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The role of aquatic macrophytes in the availability of food for young fish.

by

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ABSTRACT

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Quantitative samples from a gravel-pit lake in 1977 (April-December) showed higher geometric mean densities and biomasses of microcrustacea in the marginal weedbeds (907/l and 3107ug/l) than in the open water (225/l and 245ug/l). The weedbeds were dominated by Cyclops vernalis americanus and Ceriodaphnia pulchella and the open water by Bosmina longirostris and C. vernalis americanus. C. pulchella and B. longirostris seemed mutually exclusive. Evidence from a second gravel-pit lake (lower fish stock) indicated that this was partly caused by fish predation pressure in the first lake (higher fish stock). No microcrustacea longer than 1mm occurred in the open water. The size range in the weedbeds was 0.1-2.0mm. Diversity and abundance were highest amongst Potamogeton natans where C. pulchella was most abundant, but few microcrustacea/plant associations were found. The O+ roach diet contained microcrustacea from the open water and the weedbeds (50% numerically and 58% by weight). B. longirostris (open) was the preferred food but if not abundant the roach switched to C. pulchella (weed). Feeding was determined by prey mobility and abundance rather than by prey size. In contrast the O+ perch diet was mainly microcrustacea of weedbed origin (68% numerically and 78% by weight). Feeding was possibly size-selective. Cyclops was the main food item. Competition for food between roach and perch seemed to be minimised; diet overlaps were most common for weedbed microcrustacea. Growth of O+ roach was average in 1977 and 1978 and good in 1979. That of O+ perch was consistently average. Perch exhibited large fluctuations in first year survival. Field caging experiments provided evidence that macrophytes may be beneficial to O+ perch growth but O+ roach grew as well without them. Improved growth rates of O+ perch in the presence of macrophytes were attributed to a greater availability of macro-invertebrates and atypical feeding strategies in the absence of macrophytes.

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CONTENTS

CHAPTER 1. INTRODUCTION.

Production in a water body depends upon several sources: phytoplankton, macrophytes, epiphytes and allochthonous matter. This thesis is concerned with some aspects of the importance of the aquatic macrophytes in a gravel-pit lake in the Thames Valley, in particular their influence upon O+ roach (Rutilus rutilus (L.)) and O+ perch (Perca fluviatilis L.) populations.

Aquatic macrophytes are an integral part of the littoral zone of most freshwater lakes and play an important role in structuring and regulating littoral communities. A habitat dominated by macrophytes possesses greater differentiation in time and space in comparison with the more homogeneous open-water environment (Pieczynska and Ozimek, 1976). However, excessive plant growth can cause problems, the extent of which is illustrated by the number of methods which have been devised to control or remove aquatic weeds (Mitchell, 1974; Nichols, 1979). Extensive macrophyte growth can be a nuisance in running water, causing floods and siltation and anglers prefer weed-free waters in which to cast their lines in lakes and rivers.

This project arose out of the conflict which sometimes arises between the biological management of gravel-pit lakes, with the wish to maintain a complete ecosystem, and the requirements of anglers for relatively weed-free waters in which to fish. Rational management of a fishery requires a knowledge of the ecological role of the plants and the effects of their removal upon the managed resource, in this particular case, roach and perch populations. The main aim of this study was to determine whether O+ roach and O+ perch inhabited marginal vegetation for shelter or to obtain food. Underlying this was the premise that differences between animal communities within marginal

weedbeds and in the open-water area existed, were demonstrable and could be related to fish diet. There are of course basic differences in the diets of adult roach and perch, as perch are piscivorous while roach are omnivorous. The young of both species live in the margins in high numbers feeding on superficially similar food so that competition may possibly occur. The macrophytes could play an important role in alleviating this competition by providing a more diverse habitat containing a greater number of niches.

Aquatic macrophytes are both responsible for considerable structural complexity in the littoral zone of most water bodies and influence the physico-chemical properties of littoral water. Their role in the freshwater ecosystem has been discussed by Wetzel and Hough (1973), Pieczynska and Ozimek (1976) and Marshall and Westlake (1978). Their work can be summarised as follows. The contribution to total primary production varies with the size and trophic status of a water body and extent of the littoral but can be as much as 50% (Wetzel, 1974; Pieczynska, 1970; Moss, 1980). In addition they provide an attachment site for epiphytes which can be as productive as the pelagic phytoplankton (Allen, 1971) thereby making the littoral zone extremely important. Periphyton (the coating of sessile plants and animals on substrates in water as defined by Young (1945)) is a rich food source for grazing invertebrates (Fryer, 1968; Downing, 1981), and the diversity of habitat provided by the structural complexity of the macrophytes results in a diverse macro-invertebrate community (Macan, 1977a). Submerged macrophytes influence the littoral through the secretion of organic carbon compounds (DOM) (Wetzel and Manny, 1972). Any assessment of management practices also needs to take into consideration the effects of macrophyte removal during all stages of the life cycle as after death the macrophytes become the energy source for

the detrital food chain in the littoral (Berrie, 1975; Smock and Stoneburner, 1980). Minerals are eventually recycled thus also influencing the open-water zone (Howard-Williams and Lenton, 1975). This dynamic aspect of macrophyte biology is often ignored (Marshall and Westlake, 1978). Russian, Polish and Czech work on littoral ecology has been reveiwed by Pieczynska (1976).

The mechanisms by which macrophytes influence fish populations are not clearly understood. Certainly aquatic macrophytes are important as spawning substrates for some fish species. Mortensen (1977) found better survival of young trout in a stream with vegetation than in one which had been cleared but could not attribute this directly to the vegetation. Some species of fish rely on macrophytes for food (Hartley, 1947; Gaevskaya, 1966). Coarse fish fry usually inhabit marginal vegetation (Ridenhour, 1960; Rudenko, 1971; Shafi and Maitland, 1971; Wilkonska and Zuromska, 1978; Guma'a, 1978a). It has been assumed that the main reason for this is to obtain shelter from predation (Breck and Kitchell, 1979). It is also possible that they obtain food in the absence of competition from older fish.

The year class strength of many fish species is determined very early in life (Le Cren, 1962). Many factors can be responsible for this population regulation and while temperature is possibly of major importance (Koonce et al, 1977) other factors can also influence survival (Le Cren et al, 1977). The mechanism through which some of these factors operates is likely to be the quantity and nature of the available food at a period when the fish possess limited feeding capabilites (Grigorash et al, 1973; Braum, 1978). Spawning in the macrophytes may result in hatching in an environment containing as well as shelter, a greater diversity of food items than might otherwise occur. It is also possible that the presence of the macrophytes

alleviates competition for food between the many species of coarse fish which spawn in the spring. This aspect of the feeding biology of young coarse fish has not previously been quantitatively examined in the gravel-pit lakes and most studies have not related diet to habitat. The ecology of juvenile coarse fish populations has not been well studied because of the problems of catching small fish and obtaining accurate population estimates.

The fish populations of the gravel pit lakes in the Thames Valley in which this work was done were dominated by roach and perch and both were present in the marginal weedbeds for most of their first year. The gravel pit fish populations were dominated by younger fish (Gee, 1976) making the role of the macrophytes in providing shelter and possibly food even more important. O+ fish can be highly productive as shown by Mathews (1971) who found that they were responsible for 32% of total fish production in the River Thames.

The present study was divided into three sections. The first part of the work, in 1977, examined the microcrustacea within the marginal macrophytes and compared them to the open-water microcrustacea (crustacean zooplankton) in a gravel-pit lake. (Young coarse fish are planktivorous for much of their first year of life (Hartley, 1947; Smyly, 1952a; Lange, 1960; Lightfoot, 1976; Thorpe, 1977a; Guma'a, 1978b; Cook, 1979)). The term microcrustacea is used because while the open-water organisms were truly planktonic the macrophytes supported a mixed community of planktonic and benthic crustacea. The same quantitative sampling method was used to sample in both areas.

In the second part of this study the growth rates and diets of O+ roach and perch caught in marginal weedbeds between June and December 1977 were examined. The diets were related to the detailed information on habitat preferences of the microcrustacean food supply to determine

whether the fish were feeding in the margins or remaining there purely for shelter.

The third part of this study attempted to answer the question of whether the presence or absence of plants affected growth rates and survival rates of O+ roach and perch. This involved an experimental field study in 1978 and 1979, where the juvenile fish were held in floating cages either with or without aquatic macrophytes (simulated by plastic plants).

Hutchinson (1957) defined the terms pelagial and littoral (or infralittoral) as referring respectively to the free open-water zone and the zone of rooted aquatic vegetation. It is debateable whether the open water area of the small gravel-pit lakes could be regarded as truly pelagic as the water was relatively shallow with vegetation growing over much of the lake bottom and no part was entirely free from the influence of the margins. Therefore in any comparison with the very large lakes in America the whole of the gravel pits could be considered littoral. For the purposes of this study the terms littoral and open will be used when referring to the marginal vegetated area and the comparatively weed free open-water zone respectively.

There have been several studies of microcrustacea within littoral macrophytes and also a few which have compared macrophytic microcrustacea to open-water microcrustacea. Some obvious differences in species composition have been found. However, as will be shown, few of these studies were either quantitative or used the same sampling method in both habitats so that the differences between the two communities were not clearly defined.

The most extensive investigations of both the littoral area and the littoral in comparison with the open water are those of Straskraba (1963, 1965, 1967) in Czechoslovakia. Straskraba (1965) examined

seasonal population cycles of microcrustacea in weedbeds in Labicko backwater using a 0.5 litre large mouth bottle which was inverted under water at various depths and stations within weedbeds to provide 10 litre samples, with density expressed as numbers/litre. Straskraba (1967) also examined the effect of the fishstock on littoral zooplankton in Poltruba backwater. The littoral microcrustacea were sampled with the jar prior to fish poisoning with rotenone, and after poisoning, with a narrow glass tube, diameter 3.5 cm, so that edge effects associated with a narrow tube may have affected his estimates (George and Owen, 1978). He also compared macrophytic microcrustacean abundance with open-water abundance but he did not describe how the open water was sampled. Straskraba (1963) later made a major attempt to evaluate the contribution of the littoral zone to total lake productivity in two fishponds. He found that standing crops of zooplankton were higher in the littoral than in the open water but concluded that annual production in the littoral was lower. This work can be criticised for several reasons. Primary production from three sources (macrophytes, epiphytes and phytoplankton) was measured in the littoral but phytoplankton production was not measured in the open water (this was deduced from figures for comparable water bodies). He concluded that primary production in the littoral was lower than in the pelagic zone. The littoral zooplankton was sampled with the glass tube and compared to open-water samples of another worker. Zooplankton production was calculated as the sum of all densities obtained at fortnightly intervals, assuming a two week turnover time, regardless of taxonomic group, body size and water temperature. Such innacurate production estimates can have little value. Straskraba (1963) concluded that the littoral zone was in debt to the open water because primary production was not sufficient to support the consumers. He did not consider

whether other sources of production such as detritus and bacteria may have fuelled secondary production in the weedbeds.

Smyly (1952b, 1955, 1957) also made detailed seasonal investigations of the microcrustacea in the weeds of three moorland ponds in the Lake District. He first used a Macan grab (Smyly, 1952b). This provided a sample of 36 litres, with density expressed as numbers/litre. However, the open water was sampled with a surface tow net so that only the percentage composition and species composition of the two areas could be compared. As the grab destroyed the vegetation he then used a metal tube sampler, 7.5 cm diameter, volume 3 litres, (Smyly, 1955) recorded as 8.5 cm in Smyly (1957) where the work on macrophytic microcrustacea is summarised and pond nets and trays of open-mouthed bottles are added to the list of sampling equipment. He found marked differences in species composition of the two habitats with species normally considered truly limnetic (Hutchinson, 1967) not present in the weedbeds.

Pennak (1966) carried out a large scale survey of the "zooplankton populations in the littoral macrophyte zone" of 11 Colorado lakes, which had similar stated aims to the present study. He designed a rubber tube sampler (Pennak, 1962) to collect samples of 6-20 litres; zooplankton density was expressed as numbers/litre. The main drawback was the lack of seasonal data as he only sampled in each lake once or twice. He compared each littoral station to an immediately adjacent open-water station rather than to the truly pelagic area, although it could be argued that these open-water sites which were sometimes 12-15 m from the macrophytes in the large Colorado lakes, were comparable to the open-water areas of the smaller gravel-pit lakes. Pennak (1966) found that zooplankton numbers were higher in the open water than in the weedbeds in contrast to the findings of Straskraba (1967).

Another comparison of open-water and weedbed microcrustacea was made by Shiel (1976) in a billabong (ox-bow lake) in Australia where again the open water was only sampled at one station. Shiel examined microcrustacea in four weedbeds using a Birge cone net, mesh size 160 um, to take horizontal 20 m tows at each station. Abundance was given as percentage composition and he usually counted only one sub-sample (15 % of the total) to enumerate 100 individuals, so that considerable sub-sampling error may be attached to his counts. His discussion centres on species composition and differences between weedbeds were not clearly defined.

Very few comparisons of production in the two habitats have been made because of the large number of species with differing life cycles. Lim and Fernando (1978) compared the production of six species of Cladocera in five weedbed sites and one open-water site in a Canadian lake, using a modified Van Dorn sampler to collect duplicate samples at weekly intervals over the growing season. The two major species had similar production values in the two habitats with a higher total production of cladocerans in the littoral. However, they do not provide any information on standing crops or relative abundance and do not give the contribution of each species to total microcrustacea in each habitat.

There is more information on the microcrustacea of weedbeds alone and in particular the Chydoridae (Whiteside, 1974; Whiteside et al, 1978) but much of this data has been obtained from sediment analysis and is not an assessment of abundance in the water (Whiteside, 1970; Goulden, 1971). There have also been some detailed studies of habitat preferences of chydorids (Fryer, 1968; Fryer and Forshaw, 1979). obtained from single samples.

Quade (1969) made an interesting survey of the Cladocera

associated intimately with 12 species of aquatic macrophyte in seven North American lakes. He sampled on only one occasion using a novel sampling method consisting of diving to the lake bottom and enclosing either one plant or a small stand in a 30 x 12 x 60 cm plastic bag. His results could ony be expressed as percentage composition and while this provided accurate information on Cladoceran habitat selection it did not provide seasonal data nor did it satisfactorily sample such tycholimnetic species as Ceriodaphnia which might be of greater importance as fish food than benthic species.

Rybak, Rybak and Tarwid (1964) carried out a large scale survey of the microcrustacea of different types of littoral in 37 lakes in Poland using a Bernatowicz sampler and again only one sample was collected at each site. Their results are given as associations of species with types of littoral (sheltered, open, accessible and separate).

Most of the remaining accounts of littoral microcrustacea are studies of more specific topics which do however provide some useful information. Szlauer (1963) examined diurnal patterns of vertical migration in shallow water weedbeds using both a net and self-acting plankton samplers consisting of funnels passing upwards into inverted bottles mounted on stands. This was very similar to the very efficient pattern sampler devised by Whiteside and Williams (1975) for sampling chydorids, consisting of an 8 x 8 matrix of square funnels leading through tubes into collecting bottles, which was set overnight, restricting its use to water bodies free of vandalism. Both these samplers only collected animals moving up through the water column. The following quotation illustrates both the problems of littoral sampling and data comparability. Monakov (1969) comparing crustacea in the open water and the marginal weedbeds of the White Nile described his sampling thus; "plankton-nets, hoog-net and trowels were employed for collection

among water vegetation."

The results of these studies remain inconclusive as to the importance of marginal macrophytic microcrustacea. The obvious differences between the species composition of the two communities have been established but more important quantitative differences have not been satisfactorily examined and in no case has there been a related study of fish diet. Therefore, a detailed quantitative study of microcrustacea within the littoral weedbeds in a gravel-pit lake was carried out in 1977. A similarly detailed quantitative study of open-water microcrustacea was carried out with the same sampling equipment, a quantitative tube sampler, so that the two habitats could be accurately compared. The microcrustacean sampling programme in the first year had the following aims:-

1. To compare the species composition and standing crops of the open water and marginal weedbed microcrustacea communities.
2. To determine whether the littoral microcrustacea exhibited any habitat preferences within the marginal weedbeds, i.e. did specific associations exist between plant species and crustacean species.
3. To compare both the range of body sizes (lengths) present in the open water and the weedbeds and the body sizes of species common to both areas over the sampling season.

Many workers have related abundance and species diversity of macro-invertebrates on aquatic macrophytes to density of vegetation and structural complexity and it has been generally accepted that plants with a large surface area such as Elodea canadensis support greater numbers and more species than simple leaved plants (Krecker, 1939; Rosine, 1955; Macan, 1977b). Aquatic macrophytes can be divided into groups according to their structure; floating leaved, submerged (finely divided or straight leaved) and emergent. The sampling effort in the

weedbeds in 1977 was divided between the three main structural types (Potamogeton natans, Elodea canadensis and Sparganium erectum/Typha latifolia) to determine whether the same relationships were true for planktonic animals not so closely associated with the plant. A few associations of species of microcrustacea with plant species have been demonstrated. If it is possible to demonstrate an association of a preferred food item of the young fish with a plant species this would provide the basis for a realistic management plan for the macrophytes of the gravel-pit lakes.

In an extension of this work, a similar sampling programme was undertaken in 1978 and 1979 in another gravel pit lake in conjunction with the field experiments on the effect of the presence or absence of macrophytes on fish growth. The weedbed microcrustacea were sampled in two sites which provided a comparison of structurally different habitats, one of shallow water with dense vegetation (Elodea) and one with Typha spp. mixed with more sparsely distributed Elodea in deeper water. This gave a comparison of the open-water microcrustacean community with the litttoral vegetation and also the plant/water interface to determine how far into the lake the littoral influenced the microcrustacea.

The diet study in the first year had the following aims:

1. to examine seasonal changes in diet.
2. to determine whether the roach and perch were feeding upon open-water or littoral organisms.
3. to determine whether there was a relationship between diet and the plant species around which the fish were caught,
4. to investigate overlap in species composition of the diets of roach and perch.

5. to determine whether there was any selection in the size of food particles eaten.

One shortcoming of most fish diet studies is the lack of even general information about the food supply. Very few workers have attempted to relate diet to specific habitat except by prior knowledge of the habits of the selected food items. Mann and Orr (1969) found differences in the diets of fish caught at different sites in a stream. They related these to different species of macrophytes but the habitats themselves were not studied. Another major failing of some diet studies is that the level of identification of prey items is insufficient to determine whether inter-specific competition between fish species for food is occurring (Mann, 1973, 1978). Keast (1977) went so far as to state: "Body size rather than finer taxonomic identity is characteristically of the greater importance in fish feeding." This was in a study of diet overlaps between year classes which was based on identification of food only to order and family in most cases. Pedley and Jones (1978) discussed the importance of identification of prey to species level to determine whether trout and salmon were taking the same food species or different members of the same taxonomic group.

The few previous studies of the diet of O+ roach have included the following. Hartley (1947) made one of the earliest studies in this country but did not examine the food supply. He found that the roach were omnivorous, feeding mainly on plankton and diatoms. Lightfoot (1976) examined feeding and food of O+ roach in the River Hull where tidal effects made data interpretation difficult. Cook (1979) working on some gravel-pit lakes compared roach diets to open-water zooplankton although the fish were caught in the marginal weedbeds. Hewitt (pers. comm.) found that the diet of O+ roach in Priests Pot (Lake District) consisted entirely of Keratella sp. but no examination of the possibly

impoverished food supply was made. Lange (1960) examined the diets of several species of Russian roach from hatching to the end of the first year and compared them to non-quantitative net collections of microcrustacea from an unspecified area of the lake. The diet consisted of a variety of microcrustacea and small chironomid larvae. Grigorash et al (1973) examined the diets of O+ roach on varying occasions over nine years and although the availability of food is discussed, this was deduced from consumption figures rather than from a study of the food supply. The very small roach fed on rotifers, progressing to more mobile animals such as nauplii, small crustacea and small chironomids as they grew. All these workers agreed that the diet of small roach consisted of microcrustacea but how their choice of food related to availability was not examined.

There have been several studies of the diet of O+ perch but again the food supply has not always been investigated. Thorpe (1977a) has reveiwed most of the available information on Perca fluviatilis L. and Perca flavescens Mitchill which he regards as biologically equal. The studies most relevant to the present work are those of Smyly, 1952a; Craig, 1974a; Guma'a, 1978b and Cook, 1979. Smyly and Guma'a both examined perch diet in Lake Windermere and Guma'a (1978b) compared zooplankton in perch guts to zooplankton samples taken in the open water. In both these studies the diet consisted mainly of Copepoda and Cladocera. Craig (1974a) found that O+ perch in Slapton Ley were eating copepods and cladocerans but the food supply was not investigated. Mann (1978) observed that perch in the R. Stour consumed minnows and Ephemeroptera. He did not identify the diet more specifically. Cook (1979) carried out a detailed examination of the diet of O+ perch in the gravel-pit lakes but only compared the diet to open-water zooplankton abundance. The perch exhibited a preference for copepods and for

benthic Cladocera normally associated with vegetation. Pycha and Smith (1953) examined diets of yellow perch and found them to be feeding on a mixture of cladocera and copepods and smaller benthic invertebrates. They suggested that changes in growth rates were closely associated with changes in availability of food but the food supply was not examined. O+ perch are pelagic during the first few weeks of life (Coles, 1981) and this phase of the life cycle was not investigated. As most workers have shown that the food of both these fish species in the first year consists mainly of microcrustacea, no examination of benthic invertebrates in the weedbeds was made.

In a study of fish:food relationships it is also useful to know the size of the fish population and the relative proportions of each species under study and two population estimates of O+ roach and perch were made in 1977. These provided data on the numbers in the whole lake but as this study was concerned with the relationship of the fish to the littoral organisms and as the fish tended to spend the first year of life among the marginal macrophytes an attempt was also made to estimate numbers in these shallow regions to give information on the densities of fish when in schools. These density figures were also required for the calculation of realistic stocking densities for the field caging experiments.

Because small roach and perch are planktivorous, this study has inevitably involved some consideration of the effects of size selective predation upon zooplankton populations, about which there is a large amount of literature (Hrbacek, 1962; Brooks and Dodson, 1965; Hall _et al_, 1976; Hrbacek, 1977; Durbin, 1979). This work can be summarised as follows. Size-selective predation by planktivorous fish on zooplankton leads to the disappearance of the large species (>1.0 mm in length). Smaller herbivores, normally outcompeted by the larger filter

feeders, take their place. This results in a change in the species composition and size spectrum of the phytoplankton as the small herbivores are less efficient filter feeders and cannot take in the larger algae. While this thesis does not intend to examine this phenomenon in detail the results do show some of these effects. Macrophytes are thought to protect crustacea from fish predation (Straskraba, 1963) so that this effect is less likely to occur among the weedbeds and this in itself could lead to differences in the two microcrustacean communities under study.

Field experiments on growth rates of fish in relation to varying levels of such factors as density, food, nutrients are often carried out in small adjacent ponds. Schneider (1973a) examined the effects of density on yellow perch growth rates in small ponds, with and without macrophytes. Crowder and Cooper (1979) examined the effects of the presence or absence of macrophytes on the growth of bluegill sunfish in small ponds. This approach was initially adopted in the present study in 1977 using four small (0.05 ha.) ponds at Farnborough. However, the establishment of the fish populations proved difficult and time consuming and it was virtually impossible to make a pond weed-free. Microcrustacean sampling showed that the ponds although side by side differed biologically. Hall, Cooper and Werner (1970) also found that adjacent ponds can differ considerably. In investigations of the effects of fish predation upon littoral microcrustacea, Czech workers used netting enclosures to make fish free areas (Straskraba, 1963). It is difficult to make enclosures fish proof (Barber, 1976) and they are expensive to replicate. The gravel pits are open to the public and therefore enclosures could not be safeguarded. It was not possible because of lack of space to carry out laboratory experiments which in any case do not always relate to the field situation. However, floating

cages, widely used in fish culture, are relatively cheap and easy to make, provide replication of very similar conditions and are not subject to many of the problems which may arise in the laboratory through mechanical or electrical failure. Floating fish cages were therefore used in these experiments to investigate the influence of the presence or absence of plants upon the growth of 0+ roach and perch. The experiments were first done in 1978 using 8 cages and repeated in 1979 with 12 cages when initial problems had been solved. They were placed in the centre of the lake where they were free from human interference.

Real plants growing in the cages might have died and caused local deoxygenation and fish mortality. The logistics of getting macrophytes to grow suspended in mid-water were daunting. Therefore, plastic artificial substrates were made to simulate aquatic macrophytes. Artificial substrates have been developed mainly for use in river pollution studies as a means of obtaining uniform samples (Dickson, Cairns and Arnold, 1971). Macan and Kitching (1972) made artificial Littorella and Carex from plastic strands fastened on to a webbing base for sampling benthic invertebrates and a similar artificial seagrass has been made by Barber et al (1979). Both found that the samples of benthos so obtained were similar to but not identical with samples from the real vegetation. However, little work appears to have been done on the colonisation of artificial substrates by planktonic or semi-planktonic organisms. Preliminary experiments in the gravel pits showed that littoral microcrustacea were present around or on plastic strips suspended in the centre of the lake and Macan and Kitching (1976) obtained similar findings with plastic sheets hung in the centre of a lake.

The success of the artificial substrates as imitation macrophytes was likely to depend to some degree on the biomass of periphyton on the

plastic. Artificial substrates, usually glass slides, have been widely used for sampling periphyton (Sladeckova, 1962). Pieczynska and Spodniewska (1963) compared natural and artificial surfaces and found no significant differences in the periphyton communities in one lake and Bownik (1970) found that the life cycle and growth pattern of the plant were more important determinants of periphyton biomass than the nature of the surface. In contrast, Markosova (1980) found that the roughness of the surface was important for attracting organisms, with granite becoming coated with a higher biomass than polythene foil. However, she did not compare the artificial surfaces with plant stems. Preliminary experiments in the gravel pits showed that strips of polythene suspended in mid-water soon became coated with a thick layer of periphyton. The filter feeding portion of the microcrustacean community could be expected to colonise the substrates independently of epiphyte growth.

The experiments had the following aims:

1. to determine whether the presence of vegetation (simulated by artificial substrates) influenced the growth of O+ roach and perch.
2. to determine whether fish survival was affected by the presence or absence of vegetation.
3. to show whether the fish kept in weed and non-weed cages ate different food items which could be related to the different faunas associated with the presence or absence of the artificial substrates.
4. to show whether the roach and perch showed changes in their feeding preferences when they were kept apart from one another and also whether they exhibited greater diet overlap when feeding in isolation.
5. to determine whether differences in the diets of weed and non-weed fish could explain any observed differences in growth rates.

The microcrustacea living in the cages with and without artifical substrates were sampled quantitatively and compared with those in the

lake and the marginal weedbeds.

The extraction of gravel from the shallow river valley deposits in S.E. England has increased enormously in the last 40 years and in 1974 extraction was estimated to be 2,000 ha/year (Hartwright, 1974), 90% of this resulting in wet pits which have been left as lakes with the increasing demand for recreational water space. The work in this study was carried out mainly in two small, shallow gravel-pit lakes, one in Frimley (near Farnborough), Hampshire, and one in Yateley, Berkshire. Both are on the River Blackwater. They are described in detail in Chapter 2. The lakes belong to the Ready Mix Concrete group of companies and are two of about 60 managed as fisheries by Leisure Sport Ltd. (see Fig. 1.1). The lakes usually occur in groups and have been named by locality and then numbered for reference as shown in Table 1.1 which also gives the area, age and some water quality data for the lakes examined in this work.

The first part of the work on the differences between open water and marginal crustacea and the relationship between fish diet and marginal microcrustacea was carried out in Farnborough 18a while the caging experiments were done in Yateley 4. Other lakes examined for microcrustacea were Darenth 37, Twyford 32, Yateley 2 and four small ponds near Farnborough.

Previous biological studies on the lakes include: a survey of the fish populations of 39 lakes and population estimates in six lakes (Gee, 1976), a study of the roach in Yateley 7 (Barber, 1976), studies on the parasites of roach in Yateley 4 (Sweeting, 1976) and a study of fish/zooplankton interrelationships in Farnborough 18a and Darenth 40 (Cook, 1979).

Biologically, the gravel-pit lakes are characterised by

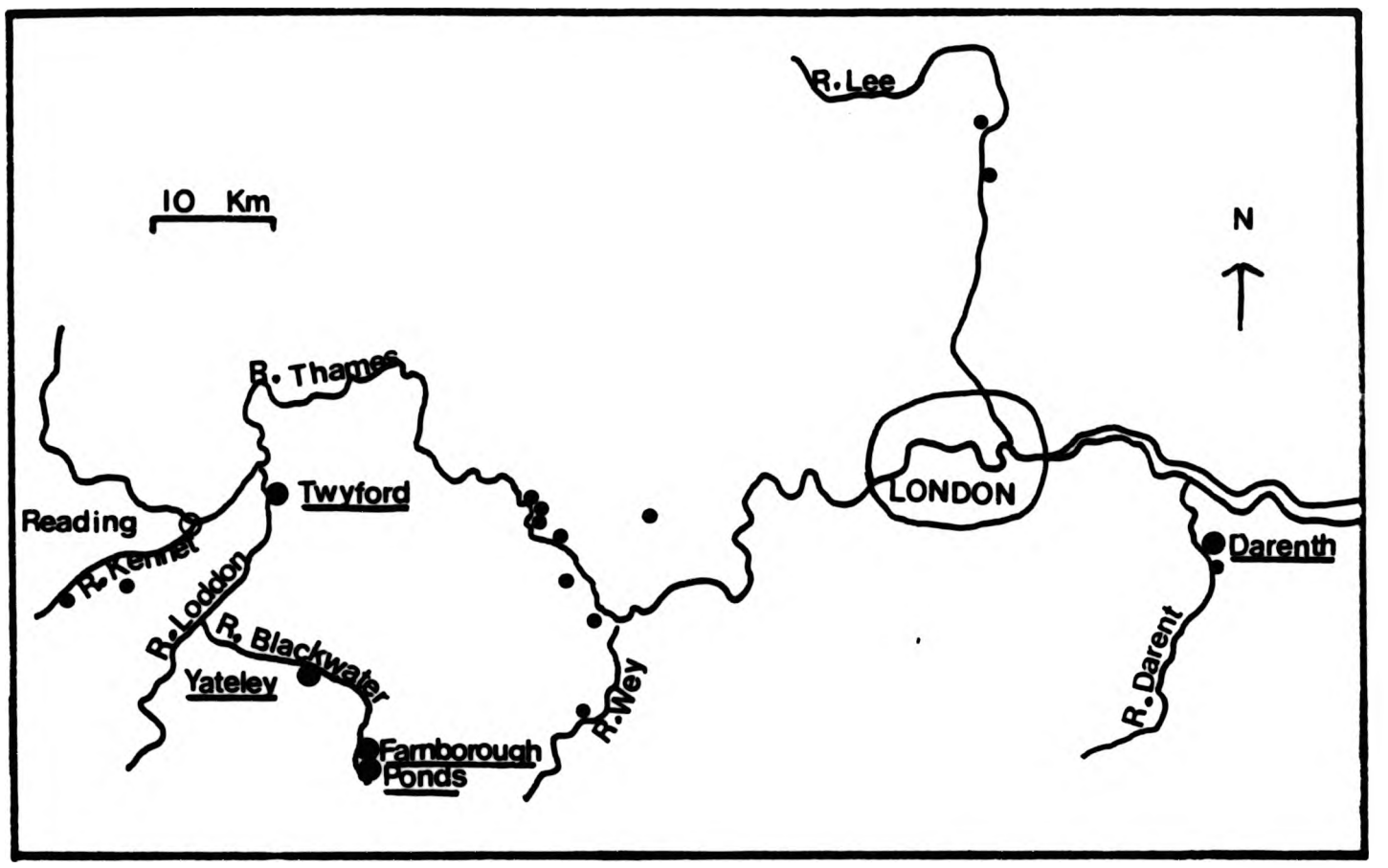


FIGURE 1.1 The location of the gravel-pit lakes.
● = the main sites of study. • = other gravel-pit lakes studied by Gee (1976).

Table 1.1 The gravel-pit lakes.

Lake	No	N.G.R.	Area	Age	pH	Cond	Ca
Farnborough	18a	SU875560	1.2	25	7.4	5.6	177
Yateley	4	SU823613	1.5	25	8.2	2.8	93
Yateley	2	"	3.7	16	8.8	2.5	68
Twyford	32	SU785753	6.0	18	8.3	3.9	125
Darenth	37	TQ559710	1.2	17	8.0	8.2	368

Area in ha. Age in years (in 1981).

Cond = conductivity in umhos x 10^{-2} Ca = calcium in mg/litre.

N.G.R. = National Grid Reference

Chemical data collected in 1971 (Barber, 1976).

variability between lakes and unpredictability between years. The following features are common to most lakes. The majority are small (average area under 9 ha) and shallow (maximum depth often only 3-4 m). They are young, mostly less than 40 years old. They lack surface inflows and are subject to water level fluctuations as the water table varies with rainfall. Water levels in adjacent pits can be different although the lakes are interconnected via buried pipes to prevent flooding. The methods of gravel extraction have changed recently so that while older lakes have vertical banks and no shallow littoral, some of the newer lakes have been dug with sloping banks and possess well developed aquatic vegetation. Some of the lakes have been landscaped and many support "high breeding densities" of birds (Catchpole and Tydeman, 1975).

Thermal stratification is rare and transient in the shallow lakes and the water is usualy well oxygenated. No water quality data have been collected since 1973 so that present levels of plant nutrients are unknown. Goodridge and Godfrey (pers. comm.) made a study of the phytoplankton in several lakes in 1973 and found that most of the lakes examined were mesotrophic with low levels of NO_3 (range; trace to 2.2 mg/litre) and PO_4 (range; trace to 0.15 mg/litre). Concentrations of calcium (Table 1.1) and silicate (range; 1 to 90 mg/litre) were high and diatoms tended to dominate the phytoplankton with blue-green algae occurring in late summer. Barber (1976) analysed water samples from most of the lakes in the Yateley complex and provided the following information on chlorophyll a levels. The average peak value in 1972 was 45 ug/litre, with the occasional value higher than this, e.g. 175 ug/litre. The average value for Yateley 4 in 1972 was 8.8 ug/litre. Munro and Bailey (1980) reported similar values for Bough Beech reservoir in Kent (mean of 9 ug/litre). Steel (1972) reported maximum

summer values of chlorophyll a of 50 ug/litre, 100 ug/litre and 150 ug/litre in three London reservoirs which are somewhat higher than the typical peak values in the gravel pits. The chlorophyll a concentrations in Yateley were also lower than those measured in some disused filter beds in E. London used for carp culture, whose water originates from the very eutrophic R. Lee (O'Grady, pers.comm.). Therefore, Yateley 4 was not a highly productive water body. Levels of chlorophyll a have not been measured in Farnborough 18a.

Many of these gravel-pit lakes are situated in urban areas or near towns and are popular coarse fisheries. Gee (1976) found that the most common fish species were roach, bream (Abramis brama (L.)), tench (Tinca tinca (L.)), perch and pike (Esox lucius L.). Other species he recorded were rudd (Scardinius erythroophthalmus (L.)), bleak (Alburnus alburnus (L.)), gudgeon (Gobio gobio (L.)), chub (Leuciscus cephalus (L.)), carp (Cyprinus carpio L.), crucian carp (Carassius carassius (L.)), minnow (Phoxinus phoxinus (L.)), ruffe (Gymnocephalus cernua (L.)), bullhead (Cottus gobio L.), stone loach (Noemacheilus barbatulus (L.)), stickleback (Gasterosteus aculeatus L.), and eel (Anguilla anguilla (L.)). The fish populations consisted predominantly of the younger age classes (0+ to 2+) and two types of fish community have been described by Gee (1976), one dominated by roach and bream and one dominated by perch and pike, the former being far more common. The lakes are visited by many anglers and some bank erosion has occurred and possibly unrecorded fish introductions and removals.

The two lakes chosen for this study, Farnborough and Yateley are 4 miles apart. Both are mature gravel-pit lakes with well developed aquatic vegetation and Farnborough supported dense populations of young roach and perch about which information already existed (Cook, 1979). At the time of the investigation the fish populations were also

relatively free of infection with Ligula intestinalis (no infected roach were found in this study) and reputedly no pike were present. Yateley was chosen for the caging experiments because although the same size as Farnborough it is rectangular in shape which meant that the fish cages could be anchored in the centre out of reach of human interference from the bank. The elongated shape of the Farnborough lake would not allow this. The two lakes are shown in Fig. 2.1.

Both Gee (1976) and Cook (1979) studied the fish populations of Farnborough 18a, but little is known about the fish in Yateley 4. The most common fish species in Farnborough were roach, rudd, perch and a high biomass of slowly growing tench (Gee, 1976; Cook, 1979). Bream appeared in 1978, introduced by anglers. Yateley 4 was known to contain roach, perch, tench and a large population of pike (Gee, 1976). There was some evidence to suggest that Yateley 4 supported a lower fish stock than Farnborough 18a. Few fish were caught despite several attempts with a variety of methods, both in this and previous studies (Sweeting, 1976; Gee, 1976). The lake was also unpopular with anglers and it was concluded that Farnborough contained more fish than Yateley. Both pike predation and infection with Ligula may have contributed to the reduced fish density in Yateley.

CHAPTER 2. SITES SAMPLED, MATERIALS AND METHODS.

2.1 Sites.

2.1.1 Farnborough 18a.

The location of Farnborough 18a is shown in Fig. 2.1 and the shape, distribution of the main species of aquatic plants and sampling sites are illustrated in Fig. 2.2. Farnborough 18 is the oldest lake in the complex at Frimley in Hampshire and now consists of 2 lakes, a and b; the latter was cut off in 1972, leaving the main lake with an area of 1.1 hectares. The elongated shape is due to the ridge and furrow method of extraction used in shallow gravel deposits which has resulted here in the long island in a and the ridge between a and b. The southern end of the lake is shallow, maximum depth 1 m, merging into reedswamp, as the lake silts up. A raised gravel spit covered with submerged aquatic vegetation runs between the two sections of the lake. The main body of the lake has a maximum depth of 3.0 m and an average depth of 1.5 m. Much of the bank drops vertically to the water but thereafter slopes gently so that a marginal fringe of aquatic vegetation has developed. The bottom sediment is mainly of mud overlying gravel, with the more exposed bays bearing clean gravel whilst the southern end has become silted. The water is coloured yellow-brown and light penetration can be low, restricting macrophytes to the shallower areas. The extent of coverage with vegetation is a changeable feature from year to year.

Information on the chemical and physical nature of the water is sparse (see Table 1.1). The water level can fluctuate and Gee (1976) measured a decrease of 0.25 m in water level over a year. An overflow pipe running into the River Blackwater prevents flooding.

The pit has not been landscaped and only isolated trees occur

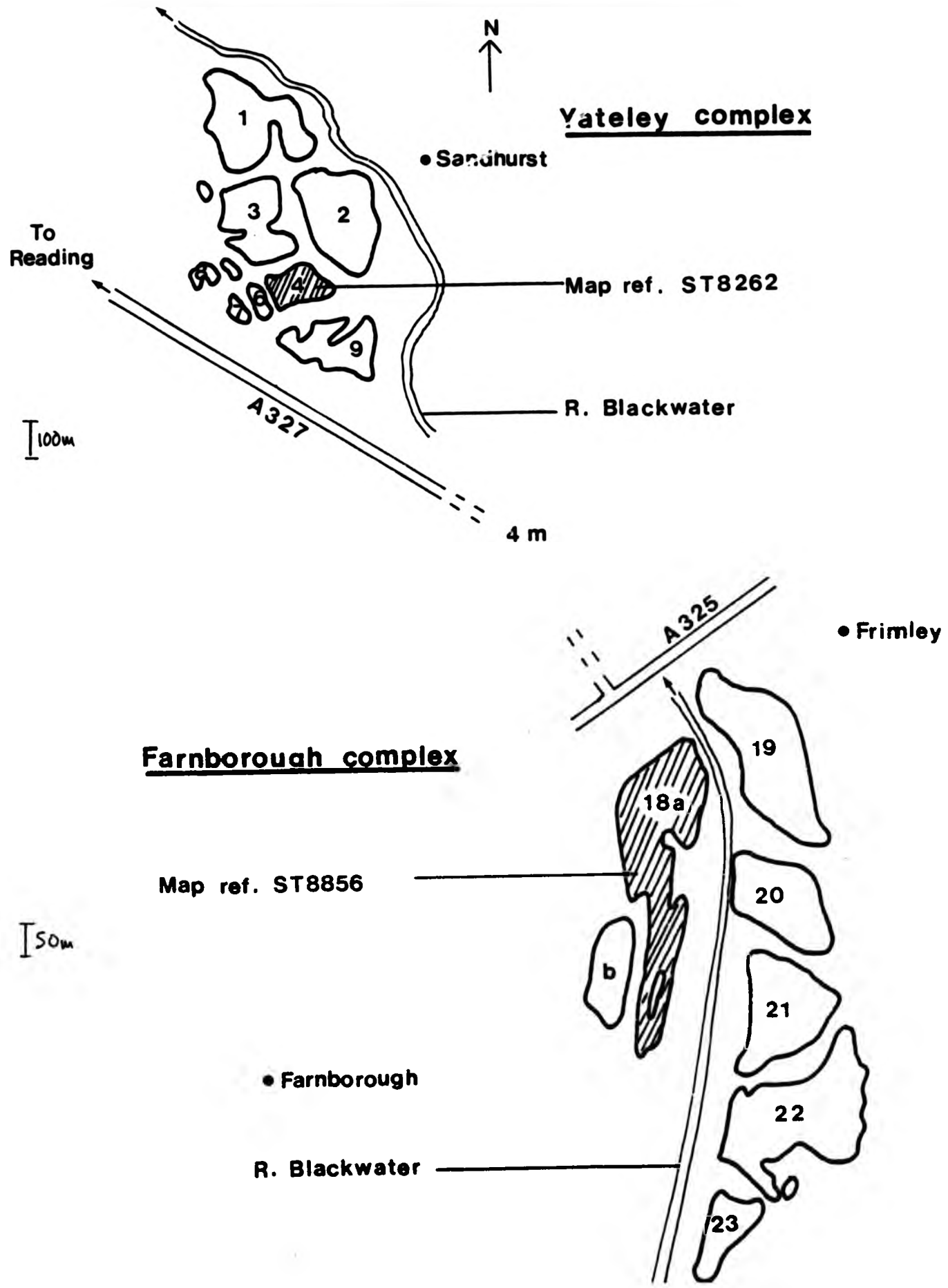


FIGURE 2.1 The gravel-pit lake complexes at Frimley, (Farnborough) Hampshire and Yateley, Berkshire, showing lake number, access points and major roads (not drawn to the same scale). The two shaded lakes were the main sites for this work. • =nearest towns.

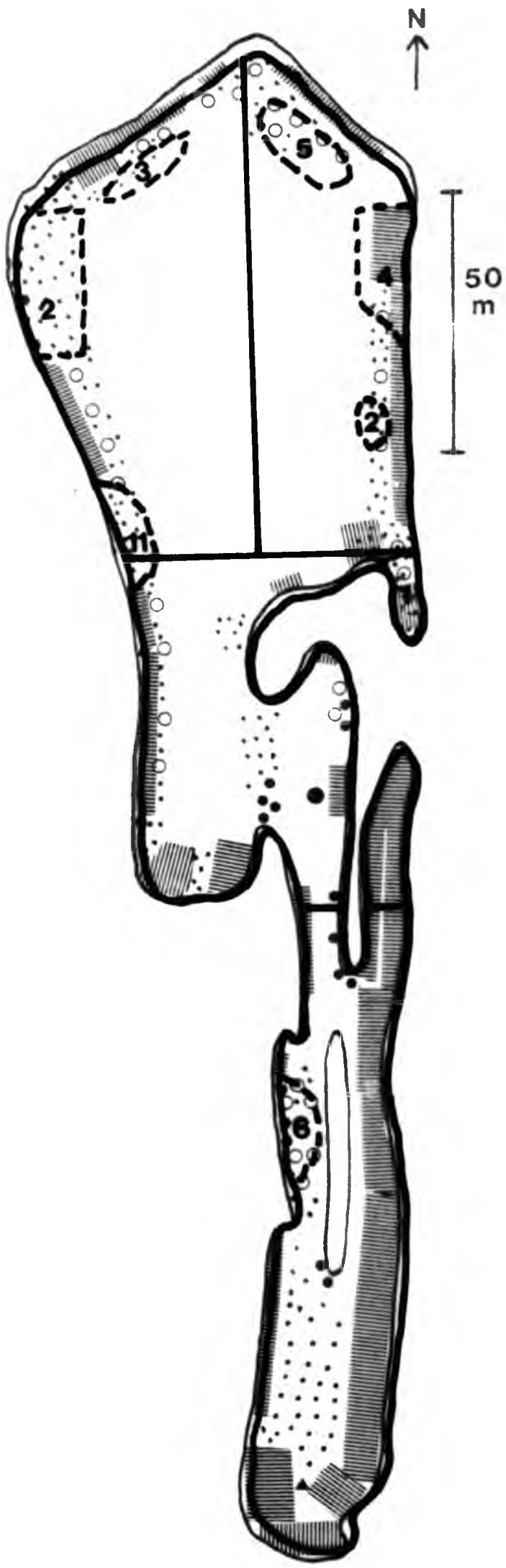
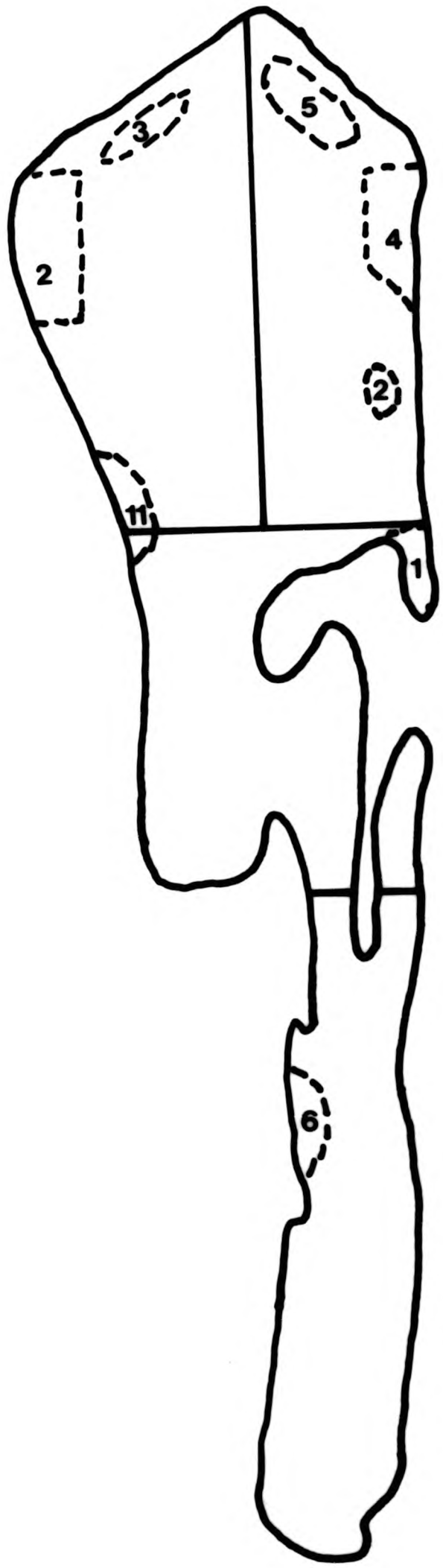


FIGURE 2.2 Map of Farnborough 18a showing the distribution of the common species of aquatic macrophytes in 1977. The overlay shows the marginal sampling sites. The weedbeds are not drawn to scale. Further information on the sites is given in Table 2.2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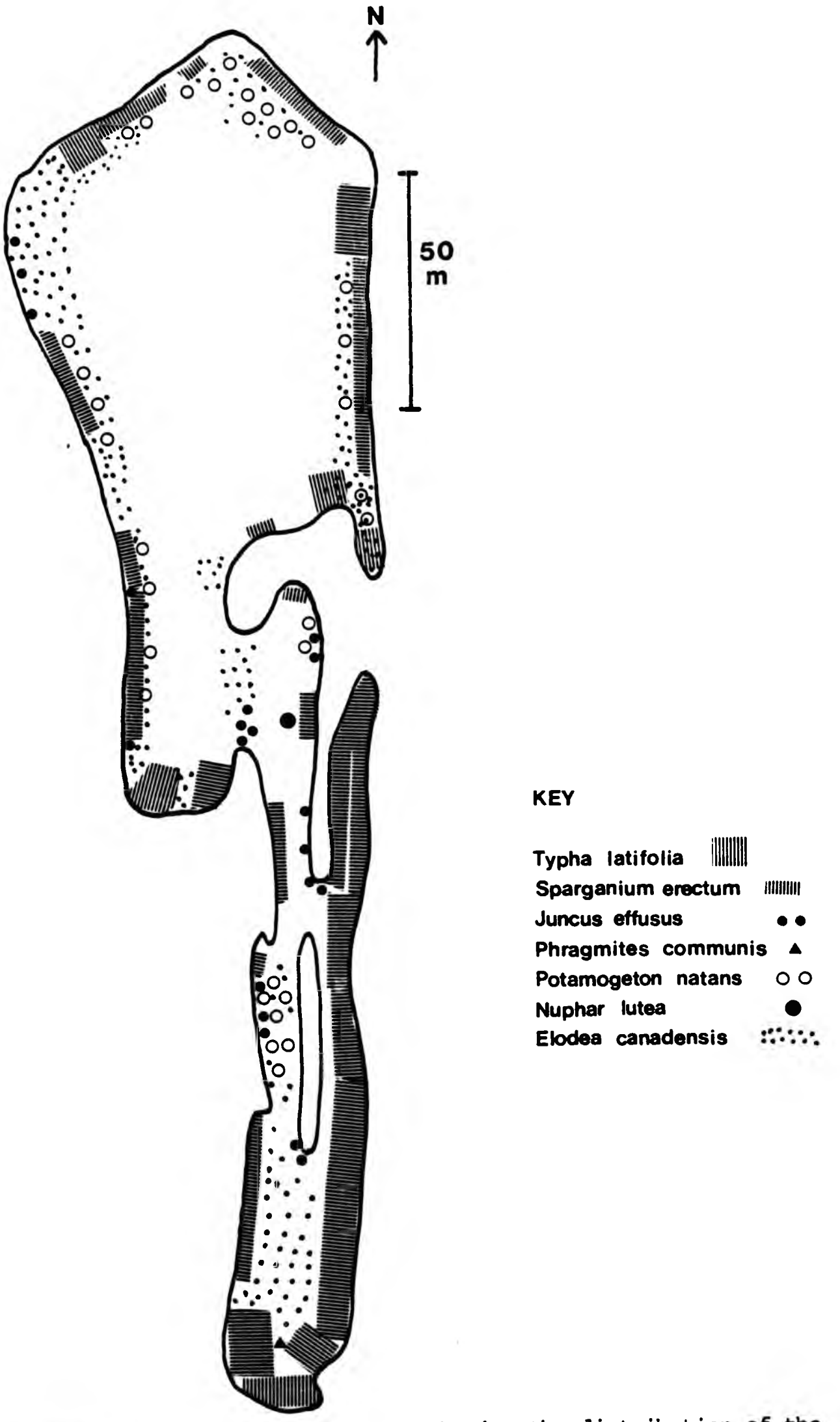


FIGURE 2.2 Map of Farnborough 18a showing the distribution of the common species of aquatic macrophytes in 1977. The overlay shows the marginal sampling sites. The weedbeds are not drawn to scale. Further information on the sites is given in Table 2.2

around the main part of the lake although the island is overgrown. The most common trees are alder (Alnus glutinosa), willows (Salix spp.) and birch (Betula pendula). Gorse (Ulex europaeus), broom (Cytisus scoparius) and brambles (Rubus spp.) are also common.

Table 2.1 lists the aquatic macrophytes observed in four gravel-pit lakes and some small ponds between 1976 and 1979. Exhaustive searches for plants were not made so that some of the less common species may have been overlooked, and also most of the plant mapping was carried out during the warmer months of the year. Macrophyte nomenclature follows Clapham, Tutin and Warburg (1962). The lakes generally contained fewer plant species than older, well established water bodies, such as some of the Norfolk Broads, (pers. obs.). Sparganium erectum was the dominant emergent plant in the main body of Farnborough 18a in 1977, growing around most of the lake in a fringe 0.5m wide. Typha latifolia was also common, particularly at the southern end of the lake. Juncus effusus grew on the more gently sloping banks in shallow water and was also abundant around the lake on top of the lake banks. Isolated specimens of Phragmites communis occurred but this reed was not common. The distribution of the emergent vegetation did not change markedly during the years of this study.

The dominant submerged plant was Elodea canadensis. The area of substrate covered varied from year to year probably due to fluctuating water levels and/or with changes in light penetration. In 1977 it grew in a broad band around the entire margin and covered the shallower regions. In 1978 it was also present in large clumps in the centre of the main body of the lake but by 1979 it had reverted to 1977 levels. Ceratophyllum demersum was present in small quantities in 1977 and had become more abundant in 1979, particularly in the shallow southern end.

Two floating leaved species were found in Farnborough 18a. Nuphar

Table 2.1 Principal aquatic macrophytes found in some gravel-pit lakes, 1977-1979.

	F	Y	PD	TW	DA
Emergent					
Equisetum fluviatile L.		x			
Typha latifolia L.	x	x	x		x
T.angustifolia L.		x			
Sparganium erectum L.	x		x		
Iris pseudacorus L.		x			
Schoenoplectus lacustris (L.) Palla				x	
Carex pseudocyperus L.		x			
Carex sp.					x
Eleocharis palustris (L.) Roem.& Schult.		x			
Juncus effusus L.		x	x		
J. effusus var compactus	x				
J. acutiflorus Hoffm.			x		
J. bulbosus L.		x			
Agrostis stolonifera L.			x		
Glyceria fluitans (L.) R.Br.	x		x		
Calamagrostis epigejos (L.) Roth		x			
Phragmites communis Trin.	x		x		
Submerged					
Elodea canadensis Michx.	x	x	x	x	x
Myriophyllum verticillatum L.		x			
M. spicatum L.					x
Ceratophyllum demersum L.	x				x
Callitriche stagnalis Scop.	x				x
Chara sp.				x	
Potamogeton pusillus L.	x				
P. obtusifolius Mert.& Koch	x				
P. crispus L.	x	x			
Floating					
Potamogeton natans L.	x		x		
Nymphaea alba L.		x			
Nuphar lutea (L.) Sm.	x				
Miscellaneous					
Ranunculus sceleratus L.				x	
R. flammula L.			x		
Alisma plantago-aquatica L.	x		x		
Rorippa nasturtium-aquaticum (L.) Hayek.		x			

F = Farnborough 18a
Y = Yateley 4
PD = ponds
TW = Twyford 32
DA = Darenth 37

lutea occurred in only one place but was increasing yearly. Potamogeton natans was very abundant, growing among the Elodea and extending into deeper water. It filled the more sheltered bays but tended to be removed by anglers and did not reach it's greatest extent until late summer. For convenience, this lake will be referred to from now on as Farnborough.

2.1.2 Yateley 4

The location of the lake is shown in Fig. 2.1 and the shape, vegetation and sampling sites are shown in Fig. 2.3 which also indicates the position of the experimental fish cages (described in Chapter 5). It is one of the older pits in the Yateley group near Sandhurst in Berkshire, and is roughly rectangular in shape with an area of 1.5 hectares. The maximum depth is 2.5 m and the average depth is 1.5 m. The low bank drops vertically into the water on the northern and western sides of the lake but the other two sides have gently sloping banks with well developed aquatic and semi-aquatic vegetation. The north and west sides of the lake are also shaded by trees. The lake is very shallow (0.5 m) around the eastern end where there is an island. The gravel bed is overlain with thick mud which probably arose partly from the decomposed leaves of the surrounding trees. The lake connects with lake no.6 across a broken bank. The site has been landscaped and the lake is surrounded by mature trees and much of the bank is overgrown with shrubs. The most common trees are willows (Salix alba), (S.alba tristis), (S.matsudana), (S.caprea), alder, and the introduced shrubs Spiraea salicifolia, Rhododendron ponticum and bamboo. Birch and balsam poplar, (Populus gileadensis) are also common.

The limited information available on water quality data has been discussed in Chapter 1 (see Table 1.1). The water was not coloured as

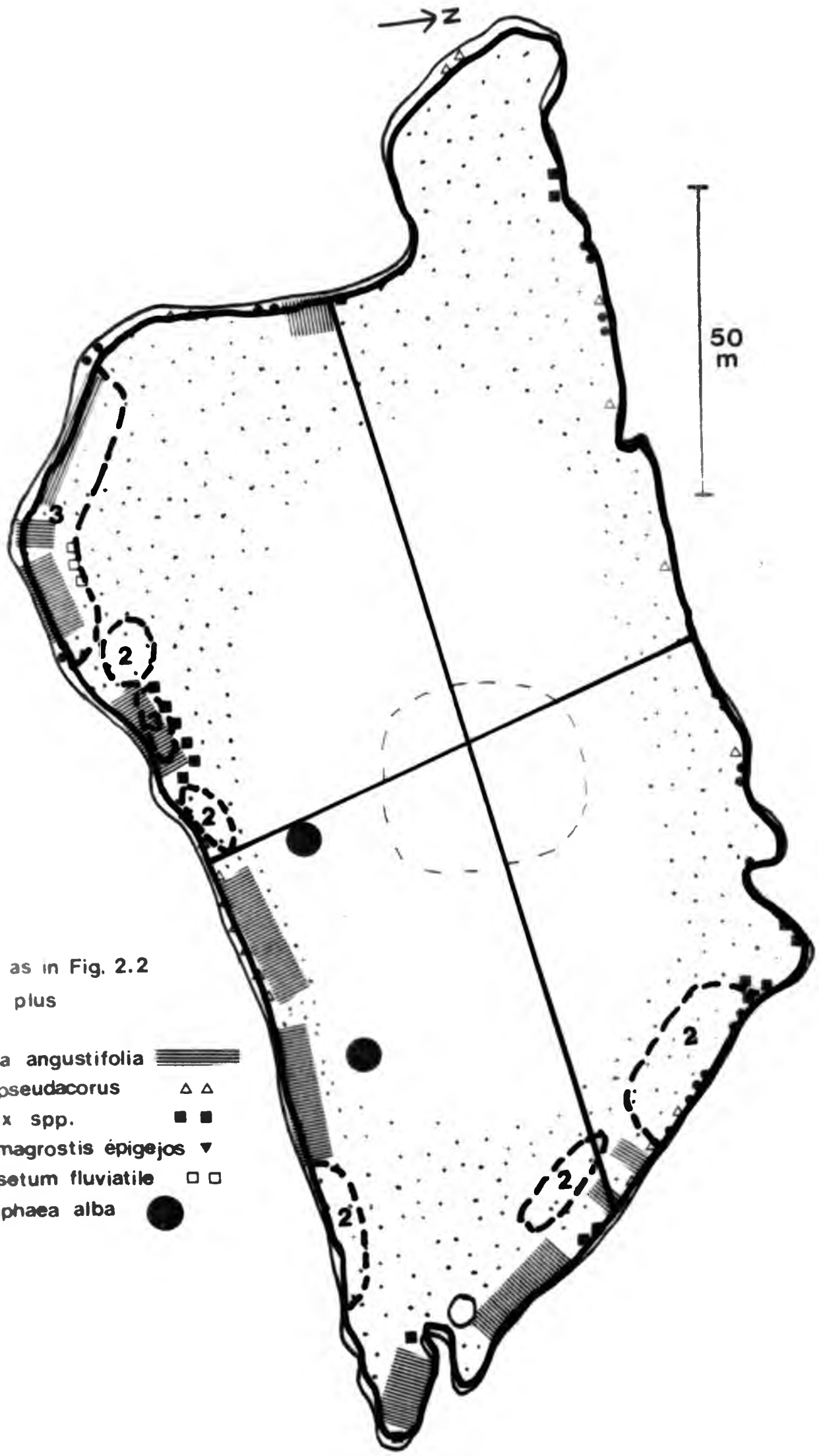
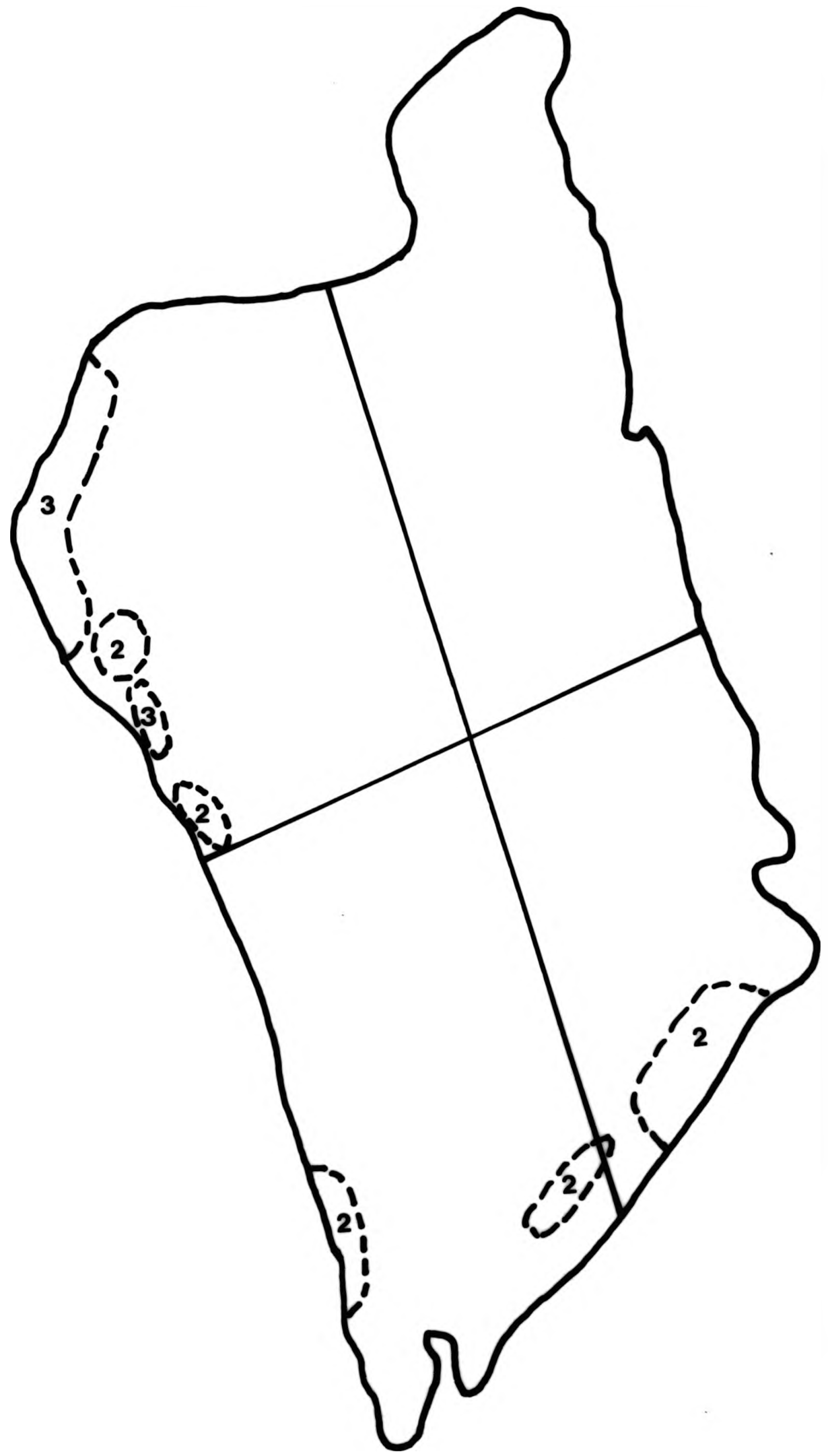


FIGURE 2.3 Map of Yateley 4 showing the distribution of the common species of aquatic macrophytes in 1978 and 1979. The overlay shows the marginal sampling sites. The weedbeds are not drawn to scale. The position of the experimental fish cages is shown by the dotted line. Further information on the sites is given in Table 2.3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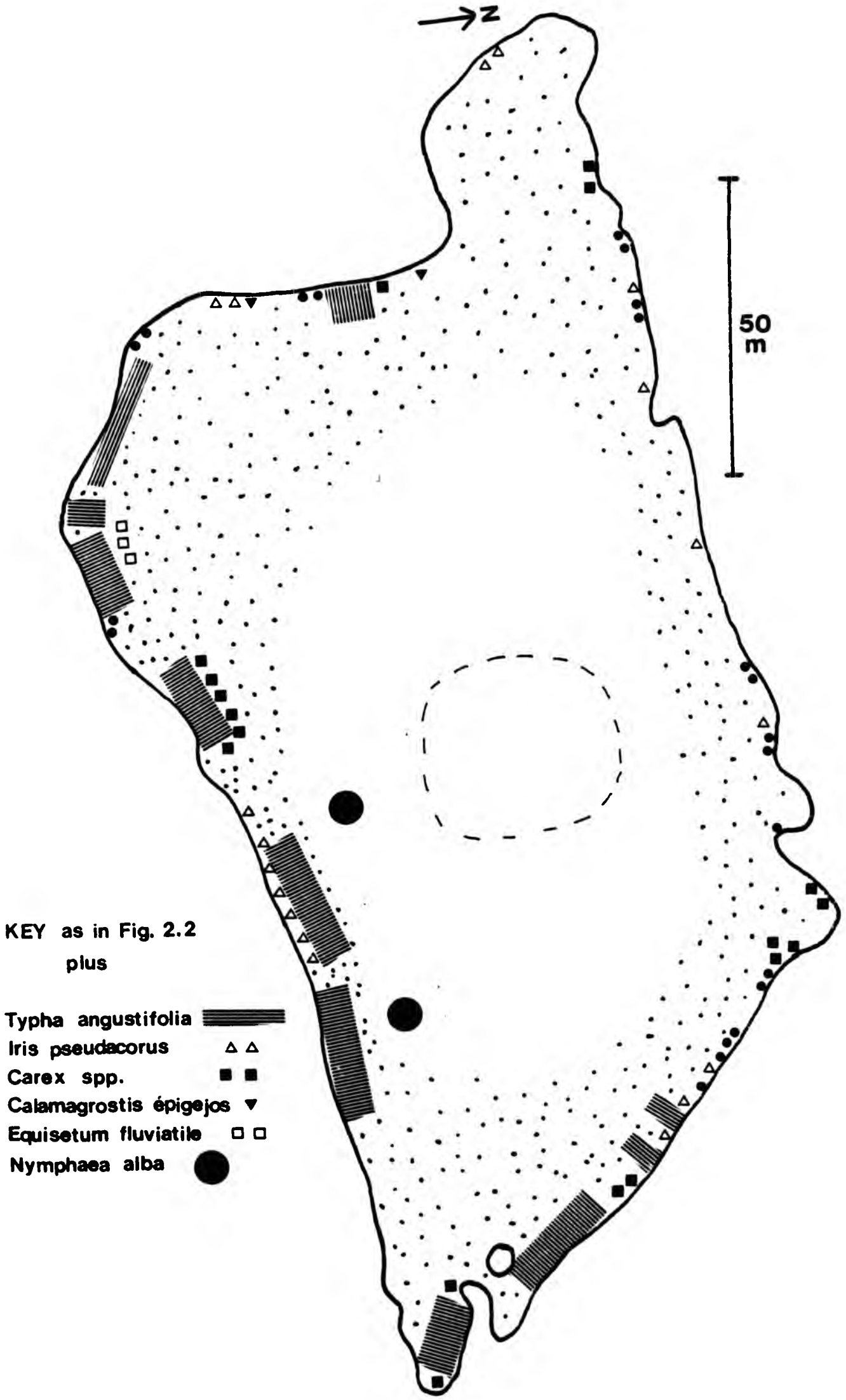

FIGURE 2.3 Map of Yateley 4 showing the distribution of the common species of aquatic macrophytes in 1978 and 1979. The overlay shows the marginal sampling sites. The weedbeds are not drawn to scale. The position of the experimental fish cages is shown by the dotted line. Further information on the sites is given in Table 2.3

in Farnborough and transparency was usually high.

The emergent vegetation in 1978 and 1979, shown in Table 2.1, consisted mainly of Typha latifolia and Typha angustifolia with Iris pseudacorus in shallower water. All were equally abundant. Juncus effusus was less common than in Farnborough but Carex pseudocyperus occurred in several shady places. Equisetum fluviatile occurred in one area and appeared to be spreading throughout 1979 but was not found in 1981. Flowering herbs were abundant along the gently sloping banks. The most common were Lythrum salicaria, Epilobium hirsutum, Mentha aquatica, Lysimachia vulgaris, Galium palustre, Roripoa nasturtium-aquaticum and Stachys palustris.

The most abundant submerged macrophyte was Elodea canadensis which covered much of the lake bottom because of the high water transparency and grew thickly on the sloping margins. The S.W. corner of the lake was overgrown with Elodea and blanket weed (Spirogyra) for much of the summer. There were two well established beds of Nymphaea alba on the southern side of the lake. For convenience, this lake will be referred to from now on as Yateley.

2.2 Microcrustacean sampling methods and analytical techniques.

2.2.1 Sampling method

A tube sampler which met the following requirements was used to collect quantitative microcrustacean samples.

1. the sampler needed to be suitable for use in both the open water area and the marginal weedbeds which contained plants in varying depths of water, as comparable quantitative samples were required. The sampling of open-water zooplankton is well documented (Bottrell et al, 1976) and there are now generally accepted techniques for their capture. However, many different kinds of samplers have been used to collect marginal

organisms (Smyly, 1957; Shiel, 1976) most of which would not have met the second requirement of this study and were not easily comparable with open water methods.

2. the weedbed should not be destroyed during sampling. Many weedbeds have been sampled with grabs or bins (Smyly, 1957; Korinkova, 1971; Macan, 1977a) but weekly sampling with such a destructive sampler would eventually result in a changed habitat.

3. the sampler was required to collect free-swimming crustacea living among the macrophytes rather than those on the bottom or those attached to the plants. Many studies of macrophytic faunal associations have involved the collection of all the organisms inhabiting all micro-habitats in a weedbed, while previous work on the gravel pits (Cook, 1979) and elsewhere (Guma'a, 1978b) has shown that the coarse fish fry feed mainly on planktonic organisms.

4. In shallow lakes with complete mixing it is necessary to sample to the bottom of the water column, as both pelagic and littoral microcrustacea undertake vertical migrations (Szlauer, 1963).

5. The sampler needed to be operable by one person.

When it is not necessary to know the vertical distribution of the animals, a tube can be used to sample zooplankton (Tonolli, 1971). The flexible tube sampler of Pennak (1962) was copied in rigid perspex. It consisted of two clear perspex tubes, internal diameter 5 cm, one tube measuring 2 m for use in the open water and the other tube of 1m for use in the margins. The tubes could be joined for sampling in deeper water if necessary. The tubes were marked off in 0.1 m graduations for measurement of the sample volume. George and Owen (1978) have criticised Pennak's tube on the grounds that the diameter (6 cm) was too narrow and would cause edge effects as it dropped through the water column and they recommend using a corrugated tube of 10 cm diameter

(which would require a closing mechanism and lifting gear). However, de Nie et al (1980) stated that a 4 cm diameter transparent tube would cause less turbulence than a wider Friedinger sampler and Bottrell et al (1976) stated that rapid closing of the sampler and minimal response by the organisms are the major factors determining the efficiency of a sampler. The tube used in this study was transparent and dropped rapidly because of its weight; both these factors would minimise zooplankton escape and the 5 cm diameter was sufficiently wide to cut down edge effects. To operate, the tube was dropped from an inflateable dinghy, through the water column to the lake bottom, taking care not to dig into the mud, and a rubber bung inserted into the top. This was sufficient to retain the enclosed water column and the tube was rapidly lifted until a hand could be placed underneath the open end to allow withdrawal from the water. The length of the core was read off to the nearest 0.05 m (=0.08 litres) and then the tube was emptied into a large container and the whole sample concentrated by filtration through 80 um mesh.

The marginal weedbed crustacea were sampled in a similar manner using the 1 m tube, as the average depth of water in the wedbeds was 0.5 m. The tube was dropped vertically through the vegetation.

These two samplers were used for all open water and weedbed sampling during this study. The 1 m tube was also used to collect microcrustacean samples within the experimental enclosures in 1978 and 1979, and therefore all samples were comparable with those of Cook (1979) who used the same sampler in his work on the lakes and also much of the work of Straskraba (1963, 1967) and Pennak (1962, 1965). The only other study of zooplankton in the gravel-pit lakes was done by Barber (1976) using an integrating pump sampler which removed water simultaneously from different depths. It is doubtful whether this

sampler did remove equal volumes from different depths and some zooplankters may have been able to outswim the suction pressure (Drenner et al, 1978).

2.2.2 Sampling programme in Farnborough.

Microcrustacean samples were collected from the marginal weedbeds from April to December in 1977, and from the open water between June to December. The average sampling interval was 13 days. Table 2.2 summarizes the volumes collected and the sites sampled.

A stratified random sampling system was used to select the sampling stations in the open water. The lake area was divided into four sections (see Fig. 2.2) and five stations were selected within each area using random numbers, (on three occasions only 3 stations were used in each area). One vertical core sample was collected at each station giving one composite sample of 20 cores. Replicate open-water samples were not taken during this part of the study for two reasons. Cook (1979) made an estimate of the sampling error using this system and found that 20 cores were sufficient to cover the zooplankton patchiness. This will be discussed further in Chapter 3. Secondly, at this stage interest was centred mainly on the comparison of the weedbed crustacea with fish diet and the open-water samples were collected to provide information on species composition and relative abundance for comparison with the marginal crustacea, so that very accurate density estimates for the open water were not required. On one sampling visit the open-water sample was not collected because the inflateable dinghy was punctured in the field.

Fig. 2.2 shows the marginal sampling sites. The main species of aquatic macrophytes sampled for microcrustacea were Elodea canadensis (site 2), Sparganium erectum and Typha latifolia (site 4) and

Table 2.2 The microcrustacean sampling programme in Farnborough in 1977.

SITE TYPE	SITE NO.	n	MEAN VOL.	RANGE	DATES OF SAMPLING
Open water		14	41.9	25-55	9.6-14.12
Elodea	2	7	11.1	7-16	7.7-9.11
	3	5			
	11	1			
	1	1			
Sp/Ty	4	9	10.9	7-15	7.7-25.10
P.natans	6	5	11.9	8-15	7.7-25.10
	5	5			
P.natans/El	12	2	11.9	7-16	7.7-9.11
	6	3			
	3	1			
Marginal weedbeds		11	16.6	6-33	23.5-27.6 26.11-14.12
Narrow tube samoler					
Elodea	1	4	3.4		9.4-27.6
Sp/Ty	4	5	2.3		9.4-15.5
Marginal		4	3.5		9.4-7.7

n = number of samples collected from each site.
The volume is given in litres with the min. and max. volumes collected from each site.
The sites are illustrated on Figure 2.1

Sp/Ty = Sparganium and Typha P. natans/El = P. natans and Elodea.

Potamogeton natans (sites 5 and 6). Sparganium and Typha are structurally similar. It was difficult to find pure stands of each species and so a site was chosen containing both but no Elodea or P. natans. On each visit to the lake one or more samples were collected from these sites and also other marginal sites depending upon the state of the vegetation and number of anglers present. It was not always possible to sample in the main sites because of the presence of anglers either in the process of fishing or having previously stirred up the water. There were also seasonal changes in the size of the weedbeds, and the degree to which a stand remained mono-specific varied. In particular, much of the Elodea became overgrown with P. natans in the autumn so that it was not often possible to sample within the two species separately. For this reason some samples were designated P. natans/Elodea. Samples referred to as marginal samples, consisted of both those taken from several sites collectively earlier in the sampling programme and those taken in the autumn when the macrophytes were dying down.

Each weedbed sample consisted of eight vertical cores collected at random within the site either by wading or from a boat. The number of cores collected was a compromise between obtaining a large volume from many cores and causing too much disturbance in the weedbed to allow sampling to continue. The average volume taken was 12 litres and sample volumes increased slightly through the summer as the vegetation extended into deeper water. Estimates of sampling error with the shorter tube sampler in a weedbed were made in 1977 and will be discussed in Chapter 3.

At the beginning of 1977, samples of marginal microcrustacea, of smaller volume, were collected with a narrower 1 m perspex tube, (internal diameter 3.2 cm). These have been included in later analyses

because they do provide information on seasonal population changes although this sampler was later replaced by the wider tube. They have been added separately to the bottom of Table 2.2.

2.2.3 The sampling programme in Yateley in 1978 and 1979.

A simplified sampling programme was undertaken in both years in Yateley, in conjunction with the caging experiments. Sampling was carried out from June to September in both years. The average sampling interval was 13 days in 1978 and six weeks in 1979. Eight sampling trips were made in 1978 and three in 1979.

The open water was sampled as previously described and one sample of 20 vertical cores was collected in 1978. In 1979 two open-water samples were taken on each occasion to obtain an estimate of sampling error. Table 2.3 summarizes this sampling programme.

The weedbed crustacea were sampled at two marginal sites as shown in Fig. 2.3. The sites were selected on the basis of plant structure rather than by species. Site 2 contained Elodea canadensis growing in shallow water in several places around the margins. Site 3 contained Elodea growing around Typha spp. bases in deeper water and including the plant/open water interface. Therefore, inshore crustacea were compared with both crustacea living at the junction of the littoral and the open-water areas, and to the fully open water region. The marginal samples were not intended to be replicates of the same area but in comparison to the open water they could be regarded as replicate samples of marginal crustacea. Fifteen vertical cores were taken at random in site 2, and 10 in site 3. In 1979 duplicate samples were collected from Elodea except on one occasion when children pulled the plants out at the site after the first sample had been taken.

Table 2.3 also shows the microcrustacean sampling programme

Table 2.3 The microcrustacean sampling programe in Yateley in 1978 and 1979.

SITE TYPE	SITE NO.	n	MEAN VOL.	RANGE	DATES OF SAMPLING
1978					
Open water		8	53.1	45-69	
Elodea	2	8	19.8	15-25	28.6-29.9
Elodea/Typha	3	8	17.5	12-25	
Cages no weed	1	7	22.5		
	2	7	22.5		
	5	5	24.7		
	6	6	24.0		
Cages weed	3	7	30.8		10.7-29.9
	4	7	28.9		
	7	7	31.1		
	8	7	29.1		
1979					
Open water		6	55.5		
Elodea	2	5	14.7		13.6-7.9
Elodea/Typha	3	3	15.1		
Cages no weed	7	3	36.2		13.6-7.9
	10	1	36.1		13.6
	12	3	35.5		13.6-7.9
	11	2	36.2		25.7,7.9
Cages weed	4	3	36.2		13.6-7.9
	6	1	36.2		13.6
	9	3	35.9		13.6-7.9
	8	2	34.9		25.7,7.9

n = number of samples collected from each site.
The volume is given in litres with the min. and max. volumes collected from each site.
The sites are illustrated on Figure 2.3

carried out in the experimental enclosures in both years. The cages were numbered and half of them contained artificial substrates. About 15 vertical cores were taken in each cage in 1978 and 20 in 1979. They were selected on a regular grid pattern across the cage to eliminate bias due to choosing too many stations either close to the sides or within particularly thick areas of artificial macrophyte.

Throughout this study all samples were filtered after collection through 80 um nylon mesh. This was not fine enough to prevent the loss of smaller rotifers and possibly some copepod nauplii but all other crustacea and larger rotifers were retained on the filter. In 1977 and 1978 all samples were preserved in 4% formalin to which sucrose was added (40 g/litre) to prevent carapace ballooning and egg loss in Cladocera (Haney and Hall, 1973). This also made it easier to measure body length and count ovigerous females. In 1979 all samples were preserved in 50% alcohol and counted soon after collection. Eosin was added to most samples to render the crustacea more visible during the sorting process.

Most of the weedbed samples required cleaning before counting. Large pieces of plant debris and occasional invertebrates such as chironomids were picked out by hand and two methods were then used to remove crustacea from the remaining mud. The first was the sugar flotation method of Anderson (1959) using a sucrose solution of specific gravity 1.12 (370 g/litre) to float organisms out of the mud. This proved very successful although some groups, in particular ostracods and male cyclopoid copepods, tended to sink with the mud. The second method was to use a set of nylon filters of mesh sizes 600 um, 271 um, and 92 um to remove fractions of different sized particles. In practise both methods were often used; the seiving removed large particles and

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broke down the mud evenly so that flotation was more successful and this combination resulted in the recovery of virtually all the organisms in a sample. The remaining mud was always examined and on the few occasions when >95% removal was not accomplished those organisms remaining in the mud were also counted to the same precision as the main sample and the two added together. It sometimes took several hours to clean a weedbed sample and it was this stage of the processing which limited the number of samples which could be examined.

2.2.5 Counting and sub-sampling.

The samples were counted in an open circular perspex counting tray with a capacity of 10 ml, clamped to the stage of a binocular microscope so that it revolved freely. The open tray possessed the advantage over a counting cell in that animals could be moved around in it if one was obscuring another, and they could be lined up against the eyepiece micrometer for measurement.

All the microcrustacean samples were sub-sampled in the following manner for counting. The sample was made up to either 50 ml or 100 ml in a beaker and stirred vigorously for several seconds to obtain a random distribution of organisms. A sub-sample of known volume was taken with a flat ended 5 ml pipette, internal diameter 6 mm. Successive aliquots were counted at x16 or x32 magnification until at least 100 specimens of each of the commoner species in the sample had been counted, in accordance with the recommendations of Lund, Kipling and Le Cren (1958) who state that a count of 100, assuming a random distribution, possesses 95% confidence limits of 82 and 122 (an error of ±20% of the mean); to obtain confidence limits within ±10% of the mean requires a count of 400.

The distribution of organisms in the subsamples was tested for

agreement with a Poisson distribution using a χ^2 test (Elliot, 1977). With very few exceptions the χ^2 values fell within the 5% significance levels so agreement with a Poisson was accepted. There was thus no evidence that a random distribution was not being obtained in the sub-sampling vessel. Fig. 2.4 shows the χ^2 values obtained from a random selection of sub-samples and one can see that the distribution in the vessel tended towards a regular distribution which would have narrower confidence limits than a Poisson.

Crustacean abundance was expressed as numbers/litre. Densities in the marginal weedbeds were expressed in this way rather than as numbers per surface area of plant (which would have required removal of the plant for measurement) as being a more realistic determination of the food available to the fish. It also simplified comparisons with the open-water samples.

2.2.6 Identification and taxonomy.

Rotifers apart from *Asplanchna priodonta* and *Conochilus hippocrepis* were not counted in this work. Other species were noted when abundant in net collections and the key of Pontin (1978) was used for identification.

All cladocerans were identified to species and the nomenclature used follows that of Flossner (1972) with two exceptions. These were the use of *Pleuroxus truncatus* instead of *Peracantha truncata* following Smirnov (1971), and *Leydigia leydigi* for *L. quadrangularis*, as in Scourfield and Harding (1966). However, Smirnov's (1971) placing of *Alona affinis* and *A. intermedia* into the genus *Biapertura* on the basis of head pore counts has not been followed.

The main problem of identification occurred in the separation of two species of *Daphnia*, as Pejler (1973) stated:

"when examining possible correlations between fish fauna and crustacean zooplankton... the work had to be based upon a taxonomic ground as firm as possible. Most crustaceans did not represent any great difficulty in this respect, the genus Daphnia, however, being an exception."

Both Daphnia longispina and D. galeata occurred in Farnborough, (confirmed by Hrbacek and Korinek, pers. comm.). While the possession of a head crest or helmet distinguished galeata from longispina, round headed specimens could not be differentiated easily and males appear identical. As neither was ever very abundant in Farnborough it was decided to count them as one category. No problems with this compromise were encountered.

The other identification problem arose over the similarity between Alona affinis and A. quadrangularis at low magnification and sometimes at high magnification. Flossner (1964) found that the shape of the post-abdomen of A. affinis can vary with habitat. During analysis of samples specimens were examined for possession of the diagnostic spinules on the claw spine (A. affinis) and it appeared that A. affinis usually occurred in weedbeds while A. quadrangularis was usually more common in the open water. This observation was used to separate indeterminate specimens. Whiteside (1974) found a similar habitat distinction in these two species. Although counted separately as far as possible on occasions when they were abundant, the counts were added together for data analysis. In following tables, the counts are given as A. quadrangularis in the open water and A. affinis in the weedbeds.

Egg bearing female cylopoid copepods were identified to species but as it is difficult to identify copepodites, all cyclopoids were counted together as one category and note made of the most abundant species of adults in each sample if sufficient egg bearing females were present. All nauplii larvae, cyclopoid and calanoid, were counted together. The key of Harding and Smith (1974) was used to identify

adult cyclopoid and calanoid copepods.

Polyvinyl lactophenol stained with lignin pink was used to mount specimens for identification.

2.2.7 Body length measurement and biomass determination.

Body length of the microcrustacea was measured under an eyepiece micrometer at x32 magnification to the nearest 25 um. Cladocera were measured from the top of the head to the base of the carapace excluding any tail spines or head crests and copepods were measured from the top of the head to the base of the furcal rami, excluding setae which can be very long but contribute little to total body weight (Burgis, 1974). Asplanchna were not measured because they shrink in formalin. The number of measurements made for each species on any date depended upon their abundance in the sample and their size; more measurements were made of species covering a large size range e.g Daphnia and Sida. 60 or more individuals of the common species were normally measured from each sample. To ensure a random selection of individuals all specimens in a sub-sample were measured.

Length/dry weight regression equations were used to calculate microcrustacean dry weight biomass from the body length measurements. Most of the regressions were obtained from the literature as shown in Table 2.4 but those for Cyclops vernalis americanus, Sida crystallina and Simocephalus vetulus were calculated from length and dry weight measurements made during this study. The results of Dumont et al (1975), the main source of information on length/weight relationships, are slightly questionable because they dried the crustacea at 110 °C, which drives off structural water and volatile fats, but in the absence of other information, their regressions were used in this study.

To obtain length/dry weight regressions for the three species

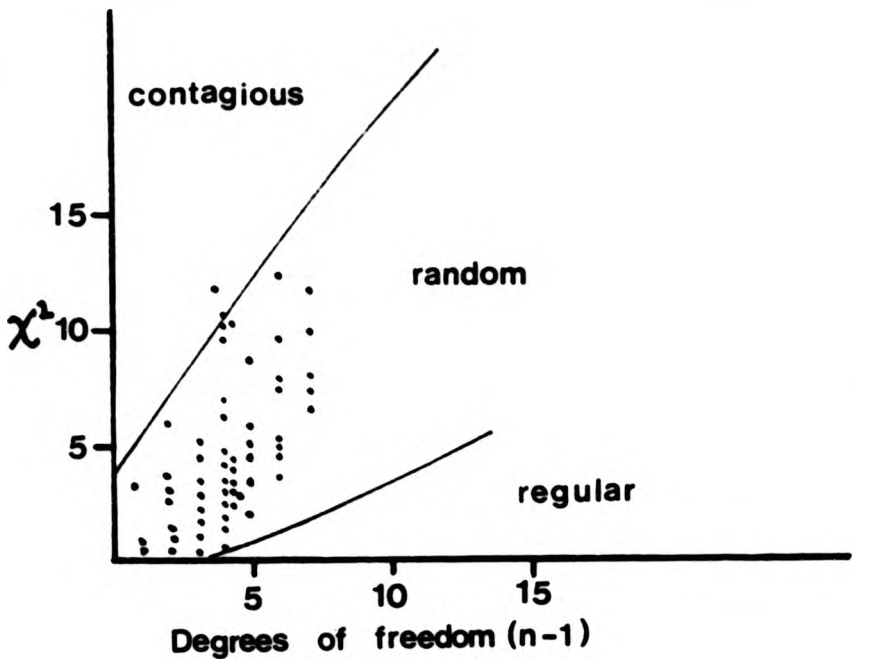

FIGURE 2.4 The 5% significance levels of χ^2 in a Poisson distribution. The points are the χ^2 values obtained from counting sub-samples of microcrustacea. n=number of sub-samples.

Table 2.4 Length/dry weight regression equations used for the estimation of crustacean dry weight biomass.

All regressions are in the form log10dry weight = a + b (log10length).

SPECIES	a	b	UNITS	SOURCE
Cyclops vernalis americanus	0.868	1.618	mm ug	3
Diaptomus gracilis	-6.102	2.33	um ug	1
Nauplii	-5.932	2.2	um ug	2
Daphnia ambigua	-6.201	2.29	um ug	1
D. longispina	0.597	2.557	mm ug	4
Ceriodaphnia pulchella*	-5.770	2.26	um ug	1
Bosmina longirostris	1.178	2.529	mm ug	5
Bosmina ovigerous	2.033	4.27	mm ug	1
Acroperus harpae	-2.043	0.85	um ug	1
Alona affinis	1.202	3.84	mm ug	1
A. rectangula**	1.472	3.48	mm ug	1
Pleuroxus aduncus***	1.551	4.03	mm ug	1
Chydorus sphaericus	1.952	3.93	mm ug	1
Sida crystallina	0.834	3.265	mm ug	3
Simocephalus vetulus	1.095	3.043	mm ug	3
Eurycercus lamellatus	0.995	3.196	mm ug	1

* The published regression was prepared for C. quadrangula.
** The regression for A. rectangula was also used for A. guttata.
*** The regression for P. aduncus was also used for P. denticulatus.

Source

1 Dumont et al, 1975
2 Burgis, 1975
3 This thesis
4 Munro in Bottrell et al, 1976
5 Bottrell in " " "

mentioned above, individual animals (>30) were dried on pre-weighed metal foil at either 60°C for about 24 hours to constant weight or in a dessicator at room temperature as recommended by Lovegrove (1966). No differences were found in the length/weight relationships obtained by the two methods. They were weighed on the 1 mg range of a Cahn electrobalance to the nearest ug. All crustacea used for these measurements had been preserved in 4% formalin and washed in several changes of distilled water before measuring and drying. Dumont et al (1975) have shown that no measurable shrinkage occurs to crustacean zooplankters preserved in formalin. The length/dry weight relationship of a species can vary with habitat and water body (Dumont et al, 1975). Therefore published regressions vary for some species, e.g Ceriodaphnia and so individuals of the more important crustacea were measured and weighed and the regression which provided the best fit to these observations was selected from those available in the literature. A separate regression was used for ovigerous Bosmina because they were very abundant on some occasions, and being small, the weight of egg was a considerable proportion of the total body weight. In order to facilitate computation of biomass, the body lengths were grouped into larger size categories (given in the apendix) selected in proportion to the size range of the species. Measurements of the smaller crustacea; nauplii, Alona guttata, A. rectangula, Chydorus and Bosmina did not require this treatment. These length frequency distributions were used only in biomass calculations and all other analyses were performed on the raw data, so that the average of the length frequencies is not always quite the same as the average of body size measurements given in later tables, e.g. 1.2% difference for Ceriodaphnia, 1.3% for Cyclops and 2.5% difference for Sida.

2.3 Fish sampling, growth measurements and gut analysis.

Treasurer (1978) reveiwed methods used for sampling O+ fish. Bagenal (1978) has also discussed the specific problems associated with the examination of young fish populations; the main ones being finding them, catching them, and handling them without harm. It is also difficult to obtain accurate population estimates of animals with a contagious distribution. Bagenal and Nellon (1980) have recently summarised methods currently in use for the study of young fish and Coles (1981) has discussed methods for catching young perch.

As the main reason for sampling the O+ roach and O+ perch was to examine their gut contents, the simplest methods available were used for their capture and no attempt was made to estimate population numbers on a regular basis.

2.3.1 Sampling and population estimates of O+ roach and perch.

In 1977 O+ fish were sampled from the marginal weedbeds for the diet study in Farnborough at fortnightly intervals from June to September with a large circular framed hand net with a buoyant rim (diameter 1 m) on a long handle. The net was pushed through a weedbed and allowed to float up so that shoals of young fish were captured without damage. Very few perch could be caught in 1977 so that the sampling effort was concentrated on the roach, although the methods used would have been equally effective for perch had they been present. Prior to this, newly hatched roach were caught in the margins with an F.B.A. pond net during the first 2-3 weeks of life. When the roach measured 3.0 cm (mid-August) a small meshed seine net (mesh size 8.0 mm) was used in conjunction with the large hand net to counteract any selection for less active fish by the hand net. The seine net measured

10 m long X 1.2 m deep with a bag and could be set in an arc around a weedbed from the bank by one operator. The average sample size was 40 fish, although on two occasions over 300 roach were collected.

The weedbed sites sampled for O+ roach and perch were usually the same as those sampled for microcrustacea although it was not always possible to catch fish from the same site or from more than one site. Normally samples were not taken from the open-water region as the young fish were usually to be found among the marginal vegetation. Evidence for this concentration of young fish in the margins is given in Chapter 4.

In 1978 and 1979 O+ roach and perch were sampled at intervals in Farnborough with both the large hand net and the minnow seine in order to obtain growth measurements for comparison with the caged fish. During an intensive search for O+ perch in September 1979 several larger fine meshed seine nets were used in an attempt to catch some perch, with little success. Fishing trips were also made to provide roach and perch for the caging experiments and are described in the next section .

Two population estimates of the O+ roach and perch were carried out in Farnborough in 1977 using 12 buoyant nets of the type described by Bagenal (1974). Twelve nets were set at one time at randomly selected open-water stations in the lake. After about 1 hour they rose and were then re-set so that normally 60 or 72 were set in one day. They provided quantitative estimates of the numbers of small (<4.0 cm) fish in the area of lake sampled. Hewitt (1979) measured the net avoidance of these nets by small roach and found it to be negligible, although Cook (1979) concluded that as they grew the roach and perch became able to avoid the nets so that more reliance can be placed on the estimates made in the spring than those made in the autumn.

In September 1977 an attempt was made to estimate the densities of

0+ roach and perch among the marginal weedbeds in Farnborough using the buoyant nets. It was hoped that the results would show whether the roach and perch displayed any tendency to congregate in specific weeds but the results were inconclusive. However, they did provide information on marginal fish densities and fish samples for diet analysis from both marginal weedy and marginal open area.

All 0+ fish caught in 1977 were killed immediately with either MS 222 or benzocaine to prevent egestion of gut contents and then preserved in 4% formalin. In the laboratory they were soaked in water for a few hours to remove the formalin, fork length was measured to the nearest mm and wet weight to the nearest mg on a 3-figure Oertling top-pan balance. Dry weights were obtained for some fish after drying on pre-weighed metal foil to constant weight in an oven at 60 °C. They were then weighed to the nearest mg on a 4-figure Oertling R42 balance. Wet weights could not be measured on very small, preserved roach, less than 1.5 cm, as they dried out on exposure to air. They were therefore dried as above for dry weight estimation only and weighed on a Cahn electrobalance to the nearest ug.

In 1978 and 1979 some of the 0+ roach and 0+ perch from Farnborough were transported live in plastic bags of oxygenated water to the laboratory for fresh length and weight measurement as the caged fish with which they were to be compared were examined fresh at the end of the experiments. They were weighed and measured immediately after being killed in MS 222. The effects of formalin upon the size of small fish have been documented (Engel, 1974) and it appears to be necessary to determine the effects for each species and lake so that preserved and fresh measurements can be compared. Fig. 2.5 shows a comparison of changes in the mean length and weight of roach and perch samples, measured before and after preservation in 4% formalin. Roach showed a

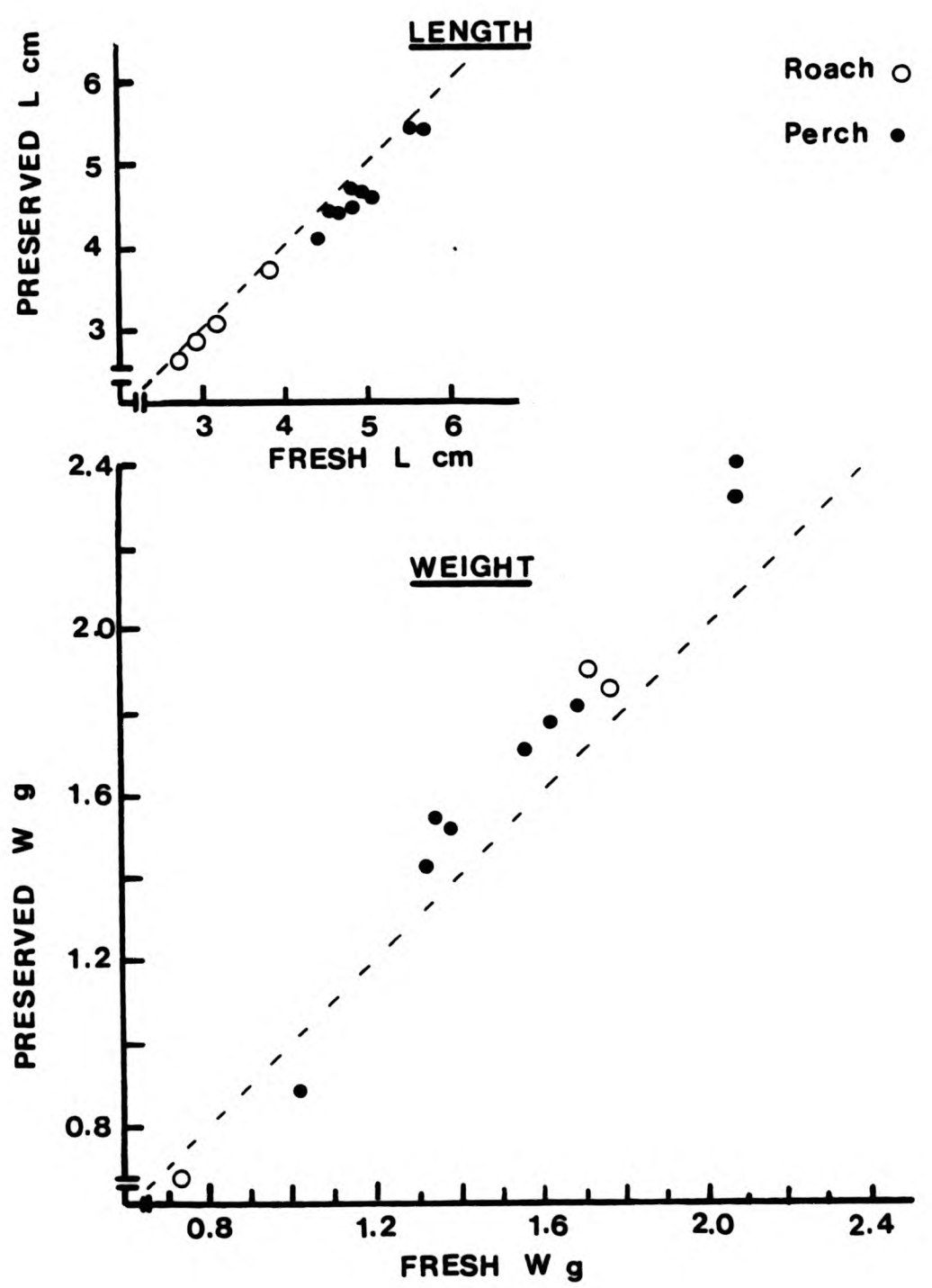

FIGURE 2.5 The relationship of preserved fork length and wet weight to fresh fork length and wet weight in 0+ roach and 0+ perch in Farnborough. The dotted line is the line of direct proportion. Each point is the mean length or weight of a sample of fish.

small and uniform decrease in length (4%) while the perch also shrank to a similar but more varied degree. The roach usually gained weight (2%) on preservation, although one sample lost weight. The perch gained more weight than the roach (5.7%), although again one sample lost weight, and the larger perch had a greater weight gain (10%) than the small perch (4.7%). These changes occurred within the first 24 hours after preservation after which length and weight remained stable. Therefore, if a length/weight regression based on preserved fish is used to predict the weight of a fresh fish the weight will be overestimated. Condition factors of preserved fish will also be overestimates as they would be based on greater weight and shorter length measurements than the fresh counterpart.

Table 2.5 The percentage increase or decrease in mean weight and length of samples of O+ roach and perch after preservation in 4% formalin.

ROACH		PERCH	
L	W	L	W
-3.0	+5.5	-7.1	-15.3
-4.9	+7.9	-1.1	+7.3
-4.5	-7.2	-3.8	+8.4
-3.6		-0.2	+4.7
		-4.9	+9.1
		-3.5	+5.3
		-5.7	+8.4
		-0.9	+10.7
		-3.3	+12.5

L = fork length in cm
W = wet weight in g

The keys of Bracken and Kennedy (1967) and Maitland (1972) were used to identify O+ fish (Young beam and rudd were also present in some samples). Roach and rudd appeared to be distinctly different in Farnborough although the possibility of roach/rudd hybrids (Wheeler, 1976) being present was not investigated.

As this study concentrated upon O+ fish which were sampled throughout the year after hatching, routine ageing was not done.

However, scales from larger roach individuals were examined to ensure that they were 0+ fish. Scales were removed from the shoulder region, washed in water and rubbed between fingers to clean them. They were mounted dry between two microscope slides and viewed through a microfilm reader. No attempt was made to age perch opercular bones. Ageing was facilitated by comparison with the scales and length frequency distributions of the 1975 and 1976 year classes of roach and perch collected from Farnborough by Cook (1979).

2.3.2 Examination of gut contents.

A sub-sample of fish from each date was taken for diet anaysis. The sub-sample was selected to be representative of the range of body lengths present in the sample. A random selection was not made as the diet of the fish could vary with the fish size, and the original sample was presumed to be a random sample from the lake population. The alimentary canal of roach is not clearly differentiated into stomach and intestine (Al-Hussaini, 1949) and so the contents of the whole gut were examined. The gut was removed from the fish and the contents scraped out into a small petri dish. The food organisms were counted in the circular counting chamber at x16 magnification and identified to species as far as possible. Larger invertebrates such as chironomids were not usually identified beyond group as they were not sampled in the lake. When the guts were full, especially in the larger fish, sub-sampling was necessary. The contents were washed into a small vial, made up to 10 ml with water and shaken violently to break up food masses. Sub-samples of 1 ml or 2 ml were removed with a flat ended 2 ml pipette and counted to the same precision for the major species as in the lake microcrustacean samples. The entire sample was also examined for both less common and larger food items such as chironomid larvae and other insects and large

Eurycercus. Roach possess pharyngeal teeth which break up food on its passage into the gut and so their gut contents were extremely fragmented. Therefore a standard procedure was adopted for identification and counting as follows:

Bosmina - head and antennules counted.

Daphnia - head counted.

Ceriodaphnia - head counted although the carapace tended to remain whole.

Cyclopoid copepods - cephalothorax with antennules counted.

Chydorids - post-abdomens identified and carapaces counted.

Chironomid larvae - head capsules counted.

Sida - carapace usually whole

Young perch possess a well differentiated stomach and intestine and these were examined separately as many published studies of perch diet refer to stomach contents only. However, because the perch were small, the contents of the stomachs and intestines were summed to provide more complete information on food eaten. This also made the data more comparable with that from the roach. It was noticed that larger food organisms remained in the stomach while smaller items were more abundant in the intestine so that examination of the stomach only could provide an incomplete record of total gut contents. Perch usually swallow their food whole and there was little difficulty in recognising and counting food items. Stomach and intestine contents were scraped separately into small petri dishes and if sub-sampling was necessary the whole sample was first examined for larger food organisms which were removed before the shaking/sub-sampling procedure which broke up insect nymphs and larger crustacea (not present in roach guts) making it difficult to piece together parts of one animal.

Body lengths of food items were measured from the gut contents of

both roach and perch to investigate whether the fish showed any size biased selection during feeding and to estimate the dry weight biomass of the diet. These measurements must be viewed with caution because they were not from a random sample of the diet, as whole organsisms were not often encountered and the carapaces became distorted in the guts making them appear larger than they were.

2.3.3 Twenty-four hour diet studies.

An examination of the changes in diet of O+ roach over 24 hours was carried out twice in Farnborough during 1977. The first study was done on 7 July when the roach had a mean length of 1.8 cm. Samples were collected from the marginal weedbeds about every two hours from 0600 hours to midnight and then at 0400 hours the next day, using the large hand-net. The 10 samples of roach were taken from five marginal sites used in rotation to allow time for the fish to return to the sampling area. The roach were all killed in MS 222 and preserved in 4% formalin and then treated as follows, detailed methods being as previously described.

1. All roach were measured and weighed.
2. A random sub-sample was taken for dry weight measurements.
3. From each time sample, a representative sub-sample of 10 roach was selected; their guts removed, dried to constant weight and weighed on a Cahn electrobalance.
4. A random sub-sample of roach was taken to measure the dry weight of the gut minus food. The guts were removed, contents scraped out and the empty alimentary canals dried and weighed on the Cahn electrobalance. This provided a relationship between fish size and empty gut weight, so that total gut weights, obtained in 3. above could be corrected for fish size, to give the dry weight of food eaten.

5. Sub-samples were taken from each time sample for enumeration of gut contents.

Microcrustacean samples were taken at the same weedbed sites on seven occasions through the day.

In September, nine samples were collected from marginal weedbeds over the same time period, although unfortunately the midnight sample was lost. They were treated in a similar manner to those above but sub-samples of fish of similar size were selected from each time sample so that it was not necessary to obtain the weight of the empty guts. In stage 5. above 10 roach from each time sample were selected and the guts bulked together for counting apart from two in which all 10 guts were examined.

2.4 The cage experiments in Yateley.

2.4.1 Fish cages.

Cage experiments were carried out in 1978 and 1979 as described in Chapter 5. Eight floating fish cages were built in 1978. They had rigid wooden frames measuring 2m x 2m by 1m deep which enclosed a constant volume of 4 m^3 of water. A cage of this size was easy to handle and could be transported to the site by van. The wooden frames could be dismantled for transport and were bolted together at the lakeside. Net bags of the same size were stretched over the outside of the frames. They had nylon collars which were fastened on to the top of the frames by copper tacks. Nylon material was used to join the mesh edges together and all sewing was done with polyester thread. The netting used was either 3 mm or 8 mm mesh knotless netting (Fields "micromesh" or "polynet") in 1978 and 3 mm mesh netting in 1979. Polystyrene blocks fastened on to the upper corners of the cages provided buoyancy and each cage was anchored off a concrete block embedded in the mud. The cages

floated free of the lake bottom (mean depth 1.5 m) and were placed in the centre of the lake but not in a fixed pattern. The cages did not appear to swing around on the anchors to any extent. Plastic netting lids which could be pulled back for sampling were fastened over the tops (which protruded above the water surface by several cm) to keep out birds.

At the end of the experiment in 1978 some of the bolts holding the cage frames together became rusted up so that the frames had to be sawn apart. Therefore, when they were rebuilt in 1979, the cages were smaller than the 4 m^3 of 1978. Table 5.1 gives the individual cage volumes. Four new cages were built in 1979 and they were made to the smaller specification of 3.2 m^3.

During the experiment in 1978 some of the material binding the netting seams together rotted. When the experiment was repeated in 1979 the old nets were resewn with new, stronger material which was also used for the four new nets.

In both years half of the cages contained artificial substrates. The cages containing the artificial substrates will be referred to as weed cages (CW) and those without as non-weed cages (CNW). Plate 1 shows a weed cage prior to immersion in the lake and Plate 2 shows the cages in position in the lake (Page 244).

2.4.2 Artificial substrates.

Preliminary experiments with artificial substrates were carried out in early 1978 to determine whether plastic strips suspended in the water column in the centre of a gravel-pit lake would become colonised with littoral microcrustacea. This did occur and so the experiments using artificial substrates to simulate macrophytes went ahead.

Four sets of artificial substrates (plastic macrophytes) were made

in 1978 and a further two sets in 1979. They were based on those described by Macan and Kitching (1972). The materials used were rigid netlon mesh for the base and several kinds of polypropylene bags cut into strips to simulate plant stems. These were plastic bags, cut into strips 1 m by 3 cm, and mesh-like vegetable bags cut into wider strips of 1 m, to simulate Elodea. These were tied onto the netlon in groups of 4 at random intervals, and in a random mixture, roughly 10 cm apart. The netlon bases were firmly tied into the bottoms of the cages with nylon twine so that fish could not become trapped underneath and a brick was placed in the centre of each to counteract the buoyancy of the plastic. The strips floated vertically in the water column within the cage and filled roughly 2/3 of the volume; some weed free water remained for the fish to move around in. During 1978 as periphyton built up on the strips, they progressively sank towards the bottoms of the cages. In 1979 therefore, small pieces of polystyrene were stapled onto the upper ends of the plastic strips to provide extra buoyancy to counteract the weight of the periphyton. This proved very successful. In 1978 the artificial substrates were suspended from buoys in the centre of the lake for at least one month before the fish were introduced to the cages to allow time for any toxic compounds to leach out of the plastic and for invertebrates to move onto them and form stable populations. In 1979, the cages with the artificial substrates in place were positioned in the lake a month before fish stocking.

Both the mats of Macan and Kitching (1972) and Barber et al (1979) contained a known density of plastic strands arranded in a regular pattern. As the microcrustacean sampling in Farnborough (Chapter 3) did not show any such relationships no attempt was made to manufacture artificial substrates with a known density of strips although the mats did contain very similar numbers of strands.

2.4.3 Fish capture for stocking the cages.

The enclosure experiments were carried out in Yateley where, because of its rectangular shape, cages placed in the centre were out of reach of people on the banks. This would not have been the case at Farnborough (see Fig. 2.2). However, in both years the O+ fish used in the experiments were taken from Farnborough because they were abundant there and easily caught whereas in Yateley O+ fish were less abundant and less easily caught by seining among the dense vegetation. It was considered preferable to use fish from a known stock rather than to attempt to compare annual growth data from Farnborough with that for fish from another water body (Weatherley, 1972). The fish were caught in Farnborough with a seine net of 3 mm mesh knotless netting with an inflateable float line described by Bubb (1980). It was set in an arc from the bank and after about one hour the float line was inflated with compressed air so that the net rose through the water trapping fish with the minimum of damage. After capture the fish were immediately placed in cooled oxygenated carriers and taken to Yateley, (10 mins. drive, see Fig. 2.1). They were then transferred to one cage to recover and the survivors counted out into the other cages. The air temperature was high in June and mortalities during transport were high, particularly of the smaller and more delicate roach, which led to more perch than roach being used in the experiments. In 1978 when large numbers of fish were required for reasons given below, several fishing trips were necessary to obtain sufficient fish and not all cages were stocked on the same date and neither were all fish held for a recovery period before stocking (see Chapter 5). In 1979 fewer fish were needed and so all were caught on one date, left in one cage for a week and then the survivors counted out into the other cages.

A large fish sample (>50) was retained on all stocking trips for

length and weight measurements which were made on freshly killed fish prior to preservation as described in section 2.3.1.

In 1978 the caged roach and perch were sampled at intervals during the experiment, using a pair of butterfly nets on long handles to catch a sample of about 20 fish. They were anaesthetised in MS 222 and length measured. Their volume was then measured by displacement of water in a volumetric flask to provide an estimation of weight. A relationship between live weight and volume was obtained in the laboratory so that the volume measured in the field could be converted to weight. Although this was not needed in the final cage growth analyses it has been mentioned because it imposed an extra stress on the fish in 1978 (in addition to that caused by the initial capture), which was not imposed in 1979. On some occasions a sub-sample was killed and preserved in 4% formalin for diet analysis. Otherwise all fish were returned alive to the cages. Between 22 August and 15 September 1978 when the experiment ended the fish were not handled so that during the last month growth in the cages continued undisturbed.

In 1979 the fish were not handled at all between stocking in July and removal in September.

At the end of the experiment in 1978 all the 0+ fish were transported to the laboratory in bags of oxygenated water, killed in MS 222 and weighed and measured fresh. In 1979 a small sub-sample from each cage was removed and killed, measured and preserved in the field for gut analysis while the remainder were treated as before. Therefore all final length measurements were made on fresh fish. Mean fresh weight was predicted from the mean fresh length using fresh length/weight linear regression equations for each set of fresh fish.

2.5 Statistical analyses and data transformations.

The SPSS computer package (Nie et al, 1975) was used for all statistical analyses and data transformations.

The microcrustacean data had a contagious distribution (negative binomial); the variance of weed samples was greater than the mean. To determine the necessary transformation to normalise this data the relationship of the variance to the mean for all the main species in all weedbed samples was calculated according to Taylor's Power Law (Elliott, 1977). However, the value of p obtained in this way did not normalise the data as well as a log10(x+1) transformation. All microcrustacean counts were therefore transformed to log10(x+1) for analysis. Cassie (1971) recommends such a transformation for plankton data (normally contagiously distributed) containing zeros.

A log10 transformation was applied to all fish size measurements (Ricker, 1958).

No common transformation could be found to normalise the fish diet data, although both an arc sin and a square root transformation were tested. Therefore, fish diet data (percentage composition) were not transformed for analysis.

CHAPTER 3. RESULTS OF THE MICROCRUSTACEAN STUDIES IN THE GRAVEL-PIT LAKES.

3.1 Introduction.

In this chapter the numerical abundance, standing crop (dry weight biomass) and species composition of the open-water microcrustacean community will be compared with those of the combined weedbed microcrustacean samples, collected in Farnborough in 1977. For this purpose, microcrustacea were sampled at fortnightly intervals in the open water of Farnborough from June to December in 1977 and weedbed crustacea were sampled from April onwards as described in Chapter 2.

Replicate samples were not routinely collected because more information about the weedbed microcrustacea could be obtained by extending the sampling effort over a variety of habitats rather than by concentrating on one or two weedbed sites. Time did not allow replication of this extensive sampling programme. However, estimates of sampling error in both regions were made and some replication of sites was carried out.

Standing crops were estimated numerically and then converted to dry weight biomass using length/dry weight regressions and the length frequency histograms obtained from body measurements as described in Chapter 2.

The microcrustacea inhabiting the three plant types will also be compared with one another in terms of numerical density, dry weight standing crop and species composition. Size measurements were also made from the microcrustacea in the different weedbed samples to determine whether there were any differences in the size frequency distributions of the crustacea inhabiting the different plant species. It was not possible to carry out any form of association analysis upon the

microcrustacean data because of both the lack of replication and the small number of sites but some associations were apparent as will be shown.

The differences between the microcrustacea in the macrophytes and the open water in Yateley in 1978 and 1979 are illustrated in Chapter 5 (results of the caging experiments) but differences between the two types of littoral samples will be discussed in this chapter. The crustacea were sampled on eight occasions in 1978 and three times in 1979. Only numerical abundance was measured, biomass was not estimated.

For additional information on the species composition of the microcrustacean communities of the gravel-pit lakes, similar samples were collected periodically in other lakes as described in Chapter 1.

Physical and chemical measurements were not part of the routine work but some data on water temperature and dissolved oxygen were collected.

3.2 Temperature and oxygen.

In 1977 and 1979 water temperature was measured during sampling trips to Farnborough and Yateley with a mercury thermometer and Fig. 3.1 shows the seasonal changes in water temperature recorded in both these lakes. In 1978 a submerged temperature and oxygen recorder (STOR) was used to record diurnal changes in water temperature and dissolved oxygen at a depth of 1 m in the centre of the lake in Yateley. Because the recorder was faulty and only worked on two occasions in 1978, little information was obtained.

In 1977 the water temperature in Farnborough rose above 14°C in May and then declined slightly before rising to the summer peak of 25°C in early July. The temperature then slowly dropped and fell below 14°C during the latter part of September. Farnborough was frozen in January

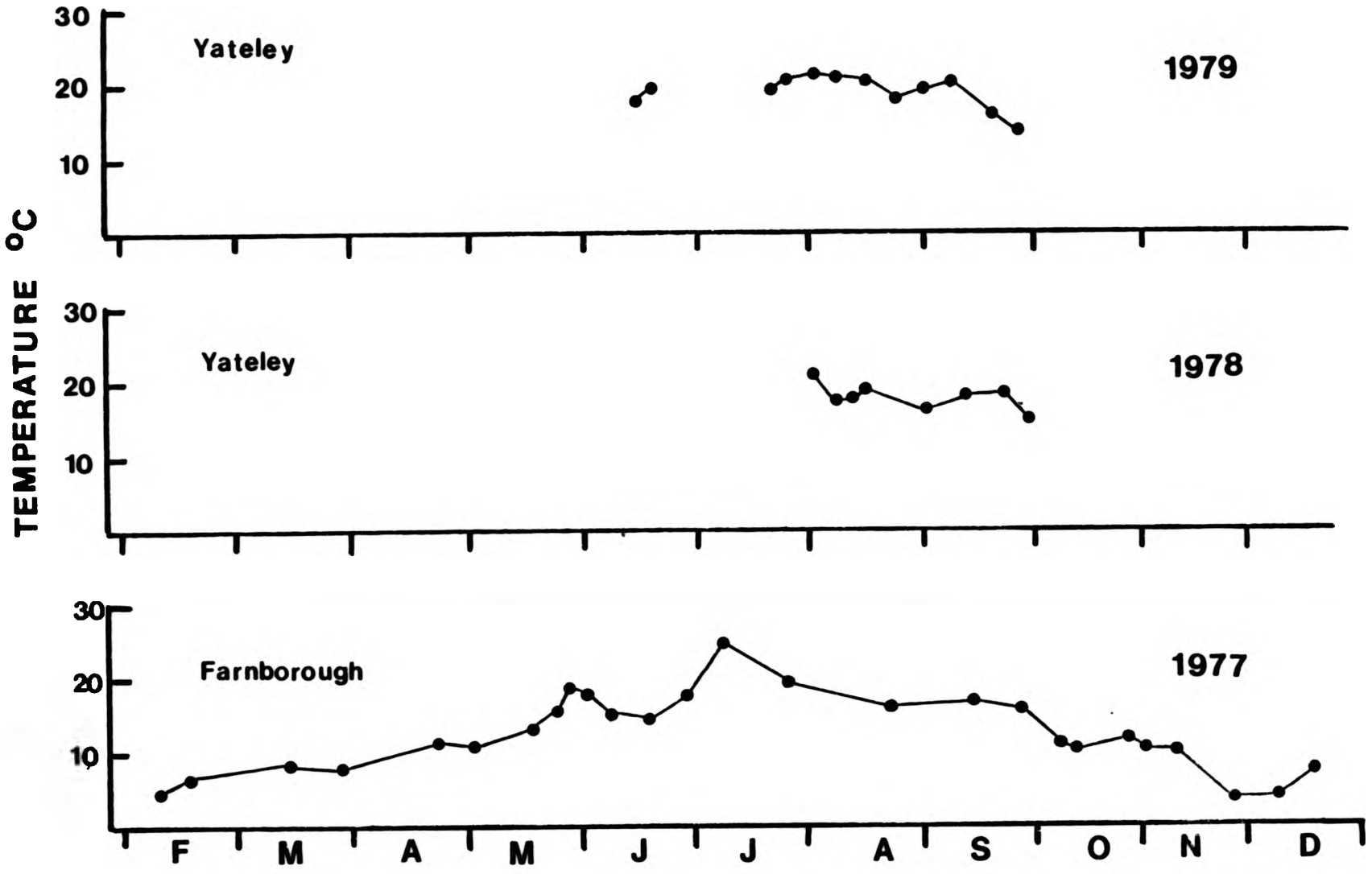

FIGURE 3.1 Surface water temperature at Farnborough and Yateley.

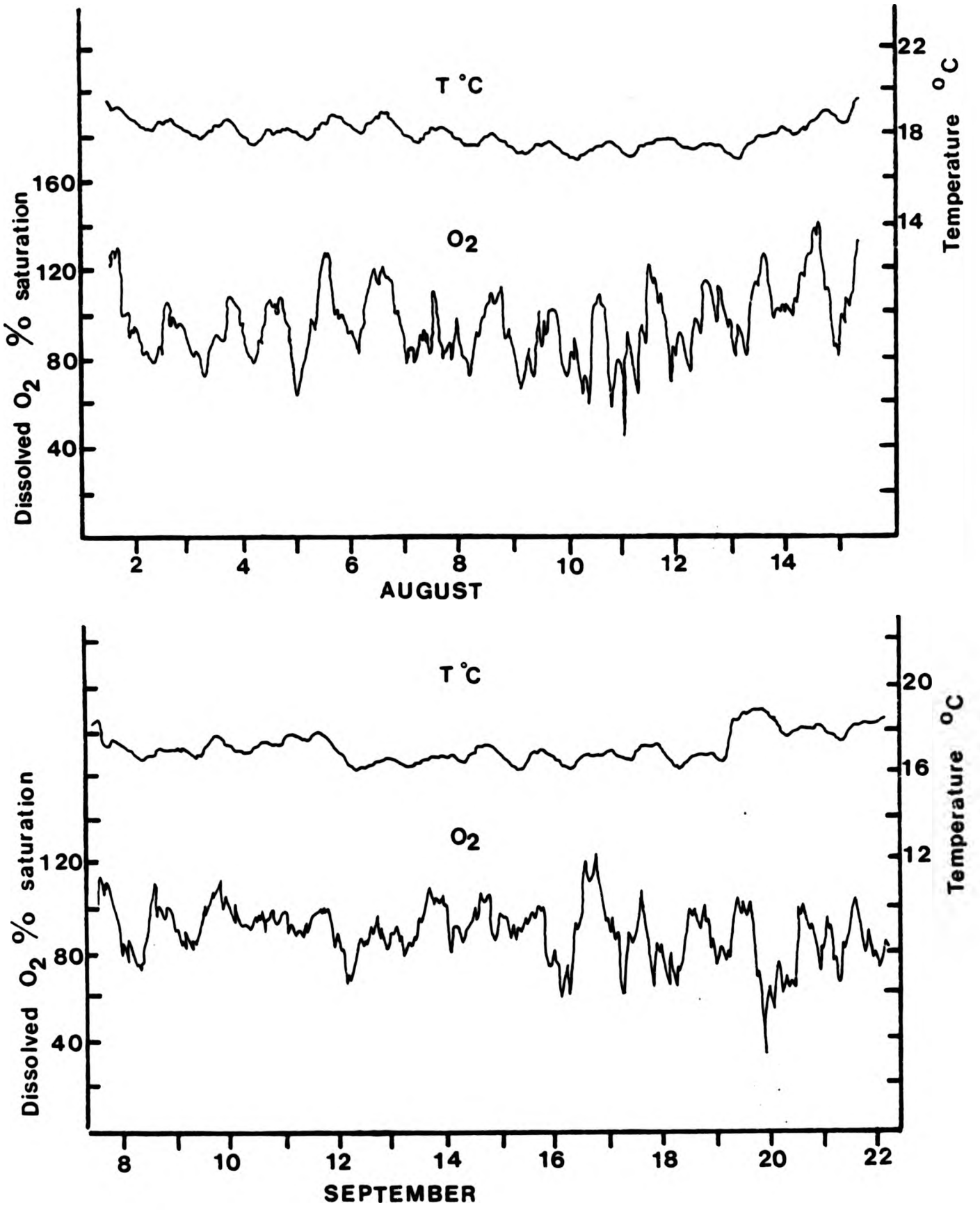

FIGURE 3.2 Diurnal fluctuations in water temperature and dissolved oxygen measured at 1 m by a Submerged Temperature and Oxygen Recorder on two occasions in Yateley in 1978.

Table 3.1 The daily minimum and maximum values of dissolved oxygen in Yateley in 1978.

2.8/ 15.8	min	77	71	77	58	75	73	68	62	52	36	64	77	96	75
	max	108	110	112	130	127	94	103	104	109	126	115	124	143	132
8.9/ 21.9	min	72	80	92	82	67	77	78	85	56	58	64	34	52	63
	max	113	115	104	103	98	112	111	103	128	114	105	107	107	110

1977 and again in early 1979. Stable thermal stratification was never encountered in these lakes but on one occasion a transient difference of a few degrees between surface and bottom water was found in the ponds, (measured on a Mackereth O_2/temperature meter). The critical temperature for fish growth is 14°C (Le Cren, 1958 while cladoceran and copepod growth and development are significantly faster above 10°C (Munro and White, 1975; Vijverberg, 1980).

The few measurements obtained in 1978 in Yateley indicated a similar temperature pattern to the previous year although the recordings suggest a slightly warmer year. In 1979 the water temperature was higher still, remaining above 20°C from mid-July to mid-September.

Gaps in the 1978 data can be partially filled in by comparison with a complete set of water temperature measurements from filter beds of the same depth in East London (O'Grady and Spillett, 1981). The highest temperature recorded there in 1978 was 22°C and the temperature fluctuated between 17°C and 20°C during the summer, so that no extreme changes appear to have been missed in the gravel pits.

Water temperature in Farnborough was usually 1°C higher in the marginal vegetation than in the open water. However, a systematic comparison over 24 hours would be needed to determine whether this difference was maintained or even increased during the day or was due to the shallower water warming up more quickly in the morning. It was not possible to do this in the present study but detailed comparisons have been made by Straskraba (1963) and Smid and Priban (1978). They found that vegetation areas tend to both warm up and cool down more quickly than the open water but over a day average temperatures are very similar.

The STOR measured daily fluctuations in water temperature and dissolved oxygen (% saturation) on two successive occasions of two weeks

each in 1978 and the results are illustrated in Fig. 3.2. Recordings were made hourly and the maximum daily fluctuation in temperature was 1 °C with a regular daily temperature pattern of evening peaks dropping to a minimum in early morning.

Dissolved oxygen was measured with a Mackereth oxygen and temperature meter in Farnborough in 1977. Levels were usually around 100% saturation and as the meter required continual servicing, recordings were discontinued in 1978 and 1979. The maximum recorded was 105% saturation in May and the lowest was 70% saturation in December. Fig. 3.2 shows the hourly fluctuations in oxygen measured by the STOR in 1978 in Yateley and Table 3.1 gives the min/max values for each day. The lowest recorded value was 34% saturation but this was exceptional and minimum values were usually around 50% or higher. Dissolved oxygen rose to a peak in late afternoon and dropped in early morning, the classical diurnal cycle. The highest value recorded was 143% saturation.

3.3 Species composition of the microcrustacea in the gravel-pit lakes.

Table 3.2 lists the species of microcrustacea found in five of the lakes and the small ponds between November 1976 and September 1979. At Farnborough and Yateley the number of species probably represents the full species diversity of microcrustacea in these lakes as these sites were visited frequently. The other lakes were only occasionally visited so that their species lists may not be indicative of the full range of species to be found. Forty three species were found in all. Only nine species of Cladocera were common to all sites, *Diaptomus gracilis* was the only calanoid copepod present in the lakes while no species of cyclopoid copepod was found at all the sites. It is unlikely that rarer benthic species were overlooked because net collections were usually

Table 3.2 Microcrustacean species found in some gravel-pit lakes between 1975 and 1979.

	F	Y	DA	TW	PD	Y7
CLADOCERA						
Sida crystallina (Muller)	x	x	x	x		
Diaphanosoma brachyurum (Lieven)		x		x		
Daphnia ambigua Scourfield	x					
D. longispina Muller	x	x	x	x	x	x
D. galeata Sars	x	x	x			
D. magna Straus				x		
Scapholeberis mucronata (Muller)	x	x	x			
Simocephalus vetulus (Muller)	x	x	x	x	x	x
Ceriodaphnia megops Sars	x	x	x			
C. pulchella Sars	x	x	x	x	x	x
Bosmina longirostris (Muller)	x	x	x	x	x	x
Macrothrix laticornis (Jurine)				x		
Ilyocryptus sordidus (Lieven)	x	x	x	x		
Eurycercus lamellatus (Fischer)	x	x	x	x		x
Graptoleberis testudinaria (Fischer)	x	x	x	x	x	x
Acroperus harpae Baird	x	x	x	x	x	x
Leydigia leydigi Schodler	x	x				
Alona intermedia Sars	x	x	x	x		
A. rectangula Sars	x	x				x
A. affinis Leydig	x	x	x	x	x	x
A. quadrangularis (Muller)	x	x	x	x	x	
A. guttata Sars	x	x	x	x	x	x
A. costata Sars	x	x		x		
Alonella excisa (Fischer)				x		
A. nana (Baird)		x	x	x		
Pleuroxus denticulatus Birge	x	x	x		x	
P. trigonellus (Muller)				x		
P. aduncus (Jurine)	x	x	x		x	
P. uncinatus Baird	x	x	x			
P. truncatus (Muller)		x	x		x	
Pseudochydorus globosus (Baird)	x	x	x	x		
Chydorus sphaericus (Muller)	x	x	x	x	x	x
Polyphemus pediculus (L.)	x	x		x		
COPEPODA						
Diaptomus gracilis Sars	x	x	x	x	x	x
Harpacticoida		x				x
Cyclops albidus (Jurine)	x	x	x	x		
Cyclops agilis (Koch, Sars)		x	x	x		
Cyclops fimbriatus (Fischer)	x					
Cyclops strenuus (Fischer)		x				
Cyclops vicinus Uljanin	x					
Cyclops viridis (Jurine)		x		x		
C. vernalis americanus (Marsh)	x			x	x	
Cyclops leuckarti (Claus)		x				

Key as in Table 2.1
Y7 = Yateley 7

made in the weedbeds to provide material for identification purposes.

The microcrustacean community of Farnborough consisted of 26 species of Cladocera, 1 calanoid and 4 cyclopoid copepods. The most common species were Bosmina longirostris, Ceriodaphnia pulchella and Cyclops vernalis americanus. Three species of Daphnia were found of which the most abundant in 1977 was Daphnia ambigua, a non-indigenous species. It was first recorded and described in this country by Scourfield (1946) and has since been recorded sporadically around London, (Green, 1966; Northcott, 1979). Cook (1979) first noticed it in both Farnborough and Yateley 7 in 1976 but it was not found in other gravel-pit lakes during this study. At the time of writing (1981) it is still common in Farnborough, and has been reported from several sites in Europe (Amoros, 1980).

Another non-indigenous species which has become established in the gravel pits is Pleuroxus denticulatus, first recorded in this country by Scourfield (1907). It has spread rapidly across Europe (Flossner and Kraus, 1977) often in association with Daphnia ambigua. It was abundant in several of the lakes and there was no diminution of population size over the study period.

Cyclops vernalis americanus was the dominant cyclopoid copepod in Farnborough. This species has been reported from several water bodies around London by Gurney (1933) and White (1975). It is planktonic and smaller than the more common littoral Cyclops vernalis (Harding and Smith, 1974). Cyclops albidus was present in low numbers in the weedbeds while only a few specimens of C. vicinus were seen in Farnborough.

The Chydoridae were represented by 15 species, which is fairly high compared to some other water bodies (Smyly, 1957).

The carnivorous rotifer Asplanchna priodonta was abundant on some

occasions in Farnborough and examination of phytoplankton net samples showed that smaller rotifers, Keratella cochlearis, K. quadrata, Polyarthra sp., Brachionus calyciflorus, Synchaeta sp. and Filinia longiseta were all very common, most probably far exceeding the crustacean zooplankton numerically.

In Yateley, 27 species of Cladocera, 1 calanoid, 1 harpacticoid and 5 species of cyclopoid copepod were found. The most common species were Bosmina longirostris, Ceriodaphnia pulchella, Diaphanosoma brachyurum, Diaptomus gracilis, Cyclops leuckarti and C. agilis. Although Daphnia longispina was more plentiful than in Farnborough it was still not particularly abundant. The Chydoridae were represented by a similar species assemblage to that in Farnborough, but also included Pleuroxus truncatus and Alonella nana. Asplanchna priodonta was on occasions very abundant in the open water and the colonial rotifer Conochilus hippocrepis was present in 1979. Other rotifers were not identified. Fryer and Forshaw (1979) reported that C. agilis was the commonest freshwater cyclopoid copepod in Britain.

The other lakes possessed similar species although there was a more limited fauna in the ponds, which were both small and new. Twyford 32 contained four species which were not found elsewhere, (Daphnia magna, Macrothrix laticornis, Alonella excisa and Pleuroxus trigonellus). Few chydorids were found in Yateley 2, a reflection of the sparser vegetation in this lake. Asplanchna priodonta, another ubiquitous species in the gravel pits, was extremely abundant in Darenth 37.

Good descriptions and information on the general ecology of most of the chydorids found in the lakes are given in Fryer (1968) and Fryer and Forshaw (1979). For the rest of this chapter Bosmina longirostris will be referred to as Bosmina; Ceriodaphnia pulchella as Ceriodaphnia;

Cyclops vernalis americanus as Cyclops; Sida crystallina as Sida and Simocephalus vetulus as Simocephalus. Because of the difficulty of distinguishing between Daphnia longispina and D. galeata during sample counting the two species will be collectively referred to as D. longispina.

3.4 Estimates of sampling error.

Cook (1979) collected separate vertically integrated samples from randomly selected open-water stations in three different lakes in 1975 using the 2 m perspex tube used in this study, to obtain an estimate of the sampling error in each lake. His results are included in Table 3.3 which shows the mean density in numbers/litre with the 95% confidence limits expressed as a percentage of the mean (all calculations done on log10(x+1) transformed counts and shown in log10 form). Bottrell et al (1976) give density estimates with confidence limits expressed in this way and those obtained here for total zooplankton in Farnborough (±3.7% of the mean) compare favourably with those of other workers for total zooplankton collected with similar samplers. Burgis (1971) obtained confidence limits in the range ±2.02% to ±5.29% of the mean in Lake George (Uganda) using a tube sampler while Grygierek (in Bottrell et al, 1976) obtained limits of ±1.9% to ±8.89%.

However, expressed in this way, the variation appears far less than it really is as the percentage of the mean is normally calculated from the antilogarithm of the confidence limits. This treatment of sample 1 gave limits of 15-17%. Burgis's Lake George data were also recalculated to give 95% confidence limits ranging from a minimum of 12% to a maximum of 41% of the geometric mean, (the ±5.29% of Table 6 in Bottrell et al, 1976). Therefore, the 95% confidence limits for total zooplankton density estimates given in Bottrell et al (1976) were in

Table 3.3 Estimates of mean density of microcrustacea in numbers/litre (log10) with the 95% confidence limits (cl) expressed as a percentage of the mean, shown in log10 form.

	WIDE TUBE					NARROW TUBE	
	OPEN 1	OPEN 2	OPEN 3	WEED 4	WEED 5	WEED 6	WEED7
	$\bar{x}$ cl	$\bar{x}$ cl	$\bar{x}$ cl	$\bar{x}$ cl	$\bar{x}$ cl	$\bar{x}$ cl	$\bar{x}$ cl
Total ind.	1.86 3.7	1.73 5.4	1.79 7.9	2.44 3.9	2.29 3.6	2.20 3.6	2.19 5.8
Copepoda	1.76 3.9	1.62 4.2	1.72 8.9	2.29 4.0	2.16 3.3	2.10 3.1	2.00 3.3
Cladocera	1.14 15	1.04 19		1.66 11	1.72 12	1.63 6.0	1.55 11
Cyclops	1.35 11	1.44 14	1.50 12	1.73 14	1.82 6.0	1.35 13	1.43 18
Bosmina	1.10 16	0.90 27		1.30 4.3	0.14 --	1.42 3.1	1.30 6.3
Daphnia	-0.8 --	0.33 51	0.90 18				
Ceriodaphnia					0.72 28		
Asplanchna				1.29 25			
Chydoridae				1.20 38	1.57 15	0.09 --	0.14 --
Sample vol litres	56.8	228.8	107.6	18.1	12.3	18.7	6.0
No. stations	12	12	8	10	7	31	10
Lake area ha	1.1	5.7	0.46				

SITES
OPEN 1 Farnborough 13.2.1975*
OPEN 2 Darenth 5.1.1975*
OPEN 3 Yateley 16.1.1975*
WEED 4 Farnborough 23.3.1978
WEED 5 Pond transect 9.8.1977
WEED 6 Farnborough 23.3.1978 **
WEED 7 " " **

* Data from Cook (1979) **narrow tube

where confidence limits are replaced by --, they were large because of low abundance in sample.

fact mainly in the range ±10% to ±40% of the mean. This level of variability is to be expected for animals with both horizontally and vertically overdispersed distributions (George, 1981). Cassie (1971) recommends that sampling programmes should aim for estimates with confidence limits of ±10%. For the rest of this section confidence limits calculated according to Bottrell et al (1976) are given first with the more normal limits (calculated from antilogs) given in brackets.

Cook's (1979) estimates for total zooplankton in the other lakes had wider confidence limits than those for Farnborough but were still acceptable. In sample Open 1 of Table 3.3 two cores were collected at each station, while in sample Open 2 a larger volume was taken at each station which has resulted in a multiplication of the effects of clumped distributions, giving confidence limits of ±5.4% of the mean, (19-24%). The greater variability in sample Open 3, ±7.9% (29-41%) of the mean was possibly due to the smaller number of stations. As 20 stations were used in the present study in comparison to the 12 examined above (Cook 1979), the sampling error attached to the use of the 2 m perspex tube was assumed to be in the region of ±3% (10-20%) for total zooplankton. As shown in Table 3.3 the copepods were more evenly distributed than the cladocerans although the density estimates for Daphnia were poor because of low abundance.

These estimates provided information on the dispersal patterns of the microcrustacea and the accuracy of the sampler. The duplicate open-water samplings carried out in Yateley in 1979 provided information on the precision of the sampling method. Table 3.4 shows the numbers/litre for total zooplankton and the major species in each sample. Total individuals/litre varied at the most by 10% and on one date by only 0.7%.

For comparison with these estimates of sampling error in the open water, a similar study was undertaken in the weedbeds with both the wide, 1 m perspex tube and also with a narrower tube, and these results are also given in Table 3.3. In sample Weed 4, ten replicate vertical cores were collected with the wide tube in the margins in Farnborough. Sample Weed 5 consisted of seven vertical cores taken along a transect line from the bank to the open-water through a bed of Sparganium in pond 3, and sample Weed 6 consisted of 31 vertical cores taken with the narrow tube in Farnborough to give the same volume as in sample Weed 4. This comparison of samplers will be discussed later.

The density estimates for total microcrustacea in the weedbeds possessed 95% confidence limits within ±4% of the mean (on log10 (x+1) transformed counts) in all cases which made them directly comparable with the density estimates in the open-water. The antilogged confidence limits for the weed samples were larger than those of sample Open 1 but smaller or the same as those of the other open-water samples. One would expect greater heterogeneity in the weedbeds but the sampling error in both habitats was of the same order of magnitude. The wide tube sampler provided fairly precise density estimates, within ±4.5% of the mean, for the more planktonic crustacea, Cyclops spp. and Bosmina, except when numbers were very low as in sample Weed 5. The high variation attached to the Asplanchna count was caused by the presence of only two individuals in one core and if this count is excluded, the confidence limits were only ±6.7% of the mean. This sampling was done in late March when the macrophytes were beginning to grow up, which accounted for the presence of Bosmina and Asplanchna in a region in which they were not found once the plants were fully grown. Some variability was expected within sample Weed 5 as the transect was across a heterogeneous site. However, the confidence limits for total numbers were smaller

Table 3.4 Comparison of duplicate open-water samples from Yateley in 1979, in numbers/litre. Each consisted of 20 vertical cores.

	13.6.79		25.7.79		7.9.79	
	1	2	1	2	1	2
Ceriodaphnia	0.4	0.9	52.0	56.0	47.0	55.0
Bosmina	0.2	0.2	154.0	177.0	0.2	0.0
Daphnia	152.0	132.0	0.2	0.3	0	0
Cyclops	73.0	33.0	206.0	231.0	106.0	166.0
Diaptomus	8.0	6.0	13.0	12.0	12.0	11.0
Nauplii	116.0	123.0	316.0	310.0	298.0	286.0
Asplanchna	13.0	15.0	59.0	49.0	28.0	36.0
Total ind	365.0	362.6	811.0	344.0	535.5	598.5
% difference	0.7		4.0		10.5	
Vol. litres	64·8	67·8	56·8	52·7	48·5	48·5

Table 3.5 Comparison of density estimates of microcrustacea in numbers/litre obtained with the wide tube (W) and the narrow tube(N) in the weedbeds in 1978.
(n)=number of vertical cores.

	W(10)	N(31)	N(10)
Total ind	275.0	159.5	154.9
Copepoda	195.0	126.0	107.0
Cladocera	45.7	42.7	36.0
Cyclops	53.8	2.4	26.8
Bosmina	19.9	26.3	21.6
Chydoridae	15.8	1.2	1.4
Asplanchna	19.5	0.5	0.9

W(10) = sample Weed 4 of Table 3.3
N(31) = sample Weed 6 of Table 3.3
N(10) is 10 cores selected at random from sample Weed 6

than for sample Weed 4. Therefore, variability within the weedbed sites sampled in the present study could be expected to be less. The chydorids appeared not to be sampled as accurately by this sampler. There were 13 species present in sample Weed 4, living in a variety of micro-habitats, giving a variable estimate and only five in the transect sample (Weed 5) where the estimate of total Chydoridae was less variable. Goulden (1971) and Whiteside (1974) found chydorids to have clumped distributions because of their association with the substrate.

A comparison between the density estimates obtained by the wide tube and the narrow tube is shown in Table 3.5. The sample of 10 wide cores is sample Weed 4 of Table 3.3 and N(31) is sample Weed 6 of Table 3.3 which gives the log10 form of the confidence limits and means. The narrow tube grossly underestimated the abundance of most groups, compared with the wide tube e.g 159/litre total instead of 275/litre total individuals. Curiously, very few Asolanchna were caught with the narrow tube although both sets of samples were taken from the same part of the lake. The narrow tube also gave lower estimates for the number of chydorids present. Although the narrow tube samples consisted of 31 cores compared to 10, the confidence limits, shown in Table 3.3, were only slightly smaller ±3.6% (14%) than those of the wide tube, ±3.9% (20-25%), so that there was more variation between the narrow tube cores. The narrow tube density estimates were recalculated from the counts of 10 randomly selected cores, (N(10), Table 3.5) and the confidence limits are shown in Table 3.3 (sample Weed 7). The total densities were still lower than for sample 4 and the confidence limits were larger than those of the 10 wide cores. This justified the early change from the narrow tube to the wide tube in 1977. It is interesting that more Bosmina were caught with the narrow tube than with the wide tube, and Szlauer (1965) found that Bosmina did not escape from a

pursuing tube as did larger animals. The higher densities possibly resulted from the same number of Bosmina being caught in a smaller volume of water than in the wide tube.

These estimates of open-water sampling error may be viewed in perspective when considered in relation to much published zooplankton work based on only one vertically integrated sample taken at a central station (George, 1981; Hrbacek, pers.comm) where no knowledge of the variability of the data is obtained. This is particularly true of work carried out in small, shallow water bodies (Duncan, 1975a). This has been justified on the grounds that thorough mixing distributes the zooplankters homogeneously. The error estimates discussed above show that this is not true and the collection of one sample should be viewed as sampling parsimoney which does not provide a full explanation of habitat variation.

3.5 Comparison of microcrustacea in the open water and in the marginal weedbeds in Farnborough in 1977.

a) Standing crops.

Total numbers/litre of microcrustacea in the open water and in the weedbeds are shown in Fig. 3.3. Each data point for the weedbeds is the geometric mean of all samples on each date. Table 3.6 gives the total numbers/litre of the individual weedbed samples. Open-water sampling commenced in June. Therefore, a spring peak in numbers of zooplankton, if it occurred, was not represented in the open-water data. The greatest density recorded in the open water was 1136 individuals/litre at the beginning of June, after which the numbers steadily declined through the year to a minimum of 40/litre in November. The geometric mean standing crop over this period was 225/litre.

Densities of microcrustacea were an order of magnitude higher in

the weedbeds, rising to a peak of 1726/litre in September. On only one occasion were numbers in the open water higher than those in the margins. Fig. 3.3 gives the geometric mean densities for all weed samples combined with the 95% confidence limits, and sample sizes are given in Table 3.6. The confidence limits were large because of small sample sizes and variation among weedbed samples which were from the different plant sites and were not intended to be replicate samples. They were combined to provide an overall comparison of open water and weedbeds.

Densities of microcrustacea in the weedbeds differed from those in the open water in that they did not decline during the summer. The peak in June was due to a high density of Bosmina, 1502/litre. This species was not normally present in the weedbeds and was presumed to have come in from the open water. Straskraba (1967) found very dense swarms of Bosmina in the lake margins during periods of peak abundance in the open water. Numbers in the margins fell slightly in August but then rose to their autumn peak as macrophyte abundance reached a seasonal peak. The lowest density found was 375/litre in December, similar to typical summer densities in the open water.

Therefore, the microcrustacean communities of these two lake regions differed in both numbers and seasonal pattern, the differences becoming more marked as the vegetation grew up around the margins. Total numbers increased in the weedbeds between June and October whereas those in the open water decreased.

Table 3.7 and Fig. 3.3(b) show standing crops of microcrustacea expressed as dry weight biomass in ug/litre. The figure gives the biomass estimate for the mean total abundance rather than the average of individual weedbed biomass estimates.

Total open water biomass in ug/litre was of the same order of

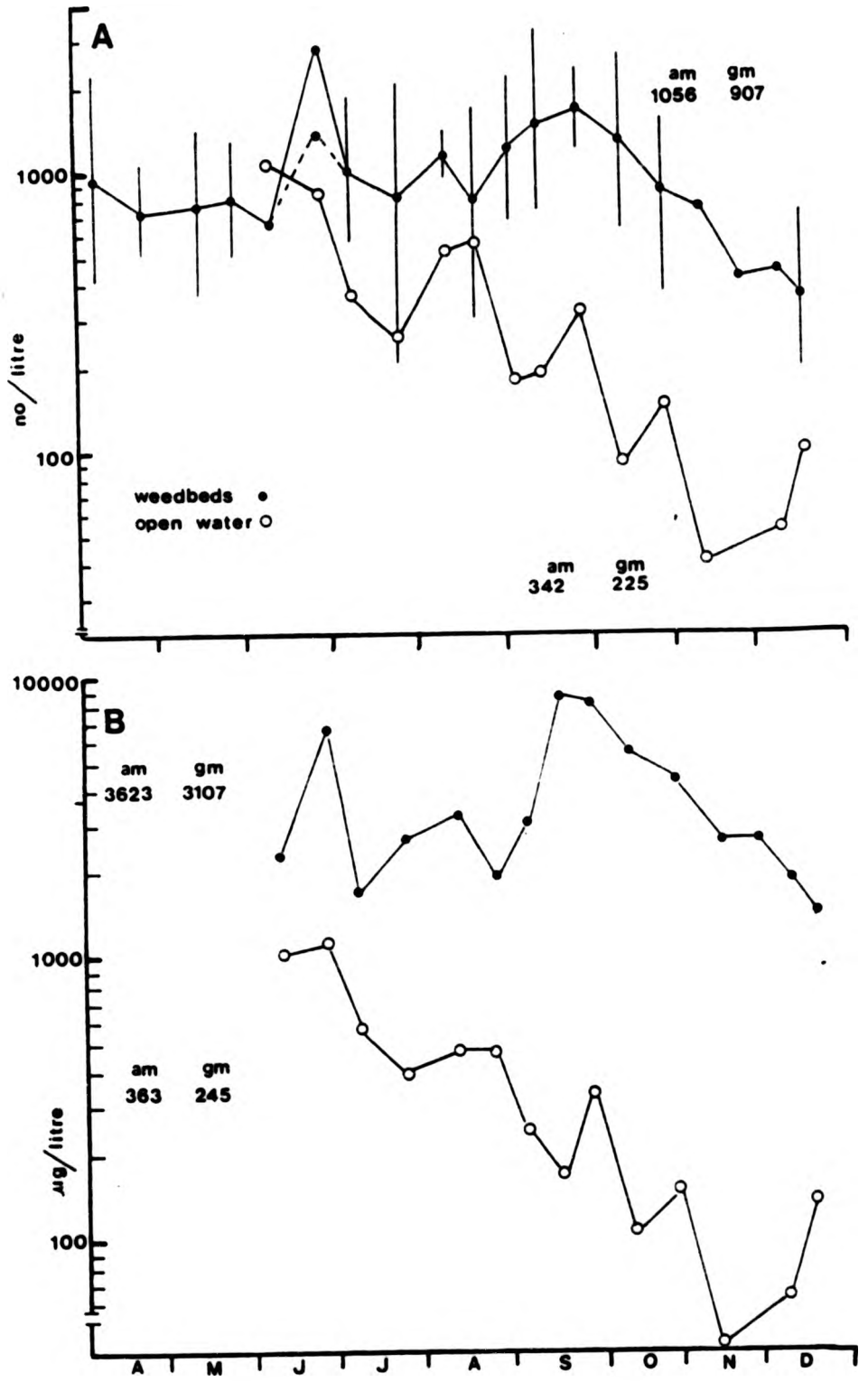

FIGURE 3.3 Total abundance of microcrustacea in the open water and in the weedbeds in Farnborough in 1977. Fig.A shows the numerical density in numbers/litre. Each weedbed point is the geometric mean of several samples with the 95% confidence limits. Fig.B shows the dry weight biomass in ug/litre. The numbers on each figure give the seasonal arithmetic (am) and geometric (gm) means for each site. The dotted line on Fig.A indicates total weedbed abundance excluding an unusually high count of Bosmina.

Table 3.6 Total numbers/litre of microcrustacea in the open water and the weedbeds in Farnborough in 1977. n=number of samples.

DATE	OPEN	ELODEA	SP/TY	P.N.	P.N./EL	$\bar{x}$ WEED	
9.4		2064	721(2)			1000(4)	narrow tube
25.4		836	575(2)			752(4)	
15.5		1082	660(2)			779(3)	
23.5		800*	998*	653*		854(3)	wide tube
9.6	1136	680*					
27.6	817	2895*					
7.7	363	1038(2)	329	2352	1631(2)	1056(7)	
25.7	265	490(2)	657	1884		759(4)	
9.8	508	1297(2)	951	1220		1182(4)	
22.8	581	1868	879	353(2)	951	721(5)	
2.9	169	2374	869	1655	956(2)	1256(5)	
12.9	200	1839	1064	1808		1524(3)	
26.9	317	2016	1560	1636		1726(3)	
10.10	95	1002	1284	1808		1325(3)	
25.10	143	1054	707	602		765(3)	
9.11	40	790			600	689(2)	
24.11		677*	277*			433(2)	
7.12	51	711*	296*			458(2)	
14.12	107	279*	411*	462*		375(3)	

Table 3.7 Total dry weight biomass in ug/litre of the open-water and weedbed microcrustacea in Farnborough in 1977.

DATE	OPEN	ELODEA	SP/TY	P.N.	P.N./EL	$\bar{x}$ WEED
9.6	1042	2541				
27.6	1085	6158				
7.7	448	2055(2)	565	3927	4818(2)	1667(7)
25.7	368	1580(2)	2290	13833		2645(4)
9.8	455	3450(2)	2280	3698		3025(4)
22.8	463	5538	2210	353(2)	3283	1852(5)
2.9	244	7424	2177	6914	2368(2)	2984(5)
12.9	165	12798	3720	11820		8074(3)
26.9	332	10570	7180	7790		7781(3)
10.10	103	3730	7533	7649		5382(3)
25.10	147	5742	3861	4064		4325(3)
9.11	43	4248			1822	2259(2)
24.11						2265(2)
7.12	61					1941(2)
14.12	131					1446(3)

* = marginal samples
SP/TY = Sparganium and Typha.
P.N = P. natans.
P.N/EL = P. natans and Elodea.

magnitude as numerical abundance in numbers/litre, falling from a peak value of 1035 ug/litre to 43 ug/litre, giving a geometric mean standing crop from June to December of 245 ug/litre. The dry weight biomass of the weedbed crustacea over this period was an order of magnitude higher than that in the open water, with a peak value of 8074 ug/litre, a minimum biomass of 1446 ug/litre in December and a mean standing crop of 3107 ug/litre. The seasonal fluctuations in biomass did not correspond to the numbers quite as closely as in the open water as there was a far greater size range of organisms present in the weedbeds (see section 3.6).

b) Species composition and diversity

The open-water microcrustacean community was dominated by Cyclops vernalis americanus and Bosmina longirostris. Fig. 3.4 shows the seasonal population changes in the open-water in Farnborough in 1977. Numbers of Cyclops remained consistently high during the summer, fluctuating around 100/litre after which the population declined rapidly in October.

The Bosmina population was markedly varied in size and each population maximum was smaller than the previous one. Cook (1979) found similar cyclical patterns of Bosmina in Farnborough in 1975 and 1976. The long sampling interval relative to the generation time (at 20°C, the time from neonate to first egg production is 2-3 days, Hrbacek (1977)) does however mean that these counts may not reflect the true population peaks.

Asplanchna was counted and is shown in Fig. 3.4 but the numbers were not included in the totals in Tables 3.6, 3.7 and Fig. 3.3 as the sampling frequency was too low for accurate estimation of rotifer numbers (Hillbricht-Ilkowska, 1965). The Asplanchna population also

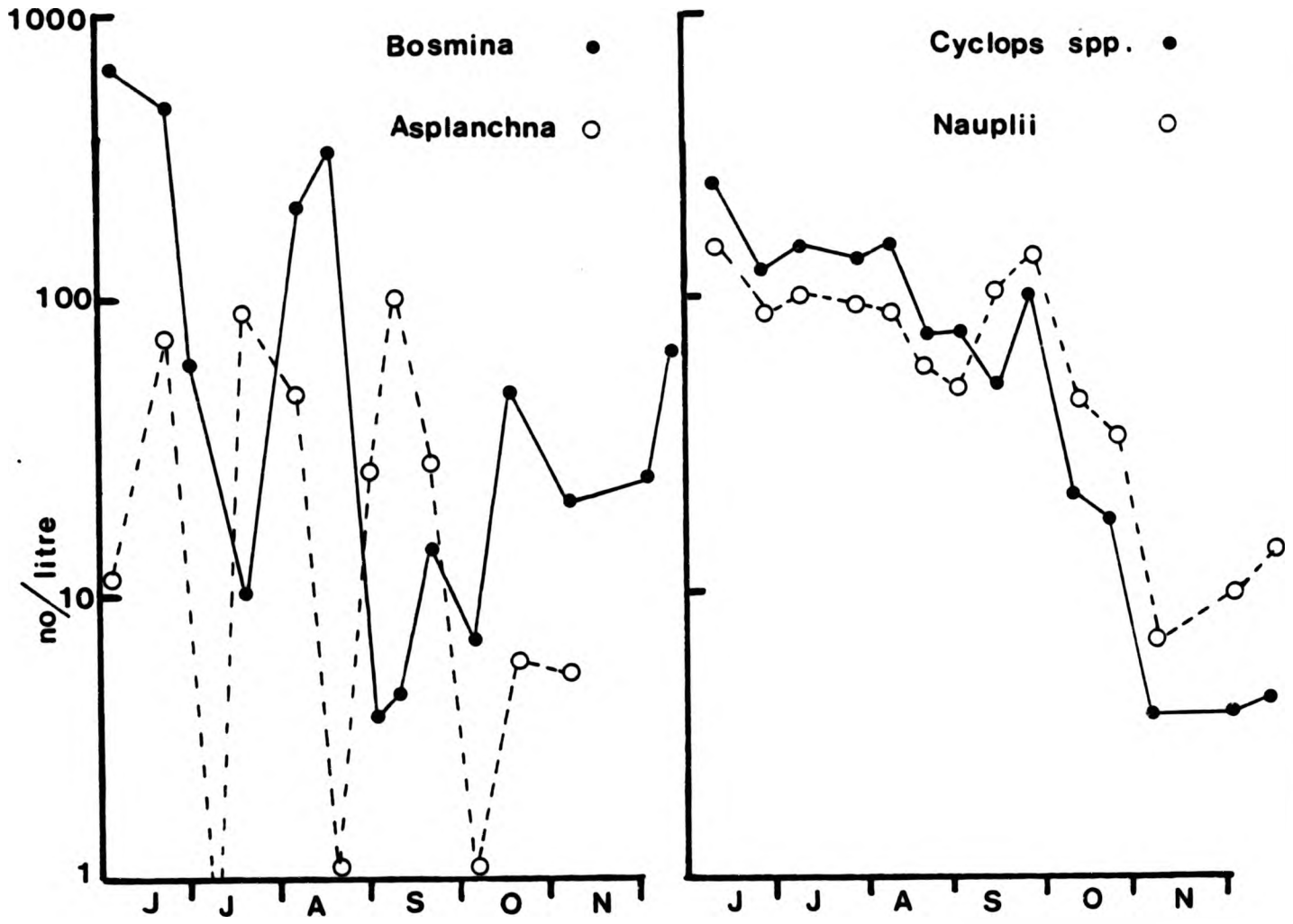

FIGURE 3.4 Abundance in numbers/litre of the major species of microcrustacea in the open water in Farnborough in 1977.

Table 3.8 Abundance in numbers/litre of the minor species of microcrustacea in the open water in Farnborough in 1977.

Date	Damb	Dlong	Diapt	Cerio	Aquad	Punc	Chydl	Chyd2
9.6	25.7	0.5	0	0.8	4.5	0.2	0	5.0
27.6	63.7	0.7	0	3.5	10.0	0	0	10.0
7.7	28.7	0.3	0	7.3	3.4	0	0	3.4
25.7	3.8	0.2	0	7.8	4.2	0.2	0	5.0
9.8	4.0	0.5	0	11.6	8.0	0.2	0	8.4
22.8	6.5	3.0	0.1	36.5	3.1	0.2	0.1	4.5
2.9	2.3	2.1	0.5	23.6	2.3	0.5	0.2	3.4
12.9	3.8	4.3	0.3	28.2	0.3	0	0	0.7
26.9	2.1	3.4	1.0	7.8	8.7	0.5	0.7	16.6
10.10	x	0.6	0.1	1.2	8.0	2.2	1.6	18.2
25.10	0.4	0.9	1.3	1.8	8.6	1.5	4.8	24.1
9.11	0	0.1	0.5	0.2	3.4	0.6	1.5	7.8
7.12	0	0	0.4	0	2.3	1.1	0.5	14.7
14.12	0.1	x	1.5	0	6.0	1.5	0.2	15.8

Other species recorded in the open water occasionally:
Ilyocryptus, Leydigia, Sida, Scapholeberis, C. megops, Graptoleberis, A. guttata, A. intermedia, P. aduncus, Simocephalus, Acroperus, A. rectangula, P. denticulatus and Eurycercus.
Key as in Table 3.9
x= <0.1/litre.

exhibited marked changes in size and there was the suggestion of an inverse relationship with Bosmina in August and September.

No other species of crustacea contributed greatly to the open-water community. Table 3.8 shows the abundance of minor species. Daphnia ambigua was fairly common in June after which the population declined and remained small throughout the summer, while D. longispina was never abundant in Farnborough, reaching a maximum density of 4.3/litre. There was a small peak of Ceriodaphnia (maximum 36.5/litre) in late August, but on the whole the daphnids contributed little to total open-water abundance.

Diaptomus gracilis was always rare in the lake. Littoral or benthic chydorids were caught in low numbers in the open water samples. The most common was Alona quadrangularis which was always present. Pleuroxus uncinatus, which inhabits vegetation free, stony bottoms (Fryer, 1968) was the next most common chydorid. The numbers of this group rose in the autumn as detritus particles were swept into the water column by wind and water mixing.

The situation in the weedbeds was more complicated because a total of 31 species was encountered in these samples of which eight were abundant at different times. Fig. 3.5 shows the seasonal changes in mean population size of the most important crustaceans. The 95% confidence limits have not been included in the interests of clarity but are given in the appendix. Differences between weed types which may have contributed to this variability will be discussed in the next section.

The most abundant crustacean in the weedbeds was the small filter feeding cladoceran, Ceriodaphnia pulchella. The population first appeared in the spring as the water temperature rose, after which

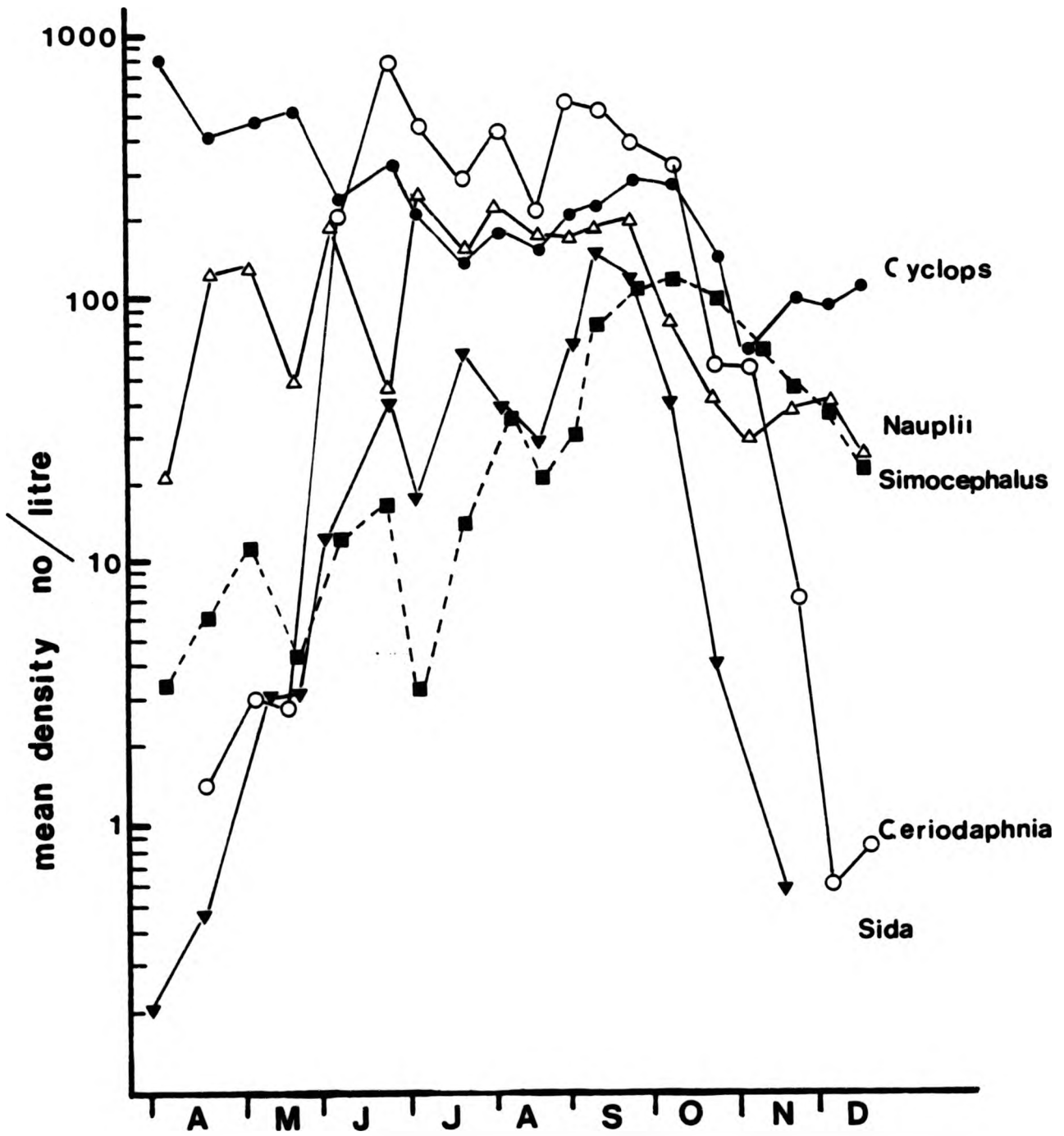

FIGURE 3.5 Geometric mean density in numbers/litre of the more important species of microcrustacea in the marginal weedbeds in Farnborough in 1977. Each point is the mean of several log10 x+1 counts.

○ Ceriodaphnia pulchella ● Cyclops spp. △ Nauplii
▼ Sida crystallina ■ Simocephalus vetulus

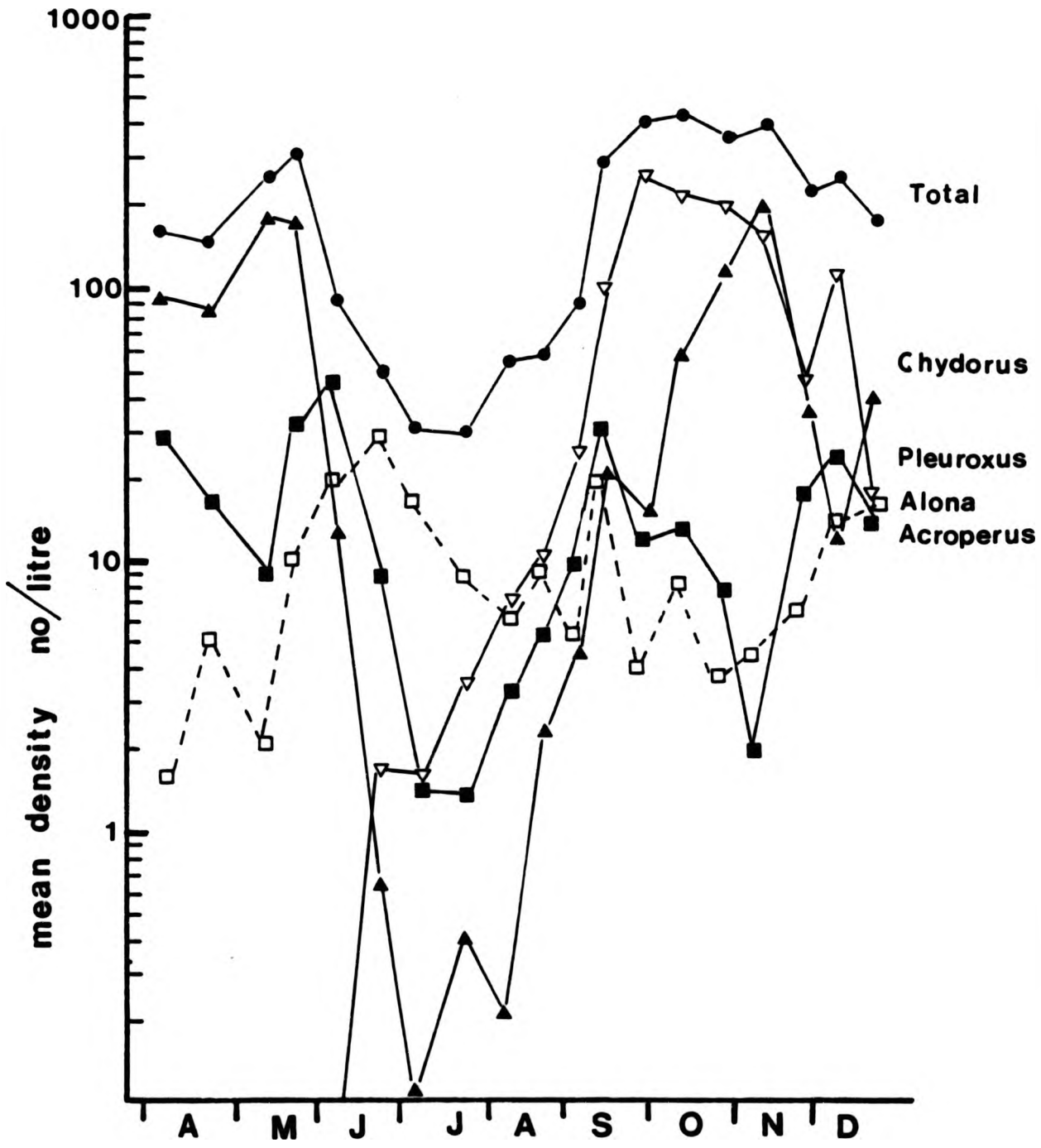

FIGURE 3.6 Geometric mean density in numbers/litre of the more important chydorids in the weedbeds in Farnborough in 1977. Each point is the mean of several log10 x+1 counts.

● Total Chydoridae ▲ Chydorus sphaericus □ Alona affinis
▽ Pleuroxus denticulatus ■ Acroperus harpae

numbers remained very high, peaking in June at 734/litre. Ceriodaphnia continued to dominate the crustacean community until the temperature dropped in September when the population declined rapidly. As noted previously, this species was uncommon in the open-water. A second larger species, C. megops was also present in low numbers in late August. It was not encountered in the open-water samples.

Cyclopoid copepods, consisting chiefly of Cyclops vernalis americanus plus a few of the larger C. albidus were also very abundant in the weedbeds. Peak density occurred in the spring (621/litre). After this numbers steadily declined following the same pattern as the open-water population, with a slight increase in October. Densities in the weedbeds were always higher than those in the open-water.

Two large semi-planktonic cladocerans were common in the weeds; Sida crystallina and Simocephalus vetulus, of which Sida was the most numerous. Numbers of both increased during the summer and Sida peaked at 150/litre in September, followed by Simocephalus (114/litre) in October. The population of Sida did not overwinter but individual Simocephalus were found during periods of lower temperatures. These are both cladocerans which can feed either on planktonic or periphytic algae (Downing, 1981) and their population increase coincided with first growth and then death and decomposition of the macrophytes, although the Sida population was probably also influenced by the presence of floating leaved plants, with which it can be associated. A similar pattern was followed by the chydorids with the addition of a May peak, as shown in Fig. 3.6. Of the 15 species found in the weedbed samples, the most common were Pleuroxus denticulatus and Chydorus sphaericus. Also periodically numerous were Alona affinis, Alona guttata, Acroperus harpae and Pleuroxus aduncus. Table 3.9 gives the density estimates for the less common species of chydorid.

Table 3.9 Geometric mean density in numbers/litre of minor species of microcrustacea in the weedbeds in Farnborough in 1977.

	Bos	Dlong	Damb	Scaph	Poly	Cmeg	Agutt	Pad	Eury	Arec	Grap	Acos	Aint	Pseud	Punc	Ilyo	Leyd
9.4	0.4	0	0	0	0	0	6.3	0.5	1.5	0	0.2	0	0.2	0	0.2	0.3	0
25.4	7.3	0	0	0	0	0	15.5	1.5	1.0	0	0	0	1.0	0	0.4	0	0
15.5	0.1	0	0	0	0	0	3.8	0	5.1	0	0.2	0	0	0	0	0	0
23.5	0.8	2.9	0	0.1	0	0	8.0	1.4	4.4	0	0	0	0	0	0	0	0
9.6	0	7.3	0	0.2	0	0	5.5	0.9	0	0	0.2	0	0	0	1.4	0	0
27.6	1502	30.8	131	0	0	0	1.8	0.3	3.6	0	0	0.3	0	0.8	0	0	0
7.7	5.4	10.6	8.5	0	0	0	1.2	0.2	1.0	x	0	0	2.8	0.1	0.4	x	x
25.7	0.1	2.5	0	x	0	1.0	3.7	2.2	0.9	0.1	0.1	0	0	0.1	0.1	0.3	1.3
9.8	0.8	0.4	0	1.7	1.2	10.2	3.0	3.5	2.8	0.1	0.4	0	0	0.7	0.2	0	0
22.8	5.1	0.1	0	1.0	0.8	0.2	2.7	9.2	1.4	0.1	0	0.7	0	0.3	0.1	0	x
2.9	0.7	0.1	x	0	0.3	3.6	2.5	9.6	2.4	0.4	0	0.5	0.2	1.5	0.1	0	0.3
12.9	0	0.2	0	0.2	0	1.7	4.9	37.6	7.4	0	1.0	1.8	0	0.7	0.3	0	0.3
26.9	0	0.3	0.1	0.1	0.3	3.4	9.3	11.1	2.7	1.1	1.3	2.8	0.1	0.4	0.2	0.1	0.3
10.10	0.1	0	0	0	0	0.6	10.1	7.1	4.2	0	0.5	0.3	0.6	0.5	0.2	0	0
25.10	0.1	0.1	0	0	0	0	12.9	2.2	5.6	0.1	0.3	0.7	0	0.7	0.2	0	0
9.11	0.7	0	0	0	0	0	18.2	2.4	12.0	4.6	0.8	0.4	0	0.8	0	0	0.2
24.11	0.4	0	0	0	0	0	32.5	2.3	11.8	6.7	0.2	0	0.6	1.2	0.3	x	0.4
7.12	8.9	0	0	0	0	0	9.0	3.1	11.3	34.1	0.4	0	1.0	0.2	0.2	0	0.8
14.12	4.2	x	0	0	0	0	21.6	9.0	4.0	18.9	0.6	0	7.2	0.1	0.1	0	0

Key
Bos=Bosmina Dlong=Daphnia longispina Damb=D.ambigua Scaph=Scapholeberis
Poly=Polyphemus Cmeg=Ceriodaphnia megops Cerio=C.pulchella Agutt=Alona guttata
Arec=A.rectangula Acos=A.costata Aint=A.intermedia Aquad=A.quadrangularis
Pad=Pleuroxus aduncus Punc=P.uncinatus Eury=Eurycercus Grap=Graptoleberis
Pseud=Pseudochydorus Ilyo=Ilyocryptus Leyd=Leydigia Diap=Diaptomus Chyd1=Chydorus
Chyd2=all chydorids x= <0.1/litre

Bosmina occurred only very occasionally in the weedbeds (see Table 3.9), so that while the open water was dominated by one small filter feeder the weedbeds were dominated by another similarly sized cladoceran, Ceriodaphnia. The two species appeared to be mutually exclusive. Comparison of Tables 3.8 and 3.9 shows that Daphnia longispina was more common in the weedbeds than in the open-water in the spring. Conversely D. ambigua was only encountered on two occasions in the weedbeds (if one excludes the large general marginal sample collected on 27 June, when several open-water species were abundant in the weedbed sample).

Tables 3.10a and 3.10b show mean densities and biomass of the major species of microcrustacea in both habitats for the period June to December, given in both arithmetic and geometric forms (log10 x+1). The comparison highlights differences in both standing crop and species composition of the two areas. Only Cyclops spp. were common and numerous in both habitats. Ceriodaphnia was relatively uncommon in the open water while Bosmina was the reverse, apart from the exceptionally high count in June already mentioned, which caused the arithmetic mean (37/litre) to be much larger than the geometric mean (2/litre); the latter therefore gives a better estimate of the minor contribution made by Bosmina to the weedbed community overall.

While Daphnia ambigua was present in the weeds in comparatively low numbers, (mean density 0.6/litre), D. longispina had a higher mean density in the margins, equal to that in the open water. Diaotomus gracilis was uncommon in both regions, although mean densities were slightly higher in the weedbeds, while the chydorids were far more numerous in the weedbeds with the exception of Pleuroxus uncinatus.

Table 3.11(a) shows the total numbers of species recorded from

Table 3.10(a) Comparison of arithmetic and geometric mean densities of microcrustacea in numbers/litre in the open water and the weedbeds in Farnborough in 1977.

	OPEN		WEEDS	
	am	gm	am	gm
Cyclops	98.5	43.4	200.5	166.1
Nauplii	79.5	57.2	172.1	121.2
Bosmina	147.2	43.0	36.7	1.7
Ceriodaphnia	9.3	4.3	390.7	142.5
Daphnia ambigua	10.1	3.3	4.6	0.6
D. longispina	1.2	0.9	4.4	0.9
Sida	0.1	0.1	57.4	16.7
Simocephalus	0.1	0.1	47.9	27.4
P. denticulatus	1.2	0.7	99.5	22.5
Chydorus	0.7	0.4	37.5	5.8
P. aduncus	0.1	0.1	11.7	4.2
Acroperus	0.2	0.2	12.5	6.6
A. affinis/quad	5.2	4.4	14.6	9.4
A. guttata	0.2	0.2	3.8	5.2
A. rectangula	0.3	0.2	4.4	0.8
Eurycercus	0.1	0.1	4.8	3.1
Diaptomus	0.4	0.3	1.2	0.6
P. uncinatus	0.6	0.5	0.3	0.2
A. intermedia	1.1	0.6	1.4	0.5
Ilyocryptus	0.1	0.1	0.1	0.1

am=arithmetic mean, gm=geometric mean.

Table 3.10(b) Comparison of arithmetic and geometric mean biomass of microcrustacea in ug/litre in the open water and the weedbeds in Farnborough in 1977.

	OPEN		WEEDS	
	am	gm	am	gm
Cyclops	198	116	726	668
Nauplii	8	6	13	10
Ceriodaphnia	10	5	454	178
Bosmina	119	30	102	1
D.ambigua	16	4	22	1
D.longispina	1	1	13	2
Sida			930	138
Simocephalus			979	653
P.denticulatus			141	44
Chydorus			37	10
P.aduncus			9	5
Acroperus			25	16
A.affinis	9	7	43	31
A.guttata			5	4
A.rectangula			3	1
Eurycercus			114	69
Diaptomus			9	3
P.uncinatus			x	x
Chydoridae	16	12	360	276

each habitat. Numbers in both increased with time to a maximum of 19 in the open water in October (the influx of chydorids from the weedbeds) and to 26 in the weedbeds in September. That many of these species were of minor importance is shown in Table 3.11(b). A maximum of three species contributed over 5% to the total density in the open water at any one time. Diversity in the weedbeds increased in the autumn and winter with up to 6 species contributing over 5%. Also shown in the table are the numbers of species making up 10% or over, (dominants as described by Pennak, 1957; Patalas, 1971). These were Cyclops and Bosmina in the open water with Ceriodaphnia, Daphnia ambigua, Alona affinis and Pleuroxus denticulatus contributing occasionally. The weedbeds were dominated by Cyclops, Ceriodaphnia and P. denticulatus.

Table 3.11 Number of microcrustacean species in the two habitats on each sampling occasion.

a) Total number of species.

Date	J	J	J	J	A	A	S	S	S	O	O	N	N	D	D
Open	9	6	7	11	12	14	12	13	16	19	19	14		17	18
Weed	15	17	23	23	22	23	24	20	26	20	20	19	21	19	19

Cyclops counted as 1 in open, 2 in weed.

b) Number of species contributing 5% or 10%+ numerically.

OPEN	J	J	J	J	A	A	S	S	S	O	O	N	N	D	D
5%	2	3	3	1	2	2	2	2	1	3	2	3	3	2	2
10%	2	2	2	1	2	2	2	2	1	1	2	2	2	1	2
WEED	J	J	J	J	A	A	S	S	S	O	O	N	N	D	D
5%	3	3	2	3	2	3	3	4	5	5	5	5	5	5	6
10%	2	3	2	3	2	2	2	4	3	3	4	5	4	2	2

Pennak (1966) has described the littoral zooplankton as possessing the same seasonal succession of numerically dominant species as occurs in the limnetic zone (Pennak, 1957), the dominants normally being one species of copepod, one cladoceran and one rotifer at any one time. In

Farnborough more than three species were equally abundant on some occasions in the weedbeds, particularly during the chydorid peak in the autumn. However, Pennak's sampling procedure may have underestimated the less mobile components of the marginal community and he does at all times restrict his discussion to zooplankton. If the analysis of the present data is restricted to truly planktonic species, these results agree with Pennak's analysis, (excepting the lack of data on rotifers).

3.6 Body length of microcrustacea in Farnborough in 1977.

Fig. 3.7 shows the seasonal changes in mean body length of the more common open-water crustacea. Points are missing when insufficient animals were present for measurement. The data were not transformed as the sample sizes were sufficiently large to normalise the distribution of measurements (see appendix), and the mode, median and mean were very similar in most cases. This also gave a more representative picture of particle size distribution in the water for comparison with fish gut contents. The open-water crustacea collected on 2 September were not measured. While many workers e.g. Burgis (1967) have only measured reproducing females, in this work all individuals in the population were measured. This enabled comparison of populations in the weedbeds and the open-water to be made with fish gut contents.

Very few microcrustacea of over 1 mm body length were found in the open water, although a few larger Diaptomus gracilis did appear in the autumn. This is typical of a water body containing a large population of planktivorous fish, (Hrbacek, 1962; Brooks and Dodson, 1965). The range of sizes was also small with the majority of microcrustacea measuring between 0.2 and 0.44 mm. Nauplii were the smallest organisms measured, with an average size of 0.18 mm. The smallest nauplii were 0.13 mm so that it was unlikely that they were lost through the 0.09 mm

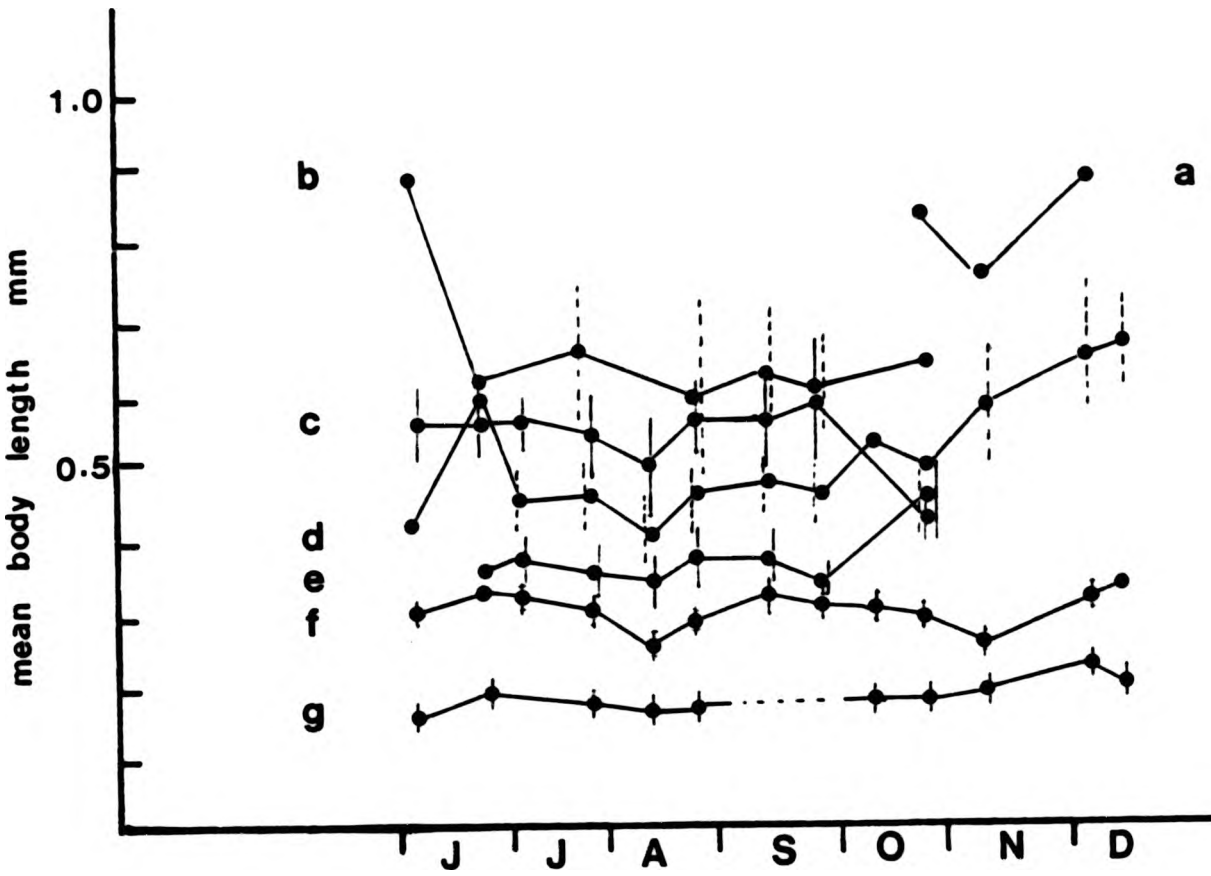

FIGURE 3.7 Mean body lengths in mm with the 95% confidence limits, of major species of microcrustacea in the open water in Farnborough in 1977. Sample sizes are given in the appendix. The confidence limits are not included on small samples (<10).
a = Diaptomus gracilis b = Daphnia longispina c = D. ambigua
d = Cyclops spp. e = Ceriodaphnia pulchella
f = Bosmina longirostris g = Nauplii

Table 3.12 Mean body length in mm of minor species of microcrustacea in the weedbeds over the sampling period. n=number of measurements.

	$\bar{x}$	min	max	n
Eurycercus	1.12	0.63	2.6	221
A. affinis	0.64	0.35	1.0	455
Acroperus	0.57	0.32	0.87	515
P. aduncus	0.43	0.30	0.77	323
A. costata	0.37	0.30	0.50	18
A. rectangula	0.32	0.25	0.55	47
A. guttata	0.29	0.17	0.38	208

Species occasionally occurring		
	$\bar{x}$	n
Scapholeberis	0.55	17
P. uncinatus	0.55	19
Leydigia	0.54	39
Diaptomus	1.14	35

mesh used for filtration. Little length overlap occurred among planktonic species, as shown by both the average sizes and the 95% confidence limits. Alona quadrangularis was the same size as Daphnia ambigua; however these two species were separated by habitat, one being planktonic and the other benthic.

Changes in the length of Bosmina, from 0.25 to 0.31 mm, although small, did coincide with major population changes, with the smallest individuals occurring during the second population peak. Whether these were in fact different varieties as found by Munro and Bailey (1980) in Bough Beech reservoir was not investigated.

The sharp increase in the average length of C. vernalis americanus in June, from 0.41 mm to 0.49 mm was due partly to the presence of males and ovigerous females in the sample. Other fluctuations were due to changes in the proportions of each developmental stage in the population. Apart from this their mean size remained around 0.45 mm in summer, rising to over 0.5 mm in the winter, when individuals of up to 1.5 mm were present. Ovigerous females had a maximum size of 1.0 mm in summer which is smaller than the 1.3-1.5 mm given by Gurney (1933) for this species. This seasonal change in body length is well documented as being an inverse relationship with increasing temperature (Vijverberg, 1980). As so few adults were found this phenomenon could not be positively demonstrated and the sudden decrease in length in August although coming after a period of high temperature was due to a large number of small copepodites in the population.

The decrease in mean length of Ceriodaphnia in the summer has been described by Burgis (1967) for egg bearing females and related again to increasing water temperature and also decreasing food measured as chlorophyll a. In Farnborough the decrease in size in the open water

was caused more by a reduction in the number of reproducing females in the open-water rather than by a marked size change and the overall reduction in size was less than that recorded by Burgis (1967) for this species, of 0.75 mm to 0.55 mm.

The mean size of Daphnia ambigua in the open water of 0.55 mm, (egg-bearers, 0.74 mm), was less than that recorded for this species by Amoros (1980) of 0.8 mm to 1.1 mm for egg bearing individuals. This species also showed a decrease in size with increasing temperature. Adult D. longispina normally measure over 1.0 mm (Scourfield and Harding, 1966) but in Farnborough this species was much smaller and few eggbearing females were found. However, this apparent reduction in size could have been due to the presence of the smaller D. galeata in the samples.

Fig. 3.8 shows the average body length of the weedbed microcrustacea, which ranged in size from 0.1 to 2.5 mm. While the more planktonic components of this community fell into a similar size range to that of the open-water zooplankton, the benthic crustacea were much larger animals. As in the open water, the common species did not overlap in size with the exception of Pleuroxus denticulatus, the introduced species which was almost the same size as Ceriodaphnia which suggests that this chydorid may not yet have quite settled into its optimum niche in the weedbeds. Table 3.12 gives the sizes of the less common and usually more benthic species, ranging from Eurycercus lamellatus, mean size 1.12 mm to Alona guttata, mean size 0.29 mm.

The seasonal fluctuations in size of Sida and Simocephalus in the weedbeds were very similar to those recorded by Green (1966) who correlated them with water temperature. Changes in mean size of Cyclops spp. in the weedbeds were caused by both varying proportions of different stages and the occasional inclusion of individuals of the

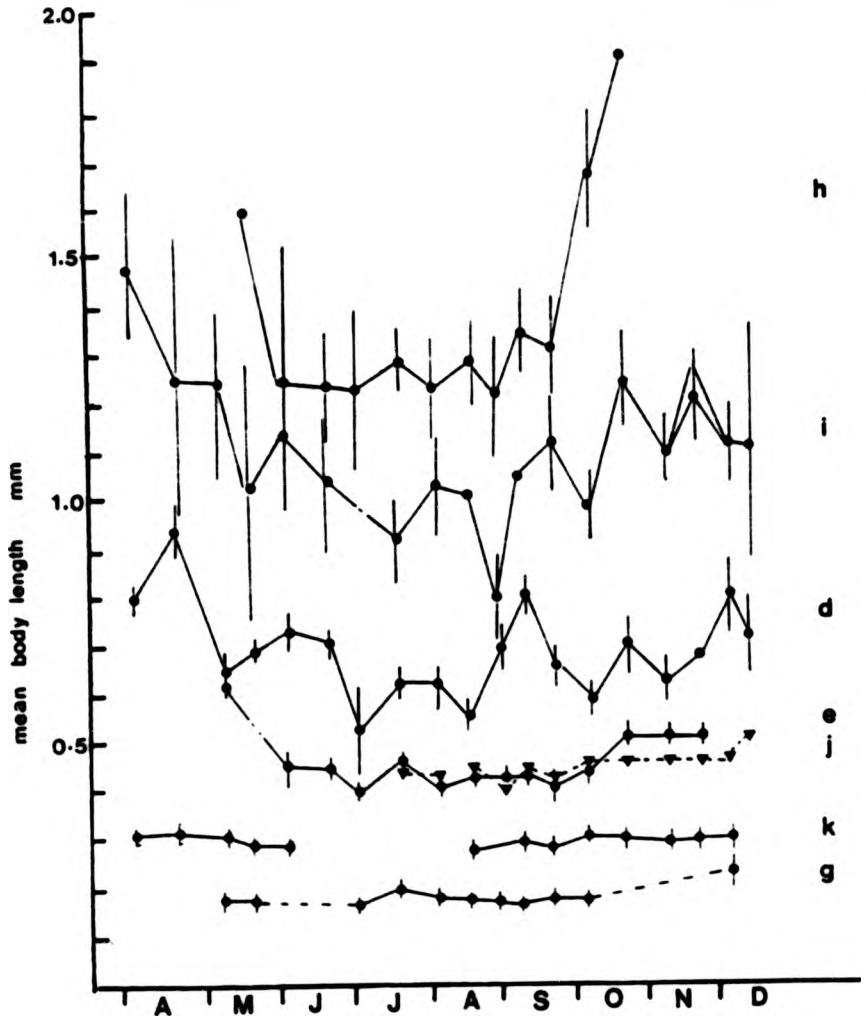

FIGURE 3.8 Mean body lengths in mm with the 95% confidence limits of major species of microcrustacea in the weedbeds in Farnborough in 1977. Sample sizes are given in the appendix. Confidence limits are not included on small samples (<10).
h = Simocephalus vetulus i = Sida crystallina d = Cyclops spp.
e = Ceriodaphnia pulchella j = P. denticulatus k = Chydorus sphaericus
g = Nauplii

Table 3.13 Comparison of average sizes of microcrustacea in mm in the open water and the weedbeds over the period 9 June to 14 December.
n = number of measurements.

	OPEN		WEEDS	
	$\bar{x}$	n	$\bar{x}$	n
Ceriodaphnia	0.37	378	0.45	1703
Bosmina	0.29	866		
Cyclops	0.51	985	0.65	1596
Nauplii	0.18	392	0.18	427
A. affinis			0.64	424
A. quadrangularis	0.54	296		
Diaptomus	0.91	46	1.12	32
P. denticulatus	0.46	93	0.46	579
P. uncinatus	0.51	48	0.55	19
D. longispina	0.61	96	1.02	121
D. ambigua	0.55	335	0.69	121

larger Cyclops albidus which were not separated during counting and measuring. Egg bearing females of C. vernalis americanus were larger in the weedbeds than in the open water.

Table 3.13 shows a comparison of the average size of species which occurred in both habitats. In most cases the weedbed individuals were larger than their open-water counterparts. These differences were significant for Cyclops and Ceriodaphnia on all occasions ($P<0.05$). The larger mean size of the cyclopoids may have been due partly to the inclusion of individuals of C. albidus, although these were not common.

Figs. 3.9, 3.10, and 3.11 show length frequency distributions of Cyclops, Ceriodaphnia and Daphnia longispina from both the open water and the weedbeds with the proportions of egg bearing females of Ceriodaphnia and Daphnia present in the samples. Differences in the mean size of Ceriodaphnia were caused by a smaller number of mature females in the open water rather than by a reduction in body length. A similar difference was observed for D. longispina. D. ambigua was significantly larger (t-test, $P<0.05$) in the weedbeds than in the open water on the two occasions when it was present in both areas. The seasonal mean size of D. longispina was larger in the open water than in the weedbeds but as it was rarely found in the open water this difference could not be tested for significance. Very few Cyclops of over 0.8 mm were present in the open water. Although some of the larger individuals in the weed samples were C. albidus, the majority were large C. vernalis americanus. The removal of larger specimens, possibly by fish predation, from the open water could occur regardless of which species was present.

A comparison of the mean particle size of the microcrustacea in both habitats is shown in Fig. 3.12. Weighted mean sizes were calculated for each date from the average size of each species

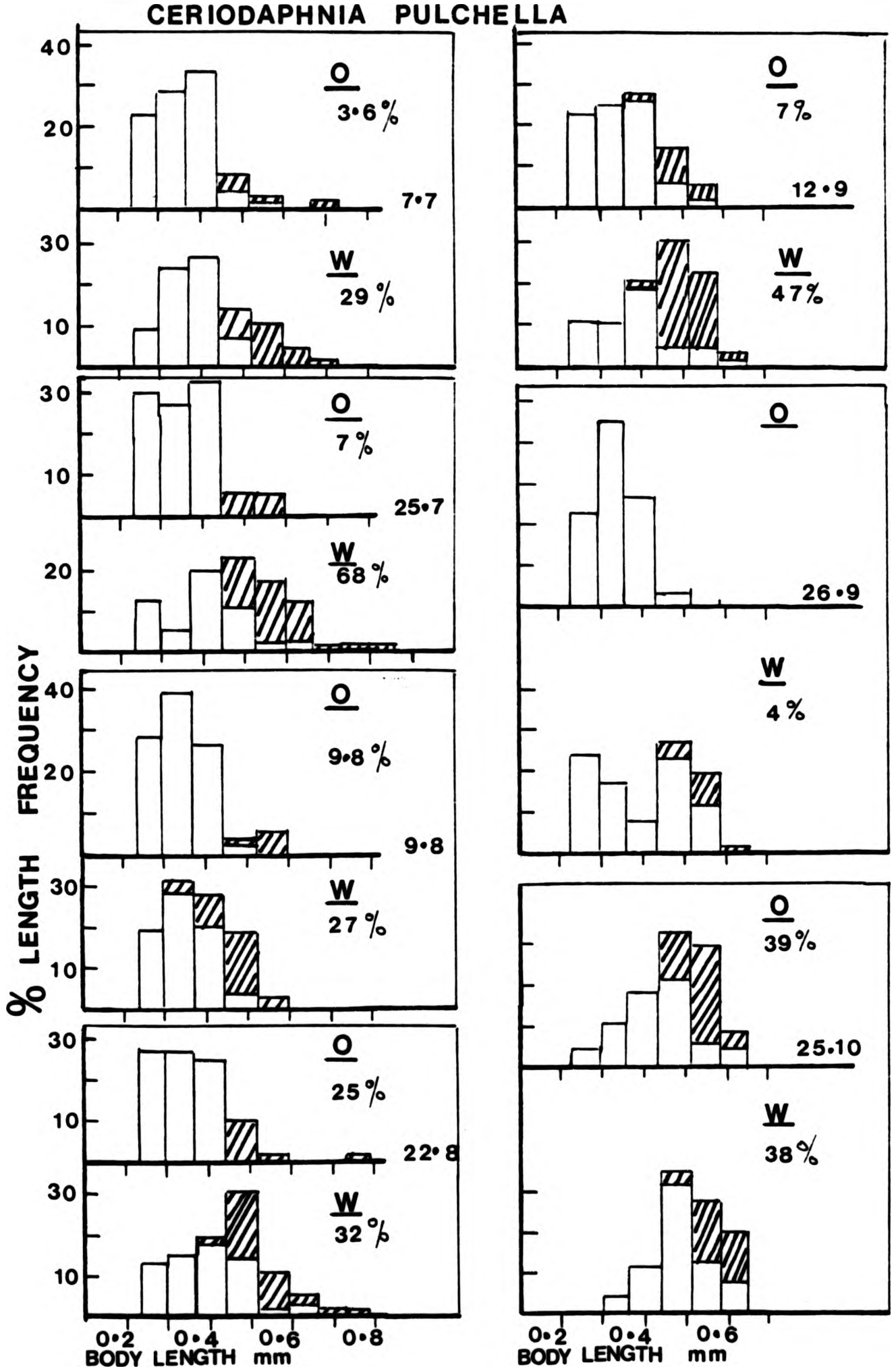

FIGURE 3.9 Percentage frequency distributions of the body lengths in mm of Ceriodaphnia pulchella from the open water (O) and the weedbeds (W) in Farnborough in 1977. The % figure on each histogram is the proportion of ovigerous females in the sample.

/// = Ovigerous females.

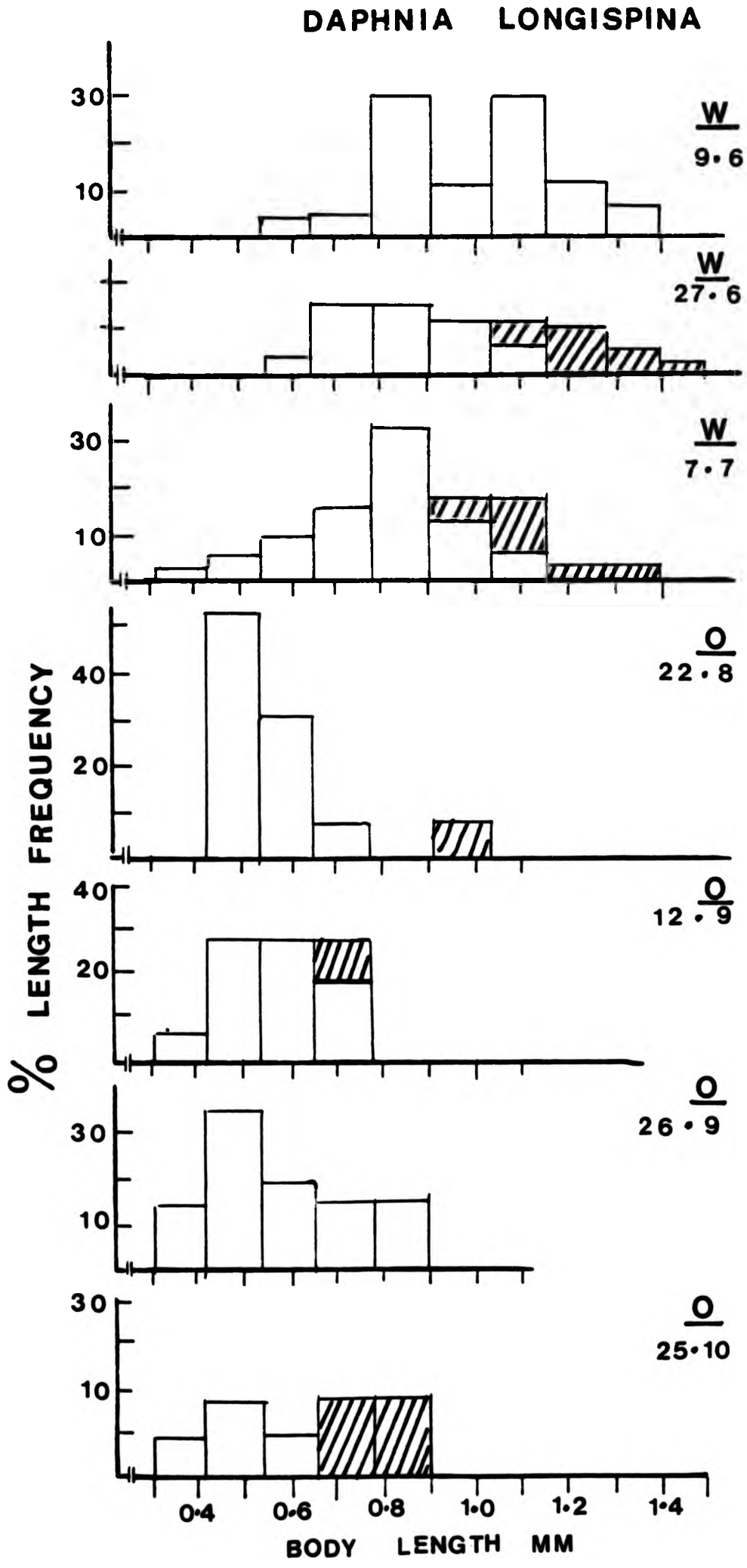

FIGURE 3.10 Percentage frequency distributions of the body lengths in mm of Daphnia longispina from the open water (O) and the weedbeds (W) in Farnborough in 1977. The 3 figure on each histogram is the proportion of ovigerous females in the sample.

/// = Ovigerous females.

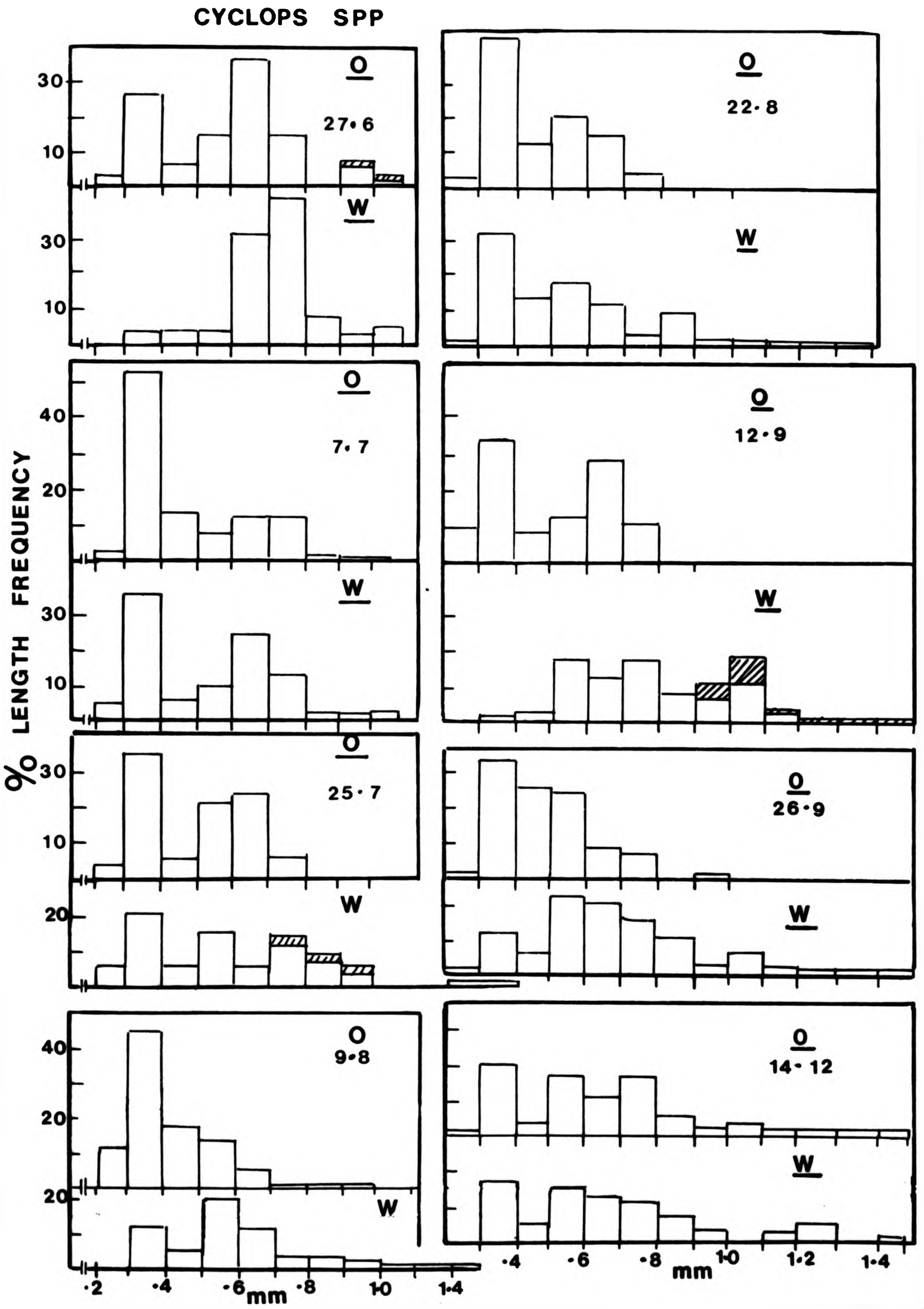

FIGURE 3.11 Percentage frequency distributions of the body lengths in mm of Cyclops spp. from the open water (O) and the weedbeds (W) in Farnborough in 1977.

multiplied by its relative abundance in the sample. This provided a better overall picture of the size of particle available as fish food. The difference between the mean size in the two habitats was emphasized by this treatment. The open-water community possessed an average weighted size of 0.32 mm, the slight increase in spring being due to the small peak of Daphnia, after which the weighted size remained constant. The weighted size in the weedbeds was greater and fluctuated according to the population dynamics of the littoral species, around a mean of 0.5 mm.

Although it could also be included in the next section, the difference between body lengths of microcrustacea collected from different weedbeds is more conveniently discussed here. On occasions when measurements were made from two or more weedbed samples, abundant species were tested for significant differences in body length, (t-test or one way analysis of variance on non-transformed data). Table 3.14 gives the mean body lengths, sample sizes and results of these statistical analyses. With few exceptions, there were no significant differences between sites. Therefore, body measurements from all weedbed sites were combined for each date for biomass estimations and/or crustacea from one site were measured and taken to be representative of all sites. Cyclops showed the greatest variation in body length with site and was usually smaller in P. natans. On 25 July both Elodea and Sparganium contained egg bearing females and seven larger individuals were present in the Sparganium sample, probably C. albidus. Neither was present in either the P. natans or the open-water samples. The highly significant difference between sites on 22 August was again due to the presence of a larger species in the Elodea sample, (see appendix). Ceriodaphnia was also significantly different in size in different sites on two occasions. This was due mainly to the

Table 3.14 Comparison of mean body length in mm of microcrustacea from different weedbeds in Farnborough in 1977. n = number of measurements.

7.7.77	P.N.		P.N./EL				SIG
	$\bar{x}$	n	$\bar{x}$	n			
Cyclops	0.56	47	0.49	105			NS
Ceriodaphnia	0.41	97	0.41	101			NS
25.7.77	**ELODEA**		**SP/TY**		**P.N.**		**SIG**
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	
Cyclops	0.67	67	0.61	107	0.54	28	*
Ceriodaphnia	0.41	72	0.49	137	0.45	67	***
Sida	1.37	59	1.21	97	1.35	52	NS
Simocephalus	0.98	36	0.86	11	0.90	7	NS
P.denticulatus	0.45	12	0.46	20			NS
22.8.77	**ELODEA**		**SP/TY**		**P.N.**		**P.N.**		**SIG**
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	
Cyclops	0.64	74	0.53	37	0.43	38	0.51	22	***
Ceriodaphnia	0.43	112	0.43	72	0.40	69	0.46	52	*
Nauplii	0.19	50			0.18	35	0.17	25	NS
Sida	1.34	37	1.44	18	1.26	37	1.19	38	NS
Simocephalus	1.06	51	1.06	34	0.92	19	0.82	17	NS
Chydorus					0.31	13	0.28	20	NS
P.aduncus	0.45	21	0.42	13	0.43	23	0.41	21	NS
P.denticulatus	0.46	23	0.47	12	0.47	5	0.46	13	NS
Acroperus	0.54	36	0.54	19					NS
A.affinis	0.70	38	0.64	18	0.56	13			*
12.9.77	**ELODEA**		**SP/TY**						**SIG**
	$\bar{x}$	n	$\bar{x}$	n					
Cyclops	0.78	57	0.82	89					NS
Ceriodaphnia	0.44	137	0.43	72					NS
Sida	1.23	35	1.40	75					*
Simocephalus	0.97	44	1.11	61					NS
P.aduncus	0.44	17	0.43	38					NS
P.denticulatus	0.42	9	0.46	35					NS
A.affinis	0.55	15	0.60	10					NS

*=P<0.05
***=P<0.001

Key as in table 3.7

presence of varying numbers of ovigerous females. This was also the case for Sida on 12 September when the Sparganium sample contained a small proportion of large ovigerous females. However, it was justifiable to use one weedbed set of measurements to estimate biomass at other sites for several reasons. These differences were less than seasonal changes in mean body length, shown in Fig. 3.8. The possibility of clumping of different developmental stages was not investigated, and there was no consistent correlation of size with specific site. Many zooplankton workers use one sample to calculate density estimates and another sample, often taken with a different sampler (usually a net) for egg counts and biomass determinations and Larsson (1978) reported no significant differences between size distributions of crustacea so obtained.

3.7 Differences between microcrustacean samples from different weedbeds.

The variation between individual weedbed samples was quite large as they were from different plant species, as shown by the confidence limits in Fig. 3.3. In a heterogeneous habitat one would expect animals to be dispersed unevenly compared with the open water. On a few occasions samples were collected from the same plant species, although not from the same site and Table 3.15 gives these density estimates for the more common species. There was usually as big a difference between samples from the same plant species as between sites except for the P. natans samples on 22 August which were uniformly low compared to the other samples taken on that date. However, a time factor was involved on two occasions, 7 July and 2 September, when the 24 hour studies of fish diet were undertaken. The times at which the weedbed samples were collected are shown in the table. Those collected on 22 August were the

Table 3.15 Comparison of numbers/litre of the more common microcrustacea from samples in the same plant type (not same site), in Farnborough in 1977.

	ELODEA					
	7.7		25.7		9.8	
Time	0300	1600				
Cyclops	209	88	213	47	182	423
Nauplii	213	107	272	71	387	469
Ceriodaphnia	772	524	224	42	551	269
Sida	30	22	156	4	51	12
Simocephalus	4	1	37	5	50	58
A.affinis	31	9	42	4	7	41
P.denticulatus	0	1	3	27	0	9
Chydorus	x	0	0	2	x	x
Chydoridae	46	15	50	70	26	95
Total ind	1344	801	963	249	1270	1325
	P.N./EL				P.N.	
	7.7		2.9		22.9	
Time	1200	1400	1900	1000		
Cyclops	342	612	225	272	58	45
Nauplii	266	389	106	198	142	80
Ceriodaphnia	1056	418	799	80	22	98
Sida	19	6	113	9	23	35
Simocephalus	11	2	14	32	4	7
A.affinis	52	11	6	8	4	2
P.denticulatus	2	x	21	62	1	5
Chydorus	x	0	10	x	4	15
Chydoridae	52	15	129	82	24	37
Total ind	1775	1499	2374	675	409	305

Table 3.16 Geometric and arithmetic mean densities in numbers/litre of minor species in the weedbeds in Farnborough in 1977.

	gm			am		
	EL	SP	PN	EL	SP	PN
Bosmina	0.6	0.6	1.2	1.2	1.1	3.0
D.ambigua	0.4	0.1	0.4	2.5	0.1	2.3
D.longispina	0.8	0.3	1.4	3.5	0.4	9.7
Scapholeberis	0.1	0.6	0.1	0.2	1.5	0.1
Polyphemus	0.1	0.2	0.4	0.1	0.3	0.9
Diaptomus	0.3	0.4	0.6	0.4	0.7	0.8

EL = Elodea
SP = Sparganium/Typha
PN = Potamogeton natans
gm = geometric mean, am = arithmetic mean.

closest in time and also the most similar pair.

Because of this variation between sites containing the same plant species, one cannot say with certainty whether observed differences in microcrustacean assemblages collected from different sites possessed any significance in an analysis of associations. However there were differences which were probably due to some degree of association of animal with plant.

The total standing crops of microcrustacea in numbers/litre and ug/litre in the three macrophyte sites between 7 July and 25 October are given in Table 3.6 and 3.7 and illustrated in Fig. 3.13. On the whole Elodea supported the highest standing crops although P. natans contained the highest arithmetic and geometric mean standing crops over this period because of the peak in numbers of both Sida and Simocephalus on 25 July. Sparganium/Typha supported the smallest communities although both numbers and biomass rose steadily though the summer suggesting a relationship with plant growth. There was a marked drop in standing crop in P. natans on one date when the crustacean assemblage bore some resemblance to that of the open water, being lower numerically although not gravimetrically, and containing representatives of the open-water community, e.g 14/litre Bosmina.

Fig. 3.14 shows the seasonal changes in numbers of the commoner species in each weedbed. One might expect least evidence for plant/crustacean associations among the planktonic species and most in the benthic species. Neither Cyclops nor Ceriodaphnia showed any association with site, although the highest geometric mean density of Ceriodaphnia was in P. natans and the lowest in Sparganium. Of the open-water zooplankton Bosmina, although rare in all weedbeds was more common in P. natans than in other sites, with a geometric mean density of 1.2/litre as compared to 0.6/litre in Elodea and Sparganium.

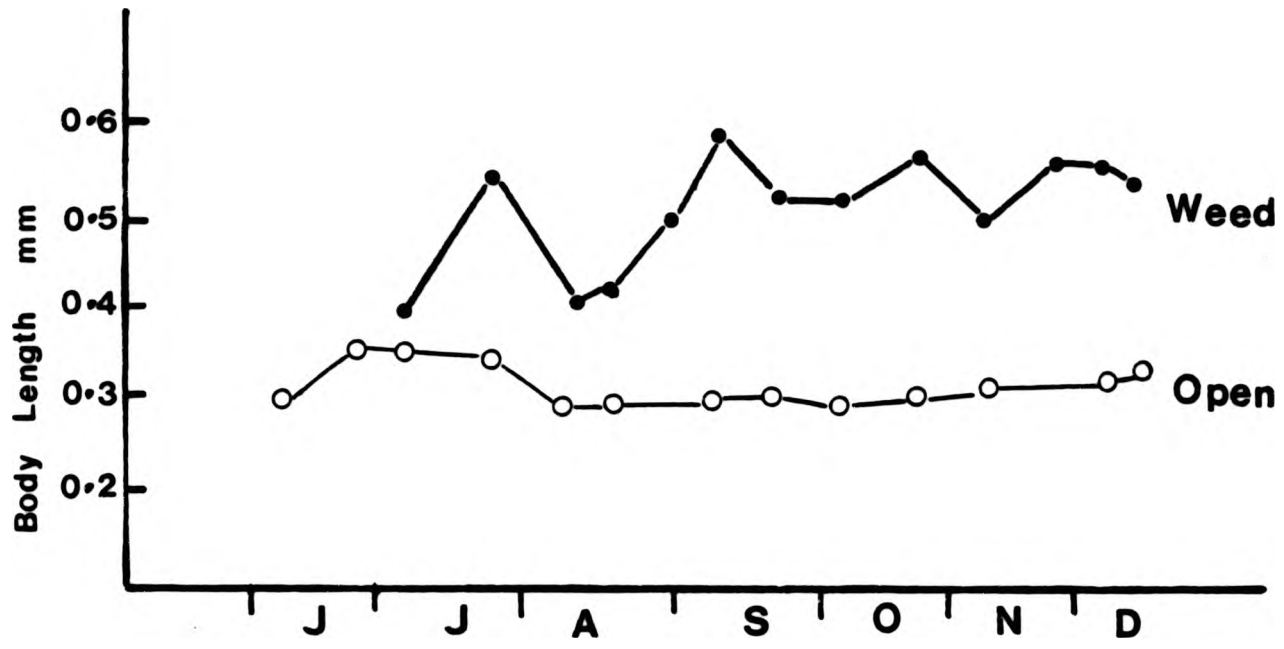

FIGURE 3.12 Weighted mean body lengths in mm of microcrustacea from the open water and the weedbeds in Farnborough in 1977.

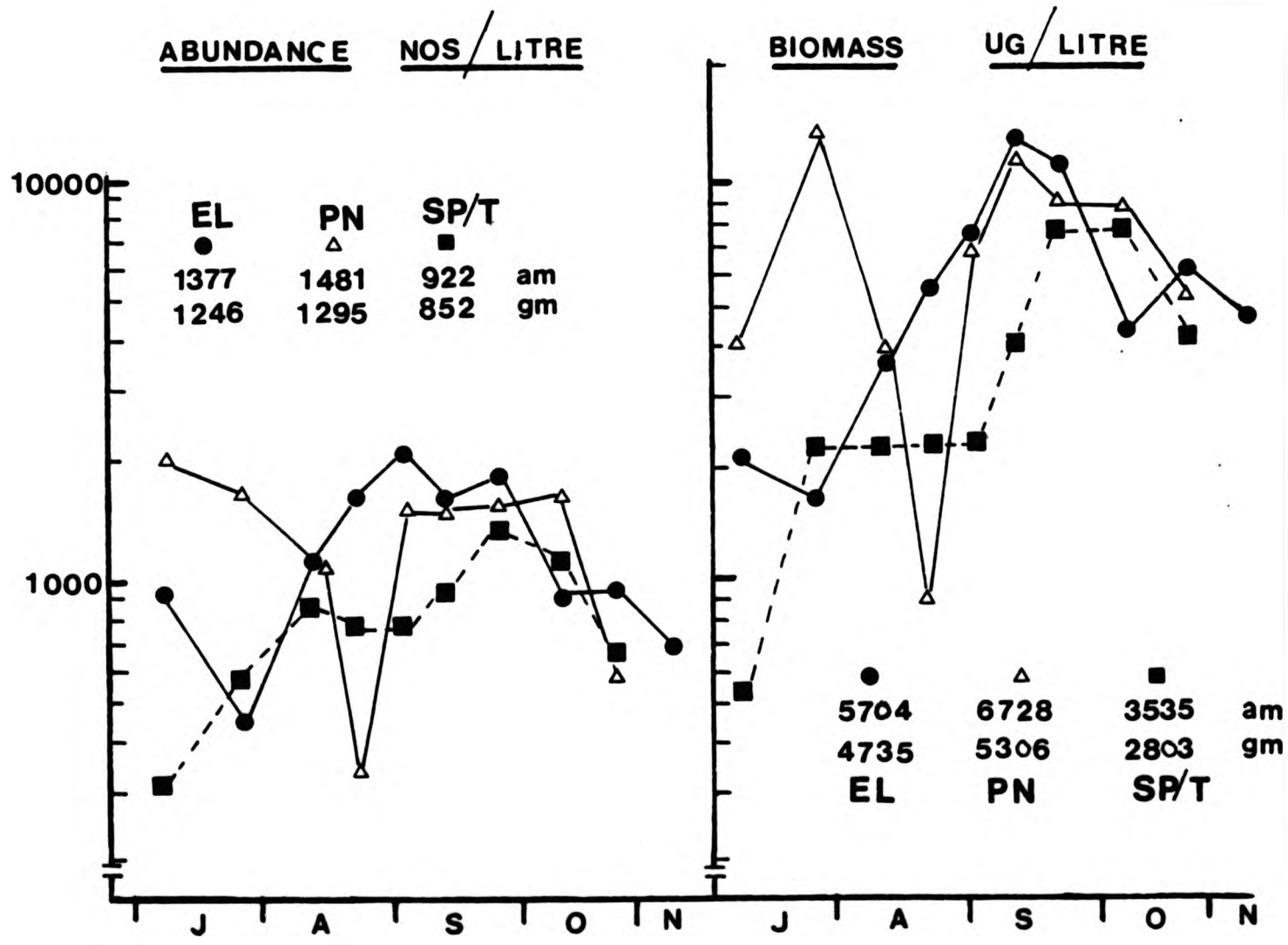

FIGURE 3.13 Numerical abundance in numbers/litre and dry weight biomass in ug/litre of total microcrustacea in the three marginal weedbed sites in Farnborough in 1977. The numbers give seasonal arithmetic (am) and geometric (gm) means for total microcrustacea at each site.
El = Elodea Pn = P. natans Sp/T = Sparganium and Typha

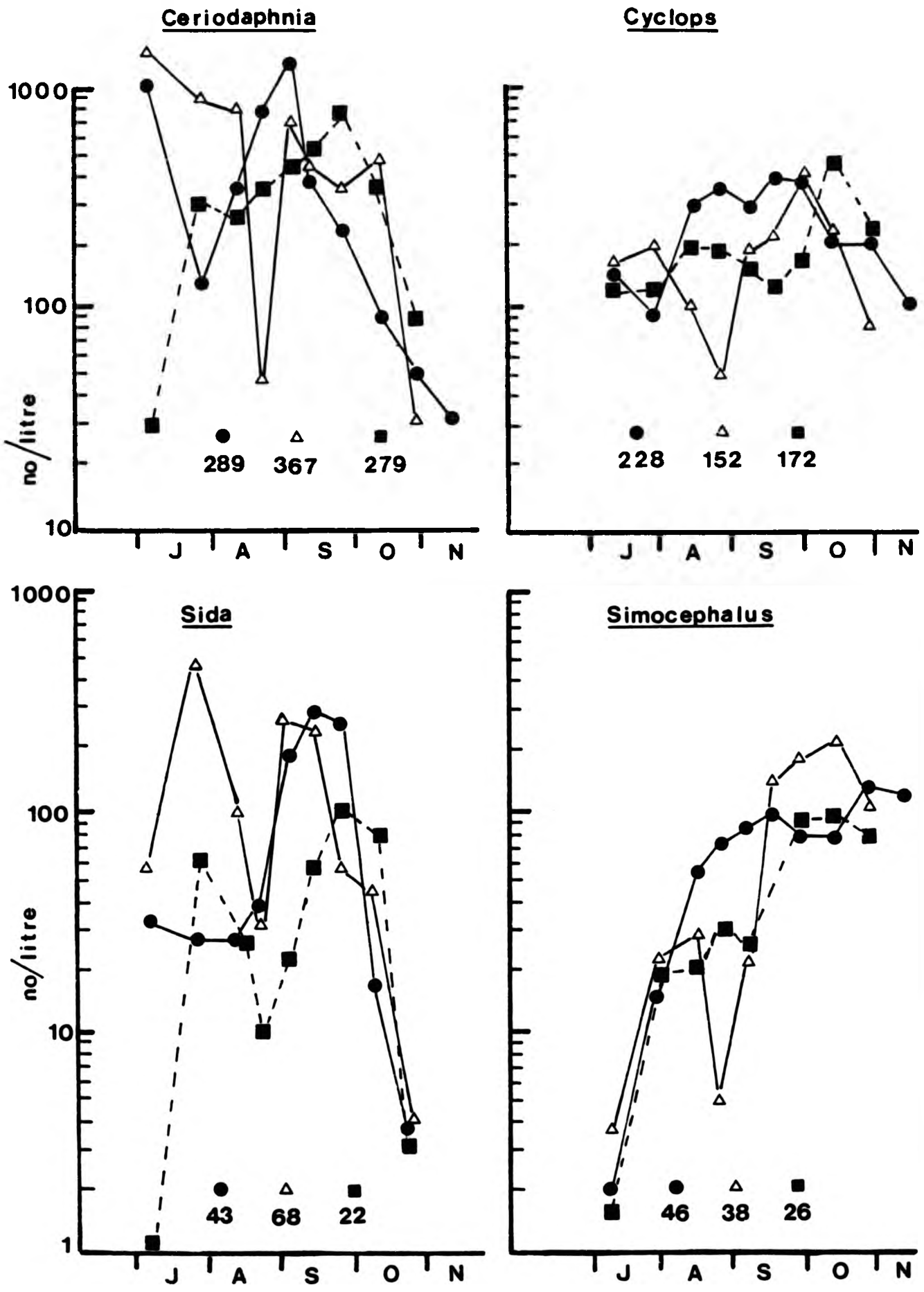

FIGURE 3.14 Numerical abundance in numbers/litre of the major species of microcrustacea in the three marginal weedbed sites in Farnborough in 1977. The numbers show the geometric means for each site.
● Elodea △ P. natans ■ Sparganium and Typha

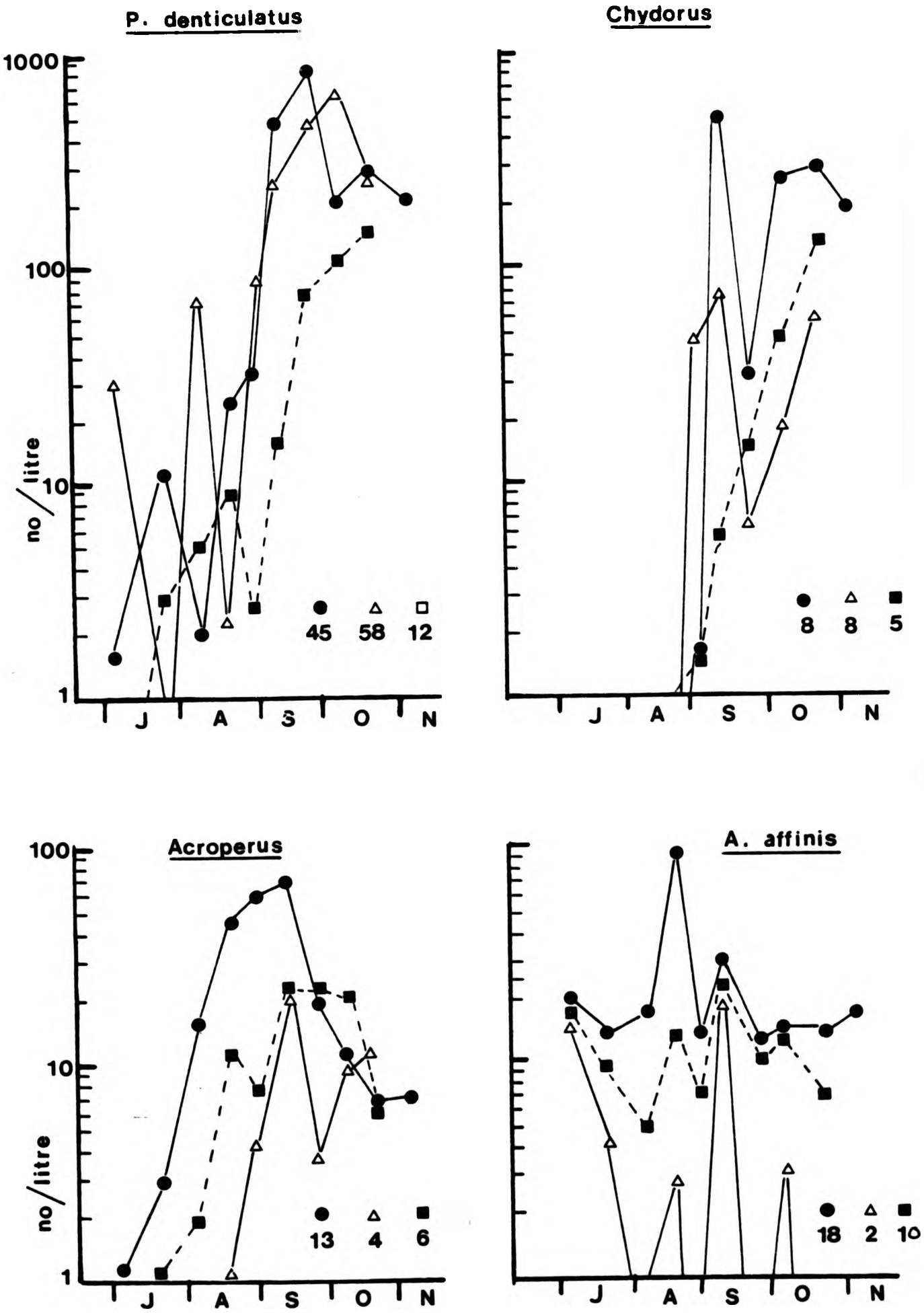

FIGURE 3.14 Cont.

Likewise, Daphnia spp. and Diaptomus gracilis were more common in P. natans, (see Table 3.16).

The Sida population occurred in two discrete peaks in all sites, the first being much greater in P. natans. However, once the population was established it became equally abundant in Elodea, although still less common in Sparganium. The association of Sida with P. natans is well documented (Langhans, 1911) so that its abundance in the other plants is interesting because the literature suggests that it is fairly immobile and remains stuck on the undersurface of the leaves, although Szlauer (1963) recorded this species as making diurnal vertical migrations. During the drop in numbers in August many mite eggs were observed on the P. natans leaves and these may have competed with Sida for attachment space (Puncochar, 1971). This may partly account for its presence in the other sites. As the Sida population declined, numbers of Simocephalus rose and to a greater level in P. natans than in other sites, so that one large cladoceran was replaced with another. This accounts for the consistently high biomass found among this plant. Simocephalus exhibited no particular association but was more common among Elodea in early August.

The Chydoridea were most abundant in Elodea, with a geometric mean of 190/litre, compared to 156/litre in P. natans and 74/litre in Sparganium. The most mobile species, Chydorus sphaericus and Pleuroxus denticulatus were also abundant among P. natans and usually less well represented in Sparganium. The more sedentary species, Acroperus harpae and Alona affinis (Fryer, 1963) showed more of an association with the surface area of the plant, being most common in Elodea and least common in P. natans. This was also true of the benthic Alona guttata, and Eurycercus was far more common in Elodea than at other sites.

Several trends can be deduced from these data. There were greater

fluctuations in the numbers of microcrustacea in P. natans whereas numbers in Elodea were more stable during the summer. Numbers in Sparganium increased steadily through the summer in phase with plant growth. It has been reported that epiphyte growth is least on young rapidly growing emergents, increasing in the autumn as the growth rate of the macrophytes slows down (Bownik, 1970).

3.8 Microcrustacea in the open water and the marginal macrophytes in Yateley in 1978.

In the gravel-pit lake at Yateley the open water microcrustacea were compared with those in Elodea in the lake margin and with those in the deeper plant/open-water boundary, termed Elodea/Typha on seven occasions between June and September in 1978. Chapter 5 illustrates the comparison beteen the open water and the combined weedbed samples. This section will discuss differences between the microcrustacea in the two marginal sites in more detail. Fig. 3.15 illustrates the seasonal changes in major species in the open water and in the two marginal sites. Table 3.17 gives the arithmetic and geometric mean densities in numbers/litre of the abundant species in the three habitats in both 1978 and 1979. As in Farnborough sampling commenced after any spring peak in zooplankton would have occurred.

The total abundance of microcrustacea in the open water varied from 167/litre to a maximum of 529/litre with a geometric mean of 366/litre, similar to open water abundance in Farnborough but differing in that the numbers remained at the same level during the sampling period instead of declining. The geometric mean abundance in Farnborough for the period June to September 1977 was 354/litre.

The open water was dominated by Cyclops spp., mainly C. leuckarti and C. agilis, which peaked in July at 200/litre, followed by a decline

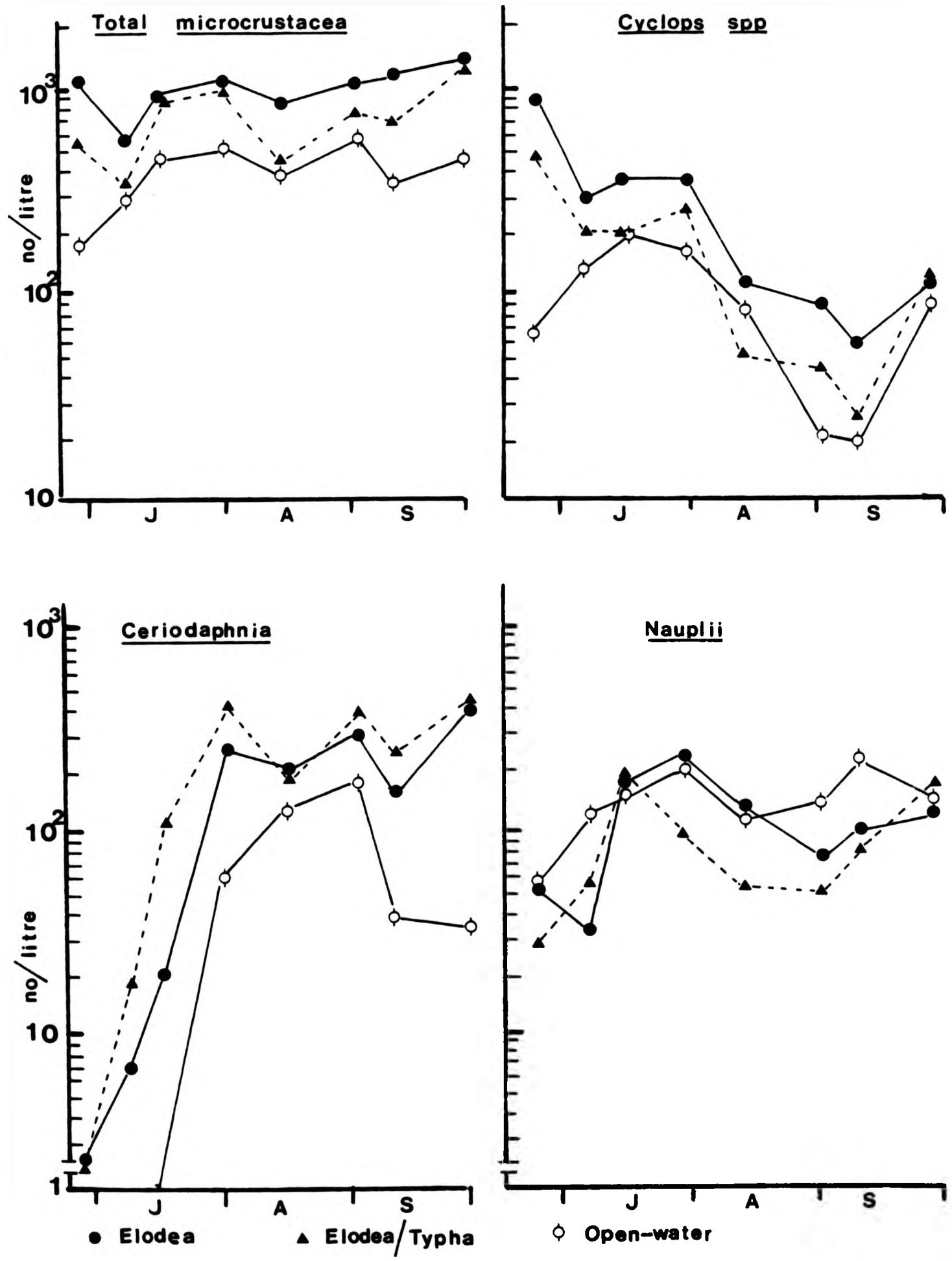

FIGURE 3.15 Abundance in numbers/litre of total microcrustacea and major species in the three sites (Open, Elodea and Elodea/Typha) in Yateley in 1978.

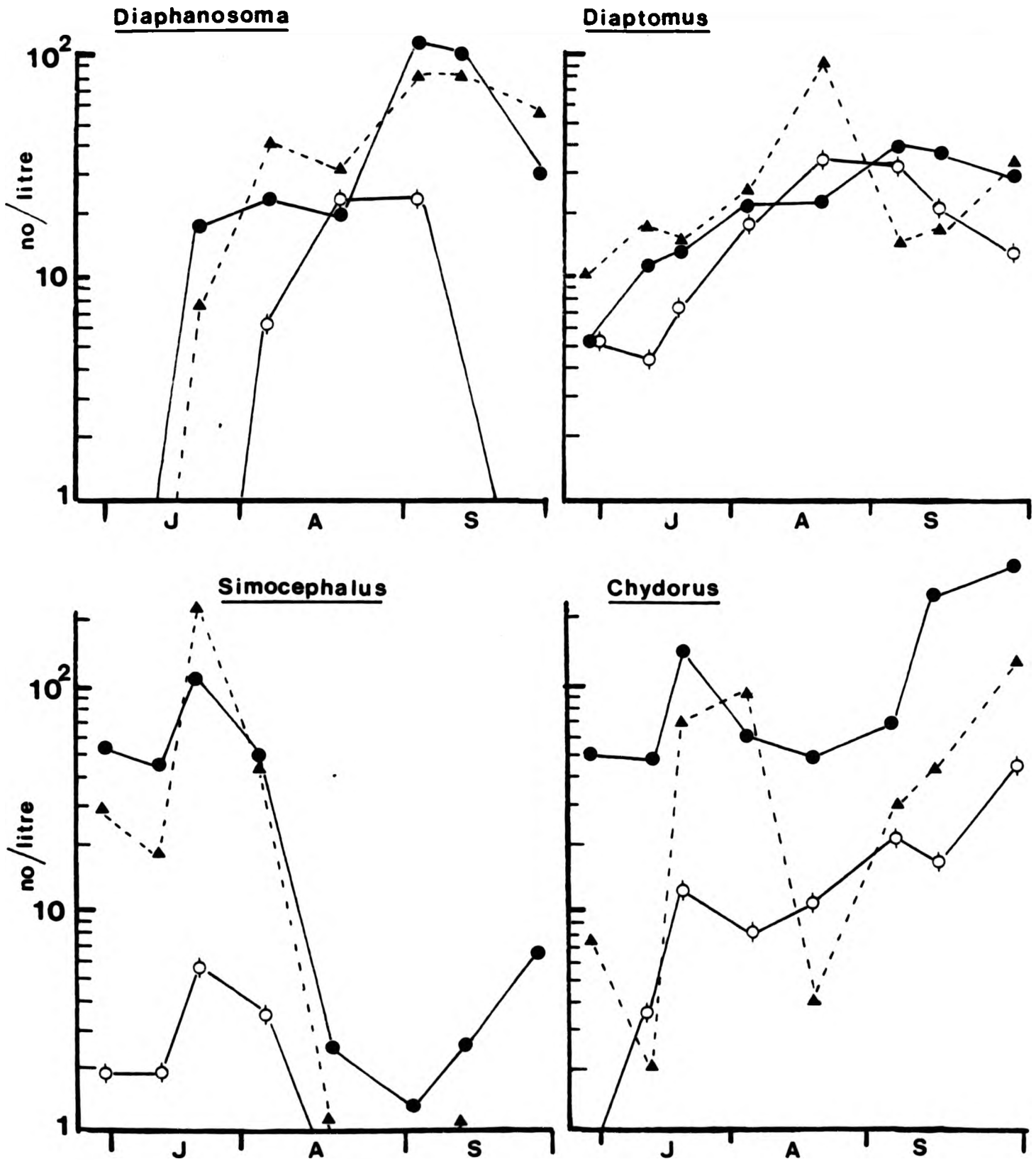

Figure 3.15 (cont.)

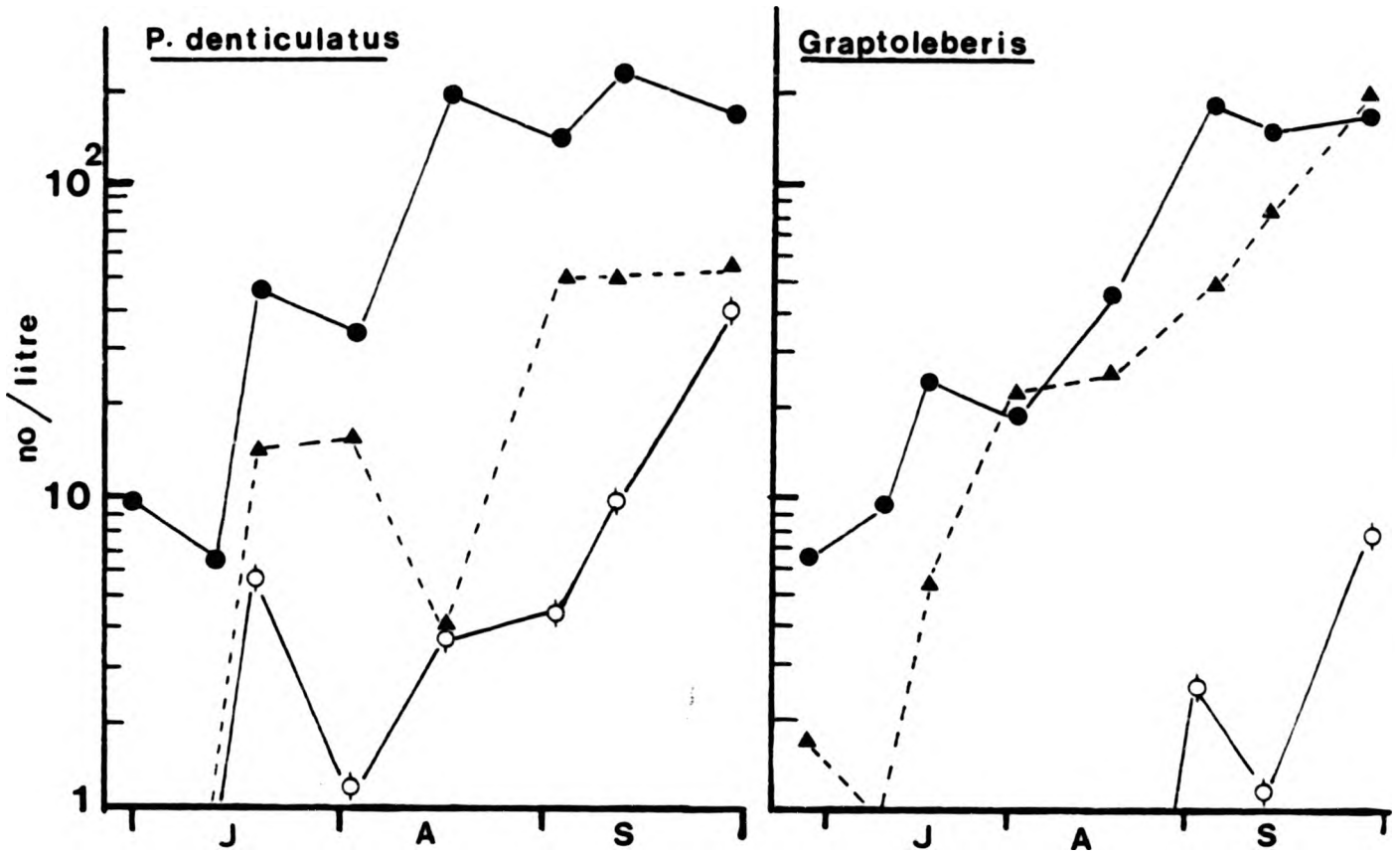

Figure 3.15 (cont.)

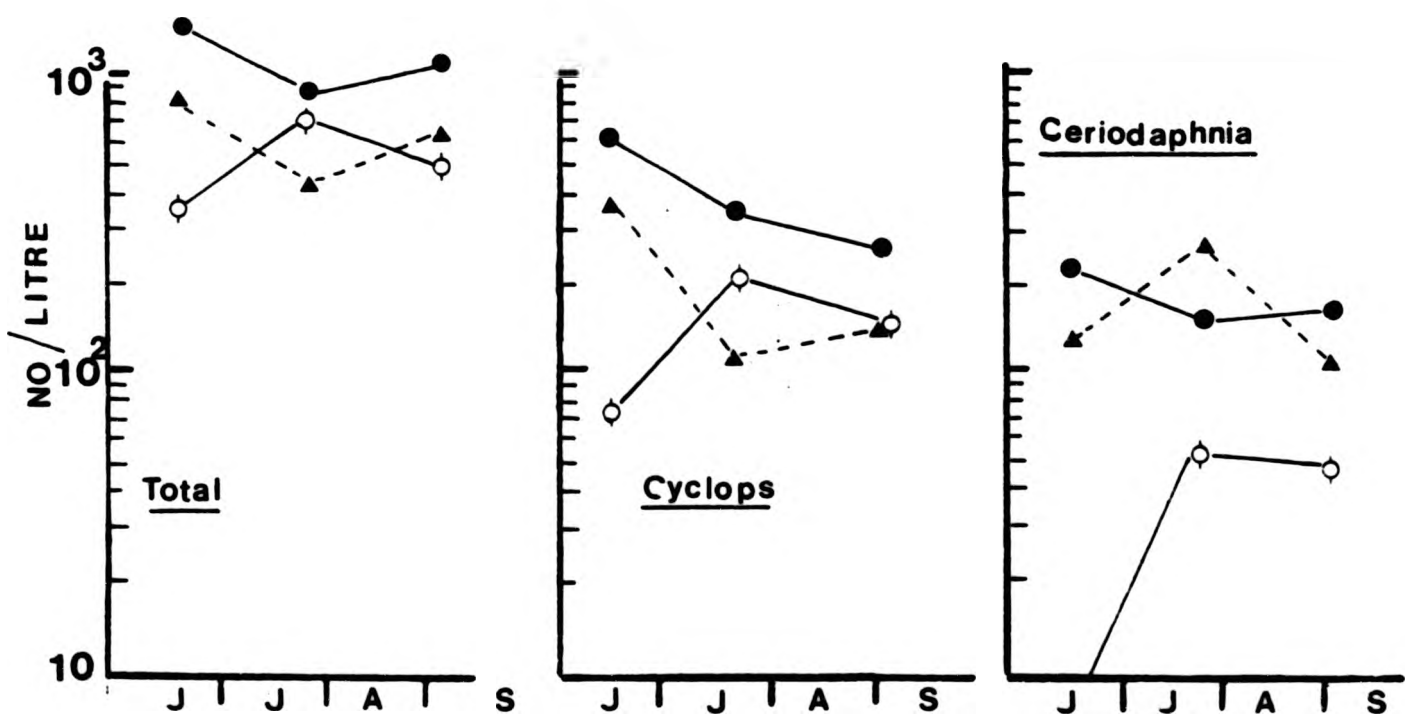

FIGURE 3.16 Abundance in numbers/litre of total microcrustacea and major species in the three sites (Open, Elodea and Elodea/Typha) in Yateley in 1979.

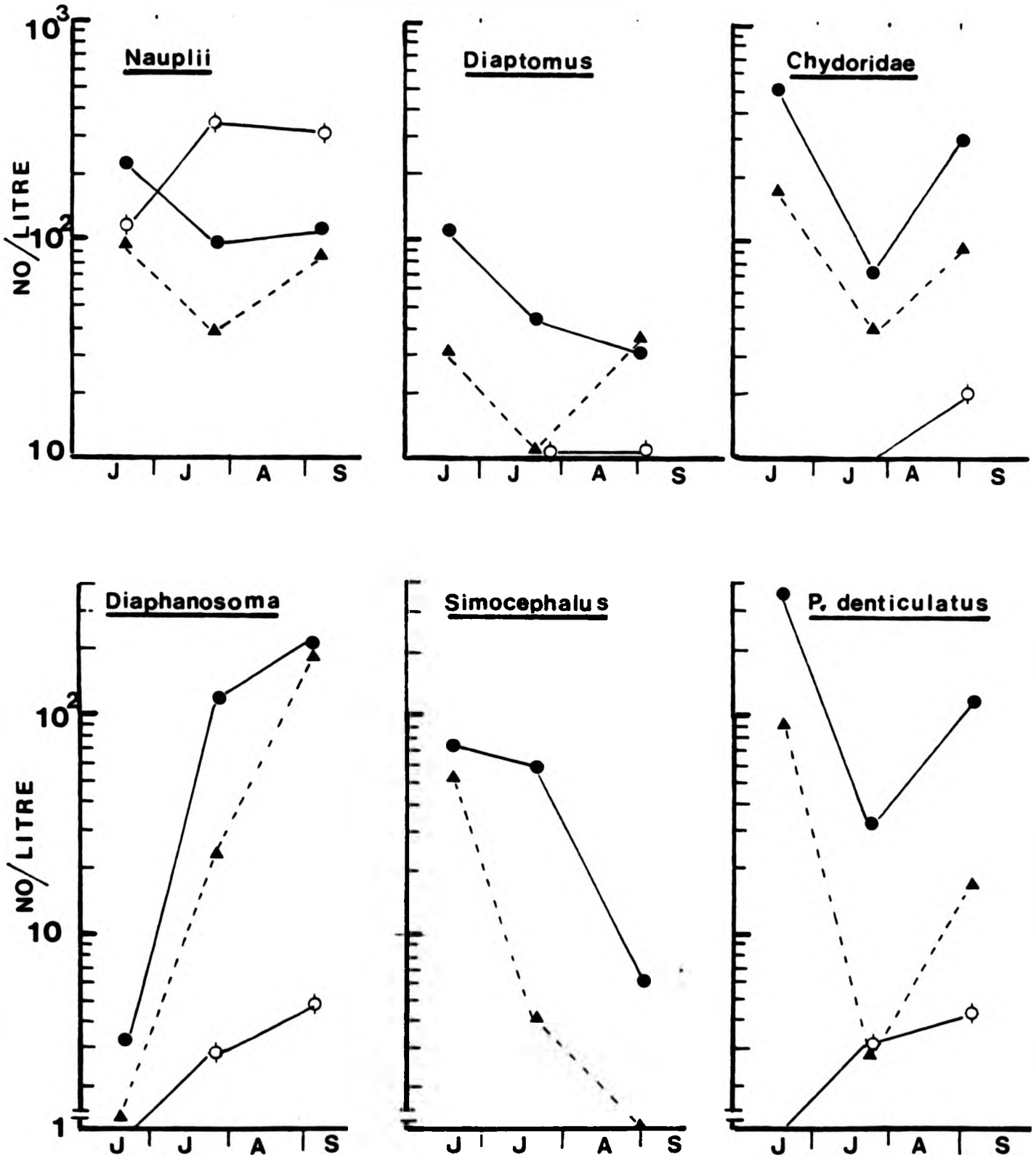

Figure 3.16 (cont.)

to 19/litre. During this decline, Ceriodaphnia and Bosmina were the most abundant crustacea in the open water, with a peak density of 163/litre and 103/litre respectively on the same date. The Ceriodaphnia population then became smaller while Bosmina exhibited a similar cyclical pattern to that found in Farnborough. Interspersed between these two crustaceans, the Asplanchna priodonta population reached a peak density of 283/litre. While the phytoplankton was not sampled, the two dominant algae in the lake were observed to be Ceratium hirundinella, abundant in August and coincident with the rise in Asplanchna, followed by Microcystis sp. during which time the filter feeders declined in number. Other species common in the open water were Diaptomus gracilis and Diaphanosoma brachyurum. Daphnia longispina was only slightly more abundant than in Farnborough with a maximum density of 34/litre. Eleven species of Chydoridae were found in the open-water samples, the most common being Chydorus sphaericus, Pleuroxus denticulatus and P. aduncus. Chydorid numbers built up through the summer to an autumn peak.

Total densities of microcrustacea were higher in the macrophytes than in the open water, as in Farnborough. Elodea supported the largest populations, with a mean density of 983/litre and a maximum density of 1375/litre. Elodea/Typha supported a geometric mean density of 696/litre with a maximum density of 1257/litre. Cyclops dominated the marginal habitats. Ceriodaphnia, Chydorus sphaericus, Pleuroxus denticulatus, Graptoleberis testudinaria and Diaphanosoma brachyurum were varyingly abundant. The carnivorous cladoceran Polyphemus pediculus was more abundant than in Farnborough, occurring in most of the weedbed samples but not in the open water. The large cladocerans Sida and Simocephalus were not as abundant as in Farnborough, Sida in particular being present in low numbers possibly because of the scarcity

of floating leaved plants.

As in Farnborough Cyclops and Ceriodaphnia were more abundant in the macrophytes than in the open water. However, while Bosmina did not occur in the weedbeds, Ceriodaphnia was more common in the open water than was Bosmina. Diaptomus was slightly more abundant in the macrophytes than in the open water. Therefore differences between the two communities were not as marked as in Farnborough and this was possibly due to the thick growths of Elodea which spread over much of the lake bottom, influencing both numbers and species composition of the open-water zooplankton. It was also possible that differences in the fishstock were responsible for differences between the microcrustacea of the two lakes as it was thought that Yateley contained fewer fish than Farnborough (see Chapter 1). This will be discussed further in section 3.10. However, of the more planktonic species, only Cyclops was more abundant in Elodea while Ceriodaphnia, Diaptomus and Diaphanosoma were most common in Elodea/Typha. The open-water species, Daphnia, Bosmina, and Asplanchna were better represented in Elodea/Typha than Elodea. Examination of Table 3.17 shows that typically open-water species were at their greatest abundance in the open water, were moderately common in Elodea/Typha and uncommon in Elodea. A reverse situation occurred with typical weed dwellers so that Elodea/Typha contained an intermediary community. There were exceptions to this pattern as Ceriodaphnia, Diaptomus and Diaphanosoma were most common in the plant/water interface. The chydorids, of which Chydorus sphaericus, Pleuroxus denticulatus and Graptoleberis were most common, were more abundant among Elodea, although interestingly, one of the less mobile species, Acroperus harpae, (Fryer, 1968), was equally common in both sites.

Therefore, the Elodea/Typha site supported a mixture of open water

and macrophyte components. The presence of vegetation resulted in a greater diversity of crustacea than would otherwise occur while because of the lower density of plants compared with Elodea, there was a greater volume of water for the filter feeders to move around in. This habitat was less well buffered than the denser marginal vegetation and greater fluctuations in numbers of some species occurred in Elodea/Typha than in Elodea.

3.9 Comparison of open water and marginal macrophytic crustacea in Yateley in 1979.

Three sets of samples were collected in 1979. The geometric and arithmetic mean densities of major species on these three dates are given in Table 3.17. Fig. 3.16 illustrates differences between the three sites. The open-water samples contained densities very similar to those of the previous year, with a geometric total mean density of microcrustacea of 467/litre (553 with Asplanchna). Individual species were also present in similar densities to those of the previous year. with Cyclops being the dominant crustacean. Ceriodaphnia was common but the sampling interval was too long for accurate estimation of the population fluctuations of Bosmina (Hillbricht-Ilkowsksa and Weglenska, 1970) and this species was only present on one sampling date. Asplanchna was again abundant in the open water.

The weedbeds contained similar densities to 1978, with Elodea supporting larger numbers of microcrustacea than Elodea/Typha. However, in 1979 no species was more abundant in Elodea/Typha than in Elodea, in contrast to 1978, except for the rarer species, Polyphemus and Scapholeberis, so that the differences between weedbed sites found in 1978 were not repeated in 1979. However, only three samples were collected and as the peak value for Ceriodaphnia was higher in

Table 3.17 Comparison of arithmetic and geometric mean densities in numbers/litre of microcrustacea in the open water and the macrophytes in Yateley 4.

	am						gm					
	1978			1979			1978			1979		
	EL	EL/TY	O	EL	EL/TY	O	EL	EL/TY	O	EL	EL/TY	O
Cyclops	277	173	100	388	198	144	195	120	77	366	172	131
Nauplii	105	91	139	142	73	241	100	76	131	133	68	210
Ceriodaphnia	166	227	51	173	152	x	70	113	15	170	144	16
Diaptomus	22	29	19	62	26	10	10	22	15	54	23	10
Diaphanosoma	39	38	6	111	69	3	15	17	2	46	21	2
Bosmina	x	x	22	6	x	55	x	x	9	x	x	5
Daphnia	x	1	7	0	1	47	x	1	3	0	1	5
Chydorus	121	46	15	5	4	1	91	23	8	4	3	0
Graptoleberis	84	53	1	10	9	x	43	14	1	9	9	0
P.denticulatus	98	26	8	67	37	3	56	11	4	120	18	2
Simocephalus	33	41	2	44	18	1	14	9	1	29	7	1
Polyphemus	10	1	x	2	2	1	3	1	x	2	2	x
Scapholeberis	2	9	x	2	3	x	2	4	x	1	1	0
Chydoridae	337	144	38	274	119	12	274	91	26	200	65	8
Asplanchna	1	5	x	0	0	32	x	1	17	0	0	27
Total ind	1021	755	384	1264	642	537	983	696	366	1227	627	467

EL = Elodea
EL/TY = Elodea and Typha
O = Open water.
x = <1.0

Elodea/Typha than in Elodea, it is possible that similar differences to those found in 1978 did occur but were not detected.

3.10 Discussion.

The results of the this work showed that differences did exist between the microcrustacean communities of the open water and marginal macrophytes in Farnborough and these differences were also found to a lesser extent in Yateley. The two communities in Farnborough were distinct in that the margins had: higher standing crops; a greater number of species; a larger average body size for those taxa occurring in both habitats, and a larger range of body sizes in the weedbeds. At the species level there was apparent mutual exclusion between Ceriodaphnia and Bosmina, the former gaining an ascendancy over the latter in the margins that it never achieved in the open water.

Before considering the nature of the communities within gravel-pit lakes an attempt should be made to consider these communities in relation to what is known about microcrustacea in S. England. There are not many natural water bodies in this area, small or large. The gravel pits are relatively recent but do possess a degree of maturity in their aquatic vegetation not found in some other man-made water bodies such as the concrete lined water supply reservoirs to which many of the published studies on crustacean zooplankton refer. Much of this discussion will concentrate on the more planktonic members of the two crustacean communities as the results of the diet study (Chapter 4) showed these to be the preferred food of the roach and perch. (The sampling method employed also provided more accurate estimates of planktonic microcrustacea than of the benthic Chydoridae).

A crustacean assemblage which might be regarded as typical of the open-water zooplankton of water bodies in S. England has been described

by Munro and White (1975) as consisting of Daphnia longispina, Cyclops vicinus and Diaptomus gracilis, from their work on Bough Beech reservoir, Kent (area 115 ha, mean depth 7.7 m) and Rye Meads sewage treatment lagoons, Herts. Munro (1977) gives a fuller semi-quantitative description of the zooplankton of Bough Beech which includes Bosmina longirostris and Asplanchna priodonta among his commoner species, although D. longispina is described as the dominant species. D. longispina, C. vicinus and D. gracilis were all uncommon in Farnborough where Cyclops vernalis americanus and Bosmina longirostris dominated the open-water zooplankton (geometric mean densities of 48/litre and 43/litre respectively). The two large filter feeders mentioned above (D. longispina and D. gracilis) were replaced in Farnborough by two smaller animals, one a filter feeder and the other a particulate grasping feeder, and the role of predator was probably taken by Asplanchna, as it is unlikely that C. vernalis americanus of the size found in Farnborough were entirely carnivorous. Comparison with other water bodies suggests that this domination of the crustacean zooplankton by cyclopoid copepods, which was also found in Yateley, is unusual, although there is evidence in the literature which suggests that a high fish stock is often accompanied by an increase in cyclopoid copepods. The crustacean zooplankton of the London reservoirs (Queen Elizabeth II, depth 17 m, mixed; and King George VI, depth 15 m, stratified) is dominated by Daphnia spp. (Duncan, 1975a). Burgis (1975) found that Cyclops vicinus contributed a small part of the biomass in QEII while C. vicinus and C. vernalis were only slightly more abundant in KGVI. This was also the case in Eglwys Nŷnydd, a Welsh reservoir (area 101 ha, mean depth 3.5 m), dominated by Daphnia hyalina with C. vicinus of secondary importance (George and Edwards, 1974). The crustacean zooplankton of Farmoor 1 reservoir near Oxford (area 51

ha, mean depth 4.6 m) was dominated by Daphnia hyalina var lacustris, with Diaptomus gracilis and Bosmina longirostris periodically abundant and Cyclops vicinus and C. strenuus present only in low numbers, (Jones et al, 1979).

The opposite to this was found in Loch Leven, Scotland, (which although further north and much larger may be compared with the gravel pits because it is a shallow, natural water body,(area 13.3 km^2, mean depth 3.9 m) where "a virtual monoculture of Cyclops strenuus abyssorum " was present in the 1970's (Johnson and Walker, 1974) although D. hyalina has recently become co-dominant possibly with increasing eutrophication (George and Owen, 1978). White (1975) working on Rye Meads sewage lagoons, found that with a high fish stock Cyclops vernalis americanus replaced Daphnia longispina and Cyclops vicinus as the dominant crustacean.

The domination by Cyclops was less marked in Yateley as a mixture of cladocerans and Asplanchna was sub-dominant. D. longispina was more abundant in Yateley than in Farnborough and as a density of 140/litre was recorded in June 1979 it is possible that greater numbers were present in the period prior to sampling. Net collections made in spring 1981 contained almost 100% Daphnia. It is well documented that fish predation can cause a change in the species composition of zooplankton communities, Bosmina often replacing Daphnia (Brooks and Dodson, 1965; Hillbricht-Ilkowska and Weglenska, 1973), and this could also have been responsible for the absence of the large cyclopoid copepods and the scarcity of Diaptomus, which was rare in Farnborough but more common in Yateley, where a lower fish stock was thought to be present. It is interesting that two lakes where cyclopoid copepods were the dominant zooplankters, Loch Leven in Scotland and Lake George in Uganda (area 250 km^2, mean depth 2.4 m) (Burgis and Walker, 1972) are both shallow,

eutrophic water bodies without permanent stratification (Burgis and Dunn, 1978), suggesting a relationship between cyclopoids and well mixed water containing particulate matter in suspension. In support of this suggestion, O'Grady (pers.comm) found that the crustacean zooplankton of a well mixed, 1.7 m deep, 0.5 ha fish pond containing a high fish stock and with high levels of particulate carbon was dominated by Cyclops spp. while an adjacent pond with a low fish stock and lower levels of particulate carbon was dominated by Cladocera. The cause of the turbidity in Farnborough was not ascertained but the lack of light penetration (which restricted macrophytes to the shallow margins) was marked, in contrast to Yateley where the water was clear to the bottom on occasions. It may have been due to dense populations of small algae which can reduce light penetration more than large algae and which are often present when fish predation has removed the large filter feeders. It is also possible that the absence of the large filter feeders from Farnborough resulted in a greater quantity of particulate matter and also smaller crustacea for the copepods to feed on. The dominance of carnivorous cyclopoids in water bodies supporting large numbers of planktivorous fish has been related to the presence of large populations of small Cladocera which are the preferred prey of the copepods (Brandl and Fernando, 1975; Jamieson, 1980). The cyclopoids in Farnborough were smaller than typical predatory copepods but may have exerted a predation pressure upon Bosmina.

The lack of data for the whole year in Farnborough could have led to the overestimation of the importance of Cyclops in the open water because the Daphnia population may have peaked earlier. However, when Daphnia spp. were present in the open water in June and July they also occurred in the weedbed samples and those collected in April did not contain any Daphnia (although the beginning of the Bosmina increase was

represented). It is unlikely that Daphnia were present in number in the lake before April because of the low water temperature (<3.0°C).

The species composition of the marginal macrophytic communities was far more complex than that of the open water although most species were present in all sites, with changes in relative abundance being of greater interest than species groupings. There is little information to be gained from a comparison of the weedbed species lists with the exhaustive lists and associations of macrophytic crustacea drawn up by Straskraba (1967) and Rybak, Rybak and Tarwid (1964) but some points are of interest. In Farnborough, Cyclops vernalis americanus although most abundant in the weedbeds, dominated the open-water community as well, suggesting a degree of flexibility on the part of this species. It is possible that the small lake area and the relatively long perimeter resulted in the margins exerting a strong influence on the species composition of the open water zooplankton. Yateley is a larger lake than Farnborough with a smaller perimeter and in it there were several cyclopoid species common at different times of the year and in different sites, with planktonic species present in the open water.

Ceriodaphnia spp. (very abundant in the marginal vegetation in Farnborough and Yateley) are often the dominant cladocerans in weedbeds. Rybak, Rybak and Tarwid (1964) in an examination of 45 littoral sites found Ceriodaphnia spp. to be dominant in 47% of the sites, although 33% of the remaining sites had Bosmina as the dominant crustacean. Bosmina did not occur among the macrophytes in Farnborough and Yateley. Hall, Cooper and Werner, (1970) found that C. reticulata was the most abundant zooplankter in some small (0.07 ha) ponds while Bosmina was rare. Neill (1975) considered Ceriodaphnia quadrangula to be an important regulator of microcrustacean community structure because of

its ability to utilise a wide range of foods efficiently.

The species assemblage found in the macrophytes was similar to that recorded from vegetation in Hampton Court Long Water by Green (1966) who did not regard Bosmina as part of this community although it was present in the open water. Fifteen species of chydorid were found in Farnborough and 17 in Yateley. This appears to be fairly typical of temperate water bodies. Smyly (1957) found 16 species in two lakes, Shiel (1976) found 18 in several weedbeds, and Green (1966) found 18 species at Hampton Court.

Smyly (1957) found no clear cut differences between the species composition of the open water and the weedbeds (apart from the absence of Daphnia from vegetation which will be discussed later) and as in this study observed that it was relative abundance which changed with habitat.

The geometric mean standing crop of open-water microcrustacea in Farnborough for the period June to December, 1977 of 249 ind./litre and 245 ug(d.w.)/litre was very similar to the annual mean standing crops reported by Cook (1979) for Farnborough; in 1975, 198 ind./litre and 144 ug(d.w.)/litre and in 1976, 329 ind./litre and 227 ug(d.w.)/litre. The geometric mean densities in Yateley in 1978 and 1979 of 366 ind./litre and 467 ind./litre were higher because the sampling period did not extend over the whole year and because the crustacean populations did not decline during the summer as they did in Farnborough in 1977. Possible reasons for this difference between the lakes will be discussed later. The standing crops in Farnborough were also similar to those reported from other small and shallow water bodies in S. England. O'Grady (pers.comm) recorded a geometric mean density of crustacean zooplankton of 218 ind./litre in a filter bed of the same depth in E.

London over a similar sampling period in 1980. Munro and Bailey (1980) in a three year study of the newly filled Bough Beech reservoir reported a peak biomass of 689 ug(d.w.)/litre in 1972 and a peak annual mean biomass of 142 ug(d.w.)/litre in 1973. These figures are lower than for Farnborough which would be more similar if the Farnborough sampling had encompassed the whole year. Munro and Bailey (1980) also quote figures for Grafham Water of similar levels. Dry weight biomass of crustacea in Queen Elizabeth II reservoir in 1973 was of the same order of magnitude as that in Farnborough, with a maximum of 1882 ug(d.w.)/litre (Duncan, 1975b). The arithmetic annual mean biomass of the two most abundant species combined in Eglwys Nynd̂d in 1970 was 580 ug(d.w.)/litre (George and Edwards, 1974, George 1976). An annual density of zooplankton of 300 ind./litre was reported for Loch Leven (Le Cren, 1978) with a peak biomass in 1970 of 1000 ug(d.w.)/litre (Burgis and Walker, 1972). The abundance of open water crustacean zooplankton in Farnborough and Yateley was therefore very similar to that in other British water bodies: the annual productivity however, may have been lower because of the mesotrophic nature of the lakes.

Comparison of the standing crops of weedbed microcrustacea recorded in this study with those found by other authors is limited because of the lack of quantitative data, discussed in Chapter 1. The most directly comparable studies are those of Straskraba (1963, 1967) and Pennak (1966) who both used a tube sampler to collect quantitative data to investigate the differences between the open water and the marginal macrophytes.

Straskraba (1967) found that the weedbeds supported higher standing crops of microcrustacea than the open water with a 10 fold difference between the two habitats, as was found in Farnborough. Straskraba (1967) provides data from other sources in agreement with

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this. The levels of abundance in the Farnborough weedbeds were also similar to those of the Labicko backwater (Straskraba, 1965) where a maximum of 1370 adult crustacea/litre was recorded. The maximum density in Farnborough was 1726/litre including copepodites and nauplii. Straskraba (1967) found maximum standing crops of 1159/litre and 384/litre in two consecutive years in Prochaskova Backwater, similar to densities in the Yateley weedbeds. At the other extreme, Rybak and Rybak (1964) reported total densities of from 0 to 100/litre in a survey of Polish littoral sites, which is extremely low. Smirnov (1963) found an order of magnitude difference between the biomass of Chydoridae in the open water and among vegetation, as was found in Farnborough.

Pennak's (1966) findings disagree with those reported here. He found smaller communities in the weedbeds and a compilation of data from all his sites (usually two per lake) gives an arithmetic mean density of 141/litre in the weedbeds and 199/litre in the open water. In 14 comparisons of weed and open sites, only 5% had higher densities in the weedbeds and the largest standing crop of crustacea was 317/litre. The tube which Pennak used was made of rubber, lighter than perspex and was lowered slowly into the shallow regions to take a "plankton sample of organisms suspended in the water." The plankters may have avoided this light tube if it dropped slowly and benthic species will have been underestimated.

The differences between the weedbeds and the open water were not so marked in Yateley as in Farnborough for two possible reasons. There was possibly a lower fishstock, resulting in the presence of large filter feeders (Diaptomus gracilis and Diaphanosoma brachyurum), and large algae e.g. Ceratium. This in turn resulted in greater light penetration than in Farnborough (although not measured) which allowed Elodea to spread over the lake bottom. Many representatives of the

littoral community were present in the open water and the numbers in the open water did not decline during the summer as in Farnborough, where the difference in total numbers between the two communities became progressively greater. Changes in total densities followed the same pattern in the three sites (Open, Elodea, Elodea/Typha), suggesting that a common factor such as temperature or food supply was involved rather than differential predation. However, the open-water and weedbed densities combined were similar to the two combined in Farnborough, the difference being in how the numbers were partitioned between sites. This may however be a questionable comparison to make because the contribution of each habitat to total lake area requires exact measurement to enable accurate comparisons to be made. Cook (1979) reported that open-water samples from Twyford 39, a lake with a high degree of vegetation cover, contained many littoral species. It would therefore appear that in these small lakes the open water can be strongly influenced by the marginal vegetation.

One of the most interesting differences between the open water and the weedbeds in Farnborough was the apparent mutual exclusion of Bosmina and Ceriodaphnia. There are thought to be two mechanisms regulating the abundance of these species. It is suggested that Bosmina, the dominant open-water cladoceran, was competitively excluded from the weeds by Ceriodaphnia. From the size efficiency hypothesis of Brooks and Dodson (1965) further discussed by Hall et al (1976) one can assume that Ceriodaphnia possessed an energetical advantage over Bosmina because of its greater body size, providing greater filtering efficiency with the ability to consume a larger size range of food particles. In microcosm experiments Neill (1975) found that Ceriodaphnia in the absence of fish predators also outcompeted other larger cladocerans (because the adults

outcompeted the juveniles of larger species). Other possible reasons for the absence of Bosmina from the vegetation were the intensive fish predation by O+ roach (Chapter 4) or unfavourable pH regimes. A very large fish population would be required for fish predation to result in total elimination of Bosmina from the weedbeds. Kairesalo (1980) found that Bosmina migrated from the littoral vegetation to the open water in the daytime and moved back at night when the pH was lower. However, if this was the case Bosmina might be expected to occur in sparse vegetation such as P. natans which would not be subject to the same extremes of pH. Bosmina did not occur in either of the marginal sites in Yateley although pH fluctuations would also probably have been less extreme in the Elodea/Typha zone. The absence of Bosmina from the littoral is not typical as some workers have found it among vegetation (Pennak, 1966; Straskraba, 1967; Lim and Fernando, 1973) although Szlauer (1963) did not regard it as a permanent inhabitant of submerged plants. Shiel (1976) found that Bosmina was significantly more common in the open water than in weedbeds as in the present study, and Dumont (1972) stated that Bosmina was very efficient at avoiding the littoral both during the day and at night. Bosmina is therefore a species which can live in both regions of a water body, actual occurrence probably being dependent upon the degree of vertebrate predation and invertebrate competition. It would be very interesting to carry out laboratory based experiments on the effects of fish predation and the presence of macrophytes upon competitive interactions between these two small cladocerans.

The cause of the large fluctuations in the Bosmina population observed in the open water is unknown. Dumont (1972) found an antagonistic relationship between Asplanchna and Bosmina involving vertical migrations in opposite directions and alternating population

peaks such as occurred in Farnborough. As Dumont concluded that Bosmina outcompeted Asplanchna for space this would not explain the Bosmina decline. The Bosmina populations may have caused food limitations during the population peaks through over-grazing.

The Ceriodaphnia population followed the same seasonal cycle as that described by Burgis (1957), appearing when the water temperature had risen above 10°C, staying consistently high during the summer and declining in the autumn. Ceriodaphnia was extremely abundant in the weedbeds, being the main contributor to the high standing crops. C. pulchella is a littoral species which may be recorded from the open water as in Yateley. It is likely that a large size range of algal particles was available to these smaller filter feeders because of the lack of large herbivorous filtrators such as Daphnia spp. in the open water. These algae would be swept into the margins, particularly into weedbeds with less dense vegetation such as P. natans and this may explain the high abundance of Ceriodaphnia in the weeds and in particular in the less densely vegetated areas. It has also been shown that Ceriodaphnia can feed on bacteria (Smyly and Collins, 1975), and Downing (1981) has described the ability of some littoral Cladocera to switch from planktonic to periphytic algal food as and when resources change. This might provide the Ceriodaphnia population with an additional competitive advantage over Bosmina in the weedbeds.

There are several possible explanations for the small populations of Ceriodaphnia in the open water in Farnborough. Gliwicz et al (1981) state that other factors being equal, differences in population size of a species can be explained by differences in food concentration or predation pressure. Food limitation due to the large numbers of Bosmina in the open water could have reduced the fecundity of the Ceriodaphnia population (Weglenska, 1971) although no evidence (egg counts) for this

was collected apart from the observation that both populations declined in the open water at the same times. It is more likely that size-selective predation by adult roach (Cook, 1979) removed the larger Ceriodaphnia individuals (see Fig. 3.9) and so lowered the populations reproductive capacity. Taylor (1980) has shown that population numbers of crustacean zooplankton are most drastically reduced by size-selective predation on the older reproducing individuals. The preference of roach for daphnids rather than copepods is well known (see Chapter 4) and the maximum size of Bosmina, of 0.5 mm was probably below the optimum food size for adult planktivores (Brooks and Dodson, 1965). The situation in Yateley (? low fish stock) suggests that the planktivorous fish were a cause of the lack of Ceriodaphnia in the open water in Farnborough because although Bosmina was absent from the vegetation Ceriodaphnia was abundant in the open water and on occasions more abundant than Bosmina.

The presence of Daphnia longispina among the vegetation in Farnborough was contrary to the findings of other workers (Smyly, 1952; Smyly, 1957; Pennak, 1966). Such limnetic plankton species as Daphnia usually do not occur in the littoral region and Smyly (1952) classified D. longispina as a species rare in vegetation. It has been suggested that limnetic species avoid shallow water and/or the shore. This phenomenon, called avoidance of the shore, or Uferflucht, which has been observed in crustacea and many rotifers, has been discussed by Siebeck (1980). He suggested that it was caused by a symmetrical optical orientation coincident with a negative geotactical orientation, related to vertical migration movements, which keeps the plankter in the open water. In the littoral zone the darkness cast by the elevated horizon forces the animal to change its orientation and move away into a more brightly lit area (the open water) in search of symmetrical optical

orientation. Littoral microcrustacea (termed facultative plankters) do not react strongly to changes in light intensity although changes in oxygen tension can cause vertical migrations (Meyer, 1980).

It has also been suggested that macrophytes secrete repellant substances affecting both rotifers (Hasler and Jones, 1949) and crustacea (Pennak, 1973). As Dorgelo and Koning (1980) found that a calanoid copepod avoided both real and plastic plants the first suggestion of avoidance of the shore appears to be more likely. This will be discussed further in Chapter 5. In Farnborough it is possible that the effects of fish predation in the open water outweighed any tendency of Daphnia to avoid the littoral as it was more abundant among the macrophytes than in the open water. It is however important to distinguish between species of Daphnia as habitat selection may markedly differ with species and Rocha (pers.comm) has shown that species of Daphnia differ considerably in their reactions to both unfavourable conditions and nearness of substrates. In Farnborough the mean size of the weedbed Daphnia was larger than their mean size in the open water, this being considerably smaller than sizes reported from other water bodies. There are two possible reasons for this. The most likely one is that size selective predation by 1+ roach, observed by Cook, (1979) removed the larger Daphnia from the open water while the 0+ roach in the margins were too small to eat them. It is also possible that the daphnid in the open water was D. galeata while D. longispina occurred in the weeds, the two species co-existing through habitat partitioning (Lane, 1975). It was noted that more crested individuals (D. galeata) were present in the open water while the majority of the weedbed dwellers had rounded heads (D. galeata or D. longispina). This emphasises the importance of identifying all organisms to species when assessing the effects of fish predation upon zooplankton communities.

Conversely, D. ambigua was rare in the weeds and being smaller, was available to the O+ fish. This "reverse to normal" situation with Daphnia preferring weeds to the open water was not found in Yateley where no Daphnia occurred in the weedbeds suggesting that the weedbeds in Farnborough provided a refuge for Daphnia from the heavy predation pressure in the open water. It is surprising to find Daphnia among vegetation as Harnisch (1950) has shown that they are limited in their ability to clean detritus from their filtering combs.

It is possible that the open water herbivores exhibited resource partitioning in their body size separation (Fig. 3.7). In a homogeneous environment one strategy for avoiding competition is for each species to select different food particles. Burns (1968) has shown that the size of food particle filtered from the water is related to body size although this is not always true (Hall et al, 1976). Patalas (1971) has called this a separation into functional niches in the water column. In the weedbeds there was a greater range of body sizes for two reasons. With the greater diversity of habitat there was probably a greater range of algal particles for the herbivores to feed on. There was less predation upon the larger crustacea as they were at the upper end of the size range taken by the O+ fish. Many of the smaller species within this size range were more benthic in habit and so protected. The overlap in sizes of the chydorids may have been due to a different type of habitat partitioning among the structurally diverse habitat (Fryer, 1968).

The association of a species with either the open water or the littoral was fairly clear-cut as shown in Table 3.18 and this agrees with similar analyses in other lakes, (Smyly, 1957; Shiel, 1976).

However, the association of crustacean species with plant species is far more difficult to examine and there have been few attempts to define such associations in any more detail than was possible from the data here. Fryer (1968) in examining the functional morphology and observing the behaviour of chydorids, obtained detailed information on habitat selection in the laboratory and he has extended this to detailed field investigations, (Fryer and Forshaw, 1979; Fryer, 1980). These studies have mostly associated species distributions with pH, water quality and geographical area in a similar manner to the surveys of Quade (1969) and Whiteside (1970). To determine exactly where in a weedbed, or on which plant species a crustacean lives by choice would require intensive sampling of each micro-habitat in the weedbed, such as under and on leaves, on the bottom etc. Such a study, although interesting, would provide little additional information on the role of the crustacea in providing food for young fish unless done in conjunction with an examination of the feeding habits of all the fish species present, whereas sampling similar to that done here does provide information on the gross distributions and availability of microcrustacea to fish which was the main objective of this work.

The only clear cut example of a macrophyte/microcrustacea association in the present study was that of Sida crystallina with P. natans which is well known (Langhans, 1911). It may be that the close attachment which Sida has with the plant, through its cervical attachment gland, makes this more readily observable than other less intimate associations which may exist but can be difficult to detect. It is interesting that Green (1966) found that Sida persisted through the winter if the temperature was not too low when Nuphar was present whereas in Farnborough P. natans died down in the autumn and Sida was not present in winter samples, suggesting that the distribution of Sida

is partly determined by the presence of floating leaved plants.

Quade (1969) states that to some extent crustacean assemblages are determined by lake type independently of plant species. An example in the gravel pits was the absence of Sida from the small ponds at Frimley although P. natans was as abundant as in Farnborough which was only 1 mile away. Although Quade did also find that the association with plant species can be stronger than that for lake type as he found higher percentage similarity coefficients relating Cladocera to plant species than Cladocera to lake, it would seem that while the absence of a plant species may prevent the establishment of an associated microcrustacean species in a water body the presence of the plant does not necessarily mean that the crustacean will also be there.

The abundance of tycholimnetic species such as Ceriodaphnia has been inversely correlated with vegetation density (Straskraba, 1965) and Fryer and Forshaw (1979) found that C. quadrangula was more abundant in Menyanthes than in other plant species. This agrees with the observations made in the present study that Ceriodaphnia was most abundant among P. natans and at the plant/water interface in Yateley, possibly an ideal situation for young fish to feed in. As Ceriodaphnia are filter-feeders, they are restricted mainly to areas where phytoplankton occurs and Brandl, Brandlova and Postolkova (1970) found that the reduction in algal photosynthesis in plant stands relative to the open water was least in Potamogeton pectinatus (60% of that in the open) and most in Elodea (12% of the open water rate). The reduction in Elodea was due to shading and it was noted in the present study that microcrustacea were sparse under a large bed of Nymphaea alba in Yateley. This conflicts with the traditional view that macrophytes support densities of invertebrates in direct proportion to the surface area of the plant. The water volume/plant density ratio may be of more

importance in determining whether a filter feeder obtains sufficient algal food in a plant stand while also being protected from vertebrate predation.

One way of analysing associations has been to examine the relationship of organisms to structural types of plants, and it has been widely accepted that finely divided plants, such as Elodea with a large surface area support the greatest numbers of species and highest standing crops (Krecker, 1939; Rosine, 1955). This was borne out to some extent in this study but there may be other attributes of the plants which attract or repell crustacea. Smyly (1952b) found abnormally low standing crops of microcrustacea in beds of Juncus and this was also observed in Farnborough. Smyly related the low abundance to a lack of oxygen caused by decomposing plant matter. On the other hand Shiel (1976) found very high standing crops and high diversity in Juncus because of the dense periphyton on the ribbed stems. This illustrates how the species of plant may not itself directly determine associations. The amount of periphyton on the plant surface or bacteria associated with the detritus which catches in the epiphytes may be the most important determinants of macrophyte/microcrustacea associations.

One method of determining whether such associations exist is to carry out association analysis, widely used in botanical studies (Kershaw, 1973). For this to be correct many more samples, either from many sites or by replication, are required than were collected in this study. Therefore, no attempt was made to statistically correlate the presence of a species with either another crustacean or with a plant species. There are also a variety of community similarity indices (Southwood, 1978) most of which do not take into account relative abundance which has been shown to be more important in this work than presence or absence as most species occurred in all the sites.

Straskraba (1967) classified littoral microcrustacea into three groups, one consisting of truly planktonic species e.g. Ceriodaphnia, Cyclops vernalis americanus; another consisting of species more closely associated with vegetation, either swimmers or creepers, e.g. Simocephalus and Sida, and thirdly, a group of species associated with the benthic substrate e.g. Pseudochydorus, Leydigia. The object of the present work was to determine whether the macrophytes exerted any influence upon fish food organisms and so a simple classification of the species found in the two gravel pits was made and is shown in Table 3.18. Species are placed in order of greatest occurrence and abundance in the open water (on the left of the table) graduating to species with their greatest occurrence and abundance in the weedbeds, on the right hand side. Few species were restricted to the open water while many more were found almost entirely in vegetation only. The anomalous presence of Daphnia longispina in vegetation in Farnborough but not in Yateley has already been discussed. The place of D. longispina was taken in the open water in Farnborough by D. ambigua. A comparison of both lakes shows that while the groupings were similar, many species occurred in one category closer to the open water in Yateley than in Farnborough, possibly as a result of the greater spread of vegetation in Yateley. The presence of the macrophytes appears to be important in determining the species composition of the microcrustacean communities. A variety of species occurred in category C, at the plant/open water boundary where the 0+ fish might be expected to feed.

In conclusion, it has been shown in this chapter that the weedbeds in these gravel pits provided the young fish with a high standing crop of microcrustacea, a greater variety of species than occurred in the open water and higher numbers of small particles of eatable size than were present in the open water. The extent to which these were utilised

Table 3.18. Grouping of microcrustacean species into the lake areas in which they were most common.

OPEN WATER A	B	C	D	MACROPHYTES E
FARNBOROUGH				
Ilyocryptus	Bosmina D.ambigua	Cyclops A.quadrangularis P.uncinatus A.intermedia Ceriodaphnia A.affinis Diaptomus	D.longispina Chydorus P.denticulatus Acroperus Graptoleberis A.rectangula	C.albidus Simocephalus Sida P.aduncus A.guttata Eurycercus Scapholeberis Polyphemus Pseudochydorus Leydigia
YATELEY				
Asplanchna	Bosmina D.longispina	Cyclops Ceriodaphnia Diaptomus Diaphanosoma Chydorus P.denticulatus P.aduncus Acroperus P.uncinatus	Simocephalus Graptoleberis A.guttata A.rectangula	Sida Polyphemus Scapholeberis P.truncatus A.intermedia Leydigia Pseudochydorus Harpacticoids.

Key
A = occur only in open water.
B = common in open water, rare in macrophytes.
C = common in both habitats, with those on the right hand side more common in macrophytes.
D = Common in macrophytes, rare in the open water.
E = occur mainly in the macrophytes

by the O+ roach and perch will be discussed in the next chapter. The interactions of fish, zooplankton and macrophytes were also brought out in this study. The macrophytes provide a refuge for crustacea from predation pressures in the open water, and they themselves exert an effect upon the open water, so that the influence of one part of this complex system is inextricably bound up with the others.

CHAPTER 4. THE GROWTH OF 0+ ROACH AND 0+ PERCH IN FARNBOROUGH IN 1977, 1978 AND 1979 AND THE RELATIONSHIP OF THEIR DIETS TO THE MICROCRUSTACEAN FOOD SUPPLY IN 1977.

4.1. Introduction.

In 1977 samples of 0+ roach and 0+ perch were obtained from Farnborough at fortnightly intervals from 9 June to 14 December. The sampling dates are given in Tables 4.2 and 4.3. On most occasions two or more samples of roach were collected from different marginal sites. Changes in growth rate during the first year and also differences in the growth rates of the two species could result from varying abilities to exploit the available food resources. Therefore, while the study of roach and perch diets in their first year in relationship to the microcrustacean food supply formed the main objective of the work in 1977, fish growth was also investigated. The diet study was not continued in 1978 and 1979, but some samples were taken so that final sizes of the fish in the experimental enclosures (Chapter 5) could be compared with those of the same fish stock in its parent lake (Farnborough). These later samples were not taken as part of a detailed fish growth study for which more frequent sampling would have been necessary, but neverthless provided information on some differences between the two species and illustrated differences in growth between years. Estimates of population size were also made as described in Chapter 2.

The specific source (i.e type) of the food supply is only one of several factors which can cause variation between the food found in consecutive fish gut samples and other factors which can influence the diet were also examined. These were the time of day of sampling, the size of the fish, and differences in preferences of individual fish. Many fish species feed at different rates through the day, with dawn and dusk peaks. Ideally one of the first steps in a feeding study should be

an investigation to determine whether the species in question exhibits any changes in feeding rate (ingestion rate) with time if only to ensure that the fish are not sampled during a period of low feeding activity. Concurrent with this, variation in gut contents with time can also be a major factor affecting diet composition. Therefore, fish were collected at regular intervals over 24 hours on two occasions, in July and in September. It was not possible to collect sufficient perch to examine their feeding periodicity but this aspect has been well documented by Thorpe (1977a) and Guma'a (1978b) who showed perch to be active during the day and inactive at night.

The problems encountered in analysing fish diet data have been widely discussed and ammended (Hynes, 1950; Windell, 1971; Hyslop, 1980) but methods commonly used have not changed in recent years, (see Ricker, 1937). The percentage composition of the diets was compared with the percentage composition of the microcrustacean samples from both the open water and the weedbeds. Variation in the numbers of organisms present in the guts of individuals can be great and it was found that expressing the results as numerical percentage composition overcame this to some extent. The main criticism of using percentage composition is that the importance of numerically abundant small organisms can be exaggerated to the detriment of larger organisms and for this reason the use of body weight is often recommended. However, in a study of food preferences, one is concerned with the proportions of food eaten relative to those available. In this instance the bulk of the food was of similarly sized microcrustacea (in comparison with other aquatic invertebrates) and therefore the data were expressed as percentage composition and then the relative contribution of each item to total food dry weight was reconstructed (Windell, 1971).

While a preference for a certain food item may be reasonably

apparent if it forms the major part of the diet, it is difficult to distinguish a genuine preference (or food selection) from dominance in the diet of species which are very abundant in the habitat. Likewise, organisms which are abundant in the water but are not eaten may not be available to the fish, because of their shape, size or behaviour. Various indices of food preference have been proposed. That of Ivlev (1961) is most commonly used. The proportion of each species in the food is compared to its relative abundance in the water body, for which it is necessary to monitor all species occurring in both sets of data. This is rarely possible in diet studies and was the main problem both in the use of this index here, and in comparing diet with food supplies in general, as rotifers and larger invertebrates, present in the guts although of low occurrence, were not sampled in the lakes. Ivlev's index does not take into account large differences in abundance as it only utilises relative proportions and requires all items to be identified to the same taxonomic level. However, it is easy to calculate and interpret and is widely used, and so, with some reservations, was used in this study,

Possible size-biased selection of food by the young fish was not intensively studied in this work but some food items were measured to determine whether there was an upper limit to the particle size which could be eaten at any stage in the life history. It was also possible that size segregation of prey occurred between roach and perch.

Much of the analysis of the roach diet data was carried out on the combined data from all samples collected on each sampling date. To show whether diet was fairly uniform throughout the population on any day and whether the food consumed showed any relationship to the micro-habitat from which the fish were taken the individual diet samples and relevant microcrustacean samples were compared.

Relatively few perch were caught in 1977 and therefore most of the analysis of diet was for roach only. Sufficient perch were however examined to enable a comparison of the species compositions of the diets to be made. The diet data for the perch were obtained from the counts of stomach and intestine contents added together. To complement the general assessment of diet overlap between the two fish species, Levins (1968) overlap coefficients were calculated. These measure the overlap of one species on another in terms of resource utilisation.

4.2 Density estimates of O+ roach and O+ perch.

O+ roach were very abundant throughout 1977 and remained catchable with the hand net and the minnow seine in the autumn and winter. In contrast O+ perch were scarce and few were caught for the diet study. The population estimates confirmed this. These estimates will be discussed in detail because they provided evidence that the young fish were most abundant in the lake margins. These estimates must be viewed with caution as the nature of the sampling method compared to the number of fish involved led to very large confidence limits. However, the estimates were of the same order of magnitude as those of Cook (1979) who used this method for detailed population studies over two years. Neither Bagenal (1974), Hewitt (1979) or Cook (1979) give the confidence limits for population estimates made with the buoyant nets.

The first population estimate was made on 7 July. Seventy buoyant nets were set at random over the whole lake during the day. 7% caught O+ roach and 3% caught O+ perch, giving estimates of total population size of 40,000 and 5,000 respectively (Table 4.1(a)). Most of the catches were made in nets set close to the lake margin. A 24 hour study of diets was also made on this day and O+ roach (but not perch) were caught with ease every two hours in the marginal weedbeds with the hand

net. The second population estimate was carried out in September. Fifty nine nets were set and again 7% caught roach giving an estimate of 1,600 while only one perch was caught. None of these fish were caught in the open water. Another 24 hour study of diets on this date showed that O+ roach were again caught easily in the weedbeds throughout the day. Although the failure of the buoyant nets to catch fish in the open water may have been due to the greater depth they had to travel through, much of Farnborough was only 1.5 m deep and Hewitt (1979) found no evidence of net avoidance by O+ roach (<3.0 cm) in water up to 3 m deep. However, it is likely that net avoidance by the larger juvenile roach did occur in September, giving an underestimate of population size.

Table 4.1 (a) Population estimates of O+ roach and O+ perch in Farnborough in 1977.

Date	Spec	n	Density n/m^2	Biomass g/m^2
7.7.77	Roach	40,478	3.7	0.16
7.7.77	Perch	5,360	0.5	0.18
2.9.77	Roach	1,630	0.15	0.15
2.9.77	Perch	1 caught		

n = total population size

(b) Estimate of marginal densities in Farnborough in 1977.

Date	Spec	Density n/m^2	Biomass g/m^2
12.9.77	Roach	3.4	3.0
	Perch	1.2	4.0

These results indicated that the O+ roach were most abundant in the marginal weedbeds in their first year. This was further borne out by the results of the estimation of marginal densities using the buoyant

nets in September 1977, shown in Table 4.1(b). Twenty seven nets were set of which 30% caught 0+ roach and 15% 0+ perch. As the nets were not designed to operate in water with dense vegetation, they may have come up fairly slowly, possibly underestimating marginal fish densities.

Although no estimates of population size were made in the following two years one can compare the relative abundance of the two species from both the numbers obtained in the fish samples, shown in Tables 4.2 and 4.3, and the effort required to catch the fish. In 1978 0+ perch were fairly abundant and easily caught while roach were scarce. In 1979 0+ roach were again common but not as easily caught as in 1977. However, although 0+ perch were caught in July 1979, nine man-days of fishing effort with a variety of seine nets in September produced one perch of 6 cm, and it was concluded that the 1979 year class of perch had suffered severe mortality during the summer.

In 1976 Cook (1979) obtained estimates of the 0+ roach and 0+ perch in Farnborough of 7,000 and 42,000 respectively in mid-summer. It appears that the first year roach and perch survived well in alternate years, with the perch being dominant in 1976 and 1978. Therefore it is interesting to compare their growth to see whether differences in year-class strength were reflected in growth rates.

4.3 Growth of 0+ roach and 0+ perch in Farnborough, 1977-1979.

Fig. 4.1 and Fig. 4.2 show the growth curves for length and weight of the roach and perch for each of the three years. Table 4.2 and Table 4.3 give the sampling dates, mean sizes and sample sizes for roach and perch respectively. (All calculations were carried out on log10 transformed measurements). The length of all fish in a sample was recorded but in some of the larger roach samples in 1977, and perch samples in 1978, a sub-sample was removed for weighing and the sample

mean weight (shown in Table 4.2) predicted from the length:weight linear regression equation obtained from the sub-sample. All the regressions were highly significant ($P<0.001$).

a) 0+ Roach.

The seasonal growth pattern for the roach was only fully observed in 1977 when growth was most rapid in July, slowed in August and increased in September after which there was no significant increase in weight or length. The larger mean size in November may have been due to gear selection as a larger meshed seine net was in use for a total population estimate of the adult fish. Growth of the 0+ roach in 1977 followed a logistic growth curve.

Gee (1978) and Cook (1979) also found that in Farnborough, the roach completed their growth by the end of September and therefore the September samples taken in 1978 and 1979 were considered a reasonable estimate of final size of 0+ roach for those years. This enabled growth to be compared in the three years. Broughton and Jones (1978) have shown that little growth of roach occurs at temperatures below 14°C, and the water temperature had dropped below this by the end of September in all three years (see Fig. 3.1).

Growth in 1977 and 1978 was similar with the roach reaching an average size of 4.2 cm/1.0 g and 4.5 cm/1.2 g respectively by the end of September. However, the 1978 roach were significantly larger throughout the sampling period as shown by the 95% confidence limits. All the 1977 roach were measured after preservation in formalin, the effects of which have been discussed in Chapter 2. The final sample in 1978 was measured fresh but the differences between the two were greater than any due to the distortions of length and weight caused by preservation. In 1979 growth was much better and the roach measured 5.9 cm/2.5 g by mid-September. These fish were also found in the lake one week earlier

Table 4.2 Growth data for 0+ roach in Farnborough, 1977, 1978 and 1979.

DATE	F.L.	W.WT	n	D.WT	n	TYPE
9.6.77	0.74		12	2.75	6	P
27.6.77	1.22		17			P
7.7.77	1.90	0.047	300	8.46	55	P
25.7.77	2.69	0.261	63	38.98	7	P
9.8.77	3.17	0.436	45	74.50	9	P
22.8.77	3.40	0.457	44	96.80	19	P
2.9.77	4.08	0.982	326	157.20	29	P
12.9.77	3.94	0.841	72	205.00		P
26.9.77	4.19	1.022	48	204.90	11	P
10.10.77	4.32	1.108	4			P
25.10.77	4.27	0.963	122	226.30	26	P
9.11.77	4.56	1.220	16			P
14.12.77	4.25	0.979	56			P
14.6.78	1.06	0.006	53			P
12.7.78	2.12	0.117	17			P
18.8.78	3.72	0.675	6			P
14.9.78	4.51	1.192	52			F
1.6.79	0.63		19			P
10.7.79	2.84	0.29	90			P
18.9.79	5.87	2.55	64			F

KEY

n = sample size

F.L. = Fork length in cm

W.WT. = Wet weight in g

D.WT. = Dry weight in mg

P = preserved

F = fresh

Annual length /weight regressions for 0+ roach in Farnborough in 1977, 1978 and 1979. All regressions are in the form log10W = a+b log10L
n = sample size

	n	a	b	r	C.L.	P
1977	517	-2.13	3.41	0.99	0.01	0.001
1978	95	-2.30	3.67	0.99	0.006	0.001
1979	154	-1.89	2.98	0.99	0.004	0.001

C.L. = 95% confidence limits of b

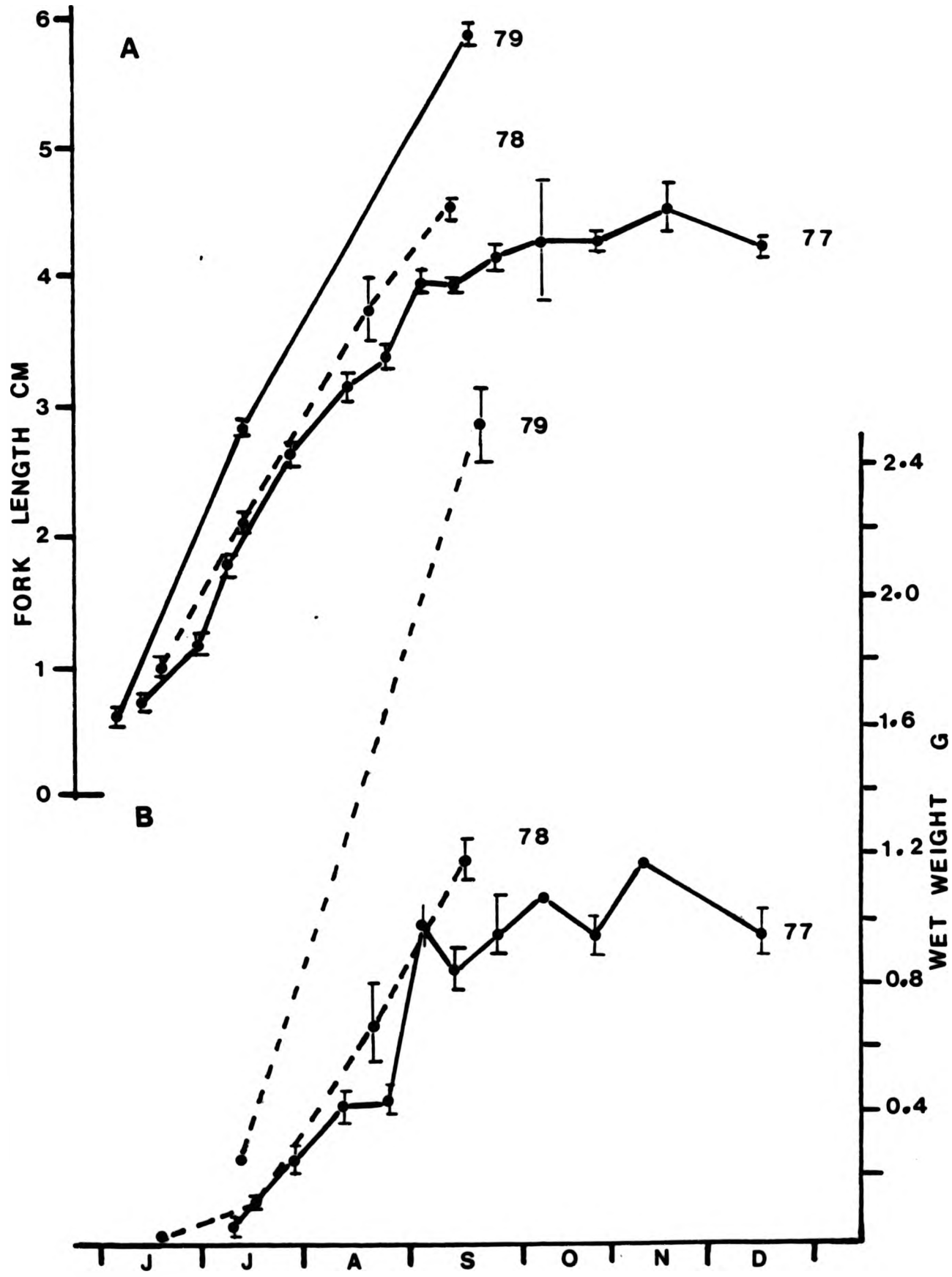


FIGURE 4.1 The growth in length (A) and weight (B) of O+ roach in Farnborough in 1977, 1978 and 1979. Each point is the geometric mean with 95% confidence limits.

Table 4.3 Growth data for 0+ perch in Farnborough in 1977, 1978 and 1979.

DATE	F.L.	W.WT	n	TYPE
7.7.77	3.00	0.351	39	P
25.7.77	4.07		4	P
2.9.77	5.68	2.782	16	P
12.9.77	5.91	3.3	6	P
31.10.77	6.35	3.700	5	P
24.5.78	0.89		53	P
14.6.78	2.24	0.136	59	P
28.6.78	3.12	0.405	102	P
18.7.78	4.04	0.941	126	P
25.7.78	4.43	0.996	126	F
22.8.78	5.55		115	F
22.8.78	5.45	2.440	28	P
10.10.78	6.59	3.273	46	F
15.7.79	3.98	0.693	39	P

KEY

F.L. = Fork length in cm

W.WT = Wet weight in g

n = sample size

P = Preserved

F = Fresh

Annual length/weight regressions for 0+ perch in Farnborough in 1977, 1978 and 1979. All regressions are in the form log10W = a+blog10L

	n	a	b	r	C.L.	P
1977	66	-1.99	3.23	0.99	0.07	0.001
1978	224	-1.91	3.01	0.99	0.04	0.001

C.L. = 95% confidence limits of b

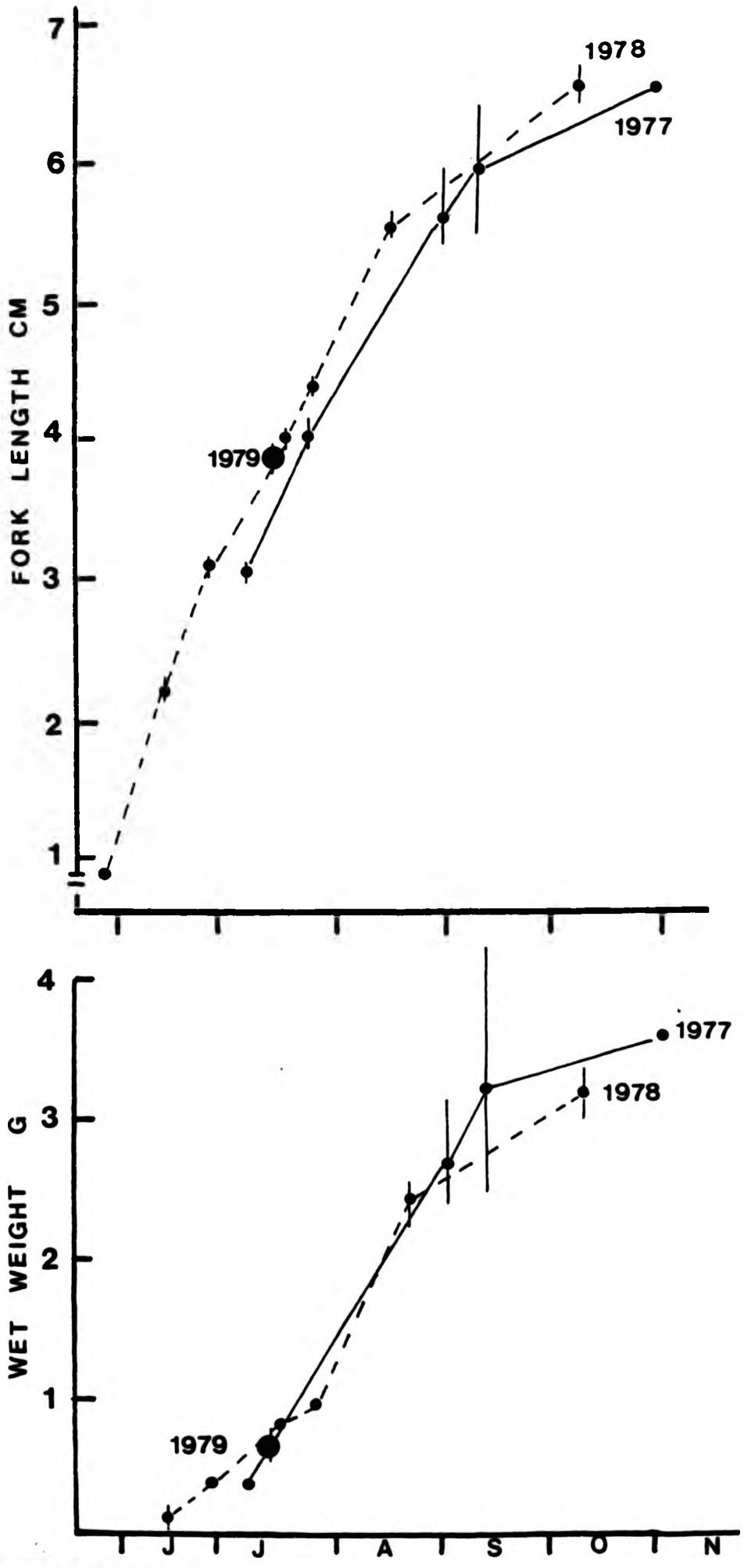


FIGURE 4.2 The growth in length and weight of O+ perch in Farnborough in 1977, 1978 and 1979. Each point is the geometric mean with 95% confidence limits.

than in previous years. Scales from the September sample were examined to confirm that they were 0+ fish.

The percentage length/frequency distributions shown in Fig. 4.3 and Fig. 4.4 confirm the initial rapid growth in June and the cessation of length increase by the end of September.

An annual length:weight relationship was established for each year from all the measurements obtained (Table 4.2). The appendix shows the data plotted on a double log scale with the fitted calculated annual linear regression lines. All these regressions were highly significant ($P<0.001$). The three annual regressions had significantly different slopes ($P<0.05$) and the greatest value of b was found in 1978. There was no evidence of separate growth stanzas with different length:weight relationships within the first year as reported by Lightfoot (1976) although changes in the regression slope with time were noted and have been reported by other workers (Broughton and Jones, 1978). It is possible that the smallest roach could have passed through a stanza in early June although the dry weight measurements for the very small fry do not suggest this. The gap in the 1977 annual length/weight relationship was caused by the lack of a mid-July sample when growth was very rapid. There was a suggestion of a different slope for the smallest fish but this may have been due to errors in weighing very small preserved fish.

The condition factor of a fish sample is an additional useful index of the length:weight relationship, and provides a simple comparison of the condition of individuals of one species of similar age or size. The condition factor (K) was calculated from the following equation:

$$K = w/l^3 \times 100$$ (Bagenal and Tesch, 1978).

The multiplication by 100 brings the value to near unity and a K factor

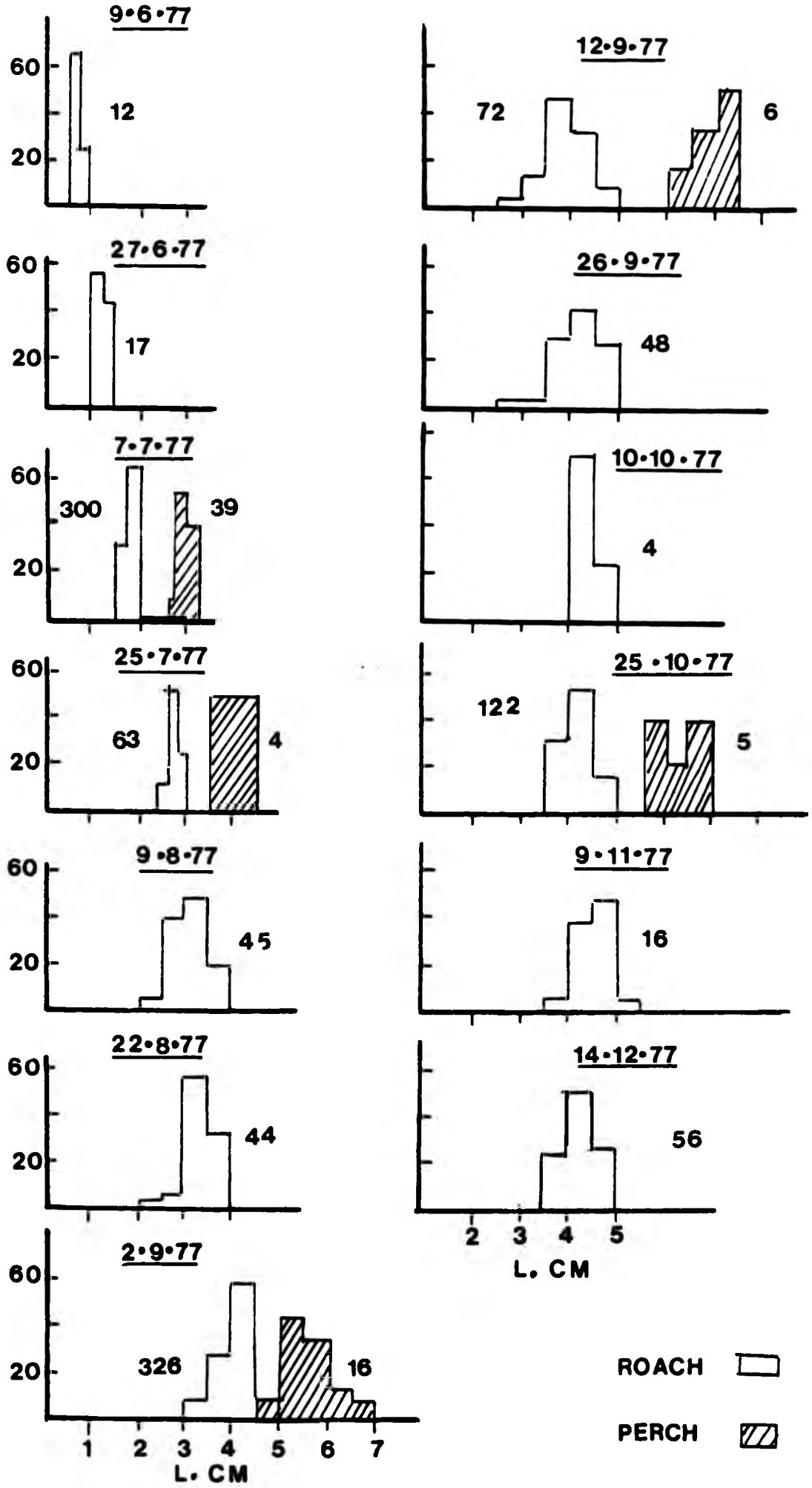


FIGURE 4.3 Percentage length frequency distributions of O+roach and O+ perch in Farnborough in 1977. Sample sizes are given on each histogram.

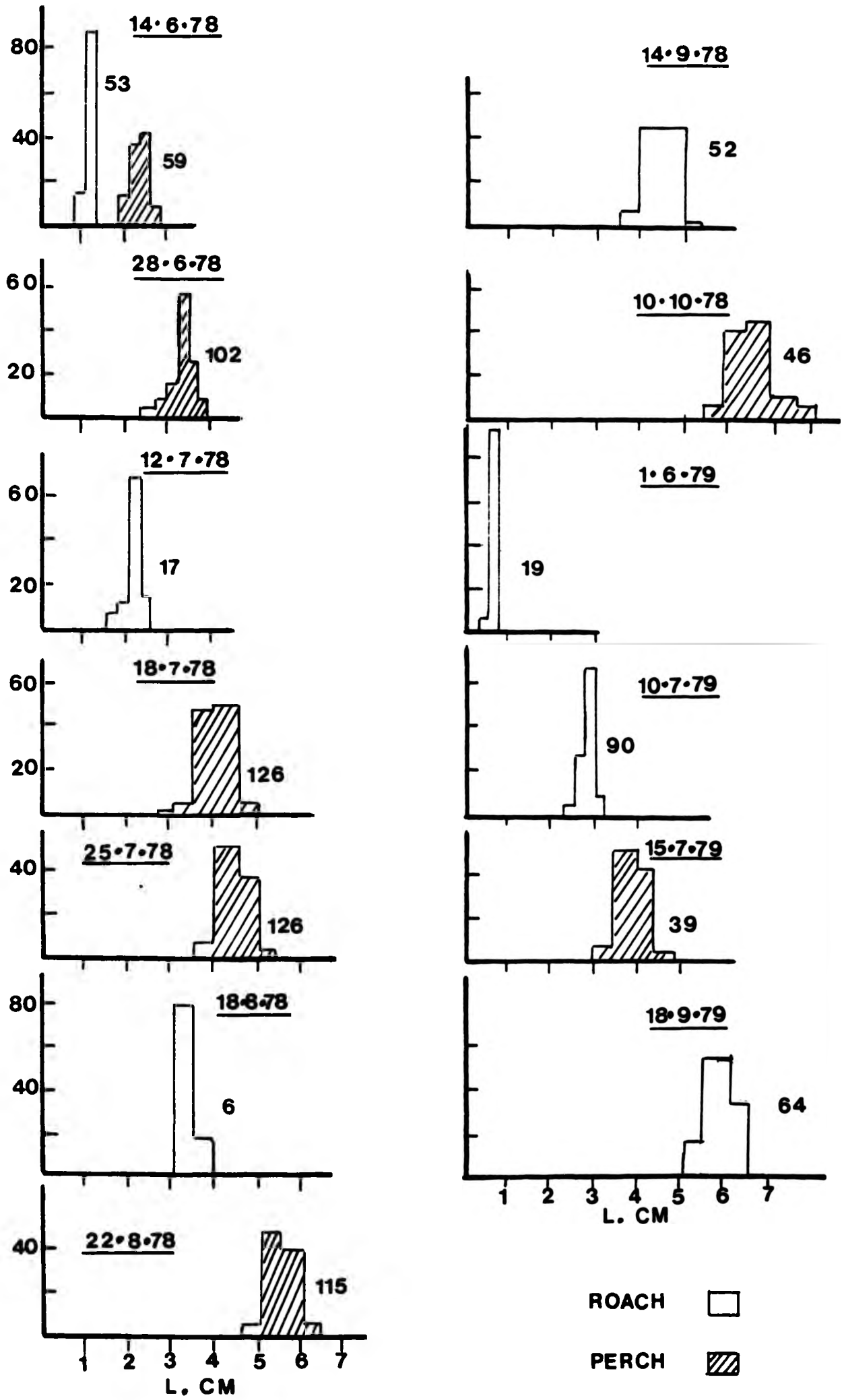


FIGURE 4.4 Percentage length frequency distributions of O+roach and O+ perch in Farnborough in 1978 and 1979. Sample sizes are given on each histogram.

of over 1 indicates a roach in good condition (Broughton et al, 1977). K was calculated for the September samples from each year (Table 4.4). They were similar in the three years with the 1978 roach possessing the best condition. Because preservation in formalin reduced length and increased weight the condition factor of the 1977 roach, of 1.4, was an overestimate.

The specific growth rate or instantaneous growth coefficient (G), (Ricker, 1958; Bagenal and Tesch, 1973) is a measure of the rate of change in size per unit time (derived from the logistic growth curve) and is a useful method of comparing growth in animals over a short time period when growth is rapid or changing (Weatherly, 1972). When calculated over longer time intervals only an average rate is obtained and ideally data should be collected over short time intervals. This was not always possible during this study but in 1977 a weekly rate was calculated for roach for comparison with temperature and food supply and an estimate of daily rate over the year was obtained for other years, using the first and last samples and time as the numbers of days elapsed. These can only be compared with caution as daily measurements are necessary to calculate an accurate daily rate and the samples in different years did not encompass exactly the same parts of the growing season. In particular the lack of the early fast growing fish may affect these annual estimates of specific growth rates.

The specific growth rate for weight was calculated thus:

$$Gw = \frac{(\log_e \bar{W}_2 - \log_e \bar{W}_1)}{\Delta t}$$ (Bagenal and Tesch, 1978)

Table 4.5 shows the calculated values and Fig. 4.5(a) shows the weekly values and water temperature plotted against time. In 1977 the specific growth rate of the 0+ roach declined with time/age in the normal manner apart from a period of accelerated growth in September before the final decline. The rapid growth between August and September was not due to

Table 4.4 Condition factors (K) of 0+ roach and 0+ perch, 1977, 1978 and 1979.

Date	Spec	K	Type
25.9.77	Roach	1.39	P
14.9.78	Roach	1.30	F
18.9.79	Roach	1.25	F
31.10.77	Perch	1.33	P
10.10.78	Perch	1.14	F

Type: P = preserved F = fresh

Table 4.5 Specific growth rates of 0+ roach and 0+ perch, 1977, 1978 and 1979.

(a) Weekly Gw

ROACH		PERCH		ROACH		PERCH	
DATE	Gw	DATE	Gw	DATE	Gw	DATE	Gw
16.7.77	0.67	16.7.77	0.38	28.6.78	0.78	21.6.78	0.55
1.8.77	0.24					5.7.78	0.30
15.8.77	0.03	15.8.77	0.90	30.7.78	0.33	21.7.78	0.06
27.8.77	0.49					8.8.78	0.22
7.9.77	-0.11	7.9.77	0.12	1.9.78	0.15	16.9.78	0.01
19.9.77	0.07						
3.10.77	0.06	6.10.77	0.06				
17.10.77	-0.06						

(b) Estimated annual mean specific growth expressed on a daily basis.

	ROACH	T	PERCH	T
1977	0.02	159	0.02	116
1978	0.06	92	0.03	118
1979	0.03	70		

T = time in days

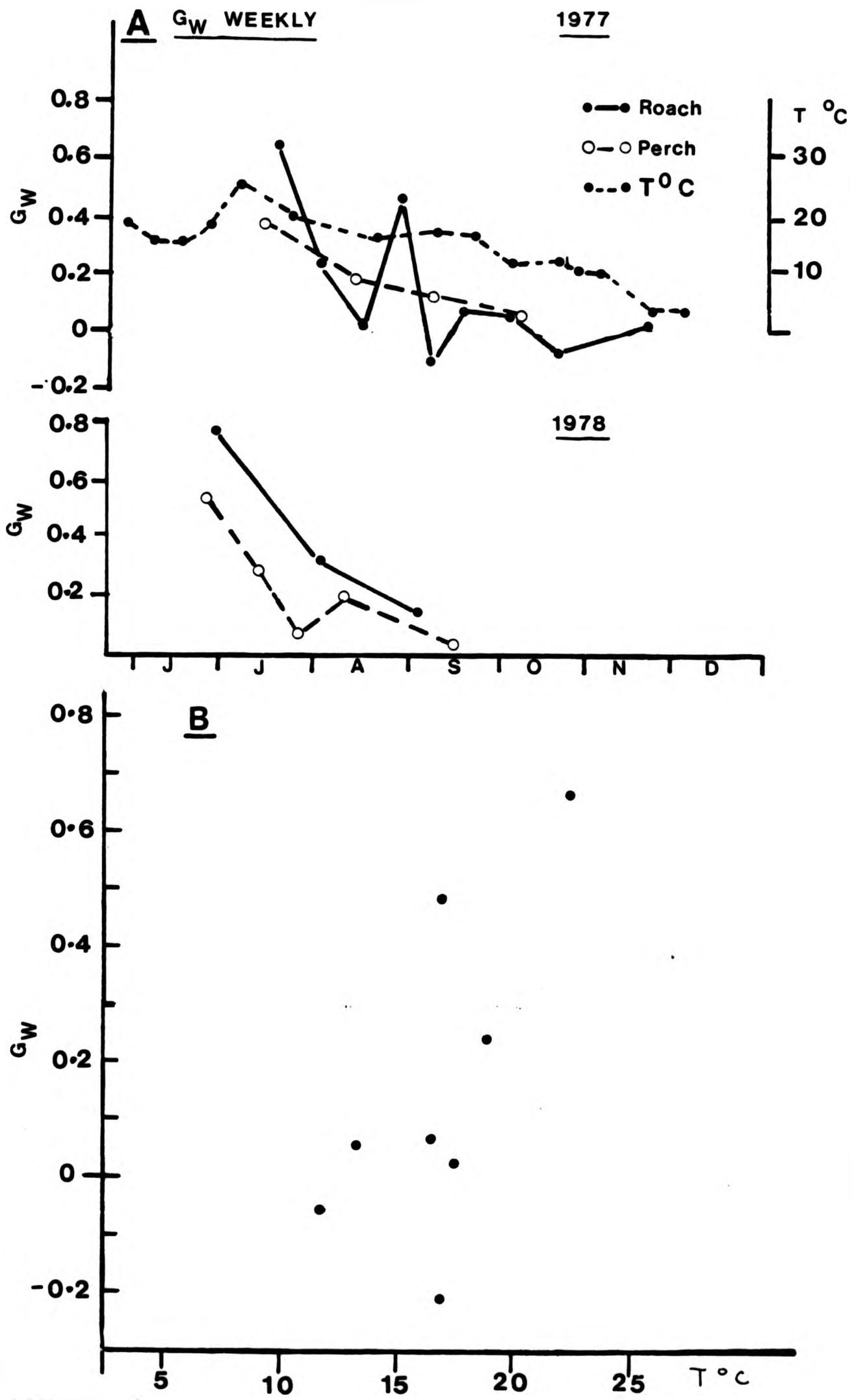


FIGURE 4.5 Specific growth rates of O+ roach and O+ perch in Farnborough in 1977 and 1978. Fig. A shows the weekly growth rates and water temperature plotted against time in 1977 and 1878. Fig. B shows the weekly growth rates of the roach in 1977 plotted against water temperature.

any recorded rise in temperature although the temperature did increase during this period after an unseasonal drop at the beginning of August, when the growth rate also slowed. Fig. 4.5(b) shows the weekly Gw values plotted against water temperature and a relationship is apparent between temperature and growth rate with the exception of two points. These may have been due to other factors overriding the fundamental control of metabolic rate by temperature, such as changes in food supply.

A comparison of the Gw calculated from the first and last samples divided by the number of days between them shows that the 1978 roach grew fastest while growth in 1977 and 1979 was similar. The greater final mean size of the 1979 roach was due to the longer growing period as they hatched earlier in the year, rather than to a higher specific growth rate.

b) O+ Perch.

Growth data obtained for O+ perch during the three years were treated in the same manner as the roach data, although since fewer perch were caught in 1977 care must be taken in comparing the growth of the two species in the three years. The effects of preservation on the perch (weight gain of 6%, see Chapter 2) also made interpretation of the results more difficult.

Little data were obtained in 1977 but in 1978 the seasonal pattern of growth was observed into September. Perch spawn earlier in the year than roach and O+ perch were first caught in May. As in the roach, most of the perch growth took place in early summer and the increase in size after August was less than in previous months. No perch were caught after October so that the point at which O+ growth ceased was not precisely known, although it is unlikely that they grew after this time

as Le Cren (1958) has shown that the majority of growth in a year occurs when the temperature is above 14°C. Growth was similar in both years and the perch reached an average size of 6.4 cm/3.7 g in 1977 and 6.6 cm/3.3 g in 1978.

In 1979 the single sample of perch obtained was of the same mean length as the samples taken on a similar date in 1978, although the weight for length of the 1979 perch was less than that of the 1978 perch. Allowing for changes caused by preservation the two year classes (1977, 1978) possessed very similar growth rates.

Table 4.3 shows the annual length:weight regressions for 1977 and 1978. The appendix shows the data plotted on a double log scale. There was no evidence of a change in the relationship with age as reported by Guma'a (1978a) for Windermere O+ perch. The condition factors of the final samples, allowing for preservation changes in the 1977 perch, were similar (Table 4.4).

Although the perch hatched earlier in the year and attained a larger size by the end of their first growing season, they had lower specific growth rates than the roach. The annual specific growth rate in 1977 was the same as for the roach, but the roach grew faster in 1978.

The percentage length frequency distributions of both species in the three years are given in Fig. 4.3 and Fig. 4.4. On most occasions there was no overlap in the sizes of the two species. Mouth gape is related to body size (Guma'a, 1978b; Cook, 1979) and the perch also have larger mouths than roach so that if they both feed size selectively, it is unlikely that direct competion for food occurs at any one time. It does mean that a wider range of food is available to the perch and the effects of their predation upon a microcrustacean population could reduce the amount of food available for the roach.

4.4 Species composition of the diets of 0+ roach and 0+ perch.

Table 4.6 gives the complete list of food items found in the guts of young roach and perch in Farnborough in 1977. 400 roach and 37 perch were examined. The mean percentage composition is given and also the percentage occurrence of each food item for all fish taken from 7 July onwards. The mean percentage composition was used rather than the mean number transformed to percentage as some important species such as Sida were only seasonally available and their importance over the year would be underestimated. Very few empty guts were found. Small items such as amoebae and algae were not counted as their contribution to the weight of the food was negligible and they may have originated from the intestines of the Cladocera. Thirty three taxonomic groups were recorded and most occurred in both fish species: comparisons should be made with care because so few perch were examined. The Cladocera formed the bulk of the diet in both fish, 78% in roach, 68% in perch, followed by cyclopoid copepods, insects and rotifers. The insects were not identified to species as they were uncommon in the guts and they were not being sampled in the lake. It is possible that soft bodied animals such as worms were being eaten but not identified as occasional bundles of chaetae were found.

The 0+ roach fed mainly upon Bosmina and Ceriodaphnia which between them formed 56% of the diet. The next most common food items were Sida, Daphnia spp. and cyclopoid copepods, mainly Cyclops vernalis americanus. The remaining food items were eaten in small quantities. The percentage occurrence shows the degree to which each species was consumed by all members of the population and further illustrates the importance of Bosmina and Ceriodaphnia in the roach diet. As further analysis of the diet data was confined to the main prey species, the rarer items will be discussed here. The chydorids formed only a small

Table 4.6. The species composition of the food of 0+ roach and 0+ perch in Farnborough in 1977, given as the mean % composition with the % occurrence of each food item in the diet of each fish species.

	ROACH		PERCH	
	$\bar{x}$ %	% occ	$\bar{x}$ %	% occ
ROTIFERA				
Keratella quadrata	3	35		
K. cochlearis	3	28		
Brachionus sp.	1	8		
Polyarthra sp.	x	1		
COPEPODA				
Cyclops spp.	6	46	31	86
Diaptomus gracilis	x	1	x	14
Nauplii l.	3	9		
CLADOCERA				
Bosmina longirostris	29	65	1	38
Ceriodaphnia pulchella	27	71	30	100
Daphnia ambigua	3	35	10	51
D. longispina	3	26	5	54
Simocephalus vetulus	x	3	1	46
Sida crystallina	11	46	15	95
Eurycercus lamellatus	1	18	1	49
Acroperus harpae	x	12	1	30
Alona aff/quad *	2	34	1	70
A. gutt/rect **	x	6	x	3
Chydorus sphaericus	1	36	x	24
Pseudochydorus globosus	x	12	x	14
Pleuroxus aduncus	x	14	x	14
P. denticulatus	x	16	x	30
P. uncinatus	x	1		
Leydigia leydigii	x	1		
AMPHIPODA				
Crangonyx pseudogracilis			x	5
OSTRACODA	x	6	x	22
NEMATODA/OLIGOCHAETA	x	1	x	30
HYDRACARINA	1	13	x	5
INSECTA				
Hemiptera	x	3	x	30
Chironomidae l.	2	41	2	76
Chironomidae p.	x	3	x	3
Trichoptera l.	x	2		
Ephemeroptera n.	x	1		
Coleoptera l.			x	11
ECTOPROCTA statoblasts	1	5		

Diatoms, dinoflagellates, testate amoebae, filamentous and unicelluar green algae were found occasionally.
x = present but contributing <1.0% to the food.

l=larvae * Alona affinis and A. quadrangularis counted together
p=pupae ** Alona guttata and A. rectangula " "
n=nymph

but constant part of the diet and of these the most common were the large Alona affinis and/or quadrangularis and Chydorus sphaericus. Chironomid larvae which occurred on the undersurface of Potamogeton natans leaves were occasionally present in the guts, as were ostracods which were difficult to count as they were broken into small fragments and may have been underestimated. No large insects apart from chironomid larvae, were found in the roach guts. Little plant material or detritus were found. For further diet analyses the principal food items were placed into the following categories; Ceriodaphnia, Bosmina, Sida, Chydoridae, Daphnia, Rotifera and other invertebrates (chironomid larvae, mites (adult and larvae), worms), labelled macro in the figures.

The diet of the young perch differed from that of the roach, with cyclopoid copepods (C. vernalis americanus plus others) making up 31% of their diet, followed by Ceriodaphnia, Sida and Daphnia spp. Again the chydorids were of lesser importance but occurred in many of the perch. The remainder of the perch diet consisted chiefly of insects, mainly chironomid larvae. Crangonyx pseudogracilis was also found in the perch guts. No rotifers or nauplii were observed, possibly because no very small perch were examined and again no plant material or algae were found. The range of insects eaten by both fish species, particularly the perch, was lower than expected, both from the literature and from personal observation of the abundance and diversity of aquatic insects in the lake. No piscivorous perch were found; the largest perch examined was 7 cm which is below the size at which they usually eat fish (Thorpe, 1977a).

4.5 Variability in diet between individual fish.

It is well known that variability in both the species composition of diet and the quantity of food eaten exists (Maitland, 1965;

Egglishaw, 1967; Mann and Orr, 1959). This leads to the problem of deciding upon a sample size large enough to encompass the variability without requiring excessive time for examination. This invariably results in a compromise where the sample is not as large as one would like and it is worth remembering this when discussing variation within and between samples. The variation found in this study was better documented for the roach than for the less abundant perch.

The greatest cause of variation in the diet data was in the total number of food organisms present in the guts of individual fish. Table 4.7 shows the arithmetic mean number of the main food species and total food particles (with 95% confidence limits expressed as a percentage of the mean) for some of the roach gut samples and all the perch gut samples. Individual fish exhibited great variation in the amount of food eaten, e.g. on 2 September, a difference of two orders of magnitude existed between the smallest amount (58) and the largest amount (1098) consumed by roach in a sample of ten fish.

The relationship of fish size to food quantity was therefore investigated to determine whether by choosing fish close to the mean length of a sample this variation could be reduced. Fig. 4.6 shows the plot of numbers of food items against body length for most of the roach examined. The maximum number of food particles increased with fish size in a curvilinear manner related to increasing fish weight and stomach capacity but the average amount eaten was variable and not related to size. While the maximum possible intake increased the amount eaten did not refect this. Within a sample no linear relationships were found correlating total food numbers with either roach length or weight (Table 4.8). The possibility that differences in the biomass of prey items might reduce the variation in food numbers was also investigated and again no significant correlation was found between the dry weight of

Table 4.7 The mean number (x) of major food items and their mean percentage composition (%) in some of the diet samples. The 95% confidence limits (C.L.) are expressed as a percentage of the mean.

ROACH		CERIO		CYCLOPS		BOSMINA		SIDA		ROTIFERS		DAPHNIA		TOTAL	N
		nos	%	nos	%	nos	%	nos	%	nos	%	nos	%		
25.7	$\bar{x}$	13	26	19	23	0.6	1.2	2.3	8	40	35	1.5	4	78	10
	C.L.	80	80	105	76	162	174	103	139	104	58	65	87	61	
22.8	$\bar{x}$	32	22	12	5	109	44	2	3	39	11	6	3	206	10
	C.L.	74	79	150	140	66	55	139	162	137	133	162	139	49	
2.9	$\bar{x}$	602	77	12	3	41	5	0.6	1	5	1	93	1	755	10
	C.L.	34	12	73	186	39	42	220	209	83	139	43	32	31	
12.9	$\bar{x}$	100	58	6	6	20	12	8	8	1.4	0.8	18	11	157	10
	C.L.	53	18	155	143	56	55	58	108	142	116	77	54	41	

PERCH		CERIO		CYCLOPS		SIDA		D.LONG		D.AMB		TOTAL	N	
7.7	$\bar{x}$	105	49	3	1.4	15	12	32	20	16	14	174	10	
	C.L.	74	37	96	74	51	72	56	40	86	86	44		
25.7	$\bar{x}$	16	20	1.3	3.9	46	53	2	1.6			75	4	
	C.L.	252	133	155	261	167	89	184	187			120		
2.9	$\bar{x}$	382	32	787	55	36	6					1246.	12	
	C.L.	66	56	69	35	72	69							
12.9	$\bar{x}$	94	14	442	49	222	31					804	6	
	C.L.	75	69	95	57	78	69							
31.10	$\bar{x}$	102	13	374	32	3	0.4	43	5	332	44	640	5	
	C.L.	249	243	185	154	215	206	254	270	135	114			

Abbreviations for specific names used in this chapter are given in Appendix 1.

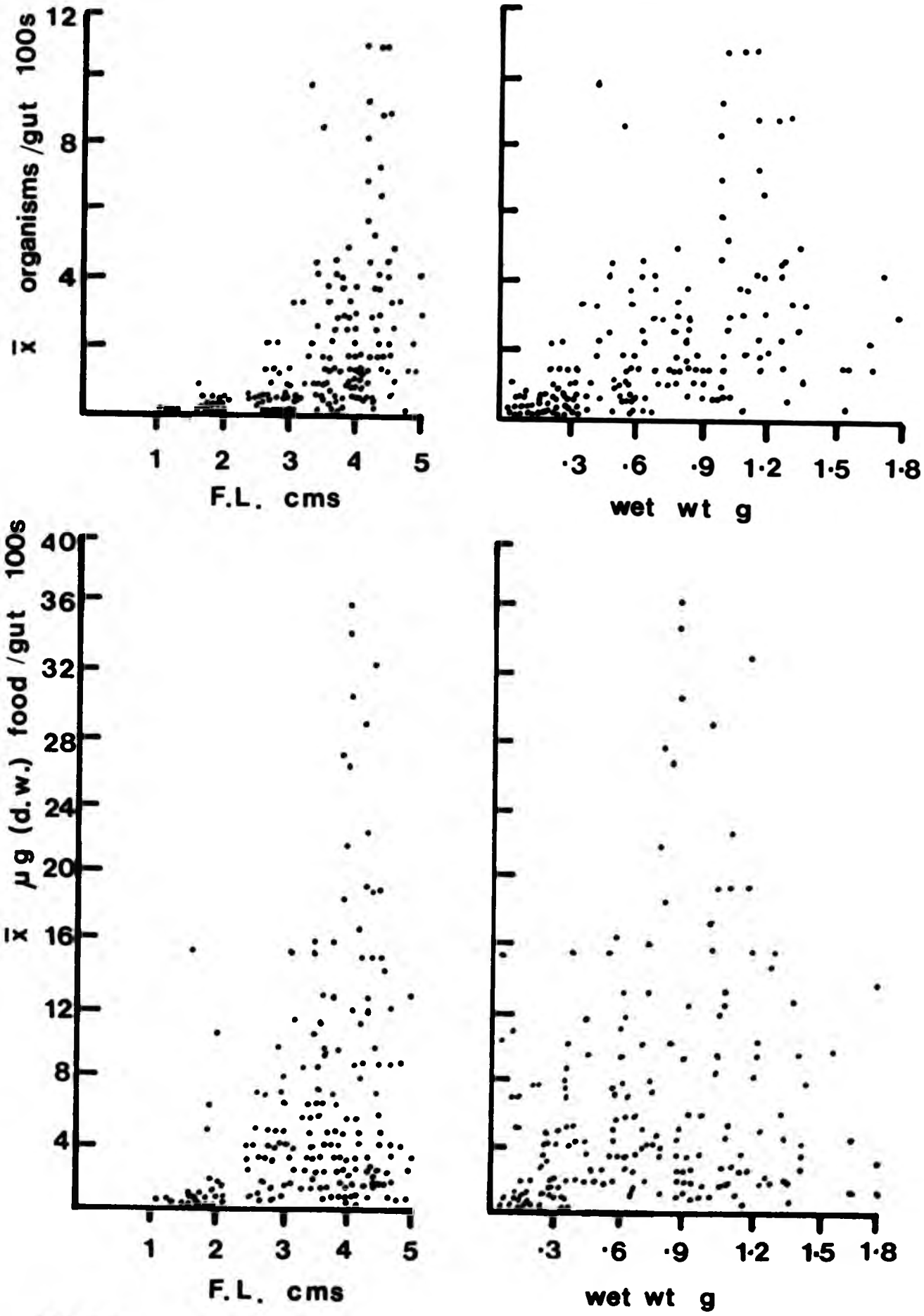


FIGURE 4.6. The relationship between food volume (numbers and dry weight biomass) and roach length and weight in Farnborough in 1977.
A. Total numbers/gut with roach fork length.
B. Total numbers/gut with roach wet weight.
C. Total dry weight of food/gut with roach fork length.
C. Total dry weight of food/gut with roach weight.

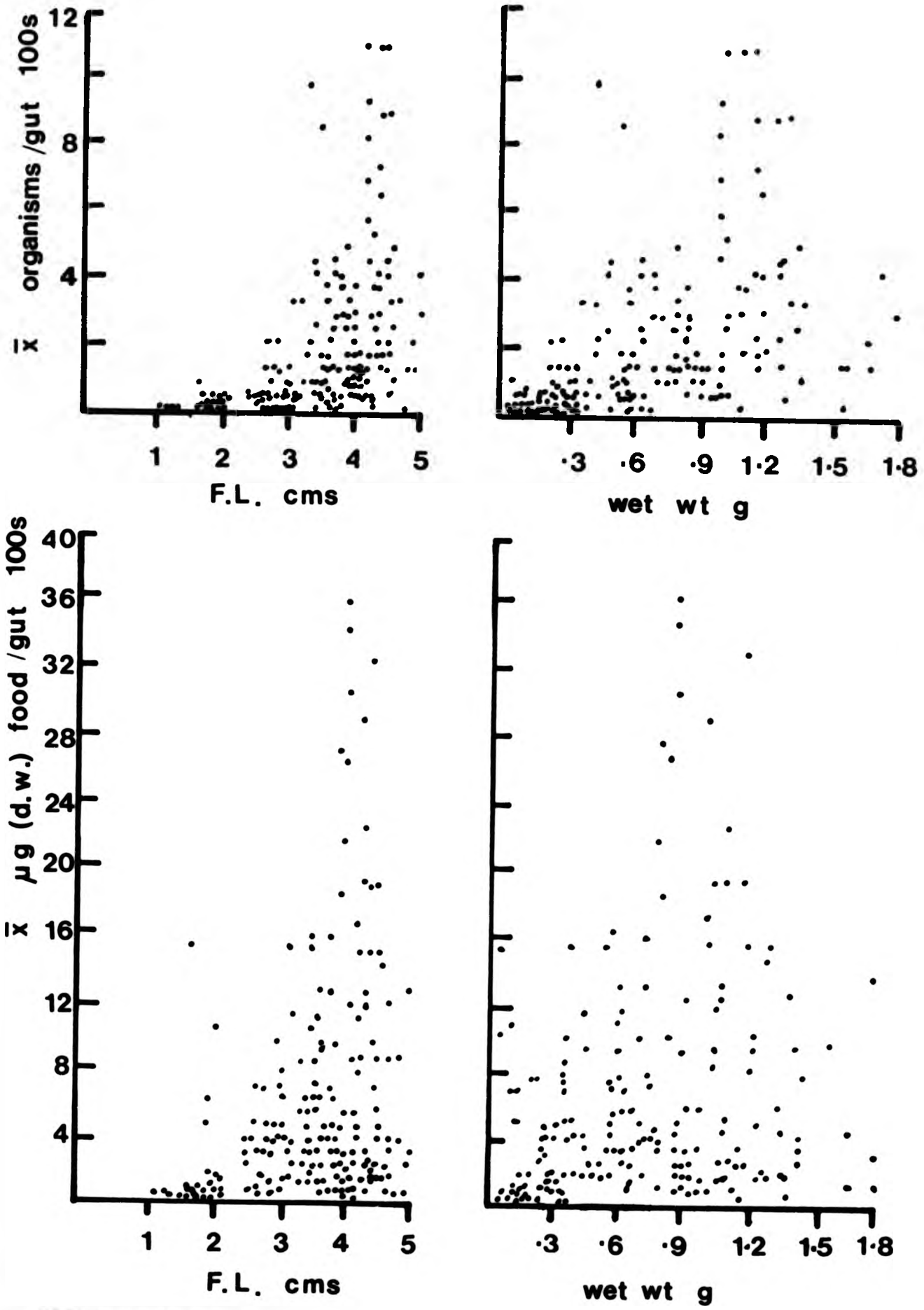


FIGURE 4.6. The relationship between food volume (numbers and dry weight biomass) and roach length and weight in Farnborough in 1977.
A. Total numbers/gut with roach fork length.
B. Total numbers/gut with roach wet weight.
C. Total dry weight of food/gut with roach fork length.
C. Total dry weight of food/gut with roach weight.

Table 4.8 Pearson correlation coefficients (r) relating total numbers of food items and their reconstructed dry weight to roach fork length and wet weight in Farnborough in 1977.

DATE	T/L	B/L	T/W	B/W	n	$\bar{x}T$	$\bar{x}B$	$\bar{x}L$
7 July	0.21	0.18	0.21	0.19	38	21	160	1.8
25 July	0.27	-0.15	-0.01	-0.16	22	59	263	2.7
9 Aug	0.32	0.32	0.28	0.28	20	145	625	3.2
22 Aug	-0.02	0.11	-0.04	0.10	15	159	430	3.4
2 Sept	0.55	0.53	0.54	0.51	20	585	1015	4.2
12 Sept	0.33	0.12	0.39	0.10	21	129	1213	4.0
26 Sept	0.39	0.10	0.37	0.10	20	214	1302	4.0
25 Oct	0.40	-0.05	0.34	-0.10	19	208	312	4.2
14 Dec	-0.27	-0.19	-0.22	-0.13	24	194	188	4.2

All roach r n = 207

T with L	0.49
B with L	0.38
T with W	0.49
B with W	0.34

T = mean total number of organisms in the guts of each sample
B = mean dry weight of organisms in μg in the guts of each sample
L = mean fork length of roach in cm W = mean wet weight of roach in g
n = sample size.

food and roach length and weight, as shown in Fig. 4.6 and Table 4.8. Similar results were obtained from an analysis of variation in perch guts.

These results suggest that little reduction in this cause of variability would result from the selection of fish close in size to the mean of the sample and the selection of the whole range of sizes present in a sample was justified. The percentage occurrence of items common in the diet was much less variable. Fig. 4.7 shows the percentage occurrence of the four most abundant species in the samples (each consisting of 10 fish). Abundant food items were most commonly present in 100% of the guts in a sample. Therefore, the samples were not biased by the presence of high numbers of a species in one or two fish. Uniformity of the species composition of the diet in perch was even more marked.

The mean numbers of each species in the diet samples were converted to percentage composition. The use of percentage composition rather than numbers reduced the range of the data to manageable proportions. Table 4.7 shows the mean percentage composition of major diet species in selected gut samples, with 95% confidence limits expressed as a percentage of the mean. The transformation to percentages did not reduce the variation as might be expected in the roach, possibly because total numbers were often less than 100 although in the perch variation was reduced by this transformation. As feeding rates were not determined, proportional representation of species in the diets was of more use than absolute numbers for comparison with proportions in the lake. The variation in total numbers consumed also made comparison of separate samples on the same date difficult and the use of percentage composition overcame this problem.

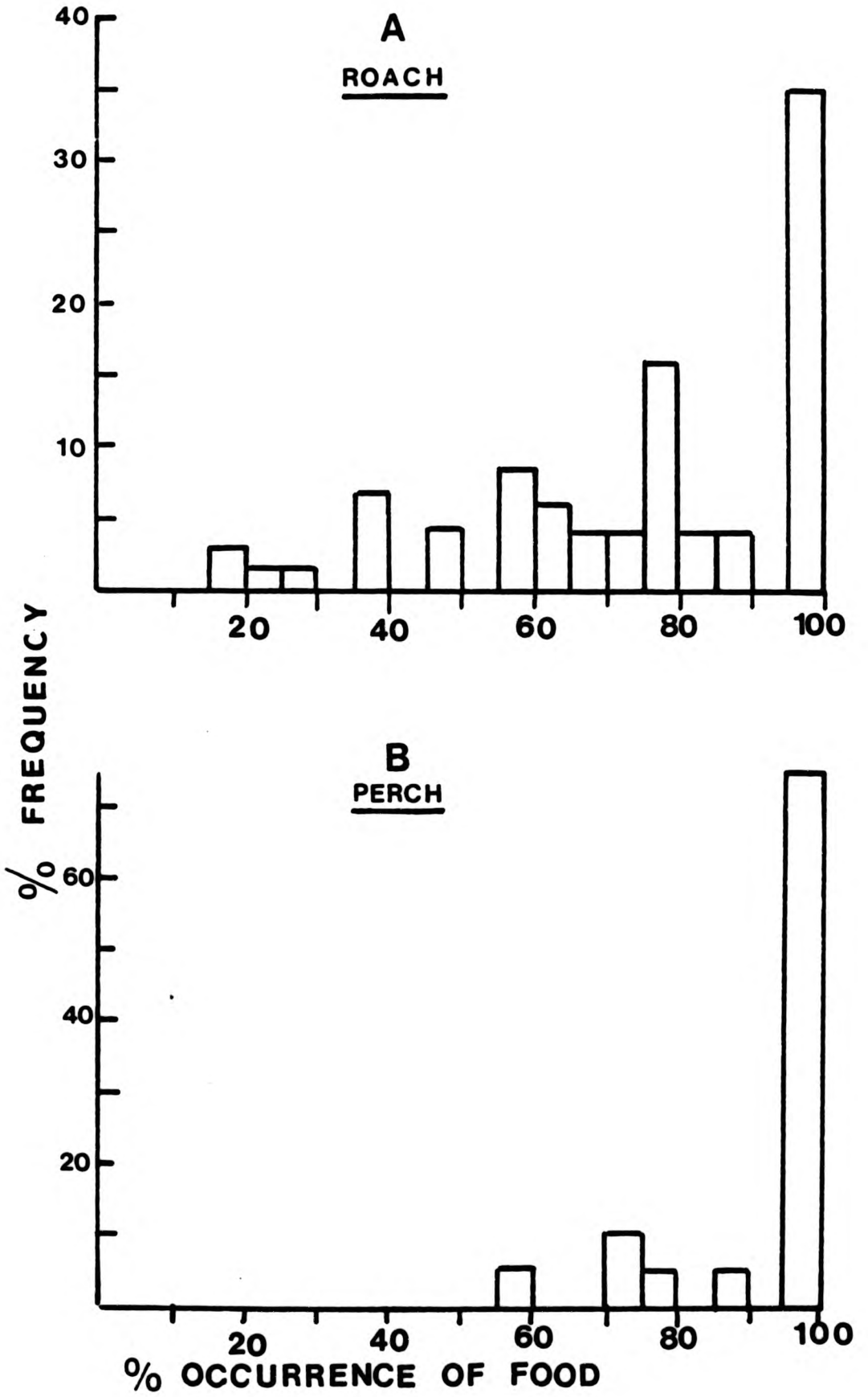


FIGURE 4.7 The frequency distribution of the percentage occurrence of major food items in the diets of 0+ roach (A) and 0+ perch (B).

4.6 Variation in diet with time in O+ roach.

Fig. 4.8. shows the results of the two 24-hour surveys of roach feeding activity, carried out as described in Chapter 2. No attempt was made to determine gut passage times or meal size. In accordance with other workers (Keast and Welsh, 1968; Thorpe, 1977b), the dry weight (mg) of the gut plus contents was expressed as a ratio of the body weight (g) and the variation of this ratio with time is shown in Fig. 4.8(a). There appeared to be two feeding peaks during the day with a significant drop at 1600 hours. The roach collected at 1400 hours were inadvertently preserved in alcohol and the weights of these fish could not be compared to the weights of fish preserved in formalin. The samples had different mean lengths, varying from 1.72 cm at 0600 hours to 1.91 cm at 1000 hours. To ensure that these proportionately large differences (10%) were not overriding time differences, a relationship was obtained to predict dry gut weight from fish length so that the dry weight of the food could be calculated, (see Chapter 2). Fig. 4.8(b) shows that the change in food dry weight with time exhibited a similar pattern to the first graph: therefore differences in fish size did not influence the results. The mean number of food items per gut, with the 95% confidence limits, for each time, are also given in Fig. 4.8. Although it has been shown that numbers vary greatly between fish, the mean numbers of food items did show the same diurnal pattern as food dry weight with the exception of the midnight sample. The greatest proportion of empty stomachs occurred at midnight (over 50%) while none were found during the day. Exact correspondance of numbers and weight was not to be expected as the examination of numbers did not incorporate any measure of the state of digestion of the food. The high number found at 2300 hours was due to the presence of 81 Bosmina in one gut. The high food weight at midnight did not match the low numbers of food

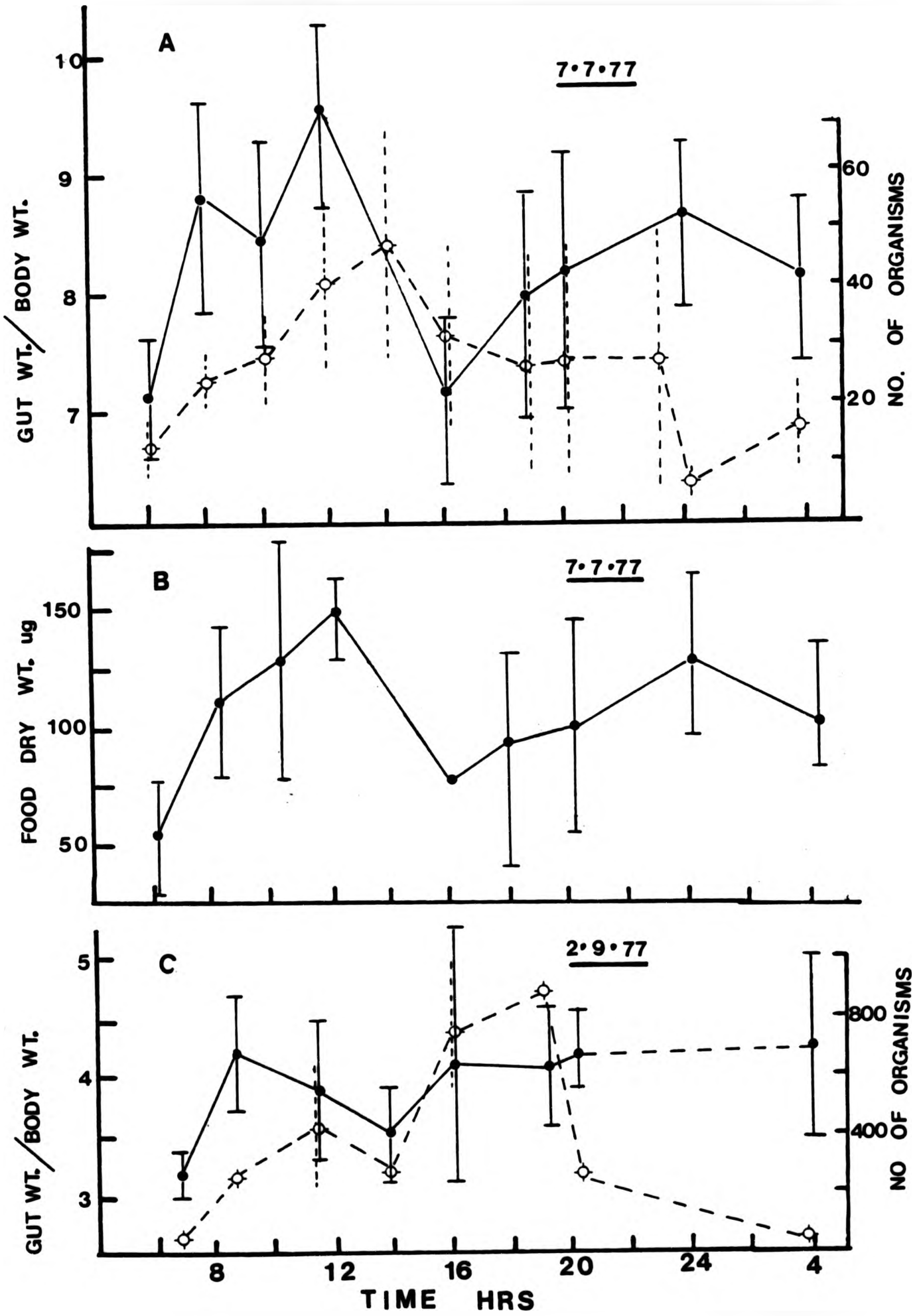


FIGURE 4.8 The results of the 24-hour studies of O+ roach diet in Farnborough in 1977.
Fig. A shows the change with time of the ratio of gut dry weight to body dry weight on 7 July, with the 95% confidence limits. The change in the mean numbers of food items in the guts with time is also shown.
Fig. B shows the change with time of the dry weight of food (ug) on 7 July, with the 95% confidence limits.
Fig. C shows the change with time of the ratio of gut dry weight to body dry weight on 2 September, with the 95% confidence limits. The mean numbers of food organisms in the guts is also shown.

items and the only explanation is that the nature of the diet changed and a small number of Daphnia were responsible for heavy food contents. There was also considerable variation in the evening samples and this may also have contributed to the lack of correlation between numbers and food weight.

As the water temperature was very high (25°C) at mid-day on 7 July and may have caused a drop in feeding activity, the study was repeated in September. On 2 September only two sets of guts were counted individually. The contents of 10 guts from each of the remaining time samples were added together for counting so that variation within samples was not measured. Fig. 4.8(c) shows the results of the September survey when a similar daily pattern was found although the high gut weights during the night were unexpected. (Unfortunately the mid-night sample was lost in the field).

On both occasions, fairly high numbers of organisms were found in the afternoon and most of the fish sampling during 1977 was in fact carried out in late afternoon.

The change in diet composition with time is shown later in the chapter, section 4.9 with the relevant weedbed samples.

4.7. Relationship of 0+ fish diet to the available food supply.

a) 0+ roach.

The percentage composition of the diet of roach caught between 7 July and 14 December 1977 is shown in Fig. 4.9. The diets of the smallest roach (less than 1.3 cm) are not shown. The newly hatched roach caught in June had been feeding upon small numbers of Polyarthra, nauplii and unicellular algae. The food of those caught at the end of June (1.0 cm) was mainly small quantities of Keratella cochlearis and Bosmina.

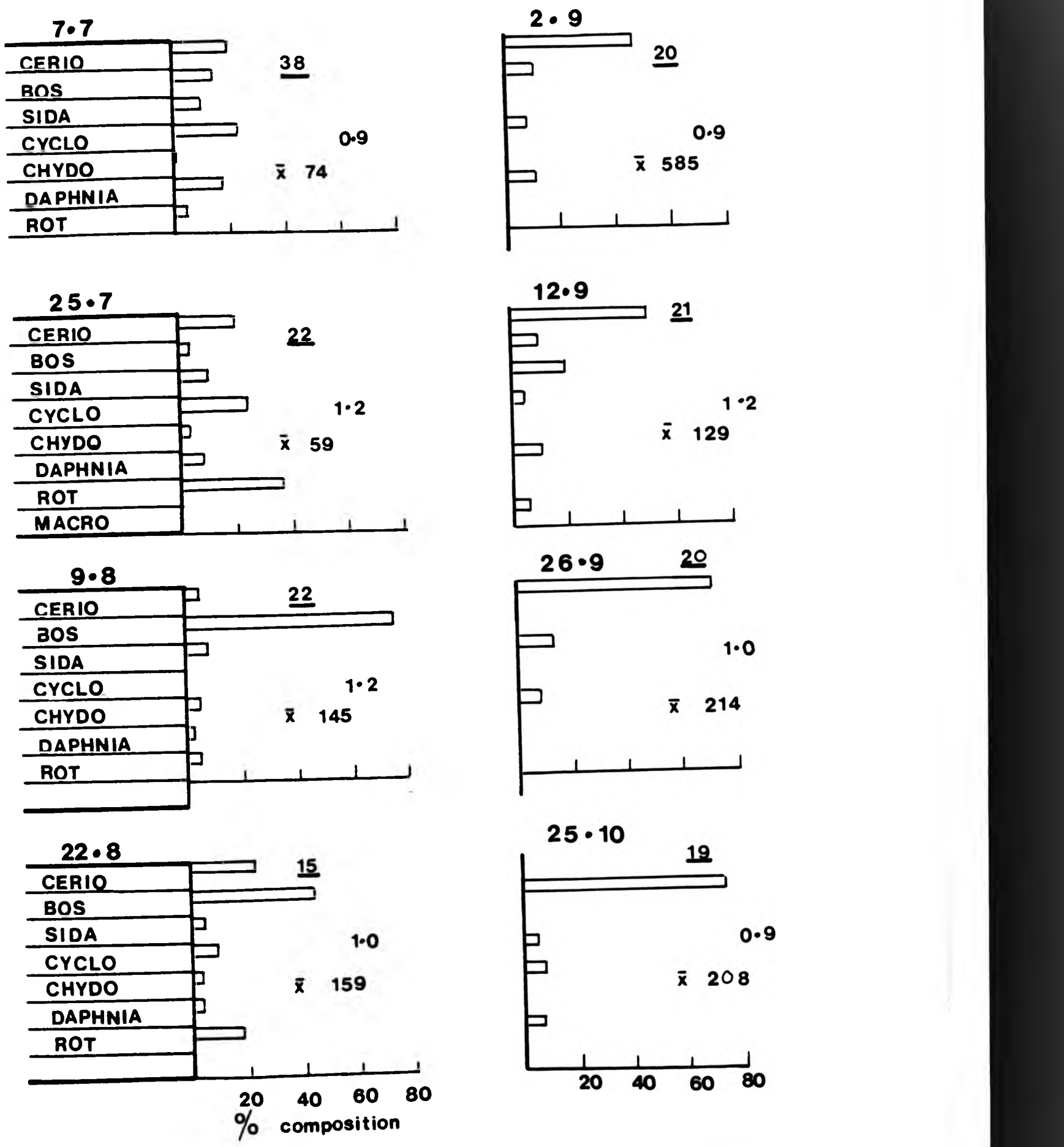


FIGURE 4.9 The percentage composition of the diet of O+ roach in Farnborough in 1977. The number of fish in each sample and the mean total number of organisms in the guts are given for each date. Cerio = Ceriodaphnia pulchella, Bos = Bosmina longirostris, Sida = Sida crystallina, Cyclo = Cyclops spp., Chydo = Chydoridae, Daphnia = Daphnia longispina and D. ambigua, Rot = Rotifers (Keratella quadrata, K. cochlearis, Brachionus).

The stomach capacity had increased greatly by 7 July and so had the diversity of diet. A large sample was examined on 7 July when the diet was predominantly of open-water origin; Daphnia longispina and D. ambigua, Bosmina and Keratella. At this time, Ceriodaphnia and Cyclops were the dominant weedbed crustacea and Cyclops dominated the open water, with Bosmina, Daphnia and Ceriodaphnia being equally sub-dominant. The presence of the large Sida in these small roach (fork length 1.8 cm) indicated that relatively large food particles could be eaten even at this early stage in the life cycle.

The predominance of open-water organisms in the guts persisted through July, with rotifers becoming more important numerically, forming 37% of the diet although Bosmina was replaced in the food by Ceriodaphnia. Cyclops made up 22% of the diet but as the same species of Cyclops was present throughout the lake one cannot ascribe this portion of the diet to either the open water or the weedbeds, although size measurements (section 4.8) suggest an open-water origin.

During August the main item in the diet was Bosmina, which was very common in the open water and formed 77% of the food on 9 August and 47% on 22 August. Daphnia ambigua was also eaten although very scarce in the open water. The plentiful Cyclops barely contributed to roach diet.

The fullest guts were found in September when numbers of crustacea in the weedbeds peaked and open-water zooplankton became comparatively scarce. Ceriodaphnia comprised over 50% of the diet throughout the month. Sida was more common in the guts than previously, possibly a function of increased fish size although it was also at peak occurrence in the weedbeds at this time.

A very small sample taken on 10 October consisted of roach feeding mainly upon Ceriodaphnia (56%), Sida (6%), and curiously statoblasts of

Ectoprocta which contributed 26% of the diet although presumably little of nutritional value as they did not appear to be digested. They were also recorded in O+ roach guts by Lange (1960). By the end of October the Ceriodaphnia population had virtually disappeared from the lake and the roach returned to open-water feeding, with Bosmina making up 77% of the food.

Roach diets were not examined again until December when although the macrophytes had died down two fairly distinct crustacean communities still persisted in the lake and the diet consisted almost entirely of Bosmina (97%). The diversity of the diet appeared to decrease with time as preferences became fixed but this was not borne out by the diversity indices (Shannon-Weaver (Southwood, 1978)) shown in Fig. 4.9. Diversity normally decreases with increasing abundance of preferred food items (Ivlev, 1961).

Table 4.9 gives a summary of the proportions of the diet arising from the two types of microcrustacean community and shows that when small, the roach fed mainly upon the open-water crustacea. This contribution became less during the summer months, dropped to 1% at the end of September and then rose during the autumn. Therefore, as roach food consumption increased during the summer, the population as a whole derived more food from the weedbed communities than from those of the open water: 48% from the open and 52% from the weeds. As the weedbed crustacea were usually also larger the biomass of food derived from this source was even greater and this will be discussed later in the chapter. Examination of individual samples shows that the following species were the dominant food items in the given number of roach samples: Ceriodaphnia 8; Bosmina 4; Sida 2; rotifers 1; chydorids 1; Daphnia 1.

The relative contributions from the open water and the weedbeds

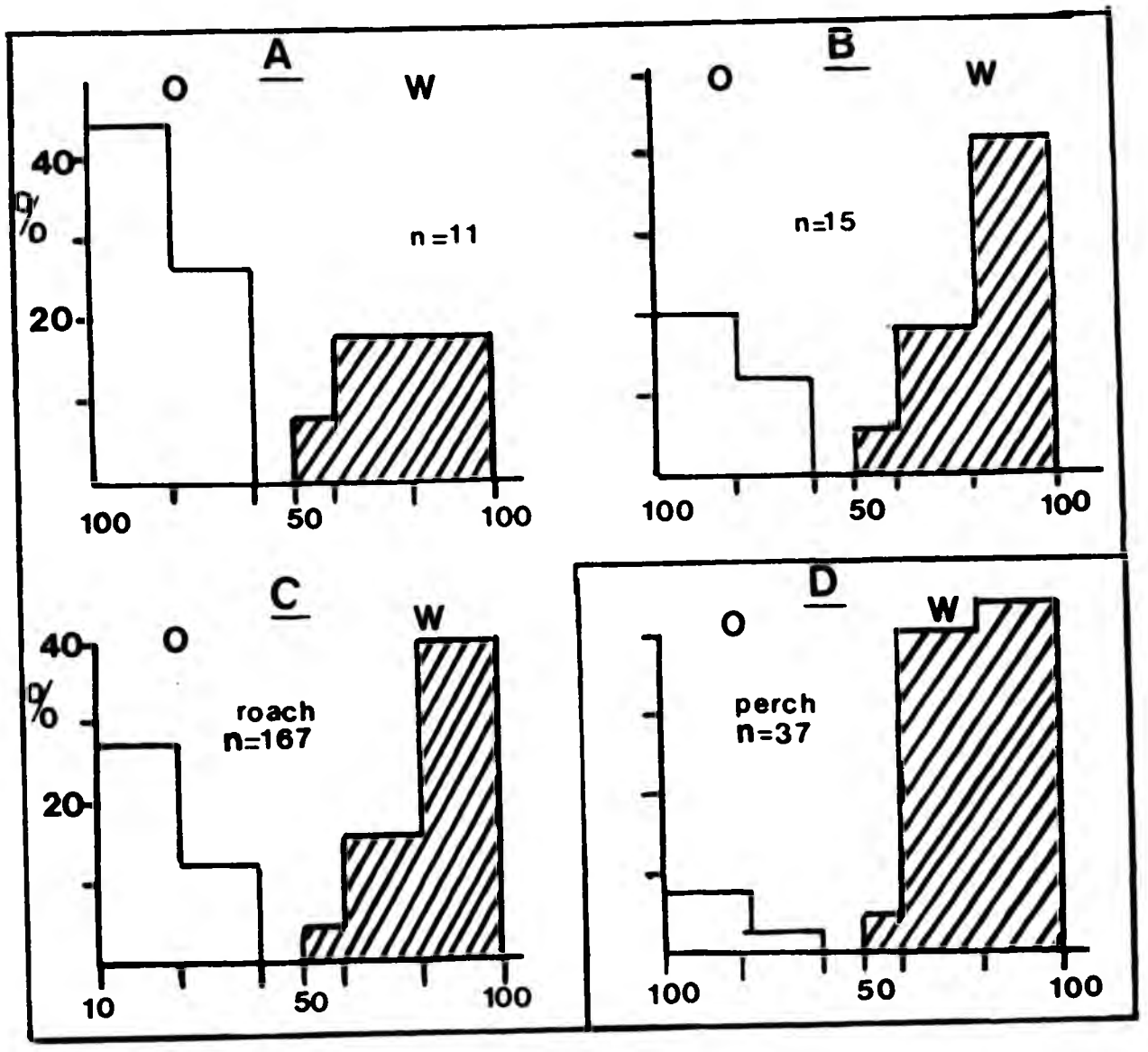


FIGURE 4.10 separation of gut contents into either open water (O) or weedbed (W) origin. Cyclops were counted as 50/50 in the O+ roach and small perch and as 30(O)/70(W) in the larger O+ perch. A. Roach gut samples, 7.7.77. B. All roach gut samples after 7.7.77. C. All individual roach guts. D. All individual perch guts.

Table 4.9. The relative proportions of open water and littoral organisms in the diets of O+ roach and O+ perch in Farnborough in 1977.

ROACH		7.7	25.7	9.8	22.8	2.9	12.9	26.9	10.10	25.10	14.12
Weed	%	31	43	17	31	73	78	98	94	9	3
Open	%	69	57	81	68	27	22	1	5	91	97
PERCH											
Weed	%	71	96			68	71			34	
Open	%	29	4			32	28			66	

summarised in Fig. 4.10. The many samples examined on 7 July are shown separately. On this occasion the roach could be divided into two groups, the larger consisting of fish with diets of open water origin. For the rest of the year, 40% of the gut samples consisted of between 80 and 100% weed crustacea. Few samples contained equal contributions from the two habitats, suggesting that the roach specialised on one or the other. A similar analysis was done on individual fish and is illustrated in Fig. 4.10. The separation of the roach into open-water and weedbed feeders was equally marked, with 60% of the guts containing weed crustacea and 66% of these being of 100% weed origin.

b) 0+ perch.

Fig. 4.11 shows the percentage composition of the diet of the few perch samples collected. The first sample was taken at the beginning of July when the fish measured 3.0 cm. The most common food item was Ceriodaphnia followed by Daphnia longispina for which the perch showed some preference, as it was not common in the open water. Other open water species such as Bosmina and rotifers were not found in the perch guts.

The diet of the small sample captured at the end of July consisted mainly of Sida, plus chironomid larvae. Again no open-water organisms had been eaten.

The perch had grown considerably by September by which time the diet had changed to a predominance of Cyclops, abundant both in the weeds and in the open water, although size measurements (section 4.8) indicate a weed origin. Ceriodaphnia made up a third of the diet. During September, the slight decline of Ceriodaphnia and rise in Sida in the weeds was reflected in the perch diet, although cyclopoid copepods continued to make up over 50% of the food.

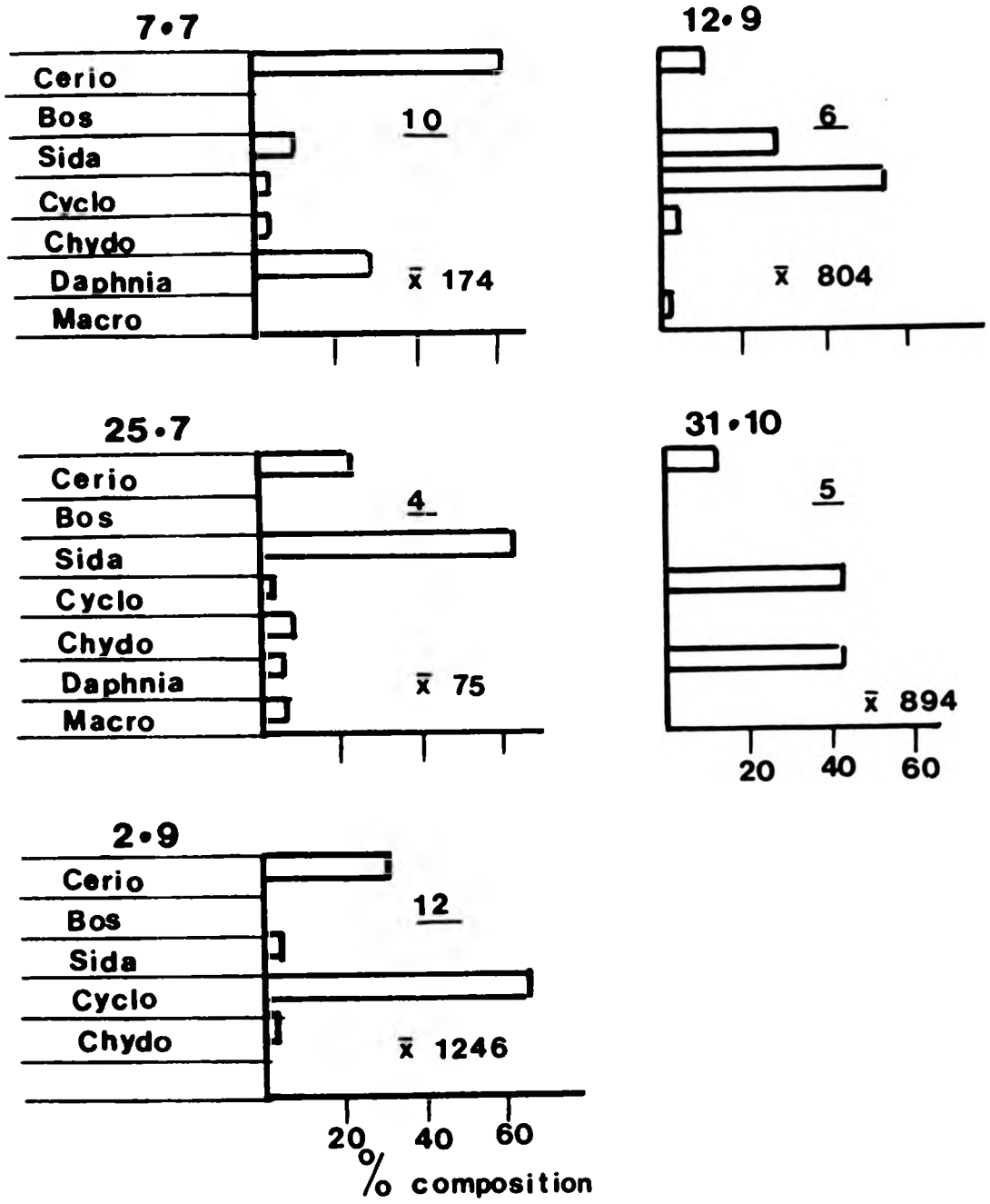


FIGURE 4.11 The percentage composition of the diet of the O+ perch in Farnborough in 1977. Sample sizes and mean total number of organisms in the guts are given. Key as in Figure 4.9

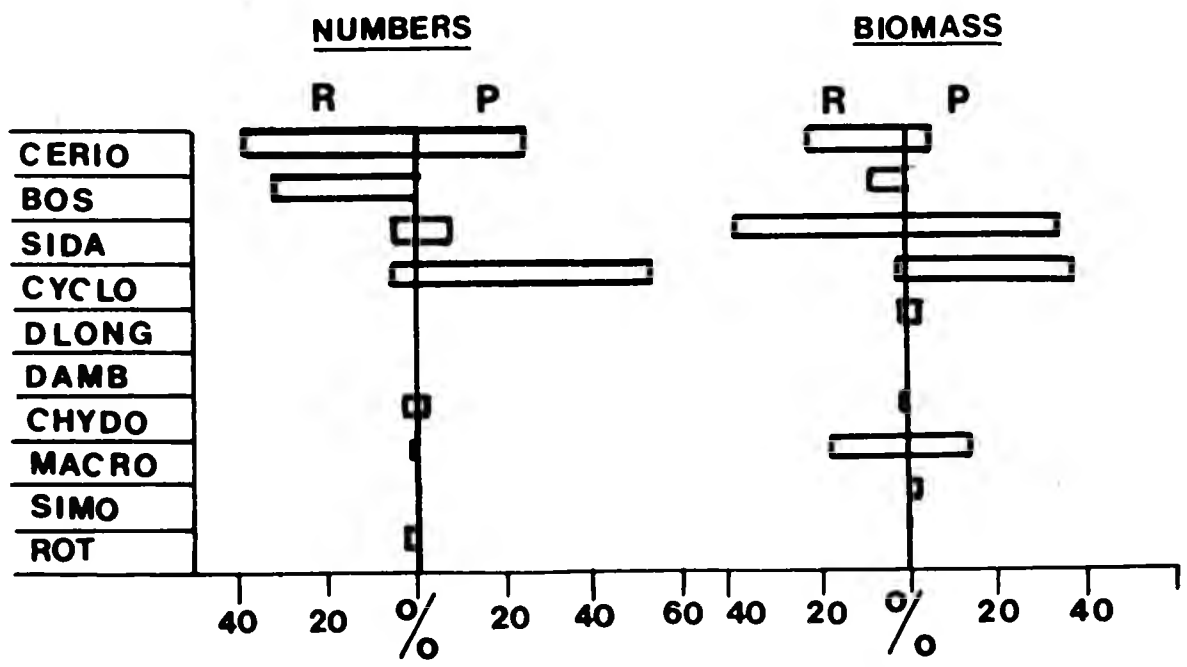


FIGURE 4.12 Graphical illustration of the overlap in the percentage composition and dry weight biomass of the diets of the O+ roach and O+ perch in Farnborough in 1977.

The food of the final sample taken at the end of October was mainly Cyclops, plus Daphnia ambigua, which although scarce in the open water comprised 37% of the food.

The relative contributions of open-water and macrophytic crustacea to the perch diet are shown in Table 4.10 and Fig. 4.10. With the exception of the October sample, the perch always consumed more weedbed crustacea than open-water crustacea and the figures for the open-water contribution may be too high because the proportions of Cyclops were divided 50/50 between open and weed in the smaller perch whereas it is more likely that the perch only took Cyclops living among the macrophytes.

c) Diet overlap.

Fig. 4.12 illustrates gross differences in species composition of the diets of the two fish species. The greater range of food items found in the roach may reflect in part the greater number of observations. The roach fed mainly upon the dominant species from the two microcrustacean communities, Bosmina from the open water and Ceriodaphnia from the weedbeds, while the perch fed mainly upon Cyclops and Ceriodaphnia, both from the weeds. Some overlap in the diet did occur over the consumption of Ceriodaphnia, Sida and Daphnia spp., although the roach usually took the smaller Daphnia ambigua while the perch ate the larger D. longispina. As discussed in the previous chapter, D.ambigua was more common in the open water while D. longispina was more abundant in the weedbeds. Overlap in the diets was more pronounced in July and had lessened considerably by September. Levins (1968) diet overlap coefficients (shown in Table 4.10) confirmed this and showed that the overlap of roach on perch was usually greater than the overlap of perch on roach.

Table 4.10 Levins diet overlap coefficients for 0+ roach and 0+ perch in Farnborough in 1977.

	R/P a_{ij}	P/R a_{ji}
7.7.77	1.22	0.38
25.7.77	0.61	0.24
2.9.77	0.51	0.51
31.10.77	0.06	0.11

The formula for the coefficients is: $a_{ij} = \frac{\Sigma Pih\ Pjh}{\Sigma Pih^2}$

Ph = the proportion of food item h in species i or species j.
Species i = roach, Species j = perch.
0 = no overlap, 1+ = complete utilisation of the same resources.

d) Electivity in roach.

Fig. 4.13 shows a comparison of percentage composition of major diet items with their percentage composition in the weedbeds and in the open water. Bosmina and Ceriodaphnia were the two most common species in the diet and consumption of Bosmina was closely related to its abundance in the open water, although peak consumption occurred prior to peak abundance so that the roach were feeding supra-proportionally upon this crustacean. When numbers of Bosmina were low in the lake the roach switched to Ceriodaphnia, the dominant crustacean in the marginal macrophytes. As soon as the Bosmina population increased in size the roach resumed feeding on it. This also corresponded to the apparent decline in the Ceriodaphnia population in the weedbeds but the lowered percentage composition was due to increased numbers of other species, and the mean numbers of Ceriodaphnia did not decline until October, (see figure 3.5) The roach did not eat Ceriodaphnia in July when it was abundant at the same time as a peak in Bosmina numbers. This suggests a preference for Bosmina followed by a switch to another abundant similarly sized crustacean when their preferred food became scarce.

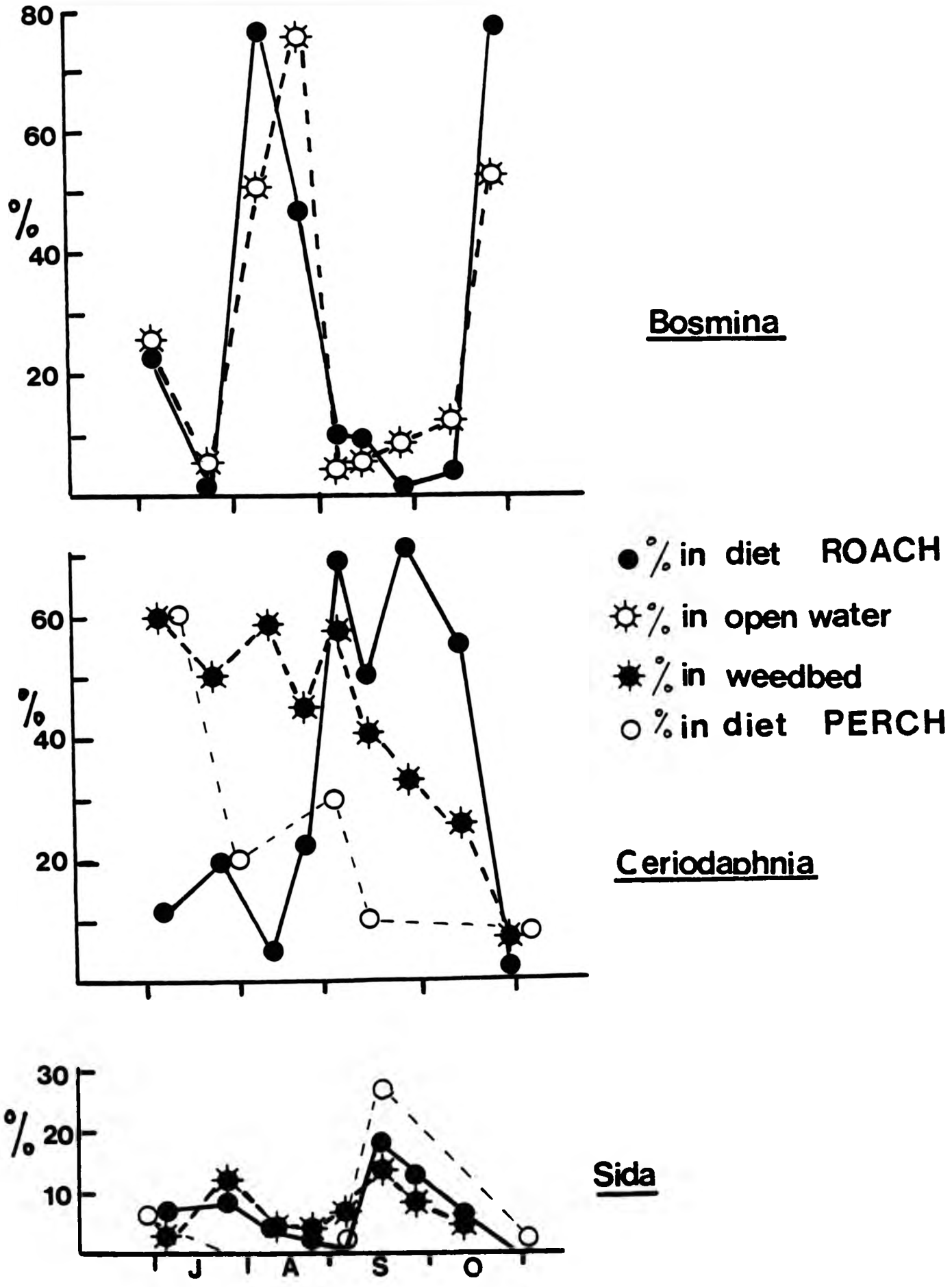


FIGURE 4.13 Comparison of the proportions of the major microcrustacean food species in the guts of the O+ roach and O+ perch, with their proportions in the microcrustacean samples from the lake, in Farnborough in 1977.

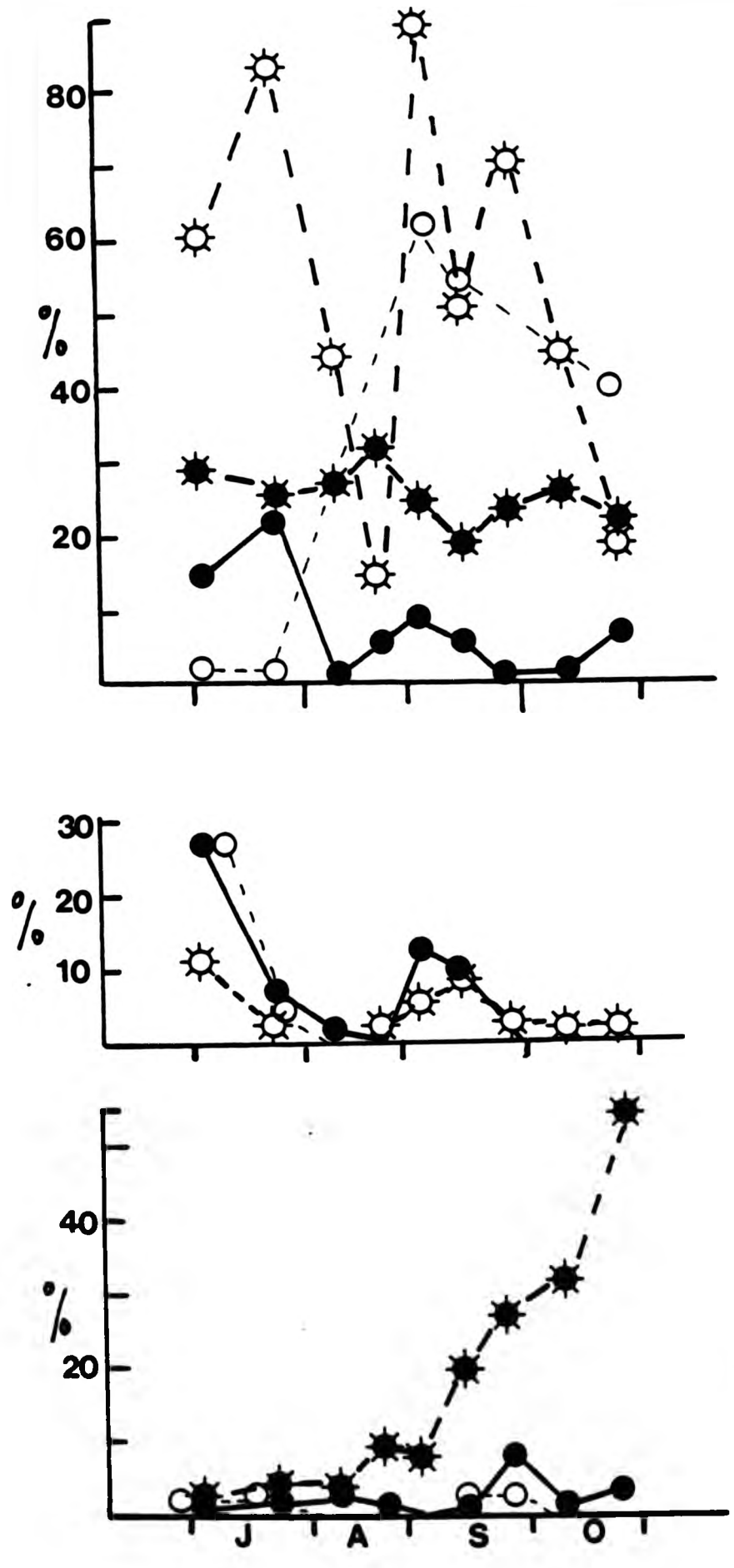


FIGURE 4.13 Cont.

The consumption of Sida was closely related to its abundance in the macrophytes with a greater proportion being eaten by the larger roach in September when most of the diet was of weedbed origin. The proportion of Daphnia in the diet was higher than its representation in the lake, suggesting a preference for this species. The consumption of both Cyclops and the chydorids showed no relationship with availability and rotifers were eaten mainly by the smaller roach. Cyclops, although abundant in the lake, was rarely eaten by the roach.

Fig. 4.13 also shows the relationship of perch diet to the available food supply and to the roach diet. The consumption of Cyclops showed little relationship to the proportions available as Cyclops although common in the gut samples, was always abundant in both the open water and the weedbeds. The proportion of Ceriodaphnia in the perch guts fell from 60% to 30% as roach consumption of this species increased but this also corresponded to the time of the switch to Cyclops by the perch. However, the perch did feed supra-proportionally upon Sida during the two population peaks of this crustacean in the weedbeds. Daphnia were only prominent in perch guts during their greatest abundance with the exception of the last sample when Daphnia ambigua formed 37% of the diet but were not detected in the open water. The chydorids in the perch guts showed no relationship with lake abundance.

Table 4.11 shows Ivlev electivity indices for 0+ roach and perch diet. The index was calculated from the following formula (Ivlev, 1961).

$$E = \frac{r - p}{r + p}$$

r = % of a species in the food, or the ration.
p = % of a species in the food supply, in the lake.

The index ranges from +1 indicating positive selection to -1 indicating positive avoidance. Calculations were performed on sample means rather

than on individual guts. The diets were first compared to the percentage composition of the weedbed crustacea and to a composite of weedbed and open-water crustacea, as although the roach were caught in the weedbeds, the open-water crustacea were also available to fish inhabiting the weed/open-water interface. The use of either weed only or open water only would introduce the bias of a restricted food supply. As Bosmina and Ceriodaphnia were also mutually exclusive in the lake the use of one or the other set of crustacean data only would result in positive indices for one of the species and negative indices for the other.

Table 4.11 Ivlev electivity indices of O+ roach and perch diets, in 1977.

ROACH	CERIO		BOS		SIDA		D.LON		CYCLOPS		D.AMB	
	OPN	W	OPN	W	OPN	W	OPN	W	OPN	W	OPN	W
25.7	-0.2	-0.3	0	1.0	0.1	-0.1	0.9	0.9	-0.1	0	0.3	1
9.8	-0.1	-0.2	0.3	1.0	0.4	0.3	0.8	0.1	-0.8	-0.7	0.6	1
22.8	0.1	-0.2	0.2	0.7	0.1	-0.2	0.5	1.0	-0.6	-0.6	0.5	1
2.9	0.2	0.2	0.9	1.0	-1.0	-1.0	0.4	0.5	-0.5	-0.4	0.7	1
12.9	0.2	0.2	1.0	1.0	-0.3	-0.4	0.6	1.0	-0.6	-0.6	0.9	1
26.9	0.5	0.4	-0.6	1.0	0.4	0.3	-0.3	0.7	-0.9	-0.9	0.3	0.9
10.10	0.4	0.4	1.0	1.0	0.1	0.3	0.9	1.0	-0.9	-0.9	0.9	1
25.10	-0.7	-0.7	0.8	1.0	-1.0	-1.0	0.3	0.7	-0.5	-0.5	0.7	1
14.12	-0.7	-0.8	0.7	1.0			0	0.5	-1.0	-1.0	0	1
PERCH	CERIO		SIDA		CYCLOP		D.LON		BOS		STIO	
	OPN	W	OPN	W	OPN	W	OPN	W	OPN	W	OPN	W
7.7	0.1	0.1	0.7	0.7	-0.9	-0.9	0.8	0.8	-0.6	0.2		
25.7	-0.1	-0.3	0.8	0.7	-0.9	-0.8	0.7	0.7	-1.0	-1.0	0.2	-0.1
2.9	-0.2	-0.2	-0.3	-0.3	0.5	0.5	0.2	0.7	-0.7	-0.2	-0.7	-0.7
12.9	-0.5	-0.5	0.5	0.4	0.7	0.7	-0.2	0.5	-1.0		0.6	-0.7
31.10	0.3	0.2	-0.1	-0.1	0.4	0.3	1.0	1.0*	-0.7	-1.0	-0.9	-0.9

* = D. ambigua

It was apparent that the indices for food selection in the roach came out the same regardless of which community the diets were compared with. The only exception was Bosmina which had a positive index when diet was

compared with the weedbeds as it did not occur there. There was little evidence of a preference for Sida and evidence of marked avoidance of Cyclops. The highest values were obtained for Bosmina and Daphnia, while the indices for Ceriodaphnia, the most common food, were never very high because of very high densities in the lake. Had the diets been compared to the open-water microcrustacea greater positive indices for Ceriodaphnia would have been obtained. The electivity indices for the perch gut contents provided more evidence for their greater preference for Cyclops than other food species. The only other evidence for selection in perch was for Daphnia.

4.8 The size of the food particles and the biomass of food eaten.

Abundant food items were measured and compared to the mean size of microcrustacea present in the lake, both in the open water and in the weedbeds. Table 4.12 shows the mean sizes and 95% confidence limits of common food items for both fish species. Error is attached to these measurements from two sources. Maceration and digestion resulted in a non-random selection of whole individuals for measurement and empty cladoceran carapaces tended to balloon out making their measurements possibly less accurate than those made from the lake microcrustacean samples.

There was no evidence for size-biased selection of Ceriodaphnia or Bosmina by the roach or perch, with no significant difference between sizes in the guts and in the lake ($P>0.05$), although the mean sizes in the guts tended to be slightly larger than those in the lake, possibly due to the ballooning effect mentioned.

Perch and roach ate the same sizes of Ceriodaphnia as shown in Fig. 4.14. The length frequency distributions of this species were compared from the guts of both fish species and from the weedbeds on two

dates as this was the item over which most diet overlap occurred. Both fish were selecting the mode of the distribution and therefore taking the most abundant size category available.

Roach ate small Cyclops while perch ate larger Cyclops. If size biased selection is discounted in both fish species, it suggests that the roach obtained Cyclops from the open water while the perch consumed them in the weedbeds. On the only occasion when they were measured from the guts of both fish species Cyclops were significantly larger ($P<0.05$) in the perch guts. Comparison with the length frequency distributions illustrated in Fig. 3.11 indicate that the fish were again tending to select the mode of the distribution. That the smaller roach were not limited to feeding upon smaller crustacea was shown by the large size of the Sida consumed. There was evidence for selection of larger individuals in the consumption of Sida and Daphnia spp. by both the roach and perch. The consumption of large items by small roach agrees with the findings of Lange (1960) who found Sida in the guts of roach of fork length 1.1 cm. Insufficient Daphnia were measured in perch guts for comparison with the roach.

A weighted mean food size was calculated for each fish species on each date, from the mean size of each food item multiplied by its abundance in the diet discounting chironomids. It is interesting that in neither fish species was there a significant increase in the mean size of the food eaten as the fish grew. The weighted mean of the perch food was always larger than that of the roach as one would expect as the perch were bigger fish with a correspondingly larger mouth gape. The size distribution in the guts depended on the species composition of the food and this in turn has been shown to depend on the availability of the various species of microcrustacea.

The mean sizes measured in the guts were used for reconstruction

Table 4.12. Comparison of the mean body lengths of major species of microcrustacea in mm, from the gut contents of the 0+ roach and 0+ perch and from the lake microcrustacean samples.

	7.7	25.7	9.8	22.8	2.9	12.9	26.9	25.10
Cerio								
Roach	0.51	0.41	0.47	0.47	0.45	0.47	0.46	
Perch	0.50				0.51	0.46		
Weed	0.41	0.46	0.41	0.43	0.43	0.43	0.41	0.52
Open	0.37	0.35	0.34	0.37		0.37	0.34	0.48
Bosmina								
Roach	0.30		0.30	0.29	0.35	0.38		0.35
Open	0.31	0.30	0.25	0.28		0.31		0.28
Cyclops								
Roach	0.38	0.35			0.48			
Perch					0.95	0.81		0.84
Weed	0.52	0.63	0.60	0.55	0.69	0.80	0.66	0.71
Open	0.46	0.48	0.40	0.46		0.49	0.47	0.51
Sida								
Roach	1.20	1.67	1.50			1.60	1.88	
Perch	1.70				1.66	1.68		
Weed	1.29	1.29	0.95	1.28	1.21	1.35	1.31	
D. amb								
Roach	0.6		0.60	0.69		0.57		
Perch	0.80						0.63	
Open	0.56	0.50	0.56		0.55	0.58	0.45	
Weed	0.68							
D. long								
Roach		1.10			0.89	0.93		
Perch	0.89							
Open		0.65		0.59		0.63		
Weed	0.87	1.28						
Weighted means								
Roach	0.47	0.45	0.35	0.34	0.47	0.65	0.61	0.33
Perch	0.69				0.81	0.95		0.70

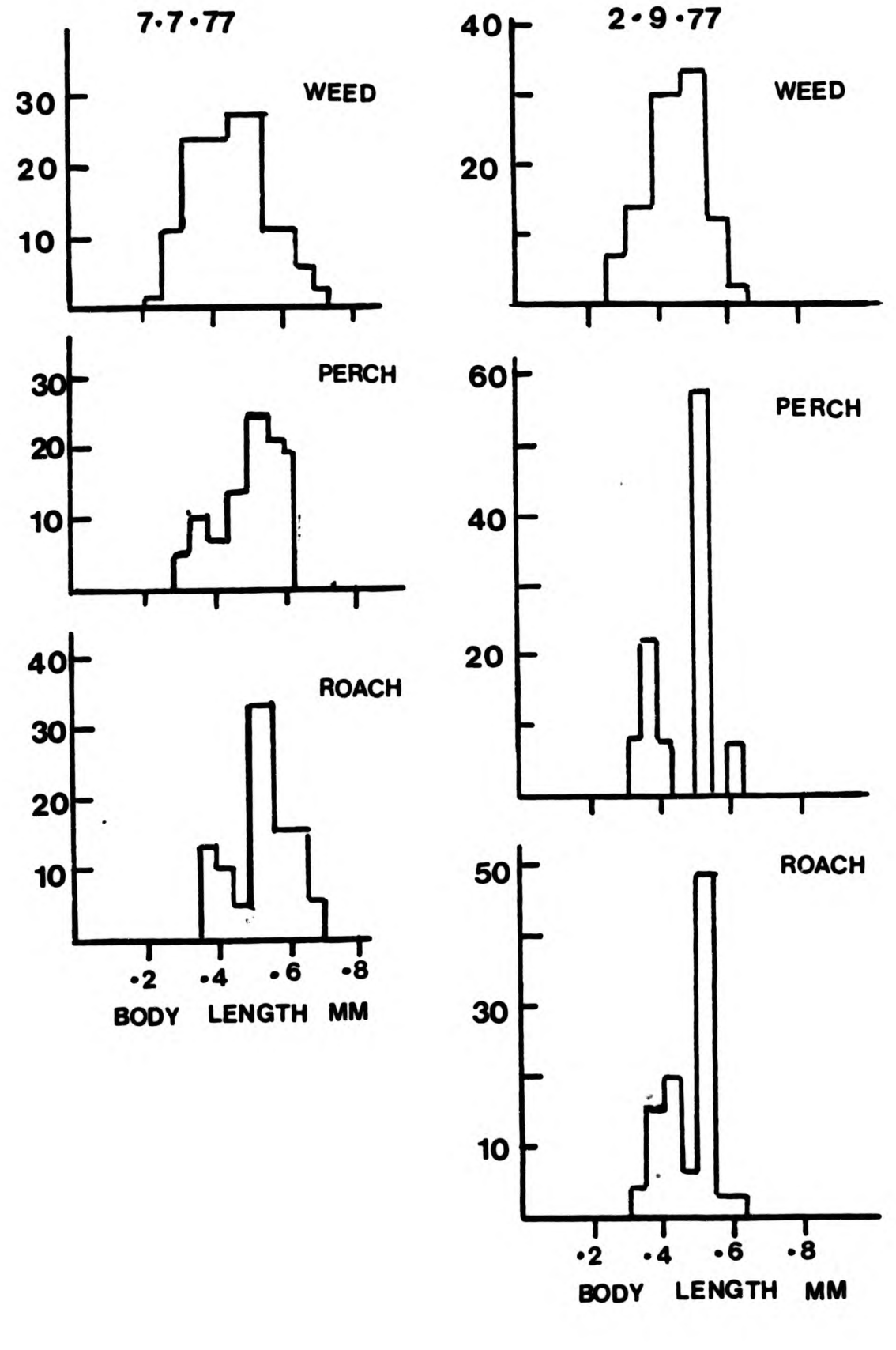


FIGURE 4.14 A comparison of the body lengths (% frequency) in mm of Ceriodaphnia pulchella from the guts of 0+ roach and 0+ perch and from the marginal weedbeds in Farnborough on two occasions in 1977.

of the dry weight biomass of the food. The dry weight corresponding to each mean length was obtained from the length/dry weight regressions in Chapter 2 and multiplied by the abundance in the gut to provide a reconstruction of biomass of food consumed. This does not equate with food volume or food weight estimates of gut contents made by other workers. All rotifers were estimated to weigh 0.1 ug (Bottrell et al, 1976). All insects were assumed to weight 60 ug in roach and 100 ug in perch. This value was obtained from length and dry weight measurements of a variety of benthic invertebrates from Farnborough and comparison with published length/dry weight regressions (Mason, 1977). These estimates will therefore be less accurate than those of the microcrustacea but as the insects were an order of magnitude heavier than the microcrustacea, their importance in the diet is apparent even when they are possibly underestimated. Vijverberg and Frank (1976) measured both the chemical composition and the calorific values of selected microcrustacea and found little differences between the energy content of Cladocera and Copepoda although Copepoda contained more lipid. Therefore, the dry weights provide an accurate measure of food value with the reservation that not all species may be digested to the same extent.

The contribution of each species to total biomass of the food of roach, shown in Fig. 4.15, was not always the same as the numerical contribution. Sida and the chironomids assumed a greater importance and the contribution of Bosmina was reduced. It has been suggested that the numbers of chironomids present in fish guts can be overestimated because they are retained longer in the guts than smaller items (Kionka and Windell, 1972) but little evidence of this was found here and different workers have found varying relationships between gut evacuation rates and particle size and prey type (Elliot, 1972; Schneider, 1973b). It

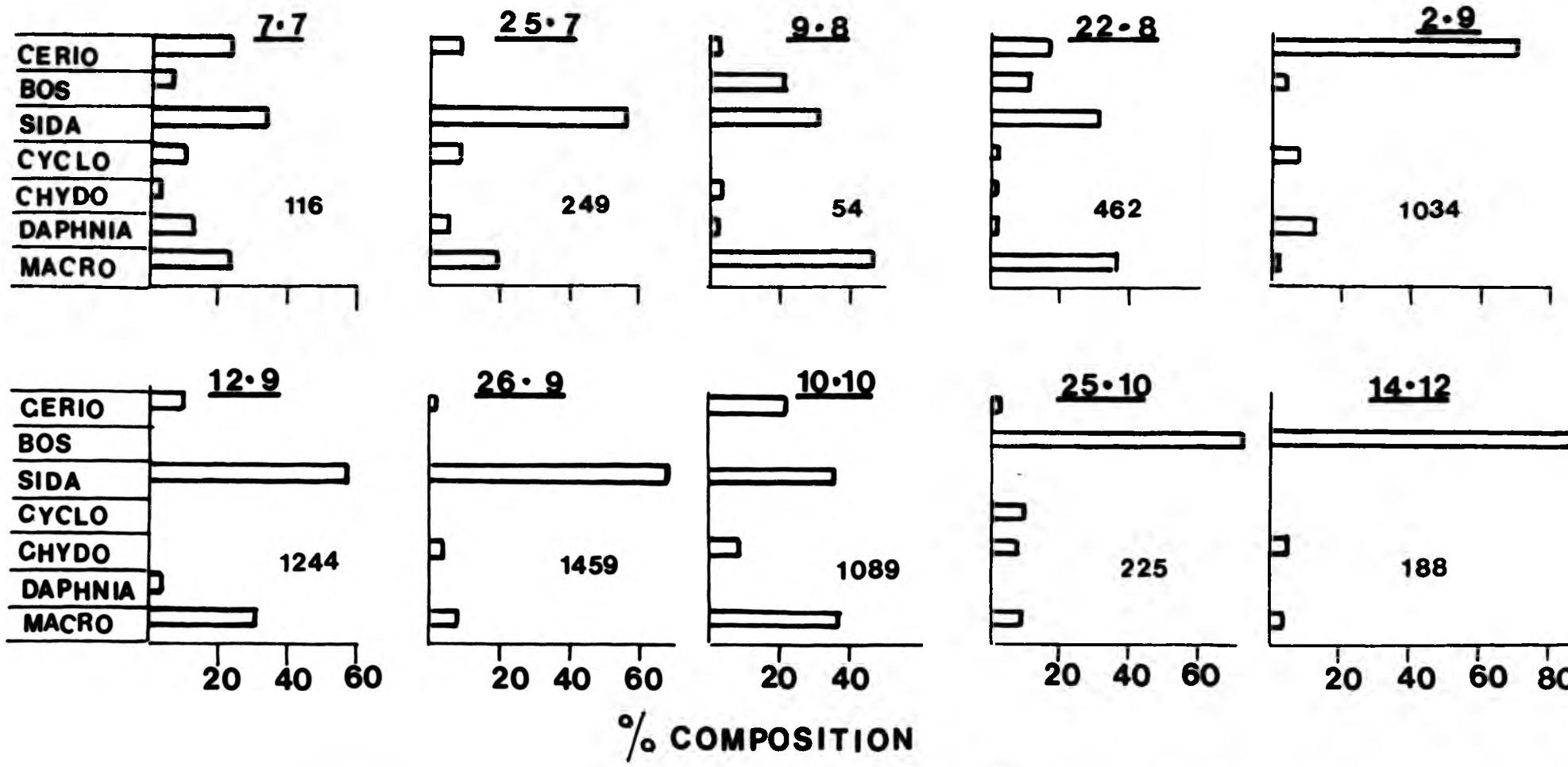


FIGURE 4.15 The percentage composition of the dry weight biomass (ug) of the food of the O+ roach in Farnborough in 1977.

was observed that while the smaller Cladocera had become totally disintegrated by the time they reached the anus Sida often appeared relatively whole although what remained may have been non-utilisable chitin.

The mean dry weight biomass of the roach food increased with time to a peak at the end of September. Some workers, e.g. Hellawell (1972) have taken similar measurements as evidence that feeding activity increases during the summer with increasing water temperature. The observations obtained here correspond most closely to the increasing size of the roach with a correspondingly greater ability to eat large quantities. The decline at the end of September was probably due to decreasing water temperatures but with no information on consumption rates food quantities cannot be related to feeding activity.

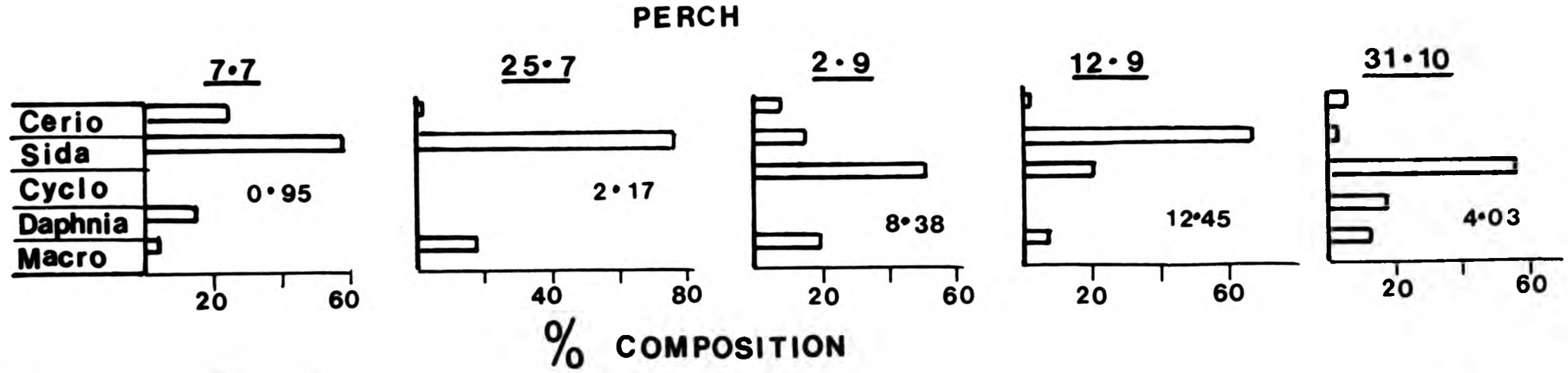
Mean dry weight biomass of the perch food, Fig. 4.15, also increased markedly with time. The relative contributions of the main species to the total biomass of food are also shown in Fig. 4.15. The importance of Sida and Cyclops became apparent and the contribution of Ceriodaphnia to total food was reduced.

In both fish species the importance of weedbed microcrustacea was emphasised by the conversion of numbers to biomass, and the relative contributions of each to total food dry weight are given in Fig. 4.16.

4.9 The relationship of roach diet to specific macrophytes.

Individual roach gut samples were compared with the microcrustacean samples collected from the same weedbeds as the roach. This comparison highlighted the variation in gut contents of the roach population.

During the two 24-hour studies, many samples of both fish and microcrustacea were collected and Fig. 4.17 shows the seven samples



	PERCH									
Contribution from weeds %	85		99		71		87		50	
	ROACH									
DATE	7·7	25·7	9·8	22·8	2·9	12·9	26·9	10·10	25·10	14·12
%	76	89	81	86	78	97	82	99	23	9

FIGURE 4.16 The percentage composition of the dry weight biomass (mg) of the food of the O+ perch in Farnborough in 1977.

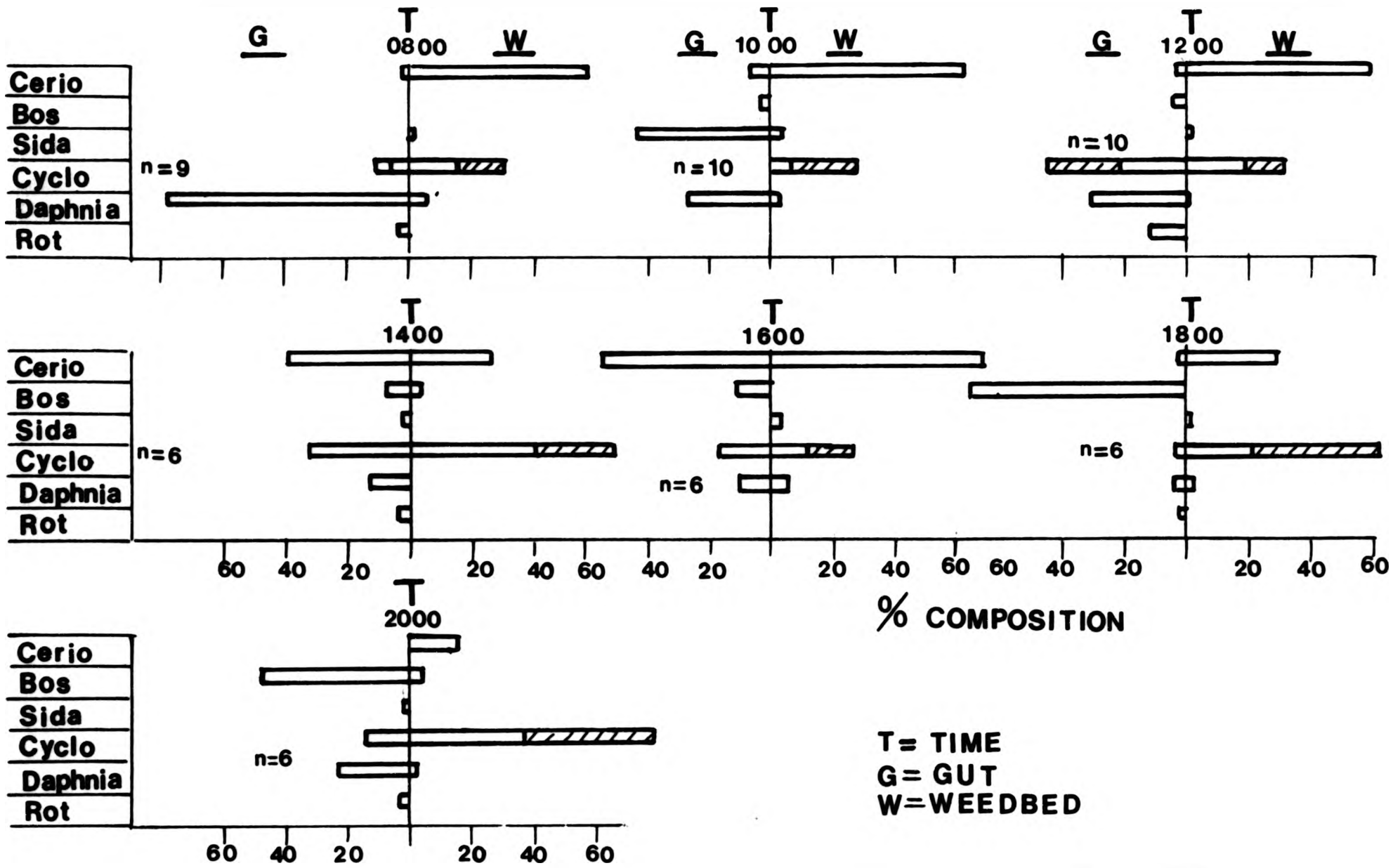


FIGURE 4.17 A comparison of the percentage composition of the diet of the 0+ roach and the weedbed microcrustacean samples collected throughout the day on 7 July, in Farnborough in 1977. /// nauplii

taken in July. The times of sampling and sampling sites are given on the figure. The percentage composition of the microcrustacea in the weedbeds was much less variable than that of the diets, apart from the last two samples which contained fewer Ceriodaphnia but were taken from within different plant stands. The diets were variable through the day and showed little relationships with the relevant weedbed samples. Points of interest are: the high proportion of Sida in the diet at 1000 hours coincided with the largest population found in the water, 54/litre among Potamogeton. The large number of Cyclops eaten at 1400 hours coincided with a peak in the samples of 612/litre. Conversely, the highest numbers of Ceriodaphnia in the weeds (1200/litre, 1400/litre) were not reflected in the diet. Bosmina was only eaten by the roach when and where Ceriodaphnia was less abundant. The Bosmina population was in decline in the open water on this date and as has been shown the roach only exerted their preference for Bosmina when it was abundant.

The percentage of open-water crustacea in the roach diet changed from 30% in early morning to 40% in the afternoon and then back to 90% in the evening. Whether this reflected fish movement in and out of the weeds or whether the diurnal vertical movements of the crustacea affected their availability is not known. Bosmina have been found to move into weeds at night (Kairesalo, 1978). The lack of Ceriodaphnia in the diet when Bosmina was consumed suggests that the roach had moved out in to the open water (Stott, 1967).

Fig. 4.18 shows the samples collected during the second 24 hour study in September. The weedbed samples were again very similar in percentage composition except for the 1700 hours sample from site 10 which contained fewer Ceriodaphnia and Sida. The diets differed in the quantity eaten during the day but were more similar in percentage composition than in July, although one sample at 2000 hours, differed as

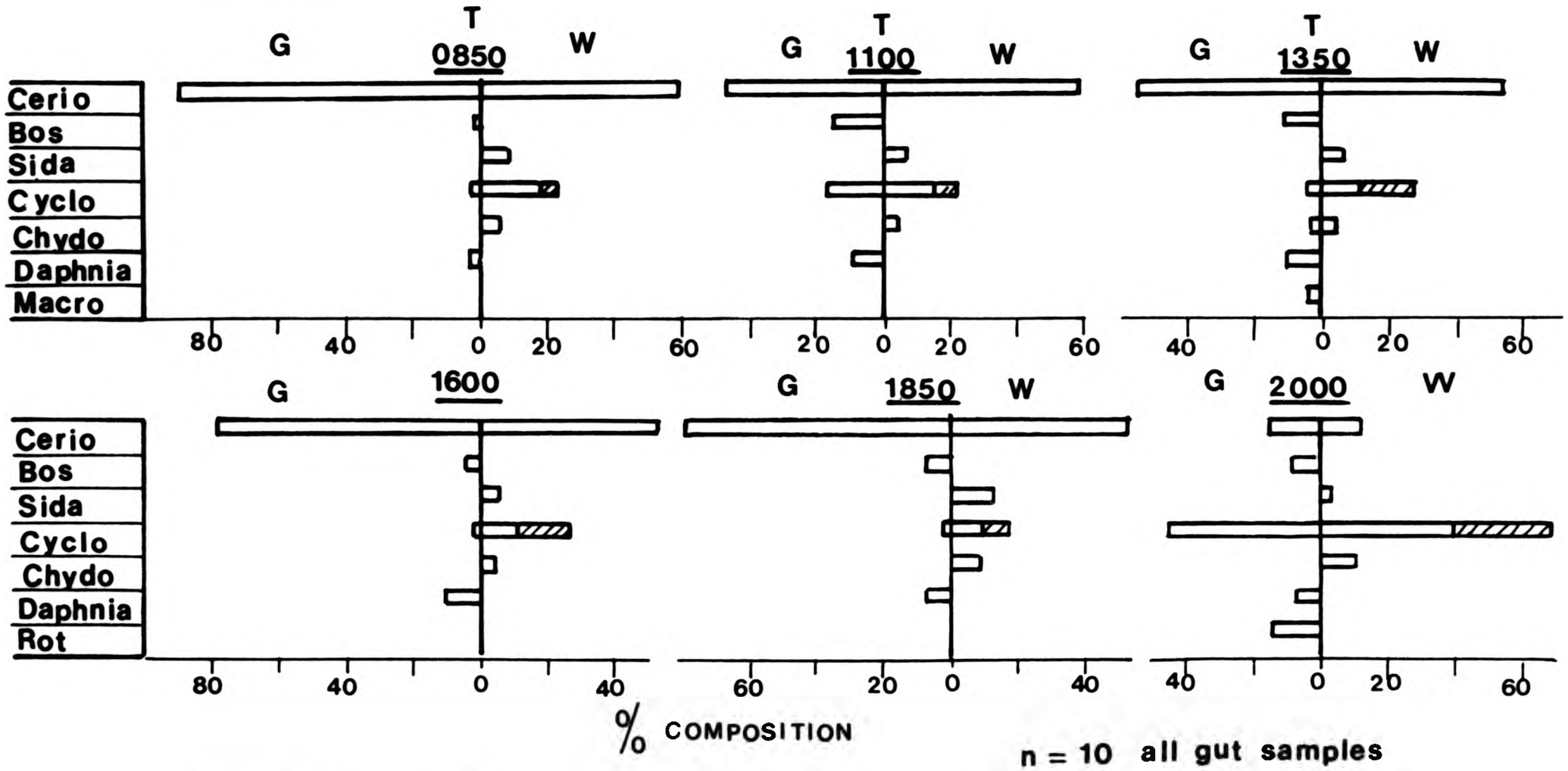


FIGURE 4.18 A comparison of the percentage composition of the diet of the 0+ roach and the weedbed microcrustacean samples collected throughout the day on 2 September, in Farnborough in 1977.

the roach had been consuming Cyclops rather than Ceriodaphnia. On this date the diets were similar to the food supply apart from the low occurrence of Sida in the guts and the consumption of Bosmina.

On other dates the roach samples were usually collected from both Elodea and Sparganium. The two samples shown for 2 September are those which have been used in all previous analyses, each containing 10 individually counted guts. Examination of Table 4.13 shows that although the numbers/litre of microcrustacea in the weedbed samples were variable, the proportions of each species were fairly similar on each date. The gut samples showed much less similarity to each other and were most variable earlier in the year. On 9 August three samples were collected, all different. Only on 26 September were samples similar. They also bore little similarity to the corresponding weedbed samples. Therefore, examination of one sample of fish for gut analysis could lead to a biased interpretation of their feeding habits. The importance of Bosmina in the diet was less apparent since on occasions when one set of roach had eaten many Bosmina the other sample had consumed Ceriodaphnia., e.g. in the two sets of roach examined in August.

There was no correlation between numbers of food items in the guts and abundance of microcrustacea in the weedbeds, although on 2 September roach caught in Elodea, where Ceriodaphnia was very abundant (1307/litre) had eaten many Ceriodaphnia, while roach caught in P. natans/Elodea where Ceriodaphnia was less abundant (80/litre) had eaten far fewer. However, this was not so on other occasions. High numbers in the guts were most often associated with open-water feeding with the roach eating many small particles. One sample taken on 12 September was from marginal open-water and the guts contained a mixture of open-water and weedbed crustacea. There were considerably more Bosmina and Daphnia in this sample so that some relationship between the area in which the

Table 4.13 Comparison of the percentage composition of individual roach gut samples (G) with the percentage composition of the microcrustacean samples (M) taken from the same sites, in Farnborough in 1977.

	25.7.77				2.9.77			
	ELODEA		SP/T		ELODEA		PN/EL	
	G	M	G	M	G	M	G	M
Ceriodaphnia	16.1	17.0	25.0	49.0	30.0	55.0	49.0	59.0
Bosmina	0.8		1.5		5.4		17.0	x
Sida	3.0	1.5	15.4	9.9	0.1	7.0		3.4
Cyclops	25.0	18.7	18.0	19.9	1.6	10.7	19.0	16.7
D.longispina	1.4*	0.9	14.0*		0.4		x	
D.ambigua	0.5		0.9		12.0		11.0	x
Keratella	51.4*		15.8*		0.6		3.3	
Chydoridae	0.7	28.0	3.4	3.7	0.1	5.4	x	6.7
Macro	0.5	28.0	2.4	15.7	0.1	17.7		
n	10		12		10		10	
Total nos.	44	249	78	657	755	2374	414	1353
Total biomass	344		151		1394		673	

	9.8.77				12.9.77			
	ELODEA		SP/T		MAR.OP		SP/T	
	G	M	G	M	G	M	G	M
Ceriodaphnia	2.5	20.3	11.3	31.4	53.4	21.7	28.9	49.2
Bosmina	87.4*		5.1*		12.4*		3.4*	
Sida	2.7	0.9	23.5	2.7	4.9	14.4	39.5	5.4
Cyclops	0.2	13.5	2.4	18.8	4.1	19.8	5.9	11.5
D.longispina	0.4		0.4		0.9		2.4	
D.ambigua	1.4		1.9		10.7		4.1	
Keratella	4.2		1.9		0.9		0.8	
Chydoridae	0.5	7.1	33.2		0.9	32.6	4.1	8.8
Macro	0.4	35.0	18.7	26.0	1.5	7.3	10.5	19.9
n	9		8		11		10	
Total nos	302	1325	32	951	157	1839	98	1064
Total biomass	527		599		622		1866	

	22.8.77				26.9.77			
	ELODEA		SP/T		ELODEA		PN	
	G	M	G	M	G	M	G	M
Ceriodaphnia	70.3*	32.0	15.4*	42.9	79.1	11.9	55.0	19.7
Bosmina	6.9*		53.0*		0.3		0.2	
Sida	12.2*	1.5*	0.9	1.1	14.2	11.4	13.0	3.2
Cyclops		28.0	5.6	19.8	0.4	17.9	2.1	22.5
D.longispina	2.8		0.6		0.1		0.1	
D.ambigua			2.1		0.4		0.1	
Keratella	0.3*		18.7*		0.3			
Chydoridae	1.3		2.3		4.6	43.9	13.9	25.5
Macro	5.4	22.0	1.0	24.0	0.9	10.9	5.3	18.4
n	5		10		10		10	
Total nos	54	951	206	879	198	2016	229	1636
Total biomass	505		360		1387		1533	

Sp/t = Sparganium and Typha Pn = P. natans
Pn/ el = P. natans and Elodea Mar.op = marginal open.
x = present <1.0% * = significantly different (P<0.05)

fish were caught and the diet may have existed.

The variation within samples has already been shown to be great. To test whether the separate gut samples were significantly different, they were compared with a t-test on non-transformed percentages. The significant differences are shown in Table 4.13. A surprising number of the dietary differences were not significant because of considerable variation within samples. Most of the obvious differences were however significant as on 22 August.

These comparisons and tests indicate the need for extensive sampling of fish populations to obtain an accurate knowledge of the diet, as the examination of any one of the samples discussed above would provide an incomplete record of the diet of the roach population on that day.

4.10 Discussion.

The examination of the roach and perch growth data has raised two interesting points in this comparison of the ecology of these two fish species. The O+ roach showed greater fluctuations in growth rate from year to year than the O+ perch, which in 1977 and 1978 attained the same size at the end of the growing season. The O+ perch exhibited marked fluctuations in year class strength, being either abundant or absent, with good first year survival being followed by failure of the next year class. There was evidence to suggest that roach growth was density dependent with intra-specific competition occurring while other factors regulated the growth and survival of the perch.

The growth rates of the roach in Farnborough in 1977 and 1978, when the average final size was 4.35 cm/1.1 g, were similar to reported growth rates of many populations in this country as shown in Table 4.14. Gee (1978) in his survey of the fish populations of the gravel pits

compared the growth of the roach to other published records and concluded that although first year growth varied considerably between lakes (the best was 9.5 cm, the poorest 3.5 cm) the roach possessed average growth rates, compared to other British populations. The 1979 year class in Farnborough attained a size of 5.9 cm by the end of September which was considerably better than in previous years, except for the 1976 year class which in the exceptionally warm summer grew to 6.8 cm (Cook, 1979). This was approaching the rapid growth rates recorded from Rye Meads (White and Williams, 1978) where the 1969 year class of roach measured 7.7 cm at end of the first year.

The seasonal pattern of growth of the O+ roach was similar to that found by other authors. White and Williams (1978) found that 1+ roach in 1969 grew slowly in April and May, after which growth was rapid through the summer, slowing in September. Growth then ceased and did not resume until May, whence a similar pattern occurred. Mann (1973) described a similar pattern for roach in the River Stour with growth occurring between May and September, and Burrough and Kennedy (1979) found that roach in Slapton Ley grew between May and September. Therefore the assumption made in this study, that the size of the roach at the end of September represented all growth for that year was justified. The period May to October was also the period of the most frequent microcrustacean sampling in 1977. It was necessary to establish the growing period of the young roach and perch since the caging experiments described in the next chapter were conducted between July and mid-September in both years.

The sizes given in Table 4.14 may not accurately represent the amount of growth which occurred in one season as they are sizes at age 1. In this study interest was centred on growth in the first year up to December, during which period the diet was also examined. Broughton and

Table 4.14. Size at age 1 of roach and perch populations.

Site	Yr.Class	L.	Method	Source
ROACH				
Darenth	1972	9.5	seine	Gee 1976
Larkfield 41		3.5	seine	" "
Yateley 4	1972	6.0	seine	" "
Yateley 4	1973	6.0	seine	" "
Yateley 7		5.4	seine	Barber 1975
Darenth	1976	6.3	seine	Cook 1979
Farnborough	1976	6.8	seine	" "
Farnborough	1977	4.2	seine	This study
Farnborough	1978	4.5	seine	" "
Farnborough	1979	5.9	seine	" "
QEII	1977	3.0	seine	Bubb (pers.comm.)
QEII	1978	5.0	seine	Bubb (pers.comm.)
Rye Meads	1968	7.7	seine(1+)	White & Williams 1978
Slapton Ley	1973	3.9	B.C.	Burrough & Kennedy 1979
Slapton Ley	1976	6.8	seine	" " "
R.Thames		4.3	B.C.	Williams 1967
R.Thames	1966	4.1	seine	Mathews 1971
R.Stour	1962	4.1	B.C.	Mann 1973
R.Stour	1965	4.6	B.C.	" "
R.Hull	1975	4.1	Drop net	Broughton & Jones 1978
R.Hull	1976	5.1	Drop net	" " "
PERCH				
Farnborough	1972	8.5	seine	Gee 1976
Twyford	1972	12.6	seine	" "
Darenth	1976	6.7	seine	Cook 1979
Farnborough	1976	6.3	seine	" "
Farnborough	1977	6.4	seine	This study
Farnborough	1978	6.5	seine	" "
Slapton Ley	1967	7.6		Craig 1974(b)
Slapton Ley	1969	9.0	B.C.	" "
Rye Meads	1969	12.0	seine	White & Williams 1978
QEII	1977	8.7	seine	Bubb (pers.comm.)
QEII	1978	8.6	seine	" " "
Windermere	1975	7.7	seine	Guma'a 1978(a) T.L.
Windermere	1976	6.5	seine	" "
Dubh Lochan		5.1	B.C.	Shafi and Maitland 1971
R.Stour		7.4	B.C.	Mann, 1978
R.Thames		6.9	B.C.	Williams 1967

B.C. = obtained by back calculation.
L. = fork length in cm unless otherwise stated.
T.L. = total length in cm
QEll = Queen Elizabeth ll Reservoir

Jones (1978) examined O+ roach growth in the River Hull and presented data both on the mean size in December and the mean size on their official birthday, 1 June, which they consider to be the size at the end of the first year. In most instances the mean length of the roach had increased between December and June, in one case from 3.5 cm to 4.2 cm. Whether this was due to differential mortality of the smaller roach in the winter or whether the fish had grown during the spring is not stated, but as mentioned above growth usually commences in May. This means that the size at age 1 and size at the end of the first growing season are not always comparable. The comparison of specific growth rates is also affected by this discrepancy as annual specific growth rates (of which there are few in literature based on direct measurements) cannot be compared with those calculated over a shorter time interval. The specific growth rates of the O+ roach in Farnborough in 1979 (see Table 4.5) show that the larger average size at the end of the first year was probably due to early hatching as the roach did not grow any faster than in other years. The early spawning may have been caused by the mild winter of 78/79 whereas in both 76/77 and 77/78 the lake was frozen over in the early part of the year.

It is possible that the growth of the O+ roach in Farnborough was density dependent as there appeared to be a relationship between abundance as expressed in sample size and the growth rate in the three years. The O+ roach population was fairly large in 1976 (Cook, 1979) although smaller than in 1977 but the good growth rate in 1976 was probably due also to the high water temperatures in that year. Growth of the small 1978 population was better than that of the more abundant 1977 population. In 1979 both young roach and perch were relatively scarce in Farnborough and unsubstantiated information from anglers suggests that many adult fish were removed from the lake during the

winter of 78/79 (by Leisure Sport Ltd.). Plankton net collections made in spring 1979 contained many large Daphnia longispina, in contrast to previous years, evidence that some change in the size of the fishstock had occurred since the previous year and this reduction in density may have led to better growth of the O+ fish. Burrough and Kennedy (1979) suggest that improved growth rates of roach in Slapton Ley were due to a reduction in population density caused by infection by Ligula intestinalis. While Broughton and Jones (1978) showed that year to year variations in growth of O+ roach could be correlated with water temperatures above 14°C, Burrough and Kennedy (1979) do not ascribe the good growth of the 1976 year class of roach to the exceptional temperatures. Broughton and Jones (1978) suggested that temperature acts mainly through the food supply but they did not carry out any population estimates to determine how density also affected growth rates. It is therefore possible that the good growth of the roach in Farnborough in 1979 was due to a reduced fish population and the absence of the perch. It could also have been due to early hatching as shown by the specific growth rates, giving a longer growing season. White and Williams (1978) attributed the fast growth rate of the roach in Rye Meads sewage lagoons to both a low density of fish and highly productive water.

The size attained by the Farnborough perch at the end of their first year (6.45 cm/3.5 g) was not particularly large compared to other British perch populations (Table 4.14). There are many references to perch growth in the literature and the Windermere population in particular has been extensively studied. However, there have been fewer studies of O+ perch growth than of adult growth. Guma'a (1978a) examined the growth of juvenile perch in Windermere and recorded average sizes at the end of the year (December) of 7.7 cm/4.0 g in 1975 and

interestingly, only 6.5 cm/3.0 g in the hot summer of 1976. Rye Meads possessed the fastest growing perch populations on record in Britain, with first year growth of 12.0 cm in 1969 (White and Williams, 1978). The slowest recorded population was that of Dubh Lochan (Ghafi and Maitland, 1971) which only grew to 5.1 cm in the first year. Gee (1978) considered that the Farnborough perch had a slower growth rate than other gravel-pit perch populations. Goldspink and Goodwin (1979) suggest that where the effect of temperature on perch growth is not apparent as in Farnborough in 1976, (when the perch grew to 5.3 cm/3.0 g (Cook, 1979)), food may be limiting and in 1976 the O+ roach were as large as the O+ perch (Cook, 1979) and increased competition for food may have resulted in poorer growth of perch.

The seasonal pattern of perch growth was found to be similar to that of roach by White and Williams (1978) and Mann (1978), with growth occurring between April or May and October, although Mann related growth to water temperatures above 12°C whereas Le Cren (1958) showed that the growth of perch was correlated with the numbers of days when the water temperature was above 14°C. Coble (1966) however could not obtain a significant relationship between the mean water temperature over the growing season and growth of yellow perch and the Farnborough perch did not show any year to year variation in growth rate which could be attributed to temperature differences. This suggests that other factors were more important than temperature as in 1976. Pycha and Smith (1955) examined O+ perch growth and survival over 11 years and found a very similar lack of variation in size at the end of the first year (mean of 6.3 cm). They also found no correlation between growth and survival. Both Alm (1946) and Le Cren (1958) found that growth of O+ perch was not density dependent. On the other hand, Mann (1978) recorded rapid growth in perch over 1 year in the River Stour and attributed it to low density

plus a diet consisting predominantly of cyprinid fry.

The large fluctuations in year class strength shown by the O+ perch in Farnborough are typical of many perch populations (Le Cren, 1958; Thorpe, 1977a). Survival of O+ perch has been significantly related to temperature only in years of extremes (Koonce et al, 1977). The measurements necessary to demonstrate whether this was the case in 1979 were not made during the present study, although no marked differences in temperature compared with other years occurred during the summer of 1979.

Year class strength has also been related to the density of older cannibalistic perch (Le Cren et al, 1977). The total perch population in Farnborough in 1976 was estimated to be 5.4 g/m^2 (17% of total fish biomass), (Cook, 1979). These were nearly all O+ perch so that it is possible that with good survival into the next year they preyed upon the 1977 year class of perch, reducing their survival, although they would be expected to take roach fry as well. A population estimate of all fish species was carried out in Farnborough in autumn 1977 and the largest category of fish caught was of perch between 8 cm and 11 cm, the 1976 year class. Few larger perch were caught and in general perch tended to be very short lived in the gravel pits (Gee, 1976). Therefore, with the poor survival of the 1977 year class and poor survival of adults of the 1976 year class (although this was not determined quantitatively) the 1978 perch would have been relatively free from predation and were indeed far more abundant than in either the preceeding or succeeding years.

To relate year class strength and growth rates to diet in both species would require a greater knowledge of the population dynamics of both the young fish and the adults than was obtained here and so further discussion of these relationships would be mere speculation.

Roach are typically fish of slow moving or still lowland waters, at the extreme of their distribution in N. England. Perch on the other hand are common in cold oligotrophic waters (and did not grow particularly well in the exceptionally warm summer of 1976) and may be at a disadvantage when inhabiting eutrophic lowland lakes populated by roach. The feeding habits of these two fish species are also basically dissimilar as roach are omnivorous and adult perch are piscivorous. Before proceeding to the discussion of feeding the variability of their diets will be discussed.

The variation in species composition of the diet of individual fish poses an analytical problem which has been discussed by many workers. Mann and Orr (1969) found that variation within diet samples was greater than that between monthly diet samples, making it impossible to determine whether diet changed significantly with season. Egglishaw (1967) found considerable variation in the numbers and weight of invertebrates in the stomachs of samples of 10 or more young salmon and trout and thought that much of it was due to the distribution of prey organisms and to the heterogeneity of the feeding environment. Variation in diets of perch has been attributed to the presence of both plankton and benthic specialists in a population (Il'ina, 1973; Chodorowoski, 1975; Noble, 1975).

Ricker (1937) in an examination of the diet of juvenile sockeye salmon stated that if two planktivorous fish ate considerably different proportions of a food species, then they must be able to distinguish and select them, with each showing different prey preferences. He referred to such variation as individual idiosyncrasy.

It is feasible that roach should exhibit less variation in diet than perch because of their shoaling habit and as has been shown in this study, their tendency to feed on aggregated prey. It was expected that

the transformation of numbers to percentage composition would reduce this variation: that this was not the case may have been due to the small range of the numbers of organisms in the guts. Eggers (1976) has shown that the numbers of aggregated prey available to individual members of a school of fish varies with the position in the school and this too may result in individual variations in diet.

As so few perch were examined little discussion of their variability can be made but no evidence of specialists on one or another type of food was obtained. Craig (1978) attempted to relate the weight of stomach contents to the size of perch but found no significant relationships, which suggests that workers who use average weights of food consumed as an indication of feeding intensity are oversimplifying the situation (Hartley, 1947; Hellawell, 1972). One notable feature of the present study was the absence of fish with empty guts. Even in the winter most guts examined contained some food, possibly accumulated and digested slowly.

The study of diurnal feeding patterns in fish and the related study of food consumption rates form a very large part of modern fish feeding biology. These topics have been less well investigated in young coarse fish. Lightfoot (1976) examined diurnal feeding cycles of 0+ roach (size 7-14 mm) in the River Hull in June and obtained results very similar to those of the present study. Two feeding peaks were recorded by Lightfoot, one at 1000 hours and one between 2000 and 2200 hours. The smallest amount of food was found in the guts at 0230 hours and the cessation of feeding was coincident with darkness. However, the lowest number of food items consumed also coincided with low tide in the river. He found considerable variation between individual fish in each time sample as was found in the present study. Grigorash et al(1973) also examined diurnal feeding patterns in lacustrine 0+ roach and

observed that there were usually two feeding peaks in a day, the larger occurring in the evening. They also recorded considerable variation in the pattern with changing season and also in different years. Guma'a (1978b) found that O+ perch had two feeding peaks at dawn and dusk and did not feed at night except in June when the nights were short. Alabaster and Robertson (1961) recorded increased activity at dawn and dusk in roach and perch and correlated it with changes in light intensity. They also found that non-lethal increases in temperature caused increased activity in fish and it is possible that the high temperature in the afternoon of 7 July may have affected the feeding pattern of the roach during the 24-hour study carried out in Farnborough.

The occurrence of two feeding peaks in a day, often at dawn and dusk is characteristic of many fish species. Keast and Welsh (1968) found such a pattern for yellow perch in Lake Opinicon, with the largest peak occurring in the evening. These two peaks were less marked in the roach in Farnborough on the second sampling occasion when no significant cessation in feeding occurred during the day.

Perch possess a well documented pattern of feeding behaviour (Thorpe, 1977a). O+ perch are planktivorous when small (Smyly, 1952a; Guma'a, 1978b; Cook, 1979). As they grow they switch to benthic feeding and finally become piscivorous. This can occur before the end of the first year. The diet of O+ perch appears to be fairly uniform. The Farnborough perch showed a preference for Daphnia and cyclopoid copepods. These species were also selected by O+ perch in Windermere (Guma'a, 1978b). The diet of O+ perch in Slapton Ley consisted of Cyclops spp., Diaptomus gracilis and Daphnia spp. (Craig, 1974a). In laboratory experiments Furnass (1979) found that O+ perch preferred

Diaptomus to Daphnia. The preference for usually larger animals may be caused by their more rapid movements which elicit a feeding response at a threshold speed of 2 cm/sec. (Boulet, 1953). Perch have been referred to as ambush predators (Guma'a, 1978b; Cook, 1979; Furnass, 1979), which sit and wait for prey to pass by, the prey movements eliciting the feeding response. The term is usually applied to solitary predators (Schoener, 1976) whereas Deelder (1955) has shown that perch hunt most efficiently in packs. Perch behaviour may however depend upon the type of prey consumed as Il'ina (1973) observed that while piscivorous perch hunted down their fish prey, planktivorous perch behaved differently, remaining fairly stationary, but in schools. Personal observations of perch movements indicated that they remained in groups even when relatively large (6.0 cm). These aspects of perch behaviour and their effects on prey consumption would merit further study.

The diet of larger O+ perch in Windermere included chironomids and other benthic invertebrates (Guma'a, 1978b). The greatest difference between the Farnborough perch and other perch populations was the exclusively planktivorous feeding habit throughout the first year, with chironomids contributing only a small portion of the food (2%). It is not known whether this was due to a greater abundance of planktonic food items or to a lack of benthos. Personal observation indicated no lack of macro-invertebrates in the weedbeds in Farnborough but the perch may have faced competition from the carp and tench present (forming a high biomass of slowly growing fish) (Gee, 1976; Cook, 1979). It is also possible that the numbers examined were too small to provide an accurate representation of all the feeding modes present in the O+ perch population as it has been shown that perch populations can contain groups with different feeding habits. Il'ina (1973) carried out a

detailed investigation of the behaviour of the progeny of a single pair of perch parents in experimental ponds. The young perch soon formed into three ecologically distinct groups; a few large piscivores, many medium sized benthic feeders and some small plankton feeders. She regarded this as evidence for plasticity of the species enabling the offspring to fill all ecological niches in the habitat. The numbers of perch assuming each role depended on the food supply and population density and all were capable of switching to other modes of feeding given the correct prey size. This appears to be a case of resource partitioning based on individual variation in initial growth rates in artificial conditions. There is no doubt that an early rapid growth rate allows perch to take full advantage of available resources by providing the fish with a choice of food. There is no reason why the three feeding modes should be present in a wild perch population particularly when other species are present. Craig (1974a) did not find any evidence of different feeding modes in the juvenile perch in Slapton Ley. As well as there being no evidence of benthic specialists in the samples collected in Farnborough, there was no obvious increase in the percentage of macro-invertebrates in the perch diets between the first samples examined (0.3%) and the last (0.6%). The peak occurrence of macro-invertebrates was 4% in the small perch examined in late July.

Various workers have found that perch take up the piscivorous habit at various sizes; 9 cm (Mann, 1978); 14 cm (Craig, 1974a); over 18 cm (Allen, 1935). Smyly (1952a) reported cannibalism in very young perch larvae in Windermere but Guma'a (1978b) found no evidence of cannibalism in young Windermere perch up to 7.7 cm. Healey (1954) found that while some perch fry were cannibals most of the population under study were plankton feeders. No fish remains were found in any of the perch guts examined from Farnborough although a variety of small

fry (rudd, tench) were available but the perch may have been too small to be piscivorous.

Poor growth leading to stunted populations of perch has been linked to the failure to become piscivorous (Alm, 1946; Deelder, 1951; Shafi and Maitland, 1971). The switch to this mode of feeding usually follows a period of benthic feeding and planktivorous perch are more unlikely to make the transition. The most important factor is probably the availability of small prey species as observed by Deelder (1951) and Mann (1978). Shafi and Maitland (1971) also observed that growth rates of adult perch in Dubh Lochan slowed down from what they considered a good start in life when forced to rely on benthic food in the absence of small fish on which to prey. Adult perch with a continuing planktivorous habit can have poor growth rates (Nyberg, 1979), possibly because the anatomy and physiology of their alimentary canal are adapted for fish eating. Nyberg (1979) considered it to be energetically disadvantageous for large perch to feed on small particles.

Jezierka (1974) showed experimentally that perch fed on fish grew better than perch fed on Tubifex. This data did not take into account density relationships as the perch were kept singly and over-fed. Data interpretation was complicated because the experiments were carried out on different sized perch at different times of the year. However, she stated that the perch fed on fish consumed a larger daily ration than those fed on Tubifex (although the data do not show this). On the other hand Healey (1954) did not find poor growth associated with the consumption of crustacean plankton in Irish lakes. However, her data are presented as percentage occurrence with no measurement of food volume so that the few sticklebacks shown as occurring in the diet may have contributed most of the bulk of the food. More convincingly, Klemetsen (1973) studied a lake in Norway where a part of the adult

perch population was planktivorous but not stunted. The perch were caught in the open water and were feeding like size-selective planktivores. These studies suggest that the relationship between perch growth and the type of feeding plus the size of the food may be more complex than generally stated. The average growth rates of the Farnborough perch may have been caused by their planktivorous habits but why this should be so cannot be satisfactorily explained.

0+ roach usually eat algae, rotifers and microcrustacea, after which the diet may include chironomid larvae and other insects. Adult roach show considerable flexibility in their feeding in contrast to perch. They can remain planktivorous with little deleterious effect on growth (White, 1975; Cook, 1979), they can become benthic feeders (Hartley, 1947; Mann, 1973) and some populations feed on macrophytes, usually when animal food is scarce (Cragg-Hine and Jones, 1969; Prejs and Jackowska, 1978). As mentioned in Chapter 1, there have been very few studies of the feeding of 0+ roach and only the investigations of Lightfoot (1976) and Cook (1979) included an examination of the food supply. A further complication is that most of these studies have been on river populations (Hartley, 1947; Mann, 1973; Lightfoot, 1976) where planktivorous feeding would not be commonly expected, although the diet of the 0+ roach examined by Lightfoot (1976) in the River Hull consisted of nauplii, rotifers and chydorids (possibly swept into the river from still backwaters).

The diet of the 0+ roach in Farnborough was truly planktonic as 78% of the food was of zooplankton (Ceriodaphnia, Bosmina, Cyclops and Daphnia). Few benthic organisms ocurred in the guts. Of the many chydorids present in the lake, only the more common species were eaten by the roach and not to any great extent. Few nauplii were eaten

although the equally small Keratella spp. were sometimes abundant in the guts suggesting that they were eaten during open-water feeding. The absence of the large Simocephalus from the diet was interesting as the larger Sida was a common diet item. Simocephalus may have been protected from predation by its more benthic habit as suggested by Brandl (1963) who reported a similar finding. The diet of the 1976 year class, recorded by Cook (1979) was very similar to that in 1977, consisting mainly of Bosmina and Ceriodaphnia, plus rotifers and some Daphnia. There were far fewer Sida in the guts but as Cook (1979) did not sample in the vegetation it is not known whether Sida was less abundant in 1976.

The term optimal foraging was introduced by MacArthur and Pianka (1966) to denote a feeding strategy which obtained maximum gain for least expenditure of energy, involving considerations of prey food value and size, pursuit, capture and handling times. This idea has been developed by other workers and reveiwed by Pyke et al (1977). Size-selective predation has been related to optimal foraging in two ways. Firstly the larger the prey the greater the amount of energy consumed in one bite, which seems to be of importance to perch. Secondly, visually hunting predators expend least energy in capturing the most visible prey which is taken to be the largest (although Zaret (1972) has shown that apparent size and real size are not always the same to the predator). However these factors do not seem to have been of importance to the O+ roach in Farnborough as the optimal diet appeared to consist of the most abundant food particles with certain attributes: small, relatively slow moving and existing in aggregations. For a shoaling fish feeding on relatively stationary planktonic food items the pursuit time is very short. Werner (1974) measured handling time (capture to swallowing) in bluegill sunfish and found that it

increased exponentially with prey size (PS) for a given fish mouth size (MS). This means that the largest prey item is not always the cheapest in terms of energy expenditure. Werner found that the optimum prey size occurred at a prey size to mouth gape ratio of 0.59 regardless of fish size in bluegills and found similar handling time/PS*MS ratios for another fish species. The mouth gape of a 4 cm roach is 1.88 mm (Cook, 1979) so that theoretically a 1 mm Daphnia could be consumed. Little evidence for size-selective predation was found in the roach in Farnborough and no increase in the size of prey with increasing fish size could be detected. Cook (1979) demonstrated a preference for large Daphnia by adult roach which at the same time also consumed larger quantities of small Bosmina, so that it is possible that the occasional large particle attracted attention and evoked a feeding response which was secondary to the main one. Larger, energetically more valuable prey items were on the whole ignored by the O+ roach, (apart from Sida which will be discussed later) suggesting that the optimal diet was one in which pursuit time was reduced to a minimum. Roach are shoaling fish and the small roach examined would have possessed a small visual field. Szlauer (1965) measured the ability of crustacea to escape a pursuing tube and found Bosmina to be the slowest. Cyclops can swim much faster and the few eaten by the roach were small. Drenner et al(1978) showed that differential capture probabilities of zooplankton by non-visually feeding fish led to consumption of Cladocera rather than Copepoda which could escape from a siphon tube. The roach appeared to prefer easily caught small food items. Other studies are in agreement with this finding. Ivlev (1961) found that roach switched to more easily caught prey when the habitat was altered to give the previously preferred food species cover. Morrison (1977) carried out prey selection experiments where roach (3.3 cm) were presented with a mixture of Diaptomus (70%),

Daphnia (20%) and Polyphemus (5%). The roach took no Diaptomus from this mixture, concentrating upon Daphnia (10%) and Polyphemus (73%). Polyphemus is very visible and slow moving and as will be shown in Chapter 5, can have an aggregated distribution in the water. Estabrook and Dunham (1976) produced a model of optimal foraging which predicted that absolute abundance of a prey item was the overriding parameter in the determination of optimal diet, and this was also the case in Farnborough. Eggers (1976) has argued that the schooling habit of fish reduces foraging efficiency, or prey consumption with the exception that when prey occurs in dense aggregations there may be some advantage to be gained from shoaling as the visual field is extended and the chances of prey encounter increased. The preference of the O+ roach for the two most abundant aggregated cladocerans was very marked.

The size-biased consumption of Sida by the O+ roach does not fit into the optimal diet of small, easily caught food particles. It is a large animal with a large black eye and was presumably very visible to the small fish (Zaret, 1972). However, relative availability of different instars is not known nor the relative mobility of juveniles and adults so that the roach (and perch) may have been eating those sizes most readily available. They were eaten during periods of peak abundance when dispersal of the Sida population would have been greatest. Roach, although planktivorous, are not filter feeders (Ricker, 1937). They possess a protrusible mouth which enables them to snap up entire food particles (Al'Hussaini, 1949) and they may have picked the Sida off the P. natans leaves. The energy content of one Sida was the equivalent of 30 Bosmina or 15 Ceriodaphnia, assuming similar calorific values per unit weight ((Vijverberg and Frank, 1976). Optimal foraging theory predicts that if easily consumed, the larger items should be preferred. However, Guissani and De Bernardi (1977)

have shown that large uncommon Bythotrephes, although selected by Coregonus in Lago Maggiore, were less well utilised (assimilated) than much smaller Daphnia, confounding optimal foraging theories, so that fish may not always take the most rewarding food. Sida was not macerated in the guts of the roach as much as the smaller Cladocera and may not have been assimilated to the same extent. Much of the weight of Sida may have consisted of chitin which is not digested so that this may be another example of roach diet being determined primarily by abundance and secondly by visibility.

The O+ roach also exhibited switching in their feeding from Bosmina in the open water to Ceriodaphnia in the weedbeds. Murdoch et al(1975) described a similar situation in the laboratory with guppies fed on Drosophila at the water surface and Tubificids on the tank bottom. As the relative abundance of each prey changed so did the diets of the guppies. They switched to disproportionate feeding on whichever prey was more abundant. The switching was caused by a change in the time spent in each part of the tank and was thought to be due to changing reward rates. When both foods were equally abundant most of the fish ate one or other prey item, exhibiting only weak preferences. This is paralleled by the results of this study where the roach fed either in the open water or in the weedbeds with very few roach having guts containing both types of food (see Fig. 4.10) at any one time.

The sampling of the microcrustacea showed that Ceriodaphnia was most abundant in weeds such as P. natans and in the plant/open water interface. Therefore it is possible that the roach inhabited the edges of the weedbeds, utilising the food resources of both areas while retaining the use of the plants for shelter if necessary. The preference for Bosmina when abundant may have also been due to its occurrence in the open water as it may have been easier to feed in this

homogeneous environment, with the switch to feeding in the habitat containing stationary structures taking place only when necessary. Crowder and Cooper (1979) showed that the feeding efficiency of bluegill sunfish dropped in weedbeds and it is possible that the visual cues of fish are upset in vegetation. Vince et al (1976) found that large fish kept in a tank containing introduced structures (grass stalks) could not feed size-selectively and they suggested that the increased structural complexity of the littoral region forced larger fish to feed in the open water while small fish remained able to exert their preferences among weeds.

Cook (1979) attempted to relate changes in the specific growth rates of the 0+ roach to changes in the consumption of Bosmina in 1976. He provided some evidence to show that consumption of Bosmina occurred at the same time as an increase in specific growth rates. However, the water temperature also fluctuated and specific growth rates can in any case fluctuate within their normal seasonal decline. The highest specific growth rates in 1977 occurred between 22 August and 2 September. The diet in that time did change from a predominance of Bosmina to a predominance of Ceriodaphnia with peak abundance of Bosmina in the lake being recorded on 22 August. Therefore, there was some evidence to show that the consumption of small particles did influence the growth rate but a much more detailed study would be required to illustrate this conclusively.

The roach can best be described as generalist feeders (Schoener, 1971) and opportunists, with flexible feeding habits and little innate preference for particular prey species. In contrast the perch exhibited marked preferences for certain prey items, Daphnia and copepods. The overlap coefficients show the generalist diet of the roach and the more specialised diet of the perch. There was little evidence to support the

statement that competition for food occurred between the two species, but a more thorough examination of the perch diets would be required to state categorically that competition did not occur.

Cook (1979) concluded that 0+ roach and perch avoided interspecific competition through resource partitioning, the roach preferring Cladocera while the perch consumed Cyclops, as was found in 1977. He also noted differences in behaviour, the roach seeking small slowly moving prey while the perch ate faster moving objects. He suggested that some spatial segregation also occurred with the perch remaining in the weedbeds while the roach roamed more widely, although no information in support of this was obtained. Gerritsen and Strickler (1977) have described two feeding strategies which can occur together; one being that of a cruising predator which consumes slow moving prey encountered in its path (the roach) and one being that of an ambush predator remaining stationary and only reacting to fast moving objects passing across its field of vision (the perch). If the roach and perch could be placed into these two categories this would enable them to co-exist in the margins of the lake.

The question of whether the macrophytes were of importance is still partly unanswered. The comparison of the diets with the microcrustacean samples showed that much of the food of the roach did come from the weedbeds as did most of the perch food. Farnborough did not contain many potential predators of the small fish as there were no pike in the lake (unconfirmed anglers reports) and few large perch, although great crested grebes were present. Indeed, the most abundant predators were probably the larger invertebrates in the weedbeds which can prey on newly hatched roach (Zuromska, 1967). Therefore the weedbeds were not absolutely necessary for cover and possibly not wholly advantageous. It is interesting that most overlap in the diets of the

two fish species did occur through the consumption of weedbed microcrustacea, Sida and Ceriodaphnia. It is possible that the diversity of the habitat allowed the two species to co-exist. It is also possible that in the absence of the macrophytes the 0+ roach would have been in direct competition with both the adult roach (Cook, 1979) and possibly the 0+ perch. If one accepts that the weedbeds were partially responsible for the size of the Ceriodaphnia population then their absence combined with the cyclical nature of the Bosmina population, further depleted by predation by the roach, would have resulted in the roach having to feed on energetically less favourable foods such as the cyclopoid copepods. Although the outcome of any competition for food would depend upon relative population sizes of the competing fish, in a lake as densely populated as Farnborough it is unlikely that good survival and growth of juvenile fish would occur if the macrophytes were removed.

CHAPTER 5. THE CAGE EXPERIMENTS IN YATELEY.

5.1 Introduction.

Enclosure experiments were carried out in Yateley in 1978 and 1979 to determine whether the presence or absence of aquatic macrophytes (simulated by artificial substrates) influenced the growth, diet and survival of 0+ roach and perch. Free-floating wooden framed cages anchored in the centre of the lake were constructed and installed as described in Chapter 2 and artificial substrates were placed in half of the cages. These will be referred to as the weed cages (CW) and those without artificial substrates as the non-weed cages (CNW).

Of the eight cages used in 1978, four were stocked with 0+ perch, (2 weed, 2 non-weed), two with 0+ roach (1 weed, 1 non-weed), as shown in Table 5.1, and two with 1+ roach (from which only the plankton data were used). The numbers of 0+ roach were limited because of high mortality during initial capture and stocking whereas the perch (which were also far more abundant in Farnborough in 1978) survived this handling better. In 1979 10 cages were stocked with 0+ perch and two with 0+ roach, (see Table 5.1) as again the roach showed poor survival during the journey from Farnborough. The fish were caught at the beginning of July in both years when the roach were about 2cm and too large to escape through the 3.0mm mesh. At the beginning of the experiment in 1978 the possibilities for growth and survival in the cages were not known and to ensure that some data were obtained, the fish were sampled and measured at regular intervals. Some were also removed for diet analysis. Therefore, although the numbers of fish in a cage had to be low enough to prevent density dependent effects interfering with growth rates and survival, sufficient fish had to be stocked to allow for mortality and for some to be removed. For this

reason large numbers of perch were used in 1978. During the planning of the experiment in spring 1978 there was little published information on the natural densities of 0+ coarse fish with which to compare those used in these experiments. In 1979 as there was now evidence that the fish would survive, they were left undisturbed, and so fewer fish were used.

One recurrent problem in enclosure experiments is that fine netting can become clogged with periphyton possibly resulting in stagnant water inside the enclosures. In 1978, there was a small amount of periphytic growth on the cages; this was removed by scrubbing once and very little reappeared after this, probably partly due to grazing by small snails which appeared in large numbers on the mesh. There was much greater periphytic growth in 1979 and this, combined with the deposition of dead Ceratium thecae on the mesh, meant that the cages had to be scrubbed every week to keep the mesh clear.

The cages provided a substrate for larger invertebrates to settle upon and many Zygoptera and other insects were observed on the tops of the cage frames. A large snail population had built up on the netting by the end of the experiment and so, as well as enclosing the water, the mesh itself provided a diversification of habitat in addition to that provided by the artificial substrates.

A few problems arose in 1978:

1. The seams and collar joining the netting of one cage rotted so that at some stage during the experiment fish movements in and out of the cage were possible. This was cage 4 (perch with weed), so that data from only three perch cages were used in the final analysis. The nets were resewn with stronger nylon in 1979 to prevent re-occurrence of this problem.
2. The artificial substrates became coated with periphyton and progressively sank to the bottom of the cages. They were modified as

described in Chapter 2.

3. In Chapter 2 it was mentioned that the cages had to be sawn apart at the end of the experiment. This caused no immediate trouble but was a problem in the next year.

In 1979 the cages were both smaller than previously and of different sizes (see Table 5.1) which resulted in slightly different stock densities in each fish cage. The mean densities for each fish species are given in Table 5.2. The weed and non-weed cages were selected so as to equalise the total volumes used for each treatment, which were 19.4 m^3 for non-weed and 19.1 m^3 for weed. It was assumed that with the lower fish densities used in 1979 these small differences in density would not affect the results. The only other problems encountered in 1979 were the net fouling already mentioned above and a bird problem as the polystyrene floats provided a perch for ducks and coots. One cage was a particularly favoured coot roost and even the addition of extra buoyancy did not prevent submersion of the cage corners at times.

Periodic measurements of dissolved oxygen and water temperature showed no differences inside and outside the cages.

The cages were emptied on 15 September in 1978 and on 11 September in 1979. The duration of the caging periods over which growth was measured were as follows;

1978 Roach	65 days	1979 Roach	63 days
Perch	52 days	Perch	58 days

5.2 Survival and growth of the 0+ roach and 0+ perch in the cages in 1978.

Table 5.1 shows the numbers and mean size of the fish at the end of the experiment. Table 5.3 shows the numbers of fish taken out of the

Table 5.1 The numbers of roach and perch in the cages at the beginning and end of the experiment, with the date of stocking and the final mean length and weight for each cage.

FISH IN					FISH OUT			CAGE
CAGE NO	TYPE	SP	NO IN	DATE	NO OUT	L	W	VOL M^3
1978								
1	CNW	R	70	1	21	4.5	1.11	4.0
3	C W	R	63	1	7	5.1	1.72	4.0
2	CNW	P	150	2/3	30	5.3	1.78	4.0
5	CNW	P	150	3	23	5.1	1.43	4.0
4	C W	P	150	2/3	CAGE BROKE UP			4.0
7	C W	P	150	3	24	5.6	2.11	4.0
1979								
11	CNW	R	43	4	26*	5.3	1.67	3.0
5	C W	R	43	4	30	5.3	1.66	3.2
1	CNW	P	31	5	31	5.3	1.43	2.8
2	CNW	P	30	5	30	5.3	1.41	3.9
7	CNW	P	34	5	34	5.0	1.24	3.3
10	CNW	P	30	5	23	5.4	1.53	3.2
12	CNW	P	30	5	21	5.2	1.35	3.2
3	C W	P	32	5	32	5.5	1.62	3.2
4	C W	P	33	5	33	5.7	1.87	3.5
6	C W	P	30	5	24	5.9	2.24	2.9
8	C W	P	30	5	15	5.3	1.52	3.1
9	C W	P	30	5	30	5.6	1.84	3.2

* + 2 Rudd

KEY

CNW = non-weed cage
C W = weed cage
R = roach
P = perch

Date 1=12.7.78
Date 2=18.7.78
Date 3=25.7.78
Date 4=10.7.79
Date 5=15.7.79

L=mean length in cm
W=mean wet weight in g

Table 5.2 Data on size of fish used, density at stocking and size of the cages.

Size of the fish at stocking			
	L	W	Date
1978 Roach	2.2	0.12	1
Perch	4.0	0.97	2
Perch	4.4	1.08	3
1979 Roach	2.8	0.29	4
Perch	4.0	0.69	5

Mean cage volume in 1979
$3.2 \pm 0.2 m^3$

Mean fish density at stocking

Roach	Perch
1978 1.99 g/m^2	39.5 g/m^2
1979 4.0 g/m^2	5.7 ± 0.4 g/m^2

Table 5.3. Total mortality and handling of roach and perch in the cages in 1978 and 1979.

TYPE	NO IN	SAMPLE	NO OUT	MORTALITY n	%	HANDLED n	%
1978							
1 CNW R	70	18	21	31	60	15	29
3 C W R	63	18	7	38	84	17	38
2 CNW P	150	30	30	90	75	45	38
5 CNW P	150	22	23	105	82	55	43
7 C W P	150	17	24	109	82	15	11
1979							
11 CNW R	43		28	15	35		
5 C W R	43		30	13	30		
CNW P	155		139	11	7		
C W P	155		134	16	10		

Initial handling at the beginning of the experiment in 1978.
Cage 1 CNW R 70 from holding cage.
Cage 3 C W R 48 from holding cage and 15 without holding
Cage 2 CNW P 150 from holding cage.
Cage 5 CNW P 150 from lake without holding
Cage 7 C W P 150 from lake without holding

The figures for 1979 perch are the means of all cages in each treatment.

Table 5.4 Mean length and weight of the 0+ roach and 0+ perch in each type of cage during the experiment in 1978.

DATE	ROACH CNW L	n	W	n	ROACH CW L	n	W	n
12.7	2.1	17	0.12	17	2.1	17	0.12	17
27.7	2.7	23	0.25	19	2.7	23	0.25	19
1.8	3.0	9	0.30*	8	3.2	11	0.37*	11
8.8	3.2	6			3.4	8		
16.8	3.7	18	0.70	7	3.7	16	0.70	7
15.9	4.5*	21	1.11*	21	5.1*	7	1.72*	7
DATE	PERCH CNW L	n	W	n	PERCH CW L	n	W	n
25.7	4.4	39	1.10	41	4.4	17	1.10	17
1.8	4.6	19	1.32	10	4.8	17	1.42	9
8.8	4.7	44			4.5	18		
16.8	4.7*	40	1.31*	10	5.1*	18	1.94*	9
22.8	4.8*	37			5.1*	6		
15.9	5.2*	53	1.65*	53	5.6*	21	2.11*	21

* significantly different P<0.05 (t-test)

Key as in Table 5.1

Table 5.5 Final mean sizes of the caged 0+ roach and 0+ perch in 1978 and 1979 with the 95% confidence limits.

		L	95% CL	W	95% CL	n
1978						
ROACH	C W	5.1	4.6-5.7	1.72	1.20-2.43	7
	CNW	4.5	4.3-4.7	1.11	0.94-1.3	21
PERCH	C W	5.6	5.5-5.8	2.11	2.07-2.15	21
	CNW	5.2	5.1-5.3	1.65	1.55-1.74	53
1979						
ROACH	C W	5.3	5.1-5.4	1.66	1.57-1.77	30
	CNW	5.3	5.2-5.5	1.67	1.56-1.79	26
PERCH	C W	5.6	5.5-5.7	1.79	1.67-1.92	134
	CNW	5.2	5.1-5.3	1.38	1.31-1.46	139

Table 5.6 Specific growth rates of the caged 0+ roach and 0+ perch in 1978 and 1979.

	ROACH			PERCH		
A 1978	CNW	CW	LAKE	CNW	CW	LAKE
Gw	0.02	0.03	0.02	0.008	0.003	0.006
Time(d)	30	30	27	30	30	49*
B 1978						
Gw	0.03	0.04	0.04	0.009	0.01	0.01
Time(d)	65	55	64	52	52	84**
1979						
Gw	0.03	0.03	0.03	0.01	0.01	?
Time(d)	63	63	70	58	58	

a = Gw calculated over the last month of the experiment.
b = Gw calculated over the duration of the experiment.
d = days
* = 22.8.78-10.10.78, ** = 18.7.78-10.10.78

Key as in Table 5.1

cages for gut analysis (sample), the numbers removed, measured and put back (handled), and the numbers which were assumed to have died during the experiment. The experiment was not designed to measure survival, and there was little consistency in the survival rates, but some points are worth noting. Both species suffered high mortality in the weed cages, while the best survival was of non-weed roach (40%). (Mortality was calculated as the percentage of the initial stock (- sample) which died.) Perch survival was similar in all three cages ($\bar{x}$=20%), further interpretation is difficult because of the lack of replication. Both handling during the initial capture and transfer, and sampling disturbance during the experiment could have been responsible for fish mortality, and the two species may also have shown different responses to these factors.

a. Roach

The percentage of roach handled was greatest in the weed cage because the sample sizes were marginally higher than from the non-weed cage and this may have contributed to their poor survival, but some of these roach were also stocked out without holding in a cage after transport whereas all the non-weed roach were kept in a holding cage for a week prior to stocking. Recalculation of the weed roach survival based upon the numbers stocked from the holding cage reduced the mortality to 77% which was more similar to that of the non-weed roach (60%) but was still high. This suggests that the initial capture and stocking affected the roach less than the subsequent handling but as this was only slightly greater in the weed roach it is also possible that some other factor such as density or dissolved O_2 was also involved.

The combined mean size of the caged roach at the end of the experiment was 4.7 cm and 1.25 g, which was slightly greater, but not

significantly different (P>0.05) from the mean size in Farnborough (4.5 cm and 1.2 g). As the density of roach was similar to that in the lake (see Table 4.1) the growth rates can be compared and it is evident that enclosure did not retard roach growth. However, the weed roach were significantly larger than the non-weed roach in both length and weight (P<0.05) and the weed roach were also larger than the Farnborough roach, (P<0.05). Fig. 5.1 shows the growth in length and weight of the caged roach and Table 5.4 summarises the growth data obtained during the experiment. The 95% confidence limits have not been included in the figure for clarity but are given in Table 5.5. Both numbers and biomass were much lower in the weed cage than the non-weed cage at the end of the experiment and this reduced density may have led to the increase in growth rate of the weed roach. The separate effects of density upon mortality and growth rate will be discussed later but it is worth noting that the weed roach were larger (but usually not significantly (P>0.05) see Table 5.4) than the non-weed roach on all sampling occasions while the effort used to catch samples was uniform which suggests that up to 16 August similar numbers were present (although on 22 August no fish could be caught in either cage). Therefore, roach in the presence of artificial macrophytes did grow better than roach without but how significant this result is it is difficult to say because of the lack of replication. It is worth noting that the roach without artificial macrophytes still grew as well as those in Farnborough.

Condition factors were calculated as described in Chapter 4. The non-weed roach had a condition factor of 1.22 whilst that of the weed roach was 1.30 and that of the roach in the lake was 1.32, indicating that the non-weed roach were marginally lighter for length than the others but all were in good condition.

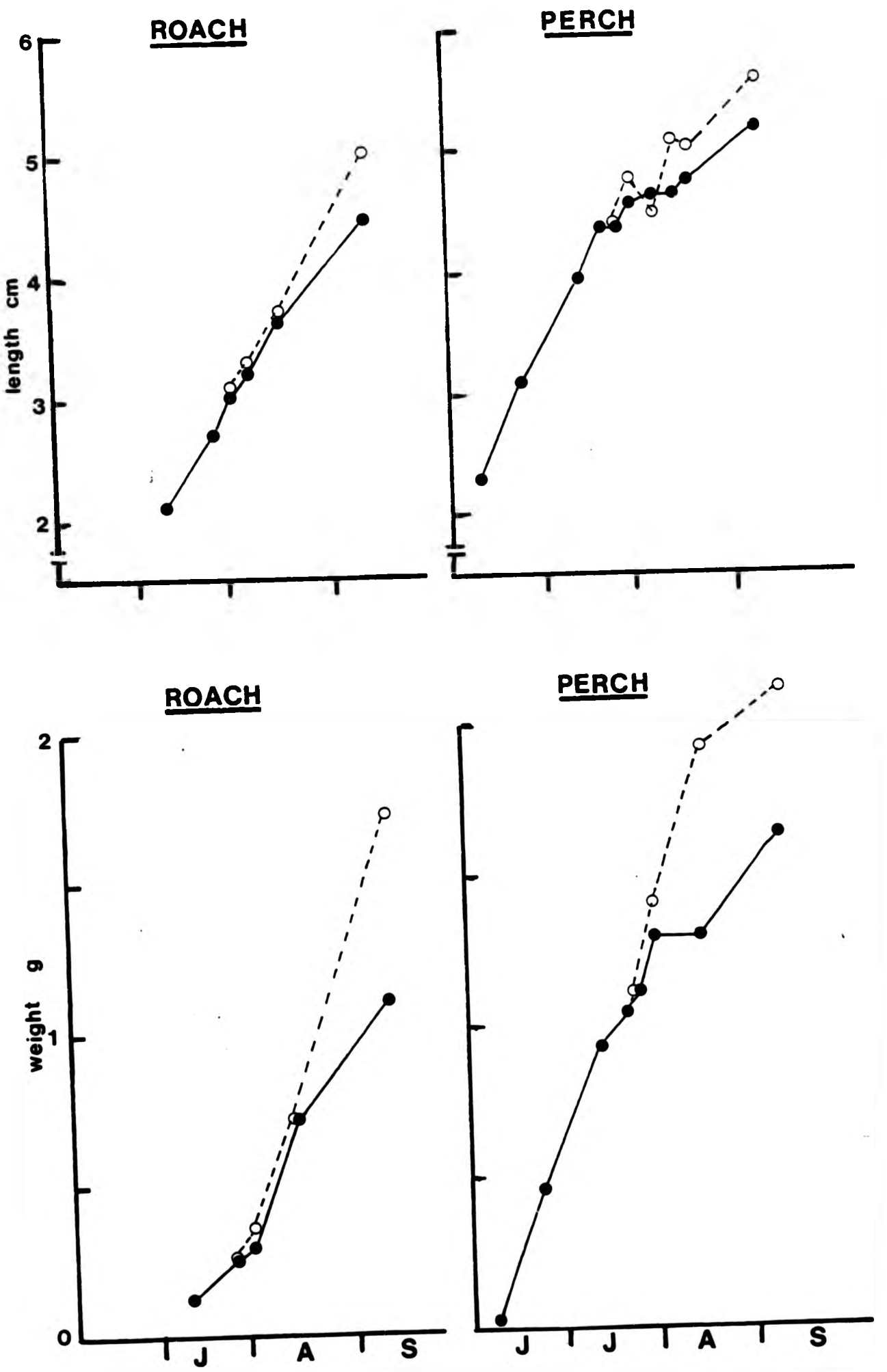


FIGURE 5.1 The growth in length and weight of the caged 0+ roach and 0+ perch in Yateley in 1978. Each point is the geometric mean of a sample.

o weed • non-weed.

Sample sizes are given in Table 5.4

A comparison of the specific growth rates (calculated as in Chapter 4) estimated on a daily basis both over the duration of the experiment and also over the last month of the experiment when the roach were not handled is shown in Table 5.6. The daily rate was calculated from the growth increments over both periods divided by the number of days, not from daily growth measurements. The difference in the growth rates of the non-weed roach over these two periods indicates that their growth slowed down over the last month as did that of the lake roach population, while the weed roach continued to grow at a fairly constant rate over the experiment and at a faster rate than the lake roach during the last month. It is also evident from the figure that the growth rate of the weed roach had not begun to level off as would be expected by mid-September as the water temperature fell below 14 °C.

b. Perch

The sample sizes of non-weed perch were usually larger than those of the weed perch because they were easier to catch and therefore more non-weed perch were handled. Despite this, their survival was better than that of the weed perch, as shown in Table 5.3. Although mortality was high in all the perch cages, handling during the experiment did not appear to be the major factor determining this mortality as the highest mortality occurred among the least handled perch in cage 7. Initial handling at stocking could have contributed to the poor survival in cage 7 as these perch were not held at the start of the experiment whereas those in cages 2 and 5 were stocked after holding for one week. The most likely cause of mortality amongst all the perch was the high stocking density which was similar to the carrying capacity for all species in many natural waters (Rudenko, 1971; Cook, 1979).

The final mean size of the caged perch was 5.3 cm and 1.77 g in

mid-September. The lake perch were not sampled between 22 August and 10 October and so the size in September was estimated from the growth curve in Chapter 4 as 6.0 cm and 2.7 g. Therefore, cage growth did not appear to be as good as lake growth. The density of perch in the cages at the start of the experiment was high (39.5 g/m^2) so that this was not surprising. However, as the density was the same in all the perch cages and the survival was similar, the growth rates of the weed and non-weed perch can be compared.

The weed perch (5.6 cm/2.11 g) were significantly larger than the non-weed perch (5.2 cm/1.65 g) at the end of the experiment (t-test, on all fish $P<0.05$), and both replicates of non-weed perch were smaller in length and weight (5.3 cm/1.78 g:5.1 cm/1.43 g) than the one remaining set of weed perch (see Table 5.1 and Fig. 5.1). Although both replicates of the non-weed perch were significantly different from one another ($P<0.05$) they were both also significantly smaller than the weed perch ($P<0.05$) which were on all but one sampling occasion larger than the combined non-weed perch. From the middle of August these differences were significant ($P<0.05$, see Table 5.3). There was a noticeable reduction in the growth rate of all the perch after stocking, as shown in Fig. 5.1 but whether this was due to handling or to overcrowding is debateable as their effects cannot be distinguished except that the largest perch (weed cage) were also those least handled but with lowest survival which would indicate that density exerted a greater effect than handling.

The weed perch had a condition factor of 1.20 which was slightly higher than that of the non-weed perch (1.17) but lower than that of the lake perch (1.25).

The specific growth rates were calculated as for roach and are given in Table 5.6. Those of the non-weed perch were faster than those

of the weed perch over the last month of the experiment. The figure for the lake perch is based on growth between the end of August and the middle of October when growth slowed down so that one can assume that it was higher during the period of the experiment. One can only speculate on whether the non-weed perch would have caught up in size with the weed perch if the experiment had been continued through September, although this is unlikely in view of the falling water temperatures.

5.3 Survival and growth of the caged roach and perch in 1979.

The experiment was repeated in 1979 with the following modifications: the roach and perch were all held for one week prior to stocking; they were not disturbed by sampling during the experiment and the perch were stocked at a reduced density. The numbers surviving in 1978 were used as an indication of the carrying capacity of the cages.

a. Roach

Table 5.3 shows the numbers of roach recovered from the cages in September 1979. In addition to the roach, cage 5(non-weed) contained two rudd of 5.5cm which were presumably mistaken for roach during stocking as very small roach and rudd can be difficult to distinguish in the field. They were included in the total for calculations of survival and final biomass in the cage as they are ecologically similar at this age but they were not included in the final growth measurements which relate only to roach. Survival was less good than expected as a third of the roach died in each cage. This represents the total mortality from all sources, both the initial handling and natural mortality during the experiment. Mortality could not be attributed to handling during the experiment in 1979 and comparison with 1978 shows that the non-weed roach (held prior to stocking) which were sampled during that experiment suffered 60% mortality. Another contributing factor could be density as

in 1978 the density was half that of 1979 because the roach were smaller which implies that while some of the mortality may have been induced by higher density in 1979, that of 1978 was mainly due to handling, overriding the beneficial effect of reduced density. It is also possible that the roach should have been given a longer holding period to recover from capture and transfer.

In 1979 the caged roach grew to a final mean size of 5.3 cm and 1.74 g which compared favourably with the previous year's growth in both the cages and the lake. However, the size of the roach in the lake was greater as they measured 5.9 cm and 2.5 g in mid-September. The possible causes of this rapid growth rate in the lake have been discussed in Chapter 4. In contrast to 1978, there were no differences at all in the size of the roach in the two cages (see Table 5.4 and Table 5.5) and as there were no differences in survival, the final biomass in each cage was also very similar. Therefore, the presence or absence of the artificial macrophytes did not appear to exert any influence upon growth and survival of the roach in 1979.

The condition factor of the caged roach was 1.17, similar to that of the lake roach, 1.22, so that neither was as heavy for length as in 1978.

The daily specific growth rates are shown in Table 5.6. They were the same for all the sets of roach and the same as that of the 1978 non-weed roach.

b. Perch

Table 5.1 gives the number of perch survivors in each cage in 1979 and Table 5.3 summarises the total numbers recovered from each treatment. Mortality in 1979 is difficult to assess because while it was thought that each cage contained 30 perch at the beginning of the

experiment, when the cages were emptied, four contained more than 30. The greatest discrepancy, in cage 7 (four extra perch and two roach) is explainable as this was the holding cage and although it was assumed to have been completely emptied at the end of the holding period it was not practical to remove the cage from the water. It is most likely that the extra one or two in the other cages arose from counting errors during stocking which only came to light at the end because the low stock density and minimal disturbance allowed very good survival. This explanation is reinforced by the fact that the total number removed at the end, 273, was similar to but lower than the 300 known to have been distributed between the cages, (by two people, rapidly on a hot day). A possible cause of the low number of survivors in cage 8 can also be given. This was the cage favoured by the coots and it is quite likely that some perch escaped.

The final mean size of the caged perch in 1979 was 5.4cm and 1.69g which was slightly longer, but lighter than the 1978 caged perch. Unfortunately, no lake perch were caught in September for comparison (see Chapter 4, section 4.2) but 1979 cage growth was poorer than any perch growth recorded in the gravel-pit lakes in other years, both during this and previous studies (Gee, 1976; Cook, 1979). Therefore, even with a reduced fish density the perch did not grow as well in the cages as in the lake. As in 1978, the weed perch were significantly larger than the non-weed perch ($P<0.05$ for length and weight) with all but one replicate being of greater length and all having a heavier mean weight, as shown in Fig. 5.2. There was some variation within treatments because the smallest sized replicate in each case was significantly different ($P<0.05$) from the largest and there was no difference between the largest non-weed replicate and the smallest weed perch but taking individual fish as replicates the overall difference

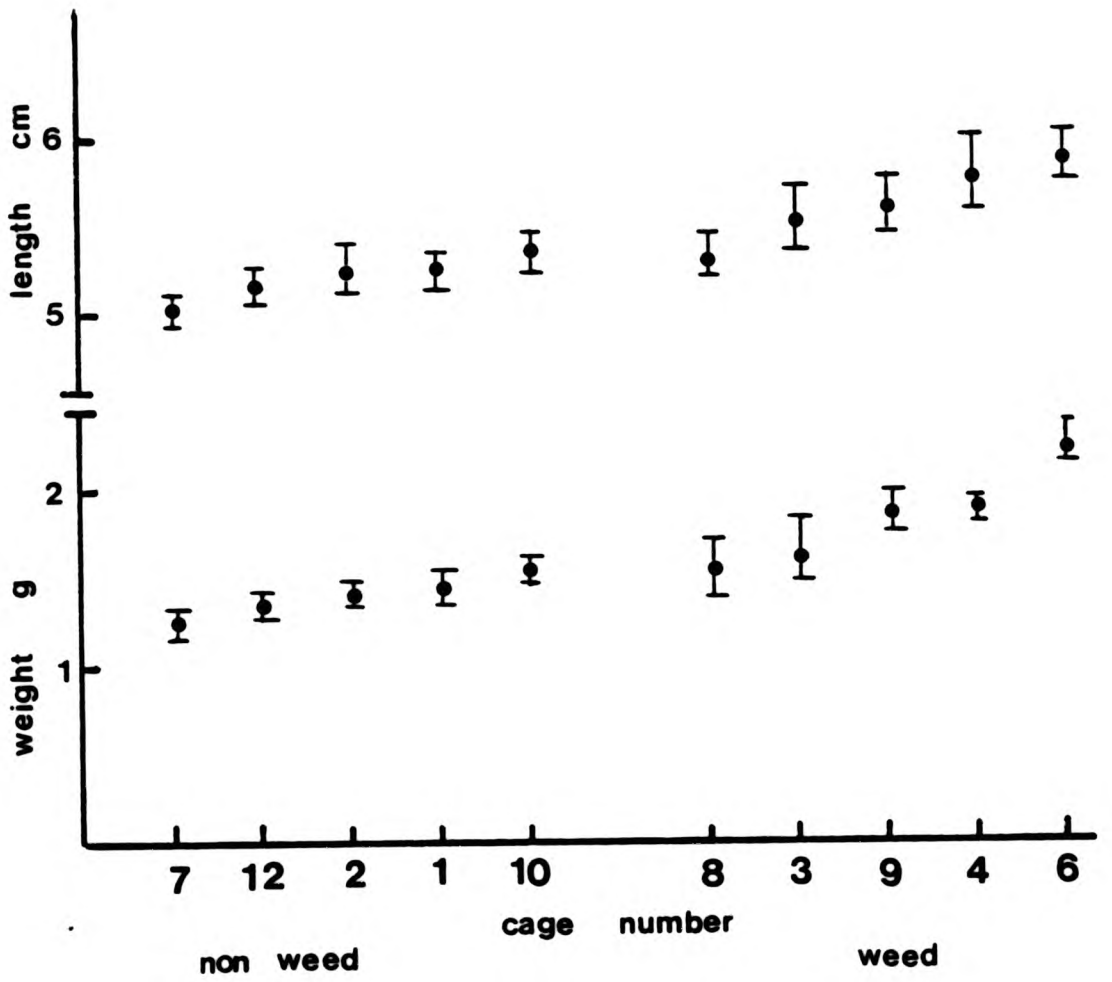


FIGURE 5.2 The geometric mean length and weight (plus 95% confidence limits) of each replicate set of O+ perch in the cages in Yateley in September 1979.
Cages 7 - 10 = non-weed cages
Cages 8 - 6 = weed cages.
Sample sizes given in Table 5.1

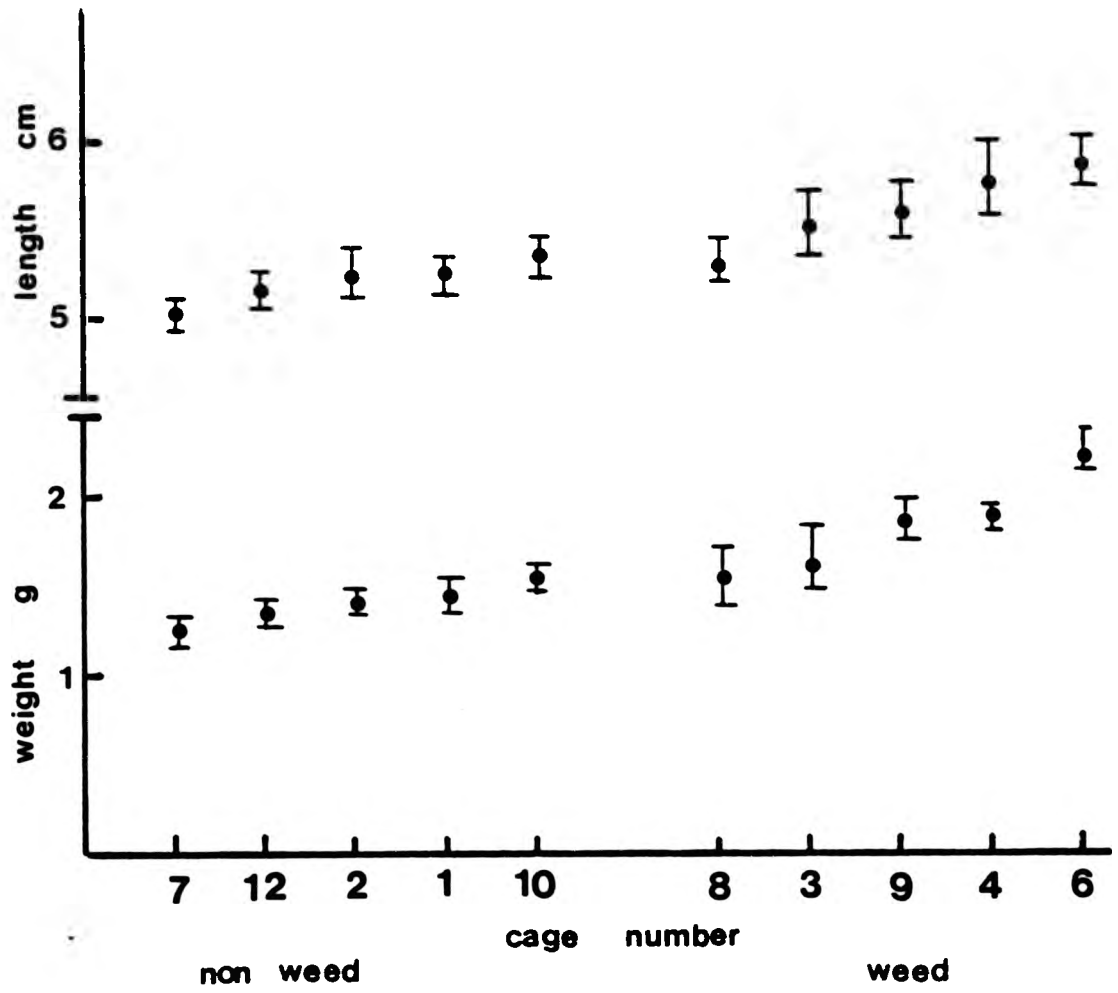


FIGURE 5.2 The geometric mean length and weight (plus 95% confidence limits) of each replicate set of 0+ perch in the cages in Yateley in September 1979.
Cages 7 - 10 = non-weed cages
Cages 8 - 6 = weed cages.
Sample sizes given in Table 5.1

was highly significant. Cage 8 which contained the smallest weed perch was the "coot cage" and it is feasible that the larger perch in this cage had escaped. The mean lengths of the weed and non-weed perch were the same as in 1978, 5.6 cm and 5.2 cm respectively. All the perch were lighter for this length than in 1979 but the perch stocked out were also lighter for length than in 1978. The condition factor of the non-weed perch was 0.98 and that of the weed perch 1.02

5.4 Estimation of fish production in the cages.

The estimation of fish production in each cage provides an alternative method of comparing fish with and without artificial substrates. Production is related to the overall performance of each cage as a fish producing unit rather than to the growth rates of individual fish, as has been previously discussed. There are various definitions of production which have been discussed by Le Cren (1972). Production here was calculated as the difference between the final biomass in a cage and the initial biomass i.e the production available for removal, or yield, discounting that lost through mortality and removal during the experiment. As samples of roach and perch were removed and measured at intervals during 1978, providing a minimum population estimate, it was theoretically possible to ascribe a mortality coefficient (Z) (Bagenal and Tesch, 1978) to the data to arrive at estimates of mean biomass present on each sampling occasion, from which production could be calculated as the sum of the growth increments. However, in practise, the exponential model did not provide a good fit to the data. An arithmetic model provided a better fit but probably overestimated survival as it assumed a constant mortality rate so that production appeared higher than it was. Therefore, the simpler method of calculating production from yield minus stock was used

although it did underestimate production, particularly if mortality was high. This also enabled the 1978 data to be compared with the 1979 data which could only be subject to this simple calculation. In 1979 the perch showed very good survival so that most of the production was present at the end of the experiment. Mean biomass was calculated as the average of the biomass present at the start (B1) and at the end (B2) (Chapman, 1978). Table 5.7 shows the production, mean biomass and $P/\bar{B}$ ratios in g/m^2 for all the cages in both years.

a. Roach.

In 1978 the production of the non-weed roach was greater than that of the weed roach despite the faster growth rate of the weed roach. This was due to greater mortality of the weed roach, as even with the increased growth rate, possibly due to the reduced density, they could not compensate for the loss in production due to mortality. As already discussed, this mortality was probably due to handling so that in 1978 the results did not provide any firm conclusions about the effects of the artificial substrates upon roach growth.

In 1979 higher stock densities in both roach cages led to greatly increased production, and $P/\bar{B}$ ratios of nearly 1.2 in both cages, similar to the average annual $P/\bar{B}$ of 1.5 proposed by Chapman (1978) as characterising natural temperate water bodies. Production and yield were slightly higher, but probably not significantly so, in the weed cage. Specific growth rates were the same as for non-weed roach in the previous year. As handling had been reduced to a minimum in 1979 the 30% mortality which occurred may have been density dependent as it was the same in both cages, and both sets of roach arrived at a final biomass similar to those reported by other workers for roach (see section 5.10). Therefore, it would seem that in 1979 the roach

Table 5.7 Stock density, production and mean biomass of the caged O+ roach and O+ perch in 1978 and 1979, all figures in g/m².

roach	STOCK	YIELD	PROD	$\bar{X}$ BIOM	P/$\bar{B}$	Gw(d)
1978						
CNW	2.10	5.83	3.73	3.97	0.94	0.03
C W	1.89	3.01	1.12	2.45	0.46	0.04
1979						
CNW	3.92	15.20	11.28	9.56	1.18	0.03
C W	4.16	16.60	12.44	10.38	1.19	0.03
PERCH						
1978						
CNW 2	38.44	13.35	-25.09	25.90		0.011
CNW 5	40.50	8.22	-32.28	24.36		0.005
C W 7	40.50	12.66	-27.84	26.58		0.013
1979						
CNW 1	7.69	15.83	8.14	11.76	0.69	0.01
CNW 2	5.30	10.85	5.55	8.08	0.69	0.01
CNW 7	7.13	12.78	5.65	9.96	0.57	0.01
CNW 10	6.51	10.99	4.49	8.75	0.51	0.01
CNW 12	6.51	8.86	2.35	7.69	0.31	0.01
$\bar{x}$	6.63	11.85	5.22	9.24	0.56	
C W 3	6.92	16.25	9.38	11.59	0.81	0.02
C W 4	6.58	17.84	11.26	12.21	0.92	0.02
C W 6	7.06	18.35	11.29	12.71	0.89	0.02
C W 8	6.78	7.48	0.70	7.13	0.10	0.01
C W 9	6.51	17.36	10.84	11.94	0.91	0.02
$\bar{x}$	6.77	15.44	8.66	11.11	0.78	

P/$\bar{B}$ = the production to biomass ratio for the duration of the experiment.
Gw(d) = the specific growth rate over the experimental period expressed on a daily basis.

fulfilled their potential in both cages regardless of their immediate environment.

b. Perch.

The perch were stocked at a high density in 1978 and the resultant mortality was such that a negative figure was obtained for production. Yields were fairly similar in the three cages, the highest being in the cage with the least handled fish.

In 1979 much lower stock densities were used. These varied slightly from cage to cage because of small differences in the numbers stocked and the size of the cage. Perch yields were similar to those of the previous year and were consistently higher in the weed cages (with the exception of cage 8, the "coot cage"). Production was also considerably higher in the weed cages but never quite as high as in the weed roach cage. The $P/\bar{B}$ ratios were low in the non-weed cages but higher and approaching 1.0 for the weed perch. Therefore, differences between weed and non-weed cages were considerable, suggesting that the artifical substrates did exert some beneficial effect upon the perch. In only two perch cages was production as high as in the roach cages and the $P/\bar{B}$ ratios were lower which suggests that the perch did not adapt to the cages as well as the roach although the presence of the artificial substrates did enable the perch to make better use of the resources available.

5.5 Summary of the growth studies.

The growth studies can be summarised as follows.

1. 0+ perch grew faster in the cages with the artificial substrates in both years, although not as fast as in the lake (Farnborough).

2. The presence of the artificial substrates enhanced roach growth in

1978. In 1979 roach growth was similar and equally good in both treatments.

3. Survival of both perch and roach was poor in 1978. This was attributed to handling stress in both species and overcrowding of the perch.

4. Survival of the perch was good in 1979, and slightly better in the weed cages while survival of the roach was not as good as expected.

5.6 The zooplankton in the lake and in the cages in 1978

The term zooplankton is used in this chapter rather than microcrustacea because the cage plankton communities were on the whole very similar to those of the open water of the lake which can correctly be termed zooplankton; they also included Asplanchna as well as copepods and Cladocera.

The zooplankton populations within the eight experimental enclosures and in the lake were sampled as described in Chapter 2, on seven occasions, from 10 July to 29 September. (The fish were placed in the cages from 12 July onwards and removed on 15 September). Four of the cages contained artificial substrates and four did not. The samples will be referred to as weed cage (CW), non-weed cage (CNW), lake marginal weedbed (LW), and lake open-water (LO), as in the previous section. The main aims of the sampling were:

1. to examine the influence of the artificial substrates upon the zooplankton, to determine whether they encouraged a more littoral type of crustacean community, i.e did they provide different environments for the two sets of fish.

2. to compare the cage zooplankton communities to open water and marginal weedbed crustacean communities in the lake to see how closely the cages reproduced these conditions.

3. to determine the similarity of replicate cages in each treatment.

All calculations were carried out on log10(x+1) transformed counts as described in Chapter 2. Where a statistical significance is attached to a result this was obtained from a t-test, between the replicate weed and non-weed cage microcrustacean samples.

The species composition of the Yateley zooplankton is given in Chapter 3, Table 3.2. The main species occurred in similar numbers in both weed and non-weed cages and in the lake. The most important components of the zooplankton occurred in the following succession: Cyclops spp. were abundant in July, followed by Asplanchna priodonta, which was replaced by Ceriodaphnia pulchella and Bosmina longirostris. The peak of Asplanchna coincided with high numbers of Ceratium in the lake followed after a pause by an increase in the numbers of Microcystis when the filter feeders decreased in number. Because the artificial substrates sank under the weight of periphyton great differences between the zooplankton populations of the weed and non-weed cages were neither expected nor found. Table 5.8 gives the total number of species recorded from each site; CNW,CN,LO,LW. The highest number of species consistently occurred in the marginal weeds as would be expected. The weed cage samples contained more species than the non-weed cage samples which were very similar to the open water in diversity. Seven species which were recorded from the marginal weedbeds were not found in the open-water of the lake; of these the following five were also absent from all the cages; Ceriodaphnia megops, Alona intermedia, A. nana, Leydigia leydigi, and Pleuroxus truncatus. The remaining pair, Pleuroxus uncinatus and Pseudochydorus globosus occurred in the cages in low numbers. Therefore, on the whole, the species composition of the cages was the same as that of the open water.

Table 5.8 The number of species in the microcrustacean samples.

	1978							1979		
	10.7	17.7	2.8	17.8	3.9	12.9	29.9	13.6	25.7	7.9
CNN	12	8	20	16	18	16	21	17	21	18
CN	15	18	22	20	21	21	21	19	22	21
LO	14	19	18	17	15	16	17	15	18	24
LN	20	33	23	18	22	25	21	21	26	26

Cyclops counted as 1 sp., nauplii not counted.

Fig. 5.3 shows the mean total numbers/litre of zooplankton in the two sets of cages, with the totals in the lake. The 95% confidence limits and range of numbers are given in Table 5.9. The confidence limits were large because of the small sample sizes. Replicate samples from each cage were not collected. The similarity between cages in each treatment is well illustrated and the four cages in each treatment can therefore be regarded as replicates. Total numbers in both weed and non-weed cages were similar on most occasions, and although the trend was towards higher numbers in the weed cages the differences were not significant ($P>0.05$). The increase in the weed cages on the last date was due to a count of 885/litre of Bosmina in one cage. The range of total numbers was always greater in the weed cages possibly due to the greater diversity of habitat. This can be compared to the differences found between weedbed samples in Farnborough. With two exceptions the totals were very similar to those of the open water but lower than those in the marginal weedbeds so that although the weed cages did not provide exactly the type of community hoped for neither did enclosure decrease the amount of available food in the cages. The agreement between the means of the non-weed cages and the open water suggests that the sampling method gave a precise measure of the amount of zooplankton in the water. The high numbers in all the cages on the second samoling date were due to very high numbers of nauplii.

Table 5.10 shows the mean total numbers/litre over the sampling

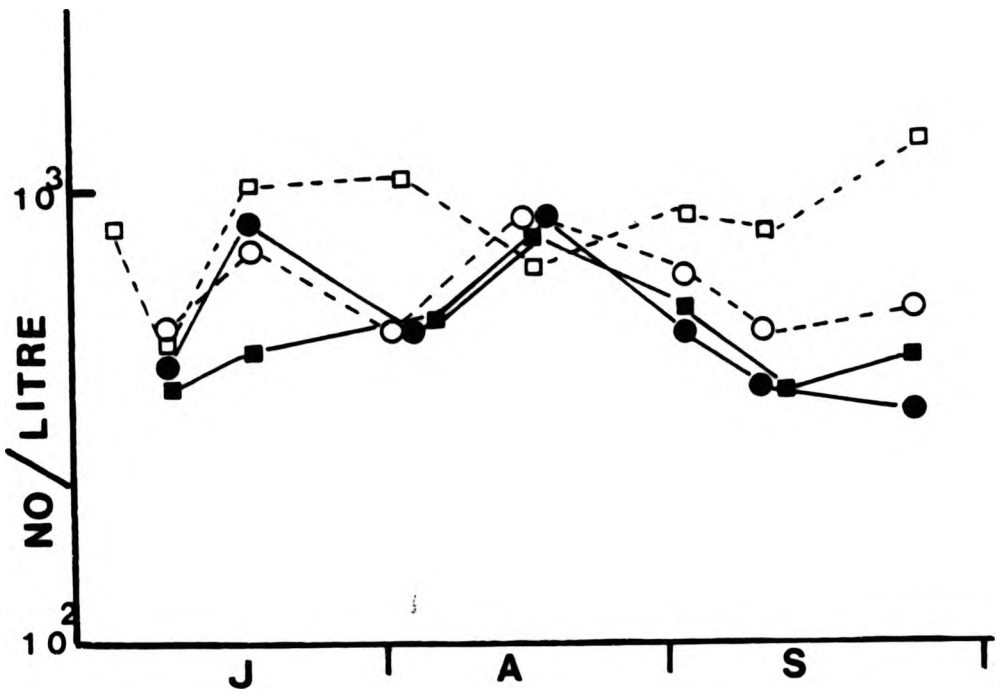


FIGURE 5.3 Abundance in numbers/litre of total zooplankton in the cages and in the lake in Yateley in 1978. Each point for the weeds and the cages is the geometric mean of several samples.

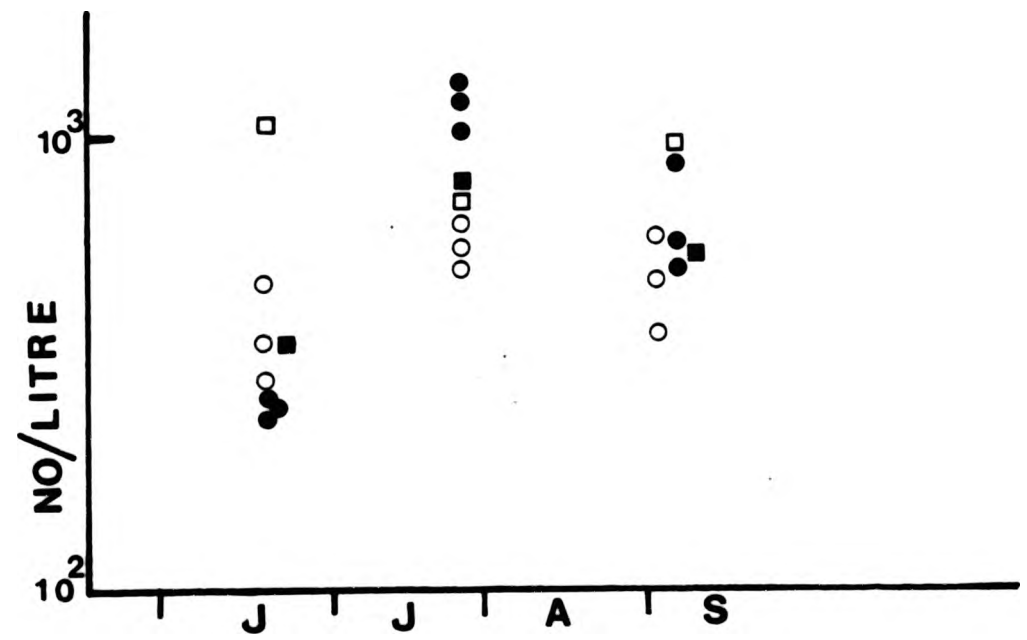


FIGURE 5.4 Abundance in numbers/litre of total zooplankton in the cages and in the lake in Yateley in 1979. Each point for the weeds and the cages is the geometric mean of several samples.

● non-weed cage □ weedbeds

○ weed cage ■ open water

Table 5.9. Geometric mean total numbers/litre of zooplankton in the cages and in the lake in Yateley 4 in 1978 and 1979.

DATE	SITE	$\bar{x}$	MIN	MAX	n	95% C.L.
1978						
10	CN	463	352	620	4	319-670
JULY	CNN	365	318	422	3	257-519
	LO	353			1	
	LN	443	343	574	2	
17	CN	750	565	1053	4	478-1176
JULY	CNN	804	668	1080	3	423-1528
	LO	425			1	
	LN	955	934	977	2	
2	CN	481	419	545	4	394-587
AUG	CNN	488	451	558	4	419-567
	LO	492			1	
	LN	1087	1080	1094	2	
17	CN	802	737	922	3	593-1085
AUG	CNN	821	765	921	4	723-934
	LO	793			1	
	LN	659	455	829	2	
3	CN	673	497	901	4	441-1027
SEPT	CNN	516	444	671	3	293-909
	LO	569			1	
	LN	859	736	1027	2	
12	CN	466	305	599	4	286-758
SEPT	CNN	363	275	440	4	259-509
	LO	362			1	
	LN	854	675	1107	2	
29	CN	500	329	1291	4	180-1385
SEPT	CNN	302	277	353	4	251-364
	LO	423			1	
	LN	1338	1296	1383	2	
1979						
13	CN	374	295	486	3	
JULY	CNN	252	243	261	3	
	LN	1191	842	1684	2	
	LO	352	363	365	2	
25	CN	577	525	640	3	
JULY	CNN	1146	1019	1232	3	
	LN	728	444	1174	3	
	LO	823	811	844	2	
7	CN	495	345	635	3	
SEPT	CNN	656	551	876	3	
	LN	968	656	1546	3	
	LO	566	535	599	2	

Key CN=weed cage
CNN=non-weed cage
LN=marginal weedbeds
LO=open water
n=number of samples
x=mean numbers/litre

Table 5.10. Geometric mean total numbers/litre zooplankton in each cage over the summer. (including Asplanchna)

CAGES		LAKE	YEAR
NON-WEED	WEED		
Cage 1 472 Cage 2 476 Cage 5 454	Cage 4 553 Cage 7 668 Cage 8 577	Open 462 weeds 936	1978
Cage 7 588 Cage 11 639 Cage 12 582	Cage 4 469 Cage 8 407 Cage 9 562	Open 553 Weeds 915	1979

Table 5.11. Geometric mean numbers/litre of the main species of zooplankton at each site over the whole sampling period.

SPECIES	1978				1979			
	CAGES		LAKE		CAGES		LAKE	
	W	NW	W	O	W	NW	W	O
Nauplii	198	187	98	147	174	241	98	210
Cyclops	71	57	125	79	136	105	261	131
Asplanchna	28	41	7	27	13	35	0	27
Ceriodaphnia	16	18	143	24	8	6	155	16
Chydorids	24	19	130	32	34	3	96	8
Diaptomus	8	15	23	16	3	10	35	10
Bosmina	8	14	x	13	3	10	1	5
Diaphanosoma	2	3	23	3	1	2	47	2
Daphnia	1	3	x	2	1	2	x	5
Polyphemus	3	1	2	x	1	3	2	x
Pleuroxus					16	1	50	2
Acroperus					9	1	15	2
Alona					1	1	3	1
Harpacticoids					11	2	7	1
Simocephalus					6	x	16	1

Key as in Table 5.1
x=less than 1

period for each cage, (the equivalent of mean annual standing crop), and here one can see that the weed cages contained slightly higher numbers of crustacea than the non-weed cages, (cages 3 and 6 were not sampled on all occasions and have been excluded). The non-weed cages were very similar to the open water while numbers in the weed cages were intermediate between the open water and the weedbeds, suggesting that the artificial substrates did exert some effect despite their tendency to sink towards the base of the cages.

Table 5.11 shows a comparison of the mean numbers of the main taxa over the sampling period, in both sets of cages, and in the two areas of the lake. Overall the cages were fairly similar but some differences were observed which can be attributed to either the presence of the artificial substrates or to the cages themselves. Asplanchna was more abundant in both types of cage than in the open water possibly because of calmer water in the cages. The slightly lower numbers in the weed cages compared to the non-weed cages could have been due to the artificial substrates as it was rarely found in the weedbed samples. Numbers of the characteristically open-water species, Diaptomus gracilis, Bosmina and Daphnia longispina, while similar in non-weed cages and the open water, were lower in the weed cages. Conversely, the chydorids, particularly Chydorus sphaericus, were more abundant in the weed cages although not as numerous as in the weedbeds. The order of abundance of species was virtually the same in the cages and the open water but different in the weedbeds which were dominated by Ceriodaphnia and chydorids. Species characteristic of the weedbeds which were not so well represented in the weed cages were Ceriodaphnia, the chydorids and Diaphanosoma brachyurum plus Simocephalus vetulus and Sida crystallina.

Fig. 5.5 shows the seasonal population changes for the main species. The confidence limits are not included in the figures because

Plate 1. An experimental fish cage (volume 4 m^3) containing artificial substrates used to simulate aquatic macrophytes in fish caging experiments in Yateley in 1978 and 1979.

Plate 2. The experimental fish cages in position in the centre of the lake, Yateley, 1979.

Plate 1. An experimental fish cage (volume 4 m^3) containing artificial substrates used to simulate aquatic macrophytes in fish caging experiments in Yateley in 1978 and 1979.

Plate 2. The experimental fish cages in position in the centre of the lake, Yateley, 1979.

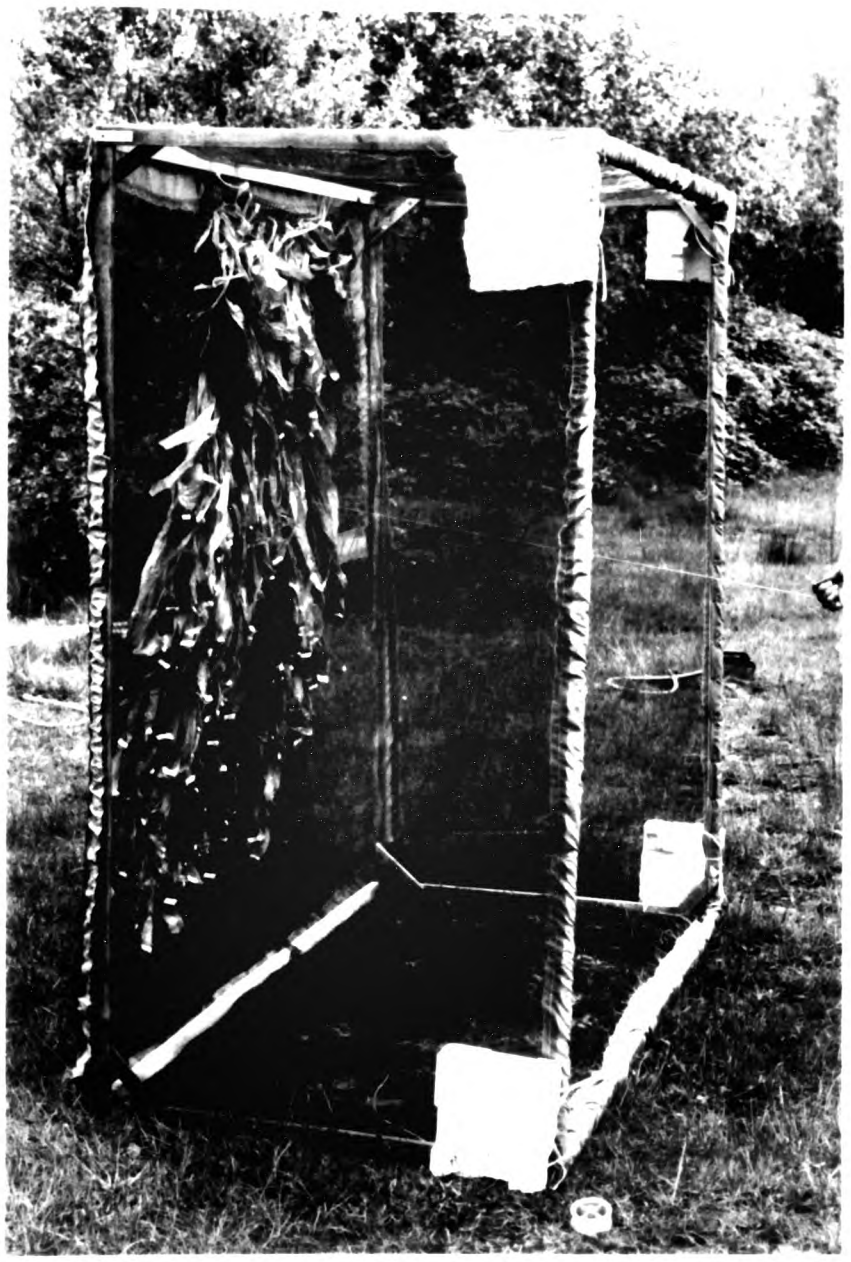


Plate 1. An experimental fish cage (volume 1 m^3) containing artificial substrates used to simulate aquatic macrophytes in fish caging experiments in Yateley in 1972 and 1973.

Plate 2. The experimental fish cages in position in the centre of the lake, Yateley, 1979.

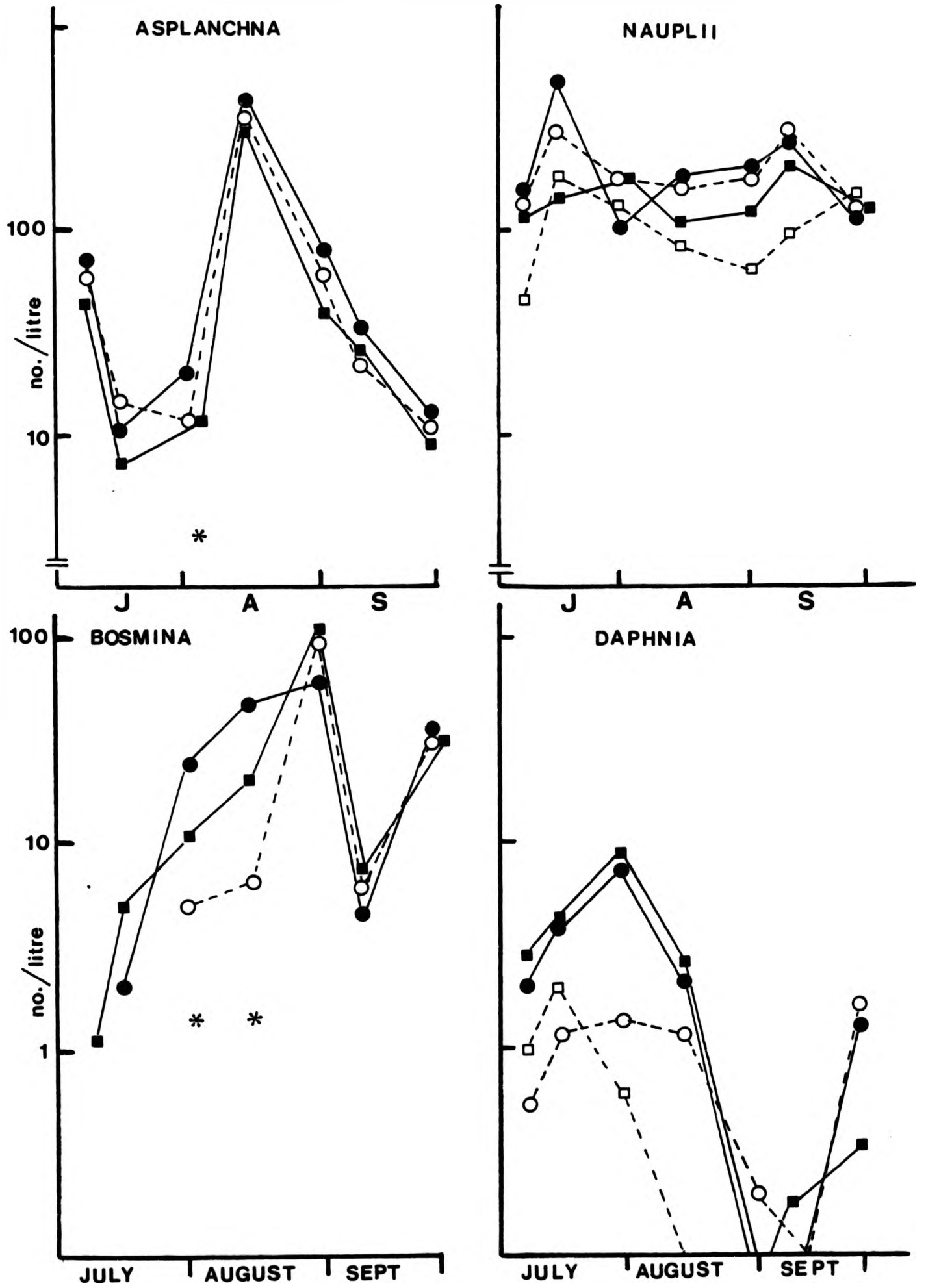


FIGURE 5.5 Abundance in numbers/litre of the major species of microcrustacea in the cages and the lake in Yateley in 1978. Densities <1.0/litre not shown but included in all analyses.
Key as in Figure 5.4. * = sig. diff. (P<0.05)

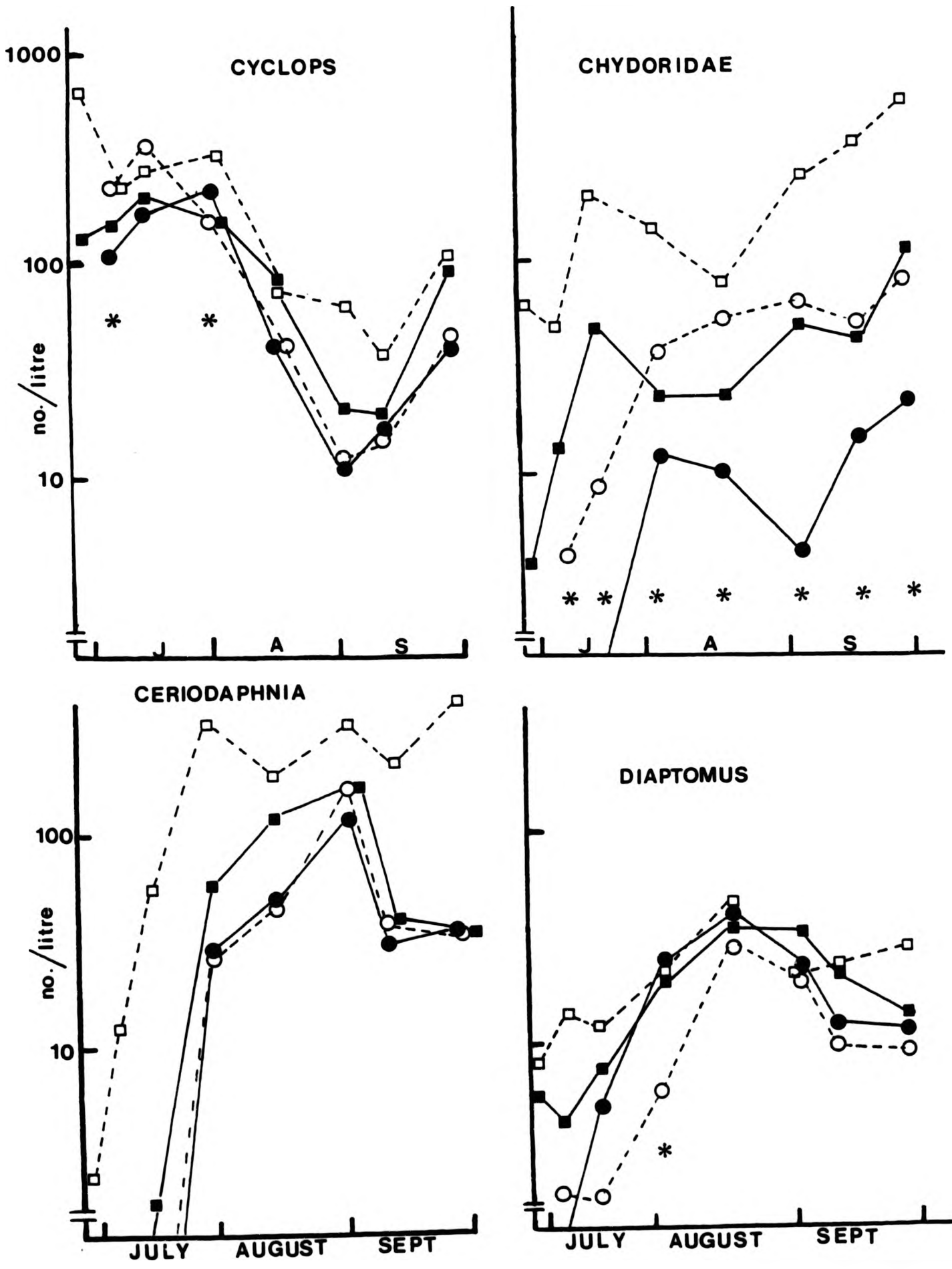


Figure 5.5 (cont.)

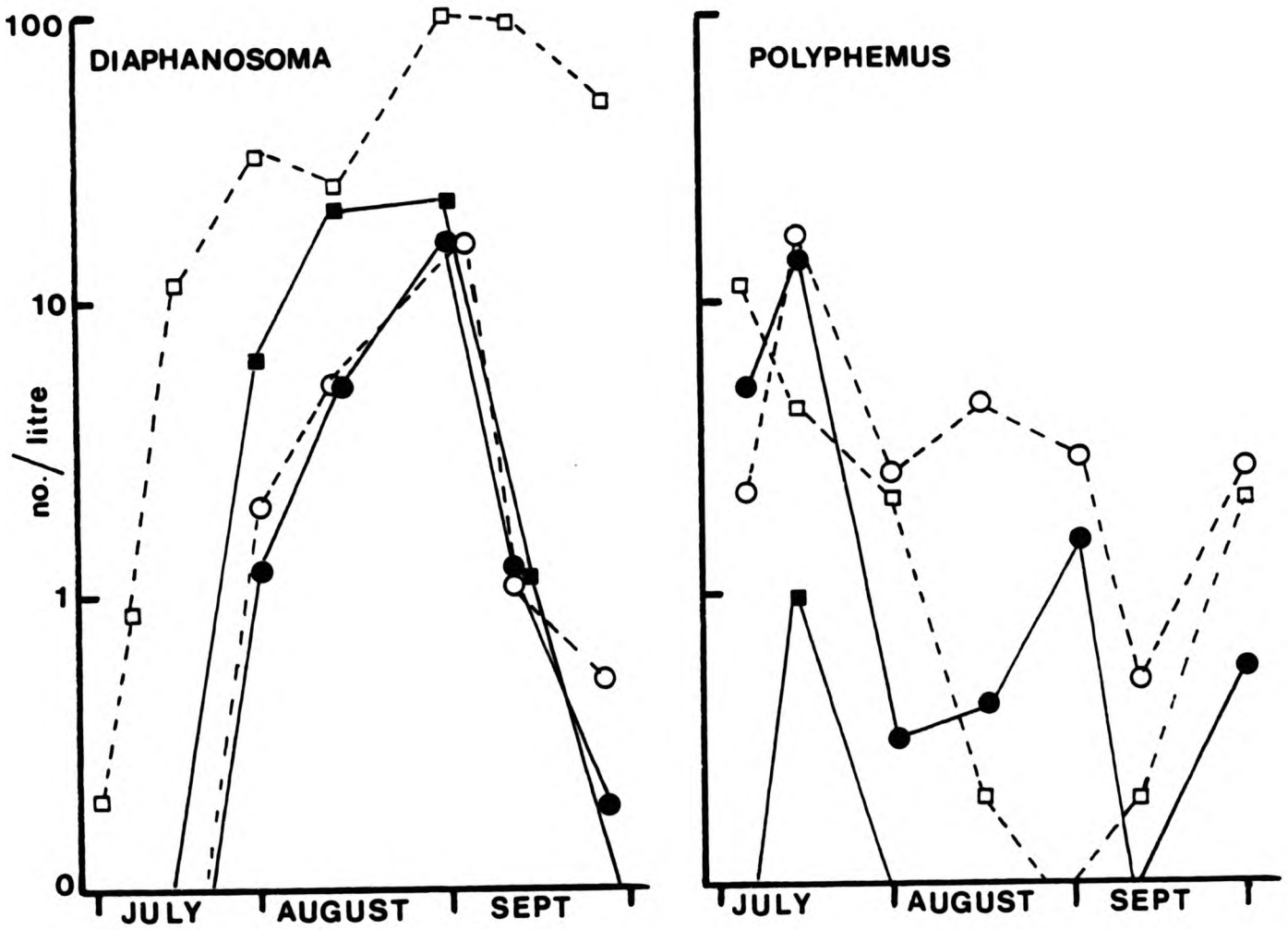


Figure 5.5 (cont.)

they would obscure the data points. They were also large because of the small sample sizes and are given in the appendix. A * on the figure denotes a significant difference on that date between the weed cages and the non-weed cages ($P<0.05$, t-test). Numbers of Cyclops were very similar in both weed and non-weed cages and more similar to numbers in the open water than the weedbeds. The weed cages contained significantly more Cyclops at the beginning of the experiment when the artificial substrates were at their best. Asplanchna was not found in the weedbeds but numbers in all the cages were similar on most occasions. Ceriodaphnia was marginally more abundant in the weed cages while Bosmina was more abundant in the non-weed cages at the beginning of the sampling period. Nauplii were more abundant in both types of cage and this may have been due again to the presence of less turbulent water. Diaptomus was always less common in the weed cages although higher numbers occurred in the margins than in the open water and this difference may possibly have been caused by fish predation. Daphnia was present in the open water and in the non-weed cages in similar numbers but was not so common in the weed cages; Daphnia is noted for avoidance of stationary objects (Pennak, 1973) but did not avoid the mesh of the cages. The greatest difference between the cage types was shown by the chydorids, mainly Chydorus, which were far more common in the weed cages than in the non-weed cages, although still not as abundant as in the weedbeds. The most noticeable effect of enclosure was shown in the high numbers of Polyphemus pediculus in the cages. While this species was only found once in the open-water samples and was not common in the weedbeds, swarms were observed around the cages on several occasions and the highest numbers recorded were 252/litre in a non-weed cage and 66/litre in a weed cage. Finally, numbers of Diaphanosoma were very similar in the cages; they were slightly lower than in the open water

and much lower than in the weedbeds.

5.7 Zooplankton samples in the cages in 1979.

In 1979 the plastic macrophytes were modified to prevent sinkage. As it was assumed that the similarities between the crustacea in the cages in 1978 were due partly to the failure of the artificial substrates, greater differences were expected in 1979 between weed and non-weed cages. In order to test this with the minimum of fish disturbance, sampling was carried out on three occasions, in June, July and September and on each occasion replicate samples of the lake open-water and marginal weedbeds were collected and three cages of each type were sampled. It was not considered necessary to collect samples from all 12 cages because the similarity between replicates of each treatment was adequately demonstrated in 1978.

Species composition of the zooplankton was almost the same as in the previous year, with the open water dominated by Cyclops, Bosmina, Asplanchna and Ceriodaphnia, plus Diaptomus and Diaphanosoma. Standing crops were also similar (see Table 5.9), but as only a few samples were collected with a long sampling interval, the seasonal population changes could not be described. One species which occurred in 1979 but was not noted in 1978 was the colonial rotifer Conochilus hippocrepis which usually could not be counted because the colonies broke up during sample filtration and sub-sampling. However, it was observed to be more abundant in the weed cages than the non-weed cages and uncommon in the open water. It was counted on one occasion in the weed cages when a mean of 164 colonies/litre was recorded (but not included in the total).

Table 5.8 shows the number of species recorded on the three sampling occasions from the different sites. In contrast to 1978, only two species recorded in the weedbeds were not found in the open water.

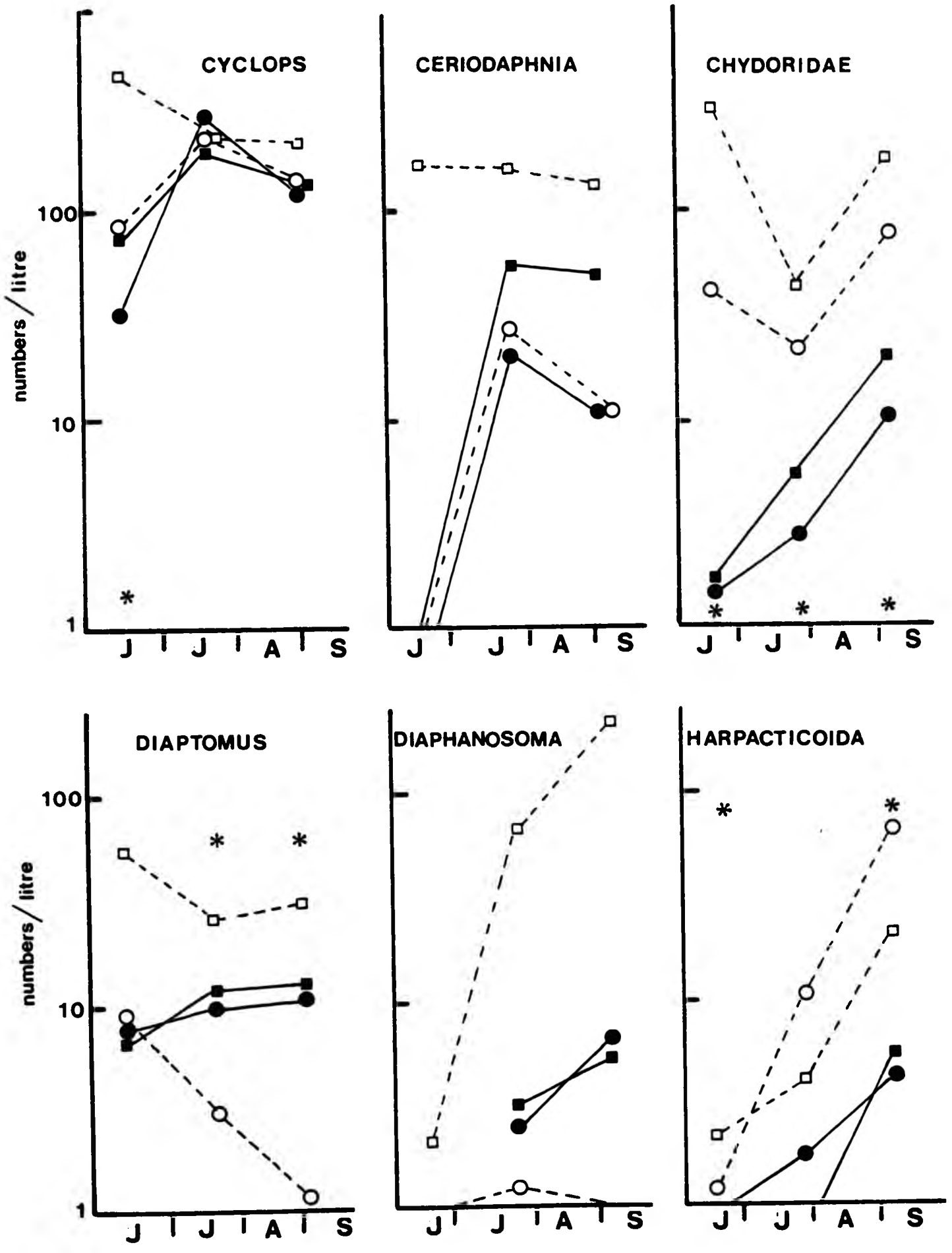


FIGURE 5.6 Abundance in numbers/litre of the major species of microcrustacea in the cages and the lake in Yateley in 1979. Densities <1.0/litre not shown but included in all analyses.
Key as in Figure 5.4. * = sig. diff. ($P<0.05$)

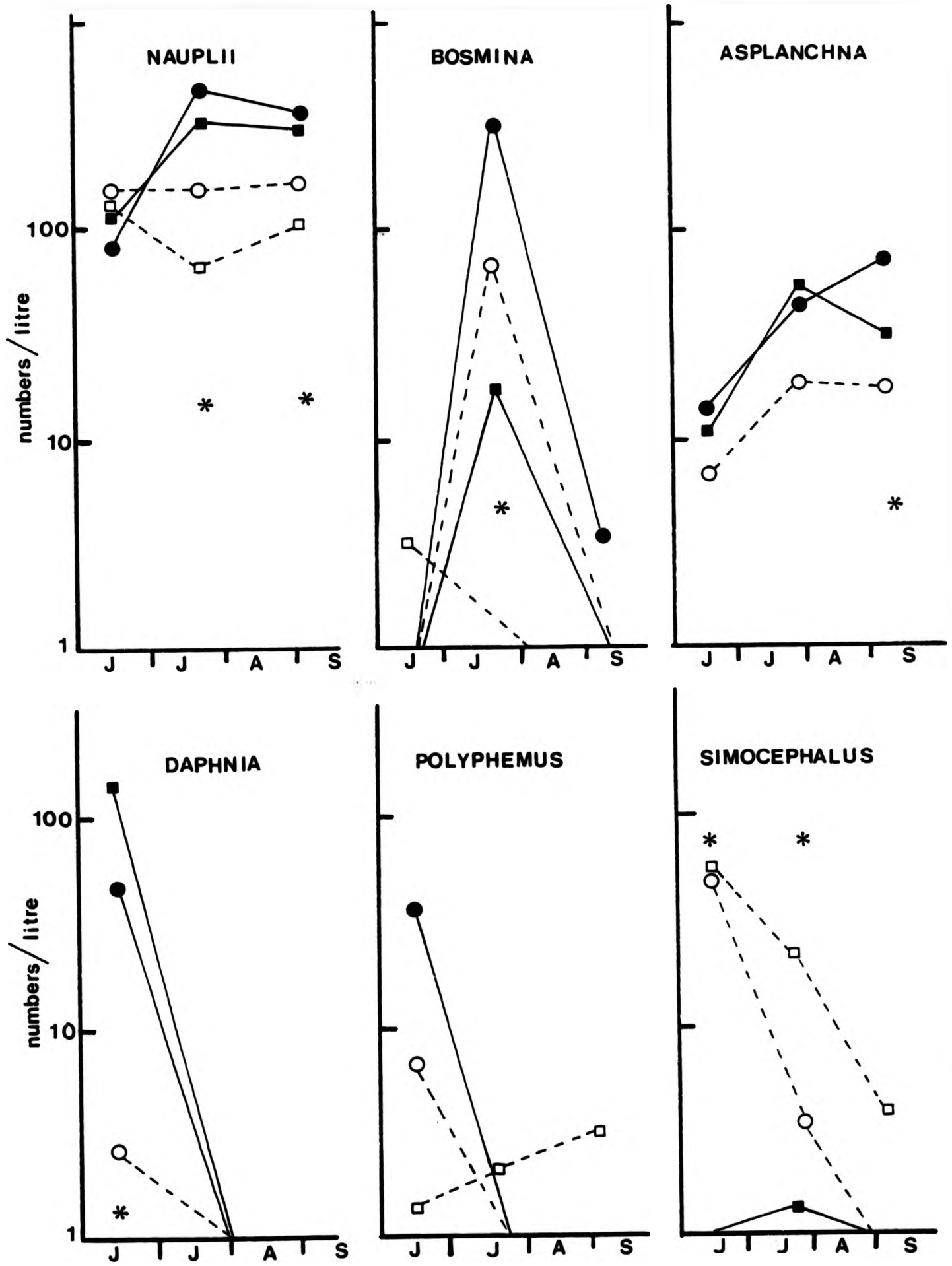


Figure 5.6 (cont.)

Four species were absent from the weed cages and five fron the non-weed cages. Asplanchna was the only organism found in the open water but not in the weedbeds. The most abundant chydorids were Pleuroxus denticulatus and Acroperus harpae in contrast to the domination by Chydorus sphaericus in 1978.

Total numbers/litre of zooplankton are shown in Fig. 5.4 and Table 5.9. Standing crops of zooplankton were very similar to those in 1978 but there were greater differences between cage types. Only on the last occasion was there any overlap between numbers in the weed and non-weed cages although the means were only significantly different in July ($P<0.05$) because of the small sample size. The non-weed cages contained higher numbers of zooplankton than the weed cages on the whole (see Table 5.9 and 5.10) and while the numbers in the weed cage remained fairly uniform in the three samples the numbers in the non-weed cages showed similar fluctuations to those in the open water. As in 1978 there was less variation between replicate cages than between treatments.

Table 5.9 shows the mean numbers/litre of the main species over the whole season. In addition to species present in 1978, harpacticoid copepods and Simocephalus vetulus contributed to the weed cage communities. Harpacticoids are usually considered to be interstitial but they were fairly common in the weed cages, (all were one species, not identified). There were more differences between cages and in particular the chydorids, Asplanchna, Diaptomus, Bosmina, Simocephalus and harpacticoids occurred in different numbers in the two types of cage.

Fig. 5.6 shows changes in the numbers/litre of the main species over the duration of the experiment. The points are joined together on the graphs for clarity although the time interval was longer than the

generation time of most of the organisms and so population changes in between are not known. Examination of those species most characteristic of the marginal weedbeds indicates that changes in the numbers of Cyclops in the cages reflected changes in the numbers in the open water although the cages did not respond similarly as Cyclops showed greater fluctuations in the non-weed cages. Numbers of Ceriodaphnia were low in both treatments while the chydorids were significantly more abundant on all occasions in the weed cages ($P<0.05$), although not as common as in the weedbeds. Simocephalus and Sida were only found in the weed cages and harpacticoids were abundant in the weed cages. Of the open-water species, Bosmina was more common in all the cages than in the open water but significantly more abundant in the non-weed cages when present in any number ($P<0.05$). Both Daphnia and Asplanchna were more numerous in non-weed cages as expected. Fluctuations in the numbers of Polyphemus bore no relationship to their presence in the weedbeds and they were more common in the non-weed cages, in contrast to 1978.

5.7.1 Larger invertebrates and ostracods in the cages.

The macro-invertebrates listed in Table 5.12 were observed in the cage samples in 1978. All were usually more common in the weed cages. On one occasion in 1979 the larger invertebrates in the cage samples were also counted; the numbers found are given in Table 5.12 which shows that there were great differences between cage types with many more animals, particularly worms and chironomids in the weed cages. The presence of Hemiptera in both types of cage may have been due to less turbulent water as they are surface dwellers.

Ostracods are not normally considered part of the plankton community and were not usually found in the plankton samples. However they were found to be common in the guts of the caged roach (see next

Table 5.12. Occurrence of macro-invertebrates in the cages in Yateley on 13.6.79.

	CN	CNN
Worms	176	1
Asellus	1	0
Crangonyx	1	0
Hydracarina	50	5
Gastropods	1	0
Zygoptera n.	0	1
Caenis sp.n.	16	1
Cloeon sp.n.	3	1
Hemiptera	30	21
Chaoborus sp.l.	4	1
Chironomidae l.	31	2
Trichoptera l.	1	0
Coleoptera ad.	1	0
Total	315	33

The table gives the average numbers in 6 samples (vol. 36 litres), not numbers/litre. The worms were mainly oligochaetes.

Table 5.13 Occurrence of ostracods in the cages in 1978 and 1979, in numbers/litre.

DATE	CN	CNN	LN
10.7.78	13	7	42
16.8.78	130	112	?
13.6.79	67	5	92
7.9.79	?	?	94

section) and so were counted in a few samples in both years. Table 5.13 gives the numbers of ostracods found in these samples in 1978 and 1979. They were noticeably more common in the weed cages, although not as abundant as in the marginal weedbeds. They were not so common in the non-weed cages and were rarely noted in the open-water samples. These counts were not included in the total numbers/litre used in this chapter nor for the calculation of percentage composition in the next section. It is possible that the ostracods were attracted both to the netting of the cages and to the artificial substrates; alternatively they may have been more vulnerable to the sampler than when living in their more usual benthic habitat.

5.8 Summary of the microcrustacean studies in Yateley.

1. In 1978 differences between the crustacean communities of the two cage types were on the whole insignificant, although the weed cages did contain larger standing crops and a greater number of species. Littoral species were usually slightly more abundant in the weed cages than the non-weed cages but the absence of open-water species from the weed cages was less marked. The failure of the artifical substrates to remain floating in the water column was a partial explanation of these similarites. Although the artificial substrates did not work very well in 1978, they did exert a considerable effect upon the larger invertebrates which were far more abundant in the weed cages than in the non-weed cages.

2. In 1979 there were differences in standing crops and species composition and on two of the three sampling occasions the non-weed cages contained higher numbers of zooplankton, caused by a greater abundance of small open-water species. Littoral species were more abundant in the weed cages and vice-versa for open-water species as

shown in Table 5.11.

3. The zooplankton in replicate cages of each treatment was very similar in both years.

4. In 1978 the zooplankton of both sets of cages resembled that of the open water. In 1979 there was a greater similarity between the weed cages and the weedbeds.

5. Although some pelagic species, e.g. Asplanchna, occurred in higher numbers in the non-weed cages than in the lake open-water, littoral species were never as abundant in the weed cages as in the weedbeds (with the exception of Polyphemus), so that while the enclosure of open water could promote an increase in the abundance of the open water community possibly through its sheltering effects, the artificial substrates did not provide a complete replica of the weedbed crustacean communities although they did provide shelter for fish and encouraged the development of a more diverse community than occurred in the open water.

6. Changes in population numbers followed the same pattern in all the cages and in the lake samples in both years with a few exceptions. Both Diaphanosoma and Diaptomus in the weed cages exhibited population changes the reverse of those which occurred in the lake in 1979.

5.9 The diet of O+ roach and perch in the cages in 1978 and 1979.

The gut contents of samples of roach and perch from weed and non-weed cages were examined on three occasions during 1978, and once in 1979. The sample sizes were usually small in 1978 as the main object of the cage experiment was to examine growth and survival rather than diet. The results presented here are from the examination of the guts of 35 roach and 60 perch in 1978 and 10 roach and 71 perch in 1979. More perch than roach were available for this diet study, in contrast to 1977

when many more roach guts were examined, so that over three years the gut contents of comparable numbers of roach and perch were counted.

Variability in diet between fish in a cage sample was similar to that found in Farnborough, as described previously, and no relationship was found between total numbers eaten and fish size. The amounts consumed were similar in magnitude and the perch showed greater variation in totals than the roach. However, differences in the relative contributions of the major species to the diets of samples from replicate cages were small, in contrast to the differences found in Farnborough between diets of fish from one site and another. This made comparison of the diets of weed and non-weed fish easier. It must be borne in mind that only periodic samples were examined and what is discussed below is gut contents rather than overall diet.

5.9.1 Species composition of the diet of the caged fish.

Table 5.14 shows the species composition of the diet of roach and perch for both years, as the mean percentage composition for all the guts examined. Comparison of the overall species composition of these fish with those in Farnborough is difficult because of differences in samples sizes, so that the caged roach appeared to have a less diverse diet than the Farnborough roach, with the opposite result for perch.

The diet of the caged roach was fairly similar in both years but differed from that of the roach in Farnborough. Ostracods formed the bulk of the diet of the caged roach and Cyclops was common in the guts. Neither was often eaten by the Farnborough roach; their preferred food items, Ceriodaphnia and Bosmina were uncommon in the guts of the caged roach. Therefore, the roach showed a degree of flexibility in their feeding, exhibiting a lack of clear-cut preferences which enabled them to take advantage of the most abundant smaller crustacea present, in

Table 5.14. Species composition of the diet of caged 0+ roach and 0+ perch in Yateley, 1978 and 1979. The mean % composition during the experiment is given for each food item.

	1978		1979	
	ROACH $\bar{x}$%	PERCH $\bar{x}$%	ROACH $\bar{x}$%	PERCH $\bar{x}$%
Rotifera				
Keratella quadrata	7	x	x	x
K. cochlearis	x	x		x
Asplanchna priodonta		x		9
Copepoda				
Cyclops spp.	13	39	25	38
Diaptomus gracilis		11		8
Harpacticoida			1	x
Nauplii	x	x		x
Cladocera				
Bosmina longirostris	5	3	x	x
Ceriodaphnia pulchella	10	17	20	25
Daphnia longispina	3	10		x
Scapholeberis mucronata	5	3		2
Simocephalus vetulus	x	x		x
Sida crystallina	x	x	x	x
Diaphanosoma brachyurum		2	x	x
Eurycercus lamellatus	2	6	x	x
Acroperus harpae		x	5	4
Alona aff/quad		x	x	x
A. gutt/rect	x	x	x	x
Pleuroxus denticulatus		x	x	2
P. aduncus	1	x		x
P. uncinatus	x			x
P. truncatus				x
Pseudochydorus globosus				x
Chydorus sphaericus	4	x	4	x
Polyphemus pediculus	10	x	x	x
Asellus aquaticus		x	x	2
Crangonyx pseudogracilis		x		x
Ostracoda	34	x	42	6
Hydracarina ad.,l.	3	x	x	x
Nematoda		x		x
Insecta				
Zygoptera n.		x		
Caenis sp. n.		1		x
Cloeon sp. n.	x	2		x
Hemiptera n.		x		x
Sialis sp. l.				x
Coleoptera l.				x
Lepidoptera l.	x			
Trichoptera l.	x	x	x	x
Chironomid l. p.	1	2	x	1
Chaoborus l.		1		x
Number of fish	35	60	10	71

n.=nymph
l.=larvae
p.=pupa
ad.=adult
x=<1%

this case ostracods. Scapholeberis and Polyphemus, both of which often occur in aggregations and are dark and presumably visible, were taken by the roach although they were not common in the zooplankton samples. Occasionally larger insect larvae occurred in the guts, including, in 1979, the aquatic caterpillars of the China Mark moths (Nymphula sp.).

The diet of the caged perch was also similar in both years, and also similar to that of the perch in Farnborough. The most commonly encountered food items in this study were cyclopoid and calanoid copepods, followed by Ceriodaphnia and Daphnia. Therefore, the perch appeared to be more conservative in their feeding, or rather to possess fairly specific food preferences. A variety of larger invertebrates were eaten including Asellus aquaticus, Crangonyx pseudogracilis and Ephemeroptera nymphs.

Therefore, there was some overlap in the species composition of the diets of the caged roach and perch with both feeding upon Cyclops and Ceriodaphnia. This differed from the situation in Farnborough where the roach ate Ceriodaphnia and the perch consumed Cyclops. Both Bosmina and rotifers were found in the guts of perch for the first time in the whole of this work.

5.9.2 Comparison of the diets of fish from weed and non-weed cages.

a) Roach 1978

Fig. 5.7 shows the percentage composition of the gut contents of roach from weed and non-weed cages in 1978 (calculated from the mean numbers in each sample). The percentage composition of the cage zooplankton samples is also shown. Comparison of the two is not straightforward because ostracods, rotifers and the larger invertebrates (called macro in the figure) were not counted in the plankton samples. Nauplii were excluded in all calculations of percentage composition of

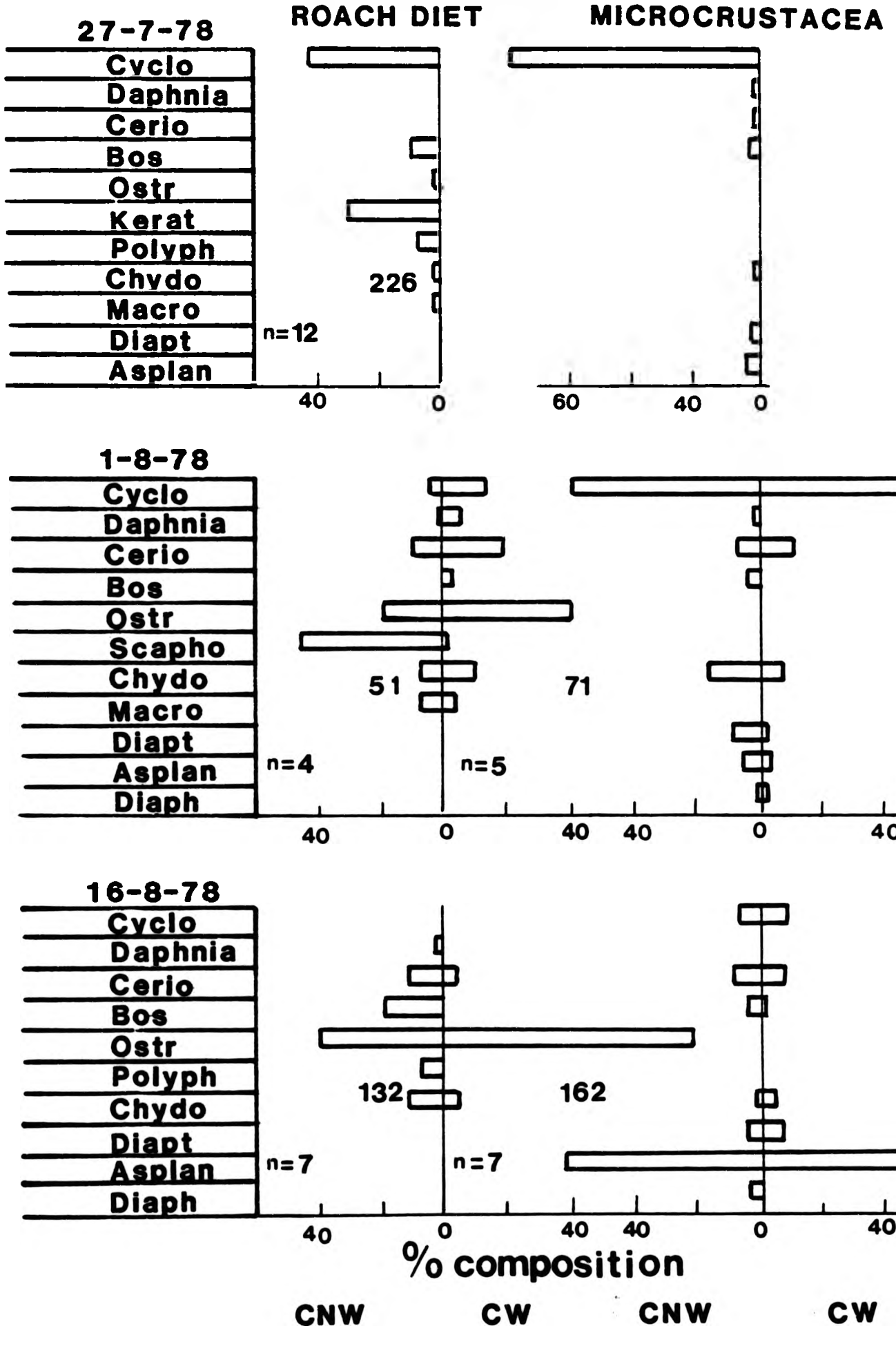


FIGURE 5.7 Percentage composition of the diet of caged roach in 1978, with the percentage composition of the zooplankton (minus nauplii). n=number of fish in the sample. The mean number of food organisms in each sample is also given.

the plankton samples in this section because they usually formed about 40% of the samples but were rarely found in the fish guts and contributed very little to the plankton biomass. Inclusion of them in the figures would also obscure the comparison between food and plankton composition.

In July only the non-weed roach were examined and their diet was dominated by open water organisms; Cyclops, rotifers (Keratella spp.) and Bosmina. Comparison with the zooplankton shows that Cyclops was the most abundant plankter in the water. Although other crustacea were far less common in the plankton, Bosmina was more abundant in the guts than would be expected from non-selective consumption. The larger invertebrates eaten were mainly caddis larvae and small mite larvae and the most common chydorids in the guts were Eurycercus and Chydorus.

In the next samples, (August), the zooplankton was similar in both cages except for the absence of Bosmina and Daphnia from the weed cages. However, the diets of the two sets of roach differed with the non-weed roach feeding mainly upon Scapholeberis, while the weed roach diet was mainly of ostracods. The high percentage composition of Scapholeberis was due to the presence of 93 individuals in one roach gut but none in the rest of the sample, possibly because it often occurs in aggregations. This is another example of the analytical problems which can arise from such variation between the fish in a sample as the rest of the diet was very similar to that of the weed roach. Both Bosmina and Daphnia were more common in the diet of the weed roach, in contrast to the occurrence of these species in the cage microcrustacean samples. The larger invertebrates were again mostly mite larvae plus occasional chironomid larvae in both cages. Chydorus was the commonest chydorid in the non-weed diet while Eurycercus and Chydorus were equally common in the weed roach diet.

The mid-August zooplankton was dominated by Asolanchna with copepods becoming less abundant, and the cages again contained very similar plankton populations. Both sets of roach were eating ostracods, which formed 33% of the diet of the weed roach. The ostracods were counted in these cage plankton samples. In the weed cage they contributed 18% of the total which made them more abundant than other crustaceans, the numbers of which had fallen during the Asolanchna population peak. 13% of the non-weed cage plankton consisted of ostracods but these roach had a more diverse diet including Bosmina and Ceriodaphnia. The mobile Chydorus was more common than other members of this group in both sets of guts and larger invertebrates were rarely encountered in the guts.

b) Perch, 1978.

Fig. 5.8 shows the percentage composition of the diets of the caged perch in 1978, with the percentage composition of the zooplankton samples. The figures for diet are the means of all perch guts examined from each treatment on each date.

In July no perch were collected from the weed cages for comparison with the non-weed perch, which were feeding mainly upon Cyclops and organisms of open-water origin, such as Daphnia and Bosmina. Eurycercus was the most abundant chydorid in the guts and the larger invertebrates were hemipterans and chironomid larvae. Cyclops, as well as being a preferred food item was also the most abundant organism in the plankton. In August all the perch had fairly similar gut contents, except for a greater number of Ceriodaphnia in the non-weed perch guts and a greater consumption of Daphnia by the weed perch. The weed perch had also eaten chironomid larvae and mayflies. By mid-August the perch had switched from feeding on Cyclops to Diaptomus as numbers of Cyclops dropped in

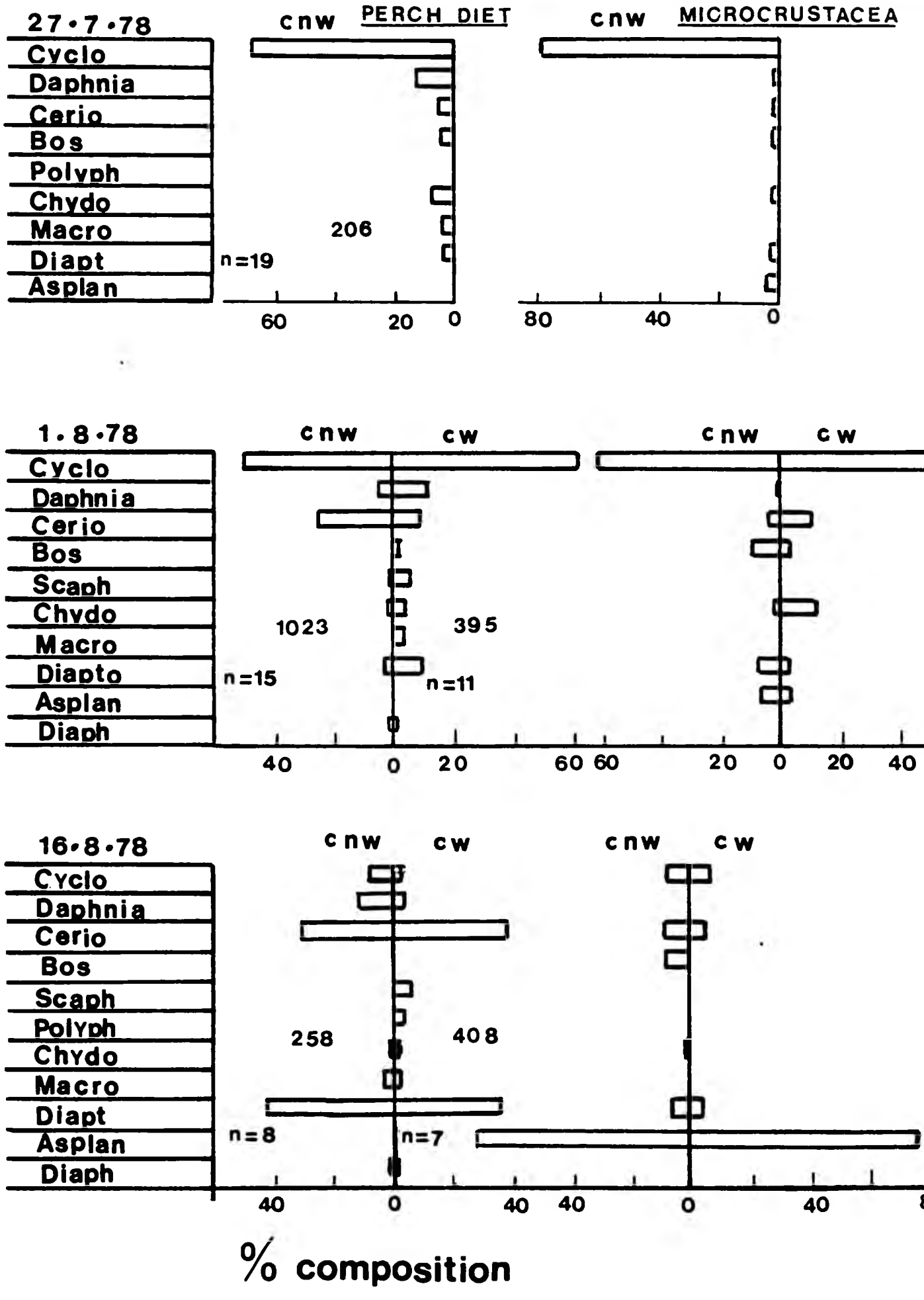


FIGURE 5.8 Percentage composition of the diet of caged perch in 1978, with the percentage composition of the zooplankton (minus nauplii). n=number of fish in the sample. The mean number of food organisms in each sample is also given.

the plankton. The diet of the weed perch was more diverse as they had been eating Scapholeberis and Polyphemus plus chironomids and Chaoborus larvae.

Therefore, on the whole, all the perch appeared to have a consistent preference for copepods plus Ceriodaphnia and Daphnia if present. The artificial substrates therefore, caused little change in the diet of the weed perch. The presence of greater numbers of the larger invertebrates in the guts of the weed perch may however have been due to the presence of the artificial substrates as they were significantly more abundant in the weed cages than in the non-weed cages (see Table 5.12).

c) Roach 1979

In 1979, 10 roach guts were examined, five from each treatment, when the cages were emptied. The percentage composition is shown in Fig. 5.9 with the percentage composition of the zooplankton samples collected four days previously. As in much of 1978, ostracods were the major diet item but on this occasion the diets of the roach were very similar, the only difference being the consumption of chydorids (Acroperus and Chydorus) and chironomids by the weed roach.

d) Perch, 1979.

In 1979 the gut contents of 71 perch, taken from nine cages on the last day of the experiment were counted. There were not enough perch in cage 8 to allow some to be killed for diet analysis. Fig. 5.9 shows the mean percentage composition of the diets of all the weed and all the non-weed perch with the percentage composition of the zooplankton. The diets of both sets of perch were very alike as all fish had been eating Cyclops and Ceriodaphnia, further evidence for the dietary conservatism

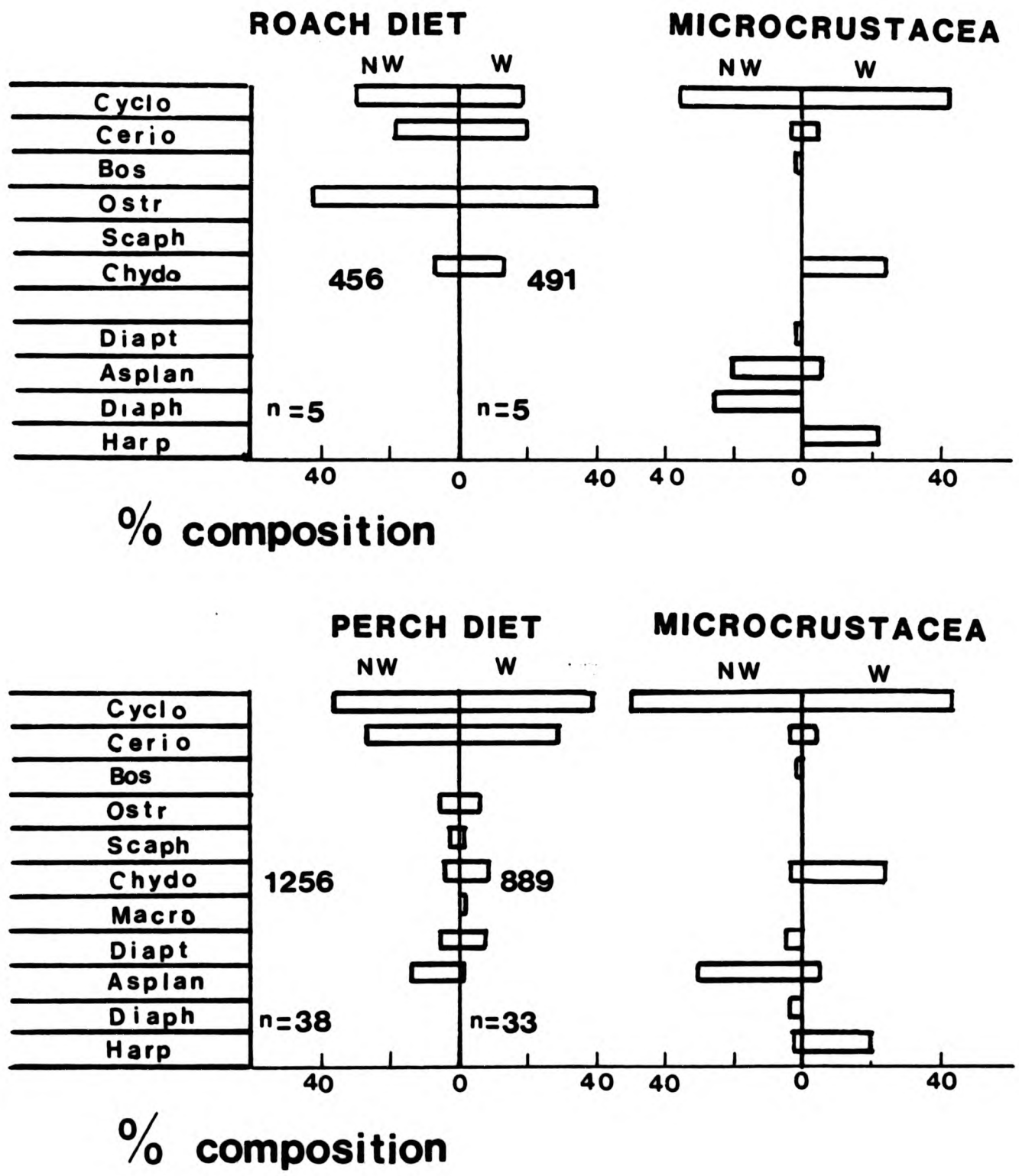


FIGURE 5.9 Percentage composition of the diet of caged roach and perch in 1979, with the percentage composition of the zooplankton (minus nauplii). n=number of fish in the sample. The mean number of food organisms in each sample is also given.

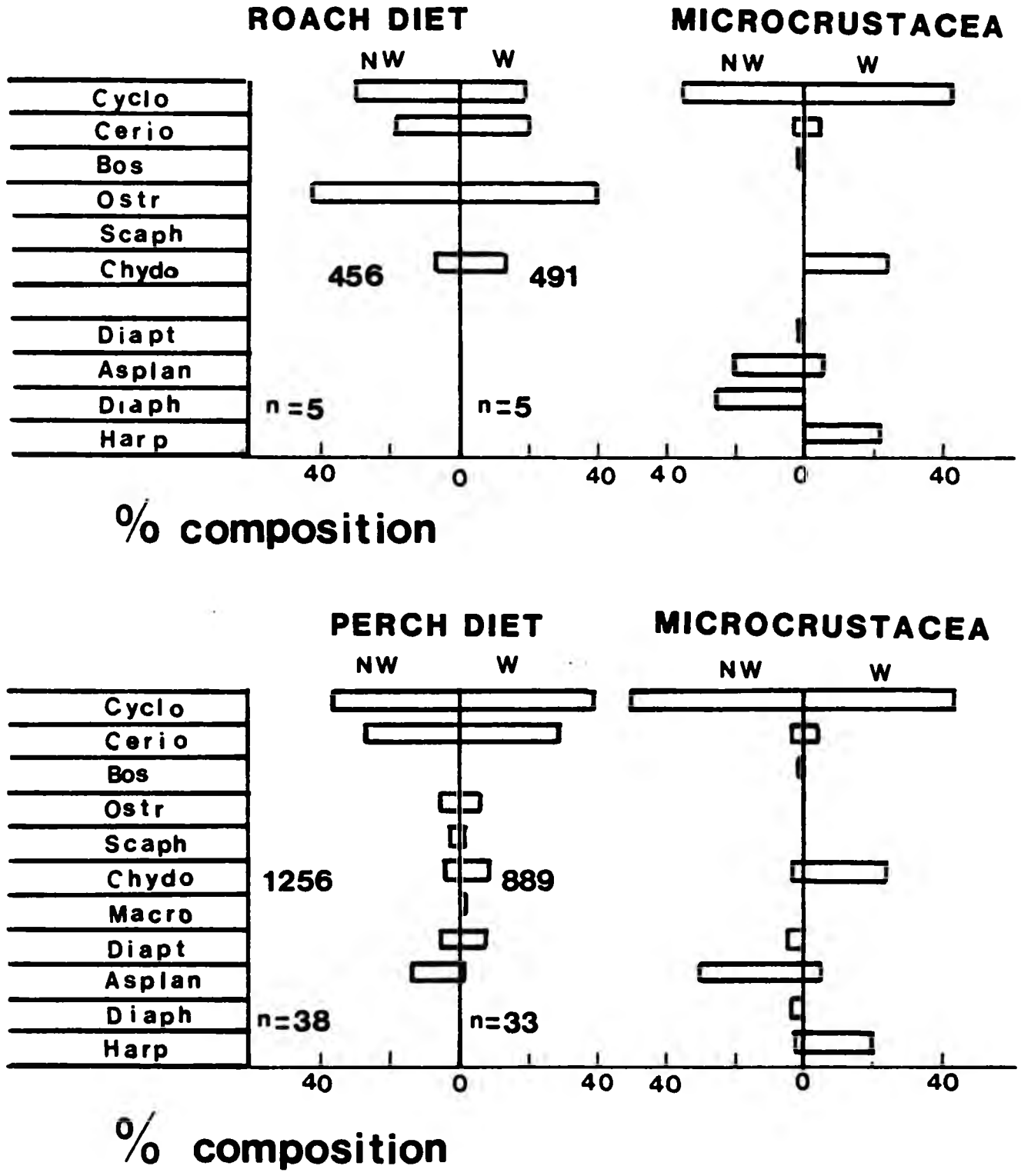


FIGURE 5.9 Percentage composition of the diet of caged roach and perch in 1979, with the percentage composition of the zooplankton (minus nauplii). n=number of fish in the sample. The mean number of food organisms in each sample is also given.

of the perch. Cyclops contributed 37% and 39% of the diet of the non-weed and weed perch respectively, and the figures for Ceriodaphnia were 28% and 29%. It is interesting that on this occasion the perch had also eaten a small quantity of ostracods. The principal difference between the two sets of perch was the inclusion of mictic Asplanchna in the food of the non-weed perch and the consumption of chydorids (Acroperus and Pleuroxus), Diaptomus, chironomid larvae and Asellus by the weed perch. These differences were significant (except Diaptomus), ($P<0.05$, t-test on individual percentage composition). The uniformity of the diet of the perch is further illustrated by the low variation between diets of separate cage samples, shown in Table 5.15. This shows the mean (plus standard deviation) of the average percentage composition of the main species in each perch cage. Considering the small sample sizes (5 and 4) the variation was not very great although the diet of the weed perch was slightly more variable than that of the non-weed perch.

e) Biomass.

The dry weight biomass of food found in the perch guts was reconstructed from the average sizes of microcrustacea eaten by the 0+ roach and perch in Farnborough in 1977 (Table 4.12). Table 5.16 shows the percentage composition of the dry weight biomass of food found in all the perch guts examined from both cage types in both years. The dry weight of the roach food was not estimated because most of it was of similarly sized particles.

The contribution of the insects to the dry weight of the perch food was markedly greater in the weed cages but otherwise the major groups were represented in similar quantites in both treatments.

Table 5.15 The mean percentage composition and standard deviation of the major food species in the 0+ perch cage gut samples in 1979.

	NON-WEED		WEED	
	$\bar{x}$	sd	$\bar{x}$	sd
Cyclops	37.0	15.1	39.0	10.6
Ceriodaphnia	23.0	6.5	29.0	13.0
Ostracods	5.6	2.0	6.6	4.9
Scapholeberis	2.8	2.3	2.1	1.7
Asplanchna	14.0	8.0	1.3	2.2
Chydoridae	4.1	2.8	10.0	7.9
Diaptomus	5.8	3.1	7.8	6.3
Macro	0.7	0.4	2.1	1.5
n =	5		4	

Table 5.16 The dry weight biomass of the gut contents of the 0+ perch in the cages in 1978 and 1979. (% composition)

	1978		1979	
	NW	W	NW	W
Cyclops	50	33	49	35
Ceriodaphnia	10	6	12	11
Ostracods			3	3
Scapholeberis		3	1	1
Chydoridae			1	2
Daphnia		3		
Diaptomus	13	22	10	12
Asplanchna			1	0
Macro	15	33	12	30

f) Diet overlap.

Dietary overlap between the two fish species appeared to be greater in Yateley when the two species were separated than when the fish were together in Farborough. Fig. 5.10 illustrates this point and shows the overall mean number of each food item in each fish species, converted to percentage composition. This can be compared with a similar treatment of the Farnborough diet data (see Chapter 4). There was considerably more overlap in Yateley in both years in the main food species, although the perch avoided ostracods in 1978. Of the 11 food categories in 1978, only two taken by the perch were not eaten by the roach (Daphnia and Diaptomus), while ostracods, Polyphemus and rotifers, which were eaten by the roach, were not found in the perch guts. However, the Levins diet overlap coefficients do not entirely agree with this (see Table 5.17). The perch in both sets of cages had completely overlapping diets but there was little overlap with the roach in 1978. The roach also had more dissimilar diets in the two treatments, as shown by the overlap coefficients. In 1979 the coefficients indicate slightly more overlap.

5.10 Summary of the diet studies.

1. The gut contents of the perch in both types of cage were on the whole very similar to one another in both years. The greatest difference was in the inclusion of macro-invertebrates in the guts of perch living among the artificial substrates. Diets of roach from weed and non-weed cages were different in 1978. Although they were the same in 1979, the analysis was based on a very small sample. These variations in diet were not usually related to the presence or absence of the artificial substrates in the cages.
2. While the perch ate the same species as the perch in Farnborough in

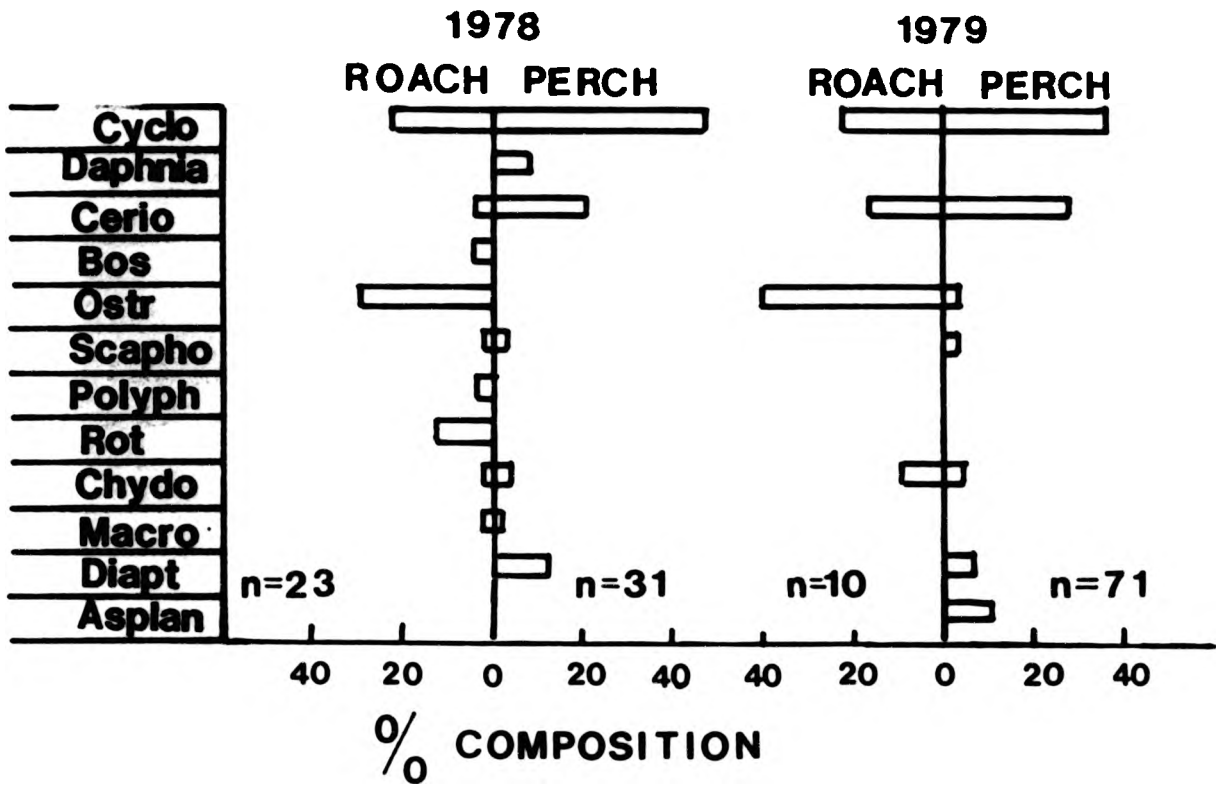


FIGURE 5.10. Comparison of the percentage composition of the diets of the 0+ roach and the 0+ perch in the cages in Yateley in 1978 and 1979.

Table 5.17 Levin's overlap coefficients for the diet of the roach and perch in the cages in Yateley in 1978 and 1979.

	PERCH		ROACH			
	NW/W	W/NW	NW/W	W/NW	P/R	R/P
1978 1.8	1.0	0.9	0.5	0.5	0.3	0.5
16.8	1.0	0.9	1.5	0.5	0.2	0.1
1979	1.0	0.9	0.9	1.1	0.7	0.6

1977, (Cyclops, Ceriodaphnia and Daphnia), the roach did not exhibit such innate preferences and consumed whatever was small, visible and abundant.

3. Dietary overlap between the two fish species was only slightly greater when they were isolated than when together in Farnborough.

4. When relatively few small crustaceans such as Ceriodaphnia and Bosmina were available, the roach in both years switched to eating ostracods and cyclopoids. As the consumption of ostracods could be regarded as peculiar to the artificial situation in which the roach were living, it is possible that in the natural situation with both fish species living together, that competition for Cyclops as food could occur.

5.11 Discussion.

The results of the caging experiments showed that the artificial substrates, despite being only partly effective in 1979, changed the habitat in some way as there were significant differences in the growth rates of the roach and perch with and without them.

a. Microcrustacea

The increasing use of artificial substrates in aquatic ecology has been primarily in the field of river pollution assessment. Many types of artificial substrate samplers have been developed (Dickson et al, 1971) to collect uniform benthic samples and there have been several attempts to measure colonisation rates. Meier et al (1979) found that a 60 day exposure period was insufficient for colonisation by all taxa, although their figures show that only four out of 23 taxa were collected after 26 days. A six week exposure time for artificial substrates was

recommended by the U.S. Environmental Protection Agency (Weier et al, 1979). These recommendations are however more applicable to macro-invertebrates in a stream habitat than to microcrustacean colonisation of the plastic macrophytes in a lake.

Macan and Kitching (1972) measured the colonisation of artificial Littorella and Carex by benthic species and found colonisation times to be fairly short, of the order of a few weeks, although the exact times are not given. Barber et al (1979) found that two weeks was a sufficient colonisation period for artificial seagrass. Therefore, the colonisation periods used in this study (over 1 month) should have been adequate for both microcrustacea and macro-invertebrates. Colonisation rates of periphyton on artificial substrates can be much faster and it is likely that this was the most important determinant of microcrustacean colonisation rates. Sladeckova (1962) measured rates of 1-2 weeks for algae and protozoa and one month for larger organisms, depending upon water temperature and water transparency. Whiteside (1974) used plastic pan scourers (Tuffy Balls) to collect chydorids and found that five days was sufficient for colonisation by algae and bacteria after which chydorids were also found on the Tuffy Balls. Markosova (1980) found that stable communities developed on artificial surfaces in open water in 10 days. Colonisation was more rapid in the open water than among vegetation because of greater light penetration into the water. It seems likely that the placing of the artificial substrates in the centre of Yateley would have speeded up periphyton colonisation and growth (Markosova, pers.comm.).

Plastic cannot of course duplicate living plant tissue. Real plants grow continuously during the summer, give off DOM (dissolved organic matter) (Wetzel and Manny, 1972) and produce O_2 and CO_2 in diurnal cycles thereby affecting the pH of the water in the weedbeds. There are

complex mineral cycles between the littoral and the open water (Howard-Williams and Lenton, 1975). Plants appear to attract some species and repell others and Otto and Svensson (1981) have discussed the production of chemicals by plants as a defence against being eaten. Some of these properties would be possessed by the periphyton on the artificial substrates but whether they give off DOM has not been documented. Certainly, Daphnia were not repelled by the artificial substrates although absent from the weedbeds.

Periphyton is a complex community of attached and motile algae plus Cladocera, worms, Protozoa, rotifers and chironomids. Some species cannot colonise plastic easily (Markosova, 1980). Cattaneo and Kalff (1978) compared the tightly attached epiphytes and the loosely attached epiphytes on natural and plastic leaves. Plastic leaves had a higher biomass of tightly attached epiphytes while the natural leaves supported a more loosely attached community, due to differences in calcium encrustation. They found no evidence for inhibition or stimulation of epiphytes by growing plants so that as a substrate plastic can be equivalent to living plants. Cattaneo and Kalff (1978) also found that the species composition of epiphytes on real and plastic plants differed. The amount of periphyton on the plastic substrates in Yateley was probably similar to that on real plants, as the lack of a living substrate giving off carbon compounds may have been compensated for by the position in the well illuminated lake centre.

Several comparisons have been made between the communities found among real and plastic plants. Macan and Kitching (1972) found that artificial Littorella and Carex contained communities very similar to those in plant stands with an occasional exception and found that densities among the artificial substrates were usually greater than among real plants. They also compared the populations in artificial

substrates positioned in different parts of the lake and found surprisingly high numbers of macro-invertebrates in the substrates suspended in mid-water, as in the present study. They concluded that macro-invertebrates were more active than previously thought. Barber et al (1979) obtained similar results although lower densities of most species were found on the artificial seagrass compared with the living Zostera. Similarly, in this study, densities of microcrustacea in the artificial substrates never equalled those in the weedbeds.

Most of the studies described above have been concerned with benthic animals and sampling has involved lifting the substrates out of the water. There appear to have been no studies such as this one where planktonic organisms were sampled from the water around the artificial substrates (while the substrates remained in situ) and compared with those inhabiting similar weedbeds.

There were some obvious differences between the artificial substrates and the weedbeds in 1979. Bosmina which did not occur among the marginal macrophytes in Yateley was present in the weed cages, suggesting that there was some property of the living plants which repelled them. Van Zon also found that Bosmina did not occur among vegetation but was present among plastic plants (pers. comm.). This appears to conflict with the previous statement that it was competition from Ceriodaphnia which excluded Bosmina from the weedbeds rather than a chemical repellant. However Ceriodaphnia was less abundant in the cages than in the weedbeds, and so would not have exerted the same competitive pressure on the Bosmina in the cages. Most of the littoral species did not occur in great abundance in the weed cages although their presence indicates their ability to colonise the artificial substrates. One complicating factor in the analysis of results was that while the substrates did not fill the cages, the samples were collected from all

over the cage so that open-water areas were also sampled. In the weedbeds, only vegetation was sampled. Initial sampling in the weed cages showed that Ceriodaphnia was more abundant in the open-water part of the cages with Bosmina, while chydorids were significantly more common among the plastic strands. The cages were not completely filled with the artificial substrates for several reasons. If members of a fish school could not see one another their behaviour may have been altered thus partially invalidating the experiment. It was not intended to force the fish to remain completely inside a weedbed but rather to give them a choice of habitat in which to move around and feed. In the cages without weeds this choice did not exist.

As the periphyton in the artificial substrates in the present study was not examined, definite reasons for the lower numbers of chydorids in the weed cages compared with the vegetation cannot be given (chydorids feed mostly on detritus and periphyton (Fryer, 1968)). Whiteside (1974) compared chydorid numbers on Tuffy Balls and in natural vegetation and found that numbers on the plastic balls were higher than in the vegetation. They were placed within the weedbeds so that only a short colonising journey was required. The lower numbers of chydorids in the non-weed cages compared with the open water indicated that the chydorids were not attracted to the mesh of the cages.

Dorgelo and Koning (1980) investigated the avoidance of plastic plants by Acanthodiaptomus denticornis. They found that this copepod avoided both real and plastic plants in the light, real plants causing greater repulsion. They suggested that this was caused by the exudation of repellants and was connected with photosynthetic activity but this does not explain why the plastic plants were also avoided. Similarly, Pennak (1973) showed that Daphnia rosea avoided plastic plants, again to a lesser extent than real plants. It is feasible that if macrophytes

exude repellants, the epiphytes do as well and this would increase with the length of time the substrate was left in the water. It seems more likely that the explanation of Siebeck (1930), that avoidance is caused by a change in optical orientation is correct. If this is the case the open-water crustacea would not be expected to avoid the plastic weeds, unless they interfered with optical stimulation of the plankters. A comparison between real plants and plastic plants, both suspended in mid-water would be required to test these theories.

One reason for lower standing crops of microcrustacea in the artificial substrates compared with the weedbeds could have been the lack of diversity of the plastic strips. Macan and Kitching (1972) found that by diversifying the surfaces of artificial substrates, a greater range of organisms was attracted to them. The artificial substrates used in Yateley were straight strips interspersed with lattice-like strips. This structure was as complex as many macrophytes and more so than Typha. As the microcrustacean sampling in Farnborough did not show any relationship between plant density and microcrustacean abundance it seems unlikely that there was a straightforward relationship between the density of plastic and microcrustacean abundance.

The effects of enclosure on the open water require examination as this itself may have caused changes in the communities. The main differences between the zooplankton in the cages and in the open water were the greater numbers of Bosmina, Asplanchna and copepod nauplii in the cages. Smyly (1976) examined the zooplankton populations inside Lund Tubes in Blelham Tarn and found enhancement of some species, notably Diaptomus and Ceriodaphnia, with an increase in nauplii caused by greater numbers of ovigerous females compared to the lake. He also found greater numbers of Chydorus in the tubes. However, the

differences were attributed to the lack of predation within the tubes rather than to enclosure itself. Polyphemus was associated with the cages and Smyly (1952b) found Polyphemus associated with P. natans leaves. It is also possible that the relatively large samples collected from the cages picked up the highly aggregated Polyphemus which was less well represented in the weedbed samples. Both the studies of Smyly and other workers using enclosures have involved complete isolation of a column of water. There do not appear to be any studies where the zooplankton within a fish cage has been examined. It is possible that enclosure caused changes in distribution of the zooplankton by disrupting the effects of natural circulating forces (wind/water movements) and changes in vertical migration resulting in a concentration of individuals within the cage (Stavn, 1971). As no information on the density of the fish in the lake was collected one cannot say whether some crustaceans were more abundant in the cages because of a lowering of the predation pressure.

One aspect of the microcrustacean results which has not been discussed is whether predation by the two fish species resulted in the microcrustacea in the roach cages being different to those in the perch cages. No such differences were found which could be attributed to differential feeding preferences. The geometric mean density over the sampling period in 1978 of Diaptomus in the perch cages was 11/litre and in the roach cages 7/litre. The figures for Cyclops were 64/litre (perch) and 63/litre (roach) and for Bosmina 9/litre (perch) and 7/litre (roach). These comparisons were complicated by the presence of both weed and non-weed cages and unequal sample size between the roach and perch so that even if changes due to predation did occur they were not demonstrable in this experiment. In 1979 cage 11 (roach, non-weed) on two occasions contained far higher numbers of Diaphanosoma than any

other cage. This was not a species eaten to any extent by either fish species but was more common in the perch guts, while none were found in the guts of non-weed roach. There was in any case no reason to expect that differences in the feeding preferences of the two fish species would cause changes in the zooplankton communities in the cages because the microcrustacea were free to move in and out through the mesh.

b. Roach and perch growth

One criticism of the caging experiments in 1978 could be that a high fish stocking density was used. The stocking density of the roach in 1978, 16.6 fish/m^2 (2 g/m^2) was high compared to density estimates obtained from Farnborough in September 1977 of 3.4 roach/m^2. Cook (1979) also estimated the numbers of O+ roach in Farnborough as 2.3 fish/m^2 in July 1975 and 3.2 fish/m^2 in June 1976. It would however be more realistic to compare these densities with the total fish biomass in natural waters. Cook (1979) obtained an estimate of total fish biomass in Farnborough of 49 g/m^2 in March 1975 decreasing to 37 g/m^2 in October 1975. Mathews (1971) carried out population estimation studies of the coarse fish in the River Thames at Reading, considered to be one of the most densely populated waters in this country. He obtained estimates for O+ roach of between 1 fish/m^2 and 19 fish/m^2, with a maximum total fish density of 82 fish/m^2 (excluding one doubtful estimate, the standing crop was still 58 fish/m^2). Growth was adversely affected at these densities but the O+ roach grew to 4.0 cm in their first year. Williams (1965) provided a standing crop estimate for this stretch of the River Thames of 47.6 g/m^2. Total biomass in Rye Meads where the fastest growth in the U.K. was recorded varied from 18.2 g/m^2 to 33 g/m^2 which White and Williams (1978) considered low. Compared to these figures for total population size the stocking densities of the roach cages in 1978 do not

appear to be high.

It is unlikely, therefore, that mortality of the roach in the cages was density dependent. The stocking density in 1979, of 13 roach/m^2 and 4.9 g/m^2 was higher than in 1978 but not excessively so. It is more likely that handling stress caused mortality. Mazeaud et al (1977) reviewed the effects of stress in fish and stated that quantitative responses to different treatments in adult coho and sockeye salmon caused a primary stress reaction in the following order; 5 minutes struggling out of water > 5 minutes at 21°C after acclimation at 11°C > 20 minutes capture in a seine net. These stresses also produced secondary effects which could occur after a time delay and such a reaction could have been the cause of mortality of the non-handled roach after stocking in 1979.

The effects of both capture and transport on young fish have been investigated, mainly in salmonids. Barton et al (1980) found that for fingerling rainbow trout initial capture was the most stressful part of a commercial stocking operation. This coupled with the stress of transport would have contributed to mortality of the caged fish. Ottaway and Simkiss (1977) found false checks on scales of 17% of adult Farnborough roach transported 30 km to Reading thus reinforcing the need to hold fish for a period after transport. Specker and Schreck (1980) found that mortalities due to transport in Coho salmon smolts occurred within hours. Mazeaud et al (1977) state that adult chinook salmon took three days to recover from transport while Barton et al (1980) found that plasma cortisol levels (used to monitor stress) did not return to basal levels until eight days after transportation. These studies indicate that species differ considerably in their reaction to stress and personal experience has shown that young roach are even more delicate than young salmonids. The differences in the stocking

procedure of the two cages in 1978 when one batch of roach was held prior to stocking was most probably the cause of the different mortality rates in the two roach cages.

It seems unlikely that the final biomass of roach of 6 g/m^2 in the non-weed cage in 1978 was sufficient to exert a density dependent effect upon the growth rate compared with 3 g/m^2 in the weed cage. It is possible that differential mortality in the weed cage removed the smaller roach although there was no overlap at all in the sizes of the two groups of roach as might be expected if differences were due to significantly different growth rates. The growth rates suggest that some differential mortality did occur as those of the surviving roach did not slow down after capture and transfer as might be expected. This was particularly marked in the weed cage.

Considering the results of the two years, the experiments indicated the flexibility of the roach in adapting to a change in conditions. Growth in the cages was never poorer than growth in the lake. The diet varied with the abundance of food and the presence or absence of the artificial macrophytes made no significant difference to growth and survival. These experiments were a simplification of the natural situation and an obvious extension of them would be to introduce a predator as Deelder (1951) has shown that roach hide in vegetation to avoid being eaten by perch.

In contrast to the roach, the perch did not grow well in the cages. Reference to Table 4.14 shows that final sizes were similar to those of the more slowly growing populations in this country. It is likely that the poor growth and survival in 1978 in all cages was due to the very high stocking density of the 0+ perch, of 38 fish/m^2 (40 g/m^2). This is comparable to the figures for total fish biomass for similar waters given above. Thorpe (1974) gives a figure of 2.4 fish/m^2 and a

biomass of 16 g/m^2 for perch in Loch Leven. One reason for stocking with such high numbers was to ensure that sufficient perch (and roach) survived to provide a shoal. (Higher numbers of roach would have been used had they been available). Feeding efficiency of perch has been shown to depend upon group behaviour and critical shoal number (Deelder, 1951) and Breder (1959) discussed the consequences of disrupting the social behaviour of fish. In deciding upon stocking numbers one also needs to consider the volume of water occupied by a school at any one time as Pitcher (1980) has shown that it is surprisingly small. It was not possible to determine how much of the mortality was due to handling stress but in 1979 perch mortality was low and as it was possible that the perch were hardier than the roach mortality in 1978 may have been density dependent. The dip in growth after stocking suggests that differential mortality did not occur. Schneider (1973a) carried out pond experiments on yellow perch and recommended the very low stocking density of 18-25 eggs/m^2 for maximum growth rates. As the stocking density of the cages was reduced in 1979 and growth of the perch was no better it appears that mortality was density dependent and the growth rate was determined by other factors, probably food availability.

The artificial substrates exerted an effect upon the perch although even in their presence growth was poorer than in the lake. As the diets were very similar in both treatments other factors must have caused the differences in growth rates. There are many accounts of the greater feeding efficiency of percids and centrarchids in open water than in vegetation (Swingle and Smith, 1941; Deelder, 1951; Crowder and Cooper, 1979; Werner and Hall, 1979) but these studies were all related to older fish consuming small fish prey. There are also many references to the effect of food type upon perch growth, (discussed in Chapter 4), which have some relevance to the cage experiments. Keast

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(1977) suggests that the zooplankton food of 0+ perch is unlikely to be limiting and if poor growth occurs it may be due to a lack of larger benthic food items when the perch make the shift from one feeding stage to the next. As previously mentioned Jezierka (1974) demonstrated that perch fed on fish grew faster than perch fed on Tubifex. Whether small differences in diets of the perch with and without macrophytes were the cause of the significant differences in growth rates will be discussed in the next section.

c. Roach and perch diet

Levels of total zooplankton abundance were similar in all cages in both years so that differences in species composition possibly reflected in dietary changes, must be looked for. The roach were significantly different in size in 1978 in the weed and non-weed cages and their diets also tended to be different, with more ostracods being eaten by the larger weed roach. It is interesting that in 1979, when both sets of roach grew to a uniformly large size and had similar gut contents, ostracods again figured prominently in the diet.

The caged roach continued the pattern of optimal foraging shown in Farnborough, with small, relatively slow moving abundant items being eaten. That the diets in the weed and non-weed cages differed suggests that the artificial substrates did influence the availability of food, possibly partly by affecting the ease with which certain species could be caught. The greater diversity of the diet of the roach in the non-weed cage in 1978 when they were smaller than the weed roach does suggest that these roach had to forage further for their food as many workers have shown that increasing diversity of diet is an indication of reduced abundance of preferred food items (Ivlev, 1961; Pyke et al, 1977). The specialisation by the faster growing roach on ostracods in

1978 and 1979 was marked. The caged roach showed little sign of a preference for Bosmina or Ceriodaphnia, neither of which was particularly common in the cages although they were more abundant in the diet of the non-weed roach.

In 1978 the roach did not markedly increase their consumption of Cyclops when isolated from perch. In 1979 Cyclops was the most abundant crustacean in the cages at the end of the experiment and also formed 20-30% of the diet of the roach. Roach did not consume Cyclops in Farnborough when both fish species co-existed. If the consumption of Cyclops by the roach was a reaction to a reduced supply of small food items it is possible that removal of macrophytes and their diverse microcrustacean fauna from Farnborough would result in competition between juvenile roach and perch for Cyclops. Conversely, Ceriodaphnia was more common in perch guts in the cages than in the lake.

There have been several studies on the supression of feeding preferences of a fish species by the competitive interactions of another species including the classic studies of Nilsson (1959, 1965) on trout and char and Werner and Hall (1969) on sunfishes in vegetation. Edlund and Magnhagen (1981) studied the co-existence of two gobiid species in the laboratory. They found that in isolation both had the same food preferences but when together the feeding patterns changed and one fish took the previous choice while the other was supressed and switched to a previously ignored food. In the caging experiments it was thought that the diets of the roach and perch would show a similar convergence when the two species were allowed to feed in isolation. That this did not occur and the perch diet remained similar to that of the perch in Farnborough suggests that the two populations in Farnborough were not competing directly for food.

The perch were significantly different in size in the weed and

non-weed cages in both years and also the same size in each treatment in each year despite being stocked at different densities. Diets appeared similar between treatments. The major difference was the greater contribution to dry weight biomass of the food by the macro-invertebrates in the weed cages. It is possible that even consumption of a few larger food items led to increased growth rates of the perch. The influence of food size upon growth rate, irrespective of consumption rates, is the basis of the size grading of commercially produced trout pellets, starting with very small crumbs for small fish and graduating to large pellets for adult fish. Wankowski and Thorpe (1979) discussed the conflicting results of studies relating fish growth at different sizes to food sizes. They found that particle size was important for juvenile Atlantic salmon and as the fish grew the size of food necessary for optimum growth rates increased. Fish fed a particle smaller than optimum for body size grew poorly. The perch in the cages may have exhibited similar responses to food size and this may be the basis for the relationship between good growth and the change from a planktonic diet to benthic feeding. Such a relationship has been shown in the field. Breck and Kitchell (1979) found that bluegill sunfish grew faster on larger prey items (Hyalella) than on zooplankton. Behavioural changes have already been mentioned. The perch normally inhabit vegetation and the pursuit of open-water prey may have expended more energy than the pursuit of vegetation dwellers. They may also have used more energy in exercising their fairly fixed preferences in the open water rather than switching to other foods. It was previously suggested that perch opt for a sit-and-wait feeding strategy while the roach are cruising predators. In this case the perch would be expected to suffer from a lack of vegetation in which to remain stationary while the cruising roach would not be affected in the same way by the lack of

vegetation.

American work has shown that the foraging efficiency of blue-gill sunfish decreased in vegetation. The results obtained here suggest the opposite. The structural complexity of the artificial substrates may not have been sufficient to exert this effect which was most marked in dense vegetation (Vince et al, 1976). There have been several studies of a more general nature relating the presence of vegetation to fish growth and survival which will be discussed in the next chapter as they are of relevance not only to the cage experiments but to the microcrustacean and diet studies in Farnborough in 1977.

In conclusion, the results of the caging experiments suggest that roach are a more adaptable species than perch although more susceptible to handling stress. The roach possess flexible feeding habits and will optimise their feeding on small, abundant, easily caught food items. The perch, in contrast, are conservative feeders. The presence of macrophytes did not appear to be necessary for good growth of roach, when not co-existing with other fish species. In the absence of marked differences in microcrustacea in the cages or in the perch diets, behavioural changes caused by the modified habitat may have caused a reduction in perch growth rates. The lack of cover may have resulted in increased swimming, possibly away from higher light intensities (Breder, 1959). The inclusion of macro-invertebrates in the diets of the weed perch may have led to better growth in comparison with the non-weed perch. Further experiments are required with both species kept together and with the addition of predators to determine more precisely how the presence of the macrophytes affects growth rates and survival.

CHAPTER 6. CONCLUSIONS.

Whatever the mechanisms by which aquatic macrophytes influence fish populations, the outcome depends upon the fish species in question and the size of the fish. The more interesting studies on interactions between macrophytes and fish populations show this and are of direct relevance to the results of the present study.

Swingle and Smith (1941) attributed stunting in bluegill sunfish lake populations partly to the presence of dense vegetation. The large amount of shelter from predation provided by the macrophytes allowed good survival of O+ fish, leading to overcrowding and stunting. Subsequently, Swingle (1968) found that fish production could be increased by the addition of macrophytes to a pond, up to a maximum coverage of 50% of the lake surface; more than this resulted in decreased foraging efficiency. In species which regulate their population size through predation on their own young (Le Cren, 1958) there are many references to macrophytes being the indirect cause of fish stunting (Alm, 1946, 1953; Deelder, 1951; DiCostanzo, 1957; Nyberg, 1979). The macrophytes allow good first year survival which leads to overcrowding of the habitat by adult fish. These in turn have only a limited food supply because the small fish prey hide in the vegetation. This situation is self-perpetuating as the reduced foraging efficiency of the adult fish no longer lowers the population size.

One reason for the drop in foraging efficiency of the adults is that the plants upset the visual cues upon which many fish depend for hunting (Werner, 1974; Werner and Hall, 1974). Crowder and Cooper (1979) showed that the success rate of bluegills in capturing *Daphnia* dropped when *Elodea* was introduced into their tank. Similarly, Vince *et al* (1976) showed that dense vegetation provided

a prey refuge for amphipods pursued by marsh killifish.

The extent to which vegetation provides a refuge for macro-invertebrates depends upon plant density. Heck and Thoman (1981) carried out experiments on the predation of shrimps by killifish in artificial seagrass. They found that only in extremely dense vegetation (674 shoots/m^2) was predation on the shrimps lowered.

Crowder and Cooper (1979) surmised that in very dense vegetation fish fed upon zooplankton because the macro-invertebrates were unavailable (could not be captured). With no vegetation zooplankton became the sole source of food. They suggested that a medium density of vegetation was of most benefit to bluegills, providing a refuge for some macro-invertebrates while not reducing foraging efficiency of the fish too greatly. They found experimentally that the highest growth rates occurred with a plant density of 100 strands/m^2.

Breck and Kitchell (1979) modelled the effects of macrophyte removal upon survival and growth of O+ bluegill sunfish. They based their model on the assumption that fish survival was positively correlated with macrophyte density. This model indicated that a reduction in survival (caused by increased predation by piscivorous adults) would lead to faster growth of the remaining young fish. These fish would switch from planktivorous feeding to benthic feeding earlier in the year. Breck and Kitchell (1979) concluded that reduced predation pressure on the zooplankton populations would result from moderate macrophyte removal. This seems a rather naive and simplistic view of a complex situation, as their model did not account for the effects of reduced recruitment and consequent changes in adult predation rates. It seems unlikely that macrophyte

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removal would cause any reduction in the predation pressure on the open-water zooplankton in Farnborough. The results of this and previous studies on the gravel pits would suggest the opposite effect. None of these studies, however, examined the effect of macrophyte removal upon the interactions between fish and littoral microcrustacea, which as shown in the present study can be extremely important to the juvenile fish.

The lowered predation pressure in densely vegetated areas could explain the extremely high densities of animals found among some weedbeds. This may mean that the explanation normally given, that plants with finely divided leaves support larger communities because of a greater surface area, may require qualification in that the greater surface area may be indirectly lowering predation rates. Elodea (the most dense vegetation present in the lake) did not support significantly higher numbers of microcrustacea in Farnborough where there was considerable predation pressure from small fish capable of penetrating dense vegetation.

Vegetation can have different effects upon young and adult fish. By providing shelter from predation macrophytes enhance juvenile survival at the expense of adult feeding efficiency in piscivorous fish. Dense vegetation also results in lowered feeding efficiencies in the young fish by providing hiding places for invertebrate prey. This is particularly marked in salmonids, where vegetation can provide both cover for prospective prey and also shelter from predation by older fish. Ware (1975) examined the predation of benthic prey by rainbow trout and found that the predation rate decreased with increasing cover, or substrate complexity in a stream, although the degree to which cover protected prey was species dependent and affected by prey behaviour.

Mortensen (1977), investigating the impact of weed cutting in a stream upon the mortality of brown trout fry, found that the mortality rate was higher in cleared streams because with a decrease in the physical complexity of the habitat, the stream supported fewer trout which are aggressive and territorial. First year salmonid survival has been related to the number of territories present in a stream (Egglishaw, 1967).

From these studies one can conclude that macrophytes provide O+ fish with a refuge from predation by piscivorous fish. The degree to which macrophyte refuges are exploited depends upon the species of adult fish present in the water body. However, if the refuge function is not used, other aspects of macrophyte presence can still be important in affecting diet and foraging efficiency of the small fish.

Increased structural complexity of a habitat leads to increased prey pursuit times and possibly capture rates (Werner, 1974). In dense vegetation the O+ fish could spend longer pursuing prey with less reward. Roach do not rise to such a challenge and as shown in Chapter 4, opt for the easiest feeding strategy in terms of energy expenditure. The variety of macrophyte forms may be important in determining the effect of vegetation upon these predation rates. A mixture of plant forms would provide both a refuge for fish from predation and support high numbers of invertebrates. Potamogeton natans is one example of a plant meeting both requirements. It provided a shelter for fish while supporting the largest microcrustacean community in Farnborough, in a relatively large volume of water causing least disruption of the visual hunting cues of the fish. The species composition of the diet of the O+ roach provided evidence that the cruising young roach

took their food from the margins of the weedbeds where P. natans was most common.

Another facet of the effect of habitat complexity upon fish feeding is in the disruption of size-selective predation. Vince et al (1976) showed that size-selective killifish could no longer select prey by size when feeding in weedbeds and this was most marked for the larger fish. Werner and Hall (1974) showed that factors which decreased predator searching efficiency reduced prey size selection in much the same way that decreasing prey abundance leads to greater diversity of diet as preferences are no longer exerted. Vince et al (1976) showed that there was a fish size/plant structure interaction and therefore a variety of macrophyte forms would be beneficial by providing littoral areas where larger fish could feed with minimal visual disruption while the smaller fish fed in more complex plant stands.

The O+ roach exhibited no size-selective feeding so that the degree of habitat complexity does not necessarily affect their feeding. It was more advantageous for the young roach to feed in the weedbeds because exploitation of the open water would have brought them into direct competition with the adult roach (Cook, 1979). Extremely dense vegetation would affect O+ perch more than O+ roach because perch feed in response to rapidly moving prey particles (Boulet, 1958) and these cues would be disrupted in weedbeds. They can also feed size-selectively (Guma'a, 1978b), and this can be disrupted in vegetation, although no evidence for size-selection was obtained in the present study. However, the removal of macrophytes would expose them to adult predation and force them into open-water feeding, to which they were not suited, to judge from the results of the cage experiments. A variety of

plant types would therefore be of benefit to perch as well as to roach.

The importance of the aquatic macrophytes in providing a bufferered environment for the young fish during the period of greatest vulnerability depends upon the size of the lake and the ratio of bank or littoral to open water. In a small lake virtually the whole area could be covered with aquatic vegetation. Consequently the effects of the macrophytes upon the ecosystem become of overriding importance because of the lack of open water.

The results of the diet study and the caging experiments suggest that the management of roach and perch populations in a fishery could be more effective if the two species were considered separately rather than as a coarse fish population. Perch have a more northerly distribution than roach (Maitland, 1972), and roach possibly grow better in eutrophic waters than oligotrophic, while perch abound and grow well in northern lakes (not responding favourably to high water temperatures in the same way as roach). Roach are a relatively plastic species, tolerating a wide range of conditions and possessing an ability to spawn on a variety of substrates. They are generalist feeders with flexible habits, omnivorous and capable of being herbivorous or carnivorous. Roach hybridise with other cyprinids with ease (Wheeler, 1976; Burrough, 1981), and may still be speciating. In contrast, perch possess fairly fixed feeding preferences partly because of their piscivorous adult habit. They are less adaptable than roach and could be termed a conservative species. Thorpe (1977a) states that perch possess a lower food conversion efficiency than some other species, and this has been implicated as one cause of declines in perch populations.

There are several references to the invasion of roach causing

a decline in other fish species in a water body. The introduction of roach to Ireland has resulted in a population explosion at the expense of the native rudd populations (Fitzmaurice, 1981). The mechanism governing this success is not clear but may be the greater ability of the roach to utilise a wide range of food resources. Burrough et al (1979) suggested that the reason for the new found dominance of roach over rudd and perch in Slapton Ley was due to the competitive superiority of the planktivorous 0+ roach.

A well documented expulsion of perch by roach occurred in the Klicava Reservoir in Czechoslovakia. Pivnicka and Svatora (1976, 1977) attributed the reduction in perch numbers to a decline in the number of female spawners, coupled with lowered fecundity and lower production rates than the roach in the same environmental conditions, as was found in the caging studies in Yateley.

The perch populations in Southern England have been reduced by outbreaks of perch ulcer disease from which the gravel-pit perch populations have never entirely recovered. This, plus competition from the roach and the lack of benthic food (possibly caused by the abundant tench) has led to them taking second place to the roach in the gravel-pit lakes.

From the results of the present study one can make suggestions as to the consequences of removing the aquatic macrophytes from gravel-pit lakes such as Farnborough.

Both roach and perch (and other coarse fish fry) would be more vulnerable to predation from older fish. This would be less serious in Farnborough than in other lakes because of the absence of pike (unconfirmed) and the low numbers of adult perch (Gee, 1976; Cook, 1979).

The surviving O+ roach would then compete with adult size selective roach for zooplankton food, already reduced by the predation pressure exerted by the adult fish (Cook, 1979). Daphnia would disappear because they would no longer have a refuge in the weedbeds. Bosmina was only intermittently available to the O+ roach in Farnborough and Ceriodaphnia was associated with the weedbeds and would also disappear. In the absence of both Bosmina and Ceriodaphnia the roach would have to expend more energy pursuing the remaining crustacea, the cyclopoid copepods. This, in turn would bring them into direct competition with the O+ perch.

The caging experiments showed that roach deprived of macrophytes did not have their growth rates reduced significantly while perch did, suggesting that the roach would outcompete the perch in a weedless situation because they are more adaptable. This would depend to some extent upon both the types of prey and the other fish species present in the water body.

The removal of macrophytes in a mixed community could therefore favour the roach. Reduced first year survival (due to greater predation by adult piscivores) could lead to better growth of the remaining roach and would be beneficial to a fishery in the long term.

Perch survival in Farnborough was poor in some years and this was possibly related to the lack of benthic food, one aspect of the study which merits further investigation. The removal of macrophytes would reduce the numbers of benthic invertebrates even more, so that the perch would have to feed entirely on plankton. Although removal of the slow growing tench might increase perch survival by reducing predation on the benthos the needs of the fishery would have to be considered before taking such a decision.

Therefore, the operation of a gravel pit as a fishery requires that managerial decisions on macrophyte removal are to some extent dictated by which species of fish would be of most value in the fishery, the results of this study indicating that in most situations the macrophytes do provide a beneficial influence.

BIBLIOGRAPHY

Alabaster, J. S. & Robertson, K. G. (1951). The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of roach (Rutilus rutilus (L.)), bream (Abramis brama (L.)) and perch (Perca fluviatilis (L.)). Anim. Behav. 9: 187-192

Al-Hussaini, A. H. (1949). On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: anatomy and histology. Quart. Journ. Micr. Sci. 90: 109-143

Allen, H.L. (1971). Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monogr. 41: 97-127.

Allen, K. R. (1935). The food and migration of the perch (Perca fluviatilis L.) in Windermere. J. Anim. Ecol. 4: 264-273

Alm, G. (1946). Reasons for the occurrence of stunted fish populations with special regard to the perch. Rep. Inst. Freshw. Res. Drottningholm. 25: 1-146

Alm, G. (1953). Maturity, mortality and growth of perch, Perca fluviatilis L., grown in ponds. Rep. Inst. Freshw. Res. Drottningholm. 35: 11-20

Amoros, C. (1980). Observations morphologiques et ecologiques sur Daphnia ambigua Scourfield, 1946 (Cladocera), espece nouvelle pour la France. Crustaceana 39: 247-254

Anderson, R. O. (1959). A modified flotation technique for sorting bottom-fauna samples. Limnol. Oceanogr. 4: 223-225

Bagenal, T. B. (1974). A buoyant net designed to catch freshwater fish larvae quantitatively. Freshwat. Biol. 4: 107-109

Bagenal, T. B. & Nellen, W. (1980). Sampling eggs, larvae and juvenile fish. EIFAC Tech. Paper No. 33: 13-36

Bagenal, T. B. & Tesch, F. W. (1978). Age and growth. In: Methods for assessment of fish production in freshwaters. 3rd. Ed. Ed. T.B.Bagenal Blackwells Scientific Press, Oxford.

Barber, W. J. (1976). Relationships between population density, feeding and growth of the roach (Rutilus rutilus L. 1758) and other coarse fish in a gravel-pit lake in Southern England. Unpublished Ph.D. Thesis, University of London.

Barber, W. E., Greenwood, J. G. & Crocos, P. (1979). Artificial seagrass- a new technique for sampling the community. Hydrobiologia 65: 135-140

Barton, B. A., Peter, R. E. & Paulencu, C. R. (1980). Plasma cortisol levels of fingerling rainbow trout (Salmo gairdneri) at rest, and subject to handling, confinement, transport, and stocking. Can. J. Fish. Aquat. Sci. 37: 805-811

Berrie, A. D. (1975). Detritus, micro-organisms and animals in fresh water. In: The role of terrestrial and aquatic organisms in decomposition processes. 17th. Symp. Brit. Ecol. Soc. Ed.J.M.Anderson an A.Macfadyen. p323-338

Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurosawa, H., Larsson, P. & Weglenska, T. (1976). A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419-456

Boulet, P. C. (1958). La perception visuelle du mouvement chez la perche et la seiche. Mem. Mus. Nat. d'Hist. Naturelle A. 17: 1-131

Bownik, L. J. (1970). The periphyton of the submerged macrophytes of Mikolajskie Lake. Ekol. Pol. 18: 503-520

Bracken, J. J. & Kennedy, M. P. (1967). A key to the identification of the eggs and young stages of coarse fish in Irish waters. Scient. Proc. R. Dubl. Soc. B. 2: 99-109

Brandl, Z. (1963). Prispevek k biologii litoralu lipenske udolni nadrze. (Contribution to the biology of the Lipno Water Reservoir). Zivocisna vyroba 8/3: 175-188

Brandl, Z., Brandlova, J. & Postolkova, M. (1970). The influence of submerged vegetation on the photosynthesis of phytoplankton in ponds. Rozpravy CSAV, rada MPV, 80(6): 33-62

Brandl, Z. & Fernando, C. H. (1975). Investigations of the feeding of carnivorous cyclopoids. Verh. int. Ver. Limnol. 19: 2959-2965

Braum, E. (1978). Ecological aspects of the survival of fish eggs, embryos and larvae. In: Ecology of freshwater fish production. Ed. S.D. Gerking. Blackwell Scientific Publications, Oxford.

Breck, J. E. & Kitchell, J. F. (1979). Effects of macrophyte harvesting on simulated predator-prey interactions. In: Aquatic macrophytes, lake management and ecosystem consequences of lake harvesting. Ed. Breck J.E., Prentki, R.T. and Loucks, O.L. Madison Centre for Biotic Systems, University of Wisconsin. pp. 211-228

Breder, C. M. Jr. (1959). Studies on social groupings in fishes. Bull. Amer. Mus. Nat. Hist. 117: 393-482

Brooks, J. L. & Dodson, S. I. (1965). Predation, body size and composition of plankton. Science 150: 28-35

Broughton, N. M., Jones, N. V. & Lightfoot, G. W. (1977). The growth of O-group roach in some Humberside waters. Proc. 8th. Brit. Coarse Fish Conf. 53-60

Broughton, N. M. & Jones, N. V. (1978). An investigation into the growth of O-group roach (Rutilus rutilus L.) with special reference to temperature. J. Fish Biol. 12: 345-357

Bubb, N. J. (1980). A large buoyant net designed to catch coarse fish fry quantitatively from shallow weed free water. Fish. Mgmt. 11: 29-34

Burgis, M. J. (1967). A quantitative study of reproduction in some species of Ceriodaphnia (Crustacea; Cladocera). J. Anim. Ecol. 36: 61-75

Burgis, M. J. (1971). An ecological study of the zooplankton in Lake George, Uganda. Unpublished Ph.D. Thesis, University of London.

Burgis, M. J. (1974). Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. Freshwat. Biol. 4: 535-541

Burgis, M. J. (1975). The biomass of cyclopoids in two Thames Valley reservoirs. Verh. int. Ver. Limnol. 19: 1834-1840

Burgis, M. J. & Dunn, I. G. (1978). Production in three contrasting ecosystems. In: Ecology of freshwater fish production. Ed. S.D. Gerking. Blackwell Scientific Publications, Oxford.

Burgis, M. J. & Walker, A. F. (1972). A preliminary comparison of the zooplankton in a tropical and a temperate lake (Lake George, Uganda and Loch Leven, Scotland). Verh. int. Ver. Limnol. 18: 647-655

Burns, C. W. (1968). The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. Limnol. Oceanogr. 13: 675-678

Burrough, R. J. (1981). Problems of natural hybridisation amongst cyprinids. Proc. 2nd. Brit. Freshw. Fish. Conf. 162-170

Burrough, R. J., Breggazi, P. R. & Kennedy, C. R. (1979). Interspecific dominance amongst three species of coarse fish in Slapton Ley, Devon. J. Fish Biol. 15: 535-544

Burrough, R. J. & Kennedy, C. R. (1979). The occurrence and natural alleviation of stunting in a population of roach, Rutilus rutilus (L.). J. Fish Biol. 15: 93-109

Cassie, R. M. (1971). Sampling and statistics. In: A manual on methods for the assessment of secondary productivity in fresh waters. Ed. W.T. Edmondson and G.G. Winberg. Blackwell Scientific Publications, Oxford.

Catchpole, C. K. & Tydeman, C. F. (1975). Gravel pits as new wetland habitats for the conservation of breeding bird communities. Biol. Conserv. 8: 47-59

Cattaneo, A. & Kalff, J. (1978). Seasonal changes in the epiphyte community of natural and artificial macrophytes in Lake Memphremagog (Que.&VT.). Hydrobiologia 60: 136-144

Chapman, D. W. (1978). Production in fish populations. In: Ecology of freshwater fish production, Ed. S.D. Gerking. Blackwell Scientific Publications, Oxford.

Chodorowski, A. (1975). Formation de populations bimodales chez les alevins de poissons carnassiers. Verh. int. Ver. Limnol. 19: 2546-2555

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962) Flora of the British Isles. 2nd. Ed. Cambridge University Press.

Coble, D. W. (1966). Dependence of total annual growth in yellow perch on temperature. J. Fish. Res. Bd. Can. 23: 15-20

Coles, T. F. (1981). The distribution of perch, Perca fluviatilis L. throughout their first year of life in Llyn Tegid, North Wales. J. Fish Biol. 18: 15-30

Cook, M. P. (1979). The interrelationships of fish and zooplankton in gravel-pit lakes. Unpublished Ph.D. Thesis, C.N.A.A.

Cragg-Hine, D. & Jones, J. W. (1969). The growth of dace Leuciscus leuciscus (L.), roach Rutilus rutilus (L.) and chub Squalius cephalus (L.) in Willow Brook, Northamptonshire. J. Fish Biol. 1: 59-82

Craig, J. F. (1974a). Population dynamics of perch, Perca fluviatilis L. in Slapton Ley, Devon. 1. Trapping behaviour, reproduction, migration, population estimates, mortality and food. Freshwat. Biol. 4: 417-431

Craig, J. F. (1974b). Population dynamics of perch, Perca fluviatilis L. in Slapton Ley Devon. 2. Age, growth, length-weight relationships and condition. Freshwat. Biol. 4: 433-444

Craig, J. F. (1978). A study of the food and feeding of perch, Perca fluviatilis L., in Windermere. Freshw. Biol. 8: 59-68

Crowder, L. B. & Cooper, W. E. (1979). The effects of macrophyte removal on the feeding efficiency and growth of sunfishes: evidence from pond studies. In: Aquatic macrophytes, lake management and ecosystem consequences of lake harvesting. Ed. Breck J.E., Prentki, R.T. and Loucks, O.L. Madison Centre for Biotic Systems, University of Wisconsin

de Nie, H. W., Bromley, H. J. & Vijverberg, J. (1980). Distribution patterns of zooplankton in Tjeukemeer, the Netherlands. J. Plankton Research 2: 317-334

Deelder, C. D. (1951) A contribution to the knowledge of stunted growth of perch (Perca fluviatilis) in Holland. Hydrobiologia 3: 357-378

Dickson, K. L., Cairns, J. Jr. & Arnold, J. C. (1971) An evaluation of the use of a basket-type artificial substrate for sampling macroinvertebrate organisms. Trans. Am. Fish. Soc. 100: 553-559

DiCostanzo, C. J. (1957). Growth of bluegill, Lepomis macrochirus, and pumpkinseed, L. gibbosus, of Clear Lake, Iowa. Iowa State College Journal of Science 32: 19-34

Dorgelo, J. & Koning, K. (1980). Avoidance of macrophytes and additional notes on avoidance of the shore by Acanthodiaptomus denticornis (Wierzejski, 1887) from Lake Pavin (Auvergne, France). Hydrobiol. Bull. 14: 196-203

Downing, J. A. (1981). In situ foraging responses of three species of littoral Cladocerans. Ecol. Monogr. 51: 85-103

Drenner, R. W., Strickler, J. R. & O'Brien, W. J. (1973). Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. J. Fish. Res. Bd. Can. 35: 1370-1373

Dumont, H. J. (1972). A competition based approach to the reverse vertical migration in zooplankton and its implication, chiefly based on a study of the interactions of Asplanchna priodonta (Gosse) with several crustacea Entomostraca. Int. Revue ges Hydrobiol. 57: 1-38

Dumont, H. J., Van de Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75-97

Duncan, A. (1975a). Production and biomass of three species of Daphnia co-existing in London reservoirs. Verh. int. Ver. Limnol. 19: 2858-2867

Duncan, A. (1975b). The importance of zooplankton in the ecology of reservoirs. Proceedings of a symposium on the effects of storage on water quality, Water Research Centre. Paper 9, 25pp.

Durbin, A. G. (1979). Food selection by plankton feeding fishes. In: Predator-prey systems in fisheries management. Ed. R.H. Stroud and H.E. Clepper. Sport Fishing Inst. Washington, D.C. p203:218

Edlund, A.-M. & Magnhagen, C. (1981). Food segregation and consumption suppression in two coexisting fishes, Pomatoschistus minutus and P. microps: an experimental demonstration of competiton. Oikos 36: 23-27

Eggers, D. M. (1976). Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. J. Fish. Res. Bd. Can. 33: 1964-1971

Egglishaw, H. J. (1967). The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. Dept. Agric. Fish. Scot. Freshw. Salm. Fish. Res. 38: 5-32

Elliot, J. M. (1972). Rate of gastric evacuation in brown trout, Salmo trutta L. J. Fish Biol. 2: 1-18

Elliot, J. M. (1977). Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publication No. 25, 2nd. Ed.

Engel, S. (1974). Effects of formalin and freezing on length, weight and condition factor of cisco and yellow perch. Trans. Am. Fish. Soc. 103: 136-138

Estabrook, G. F. & Dunham, A. E. (1976). Optimal diet as a function of absolute abundance, relative abundance and relative value of available prey. Amer. Nat. 110: 401-413

Fitzmaurice, P. (1981). The spread of roach Rutilus rutilus (L.) in Irish waters. Proc. 2nd. Brit. Freshw. Fish. Conf. 154-161

Flossner, D. (1964). Zur Cladocerenfauna des Stechlinsee-Gebiets. II Okologische Untersuchungen uber die litoralen Arten. Limnologica (Berl.) 2: 35-103

Flossner, D. (1972). Krebstiere, Crustacea: Kiemen-und-Blattfusser, Branchiopoda, Fischlause, Branchiura. Die Tierwelt Deutschlands. 60 Teil, 501pp.

Flossner, D. & Kraus, K. (1977). On the variability and taxonomy of Pleuroxus denticulatus Birge (Cladocera: Chydoridae). J. Fish. Res. Bd. Can. 34: 463-476

Fryer, G. (1968). Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. Phil. Trans. R. Soc. Lond. B. 254: 221-285

Fryer, G. (1980). Acidity and species diversity in freshwater crustacean faunas. Freshwat. Biol. 10: 41-45

Fryer, G. & Forshaw, O. (1979). The freshwater crustacea of Rhum (Inner Hebrides)- a faunistic and ecological survey. Biol. J. Linn. Soc. 11: 333-367

Furnass, T. I. (1979). Laboratory experiments on prey selection by perch fry (Perca fluviatilis). Freshwat. Biol. 9: 33-43

Gaevskaya, N. S. (1956). The role of higher aquatic plants in the nutrition of animals of freshwater basins. N.L.L. Trans. D. Maitland. 3 vols.

Gee, A. S. (1976). A comparison of growth rates of coarse fish in gravel-pit lakes in South-East England and of population structure in selected lakes. Unpublished Ph.D. Thesis, University of London.

Gee, A. S. (1978). The distribution and growth of coarse fish in gravel-pit lakes in South-East England. Freshwat. Biol. 8: 385-394

George, D. G. (1976). Life cycle and production of Cyclops vicinus in a shallow eutrophic reservoir. Oikos 27: 101-110

George, D. G. (1981). Zooplankton patchiness. Rep. Freshw. Biol. Assoc. 49: 32-44

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

George, D. G. & Owen, G. H. (1978). A new tube sampler for crustacean zooplankton. Limnol. Oceanogr. 23: 563-566

Gliwicz, Z. M., Ghilarov, A. & Pijanowska, J. (1981). Food and predation as major factors limiting two natural populations of Daphnia cucullata Sars. Hydrobiologia 80: 205-218

Goldspink, C. R. & Goodwin, D. (1979). A note on the age composition, growth rate and food of perch Perca fluviatilis (L.) in four eutrophic lakes, England. J. Fish Biol. 14: 489-505

Goulden, C. E. (1971). Environmental control of the abundance and distribution of the chydorid Cladocera. Limnol. Oceanogr. 16: 320-331

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

Grigorash, V. A., Spanovskaya, V. D. & Lebedeva, T. V. (1973). The availability of food to underyearling roach (Rutilus rutilus (L.)) in Mozhaysk Reservoir. J. Ichthyol. 12: 457-464

Guissani, G. & De Bernardi, R. (1977). Food selectivity in Coregonus sp. of Lago Maggiore: an energetical approach. Mem. Ist. Ital. Idrobiol. 34: 121-130

Guma'a, S. A. (1978a). On the early growth of 0+ perch, Perca fluviatilis, in Windermere. Freshwat. Biol. 8: 213-220

Guma'a, S. A. (1978b). The food and feeding habits of young perch, Perca fluviatilis, in Windermere. Freshwat. Biol. 8: 177-187

Gurney, R. (1933). British Freshwater Copepoda, Vol. III. Cyclopoida. Ray Society Monographs No. 20, London.

Hall, D. J., Cooper, W. E. & Werner, E. E. (1970). An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928

Hall, D. J., Threlkeld, S. T., Burns, C. W. & Crowley, P.H. (1976). The size-efficiency hypothesis and the size-structure of zooplankton communities. Ann. Rev. Ecol. Syst. 7: 177-208

Haney, J. F. & Hall, D. J. (1973). Sugar-coated Daphnia: a preservation technique for Cladocera. Limnol. Oceanogr. 18: 331-333

Harding, J. P. & Smith, W. A. (1974). A key to the British freshwater cyclopid and calanoid copepods. Freshwater Biological Association, Scientific Publications No. 18. 2nd. Ed.

Harnisch, O. (1950). Vergleichende Beobachtungen zur Nahrungserwerb von Daphnia und Ceriodaphnia. Zool Jahrb. Syst. 78: 173-192

Hartley, P. H. T. (1947). Natural history of some British freshwater fishes. Proc. Zool. Soc. Lond. 117: 129-206

Hartwright, T. U. (1974). Worked out gravel land: a challenge and an opportunity. Environ. Conserv. 1: 139-143

Hasler, A. D. & Jones, E. (1949). Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30: 359-365

Healey, A. (1954). Perch (Perca fluviatilis L.) in three Irish lakes. Scient. Proc. R. Dubl. Soc. 26: 397-407

Heck, K. L. Jr. & Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. J. exp. mar. Biol. Ecol. 53: 125-134

Hellawell, J. M. (1972). The growth, reproduction and food of the roach Rutilus rutilus (L.) of the River Lugg, Herefordshire. J. Fish Biol. 4: 469-486

Hewitt, D. P. (1979). Tests to confirm quantitative sampling of young fish by the Bagenal buoyant net. Freshwat. Biol. 9: 339-341

Hillbricht-Ilkowska, A. (1965). The effect of the frequency of sampling on the picture of the occurrence and dynamics of plankton rotifers. Ekol. Pol. A. 13: 101-112

Hillbricht-Ilkowska, a. & Weglenska, T. (1970). The effect of sampling frequency and the method of assessment on the production values obtained for several zooplankton species. Ekol. Pol. a. 18: 539-557

Hillbricht-Ilkowska, a. & Weglenska, T. (1973). Experimentally increased fish stock in the pond type Lake Warniak. Numbers, biomass and production of zooplankton. Ekol. Pol. 21: 533-551

Howard-Williams, C. & Lenton, G. M. (1975). The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. Freshwat. Biol. 5: 445-459

Hrbacek, J. (1962). Species composition and the amount of zooplankton in relation to the fishstock. Rozpravy CSAV, rada MPV, 72(10): 1-116

Hrabcek, J. (1977). Competition and predation in relation to species composition of freshwater zooplankton, mainly Cladocera. In: Aquatic microbial communities. Ed. J. Cairns. Jr. Garland Publishing Inc. p 305-353

Hutchinson, G. E. (1967). A treatise on limnology. Vol II. Introduction to lake biology and the limnoplankton. New York: Wiley. 1115pp

Hynes, H. B. N. (1950). The food of freshwater sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius) with a review of the methods used in the study of the food of fishes. J. Anim. Ecol. 19: 36-58

Hyslop, E. J. (1980). Stomach contents analysis- a review of methods and their application. J. Fish Biol. 17: 411-429

Il'ina, L. K. (1973). The behaviour of perch (Perca fluviatilis L.) underyearlings of different ecological groups in the progeny of a single pair of spawners. J. Ichthyology 13: 294-304

Ivlev, V. S. (1961). Experimental ecology of the feeding of fishes. Transl. D. Scott. Yale Univ. Press, New Haven, Conn. 302pp.

Jamieson, C. D. (1980). The predatory feeding of copepodid stages III to adult Mesocyclops leuckarti Claus. In: Evolution and ecology of zooplankton communities. Ed. C. Kerfoot, University Press, N. England. p518-537

Jezierka, B. (1974). The effect of various types of food on the growth and chemical composition of the body of perch (Perca fluviatilis L.) in laboratory conditions. Pol. Arch. Hydrobiol. 21: 467-479

Johnson, D. & Walker, A. F. (1974). The zooplankton of Loch Leven, Kinross.
Proc. R. Soc. Edinb. (B) 74: 285-294

Jones, H. R., Lack, T. J. & Jones, C. S. (1979). Population dynamics and production of Daphnia hyalina var lacustris in Farmoor 1, a shallow eutrophic reservoir. J. Plankton Research 1: 45-65

Kairesalo, T. (1980). Diurnal fluctuations within a littoral plankton community in oligotrophic Lake Paajarvi, southern Finland. Freshwat. Biol. 10: 533-537

Keast, A. (1977). Diet overlaps and feeding relationships between the year classes in the yellow perch (Perca flavescens). Env. Biol. Fish. 2: 53-70

Keast, A. & Welsh. L. (1968). Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Bd. Can. 25: 1133-1144

Kershaw, K. A. (1973). Quantitative and dynamic plant ecology. Edward Arnold Ltd. London 2nd. Ed. 308pp.

Kionka, B. C. & Windell, J. T. (1972). Differential movement of digestible and indigestible food fractions in rainbow trout, Salmo gairdneri. Trans. Am. Fish. Soc. 101: 112-115

Klemetsen, A. (1973). Pelagic, plankton-eating perch. Astarte 6: 27-33

Korinkova, J. (1971). Quantitative relations between submerged macrophytes and populations of invertebrates in a carp pond. Hidrobiologia (Bucharesti). 12: 377-382

Koonce, J, F., Bagenal, T. B., Carline, R. F., Hokanson, K. E. F. & Nagiec, M. (1977). Factors influencing year-class strength of percids: a summary and a model of temperature effects. J. Fish. Res. Bd. Can. 34: 1900-1909

Krecker, F. H. (1939). A comparative study of the animal populations of certain submerged aquatic plants. Ecology 20: 553-562

Lane, P. A. (1975). The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. Ecol. Monogr. 45: 307-335

Langhans, V. (1911). Entomostraken und Teichmacrophyten. Arch. Hydrobiol. (Plankt.) 15: 481-510

Lange, N. O. (1960). Development stages of the roach in varying ecological conditions. Trudy Inst. Morfol. Zhivot. im AN Severtsova 28: 5-40. BLLD Transl. No. RTS 10348

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

Le Cren, E. D. (1958). Observations on the growth of perch (Perca fluviatilis L.) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27: 287-334

Le Cren, E. D. (1962). The efficiency of reproduction and recruitment in freshwater fish. In: The exploitation of natural animal populations. Ed. E.D.Le Cren and M.W.Holdgate. Blackwell Scientific Publications. p 283-296

Le Cren, E. D. (1972). Fish production in freshwaters. Symp. Zool. Soc. Lond. No. 29: 115-133

Le Cren, E. D. (1976). The productivity of freshwater communities. Phil. Trans. R. Soc. Lond. B. 274: 359-374

Le Cren, E. D., Kipling, C. & McCormack, J. C. (1977). A study of the numbers, biomass and year-class strengths of perch (Perca fluviatilis L.) in Windermere from 1941 to 1966. J. Anim. Ecol. 46: 281-307

Levins, R. (1968). Evolution in changing environments: some theoretical explorations. Princeton University Press. 120pp.

Lightfoot, G. W. (1976). A study of young roach (Rutilus rutilus) in the River Hull. Unpublished Ph.D. Thesis, University of Hull.

Lim, R. P. & Fernando, C. H. (1978). Production of Cladocera inhabiting the vegetated littoral of Pinehurst Lake, Ontario, Canada. Verh. int. Ver. Limnol. 20: 225-231

Lovegrove, T. (1966). The determination of the dry weight of plankton and the effect of various factors on the values obtained. In: Some contemporary studies in Marine Science. (Ed. R.S.K. Barnes. p 429-467

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

Macan, T. T. (1977a). A twenty-year study of the fauna in the vegetation of a moorland fishpond. Arch. Hydrobiol. 81: 1-24

Macan, T. T. (1977b). The fauna in the vegetation of a moorland fishpond as revealed by different methods of collecting. Hydrobiologia 55: 3-15

Macan, T. T. & Kitching, A. (1972). Some experiments with artificial substrata. Verh. int. Ver. Limnol. 18: 213-220

Macan, T. T. & Kitching, A. (1976). The colonisation of squares of plastic suspended in freshwater. Freshwat. Biol. 6: 33-40

MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. Amer. Nat. 100: 603-609

Maitland, P. S. (1965). The feeding relationships of salmon, trout, minnows, stone loach and three -spined sticklebacks in the River Endrick, Scotland. J. Anim. Ecol. 34: 109-133

Maitland, P. S. (1972). A key to the British freshwater fishes of the British Isles (with notes on their distribution and ecology). Freshwater Biological Association Scientific Publications No. 27

Mann, R. H. K. (1973). Observations on the age, growth, reproduction and food of the roach Rutilus rutilus (L.) in two rivers in Southern England. J. Fish Biol. 5: 707-736

Mann, R. H. K. (1978). Observations on the biology of the perch, Perca fluviatilis, in the River Stour, Dorset. Freshwat. Biol. 8: 229-239

Mann, R. H. K. & Orr, D. R. O. (1969). A preliminary study of the feeding relationships of fish in a hard-water and a soft-water stream in Southern England. J. Fish Biol. 1: 31-44

Markosova, R. (1980). Effect of submerged substrates quality on the periphytic macrofauna in ponds. Vest. Cs. spol. Zool. 44: 46-52

Marshall, E. J. P. & Westlake, D. F. (1978). Recent studies on the role of aquatic macrophytes in their ecosystem. Proc. EWRS 5th. Symp. on Aquatic Weeds. 43-51

Mason, C. F. (1977). Populations and production of benthic animals in two contrasting shallow lakes in Norfolk. J. Anim. Ecol. 46: 147-172

Mathews, C. P. (1971). Contribution of young fish to total production of fish in the River Thames near Reading. J. Fish Biol. 3: 157-180

Mazeaud, M. M., Mazeaud, F. & Donaldson, E. M. (1977). Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. Soc. 106: 201-212

Meier, P. G., Penrose, D. L. & Polak, L. (1979). The rate of colonisation by macro-invertebrates on artificial substrate samplers. Freshwat. Biol. 9: 381-392

Meyers, D. G. (1980). Diurnal vertical migration in aquatic microcrustacea: light and oxygen responses of littoral zooplankton. In: Evolution and ecology of zooplankton communities. Ed. C. Kerfoot, University Press, N. England.

Mitchell, D. S. (1974). (Ed.) Aquatic vegetation and its use and control. Paris. Unesco. 138 pp.

Monakov, A. V. (1969). The zooplankton and the zoobenthos of the White Nile and adjoining waters in the Republic of the Sudan. Hydrobiologia 33: 161-185

Morrison, B. R. S. (1977). Observations on the tapeworm (Ligula intestinalis) a parasite of roach (Rutilus rutilus) in the Lake of Menteith, Perthshire. Proc. 8th. Brit. Coarse Fish Conf. 100-107

Mortensen, E. (1977). Density-dependent mortality of trout fry (Salmo trutta L.) and its relationship to the management of small streams. J. Fish Biol. 11: 613-617

Moss, B. (1980). The relative importance of different producing communities. In: The functioning of freshwater ecosystems. Ed. E.D.Le Cren & R.H.Lowe-McConnell.

Munro, I. G. (1977). The zooplankton of Bough Beech reservoir and its possible sources of origin. Trans. Kent Fld. Club. 6: 101-110

Munro, I. G. & Bailey, R. G. (1980). Early composition and biomass of the crustacean zooplankton in Bough Beech Reservoir, south-east England. Freshwat. Biol. 10: 85-96

Munro, I. G. & White, R. W. G. (1975). Comparison of the influence of temperature on the egg development and growth of Daphnia longispina O.F. Muller (Crustacea: Cladocera) from two habitats in Southern England. Oecologia (Berl.) 20: 157-165

Murdoch, W. M., Avery, S. & Smyth, M. E. B. (1975). Switching in predatory fish. Ecology 56: 1094-1105

Neill, W. E. (1975). Experimental studies of microcrustacean competition, community composition and efficiency of resource utilisation. Ecology 56: 809-826

Nichols, S. A. (1979). Macrophyte biology to management techniques: bridging the information gap. In: Aquatic macrophytes, lake management and ecosystem consequences of lake harvesting. Ed. Breck J.E. p63-78

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. (1975). SPSS: Statistical package for the social science. 2nd. Edition, McGraw Hill, New York.

Noble, R. L. (1975). Growth of young yellow perch, Perca flavescens in relation to zooplankton populations. Trans. Am. Fish. Soc. 104: 731-741

Nilsson, N.- A. (1959). On the food competition between two species of Coregonus in a North-Swedish lake. Rep. Inst. Freshw. Res. Drottningholm 39: 146-161

Nilsson, N.- A. (1965). Food segregation between salmonoid species in North Sweden. Rep. Inst. Freshw. Res. Drottningholm 46: 58-78

Northcott, D. (1979). The importance of aquatic macrophytes in the provision of crustacean zooplankton food for young fish. Proc. 1st. Brit. Freshw. Fish. Conf. 123-134

Nyberg, P. (1979). Production and food consumption of perch, Perca fluviatilis L., in two Swedish forest lakes. Rep. Inst. Freshwat. Res. Drottningholm. 58: 140-157

O'Grady, K. T. & Spillett, P. B. (1981). The production of carp (Cyprinus carpio) in disused filter beds. Proc. 2nd. Brit. Freshw. Fish. Conf. 17-28

Ottaway, E. M. & Simkiss, K. (1977). A method for assessing factors influencing "false check" formation in fish scales. J. Fish Biol. 11: 681-687

Otto, C. & Svensson, B. S. (1981). How do macrophytes growing in or close to water reduce their consumption by aquatic herbivores. Hydrobiologia 78: 107-112

Patalas, K. (1971). Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, Northwestern Ontario. J. Fish. Res. Bd. Can. 28: 231-244

Pedley, R. B. & Jones, J. W. (1978). The comparative feeding behaviour of brown trout, Salmo trutta L. and Atlantic Salmon, Salmo salar L. in Llyn Dwythwch, Wales. J. Fish Biol. 12: 239-256

Pejler, B. (1973). On the taxonomy of limnoplanktic Daphnia species in Northern Sweden. ZOON 1: 23-27

Pennak, R. W. (1957). Species composition of limnetic zooplankton communities. Limnol. Oceanogr. 2: 222-232

Pennak, R. W. (1962). Quantitative zooplankton sampling in littoral vegetation areas. Limnol. Oceanogr. 7: 487-489

Pennak, R. W. (1966). Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. Trans. Am. Microsc. Soc. 85: 329-349

Pennak, R. W. (1973). Some evidence for aquatic macrophytes as repellants for a limnetic species of Daphnia. Int. Revue ges Hydrobiol. 58: 569-576

Pieczynska, E. (1970). Periphyton in the trophic structure of freshwater ecosystems. Pol. Arch. Hydrobiol. 17: 141-147

Pieczynska, E. (1976). Selected problems of lake littoral ecology. Institute of Zoology, University of Warsaw.

Pieczynska, E. & Ozimek, T. (1976). Ecological significance of lake macrophytes. Int. J. Ecol. Environ. Sci. 2: 115-128

Pieczynska, E. & Spodniewska, I. (1963). Occurrence and colonisation of periphyton organisms in accordance with the type of substrate. Ekol. Pol. A. 11: 533-545

Pitcher, T. J. (1980). Some ecological consequences of fish school volumes. Freshw. Biol. 10: 539-544

Pivnicka, K. & Svatora, M. (1976). The abundance, growth and production of the perch population in the Klicava Reservoir during the years 1963-64 and 1967-72. Vest. Cs. spol. Zool. 40: 32-40

Pivnicka, K. & Svatora, M. (1977). Factors affecting the shift in predominance from Eurasian perch (Perca fluviatilis) to roach (Rutilus rutilus) in the Klicava Reservoir, Czechoslovakia. J. Fish. Res. Bd. Can. 34: 1571-1575

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

Prejs, A. & Jackowska, H. (1973). Lake macrophytes as the food of roach (Rutilus rutilus L.) and rudd (Scardinius erythrophthalmus). Ekol. Pol. 26: 429-438

Puncochar, P. (1971). On the ocurrence of water mites (Hydrachnellae) in the submerged vegetation of a carp pond. Proc. 3rd. Int. Congress. Acarology, Prague, 1971. 173-175

Pycha, R. L. & Smith, L. L. Jr. (1955). Early life history of the yellow perch, Perca flavescens (Mitchill) in the Red Lakes, Minnesota. Trans. Am. Fish. Soc. 84: 249-260

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. Quart. Rev. Biology 52: 137-154

Quade, H. W. (1969). Cladoceran faunas associated with aquatic macrophytes in some lakes in Northwestern Minnesota. Ecology 50: 170-179

Ricker, W. E. (1937). The food and the food supply of sockeye salmon (Oncorhynchus nerka Walbaum) in Cultus Lake, British Columbia. J. Biol. Bd. Can. 3(5): 450-468

Ricker, W. E. (1958). Computations and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191. 382pp

Ridenhour, R. L. (1960). Abundance, growth and food of young game fish in Clear Lake, Iowa, 1949 to 1957. Iowa State Journal of Science 35: 1-23

Rosine, W. R. N. (1955). The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. Ecology 36: 308-314

Rudenko, G. P. (1971). Biomass and abundance in a roach-perch lake. J. Ichthyol. 11(4): 524-535

Rybak, M. & Rybak, J. (1964). Crustacea of the summer plankton in the littoral of lakes in the Wegorzewo District. Ekol. Pol. A. 12: 147-158

Rybak, M., Rybak, J. I. & Tarwid, K. (1964). Differences in crustacea plankton based on the morphological character of the littoral of the lakes. Ekol. Pol. 12: 159-171

Schneider, J. C. (1973a). Density dependent growth and mortality of yellow perch in ponds. Fish. Res. Rep. Mich. Dep. Nat. Resources No. 1975, 18pp

Schneider, J. C. (1973b). Rate of food digestion by yellow perch (Perca flavescens) in relation to size of perch, size and type of food and temperature. Fish. Res. Rep. Mich. Dep. Nat. Resources No. 1803, 20pp

Schoener, J. W. (1971). Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404

Scourfield, D. J. (1937). An Alona and a Pleuroxus new to Britain (Alona weltneri and Pleuroxus denticulatus). J. Quekett Micr. Cl. 2(10): 71-76

Scourfield, D. J. (1946). A short spined Daphnia presumably belonging to the longispina group- D. ambigua n. sp. J. Quekett Micr. Cl. 4(11): 127-131

Scourfield, D. J. & Harding, J. P. (1966). A key to the British species of freshwater Cladocera with notes on their ecology. Freshwater Biological Association, Scientific Publications No. 5. 3rd. Ed.

Shafi, M. & Maitland, P. S. (1971). The age and growth of perch (Perca fluviatilis L.) in two Scottish Lochs. J. Fish Biol. 3: 39-57

Shiel, R. J. (1976). Associations of Entomostraca with weedbed habitats in a billabong of the Goulborn River, Victoria. Aust. J. Mar. Freshwater Res. 27: 533-549

Siebeck, H. O. (1980). Optical orientation of pelagic crustaceans and its consequences in the pelagic and littoral zones. In: Evolution and ecology of zooplankton communities. Ed. C. Kerfoot, University Press, N. England.

Sladeckova, A. (1962). Limnological investigation methods for the periphyton ("aufwuchs") community. Bot. Rev. 28: 286-350

Smid, P. & Priban, K. (1978). Microclimate in Fish pond littoral ecosystems. In: Pond littoral ecosystems, structure and functioning (Czech. IBP Wetland Project). Ed. D.Dykyjova and J.Kvet. Springer-Verlag, Ecological Studies No. 28

Smirnov, N. N. (1963), On inshore Cladocera of the Volga Water Reservoir. Hydrobiologia 21: 166-173

Smirnov, N. N. (1971). Fauna of the U.S.S.R. Crustacea. Vol. I. No. 2. Chydoridae. Academy of Sciences of the U.S.S.R. Israel Program for Scientific Translations 1974.

Smock, L. A. & Stoneburner, D. L. (1980). The response of macroinvertebrates to aquatic macrophyte decomposition. Oikos 35: 397-403

Smyly, W. J. P. (1952a). Observations on the food of the fry of perch (Perca fluviatilis Linn.) in Windermere. Proc. Zool. Soc. Lond. 122: 407-416

Smyly, W. J. P. (1952b). The Entomostraca of the weeds of a moorland pond. J. Anim. Ecol. 21: 1-11

Smyly, W. J. P. (1955). Comparison of the Entomostraca of two artificial moorland ponds in Windermere. Verh. int. Ver. Limnol. 12: 421-424

Smyly, W. J. P. (1957). Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere. Hydrobiologia 11: 59-72

Smyly, W. J. P. (1976). Some effects of enclosure on the zooplankton in a small lake. Freshwat. Biol. 6: 241-251

Smyly, W. J. P. & Collins, V. G. (1975). The influence of microbial food sources and aeration on the growth of Ceriodaphnia quadrangula (O.F.Muller)(Crustacea: Cladocera) under experimental conditions. Freshwat. Biol. 5: 251-256

Southwood, T. R. E. (1978). Ecological methods. Chapman and Hall, London. 524pp

Specker, J. L. & Schreck, C. B. (1980). Stress responses to transportation and fitness for marine survival in coho salmon (Oncorhynchus kisutch) smolts. Can. J. Fish. Aquat. Sci. 37: 765-769

Stavn, R. H. (1971). The horizontal-vertical distribution hypothesis: Langmuir circulations and Daphnia distributions. Limnol. Oceanogr. 16: 453-466

Steel, J. A. (1972). The application of fundamental limnological research in water supply system design and management. Symp. Zool. Soc. Lond. No. 29: 41-6

Stott, B. (1967). The movements and population densities of roach (Rutilus rutilus (L.)) and gudgeon (Gobio gobio (L.) in the River Mole. J. Anim. Ecol. 36: 407-423

Straskraba, M. (1963). Share of the littoral region in the productivity of two fishponds in Southern Bohemia. Rozpravy CSAV, rada MPV 73(13): 1-63

Straskraba, M. (1965). Contributions to the productivity of the littoral region of pools and ponds. I. Quantitative study of the littoral zooplankton of the rich vegetation of the backwater Labicko. Hydrobiologia 26: 421-443

Straskraba, M. (1967). Quantitative study on the littoral zooplankton of the Poltruba backwater with an attempt to disclose the effect of fish. Rozpravy CSAV, rada MPV 77(11): 7-34

Sweeting, R. A. (1976). Studies on Ligula intestinalis (L.) effects on a roach population in a gravel pit. J. Fish Biol. 9: 515-522

Swingle, H. S. (1968). Biological means of increasing productivity in ponds. FAO United Nations Fish. Rep. 44(4): 243-257

Swingle, H. S. & Smith, E. V. (1941). The management of ponds with stunted fish populations. Trans. Am. Fish. Soc. 71: 102-105

Szlauer, L. (1963). Diurnal migrations of minute invertebrates inhabiting the zone of submerged hydrophytes in a lake. Schweiz. z. Hydrol. 25: 56-64

Szlauer, L. (1965). The refuge of plancton animals before models of plancton-eating animals. Pol. Arch. Hydrobiol. XVIII 26(1): 89-95

Taylor, B. (1980). Size-selective predation on zooplankton. In: Evolution and ecology of zooplankton communities. Ed. C. Kerfoot, University Press, N. England.

Thorpe, J. E. (1974). Trout and perch populations at Loch Leven, Kinross. Proc. R. Soc. Edinb.(B). 74: 295-313

Thorpe, J. E. (1977a). Synopsis of biological data on the perches Perca fluviatilis Linnaeus 1758 and Perca flavescens Mitchill 1814. F.A.O. Fisheries Synopsis No. 113

Thorpe, J. E. (1977b). Daily ration of adult perch Perca fluviatilis L. during summer in Loch Leven, Scotland. J. Fish Biol. 11: 55-68

Tonolli, V. (1971). Methods of collection of zooplankton. In: A manual on methods for the assessment of secondary productivity in fresh waters. Ed. W.T. Edmondson and G.G. Winberg.

Treasurer, J. W. (1978). Sampling larval and juvenile fish populations in freshwater. Fish. Mgmt. 9: 6-17

Vijverberg, J. (1980). Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, the Netherlands. Freshwat. Biol. 10: 317-340

Vijverberg, J. & Frank, Th. H. (1976). The chemical composition and energy contents of freshwater copepods and cladocerans in relation to their size. Freshwat. Biol. 6: 333-345

Vince, S., Valiela, I., Backus, N. & Teal, J. M. (1976). Predation by the salt marsh killifish Fundulus heteroclitus (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. exp. mar. Biol. Ecol. 23: 255-266

Wankowski, J. W. J. & Thorpe, J. E. (1979). The role of food particle size in the growth of juvenile Atlantic salmon (Salmo salar L.). J. Fish Biol. 14: 351-370

Ware, D. M. (1973). Risk of epibenthic prey to predation by rainbow trout (Salmo gairdneri). J. Fish. Res. Bd. Can. 30: 787-797

Weatherly, A. H. (1972). Growth and ecology of fish populations. Academic press 293pp.

Weglenska, T. (1971). The influence of various concentrations of natural food on the development, fecundity and production of planktonic crustacean filtrators. Ekol. Pol. 19: 427-473

Werner, E. E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Can. 31: 1531-1535

Werner, E. E. & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55: 1042-1052

Werner, E. E. & Hall, D. J. (1979). Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256-264

Wetzel, R. G. (1974). A comparative study of primary production of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. Int. Revue. ges Hydrobiol. 49: 1-61

Wetzel, R. G. & Hough, R. A. (1973). Productivity and role of aquatic macrophytes in lakes. An assessment. Pol. Arch. Hydrobiol. 20: 9-19

Wetzel, R. G. & Manny, B. A. (1972). Secretion of dissolved organic carbon and nitrogen by aquatic macrophytes. Verh. int. Ver. Limnol. 18: 162-170

Wheeler, A. (1976). On the populations of roach (Rutilus rutilus), rudd (Scardinius erythrophthalmus) and their hybrid in Esthwaite Water, with notes on the distinctions between them. J. Fish Biol. 9: 391-400

White, R. W. G. (1975). An ecological study of fish and plankton populations in sewage effluent lagoons. Unpublished Ph.D. Thesis, University of London.

White, R. W. G. & Williams, W. P. (1978). Studies of the ecology of fish populations in the Rye Meads sewage effluent lagoons. J. Fish Biol. 13: 379-400

Whiteside, M. C. (1970). Danish Chydorid Cladocera: modern ecology and core studies. Ecol. Monogr. 40: 79-118

Whiteside, M. C. (1974). Chydorid (Cladocera) ecology: seasonal patterns and abundance of populations in Elk Lake, Minnesota. Ecology 55: 538-550

Whiteside, M. C. & Williams, J. B. (1975). A new sampling technique for aquatic ecologists. Verh. int. Ver. Limnol. 19: 1534-1539

Whiteside, M. C., Williams, J. B. & White, C. P. (1978). Seasonal abundance and pattern of chydorid cladocera in mud and vegetative habitats. Ecology 59: 1177:1188

Wilkonska, H. & Zuromska, H. (1978). Diurnal variability in occurrence of fry in the shallow littoral of the "warm" Lichenskie Lake. Rozc. Nauk. Roln. 99(H) 21: 175-191

Williams, W. P. (1965). The population density of four species of freshwater fish, roach (Rutilus rutilus (L.)), bleak (Alburnus alburnus (L.)), dace (Leuciscus leuciscus (L.)), and perch (Perca fluviatilis L.) in the River Thames at Reading. J. Anim. Ecol. 34: 173-185

Williams, W. P. (1967). The growth and mortality of four species of fish in the River Thames at Reading. J. Anim. Ecol. 36: 695-720

Windell, J. T. (1971). Food analysis and rate of digestion. In: Methods for assessment of fish production in fresh waters. Ed. W.E.Ricker, 2nd. Ed. Blackwells Scientific Publications, Oxford.

Young, D. W. (1945). A limnological investigation of periphyton in Douglas Lake, Michigan. Trans. Am. Micros. Soc. 64(1): 1-20

Zaret, T. T. (1972). Predators, invisible prey and the nature of polymorphism in the Cladocera. Limnol. Oceanogr. 17: 171-184

Zuromska, H. (1967). Some causes of mortality of roach (Rutilus rutilus L.) eggs and larvae on lake spawning grounds. Roczn. Nauk. Roln. 90(H). 3: 557-579

Appendix 1

Key to abbreviations for invertebrates

Sida	Sida crystallina
Diaph	Diaphanosoma brachyurum
D.amb	Daphnia ambigua
D.lon	D. longispina
Scaph(o)	Scapholeberis mucronata
Simo	Simocephalus vetulus
Cerio	Ceriodaphnia pulchella
Bos	Bosmina longirostris
Chydo	Chydorus sphaericus
Polyph	Polyphemus pediculus
Diapt	Diaptomus gracilis
Cyclo	Cyclops spp.
Naup	Nauplii
Harp	Harpacticoida
Asplan	Asplanchna priodonta
Rot	Keratella spp. Brachionus sp.
Kerat	Keratella quadrata/cochlearis
Ostr	Ostracoda
Macro	Macro-invertebrates
Acrop	Acroperus harpae
A.aff	Alona affinis
A.gut	Alona guttata
Eury	Eurycercus lamellatus
P.den	Pleuroxus denticulatus

KEY TO APPENDIX 2.

DATE	1977
146	26 MAY
140	26 JUNE
160	9 JUNE
178	27 JUNE
188	7 JULY
206	25 JULY
221	9 AUGUST
234	22 AUGUST
245	2 SEPT.
255	12 SEPT.
269	26 SEPT.
283	10 OCT.
298	25 OCT.
312	9 NOV.
327	24 NOV.
340	7 DECEM.
347	14 DECEM.

DATE	1978
179	28 JUNE
191	10 JULY
198	17 JULY
214	2 AUGUST
229	17 AUGUST
246	3 SEPT.
255	12 SEPT.
272	29 SEPT.

DATE	1979
164	13 JUNE
206	25 JULY
250	7 SEPT.

SITE

Farnborough

1 Open water
2 Elodea
3 Sparsanium and Typha
4 Potamogeton natans
5 P.natans/Elodea
7 General marginal

Yateley

1 Open water
2 Elodea
3 Elodea/Typha
4 Non-weed case
5 Weed case

Microcrustacea in Farnborough

SPEC1 SIDA SPEC2 D.LONGISPINA SPEC3 D.AMBIGUA SPEC4 SCAPHOLEBERIS
SPEC5 SIMOCEPHALUS SPEC6 C.PULCHELLA SPEC7 C.MEGOPS SPEC8 BOSMINA
SPEC9 ILYOCRYPTUS SPEC10 EURYCERCUS SPEC11 GRAPTOLEBERIS SPEC12 ACROPERUS
SPEC13 LEYDIGIA SPEC14 A.RECTANGULA SPEC25 A.AFFINIS SPEC16 A.GUTTATA
SPEC17 A.COSTATA SPEC18 A.INTERMEDIA SPEC19 P.DENTICULATUS SPEC20 P.ADUNCUS
SPEC21 P.UNCINATUS SPEC22 CHYDORUS SPEC23 POLYPHYEMUS SPEC 24 CYCLOPS
SPEC25 DIAPTOMUS SPEC26 NAUPLII SPEC27 PSEUDOCHYDORUS

Microcrustacea in Yateley

SPEC1 DIAPHANOSOMA SPEC2 D.LONGISPINA SPEC3 C.PULCHELLA SPEC4 BOSMINA
SPEC5 EURYCERCUS SPEC6 GRAPTOLEBERIS SPEC7 ACROPERUS SPEC8 A.RECTANGULA
SPEC9 A.GUTTATA SPEC10 P.DENTICULATUS SPEC11 P.ADUNCUS SPEC12 CHYDORUS
SPEC13 POLYPHEMUS SPEC14 CYCLOPS SPEC15 DIAPTOMUS SPEC16 HARPACTICOIDS
SPEC17 NAUPLII SPEC18 ASPLANCHNA SPEC 19 SIMOCEPHALUS SPEC20 SIDA
SPEC21 SCAPHOLEBERIS SPEC22 C.MEGOPS SPEC23 A.AFFINIS SPEC24 A.INTERMEDIA
SPEC25 A.NANA SPEC26 LEYDIGIA SPEC27 P.UNCINATUS SPEC28 P.TRUNCATUS
SPEC29 PSEUDOCHYDORUS

APPENDIX 2(A). Microcrustacean data from the open water and the weedbeds, Farnborough, 1977. Numbers / litre

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
146.	2.	1.50	12.20	0.00	0.00	10.70	1.50	0.00	0.00	0.00
146.	3.	5.70	0.00	0.00	0.40	5.80	2.60	0.00	0.00	0.00
146.	4.	4.80	0.20	0.00	0.00	3.20	4.80	0.00	4.80	0.00
160.	7.	11.70	7.30	0.00	0.20	13.30	171.60	0.00	0.00	0.00
178.	7.	44.70	30.80	130.90	0.00	16.20	753.90	0.00	1501.70	0.00
188.	2.	29.60	32.50	34.10	0.00	4.20	772.40	0.00	3.20	0.00
188.	2.	21.90	25.70	14.40	0.00	1.10	523.60	0.00	4.50	0.00
188.	3.	1.30	1.60	0.50	0.00	1.60	35.20	0.00	5.00	0.20
188.	4.	6.40	11.90	5.20	0.00	1.50	417.60	0.00	40.20	0.00
188.	5.	18.60	5.20	9.50	0.00	11.20	1056.00	0.00	4.70	0.00
188.	5.	53.50	72.20	20.90	0.00	3.70	1487.40	0.00	1.10	0.00
188.	5.	6.10	1.10	5.00	0.00	6.10	188.80	0.00	5.00	0.00
206.	2.	3.70	2.40	0.00	0.30	4.50	47.80	1.00	0.70	2.10
206.	2.	156.10	1.20	0.00	0.00	37.20	223.80	0.00	0.00	0.00
206.	3.	65.10	0.40	0.00	0.00	7.60	322.50	7.20	0.00	0.00
206.	4.	408.30	13.80	0.00	0.00	21.50	967.60	0.00	0.00	0.00
221.	2.	51.20	0.70	0.00	5.50	50.00	551.40	15.00	0.00	0.00
221.	2.	11.80	0.00	0.00	0.00	58.10	268.50	0.00	0.00	0.00
221.	3.	25.90	0.20	0.00	4.20	19.20	298.50	130.40	0.20	0.00
221.	4.	90.70	0.70	0.00	0.50	27.10	816.40	6.60	8.20	0.00
234.	2.	36.40	0.20	0.00	0.00	70.30	808.60	0.00	5.70	0.00
234.	3.	10.00	0.20	0.00	9.20	30.00	377.40	0.00	3.80	0.00
234.	4.	23.00	0.20	0.00	0.00	3.70	22.40	0.00	135.90	0.00
234.	4.	34.80	0.00	0.00	0.00	6.50	98.40	0.00	0.60	0.00
234.	5.	14.40	0.00	0.00	1.80	53.70	304.60	0.60	0.20	0.00
245.	2.	167.10	0.00	0.00	0.00	84.60	1307.30	10.10	0.00	0.00
245.	3.	21.90	0.00	0.00	0.00	26.10	495.60	12.60	1.20	0.00
245.	4.	242.10	0.40	0.00	0.00	24.00	891.20	0.00	4.00	0.00
245.	5.	113.30	0.00	0.20	0.00	13.60	799.10	2.20	0.40	0.00
245.	5.	8.80	0.30	0.00	0.00	32.20	79.50	3.10	0.00	0.00
255.	2.	264.50	0.00	0.00	0.00	93.90	398.80	0.00	0.00	0.00
255.	3.	57.30	0.70	0.00	0.20	34.40	522.80	18.40	0.00	0.00
255.	4.	221.00	0.00	0.00	0.40	135.20	483.40	0.00	0.00	0.00
269.	2.	230.30	0.60	0.00	0.00	78.80	240.00	0.00	0.00	0.20
269.	3.	100.00	0.50	0.30	0.30	81.50	869.60	8.00	0.00	0.00
269.	4.	51.80	0.00	0.00	0.00	163.90	322.30	8.40	0.00	0.00
283.	2.	16.60	0.00	0.00	0.00	77.40	100.00	0.00	0.30	0.00
283.	3.	80.00	0.00	0.00	0.00	91.00	380.70	3.40	0.00	0.00
283.	4.	40.30	0.00	0.00	0.00	208.00	492.60	0.00	0.00	0.00
298.	2.	4.20	0.00	0.00	0.00	125.00	58.00	0.00	0.40	0.00
298.	3.	3.30	0.30	0.00	0.00	75.80	91.40	0.00	0.00	0.00
298.	4.	4.00	0.00	0.00	0.00	101.30	30.50	0.00	0.00	0.00
312.	2.	0.70	0.00	0.00	0.00	120.90	36.50	0.00	0.40	0.00
312.	7.	0.60	0.00	0.00	0.00	29.80	108.50	0.00	1.10	0.00
327.	7.	0.00	0.00	0.00	0.00	31.10	0.40	0.00	0.90	0.00
327.	7.	0.20	0.00	0.00	0.00	57.10	48.30	0.00	0.00	0.10
340.	7.	0.00	0.00	0.00	0.00	70.00	1.00	0.00	13.10	0.00
340.	7.	0.00	0.00	0.00	0.00	20.80	0.40	0.00	6.00	0.00
347.	7.	0.00	0.00	0.00	0.00	12.40	0.60	0.00	3.20	0.00
347.	7.	0.00	0.20	0.00	0.00	27.40	0.90	0.00	2.60	0.00
347.	7.	0.00	0.00	0.00	0.00	34.00	1.50	0.00	8.50	0.00

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
160.	1.	0.00	0.50	25.70	0.00	0.00	0.80	0.00	685.00	0.30
178.	1.	0.00	0.70	63.70	0.00	0.00	3.50	0.00	516.10	0.00
188.	1.	0.20	0.30	28.70	0.00	0.00	7.30	0.00	65.20	0.00
206.	1.	0.00	0.20	3.80	0.10	0.10	7.80	0.00	9.20	0.40
221.	1.	0.60	0.50	4.00	0.00	0.00	11.60	0.30	204.20	0.00
234.	1.	0.20	3.00	6.50	0.00	0.00	36.50	0.00	386.10	0.10
245.	1.	0.20	2.10	2.30	0.00	0.00	23.60	0.00	3.50	0.00
255.	1.	0.00	4.30	3.80	0.00	0.10	28.20	0.00	4.50	0.00
269.	1.	0.30	3.40	2.10	0.00	0.00	7.80	0.00	14.10	0.10
283.	1.	0.00	0.60	0.04	0.00	0.00	1.20	0.00	6.30	0.04
298.	1.	0.20	0.90	0.40	0.00	0.20	1.80	0.00	55.00	0.40
312.	1.	0.00	0.10	0.00	0.00	0.40	0.20	0.00	20.00	0.20
340.	1.	0.00	0.00	0.00	0.00	0.20	0.00	0.00	22.20	0.20
347.	1.	0.00	0.04	0.10	0.00	0.10	0.00	0.00	69.70	0.04

APPENDIX 2(a) cont.

DATE	ITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
146.	2.	24.50	0.00	6.10	0.00	0.00	24.50	7.60	0.00	0.00
146.	3.	3.10	0.00	153.10	0.00	0.00	7.20	24.40	0.00	0.00
146.	4.	0.50	0.00	27.50	0.00	0.00	5.70	2.30	0.00	0.00
160.	7.	6.40	0.20	45.90	0.00	0.00	20.40	5.50	0.00	0.00
178.	7.	3.40	0.00	8.00	0.00	0.00	31.50	2.00	0.30	0.00
188.	2.	1.80	0.00	1.80	0.00	0.00	31.30	1.40	0.00	8.50
188.	2.	2.30	0.00	0.80	0.00	0.00	9.10	1.10	0.00	0.00
188.	3.	0.20	0.00	0.00	0.30	0.20	15.50	0.00	0.00	4.60
188.	4.	0.00	0.00	0.00	0.00	0.00	10.70	1.20	0.00	2.10
188.	5.	2.20	0.00	0.90	0.00	0.00	52.20	3.90	0.00	0.00
188.	5.	0.50	0.00	3.20	0.00	0.00	14.20	1.10	0.00	5.50
188.	5.	1.10	0.00	10.60	0.00	0.00	13.70	1.10	0.00	10.60
206.	2.	0.30	0.00	2.40	26.60	0.30	3.20	1.80	0.00	0.00
206.	2.	2.00	0.00	3.20	0.00	0.00	42.20	2.90	0.00	0.00
206.	3.	0.40	0.70	1.10	0.00	0.00	7.90	9.90	0.00	0.00
206.	4.	1.50	0.00	0.00	0.00	0.00	4.60	3.10	0.00	0.00
221.	2.	6.30	0.00	6.20	0.00	0.00	6.60	2.00	0.00	0.00
221.	2.	9.80	0.00	17.70	0.00	0.00	40.60	5.30	0.00	0.00
221.	3.	0.20	3.10	1.90	0.00	0.00	4.20	12.80	0.00	0.00
221.	4.	1.10	0.00	0.00	0.00	0.50	0.90	0.00	0.00	0.00
234.	2.	11.30	0.00	39.00	0.00	0.00	80.10	7.80	0.00	0.00
234.	3.	1.10	0.00	10.10	0.00	0.00	12.80	7.40	0.00	0.00
234.	4.	0.20	0.00	1.80	0.00	0.40	4.20	1.40	2.40	0.00
234.	4.	0.20	0.00	0.40	0.00	0.00	1.50	1.50	3.50	0.00
234.	5.	1.30	0.00	3.40	0.20	0.00	9.70	0.50	0.00	0.00
245.	2.	8.40	0.00	49.30	0.00	0.80	12.20	7.60	1.30	0.00
245.	3.	2.00	0.00	7.30	0.00	0.00	6.40	7.30	0.00	0.20
245.	4.	0.90	0.00	4.00	0.00	0.00	0.40	0.90	0.00	0.00
245.	5.	4.30	0.00	12.50	0.00	0.00	5.90	2.20	2.20	0.00
245.	5.	0.60	0.00	4.60	2.10	2.10	8.00	0.30	0.00	1.20
255.	2.	6.50	0.40	68.50	0.00	0.00	29.90	7.60	1.00	0.00
255.	3.	4.90	1.50	22.20	1.00	0.00	22.10	3.40	0.50	0.00
255.	4.	12.30	1.30	18.40	0.00	0.00	15.80	4.40	6.60	0.00
269.	2.	6.70	9.00	19.20	0.40	3.10	11.50	23.00	9.60	0.00
269.	3.	2.50	0.30	20.30	0.50	1.10	9.00	10.00	4.00	0.00
269.	4.	0.90	0.00	3.10	0.00	0.00	0.00	3.10	0.00	0.40
283.	2.	6.30	0.30	11.50	0.00	0.00	14.00	15.00	0.30	0.00
283.	3.	7.80	0.30	18.50	0.00	0.00	12.30	10.20	0.50	0.20
283.	4.	1.20	1.10	8.90	0.00	0.00	3.30	6.70	0.00	2.20
298.	2.	12.80	0.20	6.60	0.00	0.00	13.70	22.90	0.40	0.00
298.	3.	2.80	1.00	6.10	0.00	0.30	6.60	8.40	1.40	0.00
298.	4.	4.60	0.00	10.40	0.00	0.00	0.00	10.90	0.60	0.00
312.	2.	19.70	1.60	7.00	0.40	6.20	16.80	42.00	0.00	0.00
312.	7.	7.20	0.20	0.00	0.00	3.40	0.80	7.60	1.10	0.00
327.	7.	9.40	0.00	23.80	0.90	58.10	3.30	23.00	0.00	1.70
327.	7.	14.70	0.40	12.60	0.00	0.00	12.80	45.80	0.00	0.00
340.	7.	18.40	1.00	52.40	0.00	28.40	16.00	15.00	0.00	0.00
340.	7.	6.80	0.00	14.30	2.30	40.90	11.60	5.30	0.00	3.00
347.	7.	3.50	0.40	12.30	0.00	37.20	8.60	33.30	0.00	2.20
347.	7.	6.60	1.40	15.10	0.00	21.30	25.20	18.80	0.00	14.60
347.	7.	2.70	0.30	13.10	0.00	8.20	17.30	16.00	0.00	9.90

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
160.	1.	0.00	0.00	0.00	0.30	0.00	4.50	0.00	0.00	0.00
178.	1.	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00
188.	1.	0.00	0.00	0.00	0.00	0.00	3.40	0.00	0.00	0.00
206.	1.	0.00	0.00	0.00	0.60	0.00	4.20	0.00	0.00	0.00
221.	1.	0.00	0.10	0.00	0.00	0.00	8.00	0.10	0.00	0.00
234.	1.	0.00	0.00	0.00	0.60	0.00	3.10	0.00	0.00	0.50
245.	1.	0.00	0.00	0.00	0.00	0.00	2.30	0.00	0.00	0.20
255.	1.	0.00	0.10	0.10	0.00	0.10	0.30	0.00	0.00	0.00
269.	1.	0.00	0.10	0.00	0.00	0.10	8.70	0.40	0.00	5.10
283.	1.	0.50	0.10	1.10	0.04	0.04	8.00	0.04	0.00	3.50
298.	1.	0.40	0.00	0.30	0.00	0.30	8.60	0.10	0.00	4.40
312.	1.	0.10	0.00	0.90	0.00	0.00	3.40	0.50	0.00	0.00
340.	1.	0.50	0.40	0.20	0.10	2.20	2.40	1.00	0.00	0.40
347.	1.	0.10	0.04	0.60	0.00	0.80	6.00	0.80	0.00	0.90

APPENDIX 2(a) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27
146.	2.	0.00	12.20	0.00	290.10	0.00	605.80	0.00	0.00	0.00
146.	3.	0.00	0.00	0.00	93.20	0.00	358.00	0.80	49.80	0.00
146.	4.	0.20	0.00	0.00	276.40	0.00	473.90	0.50	0.00	0.00
160.	7.	1.40	0.90	1.40	12.40	0.00	205.70	0.00	183.00	0.00
178.	7.	2.00	0.30	0.00	0.60	0.00	323.90	0.00	45.40	0.80
188.	2.	0.00	0.00	0.00	0.40	0.00	209.60	0.40	213.30	0.40
188.	2.	0.80	0.40	0.00	0.00	0.00	88.30	0.00	106.70	0.00
188.	3.	0.00	0.20	3.00	0.00	0.00	127.30	0.00	132.60	0.00
188.	4.	0.30	0.30	0.30	0.00	0.00	612.10	0.00	388.70	0.00
188.	5.	1.70	0.40	0.00	0.40	0.00	341.90	0.40	265.90	0.40
188.	5.	29.00	0.00	0.00	0.00	0.00	142.30	0.00	526.90	0.00
188.	5.	3.30	0.00	0.60	0.00	0.00	134.00	0.00	273.20	0.00
206.	2.	27.40	5.50	0.50	1.80	0.00	46.50	0.00	70.60	0.00
206.	2.	2.90	6.70	0.00	0.00	0.00	212.70	0.00	272.10	0.00
206.	3.	3.00	1.10	0.00	0.40	0.00	124.20	0.00	104.80	0.40
206.	4.	0.00	0.00	0.00	0.00	0.00	208.70	0.00	258.40	0.00
221.	2.	0.00	3.10	0.00	0.30	0.00	182.20	0.70	387.00	1.70
221.	2.	8.90	8.90	0.90	0.20	0.00	422.60	0.00	469.40	2.20
221.	3.	5.10	8.90	0.00	0.50	0.50	179.10	0.00	255.80	0.00
221.	4.	70.10	0.00	0.00	0.00	6.10	107.90	0.90	82.40	0.00
234.	2.	24.30	20.70	0.20	0.70	0.00	342.30	0.00	420.30	0.50
234.	3.	9.80	16.80	0.00	1.10	2.20	173.70	0.00	213.10	0.60
234.	4.	0.90	8.40	0.00	4.00	0.00	57.90	0.00	142.10	0.00
234.	4.	4.70	10.10	0.00	15.30	1.70	45.30	0.00	80.30	0.00
234.	5.	77.20	1.80	0.20	0.40	1.10	266.70	0.50	212.50	0.40
245.	2.	30.30	12.60	0.00	1.70	0.40	254.40	0.40	421.20	4.60
245.	3.	2.80	10.70	0.20	1.60	0.00	143.40	0.40	128.30	1.40
245.	4.	79.60	25.70	0.00	44.60	0.40	185.70	0.90	149.30	0.40
245.	5.	20.80	30.30	0.00	9.90	0.80	225.30	0.20	106.30	3.00
245.	5.	62.00	0.00	0.30	0.30	0.00	272.40	0.00	0.00	0.30
255.	2.	424.20	18.20	0.00	23.80	0.00	364.80	0.30	135.00	1.60
255.	3.	11.20	19.10	1.40	5.40	0.00	122.50	2.20	211.40	1.00
255.	4.	223.00	148.00	0.00	76.70	0.00	223.00	0.00	238.80	0.00
269.	2.	740.00	30.70	0.20	30.70	0.00	360.60	0.60	220.80	0.40
269.	3.	70.00	54.50	0.30	14.00	0.00	160.20	1.50	150.30	0.80
269.	4.	403.80	0.00	0.00	6.10	1.30	368.40	0.90	301.10	0.00
283.	2.	197.00	28.30	0.50	249.00	0.00	193.60	1.50	90.00	0.00
283.	3.	108.60	17.00	0.20	41.00	0.00	471.20	0.00	40.30	0.80
283.	4.	635.80	0.00	0.00	18.90	0.00	205.50	3.30	179.80	0.80
298.	2.	280.00	1.10	0.40	251.00	0.00	194.20	0.20	81.00	2.60
298.	3.	137.30	14.50	0.30	120.10	0.00	202.40	4.50	30.00	0.30
298.	4.	260.70	0.00	0.00	58.70	0.00	84.60	1.20	33.70	0.00
312.	2.	202.30	1.20	0.00	171.00	0.00	106.10	5.50	50.60	1.20
312.	7.	115.70	4.20	0.00	251.20	0.00	39.10	10.60	18.90	0.40
327.	7.	27.60	2.60	0.80	8.10	0.00	45.90	1.90	36.70	0.80
327.	7.	72.80	2.00	0.00	162.70	0.00	236.10	9.60	0.00	1.80
340.	7.	290.50	0.00	0.00	20.20	0.00	120.00	0.00	54.70	0.00
340.	7.	54.10	15.80	2.60	6.40	0.00	74.60	2.50	28.00	0.40
347.	7.	21.60	12.30	0.30	8.30	0.00	55.60	4.80	62.00	0.00
347.	7.	19.50	16.50	0.00	90.00	0.00	134.90	1.10	14.90	0.20
347.	7.	13.40	3.30	0.00	88.00	0.00	226.20	0.00	19.40	0.00

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27
160.	1.	0.00	0.00	0.20	0.00	0.00	268.50	0.00	150.20	0.00
178.	1.	0.00	0.00	0.00	0.00	0.00	268.50	0.00	150.20	0.00
188.	1.	0.00	0.00	0.00	0.00	0.00	157.30	0.00	100.90	0.00
206.	1.	0.00	0.00	0.20	0.00	0.00	138.10	0.00	100.50	0.00
221.	1.	0.00	0.00	0.20	0.00	0.00	179.20	0.00	98.80	0.00
234.	1.	0.00	0.00	0.20	0.10	0.00	75.90	0.10	68.40	0.00
245.	1.	0.00	0.20	0.50	0.20	0.00	79.40	0.50	53.80	0.00
255.	1.	0.00	0.10	0.00	0.00	0.00	43.40	0.30	114.40	0.00
269.	1.	0.90	0.00	0.50	0.70	0.00	116.40	0.90	155.20	0.00
283.	1.	0.50	0.60	2.20	1.60	0.00	20.60	0.20	48.00	0.00
298.	1.	3.60	0.10	1.50	4.80	0.00	19.40	1.30	39.10	0.00
312.	1.	0.80	0.00	0.60	1.50	0.00	3.80	0.50	7.00	0.00
340.	1.	6.40	0.00	1.10	0.50	0.00	4.00	0.40	11.30	0.04
347.	1.	4.80	0.10	1.50	0.20	0.00	4.30	1.50	15.20	0.00

APPENDIX 2(B). Microcrustacean data from the cases and the lake, Yateley, 1978. Numbers / litre

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
179.	1.	0.00	33.60	0.00	0.50	2.20	0.00	0.70	0.00	0.10
179.	2.	0.00	0.00	2.90	0.00	30.50	5.70	16.90	0.50	0.50
179.	3.	0.50	0.20	2.40	0.00	2.40	1.40	14.60	0.70	5.10
191.	1.	0.00	3.10	0.30	1.20	5.00	0.00	2.60	0.05	0.05
191.	2.	0.00	0.30	7.40	0.00	34.40	9.40	32.70	0.00	1.30
191.	3.	0.20	2.20	19.70	0.20	10.80	0.70	2.30	0.00	1.10
191.	4.	0.00	2.00	0.00	1.40	0.40	0.00	0.00	0.00	0.00
191.	4.	0.40	1.10	0.00	0.40	0.90	0.00	0.00	0.00	0.00
191.	4.	0.00	3.90	0.20	0.00	1.80	0.00	0.00	0.20	0.00
191.	5.	0.00	0.20	0.00	0.20	3.20	0.00	0.20	0.00	0.00
191.	5.	0.00	0.00	0.30	0.80	2.30	0.30	0.80	0.00	0.30
191.	5.	0.00	0.60	0.60	0.40	2.70	0.00	0.00	0.80	0.00
191.	5.	0.00	1.60	0.50	1.40	0.50	0.20	0.00	0.00	0.00
198.	1.	0.10	4.20	1.80	5.10	6.50	0.40	12.30	0.60	0.60
198.	2.	17.80	0.30	21.80	0.00	19.80	25.80	35.00	1.50	0.60
198.	3.	8.00	6.10	118.70	0.00	11.70	5.00	35.60	0.00	4.30
198.	4.	0.00	0.90	0.00	1.80	0.00	0.00	0.00	0.00	0.00
198.	4.	0.00	6.20	0.00	0.00	0.80	0.00	0.00	0.00	0.00
198.	4.	0.00	8.40	0.80	8.90	0.00	0.00	0.00	0.00	0.00
198.	5.	0.00	0.60	0.60	0.00	1.80	0.00	0.00	0.00	0.00
198.	5.	0.00	2.30	0.50	0.70	1.80	0.20	0.50	0.20	0.20
198.	5.	0.00	0.00	0.50	0.50	4.60	0.00	0.00	0.00	0.90
198.	5.	0.00	3.10	1.20	1.20	1.20	0.00	0.00	0.00	0.00
214.	1.	6.50	9.60	57.80	11.50	1.90	0.00	3.30	0.00	0.10
214.	3.	42.90	1.70	403.60	0.00	4.20	20.00	11.30	0.40	1.70
214.	2.	23.20	0.00	268.50	0.60	4.50	19.70	6.10	1.90	1.90
214.	4.	3.90	10.40	28.00	16.50	1.40	0.20	0.40	0.00	0.00
214.	4.	0.80	4.50	22.00	67.80	3.20	0.00	0.60	0.00	0.00
214.	4.	1.90	6.70	25.70	10.70	1.40	0.00	0.20	0.00	0.00
214.	4.	0.00	9.90	41.60	27.20	1.20	0.00	0.30	0.00	0.00
214.	5.	4.90	2.30	28.90	2.30	1.45	0.00	0.10	0.15	0.40
214.	5.	3.90	0.80	35.00	9.40	0.80	0.00	1.30	1.30	0.80
214.	5.	0.50	2.40	17.80	4.80	1.20	0.25	0.00	0.75	1.40
214.	5.	0.75	0.60	20.90	4.80	1.90	0.05	0.30	0.20	0.45
229.	5.	4.90	2.60	53.00	22.90	0.15	0.15	0.15	0.20	1.00
229.	5.	5.70	0.50	36.80	0.70	0.00	0.00	0.00	0.00	0.25
229.	5.	5.60	0.85	47.00	9.80	0.45	0.00	0.60	0.00	0.40
246.	5.	10.10	0.00	109.20	91.60	0.00	0.15	0.20	0.05	0.25
229.	1.	19.40	2.50	111.20	20.50	0.30	0.10	2.00	0.10	0.10
229.	2.	19.80	0.00	209.00	0.00	3.30	49.10	1.40	0.90	1.90
229.	3.	30.70	0.00	189.30	0.00	0.00	2.10	1.00	0.00	0.70
229.	4.	30.70	3.80	69.10	32.10	0.30	0.00	0.00	0.00	0.30
229.	4.	4.60	1.20	54.00	77.20	0.30	0.00	0.60	0.00	0.30
229.	4.	1.20	2.60	34.30	54.00	0.00	0.00	0.00	0.00	0.00
229.	4.	3.40	1.50	40.20	33.80	0.40	0.00	0.00	0.00	0.00
229.	5.	2.80	2.60	36.90	15.70	0.20	0.00	0.00	0.20	0.20

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
246.	5.	10.10	0.00	109.20	91.60	0.00	0.15	0.20	0.05	0.25
246.	5.	26.30	0.10	221.20	143.60	0.00	0.60	1.90	1.20	0.35
246.	5.	12.70	0.75	227.50	272.30	0.00	0.30	0.30	1.65	0.00
246.	5.	15.00	0.20	146.40	26.80	0.00	0.30	1.15	0.75	0.50
246.	1.	22.00	0.00	168.10	102.70	0.20	2.40	2.20	0.50	2.90
246.	2.	116.00	0.00	280.30	0.00	0.00	203.70	1.00	2.00	0.00
246.	3.	80.00	0.00	391.00	0.30	0.40	52.30	1.10	0.00	1.00
246.	4.	25.10	0.10	98.60	39.00	0.00	0.00	0.00	0.00	0.10
246.	4.	28.10	0.10	188.80	65.10	0.00	0.20	0.00	0.10	0.00
246.	4.	6.10	0.20	73.80	78.10	0.00	0.00	0.10	0.00	0.10
255.	1.	1.20	0.20	39.50	7.50	0.20	1.10	1.60	2.30	1.60
255.	2.	104.10	0.00	160.60	0.30	0.30	168.50	0.30	0.60	3.50
255.	3.	80.00	0.20	262.60	0.30	0.00	96.70	0.00	0.00	0.50
255.	4.	1.50	0.20	42.50	4.90	0.20	0.00	0.20	0.00	0.00
255.	4.	0.90	0.10	19.00	1.90	0.10	0.50	0.30	0.10	0.00
255.	4.	1.40	0.00	20.10	6.30	0.10	0.70	0.30	0.00	0.20
255.	4.	0.90	0.20	33.80	4.70	0.00	0.00	0.10	0.00	0.10
255.	5.	0.70	0.20	52.20	3.50	0.00	0.35	0.60	0.88	0.05
255.	5.	1.20	0.30	62.40	6.30	0.50	0.80	2.65	0.80	0.30
255.	5.	1.30	0.10	24.80	16.80	0.15	1.30	2.40	0.50	0.50
255.	5.	0.55	0.00	24.00	3.30	0.05	3.10	0.60	1.50	0.85
272.	1.	0.10	0.40	32.30	28.00	1.10	7.30	6.90	3.10	1.90
272.	2.	30.00	0.00	377.80	0.00	1.40	186.90	3.00	0.00	5.10
272.	3.	59.30	0.00	424.70	1.00	4.10	250.30	5.20	2.10	2.60
272.	4.	0.30	0.50	35.40	29.10	0.10	1.80	2.30	1.00	0.70
272.	4.	0.30	6.80	56.50	56.90	0.20	2.60	0.90	2.20	0.00
272.	4.	0.10	0.70	25.70	37.60	0.10	3.20	1.30	0.50	0.00
272.	4.	0.00	0.40	25.10	24.40	0.40	5.00	0.50	0.40	0.40
272.	5.	0.30	0.50	5.65	18.00	0.40	12.80	5.85	3.25	0.70
272.	5.	0.50	0.60	29.80	98.10	0.00	6.30	4.40	1.00	0.10
272.	5.	1.15	8.30	129.40	995.20	0.50	31.10	4.65	1.50	0.75
272.	5.	0.15	0.75	38.95	15.15	0.70	15.85	5.70	5.95	1.65

APPENDIX 2(b) cont.

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
179.	1.	0.10	0.10	0.20	0.00	64.60	5.70	0.00	57.30	0.00
179.	2.	9.50	3.30	48.50	2.40	952.10	5.70	10.90	53.70	0.00
179.	3.	0.20	0.20	7.10	1.40	442.80	11.30	7.60	23.80	0.90
191.	1.	0.10	1.40	3.60	0.00	149.70	4.40	0.00	134.30	50.50
191.	2.	6.40	2.00	46.70	61.50	279.20	11.20	1.00	34.60	0.00
191.	3.	0.00	0.00	2.00	1.60	204.00	17.50	2.00	59.20	0.50
191.	4.	0.00	0.60	0.60	16.20	151.80	3.00	0.00	175.50	0.00
191.	4.	0.00	0.20	0.00	2.00	124.00	0.60	0.00	118.10	70.30
191.	4.	0.00	0.20	0.00	3.50	99.60	1.20	0.00	192.20	0.00
191.	5.	0.00	0.20	0.60	6.50	177.50	0.00	0.00	99.30	0.00
191.	5.	0.30	1.00	0.30	1.00	204.10	1.30	0.30	185.70	63.60
191.	5.	0.60	0.60	1.70	0.60	331.90	9.30	0.00	206.70	0.00
191.	5.	0.00	0.50	1.90	3.50	250.10	2.30	0.00	125.60	0.00
198.	1.	5.10	8.30	12.80	0.10	200.30	7.60	0.20	146.40	7.20
198.	2.	50.60	2.50	132.00	6.40	362.30	13.00	3.90	182.60	0.00
198.	3.	14.10	0.60	71.80	2.50	202.60	13.50	0.00	198.00	0.00
198.	4.	0.00	0.00	0.90	0.00	144.60	0.90	0.00	510.20	8.30
198.	4.	0.00	0.00	0.70	252.40	179.10	5.60	0.00	635.00	0.00
198.	4.	0.00	0.00	0.30	12.90	219.20	15.80	0.00	440.20	13.20
198.	5.	0.00	0.00	4.30	3.10	419.10	10.40	0.00	377.60	23.90
198.	5.	0.00	1.40	1.60	22.90	208.40	0.70	0.00	311.00	12.90
198.	5.	0.00	1.40	1.60	22.90	208.40	0.70	0.00	311.00	12.90
198.	5.	0.50	0.90	7.40	16.60	294.70	2.30	0.00	285.50	14.30
198.	5.	0.00	1.20	10.40	65.70	656.70	0.00	0.60	292.80	9.20
214.	1.	1.20	7.00	8.00	0.00	164.00	18.40	0.00	188.20	10.20
214.	3.	16.70	6.30	90.30	0.80	284.40	26.20	0.00	98.40	0.00
214.	2.	32.90	10.70	59.40	3.20	351.20	20.30	2.60	230.70	0.00
214.	4.	0.20	1.80	8.80	0.20	211.10	33.20	1.20	109.90	19.20
214.	4.	0.00	5.60	5.10	0.20	189.10	9.20	0.80	125.40	28.30
214.	4.	0.20	5.50	9.10	0.00	274.60	50.40	0.50	148.70	25.40
214.	4.	0.00	2.40	2.70	0.80	287.70	33.20	0.00	61.90	13.50
214.	5.	0.15	1.20	18.30	0.50	169.60	3.50	0.15	294.10	13.00
214.	5.	0.80	16.70	18.50	2.60	140.30	3.70	3.50	272.30	10.10
214.	5.	1.50	2.50	32.50	0.40	199.10	15.20	2.25	119.70	13.10
214.	5.	0.85	6.90	63.60	24.20	163.00	5.30	0.00	141.50	6.10
229.	5.	1.30	22.60	20.20	4.10	33.20	11.80	3.90	272.10	282.60
229.	5.	1.85	9.60	14.90	0.35	49.80	28.75	0.00	104.30	504.00
229.	5.	6.50	29.40	70.25	27.50	56.60	97.90	1.05	184.90	392.15
229.	5.	0.20	3.00	4.70	0.20	29.50	19.10	1.10	133.00	286.60
229.	1.	3.80	5.30	11.80	0.00	87.60	38.80	0.00	114.80	283.80
229.	2.	187.70	18.90	48.00	0.00	114.20	22.20	9.40	134.60	0.00
229.	3.	4.50	15.00	4.10	0.50	51.20	95.90	0.50	50.00	0.00
229.	4.	0.30	1.10	11.20	0.00	59.50	50.10	0.50	205.30	462.40
229.	4.	0.00	9.30	6.70	0.00	32.50	50.20	0.30	213.30	350.30
229.	4.	0.00	1.50	4.10	1.20	40.50	38.10	0.00	140.70	450.70
229.	4.	0.00	2.30	5.40	0.80	49.20	39.80	0.00	219.90	413.50

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
246.	5.	5.60	9.70	23.30	6.60	9.40	7.70	1.40	165.60	55.80
246.	5.	6.30	54.40	28.60	0.95	10.80	20.70	22.20	182.30	44.80
246.	5.	1.80	9.30	21.90	1.10	12.10	42.20	0.40	211.80	85.20
246.	5.	10.80	41.10	31.70	3.80	18.50	26.75	3.60	212.10	57.50
246.	1.	4.00	12.90	22.70	0.00	24.60	36.10	0.50	127.20	39.70
246.	2.	136.10	8.10	69.20	0.00	99.40	37.90	2.70	73.30	0.00
246.	3.	55.70	0.10	30.30	0.00	46.30	15.00	0.10	49.80	0.00
246.	4.	0.10	0.60	2.30	0.70	8.50	10.30	0.10	159.20	89.60
246.	4.	0.30	1.00	3.10	2.40	13.20	57.10	0.00	237.50	73.00
246.	4.	3.10	1.30	4.40	1.50	11.90	26.60	0.00	191.30	52.50
255.	1.	9.20	6.80	17.70	0.00	19.10	22.90	0.90	205.30	24.70
255.	2.	214.50	3.40	238.10	0.30	57.50	34.70	0.10	110.80	0.00
255.	3.	53.40	0.50	42.00	0.20	27.00	16.90	0.00	90.00	0.00
255.	4.	1.60	7.20	7.70	0.00	24.00	19.50	0.20	261.40	43.30
255.	4.	2.00	1.40	8.70	0.00	15.10	10.70	0.20	200.60	13.00
255.	4.	1.20	5.20	7.80	0.00	11.60	15.20	0.00	240.10	37.70
255.	4.	0.20	1.60	11.70	0.00	21.30	10.50	0.00	316.70	38.50
255.	5.	5.50	8.50	7.70	2.40	17.60	6.50	0.10	183.80	14.30
255.	5.	8.00	52.75	18.20	0.10	15.60	9.50	5.70	402.40	11.30
255.	5.	10.50	7.10	9.50	0.10	25.80	14.80	0.50	316.20	27.60
255.	5.	39.75	34.50	13.30	0.25	25.50	13.95	3.50	362.15	35.60
272.	1.	38.00	6.80	44.00	0.00	93.70	14.50	0.00	135.10	8.90
272.	2.	151.30	2.00	329.10	4.10	113.70	28.10	7.10	119.90	9.10
272.	3.	59.80	0.00	120.60	0.50	124.70	32.50	2.10	166.30	38.70
272.	4.	4.10	5.50	13.90	0.10	50.70	3.70	3.50	118.30	11.80
272.	4.	21.30	2.00	20.50	2.20	33.90	27.70	1.20	65.10	4.10
272.	4.	3.50	0.50	4.40	0.40	44.60	15.30	0.10	119.00	120.00
272.	4.	2.50	5.30	6.00	0.00	50.50	14.50	1.10	202.60	17.70
272.	5.	19.70	13.65	27.30	4.35	49.65	2.70	5.70	152.90	4.60
272.	5.	7.20	8.70	24.40	1.85	37.70	11.60	5.20	150.50	17.50
272.	5.	27.60	2.20	21.90	1.75	41.80	37.30	0.95	90.50	14.10
272.	5.	38.10	25.75	12.90	3.10	49.40	7.50	3.30	139.85	9.60

APPENDIX 2(b) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27
179.	1.	1.70	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
179.	2.	51.80	0.50	0.00	0.00	0.70	0.00	0.00	0.00	0.00
179.	3.	29.50	0.50	0.00	0.00	0.20	0.00	0.00	0.00	0.20
191.	1.	1.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	2.	43.50	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00
191.	3.	18.10	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00
191.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	4.	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	5.	0.50	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	5.	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
191.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	1.	5.60	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
198.	2.	102.30	0.60	0.30	0.30	0.30	0.00	0.00	0.00	0.00
198.	3.	225.60	1.20	4.30	7.40	2.50	0.00	0.00	0.00	0.00
198.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	4.	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	5.	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	5.	0.00	1.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00
198.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
214.	1.	3.50	0.50	0.10	0.00	0.00	0.00	0.00	0.00	0.00
214.	3.	48.30	5.80	7.50	8.60	0.00	0.00	0.00	0.00	0.00
214.	2.	49.90	2.60	4.20	0.00	0.00	0.00	0.00	0.00	0.60
214.	4.	4.50	0.20	0.20	0.00	0.00	0.00	0.00	0.00	0.00
214.	4.	0.90	0.00	1.10	0.00	0.00	0.00	0.00	0.00	0.00
214.	4.	2.40	0.20	0.20	0.00	0.00	0.00	0.00	0.00	0.00
214.	4.	0.00	0.50	1.00	0.00	0.20	0.00	0.00	0.00	0.00
214.	5.	4.60	0.00	0.40	0.00	0.15	0.00	0.00	0.00	0.00
214.	5.	0.55	0.50	0.85	0.00	0.15	0.00	0.00	0.00	0.00
214.	5.	3.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.00
214.	5.	4.80	2.20	0.70	0.00	0.00	0.00	0.00	0.00	0.00
229.	5.	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00
229.	5.	0.10	0.00	1.40	0.00	0.00	0.00	0.00	0.00	0.00
229.	5.	0.00	0.60	0.40	0.00	0.00	0.00	0.00	0.00	0.00
229.	5.	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00
229.	1.	0.40	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
229.	2.	2.40	3.80	1.40	0.00	0.00	0.00	0.00	0.00	0.00
229.	3.	1.20	0.20	7.90	0.00	0.00	0.00	0.00	0.00	0.00
229.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
229.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
229.	4.	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00
229.	4.	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27
246.	5.	0.00	0.05	0.30	0.00	0.00	0.00	0.00	0.00	0.00
246.	5.	0.10	0.00	0.20	0.00	0.20	0.00	0.00	0.00	0.00
246.	5.	0.00	0.00	0.10	0.00	0.10	0.00	0.00	0.00	0.00
246.	5.	0.00	0.00	0.60	0.00	0.00	0.00	0.00	0.00	0.00
246.	1.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
246.	2.	1.30	1.30	4.00	0.00	0.00	0.00	0.00	0.70	0.00
246.	3.	0.60	0.30	11.00	0.00	0.10	0.00	0.10	0.30	0.10
246.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
246.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
246.	4.	0.00	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00
255.	1.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	2.	2.60	0.00	4.20	0.00	0.60	0.30	0.00	0.60	0.30
255.	3.	1.10	1.00	11.10	0.00	0.50	0.00	0.00	0.00	0.10
255.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	5.	0.00	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00
255.	5.	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
255.	5.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
272.	1.	0.40	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	2.	8.10	0.00	5.10	0.00	0.00	0.00	0.00	2.00	0.00
272.	3.	0.50	0.00	5.20	0.00	0.00	0.00	0.00	0.00	0.00
272.	4.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	4.	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	4.	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	4.	0.20	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.90
272.	5.	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	5.	0.15	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00
272.	5.	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
272.	5.	0.30	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX 2(b) cont.

DATE	SITE	SPEC28	SPEC29
179.	1.	0.00	0.00
179.	2.	0.00	0.50
179.	3.	0.00	1.70
191.	1.	0.00	0.00
191.	2.	0.00	1.30
191.	3.	0.00	0.40
191.	4.	0.00	0.00
191.	4.	0.00	0.00
191.	4.	0.00	0.20
191.	5.	0.00	0.00
191.	5.	0.00	0.00
191.	5.	0.00	0.00
191.	5.	0.00	0.00
198.	1.	0.00	0.00
198.	2.	0.00	1.80
198.	3.	0.00	0.60
198.	4.	0.00	0.00
198.	4.	0.00	0.00
198.	4.	0.00	0.00
198.	5.	0.00	0.00
198.	5.	0.00	0.00
198.	5.	0.00	0.00
198.	5.	0.00	0.00
214.	1.	0.50	0.00
214.	3.	0.00	0.80
214.	2.	0.00	0.30
214.	4.	0.00	0.00
214.	4.	0.00	0.00
214.	4.	0.00	0.20
214.	4.	0.00	0.00
214.	5.	0.00	0.00
214.	5.	0.00	0.15
214.	5.	0.00	0.15
214.	5.	0.00	0.05
229.	5.	0.00	0.00
229.	5.	0.00	0.00
229.	5.	0.00	0.00
229.	5.	0.00	0.20
229.	1.	0.00	0.00
229.	2.	0.50	0.00
229.	3.	0.00	0.00
229.	4.	0.00	0.00
229.	4.	0.00	0.00
229.	4.	0.00	0.00
229.	4.	0.00	0.00

DATE	SITE	SPEC28	SPEC29
246.	5.	0.00	0.10
246.	5.	0.00	0.85
246.	5.	0.00	0.00
246.	5.	0.00	0.15
246.	1.	0.00	0.00
246.	2.	0.00	0.00
246.	3.	0.00	0.30
246.	4.	0.00	0.00
246.	4.	0.00	0.00
246.	4.	0.00	0.00
255.	1.	0.00	0.00
255.	2.	0.30	0.00
255.	3.	0.00	0.70
255.	4.	0.00	0.00
255.	4.	0.00	0.00
255.	4.	0.00	0.00
255.	4.	0.00	0.00
255.	5.	0.00	0.00
255.	5.	0.00	0.00
255.	5.	0.00	0.00
255.	5.	0.00	0.00
272.	1.	0.00	0.00
272.	2.	0.00	0.00
272.	3.	0.50	0.00
272.	4.	0.00	0.00
272.	4.	0.00	0.20
272.	4.	0.00	0.10
272.	4.	0.00	0.00
272.	5.	0.00	0.00
272.	5.	0.00	0.15
272.	5.	0.00	0.00
272.	5.	0.00	0.00

APPENDIX 2(C). Microcrustacean data from the cages and the lake, Yateley, 1979.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
164.	1.	0.10	151.50	0.40	0.20	0.40	0.00	0.40	0.00	0.00
164.	1.	0.00	132.40	0.90	0.20	0.70	0.00	0.30	0.00	0.10
164.	2.	3.20	0.00	220.00	16.60	17.30	4.70	40.00	1.10	7.40
164.	3.	1.40	2.30	127.00	0.00	7.40	8.10	47.00	2.30	17.10
164.	4.	0.00	52.00	0.40	0.10	1.10	0.00	0.10	0.10	0.00
164.	4.	0.00	62.90	0.10	0.00	0.10	0.00	0.10	0.00	0.10
164.	4.	0.00	34.50	0.20	0.10	0.50	0.00	0.20	0.00	0.10
164.	5.	0.00	3.10	0.30	0.00	8.20	0.40	4.00	0.00	3.50
164.	5.	0.00	1.80	0.90	0.00	10.50	0.00	2.00	0.70	4.60
164.	5.	0.00	3.60	1.20	0.00	9.20	0.50	8.60	3.50	1.70
206.	1.	2.10	0.20	52.30	153.90	0.00	0.20	1.50	0.00	0.70
206.	1.	5.40	0.30	56.50	176.60	0.00	0.40	0.50	0.10	0.80
206.	2.	209.70	0.00	228.00	0.00	2.00	12.60	6.30	1.10	0.40
206.	2.	64.00	0.00	96.00	1.20	2.90	9.30	6.50	0.40	2.20
206.	3.	24.00	0.00	220.60	0.30	0.60	6.60	2.90	0.00	2.80
206.	4.	1.23	0.10	10.70	290.40	0.00	1.80	0.60	0.00	0.00
206.	4.	9.10	2.00	74.60	283.20	0.00	0.00	0.40	0.00	0.00
206.	4.	1.10	0.00	10.80	352.70	0.20	0.00	0.80	0.00	0.00
206.	5.	1.50	0.00	13.10	80.90	0.40	0.40	14.90	1.40	1.20
206.	5.	0.60	0.00	47.90	66.30	0.30	0.90	0.90	0.30	0.30
206.	5.	1.70	0.00	35.60	55.30	0.30	1.10	3.60	1.90	2.80
250.	1.	3.20	0.00	47.10	0.20	0.40	0.00	6.60	8.60	6.20
250.	1.	8.90	0.00	56.20	0.00	0.80	0.30	7.10	3.60	5.20
250.	2.	160.60	0.00	200.30	0.00	2.30	9.20	14.90	126.00	57.60
250.	2.	285.50	0.00	115.10	0.00	0.00	20.70	29.80	18.60	4.80
250.	3.	183.40	0.00	106.90	0.00	0.20	12.80	23.40	2.40	3.20
250.	4.	0.50	0.00	5.80	1.40	0.00	0.00	4.10	1.40	0.20
250.	4.	156.10	0.30	27.00	11.10	0.00	0.00	0.50	0.00	0.80
250.	4.	1.00	0.00	7.20	1.80	0.00	0.00	3.90	2.90	0.00
250.	5.	0.20	0.10	5.40	0.00	0.10	0.20	51.30	3.30	3.90
250.	5.	0.40	0.00	17.60	0.00	0.00	1.30	21.20	0.60	1.90
250.	5.	1.10	0.00	12.50	0.00	0.00	0.50	44.70	20.20	1.60

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
164.	1.	0.80	0.00	0.00	0.50	73.10	7.60	0.20	115.80	11.80
164.	1.	0.30	0.00	0.00	0.00	83.10	5.70	0.00	123.40	10.90
164.	2.	395.70	0.00	1.60	0.50	573.00	110.10	0.50	212.60	0.00
164.	3.	91.00	0.00	0.50	2.60	350.50	30.80	5.30	93.10	0.00
164.	4.	0.40	0.10	0.00	7.80	40.80	4.50	0.00	119.10	16.10
164.	4.	0.70	0.00	0.10	86.30	17.30	12.80	0.10	72.50	7.10
164.	4.	0.80	0.00	0.10	62.30	45.40	8.00	0.00	74.60	21.60
164.	5.	12.60	0.30	0.60	2.50	98.10	1.80	0.90	186.50	4.80
164.	5.	19.20	0.00	0.40	4.20	76.30	22.80	0.90	88.40	4.50
164.	5.	29.20	1.00	0.20	22.30	89.80	8.80	2.10	229.30	13.10
206.	1.	4.60	0.00	0.10	0.00	205.70	13.10	0.10	315.90	58.80
206.	1.	1.70	0.00	0.20	0.00	230.70	11.80	0.00	309.50	48.90
206.	2.	38.50	0.40	7.70	1.30	346.20	44.90	10.00	77.60	0.00
206.	2.	28.00	0.00	1.40	5.40	314.00	45.00	4.00	113.70	0.00
206.	3.	2.80	0.00	4.90	0.60	103.70	11.30	1.40	37.90	0.00
206.	4.	0.40	0.00	1.70	0.30	261.70	11.80	0.30	598.20	46.90
206.	4.	0.70	0.00	0.10	0.00	222.40	7.50	1.00	342.60	75.30
206.	4.	0.80	0.00	1.10	0.00	385.40	12.50	7.90	490.90	23.60
206.	5.	2.50	0.00	3.20	0.30	210.70	2.00	6.00	166.40	16.00
206.	5.	11.70	0.00	4.90	0.60	215.50	5.50	21.70	0.00	18.00
206.	5.	30.10	0.30	1.90	0.00	238.90	3.00	7.20	154.70	23.50
250.	1.	4.50	0.20	3.20	0.00	105.70	12.40	6.00	298.30	28.20
250.	1.	4.60	0.00	1.80	0.50	165.90	11.40	5.50	0.00	35.60
250.	2.	275.00	0.70	27.60	9.60	371.30	25.30	63.90	140:20	0.00
250.	2.	58.40	0.00	2.70	0.50	181.90	39.90	16.30	101.00	0.00
250.	3.	17.70	0.00	7.30	3.40	140.60	36.20	7.80	89.10	0.00
250.	4.	2.50	0.00	0.00	0.00	83.60	4.40	2.10	402.00	77.40
250.	4.	1.20	0.00	0.30	0.20	212.70	25.70	1.30	319.10	119.50
250.	4.	10.30	0.00	0.60	0.00	112.10	9.70	22.20	324.50	41.80
250.	5.	11.90	0.00	5.10	0.00	134.50	0.70	73.50	208.60	33.80
250.	5.	29.30	0.00	4.50	0.00	95.80	2.00	52.00	10.00	10.00
250.	5.	21.50	0.00	2.20	0.00	167.70	1.50	72.80	260.80	14.50

APPENDIX 2(c) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25
164.	1.	0.60	0.00	0.00	0.00	0.00	0.30	0.00
164.	1.	1.00	0.00	0.00	0.00	0.10	0.00	0.00
164.	2.	68.70	0.00	0.00	0.00	11.60	0.00	0.00
164.	3.	49.70	0.50	0.00	0.00	3.70	0.00	0.90
164.	4.	0.30	0.00	0.00	0.00	0.00	0.00	0.00
164.	4.	0.10	0.00	0.00	0.00	0.10	0.00	0.00
164.	4.	0.50	0.00	0.00	0.00	0.00	0.00	0.00
164.	5.	33.30	0.10	0.00	0.00	0.40	0.00	0.00
164.	5.	57.30	0.00	0.00	0.00	0.90	0.00	0.00
164.	5.	60.80	0.00	0.00	0.00	0.50	0.00	0.00
206.	1.	1.80	0.00	0.00	0.00	0.40	0.00	0.00
206.	1.	0.90	0.00	0.00	0.00	0.00	0.00	0.00
206.	2.	82.60	2.00	0.00	100.80	0.40	0.00	0.00
206.	2.	38.00	5.40	0.00	0.00	0.70	0.40	0.00
206.	3.	3.80	1.40	0.30	16.80	0.60	0.00	0.00
206.	4.	0.20	0.30	0.00	0.00	0.20	0.00	0.00
206.	4.	0.20	0.10	0.00	0.00	0.20	0.00	0.00
206.	4.	0.00	0.00	0.00	0.00	0.40	0.00	0.00
206.	5.	1.30	0.70	0.00	0.00	2.60	0.00	0.00
206.	5.	3.40	0.60	0.00	0.00	0.90	0.00	0.00
206.	5.	7.70	1.10	0.00	0.00	0.00	0.00	0.60
250.	1.	0.80	0.00	0.40	0.70	1.90	0.00	0.90
250.	1.	0.50	0.50	0.50	0.00	2.30	0.00	1.50
250.	2.	4.80	2.30	6.90	0.00	39.20	0.00	4.60
250.	2.	7.40	0.00	4.80	0.00	4.20	0.00	1.60
250.	3.	1.20	0.50	9.60	7.40	1.50	0.00	0.30
250.	4.	0.00	0.00	0.20	0.00	0.00	0.00	0.90
250.	4.	0.00	0.00	0.00	0.00	0.20	0.00	0.00
250.	4.	0.00	0.20	0.00	0.00	12.10	0.00	0.60
250.	5.	0.00	0.20	0.20	0.00	0.30	0.00	4.00
250.	5.	0.90	0.40	1.90	0.00	0.20	0.00	0.60
250.	5.	0.50	0.40	0.20	0.00	8.60	0.00	3.60

DATE	SITE	SPEC26	SPEC27	SPEC28	SPEC29
164.	1.	0.00	0.00	0.00	0.00
164.	1.	0.00	0.00	0.00	0.00
164.	2.	0.00	0.00	0.00	0.00
164.	3.	0.00	0.00	0.50	0.00
164.	4.	0.00	0.00	0.00	0.00
164.	4.	0.00	0.00	0.00	0.00
164.	4.	0.00	0.00	0.00	0.00
164.	5.	0.00	0.00	0.00	0.00
164.	5.	0.00	0.00	0.00	0.03
164.	5.	0.00	0.00	0.50	0.00
206.	1.	0.00	0.00	0.00	0.00
206.	1.	0.00	0.10	0.00	0.10
206.	2.	0.00	0.00	0.00	0.70
206.	2.	0.70	0.40	0.40	0.40
206.	3.	0.00	0.30	0.20	0.20
206.	4.	0.00	0.00	0.00	0.00
206.	4.	0.00	0.00	0.00	0.00
206.	4.	0.00	0.00	0.00	0.00
206.	5.	0.00	0.00	0.00	0.10
206.	5.	0.00	0.00	0.00	0.30
206.	5.	0.00	0.00	0.00	0.00
250.	1.	0.00	0.00	0.00	0.00
250.	1.	0.00	0.00	0.00	0.00
250.	2.	0.60	0.00	1.20	1.70
250.	2.	0.50	0.00	0.50	0.50
250.	3.	0.70	0.20	0.20	0.20
250.	4.	0.00	0.00	0.00	0.00
250.	4.	0.00	0.00	0.20	0.00
250.	4.	0.00	0.00	0.00	0.00
250.	5.	0.00	0.00	0.00	0.00
250.	5.	0.00	0.00	0.00	0.00
250.	5.	0.00	0.00	0.00	0.50

APPENDIX 2(D). The geometric mean densities (numbers/litre) and 95% confidence limits of the major species of microcrustacea in the weedbeds in Farnborough in 1977.

	CERIO		CYCLO		NAUP		SIDA		SIMO	
	$\bar{X}$	C.L.	$\bar{X}$	C.L.	$\bar{X}$	C.L.	$\bar{X}$	C.L.	$\bar{X}$	C.L.
7.7	404	128-1278	191	104-350	239	144-398	12	4-38	4	0-173
25.7	241	32-1728	27	40-391	150	52-432	66	2-1415	13	3-56
9.8	435	188-1005	197	80-483	249	72-855	35	8-137	35	15-59
22.8	185	32-1026	133	43-409	185	87-393	21	11-42	20	4-94
2.9	517	131-2019	211	152-292	177	63-456	63	10-352	30	12-68
12.9	466	324-669	215	55-833	189	89-399	150	18-1177	76	2-436
26.9	406	76-2158	277	85-896	215	90-514	106	16-670	102	36-285
10.10	265	31-2214	265	77-908	87	13-550	38	5-258	114	30-421
25.10	54	13-211	149	43-504	43	11-165	4	3-5	99	52-185
14.12			119	20-688	26	3-169			23	6-82

	P.DEN		CHYDORUS		CHYDORIDAE	
7.7	2	1-8			30	15-50
25.7	4	0-40	1	0-2	23	7-134
9.8	7	0-130	1	0-1	51	19-129
22.8	11	1-67	2	0-11	56	13-226
2.9	25	5-117	4	0-30	90	47-172
12.9	104	1-11603	22	0-515	302	23-3747
26.9	276	12-5722	14	1-95	410	59-2817
10.10	238	25-2215	58	1-1500	425	96-1867
25.10	215	80-573	121	19-731	394	161-961
14.12	18	9-33	41	1-1095	176	55-326

APPENDIX 3. Length frequency distributions of the microcrustacea in the open water and the weedbeds in Farnborough in 1977. (mm)

Open Water F18a 1977 Length frequency distributions.

Cyclo																	
Date	0.25	0.28	0.34	0.42	0.54	0.64	0.74	0.84	0.94	1.00	1.05	1.10	1.20	1.30	1.40	1.50	1.60
9.6	14	3	30	6	9	11	2										
27.6	1		13	3	7	18	7		3,1	1,2							
7.7	1	2	58	15	8	13	13	1	,1	,1							
25.7		2	23	4	14	15	4										
9.8	8	6	48	19	15	6	1	1	1								
22.8	1	2	27	9	13	10	3										
12.9	1	6	29	6	10	24	9					,1					
26.9		1	38	29	27	8	7		1	1							
10.10			13	5	11	2	6	4					1				
25.10			13	13	21	5	4	4									
9.11		1	30	9	10	12	7	4	2	2		1		1	2	2	1
7.12			12	3	9	8	4	8	2	1	1	2	2		1		
14.12	1		15	3	14	9	12	5	2	3	1	2	2		2	1	

Bos												
Date	.175	.200	.225	.250	.275	.300	.325	.350	.375	.400	.425	.450
9.6		1	12	17	4	9	5	11	8	2		
27.6			1	19	16	12,2	11,4	4,6	8,25	3,3		,1
7.7				9	8	21	11	5,1	8	,1	2	
25.7			6,2	17,1	3	11,1	2,4	1,5	3,4	,3	,1	
9.8	3	15	18	20	5	12	3	2	1			
22.8		2	7	23	10	13,1	10,3	3,2	2,1			
12.9			1	5			1,3	2,3	1,2			
26.9			2	16	7	7	2	4	9	4	1	
10.10			2	6,1	,1	2,1	,4	1,2	1			
25.10	1		20	27,1	7,4	2,10	2,10	1,1	1,7	,1		
9.11	1	6	10	23	4	5	1	2				
7.12			2	16	9	6,7	4,11	1,7	4,2	,1		
14.12			1	16	4,1	14,1	13,5	6,3	10,13	1		

Naup													
Date	.100	.125	.150	.175	.200	.225	.250	.275	.300	.325	.350	.375	.500
9.6		6	7	7	1	1							
27.6		3	10	10	8	8	10						
25.7	1	5	13	12	9	8							
9.8		5	4	10	5								
22.8		6	9	8	4		1						
10.10	1	16	8	6	1	3	6		1				
25.10		18	6	2	1	4	8					1	
9.11		3	9	5	6	3	2	1				1	
7.12	2	7	12	11	6	4	10	3	4	4		3	
14.12		10	8	6	6	2	4		3	2		1	1

Open Water F18a 1977 Length frequency distributions.

D.lon Date	0.35	0.48	0.60	0.73	0.85	0.98
25.7			2	1		
22.8		7	4	1		,1
12.9	1	5	5	3,2	,2	
26.9	7	17	9	7	7	
25.10	1	3	1	,3	,3	

D.amb Date	0.34	0.44	0.54	0.64	0.74	0.84	0.94
9.6	12	9	15	12	12	3	
27.6			9	14,4	4,15	1,3	
7.7	6	13	19	23,4	1,8	,1	
25.7	4	5	13	4,2	2	1	
9.8	6	9	6	3,2	1,2		
22.8	1	11	7	5	2,2	,1	,1
12.9		6	4	2,1	2	,1	
26.9	2	2	6	1	4	1	
25.10		3	1				

Cerio Date	0.25	0.33	0.40	0.48	0.50	0.55	0.63	0.70	0.75
27.6	1	3	3		1				
7.7	10	11,1	14	2,2		1,2		,1	
25.7	16	15	17	3	,2	,2			
9.8	14	19	13	1,1	,2	,1			
22.8	17	17	13,2	1,2	,4	,2			,2
12.9	19	20	21,2	4,8		1,3			
26.9	12	24	14	2					
25.10	1	3	5	6,3		1,7	1,1		

A.aff Date	0.34	0.44	0.54	0.64	0.74	0.84
26.6	3	4	6	6		
7.7	2	4	4	5	1	
25.7	6	5	20	4		
9.8	5	5	5	3		
22.8	2	4	5	4		
26.9	8	11	15	8		
10.10	1	2	13	10		
25.10		4	14	14	2	
9.11	2	1	10	8	2	
7.12	4	4	11	10	5	1
14.12	1	3	7	13	7	2

Diapt Date	0.35	0.48	0.60	0.73	0.85	0.98	1.10	1.20	1.30
25.10	1	1	4	1	1	4	1	3	

Weedbeds F18a 1977 Length frequency distributions.

Cerio Date	.200	.250	.325	.400	.475	.550	.625	.700	.750	.775	.800	.825
9.6	4		13	15	3	2	14	2			1	1
27.6		7	14	53	37,6	4,21	1,17	1				
7.7	2	21	51	56	10,20		24	12	2			
25.7	1	36	18,1	58	29,38	7,42	11.26	1,1	2,2	1	1	1
9.8		12	19	17,1	11,5	2,10	7					
22.8	1	42	46	55,5	49,50	4,30	7,11	2,1	1			
2.9		10	19	40	21,25	1,16	1,1					
12.9		24	21	44,1	10,56	11,37	1,4					
26.9	1	14	11	6	14,3	8,5	1					
10.10		11	2	12,2	17,17	1,7	,1					
25.10			2	5	14,1	5,7	3,6					
9.11		1		5	17,4	10,25	2,9					
24.11				2	14,7	2,4	1,3					

Cyclo Date	.250	.275	.340	.440	.540	.640	.740	.840	.940	1.00	1.05	1.10	1.20	1.30	1.40	1.50	1.60	1.70	1.80
9.4			2	2	12	17	29	20	4	6,1	2,1	1	4		6,1				
25.4	1		3		3	2	15	15	4	9,5	5	5	3	16	4,3	1			
15.5	1		23	8	5	6	14	4	1	2		2	3	6					
23.5	1		18	12	36	32	34	20,2	2,4	11,12	1,1	3,1	1		1	1	1		
9.6			9	3		12	27	6	2,1	3,1	1,2	7,1							
27.6			2	2	2	20	25	5	2	3									
7.7	3	6	54	9	12	37	21	3	3	3	1								
25.7	2	6	44	12	31	31	11,1	25,9	12,7	6,1			2	2					
9.8	1	2	19	10	27	18	8	8	7	4	2	1	1	2					
22.8	2	1	56	24	29	23	7	14	5	3	1	2	1	2	1				
2.9			18	7	10	10	8	16,5	7,1	5	3	3		1					
12.9			1	3	25	20	26	12	9,7	17,12	2,3	3	1		,1	1,3			
26.9		1	14	6	25	22	17	11	2	6	2	2		1		1			
10.10	4		11	5	51	17	11	6	2	2			3						
25.10			10	10	13	12	10	10	7	3	1	1	5	1	1	1			
9.11			12	6	21	14	11	5	3	5	2	1			1				
24.11			9	4	17	15	6	7	1	5		1			2	3			
7.12			6	6	9	5	16	3	4	8	1	1	1	1	2	3	2		1
14.12			10	3	9	14	7	4		2		3	2	1	3	1	1		

APPENDIX 3. cont.

Weedbeds F18a 1977 Length frequency distributions.

A.sut Date	.200	.225	.250	.275	.300	.325	.350	.375
9.4					1		3	2
25.4								
23.5	1	5	2	2	11	5	3	1
9.6								
22.8								
2.9								
26.9			4	1	1		1	
10.10	2		8	4	5	1	1	
25.10		1	3	1	2	2	3	7
24.11	1	1	7	5	5	2	4	1
7.12			1	1	3	2	1	
14.12	1	1	2	3	3	3	5	2
9.11				2	8	2	2	2
25.7	2				4	1		

Acror Date	0.34	0.44	0.54	0.64	0.74	0.84	0.94
9.4		1	3	8	27		
25.4		6	1	8	10	1	
15.5	1	2	2		2	2	
23.5							
9.6	5	5	7	7	3		
27.6	2	3	1	4	2		
25.7	19	10	13	2	2		
22.8	10	14	13	23	4		
2.9	3	4	5	8	1		
12.9	2	3	6	2	1		
26.9	4	2	7	8	4		
24.11	3	1	4	9	5		
7.12	1	2	23	10	7		
25.10		5	6	2			
14.12	2	1	5	12	6		

D.lor Date	0.35	0.48	0.60	0.73	0.85	0.98	1.10	1.23	1.35	1.48
9.6			1	1	6	2	6	2	1	
27.6			2	6	6	5	3,2	,5	,3	,2
7.7	1	2	4	7	10	5,3	2,6	,1	,1	

APPENDIX 3. cont.

Weedbeds F18a 1977 Length frequency distributions.

Simo Date	0.37	0.47	0.50	0.55	0.69	0.89	1.14	1.39	1.60	1.89	2.14	2.39	2.6	2.75	2.89
9.4				1	3	4	2	7	5,2	3,9	1				
25.4			1		4		2	5	1	1		1			
15.5					3	6	2	2	5	1					
23.5				1	3	3	3	1			1				
9.6					6	5	6	7	3	2					
27.6					8	7	6	2	5	1					
25.7	1	1	1	2	14	17	7	4,1	1,3	,1					
9.8	1		3	1	26	15	11,1	5,6	1,11	,2					
22.8		1		2	38	21	18	17,11	6,7	5,5					
2.9			1	9	24	13	3		1,1	1,1					
12.9		4	1	6	30	17	12	7,3	3,16	2,4					
26.9					18	16	5	14	9	1					
10.10					30	21	18	9,2	2,3	1					
25.10		2	4		15	10	7,1	11,2	3,16	2,7					
9.11			1	2	15	21	21	8	4,2	2	1,1				
24.11				1	11	19	16	11,1	,10	,4	,3				
7.12					17	15	16	13	5	4					
14.12					2	2	4	1	2						
Sida Date															
23.5					2	1		1	1	1	1	2			
9.6			1		8	8	1	2			4	2	1		
27.6				1	5	14	10	7	5	4	,2				
7.7					3	11	4	5	4		1,1	,1			
25.7					26	47	42,1	29	28,6	7,13	,4	2	,1	,1	,1
9.8					21	17	9	5	6	10	5,1				
22.8	1		1		20	33	16	14	6,9	21,4	3,2				
2.9					10	9	9	7	3	3,1	1,1	1			
12.9					3	32	14	19	13,1	6,16	1,2	1,2	1,2		
26.9					13	19	19	9	12	4,3	2,4	,2	,1		
10.10					1	1	2	10	8	1	6	2,1			
25.10							1		1	3	1		1		
Eury Date															
9.4					3	1	1	1		1	1		2		
25.4					2	1	2	1				1			
23.5				1	4			1							
9.6															
27.6			1		2	2	2	1							
9.8					5	8	1	2	3	3					
22.8															
2.9					5	2	1	1		1					
26.9					5	1	4	2	4						
10.10					2	1	3	1	3	1	1				
25.10			1		4	3									
9.11					5	1	3	1	1	1	1				
24.11			2		15	9	4	1	2	2		3			
7.12					5	7	3	1	1	1					
14.12					3	2	3	2		2	1		1		

Appendix 4a

Population Estimates of Farnborough 0+ fish using bouyant nets (Area of net = 0.785 m^2. P=Perch and R= Roach).

Date 7.7.77

Round	n	R	P
1	12	76	3
2	11	0	0
3	12	0	0
4	12	123	0
5	11	0	23
6	12	0	0
Total	70	199	26
Est m^2		3.7	0.5
95%cl		±6.4	±1.1

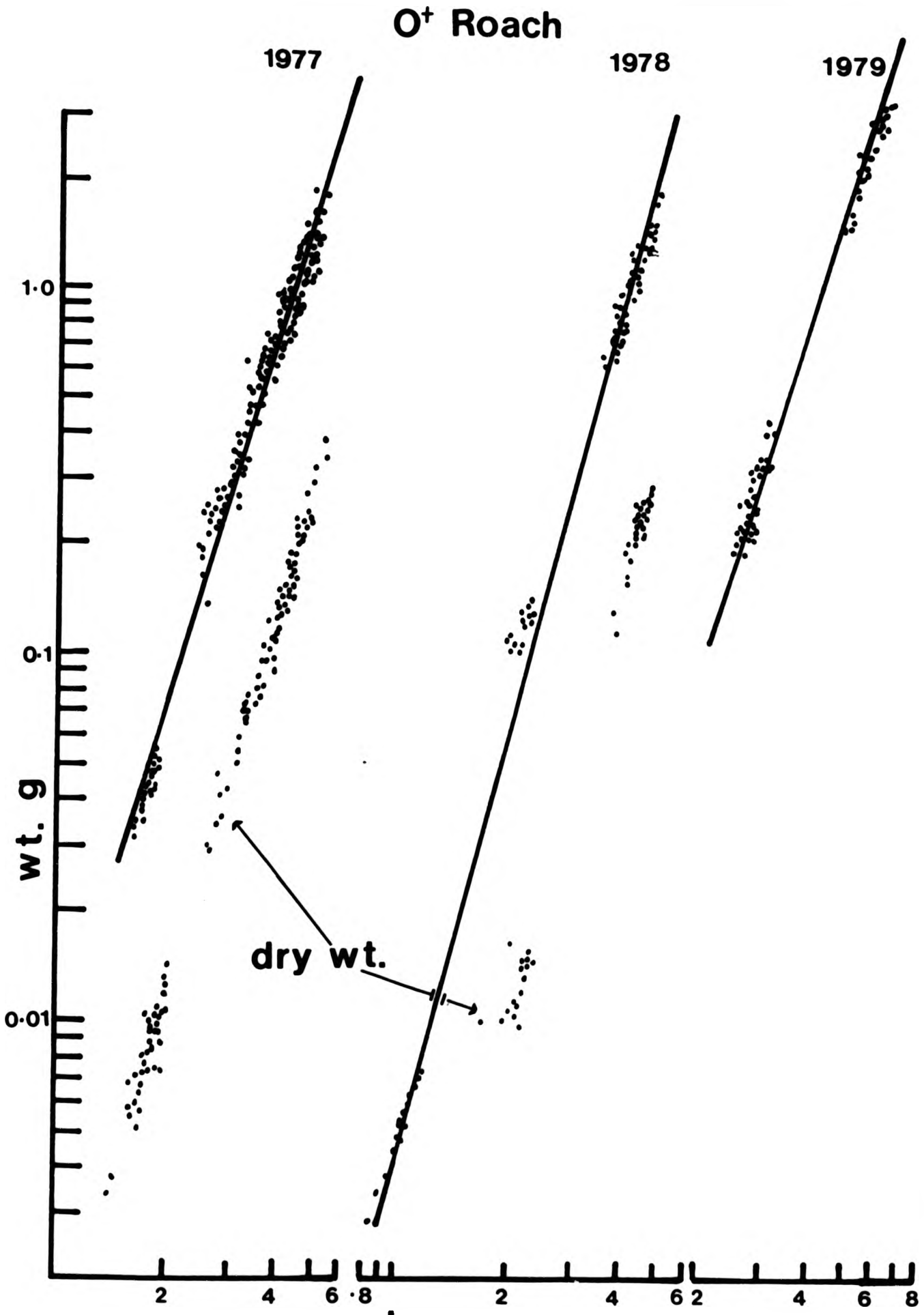
Date 2.9.77

Round	n	R	P
1	12	1	0
2	12	4	1
3	12	1	0
4	11	0	0
5	12	1	0
Total	59	7	1
Est m^2		0.15	-
95%cl		±0.2	-

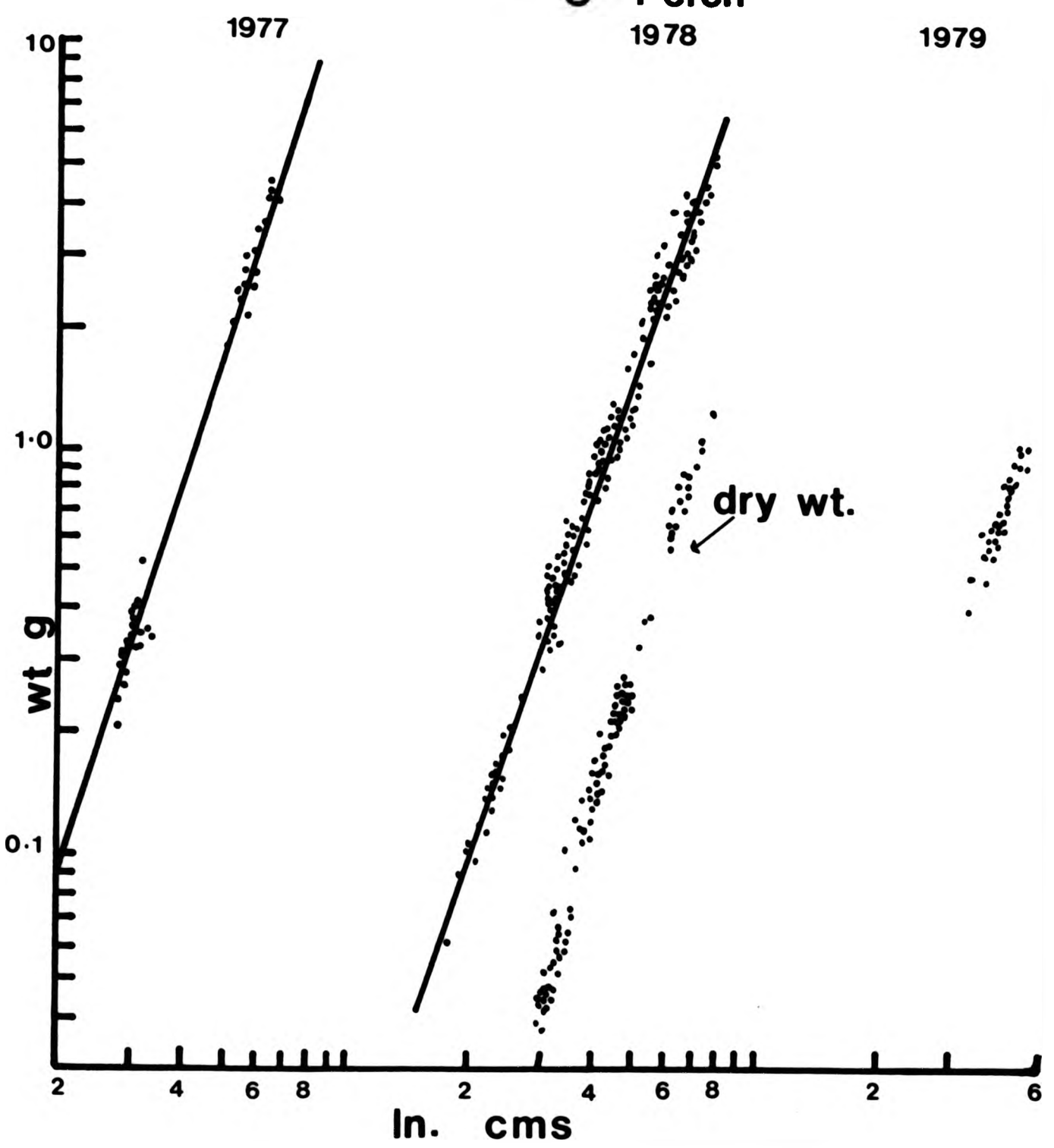
Densities in the margins

Date 12.9.77

Round	n	R	P
1	11	39	1
2	12	30	2
3	4	8	10
Total	27	77	13
Est m^2		3.4	1.2
95%cl		±2.4	±4.0



APPENDIX 4(B). Double log plot of fork length and wet weight of O+ roach from Farnborough in 1977, 1978 and 1979, with the fitted calculated annual linear regression lines. Length/dry weight data have been added where available.



APPENDIX 4(C) Double log plot of fork length and wet weight of O+ perch from Farnborough in 1977, 1978 and 1979, with the fitted calculated annual linear regression lines.

APPENDIX 5(A). Farnborough 0+ roach gut contents, 1977.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14
188.	4.	1.	3.	3.	2.	0.	0.	0.	0.	0.	0.	0.
188.	4.	1.	2.	4.	0.	12.	0.	0.	0.	0.	0.	0.
188.	4.	0.	1.	2.	0.	4.	0.	0.	0.	0.	0.	0.
188.	4.	1.	3.	4.	4.	6.	0.	0.	0.	0.	0.	0.
188.	4.	0.	1.	4.	6.	12.	0.	0.	0.	0.	0.	1.
188.	4.	0.	3.	1.	5.	8.	0.	0.	0.	0.	0.	0.
188.	2.	0.	3.	0.	17.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	3.	1.	14.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	3.	0.	1.	7.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	5.	3.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	3.	3.	0.	0.	0.	0.	0.	0.
188.	5.	1.	6.	3.	0.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	3.	18.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	1.	2.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	5.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	1.	2.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	5.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	6.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	6.	0.	3.	0.	0.	0.	0.	0.	0.	0.
188.	5.	1.	0.	1.	0.	6.	0.	0.	0.	1.	0.	0.
186.	3.	0.	50.	1.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	49.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	17.	0.	0.	0.	0.	0.	0.
188.	7.	0.	3.	1.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	9.	1.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	12.	0.	4.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	1.	3.	2.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	22.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	25.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	30.	0.	10.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	8.	3.	11.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	10.	0.	9.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	2.	1.	10.	0.	0.	0.	4.	0.	0.
188.	4.	0.	13.	9.	0.	0.	0.	0.	0.	10.	0.	0.
188.	4.	0.	2.	0.	0.	0.	0.	0.	0.	20.	0.	0.
188.	4.	0.	3.	2.	0.	0.	0.	0.	0.	22.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	34.	0.	0.
188.	4.	0.	0.	2.	1.	0.	0.	0.	0.	13.	0.	1.
188.	4.	0.	0.	1.	1.	0.	0.	0.	1.	36.	1.	0.
188.	2.	1.	0.	1.	3.	10.	0.	0.	0.	0.	0.	0.
188.	2.	0.	35.	0.	0.	9.	0.	0.	0.	0.	0.	0.
188.	2.	0.	0.	0.	0.	4.	0.	0.	0.	0.	0.	0.
188.	2.	0.	0.	0.	0.	34.	0.	0.	0.	0.	0.	0.
188.	2.	76.	0.	5.	0.	2.	0.	0.	0.	6.	0.	0.
188.	2.	0.	0.	1.	0.	6.	0.	0.	0.	0.	0.	0.
188.	2.	0.	0.	3.	9.	1.	0.	0.	0.	0.	0.	0.
188.	2.	6.	0.	0.	2.	0.	0.	0.	0.	0.	0.	0.
188.	2.	4.	24.	0.	2.	0.	0.	0.	0.	0.	0.	0.
188.	2.	0.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.
188.	6.	0.	0.	0.	2.	0.	0.	0.	0.	1.	0.	2.
188.	6.	0.	0.	0.	80.	0.	0.	0.	0.	0.	0.	1.
188.	6.	0.	0.	1.	8.	7.	0.	0.	0.	0.	0.	0.
188.	6.	0.	0.	1.	16.	0.	0.	0.	0.	0.	0.	2.
188.	6.	0.	0.	0.	6.	1.	0.	0.	0.	0.	0.	0.
188.	6.	0.	0.	1.	23.	1.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	1.	0.	8.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	2.	1.	2.	0.	0.	0.	0.	0.	2.
188.	7.	0.	0.	2.	1.	4.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	3.	1.	1.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	4.	0.	1.	0.	0.	0.	0.	0.	0.
188.	8.	16.	0.	0.	127.	12.	0.	0.	0.	0.	0.	0.
188.	8.	34.	0.	0.	9.	0.	0.	0.	0.	0.	0.	0.
188.	8.	24.	0.	0.	0.	8.	0.	0.	0.	0.	0.	0.
188.	9.	52.	1.	7.	2.	0.	1.	0.	0.	0.	0.	2.
188.	9.	43.	7.	18.	0.	0.	1.	0.	0.	1.	0.	0.
188.	9.	0.	6.	22.	2.	0.	0.	0.	0.	1.	0.	0.
188.	9.	2.	6.	13.	2.	0.	0.	0.	0.	0.	0.	0.
188.	10.	3.	4.	0.	40.	0.	0.	0.	0.	0.	0.	0.
188.	10.	2.	0.	2.	11.	0.	0.	0.	0.	0.	0.	0.
188.	10.	0.	0.	1.	19.	0.	0.	0.	0.	0.	0.	0.
188.	10.	0.	0.	1.	4.	0.	1.	0.	0.	0.	0.	0.
188.	11.	11.	1.	28.	0.	0.	0.	0.	0.	0.	0.	0.
188.	11.	1.	14.	8.	5.	0.	0.	0.	0.	0.	0.	0.
188.	11.	0.	3.	26.	20.	0.	0.	0.	0.	0.	0.	0.
188.	11.	24.	0.	24.	0.	0.	0.	0.	0.	0.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC15	SPEC16	SPEC18	SPEC19	SPEC23	SPEC24	SPEC26	SPEC27	SPEC31
188.	4.	0.	1.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	2.	0.	2.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	1.	0.	0.	0.	0.
188.	4.	1.	1.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	2.	1.	1.	0.	0.	0.	1.	0.	5.	2.
188.	5.	0.	1.	0.	0.	0.	0.	0.	4.	0.
188.	5.	0.	1.	0.	0.	0.	0.	0.	1.	0.
188.	5.	0.	4.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	1.	0.	0.	0.	1.	0.	0.	0.
188.	5.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	5.	1.	0.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	5.	0.	0.	0.	0.	0.	0.	0.	3.	0.
188.	5.	0.	1.	0.	0.	0.	0.	0.	1.	0.
188.	5.	0.	0.	0.	0.	0.	0.	0.	2.	0.
188.	5.	0.	1.	0.	0.	0.	0.	0.	3.	0.
188.	5.	0.	0.	0.	0.	0.	0.	0.	2.	0.
188.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	1.	0.	0.	0.	0.	0.	2.	0.
188.	7.	0.	1.	0.	0.	0.	0.	0.	1.	0.
188.	7.	0.	1.	0.	0.	0.	0.	0.	4.	0.
188.	7.	0.	1.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	4.	0.
188.	7.	0.	1.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	1.	4.
188.	4.	0.	1.	0.	0.	0.	0.	0.	3.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	0.	0.	0.	0.	1.	0.
188.	4.	0.	0.	0.	1.	0.	0.	0.	0.	0.
188.	4.	0.	0.	0.	7.	0.	0.	0.	1.	0.
188.	2.	7.	1.	0.	1.	0.	0.	0.	43.	0.
188.	2.	1.	0.	0.	0.	0.	0.	0.	7.	1.
188.	2.	5.	1.	0.	1.	0.	0.	0.	8.	0.
188.	2.	0.	0.	0.	0.	0.	0.	0.	1.	0.
188.	2.	0.	0.	0.	0.	0.	0.	0.	2.	0.
188.	2.	3.	1.	0.	0.	0.	0.	0.	16.	0.
188.	2.	5.	2.	0.	1.	0.	0.	0.	5.	0.
188.	2.	10.	2.	0.	1.	0.	0.	0.	14.	0.
188.	2.	7.	0.	0.	4.	0.	0.	2.	0.	0.
188.	2.	9.	3.	0.	1.	0.	0.	0.	12.	0.
188.	6.	0.	7.	0.	1.	0.	0.	0.	0.	0.
189.	6.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	6.	0.	5.	0.	0.	0.	0.	0.	1.	0.
188.	6.	0.	1.	0.	0.	0.	0.	0.	0.	0.
188.	6.	2.	1.	0.	0.	0.	0.	0.	0.	0.
188.	6.	2.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	1.	1.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	7.	0.	0.	1.	0.	0.	0.	0.	0.	0.
188.	8.	0.	3.	0.	0.	0.	0.	0.	1.	0.
188.	8.	0.	6.	0.	1.	0.	0.	0.	0.	0.
188.	8.	0.	3.	0.	0.	0.	0.	0.	8.	0.
188.	9.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	9.	4.	1.	0.	0.	0.	0.	0.	0.	0.
188.	9.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	9.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	10.	0.	2.	0.	0.	0.	0.	0.	0.	0.
188.	10.	0.	1.	1.	0.	0.	0.	0.	0.	0.
189.	10.	0.	1.	0.	0.	0.	0.	0.	1.	0.
188.	10.	0.	2.	0.	0.	0.	0.	0.	0.	0.
189.	11.	0.	0.	0.	0.	0.	0.	0.	0.	0.
189.	11.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	11.	0.	0.	0.	0.	0.	0.	0.	0.	0.
188.	11.	0.	0.	0.	0.	0.	0.	0.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
206.	1.	1.	14.	2.	0.	0.	0.	0.	0.	0.
206.	1.	0.	10.	2.	0.	0.	0.	1.	0.	0.
206.	1.	1.	8.	26.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	1.	0.	10.	1.	0.	0.	0.	0.	0.
206.	1.	0.	18.	4.	0.	0.	1.	0.	0.	0.
206.	1.	0.	2.	2.	0.	0.	0.	0.	0.	0.
206.	1.	0.	22.	23.	0.	0.	0.	0.	0.	0.
206.	1.	38.	2.	28.	4.	0.	0.	0.	0.	0.
206.	1.	56.	0.	16.	2.	4.	0.	0.	0.	1.
206.	1.	0.	0.	22.	1.	1.	0.	0.	0.	0.
206.	1.	0.	1.	0.	0.	0.	0.	0.	0.	0.
206.	2.	8.	1.	21.	0.	0.	0.	0.	0.	0.
206.	2.	34.	2.	2.	0.	0.	0.	0.	0.	0.
206.	2.	2.	3.	0.	0.	0.	0.	0.	0.	0.
206.	2.	11.	0.	1.	2.	0.	0.	0.	0.	0.
206.	2.	1.	0.	41.	0.	0.	0.	0.	0.	0.
206.	2.	95.	0.	10.	0.	0.	0.	0.	0.	0.
206.	2.	11.	2.	6.	0.	0.	0.	1.	0.	0.
206.	2.	29.	0.	0.	4.	2.	0.	0.	0.	0.
206.	2.	2.	2.	36.	0.	2.	0.	0.	0.	0.
206.	2.	1.	1.	8.	0.	0.	0.	0.	0.	0.
221.	1.	0.	0.	18.	3.	0.	0.	0.	0.	0.
221.	1.	0.	0.	35.	0.	0.	0.	0.	0.	0.
221.	1.	7.	0.	0.	47.	0.	0.	1.	0.	0.
221.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.
221.	1.	0.	5.	1.	5.	0.	0.	0.	0.	0.
221.	2.	0.	0.	5.	0.	0.	1.	8.	0.	0.
221.	2.	0.	0.	5.	0.	5.	0.	0.	0.	0.
221.	2.	2.	1.	8.	1.	0.	1.	2.	0.	0.
221.	2.	0.	0.	2.	0.	0.	0.	0.	1.	0.
221.	2.	2.	0.	7.	9.	0.	0.	0.	2.	0.
221.	2.	0.	0.	0.	1.	0.	0.	0.	0.	0.
221.	2.	2.	0.	0.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	2.	2.	0.	0.	0.	0.	1.
221.	3.	1.	0.	1.	2.	0.	0.	0.	1.	0.
221.	3.	0.	0.	5.	395.	25.	0.	0.	0.	0.
221.	3.	0.	5.	35.	230.	0.	0.	0.	0.	0.
221.	3.	0.	0.	15.	0.	0.	0.	2.	0.	0.
221.	3.	0.	5.	10.	805.	10.	0.	0.	0.	0.
221.	3.	0.	0.	0.	850.	1.	0.	0.	0.	0.
221.	3.	0.	0.	0.	0.	0.	0.	0.	1.	0.
221.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	5.	0.	1.	94.	1.	0.	0.	0.	0.
234.	1.	3.	0.	13.	2.	0.	0.	5.	2.	2.
234.	1.	0.	10.	55.	315.	35.	0.	0.	0.	0.
234.	1.	0.	0.	105.	25.	5.	0.	0.	0.	0.
234.	1.	0.	0.	38.	3.	2.	0.	0.	5.	0.
234.	1.	0.	0.	50.	170.	0.	0.	0.	5.	10.
234.	1.	0.	0.	0.	155.	0.	0.	1.	0.	0.
234.	1.	80.	1.	50.	118.	1.	0.	0.	0.	0.
234.	1.	0.	2.	4.	4.	1.	0.	0.	0.	0.
234.	1.	33.	0.	3.	98.	0.	0.	0.	0.	0.
234.	1.	0.	0.	0.	204.	0.	0.	0.	0.	0.
234.	2.	0.	0.	60.	0.	0.	0.	0.	0.	0.
234.	2.	0.	1.	60.	10.	0.	0.	0.	0.	0.
234.	2.	0.	8.	6.	12.	0.	0.	0.	0.	1.
234.	2.	0.	0.	19.	0.	0.	0.	0.	0.	2.
234.	2.	0.	0.	80.	0.	0.	0.	0.	0.	1.
245.	1.	5.	0.	380.	5.	20.	1.	0.	0.	0.
245.	1.	9.	1.	53.	63.	18.	0.	0.	0.	0.
245.	1.	0.	0.	865.	60.	170.	0.	0.	0.	0.
245.	1.	409.	0.	26.	221.	30.	0.	0.	0.	0.
245.	1.	143.	0.	37.	171.	70.	0.	0.	0.	0.
245.	1.	20.	0.	363.	76.	89.	0.	0.	0.	0.
245.	1.	38.	0.	20.	40.	11.	0.	0.	0.	0.
245.	1.	38.	0.	9.	11.	2.	0.	0.	0.	0.
245.	1.	116.	0.	34.	56.	29.	0.	0.	0.	0.
245.	1.	0.	0.	256.	8.	26.	0.	0.	0.	0.
245.	2.	10.	15.	800.	80.	175.	0.	0.	0.	0.
245.	2.	5.	0.	610.	80.	155.	0.	0.	0.	0.
245.	2.	3.	10.	905.	40.	135.	0.	0.	0.	0.
245.	2.	0.	0.	840.	15.	65.	0.	0.	0.	0.
245.	2.	74.	0.	136.	30.	42.	0.	0.	0.	0.
245.	2.	0.	0.	705.	25.	80.	0.	0.	0.	0.
245.	2.	15.	0.	690.	60.	95.	0.	0.	0.	0.
245.	2.	0.	5.	535.	60.	65.	0.	0.	0.	0.
245.	2.	15.	0.	760.	15.	85.	0.	0.	0.	0.
245.	2.	0.	0.	40.	1.	0.	0.	1.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
206.	1.	1.	0.	11.	0.	0.	0.	0.	0.	0.
206.	1.	2.	0.	23.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	1.	0.	0.	0.	0.
206.	1.	0.	0.	2.	0.	0.	0.	0.	0.	1.
206.	1.	0.	0.	1.	0.	0.	2.	3.	0.	0.
206.	1.	0.	1.	1.	0.	0.	0.	0.	0.	1.
206.	1.	2.	0.	4.	0.	0.	0.	0.	0.	0.
206.	1.	4.	0.	6.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	3.	45.	0.	0.
206.	1.	0.	0.	0.	0.	0.	10.	24.	0.	0.
206.	1.	2.	0.	14.	0.	2.	0.	0.	0.	0.
206.	1.	2.	0.	23.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	1.	0.	0.	4.	1.	0.	0.
206.	2.	0.	0.	0.	0.	0.	73.	86.	0.	1.
206.	2.	0.	0.	9.	0.	0.	2.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	4.	2.	0.	0.
206.	2.	0.	1.	5.	0.	1.	0.	1.	0.	0.
206.	2.	0.	0.	0.	1.	0.	1.	10.	0.	0.
206.	2.	0.	0.	0.	0.	1.	2.	30.	0.	0.
206.	2.	0.	0.	1.	0.	0.	102.	42.	0.	0.
206.	2.	0.	0.	7.	0.	0.	15.	20.	0.	0.
206.	2.	0.	0.	0.	0.	1.	0.	3.	0.	0.
221.	1.	0.	0.	43.	0.	0.	0.	0.	0.	0.
221.	1.	0.	0.	15.	0.	0.	0.	0.	0.	1.
221.	1.	0.	0.	0.	0.	0.	8.	4.	0.	0.
221.	1.	0.	0.	1.	0.	0.	0.	0.	0.	2.
221.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	0.	0.	8.	0.	0.	0.	0.
221.	2.	0.	0.	23.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	0.	0.	9.	0.	0.	0.	0.
221.	2.	0.	1.	17.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	1.	0.	7.	0.	0.	0.	3.
221.	2.	0.	0.	14.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	1.	0.	1.	0.	0.	0.	0.
221.	2.	0.	0.	4.	0.	0.	0.	0.	0.	0.
221.	3.	0.	0.	5.	0.	2.	0.	0.	0.	1.
221.	3.	0.	0.	0.	0.	0.	1.	1.	0.	0.
221.	3.	0.	0.	40.	0.	1.	0.	0.	0.	0.
221.	3.	0.	0.	9.	0.	2.	0.	0.	0.	1.
221.	3.	0.	0.	0.	0.	0.	15.	5.	0.	1.
221.	3.	0.	0.	1.	0.	0.	20.	0.	0.	0.
221.	3.	0.	0.	1.	0.	2.	0.	0.	1.	2.
221.	3.	0.	0.	8.	0.	2.	0.	0.	0.	1.
221.	3.	0.	0.	9.	1.	0.	0.	0.	0.	0.
234.	1.	0.	5.	5.	0.	8.	0.	0.	0.	2.
234.	1.	0.	0.	0.	0.	5.	0.	0.	0.	0.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	0.	0.	13.	0.	0.	0.	0.	0.	2.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	0.	0.	0.	0.	0.	1.	0.	0.	1.
234.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.
234.	1.	0.	0.	0.	0.	5.	0.	0.	0.	0.
234.	1.	0.	0.	0.	0.	1.	3.	0.	0.	1.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	2.	0.	0.	3.	0.	0.	0.	0.	0.	2.
234.	2.	0.	0.	2.	0.	0.	0.	0.	0.	5.
234.	2.	0.	0.	19.	0.	0.	0.	1.	1.	0.
234.	2.	0.	0.	5.	0.	0.	0.	0.	0.	0.
234.	2.	0.	0.	10.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	5.	1.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	17.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	13.	0.	0.
245.	1.	0.	0.	0.	0.	0.	3.	0.	0.	0.
245.	1.	1.	0.	0.	0.	0.	4.	5.	0.	0.
245.	1.	0.	0.	0.	0.	0.	7.	6.	0.	0.
245.	1.	0.	0.	0.	0.	0.	36.	11.	0.	0.
245.	1.	0.	0.	0.	0.	0.	1.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	10.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	5.	0.	0.
245.	2.	0.	0.	0.	0.	5.	5.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	14.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	1.	0.
245.	2.	0.	0.	0.	0.	0.	15.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	6.	0.	0.	0.	0.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC27	SPEC28	SPEC29	SPEC30	SPEC31
206.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	5.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	1.	0.	0.	0.	0.	0.	3.	0.	0.	0.	0.
206.	1.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	3.	0.	0.	0.	0.
206.	2.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
206.	2.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	1.	2.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
221.	1.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	1.	1.	1.	0.	1.	0.	0.	0.	0.	0.	0.	0.
221.	2.	1.	16.	0.	0.	0.	0.	0.	28.	0.	0.	0.
221.	2.	1.	0.	0.	0.	0.	0.	0.	0.	5.	0.	0.
221.	2.	1.	0.	0.	1.	0.	0.	0.	15.	0.	0.	0.
221.	2.	4.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.
221.	2.	15.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	2.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	2.	7.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.
221.	3.	2.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	0.	0.	0.	0.	0.	0.	0.	0.	5.	0.	0.
221.	3.	1.	0.	0.	0.	0.	0.	0.	0.	70.	0.	0.
221.	3.	0.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.
221.	3.	2.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
221.	3.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.
234.	1.	3.	0.	1.	1.	0.	2.	0.	0.	3.	0.	0.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	5.	0.	0.
234.	1.	0.	0.	1.	0.	0.	0.	0.	0.	5.	0.	0.
234.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	1.	0.	0.	0.	0.	0.	0.	0.	170.	0.	0.
234.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	195.	0.	0.
234.	1.	0.	0.	0.	0.	0.	0.	0.	0.	4.	0.	0.
234.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	2.	1.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.
234.	2.	5.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.
234.	2.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
234.	2.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	6.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	5.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	3.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	2.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	14.	0.	0.
245.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
245.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	1.
245.	2.	8.	0.	1.	0.	0.	0.	1.	0.	0.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
255.	1.	6.	0.	2.	0.	0.	0.	0.	0.	0.
255.	1.	45.	0.	15.	0.	0.	1.	0.	0.	0.
255.	1.	0.	10.	20.	5.	0.	0.	1.	0.	1.
255.	1.	0.	0.	80.	5.	0.	0.	0.	0.	2.
255.	1.	2.	0.	13.	1.	1.	0.	0.	0.	0.
255.	1.	4.	0.	14.	0.	0.	0.	0.	0.	0.
255.	1.	1.	5.	35.	5.	5.	0.	0.	0.	0.
255.	1.	0.	5.	5.	0.	0.	1.	0.	0.	0.
255.	1.	0.	0.	80.	17.	34.	0.	0.	0.	0.
255.	1.	1.	5.	20.	0.	0.	2.	0.	3.	0.
255.	2.	0.	5.	65.	25.	30.	0.	0.	0.	0.
255.	2.	0.	0.	155.	50.	10.	0.	0.	0.	0.
255.	2.	0.	5.	285.	30.	70.	0.	0.	0.	0.
255.	2.	40.	5.	35.	15.	5.	0.	1.	0.	1.
255.	2.	0.	0.	55.	10.	10.	1.	0.	0.	0.
255.	2.	0.	0.	120.	30.	15.	0.	0.	0.	0.
255.	2.	0.	0.	15.	0.	0.	0.	0.	1.	2.
255.	2.	3.	0.	180.	0.	0.	0.	2.	0.	0.
255.	2.	27.	0.	50.	13.	10.	0.	0.	0.	1.
255.	2.	0.	0.	70.	40.	15.	0.	0.	0.	0.
255.	2.	0.	0.	65.	2.	20.	0.	0.	0.	0.
269.	1.	5.	1.	360.	5.	5.	0.	0.	0.	0.
269.	1.	0.	0.	200.	0.	0.	2.	6.	0.	0.
269.	1.	0.	0.	290.	0.	0.	0.	3.	1.	0.
269.	1.	0.	0.	7.	0.	0.	0.	6.	1.	0.
269.	1.	0.	0.	17.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	105.	0.	3.	2.	6.	0.	0.
269.	1.	0.	0.	16.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	480.	0.	0.	2.	1.	1.	0.
269.	1.	3.	1.	80.	0.	0.	0.	1.	0.	0.
269.	1.	0.	0.	12.	0.	0.	1.	2.	0.	0.
269.	2.	0.	0.	55.	0.	0.	0.	3.	1.	6.
269.	2.	2.	0.	180.	0.	0.	14.	7.	1.	5.
269.	2.	1.	3.	450.	0.	1.	1.	7.	1.	3.
269.	2.	0.	0.	235.	0.	0.	0.	2.	0.	1.
269.	2.	3.	0.	230.	0.	0.	2.	6.	1.	4.
269.	2.	2.	0.	90.	0.	1.	1.	7.	0.	5.
269.	2.	33.	0.	175.	5.	0.	3.	9.	1.	1.
269.	2.	4.	0.	22.	0.	0.	33.	8.	0.	1.
269.	2.	3.	0.	49.	0.	0.	3.	11.	0.	9.
269.	2.	0.	0.	4.	0.	0.	0.	6.	0.	14.
283.	1.	1.	0.	3.	0.	0.	0.	0.	1.	1.
283.	1.	13.	0.	11.	32.	0.	1.	0.	1.	0.
283.	1.	1.	1.	3.	4.	1.	0.	1.	0.	0.
283.	1.	0.	2.	508.	0.	0.	0.	1.	4.	1.
298.	1.	17.	0.	27.	340.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	195.	0.	0.	0.	0.	1.
298.	1.	60.	1.	0.	235.	0.	1.	0.	2.	0.
298.	1.	21.	0.	0.	68.	0.	0.	0.	0.	0.
298.	1.	3.	0.	0.	57.	0.	0.	0.	0.	0.
298.	1.	5.	0.	0.	280.	1.	0.	0.	0.	0.
298.	1.	9.	1.	0.	136.	0.	0.	0.	0.	0.
298.	1.	2.	0.	1.	25.	0.	0.	0.	0.	0.
298.	1.	1.	0.	0.	24.	0.	0.	0.	0.	0.
298.	1.	0.	0.	5.	185.	0.	0.	0.	0.	0.
298.	1.	22.	0.	0.	19.	1.	0.	0.	0.	0.
298.	1.	10.	0.	0.	205.	0.	0.	0.	0.	0.
298.	1.	3.	0.	0.	103.	0.	0.	0.	0.	0.
298.	1.	50.	0.	2.	565.	4.	0.	0.	0.	0.
298.	1.	9.	0.	4.	340.	6.	0.	0.	0.	0.
298.	1.	0.	0.	1.	52.	0.	0.	0.	0.	0.
298.	1.	1.	0.	4.	104.	1.	0.	0.	0.	0.
298.	1.	3.	0.	0.	50.	0.	0.	0.	0.	0.
298.	1.	29.	0.	1.	39.	0.	0.	0.	0.	0.
347.	1.	1.	0.	0.	460.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	8.	0.	1.	1.	0.	0.
347.	1.	0.	0.	0.	44.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	85.	0.	0.	0.	0.	0.
347.	1.	1.	0.	0.	45.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	120.	0.	0.	0.	0.	0.
347.	1.	2.	0.	0.	141.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	164.	0.	0.	0.	0.	0.
347.	2.	1.	0.	0.	351.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	306.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	260.	0.	0.	0.	0.	0.
347.	1.	0.	1.	0.	235.	0.	0.	0.	0.	0.
347.	1.	1.	1.	0.	450.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	105.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	260.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	120.	1.	0.	0.	0.	0.
347.	1.	0.	0.	0.	100.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	50.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	70.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	203.	0.	0.	0.	0.	0.
347.	1.	0.	0.	1.	1.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	215.	0.	0.	0.	0.	0.
347.	1.	0.	0.	1.	343.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	387.	0.	0.	0.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
255.	1.	1.	1.	5.	0.	0.	0.	0.	0.	0.
255.	1.	0.	0.	70.	0.	0.	0.	0.	0.	0.
255.	1.	0.	5.	80.	0.	0.	1.	1.	1.	0.
255.	1.	0.	1.	85.	0.	4.	0.	0.	0.	1.
255.	1.	1.	3.	12.	0.	0.	1.	0.	0.	0.
255.	1.	0.	0.	30.	2.	0.	0.	0.	0.	0.
255.	1.	3.	2.	2.	0.	0.	0.	0.	0.	0.
255.	1.	1.	1.	60.	0.	0.	0.	0.	0.	0.
255.	1.	4.	1.	0.	0.	0.	4.	1.	0.	0.
255.	1.	1.	1.	45.	0.	0.	0.	0.	0.	0.
255.	2.	0.	0.	7.	0.	0.	1.	0.	0.	0.
255.	2.	0.	0.	4.	1.	0.	10.	0.	0.	0.
255.	2.	0.	0.	2.	1.	1.	0.	0.	0.	0.
255.	2.	0.	0.	1.	0.	1.	0.	0.	0.	0.
255.	2.	0.	0.	2.	0.	0.	1.	0.	0.	0.
255.	2.	0.	0.	8.	0.	0.	0.	0.	0.	0.
255.	2.	0.	1.	17.	0.	0.	0.	0.	0.	0.
255.	2.	2.	1.	18.	1.	0.	0.	0.	0.	0.
255.	2.	0.	0.	2.	0.	0.	0.	0.	0.	0.
255.	2.	0.	0.	4.	0.	0.	0.	0.	0.	0.
255.	2.	0.	1.	19.	0.	2.	3.	0.	0.	0.
269.	1.	0.	0.	5.	0.	5.	5.	0.	0.	0.
269.	1.	3.	4.	60.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	8.	0.	0.	0.	0.	0.	0.
269.	1.	2.	4.	33.	0.	1.	0.	0.	0.	0.
269.	1.	1.	1.	15.	0.	0.	0.	0.	0.	0.
269.	1.	0.	1.	3.	0.	0.	0.	0.	0.	0.
269.	1.	14.	2.	101.	0.	0.	0.	0.	0.	0.
269.	1.	1.	5.	1.	0.	1.	0.	0.	0.	0.
269.	1.	2.	1.	38.	0.	0.	0.	0.	0.	0.
269.	1.	0.	1.	18.	0.	3.	0.	0.	0.	0.
269.	2.	0.	8.	85.	0.	1.	0.	0.	0.	0.
269.	2.	0.	13.	12.	80.	5.	0.	0.	0.	0.
269.	2.	0.	11.	12.	20.	1.	0.	0.	0.	0.
269.	2.	1.	8.	1.	0.	0.	0.	0.	0.	0.
269.	2.	0.	5.	70.	0.	0.	0.	0.	0.	0.
269.	2.	3.	5.	33.	1.	4.	0.	0.	0.	0.
269.	2.	2.	9.	33.	0.	2.	0.	0.	0.	1.
269.	2.	8.	15.	17.	0.	5.	0.	0.	0.	0.
269.	2.	2.	9.	14.	0.	2.	0.	0.	0.	0.
269.	2.	0.	19.	28.	0.	2.	0.	0.	0.	0.
283.	1.	0.	2.	13.	0.	0.	0.	0.	0.	0.
283.	1.	1.	6.	9.	0.	1.	2.	0.	0.	1.
283.	1.	0.	5.	28.	0.	0.	0.	0.	0.	0.
283.	1.	0.	0.	4.	0.	0.	0.	0.	0.	1.
298.	1.	0.	2.	0.	0.	1.	25.	5.	0.	0.
298.	1.	0.	4.	0.	0.	0.	77.	10.	0.	0.
298.	1.	0.	8.	0.	0.	0.	35.	3.	0.	0.
298.	1.	0.	2.	0.	0.	33.	26.	1.	0.	0.
298.	1.	0.	0.	0.	0.	0.	14.	4.	0.	0.
298.	1.	0.	4.	0.	0.	0.	40.	35.	0.	0.
298.	1.	0.	4.	0.	0.	0.	34.	7.	0.	0.
298.	1.	0.	0.	0.	1.	19.	11.	11.	0.	0.
298.	1.	0.	0.	0.	0.	29.	1.	0.	0.	1.
298.	1.	0.	0.	0.	0.	1.	0.	0.	0.	0.
298.	1.	3.	4.	0.	0.	0.	12.	8.	0.	0.
298.	1.	0.	2.	0.	0.	4.	0.	0.	0.	0.
298.	1.	0.	2.	0.	0.	0.	1.	2.	0.	0.
298.	1.	0.	1.	0.	0.	0.	4.	1.	0.	0.
298.	1.	0.	2.	0.	0.	0.	4.	0.	0.	0.
298.	1.	0.	1.	0.	0.	0.	5.	1.	0.	0.
298.	1.	1.	0.	0.	3.	1.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	15.	1.	0.	1.	0.
298.	1.	1.	2.	0.	0.	0.	14.	21.	0.	0.
347.	1.	0.	2.	0.	0.	2.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	2.	0.	0.	0.	0.
347.	1.	0.	2.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	1.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	6.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	5.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	1.	0.	0.
347.	2.	0.	0.	0.	0.	4.	0.	0.	0.	0.
347.	1.	0.	1.	0.	0.	3.	0.	0.	0.	0.
347.	1.	0.	5.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	5.	0.	0.	2.	0.	0.	0.	0.
347.	1.	0.	2.	0.	0.	2.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	1.	0.	0.	3.	0.	0.	0.	0.
347.	1.	0.	2.	0.	0.	8.	0.	0.	0.	0.
347.	1.	0.	3.	0.	0.	13.	0.	0.	0.	0.
347.	1.	0.	1.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	1.	0.	0.	8.	0.	1.	0.	0.
347.	1.	0.	1.	0.	0.	2.	0.	1.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	2.	0.	0.	1.	0.	1.	0.	0.
347.	1.	0.	1.	0.	0.	4.	0.	1.	0.	0.
347.	1.	0.	5.	0.	0.	2.	0.	7.	0.	0.

APPENDIX 5(a) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC24	SPEC27	SPEC30	SPEC31
255.	1.	1.	0.	0.	0.	0.	0.	0.	0.
255.	1.	8.	0.	0.	0.	0.	0.	0.	0.
255.	1.	13.	0.	0.	0.	0.	0.	0.	0.
255.	1.	14.	0.	0.	0.	0.	0.	0.	0.
255.	1.	20.	0.	0.	0.	0.	0.	0.	0.
255.	1.	5.	0.	0.	0.	0.	0.	0.	0.
255.	1.	0.	0.	0.	0.	0.	0.	0.	0.
255.	1.	6.	0.	0.	0.	0.	0.	0.	0.
255.	1.	0.	0.	0.	0.	0.	0.	0.	0.
255.	1.	34.	0.	0.	0.	0.	0.	0.	0.
255.	2.	3.	0.	0.	0.	0.	0.	0.	0.
255.	2.	7.	0.	0.	0.	0.	0.	0.	0.
255.	2.	3.	0.	0.	0.	0.	0.	0.	0.
255.	2.	0.	0.	0.	0.	0.	1.	0.	0.
255.	2.	2.	0.	0.	0.	0.	0.	0.	0.
255.	2.	1.	0.	0.	0.	0.	0.	0.	0.
255.	2.	2.	0.	0.	0.	0.	0.	0.	0.
255.	2.	1.	1.	0.	0.	0.	0.	0.	0.
255.	2.	1.	0.	0.	0.	0.	0.	0.	0.
255.	2.	2.	0.	1.	0.	0.	0.	0.	0.
255.	2.	3.	0.	0.	0.	0.	0.	0.	0.
269.	1.	6.	0.	1.	0.	0.	0.	0.	0.
269.	1.	1.	0.	0.	1.	0.	0.	0.	0.
269.	1.	2.	0.	0.	0.	0.	0.	0.	0.
269.	1.	4.	0.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	0.	0.	0.	0.	0.	0.
269.	1.	1.	0.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	0.	0.	0.	0.	0.	0.
269.	1.	1.	0.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	0.	0.	0.	0.	0.	0.
269.	1.	0.	0.	0.	0.	0.	0.	0.	0.
269.	2.	2.	0.	1.	0.	0.	0.	0.	0.
269.	2.	3.	3.	1.	0.	0.	0.	0.	0.
269.	2.	0.	0.	0.	0.	0.	0.	0.	0.
269.	2.	0.	0.	0.	0.	0.	0.	0.	0.
269.	2.	3.	0.	0.	0.	0.	0.	0.	0.
269.	2.	1.	0.	0.	0.	0.	0.	0.	0.
269.	2.	2.	0.	0.	0.	0.	0.	0.	0.
269.	2.	1.	0.	0.	0.	0.	0.	0.	0.
269.	2.	1.	0.	0.	0.	0.	0.	0.	0.
269.	2.	0.	0.	0.	2.	0.	0.	0.	0.
283.	1.	2.	0.	1.	0.	0.	0.	0.	0.
283.	1.	17.	0.	3.	0.	0.	1.	0.	245.
283.	1.	0.	0.	0.	1.	0.	0.	0.	0.
283.	1.	3.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	2.
298.	1.	0.	0.	1.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	1.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	2.	0.	0.	0.	1.	0.	0.	10.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	1.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	2.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	30.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
298.	1.	0.	0.	0.	0.	0.	0.	1.	0.
298.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.		0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	1.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	1.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	2.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	1.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	3.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	2.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	1.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	1.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	2.	0.	0.	0.
347.	1.	0.	0.	0.	0.	0.	0.	0.	0.
347.	1.	0.	0.	0.	0.	1.	0.	0.	0.

APPENDIX 5(b) Farnborough 0+ perch gut contents, 1977.

DATE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9	SPEC10
188.	2.	23.	100.	1.	4.	0.	0.	0.	0.	0.
188.	0.	49.	110.	2.	11.	0.	1.	0.	0.	0.
188.	5.	23.	180.	1.	5.	0.	0.	0.	0.	0.
188.	2.	100.	110.	0.	3.	0.	0.	0.	0.	0.
188.	12.	26.	385.	3.	3.	0.	0.	0.	0.	0.
188.	2.	16.	24.	1.	14.	1.	4.	0.	0.	0.
188.	0.	8.	5.	1.	16.	0.	2.	0.	0.	0.
188.	0.	27.	20.	4.	67.	0.	0.	0.	0.	0.
188.	4.	21.	45.	0.	6.	0.	1.	0.	0.	0.
188.	0.	21.	71.	3.	34.	0.	0.	0.	0.	0.
206.	1.	4.	54.	0.	2.	0.	0.	0.	0.	0.
206.	0.	0.	5.	0.	0.	0.	0.	0.	0.	0.
206.	3.	0.	3.	0.	0.	0.	0.	0.	0.	0.
206.	1.	4.	3.	0.	0.	0.	1.	0.	0.	0.
255.	397.	0.	159.	0.	0.	2.	0.	0.	1.	1.
255.	898.	0.	37.	0.	0.	8.	0.	0.	0.	7.
255.	42.	0.	40.	0.	0.	8.	0.	1.	1.	6.
255.	790.	0.	26.	0.	0.	3.	2.	1.	1.	5.
255.	211.	1.	163.	0.	0.	6.	3.	0.	1.	4.
255.	311.	1.	141.	0.	0.	15.	14.	2.	0.	0.
245.	560.	1.	75.	0.	3.	38.	3.	11.	0.	0.
245.	367.	0.	1212.	0.	0.	0.	0.	0.	0.	0.
245.	46.	0.	670.	0.	0.	4.	2.	1.	0.	0.
245.	387.	0.	10.	0.	2.	3.	1.	0.	0.	0.
245.	203.	1.	231.	0.	0.	8.	3.	0.	1.	13.
245.	95.	0.	110.	0.	0.	5.	5.	0.	0.	1.
245.	87.	0.	44.	0.	0.	0.	1.	0.	0.	3.
245.	2685.	2.	628.	5.	0.	0.	2.	0.	0.	0.
245.	1190.	0.	48.	0.	0.	9.	5.	4.	0.	2.
245.	2045.	0.	400.	3.	0.	0.	1.	0.	0.	1.
245.	1322.	0.	206.	0.	0.	9.	2.	2.	0.	2.
245.	459.	0.	950.	0.	2.	4.	0.	1.	0.	0.
303.	1282.	7.	14.	1.	1.	0.	0.	0.	0.	0.
303.	525.	3.	2.	30.	356.	0.	0.	0.	0.	0.
303.	32.	0.	12.	10.	213.	0.	4.	0.	0.	0.
303.	20.	0.	15.	5.	980.	0.	0.	0.	0.	0.
303.	10.	205.	465.	0.	110.	0.	0.	0.	0.	0.

DATE	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18	SPEC19	SPEC20
188.	0.	2.	0.	0.	0.	0.	0.	0.	2.	0.
188.	0.	17.	0.	0.	0.	0.	0.	0.	0.	0.
188.	0.	25.	0.	0.	0.	0.	0.	0.	1.	0.
188.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.
188.	0.	11.	0.	0.	0.	0.	0.	0.	0.	0.
188.	0.	22.	0.	3.	0.	0.	0.	0.	0.	0.
188.	0.	23.	0.	2.	0.	0.	0.	0.	0.	0.
188.	0.	2.	0.	0.	0.	0.	0.	0.	0.	0.
188.	0.	13.	0.	1.	0.	0.	0.	0.	3.	0.
188.	0.	30.	0.	0.	0.	0.	0.	0.	0.	0.
206.	0.	54.	0.	0.	0.	0.	0.	0.	2.	0.
206.	0.	15.	0.	2.	0.	0.	0.	0.	0.	0.
206.	0.	5.	0.	8.	0.	0.	0.	0.	7.	0.
206.	0.	111.	0.	1.	0.	0.	0.	1.	3.	0.
255.	1.	184.	1.	6.	0.	0.	0.	0.	0.	0.
255.	1.	159.	0.	4.	0.	0.	0.	0.	4.	0.
255.	1.	149.	0.	1.	0.	0.	0.	0.	7.	0.
255.	0.	201.	0.	8.	0.	0.	0.	0.	3.	0.
255.	5.	548.	0.	0.	0.	0.	0.	0.	24.	0.
255.	0.	91.	2.	12.	0.	0.	0.	0.	11.	0.
245.	1.	140.	0.	3.	0.	0.	0.	0.	10.	0.
245.	0.	5.	1.	0.	0.	0.	1.	0.	8.	0.
245.	0.	65.	0.	1.	0.	0.	2.	1.	8.	0.
245.	0.	14.	1.	0.	0.	0.	0.	0.	5.	0.
245.	2.	77.	0.	3.	0.	0.	1.	0.	15.	0.
245.	2.	49.	1.	1.	0.	0.	0.	0.	27.	0.
245.	0.	18.	1.	1.	0.	0.	0.	1.	38.	0.
245.	0.	1.	0.	2.	0.	0.	0.	0.	3.	0.
245.	0.	28.	2.	3.	0.	0.	0.	0.	3.	0.
245.	1.	6.	0.	1.	0.	0.	0.	0.	6.	0.
245.	1.	24.	2.	3.	0.	0.	0.	0.	4.	0.
245.	0.	8.	0.	3.	0.	0.	0.	0.	18.	0.
303.	0.	1.	0.	0.	0.	0.	0.	1.	2.	0.
303.	0.	1.	0.	1.	0.	0.	1.	0.	2.	0.
303.	0.	1.	0.	3.	0.	0.	0.	0.	5.	0.
302.	0.	0.	0.	4.	0.	0.	0.	0.	4.	0.
303.	0.	13.	0.	7.	0.	0.	0.	0.	12.	0.

APPENDIX 5(b) cont.

DATE	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26
188.	0.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	0.	1.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
188.	1.	0.	0.	0.	0.	0.
188.	0.	0.	0.	0.	0.	0.
206.	0.	1.	0.	0.	0.	0.
206.	0.	1.	0.	0.	0.	0.
206.	0.	1.	3.	0.	0.	0.
206.	0.	4.	0.	0.	0.	0.
255.	0.	9.	1.	1.	1.	0.
255.	0.	0.	0.	0.	0.	0.
255.	3.	4.	0.	0.	0.	0.
255.	0.	25.	0.	0.	0.	0.
255.	4.	9.	1.	0.	1.	26.
255.	1.	4.	1.	0.	0.	0.
245.	0.	6.	0.	0.	0.	0.
245.	3.	0.	6.	0.	0.	1.
245.	5.	7.	1.	0.	0.	0.
245.	0.	3.	0.	0.	0.	0.
245.	0.	16.	0.	0.	0.	0.
245.	2.	3.	2.	0.	0.	0.
245.	1.	10.	3.	0.	0.	0.
245.	0.	2.	1.	0.	0.	30.
245.	0.	7.	1.	0.	0.	0.
245.	1.	4.	3.	0.	1.	0.
245.	0.	0.	4.	0.	0.	0.
245.	4.	0.	1.	0.	0.	0.
303.	0.	0.	0.	0.	0.	107.
303.	0.	0.	0.	0.	0.	1.
303.	1.	0.	0.	0.	0.	0.
303.	0.	0.	0.	0.	0.	0.
303.	0.	2.	0.	0.	1.	0.

KEY TO DIET DATA FROM FARNBROUGH, 1977

SPEC1 CYCLOPS SPEC2 D.LONGISPINA SPEC3 C.PULCHELLA SPEC4 BOSMINA
SPEC5 D.AMBIGUA SPEC6 ACROPERUS SPEC7 EURYCERCUS
SPEC8 PSEUDOCHYDORUS SPEC9 P.ADUNCUS SPEC10 P.DENTICULATUS
SPEC11 CHYDORUS SPEC12 SIDA SPEC13 OSTRACODS SPEC14 A.AFFINIS
SPEC15 K.QUADRATA SPEC16 K.COCHLEARIS SPEC17 CORIXIDS SPEC18 MITE L.
SPEC19 CHIRONOMID L. SPEC20 CADDIS L. SPEC21 INSECTS SPEC22 SIMOCEPHALUS
SPEC23 WORMS SPEC24 A.GUTTATA SPEC25 BEETLE L. SPEC26 DIAPTOMUS
SPEC27 NAUPLII SPEC28 P.UNCINATUS SPEC29 BRACHIONUS SPEC30 MAYFLIES .

APPENDIX 5(c). Yateley cased 0+ roach diet data, 1978.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9
208.	1.	0.	281.	0.	5.	51.	0.	0.	1.	0.
208.	1.	0.	75.	0.	2.	2.	0.	0.	20.	0.
208.	1.	0.	12.	0.	4.	18.	0.	0.	0.	0.
208.	1.	0.	2.	3.	1.	5.	2.	0.	0.	104.
208.	1.	0.	0.	0.	0.	13.	0.	0.	1.	16.
208.	1.	0.	445.	0.	0.	40.	0.	0.	1.	3.
208.	1.	0.	201.	0.	1.	33.	0.	0.	0.	0.
208.	1.	0.	0.	0.	0.	17.	0.	0.	0.	0.
208.	1.	0.	130.	0.	0.	38.	0.	0.	0.	0.
208.	1.	0.	9.	0.	0.	42.	0.	0.	0.	0.
208.	1.	0.	4.	2.	0.	3.	0.	0.	2.	29.
208.	1.	0.	0.	1.	0.	1.	0.	0.	1.	42.
213.	1.	0.	0.	1.	3.	0.	0.	0.	0.	0.
213.	1.	0.	8.	1.	0.	0.	0.	0.	2.	0.
213.	1.	0.	0.	1.	17.	0.	0.	0.	1.	0.
213.	1.	0.	1.	1.	0.	0.	93.	0.	1.	2.
213.	2.	0.	1.	4.	42.	2.	0.	0.	2.	0.
213.	3.	0.	0.	10.	2.	0.	3.	0.	0.	0.
213.	3.	0.	12.	3.	10.	2.	2.	0.	6.	0.
213.	3.	0.	10.	2.	11.	0.	0.	0.	5.	0.
213.	3.	0.	27.	0.	7.	3.	0.	0.	1.	0.
228.	1.	0.	0.	1.	8.	8.	0.	0.	2.	0.
228.	1.	0.	0.	3.	18.	4.	0.	0.	6.	0.
228.	1.	0.	0.	1.	26.	6.	0.	0.	4.	1.
228.	1.	0.	0.	0.	0.	1.	0.	0.	0.	17.
228.	1.	0.	0.	15.	3.	0.	13.	0.	5.	51.
228.	1.	0.	0.	2.	58.	1.	65.	0.	0.	2.
228.	1.	0.	0.	1.	6.	3.	0.	0.	2.	0.
228.	3.	0.	1.	0.	3.	2.	0.	0.	3.	0.
228.	3.	0.	0.	2.	25.	4.	0.	0.	0.	0.
228.	3.	0.	0.	0.	15.	3.	1.	0.	1.	0.
228.	3.	0.	0.	1.	21.	5.	0.	0.	2.	0.
228.	3.	0.	0.	0.	1.	1.	1.	0.	1.	0.
228.	3.	0.	0.	2.	4.	4.	0.	0.	3.	0.
228.	3.	0.	0.	1.	3.	2.	0.	0.	0.	0.

DATE	SITE	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18
208.	1.	0.	0.	2.	0.	0.	5.	0.	0.	0.
208.	1.	0.	0.	2.	0.	50.	2.	0.	0.	0.
208.	1.	0.	0.	1.	0.	7.	14.	0.	0.	0.
208.	1.	0.	0.	0.	0.	8.	0.	0.	0.	0.
208.	1.	0.	0.	2.	0.	1.	0.	0.	0.	0.
208.	1.	0.	0.	1.	0.	0.	15.	0.	0.	0.
208.	1.	0.	0.	0.	0.	1.	1.	0.	1.	0.
208.	1.	0.	0.	0.	0.	0.	0.	0.	11.	0.
208.	1.	0.	0.	0.	0.	4.	3.	0.	0.	0.
208.	1.	0.	0.	0.	0.	1.	0.	0.	7.	0.
208.	1.	0.	0.	5.	1.	8.	1.	0.	1.	0.
213.	1.	0.	0.	2.	0.	1.	1.	0.	0.	0.
213.	1.	3.	0.	3.	0.	2.	0.	0.	0.	1.
213.	1.	0.	0.	2.	0.	35.	0.	0.	0.	0.
213.	1.	0.	0.	4.	0.	4.	0.	0.	0.	0.
213.	3.	1.	0.	0.	0.	2.	0.	0.	0.	0.
213.	3.	1.	0.	1.	0.	0.	0.	2.	0.	1.
213.	3.	0.	0.	0.	0.	0.	0.	0.	0.	1.
213.	3.	1.	0.	5.	0.	41.	0.	0.	0.	0.
213.	3.	3.	0.	2.	0.	57.	0.	0.	0.	0.
213.	3.	5.	0.	4.	0.	46.	0.	0.	0.	0.
228.	1.	0.	0.	8.	0.	49.	0.	0.	0.	0.
228.	1.	1.	0.	10.	0.	62.	0.	0.	0.	0.
228.	1.	2.	0.	11.	0.	66.	0.	0.	0.	0.
228.	1.	0.	0.	1.	0.	17.	0.	0.	0.	0.
228.	1.	0.	0.	8.	0.	21.	0.	0.	0.	0.
228.	1.	1.	0.	1.	30.	0.	2.	0.	0.	3.
228.	1.	3.	0.	8.	0.	160.	0.	0.	0.	0.
228.	3.	0.	0.	3.	0.	95.	0.	0.	0.	0.
228.	3.	4.	0.	15.	0.	250.	0.	0.	0.	0.
228.	3.	3.	0.	5.	0.	170.	0.	0.	0.	0.
228.	3.	0.	0.	4.	0.	28.	0.	0.	0.	0.
228.	3.	6.	1.	11.	0.	125.	0.	0.	0.	0.
228.	3.	1.	1.	11.	0.	170.	0.	0.	0.	0.
228.	3.	1.	0.	6.	0.	110.	0.	0.	0.	0.

Site equals case number.

APPENDIX 5(c) cont.

DATE	SITE	SPEC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27
208.	1.	0.	0.	1.	0.	0.	0.	7.	3.	0.
208.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.
208.	1.	0.	0.	2.	0.	0.	0.	23.	8.	0.
208.	1.	0.	0.	1.	0.	0.	0.	2.	3.	0.
208.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
208.	1.	0.	0.	1.	0.	0.	0.	40.	2.	0.
208.	1.	0.	0.	1.	0.	0.	0.	20.	3.	0.
208.	1.	0.	0.	0.	0.	0.	0.	352.	4.	0.
208.	1.	0.	0.	0.	0.	0.	0.	14.	3.	0.
208.	1.	0.	0.	0.	0.	0.	0.	365.	3.	0.
208.	1.	0.	0.	1.	0.	0.	0.	5.	0.	0.
213.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	1.	0.	0.	2.	0.	0.	0.	0.	2.	0.
213.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	3.	0.	0.	1.	0.	1.	0.	0.	0.	0.
213.	3.	0.	0.	1.	0.	0.	0.	0.	0.	0.
213.	3.	0.	0.	1.	0.	0.	0.	0.	0.	0.
213.	3.	0.	0.	2.	0.	0.	0.	0.	1.	0.
228.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	1.	0.	1.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	10.	0.
228.	3.	0.	0.	0.	0.	0.	0.	1.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.

DATE	SITE	SPEC28	SPEC29	SPEC30	SPEC31	SPEC32	SPEC33	SPEC34	SPEC35
208.	1.	0.	0.	0.	3.	0.	0.	0.	0.
208.	1.	0.	0.	0.	1.	0.	0.	0.	0.
208.	1.	0.	0.	0.	2.	0.	0.	0.	0.
208.	1.	0.	0.	0.	4.	0.	0.	0.	0.
208.	1.	0.	0.	0.	4.	0.	0.	0.	0.
208.	1.	0.	0.	0.	2.	0.	0.	0.	0.
208.	1.	0.	0.	0.	1.	0.	0.	0.	0.
208.	1.	0.	0.	0.	1.	0.	0.	0.	0.
208.	1.	0.	0.	0.	6.	0.	0.	0.	0.
208.	1.	0.	0.	0.	4.	0.	0.	0.	0.
208.	1.	0.	2.	1.	2.	0.	0.	0.	0.
208.	1.	0.	0.	0.	0.	0.	0.	0.	0.
213.	1.	0.	0.	0.	5.	0.	0.	0.	0.
213.	1.	0.	0.	0.	1.	0.	0.	0.	0.
213.	1.	0.	0.	0.	4.	0.	0.	0.	0.
213.	1.	0.	0.	0.	1.	0.	0.	0.	0.
213.	3.	0.	1.	0.	4.	0.	0.	0.	0.
213.	3.	0.	0.	0.	2.	0.	0.	0.	0.
213.	3.	0.	0.	0.	0.	0.	0.	0.	0.
213.	3.	0.	0.	1.	4.	0.	0.	0.	0.
213.	3.	0.	0.	1.	0.	0.	0.	0.	0.
228.	1.	0.	1.	1.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	1.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	0.	0.	0.	0.
228.	1.	0.	0.	0.	2.	0.	0.	0.	0.
228.	1.	0.	0.	0.	0.	2.	0.	0.	0.
228.	1.	0.	0.	0.	2.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	2.	0.	0.	0.
228.	3.	0.	0.	0.	0.	1.	0.	0.	0.
228.	3.	0.	0.	0.	0.	1.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	1.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.
228.	3.	0.	0.	0.	0.	0.	0.	0.	0.

APPENDIX 5(d). Yateley cased 0+ perch diet data, 1978.

DATE	SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9	SPEC10	SPEC11	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16
208.	2.	0.	178.	12.	19.	19.	0.	0.	8.	0.	0.	0.	4.	1.	1.	1.	6.
208.	2.	0.	79.	4.	25.	3.	2.	0.	34.	0.	2.	0.	0.	1.	2.	0.	3.
208.	2.	2.	150.	61.	21.	12.	1.	0.	12.	1.	0.	0.	2.	0.	0.	0.	1.
208.	2.	1.	216.	7.	7.	3.	0.	0.	27.	0.	1.	1.	6.	0.	1.	0.	5.
208.	2.	1.	72.	13.	12.	1.	0.	0.	15.	0.	1.	0.	1.	0.	1.	0.	5.
208.	2.	0.	15.	1.	0.	14.	0.	0.	3.	0.	0.	0.	1.	0.	0.	0.	0.
208.	2.	0.	45.	12.	11.	16.	0.	0.	7.	0.	0.	0.	0.	0.	0.	0.	1.
213.	2.	0.	7.	2.	0.	0.	5.	1.	10.	0.	0.	0.	0.	0.	0.	0.	1.
213.	2.	2.	250.	74.	401.	19.	10.	29.	13.	1.	4.	0.	2.	0.	1.	1.	2.
213.	2.	45.	533.	74.	209.	23.	4.	23.	44.	4.	1.	2.	8.	0.	4.	0.	0.
213.	2.	0.	98.	29.	17.	2.	6.	11.	0.	1.	0.	0.	0.	0.	0.	0.	0.
213.	2.	2.	45.	1.	3.	0.	1.	4.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	2.	5.	279.	75.	126.	2.	5.	6.	19.	0.	2.	0.	0.	3.	4.	0.	2.
213.	2.	15.	465.	127.	32.	16.	8.	5.	42.	12.	0.	0.	1.	1.	0.	0.	0.
213.	2.	26.	486.	152.	142.	25.	0.	5.	61.	0.	0.	0.	1.	0.	1.	0.	0.
213.	2.	125.	305.	150.	125.	25.	0.	1.	15.	9.	0.	0.	5.	0.	0.	0.	1.
213.	2.	10.	310.	8.	20.	1.	270.	10.	4.	25.	2.	0.	1.	0.	1.	0.	0.
213.	4.	2.	37.	33.	99.	19.	11.	3.	16.	0.	0.	0.	3.	0.	6.	0.	0.
213.	4.	7.	185.	18.	44.	0.	14.	1.	17.	0.	1.	0.	2.	0.	6.	0.	3.
213.	4.	5.	183.	46.	101.	10.	0.	1.	6.	0.	0.	0.	1.	1.	2.	0.	2.
213.	4.	2.	97.	8.	9.	2.	3.	0.	4.	0.	0.	0.	0.	0.	1.	0.	0.
213.	5.	28.	406.	103.	394.	0.	0.	49.	44.	0.	0.	1.	2.	1.	4.	0.	0.
213.	5.	25.	395.	51.	50.	4.	50.	7.	4.	26.	0.	0.	5.	3.	0.	0.	0.
213.	5.	120.	880.	50.	505.	3.	0.	21.	19.	0.	1.	0.	9.	0.	3.	0.	0.
213.	5.	59.	377.	41.	320.	5.	0.	10.	26.	0.	1.	0.	1.	0.	1.	0.	1.
213.	5.	112.	1185.	77.	500.	2.	0.	5.	32.	0.	3.	0.	1.	1.	0.	0.	11.
213.	7.	9.	206.	38.	12.	2.	52.	2.	13.	3.	1.	0.	0.	1.	0.	0.	5.
213.	7.	0.	18.	8.	4.	0.	0.	0.	7.	0.	0.	0.	0.	4.	0.	0.	7.
213.	7.	133.	568.	75.	18.	4.	3.	0.	23.	0.	0.	0.	3.	8.	0.	0.	0.
213.	7.	80.	460.	42.	7.	0.	17.	5.	10.	0.	0.	0.	1.	0.	0.	0.	2.
213.	7.	115.	234.	88.	19.	0.	6.	2.	19.	0.	0.	0.	1.	2.	0.	0.	3.
213.	7.	30.	306.	43.	18.	9.	86.	3.	4.	10.	0.	1.	0.	1.	0.	0.	0.
213.	7.	8.	231.	54.	26.	1.	8.	2.	11.	0.	3.	0.	4.	0.	0.	0.	0.
228.	5.	1.	18.	4.	0.	0.	0.	0.	3.	0.	0.	0.	0.	2.	6.	0.	0.
228.	5.	31.	9.	29.	5.	0.	0.	3.	4.	0.	0.	0.	0.	0.	2.	0.	0.
228.	5.	52.	31.	34.	210.	5.	0.	9.	3.	0.	1.	0.	1.	0.	0.	0.	0.
228.	5.	64.	6.	12.	1.	0.	0.	7.	4.	0.	1.	0.	0.	0.	0.	0.	0.
228.	5.	1.	2.	3.	0.	0.	0.	0.	7.	0.	0.	0.	1.	1.	0.	0.	0.
228.	5.	284.	24.	41.	92.	41.	0.	3.	12.	2.	0.	2.	1.	0.	0.	0.	0.
228.	5.	6.	1.	0.	1.	0.	0.	0.	2.	0.	0.	0.	0.	0.	0.	0.	0.
228.	5.	308.	60.	111.	369.	51.	0.	1.	15.	0.	6.	0.	2.	1.	1.	0.	0.
228.	7.	1.	8.	4.	4.	0.	0.	2.	6.	0.	0.	0.	0.	0.	0.	0.	0.
229.	7.	4.	4.	12.	44.	0.	0.	3.	2.	0.	0.	0.	0.	0.	0.	0.	0.
228.	7.	56.	1.	9.	224.	2.	10.	17.	8.	4.	0.	0.	1.	0.	0.	0.	0.
229.	7.	0.	0.	1.	1.	0.	0.	0.	4.	0.	0.	0.	0.	0.	0.	0.	0.
226.	7.	155.	9.	20.	77.	0.	74.	7.	8.	5.	0.	0.	3.	0.	1.	0.	0.
228.	7.	27.	5.	3.	12.	0.	1.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
229.	7.	780.	87.	70.	750.	10.	103.	10.	5.	97.	0.	1.	0.	0.	0.	0.	0.

APPENDIX 5(d) cont.

DATE	SITE	SPEC17	SPEC18	'EC19	SPEC20	SPEC21	SPEC22	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27	EC28	SPEC29	SPEC30	SPEC31	SPEC32
208.	2.	0.	0.	0.	0.	1.	0.	0.	0.	0.	1.	0.	0.	0.	0.	1.	0.
208.	2.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.
208.	2.	0.	0.	0.	1.	3.	0.	0.	0.	1.	0.	0.	0.	0.	0.	2.	0.
208.	2.	0.	0.	0.	0.	2.	0.	0.	0.	0.	1.	1.	0.	0.	0.	2.	0.
208.	2.	0.	0.	0.	0.	4.	0.	0.	0.	0.	0.	0.	0.	1.	0.	2.	0.
208.	2.	0.	0.	0.	0.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
208.	2.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.
213.	2.	0.	4.	3.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.
213.	2.	0.	0.	3.	0.	4.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.	0.
213.	2.	0.	0.	2.	0.	4.	0.	0.	0.	0.	1.	0.	1.	0.	0.	1.	0.
213.	2.	0.	1.	4.	0.	1.	0.	0.	0.	0.	0.	0.	3.	0.	0.	0.	0.
213.	2.	0.	8.	1.	0.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	2.	0.	1.	1.	0.	3.	0.	0.	0.	0.	0.	0.	1.	0.	0.	0.	0.
213.	2.	0.	0.	0.	0.	11.	1.	0.	0.	2.	0.	1.	1.	0.	0.	0.	0.
213.	2.	1.	0.	0.	0.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	2.	0.	0.	0.	0.	1.	0.	0.	0.	5.	0.	0.	0.	0.	0.	0.	0.
213.	2.	0.	0.	0.	0.	2.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	4.	0.	1.	2.	0.	2.	0.	0.	0.	0.	0.	0.	1.	0.	0.	1.	0.
213.	4.	0.	5.	2.	0.	1.	0.	0.	1.	0.	0.	0.	0.	0.	0.	1.	0.
213.	4.	0.	4.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	4.	0.	0.	2.	0.	1.	0.	0.	0.	0.	0.	0.	2.	0.	0.	0.	0.
213.	5.	0.	0.	0.	0.	3.	0.	1.	0.	0.	1.	0.	1.	0.	0.	0.	0.
213.	5.	0.	0.	0.	0.	1.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	5.	1.	0.	0.	0.	2.	1.	0.	0.	0.	0.	0.	0.	0.	0.	4.	0.
213.	5.	1.	0.	1.	0.	2.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	5.	0.	0.	0.	7.	1.	0.	1.	1.	0.	3.	2.	0.	1.	0.	1.	0.
213.	7.	0.	0.	1.	0.	3.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	7.	0.	7.	0.	0.	1.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	7.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	7.	0.	0.	0.	1.	1.	0.	0.	0.	0.	0.	0.	3.	0.	0.	0.	0.
213.	7.	0.	2.	0.	0.	1.	0.	0.	0.	0.	0.	0.	2.	0.	0.	0.	0.
213.	7.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
213.	7.	0.	2.	0.	0.	2.	0.	0.	0.	0.	0.	0.	3.	0.	0.	0.	0.
228.	5.	0.	1.	2.	0.	1.	0.	1.	3.	0.	0.	0.	0.	0.	0.	0.	0.
228.	5.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	1.	0.	0.	0.
228.	5.	0.	0.	0.	0.	5.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	5.	0.	0.	2.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	5.	0.	3.	1.	3.	4.	0.	5.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	5.	0.	0.	0.	0.	3.	0.	3.	0.	0.	0.	1.	0.	1.	0.	0.	0.
228.	5.	0.	0.	2.	1.	3.	0.	0.	0.	0.	0.	0.	0.	2.	0.	0.	0.
228.	5.	0.	0.	0.	0.	2.	0.	0.	0.	0.	0.	1.	0.	0.	1.	0.	0.
228.	7.	0.	2.	0.	2.	2.	0.	2.	0.	0.	0.	0.	0.	3.	0.	0.	0.
228.	7.	0.	1.	0.	0.	1.	0.	1.	0.	0.	0.	0.	1.	2.	0.	0.	0.
228.	7.	0.	0.	0.	0.	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
228.	7.	0.	7.	1.	3.	3.	0.	1.	2.	0.	0.	0.	0.	0.	0.	0.	0.
228.	7.	0.	1.	0.	12.	4.	3.	0.	1.	0.	0.	0.	2.	0.	0.	0.	0.
228.	7.	0.	1.	0.	12.	4.	3.	0.	1.	0.	0.	0.	0.	2.	0.	0.	0.
228.	7.	0.	0.	0.	4.	4.	1.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.

APPENDIX 5(d) cont.

DATE	SITE	SPEC33	SPEC34	SPEC35
208.	2.	0.	0.	0.
208.	2.	0.	0.	0.
208.	2.	1.	0.	0.
208.	2.	0.	0.	0.
208.	2.	0.	0.	0.
208.	2.	0.	0.	0.
208.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	0.	1.
213.	2.	0.	0.	0.
213.	2.	0.	0.	0.
213.	2.	0.	1.	0.
213.	2.	0.	0.	0.
213.	4.	0.	0.	0.
213.	4.	0.	0.	0.
213.	4.	0.	0.	0.
213.	4.	0.	0.	0.
213.	5.	0.	0.	0.
213.	5.	0.	0.	0.
213.	5.	0.	0.	0.
213.	5.	0.	0.	0.
213.	5.	0.	0.	0.
213.	7.	0.	0.	0.
213.	7.	0.	0.	1.
213.	7.	0.	0.	1.
213.	7.	0.	0.	1.
213.	7.	0.	0.	0.
213.	7.	0.	0.	0.
213.	7.	0.	0.	0.
229.	5.	0.	0.	0.
228.	5.	0.	0.	0.
228.	5.	0.	0.	0.
228.	5.	0.	0.	0.
228.	5.	0.	0.	0.
228.	5.	0.	0.	0.
228.	5.	1.	0.	1.
228.	5.	0.	0.	0.
228.	7.	0.	0.	0.
228.	7.	0.	0.	1.
228.	7.	0.	0.	0.
228.	7.	0.	0.	0.
228.	7.	0.	0.	0.
228.	7.	0.	0.	0.
228.	7.	0.	0.	2.

KEY TO DIET DATA FROM YATELEY, 1978

SPEC1 DIAPTOMUS SPEC2 CYCLOPS SPEC3 DAPHNIA SPEC4 C.PULCHELLA
SPEC5 BOSMINA SPEC6 SCAPHOLESERIS SPEC7 DIAPHANOSOMA SPEC8 EURYCERCUS
SPEC9 POLYPHEMUS SPEC10 P.ADUNCUS SPEC11 P.DENTICULATUS
SPEC12 CHYDORUS SPEC13 SIDA SPEC14 OSTRACODS SPEC15 NAUPLII
SPEC16 SIMOCEPHALUS SPEC17 K.COCHLEARIS SPEC18 CLOEON SP.
SPEC19 CAENIS SPEC20 CHAOBORUS SPEC21 CHIRONOMID L. SPEC22 CHIRO. P
SPEC23 LEPIDOPT. L. SPEC24 ASELLUS SPEC25 K.QUADRATA SPEC26 CADDIS L.
SPEC27 ACROPERUS SPEC28 CORIXIDS SPEC29 INSECTS SPEC30 A.GUTTATA
SPEC31 MITE L. SPEC32 MITE AD. SPEC33 Crangonyx SPEC34 A.AFFINIS
SPEC35 NEMATODES.

Site equals case number.

APPENDIX 5(e). Yateley cased 0+ perch diet data, 1979.

SITE	SPEC1	SPEC2	SPEC3	SPEC4	SPEC5	SPEC6	SPEC7	SPEC8	SPEC9	SPEC10	SPEC11
1.	18.	16.	0.	12.	0.	5.	0.	1.	0.	0.	2.
1.	24.	76.	0.	540.	1.	1.	20.	1.	0.	0.	24.
1.	16.	286.	0.	46.	0.	0.	1.	3.	0.	0.	23.
1.	85.	1163.	0.	343.	0.	1.	9.	1.	0.	0.	19.
1.	26.	179.	0.	212.	0.	0.	8.	0.	0.	0.	15.
2.	1.	609.	0.	41.	0.	0.	2.	0.	0.	0.	0.
2.	74.	367.	0.	58.	1.	0.	1.	0.	0.	0.	0.
2.	71.	840.	0.	210.	6.	0.	13.	0.	0.	0.	4.
2.	13.	794.	0.	80.	0.	0.	6.	0.	0.	0.	4.
2.	46.	544.	0.	310.	1.	0.	46.	2.	0.	0.	2.
2.	1.	1036.	0.	55.	0.	0.	1.	0.	0.	0.	1.
2.	51.	330.	0.	1177.	15.	373.	40.	0.	5.	2.	60.
2.	8.	685.	0.	148.	2.	0.	16.	1.	0.	0.	0.
2.	16.	1162.	0.	131.	1.	0.	7.	1.	0.	0.	0.
2.	25.	326.	0.	22.	0.	0.	1.	0.	0.	0.	0.
2.	5.	65.	0.	64.	0.	3.	0.	1.	0.	0.	3.
1.	215.	132.	1.	158.	11.	212.	6.	0.	5.	6.	21.
3.	11.	93.	0.	20.	0.	6.	3.	0.	0.	2.	8.
3.	19.	0.	0.	1.	0.	0.	0.	0.	0.	0.	1.
3.	5.	349.	0.	59.	0.	0.	0.	1.	0.	0.	148.
3.	30.	444.	0.	119.	0.	0.	1.	0.	0.	0.	23.
3.	28.	84.	0.	33.	0.	0.	0.	0.	0.	0.	2.
3.	35.	382.	0.	93.	0.	0.	2.	0.	0.	0.	8.
3.	4.	120.	0.	40.	0.	0.	0.	1.	0.	0.	4.
3.	1.	29.	0.	4.	0.	2.	0.	0.	0.	0.	3.
3.	10.	204.	0.	47.	0.	0.	0.	0.	0.	0.	10.
3.	52.	89.	0.	152.	3.	179.	2.	0.	2.	1.	16.
4.	0.	16.	0.	0.	0.	0.	0.	0.	0.	0.	1.
4.	418.	146.	0.	514.	0.	50.	32.	0.	0.	0.	11.
4.	227.	336.	0.	209.	0.	6.	31.	0.	0.	0.	4.
4.	172.	49.	0.	254.	0.	146.	12.	1.	0.	0.	27.
4.	165.	452.	0.	448.	0.	0.	24.	1.	0.	0.	6.
4.	373.	98.	0.	1211.	2.	29.	38.	0.	0.	0.	9.
4.	9.	58.	0.	69.	0.	0.	1.	0.	0.	0.	0.
4.	126.	784.	0.	708.	0.	0.	21.	0.	0.	0.	7.
4.	61.	772.	0.	765.	0.	0.	19.	0.	0.	0.	8.
4.	302.	92.	0.	21.	0.	0.	6.	0.	0.	0.	1.
6.	33.	1037.	0.	550.	1.	0.	0.	1.	0.	0.	78.
6.	5.	138.	0.	23.	0.	0.	0.	0.	0.	0.	6.
6.	124.	1069.	0.	922.	0.	2.	41.	1.	0.	0.	20.
6.	6.	119.	0.	13.	0.	0.	6.	1.	0.	0.	19.
6.	76.	287.	0.	781.	1.	198.	10.	0.	4.	0.	45.
6.	144.	829.	0.	1391.	2.	37.	51.	0.	1.	0.	36.
6.	37.	565.	0.	425.	0.	0.	1.	0.	0.	0.	68.
7.	4.	116.	0.	85.	1.	0.	6.	0.	0.	0.	0.
7.	106.	521.	0.	749.	0.	3.	18.	0.	1.	0.	14.
7.	57.	250.	0.	425.	7.	15.	5.	0.	0.	0.	31.
7.	212.	215.	0.	1027.	0.	18.	13.	0.	0.	2.	65.
7.	26.	254.	0.	134.	1.	1.	1.	0.	0.	1.	1.
7.	121.	481.	0.	190.	3.	0.	4.	0.	0.	0.	5.
7.	232.	469.	1.	439.	12.	9.	10.	0.	2.	1.	20.
7.	226.	301.	0.	258.	1.	3.	11.	0.	0.	0.	8.
7.	23.	169.	0.	92.	2.	0.	5.	0.	0.	0.	3.
9.	1.	79.	0.	11.	0.	0.	0.	0.	0.	0.	2.
9.	22.	316.	0.	74.	0.	0.	3.	0.	0.	0.	2.
9.	40.	383.	0.	76.	0.	0.	3.	1.	0.	0.	7.
9.	46.	450.	0.	221.	0.	0.	0.	0.	0.	0.	0.
9.	71.	336.	0.	136.	0.	0.	1.	0.	0.	0.	0.
9.	21.	342.	0.	445.	0.	0.	0.	0.	0.	0.	19.
10.	128.	589.	0.	1825.	4.	3.	12.	0.	0.	11.	31.
10.	46.	229.	0.	266.	2.	2.	12.	0.	0.	0.	6.
10.	202.	506.	0.	339.	7.	75.	14.	0.	2.	3.	13.
10.	193.	208.	0.	119.	1.	0.	0.	0.	0.	0.	1.
10.	119.	105.	0.	470.	2.	453.	35.	0.	3.	1.	20.
10.	32.	225.	0.	458.	0.	0.	4.	1.	0.	2.	72.
12.	44.	1207.	0.	650.	0.	1.	16.	5.	0.	0.	7.
12.	48.	808.	0.	219.	1.	20.	54.	0.	0.	0.	6.
12.	14.	285.	0.	633.	5.	5.	19.	1.	0.	0.	9.
12.	8.	1677.	0.	306.	2.	0.	8.	5.	0.	0.	7.
12.	52.	513.	0.	839.	6.	1.	22.	4.	1.	0.	35.
12.	84.	149.	0.	222.	5.	26.	3.	1.	2.	0.	9.

APPENDIX 5(e) cont.

SITE	SPEC12	SPEC13	SPEC14	SPEC15	SPEC16	SPEC17	SPEC18	SPEC19	SPEC20	SPEC21	SPEC22
1.	1.	1.	7.	0.	0.	0.	0.	0.	0.	2.	0.
1.	4.	2.	46.	0.	0.	0.	0.	0.	0.	5.	0.
1.	9.	1.	47.	0.	0.	0.	1.	0.	0.	3.	0.
1.	6.	0.	122.	1.	0.	0.	0.	0.	1.	7.	0.
1.	6.	0.	26.	5.	0.	246.	1.	0.	1.	2.	0.
2.	0.	0.	21.	0.	0.	0.	0.	0.	0.	2.	0.
2.	2.	0.	55.	0.	0.	245.	0.	0.	0.	1.	0.
2.	5.	0.	109.	0.	0.	339.	0.	0.	0.	1.	0.
2.	4.	0.	36.	0.	0.	0.	0.	0.	0.	4.	0.
2.	5.	0.	64.	0.	0.	422.	0.	0.	6.	2.	0.
2.	1.	0.	15.	0.	0.	0.	0.	0.	1.	4.	0.
2.	44.	0.	195.	1.	0.	0.	0.	0.	0.	7.	0.
2.	0.	0.	11.	3.	0.	387.	0.	1.	0.	0.	0.
2.	0.	0.	1.	0.	0.	600.	0.	0.	2.	1.	0.
2.	0.	0.	3.	0.	0.	0.	0.	0.	0.	8.	0.
2.	1.	0.	5.	0.	0.	0.	0.	0.	5.	0.	0.
1.	17.	1.	140.	0.	0.	0.	0.	0.	0.	1.	0.
3.	2.	0.	33.	0.	0.	0.	0.	0.	0.	3.	0.
3.	0.	0.	2.	0.	0.	0.	0.	0.	0.	1.	0.
3.	2.	3.	150.	0.	0.	1.	0.	0.	0.	0.	0.
3.	8.	0.	217.	1.	1.	25.	0.	0.	0.	5.	0.
3.	0.	0.	15.	0.	0.	0.	0.	0.	0.	5.	0.
3.	2.	1.	75.	0.	0.	0.	0.	0.	0.	5.	0.
3.	0.	0.	25.	0.	0.	0.	0.	0.	0.	0.	0.
3.	0.	0.	1.	0.	1.	0.	0.	0.	0.	1.	0.
3.	3.	0.	28.	0.	0.	0.	0.	0.	0.	1.	0.
3.	16.	0.	77.	0.	0.	0.	0.	0.	0.	2.	0.
4.	0.	0.	7.	0.	0.	3.	0.	0.	0.	0.	0.
4.	5.	0.	35.	0.	0.	0.	0.	0.	0.	0.	1.
4.	3.	0.	325.	0.	0.	0.	0.	0.	0.	2.	1.
4.	4.	1.	63.	0.	0.	0.	0.	0.	0.	0.	0.
4.	2.	1.	38.	0.	1.	0.	0.	0.	0.	1.	0.
4.	10.	0.	70.	0.	0.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	1.	0.	380.	0.	0.	0.	0.	0.
4.	3.	3.	35.	0.	0.	0.	0.	0.	0.	3.	0.
4.	2.	1.	35.	0.	1.	0.	0.	0.	0.	2.	0.
4.	1.	0.	65.	0.	0.	100.	0.	0.	0.	3.	0.
6.	1.	6.	36.	0.	1.	0.	0.	1.	0.	19.	0.
6.	0.	3.	7.	0.	0.	2.	2.	0.	0.	44.	1.
6.	8.	0.	32.	1.	1.	0.	0.	0.	0.	0.	21.
6.	0.	24.	1.	0.	4.	0.	0.	0.	0.	6.	1.
6.	10.	0.	39.	0.	0.	0.	0.	0.	0.	1.	0.
6.	7.	0.	49.	1.	1.	0.	0.	0.	1.	6.	0.
6.	2.	0.	49.	0.	0.	0.	2.	23.	0.	15.	0.
7.	0.	0.	15.	3.	0.	615.	0.	0.	1.	2.	0.
7.	2.	0.	113.	0.	0.	0.	0.	0.	0.	3.	0.
7.	11.	0.	150.	1.	0.	228.	0.	0.	0.	0.	0.
7.	9.	0.	200.	0.	1.	0.	0.	0.	0.	4.	0.
7.	1.	0.	102.	9.	0.	426.	0.	2.	0.	5.	0.
7.	0.	0.	26.	2.	0.	0.	0.	0.	0.	8.	0.
7.	12.	0.	180.	5.	0.	338.	0.	0.	0.	2.	0.
7.	6.	0.	25.	0.	0.	0.	0.	0.	0.	1.	0.
7.	0.	0.	23.	7.	0.	814.	0.	0.	1.	1.	0.
9.	0.	4.	4.	0.	3.	0.	0.	0.	0.	25.	0.
9.	0.	2.	24.	0.	1.	0.	1.	0.	0.	15.	0.
9.	1.	1.	98.	0.	1.	0.	0.	0.	0.	25.	1.
9.	0.	0.	7.	0.	5.	0.	0.	0.	0.	11.	0.
9.	0.	0.	3.	0.	1.	0.	0.	0.	0.	0.	0.
9.	2.	49.	32.	0.	10.	0.	0.	0.	0.	5.	0.
10.	9.	0.	92.	0.	0.	0.	0.	0.	1.	0.	0.
10.	1.	0.	93.	5.	0.	1203.	0.	1.	1.	3.	0.
10.	5.	0.	67.	2.	0.	874.	0.	0.	0.	4.	0.
10.	3.	0.	137.	1.	0.	58.	0.	0.	1.	3.	0.
10.	4.	0.	30.	1.	0.	0.	0.	0.	0.	1.	0.
10.	1.	0.	78.	0.	1.	0.	0.	1.	1.	15.	1.
12.	2.	0.	22.	0.	0.	0.	0.	0.	0.	6.	0.
12.	4.	0.	58.	4.	0.	598.	0.	0.	8.	3.	0.
12.	2.	0.	78.	0.	2.	0.	0.	1.	0.	4.	0.
12.	2.	0.	31.	0.	1.	0.	0.	0.	0.	4.	0.
12.	7.	0.	74.	0.	2.	0.	0.	1.	1.	13.	0.
12.	6.	0.	64.	0.	0.	0.	0.	3.	0.	7.	0.

APPENDIX 5(e) cont.

SITE	SPEC23	SPEC24	SPEC25	SPEC26	SPEC27	SPEC28	SPEC29	SPEC30	SPEC31
1.	0.	10.	0.	0.	5.	0.	0.	0.	0.
1.	0.	18.	0.	1.	29.	0.	0.	4.	1.
1.	0.	2.	0.	0.	92.	0.	0.	0.	0.
1.	0.	9.	0.	0.	70.	0.	0.	0.	0.
1.	0.	0.	0.	0.	19.	0.	1.	1.	0.
2.	0.	1.	0.	0.	2.	0.	0.	0.	0.
2.	0.	0.	2.	0.	0.	0.	0.	0.	0.
2.	0.	1.	0.	0.	3.	0.	0.	0.	0.
2.	0.	9.	0.	0.	6.	0.	1.	0.	1.
2.	0.	0.	0.	0.	18.	0.	0.	0.	1.
2.	0.	0.	0.	0.	1.	0.	0.	0.	0.
2.	0.	1.	0.	0.	3.	0.	0.	0.	0.
2.	1.	0.	0.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.	0.	0.	0.
1.	0.	0.	0.	0.	9.	0.	0.	2.	3.
3.	0.	9.	0.	0.	27.	0.	0.	0.	0.
3.	0.	38.	0.	0.	4.	0.	0.	0.	0.
3.	0.	4.	0.	0.	371.	0.	0.	0.	1.
3.	0.	2.	0.	0.	51.	0.	0.	0.	0.
3.	0.	6.	0.	0.	12.	0.	0.	0.	1.
3.	0.	0.	0.	0.	76.	0.	0.	0.	0.
3.	1.	0.	0.	0.	0.	2.	0.	0.	53.
3.	0.	25.	0.	0.	7.	0.	0.	0.	0.
3.	0.	6.	0.	0.	151.	0.	0.	1.	0.
3.	0.	0.	0.	0.	7.	0.	0.	3.	2.
4.	0.	14.	0.	0.	1.	0.	0.	0.	0.
4.	8.	1.	0.	0.	15.	0.	0.	1.	0.
4.	0.	0.	0.	0.	35.	0.	0.	0.	0.
4.	0.	1.	0.	0.	6.	0.	0.	0.	1.
4.	0.	0.	0.	0.	39.	0.	0.	0.	0.
4.	0.	0.	0.	0.	1.	0.	0.	5.	0.
4.	0.	0.	0.	0.	7.	0.	0.	0.	0.
4.	0.	0.	0.	0.	54.	0.	0.	0.	2.
4.	0.	3.	0.	0.	45.	0.	0.	2.	0.
4.	0.	0.	0.	0.	8.	0.	0.	0.	0.
6.	1.	1.	0.	0.	52.	0.	1.	0.	0.
6.	0.	1.	0.	0.	8.	0.	0.	0.	0.
6.	0.	0.	1.	0.	0.	53.	0.	0.	0.
6.	0.	5.	0.	0.	8.	0.	0.	0.	0.
6.	0.	0.	0.	0.	204.	0.	0.	2.	0.
6.	0.	0.	0.	0.	91.	0.	0.	1.	0.
6.	0.	0.	0.	2.	162.	0.	0.	0.	0.
7.	0.	0.	1.	0.	1.	0.	0.	0.	0.
7.	0.	3.	0.	0.	50.	0.	0.	1.	1.
7.	0.	0.	0.	0.	4.	0.	0.	7.	0.
7.	0.	1.	0.	0.	3.	0.	0.	9.	1.
7.	0.	1.	1.	1.	6.	0.	1.	2.	0.
7.	0.	0.	0.	0.	6.	0.	1.	0.	0.
7.	0.	1.	0.	4.	0.	0.	2.	0.	0.
7.	0.	0.	0.	0.	7.	0.	0.	1.	0.
7.	0.	0.	0.	0.	6.	0.	0.	0.	0.
9.	0.	0.	0.	0.	12.	0.	0.	0.	0.
9.	0.	0.	0.	0.	36.	0.	0.	0.	0.
9.	2.	0.	0.	2.	108.	0.	0.	0.	0.
9.	0.	2.	0.	0.	3.	0.	0.	0.	0.
9.	0.	0.	0.	0.	13.	0.	0.	0.	0.
9.	0.	0.	0.	0.	36.	0.	0.	0.	0.
10.	0.	0.	0.	2.	19.	0.	0.	3.	6.
10.	0.	0.	0.	0.	4.	0.	0.	5.	4.
10.	0.	0.	1.	0.	4.	0.	0.	4.	0.
10.	0.	0.	0.	0.	2.	0.	0.	0.	0.
10.	0.	1.	0.	0.	2.	0.	0.	1.	0.
10.	0.	1.	0.	1.	161.	0.	0.	4.	0.
12.	0.	0.	0.	0.	31.	0.	0.	0.	1.
12.	1.	0.	0.	0.	29.	0.	0.	3.	0.
12.	0.	0.	0.	2.	9.	0.	0.	0.	2.
12.	0.	1.	0.	0.	15.	0.	0.	1.	0.
12.	0.	5.	0.	0.	11.	0.	0.	1.	1.
12.	0.	0.	0.	1.	7.	0.	0.	3.	1.

APPENDIX 5(e) cont.

SITE	SPEC32	SPEC33	SPEC34	SPEC35	SPEC36	SPEC37
1.	0.	0.	0.	0.	0.	0.
1.	0.	1.	1.	1.	0.	0.
1.	0.	0.	5.	0.	0.	0.
1.	0.	3.	1.	0.	0.	0.
1.	0.	0.	4.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	1.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	0.	0.	0.	5.
2.	0.	0.	0.	0.	0.	0.
2.	0.	0.	1.	0.	0.	0.
2.	0.	0.	0.	0.	0.	0.
1.	0.	0.	4.	1.	0.	2.
3.	0.	0.	1.	0.	0.	1.
3.	0.	0.	0.	0.	0.	0.
3.	0.	1.	0.	0.	0.	1.
3.	0.	0.	1.	0.	0.	1.
3.	0.	0.	0.	0.	0.	0.
3.	0.	0.	0.	0.	0.	1.
3.	0.	0.	0.	0.	0.	0.
3.	0.	0.	0.	0.	0.	1.
3.	0.	1.	0.	0.	0.	0.
3.	0.	1.	0.	0.	0.	0.
3.	0.	0.	0.	0.	0.	0.
3.	0.	1.	0.	0.	0.	3.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	1.
4.	0.	0.	1.	0.	0.	0.
4.	0.	0.	1.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
4.	0.	0.	0.	0.	0.	0.
6.	0.	2.	0.	1.	2.	1.
6.	0.	11.	0.	0.	2.	0.
6.	0.	0.	4.	0.	0.	2.
6.	0.	3.	3.	0.	7.	0.
6.	0.	0.	3.	0.	0.	2.
6.	0.	0.	2.	0.	0.	0.
6.	0.	0.	2.	0.	5.	3.
7.	0.	0.	0.	0.	0.	1.
7.	0.	0.	2.	0.	0.	1.
7.	0.	0.	0.	0.	0.	2.
7.	0.	0.	0.	0.	0.	2.
7.	0.	0.	1.	0.	0.	0.
7.	0.	0.	1.	0.	0.	0.
7.	0.	0.	0.	0.	0.	1.
7.	0.	0.	0.	0.	1.	0.
9.	0.	1.	0.	0.	0.	0.
9.	0.	0.	2.	0.	1.	0.
9.	0.	0.	2.	0.	0.	0.
9.	0.	0.	7.	0.	2.	2.
9.	0.	0.	3.	0.	0.	0.
9.	0.	0.	1.	0.	0.	0.
9.	0.	0.	1.	0.	1.	0.
10.	0.	0.	16.	0.	0.	3.
10.	1.	0.	6.	0.	0.	0.
10.	0.	0.	6.	0.	0.	0.
10.	0.	0.	1.	0.	0.	1.
10.	0.	0.	8.	0.	0.	0.
10.	0.	0.	121.	0.	1.	1.
12.	0.	1.	4.	0.	1.	1.
12.	0.	0.	4.	0.	1.	1.
12.	0.	1.	4.	0.	0.	0.
12.	-1.	0.	0.	0.	0.	0.
12.	0.	0.	3.	0.	2.	0.
12.	0.	0.	3.	0.	0.	0.

Key as in 5d except Spec 23 Beetle Spec 36 Pseudoclydonus Spec 37 Harpacticoida

Paper presented at the First British Freshwater Fisheries Conference, University of Liverpool, April 1979. 11pp.

THE IMPORTANCE OF AQUATIC MACROPHYTES IN THE PROVISION OF CRUSTACEAN ZOOPLANKTON FOOD FOR YOUNG ROACH

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It is known that many coarse fish fry feed extensively upon crustacean zooplankton, and for the past 2½ years I have been studying the diets of O+ roach and perch and their available food supply in a gravel pit lake in order to determine the relative contributions of both open water and weedbed dwelling crustacean zooplankton to these diets. The macrophytes may play a part in determining survival rates and the strength of the year class by affecting the food supply in the first year of life. As the resulting information is relevant to questions of macrophyte control in the management of coarse fisheries, the National Federation of Anglers have given me financial support for two years to do this work for which I am extremely grateful.

Several terms require definition as used here: 1. Aquatic macrophytes = plants which grow around the margins of many water bodies and cover much of the surface area in shallow lakes. 2. Weedbed crustacea are the free swimming crustacean zooplankton found among aquatic plants in the area often termed the littoral. They are distinct from the animals more closely associated with the plants and are found swimming among the plants as opposed to the animals which live on the plant surfaces. 3. Open water zooplankton are the true limnetic plankton found in the area called the pelagial. There are separate animal communities in these two habitats in large lakes but the demarcation of habitat is less marked in smaller water bodies (Smyly, 1952).

There were several reasons for carrying out this work which were:

1. Many shallow lakes in S. England contain dense weedbeds and are often coarse fisheries. Anglers are divided in their attitudes towards these weeds and many would like them removed for easier fishing while others do realise that good first year survival is very important for the continuation of the fishery and that the role of the plants should be known before they are indiscriminately removed.
2. Coarse fish fry congregate around the margins of lakes and in the weedbeds, but it is not known whether they go there in search of food or for shelter from predators. It is also thought that O+ roach and perch (the dominant fish species) in gravel pit lakes compete for food and possibly space and the presence of weeds may be an important regulator of this competition in providing a more diverse habitat for the fish to feed in.
3. Previous gravel pit studies on fish/zooplankton relationships have ignored the marginal crustacea and this is also true of many lake studies on fish diets and available food where the sampling of food items has taken place in the open water and the diversity of niches for crustacean food in the margins has been ignored.

The following questions were asked:

1. Do open water and weedbed crustacean plankton communities differ in species composition and numbers in a small shallow lake with extensive weedbeds?
2. If this is so, do the fish show a similar differentiation in their stomach contents i.e. can one say more particularly where they have been feeding? Another part of the study investigated possible associations of crustacean zooplankton with plant species to see whether any food items eaten by the fish were associated with certain plant species.
3. Does the presence of plants affect either growth rates or survival rates of 0+ roach and perch?

This work applies to the small, shallow lakes in S. England where the weedy margins are a considerable proportion of the lake area and vegetation rises to the surface in places as opposed to e.g., Lake Windermere where the margin is negligible compared to the amount of open water and much of the margin is devoid of plants.

METHODS

The work was carried out in a small shallow gravel pit lake in Frimley, Hampshire, Farnborough 18A. The area is only 1.1 hectares, max. depth 3.0 m and average depth 1.5 m. The lake contains dense populations of roach *(Rutilus rutilus)* and perch *(Perca fluviatilis)*, with rudd *(Scardinius erythrophthalmus)*; tench *(Tinca tinca)*, and bream *(Abramis brama)*. The dominant vegetation is *Typha latifolia*, usually growing with *Sparganium erectum*. *Elodea canadensis* covers much of the bottom and grows thickly around the margins. In the sheltered bays there are extensive stands of *Potamogeton natans* with floating leaves covering the *Elodea*. These are the principal plants within which sampling for zooplankton was carried out.

ZOOPLANKTON SAMPLING

A 2 m perspex tube was used to collect randomly selected vertical cores of water which were combined into one quantitative sample. A 1 m perspex tube was used to collect vertical cores of water in the separate weedbeds, again combined into separate quantitative samples. The samples were filtered through 80 μ mesh and the crustacea in the sample were counted and expressed as numbers/litre. Sampling commenced in April and ceased in December.

RESULTS

Zooplankton

Figure 3 shows the abundance of the open water crustacean zooplankton, expressed as numbers/litre against time in months. The drawings of the organisms are all to the same scale shown in the top of the graph. These have been included to give an indication of relative biomasses and also for those people not familiar with these animals, as in many diet studies separation of food categories has been only to Copepoda and Cladocera (i.e., copepods and *Daphnia*).

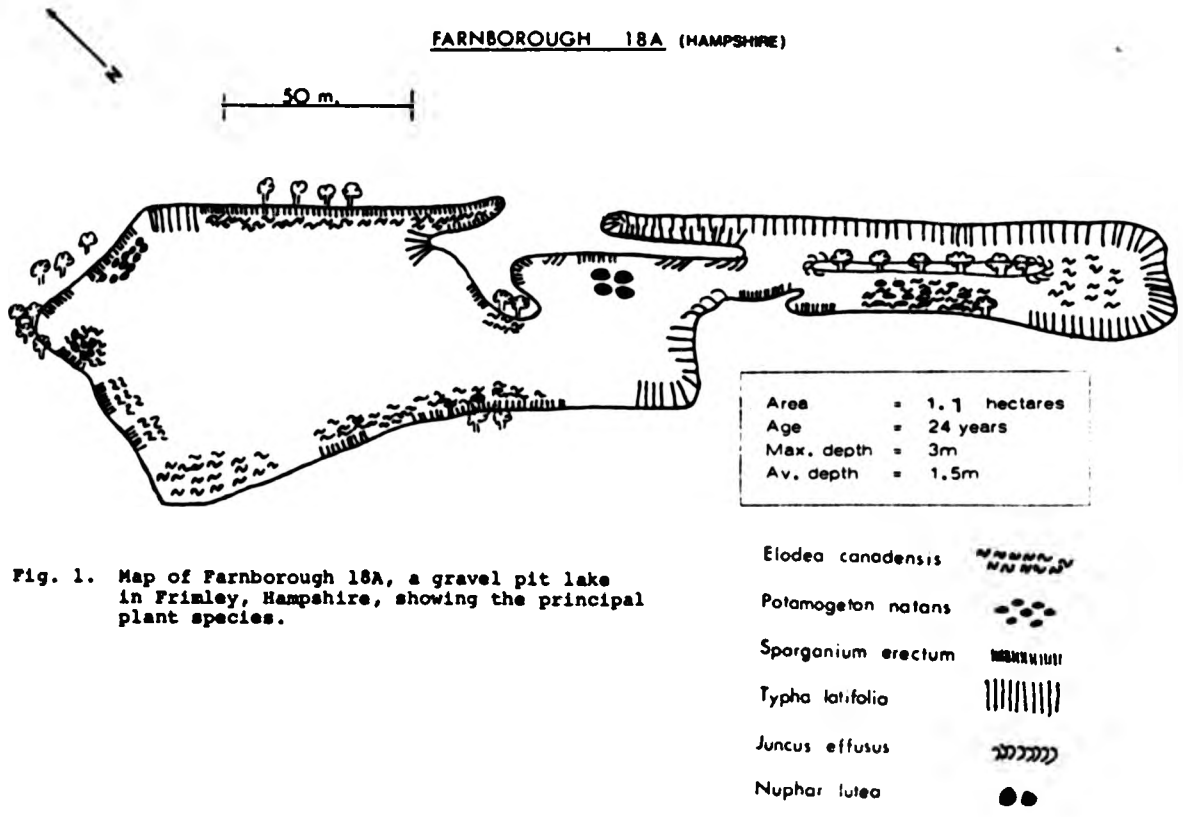

Fig. 1. Map of Farnborough 18A, a gravel pit lake in Frimley, Hampshire, showing the principal plant species.

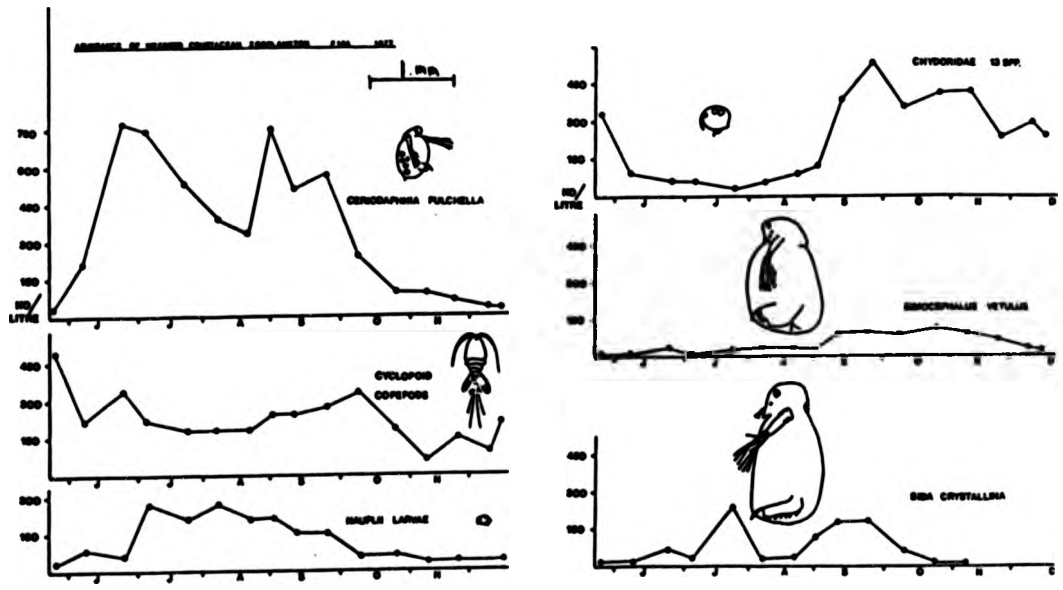

Fig. 2. The density of the more abundant weedbed dwelling crustacean zooplankton in F18A in 1977 in numbers/litre.

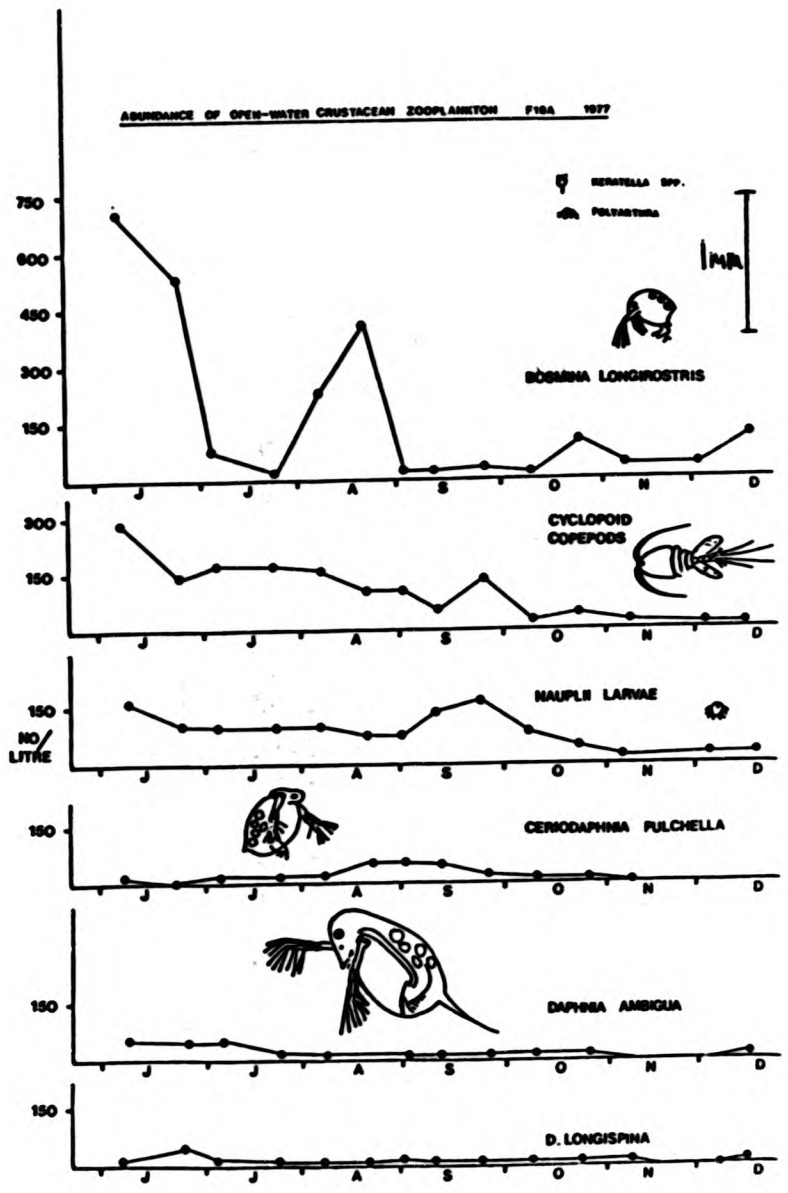

Fig. 3. The density of the more abundant open water crustacean zooplankton in F18A in 1977 in numbers/litre. (The drawing for *D. ambigua* is a generalised Daphnia.)

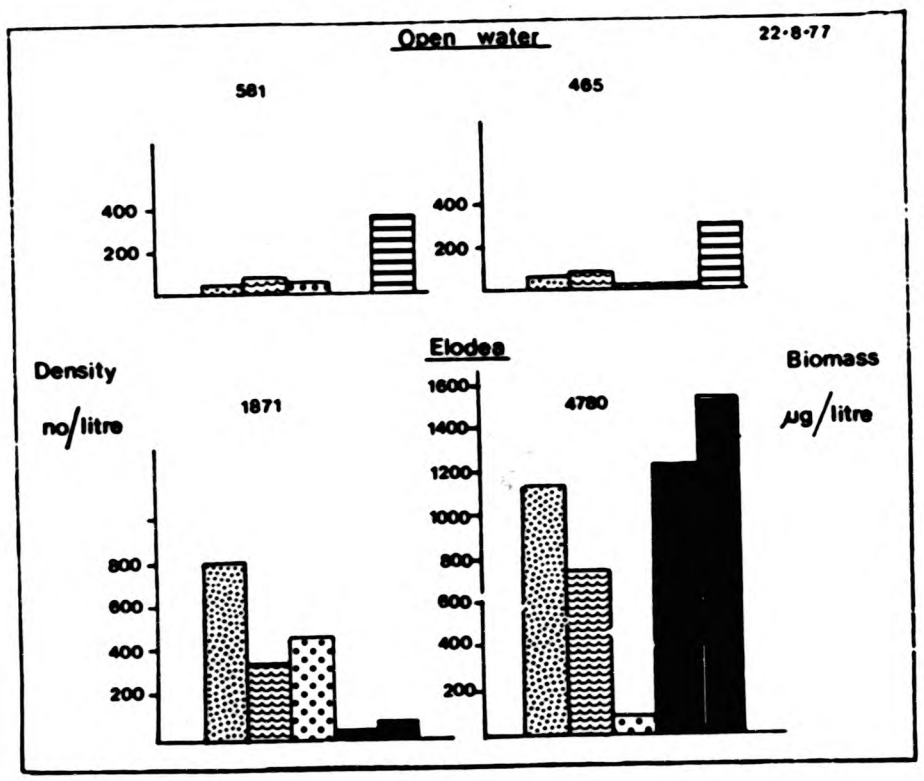

Fig. 4. Comparison of density and dry weight biomass of crustacean zooplankton in the open water and in *Elodea canadensis* in F18A on 22.8.78 (key as in Figure 5). (The numbers above each graph are the total number/litre and the total µg/litre).

Bosmina longirostris was the most numerous crustacean in the open water the population showing a fairly typical pattern of high and low numbers which has been found in previous years (M.P. Cook, pers. comm). Cyclopoid copepods and their nauplii larvae were also reasonably abundant throughout the summer. The other components of the crustacean plankton were present only in low numbers and *Daphnia* (3 spp.) were scarce. The rotifers shown to scale at the top of the graph were the most numerous open water animals but were not counted in this study as they comprised only a small portion of the standing crop because of their small size. Therefore, the open water was characterised by a dominance of small organisms and a lack of large zooplankters. This is typical of a lake with a dense fish population.

Figure 2 shows the abundance of the weedbed crustacea again as numbers/ litre against time in months. Each point is the mean of several weedbed samples. In the vegetation the dominant zooplankter was *Ceriodaphnia pulchella* which occurred in very high numbers with a slight dip in August coinciding with a peak of *Bosmina* in the open water and also with a drop in temperature (not shown). The cyclopoid copepods (different species to the open water ones) were also abundant in the weeds throughout the summer. The weedbed plankton was characterised by the presence of large numbers of the more sedentary Cladocera, the chydorids. Thirteen species were present, 3 abundantly and there were also high numbers of the two large filter feeders *Sida crystallina* and *Simocephalus vetulus*.

To summarise the differences between the vegetation and the open water;

1. Their zooplankton species composition was different, open water dominated by *Bosmina* and weedbeds by *Ceriodaphnia*. Few species were found in both habitats in any numbers, e.g. *Bosmina* and *Ceriodaphnia* appeared to be mutually exclusive while *Daphnia* spp. were not found in the weeds and conversely the large Cladocera were not found in the open water.
2. The plants supported higher numbers of animals and a greater number of species, not surprising in view of the greater diversity of habitat available in the weedbeds. Nine species (plus copepods and nauplii) were commonly found in the open water whereas 22 species (plus copepods and nauplii) were commonly found in the weeds.
3. The crustacean zooplankton biomass in the weeds was much higher than in the open water (see Figure 4). Dry weight biomass was calculated for one date, 22.8.77 from measurements of length, using my own and published (Dumont, 1975) length/dry weight regression equations. The use of biomass rather than numbers gives a more realistic estimate of the relative abundance of the organisms but in fact it made little difference to the order of dominance in the open water. However, in the weeds, in terms of biomass *Sida* and *Simocephalus* became the dominant crustacea and this was calculated for a date on which their numbers were still low. In both cases the nauplii became a negligible component.
4. There was a greater range of body size among the weedbed crustacea.

Fish

O+ roach (and perch which will not be discussed in this paper) were caught in the weedbeds from June onwards. A large hand net on a long handle was used to catch shoals and later in the year a minnow seine net (mesh 8 mm) was used. The fish were killed in MS222 and preserved in 4% formalin. The contents of the guts were removed under the microscope and the total number of food items counted in a circular perspex counting trough under the microscope. By gut contents is meant the total number of organisms contained in both the stomach and the intestine of a fish. The food items were placed in the following categories:

Rotifers; Copepods; *Daphnia; Bosmina;* Nauplii;

Macro-invertebrates which included chironomid larvae, worms, mite larvae, small Hemiptera and other insect remains; Chydorids; *Sida; Ceriodaphnia.*

The gut contents of 193 fish from 9 dates have so far been examined. The % composition of the diets is shown in Figure 5. The % composition of the food items was calculated for each fish and the mean % composition in the sample was taken for each food item. The numbers underneath are the mean number of organisms/fish and the mean fork length in cms of the sample.

The roach had a varied diet; a total of 14 spp. of crustacean zooplankton were found plus copepods, nauplii, chironomids, mite larvae, ostracods, Hemiptera and seeds, in fish ranging from 1.5 cm to 5.0 cm in length. However, over the whole season 3 species made up nearly 79% of the diet and these were in order of abundance, *Ceriodaphnia* 29%, *Bosmina* 24%, *Sida* 16%.

Figure 5 also shows the % composition of the weedbed and open water zooplankton samples. The numbers underneath are the total numbers/litre of each sample.

Bosmina is a free swimming filter feeder with a mean size of 0.3 mm and the fish consumed it when it was abundant in the open water. It formed a large part of the diet in the autumn and winter when little else was available. *Bosmina* was not found in the weedbeds. The consumption of *Ceriodaphnia* reached a peak in September, coinciding with the peak of *Ceriodaphnia* in weeds and the decline of the *Bosmina* population. *Ceriodaphnia* is also a free swimming filter feeder, slightly larger than *Bosmina*, mean size 0.45 mm, and the consumption increased with increasing fish size as well as in unison with the rise and fall of the *Ceriodaphnia* population. Therefore the roach ate nearly equal proportions of the 2 dominant zooplankters, one from the open water and one from the weeds. However the next most important food item was the large crustacean, *Sida*. This species is closely associated with the vegetation, often sticking to the undersurface of *P. natans* leaves with a sticky neck gland. As the mean size of *Sida* in the guts was 1 mm the volume of food made up by *Sida* was far greater than the volumes of either *Bosmina* or *Ceriodaphnia*.

Figure 6 shows these 3 food items superimposed. Overall there was a predominance of weedbed dwelling crustacea as the only open water organism eaten in any quantity was *Bosmina*. The rest of the diet was made up of chydorids, chironomids and a few cyclopoids with *Daphnia* and rotifers *(Keratella* and *Brachionus)* eaten by the smaller fish.

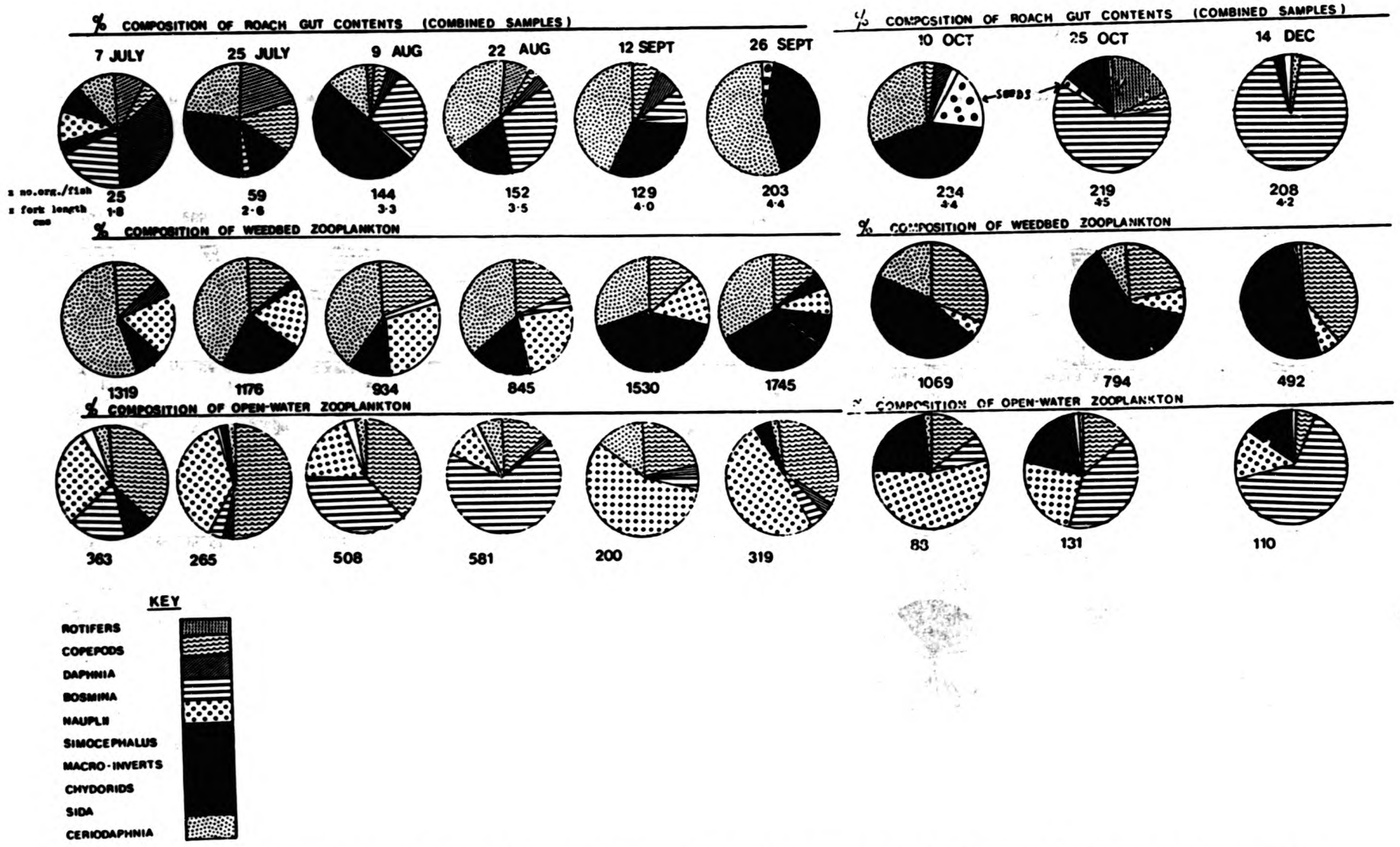

Fig. 5. The % composition of O+ roach gut contents in F18A in 1977, with the % composition of the open water and weedbed zooplankton samples.

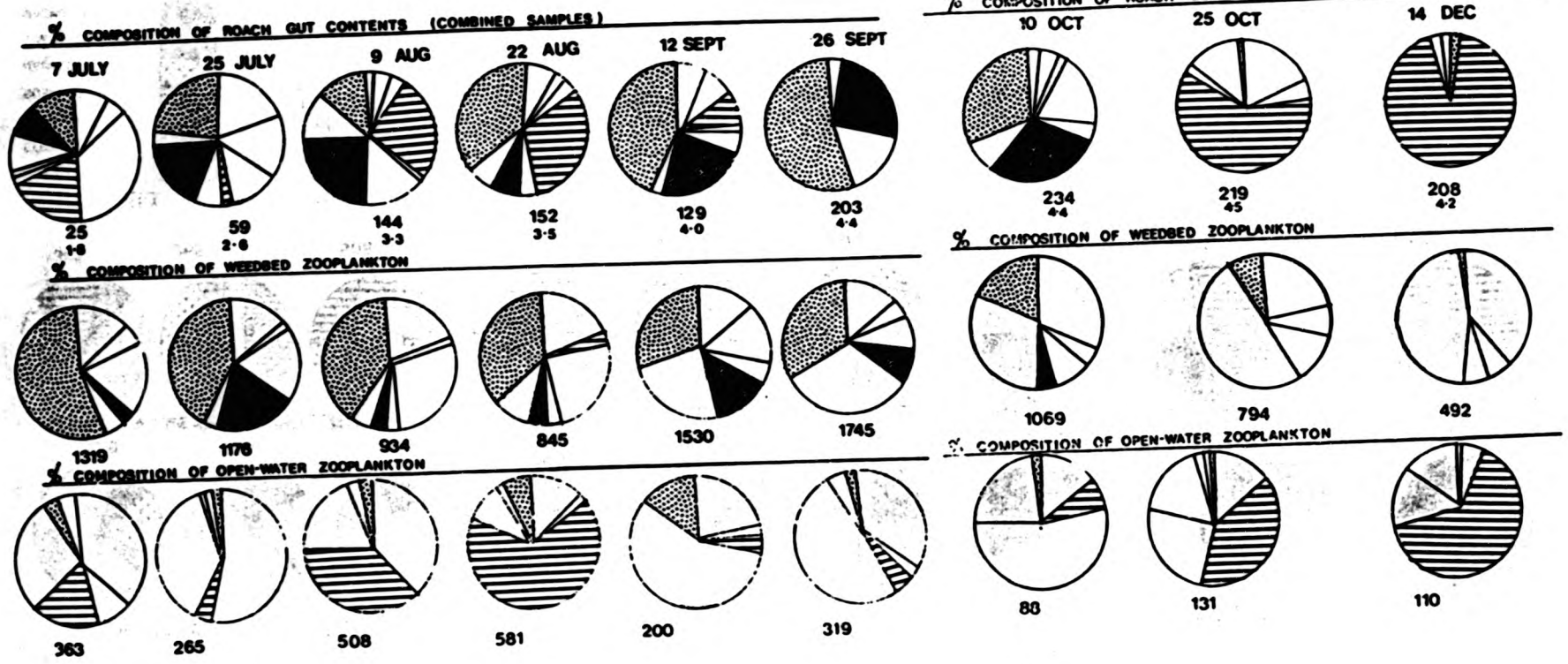

Fig. 6. As in Figure 5, with only *Ceriodaphnia pulchella, Bosmina longirostris* and *Sida crystallina* shown.

One would like to be ableoto say whether the fish showed any feeding preferences and this is usually done by calculating an electivity index (Ivlev, 1961). This was not possible with these data as different categories occurred in the diet and in the food. Therefore, I have made a comparison of numbers of the 3 major food items in the diet and in the environment in order to arrive at an estimate of electivity. Taking the numbers/litre of the 3 species in both open water and weed samples as the total available food on that day and taking the mean numbers in the gut as the total food, one can compare their relative proportions in the habitat and in the gut. Table 1 shows the results of this. The proportion of *Ceriodaphnia* eaten was always less than the proportion in the water, which was not surprising as it was so abundant in the water. More surprising was the apparent preference for *Sida* and there was a suggestion of a lesser preference for *Bosmina* particularly when *Sida* was less abundant in the water. However this was a preliminary analysis and electrivity indices have not been calculated and one cannot say more about preferences at this stage. It is interesting that *Bosmina* and *Ceriodaphnia* possessed inversely fluctuating populations in the lake although in different habitats and that the fish fed upon them in tune with the fluctuations.

TABLE 1

THE PROPORTIONS OF *Bosmina*, *Ceriodaphnia* AND *Sida* IN THE DIET AND IN THE LAKE, ASSUMING THAT THEY FORM THE TOTAL FOOD EATEN AND THE TOTAL AVAILABLE FOOD SUPPLY, a = % in the diet, b = % in the food.

Date	25.7	9.8	22.8	12.9	26.9	10.10	25.10	
Bosmina	2.5	42.7	41.4	10.6	0.5	7.1	98.6	a
	1.2	34.3	53.3	0.7	1.9	2.8	43.2	b
Ceriodaphnia	57.8	19.3	49.5	58.8	68.9	46.4	1.4	a
	68.3	60.4	43.6	72.8	75.5	78.7	53.6	b
Sida	39.6	37.8	8.9	30.4	31.3	46.5	0.0	a
	30.4	5.4	3.1	26.5	22.5	18.5	3.2	b

I have found from another investigation that *Ceriodaphnia* tends to be more abundant in the outer edges of weebeds where the water : weed ratio is higher, i.e. the vegetation is less dense, and this coupled with the known association of *Sida* with *Potamogeton natans* again a plant with a high water : weed ratio suggests that the fish were feeding in the margins of the weedbeds rather than in the centre of the vegetation. It is also interesting that the roach did not eat *Simocephalus* (similar in appearance to *Sida*) which was associated more with dense *Elodea*. Therefore they consumed a mixture of weed and open water organisms in which the weedbed items were the most important in terms of both numbers and biomass.

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CAGING EXPERIMENTS

Having shown that the fish fed upon weedbed dwelling crustacea the next step was to carry out experiments to determine whether the presence or absence of weeds affected the growth and survival rates. Enclosure experiments where parts of the lake are enclosed with mesh and the weeds removed from some areas, were not possible because of vandalism and in any case it is difficult to keep fish enclosed and very difficult to make weed free areas. Therefore, caging experiments were carried out to keep roach and perch enclosed with and without weeds in the field as opposed to the lab., in a gravel pit lake in 1978. Floating cages were used as they have the following advantages; they enclose a known volume of water, the fish are easy to catch, one can have many replicate cages, and they are easy and relatively cheap to make. Figure 7 shows how the cages were constructed. They had wooden frames, 2 m by 2 m by 1 m deep, covered with micromesh (mesh 3 mm for roach) and polynet (mesh 8 mm for perch). They had polystyrene floats and concrete anchors to hold them in the centre of the lake. They were covered with anti-bird netting lids. Eight cages were made, 4 contained weeds and 4 did not. Real weeds were not used as their usage would have posed too many practical problems. Therefore plastic macrophytes were made from polypropylene bags cut into strips and vegetable bags tied onto netlon mesh bases. It has been shown (by Macan, 1977 and others) and by my own personal observations that plastic substrates suspended in open water become colonised with communities similar to those in the weedbeds. Two cages were stocked with 0+ roach and 4 with 0+ perch (and 2 with 1+ roach, which were not used in this work). Known numbers were placed in the cages in June and their growth was monitored until September when they were finally removed. The results are not shown because the analysis is not yet complete. Interpretation of the results is difficult because of the intrusion of handling effects. Because it was not known whether the fish would survive and grow in the cages, a sample was removed from each cage weekly for measurement and then returned to the cage. This would have increased mortality and did affect the growth rates but for a sample to be completely removed each week would have required a high initial stocking density which might have introduced density-dependent effects. Therefore, the results, which were inconclusive, must be viewed with caution although there was a suggestion of better growth with weeds. However, the experiment provided information upon feeding habits of roach and perch in a controlled environment in the cages and we now know that the fish will grow in cages. The experiment will be repeated this summer using only one fish species, roach as they grew well in the cages and with more replicates and no handling. It is hoped that this experiment, combined with the previous work when fully analysed, will provide a more conclusive answer to the question of whether the macrophytes have an effect upon either growth or survival rates. This may be through the provision of food, or provision of shelter or possibly a combination of both.

REFERENCES

Dumont, H.J., van de Velde, I., Dumont, S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia (Berl.) 19, 75-97.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press. New Haven.

Fig. 7. Fish cage used for experimental work.

Fig. 8. Floating cages in the lake.

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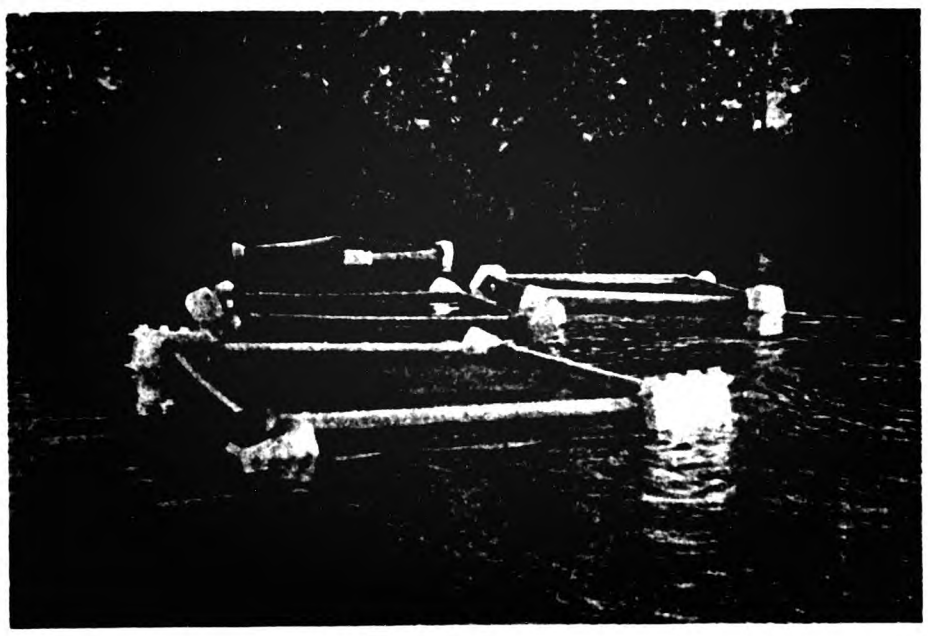

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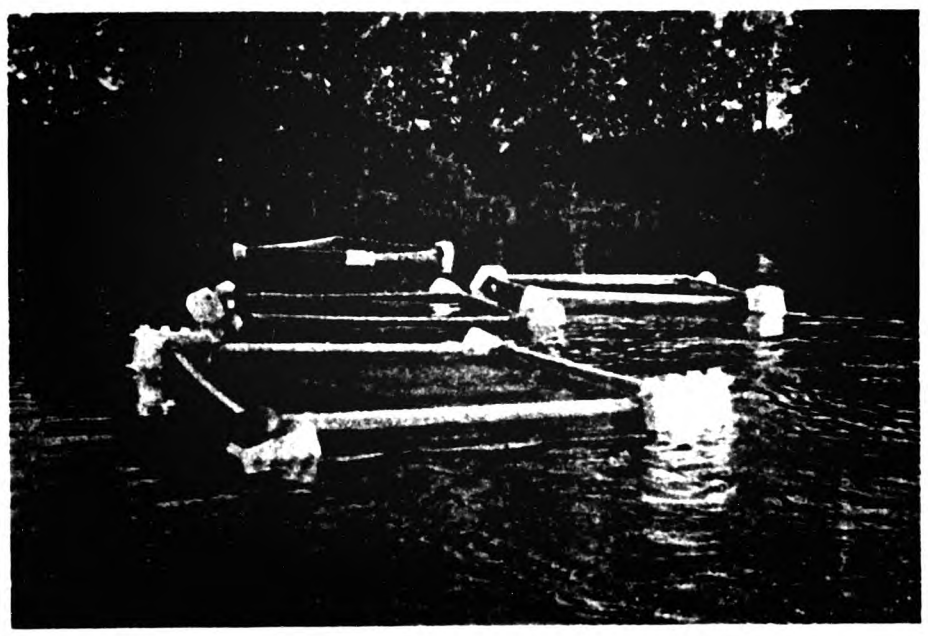

Fig. 8. Floating cages in the lake.

Macan, T.T. 1977. The fauna in the vegetation of a moorland fish pond as revealed by different methods of collecting. Hydrobiologia vol. 55. 1. 3-15.

Smyly, W.J.P. 1952. The Entomostraca of the weeds of a moorland fish pond. J. Anim. Ecol. 21, 1-11.

APPENDIX 8 The geometric mean densities and 95% confidence limits of microcrustacea in the cages in Yateley in 1978.

NON-WEED CAGES

	CERIODAPHNIA		BOSMINA		CYCLOPS		DIAPTOMUS		DAPHNIA	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.1	0-0.4	0.5	0-4	113	56-229	1.4	0-7	2	0-8
17.7	0.2	0-1.6	2	0-51	178	108-297	5	0-95	4	0-41
2.8	28	18-44	24	6-84	236	169-329	26	8-78	8	5-11
17.8	48	28-78	46	23-89	44	29-65	43	35-52	2	1-5
3.9	111	33-368	58	23-143	11	8-15	25	2-200	0.1	0-0.3
12.9	27	14-50	4	2-9	17	10-29	13	8-20	0.1	0-0.3
29.9	33	18-61	35	15-82	42	32-53	12	3-44	1.3	0-8

	CHYDORUS		POLYPHEMUS		ASPLANCHNA		NAUPLII	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.2	0-1.2	5	0-58	70		158	84-297
17.7	0.8	0-1.8	14	0-14700	10	4-23	523	335-814
2.8	6	2-12	0.3	0-1	21	12-35	108	57-195
17.8	7	3-12	0.4	0-2	413	338-506	191	137-266
3.9	3	1.3-6	1.4	0-5	74	47-116	197	126-307
12.9	9	6-12	0		30	12-73	251	184-342
29.9	6	3-23	0.5	0-3	12	4-34	113	55-245

WEED CAGES

	CERIODAPHNIA		BOSMINA		CYCLOPS		DIAPTOMUS		DAPHNIA	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.3	0-1	0.9	0-2	234	152-361	2	0-13	0.5	0-1.9
17.7	0.7	0.2-1.2	0.5	0-2	361	183-800	2	0-14	1.2	0-5
2.8	25	15-40	5	1-11	166	131-210	6	2-16	1.4	0-6.3
17.8	45	29-71	7	0-219	45	22-90	31	2-359	1.2	0-6
3.9	168	85-295	99	20-486	12	7-19	20	6-63	0.2	0-0.8
12.9	37	16-82	6	1-19	20	13-30	10	5-19	0.1	0-0.4
29.9	31	3-226	69	4-1370	44	36-54	10	1-51	1.5	0-9

	CHYDORUS		POLYPHEMUS		ASPLANCHNA		NAUPLII	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	1	0.1-3	2.2	0-9			148	85-256
17.7	5	1.2-15	17	2-115	14	7-29	314	256-385
2.8	29	11-74	3	0-31	10	5-17	192	92-398
17.8	26	3-208	5	0-257	383	185-789	174	53-571
3.9	26	18-34	2.4	0.2-9	59	38-90	191	156-234
12.9	11	6-21	0.5	0-2.6	20	8-42	303	173-530
29.8	20	12-35	2.6	1.2-5	10	4-24	125	77-203

APPENDIX 6 The geometric mean densities and 95% confidence limits of microcrustacea in the cages in Yateley in 1978.

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	CERIODAPHNIA		BOSMINA		CYCLOPS		DIAPTOMUS		DAPHNIA	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.1	0-0.4	0.5	0-4	119	66-229	1.4	0-7	2	0-8
17.7	0.2	0-1.8	2	0-51	178	106-297	5	0-95	4	0-41
2.8	28	18-44	24	6-84	236	169-329	26	8-78	8	5-11
17.8	48	28-78	46	23-89	44	29-66	43	35-52	2	1-5
3.9	111	33-366	58	23-143	11	6-19	25	2-200	0.1	0-0.3
12.9	27	14-50	4	2-9	17	10-29	13	8-20	0.1	0-0.3
29.9	33	18-61	35	19-62	42	32-53	12	3-44	1.3	0-8

	CHYDORUS		POLYPHEMUS		ASPLANCHNA		NAUPLII	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.2	0-1.2	5	0-59	70		158	84-297
17.7	0.6	0-1.6	14	0-14700	10	4-23	523	335-814
2.8	6	2-12	0.3	0-1	21	12-35	106	57-195
17.8	7	3-12	0.4	0-2	413	338-506	191	137-266
3.9	3	1.3-6	1.4	0-5	74	47-116	197	126-307
12.9	9	6-12	0		30	12-73	251	184-342
29.9	9	3-23	0.5	0-3	12	4-34	116	55-245

WEED CAGES

	CERIODAPHNIA		BOSMINA		CYCLOPS		DIAPTOMUS		DAPHNIA	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	0.3	0-1	0.6	0-2	234	152-361	2	0-13	0.5	0-1.9
17.7	0.7	0.2-1.2	0.5	0-2	361	163-800	2	0-14	1.2	0-5
2.8	25	15-40	5	1-11	166	131-210	6	2-16	1.4	0-6.3
17.8	45	29-71	7	0-219	45	22-90	31	2-359	1.2	0-6
3.9	168	95-295	99	20-468	12	7-19	20	6-63	0.2	0-0.8
12.9	37	16-82	6	1-19	20	13-30	10	5-19	0.1	0-0.4
29.9	31	3-226	69	4-1370	44	36-54	10	1-51	1.5	0-9

	CHYDORUS		POLYPHEMUS		ASPLANCHNA		NAUPLII	
Date	x	C.L.	x	C.L.	x	C.L.	x	C.L.
10.7	1	0.1-3	2.2	0-9			148	85-256
17.7	5	1.2-15	17	2-115	14	7-26	314	256-385
2.8	29	11-74	3	0-31	10	5-17	192	92-398
17.8	28	3-208	5	0-257	383	185-789	174	53-571
3.9	26	19-34	2.4	0.2-9	59	38-90	191	156-234
12.9	11	6-21	0.5	0-2.6	20	8-42	303	173-530
29.9	20	12-35	2.6	1.2-5	10	4-24	125	77-203

in the

D41685'82

END