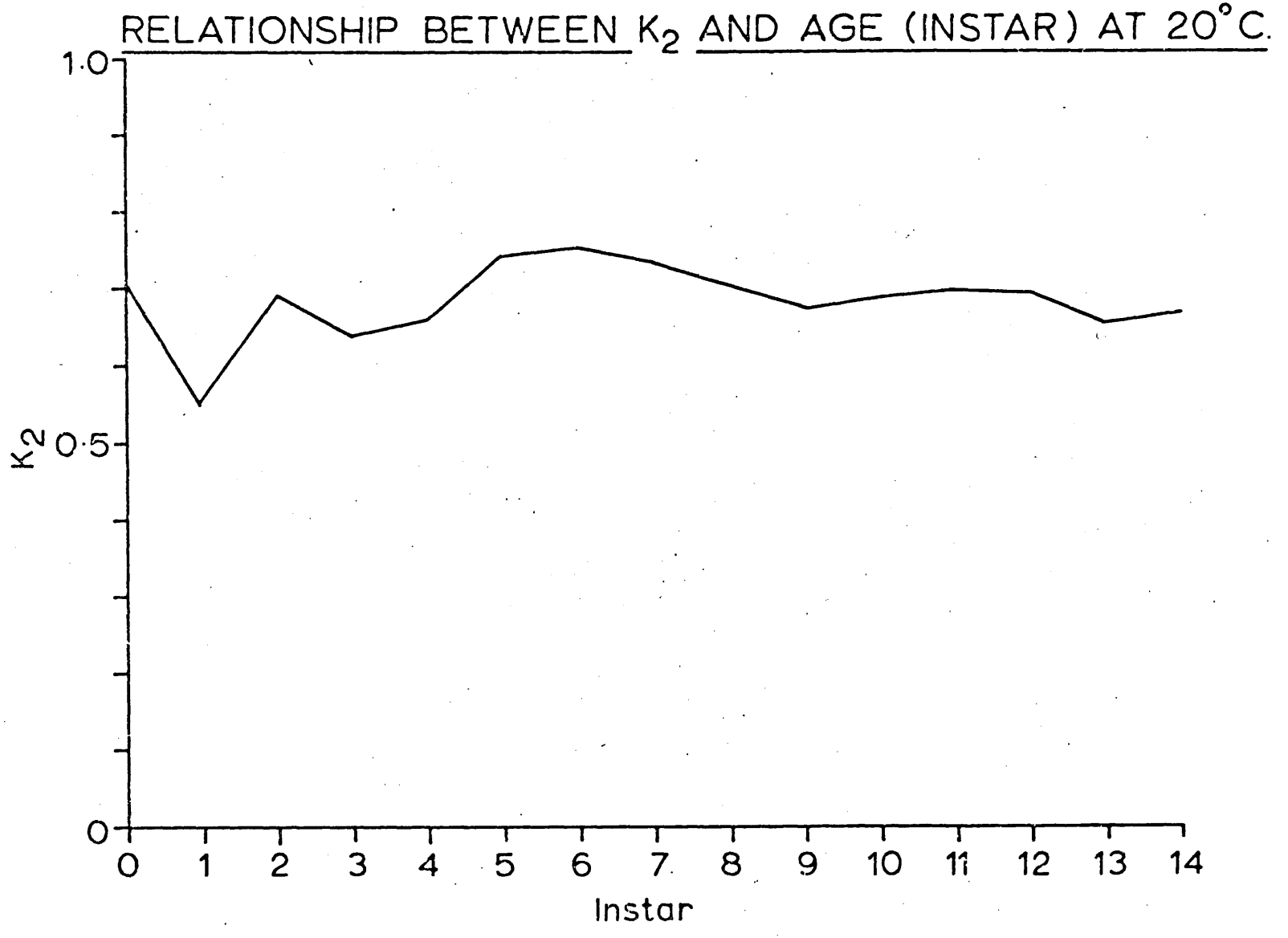

RELATIONSHIP BETWEEN K_2 AND AGE (INSTAR) AT 20°C.
1·0
0·5
0
K_2
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
Instar

Fig. 5.2.4(f).

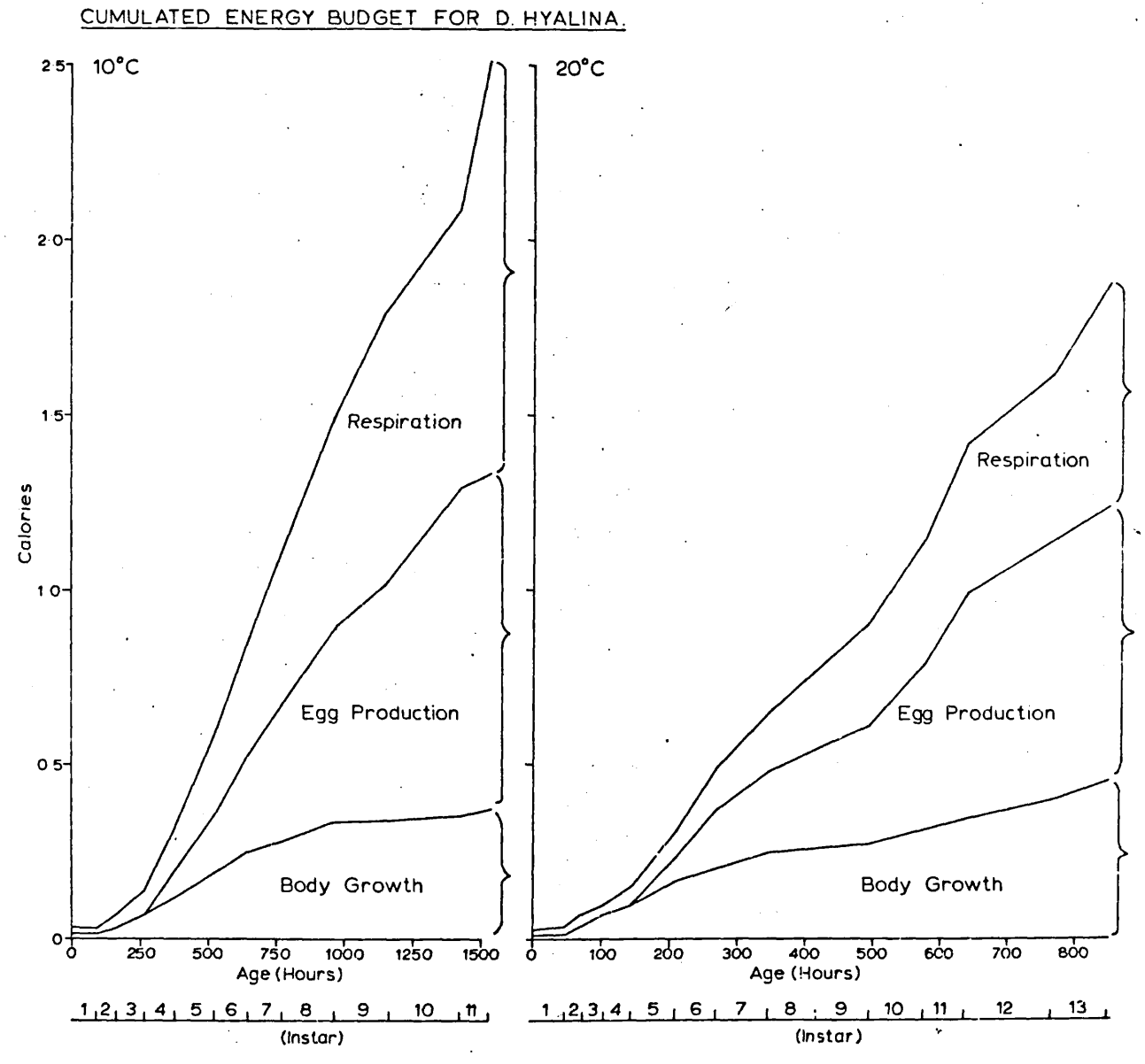

CUMULATED ENERGY BUDGET FOR D. HYALINA.
10°C
20°C
Calories
Respiration
Egg Production
Body Growth
Age (Hours)
(Instar)

Fig. 5.2.4(g).

and if this is true in representative experiments the egg production per instar should be the same at both temperatures. The figure (5.2.4(g)) also shows the energy of respiration and it can be seen that the respiration fraction is much lower at 20°C than 10°C for these animals. The importance of this is that for fully acclimated animals although the respiration rate is the same at both temperatures, the developmental time is much longer at lower temperatures and consequently more respirational energy is used.

Figure 5.2.4(h) shows the body growth (in terms of length) and respiration of individual IIc at 20°C and IXj at 10°C superimposed on the same instar scale. This figure demonstrates that apart from expected individual variation in growth and respiration rates that they are very much the same.

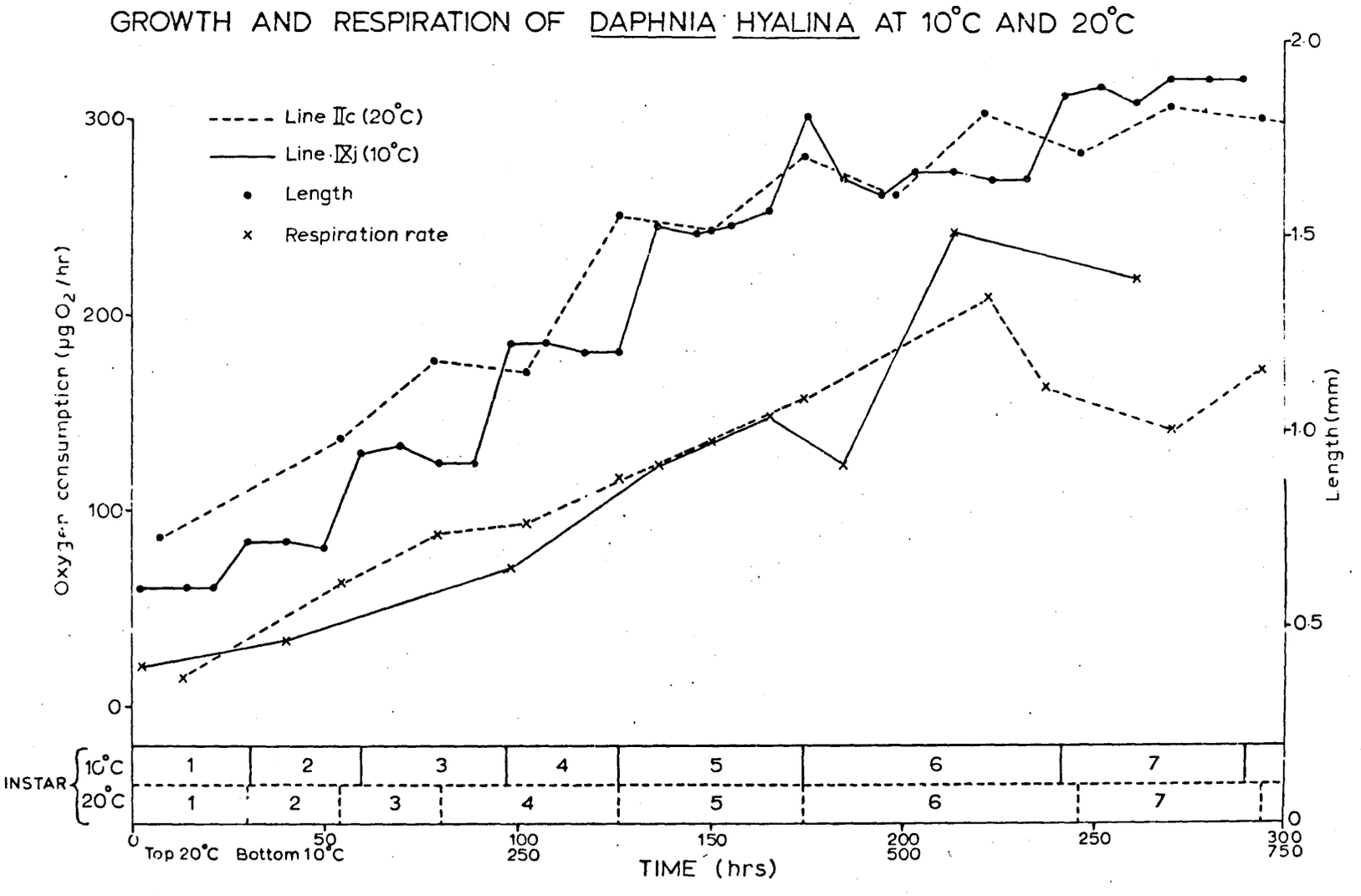

GROWTH AND RESPIRATION OF DAPHNIA HYALINA AT 10°C AND 20°C
Line IIc (20°C)
Line IXj (10°C)
Length
Respiration rate
Oxygen consumption (µg O2/hr)
Length (mm)
300
200
100
0
2·0
1·5
1·0
0·5
0
INSTAR
10°C
20°C
1
2
3
4
5
6
7
0
50
100
150
200
250
300
Top 20°C Bottom 10°C
250
500
750
TIME (hrs)

Fig. 5.2.4(h).

6. DISCUSSION

The bulk of this study dealt with the Queen Mary Reservoir and animals taken from that reservoir for further study in the laboratory. Therefore most of the comment in this section is directed mainly towards the Q.M. although that is not to say that the Queen Elizabeth Reservoir showed no interesting aspect. The recent paper of DUNCAN (1975b) draws attention to the coexistence of three species of Daphnia in the Q.E.II reservoir and undoubtedly this situation existed at the time of this study and contributed to the very different production situation described in section 5.1.8.

In studies of field populations most information is derived from a basic population estimate taken at intervals during the course of a season. This estimation is most often one of population numbers which has been further refined by sub-division into specific and/or size categories, reproductive stages, etc. It may also be a direct measure of the biomass of the population but this has more often been obtained as the product of the numerical analysis and a length-weight relationship.

The quality of the population estimate determines the reliability of any subsequently calculated information such as population dynamic indices or population production estimates. The basic population estimate may be improved in several ways. The best available technique applicable to the particular field situation must be selected. Samples may be replicated to the extent that the statistical estimate improves significantly. Unfortunately the improvement of the statistical estimate by replication of samples is no guarantee that the chosen sampling technique is the best estimator of absolute population size and care must

also be taken to gather only a manageable number of samples so that time remains for the study of other, perhaps more rewarding, facets of the problem. As LUND ET AL. (1958) demonstrate while sub-sampling algal populations, the reward (precision in this case) does not improve directly in proportion to the effort. An alternative approach is to select several different sampling methods which may sacrifice the precision obtainable for the same effort with a single replicated technique but might indicate how close to absolute population size the sampling programme approaches.

An example of this problem encountered in this study is in the difficulty in obtaining a satisfactory estimate of egg numbers in the population. This made population analyses and production estimates by standard techniques difficult. Replication of the samples may well have improved the reliability of the estimate but the alternative sampling technique using Patalas volume samples showed essentially the same problem. This indicated that an introduction of young from some other source may account for the observed discrepancies. Recent work of DUNCAN (pers. comm.) indicates that part of this difference may be accounted for by ephippial hatching from the bottom of the reservoir and that this may be considerable at certain times of the year.

Making full use of available population data by estimating production or explaining population fluctuations by means of models involves the use of other factors such as the egg developmental rate (De), the instantaneous individual growth rate (g), the respiration rate (R) and the feeding rate. These factors are themselves subject to errors in their determination which may cause gross distortion

of the real situation if incorporated into population data without reference to the existing field conditions. Each factor above is in some way a function of temperature, $f(T^{\circ})$, an easily and accurately measurable field variable. Unfortunately the relationship of these factors and temperature is not always simple or clear. Results given in this study demonstrate that the effect of temperature on respiration is not always the same in the laboratory and field situations and that an apparently simple temperature relationship such as the commonly accepted Q_{10} function may be obscured by a variety of factors such as feeding conditions, previous nutritional state or a degree of acclimatization to the existing environmental temperature as well as the more easily determinable size metabolic relationship. In fact the measured field respiration rates, admittedly confused by being of a mixed species population, depart so far from Q_{10} expectations as to make questionable the relevance of this sort of relationship to field conditions.

It is therefore advisable, when laboratory measurements of any function are to be interpolated into field data, to devise a field method (however crude) that can be used to check laboratory results in field conditions even if no obvious reason to expect a discrepancy can be seen. Workers in the area of zooplankton production use, among other factors, a value of De to calculate their production estimates. WRIGHT (1965) estimated De from the field population data *themselves* and GEORGE AND EDWARDS (1975) made in situ determinations of De. These results, where theoretically only temperature may affect the developmental rate of healthy eggs, show excellent agreement with results given by other workers from laboratory experiments, but even here extrapolation of the relationship to

unmeasured temperatures may lead to problems of interpretation. McCLAREN (1963) and BOTTRELL (1975) cast doubts on the previously accepted relationship between De and temperature and suggest several different functions that may be employed. Fortunately, in this particular example, the improved functions deviate little from the earlier function except at or beyond the extremes of the environmental temperatures encountered but empirical determinations of De in the field situation, if feasible, obviate the need to extrapolate a limited range of laboratory determinations.

Greater difficulties may be encountered when variables other than temperature may also affect a relationship. This has already been indicated in the area of field metabolism and the problem is not restricted to the zooplankton (GANF 1974). The instantaneous growth rate may be modified by food quality and quantity, the previous life history (this is usually unknown in field situations), the temperature and the genetic history of the population. The occurrence of a dwarf line in the laboratory study (line XIII in section 5.2.2) may not be uncommon in the field populations but without more sophisticated data analysis it is impossible to identify their contribution to the population production and it is only possible to apply measured factors in a blanket fashion to the population data. The effects of food quality and quantity on various growth and metabolic functions has not been examined here (or in many other studies) and is an area that requires attention. It is difficult to discover which particular food source the zooplankton are using and this may not be in proportion to the existing algal populations. NADIN-HURLEY AND DUNCAN (1976) have made a serious attempt to determine specifically what food sources are used by daphnids but it still remains to find out what nutritional

value quantitatively and qualitatively the natural diet provides.

Errors of interpolation do not only occur in the estimate of the variable to be introduced into the population data but also in the manner in which they are used. When applying variables such as growth or respiration rates determined in the laboratory, the values chosen must be applied to particular size categories that have been identified in field samples. These have often been determined on an arbitrary basis, especially if developmental stages such as instars cannot be distinguished, or on the basis of a previous study, GEORGE AND EDWARDS (1975) use the categories of the present author in STEEL ET AL. (1972) and these were determined on the previous experience of CREMER (pers. comm.). The size categories chosen are most useful if they represent a biologically identifiable stage of development such as juvenile, adult, or reproductive state even if these stages do not represent a known instar. Stages such as these usually embrace several instars and the choosing of a particular respiration rate, growth rate or weight for interpolation becomes largely guesswork (heavily biased by the experience of the worker) and this will introduce errors within the range of that particular size class. This type of error becomes large particularly when one size category embracing several instars dominates the population sample. Again a more satisfactory approach would be to measure each individual but in the available time this would be at the expense of other parts of the study. The determination of results from the field situation, even if only approximate, provides a useful indication of large discrepancies. The application of laboratory weight data to the numerical analysis of population data has to some extent

been examined in this study (section 4.1.5) and discrepancies hitherto unreported can be seen to exist. The individual variation in weight of animals of the same length (fig. 5.2.1(a)) can be considerable and is likely to be a normal field phenomenon and may be more extreme if seasonal variations are to be considered.

The conclusion to be drawn from the above part of the discussion are not that interpolation of laboratory results into field data should not be attempted but that caution should be exercised when doing so. A field measurement, even if a rather crude, may indicate areas of discrepancy. A useful function is served by erecting models and testing them with whatever data are available as this indicates areas of the study needing further, and sometimes more sophisticated, examination. If alternative methods are available for testing the same function it may be possible to arrive closer to the actual result.

Many of the results presented here reinforce the findings of other workers in this field. The seasonal changes in the zooplankton populations are much the same as found for other studies in shallow eutrophic lakes (e.g. GEORGE AND EDWARDS 1975). Similarly production levels achieved are well within the range reported in the literature but towards the upper end of the range. This again might be expected in waters rich in nutrients for algal growth supporting very large algal crops. The major contribution to this production is from D. hyalina, again a similar result to GEORGE AND EDWARDS (1975) but different from the result of JOHNSON AND WALKER (1975) in the very shallow Loch Leven where Cyclops strenuus abyssorum was the dominant zooplankter.

The reasons why D. hyalina was dominant in the O.M. during this study are complex and not well understood but may be most related to the fish populations existing in the reservoir and their controlling influence as predators of the zooplankton. Other predators of the daphnids include large populations of Asplanchna sp. occurring principally in the spring of 1969 and the occasional appearance of Leptodora kindtii as well as the continual presence of adult cyclopoid copepods.

The results of the field respiration experiments provided valuable data for making estimates of population assimilation. The results obtained compare with and expand the seasonal pattern described by CREMER AND DUNCAN (1969) for the same reservoir. The seasonal variation in respiration rates which cannot be adequately described in terms of temperature and food conditions have fundamental ecological implications especially in reference to the assimilation demands of the daphnids. This phenomenon requires further description and unfortunately no explanation of the mechanism is possible from this study although a few other workers are concerned with this problem in other animals (see NEWELL 1971). The assimilation of the zooplankton in the field situation expands the findings of STEEL ET AL. (1972) and although differing in some detail reaffirms the usefulness of these data in contributing to explain the overall relationships between zooplankton and algal ecology. The contribution of respiration as a user of energy particularly during the winter and spring can be seen in figure 5.1.6(a).

The laboratory studies have been used mainly to amplify the production and respiration studies in the field. The

length-weight relationships and growth rates of different stages were necessary to calculate production rates from the field data. The results presented here are in accord with the findings of other workers. The measurement of individual dry weights showed clearly the variation that can be expected. The laboratory respiration rates determined, partly by the author in conjunction with A. Duncan and partly by A. Duncan and G. Cremer, where acclimatization at two widely separated temperatures appears to have taken place is interesting in relation to the field respiration rates obtained. Although interpolation of these results into field data is difficult, for the reasons discussed in the earlier part of this section, they go a long way to confirming the accuracy of the field results. Whether this degree of acclimatization to temperature is a common phenomenon is open to speculation but the effect on the animals is marked. The cumulated energy budgets of individual D. hyalina (fig. 5.2.4(g)) show that for the same period of time less energy has been used for respiration by the animals at the higher temperatures and the difference has been channelled into production mainly in terms of egg production. In the field situation most of the production is by small, immature individuals, lower proportions surviving to become mature females, and these animals have a very high weight specific respiratory rate. This may account for the very high contribution of respiration to the field assimilation. This particularly applies when the temperatures are colder and the growth rates of the animals are slower thus remaining as small individuals for a longer period of time. The laboratory part of the study could well have been amplified by examining the same factors at a greater

range of temperatures but this would have made demands in terms of time and effort that were not practicable.

In conclusion, this study, although incomplete in many areas, does serve to indicate some facets of the problem that warrant further detailed study. Particular areas that escaped attention include measurements of field feeding rates and assimilation efficiencies which would be valuable in defining the trophic relationships of the zooplankton. Similarly a measure of predation on one hand and ephippial production on the other and the contribution of the River Thames might have made complete studies in their own right. Two areas that have received brief treatment in this work include production and respiration. It has been shown that production estimates depend partly on the method used to estimate them and the most satisfactory method might be determined by more theoretical work and computer simulation using selected data in different models. The respiration studies also indicate a need for further field experimentation and further studies to discover possible control mechanisms.

Finally, the present study has demonstrated to the author the value of studies that are linked with several workers linked closely and working in a common field study area. This has happened recently under the aegis of the I.B.P. programme with such groups as the Loch Leven I.B.P. project and the Lake George I.B.P. project. On a smaller scale the cooperation between J. A. Steel and A. Duncan, together with a number of other workers, while allowing scope for individuality but with the same general objectives, has allowed integrated studies beyond the scope of an individual worker to be undertaken.

7. REFERENCES

ANDERSON, B. G. (1932). The number of pre-adult instars, growth, relative growth, and variation in Daphnia magna. Biol. Bull. mar. Biol. Lab., Woods Hole, 63: 81-98.

ANDERSON, B. G. & JENKINS, J. C. (1942). A time study of events in the life span of Daphnia magna. Biol. Bull. 83: 260-272.

ANDERSON, B. G., LUMER, H. & ZUPANIC, L. J. (1937). Growth and variability in Daphnia pulex. Biol. Bull. 73: 444-463.

ANDREWARTHA, H. G. & BIRCH, L. C. (1954). The Distribution and Abundance of Animals. 782 pp. (Chicago).

ANGOLD, W. M. (1968). Studies on the distribution and population structure of zooplankton in reservoirs. Ph.D. Thesis (Science). University of London (186 pp).

ARMSTRONG, F. A. J. & WICKSTEAD, J. H. (1962). A note on the preservation of plankton samples with formalin. Journ. Cons. Int. Explor. Mer. 27(2), 129-130.

BANTA, A. M. (1926). A thelytokous race of Cladocera in which pseudo-sexual reproduction occurs. Z. indukt. Abstamm. uo Vererb Lehre 40: 28-41.

BANTA, A. M. & BROWN, L. A. (1939). Control of male and sexual egg production. In Banta et al 1939 - pp. 106-130.

BANTA, A.M., WOOD, T. R., BROWN, L. A. & INGLE, L. (1939). Studies on the physiology, genetics and evolution of some Cladocera. Carnegie Inst. Wash., Dept. Genetics, Paper No. 39 - 285 pp.

BAUDOUIN, M. F. & RAVERA, O. (1972). Weight, size, and chemical composition of some freshwater zooplankters: Daphnia hyalina (Leydig). Limnol. Oceanogr. 17(4) 645-649.

BAYLOR, E. R. & SMITH, F. E. (1953). The orientation of Cladocera to polarized light. Am. Nat. 87: 97-101.

BELLINGER, E. (1967). Ecologic a l and taxonomical studies of filter bed algae. Ph.D. Thesis. University of London.

BERG, K. (1931). Studies of the genus Daphnia O. F. Muller with especial reference to the mode of reproduction. Viderisk. Medd. fra Dansk. Naturhist. Forening. 92: 1-222.

BERG, K. (1936). Reproduction and depression in the Cladocera illustrated by the weight of the animals. Arch. für Hydrobiol. 30: 438-462.

BISHOP, J. W. (1968). Respiratory rates of migrating zooplankton in the natural habitat. Limnol. Oceanogr. 13, 1: 58-62.

BLAŽKA, P. (1966). Metabolism of natural and cultured populations of Daphnia related to secondary production. Verh. int. Ver. Limnol., 16: 380-385.

BOTTRELL, H. H. (1975). The Relationship between Temperature and Duration of Egg Development in some Epiphytic Cladocera and Copepoda from the River Thames, Reading, with a Discussion of Temperature Functions. Oecologia. 18,1: 63-84.

BRODY, S. (1945). Bioenergetics and Growth. Reinhold Pub. Co., N.Y. xii + 1023 pp.

BROOKS, J. L. (1946). Cyclomorphosis in Daphnia I. An analysis of D. retrocurva and D. galeata. Ecol. Monogr. 16: 409-447.

BROOKS, J. L. (1957). The systematics of North American Daphnia. Mem. conn. Acad. Arts Sci. 13: 5-180.

BUFFINGTON, J. D. (1969). Temperature acclimation of respiration in Culex pipiens pipiens (Diptera: Culicidae) and the influence of seasonal selection. Comp. Biochem. Physiol. 30: 865-878.

BURGIS, M. J. (1970). The effect of temperature on the development time of eggs of Thermocyclops sp., a tropical cyclopoid copepod from Lake George, Uganda. Limnol. Oceanogr. 15, 5: 742-747.

BURNS, C. W. (1968). Direct observations of the mechanisms regulating feeding behaviour of Daphnia in lakewater. Int. Rev. ges. Hydrobiol. 53: 83-100.

BURNS, C. W. (1969). Relation between filtering rate, temperature and body size in four species of Daphnia. Limnol. Oceanogr. 14, 693-700.

BURNS, C. W. & RIGLER, F. H. (1967). Comparison of filtering rates of Daphnia in lakewater and in suspensions of yeast. Limnol. Oceanogr. 12: 492-502.

COKER, R. E. & HAYES, W. J. Jr., (1940). Biological observations in Mountain Lake, Virginia. Ecology 21: 192-198.

CONWAY, E. J. (1962). Microdiffusion analysis and volumetric error. (5th edition). Crosby, Lockwood and Son Ltd.

CREMER, G. A. Zooplankton of Storage Reservoirs. Ph.D. Thesis. University of London (in prep.)

CREMER, G. A. & DUNCAN, A. (1969). A seasonal study of zooplanktonic respiration under field conditions. Verh. int. Ver. Limnol., 17: 181-190.

CUMMINS, K. W., COSTA, R. R., ROWE, R. E., MOSHIRI, G. A., SCANLON, R. M. & ZAJDEL, R. K. (1969). Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii Focke (Cladocera). Oikos 20: 189-223.

DOOHAN, M. (1973). Energetics of planktonic Rotifers applied to populations in reservoirs. Ph.D. Thesis, London University.

DUNCAN, A. (1975(a)). The importance of zooplankton in the ecology of reservoirs. The effects of storage on water quality. Water Research Centre Symposium. pp. 247-272.

DUNCAN, A. (1975(b)) Production and Biomass of Three Species of Daphnia coexisting in London Reservoirs. Verh. int. Ver. Limnol. 1975, 19: 2858-2867.

DUNCAN, A., CREMER, G. A. & ANDREW, T. (1970). The measurement of respiratory rates under field and laboratory conditions during an ecological study on zooplankton. Pol. Arch. Hydrobiol. 17: 149-160.

DUNHAM, H. H. (1938). Abundant feeding followed by restricted feeding and longevity in Daphnia. Physiol. Zool. 11: 399-407.

EDMONDSON, W. T. (1955). The seasonal life history of Daphnia in an arctic lake. Ecology 36: 439-455.

EDMONDSON, W. T. (1960). Reproductive rates of rotifers in natural populations. Mem. Ist. Ital. Idrobiol. 12: 439-455.

EDMONDSON, W. T. & WINBERG, G. G. (Eds.) (1971). A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No. 17, Blackwell, Oxford.

ELLIOT, J. M. (1971). Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication No. 25.

ELSTER, H. J. (1954). Über die Populations dynamik von Eudiaptomus gracilis Sars und Heterocope borealis Fischer in Bodensee-Obersee. Arch. Hydrobiol., Suppl. 20: 546-614.

ELSTER, H. J. (1958). Zum Problem der quantitativen Methoden in der Zooplankton forschung. Verh. int. Verein. Limnol. 13,2: 961-973.

EVANS, J. H. & McGILL, S.M. (1970). An investigation of the Coulter Counter in 'biomass' determinations of natural freshwater phytoplankton populations. Hydrobiologia 35: 401-419.

GANF, G. G. (1974). Rates of Oxygen Uptake by the Planktonic Community of a Shallow Equatorial Lake (Lake George, Uganda). Oecologia (Berl.) 15: 17-32.

GANF, G. G. & BLAŽKA, P. (1974). Oxygen uptake, ammonia and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George, Uganda). Limnol. Oceanogr. 19: 313-325.

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

GEORGE, D. G. & EDWARDS, R. W. (1974). Population dynamics and production of Daphnia hyalina in a eutrophic reservoir. Freshwat. Biol. 1974, 4: 445-465.

GLIWICZ, Z. M. (1968). The use of anaesthetizing substance in studies on the food habits of zooplankton communities. Ekol. Polska. (A). 16: 279-295.

GRAHAM, T. (1970). The zooplankton of Lough Neagh, 1968-1969. Ir. Nat. J. 265-271.

GREEN, J. (1954). Size and reproduction in Daphnia magna (Crustacea: Cladocera). Proc. zool. Soc. Lond. 124: 535-545.

GREEN, J. (1956). Growth, size and reproduction in Daphnia (Crustacea: Cladocera). Proc. zool. Soc. Lond. 126: 173-204.

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

GREZE, V. V. & BALDINA, E. P. (1964). Dinamika populacii i godovaya produktsiya Arcatia clausi Giesbr. i Centropages kroyeri v nenticheskoy zone Chernogo Morya. Tr. Sevastop. Biol. Stancii. 17, 249-261. Trans. FRBC 893.

HEGARTY, T. W. (1973). Temperature coefficient (Q_{10}), Seed Germination and Other Biological Processes. Nat. 243: 305-306.

GROVE, E. L., JONES, R. S. & MATTHEWS, W. (1961). The loss of sodium and potassium during dry ashing of animal tissue. Analyt. Biochem. 2: 221-230.

HARRIS, J. E. (1953). Physical factors involved in the vertic l migration of plankton. Q. Jl. microsc. Sci. 94: 537-550.

HALL, D. J. (1964). An experimental approach to the dynamcis of a natural population of Daphnia galeata mendotae. Ecology, 45: 94-112.

HART, R. C. & ALLANSON, B. R. (1976). The distribution and diel vertical migration of Pseudodiaptomus hessei (Mrázek) (Calanoida: Copepoda) in a subtropical lake in southern Africa. Freshwat. Biol. (1976) 6: 183-198.

HEGARTY

HEMMINGSEN, A. M. (1950). The relation of standard (Basal) energy metabolism to total fresh weight of living organisms. Reports of the Steno Memorial Hospital and Nordisk Insulin laboratorium, Vol. IV. pp. 7-58.

HEMMINGSEN, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. Reports of the steno memorial Hospital and the Nordisk Insulin laboratorium. Vol. IX Part II p. 7-10.

HOLTER, H. (1943). Technique of the Cartesian diver. C.r. Trav. Lab. Carlsberg. Ser. Chim. 24: 399-478.

HRBÁČEK, J. (1962). Species composition and the amount of zooplankton in relation to the fish stock. Roz. Cesk. Akad. Ved. 72: 3-116.

HRBACKOVA-ESSLOVA, M. (1966). The differences in the growth and reproduction at 8° and 20° of Daphnia pulicaria Forbes population inhabiting midland ponds and High Tatra lakes. Vestn. Ch. Tshsl. Zool. Spol. 30: 30-38.

HUTCHINSON, G. E. (1967). A Treatise on Limnology. Volume II. Introduction to lake biology and the limnoplankton. John Wiley. pp. 1115.

INGLE, L., WOOD, T. R. & BANTA, A. M. (1937). A study of longevity, growth, reproduction, and heart rate in Daphnia longispina as influenced by limitations in quantity of food Jour. exp. Zool. 76: 325-352.

IVLEV, V. S. (1939). Transformation of energy by aquatic animals. Int. Revue ges. Hydrobiol. Hydrogr. 38: 449-458.

IVLEV, V. S. (1945). The biological productivity of waters. Usp. sovrem. Biol. 19: 98-120. (In Russian).

JOHNSON, D. & WALKER, A. F. (1974). The Zooplankton of Loch Leven, Kinross. Proc. R. S. E. (B), 74,19: 285-294.

KAMLER, E. (1969). A comparison of the closed-bottle and flowing-water methods for measurements of respiration in aquatic invertebrates. Pol. Arch. Hydrobiol., 16: 31-49.

KIBBY, H. (1969). Energy transformations by a population of Diaptomus gracilis. Ph.D. Thesis, University of London, 224 pp.

KLEKOWSKI, R. Z. (1968). Cartesian divers micro respirometry for terrestrial animals. pp. 51-66 in Grodzinski, W. and Klekowski, R. Z. Methods of Ecological Energetics. IBP training course. Warsaw. Polish Acad. Sci.

KLEKOWSKI, R. Z. (1971). Cartesian diver micro-respirometry. pp. 290-295 In EDMONDSON & WINBERG (1971). IBP HANDBOOK No. 17 - A Manual on Methods for the Assessment of Secondary Productivity in Fresh waters.

KLEKOWSKI, R. Z. & IVANOVA, M. B. (1972). Elements of an energy budget of Simocephalus vetulus (Cladocera). Pol. Arch. Hydrobiol.

KLEKOWSKI, R. & SHUSHKINA, E. A. (1966). Energeteskii balans Macrocyclops albidus za vremya ego metamorfoza pri raznykh kontsentratsiyakh korma. Zh. obshch. Biol. 29,2: 199-208. Trans.

KONSTANTINOVA, N. S. (1961). O tempe rosta vetvistovsykh rachov i opredelenii okh produktsii. Vopr. Ikhtiol. 1,2: 362-367. FRBC Trans. 410.

KROGH, A. (1916). The respiratory exchange of animals and man. Longmans. Lond.

LANGHELT, L. (1968). Studies on the formation of zooplankton from Thames river water in the Metropolitan Water Board Reservoirs. M.Phil. Thesis (Zoology). University of London 253 pp.

LEBEDEVA, L. I. (1964). Opredelenie produktsii vetvistovsykh rachkov v vodokhranilishchakh. Tezisy 10-i nauch. konf. po izuch. vnutr. vodoemov Pribattiki, pp. 109-110.

LE SEUR, B. W. (1960). The life history of Daphnia pulex spp. Proc. Montana Acad. Sci., 19: 80-83.

LINDEMAN, R. L. (1942). The trophic-dynamic aspect of ecology. Ecology 23: 399-418.

LINDERSTRØM-LANG, K. (1937). Principle of the Cartesian diver applied to gasometric technique. Nature, Lond. 140: 108.

LINDERSTRØM-LANG, K. (1943). On the theory of the Cartesian diver microrespirometer. C.r. Tranv. Lab. Carlsberg. Ser. Chim. 24: 333-398.

LUND, J. W. G., KIPLING, C. & LE CREN, E. D. (1958). The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia. 11: 143-170.

MACARTHUR, J. W. & BAILLIE, W. H. T. (1929)(a). Metabolic activity and duration of life. I. Influence of temperature on longevity in Daphnia magna. Jour. exp. Zool. 53: 221-242.

MACARTHUR, J. W. & BAILLIE, W. H. T. (1929)(b). Metabolic activity and duration of life. II. Metabolic rates and their relation to longevity in Daphnia magna. Jour. exp. Zool. 53: 243-268.

MACFADYEN, A. (1948). The meaning of productivity in biological systems. J. Anim. Ecol. 17: 75-80.

MACFADYEN, A. (1963). Animal Ecology: Aims and Methods. (2nd edition). Pitman, 344 pp. (London).

McGILL, S. M. (1969). The ecology of the phytoplankton of a new reservoir in the Thames Valley. Ph.D. Thesis. University of London.

McLAREN, I. A. (1963). Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. Jour. Fish. Res. Bd. Can. 20: 685-727.

McMAHON, J. W. (1965). Some physical factors influencing the feeding behaviour of Daphnia magna Straus. Can. J. Zool. 43: 603-611.

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

McMAHON, J. W. & RIGLER, F. H. (1965). Feeding rate of Daphnia magna Straus in different foods labelled with radioactive phosphorus. Limnol. Oceanogr. 10: 105-113.

McNAUGHT, D. C. (1969). Developments in acoustic plankton sampling. Proc. 12th Conf. Great Lakes Res. 61-68 (Internat. Assoc. Great Lakes Research).

MARSHALL, S. M., NICHOLLS, A. G. & ORR, A. P. (1935). On the biology of Calanus finmarchius Part VI. Oxygen consumption in relation to environmental conditions. J. Mar. Biol. Assoc. U.K. 20: 1-25.

MOSHIRI, G. A., CUMMINS, K. W. & COSTA R. (1969). Respiratory energy expenditure by the predaceous zooplankter Leptodora kindtii (Focke) (Crustacea: Cladocera). Limnol. Oceanogr. 14,4: 475-486.

MUNRO, I. G. (1974). The Effect of Temperature on the Development of Egg, Naupliar and Copepodite Stages of two Species of Copepods, Cyclops vicinus Uljanin and Eudiaptomus gracilis Sars. Oecologia. 16,4: 355-368.

MURUGAN, N. & SIVARAAKRISHNA, K. G. (1973). The biology of Simocephalus acutirostratus King (Cladocera: Daphnidae) - laboratory studies of lifespan, instar duration, egg production, growth and stages in embryonic development. Freshwat. Biol. 3,1: 77-83.

NADIN-HURLEY & DUNCAN, A. (1976). A comparison of daphnid gut particles with the sestonic particles present in two Thames Valley reservoirs throughout 1970 and 1971. Freshwat. Biol. 6,2: 109-123.

NAUWERCK, A. (1959). Zur Bestimmung der Filtrierrate limnischer Planktontiere. Arch. Hydrobiol. (Suppl.), 25: 83-101.

NEWELL, R. C. (1971). The biology of intertidal animals. Logos Press (London).

OBRESHKOVE, V. (1930). Oxygen consumption in the developmental stages of a Cladoceran. Physiol. Zool. 3: 271-282.

OBRESHKOVE, V. & BANTA, A. M. (1930). A study of the rate of oxygen consumption of different Cladocera clones derived originally from a single mother. Physiol. Zool. 3: 1-8.

OBRESHKOVE, V. & KING, A. J. (1932). The effect of X-rays on the gaseous metabolism of a Cladoceran. Physiol. Zool. 5: 457-471.

OBRESHKOVE, V. & FRAZER, A. W. (1940). Growth and differentiation of Daphnia magna eggs in vitro. Biol. Bull. mar. biol. Lab., Woods Hole, 78: 428-436.

OTSUKI, A. & TAKAHISA, H. (1969). Residue from Bacterial Decomposition of Green Algal Cells as Food for Daphnia. Nature. Vol. 222 (June 21). 1 pp.

PACAUD, A. (1939). Contribution a l'écologie des cladocères. Bull. Biol. de la France et Belgique (Suppl.), 25: 1-260.

PATALAS, K. (1954). Porównawcze badania nad nowym typem samoczynnego czerpacza planktonowego i hydrochemicznego. (Comparative studies on a new type of self acting water sampler for plankton and hydrochemical investigations). Ekol. pol. Ser. A, 2, 231-242, (Engl. summ.).

PATALAS, K. (1956). Sezonowe zmiany w zespole skorupiakow pelagicznych w jeziorze Zamhowym. Polskie Archwm Hydrobiol. 3: 203-251.

PETROVICH, P. G., SHUSHKINA, E. A. & PECHEN, G. A. (1964). Raschet produktsii zooplanktona. Dokl. Akad. Nauk. SSSR 139,5: 1235-1238. In WINBERG 1971.

PETRUSEWICZ, K. & MACFADYEN, A. (1970). Productivity of Terrestrial Animals. Principles and Methods. IBP Handbook No. 13. Blackwell, Oxford.

PECHEN, G. A. & SHUSHKINA, E. A. (1964). Produktsiya planktonnykh rakoobraznykh v ozerakh razlichnogo tipa. Biol. Osnovy Rybnogo Khoz. na Vnutr. Vodoemakh Pribaltiki. Minsk, 249-256.

PRECHT, H. (1958). In Physiological Adaptation. Ed. C. L. Prosser, Washington, American Physiological Society pp 50-78. Patterns of Temperature Adaptation.

PRECHT, H., CHRISTOPHERSEN, J. & HENSEL, H. (1955). Temperatur und Leben. Verlin. Springer-Verlag, 514 pp.

PROSSER, C. L. (1962). In Comparative Physiology of Temperature Regulation Part I. (J. P. Hannon and E. Viereck, Eds.), pp. 1-44 Arctic Aeromed. Lab. Fort Wainright, Alaska.

PROSSER, C, L. & BROWN, F. A. (1961). Comparative Animal Physiology (2nd ed.). W. B. Saunders. 661 pp.

RAO, K. P. & BULLOCK, T. H. (1954). Q_{10} as a function of body size and habitat temperature. Am. Nat. 88: 33-44.

REBSDORF, A. (1966). Evaluation of some modifications of the WINKLER method for the determination of oxygen in natural waters. Verh. Int. Verein. Limnol. 16: 459-464.

RICHMAN, S. (1958). The transformation of energy by Daphnia pulex. Ecol. Monogr. 28: 273-91.

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

RIDLEY, J. E. (1964). Thermal stratification and thermocline control in storage reservoirs. Proc. Soc. Wat. Treat. Exam. 13: 275-297.

RIDLEY, J. E. A., COOLEY, P. & STEEL, J. A. P. (1966). Control of thermal stratification in Thames Valley Reservoirs. Proc. Soc. Wat. Treat. Exam. 15: 225-244.

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

RIGLER, F. H. (1961)(b). The uptake and release of inorganic phosphorus by Daphnia magna Straus. Limnol. Oceanogr. 6: 165-174.

RYTHER, J. H. (1954). Inhibitory effects of phytoplankton upon the feeding of Daphnia magna with reference to growth, reproduction and survival. Ecology, 35: 522-533.

SCHERBAKOFF, A. P. (1935). Ueber den Sauerstoffverbrauch von einigen Planktoncrustaceern. Arb. der. Limnol. Stat. zu Kossino. 19: 67-89.

SCHINDLER, D. W. (1968). Feeding, assimilation and respiration rates of Daphnia magna under various environmental conditions and their relation to production estimates. J. Anim. Ecol. 37: 369-385.

SCHINDLER, D. W. (1972). Production of phytoplankton and zooplankton in Canadian Shield Lakes. In Productivity Problems of Freshwaters (eds. Z. Kajak and A. Hillbricht-Ilkowska), pp. 311-331. Warszawa-Krakow.

SCHINDLER, J. E. (1971). Food quality and zooplankton nutrition. J. Anim. Ecol. 40: 589-595.

SCHRADER, F. (1926). The cytology of pseudo-sexual eggs in a species of Daphnia. Z. indukt. Abstamm. - u. Vererbhehre, 40: 1-27.

SMITH, M. W. (1936). Notes on the food of Daphnia pulex de Geer in fertilised waters. Trans. Am. Fish. Soc., 66: 287-290.

SOUTHWOOD, T.R.E. (1966). Ecological Methods. Methuen Lond.

STANDARD METHODS FOR THE EXAMINATION OF WATER AND WASTEWATER (1965 (12th Ed.). Amer. Public Health Association, Inc., New York.

STEEL, J. A. (1972). The application of fundamental limnological research in water supply system design and management. Symp. Zool. Soc. Lond. No. 29, 41-67.

STEEL, J. A. (1973). Reservoir algal productivity. University of Newcastle-upon-Tyne Symposium. The use of mathematical models in water pollution control. A. James (Ed.) Newcastle-upon-Tyne, 1973

STEEL, J. A. (1975). The management of Thames Valley Reservoirs. The effects of storage on water quality. Water Research Centre Symposium 371-419.

STEEL, J. A. P., DUNCAN, A. & ANDREW, T. E. (1972). The daily carbon gains and losses in the seston of Queen Mary Reservoir, England, during early and mid- 1968. In Productivity Problems of Freshwaters (eds. Z. Kajak and A. Hillbricht-Ilkowska), pp. 515-528. Warszawa-Krakow.

STRASKRABA, M. (1967). Estimation of respiration in the field of natural populations of Cladocera and Copepoda using the quantitative method of plankton sorting. Arch. Hydrobiol., 63: 497-511.

STROSS, R. G., NEESS, J. C. & HASLER, A. D. (1961). Turnover time and production of the planktonic crustacea in limed and reference portion of a bog lake. Ecology 42: 237-244

SUSHTCHENIA, L., (1958). Kolichest vennye dannye o fil'tratsionnom pitaniiplanktonnykh rachov. Nauch. Dokl. vyssh. Shk., Biol. Nauki, 1: 241-260.

SZLAUER, L. (1964). Reaction of Daphnia pulex de Geer to the approach of different objects. Pol. Arch. Hydrobiol. 8 (25) 1: 5-16

SZLAUER, L. (1965). The refuge ability of plankton animals before models of plankton-eating animals. Pol. Arch. Hydrobiol. 8(26) 1: 89-96.

SZLAUER, L. (1968). Investigations upon ability in plankton crustacea to escape the net. Pol. Arch. Hydrobiol. 15(28) 1: 79-86

TAUB, F. B. & DOLLAR, A. M. (1968). The nutritional inadequacy of Chlorella and Chlamydomonas as a food of Daphnia pulex. Limnol. Oceanogr. 14: 598-606.

TETENS-NIELSEN, E. & EVANS, D. G. (1960). Duration of the pupal stage of Aedes taeneorhynchus with a discussion of the velocity of development as a function. Oikos. 11: 200-222.

TRANTER, D. J. (1960). A method for determining zooplankton volumes. Jour. Conseil. Perm. Internatl. Explor. Mer. 25(3): 272-278

UMBREIT, W. W., BURRIS, R. H. & STAUFFER, J. F. (1949). Manometric Techniques and Tissue Metabolism. Burgess Pub. Co., Minn. 227 pp.

VERNBERG, F. J. & VERNBERG, W. B. (1970). The animal and the environment. Holt, Rinehart and Winston, Inc. N.Y. xv + 398 pp.

VOGEL, A. I. (1954). A textbook of macro- and semimicro-qualitative inorganic analysis. Longmans.

WEYMOUTH, F. W., CRIMSON, J. M., HALL, V. E., BELDING, H. S. & FIELD, J. II (1944). Total and tissue respiration in relation to body weight. Physiol. Zool. 17: 50-71.

WIGGLESWORTH, V. B. (1966). Insect Physiology. Methuen 134 pp.

WIKTOR, K. (1961). The influence of habitat factors on variations in the populations of Bosmina corregoni, Daphnia hyalina and Daphnia cuculata. Ekol. Polska., (Ser. A.) 9: 1-19. Polish text engl. summ.

WINBERG, G. G. (Ed.) (1971). Methods for the Estimation of Production of Aquatic Animals. Translated by A. Duncan. Academic Press. Lond.

WINBERG, G. G., PECHEN, G. A. & SHUSHKINA, E. G. (1965). Produktsiya planktonnych rakoobraznykh trekh ozerakh raznogo tipa. Zool. Zh. 44: 676-688. Trans. NLLRTS 6019.

WINBERG, G. G., BABITSKY, V. A., GAVRILOV, S. I., GLADKY, G. V., ZAKHARENKOV, I. S., KOVALEVSKAYA, R. Z., MIKHEYEVA, T. M., NEVYADOMSKAYA, P. S., OSTAPENYA, A. P., PETROVICH, P. G., POTAENKO, J. S. & YAKUSHKO, O. F. (1972). Biological productivity of different types of lakes. In Productivity Problems of Freshwaters (eds. Z. Kajak and A. Hillbricht-Ilkowska), pp. 383-404. Warszawa-Krakow.

WINDLE-TAYLOR, E. (1967). Forty-first report on the results of the bacteriological, chemical and biological examination of the London waters for the years 1965-1966. Metropolitan Water Board, London.

WINKLER, L. W. (1888). Die bestimmung des im Wasser gelösten Sauerstoffes. Chem. Ber. 21: 2843-2855.

WINSOR, C. P. & CLARKE, G. L. (1950). A statistical study of variation in the catch of plankton nets. J. Mar. Res. 3: 16-24.

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

ZEISS, F. R. (1963). Effects of population densities on zooplankton respiration rates. Limnol. Oceanogr., 8: 110-115.

ZEUTHEN, E. (1947). Body size and metabolic rate in the animal kingdom with special regard to marine microfauna. Comp. Rendus Lab. Carlsberg Ser. Chem. 26: 17-161.

ZEUTHEN, E. (1950). Cartesian diver respirometer. Biol. Bull., 98: 139-143.

ZEUTHEN, E. (1953). Oxygen uptake as related to body size in organisms. Quart. Rev. Biol. 28: 1-12.

8. APPENDICES

APPENDIX 4.3.

Reagents for Winkler's Determination

(a) Winkler's I

$MnSO_4 \cdot 4H_2O$ 400 g

made up to 1 litre distilled water

(b) Winkler's II

KOH 700 g

KI 150 g

made up to 1 litre distilled water

+ NaN_3 10g

dissolved in 40 mls distilled water

(c) Concentrated sulphuric acid

36N H_2SO_4

(d) Starch-soluble urea.

(e) N/320 Sodium thiosulphate solution

made up from commercially purchased ampoules of solution of known strength.

APPENDIX 5.1.1

Dry weight of daphnids and copepods. mg per V.N.H. in Q.

Date	Daphnids	Copepods	Date	Daphnids	Copepods
16.10.67	40.12	7.88	28.10	11.69	4.78
23.10	8.14	4.07	4.11	16.49	1.31
30.10	11.95	2.53	18.11	12.56	4.23
6.11	19.61	4.13	25.11	6.98	1.23
13.11	3.64	.66	2.12	17.10	4.52
20.11	23.97	3.16	9.12	2.68	4.27
27.11	7.20	2.54	16.12	8.94	.13
4.12	10.19	3.61	30.12	4.43	1.72
11.12	10.69	3.34	6.1.69	11.74	2.58
18.12	17.30	3.78	13.1	14.13	3.89
1.1.68	4.79	2.10	20.1	22.04	2.59
8.1	10.29	2.93	27.1	20.70	1.42
15.1	21.13	4.14	3.2	31.63	2.16
22.1	26.62	5.96	10.2	10.28	1.24
29.1	8.47	2.54	17.2	6.46	1.88
5.2	2.21	4.23	24.2	23.12	10.52
12.2	26.56	8.12	3.3	13.83	3.26
19.2	10.941	9.80	10.3	16.70	7.06
26.2	10.40	8.38	17.3	28.57	10.23
4.3	14.95	9.40	24.3	20.68	9.86
11.3	15.15	9.80	31.3	11.10	11.11
18.3	1.58	3.59	8.4	11.65	7.16
25.3	6.70	5.29	10.4	56.67	24.46
1.4	4.01	3.89	14.4	29.05	8.33
8.4	27.51	4.53	18.4	3.80	3.59
18.4	3.81	5.20	21.4	8.81	4.50
22.4	10.89	9.66	28.4	68.21	18.70
29.4	78.81	28.70	30.4	21.61	33.59
6.5	37.08	11.49	5.5	121.76	59.39
13.5	43.22	6.48	7.5	82.00	34.56
20.5	30.52	6.38	9.5	22.28	8.03
27.5	22.13	7.12	12.5	59.24	70.43
5.6	9.22	10.72	19.5	118.38	17.14
10.6	5.86	15.78	27.5	79.78	10.84
17.6	11.79	15.96	2.6	36.18	5.60
25.6	14.76	12.05	9.6	23.74	12.76
1.7	1.84	2.13			
8.7	9.67	6.57			
22.7	21.90	13.80			
29.7	2.25	1.90			
5.8	1.26	1.42			
12.8	5.04	1.98			
19.8	22.62	12.75			
26.8	32.96	25.15			
3.9	46.58	8.75			
9.9	20.58	7.17			
16.9	25.53	5.46			
23.9	5.19	2.22			
30.9	23.53	1.33			
7.10	19.25	5.42			
14.10	16.18	2.37			
21.10	3.19	.96			

APPENDIX. 5.1.2 .

Numbers and classes of D. hyalina per coarse V.N.H. for Q.M.

Date	Total	Eggs	>1.0 mm	1.0-1.39	1.40-1.99	>2.0
30.10.67	850	100	310	50	490	0
13.11	360	80	170	30	160	0
27.11	900	440	500	80	320	0
17.12	2470	350	1910	260	240	60
1. 1.68	2575	775	1400	475	675	25
8. 1.	870	175	560	140	170	0
22. 1.	2640	1200	1890	330	410	10
29. 1.	1307	163	1069	69	169	0
12. 2.	2280	740	1630	150	320	180
19. 2.	840	305	700	45	60	35
26. 2.	1315	260	895	230	155	35
4. 3.	1370	180	810	335	200	25
11. 3.	1225	250	670	275	270	10
18. 3.	555	25	405	70	25	0
25. 3.	470	45	395	45	10	0
1. 4.	178	26	136	16	20	6
29. 4.	15825	600	13675	1275	750	125
6. 5.	12050	0	10200	825	850	175
13. 5.	8000	25	6525	725	625	100
20. 5.	3975	50	3090	325	513	50
27. 5.	2335	30	1490	320	410	130
5. 6.	723	35	664	17	42	0
10. 6.	100	0	90	0	0	10
17. 6.	1860	0	1710	50	80	20
1. 7.	350	20	220	80	50	0
8. 7.	1750	0	1550	75	125	0
22. 7.	8575	0	8225	200	150	0
5. 8.	240	20	200	0	40	0
12. 8.	1160	0	1160	0	0	0
19. 8.	2987	170	1848	280	776	66
26. 8.	450	450	325	25	50	50
3. 9.	3888	50	3375	300	200	13
9. 9.	1960	0	1510	130	60	0
23. 9.	1440	0	1210	150	70	10
30. 9.	2962	437	2050	213	475	25
7.10.	2070	0	1710	220	140	0
14.10.	1210	160	940	70	180	20
21.10	180	0	120	0	60	0
28.10.	660	150	360	50	240	10
4.11.68	730	0	310	20	370	30
11.11.	780	0	520	80	160	20
18.11.	1810	180	1190	140	480	0
25.11.	420	140	140	30	250	0
2.12.	870	210	210	10	640	10
9.12.	200	30	150	10	40	0
16.12.	740	120	500	60	140	40
23.12.	1500	520	880	120	460	40
30.12.	390	40	300	30	60	0
6. 1.69	1080	450	670	130	250	30
13. 1.	1460	430	960	160	360	10
20. 1.	1450	760	890	160	360	40
27. 1.	930	740	550	50	310	20
3. 2.	920	660	640	70	200	10
10. 2.	1070	520	760	100	180	30
17. 2.	430	140	310	40	70	10
24. 2.	880	590	510	130	220	20
3. 3.	790	420	540	60	160	30
10. 3.	825	350	530	140	135	20
17. 3.	1940	850	1240	200	440	60

APPENDIX 5.1.2 (Contd.)

Date	Total	Eggs	>1.0 mm	1.0-1.39mm	1.40-1.99mm	<2.0mm
24. 3.	1670	1070	900	210	490	70
31. 3.	1230	180	720	140	340	30
8. 4.	420	180	190	60	170	D
10. 4.	5000	1233	2850	1233	800	117
14. 4.	1710	1510	630	310	740	30
21. 4.	290	25	216	16	50	8
28. 4.	5120	1940	4800	160	140	20
30. 4.	1380	680	1220	70	60	30
5. 5.	12025	1400	10050	1425	475	75
9. 5.	2760	0	2140	610	10	0
12. 5.	9975	2000	7575	1675	650	75
19. 5.	20045	250	15920	2025	1975	125
27. 5.	12025	625	7900	1250	2525	350
2. 6.	5440	100	4020	470	880	70
9. 6.	1330	10	890	210	230	0

APPENDIX 5.1.2

Numbers of Bosmina sp., Cyclops sp., Diaptomus sp., and Asplanchna sp. per coarse V.N.H. for Q.M.

Date	Bosmina	Cyclops	Diaptomus	Asplanchna
30.10.67	20	120	230	0
13.11.	0	20	100	0
27.11.	20	100	180	0
17.12.	0	60	130	0
1. 1.68	13	75	376	0
8. 1.	0	40	140	0
22. 1.	0	380	180	0
29. 1.	0	56	26	0
12. 2.	90	80	80	0
19. 2.	0	475	60	0
26. 2.	0	585	125	0
4. 3.	0	235	70	0
11. 3.	0	380	50	0
18. 3.	25	250	60	0
25. 3.	5	160	100	0
1. 4.	2	226	40	0
29. 4.	50	3675	225	0
6. 5.	25	1450	650	0
13. 5.	100	675	225	0
20. 5.	113	475	150	0
27. 5.	70	360	200	0
5. 6.	83	216	1411	0
10. 6.	60	390	890	0
17. 6.	280	300	1320	0
1. 7.	440	210	490	200
8. 7.	400	200	700	1600
22. 7.	125	675	2200	0
5. 8.	1210	250	230	0
12. 8.	370	170	60	0
19. 8.	233	1302	1737	0
26. 8.	0	875	6000	0
3. 9.	0	737	250	0
9. 9.	0	870	290	0
23. 9.	0	170	200	0
30. 9.	0	137	250	0
7.10.	0	70	1260	0
14.10.	0	40	440	0
21.10.	40	230	650	0
28.10.	0	60	290	0
4.11.68	20	0	240	0
11.11.	0	60	400	0
18.11.	0	130	300	0
25.11.	10	10	110	0
2.12.	10	80	160	0
9.12.	0	0	70	0
16.12.	10	30	60	0
23.12.	80	20	280	0
30.12.	0	20	70	0
6. 1.69	20	30	140	0
13. 1.	30	70	380	0
20. 1.	10	60	230	0
27. 1.	0	110	90	0
3. 2.	0	120	100	0
10. 2.	10	150	110	0
17. 2.	0	170	30	0
24. 2.	30	390	80	0
3. 3.	30	330	130	0

APPENDIX 5.1.2 (Contd.)

Date	Bosmina	Cyclops	Diaptomus	Asplanchna
10. 3.	0	220	60	10
17. 3.	20	520	190	0
24. 3.	10	230	100	0
31. 3.	20	570	80	0
8. 4.	20	280	20	20
10. 4.	30	1650	266	30
14. 4.	50	370	20	90
21. 4.	100	530	49	100
28. 4.	40	2830	160	550
30. 4.	50	3880	120	550
5. 5.	375	4150	225	7225
7. 5.	150	1925	100	11000
9. 5.	60	1090	130	7360
12. 5.	725	3825	275	14850
19. 5.	350	700	225	4075
27. 5.	400	750	250	375
2. 6.	210	350	60	230
9. 6.	90	140	630	50

APPENDIX 5.1.3

Date	VERTICAL NET HAULS				PATALAS			
	b'	r'	d'	D	b'	r'	d'	D
1.1.68	.0223	-	-	-	-	-	-	-
8.1	.0130	-.1550	.1680	.1546	-	-	-	-
22.1	.0291	.0793	-.0502	*	-	-	-	-
29.1	.0087	-.1004	.1091	.1034	-	-	-	-
12.2	.0240	.0397	-.0157	*	-	-	-	-
19.2	.0251	-.1426	.1677	.1535	-	-	-	-
26.2	.0104	.0640	-.0536	*	.0126	-	-	-
4.3	.0070	.0059	.0011	.0011	.0056	-.0583	.0639	-
11.3	.0141	-.0160	.0301	.0297	-	-	-	-
18.3	.0034	-.1131	.1165	.1100	-	-	-	-
25.3	.0086	-.0238	.0326	.0321	0	-.0694	.0694	.0670
1.4	.0163	-.1387	.1550	.1436	.0571	.2265	-.1694	*
8.4	-	-	-	-	.5344	-.1112	.6456	.4757
18.4	-	-	-	-	.0477	-.0755	.1232	.1159
29.4	.0080	.1603	-.1523	*	.0107	.3750	-.3643	*
6.5	0	-.0389	.0389	.0382	.0074	-.0274	.0348	.0342
13.5	.0005	-.0585	.0590	.0573	.0016	.0177	-.0161	*
20.5	.0024	-.0999	.1023	.0972	.0029	.0492	-.0463	*
27.5	.0028	-.0760	.0788	.0758	.0077	-.1790	.1767	.1620
5.6	.0144	-.1303	.1447	.1347	0	-.1704	.1704	.1567
10.6	0	-.3956	.3956	.3267	.0647	-.1230	.1877	.1711
17.6	0	.4176	-.4176	*	.0042	-.2975	-.2933	*
24.6	-	-	-	-	.0071	.0061	.0010	.0010
1.7	.0192	-.1193	.1385	.1293	.0047	-.1196	.1243	.1169
8.7	0	.1821	-.1821	*	.0026	.2055	-.2029	*
15.7	-	-	-	-	.0063	.0891	-.0828	*
22.7	0	.1135	-.1135	*	0	.0234	-.0234	*
29.7	-	-	-	-	.0359	-.4871	.5320	.4073
5.8	.0269	-.2554	.2823	.2460	.0671	.0044	.0627	.0608
12.8	0	.2251	-.2251	*	0	-.0715	.0715	.0690
19.8	.0170	.1351	-.1181	*	.2694	.3845	-.1151	*
26.8	.2829	-.2704	.5533	.4261	.1567	-.1436	.3003	.2594
3.9	.0042	.2695	-.2653	*	.0115	.2066	-.1951	*
9.9	0	-.1142	.1142	.1079	-	-	-	-
23.9	0	-.0220	.0220	.0218	.0084	-.1106	.1190	.1122
30.9	.0390	.1030	-.0640	*	.0219	.0925	-.0706	*
7.10	0	-.0512	.0512	.0499	.0097	-.0822	.0919	.0878
14.10	.0326	-.0767	.1093	.1035	.0295	.0794	-.0499	*
21.10	0	-.2722	.2722	.2383	0	-.3846	.3846	.3193
28.10	.0510	.1856	-.1346	*	-	-	-	-
4.11	0	.0144	-.0144	*	-	-	-	-
11.11	0	.0095	-.0095	*	-	-	-	-
18.11	.0139	.1203	-.1064	*	.0123	-.0696	-.0573	*
25.11	.0366	-.2087	.2453	.2175	.0151	-.0710	.0861	.0825

APPENDIX 5.1.3

Date	VERTICAL NET HAULS				PATALAS			
	b'	r'	d'	D	b'	r'	d'	D
2.12.68	.0266	.1040	-.0774	*	.0255	.1055	-.0800	*
9.12	.0149	-.2100	.2249	.2014	.0429	-.1741	.2170	.1951
16.12	.0137	.1869	-.1732	*	.0334	-.0060	.0394	.0386
23.12	.0291	.1009	-.0718	*	-	-	-	-
30.12	.0067	-.1924	.1991	.1805	.0390	.0010	.0380	.0373
6.1.69	.0219	.1455	-.1236	*	.0277	-.0530	.0807	.0775
13.1	.0155	.0431	-.0276	*	.0264	.0682	-.0418	*
20.1	.0335	-.0010	.0345	.0339	.0164	-.0152	.0316	.0311
27.1	.0618	-.0634	.1252	.1177	.0504	.1698	-.1194	*
3.2	.0524	-.0015	.0539	.0525	.0442	-.0088	.0530	.0516
10.2	.0311	.0216	.0095	.0095	.0372	-.1178	.1550	.1436
17.2	.0172	-.1302	.1474	.1371	.0147	-.1147	.1294	.1214
24.2	.0375	.1023	-.0848	*	.0290	.0523	-.0233	*
3.3	.0299	-.0154	.0453	.0443	.0230	.0579	-.0349	*
10.3	.0183	.0344	-.0161	*	.0195	.0132	.0063	.0063
17.3	.0281	.0940	-.0659	*	.0320	-.0312	.0632	.0612
24.3	.0470	-.0214	.0684	.0661	.0603	.0101	.0502	.0490
31.3	.0116	-.0437	.0553	.0538	.0233	-.0620	.0843	.0808
8.4	.0408	-.1343	.1751	.1606	.0163	-.0870	.1033	.0981
14.4	.1007	.2340	-.1337	*	.1432	.2003	-.0571	*
21.4	.0117	-.2637	.2754	.2407	.1339	-.1675	.3014	.2602
28.4	.0520	.4204	-.3684	*	.1264	.3256	-.1992	*
5.5	.0233	.1220	-.0987	*	.0653	.1959	-.1306	*
12.5	.0432	-.0271	.0703	.0679	.0143	-.0264	.0407	.0399
19.5	.0027	.0872	-.0845	*	.0045	-.0021	.0066	.0066
27.5	.0119	-.0852	.0971	.0925	.0159	-.0548	.0707	.0683
2.6	.0050	-.1133	.1183	.1116	.0069	-.1018	.1087	.1030
9.6	.0018	-.2012	.2030	.1837	.0038	-.0779	.0817	.0785

NOTE: - no sample

* death rate (D) negative which indicates either recruitment from ephippial hatching or river import or poor sampling.

APPENDIX 5.1.4.

PRODUCTION FIGURES CALCULATED FROM g.B. and P/B RATIOS FROM WINBERG'S METHOD

Date	P.mg.m^{-2}.day^{-1}	P/B	Date	P.mg.m^{-2}.day^{-1}	P/B
30.10.67		.090	7.10	138.37	.138
13.11		.059	14.10	94.67	.111
27.11		.052	21.10	14.38	.103
18.12		.039	28.10	46.14	.095
1.1.68	7.23	.033	4.11	46.89	.072
8.1	13.41	.031	11.11	-	.059
22.1	38.60	.033	18.11	35.85	.063
29.1	15.45	.038	25.11	12.96	.046
12.2	33.64	.031	2.12	28.67	.044
19.2	15.50	.030	9.12	5.00	.046
26.2	20.32	.025	16.12	13.96	.035
4.3	20.84	.024	23.12	-	.037
11.3	23.68	.024	30.12	6.64	.032
18.3	13.88	.036	6.1.69	14.94	.029
25.3	19.38	.048	13.1	19.06	.030
1.4	9.41	.045	20.1	28.04	.030
8.4	111.60	-	27.1	29.92	.035
18.4	16.96	-	3.2	52.18	.038
22.4	55.43	-	10.2	13.76	.031
29.4	401.57	.099	17.2	7.72	.027
6.5	172.48	.093	24.2	26.90	.027
13.5	200.55	.092	3.3	18.94	.026
20.5	131.17	.103	10.3	22.81	.030
27.5	84.89	.116	17.3	36.19	.029
5.6	75.53	.161	24.3	28.32	.038
10.6	29.10	.112	31.3	20.72	.041
17.6	101.10	.161	8.4	21.30	.043
24.6	138.19	-	14.4	59.58	.050
1.7	24.34	.166	21.4	22.23	.062
8.7	91.97	.204	28.4	282.40	.100
22.7	257.53	.224	5.5	638.96	.102
29.7	18.43	-	12.5	337.14	.115
5.8	6.48	.174	19.5	630.89	.109

APPENDIX 5.1.4 (contd.)

Date	P.mg.m^{-2}.day^{-1}	P/B	Date	P.mg.m^{-2}.day^{-1}	P/B
12.8.68	52.44	.186	27.5.69	361.50	.100
19.8	137.27	.134	2.6	208.51	.122
26.8	144.72	.141	9.6	16.22	.110
3.9	422.00	.164			
9.9	195.77	.161			
23.9	40.72	.060			
30.9	139.02	.127			

APPENDIX 5.1.7

Numbers of D.hyalina and classes per 25L from Patalas samples. for Q.M.

Date	Total	Eggs	<1.0mm	1.0-1.39mm	1.40-2.0mm	>2.0mm
26. 2.68	113	27	95	5	11	2
3. 3.	170	18	139	12	18	1
25. 3.	50	0	31	10	9	0
1. 4.	244	128	188	35	9	12
8. 4.	112	623	22	7	82	1
18. 4.	66	19	29	1	20	16
29. 4.	911	47	832	73	6	0
30. 4.	1803	101	1627	145	25	6
4. 5.	856	2	820	23	12	1
6. 5.	752	29	500	200	551	1
9. 5.	540	15	859	59	17	5
10. 5.	1187	43	865	200	112	10
12. 5.	1296	18	1149	89	43	15
13. 5.	851	8	605	108	136	2
14. 5.	348	4	309	17	17	5
20. 5.	1201	18	817	220	153	11
21. 5.	1064	12	671	164	217	12
27. 5.	343	12	227	42	74	0
5. 6.	74	0	73	1	0	0
10. 6.	40	9	19	2	11	8
17. 6.	321	4	288	17	16	0
24. 6.	335	7	284	33	13	5
1. 7.	145	2	123	14	8	0
8. 7.	611	4	583	23	4	1
15. 7.	1140	20	1045	72	21	2
22. 7.	968	6	921	23	24	0
29. 7.	32	3	29	1	2	0
5. 8.	33	7	26	0	6	1
12. 8.	20	0	18	0	2	0
19. 8.	295	304	126	54	93	22
20. 8.	805	165	571	125	101	8
26. 8.	108	56	93	4	11	0
3. 9.	564	20	517	32	15	0
23. 9.	134	4	89	26	18	1
30. 9.	256	21	167	48	37	4
7.10.	144	5	108	28	8	0
14.10.	251	30	179	22	42	8
21.10.	17	0	7	0	10	0
18.11.	194	17	98	21	73	2
25.11.	118	16	40	31	35	8
2.12.68	247	57	88	6	146	7
9.12.	73	32	35	2	36	0
16.12.	70	28	41	4	22	3
30.12.	116	71	44	15	51	6
6. 1.69.	49	26	30	4	13	2
13. 1.	79	40	47	15	15	2
20. 1.	71	18	49	7	14	1
27. 1.	223	144	152	18	51	2
3. 2.	219	132	142	12	52	7
10. 2.	96	56	71	6	18	1
17. 2.	43	12	30	5	6	2
24. 2.	62	32	46	6	10	0
3. 3.	93	38	62	10	18	3
10. 3.	102	38	66	14	17	5
17. 3.	82	41	56	6	19	1
24. 3.	88	73	44	8	34	2

APPENDIX 5.1.7 (contd.)

Date	Total	Eggs	1.0mm	1.0-1.39mm	1.40-2.0mm	2.0mm
31.3	57	16	36	8	10	3
8.4	31	6	20	2	9	0
14.4	126	137	31	21	74	0
21.4	39	44	27	3	9	0
28.4	331	364	335	13	28	5
5.5	1501	525	1104	206	167	24
12.5	1248	82	1139	56	53	0
19.5	1227	25	1006	89	128	4
27.5	883	62	626	91	156	10
2.6	433	11	331	32	68	2
9.6	251	4	192	27	30	2

APPENDIX 5.1.7

Numbers of Bosmina sp., Cyclops sp., Diaptomus sp., and Asplanchna sp. per 25 L from Patalas samples for O.M.

Date	Bosmina	Cyclops	Diaptomus	Asplanchna
26.2.68	0	28	14	0
3.3	1	31	6	0
25.3	2	15	9	0
1.4	11	135	13	0
8.4	0	25	20	0
18.4	2	76	14	0
29.4	5	130	10	0
30.4	15	414	19	0
4.5	0	190	35	0
6.5	0	48	48	0
9.5	2	210	88	0
10.5	12	27	95	0
12.5	10	146	51	0
13.5	7	56	24	0
14.5	0	32	15	0
20.5	9	64	21	0
21.5	12	84	31	0
27.5	19	34	10	0
5.6	0	22	50	0
10.6	6	28	152	0
17.6	31	10	254	0
24.6	102	40	269	0
1.7	185	17	317	0
8.7	94	40	192	0
15.7	518	26	147	0
22.7	39	55	144	0
29.7	49	11	16	0
5.8	117	7	12	0
12.8	16	11	17	0
19.8	6	17	76	0
20.8	3	135	245	0
26.8	1	39	227	0
3.9	1	27	34	0
23.9	1	14	18	0
30.9	0	3	6	0
7.10	1	5	52	0
14.10	0	9	52	0
21.10	0	14	23	0
18.11	0	10	24	0
25.11	1	7	17	0
2.12	1	10	49	0
9.12	0	4	30	0
16.12	1	4	25	0
30.12	5	6	31	0
6.1.69	1	7	13	0
13.1	5	4	18	0
20.1	0	5	19	0
27.1	1	12	18	0
3.2	5	18	11	0
10.2	0	20	9	0
17.2	0	12	8	0
24.2	4	29	7	0
3.3	1	37	8	0
10.3	1	32	5	0
17.3	3	22	10	0
24.3	2	22	2	0

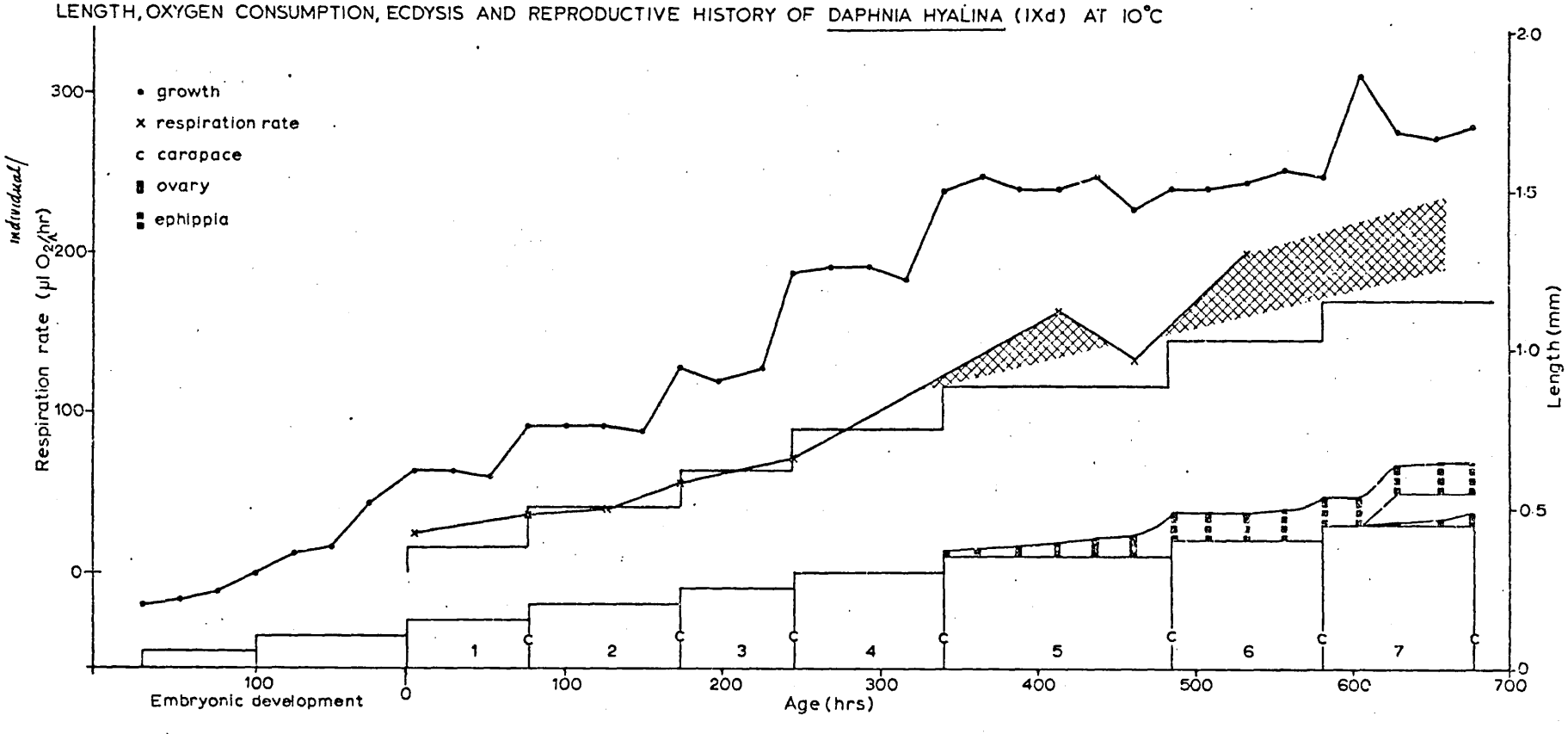
APPENDIX 5.1.7 (contd.)

Date	Bosmina	Cyclops	Diaptomus	Asplanchna
31.3	1	25	2	3
8.4	0	20	3	0
14.4	9	36	6	2
21.4	6	34	3	6
28.4	3	169	7	51
5.5	41	386	16	306
12.5	66	321	22	294
19.5	51	40	17	93
27.5	33	43	51	34
2.6	45	17	18	7
9.6	17	4	89	4

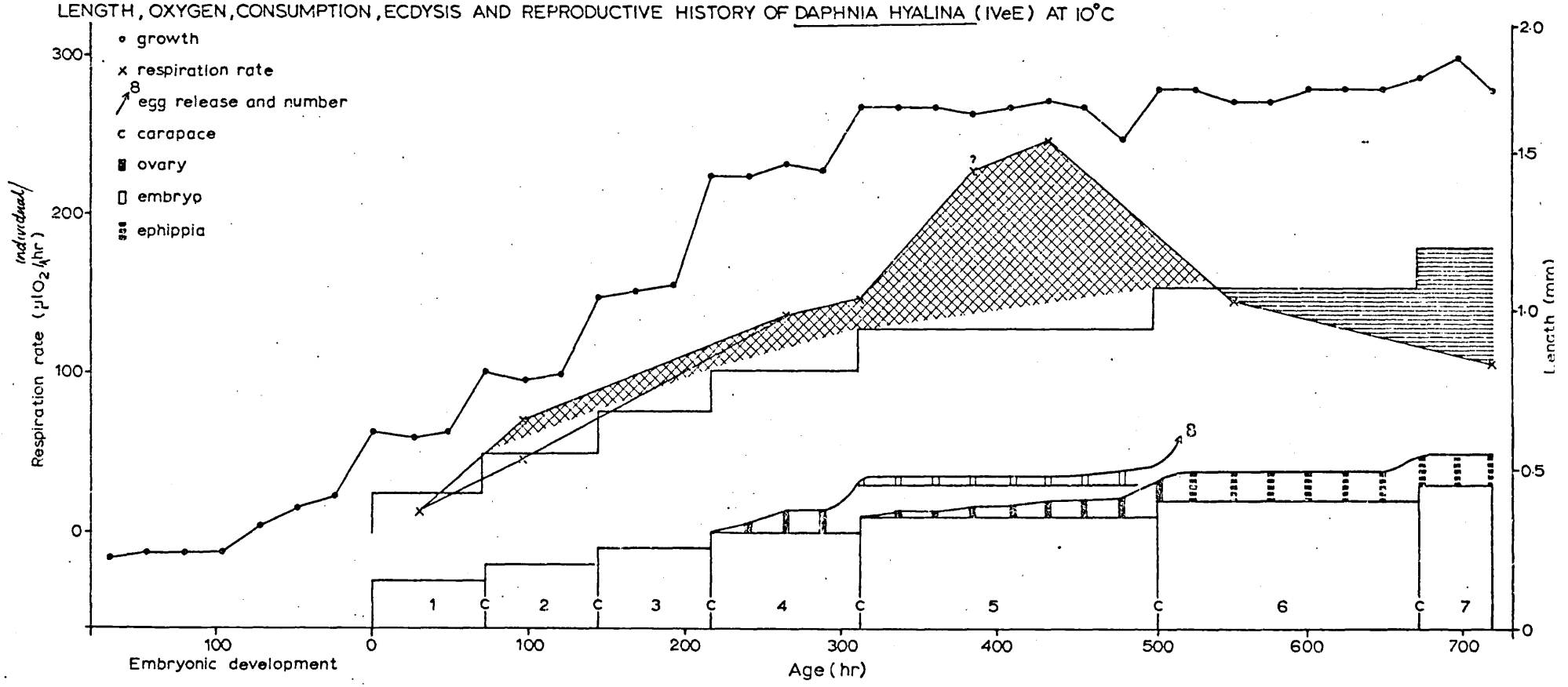
APPENDIX 5.1.8

Dry weight of daphnids and copepods. mg per V.N.H. Q.E.II

Date	Daphnids	Copepods	Date	Daphnids	Copepods
18.10.67	104.33	19.22	29.5	69.14	7.89
25.10	39.20	5.32	12.6	119.17	16.35
1.11	49.39	6.07	26.6	62.86	8.85
8.11	3.56	.30	10.7	33.54	8.36
15.11	21.14	5.21	24.7	15.13	4.15
22.11	14.52	.75	5.8	95.99	12.60
29.11	17.78	2.58	21.8	16.53	3.54
6.12	58.80	.42	25.9	54.93	4.67
13.12	7.71	.68	2.10	36.86	4.79
20.12	28.78	8.00	16.10	64.21	5.78
27.12	71.55	9.30	27.11	58.68	3.25
3.1.68	22.41	2.61	12.12	13.43	1.11
10.1	19.38	.50	1.1.69	12.22	1.74
17.1	39.80	3.58	8.1	21.03	1.87
24.1	32.81	1.36	5.2	2.83	.69
7.2	28.26	3.68	19.2	5.96	2.07
14.2	14.26	7.32	5.3	1.65	.93
21.2	38.41	4.15	19.3	2.13	2.31
28.2	48.35	1.79	2.4	3.35	1.92
6.3	23.55	.59	16.4	6.47	-
13.3	16.13	6.01	30.4	15.75	23.04
20.3	22.55	2.08	14.5	47.65	86.21
27.3	117.62	5.50	28.5	137.53	31.92
3.4	131.50	8.34	11.6	171.43	16.83
24.4.68	171.55	36.63	25.6	117.11	12.61
15.5	222.92	29.81			
22.5	65.10	11.42			



Appendix fig. 5.2.4(a).



Appendix fig. 5.2.4(b).

APPENDIX 5.3.

A. DUNCAN, G. A. CREMER and T. ANDREW

THE MEASUREMENT OF RESPIRATORY RATES UNDER FIELD AND LABORATORY CONDITIONS DURING AN ECOLOGICAL STUDY ON ZOOPLANKTON

Department of Zoology, Royal Holloway College, University of London, Englefield Green, Surrey, England

ABSTRACT

Two procedures adopted in an attempt to measure the respiratory rates throughout the year of the naturally composed macro-zooplankton in near-field conditions are described critically and in detail. Some results are presented showing the changes in the oxygen consumption per mg dry weight of the larger zooplankton from two reservoirs in the lower Thames Valley (England). An attempt is made to compare the levels of "field" respiratory rates per 5 l of the zooplankton during a period when *Daphnia hyalina* predominated with the levels obtained when laboratory respiratory rates of this species were applied to its field population numbers obtained during the same period.

INTRODUCTION

In ecological studies, the measurement of respiratory rates can provide us with information difficult to obtain in other ways, namely, how much energy is required for maintaining normal activities in a particular species and, together with measurement of growth rates, gives us another estimate of the demands this species-population makes upon its food supply, in addition to a direct one. The respiratory rate is also an extremely sensitive measure of the physiological state of an animal and its measurement helps us to distinguish the different states of metabolism exhibited by animals throughout their life cycle in response to various environmental conditions. Some ecologists have suggested that it is not necessary to measure respiratory rate to the degree of sensitivity possible because the range of metabolic levels in any species is too small for the type of productive studies with which most International Biological Programme investigations are concerned. However, if our aim is not only to produce some value or other representing the secondary biological production in terms of cal/m^2 year but also to understand why this particular value was obtained and therefore to be able to predict future values, more needs to be known about the patterns of both metabolic and growth responses of different species to their environment.

It is well known that the metabolism of animals is affected by various environmental conditions such as temperature, food concentration and qua-

lity as well as the state of development and body size of the species itself. It may also be that an animal's previous history affects its respiratory responses to its present environmental conditions. In 1966, BLAŻKA gave a very interesting paper in which he suggested that the relationship between the rate of oxygen consumption and temperature was not a simple one of temperature acclimatization. He postulated three types of metabolic regulations related in some way to food conditions which occurred in some species of the cladoceran genus Daphnia and perhaps in other crustacea; in two of these, the level of metabolism did not alter under the influence of immediate environmental change but required some time. The first of these metabolic regulatory mechanisms was revealed during a period of low winter metabolism in *Daphnia hyalina* coinciding with low concentrations of seston (less than 3 cal/l); the respiratory rate decreased proportionately to the seston concentration so that the energy reserves of these winter daphnids could last for 6–7 weeks longer. The resumption of the spring-summer levels of metabolism did not take place immediately but only after about 6–8 weeks or two or three generations. The second type of metabolic regulation is concerned with the variability of the relationship between oxygen consumption and temperature; this was detected in several daphnid species, all with similar responses. Measurement of the metabolic rate per mg body N at several temperatures from 5°–30°C at different seasons of the year in field animals as well as in well-fed laboratory cultures kept at 20°C showed that the pattern of metabolic response was different in field animals at different seasons and was different in the laboratory and field animals. BLAŻKA suggests that the field animals were exhibiting a more developed temperature acclimatization. The third type of metabolic regulation postulated concerns the varied percentage utilization of protein as a respiratory fuel under different levels of diet. Information about this was obtained by measuring the quantity of ammonia excreted as well as oxygen consumed and by assuming that all the ammonia excreted came from catabolized protein. In laboratory cultures of *D. hyalina* with a surplus of food, proteins were not used as a source of energy whereas in the field, between 12–80% of the liberated energy came from protein metabolism. The percentage of protein metabolized in this way was affected by environmental factors, being increased with increase in temperature and decreased by an increase in the level of food.

If BLAŻKA's ideas are correct and the previous nutritional history of an animal can affect its present responses to its environmental conditions, direct measurements of metabolic rates of field animals under field or simulated field conditions may enable us to detect this situation, to interpret the pattern of metabolic response to seasonal and other changes in its normal environment as well as to gain some idea of the degree of metabolic variation to be expected. During the last three years, an attempt has been made to measure the oxygen consumption of the naturally composed macro-zooplankton (retained on a 0.3 mm mesh) in as near to field conditions as possible in order to determine whether any pattern of variation in metabolism was detectable. This work was part of a study on the metabolism and secondary production of the zooplankton in three reservoirs of the lower Thames Valley whose phytoplankton was being investigated simultaneously (STEEL et al., in preparation).

METHODS

For field measurements of respiration at all seasons of the year, only the simplest, weather-proof apparatus can be employed. Simple glass stoppered flasks of 300 ml capacity protected in nalgene tubes were used, flushed and filled with reservoir water, to which were added concentrated suspensions of zooplankton filtered off through a 0.3 mm mesh from a quantitative sample. After fixation with an azide modified alkali-iodide solution, the level of dissolved oxygen was determined by the standard Winkler titration, using 50 or 100 ml sub-samples and an 0.0125 N sodium thiosulphate solution. The level of dissolved oxygen in the animal flask was compared with that of two control flasks without animals, one of which, the initial control, was fixed immediately after filling and the other, the final control, at the same time and having received the same treatment as the animal flask; the difference between the animal and final control flasks was used to calculate oxygen consumption by the zooplankton concentrate. These two controls were important in that they provided a check on the oxygen changes occurring associated with the water medium itself. The flasks were suspended in the water body itself, which thus acted as a natural water bath, usually from a buoy or raft whose wind-induced movements provided some shaking. The term, "in as near to field conditions as possible" refers mainly to temperature, the water medium used and to the period of time between the collection of animals and their re-suspension inside bottles.

Two procedures were developed during the course of the study differing in the methods employed to collect the animals (nets hauled vertically from above the bottom to the surface or volume samples taken from various depths) and in the length of exposure period (24 or 4hr); the consequences of these technical differences are described below.

The earlier procedure was developed in 1966—1967 by CREMER, whose aim was to study comparatively the seasonal changes in numbers, biomass and metabolism of the zooplankton of three reservoirs. The sampling and subsequent treatment of samples is described in more detail in CREMER and DUNCAN (1969) and was designed to provide composite collections consisting of a known number of vertical net hauls from several stations. These composite samples were considered to be representative of the water body as a whole, leaving in abeyance for the moment the question of how selectively nets sample a column of water. The net samples were convenient in that they provided an integrated sample of what was present throughout the depths. In the laboratory, the composite samples were split into equal sub-samples, using a plankton splitter designed by MOTODA (1959) and these were used for either counts and species analysis, dry weights of various components or respiratory measurements. The respiratory sub-sample was treated carefully and immediately; it was further sub-divided to provide suitable concentrations of animals whose oxygen consumption was not more than 20% of the initial oxygen concentration. It was a matter of experience to judge this, especially as the degree of sub-sampling necessary varies seasonally. Thus in May, during the peak daphnid numbers, too large a sub-sample was used resulting in a greater than 20% decrease in oxygen concentration in the animal flask so that these results had to be rejected. As the exposure period was 24 hours in order to encompass any diurnal variation, it was necessary

to use reservoir water filtered through a glass fibre pad (*GF/C*) to remove the algae and bacteria; the use of filtered water meant that the animals had no food available while in the flasks. The two control flasks were also filled with filtered water and the differences in oxygen concentration was usually less than 30% of the animal oxygen consumption. The animal and final control flasks were suspended, undarkened, from a buoy in a windy part of the reservoir near the laboratory for 24 hours. As the oxygen consumption of the macro-zooplankton was obtained by subtracting the oxygen content of the final control from that of the animal flask, any heightened initial respiration due to the disturbance of the animals by handling will be incorporated in the results, although this error is somewhat reduced because of the long exposure period; KAMLER (1969) has recently drawn attention to this error associated with closed-bottle-Winkler respirometers. To what extent lack of food for 24 hours affects the oxygen consumption of these animals is not known.

During this work, an attempt was made to estimate the oxygen consumption of not only the naturally composed zooplankton but also of its component fractions, namely the copepods, consisting of the larger copepodites and adult of *Diaptomus gracilis* and *Cyclops* spp., and the cladocerans, consisting of *Daphnia hyalina,* other species of Daphnia and the larger stages of *Bosmina longirostris.* It is possible to separate the copepods from the rest of the zooplankton by STRAŠKRABA's narcotic technique (STRAŠKRABA 1967) and to measure their oxygen consumption in a separate flask and to calculate the respiration of the cladocerans by subtraction. The effect of the mild narcotization on the respiratory rate of the copepods has not yet been tested but the animals recover very rapidly their normal swimming movements. However, the subsequent shaking to separate off the cladocerans is likely to produce a period of initial "disturbed" respiration as mentioned above.

The second procedure was developed during 1967 and 1968 by DUNCAN on one of the three reservoirs and on another during 1968 and 1969 by ANDREW. In contrast to the procedure described above, the concentration of animals suspended in the flasks was determined by the number of animals collected by the five litre PATALAS volume sampler (PATALAS 1954) and retained on a 0.3 mm mesh net disc. Moreover, all the handling of animals, from their collection to their re-suspension inside the flasks, was carried out under field conditions, as shown in Fig. 1. The period of exposure was only four hours. Animals from a known depth were washed into a flask which was then flushed out with three times its own volume of coarse filtered reservoir water from the same depth. This coarse filtered water contained all the particles or organisms which passed through the 0.3 mm mesh net disc, so that some food was available for the herbivorous species. However, due to the presence of algae, detrital particles and smaller zooplanktonic organisms, it was necessary to darken the flasks to prevent photosynthetic production of oxygen and to expose the flask for a period too short for bacterial respiration to reach a measurable level. The difference in the oxygen concentration of the initial and final controls was greater than in the first procedure when glass fibre filtered water was used, and was between 50–100% of the animal oxygen consumption for most of the year but dropped to 25% with a mean value of about 10% during peak daphnid periods. Rather than acting as a control on the changes occurring in the water medium, these differen-

ces provided an estimate of the oxygen consumption of the various organisms present, which passed through the 0.3 mm mesh. The oxygen consumption of the macro-zooplankton was calculated from the difference in oxygen content of the final control and the animal flask and will include both the initial period of heightened respiration due to disturbance and possibly darkness as well as any possible effect which the presence of animal excretory products may have on algal or bacterial respiration. The former error will be more serious than in the first procedure since it will form a greater proportion of a four hour consumption. It may be possible to eliminate by fixing an additional animal bottle after the period of disturbance, previously determined. Duplicate samples were taken at 2 m intervals down to 9 m depth or to the thermocline at weekly or fortnightly intervals.

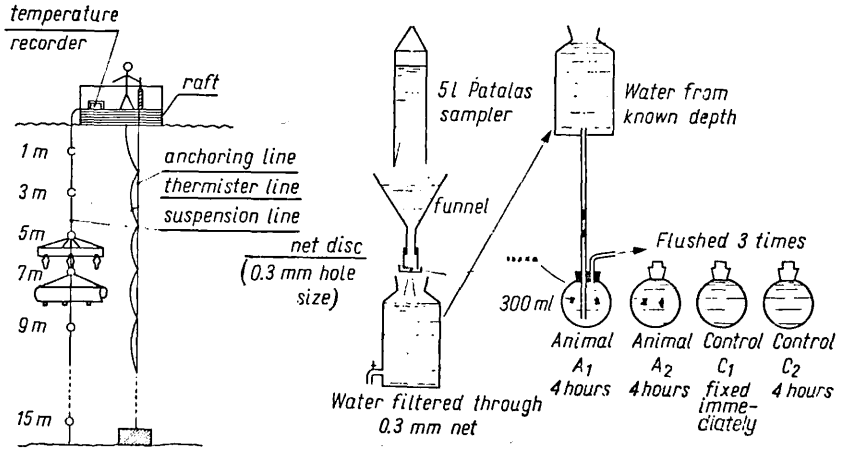


Fig. 1. Diagram showing the collection, handling and suspension of samples for "field" respirations

The time taken between the removal of animals from the reservoir to their re-suspension inside the flasks was much shorter in the second procedure. Usually all the titrations were completed on the same day and the animals filtered off to determine their dry weights. Thus it was possible to obtain quite quickly an estimate both of the standing crop and the metabolic intensity of the macrozooplankton, which is useful during periods of rapid change. Parallel samples were also taken for counts and species analysis.

One of the problems not yet solved satisfactorily is how to fix the oxygen in the animal flask. Direct fixation in the presence of the animals is the simplest technique which can be easily carried out at the edge of the reservoir; this does not seem to affect the precision of the titration carried out within an hour, ± 0.026 ml thiosulphate for a 50 ml sample, but does alter its accuracy (ANDREW, personal communication). The error which is 0.013/1 ml thiosulphate/mg dry wt. animal is the result of loss of iodine either because the manganic hydroxide which is trapped in or on the carapaces is not all dissolved on acidification or because it colours the animals' bodies and is isolated from the titration. An alternative method attempted during this work was to siphon off a sub-sample into a smaller bottle, filtered through

a coarse mesh disc to remove the animals. This produced rather variable results when performed at the edge of the reservoir because of the problems of preventing contact with air, of flushing the receiver bottle adequately to remove the film of air on its surfaces and of clogging of the netting by animals forced against it by water flow. It may be possible to use a syringe to withdraw a good sub-sample, especially if it is simultaneously fixed as in the Fox and Wingfield technique, although this method precludes any previous flushing of the syringe walls. The addition of liquid paraffin does not ensure isolation from atmospheric air and contaminates the bodies of the animals whose dry weights are desired. Transporting the flasks for fixation under laboratory conditions involves submerging them in water containers to prevent air diffusion through the ground glass joint, demands more labour, lengthens the exposure period and risks changes in temperature.

RESULTS

Figure 2 illustrates the seasonal changes in the oxygen consumption per mg dry weight of the larger zooplanktonic animals from two of the reservoirs during 1966, 1967, 1968 and 1969, measured by means of closed bottle respirometers, suspended in the reservoir for 24 or 4 hours; these measurements were performed by three different workers for various periods of time

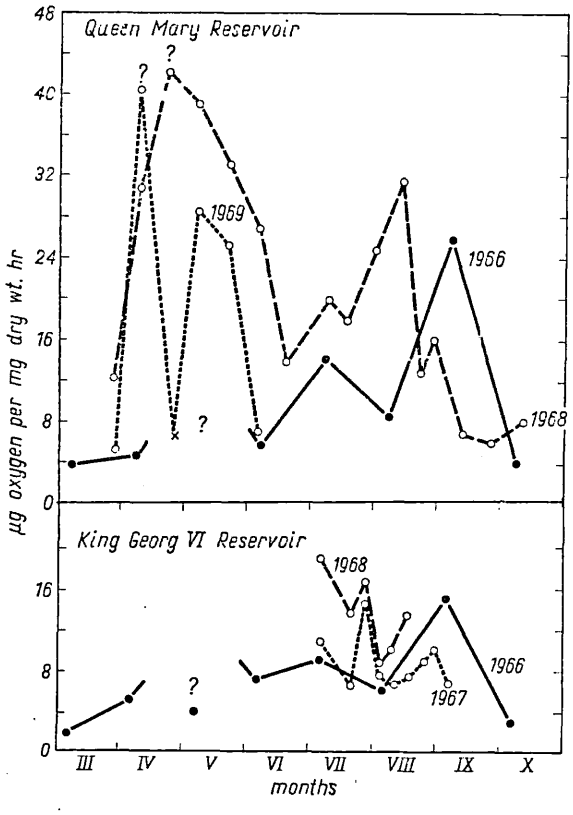


Fig. 2. Seasonal changes in the oxygen consumption per mg dry weight of macro-zooplankton from two reservoirs in 1966–1969

at monthly, fortnightly or weekly intervals. Although there is considerable variation in the maximal absolute values of metabolic rate in different years for the same reservoir, these are probably not real but reflect procedural and calculation differences associated with different exposure times, errors due to disturbance from handling, darkness, absence of food. What is striking is the similar seasonal pattern of variation in metabolic intensity revealed in consecutive years with the periods of more intense metabolism occurring during the spring, in the summer and again during the autumn. The causes of some of these periods of more intense metabolism are not yet known, although in Queen Mary Reservoir, the spring period coincides with a period of intense parthenogenetic reproduction by *Daphnia hyalina* resulting in very large standing crops of very young, small animals with a high level of weight specific respiratory rate. However, this is not the cause of the periods of more intense metabolism later in the year. Nor are these caused by the higher water temperatures prevailing at this time but rather they seem to be associated with changes in the specific composition of the zooplankton (with relatively few *Daphnia hyalina*, relatively more *Bosmina longirostris* and the appearance of considerable numbers of adult cyclopoids) and in their breeding conditions (a greater proportion of female *Diaptomus gracilis* bearing egg sacs). This is discussed in more detail in CREMER and DUNCAN (1969) but clearly more information is required about the respiratory rates of different developmental stages of these species in order to interpret the complex changes occurring in the summer and autumn.

The level and quality of food available is also likely to affect the metabolism of zooplanktonic animals. This would be best demonstrated by the direct measurement of ingestion and assimilation rates together with respiratory rates and some information on the percentage utilization of protein as a respiratory fuel, as suggested by BLAŻKA (1966); the simultaneous and frequent measurement of these would be most indicative of the food situation but difficult to achieve. However, the juxtaposition in Fig. 3 of the seston concentration, level of zooplankton biomass (predominantly cladoceran) and its weight specific respiratory rate during the summer of 1968 in the top 5 m of King George VI reservoir suggests that the overall decline in metabolic intensity of the zooplanktonic biomass may be a reflection of the dramatic decline in seston level. The alternation at almost weekly intervals of periods of high biomass levels and lower metabolism (19.VII, 1.VIII) with lower biomass levels and more intense metabolism (4.VII, 26.VII and 8–15.VIII) coincides with the occurrence in the zooplankton of either predominantly large or predominantly small daphnids.

During the spring 1968, an attempt was made to compare the respiratory rates of the zooplankton in Queen Mary reservoir obtained in two ways. The spring period was chosen because at this time the zooplankton consists mostly of *Daphnia hyalina* reproducing most intensely and resulting in its highest levels of standing crop biomass and numbers. What was compared was the mean respiratory rate of zooplankton from 5 l samples from different depths as measured in closed bottle respirometers suspended in the reservoir with rates calculated from respiratory rates of different sizes measured in the laboratory applied to the same field populations.

In the laboratory, the progeny from several large, old females containing twenty or more parthenogenetic eggs were kept separate at 20°C in condi-

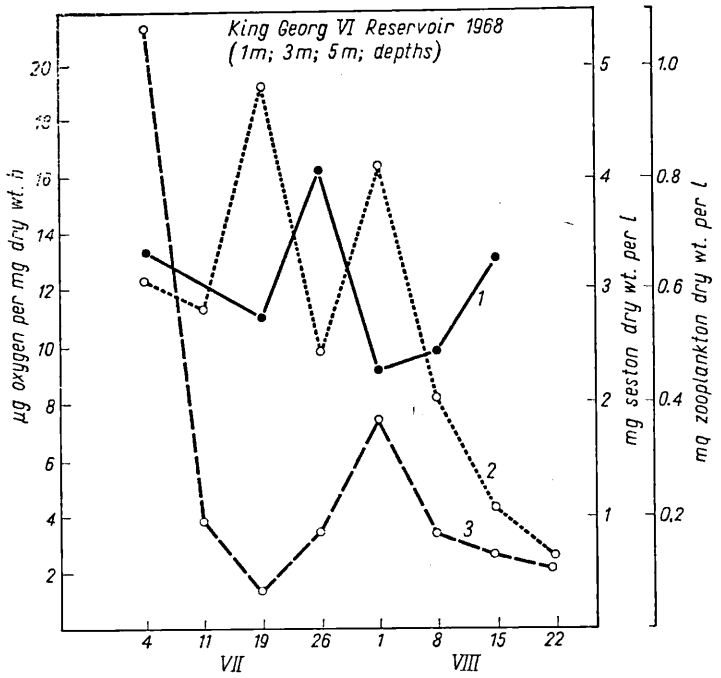


Fig. 3. Changes in the concentration of seston biomass and the oxygen consumption per mg dry weight and biomass of macro-zooplankton in one reservoir during the summer 1968. 1 — zooplankton metabolic rate, 2 — zooplankton biomass, 3 — seston biomass

tions of surplus food which was *Oocystis* spp. cultured from the reservoir populations. These old females were the precursors of the subsequent spring daphnid "bloom". The temperature was 20°C because it was the first temperature investigation to be completed in a programme studying the influence of temperature on the respiration and development of *D. hyalina*. The young released from these older females were individually named and their development followed in individual cultures until they died. Fourteen such individuals were successfully reared in dishes whose 30 ml filtered reservoir water was changed daily and replenished with surplus food. The following daily observation was made on each individual: growth as length in mm from the top of the helmet to the inflexion at the base of the spine; respiratory rate in the modified cartesian diver (Zeuthen 1950, Klekowski 1968); the occurrence of ecdysis; the reproductive state, involving the condition and size of ovary, the number of eggs and developmental state of the embryos. Figure 4 illustrates the developmental cycle of animal 11c which lived for 600 hr at 20°C up to its 10th instar when it had produced 6 broods of eggs. Such a method of investigation pioneered by Dr. R. Z. Klekowski in the study on *Macrocyclops albidus* (Jur.) (Klekowski and Shushkina 1966) provides a pattern of both the individual's and the species' life history. Thus 11c missed producing a brood of eggs during its 7th instar, for some reason, and this coincided with both a period of respiration lower than expected (horizontal hatching) and a cessation of growth in length; the stippled areas re-

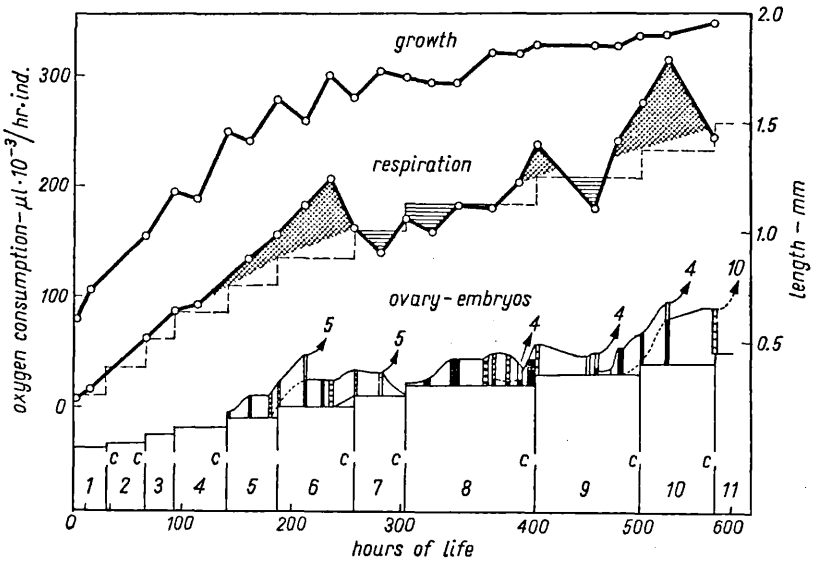


Fig. 4. The length, oxygen consumption, ecdysis and reproductive state of an individual *Daphnia hyalina* (number 11c), cultured at 20°C, fed on *Oocystis solitaria* and observed at daily intervals throughout its life span of 600hr. C — carapace instars

present the increased respiration associated with the development of an ovary and its released eggs and embryos.

For the purpose of the present comparison of metabolic rates, these fourteen life histories were employed to obtain average individual respiratory rates at 20°C for different length classes. Figure 5a illustrates the relationship between the mean oxygen consumption per hour of an individual and body length and Fig. 5b presents the numbers of different length classes of *D. hyalina* present in Queen Mary reservoir during April, May and June 1968. From these two sets of data was calculated the total oxygen consumption of the *D. hyalina* present in five litres, both at 20°C and at field temperature (whose values are given on the lower axis); the measurements at 20°C were converted to field temperatures by means of the tables based on Krogh's normal curve as published in WINBERG (1956). The two population respirations, derived from laboratory measurements applied to field numbers, are illustrated in Fig. 6 along with the field respirations per 5 l measured by means of closed-bottles suspended in the reservoir; this latter curve gives also the range of the 95% confidence limits.

Figure 6 shows that the field respirations during this period of the daphnid spring peak were considerably higher than the population respirations derived from laboratory measurements but the similar shape of the two sets of curves suggests that the same events are being described. The reasons for this difference is not known at present. It is unlikely to be due to the respiration of the other species present in the field bottles since these were not numerically abundant during this time; the mean numbers per 5 l of larger zooplanktonic species between 25.III.68 and 17.VI.68 was 131 for *D. hyalina*, 18 for *Cyclops* sp., 10 for *Diaptomus* sp. and 1 for *Bosmina* sp. As mentioned

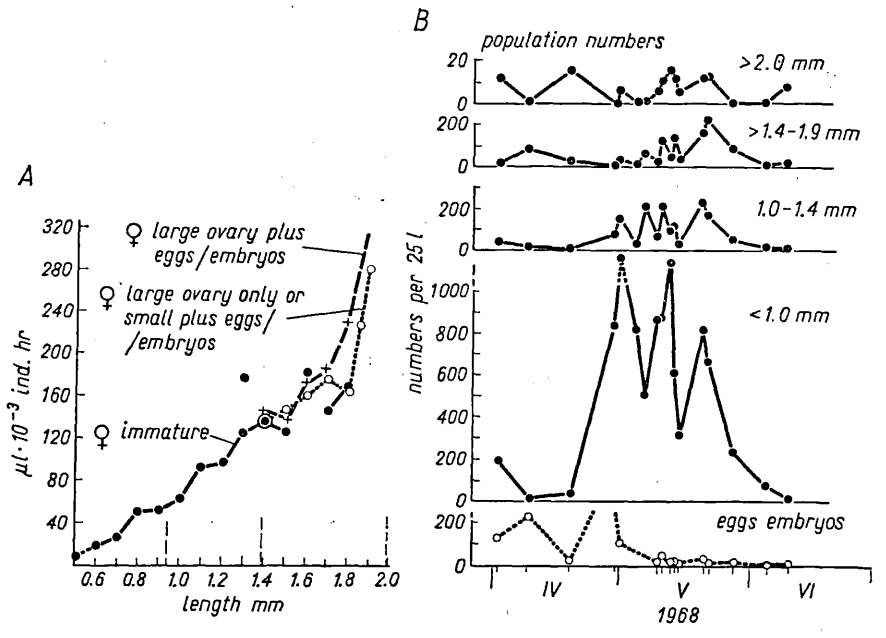


Fig. 5. A — the mean oxygen consumption of 14 *Daphnia hyalina* cultured at 20°C, the relationship between oxygen consumption and body length. B — the numbers per 25 l of *Daphnia hyalina* of different sizes in one reservoir during the spring 1968

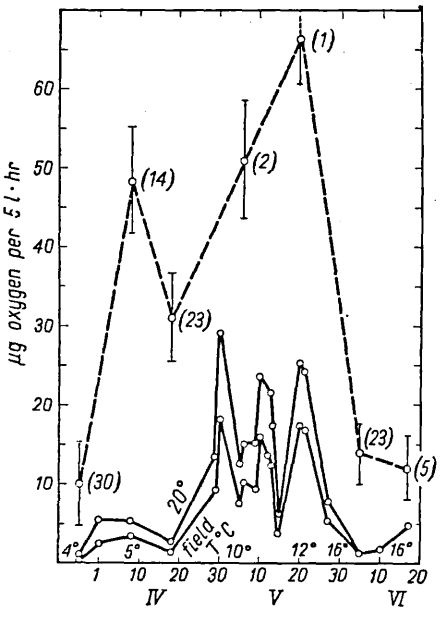


Fig. 6. A comparison of the "field" and laboratory respiration of zooplankton from Queen Mary reservoir, 1968, during a period when *Daphnia hyalina* was predominant. The methods compared were the closed-bottle-Winkler respirometer and cartesian diver respirometers. - - - field respiration at field temperature of zooplankton — mostly *D. hyalina* (± standard deviation. Numbers in brackets — ml space per daphnid); ——— laboratory respiration of *D. hyalina* applied to field populations of *D. hyalina*

earlier, any initial heightened respiration due to disturbance from handling is incorporated in the field respirations but has been excluded from the diver results which were applied to population numbers; this is a possible cause of the difference not yet measured. Another possible cause is the effect of crowding; ZEISS (1963) records that adult *Daphnia magna* confined to a space of 0.24 or 0.12 ml/individual consumed 2 to 2.5 times more oxygen at 19–21°C than those with 12 ml available per individual and, on this basis, criticises the use of microrespirometers for the measurement of daphnid respiration. The space available per daphnid is given in ml/individual in Fig. 6 (the numbers in brackets) and varied throughout the spring period. It is clear that it was minimal (between 1 and 2 ml/individual) during the greatest respiration, however, the space available for single daphnids of various ages in the cartesian divers used was between 0.01 and 0.02 ml and the respiratory rates when applied to population numbers revealed lower levels of respiration per 5 l rather than higher. An important difference between the two respirometers was the possibility for active movement; all sizes of animals in the bottles but only the smaller daphnids in the divers could swim actively during the respirometric measurements. Moreover, in both respirometers, the period of measurement lasted about 4 to 5 hours which may be a long time for a daphnid to be without food, as was the situation in the divers, whereas normal food in reduced concentration was present in the field bottles. Clearly, further investigation needs to be undertaken in order to determine the causes of the difference in level revealed in Fig. 6.

SUMMARY

1. Two procedures adopted in an attempt to measure the respiratory rates throughout the year of the naturally composed macro-zooplankton in near-field conditions are described critically and in detail. Both procedures involved the use of concentrates of zooplankton and closed-bottle-Winkler respirometers but differed in the presence or absence of food and in the duration of exposure (4 or 24 hr).

2. Some results are presented showing the changes in the oxygen consumption per mg dry weight of the larger zooplankton from two reservoirs in the lower Thames Valley (England) at different seasons of the year and during a period of rapid decline in the summer seston concentration. The possible causes of the changes revealed are discussed.

3. An attempt is made to compare the levels of "field" respiratory rates per µl of the zooplankton during a period when *Daphnia hyalina* predominated with the levels obtained when laboratory respiratory rates of this species were applied to its field population numbers obtained during the same period. The laboratory measurements were obtained from daily measurements throughout the life cycle of fourteen *D. hyalina*, cultured at 20°C and fed on *Oocystis solitaria* by means of Zeuthen's stoppered cartesian diver, an approach pioneered by KLEKOWSKI in *Macrocyclops albidus* Jur. (KLEKOWSKI and SHUSHKINA 1966). The pattern of changes in the population respiratory rate throughout this period of spring peak abundance given by the two methods was very similar but the levels differed. Possible causes of this difference are discussed.

Acknowledgements

The authors wish to acknowledge their indebtedness both to WINDLE TAYLOR, C. B. E., Direct of Water Examination of the Metropolitan Water Board, for his permission to work on the reservoirs of the lower Thames Valley and to Doc. Dr.

R. Z. Klekowski for so generously passing on his experience both in the techniques of the Zeuthen stoppered cartesian diver and in its application to ecological problems.

REFERENCES

Błażka, P. 1966. Metabolism of natural and cultured populations of Dapnia related to secondary production. *Verh. int. Ver. Limnol.*, 16, 380–385.

Cremer, G. A., Duncan, A. 1969. A seasonal study of zooplanktonic respiration under field conditions. *Verh. int. Ver. Limnol.*, 17, 181–190.

Kamler, E. 1969. A comparison of the closed-bottle and flowing-water methods for measurements of respiration in aquatic invertebrates. *Pol. Arch. Hydrobiol.*, 16, 31–49.

Klekowski, R. Z. 1968. Cartesian diver microrespirometry for terrestrial animals. In: W. Grodziński, R. Z. Klekowski [Eds.] *Methods of ecological bioenergetics*, 51–66, Warszawa–Kraków, Pol. Acad. Sci.

Klekowski, R. Z., Shushkina, E. A. 1966. Ernährung, Atmung, Wachstum und Energie-Umformung in *Macrocyclops albidus* (Jurine). *Verh. int. Ver. Limnol.*, 16, 399–418.

Motoda, S. 1959. Devices of simple plankton apparatus. *Mem. Fac. Fish. Hookaido Univ.*, 7, 73–94.

Patalas, K. 1954. Porównawcze badania nad nowym typem samoczynnego czerpacza planktonowego i hydrochemicznego [Comparative studies on a new type of self acting water sampler for plankton and hydrochemical investigations]. *Ekol. pol. Ser. A*, 2, 231–242, [Engl. summ.].

Straškraba, M. 1967. Estimation of respiration in the field of natural populations of Cladocera and Copepoda using the quantitative method of plankton sorting. *Arch. Hydrobiol.*, 63, 497–511.

[Winberg, G. G.] Винберг, Г.Г. 1956. *Интенсивность обмена и пищевые потребности рыб* [Rate of metabolism and food requirements of fishes]. Minsk, Izd. Belgosuniversiteta. [Engl. ed.: Transl. Ser., 194, Fish. Res. Board of Canada].

Zeiss, F. R. 1963. Effects of population densities on zooplankton respiration rates. *Limnol. Oceanogr.*, 8, 110–115.

Zeuthen, E. 1950. Cartesian diver respirometer. *Biol. Bull.*, 98, 139–143.

PRODUCTIVITY PROBLEMS OF FRESHWATERS. WARSZAWA — KRAKÓW 1972
Proceedings of the IBP-UNESCO Symposium on Productivity Problems of Freshwaters
Kazimierz Dolny, Poland, May 6—12, 1970
EDITORS: Z. KAJAK, A. HILLBRICHT-ILKOWSKA

James A. P. STEEL, Annie DUNCAN and Tony E. ANDREW

Metropolitan Water Board,
Queen Elizabeth 11 Reservoir,
Molesey Road, West Molesey, Surrey, England

Royal Holloway College (University of London),
Englefield Green, Surrey, England

The New University of Ulster,
Coleraine, Northern Ireland

The daily carbon gains and losses in the seston of Queen Mary Reservoir, England, during early and mid 1968

The aim of the contribution is to describe the seasonal changes in the daily rates of carbon "gains" and "losses" in the seston of Queen Mary Reservoir during 1968, in order to indicate the possible temporal and quantitative trophic inter-relationships between the basin's phytoplankton and herbivorous zooplankton. The methods adopted for measurement and computation of the various parameters involved are described: net primary production, algal numbers, chlorophyll, total particulate carbon, algal immigration and emigration, time-depth temperature and silica distributions and, for *Daphnia hyalina* Leydig, the numerical density, length frequency distribution, individual body weight, duration of developmental cycle, mean respiratory rate and daily assimilation. The weekly sampled biomasses of *D. hyalina*, algae and detritus illustrate the statics of the situation and the daily carbon "gains" and "losses" in the reservoir seston its dynamics; a computed balance between these daily "gains" and "losses" provide an estimate of the required increase and decrease or of the goodness, or poorness, of the attempt to balance the incoming and outgoing carbon fluxes.

1. INTRODUCTION

The aim of the contribution is to describe the seasonal changes in the daily rates of carbon "gains" and "losses" in the seston of Queen Mary reservoir during 1968, in order to indicate the possible temporal and quantitative trophic inter-relationships between the basin's phytoplankton and herbivorous zooplankton. It represents a first attempt to integrate the results from Ph.D. theses and co-operative studies designed to form a parallel investigation involving two or three trophic levels and has proved more successful in the first half of the year than during the late summer period.

2. DESCRIPTION OF THE RESERVOIR

Queen Mary Reservoir is one of several being studied which are situated in the Thames valley and which form part of the Metropolitan Water Board's storage system for the London water supply. These reservoirs are wholly man-made, consisting of a basin excavated to the London clay and surrounded by an embankment of materials with a clay core "keyed" into the lower clay. Queen Mary Reservoir is the largest of the Board's reservoirs at present and its major supply reservoir; its area is 290 ha, depth 12 m and volume 30×10^6 m^3. Normally between 1 and 2% of its total volume passes through it every day. The reservoir is roughly circular with a baffle wall delimiting the outlet area to approximately one third of the whole. Water enters the basin through pipes with submerged orifices and impinges upon a small wall which thus absorbes most of the momentum of the inlet water and restricts any mixing to the space between the pipes and the wall. The reservoir is filled from the River Thames, an enriched calcareous river with the following nutrient levels: NH_3–N — 0.1-1.2 mg/l, NO_3–N — 5 mg/l, orthophosphate — 1-2 mg/l, SiO_2 — 15-20 mg/l, $CaCO_3$ — 250 mg/l (Windle Taylor 1967).

The large area, shallowness and volume transported per day generally ensures that this reservoir is isothermal for most of the summer. However, when periods of intense radiation coincide with relative stillness, some degree of stratification appears but usually only involves the bottom metre of the reservoir, there being some chemical deterioration. Such conditions do not usually persist for very long periods and the reservoir then de-stratifies. The period of stratification is not usually long enough for gross deterioration of the bottom waters and overturns do not affect the quality of the general water mass, although such overturns may, of course, affect biological production. Thus, this reservoir is characterized by intermittent stratification with, perhaps, three mixings per year (Windle Taylor 1967).

3. METHODS

3.1 The samples upon which this study is based were taken at weekly intervals between 9—11 a.m. from the outlet raft (Fig. 1). In an earlier investigation (Steel et al., in preparation), this reservoir was sampled from three major areas, the inlet (A), tip of baffle (B) and outlet (C). In each area, depth samples were obtained from two or more stations and then bulked so as to

provide a composite sample from that area. Subsequent comparison of the chemical and biological data of the composite samples indicated sufficient homogeneity of the organisms being considered here for the outlet samples to be taken as representative of the whole. Measurements of vertical extinction coefficients of the outlet water during 1968 indicate, after some period of closure of the reservoir, the presence of river water within two days. This would seem to support the presence of a fairly high degree of horizontal mixing implicit in the sampling results.

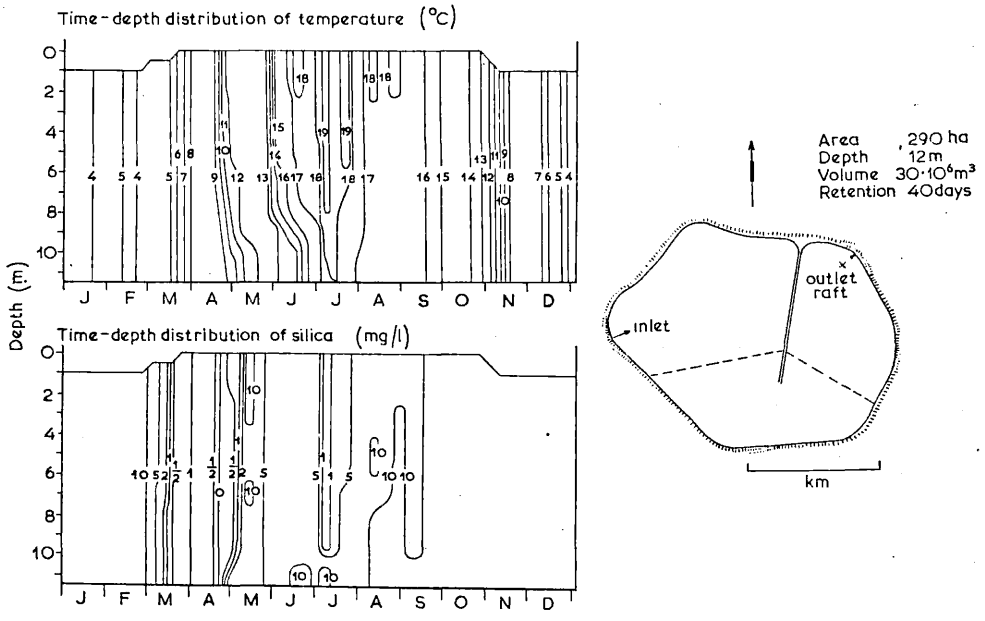


Fig. 1. Map of Queen Mary Reservoir and its time-depth distribution of temperature and dissolved silica during 1968

3.2 Net primary production has been computed from an assessment of the total daily gross production reduced by an assumed daily respiratory loss. The daily gross production was determined by short-term (4—6 hours) exposure of replicate light and dark bottles at various depths, any change of oxygen being measured by Winkler's titration, the dosing reagents of which were modified to 50% Pomeroy-Kirschmann concentration. The iodine was released by phosphoric acid and a 100 ml aliquot titrated with N/80 thiosulphate in a Smith's Free Piston Burette, using fresh starch indicator. The resultig profile was planimetrically integrated with respect to depth and converted to a daily rate per unit area by a day rate conversion factor determined as part of the main study. The daily respiratory loss per unit volume was assessed from the respiratory rate in the dark and assumed to be constant throughout the 24 hours. The time course of change in oxygen concentration over 24—30 hours was measured and the linear or near-linear portion of the result regressed. In order to convert this day rate per unit volume to a day rate per unit area, it was multiplied by an assumed mixing depth assessed from vertical distribution of counts and chlorophyll data. Thus, net production:

$$NP = \Sigma nP - n \cdot R \cdot 24 \cdot z_m$$

(Talling 1957) where: ΣnP = the daily integrated gross production, n = the phytoplankton concentration per unit volume, R = the respiratory rate per unit phytoplankton, z_m = the mixed depth.

This net production in terms of oxygen was then converted to carbon net production assuming a PQ of one.

3.3 Phytoplankton counts were performed using a clarified membrane filter technique (Steel 1969) in conjunction with Utermöhl sedimentation-counting with an inverted microscope. Occasional size measurements were performed so as to allow volume assessment.

3.4 Chlorophyll was measured by filtration of 1—2 l samples onto Whatman GFC glass fibre filter papers with an addition of $MgCO_3$. These were extracted in 90% acetone for 24 hours in the dark at −4°C. The samples were then filtered through either sintered glass or glass fibre and their optical density (OD) determined in a Beckman DB spectrophotometer. Chlorophyll concentration was determined as 11.9 OD_{663} mg/m^3 (Talling and Driver 1961).

3.5 Total particulate carbon was determined by wet oxidation of the total particulate material with a potassium dichromate-sulphuric acid oxidant together with a silver sulphate catalyst. The oxygen demand was determined by back titration with N/80 ferrous ammonium sulphate and equivalence to C was used to assess total C. The particulate carbon was separated by filtration of 1.0—0.1 l of sample, after removal of the larger zooplankton, through Whatman GFC glass fibre paper previously treated in a muffle furnace for at least 0.5 hour at 550°C. A regression of total particulate carbon and computed total plant volume was then used to assess plant carbon and this subtracted from the total particulate carbon was taken to be detrital (tryptonic) carbon.

3.6 Algal immigration was computed from a knowledge of the volume of river water flowing into the basin each day and the concentration and size of those phytoplankters which also were forming the reservoir's standing crop. From this data, and using the above carbon/volume relationship, a total daily input per unit area was calculated, assuming "instantaneous" mixing.

3.7 Algal emigration was computed in an exactly similar fashion, but using the reservoir phytoplankton standing crop.

3.8 The time-depth temperature distribution (Fig. 1) was constructed from the data automatically recorded from twelve resistance thermometers placed at 1 m intervals throughout the depth at the outlet raft.

3.9 The time-depth silica distribution (Fig. 1) was constructed from silica determinations by an acid molybdate method; the developed yellow colour was read at 420 mμ in a Beckman DB spectrophotometer.

3.10 The numerical density and length frequency distribution of populations of *Daphnia hyalina* Leydig, the only daphnid and the main planktonic herbivore present, were based upon averages of samples collected by means of a 5-litre Patalas volume sampler at five depths which were then filtered through a coarse mesh net (aperture size — 0.26 mm) in situ. Total counts were made of all the organisms retained on this net, through which few small daphnids could pass. The following daphnid stages were recorded: eggs or embryos, less than 1 mm length, 1.00—1.39 mm, 1.40—1.99 mm, greater than 2.00 mm; number of individuals with eggs or embryos; numbers of eggs or embryos per individual. Simultaneously, vertical hauls with coarse and fine plankton nets were taken to provide larger samples but these net samples collected only one third of the daphnids collected by the volume sampler for the same volume of water filtered and have not been used in the calculations.

3.11 Individual body weights of daphnids for the field size classes were obtained from a length-body weight regression based upon measurement of several hundred field individuals using a Cahn electrobalance. The carbon content was 44% of the dry weight.

3.12 The duration of the developmental cycle and the mean respiratory rates of daphnids of different lengths at 10 and 20°C were determined experimentally (Duncan, Cremer and Andrew, in preparation); in each case, about 20 individuals, fed on an excess supply of *Oocystis solitaria* Wittrock, were reared under controlled temperature conditions, from newly released young of known age until their death. At both temperatures, the oldest individual had attained the 10th-11th instar but was about 600 hours old at 20°C and 1,200 hours old at 10°C. Rates of oxygen consumption were measured by means of Zeuthen's stoppered cartesian diver (Zeuthen 1950, Klekowski 1968) at 24 hourly or 48 hourly inter-

vals. Respiratory rates for other temperatures were obtained from diver measurements of field individuals. The developmental period for other temperatures were calculated from the measured durations on the basis of Krogh's normal curve (Winberg 1968). An RQ = 1.0 was assumed for converting oxygen consumption to carbon production.

3.13 Daphnid daily assimilation (as carbon per unit area) has been calculated as the sum of their daily production and respiration, assuming that no natality or mortality occurred during the 24 hours being considered; this under-estimates the "grazing demands" of the population since the assimilation efficiency in Cladocera is usually less than 50% (Richman 1958, Klekowski and Ivanowa — personal communication on *Simocephalus vetulus*) and diver respiratory rates probably represent something less than active metabolism. Daphnid production was calculated from numbers and size frequency distribution in the weekly samples, the maximal dry body weight attained by the field length classes and the duration of development at different temperatures. Thus,

$$\sum_{i=1}^{5} N_i \cdot \frac{(w_{t\,\max} - w_{(t-1)\,\max})}{D_t} \cdot 0.44$$

where: N_i = the average number of a field size class per unit area [five field classes are involved (eggs/embryos, less than 0.1 mm, 1.0—1.39 mm, 1.40—1.99 mm and greater than 2.0 mm)]; $(w_{t\,\max} - w_{(t-1)\,\max}) \cdot 0.44$ = the difference between the maximal dry weights of individuals belonging to successive field classes, converted to carbon; D_t = the duration in days of the development of the field classes at field temperatures.

The population respiration was calculated from mean respiratory rates per hour for different instars at different temperatures, assuming that the rate of oxygen consumption was constant throughout 24 hours; no account has been taken of any possible food effects upon either the respiratory rate or duration of development. Thus,

$$\sum_{i=1}^{5} N_i \cdot R_{it} \cdot 24 \cdot 0.4$$

where: R_{it} = the oxygen consumption per hour of an individual at the field temperature; this is converted to carbon production per day, assuming an RQ = 1.

3.14 Inter-sample computation: As the carbon fluxes associated with the biomass changes relate to "inter-sample" periods, it was necessary to estimate the values of the other carbon fluxes at similar times. Such "inter-sample" values have been obtained by assuming a linear rate between samples, that is,

$$a_{\substack{\text{inter} \\ n \to n+1}} = \frac{a_{n+1} - a_n}{7}$$

where: a = a parameter determined on or computed for sample days n and $n+1$ at weekly intervals.

Some earlier model work on this system indicates that, with respect to the various rates involved and the sampling frequency, such an assumption would not invalidate the relationship detailed in what follows.

4. RESULTS

Figure 2 illustrates the qualitative and quantitative algal history at 1 m depth throughout the period considered. It may be seen that the algae of this eutrophic basin are dominated by diatoms. There are usually much larger crops of blue-

-green algae, however, the very poor late summer of 1968 seems to have greatly reduced their abundance. A particular characteristics of those algal crops which do exist is their "dynamic" nature; they are usally either increasing or decreasing, any quasi steady state being maintained for only short periods. Figure 2 also illustrates the seasonal changes in the numerical abundance of five length groups of *Daphnia hyalina*, the two larger of which are reproductive. The fact that the group less than 1.0 mm is more abundant than the numbers of eggs-embryos implies that the larger reproductive sizes have been inadequately sampled.

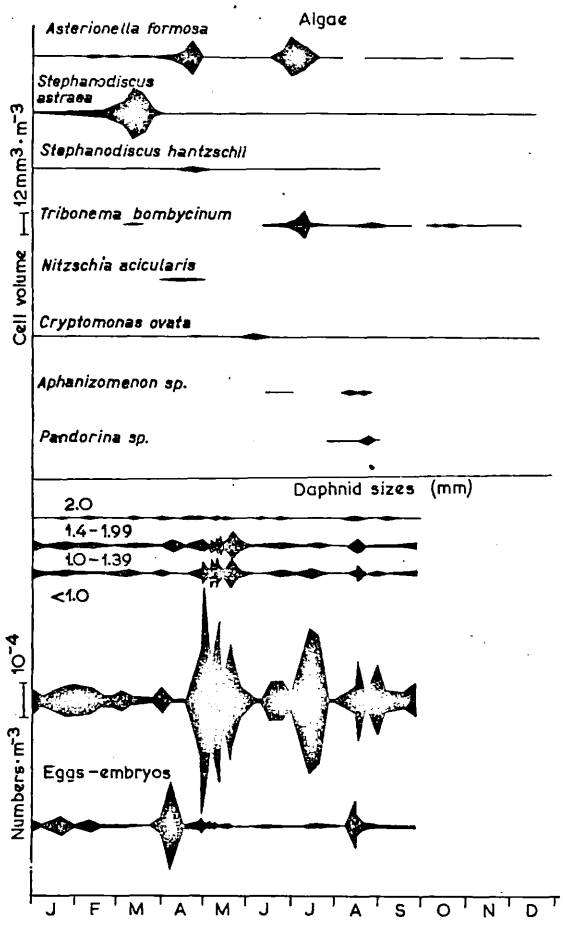


Fig. 2. Weekly sampled species composition of phytoplankton and size-frequency distribution of *Daphnia hyalina*

Figure 3 presents the weekly sampled biomasses of *Daphnia hyalina*, algae and detritus. The daphnid biomass was calculated from the product of arithmetic mean concentration of each size group and the group mean dry weight, multiplied by the total depth. Figures 2 and 3 show the considerable overwintering population of *Daphnia* as well as its three periods of reproductive activity. An

estimate of the detrital carbon biomass was obtained from regression analyses on particulate chlorophyll and carbon concentration. The zero chlorophyll-carbon was taken to represent detrital carbon. This concentration was multiplied by the total depth to obtain biomass. Subtraction of that biomass from the total particulate carbon biomass is an estimate of the algal carbon biomass. This estimate is supplemented by values based upon algal volume and total particulate carbon regression analyses, the resulting coefficients being taken as an indication of the value of the carbon-volume relationship of the algae. This relationship was used to ensure that the chlorophyll-carbon analyses were restricted to more or less steady values of the carbon/chlorophyll ratio. The algal biomass has a largest value (32 g $C \cdot m^{-2}$) at the end of the spring bloom of *Stephanodiscus astraea* Grunow. The subsequent lesser peak (about 15 g $C \cdot m^{-2}$) is almost coincident with a diatom maximum in the River Thames. The final biomass of August is,

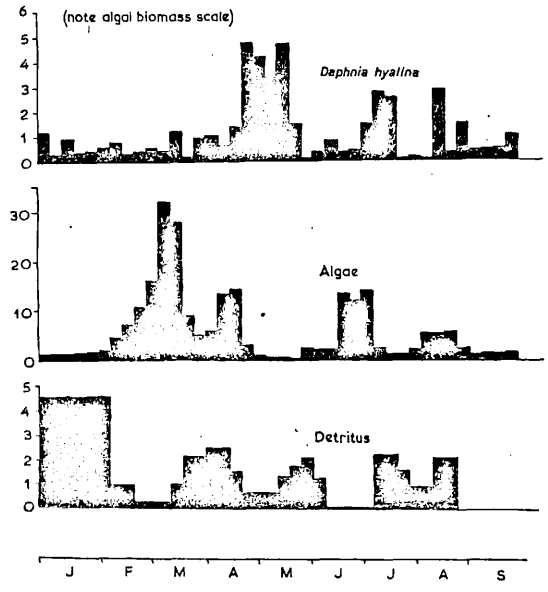


Fig. 3. Weekly sampled biomasses of *Daphnia hyalina*, algae and detritus as g carbon $\cdot m^{-2}$

as already indicated, much reduced from "normal", and would usually also be of the order of 15 g $C \cdot m^{-2}$. The January and early February detrital biomass (4.5 g $C \cdot m^{-2}$) is a result of the large silt suspensions in the high winter flows of the River Thames. The post-algal peak "levels" (about 2.5 g $C \cdot m^{-2}$) are presumably partially the result of the manner of estimate, that is, it includes as non-chlorophyllous carbon bacteria, rotifers and Protozoa, although some loss of these will occur due to the pore size of the glass fibre filters used and/or fragmentation of the organisms.

Figure 4 illustrates the main daily carbon "gains" and "losses" in the reservoir during 1968, where daily carbon "gains" are represented by the rate of

phytoplankton net carbon fixation ($+NP$) plus the daily addition of river algal and detrital carbon (algal and detrital immigration) and any decrease in either algal ($-\Delta B/\Delta t$) or detrital ($-\Delta C/\Delta t$) biomass. The daily carbon "losses" are the algae and detritus carried out of the basin (algal and detrital emigration), any increase in either algal ($+\Delta B/\Delta t$) or detrital ($+\Delta C/\Delta t$) biomass, any negative net

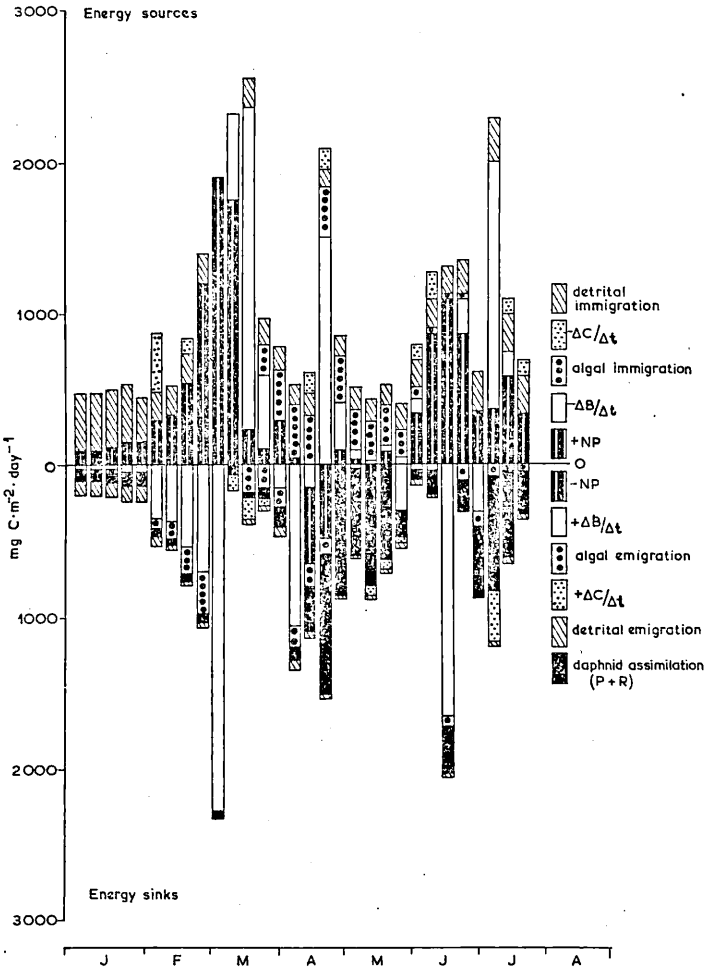


Fig. 4. Computed inter-sample daily carbon fluxes (expressed in terms of mg $C \cdot m^{-2} \cdot day^{-1}$)

production ($-NP$) plus the carbon which must have been assimilated daily by the daphnid population present [daphnid assimilation ($P+R$)], these being the main planktonic herbivore. A computed balance between these daily "gains" and "losses" was then set up, the required increases and decreases being shown in Figure 5.

Figures 3 and 4, respectively, illustrate the statics and dynamics of the situation, and thus in what follows any quoted biomass estimate will be found in Figure 3 whereas any cited rate can be read off from Figure 4.

In the early part of the year, what algal biomass was present (between 1—2 g $C \cdot m^{-2}$) is dominated by a large variety of *Stephanodiscus astraea* (cell size: 15—18 by 40—50μ) and data on both net production (up to 2,000 mg $C \cdot m^{-2} \cdot day^{-1}$) and changes in the standing crop (up to 2,500 mg $C \cdot m^{-2} \cdot day^{-1}$) suggest that nearly all the production is being manifest as new algal biomass. This state of affairs continued until early March when the basin was shut in; within the next

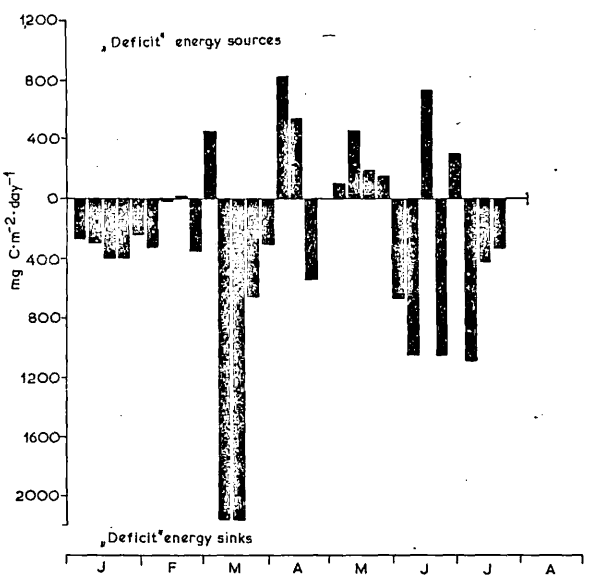


Fig. 5. The required carbon fluxes for numerical balance of Figure 4

ten day, further net production reduced the silica concentration within the basin to nearly zero (Fig. 1) and this coincided with the maximal algal biomass of 32 g $C \cdot m^{-2}$. This was then followed by an algal biomass reduction to approximately 10 g $C \cdot m^{-2}$ due to settlement of the moribund *S. astraea*.

During the same period, and up to mid-April, when the biomass of *Daphnia hyalina* was low (less than 1 g $C \cdot m^{-2}$), daphnid assimilation was also at a very low level (about 100 mg $C \cdot m^{-2} \cdot day^{-1}$); the food available was either nutritively poor detrital material (4 g $C \cdot m^{-2}$) or, during February, March and April, large populations of the relatively inedible diatom, *S. astraea*. Although as many as 60% of the mature-sized daphnids (which were not very numerous) were bearing eggs, the low number of eggs per female (about 4.0/female) seemed to confirm the poor quality of the food available.

The basin was then re-opened to the river in late March and the consequence was an introduction of more silica as well as the diatoms, *Asterionella formosa* Hassall and *Stephanodiscus hantzschii* Grunow, from the river. A rapid growth of *S. hantzschii* and, to a lesser extent *A. formosa*, took place within the river during the first three weeks in April, thus producing a greater algal immigration (300 mg $C \cdot m^{-2} \cdot day^{-1}$) into the reservoir. Just after the main growth of *Stepha-*

nodiscus astraea, when the daphnid biomass was still at a relatively low level (about 1 g $C \cdot m^{-2}$), this algal immigration, plus some degree of basin net production, were sufficient to produce a second growth of *A. formosa* and *S. hantzschii* (15 g $C \cdot m^{-2}$). Towards the peak of this growth in late April, Figure 4 demonstrates that there was virtually no net production within the basin and, in fact, there seemed to be a large column respiratory deficit (up to 500 mg $C \cdot m^{-2} \cdot day^{-1}$). Meanwhile, the high biomass levels were being maintained by algal immigration.

By the beginning of April, a striking increase in the number of eggs per female daphnid (14.0/female) took place and remained high (10 eggs/female) until the end of April; this coincided with the better quality of the food available in the actively growing cells of the river diatoms. By the end of April and during May, a major change occurred, namely, the appearance of a large increase in daphnid biomass (up to 5 g $C \cdot m^{-2}$) whose daily assimilation level reached values of 1,000 mg $C \cdot m^{-2} \cdot day^{-1}$ and, concomitantly, the plant biomass decreased to a low level (to about 0.5 g $C \cdot m^{-2}$). This reduction occurred although the same level of algal immigration (270 mg $C \cdot m^{-2} \cdot day^{-1}$) from the river was sufficient earlier to support much larger basin plant biomasses. The immigrant algae consisted of smaller diatoms (*S. hantzschii* with a cell size of 8—10 by 8—10μ and *A. formosa* with a cell size of 2—4 by 60—120μ) and these appear to be the sole potential food available to support these high daphnid assimilations apart from the detrital carbon immigration of about 136 mg $C \cdot m^{-2} \cdot day^{-1}$. It therefore appears that the daphnid population at this time was being maintained entirely by the immigrant river algae and detritus, which, however, was being voraciously grazed down so that no measureable basin net production was detectable. At the end of April and beginning of May, considerable numbers of adult *Cyclops vicinus* Uljanin and the predacious rotifer *Asplanchna* sp. were present and may have cropped the smaller daphnids; this effect has not as yet been demonstrated.

This situation continues until the end of May and early June, when the river population of algae declines so that the algal immigration level drops to 85 mg $C \cdot m^{-2} \cdot day^{-1}$ and, consequently, the daphnid biomass falls to their low summer value (0.5 g $C \cdot m^{-2}$) with a daily assimilation rate of barely 200 mg $C \cdot m^{-2} \cdot day^{-1}$ during June. Throughout this period (end of May to July) the main food available was again detrital carbon (270—85 mg $C \cdot m^{-2} \cdot day^{-1}$) upon which the daphnids could only produce 2 or fewer eggs per female.

In the absence of any serious levels of herbivorous grazing in mid-June, the basin production attains values of about 1,000 mg $C \cdot m^{-2} \cdot day^{-1}$ which results, by the end of June and beginning of July, in a further increase in the algal biomass (up to 14 g $C \cdot m^{-2}$), consisting of *Asterionella formosa* and *Tribonema bombycinum* Derbes et Solier, the former being twice more abundant than the latter. During the second week in July, the concentration of *Asterionella* decreased as that of *Tribonema* increased, resulting in a reversal of dominance, although the biomass remained at much the same level (10—14 g $C \cdot m^{-2}$).

However, after some delay, daphnid assimilation demands increased up to

900 mg $C \cdot m^{-2} \cdot day^{-1}$ in mid-July and remained at more than 300 mg $C \cdot m^{-2} \cdot day^{-1}$ until the beginning of August, during which period, the algal biomass was rapidly reduced to 1 g $C \cdot m^{-2}$, even although some net production (500—700 mg $C \cdot m^{-2} \cdot day^{-1}$) was still taking place. It would appear that the basin production is not being maximally exploited by the cladocerans during this period which could be the result of predation. During July, the only invertebrate carnivore present in large numbers was *Asplanchna* sp. whereas, later during August, when the rotifer numbers were still high, the predacious *Leptodora kindtii* (Focke) and adult cyclopoids were also present. Any cropping effect by these predators has not yet been assessed quantitatively and nothing is known about the numbers of young fish larvae in the reservoir.

At the present state of this investigation, it is not possible, as had been hoped, to continue to the end of the year such interpretations of the changes in algal and daphnid biomasses because of various difficulties, one of which is the assessment of "mixed depth" for net production and respiratory calculations for blue-green algae.

5. SUMMARY AND DISCUSSION

It is suggested that the following sequence of biological events occurred in Queen Mary Reservoir during the first half of 1968:

1. A period of low "holding" net primary production, light-limited, which together with immigrant detrital carbon, supports the low winter daphnid population with a characteristically low egg number per female.

2. This is followed by a period of high basin net production but little river algal immigration; the still high level of detrital carbon immigration provides the sole support of the daphnid biomass since the dominant alga is of an almost inedible size. The net production results in very high algal biomasses of *Stephanodiscus astraea.*

3. Nutrient limitation takes place in the relatively quiescent conditions of the enclosed basin; there is a period of sedimentation of the senescent diatom.

4. The opening of the basin to the river brings in new silica and new algae from the river, *Stephanodiscus hantzschii* and *Asterionella formosa.* The resulting basin net production plus the continual algal immigration results in new levels of algal biomass.

5. The river algal biomass then attains maximum levels, resulting in a decline in the level of river silica. This also causes a decrease in the level of silica in the basin and, coinciding with this, high levels of deficit algal respirations were measured. The algae of river origin are smaller diatoms, apparently grazeable by daphnids, since large increases in daphnid biomass, produced by increased egg production per female, coincides with reductions in diatom biomass.

6. This situation of low diatom biomass plus the relatively constant, fairly high input of river diatoms changes when the river diatom population declines. The daphnid population, although possibly subject to predation by rotifer and adult cyclopoid predators, appears to overgraze its food supply and its biomass falls to very low levels.

7. In the absence of daphnids, further net production by the summer population of *Asterionella* and *Tribonema* results in new algal biomass.

8. After some delay, an increase in daphnid biomass then occurs and the grazing power of this new daphnid population, possibly also subject to predation by *Asplanchna* coincides with a reduction in the plant biomass to low levels.

Figure 5 is indicative of the goodness, or poorness, of the attempt to balance the incoming and outgoing carbon fluxes; the biomasses illustrated in Figure 3 represent temporary resting places of carbon in its passage through the trophic system of the basin-ecosystem, with complete capability to effect such a balance, "deficit" sources and sinks would be unnecessary and Figure 5 would just show a zero line. The deviation from perfect balance shown in Figure 5 is some measure of the imperfections of our field sampling, measurement and computation techniques; these result from (1) non-measurement of parameters of importance (bacterial production, diatom sedimentation, herbivore grazing directly, young fish predation); (2) imperfect measurement of other parameters (algal respiration, active metabolism of daphnids, adequate field sampling, particularly of the larger daphnid sizes); (3) imperfect computation by which we mean inadequate understanding of the relevant factors influencing organisms in nature and under the conditions of measurement, resulting in imperfect transfer coefficients.

The larger sink fluxes in Figure 5 are those of mid-March, that is, immediately after the spring maximum of *Stephanodiscus astraea*. The requirement is almost entirely to satisfy a large reduction in algal biomass ($-\Delta B/\Delta t$) (approximately about 2,000 mg $C \cdot m^{-2} \cdot day^{-1}$) and the net production of that reducing biomass. It would seem reasonable to ascribe this reduction to sedimentation, and some field measurements made during the post-bloom spring period confirm that such a value for sedimentation is reasonable for that time. The other moderately large sink fluxes are those of June and July, in which probably all the errors play a part. Thus an unknown amount of sedimentation will have taken place and, as there was only partial circulation of the water column, much greater difficulty exists in estimating the "mixed depth". Adequate assessment of such an effect is important for the estimation of net production and over- or underestimation may well be due to an under- or overestimate of this depth. It is quite possible that such a "mixed depth" may not in fact exist for the whole of the 24 hours.

It had been hoped to continue this mode of approach throughout the year, however this has not proved possible for the biomasses of late August and early September. As this was a mixture of blue-green and motile green algae, it has been impossible to obtain an objective estimate of their circulated depth from a single sampling station. Choice of what seemed a reasonable depth, based on their

vertical distribution at the outlet, led to some very large estimates of their net production (2,000 mg $C \cdot m^{-2} \cdot day^{-1}$) which could only be balanced by a "deficit" sink of approximately 1,500 mg $C \cdot m^{-2} \cdot day^{-1}$. The buoyancy and motility of the organisms makes it unlikely that such a deficit could be explained by sedimentation. It would seem, therefore, that the net production was being overestimated, due probably to some overestimate of the gross production and the difficulties of obtaining a meaningful column respiration.

Although the attempt to equate the carbon fluxes then being measured has been only partially successful, it has proved useful in revealing where subsequent work should be concentrated.

The contribution of J.A.P. Steel is by permission of Dr. E. Windle Taylor, Commander of the British Empire, Director of Water Examination of the Metropolitan Water Board. A. Duncan and T.E. Andrew wish to thank Dr. E. Windle Taylor for permission to sample in Queen Mary Reservoir and for generous help from his staff. T.E. Andrew was in receipt of a Studentship from the Natural Environmental Research Council which he gratefully acknowledges.

REFERENCES

Duncan, A., Cremer, G.A., Andrew, T.E. (in preparation) — On life cycle energy budgets of *Daphnia hyalina* Leydig at 10 and 20°C and in excess of food.

Klekowski, R.Z. 1968 — Cartesian diver technique for microrespirometry (IBP Meeting on Methods of Assessment of Secondary Production in Freshwaters) — Prague, 26 pp. (mimeographed).

Richman, S. 1958 — The transformation of energy by *Daphnia pulex* — Ecol. Monogr. 28: 273—291.

Steel, J.A.P. 1969 — A membrane filter method for counting algae — J. Soc. Wat. Treat. Examin. 18: 343—346.

Steel, J.A.P., Bellinger, E., Colling, R.L., Duncan, A., Cremer, G.A. (in preparation) — A limnological survey of three storage reservoirs in the lower Thames valley, England.

Talling, J.F. 1957 — The phytoplankton population as a compound photosynthetic system — New Phytol. 56: 133—149.

Talling, J.F., Driver, D. 1961 — Some problems in the estimation of chlorophyll-a in phytoplankton (Proc. of the Conference on Primary Productivity Measurement. Hawaii) — U.S. Atomic Energy Commission Publication, TID, 7633: 142—146.

Winberg, G.G. (editor) 1968 — Metody opredeleniya produkcii vodnykh zhivotnykh [The methods for the estimation of production of aquatic animals] — Minsk, 242 pp.

Windle Taylor, E. 1967 — Forty-first report on the results of the bacteriological, chemical and biological examination of the London waters for the years 1965—66 — Metropolitan Water Board, London.

Zeuthen, E. 1950 — Cartesian diver respirometer — Biol. Bull. 98: 139—143.