ENERGETICS OF PLANKTONIC ROTIFERS APPLIED TO POPULATIONS IN RESERVOIRS.

Margaret Doohan B.Sc (London)

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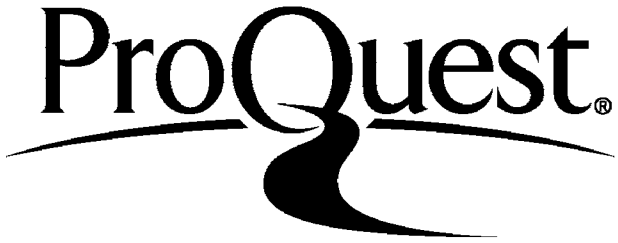


Abstract

In this thesis field data are given on the seasonal variation in standing crop of rotifers, the egg numbers and the eggs per female in two Thames Valley reservoirs, the Queen Mary and the Queen Elizabeth II. These sites are described and basic physicochemical and seston data given from other sources. The occurrence and seasonal distribution of six rotifer species is described in detail and the relationship between the total standing crop and some physicochemical characteristics is discussed. The logistic equation is used to calculate the rates of change of some species and these are discussed in relation to temperature, seston, and bacteria.

The population dynamics of Keratella quadrata are discussed and birth-rates and production of egg-bearing rotifers calculated using Edmondson's (1960, 1965) method. The production/biomass ratio is then calculated seasonally for egg-bearing rotifers and discussed in relation to current literature. The Q_{10} relationship is used to assess relative temperature dependence of rotifers in different environments.

Respiration rates of several rotifer species given at reservoir temperature and regressions of respiration/dry weight, respiration/temperature are given together with Q_{10} values. Finally respiration of the reservoir populations is calculated and related to production, indicating a constant relationship through out the season. Annual assimilation and consumption only are given, assimilation being calculated from Production plus respiration, and a mean assimilation efficiency of 60% being assumed. This was made necessary by inconclusive feeding experiments which are nevertheless recorded in the text.
An energy budget for adult Brachionus plicatilis is given as a demonstration of the validity of the methods used, and an indication of what might be achieved in the field situation in the future.

Contents

Introduction

Over recent years staff and students of the Zoology Department of Royal Holloway College have been collaborating closely with the Metropolitan Water Board in studies of various kinds on the Board's reservoirs in the Thames Valley near Staines and Walton-on-Thames. Post-graduate workers working with Dr. A. Duncan have complemented her own work on the energetics of the herbivorous Crustacean populations, particularly the Daphnids, and at present Dr. M. Burgis is working on the cyclopoid Copepods. The staff of the Metropolitan Water Board provide data of a routine kind on the physico-chemical characteristics of the reservoir and on the phytoplankton, whilst the Assistant Senior Biologist, Mr. A. Steel, is also involved in fundamental research on energy transformations in the phytoplankton throughout the year. To expand the picture of energy flow from seston to herbivorous zooplankton, work on the rotifer population was initiated.

The work described in this thesis had therefore two purposes:

1. To form a part of a much wider research project on energy flow through aquatic ecosystems as part of the I.B.P. U.K./P.F./14 project. For this purpose bacic numerical, taxonomic and physiological data on rotifers were required.

2. To look for generalised relationships between the physiological characteristics of rotifers and more easily obtainable information such as ambient temperature, numbers of animals, mean size of animal. At the same time it was hoped to simplify and develop some of the techniques involved in working with very small animals or at least delineate the extent of their reliability.

These two aims were largely fulfilled except for the one failure in obtaining reliable ingestion rates for reservoir populations at reservoir food concentrations. In anticipation of this eventuality, work on a laboratory

population of Brachionus plicatilis was initiated at the kind invitation of Prof. A. Ruttner-Kolisko and Prof. H. Loffler of the Limnological Institute of the Austrian Academy of Sciences. Some of this work is presented here as a confirmation of the reliability of the experimental methods used on field animals. Work on age- and therefore, size related respiration rates of B. plicatilis has been omitted as unrelated to the rest of the thesis, since it was found impossible to measure accurate size differences within individual reservoir species, much less determine the size of every rotifer used in respiration or ingestion experiments. This work will therefore be published separately.

The thesis falls naturally into two main sections. The first describes field data and attempts to relate background information to the standing crop and rates of change of the rotifer population. In the second main section laboratory work is the main data source but this is applied wherever possible to the field situation.

Before the start of I.B.P. no work of this kind had been attempted on rotifer populations despite their importance in some bodies of water, and even now, the data presented here represent one of the most comprehensive ecological energetic studies of planktonic rotifers. No previous work has combined laboratory and field data in this way. I.B.P. work edited by Kajak and Hillbricht-Ilkowska (1972) is largely field work with biomass and production estimates based on indirect conversion factors of which the validity has not previously been assessed. Data of Galkovskaya in Winberg (1971) give field estimates of production, and laboratory determinations of respiration and consumption but the various ecological efficiencies given do not combine field and laboratory data, and the methods used are not clear even in the sources (Galkovskaya 1963. Erman 1956, 1962). Production estimates based on Edmondson's (1960) method have also been produced by Hillbricht-Ilkowska (1967) with Weglenska (1970) and

with Pourriot (1970), also Lewkowicz (1971), Andronikova et al (1972), Alimov et al (1972), but only Hillbricht-Ilkowska and Pourriot (1970) have given additional data on egg development rates which form the basis of these production estimates. The present work besides adding some data also attempts to generalis the relationship between egg development rate and temperature for several planktonic rotifer species.

Respiration rates of rotifers have previously been measured by Galkovskaya (1963), Belyatskaya (1959) Pourriot and Deluzarches (1970), but no relationships between temperature and respiration or between production and respiration have been produced, since no other attempts have been made to determine production and respiration simultaneously on a seasonal basis.

The experimental approach owes much to the work of Prof. Klekowski at the Dept. of Experimental Hydrobiology in Warsaw, an approach developed by Dr. Dunca to provide a realistic synthesis of laboratory and field data such as that attempted here for rotifers. Pilarska (in press 1971) from Klekowski's laboratory, has produced an energy budget for laboratory populations of Brachionus rubens in different concentrations of food, but no attempt was made to relate this to the field situation.

All work on rotifers prior to the studies cited above have been either taxonomy and general ecology or experimental work on reproduction, Taxonomy and ecology have been reviewed by Hutchinson (1967) and it was considered unnecessary to review the few subsequent papers, relevant ones being cited in the text of this thesis. Mixis experiments have been reviewed and a more satisfactory explanation given by Birky and Gilbert (1971) but work of this nature was not undertaken for this thesis. Halbach (1970) gives and excellent review of factors affecting aspects of rotifer life histories other than mixis in laboratory experiments, so that the last three sources quoted virtually cover all aspects of rotifer biology not referred to or connected with the subject of this thesis.

Acknowledgements

I wish to thank Prof. P.M. Butler who provided facilities in the Zoology Department of Royal Holloway College, and the technical staff of the department particularly the chief technician M.C. Colthorpe for photographic and other help, and Mr. and Mrs. N. Nadin-Hurley. I acknowledge with thanks the stimulating advice, assistance and criticism of my superviser, Dr. A. Duncan and the generous help of all kinds provided by the staff of the Metropolitan Water Board who permitted the project to be done on their reservoirs.

Many others, too numerous to mention specifically, have assisted technically or by discussion in this thesis, these too I wish to thank.

The work was conducted during the tenure of a Natural Environment Research Council Studentship which is gratefully acknowledged.

Table 1

Sampling Statistics on Total Numbers of Rotifers

Vertical Net Hauls

N	Mean	S.D.	S.D. x t (10% level)	S.D. x t (as %)
5	474.4	72.7	154.8	32

Patalas Series (Filtered through 180 mesh net)

N	Mean	S.D.	S.D. x t (10% level)	S.D. x t (as %)
4	838	115.3	271	32

4m. Patalas Samples (Filtered)

N	Mean	S.D.	S.D. x t (10% level)	S.D. x t (as %)
4	73.5	10	23.5	32

Filtered Patalas Series = 2.5 x Vertical Net Haul

Unfiltered Patalas = 2.5 x Filtered Patalas.

Overall conversion factor for net hauls = 6

$$\text{Net area} = \frac{1 m^2}{14.08}$$

$$\therefore 1 m^2 \text{ column} = \text{Net haul} \times 14.08 \times 6$$

$$= \text{Net haul} \times 84.5$$

Methods

Ecology and Population Studies

Quantitative Sampling of Rotifers

Rotifers were collected on alternate weeks from each reservoir except during the spring and autumn peaks when more frequent samples were taken from the Q.M. reservoir. Collections were made with an F.B.A. phytoplankton net (180 meshes to the inch) and duplicate vertical net hauls were taken throughout the depths, the net being washed carefully after each haul. Likens and Gilbert (1970) point out that this size of mesh may not collect young or soft-bodied rotifers. No account was taken of this during sampling but the net hauls were subsequently calibrated using a series of 5 litre Patalas samples taken throughout the depths during the spring bloom of 1972.(See Table 1)

The two net hauls were preserved separately in 10% formalin after fixing in 4% formalin. Usually one complete haul was used for a count but if the more numerous species were present in numbers less than 40 then both net hauls were used. During the spring and autumn peaks subsamples were taken with a 5ml. Stempel pipette after the sample volume had been made up to 250ml. When the total number of rotifers counted was 100, the coefficient of variation of 5 Stempel subsamples was only 12%, but when the total was 40 the coefficient increased to 44%. As far as possible 100 animals of each species were counted, otherwise 40. In winter and occasionally in June, counts of both net hauls were less than 40 animals. Calculations of rates of change based on such low counts are noted in the tables of results.

The numbers per vertical net haul were transformed into numbers per metre^2 column by multiplying by 84.5. This figure was obtained from

i) a comparison of the mean number of rotifers in a vertical net haul with that in a Patalas column filtered through a

a net with the same mesh,

ii) a comparison of Patalas samples taken at 4 metres when filtered and when sedimented in a separating funnel with Lugol's iodine,

iii) a comparison of the area of the net with a square metre.

The variation in samples taken by the different methods is given in Table 1. Standard deviation times t for the small number of samples used was 32% of the mean for net hauls, Patalas series, and individual Patalas samples. The 2.5 factor difference between filtered and sedimented Patalas samples was the same in egg-bearing and non-productive females of Keratella quadrata (Muller), and was therefore applied to all small rotifers. Numbers of Asplanchna priodonta did not differ in the filtered and unfiltered samples so the factor was omitted from calculations.

Wherever comparisons of the rotifer numbers in the two reservoirs were made, the metre^2 column data was transformed into numbers per metre^3 by dividing by the depth of the reservoir at the date in question.

Samples for experimental work were collected with the net already described and passed through a 60 mesh filter to remove larger Cladocera and Copepoda. The remainder was stored in large Thermos flasks for transporting to the laboratory. Reservoir water for feeding during experiments was collected in a 5 litre Patalas at 3m. depth and carried back in a Thermos without being filtered or concentrated in any way.

Quantitative Sampling of Bacteria

Samples were taken with a 5l. Patalas and the water was flushed directly into 2 sterile bottles. Two Patalas samples were used at first but since there was no significant difference between the pairs of bottles filled from them ($t = 0.63$, $P > 0.1$) a single sample was used later and two bottles filled from it. Within an hour of arriving in the laboratory 1 ml.

sub-samples of serial dilutions were taken aseptically from each bottle and poured plates prepared using casein-peptone agar. (Collins 1960) The plates were incubated at 20°C. for ten days before colony counts were made on the most suitable dilution (30→300 colonies per plate) Results were then converted to numbers per ml.

Development Rates

The development rates of rotifer eggs were determined by the method described by Edmondson (1960) which is an adaptation of that designed by Elster (1945) for copepods. The method assumes that in a large sample of egg-bearing females, the ages of the eggs will be randomly distributed and the last eggs to hatch will have been produced just prior to sampling.

Individual egg-bearing females were placed each in 1ml of reservoir water in the cavities of a haemagglutination tray and placed in a constant temperature tank maintained at reservoir temperature. For each experiment 40-50 animals were used. The dishes were inspected at 2-4 hour intervals depending on the temperature of incubation and consequently on speed of development. At each inspection the number of animals still carrying eggs was noted until the last egg hatched. The regression of the number of females still carrying eggs against time was calculated, and the mean development time read off where the time cut the time axis.

This method was used at field temperatures on five occasions for Keratella quadrata and a linear relationship between the reciprocal of development time and temperature was established and calculated. From this relationship, development rate in the reservoir was calculated at two week intervals and used for estimating birth rate, death rate and production.

Birth rate and death rate

For planktonic rotifers Edmondson (1960) has shown that $B_r = \frac{E}{D}$ where B_r is the finite birth rate, $\frac{1}{D}$ the development rate of the eggs, per

female in a sample or population.

The instantaneous birth rate, b', that is, the rate at which animals are added to an initial population of one is obtained from the natural logarithm of B_r.

$$b' = l_n (B_r + 1)$$

This method was used to calculate the birth rate of Keratella quadrata in both reservoirs.

The rate of change of the numbers in the field population was obtained from the logistic equation

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

where N_o and N_t are the numbers of animals observed at the beginning and end of the period for which the birth rate was calculated. r is the rate of change and t the days between sampling.

The death rate d' was calculated from the observed rate of change and the experimentally determined birth rate.

$$r' = b' - d'$$

d' is the instantaneous death rate. The finite death rate d, used in production calculations, was obtained from

$$d' = l_n (1+d)$$

These calculations assume a constant birth and death rate between samples which is probably not strictly accurate, particularly during the times of rapid increase in rotifer standing crop. During this period therefore samples were taken at weekly and even three day intervals in the Q.M. reservoir to see if birth rates calculated at different sampling intervals made substantial changes in expected population numbers.

The parameters calculated by the methods described in this section were used on Keratella quadrata data from both reservoirs to obtain production estimates.

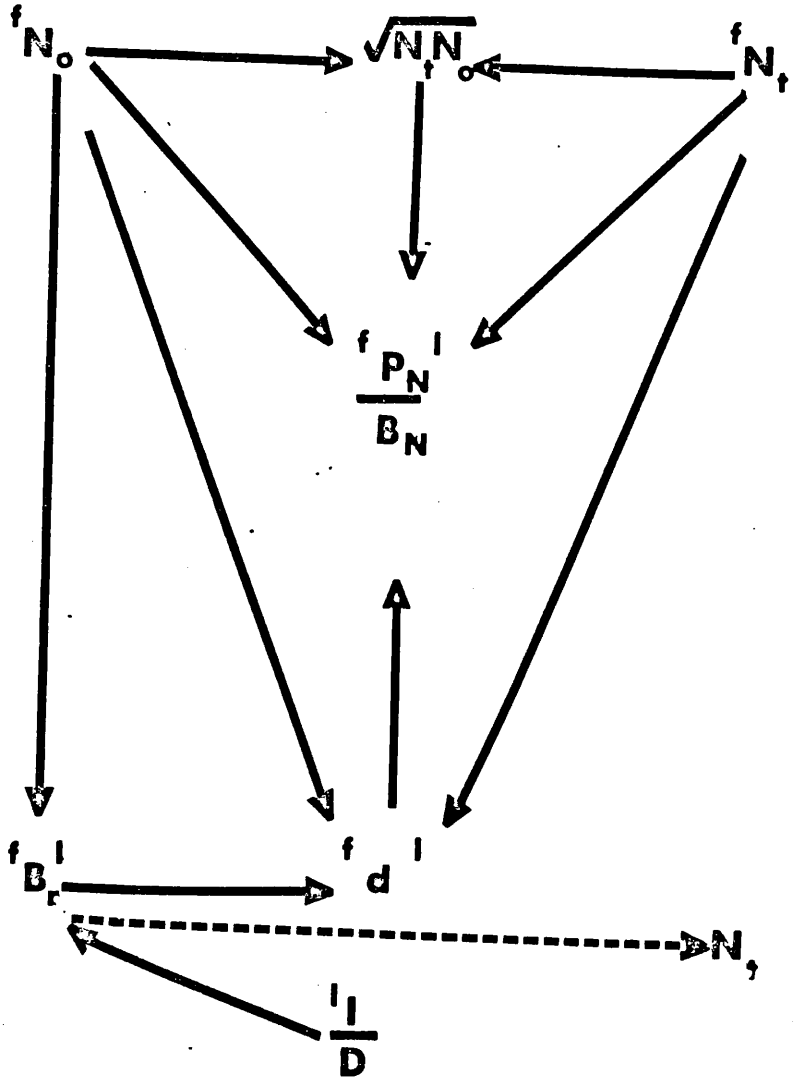

$^{f}N_{o}$
$\sqrt{N_f N_o}$
$^{f}N_{f}$
$^{f}\frac{P_N}{B_N}{}^{I}$
$^{f}B_r{}^{I}$
$^{f}d{}^{I}$
N_f
$\frac{I}{D}{}^{I}$

Fig. 1. Relationship between various parameters used in population dynamics

F = Field data
L = Laboratory data

Production of Rotifers

Production in terms of number of individuals added to the population per unit time was at first calculated by the method described by Galkovskaya in Winberg (1971 and derived from Edmondson (1960) Production = $[\bar{N}.d.t.] + N_t - N_o$ The formula was accepted uncritically but it became clear that the resulting production, when divided by the initial number of females present (N_o), was in most instances almost identical with the birth rate (B_p). The discrepancies seemed to result from errors involved in low counts or differences caused by the use of the exponential in determining d' from b'-r'. Since the birth-rate is based on egg numbers not numbers of young animals, egg mortality is included in the determination of d or assumed to be nil. It is therefore inevitable that net production per individual should be the same as the birth rate. Appendix II demonstrates the similarity for Keratella quadrata, and subsequent calculations were based on birth rate only.

To be an accurate assessment of production the birth rate should be based on the number of adults added to the population unless 100% egg viability can be assumed. In the experiments previously described to determine development times of the eggs of K. quadrata using forty to fifty egg bearing females in each of five experiments, all eggs hatched. This was also the case in two experiments on Polyarthra vulgaris.

Figure I shows the relationship between the parameters used in production calculations by the two methods described above. L. signifies laboratory determinations and F. means field sampling.

Feeding

The accurate determination of the feeding rates of rotifers under field conditions has not been attempted before due to the technical difficulties involved. Several attempts were made to overcome these difficulties but with little success.

Field feeding experiments

Initial experiments to test the feeding rates of rotifers in the field made use of the method devised by Gliwicz (1968). This involves the narcotisation of different sections of the zooplankton community using physostigmine salicylate. 250ml. round-bottomed flasks with ground glass stoppers were filled at the reservoirs from a depth of 3 metres, and transported as quickly as possible to the laboratory. Two series of flasks were set up as follows.

F.	F.R.	C A	C
No narcotic All zooplankton feeding	Narcotic 1.10^{-5} g/ml. Rotifers feeding. Others narcotised.	Narcotic 5.10^{-5} g/ml . All zooplankton narcotised.	Fixed in Lugol's iodine.

F, FR and C A were suspended upside down at 3 metres in a local pond and left for 24 hours. After this the zooplankton in each flask was counted and samples of phytoplankton were sedimented with Lugol's iodine and counted on an inverted microscope. Plate counts of bacteria were also attempted. Flask C acted as the initial count for phytoplankton and bacteria.

Gliwicz demonstrated that physostigmine salicylate has no effect on bacteria and phytoplankton. Tests were made of its effects on the reservoir zooplankton and confirmed the findings of Gliwicz that a concentration of 1.10^{-5} g/ml. is sufficient to narcotise all zooplankton except the rotifers but it acts slowly on nauplii (about 20 minutes)

The concentration of zooplankton proved to be too low for these experiments to be continued, and later attempts at field feeding experiments involved the use of radioactive tracers.

Laboratory feeding experiments

Simple direct counting techniques were tested initially with laboratory populations of Brachionus rubens and Keratella quadrata collected from local ponds. Experimental vessels were solid watch glasses containing known quantities of uni-algal cultures derived from reservoirs and ponds. Food species were Oocystis solitaria, Scenedesmus sp and Chlorella sp.

Two sets of vessels were set up as follows:

F	C	I
Algal cultures. Rotifers at a concentration of 10 per ml.	Algal culture only	1 ml. of culture fixed with Lugol's iodine at start of experiment

After a known feeding period at 20^{0}C, the algae in F and C were fixed

and sub-sampled for counting. Oocystis and Scenedesmus were counted in 1 ml. counting cell divided by a grid into micro-litres. Chlorella was counted in a haemocytometer of capacity 0.01 ul. Counts were replicated until at least 100 cells had been counted in each case giving a counting efficiency of 20% (Lund et al 1958)

Since periods of feeding were never more than 4 hours the exponential formula was not needed to calculate feeding rate as the concentration in C did not differ notably from that in I

$$\text{Feeding rate (Cells/ind./Hr.)} = \frac{C_c - C_F}{10t}$$

where C_c represents the concentration in the control vessel C after time t, and C_F is the final concentration in the feeding vessel.

Radioactive feeding experiments

An adaptation of the method used by Marshall and Orr (1955) and Sorokin (1968) and reviewed by Rigler in Edmondson and Winberg (1971) was used to determine the feeding rate of rotifers in ^{14}C labelled algae. Preliminary experiments were performed on cultured animals and algae but the method was adapted later for use under field conditions.

Algae were labelled by adding up to 10 uCi of labelled sodium bicarbonate to 100 ml. of culture. In cultures in the log. phase of growth, uptake was very rapid, but all feeding experiments were undertaken 24 hours later to ensure maximum uptake. During labelling, cultures were kept in flasks, closed with ground glass stoppers to prevent leakage of $^{14}CO_2$, in a growth room with extra blue light to enhance carbon fixation.

Feeding chambers were haemagglutination trays with 1 ml. cavities. Algae were first counted in a haemocytometer then 5 or 10 ml, according to the concentration, were filtered on to an HA Millipore filter under pressure and washed in 15 ml. of reservoir water, then 15 ml. of distilled water.

When Dunaliella salina was being treated in this way three washes of distilled water were used, as the algae is in a saline medium and there is danger of salts crystallising on the filter. The filter was then dried at 50°C and left in a dessicator until counting.

1 ml. of algal culture was placed in each feeding vessel and ten rotifers added using a braking pipette to reduce the amount of water added. By direct observation the time needed to fill the gut had been determined and rotifers were fed for 20 minutes to half an hour according to the species, and for one hour in the large rotifer Brachionus plicatilis (Muller). After the feeding period, the animals were rinsed carefully in three changes of reservoir water, algal culture medium or distilled water and transferred to a Millipore HA filter for a final washing under pressure in distilled water. The filters were then dried and stored as mentioned previously. During all these transfers no defaecation was observed in the species studied and therefore the results indicate the amount of food in the gut.

Radioactive counts were done on a Panax liquid scintillation counter using a toluene-based scintillant consisting of 0.5 gm per litre dimethyl POPOP and 4 gm. per litre paraterphenyl. Dried filters were placed in 10 ml. of scintillant and the vials left in the refrigerator to adjust to 5°C, the temperature giving optimal counting efficiency of 85%. In all cases the time taken to record 1000 counts was noted so that counting was accurate to within 95%. (Lund et al 1958)

Each experiment consisted of the following sets of counts:

a) Source - 3 x 1000 counts to test machine efficiency.

b) Background - Clean HA Millipore in scintillant

c) Algal count

d) Rotifer count

e) Last washing water. In early trials this was found to differ

negligibly from a), and thereafter it was omitted.

Feeding rate was calculated as follows:

$$\text{Cells ingested/animal/hour} = \frac{60}{t} \times \frac{R_R \cdot V \cdot N_A}{N_R \cdot R_A}$$

where t = Length of experiment in minutes

R_R = C.p.m. in rotifer vial

N_R = No. of rotifers in vial

V = Volume of algae counted

N_A = No. of algae per ml.

R_A = C.p.m. in algae vial

The volume of water cleared by an animal in an hour was calculated from the same formula omitting the term N_A.

This experimental procedure was also followed using rotifers from the reservoir in reservoir water. Water at reservoir temperature was cleared of zooplankton by means of a pipette and labelled sodium bicarbonate was added at a concentration of 10 uCi per 100 ml. water. Two procedures were followed after 24 hours.

a) Water was filtered through a membrane filter of pore size 12u to remove all algae too large for rotifers to eat. The feeding experiments were then conducted as described above.

b) Feeding experiments were conducted in unfiltered water but the control count was taken after passing the water through a 12u filter. The filtrate was subsequently re-filtered for counting purposes through an HA Millipore (pore size 0.45u).

Similar experiments were also conducted using labelled glucose at so low a concentration that only bacteria would take it up. (Wright and Hobbie 1966) The labelled bacteria were then used as food for rotifers. Bacteria numbers were calculated from the plate counts already described, whilst phytoplankton numbers were supplied by Mrs. C. Nadin-Hurley who did fortnightly counts on sedimented reservoir samples using an inverted microscope.

Rotifers used on different occasions for the above experiments were Keratella quadrata, Polyarthra sp and Synchaeta pectinata. In all cases self-absorption was found to be negligible, nor was there any significant uptake of labelling from the medium by the rotifers provided adequate washing procedures were carried out.

Assimilation experiments

These were conducted only on Brachionus plicatilis in a culture of Dunaliella salina, as part of an energy budget constructed for this species. Groups of 4 animals were fed for 2,4,6,24,26,28,41,43 and 45 hours in 1 ml. of labelled algal suspension. All animals were adults just beginning egg production. After feeding they were transferred to unlabelled food for an hour before washing, drying and counting as described above. The assimilation per hour was determined from the formula used for consumption, but since radioactive food from the gut was replaced by unlabelled food, the result is the amount of labelled food already incorporated into the body.

The consumption and assimilation of Brachionus plicatilis were converted into calories taking the calorific value of Dunaliella to be 0.436×10^{-6} cal. per cell. This is one third that of Chlamydomonas (Richman 1958) to which Dunaliella is related and of which it is about one third the volume.

Respiration Measurements.

Respiration rates were determined at field temperatures in filtered (double glass fibre) reservoir water using stoppered Cartesian divers with a gas phase (diver constant) of less than 1 Ul. (Linderstrom-Lang 1943, Zeuthen 1943, 1950a), 1955, Hotler and Zeuthen 1966 (review) Kleckowski 1971).

The respirometer is a constant volume, changing pressure system which measures the change in buoyancy of the diver caused by the consumption of oxygen from the gas phase by respiration of the experimental animal. The carbon-dioxide produced is absorbed by 0.1N NaOH in the diver head. A manometer containing Brodie's fluid records the pressure change necessary to make the diver float at equilibrium level at measured time intervals. The

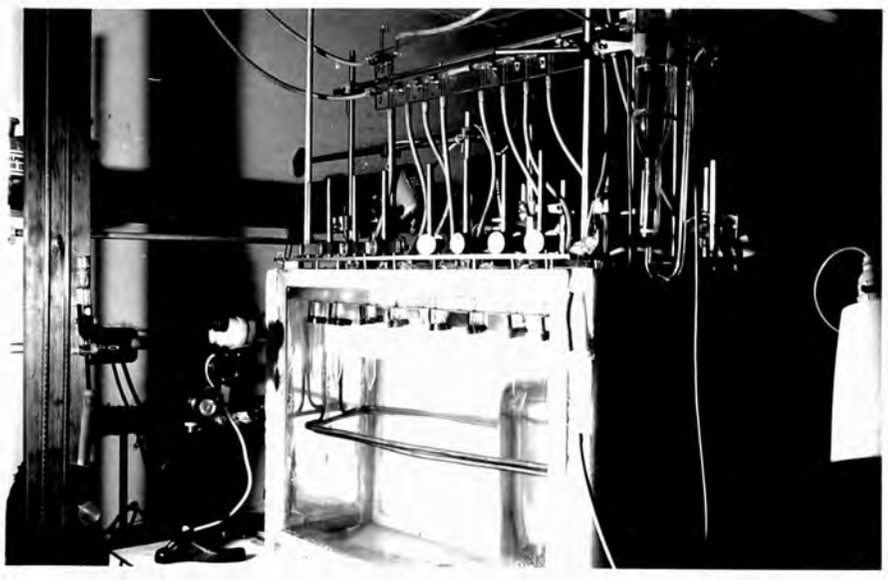


Fig. 2. Cartesian diver respirometry apparatus

pressure change is converted to oxygen consumption at N.T.P. by Boyle's Law

$$\Delta V_{o2} = \frac{V_g \cdot \Delta P}{P_o} \cdot \frac{273}{T^oC}$$

where ΔV_{o2} = Oxygen consumption at N.T.P.

V_g = Volume of diver gas phase

ΔP = Change in pressure

P_o = Normal pressure (10,000 mm. of Brodie's fluid)

T^oC = Temperature in degrees Celsius

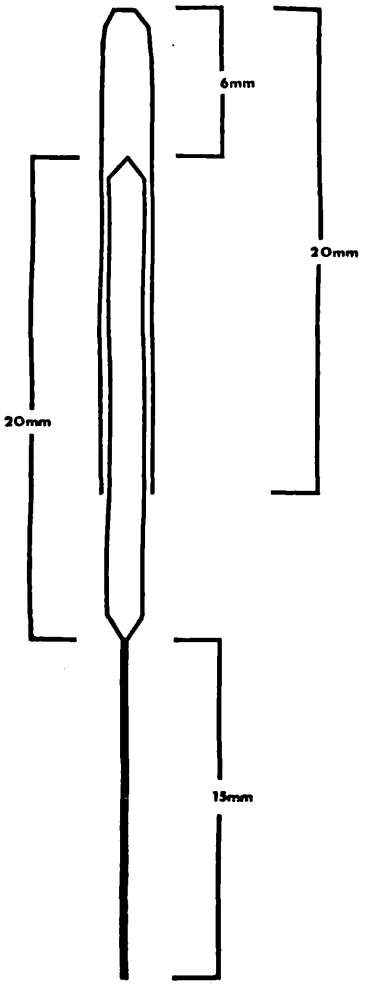
Respiration rates are measured with the diver submerged in 0.1N NaOH in a closed vessel connected by means of a manifold to a manometer. Before loading the vessels with a diver they are flushed through with CO_2-free air. Up to eight vessels can be in operation at any one time since each is separated from the others by a two-way tap. All the vessels are submerged in a constant temperature tank (see Fig 2) with the temperature controlled by a 200 watt carbon filament lamp connected to a mercury contact thermometer. At low temperatures a refrigeration unit operates also. An electrical stirrer ensures uniform temperature throughout the bath and polystyrene sheets improve the insulation so that the temperature is controlled to $\pm$ 0.05°C. Ambient temperature seldom differed from 15°C in the basement where the tank was set up.

Divers were made from the Pyrex capillaries pulled in an oxygen flame from 1 cm. bore glass tubing. The diver must combine sufficient strength to resist constant handling with sufficient lightness to enable it to float with a diver constant small enough to allow accurate measurements of low respiratory rates. Klećkowski (1971) recommends that the ratio between the inner and outer diameters of the diver head be about 0.9, and the ratio between the enclosed gas phase in the diver tail and the diver constant be less than 4 to allow for rapid response to pressure changes.

The divers used in the present work has a gas phase of less than 1ul

CARTESIAN

DIVER



DIMENSIONS OF

HEAD. V_g 0·65 µl.

Internal diameter < 0·6 mm

Length of V_g > Int. diam.

$\frac{\text{Int. diam.}}{\text{Ext. diam.}} \geq 0{\cdot}9$

Fig. 3. Cartesian diver respirometer

and were constructed without the expanded head to reduce the chance of rapidly swimming animals leaving the diver head before the insertion of the gas phase. The reduced gas phase made necessary a modification of the original diver plan according to the proportions shown in Fig 3. The sizes given approximate to those used for divers with a gas phase of 0.625 ul. but the proportions need further modification as the ratio of the internal to external diameter of the Pyrex capillary approaches 0.9.

Divers are usually loaded in two stages, first with the animal, then with the gas phase in a calibrated braking pipette. This method failed due to the rapid movement of the rotifers. A calibrated braking pipette was therefore loaded first with the V_g required to float the diver in use and then an individual or several rotifers were picked up with the same braking pipette. Careful breath control was necessary to prevent excess water being taken into the braking pipette and so overloading the diver head. It was found that a length of water up to 10 mm. containing the rotifers was satisfactory. With more water there is danger of flushing out the rotifer before the air bubble has been inserted, or placing the bubble so low in the diver that its centre of gravity is disturbed and will not float upright.

The length of the air bubble in the braking pipette can be read with an accuracy of $\pm$ 0.25 mm. This introduces errors into the size of the V_g. recorded for the diver, the magnitude of the error varying in proportion to the relative sizes of the V_g. and the calibration of the braking pipette used to load it. Table 2 shows the pipette and diver calibrations used in the present work and the errors involved. The maximum error in the V_g. was $\pm$ 5.0%. Any respiration rates involving a greater error were discarded.

The manometer could be read with an accuracy of $\pm$ 0.5 mm of Brodie's fluid. The smallest pressure change recorded was 12mm giving an error of $\pm$ 4.2%. Therefore the maximum error involved in the respiration rates given was $\pm$ 6.8%. ($\pm \sqrt{e_1^2 + e_2^2}$)

gas diffusion in central run of divers; equilibrium-time

Table 2

$$\% \text{ Error in Diver} = \frac{0.25 \times A}{B} \times 100$$

Length of V_g in pipette	Pipette Calibration (A)	Diver Calibration (B)	% Error in diver
8 mm ± 0.25 mm	0.255	2.04	± 3.13
10	0.161	1.61	2.5
9	0.156	1.42	2.75
9	0.156	1.51	2.58
10	0.166	1.66	2.5
10	0.157	1.57	2.5
45	0.039	1.76	0.55
11	0.154	1.69	2.28
16	0.154	2.46	1.57
20	0.090	1.8	1.25
5	0.154	0.78	4.9
10	0.075	0.75	2.5
15	0.074	1.11	1.67
5	0.125	0.625	5.0
5	0.115	0.575	5.0

Table 3

RESERVOIR DIMENSIONS		
	Q.M.	Q.E.II
Area (hectares)	290	128
Depth (metres)	12	17.2
Volume (m^3)	$30x10^6$	$20x10^6$

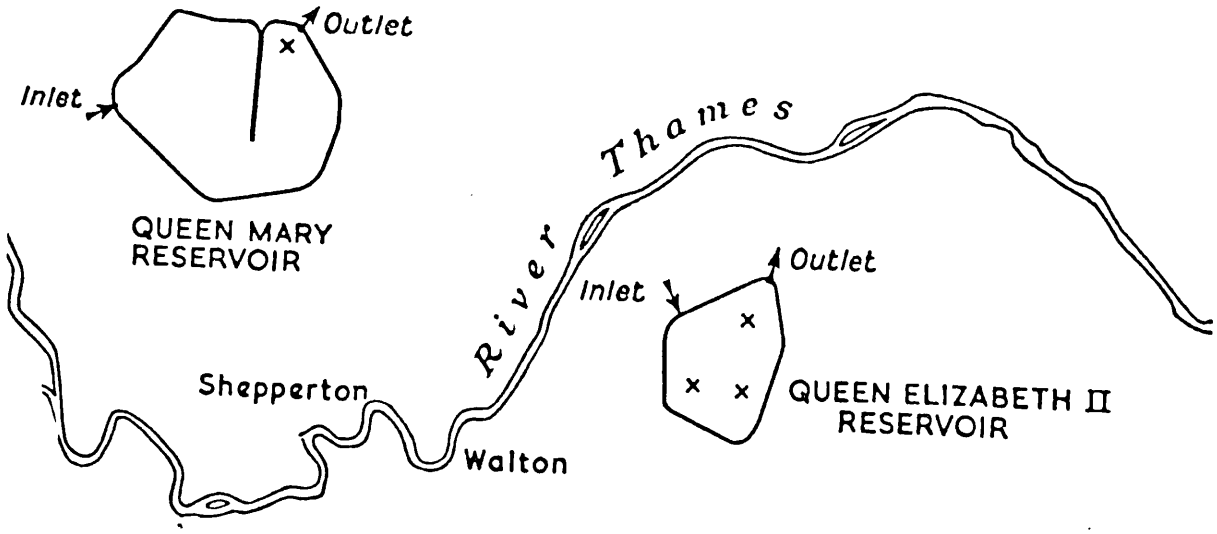

Outlet
Inlet
QUEEN MARY
RESERVOIR
River Thames
Outlet
Inlet
QUEEN ELIZABETH II
RESERVOIR
Shepperton
Walton

Fig. 4. Area surrounding Queen Mary and Queen Elizabeth II reservoirs. (Metropolitan Water Board)

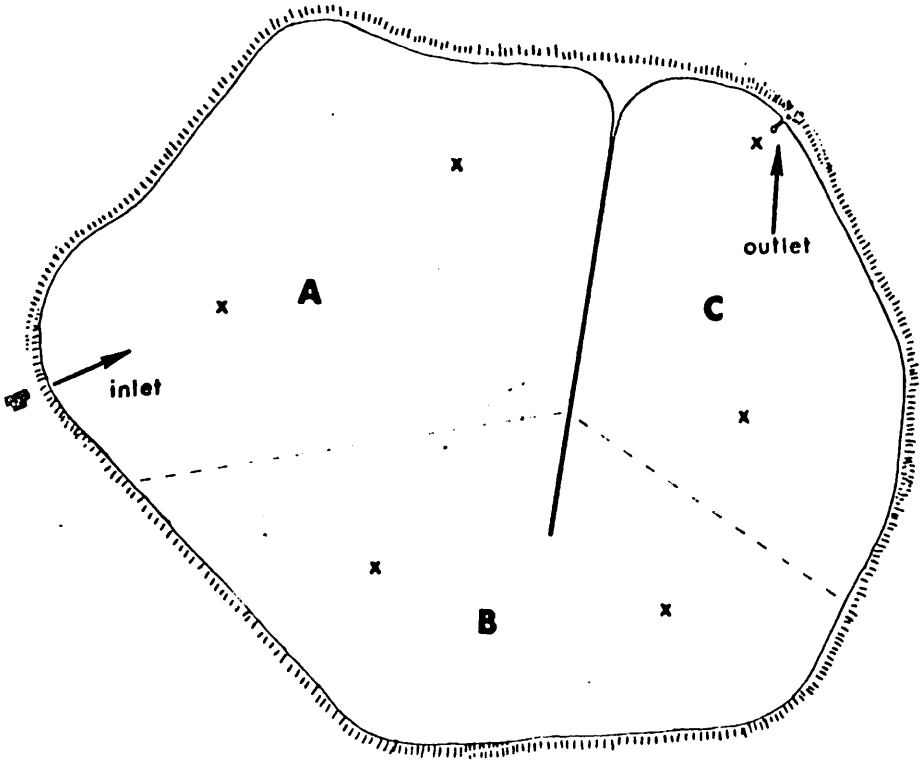

A
B
C
inlet
outlet

Fig. 5. Plan of Queen Mary Reservoir

Description of Sampling sites

The water bodies sampled in this work were the Queen Mary and Queen Elizabeth II reservoirs of the Metropolitan Water Board. They were used by courtesy of the Director of Water Examination and of the Senior Biologist, Dr. J. Ridley, who together with his staff, also provided the physico-chemical data. Their work, together with that of the Senior Assistant Biologist, Mr. A. Steel, who provided phytoplankton data and much helpful advice and discussion, is gratefully acknowledged.

The two reservoirs are in the Thames Valley (Figure 4) and are supplied with water from the River Thames, a eutrophic, calcareous river with the following nutrient levels:

NH_3-N : 0.1 - 2.0 mg/litre; NO_3-N : 5 mg/litre;

ortho phosphate : 1.2 mg/litre; SiO_2 : 15-20 mg/litre;

$CaCo_3$: 250 mg/litre. (Windle-Taylor 1964)

Queen Mary Reservoir (Q.M.)

This was the major supply reservoir of the Metropolitan Water Board and was in constant use during the course of the present work. Its dimensions are given in Table 3. Usually 1% to 2% of the total volume flows in and out daily. Water is pumped in from the R. Thames through submerged pipes and its momentum is slowed by contact with a small wall near the mouths of the pipes. Since the reservoir is shallow but with a large area and a constant flow, it is isothermal for most of the year. A transient thermocline may form in June and July but the stratification is generally restricted to one or two metres from the bottom and no serious deterioration of the water quality occurs. The outlet area of the reservoir (Figure 5) is delimited from the remaining two-thirds of the basin by a baffle. Samples were taken from within this area at the outlet raft. Surveys made with vertical net hauls (60 mesh to the inch) indicated little variation in biomass over the

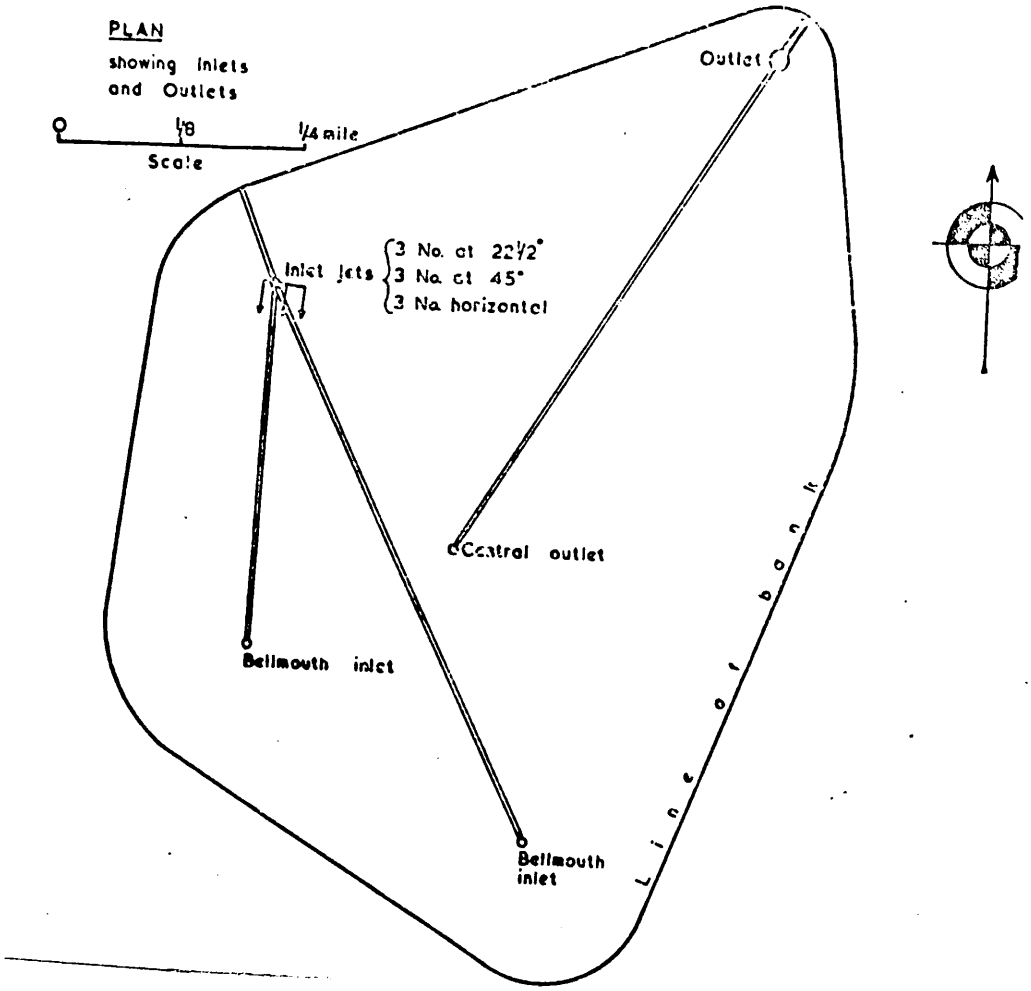
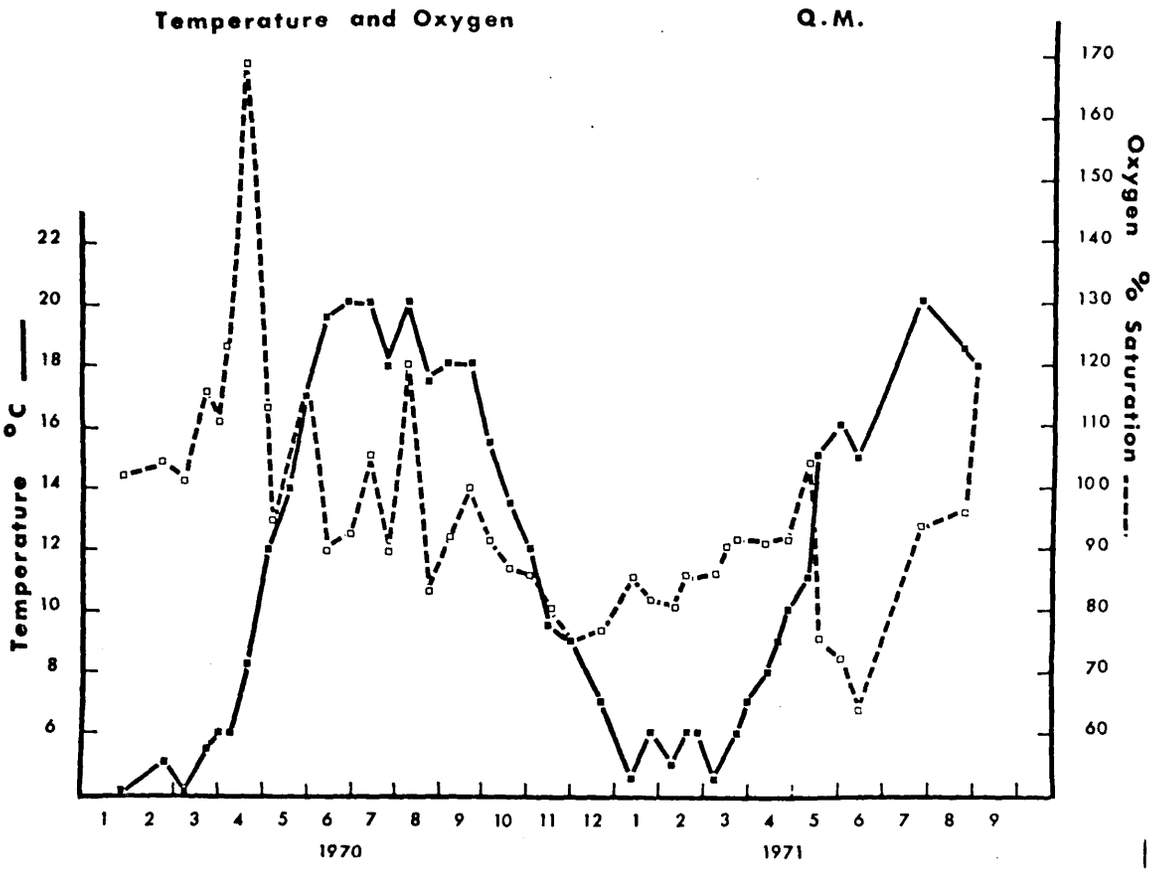

PLAN
showing inlets
and Outlets
1/8
1/4 mile
Scale
Outlet
Inlet jets
3 No. at 22½°
3 No. at 45°
3 No. horizontal
Central outlet
Bellmouth inlet
Bellmouth
inlet
Line of bank

Fig. 6. Plan of Queen Elizabeth II Reservoir

area of the reservoir apart from an increase adjacent to the inlet and a decrease in the area of "dead water" alongside the baffle. (Duncan, Andrew, personal communication) It was considered therefore that samples from the one site would be sufficiently representative of the whole reservoir.

Queen Elizabeth II Reservoir (Q.E.II)

This reservoir also was in constant use during this work with 0.8% to 2.0% of its total volume passing through it each day. Its dimensions are given in Table 3. A specially designed jetting system for introducing water into the reservoir maintains isothermal conditions throughout the year despite the depth of the reservoir. A full description of this jetting system is given in Ridley, Cooley and Steel (1966). With the jets in operation the chances of the same water entering and leaving the reservoir on the same day show a normal distribution, (Steel, personal communication) so that Q.E.II is virtually a homogeneous body of water. The reservoir is an irregular pentagon (Figure 6), and samples were taken from the tower nearest the outlet pier.


Temperature and Oxygen
Q.M.
Temperature °C
Oxygen % Saturation
22
20
18
16
14
12
10
8
6
170
160
150
140
130
120
110
100
90
80
70
60
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

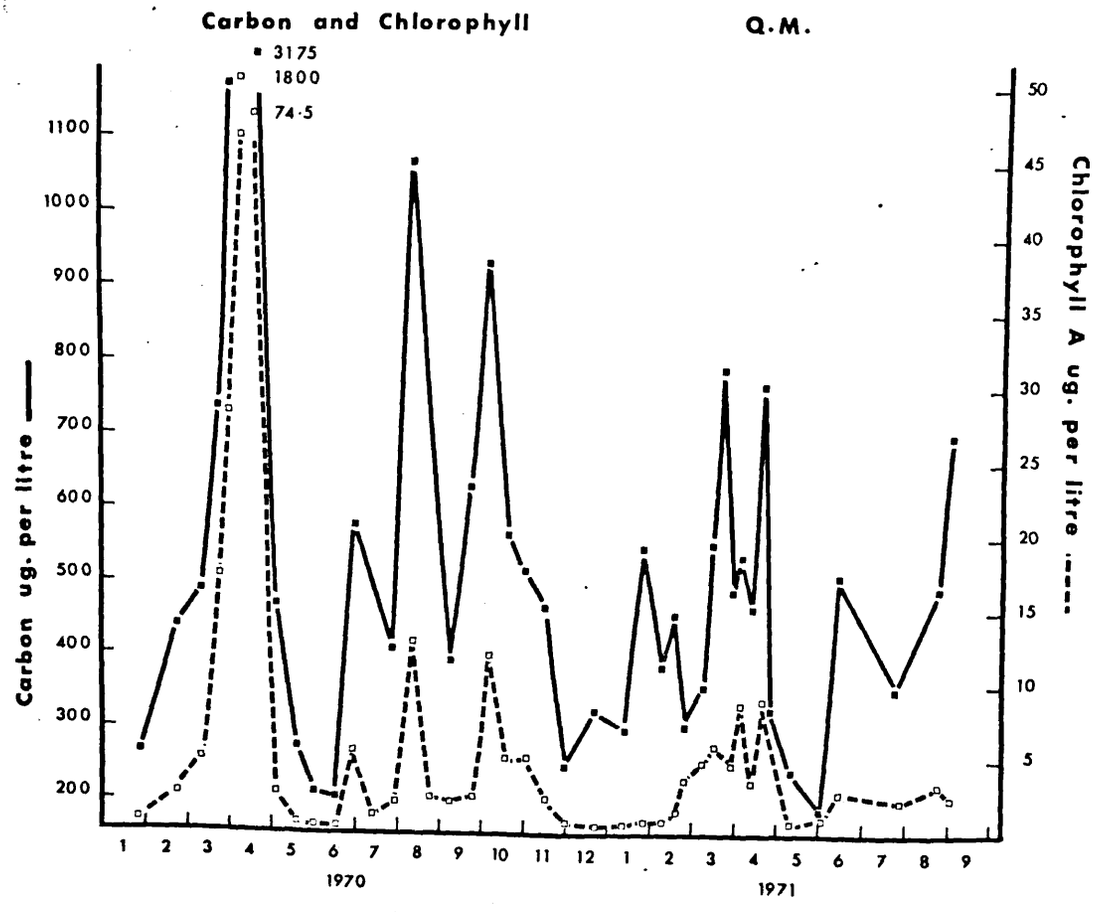

Carbon and Chlorophyll
Q.M.
3175
1800
74·5
Carbon ug. per litre
Chlorophyll A ug. per litre
1100
1000
900
800
700
600
500
400
300
200
50
45
40
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 7. Seasonal variation in temperature and oxygen in Q.M. reservoir.

Fig. 8. Seasonal variation in carbon and chlorophyll A in Q.M. reservoir

PHYSICO-CHEMICAL CHARACTERISTICS OF THE RESERVOIRS

In Figures 7 - 12, some of the physical and chemical characteristics of the two reservoirs which may have some bearing, either directly or indirectly on the rotifer populations are presented graphically. Short comments are included in this section but the interrelationships of these various factors will only be considered in connection with the rotifers which are the subject of this thesis.

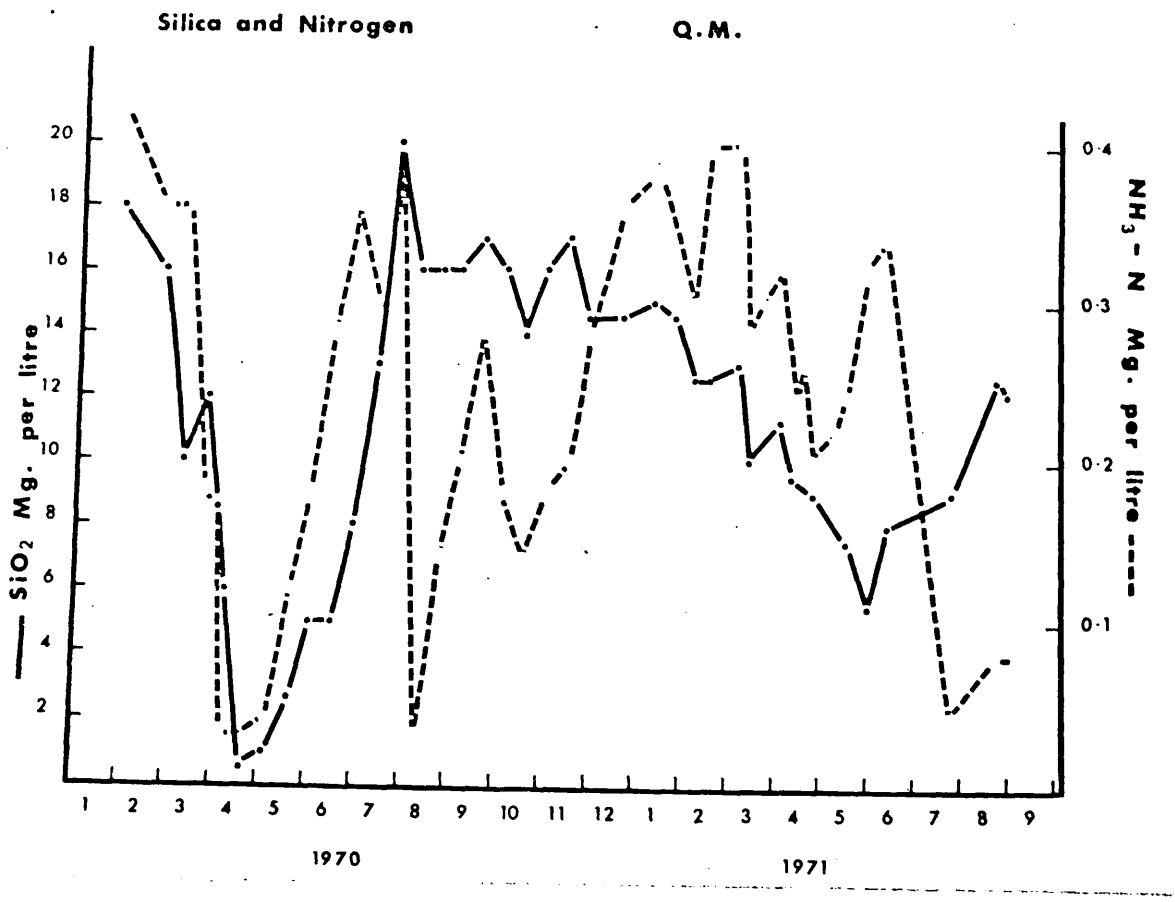
Queen Mary Reservoir

Temperature

Figure 7 shows the seasonal variation in temperature and percentage saturation of dissolved oxygen at 3 metres in Q.M. There was a steady increase in temperature from about 4°C to 20°C. during the spring period of both years followed by a steady decline beginning in August or September. The maximum temperature difference between the top and bottom of the water body in summer of 1970 was 5°C. In summer 1971 it was only 3.5°C. Over the summer months temperature fluctuated around 18°C - 20°C. during 1970 and around 4°C - 6°C. in the winter. In 1971 a temperature of 20°C was reached only in July but the steady increase over the spring period was still clearly defined.

Dissolved oxygen

Dissolved oxygen never fell below 60% saturation and a super-saturation value of 168% occurred in April 1970. During the summer, the value for the hypolimnion, that is below 10m, went as low as 5% but the epilimnion remained at over 80% saturation. The highest value recorded for April 1971 was only 99% but correspondingly the hypolimnion in June never had a value below 15% saturation and this was recorded only on one occasion (June 7th). In August/ September of both years values about 120% were recorded.


Silica and Nitrogen
Q.M.
— SiO_2 Mg. per litre
---- NH_3 - N Mg. per litre
1970
1971

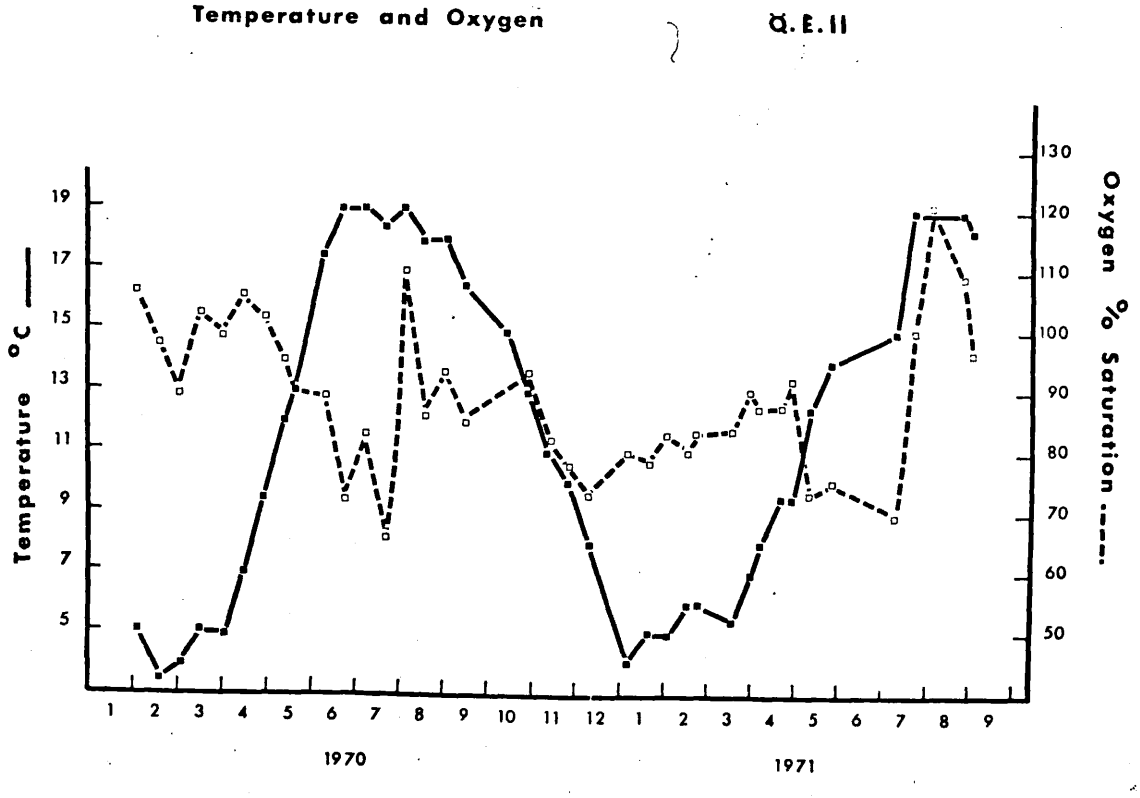

Temperature and Oxygen
Q.E.II
Temperature °C ——
Oxygen % Saturation ----
1970
1971

Fig. 9. Seasonal variation in silica and ammonia nitrogen in Q.M. Reservoir.

Fig. 10. Seasonal variation in temperature and oxygen in Q.E.II reservoir.

Carbon

Peak carbon concentrations (Fig. 8) occurred coincident with the higher values of dissolved oxygen during March/April of both years but the highest recorded value in spring 1970 was 3175ug/litre compared with only 770 ug. the following year. A second peak occurred in August 1970 with a smaller one two months later. There were also indications of this condition in October 1971 when the present study was terminated.

Chlorophyll A

Figure 8 also shows the amount of chlorophyll A in ug./litre. The spring peak coincided with the carbon and dissolved oxygen peaks in 1970 but no significant peak occurred in spring 1971. August and October 1970 had values of 12.98 ug. and 12.014 ug. per litre of chlorophyll A, coinciding with high carbon values and with increases in dissolved oxygen concentration. (Fig 7)

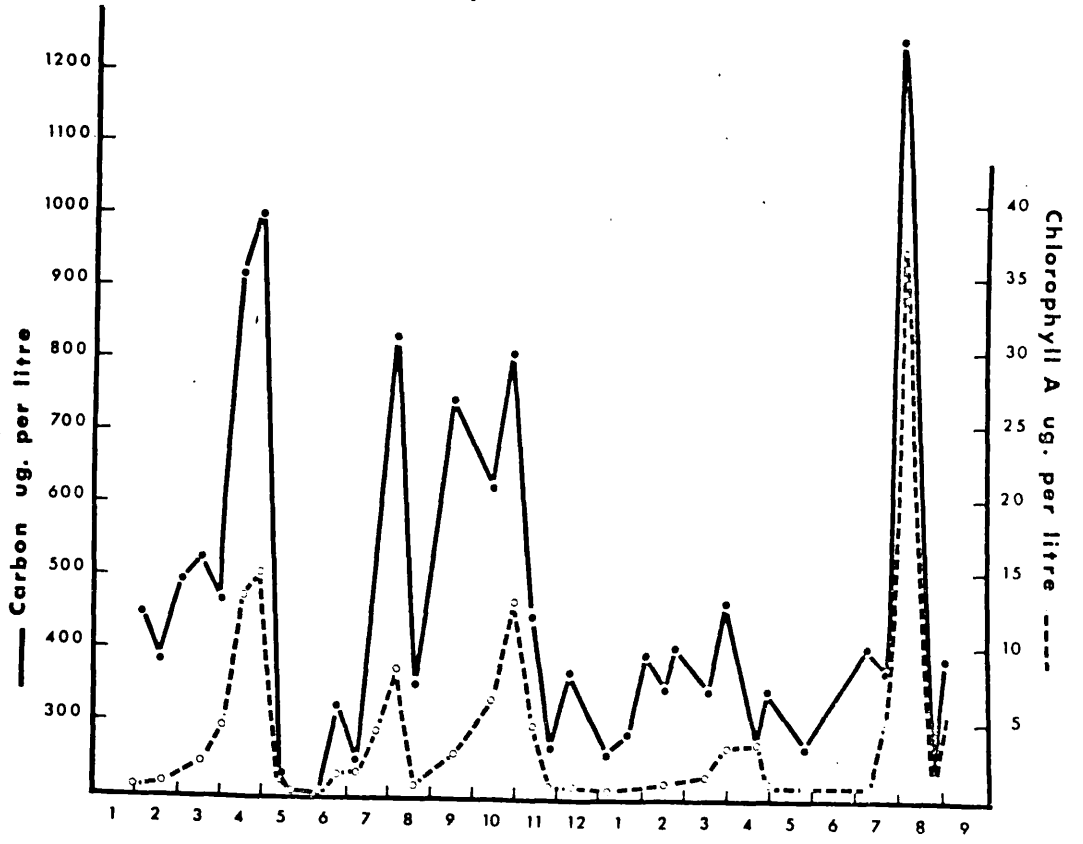
Silicon dioxide

Concentrations of silicon dioxide (Fig. 9) were fairly high throughout the year with a markedly low value of 0.5 mg./litre in April 1970. Such a low value was not repeated during the following year when the minimum recorded in April was 9.0 mg./litre, but the spring minimum, 5.5 mg. occurred later, at the beginning of June.

Ammonia nitrogen

The lowest recorded value of ammonia nitrogen (Fig. 9) occurred in April 1970 just prior to the minimum silicon dioxide concentration. Recovery paralleled that of silica concentration but slightly preceded it, and another low value was recorded in August bearing no relationship with the silica concentration. The following year the minimum spring value was 0.20 mg./litre, more than six times that of 1970, and again it preceded the silica minimum by about four to five weeks. July 1971 showed another low value corresponding to the August minimum of the previous year.

Carbon and Chlorophyll **Q.E.II**



Silica and Nitrogen **Q.E.II**

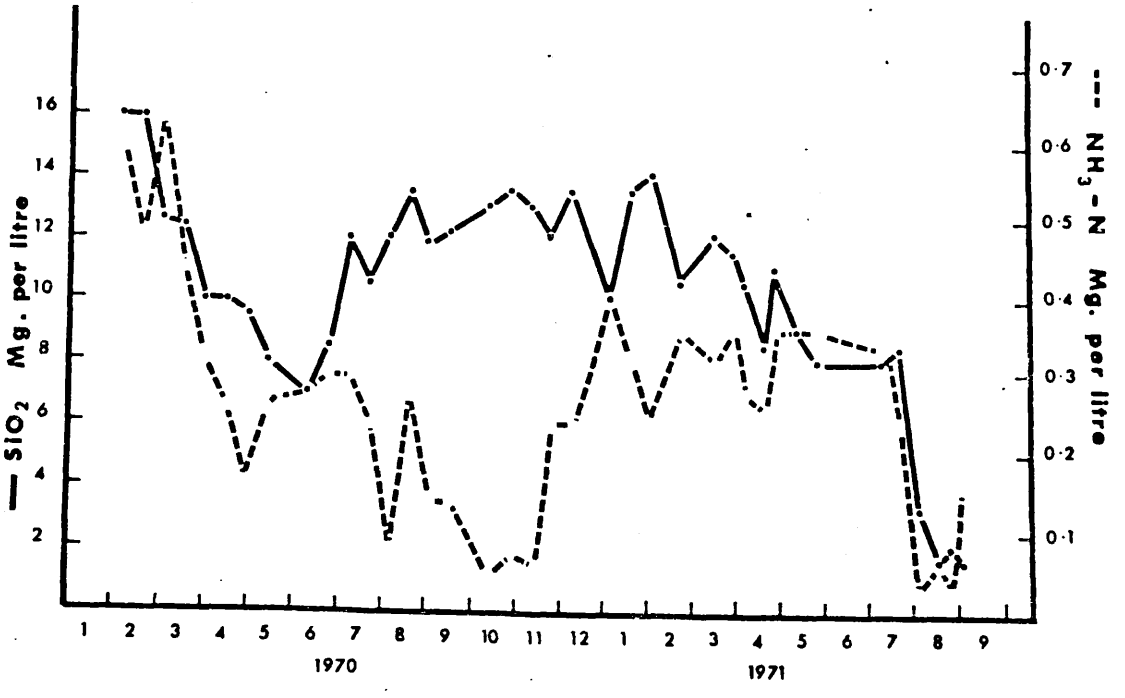


Fig. 11. Seasonal variation in carbon and chlorophyll A in Q.E.II reservoir.

Fig. 12. Seasonal variation in silica and ammonia nitrogen in Q.E.II reservoir.

Queen Elizabeth Reservoir

Temperature

The seasonal variation in temperature is virtually the same for this reservoir as for Q.M. at 3 metres. (cf. Fig. 10 and Fig 7) but the maximum recorded difference in temperature between the top and the bottom in June was only 2°C in 1970 and 1°C in 1971. For the rest of the year isothermal conditions prevailed.

Dissolved oxygen

Though the percentage saturation never fell below 70% (Fig. 10) and the winter values for 1970-1971 were very similar to those of Q.M., the exceptionally high value obtaining in Q.M. in April 1970 (Fig. 7) did not occur in Q.E.II. The highest recorded value was 105.4% in the middle of April 1970, and in April 1971 the highest value was 92%. In both years the highest overall values were recorded in August, 110% in 1970 and 121% in 1971.

Carbon

The peak carbon value (Fig. 11) for 1970 occurred during April and was about 1,000 ug./litre, which was only on third that of Q.M. shown in Fig. 8. In the autumn of 1970 this discrepancy was not so marked but higher values were still recorded in Q.M. In 1971, the spring peak of carbon hardly occurred at all in Q.E.II, the highest value being 460 ug./litre at the end of March, but 1,235 ug./litre were recorded in August of that year.

Chlorophyll A

Peaks of chlorophyll A coincided with those of carbon concentration with again a notable absence of a spring peak in 1971. The highest value obtained over the sampling period was 37.9 ug./litre during August 1971. (Fig. 11)

Silicon dioxide

The silica concentration (Fig 12) was consistently higher in Q.E.II

than in Q.M., with only a slight fall in concentration during May and June of both years. From July 1970 to January 1971, the concentration in Q.E.II remained slightly but consistently below that of Q.M. but from January to July 1971, the values were very similar in both reservoirs. The slight increase in concentration noted in Q.M. in August did not occur in Q.E.II where instead there was a significant fall in concentration to only 1.7 mg/litre, the lowest value recorded in this reservoir during the sampling period.

Ammonia nitrogen

Apart from the minimum values recorded in April and August 1970 in Q.M., the nitrogen concentration was consistently lower in Q.E.II. The lowest recorded values were in August 1971 and also October 1970, but the highest concentration recorded, 0.64 in March 1970, was never approached again during the period investigated.

SESTON DATA

The data in this section, some of which is presented graphically in Fig. 13 and 14, was kindly provided by Mrs. J. Nadin-Hurley during her tenure of a N.E.R.C. research assistantship for work on zooplankton feeding in the reservoirs. Her work is gratefully acknowledged.

Counts were made on a Wild inverted microscope after sedimentation of sub-samples with Lugol's iodine. Different magnifications and dilutions were used according to the size and concentration of the particles being counted. At least one hundred particles were counted in each case. (Lund, Kipling and LeCren 1958). Tables 8 - 11 contain counts per ml. of sections of the total seston selected on the basis of size and/or edibility using the criteria of Gliwicz (1969) and Edmondson (1965).

Queen Mary

Flagellates

Table 8 gives the number per ml. of the components of the flagellate population of the Q.M. reservoir. Rhodomonas spp., Cryptomonas spp. and some small flagellates less than 3u in diameter formed the major components with Dinobryon sp. and Synura sp. occasionally appearing in the samples. The small flagellates may be gametes or zoospores of other algae but so far they have not been identified with certainty. They formed the principal component of the phytoplankton in February and March of both years but were absent at other times of the year.

The populations of Rhodomonas and Cryptomonas fluctuated somewhat throughout the year with the highest numbers occurring during the period when small flagellates were dominant, and also in September 1970.

Detritus

The amount of detritus was assessed on particle number rather than size and it was classified into several groups according to its appearance. The

flocculent detritus (Table 9) consisted of small particles from 1-5 u in diameter which were capable of aggregating into larger clumps. This was the main constituent of the total detritus which also comprised black, particulate matter and some hyaline fractions.

The largest amount of detritus assessed as particles per ml. was recorded at the beginning of April 1970, but apart from this the fluctuations are fairly irregular with very low values in June of both years.

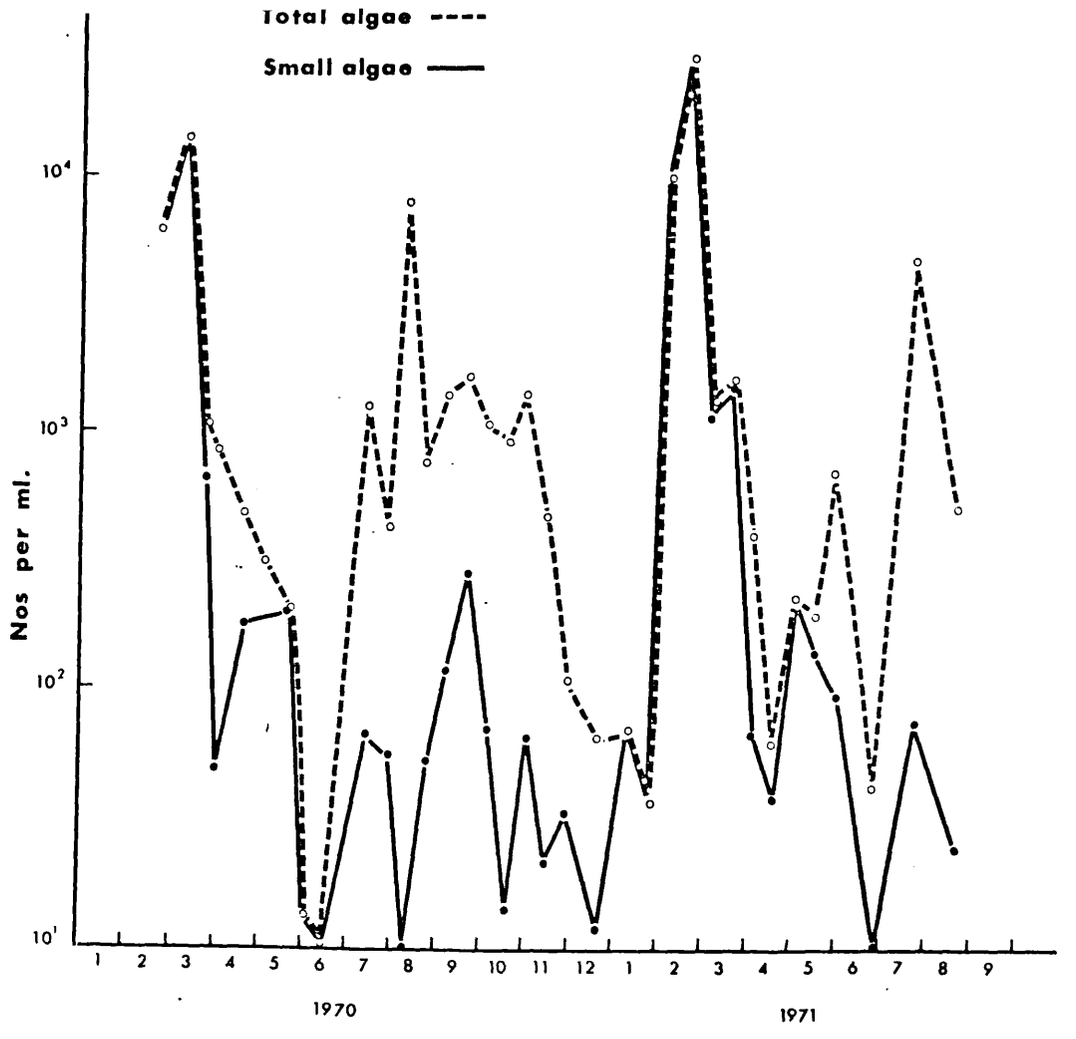
Total phytoplankton

At periods when the small flagellates were dominant, total algal counts were numerically the highest of the year but other high values occurred in August 1970 and in July 1971 when Tribonema bombycinum was an important component of the phytoplankton. September and October 1970 had algal counts greater than 1,000 cells per ml. at a time when the blue-green algae, Anabaena spp. dominated the phytoplankton with Tribonema and Microcystis aeruginosa and was joined later by the diatom Melosira sp. The spring diatom bloom in 1970 developed in March and persisted throughout April. It was dominated by Stephanodiscus astraea but Asterionella formosa and S. hantzchii also occurred. These three diatoms were present in 1971 but nc large bloom occurred. (Fig. 13)

Zooplankton

Studies on the zooplankton other than rotifers have been undertaken in recent years by Dr. A. Duncan, G. Cremer, and T. Andrews. A species list was given in the 41st M.W.B. Report for the period prior to 1964. Since then a change in dominance seems to have occurred from Daphnia hyalina to the larger D. magna and D. pulex. (A. Duncan, personal communication). Cyclops vicinus was the dominant predatory zooplankter but Leptodora kindtii appeared in a few samples in the summer.

JULY - SEPT


Total algae ----
Small algae ——
Nos per ml.
10^4
10^3
10^2
10^1
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Q.E.II

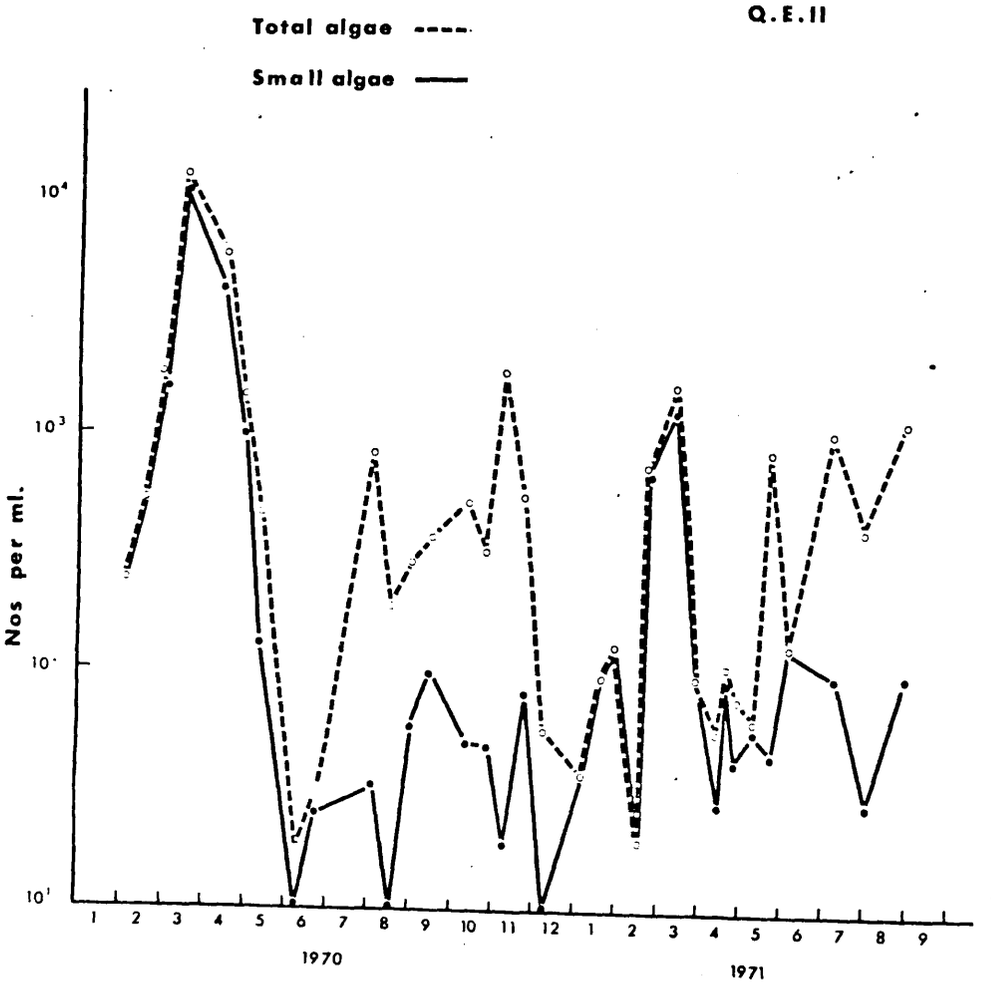

Total algae ----
Small algae ——
Nos per ml.
10^4
10^3
10^2
10^1
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 13. Seasonal variation in total algae and small algae in Q.M. reservoir.

Fig. 14. Seasonal variation in total algae and small algae in Q.E.II reservoir.

Queen Elizabeth II

Flagellates

Table 10 gives the numbers per ml. of the flagellate population of Q.E.II. February and March 1970 presented a similar picture in this reservoir to that in Q.M. but counts for the following year were lower by one or two orders of magnitude due mainly to a failure of the small flagellates to reach their usual peak. Rhodomonas spp. reached similar values in spring 1971 as in the previous year but Cryptomonas spp. were considerably fewer in number throughout 1971.

Detritus

Though overall the detritus values in Q.E.II were slightly higher than in Q.M., the large quantities recorded in Q.M. 1970 did not occur in Q.E.II. The highest value recorded was 23,174 particles per ml. in March 1971, but for the rest of the year, apart from significantly low values in June 1970 and May 1971, the amount of detritus showed irregular fluctuations.

Total phytoplankton

Apart from the occasions when the total phytoplankton reflected the number of small flagellates, the numbers shown in Table II were at their highest in November 1970 and July and September 1971. The November peak the blue-green algae Anabaena spp. and Microcystis aeruginosa which were probably partly responsible for the high numbers in July also. In July and September, the filamentous Xanthophyte, Tribonema bombycinum was dominant. As in the Q.M., the diatom bloom in spring was dominated by Stephanodiscus astraea and Asterionella formosa with Melosira sp. appearing in autumn (Fig. 14)

Zooplankton.

Zooplankton composition was similar in both reservoirs.

Table 4

Physico-chemical data for Q.M. Reservoir at 3m.

Date	Temperature °C	Dissolved % Saturation	Oxygen mg/litre
26/1	4	102	12.6
23/2	5	104	12.8
9/3	4	102	12.8
23/3	5.5	116	14.1
1/4	6	111	13.2
7/4	6	123	14.6
20/4	8.5	168	19.3
4/5	12	113	11.9
19/5	14	94	9.4
1/6	17	115	10.9
15/6	19.5	90	7.2
29/6	20	93	8.3
13/7	20	105	9.4
27/7	18	90	8.3
10/8	20	120	10.8
24/8	17.5	83	7.8
7/9	18	92	7.8
21/9	18	100	11.0
5/10	15.5	91	8.9
19/10	13.5	87	8.9
2/11	12	86	9.1
16/11	9.5	80	8.9
30/11	9	75	8.5
21/12	7	77	9.1
12/1	4.5	85	10.6
25/1	6	82	10.3
9/2	5	81	10.0
18/2	6	85	10.3
25/2	6		
8/3	4.5	86	10.7
15/3	5	90	10.8
22/3	6	91	11.0
30/3	7	84	9.9
5/4	7.5	91	10.6
13/4	8	92	10.6
20/4	9	91	10.3
26/4	10	99	10.8
10/5	11		
17/5	15	75	7.4
1/6	16	72	7.0
14/6	15	64	6.4
26/7	20	93	8.4
23/8	18.5	96	8.8
2/9	18	119	11.0

Table 5

Physico-chemical data for Q.M. Reservoir at 3m.

Date	SiO_2 mg/litre	Carbon ug/litre	Chlorophyll A ug/litre	NH_3-N mg/litre
26/1	18	271.5	0.502	0.44
23/2	16	441.17	2.612	0.36
9/3	10	489.34	4.925	0.36
23/3	12	791.17	17.4	0.18
1/4	8.5	1151.67	28.45	0.17
7/4	6	1800	47.47	0.03
20/4	0.5	3175	74.57	0.03
4/5	1.0	471.67	2.682	0.04
19/5	2.7	273.34	0.614	0.12
1/6	5	216.7	0.3	0.18
15/6	5	209.17	0.463	0.28
29/6	8	580.84	5.38	0.36
13/7	16		1.49	0.03
27/7	20	408.34	2.053	0.38
10/8	16	1046.7	12.98	0.03
24/8	16		2.395	0.14
7/9	16	396	2.122	0.20
21/9	17	629.7	2.528	0.28
5/10	16	912.5	12.014	0.18
19/10	14	565.84	4.902	0.14
2/11	16	518	5.045	0.18
16/11	17	468	2.15	0.20
30/11	14.5	254.17	0.737	0.28
21/12	14.5	324.5	0.52	0.36
12/1	15	304	0.57	0.38
25/1	14.5	549	0.88	-
9 /2	12.6	385	0.89	0.30
18/2	12.6	459	1.44	0.40
25/2		303	3.77	-
8/3	13	360	4.85	0.40
15/3	10	557	5.94	0.28
22/3		770	5.5	0.30
30/3		487	4.9	-
5/4	11.4	534	8.67	0.32
13/4	9.5	465	3.4	0.24
20/4	9.3	745	9.08	0.26
26/4	9	331		0.20
10/5		243	0.70	0.22
17/5	7.5			0.24
1/6	5.5	195	1.29	0.32
14/6	8.0	510	2.85	0.34
26/7	9.0	355	2.37	0.04
23/8	12.6	490	3.34	0.08
2/9	12.2	680	2.65	0.08

Table 6

Physico-chemical data for Q.E.II Reservoir at 3m.

Date	Temperature °C	Dissolved % Saturation	Oxygen mg/litre
4/2	5	106	13
18/2	3.5	98	12.4
2/3	4	89.6	11.4
16/3	5	102.8	12.7
1/4	5	99.8	12.2
15/4	7	105.4	12.5
29/4	9.5	102	11.4
13/5	12	95	10.2
20/5	13	90	9.2
10/6	17.5	89.4	8.5
24/6	19	72	6.6
8/7	19	83	7.5
22/7	18.5	66.4	6.2
5/8	19	110	10
19/8	18	86.4	8
2/9	18	93	8.6
16/9	16.5	85.4	8
14/10	15	99	9.8
28/10	13	93	9.6
12/11	11	82	9.0
25/11	10	78	8.6
9/12	8	73	8.3
6/1	4	80	10.0
20/1	5	79	9.7
3/2	5	83	10.2
17/2	6	81	9.8
24/2	6	83	10
17/3	5.5	84	10.3
31/3	7	90	10.7
7/4	8	88	10.3
21/4	9.5	88	9.8
28/4	9.5	92	10.3
12/5	12.5	73	7.6
26/5	14	75	7.6
9/7	15	70	7.0
21/7	19	100	9.1
4/8	19	121	11.0
18/8	19		12.6
25/8			
1/9	18.5	97	8.9

Table 7

Physico-chemical data for Q.E.II Reservoir at 3m.

Date	SiO_2 mg/litre	Carbon ug/litre	Chlorophyll A ug/litre	NH_3-N mg/litre
4/2	16	452.28	0.633	0.60
18/2	16	386.29	0.823	0.48
2/3	12.6	496.71	1.423	0.64
16/3	12.4	525.14	2.434	0.44
1/4	10	469	4.944	0.32
15/4	10	915.14	13.8	0.26
29/4	9.5	999.28	15.143	0.16
13/5	8	231.43	0.854	0.26
20/5	7.7	203.43	0.816	0.27
10/6	7	166.67	0.4	0.28
24/6	8.5	326.43	1.578	0.32
8/7	12	250	1.706	0.32
22/7	10.5		4.55	0.24
5/8	12	830.57	8.914	0.08
19/8	13.5	355.57	0.79	0.28
2/9	11.8			0.14
16/9	12.2	742.286	3.094	0.14
14/10	13	624.28	6.756	0.04
28/10	13.5	808.57	13.26	0.07
12/11	13	447	4.98	0.60
25/11	12	286	0.934	0.24
9/12	13.5	371	0.864	0.24
6/1	10	261	0.46	0.40
20/1	13.5	285	0.59	0.32
3/2	14	396	0.83	0.24
17/2		348	0.91	
24/2	10.5	400	1.31	0.36
17/3	12	345	1.38	0.32
31/3	11.5	460	3.47	0.36
7/4	10.5			0.28
21/4	8.5	275	3.79	0.26
28/4	11.0	342	1.08	0.36
12/5	9			0.36
26/5	8.0	270	0.83	0.36
9/7	8.0	400	0.78	0.34
21/7	8.4	370	5.1	0.24
4/8	3.3	1235	37.9	0.03
18/8	1.7			0.06
25/8		240	1.10	0.03
1/9	1.7	392	6.05	0.16

Table 8

Seston Data for Q.M. Reservoir (Nos. per ml)

Date	Small flagellates	Rhodomonas	Cryptomonas	Total flagellates
23/2	6,030	190	-	6220
9/3	14,400	109	18	14532
23/3	217	183	106	512
1/4	49	-	-	49
7/4				
20/4	23	112	31	176
4/5				
19/5		98	34	161
1/6		11	2	13
15/6				
29/6				
13/7		42	12	64
27/7		35	20	55
10/8				
24/8		39	13	52
7/9		96	20	116
21/9		192	82	274
5/10		58	12	70
19/10		12	2	14
2/11		35	17	61
16/11		13	4	19
30/11		20	11	33
21/12		9	3	12
12/1	45	19	2	66
25/1		20	11	31
9/2	9,600	-	3	9694
22/2	28,100	32	62	28194
25/2				
8/3	42	364	55	487
11/3				
22/3	670	684	14	1390
30/3				
5/4	47	4	6	57
8/4				
19/4		18	8	26
22/4				
29/4				
6/5	42	114	10	166
17/5		88	17	105
1/6		30	1	41
28/6		6		6
26/7		42	30	72
23/8		14	10	24
6/9				

Table 9

Seston Data for Q.M. Reservoir

Date	Flocculent Detritus	Total Detritus	Small Diatoms	Total small algae	Total algae
23/2	1340	1945	93	6313	6350
9/3	870	1301	364	14896	14911
23/3	2380	3645	161	673	1084
1/4	15650	21695		49	859
7/4					
20/4	3920	5453		176	492
4/5	4240	6382			311
19/5	7960	11408	37	198	204
1/6	570	910		13	13
15/6	86	129		0	2
29/6					
13/7	480	715		64	1264
27/7	900	1420		55	403
10/8	1020	1449		0	7948
24/8	1300	1766		52	750
7/9	1490	2670		116	1392
21/9	2980	3600		274	1611
5/10	1920	2420		70	1062
19/10	2220	2690		14	929
2/11	1230	1840	4	65	1349
16/11	1950	2320	2	21	472
30/11	2690	3910		33	109
21/12	3720	4180		12	64
12/1	1150	1439		66	66
25/1	134	545	6	37	38
9/2	2980	3073	94	9788	9795
22/2	3370	7060	58	28252	28257
25/2					
8/3	2662	4038	638	1125	1216
11/3					
22/3	2772	3973	53	1443	1528
30/3					
5/4	420	514	10	67	396
8/4					
19/4	1220	1747	12	38	59
22/4					
29/4					
6/5	1540	1924	48	214	214
17/5	4520	7257	33	138	197
1/6	346	455	53	94	683
28/6	1450	5933		6	40
26/7	1175	2606		72	4062
23/8	4050	6025		24	488
6/9					

Table 10

Seston Data for Q.E.II Reservoir

Date	Small flagellates	Rhodomonas	Cryptomonas	Total flagellates
4/2	127	48	21	196
18/2	340	35	12	387
2/3	1240	92	47	1407
16/3	10600	67	32	10714
3/4				
13/4	3900	103	49	4078
29/4	624	124	61	848
11/5	24	21	6	53
22/5				
8/6		3	2	5
22/6		20	5	25
8/7				
20/7				
3/8		29	4	33
17/8		-	6	6
1/9		39	12	58
15/9		62	24	99
12/10		30	14	50
26/10		42	5	49
9/11		14	3	19
24/11		49	21	81
8/12		3	2	7
6/1	22	13	2	37
20/1	42	35	18	95
2/2	25	33	12	70
17/2	-	12	-	12
25/2	430	91	37	568
15/3	700	96	20	821
29/3	60	30	-	95
15/4	-	11	7	19
22/4	27	23	14	64
27/4	37	3	-	40
11/5	5	28	12	45
24/5	-	13	3	16
7/6	21	35	-	56
19/7		58	10	68
2/8		22	6	28
16/8				
1/9		80	15	95

Table 11

Seston Data for Q.E.II Reservoir

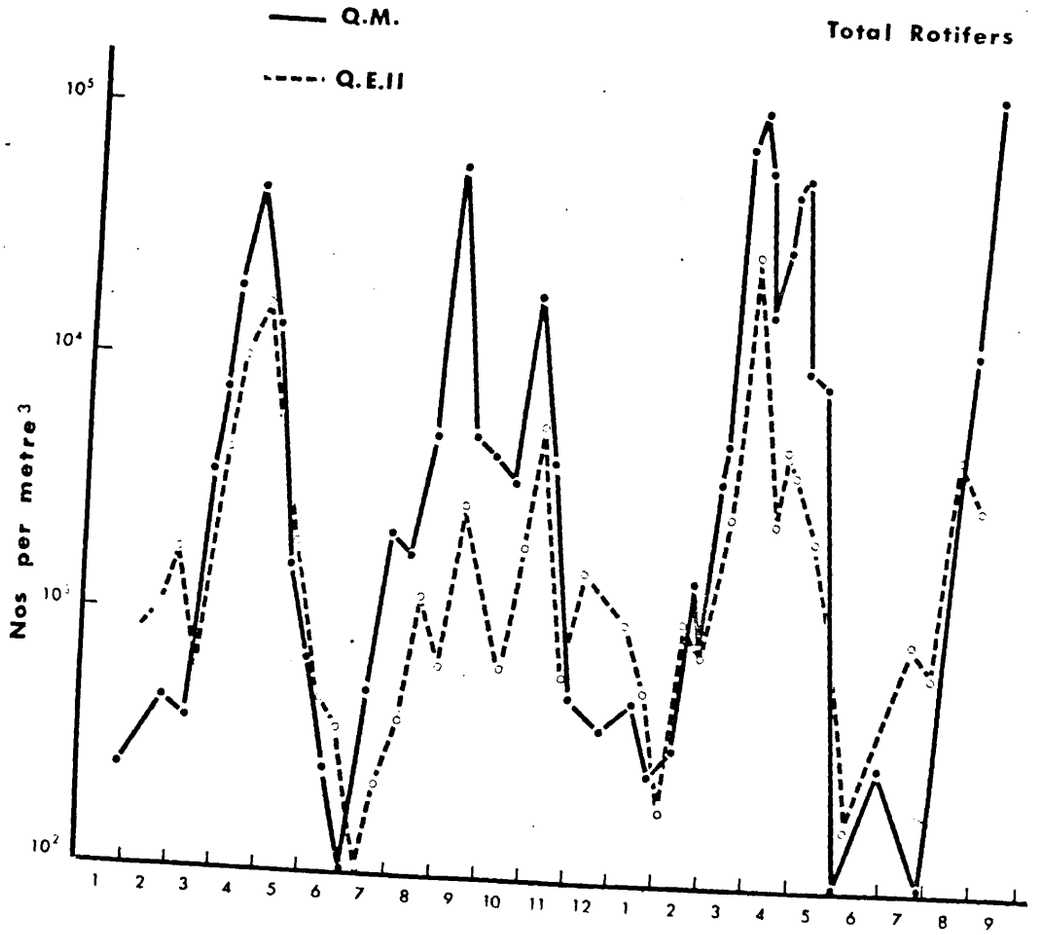
Date	Flocculent Detritus	Total Detritus	Small Diatoms	Total small algae	Total algae
4/2	2502	2712	49	245	245
18/2	2133	2400	130	517	526
2/3	2330	2890	169	1576	1747
16/3	2440	3027	247	10961	11558
3/4					
13/4	3570	4180	198	4276	5944
29/4	3690	4491	152	1000	1506
11/5	4120	5906	77	130	475
22/5					
8/6	90	136		5	17
22/6	230	334		25	31
8/7					
20/7					
3/8	1040	1186		33	859
17/8	2350	3362		6	187
1/9	3100	3560		58	290
15/9	2400	3300		99	360
12/10	430	920		50	530
26/10	690	1250		49	320
9/11	2900	3500		19	1850
24/11	3620	4890		81	550
8/12	2200	2700		7	57
6/1	990	1149		37	37
20/1	2010	2406		95	95
2/2	960	1071	54	124	124
17/2	3690	5000	8	20	20
25/2	936	1074	107	675	733
15/3	2400	3087	465	1286	1546
29/3	14933	23174	-	95	95
15/4	1080	1240	9	28	56
22/4	1240	1760	26	90	104
27/4	2660	2948	2	42	78
11/5	1080	1513	10	55	63
24/5	79	117	29	45	843
7/6	1760	2252	72	128	128
19/7	1490	2260	29	97	1019
2/8	3325	4653		28	404
16/8					
1/9	4975	7477		95	1151

Standing Crop and Occurrence of Rotifers

In the course of this work, twenty species of rotifers were found in the two reservoirs investigated, of which one species, Conochilus unicornis was confined to Q.E.II. (Table 12) The standing crop of the majority of these species was so low as to prevent statistically significant comparisons of their abundance (Table 13). Only six species have therefore been selected for detailed study, the others being included in total standing crop data. All the species found were Monogononta, rotifers in which a sexual, mictic phase may occur in a generally asexual, amictic life cycle. Birky and Gilbert (1971) have summarised the general conclusions of recent reviews of the control of mixis. (See also Pourriot 1965a), Hutchinson 1967), and Wesenberg-Lund (1930) points out that generally pelagic lake rotifers have a sexual period following a population maximum. Of the six species selected for detailed study, only one, Polyarthra vulgaris appeared to have a sexual phase. This occurred in autumn at the time of peak population density. For this species, numbers of mictic females have been included in population estimates, but the number of eggs per female was calculated from amictic eggs only.

Total rotifer population

Figure 15 represents the standing crop of rotifers per cubic metre in the two reservoirs. Peak numbers occurred in late April or early May, and again in September to November. The spring peak consisted largely of Synchaeta oblonga, Synchaeta pectinata, Keratella cochlearis, Keratella quadrata, Polyarthra vulgaris, and Asplanchna priodonta, but the species diversity (Table 13) was also increased so that the rotifer population besides being at its most numerous was also most varied. The autumn peak consisted of fewer species and was dominated by Polyarthra vulgaris, Keratella quadrata and, in Q.M. only, Synchaeta pectinata. In September, Pompholyx sulcata was present in both reservoirs in fairly high numbers, and Conochilus


Q.M.
Q.E.II
Total Rotifers
Nos per metre³
10⁵
10⁴
10³
10²
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

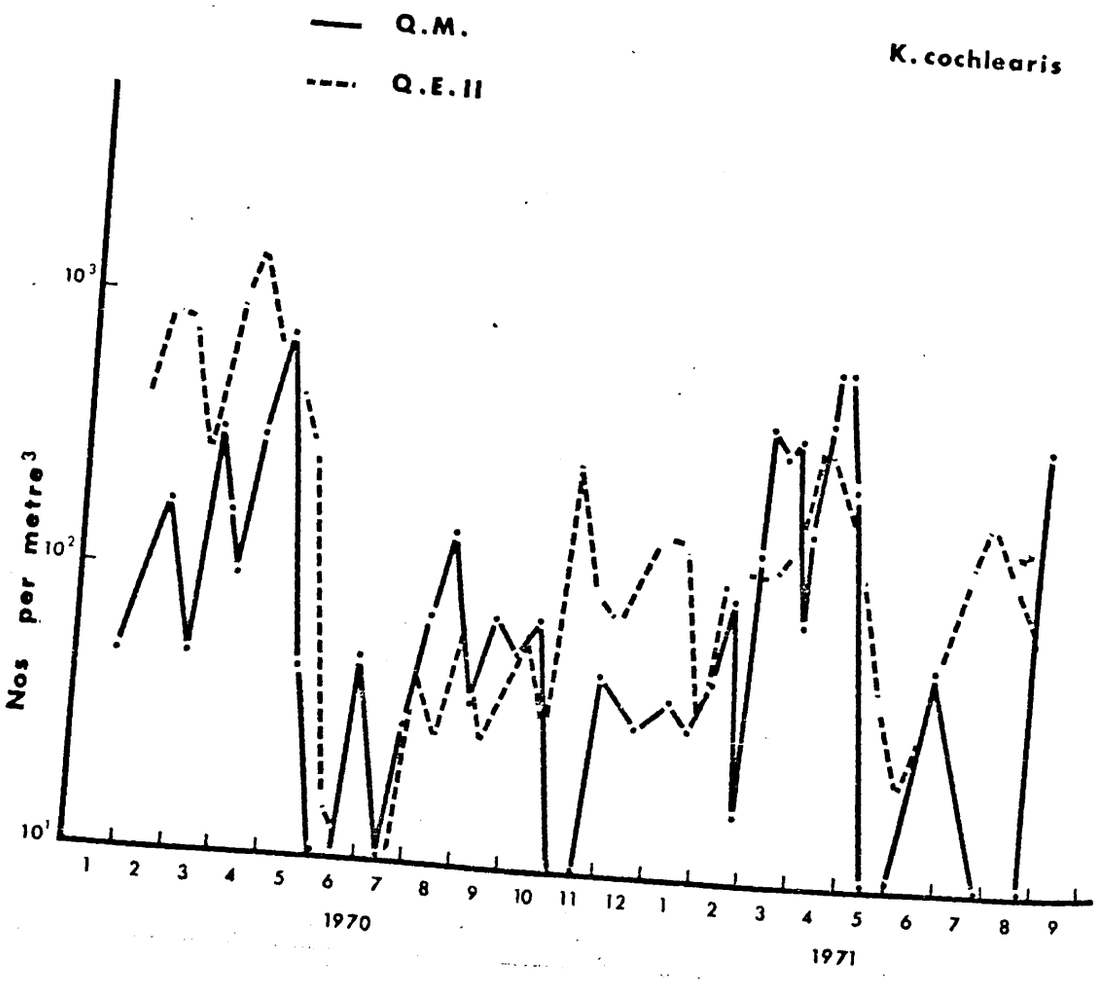

Q.M.
Q.E.II
K. cochlearis
Nos per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 15. Seasonal variation in total rotifers in Q.M. and Q.E.II

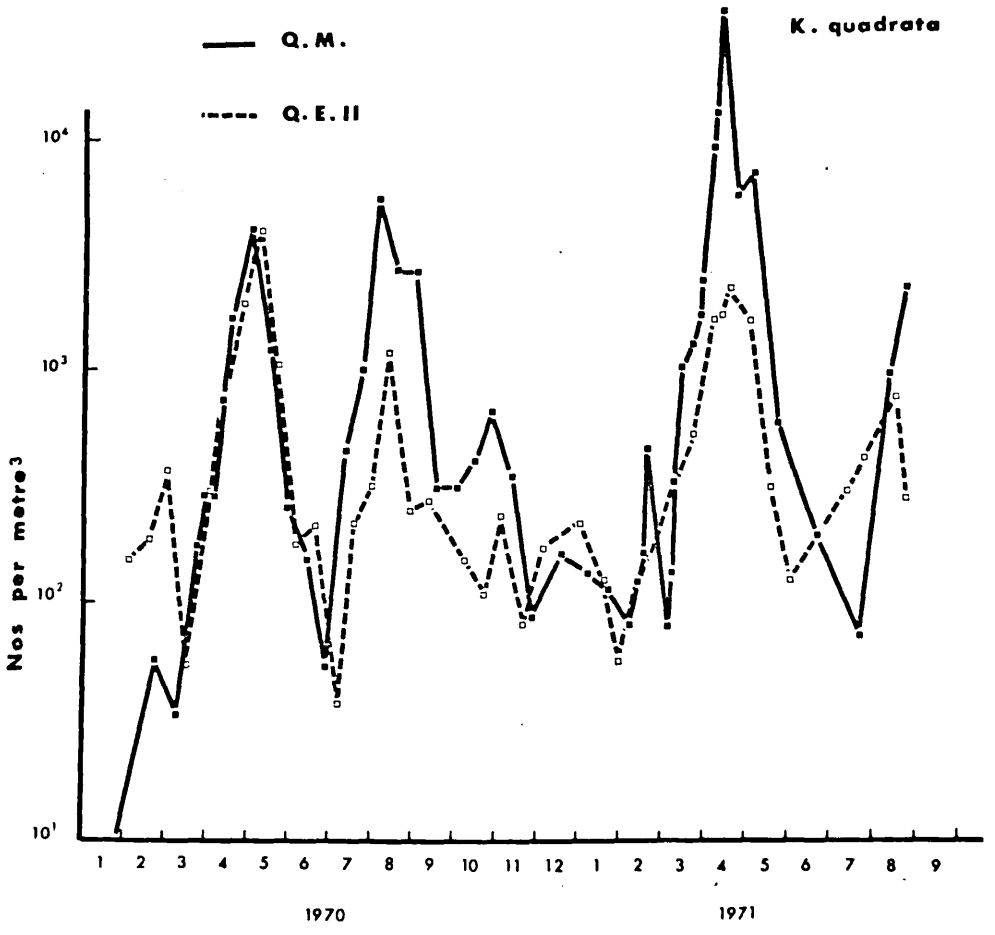
Fig. 16. Seasonal variation in K. cochlearis in Q.M. and Q.E.II

unicornis was prominent in Q.E.II during the winter months. (November - January)

Peak numbers in Q.M. were consistently higher than in Q.E.II during peaks, but comparisons at other times of the year were not feasible because of the low population densities. Lowest standing crops occurred in both reservoirs in June and July when the total population was sometimes less than 100 per cubic metre. The mean number of rotifers present during the spring maximum and throughout 1970 confirms the higher productivity of the Q.M. reservoir. (Table 14) Comparisons of absolute peak numbers may be misleading when dealing with rotifer populations since the decline following a maximum is extremely rapid and unless sampling is very frequent one could miss the actual peak numbers. Comparison of means over the peak period was felt to be a more effective method. The mean spring numbers for 1971 differed markedly in the two reservoirs. That of Q.M. is seven times that of Q.E.II indicating an increase in productivity in Q.M. which was caused by significant increases in populations of only certain species of rotifers.

Keratella cochlearis

This species was present, though in low numbers, throughout the year and was the only species with a larger standing crop in Q.E.II for several weeks. (Figure 16) The spring mean for 1970 in Q.E.II was three times that of Q.M. but the following year the usual pattern of increased numbers in Q.M. occurred. Larsson (1971) found that in Blankvatn, a meromictic lake, K. cochlearis was present in all combinations of oxygen concentration and temperature, but George and Fernando (1968) considered it a cold stenotherm since in Paradise Lake it was absent at temperatures greater than 14°C. Wesenberg-Lund (1930) calls it a perennial species with a maximum in May. Einsle (1967) found that in Mindelsee, where the summer temperature is less than 20°C, maxima occur in the middle of April and end of September.


K. quadrata
Q.M.
Q.E.II
Nos per metre³
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

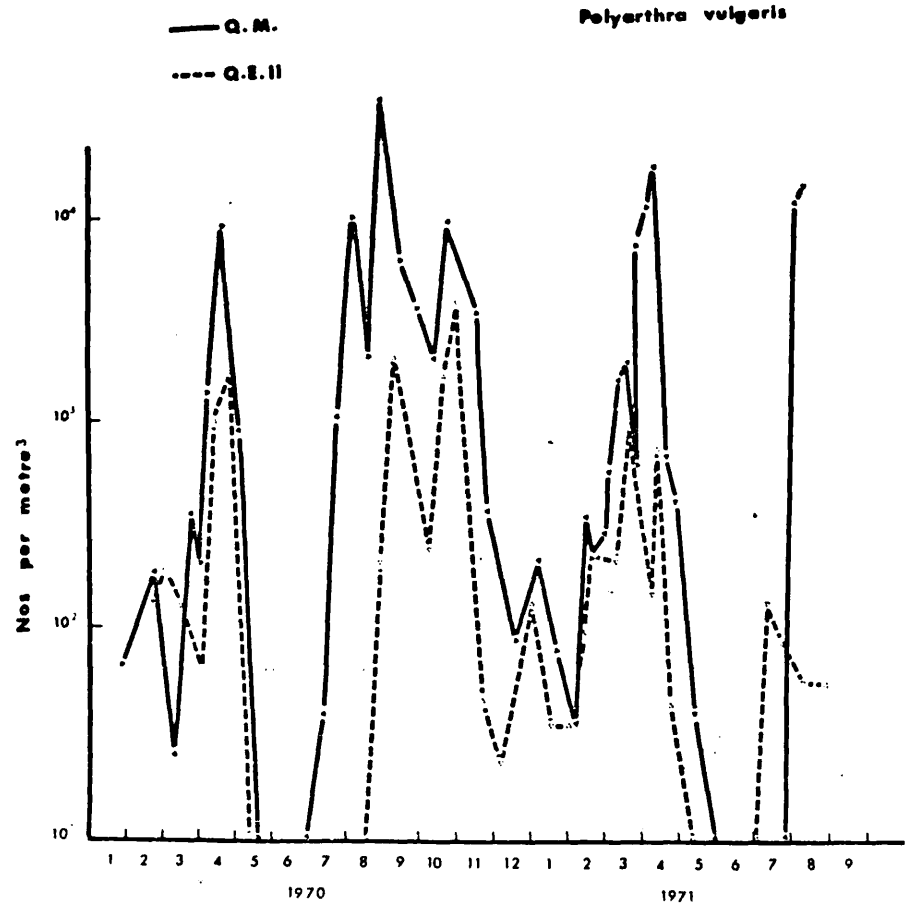

Polyarthra vulgaris
Q.M.
Q.E.II
Nos per metre³
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 17. Seasonal variation in K. quadrata in Q.M. and Q.E.II

Fig. 18. Seasonal variation in Polyarthra vulgaris in Q.M. and Q.E.II

In Q.M. and Q.E.II Einsle's findings were most closely corroborated, with prominent spring maxima and indications of a second maximum in September at least in 1971. The early peak occurs at temperatures of 5°-7°C, but the autumnal one at about 18°C so in these reservoirs, K. cochlearis is less temperature - restricted than in Paradise Lake and could rather be described as a eurythermal species, surviving a temperature range of 4°-21°C.

Keratella quadrata

Figure 17 shows the seasonal variation in numbers per cubic metre of K. quadrata. This was the only rotifer present in significant numbers throughout the year, and like K. cochlearis it had both spring and autumn maxima, both of which were very pronounced. In spring 1970 the maximum numbers in the two reservoirs were virtually identical as were the mean numbers over that period, and the peak occurred about two weeks later than the peak of the other species studied. In autumn of that year, the maximum standing crop was considerably higher in Q.M., and in the succeeding spring the difference was augmented still further, with the Q.M. mean standing crop about eight times that of Q.E.II. This trend continued into September 1971 and seems to indicate a change in the Q.M. reservoir tending to differentiate it from Q.E.II in 1971 season.

K. quadrata was described by Wesenberg-Lund (1930) as a perennial species with a significant minimum in summer and with mixis occurring only in ponds. The species is widely distributed but is often replaced at low temperatures by K. hiemalis (Amrén 1964). Though winter temperatures in Q.M. and Q.E.II were low enough to permit the occurrence of K. hiemalis, no specimens were found.

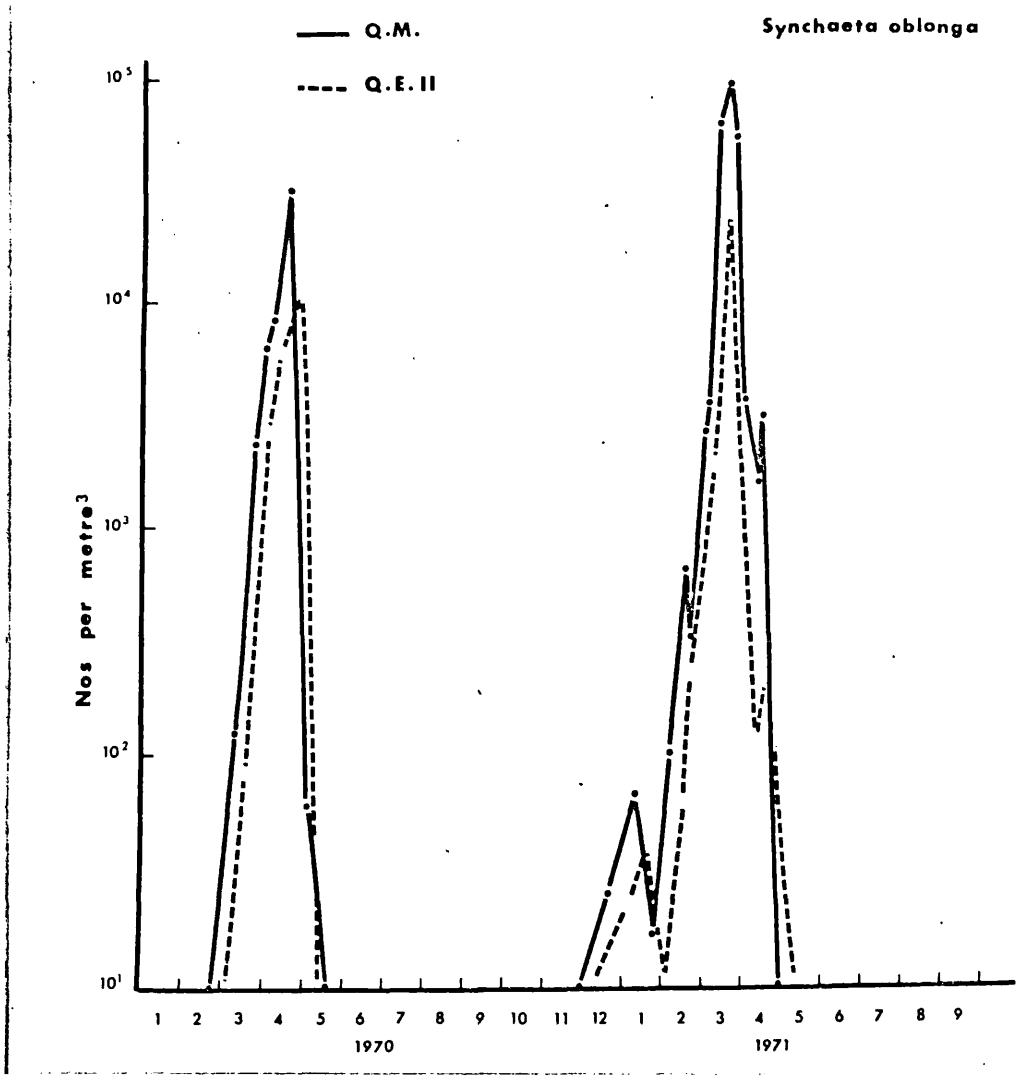
There were indications of morphological variation in K. quadrata but specimens with long and short spines were found in the same samples during early spring. No seasonal cyclomorphosis was noticed during counting but

accurate measurements were not taken regularly. The differences in morphology noticed in spring may indicate the presence of first or second generation rotifers hatched from resting eggs. (Amrén 1964b) Since mixis was never observed these rotifers may indicate the influence of the Thames population or more probably that of the littoral population of K. quadrata, since littoral zone rotifers are often similar to pond species which have regular periods of mixis.(Wesenberg-Lund 1930)

Polyarthra vulgaris

This species is difficult to distinguish from P. dolichoptera and from small specimens of P. major, particularly when specimens are preserved and the ventral appendages characteristic of P. vulgaris are no longer visible. When the largest specimens from Q.M. and Q.E.II were examined alive, the ventral appendages were quite obvious, and therefore all specimens were referred to Polyarthra vulgaris. Langhelt (1965) sampled the River Thames and the Q.M. and classified the Polyarthra she found as P. longiremis. This species is fairly easily distinguished from P. vulgaris and the possibility that there has been a change over the past seven years cannot be overlooked.

P. vulgaris had very high spring and autumn maxima in both reservoirs (Figure 18), but disappeared entirely from the pelagial zone in summer for a period of about two months. No mictic females were found during the spring maxima so the population can only have been renewed from the littoral zone in the autumn. During the autumn peaks in both reservoirs mictic females carrying male eggs were found but few resting eggs were noticed. Polyarthra spp. are noted for the ease with which they drop their eggs. Many amictic eggs were found loose in preserved samples and it was assumed therefore that the preservative rather than the actual sampling caused loss of eggs. Whether this was also the case with resting eggs is not known. If the autumn maxima were augmented by mass hatching of resting eggs one would expect to see


Synchaeta oblonga
Q.M.
Q.E.II
Nos per metre³
10⁵
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

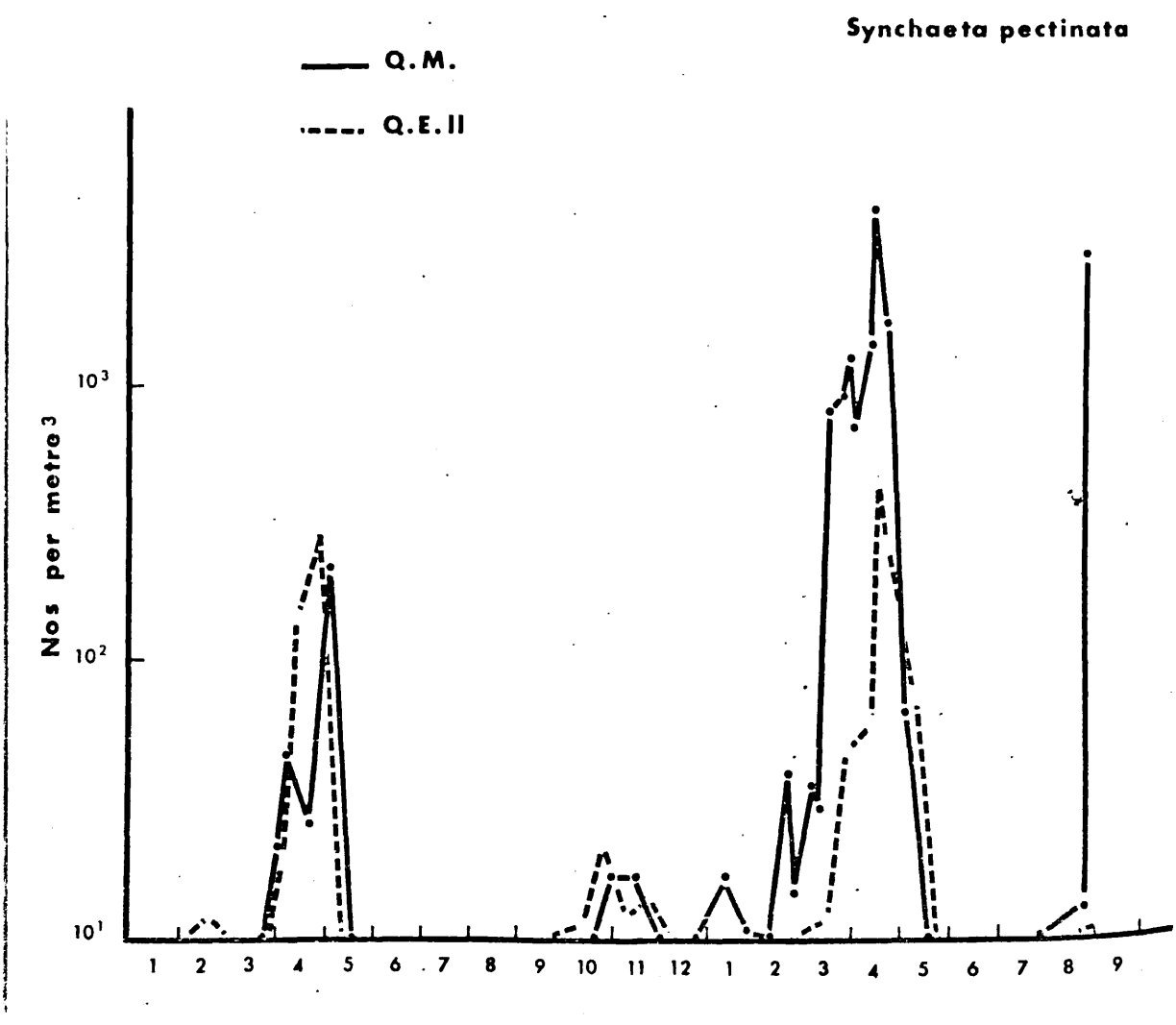

Synchaeta pectinata
Q.M.
Q.E.II
Nos per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Fig. 19. Seasonal variation in Synchaeta oblonga in Q.M. and Q.E.II

Fig. 20. Seasonal variation in S. pectinata in Q.M. and Q.E.II

the morphological differences recorded by Nipkow (1952) in first generation P. vulgaris. Such differences were only noticed, and then very rarely in spring.

Synchaeta oblonga

Wesenberg-Lund (1930) states that all observations of this species show an active life of only four to six weeks with the rest of the year spent as a resting egg though no sexual period had been observed. Observations of this species in Q.M. and Q.E.II were very similar to this. After an extremely rapid period of exponential increase in population numbers to a peak surpassing that of all other species (Figure 19), it declined with even greater rapidity and was absent from the reservoirs until the following spring. Peak numbers occurred in March or April, that is coincident with those of P. vulgaris and K. cochlearis but slightly earlier than that of K. quadrata. It was only present in spring, and as Wesenberg-Lund (1930) also observed, never occurred later than May. There seems to be no record of this species at temperatures exceeding 12°C. and it seems likely that this is a cold stenotherm of fairly limited distribution in lakes. In Denmark it was considered a pond form only (Wesenberg-Lund 1930). If resting eggs do occur in the reservoir, and this seems the only way to account for the sudden appearance of this species, then it is probable that they are restricted to the littoral zone where pond species often occur in high numbers.

Synchaeta pectinata

This species contributed to the substantially increased productivity of Q.M. in 1971 compared with the previous year. (Figure 20) Mean numbers during spring 1970 were similar in both reservoirs, and though the species re-appeared in October and November of that year, the numbers were extremely low and could hardly be said to constitute an autumn peak. In spring 1971, the mean number present in Q.M. was more than twenty times that of the previous

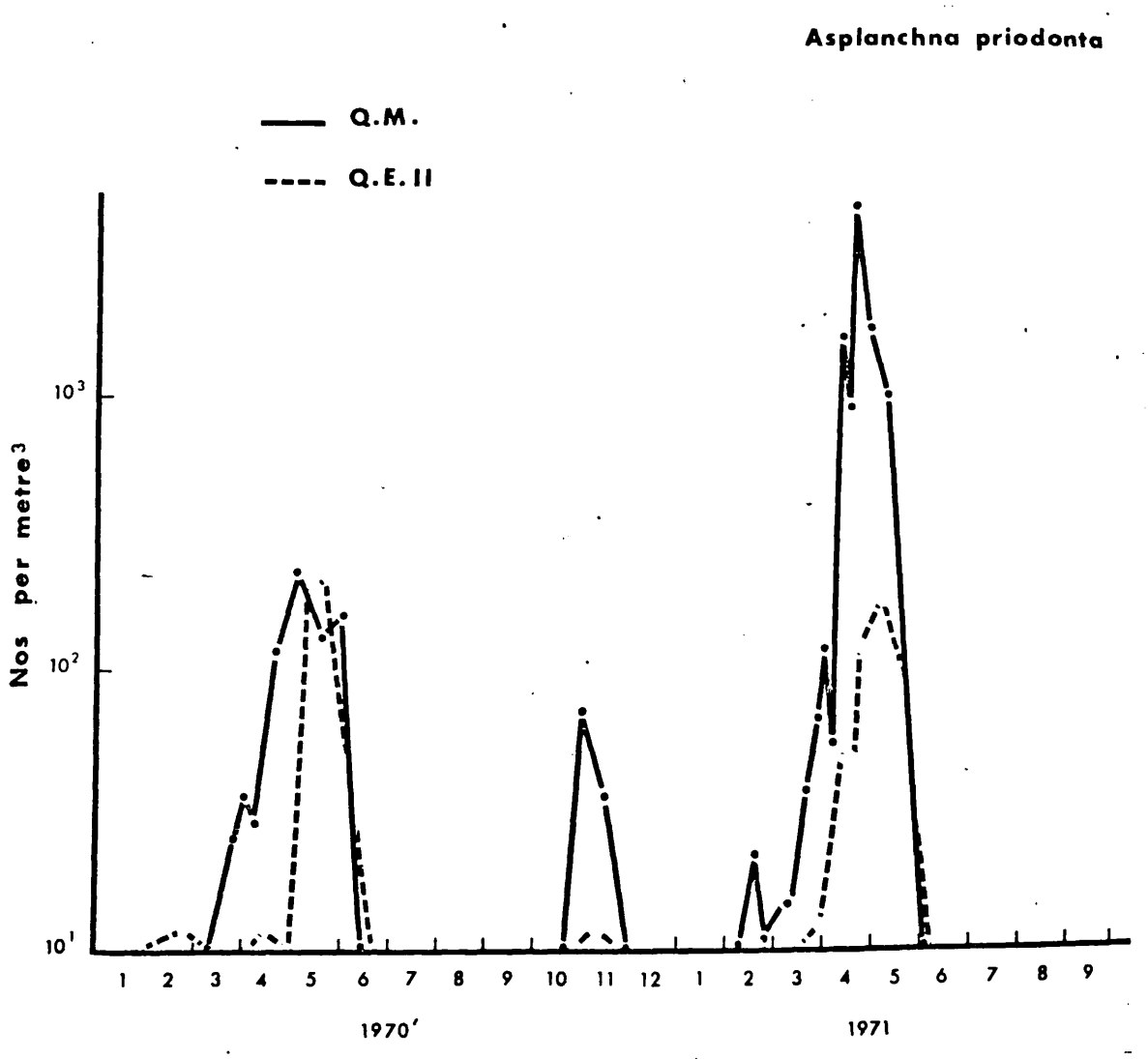

Asplanchna priodonta
Q.M.
Q.E. II
Nos per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970'
1971

Fig. 21. Seasonal variation in Asplanchna priodonta in Q.M. and Q.E.I.

year whilst the population had also doubled in Q.E.II. August 1971 also indicated that an autumn peak of this species would occur in Q.M. Wesenberg-Lund (1930) records this species as rare in lakes. Langhelt (1965) does not record it in the River Thames, so possibly this species, like S. oblonga has its population renewed from the littoral.

Asplanchna priodonta

This rotifer is a truly planktonic form, restricted to open water bodies with little standing vegetation. No evidence of mixis was found though males have been observed in previous years (Pontin, personal communication). Peak abundance (Figure 21) occurred in early May, and as with the other rotifers, Q.M. reservoir in spring 1971 was considerably more productive than in the previous year. A. priodonta has been described as a predator and some specimens were found with loricas of Keratella quadrata and K. cochlearis in the stomach during peak abundance of these species. Though high numbers of this food were also available in autumn, no autumnal peak of Asplanchna was apparant though it did reappear in very low numbers in November.

Quantitative samples were not taken from the littoral zone of the reservoirs but occasional samples taken for experimental work contained rotifers of the six species described above. The possibility therefore of a sexual phase occurring in the littoral zone and augmenting or initiating the pelagial population cannot be ignored.

Table 12

SPECIES OF ROTIFERS IN Q.M. AND Q.E.II RESERVOIRS 1970-1971

Order: MONOGONONTA

Sub-order: PLOIMA

Family: Brachionidae

Keratella cochlearis	Gosse
Keratella quadrata	Müller
Brachionus urceolaris	Müller
Brachionus calyciflorus	Pallas
Euchlaris dilatata	Ehrenberg
Notholca squamula	Müller
Notholca acuminata	Ehrenberg
Kellicottia longispina	Kellicott
Lepadella patella	Müller

Family: Synchaetidae

Synchaeta oblonga	Ehrenberg
Synchaeta pectinata	Ehrenberg
Polyarthra vulgaris	Carlin

Family: Notommatidae

Cephalodella forficata	Ehrenberg

Family: Trichocercidae

Trichocerca stylata	Gosse

Family: Asplanchnidae

Asplanchna priodonta	Gosse

Family: Lecanidae

Lecane sp.

Sub-order: FLOSCULARIACEAE

Family: Conochilidae

Conochilus unicornis	Rousselet (Q.E.II only)
Conochiloides natans	(Seligo)

Family: Testudinellidae

Filinia longiseta	Ehrenberg
Pompholyx sulcata	Gosse

Table 13a

Q.M. Reservoir Rotifera per vertical net haul.

1970	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Keratella cochlearis	6	12	23	24	47	1	4	13	5	7	2	4
Keratella quadrata	5	7	13	69	422	23	81	432	136	45	42	18
Polyarthra sp.	1	19	22	453	56		35	612	2162	333	497	10
Synchaeta oblonga			152	2021	5							3
Synchaeta pectinata		1	1	9	35		6	8	143	5		2
Asplanchna priodonta	2	5	5	12	456	17					10	1
Brachionus urceolaris	1	1		6								
Brachionus calyciflorus	1	1	1	10	3	7	2				2	
Lecane sp.		3	5	19	20					2		1
Filinia longiseta				2	4					7	2	
Notholca squamula		5	14	31	39					5		4
Notholca acuminata				4	21							
Kellicottia longispina				1	1							
Pompholyx sulcata							1	3	5	18	20	
Trichocerca stylata									47	22		
Conochiloides natans										10	3	
Euchlanis dilatata		2									3	
Cephalodella forficata			1	3								1
Lepadella patella	2											
Conochilus unicornis												

1971	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec.
Keratella cochlearis	4	7	27	54	17	7		12	51			
Keratella quadrata	14	11	68	1442	740	18	9	110	255			
Polyarthra sp.	17	23	122	929	27			1408	15712			
Synchaeta oblonga	5	42	4893	1525								
Synchaeta pectinata	4	5	125	565	10			4	912			
Asplanchna priodonta		3	9	467	407							
Brachionus urceolaris												
Brachionus calyciflorus		1	1	92								
Lecane sp.		1	6	9	2							
Filinia longiseta			4	13	2							
Notholca squamula			6	21								
Notholca acuminata			1	7	2							
Kellicottia longispina												
Pompholyx sulcata												
Trichocerca stylata												
Conochiloides natans												
Euchlanis dilatata												
Cephalodella forficata		1										
Lepadella patella												
Conochilus unicornis												

Table 13b

Q.E.II Reservoir Rotifera per vertical net haul

1970	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Keratella cochlearis		127	95	185	75	2	1	7	9	9	37	14
Keratella quadrata		32	40	182	473	28	24	136	48	24	27	30
Polyarthra sp		22	28	181					207	169	324	4
Synchaeta oblonga		5	7	1233								
Synchaeta pectinata		4	1	7						7	7	2
Asplanchna priodonta				3	71	6					4	1
Brachionus urceolaris		1			7	4		1				
Brachionus calyciflorus		1	3	22	9	6		1	5		3	2
Lecane sp		1	11	33	17	1			5	1	5	3
Filinia longiseta		1	3	1					5	2		4
Notholca squamula		2	30	13				2			2	3
Notholca acuminata				11								1
Kellicottia longispina		1	1									
Pompholyx sulcata									30		12	
Trichocerca stylata							1			10		
Conochiloides natans											3	17
Euchlanis dilatata		1									1	
Cephalodella forficata		2	1	5						11		
Lepadella patella			1									
Conochilus unicornis											98	194

1971	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Keratella cochlearis	29	18	25	61	17	5	26	33	15			
Keratella quadrata	29	21	70	309	162	21	51	100	49			
Polyarthra sp.	15	25	98	54			24	12	10			
Synchaeta oblonga	5	24	2409	28	1							
Synchaeta pectinata	1		30	114	18		1		2			
Asplanchna priodonta			3	29	61	4						
Brachionus urceolaris												
Brachionus calyciflorus		1	1	28	26	2						
Lecane sp		1	6	28	1							
Filinia longiseta				2	1							
Notholca squamula			5	14								
Notholca acuminata			1	2								
Kellicottia longispina												
Pompholyx sulcata							61	362	247			
Trichocerca stylata												
Conochiloides natans												
Euchlanis dilatata	3											
Cephalodella forficata	14	1		2								
Lepadella patella												
Conochilus unicornis	30											

Table 14a

Mean Numbers of Rotifers for February-May (inclusive) per M^3

Reservoir	Q.M.	Q.E.II	Q.M.	Q.E.II
Species	1970		1971	
Keratella cochlearis	242.6	690.5	272.9	174.2
Keratella quadrata	972.4	965.7	5001.5	779.9
Polyarthra vulgaris	1,498.9	388.4	2,967.4	230.8
Synchaeta oblonga	6,290.0	2,239.3	16,454.9	2,789.1
Synchaeta pectinata	39.7	55.3	792.0	90.8
Asplanchna priodonta	72.7	49.0	732.5	48.2
Overall mean	10,548.5	4,736.9	29,359.8	4,606.0

Table 14b

Mean Numbers of Rotifers for 1970 per M^3

Reservoir	Q.M.	Q.E.II
Keratella cochlearis	110.6	291.7
Keratella quadrata	928.6	513.4
Polyarthra vulgaris	1,692.8	471.1
Synchaeta oblonga	2,832.3	842.3
Synchaeta pectinata	15.4	239.7
Asplanchna priodonta	36.0	21.1
Overall mean	7,638.8	2,514.7

Table 15a

Q.M. Reservoir Data for January 1970 - September 1971

Numbers of Rotifera per M^3

Date	Total Rotifer	Keratella cochlearis	Keratella quadrata	Polyarthra spp	Synchaeta oblonga	Synchaeta pectinata	Asplanchna priodonta
26/1	244.9	50.7	8.5	67.6		10.6	3.5
23/2	447.7	177.4	50.7	185.9			10.6
9/3	380.2	50.7	33.8	25.3	186.0	7.1	7.1
23/3	3,556.6	329.5	177.4	354.8	2,373.9		24.7
1/4	7,594.7	168.9	287.2	202.7	6,302.2	21.1	35.2
7/4	10,914.8	92.9	287.2	1,368.6	8,549.4	45.8	28.2
20/4	46,479.4	322.6	1,643.5	9,000.9	32,839.7	25.6	115.2
4/5	13,501.4	752.6	4,085.8	844.9	61.4	217.6	226.4
19/5	1,513.0	46.1	1,213.4	7.7	7.7		134.4
1/6	691.2	7.7	253.4				153.6
15/6	253.4	7.7	153.6				6.4
29/6	69.1	53.8	53.8				6.4
13/7	514.6	0	433.9	38.4	15.4		
27/7	2,173.4	30.7	975.4	1,021.4			3.2
10/8	1,728.0	76.8	5,299.2	10,099.2			
24/8	5,068.8	153.6	2,611.2	1,996.9			
7/9	59,343.4	38.4	2,511.4	38,016.0			
21/9	5,184.0	76.8	307.2	5,894.4			
5/10	4,300.8	57.6	307.2	3,379.2	76.9		
19/10	3,456.0	76.8	384.0	1,881.9			
2/11	10,898.0	0	633.6	8,701.4		17.6	70.4
16/11	4,139.5	0	337.8	3,210.2	126.7	17.6	35.2
30/11	506.9	50.7	84.5	354.8			
21/12	371.7	33.8	152.0	84.6	25.3	7.1	3.5
12/1	490.0	42.2	126.7	202.7	67.6	17.6	
25/1	262.0	33.8	109.8	76.0	16.9	10.6	
9/2	321.0	50.7	76.0	33.8	101.4		7.1
22/2	1,478.4	101.4	152.0	321.0	650.5	38.7	21.1
25/2	760.3	16.9	422.4	219.7	321.0	14.1	10.6
8/3	3,556.6	143.6	76.0	270.4	2,618.9	35.2	14.1
11/3	4,899.8	422.4	126.7	532.2	3,573.5	28.2	14.1
22/3	71,723.5	337.9	929.3	1,436.2	63,529.0	809.6	35.2
30/3	103,817.5	388.6	1,148.9	1,867.0	95,631.4	887.1	63.4
5/4	58,941.7	84.5	1,529.1	557.6	55,587.8	1,228.5	112.7
8/4	16,169.5	177.4	2,162.7	7,882.0	3,624.2	682.9	52.8
19/4	29,521.9	445.4	8,256.0	10,644.5	1,582.0	1,379.2	1,587.2
22/4	47,923.2	691.2	11,212.8	16,742.4	3,148.8	4,256.0	864.0
29/4	53,299.2	691.2	32,563.2	614.4		1,664.0	4,864.0
6/5	9,945.6	268.8	5,068.8	384.0		64.0	1,648.0
17/5	8,678.4	0	6,297.6	38.4			960.0
1/6	53.8	0	537.6				
28/6	297.6	61.4	180.5	7.7		3.2	
26/7	69.1	0	69.1				
23/8	11,842.6	9.2	844.8	10,813.4		12.8	
6/9	130,821.1	391.7	1,958.4	12,066.8		2,918.4	

Table 15a cont.

Q.M. Reservoir Data for January 1970 - September 1971.

Egg Numbers per M^3

Date	Keratella cochlearis	Keratella quadrata	Polyarthra spp.	Asplanchna priodonta
26/1	16.9			
23/2	84.5	8.5	92.9	
9/3	25.3	16.9	8.5	
23/3	228.1	153.0	152.0	
1/4	109.8	270.4	211.2	
7/4	67.6	270.4	1343.2	16.9
20/4	138.2	1167.4	1382.4	86.4
4/5	122.9	307.2		518.4
19/5		61.4		16.0
1/6		30.7		6.4
15/6				
29/6		7.7		
13/7		180.5		
27/7		487.6	50.7	
10/8		92.1	1612.8	
24/8		345.6	307.2	
7/9			15552.0	
21/9		115.2	268.8	
5/10		131.6	115.2	
19/10		164.3	M 38.4	
			76.8	
2/11		168.9	M1013.8	
16/11		42.2	M 126.6	
			126.6	
30/11		8.5	M 16.9	
21/12		8.5		
12/1	16.9	33.8		
25/1	16.9	16.9	8.5	
9/2	25.3			
22/2	8.5	67.6	92.9	7.1
25/2	9.3	16.9	92.9	3.5
8/3	16.9	50.7	278.8	10.6
11/3	169.0	76.0	481.6	14.1
22/3	236.5	506.9	3125.8	
30/3	67.6	582.9	2331.7	14.1
5/4	76.0	963.1	506.9	45.8
8/4		980.0	447.7	7.1
19/4	384.0	2357.8	829.4	304.0
22/4		4224.0	2918.4	416.0
29/4		4070.4	230.4	992.0
6/5		268.8		
17/5		384.0		16.0
1/6				
28/6		53.8		
26/7		7.7		
23/8		168.9	2168.9	
6/9			2396.0	

Table 15b

Q.E.II Reservoir Data for January 1970 - September 1971

Numbers of Rotifera per M^3

Date	Total Rotifers	Keratella cochlearis	Keratella quadrata	Polyarthra app	Synchaeta oblonga	Synchaeta Pectinata	Asplanchna priodonta
4/2	805.4	399.9	152.1	118.3		7.0	4.7
18/2	1,036.3	870.2	182.2	123.9		11.7	
2/3	1,745.9	799.8	369.6	185.8		7.0	
16/3	602.6	264.7	50.7	129.5	84.5	4.7	
3/4	4,471.8	996.9	297.8	61.9	2675.2	18.8	2.3
13/4	10,024.9	1,526.3	743.4	985.6	6026.2	140.8	11.7
29/4	16,637.3	570.2	1900.8	1890.2	11367.8	308.0	8.8
11/5	5,327.5	491.0	3954.7				198.0
22/5	1,980.0	295.7	1040.2				215.6
8/6	406.6	15.8	179.5				37.4
22/6	274.6	10.6	205.9				2.3
8/7	37.0	0	37.0				
20/7	221.8	5.3	211.2				
3/8	396.0	47.5	300.9	5.3			
17/8	1,214.4	26.4	1135.2				
1/9	649.4	68.6	242.9	205.9		6.6	
15/9	2,772.0	26.4	264.0	1980.0			
12/10	633.6	68.6	147.8	227.0		11.0	
26/10	1,900.8	26.4	105.6	1557.6		22.0	
9/11	5,603.8	309.8	225.3	3604.5		11.7	11.7
24/11	608.2	101.4	78.8	45.0		14.1	9.4
8/12	1,548.8	78.8	168.9	22.5		4.7	2.2
6/1	1,008.1	163.3	208.4	129.5	22.5	4.7	
20/1	444.9	157.7	118.3	33.8	39.4	2.4	2.2
2/2	191.5	33.8	56.3	33.8		2.4	
17/2	1,019.4	123.9	118.3	90.1	61.9	7.0	4.4
25/2	791.3	126.7	146.4	216.8	233.7	2.4	4.0
15/3	2,624.5	123.9	304.1	197.1	1898.0	11.7	2.2
29/3	27,253.2	157.7	478.7	906.8	25231.4	46.9	11.7
15/4	2,511.9	405.5	1453.0	135.2	112.6	58.7	37.6
22/4	4,678.1	316.8	1584.0	686.4	211.2	444.4	35.2
27/4	3,938.9	274.6	1953.6	42.2	126.7	255.2	118.8
11/5	2,233.4	132.0	1415.0		10.6	74.8	173.8
24/5	818.4	47.5	290.4		5.3	4.4	94.6
7/6	176.9	21.1	118.3				9.9
19/7	879.1	134.7	269.3	124.1		6.6	
2/8	660.0	211.2	369.6	79.2			
16/8	4,699.2	132.0	686.4	52.8			
1/9	3,020.2	79.2	258.7	52.8		11.0	

Table 15b cont.

Q.E.II Reservoir Data for January 1970 - September 1971

Egg Numbers per M^3

Date	Keratella cochlearis	Keratella quadrata	Polyarthra app.	Asplanchna priodonta
4/2	90.1	16.9	11.9	
18/2	318.2	36.6	19.7	
2/3	191.5	95.8	16.9	
16/3	67.6	22.5	22.5	
3/4	399.9	292.9	28.2	
13/4	1030.6	585.7	275.9	
29/4	269.3	718.1	369.6	6.6
11/5	63.4	543.8		55.0
22/5		26.4		30.8
8/6				2.2
22/6		10.6		
8/7		5.3		
20/7		31.7		
3/8	26.4	153.1		
17/8		15.8		
1/9		26.4		
15/9			132.0	
12/10	15.8	15.8	15.8	
26/10		5.3	M79.2	
			132.0	
9/11	112.6		M28.2	
			253.4	
24/11				
8/12		5.6	11.4	
6/1	45.0	16.9	5.6	
20/1	61.9	28.2		
2/2		22.5		
17/2	11.3	16.9	11.3	
25/2	73.2	22.5	70.4	
15/3	50.7	95.8	11.3	
29/3	45.0	95.8	39.4	
15/4	67.6	332.3	16.9	7.0
22/4	105.6	770.9	105.6	8.8
27/4	63.4	485.8	31.7	26.4
11/5		132.0		15.4
24/5		21.1		2.2
7/6		15.8		
19/7	26.4	15.8		
2/8	26.4			
16/8	26.4	105.6		
1/9				

Table 16a

Q.M. RESERVOIR DATA FOR JANUARY 1970 - SEPTEMBER 1971

EGGS PER FEMALE

DATE	KERATELLA COCHLEARIS	KERATELLA QUADRATA	POLYARTHRA SPP.	ASPLANCHNA PRIODONTA	TOTAL SMALL ROTIFERS
23/2	0.48	0.17	0.5		0.38
9/3	0.50	0.50			0.50
23/3	0.69	0.86	0.43		0.66
1/4	0.65	0.94	1.04		0.88
7/4	0.73	0.94	0.98	0.60	0.88
20/4	0.43	0.71	0.15	0.75	0.43
4/5	0.16	0.07		2.29	0.12
19/5		0.05		0.12	0.05
1/6		0.12			0.12
15/6					
29/6		0.14			0.14
13/7		0.42			0.42
27/7		0.50	0.45		0.48
10/8		0.01	0.16		0.09
24/8		0.13	0.15		0.14
7/9			0.41		0.41
21/9		0.38	0.05		0.22
5/10		0.43	0.03		0.23
19/10		0.43	0.04		0.24
2/11		0.27			0.27
16/11		0.13	0.04		0.09
30/11		0.10			0.10
21/12		0.05			0.05
12/1		0.27			0.27
25/1		0.15			0.15
9/2					
22/2	0.25	0.44	0.29		0.33
25/2		0.04	0.42		0.23
8/3	0.65	0.67	1.03	0.75	0.78
11/3		0.60	0.90	1.0	0.75
22/3	0.50	0.55	2.18		1.08
30/3	0.61	0.51	1.25	0.22	0.79
5/4	0.80	0.63	0.91	0.41	0.78
8/4	0.43	0.45	0.06	0.13	0.31
19/4		0.29	0.08	0.19	0.19
22/4	0.56	0.38	0.17	0.48	0.37
29/4		0.13	0.38	0.20	0.26
6/5		0.05			0.05
17/5		0.06		0.01	0.06
1/6					
28/6		0.21			0.21
26/7		0.11			0.11
23/8		0.20	0.02		0.11
6/9			0.02		0.02

Table 16b

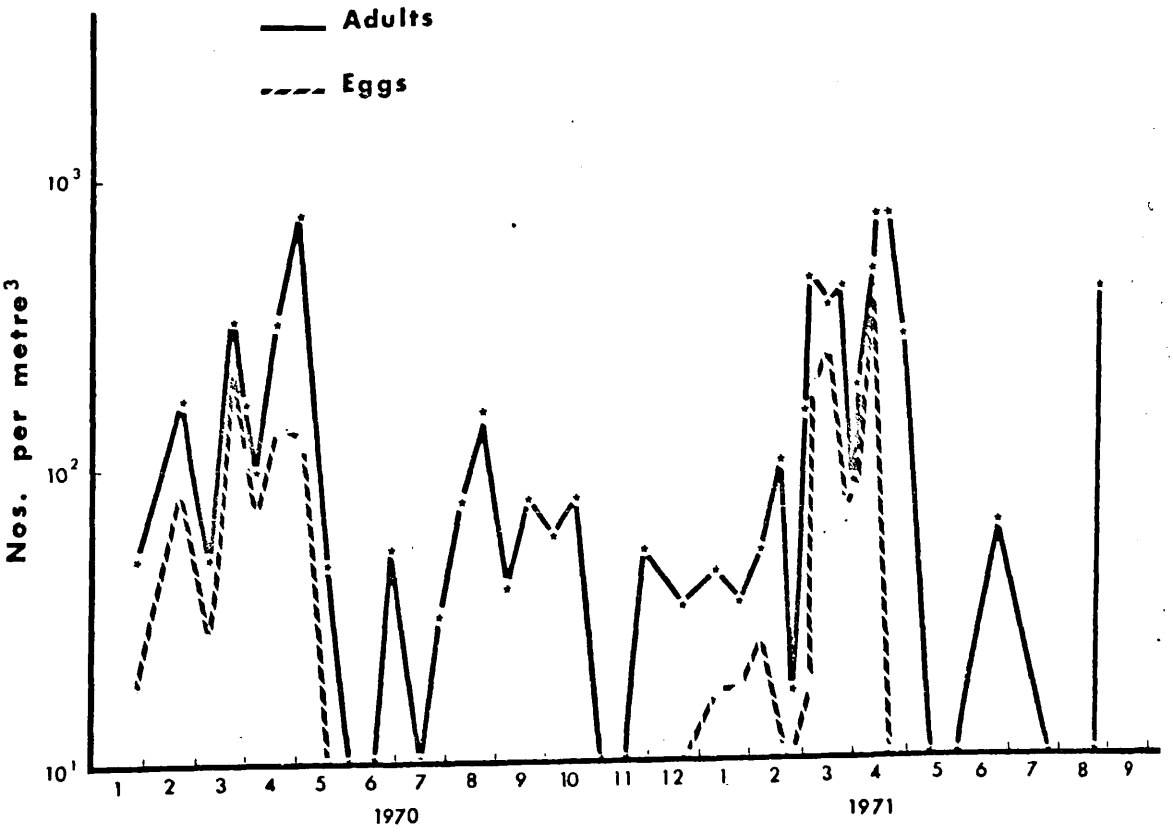
Q.E. II RESERVOIR DATA FOR FEBRUARY 1970 - SEPTEMBER 1971

EGGS PER FEMALE

DATE	KERATELLA COCHLEARIS	KERATELLA QUADRATA	POLYARTHRA SPP.	ASPLANCHNA PRIODONTA	TOTAL SMALL ROTIFERS
4/2	0.23	0.24	0.10		0.19
18/2	0.36	0.12	0.16		0.21
2/3	0.24	0.24	0.09		0.19
16/3	0.26	0.44	0.17		0.29
3/4	0.40	0.98	0.45		0.61
13/4	0.68	0.79	0.28		0.58
29/4	0.47	0.38	0.20	0.75	0.35
11/5	0.13	0.14		0.28	0.13
22/5		0.03		0.14	0.03
8/6					
22/6		0.05			0.05
8/7		0.14			0.14
20/7		0.15			0.15
3/8	0.56	0.51			0.53
17/8		0.01			0.01
1/9		0.11			0.11
15/9			0.67		0.67
12/10	0.23	0.11	0.70		0.35
26/10		0.05	0.08		0.06
9/11	0.36		0.07		0.22
24/11					
8/12		0.03			0.03
6/1	0.28	0.08			0.18
20/1	0.39	0.24			0.32
2/2		0.40			0.40
17/2		0.14			0.14
25/2	0.58	0.15	0.32		0.35
15/3	0.41	0.31			0.36
29/3	0.29	0.20	0.04		0.18
15/4	0.17	0.23	0.12	0.19	0.17
22/4	0.33	0.49	0.15	0.25	0.32
27/4	0.23	0.25		0.22	0.24
11/5		0.09		0.09	0.09
24/5		0.07			0.07
7/6		0.14			0.14
19/7	0.20	0.06			0.13
2/8	0.13				0.13
16/8	0.20	0.15			0.17

Keratella cochlearis

Q.M. Reservoir



Keratella cochlearis

Q.E.II

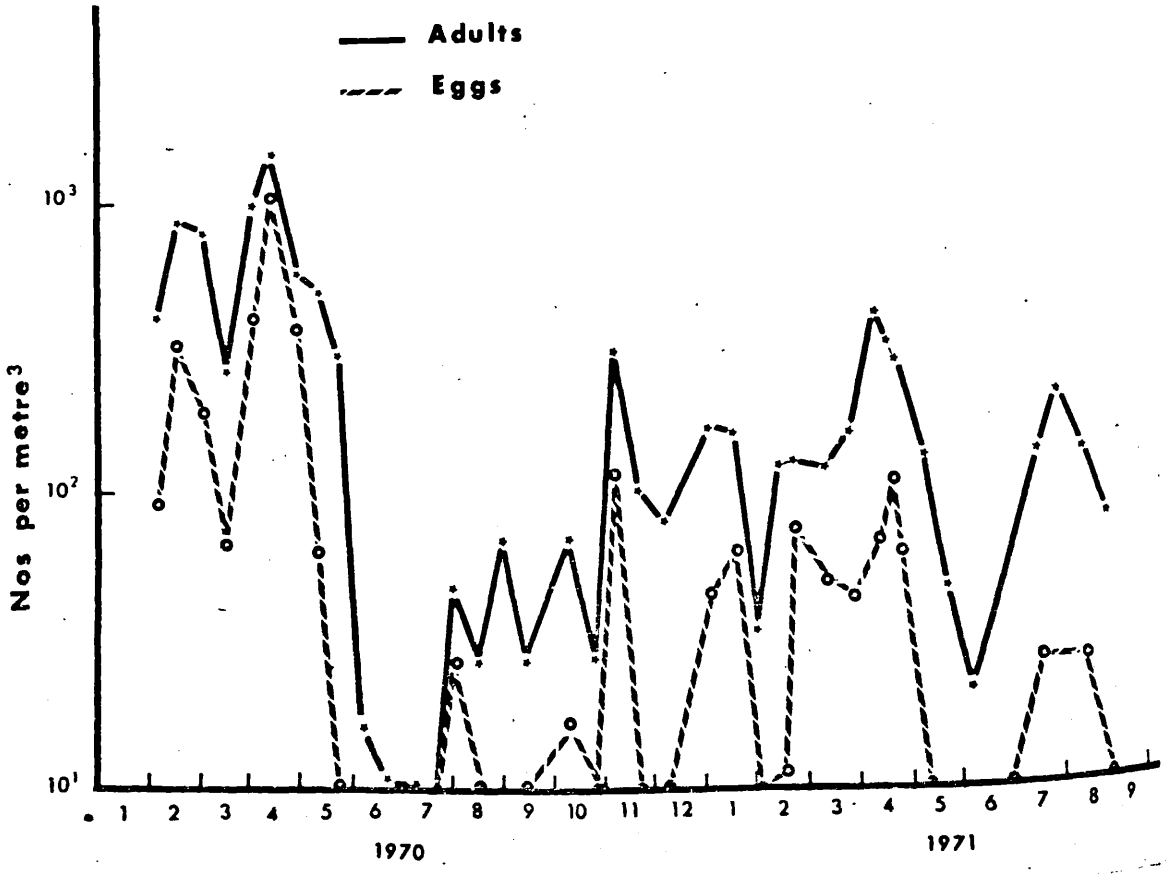


Fig. 22. Adult standing crop and eggs of K. cochlearis in Q.M.

Fig. 23. Adult standing crop and eggs of K. cochlearis in Q.E.II

Egg Numbers and Ratios

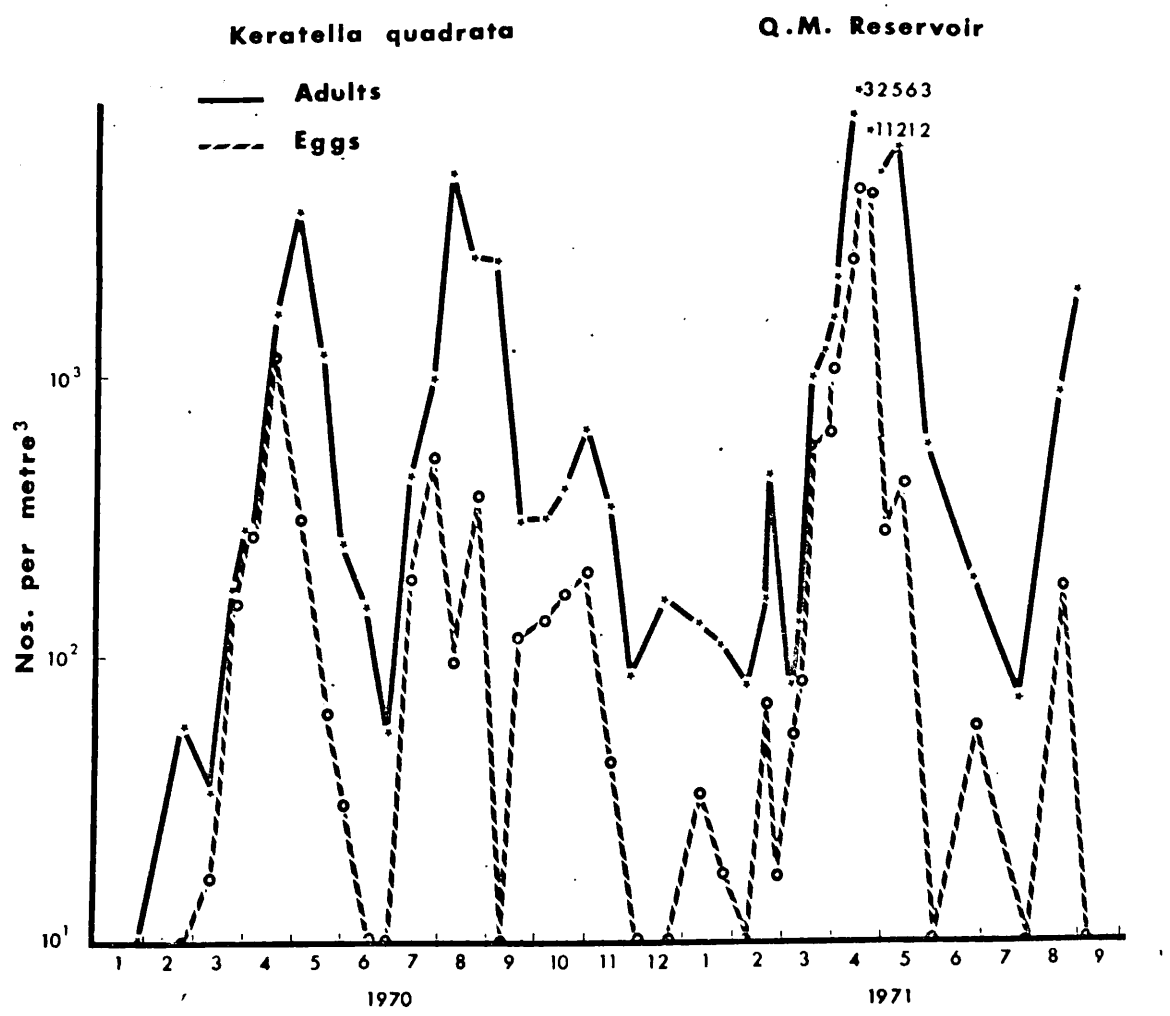
Many planktonic rotifers carry their eggs for the time prior to hatching. The interval between the laying of successive eggs varies according to availability of food (Edmondson 1965) and in culture female Brachionidae may carry up to three or four amictic eggs. In the reservoir populations, females carrying more than one egg were only rarely seen.

Keratella cochlearis

Figure 22 shows the number of adults and number of eggs per cubic metre in Q.M. reservoir. Peaks of egg numbers generally coincided with maximum numbers of females probably because of the rather long sampling interval. In April of both years, when samples were taken more frequently, the egg peak occurred just prior to the adult peak. In 1970 this represented 0.73 eggs per female (Table 16) whilst in 1971 the peak was 0.80 eggs per female. In Q.E.II (Figure 23) maximum egg ratio occurred in April 1970 but this was only 0.68, lower than in Q.M. Nevertheless the peak standing crop of adults was higher in Q.E.II due to the higher initial population surviving the winter at the beginning of 1970. The following year the situation was reversed and in Q.M. for several weeks in succession high ratios obtained. Again the initial population was higher in Q.E.II but egg ratios remained very low over the spring peak, only once reaching more than 0.50 eggs per female.

Keratella quadrata

The longer life cycle of this species was demonstrated by the occurrence of egg peaks always slightly before the population peak. (Figures 24 and 25) Since the sampling interval was 14 days it would appear that K. quadrata can survive at least 14 days in the reservoir. A related species, K. valga can survive up to 22 days whilst mean survival time in the laboratory for a rotifer has been given as 11.2 days. (Larsson 1971, Hutchinson 1967) During this period, egg production varies with food and temperature (Edmondson 1965) with


Keratella quadrata
Q.M. Reservoir
Adults
Eggs
*32563
*11212
Nos. per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

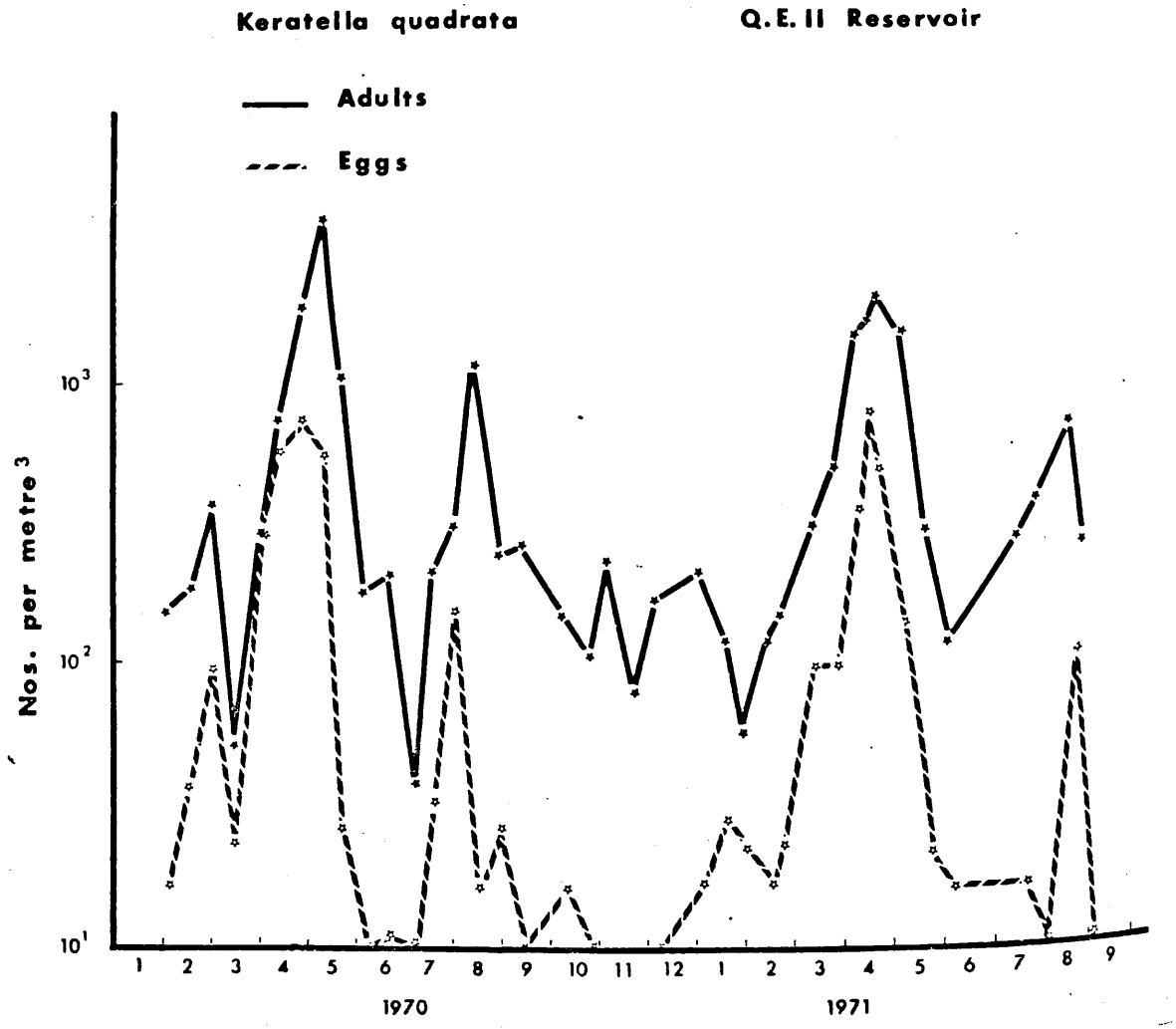
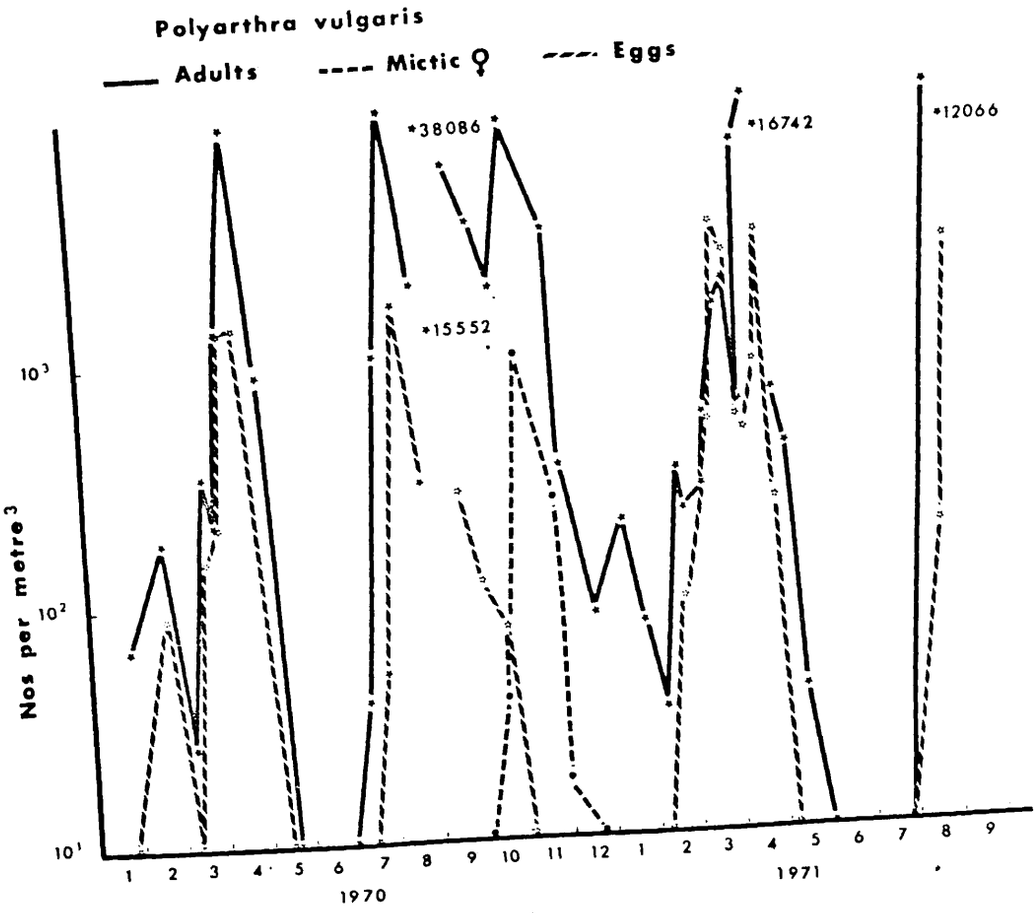

Keratella quadrata
Q.E. II Reservoir
Adults
Eggs
Nos. per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 24. Adult standing crop and eggs of K. quadrata in Q.M.

Fig. 25. Adult standing crop and eggs of K. quadrata in Q.E.II.

Q.M.



Q.E.II Reservoir

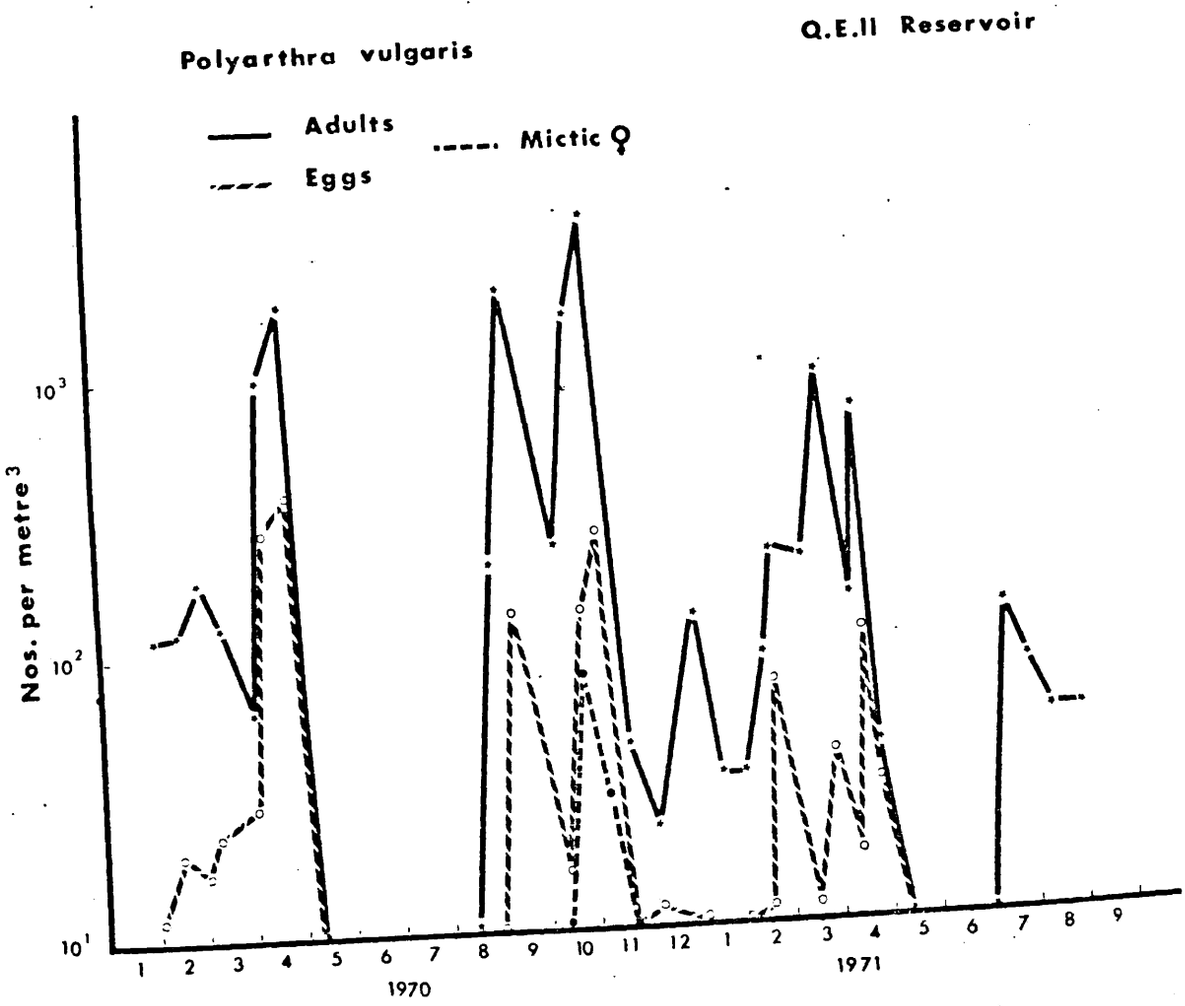


Fig. 26. Adult standing crop and eggs of Polyarthra vulgaris in Q.M.

Fig. 27. Adult standing crop and eggs of Polyarthra vulgaris in Q.E.II

the former affecting the number of eggs a female is carrying and the latter modifying the egg ratio by changing the development time.

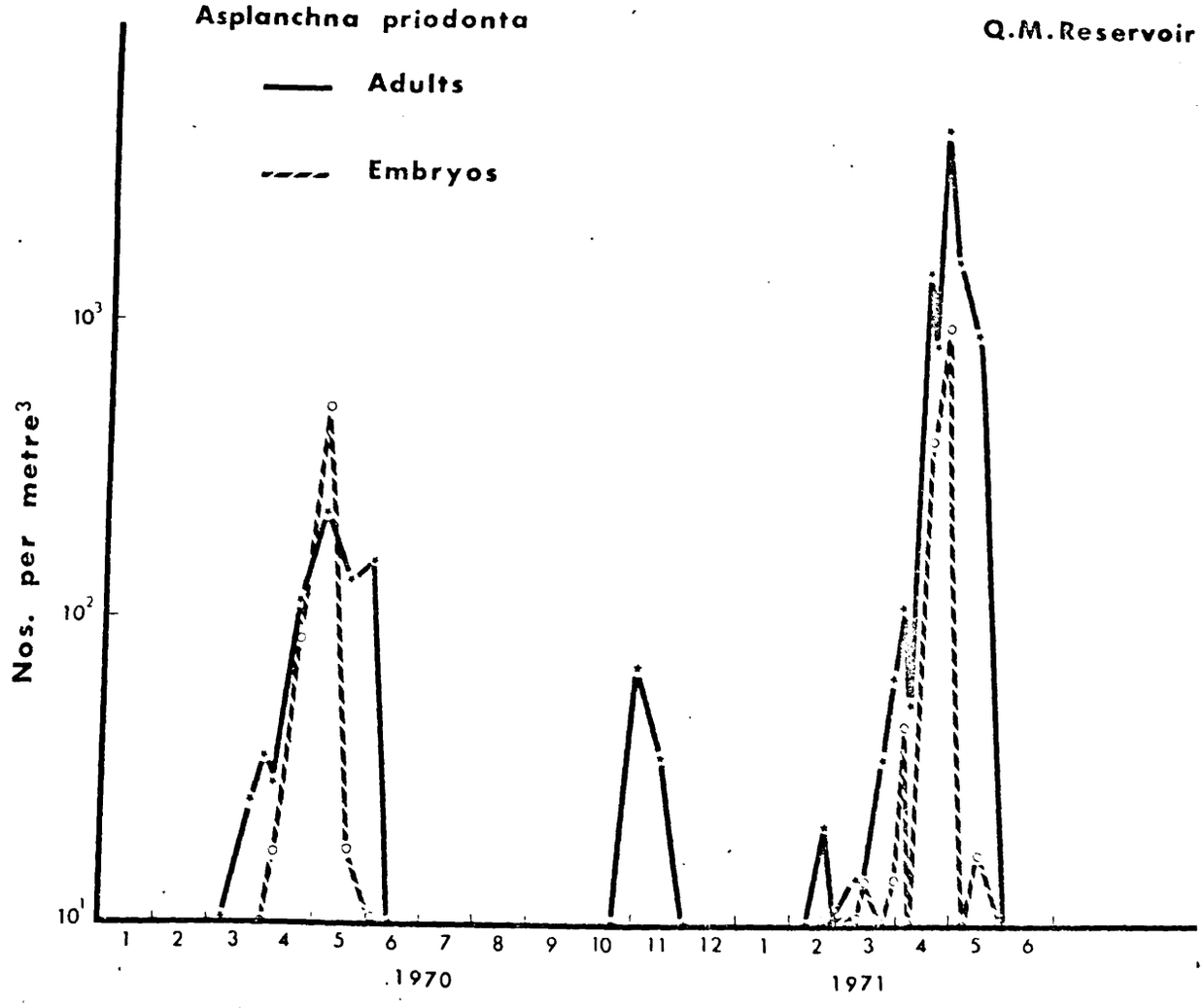
Egg ratios (Table 16) were higher just before the spring bloom reaching 0.94 in Q.M. in 1970 and 0.98 in Q.E.II. The high ratios persisted longer in Q.M. but the larger overwintering population in Q.E.II produced almost identical peak populations in the two reservoirs. In spring 1971 the Q.E.II egg ratio was consistently low, never exceeding 0.49 and generally fluctuating around 0.20. Though the Q.M. population did not have as high ratios as in 1970, ratios between 0.51 and 0.67 persisted throughout March and at the beginning of April.

Polyarthra vulgaris

Many eggs of this species were found loose in sample bottles. They are readily distinguishable from those of other genera by a number of large fat globules. Nipkow (1952) found that newly hatched P. dolichoptera were filled with fat. Since newly laid eggs are less likely to be detached from the adult than those nearing term, the presence of the fat globules might be a useful diagnostic feature for amictic eggs of this genus. (See also Wesenberg-Lund 1930 Plate XI, Pourriot 1965b) Plate II)

P. vulgaris had very high egg ratios in Q.M. in spring 1970 and 1971. The first year, the maximum was 1.04, the second 2.18, and correspondingly, the mean population present over the spring period was doubled in 1971 compared with the previous year. (Figure 26 and 27) The maximum egg ratio in Q.E.II in 1970 (Table 16) was only 0.45 in spring, but a higher value was obtained in October when a second, larger population peak developed. Just prior to that peak, the egg ratio reached 0.70. The following spring however the population and the egg ratios were extremely low, the latter never exceeding0.32.

P. vulgaris was the only species with a sexual phase. In both reservoirs


Asplanchna priodonta
Q.M. Reservoir
Adults
Embryos
Nos. per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6
1970
1971

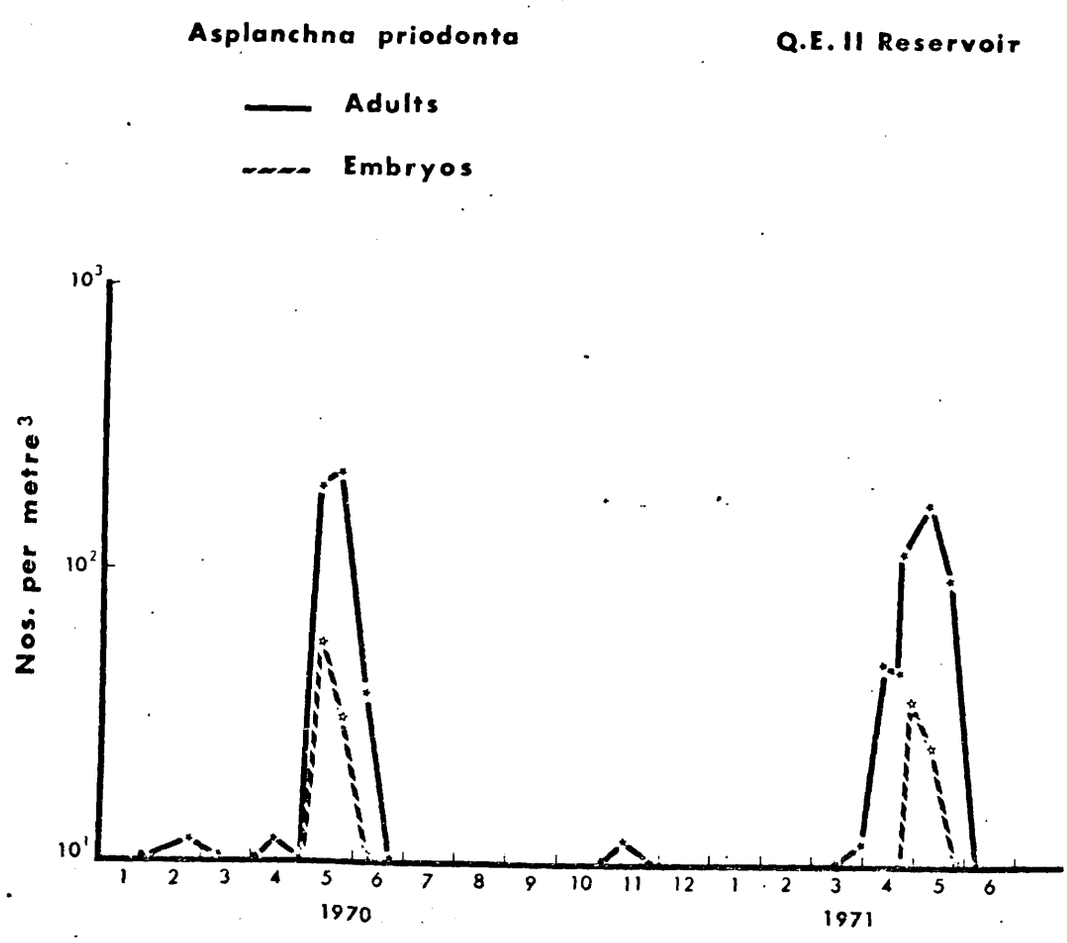

Asplanchna priodonta
Q.E. II Reservoir
Adults
Embryos
Nos. per metre³
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6
1970
1971

Fig. 28. Adult standing crop and embryos of Asplanchna priodonta in Q.M.

Fig. 29. Adult standing crop and embryos of Asplanchna priodonta in Q.E.II

mictic females carrying male eggs were only found in autumn 1970 at the peak of population numbers. In Q.M. maximum numbers of mictic females occurred during the decline of amictic egg production, but in Q.E.II both types of egg were produced in fairly large numbers just prior to the population peak. This difference in such similar populations suggests as Birky and Gilbert (1971) demonstrate, that an environmental factor, independent of population size, controls the appearance of mixis.

Asplanchna priodonta

This species is viviparous but it is a simple matter to count developing embryos in the body of the transparent adult. A. priodonta plays a relatively small part in the rotifer population of Q.E.II (Figure 29) and the egg ratios during the spring when the size of the population in increased are very low, only once exceeding 0.70 (Table 16) In the Q.M. reservoir the spring populations were quite large (Figure 28) and many females were found containing several embryos in different stages of development. In 1970, the maximum egg ratio was 2.29, in 1971 it was 1.0 (Table 16) and though the population increased rapidly the numbers were not maintained.

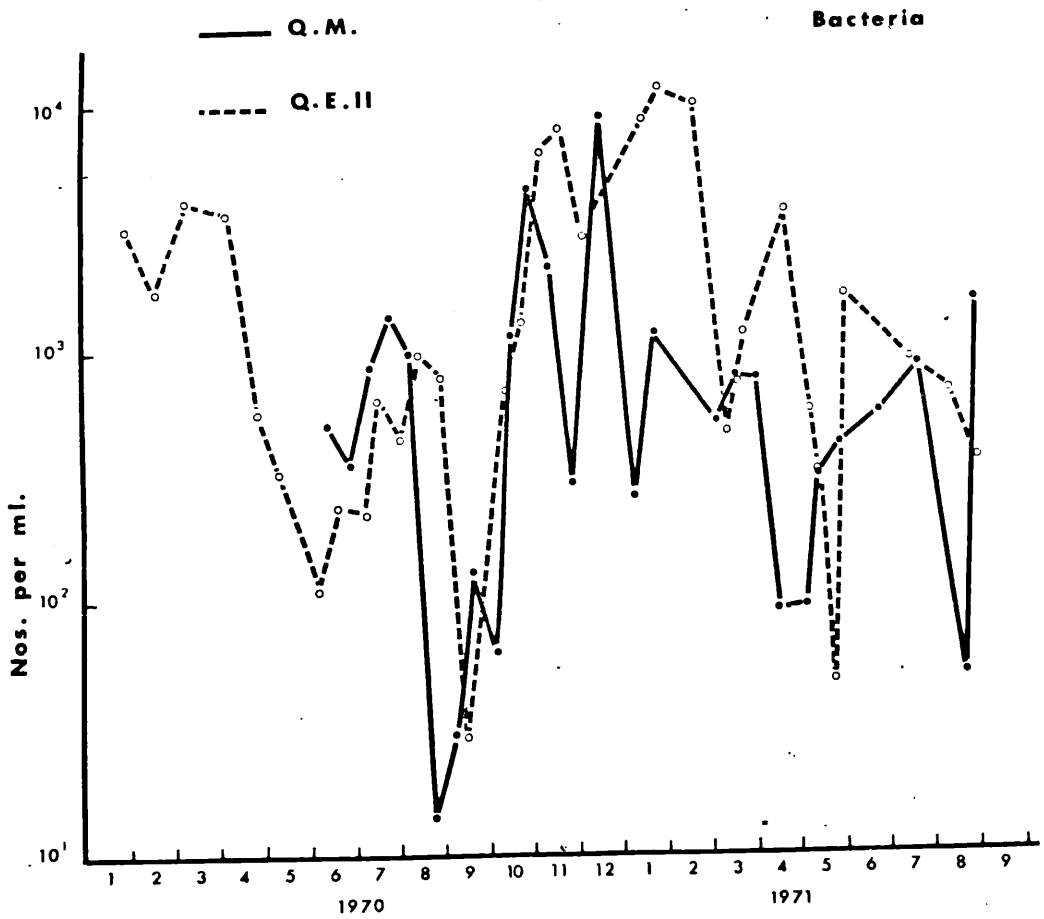

Q.M.
Q.E.II
Bacteria
Nos. per ml.
10^4
10^3
10^2
10^1
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 30. Bacteria standing crop in Q.M. and Q.E.II

Standing Crop of Bacteria

Figure 30 shows the results of plate counts of bacteria collected with a Patalas sampler. The data used for the earlier part of 1970 in Q.E.II were obtained by transferring those of Price (unpublished Ph.D. thesis) derived from Friedinger samples from the same reservoir. Curzon (unpublished) found that the relationship between plate counts derived from Patalas and Friedinger samples taken on the same day could be expressed by the equation

$$y = 0.87x + 0.654 \quad (r = 0.89)$$

where y was Patalas data and x Friedinger data in numbers per ml. This relationship was used to transform Price's data to make it comparable with the rest of the year.

The crudity of the plate count method only allows for comparison of major variations in bacteria standing crop, (Collins and Willoughby 1957) and though much data is available from elsewhere, the many different plating and counting techniques in use make direct numerical comparisons impossible.

Peak numbers of viable, colony forming bacteria occurred in both reservoirs over the winter months and high counts persisted until April or May when the first major crash occurred. This contrasts with the findings of Taylor (1949b) only in the dating of the fall in numbers which in the English Lakes generally occurs in March. However Willoughby and Collins (1966) point out the great incidental variations which can occur over very short periods, increased rainfall for example being followed by increased bacteria numbers. (Collins and Willoughby 1962)

Numbers throughout June and July were very low falling to a minimum at the beginning of September or end of August, but numbers increased again in October and November and remained high over the winter months. The maximum number of bacteria recorded during the period over which samples were taken were 12,000 cells per ml in Q.E.II in February 1970 (Table 17), but the maximum

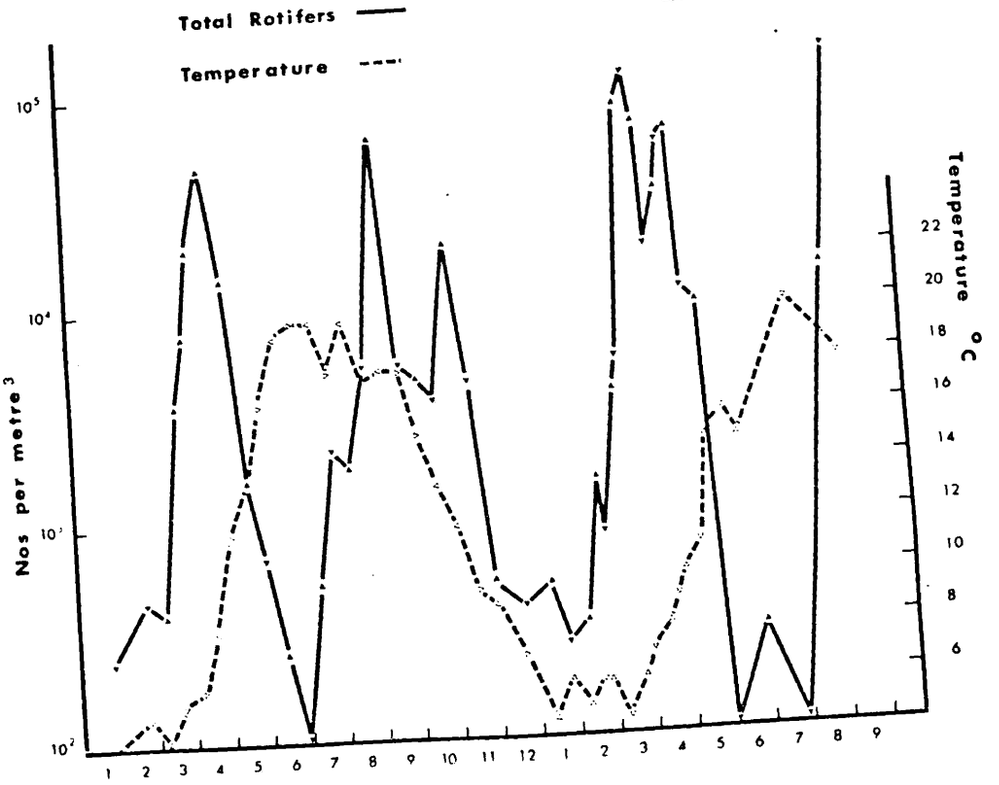
recorded in Q.M. was 8,700 per ml. in December. The values are of the same order of magnitude as numbers of epilimnetic bacteria in Esthwaite Water (Jones 1971) which, compared with the other English Lakes, is relatively rich in nutrients. Jones used a slight modification of the casein-peptone agar used in the present work but it was felt that numbers would still be comparable.

Table 17

Standing Crop of Bacteria for Q.M. and Q.E.II

Q.M.		Q.E.II		
Date	Bacteria in nos. per ml.	Date	Bacteria in nos. per ml.	
15/6	500	30/1	3219	
29/6	351	17/2	1740	
13/7	855	10/3	4002	
27/7	1377	7/4	3654	Price
10/8	993	28/4	566	
24/8	14	12/5	322	
7/9	30	19/5	1349	
21/9	128	8/6	110	
5/10	64	22/6	235	
19/10	1173	8/7	223	
2/11	4590	20/7	640	
16/11	2200	3/8	445	
30/11	295	17/8	963	
21/12	8700	1/9	793	
12/1	259	15/9	28	
25/1	1175	12/10	670	
8/3	515	26/10	1303	
22/3	785	9/11	6350	
5/4	760	24/11	7875	
19/4	90	8/12	2840	
6/5	96	20/1	8500	
17/5	310	2/2	12300	
1/6	415	25/2	1080	
28/6	545	15/3	456	
26/7	850	29/3	1170	
23/8	50	27/4	3650	
6/9	1583	11/5	575	
		24/5	46	
		7/6	1685	
		19/7	870	
		16/8	678	
		1/9	365	

Q. M.


Total Rotifers
Temperature
Nos per metre³
Temperature °C
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Q.E.II

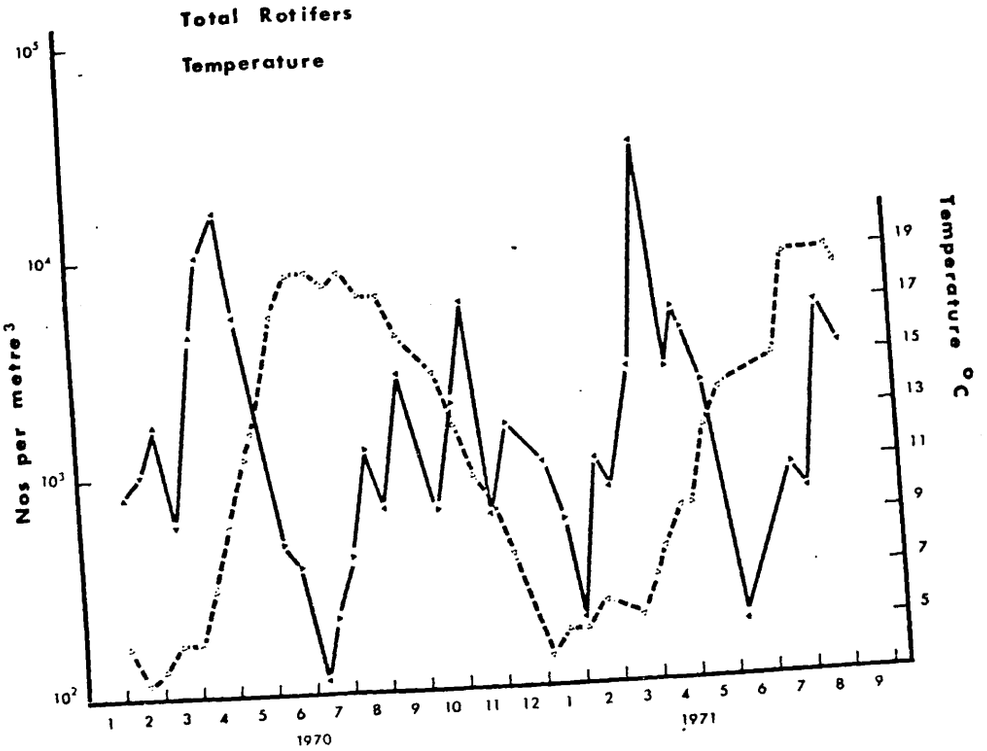

Total Rotifers
Temperature
Nos per metre³
Temperature °C
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 31. Rotifer standing crop and temperature in Q.M.

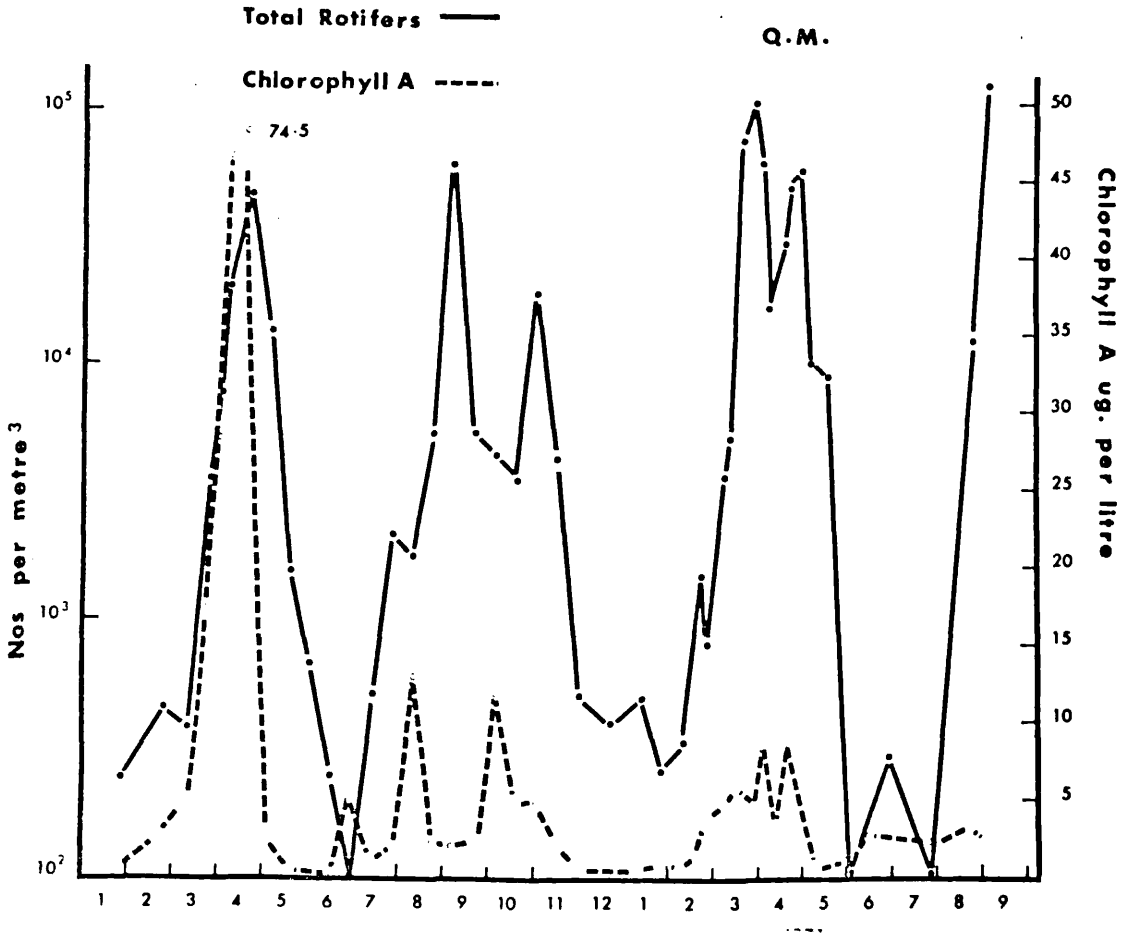
Fig. 32. Rotifer standing crop and temperature in Q.E.II

Discussion: Relationship between physico-chemical data, seston and rotifer standing crop

Rotifer standing crop and temperature

Figures 31 and 32 show the rotifer standing crop and temperature plotted on the same axes. The most notable point was that in both reservoirs the rotifer populations were at their maximum when the temperature was either steadily increasing or steadily decreasing. The rate of change of temperature was calculated from the slope of the line relating time to temperature and found to be 1.5°C in ten days. What effect a changing temperature might have on development rate and other metabolic processes could not be determined. It is probable however that so slight a change in temperature in comparison with the shortness of the period required for egg development (see later) would have little effect on any one generation of rotifers, but the relationship between changing temperature and acclimation in poikilotherm metabolism has not been studied except by Newell (1969). This author demonstrates the relative independence of standard metabolism on temperature but the rate of activity of an animal differs markedly with short term fluctuations in temperature. Such adjustments to ambient temperature must occur during spring and autumn in the reservoirs so that the zooplankton is never deeply acclimated.

It has been shown earlier that of the species investigated here only one, Synchaeta oblonga could be described as a cold stenotherm. The rest were present at various temperatures within the range 5° - 20°C. which represents the limits of the seasonal variation in temperature in the reservoirs. Despite this, the total standing crop of rotifers began to decline when the temperature was only about 14°C (see figures 31 and 32), and remained at low levels when the temperature was at its highest. The autumn increase in rotifer populations began in both reservoirs when the temperature was fairly steady. The standing crop remained high when the


Total Rotifers
Chlorophyll A
Q.M.
74·5
Nos per metre³
Chlorophyll A ug. per litre
10⁵
10⁴
10³
10²
50
45
40
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

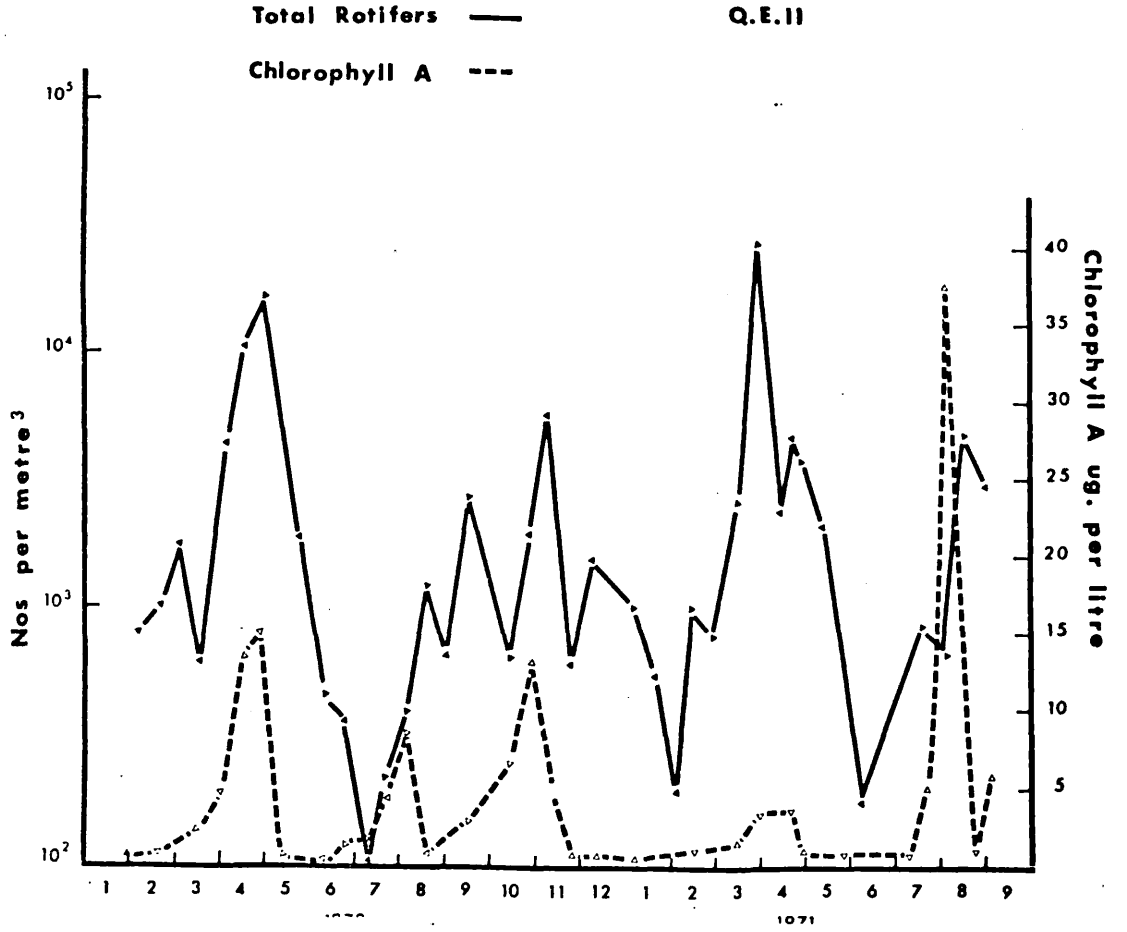

Total Rotifers
Chlorophyll A
Q.E.II
Nos per metre³
Chlorophyll A ug. per litre
10⁵
10⁴
10³
10²
40
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Fig. 33. Rotifer standing crop and chlorophyll A in Q.M.

Fig. 34. Rotifer standing crop and chlorophyll A in Q.E.II

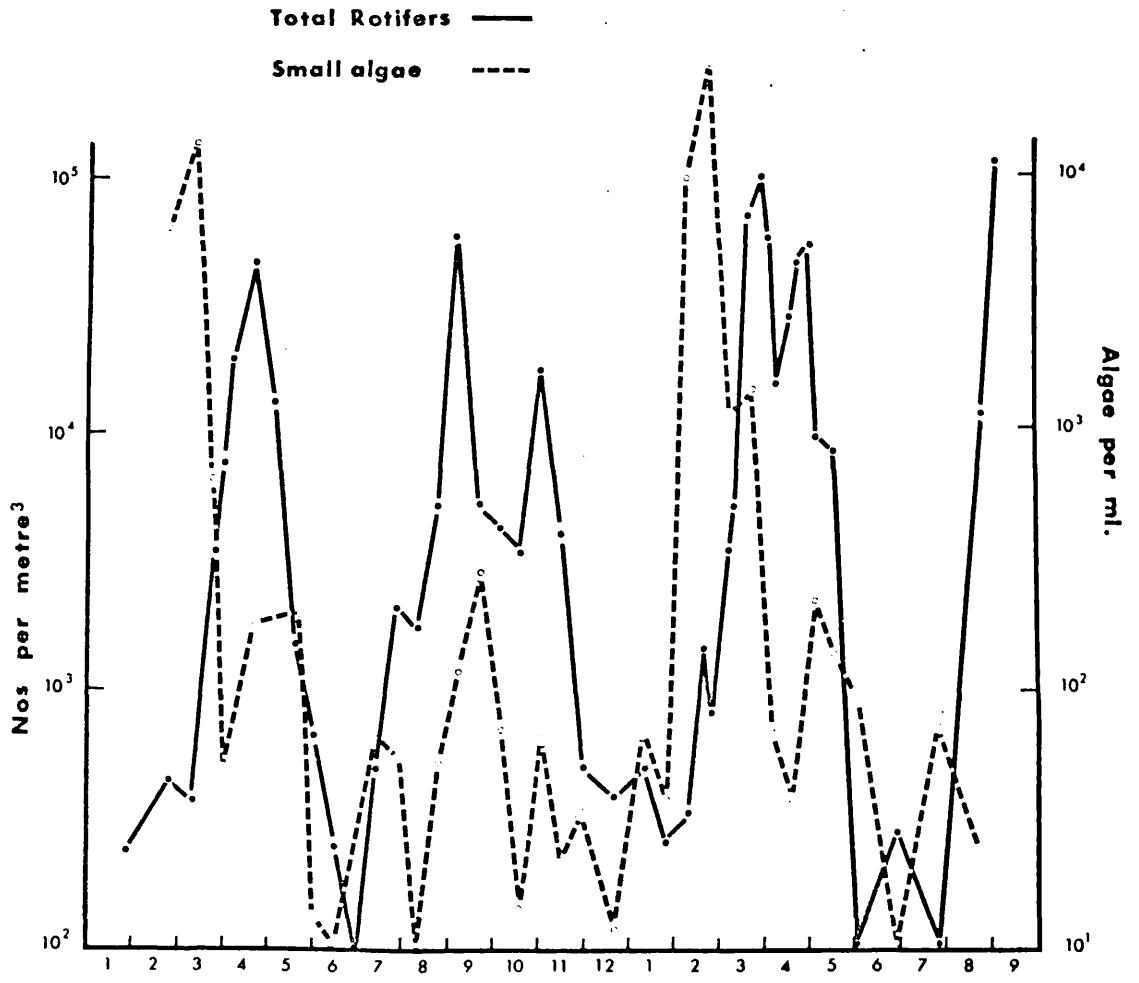
temperature began to fall but when it reached 7° - 8°C, the decline in the rotifer population began.

It is clear therefore that temperature could not trigger the sudden increase in rotifer numbers either in spring or autumn, nor could metabolic changes related to temperature account for the sudden decline from peak numbers. Some other factor must be considered. The most obvious one is food. Assuming that the single most important factor determining the availability of food for planktonic animals is size of particle (Jorgensen 1966), then the food available for planktonic rotifers must consist of some combination of algae, bacteria and detritus (Pourriot 1965). Therefore it was considered valuable to compare the rotifer standing crop with a series of factors related to available food before examining the feeding relationship in more detail.

Rotifer standing crop and chlorophyll A

Chlorophyll A is often used as an indicator of the standing crop of algae even though it is known that relationship between chlorophyll and algal biomass is extremely variable. (Bowles and Quennell 1970) In figures 33 and 34, chlorophyll A is plotted with the rotifer standing crop.

In most instances peaks of chlorophyll almost coincided with peaks of rotifer abundance but at this stage no causal relationship could be inferred since the spring peaks of chlorophull A consisted mainly of large diatoms such as Stephanodiscus astraea and Asterionella formosa and the autumn peaks were mainly Tribonema, Anabaena and Microcystis. All these would seem, according to the criteria of Gliwicz (1969) and Pourriot (1965), to be too large to provide food for most of the reservoir rotifers. That food was provided by organic matter other than the algae named above was perhaps suggested also by the situation in both reservoirs in spring 1971. No noticeable reduction in peak standing crops of rotifers occurred in 1971


Total Rotifers
Small algae
Nos per metre³
Algae per ml.
10⁵
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Q. E. II

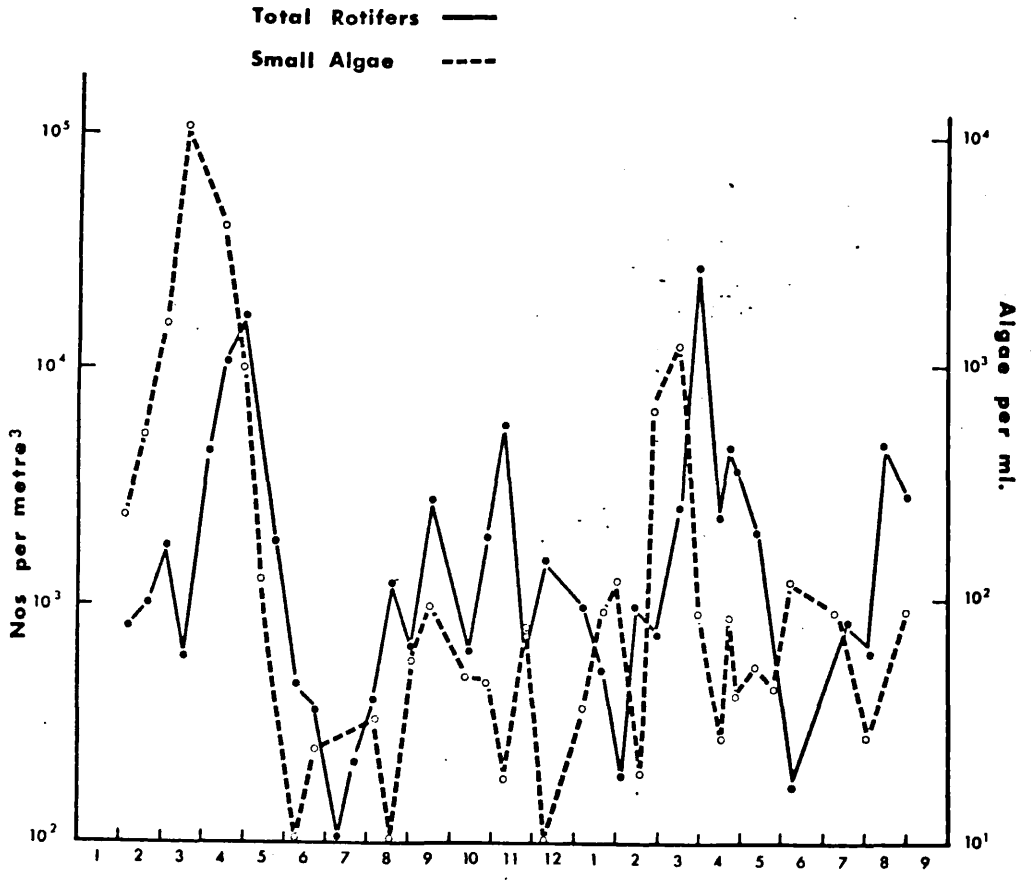

Total Rotifers
Small Algae
Nos per metre³
Algae per ml.
10⁵
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Fig. 35. Rotifer standing crop and small algae in Q.M.

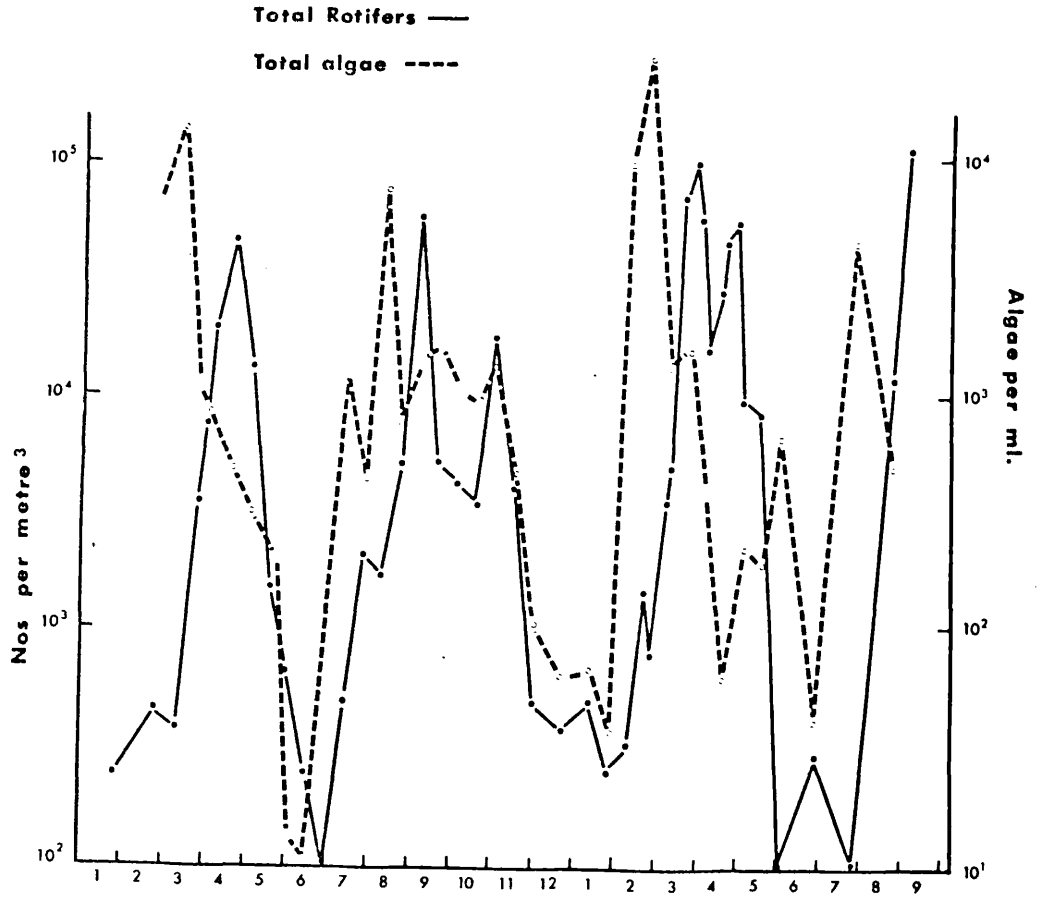
Fig. 36. Rotifer standing crop and small algae in Q.E.II

compared with the previous spring but the chlorophyll content was reduced to 9.08ug/litre in Q.M. compared with 74.57 the previous year, and in Q.E.II the spring peak of 1971 was only 3.79ug/litre compared with 15.14 in 1970. Similarly in autumn 1971, though the chlorophyll content was never more than 3.34ug/litre in Q.M., the highest rotifer standing crop of the entire sampling period, 130,800 per cubic metre, was recorded, whilst in Q.E.II with a peak chlorophyll of 37.9ug/litre, the largest rotifer population was only 4,700 per cubic metre, lower than both spring peaks and slightly less than that of the previous autumn. It seems therefore that only in cases where the phytoplankton is dominated by one species or by a group of species of similar size and chlorophyll composition can a comparison of smaller herbivorous zooplankton standing crop with chlorophyll show genuine feeding relationships. This is probably the case for example in Lake George, Uganda, where Burgis (1971) found a clear increase in the standing crop of Lecane bulla with increase in chlorophyll A. The Lake George phytoplankton consists predominantly of blue-green algae, chiefly Microcystis, and the rotifer is associated with clumps of these algae in the open water of the lake.

Rotifer standing crop and total small algae

Figures 35 and 36 show the rotifer standing crop in relation to the numbers of small algae. These algae were selected from the counts of Mrs. C. Nadin-Hurley on the basis of their suitability as food according to the criteria of Pourriot (1965) which includes a wider size range than that described by Gliwicz (1969). In spring of both years in both reservoirs the peak of rotifers occurred immediately after that of the small algae which at this time were mainly flagellates less than 3u long. The population of rotifers appeared therefore to begin increasing from the low winter population at a time when this food source was most abundant. Edmondson(1965) found strong correlations between the reproductive rate

Q.M.


Total Rotifers
Total algae
Nos per metre 3
Algae per ml.
10⁵
10⁴
10³
10²
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Q. E. II

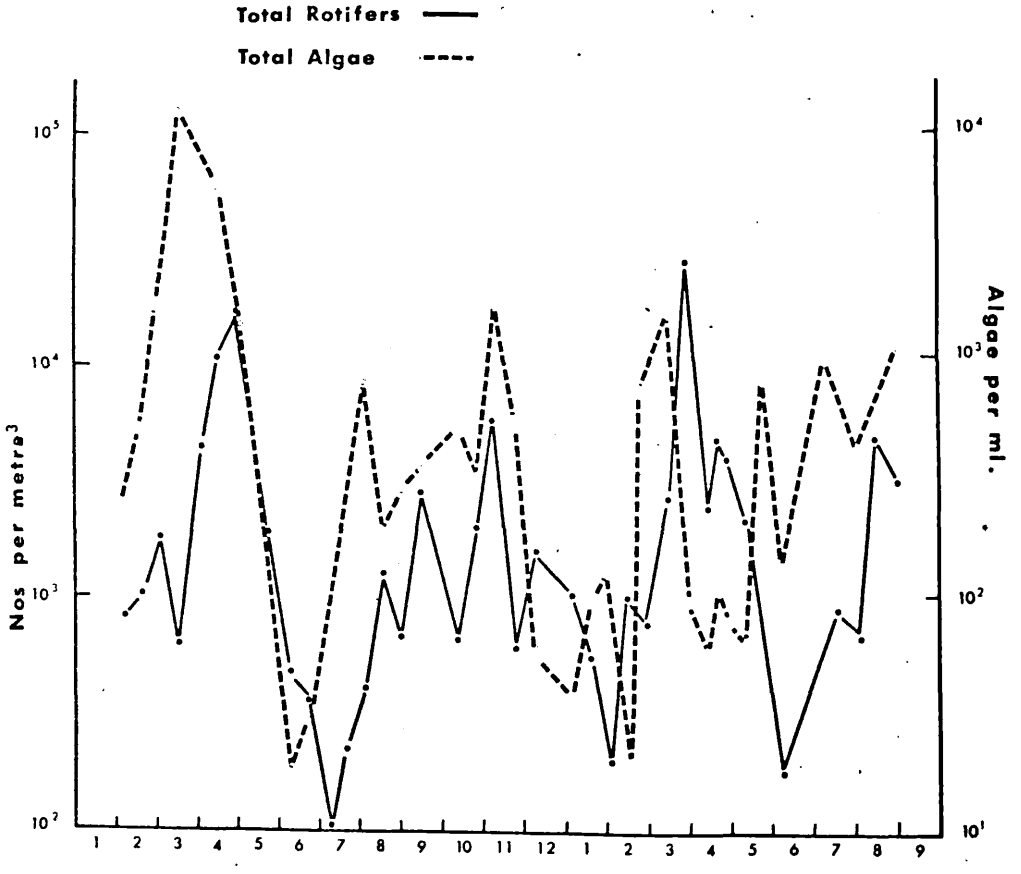

Total Rotifers
Total Algae
Nos per metre³
Algae per ml.
10⁵
10⁴
10³
10²
10⁴
10³
10²
10¹
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9

Fig. 37. Rotifer standing crop and total algae in Q.M.

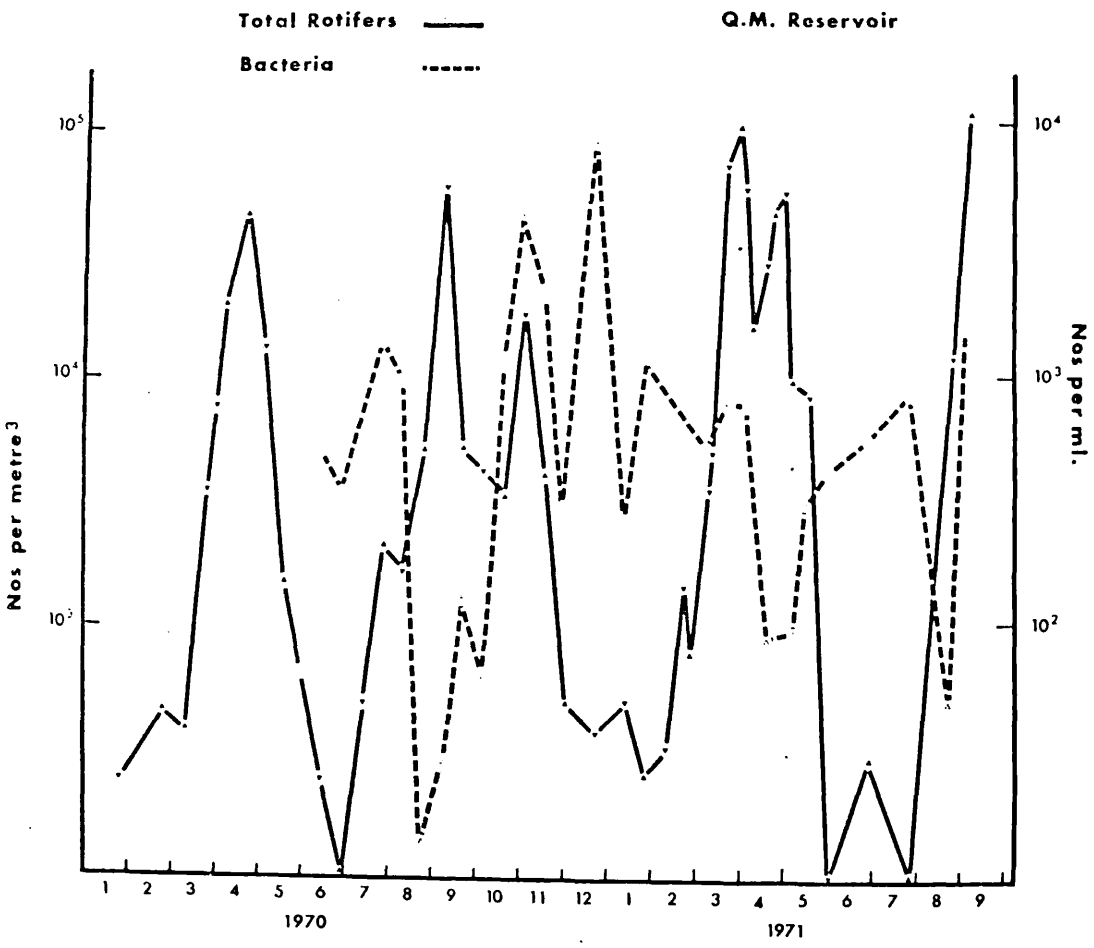
Fig. 38. Rotifer standing crop and total algae in Q.E.II

of K. cochlearis and small algae in four of the English lakes. In the reservoirs, a rapidly increasing rotifer population seemed to be related to a high standing crop of small algae but this relationship only held in the spring and even then there was a time lag of at least one sampling interval between the suggested cause and its effect. The autumn population of rotifers began to increase in abundance when the standing crop of small algae per ml. was less than one hundred (Q.E.II) or only a little over this number (Q.M.) This is far below the concentration usually present in rotifer ponds and cultures, (cf. Pourriot 1957,1958, 1965; Erman 1962; Galkovskaya 1963; Ito 1955, 1957; Pennington 1941), and would be inadequate to maintain the population if no other food source were available.

The small algae included in Figs 35 and 36 were not reflected in the Chlorophyll A picture (cf. Figs 33 and 34) of which the highest concentration in spring occurred after the peak of small algae, and the highest autumn concentrations were independent of the numbers of small algae present at the time.

Rotifer standing crop and total number of algae

The lack of a relationship between rotifer standing crop and both chlorophyll A and small algae in the autumn suggested the presentation of the data shown in Figs 37 and 38. Edmondson (1965) mentions the possibility of blue-green algae such as Anabaena serving as food for rotifers if the algal filaments break up or cells become detached in large numbers. He does not however examine this possibility in his work. In the same paper he describes the feeding mechanism of Polyarthra spp, which, unlike the Brachionidae such as Keratella cochlearis and K. quadrata, not only creates a current of water drawing in small suspended particles but also performs a strong pumping action with the relatively rigid mastax so that larger, soft particles can be distorted and sucked between the jaws. In this way, short


Total Rotifers
Bacteria
Q.M. Reservoir
Nos per metre3
Nos per ml.
10^5
10^4
10^3
10^2
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

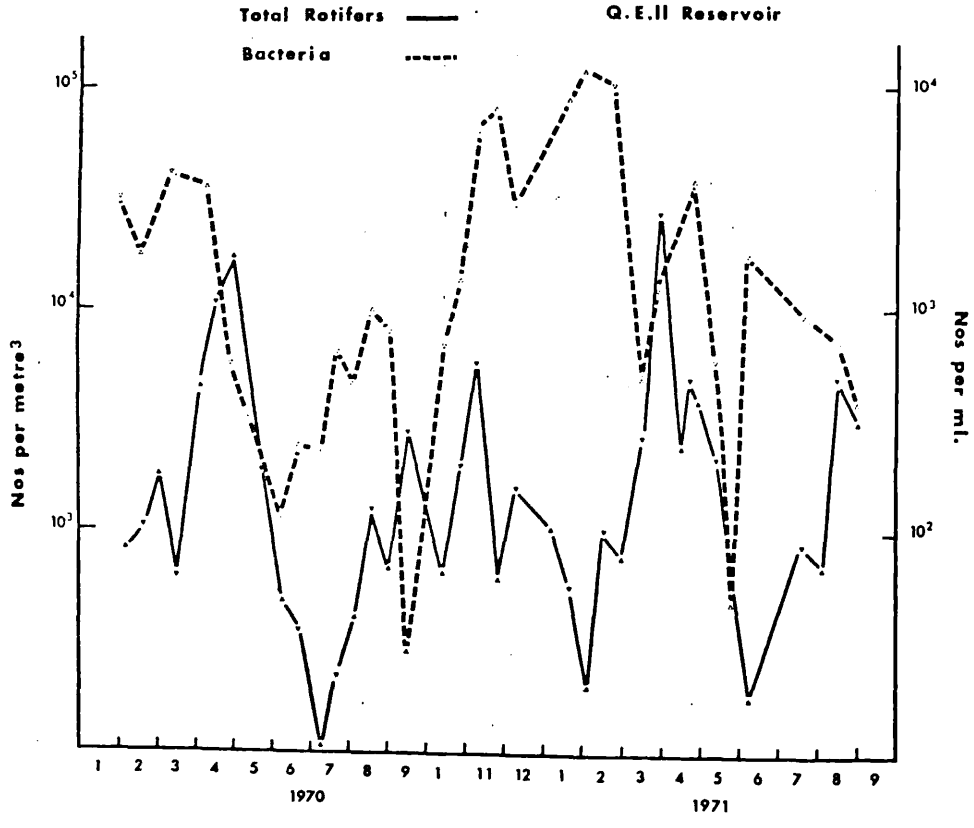

Total Rotifers
Bacteria
Q.E.II Reservoir
Nos per metre3
Nos per ml.
10^5
10^4
10^3
10^2
1 2 3 4 5 6 7 8 9 1 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 39. Rotifer standing crop and bacteria in Q.M.

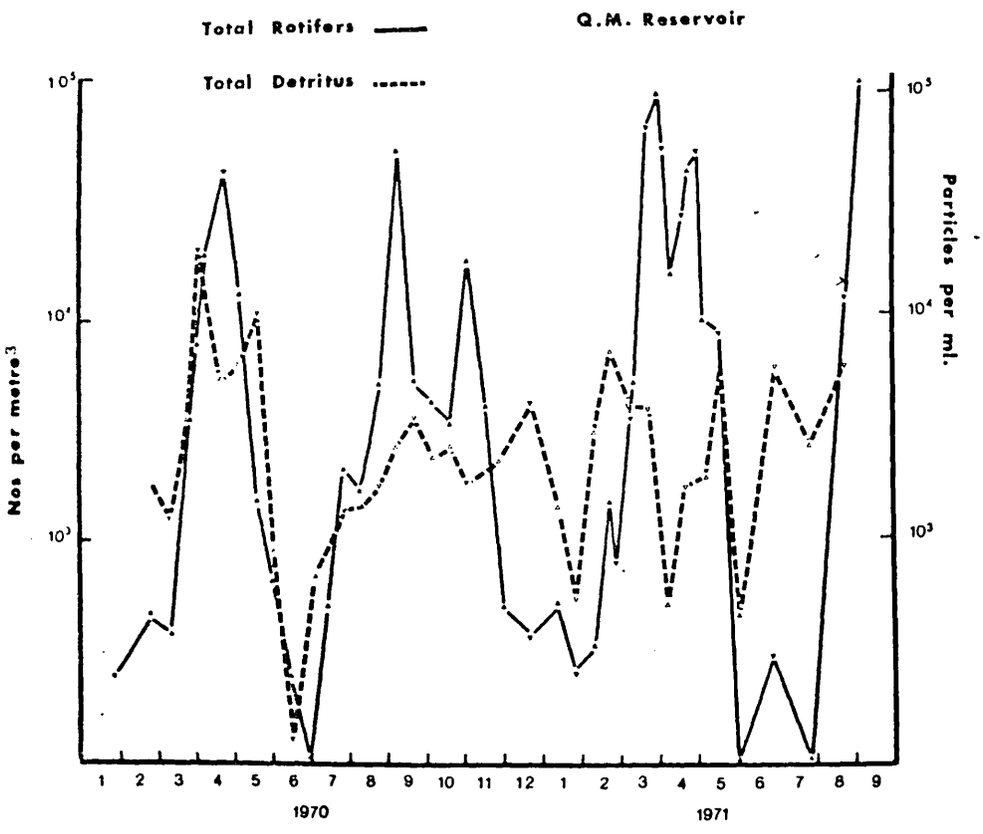
Fig. 40. Rotifer standing crop and bacteria in Q.E.II

lengths of blue-green algal filaments could form part of the food of this species. In a similar way Tribonema filaments could become edible when broken down. No information is available on the digestibility of either of these algae by any rotifer species.

The spring peak of total algae in both reservoirs shown in Figs 37 and 38 did not fall off so rapidly as that of small algae (cf also Figs 13 and 14), being broadened, as it were, by the increase in the number of diatoms. Nevertheless the peaks reflected each other to a considerable extent. This was not the case in the autumn where the total number of algae increased just prior to the autumn build-up of rotifers whilst the number of small algae fluctuated at a very low level. The relationship between the autumn peak of algal numbers including Tribonema and Anabaena, and the rotifer peak, showed a similar time lag to that between the spring peak of small algae and that of the rotifers. Since the autumn peaks of rotifers were dominated by Polyarthra vulgaris, the feeding relationship suggested above might contribute to the decline of the autumn blue-green algae bloom. The extension of this bloom into October and November was due largely to Microcystis which, being embedded in a mucilaginous matrix is least susceptible to the centrifugal action of the rotifer corona. Pourriot (1965) quotes Edmondson as finding a strong correlation between Polyarthra vulgaris and Cryptomonas. This alga was present throughout the year in both reservoirs but with numbers too low to be significant. (See tables 8 and 10)

Rotifer standing crop and bacteria

Bacteria have also been suggested as possible food for planktonic animals (Rodina 1947, Gliwicz 1969). Figures 39 and 40 give no suggestion that a consistent relationship existed in the reservoirs. Though bacteria numbers did fall off near the spring peaks of rotifers there were increases in bacteria numbers during autumn peaks. These inconsistencies may in part


Total Rotifers
Total Detritus
Q.M. Reservoir
Nos per metre³
Particles per ml.
10⁵
10⁴
10³
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

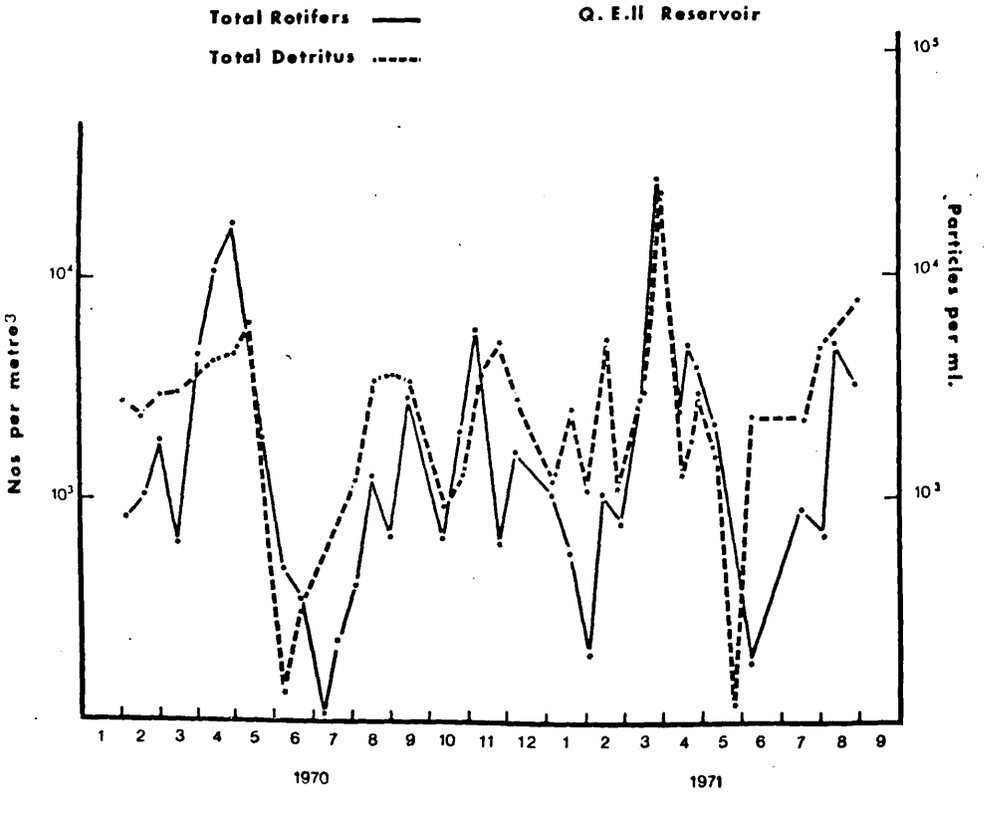

Total Rotifers
Total Detritus
Q. E.II Reservoir
Nos per metre³
Particles per ml.
10⁵
10⁴
10³
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 41. Rotifer standing crop and total detritus in Q.M.

Fig. 42. Rotifer standing crop and total detritus in Q.E.II

be due to changes in dominance within the rotifer population causing a shift in grazing pressure. Edmondson (1965) suggests that very small particles may be outside the feeding range of Polyarthra. This species dominated the autumn peak when increases in bacteria numbers associated with a rapid build up of blue-green algae would not be removed by a grazer which prefers larger particles.

Rotifer standing crop and detritus

Figures 41 and 42 show the rotifer standing crop and the numbers of detritus particles per ml. taken from Tables 9 and 11. In Q.M. the spring peak of rotifers in 1970 coincided with a high detritus content and the low summer population in 1970 occurred when there was very little particulate matter in the reservoir. During the rest of the sampling period, the detritus in Q.M. fluctuated randomly in relation to the rotifer population though there was some tendency in January and June for low population numbers to occur coincidentally with low detritus counts.

In Q.E.II the relationship between the rotifer population and detritus was very much clearer though the time lag between the peaks and depressions of these two parameters was not consistent. Nevertheless it can be said that in general a high content of particulate matter, unidentifiable biologically, occurred during periods when rotifer populations were at their highest and this was particularly clear in Q.E.II.

Summary

Figs 31 - 42 suggest therefore that the influence of temperature on the rate processes of rotifers in these reservoirs was strongly modified by food availability. Though the best method of determining food influence is by comparing rates of change of the food and grazing populations, nevertheless some ideas can be gleaned from comparisons of standing crop data.

In spring when rotifer populations were high all food sources, bacteria, small algae and detritus were available in considerable numbers, with the small algae, mainly flagellates, rising to peak numbers whilst the rotifer population appeared to be increasing most rapidly. Bacteria, other small algae apart from flagellates, and detritus were all available during the winter months, and the temperature was not so markedly lower than the spring that this factor could be responsible for limiting the rotifer population. It seems therefore that the appearance in great numbers of a food qualitatively better than bacteria or detritus initiated the great increase in the rotifer population in the spring.

During June and early July the reservoirs were virtually devoid of algae, detritus and rotifers, but Bettrell(personal communication) found the highest phytoplankton and zooplankton numbers in the River Thames in June. The rotifer populations of the Thames and the reservoirs are qualitatively and quantitatively very different, but one cannot ignore the influence that dying plankton and decaying organic matter carried in from the Thames would have on the biologically"empty" reservoirs. The increase in detritus (Figs 41 and 42) and in the total number of algae (Figs. 37 and 38) in July and August in the reservoirs must be related to the inflow from the Thames since no physico-chemical change occurred in the reservoirs. These increases preceded the increase in the rotifer populations in July and August and probable triggered this increase. The contrast with the spring picture where small flagellates initiated the bloom of rotifer may in part be caused by qualitative differences in the detritus. In July the detritus coming into the reservoirs from the Thames would be rich in organic matter carrying as it does blooms of phytoplankton and zooplankton. On the other hand the winter detritus could not be derived from biological material but would be mainly mineral particles washed into the Thames by flood water. The peak

of suspended material in the Thames was in February (Bottrell, personal communication) and was not related to high algae or zooplankton numbers.

Rates of change of rotifer populations

Comparisons of standing crop data between ecosystems convey little valuable information if they are not coupled with data concerning the rates at which populations are increasing or declining. The same standing crop value may be the result of a population slowly increasing in numbers in one ecosystem and the maximum population produced by a sudden bloom in another ecosystem. The organism-environment interaction is different in these two cases and the difference becomes more apparent when rates of change are compared.

The logistic equation $N_t = N_o e^{rt}$ was used to calculate r, the rate of change of the population.

N_o = The number of animals at time o

N_t = The number of animals after time t

e = The base of natural logarithms.

N_t and N_o were obtained from the standing crop data recorded in Tables 12-17 and shown graphically in Figures 15-30, whilst t was the interval between samples. By this method rates of change were calculated for the whole rotifer population as a unit, then for six species singly: Keratella cochlearis, K. quadrata, Polyarthra vulgaris, Synchaeta oblonga, S. pectinata, and Asplanchna priodonta. The results are recorded in Appendix I

The seasonal variation in r is reflected in the size of the standing crop and can be visualised relatively easily from Figs. 15-30 from the slopes of lines connecting one point to the next. It was therefore considered superfluous to plot the seasonal pattern of fluctuations in r since the discussion would be similar to that of the standing crop data. The values of r are therefore grouped according to ambient temperature in Figures 43-49.

Physiological rate processes are extremely temperature sensitive but the value of r, since it involves population survival is also influenced by

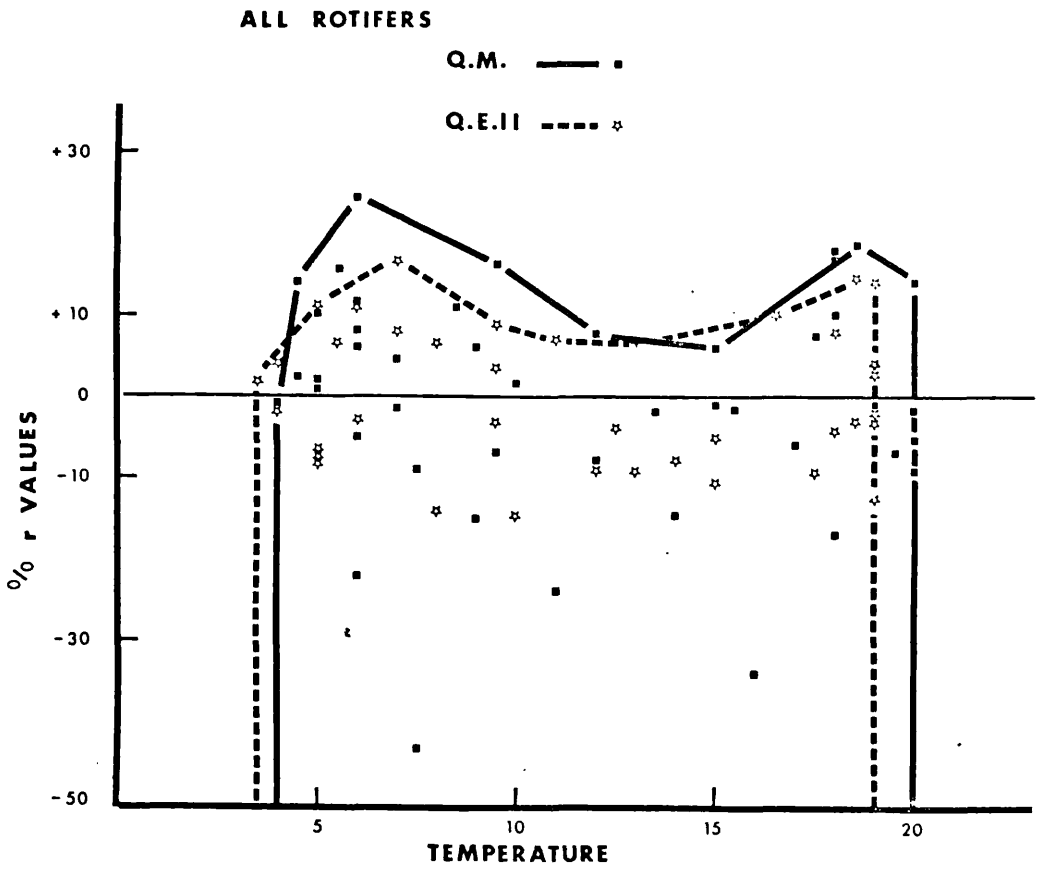
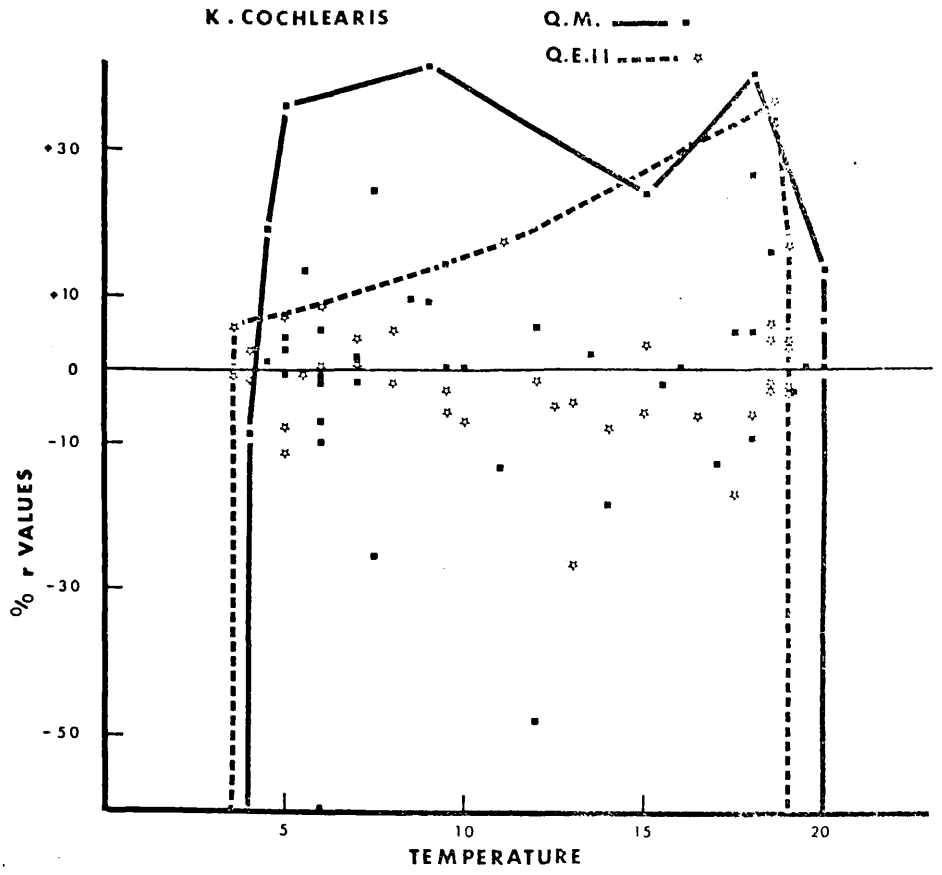

ALL ROTIFERS
Q.M.
Q.E.II
+30
+10
0
-10
-30
-50
% r VALUES
5
10
15
20
TEMPERATURE

Fig. 43. Rates of change of whole rotifer population against temperature in Q.M. and Q.E.II


K . COCHLEARIS
Q.M.
Q.E.II
+30
+10
0
-10
-30
-50
% r VALUES
5
10
15
20
TEMPERATURE

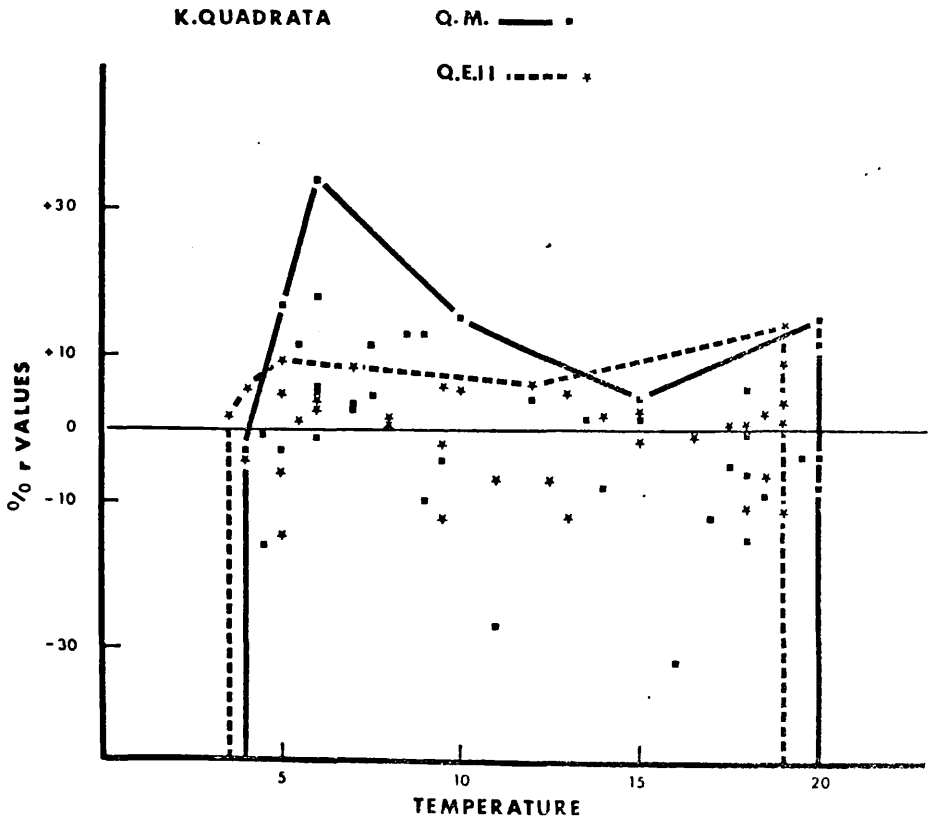

K.QUADRATA
Q.M.
Q.E.II
+30
+10
0
-10
-30
% r VALUES
5
10
15
20
TEMPERATURE

Fig. 44. Rates of change of K. cochlearis against temperature in Q.M. and Q.E.II

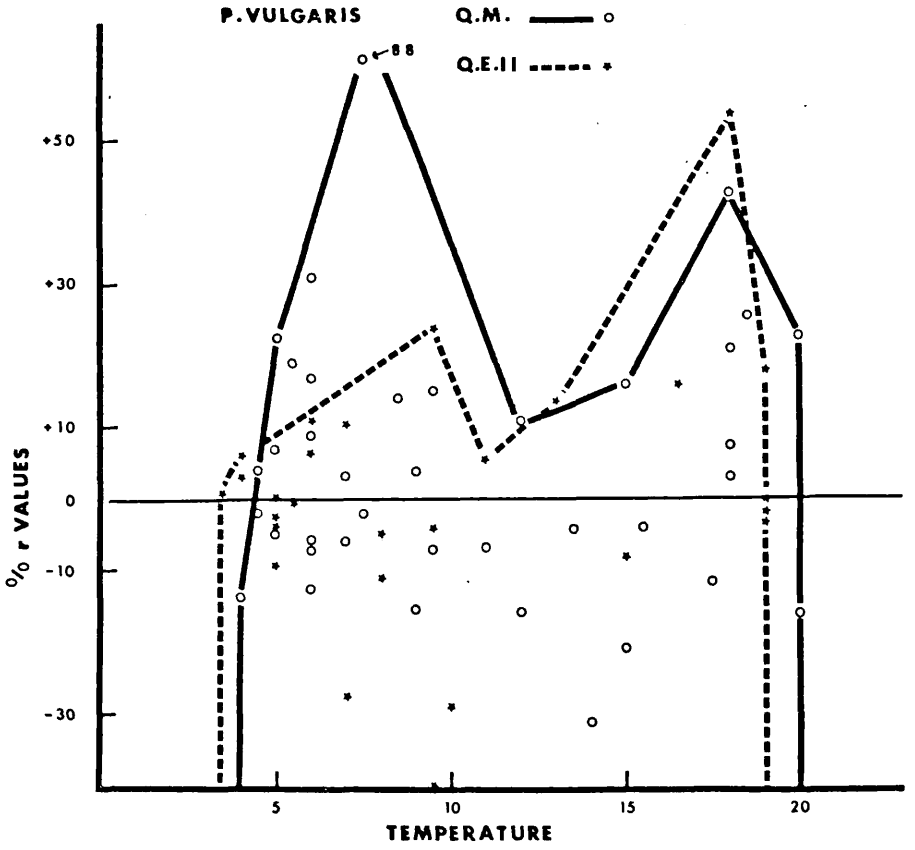
Fig. 45. Rates of change of K. quadrata against temperature in Q.M. and Q.E.II

food conditions, competition and predator/prey relationships. By grouping the r values according to temperature the influence of other factors is demonstrated whenever there is a departure from the expected increase in rate with rising temperature within the temperature limit of the organism under examination. Factors influencing a declining population are likely to be more complex than those influencing population increase and therefore only positive rates of change will be discussed in detail. Positive rates of change imply that the birth-rate of the population is greater than the death rate.

Figure 43 shows the rates of change of the entire rotifer population plotted against temperature. Maximal positive rates of change occurred between 5° and 8°C. with a noticeable decline from 8° to 16.5°C followed by another subsidiary peak at 18.5°C. The values for the Q.E.II reservoir were in general lower at any one temperature than those for Q.M.

When the rates of change for different species were considered separately four species followed the same general temperature pattern as the whole population. These were K. cochlearis, K. quadrata, Polyarthra vulgaris and Synchaeta pectinata (Figs 44-46, 48), but only the last species followed the same pattern in both reservoirs with the Q.E.II values lower than the Q.M. The other three species followed the generalised temperature distribution only in Q.M. In Q.E.II, K. cochlearis showed no noticeable peak at the lower temperatures, whilst K. quadrata and P. vulgaris both had higher rates of change at the upper end of the temperature range.

The two remaining species, S. oblonga and A. priodonta showed different temperature relations from the generalised picture. S. oblonga (Fig. 47) had r values of 19% or over in the temperature range from 5°-10°C. in Q.M. but there was a maximum value of 51% at 5°C. in Q.E.II, followed by a noticeable and steady decline over the remainder of the temperature range. A. priodonta (Fig. 49) had the same pattern in both reservoirs but with


P.VULGARIS
Q.M.
Q.E.II
.88
+50
+30
+10
0
-10
-30
% r VALUES
5
10
15
20
TEMPERATURE

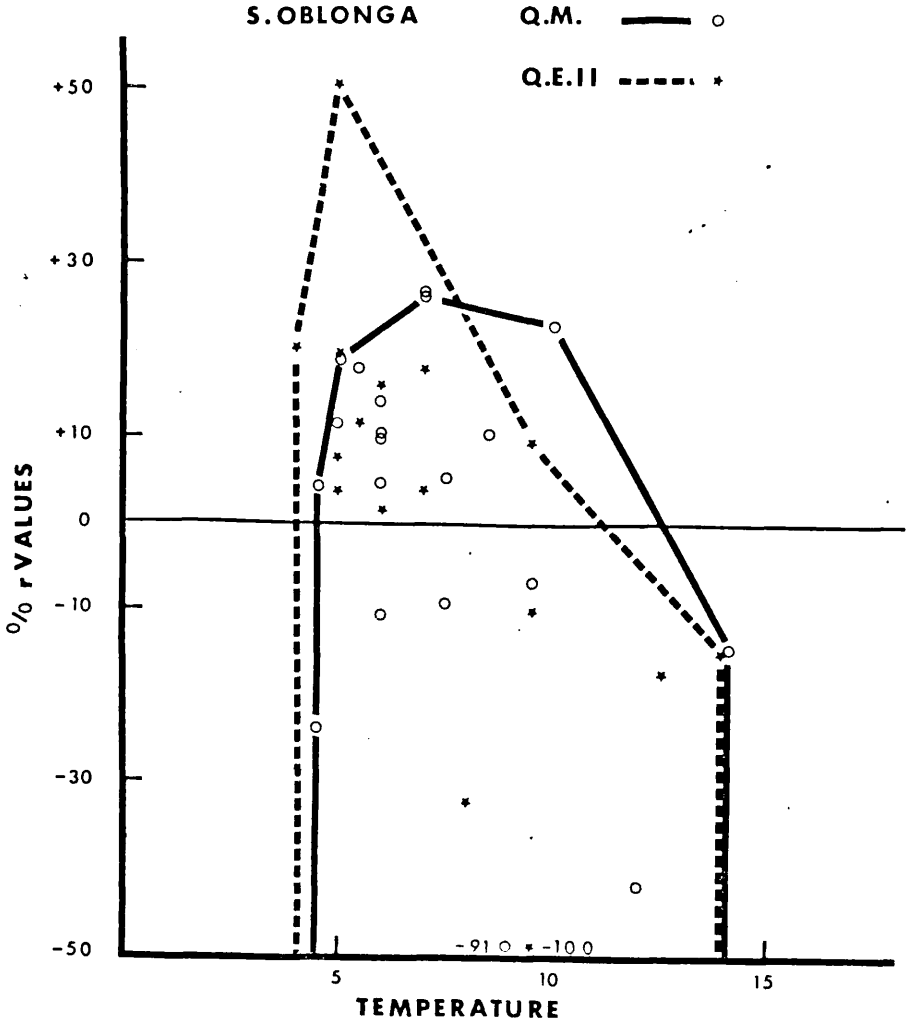
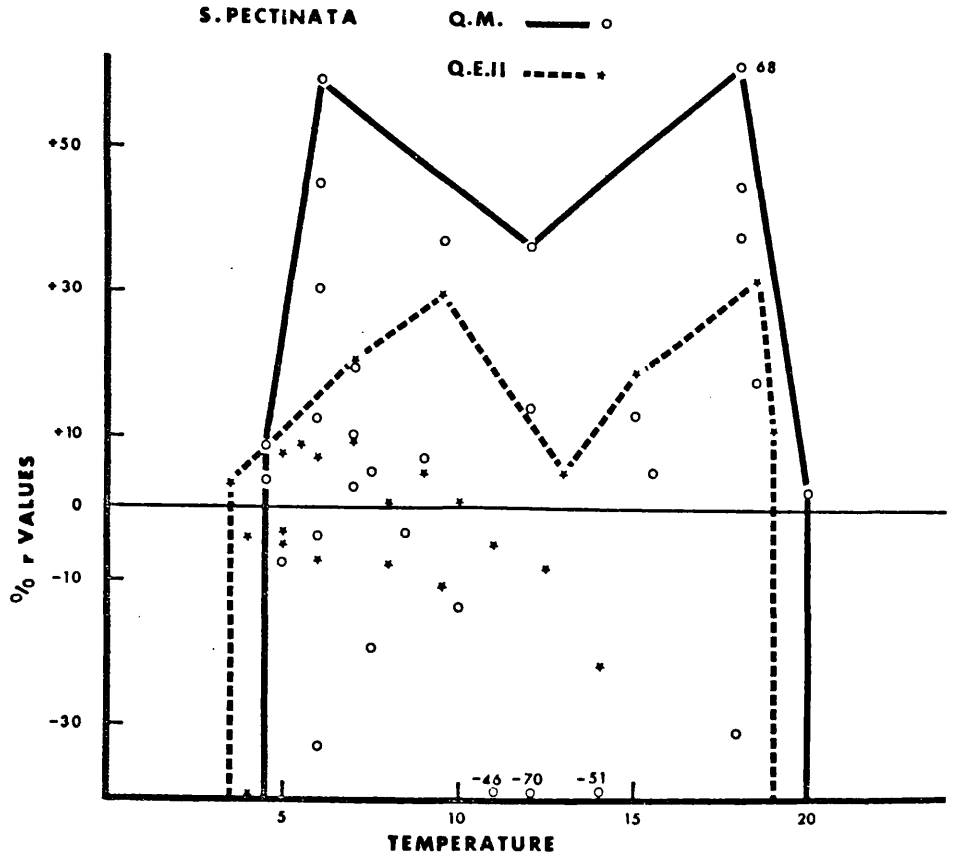

S.OBLONGA
Q.M.
Q.E.II
+50
+30
+10
0
-10
-30
-50
% r VALUES
-91 ○ * -100
5
10
15
TEMPERATURE

Fig. 46. Rates of change of P. vulgaris against temperature in Q.M. and Q.E.II

Fig. 47. Rates of change of Synchaeta oblonga against temperature in Q.M. and Q.E.II


S. PECTINATA
Q.M.
Q.E.II
68
+50
+30
+10
0
-10
-30
% r VALUES
-46
-70
-51
5
10
15
20
TEMPERATURE

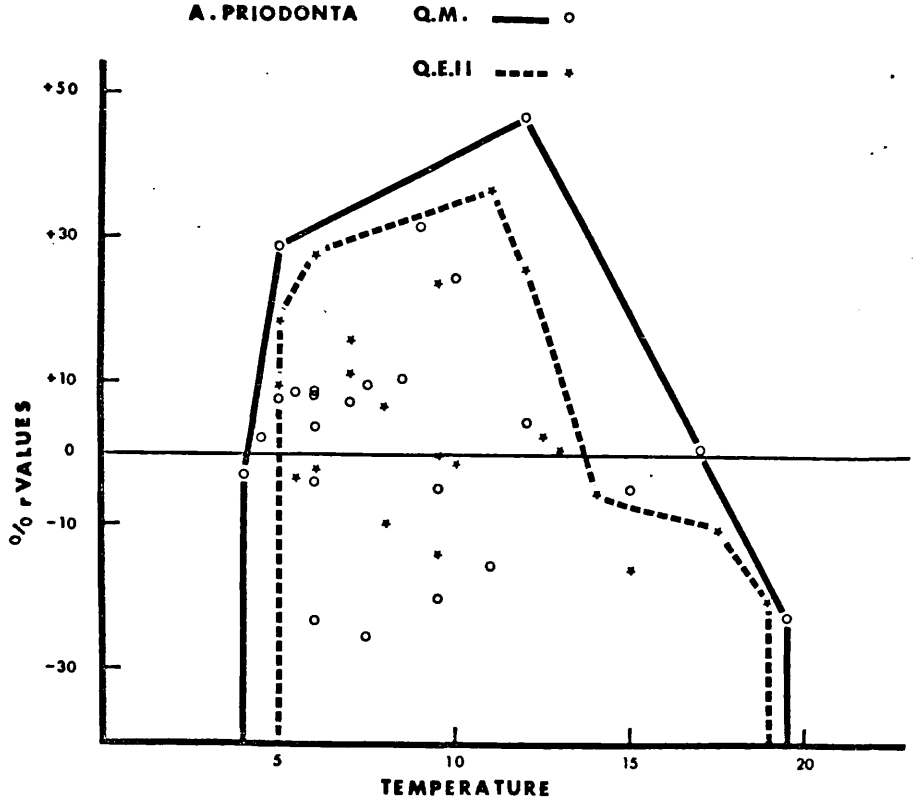
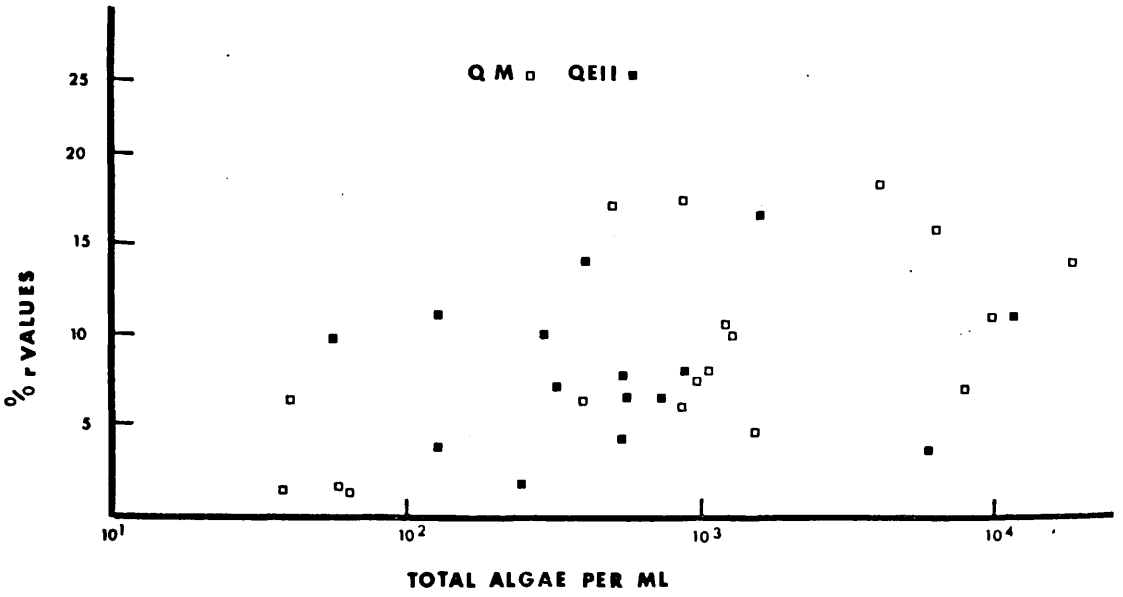

A. PRIODONTA
Q.M.
Q.E.II
+50
+30
+10
0
-10
-30
% r VALUES
5
10
15
20
TEMPERATURE

Fig. 48. Rates of change of S. pectinata against temperature in Q.M. and Q.E.II

Fig. 49. Rates of change of Asplanchna priodonta against temperature in Q.M. and Q.E.II

slightly lower r values in Q.E.II. High positive values occurred over the range from 5°-12°C. followed by a rapid decline and no return to these values in the 18°-20°C. range, though the population was present at these temperatures.

ALL ROTIFERS



ALL ROTIFERS

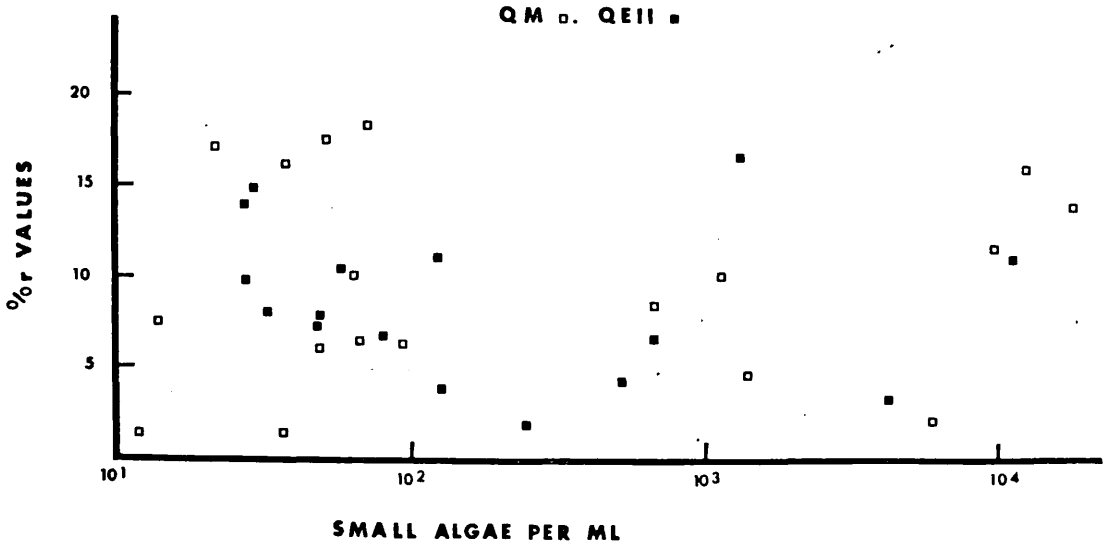


Fig. 50. Positive rates of change of all rotifers against total algae in Q.M. and Q.E.II

Fig. 51. Positive rates of change of all rotifers against small algae in Q.M. and Q.E.II

Rates of change and seston

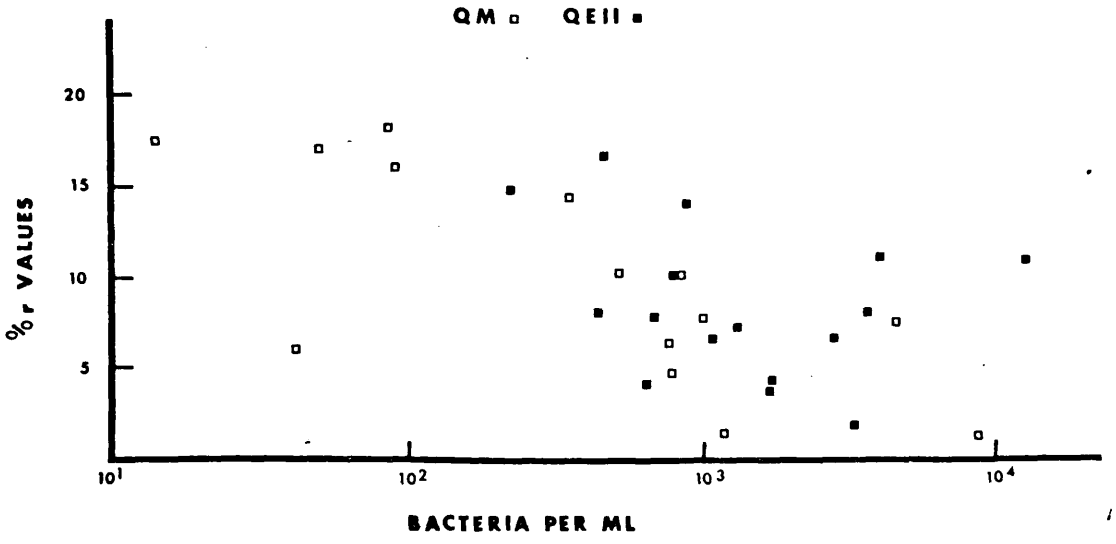
Figs. 50-53 show the positive rates of change of the rotifer population as a whole plotted against different groups of seston. The seston data were taken at time o, that is at the beginning of the period for which the rate of change was calculated. Unfortunately some gaps in the seston data prevented all the positive rates of change being included on the graphs, but all those for which seston data were available are plotted. The number of points in each section of the graph is clearly not important in the discussion of the influence of seston on r values, since it is a function of the frequency of occurrence of certain concentrations of seston. What might be significant is the concentration at which the highest rates of change occurred, and this parameter will be the basis of the present discussion.

Fig. 50 shows the rates of change of the rotifer population plotted against total algae per ml. The highest rates of change occurred at concentrations greater than 400 cells per ml. When the same data were plotted against small algae in Fig. 51, the high rates separated into two groups, one small group at high concentrations and another larger one at concentrations less than 80 cells per ml. The data in Fig. 52 show an interesting contrast with Fig. 50. The highest rates of change occurred when the bacteria population was at its lowest. The data in Fig. 53 show no trend of increasing or decreasing rates with detritus content. Positive rates of change were grouped randomly over the whole range of detritus concentrations.

Discussion

Pilarska (personal communication) found that the optimal food concentration for cultures of Brachionus rubens at 20°C. was one million cells per ml. of Chlorella vulgaris. At this concentration maximum reproductive rate was realised and animals survived to physiological death. For B. calyciflorus Galkovskaya (1963) states that the relative growth rate ($e^r - 1 \times 100\%$)

ALL ROTIFERS



ALL ROTIFERS

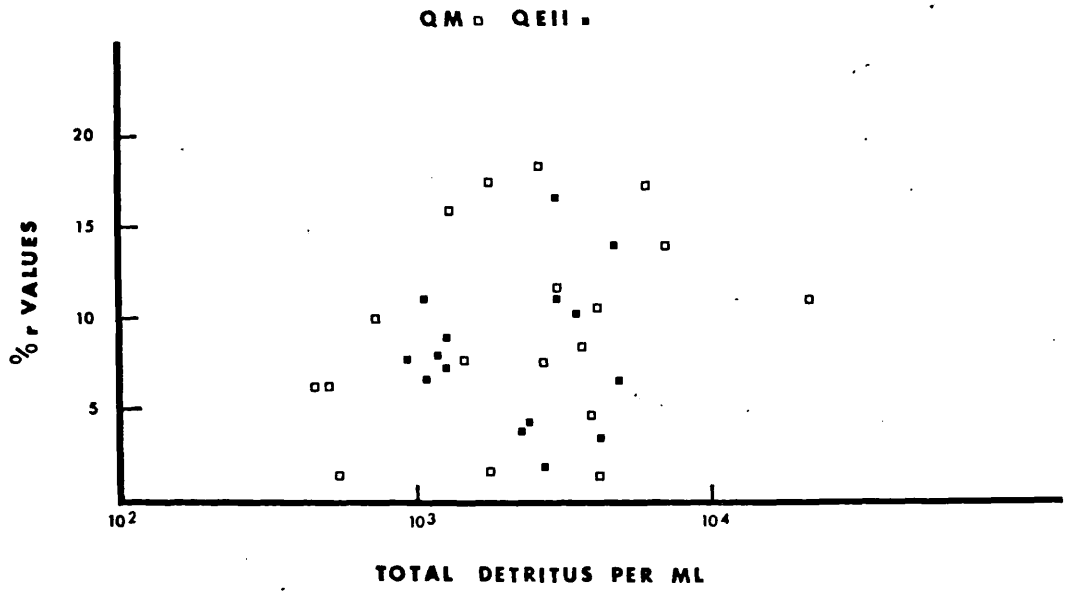


Fig. 52. Positive rates of change of all rotifers against bacteria in Q.M. and Q.E.II

Fig. 53. Positive rates of change of all rotifers against total detritus in Q.M. and Q.E.II

reached a maximum at three million cells per ml. though Table 1 in her paper gives the same rate of growth per day at both one million and three million cells per ml. with a further increase at five million cells per ml. when single animals were used to initiate the population. Halbach (1972) found that one million cells per ml. was optimal for B. calyciflorus. Despite this discrepancy it is clear that optimal food concentrations in all the above work were very high indeed. Such concentrations never existed in the reservoirs even when available algae, bacteria and detritus were added together, and the maximum rate of change for the rotifer population as a whole was only 24% whereas Galkovskaya (op. cit) in cultured animals found a maximum of 202% per day which was equivalent to a relative daily growth rate of 175%. It seems therefore that the reservoir population, even when most productive, were limited by food availability. Data analysed by Edmondson (1946) from Carlin, Ahlstrom, Chandler, Colditz and Kreutner for different species in the field has a range of maximum r values from 4 to 48 with the majority in the teens and twenties. Edmondson also suggests that food deficiency causes these low rates. As was pointed out previously, in early spring the total number of algae was strongly influenced by very high concentrations of small flagellates which were present for only a short period. In autumn no flagellates occurred but high rates of change were nevertheless frequent, probably as a consequence of organic matter becoming available after the June blooms in the Thames when higher temperatures in the reservoirs would augment the birth rate. (See standing crop section) Consequently when rates of change were plotted against numbers of small algae (Fig. 51) and against temperature (Fig. 43) two groups of high values were apparent.

The role of bacteria and detritus as food for rotifers has been discussed and in part reviewed by Pourriot (1965), who bases much of his discussion on cultured animals. He presents some evidence that certain rotifer

species, even herbivorous forms, are capapble of selection among particles of the same size, some species "preferring" living food to detritus. He separates rotifer species into four categories according to their feeding habits:

1. Exclusively herbivors e.g. Synchaeta spp., Polyarthra dolichoptera.
2. Mixed feeders e.g. Philodinidae, Proales fallaciosa
3. Bacteria feeders e.g. Dipleuchlanis propatula
4. Exclusively detritus feeders e.g. Pedalia mira and Conochilus sp.

He mentions the lack of evidence on the role of detritus in the feeding of some Brachionidae known to feed on phytonannoplankton. The availability of food particles in the Q.M. and Q.E.II reservoirs strongly suggests that the planktonic rotifers of these habitats must be largely omnivorous for most of the year, though they were most productive during algal blooms. Pourriot (op. cit.) suggests that a study of reproductive rate is the best method of determining the nutritional value of a particular food since on poor food rotifers can maintain themselves without appreciably increasing in numbers. Reproductive rates can be determined by Edmondson's (1960) method in those rotifers which carry their eggs and this has been done in the present work. But in field populations which drop their eggs no method has been devised for determining birth rates. In this case comparative work is best done using the rather cruder measure of rates of change.

Bacteria seem to be of little importance to the total population of rotifers in the reservoirs, high rates of change only occurring when bacteria numbers were at their lowest. Since in Fig. 52 the bacteria numbers plotted were those present at the beginning of a period of population increase, one cannot explain the preponderance of higher rates of change at the lower end of the bacteria scale by postulating that efficient grazing kept down the bacteria population. If two static measurements of standing crop were being

compared this could be the explanation. The value of comparisons of rates of change in both herbivore and food populations cannot be overestimated but unfortunately it was not possible to determine the rates of change of bacteria and algae populations in the present work.

The scattering of positive rates of change over the whole range of detritus concentrations (Fig. 53) suggests that whilst it might provide a basic food source for the rotifer population or for some component of it, detritus cannot be solely responsible for the sudden rapid increases in the population which occurred in spring and autumn. However since rates of change are temperature dependent through their dependence on the birth rate, less nutritious food could produce rates of change similar to those in good food if the temperature were higher. A hypothetical case will illustrate this. K. quadrata has an egg development rate of 1.22 per day at 20°C, and 0.28 at 5°C (Appendix II) These values are extremes of reservoir temperatures in autumn and spring respectively. If food is so poor in autumn that the number of eggs per female is only 0.5, then the birth rate using Edmondson's (1960) method would be 0.61 per day. If good food in spring produced an egg ratio of 2 per female, then the birth rate would be 0.56, lower than the autumn rate despite the greater number of eggs per female in the population. An increased mortality in poor food in autumn might counterbalance the birth rate, but as Pourriot (op. cit.) points out and much experimental work demonstrates (Jennings and Lynch (1928) King (1970), Meadow and Barrows (1971), Halbach (1972)) fertility diminishes much more rapidly in poor food than does length of life, (See also Table 21) and length of life of Philodina acuticornis odiosa increased by as much as three days when temperature rose by 1°C (Meadows, unpublished data). It is suggested therefore that the small flagellates occurring in high numbers in early spring trigger the sudden increase in the rotifer population and that at these low temperatures the effect of food

predominates. In autumn, the arrival of quantities of detritus and dying algae from the summer bloom in the Thames would be sufficient to trigger the population increase because of the higher ambient temperature. Nevertheless at the food levels available in the reservoirs, competition between species in the early stages of population increase must largely determine the relative proportions of different species contributing to the peak standing crops. The first species off the mark, so to speak, can exploit available food and attain maximum rates of change before the populations of other species build up. This must be particularly true for the small herbivorous species of similar sizes which form the greater part of the reservoir populations.

Production of reservoir rotifers

Development rates

The only species of which the development rate was fully investigated was Keratella quadrata. The low numbers of ovigerous females in other species prevented adequate investigation, whilst the difficulty of maintaining Polyarthra vulgaris in small volumes of water without specimens becoming attached to the surface film only allowed two satisfactory determinations to be made on this species. Table 18a) gives the results of these measurements for K. quadrata The linear regression equation relating development rate ($\frac{1}{D}$) of Keratella quadrata to temperature was $y = 0.0619x + 0.044$. where x was measured in degress Celsius and y was the proportion of an egg developing in one day, i.e. the reciprocal of the development time.

Table 18b) also shows the Q_{10} values calculated at $5^{\circ}C$ intervals over the range of temperatures within which K. quadrata was present. From 10° - $20^{\circ}C$ typical Q_{10} values of about 2 occurred but from 5° - 10° twice the usual value was obtained indicating a more powerful temperature effect at low temperatures than at higher ones.

Discussion

Amren (1964) has published detailed results of his determinations of development times and rates for K. quadrata in some ponds on Spitsbergen. The temperature range of the ponds over which K. quadrata was present was narrower than that in the reservoirs, covering only 0.6° - $11.8^{\circ}C$. The maximum recorded temperature was $9.7^{\circ}C$, the minimum, was $0.6^{\circ}C$. Development times were studied over the temperature range 3.7° - $12.9^{\circ}C$ and tests at $19^{\circ}C$ did not allow development at all. Amren commented on the high degree of temperature dependence in this pond variety of K. quadrata. Fig. 54 shows his values of development time and those of the reservoir variety on the same scale with the curve connecting Amren's data extrapolated to meet the curve

EGG DEVELOPMENT TIME OF K. QUADRATA

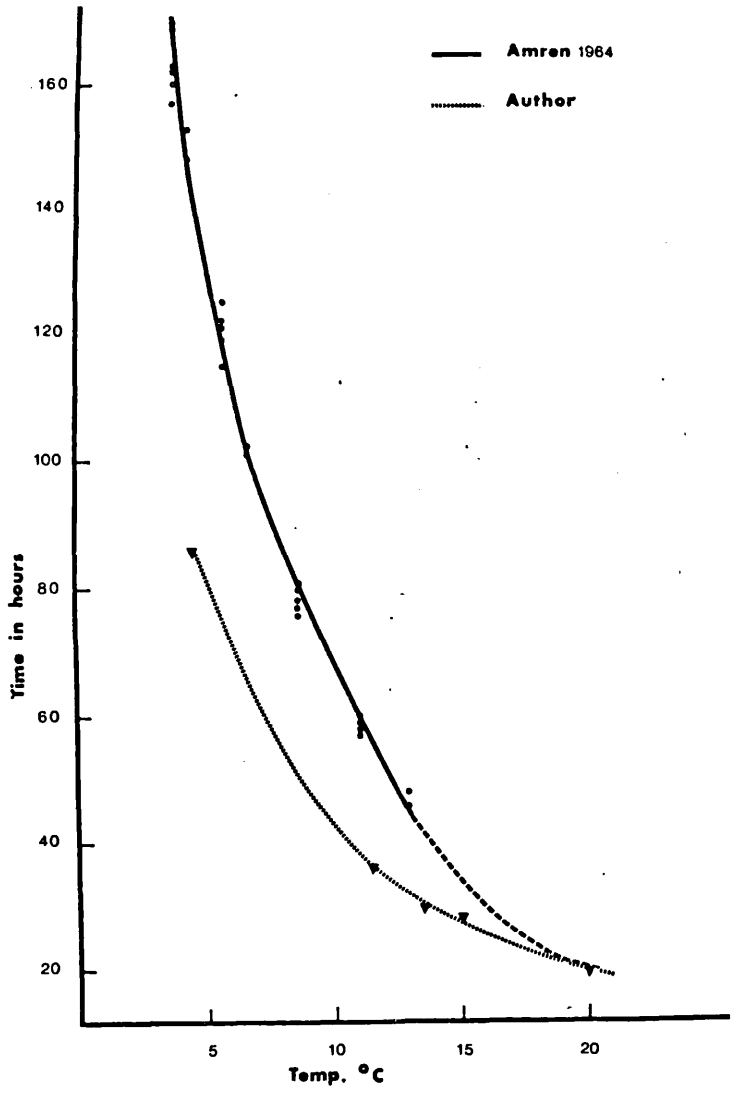


Fig. 54. Development time of eggs of K. quadrata in relation to temperature

Table 18a)

Time and rate of egg development in K. quadrata

Temperature	Time in Hours	Rate per day
20°C	19.6	1.22
15°	28.3	0.85
13.5°	30.3	0.79
11.5°	36.0	0.67
5°	86.0	0.28

Table 18b)

Q_{10} of egg development for K. quadrata

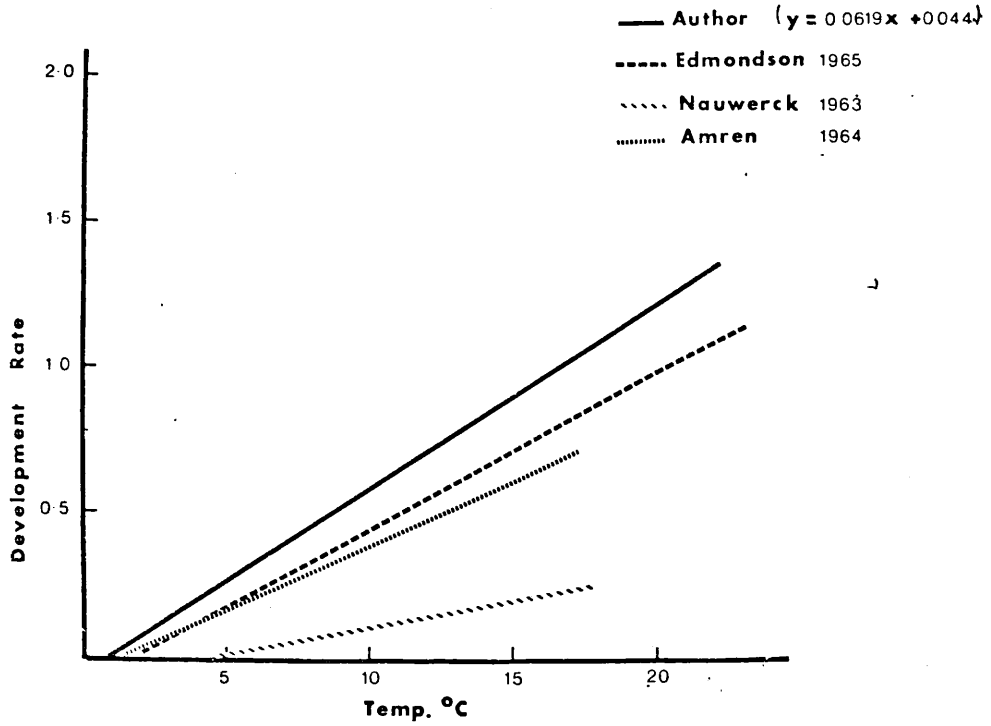
Temperature range	Q_{10}	Q_{10} (calculated from Amren 1964)
5-10°C	4.28	5.66
10-15°C	2.16	2.40
15-20°C	2.04	

from the reservoir variety at 20°C. to facilitate visual comparisons. As with the reservoir samples the degree of temperature dependence of development times was more marked at lower temperatures, but also for each temperature range the variety from the cold water pond showed a greater temperature dependence and a longer development. The Q_{10} values, which indicate the degree of temperature dependence of a rate process, were also calculated from Amren's data. These are given in Table 18b. The first one particularly is higher than the values for the reservoir. Rao and Bullock (1954) showed that the Q_{10} of respiration is generally higher in organisms previously adapted to colder temperatures.

Nauwerck (1963) used the time between the egg maximum and the population maximum in Lake Erken as an estimate of the development time of the eggs of K. quadrata. He found it was 200 hours at 11°C. This is considerably longer than in the Spitsbergen ponds or the reservoirs but Amren's explanation, that the Spitsbergen variety was adapted to cold water and therefore had a shorter development time does not account for the eurythermal reservoir form having the shortest development time of the three. Nauwerck's development times for K. cochlearis also, were considerably higher than Edmondson's (1965) for the same species. The sampling interval of one week used by Nauwerck may have been too long to define the precise maxima of egg numbers and population and the curve for K. quadrata given in his Figure 32 is defined by only two points.

Fig. 55 shows development rates of K. quadrata using reservoir data, Amren (1964), Edmondson (1965) and Nauwerck (1963). Since Edmondson gives the rate of development of K. quadrata at only two temperatures it was considered more convenient to compare all the available data as straight-line relationships, that is in the reciprocal ($\frac{1}{D}$) form. Nauwerck's values were read off from his Fig. 32 and may not therefore be as accurate as the others, nevertheless they are certainly comparable. It is clear from Fig. 55 that Nauwerck's

Development Rate of K.quadrata



EGG DEVELOPMENT RATES

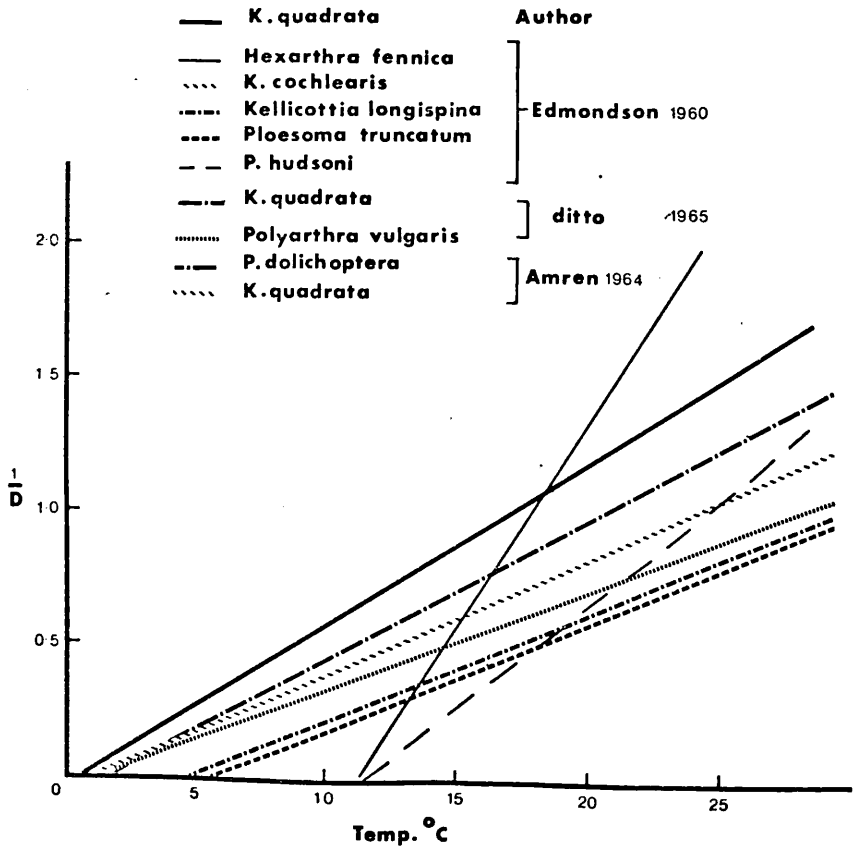


Fig. 55 Development rates of eggs of K. quadrata after various authors

Fig. 56 Development rates of eggs of various planktonic rotifers after several authors.

results are very different from the other data, with the reservoir development rates the highest of the four sets of data. Nauwerck considers the Erken variety to be a warm stenotherm, and whereas the other lines in Fig. 55 cut the temperature axis between 0° and 2°C., that from Lake Erken cuts it at 4.4°. The Q_{10} for Nauwerck's development rates over the range 7° - 12°C, that is over the interval delimited by the measured values, was 7.84 indicating a very strong temperature dependence. These data suggest therefore that animals subjected to narrow temperature ranges are more dependent on temperature in their rate processes than eurythermal forms. Rao and Bullock (1954) suggest that this should be the case but little evidence has been accumulated to support it. This point will be considered again the the respiration section of this thesis.

Fig. 56 shows egg development rates of various rotifers calculated by the egg ratio method by different workers, mainly Edmondson as reviewed in Hutchinson (1967), and also Amren (1964) and Edmondson (1965) and the present data on K. quadrata. The only obvious deviations from the general trend of the results shown in Fig. 56 are Hexarthra fennica and Ploesoma hudsoni. The data for Hexarthra probably need revision (Edmondson, personal communication) so that apart from Ploesoma hudsoni a generalised relationship for all the planktonic rotifers in Fig. 56 would be equivalent to that for K. cochlearis of Edmondson (1965). Using the basic equation for a straight line joining two points of which the co-ordinates are known, this relationship can be described by the line $y = 0.044x - 0.11$, the co-ordinates of the two points given by Edmondson being (10, 0.33) and (20, 0.77). For rough estimates of production of planktonic rotifers this equation would be adequate and has been used for those rotifers from the reservoirs which carry their eggs. The more specific equation was used for K. quadrata based on the results previously described and summarised in Appendix II.

Dry weights

The method used to determine the dry weights of rotifers was described in Dochan and Rainbow (1971) which is included in the Appendices to this thesis. Table 19 shows the results of these and other dry weight determinations relevant to production estimates of the reservoir rotifers. Not all the rotifers in the reservoirs could be weighed directly, either because of difficulties in handling sufficient numbers in a fresh condition to weigh them effictively or because they were non-loricate forms and therefore not susceptible t direct weighing. Brachionus plicatilis is a brackish water rotifer, relatively easy to culture for which an energy budget was constructed to provide a basis for comparison with reservoir data.

Table 19

Dry weights of some planktonic rotifers

Species	Weight in ug
K. quadrata	0.075
K. quadrata + one egg	0.143
P. vulgaris	0.043
S. oblonga	0.022
B. plicatilis	0.202

Table 20

Volumes and weights of some planktonic rotifers

Species	Volume (u^3)	Wet Weight (ug) (Kosova 1961)	Dry Weight (ug)
K. quadrata	1. 1×10^5	0.70	0.075
P. vulgaris	2. 5.5×10^4	0.60	0.043
S. oblonga	2. 1.0×10^4	0.10	0.022
B. plicatilis	3. 3×10^6	2.0	0.202

1. Nauwerck (1963)
2. Modified from Nauwerck (1963)
3. Ruttner-Kolisko (1972)

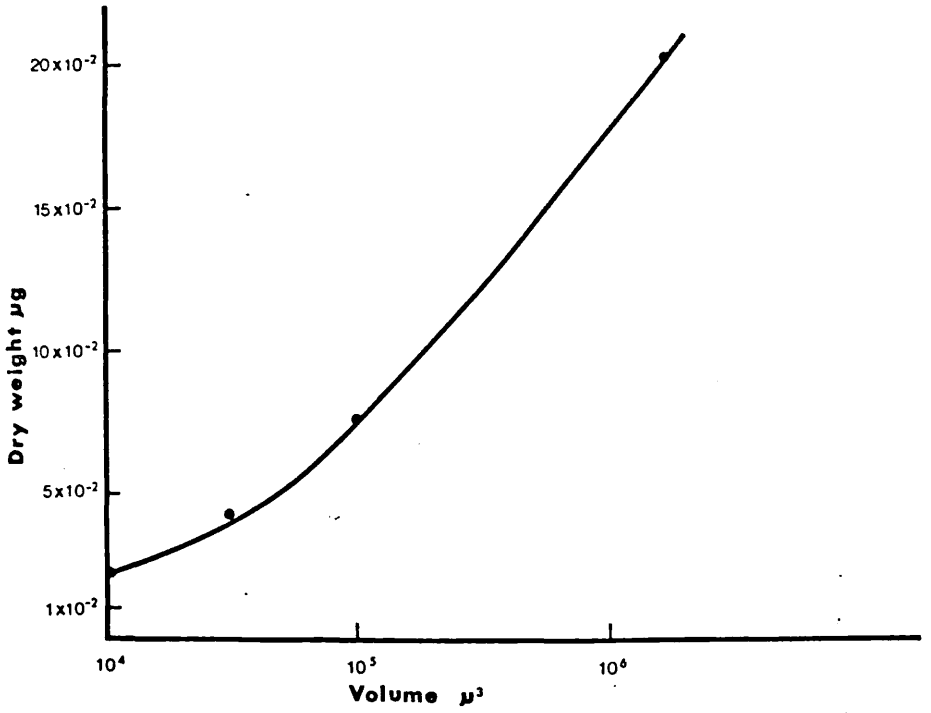
Volume/Dry Weight Relationship

Fig. 57 illustrates an attempt to determine dry weights of rotifers other than those weighed directly. The relationship is tenuous, being based on only four points but it was considered that this method would give a closer approximation to the dry weight of different species than arbitrary methods using a generalised conversion factor.

The curve was obtained using animals for which both volumes and dry weight were available. The volume of B. plicatilis was derived by Ruttner-Kolisko (1972), that of K. quadrata from Nauwerck (1963) and those of P. vulgaris and S. oblonga modified from Nauwerck on the basis of the size relations of these species in the reservoir. Dry weights were obtained by the metho described earlier.

Subsequent to the preparation of this thesis, a paper by Kosova (1961) was obtained which gives the wet weight of rotifers of different species and sizes. Table 20 gives the volumes, dry weights and Kosova's wet weights for the four species used in the graph. The values given suggest that 10% of Kosova's wet weight would be a good approximation to the dry weight. It would be useful to check the agreement between her data and direct measures of dry weight for other species.

Volume / Dry weight Relationship



K. quadrata Q.M.

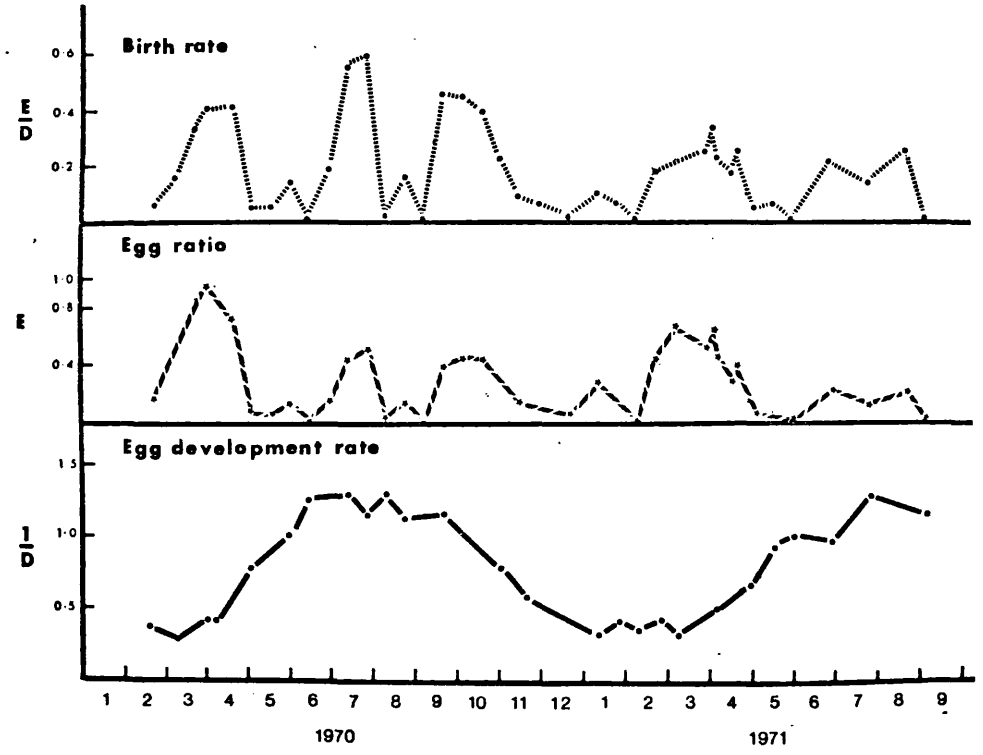


Fig. 57 Volume/dry weight relationship for planktonic rotifers

Fig. 58 Development rate of eggs, egg ratios and birth rates of K. quadrata in Q.M. reservoir

Population dynamics of Keratella quadrata

Appendix II contains the parameters of the population dynamics of K. quadrata in both reservoirs together with production estimates calculated by Galkovskaya's (1971) method which was already discussed in the methods section of this thesis. Egg development rate $(\frac{1}{D})$ which was discussed earlier, fluctuated with temperature alone throughout the year. The number of eggs per female based on numbers present at the beginning of each sampling interval fluctuated independently of temperature. This parameter has been discussed in the section on egg numbers and ratios. When the egg ratio is combined with the development rate according to Edmondson's (1960) method, the resulting birth rate is clearly dependent on both temperature and food. The affect of food quality on birth rates of K. quadrata was determined in a pilot experiment on a pond sample kept in the laboratory at 15°C. for a period of ten days. The development rate was determined at 15°C and found to be 0.96. If the production of one egg is dependent on food it is reasonable to assume that the period between the production of successive eggs should vary with food whilst the development rate remains constant at a given temperature. Rotifers were kept in pond water filtered through double glass fibre and four dishes were prepared:

a) containing filtered water only.

b) filtered water plus Scenedesmus sp.

c) filtered water plus Oocystis sp.

d) filtered water plus Chlorella sp.

Scenedesmus sp. and Oocystis sp. were from cultures initiated with reservoir algae, whilst the Chlorella sp. cultures were initiated with algae from the same pond as Keratella. This alga predominated in the pond throughout the period when the rotifers were present. Water was changed and algae renewed every two days.

The results of this experiment are presented in Table 21. The length of the period between eggs clearly decreases as food quality improves and where this period is less than one day the higher proportion of eggs carried in twos distinguishes the shorter inter-egg period. For eggs to be carried in twos the inter-egg period must be shorter than the length of time from laying to hatching. Table 21 indicates that with the short inter-egg period and the higher proportion of eggs carried in twos in improved food conditions the birth rate is substantially increased despite the egg development rate being held constant. The mean number of eggs produced by a female in one day is therefore a good indicator of food conditions.

Fig. 58 is a graph of development rate, egg ratios and birth rate plotted on a seasonal basis for Q.M. reservoir, in an attempt to demonstrate the relative importance of temperature and food in determining the birth rate. Appendix II contains the same data for Q.E.II but as the pattern and discussion would be essentially the same for both reservoirs this data has not been plotted.

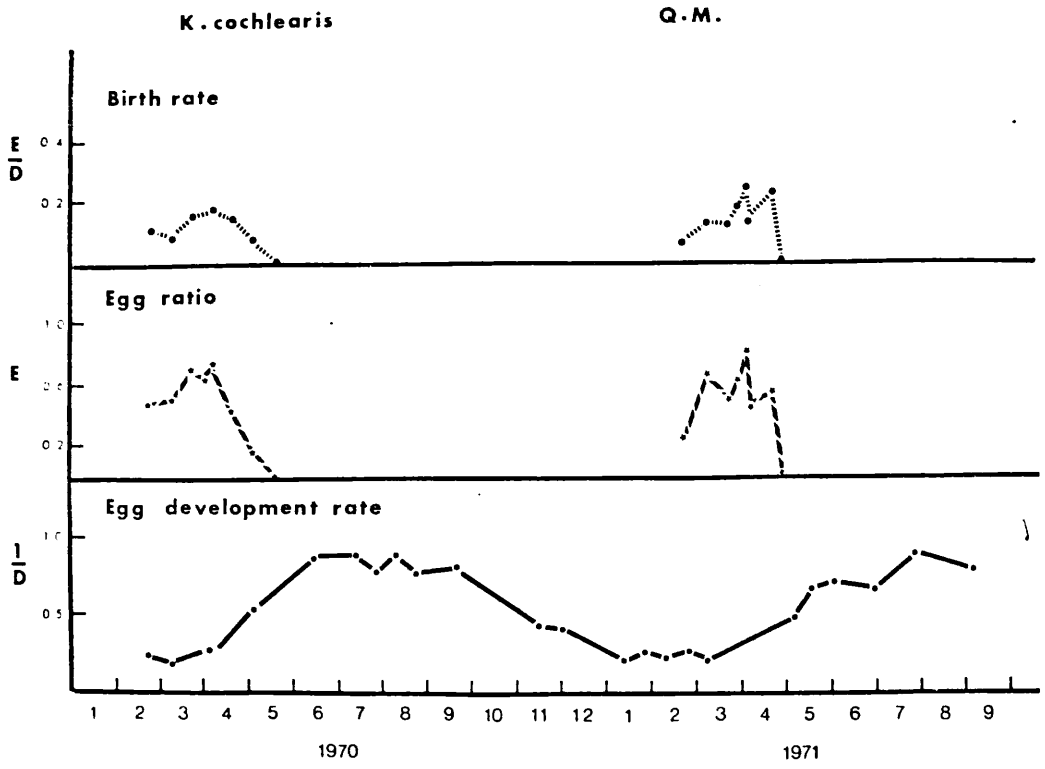
Figure 58 shows clearly that it was the egg ratio rather than the egg development rate which exerted the strongest influence on the birth rate, and therefore food is the more important factor limiting the population of K. quadrata in the reservoir. Since temperatures were higher in autumn and hence development rates more rapid, the influence of food was of less importance than in the spring. The birth-rate therefore increased relatively more in the autumn in response to a similar increase in egg ratio than it did in spring. This also is clear from Figure 58.

The birth rate in Q.M. reservoir fluctuated from zero values to 0.58 per individual per day or an instantaneous rate of 0.457 during August 1970 (Appendix II and Figure 58). In Q.E.II the maximum birth rate was 0.62 per individual per day or an instantaneous rate of 0.482 in August 1970. In general the highest death rates occurred during periods of high birth rates and immediately following them.

The only detailed treatment of the population dynamics of K. quadrata is by Amren (1964). The finite birth rates he gives for field populations cover a similar range to those in the present work despite differences in the temperature regimes of the habitats. The highest birth rate in the Spitsbergen ponds was 0.53 at a temperature of 9.6°C, whilst in the reservoirs the highest was 0.62 at a temperature of 19°C. The difference in the effective temperature is probably related to the temperature range of the rotifer in each environment (See rates of change section). During periods of high birth rates in Spitsbergen the death or elimination rates were often negative. Amren considered this to be the result of continued hatching of resting eggs masking the deaths of adults. Resting eggs were never observed in the reservoir and few negative death rates occurred. In fact the reverse situation to Spitsbergen occurred in the reservoirs with high birth rates and death rates coinciding. It seems reasonable to suggest that the high death rates during periods of rapid population expansion were due to deaths of young animals either by selective predation or by intra- and interspecific competition for food. As was mentioned in the section on rates of change, the food situation in the reservoir was, even at its best, considerable poorer than is usual in culture experiments, and it would appear that food might be limiting the reservoir population which was low in comparison with other situations (Hutchinson 1967). For example Ito (1957) had cultures with more than 8×10^6 adults of Brachionus plicatilis per cubic metre with no algae as food, whilst in the reservoir the maximum total number of rotifers per cubic metre was less than 0.2×10^6.

Birth rates of other egg-bearing rotifers

Besides Keratella quadrata there were only two other rotifers in any number which carried their eggs from laying to hatching and therefore could be studied using Edmondson's (1960) egg ratio method. These were K. cochlearis and P. vulgaris. The regression relating development rate to temperature for


K. cochlearis
Q.M.
Birth rate
E/D
0.4
0.2
Egg ratio
E
1.0
0.5
0.2
Egg development rate
1/D
1.0
0.5
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

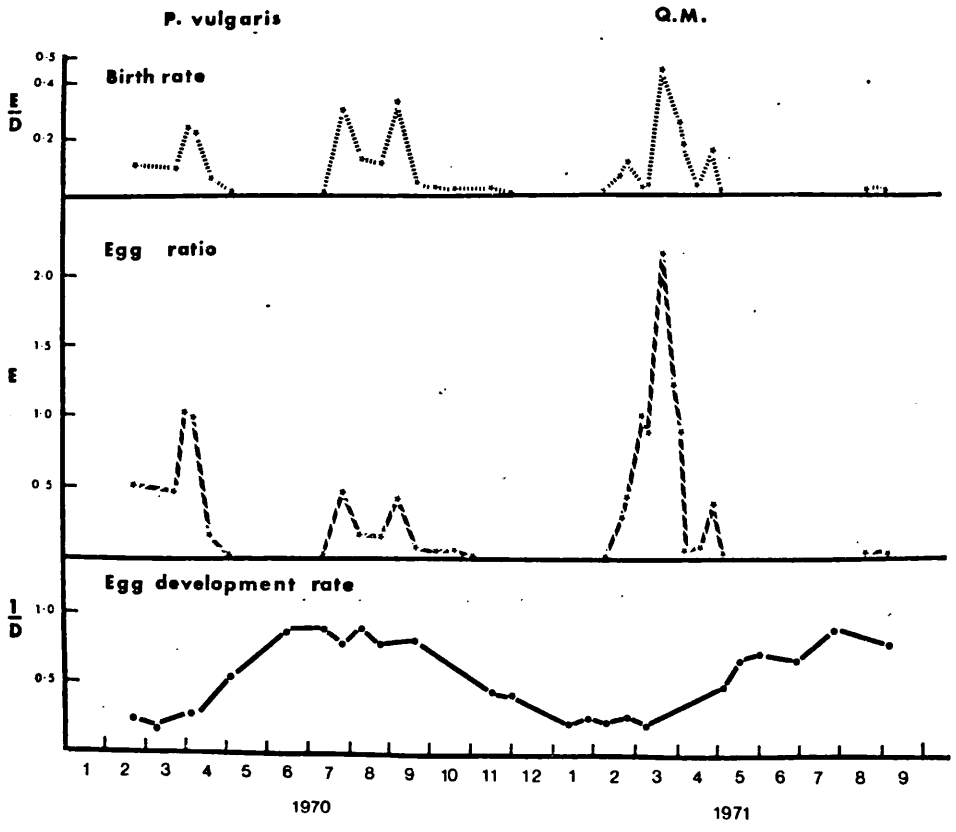

P. vulgaris
Q.M.
Birth rate
E/D
0·5
0·4
0·2
Egg ratio
E
2·0
1·5
1·0
0·5
Egg development rate
1/D
1·0
0·5
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 59 Development rate of eggs, egg ratios and birth rates of K. cochlearis in Q.M. reservoir

Fig. 60 Development rate of eggs, egg ratios and birth rates of P. vulgaris in Q.M. reservoir.

K. cochlearis was used in both cases since this relationship (See earlier) seemed to represent the mean of the development rate determinations for most rotifers studied up to the present time. Appendix III contains the birth rates of these two species in both reservoirs calculated when eggs were to be found. The gaps in the table therefore do not necessarily represent on absence of the particular species but an absence of reproducing individuals, at least in the case of K. cochlearis. Real absences have already been recorded in the section on standing crop. The birth-rate data is represented graphically in Figs 59 and 60.

K. cochlearis had a birth rate less than 0.25 in both reservoirs throughout the period for which samples were taken, except for a value of 0.385 in August 1970 in Q.E.II caused by a sudden appearance of eggs. This value is perhaps best ignored. Egg members were so low in autumn of both years in Q.M. that no valid birth rates could be calculated. Birth rates were however calculated for K. cochlearis in Q.E.II of both years when the values were as high or higher than most of the value obtained in spring.

In the case of P. vulgaris high birth rates were frequent in spring and autumn in both reservoirs except for spring 1971 in Q.E.II when both the birth rate and the population remained very low. In autumn 1971 sampling was too infrequent to give an accurate picture of the birth rate of P. vulgaris. No eggs were recoreed in Q.E.II and the birth rate was very low in Q.M. Despite this the standing crop in Q.M. was very high. (Table 15)

As in the case of K. quadrata the birth rate of K. cochlearis and P. vulgaris as shown in Figs 59 and 60 showed greated dependence on egg ratios than on the development rate and hence were limited by food rather than temperature. This confirms the evidence presented in the section on rates of change and the discussion relating algae and bacteria to the rates of change would be of equal validity in this section.

Production of egg-bearing rotifers

As already discussed in the methods section of this thesis and as Edmondson(1965) suggested, the birth rate of egg-bearing reservoir rotifers could be a sufficiently close approximation to the production in view of the relatively small increase in size which occurs after hatching. However in transforming birth rate data into dry weight the weight of the fully grown adult has been used as the conversion factor in this thesis. This means that the production of an individual in terms of its own growth has been added to the production of the egg from which the individual hatched. In the case of K. quadrata, the only rotifer for which egg weight was known, this involved the addition of only 0.007ug. to the weight of the egg. Appendix IV contains the production estimates per m^2 column based on the weights derived from Figure 57 and, for convenience Appendix V contains corresponding standing crop data also converted to dry weight. Since both production and biomass estimates were based on the same dry weight value, the birth-rate and the P/B ratio are identical when the latter is an instantaneous measurement. The P/B ratio has been used particularly in Russian and Polish work (Kajak and Hillbricht - Ilkowska 1972, Hillbricht-Ilkowska 1967, Lewkowicz 1971) as an estimate of how frequently a population is replaced during its vegetative season. It can therefore be used to determine turnover time as defined by Cummins et al (1969) when production is measured over the vegetative season, and biomass calculated as the mean for the whole season. The season in the reservoir was taken as the whole year even though Polyarthra vulgaris was totally absent for about six weeks. In this way comparisons between the three egg-bearing rotifers could be made.

Table 22 contains the mean biomass, annual production and the P/B values for K. quadrata, K. cochlearis, and P. vulgaris. Biomass and production were also converted to calories assuming 1ug dry weight to be equivalent to

5 calories (Winberg 1972). One of the most interesting points these data showed was that despite differences between the mean standing crops of each species in the two reservoirs, the P/B ratio for any one species was virtually the same in both environments. Hillbricht-Ilkowska and Weglenska (1970) point out that both production and biomass are different in lakes of different trophic characteristics, both being about one third lower for rotifers in a mesotrophic lake compared with a eutrophic one. When P/B ratios were calculated on the data presented in Table 1 of the Polish paper they were found to be 30.14 and 28.9 in the eutrophic lake, and 34.8 and 31.6 in the mesotrophic one for the entire rotifer population, but these were for periods of six months only. Galkovskaya (1971) proposes the simple multiplication of a P/B value calculated over one day to produce the monthly P/B. In the case of rotifer populations this method can be of little value unless one can assume that the standing crop and birth rate have remained the same throughout the month. Clearly if one could validly assume this one would have sufficient data to calculate a monthly P/B without using the daily one, which, as was pointed out earlier, is equivalent to the birth rate in the case of rotifers.

Because of the problem described above, comparisons of annual P/B ratios with those based on shorter vegetative seasons can only be tentative. Nevertheless the overall P/B values given in Table 22 were clearly very similar to those calculated from the data on the Mazurian Lakes given by Hillbricht-Ilkowska and Weglenska (1972). Andronikova et al (1972) give a P/B value of 35.3 for rotifers in Red Lake in the north-west U.S.S.R. for the same six month period as in the Mazurian Lakes. Lewkowicz (1971) gives production and biomass data for several rotifer species in experimental fish ponds in Gotysz. The P/B values for a four month period in fertilised and unfertilised ponds were calculated for species related to those used here. For K. quadrata the values ranged from 27 to 33: for K. cochlearis from 22.3 to 24.1; for P. trigla vulgaris

from 27.7 to 35.6. The P/B values showed no relationship with the degree of fertilisation of the ponds. All these values are close to the reservoir data given in Table 22 despite the differing lengths of the vegetative seasons. It is possible that low production values in winter and their absence in summer cancelled out the high values obtained in the reservoirs during the early spring and so made the annual P/B comparable with the values calculated for shorter periods in the work quoted. Alternatively it could be that were more data available a P/B of about 30 over the vegetative season could be taken as fairly standard for planktonic rotifers in temperate situations.

However in Russian lakes 30 km. from the Arctic Circle a seasonal P/B of only 14 was obtained (Alimov et al 1972) Schindler (1972) found in Canadian Lakes covered with ice for 5 to 7 months a year that the mean daily P/B for rotifers equalled values obtained by Patalas (1970) in a thermally polluted lake. Schindler also remarked that the fact that maximum daily P/B ratios occurred when the lake had maximum heat content was not surprising. Bearing in mind what has been said about the daily P/B being equivalent to the birth rate, and the greater influence of egg numbers rather than development rate on the latter in the reservoirs one could be surprised by the results given by Schindler. One is led to conclude that temperature and food must influence production in different ways in cold and warmer environments and to suggest that simple graphical comparisons of development rates, egg ratios and birth rates such as those in Figures 58 - 60 would help to clarify this difference.

Table 21

Culture experiment on Keratella quadrata

Temperature: 15°C. Development rate: 0.96

Food species	Filtered water	Scenedesmus sp.	Oocystis sp.	Chlorella sp.
Average inter-egg period	7.5 days	5 days	< 1	< 1
Percentage eggs carried in twos	0	0	25	49
Eggs laid per adult per day	0.018	0.083	0.34	0.67
$\frac{E}{D} = B_r$ (daily)	0.017	0.079	0.326	0.641
b'	0.017	0.076	0.282	0.495

Table 22

Mean biomass and annual production estimates for 1970 in terms of ug. dry weight and calories

	Mean Biomass		Annual Production		
Queen Mary	ug.	Calories x 10^{-3}	ug.	Calories x 10^{-3}	P/B
K. quadrata	759.66	3,789.3	32,919.35	164,596.75	43.33
K. cochlearis	44.75	223.75	1,350.5	6,752.5	30.18
P. vulgaris	774.60	3,873.0	16,483.4	82,417.0	21.28
Overall values	526.34	2,631.70	16,917.75	84,588.75	32.14
Queen Elizabeth					
K. quadrata	648.40	3,242.0	28,824.05	144,120.25	44.45
K. cochlearis	184.22	921.1	6,763.45	33,817.25	36.71
P. vulgaris	637.85	3,189.25	14,833.60	74,168.0	23.26
Overall values	490.16	2,450.8	16,807.03	84,035.15	34.29

Table 23

Respiration Rates of Reservoir Rotifers
(All adults without eggs unless otherwise stated)

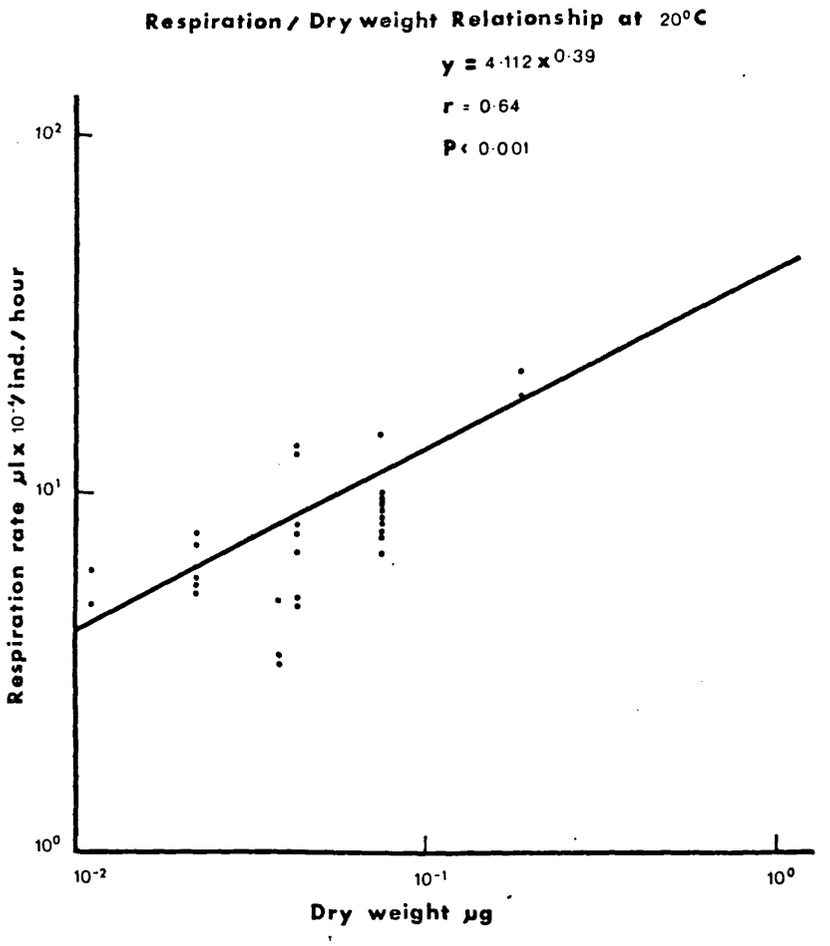
Species	Temperature (°C)	Rate at 20°C (Krogh's)	Rate (ul x 10^{-4}/hour)	Notes
Keratella cochlearis	12.5	5.01	2.32	
	12.5	3.33	1.54	
	12.5	3.50	1.62	
Keratella quadrata	6.8	8.92	2.24	
	10.0	9.40	3.52	
	10.0	14.39	5.39	
	10.0	6.78	2.54	
	10.5	7.72	2.89	
	10.6	9.55	3.98	
	10.6	9.29	3.87	
	10.6	7.42	3.09	
	10.6	4.42	1.84	
	10.6	6.38	2.66	Young
	10.6	5.30	2.21	
	12.0	0.48	0.22	
	12.0	0.26	0.12	Newly hatched.
	12.0	1.77	0.82	
	13.0	8.03	4.14	
	13.0	2.17	1.12	Young
	15.5	9.78	6.23	
	15.5	8.48	5.4	
	15.5	8.18	5.21	
	15.5	5.04	3.21	Young?
	15.5	8.71	5.55	
Synchaeta pectinata	9.3	18.39	6.03	
	9.3	20.16	6.61	
Notholca squamula	9.0	6.10	2.0	
	9.0	4.88	1.6	
Synchaeta oblonga	6.5	5.55	1.22	
	6.5	5.78	1.27	
	9.3	7.72	2.53	
	9.3	5.40	1.77	
	9.6	7.16	2.68	
Polyarthra vulgaris	10.5	13.40	5.02	
	10.5	6.70	2.51	
	10.5	7.66	2.87	
	10.5	12.79	4.79	
	10.5	8.09	3.03	
	18.0	5.02	4.18	
	18.0	4.79	3.99	

Respiration Rates

Only in recent years have attempts been made to measure the respiration rates of planktonic rotifers. Pourriot and Deluzarches (1970), Belyatskaya (1959) and Galkovskaya (1963, 1971) dealt with Brachionus calyciflorus, one of the larger planktonic rotifers. Belyatskaya and Galkovskaya both used large Cartesian divers but the former worker put up to twenty five animals in divers of 45-150 ul gas phase. Pourriot and Deluzarches, using a micro-Winkler technique, demonstrated the effect of crowding on the respiratory rates of several rotifer species as Zeiss (1963) had done for Daphnia magna. The former authors showed that in the case of rotifers, the reduced rate in more concentrated cultures was not correlated with reduced oxygen tension in the medium. The value of the small divers used in the present work lies in their elimination of the crowding effect, and since planktonic rotifers are constantly active even in the relatively confined space in the diver head, an accurate assessment of a fairly normal active respiratory rate is feasible. Pilarska (personal communication) has used similar but slightly larger Cartesian divers for Brachionus rubens from cultures.

In the present work respiration rates were determined at field temperatures to avoid the effects of incomplete or uncertain acclimation (See Bullock 1955). The following species were used, giving a representative size range for all herbivorous rotifers: Keratella cochlearis, K. quadrata, Synchaeta oblonga, S. pectinata, Polyarthra vulgaris, and Notholca squamula. All the rates measured at different temperatures fell within the range 0.1 - 0.7 x 10^{-3} ul. per individual per hour, that is 0.48 - 3.38 x 10^{-6} calories per individual per hour. for adult animals (See Table 22.)

To facilitate comparisons with other work the data at various temperatures were converted to 20°C. using factors obtained from the "normal curve" described by Krogh (1914) and quoted in Winberg (1971). Though the limitations of this


Respiration / Dry weight Relationship at 20°C
y = 4·112 x^0·39
r = 0·64
P < 0·001
Respiration rate µl x 10⁻² / ind. / hour
10²
10¹
10⁰
10⁻²
10⁻¹
10⁰
Dry weight µg

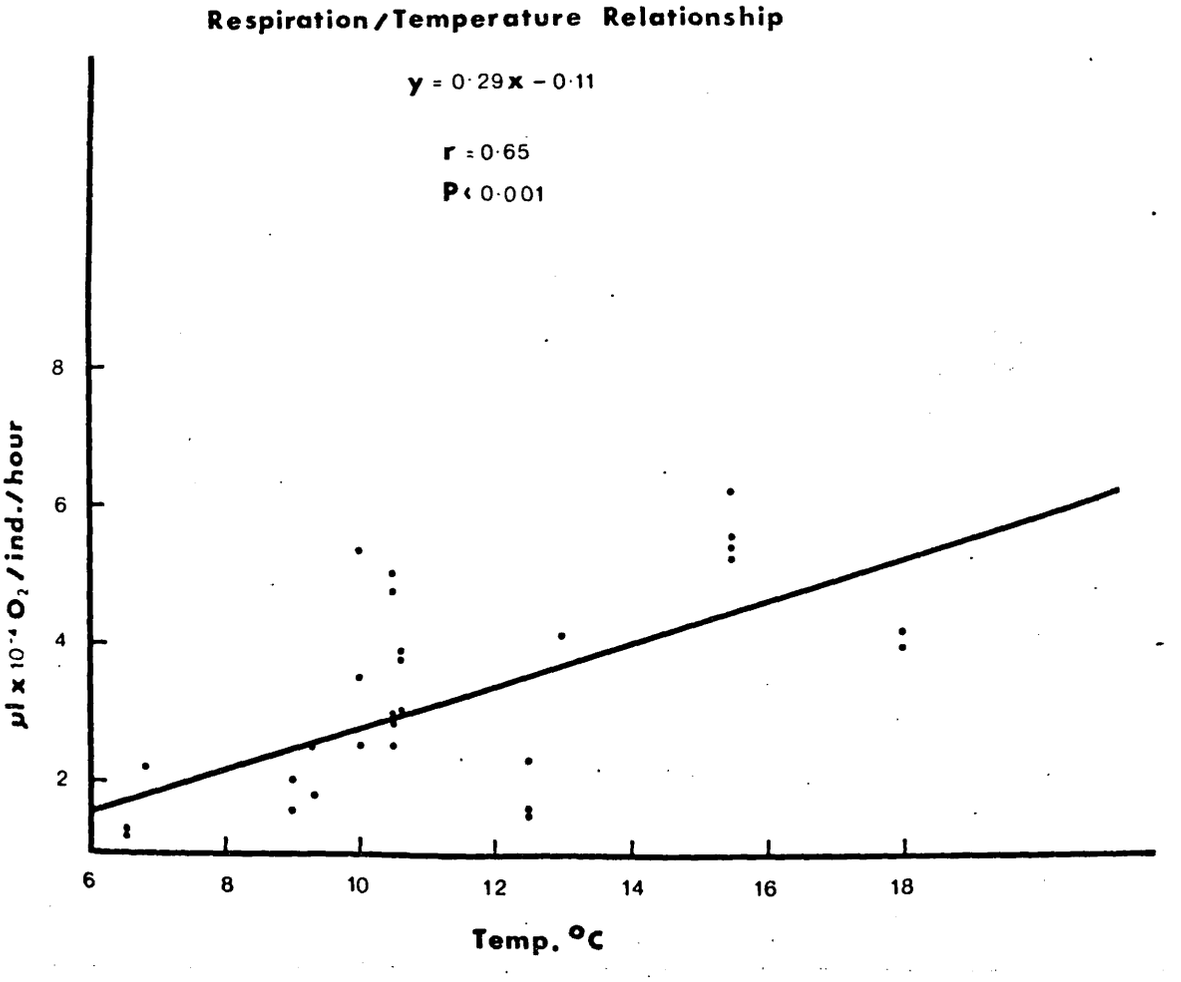

Respiration / Temperature Relationship
y = 0·29 x − 0·11
r = 0·65
P < 0·001
µl x 10⁻¹ O₂ / ind. / hour
8
6
4
2
6
8
10
12
14
16
18
Temp. °C

Fig. 61 Respiration rate/dry weight relationship for small planktonic rotifers, converted to 20°C. by Krogh's curve.

Fig. 62 Linear relationship between respiration and temperature for small planktonic rotifers.

method are discussed later, it was thought best to use the relationship already used in previous work of this kind. The converted data is also shown in Table 22. The mean respiration rate at 20°C was calculated for all adults and the variance was found to be almost 100% ($\bar{x}$ = 7.57, variance = 7.08). This strongly suggested that though all the respiration rates for planktonic rotifers are within the same orders of magnitude, individual variation due to size as well as species cannot be entirely ignored. Since however it was impossible to determine the respiration rates of all the reservoir rotifers or even some of them at more than a few temperatures within their range, some attempt was made at generalising the respiration picture to include rotifers of various sizes and species whose respiration rates had not been measured.

Respiration rates, size and temperature

Figure 57 was used to obtain the dry weights of the rotifers for which respiration had been measured. Figure 61 is the double-logarithmic plot of respiration rate against dry weight. Only K. cochlearis is significantly misplaced from the general trend of size-dependent respiration. This species is heavily loricated for its size, a factor which probably accounts for its displacement since there would be less respiring tissue in relation to its overall weight than in the other species investigated. However the regression was calculated including K. cochlearis and the relationship could be expressed as $y = 4.112 \times^{0.39}$ with r = 0.4, $P < 0.001$. This is a highly significant correlation indicating that the rate of respiration increases much less rapidly than the dry weight of rotifers.

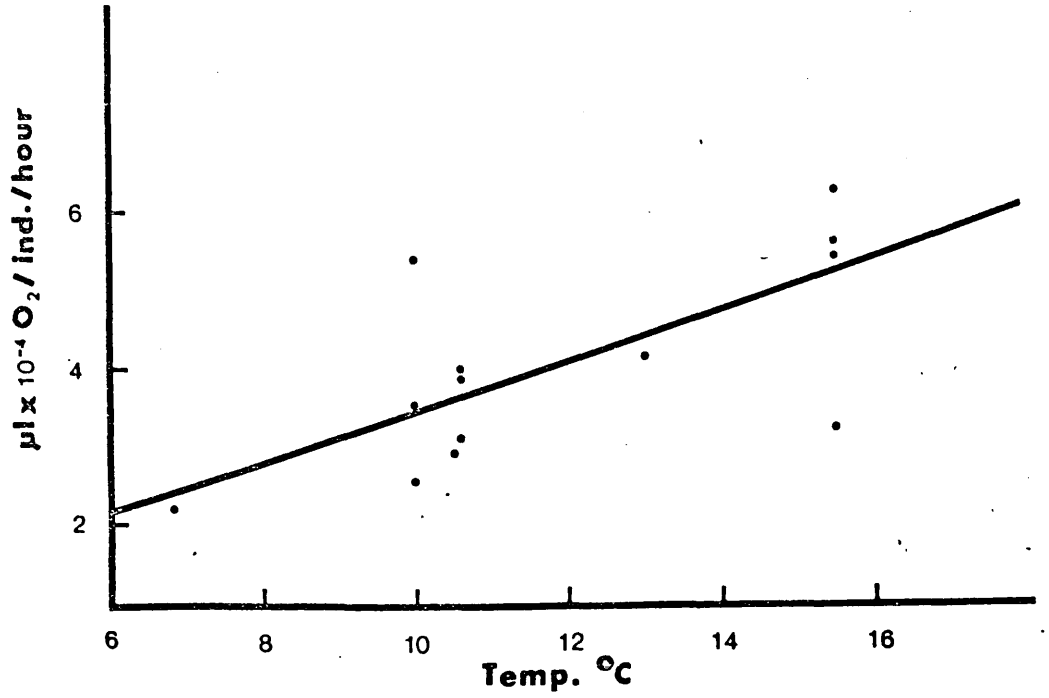
Figure 62 shows the linear relationship obtaining between temperature and respiration rates of the smaller rotifers. The scatter due to size is very apparent, nevertheless the regression equation, y = 0.29 x - 0.11, gave a correlation coefficient of 0.65 with $P < 0.001$. An exponential relationship was also tested on the same data and this too was significant with $P < 0.001$.

Respiration / Temperature (K.quadrata)

$y = 0 \cdot 302 + 0 \cdot 433$

$r = 0 \cdot 69$

$P < 0 \cdot 01$



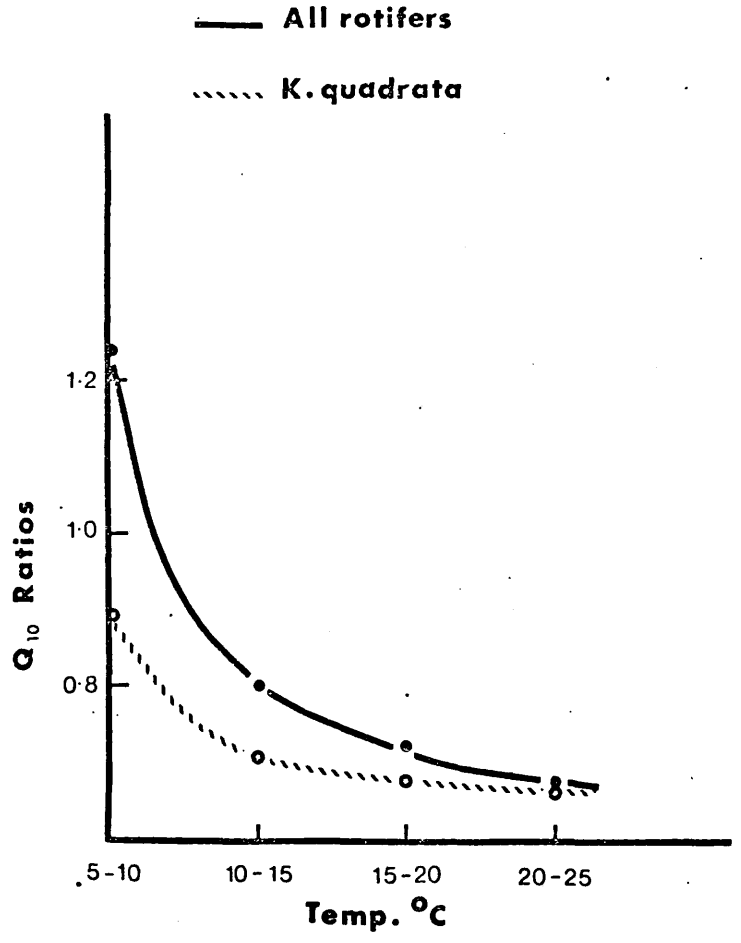


Fig. 63 Linear relationship between respiration rate and temperature for K. quadrata

Fig. 64 Ratio between Q_{10} for rotifers and the Q_{10} values obtained by Krogh plotted against temperature.

The regression equation was $y = 0.344e^{0.09x}$. Since the linear regression was equally significant, this simpler relationship was used in subsequent calculations. This choice will be discussed later in the light of other work.

The respiration rate of K. quadrata had been determined at several temperatures. Figure 63 shows the linear relationship between respiration and temperature for this species expressed by the equation $y = 0.302x + 0.433$ with $P < 0.01$ for a correlation coefficient of 0.69. The exponential relationship was equally significant and could be expressed by the equation $y = 0.43e^{0.08x}$. Again the simpler relationship was used subsequently but for work with field data involving all the rotifers, the more generalised relationship obtained from all the respiration rates was used. This differed negligibly in slope from the temperature/respiration regression for K. quadrata but was different in level. How significant this difference was may be assessed by comparison with the respiration rates of B. plicatilis measured at different stages in its life history which are to be published separately.

Discussion

Respiration - size relationship

The relationship between size and respiration rate has been discussed and reviewed by many authors including extensive work by Brody(1945), Hemmingsen (1950, 1960), Bertalanffy (1957) and Zeuthen (1947, 1953, 1970). Zeuthen (1953) suggested that metabolism is related to cell surface and therefore would increase with the two-thirds power of the weight in poikilotherm animals. Therefore the equation relating metabolism to weight could be expressed as $y = ax^{0.67}$ where y is the metabolic rate, x body weight and a the intercept on the y axis.

Hemmingsen (1950, 1960) for an extensive range of poikilotherms, showed that metabolism is more nearly related to the three-quarters power of the body weight, and accounts for the discrepancy between his result and that of Zeuthen by relating metabolism to respiring surfaces which may be increased by

vascularisation, ventilation of internal surfaces etc. These generalised relationships covering a size range from 10^{-12} - 10^{6} grams may not hold for narrower ranges or particular taxonomic groups (Zeuthen 1970, Newell 1970). For the rotifers studied here, metabolism increased with a little over one-third power of the body weight. This is in complete contrast to the work of Zeuthen (1953) who suggested that in small metazoan poikilotherms, the slope relating metabolism to dry weight was 0.9 -1.0. However the data he included referred only to marine larvae and all were larger than 0.1 ug. in weight. It has often been noted that the metabolism of young stages is greater per unit weight than that of adults or larger animals of the same species. This perhaps accounts for the steep slope of the metabolism/weight relationship in marine larvae.

Bearing in mind that rotifers have a fixed number of nuclei in the various organs of the body (Hyman 1951) and that therefore the greatest metabolic demand in adults is that of egg production, it is theoretically possible that the rotifers increased size consists largely of non-metabolising substances: yolk, lorica. If the size increase between the species included here is due largely to the expansion of cytoplasm in mainly syncytial organs and tissues (Hyman 1951) the metabolic rate may not substantially increase with size. The slope of 0.39 may therefore be related to this particular taxonomic group which contains some of the smallest metazoa with a very unusual growth pattern and, in some cases at least, a considerable volume of non-respiring material. In this connection however Schiemer and Duncan (in preparation) have found no such unusual b value in nematode species, a group related to rotifers with a similar growth pattern but no lorica.

Respiration/Temperature Relationship

Newell(1970)summarises considerable evidence that temperature does not influence active and standard metabolism in the same way. In nature, planktonic

rotifers, particularly those without a foot and certainly those confined to the pelagial, are seldom inactive. This activity continued in the Cartesian diver respirometers and therefore all measurements of respiration are of active metabolism.

Haldrow and Boyd (1967) distinguished between the effects of T^{o} on active and standard metabolism in Gammams oceanicus and showed that the active rate of respiration is affected by temperature changes to a greater extent than the standard rate. The Q_{10} value was lower for relatively inactive animals than for active animals in the same temperature range. Rao and Bullock (1954) showed that the Q_{10} also varies with the temperature to which the organism has previously been adapted being lower for animals adapted to warmer temperatures. These writers also point out that it is natural to look for lower Q_{10} in animals subject to wide fluctuations in temperature but they found sparse evidence of this correlation. However Davies (1966) showed that Patella vulgata had a lower Q_{10} higher up the shore. This was correlated with a higher environmental temperature and greater temperature fluctuations than those lower down the shore, and than Patella aspera which is confined to the lower shore.

It is clear therefore that there are several opinions as to what the Q_{10} value really demonstrates, so much so that Bělehrádek (1930) suggested it was of little use for comparative purposes. The various opinions have been summarised and discussed by Newell(1970) and it seems that provided other variables, such as size and activity are eliminated, comparative work with Q_{10} might be of some value. (See Rao and Bullock 1954).

In all the cases mentioned so far, and in the review of Newell(1970) the relationship between temperature and metabolism was considered to be linear when the logarithm of the respiration rate was plotted against temperature. This differs slightly from the empirical formula of Arrhenius where

the linear relationship is between the log. rate of an enzyme reaction and the reciprocal of temperature. If the Arrhenius or the exponential relationship hold, then the Q_{10} is constant over a particular temperature range, but this seldom occurs in nature. (Barrington 1968) The early data of Krogh (1914) whose "normal" curve has frequently been used as a expression of the standard relationship between respiration rate and temperature allows for changing Q_{10} value in contrast to the Arrhenius formula.

As already recorded, the data presented here shows a very significant linear relationship with temperature. In only one other case has such a relationship been established. This was the heart rate of frogs measured during the summer by Barcroft and Izquierdo (1930) and also shown for excised hearts in Barcroft (1938). In the latter case particularly, the relationship is more obviously linear in the higher temperatures, that is at temperatures operating in the field situation. Cremer and Duncan (1969) found a discrepancy between field respirations of Cladocera and Copepoda and the theoretical values obtained from a respiration/temperature relationship. In all other published work animals have been acclimated to different temperatures and therefore it is the respiration rates of acclimated animals that have shown the exponential relationship with temperature, nor have these animals been kept always within their normal temperature range.

In the present work, the temperature dependence of active metabolism as demonstrated by the linear plot (Fig. 62) is slight, giving a slope of only 0.29. The Q_{10} was calculated for $5^{\circ}C$ intervals throughout the range and slightly beyond it at higher temperatures, for all rotifers and for K. quadrata. The results are summarised in Table $\frac{24}{23}$ which also includes the values of Q_{10} derived from Krogh's curve by Winberg (1971) and the ratio between these two values. As with the data of Krogh (1914), there is a steady decrease in the Q_{10} value with each successive $5^{\circ}C$ rise in temperature but the ratio between

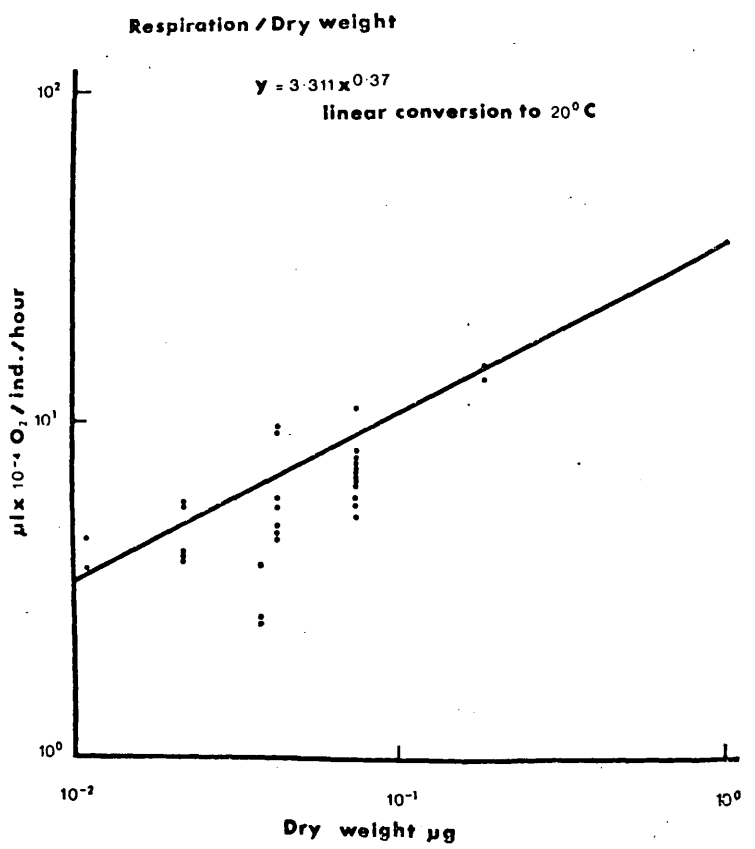

Respiration / Dry weight
y = 3·311x^0·37
linear conversion to 20° C
10²
10¹
10⁰
µl x 10⁻⁴ O₂ / ind. / hour
10⁻²
10⁻¹
10⁰
Dry weight µg

Fig. 65 Respiration/dry weight relationship for small planktonic rotifers converted to 20°C. by the relationship described in Fig. 62.

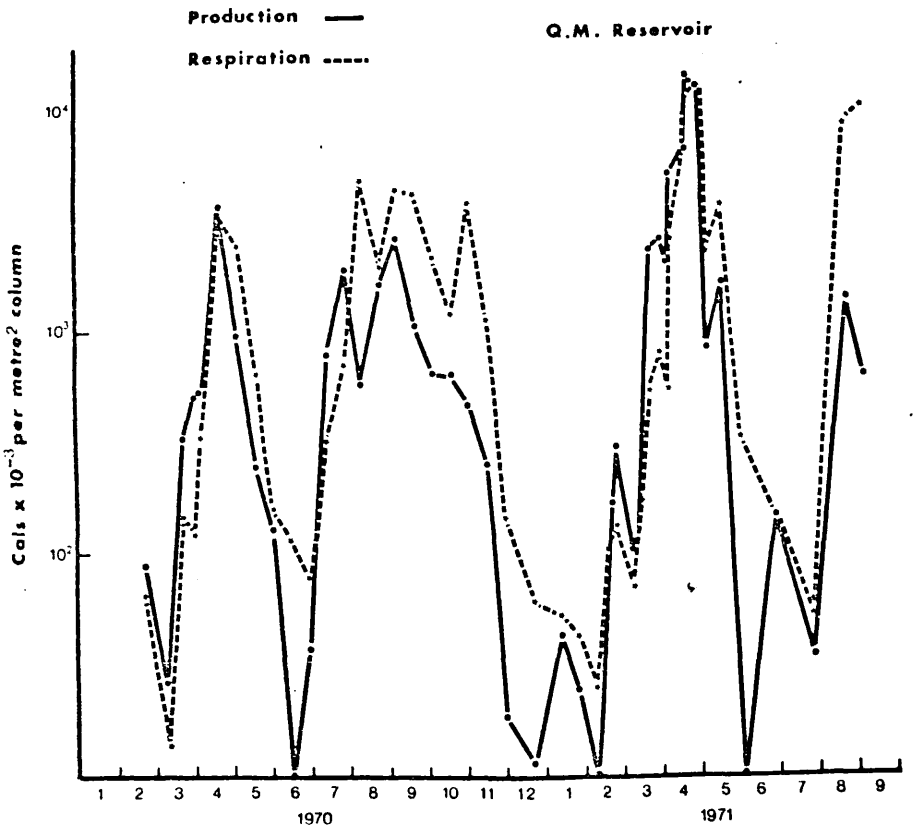
the Q_{10} for rotifers and that obtained by Krogh is not constant at different temperature intervals. When the ratio is plotted against temperature a clear curvilinear relationship obtains with the higher ratio at the lower temperature (Fig. 64). This may indicate a lesser degree of temperature dependence in rotifers than can be predicted from Krogh's curve and this relative independence is greater at temperatures above 15°C. Many Bdelloidea and a number of Monogononta have been noted for their resistance to high temperatures even in the active state (Hyman 1951). Resistance to extreme cold has only been recorded in Bdelloidea and then in an inactive, resistant condition. (Hyman 1951) The degree of temperature independence demonstrated by the Q_{10} relationship also lends support to the suggestion (see earlier) that food conditions rather than temperature effects are responsible for the decline of the rotifer population during the summer months.

The linear relationship between temperature and respiration was also used to convert respiration data to 20°C. Fig. 65 is a double log. plot of respiration and dry weight for comparison with Fig. 61 which is based on Krogh's conversion factor. The new relationship produced a respiration/weight regression which could be expressed as $y = 3.311x^{0.37}$. This equation differs negligibly from that using Krogh's factors particularly in its slope. It is suggested therefore that within the normal temperature limits of a species the relationship between field temperature and respiration rate measured at that temperature is linear. Beyond these limits the relationship becomes curvilinear even when animals are acclimated. In this connection it is interesting to recall that Bottrell (personal communication) has found a curvilinear relationship between the rates of development of some fresh-water zooplankton and temperature, in contrast to Elster (1954) Edmondson (1960), Amren (1964) Burgis (1970) and the present work on rotifers, all of which show a linear relationship. This discrepancy can perhaps also be accounted for by differences in the range of temperature values used for the determinations.

Table 24

Q_{10} values for respiration rates of rotifers

Temperature	5°-10°C	10-15	15-20	20-25
A Reservoir rotifers	4.33	2.31	1.79	1.56
B K. quadrata only	3.17	2.07	1.69	1.51
C Krogh's value	3.5	2.9	2.5	2.3
Ratio $\frac{A}{C}$	1.24	0.80	0.72	0.68
Ratio $\frac{B}{C}$	0.91	0.71	0.68	0.66


Production
Respiration
Q.M. Reservoir
Cals x 10^{-3} per metre^2 column
10^4
10^3
10^2
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

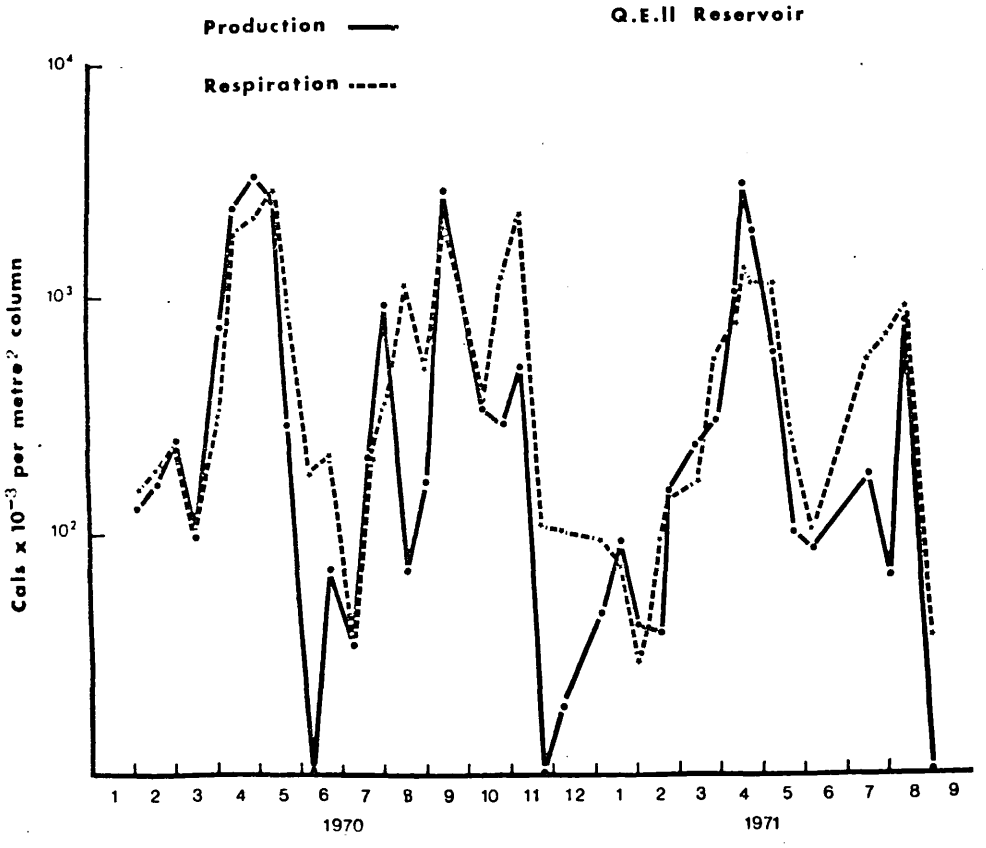

Production
Respiration
Q.E.II Reservoir
Cals x 10^{-3} per metre^2 column
10^4
10^3
10^2
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
1970
1971

Fig. 66 Seasonal variation in production and maintenance cost for rotifers in Q.M. reservoir

Fig. 67 Seasonal variation in production and maintenance cost for rotifers in Q.E.II reservoir.

Respiration rates of field populations of egg-bearing rotifers

The equation calculated from determinations of the respiration rates of various reservoir rotifers, namely $y = 0.29x - 0.11$, where y is the respiration rate in microlitres x 10^{-4} of oxygen per individual per hour, and x is the ambient temperature, was used to determine the overall daily oxygen consumption in one metre^2 column of the reservoirs for populations of K. quadrata, K. cochlearis, and P. vulgaris. These data are presented in Appendix VI where they are also converted into calories x 10^{-3}. Assuming a mixed diet, one millilitre of oxygen was taken to be 4.83 calories (Ivlev 1945).

Oxygen consumption measurements calculated by the method described above are dependent on only two factors, namely, temperature and population numbers. High population densities in spring and autumn were therefore reflected in the high maintenance costs and the higher temperatures in autumn enhanced the utilisation of energy for respiration. Nevertheless highest maintenance costs were found in spring 1971 in Q.M. when very high densities of K. quadrata and and P. vulgaris were seen. Since only rotifers which carry their eggs were included in the present analysis, the large population of S. pectinata, which occurred in autumn 1971 in Q.M., were not reflected in the respiration rates calculated here.

During the winter months in both reservoirs maintenance costs were minimal as were production estimates. Figures 66 and 67 show the seasonal picture of production and respiration rates in calories x 10^{-3} per m^2 column for the two reservoirs. The trends reflected each other fairly closely with the greatest discrepancies occurring when the production was declining. At these points, respiration rate seemed to decline less rapidly than did production, possibly because production estimates reflected the food situation.

Pilarska (personal communication) has been able to show in cultures of Brachionus rubens that the respiration rate is virtually independent of food

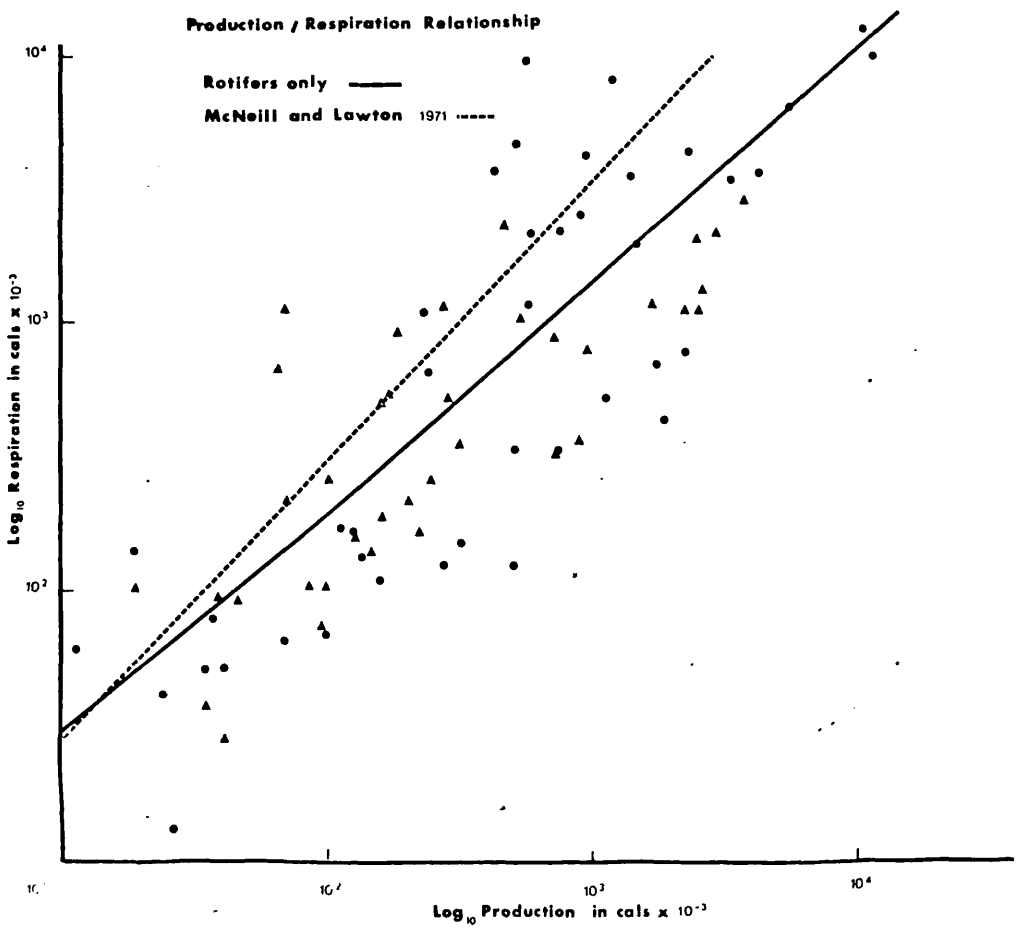

Production / Respiration Relationship
Rotifers only
McNeill and Lawton 1971
10^4
10^3
10^2
10^2
10^3
10^4
Log_{10} Respiration in cals x 10^{-3}
Log_{10} Production in cals x 10^{-3}

Fig. 68 Production/respiration relationship for rotifers in Q.M. and Q.E.II. ($\log R = 0.79 \log P + 0.69$)

concentration. One could expect this of opportunistic animals such as planktonic rotifers which seldom survive adverse conditions except as resting stages.

Figure 68 combines production and respiration estimates per m^2 column in the form of a double log regression. The equation was log R = 0.79 log P + 0.69 and the correlation was highly significant ($r = 0.82$, $P<0.001$). This form of calculation may have covered the variation in respiration and production estimates caused by temperature and food conditions. On the other hand it could be that since food conditions were also dependent on temperature, any improvement was offset by increased maintenance costs due to the rise in temperature. It is therefore feasible that the relationship between food-influenced production and temperature-influenced respiration should remain constant throughout the year.

The only other workers who have calculated the maintenance costs of rotifer populations in field situations are the Russian workers referred to in the production section and whose work is recorded in Kajak and Hillbricht-Ilkowska (1972). The methods by which maintenance costs were calculated in the Russian work are not given though Alimov et al (1972) base those of Cladocera on the relationship between wet weight and oxygen consumption derived by Sushcheniya (1968). No methods at all are given by Anchronikova et al (1972), and all the work gives the total seasonal maintenance cost rather than the variation throughout the season. There is therefore no published work on rotifers with which to compare Figure 68, though Cremer and Duncan (1969) give data for Cladocera and Copepoda from which a similar relationship might be computed.

However, Engelmann (1966) related annual production to annual maintenance costs for several terrestrial invertebrates and compared the regression he obtained with a similar one for homiotherms though he did not analyse them

statistically. For poikilotherms he obtained the regression log R = 0.62 + 0.86 log P. McNeill and Lawton (1970) brought together additional data and recalculated the same regression as log R = 1.0733 log P + 0.3757, omitting those data which assumed a P/R ratio. The slope of this line did not differ significantly from 1.0, but when the data for short-lived poikilotherms only was recalculated the regression became log R = 1.1740 log P +0.1352 where the difference between 1.1740 and 1.0 was significant.

Annual production and respiration were calculated for the two reservoirs studied here and the results are presented in Table 25. The annual production estimates were very similar for both reservoirs but it appeared that the annual maintenance costs were higher in Q.M. than Q.E.II. Nevertheless, despite this apparent difference, when the production estimates were fitted to the equation of McNeill and Lawton (1970) quoted above, the respiration data were found to be within the 95% confidence limits calculated by these authors (log R $\pm$ 0.5544) for the data they used. This again implies that seasonal variation in maintenance cost and production cancel each other out to such an extent that the relationship between the total annual cost and the total annual output remains constant. When the data of Alimov et al (1972) and Andronikova et al (1972) for total herbivorous rotifers are fitted to McNeill and Lawton's equation, these data also fall within the 95% confidence limits even though they are calculated for vegetative seasons shorter than one year.

Table 25

Annual Production and Maintenance Costs of rotifer populations in Q.M. and Q.E.III reservoirs.

	Total P (cals)	Total R (cals)
Q.M.	264.79	497.24
Q.E.II	252.11	272.406

Table 26

Feeding rates of rotifers

Species	Source	T°C	Food Species	Food Concentration cells/ml	Method used	Consumption ul/ind./hr	Consumption Cells/ind./hr
K. quadrata	Pond	20°	Chlorella	152 x10^4	Direct count	1.8	2.8 x 10^3
				50 x10^6	Tracer	3.15	157 x 10^3
	Pond	20°	Oocystis	74 x10^4	Direct count	2.3	1.7 x 10^3
	Pond	23.5°	Chlorella	40.2 x10^3	Tracer	2.52	101 x 10^3
						4.6	184 x 10^3
						2.6	104 x 10^3
B. rubens	Pond	20°	Scenedesmos	79.6 x10^4		1.4	1.14x 10^3
				85 x10^4	Direct	1.6	1.36x 10^3
				86 x10^4	count	1.0	0.9 x 10^3
				86 x10^4		1.4	1.18x 10^3
P. vulgaris	Reservoir	20°	Small flagellates	480 x10^3	Tracer	0.84	424
			Cryptomonas	55.7 x10^3	Tracer	0.39	22
	Reservoir	5°	Bacteria	785	Tracer	1.09	
S. pectinata	Reservoir	8°	Algae	77	Tracer	1.06	
						1.29	

Food Consumption of rotifers

Several experiments to determine food consumption under natural conditions were conducted using the method described by Gliwicz (1968), but the errors involved in the counting method were so great and the numbers of rotifers so low that the work had to be abandoned without its having produced any significant results.

Attempts were then made to determine feeding levels in different concentrations of food using cultured animals in the hope that such work could be related to concentrations in the field and also compared with other work in the literature (Erman 1956, 1962, Galkovskaya 1963, Ito 1955, Ito and Iwai 1957, Pourriot 1957, Pennington 1941, King 1967.) In this way it was hoped to generalise the relationships between feeding rate, temperature and food concentrations in a way similar to the production and respiration data. The direct counting method described in the methods section of this thesis was employed at first until there was the possibility of using radioactive tracers. The tracer technique, particularly when using field population, required considerable work, and because of the small size of the animals used was even more time-consuming than the direct counting method. It had the advantage however of enabling fewer animals to be used in less concentrated food suspensions than were required for the direct counting method. The only meaningful results using these last two techniques are recorded in Table 26, but subsequent work on the consumption and assimilation of B. plicatilis indicated the value of the tracer technique for herbivorous rotifer populations under almost field conditions. Gliwicz's (1968) method requires high concentrations of rotifer relative to other planktonic animals, and the variation in the results, though not recorded, must necessarily be high, as it is in all counting methods.

The results in Table 26, though very variable, fit the graph given by Galkovskaya (1963) Unfortunately the data from which this graph was constructed

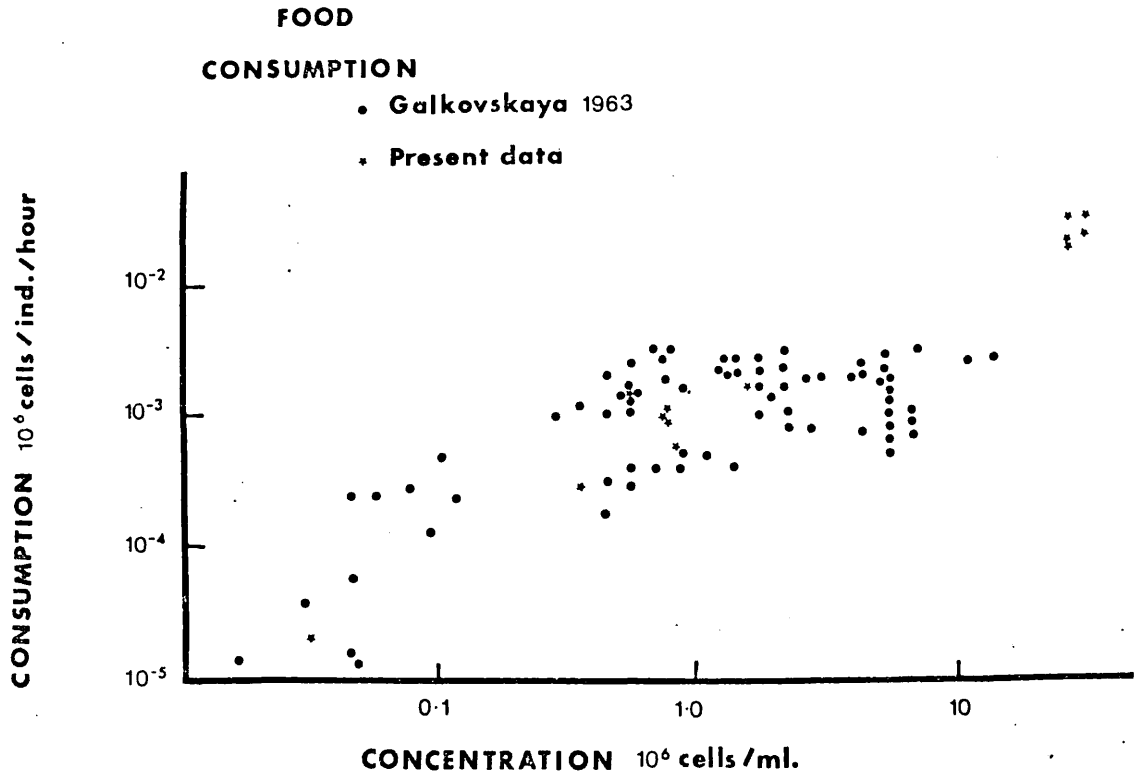

FOOD
CONSUMPTION
• Galkovskaya 1963
* Present data
CONSUMPTION 10⁶ cells / ind. / hour
10⁻²
10⁻³
10⁻⁴
10⁻⁵
0·1
1·0
10
CONCENTRATION 10⁶ cells / ml.

Fig. 69 Ingestion rate of planktonic rotifers in relation to food concentration. (Modified after Galkovskaya (1963)

were not given in the paper so it was impossible to calculate the mathematical relationship between food concentration and consumption. The graph (Figure 69) indicates however that the results vary by as much as a factor of ten at maximal feeding rates whilst the range below this covers 1.5 log cycles, that is, the total range is only a little over twice the experimental variation at any one food concentration. Clearly a much greater refinement of technique is required before valid quantitative estimates of the consumption of field populations of rotifers can be obtained.

The only data of this kind are the last three sets recorded in Table 26 These indicate, when compared with the culture data which precede them, that the reservoir populations cannot rely on one food source alone but must depend on bacteria, algae and detritus particules of the right size, otherwise they would be consuming less than one particle per hour. Nevertheless, the filtering rates were similar to those observed in other rotifers and one must therefore assume that within the volume of water filtered other particles which were not labelled with ^{14}C were providing food. The relative proportions of labelled and unlabelled food varies throughout the year as proportions of algae, bacteria and detritus fluctuate. Nothing further could be deduced concerning the food supply of the rotifers in the reservoirs, but by adding the calories required for production and respiration it was possible to determine how much food must be assimilated by the population at various periods of the year.

An energy budget for adult Brachionus plicatilis O.F. Muller

The study of the energetics of field populations should also involve laboratory work from which generalisations, such as those contained in the respiration and production sections of this thesis, can be made (cf Engelmann 1966). Such generalisations can often be supported by detailed ecological studies such as those of Hall et al (1970) but these are extremely time-consuming and involve large numbers of workers simultaneously. The opportunity of preparing a complete energy budget for Brachionus plicatilis to serve as a comparison with reservoir populations was given by Prof. H. Loffler and Prof. A. Ruttner-Kolisko at the Biologische Station of the Austrian Academy of Sciences at Lunz-am-See, Austria. Rotifers may be of considerable importance in the energy flow through pond and lake ecosystems because of their rapid life histories and high reporductive potential. Whilst some data is available on feeding, respiration and production of these animals (see references in rest of text), so far no complete energy budget has been published. King (1967) provided comprehensive data on Euchlanis dilatata omitting respiration but giving very useful observations and a valuable discussion of ecological efficiencies in rotifers. The present work give complete data for and energy budget and ecological efficiencies of adult Brachionus plicatilis.

Cultures of the rotifer were obtained from stocks at the Biologische Station, Lunz-am-See by courtesy of Prof. Ruttner-Lolisko, and the cultures were maintained and aged by her research assistant. Excess Dunaliella salina provided the food, and experimental cultures were maintained at 20°C. in sea water. All experimental work was performed at 20°C. on animals whose ages were known to the nearest hour. Methods already described earlier were employed in the work but any slight modifications will be mentioned where relevant. Age-specific respiration was studied but since such data on consumption and assimilation has not been obtained it will be discussed separately from the

adult energy budget. Ruttner-Kolisko (1972) provided data on the volumes of animals of known age.

Table 27

Respiration rates of individual Brachionus plicatilis in ul. $O_2 \times 10^{-4}$ per individual per hour

Stage	Egg	Adult	Adult + one egg	Adult + two eggs	Adult + three eggs	Post oviger- ous Adult	Senile Adult	Total oviger- ous Adults
	5.242	20.405	43.725	54.219	59.758	53.224	13.281	
	7.652	29.15	47.223	61.215	54.802	57.318	12.826	
		31.482	59.47	71.126	63.839	47.066	12.243	
		23.3	51.26	50.049		43.338		
		20.504	47.532	58.25		65.005		
		21.669	35.416	61.215				
		23.766						
		24.698						
		27.494						
		25.069						
		23.32						
Mean + S.E. Mean	6.447	26.623 ± 2.36	47.438 ± 8.37	59.346 ± 7.56	59.466	53.190	12.783	54.607 ± 4.97
S.D.xt			±20.49	±18.52				±19.25
Mean ± S.E in Calx10^{-6}	3.11	11.89 ± 1.14	22.91 ± 4.04	28.66 ± 3.65	28.72	25.69	6.17	26.375 ± 2.4

Table 28

Consumption of Dunaliella salina by Brachionus plicatilis

Rotifers per experiment	Foodcells x 10^3 per ml.	Activity in C.P.M. per ml.	Activity in C.P.M. per rotifer	ul. cleared/ indiv/hr.	Cells Eaten/ indiv/ Hour	Consumption - Mean Assimil.	Consumption in cals. x 10^{-6}
16	1440	24907	11.72	0.94	1353.6	1205.7	525.69
15	1440	24907	8.58	0.68	979.2	831.3	362.45
13	775	14925	16.96	1.14	883.5	735.6	320.72
13	775	14925	18.41	1.23	928.7	780.8	340.43
13	970	16000	12.04	0.75	727.5	579.6	252.71
12	970	16000	10.20	0.64	620.8	472.9	206.18
23	590	9600	14.44	1.5	885.0	737.1	321.38

Mean Consumption = 763.28 Cells/individual/hour

Mean $\pm$ S.E. (Mean) = 332.79 $\pm$ 93.25 Cals x 10^{-6}/ind/hr.

$\pm$ S.Dxt = $\pm$ 246.7

Table 29

Assimilation of Dunaliella salina by Brachionus plicatilis

Rotifers per experiment	Time in labelled food	Food cells x 10^3 per ml	Activity in C.P.M. per ml.	Activity in C.P.M. per rotifer	ul. per indiv. per hour assimil.	Cells per indiv. per hr. assimil.	Cal x 10^{-6} assim. per hr.
24	2 hrs	350	8230	9.12	0.56	196	85.46
22	4	↓	↓	12.36	0.38	133	57.99
24	6	↓	↓	20.49	0.42	147	64.09
16	24	590	9600	43.37	0.19	112	48.83
12	26	↓	↓	68.50	0.27	159	69.32
12	28	↓	↓	72.80	0.27	159	69.32
15	41	↓	↓	76.89	0.20	118	51.45
16	43	↓	↓	106.74	0.26	153	66.71
15	45	↓	↓	113.03	0.26	153	66.71

Mean Assimilation = 147.9 Cells/individual/hour

Mean $\pm$ S.E. (Mean) = 64.43 $\pm$ 9.95 Cals x 10^{-6}/ind./hour

$\pm$ S.D x t = $\pm$ 29.85

Results

Table 27 shows the respiration rates of individual adult Brachionus plicatilis in microlitres x 10^{-4} of oxygen per hour and in calories x 10^{-6} per hour. Prior to egg production the rates are relatively uniform but ovigerous females have a rate more than double this. The higher rate appears to be independent of the number of eggs the female is carrying since 95% confidence limits of the mean of all ovigerous females cover the range of values contained in each separate category of ovigerous female although the number of determinations is low. The mean respiration rate of all ovigerous females is therefore used in the budget, since in an actively growing culture mature females are seldom without an egg.

The consumption data in Table 28 show much greater variability than either respiration or assimilation, but since the variation was not closely correlated with the concentration of the feeding suspension a mean value for all the experiments was calculated.

According to Galkovskaya (1963) feeding intensity of Brachionus calyciflorus Pallas is dependent on all concentration in the medium up to 0.5 x 10^6 cells per ml. Above this concentration feeding intensity is maximal. The lowest concentration used in the present work is within the maximal range given for this related rotifer species.

The concentration of food used in the assimilation experiments (Table 29) was lower than in most of the feeding experiments but again there is no regular variation with concentration. The accuracy of the mean value (S.E. = $\pm$ 15%) coupled with the irregularity of the variation in the data, does not justify rejection of values from the lower food concentrations.

Schindler (1968) points out that in Daphnia magna respiration of assimilated ^{14}C begins after 16-24 hours after which true assimilation cannot be measured. The results presented here do not suggest that this has occurred

Table 30

Data for production estimates for Brachionus plicatilis

Category	Mean dry weight	Calculated Cal. value (assuming 50% D. Weight = Carbon)
Adult	0.158 ug.	790×10^{-6} Cal.
Adult + 1 egg	0.250	1290×10^{-6}
Egg	0.092	500×10^{-6}

Table 31

Hourly reproductive production of B. plicatilis

Category	Proportion of egg produced per hour		Mean	Cal. val. of egg	Hourly Production
Female + 1 egg		4% of an egg	7.3%	500×10^{-6}	36.5×10^{-6} cals
2 eggs	4	8% of an egg			
3 eggs	8	16% of an egg			

Table 32

Elements of an energy budget for adult Brachionus plicatilis in cal $\times 10^{-6}$ per adult per hour

		Measured $\pm$ S.E.	Calculated
Consumption	(C)	332.79 ± 93.25	
Assimilation	(A)	64.43 ± 9.95	62.875 (P+R)
Respiration	(R)	26.375 ± 2.4	
Production (eggs)	(Pr)	36.5	34.9
Faeces	(F)		268.36 (C-A)

Efficiencies: $\frac{A}{C} = 0.194$, $\frac{Pr}{C}$ $(K_1) = 0.11$ $\frac{Pr}{A}$ $(K_2) = 0.57$

during the period of the experiment since there was no fall off in activity of the rotifers. This probably requires further investigation.

Table 30 shows the dry weights obtained by cumulation and the calorific values of individual adults and eggs. These values provided the basis for production estimates. Egg development time in rotifers has been shown to be closely dependent on temperature (Edmondson 1960). In cultures of Brachionus plicatilis kept at 20°C, Ruttner-Kolisko (personal communication) found that the eggs take 24-26 hours from laying to hatching. The percentage of egg development occurring in one hour will vary according to the number of eggs the female is carrying. This data is recorded in Table 31, and the hourly production converted to calories using the data from Table 30. As for the respiration data, oviperous females were treated as one group irrespective of the number of eggs they were carrying.

Table 32 shows the elements of an energy budget for reproducing adult Brachionus plicatilis. The second estimate of reproductive production was calculated by Winberg's "physiological method" applied by Galkovskaya (1971) to rotifer populations in the field. This involves the determination of nett production efficiency (K_2 or $\frac{P}{A}$) and the metabolic loss (T) or respiration rate. production is then equal to $\frac{TK_2}{1-K_2}$ The result obtained by this method is very close to that determined from dry weight and calorific values of the eggs.

Assimilation calculated as P + R is within the limits of accuracy of the mean assimilation measured radioactively and differs from it by only 2-4%. However the assimilation measured radioactively must also include some kind of growth factor when measurements were continued for several hours. This could be metabolic activity in the ovary or vitellarium since growth in size has definitely stopped by the time eggs are produced.

Discussion

a) Respiration

Earlier work on rotifer respiration has already been reviewed in the section on respiration of reservoir rotifers. These usually involved large numbers of animals. In the present work, using animals of known age, individual differences between animals of the same age became apparent and also between adults. When the respiration rate of all the eggs carried is subtracted from the total respiration rate, the rate for an ovigerous female is still higher than that of a pre-ovigerous adult. This is probably due to increased metabolic activity in the ovary and vitellarium, which continues for about forty-eight hours after the laying of the last egg. During the post-ovigerous period, the body of the female seems to accumulate large quantities of yolk and the respiratory rate is as high as that of the reproducing females. As the animal ages the yolk is dispersed but the gut remains empty and at this stage the respiratory rate decreases below that of young adults without eggs.
Apart from that of the oldest adults, these different respiratory rates all fall within the range of values obtained by Pourriot and Deluzarches for large numbers of Brachionus calyciflorus of unknown age distribution under different experimental conditions (1.57 → 6.2 ul x 10^{-3} /ind./hr.) The values obtained by Belyatskaya (2.24 x 10^{-3} ul) and Galkovskaya (5.04 x 10^{-3}) also fall within this range. It is important therefore that mean respiration values for a population even of animals as small as rotifers be determined on animals of known state if they cannot be measured individually. This is even more important where actively growing cultures are concerned, since the age-specific respiration rate is even more variable (See later)

b) Feeding

The only published work on the feeding rate of B. plicatilis is that of Ito (1955) in which the food was Synechococcus sp. The mean volume filtered

per individual per hour was 3.04 ul, corresponding to a cell consumption of 24.32×10^3 in a food concentration of 8×10^6 cells per ml. This is very much higher than the values obtained in the present work using Dunaliella salina. Galkovskaya (1961) suggests that the food consumption of B. calyciflaris increases with cell concentration in the feeding medium, up to a maximum at about 0.5×10^6 cells per ml, when the rate levels off. King (1967) found a similar effect with Euchlaris dilatata feeding on Chlamydomonas reinhardii, but no levelling off occurred with Euglena as food in the concentrations he used. This indicates, as Erman (1962) suggested, that when interspecific comparisons of food are made feeding rate varies more with the quality of the food offered than with its concentration. He found that in the case of B. calyciflorus the filtering rate ranged from 1.3 → 13.3 ul/ind./hour according to the nature of the food offered. The difference between Ito's results and the ones presented here are probably a consequence of the differences between the quality of the food offered rather than of its concentration.

With a food concentration greater than 0.5×10^6 cells/ml. the filtering rate of Brachionus calyciflorus (Galkovskaya 1963) and of B. rubens (Erman 1956) is about 1ul/individual/hour. Rates obtained for B. plicatilis agree with this but the results of Galkovskaya and Erman show considerable variation despite the large numbers of animals used for each determination. The maximum feeding rates obtained by Galkovskaya vary by a factor of ten. The variability of the B. plicatilis results is much reduced by the use of radioactive techniques and these, together with rates obtained by Pennington (1941) for B. calyciflorus and the present author's unpublished data for B. rubens and Keratella quadrata all fall within the same range. Until more refined methods are available for the determination of feeding rates of very small animals, it is probable that all Brachionidae will fit Galkovskaya's graph. As with respiration data, the need to use large numbers covers individual variation. Small animals vary

by small amounts, but have proportionately the same variability as larger ones. Refined techniques would demonstrate individual variation whereas accurate techniques used with large samples mask individual variation by substituting a spuriously accurate mean. This is probably the case with the results of the radioactive work used here.

c) Assimilation and Assimilation Efficiency

Galkovskaya (1963, 1971) gives assimilation efficiencies $\frac{A}{C}$ for B. calyciflorus ranging from 0.21 → 0.78 with the lower efficiencies apparently occurring in higher food concentrations. The only other value for rotifers is given by Sorokin and Mordukhay-Boltovskaya (1962) for Asplanchna which is a predator. Their values, quoted by Galkovskaya, are 0.16 - 0.22. The efficiency of B. plicatilis (Table 6) is very low, particularly for an animal feeding on a naked alga. This is probably due to the excess of available food in the medium. Feeding is a continuous process in planktonic rotifers and little or no rejection of particles of the right size and nature occurs in the gullet. In excess food therefore, particles pass through the gut too quickly to be effectively digested. King (1967) noted that undigested algae appeared in the faeces of Euchlanis dilatata only at the most concentrated food level. Many cells of Dunaliella seen in the faeces of B. plicatilis were still green and apparently intact, but they were no longer motile and therefore not available as food. The assimilation data might have been checked using the relation A = C-F if labelled faces had been collected during experiments, but the difficulties of separating faecal material from labelled algae and medium were not overcome. The similarity between the calculated assimilation (P+R) and the experimental result gives confidence in the radioactive technique employed.

McNeill (1970) found that the assimilation efficiency of Leptopterna Dolabrata, a mirid, ranged from 0.28 to 0.36. Since the mirid feeds largely on cell contents only, one would expect its efficiency to compare well with

that of an animal feeding on a naked cell. Similarly Wiegert's (1964) work on Philaenus spumarius a plant fluid feeder, shows a very high assimilation efficiency, 0.30 0.36 for nymphs, 0.66 for adults. However neither of these animals feeds continuously and again it is the rate of movement of food through the gut in a rotifer which reduces the assimilation efficiency relative to that of other species feeding on readily assimilated food material.

d) Production and Production Efficiencies

Since the present paper deals with adult rotifers, only reproductive production has been calculated. The gross production efficiency $\frac{P}{C}$ or K, (Ivler 1945) is quite low for a herbivore but is nevertheless within the range of values given by Galkovskaya (1963) for B. calyciflorus, 0.04→0.36, which probably also excludes body growth. The low efficiency is clearly a function of the poor assimilation efficiency since the nett production efficiency $\frac{P}{A}$, or K_2 (Ivler 1945) corresponds to the higher range of values given for B. calyciflorus 0.20→0.69, and corresponds closely to the values for the growth of Philaenus spumarius nymphs (Wiegert 1945) 0.53 and to McNeills (1970) values for Leptopterna dolabrata 0.50→0.58 which include both growth and reproduction. Although increase in size is not negligible in a rotifer it is nevertheless small in comparison with its extraordinary reproductive potential. It is therefore theoretically possible that $\frac{Pr}{A}$ for an adult rotifer should equal $\frac{Pg + Pr}{A}$ where Pg is growth for other animals feeding on easily assimilated material, or the $\frac{Pg}{A}$ for an actively growing nymph of similar feeding habits. McNeill relates the high nett efficiency of his animal to the fact that the mirid is sedentary. This is hardly the case in a rotifer. Though B. plicatilis has a foot and can remain attached to a surface, this seldom occurs in a healthy growing culture and when it does ciliary currents continue at the same rate as when the animal is moving.

Adult B. plicatilis is highly efficient at converting assimilated food into reproductive production, but much less efficient at converting available food

material into body material which could be used by the next trophic level. Under conditions where food is less readily available, the gross production efficiency may be higher. Galkovskaya (1963) found that B. calyciflorus achieved maximal reproductive production in the highest food concentrations. (3×10^6 cells/ml). This coincided with both maximal consumption and maximal gross and nett production efficiencies. However the work recorded by her in 1971 does not show this correspondence between K_1, K_2 and food concentration but shows a steady increase in K_1 as food concentration decreases while K_2 fluctuates irregularly showing no correlation with either of the other parameters. This seems to be more realistic since K_2 is a measure of the physiological state of the animal and therefore would be affected only indirectly by environmental conditions. Further work on animals cultured in different food levels is needed to ascertain the quantity of available food which gives maximal K_1 without reducing K_2. A budget determined at this food level would give the energy relations of an animal at its most efficient, and provide a standard for comparison with field situations.

Table 33

Annual Assimilation and Consumption of egg-bearing rotifers in one m^2 column

	Assimilation	Consumption
C.M.	762.03 cals.	11,430.45 cals.
C.E.II	524.52	7,867.80

Annual Assimilation and Consumption

By adding together the annual production and maintenance cost for each of the reservoir populations, it was possible to asses the amount of food assimilated annually by the rotifer population of one metre^2 column in each reservoir. These results, in calories, are given in Table 33.

Andronikova et al (1972) give data from Red Lake on assimilation and consumption of herbivorous rotifers which would suggest an assimilation efficiency of 81%. Similarly Alimov et al (1972) also suggest assimilation efficiencies in Lake Krivoe of 92%, and Lake Krugloe 80%. These seem extremely high though possible in low concentrations of easily assimilated food such as naked flagellates. Pilarska (personal communication) found in cultured B. rubens an efficiency of 20%, and the author's work on B. plicatilis gave one of 19%, but both of these were in dense concentrations of food. Data in Winberg (1971) for B. calyciflorus show that assimilation efficiencies vary, in this case from 25% to 78%, roughly in accordance with food concentration. Bearing this is mind, a mean assimilation efficiency for the year in the reservoirs was taken to be 60%. This was applied to the annual assimilation data to give the annual consumption which is recorded in Table 33. Until more detailed information is obtained about the feeding rate of reservoir rotifers or at least the assimilation efficiency in the field, it was not considered opportune to attempt a seasonal assessment of food consumption.

Cummins and Waycheck (1971) give the calorific values of a variety of organisms taken from the literature. If the reservoir rotifers assimilated only Chrysophyceae and Chlorophyceae, taking the mean calorific value of these algae given by the above authors as 3,800 cals. per gram dry weight, then the rotifers in one m^2 column of Q.M. consumed in 1970 approximately 3 grams dry weight of algae, whilst in Q.E.II they consumed about 2 grams. The total annual biomass calculated from Appendix V for egg-bearing rotifers was 0.6 grams in

Q.M. and 0.4 grams in Q.E.II. This means that over one year the population would consume in both reservoirs, five to six times its own weight of algae, and therefore the mean algal biomass required to support the rotifers must be approximately 8 mg. in Q.M. and 5 mg. in Q.E.II per m^2 column. If these weights are converted to cell numbers taking the weight of 10^6 small algae to be 4ugm. (Lund 1964) then the mean requirement of rotifers in one m^2 column of Q.M. is only 2,000 x 10^6 cells, (170 per ml) and in Q.E.II, 1,250 x 10^6 cells (80 per ml). When these figures are compared with Tables 9 and 11 it is clear that when the rotifer demand was at its highest in March and April, algae were present in sufficient numbers to support the population, but in autumn, when the rotifer population was again very high some other food source would be required. Another point is also brought to mind. Cultures of rotifers are often maintained at food concentrations of over 10^6 cells per ml. The present work indicates that this is far in excess of their requirements and one should be wary of extrapolating from laboratory to field in this particular matter

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APPENDIX I

RATES OF CHANGE OF ROTIFER POPULATIONS CALCULATED FROM $N_t = N_o e^{rt}$

A. Q.M. RESERVOIR

Date	t	r values					
		Keratella cochlearis	Keratella quadrata	Polyarthra vulgaris	Synchaeta oblonga	Synchaeta Pectinata	Asplanchna priodonta
23/2	28	0.045		+0.072			+0.078
9/3	14	-0.090	-0.029	-0.142			-0.029
23/3	14	0.134	0.118	+0.189	+0.182		+0.089
1/4	9	-0.074	0.054	-0.062	+0.108	+0.595	+0.040
7/4	6	-0.100	0	+0.318	+0.051	+0.129	-0.037
20/4	14	0.096	0.131	+0.141	+0.103	-0.035	+0.107
4/5	15	0.057	0.061	-0.158	-0.419	+0.143	+0.045
19/5	15	-0.186	-0.081	-0.313	-0.139	-0.519	-0.035
1/6	13	-0.138	-0.120				+0.010
15/6	14	0	-0.036				-0.227
29/6	14	0.139	-0.075				
13/7	14	0	0.151				
27/7	14	0.416	0.058	+0.432		+0.457	
10/8	14	0.065	0.121	+0.234		+0.028	
24/8	14	0.050	-0.051	-0.117			
7/9	14	-0.099	-0.003	+0.210		+0.687	
21/9	14	0.050	-0.150	+0.031		-0.317	
5/10	14	-0.021	0	-0.040		+0.050	
19/10	14	0.021	0.016	-0.042			
2/11	14	-0.481	0.045	+0.103		+0.369	+0.468
16/11	14	0	-0.045	-0.071			-0.050
30/11	14	0.445	-0.100	-0.157			
21/12	21	-0.019	0.029	-0.068	+0.264	+0.203	
12/1	22	0.010	-0.008	+0.040	+0.045	+0.042	
25/1	13	-0.017	-0.011	-0.075	-0.107	-0.039	
9/2	15	0.027	-0.025	-0.054	+0.119		+0.284
22/2	13	0.053	0.053	+0.173	+0.143	+0.458	+0.084
25/2	3	-0.600	0.341	-0.126	-0.235	-0.337	-0.232
8/3	11	0.194	-0.156	+0.019	+0.191	+0.083	+0.026
11/3	3	0.360	0.170	+0.225	+0.104	-0.075	0
22/3	11	-0.020	0.181	+0.090	+0.262	+0.305	+0.083
30/3	8	0.018	0.027	+0.033	+0.051	+0.011	+0.073
5/4	6	-0.254	0.048	-0.201	-0.090	+0.054	+0.096
8/4	3	0.247	0.116	+0.883	-0.910	-0.195	-0.253
19/4	11	0.092	0.130	+0.036	-0.067	+0.073	+0.318
22/4	3	0.146	0.102	+0.151	+0.229	+0.376	-0.202
29/4	7	0	0.152	-0.472		-0.134	+0.247
6/5	7	-0.135	-0.266	-0.067		-0.465	-0.155
17/5	11	-0.727	0.020	-0.209			-0.049
1/6	15	0	-0.318	-0.403			
28/6	27	0.241	0.045	+0.164		+0.132	
26/7	28	0	-0.034	-0.158			
23/8	28	0.165	0.089	+0.259		+0.177	
6/9	14	0.268	0.060	+0.078		+0.388	

APPENDIX I

RATES OF CHANGE OF ROTIFER POPULATIONS CALCULATED FROM $N_t = N_o e^{rt}$

B. Q.E.II RESERVOIR

r values

Date	t	Keratella cochlearis	Keratella quadrata	Polyarthra vulgaris	Synchaeta oblonga	Synchaeta Pectinata	Asplanchna priodonta
18/2	14	0.056	0.018	+0.003		+0.037	
2/3	12	-0.007	0.059	+0.034		-0.037	
16/3	14	-0.079	-0.147	-0.026	+0.510	-0.029	
3/4	18	0.074	0.098	-0.041	+0.192	+0.077	+0.198
13/4	10	0.043	0.092	-0.277	+0.081	+0.202	+0.161
29/4	16	-0.058	0.063	-0.045	+0.044	+0.053	-0.140
11/5	12	-0.013	0.061			-0.709	+0.259
22/5	11	-0.046	-0.121				+0.008
8/6	17	-0.172	-0.103				-0.103
22/6	14	-0.029	0.010				-0.202
8/7	16	-0.321	-0.107				
20/7	12	0.370	0.145				
3/8	14	0.157	0.025				
17/8	14	-0.060	0.095				
1/9	15	0.064	-0.103	+0.540			
15/9	14	-0.064	0.006	+0.162			
12/10	27	0.035	-0.021	-0.080		+0.192	
26/10	14	-0.268	-0.024	+0.138		+0.050	
9/11	14	0.171	0.050	+0.055		-0.050	+0.369
24/11	15	-0.074	-0.070	-0.292		+0.012	-0.015
8/12	14	-0.018	0.004	-0.050		-0.078	-0.099
6/1	29	0.025	0.007	+0.060	+0.201	0	
20/1	14	-0.003	-0.041	-0.096	+0.040	-0.049	+0.099
2/2	13	-0.119	-0.057	0			
17/2	15	0.087	0.049	+0.065	+0.016	+0.073	+0.284
25/2	8	0.003	0.027	+0.110	+0.166	-0.073	-0.020
15/3	18	-0.001	0.041	-0.005	+0.116	+0.089	-0.030
29/3	14	0.017	0.013	+0.109	+0.185	+0.099	+0.115
15/4	17	0.056	0.081	-0.112	-0.318	+0.013	+0.068
22/4	7	-0.026	0.022	+0.242	+0.099	+0.298	0
27/4	5	-0.029	0.042	-0.558	-0.102	-0.111	+0.243
11/5	14	-0.052	-0.023		-0.177	-0.088	+0.027
24/5	13	-0.079	-0.122		-0.053	-0.218	-0.047
7/6	14	-0.058	-0.069				-0.161
19/7	42	0.044	0.021	+0.181		+0.111	
2/8	14	0.032	0.023	-0.032			
16/8	14	-0.034	0.044	-0.029			
1/9	16	-0.032	-0.061	0		+0.323	

APPENDIX I (b)

RATES OF CHANGE OF TOTAL ROTIFER POPULATION

Q.M.		Q.L.II	
Date	r value	Date	r value
23/2	0.0215	18/2	0.0181
9/3	-0.0117	2/3	0.0434
23/3	0.1597	16/3	-0.0760
1/4	0.0843	3/4	0.1113
7/4	0.0605	13/4	0.0807
20/4	0.1103	29/4	0.0357
4/5	-0.0824	11/5	-0.0949
19/5	-0.1459	22/5	-0.0900
1/6	-0.0602	8/6	-0.0931
15/6	-0.0717	22/6	-0.0280
29/6	-0.0928	8/7	-0.1253
13/7	0.1434	20/7	0.1493
27/7	0.1029	3/8	0.0411
10/8	-0.0164	17/8	0.0804
24/8	0.0769	1/9	-0.0417
7/9	0.1757	15/9	0.1037
21/9	-0.1741	12/10	-0.0547
5/10	0.0155	26/10	0.0785
19/10	-0.0156	9/11	0.0726
2/11	0.0752	24/11	-0.1480
16/11	-0.0692	8/12	0.0668
30/11	-0.1500	6/1	-0.0148
21/12	-0.0148	20/1	-0.0584
12/1	0.0126	2/2	-0.0649
25/1	-0.0482	17/2	0.1115
9/2	0.0136	25/2	-0.0317
22/2	0.1175	15/3	0.0666
25/2	-0.2216	29/3	0.1672
8/3	0.1403	15/4	-0.1402
11/3	0.1068	22/4	0.0981
22/3	0.2440	27/4	-0.0344
30/3	0.0462	11/5	-0.0405
5/4	-0.0943	24/5	-0.0773
8/4	-0.4312	7/6	-0.1094
19/4	0.0634	19/7	0.0382
22/4	0.1616	2/8	-0.0205
29/4	0.0152	16/8	0.1402
6/5	-0.2398	1/9	-0.0276
17/5	-0.0124		
1/6	-0.3389		
28/6	0.0634		
26/7	-0.0522		
23/8	0.1837		
6/9	0.1717		

APPENDIX II

POPULATION DYNAMICS OF KERATELLA QUADRATA

A. Q.M. RESERVOIR

Date	T°C	$\frac{1}{D}$	E	$B=E/\Phi$	b'	r	(b-r)	d $N_t-N_o + \sqrt{N_t N_o}.d.t$	Production per m^2	Mean daily production per col.	Mean daily production per individual
23/2	5	0.35	0.17	0.06	0.058						
9/3	4	0.29	0.50	0.15	0.140	-0.029	0.087	59.72	4.27		0.062
23/3	5.5	0.38	0.86	0.33	0.285	0.118	0.022	277.30	19.81		0.154
1/4	6	0.41	0.94	0.39	0.329	0.054	0.231	271.08	30.12		0.08
7/4	6	0.41	0.94	0.39	0.329	C	0.329	112.02	18.67		0.39
20/4	8.5	0.57	0.71	0.40	0.337	0.131	0.198	6082.36	434.45		0.362
4/5	12	0.78	0.07	0.05	0.049	0.061	0.276	26639.83	1775.99		0.374
19/5	14	0.91	0.05	0.05	0.049	-0.081	0.130	3245.32	216.35		0.053
1/6	17	1.09	0.12	0.13	0.122	-0.120	0.169	671.92	51.69		0.05[illegible]
15/6	19.5	1.25	0	0	0	-0.036	0.158	682.92	48.78		0.135
29/6	20	1.28	0.14	0.18	0.166	-0.075	0.075	-8.11	-0.58		-0.003
13/7	20	1.28	0.42	0.54	0.432	0.151	0.015	1555.2	111.09		0.397
27/7	18	1.15	0.50	0.58	0.457	0.058	0.374	8590.08	613.57		0.514
10/8	20	1.28	0.01	0.01	0.01	0.121	0.336	31209.54	2229.53		0.535
24/8	17.5	1.12	0.13	0.15	0.140	-0.051	0.061	991.52	70.82		0.010
7/9	18	1.15	0	0	0	-0.003	0.143	9741.75	695.84		0.148
21/9	18	1.15	0.38	0.44	0.365	-0.150	0.150	-411.34	-29.38		-0.0[illegible]
5/10	15.5	1.0	0.43	0.43	0.358	0	0.365	3477.2	248.37		0.4[illegible]
19/10	13.5	0.88	0.43	0.38	0.322	0.016	0.342	3737.53	266.97		0.424
2/11	12	0.78	0.27	0.21	0.191	0.045	0.277	4202.67	300.19		0.348
16/11	9.5	0.63	0.13	0.08	0.077	-0.045	0.236	2335.92	166.85		0.216
30/11	9	0.59	0.10	0.06	0.058	-0.100	0.177	342.49	24.46		0.087
21/12	7	0.47	0.05	0.02	0.020	0.029	0.029	231.6	11.03		0.058
12/1	4.5	0.32	0.27	0.09	0.086	-0.008	0.028	100.31	4.56		0.020
25/1	6	0.41	0.15	0.06	0.058	-0.011	0.097	232.56	17.89		0.091
9/2	5	0.35	0	0	0	-0.025	0.083	140.15	9.34		0.061
22/2	6	0.41	0.44	0.18	0.166	0.053	-0.053	126.72	9.75		0.054
25/2	6	0.41	0.04	0.16	0.148	-0.341	-0.175	450.56	150.19		0.036
8/3	4.5	0.32	0.67	0.21	0.191	0.156	0.304	589.07	53.55		0.179
11/3	5	0.35	0.60	0.21	0.191	0.170	0.021	95.28	31.76		0.194
22/3	6	0.41	0.55	0.23	0.207	0.181	0.010	1400.51	127.32		0.223
30/3	7	0.47	0.51	0.24	0.215	0.027	0.180	3080.17	385.02		0.224
5/4	77.5	0.50	0.63	0.32	0.278	0.048	0.167	3085.68	514.28		0.233
8/4	7.5	0.50	0.45	0.23	0.207	0.116	0.162	2665.37	888.46		0.295
19/4	9	0.59	0.29	0.17	0.157	0.130	0.077	83030.9	7548.26		1.020
22/4	9.5	0.63	0.38	0.24	0.215	0.102	0.055	8490.05	2830.02		0.160
29/4	10	0.66	0.13	0.09	0.086	0.152	0.063	55081.85	7868.84		0.225
6/5	11	0.72	0.05	0.04	0.039	-0.266	0.352	19335.84	2762.26		0.117
17/5	15	0.93	0.06	0.06	0.058	0.020	0.019	4531.59	411.96		0.0[illegible]
1/6	16	1.03	0	0	0	-0.318	0.318	-5430.63	-362.04		-0.339
28/6	15	0.97	0.21	0.20	0.182	0.045	-0.045	232.32	8.60		0.048
26/7	20	1.28	0.11	0.13	0.122	-0.034	0.216	1206.3	43.08		0.210
23/8	18.5	1.19	0.20	0.24	0.215	0.089	0.033	1967.88	70.28		0.159
6/9	18	1.15	0	0	0	0.060	0.155	7587.95	542.0		0.230

APPENDIX II.

POPULATION DYNAMICS OF BERATELLA QUADRATA

B. G.E.II RESERVOIR

Date	T°C	$\frac{1}{D}$	E	B=E/d	b'	r	d (b-r)	Production $\frac{N_t - N_o}{\sqrt{N_t N_o}.d.t}$	Mean daily production per m^2 col.	Mean daily production per individual
4/2	5	0.35	0.24	0.08	0.077					
18/2	3.5	0.26	0.12	0.03	0.030	0.018	0.059	472.59	33.76	0.079
2/3	4	0.29	0.24	0.07	0.068	0.059	-0.029	499.84	41.65	0.060
16/3	5	0.35	0.44	0.15	0.140	-0.147	0.215	328.58	23.47	0.066
3/4	5	0.35	0.98	0.34	0.293	0.098	0.042	855.4	47.52	0.155
13/4	7	0.47	0.79	0.37	0.315	0.092	0.201	3807.72	380.77	0.324
29/4	9.5	0.63	0.38	0.24	0.215	0.063	0.252	17157.18	1072.32	0.349
11/5	12	0.78	0.14	0.11	0.104	0.061	0.154	20392.17	1699.35	0.232
22/5	13	0.84	0.03	0.03	0.030	-0.121	0.225	7220.2	656.38	0.121
8/6	17.5	1.12				-0.103	0.133	486.68	28.63	0.025
22/6	19	1.22	0.05	0.06	0.058	0.010	-0.010	70.40	5.03	0.010
8/7	19	1.22	0.14	0.17	0.157	-0.107	0.165	215.72	13.48	0.058
20/7	18.5	1.19	0.15	0.18	0.166	0.145	0.012	475.37	39.61	0.530
3/8	19	1.22	0.51	0.62	0.482	0.025	0.141	1660.62	118.62	0.176
18/8	18	1.15	0.01	0.01	0.010	0.095	0.387	5467.92	390.57	0.792
1/9	18	1.15	0.11	0.12	0.113	-0.103	0.113	140.89	9.39	0.007
15/9	16.5	1.06				0.006	0.107	1096.21	78.30	0.116
12/10	15	0.97	0.11	0.01	0.01	-0.021	0.021	- 11.05	- 0.41	-0.015
26/10	13	0.84	0.05	0.04	0.04	-0.024	0.034	45.96	3.28	0.010
9/11	11	0.72				0.050	-0.010	281.6	20.11	0.050
24/11	10	0.66				-0.070	0.070	43.71	2.91	0.009
8/12	8	0.54	0.03	0.02	0.02	0.050	-0.054	225.3	16.09	0.056
6/1	4	0.29	0.08	0.02	0.02	0.007	0.013	78.29	2.70	0.006
20/1	5	0.35	0.24	0.08	0.077	-0.041	0.061	109.9	7.85	0.020
2/2	5	0.35	0.40	0.14	0.131	-0.057	0.134	224.43	17.26	0.085
17/2	6	0.41	0.14	0.06	0.058	0.049	0.082	415.03	27.67	0.136
25/2	6	0.41	0.15	0.06	0.058	0.027	0.031	151.99	18.10	0.155
15/3	5.5	0.38	0.31	0.12	0.113	0.041	0.017	555.68	30.87	0.059
29/3	7	0.47	0.20	0.09	0.086	0.013	0.100	1838.73	131.34	0.138
15/4	8	0.54	0.23	0.12	0.113	0.081	0.005	2613.07	153.71	0.074
22/4	9.5	0.63	0.49	0.31	0.27	0.022	0.091	3195.28	456.47	0.117
27/4	9.5	0.63	0.25	0.16	0.148	0.042	0.228	6990.07	1398.01	0.298
11/5	12.5	0.81	0.09	0.07	0.067	-0.023	0.171	10295.54	735.40	0.166
24/5	14.0	0.91	0.07	0.06	0.058	-0.122	0.189	1645.48	126.58	0.074
7/6	15	0.97	0.14	0.14	0.131	-0.069	0.127	432.4	30.89	0.065
19/7	19	1.22	0.06	0.07	0.068	0.021	0.110	2686.67	63.97	0.139
2/8	19	1.22				0.023	0.045	809.3	57.81	0.069
16/8	19	1.22	0.15	0.18	0.166	0.044	-0.044	844.8	60.34	0.045
1/9	18.5	1.19				-0.061	0.227	5725.42	357.84	0.318

Appendix III

Birth rates of egg-bearing reservoir rotifers

Queen Mary Reservoir

Date	$\frac{1}{D}$	Polyarthra vulgaris (b')	Keratella cochlearis (b')
23/2	0.22	0.104	0.104
9/3	0.18		0.086
23/3	0.24	0.095	0.157
1/4	0.26	0.239	0.157
7/4	0.26	0.223	0.174
20/4	0.37	0.058	0.148
4/5	0.53		0.077
19/5	0.62		
1/6	0.75		
15/6	0.86		
29/6	0.88		
13/7	0.88		
27/7	0.79	0.308	
10/8	0.88	0.131	
24/8	0.77	0.113	
7/9	0.79	0.278	
21/9	0.79	0.039	
5/10	0.68	0.020	
19/10	0.59	0.020	
2/11	0.53		
16/11	0.42	0.020	
30/11	0.40		
21/12	0.31		
12/1	0.20		
25/1	0.26		
9/2	0.22		
22/2	0.26	0.077	0.058
25/2	0.26	0.104	
8/3	0.20	0.020	0.122
11/3	0.22	0.020	
22/3	0.26	0.451	0.122
30/3	0.31	0.329	0.174
5/4	0.33	0.262	0.231
8/4	0.33	0.182	0.131
19/4	0.40	0.030	
22/4	0.42	0.068	0.215
29/4	0.44	0.157	
6/5	0.48		
17/5	0.66		
1/6	0.70		
28/6	0.66		
26/7	0.88		
23/8	0.81	0.020	
6/9	0.79	0.020	

Appendix III

Birth rates of egg-bearing reservoir rotifers

Queen Elizabeth Reservoir

Date	$\frac{1}{D}$	Polyarthra vulgaris (b')	Keratella cochlearis (b')
4/2	0.22	0.020	0.049
18/2	0.15	0.020	0.049
2/3	0.18	0.020	0.040
16/3	0.22	0.039	0.058
3/4	0.22	0.095	0.086
13/4	0.31	0.086	0.191
29/4	0.42	0.077	0.182
11/5	0.53		0.068
22/5	0.57		
8/6	0.77		
22/6	0.84		
8/7	0.84		
20/7	0.81		
3/8	0.84		0.385
17/8	0.79		
1/9	0.79		
15/9	0.73	0.399	
12/10	0.66	0.378	0.140
26/10	0.57	0.049	
9/11	0.48	0.030	0.157
24/11	0.44		
8/12	0.35		
6/1	0.18		0.049
20/1	0.22		0.086
2/2	0.22		
17/2	0.26		
25/2	0.26		0.140
15/3	0.24	0.077	0.095
29/3	0.31		0.086
15/4	0.35	0.010	0.058
22/4	0.42	0.039	0.131
27/4	0.42	0.058	0.095
11/5	0.55		
24/5	0.62		
7/6	0.66		
19/7	0.84		0.157
2/8	0.84		0.104
16/8	0.84		0.157
1/9	0.81		

Appendix IV

Daily Production of rotifers in terms of dry weight (ug) per m^2 col.

Queen Mary

Date	Keratella quadrata	Keratella cochlearis	Polyarthra vulgaris	Total
23/2	2.23	7.10	8.36	17.69
9/3	3.55	1.67	0	5.22
23/3	37.97	19.77	7.27	65.01
1/4	70.94	10.14	20.88	101.96
7/4	70.94	6.13	27.57	104.64
20/4	457.39	19.87	247.53	724.79
4/5	166.29	24.01		190.30
19/5	49.39			49.39
1/6	25.65			25.65
15/6	0			0
29/6	7.40			7.40
13/7	154.65			154.65
27/7	368.01		5.58	373.59
10/8	46.63		62.92	109.55
24/8	301.59		10.76	312.35
7/9	0		501.81	501.81
21/9	92.59		110.23	202.82
5/10	90.90		33.45	124.35
19/10	102.22		18.63	120.85
2/11	90.60		0	90.60
16/11	19.59		28.89	48.48
30/11	3.72			3.72
21/12	2.28			2.28
12/1	8.24			8.24
25/1	4.83			4.83
9/2	0			0
22/2	19.01	2.23	10.59	31.83
25/2	46.89	0	9.88	56.77
8/3	10.87	6.61	2.43	19.91
11/3	18.12	0	4.79	22.91
22/3	144.04	15.54	278.62	438.20
30/3	184.98	25.65	263.25	473.88
5/4	319.58	7.43	63.01	390.02
8/4	335.22	8.87	614.79	958.88
19/4	1,071.63	0	152.22	1,223.85
22/4	1,985.79	62.35	534.08	2,582.22
29/4	2,328.27		45.96	2,374.23
6/5	161.69			161.69
17/5	304.80			304.80
1/6	0			0
28/6	27.20			27.20
26/7	6.99			6.99
23/8	149.61		107.05	256.66
6/9	0		119.46	119.46

Appendix IV

Daily Production of rotifers in terms of dry weight (ug) per m^2 col.

Queen Elizabeth II

Date	Keratella quadrata	Keratella cochlearis	Polyarthra vulgaris	Total
4/2	13.23	11.40	1.60	26.23
18/2	6.70	24.80	1.67	33.17
2/3	30.16	17.99	2.51	50.66
16/3	7.98	8.74	3.30	20.02
3/4	98.26	49.35	3.81	151.42
13/4	263.18	167.13	54.70	485.01
29/4	489.65	62.95	99.80	652.40
11/5	493.55	20.43		513.98
22/5	38.28			38.28
8/6	0			0
22/6	14.50			14.50
8/7	6.98			6.98
20/7	42.24			42.24
3/8	174.32	11.10		185.42
17/8	14.53			14.53
1/9	33.03			33.03
15/9	0		544.90	544.90
12/10	1.89	5.82	59.21	66.92
26/10	5.07		52.34	57.41
9/11	0	27.88	70.29	98.17
24/11	0			0
8/12	3.80			3.80
6/1	4.69	4.65		9.34
20/1	10.29	7.81		18.10
2/2	8.28			8.28
17/2	7.81			7.81
25/2	9.67	10.07	10.73	30.47
15/3	38.78	6.69		45.47
29/3	46.68	7.81	5.44	59.93
15/4	185.26	13.38	3.45	202.09
22/4	514.48	25.34	27.46	567.28
27/4	346.96	15.82		362.78
11/5	113.20			113.20
24/5	20.44			20.44
7/6	17.39			17.39
19/7	21.97	12.93		34.90
2/8	0	13.52		13.52
16/8	137.28	12.67		149.95
1/9	0	0		0

Appendix V

Standing crop of egg-bearing rotifers in terms of dry weight (ug) per m^2 column

Queen Mary Reservoir

Date	Keratella quadrata	Keratella cochlearis	Polyarthra vulgaris	Total Biomass (ug)
23/2	38.03	67.42	79.93	185.38
9/3	25.34	19.27	10.89	55.50
23/3	133.07	125.19	152.58	410.84
1/4	215.42	63.20	87.18	366.80
7/4	215.42	35.32	588.50	839.24
20/4	1,355.90	134.84	4,257.46	5,748.20
4/5	3,370.77	314.59	399.64	4,085.00
19/5	1,001.07	19.27	3.64	1,023.98
1/6	209.07	3.21		212.28
15/6	126.72	3.21		129.93
29/6	44.37	22.48		66.85
13/7	357.98	0		357.98
27/7	804.69	12.84	18.16	835.69
10/8	4,371.84	32.10	483.13	4,887.07
24/8	2,154.24	64.20	94.45	2,312.89
7/9	2,071.89	16.05	1,798.16	3,886.10
21/9	253.44	32.10	2,788.05	3,073.59
5/10	253.44	24.08	1,598.36	1,875.88
19/10	316.80	32.10	890.13	1,239.03
2/11	475.20	0	3,741.62	4,216.82
16/11	253.35	0	1,380.40	1,633.75
30/11	63.36	19.27	152.58	235.21
21/12	114.03	12.84	36.38	163.25
12/1	95.04	16.05	87.18	198.27
25/1	82.35	12.84	32.69	127.88
9/2	57.02	19.27	14.53	90.82
22/2	114.03	38.53	138.03	290.59
25/2	316.80	6.43	94.45	417.68
8/3	57.02	54.58	116.25	227.85
11/3	95.04	160.51	228.85	484.40
22/3	696.96	128.41	617.55	1,442.92
30/3	861.71	147.68	802.82	1,812.21
5/4	1,146.83	32.10	239.76	1,418.69
8/4	1,622.03	67.42	3,389.24	5,078.69
19/4	6,811.20	186.18	5,034.84	12,032.22
22/4	9,250.56	288.92	7,919.16	17,458.64
29/4	26,864.64	288.92	290.60	27,444.16
6/5	4,181.76	112.36	181.63	4,475.75
17/5	5,195.52	0	18.16	5,213.68
1/6	443.52	0	0	443.52
26/6	148.91	25.67	3.64	178.22
26/7	57.02	0	0	57.02
23/8	696.96	3.85	5,114.75	5,815.56
6/9	1,615.68	163.73	5,707.61	7,487.02

Appendix V

Standing crop of egg-bearing rotifers in terms of dry weight (ug) per m^2 column

Queen Elizabeth Reservoir

Date	Keratella quadrata	Keratella cochlearis	Polyarthra vulgaris	Total Biomass (ug)
4/2	171.09	227.93	76.29	475.31
18/2	218.61	495.99	79.93	794.53
2/3	443.52	455.86	119.87	1,019.25
16/3	57.02	150.89	83.54	291.45
3/4	334.98	568.22	39.96	943.16
13/4	836.37	869.98	635.71	2,342.06
29/4	2,280.96	346.70	1,300.47	3,928.13
11/5	4,745.66	298.54		5,044.20
22/5	1,248.21	179.78		1,427.99
8/6	215.42	9.62		225.04
22/6	247.10	6.43		253.53
8/7	44.37	0		44.37
20/7	253.44	3.21		256.65
3/8	361.17	28.89	3.64	393.70
17/8	1,362.24	16.05		1,378.29
1/9	291.47	41.72	141.67	474.86
15/9	316.80	16.05	1,362.24	1,695.09
12/10	177.39	41.72	156.19	375.30
26/10	126.72	16.05	1,071.63	1,214.40
9/11	253.44	176.56	2,324.89	3,008.33
24/11	88.70	57.78	29.05	175.53
8/12	190.08	44.94	14.53	249.55
6/1	234.45	93.09	83.54	411.08
20/1	133.07	89.88	21.80	244.75
2/2	63.36	19.27	21.80	104.43
17/2	133.07	70.63	58.13	261.83
25/2	164.75	72.23	139.86	376.84
15/3	342.14	70.63	127.14	539.91
29/3	538.56	89.88	584.86	1,213.30
15/4	1,634.67	231.15	87.18	1,953.00
22/4	1,900.80	192.61	472.24	2,565.65
27/4	2,344.32	166.94	29.05	2,540.31
11/5	1,698.03	80.26		1,778.29
24/5	348.48	28.89		377.37
7/6	133.07	12.84		145.91
19/7	323.15	81.87	85.37	490.39
2/8	443.52	128.41	54.49	626.42
16/8	823.68	80.26	36.33	940.27
1/9	310.46	48.15	36.33	394.94

Appendix VI

Daily Production and Respiration Data per m^2 column

Queen Mary

Date	P. ug.	P. cals x 10^{-3}	R. ul. O2	R. cals x 10^{-3}
23/2	17.69	88.45	13.31	64.31
9/3	5.22	26.1	2.77	13.37
23/3	65.01	325.05	30.82	148.84
1/4	101.96	509.80	25.78	124.50
7/4	104.64	532.20	68.41	330.43
20/4	724.79	3,623.95	683.29	3,300.30
4/5	190.30	951.50	505.63	2,442.21
19/5	49.39	246.95	132.14	638.25
1/6	25.65	128.25	33.23	160.48
15/6	0	0	23.63	114.14
29/6	7.40	37.00	16.16	78.04
13/7	154.65	773.25	65.18	314.82
27/7	373.59	1,867.95	140.91	680.58
10/8	109.55	547.75	960.99	4,641.60
24/8	312.35	1,561.75	388.96	1,878.70
7/9	501.81	2,509.05	856.83	4,138.47
21/9	202.82	1,014.10	846.98	4,090.92
5/10	124.35	621.75	433.91	2,095.81
19/10	120.85	604.25	235.64	1,138.12
2/11	90.60	453.00	755.02	3,646.74
16/11	48.48	242.40	255.66	1,089.92
30/11	3.72	18.60	29.40	142.01
21/12	2.28	11.40	12.46	60.19
12/1	8.24	41.20	10.70	51.71
25/1	4.83	24.15	8.59	41.49
9/2	0	0	5.16	24.93
22/2	31.83	159.15	22.47	108.54
25/2	56.77	283.85	25.78	124.51
8/3	19.91	99.55	14.11	68.16
11/3	22.91	114.55	34.73	167.96
22/3	438.20	2,191.00	105.76	510.80
30/3	473.38	2,369.40	156.88	757.74
5/4	390.02	1,950.10	107.86	520.98
8/4	958.88	4,794.40	507.83	2,452.83
19/4	1,223.85	6,119.25	1,276.83	6,167.10
22/4	2,528.22	12,911.10	2,004.10	9,679.81
29/4	2,374.23	11,871.15	2,494.64	12,049.11
6/5	161.69	808.45	443.38	2,141.52
17/5	304.80	1,524.00	709.23	3,425.56
1/6	0	0	64.29	310.53
28/6	27.20	136.00	27.94	134.94
26/7	6.99	34.95	10.38	50.14
23/8	256.66	1,283.30	1,620.19	7,825.50
6/9	119.46	597.30	1,944.90	9,393.86

Appendix VI

Daily Production and Respiration Data per m^2 column

Queen Elizabeth II

Date	P. ug.	P. cals x 10^{-3}	R. ul. O_2	R. cals x 10^{-3}
4/2	26.23	131.15	32.33	156.17
18/2	33.17	165.85	38.93	188.04
2/3	50.66	253.30	52.16	251.92
16/3	20.02	100.10	21.46	103.67
3/4	151.42	757.10	65.44	316.09
13/4	485.01	2,425.05	225.01	1,086.79
29/4	652.40	3,262.00	443.80	2,143.56
11/5	513.98	2,569.90	575.31	2,778.77
22/5	38.28	191.40	187.75	906.82
8/6	0	0	37.28	180.06
22/6	14.50	72.50	44.89	216.82
8/7	6.98	34.90	7.67	37.03
20/7	42.24	211.20	43.73	211.20
3/8	185.42	927.10	73.36	354.32
17/8	14.53	72.65	227.93	1,100.92
1/9	33.03	165.15	101.53	490.40
15/9	544.90	2,724.50	408.02	1,970.73
12/10	66.92	334.60	72.20	348.75
26/10	57.41	287.05	237.46	1,146.95
9/11	98.17	490.85	458.99	2,216.92
24/11	0	0	22.62	109.27
8/12	3.80	19.00	21.51	103.88
6/1	9.34	46.70	18.95	91.51
20/1	18.10	90.50	14.94	72.18
2/2	8.28	41.40	5.98	28.87
17/2	7.81	39.05	19.50	94.19
25/2	30.47	152.35	28.75	138.88
15/3	45.47	227.35	35.53	161.97
29/3	59.93	299.65	106.66	515.18
15/4	202.09	1,010.45	158.62	766.14
22/4	567.28	2,836.40	263.27	1,271.61
27/4	362.78	1,813.90	231.04	1,115.90
11/5	113.20	566.00	209.11	1,009.99
24/5	20.44	102.20	51.25	254.52
7/6	17.39	86.95	21.49	103.80
19/7	34.90	174.50	109.49	528.85
2/8	13.52	67.60	136.86	661.02
16/8	149.95	749.75	180.65	872.55
1/9	0	0	78.92	381.17

APPENDIX VII

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Determination of Dry Weights of Small Aschelminthes (< 0.1 µg)

MARGARET DOOHAN and VICTORIA RAINBOW*
Zoology Department, Royal Holloway College, University of London, Englefield Green, Surrey, England

Received January 13, 1971

* Present address: Department of Biology, University of Stirling, Scotland.

A method is described here by which the individual dry weight may be determined for Rotifera and Nematoda of less than 0.1 μg dry weight. Fresh weights of rotifers and nematodes have previously been obtained either by the weighing of scale models of known density and volume or by approximating the animal shape to geometrical figures from which weight can be calculated (Andrássy, 1956; Overgaard-Nielsen, 1949; Neuwerck, 1963). Dry weights for groups of nematodes (>10 μg), using a relatively coarse balance, were obtained by Wieser (1960), and Fernando weighed groups of 100000 larvae of *Necator americanus* to the nearest 0.01 mg on a semi-micro balance (Fernando, 1963). No previous attempts have been described for rotifer dry weights although Depoorter and Magis report that 12000 washed eggs of *Brachionus leydigi,* dried at 80° C, weighed 630 μg (Depoortere and Magis, 1967). By cumulating relatively small groups of dried animals, we have been able to detect differences in dry weight of 0.005 μg/individual.

The rotifers used were *Keratella quadrata* (O.F. Muller) of mean length 141.7 ± 14 μ. The nematodes were the free-living stages of a mammalian parasite, *Nematosporoides dubius* (Bayliss) divided into 24-hour age groups, the first batch being hatched 48 hours after the eggs were passed from the host animal and placed in culture, the last being seven days old; the length range was $393 \rightarrow 581$ μ.

Homogeneous samples of approximately 50 rotifers were accurately counted, briefly washed in distilled water and dried on cavity slides in a $CaCl_2$ desiccator at room temperature for at least 48 hours (Lovegrove, 1966). After this period a sample was transferred with tungsten needles or fine hairs to the scale pan of a Cahn Gram Electrobalance (10^{-7} g;

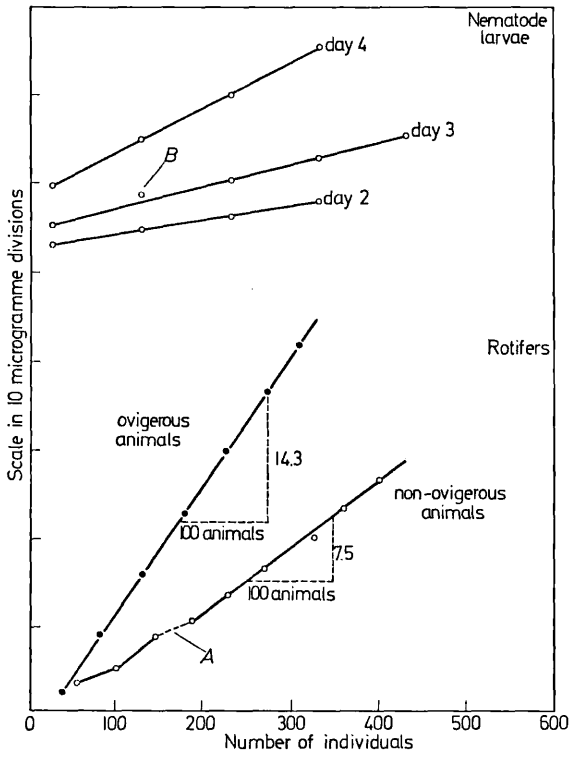

Fig. 1. The dry weight of *Keratella quadrata* and larval *Nematosporoides dubius* from cumulated samples of 50 or 100 individuals. *A* Known loss of animals from scale pan. *B* Probable increase in moisture content of sample

sensitivity, 0.2 µg; accuracy, 0.05% of the scale range), all damaged animals being discarded. Weighings were within the 1 mg range of the balance scale and each weighing was delayed for a short period to allow moisture absorbed during transfer to be removed by silica gel in the balance chamber. After the first reading, the balance was not returned to zero but a second sample was added to the loaded scale pan and the new weight recorded. This process was continued until up to 400 rotifers had been accumulated and weighed. The method gives equally satisfactory results after only four or five sets of cumulated weighings.

Fig. 1 shows the linear relationship between ovigerous or non-ovigerous rotifer numbers and their dry weights; since weights are cumulated an absolute scale of weight is not necessary and therefore the vertical axis is simply marked in 10 µg divisions. From the line fitted

by eye, the weight of 100 individuals was read off and the weight of one calculated. The table presents the mean weight of one individual *Keratella*, without eggs and carrying one egg. Five replicate weighings of a single sample containing approximately 90 animals gave a mean sample weight and standard error of 6.62 ± 0.07 µg. The cumulation of samples provides an automatic check on loss of animals during transfer to the scale pan or possible gain in moisture content during the weighing (see Fig. 1). A regression could be calculated (and has been for other results) but it was not considered necessary for this data.

The nematodes were treated in the same way as the rotifers, using samples of 100 larvae and cumulating up to 600 individuals. However, their number could be accurately determined only before drying and not immediately prior to weighing since they tend to stick together so that those lost during transfer to the pan could not be counted. The mean individual dry weights obtained are presented in the Table. This demon-

Table. *Mean dry body weight of* Keratella quadrata (Rotifera) *and larval* Nematosporoides dubius (Nematoda)

Keratella quadrata (Muller)		*Nematosporoides dubius* (Bayliss)	
Reproductive state	Mean individual weight (µg)	Age of larvae in days	Mean individual weight (µg)
Ovigerous ♀	0.143	day 2	0.016
Non-ovigerous ♀	0.075	day 3	0.026
Egg (by subtraction)	0.068	day 4	0.054

strates the usefulness of the technique for distinguishing different dry weights of various developmental stages of a very small species such as this nematode, from which a growth curve in terms of dry weight rather than calculated wet weight can be derived. Processes involving changes in hydration render wet weight estimates unreliable for comparisons of metabolism of different growth stages of a species or between different groups of species. Accurate dry weights are essential for this purpose.

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Margaret Doohan
Zoology Department
Royal Holloway College
University of London
Englefield Green, Surrey/England