THE UNIVERSITY OF HULL

The vertical distribution and migration of planktonic rotifers in a hypereutrophic tarn

being a thesis submitted for the degree of
Doctor of Philosophy
in the University of Hull

by Lesley J. Stewart M.A. (Cantab.)

May 1988

ABSTRACT

The planktonic rotifers of Priest Pot were studied from January 1983 to September 1984. Routine weekly samples from January 1983 to March 1984 provided a uniquely detailed data set giving information on the vertical distribution of the rotifer community in relation to the environmental conditions. Seasonal abundance of the rotifers was also noted. Diel studies in 1983 investigated the vertical migration of the community and experimental work in 1984 produced new information on the causes of migration in planktonic rotifers.

Sixteen species were found but six of these were very rare. The remaining ten were divided into perennial species (*Keratella cochlearis*, *K.quadrata*, *Polyarthra vulgaris*, *Synchaeta kitina* and *S.pectinata*), spring-autumn species (*Brachionus calyciflorus*, *B.angularis* and *Filinia terminalis*) and summer-autumn species (*Anuraeopsis fissa* and *F.brachiata*) according to their periods of occurrence and abundance.

When the tarn was isothermal most of the rotifer species were homogeneously distributed in the water column. This was only altered when algal blooms occurred in spring and autumn, causing some species to aggregate at depths with high chlorophyll concentrations, and when the rotifers were hatching from resting eggs, producing large populations in one section of the water column before dispersal. When the tarn was stratified, from May to September, all the rotifers were confined to the epilimnion by the anoxic water of the bottom two metres.

F.brachiata, B.calyciflorus, B.angularis and P.vulgaris were concentrated nearer the surface than the other species. K.cochlearis and K.quadrata were aggregated just above the oxycline and A.fissa often occurred in very low oxygen concentrations and always had maxima at the oxic-anoxic boundary. These stratified distributions are linked to food availability and show clearly the oxygen and temperature requirements of the different species.

Diel studies in 1983 showed that most of the rotifer species can perform vertical migrations. These were more often a reverse migration (up during the day and down at night) than the expected normal migration (down during the day and up at night) commonly found in studies of crustaceans. The movements were not only linked to the photoperiod but also showed some response to changing chlorophyll levels and to oxygen concentration in the water column. One species, A.fissa, did not show a response to either light or chlorophyll stimuli but its distribution was linked to movements of the oxic-anoxic boundary.

Experimental work on the vertical migration of the rotifers produced further evidence that reverse migrations are more common in rotifers than the classical "normal" migration. Manipulation of the community using altered photoperiods showed light to be a controlling stimulus for the migrations. It is suggested that the migration is a result of a circadian rhythm entrained to the exogenous 24 hour cycle by the changing light intensity.

ACKNOWLEDGEMENTS

I should like to take this opportunity to thank Dr D.G.George of the Freshwater Biological Association (FBA) for all his help, advice and encouragement during the course of this study and Dr R. Goulder of Hull University for helpful discussions and support. At the FBA's Windermere Laboratory I am grateful to: Professor J.G. Jones for allowing the use of the bacteriology department's equipment and Bernard Simon for training in direct counts; Dr J. Hilton for the use of the analytical laboratory (with thanks to Nigel Hetherington and Eric Rigg for the analyses); Dr E. Tipping for the use of the spectrophotometer; Dr A. Irish and Steve Gardener for assistance with the computing and Margaret Hurley for advice and discussion on the statistics and computing.

I would like to say a big thank you to all the people who helped with sampling, both the routine sampling and the overnight migration studies, especially to Nicholas White, Ralph Sutton, Janice Fletcher, Justin Wood and most of all Diane Hewitt who also helped with advice and discussions.

Without the skill and hard work of the FBA workshop staff this work could not have been done. Jim Crompton, Brian Winstanley and Paul Hodgson built both the sampling heads used in the routine sampling and the experimental tube used in 1984. The electronics staff, especially Colin Cunningham, produced the ZX81 counter which speeded up and greatly assisted the rotifer counts.

I am grateful to all the other staff at the FBA who made my four years in Windermere so enjoyable as well as profitable, especially Dr D.J.J. Kinsman and Dr R.T. Clarke for allowing me to use the facilities at the Windermere Laboratory.

Finally I would like to say thank you to my parents for their support and patience with both me and the thesis and to Bernard for everything.

CONTENTS

Chapter One

Chapter Two

Site description with notes on some environmental variables

Chapter Three

A species list of the rotifers found in Priest Pot with notes on their taxonomy

Chapter Four

Methods used in routine sampling

Chapter Five

The horizontal distribution of the planktonic rotifers in Priest Pot

Chapter Six

The seasonal succession of the planktonic rotifers in Priest Pot

Chapter Seven

The vertical distribution of the planktonic rotifers in Priest Pot

Chapter Eight

The vertical migration of planktonic rotifers in Priest Pot

Chapter Nine

Experimental investigations of the vertical migration of the planktonic rotifers in Priest Pot

CHAPTER ONE

Introduction

Rotifers are frequently overlooked in plankton studies because their small size often makes them a relatively minor part of the biomass. However, in terms of production their importance is greater because of their rapid turnover times and their ability to utilize very small food particles (<5 um) such as detritus and bacteria. A knowledge of their habitat requirements and preferences is, therefore, important. Few studies of rotifers have included the detailed data on the environmental conditions which are required for a full explanation of the rotifers' behaviour.

In this thesis I examine some of the factors influencing the spatial and temporal distribution of planktonic rotifers in Priest Pot, a hypereutrophic pool in the English Lake District. This small tarn has previously been the site of various studies based at the Windermere Laboratory of the Freshwater Biological Association. The ciliate community has been studied by Goulder (1980) and later by Finlay & Berninger (1984). These investigations and unpublished observations by Hewitt showed stratification of the rotifer community and a more detailed study was therefore planned.

Priest Pot is unusual in that the zooplankton of its open water contains almost no adult crustacea and only a few copepod nauplii. The predominant metazoans are the rotifers, making it a particularly interesting system to study. It is also shallow (less than four metres deep) so detailed profiles can be obtained using relatively small numbers of samples. These two facts coupled with the previous work on the tarn make Priest Pot an ideal site for a detailed survey of rotifer ecology.

Miracle (1977) states that rotifer populations tend to assume marked vertical distributions with well defined maxima at a given depths. Pejler (1962) suggests that such between-species differences in the vertical distribution of rotifers may be a means of avoiding competition. In some European and North American studies marked vertical distributions have been found. Miracle & Vicente (1983) found accumulations near and in the chemocline in Spanish meromictic lakes. Axelson (1961) in Sweden and Stemberger (1974) and Stemberger _et al._, (1979) in North America both noted the importance of the thermocline in determining the stratification of the rotifer community. Schindler & Noven (1971) found that the maximum density of rotifers was always concentrated near the region of maximum phytoplankton abundance. However, British studies have not, so far, shown this. In the homogeneous environment of Loch Leven, May (1980) found that the rotifers were evenly distributed through the water column with no real differences between depths. Elliott (1977) found slight variation between depths in a much deeper Cumbrian lake but no well defined maxima were observed. In a tightly stratified environment, however, rotifers might be more likely to show marked vertical distributions. Previous work on the ciliates in Priest

Pot by Fenchel & Finlay (1984) showed that the tarn has a very marked oxycline during the summer and the ciliates have vertically stratified distributions. A fine scale study of the rotifers, to investigate any similar distributions was therefore planned. It was hoped that the data obtained would also provide information on the seasonal succession of rotifers in addition to detailed vertical profiles.

A number of workers have studied the seasonal succession and temporal dynamics of planktonic rotifers. Investigations have been carried out in all the Scandinavian countries : in Norway by Larsson (1971), in Sweden by Carlin (1943), Pejler (1957a, b, 1961) and Nauwerck (1963), in Denmark by Wesenberg-Lund (1904, 1930) and in Finland by Hakkari (1969) and Granberg (1970). In the rest of Europe there has been work by Ruttner (1930), Ruttner-Kolisko (1975, 1977, 1980) and Herzig (1979) in Austria, by Hofmann (1980) in Germany and by Pourriot (1965) in France. In North America there have been investigations by Pennak (1949), George & Fernando (1969), Baker (1979) and Moore (1980). However, work on British freshwaters in recent years is scarce. Elliott (1977) carried out a detailed investigation of Grasmere, an oligotrophic lake in the English Lake District, and Loch Leven, a eutrophic lake, was the subject of an intensive study by May (1980). Doohan (1973) used two Thames Valley reservoirs as sites for an investigation into rotifer energetics which also considered the seasonal dynamics of the six most abundant species.

Rotifer species are often described according to the temperatures at which they occur i.e. eurytherms, cold stenotherms, warm stenotherms. Hutchinson (1967) grouped rotifers according to their seasonal occurrence. He used a detailed study of the Swedish lake Motalastrom, by Carlin (1943) as a basis for his system. The rotifers were divided into three groups : perennial forms with spring/summer maxima, winter to early spring forms and summer forms. Larsson (1971) took this system and modified it for the Norwegian lake Blankvatn. He suggested that Hutchinson's winter to early spring forms were perennial forms which, unable to inhabit the warm epilimnion in the summer, spent this period at the chemocline, while the perennial forms named by Hutchinson remained in the epilimnion throughout. Hence Larsson's new categories : perennial surface forms, perennial chemocline forms and summer surface forms. Both these systems are based on Scandinavian lakes which experience a different climate to those in the English Lake District. They undergo long, cold winters with ice cover, warm summers and the intervening seasons are short. On the west coast of Britain the climate is not continental. The winters are milder and spring and autumn are longer. To take account of these climatic differences a third system of classification was fitted to the rotifers of Grasmere by Elliott (1977) : spring to autumn species, spring to early summer species and summer to autumn species.

Vertical migration is a well documented phenomenon in the planktonic crustacea (see reviews by Cushing, 1951; Hutchinson, 1967; Longhurst, 1976) but for the rotifers there are relatively few accounts of diel movements. The definition of migrations used throughout this thesis is that a normal migration involves movement down during the day and up at night resulting in the plankton being deeper in the water column during the hours of daylight while a reverse migration is exactly that; the plankton being higher in the water column during the day and moving down at night. George & Fernando (1970) studied the vertical migrations of the rotifers in Sunfish Lake, Ontario and found a variety of migration patterns. _Keratella quadrata_ performed a reverse migration in March but in the previous February had been recorded performing a normal migration. _Polyarthra vulgaris_ and _Filinia terminalis_ also showed both normal and reverse migrations . This observation of different migrations by the same species is supported by the findings of other workers (Pennak, 1944; Larsson, 1971; Schindler & Noven, 1971; Fairchild _et al_., 1977; & Cruz-Pizarro, 1978). There is a higher proportion of reverse migrations in the rotifer literature than would be expected from the work on crustaceans. Hutchinson (1967) describes reverse migration as aberrant behaviour but in rotifers it is at least as common as the so-called normal migrations. Such reverse patterns of migration are, however, commonly reported in motile phytoplankton i.e. by Talling (1971), George & Heaney (1978) and Lund & Reynolds (1982). A link between the rotifer migrations and those of the algae has not yet been recorded.

Diel studies in Priest Pot described in this thesis were designed to investigate not only changes in the vertical distribution of the rotifers but also changes in the environmental conditions and the sampling was performed frequently throughout 24 h. Further experimental work in Priest Pot subjected the rotifer community to conditions of constant darkness and to a shortened photoperiod in an attempt to investigate the importance of light to rotifer migration.

Experimental enclosures have frequently been used in zooplankton studies (Heaney & Eppley, 1981; Booker et al., 1976) but have always been in a laboratory. The use of a relatively small enclosure in the field is a new departure. Dumont (1972) used small, square enclosures in Lake Donk to investigate the effect of changing the composition of the plankton community on the migrations. However the work in Priest Pot described in this thesis is the first time such an approach has involved simulated light conditions. With the experimental apparatus it was possible to manipulate the conditions to which the natural rotifer community was subjected.

Information about migrations in naturally changing light conditions is limited. In the Arctic some studies of crustacean migration have been performed in the 24 h daylight of the arctic summer. The bad weather conditions during the winter have, however, so far prevented any studies in the 24 h arctic nights. Bogorov (1946) found no migrations in conditions of uninterrupted daylight but in autumn, with alternating day and night, there was clear evidence of diurnal vertical migrations. In Spitsbergen, Digby (1960,1961) found some migrations under midnight sun conditions but the evidence was equivocal. Burris (1980) found normal migrations in two Synchaeta spp. under intermediate light conditions in the Gulf of Finland. He also observed a reverse migration in K.quadrata. In the North American Arctic Buchanan & Haney (1980) found no migration under continuous light but migrations were initiated when the photoperiod reached L:D 20:4. Ruttner (1909) studied rotifer migrations under ice in Lunzer See and found some migrations under ice but not under snow-covered ice. The migrations could be initiated by removing the covering of snow from the ice.

This study provides a detailed picture of the vertical distribution of the rotifers in Priest Pot in relation to the environmental conditions. It also investigates their vertical migration both under natural conditions and in simulated photoperiods. The routine sampling gives details of the seasonal succession of rotifer species in 1983-4. An attempt is made to link the behaviour of the rotifers with their environment.

CHAPTER TWO

Site Description with Notes on some Environmental Variables

2.1 General Description

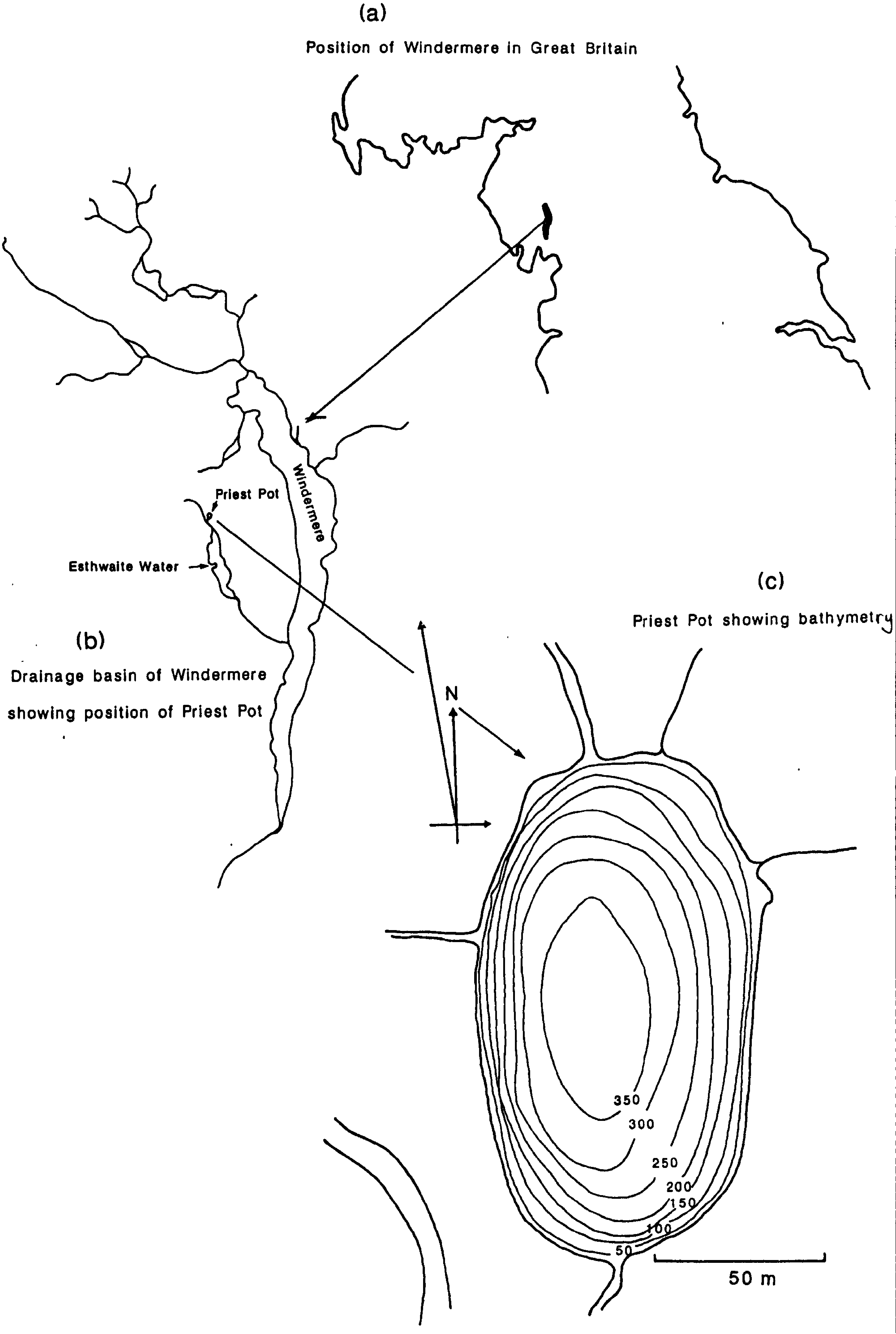
Priest Pot is a small, hypereutrophic tarn in the English Lake District (National Grid Reference SD 357 978). It has an area of one hectare, a mean depth of 2.32 m and a maximum of 3.94 m. Situated at the north end of Esthwaite Water, it is adjacent to the North Esthwaite Fen, a National Nature Reserve since 1954. During the summer months, from May to September, it is tightly stratified with often only the top 1.5 m remaining oxygenated.

Figure 2.1 shows both the position of the tarn in the Lake District and the results of a bathymetric survey carried out in 1982. The survey shows Priest Pot as a shallow basin, the west bank slightly steeper than the east but otherwise regular in shape. It has an outflow at its southern end and two main inflows, one at the north end and another on the western side.

The tarn is probably the relic from a deep basin formed by the retreating glaciers (Marler, 1952). It has become separated from Esthwaite Water by a bank of alluvium on which fen carr vegetation has developed. This vegetation has encroached on the tarn and is gradually reducing it in size. At present the calculated area of the tarn is 10008 m^2 compared with 13210 m^2 in 1881, and the maximum depth, recorded in November 1982, was more

Figure 2.1. Geographical and bathymetric details of Priest Pot. (a) The position of Windermere in the British Isles, (b) the drainage basin of Windermere showing the position of Priest Pot and (c) the bathymetric details of Priest Pot.

Figure 2.1. Geographic and Bathymetric details of Priest Pot



(a)

Position of Windermere in Great Britain

(b)

Drainage basin of Windermere showing position of Priest Pot

(c)

Priest Pot showing bathymetry

than a metre less than the depth given by Belcher et al. in 1966.

It is fed by three slow-flowing drainage ditches, one carrying farm-yard run-off. The input of farm effluent and the run off from surrounding fields combine to give Priest Pot very high nutrient levels. Belcher et al. (1966) give concentrations of ammonia, nitrate and orthophosphate of 282 ug N l^{-1}, 270 ug N l^{-1} and 21.2 ug P l^{-1} respectively and the values obtained in this study agree with these. Gorham (1966) assessed the tarn's fertility as very high on the basis of carbon to sulphur ratios.

The phytoplankton has been the subject of various morphological and taxonomic studies : nanoplanktonic flagellates (Belcher, 1968, 1969; Swale, 1968; Belcher & Swale, 1967), Volvocales (Belcher, 1964; Belcher & Swale, 1963) and Chlorococcales (Belcher & Swale, 1962). There have also been ecological studies on the algae. Silica depletion in the tarn was linked to diatom populations by Belcher et al. (1966) and an inverse relationship between phosphate concentrations and population growth in a new species of chrysomonad, Ochromonas ostreaeformis was shown by Swale & Belcher (1966). Vincent (1980a, b) carried out a physiological study of a population of Scenedesmus from the hypolimnion and concluded that its survival below the 1% light level in anoxic water was due to its heterotrophic metabolism.

Rotifers dominate the zooplankton of Priest Pot in oxygenated water, but during stratification the bottom two metres or more may be anoxic. This hypolimnion is populated by ciliates, most notably Loxodes magnus Stokes and L.striatus Penard. These were the subject of a detailed study by Goulder (1980) and more recently by Finlay et al. (1983) and Fenchel & Finlay (1984). The rotifers have previously been studied in relation to the fish population of the tarn (Hewitt & George, 1987).

2.2 Physicochemical conditions in the tarn during the study

2.2.1 Temperature (Fig.2.2.a)

The temperature during the winter of 1983 fell below 4°C in February when there was ice cover but then increased steadily through the spring. The tarn remained isothermal until early May but as the surface warmed up to more than 12°C the tarn began to stratify and throughout the summer the surface waters were up to 10°C warmer than the hypolimnion although there was not a steep thermocline. The tarn cooled slightly during August and by September had reverted to an isothermal state which was maintained for the remainder of the study. By late October the tarn had cooled to 8°C and the temperature continued to fall until by mid-December it was below 4°C and remained thus until late February 1984.

2.2.2 Oxygen (Fig.2.2.b)

The oxygen in the deeper water became depleted from May onwards and from late in May the 1.5 m of the water column above the sediment contained almost no oxygen. It remained anoxic until early September when mixing

Figure 2.2. (a) Temperature isopleth diagram for the sampling period 1983 to 1984. (b) Oxygen isopleth diagram for the period 1983 to 1984. Temperature measured in °C and oxygen in mg l^{-1}.

Figure 2.2.a Temperature

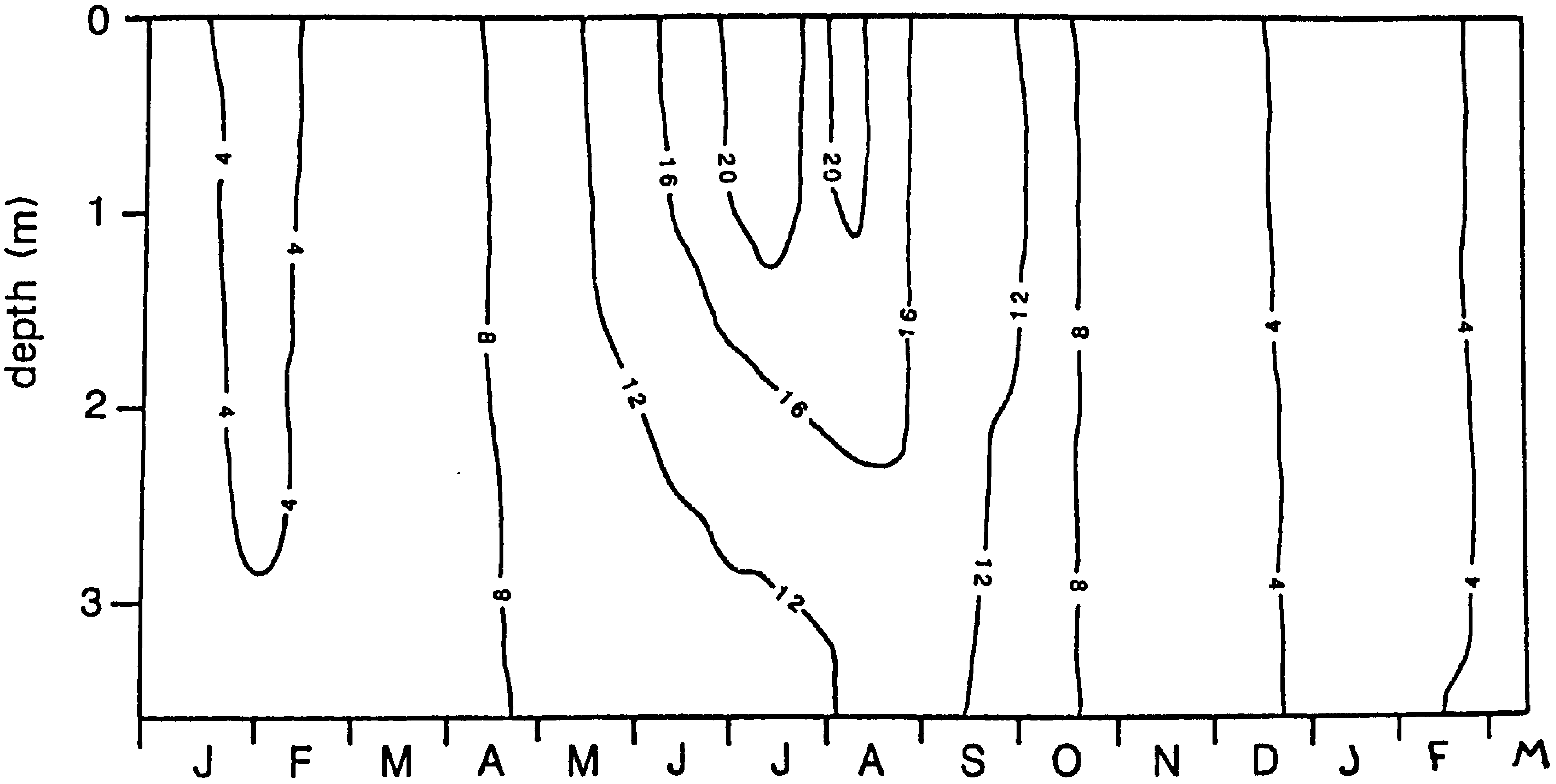
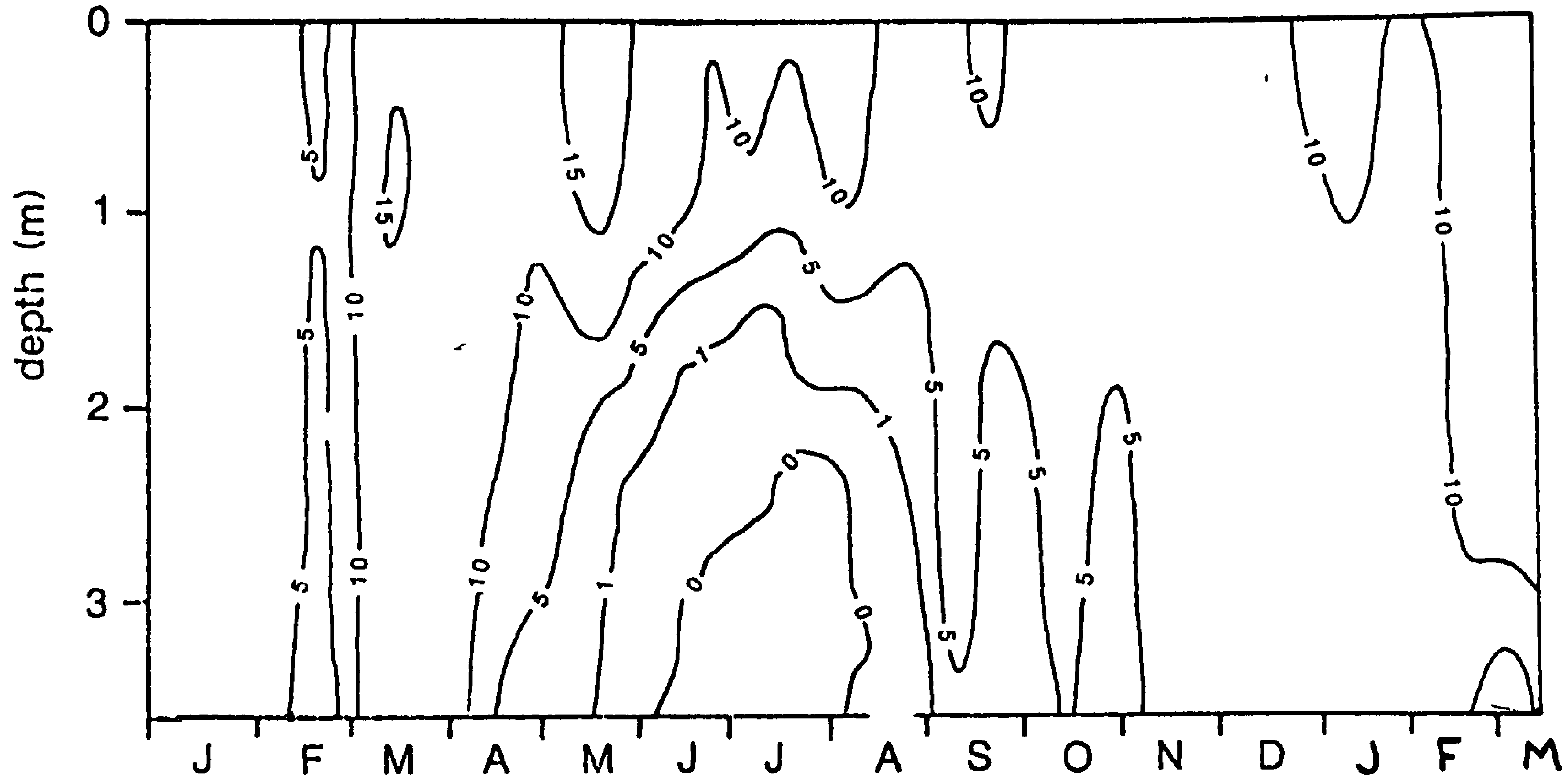


Figure 2.2.b Oxygen



occurred. Although on two occasions during the autumn the oxygen levels in the deeper water again began to decrease, the water column soon mixed again and the tarn remained well mixed throughout the rest of the study.

In the epilimnion, the oxygen level fluctuated, reaching peaks over 15 mg l^{-1} during the algal blooms in April and May but remaining between 5 and 10 mg l^{-1} for much of the year.

2.2.3 Nitrate (Fig.2.3.a)

Nitrate levels in Priest Pot were always high and sometimes exceeded 1000 ug N l^{-1} during the spring of 1983. Concentrations fell from mid-May onwards and were less than 100 ug N l^{-1} by mid-June. For much of the summer the values recorded were well below 50 ug N l^{-1}, at times they went below the detection limit of the method used (14 ug N l^{-1}). After the breakdown of stratification in early September, levels began to rise and by October were again over 500 ug N l^{-1}.

2.2.4 Ammonia (Fig.2.3.b)

Ammonia levels were high throughout the winter, more than 500 ug N l^{-1}, but dropped from February onwards. In mid-April levels began to rise in the bottom metre of the tarn and as the tarn stratified in late May the ammonia concentration increased to between 1000 and 5000 ug N l^{-1} in the hypolimnion until mixing in September. The levels in the epilimnion during the summer were much lower, always below 100 ug N l^{-1} and frequently below 50 ug N l^{-1}. On mixing, the levels rose and the

Figure 2.3.(a) Nitrate isopleth diagram for the period 1983 to 1984. (b) Ammonia isopleth diagram for the period 1983 to 1984. Both measured as ug N l^{-1}.

Figure 2.3.a. Nitrate

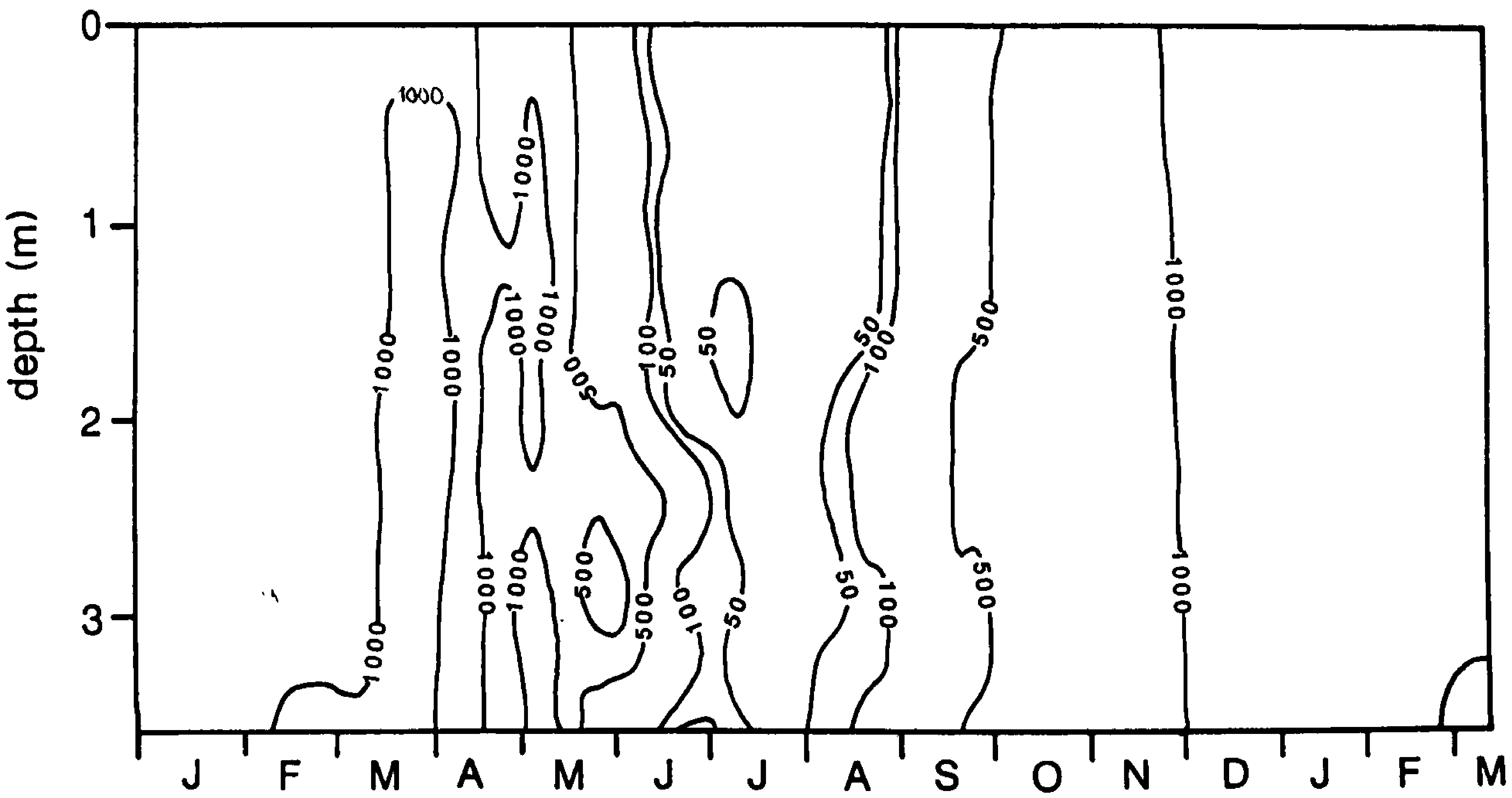
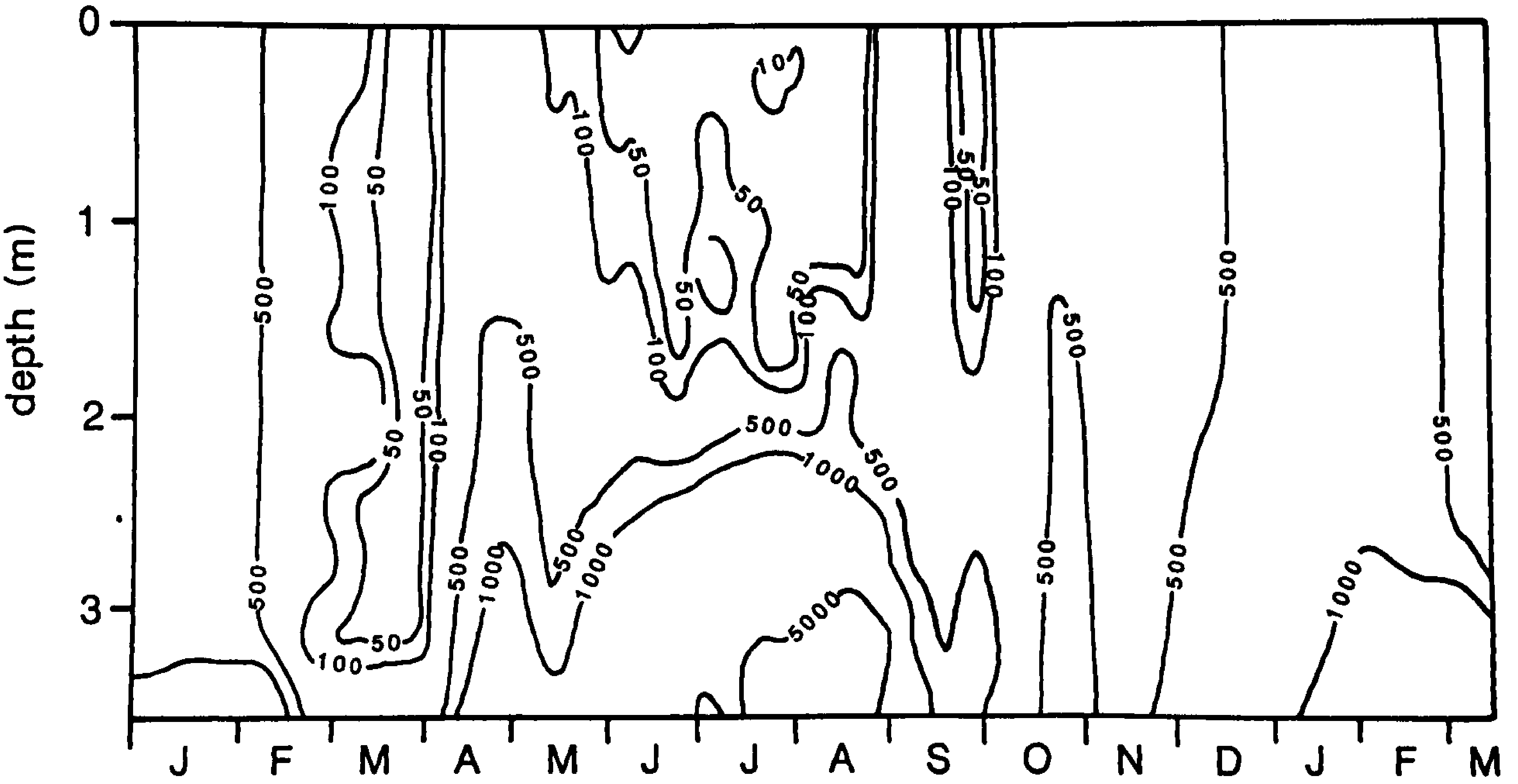


Figure 2.3.b. Ammonia



concentration of ammonia in the water column increased until by late November it was more than 500 ug N l^{-1} and remained high until the following March.

2.2.5 Total Phosphorus (Fig.2.4.a)

According to Wetzel (1975) most surface waters contain between 10 and 50 ug P l^{-1}. The levels found in Priest Pot were higher, often above 250 ug P l^{-1} and in the hypolimnion in summer rose to more than 2500 ug P l^{-1}. During the winter the concentrations were lower, falling below 100 ug P l^{-1} in 1983/4 but even these values are high when compared to other water bodies. Vollenweider (1968) showed that in general the total phosphorus levels increase with increasing lake productivity. He gives a level for hypereutrophic lakes of more than 100 ug P l^{-1} which is easily exceeded in Priest Pot.

2.2.6 Orthophosphate (Fig 2.4.b)

The concentrations of orthophosphate in the tarn stayed between 10 and 50 ug P l^{-1} until April when they fell below 10 ug P l^{-1} and remained low until early May. During the summer, levels in the epilimnion remained below 50 ug P l^{-1} but only fell below 10 ug P l^{-1} for a week in late July. The highest values in the top two metres occurred in early September after mixing. At this time the concentrations were above 100 ug P l^{-1} for a short period before falling below 50 again and remaining low throughout the winter. However, even when the orthophosphate was at its lowest concentrations it is unlikely that it was limiting to phytoplankton growth as

Figure 2.4. (a) Total soluble phosphorus isopleth diagram for the sampling period 1983 to 1984. (b) Orthophosphate isopleth diagram for the period 1983 to 1984. Both measured as ug P l^{-1}.

Figure 2.4.a Total phosphorus

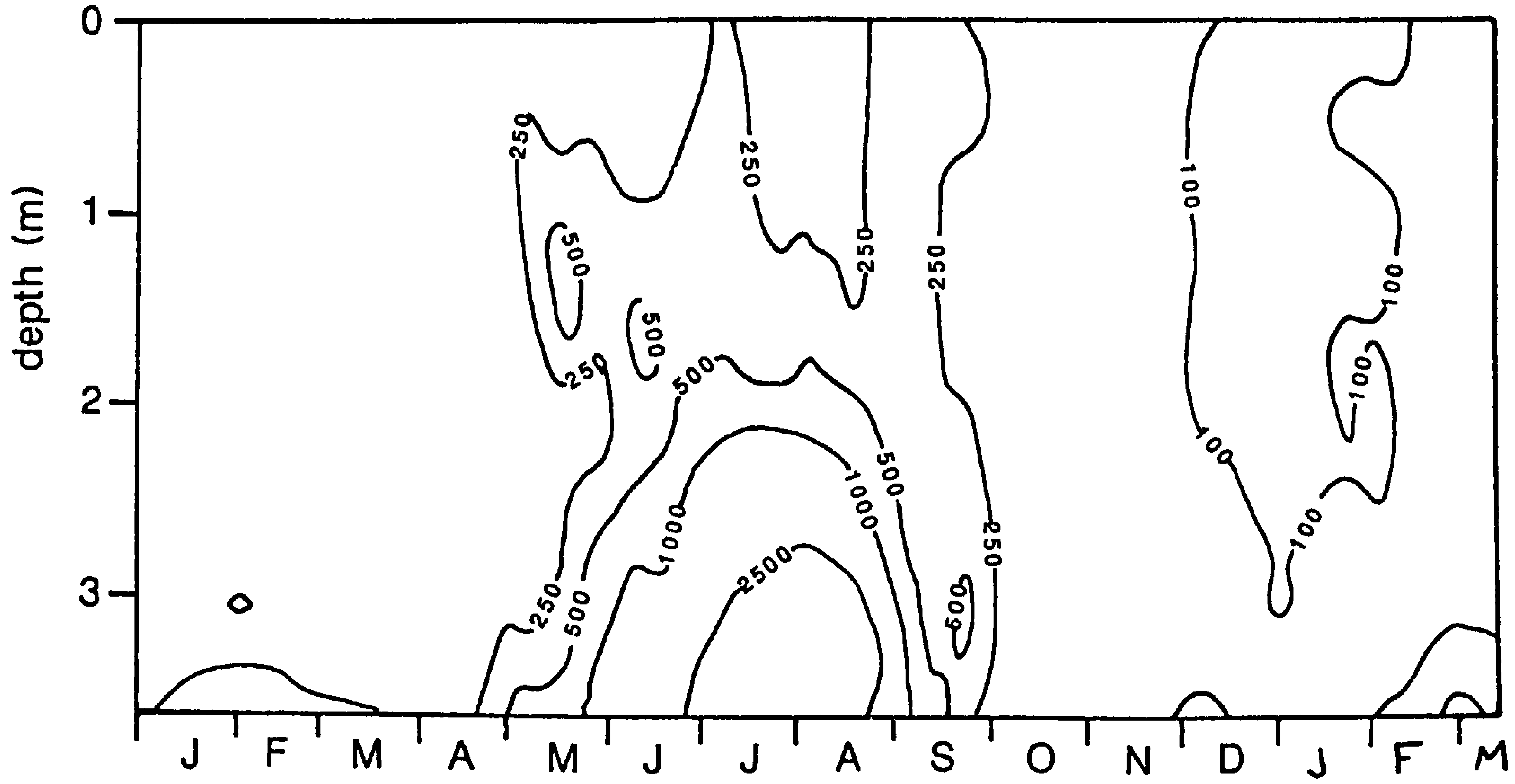
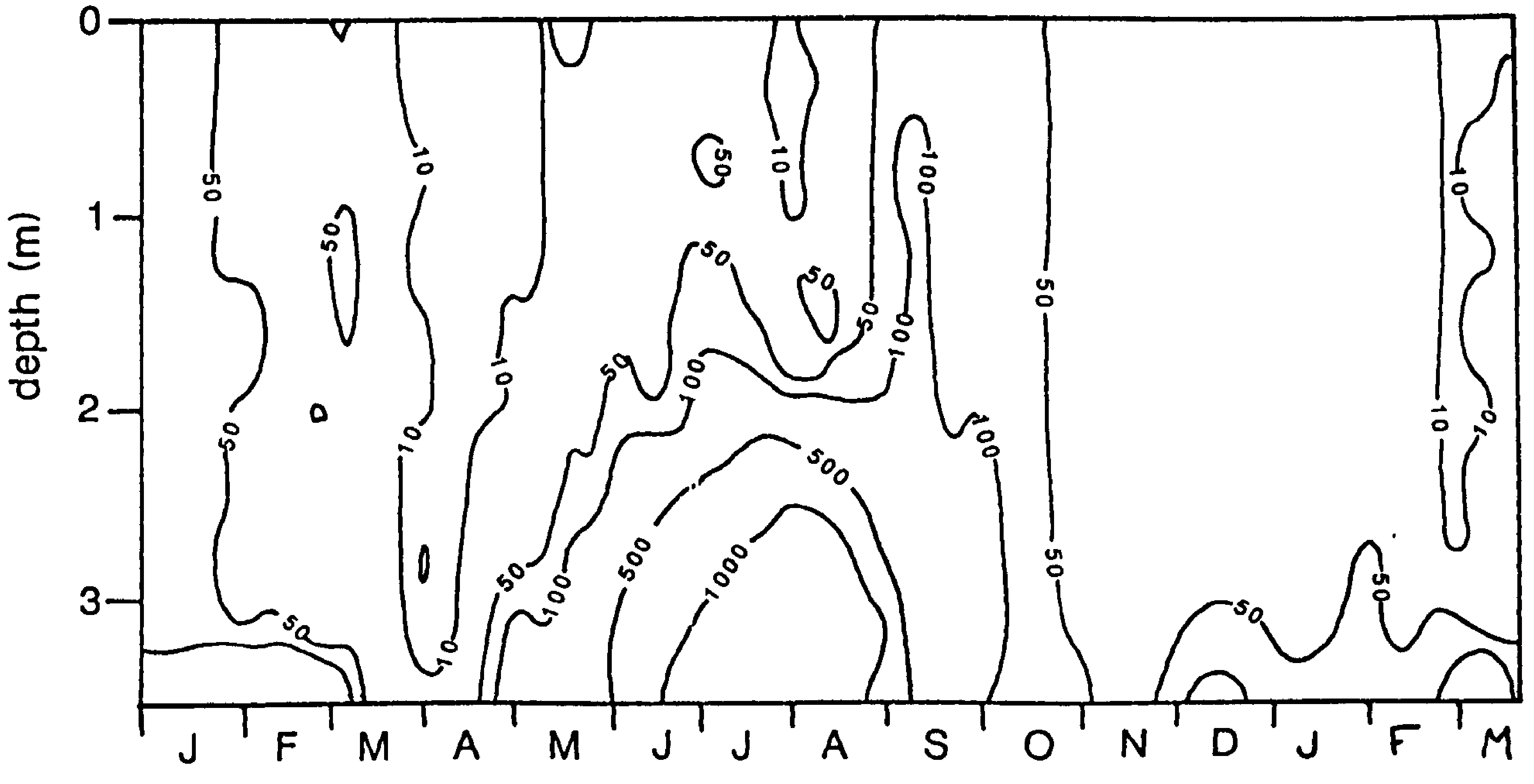


Figure 2.4.b Orthophosphate



the lowest values for Priest Pot would be considered average in other water bodies.

2.2.7 Dry Weight (Fig.2.5.a)

The measurements of dry weight were started in May and continued until mid-November. During this time the levels were above 10 mg l^{-1} until early October when they fell below 5 mg l^{-1}. In May the dry-weight values reached surprisingly high levels with peaks between 1 and 2 metres depth of 85 mg l^{-1} and 137 mg l^{-1} on successive weeks. These peaks were mainly caused by a bloom of dinoflagellates which had gone by the end of the month. High numbers of rotifers at this time and during the summer contributed to the high dry weight values in the epilimnion. The levels also rose in the hypolimnion and remained over 25 mg l^{-1} until mixing took place in September. After destratification the amount of particulate matter decreased and fell below 10 mg l^{-1} in mid-October. However, these levels are still high compared to other water bodies.

2.2.8 Chlorophyll a (Fig.2.5.b)

Measurements of the chlorophyll a equivalent showed a fluctuating algal population. Values were always quite high, usually more than 100 ug l^{-1}. However, there was a series of population peaks through the year. A slight increase, dominated by the colonial chrysophyte Synura, occurred in early April. This was followed in mid to late May by the highest chlorophyll a values found during the study (> 2000 ug l^{-1}) caused by a bloom of the

Figure 2.5. (a) Isopleth diagram for dry weight of particulate matter in the tarn for the sampling period 1983 to 1984 measured in mg l^{-1}.
(b) Chlorophyll a isopleth diagram for the sampling period 1983 to 1984. Chlorophyll a equivalent measured in ug l^{-1}. (c) Bacterial numbers (by direct count) isopleth diagram for the sampling period 1983 to 1984. Values are given in no. $ml^{-1} x\ 10^{-6}$.

Figure 2.5.a Dry Weight

Figure 2.5.b Chlorophyll a

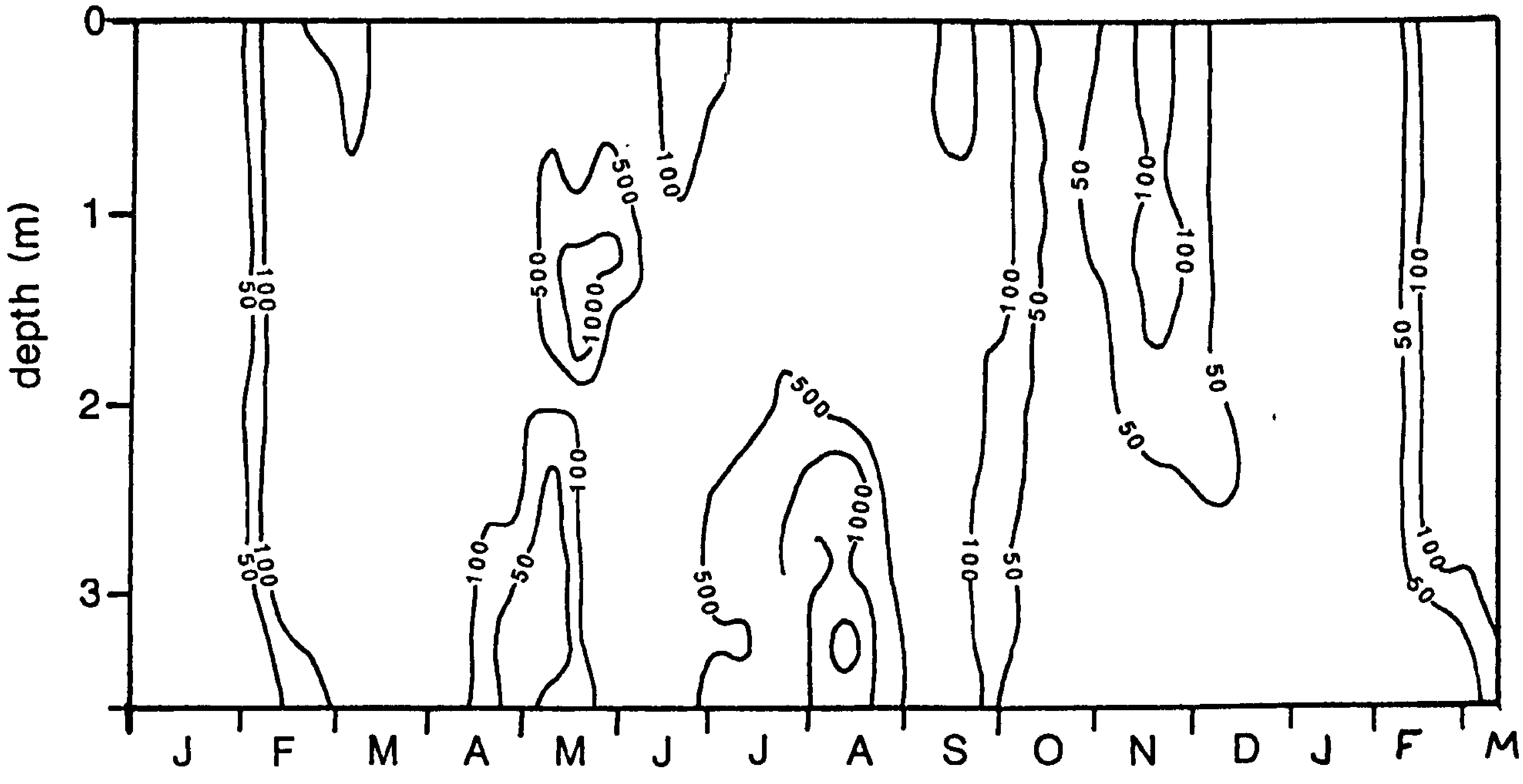
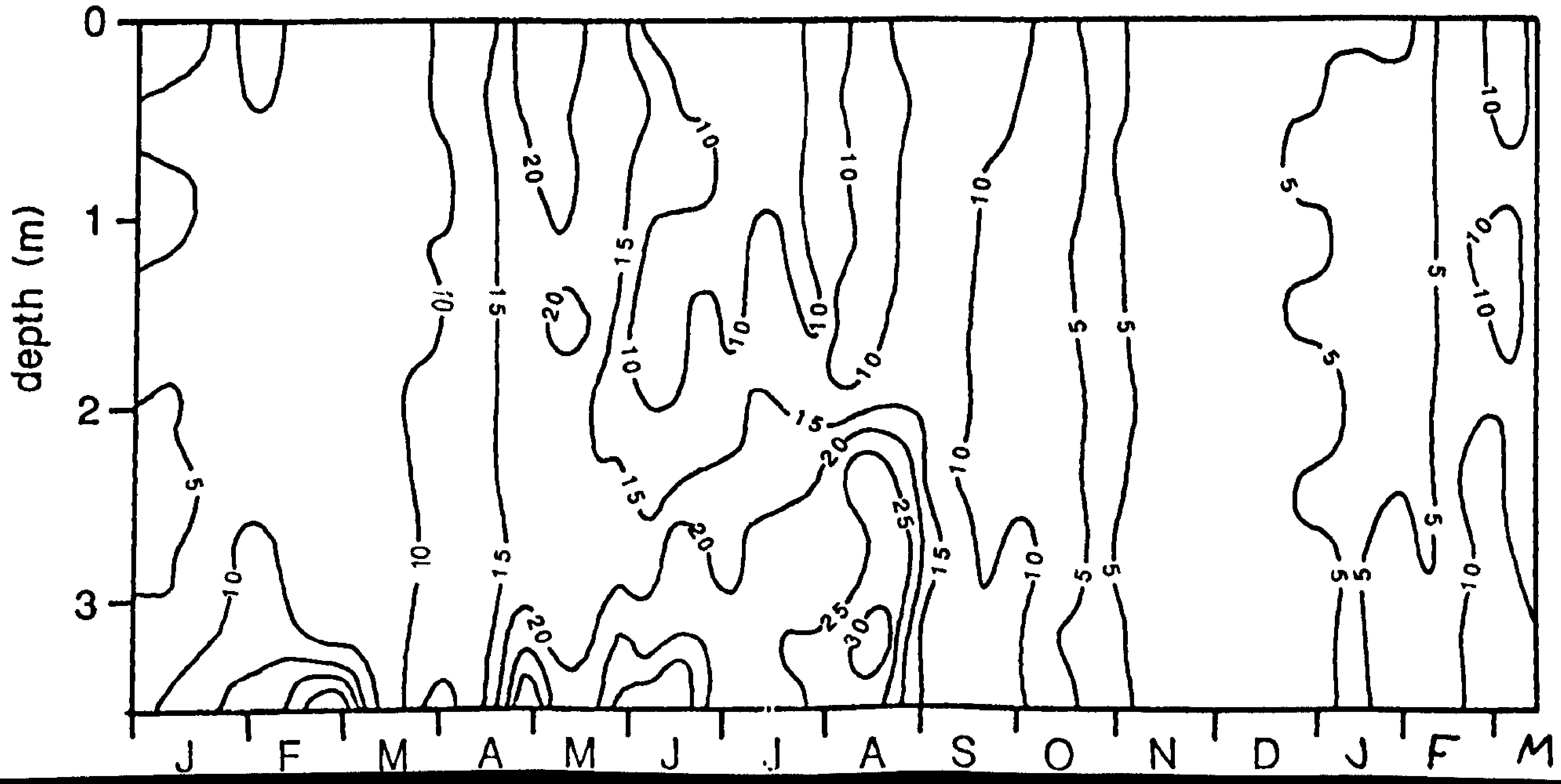


Figure 2.5.c Bacteria



dinoflagellate *Peridinium lomnickii*. During the summer the amount of chlorophyll *a* in the epilimnion was lower. At this time desmids and small green algae were dominant in the phytoplankton. Concentrations in the hypolimnion increased in July and August to more than 1000 ug l^{-1}. This was probably caused by a large community of photosynthetic bacteria in the anoxic water. In mid-September, after the stratification had broken down, another maximum occurred caused by the same chrysophyte. Chlorophyll *a* then fell and remained low until November when there was a slight increase which lasted for a fortnight. The chlorophyll *a* concentration then remained below 50 ug l^{-1} until the following February.

The chlorophyll readings show two quite different communities both bearing chlorophyll. The epilimnetic phytoplankton has a series of spring blooms followed by lower numbers during the summer and only a small recovery in the autumn. There is however a second photosynthetic community in the hypolimnion which produces very high chlorophyll concentrations for three months in summer. Although Vincent (1980a, b) observed *Scenedesmus* populations in the hypolimnion of Priest Pot they were not seen in large numbers in the samples during this study. This second community is therefore likely to be bacterial as it is coincident with very high direct counts. Only the former community is readily available as a food source to the rotifers, the latter being confined to the anoxic hypolimnion.

2.2.9 Bacteria (Direct Counts) (Fig.2.5.c)

Direct counts of the bacteria showed very high values at times. Numbers in the oxic water were highest during May, just before the peak of *Peridinium lomnickii* but after that of *Synura*. Throughout the summer, values around $10^7 ml^{-1}$ were obtained in the epilimnion but values more than double this occurred in the anoxic waters of the hypolimnion where there were high densities of *Ochrobium* at the oxycline and photosynthetic bacteria throughout. After mixing, this anaerobic community crashed but the counts remained above $10^7 ml^{-1}$ until October when they fell and remained low (c.5 x $10^6 ml^{-1}$) throughout the winter. However, in both 1983 and 1984 there were slight increases after the ice cover in January and February had melted.

CHAPTER THREE

A Species List of the Rotifers found in Priest Pot with Notes on their Taxonomy

3.1 General Considerations

Rotifers are small metazoans, characterized by a ciliated corona and specialized jaws. They were first described by Leeuwenhoek in 1703, although an earlier description by the Reverend John Harris is almost certainly of a bdelloid rotifer. Leeuwenhoek termed them "wheel animalcules" on account of their ciliated corona and for almost the next two centuries they were classed as Infusoria. More species continued to be discovered throughout the eighteenth century, Linnaeus including several in the tenth edition of his Systemae Naturae under zoophytes in 1758. The term rotifer (literally the Latin for wheel animal) was first introduced by Cuvier in 1798 but at this time they were still classed with the Protozoa and coelenterates. It was not until 1812 that they were recognized as being more complex than both these groups by du Trochel and separated from them. They continued, however to be included in the Infusoria. In 1838, Ehrenberg repeated du Trochel´s separation in his work "Die Infusorienthierchen" and introduced the name Rotatoria by which they are now known (although there is still some dispute (Ricci 1983)). Metschnikoff, in 1864, separated the rotifers from the gastrotriches to which, he said, they were closely related and it was Zelinka who, in 1889, moved them from the Infusoria to their present position in the Phylum Aschelminthes, although some workers still afford them phyletic status.

Three classes exist : Seisonidea which contains marine species, Digononta (or Bdelloidea) which are soft bodied forms from mainly benthic, interstitial or phytal habitats, rarely occurring in the plankton, and the Monogononta which contains almost all the planktonic forms and to which all the rotifers found during this study belong.

The taxonomy of the rotifers is complicated by the presence of polymorphisms. In order to deal with this problem, many species, varieties and "formenkreis" have been described. However, many of these varieties are difficult to distinguish and even the experts disagree on some classifications. The rotifers from Priest Pot have been identified using the keys in Ruttner-Kolisko (1974) and Voigt & Koste (1978) and any anomalies are discussed in the notes below. A full species list is given in Table 3.1

Many rotifers have a rigid or semi-rigid lorica, e.g. the Brachionidae, but others such as Synchaeta spp. and Polyarthra spp. are illoricate. The loricate forms are often classified solely on the characteristics of the lorica, e.g. shape, spines, facets etc. and many remain recognizable after preservation. However, the soft-bodied forms contract and distort on contact with fixatives, making identification impossible and even recognition of known species difficult. For this reason the species were usually identified from live samples. In some cases, however, where their occurrence was sporadic or brief,

Table 3.1 A Species List of the planktonic Rotifers in Priest Pot

Order : Ploima

Family : Brachionidae

Genus : Keratella

Keratella cochlearis (GOSSE 1851)
Keratella quadrata (MULLER 1786)
Keratella serrulata (EHRENBERG 1838)

Genus : Brachionus

Brachionus calyciflorus PALLAS 1760
Brachionus angularis GOSSE 1851

Genus : Anuraeopsis

Anuraeopsis fissa (GOSSE 1851)

Genus : Euchlanis

Euchlanis sp.

Family : Lecanidae

Genus : Lecane

Lecane sp.

Family : Trichocercidae

Genus : Trichocerca

Trichocerca pusilla (JENNINGS 1903)

Family : Asplanchnidae

Genus : Asplanchna

Asplanchna priodonta GOSSE 1850

Family : Synchaetidae

Genus : Synchaeta

Synchaeta pectinata (EHRENBERG 1832)
Synchaeta kitina ROUSSELET 1902

Genus : Polyarthra

Polyarthra vulgaris CARLIN 1943

Order : Flosculariacea

Family : Testudinellidae

Genus : Filinia

Filinia terminalis (PLATE 1886)
Filinia brachiata (ROUSSELET 1901)

Family : Hexarthridae

Genus : Hexarthra

Hexarthra mira (HUDSON 1871)

this was not possible and the identification of these species is therefore tentative.

3.2 Annotated Species List

3.2.1 Genus : Keratella (Bory de St.Vincent 1822)

The taxonomy of this genus is based on characteristics of the lorica, the length and shape of the spines and the patterning of the facets. However, these can vary widely and as a result many of the *Keratella* species show polymorphisms which complicate their identification.

Lauterborn noted the changes in spine length in *K.cochlearis* Gosse 1851 and published detailed information on the so-called Lauterborn cycles (von Lauterborn,1900,1904). Forms of *K.cochlearis* vary in the *tecta* series from spineless (*K.cochlearis* f.*tecta*) through to long spined (f.*macracantha*). Changes in the facets produce two other series, the *hispida* series and the *irregularis* series. Pejler (1962) shows that the changes in spine length are caused by external factors and as such are of little importance taxonomically. The species in Priest Pot most closely resembled the *K.cochlearis* f.*typica* of Ruttner-Kolisko (1974) and although spineless forms are known to occur under conditions of rapid development in warm water and in eutrophic environments, they were, surprisingly, not found in the Priest Pot population.

The type of the genus, *Keratella quadrata* Muller 1786, also shows polymorphisms. Ruttner-Kolisko (1949) detailed the wide range of spine lengths found in nature, but unlike *K.cochlearis*, this species shows no change in the facets on the lorica. No temporal variation was found in the spine length of the Priest Pot population, they were of the typical form.

Only one individual of *K.serrulata* (Ehrenberg, 1838) was found during the investigation.

3.2.2 Genus : *Brachionus* Pallas 1776

This genus is also classified exclusively on features of the lorica. Several features are used : number and form of anterior spines, shape of the lorica margins, form of the foot opening and presence of caudal spines. As they can all vary independently of each other many forms have been described and their correct classification is the cause of much discussion.

The larger species in Priest Pot was clearly *B.calyciflorus* Pallas 1766. This can have a wide range of spine lengths. Gilbert (1966, 1967) showed that an increase in the length of the postero-lateral spine was linked to the presence of *Asplanchna* in the water, a fact previously noted by de Beauchamp (1952 a, b). The population in Priest Pot showed none of this variation, its postero-lateral spines were either reduced or absent.

The other species was smaller and squarer with much reduced spines and was identified as *B.angularis* Gosse 1851.

3.2.3 Genus : *Anuraeopsis* (Lauterborn, 1900)

This genus is usually described as tropical, but one species, *A.fissa* (Gosse, 1851) has been found in temperate waters. Pejler (1957 b) found A.fissa in a small pond in Lapland and other records from this latitude exist. It is known to be a warm stenotherm but can survive in colder environments where the summer temperatures are favourable. The genus was revised by Berzins (1962) and most of the tropical species were renamed as forms of A.fissa which showed a geographical disribution from A.fissa f.navicula around the equator to A.fissa f.fissa in Europe. This latter form is found all over Europe, Berzins describes it as the typical form and it was this form which occurred in Priest Pot. In this study the population has been named A.fissa (Gosse, 1851) following the classification in Ruttner-Kolisko (1974).

3.2.4. Genus : Euchlanis (Ehrenberg, 1832)

Euchlanis is a genus in which about twenty forms have been described, but only one species, E.dilatata (Ehrenberg, 1832) is regularly planktonic. The classification is based exclusively on the shape of the lorica and the few individuals found in Priest Pot were similar to descriptions of E.dilatata in the literature. However, fewer than ten individuals were found during the study, all of them after preservation, so the classification is only certain to the generic level.

3.2.5 Genus : Lecane (Nitzsch, 1827)

The species of this genus are mainly littoral or benthic, and are rarely found in the plankton. Only two individuals were found during the fifteen months of routine sampling and it is likely that they had come from the littoral zone and were only accidentally in the pelagic waters. They were not identified beyond genus as their appearance in the plankton was of little significance.

3.2.6 Genus : Trichocerca (Lamarck, 1801)

Trichocerca species are characterized by asymmetrical toes, the left being of varied length while the right may be reduced or absent. The genus contains many described forms but only a few are planktonic. No live animals were obtained for examination but investigation of the preserved individuals suggested that the population in Priest Pot may be *T.pusilla* (Jennings 1903). The species has a short body (length:breadth about 2:1) and a left toe approximately half the length of the body. Ruttner-Kolisko (1974) gives a size range of 70 to 110 um for body length and the Priest Pot individuals were within this. In 1983 the species occurred only sporadically but in 1984 a larger population appeared in late summer and was present during the experimental phase of this study. It is tentatively named *T.pusilla*.

3.2.7 Genus : Asplanchna (Gosse, 1850)

Asplanchna species are illoricate with a saccate body. They are classified by means of some very variable features : the body size, shape of the vitellarium and number of nuclei in it, trophi, resting eggs, gastric glands and excretory organs. The population in Priest Pot appeared for less than a month in the summer and no live individuals were examined. However,their spherical vitellarium and estimated size before preservation make it likely that they were *A.priodonta* (Gosse, 1850).

3.2.8 Genus : *Synchaeta* (Ehrenberg, 1832)

The genus *Synchaeta* contains marine and brackish as well as freshwater species and most have a temperate distribution. They are illoricate which makes identification after preservation almost impossible. Even in the extended state there are still problems with their taxonomy. The rotifer community in Priest Pot contained two populations of *Synchaeta* species; one between 100 and 150 um in length, the other about 300 um. This size difference allowed separation of the two species even in their contracted state. Examination of live specimens suggested that the smaller form was *S.kitina* (Rousselet, 1902). Both Ruttner-Kolisko (1974) and Pontin (1978) give *S.kitina* as a synonym for *S.tremula* (Muller, 1786) although Kutikova (1970) gives it as a separate species. Its size, period of occurrence and comb-like uncus make it similar to the species found by May (1980) in Loch Leven. The population in Priest Pot was therefore named *S.kitina*.

The larger species was identified as *S.pectinata* (Ehrenberg, 1832) on account of its larger size and its bell-like shape. Examination of the mastax of this form showed no combing on the uncus similar to that found on the trophi of *S.kitina*. The uncus of *S.pectinata* is described as "with one pointed tooth" by Ruttner-Kolisko (1974) so the lack of combs in the Priest Pot population supports its identification as *S.pectinata*.

3.2.9 Genus : *Polyarthra* (Ehrenberg, 1834)

The genus is divided into groups by Ruttner-Kolisko (1974) and the "formenkreisen" and species are differentiated mainly by size and by the shape and measurements of the blades. These measurements can vary within one population and an overlap in size occurs between both "formenkreisen" and species. The relative measurements (ratios of blade width to blade length and of body length to blade length), however, are fairly constant. The first generation hatched from resting eggs bear no blades and were initially classified separately in the genus *Anarthra*. However, they are now included in the appropriate species of *Polyarthra*.

Carlin (1943) carried out a sub-division of the genus and produced a series of groups. One of these, the *P.vulgaris*/*dolichoptera* group, is the one to which the Priest Pot population belongs. This group is known to contain many intermediate forms between the terminal members *P.vulgaris* (Carlin, 1943) and *P.dolichoptera* (Idelson, 1925) and the characteristics of the specimens examined from Priest Pot suggest that it is a form near the *P.vulgaris* end of the series. *P.vulgaris* has short,serrated blades with a large width to length ratio and tends to be larger than the longer, narrower bladed *P.dolichoptera*. The study population bore blades only slightly longer than expected for *P.vulgaris* and for much of the year was within the correct size range. Although at times there was a proportion of the population smaller than the stated range of *P.vulgaris*, all the other characteristics were closer to the descriptions of this species than to those of P.dolichoptera. It was therefore identified as P.vulgaris (Carlin, 1943) for the purposes of this study although it may be an intermediate form.

3.2.10 Genus : Filinia (Bory de St.Vincent)

Members of this genus are illoricate with two skipping bristles and one or two caudal bristles. Three groups exist, separated by characteristics of these bristles, but the major one is the longiseta/terminalis group which has been widely discussed in the literature (Pejler, 1957 a; Hofmann, 1982; Ruttner-Kolisko, 1980). F.terminalis (Plate, 1886) is described as a cold stenotherm and its skipping bristles are smooth. In contrast, F.longiseta (Ehrenberg, 1834) is a thermophile and its skipping bristles bear small spines along their length. The population in Priest Pot generally occurred at temperatures below 15°C and had no spines on its bristles. On this evidence it was identified as F.terminalis.

The cornuta/brachiata group is less well documented. It contains two species, differentiated by the length of the skipping bristles and presence or absence of a lip on the corona. F.brachiata (Rousselet, 1901) has bristles from half to the full length of the body and a distinct lip. The bristles of F.cornuta (Weisse, 1847) are much shorter and the lip is not so prominent. Although examination of the study population showed that the lip was not particularly pronounced, from the length of the bristles it could be identified as F.brachiata.

3.2.11 Genus : Hexarthra (Schmarda, 1854)

The members of this genus are illoricate but bear six arm-like appendages which themselves bear bristles by which they can be recognized even after preservation. Most are warm water species and many live in salt or brackish water. The population in Priest Pot occurred sporadically and no live animals were examined. However, investigation of a preserved specimen showed some of the characteristics of *H.mira* (Hudson, 1871); it had two club-shaped appendages at the posterior end, and the bristles on its arms were inserted singly. *H.mira* is the only species of *Hexarthra* found in Britain according to Pontin (1978) and in Hussey (1981) there is only one record of a second species, *H.oxyuris* by Bryce & Garner (1944). It seems likely that the identification of this population as *H.mira* is correct.

CHAPTER FOUR

Methods used in Routine Sampling

4.1 Methods used in the field

4.1.1 Obtaining the samples

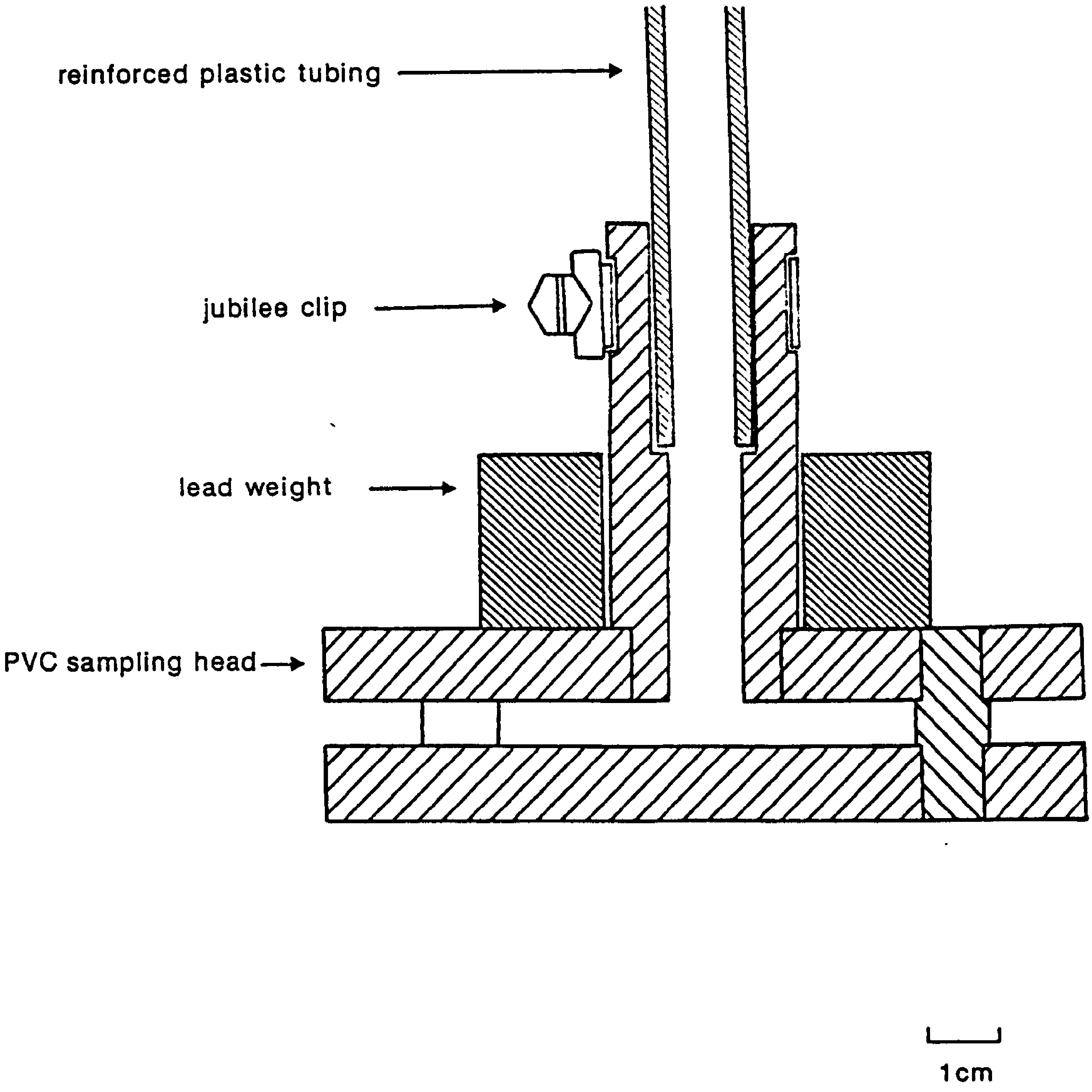
Routine samples were collected from the tarn at regular intervals from January 1983 to March 1984. They were taken weekly, except from December to February when the interval was a fortnight and during ice cover* when sampling was not possible. The collection methods used were designed to provide information on both the vertical distribution of the rotifers in the water column and seasonal changes in population density. Sampling was from the centre buoy where the tarn was 3.5 to 3.7 m deep.

A peristaltic pump (Glen Creston Ltd., Stanmore, Middlesex, U.K. cat.no. 60 225 WAB) powered by a 12 volt car battery was used to pump water from selected depths through a 5 metre length of reinforced plastic tubing. The tube was fitted with a "laminar flow" sampling head (Fig.4.1) as described by Cunningham & Davison (1980), which allowed discrete water samples to be collected at intervals of only 5 cm. When the tarn was isothermal the samples were taken at 0.40 m depth intervals throughout the column but after the onset of stratification in May the interval was changed to 0.20 m above the oxycline and 0.60 m below. During stratified conditions an extra sample was taken at the oxycline. Up to six litres of water were taken at each depth, a smaller volume was sufficient during periods of high rotifer numbers.

* (for 2 weeks in February 1983)

Figure 4.1. The laminar flow sampling head used in the routine sampling during 1983 and 1984.

Figure 4.1 The Laminar Flow Sampling Head



Processing of samples was begun immediately on return to the laboratory.

4.1.2 Physical Data

Oxygen concentration, temperature and light intensity were measured in the tarn at the time of sampling. Oxygen and temperature profiles were obtained using a temperature compensated, dissolved oxygen probe with thermistor (Yellow Springs Co. Inc., Yellow Springs, Ohio, U.S.A. YSI 5739). A standard probe with a built-in stirrer (YSI 5795A) was used at 0.25 m depth intervals up to July, after this the stirrer was detached and the probe was fitted to the laminar flow sampling head. Measurements were then taken at the sampling depths.

Light measurements were taken using a Lambda flat plate sensor (Lambda Instrument Co. Inc., Lincoln, Nebraska, U.S.A.) and a Fluke multimeter (Fluke (Nederland) B.V., Tilburg, The Netherlands) at 0.10 m intervals.

4.2 Treatment of samples in the laboratory

4.2.1 Sub-samples for rotifer counts

Sub-samples were taken for quantitative analysis of the rotifer populations. As rotifer numbers increased the volume of the sub-samples was decreased from 4 litres in mid-winter to 1 litre throughout the summer. A series of concentration steps was required before the samples could be stored for counting.

From May to October, one litre was sufficient and this was concentrated by sedimentation in a series of glass measuring cylinders, down to a volume of 10ml. Non-acetic Lugol's solution (10g I, 20g KI, 200ml distilled water) was added as a fixative and as a killing agent. The samples were left for at least 48 hours at each step in the concentration process to ensure that all the rotifers had settled out. The concentrated samples of 10ml were fixed with a further 5 drops of Lugol's solution and stored in screw top vials until counted.

Larger sub-samples were concentrated initially by a reverse filtration method (Dodson & Thomas, 1964) through a 35 um nylon mesh. This is a gentle method that reduces damage to the plankton that is filtered. The mesh was fixed, using epoxy resin (Araldite), across a cylinder of plastic cut from a sample bottle. This nested inside a pyrex beaker containing the sub-sample. The filtrate entering the plastic cylinder through the mesh was removed by bailing to maintain the head of water in the beaker. Further concentration of the samples was by sedimentation and followed the process described previously.

4.2.2 Algal Samples

10 to 15ml of each sub-sample were fixed with Lugol's solution and stored in glass vials for future microscopic examination.

4.2.3 Direct Counts of Bacteria

Direct counts were carried out on the day of sampling using the incident light (epifluorescence) method of Jones & Simon (1975).

About 100ml of tarn water were filtered to provide pre-filter diluent, first through a Whatman GF/C filter, then a 0.22 um pore size Millipore cellulose membrane. A 5ml sub-sample was mixed with the fluorochrome acridine orange in the ratio 100:1, giving a final concentration of 10 ug l^{-1}, and allowed to stand for three minutes. The filters used for the direct counts were 0.22 um cellulose membranes dyed black with DYLON^{C}, no.8 ebony black. Details of the method for dyeing the membranes are given in Jones & Simon (1975). 5ml of pre-filter diluent and 1ml of dyed sample were filtered, the diluent being necessary to ensure even distribution of bacteria on the membrane. The membrane was immediately transferred to a film of immersion oil, covered by a further drop of oil, and counted within an hour of filtration. Between filtration and counting the mounted membranes were refrigerated to prevent reduction of the counts.

Counting was done on a Leitz Orthoplan microscope with a Ploem illuminator, the light source was a 200 W mercury vapour lamp. Illumination was through a Calflex B1/K2 interference heat filter, a 1.5 mm BG12, 2x KP490 (=KP500) interference filters and a dichroic mirror/suppression filter combination TK510/K515. The image was viewed through a K530 barrier filter. The bacteria were counted using a total magnification of x1250. An eye-piece graticule was used to define the counting area.

It was necessary to count at least 400 bacteria per membrane to be 95% certain that the actual number was within plus or minus 10% of the count (Jones,1979).

4.2.4. Chlorophyll a determinations

A 250ml sub-sample of water was passed through a 47 mm Whatman GF/C filter on a Millipore filter apparatus, then the filter was boiled in 10ml of methanol. The resulting chlorophyll extract was either read immediately or covered with plastic film and stored in a refrigerator for not more than 24 hours. A scanning spectrophotometer (Pye Unicam SP8-100 ultra-violet spectrophotometer) was used to measure the absorbance in a 1 cm cell over a range of wavelengths, from 500 nm to 800 nm. Using this value and the multiplication factor from Talling & Driver (1963), a value for chlorophyll a equivalent as ug ml^{-1} in the solvent was obtained (Golterman et al., 1978). A further conversion, using a factor dependent on the volume filtered, gave the concentration of chlorophyll a in the tarn in ug l^{-1}. During periods of high algal concentration it was sometimes necessary to reduce the volume of the sub-sample because the filters rapidly became blocked.

4.2.5 Dry Weights

47 mm Whatman GF/F filters were dried separately in Petri dishes in an oven at 60°C for 24 hours, then transferred to a desiccator for storage until required. On the sampling day they were weighed accurately on a Mettler balance. 250ml of each water sample were filtered using a Millipore filter assembly and a small vacuum pump. The filters were then redried in the oven at 60°C for at least 24 hours, allowed to cool in a desiccator

and reweighed. The quantity of particulate matter in the samples could then be calculated by difference. During periods of high algal numbers, as in the chlorophyll extractions, a smaller sub-sample was used.

4.2.6. Chemical Analysis

Chemical analyses were carried out by the staff of the analytical laboratory of the Freshwater Biological Association, Windermere.

Nitrate was determined using the hydrazine-copper reduction method (Hilton & Rigg, 1983) on a discrete analyser - a Pye Unicam AURA system (AC1) automatic chemistry unit with an SP6-550 ultra-violet/visible spectrophotometer and a Hewlett-Packard 9815A calculator. This same equipment was used to measure ammonia as indophenol blue after treatment of the sample with phenol nitroprusside and alkali hypochlorite reagents; a method modified from Chaney & Marbach (1962) and given by Mackereth et al. (1978).

Two phosphorus determinations were carried out. Soluble reactive phosphorus was measured using a method modified from Murphy & Riley (1962) and Stephens (1963). The sample was reduced to molybdo antimonyl phosphoric acid using an acidic molybdate solution containing antimony and ascorbic acid as reductant and read spectrophotometrically. Total dissolved phosphorus was determined as phosphate after autoclaving with acid persulphate (Eisenreich et al., 1975).

4.3 Method used in Counting

The rotifer samples were counted using a Nikon Optiphot microscope at a total magnification of x100. Glass Sedgewick-Rafter cells were used as counting chambers in preference to plastic cells as the latter become badly scratched. A 1ml sub-sample was taken from each concentrated 10ml sample and transferred to the counting chamber in the manner described by Jones (1979). At times it was necessary to carry out a dilution before sub-sampling. When rotifer numbers were at their highest, alternate columns on the Sedgewick-Rafter cell were counted. This method halved the volume counted whilst still scanning the length of the cell, thereby minimising any possible inaccuracies caused by a differential spread of organisms. Since the coverslips provided with the Sedgewick-Rafter cells by the supplier (Graticules Ltd., Tonbridge, Kent) were too thick to allow the use of the x40 objective, thinner coverslips (no.1) were used.

The counting was carried out using a modified Sinclair ZX81 (Cunningham & Purewal, 1983) in place of mechanical counters.

CHAPTER FIVE

The Horizontal Distribution of Rotifers in Priest Pot

5.1 Introduction

The distribution of zooplankton is not always homogeneous in the horizontal plane. In some water bodies aggregations of zooplankton develop and these patches can affect any estimates of population density. A review of zooplankton patchiness by George (1981) covers the problems of patchiness and its detection.

The horizontal distribution of rotifers has not been widely studied. Preissler (1977a,b 1980) investigated avoidance of shore and suggested that this behaviour was present in rotifers. In Loch Leven, May (1980) found a random distribution in the rotifers of the pelagic zone but this is a well mixed lake. Priest Pot is sheltered by trees and is stratified for part of the year and under these conditions the rotifers could become aggregated.

5.2 Methods

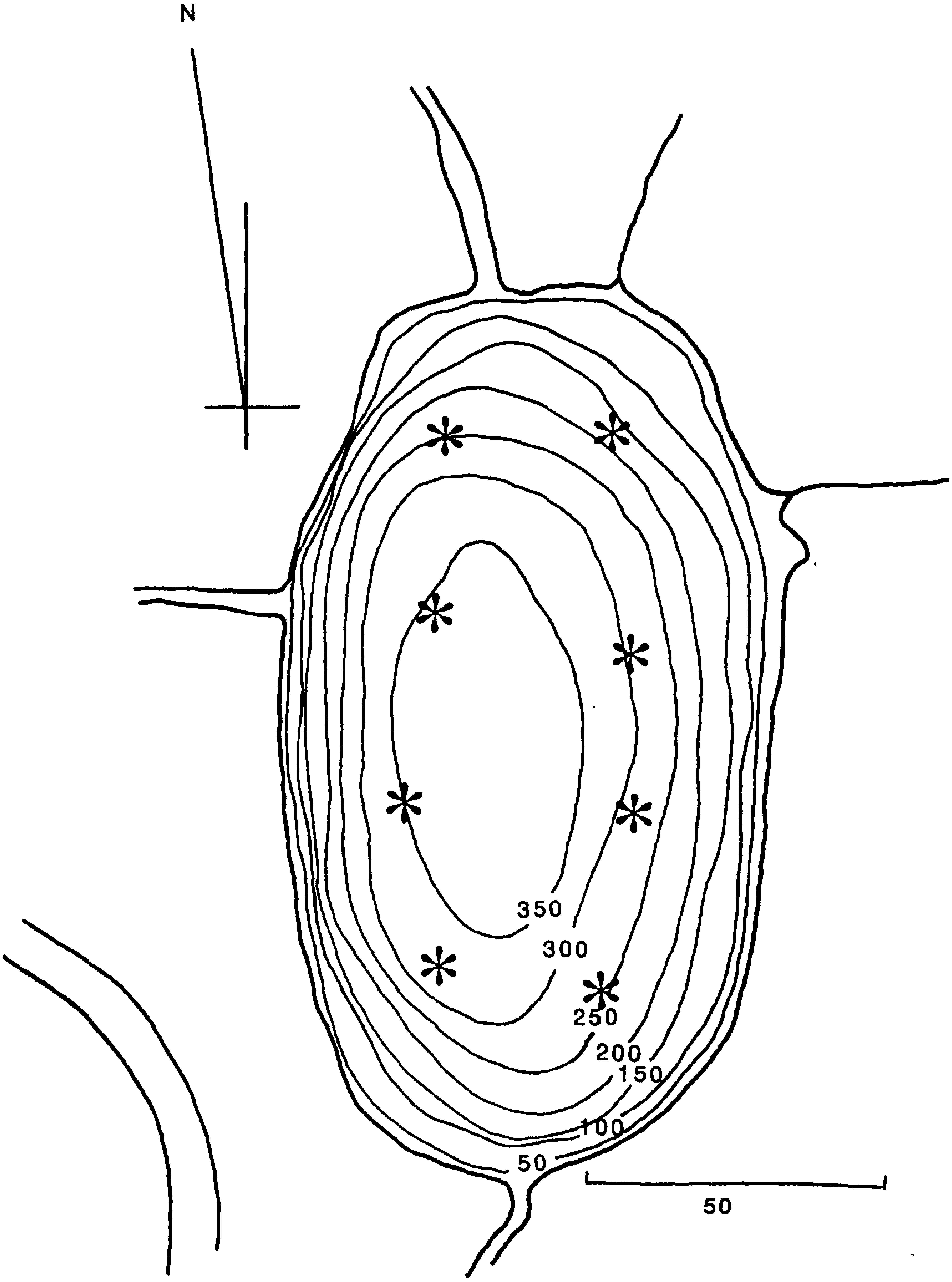
Eight sampling sites were chosen to cover that part of Priest Pot deeper than 2.5 m (Fig.5.1). Integrated water samples were taken at each site using a 3 m flexible rubber tube, 2 cm internal diameter*. Two or three samples were taken at each site to provide enough water for a 2.5 litre sub-sample. This was concentrated to 10 ml in the laboratory following the reverse filtration/sedimentation method described in Chapter Three. Fixation and preservation were in non-acetic Lugol's iodine. One ml sub-samples, representing 250 ml

* weighted at one end

Figure 5.1. Priest Pot showing the position of the eight sampling sites used in the horizontal distribution investigation.

Figure 5.1

Sampling Sites for Horizontal Distribution Investigation



of original tarn water, were then counted in a Sedgewick-Rafter cell. Occasionally some samples were contaminated with mud and were uncountable. On these dates fewer than eight samples were counted. Samples were taken weekly* until the end of May when bi-weekly sampling was started.

The data were treated in three ways : the population density at one site was plotted against the mean population density from all sites, an index of dispersion was calculated as a test for non-randomness and a patchiness index was calculated as a measure of aggregation.

5.3 Comparison of one site with the mean of all sites

The comparison was carried out on total rotifer numbers and then on four individual species. Although the horizontal samples were only counted up to July, they give an adequate size data set for investigation.

The data for total rotifer numbers show a good fit to a straight line until values exceed 20,000 ind l^{-1} (Fig.5.2), above this value there is more scatter. When the four dominant species are considered individually, similar findings appear. The close relationship between the data from one site and the mean of all the sites indicates that there is little variation between sites.

5.4 Index of Dispersion

A test for non-randomness was performed using the index :

$$\frac{s^2(n-1)}{\bar{x}}$$

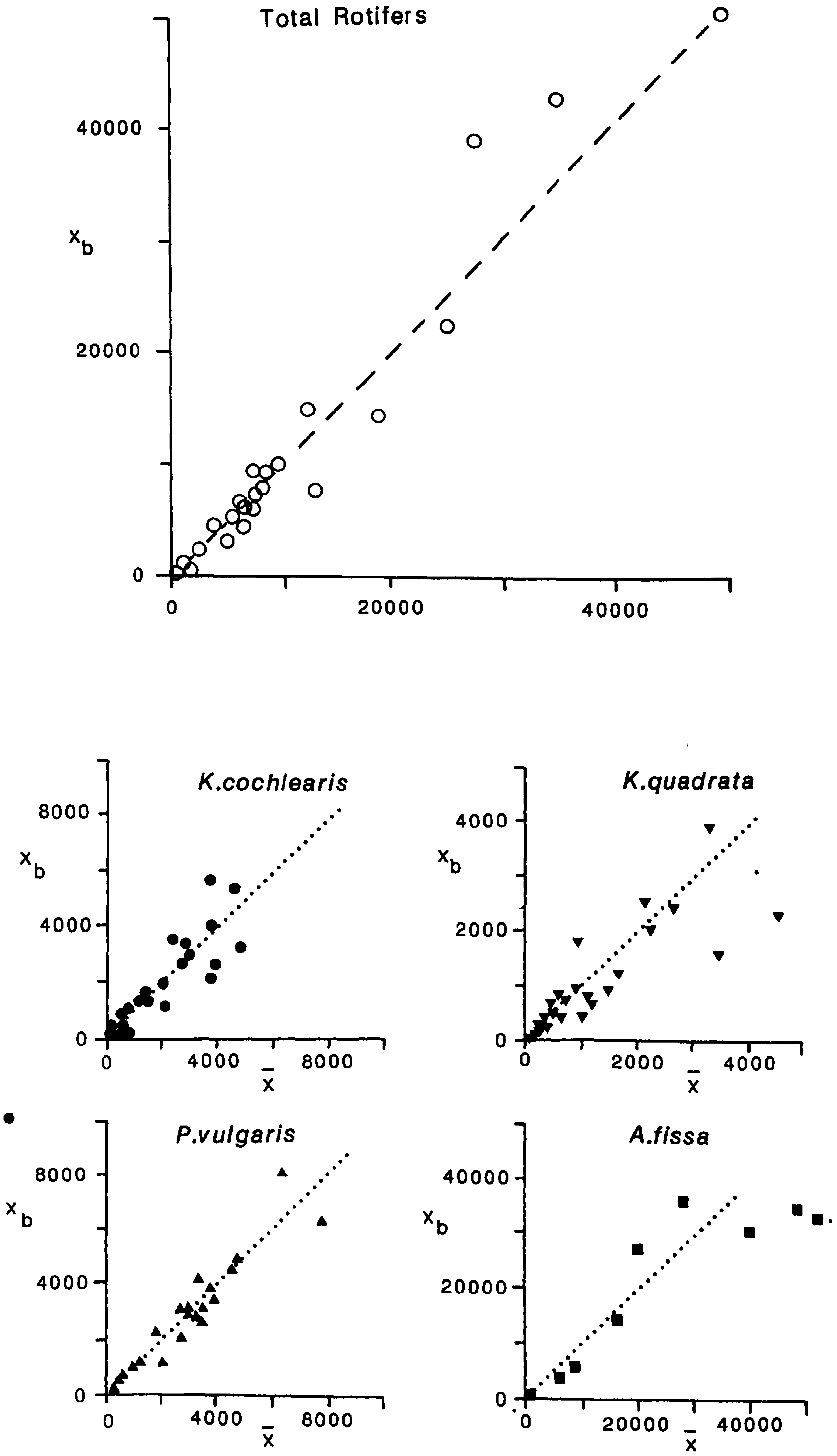
This index is n-1 for a random distribution, zero for

---

* From January

Figure 5.2. A comparison of the mean number of rotifers at one sampling site (x_b) with the mean number of all sites ($\bar{x}$), carried out for total rotifer numbers and for four individual species: *Keratella cochlearis*, *K.quadrata*, *Polyarthra vulgaris* and *Anuraeopsis fissa*.

Figure 5.2


Total Rotifers
40000
x_b
20000
0
0
20000
40000
K.cochlearis
8000
x_b
4000
0
0
4000
8000
$\bar{x}$
K.quadrata
4000
x_b
2000
0
0
2000
4000
$\bar{x}$
P.vulgaris
8000
x_b
4000
0
0
4000
8000
$\bar{x}$
A.fissa
40000
x_b
20000
0
0
20000
40000
$\bar{x}$

maximum regularity and $\Sigma x(n-1)$ for maximum contagion (M.Elliott 1977). The index was calculated for total rotifer numbers and the values are given in table 5.1.

For a 5 % level of testing, the χ^2 value for the index should be between 1.69 and 16.01 for randomness. All but one of the χ^2 values are clearly greater than this, indicating that the rotifer community was aggregated when the samples were taken.

5.5 Lloyd's Index of Patchiness

A measure of patchiness of a population based on the mean crowding statistic of Lloyd (1967) was used to further investigate the aggregation of the rotifers in the tarn. The mean crowding estimate ($\overset{*}{x}$) is given by :

$$\overset{*}{x} = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1\right)$$

and the ratio of mean crowding ($\overset{*}{x}$) to mean density ($\bar{x}$) is taken as the index of patchiness. This index equals unity for random distributions, is less than unity for regular distributions and is greater than unity for aggregated distributions. The indices obtained were sorted into categories with values between 1 and 1.05, 1.051 and 1.1, 1.11 and 1.15 etc.. The number of indices within each range was noted and plotted as histograms for total rotifers and for the four individual species (Fig.5.3). Almost all the indices calculated were below 1.3, all but two of those for total rotifer numbers were between 1 and 1.1. The frequency histograms all show highest frequency between 1 and 1.1 and the mean patchiness index for each species is also close to unity. However, for the large values of $\bar{x}$ involved, the index should be less than

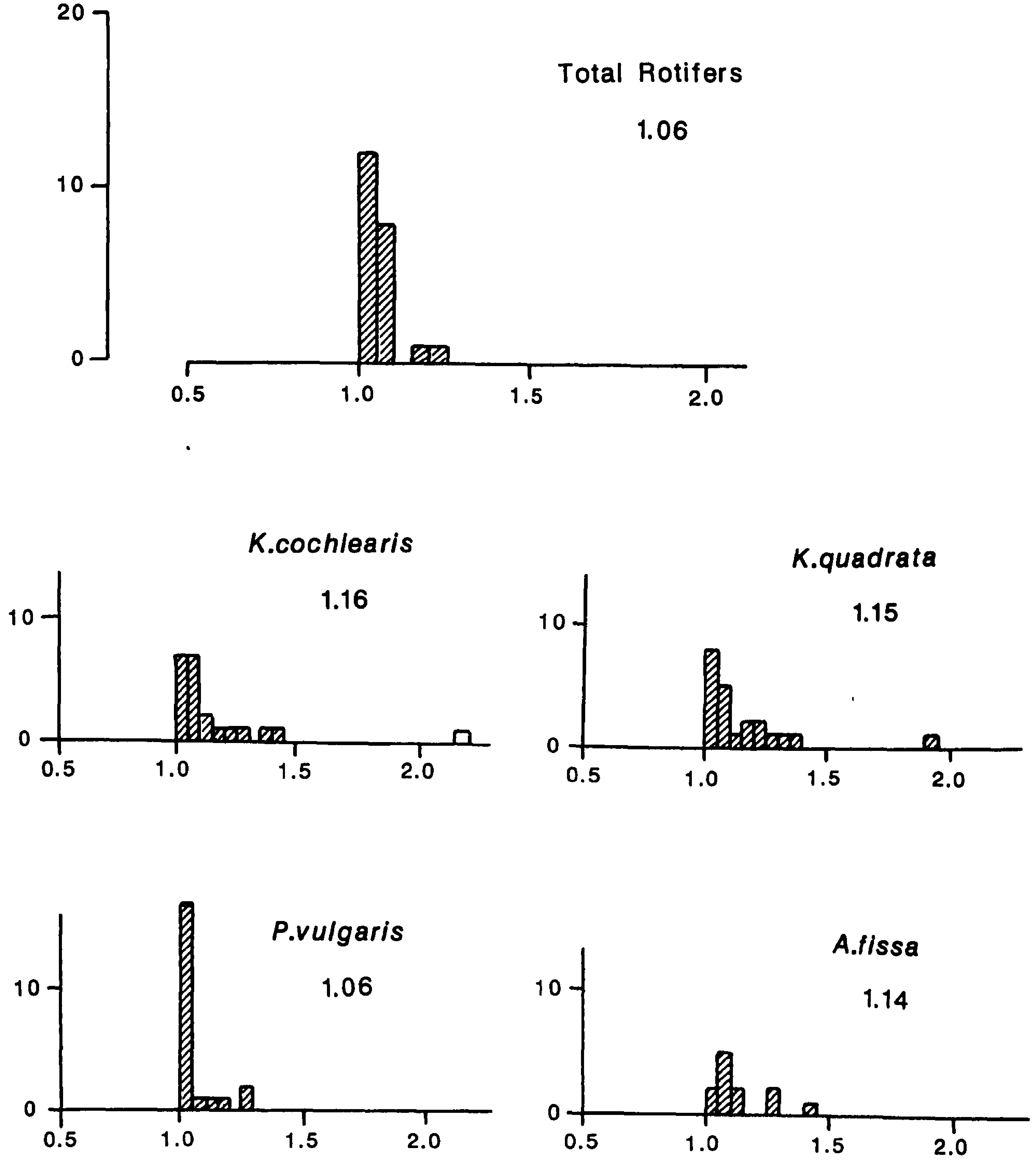
Table 5.1 Indices of dispersion for the total rotifer community

Date	$\frac{(n-1)s^2}{X}$	χ^2	Significance
23.3.83	1687.11	159	*
28.3.83	145.71	180	*
5.4.83	81.98	46	*
11.4.83	29.23	678	*
18.4.83	227.97	92	*
25.4.83	39.76	189	*
2.5.83	32.26	522	*
9.5.83	349.44	68	*
16.5.83	208.28	53	*
23.5.83	234.32	79	*
31.5.83	379.56	141	*
6.6.83	179.12	92	*
13.6.83	971.72	149	*
16.6.83	385.93	74	*
20.6.83	437.16	42	*
27.6.83	363.70	66	*
1 .7.83	251.76	117	*
7.7.83	383.11	4	ns
11.7.83	658.39	23	*
14.7.83	622.36	23	*
18.7.83	454.67	45	*
25.7.83	574.94	34	*

*$p < 0.05$; ns, not significant

Figure 5.3. Histograms showing the range of Lloyd's Indices of Patchiness and the number of indices in each range for total rotifer numbers and the four species: *Keratella cochlearis*, *K.quadrata*, *Polyarthra vulgaris* and *Anuraeopsis fissa*.

Figure 5.3


20
10
0
Total Rotifers
1.06
0.5
1.0
1.5
2.0
K.cochlearis
1.16
K.quadrata
1.15
P.vulgaris
1.06
A.fissa
1.14

1.00016 to indicate randomness (using χ^2 tables for confidence levels). It would therefore appear that the samples taken show some degree of aggregation.

5.6 Discussion

Although initially the horizontal distribution of the rotifer community appeared to be random, further investigation showed that the horizontal distribution showed a degree of aggregation. However, with the large population sizes found in Priest Pot, any effects of this patchiness would be minimal and they would be unlikely to affect the results of the vertical distribution studies carried out in Priest Pot during 1983 and 1984. It is possible that any anomalous values could be the result of a non random distribution of the rotifers but in general the results of this horizontal distribution investigation should not affect the other results in this study. The studies carried out in 1984 on an enclosed population (Chapter Nine) would obviously not be affected by patchiness and the similarity between the results from those studies and those on the populations in the tarn are a further indication that any patchiness effects are minimal.

CHAPTER SIX

The Seasonal Succession of the Rotifers in Priest Pot

6.1 Introduction

The many ecological studies performed on planktonic rotifers have shown seasonal changes in their abundance and a succession of species through the year. Previous work on British freshwaters includes studies on seasonal changes of the planktonic rotifer community in Thames reservoirs (Doohan, 1973), an oligotrophic lake (Elliott,1977) and a eutrophic loch (May,1980). The routine sampling in Priest Pot showed evidence of changes in abundance and in species composition and adds a hypereutrophic tarn to the list above.

6.2 Methods

The data from the regular weekly samples were used to obtain a mean number of rotifers per litre on each date for each species. Using these values it was possible to plot the seasonal succession of the rotifers over the fifteen-month study. The mean values of individuals per litre varied from zero to more than 100,000. Although a cube root or logarithm transformation of the data would have made the figures more directly interpretable as rates of increase, it was decided to plot numbers per litre as this showed the fluctuations more effectively. The population changes were then compared with other environmental variables in an effort to explain some of the variation. An attempt was made to classify the rotifers into groups according to their times of maximum abundance. As the patterns of occurrence in Priest Pot did not fit well into any of the three systems described in Chapter One ; those of Hutchinson (1967), Larsson (1971) and Elliott(1977), a fourth system is defined for the Priest Pot community.

6.3 General Description of the Total Rotifer Community

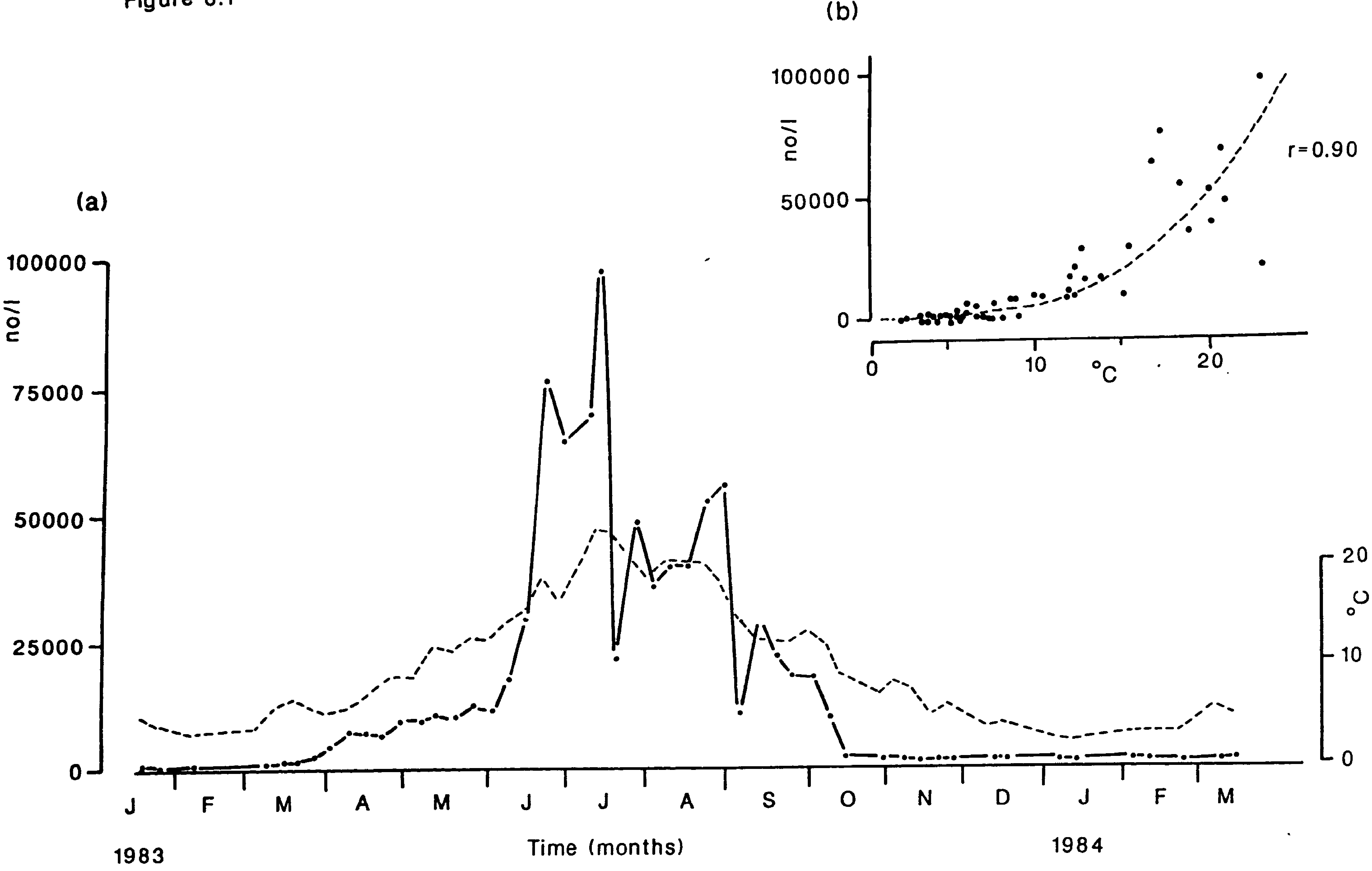
The total rotifer community over the fifteen-month study period not surprisingly showed much higher numbers during the warmer seasons. For most of the summer numbers were above 10000 l^{-1} (Fig.6.1.a), a concentration very much higher than that found in most other waters. A list of some Scandinavian lakes in Larsson (1978) reveals that in oligotrophic waters numbers rarely approach 100 l^{-1}. In eutrophic waters, numbers as high as 8000 l^{-1} have been recorded by Orcutt & Pace (1984), while Eloranta (1982) found up to 15000 l^{-1} of *Keratella cochlearis* in a warm water effluent-pond but no published values, reach those recorded in Priest Pot.

The temperature in the tarn (Fig.6.1.a) increased steadily from March onwards and during the summer reached 23.5°C before decreasing. Throughout the winter months the water temperature was rarely more than 5 °C and periods of ice cover occurred at the beginning of both years.

The temperature data and the total rotifer numbers were entered into the "curvefitter" program (Warme 1980, Interactive Microware Inc.) on an Apple IIe microcomputer

Figure 6.1. Total rotifer numbers per litre during the sampling period January 1984 to March 1984. (a) The total rotifer numbers and the mean temperature in the oxygenated part of the water column over the fifteen months of routine sampling. Rotifer numbers (——) and temperature (---). (b) Total rotifer numbers correlated with the mean temperature in the tarn showing a positive correlation significant at the 1% level.

Figure 6.1


(a)
100000
75000
50000
25000
0
no/l
20
10
0
°C
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
Time (months)
1984
(b)
100000
50000
0
no/l
0
10
20
°C
r=0.90

and the resulting geometric curve (Fig.6.1.b) showed significant correlation although scatter increased above 15°C.

Chlorophyll a equivalent measurements showed a series of maxima through the year, Fig.6.2.a, with both spring and autumn blooms. Values were lower through the summer but were still around 200 ug l^{-1} which would be considered high in many water bodies. Examination of algal samples showed that in April and September the phytoplankton was dominated by a species of Synura, a colonial chrysophyte. The large peak of chlorophyll a in May was predominantly the dinoflagellate Peridinium lomnickii. During the summer, when chlorophyll a levels in the epilimnion were quite low, the phytoplankton consisted mainly of small green algae and desmids. The succession of species in the phytoplankton found by examination of the algal samples shows that the period of maximum food availability is not necessarily coincident with the period of maximum chlorophyll a equivalent values, the size of particle present being an important factor. Using "curvefitter", the relationship between chlorophyll and total rotifer numbers was investigated (Fig.6.2.b).

The bacterial counts, Fig.6.3.a, showed high values in spring but fluctuating values during the rest of the year. The values during the summer are means of the epilimnion counts. This exclusion of the anoxic waters lowers these values considerably but it gives a more realistic estimate of the bacterial numbers available to

Figure 6.2. Chlorophyll a equivalent in ug l^{-1} during the sampling period January 1983 to March 1984. (a) Chlorophyll a equivalent in the oxygenated part of the water column over the fifteen months of routine sampling. (b) Total rotifer numbers correlated with mean chlorophyll a concentration showing a wide scatter of points .

Figure 6.2

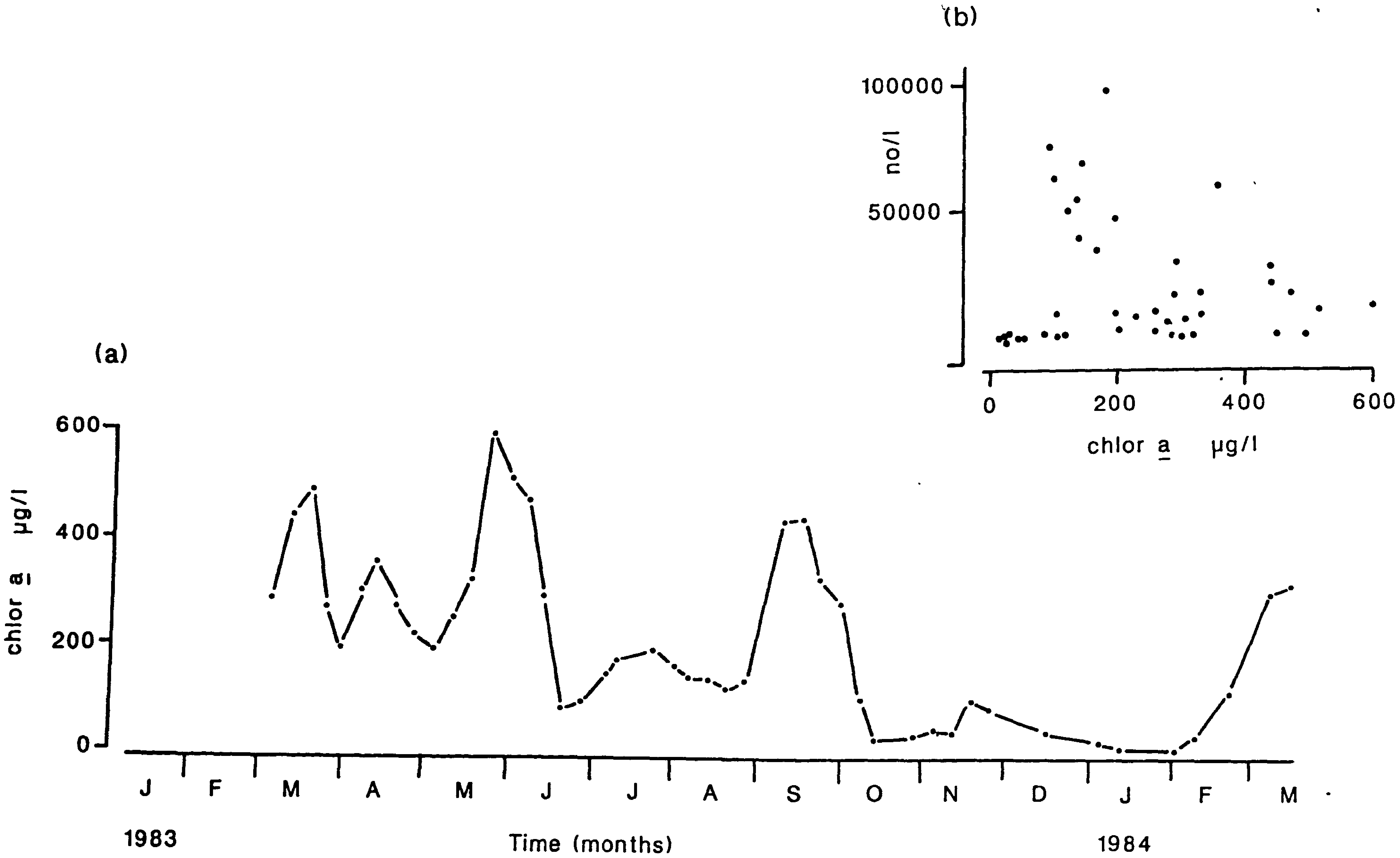
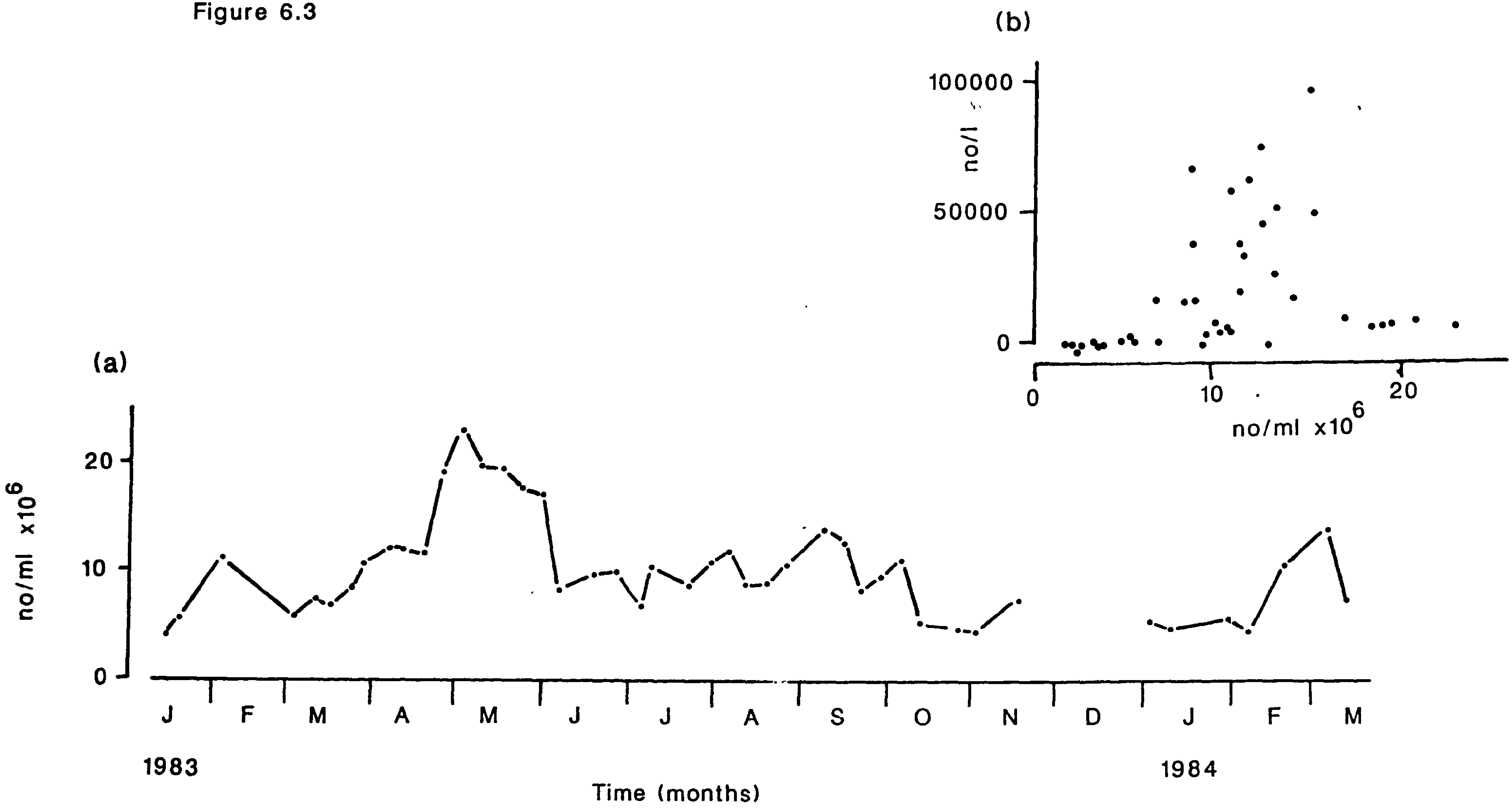

(a)
chlor a µg/l
600
400
200
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
Time (months)
1984
(b)
no/l
100000
50000
0
200
400
600
chlor a µg/l

Figure 6.3. Bacterial numbers (obtained by direct counts) as no. ml^{-1}x 10^{-6} during the sampling period January 1983 to March 1984. (a) Bacterial numbers over the fifteen months of routine sampling. (b) Total rotifer numbers correlated with bacterial numbers showing a wide scatter of points.

Figure 6.3


(a)
no/ml x10^6
0
10
20
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
1984
Time (months)
(b)
no/l
100000
50000
0
0
10
20
no/ml x10^6

the rotifers. The relationship between bacteria and rotifer numbers was investigated (Fig.6.3.b).

The temperature relationship was as expected. The relationship with chlorophyll showed that quality was more important than quantity i.e. the species of algae present was more important to the rotifers than just the concentration of chlorophyll in the tarn. The bacterial relationship may be important for some species.

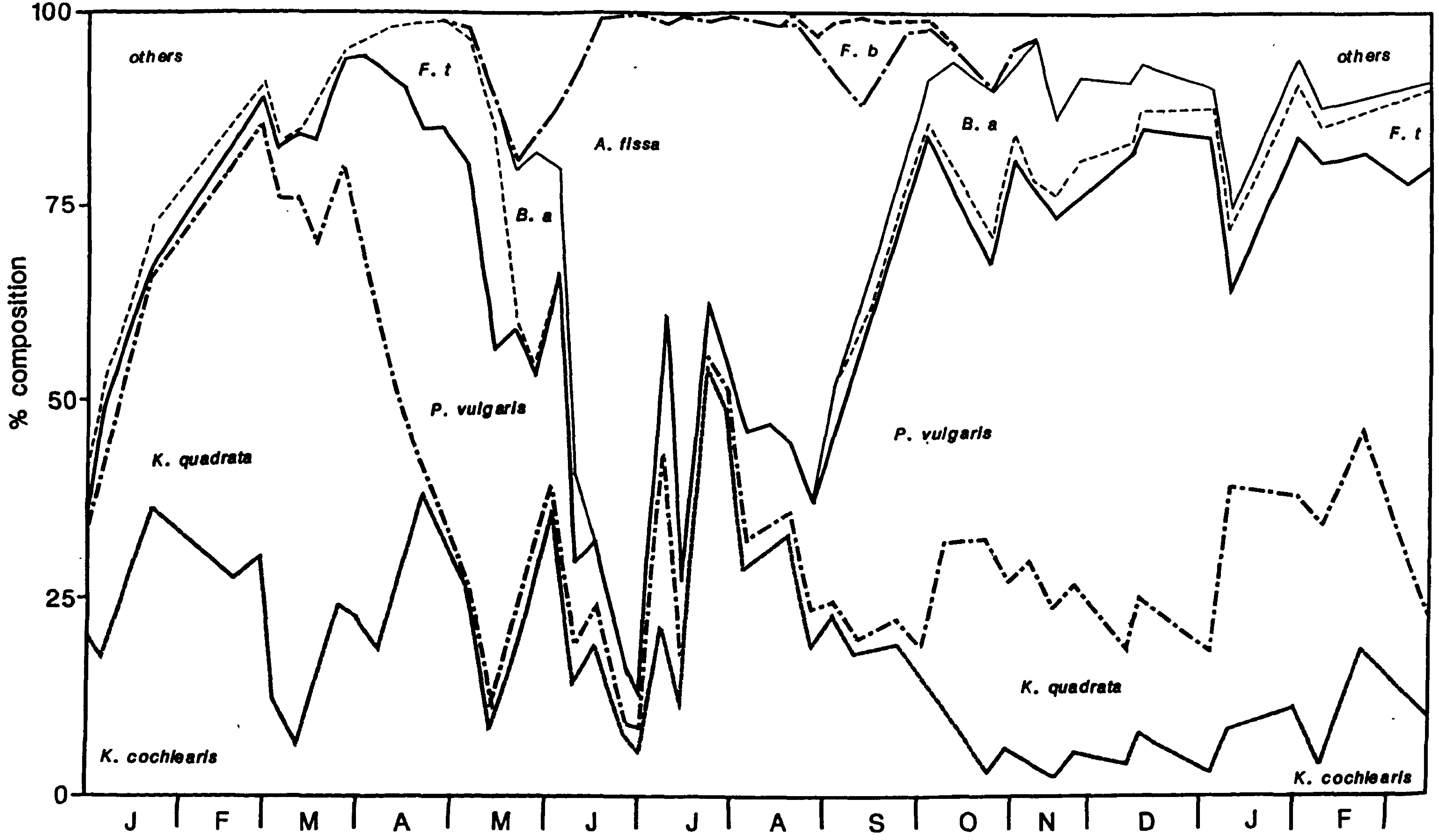
6.4 The Percentage Composition of the Zooplankton

Figure 6.4 summarizes the general pattern of seasonal succession in the rotifer community with all the population densities reduced to a proportion (%). At the start of sampling, in mid-January, the rotifer community was dominated by Synchaeta species (50%) although actual numbers were very low. In early February, Keratella quadrata and K.cochlearis increased in numbers and importance; K.quadrata was dominant in the community throughout February, March and early April. The Polyarthra vulgaris population developed in early April and replaced K.cochlearis as the dominant species. At the same time, numbers of F.terminalis increased. Throughout April and May the community was almost entirely P.vulgaris (40%), K.cochlearis (35%) and F.terminalis (10%), with the other species constituting only 5% of the total. In early June a population of B.angularis developed to become 20% of the rotifer community and K.cochlearis again increased in importance. However, by mid-June, the warm stenotherm A.fissa had appeared and

Figure 6.4. The percentage composition of the rotifer community during the fifteen month sampling period.

The category 'others' includes both Synchaeta species and the sporadic species.

Figure 6.4



F. t, *Filinia terminalis*; F. b, *Filinia brachiata*; B. a, *Brachionus angularis*.

was increasing rapidly in numbers until by late June/early July it constituted more than 80% of the rotifer community. It continued to dominate the zooplankton of the epilimnion throughout the summer until late September although, on 18 July the A.fissa population crashed to less than 40% of the community and after that was rarely more than 55% of the total rotifers. In early August a large peak of K.cochlearis made up more than 50% of the community but this was the only time during the fifteen month sampling period that it was the major species although it was frequently a co-dominant. Howevever, unlike most other species, it rarely fell below 5% and was usually more than 10% of the rotifer community. F.brachiata, a species usually found as rare or sporadic, occurred in late summer in numbers high enough to make it up to 10% of the total community. From late September onwards, P.vulgaris dominated the rotifers, usually being more than half the community. B.angularis had a second period of population development from October to January, F.terminalis also became a significant percentage of the community again in the autumn and continued to be present throughout the winter months, a seasonal distribution typical of a cold stenotherm. K.quadrata constituted more than 10% of the rotifers throughout the winter months. It appears that the two species of Keratella alternated dominance; K.quadrata was often dominant during the cooler periods of the year while K.cochlearis was most important from May to October. Synchaeta increased in importance in the autumn and constituted around 10% of the rotifers throughout the winter of 1983/84.

6.5 Details of the Seasonal Occurrence of Rotifer Species in Priest Pot

6.5.1 Definition of successional categories

The rotifers in the tarn were found to fall into three categories : perennial species, spring and autumn species and summer to autumn species. Table 6.1 shows this division and the temperatures between which the populations occur. Most species showed a decline in numbers when the surface temperature reached 23.5°C and the temperature in the epilimnion was more than 22°C. There were very low numbers of rotifers below 6°C.

The population densities of the rotifer species throughout the fifteen month study are shown in Figures 6.5 to 6.8.

6.5.2 Perennial Species

Some species had very wide temperature tolerances and occurred throughout the year, with low numbers during the winter followed by a series of peaks from mid-spring onwards.

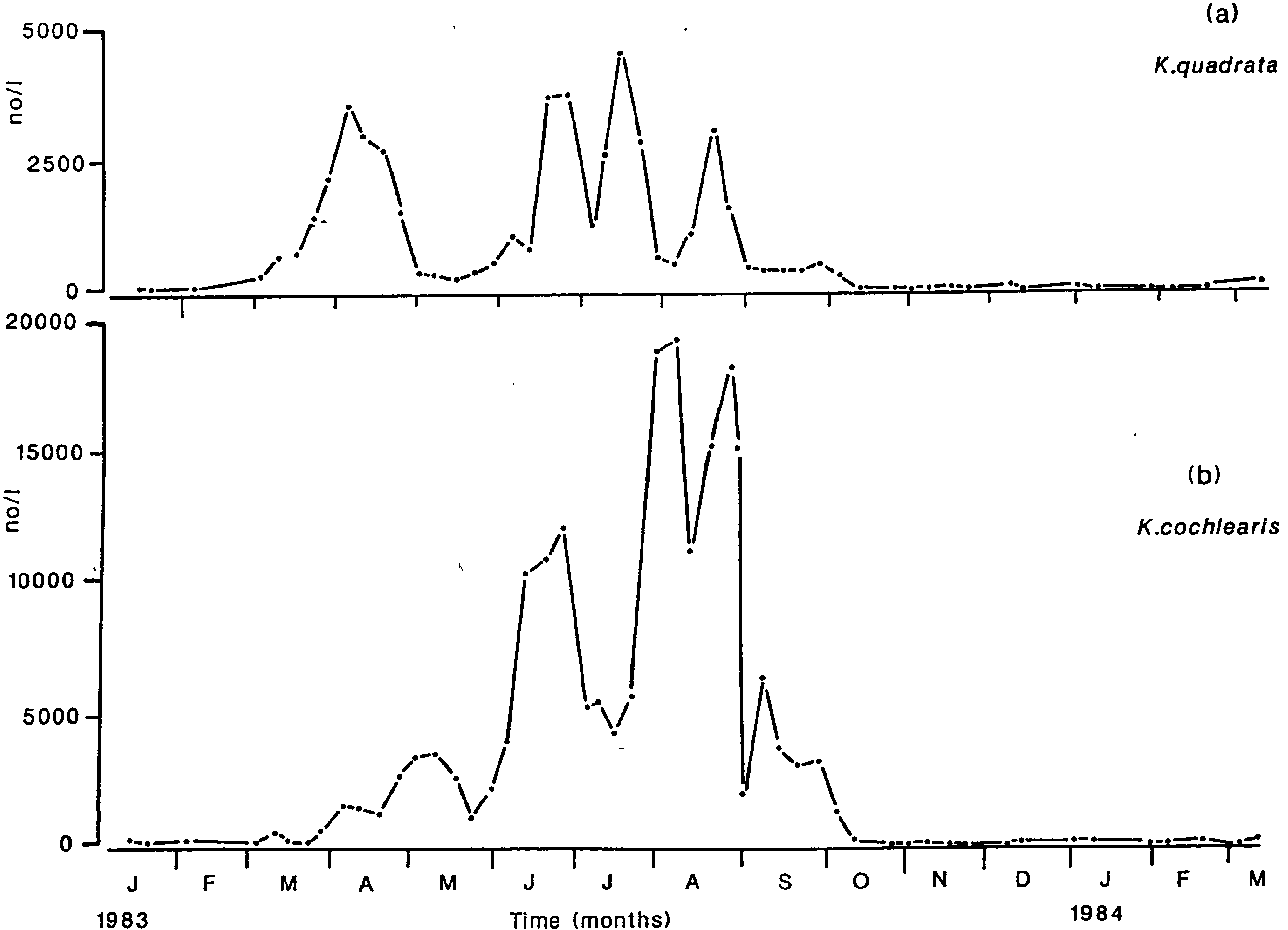
K.quadrata, Fig.6.5.a, was the first to reach a peak, with densities up to 3000 l^{-1} in late March/early April. This was followed by peaks in May of both K.cochlearis (Fig.6.5.b) and P.vulgaris (Fig.6.6.a) of 3500 l^{-1} and 500 l^{-1} respectively. During the summer, all three species showed a series of peaks although K.cochlearis was the most abundant, with almost 20000 l^{-1} in August. P.vulgaris had smaller peaks in July and August after a

Table 6.1 The division of the Priest Pot rotifer population according to their seasonal abundance.

Species	Months of greatest abundance	Temperature range (°C)
Perennial		
K. cochlearis	April - September	3 - 24
K. quadrata	February - September	3 - 24
P. vulgaris	March - September	3 - 24
S. kitina	-	3 - 24
S. pectinata	-	3 - 21
Spring/Autumn		
B. calyciflorus	April - May	9 - 16
B. angularis	April - May, September	9 - 16
F. terminalis	April - May, September	3 - 16
Summer/Autumn		
A. fissa	May - August	9 - 24
F. brachiata	June - September	9 - 21

Figure 6.5. The seasonal abundance of the planktonic rotifers in Priest Pot from January 1983 to March 1984. (a) *Keratella quadrata* and (b) *Keratella cochlearis*.

Figure 6.5


(a)
K.quadrata
5000
2500
0
no/l
(b)
K.cochlearis
20000
15000
10000
5000
0
no/l
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
Time (months)
1984

maximum of 8000 l^{-1} in June. In late September its numbers increased again to form an autumn maximum before decreasing to low winter levels. During the summer, *K.quadrata* fluctuated between 500 and 4500 l^{-1}. All three species had declined to below 200 l^{-1} by the end of October but remained present in the plankton throughout the winter.

The two species of *Synchaeta* were also perennial (Fig.6.6.b and 6.6.c), but were at much lower densities, less than 1000 l^{-1}, with small maxima in spring and summer.

6.5.3 Spring and Autumn Species

Other species seemed to be inhibited by the low temperatures and did not start to increase in numbers until May when the temperature rose above 10°C. *Brachionus angularis*, Fig.6.7.a, increased to a maximum of almost 5000 l^{-1} in late May-early June then rapidly decreased to very low numbers through the summer until a second, much smaller peak in October. *Brachionus calyciflorus*, Fig.6.7.b, also increased to a maximum of 2700 l^{-1} at this time but was then at very low numbers or of only sporadic occurrence for the rest of the year.

A third species, *Filinia terminalis*, did not start to increase in numbers until late April but then rapidly rose to a first peak in late May, Fig.6.7.c. A second peak (8000 l^{-1}) in June was followed by a decline.Only sporadic occurrences were found through the summer until a slight recovery to 200 l^{-1} in October.

Figure 6.6. The seasonal abundance of the planktonic rotifers in Priest Pot from January 1983 to March 1984. (continued). (a) *Polyarthra vulgaris*, (b) *Synchaeta kitina* and (c) *Synchaeta pectinata*.

Figure 6.6

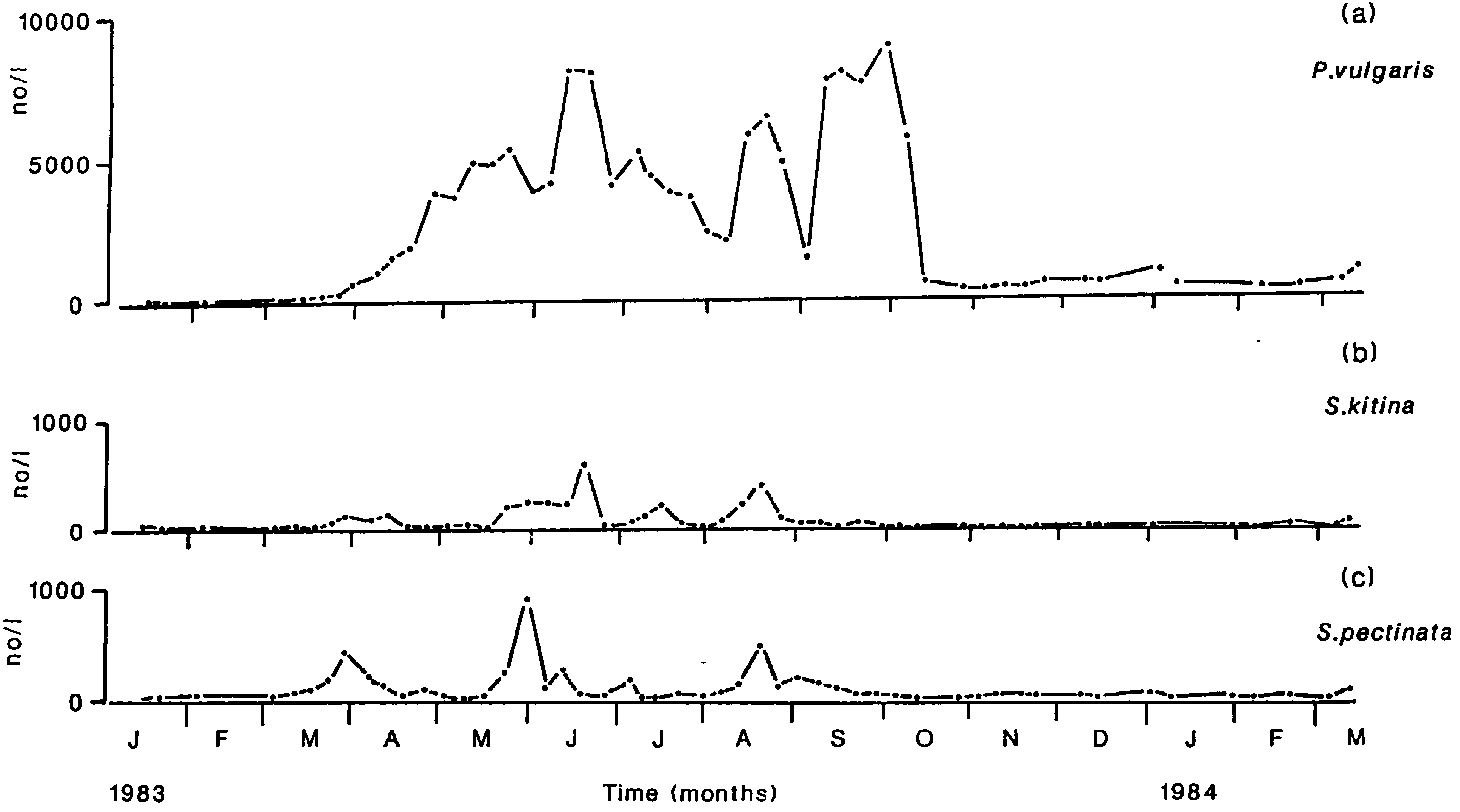
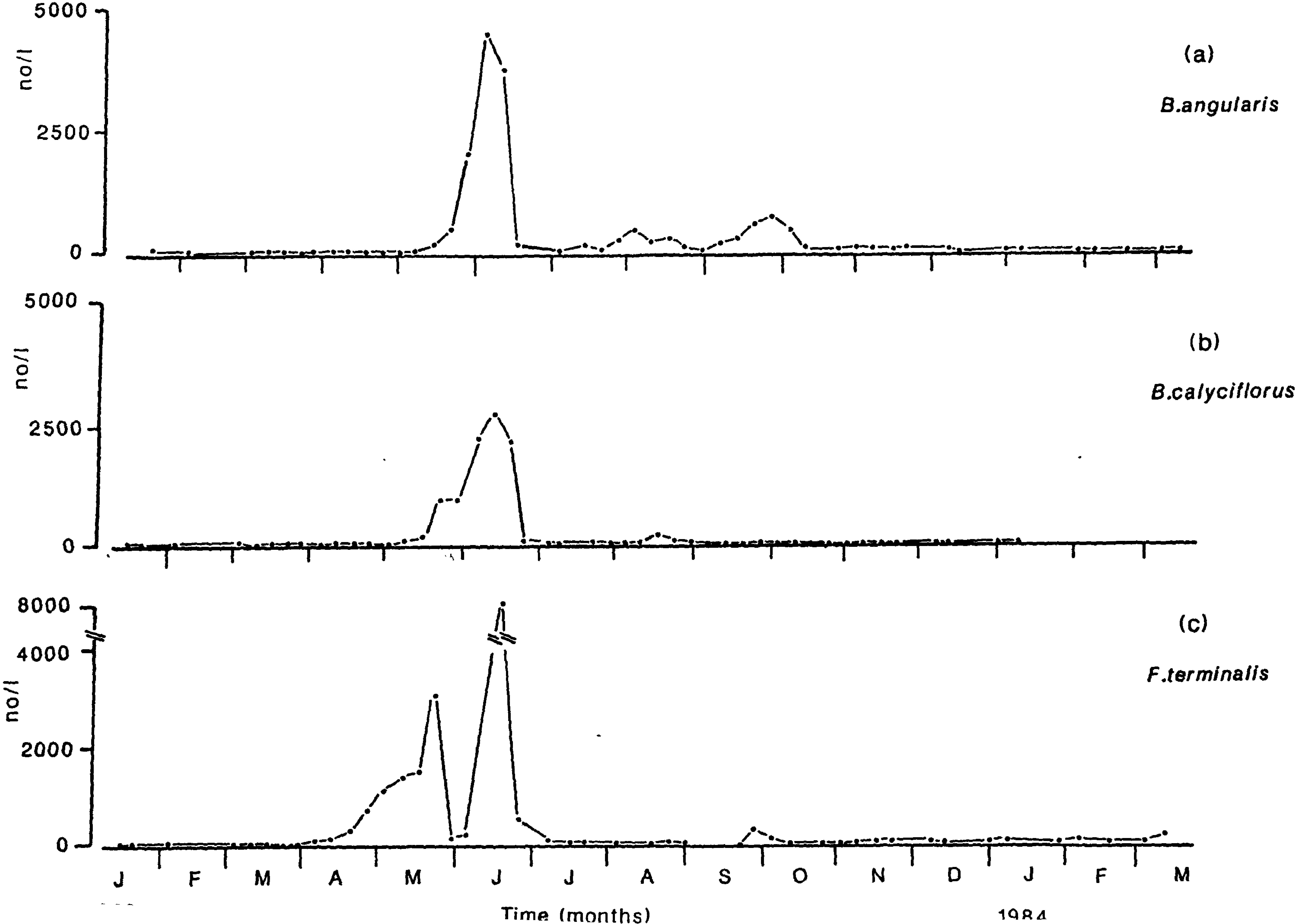

(a)
P.vulgaris
10000
5000
0
no/l
(b)
S.kitina
1000
0
no/l
(c)
S.pectinata
1000
0
no/l
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
Time (months)
1984

Figure 6.7. The seasonal abundance of the planktonic rotifers in Priest Pot from January 1983 to March 1984 (continued). (a) *Brachionus angularis*, (b) *Brachionus calyciflorus* and (c) *Filinia terminalis*.

Figure 6.7


5000
2500
0
no/l
(a)
B.angularis
5000
2500
0
no/l
(b)
B.calyciflorus
8000
4000
2000
0
no/l
(c)
F.terminalis
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
Time (months)
1984

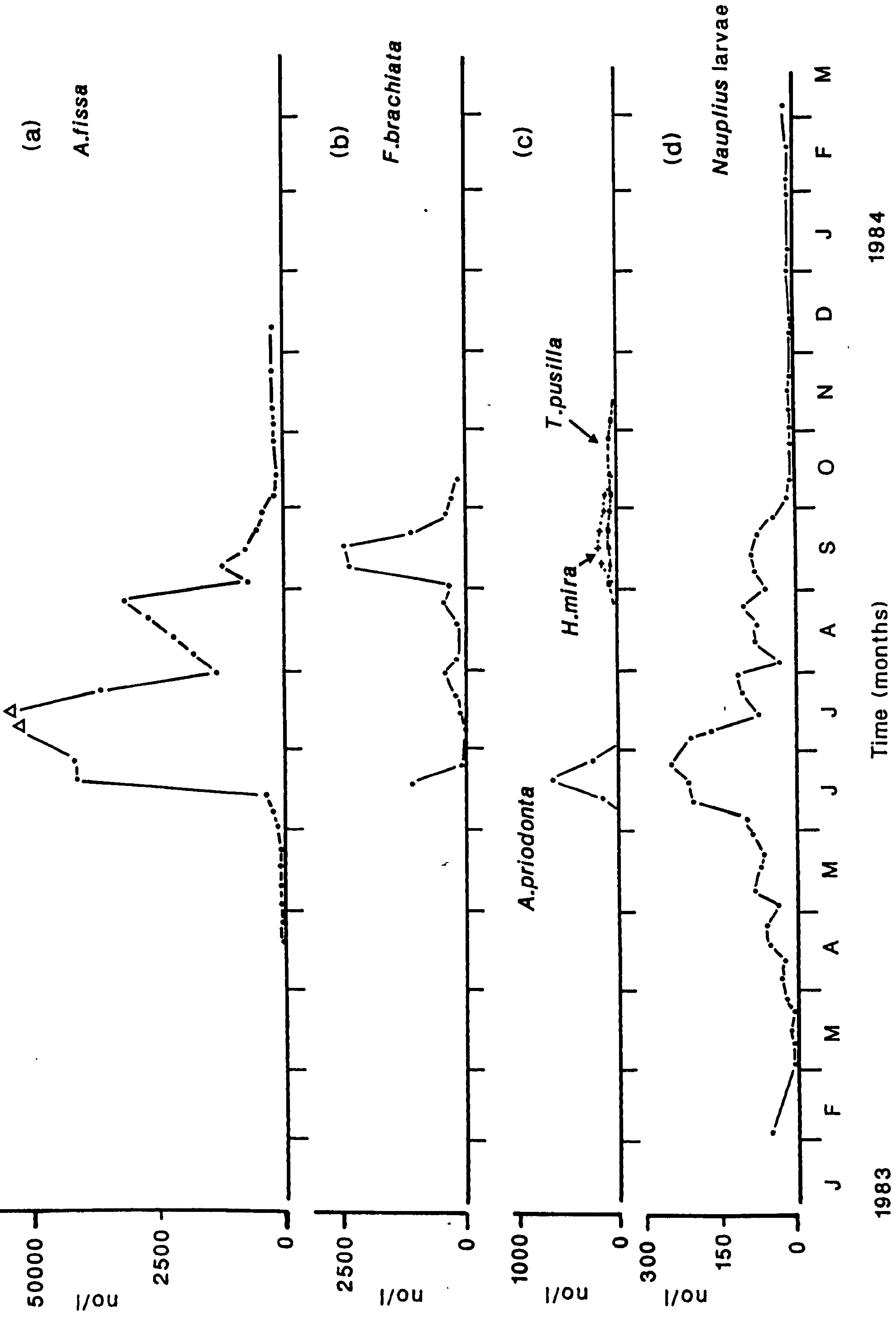
6.5.4 Summer to Autumn Species

The two most abundant summer-autumn species, A.fissa and Filinia brachiata, did not appear until the water was warmer. The former, Fig.6.8.a, appeared in mid-April when the temperature rose above 8 °C but did not reach high densities until the temperature had reached 12°C at the end of May. It then remained at high levels, up to 100000 l^{-1}, through the summer, recovering back to high levels in August after a sudden drop during the hottest week of July. After September, numbers declined as the temperature fell below 12°C and by mid-November it was absent. F.brachiata, Fig.6.8.b, had only a brief appearance in June followed by a large population after the temperature had reached 18°C. The density increased to a peak in mid-September of 2200 l^{-1} before disappearing from the plankton at the end of October.

The three other summer-autumn species, Fig.6.8.c, were much lower in numbers. Asplanchna priodonta appeared, reached a density of 600 l^{-1} and disappeared again in the course of four weeks in late June-early July. This coincided with peaks of K.cochlearis, K.quadrata and P.vulgaris. Hexarthra mira occurred sporadically during the autumn with never more than 10 l^{-1} and a species of Trichocerca, probably T.pusilla, occurred after mixing at densities up to 100 l^{-1} until mid-October.

Figure 6.8. The seasonal abundance of the planktonic rotifers in Priest Pot from January 1983 to March 1984 (continued). (a) *Anuraeopsis fissa*, (b) *Filinia brachiata*, (c) *Asplanchna priodonta*, *Hexarthra mira* and *Trichocerca pusilla* and (d) *Nauplius larvae*.

Figure 6.8



(a)
A.fissa
50000
2500
0
no/l
(b)
F.brachiata
2500
0
no/l
(c)
A.priodonta
H.mira
T.pusilla
1000
0
no/l
(d)
Nauplius larvae
300
150
0
no/l
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1983
1984
Time (months)

6.5.5 Nauplius Larvae

The only crustaceans found in the zooplankton , apart from sporadic findings of copepodites, were nauplius larvae which were not identified further, Fig.6.8.d. They had a fluctuating population with peaks up to 100 l^{-1} for six months, from April to October, and a maximum of 230 l^{-1} in late June.

6.6 Discussion

The changes in abundance found in the rotifers of Priest Pot are similar to those already recorded in the literature but many species show variation in their times of maximum density compared to those previously published.

K.quadrata in most studies is found in highest numbers in the spring (Einsle, 1967; Ferrari & Rossi, 1976; Eloranta, 1982) or spring and autumn (Baker, 1979; Herzig, 1979; Pennak, 1949), but summer peaks have been found by Nauwerck (1963), Moore (1980) and Bosselmann (1981). In Priest Pot the population had peak numbers in all three seasons.

Pejler (1957 b) called *K.cochlearis* a eurytherm but George & Fernando (1969) found it to be a cold water stenotherm. In Priest Pot it is the former with population peaks coinciding with algal and bacterial population maxima in spring and its highest numbers found in August 1983 with smaller peaks in June and September. This is a similar distribution to those found by Lozeron (1902), Nauwerck (1963), Bosselmann (1979) and Moore (1980). However *K.cochlearis* is a very widespread species and many other studies have found quite different times of maximum density.

Ruttner-Kolisko (1974) describes *P.vulgaris* as eurythermous and in Priest Pot it behaves as a eurytherm, having a series of peaks throughout the year with high numbers from March to October. In the literature it has been found with maxima in summer by George & Fernando (1969), Duffy & Liston (1978), Larsson (1978) and Moore (1980), in spring by Michael (1968) and Adalsteinsson (1979), in autumn by Stemberger (1974) and Orcutt & Pace (1984) and in a combination of these by Einsle (1967), Ferrari & Rossi (1976), Ruttner-Kolisko (1977) and Herzig (1979). The species appears to have tolerance to a wide range of temperatures and the variations in the times of its population maxima in the different lakes are probably caused by another factor, such as food availability.

The *Synchaeta* species were both most abundant in spring and early summer, a finding similar to those of Nauwerck (1963) and Doohan (1973). Pejler (1963) has also described them as eurythermal.

The spring-summer forms *B.angularis*, *B.calyciflorus* and *F.terminalis* show changes in abundance similar to those already recorded in the literature. *B.angularis* has usually been found at maximum numbers in the spring (Pourriot, 1965; Michael, 1968; Cowell *et al*., 1975; Eloranta,1982) but Herzig (1979) found it in summer and autumn in Neusiedlersee.The spring peak of *B.calyciflorus* found in Priest Pot was similar to those found by Cowell *et al*. (1975), Herzig (1979) and Pourriot *et al*. (1982).

However it did not show the autumn peak found by Pennak (1949) and Pourriot (1965).

F.terminalis has been described as a cold water stenotherm (Pejler, 1957 a) and in Priest Pot it is sporadic above 12°C. In some lakes it has population peaks in spring before disappearing from the plankton (Pejler, 1961; Nauwerck, 1963; Pourriot, 1965; Herzig, 1979; Kasprzak & Ronneberger, 1982) but other workers have shown that as the epilimnion warms up in spring the F.terminalis moves down in the water column and remains in the cooler hypolimnion throughout the summer (George & Fernando, 1969; Larsson, 1971; Ruttner-Kolisko, 1980; Hofmann 1982). The occurrence of similar behaviour will be discussed in the following chapter. An autumn peak by this species was found by Elliott (1977) and Ruttner-Kolisko (1977) but was not found in Priest Pot.

The summer-autumn forms include two species which only occurred at very low numbers, Trichocerca sp. and H.mira. A.priodonta only appeared in the samples for four weeks in June. Previous work has frequently shown their maximum abundance in summer (Pejler, 1961; Granberg, 1970; Herzig, 1979; Burns & Mitchell, 1980) although other investigations have found autumn peaks (Nauwerck, 1963; Pourriot, 1965; Hakkari, 1969) and spring peaks (Pennak, 1944; Doohan, 1973). Adalsteinsson (1979) found it at maximum numbers when the other rotifers reached a peak and in Priest Pot the peak of Asplanchna coincided with that of total rotifers.

A.fissa is usually described as a warm water stenotherm, all the other species in the genus are tropical. In Priest Pot it occurred throughout the summer and autumn, a similar finding to those of Pourriot (1965) and of Orcutt & Pace (1984). Other studies have found it to have peaks in spring and autumn (Michael, 1968; Cowell *et al.*, 1975; Eloranta, 1982) and Pejler (1957 b) found it under ice in Northern Swedish Lapland.

F.brachiata appeared in Priest Pot when the water was at its warmest but persisted until October when the temperature fell below 10°C. There is little literature on this species but Ruttner-Kolisko (1974) describes it as a warm water stenotherm. It may be that the resting eggs of this species require warm conditions for hatching but that the adult rotifers can survive in a wider range of temperatures.

CHAPTER SEVEN

The Vertical Distribution of the Planktonic Rotifers in Priest Pot

7.1 Introduction

A number of studies have shown that rotifer populations have a wide variety of vertical distributions; some species are clearly epilimnetic while others are characteristic of deeper waters. In the sheltered waters of Priest Pot many species of rotifers are able to aggregate in the water column, both when the tarn is isothermal and when it is stratified. In this chapter the data from the routine samples are discussed with reference to the vertical distribution of the rotifers.

7.2 Treatment of the Data

The data obtained during 1983 and 1984 were entered into the MICRORIM data base package (MICRORIM Inc., Bellevue, Washington, U.S.A.) for sorting, then transferred to the NERC Honeywell main frame computer at Bidston for plotting depth/time isopleth diagrams. The Surface II graphics system, designed for geological contouring, was used to obtain depth/time contours for each rotifer species and for selected environmental variables. Some of these figures have already appeared in the site description in Chapter Two, namely the oxygen (mg/l), temperature (C), chlorophyll *a* equivalent (mg/l) and bacteria (direct counts; no/ml). Two isopleth diagrams are also provided as transparent overlays : one shows the temperature structure and the other shows the vertical distribution of chlorophyll. Both include a stippled area showing the extent of the anoxic water. These can be used with each species isopleth diagram to show responses to thermal conditions, anoxia and food availability.

To simplify analysis, the mean depth of each species was calculated using the weighted expression :

$$\bar{D} = \sum_{i}^{tot} D_i \, N_i^2 / \sum_{i}^{tot} N_i^2$$

where D_i is the depth of the ith sample and N_i the concentration of animals at that depth. Variations in the mean depth (D) of a population can often demonstrate the way in which that population tends to concentrate at a particular depth. If a population is homogeneously distributed in the water column its mean depth will equal the mean depth of the sampling units (S). If the animals concentrate at a particular depth then their mean depth will differ from the value of S. When the tarn was isothermal, the value of S was constant at 1.8 m, however during stratification the depth of the oxycline fluctuated so a range of S values was obtained for this period. D values were calculated for each sampling date for each species. To summarize general trends, frequency diagrams of mean depths were then plotted for the isothermal and stratified periods separately. The overall mean depths for each species and the values of S were also marked on the diagrams to illustrate the variation of the distributions.

Histograms were also plotted for both temperature at D and for light intensity at D for each species showing the frequency of different values. The D values for each species were also compared to the D value of the chlorophyll distribution and with the depth of the oxycline.

7.3 The Vertical Distribution of each Rotifer Species found in Priest Pot

7.3.1 *Keratella cochlearis* (Fig.7.1)

When the tarn was isothermal *K.cochlearis* was often homogeneously distributed in the water column (Fig.7.2.a). However, its distribution was stratified in both February and March when the population was increasing from the low winter levels. The numbers first increased in the bottom metre of the water column (Fig.7.2.b) before the population became more evenly distributed. In both spring and autumn there were algal blooms and at these times *K.cochlearis* showed stratified distributions even though the water column was isothermal. Its distribution showed maxima which coincided with the vertical distribution of the chlorophyll *a* in both May (Fig.7.2.c) and September (Fig.7.2.d). During the remainder of the period when the tarn was isothermal the population showed little aggregation.

Once the tarn had become stratified however, this species was frequently found concentrated just above the oxycline (Fig.7.2.e) and their vertical distribution always showed some aggregation. This increase in numbers

Figure 7.1. Isopleth diagram showing the vertical distribution of *Keratella cochlearis* in Priest Pot from January 1983 to March 1984.

Figure 7.1 *Keratella cochlearis*

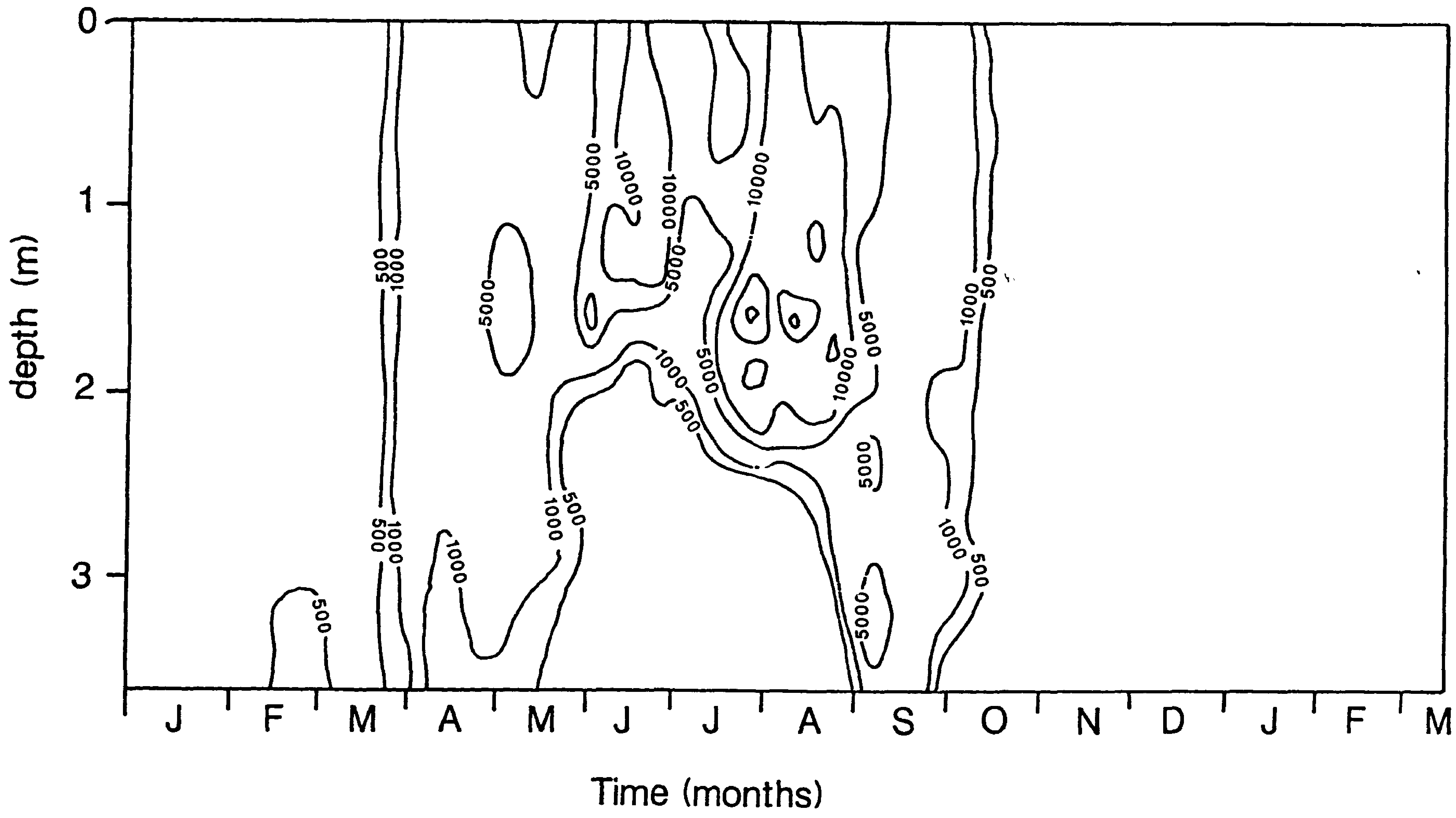
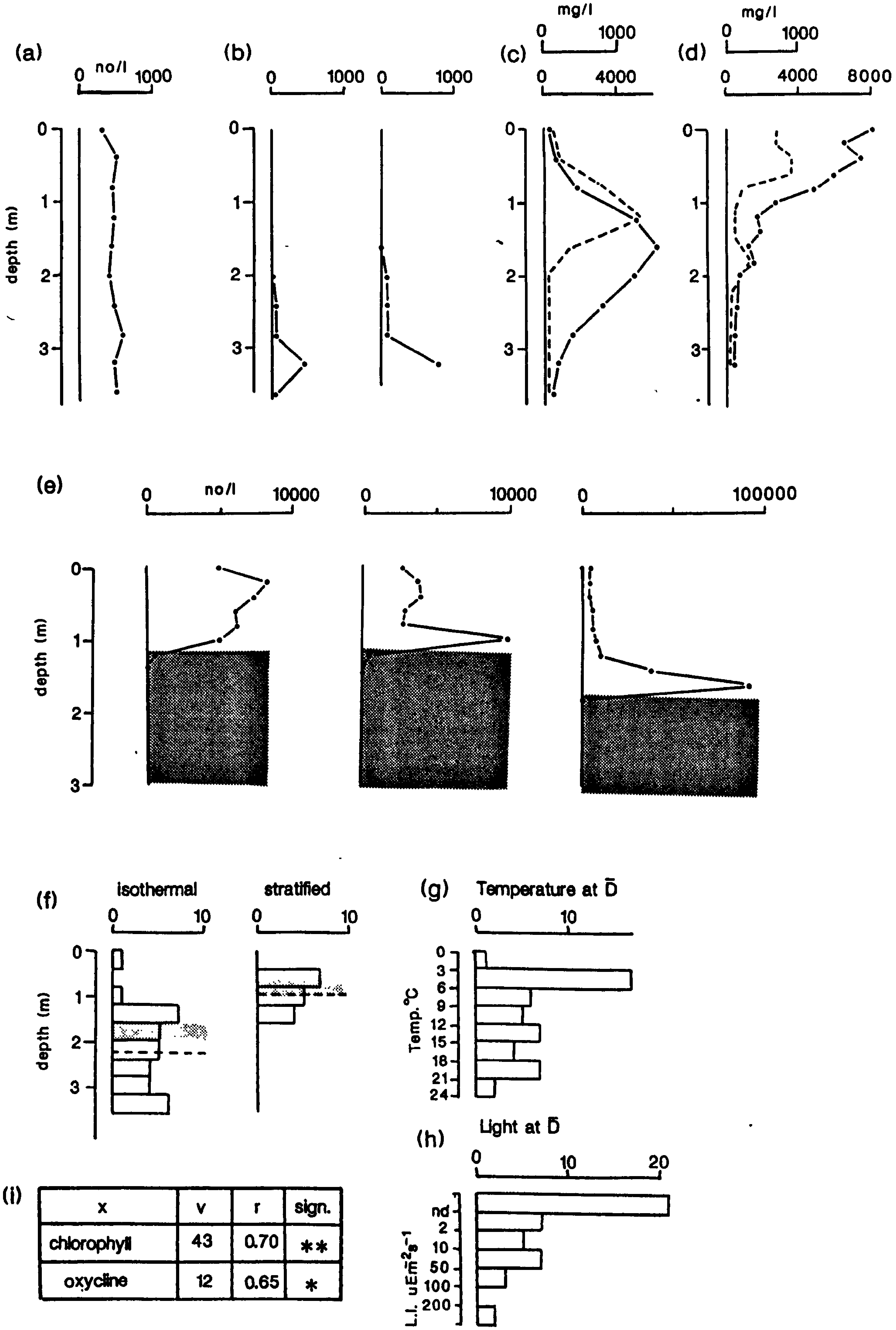


Figure 7.2. The vertical distribution of Keratella cochlearis. (a) A homogeneous distribution during isothermal conditions, (b) the initial distribution of K.cochlearis in early March showing highest numbers in deep water, (c) and (d) peaks of K.cochlearis in high chlorophyll a concentrations (---) during isothermal conditions, (e) during stratified conditions K.cochlearis frequently had large peaks near the oxycline, (f) Histogram showing distribution of the mean depths of K.cochlearis in both isothermal and stratified conditions. The broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (g) histogram of distribution of the temperatures at the mean depths for K.cochlearis indicating the range of temperatures tolerated by this species, (h) histogram of distribution of light intensities measured at the mean depths for K.cochlearis and (i) table showing the results of correlations between mean depth of chlorophyll and mean depth of the rotifers and depth of oxycline and mean depth of the rotifers.

Figure 7.2 *Keratella cochlearis*



(i)

x	v	r	sign.
chlorophyll	43	0.70	**
oxycline	12	0.65	*

just above the oxycline may be linked to food availability since this species is known to feed on bacteria (Pourriot, 1977).

Figure 7.2.f shows the frequency histograms for the D values during the time when the tarn was isothermal and during stratification. The water column was divided into nine depth ranges from 0 m to 3.6 m, the number of D values in each range noted and plotted on the histograms as shown. The overall mean depth is indicated by a broken line and the range of S values shown as a stippled area (where S is the mean depth of the sampling units and thus the expected mean depth for a homogeneously distributed population).

When the tarn was isothermal the overall mean depth of the population was 2.25 m and most individual D values were below 1.0 m depth. During the stratified period the mean depths were higher, around 1 m , with an overall mean of 0.97 m. The frequency distribution of temperatures at the mean depth illustrates the wide range of temperatures tolerated by this species and supports its description as a eurytherm, (Fig.7.2.g). Almost half of the mean depths were at undetectable light intensities (Fig.7.2.h) and this data indicates an avoidance by the rotifers of high light levels (> 200 uE m^{-2} s^{-1}). The mean depths of K.cochlearis were related to both the distribution of the chlorophyll and the position of the oxycline, the correlations being significant at the 1% and at the 5% levels respectively (Fig.7.2.i).

In Priest Pot, K.cochlearis was often concentrated near the oxycline during the summer but at other times, when the tarn was isothermal, it was homogeneously distributed. Exceptions occurred when the chlorophyll distribution was stratified and when the population first increased in the spring.

Concentrations of K.cochlearis at low oxygen levels have been described by Axelson (1961), Ruttner-Kolisko (1977) and Miracle & Vicente (1983) although Einsle (1967) always found low numbers in the samples nearest the oxycline. Stemberger (1974) and Stemberger et al. (1979), in Lakes Michigan and Huron respectively, found K.cochlearis concentrated in the metalimnion and at the base of the epilimnion during stratification. In isothermal conditions distributions are described that vary from homogeneous in a warm water effluent pond (Eloranta, 1982) to peaks occurring at various depths from week to week (Larsson, 1971; Elliott, 1977; Duffy & Liston, 1978; Bosselmann, 1979). A correlation between K.cochlearis and densities of Cryptomonas sp. was found by Granberg (1970) and Nauwerck (1963) linked the rotifers' distribution to the presence of chrysomonads. These results, added to those obtained in Priest Pot show both oxygen and chlorophyll to be important factors in determining the vertical stratification of the population.

7.3.2 Keratella quadrata (Fig.7.3)

When the tarn was isothermal, K.quadrata was homogeneously distributed in the water column on many of the sampling occasions (Fig.7.4.a). However, in March

Figure 7.3. Isopleth diagrams showing the vertical distribution of _Keratella quadrata_ in Priest Pot from January 1983 to March 1984.

Figure 7.3 *Keratella quadrata*

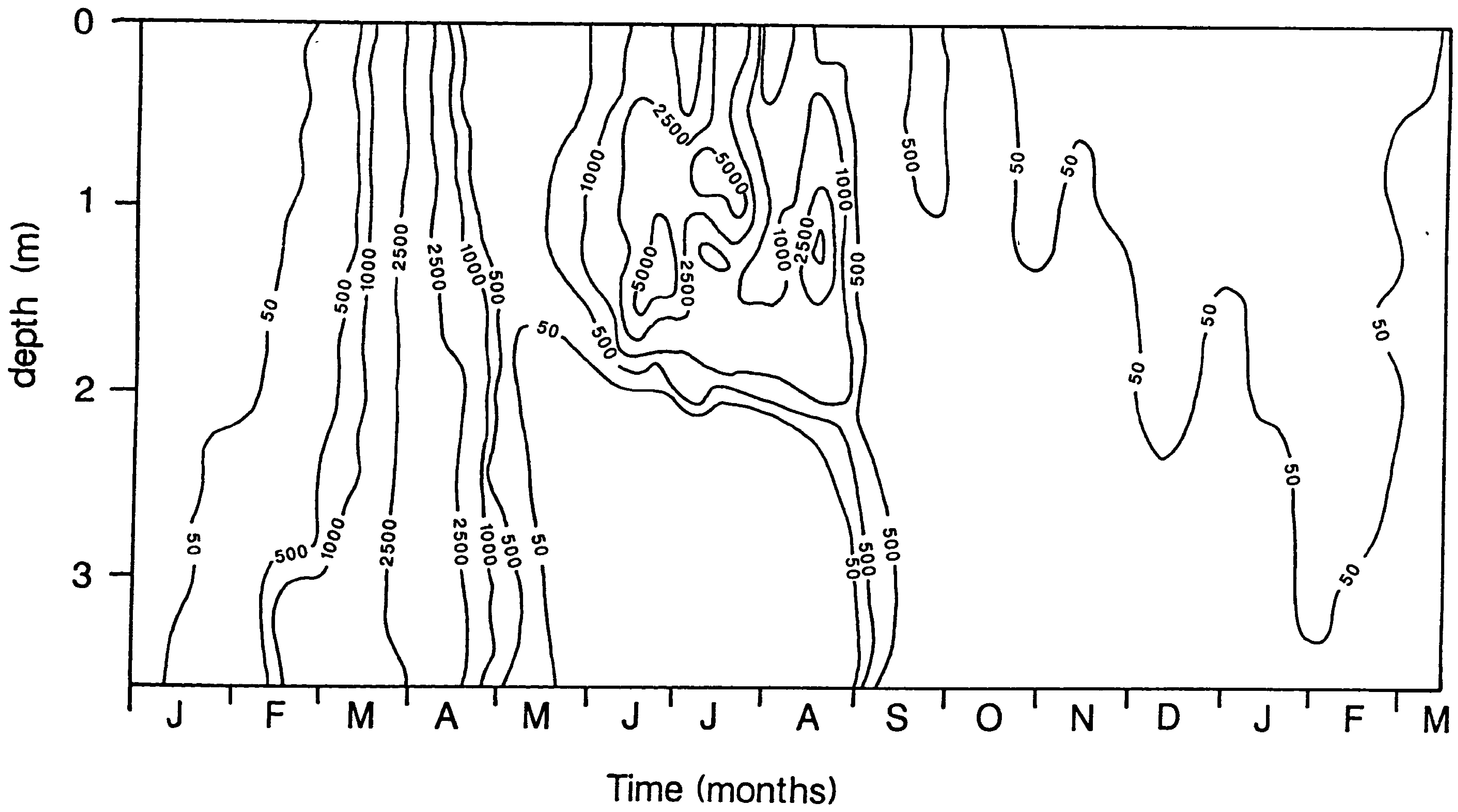
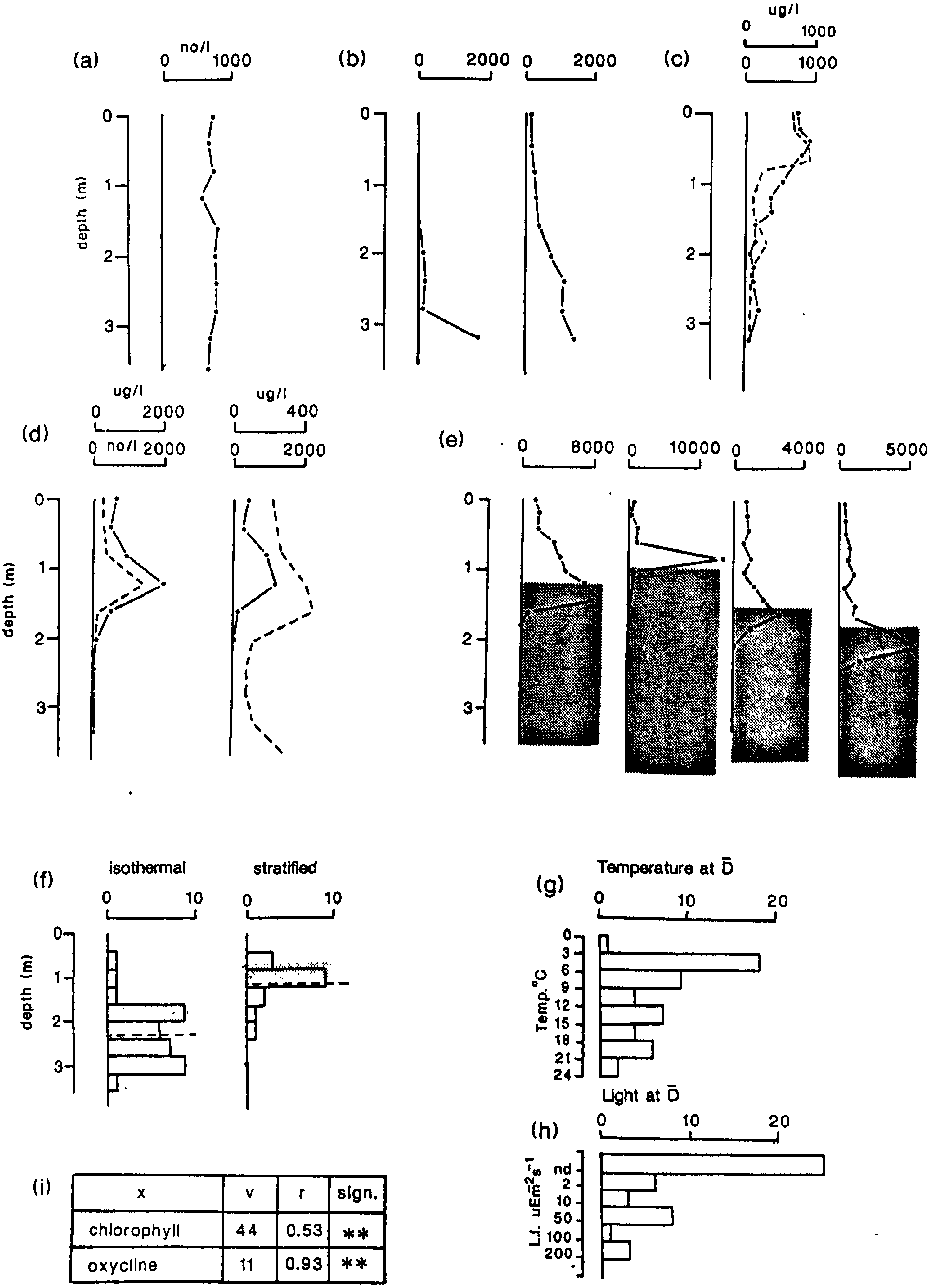


Figure 7.4. The vertical distribution of *Keratella quadrata*. (a) Homogeneous distribution during isothermal conditions, (b) the initial distribution of *K.quadrata* in early March showing highest numbers in deepest waters, (c) a peak of *K.quadrata* developed coincident with high chlorophyll *a* concentrations (---) during isothermal conditions, (d) peaks of *K.quadrata* coincident with high chlorophyll *a* concentrations during stratified conditions, (e) *K.quadrata* showed highest numbers near the oxycline during stratified conditions, the profiles for four dates in the summer are shown, (f) histogram showing distribution of the mean depths of *K.quadrata* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (g) histogram of distribution of the temperatures at the mean depths of *K.quadrata*, indicating the range of temperatures tolerated by this species, (h) histogram of distribution of the light intensities measured at the mean depths for *K.quadrata* and (i) table showing the results of the correlations: mean depth of chlorophyll *a* against mean depth of *K.quadrata* and depth of the oxycline against mean depth of *K.quadrata*.

Figure 7.4 *Keratella quadrata*



(i)

x	v	r	sign.
chlorophyll	44	0.53	**
oxycline	11	0.93	**

when the population was increasing from the low winter levels, its distribution was stratified. The numbers first increased in the bottom metre of the water column (Fig.7.4.b) before becoming more evenly distributed. The distribution of the K.quadrata population showed maxima which coincided with the vertical distribution of the chlorophyll a in both isothermal conditions (Fig.7.4.c) and in the stratified water column (Fig.7.4.d). When the tarn became stratified the animals became confined to the epilimnion. The isopleth diagram (Fig.7.3) shows a series of maxima in the epilimnion between 1 m and 2 m through the summer with lower values near the surface and Figure 7.4.e illustrates the position of these maxima in relation to the oxycline on four dates during the summer.

When the tarn was isothermal the overall mean depth of the population was 2.34 m and almost all the individual D values were below 1.4 m. During the stratified period the overall mean rose to 1.15 m, one of the deepest overall mean depths shown by the rotifers in Priest Pot (Fig.7.4.f). The temperatures at the D (Fig.7.4.g) showed, as with K.cochlearis, the wide range of temperature tolerated by this eurythermal species and over half the mean depths were again in undetectable light (Fig.7.4.h). The correlation of D with the D of chlorophyll showed a positive relationship with significance at the 1% level, indicating either the importance of food in determining the species' vertical distribution or a common response to the light stimulus. The depth of the oxycline, however, seemed to be a more important factor, with a correlation significant at the 0.1% level (Fig.7.4.i).

K.quadrata in Priest Pot tended to be homogeneously distributed in the water column during isothermal periods but was concentrated in the deeper strata of the epilimnion when the tarn was stratified. The vertical distribution of the animals was closely related to the movements of the oxycline.

Elliott (1977) found K.quadrata in higher numbers in the lower strata of Grasmere in the English Lake District, Stemberger (1974) found them in a peak at the metalimnion of Lake Michigan and in the Laguna de la Cruz Miracle & Vicente (1983) described a distribution both in the mixolimnion and at the chemocline. Three other studies showed peaks nearer the surface; Kosicki (1960), Nauwerck (1963) and Einsle (1967), but these were transitory and were either followed by extinction or by unform distributions. No studies have previously linked their distribution with chlorophyll levels although in Priest Pot they were clearly an important factor in determining the distribution of the population.

7.3.3 Brachionus calyciflorus (Fig.7.5)

B.calyciflorus was only abundant for a short period in May and June.It appeared in early May in the surface metre of the tarn even though the water at this time was isothermal (Fig.7.6.a). It was subsequently confined to the epilimnion as the tarn stratified in late May, three weeks after this species′ appearance (Fig.7.6.b). Its distribution showed maxima around one metre which at

Figure 7.5. Isopleth diagram showing the vertical distribution of Brachionus calyciflorus in Priest Pot from January 1983 to March 1984.

Figure 7.5 *Brachionus calyciflorus*

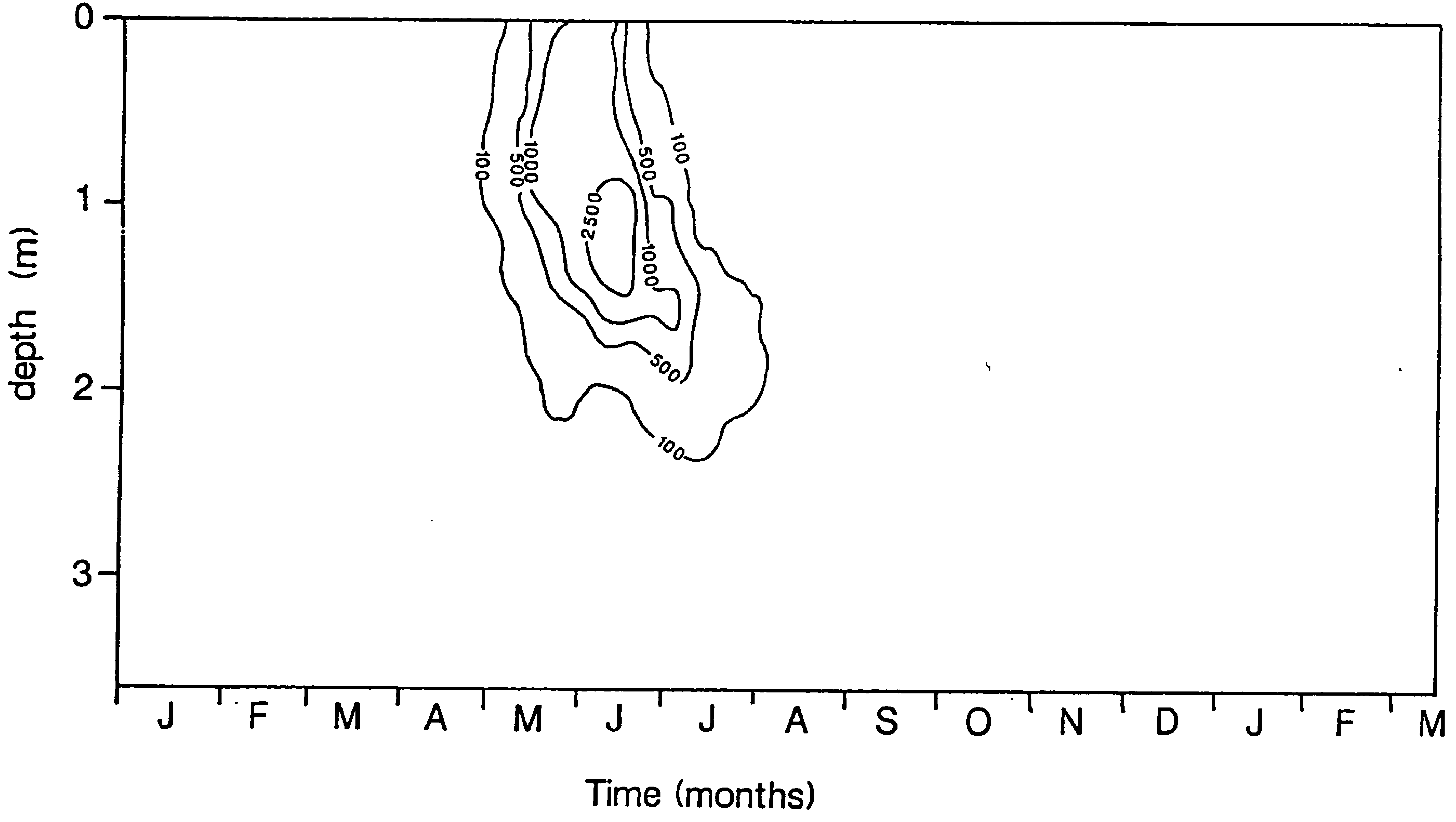
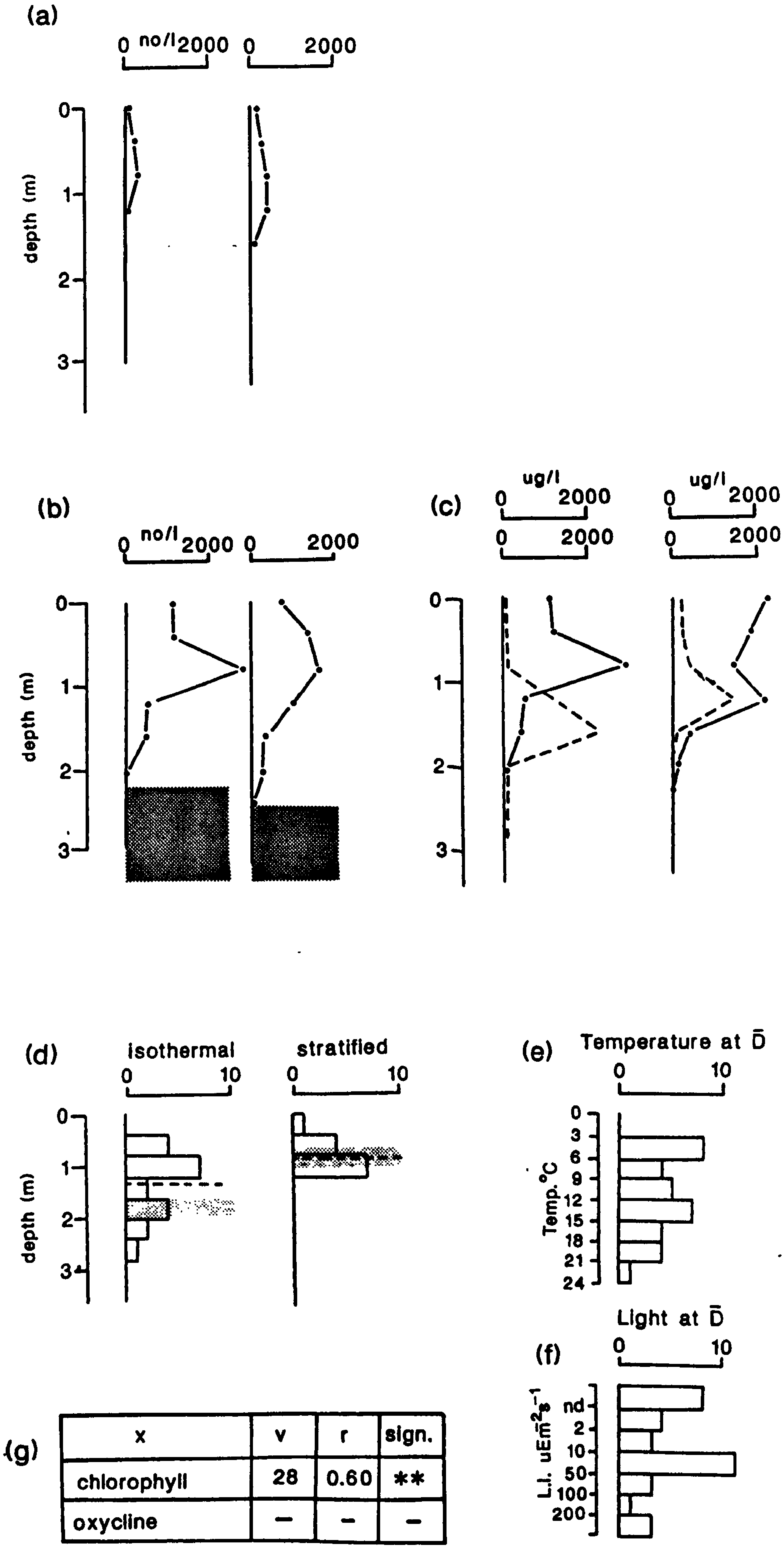


Figure 7.6. The vertical distribution of *Brachionus calyciflorus*. (a) the initial distribution of *B.calyciflorus* showing highest numbers in the surface metre of the tarn, (b) after stratification the distribution of *B.calyciflorus* was confined to the epilimnion well above the oxycline, (c) two dates on which the chlorophyll *a* levels (---) had a maximum at one particular depth, on the first date the *B.calyciflorus* population was not linked to the distribution of chlorophyll *a* but on the second it showed a coincident peak, (d) histogram showing distribution of the mean depths of *B.calyciflorus* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (e) histogram of distribution of the temperatures at the mean depths of *B.calyciflorus* indicating the range of temperatures tolerated by this species, (f) histogram of distribution of the light intensities measured at the mean depths for *B.calyciflorus* and (g) table showing the result of a correlation of mean depth of chlorophyll *a* against mean depth of *B.calyciflorus*.

Figure 7.6 *Brachionus calyciflorus*



x	v	r	sign.
chlorophyll	28	0.60	**
oxycline	–	–	–

times coincided with the vertical distribution of the chlorophyll *a* in the epilimnion but at other times bore little relation to it (Fig.7.6.c).

A comparison of the isopleth diagram (Fig.7.5) with the temperature structure overlay indicates an intolerance of temperature extremes. The population was greatest when the water temperature was between 12°C and 16°C. As it rose above 20°C the population declined and became sporadic.

When the tarn was isothermal more than half the D values were[*] shallower than 1.2 m with an overall mean of 0.87 m (Fig.7.6.d). The frequency histogram of temperature at D shows fewer below 9 °C and above 18°C than in the previous two species, indicating a sensitivity to extremes of temperature (Fig.7.6.e). The light intensities at D show that this species is found at higher light intensities than the two *Keratella* species which was also indicated by the higher values of D. As numbers were very low for most of the stratified period the relationship between the D values of the rotifer population and the depth of the oxycline was not tested. The relationship with the D values of chlorophyll *a* was tested, however, and again showed a significant correlation between the position of the rotifers and the position of their possible food source.

In Priest Pot, *B.calyciflorus* was mainly confined to the top two metres both when the tarn was isothermal and when it had stratified. At times its distribution was linked to that of chlorophyll *a*.

[*] deeper than 1.2 m and the overall mean depth was 1.3 m, almost one metre closer to the surface than the two species of Keratella. After stratification all the mean depths were

---

Very few ecological studies have described the distribution of B.calyciflorus. Miracle & Vicente (1983) found a bimodal distribution in the mixolimnion at temperatures over 20°C. Numbers in Priest Pot fell at temperatures over 16°C so the sensitivities of these two populations are obviously different.

7.3.4 Brachionus angularis (Fig.7.7)

This other Brachionus species was also most abundant in June but appeared a week earlier than B.calyciflorus. It appeared in the surface two metres even though the tarn was isothermal and it remained confined to this section of the water column even after stratification (Fig.7.8.a). In the autumn, when the tarn again became isothermal, the population was evenly distributed in the top two metres until 26 September when an aggregation coincident with increased chlorophyll levels occurred in the surface metre of the water column (Fig.7.8.b)

When the tarn was stratified the B.angularis frequently showed a stratified vertical distribution, with maxima coincident with increased chlorophyll a values (Fig.7.8.c). The largest population was found before the temperature rose above 16°C and was concentrated in the top one and a half metres (Fig.7.7 and overlay A). In July numbers fell and remained low until after mixing in the autumn.

When the tarn was isothermal the overall mean depth of the population was 1.72 m and the individual D values were quite evenly distributed. When the tarn was stratified the overall mean depth was almost halved to

Figure 7.7. Isopleth diagram showing the vertical distribution of *Brachionus angularis* in Priest Pot from January 1983 to March 1984.

Figure 7.7 *Brachionus angularis*

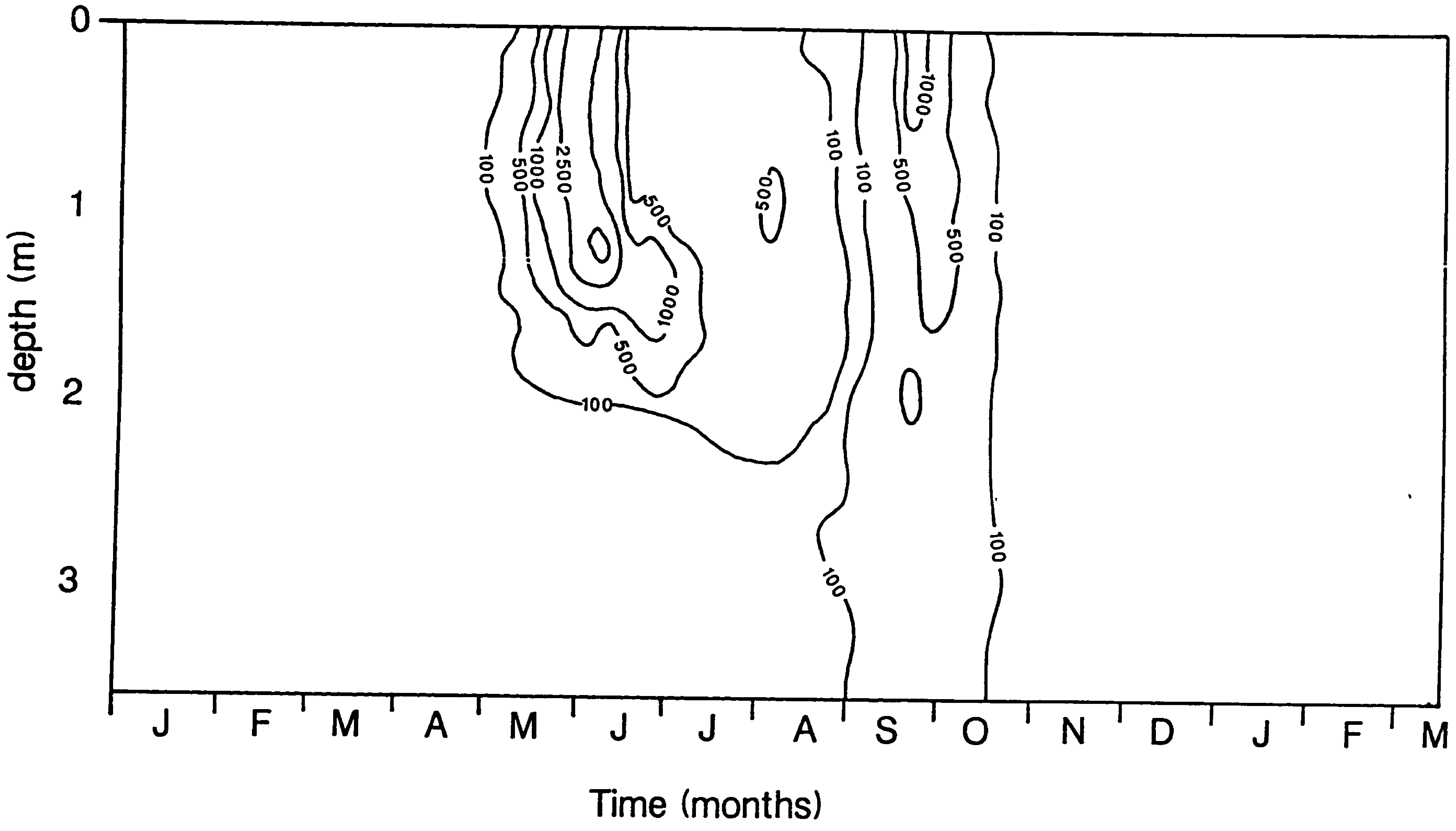
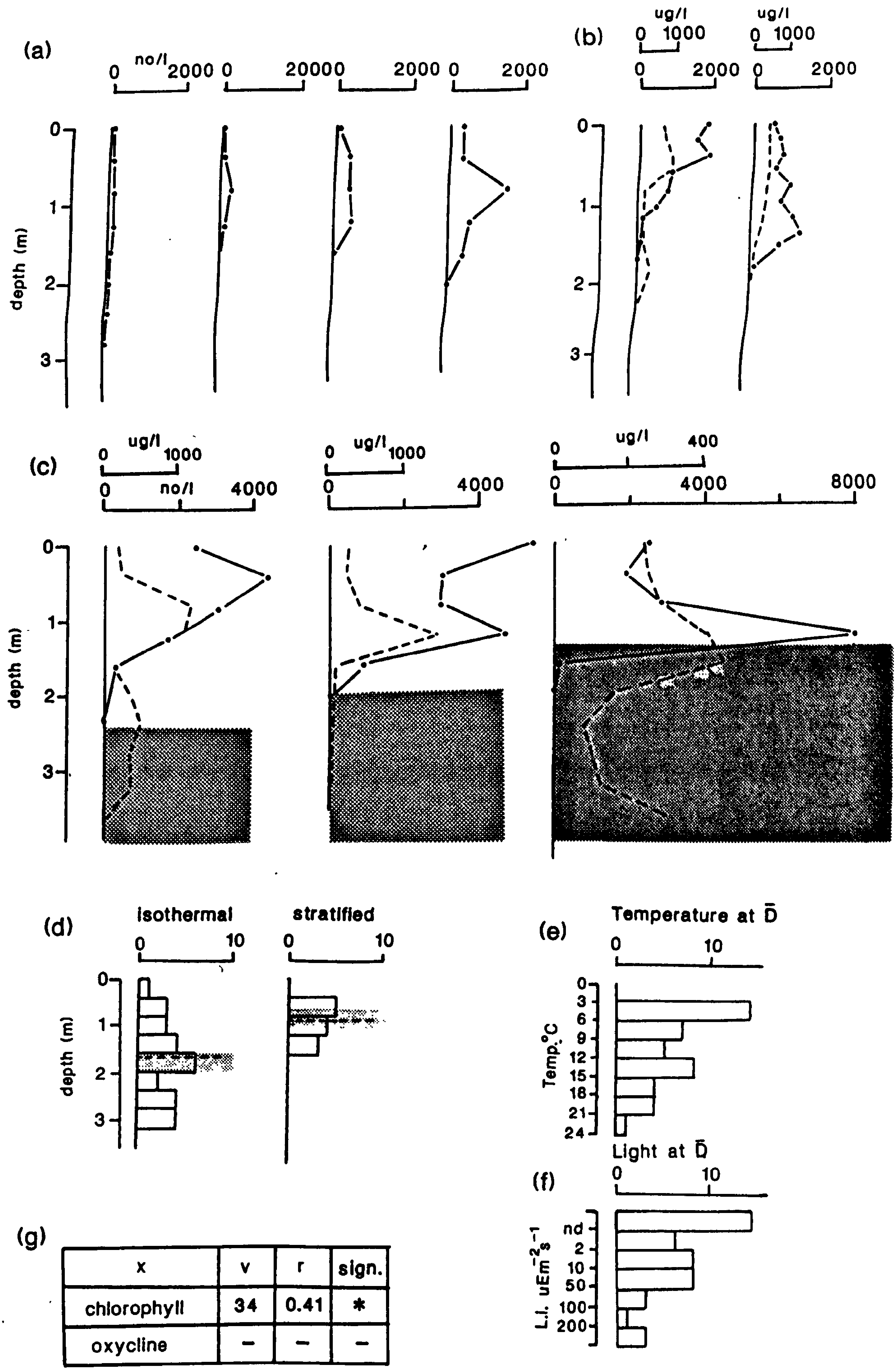


Figure 7.8. The vertical distribution of *Brachionus angularis*. (a) The initial distribution of *B.angularis* showing highest numbers in the surface metre of the tarn (b) during isothermal conditions the rotifers had coincident maxima with chlorophyll *a* maxima (---) but were more uniformly distributed on dates when the chlorophyll *a* profile was uniform, (c) after stratification the rotifers were confined to the epilimnion but on the three dates shown had maxima coincident with chlorophyll *a* peaks, (d) histogram showing distribution of the mean depths of *B.angularis* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (e) histogram of distribution of the temperatures at the mean depths of *B.angularis* indicating the range of temperatures tolerated by this species, (f) histogram of distribution of the light intensities measured at the mean depths for *B.angularis* and (g) table showing the result of a correlation of mean depth of chlorophyll *a* against mean depth of *B.angularis*.

Figure 7.8 *Brachionus angularis*



x	v	r	sign.
chlorophyll	34	0.41	*
oxycline	–	–	–

0.91 m and all the mean depths were between 0.4 m and 1.6 m (Fig.7.8.d). The frequency histogram of temperatures at D (Fig.7.8.e) showed lower frequencies below 6 C than the two Keratella species but the range of temperatures tolerated was greater than that of B.calyciflorus. The shallower mean depths of this species moved its population into the base of the euphotic zone and only a third of the D values were in undetectable light intensities (Fig.7.8.f). As with B.calyciflorus, numbers were very low for much of the stratified period so a correlation statistic was not calculated for D of B.angularis with depth of oxycline. The relationship with D of chlorophyll was investigated but was significant at only the 5% level (Fig.7.8.g), less than in the previous species, possibly because the feeding habits of B.angularis concentrate on bacteria and detritus (Pourriot, 1977).

In Priest Pot, B.angularis tended to concentrate in shallower depths than the two Keratella species but below the other species of Brachionus. The population was mainly confined to the top two metres of the water column in both isothermal and in stratified conditions.

Few accounts of vertical distribution occur in the literature for this species. Eloranta (1982) found no stratification in a warm-water effluent pond during one year but found high numbers in the top four metres in the following year.

7.3.5 Polyarthra vulgaris (Fig.7.9)

P.vulgaris was present throughout the year but only at very low numbers before the beginning of April. When the tarn was isothermal, the population was homogeneously distributed (Fig.7.10.a) until the algal bloom in spring. During May the population generally showed maxima coincident with high chlorophyll a values (mainly Peridinium) even though the tarn was still isothermal (Fig.7.10.b). In the autumn a bloom of Synura sp. aggregated in the surface metre of the tarn and P.vulgaris had a maximum coincident with it (Fig.7.10.c). At other times in isothermal conditions the population was more evenly distributed. When the tarn was stratified P.vulgaris was confined to the epilimnion. Its distribution varied from relatively homogeneous to showing a distinct maximum (Fig.7.10.d). In all cases, numbers fell near the oxycline and the peaks of P.vulgaris were above the high chlorophyll levels in the top of the hypolimnion.

When the tarn was isothermal the overall mean depth was 2.01 m and the individual D values show a tendency to avoid the surface metre of the tarn. During stratification, however, the population was mainly concentrated above 1.2 m, an overall mean depth of 0.83 m placing it above both the Brachionus species although in isothermal conditions it had been deeper than either of them (Fig.7.10.e). The temperatures at D showed the wide range of temperatures tolerated by this species (Fig.7.10.f) and almost half the light intensities at D were undetectable (Fig.7.10.g). The positive correlation between the D of P.vulgaris and the D of the chlorophyll, significant at the 1% level, showed the possible effect

Figure 7.9. Isopleth diagram showing the vertical distribution of *Polyarthra vulgaris* in Priest Pot from January 1983 to March 1984.

Figure 7.9 *Polyarthra vulgaris*

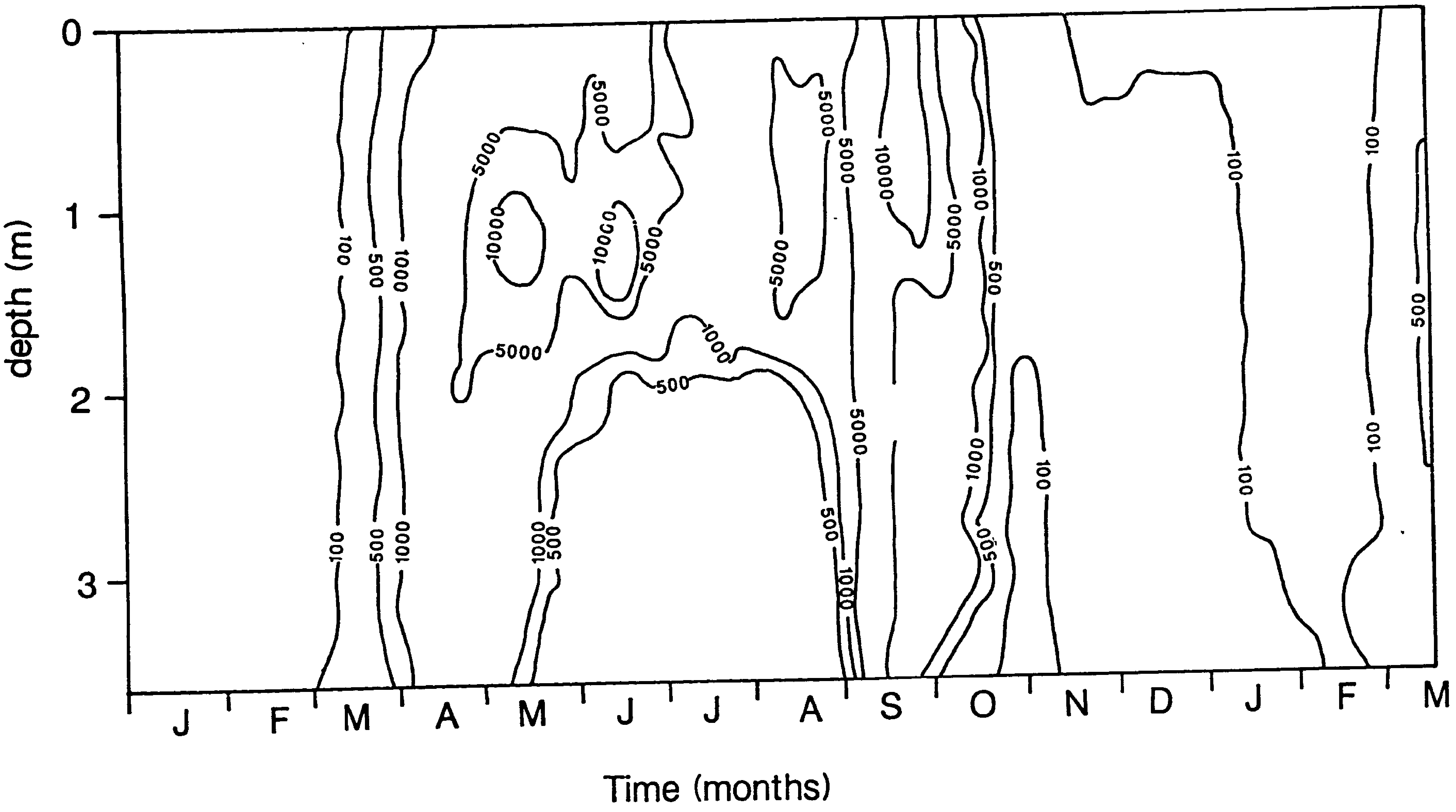
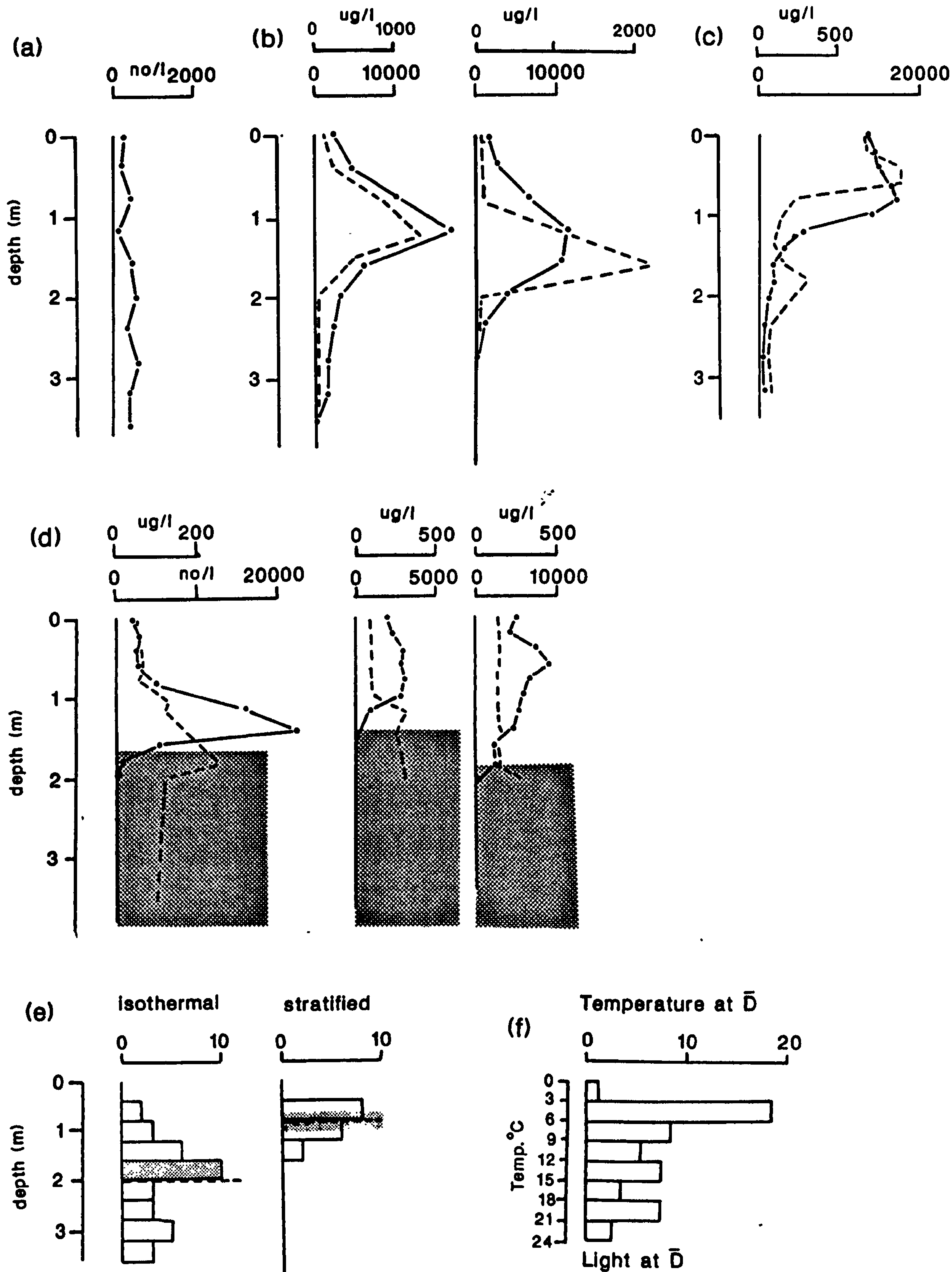


Figure 7.10. The vertical distribution of *Polyarthra vulgaris*. (a) In isothermal conditions the distribution of *P.vulgaris* was often uniform, (b) on two dates when *Peridinium lomnickii* blooms produced high chlorophyll *a* concentrations (---) in the second metre of the tarn the rotifers showed maxima coincident with the algal peaks, (c) the autumn bloom of *Synura* also produced coincident peaks in *P.vulgaris*,(d) during stratified conditions the rotifers showed coincident peaks with the chlorophyll *a* distribution on some dates (L.H. profile) but at other times their distribution was uniform throughout the epilimnion (e) histogram showing distribution of the mean depths of *P.vulgaris* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (f) histogram of distribution of the temperatures at the mean depths of *P.vulgaris* indicating the range of temperatures tolerated by this species, (g) histogram of distribution of light intensities measured at the mean depths for *P.vulgaris* and (h) table showing the results of correlations between the mean depth of chlorophyll *a* and depth of the oxycline against mean depth of *P.vulgaris*.

Figure 7.10 *Polyarthra vulgaris*



(h)

x	v	r	sign.
chlorophyll	41	0.72	* *
oxycline	12	0.68	*

of food availability on the rotifers' distribution. The depth of the oxycline was also correlated with the D of _P.vulgaris_, at the 5% level, but the profiles showed the rotifers to be avoiding it rather than concentrating near it as in the _Keratella_ species.

In Priest Pot the distribution of _P.vulgaris_ was homogeneous when the tarn was isothermal except during the periods of high algal numbers, when the rotifer distributions developed maxima coincident with those of chlorophyll. During the stratified period their distributions indicated an avoidance of low oxygen levels which overrides the species' tendency to concentrate where chlorophyll levels increase.

Fairchild _et al_. (1977) showed a correlation between _P.vulgaris_ populations and both chlorophyll values and chrysomonad densities. A sensitivity to low oxygen concentrations has been previously described by Pejler (1957 b) and other workers support this (Nauwerck, 1963; Einsle, 1967; George & Fernando, 1969; Larsson, 1971). Stemberger (1974) and again Stemberger _et al_. (1979) found peaks in the metalimnion above the _K.cochlearis_ maxima and Berzins (1958), Axelson (1961) and Elliott (1977) all found _P.vulgaris_ in greater densities in the upper strata.

7.3.6 _Filinia terminalis_ (Fig.7.11)

The species began to increase in numbers at the beginning of April and, like the two species of _Keratella_, it first increased in the deep water (Fig.7.12.a) before spreading through the whole water column (Fig.7.12.b). In the autumn, when the tarn was again isothermal, the population had a second period of abundance which again started in the bottom metre of the water column (Fig.7.12.c) but the following week the peak had shifted up a metre, the deeper water having become anoxic. When the tarn first began to stratify the population had developed a slight maximum in the top metre of the tarn. As the temperature near the surface increased, the population moved down but as this occurred at the same time as the start of stratification, the population became confined to a narrow band where the oxygen concentration was low but sufficient and temperature was below 16°C. This band became increasingly narrow as the oxycline moved further up in the water column until there was no longer a zone where both the temperature and the oxygen requirements of F.terminalis were satisfied. In Figure 7.12.d. this can be seen as the bar denoting the 16°C contour moves down until it occurs within the stippled anoxic zone. After this occurred on 27 June 1983 F.terminalis was sporadic until the autumn.

The overall mean depth of the population when the tarn was isothermal was 2.44 m, the deepest of all the species studied, and all the individual mean depths were below 1.2 m. There were only five results during the period of stratification but of these, 3 had D values below 1.2 m and the overall mean depth of 1.26 m was one of the deepest found in this study (Fig.7.12.e). The frequency distribution of temperatures at D shows clearly

Figure 7.11. Isopleth diagram showing the vertical distribution of *Filinia terminalis* in Priest Pot from January 1983 to March 1984.

Figure 7.11 *Filinia terminalis*

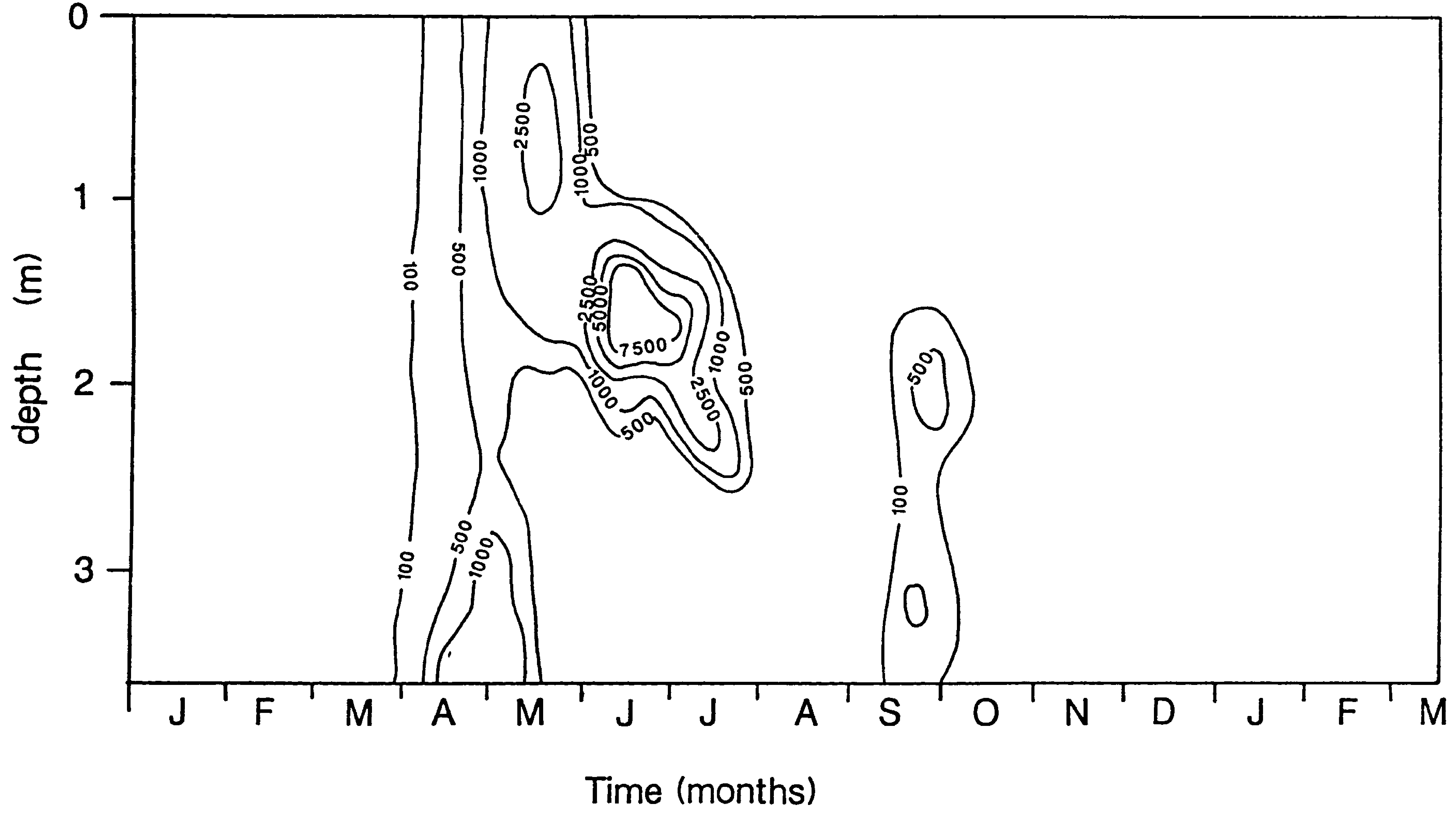


Figure 7.12. The vertical distribution of _Filinia terminalis_. (a) When the rotifers first appeared in the tarn they were concentrated in the deeper water, (b) during isothermal conditions they occurred throughout the water column, (c) in the autumn, a second period of abundance again started in the deeper water but the deeper water became anoxic (□— □ , oxygen profile) and the peak of rotifers was shifted upwards, (d) after stratification, _F.terminalis_ was confined to a narrow band where oxygen concentration was sufficient but temperature was below 16°C. As the bar denoting the 16°C contour moves down on successive profiles the rotifers can be seen to be forced down until, when the bar reaches the stippled hypolimnion the rotifers are forced out altogether, (e) histogram showing distribution of the mean depths of _F.terminalis_ in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (f) histogram of distribution of the temperatures at the mean depths of _F.terminalis_ indicating the range of temperatures tolerated by this species, (g) histogram of distribution of the light intensities measured at the mean depths of _F.terminalis_ and (h) table showing the result of a correlation between the mean depth of Chlorophyll _a_ against mean depth of _F.terminalis_.

Figure 7.12 *Filinia terminalis*

x	v	r	sign.
chlorophyll	15	0.46	ns
oxycline	–	–	–

this species sensitivity to temperatures over 15°C (Fig.7.12.f) and the high proportion of undetectable light intensities at the mean depths indicates the depth of the population (Fig.7.12.g). There was no relationship with chlorophyll, the correlation coefficient between the values of D for the rotifers and D for the chlorophyll being insignificant (Fig.7.12.h), which is to be expected for a bacterial feeder like F.terminalis. No correlation coefficient was calculated with the depth of the oxycline because only five dates were available.

In Priest Pot the F.terminalis population is limited by temperatures above 15°C. The vertical distribution of this species is generally homogeneous until temperature and oxygen conditions confine them to a rapidly decreasing section of the water column before excluding them from the tarn altogether.

The distribution of this species has been much discussed in the literature. Ruttner-Kolisko (1980) describes the distribution of F.terminalis in low oxygen (< 2 mg l^{-1}) at temperatures between 12 and 15°C. She states that they show facultative anaerobiosis. In Esthwaite Water, where the oxycline during the summer reaches up to the 10 to 12°C isotherm, there are no F.terminalis during the stratified period. In Windermere, a deeper lake, there is space for them to survive all the year round in oxygenated water at 10°C. In Plußsee, Hofmann (1982) found a population of F.terminalis moving down as the temperature in the water increased in May, followed by a decline in numbers. Other studies have found this species occurring in low oxygen conditions ;

Ruttner-Kolisko (1977) found more than 50% of the population at 8 m where oxygen readings were zero in Lunzer Obersee, Larsson (1971) found a maximum in 0 - 2 mg O_2 l^{-1} by the chemocline and the population studied by Elliott (1977) in Grasmere had higher numbers in the lower strata in 9 - 47% oxygen. Pejler (1961) found this species in a narrow band at the bottom of Osbysjon in the summer, Axelson (1961), George & Fernando (1969) and Kasprzak & Ronneberger (1982) describe maxima in the hypolimnion while Guerrero _et al_. (1978) and Miracle & Vicente (1983) both describe distributions with peaks around the chemocline. All the populations of _F.terminalis_ studied show distributions skewed towards deeper water with low oxygen tensions but in many cases this is a result of increased temperatures in the surface water. The pattern of distribution in Priest Pot shows a response to increasing temperature followed by a decline in numbers as conditions become anoxic very similar to those described in the literature.

7.3.7 _Filinia brachiata_ (Fig.7.13)

This second species of _Filinia_, unlike the cold stenotherm _F.terminalis_, did not appear in the tarn until the summer. It was only present in isothermal conditions for a month after stratification had broken up in early September. During this time the population showed two distributions. On 19 September, when the tarn was isothermal, the rotifers were relatively evenly distributed through the water column (Fig.7.14.a). The following week, on 26 September, they were mainly

Figure 7.13. Isopleth diagram showing the vertical distribution of _Filinia_ _brachiata_ in Priest Pot from January 1983 to March 1984.

Figure 7.13 *Filinia brachiata*

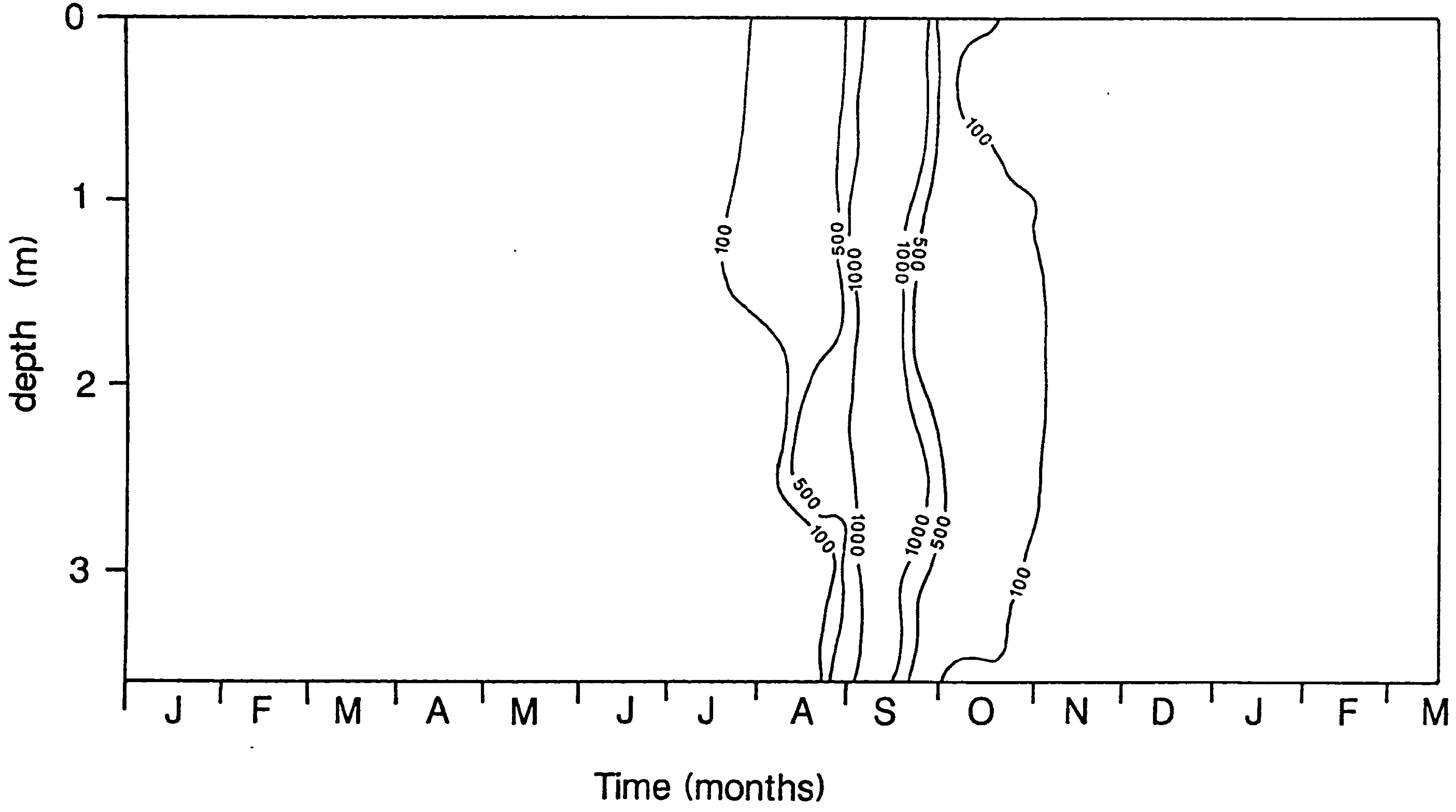
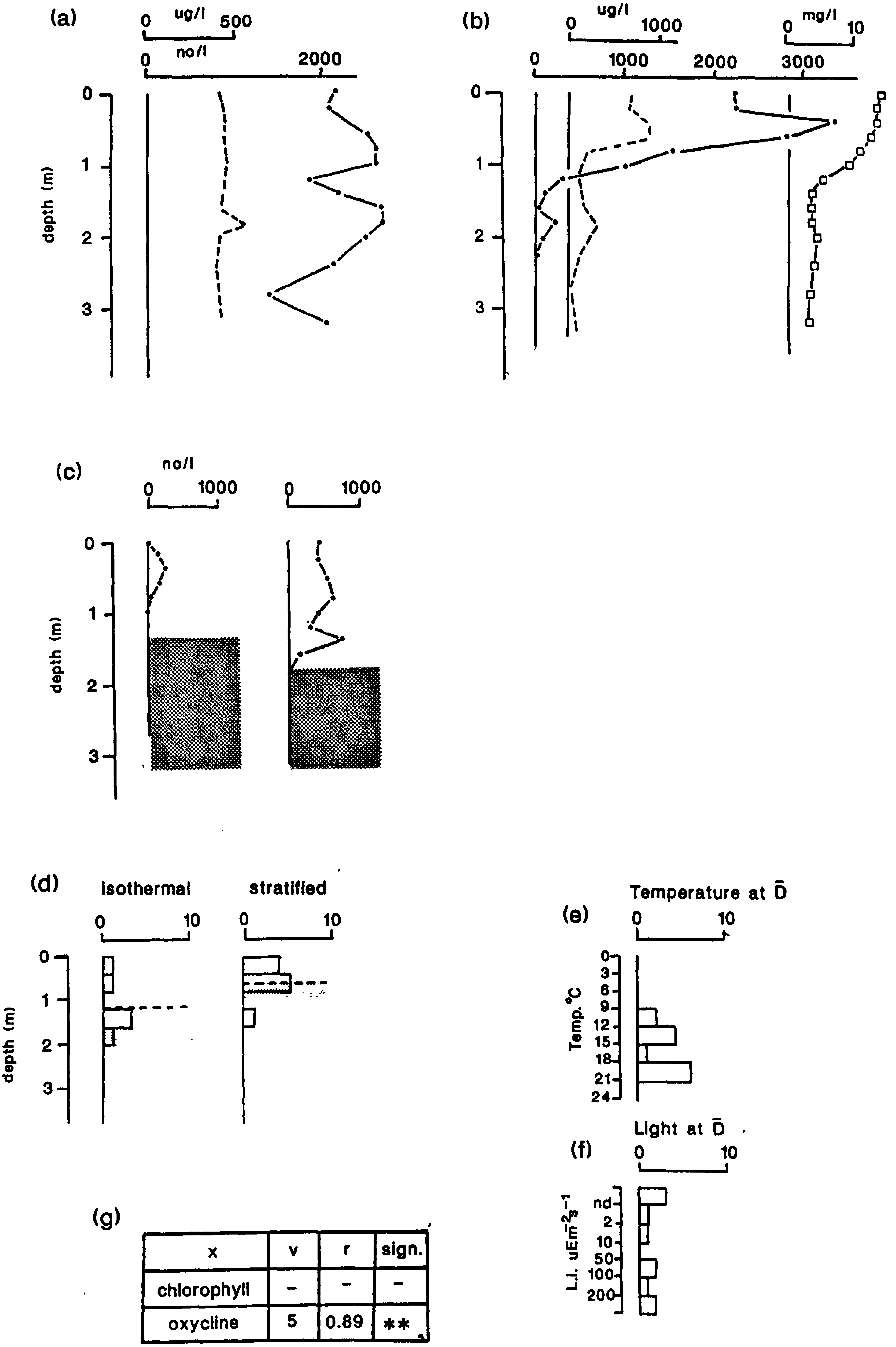


Figure 7.14. The vertical distribution of *Filinia brachiata*. (a) In isothermal conditions, *F.brachiata* showed a relatively even distribution, (b) in late September a surface peak occurred either linked to the coincident peak of chlorophyll *a* (---) or to the depletion of oxygen (□—□)in the deeper waters, (c) during the earlier stratified period *F.brachiata* avoided the low oxygen concentrations near the oxycline, (d) histograms showing distributions of mean depths of *F.brachiata* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (e) histogram of distribution of the temperatures at the mean depths of *F.brachiata* indicating the range of temperatures tolerated by this species, (f) histogram of distribution of light intensities measured at the mean depths of *F.brachiata* and (g) table showing the result of a correlation between the depth of the oxycline and the mean depth of *F.brachiata*.

Figure 7.14 *Filinia brachiata*



(g)

x	v	r	sign.
chlorophyll	–	–	–
oxycline	5	0.89	**

restricted to the top metre (Fig.7.14.b) either in response to the depletion of oxygen to 3 mg l^{-1} in the deeper water or, perhaps, to the higher values of chlorophyll in the surface waters caused by a bloom of *Synura* sp. The population declined rapidly after the end of September and no *F.brachiata* were found in the tarn after mid-October.

In stratified conditions the rotifers were always confined to the epilimnion. In June and July there were sporadic occurrences but only in late August did the population become more established and was concentrated in the top metre (Fig.7.14.c), well above the low oxygen levels near the oxycline.

The frequency distributions of the D values show the species higher in the water column than most other species (Fig.7.14.d). When the tarn was isothermal it was the highest, with an overall mean depth of 1.15 m and during stratification the overall mean depth was 0.63 m. The range of temperatures at D clearly shows the species to be a warm stenotherm with no appearances below 9°C and most between 15 and 21°C (Fig.7.14.e). The range of light intensities at D (Fig.7.14.f) reflected the position of this species near the surface. The correlations with ~~both chlorophyll a and~~ the depth of the oxycline were significant at the 1% level (Fig.7.14.g).

The distribution of *F.brachiata* in Priest Pot was concentrated nearer the surface than that of any other species. Their position was linked to the distribution of chlorophyll and also to the depth of the oxycline. In

September they showed a sensitivity to oxygen concentrations of less than 3 mg l^{-1} which may partly explain their preference for surface waters. A search of the literature found no ecological descriptions of this species, previously it has only been found as a rarity. This is, therefore, almost certainly the first detailed description of this species' behaviour.

7.3.8 Anuraeopsis fissa (Fig.7.15)

When the temperature in the tarn reached 8°C A.fissa started to appear sporadically in the samples. The first record of its presence was on 18 April but it was not until the end of May that its population reached 1000 l^{-1}, by which time the tarn had become stratified. When the tarn returned to isothermal conditions in September A.fissa was still numerous and remained so for six weeks before its numbers dropped. In isothermal conditions, this rotifer showed a variety of distributions. During the first two weeks of September the population was uniformly distributed through the top two metres of the tarn but aggregated into a large peak around 3 m depth (Fig.7.16.a). On 19 September they had become uniformly distributed through all the samples (Fig.7.16.b) but the deep peak had returned in the last week of September (Fig.7.16.c) and on this occasion was in depleted oxygen concentrations (2.2 mg l^{-1}). On 3 October an oxic-anoxic boundary had developed between 2.0 m and 2.4 m and, although the population had declined to a mean density of 2570 l^{-1}, the A.fissa showed a definite maximum between 1.6 m and 2.0 m just above it. Numbers continued to fall and by late October there were only sporadic occurrences. Just as its appearance had coincided with the temperature in the tarn rising above 8 °C, so its disappearance occurred as the temperature fell below 8°C. This can be seen from Fig.7.15 and overlay A and it indicates the lower limit of this species' temperature tolerance.

In stratified conditions A.fissa reached very high numbers, up to 200000 l^{-1} on some dates. A similar distribution was found throughout the summer, a peak of rotifers always occurring just above or on the 1 mg O_2 l^{-1} boundary. The position of this peak in the water column varied as the depth of the oxic-anoxic boundary fluctuated (Fig.7.16.d).

There was little difference between the overall mean depth in isothermal conditions and that during the stratified period but the former, at 1.67 m, placed A.fissa in the middle of the species present whilst the latter, at 1.30 m, was the deepest of all the species (Fig.7.16.e). The range of temperatures at D starts at 9°C indicating the species' status as a warm stenotherm (Fig.7.16.f). All but one of the light intensities at D were below 50 uE m^{-2} s^{-1} illustrating the depth of this species in the water column (Fig.7.16.g). Fewer D values were in undetectable light intensities than for other species probably because when A.fissa was present from May to October, the incident light was higher than during the winter. There was no relationship with chlorophyll but the depth of the oxycline was obviously an important factor in determining the distribution of this species and it was positively correlated with the mean depth of

Figure 7.15. Isopleth diagram showing the vertical distribution of _Anuraeopsis fissa_ in Priest Pot from January 1983 to March 1984.

Figure 7.15 *Anuraeopsis fissa*

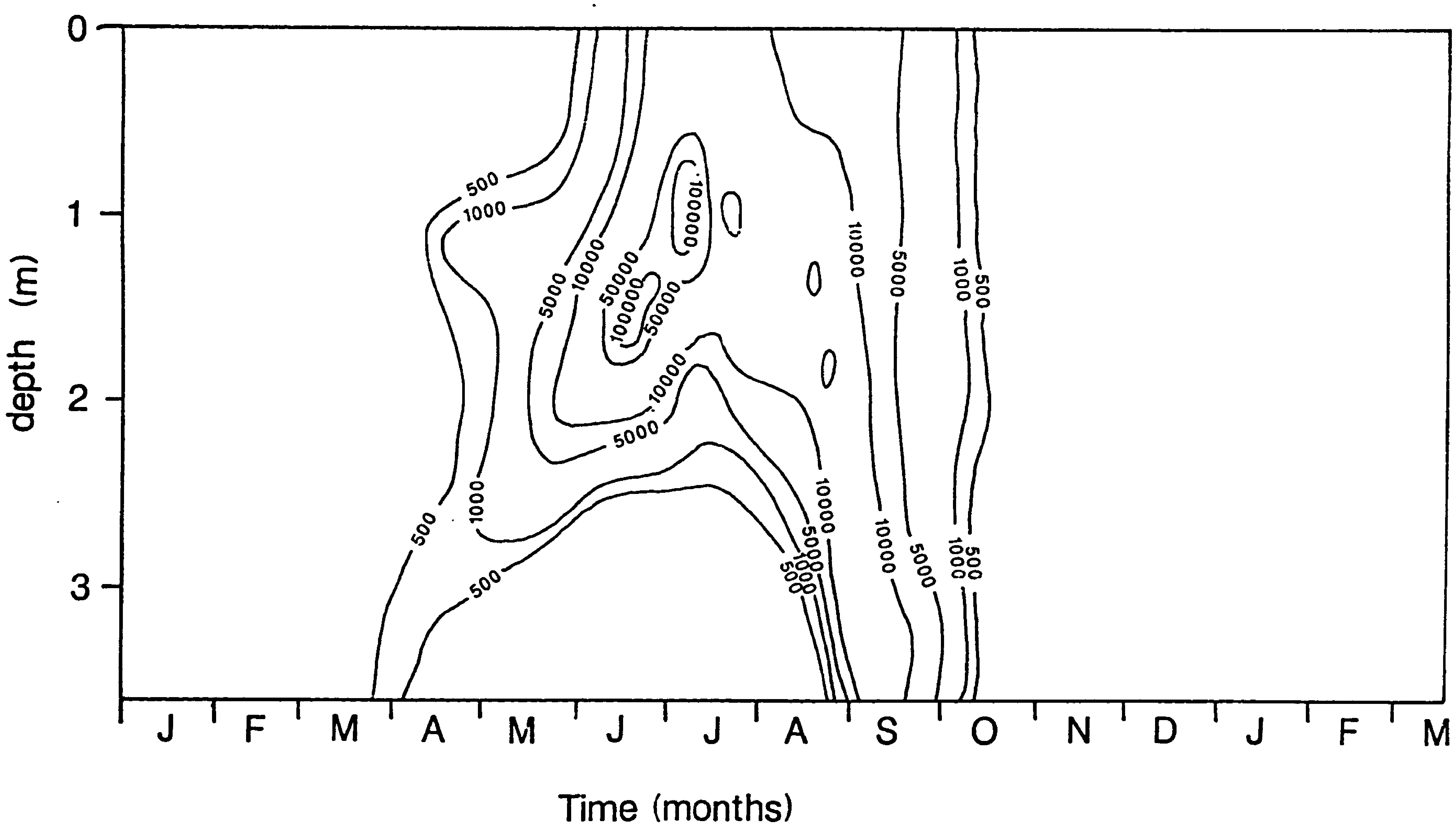
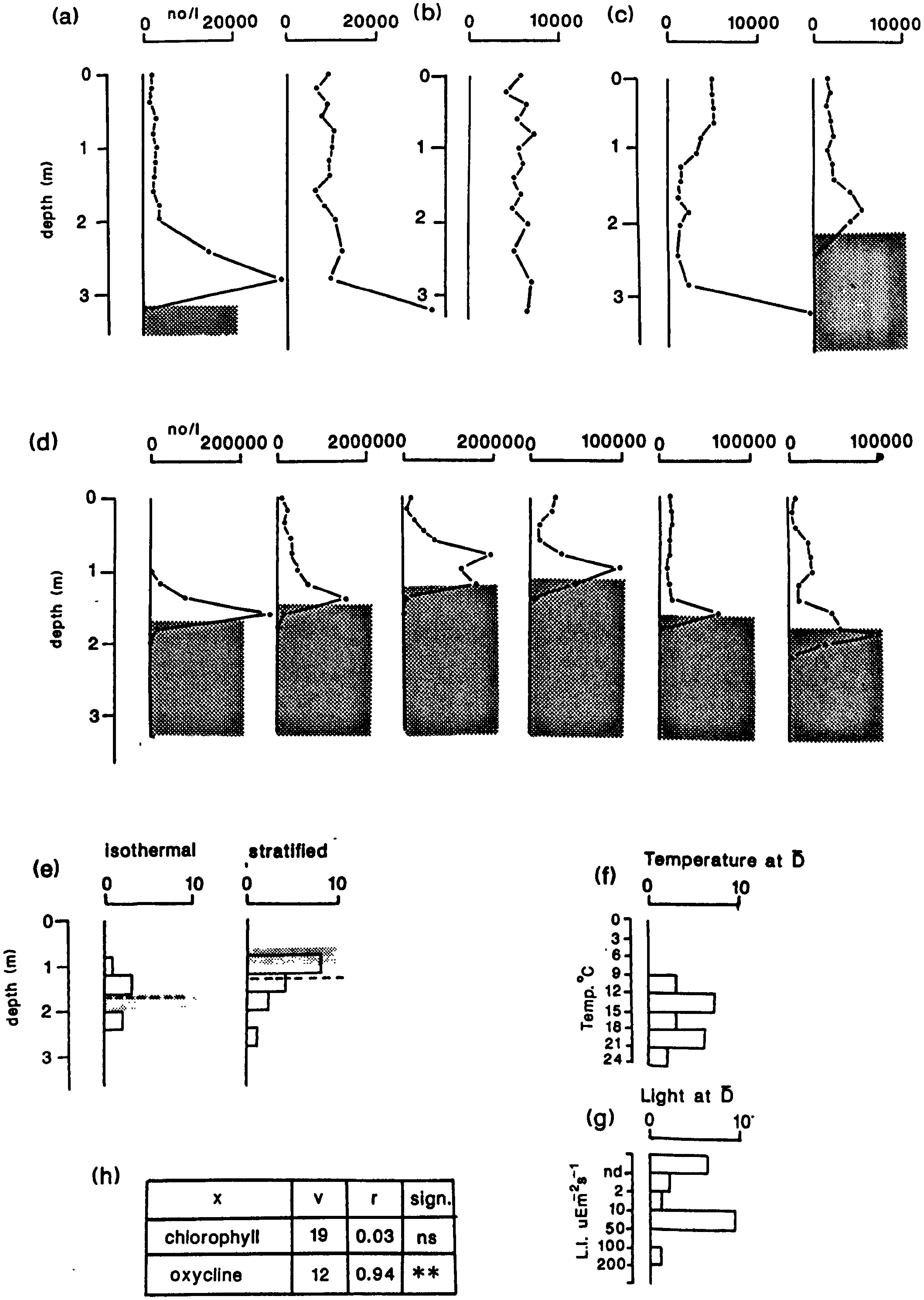


Figure 7.16. The vertical distribution of *Anuraeopsis fissa*. (a) In isothermal conditions in September a large peak was found around 3m depth, (b) by mid-September their distribution was even throughout the water column, (c) when the oxygen in the deeper water became depleted in late September the rotifers displayed maxima near the oxic-anoxic boundaries, (d) throughout the stratified summer period *A.fissa* always had a maximum near the oxycline, (e) histogram showing distribution of the mean depths of *A.fissa* in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (f) histogram of distribution of the temperatures at the mean depths of *A.fissa* indicating the range of temperatures tolerated by this species, (g) histogram of distribution of the light intensities measured at the mean depths of *A.fissa* and (h) table showing the results of correlations of the mean depth of chlorophyll *a* and the depth of the oxycline against the mean depth of *A.fissa*.

Figure 7.16 *Anuraeopsis fissa*



x	v	r	sign.
chlorophyll	19	0.03	ns
oxycline	12	0.94	**

A.fissa at the 1% level (Fig.7.16.h).

The distribution of the population in Priest Pot was strongly associated with the oxycline and A.fissa was the species most tolerant of low oxygen concentrations. In both isothermal and stratified conditions A.fissa was always found at a maximum where oxygen concentrations fell.

Pejler (1961) found maxima in Osbysjon in a narrow zone close to the bottom of the lake, Guerrero *et al*. (1978) described a plate of A.fissa just above the chemocline and Miracle & Vicente (1983) found it largely restricted to the chemocline in low oxygen concentrations and noted its tolerance of anaerobic conditions. Guerrero *et al*. linked its distribution to bacterial feeding and this may be a cause of the maxima in Priest Pot. Eloranta (1982) found no stratification in a warm-water effluent pond from August to October but during this time the epilimnion was mixed by pumps which may have prevented the development of aggregations.

In Priest Pot this species was different to all the others present not only in its tolerance of low oxygen concentrations but in its lack of any relationship with chlorophyll *a* values; as a bacterial feeder the oxic-anoxic boundary and the top of the hypolimnion were far more important to it.

7.3.9 Synchaeta kitina (Fig.7.17) and Synchaeta pectinata (Fig.7.18)

The two species of Synchaeta in Priest Pot were never present at high population densities. S.kitina was usually below 500 l^{-1} and S.pectinata rarely rose above 1000 l^{-1}. Before stratification they were mainly uniformly distributed in the water column but during the summer they sometimes showed marked concentrations. However, their numbers fluctuated widely during this time and on some occasions they were absent from the samples.

The frequency histograms of mean depths show the overall means of both species to be quite shallow in the tarn when it was isothermal; S.kitina had an overall D of 1.38 m and S.pectinata one of 1.30 m. During stratified conditions they moved up, most mean depths were above 1.2 m, with overall means of 0.82 m and 0.61 m respectively (Fig.7.19.a). The D values did not show any obvious temperature preferences (Fig.7.19.b) but the light at D showed fewer undetectable light intensities than in most other species, an indication of their position in the upper waters. S.kitina correlated significantly with both chlorophyll (at the 1% level) and with the depth of the oxycline (at the 5% level). S.pectinata only showed significance with chlorophyll (at the 1% level), but as numbers were so low the accuracy of these correlations may be doubtful.

In the literature S.kitina is normally described as a cold water species but in Priest Pot it was found throughout the year. Hakkari (1969) and Larsson (1971) found it mainly in the upper waters but Stemberger et al. (1979) found it limited to the hypolimnion in late summer. S.pectinata has been described showing uniform distributions (George & Fernando, 1969), peaks at depth

Figure 7.17. Isopleth diagram showing the vertical distribution of *Synchaeta kitina* in Priest Pot from January 1983 to March 1984.

Figure 7.17 *Synchaeta kitina*

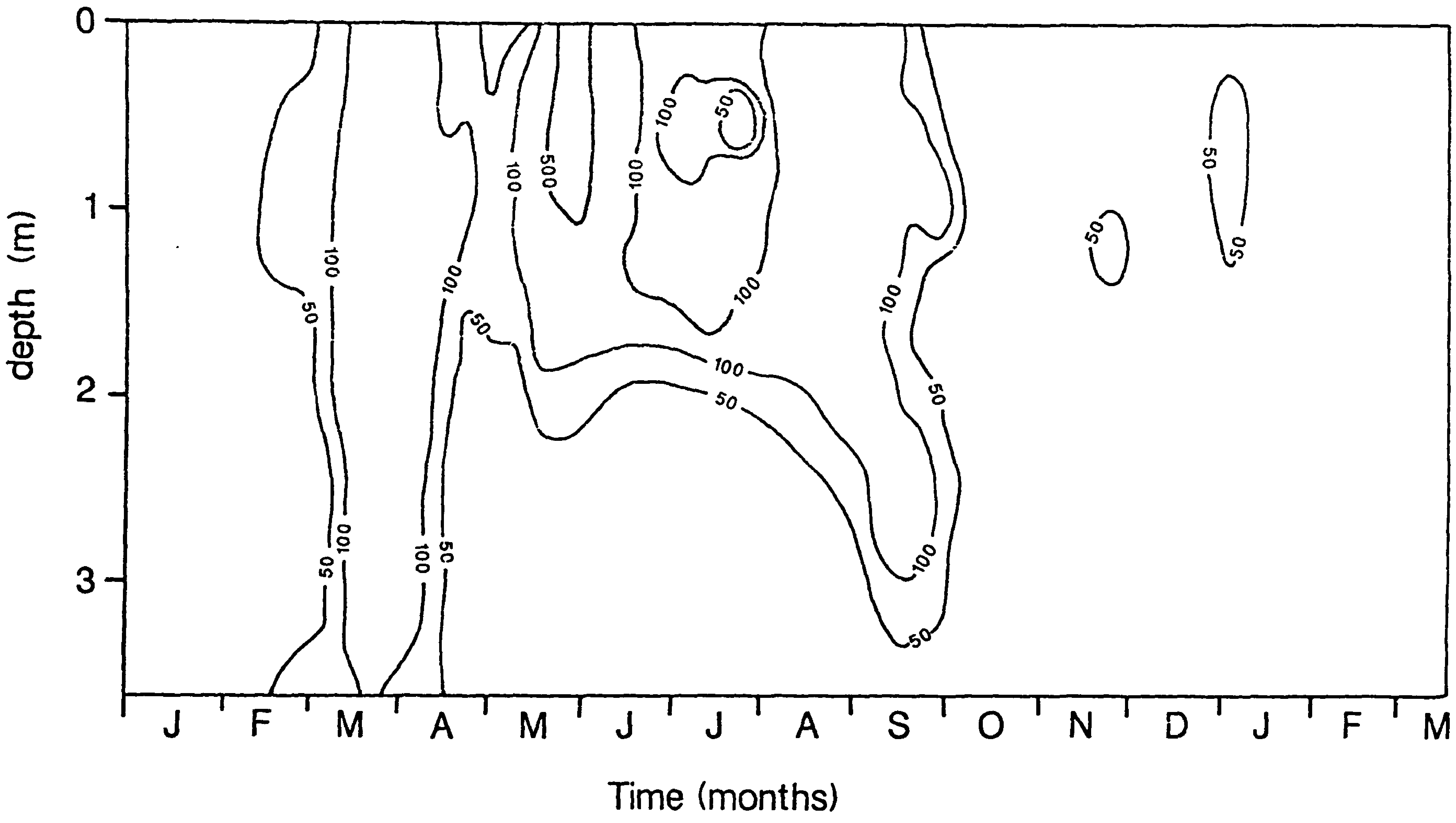


Figure 7.18. Isopleth diagram showing the vertical distribution of *Synchaeta pectinata* in Priest Pot from January 1983 to March 1984.

Figure 7.18 *Synchaeta pectinata*

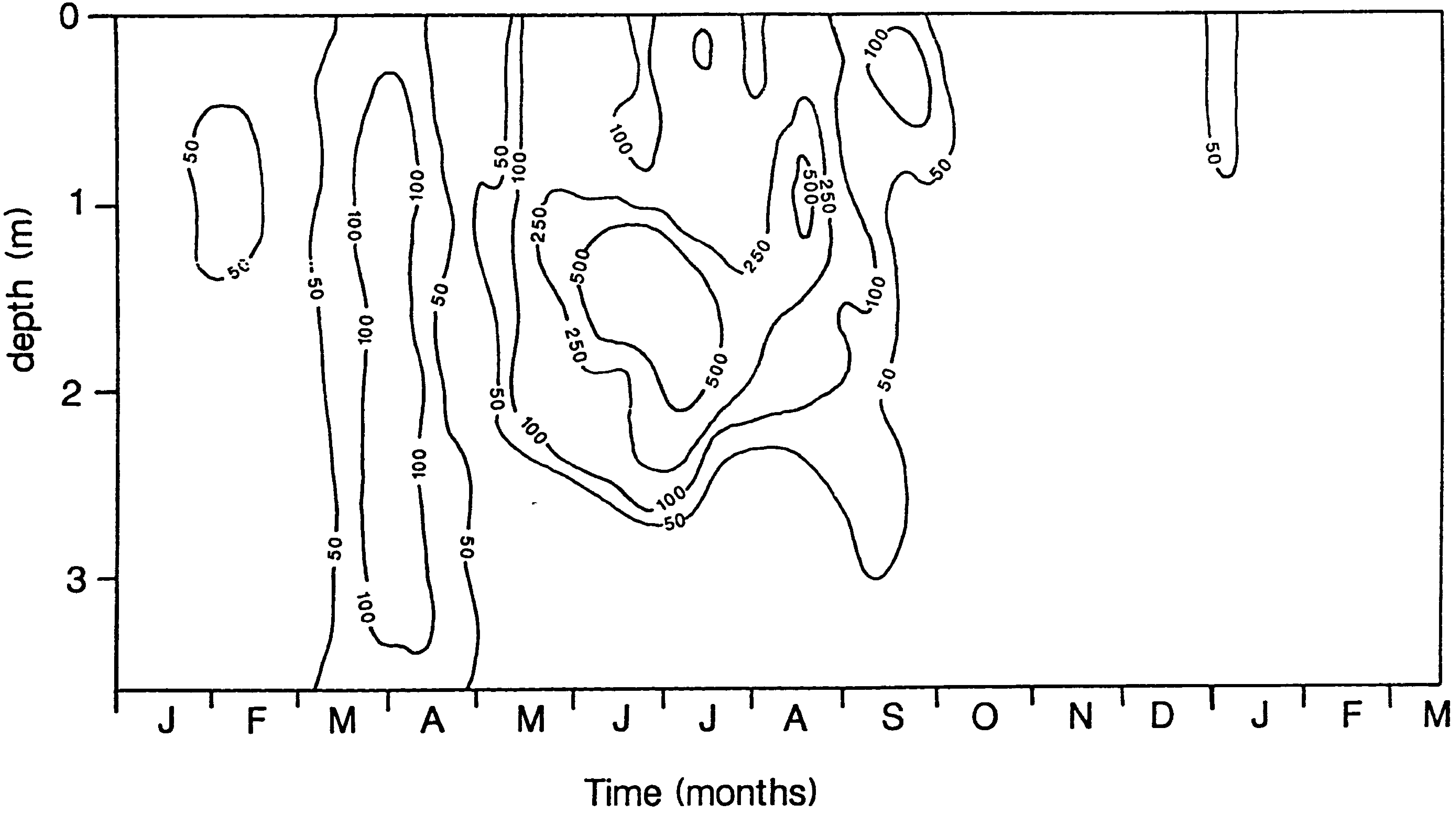
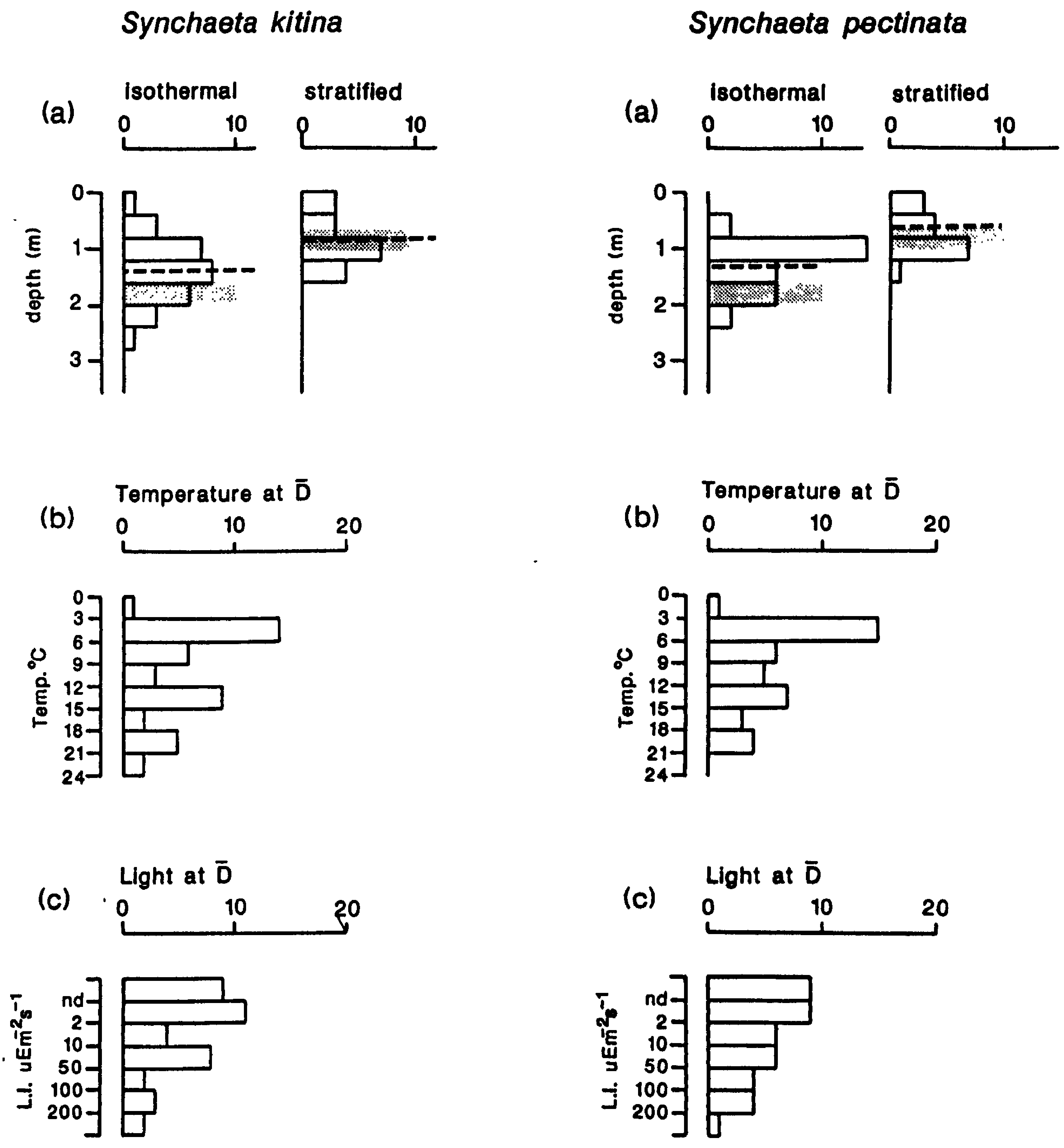


Figure 7.19. The vertical distributions of *Synchaeta kitina* (L.H.S.) and *Synchaeta pectinata* (R.H.S.). (a) Histograms showing the distribution of the mean depths of the two species in both isothermal and stratified conditions, the broken line indicates the overall mean depth and the shaded bar the expected mean depth for a random distribution, (b) histograms of distribution of the temperatures at the mean depths of the rotifers indicating the range of temperatures tolerated by these species, (c) histograms of distribution of light intensities measured at the mean depths of *S.kitina* and *S.pectinata* and (d) table showing the results of correlations between the mean depths of chlorophyll *a* and the depth of the oxycline against the mean depths of *S.kitina* and *S.pectinata*.

Figure 7.19



(d)

x	v	r	sign.
chlorophyll	35	0.35	**
oxycline	10	0.61	*

(d)

x	v	r	sign.
chlorophyll	35	0.54	**
oxycline	8	0.30	ns

in spring and near the surface in the summer (Hakkari, 1969) and a peak at depth in spring (Kasprzak & Ronneberger, 1982). In Priest Pot, although the small populations make any generalizations likely to contain inaccuracies, both species show a tendency to concentrate in the surface waters.

7.3.10 Sporadics and Rarities

Hexarthra mira and Trichocerca pusilla both appeared in the water samples but too rarely to build up any picture of their depth preferences.

Asplanchna priodonta occurred for only two weeks in June but on 20 June it was stratified with a peak at 1 m. This coincided with the top of the deep water chlorophyll peak but as Asplanchna is a carnivorous rotifer it seems unlikely that there was a direct link. It may have been feeding on the other rotifers aggregated at this depth because of the chlorophyll. High numbers of K.quadrata and P.vulgaris occurred there although neither was at its maximum but K.cochlearis displayed a bimodal distribution with peaks above and below this depth. There is insufficient evidence from only one date to state that the distributions of Asplanchna and the other rotifers were linked but it is possible that they were.

7.4 Discussion

The information obtained during the 1983/84 routine sampling produced a detailed picture of the vertical distribution of the members of the rotifer community in relation to their environment. The distributions showed stratification of the populations, both in the summer, when an epilimnion and anoxic hypolimnion were present, and during the rest of the year when the tarn was usually isothermal. Although there are many descriptions in the literature of the vertical distribution of rotifers, few also provide details of the environment. In this study it was possible to correlate some of the high population densities with environmental factors such as temperature, chlorophyll and oxygen concentration.

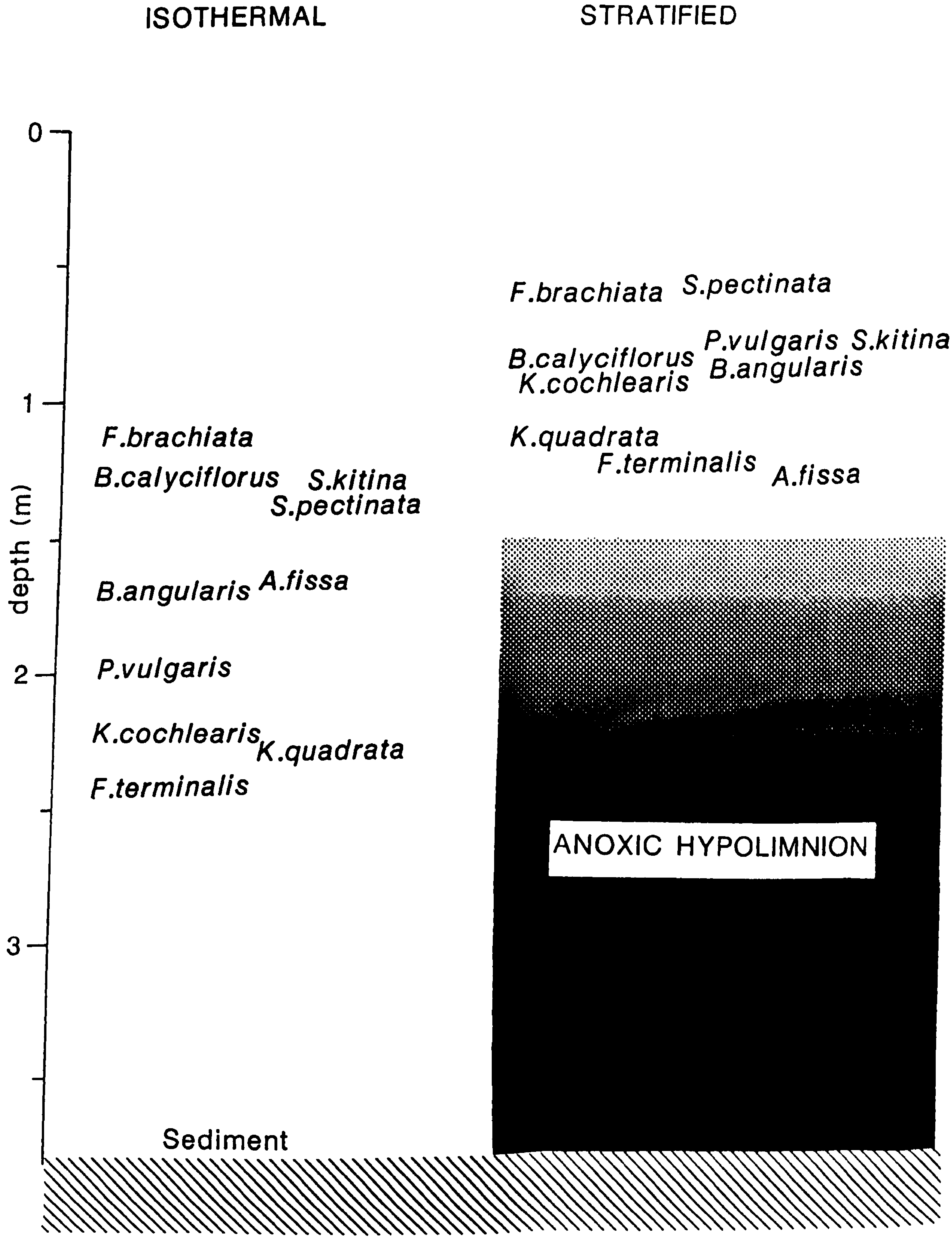
The calculation of mean depths for all the species allowed generalizations to be made about their vertical distributions. Figure 7.20 shows the overall mean depths of the different species in relation to each other both during mixed conditions (Fig.7.20.a) and when the tarn was stratified (Fig.7.20.b). When the tarn was isothermal four species had overall mean depths below 2.0 m. P.vulgaris was just below with an overall D of 2.01 m while the other three species were deeper; K.cochlearis at 2.25 m, K.quadrata at 2.34 m and F.terminalis the deepest at 2.44 m. The remaining species had overall mean depths between 1.0 m and 2.0 m, the highest in the water column being F.brachiata at 1.15 m.

This spread of species through the water column is one of the ways in which Pejler (1962) suggests that rotifers can avoid competition. In Priest Pot it allows up to ten species to be present and although their maxima sometimes overlap it is likely that this spatial separation is one of the causes of the diversity of the rotifer community. This is not a full explanation however, as various other studies have found several

Figure 7.20. The overall mean depths of each species during isothermal conditions (a) and during stratified conditions (b).

Figure 7.20

Overall mean depths of each species in isothermal and in stratified conditions



species present and no vertical stratification in their numbers (May, 1980; Eloranta, 1982). When the tarn is stratified the species are compressed into a relatively shallow epilimnion but within this the surface species maintain their position above the deeper species.

The oxycline is clearly a major factor influencing the rotifers' distribution. However, not only does it force them up out of the deeper waters into the epilimnion where oxygen is still available but it also seems to be a preferred position in the water column, many species occurring with large maxima on or just above it. *K.quadrata* and *A.fissa* were the two species most tolerant of the low oxygen concentrations near the oxycline. *K.cochlearis* also occurred close to the oxycline but other species tended to concentrate further away. *P.vulgaris* showed a marked intolerance to the low oxygen levels near the oxycline and its mean depth changed greatly on stratification. The development of anoxic conditions in the deeper waters forced some species into a very narrow zone, little more than a metre, at the surface, while allowing those species capable of surviving in low oxygen concentrations to exploit the increased bacterial populations at the oxic-anoxic boundary.

Temperature was important to some species, the cold stenotherms disappeared from the surface waters, taking refuge in the cooler, deeper water before disappearing altogether as this too warmed up or became anoxic. This could most clearly be seen in *F.terminalis* and has been documented before by Ruttner-Kolisko (1980) and Hofmann

Table 7.1 A summary of the observations on the vertical distribution of the planktonic rotifers in Priest Pot

				Overall $\bar{D}$	
Species	Temp. range	Chlorophyll	Oxycline	Isothermal	Stratified
K.cochlearis	3-24	**	*	2.25	0.97
K.quadrata	3-24	**	**	2.34	1.15
B.calyciflorus	9-16	**	-	1.30	0.87
B.angularis	9-16	*	-	1.72	0.91
P.vulgaris	3-24	**	*	2.01	0.83
F.terminalis	3-16	ns	-	2.44	1.26
F.brachiata	9-21	-	**	1.15	0.63
A.fissa	9-24	ns	**	1.67	1.30
S.kitina	3-24	**	*	1.38	0.82
S.pectinata	3-21	**	ns	1.30	0.61

**, significant at 1% level; *, significant at 5% level; ns, not significant.

(1982). Most species, however, were tolerant of the temperature changes occurring in Priest Pot and the two warm stenotherms, A.fissa and F.brachiata, were not present in conditions where temperature in the oxygenated waters varies significantly with depth.

The light intensity may have been the reason most rotifers were less abundant in the top half metre, as all species seemed to avoid light intensities greater than 200 uE m^{-2} s^{-1} most having mean depths well below 50 $uEm^{-2}s^{-1}$ (often at undetectable light intensities).

The mean depth of the chlorophyll was positively correlated with all the species except F.terminalis and A.fissa (both of which are described by Pourriot (1977) as feeding mainly on bacteria). It is certain that at times algal densities were an important determining factor in the distribution of the rotifer populations. However, it is also possible that some of the correlation was due to both the algal and the rotifer populations responding to some other environmental factor.

Table 7.1 summarizes the observations on the vertical distributions and their possible causes. The depth of the oxycline sets a clear limit to the depth of water available to the aerobic rotifers. However, it is clear that its effect is less on some species than on others and some are able to exploit a food resource unavailable to the less tolerant species. Food availability is also sometimes important in explaining maxima. In Priest Pot the rotifer community is divided into surface species and deep water species, those that can tolerate low oxygen and those that cannot and those that are correlated with algal distributions and those that are primarily bacterial feeders. These divisions show the co-existence of many species within a relatively small volume of water and the exploitation of a wide variety of conditions.

CHAPTER EIGHT

The Vertical Migration of Planktonic Rotifers in Priest Pot

8.1 Introduction

The vertical distribution of rotifers may change from month to month or from week to week, as discussed in the previous chapter, or in a daily rhythm as a result of vertical migrations. There are numerous studies of diel migration in planktonic crustaceans (see reviews by Cushing, 1951 and Longhurst, 1976) but relatively few accounts of diel movement in rotifers. Most accounts of rotifer migration describe the general pattern of movement without relating these movements to changes in the environment. In an attempt to produce a more detailed study of rotifer migration and to relate the movements to changes in the animals′ physical, chemical and biotic environment, four twenty-four hour studies were carried out in 1983 ; in April, when the tarn was isothermal, in May and September, when stratification was weak, and in July when stratification was most intense. A fifth study, performed in November, gave insufficient data because rotifer numbers were very low.

8.2 Sampling Details

In all the twenty-four hour studies the sampling procedure was similar to that used for the routine weekly samples. A peristaltic pump and laminar flow sampling head were used to collect the samples from the chosen depths. Oxygen and temperature profiles were measured using a Yellow Springs probe and meter and light profiles were taken with a Lambda light sensor and Fluke multimeter. The sampling was always at the centre buoy. Sub-samples of water for chlorophyll extraction were processed within 12-24 hours and chlorophyll *a* equivalent values were read on a scanning spectrophotometer after extraction in hot methanol. Processing of all the rotifer samples was begun within two hours of collection. In April, when rotifer numbers were low, two-litre sub-samples were concentrated by reverse filtration through a 35 um filter before sedimentation. On the other three dates, when rotifer numbers were higher, one litre samples were concentrated directly by sedimentation to a final volume of 10ml. Non-acetic Lugol's iodine was used as a killing agent and fixative. Subsequently, 1ml sub-samples of the sedimented concentrate were transferred to a glass Sedgewick-Rafter cell for counting. A modified Sinclair ZX81 microcomputer was used instead of mechanical counters to keep the tally.

In April the samples were collected every three hours but on the other three dates the sampling was more frequent around sunrise and sunset. The sampling depth interval was also varied according to conditions in the tarn. In April, May and September the interval was 0.4 m but in July the interval was changed to 0.2 m in the epilimnion with additional samples taken at 1.4,1.8 and 2.8 m in the anoxic hypolimnion.

The numbers of animals collected from each depth were converted to percentages and their vertical distribution displayed on this relative scale. Since many of these vertical distributions were skewed, the mean depth (D) was calculated using the weighted expression :

$$\bar{D} = \sum_{i}^{tot} D_i N_i^2 / \sum_{i}^{tot} N_i^2$$

where D_i is the depth of the ith sample and N_i the concentration of animals at that depth.

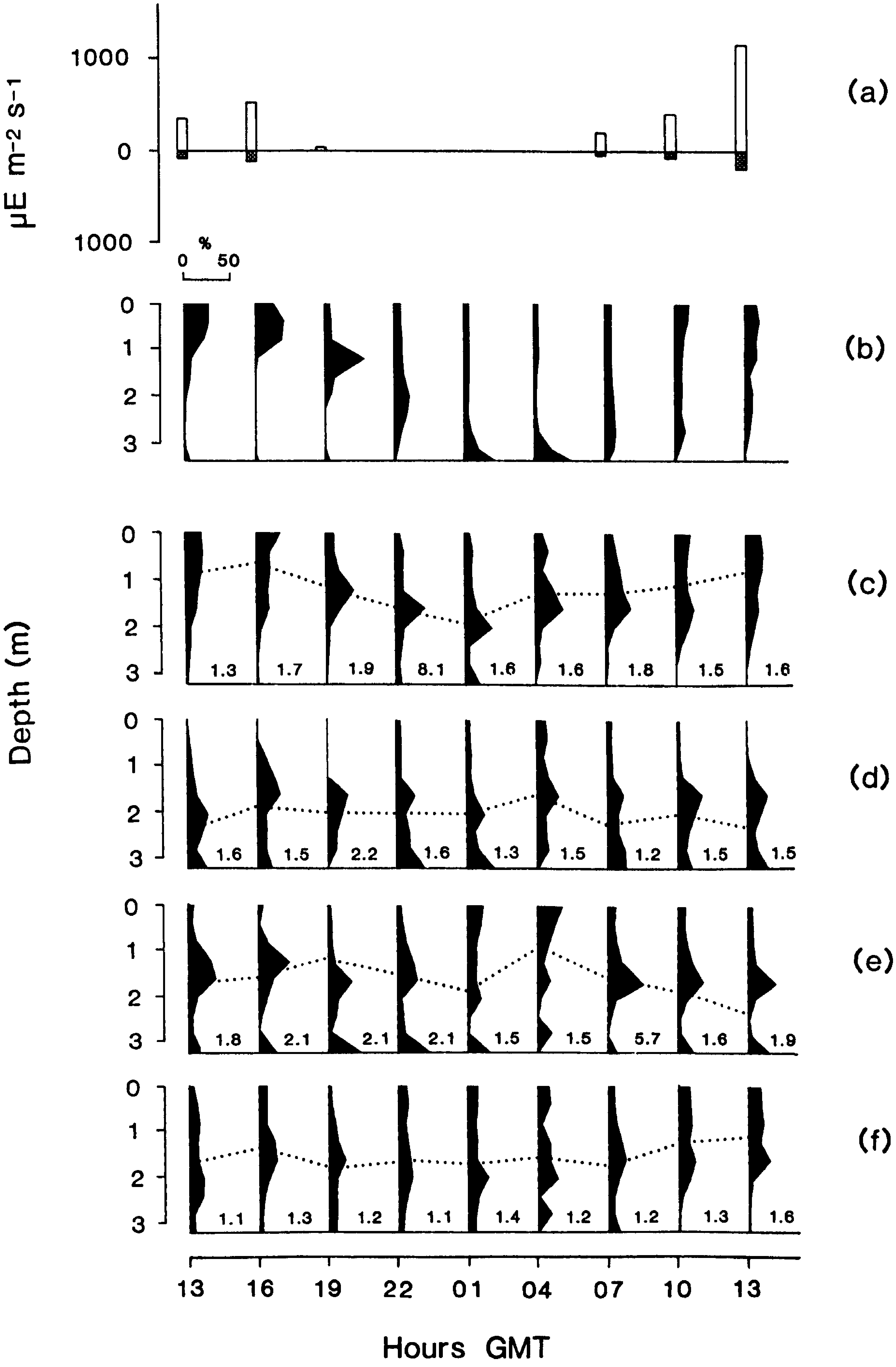
8.3 Results

Figure 8.1 shows the diel change in the vertical distribution of the four most abundant rotifer species in Priest Pot on 13-14 April 1983. At this time the tarn was isothermal at 7-8°C and the water column well mixed, with oxygen concentrations ranging from 10-16 mg l^{-1}. The weather over the two days was wet with winds of up to 8 m s^{-1} during daylight hours; the sun rose at 05:00h and set at 19:00h GMT. The mean concentration of chlorophyll *a* in the water column was 270 ug l^{-1} and 80-90% of incident light was attenuated in the top 0.5 m (Fig.8.1.a). The phytoplankton was dominated by a *Synura* species (Chrysophyceae) which performed a pronounced reverse migration, moving away from the surface at night and returning the following day (Fig.8.1.b).

The vertical movements of *Keratella cochlearis* (Fig.8.1.c) closely followed the *Synura*. During the day more than 50% of the population was in the top metre of the column. After dusk a peak developed at 1.20 m and moved downwards through the night until it reached 2.00 m at 01:00h. During the day the population dispersed upwards again. The diel movements of *Keratella quadrata* (Fig.8.1.d) were less pronounced than *K.cochlearis*, but

Figure 8.1. The vertical migration of the rotifers in Priest Pot on April 13/14 1983. (a) The light intensity at the surface (open blocks) and at 0.5 m depth measured in $uEm^{-2}s^{-1}$. (b) Chlorophyll a profiles. The chlorophyll a at each depth is the quantity present in the sample from that depth, expressed as a percentage of the total chlorophyll a in the profile. (c to f) Rotifer profiles with the mean depths joined by dotted lines. The numbers have been converted to percentages in the same way as the chlorophyll a values. Species illustrated are (c) Keratella cochlearis, (d) Keratella quadrata, (e) Filinia terminalis and (f) Polyarthra vulgaris.

The values given by each profile represent Lloyd's Index of patchiness calculated using the equation given on page 52. The index is unity for random distributions, less than unity for regular distributions and greater than unity for aggregated distributions.



μE m-2 s-1
1000
0
1000
(a)
0 % 50
Depth (m)
0
1
2
3
(b)
(c)
1.3
1.7
1.9
8.1
1.6
1.6
1.8
1.5
1.6
(d)
1.6
1.5
2.2
1.6
1.3
1.5
1.2
1.5
1.5
(e)
1.8
2.1
2.1
2.1
1.5
1.5
5.7
1.6
1.9
(f)
1.1
1.3
1.2
1.1
1.4
1.2
1.2
1.3
1.6
13
16
19
22
01
04
07
10
13
Hours GMT

this species also moved into deeper water at night. In contrast, Filinia terminalis (Fig.8.1.e) performed a very definite nocturnal migration even though a proportion of the population stayed near the bottom. This lower peak contained up to 34% of the F.terminalis in the column. The other peak occurred at 1.20 m and 1.60 m during the day and evening but moved to the surface at night before sinking again the following day. The only other abundant species, Polyarthra vulgaris (Fig.8.1.f) showed no clear pattern of movement except perhaps a tendency to move deeper at night. During this diel study the overall rotifer numbers increased threefold. This could have been the result of the winds concentrating the rotifers into patches which then affected the results by drifting through the sampling point.

The tarn began to stratify in May and by the 23rd of the month a pronounced oxycline had formed between 2.0 and 2.5 m (Fig.8.2.b). The hypolimnetic temperature was now 10 °C and the temperature in the epilimnion ranged from 11 to 16°C. The weather was cool with winds of up to 5 $m\ s^{-1}$ at times; the sun rose at 04:00h and set at 20:15h GMT. The average concentration of chlorophyll a in the water column was 434 $ug\ l^{-1}$ and the proportion of incident light attenuated in the top 0.5 m ranged from 60 to 80% (Fig.8.2.a). The phytoplankton was dominated by the large, motile dinoflagellate Peridinium lomnickii which, on the afternoon of 23 May, was concentrated at a depth of 1.5-1.6 m but on the morning of the 24th moved towards the surface in a definite reverse migration.

Throughout the twenty-four hour period, the rotifers

Figure 8.2. The verical migration of the rotifers in Priest Pot on May 23/24 1983. (a) Light intensity at the surface (open blocks) and at 0.5 m depth (shaded blocks) measured in $uEm^{-2}s^{-1}$. (b) Chlorophyll a profiles, the oxycline is marked as a solid line. (c to f) Rotifer profiles with the mean depths joined by a dotted line. Species shown are (c))Keratella cochlearis, (d) Keratella quadrata, (e) Filinia terminalis, (f) Polyarthra vulgaris, (g) Brachionus calyciflorus and (h) Brachionus angularis.

The values given by each profile represent Lloyd's Index of patchiness calculated using the equation given on page 52. The index is unity for random distributions, less than unity for regular distributions and greater than unity for aggregated distributions.

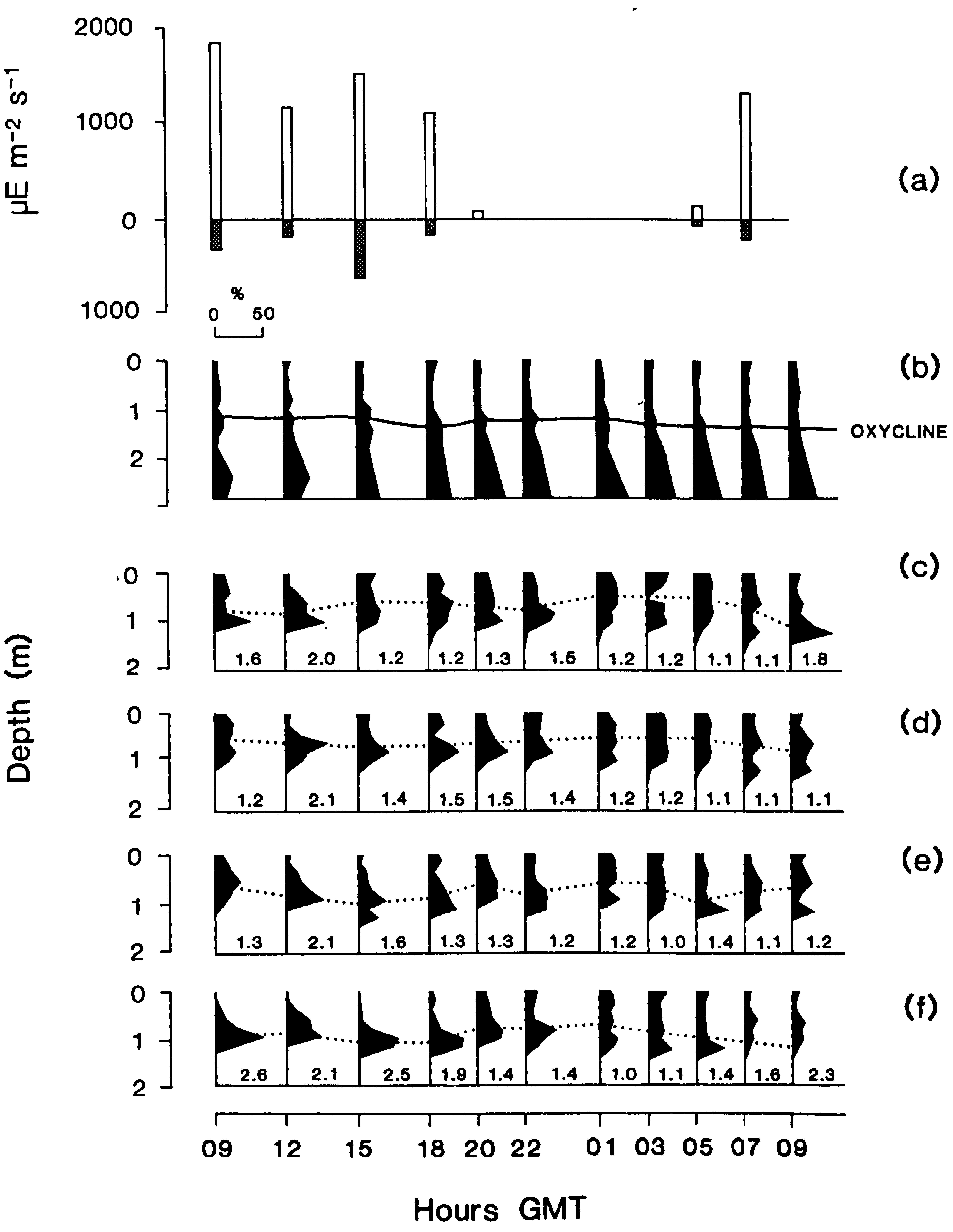

μE m⁻² s⁻¹
2000
1000
0
1000
0 % 50
(a)
(b)
OXYCLINE
(c)
1.3 1.7 1.7 1.7 1.7 1.7 2.0 1.6 1.8 2.6 1.4
(d)
1.3 2.4 1.6 1.9 2.1 1.1 1.2 1.6 1.6 1.6 1.6
(e)
1.6 1.5 1.7 1.5 1.6 2.0 1.5 2.5 1.3 1.4 1.9
(f)
1.5 2.0 1.4 1.7 1.7 1.6 1.4 1.6 1.4 1.4 1.4
(g)
(h)
Depth (m)
0
1
2
3
09 12 15 18 20 22 01 03 05 07 09
Hours GMT

were confined to the top 2.25 m of oxygenated water. The rotifer migrations were not especially pronounced but *K.cochlearis* (Fig.8.2.c) and *P.vulgaris* (Fig.8.2.f) moved deeper at night and *F.terminalis* (Fig.8.2.e) performed a weak nocturnal migration. The movements of *K.quadrata* (Fig.8.2.d) were irregular and the depth distributions frequently bimodal. The two species of *Brachionus*, *B.calyciflorus* (Fig.8.2.g) and *B.angularis* (Fig.8.2.h), showed no definite movement but they did show distributions markedly different to those of the two species of *Keratella* and of *P.vulgaris*. These three species were concentrated around the depth of the algal maximum throughout the study while *B.calyciflorus*, *B.angularis* and also *F.terminalis* all had their highest numbers in the surface metre of the tarn while population densities were much lower at the algal maximum.

On the 18 and 19 July, epilimnetic temperatures ranged from 20 to 24 °C and a very steep oxycline had formed between 1.1 and 1.3 m (Fig.8.3.b). The weather was calm and sunny and the sun rose at 04:00h and set at 20:30h GMT. The mean concentration of chlorophyll *a* in the epilimnion was 203 ug l^{-1} and the hypolimnion contained a dense population of photosynthetic bacteria (Fig.8.3.b). This showed up as a large peak of chlorophyll *a* because the extraction method shifted the peak absorbance wavelength of the bacterial chlorophyll to 665 nm. The proportion of incident light attenuated in the top 0.5 m (Fig.8.3.a) ranged from 60 to 80% of surface light intensity.

Figure 8.3. The vertical migration of the rotifers in Priest Pot on July 18/19 1983. (a) Light intensity at the surface (open blocks) and at 0.5 m depth (shaded blocks) measured in $uEm^{-2}s^{-1}$. (b) Chlorophyll a profiles with the oxycline marked by a solid line. (c to f) Rotifer profiles with the mean depths at each time joined by a dotted line. Species illustrated are (c) *Keratella cochlearis*, (d) *Keratella quadrata*, (e) *Polyarthra vulgaris* and (f) *Anuraeopsis fissa*.

The values given by each profile represent Lloyd's Index of patchiness calculated using the equation given on page 52. The index is unity for random distributions, less than unity for regular distributions and greater than unity for aggregated distributions.



µE m-2 s-1
2000
1000
0
1000
(a)
%
0 50
(b)
0
1
2
OXYCLINE
Depth (m)
(c)
0
1
2
1.6 2.0 1.2 1.2 1.3 1.5 1.2 1.2 1.1 1.1 1.8
(d)
0
1
2
1.2 2.1 1.4 1.5 1.5 1.4 1.2 1.2 1.1 1.1 1.1
(e)
0
1
2
1.3 2.1 1.6 1.3 1.3 1.2 1.2 1.0 1.4 1.1 1.2
(f)
0
1
2
2.6 2.1 2.5 1.9 1.4 1.4 1.0 1.1 1.4 1.6 2.3
09 12 15 18 20 22 01 03 05 07 09
Hours GMT

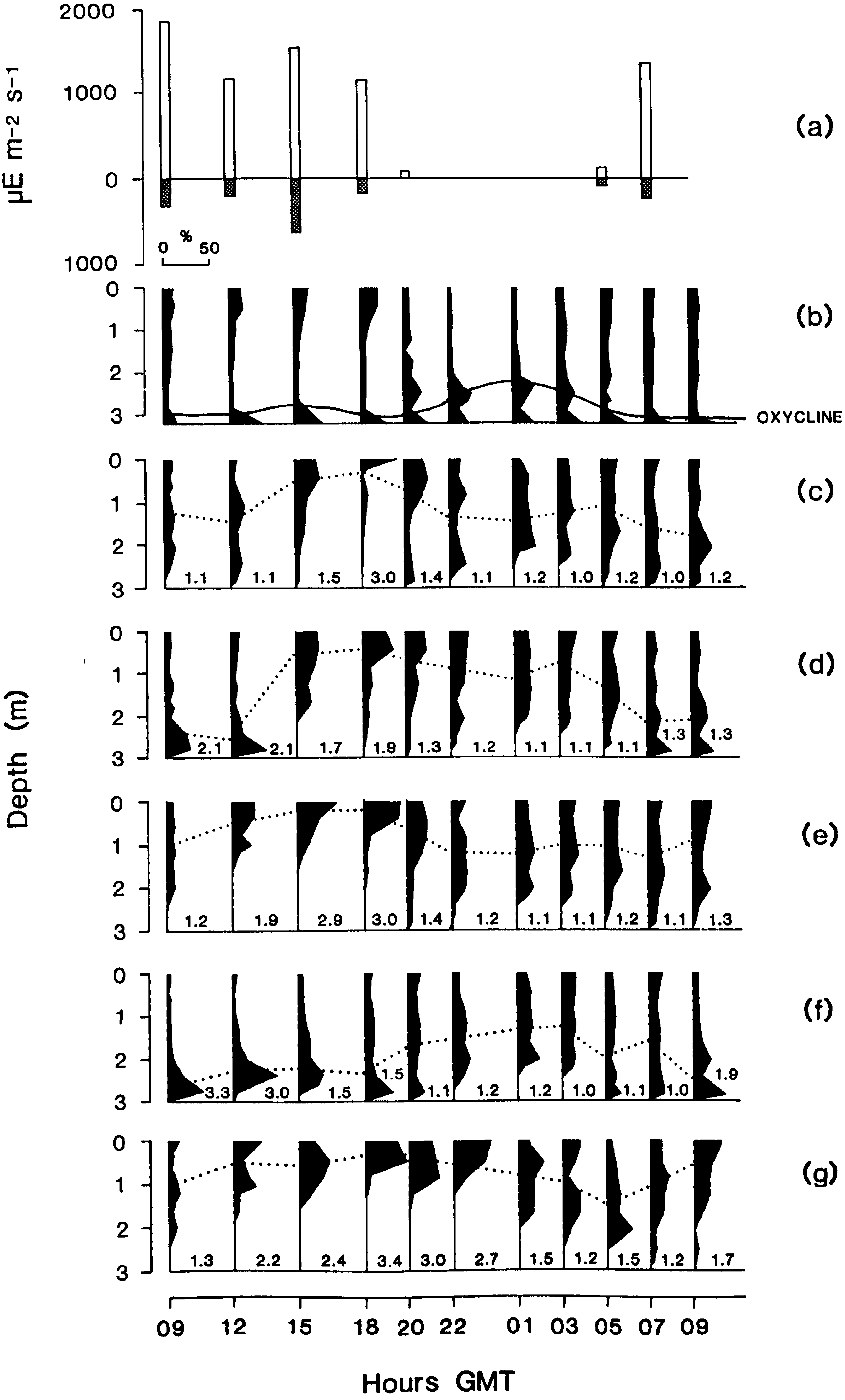
Four species of rotifer were abundant in the tarn: *K.cochlearis*, *K.quadrata*, *P.vulgaris* and *Anuraeopsis fissa*. There was no clear pattern of migration, but all four species dispersed upwards during the night and most reaggregated at depth the following day (Fig.8.3.c-f). Throughout the twenty-four hour period, *A.fissa* tended to remain deeper in the water column than the other three species and at times considerable numbers were recovered from anoxic water.

In early September the tarn was beginning to destratify. By 5 September, the water column was relatively well mixed but there was still some deoxygenation above the sediment (Fig.8.4.b). The boundary of the deoxygenated water moved upwards in late evening as photosynthetic oxygen production declined. The weather was dry with winds of 6 m s^{-1} gusting to 12 m s^{-1}; the sun rose at 05:00h and set at 18:30h GMT. The proportion of incident light reaching a depth of 0.5 m ranged from 80 to 100% of surface light intensities (Fig.8.4.a). The chlorophyll *a* profiles (Fig.8.4.b) show considerable vertical movement in the epilimnion. The phytoplankton was dominated by the Chrysophyte *Synura* which migrated towards the surface in late afternoon and became concentrated above the oxycline at night.

Five species of rotifers were abundant in the plankton. *K.cochlearis* (Fig.8.4.c), *K.quadrata* (Fig.8.4.d) and *P.vulgaris* (Fig.8.4.e) followed the upward movement of the algae quite closely but dispersed downwards during the night. They all became concentrated in the top 0.5 m of the tarn at 18:00h. *K.cochlearis* was

Figure 8.4. The vertical migration of the rotifers in Priest Pot on September 5/6 1983. Light intensity at the surface (open blocks) and at 0.5 m depth (shaded blocks) measured in $uEm^{-2}s^{-1}$. (b) Chlorophyll _a_ profiles with the oxycline marked as a solid line. (c to g) Rotifer profiles with the mean depths at each time joined by a dotted line. The species illustrated are (c) _Keratella cochlearis_, (d) _Keratella quadrata_, (e) _Polyarthra vulgaris_, (f) _Anuraeopsis fissa_ and (g) _Filinia brachiata_.

The values given by each profile represent Lloyd's Index of patchiness calculated using the equation given on page 52. The index is unity for random distributions, less than unity for regular distributions and greater than unity for aggregated distributions.


2000
1000
0
1000
µE m⁻² s⁻¹
0 % 50
(a)
(b)
OXYCLINE
(c)
1.1 1.1 1.5 3.0 1.4 1.1 1.2 1.0 1.2 1.0 1.2
(d)
2.1 2.1 1.7 1.9 1.3 1.2 1.1 1.1 1.1 1.3 1.3
(e)
1.2 1.9 2.9 3.0 1.4 1.2 1.1 1.1 1.2 1.1 1.3
(f)
3.3 3.0 1.5 1.5 1.1 1.2 1.2 1.0 1.1 1.0 1.9
(g)
1.3 2.2 2.4 3.4 3.0 2.7 1.5 1.2 1.5 1.2 1.7
Depth (m)
0 1 2 3
09 12 15 18 20 22 01 03 05 07 09
Hours GMT

dispersed throughout the column at first but it moved upwards to form a peak at the surface at 18:00h before redispersing during the night. On the second day a peak developed at 2.00 m. Although the population of K.quadrata was declining in September it showed a significant movement upwards from a peak in the bottom metre of the epilimnion to one at the surface before dispersing again. P.vulgaris was quite dispersed in the water column but at 18:00h more than 80% of the population became concentrated in the top 0.5 m. The movements of Filinia brachiata (Fig.8.4.g) were more irregular. This species also moved towards the surface in late afternoon but did not disperse until well into the night. The movements of A.fissa (Fig.8.4.f) were quite unlike those of the other rotifers. This population had a maximum directly above the oxycline and tended to vary its position as the depth of the oxycline changed.

Fig.8.5 shows the light intensity experienced over 24 h by four rotifer species at their estimated mean depths. All the rotifers tended to aggregate in a relatively narrow range of light conditions. In summer, surface light intensities may exceed 1500 uE $m^{-2}s^{-1}$ but the rotifers were most frequently found at intensities below 100 uE $m^{-2}s^{-1}$.

In Fig.8.6 the oxygen concentration experienced over 24 h by three rotifer species, K.cochlearis, P.vulgaris and A.fissa, at their estimated mean depths is shown. It shows that K.cochlearis and P.vulgaris were often abundant in well oxygenated water whereas A.fissa tended

Figure 8.5. The light intensity experienced over 24 h by four rotifer species, *Keratella cochlearis*, *Keratella quadrata*, *Polyarthra vulgaris* and *Anuraeopsis fissa*, at their mean depths. The four dates shown are △ April 13/14 ○ May 23/24, ● July 18/19 and □ September 5/6 1983.


K.cochlearis
μEm^{-2}s^{-1}
100
0
0
12
24
K.quadrata
100
0
0
12
24
P.vulgaris
100
0
0
12
24
A.fissa
100
0
0
12
24
hours
GMT

Figure 8.6. The oxygen concentration experienced over 24 h by three rotifer species, *Keratella cochlearis*, *Polyarthra vulgaris* and *Anuraeopsis fissa*, at their estimated mean depths. The four dates shown are △ April 13/14, ○ May 23/24, ● July 18/19 and □ September 5/6.1983.

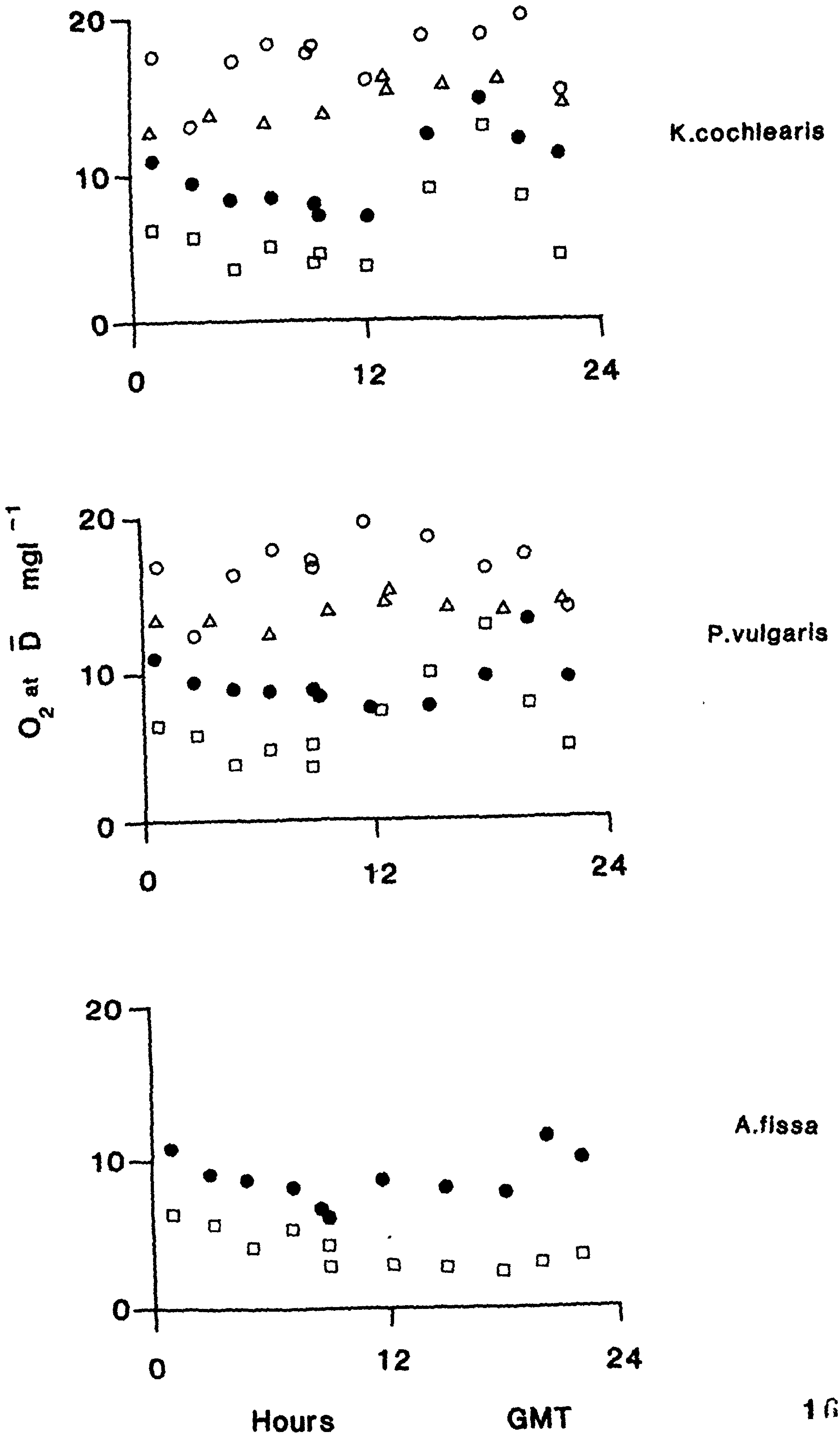
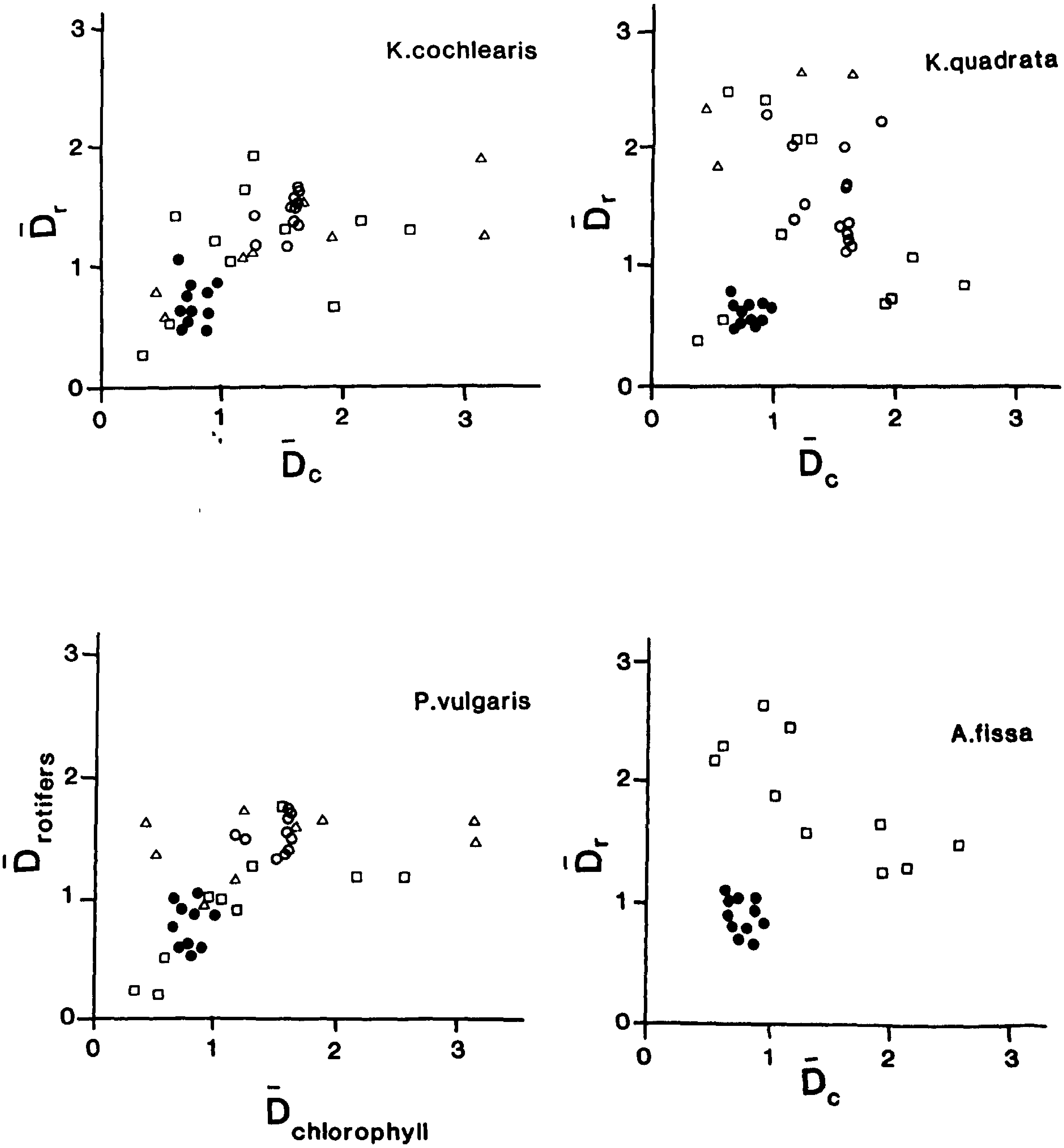
20
10
0
0
12
24
K.cochlearis
O_2 at $\bar{D}$ mgl^{-1}
20
10
0
0
12
24
P.vulgaris
20
10
0
0
12
24
A.fissa
Hours GMT

Figure 8.7. The mean depths of four rotifer species plott against the mean depths of the chlorophyll distributions. The four rotifer species are *Keratella cochlearis*, *Keratella quadrata*, *Polyarthra vulgaris* and *Anuraeopsis fissa* and the dates are △ April 13/14, ○ May 23/24, ● July 18/19 and □ September 5/6.


K.cochlearis
K.quadrata
P.vulgaris
A.fissa
$\bar{D}_r$
$\bar{D}_c$
$\bar{D}_{rotifers}$
$\bar{D}_{chlorophyll}$
0
1
2
3

to aggregate at lower oxygen concentrations.

Fig.8.7 shows that the vertical distribution of K.cochlearis and P.vulgaris was strongly related to the vertical distribution of the phytoplankton. In contrast, the vertical distribution of K.quadrata and A.fissa bore little relationship to the movements of the phytoplankton in the epilimnion.

8.4 Discussion

The various patterns of rotifer migration observed in Priest Pot in 1983 are summarized in Table 8.1. The individual species did not follow any consistent pattern of movement. Upward nocturnal, reverse and irregular migrations could be undergone by the same species over different twenty-four hour periods. The migrations with the highest amplitudes were recorded in April and September when the rotifers were free to move through a 3 m oxygenated water column. In summer the intense physical and chemical stratification in the tarn confined the rotifers to the top 1-2 m and the amplitudes of migration were correspondingly reduced. The maximum ascending and descending velocities recorded in Table 8.1 are similar to those reported by George & Fernando (1970) for rotifers in the much deeper Sunfish Lake, Ontario.

Most of the dominant rotifers in Priest Pot performed reverse migrations at some time during the year. Reverse migration is usually thought of as abnormal behaviour in planktonic crustaceans (Hutchinson, 1967) but has often been reported in planktonic rotifers. George & Fernando (1970) found that both P.vulgaris and F.terminalis

TABLE 8.1. SUMMARY OF THE RESULTS FROM THE FOUR TWENTY-FOUR HOUR STUDIES PERFORMED IN 1983.

SPECIES	DATE	TYPE	AMPLITUDE of MIGRATION (m)	MAXIMUM SPEED of ASCENT cmsec^{-1}	MAXIMUM SPEED of DESCENT cmsec^{-1}
K.cochlearis	April	R	1.36	.006	.005
	May	R	.48	.003	.003
	July	N	.59	-	-
	Sept	MR	1.39	.008	.009
K.quadrata	April	R	1.11	.004	.006
	May	I	.89	.008	.003
	July	N	.23	-	-
	Sept	MR	2.09	.018	.012
P.vulgaris	April	I	.73	.005	.004
	May	R	.40	-	-
	July	N	.46	-	-
	Sept	MR	1.07	.005	.007
F.terminalis	April	N	1.63	.009	.006
	May	N	.59	.005	.004
F.brachiata	Sept	I	1.28	.007	.008
A.fissa	July	N	.48	-	-
	Sept	N	1.43	.012	.009

R : reverse migration
N : nocturnal upward migration
I : irregular movements
MR : modified reverse migration

performed reverse migrations under snow-covered ice. Similar migrations were recorded in high mountain lakes for *K.quadrata* by Pennak (1944) and for *K.cochlearis* by Cruz-Pizarro (1978). Reverse migration of *Asplanchna priodonta* was found in a eutrophic pond by Dumont (1972). In this case the movement was an almost exact reverse of that shown by the cladoceran, *Bosmina*. This was explained as interspecific competition, the *Asplanchna* were thought to be avoiding the very high concentrations of cladocerans. At lower population densities of *Bosmina* the rotifer showed a normal nocturnal migration.

In Priest Pot the most pronounced reverse migrations were associated with similar diel movements of the phytoplankton. Diel vertical migrations of motile phytoplankton have frequently been reported in lakes (Talling, 1971; George & Heaney, 1978; Lund & Reynolds, 1982). The range of movements is quite varied but many species tend to move away from the surface at night and accumulate in mid-water. This is similar to the behaviour shown by the chrysophyte algae in Priest Pot in both April and September. Such deep water maxima are sometimes associated with nutrient depletion (Heaney & Eppley, 1981) but the evidence for nutrient scavenging is equivocal. It is not at all clear why the rotifers should follow the migrating phytoplankton in Priest Pot as *Synura* and *Peridinium*, the dominant species, are probably too large to ingest (Pourriot, 1977). It may be possible for some of the rotifers to feed on the colonial form, *Synura*, by taking single cells from the colony (A.Ruttner-Kolisko, personal communication). The spatial association between the rotifers and the phytoplankton may, however, not be related to feeding but may simply reflect a common response to incident light (George, 1983).

The only rotifer species which persistently moved independently of the phytoplankton was A.fissa. This species was found associated with low oxygen levels throughout its occurrence in 1983. In both July and September it was found in the highest numbers near the oxycline and in the latter study it showed active movement to maintain this position as the depth of the oxycline fluctuated. It is known that A.fissa feeds almost exclusively on detritus and bacteria (Pourriot, 1977) and this may be why it was invariably associated with the oxycline where bacterial numbers are high.

CHAPTER NINE

Experimental Investigations of the Vertical Migration of the Planktonic Rotifers in Priest Pot

9.1 Introduction

The diurnal studies carried out in 1983 showed that the planktonic rotifers in Priest Pot perform some degree of vertical migration. In 1984 an *in situ* experimental system was designed to investigate the effects of incident light on these vertical movements.

9.2 General Principles

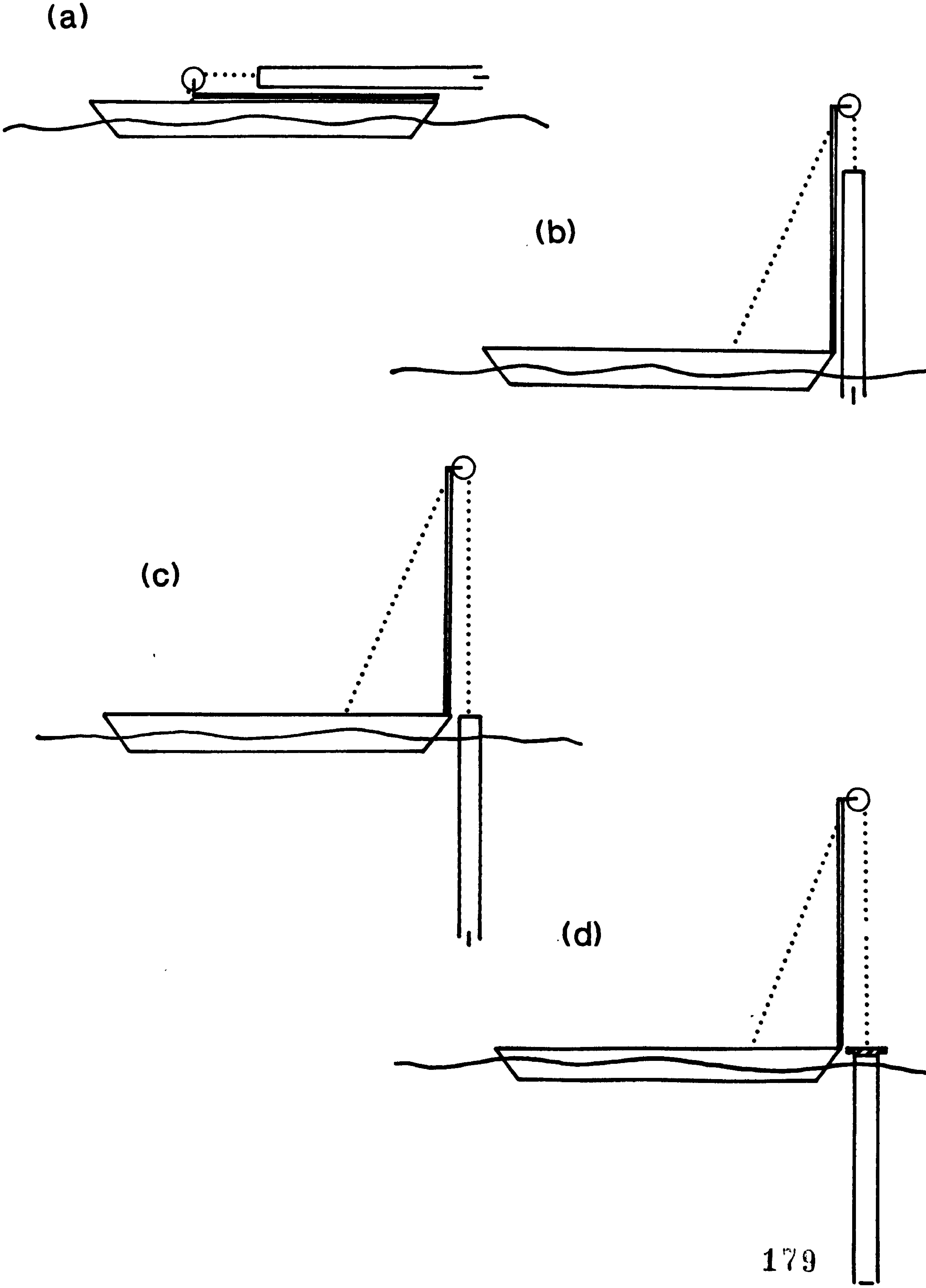
Phytoplankton migrations have been investigated in the laboratory using tubes in which field conditions are simulated. Eppley *et al*. (1968) used a 3 m by 10 m tube to reproduce a marine environment and observed vertical migrations in two dinoflagellates, *Gonyaulax polyedra* and *Cachonina niei*. A smaller tube (0.25 m by 2.02 m) was used by Heaney & Eppley (1981) to investigate further the migrations of dinoflagellates in marine waters. Booker *et al*. (1976) simulated the conditions found in a freshwater lake using a polyvinylchloride (PVC) cylindrical tube about 0.25 m by 2 m, illuminated from above and covered at the bottom. This was used in studies on the stratification of *Anabaena flos-aquae*. The freshwater dinoflagellate, *Ceratium hirundinella*, was studied by Heaney & Furnass (1980) in PVC tubes (0.15 m by 1.63 m). Vertical migrations were induced in the *Ceratium* using an artificial light system to provide a 12:12 hour light:dark cycle.

Large experimental enclosures have been installed in lakes to manipulate enclosed plankton communities. The Lund tubes in Blelham Tarn in the English Lake District, described by Lund & Reynolds (1982), enclosed c.18000 m^3 and were permanent enclosures in which long term ecological and experimental studies of the phytoplankton and the zooplankton were performed.

The tube used in Priest Pot was more similar to the laboratory tubes than to the large, permanent enclosures both in terms of size and time scale of use. It was designed to be removed from the tarn after each experiment, then replaced in position before the next. The epilimnion of Priest Pot in the summer is rarely deeper than two metres so the tube used was built to enclose a column of water about 2.5 m in depth. A flat bottomed boat was fitted with stabilizing outriggers and modified to hold a metal cradle to which the tube could be strapped (Fig. 9.1.a). This cradle pivoted near one end and, with the help of counterweights, the tube could be raised into an upright position (Fig. 9.1.b) from which it could be lowered vertically into the tarn (Fig. 9.1.c) to enclose a relatively undisturbed column of water containing the natural plankton community. The tube could then be sealed by a hinged door at the bottom and made light tight by the addition of a lid at the top (Fig. 9.1.d). The column of water so enclosed could then be used for experiments concerning the effect of incident light on the rotifer movements.

Figure 9.1. Schematic diagram illustrating how the equipment is used. (a) The tube in position on the boat, strapped to the gantry. (b) The gantry swung into the upright position with the butterfly valve open. (c) The column lowered into the tarn. (d) The tube sealed by closing the butterfly valve and made light tight by the addition of a light tight lid at the top.

Figure 9.1



A series of experiments were carried out in Priest Pot during the late summer of 1984 using the experimental tube.

(1) In order to determine how much, if at all, the tube changed the behaviour of the enclosed rotifers a 24hr study was performed in July with almost simultaneous sampling inside and outside the tube.

(2) Investigations into the effect of the light environment on the migrations were carried out.

(a) the effect of the absence of light was investigated by cutting out all light from the tube throughout a 24 h sampling period.

(b) the response of the enclosed community to a 4:4 hour light:dark cycle was investigated on two separate occasions for periods of 10.5 and 12 hours respectively.

9.3 Constructional Details

The tube was made from sheets of aluminium, 16 S.W.G., which were formed into cylinders 30 cm in diameter and strengthened with hoops of PVC. The tube was built in two sections which could be bolted together to form a single 3 m tube (Fig. 9.2.a).

The top section was 1.20 m in length and was fitted with a bridle to which a rope could be attached for raising and lowering the whole apparatus. The lower section was 1.80 m in length and was fitted with a perspex door that could be operated from the surface by wires (Fig. 9.2.b).

Figure 9.2.a. A sectional view of the column.

Figure 9.2.b. A sectional view of the butterfly valve showing the closing mechanism.

Figure 9.2.c. The sampling head showing the position of the combined temperature and oxygen probe and the light sensor.

Figure 9.2.a.

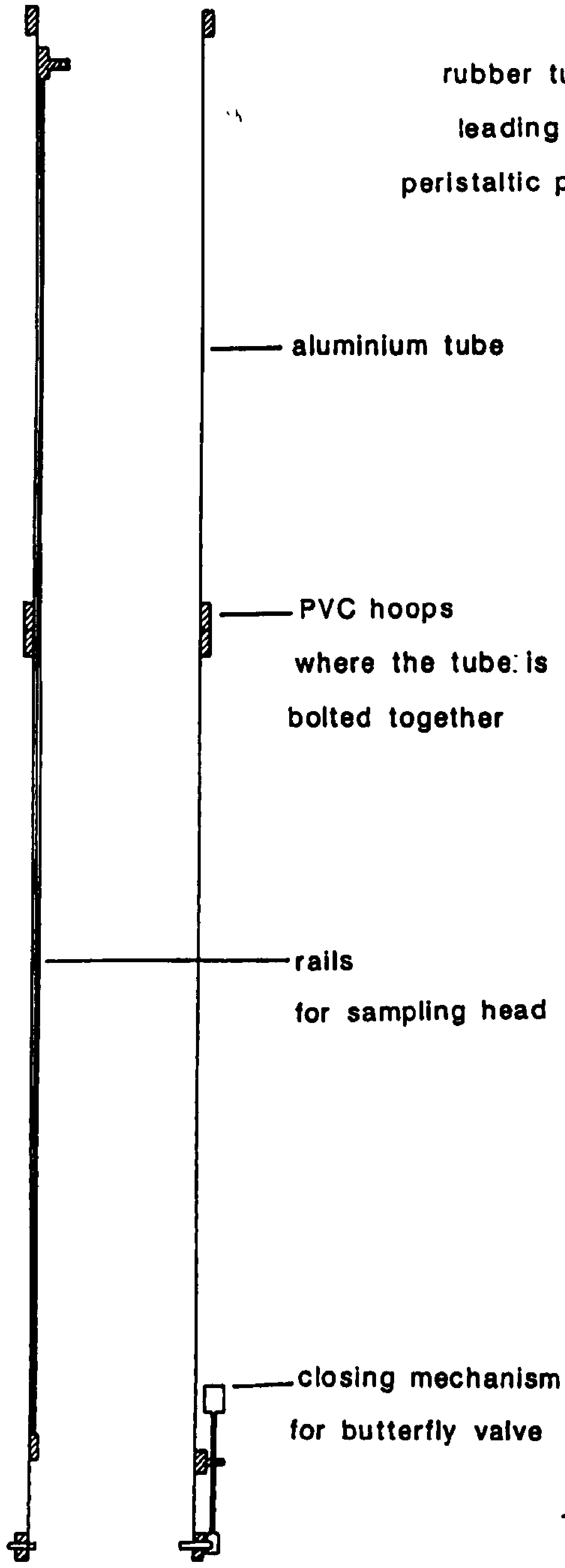


Figure 9.2.c.

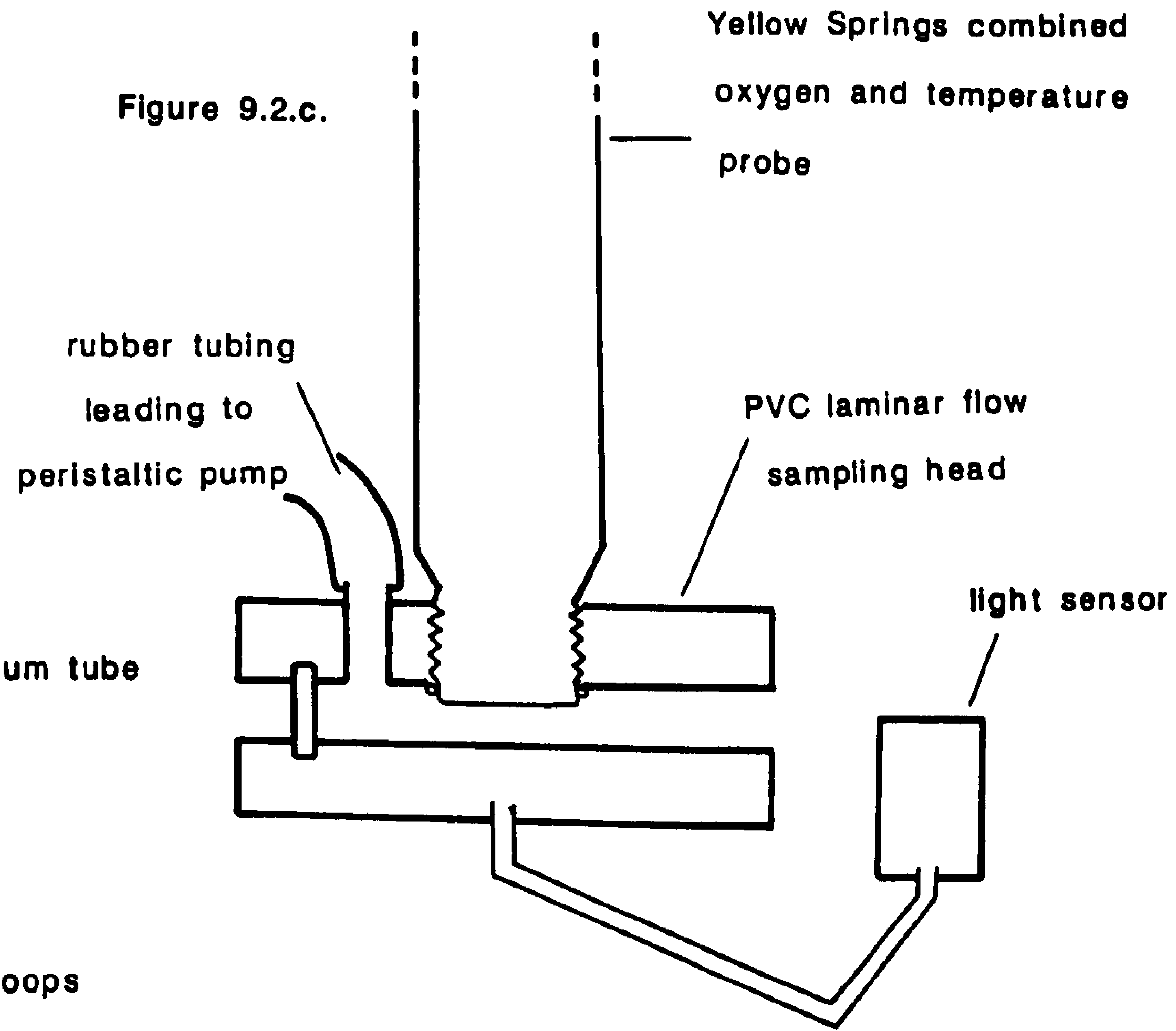
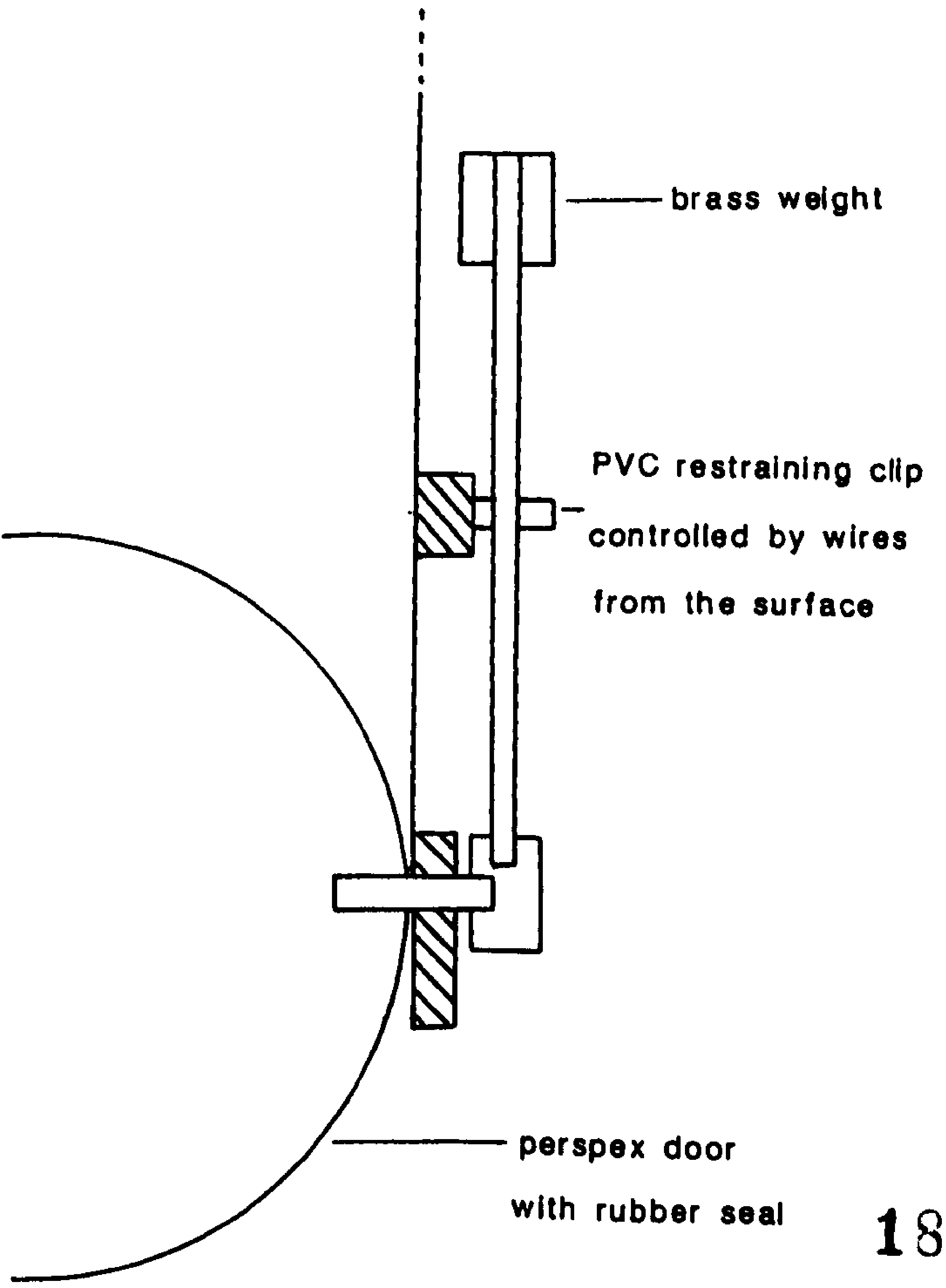


Figure 9.2.b.



A sampling head ran on rails along the inside of the tube, for this purpose a PVC pulley and block were attached to the inside of the tube, 30 cm from the top. A 3 cm diameter hole was cut in the aluminium just above the pulley, through which the sampling tube and probe leads could pass. A guard of black bristle was fitted to the hole to prevent the entry of light. Two aluminium rails were inserted into the PVC block at the top of the tube and ran to a similar block in the lower section. The rails were held rigid, 1 cm from the tube wall and provided a guide for the carriage on which the sampling head was mounted (Plate 9.1). This carriage ran along the guide rails holding the head a set distance from the walls of the tube. This distance was adjustable and was set at 15 cm for the experiments described here. The carriage was weighted with lead rings to ensure smooth running and had a PVC clamp attached which held a Yellow Springs combined oxygen and temperature probe onto which the sampling head fitted.

The sampling head (Fig.9.2.c , Plate 9.2) was a miniature version of the laminar flow head already described. The Yellow Springs probe screwed into the top plate of the head and held the sampling head perpendicular to the rails. The plastic tubing through which the samples were collected was 3mm inside diameter and was fitted to the top plate close to the probe. This ensured a flow of water across the probe membrane as the samples were taken. A Macam quantum radiometer/photometer Q101 (Macam Photometrics Ltd.,10 Kelvin Sq., Livingston,

Plate 9.2. The sampling head showing the carriage on which it runs, the temperature-oxygen probe and the light sensor.

Scotland) was fitted to a metal support at the side of the head. The probe lead was marked at 5 cm intervals to a depth of 2.5 m starting where the head was just below the water surface. The sensor lead and sampling tube were attached to it.

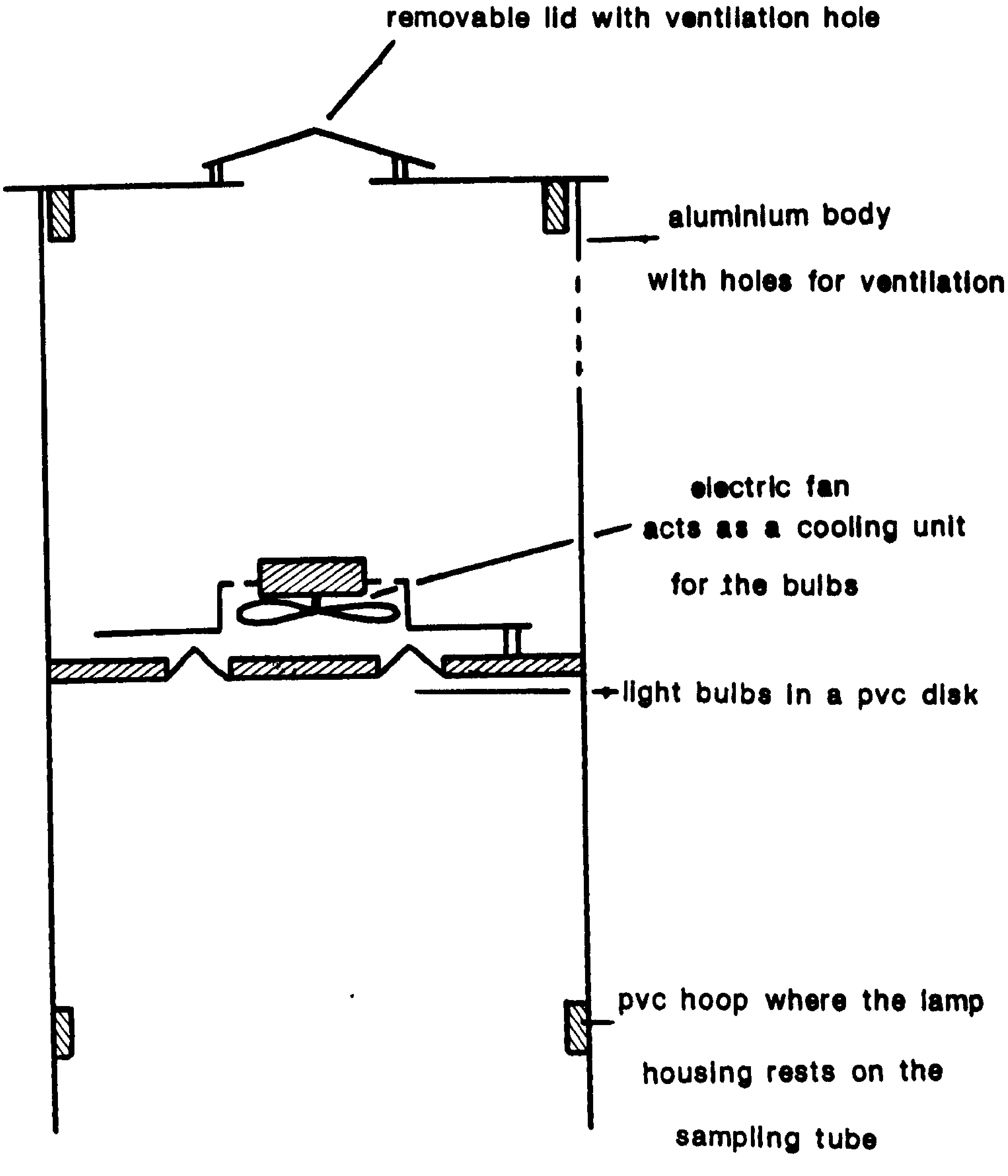
The assembled tube, once placed in position on the gantry, could be raised from a horizontal to a vertical position, Plate 9.3, in which the gantry was fixed using wire stays. The tube could then be lowered gently into the tarn with the perspex door open. A rope and webbing straps were used to hold the tube still once it was in position and a platform built out from the sampling boat allowed easy access to the equipment.

The lamps for illuminating the system were mounted in an aluminium cylinder, Fig. 9.3, which fitted over the top of the tube, Plate 9.4, making a light tight seal. A longer bridle was fitted to the tube once in position which fitted over the lamp housing. Four twelve volt projector bulbs were used to give a total illumination of 300 W. They stood in recessed holes in a metal plate which cut out light from all other sources. The lights were wired to a rheostat which gave five steps of illumination between complete darkness and maximum intensity, allowing simulation of dawn and dusk. An electric fan was fitted behind the lights, Plate 9.5. This reduced the heating effects from the light bulbs and prevented unnatural temperature changes occurring in the enclosed water column. The lights were powered by four 12 volt car batteries connected in parallel. These also ran the peristaltic pump that was used to collect the

Plate 9.3. The gantry being raised into an upright position for lowering of the tube into the tarn.

Figure 9.3. A sectional view of the lamp housing.

Figure 9.3


removable lid with ventilation hole
aluminium body
with holes for ventilation
electric fan
acts as a cooling unit
for the bulbs
light bulbs in a pvc disk
pvc hoop where the lamp
housing rests on the
sampling tube

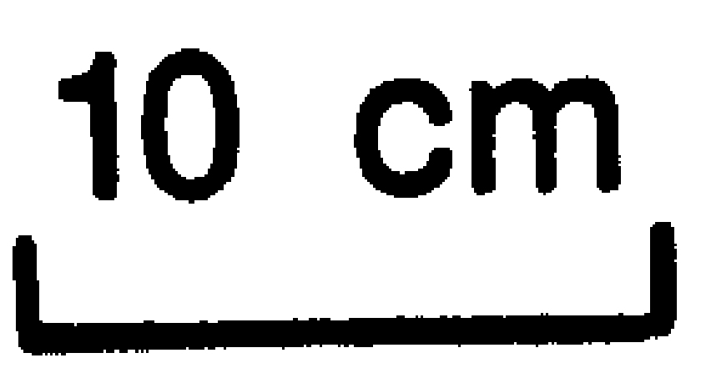
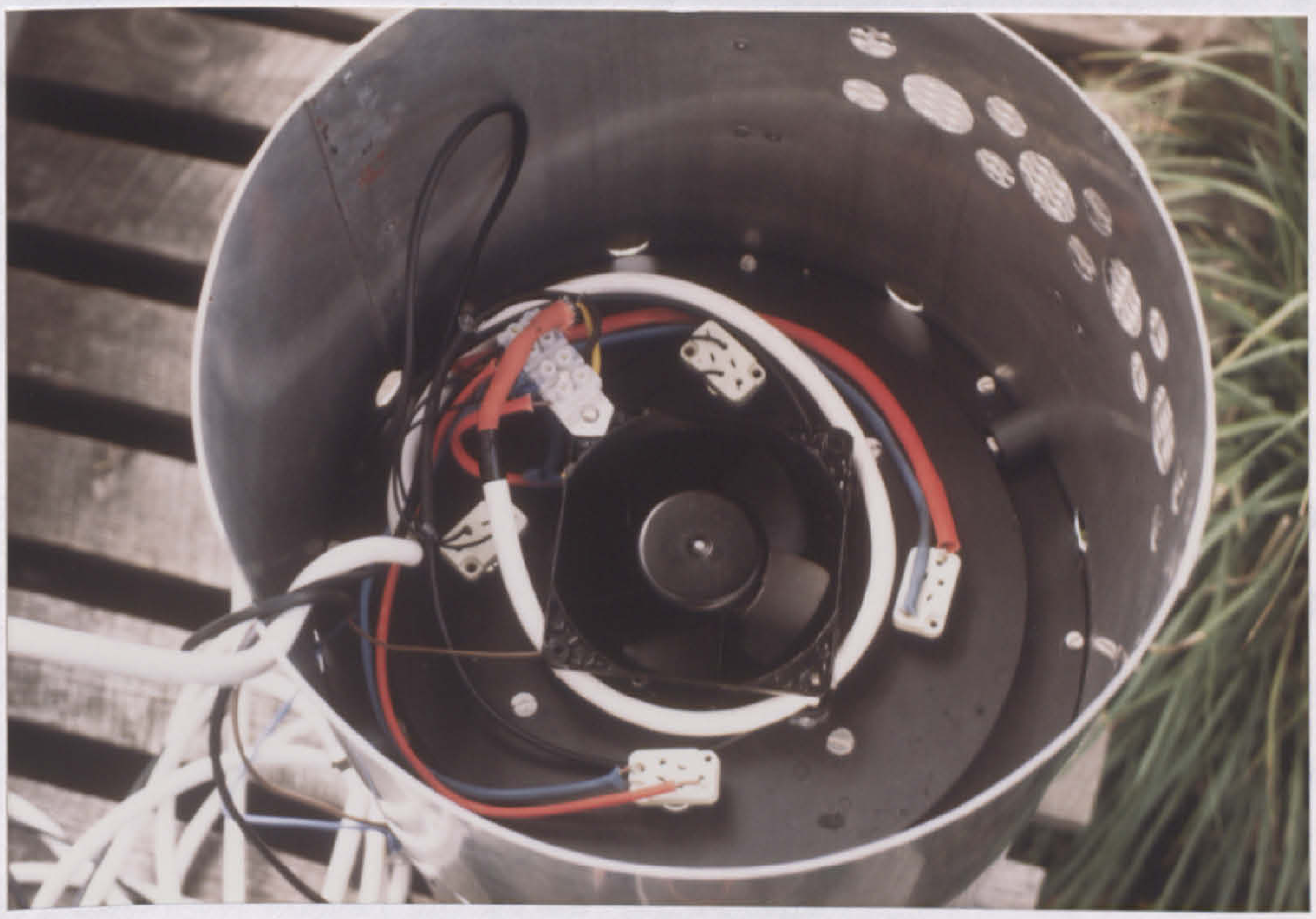

10 cm

Plate 9.5. A view of the top of the lamp housing showing the electric fan used for cooling the light bulbs.



samples. The fan was run on a separate circuit from a Cyclon rechargeable 12 V, 5 Ah lead acid battery.

9.4 Operation

The sectioned tube was transported out to the moored boat in its constituent pieces and assembled in situ as this was found to be the easiest procedure. The two aluminium cylinders were placed on the cradle and bolted together. A new membrane was fitted to the Y.S.I. probe and the probe re-calibrated before the sampling head and probe were assembled, attached to the carriage and placed on the aluminium rods. These rods were then secured into the drilled PVC blocks inside the tube and the sampling carriage checked to ensure that it was free running. The rope over the gantry pulley system was then shackled to the tube's bridle and the webbing straps tightened around the lower section of the tube. The apparatus was then ready for installation in the tarn as described in 9.2.

9.5 General Methods used in Sampling

In the first experiment, the sampling procedure in the tarn, alongside the experimental tube, was similar to that used throughout the fifteen months of routine sampling and has been described in Chapter Four. Water samples were pumped through a laminar flow sampling head from various depths down a water column. A Yellow Springs combined oxygen and temperature probe was attached to the sampling head and profiles were obtained at the time of sampling. Light profiles were measured using a Macam quantum radiometer/photometer Q101. This had been fitted to a punched metal disc to ensure that the photocell remained upright and level in the water.

Inside the tube, the water samples were taken using a peristaltic pump fitted with an adaptor to allow the use of a smaller bore tubing. Profiles of oxygen, temperature and light were taken concurrent with the samples.

A Turner Designs field fluorimeter, model 10-005, (Turner Designs, 2247 Old Middlefield Way, Mountainview, California, 94043, U.S.A.) was used to obtain estimates of algal density both in the tarn and in the tube. However it was found to be too sensitive for the very large concentrations found in Priest Pot and most of the readings were beyond the range of the equipment.

The samples taken, both inside the tube and in the tarn, were 100ml in volume and were fixed immediately with Lugol's iodine. On return to the laboratory the samples were concentrated by sedimentation to 2ml and a 1ml sub-sample of each was then counted in a glass Sedgewick-Rafter cell as described previously.

The estimated mean depths of the populations were calculated from the rotifer data and the migrations plotted as in Chapter Eight.

9.6 A Comparison of Tube and Tarn (17/18 July 1984)

9.6.1 Sampling Details

The tube was put into position in the tarn at 09:00 h on 17 July to allow an acclimatization period before the sampling started. Water samples were taken and profiles measured inside the tube and outside in the tarn at five times : 16:00 h, 22:00 h, 01:00 h, 04:00 h and 10:00 h.

In the tarn the sampling interval was 0.20 m from the surface to 2.00 m and a twelfth sample was taken at a depth of 2.50 m. The same sampling interval was used inside the tube down to 1.80 m (the extent of the guide rails).

9.6.2 Results

A comparison between the temperature and oxygen profiles in the tarn and in the enclosed water column show no great differences between the two environments (Fig.9.4), although the oxycline is somewhat depressed in the tube, the change from hypoxic to anoxic water being more gradual than in the tarn. The light profiles showed a decrease in light penetration in the tube (Fig.9.5).The lower light intensities were caused by the shading effect of the walls of the tube. There were no fundamental differences in the behaviour of the two communities (Fig.9.6).

Six species were present in significant numbers, of which two showed reverse migrations, two performed nocturnal migrations and the remaining two showed little movement.

Keratella cochlearis (Fig.9.6.b) showed the migration of the greatest amplitude (1.13 m in the tarn, 0.90 m in the tube) with a very definite downward movement which started before "dusk" and continued until 01:00 h. The direction of the movement then changed and the population moved upward in the water column, becoming more dispersed as it did so. This upward movement started before there was a detectable light level (<2.5 uE $m^{-2}s^{-1}$). The peak

Figure 9.4

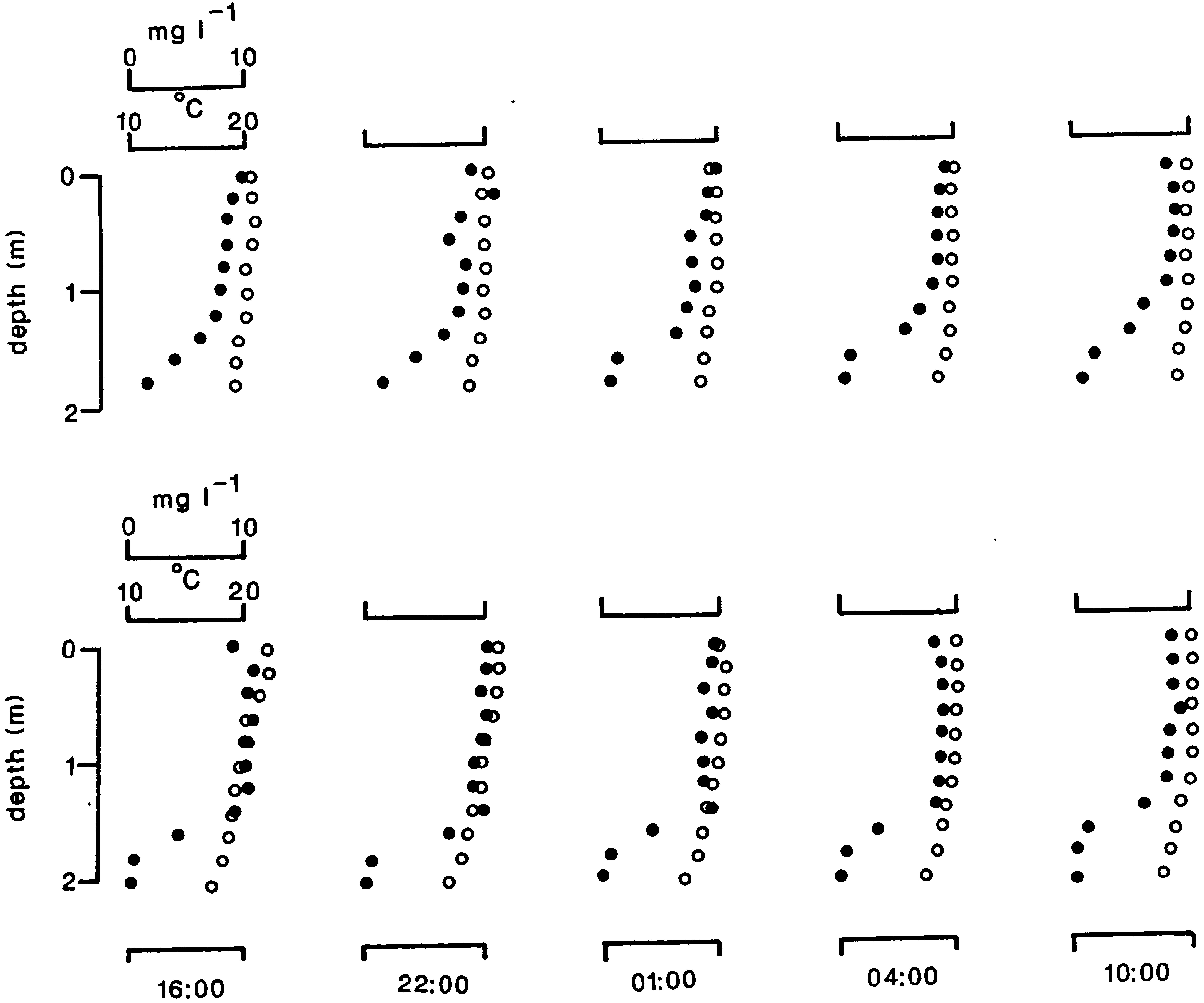
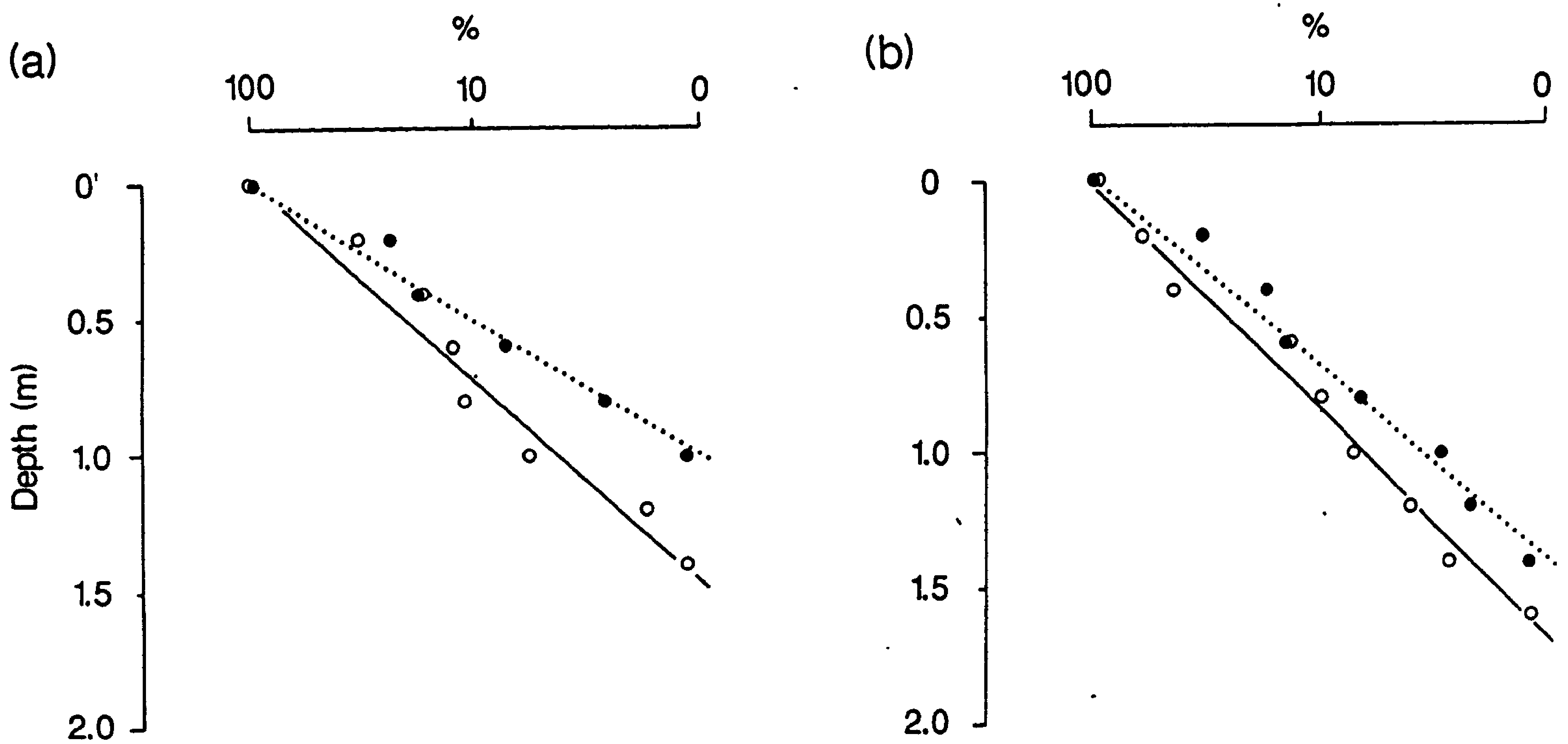


Figure 9.5. The light profiles in the tube and the tarn shown as semi-logarithm plots. The light penetration in the tube (●) was reduced compared to that in the tarn (o). Two profiles are shown (a) at 10:00 h and (b) at 16:00 h.

Figure 9.5



at night occurred at the base of the epilimnion, near the low oxygen levels.

The other reverse migration was performed by Polyarthra vulgaris (Fig.9.6.d) but was less marked. In the unenclosed population of the tarn there was a downward movement in the late afternoon and early evening to form a maximum at a depth of 1.80 m. This maximum became smaller as the night progressed, decreasing from almost 40% to just over 20%, and had dispersed slightly through the epilimnion by 10:00 h the following morning. The population in the tube was already concentrated at the base of the epilimnion when the investigation started and remained there until the morning, when a marked dispersal upwards took place between 04:00 h and 10:00 h.

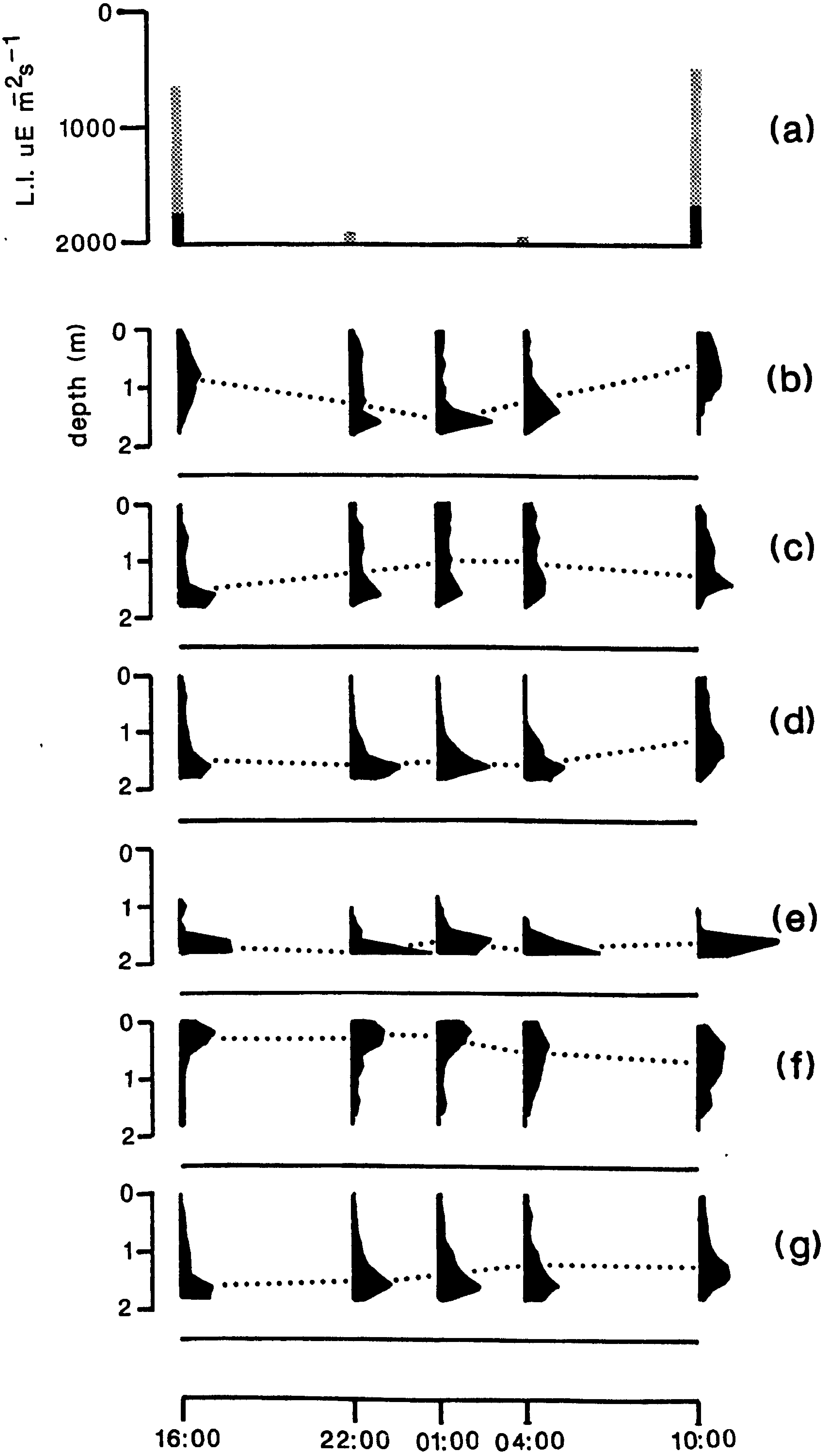
Although the tarn and enclosed populations of Brachionus angularis started off at 16:00 h with very different distributions, their movements from the late evening onward were similar (Fig.9.6.c). In the tube the population performed a nocturnal migration with an amplitude of almost half a metre, being more dispersed in the water column during the hours of darkness. In the tarn there was a similar pattern of movement but the population at 16:00 h was dispersed through the water column and moved down to a peak in the lower half metre of the epilimnion at dusk before the nocturnal migration occurred.

Filinia brachiata moved down throughout the night and early morning in both the tube and the tarn but was always concentrated in the top metre of the water column (Fig.9.6.f). In this way its population maxima were

Figure 9.6. The vertical migration of the rotifers in the tarn and in the tube, a comparison. (a) The light intensity at the surface (shaded blocks) and at 0.5 m depth (filled blocks). Six species are shown (b) *Keratella cochlearis*, (c) *Brachionus angularis*, (d) *Polyarthra vulgaris*, (e) *Filinia terminalis*, (f) *Filinia brachiata* and (g) *Anuraeopsis fissa*.

Figure 9.6 IN THE TARN

Figure 9.6 IN THE TUBE



always completely separate from those of the other Filinia species present, F.terminalis, the majority of which remained in a tight band below a depth of 1.50 m (Fig.9.6.e).

Anuraeopsis fissa remained concentrated in the second metre of the water column (Fig.9.6.g). The peaks at the base of the epilimnion were more marked in the enclosed population. In the tarn there was a slight rise during the night as the population dispersed.

9.7 Effect of the Absence of Light on Migrations (16 August 1984)

9.7.1 Sampling Details

The tube was placed in the tarn in the late afternoon on the 15th August and the light system was fitted, to act as a blackout, before the first samples were taken at midnight. The light system cut out all natural illumination from the enclosed water column.

Samples were taken from the tube at four-hour intervals from 00:00 h to 24:00 h on 16 August with simultaneous oxygen and temperature profiles. The light in the tube was checked periodically and at no time during the experiment was there a detectable light level. The sample interval was 0.20 m from the surface to 1.80 m inclusive.

9.7.2 Results

Without the stimulus of light there were less striking migrations than those previously found in the tarn but the distributions of most populations did change.

P.vulgaris (Fig.9.7.d) and A.fissa (Fig.9.7.f) both showed only small changes in distribution, the former only varying from a tight peak in the bottom half metre of the column at 16:00 h while the Anuraeopsis population had a much less well defined peak in the deeper water which dispersed upwards during the evening.

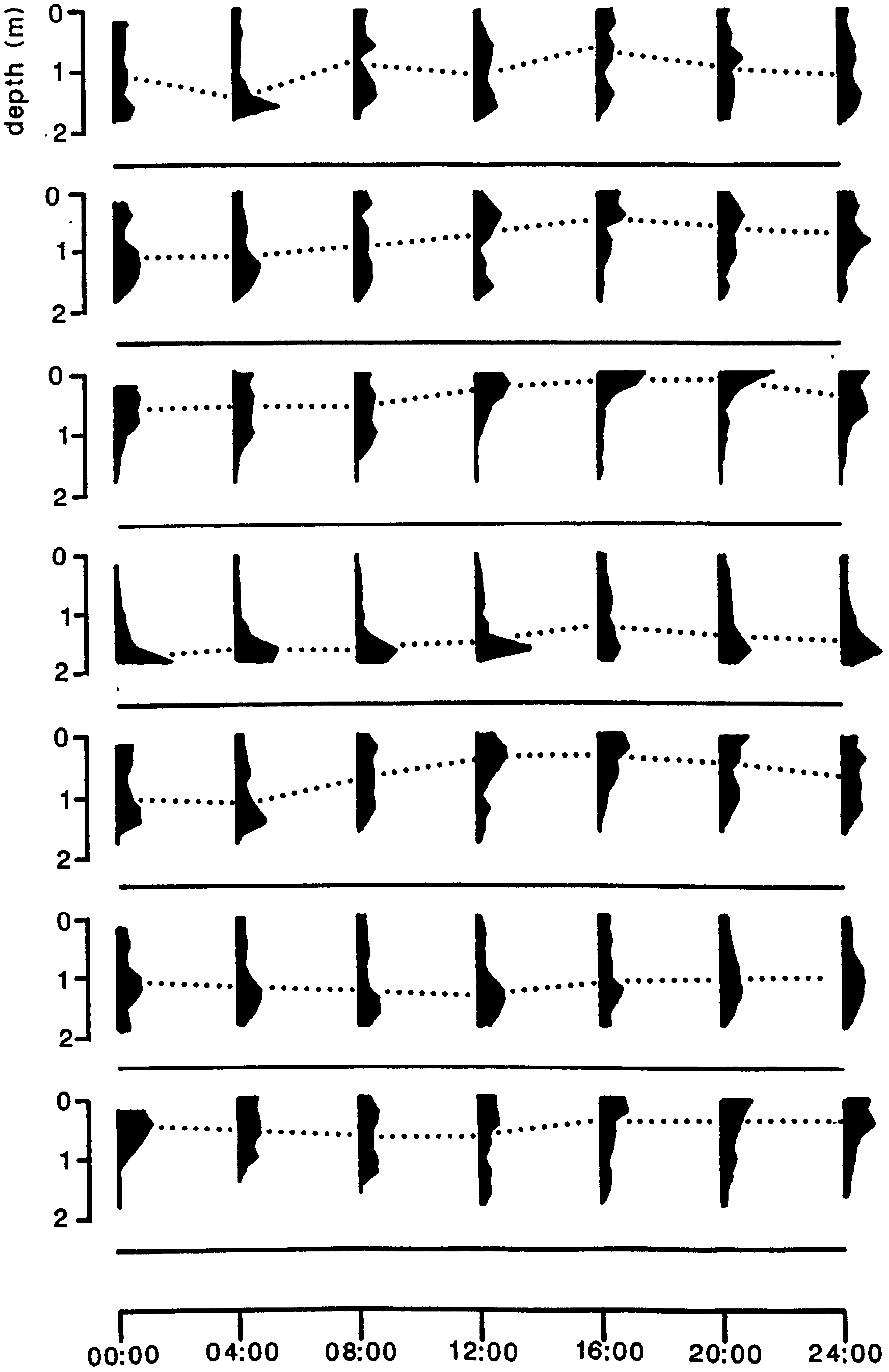
F.brachiata (Fig.9.7.g) showed the least fluctuation in mean depth (amplitude 0.29 m) but its distribution varied from a surface concentration through more dispersed distributions during the hours of daylight and back to a surface peak by the following midnight (a normal migration pattern).

The movements of K.cochlearis (Fig.9.7.a) were similar to a reverse migration although at midday there was a slight sinking. The population formed into a tight peak in the bottom half metre at 04:00 h but was more dispersed during the rest of the experiment.

The three remaining species all performed reverse migrations, most marked in B.angularis (Fig.9.7.c) which was concentrated in the top half metre of the water column during the afternoon and early evening. Both Trichocerca sp. (Fig.9.7.e) and K.quadrata (Fig.9.7.b) also moved up from peaks below 1 m to concentrate in the top half metre from 12:00 h to 20:00 h before dispersing down by midnight. These two migrations had amplitudes of 0.80 m and 0.68 m respectively while that of B.angularis occurred over a smaller distance and had an amplitude of only 0.48 m although the change in distribution was

Figure 9.7. The vertical migration of the rotifers under conditions of permanent darkness (August 16 1984). Seven rotifer species are illustrated (a) *Keratella cochlearis*, (b) *Keratella quadrata*, (c) *Brachionus angularis*, (d) *Polyarthra vulgaris*, (e) *Trichocerca* sp., (f) *Anuraeopsis fissa* and (g) *Filinia brachiata*.

Figure 9.7



greatest from 15% to 45% of the population at the surface.

9.8 Response of the Rotifers to a changed Photoperiod (23 and 30 August 1984)

9.8.1 Methods

On both occasions the tube was put into the tarn late on the previous evening and the light system fitted after it was dark. On 23 August the lights were powered by four 12 V car batteries but these became exhausted hence on 30 August, when the experiment was repeated, a second set of batteries was obtained and used to power the lamps during the second "day".

Between 08:30 h and 09:00 h the artificial light regime began. Using the rheostat the lights were turned on in five steps of increasing intensity, ten minutes apart, resulting in full illumination after one hour of "dawn". The lights and fan were then left on for three hours of "day" before they were dimmed over five progressive steps ("dusk"), again at ten minute intervals, to total darkness. The light system was then left off for three hours of "night" before "dawn" was repeated. On the first occasion (23 August) the batteries ran down at the start of the second "day" so sampling was finished at "midday". However, the use of a second set of car batteries on 30 August allowed sampling to continue until the second "dusk".

9.8.2 Results from 23 August

The temperature and oxygen profiles taken during the experiment show an increase in temperature throughout the duration of the experiment in the top half metre of the water column but below this it remained relatively stable (Fig.9.8.a) while the oxygen (Fig.9.8.b) showed a small increase during the hours of illumination and a decrease in darkness. The changing light intensity is shown in Fig.9.9.a.

There were six species present, two of which showed little movement while of the other four three performed reverse migrations and one a nocturnal migration.

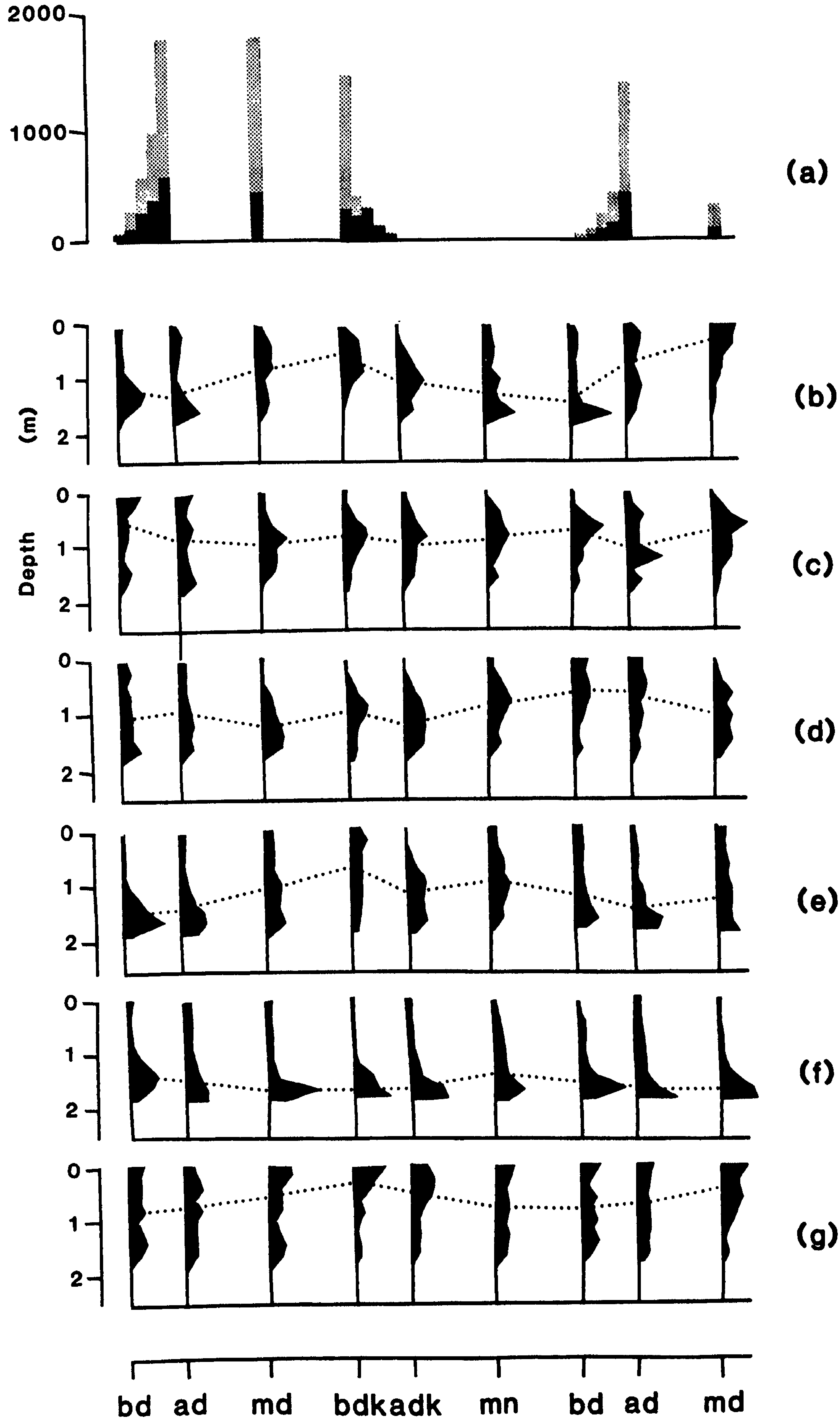
K.cochlearis showed the most striking reverse migration with an amplitude of 1.15 m and a very rapid response to the changes in illumination (Fig.9.9.b). At first the population was concentrated around 1.0 m to 1.5 m. After "dawn" the peak had shifted down slightly but the population then dispersed upwards so that ninety minutes later, at"midday", their distribution was even through the water column. This upward movement continued over the next ninety minutes and after three hours of illumination the population was concentrated in the top metre of the water column. After one hour of "dusk" the distribution had undergone a startling change and few rotifers were left in the top half metre. The mean depth of the population had increased by about half a metre, from 0.55 m to 1.09 m, implying a swimming speed of 150 um sec^{-1} (0.015 cm sec^{-1}). This downward movement continued over the next ninety minutes and a peak developed at 1.6 m that contained 30% of the population.


(a)
°C
15
25
depth (m)
0
1
2
(b)
mg l⁻¹
0
10
depth (m)
0
1
2
bd
ad
md
bdk
adk
mn
bd
ad
md

Figure 9.9. The vertical migration of the rotifers in the experimental column under a changed photoperiod. bd, Before dawn; ad, after dawn; md, midday; bdk, before dusk; adk, after dusk and mn, midnight.

(a) The light intensity at the surface of the tube (shaded blocks) and at 0.5 m depth (filled blocks).

Six species are shown (b) *Keratella cochlearis*, (c) *Keratella quadrata*, (d) *Brachionus angularis*, (e) *Polyarthra vulgaris*, (f) *Anuraeopsis fissa* and (g) *Filinia brachiata*.


2000
1000
0
(a)
Depth (m)
0
1
2
(b)
(c)
(d)
(e)
(f)
(g)
bd
ad
md
bdk
adk
mn
bd
ad
md

After a further ninety minutes of darkness this proportion had increased to 40%. A second rapid response was found after the second "dawn", the mean depth changed by almost 0.70 m in one hour, implying an upward swimming velocity of 186 um sec^{-1} (0.019 cm 1sec^{-1}), and the population became evenly distributed through the tube. After ninety minutes of constant illumination their continued upward movement had resulted in a concentration of 60% of the population in the top half metre.

Both *P.vulgaris* (Fig.9.9.e) and *F.brachiata* (Fig.9.9.g) also performed reverse migrations but, although their cycle closely followed the changes in the light climate, they were slower in their responses to the changing illumination than the *K.cochlearis*. Their reverse migrations reached points nearest the surface at the sampling time before "dusk", after three hours of "daylight". On the second "day", *F.brachiata* had a slightly quicker response and a peak had developed in the surface metre by "midday".

B.angularis was the only species to perform a migration similar to a nocturnal migration (Fig.9.9.d). There was little change in its distribution until the lights were turned off. This initiated an upward dispersal and slight concentration in the surface metre. This movement stopped at the second "dawn" and was reversed by the presence of light.

Two species, *K.quadrata* (Fig.9.9.c) and *A.fissa* (Fig.9.9.f) showed only slight movements. The former sank away from the surface each time the lights were turned on, more pronouncedly at the second "dawn". A.fissa remained concentrated in the bottom half metre of the tube, although there was a slight upward dispersal during the three hours of darkness and increased concentration during the periods of illumination.

9.8.3 Results from 30 August 1984

In this repeat of the investigation into the response of rotifers to a changed light cycle, the temperature profiles (Fig.9.10.a) remained very similar throughout the duration of the experiment but the oxygen profiles (Fig.9.10.b) showed differences as the illumination changed, photosynthesis during the "daylight" hours causing an increase in the surface metre which then was depleted during the hours of darkness. The changes in light intensity throughout the experiment are shown in Fig.9.11.a.

Nine rotifer species were present in the zooplankton and of these, five showed a reverse migration in response to the illumination, while the other four showed little change.

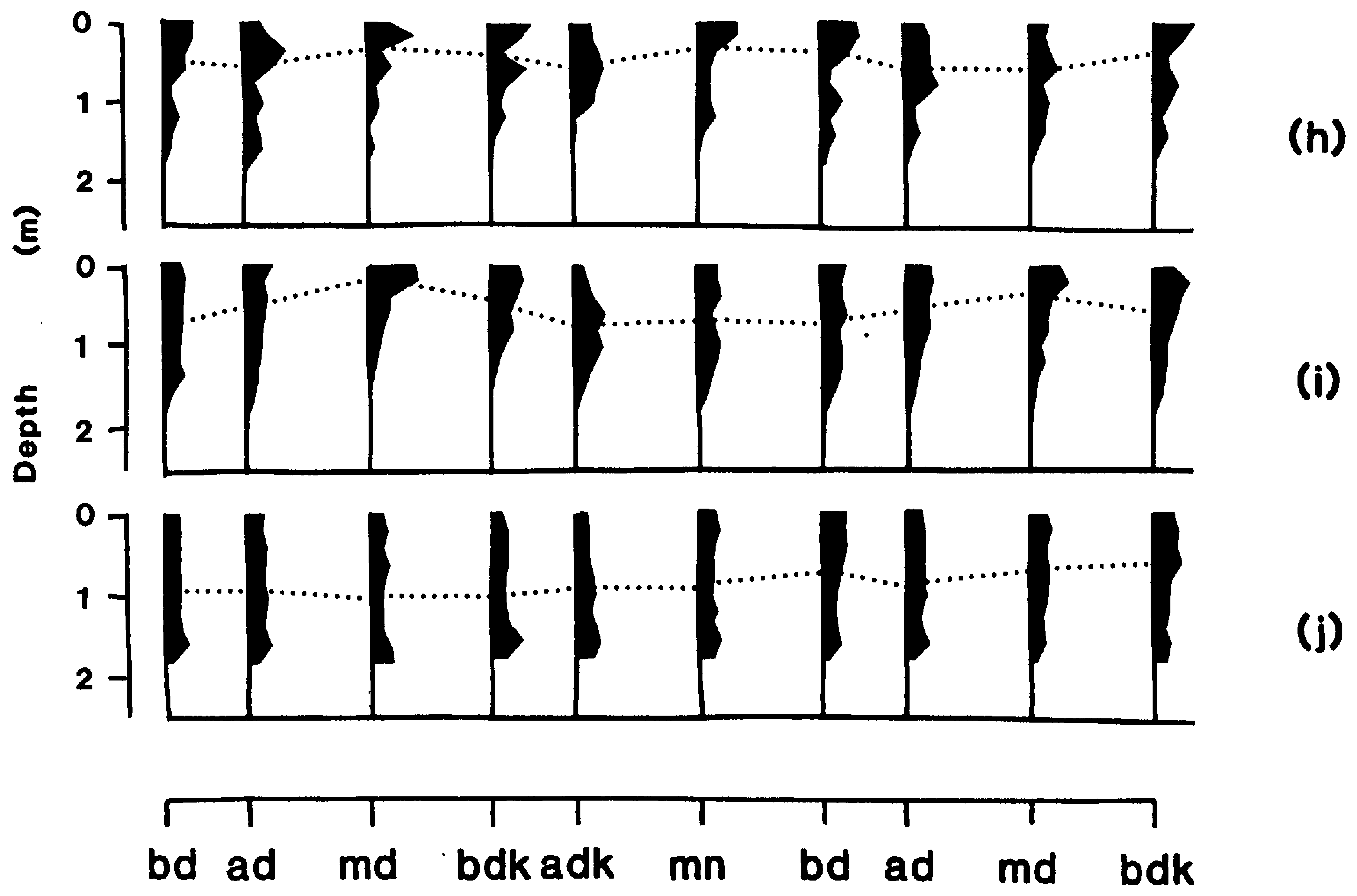
K.cochlearis again displayed a marked reverse migration (Fig.9.11.b) with changes in the mean depth of 0.75 m over one hour at "dusk" and 0.71 m over one hour at "dawn". These changes implied swimming speeds of around 200 um sec^{-1} (0.02 cm sec^{-1}). At the start of the study the population was evenly dispersed through the epilimnion. By "midday", after ninety minutes of full illumination, a concentration had developed at the surface containing 30% of the population. After a further

Figure 9.10. The temperature and oxygen profiles taken on 30 August 1984. (a) Temperature in °C and (b) oxygen in mgl^{-1}. bd, Before dawn; ad, after dawn; md, midday; bdk, before dusk; adk, after dusk and mn, midnight.


°C
15
25
mg l^{-1}
depth (m)
0
1
2
depth (m)
0
1
2
bd
ad
md
bdk
adk
mn
bd
ad
md
bdk

Figure 9.11. The vertical migration of the rotifers in the experimental tube under a changed photoperiod on August 30 1984. bd, Before dawn; ad, after dawn; md, midday; bdk, before dusk; adk, after dusk and mn, midnight. (a) The light intensity at the surface of the tube (shaded blocks) and at 0.5 m depth (filled blocks) in $uEm^{-2}s^{-1}$. Nine species are illustrated. (b) *Keratella cochlearis*, (c) *Keratella quadrata*, (d) *Brachionus angularis*, (e) *Polyarthra vulgaris*, (f) *Filinia terminalis*, (g) *Filinia brachiata*, (h) *Synchaeta* sp., (i) *Trichocerca* sp. and (j) *Anuraeopsis fissa*.


2000
1000
0
(a)
0
1
2
(b)
Depth (m)
0
1
2
(c)
0
1
2
(d)
0
1
2
(e)
0
1
2
(f)
0
1
2
(g)
bd
ad
md
bdk
adk
mn
bd
ad
md
bdk


0
1
2
0
1
2
0
1
2
Depth (m)
(h)
(i)
(j)
bd
ad
md
bdk
adk
mn
bd
ad
md
bdk

ninety minutes this had increased and 40% of the <u>K.cochlearis</u> were in the surface 0.20 m. In the sixty minutes over which the illumination was progressively reduced to darkness, the population moved to a peak around 1.4 m. This peak sank to 1.6 m and developed to more than 35% over the next three hours of darkness. After one hour of "dawn" the distribution had changed from having a marked peak at 1.60 m to an almost uniform distribution throughout the column with slightly higher numbers in the surface half metre. Over the following three hours the population concentrated into a peak at the surface containing more than 50% of the <u>K.cochlearis</u>. This cycle of reverse migration had an amplitude of 1.21 m and patchiness indices showed very significant changes in distribution.

<u>K.quadrata</u> (Fig.9.11.c) was slower in its responses but during both periods of "daylight" the population became concentrated in the top half metre of the water column. After "dusk" this peak dispersed downwards quite rapidly and during the hours of darkness the population was evenly distributed.

The response of <u>P.vulgaris</u> (Fig.9.11.e) showed an upward movement during the first period of "daylight" followed by sinking and dispersal during the "night", a peak developing below 1.5 m after three hours without light. However, the population did not respond so rapidly during the second period of illumination. Although it became dispersed through the water column with a slight concentration in the top half metre, it was not as tight a distribution as the previous day.

Trichocerca sp., although numbers were low, also performed a reverse migration (Fig.9.11.i) showing concentration in the top half metre during "daylight" and dispersal at "night".

The movements of *F.brachiata* (Fig.9.11.g) were less marked. There was always a concentration of the population in the surface waters but it increased during the periods of illumination.

The other four species did not perform migrations. *Synchaeta* sp. (Fig.9.11.h) and *B.angularis* (Fig.9.11.d) showed irregular movements; *Synchaeta* having peaks at the surface during both light and dark phases which dispersed then reformed, while *B.angularis* had occasional small peaks below 1.5 m. *A.fissa* (Fig.9.11.j) remained evenly distributed throughout the study. *F.terminalis* showed a very similar distribution to that found on 17 July. There were almost no individuals above a depth of one metre and the majority (c.75%) of the population was at 1.80 m (Fig.9.11.f). The population had appeared in the plankton since 23 August either after disappearing completely from the tarn or, more likely, after being concentrated below the reach of the tube.

9.9 Discussion

At the start of the experimental study it was not certain that this type of approach - extending laboratory methods into the field - would work. The tube could have caused problems by changing the conditions found in the enclosed water column so rapidly and so radically that any attempt at a comparison between the enclosed populations and those in the tarn would have been invalid. However, preliminary tests showed that the physical conditions inside the tube were comparable with those in the tarn while the full twenty-four hour study in July, described here, provided evidence that the behaviour of the rotifer communities were also similar.

This preliminary finding, that any behaviour found in the tube would be representative of that expected of the natural population allowed further experiments to be performed, investigating the responses of the rotifer community to changes in the environment.

The method of <u>in situ</u> experimentation used here removed the problems involved in reproducing the field conditions artificially in the laboratory and the difficulties of maintaining a rotifer community representative of that present in the field. It has severe limitations, as its use is only feasible where rotifer numbers are high and the experimental tubes would have to be designed for the depth of site involved. However, in Priest Pot, the shallowness of the tarn, the density of the rotifer populations and the predictability of the environment made it a very efficient method.

The experiments carried out in August showed that it was possible to induce vertical migrations that followed an artificial light regime. Most of the species present showed some response to the changed illumination (Table 9.1). It would seem likely, therefore, that light is an important factor in the timing of vertical migrations in rotifers and in the maintenance of a stratified distribution in the water column.

The swimming speeds calculated for some species were similar to those found by George & Fernando (1970) in the rotifers of mountain lakes and by Worthington (1931) in Lake Lucerne for the copepods *Eudiaptomus gracilis*, *Mixodiaptomus laciniatus* and *Mesocyclops leuckarti*.

K.cochlearis showed the most marked vertical migration in response to the altered light regime. The response was the same in both experiments, a reverse migration with rapid sinking at dusk and an equally rapid rise at dawn with obvious preferred day and night depths. The swimming velocities implied by the variation of the mean depth of the population were greater than those found in 1983 (Table 8.1).

Work on crustaceans has shown vertical migrations induced in response to an artificial light regime (Harris & Wolfe, 1955), but as far as I know this is the first case of rotifer migrations being manipulated. Harris & Wolfe studied *Daphnia magna* in water to which indian ink had been added to produce a rapid change in light intensity over a short vertical distance. They induced a twilight migration (down in bright illumination, rising as light declines then sinking in darkness) which could be reproduced with a cycle of from two to thirteen hours duration.

A further examination of Table 9.1 reveals the frequency of reverse migrations. Although nine migrations were observed, only two of them (those of *B.angularis*) were the expected nocturnal migration. The other seven were reverse migrations, most marked in *K.cochlearis* but

Table 9.1. The vertical migrations shown by the rotifers in Priest Pot under different light regimes.

Species	17/18 July (normal)	16 August (no light)	23 August (3 h cycle)	30 August (3 h cycle)
Keratella cochlearis	Reverse 0.90[*]	Reverse 0.79	Reverse 1.15	Reverse 1.21
Keratella quadrata	-[**]	Reverse 0.68	NM[***] 0.50	Reverse 0.58
Brachionus angularis	Normal 0.49	Reverse 0.48	Normal 0.61	Normal 0.40
Polyarthra vulgaris	Reverse 0.47	NM 0.54	Reverse 0.81	Reverse 0.98
Filinia terminalis	NM 0.18	-	-	NM 0.19
Filinia brachiata	Normal 0.36	Normal 0.29	Reverse 0.48	Reverse 0.69
Anuraeopsis fissa	Normal 0.49	NM 0.32	NM 0.31	NM 0.44

[*] Amplitude of movement (lowest mean depth - the highest mean depth.

[**] -, Not present in the samples.

[***] NM, No migration.

also occurring in K.quadrata, P.vulgaris, and F.brachiata. As mentioned previously, the literature on migration is of the view that reverse migrations are an aberrant behaviour pattern, but work on rotifers reveals several cases to which these results may be added.

Circadian rhythms are common in nature and have been the subject of detailed studies in plants, arthropods and even in the allergic responses of man. Endogenous rhythms of migration are known for crustacean zooplankton (Esterley, 1917; Harris, 1963) but have never been described for planktonic rotifers.

In Priest Pot, the rotifers showed the same migrations when submitted to a regime of total darkness as in normal illumination indicating that they may indeed have an endogenous rhythm. Although the experiment only covered one period of the light cycle it would still appear that the migration of rotifers is effected by an internal clock.

Circadian clocks usually have a periodicity close to the twenty-four hour exogenous rhythm and are thought to be brought into phase with the normal day-night cycle by a "zeitgeber" or entraining agent. In many studies light has been the major "zeitgeber" and in Priest Pot this would also seem to be the case. Under normal illumination the migration of the rotifers had the expected 24 h periodicity and this was also the case when there was no light stimulus. However, when the periodicity of the light cycle was changed , that of the migration was similarly affected. This indicates that in Priest Pot light was a "zeitgeber" to the rotifers´ endogenous rhythm and instead of the expected 24 h rhythm seen in total darkness, a new cycle of migration appeared, entrained to the shorter light - dark cycle provided.

CHAPTER TEN

General Discussion

Sixteen species of rotifers were found in the plankton of Priest Pot but six of these were very rare. The remaining ten were divided into perennial species (K.cochlearis, K.quadrata, P.vulgaris, S.pectinata and S.kitina), spring/autumn species (B.calyciflorus, B.angularis and F.terminalis) and summer/autumn species (A.fissa and F.brachiata) according to their periods of occurrence and abundance. Detailed information of these species' vertical distribution and seasonal occurrence is summarized in Table 10.1. It is obvious that temperature is a major factor influencing the seasonal composition of the rotifer community. May (1980) emphasized this point for the rotifers in the eutrophic Loch Leven and the same is true for Priest Pot. Other environmental variables are also important, however, in producing the vertical distributions and migrations characteristic of some species. Their effects will be discussed in relation to the existing rotifer literature.

In the past, studies of rotifers have emphasized the importance of temperature as a controlling factor in their occurrence. Many species are described according to their temperature preferences : warm stenotherms, cold stenotherms and eurytherms, and seasonal succession of rotifer species in a water body is a common phenomenon. Carlin (1943) showed a succession of Polyarthra species throughout the year; the small slender-bladed P.dolichoptera abundant in May being followed by

Table 10.1

SPECIES	SEASONAL ABUNDANCE	VERTICAL DISTRIBUTION				TEMPERATURE RANGE (°C)	CHLOROPHYLL CORRELATION
		ISOTHERMAL		STRATIFIED			
	J F M A M J J A S O N D	Overall	Range	Overall	Range		
Perennial							
K.cochlearis		2.25	0.40–3.57	0.97	0.46–1.55	3–24	**
K.quadrata		2.34	0.55–3.38	1.15	0.55–1.74	3–24	**
P.vulgaris		2.01	1.12–3.56	0.83	0.55–1.29	3–24	**
S.kitina		1.38	0.40–2.51	0.82	0.27–1.40	3–24	**
S.pectinata		1.30	0.60–2.38	0.61	0.25–1.06	3–21	**
Spring/Autumn							
B.calyciflorus		1.30	0.50–2.60	0.87	0.36–1.19	9–16	**
B.angularis		1.72	0.29–3.12	0.91	0.43–1.51	9–16	*
F.terminalis		2.44	1.37–3.55	1.26	0.75–1.60	3–16	ns
Summer/Autumn							
A.fissa		1.67	1.13–2.65	1.30	0.94–1.71	9–24	–
F.brachiata		1.15	0.40–1.79	0.63	0.32–0.82	9–21	–

P.vulgaris in June, *P.major* in July and September and finally *P.remata* in October, all of which are larger with broader blades. Pejler (1957 a,b) and Larsson (1971) also showed species succession in other Scandinavian water bodies. In Priest Pot it became clear that the rising temperatures in early summer encouraged the appearance of the warm stenotherms *A.fissa* and *F.brachiata* whilst inhibiting the populations of *B.calyciflorus*, *B.angularis* and *F.terminalis*. Even the perennial species were most abundant when the temperatures were above 8°C although small populations survived in the low winter temperatures. With the cold stenotherms the rising temperatures at the surface produced a vertical distribution with aggregation in the deeper, cooler water. In Priest Pot this occurred in both *F.terminalis* and *B.calyciflorus*. Ruttner-Kolisko (1980) found the same change in distribution for *F.terminalis* as Windermere warmed up. In water bodies that stratify during the summer, this downward movement can result in extinction of species as they are pushed down into anoxic water. This has been documented for *F.terminalis* in Esthwaite Water by Ruttner-Kolisko (1980) and in PluBsee by Hofmann (1982). It was the cause of *F.terminalis*'disappearance from the plankton in Priest Pot.

Rotifers are aerobic although some workers have found them in very low oxygen concentrations (Larsson, 1971; Miracle & Vicente, 1983). In lakes which stratify, the metazoan zooplankton is confined to the oxygenated waters. Priest Pot is stratified from May to September and during this time has a very narrow band of water between the oxygenated epilimnion and the anoxic hypolimnion, in some cases the transition occurs over less than 5 cm. The oxic-anoxic boundary appeared to be very important to the distribution of the rotifers, not only in its role as a barrier cutting them off from the lower two thirds of the tarn but as a site for aggregation. All the rotifer species were forced up into the epilimnion by the oxycline but some showed a remarkable tolerance of the low oxygen concentrations at this boundary and formed large maxima coincident with it. Others could not move up as the surface waters were warmer than they could tolerate. These species, as described in the previous section, disappeared from the zooplankton as the oxycline moved up. Some species were sensitive to the low oxygen concentrations and were forced higher into the epilimnion. P.vulgaris has been previously noted for its intolerance of low oxygen concentrations (Pejler, 1957 b) and its vertical distribution in Priest Pot supported this. Few species are noted for their preference for anoxic conditions but studies have occasionally found maxima of certain rotifers in very low or absent oxygen (Miracle & Vicente, 1983). In Priest Pot the vertical distribution of A.fissa was strongly correlated with the position of the oxycline and on an occasion when the depth of the oxic-anoxic boundary fluctuated through 24 hours the aggregations of A.fissa moved to remain coincident with this area of low oxygen concentration, performing a vertical migration.

The chlorophyll *a* equivalent values and the direct counts of bacteria gave some measure of the food available to the rotifers. The species that were most abundant in Priest Pot were microphagous filter feeders. Both Nauwerck (1963) and Pourriot (1977) state the importance of detritus and bacteria to many of the rotifer species found in Priest Pot. They also cite chrysomonads as an important part of the diet of *K.cochlearis*, *K.quadrata* and *P.vulgaris*. The algal blooms in Priest Pot in April and September were caused by large numbers of the chrysomonad *Synura* sp.. Some rotifer species had population increases at these times which may have been linked to the increased quantities of algal food avaiable. The vertical distributions of *K.cochlearis*, *K.quadrata* and *P.vulgaris* showed aggregations coincident with the highest chlorophyll values and on two occasions, April 13/14 and September 5/6 1983 , a vertical migration was found that followed the movements of the algae. Nauwerck (1963) found positive correlations between rotifer numbers and chrysomonad populations and others found links between algal numbers and rotifer numbers (Granberg, 1970; Schindler & Noven, 1971).

A.fissa and *F.terminalis* are both known as detrital or bacterial feeders (Pourriot, 1977) and *F.brachiata* is probably similar in its requirements. The first two species showed no response to changing chlorophyll concentrations in Priest Pot but did seem to show some link with bacterial numbers. The oxic-anoxic boundary in

Priest Pot is rich in bacteria, the direct counts showed higher numbers in the hypolimnion, and the aggregations of certain species of rotifers at the oxycline are almost certainly linked to bacterial feeding. Larsson (1971) found F.terminalis in waters where oxygen concentrations were low and bacteria were numerous.

The importance of light in the distribution of plankton is well documented if not well understood. Work on Daphnia by Harris (1963), Harris & Wolfe (1955), Ringelberg (1964) and others showed light responses controlling both movement and orientation in the water. Much less work has been done on the rotifers. The eye spot of a rotifer is a much simpler organ than the daphnid eye but Viaud (1940,1943 a,b) performed a series of experiments on four species of planktonic rotifers and showed phototactic responses. Pourriot has also studied the light responses of rotifers. The hatching of the resting eggs of Brachionus rubens and B.plicatilis was found to require light (Blanchot & Pourriot, 1982 a,b) and Notommata copeus reproduced parthenogenetically in a short photoperiod (L:D 14:10) but in a long photoperiod (L:D 17:7) the sexual phases appeared (Pourriot, 1981; Pourriot et al., 1981). However no work has been published on the importance of the photoperiod to the vertical distribution of rotifers. The diel studies in Priest Pot showed that migrations were performed by some of the rotifer species present. Although chlorophyll was important on two occasions, the basic rhythm was linked to the day-night cycle in all cases. The experimental work using the aluminium tube aimed to investigate the importance of light and photoperiod in determining the migrations. Unlike the larger crustacean zooplankton, the usual migration of rotifers is what the literature terms a "reverse" migration (up during the day and down at night). The work on Crustacea has always stated that this is aberrant behaviour and the expected movement is a "normal" migration (down during the day and up at night) (Cushing, 1951; Hutchinson, 1967; Longhurst, 1976). The reasons put forward for vertical migrations are many and varied. One of the most often cited is that it is a predator avoidance behaviour; the zooplankton only move into the surface waters to feed on the higher algal numbers there when it is dark and the predators who hunt by sight cannot locate them (Zaret & Suffern, 1976). This theory does not fit all the cases of vertical migration observed and is little help in explaining rotifer migration in Priest Pot as their predators are mainly non-visual feeders (Crustacea and roach fry).

The tube experiments are fundamentally important as they are the first attempt at moving the cylinder apparatus of Heaney & Eppley (1981) into the field. Dumont (1972) used square enclosures in Lake Donk but these were very simple apparatuses and he used them as enclosures in which to manipulate the plankton community structure without changing the abiotic conditions.

In Priest Pot the rotifers performed migrations with the same period as the usual day-light photoperiod. When subjected to total darkness over a 24 h period most still performed the same migration. It seems that they had become entrained to a 24 h cycle but that the control was at least partly endogenous. The migrations could be an example of a circadian rhythm that has become entrained to the 24 h photoperiod by an exogenous stimulus e.g. light. A circadian rhythm is a cyclical variation in behaviour, or in some metabolic or physiological process, with a periodicity around 24 hours. It may be endogenous and persist even when external conditions are held constant or it may be exogenous and fail to persist in a constant environment. An endogenous circadian rhythm may be entrained to exactly 24 h periodicity by an external stimulus e.g. light or temperature. This entraining agent is termed the zeitgeber and in the case of the rotifer migrations in Priest Pot is almost certainly light. This theory was supported by the fact that a changed photoperiod resulted in a changed migration cycle. The two experiments in the tube, using a L:D cycle of 3:3 with 1 hour of changing light intensity between to simulate dawn and dusk, produced migrations in some of the rotifers with the same period as the light cycle. This showed clearly the importance of light in controlling vertical migration in some species. It also showed that for other species, e.g. A.fissa and F.terminalis, the photoperiod is not important. Their vertical distribution was linked to the oxic-anoxic boundary and was not affected by the changing light intensity. The fact that these two species are bacterial or detrital feeders while the others, which responded to light, were predominantly algivores could be evidence that the migration of the rotifers is mainly a means of following a migrating food source. Many algae migrate and they almost always go up during the day and down at night. If the rotifers follow this then they remain in areas of high algal density throughout the 24 hours. Entrainment to the photoperiod would enable them to do this and would explain why, even at times when the phytoplankton consists of non-migrating species of algae, the rotifers often still perform a reverse migration. In rotifers, therefore, it would seem that the migration may be behaviour aimed at providing "optimum foraging".

Although in isothermal conditions the vertical distribution of the rotifers was often homogeneous, the presence of high algal densities or other changed environmental conditions produced definite aggregations. In some species their distribution was often linked to chlorophyll and changed over 24 h to remain in areas of high algal numbers. Their migrations were entrained to the 24 h photoperiod. Other species were bacterivores and detritivores and their distributions were linked to the high bacterial numbers at the oxic-anoxic boundary. They showed little or no response to changing chlorophyll or changing light. Temperature is the major factor determining the presence or absence of species but other environmental factors, namely oxygen, food availability and light, are clearly important influences on the temporal and spatial distribution of the planktonic rotifers of Priest Pot.

SUMMARY

The planktonic rotifers in Priest Pot, a hypereutrophic tarn in the English Lake District, were studied over a 20 month period during 1983 and 1984. Routine weekly samples provided a uniquely detailed data set giving information on the seasonal composition and the vertical distribution of the rotifer community in relation to the environmental conditions: oxygen, temperature, light, chlorophyll *a*, bacteria and water chemistry. The distribution of the rotifers varied between species and was correlated with temperature, oxygen and chlorophyll *a* concentrations. Aggregations of some species were found at the oxic-anoxic boundary while others were more concentrated in the surface waters. Diel studies in 1983 investigated the vertical migration of the community and found that most of the rotifer species performed reverse migrations (up during the day and down at night) as opposed to the expected normal migration (down during the day and up at night) found in studies of crustaceans. Experimental work submitting enclosed populations in the field to altered photoperiods showed light to be a controlling stimulus. The migration is thought to be a result of a circadian rhythm entrained to the exogenous 24 hour cycle as the movement continued with no light but changed to follow a shortened photoperiod.

REFERENCES

Adalsteinsson, H. (1979). Zooplankton and its relation to available food in lake Myvatn. Oikos 32:162-194.

Axelson, J. (1961). Zooplankton and impoundment of two lakes in Northern Sweden (Ransaren and Kultsjon). Report of the Institute of Freshwater Research, Drottningholm 42:84-168.

Baker, R.L. (1979). Birth rate of planktonic rotifers in relation to food concentration in a shallow eutrophic lake in Western Canada. Canadian Journal of Zoology 57:1206-1214.

Belcher, J.H. (1964). Some new and uncommon British Volvocales III. British Phycological Bulletin 2:307-312.

Belcher, J.H. (1968). Lorica construction in Pseudokephyrion pseudospirale Bourrelly. British Phycological Bulletin 3:495-499.

Belcher, J.H. (1969). A morphological study of the phytoflagellate Chrysococcus rufescens Klebs in culture. British Phycological Journal 4:105-117.

Belcher, J.H. & E.M.F. Swale (1962). Some Chlorococcales new to Britain. British Phycological Bulletin 2:121-125.

Belcher, J.H. & E.M.F. Swale (1963). Some new and uncommon British Volvocales II. British Phycological Bulletin 2:210-218.

Belcher, J.H. & E.M.F. Swale (1967). Chromulina placentula sp.nov. (Chrysophyceae) a freshwater nannoplankton flagellate. British Phycological Bulletin 3:257-267.

Belcher, J.H., E.M.F. Swale & J. Heron (1966). Ecological and morphological observations on a population of Cyclotella pseudostelligera Hustedt. Journal of Ecology 54:335-340.

Berzins, B. (1958). Ein Planktologische Querprofil. Report of the Institute of Freshwater Research, Drottningholm 39:5-22.

Berzins, B. (1962). Revision der Gattung Anuraeopsis Lauterborn (Rotatoria). Kungliga Fysiografiska sallskapets i Lund forhandligar 32:33-47.

Blanchot, J. & R. Pourriot (1982a). Effets de l´intensite d´eclairement et de la longeur d´onde sur l´eclosion des oeufs de duree de Brachionus rubens (Rotifere). Compte rendu hebdomadaire des seances de l´Academie des Sciences. Paris 295:123-125.

Blanchot, J. & R. Pourriot (1982b). Influence de trois facteurs de l´environnement, lumiere, temperature et salinite, sur l´eclosion des oeufs de duree d´un clone de Brachionus plicatilis (O.F.Muller). Rotifere. Compte rende hebdomadaire des seances de l´Academie des sciences. Paris 295:243-246.

Bogorov, B.G. (1946). Peculiarities of diurnal vertical migrations of zooplankton in polar seas. Journal of Marine Research 6:25-32.

Booker, M.J., M.T. Dinsdale & A.E. Walsby (1976). A continuously monitored column for the study of stratification by planktonic organisms. Limnology and Oceanography 21:915-919.

Bosselmann, S. (1979). Population dynamics of Keratella cochlearis in Lake Esrom. Archiv fur Hydrobiologie. Stuttgart 87:152-165.

Bosselmann, S. (1981). Population dynamics and production of Keratella hiemalis and K. quadrata in Lake Esrom. Archiv fur Hydrobiologie. Stuttgart 90:427-447.

Bryce, D. & W.E. Garner (1944). List of British Rotifera 17pp. unpublished copies in possession of Quekett Microscopical Club of British Museum (Natural History).

Buchanan, C. & J.F. Haney (1980). Vertical migrations of zooplankton in the Arctic : a test of the environmental conditions. Special Symposium volume 3 American Society of Limnology and Oceanography pp.69-79. (Ed. W.E. Kerfoot).

Burns, C.W. & S.F. Mitchell (1980). Seasonal succession and vertical distribution of zooplankton in Lake Hayes and Lake Johnson. New Zealand Journal of Marine and Freshwater Research 14:189-204.

Burris, J. (1980). Vertical migration of zooplankton in the Gulf of Finland. American Midland Naturalist 103:316-321.

Carlin, B. (1943). Die Planktonrotatorien des Motalastrom - zur Taxonomie und okologie der planktonrotatorien. Meddelanden fran Lunds universitets Limnologiska institution 5:1-255.

Chaney, A.L. & E.P. Marbach (1962). Modified reagents for determination of urea and ammonia. Clinical Chemistry 8:130-132.

Cowell, B.C., W.D. Craig & R.C. Adams (1975). A synoptic study of the limnology of Lake Thonotosassa, Florida. Part I Effects of primary treated sewage and citrus wastes. Hydrobiologia 46:301-345.

Cruz-Pizarro, L. (1978). Comparative vertical zonation and diurnal migration among Crustacea and Rotifera in the small high mountain lake La Caldera (Granada, Spain). Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie 20: 1026-1032.

Cunningham, C.R. & W. Davison (1980). An opto-electronic sediment detector and its use in the chemical micro-profiling of lakes. Freshwater Biology 10:413-418.

Cunningham, C.R. & J.S. Purewal (1983). A microcomputer based aid for counting plankton samples. Journal of Plankton Research 5:783-786.

Cushing, D.H. (1951). The vertical migration of planktonic crustacea. Biological Reviews 26:158-192.

de Beauchamp, P.M. (1952 a). Un facteur de la variabilite chez les rotiferes du genre Brachionus. Compte rendu hebdomadaire des seances de l´Academie des sciences., Paris 234:573-575.

de Beauchamp, P.M. (1952 b). Variation chez les rotiferes du genre Brachionus. Compte rendu hebdomadaire des seances de l´Academie des sciences., Paris 235:1355-1356.

Digby, P.S.B. (1960). Midnight sun illumination above and below the sea surface in the Sorgat, N.W. Spitsbergen, and its significance to plankton. Journal of Animal Ecology 29:273-297.

Digby, P.S.B. (1961). The vertical distribution and movements of marine plankton under midnight sun conditions in Spitsbergen. Journal of Animal Ecology 30:9-25.

Dodson, A.N. & W.H. Thomas (1964). Concentrating plankton in a gentle fashion. Limnology and Oceanography 9:455-456.

Doohan, M. (1973). Energetics of planktonic rotifers applied to populations in reservoirs. PhD. Thesis University of London.

Duffy, W.G. & C.R. Liston (1978). Seasonal abundance of planktonic rotifers in a nearshore area of central lake Michigan. Journal of the Great Lakes Research 4:46-49.

Dumont, H.J. (1972). A competition based approach of the reverse vertical migration in zooplankton and its implications chiefly based on a study of the interactions of the rotifer Asplanchna priodonta (Gosse) with several Crustacea Entomostraca. Internationale Revue der gesamten Hydrobiologia und Hydrographie 57:1-38.

Einsle, U. (1967). Uber das jahrezeitliche Auftreten der Planktonrotatorien in Mindelsee. Mitteilungen des Badischen Landesvereins fur Naturkunde und Naturschutz N.F. 9:513-527.

Eisenreich, S.J., R.T Bannerman & D.E. Armstrong (1975). A simplified phosphorus analysis technique. Environmental Letters 9:45-53.

Elliott, J.I. (1977). Seasonal changes in the abundance and distribution of planktonic rotifers in Grasmere (English Lake District). Freshwater Biology 7:147-166.

Elliott, J.M. (1977). Some methods for the analysis of samples of benthic invertebrates. Freshwater Biological Association Scientific Publication No.25.

Eloranta, P.V. (1982). Zooplankton in the Vasikkalampi pond, a warm water effluent recipient in central Finland. Journal of Plankton Research 4:813-837.

Eppley, R.W., O. Holm-Hansen & J.D.H. Strickland (1968). Some observations on the vertical migration of dinoflagellates. Journal of Phycology 4:333-340.

Esterley, C.O. (1917). The occurrence of a rhythm in the geotropism of two species of plankton copepods when certain recurring external conditions are absent. University of California Publications in Zoology 16:393-400.

Fairchild, G.W., R.S. Stemberger, L.P. Epskamp & H.A. Debaugh (1977). Environmental variables affecting small scale distributions of five rotifer species in Lancaster Lake, Michigan. Internationalen Revue der gesamten Hydrobiologie und Hydrographie 62:511-521.

Fenchel, T. & B.J. Finlay (1984). Geotaxis in the ciliated protozoan Loxodes. Journal of Experimental Biology 110:17-33.

Ferrari, I. & O. Rossi (1976). Composition and seasonal succession of the zooplankton in Lake Mergozzo (Northern Italy). Memorie dell´Istituto italiano di idrobiologia Dott. Marco de Marchi. Milano. 33:85-104.

Finlay, B.J. & U.G. Berninger (1984). Co-existence of congeneric ciliates (Karyorelictida : Loxodes) in relation to food resources in two freshwater lakes. Journal of Animal Ecology 53:929-943.

Finlay, B.J., A.F.W. Span & J.M.P. Harman (1983). Nitrate respiration in primative eukaryotes. Nature, London 303:333-336.

George, D.G. (1981). Zooplankton patchiness. Report of the Freshwater Biological Association 49:32-44.

George, D.G. (1983). Interrelations between the vertical distribution of Daphnia and chlorophyll a in two large limnetic enclosures. Journal of Plankton Research 5:457-475.

George, D.G. & S.I. Heaney (1978). Factors influencing the spatial distribution of phytoplankton in a small productive lake. Journal of Ecology 66:133-155.

George, M.G. & C.H. Fernando (1969). Seasonal distribution and vertical migration of planktonic rotifers in two lakes in Eastern Canada. Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie 17:817-829.

George, M.G. & C.H. Fernando (1970). Diurnal migration in three species of rotifers in Sunfish Lake, Ontario. Limnology and Oceanography 15:218-223.

Gilbert, J.J. (1966). Rotifer ecology and embryological induction. Science. New York 151:1234-1237.

Gilbert, J.J. (1967). Asplanchna and posterolateral spine production in Brachionus calyciflorus. Archiv fur Hydrobiologie. Stuttgart 64:1-62.

Golterman, H.L., R.S. Clymo & M.A.M. Ohnstad (1978). Method for physical and chemical analysis of freshwaters. IBP Handbook No.8. Blackwell Scientific Publications. Oxford.

Gorham, E. (1966). Some chemical aspects of wetland ecology. Proceedings of the 12th Annual Muskeg Research Conference. pp. 17.

Goulder, R. (1980). The ecology of two species of primitive, ciliated protozoa commonly found in standing freshwaters (Loxodes magnus Stokes and L.striatus Penard). Hydrobiologia 72:131-158.

Granberg, K. (1970). Seasonal fluctuations in numbers and biomass of the plankton of Lake Paajarvi, southern Finland. Annales zoologici Fennici 7:1-24.

Guerrero, R., C. Abella & M.R. Miracle (1978). Spatial and temporal distribution of bacteria in a meromictic karstic lake basin: relationships with physicochemical parameters and zooplankton. Verh. int .Verein. theor. angew. Limnol. 20, 4, 2264-2271.

Hakkari, L. (1969). Zooplankton studies in the Lake Langelmavesi, South Finland. Annales zoologici Fennici 6:313-326.

Harris, J.E. (1963). The role of endogenous rhythms in vertical migration. Journal of the Marine Biological Association U.K. 43:153-166.

Harris, J.E. & U.K. Wolfe (1955). A laboratory study of vertical migration. Proceedings of the Royal Society, B. 144:329-354.

Heaney, S.I. & R.W. Eppley (1981). Light, temperature and nitrogen as interacting factors affecting diel migrations of dinoflagellates in culture. Journal of Plankton Research 3:331-344.

Heaney, S.I. & T.I. Furnass (1980). Laboratory models of diel vertical migration in the dinoflagellate Ceratium hirundinella. Freshwater Biology 10:163-170.

Herzig, A. (1979). The zooplankton of the open lake. In: Neusiedlersee, the limnology of a shallow lake in central Europe. pp. 281-335 (Ed. Loffler). Junk. The Hague. pp281-335.

Hewitt, D.P. & D.G. George (1987). The population dynamics of Keratella cochlearis in a hypereutrophic tarn and the possible impact of predation by young roach. Hydrobiologia 147:221-227.

Hilton, J. & E. Rigg (1983). Determination of nitrate in lake water by the hydrazine-copper reduction method for use on a discrete analyser : performance statistics and an instrument induced difference from segmented flow conditions. Analyst. London 108:1026-1028.

Hofmann, W. (1980). On morphological variation in Keratella cochlearis populations from Holstien lakes (Northern Germany). Hydrobiologia 73:255-258.

Hofmann, W. (1982). On the coexistence of two pelagic Filinia species in Lake PluBsee I. Dynamics of abundance and dispersion. Archiv fur Hydrobiologie. Stuttgart 95:125-137.

Hussey, C.G. (1981). A checklist and bibliography of records of Rotifera (Rotatoria) in Britain. London. British Museum (Natural History) 8pp 10fiche.

Hutchinson, G.E. (1967). A treatise on Limnology, vol. 2. John Wiley and Sons, Inc. New York.

Jones, J.G. (1979). A guide to methods for estimating microbial numbers and biomass in freshwater. Freshwater Biological Association Scientific Publication no.39.

Jones, J.G. & B.M. Simon (1975). An investigation of errors in direct counts of aquatic bacteria by epifluorescence microscopy with reference to a new method for dyeing membrane filters. Journal of Applied Bacteriology 39:317-329.

Kasprzak, P. & D. Ronneberger (1982). Vergleichende untersuchungen zur Struktur und Dynamik des Zooplanktons im Stechlinsee, Nehmitsee und Haussee 1978/79. Limnologica (Berlin) 14:263-295.

Kosicki, S. (1960). The vertical distribution of pelagic Rotatoria during the summer stagnation in Lakes Mikolajskie and Snardwy. Polskie Archivum Hydrobiologii 8:9-62. (paper in polish with english summary).

Kutikova, L.A. (1970). Kolovratki Fauna USSR. Fauna USSR 104 Akademia Nauk.

Larsson, P. (1971). Vertical distribution of planktonic rotifers in a meromictic lake; Blankvatn near Oslo, Norway. Norwegian Journal of Zoology 19:47-75.

Larsson, P. (1978). The life cycle, dynamics and production of zooplankton in Ovre Heimdalsvatn. Holarctic Ecology 1:162-218.

Lloyd, M. (1967). "Mean crowding". Journal of Animal Ecology 36:1-30.

Longhurst, A.R. (1976). Vertical migration. In : The Ecology of the Seas (Ed. D.H. Cushing & J.J. Walsh). Blackwell. Oxford. pp116-137.

Lozeron, H. (1902). Sur la repartition verticale du plancton dans le lac de Zurich de decembre 1900 a decembre 1901. Vierteljahrschrift der Naturforschenden Gesellschaft in Zurich 47:115-198.

Lund, J.W.G. & C.S. Reynolds (1982). The development and operation of large limnetic enclosures in Blelham Tarn, English Lake District, and their contribution to phytoplankton ecology. Progress in Phycological Research vol.1 pp. 2-65 (Ed. F.E. Round & D.J. Chapman). Elsevier Biomedical Press. Amsterdam.

Mackereth, F.J.H., J. Heron & J.H. Talling (1978). Water Analysis. Freshwater Biological Association. Scientific Publication No. 36.

Marler, P. (1952). A preliminary study of the post-glacial history of the Esthwaite Valley. Thesis, University of London.

May, L. (1980). The ecology of planktonic rotifers in Loch Leven. Ph.D. Thesis, Paisley College of Technology.

Michael, R.G. (1968). Studies on the zooplankton of a tropical fish pond. Hydrobiologia 32:47-68.

Miracle, M.R. (1977). Migration, patchiness and distribution in time and space of planktonic rotifers. Archiv fur Hydrobiologie Beihefte Ergebnisse der Limnologie 8:19-37.

Miracle, M.R. & E. Vicente (1983). Vertical distribution and rotifer concentration in the chemocline of meromictic lakes. Hydrobiologia 104:259-267.

Moore, J.W. (1980). Seasonal cycles of zooplankton and related phytoplankton development in three shallow mesotrophic lakes in Northern Canada. Internationalen Revue der gesamten Hydrobiologie und Hydrographie 65:357-378.

Murphy, J. & P. Riley (1962). A modified single solution method for the determination of phosphate in natural waters. Analytica chimica Acta 27:31-36.

Nauwerck, A. (1963). Die Beziehungen zwischen Zooplankton und phytoplankton im See Erken. Symbolae botanical upsalienses 17:1-163.

Orcutt, J.D., Jr. & M.L. Pace (1984). Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. Hydrobiologia 119:73-80.

Pejler, B. (1957a). On variation and evolution in planktonic rotatoria. Zoologica Bidrags fran Uppsala 32:1-66.

Pejler, B. (1957b). Taxonomical and ecological studies on planktonic rotatoria from northern Swedish Lapland. Kungliga Svenska vetenstapsakademiens handlingar Uppsala u. Stockholm 6:1-68.

Pejler, B. (1961). The Zooplankton of Osbysjon, Djursholm I. Seasonal and vertical distribution of the species. Oikos 12:225-248.

Pejler, B. (1962). The zooplankton of Osbysjon, Djursolm. II. Further ecological aspects. Oikos 13:216-231.

Pejler, B. (1963). Regional-ecological studies of Swedish freshwater zooplankton. Zoologica Bidrags fran Uppsala 36:407-515.

Pennak, R.W. (1944). Diurnal movements of zooplankton organisms in some Colorado mountain lakes. Ecology 25:387-403.

Pennak, R.W. (1949). Annual limnological cycles in some Colorado reservoir lakes. Ecological Monographs 19:235-267.

Pontin, R.M. (1978). A key to the freshwater planktonic and semi-planktonic rotifera of the British Isles. Freshwater Biological Association Scientific Publication no.38.

Pourriot, R. (1965). Recherches sur l´ecology des Rotiferes. Vie et Milieu Supplement 21:1-224.

Pourriot, R. (1977). Food and feeding habits of the Rotifera. Archiv fur Hydrobiologie. Beihefte Ergebnisse der Limnologie 8:243-260.

Pourriot, R. (1981). Influence des trois facteurs de l´environnement lumiere, temperature et salinite, sur l´eclosion des oeufs de duree dun clone de Brachionus plicatilis (O.F. MULLER). Rotifere. Compte rendu hebdomadaire des seances de l´Academie des sciences 295:243-246.

Pourriot , R., P. Clement & A. Luciani (1981). Perception de la photoperiode par un Rotifere : hypotheses sur les mecanismes. Archives zoologique experimentale et generale 122:317-327.

Pourriot, R., D. Benest & C. Rougier (1982). Processus d´eclosion des oeufs de duree de Brachionus calyciflorus Pallas (Rotifere). Comparaison de deux clones. Vie et Milieu 32:83-87.

Preissler, K. (1977a). Do rotifers show avoidance of shore ? Oecologia (Berlin) 27:253-260.

Preissler, K. (1977b). Horizontal distribution and "avoidance of shore" by rotifers. Archiv fur Hydrobiologie. Beihefte Ergebnisse der Limnologie 8:43-46.

Preissler, K. (1980). Field experiments on the optical orientation of pelagic rotifers. Hydrobiologia 73:199-203.

Ricci, C. (1983). Rotifera or Rotatoria ? Hydrobiologia 104:1-2.

Ringelberg, J. (1964). The positively phototactic reaction of Daphnia magna Straus : a contribution to the understanding of vertical migration. Netherlands Journal of Sea Research 2:319-406.

Ruttner, F. (1909). Uber die Anwendung von filtration und Zentrifugierung bei den planktologischen Arbeiten an den Lunzer Seen. Internationalen Revue der gesamten Hydrobiologie und Hydrographie 2:174-181.

Ruttner, F. (1930). Des Plankton der Lunzer Untersees seine Verteilung in Raum und Zeit wahrend der Jahre 1908-1913. Internationalen Revue der gesamten Hydrobiologie und Hydrographie 23:1-138.

Ruttner-Kolisko, A. (1949). Zum Formweschel und Artproblem von Anuraea aculearis (Keratella quadrata). Hydrobiologia 1:425-467.

Ruttner-Kolisko, A. (1974). Plankton Rotifers Biology and Taxonomy. Die Binnengewasser Supplement 26 English Translation.

Ruttner-Kolisko, A. (1975). The vertical distribution of plankton rotifers in a small alpine lake with a sharp oxygen depletion (Lunzer Obersee). Verhandlungen der Internationalen vereinigung fur theoretische und angewandte Limnologie 19:1286-1294.

Ruttner-Kolisko, A. (1977). Population dynamics of rotifers as related to climatic conditions in Lunzer Obersee and Untersee. Archiv fur Hydrobiologie. Beihefte Ergebnisse der Limnologie 8:88-93.

Ruttner-Kolisko, A. (1980). The abundance and distribution of Filinia terminalis in various types of lake as related to temperature, oxygen and food. Hydrobiologia 73:169-175.

Schindler, D.W. & B. Noven (1971). Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the experimental lakes area, north western Ontario. Journal of the Fisheries Research Board of Canada 28:245-256.

Stemberger, R.S. (1974). Temporal and spatial distributions of planktonic rotifers in Milwaukee Harbour and adjacent Lake Michigan. Proceedings of the 17th Conference on Great Lakes Research 17:120-134.

Stemberger, R.S., J.E. Cannon & F.J. Bricker (1979). Spatial and seasonal structure of rotifer communities. U.S. Environment Protection Agency 600/3-79-085.

Stephens, K. (1963). Determination of low phosphate concentrations in lake and marine waters. Limnology and Oceanography 8:361-362.

Swale, E.M.F. (1968). A study of the nannoplankton flagellate Pedinella hexacostata Vysotskii by light and electron microscopy. British Phycological Journal 4:65-86.

Swale, E.M.F. & J.H. Belcher (1966). Ochromonas ostreaformis nov.sp., a large compressed chrysomonad. New Phytologist 65:267-272.

Talling, J.F. (1971). The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitteilungen der Internationalen Vereinigung fur theoretische und angwandte Limnologie 19:214-243.

Talling, J.F. & D. Driver (1963). Some problems in the estimation of chlorophyll a in phytoplankton. US Atomic Energy Commission, Division of Technical Information TID-7633:142-146.

Viaud, G. (1940). Recherches experimentales sur le phototropisme des rotiferes I. Bulletin biologique de la France et de la Belgique, Paris 74:249-308.

Viaud, G. (1943a). Recherches experimentales sur le phototropisme des Rotiferes II. Memoire. Bulletin biologique de la France et de la Belgique, Paris 77:68-93.

Viaud, G. (1943b). Recherches experimentales sur le phototropisme des Rotiferes III. Stroboscopie des mouvement ciliaires. Mouvement ciliaires et phototropisme. Bulletin biologique de la France et de la Belgique, Paris 77:224-242.

Vincent, W.F. (1980a). The physiological ecology of a Scenedesmus population in the hypolimnion of a hypertrophic pond I. Photoautotrophy. British Phycological Journal 15:27-34.

Vincent, W.F. (1980b). The physiological ecology of a Scenedesmus population in the hypolimnion of a hypertrophic pond II. Heterotrophy. British Phycological Journal 15:35-41.

Voigt, M. & W. Koste (1978). Rotatoria. Die Radertiere Mitteleuropas. Berlin Bebruder Borntraeger pp720.

Vollenweider, R.A. (1968). Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Water Management research OECD.DAS/CSI/68.27 pp159+20+61.

von Lauterborn, R. (1900). Der formenkreis von Anuraea cochlearis. Ein Beitrag zur Kenntnis der Variabilitat bei Rotatorien. I Teil: Morphologische Gliederung des Formenkreises. Verhandlungen des Naturhistorisch-medizinischen Vereins zu Heidelberg 6:412-448.

von Lauterborn, R. (1904). Der Formenkreis von Anuraea cochlearis. Ein Beitrag zur Kenntnis der Variabilitat bei Rotatorien. II Teil: Die cyklische oder temporale Variation von Anuraea cochlearis. Verhandlungen des Naturhistorisch-medizinischen Vereins zu Heidelberg 7:529-1.

Warme, P.K. (1980). Curve Fitter. Interactive Microware, Inc. State College, Pa 16801 U.S.A.

Wesenberg-Lund, C. (1904). Studier over de Danske soers plankton. Copenhagen. Gyldendalske Boghandel Nordisk Forlag. pp. 223.

Wesenberg-Lund, C. (1930). Contributions to the biology of the Rotifera II. The periodicity and sexual periods. Kobenhavn. Andr. Fred. Host & Son. Kungliga Hof-Boghandel.

Wetzell, R.G. (1975). Limnology. Saunders. Philadelphia 743 pp.

Worthington, E.B. (1931). Vertical movements of freshwater macroplankton. Internationale Revue der gesamten Hydrobiologie und Hydrographie 25:394-436.

Zaret, T.M. & J.S. Suffern (1976). Vertical migration as a predator avoidance mechanism. Limnology and Oceanography 21:804-813.

PUBLICATIONS

STEWART, L.J. & GEORGE, D.G. (1987).
Environmental factors influencing the vertical migration of planktonic rotifers in a hypereutrophic tarn.
Hydrobiologia, 147, 203-208.

STEWART, L.J. & GEORGE, D.G. (1988).
An *in situ* experimental column for the study of vertical migration in plankton.
Freshwater Biology (in press).

FINLAY, B. J., BERNINGER, U.-G., STEWART, L.J., HINDLE, R.M. AND DAVISON, W. (1987).
Some factors controlling the distribution of two pond dwelling ciliates with algal symbionts (*Frontonia vernalis* and *Euplotes daidaleos*).
Journal of Protozoology, 34, 349-356.