A study of the planktonic rotifers (Rotatoria) of Grasmere

Elliott, Judith I.

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Abstract

The planktonic rofiters of Grasmere, a small lake in the English Lake District, were studied from August 1969 to December 1972. Twenty-four species were recorded but five were very rare. The remaining species were divided into three groups according to their seasonal occurrence: spring-autumn species (Keratella quadrata, K. cochlearis, Gastropus stylifer, Asplanchna priodonta, Kellicottia longispina, Conochilus hippocrepis), spring-early summer species (Polyarthra dolichoptera, Synchaeta tremula, S. pectinata, S. stylata, S. oblonga, C. unicornis), summer-autumn species (Polyarthra vulgaris, P. major, Filinia terminalis, S. grandis, Ploesoma hudsoni, Trichocerca capucina, T. similis). The months in which each species were abundant are given.

Keratella quadrata and Filinia terminalis were most abundant in the deepest stratum, Kellicottia longispina and Conochilus spp. were most abundant in the upper and middle strata, Trichocerca spp. showed no pronounced vertical distribution, and all the remaining species were most abundant in the upper stratum. Keratella cochlearis, Kellicottia longispina and Synchaeta spp. (temperature only) attained their highest densities over a wide range of temperature and oxygen concentration, and Filinia terminalis, Conochilus spp., Asplanchna priodonta, K. quadrata, Polyarthra spp., Synchaeta spp. (oxygen only) attained their highest densities within a narrow range of temperature and oxygen concentration. Optimum ranges are given for each species.

Major changes in abundance occurred between 1971 and 1972 when Asplanchna priodonta, Kellicottia longispina, Conochilus unicornis and Filinia terminalis increased in abundance, and Keratella quadrata, Gastropus stylifer, C. hippocrepis, Polyarthra spp., Synchaeta spp. and Ploesoma hudsoni decreased in abundance. These changes are discussed in relation to the temperature and oxygen requirements of each species and also to the probable enrichment of the lake after the opening of a new sewage works in June 1971.

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Judith I. Elliott.

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CONTENTS

SECTION 1

INTRODUCTION

1. Introduction.

1.1 The purpose of the present study.

There is little information on the planktonic rotifers of the English Lake District. Wailes (1939) and Galliford (1947, 1949) recorded the rotifers found in Windermere, Thirlmere, Esthwaite Water and Blelham Tarn, and Ruttner-Kolisko (1970) discovered a new species, Synchaeta calva, in Windermere, Thirlmere and Blelham Tarn. Edmondson (1965) estimated the reproductive rate of Polyarthra vulgaris Carl. in Windermere, Keratella cochlearis (Gosse) and Kellicottia longispina (Kell) in Windermere, Esthwaite Water and Blelham Tarn, and also investigated the relationship between reproductive rate and the abundance of food organisms.

In 1969, Dr. Ruttner-Kolisko worked for six months in the Windermere laboratory of the Freshwater Biological Association and studied the seasonal abundance of rotifers in several lakes. She suggested that a detailed study of the rotifers of one lake would be most useful. Therefore the present study commenced and its chief purpose was to investigate the seasonal changes in the population of planktonic rotifers in Grasmere. Grasmere was chosen because there was a good population of rotifers, several aspects of the lake were already being studied and a new sewage treatment plant was to be constructed during the course of this investigation.

1.2 A short review of the literature on the ecology of planktonic rotifers.

The rotifers or "wheel animalcules" are small, pseudocoelomate animals which possess a ciliary organ or "corona" at the anterior end and a pharynx or "mastax" provided with internal jaws or "trophi". Rotifers were separated from the Protozoa under the name Rotatoria by Ehrenberg (1838), but other workers (e.g. Dutrochet 1812) had recognised them as a natural group under the name Rotifera. Hyman (1951) preferred the latter name and placed the class Rotifera in the phylum Aschelminthes. More recent workers (e.g. Voigt 1957, Bartos 1959, Rudescu 1960, Ruttner-Kolisko 1972) prefer the name Rotatoria and this name is most frequently used by workers on this group. The interrelationships and possible origins of the Rotatoria have been discussed by Hyman (1951) and Ruttner-Kolisko (1963).

Of the three orders of rotifers (Seisonacea, Bdelloidea, Monogononta), only the Monogononta are found in the freshwater plankton. There are three suborders in the Monogononta, namely Ploima, Flosculariacea, Collothecacea, and each suborder contains both benthic and pelagic species. The pelagic species are among the most characteristic members of the plankton, and most species show the following features that are an adaptation to a pelagic life: thinness of cuticle and transparency (e.g. Asplanchna, Synchaeta), stout or sacciform shape, a foot which is ventrally displaced or greatly reduced, and structures for buoyancy such as oil droplets or jelly (e.g. Conochilus) or long projecting spines (e.g. Kellicottia, Keratella, Filinia, Polyarthra). The evolution of the planktonic Rotatoria from periphytic and benthic forms has been discussed in detail by Pejler (1957a). Genera which occur most frequently and abundantly in the plankton of lakes are *Keratella*, *Kellicottia*, *Polyarthra*, *Synchaeta*, *Filinia* and *Asplanchna* (Edmondson 1959).

The distribution of many species of rotifers is potentially cosmopolitan, i.e. they are of world-wide occurrence (Rousselet 1909, Edmondson 1944), but some species have a more limited geographical distribution. Green (1972) compared the planktonic rotifer fauna of Lake Albert in Africa (Green 1967a) with that of nine localities in the Old World Northern Hemisphere (most northern locality was Spitsbergen). He found that as latitude increased, the similarity between localities decreased, and he recognised four major groups of species:

1) Cosmopolitan- occurring on at least three continents, and in cool temperate as well as tropical areas, e.g. *Euchlanis dilitata* Ehrenberg has been recorded from Spitsbergen (Amren 1964b), Uganda (Green 1967a), Greenland (Levinson 1914), Tierra del Fuego (Thomasson 1955a), and New Zealand (Russell 1960).

2) Cosmotropical- occurring on two or more continents in the tropics, but absent from cool temperate regions, e.g. *Brachionus caudatus* Barrois and Daday, *Keratella tropica* (Apstein).

3) Arctic-temperate- occurring in Arctic or Antarctic areas but also in cool temperate regions, e.g. *Notholca* spp. (Carlin 1943, Pejler 1962a).

4) American- occurring only in the Americas, e.g. *Brachionus gessneri* Hauer (Hauer 1956, 1965).

Green (1972) also found that in the ten localities ranging from Lake Albert to Spitsbergen, the following nine genera accounted for 40-72% of the total species in each locality:

Brachionus, Keratella, Lecane, Notholca, Ploesoma, Polyarthra, Synchaeta, Trichocerca, Testudinella. There is a large variation in the number of species of rotifers found in the plankton of different lakes, e.g. 91 species, 7 genera and 1 order from Terwilliger's Pond (U.S.A.) over eight months (Ahlstrom 1933), 97 species from the series of lakes and rivers of Motalaström (Sweden) over six years (Carlin 1943), 62 species from Lake Albert (Uganda) over one year (Green 1967a), 60 species from about seventy lakes and ponds in central Sweden (Pejler 1957c), 47 species from Lake Baikal (U.S.S.R.) over many years (Kozhov 1963), 38 species from over forty ponds and lakes in northern Swedish Lapland (Pejler 1957b), 34 species from lakes in the Ocqueoc River system (U.S.A.) over four years (Beach 1960), 34 species from Lake Balaton (Hungary) over two years (Zankai and Ponyi 1971), 33 species from Lago di Scanno (Italy) over eight years (Cannicci 1962), 32 species from Lago Maggiore (Italy) over thirteen months (Tonolli 1962), 30 species from Lake Stechlinsee (Germany) over three years (Koch-Althaus 1963), 21 species from Paradise Lake (Canada) over one year and 10 species from Sunfish Lake (Canada) over seventeen months (George and Fernando 1969), 14 species from lakes, ponds and puddles in Spitsbergen over two summers (Amren 1964b), and 10 species from Lake Blankvatn (Norway) over twenty two months (Larsson 1971). Pennak (1957) surveyed twenty seven lakes in Colorado and found up to 10 species per sample (mean 4.8). From a survey of the literature, he found a range up to 19 species per sample (mean 5.5), but this figure is lower than those given by other workers, e.g. Carlin (1943), Tonolli (1962). Therefore the number of species found in a given locality over one year or longer ranges from

10 to about 100, but single samples contain a much lower number of species.

Although most species of rotifers are dioecious (exception: order Bdelloidea), the males are greatly reduced in size and morphology, and usually appear for brief periods. In the Ploima, the males are usually reduced to one-half to one-eighth the size of the females, but the males in the Flosculariacea and Collothecacea are often less than one-tenth the size of the female. Three kinds of eggs are produced in the Monogononta: thin-shelled "amictic" eggs that cannot be fertilised and that develop parthenogenetically into females; smaller thin-shelled "mictic" eggs that if not fertilised develop into males; and thick-shelled "dormant" or "resting" eggs that are fertilised mictic eggs and that hatch into amictic females. Parthenogenetic eggs hatch in one to three days but dormant eggs require six to eight weeks. Females are either mictic or amictic, and one female cannot produce both kinds of eggs. The females of planktonic rotifers usually have the adult form and structure when they hatch, and sexual maturity is attained in a few days. Males are usually sexually mature when they hatch, and do not grow. In the typical heterogenous life history of the Monogononta, amictic females hatch from dormant eggs, then a series of parthenogenetic generations hatch from amictic eggs and are finally succeeded by a sexual generation whose mictic females and small males produce large mictic dormant eggs. The heterogenic alternation of generations combines the advantage of quick multiplication during the parthenogenetic phase with the essential recombination of genes by mating in the mictic stage (Ruttner-Kolisko 1969). Hutchinson (1967) considers that this life cycle is strong evidence for the hypothesis that rotifers became established early in their history in freshwater and that the species now found in the sea are secondarily marine.

The dormant eggs usually have thickened and sculptured external walls, and enable the species to survive when conditions are unfavourable, e.g. drought and low temperatures. The females hatching from these dormant eggs are sometimes morphologically different from the later amictic females, e.g. the early females sometimes lack appendages in Polyarthra (Nipkov 1952) and Filinia (Sudzuki 1964, Ruttner-Kolisko 1972). In most planktonic species (e.g. Keratella, Kellicottia, Brachionus, Polyarthra, Filinia, Conochilus and a few species of Synchaeta) eggs are carried by amictic females and Asplanchna is viviparous, but other species (Ploesoma, Gastropus and most species of Synchaeta) lay their eggs in the water (Edmondson 1960) or on water plants (e.g. Euchlanis). Most species of Trichocerca lay their eggs on other organisms which include other species of rotifers (Wesenberg-Lund 1930, Pourriot 1970), and Trichocerca capucina (Wierz.-Zach.) has been described as a cuckoo among the rotifers (Rudlin 1949).

Some species do not have a sexual phase with the production of dormant eggs (acyclic), whereas the sexual phase of other species usually coincides with the period of maximum population density and may occur once (monocyclic species), twice (dicyclic species), or several times (polycyclic species) in a year (Wesenberg-Lund 1923, 1930). Among the perennial planktonic rotifers in Motalaström, sexual periods were observed in all species except Keratella cochlearis and Kellicottia longispina (Carlin 1943). Pejler (1957b) observed the formation of resting eggs in Kellicottia longispina in Lapland lakes and described the male for the first time. No sexual periods were observed in Keratella quadrata (O.F.Müller) in Lunzer Obersee (Ruttner-Kolisko 1949) and Carlin (1943) observed only one Keratella quadrata with resting eggs in Motalaström over six years. In Keratella hiemalis (Carlin), resting eggs can be formed without fertilisation and males may never occur (Ruttner-Kolisko 1946). Pejler (1957a) recorded 38 species in Lapland and found 26 species with males or male eggs, 5 species with resting eggs but apparently no males, and 7 species with no males or resting eggs. Although it is generally agreed that the appearance of mictic females in the sexual phase is related to environmental factors, it is not known which factor or combination of factors is important (Halbach and Halbach-Keup 1972). The various suggestions include starvation (Nussbaum 1897), optimal feeding (Whitney 1916b, 1917, 1919), brief starvation after optimal feeding (Mitchell 1913), changes in the nature of the food (Whitney 1914a, b; 1916a, b; Hodgkinson 1918, Luntz 1926, Watzka 1928, Pourriot 1957a), changes in pH or bicarbonate or oxygen (Tauson 1925), the shock effect of a sudden decrease in water temperature (Ruttner-Kolisko 1964), high population density and crowding (Buchner 1936, 1941a, b), and high ratios of amictic females to the volume of the medium (Gilbert 1963). All these results were obtained from experiments on rotifers in cultures, but Carlin (1943) found that a sexual phase in the field does not occur in species with a low density and is therefore limited to species showing a maximum population density at any given time.

Numerous studies have been made in laboratory cultures to determine the life span of rotifers and their egg production at different temperatures (see references in Hyman 1951, Hutchinson 1967, Ruttner-Kolisko 1972). From the results of her own work and those of other workers, Ruttner-Kolisko (1963) concludes that a heterogonic rotifer inhabiting a small body of water will live for about ten days and will produce one youngster daily from the third day onwards. Therefore, about 10^{12} individuals can develop from one egg in the course of sixty days with a normal death rate, and the first descendants will have gone through almost thirty generations, the last through only six. Pelagic species of large lakes have a longer life span of about two weeks, produce one egg in about forty eight hours, and can therefore produce about 10^{6} individuals from one egg in sixty days. As rotifers can reproduce very rapidly in the parthenogenetic phase, it is not surprising that variability within genera is very great and it is therefore difficult to determine clear species boundaries.

Edmondson (1960, 1964, 1965, 1968) has developed a series of equations to measure and compare rates of birth, death and reproduction, and has used these rates to analyse the population dynamics of planktonic rotifers. He found that the reproductive rate of <u>Keratella cochlearis</u>, <u>Kellicottia longispina</u> and <u>Ploesoma truncatum</u> (Levander) in Bare Lake (Alaska) was correlated with both temperature and Secchi disk transparency which was a rough inverse measure of the standing crop of phytoplankton (Edmondson 1960). He later found that both temperature and the abundance of a particular food organism had an apparent effect on the reproductive rates of <u>Keratella cochlearis</u>, <u>Kellicottia longispina</u> and <u>Polyarthra vulgaris</u> in four lakes in the English Lake District

(Edmondson 1960). These studies are excellent examples of a quantitative approach to the population dynamics of rotifers and also demonstrate that food is an important factor in the regulation of population numbers.

The feeding habits of planktonic rotifers vary between species. Some species produce a current that brings small particles and organisms to the rotifer, and have trophi of the chewing type, e.g. Brachionus, Euchlanis, Keratella, Kellicottia. Other species are carnivores which either trap their prey, e.g. Collothecacea, or seize their prey with trophi of the forceps type e.g. the pelagic Trichocercidae, Synchaetidae, Gastropodidae and Asplanchnidae of the suborder Ploima. Some species which seize their prey also chew their prey after capture, but other species suck out the contents by means of a piston apparatus, e.g. species in the Gastropodidae feeding on Dinoflagellates (Kolisko 1938).

The feeding of rofiters have been studied in the field (Dieffenbach and Sachse 1911, Naumann 1923, Myers 1941, Pejler 1957b, Pourriot 1965a) and in laboratory cultures (de Beauchamp 1938, Pourriot 1957b, 1965, 1970). Species which feed by sedimenting particles show food preferences. Brachionus spp. prefer a diet of Protococcales, Euglenoidina and Volvocales (de Beauchamp 1938, Pourriot 1957b, 1965a) and also readily eat cryptomonads and euchlorophyceans (Rezvoj 1926). Filinia eats smaller food (diameter < 10 u) and appears to exist chiefly on organic detritus and bacteria (Naumann 1923, Nauwerck 1963, Pourriot 1965a). Kellicottia longispina, Keratella, and planktonic species of Collotheca also feed on small particles (10-12 u), and although they chiefly feed on sedimentary particles, Kellicottia and Keratella can capture larger food organisms, e.g. Cryptomonas (Pourriot 1963). Polyarthra also feeds chiefly on Cryptomonas (Dieffenbach and Sachse 1911), and the reproductive rate of Polyarthra vulgaris was strongly correlated with numbers of Cryptomonas in Windermere (Edmondson 1965).

Raptorial species also feed on a variety of food organisms. Ascomorpha sucks out dinoflagellates (Myers 1941, Carlin 1943, Pejler 1957b), and species of Synchaeta, Ploesoma and Asplanchna feed on algae, protists, other rotifers and even small Crustacea (Rezvoj 1926, Pejler 1957b, Pourriot 1965a). Trichocerca spp. usually feed on filamentous algae and small particles, but they can also suck out the contents of desmids (Pourriot 1970), and T. capucina can seize, pierce and suck out the contents of eggs of Keratella quadrata (Rudlin 1949).

Pejler (1957b) notes that there are several examples of coexisting species which differ in size and are therefore feeding on slightly different food. The form of the mastax differs in species of the genera Synchaeta, Asplanchna and Trichocerca, and this diversity in the trophi is probably also correlated with different feeding habits in these raptorial species. Therefore, as a result of these different food preferences and feeding habits, the rotifers probably occupy fairly discrete niches in the plankton community.

Many workers have investigated the phenomenon of "cyclomorphosis" in rotifers. This seasonal change in body form, especially in the length of the projecting spines of the lorica, has been well documented for the planktonic Ploima, e.g. Keratella, Brachionus, Notholca, Asplanchna. Cyclomorphosis occurs in other planktonic organisms, and Wesenberg-Lund (1900) proposed that these organisms enlarge their surfaces during summer by body or spine elongation and thus increase their buoyancy with the decrease in the specific weight of the water with increasing temperature. Dieffenbach and Sachse (1911) associated cyclomorphosis with changes in the food supply; long-spined forms occur when food is abundant and short-spined forms occur when food is sparse, but Rauh (1963) suggested that a scarcity of food should result in greater length of body and spines. Other workers have concluded that cyclomorphosis is not due to environmental factors, but is related to successive parthogenetic generations (Lauterborn 1900, 1904, Krätzschmar 1908, Hartmann 1920, Lange 1913, 1914).

The term cyclomorphosis implies that there is a successive, one-way variation which follows an inherent pattern. As environmental factors may influence this pattern in rotifers and some species may show no seasonal change in body form, the term "temporal variation" should be used until a real cyclomorphosis can be demonstrated (Björklund 1972). One classical example of temporal variation is the study on _Keratella quadrata_ by Krätzschmar (1908). Carlin (1943) later found that some of Krätzschmar's material was really _K. hiemalis_. Ruttner-Kolisko (1949) found no temporal variation in _K. quadrata_ taken from the same lake (Lunzer Obersee) as Krätzschmar's specimens, but did observe a temporal variation in specimens from a smaller, shallow lake. Carlin (1943) found a temporal variation in _K. quadrata_ and most of the perennial planktonic species in Motalaström, and also found that size was negatively correlated with temperature but was apparently unrelated to periods of sexual reproduction or maximum abundance. The first generation of _K. quadrata_ was spine-less in ponds on Spitsbergen but spine length increased in successive generations (Amren 1964a). There was no correlation between the size variation and environmental factors. In contrast to the views of other workers, Gallagher (1957) proposed that cyclomorphosis in K. cochlearis is directly related to temperature. A large number of workers have studied temporal variation in rotifers and the more recent records are published in Ahlstrom (1943), Carlin (1943), Margalef (1947), Berzins (1955), Buchner, Mulzer and Rauh (1957), Gallagher (1957), Pejler (1957a, 1962b), Green (1960). Hutchinson (1967) includes a large amount of information on rotifers in his extensive review of cyclomorphosis in the plankton. He notes that although cyclomorphosis is clearly determined by environmental factors, both known and unknown, there may also be inherent diversity in the reactions of different races or species to these factors. At present there is no general agreement on the adaptive significance of cyclomorphotic changes or temporal variations.

Although a diel migration of zooplankton is well documented (references in Hutchinson 1967), there are few records for rotifers. Most of the records are for one 24-hour period, and consequently the rotifers are said to show nocturnal, reverse or no migration (Kikuchi 1930, Ruttner 1930, 1937, 1943, Pennak 1944, Pejler 1957b, Kubicek 1964). The only detailed study appears to be that of George and Fernando (1970) who found that the same species can show nocturnal upward migration at one season and the reverse at another. Polyarthra vulgaris exhibited nocturnal migration in June, July, August and February, and reverse migration in March and April. A similar pattern was shown by Filinia terminalis (Plate) with reverse migration in April, and no apparent nocturnal migration was seen in Keratella quadrata. Larsson (1971) compared the day-night variations in the vertical distribution of rotifers in lake Blankvatn and found that Kellicottia longispina was the only species to show a diel migration which occurred only in August with greater numbers near the surface at night. Although there is little information on diel migration in rotifers, several workers have shown that the vertical distribution of rotifers varies between species, especially in thermally stratified lakes (Ruttner 1930, Campbell 1941, Pejler 1957b, 1961, Nauwerk 1963, Gilyarov 1965, Green 1967b, George and Fernando 1969, Larsson 1971, Klimowicz 1972). Berzins (1958) has probably made the most detailed study of both the vertical and horizontal distribution of zooplankton in a stratified lake. These studies indicate that most species attain their highest numbers in the epilimnion where phytoplankton production is greatest, and the numbers of rofiters generally decrease with increasing depth. This general pattern can be greatly distorted when an algal bloom with its associated rofiters descends to depths at which large numbers of rofiters are not usually found. In highly eutrophic waters, a marked decrease in oxygen in the upper layers can produce a temporary predominance of hypolimnic species. The density of some species (e.g. Keratella hiemalis, Filinia terminalis, Polyarthra dolichoptera Idelson) is greatest in the hypolimnion and this may be due to temperature, food or light conditions. K. hiemalis is generally regarded as a cold-water stenotherm, and Filinia terminalis and Polyarthra dolichoptera were also calssified as cold-water stenotherms, but Pejler (1961) found both species at temperatures up to 19°C in a shallow unstratified lake. Hypolimnic species are often found in greatest numbers just below the thermocline, and this distribution pattern probably reflects the rain of particulate food, such as faeces, bacteria and dead organisms, from the epilimnion. Light may also be an important factor which determines the vertical distribution of rofiters. Ruttner-Kolisko (1972) studied the vertical distribution of four species in Windermere in April when the lake was unstratified with differences between the surface and bottom (depth 40 m) of only 0.5°C and 3% saturation of oxygen. Although the environmental conditions were near uniform, the rotifers showed a definite pattern of vertical distribution with greatest numbers near the surface for Asplanchna priodonta Gosse and Keratella cochlearis, between 5 and 25 m for K. quadrata, and between 15 and 20 m for Filinia terminalis. Ruttner-Kolisko concludes that these distributions could only be due to an active vertical movement corresponding to the light gradient. These distribution patterns correspond very closely to those observed during the period of stratification.

Several workers have studied seasonal succession in planktonic species of rotifers and seasonal changes in their numbers (Wesenberg-Lund 1904, 1930, Ruttner 1930, Ahlström 1933, Carlin 1943, Davis 1954, 1969, Beach 1960, Pejler 1961, Koch-Althaus 1963, George and Fernando 1969, Granberg 1970, Larsson 1971). The species have usually been divided into groups according to their time of occurrence and periods of abundance. Carlin (1943) recognised three groups; winter and early spring species (e.g. Synchaeta lakowitziana Lucks, Keratella hiemalis, Notholca caudata Carlin), perennial species with late spring and early summer maxima (e.g. Keratella cochlearis, Kellicottia longispina, Asplanchna priodonta, Polyarthra vulgaris Carlin, Keratella quadrata), seasonal summer species (e.g. Gastropus stylifer Imhof, Ascomorpha ecaudis Perty, Ploesoma hudsoni Imhof). Some species cannot be placed in these three categories, and may have several maxima between May and October (e.g. Synchaeta spp.), or show temporal succession for species of the same genus (e.g. Polyarthra spp.). Some workers (e.g. Larsson 1971) have only recognised perennial and summer species, and it is clear that the periods of occurrence for a particular species can vary considerably between localities, e.g. Conochilus unicornis Rousselet has been reported as a summer form (Ahlström 1933, Chandler 1940, Davis 1969, Larsson 1971) and as a perennial form (Carlin 1943, Nauwerk 1963, Granberg 1970).

Several factors have been suggested to explain the vertical distribution and seasonal changes of each species. Although some correlations have been found, it is rarely clear if these are direct correlations, and contradictory results have often been obtained from different localities. However, it is clear that many species have definite environmental requirements. Therefore, if these requirements are known, the species can be used as indicators of the environment.

Ruttner-Kolisko (1971) has shown that rotifers can be used as indicators of the chemical conditions in inland waters of high salinity, and she listed species which were characteristic of freshwater, waters with a low or high salt content, and soda-waters. Several workers have reported definite pH ranges for different species, (e.g. Tauson 1926, Myers 1937, Russell 1949, Galliford 1954) but as other chemical factors may be correlated with pH, the actual limiting factor may not be pH but one of the other factors. Ahlström (1940) concluded that Brachionus is limited almost entirely to alkaline water (pH >6.6), but Strøm

(1944) found B. angularis (Gosse) in high mountain lakes of low conductivity. Pourriot (1965a) examined the distribution of rotifers in three pH ranges, 4.4 - 6.0, 5.8 - 7.0, > 7.0, and found that some species occurred in all three ranges (e.g. Polyarthra dolichoptera, Conochilus hippocrepis (Schrank)), most species occurred at pH > 7.0, and most planktonic species of large lakes occurred at pH values > 5.8. Pejler (1957c) doubts the importance within rather wide limits of either pH or total ionic concentration in determining the distribution of planktonic rotifers, and suggests that the apparent correlations are chiefly due to some species being characteristic of water of low or high primary productivity. Many workers have reported a correlation between the distribution of rotifers and water temperature, and have recognised apparent cold-water stenotherms which are found in the colder hypolimnion of stratified lakes and which can tolerate low concentrations of oxygen, e.g. Filinia terminalis, Keratella hiemalis, Polyarthra dolichoptera. The problems of separating the effects of temperature and oxygen from those of food supply have already been discussed. Pourriot (1965a) is one of the few workers who has examined the effects of several environmental factors (temperature, oxygen, pH, alkalinity, concentration of dissolved salts and organic substances, availability of food) on the distribution of rotifers, and has demonstrated that the distribution of some species is apparently correlated with one or more of these factors. Predation is another factor which may affect population size. Edmondson (1960) found a correlation between the numbers of the predator Asplanchna, and the death rate of the prey species, Keratella cochlearis. Hillbricht-Ilkowska (1962) found that the numbers of K. cochlearis increased as the number of carp fry in ponds increased. She suggested that the rooting habits of the carp increased the amount of seston in the pond and thus increased the amount of available food for the rotifers.

It is clear that the availability of food is a very important factor affecting the population size and distribution of rotifers. As different species have different food preferences and feeding habits, variations in the food supply will not affect different species in the same way. Food is obviously the prime factor when rotifers are used as indicators of trophic conditions. Pejler (1957c, 1965) concludes that the following species avoid the most highly productive waters: Ascomorpha ovalis Bergendal, Asplanchna herricki de Guerne, Synchaeta grandis Zacharias, Ploesoma hudsoni. Therefore these species may be indicators of oligotrophy. Kellicottia longispina, Polyarthra vulgaris and Conochilus unicornis are usually very conspicuous in extremely oligotrophic waters. A possible reason for the absence of S. grandis and P. hudsoni from eutrophic waters is that an abundance of non-edible algae is an obstacle to these carnivorous species when they are hunting and catching their prey (Pejler 1965). Pejler considers that the following species are typical of eutrophic waters: Brachionus spp., Keratella cochlearis, Anuraeopsis fissa (Gosse), Trichocerca spp., Polyarthra euryptera (Wierz), Pompholyx sulcata (Hudson) and Filinia longiseta (Ehrenberg). The intraspecific form, K. cochlearis f. tecta, is an excellent indicator of eutrophy (Pejler 1962b). There is some similarity between these lists of Pejler and those of Ruttner-Kolisko (1972) who gives the following species for oligotrophic lakes: Synchaeta (oblonga Ehrenberg, tremula Müller, pectinata Ehrenberg), Polyarthra (vulgaris-dolichoptera group), Keratella cochlearis, Conochilus unicornis, Kellicottia longispina, Asplanchna priodonta and Filinia terminalis. Eutrophic lakes usually contain some of these species, but in greater numbers together with the following: Euchlanis dilitata, Trichocerca spp., Pompholyx sulcata, Keratella quadrata, Filinia (longiseta-limnetica group). There is therefore a strong possibility that rotifers can be used as indicators of eutrophication, both natural and that due to man, but more work is clearly needed on this subject.

In this short review of the literature, it has been impossible to include references to all work on the ecology of planktonic rotifers, but an attempt has been made to consider the more important aspects of their ecology. Longer and more detailed reviews of the literature have been made by Hutchinson (1967) and Ruttner-Kolisko (1972).

SECTION 2

DESCRIPTION OF GRASMERE

2. Description of Grasmere

2.1 Morphometry of the lake.

Grasmere is a small lake (length 1.609km, breadth 685m) situated at an altitude of 61.6m above sea level on rocks of the Borrowdale volcanic series. It is the most northerly lake in the group which includes Windermere and is surrounded by mountains (heights up to 609.6m) which form the major part of the catchment area. The main inflow and outflow is the River Rothay, which enters the lake from the north and leaves from the south east. An island lies between the two basins of the lake, a smaller shallow basin in the north west and a deep larger basin in the south east (Fig. 1.).

The lake is fairly shallow with a depth of less than 5m for about half of the total surface area of $0.644km^2$. The total volume of the lake is about $5x10^6m^3$, the mean depth is 7.744m and the maximum depth is 21.5m at the point where all samples were taken.

Before the building of the new sewage works which discharges treated effluent into the River Rothay before it enters the lake, dwellings had private septic tanks and some establishments discharged effluent directly into the River Rothay. This effluent plus ground seepage undoubtedly contributed some enrichment to the lake.

Apart from a group of beeches at the south east end, there are generally few trees surrounding the lake. The margins of the lake are fringed with <u>Phragmites communis</u> which forms a dense stand near the inflow.

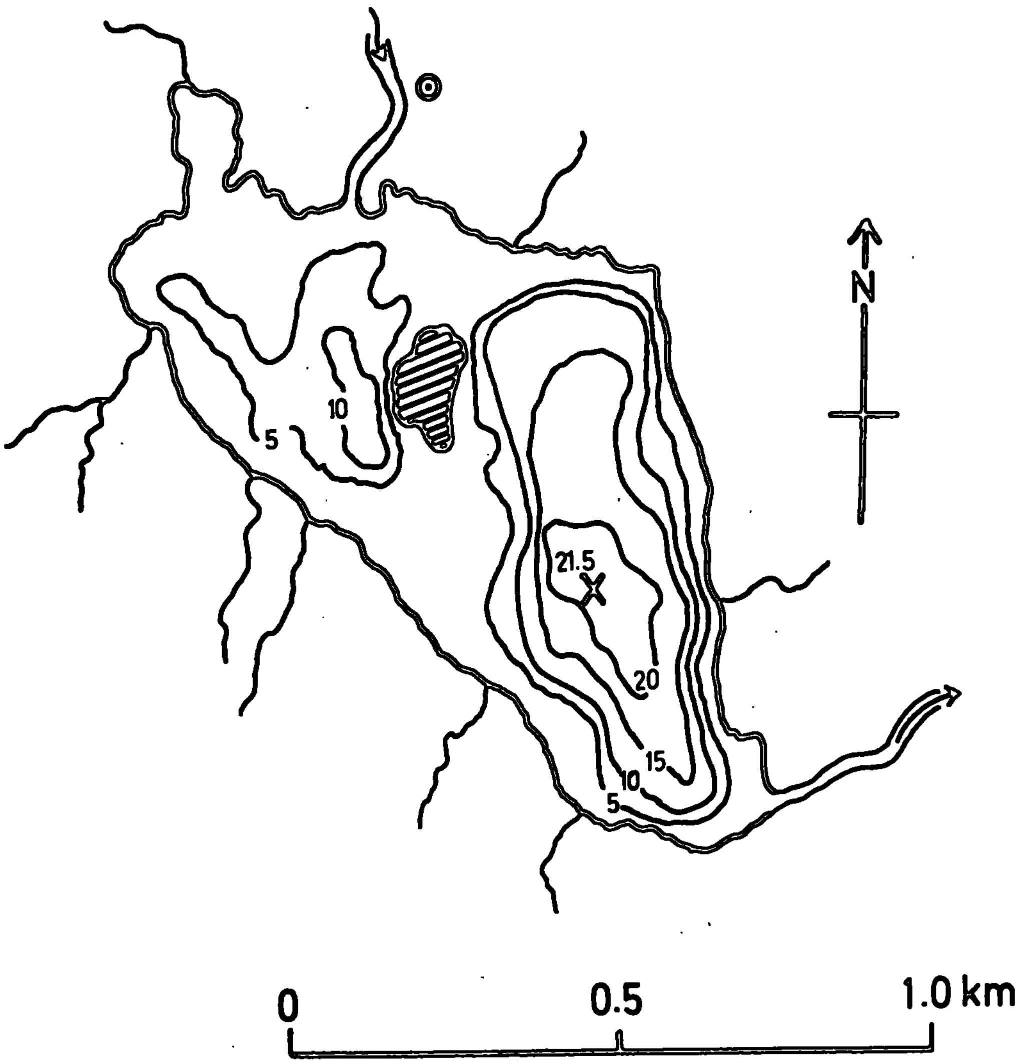

Fig. 1 Map of Grasmere showing depth contours in metres and position of sàmpling point (X) and sewage works (O).

2.2 Seasonal changes in temperature.

As the four samples of rotifers were taken in vertical hauls over depths of 20-15m, 15-10m, 10-5m, 5-0m, the seasonal changes in water temperature are given separately for each of these four strata (Fig. 2.). Temperature changes within Grasmere follow a regular annual pattern. The lake is stratified from May to late October and the depth of the thermocline increases from 6-7m from the surface in May to 14-15m in October. Rapid cooling in October and November produces a uniform temperature of 3-4°C during the winter months, and thin patches of ice occasionally form. This low temperature is maintained until March and then gradually increases to 6-7°C at the end of April when stratification commences.

In 1970, the temperature of the surface stratum (0-5m) increased from a uniform 7°C at the end of April to a range of 15-21°C in mid June, and then decreased to 14°C in September. During the same period, the temperature of the 5-10m stratum increased from 7°C to a range of 8-15.5°C, while the range in the 10-15m stratum was only 7-8°C. The temperature of the bottom stratum (15-20m) remained low at 6.5-7°C throughout the summer, increased in October when the thermocline descended into the upper layers of this stratum and then increased to 9°C during the autumn overturn and mixing of water in late October.

A similar seasonal pattern was observed in 1971 but the temperatures in all four strata were slightly lower, particularly in the 10-15m stratum.

In 1972, stratification took longer than in previous years and the thermocline was not established until late June. This

Figs. 2 and 3.

Fig.2 Maximum and minimum water temperature (^{o}C) in each stratum (depth strata were 0-5m,5-10m,10-15m and 15-20m from surface) from August 1969 to December 1972. (N.S. indicates the periods in which no samples were taken).

Fig.3 Maximum and minimum dissolved oxygen (% saturation) in each stratum (depth strata were 0-5m,5-10m,10-15m 15-20m from surface) from August 1969 to December 1972. (N.S. indicates the periods in which no samples were taken).

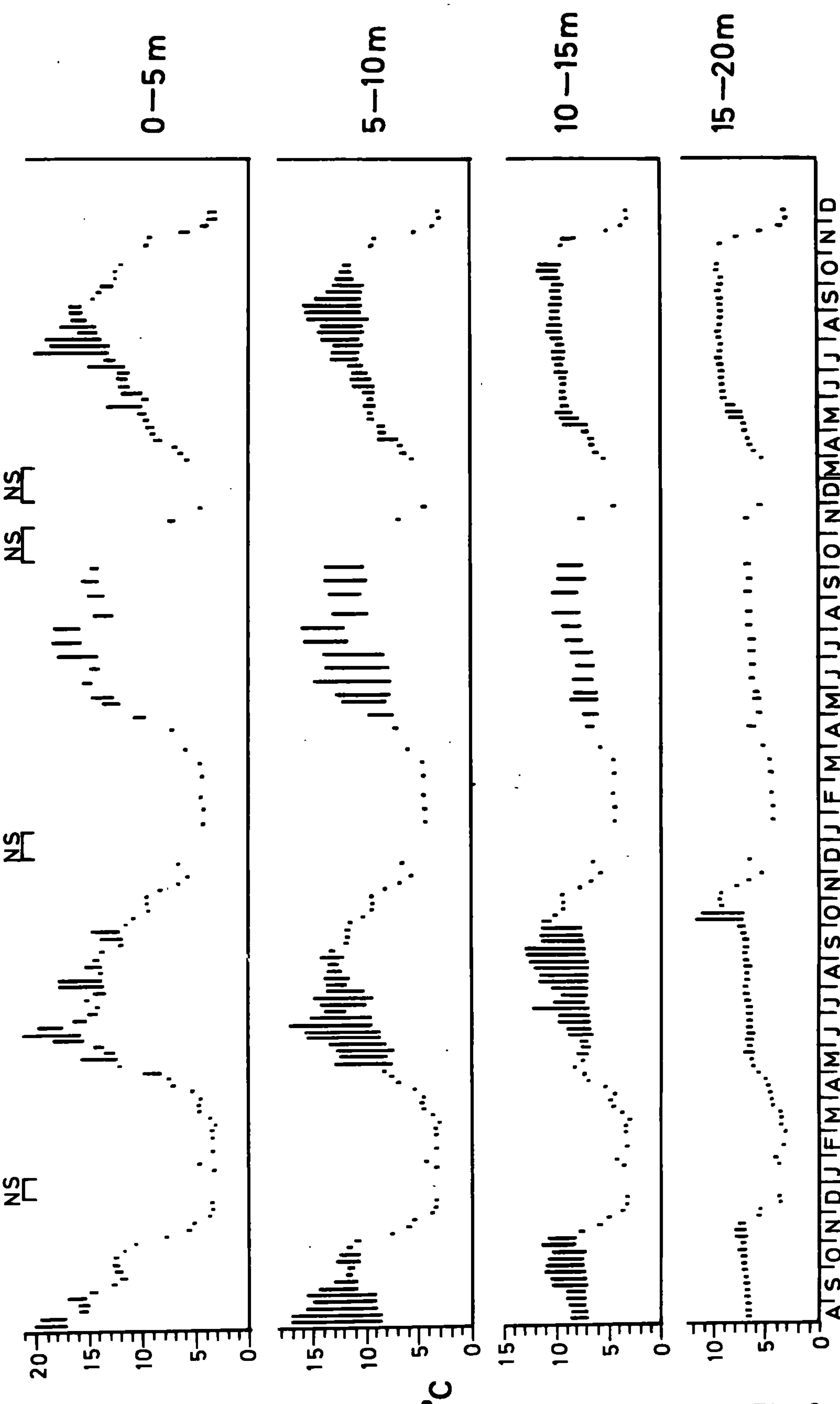
0—5 m
5—10 m
10—15 m
15—20 m
°C
NS
NS
NS
NS
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D M A M J J A S O N D
1969
1970
1971
1972

Fig.2.

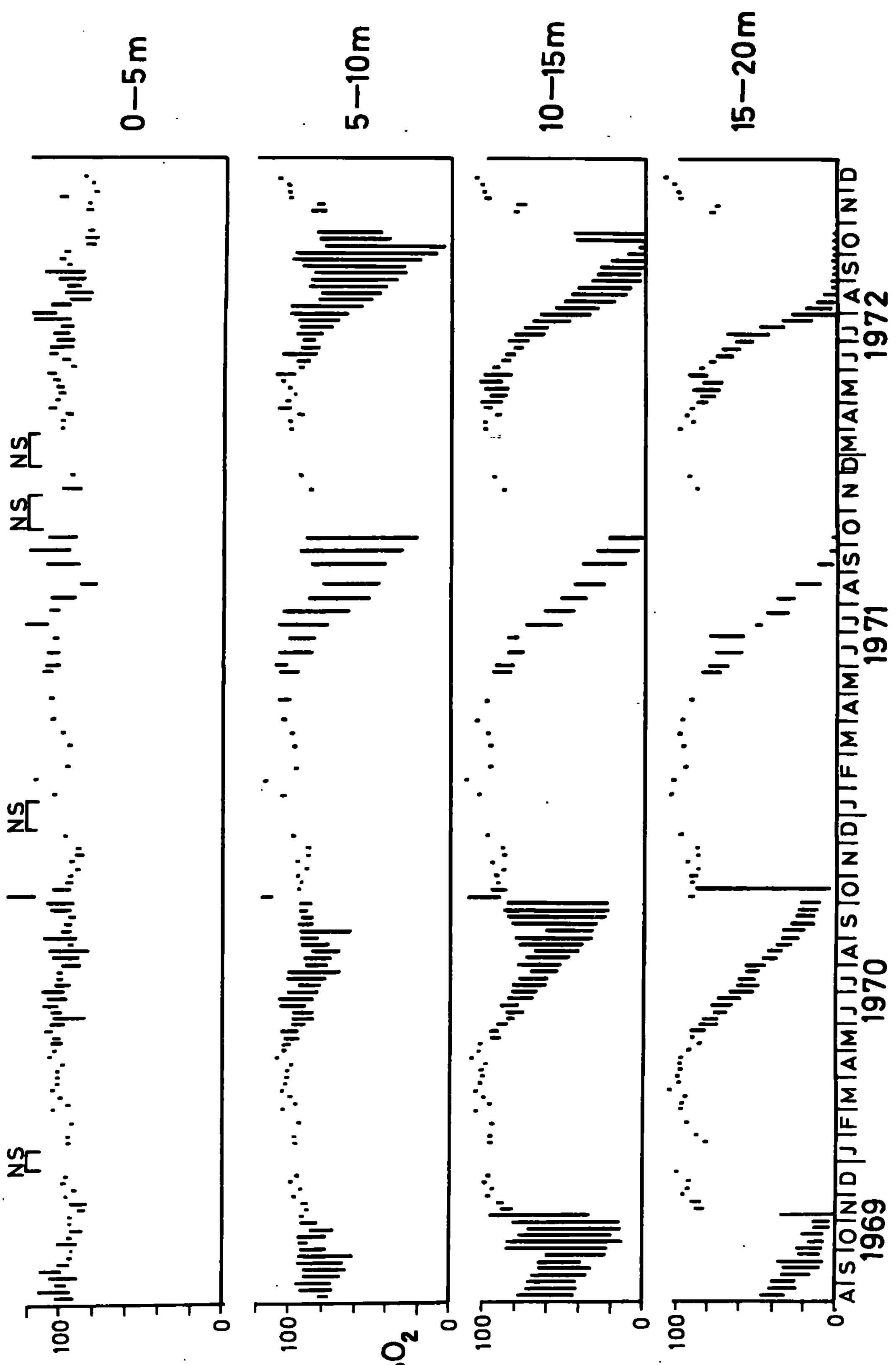
0–5m
5–10m
10–15m
15–20m
NS
NS
NS
NS
%O$_2$
100
0
100
0
100
0
100
0
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D M A M J J A S O N D
1969
1970
1971
1972

Fig.3.

delay was possible due to the low air temperatures and high winds in May and June. Although the thermocline remained in the 5-10m stratum throughout most of the summer, and was therefore nearer the surface than in previous summers, the temperature of the bottom stratum (15-20m) remained at between 9 and 10°C.

2.3 Seasonal changes in dissolved oxygen.

In all four years, after the autumn overturn and mixing of water in October, the percentage saturation of oxygen was fairly uniform at all depths and remained at around 95-100% until early May (Fig. 3.). Throughout the summer, differences in percentage oxygen concentration at different depths became marked. During the summer period of stratification, the percentage saturation in the surface stratum (0-5m) remained high and rarely fell below 80%. The major changes occurred in the hypolimnion in which there was an oxygen deficit which increased throughout the summer period.

In 1969 and 1970, the percentage saturation in the 5-10m stratum decreased slightly throughout the summer period to a minimum of 60%, and the range of percentage saturation in the 10-15m stratum increased markedly throughout the summer. In the bottom stratum (15-20m), the percentage saturation had a small range and gradually decreased throughout the season from over 80% in May to minimum values of less than 2% in late October.

In 1971 and 1972 the summer changes in percentage saturation were markedly different from those in 1969 and 1970. The range of percentage saturation in the 5-10m stratum was wider than in previous years and increased to 20-85% in 1971 and 4-80% in 1972.

In contrast to this change, the percentage saturation in the 10-15m stratum had a narrower range than in the two previous years and decreased to a lower minimum value which reached less than 1% in 1972. Therefore the summer changes in percentage saturation in the 10-15m stratum in 1971 and 1972 were very similar to those in the 15-20m stratum in 1969 and 1970. As the percentage saturations were lower in the 10-15m stratum in 1971 and 1972, there was a marked decrease in percentage saturation in the bottom stratum (15-20m) and very low oxygen concentrations were recorded in September and October 1971 and in August, September and October 1972. Therefore the rate of oxygen consumption in the hypolimnion was higher in 1971 and especially 1972 than in 1969 and 1970. The most probable explanation for these changes is that they are due to the effects of the effluent from the new sewage works which started to operate in June 1971.

SECTION 3

METHODS

3. Methods

3.1 Sampling procedure in the field.

Samples were taken with a closing net (length 76cm, mesh size 68 meshes/cm, aperture 0.075mm) which was attached to a circular steel collar (Fig. 4.). This surrounded a circular shutter which was closed by a strong spring activated by a lead messenger (Plates 1-3). A bucket with a tap was attached to the apex of the net and the whole sampler was supported by a metal frame weighted at the lower end. As the diameter of the mouth of the sampler was 12.2cm, the effective sampling area was 116.9cm^2. Therefore the net sampled approximately 58 l for a vertical haul over a stratum of 5m. It is probable that the efficiency of the net was not more than about 80% (Welch 1948, p248).

All samples were taken at the deepest part of the lake (Fig. 1.). The net with the shutter open was suspended on the end of a nylon rope graduated at metre intervals, then was lowered to a depth of 20m and finally was hauled vertically (rate about 0.5m/sec) to 15m. After the messenger had been released and the shutter closed, the net was hauled to the surface and the contents of the bucket (plankton in about 130cm^3 of lake water) were emptied into a bottle. This procedure was repeated for samples over strata of 15-10m, 10-5m and 5-0m. Therefore four samples were taken on each sampling occasion. Temperature and dissolved oxygen were measured at metre intervals with a Mackereth (1964) oxygen electrode. pH was measured in the laboratory.

Hillbricht-Ilkowska (1965) has found that samples taken every fourteen days and every 3-5 days may provide different pictures

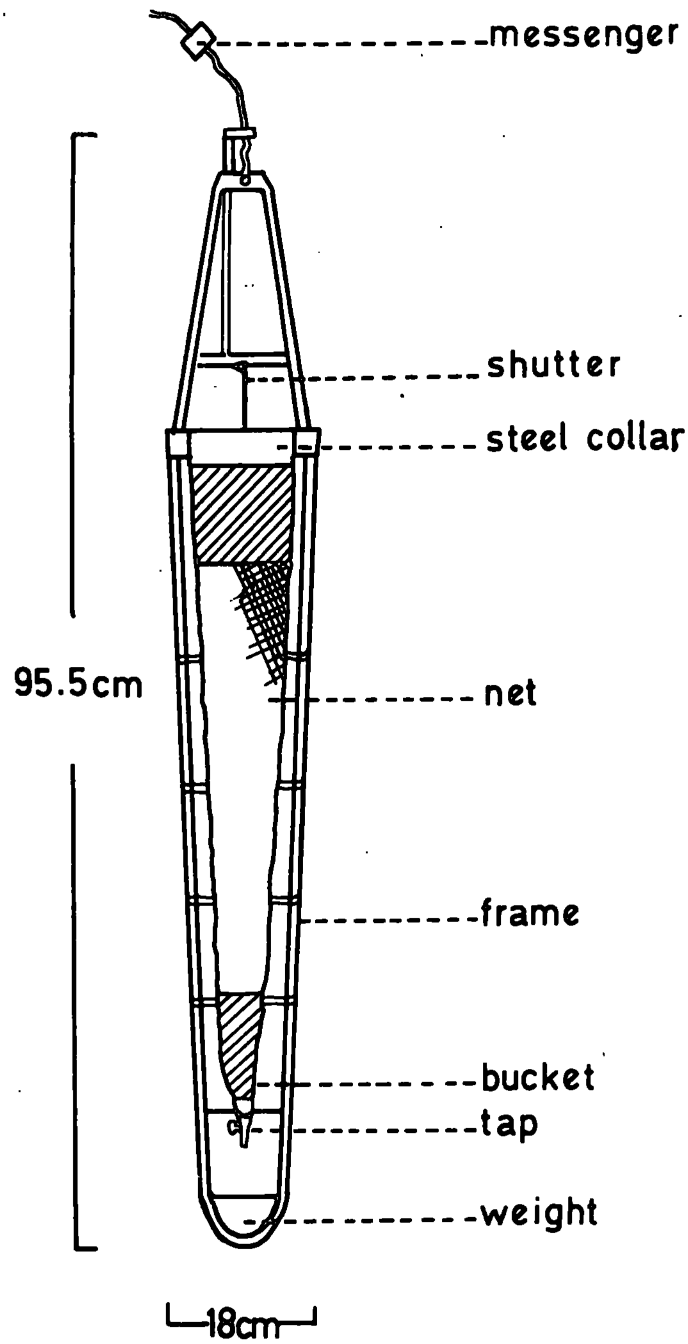

Fig.4 Diagram of closing net with shutter open.

Plate 1. Closing net.

Plate 2. Closing net with shutter open.

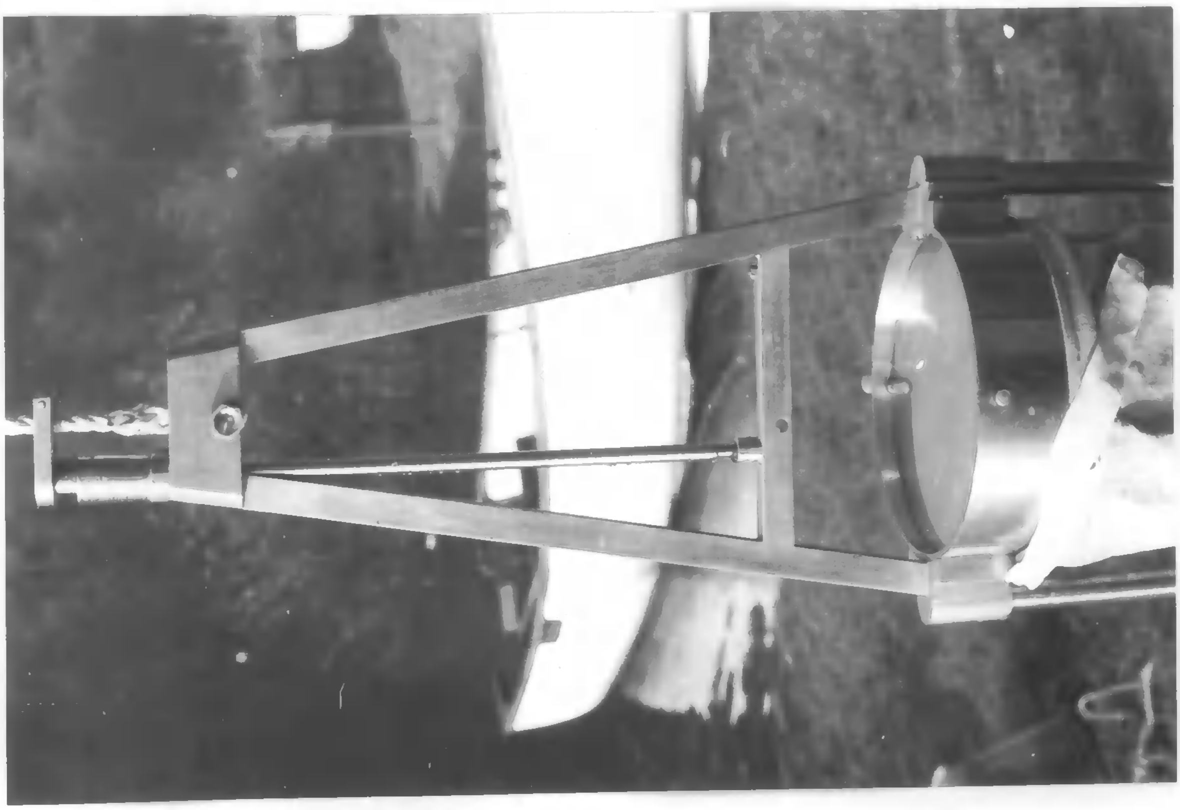

Plate 3. Closing net with shutter closed.

of the numbers and composition of planktonic rotifers, but the distortion caused by the longer sampling period is relatively greater for sporadic rarely-occurring species than for frequently-occurring species. In the present study, sampling was at weekly intervals from August to December 1969, March to December 1970, at intervals of two weeks from March to December 1971 and at weekly intervals from March to December 1972. It was assumed that numbers were close to zero in January and February and this assumption was checked in January 1970 and January and February 1973. Samples could not be taken in some weeks because of ice, strong winds or other climatic factors.

3.2 Sampling procedure in the laboratory.

As it is easier to identify live rotifers, the samples were usually examined within one hour after collection. Two filters were used to separate and concentrate a sample. Each filter was a plastic tube (length 7.5cm, diameter 4cm) with a bottom of nylon sifting cloth. Crustacea and the large rotifers (Asplanchna priodonta Gosse, Conochilus hippocrepis (Schrank), C. unicornis Rousselet) were separated from the rest of the sample by pouring each sample through a coarse filter (24 meshes/cm, aperture 0.282mm). The filter was then washed several times with a small volume of lake water until all the large rotifers and Crustacea had been transferred into a glass crucible. This fraction of the sample was examined later. The filtrate was now filtered through a fine filter (55.5 meshes/cm, aperture 0.096mm) which was washed several times until all the contents had been transferred into $30cm^3$ of lake water. This concentrated sample was first stirred to ensure that the rotifers were randomly distributed throughout the sample and then a subsample of $10cm^3$ was poured into a sedimentation tube which was similar to that described in detail by Lund et. al. (1958). Each tube consisted of a cylinder of plexiglass with a microscopical cover glass cemented onto one end to serve as a floor. Two drops of Lugol's solution (a saturated solution of iodine in potassium iodide) were added to kill, stain and weight the rotifers which settled to the bottom. The relationship between the height and diameter of a sedimentation tube influences the rate of sedimentation. It was found in preliminary experiments that one hour was sufficient for all rotifers to settle to the bottom. The remaining $20cm^3$ of the sample were examined later. This procedure was repeated for each of the four samples. The four crucibles containing the largest rotifers were now examined under a binocular microscope and all rotifers were counted whilst they were removed by means of a fine pipette. Only the colonies of <u>Conochilus hippocrepis</u> and <u>C. unicornis</u> were counted. The second group of four crucibles containing the $20cm^3$ of each sample were now examined and all species of rotifers were identified whilst they were still alive. Difficult and unknown species were removed and identified under a high-power microscope. Finally all the rotifers in each sub-sample of $10cm^3$ were counted on an inverted microscope with a 16mm objective and x6 eyepieces. The counts from the sub-sample were multiplied by three and added to the total counts of large rotifers. Several smaller rotifers were occasionally removed in the first filtration and were counted with the large rotifers.

It was assumed that the rotifers were randomly distributed in the concentrated sample before the sub-sample was taken.

This assumption was checked several times by dividing the sample into three sub-samples and counting the rotifers in each sub-sample of $10cm^3$. The three counts for total numbers and for each species were tested for agreement with a Poisson series using the χ^2 test (variance to mean ratio) (Elliott 1971, section 4.1.2). Typical results are given in Table 1. As all χ^2 values except one were between the 5% significance levels, agreement with a Poisson series was accepted at the 95% probability level ($P > 0.05$). The single exception (Keratella cochlearis, 5-10m, 12 August 1969) was only just significantly clumped ($P < 0.05$), and this same species was randomly distributed in the other samples. Therefore the assumption of a random distribution of rotifers in the concentrated sample appeared to be valid, and the counts from the sub-sample were used to estimate the mean numbers in the concentrated sample.

Table 1. Examples of counts in sub-samples and χ^2 values from test for agreement with a Poisson series. 5% significance points are 0.05 and 7.38. Significant departure from a Poisson series is indicated by an asterisk: $^*P < 0.05$.

12 August 1969

Sample from:	0–5m				5–10m				10–15m				15–20m			
Sub-sample:	1	2	3	χ^2	1	2	3	χ^2	1	2	3	χ^2	1	2	3	χ^2
Asplanchna priodonta	46	42	38	0.76	8	15	12	2.12	1	1	3	1.60	3	2	6	2.37
Ascomorpha saltans	12	6	7	2.48	3	1	1	1.60	0	0	0		0	0	0	
Conochilus hippocrepis	86	106	96	2.08	25	20	25	0.71	0	0	0		0	0	0	
Filinia terminalis	6	2	4	2.00	2	0	1	2.00	0	1	0	2.00	27	19	30	2.55
Gastropus stylifer	68	86	78	2.10	39	57	60	4.96	2	2	7	4.55	18	21	16	0.69
Kellicottia longispina	28	30	33	0.42	7	2	5	2.72	0	0	0		1	0	1	1.00
Keratella cochlearis	374	348	367	1.00	179	135	184	8.76*	13	11	17	1.37	43	35	51	2.95
Polyarthra spp.	226	260	241	2.40	29	34	36	0.79	2	2	1	0.40	3	7	6	1.62
Synchaeta stylata	88	78	70	2.07	0	0	0		0	0	2	4.03	0	0	0	
S. tremula	26	15	22	2.95	4	4	2	0.80	0	0	0		0	0	0	
Trichocerca similis	8	6	8	0.36	29	36	31	0.81	0	2	0	4.03	3	1	4	1.75
T. pusilla	6	14	8	3.71	7	3	6	1.62	0	0	0		1	0	0	2.00
Total number	974	993	972	0.27	332	307	363	4.71	18	19	30	3.97	99	85	114	4.23

Table 1 continued..

3 October 1972

Sample from:	0–5m				5–10m				10–15m				15–20m			
Sub-sample	1	2	3	χ^2	1	2	3	χ^2	1	2	3	χ^2	1	2	3	χ^2
Filinia terminalis	0	0	1	2.00	2	2	1	0.40	1	0	1	1.00	5	3	7	1.60
Gastropus stylifer	0	0	0		0	0	0		1	0	1	1.00	0	1	0	2.00
Kellicottia longispina	48	50	52	0.16	45	44	34	1.81	31	27	19	2.91	9	7	7	0.35
Keratella cochlearis	40	25	24	5.42	12	14	23	4.20	18	17	11	1.87	14	10	11	0.74
K. quadrata	0	0	0		0	0	0		0	0	0		0	1	0	2.00
Polyarthra vulgaris	0	0	0		0	0	1	2.00	1	1	0	1.00	1	0	0	2.00
Synchaeta spp.	2	2	1	0.40	3	1	1	1.60	0	0	1	2.00	1	0	1	1.00
Trichocerca capucina	0	0	0		1	2	0	2.00	0	2	0	4.03	0	0	1	2.00
Total number	90	77	78	1.28	63	63	60	0.10	52	47	33	4.41	30	22	27	1.24

SECTION 4

RESULTS

4. Results

4.1 Planktonic species of rotifers found in Grasmere with notes on their taxonomy, temporal variation and feeding.

A total of twenty-four planktonic species were recorded during the present study. These are listed in Table 2 together with their size ranges, and illustrated in Figs. 5-8. The nomenclature follows that of Voigt (1957) and Ruttner-Kolisko (1972), and the more important taxonomic features are now summarised.

Keratella cochlearis (Fig. 5A.) is probably the most common planktonic rotifer in temperate regions and numerous forms have been recorded (Hudson and Gosse 1886, Lauterborn 1900, Voigt 1904, Carlin 1943, Haüer 1952, Pejler 1962b, Sudzuki 1964). The taxonomic problems caused by these numerous forms have been discussed by Pejler (1957a). Only the typical form was recorded in Grasmere. This has one posterior and six anterior spines, and an hexagonal sculpturing pattern on the lorica. In lateral view, the ventral plate and posterior spine form a slightly convex curve.

Keratella quadrata (Fig. 5B.) was of a normal type with two slightly curved posterior spines about one-third as long as the body, and six short anterior spines. The sculpturing on the lorica was fairly constant, but in a few specimens the fork on the dorsal surface of the lorica, just anterior to each posterior spine, was indistinct.

Kellicottia longispina (Fig. 5F.) was of the normal type with no distortion of the spines. It has one long posterior and one long, two medium and three short anterior spines. The long anterior spine was never as long as the posterior spine.

The three *Trichocerca* species, namely *capucina*, *similis* and

Table 2. Planktonic species of rotifers in Grasmere.

Size range is given in parentheses after each species.

Order Monogononta

Sub-Order 1. Ploima

Family Brachionidae

Euchlanis dilitata Ehrenberg 1832 (200-600 µ)

Keratella cochlearis (Gosse) 1851 (150-200 µ)

K. quadrata (O.F.Müller) 1786 (200-290 µ)

Kellicottia longispina (Kellicott) 1879 (450-800 µ)

Family Trichocercidae

Trichocerca capucina (Wierzejski & Zacharias) 1893 (200-300 µ)

T. similis (Wierzejski) 1893 (150-200 µ)

T. pusilla (Jennings) 1903 (70-110 µ)

Family Gastropodidae

Gastropus stylifer Imhof 1891 (120-230 µ)

Ascomorpha saltans Bartsch 1870 (100-150 µ)

A. ecaudis Perty 1850 (130-200 µ)

Family Asplanchnidae

Asplanchna priodonta Gosse 1850 (500-1500 µ)

Family Synchaetidae

Polyarthra vulgaris Carlin 1943 (100-150 µ)

P. major Burckhard 1900 (150-170 µ)

P. dolichoptera Idelson 1925 (90-120 µ)

Synchaeta grandis Zacharias 1893 (530-565 µ)

S. stylata Wierzejski 1893 (200-300 µ)

S. tremula (O.F. Müller) 1786 (170-250 µ)

S. pectinata Ehrenberg 1832 (300-500 µ)

S. oblonga Ehrenberg 1832 (150-230 µ)

Ploesoma hudsoni (Imhof) 1891 (300-500 µ)

Sub-Order 2. Flosculariacea

Family Testudinellidae

Filinia terminalis (Plate) 1886 (235-320 μ)

Family Conochilidae

Conochilus hippocrepis (Schrank) 1830 (500-800 μ)

C. unicornis Rousselet 1892 (290-375 μ)

Sub-Order 3. Collothecacea

Family Collothecidae

Collotheca mutabilis (Hudson) 1885 (200-500 μ)

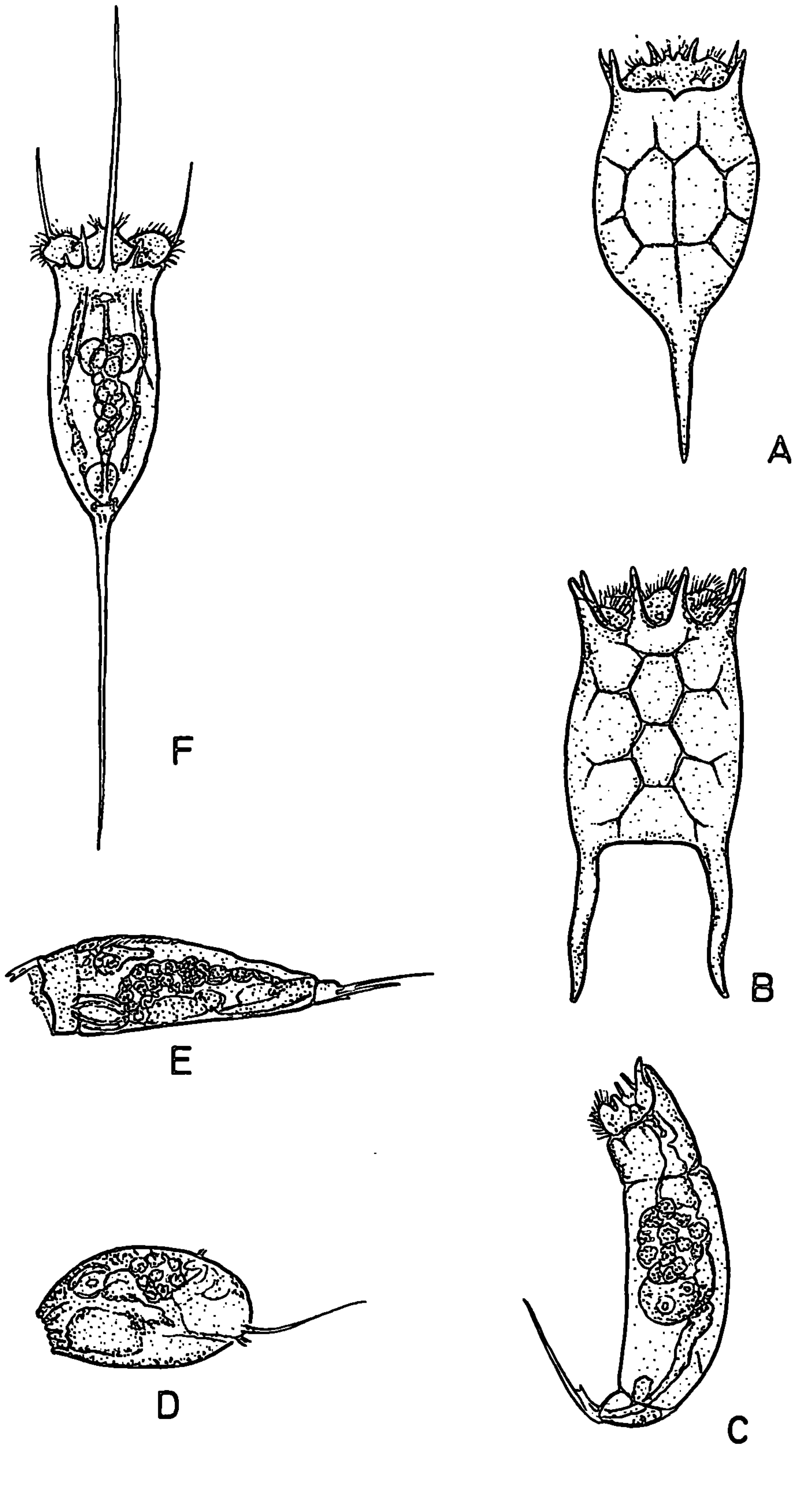

Fig.5 A, _Keratella cochlearis_, B, _K. quadrata_,

C, _Trichocerca capucina_, D, _T. pusilla_, E, _T. similis_,

F, _Kellicottia longispina_.

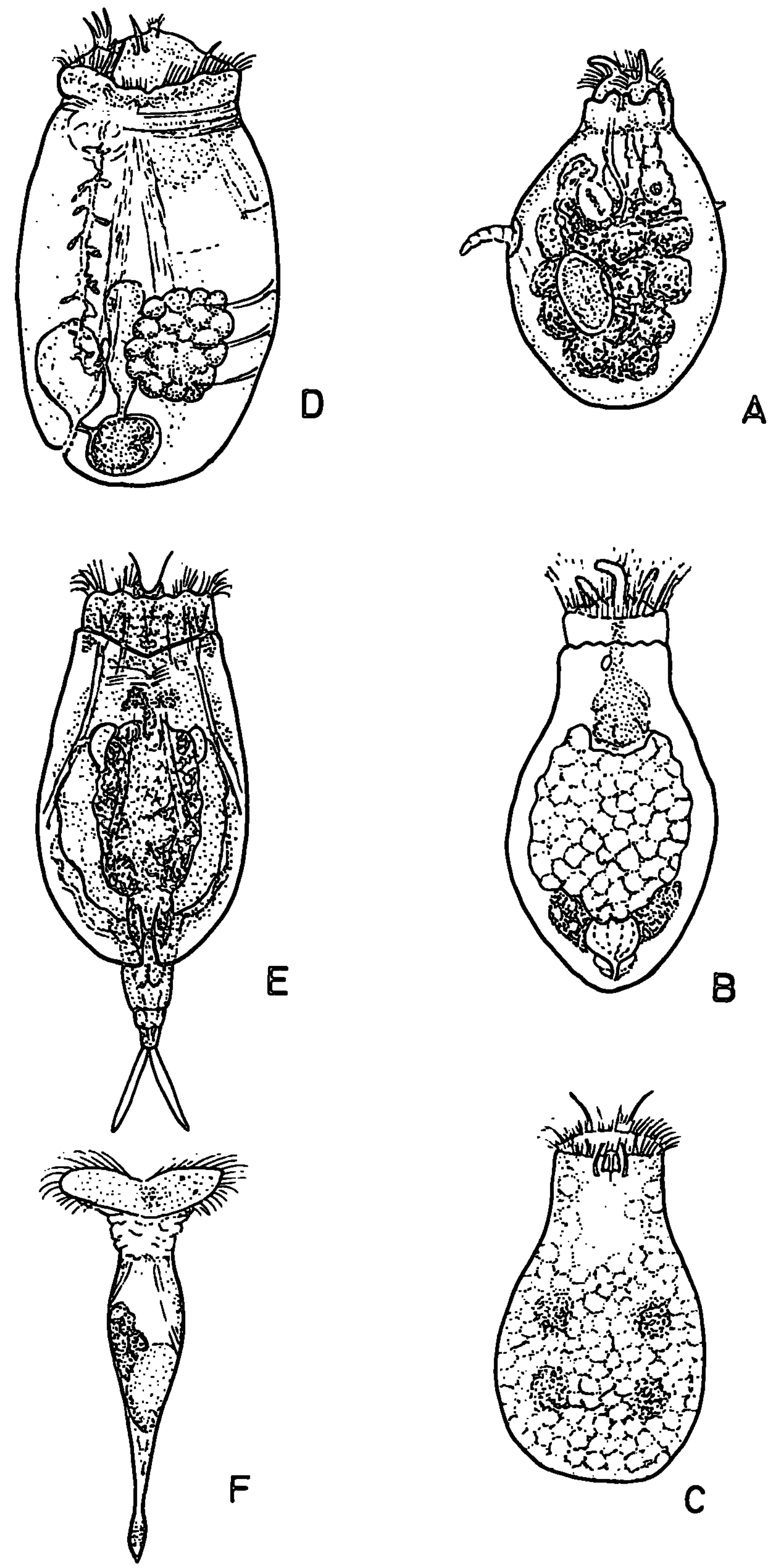

Fig. 6 A, Gastropus stylifer, B, Ascomorpha saltans, C, A. ecaudis, D, Asplanchna priodonta, E, Euchlanis dilitata, F, Collotheca mutabilis.

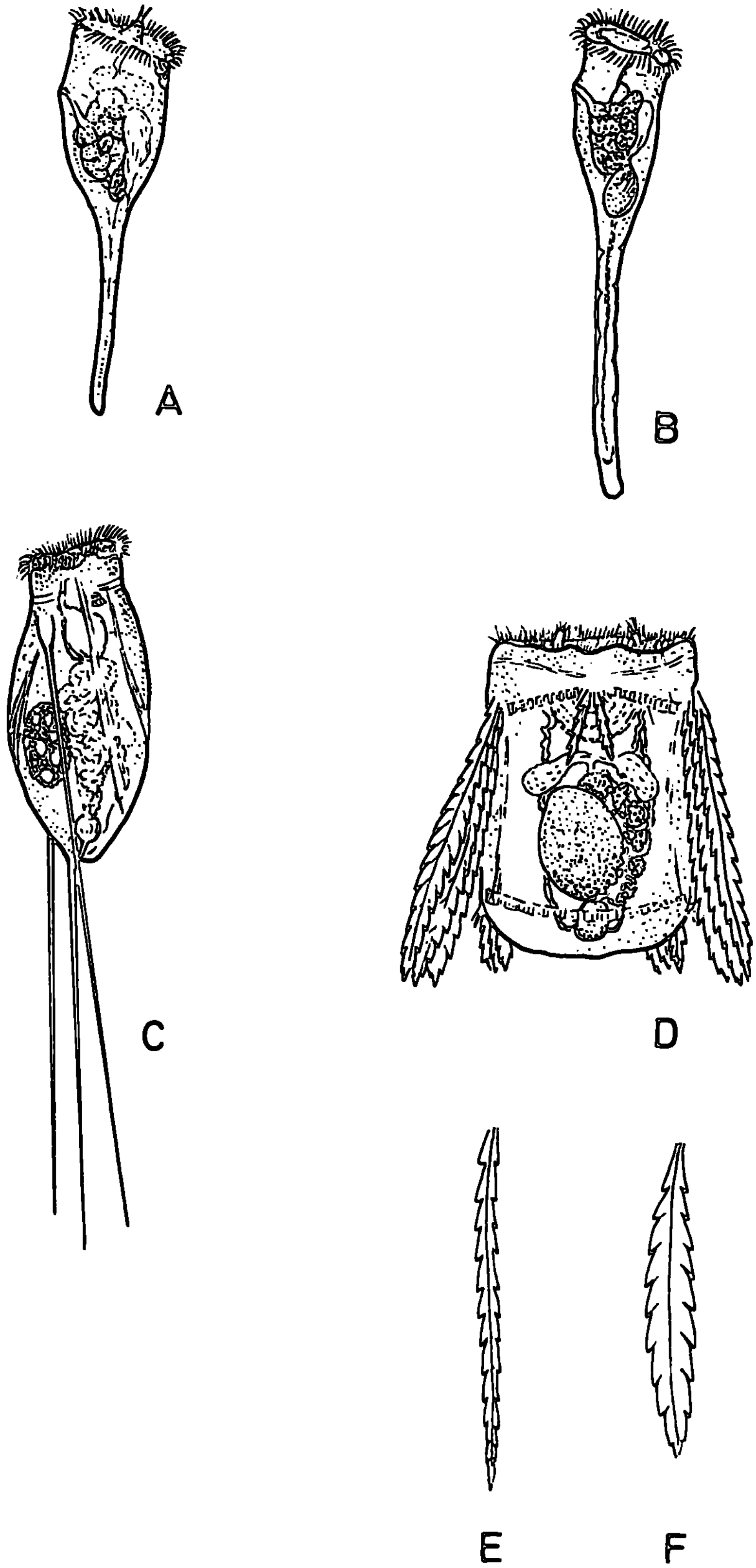

Fig.7 A, Conochilus unicornis, B, C. hippocrepis, C, Filinia terminalis, D, Polyarthra vulgaris, E, fin of P. dolichoptera, F, fin of P. major.

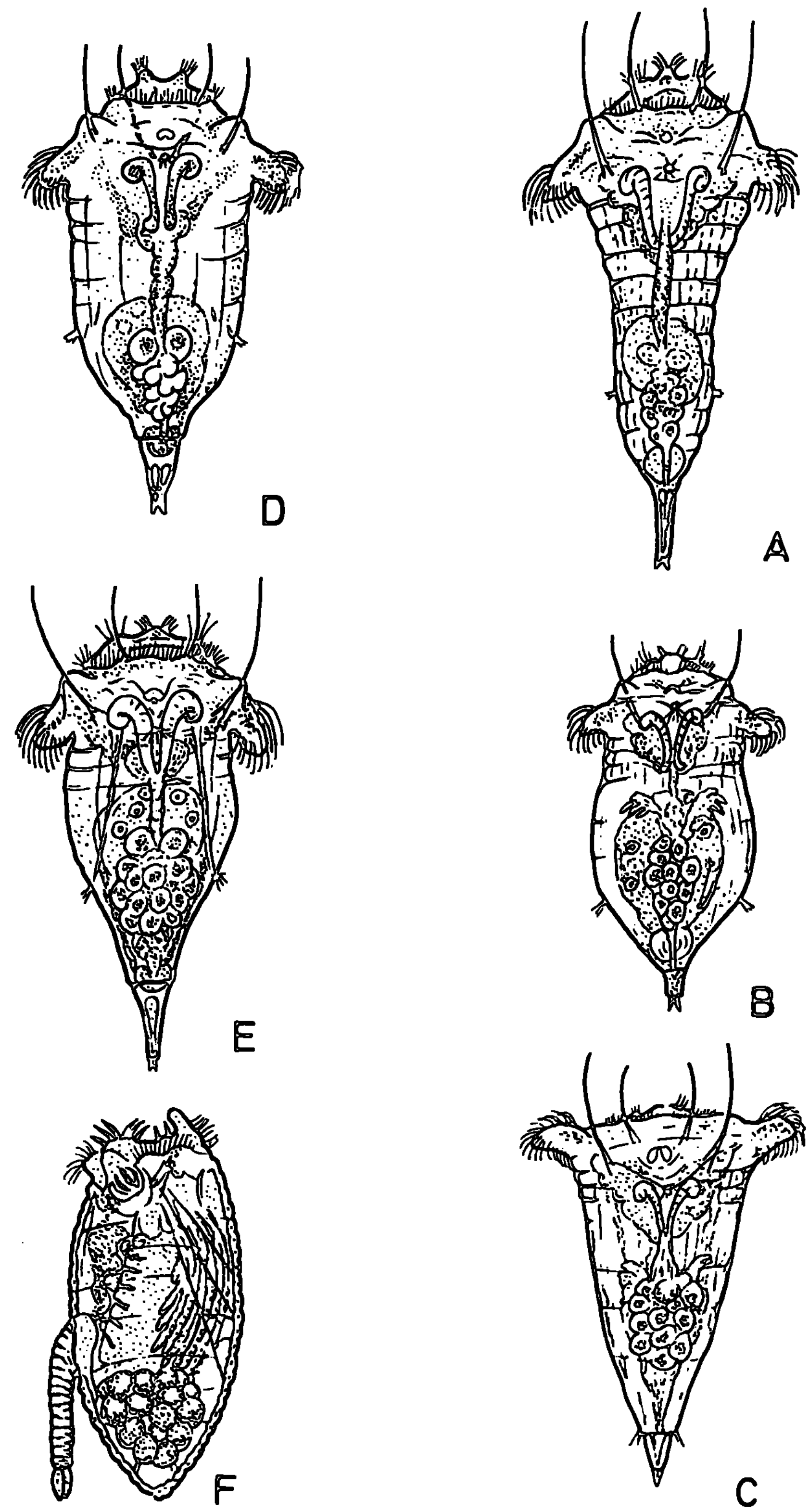

Fig. 8 A, Synchaeta grandis, B, S. oblonga, C, S. tremula, D, S. pectinata, E, S. stylata, F, Ploesoma hudsoni.

pusilla, (Figs. 5C,D,E.) possessed the usual key characters and were fairly easy to separate on the basis of total length, length of toe, and shape of the anterior projections of the lorica. All these characters were also visible in dead material.

Gastropus stylifer (Fig. 6A) with pink body fluid, a bright red eye spot and slate grey stomach containing orange oil droplets could not be confused with any other rotifer. Asplanchna priodonta (Fig. 6D.) was distinguished by its size, transparency, lack of a foot and lack of apical projections.

The genus Polyarthra (Figs. 7.C,D,E.) (reviewed by Nipkov 1952) has been the subject of much investigation in recent years. Carlin (1943) reorganised the genus and established a new system of classification. Since then, a series of introgressive forms between P. vulgaris and P. dolichoptera, and P. vulgaris and P. major have been recorded by Pejler (1956, 1957a) from ponds in Central Sweden and also from ponds and Lake Torneträsk in Lapland. At present there is some disagreement between workers on the taxonomic position of some species, and whether they should be considered true species, sub-species or only different forms of the same species (Carlin 1943, Anderson 1949, 1953, Nipkov 1952, Pejler 1956, Sudzuki 1964).

Polyarthra vulgaris (Fig. 7D.) in Grasmere has the following features described by Carlin (1943) and used as key characters by Ruttner-Kolisko (1972); body length 100–150 μ, ratio of fin width to length 1.5, the fins having well defined small teeth. A small pair of toothed setae situated on the ventral surface near the mastax are characteristic.

The typical body length of P. major (Fig. 7F.) was given as 136–180 μ by Voigt (1957), whereas Sudzuki (1964), Pourriot (1965) and Ruttner-Kolisko (1972) consider that the body length exceeds 150 μ with the fins 20-40 μ in width. For the purposes of this study, the following features described by Ruttner-Kolisko (1972) were used to identify P. major: body length 150-170 μ with leaf-shaped broad fins. P. dolichoptera (Fig. 7E.) is smaller than either P. vulgaris or P. major and has narrow, markedly toothed fins which are much longer than the body.

Two species of Conochilus (C. unicornis, C. hippocrepis) (Figs. 7.A,B.) were found in Grasmere. Individuals of C. unicornis are generally much smaller than C. hippocrepis, form smaller colonies with 8-15 individuals and have fused lateral antennae. C. hippocrepis colonies contain 30-50 slender individuals, each bearing a pair of unfused lateral antennae. Chlamydomonas gloeophila Skuja was observed in the centre of the colony.

The taxonomy of the genus Filinia has been discussed by Carlin (1943), Pejler (1957a,b), Sudzuki (1964) and Hutchinson (1964). Pejler considers F. limnetica (Zacharias) to be a synonym for F. longiseta, and F. major (Colditz) to be a synonym for F. terminalis. Ruttner-Kolisko (1972) appears to follow this system in her key. However, Sudzuki (1964) regards F. terminalis as a simple form of F. longiseta. One of the important morphological features is the position of the insertion of the posterior appendage. In F. terminalis, this is either terminal or on the ventral surface of the body not more than 15 μ from the apex, whereas in F. longiseta, it is always inserted at about 25 μ from the apex. The appendages of F. longiseta bear spines which are clearly visible. These spines are extremely fine or absent in F. terminalis. The average ratio of the lengths of the lateral appendages to the length of the posterior appendage is usually

1.2 in F. terminalis and 2.0 in F. longiseta (Ruttner-Kolisko 1972). Measurements of F. terminalis from Grasmere gave a mean ratio of 1.4 with a range of 1.3 - 1.6. Many varieties have been described (Pejler 1957a, Sudzuki 1964, Larsson 1971) in the longiseta - terminalis group and there is still doubt about the true position of species within this group (see review by Hutchinson 1964). Pejler (1957a) and Ruttner-Kolisko (1972) have suggested that F. terminalis occurs at a water temperature less than 15°C and F. longiseta occurs at 15-20°C. In view of all the evidence, it was decided that the species of Filinia in Grasmere was F. terminalis.

Five species of Synchaeta (Fig. 8,A-E.) were found in the samples, but could only be identified when alive. As individuals of this genus contract when dead, it was impossible to separate the species in the counting chamber, and therefore only the total numbers in the genus were recorded. Individuals of S. grandis (Fig. 8A.) ranged from 530-565 µ in length and 270-283 µ in width. The overall length of S. tremula (Fig. 8C.) was generally 170-250 µ but some of the first individuals to appear at the beginning of the season were noticeably smaller (110-150 µ).

Asplanchna priodonta was the only species whose males were observed in the samples. The males were present in May and June when the population was at a maximum. A second sexual phase in August was not observed in 1969, 1970, 1971 and 1972, but has been observed in 1973. As small numbers of Keratella cochlearis, K. quadrata and Kellicottia longispina were present throughout the winter, it is probable that there was no sexual phase in these species. The absence of males of other species in the samples may be due to their small size which allowed them to pass through the sampling net.

A marked temporal variation was not observed in any species. Individuals of Keratella quadrata tended to be slightly larger in spring. When Polyarthra vulgaris first appeared in the samples in early summer, some individuals lacked lateral fins and were presumably females which had hatched from dormant mictic eggs (Nipkov 1952), and which were once erroneously called Anarthra aptera (Hood 1895). A temporal variation in Keratella cochlearis was observed for the first time in the summer of 1973 when the tecta form (Pejler 1962b) appeared in the samples.

Of the twenty-four species occurring in Grasmere, ten feed by sedimenting small food particles (Euchlanis dilitata, Keratella spp., Kellicottia longispina, Polyarthra spp., Filinia terminalis, Conochilus spp.). The three Trichocerca spp. suck out the contents of algae, and T. capucina can feed on the eggs of Keratella quadrata. Gastropus stylifer and the two Ascomorpha spp. seize and suck out the contents of dinoflagellates, and A. saltans was seen to grasp and feed on S. tremula. The five species of Synchaeta, Asplanchna priodonta and Ploesoma hudsoni all seize their prey which can be algae, protozoa and other rotifers. Individuals of Asplanchna priodonta were seen with Tabellaria (Bacillariophyceae) and Keratella cochlearis in their stomachs, and the large predator Ploesoma hudsoni was observed eating small Synchaeta. Collotheca mutabilis feeds by trapping its prey and is therefore different from all the other species.

4.2 Seasonal occurrences of the different species.

The species were arranged in four groups according to their seasonal occurrence and the percentage of the total number of sampling occasions on which each species was taken (Table 3, Fig. 9.).

Table 3. Number of sampling occasions and percentage of total number of sampling occasions on which each species was taken in 1970, 1971, 1972 and in all three years.

	1970	1971	1972	Total
	No (%)	No (%)	No (%)	No (%)
Total number	41 (100)	17 (100)	33 (100)	91 (100)
Group A				
Kellicottia longispina	37 (90)	14 (82)	32 (97)	83 (90)
Keratella cochlearis	34 (83)	17 (100)	31 (94)	83 (90)
Gastropus stylifer	26 (63)	13 (76)	18 (55)	57 (63)
Keratella quadrata	28 (68)	12 (71)	14 (42)	54 (59)
Conochilus hippocrepis	24 (59)	10 (59)	17 (52)	51 (56)
Asplanchna priodonta	28 (68)	8 (47)	12 (36)	48 (53)
Group B				
Synchaeta stylata	19 (46)	6 (35)	16 (48)	41 (45)
Conochilus unicornis	20 (49)	3 (18)	15 (45)	38 (42)
Polyarthra dolichoptera	17 (41)	4 (24)	10 (30)	31 (34)
Synchaeta tremula	13 (32)	4 (24)	13 (39)	30 (33)
Synchaeta pectinata	15 (37)	0 (0)	10 (30)	25 (27)
Synchaeta oblonga	16 (39)	3 (18)	5 (15)	24 (26)
Group C				
Polyarthra vulgaris	15 (37)	9 (53)	18 (55)	42 (46)
Filinia terminalis	9 (22)	1 (6)	17 (53)	27 (30)
Synchaeta grandis	13 (32)	2 (12)	2 (6)	17 (19)
Ploesoma hudsoni	11 (27)	5 (29)	0 (0)	16 (17)
Trichocerca capucina	0 (0)	5 (29)	10 (30)	15 (16)
Trichocerca similis	5 (12)	1 (6)	7 (21)	13 (14)
Polyarthra major	5 (12)	3 (18)	0 (0)	8 (9)
Group D				
Collotheca mutabilis	2 (5)	2 (12)	2 (6)	6 (7)
Ascomorpha saltans	0 (0)	3 (18)	1 (3)	4 (5)
Trichocerca pusilla	2 (5)	0 (0)	0 (0)	2 (2)
Ascomorpha ecaudis	1 (2)	0 (0)	0 (0)	1 (1)
Euchlanis dilitata	0 (0)	0 (0)	1 (3)	1 (1)

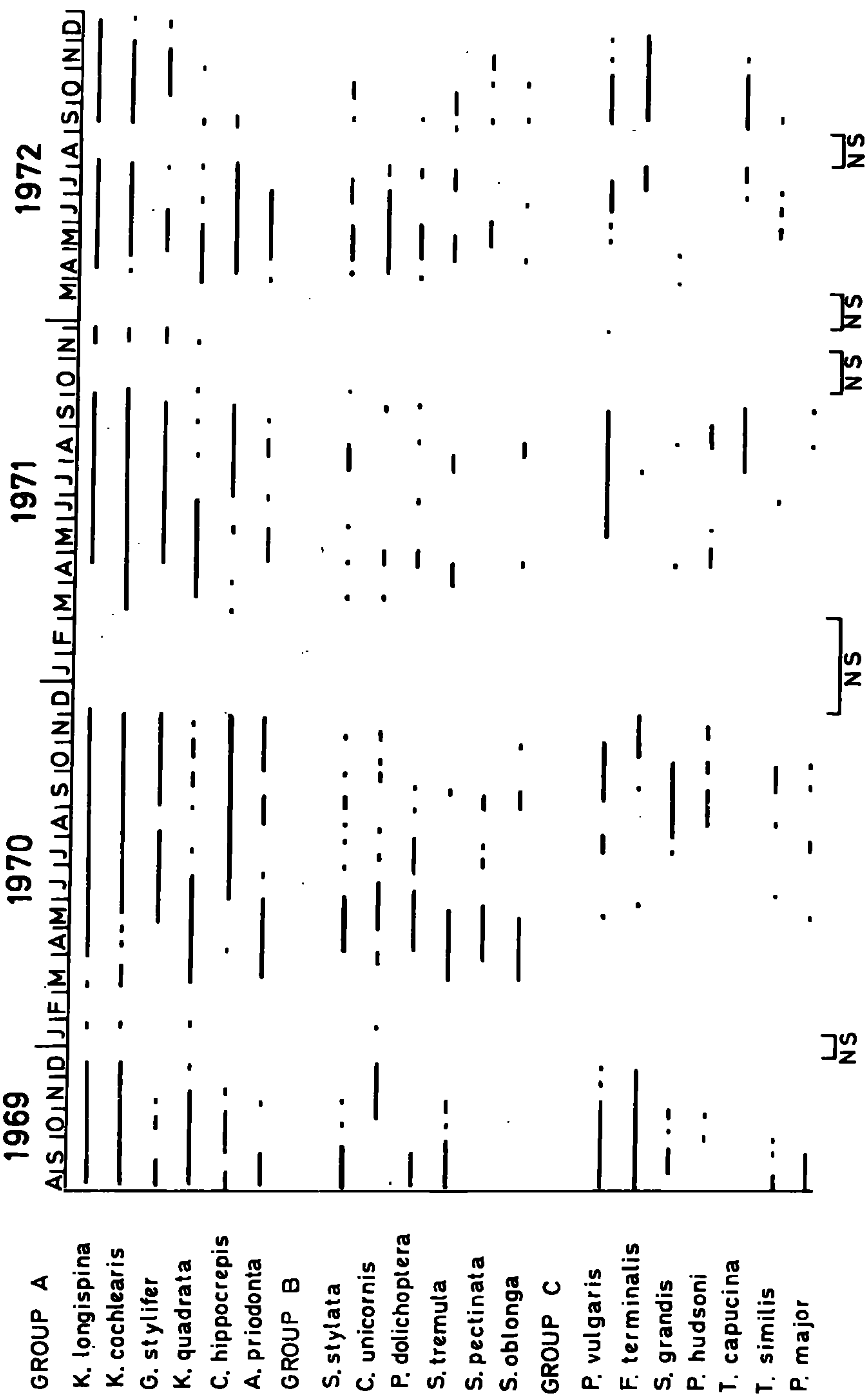

Fig. 9. Seasonal occurrence of planktonic rotifers in Grasmere.

(N.S. indicates the periods in which no samples were taken).

Although there were some differences between years, the following general conclusions can be made about the occurrence of each species.

Group A includes all species which occurred from spring to autumn and which were taken on more than 50% of the total sampling occasions. Each species, except Asplanchna priodonta in 1972, occurred on more than 40% of the sampling occasions in each year. Kellicottia longispina, Keratella cochlearis and K. quadrata were occasionally taken in winter and occurred almost continuously from March to November in all years. Gastropus stylifer and Conochilus hippocrepis also occurred from spring to autumn but their first appearance in the samples was usually later than the preceding three species. A. priodonta occurred early in the season, then again in August after a period of absence, and for a third period at the end of the season in 1970.

Group B includes all species which occurred chiefly in spring and early summer, but in some years there was a second major period of occurrence towards the end of the season, e.g. Conochilus unicornis in 1969, Synchaeta pectinata, S. stylata and S. tremula in 1972. There were some notable differences between years. In 1971, the frequency of occurrence of C. unicornis was greatly reduced and S. pectinata was never taken in the samples.

The seven species in Group C occurred chiefly in summer and autumn, but all except Polyarthra vulgaris showed a large variation between years in their frequency of occurrence. Filinia terminalis was very rare in 1971, but was taken frequently in 1969, 1970, and 1972. Synchaeta grandis occurred regularly over a three month period in 1969 and 1970, but was very rare in 1971 and 1972. Ploesoma hudsoni was very rare at depths below 5m, and was not taken in 1972. Although Trichocerca capucina was only taken in 1971 and 1972, it had been taken earlier in 1969 by Dr. Ruttner-Kolisko. Polyarthra major was rare in 1971 and was not taken in 1972.

The five rare species in Group D were only taken on less than seven sampling occasions. As Ascomorpha saltans, A. ecaudis and Euchlanis dilitata are chiefly littoral species which occur amongst macrophytes, they rarely occur in the plankton. Carlin (1943) states that Trichocerca is usually a genus of eutrophic ponds, and he found that the planktonic occurrence of the genus in lakes appeared to correspond to short periods when the phyto-plankton reaches maxima comparable to those of small productive lakes. This relationship may explain the brief appearance of Trichocerca pusilla (Group D), and the erratic appearance of T. capucina and T. similis (Group C) in Grasmere.

4.3 Major differences between the numbers taken in each stratum and in each year.

As the five rare species in Group D were taken on less than four sampling occasions in each year (Table 3), they cannot be considered separately in this section. The total numbers of these five species are recorded for each sample in Appendix Table 1. Of the remaining nineteen species, the three species in the genus Polyarthra and the five species in the genus Synchaeta could only be identified to genera after they had been fixed with iodine prior to counting (see methods, section 3.2). The total numbers of these two genera and the remaining eleven species are recorded for each sample in Appendix Table 2. These thirteen taxa were arranged in the same order as that used in Table 3, but it was necessary to combine groups B and C because the genera Synchaeta and Polyarthra were not separated into species. The percentage contributions of each taxon to the total numbers of rotifers taken from each stratum in each year are compared in Table 4. Group A contained all the abundant species except the genus Synchaeta whereas in groups B and C, only the genus Synchaeta contributed more than 8% to the total numbers. The five species in group D always contributed less than 1% to the total numbers.

As a large change in one percentage can markedly affect the other percentages, comparisons between percentages can be misleading. Therefore mean numbers per sample were also calculated for each taxon and these are compared in Table 5. Mean numbers rather than total numbers were used in these comparisons because the total number of samples varied between years (Table 3). The comparisons between mean numbers also showed that the most abundant species were in group A, and the mean numbers of these six species and the genera Synchaeta and Polyarthra were greater than 20 per sample in at least one stratum or year. Mean numbers of the remaining five species in groups B and C were never greater than 8 per sample, and the combined numbers of the five species in group D were never greater than one per sample. Therefore the species which occurred in most months of the year (group A), also made the greatest contribution to the total numbers taken in a year.

In each year, the mean numbers of all rotifers decreased from the surface stratum (0-5m) to the deepest stratum (15-20m), and this decrease was most marked between the strata above and below 10m (Table 5, Fig. 10.). A similar decrease in numbers with depth was shown by Kellicottia longispina in 1970, Keratella cochlearis

Table 4. Percentage contribution of each species or genus to total numbers of rotifers taken from each stratum in each year (species in group D and in the genera *Synchaeta* and *Polyarthra* are listed in Table 3).

Stratum	0 - 5m			5 - 10m			10 - 15m			15 - 20m		
Year	1970	1971	1972	1970	1971	1972	1970	1971	1972	1970	1971	1972
Group A												
Kellicottia longispina	22.1	14.0	22.6	26.5	35.1	29.4	26.0	17.4	23.6	22.0	13.2	34.8
Keratella cochlearis	19.6	33.9	12.0	15.7	23.8	12.7	22.0	31.6	18.1	20.8	30.1	17.3
Gastropus stylifer	9.4	4.7	0.4	6.1	4.4	0.6	7.1	16.5	1.0	6.9	8.7	0.8
Keratella quadrata	0.5	0.3	0	3.1	0.6	0.1	16.0	13.2	0.4	22.1	24.0	1.6
Conochilus hippocrepis	5.9	2.8	1.7	23.1	4.1	3.2	7.7	2.5	0.2	4.9	0.7	0
Asplanchna priodonta	10.1	20.8	57.2	3.7	16.4	48.4	2.1	5.3	47.4	1.4	1.9	35.8
Groups B & C												
Synchaeta spp.	24.1	15.4	3.3	13.2	9.8	2.7	12.8	7.1	2.5	9.7	13.2	2.6
Polyarthra spp.	5.7	7.3	1.4	5.4	3.7	0.7	3.8	4.0	0.9	4.1	5.9	1.4
Conochilus unicornis	2.0	0	0.6	2.5	1.0	0.4	1.2	1.4	3.0	1.4	0.3	2.5
Filinia terminalis	0.1	0	0.3	0.2	0	1.3	0.4	0	2.1	5.6	0.1	2.5
Ploesoma hudsoni	0.6	0.2	0	0.3	0	0	0.4	0.1	0	0.3	0	0
Trichocerca capucina	0	0.3	0.2	0	0.8	0.2	0	0.7	0.3	0	1.0	0.3
T. similis	0	0	0	0.1	0.1	0	0.3	0	0.1	0.3	0	0.3
Group D	0	0.1	0.1	0	0	0	0.1	0	0.2	0	0.8	0.1
Total numbers	9820	5470	21313	8013	4868	13133	5536	2090	7780	4001	1618	7004

Table 5. Mean numbers per sample of each species or genus of rotifers taken from each stratum in each year (species in group D, and in the genera <u>Synchaeta</u> and <u>Polyarthra</u> are listed in Table 3).

Stratum	0 - 5m			5 - 10m			10 - 15m			15 - 20m		
Year	1970	1971	1972	1970	1971	1972	1970	1971	1972	1970	1971	1972
Group A												
<u>Kellicottia longispina</u>	52.9	45.2	146.0	51.8	100.4	117.0	35.1	21.4	55.7	21.5	11.5	73.8
<u>Keratella cochlearis</u>	46.9	109.1	77.3	30.6	68.2	50.6	29.7	38.8	42.6	20.3	28.6	36.7
<u>Gastropus stylifer</u>	22.4	15.2	2.6	12.0	12.7	2.5	9.5	20.3	2.4	6.8	8.3	1.7
<u>Keratella quadrata</u>	1.2	1.1	0.5	6.1	1.8	0.5	21.7	16.3	1.1	21.6	22.8	3.5
<u>Conochilus hippocrepis</u>	14.2	0.9	11.0	45.2	11.7	12.7	10.4	3.2	0.5	4.8	0.7	0
<u>Asplanchna priodonta</u>	24.2	67.1	369.7	7.3	46.9	192.7	2.8	6.6	111.7	1.4	1.8	76.0
Groups B & C												
<u>Synchaeta</u> spp.	57.8	49.6	21.2	25.7	28.1	10.7	17.3	8.8	6.0	9.5	12.5	5.6
<u>Polyarthra</u> spp.	13.6	23.5	8.8	10.5	10.6	2.9	5.1	4.8	2.2	4.0	5.6	3.0
<u>Conochilus unicornis</u>	4.7	0.2	4.1	4.9	3.0	1.8	1.6	1.7	7.1	1.4	0.4	5.3
<u>Filinia terminalis</u>	0.1	0	2.0	0.4	0	5.1	0.6	0	4.9	5.5	0.2	5.4
<u>Ploesoma hudsoni</u>	1.3	0.6	0	0.6	0	0	0.5	0	0	0.4	0	0
<u>Trichocerca capucina</u>	0	1.1	1.5	0	2.5	1.1	0	0.9	0.9	0	0.9	0.6
<u>T. similis</u>	0	0	0.1	0.2	0.4	0.2	0.5	0	0.3	0.4	0	0.5
Group D	0.1	0.4	1.0	0.1	0.2	1.0	0.1	0.[illegible]	0.5	0.1	0.8	0.2
Total numbers	239.5	321.8	645.8	195.4	286.4	398.0	135.0	122.9	235.8	97.6	95.2	212.2

Fig. 10

Fig. 10 Mean numbers per sample of each species or genus of rotifers taken from each stratum in each year. The least abundant species (mean numbers 8 per sample) are included in other species, and are listed in Tables 3 and 4.

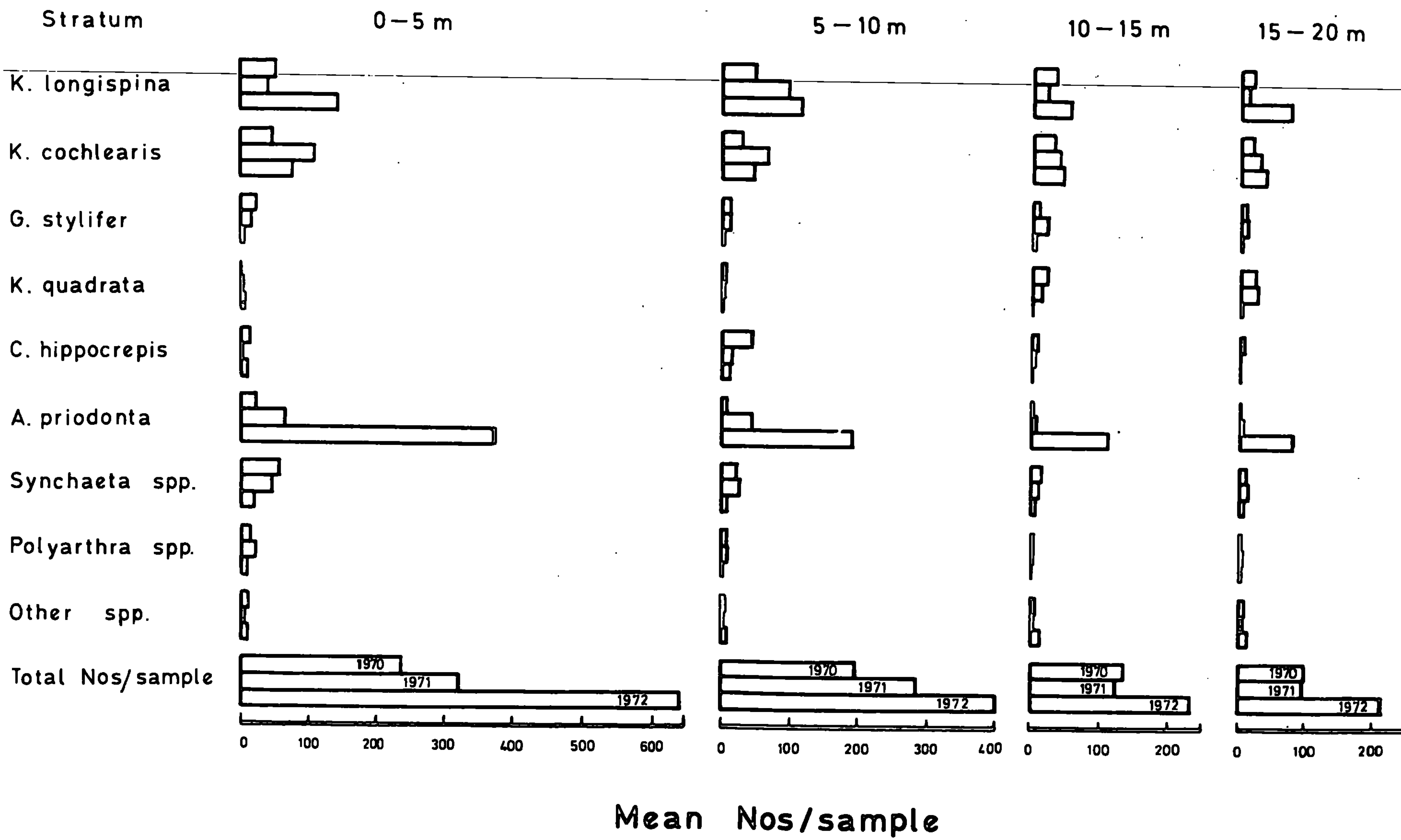
Stratum
0 – 5 m
5 – 10 m
10 – 15 m
15 – 20 m
K. longispina
K. cochlearis
G. stylifer
K. quadrata
C. hippocrepis
A. priodonta
Synchaeta spp.
Polyarthra spp.
Other spp.
Total Nos/sample
1970
1971
1972
0
100
200
300
400
500
600
Mean Nos/sample

Fig. 10.

in all years, Gastropus stylifer in 1970 and 1972, Asplanchna priodonta in all years, Synchaeta spp. in 1970 and 1972, Polyarthra spp. in 1970, and Ploesoma hudsoni in 1970 and 1971. Although the mean numbers of these species did not always decrease progressively with depth, the exceptions were usually due to a small increase in mean numbers in one stratum and were probably not significant. Therefore these five species and two genera were all most abundant in the surface layers. The mean numbers of two species, namely Keratella quadrata and Filinia terminalis, followed exactly the reverse pattern and progressively increased with depth in all years. Conochilus hippocrepis was the only species whose mean numbers increased from the 0-5m stratum to the 5-10m stratum, and then decreased with depth. The mean numbers of C. unicornis were also at a maximum in the 5-10m stratum in 1970 and 1971, but were at a maximum in the 10-15m stratum in 1972. Mean numbers of the two Trichocerca spp. were too low to show any definite pattern with depth. Therefore five species (K. longispina, K. cochlearis, G. stylifer, A. priodonta, P. hudsoni) and two genera (Synchaeta, Polyarthra) were most abundant in the surface stratum, two species (K. quadrata, F. terminalis) were most abundant in the deepest stratum, two species (Conochilus spp.) were most abundant in the middle strata, and two species (Trichocerca spp.) showed no pronounced vertical distribution.

The mean numbers of all rotifers increased slightly from 1970 to 1971, and greatly from 1971 to 1972. This increase was chiefly due to the large increase in the numbers of Asplanchna priodonta at all depths and also to the increased numbers of Kellicottia longispina in 1972. There were no marked differences between the mean numbers of Keratella cochlearis in the three years. Mean numbers of Gastropus stylifer, K. quadrata, Conochilus hippocrepis, Synchaeta spp. and Polyarthra spp. decreased markedly from 1971 to 1972. The mean numbers of the rarer species (< 8/ sample in Table 5) did not always show a definite increase or decrease between years. Mean numbers of C. unicornis decreased in the 5-10m stratum and increased in the 10-15m and 15-20m strata from 1970 to 1972. Filinia terminalis almost disappeared in 1971 but was taken in highest numbers in 1972. Ploesoma hudsoni almost disappeared in 1971 and was not taken in 1972. Trichocerca capucina was not taken in 1970, and T. similis almost disappeared in 1971. Therefore, from 1971 to 1972, the mean numbers increased for two species (A. priodonta, K. longispina) in all strata and for one species (C. unicornis) in the two lower strata, and decreased for two genera (Synchaeta, Polyarthra) and four species (G. stylifer, K. quadrata, C. hippocrepis, P. hudsoni) in all strata, and for one species (C. unicornis) in the 5-10m stratum. F. terminalis should probably be included with the species which increased in numbers.

4.4 Seasonal changes in the abundance and vertical distribution of the different species.

Numbers of the rare species in group D were usually too low for any comparisons to be made. Collotheca mutabilis, Ascomorpha saltans, and Trichocerca pusilla were taken from all strata, but A. ecaudis was not taken from the 0-5m stratum on the one occasion on which it occurred and Euchlanis dilitata was not taken from the 10-15m stratum. The numbers of each species were usually very low (< 10 per sample), but slightly higher numbers of T. pusilla (range 15-80 per sample) were taken from strata 0-5m and 5-10m in August 1969. This was the only month in which T. similis was taken in high numbers, especially from strata 0-5m and 5-10m (range 3-149 per sample). In all other samples, the numbers of this species were very low (< 10) or the species was absent. T. capucina was never taken in high numbers (maximum 15 per sample), but usually occurred in similar numbers in all strata when it was present. The numbers of Ploesoma hudsoni were only greater than 10 in 1970, when it occurred in all strata and when its major period of occurrence was from late August to mid-September with maximum numbers of 33 per sample in the 0-5m stratum. The numbers of the remaining eight species and two genera are compared in Figs. 11-17. The periods in which the lake was stratified were estimated from Figs. 2 and 3, and are shown at the top of each figure.

Filinia terminalis occurred in only one sample in 1971 and numbers were very low in 1970. The chief period of occurrence was from August to November and the lowest numbers usually occurred in the 0-5m stratum (Fig. 11.). There was little difference between the numbers taken in the three lowest strata in 1972, but numbers were highest in the lowest stratum (15-20m) in 1970 and especially in 1969 when very high numbers were taken in the samples. The major peaks in numbers occurred during the period of stratification in 1969 and large numbers of this species must have lived at very low O_2 concentrations in the lowest stratum (range about 10-20% saturation). This was also true in 1972 when Filinia was taken at extremely low O_2 concentrations which were close to zero in the 15-20m stratum in September and October (see Fig. 3.). In both

Figs. 11-18.

Figs 11-18. Numbers taken in each sample from each stratum from August 1969 to December 1972. (N.S. indicates the periods in which no samples were taken. The shaded bars at the top of the figures indicate the periods in which the lake was stratified).

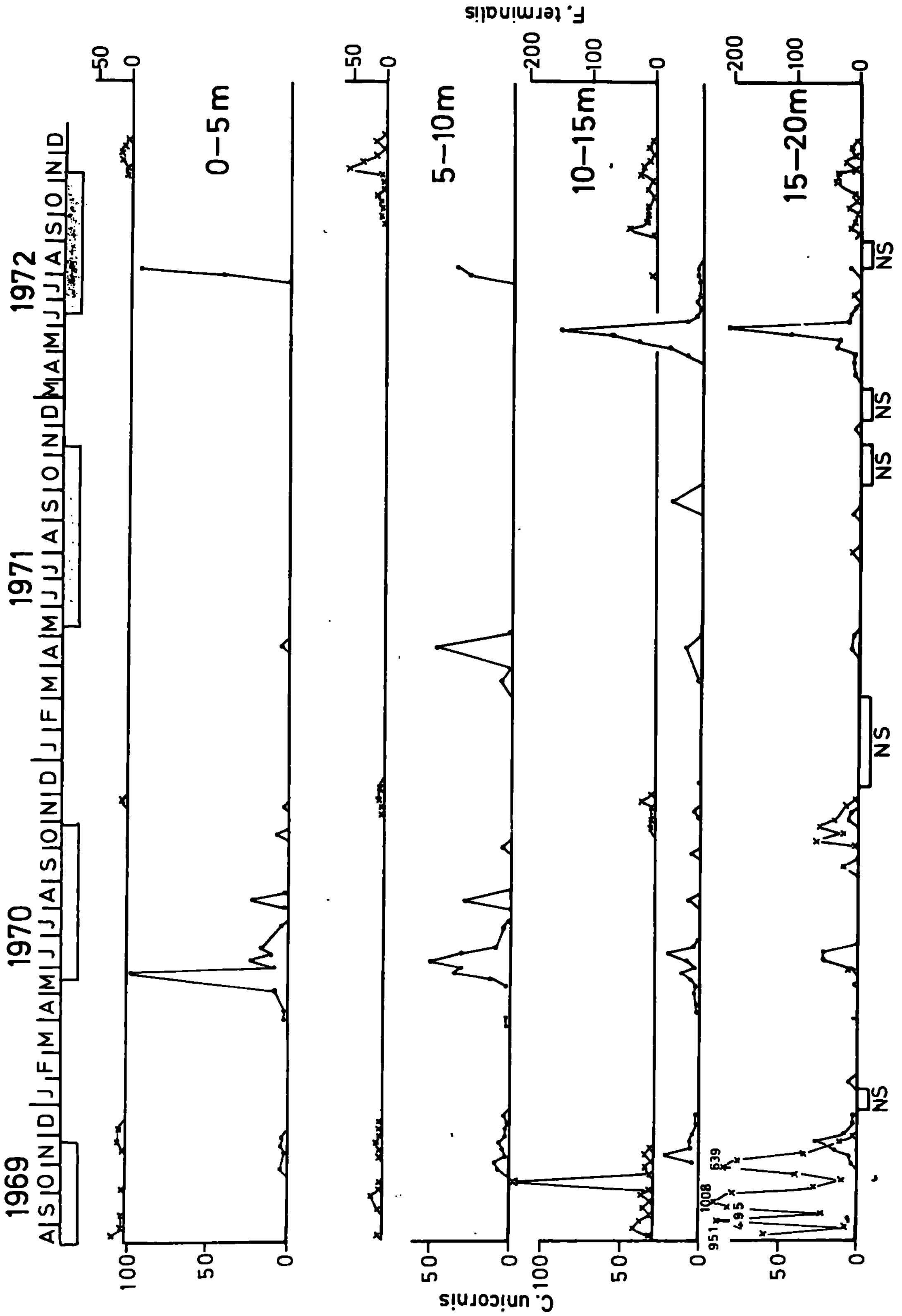

Fig. 11 Conochilus unicornis (.-.)

Filinia terminalis (x-x)

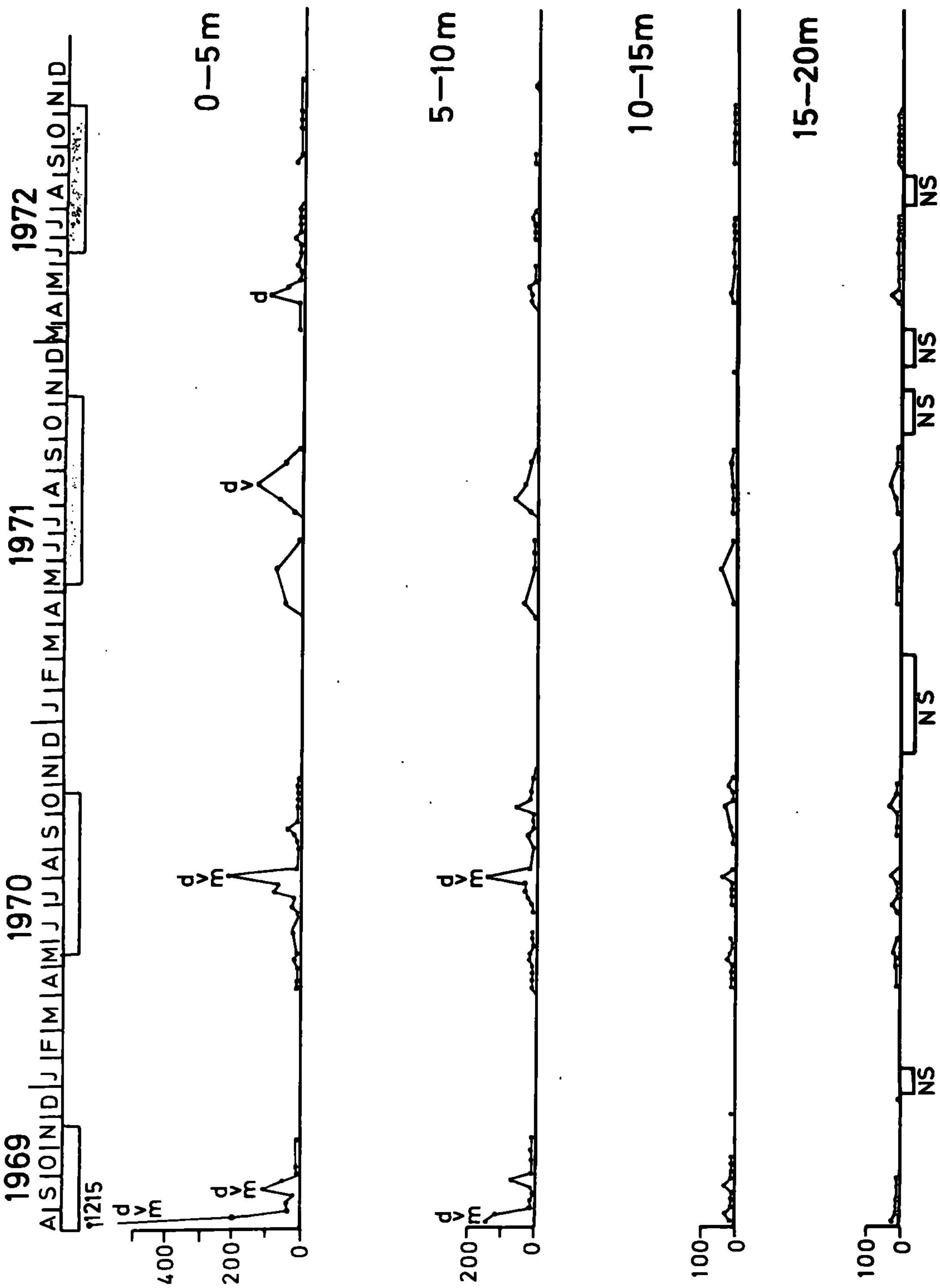

Fig. 12 Polyarthra spp.

d=dolichoptera, v=vulgaris, m=major

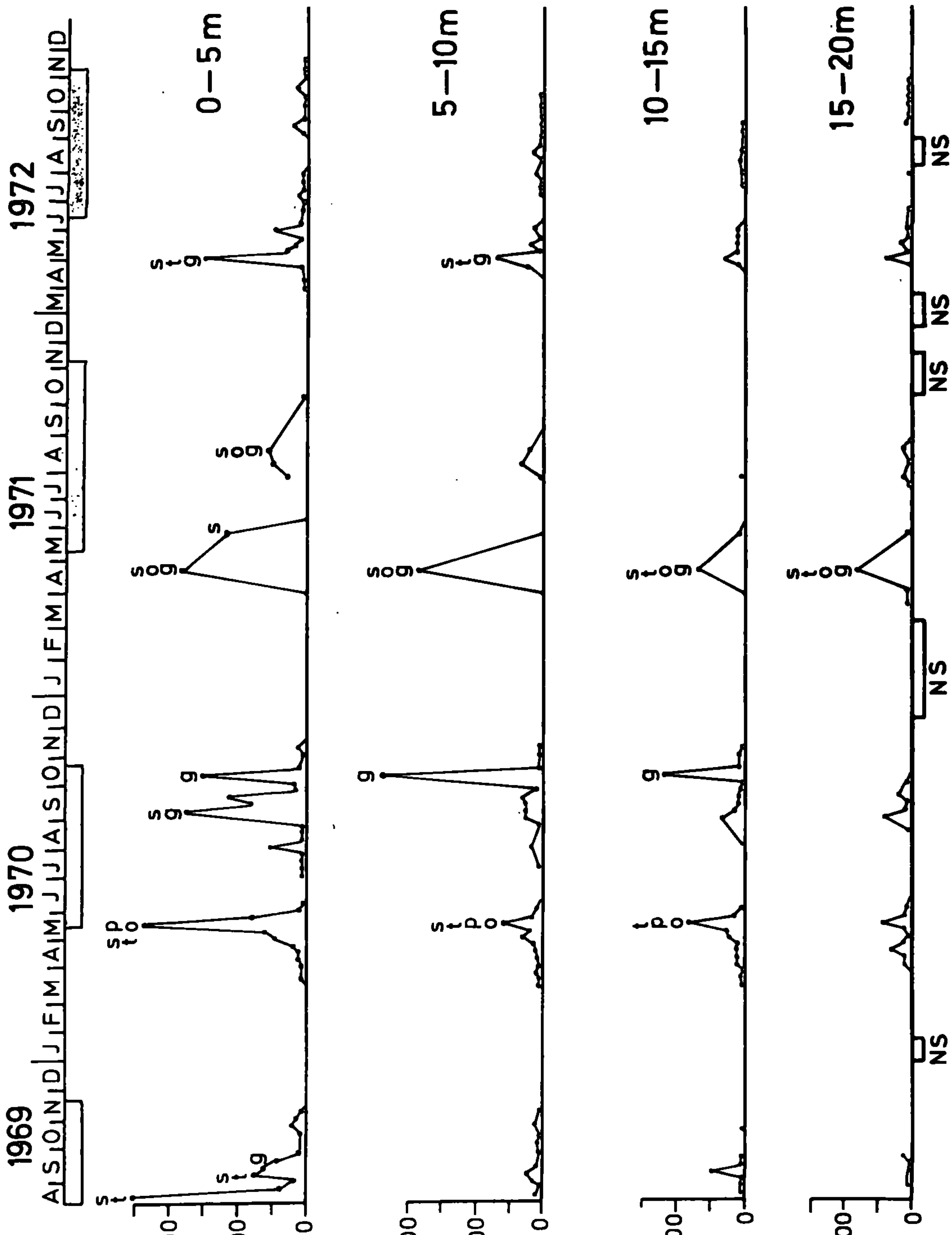

Fig 13 Synchaeta spp.

s=stylata, t=tremula, p=pectinata, o=oblonga, g=grandis.

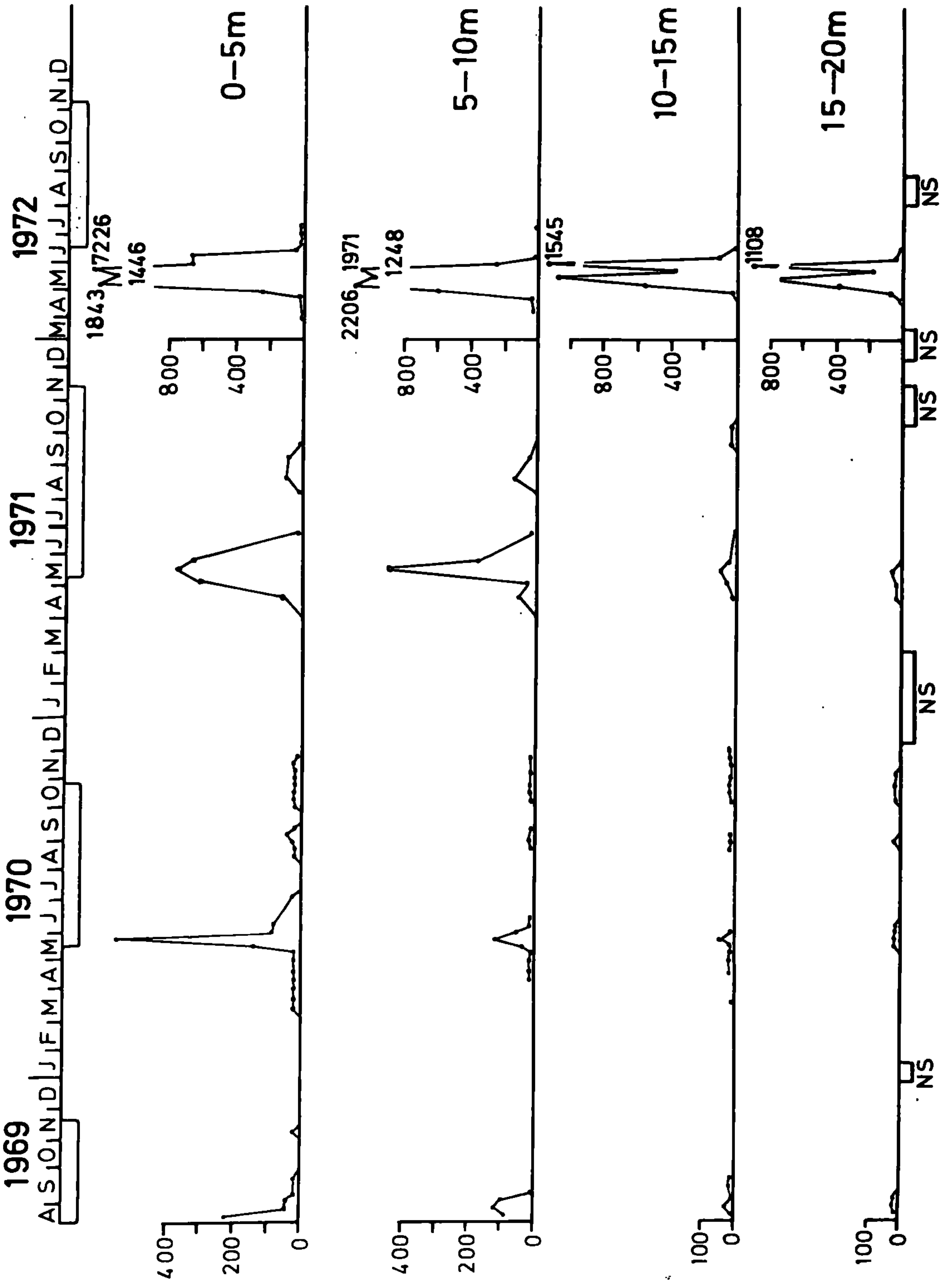

Fig.14 Asplanchna priodonta

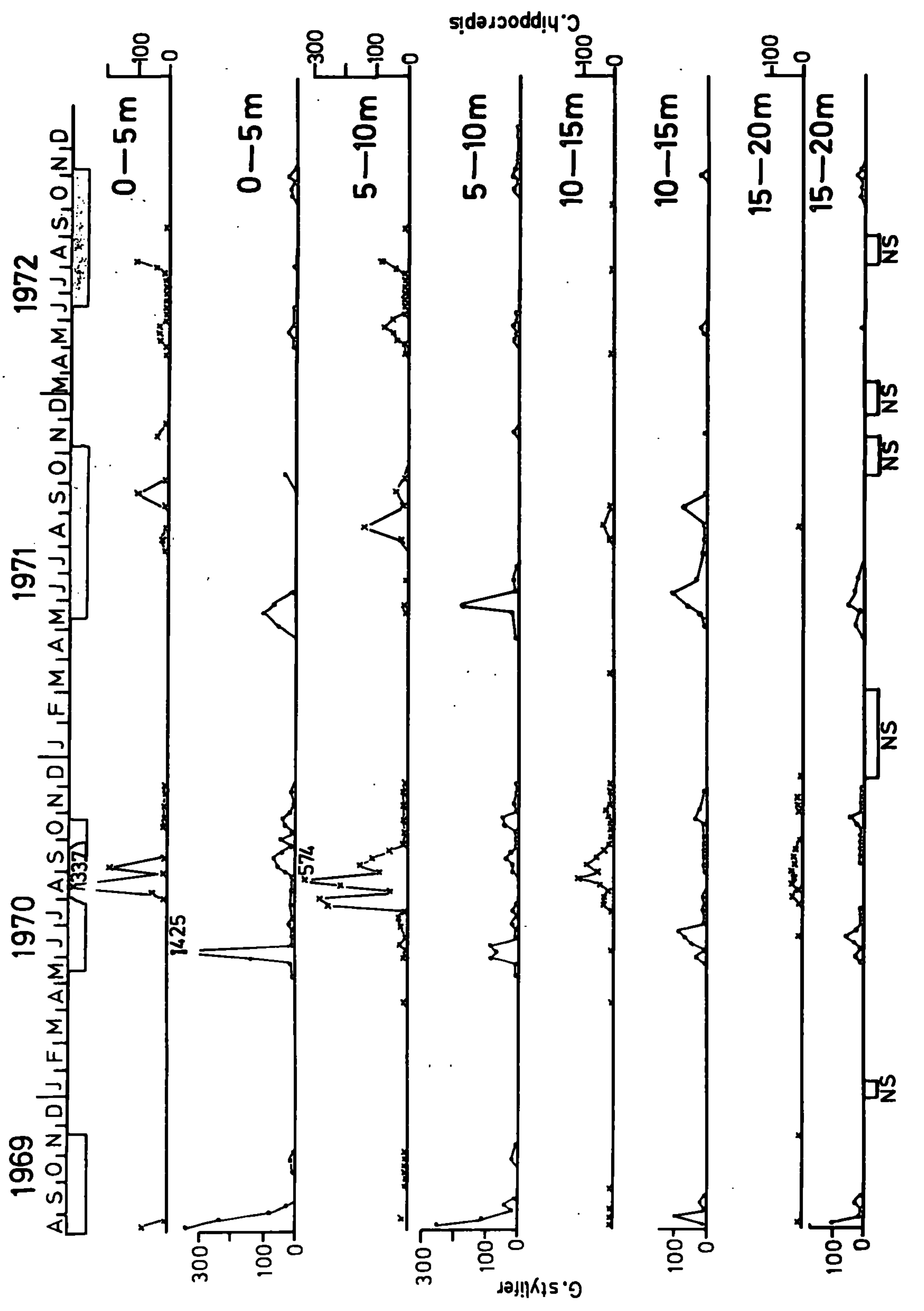

Fig. 15 Gastropus stylifer (.-.), Conochilus hippocrepis (x-x)

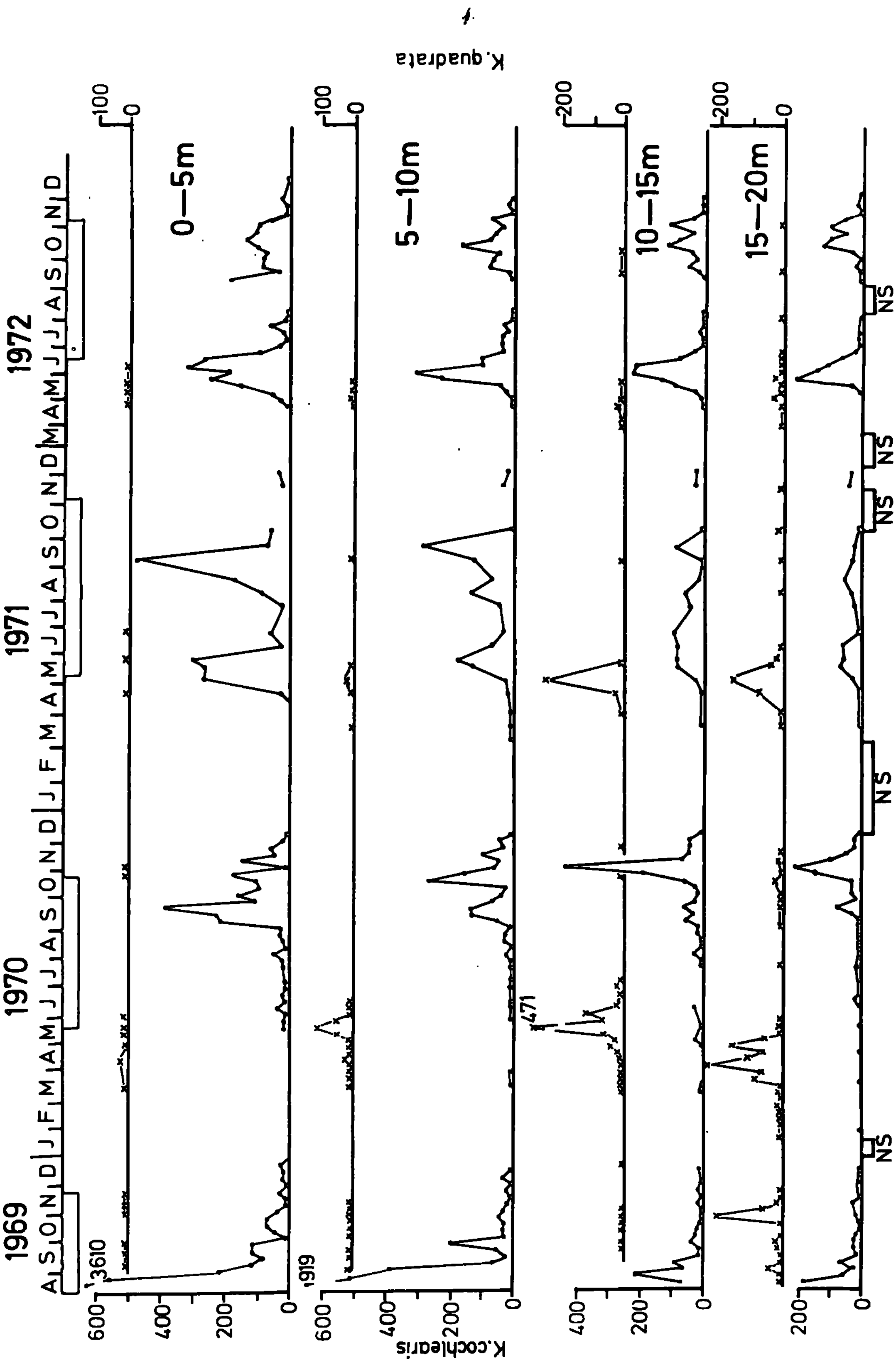

Fig. 16 Keratella cochlearis (.-.), K. quadrata (x-x)

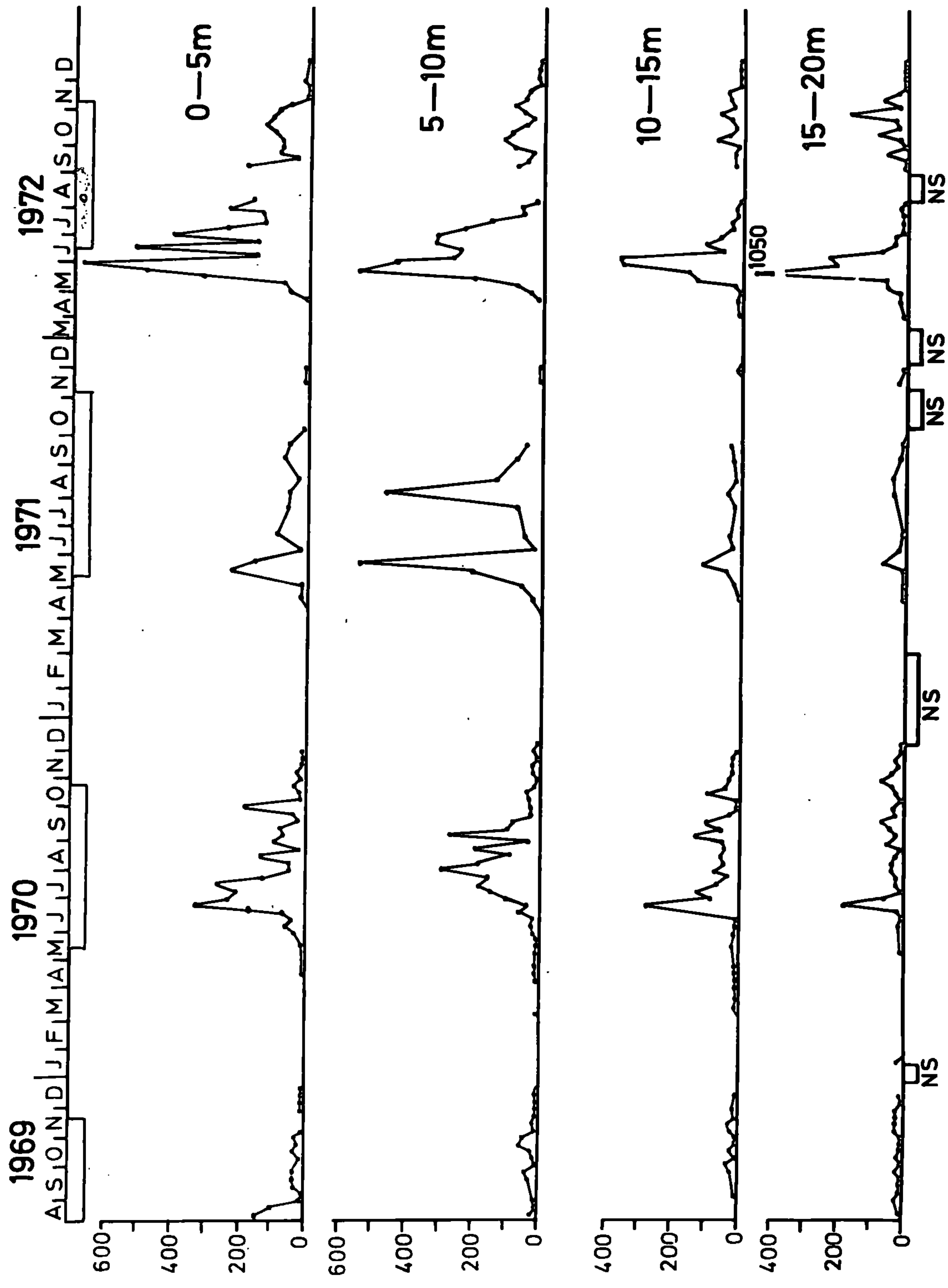

Fig.17 Kellicottia longispina

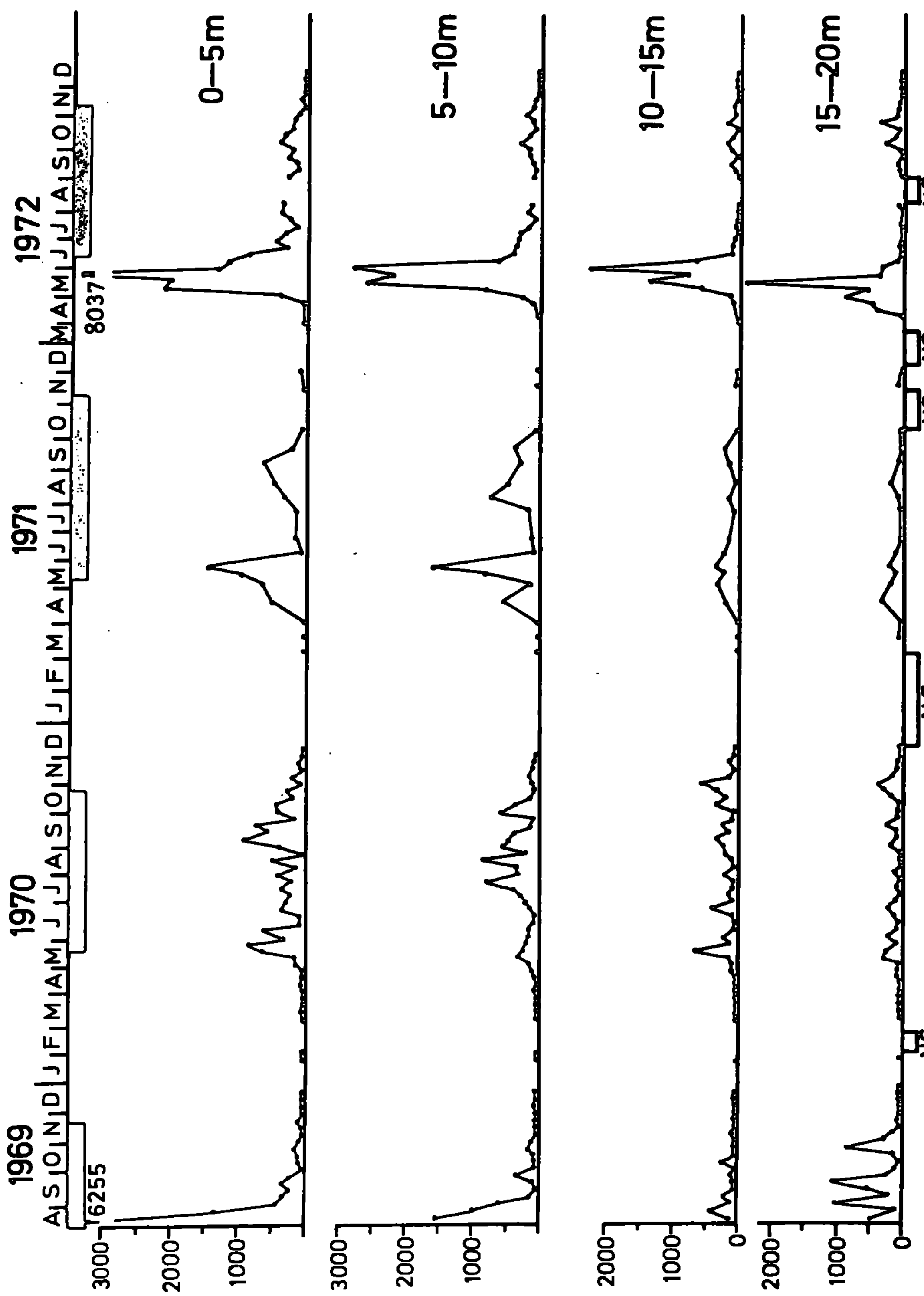

Fig. 18 Total numbers of all species

1970 and 1972, the numbers increased slightly in November during the period of overturn. Therefore the numbers of F. terminalis varied considerably between years, but were usually greatest in the lower strata and often at very low O_2 concentrations.

The numbers of Conochilus unicornis usually decreased with depth and were usually highest at the beginning of the period of stratification (Fig. 11.). There was a slight decrease in numbers from 1970-1971 and a slight increase from 1971-1972. Peaks in numbers occurred just before stratification in the lower strata (10-15, 15-20m) in 1972, and just after stratification in the upper strata (0-5, 5-10m) in 1972 and in all strata in 1970.

Polyarthra spp. occurred chiefly during the period of stratification with a slight decrease in numbers from upper to lower strata and with a peak in numbers in July or August (Fig. 12.). All three species (P. dolichoptera, P. vulgaris, P. major) were present during the peak in numbers in 1969 and 1970, but only two species (P. dolichoptera, P. vulgaris) were present during the peak for 1971, and there was no obvious peak in 1972. Although no counts were made, P. dolichoptera appeared to be the predominant species in April, and P. vulgaris and P. major were predominant in July and August. There was no obvious difference in numbers between 1970 and 1971, but numbers decreased slightly from 1971 to 1972. Therefore these species were fairly abundant for a short period in the middle of the summer and chiefly occurred in the upper strata.

Synchaeta spp. also occurred chiefly during the period of stratification with a decrease in numbers from upper to lower strata, but one peak in numbers occurred at the start of stratification in May 1970 and before the start of stratification in April 1971 and

1972 (Fig. 13.). The number of peaks in numbers varied between years and all five species did not occur together during each peak. In the first peak in the year, four species were present in 1970 (S. stylata, S. tremula, S. pectinata, S. oblonga), and three species were present in 1971 (S. stylata, S. oblonga, S. grandis), and in 1972 (S. stylata, S. tremula, S. grandis). S. grandis was usually the only species present in the final peak at the time of the autumn overturn, but this species was very rare in 1971 and 1972. Although there were some differences between years, it appeared that S. tremula and S. pectinata were most abundant in April and May, S. stylata and S. oblonga were most abundant in April and May and also in August and September, and S. grandis was most abundant from August to October. There was a marked decrease in numbers of all species from 1971 to 1972. Therefore the five Synchaeta spp. were abundant at different times of the year and chiefly occurred in the upper strata.

There were two distinct periods of occurrence for Asplanchna priodonta, the first from March to July and the second from August to October or November (Fig. 14.). The major peak in numbers occurred only in the first of these periods and usually at the onset (1970, 1971), or just before (1972), the period of stratification. There was no obvious peak in numbers during the second period of occurrence and this period was inexplicably absent in the lowest stratum (15-20m) in 1971, and in all strata in 1972. Numbers usually decreased from the upper to lower strata in 1972. There was clearly a large increase in numbers from 1971 to 1972. Therefore this species was most abundant in May and June, and usually in the upper strata.

Conochilus hippocrepis occurred chiefly during the period of stratification in 1970 and 1971 with maximum numbers in July, August and September (Fig. 15.). The numbers were considerably lower in 1972, especially in the lower strata (10-15m, 15-20m), and the period of occurrence was chiefly before and in the first half of the period of stratification. When the numbers were high, they were usually greatest in the two upper strata. *Gastropus stylifer* occurred chiefly during the period of stratification, but the numbers decreased considerably from 1971 to 1972 (Fig. 15.). Definite peaks in numbers were seen in 1970 and 1971 when they occurred in late May or early June with a decrease in numbers from upper to lower strata. The peak in August 1969 cannot be explained.

Apart from *Filinia terminalis*, *Keratella quadrata* was the only other species whose numbers increased from the upper to the lower strata (Fig. 16.). Numbers decreased considerably from 1971 to 1972. The chief peaks in numbers occurred in the lowest stratum (15-20m) in April and in the 10-15m and 5-10m strata at the start of stratification in May. Therefore this species was most abundant in April and May, and chiefly occurred in the lower strata. *K. cochlearis* probably occurred throughout the year but the numbers were very low in winter. It chiefly occurred from April to November and there was one autumn peak in numbers in 1970 and a spring and autumn peak in 1971 and 1972 (Fig. 16.). The autumn peak in 1970 occurred in September in the upper stratum (0-5m), at the end of stratification in mid-October in the 5-10m stratum, and in late October in the 10-15m and 15-20m strata. The spring peak in 1971 and 1972 occurred at the start of stratification in May 1971 and June 1972, and the autumn peak occurred during stratification in September 1971 and in September-October 1972. The numbers usually decreased with depth, and there was no noticeable decrease or increase in numbers from 1970 to 1972. Therefore this species was most abundant in September and October in all years and in May or June 1971 and 1972, and chiefly occurred in the upper strata.

Kellicottia longispina was present throughout the year with low numbers in winter. It chiefly occurred during the period of stratification but high numbers occurred in all strata just before the start of stratification in 1972 (Fig. 17.). There was a large variation in the number of peaks occurring in each year. Several peaks occurred from June to September in 1970. An early peak occurred in May 1971 in all strata with a second peak in August 1971 and in the 5-10m stratum. A definite peak occurred at the end of May 1972 and was followed by other peaks in June, July and August in the upper stratum (0-5m). The numbers increased slightly in the 5-10m stratum from 1970 to 1971 and markedly in all strata from 1971 to 1972. A decrease in numbers with depth was only clearly shown in 1969 and 1970. In 1971, numbers increased from the 0-5m stratum to the 5-10m stratum and then decreased. In 1972 numbers decreased with depth in the three upper strata but increased in the lowest stratum (15-20m). Therefore there were large fluctuations in the abundance of this species from May to September and although the numbers were generally higher in the upper strata, high numbers were recorded in the lowest stratum (15-20m) in 1972.

The seasonal changes in the total number of rotifers taken in each sample are compared in Fig. 18. Numbers were generally higher from May to October with most of the peaks occurring during the period of stratification, except in 1972 when there was a peak in May before the onset of stratification. From Figs. 11 to 17, it is possible to list the principal species which were responsible for the major peaks. The major peak in 1969 was chiefly due to Keratella cochlearis, Gastropus stylifer, Synchaeta stylata, S. tremula and Polyarthra spp. There were several small peaks in 1970 during the period of stratification, but no major peaks. Kellicottia longispina, Keratella cochlearis, Asplanchna priodonta and Synchaeta stylata were the predominant species in the peak of May 1971, Kellicottia longispina was almost entirely responsible for the peak in the 5-10m stratum in August 1971, and the peak in September 1971 was chiefly due to K. cochlearis. The major peak in May 1972 was almost entirely due to Asplanchna priodonta which contributed 7,226 individuals to the total of 8,037.

The total numbers generally decreased from the upper to the lower strata. It is remarkable that rotifers occurred regularly, but in small numbers, in the lowest stratum (15-20m) in late September and October 1971, and in late August to October 1972 when oxygen concentrations were extremely low (ranges were 1-4% saturation for September to October 1971 and 0-4.5% saturation for late August to October 1972). The following species occurred at these very low oxygen concentrations in the lowest stratum, Kellicottia longispina, Keratella cochlearis, K. quadrata, Gastropus stylifer, Synchaeta oblonga, S. pectinata, S. stylata, S. tremula, Polyarthra vulgaris, Filinia terminalis and Trichocerca capucina.

4.5 Occurrence and abundance of the different species in relation to temperature and oxygen concentration.

pH, temperature and dissolved oxygen were measured at metre intervals at the sampling point. pH values varied between 5.6 and 7.3 in 1969 (August - December only), 5.2 and 7.3 in 1970, 5.9 and 8.7 in 1971, 5.6 and 8.8 in 1972. No correlations were found between pH and the occurrence or numbers of the rotifer species in Grasmere. Ranges of temperature and dissolved oxygen in each stratum are given for each sampling occasion in Figs. 2 and 3. These values were used to determine the ranges within which each species or genus occurred (Table 6). It is obvious that all taxa occurred over a wide range of temperature and oxygen concentration. Numbers of the five rare species in group D were too low for any comparisons to be made. Very little information was available for the three rare species in group C, namely Trichocerca similis, T. capucina and Ploesoma hudsoni. The numbers of the last two species never exceeded 50 per sample, and the numbers of T. similis exceeded 50 only in August 1969 at high temperatures and oxygen concentrations (ranges 15.5-17^{o}C, 80-95% saturation).

The numbers of the remaining eight species and two genera frequently exceeded 50 individuals per sample, and these records are compared in Figs. 19-25. Each point on a figure indicates the median temperature (^{o}C) and oxygen concentration (% saturation) on a sampling occasion when the numbers of a taxon exceeded 50 per sample. Higher densities (>150, >250, >500 per sample) are also shown on the figures, and the outer line includes all the different combinations of temperature and oxygen concentration

Table 6. Ranges of temperature (^{o}C) and dissolved oxygen (% saturation) in Grasmere for the occurrence of each species or genus.

	Temperature	Oxygen
Kellicottia longispina	3.5 - 21	0 - 125
Keratella cochlearis	3.5 - 21	0 - 125
K. quadrata	3.5 - 17	0 - 111
Gastropus stylifer	6 - 21	0 - 125
Conochilus hippocrepis	4.5 - 20	3 - 120
Asplanchna priodonta	4.0 - 21	2 - 125
Synchaeta spp.	3.5 - 20	0 - 125
Polyarthra spp.	4.5 - 21	0 - 125
C. unicornis	4.5 - 21	3 - 125
Filinia terminalis	3 - 20	0 - 115
Trichocerca capucina	7 - 18.5	0 - 120
T. similis	7 - 20	1 - 115
Ploesoma hudsoni	7 - 15	7 - 115

Figs. 19-25

Figs. 19-25. Occurrence and abundance in relation to temperature (^{o}C) and oxygen concentration (% saturation) Occurrences are only recorded in the figure when the numbers of a species exceeded 50 per sample. The continuous line includes all the different combinations of temperature and oxygen concentration occurring in Grasmere during the present study. The broken line includes the area where highest densities were found.

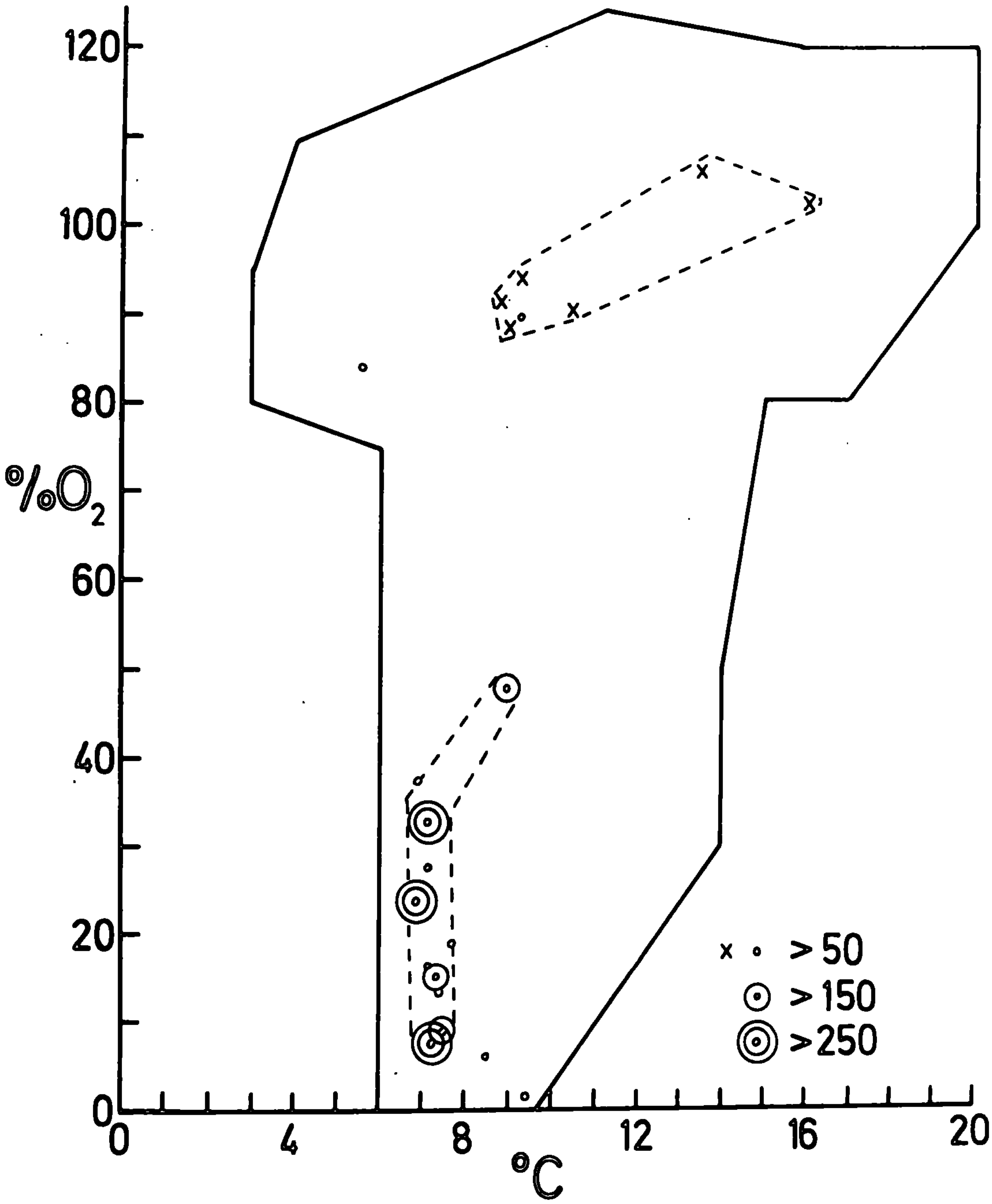

Fig.19 Conochilus unicornis (x), Filinia terminalis (.)

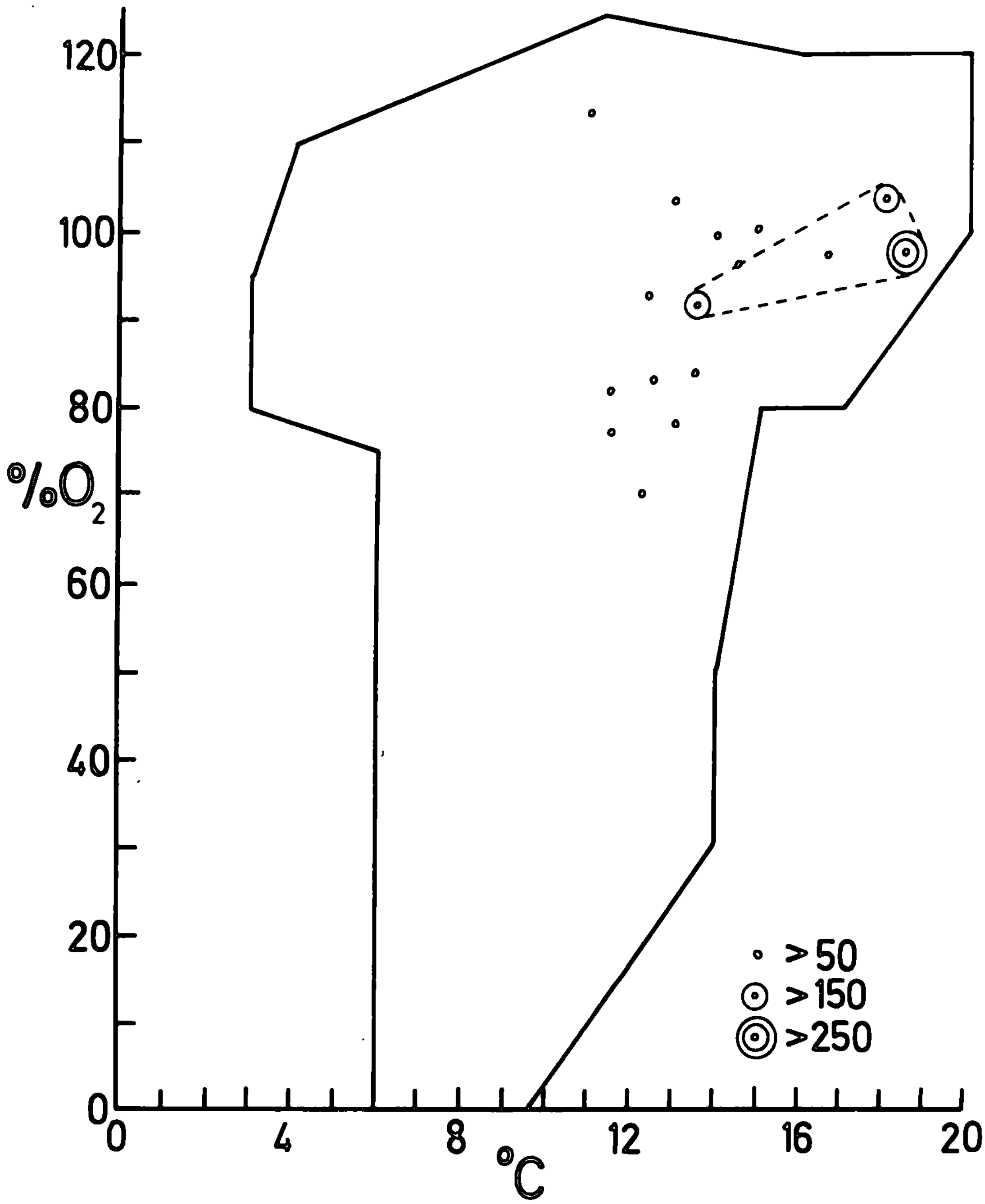

Fig. 20 Polyarthra spp.

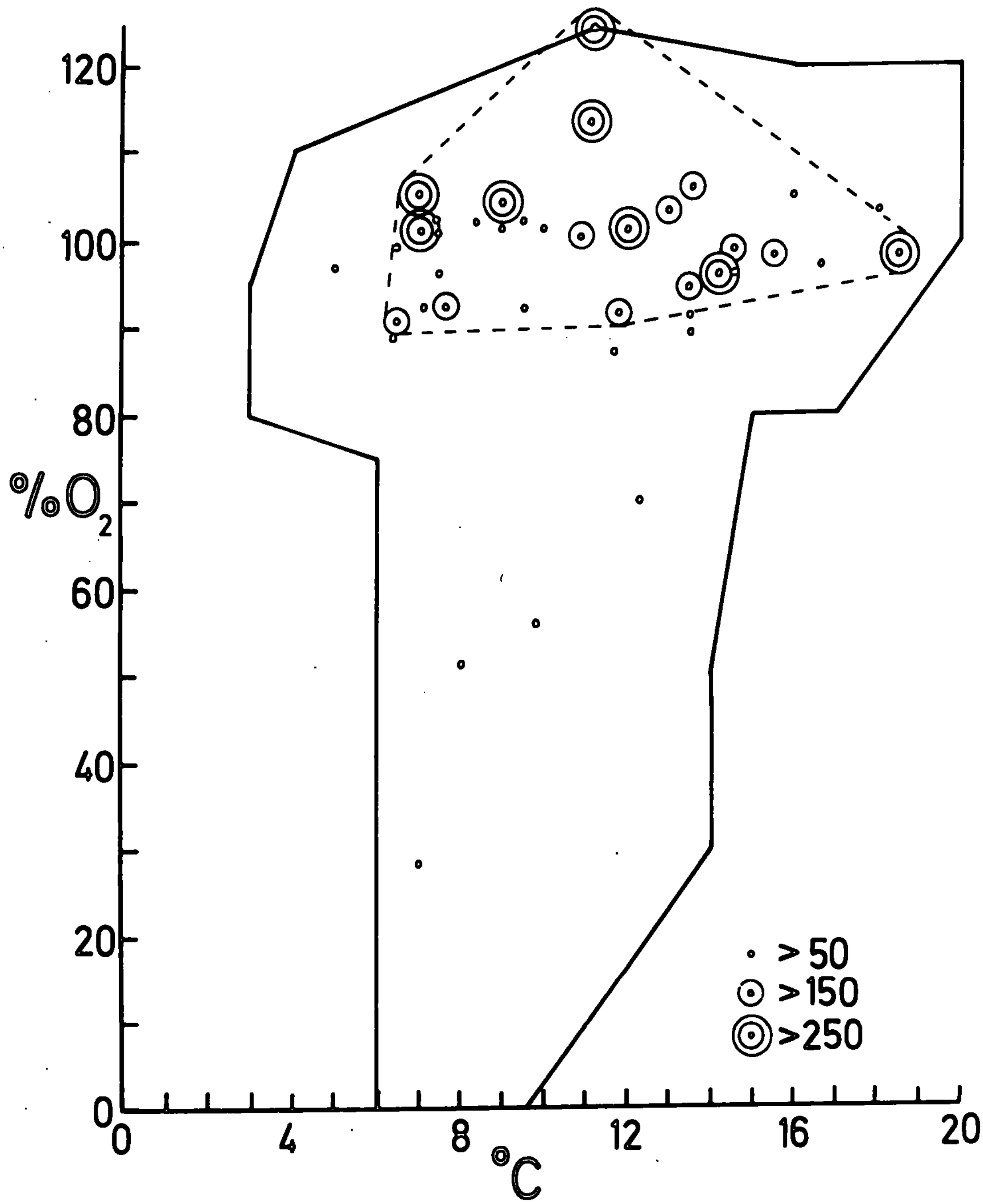

Fig. 21 Synchaeta spp.

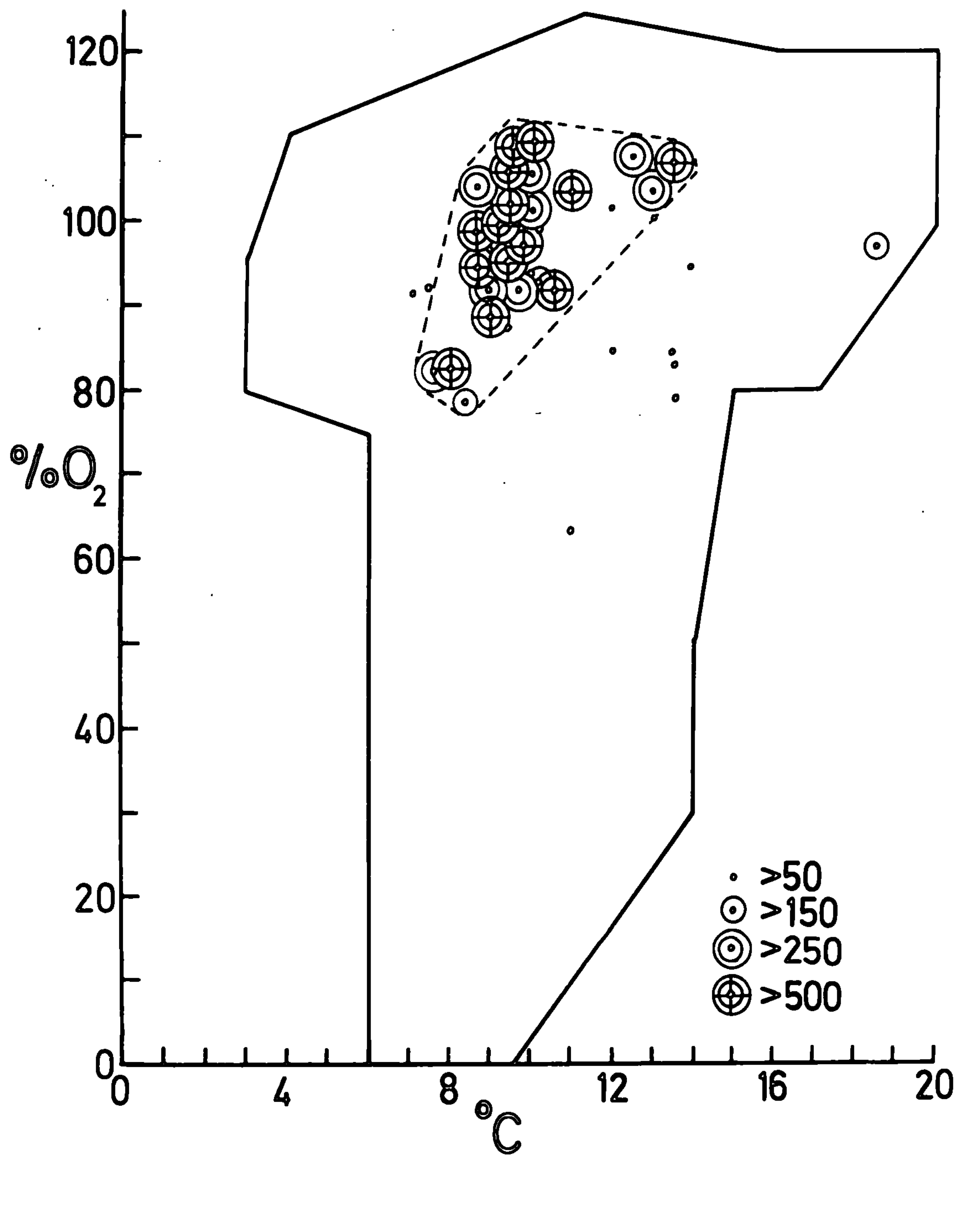

Fig. 22 Asplanchna priodonta

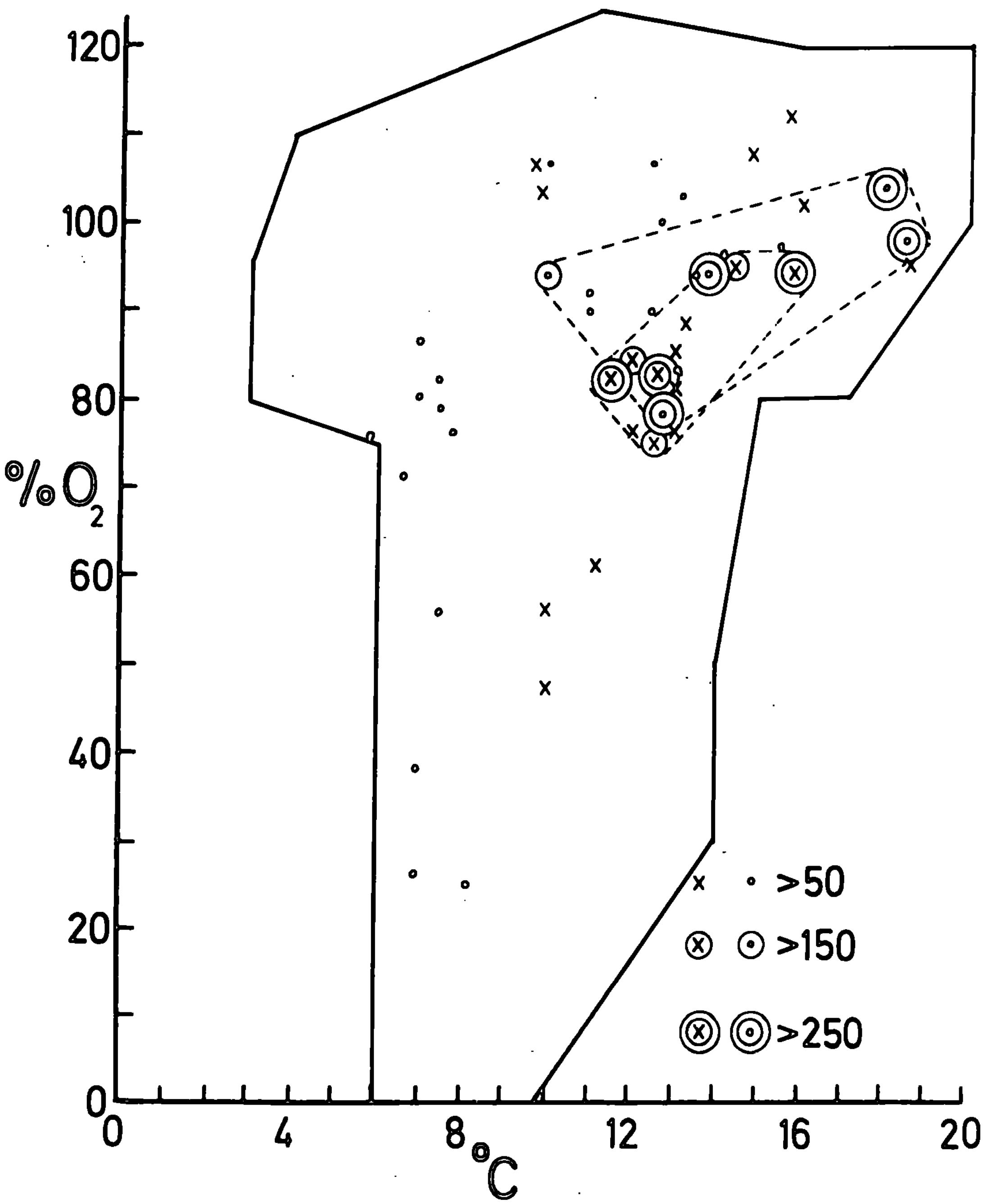

Fig.23 Gastropus stylifer (.), Conochilus hippocrepis (x)

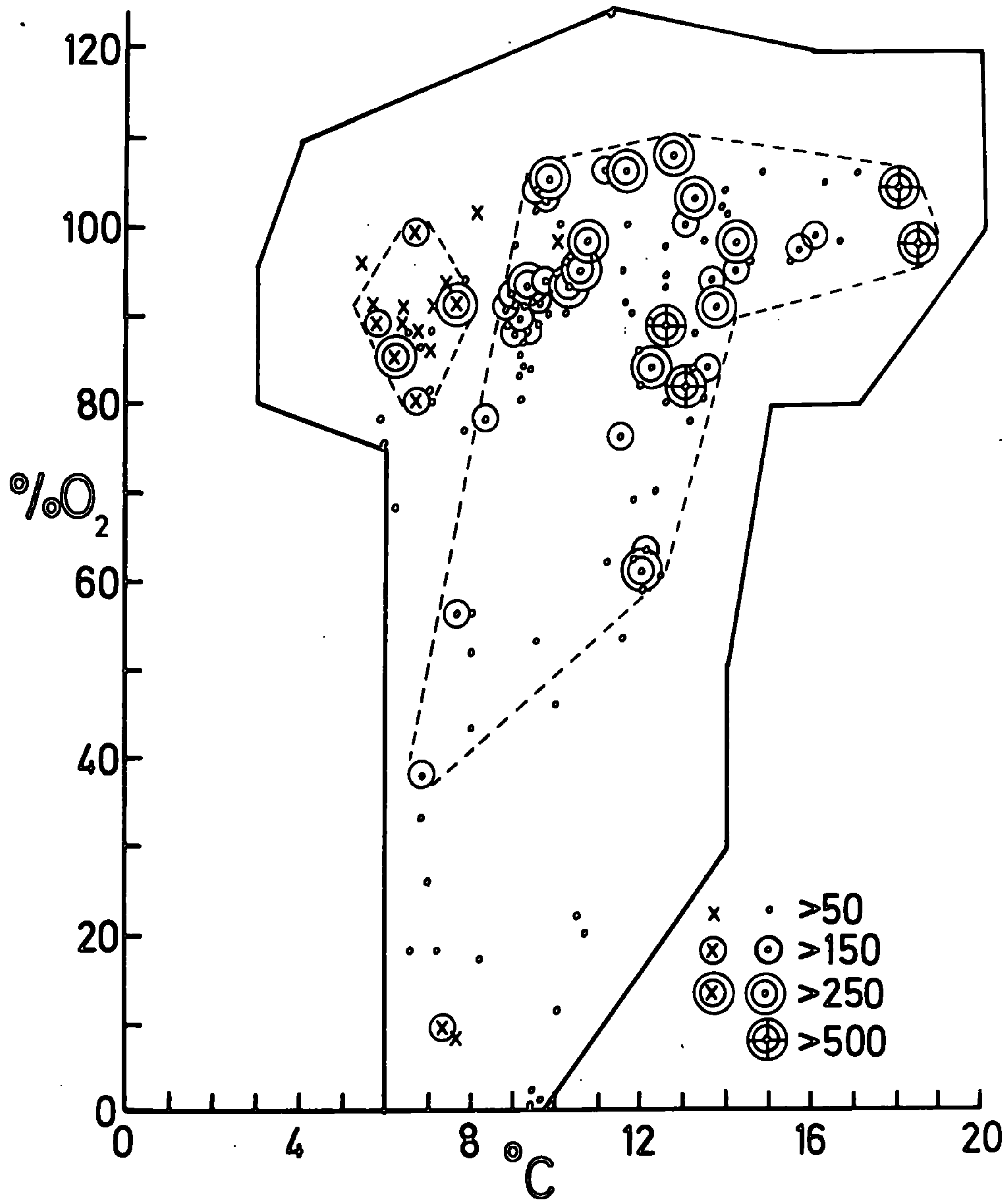

Fig. 24 Keratella cochlearis (.), K. quadrata (x)

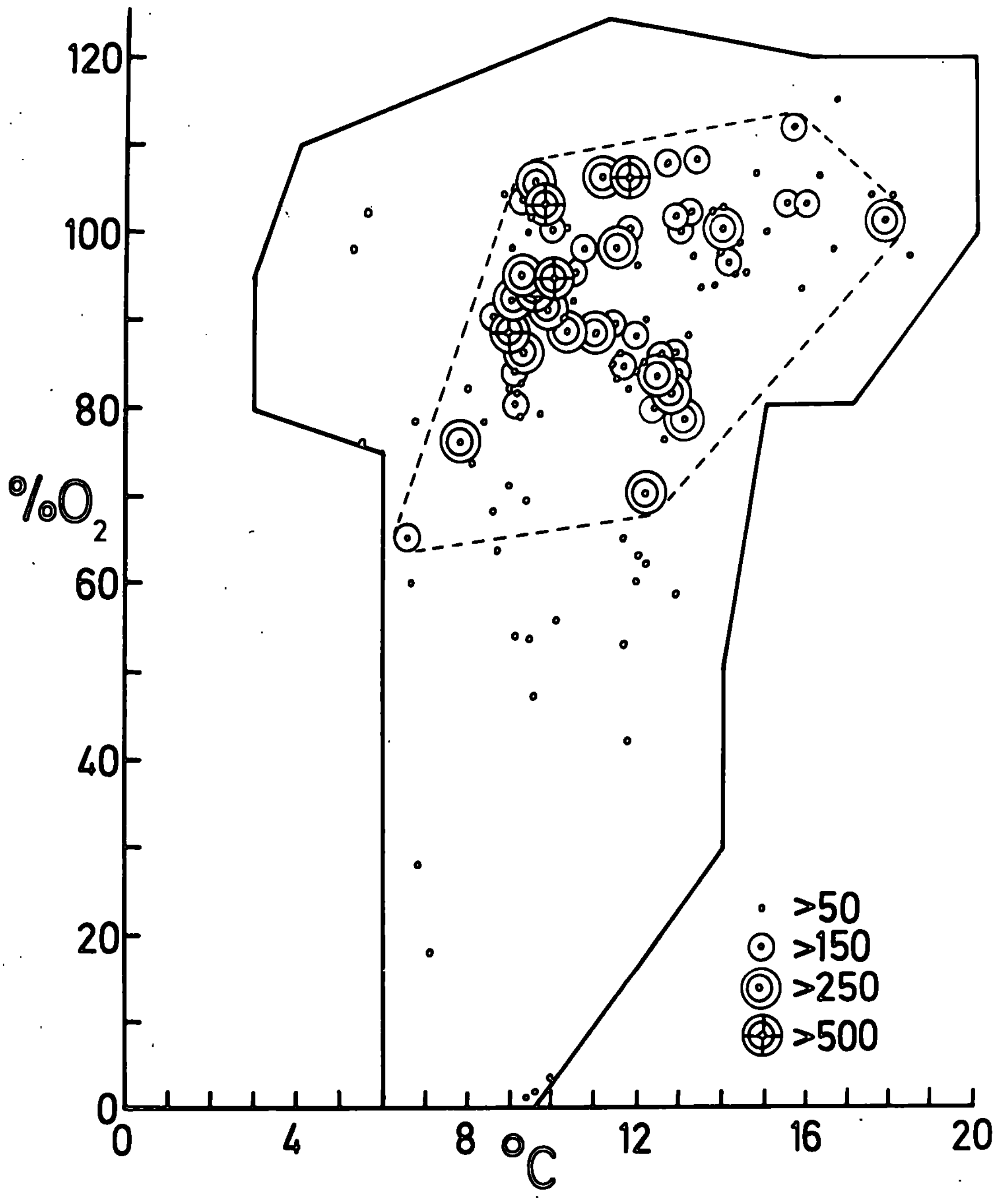

Fig. 25 <u>Kellicottia longispina</u>

occurring in Grasmere during the present study.

The numbers of *Filinia terminalis* (Fig. 19.) reached their highest values (> 150 per sample) at low temperatures (6.8-9°C) and low oxygen concentrations (9-47% saturation). In direct contrast to this species, *Conochilus unicornis* (Fig. 19.) reached densities above 50 individuals per sample at only high oxygen concentrations (86-106% saturation) and fairly high temperatures (8.5-16°C). Therefore both these species were only abundant within a limited range of temperature and oxygen concentration, and the optimum ranges for each species were markedly different.

Although the numbers of *Polyarthra* spp. (Fig. 20.) rarely exceeded 50 individuals per sample in the present study, the limited records clearly indicate that the highest densities (>150 per sample) were only attained at high oxygen concentrations (92-103% saturation) and high temperatures (13.5-18.5°C).

The numbers of *Synchaeta* spp. (Fig. 21.) reached high densities (>150 per sample) only at very high oxygen concentrations (> 90% saturation) but appeared to be less limited by temperature. High numbers were recorded over a wide range (6.5-18.5°C), but this apparent wide tolerance to temperature could be due to the different species attaining their maximum abundance at different temperatures.

Apart from one value, all the records of high densities (>150 per sample) for *Asplanchna priodonta* (Fig. 22.) were located within a narrow range of temperature and oxygen concentration (7.7-13.5°C and 77-109% saturation). Therefore this species was not abundant at low oxygen concentrations (<77% saturation) or at extreme temperatures (<7.7°C and 13.5°C).

The numbers of both Gastropus stylifer and Conochilus hippocrepis (Fig. 23.) exceeded 50 per sample over a wide range of temperature and oxygen concentration. Their maximum numbers (>150 per sample) occurred over narrower ranges of 10-18.5°C and 78-104% saturation for G. stylifer, and 11.5-15.7°C and 75-95% saturation for C. hippocrepis. Therefore both species were most abundant at high oxygen concentrations and fairly high temperatures.

There were relatively few records for Keratella quadrata (Fig. 24.) but, apart from one value, all the high densities (>150 per sample) were located in a narrow range of low temperature (5.7-7.7°C) and high oxygen concentration (80-99% saturation). Therefore, this species apparently requires very specific conditions of temperature and dissolved oxygen before high densities are attained. In contrast to K. quadrata, K. cochlearis was abundant over a wide range of temperature and oxygen concentration (6.8-18.5°C, and 37-107% saturation). Within this wide range, the highest densities were chiefly found at oxygen concentrations above 80% saturation and temperatures greater than 9°C. Kellicottia longispina (Fig. 25.) was also abundant over a wide range of temperature and oxygen concentration (7.8-17.9°C, and 65-112% saturation).

Therefore the most abundant species in Grasmere attained their highest densities over either a wide range of temperature and oxygen concentration, i.e. Keratella cochlearis, Kellicottia longispina, Synchaeta spp. (temperature only), or a narrow range of temperature and oxygen concentration, i.e. Filinia terminalis, Conochilus unicornis, C. hippocrepis, Asplanchna priodonta, Keratella quadrata, Polyarthra spp., Synchaeta spp. (oxygen concentration only).

SECTION 5

DISCUSSION AND GENERAL CONCLUSIONS

5. Discussion and general conclusions

A total of thirteen genera and twenty-four species were recorded from the plankton of Grasmere. Edmondson (1959) proposed that the genera Keratella, Kellicottia, Polyarthra, Synchaeta, Filinia and Asplanchna were the most frequent and abundant genera in the plankton of lakes, and all six genera occurred in Grasmere. Green (1972) found that only nine genera accounted for most of the species found in a wide geographical range of localities. Only five of these genera occurred in Grasmere, namely Keratella, Polyarthra, Synchaeta, Ploesoma, Trichocerca and the four genera absent from Grasmere were Brachionus, Lecane, Notholca, Testudinella. Several workers have recorded a higher number of species (see review of literature in section 1.2), and the number in Grasmere is comparable to those found in Lake Stechlinsee (Koch-Althaus 1963) and in Paradise Lake (George and Fernando 1969). The only localities where fewer species have been recorded are Sunfish Lake (George and Fernando 1969), Spitsbergen (Ahmren 1964b), and Lake Blankvatn (Larsson 1971). It is therefore clear that Grasmere cannot be considered to be a lake rich in species of planktonic rotifers.

As small numbers of Keratella cochlearis, K. quadrata and Kellicottia longispina were present throughout the winter, there was probably no sexual phase in these species. This conclusion is supported by the observations of Carlin (1943) who found no sexual periods in K. cochlearis and Kellicottia longispina, and only one K. quadrata with resting eggs in Motalaström over six years.

Although many workers have recorded a temporal variation in the body form of planktonic rotifers and have concluded that a definite cyclomorphosis occurs, no marked seasonal change in body form was observed for any of the species in Grasmere. This absence of a temporal variation cannot be explained but it may indicate that fluctuations in environmental factors were not so great as those found in localities where a temporal variation exists. The absence of appendages in females which had hatched from dormant mictic eggs was seen in *Polyarthra*, as also recorded by Nipkov (1952), but not in *Filinia* as recorded by Sudzuki (1964).

The most important results for each of the principal species in Grasmere are summarised in Table 7. There was not enough information on the rare species in group D and the *Trichocerca* spp. in group C to justify their inclusion in this table.

Apart from the rare species in group D, three broad categories were recognised: A, spring-autumn species; B, spring-early summer species; C, summer-autumn species. Carlin (1943) separated the species in Motalaström into slightly different categories, namely winter and early spring species, perennial species with late spring and early summer maxima, seasonal summer species; and Larsson (1971) divided the species in Lake Blankvatn into only perennial and summer forms.

The six species in group A in Grasmere included only three truly perennial species, *Kellicottia longispina*, *Keratella cochlearis* and *K. quadrata*. These species were also classified as perennial by Carlin (1943), Davis (1954), Koch-Althaus (1963), George and Fernando (1969), Larsson (1971). In contrast to these observations, Beach (1960) classified *K. quadrata* as a rare cold water form in the Ocqueoc River System and George and Fernando (1969) found that *K. cochlearis* was also a cold water form with only one peak in January in Sunfish Lake and two peaks in January and May-June in Paradise Lake. Both spring and autumn peaks occurred in the numbers of *K. cochlearis* in Grasmere (Table 7),

Table 7. Summary of results for principle species in Grasmere, summarising seasonal occurrence (groups A,B and C), seasonal abundance (months in which a species was abundant), vertical distribution (stratum in which a species was usually most abundant: U=upper stratum, M=middle strata, L=lowest stratum), differences in abundance between years (o=no marked change in abundance, -= marked decrease in numbers, += marked increase in numbers), and ranges of temperature (°C) and oxygen concentration (% saturation) within which the highest densities were attained.

Seasonal occurrence	Seasonal abundance A.	M.	J.	J.	A.	S.	O.	N.	vert dist	Between years 70-71	71-72	High Densities °C	%O_2
A) Spring-autumn spp.													
Keratella quadrata	---	---							L	o	-	5.7 - 7.7	80 - 99
Gastropus stylifer		---	---						U	o	-	10.0 - 18.5	78 -104
Asplanchna priodonta		---	---						U	+	+	7.7 -13.5	77 -109
Kellicottia longispina		---	---	---	---	---			UM	o	+	7.8 -17.9	65 -112
Keratella cochlearis		---	---			---	---		U	o	o	6.8 -18.5	37 -107
Conochilus hippocrepis				---	---	---			UM	-	-	11.5 -15.7	75 - 95
B)Spring-early summer													
Polyarthra dolichoptera	---								U	o	-	- -	- -
S.tremula, S.pectinata	---	---							U	o	-	6.5 -18.5 (S.tremula, S.pectinata, S.stylata, S.oblonga)	90 -125
S.stylata, S.oblonga	---	---			---	---			U	o	-		
Conochilus unicornis		---	---						UM	-	+	8.5 -16.0	86 -106
C)Summer-autumn													
Polyarthra vulgaris/major				---	---	---			U	o	-	13.5 -18.5	92 -103
Synchaeta grandis					---	---	---		U	o	-	- -	- -
Filinia terminalis					---	---	---	---	L	-	+	6.8 -9.0	9 - 47
Ploesoma hudsoni						---			U	-	-		

and a similar autumnal peak has been recorded in Terwilliger's Pond in Ohio (Ahlstrom 1933), in Lake Erie (Davis 1954), in Mindelsee (Einsle 1967), and in Lake Balaton (Zankai and Ponyi 1970). The remaining three species in group A - Asplanchna priodonta, Conochilus hippocrepis and Gastropus stylifer did not occur in winter. Carlin (1943) classified A. priodonta as a perennial species which may disappear almost completely for a few weeks in July. This species was not perennial in Grasmere, but there was a similar absence in July after the sexual phase in May and June. G. stylifer occurred from spring to autumn with maximum numbers in May and June in Grasmere. This species was a perennial in Stechlinsee (Koch-Althaus 1963) but in Motalaström (Carlin 1943) and in Paradise Lake (George and Fernando 1969), it only occurred in summer with maximum numbers in June and July.

The six species in group B (Table 7) occurred chiefly in spring and early summer with maximum numbers in April, May or June but there was a second maximum in August and September for two species (Synchaeta stylata, S. oblonga). Carlin (1943) classified Polyarthra dolichoptera as a winter and early spring species in Motalaström. Although this species was absent in winter in Grasmere, its maximum numbers also occurred in early spring. Conochilus unicornis is also in this group, and therefore its occurrence in Grasmere agrees with the records of some other workers (Ahlstrom 1933, Chandler 1940, Davis 1969, George and Fernando 1969, Larsson 1971), but not with those who have classified this species as a perennial form (Carlin 1943, Nauwerck 1963, Granberg 1970). The maximum numbers of Synchaeta tremula and S. pectinata occurred in April and May in Grasmere. S. tremula was classed as a summer form by Carlin (1943), Pejler (1957c) and Larsson (1971), but Carlin found several peaks between June and September. S. pectinata reached maximum numbers in May in Paradise Lake (George and

Fernando 1969), but not until August and September in Motalaström (Carlin 1943). Numbers of the two remaining Synchaeta spp. in group B were also at a maximum in April and May, but reached a second peak in August and September. Both species are classified as summer species by Carlin (1943), but he found that S. oblonga had several maxima between May and October with almost complete disappearance of this species between peaks, and that S. stylata was almost entirely confined to late summer with maximum numbers in August.

The species in group C occurred from summer to autumn. Polyarthra vulgaris has been classified as a perennial form with maximum abundance in late spring and early summer (Carlin 1943), or in summer to autumn (Nipkov 1952, Larsson 1971), or in both spring and autumn (George and Fernando 1969). In Grasmere this species was most abundant from mid-July to mid-September, and no spring or early summer peak was observed. The seasonal occurrences of P. major in Grasmere and Motalaström (Carlin 1943) were similar. Synchaeta grandis was a summer form with maximum numbers in May and June in Motalaström (Carlin 1943), but the occurrence and maximum numbers of this species were later in Grasmere. Filinia terminalis is usually regarded as a winter and early spring species with maximum numbers in spring (Carlin 1943, Larsson 1971). George and Fernando (1969) found a similar seasonal pattern in the shallow Paradise Lake (6m) but in the deeper Sunfish Lake (19m), large numbers were present in the hypolimnion in summer. When F. terminalis occurred in fairly high numbers in Grasmere, it was abundant from August to November, but only in the hypolimnion. Ploesoma hudsoni was never abundant in Grasmere but its numbers increased slightly from late August to mid-

September. This species was a seasonal summer species in Motalaström with maximum numbers usually in June and July (Carlin 1943), and therefore slightly earlier than in Grasmere.

Nearly all the species in Grasmere were most abundant in the upper stratum (Table 7). The two exceptions, with greatest numbers in the lowest stratum, were Keratella quadrata and Filinia terminalis. Numbers of the Trichocerca spp. in group C and the rare species in group D were too low to show any definite vertical distribution. The vertical distributions of the remaining species are in general agreement with the results of other workers (Campbell 1941, Berzins 1958, Pejler 1961, George and Fernando 1969, Larsson 1971, Klimowicz 1972). As vertical distribution is most pronounced during stratification, most workers have assumed that it is chiefly due to the different environmental requirements of each species. However, some species in Grasmere (e.g. Keratella quadrata, K. cochlearis, Conochilus spp., Asplanchna priodonta, Synchaeta spp., Polyarthra dolichoptera) showed a definite vertical distribution pattern when the lake was unstratified and temperature and oxygen conditions were nearly uniform. This vertical distribution of species before stratification was most marked in 1972 when the start of stratification was later than in other years. These results support the earlier observation of Ruttner-Kolisko (1972) who found that Asplanchna priodonta, Keratella cochlearis, K. quadrata and Filinia terminalis showed a definite pattern of vertical distribution in Windermere when the lake was unstratified in April. She concluded that these distributions could only be due to an active vertical movement corresponding to the light gradient, and it is remarkable that the patterns of vertical distribution were very close to those observed during the period of stratification.

Although each species occurs over a wide range of some environmental factors (e.g. ranges of temperature and oxygen in Table 6), each species is usually most abundant within a fairly narrow range of each environmental factor. No evidence was available from the results of the present study to suggest any correlation between pH and the abundance of each species, and no information is available for other chemical factors. Although several workers have reported definite pH ranges for different species (Tauson 1926, Myers 1937, Ahlstrom 1940, Russell 1949, Galliford 1954), Pejler (1957c) doubted the importance, within rather wide limits, of either pH or total ionic concentration, and he produced evidence which suggests that the apparent correlations are chiefly due to different levels of production rather than variations in water chemistry. In an extensive study of the effects of several environmental factors on the distribution of rotifers, Pourriot (1965a) found that most planktonic species from large lakes occurred at pH values greater than 5.8, and pH values in Grasmere rarely fell below this value.

The most abundant species in Grasmere occurred over a wide range of oxygen and temperature (Table 6). It is remarkable that the following species occurred at oxygen concentrations close to zero: Kellicottia longispina, Keratella cochlearis, K. quadrata, Gastropus stylifer, Synchaeta oblonga, S. pectinata, S. stylata, S. tremula, Polyarthra vulgaris, Filinia terminalis, Trichocerca capucina. Pejler (1957b), Pourriot (1965a) and Larsson (1971) also found that rotifers can tolerate extremely low oxygen concentrations and Beadle (1963) found two species of rotifers in the anaerobic environment of a permanently stratified tropical crater lake. Polyarthra dolichoptera and Filinia terminalis are usually regarded as cold water stenotherms, but were found at fairly high temperatures in Grasmere (Table 6) and have been recorded at high temperatures by other workers (Edmondson and Hutchinson 1934, Thomasson 1955b, Pejler 1961, Pourriot 1965a).

In contrast to their occurrence within wide limits of temperature and oxygen, most species were most abundant within narrow ranges of temperature and oxygen concentration (see summary of ranges in Table 7). Only two species, Keratella cochlearis and Kellicottia longispina, were abundant within a fairly wide range of temperature and oxygen concentration. Other workers have found that these species are abundant over a wide range of temperature (Wesenberg-Lund 1930, Carlin 1943, Pourriot 1965a, Larsson 1971) and oxygen concentration (Larsson 1971), but K. cochlearis was found to be a cold water stenotherm by George and Fernando (1969), and K. longispina was found only in the hypolimnion between 5-10^{o}C by Yamamoto (1959). Synchaeta spp. were abundant only at oxygen concentrations greater than 90% saturation but at temperatures within a wide range from 6.5-18.5^{o}C. S. pectinata has been found to be most abundant at low temperatures by some workers (Wesenberg-Lund 1930, Ruttner 1937, Pourriot 1965a, Ruttner-Kolisko 1972), but other workers consider this species to be a eurytherm (Carlin 1943, Pennak 1949, Pejler 1957c). S. tremula and S. oblonga are usually most abundant at low temperatures (Wesenberg-Lund 1930, Pawlowski 1958, Pourriot 1965a) and have even been considered cold water stenotherms (Pejler 1957c, Nauwerck 1963). These different optima may explain the apparently wide range of temperature within which Synchaeta spp. occurred in Grasmere.

If abundance rather than occurrence is considered, Keratella quadrata and Filinia terminalis are clearly cold water stenotherms which are most abundant in the hypolimnion. These observations agree with those of earlier workers for F. terminalis (Slonimski 1926, Carlin 1943, Pourriot 1965a, Larsson 1971, Ruttner-Kolisko 1972), and for K. quadrata (Beach 1960, Koch-Althaus 1963, George and Fernando 1969). Although both species were abundant at low temperatures, only F. terminalis was abundant at low oxygen concentrations whereas K. quadrata was only abundant at oxygen concentrations above 80% saturation. George and Fernando (1969) found that K. quadrata could not tolerate the oxygen deficiency in the hypolimnion towards the end of the period of thermal stratification, but this species was found in small numbers at low oxygen concentrations in Grasmere.

Asplanchna priodonta was most abundant at high oxygen concentrations and at temperatures which were neither high nor low in Grasmere, but Pourriot (1965a) considers this species to be a eurytherm.

The remaining species (Gastropus stylifer, Conochilus spp., Polyarthra spp.) were most abundant at high oxygen concentrations and fairly high temperatures. There is little information in the literature on G. stylifer but Pourriot (1965a) classifies this species as a warm water stenotherm. Hubault (1947) and Larsson (1971) also found that C. unicornis was most abundant at high oxygen concentrations and high temperatures, and Pourriot (1965a) classified C. hippocrepis as a warm water form. P. dolichoptera is usually considered to be a cold water stenotherm (Nauwerck 1963, Pourriot 1965a, Ruttner-Kolisko 1972). Although no ranges can be given for this species in Grasmere, it was most abundant in spring and early summer when temperatures were fairly low and oxygen concentrations were high. Carlin (1943) notes that this species disappears at temperatures between 15°C and 18°C, but Pourriot (1965a) found large populations at 17°C in June and at 21°C in August. Pourriot (1965a) classifies P. major as a warm water stenotherm and P. vulgaris as a warm water form. Carlin (1943) found that the latter species reached its maximum numbers between 15°C and 20°C. These results are in agreement with those of the present study, but Ruttner-Kolisko (1972) considers that both species are eurytherms in water with a high oxygen concentration and Larsson (1971) found that P. vulgaris/major was most abundant at low temperatures between 0°C and 4°C.

Pourriot (1965a) notes that in larger lakes, the distribution of rotifers in relation to temperature is less marked than in small bodies of water. He also notes that the contradictory results of some workers probably indicates that factors other than temperature and oxygen concentration affect the distribution and abundance of rotifers. One major factor is the availability of suitable food for each species, and this factor is clearly important in considering the differences in abundance between years in Grasmere.

The major changes in abundance occurred between 1971 and 1972. Four species increased and twelve species decreased in abundance (Table 7). All the twelve latter species attained their highest densities within a narrow range of oxygen concentration. Their reduced numbers may therefore be partially correlated with the lower oxygen concentrations in all except the upper stratum in 1972. Although all these species except Synchaeta spp. were also abundant within a fairly narrow range of temperature, there was no marked difference between the temperature ranges in 1971 and 1972. The only species which did not decrease or increase markedly in numbers between 1971 and 1972 was K. cochlearis and one species which increased was Kellicottia longispina. As these were the only two species which attained their highest densities over a wide range of temperature and oxygen concentration, they were probably least affected by the marked decrease in oxygen concentration from 1971 to 1972. The wide optimum ranges of temperature and oxygen concentration for these species may also explain their seasonal abundance over a long period. Another species which increased in abundance from 1971 to 1972 was Asplanchna priodonta. Although this species was most abundant within a fairly narrow range of temperature and oxygen concentration, it reached its maximum abundance before the lake was stratified and was therefore unaffected by the marked decrease in oxygen concentration from 1971 to 1972. There was no obvious reason for the marked increase in numbers of Conochilus unicornis from 1971 to 1972. Filinia terminalis was the fourth species which increased from 1971 to 1972. This species and K. quadrata were the only species which were most abundant at low temperatures in the lowest stratum, but F. terminalis was the only species which was abundant at low oxygen concentrations. Therefore this species was probably unaffected by the marked decrease in oxygen concentration from 1971 to 1972.

Although the decrease in oxygen concentration may partially explain these marked changes in abundance from 1971 to 1972, changes in the availability and abundance of food must also have been important. The new sewage works started to operate in June 1971, and the treated effluent contributes some enrichment to the lake. This enrichment has probably affected the trophic status of the lake, but it would be unwise to make any definite conclusions from only one comparison between years. However, it is interesting to consider the opinions of other workers on the role of rotifers as indicators of trophic conditions.

Pejler (1957c, 1965) places S. grandis and Ploesoma hudsoni amongst the species which avoid highly productive lakes. Therefore, as a lake changes from oligotrophic to eutrophic, these species may decrease in abundance or virtually disappear as apparently occurred in Grasmere. One possible reason for the absence of these species from more productive waters is that an abundance of non-edible algae is an obstacle to these carnivorous species when they are hunting and catching their prey (Pejler 1965). Pejler (1957c, 1965) also notes that Kellicottia longispina, Polyarthra vulgaris and Conochilus unicornis are usually conspicuous in oligotrophic waters, and Pourriot (1965a) notes that K. longispina, P. hudsoni and C. hippocrepis avoid highly productive waters. These species would therefore be expected to decrease in abundance with eutrophication and this occurred for P. vulgaris, C. hippocrepis, P. hudsoni, but not for K. longispina and C. unicornis in Grasmere. Ruttner-Kolisko (1972) records the following species as typical of oligotrophic lakes: Synchaeta oblonga, S. tremula, S. pectinata, Polyarthra (vulgaris-dolichoptera group), Keratella cochlearis, C. unicornis, K. longispina, Asplanchna priodonta and Filinia terminalis; but notes that some of these species may occur in greater numbers in eutrophic lakes together with Euchlanis dilitata, Trichocerca spp., Pompholyx sulcata, K. quadrata, Filinia (longiseta-limnetica group). All the "oligotrophic" species were present in Grasmere, but only K. quadrata of the "eutrophic" species was fairly common in Grasmere, Trichocerca spp. and Euchlanis dilitata were rare and the other two species were never found. Pejler (1962b) considers that Brachionus spp., Polyarthra *euryptera* and *Anuraeopsis fissa* are also typical of eutrophic waters but none of these species was recorded in Grasmere. The *tecta* form of *K. cochlearis* is regarded by Pejler (1962b) as an excellent indicator of eutrophy and was found for the first time in Grasmere in the summer of 1973.

A marked increase in total numbers of rotifers also occurred from 1971 to 1972 in Grasmere, and this increase was also probably due to the enrichment of the lake with an increased food supply of phytoplankton and planktonic bacteria. The importance of planktonic bacteria as a food supply must not be underestimated. Olah (1969) and Zankai and Ponyi (1970) found that a quantitative increase in planktonic bacteria was closely followed by an increase in the rotifer population of Lake Balaton, and Pourriot (1965a) found that several species utilised bacteria as a source of food.

Therefore some of the changes in the abundance of different species in Grasmere apparently indicate an evolution towards more eutrophic conditions, but the information on indicator species is limited and often contradictory. There is clearly a need for a long-term study on the rotifer population of Grasmere, and also on the allied problem of the relationship between the abundance of each species and its food supply.

SECTION 6

SUMMARY

6. Summary

1. The planktonic rotifers of Grasmere, a small lake in the English Lake District, were studied from August 1969 to December 1972. Weekly or fortnightly samples were taken with a closing net which was hauled vertically over five metres and thus provided samples from strata of 0-5m, 5-10m, 10-15m, 15-20m.

2. Twenty-four planktonic species were recorded from Grasmere but the following species were very rare: Collotheca mutabilis, Euchlanis dilitata, Ascomorpha saltans, A. ecaudis and Trichocerca pusilla. The remaining species were divided into three groups according to their seasonal occurrence: spring-autumn species, Keratella quadrata, K. cochlearis, Kellicottia longispina, Gastropus stylifer, Asplanchna priodonta and Conochilus hippocrepis; spring-early summer species, Polyarthra dolichoptera, Synchaeta tremula, S. pectinata, S. stylata, S. oblonga and Conochilus unicornis; summer-autumn species, Polyarthra vulgaris, P. major, Filinia terminalis, Synchaeta grandis, Ploesoma hudsoni, Trichocerca capucina and T. similis. The months in which each species was abundant are given.

3. K. cochlearis, G. stylifer, A. priodonta, P. hudsoni, Synchaeta spp., Polyarthra spp. were usually most abundant in the upper stratum, K. quadrata and F. terminalis were most abundant in the deepest stratum, Kellicottia longispina and the two Conochilus spp. were most abundant in the upper and middle strata, and Trichocerca spp. showed no pronounced vertical distribution.

4. The most abundant species attained their highest densities over either a wide range of temperature and oxygen concentration, K. cochlearis, K. longispina, Synchaeta spp. (temperature only),

or a narrow range of temperature and oxygen concentration, F. terminalis, Conochilus spp., A. priodonta, K. quadrata, Polyarthra spp., Synchaeta spp. (oxygen concentration only). Optimum ranges for temperature and oxygen concentration are given for each species.

5. Major changes in abundance occurred between 1971 and 1972. A. priodonta, K. longispina, C. unicornis and F. terminalis increased in abundance, the numbers of K. cochlearis remained fairly constant, and K. quadrata, G. stylifer, C. hippocrepis, Polyarthra spp., Synchaeta spp. and P. hudsoni decreased in abundance. The various reasons for these changes are discussed, especially in relation to the temperature and oxygen requirements of each species and also in relation to the probable enrichment of the lake after the opening of a new sewage works in June 1971.

6. It is concluded that there is a need for a long-term study on the rotifer population of Grasmere and also on the relationship between the abundance of each species and its food supply.

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SECTION 7

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APPENDIX TABLES 1 and 2.

Appendix Table 1.

Year	1969						1970											1971				1972				
Month	August			Sept		O	Ap	Jl	August			Sept		O	Nov			My	Jn	Ag	S	Jn	Jl	S	Oct	
Date	12	19	26	2	30	21	28	7	11	18	25	2	15	6	9	16	23	24	7	17	6	20	25	5	3	24
0-5m																										
Euchlanis dilitata																										3
Trichocerca similis	35	4	3		3																	3				
T. pusilla	50	80	21																							
Ascomorpha saltans	2	2																	3							3
Collotheca mutabilis								3							1				3					27		
Total	87	86	24		3			3							1				6			3		27		6
5-10m																										
Euchlanis dilitata			3																							
Trichocerca pusilla	26	30	15						1			2														
Ascomorpha saltans	5																									
A ecaudis							1																			
Ploesoma hudsoni						9				3	6		12	3		1										
Collotheca mutabilis	1			1														3						3		
Total	32	30	18	1		9	1		1	3	6	2	12	3		1		3						3		

Appendix Table 1 cont.

Year	1969						1970											1971				1972				
Month	August			Sept		O	Al	Jy	August			Sept		O	Nov		My	My	Jn	Ag	S	Jn	Jy	S	Oct	
Date	12	19	26	2	30	21	28	7	11	18	25	2	15	6	9	16	23	24	7	17	6	20	25	5	3	24
10-15m																										
Trichocerca pusilla		6																								
Ascomorpha saltans																										6
A. ecaudis							3																			
Ploesoma hudsoni											12			1		5	3				3					
Collotheca mutabilis																								9		
Total		6					3				12			1		5	3				3			9		6
15-20m																										
Euchlanis dilitata		6																								
Trichocerca capucina																				9	7		9	9	1	
Ascomorpha saltans		6																		10	3					
Trichocerca pusilla	1																									
Ascomorpha ecaudis							3																			
Ploesoma hudsoni					3						6		3	3		3										
Collotheca mutabilis																						3		3		
Total	1	12			3		3				6		3	3		3				19	10	3	9	12	1	

Appendix Table 2. Abbreviations of species and genera.

Kc = *Keratella cochlearis*

Kq = *K. quadrata*

Kl = *Kellicottia longispina*

Tc = *Trichocerca capucina*

Ts = *T. similis*

Gs = *Gastropus stylifer*

Ap = *Asplanchna priodonta*

P = *Polyarthra* spp.

S = *Synchaeta* spp.

Ph = *Ploesoma hudsoni*

Ft = *Filinia terminalis*

Cu = *Conochilus unicornis*

Ch = *C. hippocrepis*

OS = Other species

T = Total

Appendix Table 2.

Year	1969											
Month	August			September					October			
Date	12	19	26	2	9	16	23	30	7	14	21	28
0-5m												
Kc	3610	560	219	118	84	117	117	12	45	63	63	36
Kq				3		1		3				3
Kl	145	100	9	6	33	36	36		18	36	21	27
Tc												
Gs	385	290	78	24					3		6	
Ap	220	32	32	4		1						
P	1215	200	39	39	18	112	54	6	12			
S	500	70	30	150	123	75	12			15	39	27
Ph											3	
Ft	20	1		3				3				
Cu											3	
Ch	73	4										
OS	87	86	24					3				
T	6255	1343	431	347	258	342	219	27	78	114	135	93
5-10m												
Kc	919	515	390	69	30	54	195	30	33	30	42	33
Kq			10		3	1			3	3	1	9
Kl	20	5	10			30	45	3	18	21	54	45
Tc												
Ts	149	65	55			1						
Gs	254	110	20	36						3	9	
Ap	90	130	90									
P	146	115	10	12	3	12	69	12		6	3	
S	20	5	30	48	12		3	1	6		18	
Ft	4				6		18	3	3			
Cu											7	9
Ch	9	17					3		3	1	1	1
OS	32	30	18	1							9	
T	1543	992	633	166	54	98	333	49	66	64	144	97

Appendix Table 2. cont.

Year	1969							1970											
Month	November				December			Jy	March					April				May	
Date	5	11	18	25	2	9	16	20	3	10	17	24	31	7	14	21	28	5	12
0-5m																			
Kc	9	9	24	3	8	9	12												6
Kq	3		3							1				19				5	9
Kl	3			6	2	1	3								2				6
Tc																			
Gs															=			3	
Ap	1									1	1		2	5	1		8	3	140
P	3													3	3		6	15	9
S	7										4		4	12	13	33	87	123	468
Ph																			
Ft		3	6		6														
Cu		1	2	2															
Ch																			
OS																			
T	26	13	35	11	16	10	15	0	0	2	5	0	7	40	19	33	101	156	638
5-10m																			
Kc	15	9	15	6	33	3				3	3								
Kq	3	1								3	1	3	3	15	4	9	3	45	111
Kl	3	12	9	3	3	3			1					3	1	3		6	6
Tc																			
Ts																			
Gs	3																	3	
Ap														3	4		5	2	40
P	3													6	3	3	8	15	18
S	6									1	1	12	9	12	15	27	57	36	111
Ft	3	3	6	3	3	3													
Cu	2	4	6	2	2	1	3					1	1					2	11
Ch														1					
OS																	1		
T	38	29	36	14	41	10	3	0	1	7	2	19	13	40	27	42	74	109	297

Appendix Table 2. cont.
0-5m
Year 1970

Month	May		June					July				August			
Date	19	26	2	9	16	23	30	7	14	21	28	4	11	18	25
Kc	6	5	40	6	9	3	3		9	9	48	3	15	21	24
Kq		10													
Kl		30	55	42	69	324	225	201	264	123	42	48	135	15	96
Tc															
Gs	12	1135	425	6	6	3	9	3	3	3		3			27
Ap	547	83	85			6							9	1	21
P			20			3	24	18	75	60	210	3			
S	159	10	5				9	3	1	6	105	3	3	6	203
Ph															6
Ft															
Cu	98	7	22	9	15			3				22			
Ch												45	337		10
OS								3							
T	822	280	652	63	99	339	270	231	352	201	405	127	499	43	390

5-10m

Kc	3		5	6		6	3		3	3	15	3	18	24	9
Kq	45	3	5	1											
Kl	3	10	15	18	57	45	101	150	180	105	294	183	81	198	33
Tc															
Ts			5												
Gs	9	80	75	96	6	3	9	3	9			6			15
Ap	118	65	12	6										12	3
P	3	5	1			3	9	27	33	33	144	6			3
S	24	10						3			30			9	48
Ft															
Cu	35	30	50	30	8			3				28			
Ch		10	6	13	1		15	21	6	234	285	50	212	574	90
OS													1	3	6
T	240	213	174	170	72	57	137	207	231	375	768	376	312	820	207

Appendix Table 2. cont.

Year	1970													
Month	September					October				November				Dec.
Date	2	8	15	22	29	6	13	21	26	2	9	16	23	7
0-5m														
Kc	210	225	384	102	156	96	102	170	9	141	48	54	15	3
Kq								3	3					
Kl	66	72	21	39	180	9	15	33	12	21	3	9	10	
Tc														
Gs	54	60	36	9	39	6	24	36	12	2		6		
Ap	36	6			3	3	12	3	1	14		1		
P	12	18	41	3		9	3	6	9	3				
S	342	159	228	27	30	300	9		3	15				
Ph	9	4	33				1			1	1			
Ft												6		
Cu							6				1			
Ch	177						9	2		1		2	1	
OS											1			
T	906	544	743	180	408	423	181	253	49	198	54	78	26	3
5-10m														
Kc	51	132	138	69	39	24	261	150	60	45	99	36	42	6
Kq														
Kl	270	99	81	21	27	27	36	12	9	15	15	6	9	3
Tc														
Ts			5											
Gs	15	30	12	3	3	6	36	45	6	12		6	3	
Ap		6				3	3	3		10		3		
P		12	9	3	3	55	12	12		3				
S	48	48	57	15		469	6		3	3				
Ft										3	3	6		6
Cu					3									
Ch	146	105	47	11		2		5		6		8	4	
OS	2		12			3						1		
T	532	432	361	122	75	589	354	227	78	97	117	66	58	15

Appendix Table 2. cont.

Year 1971

Month	March			Apl.	May			June		Jly.	August		Sept.		Oct.	Nov.	
Date	2	16	30	19	3	17	24	7	21	21	2	17	6	20	4	15	28
0-5m																	
Kc				12	264	261	300	24	60	21	90	171	477	69	57	12	36
Kq				9			3		6								
Kl				15	15	216	153	18	90	60	51	12	66	51	12	3	6
Tc											9	6	3				
Gs					51	99	66	9	3						24	3	3
Ap				48	290	374	319		3		6	59	41				
P				48			75		6	24	69	123	48	6			
S				369			225			45	93	108			3		
Ph				1	3		3					3					
Ft																	
Cu				3													
Ch										2	15		3	97			36
OS								6									
T	0	0	0	505	623	950	1144	57	168	152	333	482	638	223	96	18	81
5-10m																	
Kc	3	3	1	9	18	129	174	69	33	45	138	69	126	285	7	30	21
Kq		3		3	21								3				
Kl				21	60	204	546	18	51	72	465	138	78	48		3	3
Tc											12	15	15				
Ts									6								
Gs				3		15	174	6	9							9	
Ap				41	25	444	183		3			72	29				
P				39			6	3	6	15	63	33	15				
S			3	369			9			3	57	36					
Ft																	
Cu		6		45													
Ch						4	3		2		13	132	18	27			
OS							3										
T	3	12	4	530	124	796	1098	96	110	135	748	495	284	360	7	42	24

Appendix Table 2. cont.

Year 1972

Month	Mch.	April			May				June				July		
Date	28	4	18	25	8	16	23	30	6	13	20	27	4	11	18
0-5m															
Kc			6	30	57	153	243	186	318	264	96	36	18	21	63
Kq	<1		1		6	6			3						
Kl			3	60	78	321	489	573	153	519	159	408	246	132	142
Tc												12			
Gs				3	3	18	6			3					
Ap	<1		21	256	1843	1446	7226	660	687	40	15	3	2		
P	<1		12	99	45	3	6	18		6	6	24	12	12	9
S	<1	2	11	294	60	39	18	99	6		6	6	18	12	9
Ph															
Ft													6		
Cu															
Ch			2	4	48	50	49	17	7	6	6	3	2	2	5
OS											3				
T		2	56	746	2140	2036	8037	1553	1174	838	291	492	304	179	228
5-10m															
Kc			6	9	24	48	228	306	111	111	33	39	36	24	30
Kq	<1		2	9	3	3									
Kl			12	39	87	216	551	435	270	249	327	318	231	150	53
Tc															
Ts								3					3		
Gs					12	6	12	3	3						
Ap	<1		29	38	601	2206	1248	1971	251	14			1		
P	<1		14	15	224	3		3				3	6	6	9
S	<1		47	135	12	33	9	21					3	3	4
Ft															
Cu															
Ch			10	8	31	46	129	44	9	5	7	6	4	1	2
OS															
T		0	120	253	794	2561	2177	2786	644	379	367	366	284	184	98

Appendix Table 2. cont

Year 1972

Month	Jly	Aug	September				October					November				December		
Date	25	1	5	12	19	26	3	10	17	24	31	7	14	21	27	4	11	18
0-5m																		
Kc	18	9	189	36	90	87	89	104	139	110	98	57	9	9	15			1
Kq																		
Kl	240	165	15	51	75	168	150	288	116	85	74	30	24	21	12	18	3	
Tc	3	3	9	6	3	12		3										
Gs	6							9	9	6	18	6						
Ap																		
P	12			15	3				3	3	1					1		
S	9		18	39	6	5	5	17	18		6	6	6					
Ph																		
Ft							1					6	6	18	15	12	1	
Cu	42	94																
Ch	60	102	1															
OS			27							6								
T	390	373	259	147	177	267	245	411	285	210	197	105	45	48	42	31	4	1
5-10m																		
Kc	3	3	6	18	75	66	49	168	78	58	39	72	9	15	6			
Kq																		
Kl	63	18	87	45	33	93	123	95	54	33	63	90	54	39	10	12	11	1
Tc	3	3	6	6	9		3	3	3									
Ts																		
Gs									9	3	15	12	3	3			1	1
Ap																		
P	6			3	3										1			
S	15		6	27	12	3	5	9	6		1	3						
Ft						6	6	9	15			6	57	39	15		16	
Cu	26	33																
Ch	44	70	2	1														
OS			3															
T	160	127	110	100	132	168	186	284	165	94	118	183	123	96	32	12	28	2

Appendix Table 2. cont.

Year 1969

Month	August			September					October				November			
Date	12	19	26	2	9	16	23	30	7	14	21	28	5	11	18	25
10-15m																
Kc	67	213	66	93	12	18	39	24	18	9	6	6	12	3	12	6
Kq						6	3		3			3				
Kl				3			15	30	3	24	9	3	18	21	3	3
Tc																
Ts	2	9														
Gs	13	108	9	21	3											
Ap	7	28	15		7	1										
P	13	30	9	6	3	33	9	3	3	6						3
S	2	5	6	96	6	6				3						
Ft	1	27	18		12	3	15	6	222	3	9	3	9			
Cu												4	21	4	5	4
Ch	1	5	1			1									1	
OS		6														
T	172	431	124	219	43	68	81	63	249	45	24	19	60	28	21	16

15-20m																
Kc	185	54	24	72	15	24	21	15	6	9	18		24	9	3	6
Kq	9	3	42	3	6	15	21	3		6	207	57	21		3	
Kl	2			15	6	6	3	15	3	9	3	6	15	15	12	15
Ts	9	15	3			1										
Gs	100	12	6	51												
Ap	16	6	8													
P	22	3		3		6	6									
S		3		9	3	21										
Ft	149	12	951	53	495	1008	195	66	18	96	639	180	81		24	3
Cu												2	4	13	26	5
Ch	6													4		
OS	1	12						3								
T	499	120	1034	206	525	1081	246	102	27	120	867	245	145	41	68	29

Appendix Table 2. cont.

Year	1969			1970															
Month	December			Jn	March					April				May				June	
Date	2	9	16	20	3	10	17	24	31	7	14	21	28	5	12	19	26	2	9
10-15m																			
Kc		3			6	3							3		6			25	
Kq		1			3	3	7	3	6	9	13	42	21	63	471	69	120	20	
Kl		1				3			1	3	4	3			12		10	5	3
Tc																			
Ts																		10	
Gs																6	30	10	54
Ap							1				1		1	2	6	50	13		
P										3	3	3	3	21	12	3	10		
S						2	1	1	15	15	12	18	42	48	156	24	8		
Ft																			
Cu		1	1						1	1			2	2	5	11	2	8	20
Ch										1								4	
OS													3						
T	0	6	1	00	9	11	9	4	23	32	33	66	75	136	668	163	193	82	77
15-20m																			
Kc	2	3		3			1				3					3		6	18
Kq	10			6	3	6	7	15	5	12	6	78	60	255	102	66	155	45	1
Kl	1	2		18										3				6	3
Ts																			
Gs																12	20	10	36
Ap															1	1	11	15	
P		1								3			3	3	15		6		
S									18	18	60	18	1	15	87	12	7		
Ft		3															10		
Cu		1	1	4					1					1			3		21
Ch																			
OS													3						
T	3	11	1	31	3	6	8	15	24	33	69	96	67	277	205	94	212	82	79

Appendix Table 2. cont.

Year 1970																		
Month	June			July				August				September					October	
Date	16	23	30	7	14	21	28	4	11	18	25	2	8	15	22	29	6	13
10-15m																		
Kc					6	3	15	3	6	15	18	51	36	63	27	18	24	60
Kq	9	18																
Kl		279	81	123	66	33	87	45	51	42	45	129	57	96	24	6	6	96
Tc																		
Ts									3					3		3		
Gs	72	90	9	3	9		6				6	6	6	6	3	3		9
Ap										1	9	3					1	
P			3	3	6	9	39	3				3	9	12			33	3
S							1				63	21	12	12	3	3	242	3
Ft																		
Cu	2							7							4			
Ch					3	24	21	12	38	109	34	79	35	20	8	2		2
OS											12						1	
T	83	387	93	129	90	69	169	70	98	167	187	292	155	212	69	35	307	173
15-20m																		
Kc	3	9			12	3	6	3	3	9	9	9	30	78	21	30		33
Kq	6				3						3			9	3	3		21
Kl	18	180	54	6	24	21	30	33	27	18	51	21	39	66	24	27	9	18
Ts														6		3		6
Gs	54	15	9	6	6							9	9	9		9	6	21
Ap											12						3	
P		9	21	6	9	9	24						3	9		3	33	
S									3		81	15	12	36		6		
Ft														18				66
Cu	20																	
Ch	4					9	21	2	26	22	27	18	19	17		1		1
OS											6			3			3	
T	105	213	84	18	54	42	81	38	59	49	189	72	112	251	48	82	54	166

Appendix Table 2. cont.

Year	1970							1971									
Month	Oct		November				D	March			A	May			June		J
Date	21	26	2	9	16	23	7	2	16	30	19	3	17	24	7	21	21
10-15m																	
Kc	189	432	69	45	45	45	6		3		3	27	84	84	87	96	45
Kq	9				3					1	27	246					
Kl	39	30	21	18	15	6					2	18	48	105	24	33	21
Tc																	3
Ts																	
Gs	36	24			3							12	24	63	111	30	15
Ap	9	8		4	3	3					12	30	45	19			
P	9	18	3								4			45		3	6
S		9									138			9			3
Ft	3	3			18												
Cu			2						1		9						
Ch	5	17	4		8	1	3						6				
OS					5	3											
T	299	541	99	67	100	58	6	3	4	1	195	333	207	325	222	162	93
15-20m																	
Kc	147	204	99	46	21	21	3		3		3	27	60	54	60	12	24
Kq	6	3	6						3	6	126	153	33	24	12		
Kl	36	70	36	16	21	3	3				3	9	9	63	15	9	
Ts																	
Gs	36	3		4	3							18	12	54	30	21	
Ap	3	10									3	5	18	5			
P	3	6									9	9	6	15			3
S									6	3	162			3			12
Ft	21	63	33		15												3
Cu		5	3								2	1					
Ch		8	10	10	1		2			1							
OS						3											
T	252	372	187	76	61	27	8	0	12	10	308	222	138	218	117	42	42

Appendix Table 2. cont

Year	1971							1972									
Month	August		Sept		O	Nov		M	April			May				June	
Date	2	17	6	20	4	15	28	28	4	18	25	8	16	23	30	6	13
10-15m																	
Kc	60	20	3	90	7	27	24			2	9	30	96	131	228	219	81
Kq			3					<1	1	10	6			9			
Kl	39	16	21	30			6		1	12	6	21	132	162	357	360	57
Tc			9	3													
Ts																	
Gs	3	3	75			9							12	15	3		
Ap		2	4					<1			20	560	1074	378	1545	106	2
P	6	3	9	3			3	<1		10	15				6		3
S								<1		16	54	24	24	24	18	3	
Ft																	
Cu				19							9	20	39	56	88	8	3
Ch	7	29	9							10							
OS			3														
T	115	73	136	145	7	36	33		2	60	119	655	1377	775	2245	696	149
15-20m																	
Kc	33	54	30	28	18	45	36		1		6	12	36	213	141	108	66
Kq	3		6		15	6		<1			54	6	12	24	3		
Kl	30	36	12	9		15	3			1	18	24	60	60	1050	213	234
Ts														3			3
Gs					3	3							3	6			
Ap								<1			74	384	729	178	1108	32	3
P	12	30	9	3				<1		3	33	6	3		3		3
S	9	18						<1		6	84	12	24	12	12		
Ft																	
Cu				2			1		1	2	1	14	12	43	83	6	5
Ch	2	9															
OS		19	10														
T	89	166	67	42	36	69	40		2	12	270	458	879	539	2400	359	314

Appendix Table 2. cont.

Year 1972

Month	June		July				A	September				October					Nov.	
Date	20	27	4	11	18	25	1	5	12	19	26	3	10	17	24	31	7	14
10-15m																		
Kc	33	9	9	15	9	6	9	3	12	51	21	46	114	75	36	111	33	12
Kq									6				3					
Kl	111	63	30	33	21	18	9	25		27	15	77	48	24	37	63	30	36
Tc						9	3	3	6	6		2						
Ts	3		3															
Gs												1	1	3	6	27	6	3
Ap																		
P		6	6	3	3				3			3	6		3	3		3
S				6		3		3	9	9		1	3					
Ft						3			39	12	12		10	6		12	3	24
Cu	1	3	1		1	3	3											
Ch						4			3									
OS								9							6			
T	148	81	49	57	34	46	24	43	78	105	48	130	185	108	88	216	72	78

15-20m	20	27	4	11	18	25	1	5	12	19	26	3	10	17	24	31	7	14
Kc	33	12	21	15	6	6	3	3	9	21	9	35	129	99	51	101	54	6
Kq	3					6			3							3		
Kl	72	39	36	18	10	12	12	9	9	57	3	23	90	21	37	180	21	72
Ts									9	3								
Gs													6	6	6	21	9	
Ap																		
P		6	3	6	3				6	9	3	1	3	3		6		
S	3					3			12	3		2	6	3		3		
Ft			6				3		12	6		15	3	3		69	27	9
Cu	2						5											
Ch																		
OS	3					9		12				1						
T	116	57	66	39	19	36	23	24	60	96	15	77	237	135	94	174	111	87

Appendix Table 2. cont

Year	1972				
Month	Nov.		December		
Date	21	27	4	11	18
10-15m					
Kc	3	3			
Kq					
Kl	42	9	4	6	2
Tc					
Ts					
Gs	3				
Ap					
P					
S					
Ft	18	9	4	9	
Cu					
Ch					
OS					
T	66	21	8	15	2
15-20m					
Kc	15		1		
Kq					
Kl	24	3	9	9	8
Ts					
Gs					
Ap					
P					
S					
Ft	18	6	9		
Cu					
Ch					
OS					
T	57	9	19	9	8