TROPHIC INTERRELATIONSHIPS, LIFE-HISTORIES AND TAXONOMY OF SOME INVERTEBRATES ASSOCIATED WITH AQUATIC MACROPHYTES IN LAKE GRASMERE

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ABSTRACT

Ecological studies were made on macrophyte-associated invertebrates at 13 sites within the macrophyte zone of Lake Grasmere, Cass, Canterbury, South Island, New Zealand (43°05'S, 171°45'E; 583 m a.s.l.). A pilot survey (14 April 1976) and a quantitative sampling program (September 1976 - October 1977) were carried out using a new cylinder-sampler (which is described). Non-quantitative samples were taken also to provide additional information.

About 113 species of aquatic invertebrates were collected from Lake Grasmere and its immediate environs including at least 75 species that were associated with submerged macrophytes. Chironomidae (17 spp.), Crustacea (16 spp.), and Trichoptera (12 spp.) were best represented. Thirty species were new records for the Cass district.

Cluster analysis was used to simplify the analyses of data from the quantitative sampling program and dendrograms of site groups and species groups were derived. Four site groups were delimited on the basis of similarity in the composition of associated invertebrate communities. Ten species groups were identified on the basis of each species' distribution. The characteristics of the site groups and species groups are discussed. The 13 taxa of species group 6 occurred at all sites sampled and comprised over 95% (by numbers) of the fauna at each site group. Overall, Mollusca (mainly *Potamopyrgus antipodarum*) (55.9%), Crustacea (16.4%) and Coelenterata (*Chlorohydra viridissima*) (14.8%) were the numerically dominant groups on macrophytes. Seasonal changes in invertebrate communities at the site groups were considered using diversity indices and community similarity indices.

The trophic relationships of *Paroxyethira hendersoni*, *P. tillyardi*, *Hudsonema amabilis*, *Triplectides cephalotes* (Trichoptera), *Nymphula nitens* (Lepidoptera), *Xanthocnemis zealandica* (Odonata) and *P. antipodarum* (Mollusca) were investigated using faecal analysis. Emphasis was placed on size- or instar-related dietary changes. *N. nitens* and *T. cephalotes* fed primarily on tissue of aquatic macrophytes; the two *Paroxyethira* spp. and *P. antipodarum* were herbivorous browsers on periphyton; *X. zealandica* was a predator (especially on Oligochaeta, Cladocera, Acarina and *P. antipodarum*); and *H. amabilis* was omnivorous. Notes on the gut contents of Chironomidae are presented.

Life-history information was collected for seven species of Trichoptera, *N. nitens* and *X. zealandica*. Most species had slow seasonal life-histories, with emergence during spring and summer. Exceptions were *Oxyethira albiceps* and *P. hendersoni* (non-seasonal, perhaps bivoltine) and *X. zealandica* (non-seasonal, predominantly a three year life-history).

Taxonomic studies included the production of keys to larvae of Hydroptilidae and Chironomidae and adult males of the New Zealand Chironomidae. The fifth instar larva of *Paroxyethira tillyardi* is described and the habitats and distributions of the New Zealand species of Hydroptilidae are discussed. The male of *Eukiefferiella* sp. (Chironomidae: Orthocladiinae) is described; illustrated notes on chironomid larvae and pupae from Lake Grasmere are presented and problems in chironomid systematics are discussed.

CHAPTER I

GENERAL INTRODUCTION

The ecology of invertebrates living in macrophyte zones of lakes in New Zealand has received little attention from biologists, partly because sampling is difficult. Accurate quantitative work is hard to achieve because of the variable density of vegetation, although qualitative data can be obtained simply by sweeping through vegetation with a hand-net (Winterbourn & Lewis 1975). Surveys of the faunas associated with submerged aquatic macrophytes in some New Zealand lakes have been made (e.g., Armstrong 1935, Cunningham *et al.* 1953, Winter 1964, Fish 1966, Stout 1969b, 1970, 1975a, 1977, Greig 1973) but only a little is known about the biology of many of the invertebrates concerned (see Marples 1962, Pendergrast & Cowley 1966, Stout 1975a, 1977, Winterbourn & Lewis 1975, Chapman & Lewis 1976, Cowley 1978, Winterbourn & Gregson in press). On the other hand, there have been several detailed studies of Hemiptera, Odonata, Trichoptera and Mollusca (e.g., Babington 1967, Winterbourn 1970b, Young 1970, Crumpton 1979, Deacon 1979).

The present study was initiated in an attempt to overcome this deficiency in the knowledge of the macroinvertebrate fauna and was aimed initially at documenting the taxonomic composition of macrophyte-associated invertebrate communities to provide a background for further work on trophic interrelationships and life-histories. Field work was carried out at Lake Grasmere in inland Canterbury, South Island, New Zealand. This lake is readily accessible and is close to the University of Canterbury's Field Station at Cass, but was chosen primarily because it is perhaps the most intensively studied high-country lake in the Cass district. The scientific endeavour at Cass has been summarised by Burrows (1977) (see also Chapter II of this study). Aspects of Lake Grasmere that have been investigated include the catchment (McLeod & McLeod 1977, Gibson 1978), physical and chemical features (Stout 1969a, b, 1975a, b, 1972, 1977, Irwin 1972), bacterial populations (Ramsay 1972, 1974, 1976), phytoplankton (Stout 1969a, 1972, 1975a, 1977, Flint 1975), zooplankton (Stout 1969a, 1972, 1975a, 1977), periphyton (Greig 1976) and benthic invertebrates (Jamin 1976, Timms in prep.). Invertebrate communities associated with

macrophytes have been discussed only briefly by Stout (1969b, 1975a, 1977) and Winterbourn & Lewis (1975). Greig (1976) investigated the production and trophic relationships of a littoral population of a mayfly *Deleatidium* sp.

The aims of the present study were to examine the invertebrate communities present on macrophytes (native and adventive species), and to elucidate the trophic relationships and life-histories of some of the invertebrates characteristic of the macrophyte zone. An unexpected addition to work originally envisaged was the taxonomic study of larval Hydroptilidae (Trichoptera) and of Chironomidae. The interest in Chironomidae arose when enumeration of light-trap collections of adult insects (initially for Trichoptera) revealed the presence of large numbers of 'unidentified Diptera' which tempted me into trying to identify them. The identification of adults led naturally to attempts to identify larvae and later, because of deficiencies in larval systematics of New Zealand Chironomidae, to more wide-ranging taxonomic investigations (see Stark in press and Chapter VI present study).

CHAPTER II

STUDY AREA

2.1 INTRODUCTION

All field work was carried out at Lake Grasmere, Canterbury, near the Southern Alps in the South Island of New Zealand (Figs 2.1 and 2.2). This lake was chosen because of the relatively extensive background of scientific study available and its proximity to the Cass Field Station, a convenient base.

The purpose of this chapter is to outline briefly the features of Lake Grasmere, the climate and previous scientific work on the lake.

2.1.1 Location, Formation and Catchment of Lake Grasmere

Lake Grasmere is one of five small lakes situated close together in the catchment of the Waimakariri River (Fig. 2.1) (Stout 1969a). The lake is at a latitude of 43°05' South, longitude 171°45' East and altitude 583 m a.s.l. Like nearby Lake Sarah, it was dammed by morainic ice-eroded rock and postglacial fan-building, and has been in existence since the Poulter glacial advance (about $17 - 13 \times 10^3$ years before present) (Gage 1959, 1977).

The catchment (1,850 ha) is primarily tussock country and 50% of it is now used for agriculture (Gibson 1978). Agricultural modification of the catchment has occurred during the last 100 years, although most change has taken place in the last 20 years. In 1956, aerial topdressing and oversowing was begun. In 1964, cultivation and pasture improvement of 75 ha to the west of the lake was undertaken, and in 1973 a border dyke irrigation system began operating so that by March 1977 117 ha were being irrigated. A small reserve of mountain beech forest (*Nothofagus solandrii* var. *cliffortiodes*) is present on Long Hill (along the eastern side of the lake). The reader is referred for more detailed information to Gage (1959, 1977), Bradshaw (1977) and Soons (1977) (geology and geomorphology); McLeod & Burrows (1977), McLeod & McLeod (1977) and Gibson (1978) (history, farming and catchment of Lake Grasmere).

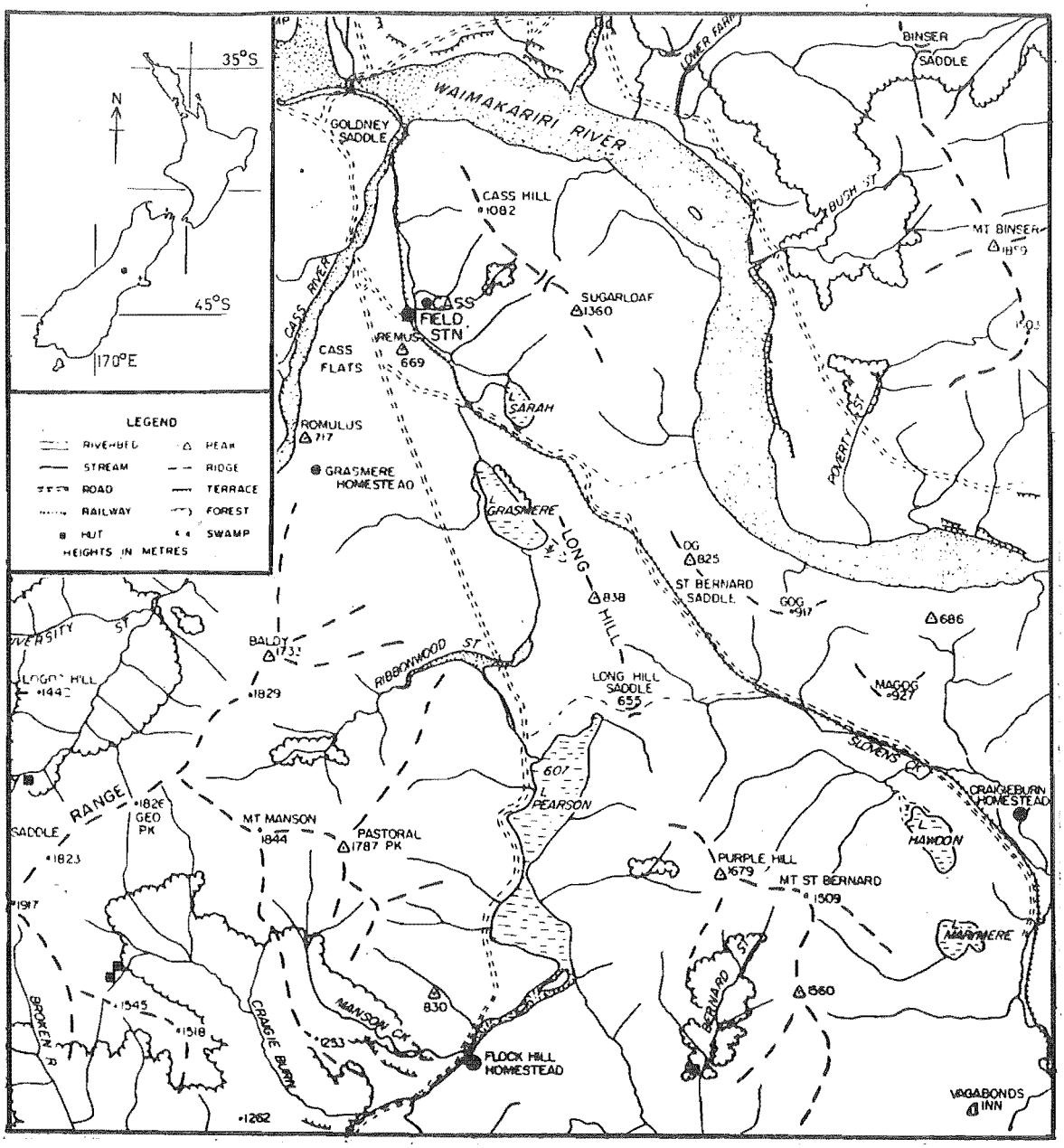


Fig. 2.1 The study area. The inset shows the location of Cass (●) and Christchurch (+) in the South Island of New Zealand. Scale of study area map: 1 cm = 1 km. (Modified from Burrows 1977.)

2.2 CLIMATE

Lake Grasmere is located in an area of steep annual rainfall gradient, with high values in the west and low values in the east. It lies on the 1,250 mm mean annual isohyet (Greenland 1977). Monthly variation in rainfall is small, ranging from a mean of 89 mm in February to 130 mm in October at the Cass Field Station (Greenland 1977). Snow may fall in the Cass Basin on a few occasions in most winters, but seldom persists for any length of time.

High summer temperatures and relatively mild winters (moderated by northwesterly winds) are characteristic of Cass. Extremes of shade

air temperature recorded at the Cass Field Station (1961-1964) were -16°C and 37°C, with a mean annual air temperature for the same period of 9°C.

The climate at Cass and Lake Grasmere is dominated by wind, with a reported average annual wind speed of 4.9 m sec^{-1} (from two years' data at the Cass Field Station; Greenland 1977). Observations on wind directions at the Cass Field Station showed that winds from the northwesterly quarter occurred 51% of the time. Only 20% of the observations indicated calm conditions, and this is likely to be an over-estimate since most observations were taken in the mornings, which are normally calmer than later in the day. Percentage frequencies of winds from other directions were, southeast to northeast 16% and south to southwest 13%.

Greenland (1977) provides further information on the climate of the Cass area.

2.3 LAKE GRASMERE

Lake Grasmere (Fig. 2.2 and Plate 2.1) has an area of approximately 63 ha, a maximum depth of 15 m (mean depth 7.8 m), and a total length of 1.5 km (Irwin 1972, Stout 1977). The water level fluctuates by at least a metre during the year, and also differs between years, usually lowest in July/August and highest in spring (Stout 1975a). There is one inlet stream (Ribbonwood Stream), and several inlet springs that originate from neighbouring alluvial fans (Stout 1972). The single outlet (Grasmere Stream) leaves the northern end of the lake.

2.3.1 Physical Features

Thermal stratification is a very rare occurrence as the water is frequently mixed by prevailing northwesterly winds. The maximum surface water temperature (recorded in mid lake) has ranged between 19°C and 21°C in different summers, and temperatures in December and January may vary by as much as 4°C between years (Stout 1975a). The winter low is usually 3 - 4°C and ice may form over all or part of the lake. During the study period, lake water temperatures were within previously recorded limits (Fig. 2.3), and ice covered about seven-eighths and one-third of the lake's area in the winters of 1976 and 1977 respectively. Ice was thickest along the eastern shore (under the beech forest), and the more wind-exposed and less-shaded southern and western sides of the lake remained ice-free. The lake warmed more quickly and reached a higher maximum temperature in 1977 - 1978 than in 1976 - 1977 (Fig. 2.3).

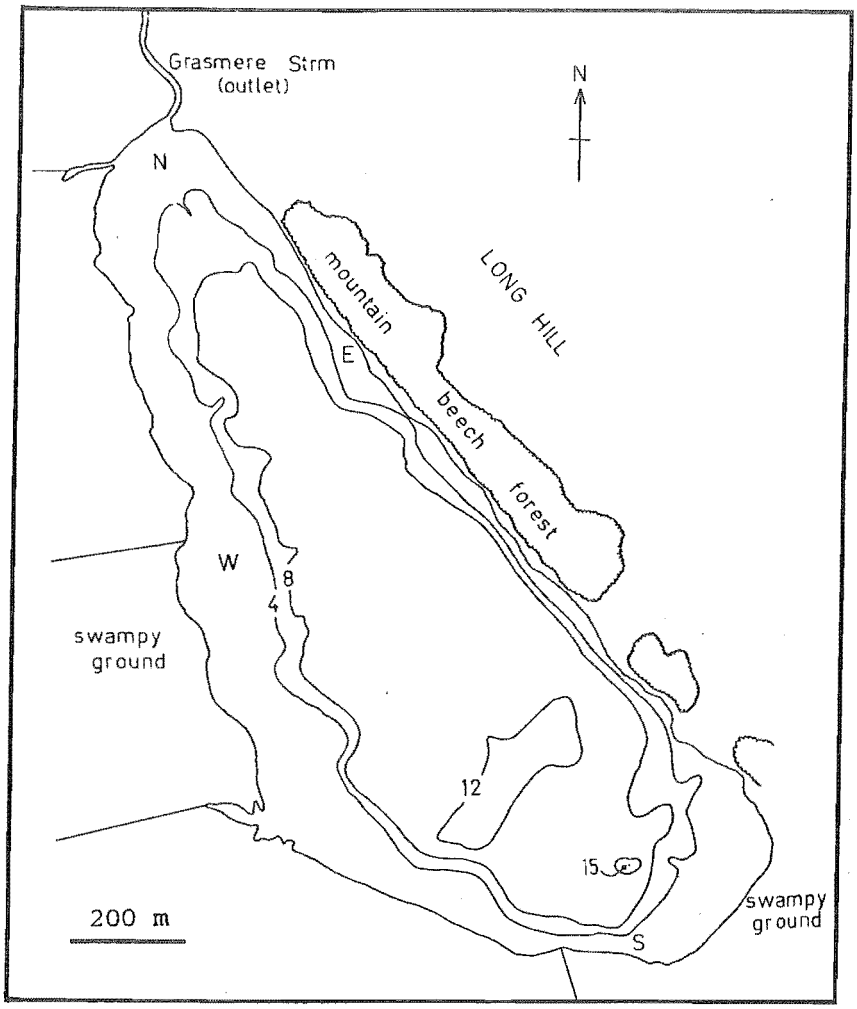


Fig. 2.2 Map of Lake Grasmere showing four main sampling areas (N, S, E and W), the 4 m, 8 m and 12 m depth contours and the deepest point of the lake (15 m).

Light penetration, measured using a Secchi disc, is variable. Extremes of 0.42 m (September 1970 following heavy rains) and 8.2 m (May 1970) have been recorded (Stout 1972, 1977), with fluctuations being related to silt loads or plankton densities. The average Secchi disc value recorded in mid lake by Stout (1972) was 2.8 m. Secchi disc readings were taken on eight occasions during 1976 - 1977 and ranged from 1.7 m (October 1977) to 5.0 m (April 1977) (Fig. 2.3). The average of these values was 3.0 m. Low Secchi disc values during the study period all followed periods of high rainfall (data from weather records kept at the Cass Field Station).

2.3.2 Chemical and Biological Features

The chemical features of Lake Grasmere and its inlets have been discussed by Stout (1969a, 1972, 1975a, 1977), and only the features salient to the present study are outlined here.

Plate 2.1 Lake Grasmere from the southern end (opposite).

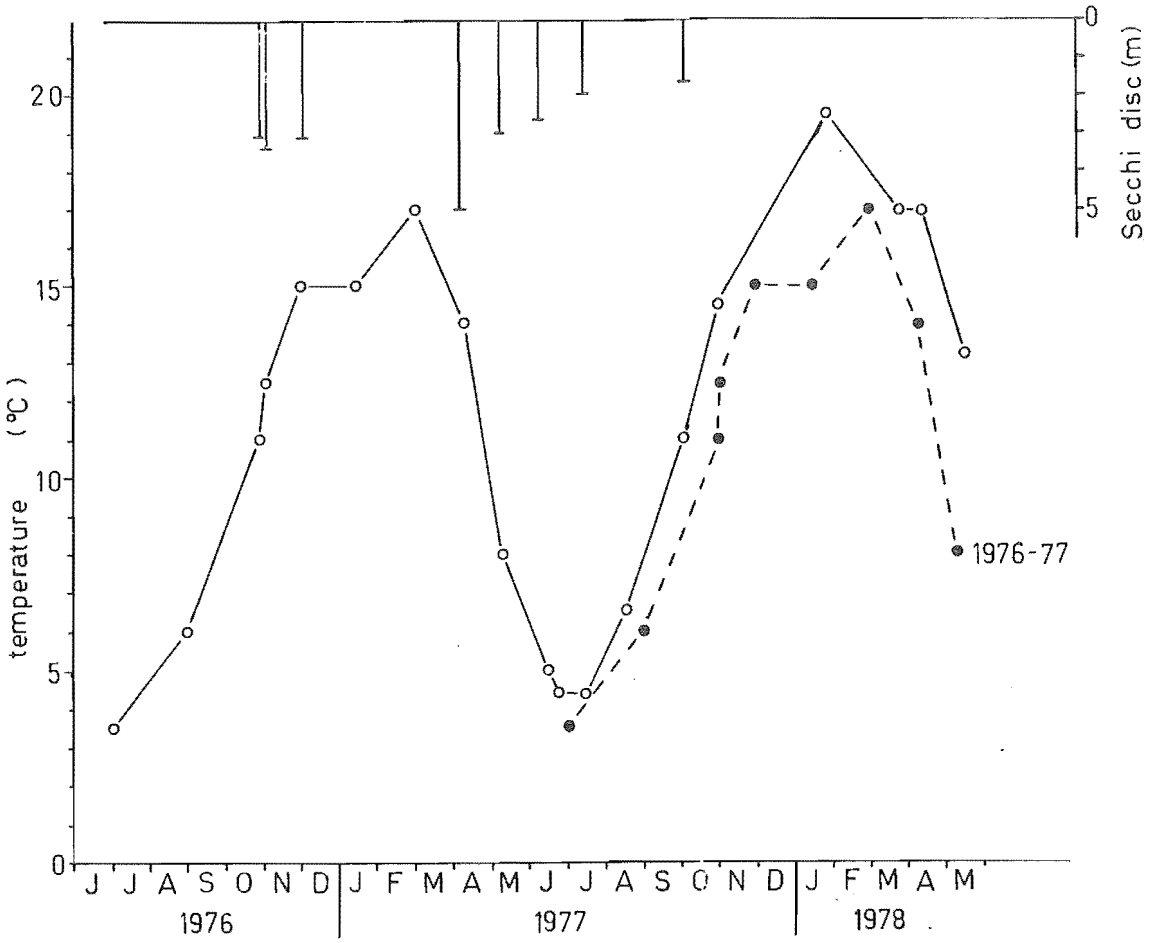


Fig. 2.3 Open-water temperatures and Secchi disc readings taken in Lake Grasmere between July 1976 and May 1978. The dashed line represents temperature measurements of 1976 - 1977 superimposed on those for 1977 - 1978. Ice was present on the lake on 3 July and 25 July 1976 and 13 July 1977.

The frequent mixing and extensive macrophyte beds ensure that the lake water is usually well oxygenated at all depths, although values as low as 36% oxygen saturation have been recorded (following a few days of exceptional summer calm) (Stout 1977). The pH of the lake water is normally close to neutral, except during algal blooms (which may occur during February or March) when a pH of 8.3 has been recorded (Stout 1969). Lake Grasmere has amongst the highest values of bicarbonate alkalinity and conductivity for the Cass lakes, but these values are not particularly high compared with values from some North Island lakes. Low Ca (6.6 - 11.7 g m^{-3}) and Mg (1.17 - 1.42 g m^{-3}) values, and high Si content (up to 8 g SiO_2 m^{-3}) are notable for their likely effects on the decreased occurrence of larger crustaceans and molluscs (Ca and Mg) and increased occurrence of diatoms (Si) (Stout 1977).

Ramsay (1972, 1974, 1976) studied the heterotrophic bacteria in the open water, in water over the macrophytes, on *Elodea*, and on the mud.

She found that the numbers of bacteria in water over *Elodea* were low, but increased in autumn and winter, and that mature and moribund leaves showed greater bacterial uptake activity than young leaves and new growth. Bacteria tended to increase after zooplankton (but not phytoplankton) blooms and (near an inflowing spring) after rainfall.

The phytoplankton of Lake Grasmere is dominated by diatoms (*Asterionella formosa, Diatoma elongatum, Melosira granulata* var. *angustissima* and *Cyclotella* sp.) with changes in the dominant species from year to year (Stout 1972, 1975a,1977). Filamentous green algae (*Mougeotia* sp. and *Gloeotila pelagica* var.) and colonial green algae (*Eudorina elegans* and *Volvox* sp.) may occur also, but blue-green algae are not common (Stout 1975a,1977). Values for phytoplankton Chlorophyll *a* as high as 8 mg m^{-3} (mean annual value 4.9 mg m^{-3}) have been recorded (Stout 1969a,1972, 1975a,1977). Lowest values usually occur in May and June (Stout 1972) but marked variations may occur from year to year (Stout 1977).

The zooplankton is dominated by two cladocerans (*Ceriodaphnia dubia* and *Bosmina meridionalis*) and several species of rotifer (Stout 1975a). Other members of the zooplankton, present at various times of year, are the water mite *Piona uncata exigua* and young stages of the cyclopoid copepod *Eucyclops serrulatus*. Seasonal fluctuations of zooplankton, both numbers and species present, can be related, at least in part, to amount and species composition of the phytoplankton (Stout 1975a).

The adventive *Elodea canadensis* is the most abundant macrophyte in Lake Grasmere and forms extensive beds in water down to about 7 - 8 m deep. It is not present in water less than about 0.5 m deep except in occasional small clumps in sheltered areas, and is sparse and stunted at the wind-exposed southern end of the lake. *Isoetes alpinus* may be found in shallow water, especially along the stony/rocky eastern shore, and also in southern and western areas. The stoneworts, *Chara* sp. and *Nitella* sp., grow at depths between 1m and 2 m, especially where the bottom is silty (for example, in places along the eastern and southern shores). The stoneworts are present in more luxuriant beds below the *Elodea* zone in water more than 7 - 8 m deep (Stout 1977). *Myriophyllum propinquum* and *Ranunculus fluitans* are present, in a narrow band, along the eastern shore at the upper margin of the *Elodea* zone, in water about 1 m deep. Patches of *M. propinquum* may be found in other areas of the lake, especially at the southern end. *Potamogeton cheesemanii*

has a very patchy distribution and was not common during the study period. This species exhibits pronounced die-back in winter (Stout 1975a,1977) and new shoots were observed in silty areas in the northern and western areas of the lake in early November 1976. Seasonal changes in macrophyte biomass were marked (except for *M. propinquum*) during the present study (Fig. 2.4). *E. canadensis* had the greatest biomass of the four macrophytes examined and showed the greatest seasonal change. It has perennial shoots that remain green in winter when there was no obvious die-back, although there was some reduction in standing crop (Fig. 2.4). Relatively high water transparency in April 1977 (Fig. 2.3) may have contributed to increased productivity and hence biomass of *E. canadensis* at this time (Fig. 2.4).

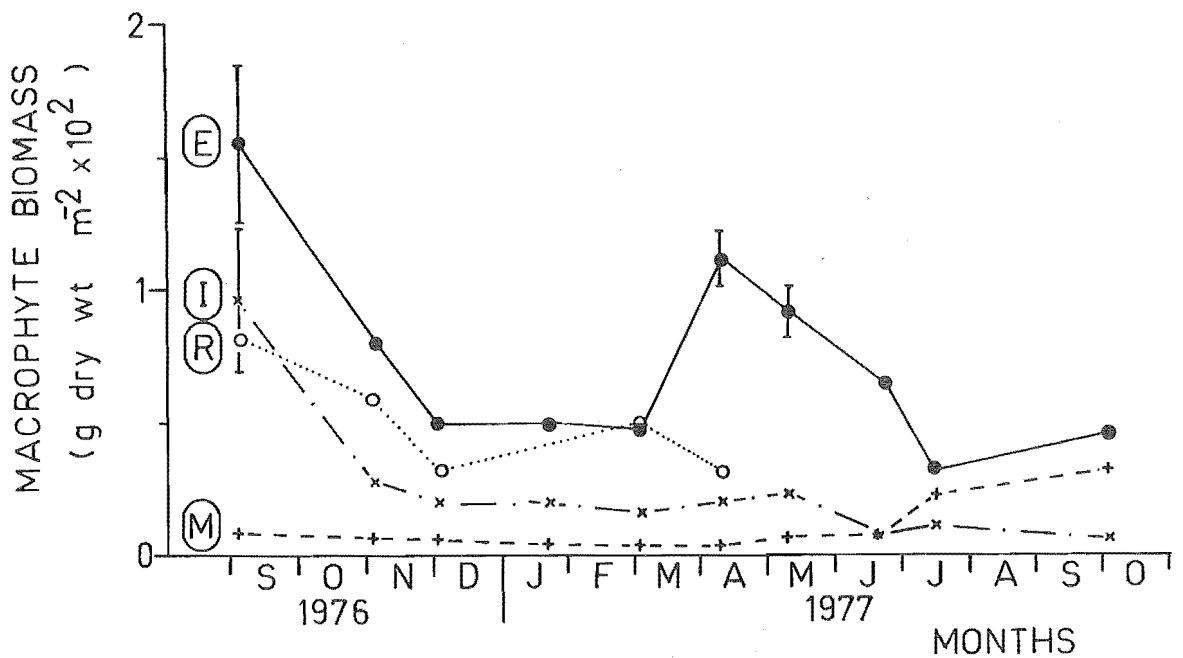


Fig. 2.4 Changes in biomass of four species of aquatic macrophyte (*Elodea canadensis* (E), *Isoetes alpinus* (I), *Ranunculus fluitans* (R), and *Myriophyllum propinquum* (M), (September 1976 - October 1977). All standard errors were less than 10 g m^{-2} unless indicated. Data from quantitative sampling program (see Chapter III).

Extensive growths of filamentous green algae may be present on macrophytes and stony substrates at certain times of year. During the study period they were most prominent in May and October 1977.

Invertebrate communities associtated with the submerged aquatic macrophytes of Lake Grasmere have been discussed briefly by Stout (1969a,

1975a,1977) and Winterbourn & Lewis (1975). Work by Jamin (1976) and Timms (in press) has documented the benthic fauna. Greig (1976) investigated the trophic relationships and production of a littoral population of a mayfly *Deleatidium* sp. No ecological studies have been made in the lake on invertebrates associated with the macrophytes.

Lake Grasmere contains several species of fish, including brown (*Salmo trutta*), rainbow trout (*S. gairdnerii*), long-finned eel (*Anguilla dieffenbachii*), probably short-finned eel (*A. australis schmidtii*), upland bullies (*Gobiomorphus breviceps*) and Koaro (*Galaxias brevipinnis*) (Stout 1975a).

Lake Grasmere is a Wildlife Refuge for waterfowl and large numbers of birds are often present on the lake (see Stout (1975a) for further details). A number of these birds feed in the lake and nutrients are added to the lake in their faeces (especially by Canada Geese (*Branta canadensis*)).

CHAPTER III

QUANTITATIVE SAMPLING PROGRAM

3.1 AIMS OF THE QUANTITATIVE SAMPLING PROGRAM

The background to scientific work on Lake Grasmere has been discussed in Chapter II. Various aspects of the lake, and its associated organisms, have been studied over the years, but information on the invertebrates of the macrophyte zone is limited to preliminary descriptions (Stout 1969a,1975a,1977; Winterbourn & Lewis 1975). Only three studies have been concerned primarily with macroinvertebrates. Greig (1976) studied the ecology of a littoral population of *Deleatidium* sp. (Ephemeroptera), especially its trophic relationships and predation, but his study was based on wave-exposed stony substrates at the southern end of the lake where a specialised lake fauna exists. Jamin (1976) and Timms (in prep.) have investigated the benthos.

In an attempt to overcome this deficiency in knowledge of the invertebrate fauna, a monthly sampling program was proposed with the following aims in mind:-

1. To document the taxonomic composition of the phytomacrofauna of Lake Grasmere.

Preliminary surveys of Lake Grasmere early in 1976 showed that there were many species of invertebrates present in the macrophyte zone that had not previously been recorded. In order to provide the necessary foundation for proposed work on the trophic interrelationships and life histories of the dominant invertebrates it was felt essential that more complete information be collected.

2. To characterise and compare the invertebrate communities present on different macrophyte species.

The macrophyte zone of Lake Grasmere comprised beds of *Elodea canadensis*, *Myriophyllum propinquum*, *Isoetes alpinus*, *Ranunculus fluitans*, *Potamogeton cheesemani*, *Chara* sp., and *Nitella* spp. although only the first four named were extensive enough to make regular sampling practical. In particular, a comparison of the communities on the adventive *E. canadensis* with those on the native *M. propinquum* was considered potentially interesting.

3. To compare communities from several areas and depths within the lake.

Within the littoral zone of lakes, environmental factors such as water depth, wave exposure, substrate, amount of organic material and degree of shading can contribute to variability between communities. It was decided, therefore, that the sampling program should encompass a range of sites within the lake where differences in environmental parameters might be expected. It was hoped that such an approach would yield information of more general applicability to other lakes in New Zealand than would intensive sampling at any one site.

4. To analyse trends in seasonal changes in invertebrate abundance.

Detailed analysis of the seasonal changes in invertebrate abundance was not considered to be a primary aim of this study. The sampling and processing effort required to obtain statistically reliable information would have been prohibitive. Nevertheless, the information obtained, although based on relatively few samples, and low numbers of many species, was thought to be worth presenting with the proviso that the various deficiencies were realised. In addition, it was considered important to gauge the extent that seasonal changes in the invertebrate communities can influence the conclusions drawn from information collected each month when analysed on an annual basis. If seasonal changes are very pronounced the annual overview may not be a good representation of the average situation or it could be influenced markedly by the particular months in which samples were collected. Conversely, where seasonal changes are minimal the effect of dates of sampling on the annual overview should be negligible.

5. To supplement invertebrate life history information.

Most of the invertebrates collected for life history analysis were obtained separately (Chapter V), but the quantitative sampling program was expected to provide additional specimens of the species under study.

3.2 METHODS

3.2.1 Sampling Methods

(a) The problem of sampling. Sampling of littoral macrofaunal communities has many problems particularly as the littoral macrophyte zone tends to be more diverse than benthic habitats (Welch 1948). When designing a sampling device or assessing the applicability of a given

device to a certain situation there are many points to consider. Resh (1979) recently reviewed the sources of error in benthic sampling, sampling reliability, and the role that life history information can play in the development of appropriate designs for benthic investigations. Many of these considerations are applicable also to the sampling of submerged aquatic macrophyte communities. Sampling variability can be dependent upon the choice and operation of the sampling device, environmental features, field and laboratory sorting procedures, and biological features of the study organisms.

A wide range of methods and equipment has been devised for sampling invertebrate communities on aquatic macrophytes (Edmondson & Winberg 1971, Elliott & Tullett 1978, Merritt, Cummins & Resh 1978). For example:

i. hand collection (Krecker 1939, Entz 1947, Müller-Liebenau 1956, Matlak 1963, Harrod 1964, Bownik 1970, Laupy 1977);

ii. hand-net sweeps (Stube 1958, Lawton 1970b, Liddle, Happey-Wood & Buse 1979);

iii. mesh bag placed over plant which is then cut off, sealed in bag and removed (Andrews & Hasler 1943, Welch 1948, Rosine 1955, Mrachek 1966, Higler 1980);

iv. frame, cylinder or box samplers (including grabs and corers) with a variety of closing mechanisms (Whitehead 1935, Macan 1949, Smyly 1952, Gerking 1957, Garnett & Hunt 1965, Gillespie & Brown 1966, Korinkova 1971, Mackie & Qadri 1971, Ladle, Bass & Jenkins 1972, McCauley 1975, Soszka 1975a, Minto 1977);

v. artificial macrophyte substrates (Glime & Clemons 1972, Macan & Kitching 1972, 1976, Soszka 1975b, Higler 1977, 1980, Macan 1977).

For quantitative studies, hand collection and hand-net methods are generally considered unsuitable (McCauley 1975). However, there is some evidence that a 'standard sweep' hand-net method can give reasonably quantitative results, although for some invertebrates it can be very selective (because of invertebrate behavioural differences) (Macan 1963, 1966). Several sampling methods are best employed with the aid of SCUBA (notably the mesh bag methods in iii. above), otherwise sampling depth is severely limited. Similarly, artificial macrophyte substrates (v. above) are more readily used if SCUBA divers are available, especially for their retrieval. There is some evidence that

techniques of phytomacrofaunal community analysis based on artificial substrates can introduce systematic bias. For example, Soszka (1975b) found that Lepidoptera larvae, which burrow in and feed on macrophyte tissue, not unnaturally were absent from plastic *'Potamogeton perfoliatus'* while present on the real plants. In addition, artificial plants cannot exhibit seasonal changes (in tissue quality, growth form, etc.) which are certain to influence associated animal communities. Furthermore, artificial macrophyte substrates are still relatively untried and, in my opinion, cannot replace sampling of natural macrophyte communities until the various sources of error are recognised and accounted for. Grabs, corers and similar sampling devices (iv) also are not without problems. The equipment required is often more expensive, more complicated and more likely to give trouble. With many samplers, difficulty is experienced in separating the phytomacrofauna from the benthos, there is often a pronounced 'edge effect' and the different growth forms and densities of macrophytes may adversely affect sampling reliability (Resh 1979). However, devices of the grab type seem to offer most promise when it is necessary to obtain samples using a boat and when a range of depths has to be encompassed.

These considerations prompted the design and construction of a cylindrical, pole-mounted sampler that could be operated from a small boat and sample down to a depth of four metres (Stark 1980).

(b) The design and operation of the cylinder-sampler. The sampler (Plate 3.1) is a pole-mounted cylinder (600 mm long × 100 mm internal diameter 'Alkathene' tubing) that can be closed at each end. Stainless steel jaws 2 mm thick (Plate 3.1 b), one with a serrated edge, close with a strong rubber strip-powered scissor action across the lower end of the cylinder to cut off and contain the sample of vegetation and its macrofauna. The top of the sampler comprises a rotating sieve (200 µm mesh) set at an angle of 45° to the long axis of the cylinder. Four 20 mm-diameter holes in the side wall of the sieve provide through-flow for water as the sampler is lowered and can be closed off by rotation of the sieve. The cylinder is attached to an aluminium pole (2.2 m long × 15 mm internal diameter) by a hinge at its lower end and a sliding spring-loaded catch near its upper end. A further length of aluminium tubing (2 m long × 15 mm external diameter) when slid 200 mm inside the permanently attached pole and fastened with a bolt and wing-nut, enables samples to be obtained down to a lake-depth of four metres. (The detachable pole has a brass adaptor that takes the thread of a standard hand-net ring, allowing it also to be

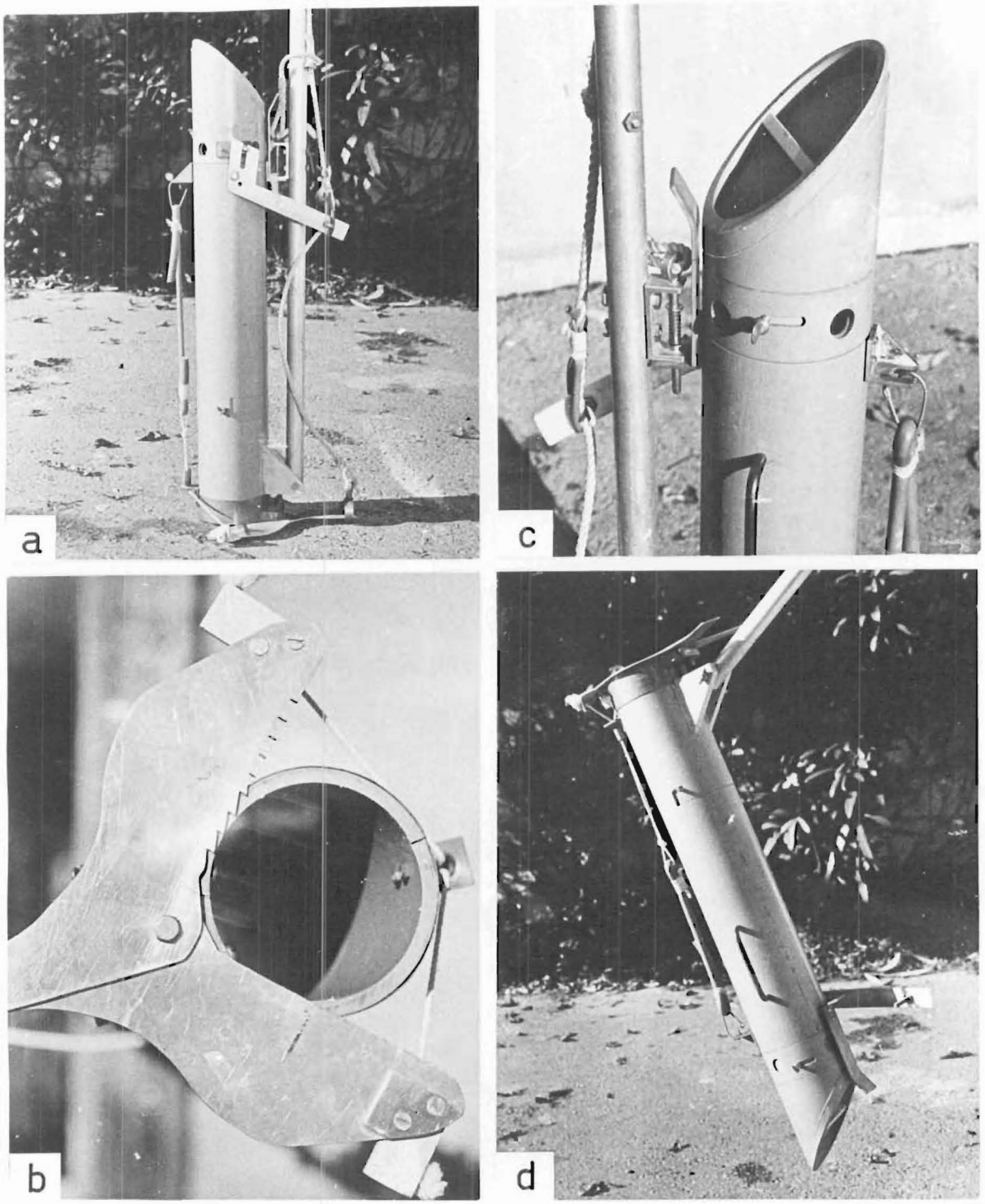


Plate 3.1

a. General view of the sampler in the set position. Note: trigger rope with jaw clamp on lower end, rubber loop over end of sieve rotation lever, cylinder hinge release catch, and rubber "spring" arrangement (at left).

b. Jaws, in the set position as seen from below.

c. The sieve end with holes open and showing the locating bolt which retains the sieve.

d. Sampler in the retrieval position.

used to collect non-quantitative samples with a hand-net.) A strong nylon rope, running through brass eye-bolts attached to the aluminium pole, controls sieve rotation, jaw release, triggering and release of the cylinder from its upper fastening. The sampled area is 0.008 m^2.

The sampler is set in the following manner (Plate 3.1 a):

i. The top end of the cylinder is fastened to the pole by the spring-loaded catch.

ii. The jaws are held open by a brass clamp on the end of the triggering rope.

iii. The sieve is rotated so that the four laterally placed holes are open, and a rubber loop attached to the triggering rope is slipped over the end of the lever which controls sieve rotation. It is important that the triggering rope is positioned as in Plates 3.1 a and c to facilitate smooth operation.

The sequence of operation is as follows:

i. The sampler is allowed to descend over the macrophyte bed under its own weight. It was found that less variable replicate samples were obtained in this manner, rather than by delicate attempts, incorporating lateral movements, to position the sampler.

ii. When the sampler reaches the substrate the triggering rope is pulled and the following three operations occur in sequence -

(a) the sieve rotates to close off the four 'irrigation' holes;
(b) the jaws are released cutting off and enclosing the sample;
and (c) the cylinder is released from its upper fastening.

iii. The sampler is raised with the sieve end at the bottom and the water drains out (Plate 3.1 d).

iv. The sieve is removed by unscrewing a small locating bolt and the sample washed into a plastic bag (and preserved if desired). Once the sieve has been replaced the above sequence can be repeated for taking the next sample.

Table 3.1 summarises various considerations (adapted from Resh 1979) involved in the quantitative sampling of animal communities on macrophytes, and methods used in the present study to minimise any inherent or created problems. The sampler incorporates several design features that improve its efficiency. A significant error in quantitative sampling of aquatic macrophytes may arise due to the 'bow

wave' of a descending sampler pushing aside the macrophytes or causing the invertebrates with the most developed escape responses to flee. It was found that sampling was easier and a greater number of invertebrates were collected when the sampler was allowed to descend under its own weight and if the sieve was not in place. A lid is essential, however, because once a macrophyte has been cut off it tends to float upward out of the sampler. In order to increase water flow through the sampler (and thus decrease the 'bow wave' and to retain the sample) the four 20 mm-diameter holes were placed laterally on the sieve and the lever system was designed to close these off during sample collection. This design reduced the visible disturbance to the macrophyte bed in the region of the descending sampler and, presumably, led to a reduction of the 'edge effect' (see Elliott 1977). The term 'edge effect' describes the unsystematic errors that influence measures of invertebrate density by, for example, the edge of the sampler brushing invertebrates from plant stems or causing those species with the most developed escape responses to flee.

Mesh size of sampling equipment may influence markedly the estimation of population size, distribution and community structure (Malley & Reynolds 1979). The mesh must be fine enough to capture the smallest life history stages required and not so fine that clogging is a problem. The final design of the sieve arrangement on the cylinder sampler was the result of much experimentation. It was found that if the sieve was placed at right angles to the long axis of the cylinder (i.e. a circular sieve) clogging of the desired µm mesh with fine sediment and filamentous algae was a major problem when the sampler was used in the manner described above (i.e. the sieve at the bottom when the sampler is retrieved). A coarser mesh would have allowed too many smaller animals to escape. The solution was to incline the sieve at an angle of 45° to the long axis of the sampler so that the filtering area was increased by 42% and any sediment or algae collected was washed down to the bottom angle of the sieve. This left the greater part of the sieve clear for more efficient drainage.

The sampler was found to be most effective in macrophyte beds where plant growth was vertical. It was difficult to obtain samples where macrophyte stems were very short (i.e. less than about 30 mm, e.g. *Isoetes alpinus* at some sites) or very long (i.e. greater than about 1 m, e.g. *Elodea canadensis* in deeper water) or from plant species whose growth forms were not relatively rigid or upright (e.g. *Ranunculus*

fluitans and *Potamogeton cheesemani)*. At the times of year when growth of filamentous algae was extensive, difficulty was experienced in obtaining quantitative samples. This was especially so in zones of *Elodea canadensis* where the filamentous algae and macrophytes formed an almost impenetrable mat. In such conditions it is very difficult to obtain adequate quantitative samples.

Table 3.1 Factors affecting quantitative sampling of animal communities on littoral aquatic macrophytes (adapted from Resh 1979) and methods used in the present study to overcome the problems.

Factor	Problems	Remedy
Vegetation	Loss of organisms during removal; inability to enclose macrophyte or to close sampler.	Completely enclosed sampler after triggering powerful rubber-powered cutting jaws.
Depth	Design of sampler limits working depth.	Sampler mounted on extendable aluminium pole with simple triple-action trigger mechanism; sampling possible down to 4 m lake depth.
Disruption of substrate by shockwave of sampler	Loss of small organisms and those with well-developed escape responses; incomplete sampling of macrophyte.	Closeable vents on rotating sieve to give better flow-through of water when sampler descending; care with sampler operation.
Mesh size	Coarse - miss small life history stages. Fine - blockage by fine sediments leading to reduced sampling efficiency.	Used 200 µm mesh angled to provide efficient drainage when sampler lifted.
Sampler dimensions	Large - increased sorting time; may not detect aggregations (Elliott 1977). Small - may not detect aggregations; variability increased due to edge effect.	Compromise: the need for short sorting time biased the choice in favour of a small sampler.
Operator inconsistency	Systematic error in population estimates (Needham & Usinger 1956).	Single operator.
Number of replicates	Time involved vs adequacy of representation of community sampled.	Depends on aims of study.
Weather conditions	Can influence micro-distribution of invertebrates.	Sample in similar conditions each time.

3.2.2 Pilot Survey and Analysis of Sample Variability

A pilot survey was undertaken on 14 April 1976 during which 33 samples (Appendix 1) were obtained using the cylinder-sampler. The data from this survey were examined for variability between replicates to determine the number of samples needed to estimate invertebrate abundance to a specified level of precision.

Elliott (1977) and Resh (1979) discussed, in detail, the problems of the size and numbers of samples required to estimate the densities of benthic invertebrate populations to a desired level of precision and these considerations relate equally well to phytomacrofaunal communities. Ideally, the solutions to these problems are dependent upon the aims of the investigation alone, but in practice the choice of sample size and/or the number of replicates is usually dictated by practical, rather than statistical, considerations. A quantitative study aims to estimate the *density* of each taxon (usually species) in the habitat (commonly used in phytomacrofaunal studies are numbers/m^2 of substrate or numbers/g (wet or dry wt) of macrophyte). On the other hand, a faunal survey usually aims to discover which species are present and perhaps estimate their *relative abundance* at each site.

The quadrat or sample size most suitable for any particular investigation of the density or distribution of a population is dependent upon the nature of its dispersion; i.e. whether its distribution is random, regular or contagious. Contagious or aggregated distributions describe the dispersions of most biological populations (Elliott 1977), which is not surprising considering the spatial variation in the influences of environmental factors.

Several workers (e.g. Beall 1939, Finney 1946, Taylor 1953) have concluded that a small sampling unit is more efficient for estimating population densities than a larger one when the dispersion of a population is contagious. More smaller samples can be collected and processed with the same effort, the catch is more representative since many small units cover a wider range of habitat than a few large units, and many small units (with more degrees of freedom) are more statistically reliable than a few large units. Although a small sample size may be the ideal theoretical solution, there are practical factors which set a lower limit to the dimensions of the sampling unit (e.g. the growth form of the macrophyte species), and, as sample size decreases, the 'edge effect' becomes more pronounced. As samplers become smaller, the edge becomes greater relative to the area sampled

and the potential for error in the density estimate increases. The size of the area sampled in this study (0.008 m^2) was dictated by the density of invertebrates in the habitats to be sampled (estimated from preliminary sampling prior to the pilot survey) which influences sample processing time, and the size of cylinder available for its construction.

Because variation due to contagious distributions is often encountered in sampling natural populations, a single small sample is likely to be statistically inaccurate. The simplest way to overcome this is to take a large number of replicates (greater than 50). However, this is rarely practicable, especially if samples are to be collected at frequent intervals or from a number of habitats. Elliott (1977) suggested that a standard error equal to ±20% of the mean was reasonable for benthic sampling. Then -

$$\text{the index of precision, } D = 0.2 = \frac{\text{standard error}}{\text{arithmetic mean}} = \frac{1}{x}\sqrt{\frac{s^2}{n}}$$

where s^2 = variance, and n = number of replicates required. If dispersion is contagious (a reasonably safe assumption for most biological populations) a negative binomial is known to be a suitable model for data obtained from a series of replicate samples. Then -

$$D = \frac{1}{x}\sqrt{\frac{\bar{x}}{n} + \frac{\bar{x}^2}{nk}} = \sqrt{\frac{1}{n\bar{x}} + \frac{1}{nk}}$$

$$\text{and} \quad n = \frac{1}{D^2}\left(\frac{1}{\bar{x}} + \frac{1}{k}\right) = 25\left(\frac{1}{\bar{x}} + \frac{1}{k}\right) \quad \text{for 20\% error} \quad \ldots\ldots\ldots \quad (1)$$

where k = common k and $\frac{1}{k}$ is a measure of excess variance or clumping of individuals in a population $\left(k = \frac{\bar{x}^2}{s^2 - \bar{x}}\right)$. As $\frac{1}{k}$ approaches 0 ($k \to \infty$) the distribution tends to random, and as $\frac{1}{k}$ tends to infinity ($k \to 0$) the distribution converges to the logarithmic series (Fisher, Corbet & Williams 1943). Given the number of replicates (n) actually collected, it is possible to calculate the index of precision achieved using the following expression:

$$D = \sqrt{\frac{\frac{1}{\bar{x}} + \frac{1}{k}}{n}} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

Equations (1) and (2) were applied to data (Appendix 1) from replicates collected during the pilot survey (Tables 3.2 and 3.3). The number of replicate samples required to estimate reliably the densities of invertebrate taxa within 20% of the mean was very variable, depending upon the habitat sampled, the taxa in question and the units of density used (Table 3.2). When invertebrate density

was expressed in terms of numbers per sample, between 1 and 76 replicates were required (depending upon the taxon and the habitat) and when density was expressed as numbers per g dry weight of macrophyte,

Table 3.2 Number of replicate samples (n) required for various invertebrate taxa from different macrophyte habitats to estimate the density* within 20% of the mean. Data from the pilot survey (14 April 1976) (Appendix 1).
* n for numbers/sample (n for numbers/g dry wt macrophyte).
Habitat codes given in Table 3.4.

Habitat:	N *E*	S *I*	E *E* 2	E *I*	W *E* 1	W *E* 2	W *I*
Number of samples taken:	8	2	5	4	3	4	2
Taxa							
Coelenterata	57(39)	29(38)	15(13)	41(35)	22(33)	50(43)	6(5)
Annelida	23(17)	-(-)	49(78)	-(-)	7(4)	76(83)	23(22)
Crustacea	13(22)	26(37)	14(22)	26(37)	23(24)	27(25)	13(14)
Insecta	34(33)	7(1)	3(2)	17(24)	17(14)	26(27)	12(13)
Acarina	12(6)	1(10)	3(14)	30(42)	3(12)	9(15)	9(10)
Mollusca	5(4)	18(5)	5(7)	12(19)	3(1)	11(9)	24(25)
Total invertebrates	5(4)	14(3)	5(6)	13(21)	4(2)	6(7)	22(23)

Table 3.3 Number of replicate samples (n) required to estimate the dry weight in grams of macrophyte within 20% of the mean for nine habitat types, and the index of precision (D) achieved if two * or three ** replicates are taken. Data from the pilot survey on 14 April 1976 (Appendix 1). Habitat codes given in Table 3.4.

Habitat:	N *E*	S *E*	S *I*	E *E* 2	E *R*	E *I*	W *E* 1	W *E* 2	W *I*
n	3.3	6.6	6.1	1.3	2.4	2.5	2.0	2.3	<1.0
D* n=2	0.26	0.36	0.35	0.11	0.21	0.22	0.20	0.22	0.02
D**n=3	0.21	0.30	0.29	0.08	0.18	0.18	0.16	0.15	0.02

up to 83 replicates were found to be required. Less variability was seen in the total invertebrate density, especially from *E. canadensis* zones where fewer than eight samples were required to obtain the desired precision. Generally, the number of samples required to estimate reliably the invertebrate density, either as numbers per sample or numbers per g dry weight of macrophyte, within desirable limits of statistical precision, was unacceptably high for the sole investigator since a prime aim was the investigation of several habitat types. Consequently, it was decided to collect between one and three samples from each of 13 habitats (Table 3.4) during the main quantitative sampling program.

Table 3.4 Sample types and number of replicates to be collected during the quantitative sampling program (see Fig. 2.2 for sampling areas and Table 3.5 for details of sampling sites).

Site code	Sampling area	Macrophyte	Lake depth (m)	No. of samples/ month
E *E* 1	EAST	*Elodea canadensis*	1	1
E *E* 2	"	*Elodea canadensis*	2	3
E *I*	"	*Isoetes alpinus*	0-1	2
E *R*	"	*Ranunculus fluitans*	1-2	1
E *M*	"	*Myriophyllum propinquum*	1-2	2
W *E* 1	WEST	*Elodea canadensis*	1	1
W *E* 2	"	*Elodea canadensis*	2	3
W *E* 3	"	*Elodea canadensis*	3	1
W *E* 4	"	*Elodea canadensis*	4	1
W *I*	"	*Isoetes alpinus*	0-1	1
S *I*	SOUTH	*Isoetes alpinus*	0-1	2
S *M*	"	*Myriophyllum propinquum*	0-1	2
N *E* 2	NORTH	*Elodea canadensis*	2	3
				23

Table 3.3 shows the number of replicates required to estimate the dry weight of macrophyte, within 20% of the true mean value, for nine habitats from the pilot survey. Also shown is the influence of the number of replicates (viz., two or three) on the index of precision (D) of the macrophyte dry weight estimate. In most cases (six out of nine),

triplicate (n = 3) samples yielded dry weight estimates within 20% of the true values. Duplicate (n = 2) samples, on the other hand, reduced the precision by an average of just over 4.2%.

3.2.3 The Main Quantitative Sampling Program

(a) Field procedure. The monthly sampling regime used (Table 3.4) resulted from a consideration of sample collection logistics, the available time per month for sample processing, the variability in samples, and the aims of the study. Given the range of communities to be sampled, the number of replicates of each sample type was severely limited for practical reasons and, as outlined above (p. 21), the number of samples required to obtain a reasonable level of statistical precision (± 20% of the mean density) was far in excess of the number I was able to process in the time available. However, as already stated (p. 12), I considered it more important to investigate a wide range of invertebrate/macrophyte community types than concentrate on one specific community.

The monthly quantitative sampling program was begun in September 1976 and continued until October 1977. Thirteen sampling sites, in four areas of Lake Grasmere (Fig. 2.2) were selected to cover a range of macrophytes and environmental conditions (Table 3.5). Sampling effort was concentrated on *Elodea canadensis* communities since this macrophyte represented about 90% of the macrophyte-covered area of the lake. The endemic *Isoetes alpinus*, the most abundant macrophyte in water less than 1 m deep, and, especially, *Myriophyllum propinquum* (also an endemic species) were expected to provide interesting comparisons with the adventive *E. canadensis*. The wide range of habitats investigated was intended to provide data that could be used in comparison with macrophyte communities of other high-country lakes.

A total of 180 samples were obtained with the cylinder-sampler, from the 13 macrophyte habitats in Lake Grasmere on ten occasions during the sampling period (Table 3.6). The samples were collected between 1100 h and 1600 h N.Z.S.T. from four main sampling areas, which were termed North, South, East, and West (Fig. 2.2). Once samples had been collected, they were transferred to 400 × 300 mm plastic bags and preserved with 4% formalin.

Deviations from the proposed sampling regime were due to ice preventing sampling (13 July 1977) or particularly strong north-westerly winds and excessive growths of filamentous green algae

Table 3.5 Physical features of the sampling sites (see Table 3.4 for details of site codes, macrophytes and lake depths and Fig. 2.2 for location of the four main sampling areas).

Site code	Wave action	Substrate	Remarks
E *E* 1	weak-moderate	Mostly inorganic but organic inputs from overhanging beech forest canopy. Shore steeply shelving below 0.5 m. Sand - large rocks and boulders.	Extensive shading by beech canopy and hillside (especially in winter). *Myriophyllum* and *Ranunculus* comprise a narrow, mixed band near upper margin of *Elodea* bed.
E *E* 2	" "		
E *I*	" "		
E *M*	" "		
E *R*	" "		
N *E* 2	moderate	Highly organic (decomposition products of macrophytes). Gentle slope near shore, several sudden changes in region of 2 - 4 m. Firm to loosely-packed, fine particulate sediments.	Extensive macrophyte growth acts as source of, and trap for, organic detritus. *Isoetes* present in small clumps or in areas up to 20 m^2.
W *E* 2	weak		
W *E* 3	"		
W *E* 4	"		
W *E* 1	moderate		
W *I*	"		
S *I*	strong	Much organic material deposited by wave action (due to prevailing NW winds). Uneven, stony sediments with coarse particulate organic material trapped in macrophyte beds.	Strong wave action and possible influence of inlet stream (spring A, Stout 1972) produce stream-like habitat at lake edge.
S *M*	"		

Table 3.6 Sampling dates and numbers of samples collected from the 13 macrophyte habitats in Lake Grasmere during the quantitative sampling program (see Table 3.4 for key to site codes).

Site: / Date	N *E* 2	S *I*	S *M*	E *E* 1	E *E* 2	E *I*	E *M*	E *R*	W *E* 1	W *E* 2	W *E* 3	W *E* 4	W *I*
2/ 9/76	3	1	1	1	3	2	-	1	1	3	1	1	1
2/11/76	3	2	1	1	3	2	2	1	1	3	1	1	2
2/12/76	3	1	1	1	3	2	2	2	1	3	1	1	1
20/ 1/77	3	1	1	-	3	-	1	-	1	3	1	1	1
2/ 3/77	3	2	1	1	3	2	1	1	1	3	1	1	1
8/ 4/77	3	2	1	1	3	1	1	1	1	3	1	1	-
10/ 5/77	3	-	1	1	3	1	1	-	1	3	1	1	1
20/ 6/77	3	1	1	-	3	2	1	-	1	3	1	1	1
13/ 7/77	3	2	1	-	-	-	-	-	1	3	1	1	1
3/10/77	3	-	-	-	4	1	1	-	-	3	-	-	-
	30	12	9	6	28	13	10	6	9	30	9	9	9

(3 October 1977). The departure from sampling at monthly intervals was primarily due to adverse weather conditions delaying sampling trips. Samples of *R. fluitans* (E*R*, Tables 3.4 and 3.6) were very difficult to obtain due to both the growth form and relative rarity of this plant, which was confined to a narrow band in the eastern sampling area (Fig. 2.2). Sampling of this habitat was discontinued after April 1977.

Lake temperature measurements, Secchi Disc readings and weather observations were made at each time of sampling as variations in these factors may affect sampling efficiency and/or distributions and life histories of many aquatic invertebrates.

(b) Laboratory procedures. Samples were washed through a series of Endecott sieves (3350, 1400, 500 and 200 µm mesh) to separate animals from plant material, and macrophyte stems were examined to ensure that all invertebrates had been removed. Invertebrates were stored in 70% alcohol to await further sorting. Dry weights (after three days at 66°C) of macrophyte per sample were determined.

Macroinvertebrates were sorted under a stereoscopic dissecting microscope at magnifications ranging from 12.5 to 40 ×. Identification of some species, notable Oligochaeta and Chironomidae, necessitated the preparation of slide-mounted specimens. The mounting medium used was lactophenol-PVA incorporating Lignin Pink, which stains chitinised material. Sometimes 10 - 20 seconds in hot KOH was required to clear midge larvae, although animals mounted directly in lactophenol-PVA became clearer with time. Slides were dried for about one week at 66°C, examined, and stored in cardboard slide trays. Macroinvertebrates, once sorted, counted (and measured for use in life-history analyses where applicable: Chapter V) were stored in ethylene glycol.

3.3 RESULTS AND DISCUSSION

3.3.1 Sampling Variability

The pilot survey was the first occasion on which the cylinder-sampler was used and I found that some expertise was required to obtain good samples. Subsequent modifications to the sampler (including redesigning the sieve end of the cylinder) and practice in its operation, improved the repeatability of sampling. It was probable, therefore, that replicate samples taken in the pilot survey were more

variable than similar sets of samples collected later during the main quantitative sampling program. I decided that the best way to test this was to make a paired comparison of indices of precision (D) derived from the pilot survey (column one in Appendices 4.1 to 4.5) with those derived from samples collected on 8 April 1977 during the main quantitative sampling program (Appendices 4.1 to 4.5). As these collections were made at almost exactly the same time of year, when environmental conditions (e.g., macrophyte growth form, presence/absence of filamentous algae) were most likely to be similar, any change in the variability of replicates between dates should have been due primarily to sampling experience.

The statistical test chosen to assess the significance of these comparisons was Wilcoxon's Signed Ranks Test (1945) as described in Langley (1968). The purpose of this simple test is to compare two random samples of matched measurements. If there is no significant difference between two sets of paired measurements, chance differences should consist of about equal numbers of plus and minus differences. The test takes into account not only the direction of the differences, but also the size of the differences between matched pairs (cf. Wilcoxon's Sum of Ranks Test *in* Langley 1968). This feature increases the sensitivity of the test to a point where it compares very favourably with the t Test. Wilcoxon's Signed Ranks Test was preferred to the t Test because it is 'distribution free' and applies to matched measurements (see Langley 1968).

Replicate samples were taken from only four habitats on 8 April 1977 during the quantitative sampling program (Appendices 4.1, 4.2, 4.3, 4.5). Indices of precision of invertebrate density (for the taxa shown in Table 3.2) from these replicates were compared with those from the pilot survey. In addition, as the accuracy of density measurements is influenced by the units of density, calculations were performed with data where densities were expressed in terms of numbers/sample (= numbers/ 0.008 m^2) and in terms of numbers/g dry wt of macrophyte.

In two habitats (N *E* 2 m and W *E* 2 m) the probability of there being no significant difference between the precision of the invertebrate density estimates (i.e., numbers/sample and numbers/g dry wt of macrophyte) from the two dates was 5%. This difference was deemed to be *probably significant* ($P \leqslant 5\%$) and inspection of the original data (Appendices 4.1 to 4.5) showed that the quantitative sampling program revealed the lesser sampling variability. The quantitative sampling program gave density estimates in terms of numbers/sample for habitat S *I* which were probably

significantly better (5% probability of no significant difference) than those from the pilot survey whereas with density expressed as numbers/g dry wt of macrophyte the difference was not significant. For habitat E*E* 2 m, there was no significant difference in sampling variability between the two dates for either units of density. However, in no cases did the pilot survey yield indices of precision of invertebrate density estimates that were better than those obtained from like replicates collected on 8 April 1977. Thus, the expectation that sampling performance would be improved by experience probably had some statistical basis.

In order to assess the precision of the invertebrate density and macrophyte dry weight estimates, equations (1) and (2) (p. 19) were applied also to replicate samples collected during the main quantitative sampling program. However, it is not possible to apply these statistics to habitats or times when only one sample was collected (e.g., S*I*, 2 September 1976, Appendix 2.2). Appendices 4.1 to 4.6 show indices of precision of invertebrate density and macrophyte dry weight estimates for replicate samples from eight macrophyte habitat types based on data collected during the quantitative sampling program. Wilcoxon's Signed Ranks Test was applied to paired D values in three ways to determine -

i. whether, for a given month, numbers/sample or numbers/g dry wt of macrophyte gave a significantly better estimate of invertebrate density for each taxa within each habitat,

ii. whether, for each taxon and total invertebrates, numbers/sample or numbers/g dry wt of macrophyte gave a significantly better estimate of invertebrate density (all habitats combined), and

iii. whether numbers/sample or numbers/g dry wt of macrophyte gave a significantly better estimate of invertebrate density when data from all habitats, times and taxa were combined.

Table 3.7 presents the results of these significance tests for five habitats. All non-significant results have been omitted and there were insufficient data pairs for habitats E*R* and W*I* to permit the application of Wilcoxon's Signed Ranks Test. Where there was a significant difference between the reliability of invertebrate density estimates on each sampling date, it was usually numbers/sample which gave the better estimate (column i, Table 3.7). The exception was

Table 3.7 Significance levels for Wilcoxon's Signed Ranks Test applied to paired indices of precision (D) of invertebrate density (numbers/sample vs numbers/g dry wt of macrophyte). In each case the unit of density that gave the significantly less variable (= better) density estimate is given (i) for each sampling date, (ii) for each taxon, and (iii) overall. All non-significant results are omitted. (See Table 3.4 for site codes.)

	(i)	(ii)	(iii)
Significance level:	5%*	5%*	1%**
Habitat			
N *E* 2		Mollusca, No./g	
S *I*	2/3/77 No./sample		No./sample
E *E* 2	2/12/76, 20/1/77, 2/3/77, 3/10/77 No./sample	Insecta, No./sample	No./sample
E *I*	2/3/77, No./g		
W *E* 2	2/3/77, 20/6/77 No./sample		

* 5% level = difference probably significant.
** 1% level = difference almost certainly significant.

habitat E *I* on 2 March 1977 when numbers/g dry wt of macrophyte gave the less variable estimate. The densities of only two major taxa (column ii, Table 3.7) were probably significantly better ($P \leqslant 5\%$) estimated in terms of one unit of density relative to the other. In habitat N *E* 2 m, the density of Mollusca was probably significantly ($P \leqslant 5\%$) more accurately estimated in terms of numbers/g dry wt of macrophyte rather than numbers/sample. This is possibly because Mollusca (here represented exclusively by *Potamopyrgus antipodarum* and *Gyraulus corinna*) graze on periphyton on plant surfaces and the available plant surface (which, for any one plant species, is proportional to the biomass of the plant) is likely to be an important factor in their dispersion. The density of Insecta from habitat E *E* 2 m, on the other hand, was probably significantly ($P \leqslant 5\%$) more

accurately assessed in terms of numbers/sample, suggesting that their dispersion in this habitat was on an areal basis (i.e., unit area of lake bottom) and not intimately related to the available area of plant surfaces. Overall data from only two sites (S *I* and E *E* 2 m, column iii, Table 3.7) showed a difference in the reliability of density estimates which was almost certainly ($P < 1\%$) in favour of numbers/sample. Both these sites were relatively difficult to sample, the former due to wave action and resultant patchiness of macrophytes and uneveness of substrate and the latter due to the steeply shelving, rocky substrate.

In conclusion, given that invertebrate density estimates within 20% of the true mean values are usually considered desirable for quantitative sampling programs of this nature;

1. The pilot survey indicated that the numbers of samples required to achieve this precision varied according to the invertebrate taxa, sampling date, macrophyte habitat, and units of density and was considered beyond the limits of practicality for this study.

2. A comparison of samples from April 1976 (pilot survey) and April 1977 showed that sampling variability was reduced in the main quantitative sampling program relative to the pilot survey, suggesting that experience in sampling and modifications to the sieve end of the sampler were factors influencing the reliability of invertebrate density estimates obtained.

3. For most sampling dates, habitats, and taxa in the main quantitative sampling program there was no significant difference between the reliability of density estimates derived from densities expressed as numbers/sample or as numbers/g dry wt of macrophyte. Numbers/sample provided less variable invertebrate density estimates in most of those instances where there was a statistically significant difference.

3.3.2 Community Species Composition

A total of almost 96,000 animals belonging to at least 113 species (Table 3.8) were collected from Lake Grasmere and its immediate environs. These included over 64,000 aquatic invertebrates belonging to about 75 species collected during the main quantitative sampling program from 13 aquatic sites (Appendix 2 and Table 3.9). Ten taxa (*Simocephalus vetulus*, *Liodessus plicatus*, *Rhantus pulverosus*, Helodidae, *Polyplectropus puerilis*, *Psilochorema nemorale*, *Pycnocentria evecta*, Tipulidae, *Paradixa* sp., and Stratiomyidae) were not collected in quantitative samples but

were found in hand-net collections from the lake. None of these taxa (with the exception of *S. vetulus*, a weed dwelling Cladoceran that was not common during the study period) is considered characteristic of macrophyte zones in lakes. The dytiscid beetles (*L. plicatus* and *R. pulverosus*) are most common in ponds, although they do occur at low densities in macrophyte zones of lakes (Pendergrast & Cowley 1966). The remaining species are characteristic of benthic sediments or stony substrates and flowing waters. Five species were represented in all the quantitative samples by two or fewer individuals (*Placobdella maorica*, *Procordulia grayi*, *Antiporus strigosulus*, *Triplectides obsoleta* and *Oecetis iti*), and a further five by between three and ten individuals (*Deleatidium* sp., *Zelandobius furcillatus*, *Sigara arguta*, *Arrenurus* sp. and *Physastra variabilis*). The damselfly larva, *Austrolestes colensonis*, was not recorded from the lake during the intensive sampling period but has been collected subsequently (29 September 1980), and was recorded (between March 1969 and January 1970) by Crumpton (1977).

Table 3.8 Aquatic macroinvertebrates collected from Lake Grasmere, Cass, April 1976 - December 1978. L = light-trapped adults only and H = hand-collected adults only, from lake shore. * = new record for Lake Grasmere (*cf.* Stout 1975a)). ** = new record for the Cass district (*cf.* checklist in Burrows (1977)).

COELENTERATA	
Hydrozoa	
Hydridae	
Chlorohydra viridissima (Pallas, 1766)	
PLATYHELMINTHES	
Turbellaria	
Tricladida	
Cura pinguis (Weiss, 1909)	
ECTOPROCTA	
Phylactolaemata	
Plumatellidae	
Plumatella repens (Linnaeus, 1758)	
NEMATODA	
Nematoda indet.	*
Mermithidae indet.	*
ANNELIDA	
Oligochaeta	
Lumbricidae	
Eiseniella tetraeda (Savigny, 1826)	

Lumbriculidae		
Lumbriculus variegatus (Müller, 1774)	*	
Naididae		
Chaetogaster sp.	*	**
Tubificidae		
Aulodrilus pluriseta (Piguet, 1906)	*	**
Limnodrilus hoffmeisteri Claparède, 1862	*	**
Hirudinea		
Glossiphoniidae		
Glossiphonia multistriata Mason, 1974		
Placobdella maorica Benham, 1906		
ARTHROPODA		
Crustacea		
Cladocera		
Bosminidae		
Bosmina meridionalis Sars, 1904		
Chydoridae		
Alona guttata Sars, 1862		
Graptoleberis testudinaria (Fischer, 1848)	*	
Leydigia ?australis Sars, 1885	*	**
Chydorus sphaericus (O.F. Müller, 1785)		
Daphniidae		
Ceriodaphnia dubia Richard, 1895		
Simocephalus vetulus (O.F. Müller, 1776)		
Macrothricidae		
Ilyocryptus sordidus (Lièvin, 1848)	*	
Neothrix armata Gurney, 1927	*	
Ostracoda		
Cypridae		
Cypridopsis vidua (O.F. Müller, 1776)		
Scottia insularis Chapman, 1963	*	**
Herpetocypris pascheri Brehm, 1929	*	
Prionocypris marplesi Chapman, 1963	*	**
Cytheridae		
Gomphocythere duffi (Hornibrook, 1955)	*	
Darwinulidae		
Darwinula repoa Chapman, 1963	*	
Copepoda		
Cyclopidae		
Eucyclops serrulatus (Fischer, 1851)		
Insecta		
Ephemeroptera		
Leptophlebiidae		
Deleatidium sp. Eaton, 1899		
Odonata		
Lestidae		
Austrolestes colensonis (White, 1846)	*	
Coenagrionidae		
Xanthocnemis zealandica (McLachlan, 1873)		
Corduliidae		
Procordulia grayi (Selys, 1871)		
Plecoptera		
Eustheniidae		
Stenoperla prasina (Newman, 1845)		
Austroperlidae		
Austroperla cyrene (Newman, 1845)		
Gripopterygidae		
Zelandobius furcillatus Tillyard, 1923	*	

Hemiptera		
Corixidae		
Sigara arguta (White, 1878)		
Diaprepocoris zealandiae Hale, 1924	*	
Coleoptera		
Dytiscidae		
Liodessus plicatus (Sharp, 1882)		
Antiporus strigosulus (Broun, 1880)	*	
Rhantus pulverosus (Stephens, 1828)	*	
Helodidae indet.		
Diptera		
Tipulidae		
Zelandotipula sp.	H	
Leptotarsus (Macromastix) minutissima (Alexander, 1922)	H	
Limonia (Dicranomyia) otagensis (Alexander, 1924)	**	H
L. (D.) ?vicarians (Schiner, 1868)	L	
L. (D.) sp. A	**	H
L. (D.) sp. C	**	H
Metalimnophila sp.	H	
Aphrophila neozelandica (Edwards, 1923)	HL	
Erioptera (Trimicra) pilipes (Alexander, 1922)	HL	
Amphineurus 4 spp. (none named)	**	HL (2 spp.)
Molophilus sp.	H	
Chironomidae		
Tanypodinae		
Pentaneura harrisi Freeman, 1959	**	H
Ablabesmyia mala (Hutton, 1902)	*	**
Gressittius antarcticus (Hudson, 1892)	*	
Macropelopia languidus (Hutton, 1902)	L	
M. umbrosa (Freeman, 1959)	*	**
Podonominae		
Parochlus spinosus Brundin, 1966	*	HL pupae
Diamesinae		
Maoridiamesa harrisi Pagast, 1947	H	
Lobodiamesa campbelli Pagast, 1947	H	
Orthocladiinae		
Syncricotopus pluriserialis (Freeman, 1959)	*	
Cricotopus zealandicus Freeman, 1959	*	
Metriocnemis lobifer Freeman, 1959	**	H
Corynoneura donovani Forsyth, 1971	*	**
Lymnophyes vestitus (Skuse, 1889)	*	**
Orthocladiinae indet. sp. A	*	**
Orthocladiinae indet. sp. B	*	**
Orthocladiinae indet. sp. C	*	**
Chironominae		
Chironomus zealandicus Hudson, 1892		
Chironomus sp.a	*	**
Xenochironomus canterburyensis (Freeman, 1959)	*	**
Cladopelma curtivalva (Kieffer, 1917)	*	**
Harrisius pallidus Freeman, 1959	H	
Polypedilum pavidus (Hutton, 1902)	**	L
P. canum Freeman, 1959	**	H
Tanytarsus vespertinus Hutton, 1902	*	
Calopsectra funebris (Freeman, 1959)	*	**
Dixidae		
Paradixa sp.	*	
Stratiomyidae		
Stratiomyidae indet.		

Trichoptera		
Hydropsychidae		
Aoteapsyche colonica (McLachlan, 1871)	HL	
A. tepoka (Mosely, 1953)	HL	
Polycentropodidae		
Polyplectropus puerilis (McLachlan, 1868)	*	
Rhyacophilidae		
Hydrobiosis umbripennis McLachlan, 1868	L	
H. parumbripennis McFarlane, 1951	L	
H. harpidiosa McFarlane, 1951	L	
H. frater McLachlan, 1868	L	
H. clavigera McFarlane, 1951	L	
Psilochorema nemorale McFarlane, 1951		
Ps. bidens McFarlane, 1951	L	
Ps. leptoharpax McFarlane, 1951	L	
Costachorema xanthoptera McFarlane, 1939	L	
C. callistum McFarlane, 1939	L	
Conoesucidae		
Pycnocentria evecta McLachlan, 1868		
Pycnocentrodes aureola (McLachlan, 1868)		
Hydroptilidae		
Oxyethira albiceps (McLachlan, 1862)		
Paroxyethira hendersoni Mosely, 1924		
P. tillyardi Mosely, 1924	*	**
Leptoceridae		
Oecetis iti McFarlane, 1964	*	
O . unicolor (McLachlan, 1868)	*	
Hudsonema amabilis (McLachlan, 1868)	*	
Triplectides cephalotes (Walker, 1852)		
T. obsoleta (McLachlan, 1862)	*	
Lepidoptera		
Pyralidae		
Nymphula nitens (Butler, 1880)		
Acari		
Cryptostigmata		
Hydrozetidae		
Hydrozetes lemnae (de Coggi, 1899)	*	**
Malaconothridae		
Trimalaconothrus novus (Sellnick, 1929)	*	**
Astigmata		
Acaridae		
Rhizoglyphus robini Claparède, 1869	*	**
Prostigmata		
Arrenuridae		
Arrenurus (Arrenurus) sp.	*	**
Pionidae		
Piona (Piona) uncata exigua Viets, 1949		
Mollusca		
Gastropoda		
Planorbidae		
Gyraulus corinna (Gray, 1850)		
Physastra variabilis (Gray, 1843)		
Hydrobiidae		
Potamopyrgus antipodarum (Gray, 1843)		
Bivalvia		
Hyriidae		
Hyridella menziesi (Gray, 1843)		
Sphaeriidae		
Sphaerium novaezelandiae Deshayes, 1851		

Table 3.9 Macroinvertebrates collected in quantitative samples, Lake Grasmere, Cass, September 1976 - October 1977. Percentage composition by number of total fauna collected from each site and, in brackets, mean numbers per sample (= 0.008m²). * = < 0.1% of the total fauna or < 0.1 individuals per sample. - = not present. Site codes as in Table 3.4, raw collection data in Appendix 4. (*Plumatella repens* was recorded as present at every site but was not quantified.)

Taxa	SITES																					
	NE 2		SI		SM		EE 1		EE 2		EI		EM		ER		WE 1		WF 2		WE 3		WE 4		WI	
COELENTERATA																										
Chlorohydra viridissima	3.1	(11.1)	2.3	(5.3)	0.8	(3.1)	8.1	(42.7)	9.0	(35.0)	2.6	(3.9)	9.4	(16.3)	1.3	(2.0)	1.4	(6.1)	22.9	(80.2)	49.3	(300.9)	49.8	(267.2)	1.0	(4.8)
PLATYHELMINTHES																										
Cura pinguis	0.1	(0.4)	0.3	(0.6)	0.1	(0.4)	0.4	(2.0)	0.3	(1.0)	0.5	(0.7)	0.4	(0.6)	0.1	(0.2)	0.1	(0.6)	0.1	(0.4)	0.2	(0.9)	0.1	(0.7)	1.1	(4.9)
NEMATODA	0.3	(1.0)	1.2	(2.6)	0.5	(1.8)	0.1	(0.5)	0.1	(0.4)	0.3	(0.5)	0.1	(0.1)	0.1	(0.2)	0.5	(2.2)	0.1	(0.2)	-	-	-	-	1.4	(6.6)
OLIGOCHAETA (except *Chaetogaster*)	5.2	(18.3)	7.4	(16.8)	1.0	(4.0)	0.8	(4.0)	1.9	(7.3)	0.4	(0.6)	*	(0.1)	0.3	(0.5)	7.7	(34.9)	6.1	(21.5)	0.9	(5.3)	0.5	(2.4)	1.0	(4.7)
Chaetogaster sp.	1.4	(5.0)	2.1	(4.8)	1.4	(5.2)	0.2	(1.0)	0.3	(1.0)	0.3	(0.5)	1.7	(2.9)	0.2	(0.3)	6.0	(27.3)	2.0	(7.2)	2.2	(13.2)	3.5	(18.7)	1.5	(6.9)
HIRUDINEA																										
Glossiphonia multistriata	0.1	(0.3)	*	(*)	-	-	*	(0.2)	-	-	-	-	-	-	-	-	-	-	-	-	*	(0.1)	-	-	-	-
Placobdella maorica	*	(*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRUSTACEA																										
Cladocera	8.0	(28.5)	8.1	(18.3)	4.8	(18.6)	0.6	(3.2)	1.0	(4.0)	5.4	(8.0)	2.8	(4.8)	1.1	(1.7)	7.6	(39.4)	8.6	(30.0)	9.2	(56.3)	3.2	(17.1)	5.8	(26.8)
Ostracoda	*	(*)	0.3	(0.6)	0.9	(3.6)	0.8	(4.2)	0.7	(2.6)	0.8	(11.7)	0.1	(0.2)	0.2	(0.3)	1.0	(4.3)	*	(*)	*	(0.3)	0.1	(0.4)	6.2	(28.3)
Copepoda																										
Eucyclops serrulatus	18.4	(65.3)	3.8	(8.7)	3.4	(13.0)	6.2	(32.7)	6.5	(25.5)	23.4	(34.8)	5.0	(8.7)	5.2	(8.2)	8.3	(37.0)	9.0	(31.7)	11.4	(69.8)	7.9	(42.1)	12.8	(58.6)
INSECTA																										
Ephemeroptera																										
Deleatidium sp.	-	-	*	(*)	-	-	-	-	-	-	0.1	(0.1)	-	-	-	-	*	(0.1)	-	-	-	-	-	-	-	-
Odonata																										
Procordulia grayi	*	(*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	(0.1)	-	-
Xanthocnemis zealandica	*	(*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	(0.8)	0.1	(0.3)	*	(0.2)	-	-	-	-
Plecoptera																										
Zelandobius furcillatus	-	-	0.1	(0.2)	*	(0.1)	-	-	-	-	0.2	(0.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera																										
Diaprepocoris zealandiae	*	(*)	0.1	(0.2)	0.1	(0.2)	*	(0.2)	0.1	(0.3)	0.1	(0.1)	-	-	-	-	-	-	*	(*)	-	-	-	-	-	-
Sigara arguta	*	(*)	-	-	*	(0.1)	-	-	-	-	-	-	0.1	(0.1)	0.1	(0.2)	-	-	-	-	*	(0.2)	-	-	-	-
Coleoptera																										
Antiporus strigosulus	-	-	-	-	-	-	*	(0.2)	-	-	0.1	(0.1)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera																										
Oxyethira albiceps	-	-	0.1	(0.3)	-	-	-	-	-	-	-	-	-	-	-	-	0.2	(0.8)	-	-	-	-	-	-	*	(0.1)
Paroxyethira hendersoni	0.9	(3.1)	3.8	(8.6)	3.0	(11.7)	0.5	(2.5)	0.2	(0.8)	2.4	(3.6)	3.2	(5.5)	0.2	(0.3)	0.8	(3.8)	0.8	(2.8)	0.4	(2.2)	0.3	(1.7)	5.5	(25.0)
P. tillyardi	*	(*)	*	(*)	-	-	0.9	(4.8)	0.6	(2.4)	1.1	(1.7)	1.4	(2.5)	3.1	(4.8)	0.1	(0.2)	0.1	(0.2)	-	-	0.1	(0.3)	0.3	(1.4)
Pycnocentrodes aureola	-	-	-	-	0.2	(0.9)	*	(0.2)	*	(0.1)	0.1	(0.2)	-	-	-	-	*	(0.1)	-	-	-	-	-	-	-	-
Triplectides cephalotes	*	(*)	0.1	(0.3)	0.3	(1.2)	-	-	-	-	-	-	0.1	(0.1)	-	-	0.1	(0.3)	*	(*)	-	-	-	-	0.2	(0.8)
T. obsoleta	-	-	-	-	*	(0.1)	-	-	*	(*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hudsonema amabilis	*	(*)	-	-	0.1	(0.4)	*	(0.2)	0.2	(0.9)	0.3	(0.5)	0.6	(1.0)	0.5	(0.8)	*	(0.1)	-	-	-	-	-	-	-	-
Oecetis unicolor	-	-	0.1	(0.2)	-	-	-	-	-	-	-	-	-	-	-	-	*	(0.1)	-	-	-	-	-	-	-	-
Oe. iti	-	-	*	(*)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	(0.1)
Lepidoptera																										
Nymphula nitens	-	-	*	(*)	0.3	(1.0)	0.1	(0.3)	*	(0.1)	0.1	(*)	0.6	(1.1)	-	-	-	-	-	-	-	-	-	-	0.1	(0.3)
Diptera																										
Chironomidae	0.8	(2.8)	5.2	(11.7)	6.0	(23.3)	0.4	(1.8)	0.5	(2.0)	3.3	(4.8)	1.4	(2.5)	1.3	(2.0)	2.5	(11.4)	1.3	(4.6)	1.2	(7.2)	1.1	(5.8)	3.3	(15.2)
Acari																										
Arrenurus n.sp.	-	-	-	-	-	-	-	-	*	(*)	-	-	-	-	-	-	*	(0.1)	*	(*)	-	-	-	-	*	(0.1)
Piona uncata exigua	1.8	(6.3)	0.9	(2.1)	0.5	(1.8)	1.7	(9.0)	2.0	(7.7)	1.0	(1.5)	2.0	(3.5)	2.3	(3.7)	0.5	(2.4)	1.9	(6.7)	0.8	(5.0)	0.9	(4.7)	0.4	(2.0)
Hydrozetes lemnae	0.9	(3.1)	4.5	(10.2)	2.2	(8.7)	2.3	(12.0)	1.4	(5.5)	4.3	(6.3)	4.7	(8.2)	5.7	(9.0)	0.5	(2.3)	0.8	(2.7)	1.2	(7.3)	1.7	(9.2)	3.4	(15.3)
Trimalaconothrus novus	0.5	(1.9)	0.3	(0.7)	0.9	(3.6)	0.3	(1.5)	0.1	(0.3)	3.4	(5.0)	0.3	(0.5)	0.4	(0.7)	0.2	(0.6)	0.2	(0.8)	0.1	(0.7)	0.8	(4.3)	4.0	(4.3)
Mollusca																										
Gyraulus corinna	10.7	(38.0)	8.1	(18.3)	5.7	(22.1)	0.7	(3.7)	1.9	(7.3)	1.5	(2.2)	0.8	(1.3)	1.0	(2.2)	9.3	(42.3)	7.4	(26.1)	3.7	(22.4)	5.2	(27.7)	5.0	(23.0)
Physastra variabilis	-	-	-	-	-	-	-	-	0.1	(0.2)	0.1	(*)	0.1	(0.1)	-	-	-	-	-	-	-	-	-	-	-	-
Potamopyrgus antipodarum	47.7	(169.2)	50.5	(113.8)	67.7	(262.7)	75.5	(398.3)	72.7	(283.0)	48.3	(71.8)	65.5	(113.9)	76.9	(189.8)	52.9	(240.2)	38.5	(134.9)	19.3	(117.4)	25.0	(134.3)	45.3	(207.8)
Sphaerium novaezelandiae	-	-	0.6	(1.3)	0.1	(0.6)	0.4	(2.3)	0.4	(1.5)	0.1	(*)	-	-	0.1	(*)	0.2	(0.7)	0.1	(0.2)	0.1	(0.2)	-	-	1.4	(6.3)

3.3.3 Known Habitat Requirements of Some Freshwater Invertebrates

The purpose of this section is to review previous knowledge of the habitat requirements of many of the species collected in quantitative samples from Lake Grasmere, in order to provide a background for interpretation of the association of species in species groups (see p. 52).

PLATYHELMINTHES

Cura pinguis, a triclad, is found under stones, on plants, in ponds with muddy bottoms and in stable rivers (Nurse 1950) and also on dense submerged macrophyte beds in lakes (Winterbourn & Lewis 1975).

ANNELIDA

Oligochaeta

Lumbriculus variegatus and *Eiseniella tetraedra* have been recorded from macrophyte zones in other lakes in New Zealand (Winterbourn & Lewis 1975) and the former was the most abundant oligochaete in the mud below the macrophyte zone of Lake Grasmere (Jamin 1976, Timms in prep.). *L. variegatus* is known from a wide range of habitats but favours quiet reaches of flowing waters and ponds with silt, mud and roots in the littoral zone (Pickavance 1971). A *Lumbriculus*-dominated community is not considered indicative of organically polluted conditions (Brinkhurst 1965) but rather of waters supporting abundant submerged vegetation and/or a substrate of sand, silt, gravel or coarse detritus (Winterbourn & Stark 1978). The naidid oligochaete, *Chaetogaster* sp., is represented in the psammon (= fauna and flora living in interstitial water between grains of sand in the substrate) (Winterbourn & Lewis 1975) but may be found in the mantle cavity of *Gyraulus* sp. (near Dunedin especially, according to Marples 1962).

CRUSTACEA

Cladocera

Bosmina meridionalis is a filter-feeding planktonic cladoceran found in many lakes and reservoirs throughout New Zealand. *Graptoleberis testudinaria* on the other hand is characteristic of macrophytic habitats where it glides over stems and leaves, grazing on bacteria and small particles on their surfaces (Lewis 1976). *Alona guttata* is characteristic also of macrophyte zones (Stout 1975a, Winterbourn & Lewis 1975). *Chydorus sphaericus* has similar habits to *G. testudinaria* except that it feeds on filamentous algae and is not infrequently recorded from the open-water plankton (Lewis 1976). *Ceriodaphnia dubia* is found in most lakes and ponds throughout New

Zealand and is regarded as planktonic. *Ilyocryptus sordidus* is a cosmopolitan macrothricid cladoceran that has a truly benthic habit living in soft bottom deposits of ponds and lakes, and *Neothrix armata* frequents similar habitats although it has been recorded only in benthic samples from several lakes in the Rotorua (North Island) district (Lewis 1976) prior to this record.

Ostracoda

Six species of ostracods were identified from Lake Grasmere. All are characteristic of benthic (*Scottia insularis, Herpetocypris pascheri, Prionocypris marplesi, Gomphocythere duffi* and *Darwinula repoa*) or macrophytic habitats (*Cypridopsis vidua* and *D. repoa*) (Chapman 1976).

Copepoda

Eucyclops serrulatus, an herbivorous cyclopoid copepod that creeps over macrophyte stems or benthic substrates, was the only copepod recorded from quantitative samples. It is known from lakes, ponds, rivers, and even brackish waters in coastal situations (Chapman & Lewis 1976).

INSECTA

Ephemeroptera

The leptophebiid mayfly *Deleatidium* sp., probably New Zealand's most common aquatic insect genus, is widespread in streams and rivers and is found also in lakes on wind-exposed shores (Penniket 1969, Winterbourn & Lewis 1975, Greig 1976). The taxonomy of *Deleatidium* spp. is most uncertain.

Odonata

Austrolestes colensonis is common in small pools and swamps and may be found at the edges of lakes where there are plant species suitable for oviposition. It is not found in habitats where there is significant water movement or wave action (Crumpton 1975, 1977). *Xanthocnemis zealandica* is found in similar habitats to *A. colensonis* and is distributed widely in New Zealand. It is associated usually with aquatic vegetation and, unlike *A. colensonis*, may be found in slow-flowing streams (Crumpton 1977). Within-habitat distribution of *X. zealandica* is patchy in heterogeneous environments (e.g., *Typha* beds, Lake Sarah) but more even in uniform habitats (e.g., Isaac's Pond) (Deacon 1979). The endemic anisopteran, *Procordulia grayi*, is fairly widespread in bottom sediments of ponds and lakes both in the Canterbury high-country, and in lowland areas of Canterbury and Westland (Crumpton

1977). More generally, larvae may be found in suitable habitats in New Zealand south of the Waikato (North Island) in lakes, ponds and occasionally deep rivers. Small larvae frequent deep water (3 m +) whereas later instars occur nearer the shore (R.J. Rowe, pers. comm.).

Plecoptera

The only stonefly recorded in quantitative samples, *Zelandobius furcillatus*, has been recorded from open stable streams and, like *Deleatidium*, wind-exposed lake shores (Stout 1977).

Hemiptera

Sigara arguta is the most common corixid in New Zealand and is found in most still waters, such as in sheltered places in large lakes, along margins of estuaries (sometimes brackish), in ponds and in slack-water areas of rivers and streams (except those in the South Island with shingle beds) (Young 1962). In lakes and large ponds it is often associated with *Diaprepocoris zealandiae*. *D. zealandiae* is common in high country lakes of the South Island and in larger ponds, lagoons, and canals in coastal areas. It is less common in slow water areas of deep streams. The presence of aquatic macrophytes (especially *Elodea*, *Myriophyllum* or *Ranunculus*) or *Typha* beds are an essential feature of its habitat and the water must be more than 0.3 m deep, at least in places (Young 1962).

Coleoptera

The only dytiscid in quantitative samples, *Antiporus strigosulus*, has been recorded mostly from ponds, tarns, and among vegetation in lakes (Stout 1969b, 1977), temporary rainwater ponds and some streams (Ordish 1966). The genus (as unidentified larvae) has been found also in thermal waters of Lake Rotowhero up to 34°C (Winterbourn 1968).

Diptera : Chironomidae (see Chapter VI)

Trichoptera (see Chapter VI for Family Hydroptilidae)

Cowley (1978) stated that the sericostomatid caddisfly *Pycnocentrodes aureola* was found on rocks in streams, although he did examine some material from the rocky shore of Lake Grasmere. Since the larval case is always made of small stones and sand (and is relatively heavy for the size of the larva), the larva must be associated with substrates including fine mineral particles.

Five species of leptocerid caddisflies were collected from macrophytic habitats of Lake Grasmere but only three were common. *Oecetis unicolor* was first studied by Babington (1967) in Lake Rotorua

(North Island) where it was found in water up to 0.6 m deep living in the upper 6 - 7 mm of sand on the bottom, and also in loosely-growing macrophytes close to the substrate. It is common in many lakes that have clean sandy areas of beach and it occurs also in rivers and streams in similar habitats (Cowley 1978). M.L. Ling (pers. comm. to Cowley 1978) recorded its presence in the Ohau Channel between Lakes Rotorua and Rotoiti in water up to 2 m deep where there was moderate water flow and Timms (1980) recorded it down to 46 m in Lake Rotoiti (South Island).

Hudsonema amabilis is probably the most widespread of the leptocerid caddisflies found in New Zealand. It is present in rivers and streams and also in lakes especially (but not exclusively) near the shore where there is some wave action, and near inlet or outlet streams (Cowley 1978) but may occur at greater depths (e.g., down to 20 m in Lake Rotoroa, Nelson lakes, South Island (Timms 1980)).

One of the largest leptocerids in New Zealand is *Triplectides cephalotes*, which is one of the most common still-water caddisflies in the country. It is found throughout New Zealand in lakes that have suitable macrophyte zones but is absent from high-altitude tarns. It is known also from temporary ponds and neglected (?) swimming pools (Cowley 1978). Babington (1967) noted that in the macrophyte zone of Lake Rotorua (North Island), larvae were most common in water less than 1 m deep on plants less than 0.3 m high. However, B.T. Coffey (pers. comm. to Cowley 1978) observed *T. cephalotes* larvae on *Lagarosiphon* down to a depth of 6 m in the Nelson lakes (South Island) and Timms (1980) recorded it down to 21 m in Lake Rotoroa and 12 m in Lake Rotoiti (Nelson lakes).

Lepidoptera

Nymphula nitens, New Zealand's only moth with an aquatic larva, is almost always associated with macrophytes (Marples 1962) although it has been recorded from benthic habitats (Forsyth 1978, Timms 1980 and in prep.). In these benthic situations, macrophytes must have been nearby because the larva is an obligate herbivore (feeding on living plant material) (see Chapter IV). This species is widespread in New Zealand and is present also in South Australia (Pendergrast & Cowley 1966).

ACARI

Piona uncata exigua is the most commonly occurring water mite in New Zealand and is usually found in small lakes or large ponds. This

species has strong swimming setae on its legs and, unlike most other aquatic mites, may be well represented in the plankton (Stout 1969a).

Hydrozetes lemnae is an aquatic oribatid (= cryptostigmatid) mite that inhabits rootlets, stems and leaf sheaths of aquatic plants. The Group Oribatei comprises mostly non-predatory mites that feed only on dead moss or macrophyte tissue (i.e., mycophages or saprophages) in moist to submerged habitats (Krantz and Lindquist 1979). This particular species is widespread in New Zealand (Dr G.W. Ramsay pers. comm.) and one of the few published records is from the outflow channels of hot springs near the Hurunui River (Canterbury, New Zealand) at temperatures up to 41°C (Stark, Fordyce & Winterbourn 1976). Another oribatid, *Trimalaconothrus novus*, has been recorded from localities near Queenstown and Dargaville (Dr G.W. Ramsay pers. comm.) and hot springs near the Hurunui River (Stark, Fordyce & Winterbourn 1976). Members of this genus are known to feed on green plants and are common on mosses in moist, semi-aquatic or submerged habitats (Krantz & Lindquist 1979). In the hot springs, *T. novus* was found in association with the blue-green algal mat up to 41°C. In general however aquatic oribatids in New Zealand, although found in a variety of habitats, have been little studied (Stout 1976).

MOLLUSCA

Gastropoda

Gyraulus corinna, the most common planorbid mollusc in New Zealand freshwaters, is an endemic species but little is known about it. *G. kahuica*, regarded by some (e.g., Ponder pers. comm. to Winterbourn 1973) as a subspecies of *G. corinna*, acts as an intermediate host for larval trematodes (Winterbourn 1973).

Physastra variabilis has a wide distribution in still waters in New Zealand but rarely is common. It is particularly sparse in the vicinity of towns and in water bodies that are influenced by man's activities. *P. variabilis* is most common in lakes and ponds in remote areas, but seems to be unable to compete effectively with the closely related *Physa* sp. which has replaced it in certain habitats (Winterbourn 1973).

Potamopyrgus antipodarum, a hydrobiid gastropod, is certainly the most common and widespread of New Zealand's freshwater molluscs and is found in almost all kinds of fresh waters except temporary ponds. It also inhabits brackish waters (Winterbourn 1970b, 1973).

Bivalvia

Sphaerium novaezelandiae is the most common sphaeriid clam in New Zealand and may be found in mud from both vegetated and unvegetated areas of lakes as well as in streams that have suitable substrates (Winterbourn 1973).

3.3.4 Invertebrate Community Relationships

(1) Invertebrate communities on different macrophytes

The invertebrate communities found on four species of submerged aquatic macrophyte were examined during the quantitative sampling program: the adventives *Elodea canadensis* (142 samples) and *Ranunculus fluitans* (10), and the endemics *Isoetes alpinus* (42) and *Myriophyllum propinquum* (19) (see Mason 1975). Thirty-seven invertebrate taxa were recognised.

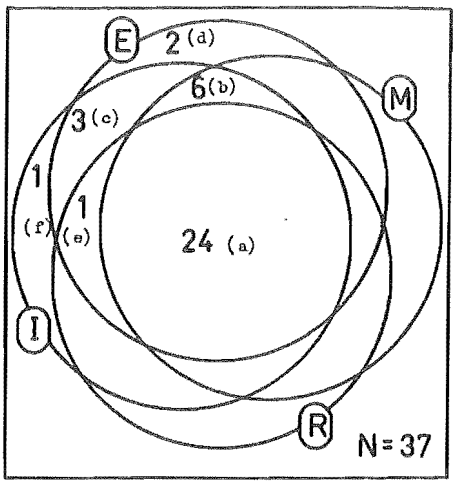
Only 25 invertebrate taxa (Fig. 3.1) were collected in samples of *R. fluitans* and these taxa (with the exception of *Xanthocnemis zealandica* (e)) were present also on the three other macrophytes.

Thirty-six invertebrate taxa were collected from samples of *E. canadensis* (Fig. 3.1). The *E. canadensis* zones comprised about 90% of the macrophyte-covered area of Lake Grasmere and, therefore, provided a very extensive habitat for invertebrates. *Oecetis iti* (which was found only on *Isoetes*) was the only species not recorded from *E. canadensis* and *Placobdella maorica* and *Procordulia grayi* were unique to it. These last two species were found only occasionally and their apparent absence from other plants may reflect the fewer samples collected from other macrophytes.

I. alpinus was the habitat of 35 taxa, lacking only the two species unique to *E. canadensis* (d, Fig. 3.1). However, many of the taxa recorded from this plant were not common on it (groups b, c, d, e and f, Fig. 3.1) (see also Table 3.8).

The fauna collected from *M. propinquum* (30 taxa) comprised only the 24 taxa shared by all four macrophytes and six shared with *Elodea* and *Isoetes*.

The proportion of insects in those groups not present in communities on all macrophytes (b - f, Fig. 3.1) was high, suggesting that the insects had quite specific habitat requirements (at least in terms of macrophyte preferences).



(a) *Chlorohydra viridissima*
Cura pinguis
Plumatella repens
NEMATODA
OLIGOCHAETA
Chaetogaster sp.
Glossiphonia multistriata
CLADOCERA
OSTRACODA
Eucyclops serrulatus
Sigara arguta
Diaprepocoris zealandiae
Oxyethira albiceps
Paroxyethira tillyardi
P. hendersoni
Hudsonema amabilis
Nymphula nitens
CHIRONOMIDAE
Piona uncata exigua

Hydrozetes lemnae
Trimalaconothrus novus
Gyraulus corinna
Potamopyrgus antipodarum
Sphaerium novaezelandiae

(b) *Antiporus strigosulus*
Zelandobius furcillatus
Pycnocentrodes aureola

Triplectides cephalotes
Oecetis unicolor
Physastra variabilis

(c) *Deleatidium* sp.
Triplectides obsoleta

Arrenurus sp.

(d) *Placobdella maorica*

Procordulia grayi

(e) *Xanthocnemis zealandica*

(f) *Oecetis iti*

Fig. 3.1 Venn diagram of the distribution of invertebrate taxa among the four most abundant macrophyte species in Lake Grasmere. Data from quantitative samples (April 1976 - October 1977). Numbers of samples; *E. canadensis* = 142, *I. alpinus* = 42, *M. propinquum* = 19 and *R. fluitans* = 10.

The units of invertebrate density used to compare communities on different macrophytes (or even on the same macrophyte between times) can have a marked effect on comparisons and subsequent interpretation (Fig. 3.2). When total invertebrate density was expressed as numbers/m^2 of lake bottom ((a) Fig. 3.2) *E. canadensis* appeared to represent the most productive habitat, followed by *Myriophyllum* and *Isoetes*. *Elodea* tended to grow in the densest beds, whereas the growth of *Myriophyllum* was much more open. *Isoetes* could reach high stem densities but was more often clumped and the inclusion of benthic invertebrates in samples was significant.

When densities were expressed as numbers/g (dry wt) of macrophyte ((b) Fig. 3.2) the highest values were found on *Isoetes* because this macrophyte had a lower biomass per sample than either *Elodea* or *Myriophyllum* but invertebrate numbers were not decreased

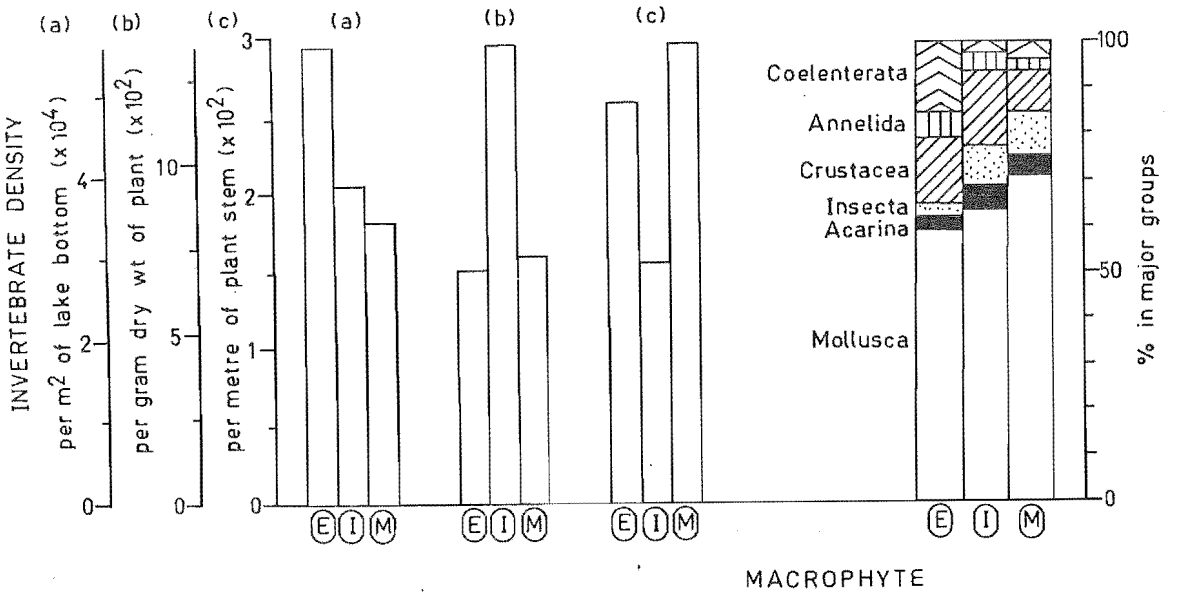


Fig. 3.2 Invertebrate density and community composition (%) from samples of *Elodea canadensis* (E) 143 samples, *Isoetes alpinus* (I) 42 samples and *Myriophyllum propinquum* (M) 19 samples collected from Lake Grasmere between April 1976 and October 1977.

proportionately. In addition, since *Isoetes* stem lengths were short, invertebrates characteristic of benthic habitats probably were included in samples. *Elodea* and *Myriophyllum*, which had similar general growth forms, harboured communities of similar density.

The third measure of invertebrate density, numbers per length (metres) of plant stem ((c) Fig. 3.2) altered the ranking once again. In this case the order of increasing invertebrate was reflected by available area of plant surface, especially as a substrate for grazers on 'Aufwuchs' (= diatoms, etc., on plant surfaces). *Myriophyllum*, with its finely divided leaves (cf. *Elodea*) presented the greatest surface area, and *Isoetes*, with erect, spike-like leaves crowded on short stem bases, the least. There was a good relationship between numbers of invertebrates/g (dry wt) of macrophyte and numbers per length of plant stem for macrophytes of similar growth form (i.e., *Elodea* and *Myriophyllum*, but not *Isoetes*).

Total invertebrate densities on *R. fluitans* are not shown in Fig. 3.2 because only ten quantitative samples were collected during the pilot survey and main quantitative sampling program and the lengths of stems were too difficult to measure accurately. The limited information available suggests that invertebrate densities on *Ranunculus* were less than on the other plants both in terms on numbers/m^2 of lake bottom (3.2×10^4) and numbers/g (dry wt) of macrophyte (5.3×10^2).

The most valid density units to use depends upon the aims of any investigation (together with practical considerations). For example, if the aim was to determine the total population of a taxon in a particular habitat it would be best to use units such as numbers/m^2 of lake bottom. This would enable total numbers to be estimated by multiplying the density, expressed as above, by the area of habitat. However, for comparison of densities of invertebrates between different species of macrophytes it is better to use units that are based on a property of the particular plant species such as numbers/unit weight of macrophyte, numbers/unit length of macrophyte stem or numbers/surface area of macrophyte. As can be seen in Fig. 3.2 the comparison of densities of invertebrates on the different macrophytes is extremely dependent upon the units used. Numbers/g (dry wt) of macrophyte (e.g., Fig. 3.9) are preferred for comparison of invertebrate communities on different macrophytes since differences in invertebrate abundances between plants are more easily interpreted in these units.

The percentage taxonomic composition of invertebrate communities present on any species of macrophyte is, of course, independent of the units of density when invertebrate densities are numerically based (cf. biomass of invertebrates basis). Mollusca were the most numerous major group on all macrophytes examined (Fig. 3.2), especially on *R. fluitans**, but none of the invertebrate communities contained the other major taxa in the same order of rank. Coelenterata formed a higher proportion of the invertebrate communities on *E. canadensis* (15.4%) (especially at sites in the western sampling area) than on other plants. Crustacea were the only other group to contribute more than 10% to the invertebrate communities on any of the macrophytes (*Elodea* and *Isoetes* Fig. 3.2). Insecta comprised a markedly larger percentage of the fauna on native compared with adventive macrophytes (Fig. 3.2 *). The densities of insects/m^2 of lake bottom on *Isoetes* and *Myriophyllum* were 2.4 times greater than on *Elodea*, and on *Ranunculus* only 0.7 times that on *Elodea*. Densities in terms of numbers of invertebrates/g (dry wt) of macrophyte were 6.6 times (*Isoetes*), 4.0 times (*Myriophyllum*) and 0.9 times (*Ranunculus*) the density on *Elodea*; and in terms of insects/m of plant stem 2.0 times (*Isoetes*) and 4.4 times (*Myriophyllum*). The native macrophytes therefore were strongly colonised by insects in Lake Grasmere despite their limited distributions.

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* *Ranunculus fluitans*; Coelenterata 0.7%, Annelida 0.5%, Crustacea 4.1%, Insecta 2.9%, Acarina 5.1%, Mollusca 86.6%.

Trichoptera (especially Hydroptilidae) and Chironomidae together comprised 92.0% (*Elodea*), 97.6% (*Isoetes*), 94.7% (*Myriophyllum*) and 94.4% (*Ranunculus*) of the insects on each of the four species of macrophyte (Appendices 1 and 2.8). Acarina were better represented on macrophytes other than *Elodea*, but the apparent occurrences of Annelida and Crustacea on plants were probably enhanced by inclusion, in samples, of benthic and planktonic animals respectively

(2) Invertebrate communities at different depths

Quantitative samples of invertebrates on submerged aquatic macrophytes were collected from lake water depths ranging from 1 - 4 m. The numbers of taxa present at each of the four depths are depicted in Fig. 3.3.

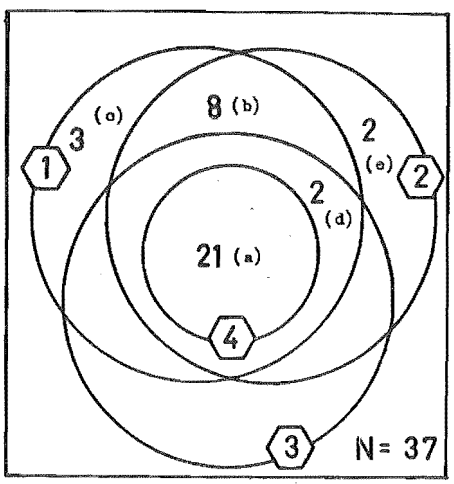
(a) *Chlorohydra viridissima*
Cura pinguis
Plumatella repens
OLIGOCHAETA
Chaetogaster sp.
CLADOCERA
OSTRACODA
Eucyclops serrulatus
Xanthocnemis zealandica
Diaprepocoris zealandiae
Paroxyethira hendersoni
Paroxyethira tillyardi
Triplectides cephalotes
Oxyethira albiceps
Nymphula nitens
CHIRONOMIDAE
Piona uncata exigua
Hydrozetes lemnae
Trimalaconothrus novus

(b) NEMATODA
Antiporus strigosulus
Pycnocentrodes aureola
Triplectides obsoleta

(c) *Deleatidium* sp.
Zelandobius furcillatus

(d) *Glossiphonia multistriata*

(e) *Placobdella maorica*



Gyraulus corinna
Potamopyrgus antipodarum
Sphaerium novaezelandiae

Hudsonema amabilis
Oecetis unicolor
Arrenurus sp.
Physastra variabilis

Oecetis iti

Sigara arguta

Procordulia grayi

Fig. 3.3 Venn diagram of the distribution of invertebrate taxa collected in quantitative samples of submerged aquatic macrophytes from four depths in Lake Grasmere (April 1976 - October 1977). Numbers of samples collected = 1 m 94, 2 m 101, 3 m 9 and 4 m 9.

Of 37 taxa, 22 were recorded from all depths sampled, but only 17 of these were found on all macrophytes examined (Fig. 3.1). These comprised the 13 species that occurred at every *site* sampled plus *P. repens, P. tillyardi, S. novaezelandiae* and *O. albiceps*. There was a general decline in numbers of taxa with depth. At 1 m, 35 taxa were recorded, including the species characteristic of stream-like environments (e.g., *Deleatidium* sp. and *Z. furcillatus*) or sandy substrates (*Oecetis iti*) which were unique to this depth. Eight taxa were shared by 1 m and 2 m and two by 1 m, 2 m and 3 m. Only two taxa were not collected in samples from 1 m (*P. maorica* and *P. grayi*) and these, relatively rare, species were found only in *Elodea* samples from 2 m depth. Their apparent absence from other depths may be a consequence of their rarity combined with decreased sampling effort at depths other than 2 m. Nearly 50% of all quantitative samples were collected from this depth (Table 3.6). Despite low numbers of quantitative samples collected from 3 m and 4 m (all in the *Elodea* zone), the lower numbers of taxa (22 and 24, Fig. 3.3) collected reflect the true situation as indicated by extensive non-quantitative sampling using a 200 µm mesh hand-net in these habitats.

Considerable changes in invertebrate density and community composition occurred with depth in the *Elodea* zone in the western sampling area (Fig. 3.4). Invertebrate communities were dominated by molluscs (1 - 2 m) and *Chlorohydra* (3 - 4 m) with Crustacea the next most common group. Other salient features were the relatively minor contributions of Insecta and Acarina at all depths (1.2 - 5.2%) and the relatively similar percentage representation of Crustacea (16.8 - 18.5%) over the depth range 1 - 3 m. *C. viridissima* densities were highest where *Elodea* was growing in water 3 m deep (although the *Chlorohydra* on plant stems could be as close to the surface as 1 m). The seasonal peak in abundance of *Chlorohydra* (8 April 1977) was correlated with the maximum Secchi Disc reading (5.0 m) obtained during the study. Increased water transparency and consequent increased light penetration at this time may enhance the production of the symbiotic zoochlorellae (which give *Chlorohydra* its green colour) and hence boost *Chlorohydra* abundance. Maximum values of water transparency (Secchi Disc reading *ca.* 8.2 m) have been recorded in previous years in April and May (Stout 1972). Low light penetration (i.e., low Secchi Disc readings) in other months probably limits *Chlorohydra* abundance. Densities of Annelida, Insecta and Mollusca showed a general decrease with depth as fewer animals with bottom-dwelling habits were included in samples and periphyton levels on

plant surfaces diminished. Qualitative differences in periphytic coatings were easily assessed visually or by the slimy nature of the plant surfaces (see also Chapter IV, p. 87).

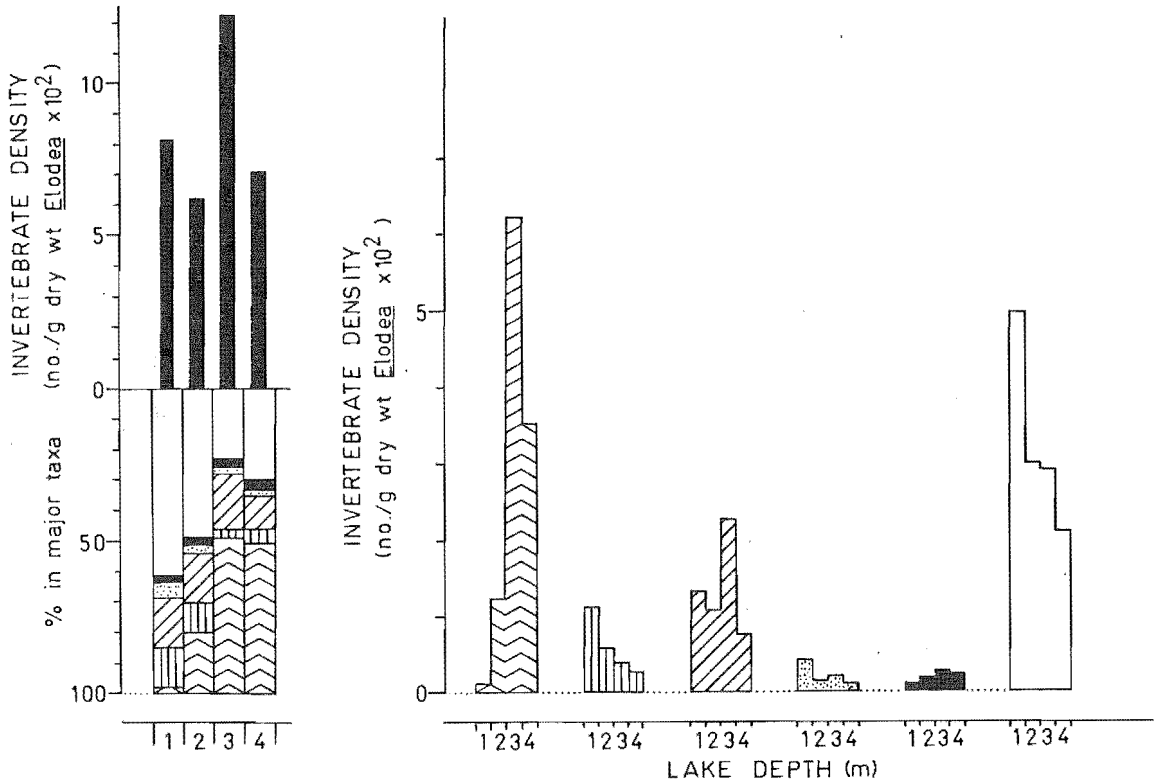


Fig. 3.4 Total invertebrate density, percentage composition of community in terms of major taxa, and changes in abundance of major taxa between 1 m and 4 m (lake depth) in the *Elodea canadensis* zone in the western sampling area of Lake Grasmere (April 1976 - October 1977). (Numbers of samples: 1 m = 9, 2 m = 34, 3 m = 9, 4 m = 9.)

(3) Site groups and species groups

(a) Introduction. Thirty-seven invertebrate taxa were recognised in quantitative samples from 13 sites in the macrophyte zone of Lake Grasmere (Table 3.9). In order to simplify the analysis of the factors affecting associations of invertebrates with macrophyte species and with other habitat characteristics (e.g., substrate, depth and wave exposure) it was necessary to reduce the number of possible comparisons. I decided to use a clustering method of data reduction aimed at aggregating sites with similar invertebrate communities into groups (site groups) and creating species groups consisting of taxa that showed similar site preferences. This treatment decreases the number of comparisons required for determination of factors affecting community

composition and (since data from individual sites are combined) provides a more substantial data base for comparative analyses.

Cluster analysis is a numerical method of classification in which entities (such as sampling sites) are grouped according to the similarity of the attributes (for example, species) associated with each entity. In this type of classification, the groups of similar entities are related to one another by a two-dimensional hierarchical tree structure called a dendrogram (e.g., Figs. 3.5 and 3.6). A dendrogram is defined as a diagrammatic illustration of relationship based upon degree of similarity or dissimilarity where the level of branching indicates relative similarity or dissimilarity. In addition to depicting relationship between entities, the order of the entities should correlate with a gradient of some kind. In a dendrogram such as Fig. 3.5 the order of sites may be correlated with, for example, a gradient of substrate type, wave exposure, or macrophyte growth form.

Many different similarity/dissimilarity measures and/or clustering strategies are available and dendrograms resulting from their use may differ markedly according to the procedures adopted (see Clifford & Stephenson 1975).

The choice of methods is often related to the nature of the data. Ecological data with many zero entries and a few outstandingly high entries suggest transformation (for example, $\log_{10}$ (n + 1)), use of the Bray-Curtis dissimilarity measure and a flexible or group average sorting strategy. The final choice of methods depends upon how the data can be interpreted usefully by the biological user and thus to a large extent the 'best' methods to use are those that result in 'sensible' classifications. The effectiveness of a classification may be considered in two ways: the first is whether or not the clusters comprise like grouped with like on the basis of intrinsic data (i.e., data used in dendrogram formation, such as species' abundances and distributions) and the second depends upon the extent to which groupings obtained by intrinsic data reflect extrinsic attributes (e.g., environmental features).

(b) Data processing. For the purposes of computer analyses, five species (*Plumatella repens, Placobdella maorica, Procordulia grayi, Triplectides obsoleta* and *Oecetis iti*) were not considered since they were either not quantified (*P. repens*) or were represented in quantitative samples by only one or two specimens (Appendix 2). Five further taxa (Oligochaeta, Nematoda, Cladocera, Ostracoda and

Chironomidae) were not identified to species due to taxonomic shortcomings at the time of the analyses.

A species X sites matrix or two-way table (similar to Table 3.9; containing species densities as numbers of invertebrates per sample summed over all sampling dates) was constructed using information collected during the quantitative sampling program (September 1976 - October 1977) (Appendix 2). To facilitate cluster analyses, because attribute values (i.e., individual invertebrate species' abundances) covered a wide range (between 0 and about 400 individuals per sample, Table 3.9) this matrix was transformed using a $\log_{10}$ (n + 1) transformation. Dendrograms depicting the degree of association of site groups (Fig. 3.5) and species groups (Fig. 3.6) were derived with the aid of Professor W. Stephenson (University of Queensland, Australia) using the Bray-Curtis dissimilarity measure and a group fusion sorting strategy.

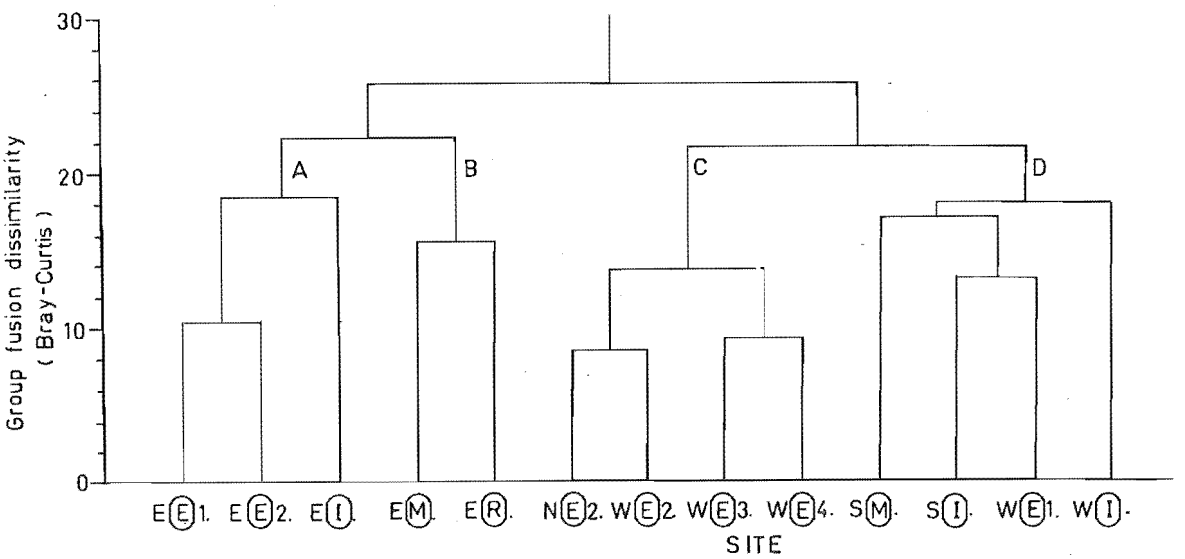


Fig. 3.5 Site group dendrogram. (All quantitative samples combined, September 1976 - October 1977).

The Bray-Curtis measure, which is considered desirable where differences in species dominance and zeros (i.e., species absence) are involved, defines the dissimilarity of two sites (or individuals) as

$$\frac{\sum_{1}^{n} | x_{1j} - x_{2j} |}{\sum_{1}^{n} (x_{1j} + x_{2j})}$$

where n is the number of attributes (for example, species) x_{1j} and x_{2j} are the values (for example, sites) (Clifford & Stephenson 1975).

Various attempts have been made to replace, with tests of significance, personal judgments of the results of classification. These tests, which are of four main types, are open to criticism on theoretical grounds, but in practice tend to confirm common sense judgments (see Clifford & Stephenson 1975, for more complete discussion). The 'pseudo F test' (Prof. W. Stephenson, pers. comm.) was used to find out which species 'conformed noticeably' (see Stephenson, Williams & Cook 1974) to their site groups by applying the test to the rows of a species X sites two-way table. Species that 'conform noticeably' to their site groupings usually are characterised by marked differences in numerical dominance and/or constancy of occurrence in different site groups.

(c) Site groups. The associations of sites, in terms of their invertebrate communities are depicted in the site group dendrogram (Fig. 3.5). The aim of this cluster analysis was to aggregate sites with similar invertebrate communities into groups in order to simplify the determination of factors affecting community composition. A compromise is necessary between excessive clumping (leading to over-simplification and loss of information) and no aggregation at all. Arguments can be presented favouring various numbers of site groups. For example, six site groups could be chosen [viz., (E *E* 1 and E *E* 2), (E *I*), (E *M* and E *R*), (N *E* 2, W *E* 2, W *E* 3 and W *E* 4), (S *M*, S *I* and W *E* 1) and (W *I*)] since E *I* and W *I* are the two single sites whose invertebrate communities differ most from those at any other sites. In this respect they may deserve 'group' status. However, environmental conditions (for example, wave action and sediment type) at these two sites (Table 3.5) are not sufficiently different from those at the other sites in groups A and D respectively (Fig. 3.5) to warrant separation. Consequently, four site groups (A, B, C, D) were chosen using knowledge of both the environmental features (Table 3.9) and invertebrate community composition (Table 3.8) at the sites to determine the component sites of each group.

Physical features of the site groups. The physical features of the study area have already been considered (Chapter II) (Table 3.9) and the following discussion emphasises the main points in the light of the composition of the site groups.

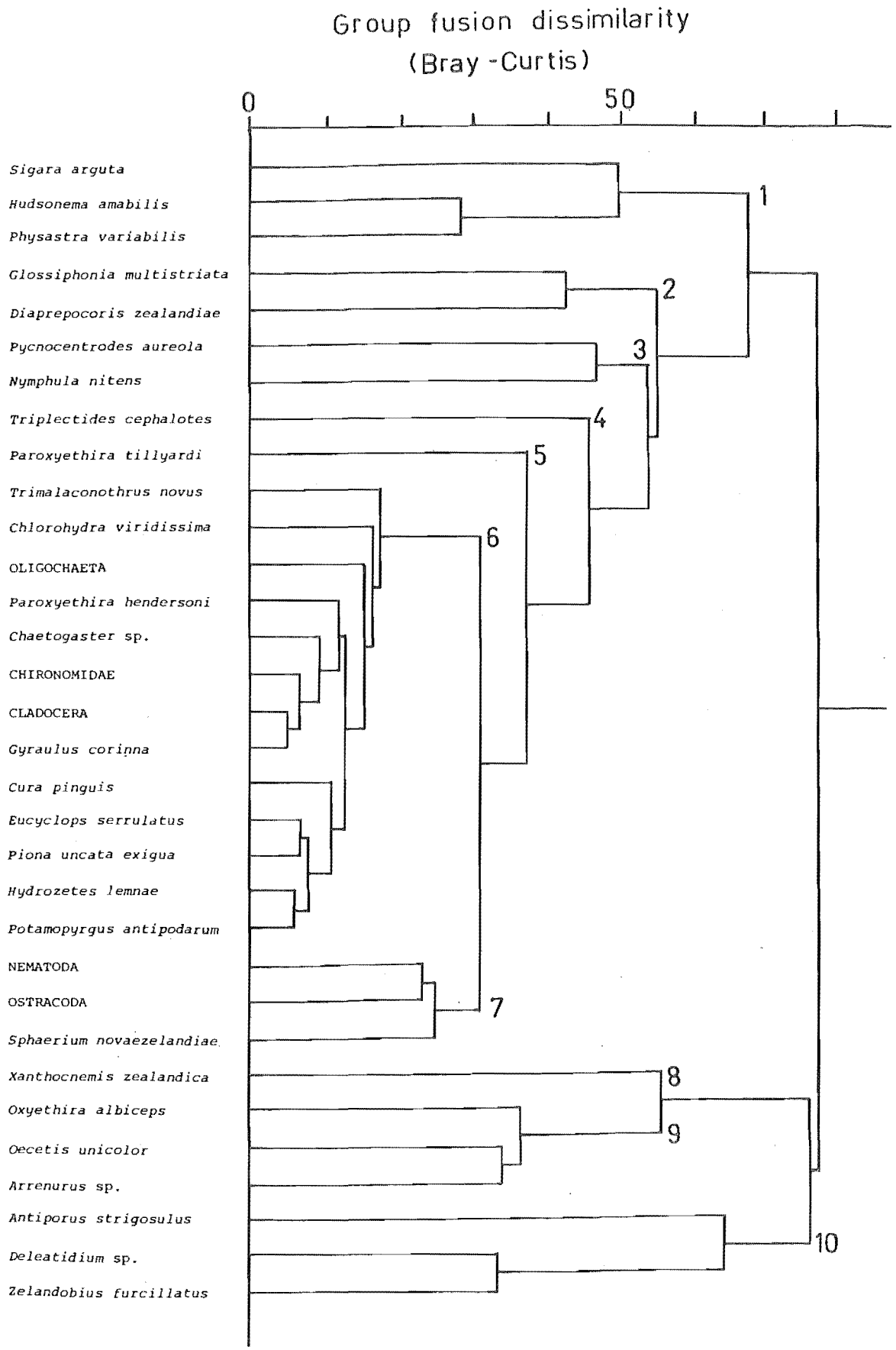


Fig. 3.6 Species group dendrogram. (All quantitative samples combined, September 1976 - October 1977).

Site group A

The three sites (E *E* 1, E *E* 2 and E *I*) comprising this group are on the eastern side of Lake Grasmere (Fig. 2.1) where the substrate ranges from sand and stones to large rocks and boulders. Prominent features are the inputs of branches and leaves from overhanging mountain beech trees (*Nothofagus solandrii* var. *cliffortiodes*) and the shading effect of the adjacent hillside and trees, especially when the sun is low in winter. Wave action is weak to moderate.

Site group B

This group comprises sites E *M* and E *R* and shares the physical features of site group A. The important feature here is the very restricted distribution of the macrophytes *Myriophyllum propinquum* and *Ranunculus fluitans*. In this area of the lake they occured only in a very narrow band (less than 1 m wide) between the *Isoetes* and *Elodea* zones in water about 1 m deep.

Site group C

This relatively homogeneous group comprised four sites (N *E* 2, W *E* 2, W *E* 3 and W *E* 4) within an extensive monoculture of *Elodea canadensis* and represented the dominant macrophyte habitat in the lake (about 90% of the macrophyte-covered area). Wave action is only moderate to weak since the water is deeper (2 - 4 m) and the substrates are highly organic, comprising silt and fine particles resulting from the decomposition of the macrophytes. Sites within this group have more similar invertebrate communities than those comprising any other site group. N *E* 2 and W *E* 2 were the two least dissimilar sites sampled (Fig. 3.5), which is not surprising since they are at the same depth (2 m) in the same extensive *Elodea* monoculture (Fig. 2.1).

Site group D

This group is the most heterogeneous of the four site groups chosen. This heterogeneity is reflected in both the environmental features of the sites (Table 3.5) and in the low degrees of dissimilarity between sites in the site group dendrogram (Fig. 3.5). The sites are all shallow, being in water less than 1 m deep, with moderate to strong wave action especially during prevailing north-westerly winds. The two southern sites (S *I* and S *M*) are influenced also by various inlet streams arising from springs in swampy ground

near the lake edge (especially Inlet A, Stout 1972 Fig. 1) (Fig. 2.1). The substrates range from mud (western sites) to stones (southern sites) with large accumulations of organic material, mostly derived from macrophyte decomposition. At the southern end of the lake in the zone subjected to strong wave action (i.e., in water less than 1 m deep) macrophyte growth is relatively sparse and plants found in clumps act as sediment and organic matter traps. Between these clumps, finer sediments may be eroded away leaving a more stony bottom. The lake bottom in this region of the littoral zone is relatively uneven comprising small humps of macrophytes with hollows between. The conditions in these zones are more reminiscent of lotic than most lentic situations.

Discussion. The site group dendrogram (Fig. 3.5) highlights the marked difference between invertebrate-macrophyte communities of the eastern sampling zone (site groups A and B) and communities in other areas of the lake (site groups C and D). Site group B comprises communities whose occurrence was restricted to a very narrow band along the shore, although it is otherwise surprising that these sites do not show greater similarity to site E *E* 1 from site group A since this site is in very close proximity to the sites of group B. Site group C, on the other hand, represents about 90% of the macrophyte-covered area of the lake and is the most homogeneous group, being virtually a monoculture of *Elodea canadensis*. Site group D, the most heterogeneous assemblage, is characterised by highly organic substrates and marked development of periphytic coatings on plant surfaces.

An environmental gradient which may be correlated with the order of site aggregation (i.e., E *E* 1, E *E* 2, ... W *E* 1, W *I* as on Fig. 3.5) is the degree of organic matter accumulation in the substrate and on plant surfaces. The eastern sites (site groups A and B) are characterised by relatively 'clean' macrophyte surfaces with only moderate periphytic development (due perhaps to a shading effect of the hillside) and substrates that are sandy/stony with very coarse particulate organic matter (beech leaves, twigs, etc.). Site group C has relatively silty substrates with high organic content (decomposing macrophyte material) whereas sites in group D have a variety of substrate types with macrophytes notable for their relatively stunted growth (due perhaps to wave action and shallowness of the water) and very thick coatings of periphyton and organic debris. The above gradient to some extent is due to the effect of wave action. Site groups A and B probably represent 'erosional'sites where fine organic material is removed from

the substrate by the moderate wave action, whereas sites in group D, which are subjected to the strongest wave action, are net 'depositional' sites due to the effects of the prevailing northwesterly winds. Sites in group C on the other hand are not subjected to strong wave action as they are in deeper water and consequently there is not likely to be any removal or addition of organic material to or from other areas. The substrates here are primarily the result of *in situ* decomposition of *Elodea canadensis* and organic matter processing by invertebrates.

(d) Species groups.

Description of the species groups and their occurrence at the site groups.

Introduction. The purpose of this section is to outline the taxonomic composition of the species groups and to account for this composition using knowledge of the habitat requirements of the invertebrate species (see p. 34) and distributional information from sampling invertebrate-macrophyte communities in Lake Grasmere (Table 3.9, Appendix 2).

Because clustering strategies are 'group-size dependent' (Stephenson, Williams & Lance 1970), groups that differ greatly in size should not be selected by defining a fixed level of dissimilarity. Instead, groups are best selected by following down the dendrogram until the species remaining in a group subjectively have similar distributions among the site groups. In other words, species groups should be selected so that they make ecological sense.

In this manner, ten species groups (numbered 1 - 10, Fig. 3.6) were selected from the species group dendrogram. Knowledge of each species' distribution, from data obtained during the quantitative sampling program (Table 3.9 and Appendix 2), was used to delimit species groups.

The representation of each species group at each site group (Tables 3.10 and 3.11) was determined by calculating the mean number of individuals of the species group per sample at the site group and then expressing this as a percentage of the sum of values for all site groups. The percentage representation was adjusted to give equal weight to each site group, since different numbers of samples were taken from each (Table 3.17). Thus, the site group that has the highest mean numbers of a species group per sample has the highest percentage

occurrence of that species group. If the percentage occurrence had been calculated using total numbers of individuals collected from each site group, the percentage representation of a species group would be biased in proportion to sampling effort. This would tend to obscure any preferences that certain species groups may have for different macrophytes, substrates, sampling areas of other environmental features and also make interpretation of the dendrograms, which were derived on a mean numbers per sample basis, more difficult.

Table 3.10 Percentage representation of species groups (by mean numbers of individuals per sample) at site groups, and the percentage of total invertebrate numbers per sample occurring at each site group (September 1976 - October 1977).
- = not present.

Species groups	Site groups			
	A	B	C	D
1	39.0	51.8	2.3	6.9
2	49.3	-	29.4	21.3
3	18.1	45.0	-	36.9
4	-	8.4	12.1	79.4
5	38.6	52.3	2.8	6.3
6	26.8	12.9	32.1	28.2
7	21.6	2.3	3.6	72.5
8	-	-	48.6	51.4
9	3.0	-	1.5	95.5
10	53.6	-	-	46.4
% Total numbers	26.8	13.1	31.4	28.7

Species group 1

This species group comprised the hemipteran *Sigara arguta*, the trichopteran *Hudsonema amabilis*, and the gastropod mollusc *Physastra variabilis*. These species seem to have little in common. Although they are all distributed widely (although not necessarily abundantly) throughout New Zealand this is a feature shared by many species in other groups and does not explain their association here. *H. amabilis* and

P. variabilis 'conformed noticeably' to site groups A and B ($P < 0.01\%$ pseudo F test) although the species group was otherwise relatively weakly clustered (Fig. 3.6) and most common at site group B (Table 3.10). The presence of sandy/stony/rocky substrates (rather than very fine organic sediments), the steeply shelving lake shore, and the relatively weak wave action may be key factors in their occurrence. These species were most common in shallow water: *S. arguta* in sheltered areas; *H. amabilis* (on *Myriophyllum* and *Ranunculus* and especially mineral substrates) and *P. variabilis* both in the eastern sampling area. *H. amabilis* was the third most abundant caddisfly in the macrophyte zones of the lake (after the two *Paroxyethira* species) but *P. variabilis* was outnumbered by *Potamopyrgus antipodarum* by at least 1,200 to one (Table 3.9, Appendix 2).

Species group 2

This species group comprised two weakly clustered species; the leech *Glossiphonia multistriata* and the hemipteran *Diaprepocoris zealandiae*, neither of which 'conformed noticeably' to any site groups. *G. multistriata* has been recorded previously on stones and macrophytes in Lake Grasmere (Stout 1977) and *D. zealandiae* was the more common of the two corixids in the lake (Table 3.9). A common factor linking these two species in Lake Grasmere seems to be an association with *Elodea canadensis*. Ninety-two percent of *G. multistriata* and 75% of *D. zealandiae* collected during the quantitative sampling program were associated with this macrophyte from site groups A and C (Table 3.9). This species group was most common at site group A and present also at site groups C and D (Table 3.10).

Species group 3

Pycnocentrodes aureola (Trichoptera) and *Nymphula nitens* (Lepidoptera) were associated at a high level of dissimilarity (Fig. 3.6) suggesting that their association is relatively weak. Neither 'conformed noticeably' to any site groups. *P. aureola* was not common on macrophytes in Lake Grasmere (Table 3.9) but was very common in shallow water on mineral substrates. Conversely, *N. nitens*, during 1976 and 1977, was found most often associated with shoot tips of *Myriophyllum* (Table 3.9). In 1978, however, when densities of *N. nitens* increased dramatically (see Chapter V) many more larvae were found associated with other macrophytes such as *E. canadensis*. This species group was most common in site groups B, D, and A (Table 3.10) with preference for sites where macrophyte stem lengths were short (0.1 - 0.3 m) (Table 3.9).

Species group 4

Triplectides cephalotes (Trichoptera) was the sole member of this species group and 'conformed noticeably' to site group D ($P < 0.01$, pseudo F test). It was present also in site groups C and B (Table 3.10). These records support earlier observations on preference for shallow water sites. Cowley (1978) recorded larvae living amongst stones on a rocky beach in Lake Grasmere, although my observations suggest that a greater proportion of the population in the lake is associated with aquatic macrophytes.

Species group 5

The sole occupant of this species group, the hydroptilid caddisfly *Paroxyethira tillyardi*, 'conformed noticeably' to eastern sites (site groups A and B) ($P < 0.01$, pseudo F test). Nearly 90% (in terms of mean numbers per sample) were collected from these areas (Table 3.10) and those collected from other areas preferred shallow sites (Table 3.9). A distinct preference for sandy/stony substrates rather than silty/muddy substrates was evident.

Species group 6

The species group comprised thirteen taxa (Table 3.11) whose common feature was their occurrence at all sites sampled. Six taxa 'conformed noticeably' to even representation at all site groups (Oligochaeta ($P < 0.05$), *Chaetogaster* sp. ($P < 0.01$), Cladocera ($P < 0.001$), *Eucyclops serrulatus* ($P < 0.05$), Chironomidae ($P < 0.001$), and *Gyraulus corinna* ($P < 0.001$)).

Species group 6 contains the eleven most common taxa (by total numbers collected during the quantitative sampling program) and the 13th and 16th ranked species and comprises species that are characteristic of macrophyte zones of lakes (see Winterbourn & Lewis 1975). This group makes up over 95% (by numbers) of the fauna at each site group (see Tables 3.17 and 3.18 and associated discussion).

P. antipodarum was the most common macroinvertebrate at almost every site (Table 3.9) averaging over 50% by numbers in all quantitative samples combined. *C. viridissima*, the second most common species, was especially common on *E. canadensis* in site group C (Tables 3.9 and 3.11). There was a marked seasonality in its occurrence (see Figs. 3.9a, 3.10 - 3.13) and marked change in abundance with depth (Fig. 3.4). The third most abundant species, the copepod *E. serrulatus*, was most common also at site group C (Table 3.11) where reduced wave action probably enhanced

its abundance. *G. corinna*, the fourth most common macroinvertebrate on macrophytes in Lake Grasmere, was found also on rocky and sandy substrates. On plants it was present mostly at site groups C and D (Table 3.11).

Table 3.11 Percentage occurrence of the taxa of species group 6 among the four site groups (on a mean numbers per sample basis).

Taxon	Site group			
	A	B	C	D
Trimalaconothrus novus	18.4	6.1	17.7	57.8
Chlorohydra viridissima	20.5	8.1	67.8	3.6
OLIGOCHAETA (except *Chaetogaster*)	13.9	0.7	44.1	41.3
Paroxyethira hendersoni	8.6	17.8	13.7	59.9
Chaetogaster sp.	4.0	8.9	38.5	48.6
CHIRONOMIDAE	11.1	9.4	17.8	61.7
CLADOCERA	7.8	5.7	48.7	37.8
Gyraulus corinna	8.7	2.2	48.2	40.9
Cura pinguis	30.1	12.4	14.1	43.4
Eucyclops serrulatus	25.0	7.4	43.5	24.2
Piona uncata exigua	34.6	19.8	34.1	11.5
Hydrozetes lemnae	23.1	29.9	14.6	32.4
Potamopyrgus antipodarum	34.5	16.6	20.7	28.2

Cladocera from quantitative samples were not identified to the specific level prior to April 1977. However, seven species were identified from samples collected between April and October 1977 inclusive. During this period cladoceran species composition (on a mean numbers per sample basis; all sites combined) was as follows: *Bosmina meridionalis* 40.1%, *Graptoleberis testudinaria* 36.9%, *Alona guttata* 17.1%, *Chydorus sphaericus* 6.3%, *Ceriodaphnia dubia* 0.6%, *Ilyocryptus sordidus* 0.2%, and *Neothrix armata* 0.1%. *Leydigia ?australis* and *Simocephalus vetulus* occurred also but were not collected in quantitative samples.

Distinct differences in species composition of Cladocera occurred in each site group (Table 3.12). *G. testudinaria* was most abundant at site group C. These two species constituted nearly 85% of cladocerans collected and *A. guttata* and *C. sphaericus* were the

only other species to contribute more than 10% by numbers at any site groups between April and October 1977.

Table 3.12 Species composition (%) of Cladocera in quantitative samples from each site group and total numbers of each species collected (April - October 1977).

Species	Total numbers collected	Site group A	B	C	D
Bosmina meridionalis	1168	20.5	-	67.3	9.0
Graptoleberis testudinaria	763	53.9	75.0	29.2	41.3
Alona guttata	240	20.5	-	1.0	38.2
Chydorus sphaericus	99	5.2	25.0	2.2	10.1
Ceriodaphnia dubia	12	-	-	0.4	0.9
Ilyocryptus sordidus	2	-	-	-	0.4
Neothrix armata	1	-	-	-	0.2

Cladoceran densities (Table 3.13) were much lower in the eastern sampling area (site groups A and B) than elsewhere. There was clearly a greater planktonic influence on the phytomacrofaunal communities at site group C. Indicative of this influence was the prevalence of the planktonic *B. meridionalis* at site group C and the presence of *C. dubia* exclusively at site groups C and D (although only a few individuals were collected, Table 3.12) (Table 3.13).

Table 3.13 Percentage representation of each cladoceran species (by mean numbers per sample) between the four site groups, and overall mean numbers per sample (all species combined) at each site group (April - October 1977).

Species	Site group A	B	C	D
Bosmina meridionalis	2.4	-	88.5	9.1
Graptoleberis testudinaria	6.8	5.9	41.6	45.7
Alona guttata	5.6	-	3.0	91.4
Chydorus sphaericus	3.8	11.5	18.6	66.1
Ceriodaphnia dubia	-	-	36.7	63.3
Ilyocryptus sordidus	-	-	-	100.0
Neothrix armata	-	-	-	100.0
mean numbers/sample	3.9	2.4	44.0	34.1

G. testudinaria, *A. guttata*, and *C. sphaericus* are all weed dwelling species with distributions biased towards site groups D, or C (Table 3.13). These areas (cf. site groups A and B) had more available macrophyte substrates and/or greater quantities of organic material and periphyton amongst or adhering to the stems of macrophytes. It is likely, therefore, that the distributions of the weed dwelling cladocerans were in response to available food or attachment sites.

Besides *Chaetogaster* sp., four oligochaetes were recorded from macrophyte zones of Lake Grasmere (Table 3.8), although they were more common in mud than on macrophyte surfaces. Although oligochaetes from quantitative samples were not identified to species on a regular basis, *Lumbriculus variegatus* and *Chaetogaster* sp., and to a lesser extent, *Eiseniella tetraedra* were the dominant species on macrophytes. The oligochaetes (including *Chaetogaster* sp.) were most common in site groups C and D (Table 3.11) where the presence of large quantities of organic detritus amongst the macrophytes was likely to be the main influence upon their distribution.

Chironomidae were not identified specifically during original processing of quantitative samples due to taxonomic difficulties and, therefore, were lumped in the dendrogram analyses. Subsequently, further identifications have been possible (Stark in press) and ten taxa have been recognised (see also Chapter VI, Appendix 3 and Table 3.14).

Table 3.14 Species composition (%) of Chironomidae in quantitative samples from each site group and all sites combined (September 1976 - October 1977).

Taxa	Total numbers collected	Site group A	B	C	D	Overall
Cricotopus spp.	761	43.7	91.9	87.9	64.5	70.4
Macropelopia/Gressittius	147	45.2	-	10.3	9.5	13.5
Tanytarsus vespertinus	98	-	-	-	16.9	9.1
Orthocladiinae A	27	-	-	-	4.7	2.5
Ablabesmyia mala	25	8.7	5.4	0.3	1.9	2.3
Orthocladiinae B	10	-	2.7	-	1.6	0.9
Chironomus zealandicus	6	0.8	-	1.2	0.2	0.6
Orthocladiinae C	4	-	-	-	0.7	0.4
Pentaneura sp.	2	1.6	-	-	-	0.2
Syncricotopus pluriserialis	1	-	-	0.3	-	0.1

Distinct differences in chironomid species composition occurred in each site group (Table 3.14). *Cricotopus* (perhaps two species) was the dominant chironomid at three site groups (B, C and D) and in terms of overall abundance. At the remaining site group (A), the abundance of *Cricotopus* spp. was similar to that of *Macropelopia/ Gressittius* (two ? species). All these taxa comprised nearly 85% of chironomid larvae collected during the quantitative sampling program. *T. vespertinus* was the only other species representing more than 10% of chironomid numbers at any site group and was found exclusively at site group D.

Table 3.15 Percentage representation of each chironomid species (by mean numbers per sample) in the four site groups, and overall mean numbers per sample (all species combined) at each site group (September 1976 - October 1977).

Taxa	Site group			
	A	B	C	D
Cricotopus spp.	7.0	12.7	23.0	57.3
Macropelopia/Gressittius	39.1	-	14.7	46.2
Tanytarsus vespertinus	-	-	-	100.0
Orthocladiinae A	-	-	-	100.0
Ablabesmyia mala	35.8	19.1	2.0	43.1
Orthocladiinae B	-	20.0	-	80.0
Chironomus zealandicus	21.7	-	52.2	26.1
Orthocladiinae C	-	-	-	100.0
Pentaneura sp.	100.0	-	-	-
Syncricotopus pluriserialis	-	-	100.0	-
mean numbers/sample	2.7	2.3	4.4	14.8

Chironomid densities were much higher at site group D than elsewhere (Table 3.15) due to greater species richness resulting from increased habitat heterogeneity and the inclusion of bottom-dwelling animals in samples. All but one (*C. zealandicus*) of the species occurring at site group D was most common at this most heterogeneous group. *Cricotopus* spp. favoured site groups C and D, whereas the predatory Tanypodinae (especially *Macropelopia/Gressittius* and *A. mala*) were most abundant at shallow sites (site groups A and D) (Table 3.15). *C. zealandicus*, a species common in the benthos below the macrophyte

beds of Lake Grasmere (Timms in prep.), was infrequently collected from macrophytes but was most represented at site group C (the *E. canadensis* 'monoculture').

Three species of Acarina were included in species group 6. *Hydrozetes lemnae* was well represented at all site groups (Table 3.11) but had highest densities at shallow sites in site groups A and D (Table 3.9). *Piona uncata exigua* was most common at site groups A and C (Table 3.11), especially at sites characterised by *E. canadensis* (Table 3.9). Lowest densities were recorded from shallow sites with moderate to strong wave action (mainly site group D). This distribution is consistent with the known planktonic/littoral habits of *Piona* (Stout 1969b,1976, Winterbourn & Lewis 1975). The third species, *Trimalaconothrus novus*, was very common in clumps of *I. alpinus*, especially near the leaf bases. In July 1976 white nymphs were found inside a decomposing *Isoetes* stem indicating that such sites may be used for egg-laying. *T. novus* was most common at site group D (Table 3.11).

Paroxyethira hendersoni was the most common trichopteran living in Lake Grasmere (Table 3.9) and the most frequently taken as adults in hand net (Appendix 5.3) and light trap (Appendix 5.4) collections from the lake shore. It was best represented at site group D (Table 3.11), especially at sites W *I* and S *M* (Table 3.9). There appeared to be a distinct preference for zones of *I. alpinus* and *M. propinquum* that occurred in shallow water.

The remaining member of this species group is the flatworm *Cura pinguis*. This species was distributed widely in Lake Grasmere but was most common at site groups D and A (Table 3.11) and especially at sites W *I*, E *E* 1 and E *E* 2 (Table 3.9).

Species group 7

This species group comprised three taxa characteristic of benthic habitats. All 'conformed noticeably' to site groups A and D (Nematoda, pseudo F test, $P < 0.01$; Ostracoda, $P < 0.01$; *Sphaerium novaezelandiae*, $P < 0.05$).

Nematoda and Ostracoda (except for the very distinctive *Gomphocythere duffi*) were not identified to species during the quantitative sampling program due to taxonomic shortcomings. However, six species of Ostracoda (Table 3.8) have been identified subsequently (Dr M.A. Chapman, pers. comm.). All are characteristic of benthic (*Scottia insularis, Herpetocypris pascheri, Prionocypris marplesi,*

G. duffi and *Darwinula repoa*) and macrophytic (*Cypridopsis vidua* and *D. repoa*) habitats (Chapman 1976). By far the most common species in samples was *D. repoa*. *S. insularis* (a small dark green species that occurred in large numbers in highly organic substrates near the swampy inlet stream, but not in quantitative samples) and *P. marplesi* have hardly ever been recorded since they were described by Chapman (1963) (Dr M.A. Chapman, pers. comm.).

S. novaezelandiae was present in all sandy to muddy habitats in the macrophyte zones of Lake Grasmere and it occurs in the benthos as well (Jamin 1976, Timms in prep.).

Species group 7 was most common at site groups D and A (Table 3.10). There was a trend to decreasing abundance of these taxa with depth (or increasing height of macrophyte) as the bottom faunal influence on samples decreased. This difference was marked especially in the western sampling zone: W *I* was the most preferred site (with the shortest macrophyte), followed by W *E* 1, with a marked reduction in representation where macrophyte stems were longer, in deeper *E. canadensis* zones (W *E* 2 - W *E* 4) (Table 3.9) of site group C.

Species group 8

The larva of the common red damselfly, *Xanthocnemis zealandica*, was the sole member of this species group and did not 'conform noticeably' to any site groups. *X. zealandica* was not common in Lake Grasmere during most of 1977 and was collected rarely in quantitative samples. An indication of the difference in its abundance between 1976 and 1977 is given by Fig. 5.13 (p. 134) where similar effort with a hand-net yielded approximately seven times as many larvae in the last four months of 1976 as in the same period the following year. The extensive northern and western zones of *E. canadensis* (site group C) were the favoured habitat in the lake (Table 3.9) and it was from these areas that animals were collected most readily for life history information and faecal analyses (Chapters IV and V). In terms of site groups, *X. zealandica* was represented almost equally in groups C and D, the latter due entirely to site W *E* 1 (Tables 3.9 and 3.10).

Species group 9

Oxyethira albiceps (Trichoptera: Hydroptilidae), *Oecetis unicolor* (Trichoptera: Leptoceridae) and *Arrenurus* sp. (Acari: Prostigmata: Arrenuridae) comprised this species group but did not 'conform noticeably' to any site groups.

O. albiceps was collected in quantitative samples only from western and southern areas (site group D) although it was taken occasionally in hand-net sweeps from deeper *E. canadensis* zones in the western sampling area (site group C), especially when the biomass of green filamentous algae was high (e.g., October 1977). Highest densities, however, were found on algal covered stones at the southern end of the lake.

O. unicolor was collected in quantitative samples from only two sites (W *E* 1 and W *I*, Table 3.9) in site group D. In addition, it was present on sandy substrates in the southern zone, and in greatest densities near the outlet stream at the northern end of the lake where substrates were sandy and the water less than 1 m deep.

The undescribed species of *Arrenurus* was best represented at sites W *E* 1 and W *I* (site group D) but was present also at E *E* 2 (site group A) and W *E* 2 (site group C). The known New Zealand species of *Arrenurus* (*A. rotoensis* and *A. lacus*) have been recorded only from ponds and small lakes (Stout 1953b) but little is known of their ecology.

Species group 9 was characteristic of site group D although it is likely that macrophyte zones are not the preferred habitats since *O. albiceps* was most abundant on algal covered stones, *O. unicolor* on sandy substrates and *Arrenurus* sp. also probably has benthic habits.

Species group 10

The tenth species group comprised the dytiscid beetle *Antiporus strigosulus*, the mayfly *Deleatidium* sp. and the stonefly *Zelandobius furcillatus*. Only the first named 'conformed noticeably' to any site group (site group A, $P < 0.05$, pseudo F test).

A. strigosulus was not abundant in Lake Grasmere and was recorded (as one adult and one larva) in quantitative samples at two sites (Table 3.9) in site group A. Non-quantitative hand-net collections suggested that *A. strigosulus* was present in shallow habitats in the eastern area of the lake, occasionally near the outlet stream in the northern area and in the shallow sites in western and southern areas of the lake. It is an active swimmer and its abundance would almost certainly be underestimated using the quantitative sampler.

Only three specimens of *Deleatidium* sp. were collected in quantitative samples, from two sites in site group D (S *I* and W *E* 1) and one in site group A (E *I*) (Table 3.9). Greatest numbers were present along eastern and southern stony shores of Lake Grasmere where

the wave action and substrates created conditions that were more typical of streams. *Deleatidium* could not be regarded as a permanent member of the invertebrate communities on aquatic macrophytes in this lake.

Seven specimens of *Z. furcillatus* were collected in quantitative samples from two sites in site group D (S *I* and S *M*) and one in site group A (E *I*) (Table 3.9). All three of these shallow water sites had stony substrates and were subjected to wave action.

Species group 10 was represented only at site groups A and D and mostly at sites with stony substrates and moderate to strong wave action.

3.3.5 Seasonal Changes in Invertebrate Communities at the Site Groups

(1) Introduction

The following discussion is concerned with seasonal changes in community structure at each of the four site groups in general terms only. As stated earlier (p. 21) it was anticipated that, since logistic considerations prevented very intensive sampling, the data obtained could not be subjected to detailed month-by-month analysis. Therefore, a variety of indices of species diversity and community similarity are used here in an attempt to examine general seasonal trends in the relative abundance of the taxonomic groupings of Coelenterata, Annelida, Crustacea, Insecta, Acarina and Mollusca and seasonal trends in overall community composition at each site group particularly in relation to any marked changes in between-site comparisons. More detailed analyses of the seasonality of certain species are described in Chapter V.

(2) Procedure

(a) Species diversity. One of the measurable characteristics of any collection of organisms is its 'diversity'. Diversity in this context refers to the degree of uncertainty attached to the specific identity of any randomly selected individual from a collection of organisms. A collection in which all individuals belong to one species has no diversity whereas one in which every individual belongs to a different species has maximum diversity because it is impossible to predict the identity of the next species. A great variety of indices have been derived to measure diversity (Pielou 1966).

Species diversity has two components: (i) the number of species (i.e., species richness) and (ii) equitability or evenness of the

allotment of individuals among the species. Thus, both a greater number of species and a more even or equitable distribution of individuals among the species will contribute to increased diversity.

A commonly used diversity index is that derived independently by Shannon and Wiener (Shannon & Weaver 1949)

$$H' = - \sum_{i=1}^{s} p_i \log p_i$$

where H' is the population value of the average diversity of a sample from an indefinitely large population; s is the number of species, and p_i is the proportion of the ith species in the population.

Since species diversity has two components it is of interest to know how each contributes to total diversity. To this end we may also calculate, separately, indices of species richness and species evenness.

Species richness (although in its simplest form the number of species) can be calculated from

$$d = \frac{S}{\log N}$$

where S = the number of species and N = the number of individuals (i.e., a measure of sample size) (Odum, Cantlon & Kornicker 1960, Whittaker 1975). This index (= Whittakers index of species richness) corrects for the effects of sample size since a larger sample may be expected to contain a greater number of species than a smaller one.

The index of species evenness used here was derived by Pielou (1966),

$$J' = \frac{H'}{H'_{max.}} = \frac{H'}{\log S}$$

In this case, species evenness is defined as the ratio of observed species diversity (H') to maximum species diversity ($H'_{max.} = \log S$).

(b) Community similarity indices. Two community similarity indices were used to determine the times of year when most change occurred in the composition of the animal communities at the different site groups. These indices were the coefficient of community (CC) and the percentage similarity of community (PSc) (Jaccard 1932, Whittaker & Fairbanks 1958, Johnson & Brinkhurst 1971, Barton & Hynes 1978). CC measures the percentage of species shared by two samples, community types or habitats among the total number of species represented in both.

Thus, $CC = \frac{c}{a+b-c}$ in which a is the number of species in the first sample, b the number in the second sample and c the number in common.

The second index, one of the most widely used indices of its type, compares animal communities by the numbers of individuals of each species shared by the two samples, communities or habitats.

$PSc = 100 - 0.5 \Sigma |a-b| = \Sigma \min (a,b)$ where a and b are, for a given species, the percentage of samples A and B which that species represents.

By calculating CC and PSc values between adjacent sampling dates one can determine when there is the greatest change in the composition of the animal communities. The lower the values of CC or PSc (i.e., the lower the degree of similarity) the greater the change between samples. In addition, by applying the indices to replicate samples (i.e., samples that are assumed to be very similar: CC and PSc should approach 100%) one can not only test sampling replicability, but also set up criteria to assess degrees of affinity between samples. Johnson & Brinkhurst (1971) considered that high affinity between stations (= samples) was indicated when the values of CC and PSc between stations did not fall below the lowest values of the indices within stations, as assessed from the values obtained from the comparison of replicate samples.

CC measures relative similarity in terms of species composition and may overvalue minor species to the neglect of differences in dominance. This index is very simply applied, however, because it requires only presence/absence data. This simplicity is also its major disadvantage because abundant and rare species are given equal weight. PSc, by contrast, measures relative similarity of numerical composition in terms of species populations and usually leads to grouping of communities by dominants or most abundant species. Its weakness may be in overvaluing the sharing of dominants to the neglect of differences in overall community composition, which is the result also of the presence of rarer species. Used together the two indices are of more value than any single index. By comparing their relative values it is possible to determine, for example, whether high affinity of samples is due to the sharing of most species and/or to the occurrence of species in about the same proportions.

(3) Results

(a) Species diversity. Species diversity tended to be lower in eastern sampling zones (site groups A and B) than in other areas (Fig. 3.7a).

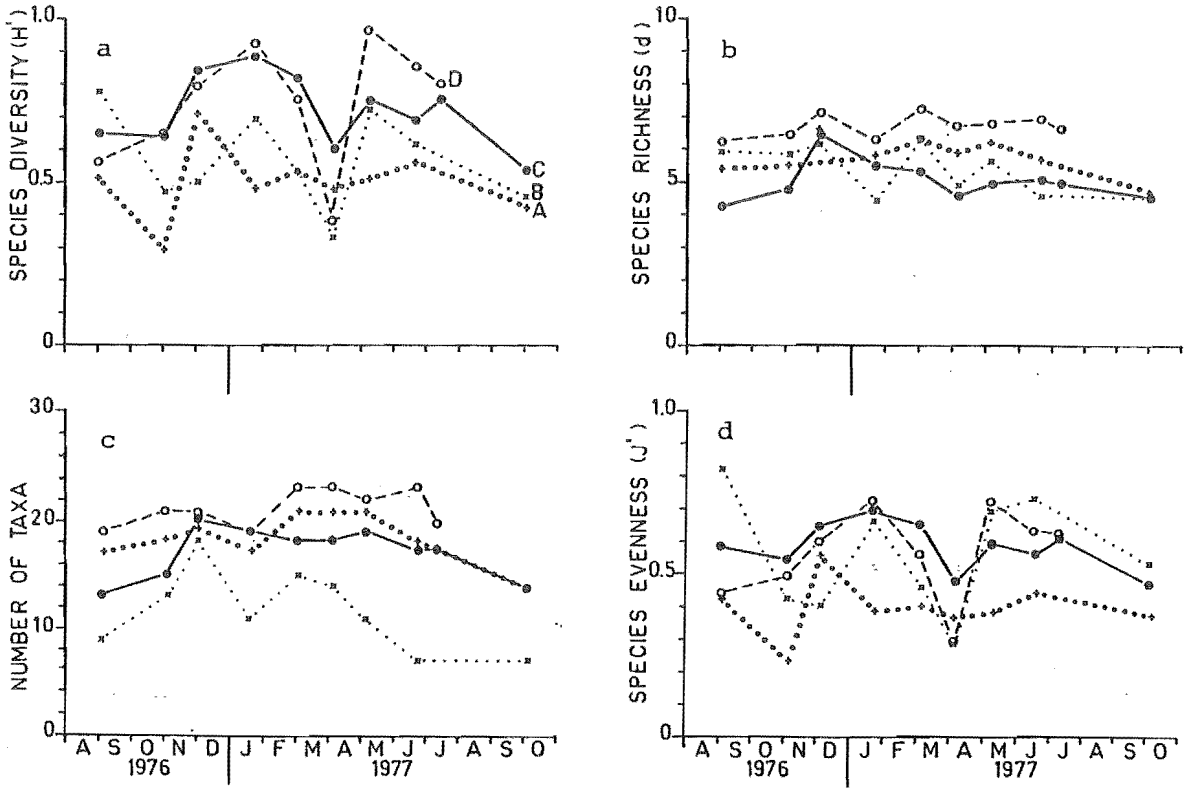


Fig. 3.7 Seasonal changes in (a) species diversity, (b) species richness, (c) number of taxa, and (d) species evenness for each site group during the time of the quantitative sampling program.

In general, diversity was highest during the summer and late autumn-winter at most site groups. Site group A showed the least seasonal change in diversity. It did not exhibit the prominent decrease in April 1977 (Fig. 3.7a) shown by the other site groups, a decrease due to dramatic changes in *P. antipodarum* (especially at site groups B and D) and *C. viridissima* (especially at site group C) (see also Figs. 3.9a and f).

Whittaker's index of species richness suggested there was relatively little change in species richness during the sampling period (Fig. 3.7b). Site group D, the most heterogeneous group, always had the highest species richness followed, on average, by site groups A, B and C in that order. This order reflected the order of site group heterogeneity (see discussion on physical features of site groups). On a numbers of taxa basis (which is another way of expressing species richness) the series of decreasing species richness at the site groups was D, A, C, B. This series did not reflect the order of site group heterogeneity quite as well as Whittaker's index although seasonal variations were more apparent (Fig. 3.7c). Sampling of the habitats

of site group B, which were very restricted in distribution, was difficult and fewer samples were collected than from the other site groups, especially after April 1977 (Table 3.16). The number of taxa

Table 3.16 Numbers of samples collected from the site groups (September 1976 - October 1977).

Site group	Sampling date 2/9	2/11	2/12	20/1	2/3	8/4	10/5	20/6	13/7	3/10	Total
A	6	6	6	3	6	5	5	5	0	5	47
B	1	3	4	1	2	2	1	1	0	1	16
C	8	8	8	8	8	8	8	8	8	6	78
D	4	6	4	4	5	4	3	4	5	0	39

collected (Fig. 3.7c) from site group B correlated well with the numbers of samples collected (Table 3.16). This suggests that Whittaker's index of species richness (which accounts for the influence of sample size variations on species richness) provided a more realistic assessment of the species richness of this habitat.

The second component of species diversity (i.e., species evenness) showed seasonal variation (Fig. 3.7d) that was almost identical in pattern to the changes in total diversity. This indicates that the seasonal pattern of species diversity was due primarily to changes in species dominance rather than in number of species present.

(b) Community similarity. CC and PSc values between adjacent sampling dates were calculated for each of the site groups and plotted midway between sampling dates (Fig. 3.8). For site group A CC and PSc had similar numerical values. There was least change in community composition during autum - early winter and most change in November - December. The decline in CC and PSc evident between June and October 1977 probably was mostly a function of the length of this time interval (since, even with a constant rate of seasonal change, more change might be expected to occur over a longer period). For most of the year, PSc was higher than CC suggesting that there was more change in species dominance than species presence or absence. Comparison of the community composition on 3 October 1977 with that on 2 September and 2 November 1976 (Fig. 3.8A) suggested there was marked similarity in abundance of

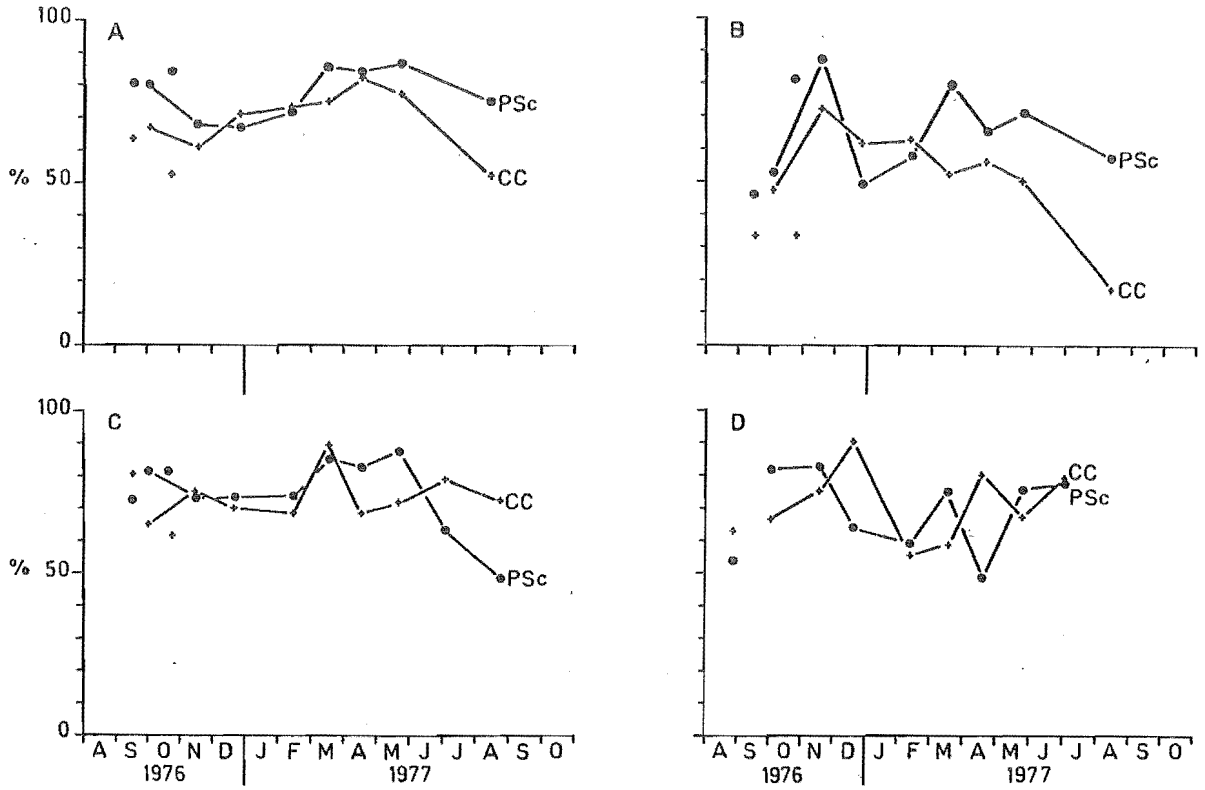


Fig. 3.8 A-D CC and PSc values calculated between adjacent sampling dates (and plotted midway between them) for invertebrate communities at each site group. Unlinked symbols represent comparisons of the last 1977 samples (i.e., July or October) with the nearest months in 1976 (i.e., September and November).

dominant species (PSc values over 80%) but greater variation in taxonomic composition (CC values 52 - 63%) between years. These differences between years were due primarily to reduced species richness in October 1977 (14 taxa) compared with the similar period in 1976 (17 - 18 taxa) (Fig. 3.7c).

There was greater seasonal variation in CC and PSc in site group B (Fig. 3.8B) than in site group A. Most change in abundance of dominant species (i.e., lowest PSc values) occurred between September and November 1976 and also between December 1976 and January 1977. As with site group A, CC was lower than PSc for most of the year (and low in real terms, i.e., few species) suggesting that there was considerable variation in the taxonomic composition of the community. This variation was reflected also in species richness (Figs. 3.7b and c). Although the invertebrate community at site group B showed the most seasonal change not only in community composition (as indicated by CC and PSc values, Fig. 3.8) but also in the number of taxa present (Fig. 3.7c), species evenness (Fig. 3.7a) and total invertebrate densities (Fig. 3.11),

the number of samples collected (16) was considerably fewer than the number from other site groups and the seasonal distribution of sampling effort was uneven (Table 3.16). Consequently it is difficult to separate real changes in community composition from those arising as an artefact of biased sampling effort.

The data for site group C should be the most reliable since this was the most homogeneous assemblage of sites (see Table 3.9) and was based on the largest number of samples (Table 3.16). There was very little seasonal change in species composition, with CC values between sampling dates ranging from 64.7% to 89.5% with the main peak between March and April 1977 (Fig. 3.8C).

Lower values were caused by the intermittent presence of uncommon species (e.g., leeches and some insect species). High PSc values between most sampling dates suggest that the percentage abundance of the commonest species was consistent also. The three highest PSc values (around 85%) occurred between the autumn and winter months when the communities were dominated by *C. viridissima* (Fig. 3.9a) and *P. antipodarum* (Fig. 3.9f). The low PSc between July and October 1977 was primarily due to the switch from a *C. viridissima* (15%) and *P. antipodarum* (25%) dominated community to one dominated by *P. antipodarum* (70%) alone. Comparison of the October 1977 samples with those from September and November 1976 showed that the communities had similar abundances of dominant species (high PSc) and taxonomic compositions (high CC) implying that changes in community composition occurred in an annual cycle (Fig. 3.8C). However, since only one cycle was investigated, it is not possible to say whether this would always be so.

In the most heterogeneous site group, D, variations in CC between sampling dates (Fig. 3.8D) were, in the main, due to the intermittent presence of various insect taxa, especially in January, March and June 1977. Fluctuations in PSc, an index that is influenced markedly by dominants, were due to particularly low percentage contributions of *P. antipodarum* to the invertebrate community, caused, in part, by increased representation of Cladocera and Oligochaeta (January 1977) and *Chaetogaster*, Cladocera, Copepoda, and Insecta (May 1977) relative to neighbouring months (Figs. 3.9b, c and d). The habitats of site group D were not sampled in October 1977 and the comparison of July 1977 with September 1976 (Fig. 3.8D) suggests that communities present in these months differed, especially in terms of the percentage representation

of dominant taxa (e.g., Oligochaeta and *P. antipodarum*) (Figs. 3.9b and f). The numbers of taxa present were quite similar (19 in September 1976 and 20 in July 1977) but only 62.5% of the taxa were shared (Fig. 3.8D).

3.3.6 Seasonal Changes in the Abundance of Major Taxa at the Site Groups

In detailed analysis of seasonal changes in the abundance of major taxa there were often marked variations that were difficult to explain. Sampling on some dates was more difficult than others and it is possible that between-date comparisons may be subject to greater error than comparison of samples from one date. This could be due to the influences of recent weather conditions (periods of high winds, heavy rain, etc.) compounded with true seasonal changes and/or sampling variability, weather conditions at the time of sampling and the time of day of sampling (although these last two factors were standardised as far as was possible).

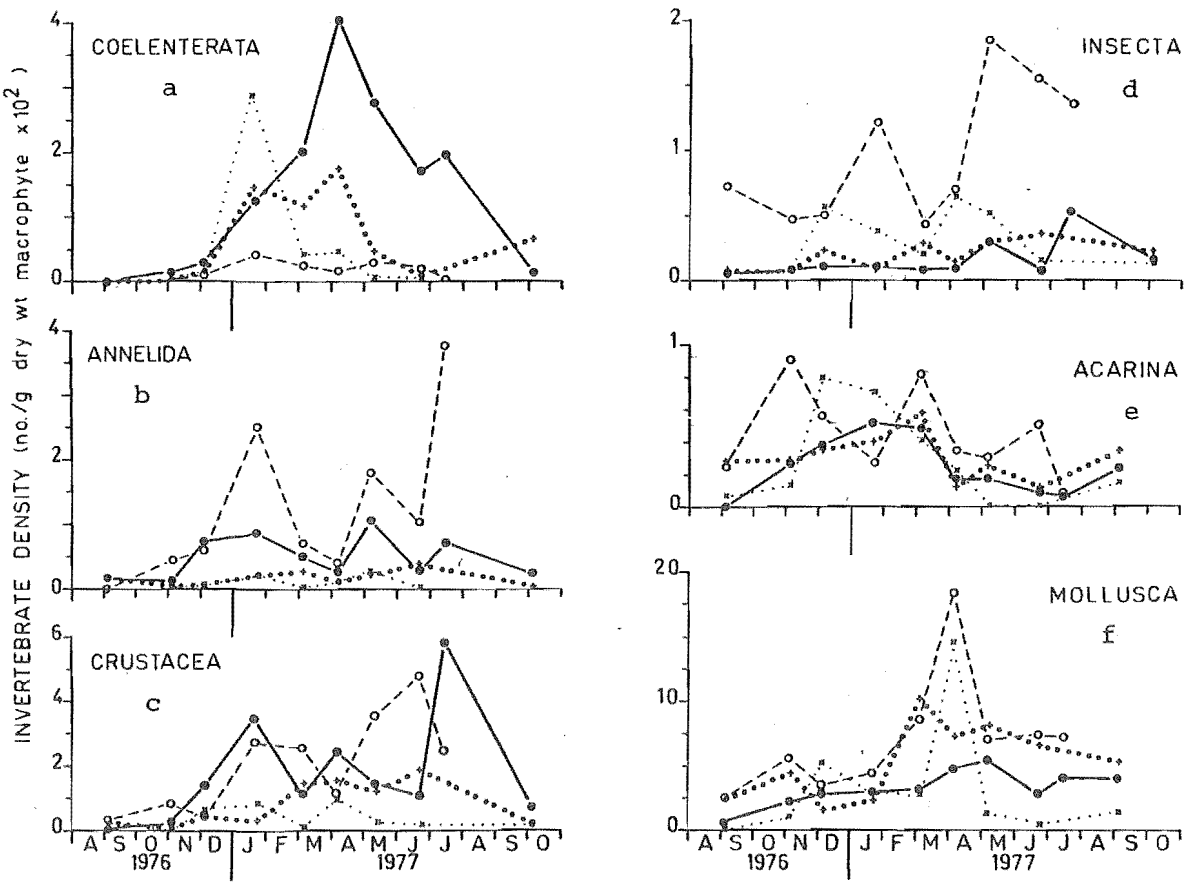


Fig. 3.9 a - f Seasonal changes in abundance of major taxa at each site group. (September 1976 - October 1977.)

▪·····▪ = site group A, ▪·····▪ = site group B,
●——● = site group C, ○----○ = site group D.

General aspects of seasonal changes in the abundance of major taxa at each of the site groups (Fig. 3.9) will be discussed, but detailed analyses will not be attempted. Seasonal changes in total invertebrate density (numbers per gram dry weight of macrophyte) and percentage composition of invertebrate communities at each site group are shown in Figs. 3.10 - 3.13.

(1) Site group A

The invertebrate community at site group A was dominated by Mollusca (mainly *P. antipodarum*) (48.2 - 89.8%) in all months sampled (Fig. 3.10). Peak abundances of molluscs occurred in March 1977, when the population was dominated by small individuals, and lowest numbers were present in December and January (Fig. 3.9f).

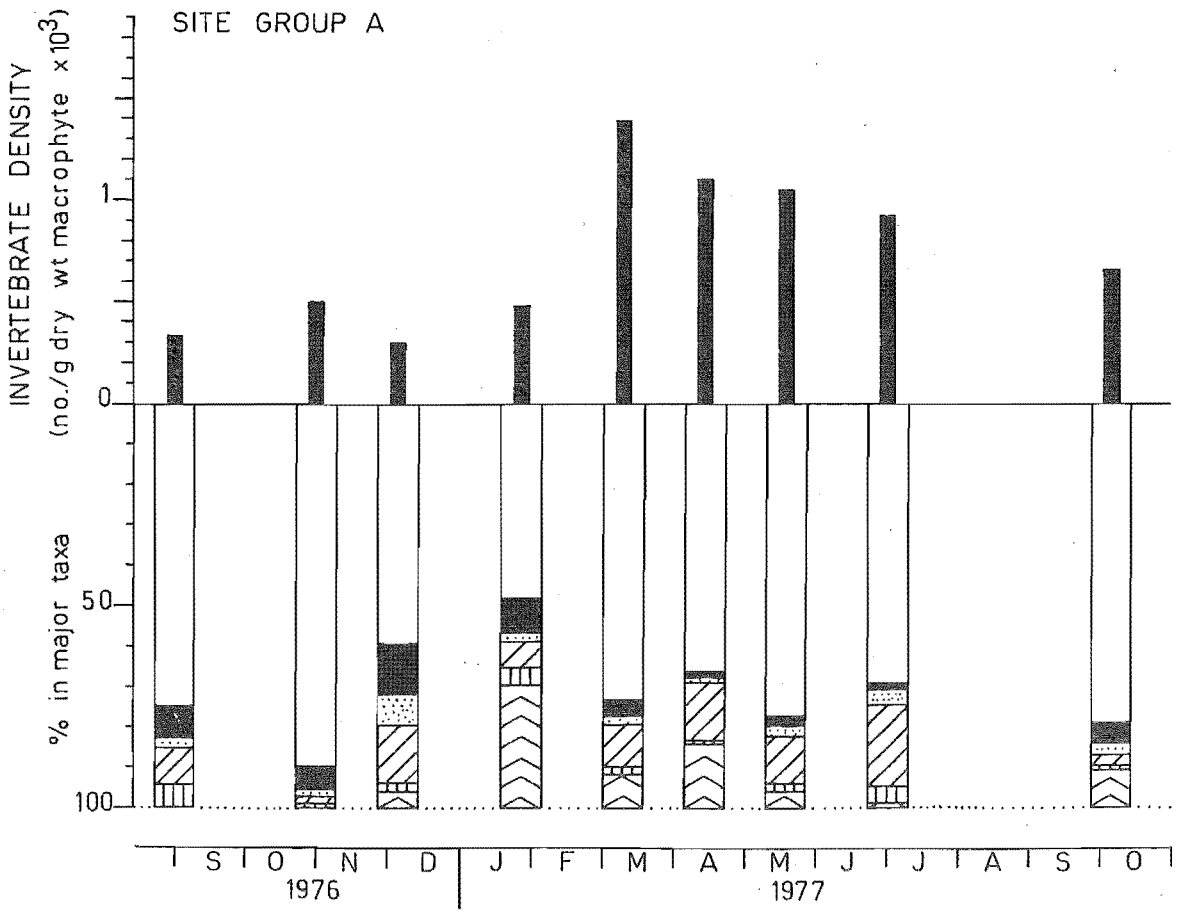


Fig. 3.10 Seasonal changes in total invertebrate density and percentage composition of invertebrate communities (in terms of major taxa) at site group A during the sampling period. (Key to major taxa given in Fig. 3.2.)

Crustacea were usually the next most numerous group (1.9 - 19.8%, Fig. 3.10) with highest densities in autumn and winter (Fig. 3.9c), but sometimes *C. viridissima* with a greater seasonal range (0.2 - 30.5%)

made a larger percentage contribution to the community (Fig. 3.10). Highest densities of *C. viridissima* were present between January and April (Fig. 3.9a). Densities of Acarina increased from September 1976 to March 1977 (Fig. 3.9e) with dominant species being *H. lemnae* and *P. uncata exigua* (see life-history section). The percentage contribution of mites to the community at site group A ranged from 1.3% (April 1977) to 12.1% (December 1977) (Fig. 3.10). Insecta never reached high densities at site group A and seasonal changes in abundance were difficult to interpret since low numbers of individuals of ten species contributed to the pattern (Fig. 3.9d). Generally, peaks in abundance were due to Hydroptilidae (December 1976, May 1977), Chironomidae (March, May and June 1977) and *H. amabilis* (June 1976). Annelida were always present in low numbers at the sites of group A and never comprised greater than 5% of the fauna at any time (Fig. 3.10). They were most abundant (about 40 per gram dry weight of macrophyte) in June 1977 (Fig. 3.9b). Overall invertebrate densities at site group A were highest in March 1977 and lowest in December 1976 (Fig. 3.10).

(2) Site group B

At site group B, two macrophytes (*Myriophyllum propinquum* and *Ranunculus fluitans*) were sampled but both species were collected on only four occasions (November and December 1976, March and April 1977). In September 1976 only *R. fluitans* was collected, and in each of the remaining four months only *M. propinquum* (Appendices 2.7 and 2.8). However, at most times when both *Myriophyllum* and *Ranunculus* were collected there was a high correlation between the percentage composition of invertebrate communities (by major taxa) on both plants (2 Nov. 1976 Spearman's Rank Correlation Coefficient (Rs) = 0.886, Students t = 3.816, $P < 0.010$; 2 Dec. 1976 Rs = 0.829, t = 2.960, $P < 0.025$; 8 Apr. 1977 Rs = 0.886, t = 3.816, $P < 0.010$). Only in March 1977 was there no significant correlation (Rs = 0.421, t = 0.929, NS) due to a small sample of *Ranunculus* on this date (Appendix 2.8). Consequently, since there was normally no significant difference between the invertebrate communities on *Myriophyllum* and *Ranunculus* (in terms of the percentage composition of major taxa), the absence of a collection of *Ranunculus* or *Myriophyllum* should not change markedly the overall pattern of community composition at site group B as shown on Fig. 3.11).

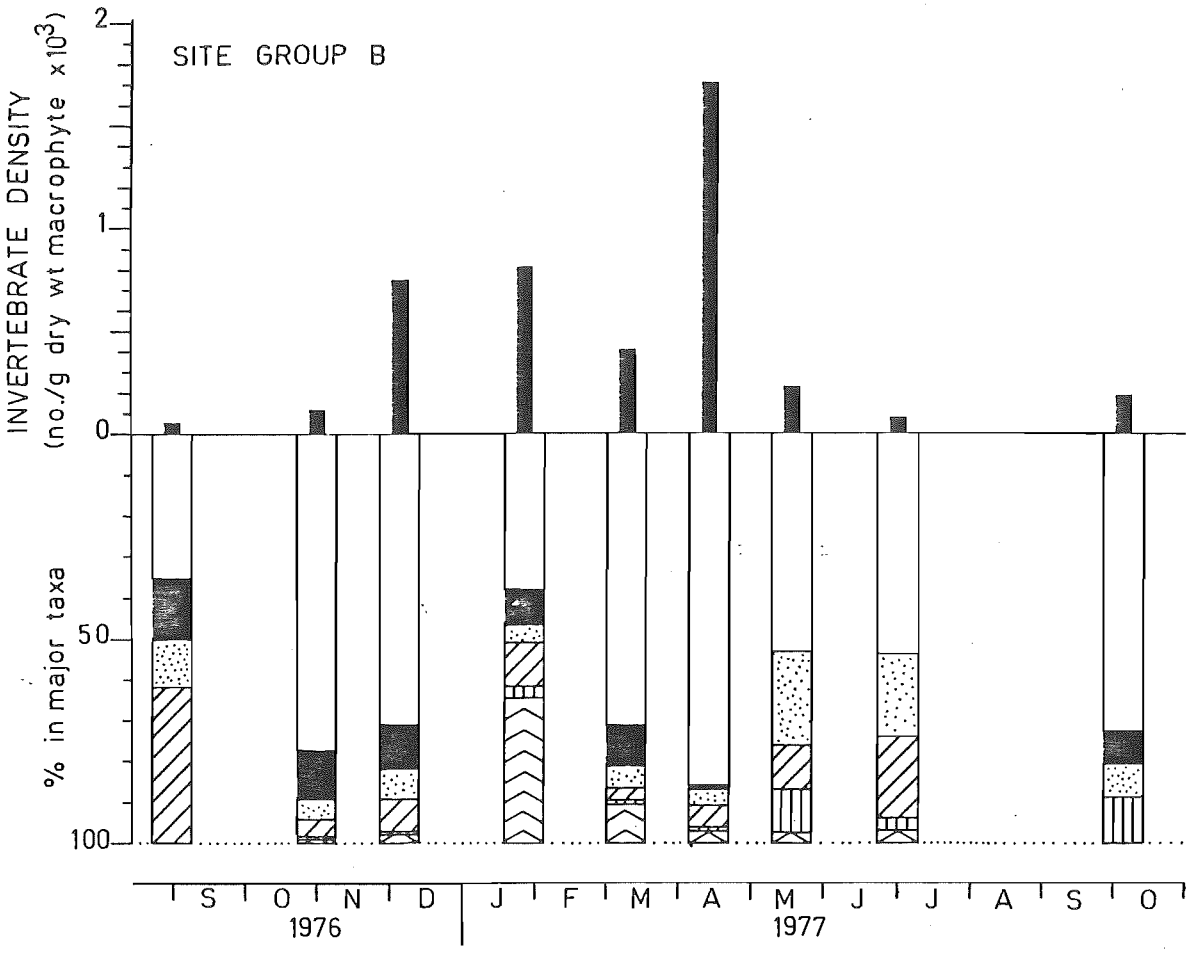


Fig. 3.11 Seasonal changes in total invertebrate density and percentage composition of invertebrate communities (in terms of major taxa) at site group B during the sampling period. (Key to major taxa given in Fig. 3.2.)

Usually the invertebrate community at site group B was dominated by Mollusca (35.3 - 85.9%). Only in September 1976 was the percentage representation of Mollusca exceeded by that of another group, viz., Crustacea (38.2%, Fig. 3.11). The pattern of molluscan abundance at site group B showed certain similarities to that at site group A although peak densities occurred one month later (in December 1976 and April 1977). The decline in abundance of Mollusca (Fig. 3.9f), and most of the other taxa, after April 1977 at site group B was due to die-back of *Myriophyllum* and *Ranunculus* in winter (and consequent sampling difficulties). *C. viridissima* again showed marked seasonality with peak abundance in January 1977 (Fig. 3.9a), and absence in September 1976 and October 1977. *Chlorohydra* comprised between 0 and 35.4% of the invertebrate community of this site group (Fig. 3.11). Abundance of Annelida was similar to that at site group A with relatively low numbers present at all times of year (Fig. 3.9b), although at this site this group comprised up to 10.8% of the community in May and October

1977 (Fig. 3.11). Densities of Crustacea at site group B were, on average, lower than at any of the other site groups (Fig. 3.9c), but the seasonal pattern was much the same as at site group C if allowance is made for the absence of samples for July 1977. Peaks in abundance of Crustacea occurred in January and April 1977. Insecta comprised between 3.9% and 22.6% of the community at site group B (Fig. 3.11) with peak abundances in December 1976 and April 1977. The major contributors to the December peak were Hydroptilidae (86.7%) and of these 90.8% were early instars (i.e., pre-cased = pre-fifth instar larvae). The April peak was due to pre-cased Hydroptilidae and also Chironomidae larvae. Acarina at site group B showed a clear seasonal pattern of abundance, not unlike that at site groups A and C, with a summer peak and a winter low (Fig. 3.9c). *H. lemnae* was the dominant mite up to and including January 1977 and thereafter *Piona* comprised a greater proportion of the declining population. Overall invertebrate densities at site group B generally were highest in summer and lowest in winter (Fig. 3.11). Very large numbers of small *P. antipodarum* were responsible for the greater part of the peak in invertebrate abundance in April 1977 (Figs. 3.9f and 3.11).

(3) Site group C

Mollusca were the dominant group in eight of the ten months sampled (Fig. 3.12) although the dominance was not as marked as at the other three site groups (Figs. 3.10, 3.11 and 3.13). Between 30.4% and 72.3% of the community at site group C comprised Mollusca, with the highest densities of *P. antipodarum* and *G. corinna* in April and May. Seasonal fluctuations in mollusc abundance in this, the most stable habitat type, were less marked and densities were generally lower than those at other site groups (Fig. 3.9f). *Chlorohydra* and Crustacea were almost equally numerous members of the community at site group C. Seasonality in abundance of *Chlorohydra* was very marked with peak numbers in April 1977; numbers in September and October were low. *Chlorohydra* comprised between 2.7% and 34.5%, by numbers, of the community at this site group (Fig. 3.12). There were also marked changes in abundance of Crustacea with peaks in January (Copepoda 53%, Cladocera 46%), April (Copepoda 86%) and July (Cladocera 84%) 1977 (Fig. 3.9c). Copepoda (*Eucyclops serrulatus*) were more abundant than Cladocera (mainly *Bosmina* and *Graptoleberis*) in all months sampled except September 1976 and July 1977. Ostracoda were of minor importance numerically in the habitats of this site group. Annelida were more

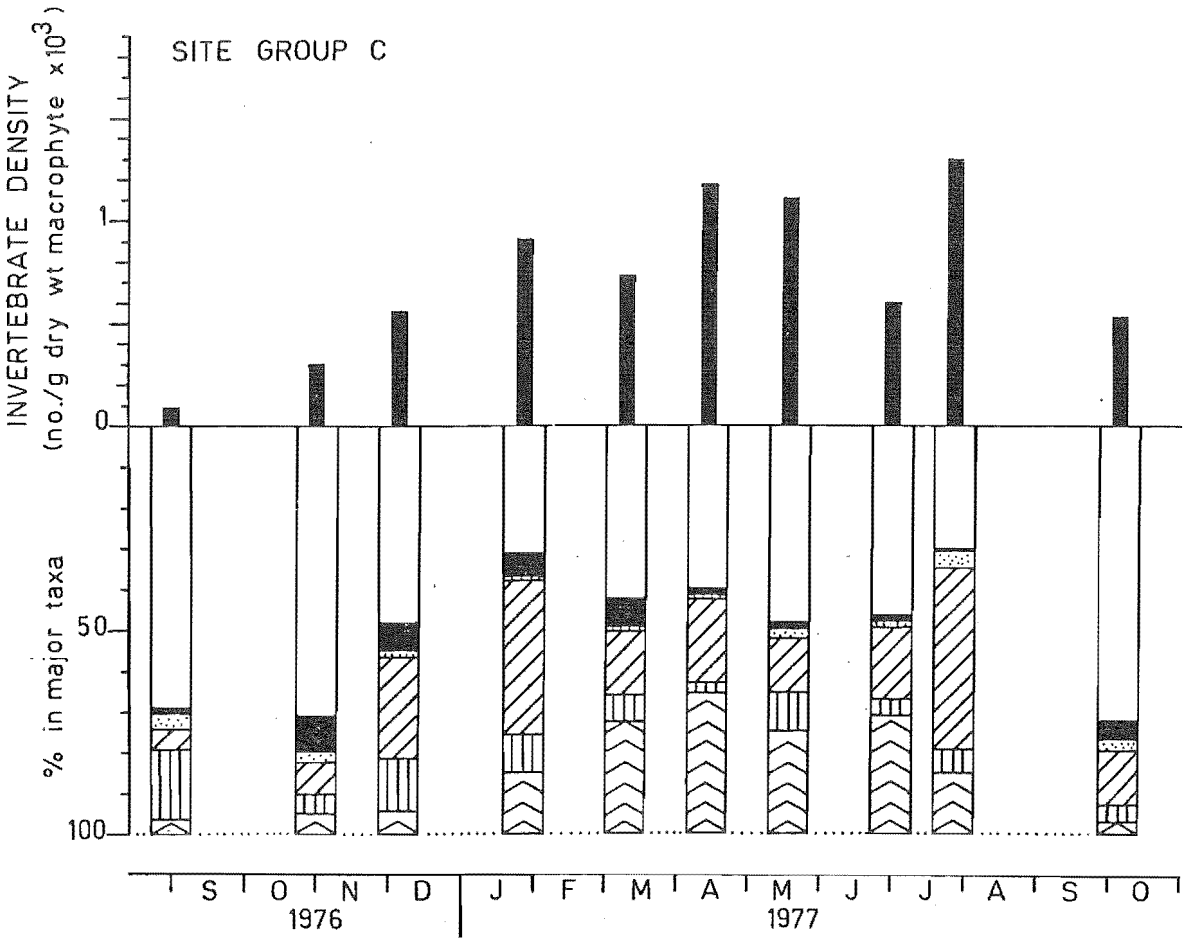


Fig. 3.12 Seasonal changes in total invertebrate density and percentage composition of invertebrate communities (in terms of major taxa) at site group C during the sampling period. (Key to major taxa given in Fig. 3.2.)

common in invertebrate communities at site groups C and D than in groups A and B (which were in the eastern sampling zone). At site group C, Annelida comprised between 2.4% and 17.1% of invertebrate numbers with peak densities over the 1976 - 1977 summer, in May 1977 and July 1977. Unidentified Oligochaeta contributed most to the pattern of abundance but the May peak was boosted by high numbers of *Chaetogaster* (Fig. 3.9b). Acarina abundance at site group C showed a clear seasonal pattern with a summer peak and winter low (Fig. 3.9e). This same trend was seen also at the other site groups. As at site group B, *H. lemnae* was dominant early in the sampling period (up to January 1977) and *Piona* thereafter. *T. novus* was present in much higher densities in January and March 1977 than at other times (see Appendix 2). The representation of Acarina in the community at site group C varied from 0.5% (July 1977) to 9.0% (November 1976). The *Elodea* monoculture that comprised site group C was generally the poorest macrophyte habitat in

Lake Grasmere for Insecta. Insecta comprised between 0.8% and 4.4% of the community at this site group and the peaks in seasonal abundance were almost entirely due to Chironomidae larvae (May and July 1977, Fig. 3.9d).

Overall invertebrate densities at site group C were lowest in September with peaks in January (Crustacea, Acarina), April/May (*Chlorohydra*, Crustacea), and July (Crustacea) (Fig. 3.12).

(4) Site group D

Mollusc densities at site group D showed similar patterns of seasonal abundance to those at the other site groups. The peak in abundance in April 1977 was in common with site group B (Fig. 3.9f). Mollusca comprised between 47.4% and 87.1% of the community at site group D (Fig. 3.13). Crustacea were the next most common group (5.3 - 31.1%, Fig. 3.13) with peak abundances in late summer and autumn - early winter. Ostracoda were common at all sites of site group D (and at site group A but not at other site groups) and contributed most to crustacean abundance in November 1976 and May 1977. In January 1977 Cladocera (84%) dominated the Crustacea, whereas Copepoda were dominant in March (57%) and June (64%). In May, the percentages of Copepoda and Cladocera were about equal (39 - 40%) with Ostracoda (20%) comprising the balance of the Crustacea. Site group D encompassed the most frequented habitats for insects in Lake Grasmere, both in terms of numbers of taxa (14 species plus about nine species of Chironomidae) and numerical abundance (Fig. 3.9d). Insecta constituted between 3.3% and 18.4% of the fauna at this site group (Fig. 3.13) and showed marked seasonality. Peaks in abundance, mainly *Paroxyethira hendersoni* and Chironomidae, occurred in January and May - July 1977 (Fig. 3.9d). Annelida were also most represented in site group D (0.6 - 25.3%, Fig. 3.13) relative to the other site groups. The pattern of abundance was similar to that at site group C except that peaks were more pronounced. As at site group C, the May peak was boosted by large numbers of *Chaetogaster*. The July peak was mostly unidentified oligochaetes (84%) and the January peak comprised about 57% unidentified oligochaetes and 43% *Chaetogaster*. Site group D comprised sites in which mites, especially the oribatids *H. lemnae* and *T. novus*, were well represented. The early dominance of *H. lemnae* (to January 1977) was a feature shared with the other site groups, however the dominance of *Piona* was short-lived (only March 1977).

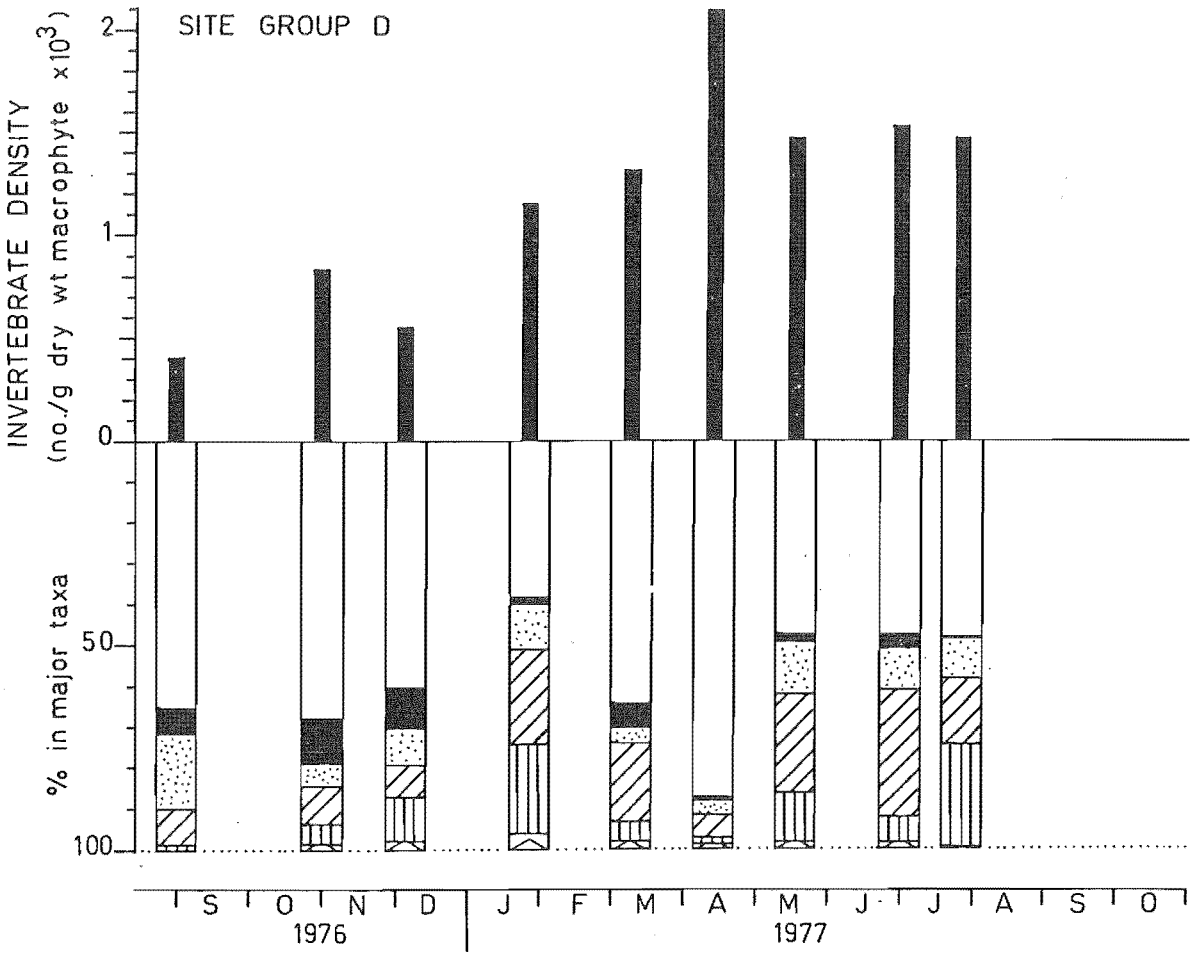


Fig. 3.13 Seasonal changes in total invertebrate density and percentage composition of invertebrate communities (in terms of major taxa) at site group D during the sampling period. (Key to major taxa given in Fig. 3.2.)

H. lemnae (April and October 1977) and *T. novus* (May, June and July 1977) were dominant thereafter. Larval *T. novus* were most abundant in late summer and autumn (see Appendix 2). Mites comprised between 1.7% and 11.0% of the fauna at site group D (Fig. 3.13). *Chlorohydra* was not well represented at this site group (0 - 3.7%) (Fig. 3.13). However the seasonal pattern of abundance was similar to that at site group B with maximum numbers in January 1977.

Total invertebrate abundance at site group D was usually greater than at any other site group but the seasonal pattern was most similar to that at site group A and was influenced to the greatest extent by mollusc abundance (mainly *P. antipodarum*).

3.4 CONCLUSIONS

3.4.1 The Composition of Invertebrate Communities at the Site Groups in Terms of Species Groups and Major Taxa

The most notable feature of the taxonomic composition of invertebrate communities of the macrophyte zones of Lake Grasmere was the numerical dominance exhibited by a relatively small number of species. The 13 taxa of species group 6 comprised between 95.5% (site group D) and 99.7% (site group C) by numbers of the invertebrate communities at the site groups (Table 3.17). The dominance of species group 6 (which comprised those species that occurred at every site sampled) was, to a large extent, due to *P. antipodarum* which was numerically dominant at each site group (36.2 - 70.6%) (Table 3.18). Only at site group C was its dominance approached by *C. viridissima* (24.9%). Furthermore, only six taxa (*P. antipodarum, C. viridissima, E. serrulatus, G. corinna,* Cladocera, and *H. lemnae*) contributed more than 5% (by numbers) to the fauna at any site group. The numerical contribution of the remaining nine species groups to invertebrate abundance was minor (0.3 - 4.5%) (Table 3.18). These minor species groups (i.e., all except species group 6) contributed to varying degrees to the communities of the four site groups (Table 3.17). The benthic species of group 7 were next in abundance to species group 6 at site groups D (3.8%), A (1.2%) and C (0.2%) whereas at site group B species group 5 (= *P. tillyardi*) filled second place (2.01%). No other species group contributed more than 0.75% to the invertebrate community at any site group (Table 3.17). Marked differences were evident in the contributions of three species groups to the communities at site groups A and B on the one hand, and C and D on the other. Species groups 1 and 5 were more prominent members of the communities at eastern sites (A and B) than in other areas, whereas *X. zealandica* (species group 8) was found only in site groups C and D (Table 3.17). Although Mollusca were the dominant taxonomic group (by numbers) in the invertebrate communities at each site group (43.7 - 72.6%) (Table 3.19) and *P. antipodarum* was the most common species at all sites, there were marked differences in the distributions of *G. corinna, P. variabilis* and *S. novaezelandiae* (Tables 3.9 and 3.20).

Crustacea and Coelenterata were the only other major taxa that constituted greater than 10% of the fauna of any site group (Table 3.19). *C. viridissima* (Coelenterata) was a prominent component of the community at site group C (primarily due to its seasonal appearance at very high densities), whereas Crustacea constituted greater than 10% of the communities at site groups C (due to planktonic immigrants), D and A. Annelida had proportionately greater representation at sites with benthic influences (especially at site group D). Mites (except for

site group B) and insects (except for site groups B and D) were less than 5% of the fauna at any site group.

Table 3.17 Percentage contribution (by numbers) of the individual taxa of the different species groups to invertebrate communities of the site groups (September 1976 - October 1977). * = < 0.01%, - = not present. (See also Table 3.18 for details of species group 6.)

Taxa	Site group A	B	C	D
Species group 1	0.25	0.67	0.01	0.04
Sigara arguta	-	0.07	0.01	*
Hudsonema amabilis	0.21	0.56	*	0.04
Physastra variabilis	0.04	0.04	-	-
Species group 2	0.09	-	0.05	0.04
Glossiphonia multistriata	0.02	-	*	*
Diaprepocoris zealandiae	0.07	-	0.04	0.03
Species group 3	0.08	0.41	-	0.15
Pycnocentrodes aureola	0.04	-	-	0.06
Nymphula nitens	0.04	0.41	-	0.09
Species group 4 *(Triplectides cephalotes)*	-	0.04	0.02	0.17
Species group 5 *(Paroxyethira tillyardi)*	0.73	2.01	0.05	0.11
Species group 6 (see Table 3.18)	97.61	96.61	99.66	95.47
Species group 7	1.20	0.26	0.17	3.76
Nematoda	0.12	0.07	0.12	0.87
Ostracoda	0.71	0.15	0.03	2.31
Sphaerium novaezelandiae	0.37	0.04	0.02	0.58
Species group 8 *(Xanthocnemis zealandica)*	-	-	0.04	0.05
Species group 9	*	-	*	0.17
Oxyethira albiceps	-	-	-	0.08
Oecetis unicolor	-	-	-	0.08
Arrenurus sp.	*	-	*	0.01
Species group 10	0.04	-	-	0.03
Antiporus strigosulus	0.01	-	-	-
Deleatidium sp.	*	-	-	0.01
Zelandobius furcillatus	0.03	-	-	0.02

The ranking of major taxa at each site group on a percentage by numbers basis (e.g., at site group A : Mollusca = 1, Crustacea = 2, Coelenterata = 3, Acarina = 4, Insecta = 5 and Annelida = 6, Table 3.19) tends to bias representation in favour of taxa with high densities that

may be highly seasonal (e.g., Coelenterata at site group C). A more realistic assessment of the year-round ranking of taxa in the communities at site groups may, perhaps, be obtained by using a points method that gives equal weight to each month's samples from each site group (see Sanders 1960). Table 3.21 lists the biological index values of the major taxa determined first by ranking the taxa according to abundance from 1 to 6 for each month for each site group. A rank of 1 is then given a value of ten points, a rank of 2 nine points, and so on, and the points added to give the biological index value. Thus, if a taxon is ranked first in each of, say, ten months it will gain 100 points, the highest possible score. The highest possible biological index value for taxa in site groups A, B and D was 90 (nine months' data) and for site group C 100 (ten months' data).

Table 3.18 Percentage occurrence (by numbers) of invertebrate taxa comprising species group 6 at each site group. Data from all quantitative samples combined (September 1976 - October 1977).

Taxa	Abundance ranking	Site group A	B	C	D
Potamopyrgus antipodarum	1	70.56	69.47	36.17	53.88
Chlorohydra viridissima	2	8.11	6.52	24.94	1.31
Eucyclops serrulatus	3	8.37	5.06	12.44	7.56
Gyraulus corinna	4	1.59	0.82	7.53	6.99
CLADOCERA	5	1.44	2.16	7.67	6.50
OLIGOCHAETA (except *Chaetogaster* sp.)	6	1.49	0.15	4.01	4.12
Chaetogaster sp.	7	0.25	1.15	2.07	2.87
Hydrozetes lemnae	8	1.90	5.06	1.03	2.49
CHIRONOMIDAE	9	0.79	1.38	1.08	4.09
Piona uncata exigua	10	1.81	2.12	1.52	0.56
Paroxyethira hendersoni	11	0.50	2.12	0.68	3.24
Trimalaconthrus novus	13	0.49	0.34	0.41	1.45
Cura pinguis	16	0.31	0.26	0.12	0.42
All other taxa (see Table 3.17)		2.39	3.39	0.33	4.52

Table 3.19 Contribution of the major taxa (% by numbers) to the composition of invertebrate communities at the site groups, and for all site groups combined. (Data from all quantitative samples combined, September 1976 - October 1977.)

Taxa	Site group				Overall
	A	B	C	D	
Coelenterata	8.11	6.52	24.94	1.31	14.75
Annelida	2.19	1.63	6.36	8.29	5.57
Crustacea	10.52	7.37	20.14	16.37	16.40
Insecta	2.42	6.59	1.92	8.07	3.61
Acarina	4.20	7.52	2.96	4.51	3.80
Mollusca	72.56	70.37	43.72	61.45	55.87

Table 3.20 Percentage composition of Mollusca at each site group (all quantitative samples combined, September 1976 - October 1977).

Taxa	Site group			
	A	B	C	D
Gyraulus corinna	2.21	1.16	17.29	11.38
Physastra variabilis	0.07	0.05	-	-
Potamopyrgus antipodarum	97.21	98.73	82.66	87.68
Sphaerium novaezelandiae	0.51	0.05	0.05	0.94

Ranking of major taxa within site groups using biological index values (Table 3.21) gave a slightly different indication of their numerical importance at the site groups compared with the overall percentage composition of taxa (Table 3.19). The differences were most marked at site group B where Mollusca were the only group to retain their (first) ranking. The most notable difference at site group B was in the ranking of mites which were second on an overall percentage basis (Table 3.19) but only fourth on a points basis (Table 3.21). This change was due to marked seasonal variation in mite abundance at this site group (Fig. 3.18).

At the other three site groups the differences between the percentage and points methods were less marked and, except at site group D, involved single changes of only one rank. At site group D the extreme seasonality of Annelida (Fig. 3.9b) resulted in a higher ranking on a percentage basis (Tables 3.19 and 3.21). Although most differences appear relatively minor I believe that the biological index values give a more realistic overall assessment of the numerical importance of each of the major taxa at each site group. This method of evaluation is not influenced markedly by seasonal 'explosions' of abundance, except in so far as they affect ranking within the particular month/s of great abundance.

Table 3.21 Biological index values for major taxa at each of the four site groups (September 1976 - October 1977). Values for site groups A, B and D based on 9 months' data; site group C, 10 months' data.

Site group	Taxon	Rank 1	2	3	4	5	6	Biological index value
A	Mollusca	9						90
	Crustacea		5	2	2			75
	Acarina		1	4	2	2		67
	Coelenterata		3	2		1	3	64
	Insecta				5	3	1	58
	Annelida			1	1	2	5	52
B	Mollusca	8	1					89
	Crustacea	1	2	3	1	2		71
	Insecta		2	3	3	1		69
	Acarina		3	2	1	1	2	66
	Coelenterata		1	1	2	5		61
	Annelida		1	1	1	2	4	56
C	Mollusca	8	2					98
	Crustacea	2	2	6				86
	Coelenterata		4	2	1	2	1	76
	Annelida		1	1	6	2		71
	Acarina		1	1	2	3	3	64
	Insecta				1	3	6	55
D	Mollusca	9						90
	Crustacea		5	3		1		75
	Insecta		1	3	4	1		68
	Acarina		1	2	1	4	1	61
	Annelida		2	1	3	2		59
	Coelenterata					1	8	46

3.4.2 Comparison of Species Diversity and Invertebrate Density at Different Site Groups

Seasonal changes in species diversity, species evenness, species richness, and invertebrate densities have been discussed in previous sections. The following discussion is concerned with the differences or similarities in overall community composition at the site groups (all data combined, 2 September 1976 - 3 October 1977).

Overall species diversity was highest at site groups C and D with diversity at site group C having a greater evenness component than at site group D (Table 3.22). The *E. canadensis* 'monoculture' of site group C was the most homogeneous macrophytic habitat in Lake Grasmere and the one least subject to seasonal change (e.g., Fig. 3.8C). These factors tend to enhance species evenness.

The communities at site group D had 32 taxa, and the highest species richness component of diversity, whereas only 26 taxa were collected from site group C and this, when related to sample sizes, resulted in the relatively low value for Whittaker's species richness for site group C (Table 3.22). Habitat heterogeneity, which makes available a greater number of niches, was considered to be the main cause of high diversity (especially species richness) at site group D.

Table 3.22 Overall species diversity (H'), species evenness (J'), species richness (d), numbers of taxa, mean invertebrate densities (numbers per sample and numbers per g dry wt of macrophyte) and numbers of samples for each of the four site groups (September 1976 - October 1977).

	Site group			
	A	B	C	D
H'	0.54	0.57	0.80	0.80
J'	0.38	0.43	0.56	0.53
d	6.43	6.42	5.80	7.69
No. of taxa	27	22	26	32
Mean invertebrate density: No./sample	334.83	167.30	392.99	369.90
No./g	690.83	446.75	651.36	1064.65
No. of samples	47	16	78	39

The eastern sites (site groups A and B) were different, with lower total diversity and species evenness (Table 3.22). Whittaker's species richness values were similar for both of these site groups due to the relatively lower number of taxa collected from site group B being compensated for by (or perhaps related to) lower numbers of invertebrates in samples or fewer samples collected from site group B (Table 3.22). Species groups 2, 8, 9 and 10 were not collected in samples from site group B (Table 3.17) during the quantitative sampling program. Certain species (especially in species groups 2 and 10) possibly may have been present since they occurred in the adjacent sites of site group A (Table 3.17). It is likely, therefore, that the similar species richness values, as indicated by Whittaker's index, are a true indication of similarities between invertebrate communities at site groups A and B (Table 3.22).

Invertebrate densities at eastern sites (site groups A and B) tended to be lower than elsewhere when expressed as numbers of invertebrates per sample. Highest densities were recorded from the most homogeneous site group (C) and lowest densities from the least intensively sampled site group B (Table 3.22). Expression of invertebrate density as numbers per g dry wt of macrophyte habitat altered the situation. Highest densities were then recorded from site group D and lowest again from site group B. Site groups dominated by *E. canadensis* (C and A) showed the least proportional increase in density relative to other site groups when invertebrate densities were converted from nos./sample to nos./g dry wt of macrophyte (Table 3.22). The stunted macrophytes and the inclusion of benthic animals at site group D were considered to contribute to high invertebrate densities on a numbers/dry wt of macrophyte basis.

3.4.3 Community Similarity

Table 3.23 presents average values of CC and PSc between sampling dates and for replicate samples from individual sites for each site group. Replicate samples are, by definition, expected to be of similar composition since they are collected from the same area of the habitat on the same sampling date. PSc values for replicate samples were high (> 66%) suggesting that the sampling method was good for estimating the percentage abundance of the commoner species. Generally, values of CC were lower and more variable (42 - 70%) indicating that, especially in some habitats (e.g., E *I* and E *M*), there was a greater

proportion of relatively uncommon species and the sampling procedure was not adequate for these species.

Average values of CC and PSc between sampling dates cannot be compared directly with values from replicate samples since the time periods between sampling dates influence markedly the numerical values of CC and PSc obtained.

However, an indication of the overall amount of seasonal change in invertebrate abundance was obtained by sum of squares analysis of a 'site X times' matrix of invertebrate densities (in terms of numbers/sample) (i.e., 13 sites X 10 sampling times). The sum of squares variation in total invertebrate density at sites was 21,499.6 and over times was 43,843.5. This shows that there was 2.039 times more 'variation heterogeneity' in times than sites. In other words, temporal changes were more pronounced than spatial variations.

Table 3.23 Average values of CC and PSc (± standard deviation) between sampling dates and for replicate samples from individual sites, for each site group (September 1976 - October 1977).

	CC	PSc
Site group A (between dates)	69.87 ± 9.65	77.02 ± 7.97
E *E* 2 (replicates)	59.40 ± 12.36	83.53 ± 8.05
E *I* (replicates)	42.00 ± 7.25	66.20 ± 4.55
Site group B (between dates)	52.26 ± 16.48	64.94 ± 13.30
E *M* (replicates)	47.00 ± 4.24	79.00 ± 2.83
Site group C (between dates)	73.08 ± 7.42	74.30 ± 12.22
N *E* 2 (replicates)	68.37 ± 14.77	74.73 ± 13.13
W *E* 2 (replicates)	69.97 ± 11.58	69.07 ± 12.01
Site group D (between dates)	71.52 ± 11.77	70.45 ± 12.25
S *I* (replicates)	65.75 ± 14.01	74.25 ± 11.38
W *I* (duplicate)	55.60 -	71.63 -

CHAPTER IV

TROPHIC INTERRELATIONSHIPS OF SOME MACROPHYTE-ASSOCIATED INVERTEBRATES

4.1 INTRODUCTION

In recent years it has become increasingly apparent that knowledge of trophic relationships is a necessary prerequisite to an understanding of energy flow and community dynamics in freshwater ecosystems (e.g., Cummins 1973). Compared with rocky shore, stream and sediment habitats, the macrophyte beds of a lake present, to the animals that live in them, a habitat of much greater physical and chemical complexity. Because of this, and formidable problems of sampling (see Chapter III), it is not surprising that the investigation of macrophyte-zone animals of lakes has progressed little beyond the stage of observation and lags behind studies of stream animals (Moss 1980).

Very complex food webs must exist within macrophyte beds (Moss 1980). The study of trophic relationships in freshwater communities reveals a great diversity of available foods and a variety of methods of resource utilisation (Anderson & Cummins 1979). Because of such complexity, attempts have been made to elucidate nutritional relationships of aquatic invertebrates by defining trophic categories in terms of the food itself (herbivores, detritivores, carnivores, i.e., trophic levels) or according to the way it is obtained (e.g., the shredder, collector, scraper and predator functional groups of Cummins (1973)). Almost all stream invertebrates are omnivores but usually take a greater proportion of plant or animal food at particular stages of their life histories (Moss 1980). Dietary shifts in later instars are well documented for a number of species (Winterbourn 1971b, Crosby 1975, Fuller & Stewart 1977, Anderson & Cummins 1979). In these instances difficulties are encountered in assigning invertebrates to functional groups. Nevertheless, the concept of functional groups has proven useful in analysing the partitioning of food resources on a community basis in lotic ecosystems (Cummins 1973, 1974, Merritt & Cummins 1978, Mackay & Wiggins 1979, Wiggins & Mackay 1978, Cowie 1980).

The food habits of freshwater invertebrates in New Zealand are relatively little known. Although recent works by Winterbourn (1974),

Crosby (1975), Devonport & Winterbourn (1976), Winterbourn & Davis (1976), Winterbourn (1978) and Cowie (1980) have documented the specific food habits of a number of stream insects (mainly Megaloptera, Ephemeroptera, Plecoptera and Trichoptera), very little work has been done on invertebrates living in lentic environments. Babington (1967) examined the gut contents of three species of leptocerid (Trichoptera) larvae but not in detail, and Greig (1976) investigated the feeding of a species of the more typically lotic *Deleatidium* (Ephemeroptera) in Lake Grasmere. Most information on the diets of lake-dwelling invertebrates in New Zealand is non-quantitative and based solely upon observation or generalisations from work on related overseas species. Consequently, a primary aim of this study was to obtain quantitative information on the food habits of a number of lake-dwelling invertebrates in order to gain some insight into the organisation of food webs within the macrophyte zone.

The choice of study animals was influenced by several considerations, including that they had to be present in large enough numbers to make regular sampling practicable. I wanted to examine the food habits of a range of invertebrates that could be expected to belong to different functional groups (e.g., a shredder, *Nymphula nitens* (Lepidoptera) and a predator, *Xanthocnemis zealandica* (Odonata)). Also, it was anticipated that a study of closely related species or genera (e.g., the two hydroptilid caddisflies, *Paroxyethira hendersoni* and *P. tillyardi,* and the two leptocerid caddisflies, *Hudsonema amabilis* and *Triplectides cephalotes*) and more detailed examination of species that had been investigated previously in other lakes and ponds (e.g., *T. cephalotes* and *H. amabilis* (Babington 1967), *X. zealandica* (Crumpton 1979) would provide interesting comparative data. A further logical choice, in view of its numerical dominance in the macrophyte beds of Lake Grasmere, and abundance in other freshwater habitats, was the snail, *Potamopyrgus antipodarum*.

The food habits of freshwater invertebrates have been studied using a variety of methods, viz., field observations (Welch 1924, Berg 1941, Bay 1972), laboratory observations (Welch 1916, 1924, Berg 1941, Nielsen 1948, Babington 1967, Satija 1974), food preference experiments (Lawton 1970a,Skoog 1978, Anderson & Cummins 1979 and references therein, Anderson & Sedell 1979 and references therein), gut content analyses (Muttkowski & Smith 1929, Slack 1936, Nielsen 1948, Hanna 1957, Mecom & Cummins 1964, Babington 1967, Tarwid 1969, Thut 1969, Winterbourn 1971a, 1971b, 1973, 1974, 1978 , Satija 1974, Crosby 1975, Soszka 1975b, Devonport & Winterbourn 1976, Winterbourn & Davis 1976, Crumpton 1979,

Cowie 1980), faecal analyses (Pritchard 1964, Lawton 1970a, Soszka 1975b, Skoog 1978, Thompson 1978a and b), serological techniques (Davies 1969, Davies, Wrona & Linton 1979) and radioactive tracers (Rodina & Troshin 1954, Sorokin 1966, Hargrave 1970, Sedell 1972, Nash 1974, Greig 1976).

Gut content analyses have been the usual methods used to determine the general nature of food ingested by freshwater invertebrates. Resistant remains - spines, mouthparts, carapaces, diatom frustules and macrophyte cell walls - give clues to what has been ingested, but soft-bodied prey (e.g., flatworms (Davies 1969, Davies & Reynoldson 1969, 1971)) may leave no trace. In addition, the presence of a material in the digestive tract does not prove nutritional importance and differential rates of digestion of food items also renders the nutritional interpretation of visual gut content analyses difficult (Cummins 1973). The most rapidly digested items, and therefore the least likely to be observed, might be of greatest nutritional significance. In spite of these problems, gut content analyses have proven useful in giving an indication of the trophic relationships of aquatic invertebrates.

The technique of faecal analysis was chosen in this study. It has disadvantages similar to those described above for gut content analyses, but is less time consuming and more easily applied to invertebrates that are too small to dissect easily.

Comparisons of faecal pellet analyses and gut content analyses made early in the study showed no significant qualitative differences between the two methods. Since most investigators have equated the composition of gut contents with food intake (i.e., ingestion), I have assumed, for simplicity in the following discussion, that the composition of the faeces agrees with the composition of food ingested.

4.2 METHODS

4.2.1 Faecal Analysis

(1) Field procedure. The species whose faecal material was analysed quantitatively (Table 4.1) were collected from areas of the lake where they were most abundant. *P. tillyardi*, *H. amabilis* and *P. antipodarum* were collected from shallow beds of *E. canadensis* and *I. alpinus* in the eastern sampling area; *X. zealandica*, *P. hendersoni* and *T. cephalotes* from the *E. canadensis* 'monoculture' in the northern and western sampling areas; and *Nymphula nitens* from *M. propinquum* in the eastern sampling zone. The animals were obtained using a 200 µm

Table 4.1 Size classes of invertebrates used in faecal analyses. htl = hind-tibia length, hw = head width, tsh = total shell height.

Species (parameter measured)	Size group	Size range (mm)	Instar
Xanthocnemis zealandica (hw)	1	⩽ 2.0	
	2	2.1 - 3.0	
	3	⩾ 3.1	F
Nymphula nitens (hw)	1	⩽ 0.875	
	2	0.876 - 1.100	
	3	⩾ 1.101	
Paroxyethira hendersoni (hw)		0.23	F
Paroxyethira tillyardi (hw)		0.18	F
Hudsonema amabilis (htl)		⩽ 0.30	2
		0.31 - 0.45	3
		0.46 - 0.75	4
		⩾ 0.76	5
Triplectides cephalotes (htl)		⩽ 0.50	2
		0.51 - 0.80	3
		0.81 - 1.50	4
		⩾ 1.51	5
Potamopyrgus antipodarum * (tsh)		⩾ 3.50	

* *P. antipodarum* of a smaller size class (tsh < 3.50 mm) were collected also but densities of food material on filters were not enough to make enumeration worthwhile. The division between the size classes represents the size at which *P. antipodarum* become mature (Winterbourn 1970b).

mesh hand-net on the end of a 2 m aluminium pole. The net was moved to and fro through the appropriate submerged macrophyte beds and its contents were emptied into a white tray for sorting. All individuals of the chosen species were removed from the sample in the tray and isolated individually in 40 mm × 25 mm snap-top glass tube vials containing about 3 ml of

filtered tap water. This procedure was continued until at least ten individuals of the dominant size classes had been collected. The remainder of each sample was transferred to a plastic bag and preserved with formalin for subsequent microscopic sorting and use in life-history analyses (Chapter V).

The species under study required different treatments to obtain best results. All were washed in filtered water prior to isolation and the cases of *T. cephalotes* larvae were removed to minimise contamination by non-faeces-derived material, and so that the starved larvae could not feed on their cases. Hydroptilidae, because of their minute size, yielded best results when several individuals were placed in each vial.

(2) Laboratory procedure. The isolated invertebrates were left to produce faeces over a period of 12 to 24 hours. The animals were then removed from the vials, measured, and preserved in 70% alcohol. About 1 ml of absolute alcohol was added to each of the vials to prevent bacterial or fungal interference occurring prior to further treatment. The lid of each vial was labelled with the size of the invertebrate from which the faeces had been obtained.

The contents of each vial were transferred into a plastic 15 × 50 mm vial, using filtered water as necessary, and subjected to 10 - 30 seconds of ultrasonic vibration in a Bransonic 3 ultrasonic generator half-filled with water. This broke up the faecal material and dispersed it evenly throughout the liquid. Plastic vials withstood the rigours of repeated ultrasound better than glass. The suspended faecal material was washed into a small (16 mm internal diameter) Millipore funnel and filter column fitted with a 0.45 µm pore size filter paper. The filter column was fitted with a perspex 'reduction disc' of my own design to reduce the filtering area to 10 mm diameter. The aim of this was to increase the density of faecal material on the filter and so facilitate enumeration, and to keep individuals' faeces separate as far as possible.

The filter paper used was Gelman Metricel GA-6 (pore size 0.45 µm) which was obtained in 200 × 250 mm sheets (Part No. 60180). Squares of 12 × 12 mm (approx.) were cut, ready for use, with a sharp scalpel. (This method was considerably more economical than that using ready-made 25 mm diameter filters (Part No. 60172) and also enabled up to four filters to be mounted on each microscope slide, thus saving on materials, storage space and handling time). After filtration, under low vacuum,

the filter papers were allowed to dry, under cover, at room temperature. They were then mounted on standard microscope slides using lactophenol-PVA stained with Lignin Pink. After about a week in a slide-drying oven (at 66°C) the slides could be examined.

Slide-mounted filters were examined at 450× magnification under phase contrast using a Meopta C36 Bi Microscope (Type 56243). Six fields of view were examined per filter. Diatom genera or species were recognised and counted and the projected areas of macrophyte, detritus, filamentous algae, and animal remains were estimated using a gridded eyepiece. The counts of each diatom genus or species were converted to an areal basis by multiplying by standard areas (Table 4.2) calculated from measurements of several diatoms of the same type and size. Patrick (1959), Barber (1962), and Weber (1971) were useful aids to identification, as were a preliminary list of diatom genera from stony substrates in Lake Grasmere given by Greig (1976) and the list of planktonic diatoms recorded by Stout (1972).

In order to facilitate the identification of animal remains in faecal pellets, a reference collection of potential prey invertebrates was prepared (using hot KOH, as necessary, to digest away soft tissues). Some of the criteria by which prey items were recognised are shown in Fig. 4.1. In addition, Nematoda were occasionally present intact in faecal pellets; the cladoceran, *Simocephalus vetulus* was recognised by the characteristic postabdomen and carapace; the cyclopoid copepod *Eucyclops serrulatus* was represented by typical limb segments and furcal rami; and ostracods were recorded as prey by the presence of valves and limbs. Among the insects recorded as prey items, hydroptilid caddisfly larvae were identified by the species-specific shapes of the frons, tarsal claws, and prothoracic sternites (see Chapter VI). Mandibles and limb segments were useful also but did not enable specific identification. Chironomid larvae were also readily identifiable, using head capsules, which often remained intact, or mandibles, labial plates and posterior proleg claws (see Chapter VI). In addition to the distinctive radula teeth, the gastropod mollusc *Potamopyrgus antipodarum* was recognised by the presence of shell fragments.

The sizes of *P. antipodarum* ingested were determined by measuring the total length (l) of an inner marginal tooth of the radula (Fig. 4.1J). All inner marginal teeth in the radula of snails of a given size were the same size. The following relationship was found between total shell height of *P. antipodarum* and the length of the

Table 4.2 Standard areas used to calculate the projected areas of diatoms in the faecal analyses of freshwater invertebrates from Lake Grasmere. Specific names of diatoms should be regarded as tentative (especially those species previously unrecorded from the Cass area). Previously recorded genera/species are denoted by the following superscripts:

S = phytoplankton, Lake Grasmere (Stout 1972)
G = periphyton on stones, Lake Grasmere (Greig 1976)
B = streams at Cass (Barber 1962)
D = Middle Bush Stream, Cass (Davis & Winterbourn 1977)
C = Cass area (checklist *in* Burrows 1977).

Diatom Genus	projected area ($mm^2 \times 10^{-4}$) (specific name/s)			
Asterionella[G]	3.10 *(formosa)*[S,C]			
Cocconeis[G,D]	2.18 *(placentula)*[B,C]			
Cyclotella[G]	1.77 *(kuetzingiana)*[S,C]			
Cymbella[G,D]	16.30 *(cistula)*[C]			
Diatoma	2.70 *(elongatum)*[S,B,C]	10.50 *(hiemale)*[C]		
Epithemia[G,D]	5.3 *(sorex)*[C]	12.20 *(turgida)*[B,C]		
Eunotia	8.00 *(cassiae)*[B]			
Fragilaria[G]	1.68 *(construens)*[B,C]	3.05 *(leptostaurum)*		
Gomphonema[G,D]	5.00 *(constrictum)*[C]	10.50 *(herculeana)*[C]	0.44 *(olivaceum)*	
Melosira[G]	2.02 *(granulata)*[S,B,C]			
Navicula[G]	6.80 *(radiosa)*[B,C]	4.73 *(reinhardii)*		
Opephora	20.0 *(martyi)*[B,C]			
Pinnularia	28.70 *(gibba)*[B,C]			
Rhoicosphenia[D]	3.24 *(curvata)*			
Rhopalodia[G,C]	1.70 (sp.)			
Stephanodiscus	2.85 *(dubius)*			
Synedra[G]	1.63 *(actinastroides)*	5.75 *(acus)*[C]		
Tabellaria	1.00 *(flocculosa)*[B,C]			

inner marginal tooth by dissecting radulae from snails of various sizes (2.6 mm to 8.6 mm tsh), mounting them on microscope slides, and measuring a number of teeth.

P. antipodarum tsh = 94.013 (length of inner marginal tooth) - 3.224 mm ($r = 0.998$).

Therefore, this equation was used to determine the sizes of *P. antipodarum* ingested by *H. amabilis* and *X. zealandica* larvae.

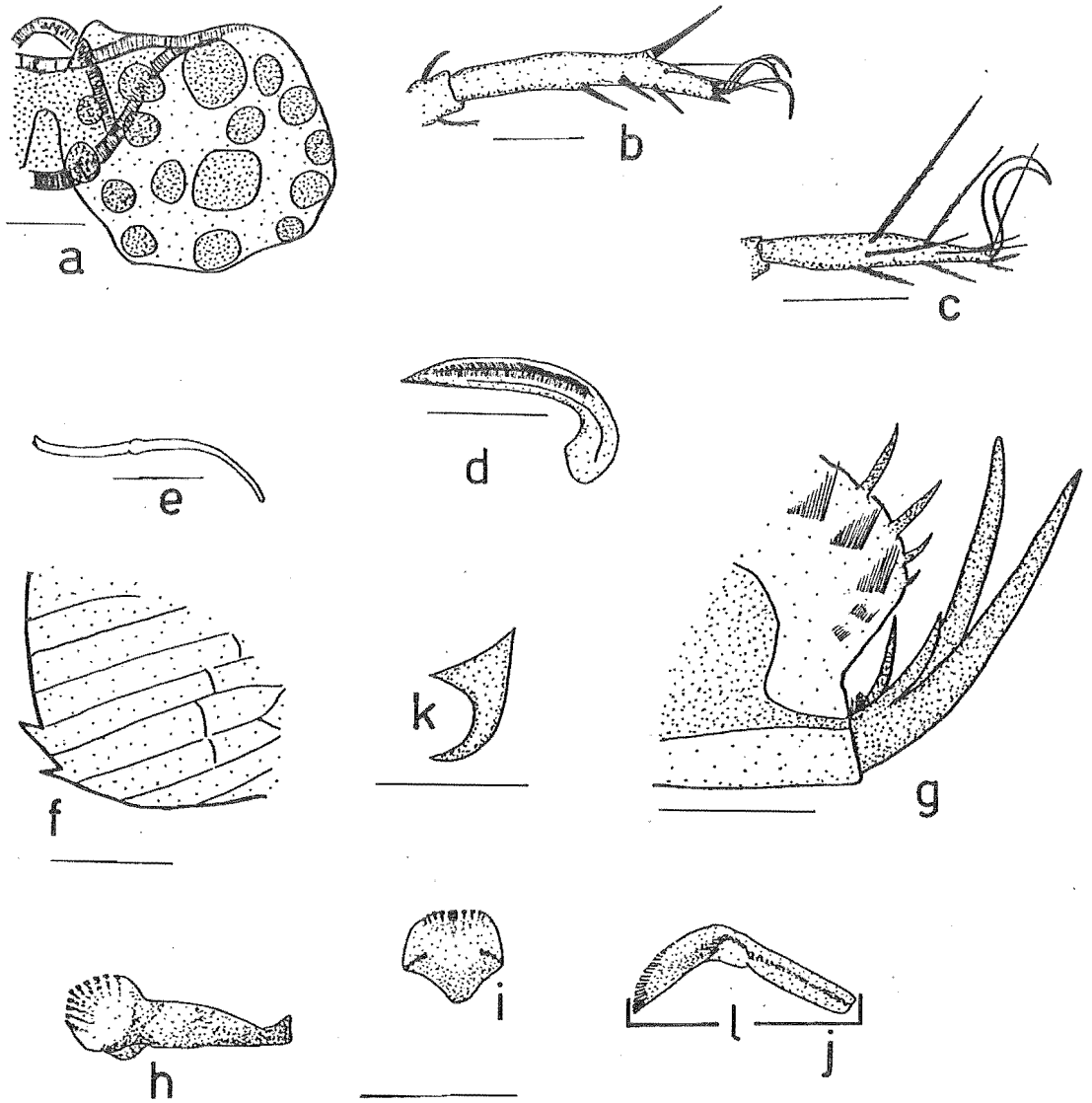


Fig. 4.1 Skeletal remains used to recognise prey items in faecal analyses. (Scale bars = 0.05 mm)

Acarina	a. *Piona uncata exigua:* part of genital plate of male.
	b. *Trimalaconothrus novus:* tarsus and tarsal claws of hind limb.
	c. *Hydrozetes lemnae:* tarsus and tarsal claws of hind limb.
	d. *Piona uncata exigua:* mandibular claw.
Oligochaeta	e. *Lumbriculus variegatus:* seta.
Cladocera	f. *Graptoleberis testudinaria:* postero-lateral margin of valve.
	g. *Alona* sp. postabdominal claws.
Mollusca	h. i. j. *Potamopyrgus antipodarum:* radula teeth (lateral, central and inner marginal) (showing length measurement, see pp. 92, 101-103 & 114-115).
Chironomidae	k. *Calopsectra funebris:* hook from posterior proleg.

The number of prey items present in each pellet was estimated easily for most prey species from the number of mandibles, head capsules, genital plates, etc. Oligochaetes and *P. antipodarum*, however, were recorded only as single occurrences whenever their characteristic remains were found in each pellet.

Most of the major food categories recognised during this study are well known (viz., diatoms, detritus, macrophyte, filamentous algae and animal remains) but the final category remains a mystery. S.R.T's, ('small round things') denoted by the diagonal striping on Fig. 4.2 (and subsequent figures), were about 9 µm in diameter and composed of a 'solid' core surrounded by a 'membrane' with a narrow space between. They were not like eggs of invertebrates, but rather were most likely to be of plant or fungal origin (pollen or spores?). They were never important quantitatively.

The importance of careful preparation of permanent slide-mounts of faecal material during studies of food habits should not be underestimated because ability to recognise various food items (especially fragments of prey) improves with experience. It is extremely valuable to be able to refer back to 'problem' slides which, in many cases, can be successfully re-analysed.

4.2.2 Periphyton Analysis

Lengths of macrophyte stem (*E. canadensis* and *M. propinquum*) were collected from various sites in each of the sampling areas of Lake Grasmere. The stems were stored in 70% alcohol prior to further treatment.

Lengths of 15 mm were cut in series down each stem beginning at the shoot tip. The periphytic coating of each length was removed by repeated ultrasonic vibration and washing in filtered water. Five cycles of ultrasonic treatment (30 seconds each) and washing with filtered water were sufficient to remove practically all of the periphyton from the plant surfaces. This was confirmed by microscopic examination of the plant surfaces and by examination of the filtrate from a sixth washing, which showed that very few diatoms remained attached to the plant. The washings from each section of stem were filtered through a Millipore filter column, and each filter paper was mounted on a microscope slide. Slide-mounted filters were examined as for invertebrate faeces (p. 92).

4.3 RESULTS AND DISCUSSION

4.3.1 Introduction

The results of faecal analyses are presented together with preliminary investigations on the nature of the periphytic coating on macrophytes, as a potential source of food. A comparison of the faecal analyses of the seven species examined (all months and instars or size classes combined) is given in Fig. 4.2. Where appropriate, differences in food habits between size classes or instars of the study species are discussed later, and the findings compared with previous work on the same, or related species from New Zealand or overseas.

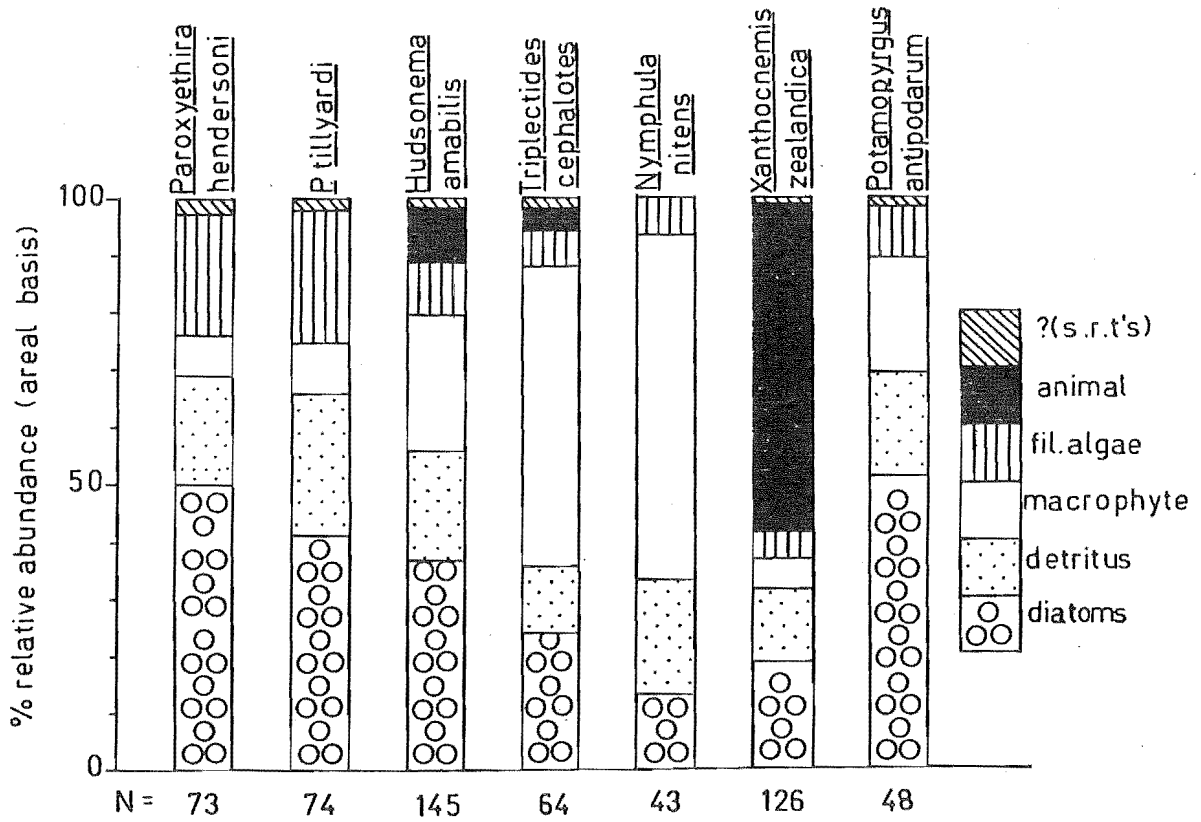


Fig. 4.2 Composition of faecal material of seven invertebrate species from Lake Grasmere, in terms of major food categories, on a projected area basis (July 1976 - November 1977). (All size classes combined, N = number of individuals examined.) Also given is the key to food categories (as used on this, and subsequent figures).

Very few obvious seasonal changes were apparent in either the composition of the faecal material in terms of major food categories (i.e., diatoms, detritus, macrophyte tissue, filamentous algae, animal remains and S.R.T's), or the generic composition of the diatom category.

4.3.2 Periphyton Analyses

Although initially I had intended to compare the composition of faecal material with the composition of available food in the environment on a regular basis (from periphyton and invertebrate sampling), it soon became apparent that this was not a practical proposition. The seven species whose faecal pellets were analysed were collected from different areas of the lake (see p. 89) and, in some cases, were undoubtedly feeding in different microhabitats. The work involved in regular quantitative sampling of periphyton from different microhabitats and different areas of the lake proved to be prohibitive. However, a few generalisations can be drawn from the limited number of quantitative periphyton analyses made and the more extensive qualitative studies.

Pieczyńska (1964) found that there was greater variability in species composition in old than young periphyton, and that various types of substrate had very similar communities provided that they were located in the same environment (e.g., in the same part of the littoral zone). This was also the case in the present study. Semi-quantitative and qualitative examinations showed great similarity in the composition of periphyton communities on different macrophytes from the same sampling areas in Lake Grasmere. On the other hand, certain differences were evident between periphytic communities from different areas of the lake. Notable amongst these differences was the apparently greater representation of *Rhoicosphenia* in diatom communities in the eastern sampling area compared to the western zone. Most other differences were minor and would add only confusion if attempts were made to correlate them with, for example, the food preferences of periphyton-feeding invertebrates.

Table 4.3 gives a typical example of the change in composition of the periphyton community in a 'transect' down a stem of *E. canadensis*. There was a dramatic increase in the quantity of periphyton with age of the plant stem, as measured microscopically in terms of relative densities of periphytic organisms on membrane filters (Table 4.3 (a)). Diatoms comprised the greatest percentage of the community and there was a general trend to increased abundance and species richness with age down the plant stem reflecting the duration of stem exposure to potential colonisation. Although detritus made a greater percentage contribution to the periphyton community of the shoot tip, the quantities of detritus on older parts of the stem (in absolute terms) were higher (up to 2.5 times those on the shoot tip, Table 4.3 (a)).

Table 4.3 Composition of periphyton communities on successive 15 mm lengths of *Elodea canadensis* stem collected from the eastern sampling area of Lake Grasmere (8 April 1977).
(a) Percentage composition and relative amounts of periphyton.
(b) Numerical composition (%) of the diatom category and total numbers of diatoms.

(a)	Distances down *E. canadensis* stem				
	Shoot tip	15 - 30 mm	30 - 45 mm	45 - 60 mm	60 - 75 mm
Diatoms	83.4	95.0	94.6	98.3	97.0
Detritus	16.6	5.0	5.4	1.1	2.0
Filamentous algae	-	-	-	0.6	1.0
Relative periphyton density (by projected area)	1 :	7.6 :	7.7 :	19.5 :	20.8
(b)					
Cocconeis	97.2	94.8	95.7	98.4	98.7
Epithemia	2.8	1.0	0.7	0.2	0.3
Diatoma	-	2.6	2.0	0.1	0.5
Synedra	-	-	0.3	0.7	0.2
Navicula	-	-	0.7	0.2	0.2
Rhoicosphenia	-	1.0	0.3	-	0.1
Gomphonema	-	0.3	0.3	0.4	-
Cyclotella	-	0.3	-	-	-
Total numbers of diatoms	36	304	302	842	876

4.3.3 Invertebrate Faecal Analyses

(1) *Paroxyethira hendersoni* and *P. tillyardi* (Trichoptera: Hydroptilidae). More than 90% of the faecal material of final instar larvae of the two species of *Paroxyethira* was browsed from plant surfaces and the remainder was macrophyte tissue itself (Fig. 4.2). Diatoms predominated over other food categories in most months (Appendices 6.1a and 6.2a) and overall (Fig. 4.2). Detritus and filamentous algae were almost equally represented in the faeces of both species, with the former perhaps marginally more abundant in faeces of *P. tillyardi* (Appendices 6.1a and 6.2a). Macrophyte tissue never contributed more

than 15% to the composition of the faecal material of either species and was usually around 8%.

Cocconeis was the most represented diatom genus in the faeces of both species, and *Gomphonema* and *Epithemia* each contributed more than 5% of diatom numbers overall (Appendices 6.1b and 6.2b). *Rhoicosphenia* had relatively greater representation in the faeces of *P. tillyardi* than *P. hendersoni*, probably because it was relatively more abundant where the former was collected. On the other hand, *Asterionella*, a diatom that may be present in the phytoplankton (Stout 1972), was recorded only in the faeces of *P. hendersoni*. *P. hendersoni* was collected from an *E. canadensis* zone underlying open water in the northern and western sampling areas.

A higher percentage of individual *P. tillyardi* larvae than *P. hendersoni* larvae had each of the major food categories in their faeces (diatoms:- *P. tillyardi* 98.7%, *P. hendersoni* 76.7%; detritus:- 98.7%, 76.7%; macrophyte:- 66.2%, 56.2%; filamentous algae:- 87.8%, 69.9%).

Differences in food habits between the two species of *Paroxyethira*, in Lake Grasmere, were probably related to differences in available food in the respective collection areas, rather than selective feeding.

Most Hydroptilidae make exclusive use of filamentous algae by piercing and sucking the cell contents (Nielsen 1948, Wiggins 1978, Mackay & Wiggins 1979). However, Nielsen (1948) observed that the structure of the mouthparts did not exclude the possibility that solid food could be ingested. Of five genera (*Agraylea*, *Hydroptila*, *Oxyethira*, *Orthotrichia* and *Ithytrichia*) he examined, the first four normally fed on the sap of filamentous algae, but *Oxyethira* was observed (in the laboratory) ingesting delicate filamentous algal threads, and diatoms were also found in its alimentary canal. *Ithytrichia*, on the other hand, fed exclusively on solid food, viz., very small diatoms. The structure of the mouthparts suggests that they are used to scoop up periphyton from surfaces. Nielsen (1948) did not indicate whether *Oxyethira* ingested filamentous algal cells or diatoms in nature, but it was interesting that this genus was the only one of the five that he found in acid waters and deep water where filamentous algae were not present. *Ithytrichia* was restricted to fast-flowing water also where filamentous algae did not grow.

Soszka (1975b) analysed the gut contents of 120 hydroptilids of the genera *Agraylea, Hydroptila, Orthotrichia* and *Oxyethira* and found that periphytic algae (diatoms 62%, other periphytic algae 35%) were the main food. In only one case was a small fragment of macrophyte tissue found.

Disney (1972), in a most unusual record, has observed larvae of *Orthotrichia* in Africa sucking the fluids from the eggs and immobile pupae of black flies (Diptera: Simuliidae).

The food habits of New Zealand Hydroptilidae had not been examined quantitatively previously. Cowley (1978) observed that *Oxyethira albiceps* was common where filamentous algae abound, sucking the contents from cells. Although I did not examine the gut contents of *O. albiceps* quantitatively, whole mounts of larvae on microscope slides contained fragments of cell walls of filamentous algae, suggesting that feeding was not solely by piercing and sucking, although the guts never appeared to be full of solid material as was the case with the *Paroxyethira* species.

Cowley (1978) noted that the mouthparts of *Paroxyethira hendersoni* were very similar to those of *O. albiceps* implying, perhaps, similar food habits, although this was not stated. The present work, however, confirms the view of Leader (1970) who said "it should be noted that the normal food of hydroptilid larvae is generally thought to be the sap of algae, feeding being accomplished by piercing single algal cells and sucking out the contents, but the guts of *Paroxyethira* spp. are always found to be full of diatoms, and the mouthparts appear to be better adapted for sweeping up a diatomaceous carpet than for biting cell walls".

(2) *Hudsonema amabilis* (Trichoptera: Leptoceridae). Caddisfly larvae of the family Leptoceridae have been recorded as carnivorous (Hicken 1967, Winterbourn 1971a, Satija 1974, Resh 1976, Mackay & Wiggins 1979), phytophagous (Mackay & Wiggins 1979), detritivorous (Resh 1976) and omnivorous (Slack 1936, Babington 1967).

The overall composition of the faecal material of *H. amabilis* (instars 2 - 5) in Lake Grasmere was indicative of omnivorous food habits (Fig. 4.2). Diatoms accounted for a reasonably constant percentage (30 - 40%) of the food of instars 2 to 5 (Fig. 4.3) and the major changes with increasing age were the reduction in the detrital component and the increased presence of macrophyte and prey items. Greater detrital feeding in early instars has been documented for many herbivore-

detritivore species (Coffman, Cummins & Wuycheck 1971) and a shift from algal or detrital feeding to predation has been demonstrated in the later instars of several caddisflies (Winterbourn 1971b, Wiggins 1977).

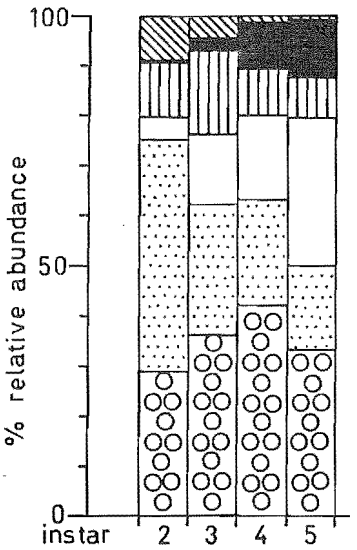


Fig. 4.3

Food habits of the last four larval instars of *Hudsonema amabilis*, in terms of major food categories, on a projected area basis (from faecal analyses) (September 1976 - November 1977). Number of larvae examined: 2nd instar = 11, 3rd instar = 18, 4th instar = 50, 5th instar = 66. N.B. greater numbers of larvae were examined non-quantitatively (see Tables 4.4 and 4.5).

Almost all *H. amabilis* larvae examined had ingested diatoms and detritus and most had fed on filamentous algae (Table 4.5). The number of larvae that had fed on macrophyte tissue and animal food items increased progressively from the second to the fifth instar.

A greater range of prey items was recorded in the faeces of fifth instar larvae than in those of earlier stages (Table 4.4). The most notable change between instars was the increased predation on *Potamopyrgus antipodarum* and mites. These data suggest that *P. antipodarum* was the most preyed upon species, and this may be because it was the most common of the potential prey in the habitat (Table 3.9, p. 33). *H. amabilis* larvae have been observed feeding upon *P. antipodarum* in the laboratory (see Wilson 1980), on chironomids by Babington (1967), and on small mayflies and *P. antipodarum* by Cowley (1978).

P. antipodarum of increasingly larger size may be eaten by later instars of *H. amabilis* (Fig. 4.4). Ninety-six percent of snails eaten by fifth instar larvae were greater than 4 mm tsh (cf. 36% of those eaten by fourth instar larvae). Wilson (1980) found in the laboratory that third and fourth instar larvae only ate snails of greater than 3 mm tsh and that second instar larvae did not eat *P. antipodarum*. My data is in general agreement with that of Wilson (1980), although I recorded

Table 4.4 Percentage of *Hudsonema amabilis* larvae in instars 2 - 5 whose faeces contained various prey items (September 1976 - November 1977). N = number of larvae examined.

Prey category	Instar 2	3	4	5
N	11	18	87	121
Nematoda	-	-	-	1.6
Oligochaeta	-	5.6	4.6	5.7
Cladocera				
Graptoleberis testudinaria	-	-	-	1.6
Bosmina meridionalis	-	-	-	1.6
Copepoda				
Eucyclops serrulatus	-	5.6	2.3	-
Chironomidae	9.1	-	2.3	-
Trichoptera				
Paroxyethira spp.	-	-	1.2	2.5
Acarina				
Piona uncata exigua	-	-	1.2	3.3
Hydrozetes lemnae	-	5.6	5.8	9.0
Trimalaconothrus novus	-	-	2.3	3.3
Mollusca				
Potamopyrgus antipodarum	-	5.6	23.0	31.2
Unidentified exoskeleton	-	5.6	11.5	10.7

P. antipodarum remains in the faeces of only one third instar *H. amabilis* larva, and the remains of several snails of less than 3 mm tsh in the faeces of third, fourth and fifth instar larvae. Wilson (1980) postulated that fourth and fifth instar *H. amabilis* larvae could not feed on snails of total shell height less than 3 mm and 4 mm respectively because their heads were too wide to enter the snail's shell aperture to get behind the operculum. Unfortunately, this argument is false due to errors in her head width measurements. Final instar larvae (mean head width about 0.70 mm) are capable of entering the aperture of *P. antipodarum* shells as small as 1.0 - 1.9 mm tsh (minimum aperture diameter 0.803 mm (from Wilson 1980)). Therefore, whereas *H. amabilis* larvae may retain the ability to ingest small snails, they may find large snails a better proposition.

The overall pattern of food habits of each instar was reflected in the seasonal data (Appendix 6.3). The ranking of major food categories in individual months usually was similar to the overall

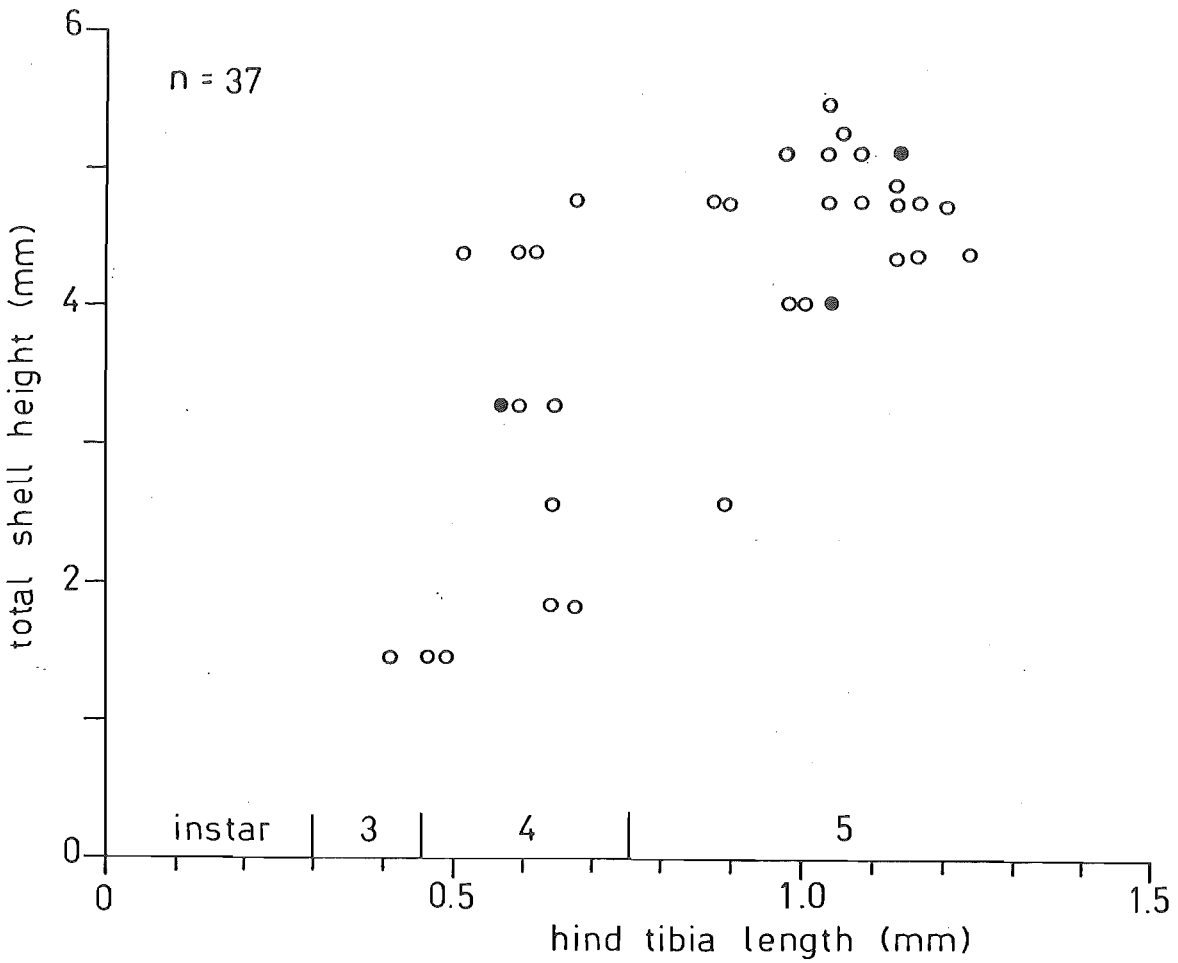


Fig. 4.4 Sizes (calculated from radula teeth) of *Potamopyrgus antipodarum* whose remains were found in the faeces of *Hudsonema amabilis* larvae of various sizes (September 1976 - November 1977). Solid circles = two records.

ranking for each instar. Few clear seasonal trends were evident, although from November to January the representation of prey items in the faeces of fifth instar larvae was greater than at other times, suggestive of increased emphasis on higher quality food prior to pupation (see Anderson & Cummins 1979).

Cocconeis was the most common diatom (63 - 81%) in the faeces of the last four instars of *H. amabilis*. No other diatom genus contributed more than 10% by numbers to the overall diatom category for any instar, although some genera were more prominent in certain months (Appendix 6.4). *Rhoicosphenia* and *Epithemia* (instars 2 - 5), *Asterionella* (instars 2 and 5), *Cyclotella* (instars 2, 3 and 5) and *Gomphonema* (instars 2 and 3) were all well represented at various times of year (Appendix 6.4).

Table 4.5 Percentage of *Hudsonema amabilis* larvae in instars 2 - 5 whose faeces contained each of the major food categories (September 1976 - November 1977) (N = number of larvae examined).

Major food category	Instar 2	3	4	5	Overall
N	11	18	87	121	237
Diatoms	90.9	94.4	98.9	100.0	98.7
Detritus	100.0	94.4	98.9	97.5	97.9
Macrophyte	27.3	66.7	73.6	91.7	80.2
Filamentous algae	72.7	77.8	87.4	84.3	84.4
Animal	9.1	27.8	48.3	62.8	52.3
S.R.T's	27.3	44.4	18.4	22.3	22.8

A study of the larval food habits of *H. amabilis* in Lake Rotorua (North Island) by Babington (1967) showed that the larvae had catholic feeding habits, a feature that is confirmed by the present work. The gut contents of ten larvae she collected in September were dominated by animal remains (including entire tiny caddis larvae, insect head capsules, thoracic plates, wings and legs), with egg cases, macrophyte tissue and algae also present. In the guts of a further ten larvae collected in March, however, diatoms and filamentous algae were most prominent, followed by macrophyte tissue and egg cases. No animal fragments were found. Babington (1967) attributed this seasonal change in food habits to a change in available food in the habitat. The same seasonal pattern of change in food habits was not observed in the present study (Appendix 6.3). Animal remains were present in the faeces of larvae collected in most months (the exceptions being second and third instar larvae when low numbers of larvae were collected), but could not be referred to as the *dominant* food category at any time. However, the conclusion that availability is the key to trophic relationships is supported, for example, by the species composition of the prey taken, and the wide range of diatom genera eaten.

(3) *Triplectides cephalotes* (Trichoptera: Leptoceridae). The faecal material of second to fifth instar *T. cephalotes* was dominated by macrophyte tissue (Fig. 4.2 and Fig. 4.5) although diatoms, detritus, filamentous algae, prey and S.R.T's were also recorded. The food

habits of second and third instar larvae were very similar (Fig. 4.5) but the faeces of only two second instar larvae were examined. Macrophyte tissue was ingested to a relatively greater degree by fourth and fifth instar larvae, mainly at the expense of detritus and filamentous algae.

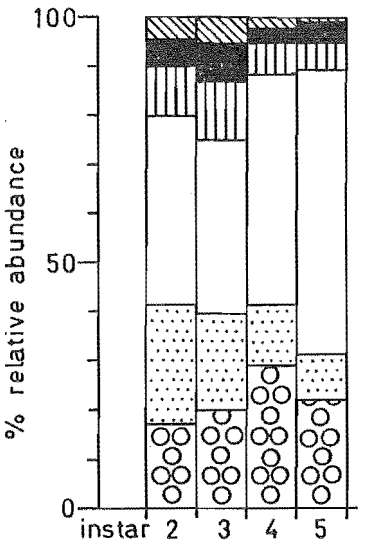


Fig. 4.5

Food habits of the last four instars of *Triplectides cephalotes*, in terms of major food categories, on a projected area basis (from faecal analyses) (September 1976 - November 1977). Number of larvae examined: 2nd instar = 2, 3rd instar = 8, 4th instar = 23, 5th instar = 31.

Table 4.6 Percentage of *Triplectides cephalotes* larvae in instars 2 - 5 whose faeces contained various prey items (September 1976 - November 1977). (N = number of larvae examined.)

Prey category	Instar 2	3	4	5
N	2	8	23	31
Oligochaeta	-	-	4.3	3.2
Cladocera				
Graptoleberis testudinaria	50.0	-	8.7	21.6
Bosmina meridionalis	-	37.5	-	-
Trichoptera				
Paroxyethira hendersoni	-	-	-	3.2
Acarina				
Hydrozetes lemnae	-	-	-	6.5
Mollusca				
Potamopyrgus antipodarum	-	-	-	6.5
Unidentified exoskeleton	-	-	4.3	-

A very limited range of animal food items was found in the faeces of *T. cephalotes* larvae (Table 4.6) and cladocerans were the only group represented in the faeces of all instars examined. The data for the second and third instars should be regarded with caution due to the small sample size. Bearing this in mind, it is likely however that the carnivorous habit assumes a greater role in progressively later instars. As with *H. amabilis*, the fifth instar had the greatest prey diversity, but with only 29% of larvae examined having prey remains in their faeces (Table 4.7), carnivory may be an irregular occurrence. Eighty-six percent of all prey items found in faeces of *T. cephalotes* were from fourth and fifth instar larvae collected between November and January, but only 59% of the animals examined were collected during the same period (Appendix 6.5). This suggests that animal food was taken to a greater extent in summer and may be another example of increased carnivory prior to moulting into the final instar or pupation (see Anderson & Cummins 1979).

Almost all individuals in instars 2 - 5 had ingested diatoms, detritus and macrophyte tissue (Table 4.7), the first two a likely consequence of a preference for the last. Filamentous algae were ingested by a progressively smaller proportion of later than earlier instars.

Table 4.7 Percentage of *Triplectides cephalotes* larvae in instars 2 - 5 whose faeces contained each of the major food categories (September 1976 - November 1977). (N = number of larvae examined.)

Major food category	Instar 2	3	4	5	Overall
N					
Diatoms	100.0	100.0	100.0	100.0	100.0
Detritus	100.0	100.0	100.0	100.0	100.0
Macrophyte	100.0	100.0	100.0	96.8	98.4
Filamentous algae	100.0	75.0	69.6	48.4	60.9
Animal	50.0	37.5	17.3	29.0	26.6
S.R.T's	100.0	87.5	52.2	51.6	57.8

Interpretation of patterns of seasonal change in the contributions of major food categories (Appendix 6.5) and diatom genera (Appendix 6.6) to the food of *T. cephalotes* was made difficult by the low numbers of larvae available for examination in some months. In ten out of 18 months, the faeces of three or fewer *T. cephalotes* larvae were analysed. Macrophyte tissue was the top-ranked contributor to the food of larvae in most months for instars 2 to 5 (Appendix 6.5), with detritus (3rd instar), and diatoms (2nd instar) dominant when macrophyte was not. *Cocconeis* was the best represented diatom in the faeces of most larvae throughout the year (Appendix 6.6). *Gomphonema, Epithemia* and *Rhoicosphenia* were next in abundance for both fourth and fifth instar larvae (although not in the same ranking order).

T. cephalotes has an almost obligatory relationship with aquatic macrophytes. Babington (1967) observed larvae chewing leaf margins of *E. canadensis, Potamogeton cheesemanii* and *P. ochreatus* in Lake Rotorua (North Island). Older leaves, especially of *E. canadensis*, were preferred and new growth was not eaten. *T. cephalotes* larvae normally construct their cases from potential food items, and in the macrophyte zones of Lake Grasmere, *E. canadensis* leaves and stems, and hollow stems of *I. alpinus*, are most commonly utilised. Sometimes stones or *P. antipodarum* shells may be incorporated (as noted also by Cowley (1978)). At times of food shortage (for example, isolated larvae in the laboratory) larvae may eat their own cases, or those of others.

Babington (1967) found that macrophyte tissue was the dominant food item in gut contents in September (up to 50% by projected area) and March (when filamentous algae were almost equally important). In March, the guts of some individuals were almost completely full of diatoms. These data are in agreement with the results of this study.

Few trichopteran larvae use green plants for food *and* case construction (Mackay & Wiggins 1979). The use of plant materials and silk (as opposed to sand and stones) by larvae such as *Triaenodes* (Moretti 1942, *in* Mackay & Wiggins 1979) and *T. cephalotes* (Babington 1967, Cowley 1978, present study), has enabled these larvae to leave the bottom substrate to which they would otherwise have been restricted. None of these larvae can swim without their cases, and Mackay and Wiggins (1979) suggest that the slender plant and silk-based cases serve a hydrostatic or hydrodynamic function in making macrophyte energy resources available.

Phytophagous leptocerids include one of the few larval trichopteran pests; the larva of *Triaenodes*, which can be a pest of rice crops (Moretti

1942, *in* Mackay & Wiggins 1979). (The only other larval Trichoptera that assume pest status in crops belong to the family Limnephilidae, which is not represented in New Zealand.) Although the opportunity for trichopteran larvae to become pests in New Zealand is limited (because there is little, if any, commercial production of aquatic plants), the use of phytophagous larvae (such as *T. cephalotes*) in the biological control of nuisance aquatic macrophytes (by artificially increasing larval densities) is a possibility. B.T. Coffey (pers. comm. to Cowley 1978) has observed large larvae of *T. cephalotes* on defoliated stems of *Lagarosiphon* indicating that larvae can reduce the standing crop of the plant.

(4) *Nymphula nitens* (Lepidoptera: Pyralidae). The food habits of *N. nitens* in New Zealand have not been studied previously but it has been assumed, by analogy with the habits of overseas species, that living macrophyte tissue is the main food. Winterbourn and Lewis (1975) suggested that *N. nitens* and *T. cephalotes* were "perhaps the only inhabitants of the macrophyte beds that eat the living plants".

In Lake Grasmere, *N. nitens* larvae are phytophagous (Fig. 4.2). Nearly 60% (by projected area) of faecal material was macrophyte tissue. Detritus (20.0%), diatoms (13.6%), and filamentous algae (6.6%), which contribute to the periphytic coating on plant surfaces, would almost certainly have been ingested while chewing on macrophyte tissues.

Because limited numbers of larvae were available and the size ranges of instars were uncertain, three arbitrarily chosen size classes of *N. nitens* were considered for food comparisons (Table 4.1).

Macrophyte tissue contributed an increasing proportion to the diet of larvae as they got larger (Fig. 4.6), and comprised 38.0%, 60.5%, and 71.0% of the faeces of larvae of the first, second, and third size classes respectively. The parallel reduction in the contributions of detritus and diatoms resulted from the ingestion by larger larvae of larger fragments of macrophyte (with less periphyton relative to plant tissue than smaller fragments). In addition, larger larvae were able to eat their way into plant stems where they could ingest tissue that was not coated with diatoms or detritus.

Seasonal changes in food habits (Appendix 6.7) were difficult to interpret due to the difficulty of separating seasonal effects from individual variation between larvae since, in most months, sample sizes were small (see Chapter V, p. 132). Filamentous algae were most prominent in August/September and diatoms least represented from August

to November in the faeces of all three size classes (Appendix 6.7a). Detritus showed marked seasonal variation in contribution but no consistent pattern. Macrophyte tissue made a consistently large contribution to the ingested food of each size class in most months. Lowest values were found in June (size groups 2 and 3), July and September (size group 1).

Cocconeis was the dominant diatom in the faeces of *N. nitens* throughout the year. Diatom species richness was lowest, and the dominance of *Cocconeis* most marked, in the faeces of larvae in the largest size class (Appendix 6.7b).

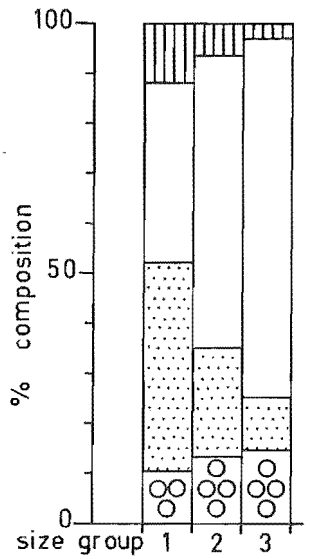


Fig. 4.6

Food habits of three size classes of *Nymphula nitens*, in terms of major food categories, on a projected area basis (from faecal analyses) (July 1976 - August 1977). See Table 4.1 for size ranges of the size classes. Number of larvae examined: size class 1 = 8, size class 2 = 28, size class 3 = 7.

Table 4.8 Percentage of *Nymphula nitens* larvae in three size classes whose faeces contained each of the major food categories (July 1976 - August 1977) (N = number of larvae examined).

Major food category	Size class 1	2	3	Overall
N	8	28	7	43
Diatoms	100.0	100.0	100.0	100.0
Detritus	100.0	100.0	100.0	100.0
Macrophyte	100.0	100.0	100.0	100.0
Filamentous algae	87.5	85.7	85.7	86.0

Cocconeis was the most common diatom on macrophytes and one of the first species to colonise new surfaces (see p. 98). The generic

composition of diatoms in the faeces of larvae of the third size class suggests that these larvae were feeding on shoot tips of macrophytes. This was confirmed by observation; small larvae were distributed more evenly over the plants but large larvae were invariably found where there was new growth.

All larvae examined had ingested diatoms, detritus, and macrophyte tissue (Table 4.8). A similar proportion (about 86%) of larvae of each size class had fed upon filamentous algae.

Cummins (1973) noted that there was a paucity of good quantitative data on the food habits of aquatic Lepidoptera, despite their being widely distributed in freshwaters. Welch (1916) observed that larvae of *Nymphula maculalis* fed on yellow water-lily (*Nymphaea americana*) in Douglas Lake (Northern Michigan, U.S.A.) and Berg (1941) found larvae of *Acentropus niveus* only at the tips of shoots (or near the tips) of *Elodea canadensis* and *Ceratophyllum* sp. where they fed on "the youngest and tenderest leaves". Also, larvae construct "houses" with silk threads, from pieces of leaves of the food plant. These observations are consistent with those of the present study, where larvae were found most commonly in the shoot tips of *Myriophyllum propinquum* and, when densities were high (e.g., March 1978), on *E. canadensis*. At high larval densities, *N. nitens* can have a marked defoliating effect, and may be the most promising indigenous species for use in biological control of nuisance aquatic macrophytes.

Soszka (1975b) provided the first quantitative data on the diet of aquatic Lepidoptera (*Paraponyx stratiotata* and *A. niveus*). Both species had identical food habits and, as for *N. nitens*, all larvae examined (n = 100) fed primarily on the tissue of vascular plants. The percentage composition of gut contents (on a projected area basis) was approximately 53.0% macrophyte, 17.6% diatoms, 17.6% other algae, 5.9% detritus and 5.9% invertebrates (viz., fragments of Cladocera, Oligochaeta, and Rotatoria) (determined from Fig. 2, p. 398, Soszka 1975b). Although no animal fragments were recorded in the faeces of *N. nitens*, the remaining food categories were similar to those recorded by Soszka (1975b). Differences in percentage composition were probably due to differences in available food.

In experiments with artificial substrates, Soszka (1975b) found that lepidopteran larvae were the only macroinvertebrates in Mikolajskie Lake that did not occur on plastic plants. This emphasises the importance of fresh macrophyte tissue as an essential food of aquatic Lepidoptera.

(5) *Xanthocnemis zealandica* (Odonata: Coenagrionidae). Odonatans provide perhaps the best examples of how similarity in morphology confers similarity in food habits. The presence of the modified labium in all larval Odonata is considered sufficient evidence to conclude that all species are predaceous, even though the food habits of only a few species have actually been studied (Cummins 1973). Odonatan larvae are among the more convenient predators to investigate for field-consumed prey because the faecal material is passed in pellets enclosed by a peritrophic membrane.

Methods of faecal pellet analysis have been used to study the prey of zygopteran (= damselfly) larvae (Lawton 1970a, Pearlstone 1973, Thompson 1978a & b) and anisopteran (= dragonfly) larvae (Corbet 1957, Pritchard 1964, Staddon & Griffiths 1967). Other studies have utilised gut content analyses (Chutter 1961, Macan 1964, Fischer 1966, 1967, Crumpton 1979).

A wide range of prey types are taken by odonate predators, but certain groups have not been recorded in gut contents or faecal pellets. These include adult Coleoptera and larval Trichoptera (Chutter 1961, Lawton 1970, Pearlstone 1973, Thompson 1978a & b), and corixids have been noted as prey of zygopteran larvae only by Crumpton (1979). The presence of remains of hydroptilid caddisfly larvae in faecal pellets of *X. zealandica* (present study) is thus the first record of predation on Trichoptera. Serological studies have shown that damselfly larvae may prey upon triclads (Davies 1969), but these (and coelenterates and leeches) are likely to be the only prey species completely overlooked by faecal pellet (or gut content) analysis (Davies & Reynoldson 1971). It was not possible to eliminate this minor source of error given the time and resources available, and none of these potential prey were common in the microhabitat of *X. zealandica* in Lake Grasmere.

Few studies of the trophic relationships of Odonata have recognised non-animal 'food' materials in gut contents or faecal pellets. However, Thompson (1978a) recorded plant detritus (which appeared as a fine brown material) in faecal pellets, some of which he contended was derived from the gut contents of prey organisms and the remainder picked up accidentally during prey capture.

As expected, the faeces of *Xanthocnemis zealandica* were dominated by animal remains, but all of the other major food categories (Fig. 4.2) were also recorded. It is probable that non-animal food items were either ingested accidentally when striking at prey, or were derived from

prey gut contents. Diatoms, detritus, and prey items were found in faecal pellets of all *X. zealandica* larvae examined (Table 4.9).

Table 4.9 Percentage of *Xanthocnemis zealandica* larvae in three size classes whose faecal pellets contained each of the major food categories (September 1976 - November 1977) (N = number of larvae examined).

Major food category	Size class 1	2	3	Overall
N	26	53	47	126
Diatoms	100.0	100.0	100.0	100.0
Detritus	100.0	100.0	100.0	100.0
Macrophyte	73.1	88.7	83.0	83.3
Filamentous algae	84.6	81.1	72.3	78.6
Animal	100.0	100.0	100.0	100.0
S.R.T's	11.5	39.6	29.8	30.2

Since the instars of *X. zealandica* could not be determined, and larval densities were low (which limited sample sizes), only three size classes were chosen for the purpose of faecal analyses (Table 4.1). The third (= largest) size class approximated the final instar (see Deacon 1979).

There was very little difference in food habits (in terms of major food categories) between the three size classes of *X. zealandica* larvae examined (Fig. 4.7). Differences in food habits between size classes were evident when the composition of the prey category was considered (Table 4.10). A high proportion of larvae of all sizes fed on Cladocera (mainly *Graptoleberis testudinaria*) and Oligochaeta. Mites (especially *Hydrozetes lemnae* and *Piona uncata exigua*), hydroptilid caddisfly larvae and, especially *Potamopyrgus antipodarum* had greater representation in faecal pellets of larger *X. zealandica* larvae. Conversely, chironomid larvae were found more often in the pellets of smaller larvae.

Final instar *X. zealandica* larvae apparently spend most of their time in a head down posture close to the bottom of stems (the "hunting" position) (Rowe 1978). Nevertheless, some larvae may be found at the tops of stems (facing up) and Rowe (1978) suggested that this was either in preparation for emergence or a method of avoiding intraspecific conflict.

Table 4.10 Percentage of *Xanthocnemis zealandica* larvae in three size classes whose faecal pellets contained various prey items (September 1976 - November 1977) (N = number of larvae examined).

Prey category	Size class 1	2	3
N	26	53	47
Oligochaeta	65.4	73.6	76.6
Cladocera			
Graptoleberis testudinaria	73.1	75.5	61.7
Bosmina meridionalis	26.9	17.0	10.6
Simocephalus vetulus	-	-	4.3
Copepoda			
Eucyclops serrulatus	-	-	2.1
Ostracoda	-	1.9	-
Chironomidae			
Tanypodinae *(Gressittius antarcticus)*	3.9	-	-
Orthocladiinae	15.4	9.4	6.4
Tanytarsini *(Tanytarsus vespertinus)*	-	1.9	-
Trichoptera			
Hydroptilidae	11.5	22.6	21.3
Unidentified	3.9	-	-
Acarina			
Hydrozetes lemnae	11.5	22.6	27.7
Trimalaconothrus novus	-	1.9	2.1
Piona uncata exigua	11.5	20.8	34.0
Mollusca			
Potamopyrgus antipodarum	-	15.1	42.6
Unidentified exoskeleton	11.5	7.6	6.4

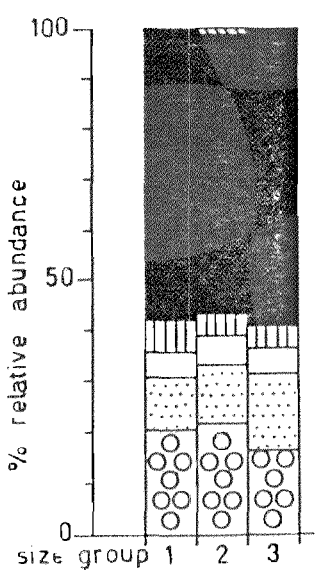


Fig. 4.7

Food habits of three size classes of *Xanthocnemis zealandica*, in terms of major food categories, on a projected area basis (from faecal pellet analyses) (September 1976 - November 1977). Number of larvae examined: size class 1 = 26, size class 2 = 53, size class 3 = 47.

The food habits of final instar larvae recorded here (viz., the high contributions of oligochaetes, benthic cladocerans, Acarina, and *P. antipodarum* (see Chapter III, p. for discussion of the habits of these groups)) are consistent with the abundance of potential prey in the collection area (Table 3.9, N E 2, W E 2, p. 33).

Crumpton (1979) studied the food habits of *X. zealandica* in two ponds near Christchurch (South Island, New Zealand) but did not separate larvae of different sizes. Oligochaeta, Ostracoda, Cladocera and chironomid larvae were most frequently represented in crop contents. Predation on tiny zygopteran larvae (i.e., cannibalism) was recorded in 9.4% of crops examined. I found no instances of cannibalism in an examination of 126 faecal pellets, and Rowe (1978 and pers. comm.), in many hours of observation, has observed cannibalism only in crowded transport containers. Work on related species overseas shows that the incidence of cannibalism is very low. Lawton (1970a) identified 2,000 prey items from *Pyrrhosoma nymphula* and found only two zygopteran remains, and Chutter (1961) found only one instance (in 600 crops) where a zygopteran (a different species) had been eaten by *Pseudagrion*.

X. zealandica larvae ingested *P. antipodarum* of all sizes available in Lake Grasmere (range 1.48 - 5.24 mm tsh determined using the tsh versus length of inner marginal tooth regression, p. 93). Final instar larvae (= size class 3) showed a preference for larger snails than did *X. zealandica* of size group 2, but both size classes retained the ability to feed on small snails (Fig. 4.8). *X. zealandica* larvae smaller than 2 mm h.w. were not recorded as predators of *P. antipodarum*. Crumpton (1979) did not record *P. antipodarum* in crop contents of *X. zealandica* despite its presence (few to common, all year round) in the habitat (Crumpton 1978).

Seasonal changes in the composition of faecal pellets by major food categories, and the generic composition of the diatom category are given in Appendices 6.8 and 6.9. Since non-prey food items may be regarded as somewhat incidental to the nutrition of damselfly larvae, seasonal changes in the representations of prey items only, are considered.

The overall pattern of prey taken (Table 4.10) for each size class was reflected in seasonal data (Table 4.11) with Oligochaeta, Cladocera, Acarina and *P. antipodarum* most represented in faecal pellets. No marked seasonal changes were evident, reflecting year-round availability of the prey items recorded (see Appendices 2.1 and 2.10).

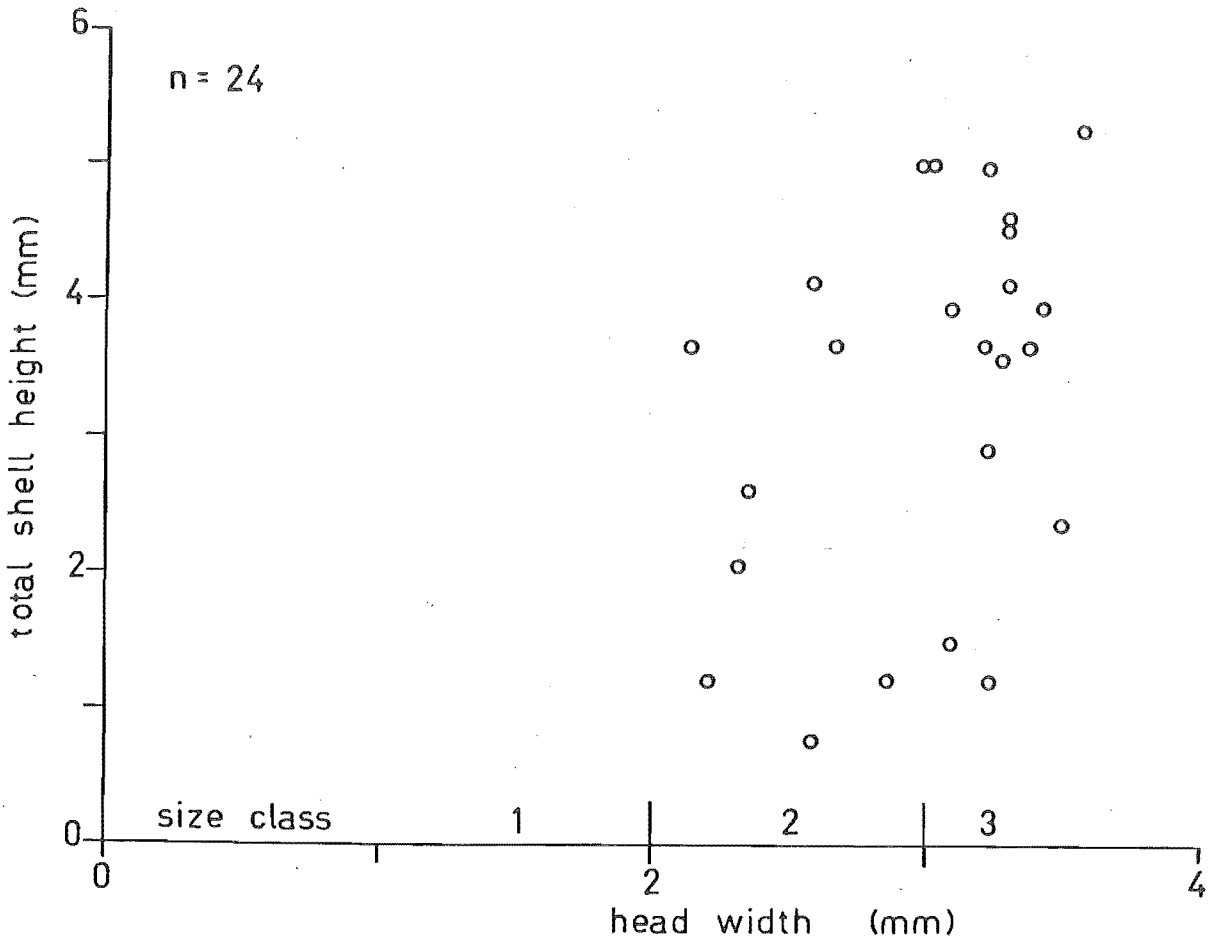


Fig. 4.8 Sizes of *Potamopyrgus antipodarum* (calculated from radula teeth) whose remains were found in the faecal pellets of *Xanthocnemis zealandica* larvae (September 1976 - November 1977).

(6) *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae).

P. antipodarum is the dominant mollusc, if not the dominant macroinvertebrate, in many New Zealand lakes (Forsyth 1975a, Stout 1975b, Winterbourn & Lewis 1975). Nash (1974) made a preliminary study of feeding and assimilation of *P. antipodarum* using radiotracer techniques and Winterbourn (1970a) observed that epipelic and epiphytic periphyton was the main food. Marshall (1974) stated that *P. antipodarum* was an epipelic detritivore and these observations were confirmed by Towns (1976).

These statements on the food habits of *P. antipodarum* were confirmed for Lake Grasmere animals by faecal analyses and observations made during this study. *P. antipodarum*, in aquaria, were seen browsing over plant surfaces and on periphyton growing on the glass sides. Feeding trails were visible on the sides of aquaria (where the periphytic coating had been rasped off) and there was no visual evidence of selective feeding.

Table 4.11 Seasonal occurrence of prey items in faecal pellets of *Xanthocnemis zealandica* (September 1976 - November 1977) 1 = present in faecal pellets of size class 1; 2 = present in faecal pellets of size class 2; 3 = present in faecal pellets of size class 3; - = absent; * = larval size classes not present. (See Table 4.1 for size ranges of size classes and Appendix 6.8 for numbers of larvae examined.)

Prey category	Sampling dates						
	1976			1977			
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	21 Nov.
Oligochaeta	-,2,3	1,2,3	1,2,3	1,2,3	*,2,3	1,-,3	*,*,3
Cladocera							
Graptoleberis testudinaria	1,2,-	-,2,3	1,2,3	1,2,3	*,2,-	1,2,3	*,*,3
Bosmina meridionalis	1,2,3	1,2,3	-,-,3	1,-,-	*,-,3		
Simocephalus vetulus	-,-,-	-,-,-	-,-,-	-,-,3	*,-,-	-,-,-	*,*,3
Copepoda							
Eucyclops serrulatus	-,-,-	-,-,-	-,-,-	-,-,3	*,-,-	-,-,-	*,*,-
Ostracoda	-,-,-	-,-,-	-,-,-	-,-,-	*,2,-	-,-,-	*,*,-
Chironomidae							
Tanypodinae	1,-,-	-,-,-	-,-,-	-,-,-	*,-,-	-,-,-	*,*,-
Orthocladiinae	1,2,-	-,2,-	1,-,3	-,-,3	*,-,-	-,2,3	*,*,-
Tanytarsini	-,-,-	-,-,-	-,2,-	-,-,-	*,-,-	-,-,-	*,*,-
Trichoptera							
Hydroptilidae	-,-,-	1,2,3	1,2,3	-,-,3	*,-,-	-,2,3	*,*,3
Unidentified	1,-,-	-,-,-	-,-,-	-,-,-	*,-,-	-,-,-	*,*,-
Acarina							
Hydrozetes lemnae	-,-,3	1,2,3	1,2,3	-,2,3	*,2,-	-,-,-	*,*,3
Trimalaconothrus novus	-,2,-	-,-,-	-,-,-	-,-,-	*,-,-	-,-,3	*,*,-
Piona uncata exigua	1,-,-	1,-,3	1,2,3	-,-,3	*,2,-	-,2,3	*,*,3
Mollusca							
Potamopyrgus antipodarum	-,2,3	-,2,3	-,2,3	-,2,3	*,2,-	-,-,3	*,*,3
Unidentified exoskeleton	1,2,3	1,-,3	-,-,-	-,2,-	*,-,-	1,-,3	*,*,-

The faecal contents of *P. antipodarum* (in terms of major food categories) were similar to those of the two *Paroxyethira* species (Fig. 4.2). Diatoms were the main food items, followed by macrophyte fragments, detritus, filamentous algae and S.R.T's. On this level, the main differences between these species were the increased representation of macrophyte tissue and the decreased representation of filamentous algae in the faeces of snails compared with hydroptilids. The radula of *P. antipodarum* is capable of rasping off the epidermal layer of macrophyte tissue, whereas the scooping mouthparts of *Paroxyethira* spp. (cf. *Ithytrichia*, Nielsen 1948) seem able only to scrape off the periphytic coating. Also, Nielsen (1948) observed that the structure of the mouthparts of algal piercing and sucking hydroptilids differed little from those that had taken up a browsing habit. These functional differences between the mouthparts of *P. antipodarum* and the *Paroxyethira* spp. may account for the observed differences in their faecal composition.

All *P. antipodarum* whose faeces were analysed had fed upon diatoms and detritus, and most on macrophyte (95.8%) and filamentous algae (81.3%). S.R.T's were recorded in the faeces of 35.4% of snails examined (mainly in June 1977 when S.R.T's were most abundant (Appendix 6.10)). No animal remains were found in faeces of *P. antipodarum*.

There were marked seasonal changes in the relative contributions of major food items eaten by *P. antipodarum* (Appendix 6.10d) but, as with most of the other species studied, it is difficult to explain them. Diatoms were the most common food items in all months in which analyses were done, except April 1977 (when macrophyte, detritus and filamentous algae were more common). Detritus and macrophyte tissue were usually next to diatoms in ranking and contributed similar amounts in most months. Filamentous algae comprised less than 12% of the faeces (by projected area) in all months except April 1977 (22.4%).

The generic composition of the diatom category in the faeces of *P. antipodarum* (Appendix 6.10b) was distinctly different from that of any of the other species studied. *Rhoicosphenia* and *Cocconeis* made approximately equal overall contributions and *Epithemia* had greater representation in the faeces of *P. antipodarum* than in those of the other animals. Since most *P. antipodarum* were collected from short-stemmed *I. alpinus* beds, in the eastern sampling zone of Lake Grasmere, it is possible that they may have been feeding closer to, or on, the bottom (on periphyton-covered rocks or beech tree debris). *Rhoicosphenia* and *Epithemia* are two of the most common diatom genera in Middle Bush Stream, Cass (Davis & Winterbourn 1977) where such substrates may be

found, so it is possible that these diatom genera also were more abundant in Lake Grasmere in the habitat where these *P. antipodarum* were feeding.

(7) Observations on the gut contents of Chironomidae. During the course of taxonomic studies on New Zealand chironomids, many larvae were mounted on slides usually without treatment with KOH so that their gut contents were often visible. Since little is known about the food habits of the New Zealand species, I considered it useful to document these observations.

Tanypodinae

Larvae of the subfamily Tanypodinae generally are considered to be predaceous (Cummins 1973), although Davies and McCauley (1970) recorded the presence of algae as well as animal remains in digestive tracts of Tanypodinae from Marion Lake (Canada).

Large numbers of *Gressittius/Macropelopia* were examined from lakes throughout the South Island of New Zealand, and in most cases, diatoms and detritus dominated the gut contents. In many larvae, very large diatoms (e.g., *Stauroneis* (?) up to 2.8 mm long) were present. Other chironomids (e.g., *Chironomus zealandicus*) and Cladocera (especially *Graptoleberis testudinaria* and *Bosmina meridionalis*) were the main animal prey items seen.

The gut contents of *Ablabesmyia mala* invariably contained prey items including chironomids (notably *Tanytarsus vespertinus* in Lake Grasmere), Cladocera (especially *G. testudinaria* in Lake Grasmere), and Copepoda.

Orthocladiinae

Orthocladine chironomids are normally detrital-algal feeders (Cummins 1973). Observations on the gut contents of *Syncricotopus pluriserialis*, *Cricotopus* spp., *Rheocricotopus* sp. (= Orthocladiinae B) and Orthocladiinae C (see Chapter VI) supported this contention.

Chironominae

Algal-detrital feeders, leaf-miners and wood-dwellers are known in this subfamily (Cummins 1973).

Tribe Chironomini

Harrisius pallidus, a wood-dwelling species, is closely related to the genus *Stenochironomus*, whose members are leaf-miners or wood-

dwellers (A. Borkent pers. comm.). Digestive tracts of *H. pallidus* were always full of wood fragments. *Paucispinigera* spp. may also feed on wood, but in fine particulate form, from amongst sediments or on the surfaces of logs. Guts of this genus may also contain large quantities of inorganic material, as well as detritus and diatoms.

The guts of *Chironomus zealandicus* examined were normally full of fine particulate organic and inorganic material.

Tribe Tanytarsini

The gut contents of *Calopsectra funebris, Tanytarsus vespertinus* and *Corynocera* sp. were dominated by detritus and diatoms, with large quantities of mineral particles in some larvae (especially *C. funebris*).

CHAPTER V

LIFE-HISTORY INFORMATION ON SELECTED INSECTS

5.1 INTRODUCTION

Although the study of life-histories of aquatic insects in New Zealand has advanced significantly over the last ten years or so (e.g., Winterbourn 1966, 1974, 1978, Norrie 1969, Michaelis 1973, Crosby 1975, Hopkins 1976, Winterbourn & Davis 1976, Towns 1976, Cowie 1980) most work has concerned stream insects. Life-history studies by Babington (1967) (three leptocerid caddisflies), Deacon (1979) and Crumpton (1979) (Odonata), and Young (1970) (Hemiptera), are among the few investigations of pond- or lake-dwelling insects. Brief life-history notes are provided, usually as part of taxonomic studies, for a number of other species by Forsyth (1971, 1979), Forsyth & McCallum (1978a & b) (Chironomidae), Leader (1972) (Hydroptilidae), and Cowley (1978) (Trichoptera).

Life-history information interrelates with, and is a necessary complement to, the study of the taxonomy of aquatic insects (Oliver 1979). For example, knowledge that certain immature stages and adults belong to the same species aids in the search for distinguishing taxonomic characters in one or all of the life stages. In addition, a life-history study may reveal morphological or behavioural differences that result in the recognition of two species where only one was thought to be present (Oliver 1979). Information on the seasonality of abundance of various life stages is important in the elucidation of food webs and trophic interrelationships (Cummins 1973, Chapter IV of present study) since different stages may have different food habits. There is evidence also that interspecific competition may be reduced by life-history asynchrony such that maximum numbers of major feeding stages (i.e., final instar larvae) of potential competitors are separated temporally to some degree (see Winterbourn 1971a).

This study is concerned primarily with the life-histories of the insects whose feeding relationships were also studied (see Chapter IV), although information was collected on a number of other species as well. Since I was most concerned with aquatic insects in their association with macrophytes, the emphasis was on the larval stages. Information obtained on other life-history stages (especially the egg) is more limited. Nevertheless, for most species it was possible to determine the main life-history patterns.

5.2 METHODS

Aquatic stages of insects were collected in quantitative samples and non-quantitative hand-net collections (see Chapter III for details of sample collection and processing). Limited numbers of adult insects were obtained by sweep-netting lakeside vegetation (Appendices 5.1, 5.3, 5.5 and 5.7) particularly at the southern end of the lake, and by light-trapping (Appendices 5.2, 5.4, 5.6 and 5.7).

Maximum head width or hind tibia length were measured (on material preserved in 70% alcohol) in order to assign individual larvae to instars or size classes. Maximum head widths (hw) were measured for *Pycnocentrodes aureola*, *Oecetis unicolor* and *Nymphula nitens* at ×40 magnification, and at ×25 for *Xanthocnemis zealandica*, using a binocular microscope fitted with a linear eyepiece micrometer. It was inconvenient to measure head widths of the two larger leptocerid caddis larvae *(Hudsonema amabilis* and *Triplectides cephalotes)* since their greatly elongated meta-thoracic limbs hampered correct orientation. As preserved larvae tend to lie naturally on their sides, with their elongated limbs oriented approximately in the focal plane of the microscope, the length of the hind tibia (the longest leg segment) was measured instead. As a check on reliability for instar determination, and to enable comparisons to be made with studies in which head width was used, both structures were measured for a number of individuals, including some collected during different seasons.

Linear regressions of hind tibia length (htl) versus head width (hw) were fitted by the least squares method for 69 *H. amabilis* (Fig. 5.1) and 39 *T. cephalotes* (Fig. 5.2) larvae. Measurements of hind tibia length provided a convenient and unambiguous method for assigning individuals of these species to their appropriate instars, and being between 6% and 55% greater than head width (for smallest and largest larvae respectively) for *H. amabilis*, and 22% and 69% greater for *T. cephalotes*, there was less error involved in their measurement with an eyepiece micrometer. The relationship between htl and hw for *H. amabilis* has been substantiated by a more intensive study of a lowland population in the Avon River, near the Student Union building, on the Ilam campus of the University of Canterbury (C.L. McLay and K.W. Fraser pers. comm.).

Since the number of instars of *X. zealandica* could not be determined precisely (but is likely to vary between 12 and 14, R.J. Rowe pers. comm.), its life-history pattern was demonstrated by

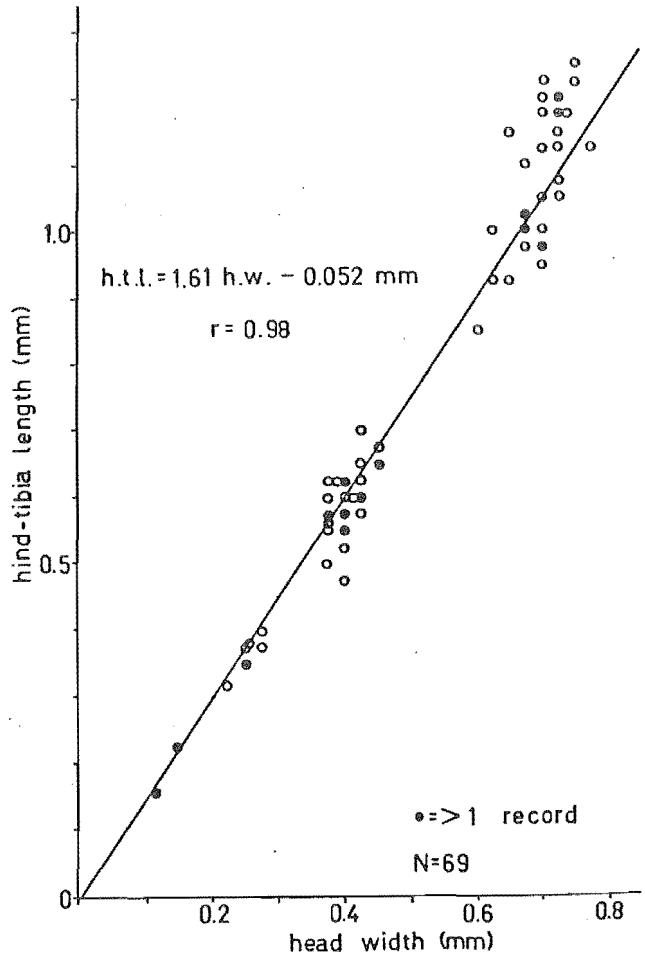


Fig. 5.1

Hind tibia length (htl) versus head width (hw) for *Hudsonema amabilis* with least square regression line and equation.

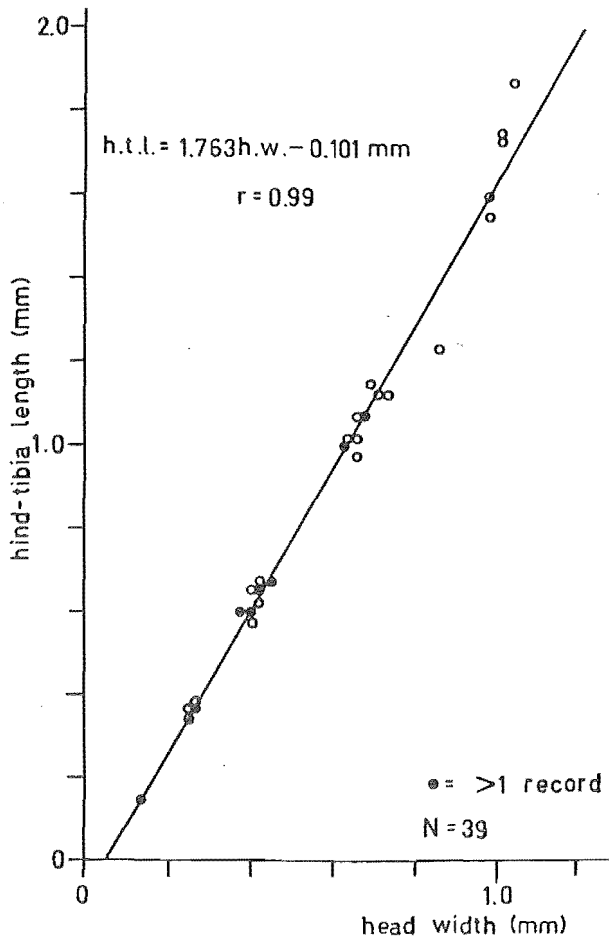


Fig. 5.2

Hind tibia length (htl) versus head width (hw) for *Triplectides cephalotes* with least square regression line and equation.

separating monthly collections of larvae into component cohorts (see Deacon 1979). Cohorts (or year classes) of larvae comprised individuals of similar size range, which could sometimes be distinguished by inspection of monthly size-frequency data. At other times, it was necessary to use Taylor's method for polymodal analysis (Taylor 1965) to separate cohorts (see Deacon 1979).

5.3 RESULTS AND DISCUSSION

5.3.1 *Hudsonema amabilis* (Trichoptera: Leptoceridae)

Measurements of larval hind tibia lengths formed five groups indicating the presence of five larval instars (Fig. 5.3). Instars were distinctly separate in most months, although the combination of htl measurements from all larvae collected between April 1976 and March 1978 slightly obscured the separation between instars, suggesting that the size limits of the instars may be somewhat flexible. Size variation within each instar increased with age.

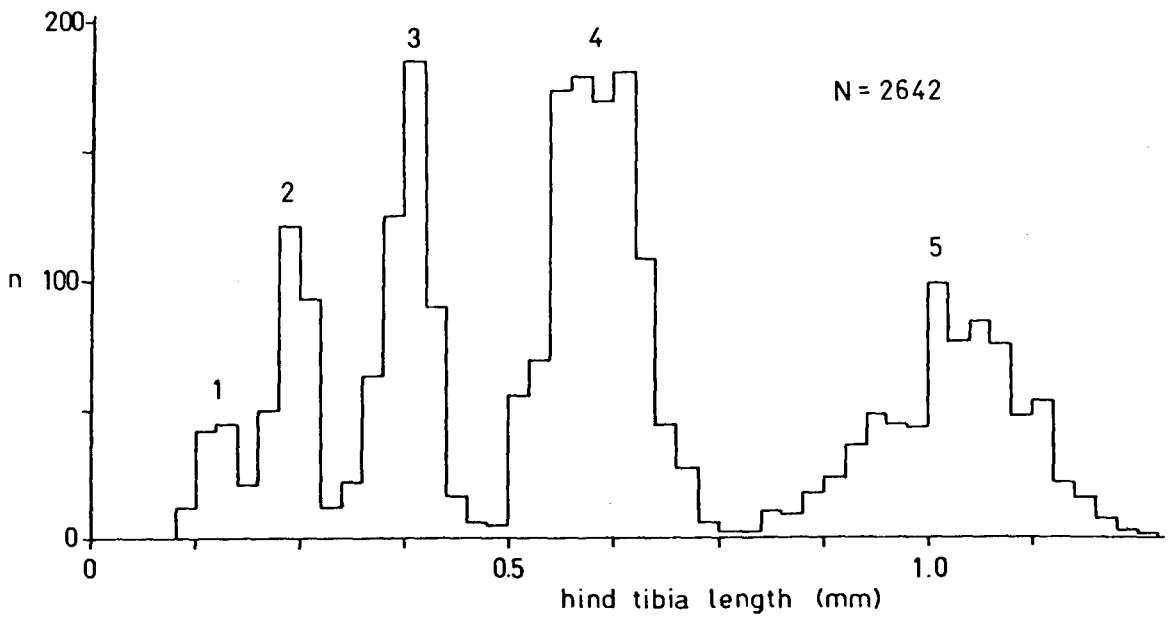


Fig. 5.3 Size frequency distribution of hind tibia lengths of *Hudsonema amabilis* larvae (all data combined, April 1976 - March 1978).

The numbers of larvae taken on each sampling date between July 1976 and March 1978, percentage of larvae in each instar, and mean size of larvae in the most abundant instar are shown in Fig. 5.4. First instar larvae were taken from January to April, although one was found in September (1976). Growth was rapid between March and June so that most larvae overwintered in the fourth instar. As lake temperatures rose the following spring, larvae entered a period of rapid growth culminating in emergence.

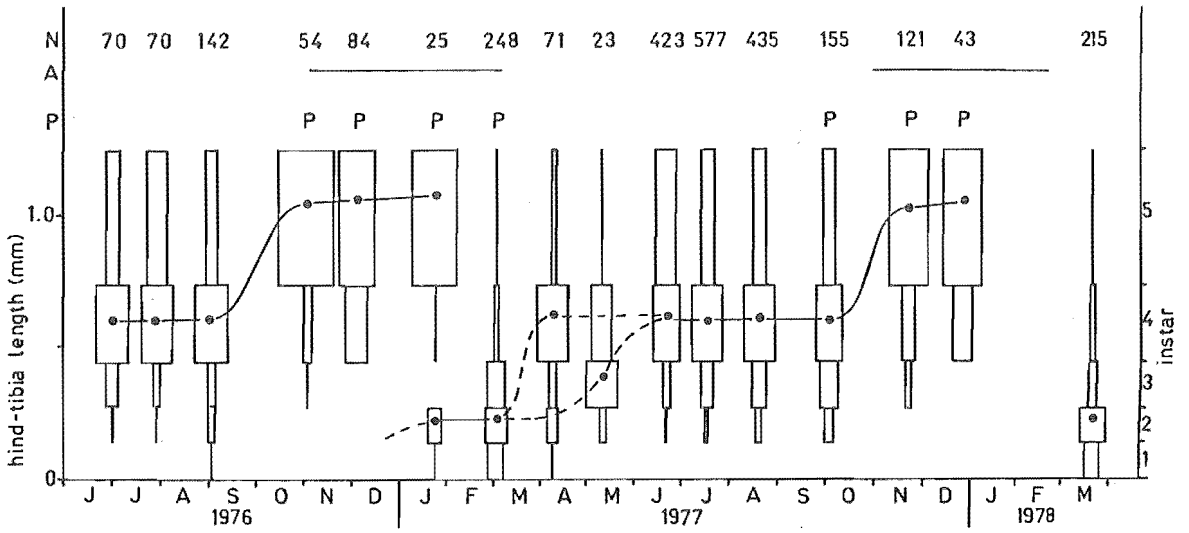


Fig. 5.4 Life-history pattern of *Hudsonema amabilis* (July 1976 - March 1978) showing the percentage of larvae in each instar, and periods of adult (A) and pupal (P) abundance. Solid circles indicate the mean sizes of larvae in the dominant instars. N = number of larvae collected.

First and second instar larvae were found mainly on the stony bottom in macrophyte-free, shallow (less than 0.3 m deep) water near the lake edge whereas many later instar larvae also occurred on macrophytes. Most pupae were seen attached to rocks and submerged beech tree logs, although some were attached to macrophytes. Since my samples were collected primarily from macrophytes, early instar larvae and pupae are probably under-represented.

Adults of *H. amabilis* were the most common leptocerid caddisflies taken in hand-net and light-trap collections and were recorded in November, December, and January (Appendices 5.3 and 5.4). The presence of pupae and final instar larvae (Fig. 5.4) indicate a flight period extending from early November to early March at Lake Grasmere. McFarlane (1977) recorded adults in light-trap collections from the Winchmore Irrigation Research Station, about 140 m a.s.l., in inland mid-Canterbury, from 2 November to 26 April whereas around Auckland, in the North Island, adults have been collected from early August to late April (Cowley 1978).

The life-history pattern observed at Lake Grasmere, and the size ranges of the instars (Fig. 5.1) are essentially the same as those found in McLay and Fraser's larval study in the Avon River (pers. comm.). This suggests that the factors responsible for the timing of the life-history, and growth of larvae, were similar in both places.

5.3.2 *Triplectides cephalotes* (Trichoptera: Leptoceridae)

The size frequency distribution of larvae indicated the existence of five instars (Fig. 5.5). The identity of the first instar was confirmed by measurement of larvae taken from gravid females since females of this species are ovoviviparous, giving birth directly to 500 - 600 first instar larvae (Pendergrast & Cowley 1966).

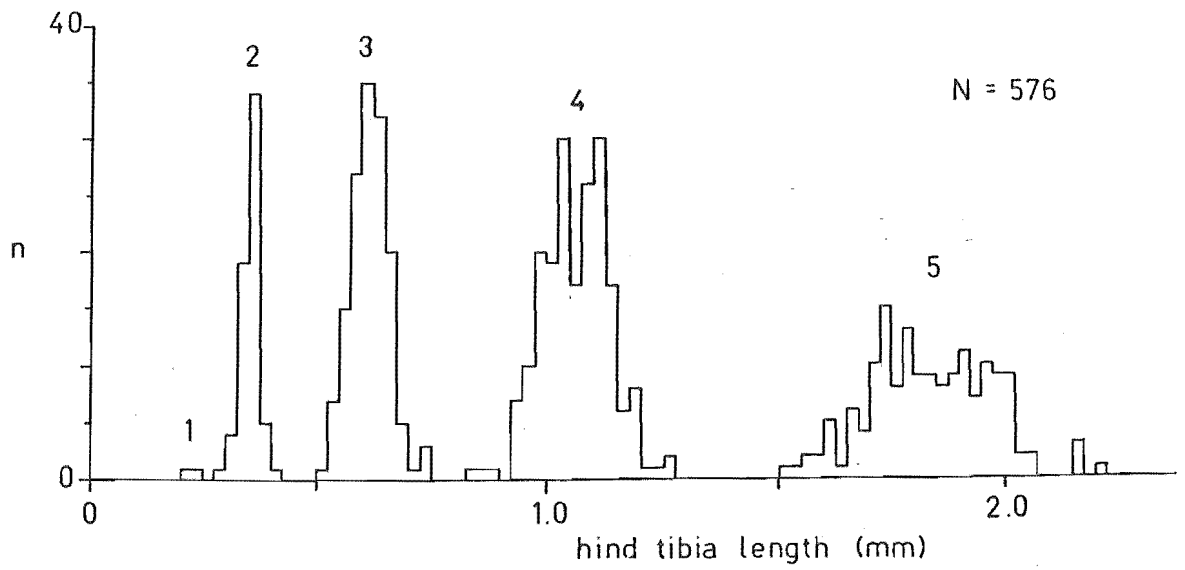


Fig. 5.5 Size frequency distribution of hind tibia lengths of *Triplectides cephalotes* larvae (all data combined September 1976 - March 1977).

Although most instars were present in most months (Fig. 5.6), suggesting that larval recruitment and growth were not well synchronised, the general pattern of growth of the main component of the population could be followed. Very few first instar larvae were collected in field samples (and only in April 1977). Since larvae, rather than eggs, are released by the females, it is probable that a rapid moult into the second instar occurs to take advantage of the release of young at a relatively advanced stage. First instar larvae could be recruited to the population between late December and April. This could not occur at the onset of the adult flight period because time would be required for development to the first instar inside the adult females. After a period of rapid growth, most larvae (40 - 70%) spent the winter in the third instar (cf. *H. amabilis*, the fourth instar), and passed through the final two instars from late October to January. Pupae were found attached to macrophytes from early November to late March (Fig. 5.6), but adults were taken only in December and January (Appendices 5.3 and 5.4). Although there were no adult collections taken in February, and adult *T. cephalotes* were not taken in March, it was probable that the

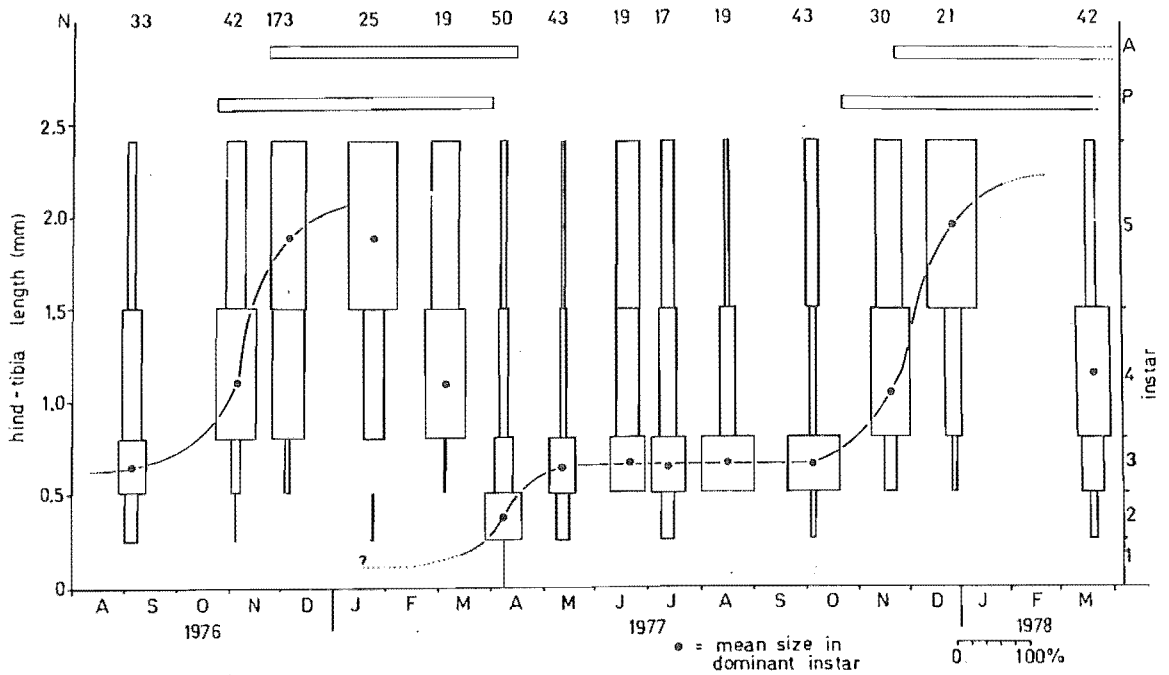


Fig. 5.6 Life-history pattern of *Triplectides cephalotes* (September 1976 - March 1978) showing the percentage of larvae in each instar and periods of adult and pupal abundance. N = number of larvae collected.

flight period extended from about the end of November to April (based on pupal evidence). McFarlane (1977) noted a flight period from 23 November to 19 April at the Winchmore Irrigation Research Station on the Canterbury Plains, and Cowley (1978) collected adults from September to mid May around Auckland in the North Island.

Cowley (1978) found final instar larvae in a swimming pool in Auckland on 30 January, and suggested that the first instar larvae could not have been present before mid December (presumably because there was no water in the pool before then). This indicates that, at least in warmer areas of New Zealand and at the inflated temperatures often found in swimming pools, the life-history can be short.

5.3.3 *Pycnocentrodes aureola* (Trichoptera: Conoesucidae).

Limited life-history information was collected for *P. aureola*, a conoesucid caddisfly that lives on stony or rocky substrates, rather than macrophytes, in Lake Grasmere (and more commonly in streams (Cowley 1978)).

Larval instars could not be distinguished on the basis of head width measurements (Fig. 5.7), but there was apparently only one cohort present during the year, and a univoltine life-history pattern (Fig. 5.8).

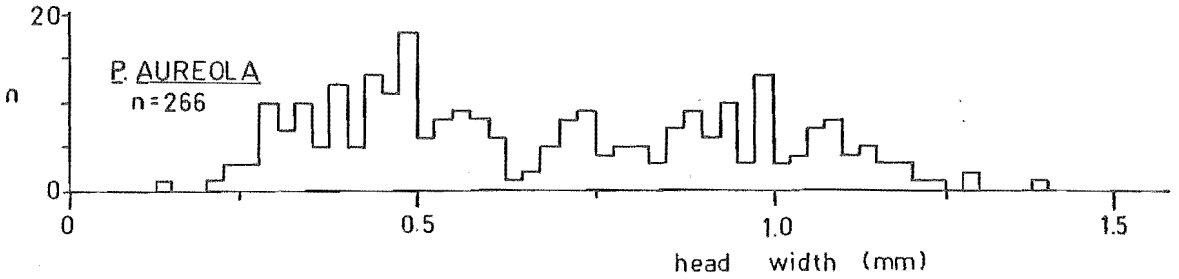


Fig. 5.7 Size frequency distributions of *Pycnocentrodes aureola* (all data combined, March 1977 - March 1978).

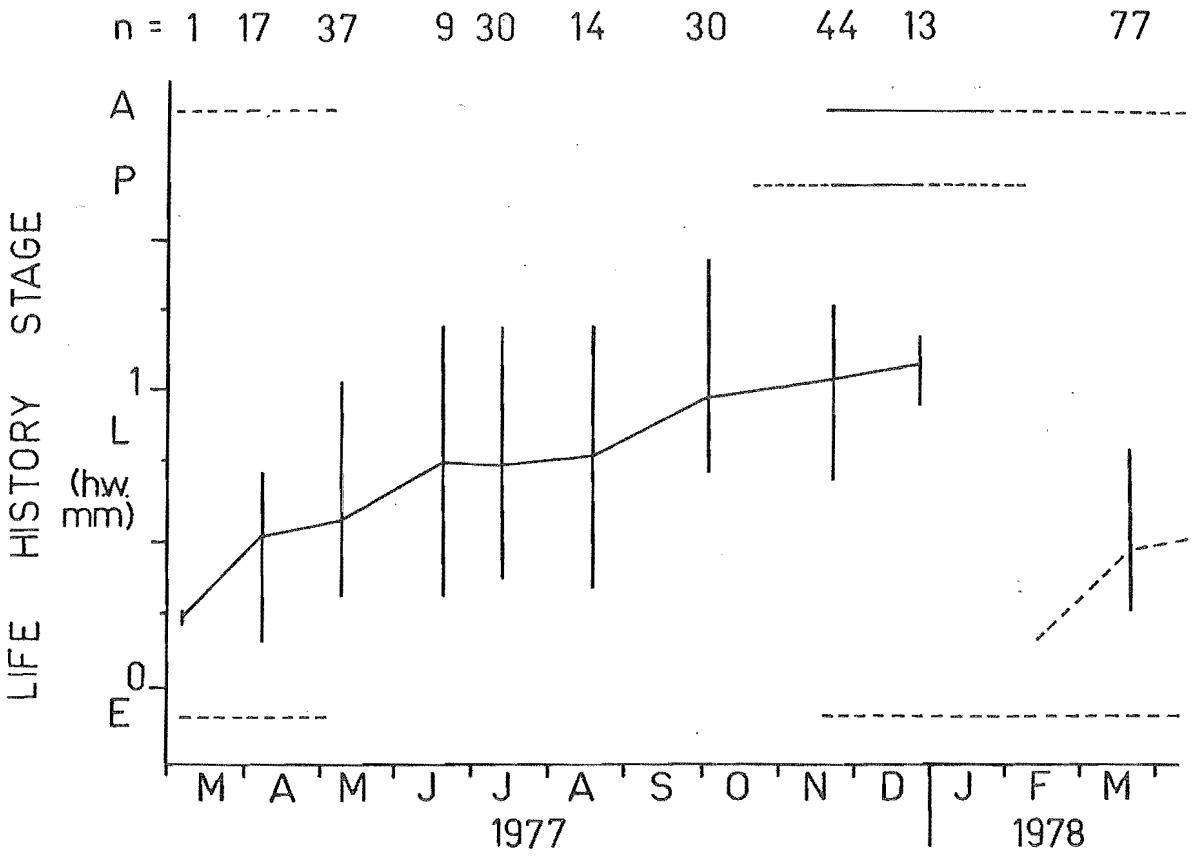


Fig. 5.8 Diagrammatic representation of the life-history of *Pycnocentrodes aureola* (March 1977 - March 1978). Vertical bars show the size ranges of larvae collected each month; mean sizes are joined. Presence of eggs (E), pupae (P), and adults (A) are also shown. n = number of larvae sampled. Dashed lines represent life-history stages that were presumed to be present but were not recorded.

Spherical egg masses characteristic of *P. aureola* were found amongst rocks, stones and debris in shallow water along the eastern shore of Lake Grasmere from mid November to early May, and pupae were recorded in November and December (but may have been present also in October, January and early February). Adults were taken in hand-net and light-trap collections from early November to late January, occasionally in

very large numbers (Appendices 5.3 and 5.4). Norrie (1969) collected adults throughout the year near Auckland, and Cowley (1978) recorded the presence of larvae and pupae at all times, although adults were more common in spring and summer. McFarlane (1977) noted a flight period from mid October to early May at Winchmore in the South Island. However, it seems that the flight period at Lake Grasmere was shorter, since adults were not collected on 27 October (1978), 2 March and 8 April (1977) (Appendices 5.3 and 5.4).

5.3.4 *Oecetis unicolor* (Trichoptera: Leptoceridae)

O. unicolor was most common in Lake Grasmere on sandy substrates and amongst low macrophytes, especially near the outlet stream. It was not collected often in samples from macrophytes (see Chapter III).

In Lake Grasmere, *O. unicolor* apparently has an annual life-history with a single cohort present in any one year (Fig. 5.9). The pattern is virtually identical to that for *P. aureola* (see Fig. 5.8), and also for animals collected from Lake Pearson by Dr B.V. Timms (pers. comm.). No attempt was made to locate eggs, and pupae were not recorded.

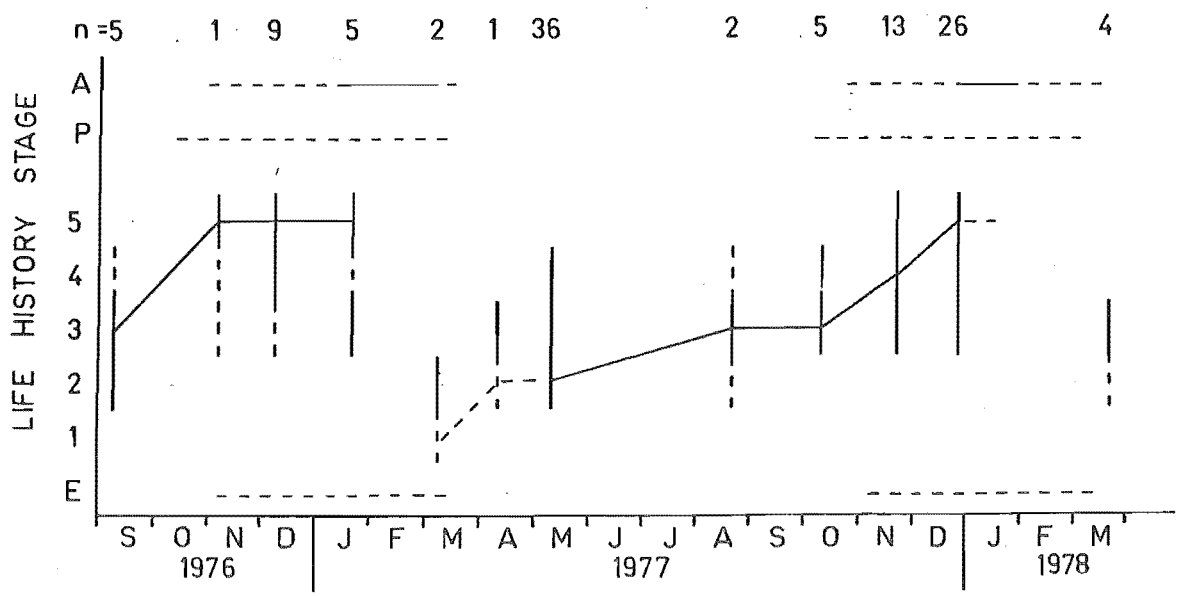


Fig. 5.9 Diagrammatic representation of the life-history of *Oecetis unicolor* (September 1976 - March 1978). Vertical bars show the range of instars present each month; dominant instars are joined. Presence of eggs (E), pupae (P), and adults (A) are also shown. n = number of larvae sampled. Dashed lines represent life-history stages that were presumed to be present but were not recorded.

Adults of *O. unicolor* were collected in December and January (Appendices 5.3 and 5.4), but since larvae were most common at the opposite end of the lake to that where most collections for adults were made, these collections are unlikely to be a reliable indication of the flight period. Cowley (1978) collected adults from October to mid April, but suggested that the flight period was longer than this because gravid females were taken in April. McFarlane (1977) recorded adults in light-trap collections from Winchmore between mid October and late March, and the seasonal abundance of larval instars in Lake Pearson (about 2.5 km from Lake Grasmere) during 1978 - 1979 indicated that adults emerged mainly in December, January, and February (B.V. Timms pers. comm.).

5.3.5 *Oxyethira albiceps, Paroxyethira hendersoni* and *P. tillyardi* (Trichoptera: Hydroptilidae)

Since specific separation of larvae of the first four instars of New Zealand hydroptilids is not yet possible (see Chapter VI), and there is little intraspecific size variation in final instar larvae of all three species, I did not measure larvae collected on a regular basis for life-history analyses. However, information on the presence and abundance of final instar larvae and pupae obtained in the quantitative sampling program (Appendix 2) and non-quantitative hand-net collections, and adults from hand-net and light-trap samples (Appendices 5.3 and 5.4), has enabled the elucidation of certain features of their life-histories.

O. albiceps was rare in quantitative samples from macrophytes but more common on stony substrates amongst filamentous algae at the southern end of the lake where final instar larvae occurred throughout the year. Adults were collected in six months of the year (January, March, May, October, November, and December) (Appendices 5.3 and 5.4), but it is likely that emergence can occur in almost any month (since pupae were recorded even in mid June). Cowley (1978) noted the presence of all life-history stages throughout the year, and McFarlane (1977) collected most adults in light-traps at Winchmore between September and May, although some were collected during the remainder of the year.

Final instar larvae and pupae of *P. hendersoni*, the most common hydroptilid in Lake Grasmere, were collected in almost every month in which samples were taken (Appendices 2, 5.3 and 5.4), although pupae were not recorded in July. Most emergence seemed to occur between

October and March or April (Appendix 5.3). McFarlane (1977) noted a flight period from early November to mid May at Winchmore, and Cowley (1978) stated that adults could be found at any time of year.

Final instar larvae of *P. tillyardi* were recorded in all collections, but pupae were found only in December and January (despite intensive searching at other times), and adults mainly in December and January but occasionally as late as March (Appendices 2, 5.3 and 5.4). This species had the shortest flight period of the three hydroptilids (and, in fact, of all insects studied) in Lake Grasmere and, apparently, a well synchronised emergence.

5.3.6 *Nymphula nitens* (Lepidoptera: Pyralidae)

I was not able to determine the number of larval instars in this species by rearing or inspection of raw size frequency data (Fig. 5.10), but application of Dyar's rule, which states that there is a geometric increase in the size of a sclerotised structure with each instar in insects (Crosby 1973), indicated that there were probably nine larval instars (indicated on Fig. 5.10). The head width increased by a factor of 1.28 - 1.29 at each moult. The size of the first instar larvae (hw = 0.20 mm) was established from larvae hatched from eggs found on *Myriophyllum propinquum*.

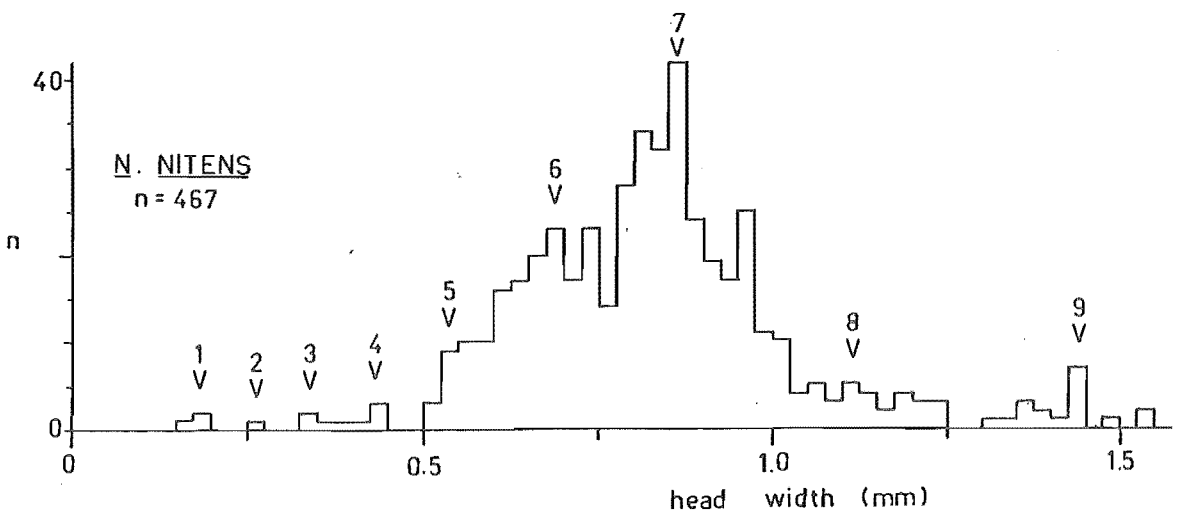


Fig. 5.10 Size frequency distributions of *Nymphula nitens* (all data combined, July 1976 - March 1978).

N. nitens has a univoltine life-history pattern in Lake Grasmere (Figs. 5.11 and 5.12). First instar larvae were collected in January, and grew rapidly until late March when most were probably in instars 5 to 7. There was very little growth in winter when mid-lake water temperatures were below 11 or 12°C (see Fig. 2.3). Growth resumed in October and continued through to emergence in December and January.

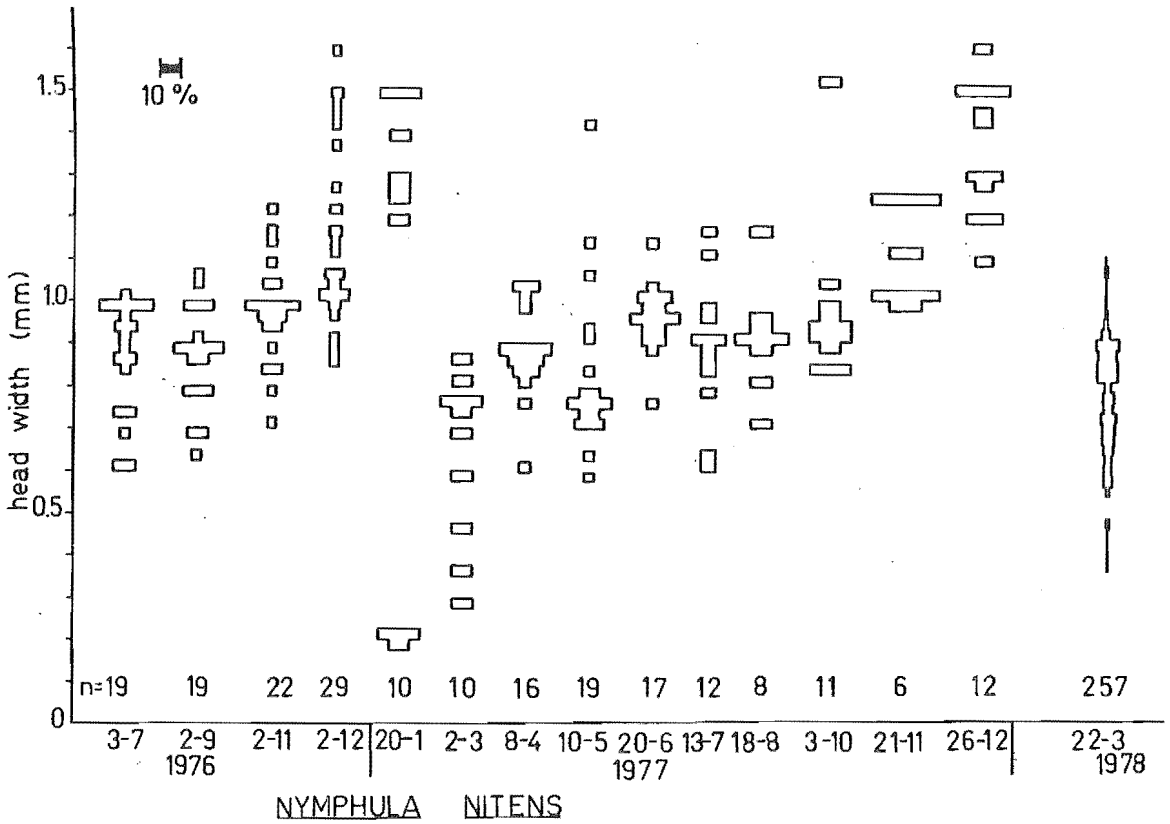


Fig. 5.11 Size frequency distribution of *Nymphula nitens* larvae collected from Lake Grasmere between July 1976 and March 1978. n = number of larvae sampled.

The mean sizes of *N. nitens* larvae were greater in 1977 - 1978 than at corresponding times the previous year (Fig. 5.11), suggesting more rapid growth in 1977 - 1978. This may have been associated with higher water temperatures (1.5 - 5.0°C higher from August 1977 to February 1978 than in the same period of 1976 - 1977, Fig. 2.3). Also, numbers of larvae collected (with similar sampling effort) from the lake in early 1978 were about 25 times (1977) and ten times (1976) greater than in the previous two years (Fig. 5.11). In March 1978, larvae were found on their preferred food plant (*M. propinquum*), and in large numbers also on *Elodea canadensis*. The occurrence of many larval cases constructed of *E. canadensis* leaves bound by silk threads, and observations of partly defoliated macrophyte stems, were striking evidence of the impact of high larval densities.

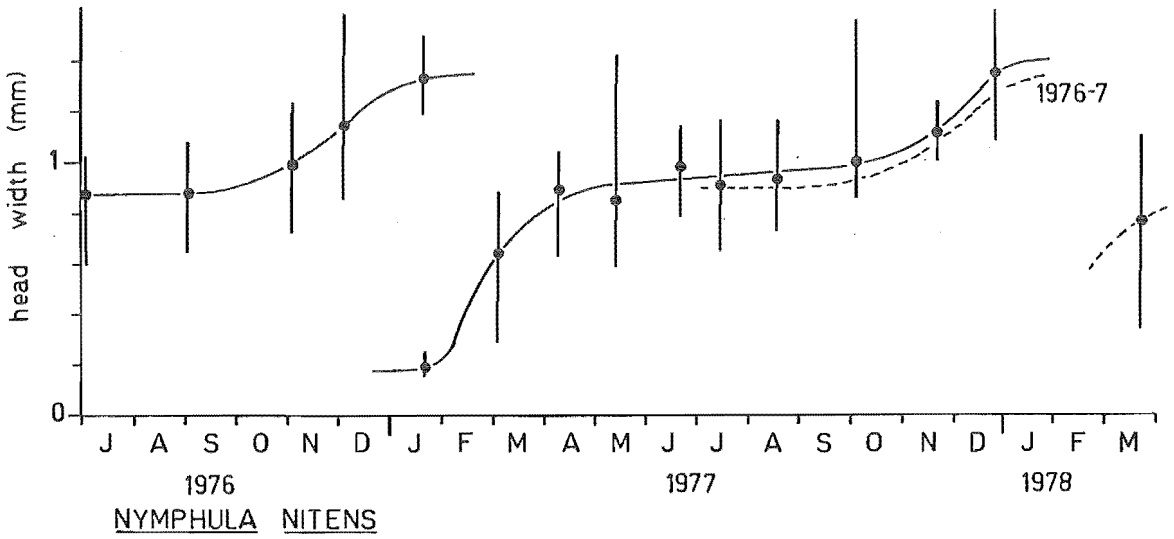


Fig. 5.12 Life-history pattern of *Nymphula nitens* (July 1976 - March 1978) showing mean size, and range of sizes of larvae in each month sampled. The dashed line represents the growth curve of 1976 - 1977 superimposed on that for 1977 - 1978.

5.3.7 *Xanthocnemis zealandica* (Odonata: Coenagrionidae)

Deacon (1979) found that *X. zealandica* at Lake Sarah (about 1 km from Lake Grasmere) had a three-year life-cycle, but that some larvae could complete development in two years (cf. a lowland population where a two-year life-history was the rule). Part of my study period (September 1976 - March 1977) overlapped with that of Deacon (1979), and his more complete data facilitates the interpretation of the life-history of *X. zealandica* at Lake Grasmere.

Fig. 5.13 shows the size frequency distribution of larvae with cohorts (i.e., larvae of the same year-class) numbered 1 - 4, and approximate growth curves of component cohorts. The striking feature of Fig. 5.13 is the poor representation of cohorts 3 and 4, whose absence is unlikely to be due to sampling inadequacy since large numbers of young larvae were taken in September 1980 (Fig. 5.13). Instead, their low representation may indicate poor recruitment of these year classes, which could have been the result of any one (or more) of a number of factors (e.g., poor parental emergence, mating success, oviposition success, hatching success or survival of small larvae).

Eggs are laid during the summer inside the stems and leaves of floating plant material or rooted macrophytes that reach near the water surface. The first winter is spent as early instar larvae (e.g., cohort 4, Fig. 5.13), but by the following March some larvae have reached 1.5 mm hw. Little growth occurs during the second winter (e.g., cohort

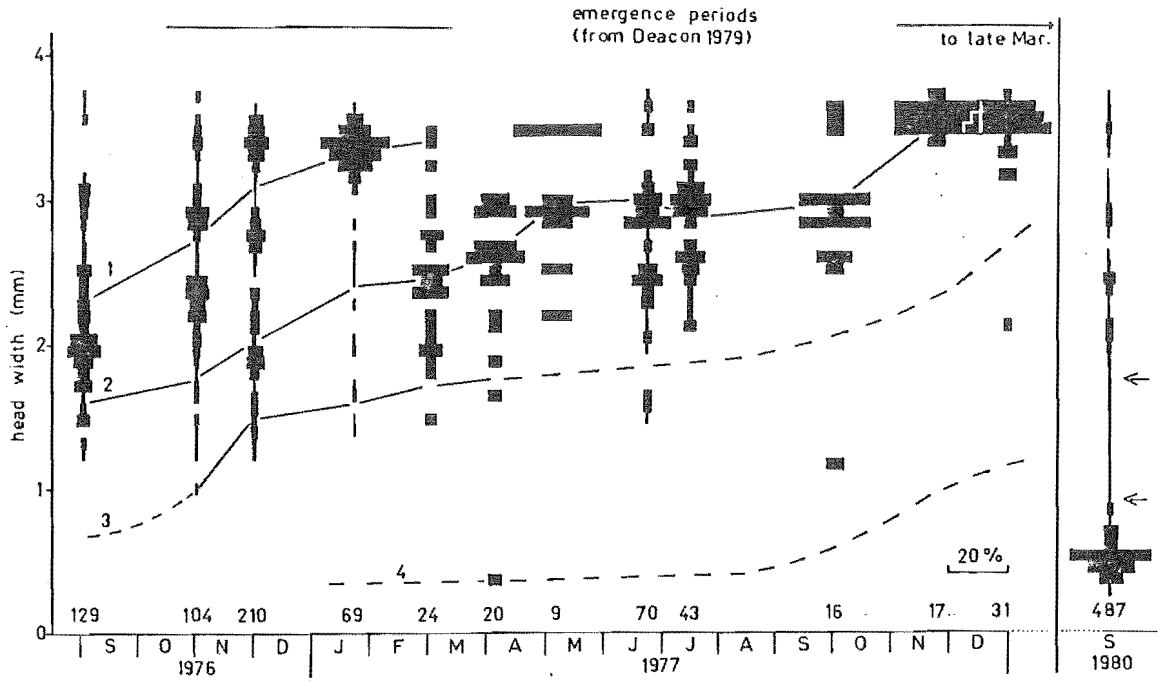


Fig. 5.13 Size frequency distribution of *Xanthocnemis zealandica* from Lake Grasmere (September 1976 - December 1977), with an additional collection from September 1980). Lines indicate approximate growth curves of component cohorts. The dashed lines are based on data from Deacon (1979) in the absence of larval representation in samples from Lake Grasmere. Also shown are the presumed emergence periods (from Deacon 1979) and numbers of larvae collected. Arrows at left of September 1980 size frequency distribution indicate approximate divisions between cohorts.

3, Fig. 5.13), but early in the next year some larvae reach the F-1 and final instars (e.g., cohort 2 in March 1977, Fig. 5.13). However, most larvae spend the third winter (when, once again, there is little growth) as F to F-3 instar larvae (e.g., cohort 2 in winter 1977, Fig. 5.13) and emergence occurs the following summer. The pattern of larval growth, in summary, is three winters of very little growth, each followed by a period of rapid growth during the summer, with the third culminating in emergence.

Adults were collected from early December 1976 to 8 April 1977, and again on 9 October 1978 (Appendix 5.7). Deacon (1979) found that emergence could start on different dates at various sites, but only when the water temperature had risen to 10 - 12°C. At Lake Sarah (lake shore site), the emergence period ranged from 126 (1976 - 1977) to 147 (1977 - 1978) days, beginning between 14 and 22 November in 1976, and 6 and 14 November in 1977 (Deacon 1979). The termination of emergence was between 16 and 20 March in 1977, and 26 March and 2 April in 1978. These dates may apply equally well to the emergence of *X. zealandica* from Lake Grasmere since the temperature regimes of the two lakes are

usually similar (Stout 1969a, Deacon 1979, cf. present study). Deacon (1979) noted a temperature range from 4°C to 20°C in Lake Sarah between early July 1977 and late April 1978, which is the same as that recorded in the present study (Fig. 2.3) from Lake Grasmere. The earlier warming of Lake Grasmere in 1977 - 1978 (cf. 1976 - 1977), and presumably also Lake Sarah, is consistent with the earlier emergence of *X. zealandica* in 1977 - 1978 (as noted by Deacon (1979)). The collection of nine adults on 9 October 1978 from the southern end of Lake Grasmere, suggests that emergence in that year was even earlier than in the two preceding years.

CHAPTER VI

TAXONOMY OF THE NEW ZEALAND HYDROPTILIDAE (TRICHOPTERA) AND CHIRONOMIDAE (DIPTERA)

6.1 INTRODUCTION

Invertebrates collected during the course of this study that could not be identified readily to the specific level, in particular, adult and larval Chironomidae and the larva of a species of *Paroxyethira* (Hydroptilidae), stimulated an interest in the taxonomy of these groups. I intended, initially, to identify specimens collected from Lake Grasmere (both larvae and pupae from aquatic habitats and adults collected in light-traps or hand-nets), but this work developed into a more intensive study of the taxonomy of hydroptilids and chironomids and the construction of keys to the New Zealand species (see also Stark in press).

This chapter presents keys to the larval Hydroptilidae and to the larval and adult male Chironomidae of New Zealand constructed from the literature and from my own taxonomic investigations, and discusses taxonomic problems concerning these groups. Distributional records and habitat notes are included where possible, since these can be useful aids to taxonomic studies. Descriptions of the larva of *Paroxyethira tillyardi* and the adult males of two unnamed chironomids (subfamily Orthocladiinae) are given together with notes and figures of chironomid larvae and pupae from Lake Grasmere.

6.2 TAXONOMY OF THE LARVAE OF NEW ZEALAND HYDROPTILIDAE

Of the six species of Hydroptilidae described from New Zealand, one is in the widespread genus *Oxyethira* Eaton 1873 and five in the endemic *Paroxyethira* Mosely 1924. Adequate descriptions of adults were given by Mosely (1924) and Leader (1972), and a key to adults by Leader (1972). The larvae of only two species (*O. albiceps* and *P. hendersoni*) have been described by Cowley (1978) who referred also to previous work on the family in New Zealand.

The following key to larvae and pupae of the New Zealand species of hydroptilids includes all of the described species, although it is not yet possible to distinguish between *P. eatoni*, *P. hintoni* and *P. kimminsi*. Pharate adults (i.e., late pupae that show the

characteristic adult genitalia) must be examined to enable specific identification of these species (see key in Leader 1972).

Efforts to differentiate the species further have been frustrated by a paucity of larval material of *P. kimminsi* (especially) and *P. hintoni*. The marked similarity between adults of *P. kimminsi* Leader 1972 and *P. eatoni* Mosely 1924 deserves further consideration when more material is available. In addition to the characters used in the key, the morphology of larval prosternal plates was examined and four species-groups were evident (Fig. 6.1). However, no further differentiation of species was possible.

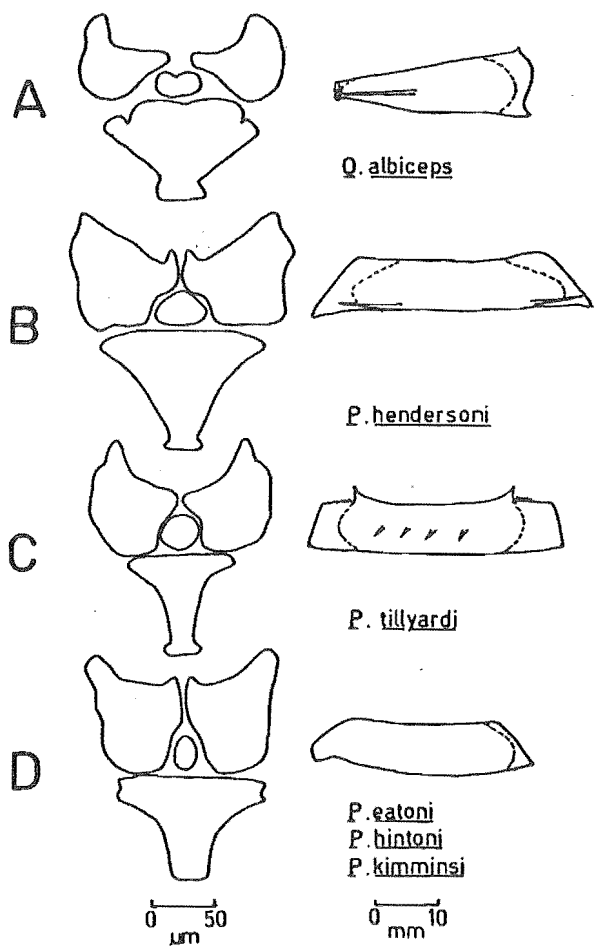


Fig. 6.1

Larval prosternal plates and cases of New Zealand Hydroptilidae.

There has been some suggestion that more than one species of *Oxyethira* is present in New Zealand (Michaelis 1977, A.G. McFarlane pers. comm.). This belief appears to be based on the considerable size variation among larvae, pupae and adults and minor differences in larval case morphology of specimens from some areas. I do not consider that, at present, there is evidence sufficient to warrant the erection of another species. Towns (1976) also found no evidence to support the existence of more than one species.

6.2.1 Key to the Larval Hydroptilidae of New Zealand (from Stark in press)

1. With a case 2
- Without a case; either instars 1-4 (of any species), or 5th instar larvae which have lost their cases 5

2. Case the shape of a flask or axehead (Fig. 6.1A) .... *Oxyethira albiceps* (McLachlan)
[Widely distributed in freshwaters from sea-level to about 900 m. All life history stages exhibit considerable variation in size and may be found throughout the year. (Cowley 1978)]
- Case approximately rectangular. (Fig. 6.1 B-D) ..... *Paroxyethira* 3

3. Case with spine-like projections which interrupt its otherwise smooth outline 4
- Case without projections (Fig. 6.1D) ..... *P. eatoni* Mosely
..... *P. kimminsi* Leader
..... *P. hintoni* Leader
[These three species are not well known and as yet their larvae cannot be separated. *P. eatoni* inhabits small ponds, seeps, tarns and the quieter stretches of streams and often is associated with filamentous algae and diatoms. *P. kimminsi* is known only from quieter parts of streams in the Waitakere Ranges near Auckland. *P. hintoni* is known from mountain streams above 600 m. (Leader 1972)]

4. Case with two horizontal projections at each end (Fig. 6.1B) .... *P. hendersoni* Mosely
[Larvae occur widely in a variety of freshwater habitats from sea level to at least 1320 m. Case shape and size can be highly variable. (Cowley 1978, Leader 1970, Leader 1972)]
- Case with up to four lateral and two dorsal projections; often darkly pigmented, sometimes black (Fig. 6.1C)... *P. tillyardi* Mosely
[Known only from lakes where larvae are found on algal-coated macrophytes and stones. Larval cases vary considerably in shape and in number and development of spines.]

5. Prothorax narrower than head; abdomen tapering gradually posteriorly and possessing long setae; anal appendages long and slender ..... Instars 1-4, all species
[At present it is not possible to separate early instars of the six species. (Leader 1972)]

- Prothorax as broad as or broader than head; abdomen large and swollen, usually laterally flattened ..... Final instar larvae [*P. hendersoni* and *P. tillyardi* possess a complex spine on the median of the ventral prolongation of the protarsus but this spine is absent from *O. albiceps*. In addition, the tarsal claw of the hind limb of *P. hendersoni* is about 20 times as long as its basal width whereas it is only 10 times as long in *P. tillyardi*. The condition in the other *Paroxyethira* species is not known.]

6.2.2 Distribution of the New Zealand Species of Hydroptilidae

O. albiceps was considered by Leader (1972) to be by far the most abundant and widespread of the New Zealand Hydroptilidae, being recorded from Dargaville in the North Island to Dunedin in the South Island (Fig. 6.2A), from lakes and streams between sea level and about 900 m a.s.l. Cowley (1978) suggested that, in most freshwater habitats, its distribution was related more to food availability (probably filamentous algae) than to current speed or substrate. *O. albiceps* may be found in virtually any freshwater habitat with sufficient filamentous algae and this is reflected in its wide distribution within New Zealand and its presence on Chatham Is., Auckland Is., Campbell Is., Snares Is. and Antipodes Is. (Wise 1972, 1973, 1978).

P. hendersoni also is found throughout New Zealand (Fig. 6.2B) in lowland lakes and ponds, on aquatic macrophytes at the edges of large rivers (Leader 1972) and in the outlet stream of L. Turbott, Auckland Is. (Wise 1972). I have found this species in a wide variety of fresh water habitats (viz., most freshwater bodies containing macrophytes, filamentous algae and/or diatoms) and have records of adults from 1320 m a.s.l. (Lake Sylvester, N.W. Nelson, February 1966, A.G. McFarlane coll.).

*P. tillyardi**, however, has been found only in lakes, where the larvae occur on filamentous algal or diatom encrusted macrophytes or stones. Leader (1972) stated that *P. tillyardi* appeared to be a highly localised insect because, despite intensive collecting, it was known (as an adult) from only two places (Lake Ianthe on the West Coast of

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* All references to *P. tillyardi* in Leader (1970) are actually *P. hendersoni* since Leader misassociated *P. tillyardi* adults with *P. hendersoni* larvae from Lake Ianthe. I have found the larvae of both species in samples collected by Dr K. Deacon from this lake.

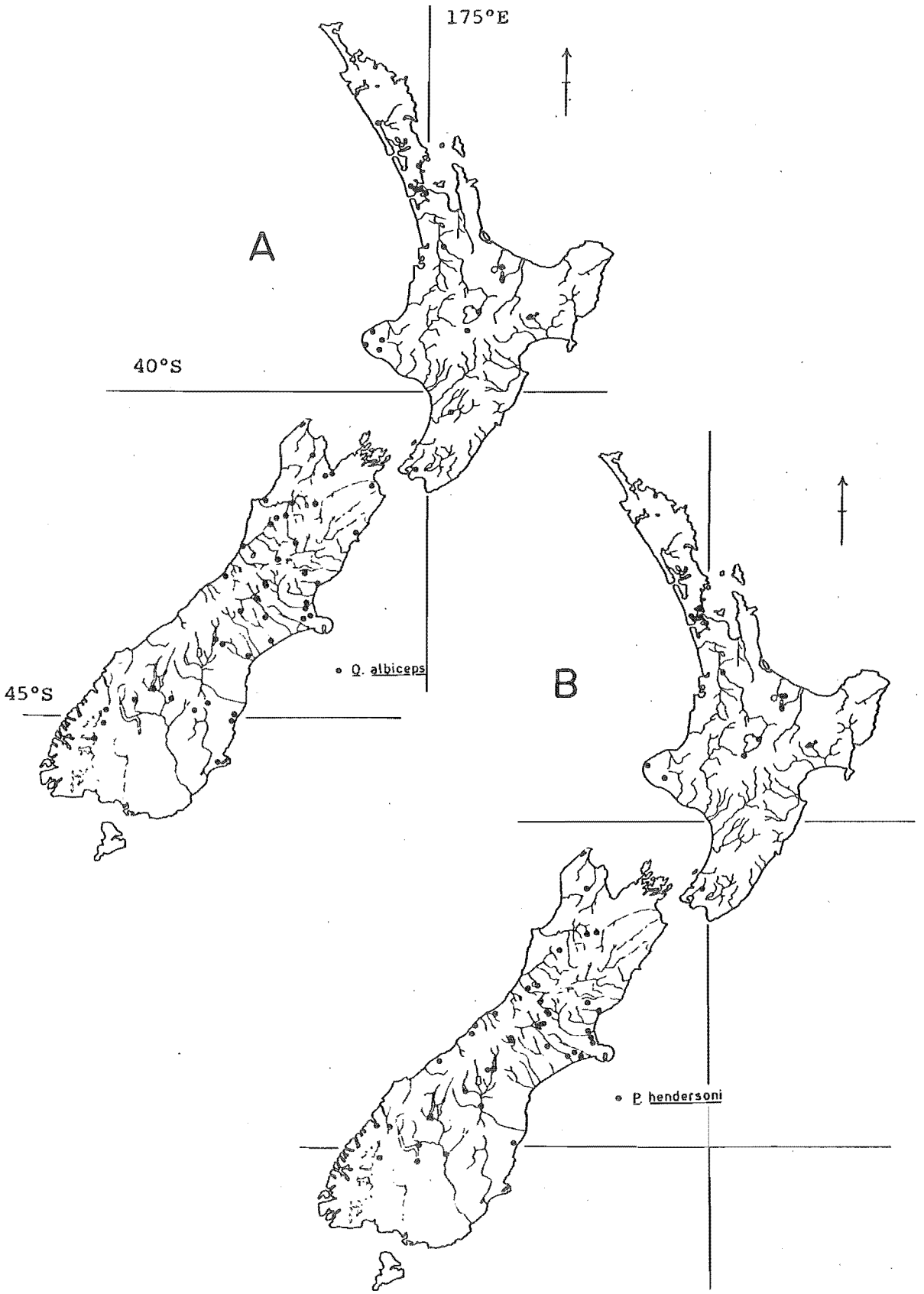


Fig. 6.2 Distribution of (A) *Oxyethira albiceps* and (B) *Paroxyethira hendersoni*.

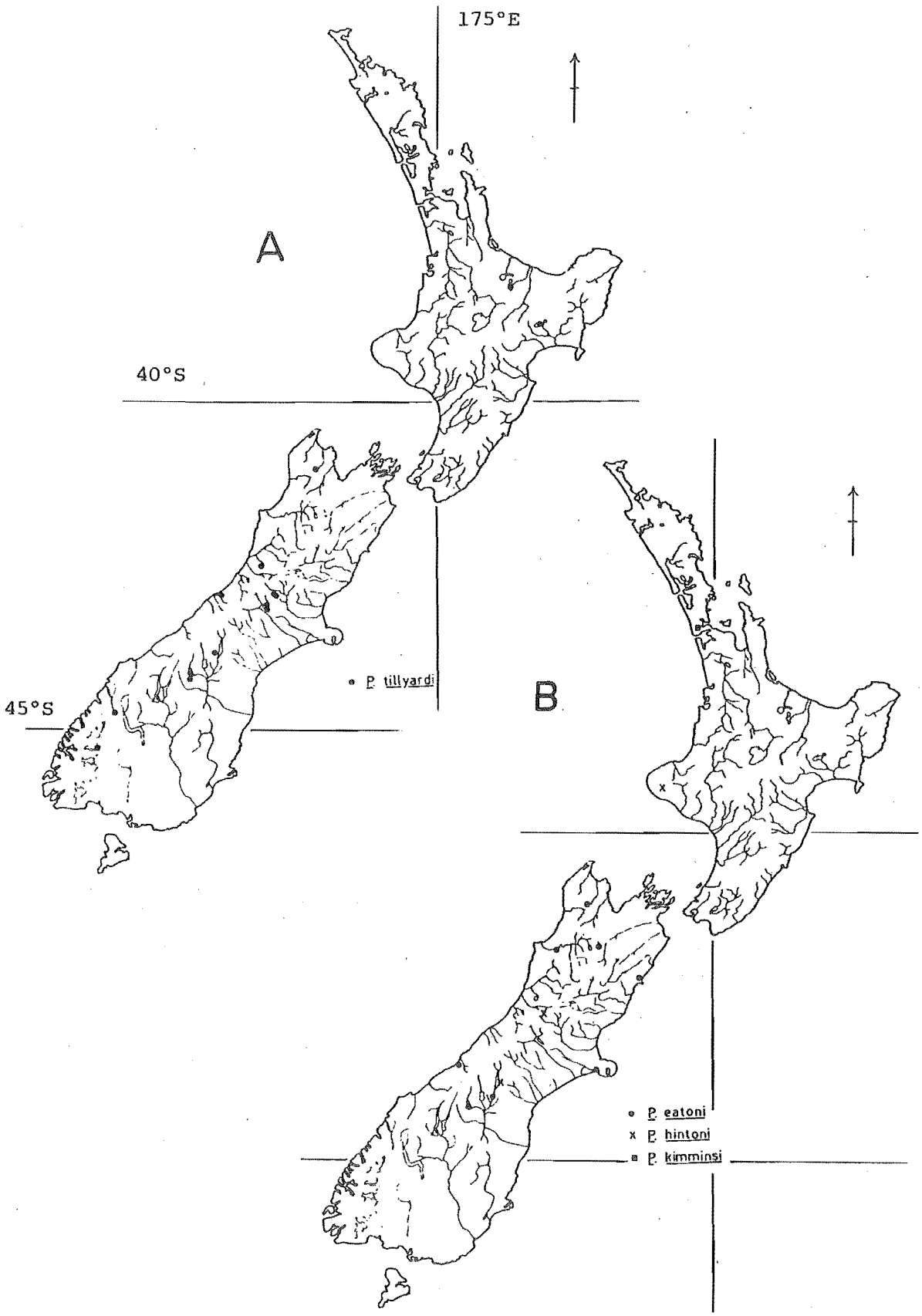


Fig. 6.3 Distribution records of (A) *Paroxyethira tillyardi* and (B) *P. eatoni*, *P. hintoni* and *P. kimminsi*.

the South Island and the Tarawera region, North Island). *P. tillyardi* has a very short flight period (see Chapter V) and would seem to be comparatively rare if its presence was determined solely on the basis of adult records. Larvae are present all year round, and I have found them in collections from at least 14 different lakes throughout New Zealand (Fig. 6.3A). The geographical range of *P. tillyardi* appears to be limited by the presence of suitable larval habitats, hence, for example, its absence from the Canterbury Plains.

P. eatoni, *P. hintoni*, and *P. kimminsi* are poorly known as larvae and, as yet, cannot be distinguished from one another in the absence of pharate adult or adult associations. *P. kimminsi* is known only from its type locality in the Waitakere Ranges, Auckland (Cascades Stream). Leader (1972), who described the adults, also recorded the presence of larvae and pupae associated with filamentous algae and diatoms on the sides of stones in quieter parts of the stream. Maximum abundances of immature stages occurred in summer. Towns (1976) also recorded its presence in the same area (Fig. 6.3B). *P. hintoni* was described by Leader (1972) from adults collected near the TePopo Stream (Mount Egmont, altitude 700 m) and he also collected adults and recorded immature stages in a small stream flowing into the north side of Lake Tekapo (altitude 600 m+) (Fig. 6.3B). I have also examined specimens from the Edwards River in the Arthur's Pass National Park (760 m a.s.l., 20 January 1939, A.G. McFarlane coll.) (Fig 6.3B). Thus, this species seems to be restricted to streams above about 600 m a.s.l. *P. eatoni* is more widely distributed (Fig. 6.3B). The adult male was described by Mosely (1924) from the Tekapo River in the Mackenzie County, South Island, and the female by Leader (1972) who did not mention a type locality. Dr J.P. Leader (pers. comm. 22 March 1977) has found larvae only at one place - 'in a stream running underneath a railway bridge near Inangahua' (West Coast, South Island). Adults of this species are 'commonly caught in light-traps around the North Island lakes' (Dr J.P. Leader pers. comm. 22 March 1977). I have examined adult material from Lake Moeraki (3 February 1965, A.G. McFarlane), Lake Ohau (12 March 1966, A.G. McFarlane), Lake Rotoiti (South Island) (22 November 1978, B.V. Timms) and larvae and pupae from tarns and seeps near Lake Sylvester (1320 m a.s.l., A.L.P. coll. *in* A.G. McFarlane colln), 'Kaituna', Banks Peninsula (13 September 1964, J.G. Penniket) and a small pond in the bed of the Puhipuhi River near Kaikoura (6 November 1978, J.D.S.). It seems likely, since larvae have not been collected

from lakes, that the preferred habitat of larvae is small ponds, seeps, tarns or slow-flowing backwaters of streams and rivers in association with filamentous algae and diatoms as at the Puhipuhi River.

6.2.3 Description of the Larva of *Paroxyethira tillyardi* (Figs 6.4, 6.5e,f)

Paroxyethira tillyardi Mosely 1924.

Mosely 1924, *Transactions of the New Zealand Institute* 55: 670-673.

LARVA (final instar): larval length variable 2.2 - 3.6 mm; case length 2.7 - 4.0 mm, depth 0.9 - 1.0 mm.

CASE. The case of *P. tillyardi* varies greatly in size, colour and the number (0 - 4 per side) of the lateral and size of the dorsal projections (Fig. 6.5e,f). It can be up to 4 mm long (usually 3.6 - 3.7 mm) and 1.0 mm deep. The distance between the dorsal processes varies between 1.2 and 1.6 mm. The case is constructed of medium to dark brown-black semi-transparent secretion and is usually lighter in colour towards each end. The two ends of the case are identical.

HEAD (Fig. 6.4b). Length 0.25 mm, width 0.19 mm, L/W = 1.32. Only slightly elongate, oval, almost parallel-sided. Pigmentation dark brown-black with pale brown around large eyes. Frontoclypeal apotome wider across lower half than upper. Antennae prominent with lateral bristle at least 1.5× antennal length. Pregula with narrow lateral arms; postgula a crescent-shaped plate (Fig. 6.4c). Mandibles asymmetrical, with two outer basal bristles. Left mandible with a well-formed inner brush of hairs (Fig. 6.4d). Facial hairs very long, some 2× length of head capsule.

THORAX. All three notal plates well formed. Mesonotum and metanotum similar in length and breadth (0.16 - 0.18 × 0.23 - 0.26 mm) (L × W) and clearly wider than pronotum.

Prothorax. Length 0.18 mm, width 0.21 mm, L/W = 0.86. Pronotum with straight anterior edge and evenly curved anterolateral angles. Pigmentation mid-dark brown, lighter anteriorly and laterally. Anterior edge of pronotum bearing (from midline laterally), 1 short, 1 long, 2 short, 1 long and 5 short setae, and, on the dorsal surface 2 pairs of medium length setae. Prosternum (Fig. 6.1) with a single T-shaped oral sternite.

Meso- and metathorax. Well-formed; pigmentation mid-dark brown, darker posteriorly. Mesosternal region with small, elongate trapezoid sclerite on mid ventral axis and 2 irregular, transversely elongate anal plates. Metasternum with weakly sclerotised Y-shaped oral

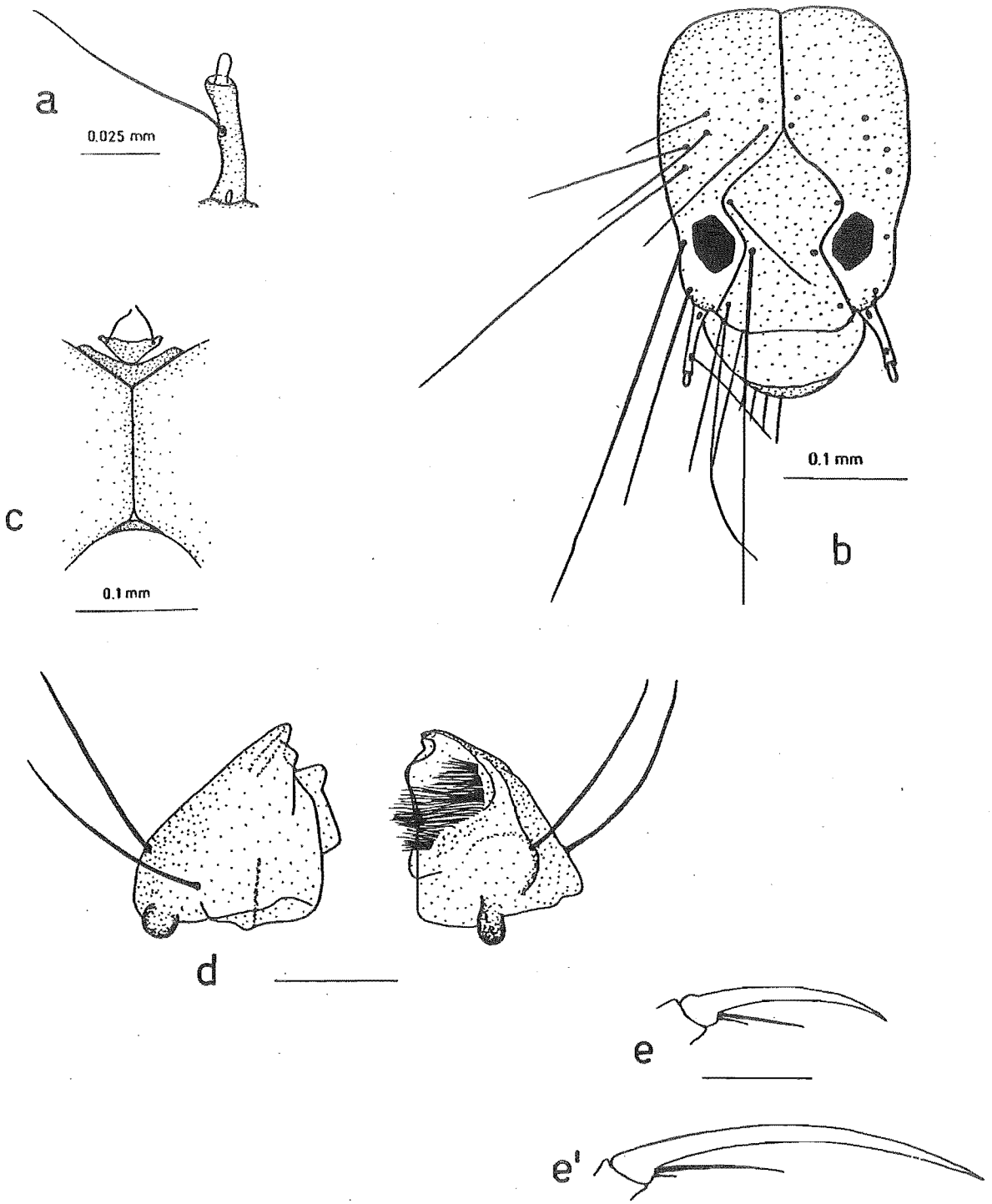


Fig. 6.4 *Paroxyethira tillyardi:* a. antenna, b. head, c. gular region, d. mandibles, e. claw of hind limb (e' = claw of hind limb of *P. hendersoni*). All scale bars 0.05 mm unless indicated otherwise.

sternite and 2 very narrow, transversely elongate anal sternites.

Legs. Forelegs short, sturdy, Middle and hind legs longer and thinner; pretarsal claws relatively stout (cf. *P. hendersoni* Fig. 6.4e, e'). Forelegs uniform pale brown-gold. Tibia with peg-like projection bearing 2 distal setae - one blade-like and one stout - and a complex comb-like spine on the inner base. Ventral edge of femur with several prominent setae arising from slight projections.

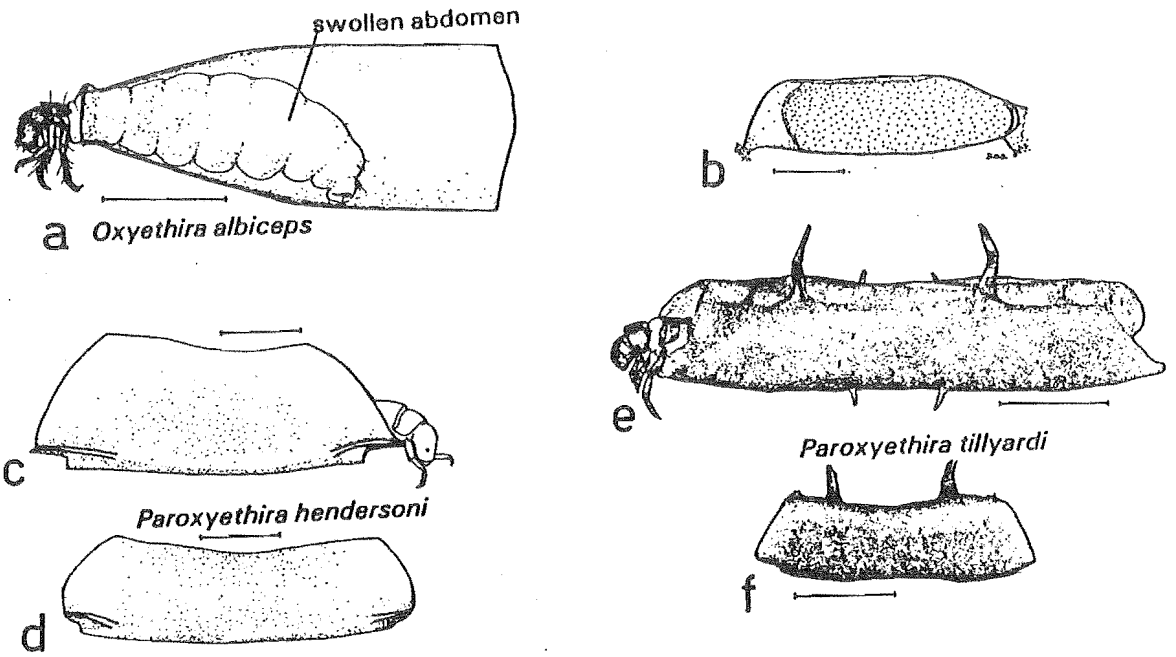


Fig. 6.5 a. *Oxyethira albiceps* cased larva; b. *Paroxyethira eatoni* pupal case; c. *P. hendersoni* cased larva; d. *P. hendersoni* case; e. *P. tillyardi* cased larva; f. *P. tillyardi* case. (Scale bars = 1 mm)

ABDOMEN lime green (bright yellow rapidly leaching to white when preserved in 70% alcohol), without gills. Segments 1 and 9 small, clearly defined. Segments 2 - 8 large, segments 4 - 6 largest. Segment 9 with a medium-sized, oval tergite bearing 4 pairs of hairs, the middle pair very long. Segments 3 - 7 with a minute chitinous ring mid-dorsally. Anal appendages shortened. Segment 10 short, compact. Dorsal supporting plate with 2 setae, one on surface the other arising from a notch in distal edge. Claw with a short, strong primary hook and 4 small auxiliary hooks, the second pair very slender.

SPECIMEN LOCALITIES*

South Island. NN - Boulder L. 27 October 1963 V.M. Stout, MC - L. Coleridge 14 January 1968 A.G. McFarlane; L. Grasmere 14 April 1976 - 21 October 1980; WD - L. Brunner 10 January 1965 V.M. Stout; MK - L. Ohau 19 February 1976 V.M. Stout; FD - L. Te Anau 30 September 1976 V.M. Stout; L. Lochie January 1962 G.A. Knox.

* Code system for specimen localities follows that recommended by Walker & Crosby (1979).

DIAGNOSIS

The presence of a complex comb-like spine on the inner base of the fore-tibia separates larvae of *Paroxyethira* from *Oxyethira*.

P. tillyardi differs from other *Paroxyethira* species in the form of the prosternal plates, the darker pigmentation (especially of the head and thorax), and the more robust limbs. The larval case is very different from those of the other species (Fig. 6.5).

6.3 TAXONOMY OF NEW ZEALAND CHIRONOMIDAE

Few larvae of New Zealand Chironomidae have been described (Brundin 1966; Forsyth 1971, 1975b, 1979; Sublette & Wirth 1980) and consequently identification, even to the generic or tribal level, has been a problem. On the other hand, adult taxonomy is reasonably well advanced as a result of the work of Pagast (1947), Freeman (1959, 1961), Brundin (1966), Forsyth (1971, 1975b) and Sublette & Wirth (1980).

The following keys to larvae and adult males of freshwater chironomids known from the main islands of New Zealand include all described species of the subfamilies Tanypodinae, Podonominae, Diamesinae and Chironominae (and four undescribed Chironominae). Orthocladiinae, Telmatogetoninae (marine) and chironomids known only from New Zealand's subantarctic islands (see Sublette & Wirth 1980) are not included. Orthocladiinae systematics is confused by various conflicting systems of nomenclature, many synonymies (see, for example, Hamilton, Saether & Oliver 1969), and the proliferation of very narrow generic diagnoses (as evidenced by, for example, eight monotypic genera erected by Sublette & Wirth (1980) for orthoclads from New Zealand's Subantarctic islands). The existence of many undescribed species makes it inadvisable to construct keys to New Zealand Orthocladiinae.

The following keys to the subfamilies and species of larval Chironomidae, complete with introduction, are based on the literature and my own taxonomic investigations. These keys are included in the compilation of keys to the freshwater insects of New Zealand by Winterbourn and Gregson (in press) and are the most comprehensive keys to New Zealand chironomids constructed to date.

The identification of chironomid larvae is not easy since taxonomic knowledge of larvae lags behind that of adults. Therefore, it is often necessary to establish the link between adult and larval stages of a species to enable specific identification. The importance of life history information (in the broadest sense, the ecology of a species) in this regard should not be underestimated. Behavioural features, microhabitat preferences and data on abundance can all be

useful in associating life-history stages. Often a clue to larval identity can be obtained by association with adults collected in the region of the larval habitat although there is always the danger of misassociation. Pupae can be especially useful because they develop adult characteristics (e.g., genitalia) and it may then be possible to associate adults, pupae and larvae through field collections. The best method, and the one least subject to misinterpretation, is that of rearing individually isolated larvae, through the pupal stage, to emergence as the adult. One then has larval head capsules, pupal exuviae and adults for examination. If due care is taken to duplicate environmental conditions (especially temperature, current speed, substrate and food supply) rearing is not difficult for many species (e.g., several species reared by Forsyth (1971) took 12-25 days at 20-25°C to grow from egg to adult). Identification of chironomid larvae relies on features of both the head and body and usually requires the mounting of specimens on slides. The following procedure is recommended: Colours of specimens should be noted before they are killed and stored in 70% alcohol. To mount a larva on a slide, the body should be separated from the head and mounted on its side whereas the head should be placed ventral side up. It is often best to boil the head in 5-10% KOH (10 min or less) to digest away muscle tissue prior to mounting on the slide. A good mounting medium is lactophenol-PVA. Sometimes, temporary mounts in water are useful for examination of the fine structures of mouthparts. The nature of the taxonomic characters used in the keys will become evident on referring to the figures; anatomical terminology used follows that of Mason (1973).

I would like to emphasise that the keys must be used with caution as the New Zealand fauna is relatively poorly known. Especially within the subfamily Orthocladiinae, there are many undescribed species, a number of which are extremely similar as adults and, as yet, not separated as larvae. Overseas keys (Bryce & Hobart 1972, Mason 1973, Martin 1974, 1975, Oliver, McClymont & Roussel 1978) also may be useful for identifying larvae at the generic level.

Nomenclature used below is that employed by most contemporary European workers (e.g., Brundin 1966, Fittkau 1962). As such, it is in line with recent work in Australia (J. Martin, pers. comm.) and current trends in North America (Hamilton, Saether & Oliver 1969, Saether 1977). The European classification employs smaller genera than those traditionally used by most North American taxonomists and past New Zealand workers (Forsyth 1971, Freeman 1959).

As the distributions and habitat requirements of most species are poorly known, few annotated notes on biology are appended.

6.3.1 Keys to Larval Chironomidae of New Zealand

[Subfamilies or tribes marked with a single asterisk have not been recorded from New Zealand. **Orthocladiinae, Clunioninae and Telmatogetoninae are poorly known in this country as larvae and are not keyed further.]

Key to subfamilies

1. Head capsule with fork-shaped lingua; antennae retractile into sheaths embedded in head (Fig. 6.6a,c) ..... Tanypodinae, p. 150
- No fork-shaped lingua; antennae not retractile 2

2. Premandibles absent 3
- Premandibles present (Fig. 6.6d) 4

3. Posterior procerci (= preanal papillae) 5 to 10 times as long as wide; antennae 4 or 5 segmented, third segment may be annulated; hypopharynx with ventral lamellae projecting forward .... Podonominae, p. 151
- Posterior procerci lacking; antennae 3-segmented, not annulated; labial plate without teeth, anterior margin nearly straight; body heterogeneously sclerotised, partly covered with plates of differing forms and bearing strongly developed setae .... Aphroteniinae*

4. Paralabial plates with striations (Fig. 6.6e) (exception: *Harrisius pallidus*, paralabial plates indistinct) .... Chironominae, p. 153
- Paralabial plates, if present, without striations (Fig. 6.6d) 5

5. Third antennal segment with annulations OR head, in dorsal or ventral view, tapering towards the front (i.e., tending toward trapezoid shape), occipital margin with distinct, deep-black neck (Fig. 6.7a), head colour either dark reddish-brown or light yellow, head capsule often with numerous long setae ..... Diamesinae, p. 152
- Not as above; third antennal segment never annulated 6

6. Freshwater species (some terrestrial or semiterrestrial); labial plate variable, usually convex anteriorly, its central three-quarters always with teeth (Fig. 6.6d) ..... Orthocladiinae,** p. 157
- Generally marine (intertidal) ..... Clunioninae & Telmatogetoninae**

Key to larval Tanypodinae

1. Paralabial combs (Fig. 6.6c) absent; abdominal segments slender, without hair fringe; anal gills slender ..... Tribe Pentaneurini, 2
- Paralabial combs, or a row of free chitin points present; abdominal segments broad, usually with hair fringe 3

2. Maxillary palp with more than one basal segment (Fig. 6.6f); lingua with 5 teeth ..... *Ablabesmyia mala* (Hutton)
[Found in lakes, ponds and streams. Sublette & Wirth 1980, Hutton 1902, Freeman 1959]
- Maxillary palp with a single basal segment; lingua with 5 teeth ..... other Pentaneurini
[One described species, *Pentaneura harrisi* Freeman, and at least one undescribed species. There is some doubt concerning the generic placement of Australasian *Pentaneura* (J. Martin pers comm.). Found in streams and lakes. Freeman 1959, Forsyth 1971]

3. Antennae at least half as long as head; a row of free chitin points present in place of paralabial comb; lingua with 6-7 teeth ..... Tribe Coelotanypodini*
- Antennae at most one third as long as head; paralabial combs present 4

4. Mandible with thick, bulging basal portion; 6 anal gills ..... Tribe Tanypodini*
- Mandible not as above (Fig. 6.6c); 4 anal gills 5

5. Lingua with 4 yellow teeth of equal length, OR lingua with 5 black teeth; superlingua scale-like with toothed edge ..... Tribe Macropelopiini (in part)*
- Lingua with 5 reddish-yellow or brownish-black teeth; superlingua two-pointed 6

6. Mandible with large two-pointed tooth; labial plate with long pustule-like appendages latero-basally; paralabial combs each with 13 teeth ..... Tribe Anatopyniini*
- Mandible with two small teeth close together; no pustule-like appendages; paralabial combs each with, at most, 9 teeth; toothed margin of lingua concave or straight ..... Tribe Macropelopiini (in part)
[Larvae keying here belong to the genera *Macropelopia*, *Apsectrotanypus* or *Gressittius*. Ten species have been described as adults from New Zealand: *Gressittius antarcticus* (Hudson), *Macropelopia apicincta*

(Freeman), *M. languidus* (Freeman), *M. debilis* (Hutton), *M. quinquepunctata* (Freeman), *M. flavipes* (Freeman), *M. apicinella* (Freeman), *M. umbrosa* (Freeman) and the species *quadricincta* Freeman and *cana* Freeman which may belong in *Apsectrotanypus* (J. Martin pers. comm.). Larvae of few of the above species have been recognised and genera and species are separated easily only as adults. Members of the tribe occur in many freshwater habitats. Forsyth 1971, Freeman 1959, Hutton 1902, Sublette & Wirth 1980]

Key to larval Podonominae

[The diagnoses of New Zealand podonomid larvae leave much to be desired. Tentative larval identifications should be checked by examination of pupae or adult males.]

1. Posterior procerci (= preanal papillae) uniformly pigmented ..... Tribe Podonomini, 2
- Posterior procerci black basally, hyaline (= transparent) distally ..... Tribe Boreochlini*

2. Antennae comparatively short and stout, third segment annulated in most New Zealand species; middle tooth of labial plate considerably broader and longer than the first of 7 laterals (Fig. 6.6g); mandible with an apical group of 7 dark teeth (Fig. 6.6h) ..... *Parochlus* spp.
[Ten species have been described: *P. conjungens* Brundin, *P. aotearoae* Brundin, *P. spinosus* Brundin, *P. maorii* Brundin, *P. ohakunensis* (Freeman), *P. carinatus* Brundin, *P. pauperatus* Brundin, *P. novaezelandiae* Brundin, *P. longicornis* Brundin and *P. glacialis* Brundin. Specific determination is possible only by examination of pupal material although *P. conjungens* and *P. glacialis* can be identified as adult males. Common in mountain streams. Brundin 1966]
- Antennae short and stout, third segment never annulated; middle tooth of labial plate small, hardly broader or longer than the first of 7 or 8 laterals; head often broad and triangular but may be slender and parallel-sided ..... *Podonomus* spp.
[Three species have been described: *P. parochloides* Brundin, *P. waikukupae* Brundin and *P. pygmaeus* Brundin. Adult males are preferred for specific determination. Found in mountain streams. Brundin 1966]

[The larva of *Zelandochlus latipalpis* Brundin (recorded from Franz Josef and Fox Glaciers) was described by Dumbleton (1973), however, insufficient detail was given for this species to be included in the key.
Larvae of *Podochlus* spp. are not known. Four species have been described: *P. grandis* Brundin, *P. stouti* Brundin, *P. cockaynei* Brundin and *P. knoxi* Brundin. Specific identification is possible by examination of pupae or adult males. *Podochlus* larvae probably inhabit mountain streams. Brundin 1966]

Key to larval Diamesinae

1. Third antennal segment annulated 2
- Third antennal segment not annulated 3

2. Dorsal surface of head with numerous large protuberances .... Tribe Boreoheptagyini*
- Dorsal surface of head without such protuberances .... Tribe Diamesini*

3. Paralabial plates well developed, extending beyond the labial plate by at least one half of the width of the labial plate. Paralabials with distinct beard of large, black hairs, or, hairs absent and central portion of labial plate with narrow concavity between two median teeth ..... Tribe Prodiamesini*
- Paralabials not developed as above 4

4. Anterior margin of labial plate virtually straight, middle one third of plate (at least) without teeth; premandibles not well developed and ending in a single blade ..... Tribe Protanypini*
- Labial plate distinctly convex (Fig. 6.7b,c); premandibles well developed and ending in more than one blade 5

5. Antennae 4-segmented, basal segment more than twice the length of segments 2, 3 and 4 together; head yellow and body light green; long posterior prolegs; labial plate light yellow, median tooth nearly one half plate width and smoothly rounded, flanked by 7 darker laterals (Fig. 6.7c) ..... Tribe Lobodiamesini
[This tribe is monotypic, containing one species *(Lobodiamesa campbelli* Pagast) which is found characteristically in small, slow-flowing mountain streams. Brundin 1966, Pagast 1947]
- Antennae 5-segmented ..... Tribe Heptagyini
[Five species of *Maoridiamesa* belong in this tribe. They have

very dark, conspicuously triangular heads with black occipital margins produced into pronounced necks with two ventral, posteriorly directed, projections and dorsolateral incisions (Fig. 6.7a) labial plate with 15 teeth, median tooth broad, second laterals small, third laterals very large (Fig. 6.7b). Larvae of the five species, *M. harrisi* Pagast, *M. intermedia* Brundin, *M. stouti* Brundin, *M. glacialis* Brundin and *M. insularis* Brundin (Campbell Island) inhabit mountain streams and some lowland rivers, but only adult males or pupae can be identified easily. Brundin 1966, Pagast 1947]

Key to larval Chironominae

[The larvae of *Tanytarsus albanyensis* Forsyth, 1971 and *Ophryophorus ramiferus* Freeman 1959 are not known.]

1. Antennae arise from prominent tubercles (prominences), as long as wide or longer; first antennal segment long and curved; striated paralabial plates often nearly four times as wide as long and nearly touching in the midline (Fig. 6.7r) ..... Tribe Tanytarsini, 3
- Antennal tubercles much wider than long, first segment not long and curved; striated paralabial plates usually (but not always) more fan-shaped (Fig. 6.7k) 2

2. Paralabial plates nearly touching in the midline, about four times wider than long ..... Tribe Pseudochironomini
[One species, *Riethia zeylandica* Freeman has been described from New Zealand. The larva is unknown. Freeman 1959]
- Paralabial plates distinctly separated (or indistinct in *Harrisius* (Fig. 6.7i)) ..... Tribe Chironomini, 7

3. Labial plate with 11, 13 or 15 teeth; mandibles with obvious teeth 4
- Labial plate with 3 teeth (may appear like 5) (Fig. 6.7o); mandibles without obvious teeth (Fig. 6.7p) ..... *Corynocera* sp.
[Undescribed larvae of this genus have been recorded from several lakes in New Zealand.]

4. Labial plate with 11 or 15 teeth 5
- Labial plate with 13 distinct, unicolourous teeth (or 11 if the median tooth is considered trifid) (Fig. 6.7q) .... *Calopsectra* Kieffer sp.
[All life history stages of this species, collected from the Hurunui River hot springs, await description.]

5. Anterior margin of labial plate strongly convex and with 11 teeth, median tooth rounded and unicolourous with no sign of notching (Fig. 6.7r) ..... *Tanytarsus vespertinus* Hutton
[This species has been recorded from lakes and rivers in lowland and upland areas. Freeman 1959, Hutton 1902]

- Median tooth of labial plate not unicolourous and/or not uniformly rounded 6

6. Median tooth of labial plate with basal, lateral notches (i.e., trifid); labial plate unicolourous and strongly convex (Fig. 6.7s) ..... *Paratanytarsus agameta* (Forsyth)
[This species has been recorded from shallow ponds and some lakes in the northern third of the North Island. Forsyth 1971, Kieffer 1921]

- Median tooth of labial plate not unicolourous and with slight lateral notching (Fig. 6.7u), which may make it appear to comprise 5 teeth in newly moulted larvae (Fig. 6.7t); labial plate only slightly convex ..... *Calopsectra funebris* (Freeman)
[This species can be found in rivers, lakes, ponds, swamps and some oxidation ponds. Forsyth 1971, Freeman 1959, Sublette & Wirth 1980]

7. Antennae 6-segmented (Fig. 6.7e) 8

- Antennae 5-segmented 9

8. Paired median teeth of labial plate smaller than first laterals, second laterals small and on the side of third laterals, 16 teeth (Fig. 6.7d,f) (early instars *may* have 15 teeth, i.e., only *one* small median tooth) ..... *Paucispinigera* spp.
[One described species, *P. approximata* Freeman (Fig. 6.7d,e), and one undescribed species. The larva of the latter species (known from Lakes Gault and Matheson) has minute middle and second lateral teeth on the labial plate (Fig. 6.7f). *P. approximata* inhabits beech forest streams and some lakes, especially those with beech-derived organic substrates. Freeman 1959]

- Paired median teeth of labial plate lighter than laterals and larger than first laterals which are on the sides of second laterals (Fig. 6.7g) ..... *?Microtendipes* Kieffer sp.
[Known from a single larva collected in Blue Lake, Tongariro.]

9. Labial plate concave anteriorly, the middle tooth wide and light, flanked by oblique rows of darker laterals (Fig. 6.7h). Maxillary palps prominent ..... *Cryptochironomus* Kieffer sp. [Recorded from Waitomo Stream, North Island.]

- Labial plate not as above 10

10. Labial plate concave anteriorly with 8 low, rounded, black teeth; paralabial plates indistinct; mandibles triangular and darkly pigmented (Fig. 6.7i) ..... *Harrisius pallidus* Freeman [The larva of this species occurs inside partly decomposing wood in mountain-streams. Freeman 1959]

- Labial plate not as above 11

11. Labial plate with 14 teeth, the paired median and second laterals largest and even in height (Fig. 6.7j) ..... *Polypedilum* spp. [Ten described species and possibly several undescribed species all belonging to the subgenus *Polypedilum: Polypedilum pavidus* (Hutton), *P. longicrus* Kieffer, *P. opimus* (Hutton), *P. harrisi* Freeman, *P. digitulus* Freeman, *P. cumberi* Freeman, *P. ignavus* (Hutton), *P. canum* Freeman, *P. luteum* Forsyth, and *P. alternans* Forsyth. *P. ignavus* may be a synonym of *P. canum*. Specific determination is possible only by examination of adult males. The genus is represented in a wide range of freshwater habitats: *P. pavidus* is common in the littoral zone of eutrophic lakes and some oxidation ponds, *P. opimus* and *P. harrisi* inhabit small streams and seepages and *P. luteum* probably occurs in running waters. Forsyth 1971, Freeman 1959, Hutton 1902, Kieffer 1921]

- Labial plate *usually* with an odd number of teeth (if even then greater than 14) 12

12. Eighth abdominal segment with one or two pairs of ventral tubules (= blood gills) (Fig. 6.6b) 13

- Eighth abdominal segment without ventral tubules 14

13. Two pairs of ventral tubules (Fig. 6.6b), variable in length, usually as long as segment 8; labial plate with 15 teeth (Fig. 6.7k); two pairs of anal gills, each less than half the length of segment 8, directed posteriorly ..... *Chironomus zealandicus* Hudson [This is the "thummi" type of the common, red "blood worm" and is found in the benthos of lakes, streams and eutrophic waters such as oxidation ponds. The larva of *Chironomus analis* Freeman appears to be morphologically indistinguishable from "thummi" type *C. zealandicus* but differs cytologically. Forsyth 1971, Freeman

1959, Hudson 1892, Hutton 1902]

- One pair of ventral tubules (arising distally on abdominal segment 8) with pointed ends; labial plate convex with 15 teeth (if first laterals are considered to be formed by lateral notches of the large median tooth); paralabials with finely serrated anterior edge and pointed ends (Fig. 6.71); anal gills bulbous towards apex and directed laterally .... *Kiefferulus opalensis* Forsyth
  [Found on wood and among roots of *Juncus* sp. in ponds and lakes. Forsyth 1975b]

14. Labial plate with 13 teeth, the outer lateral pair (i.e., 6th laterals) each with a slight notch, 5th laterals small (Fig. 6.7m) ..... *Cladopelma curtivalva* (Kieffer)
  [This larva, which is common in lakes, was described erroneously by Forsyth (1971) as *Chironomus (Cryptochironomus) cylindricus*. Forsyth 1971, Freeman 1961]
- Labial plate not as above, with 15 or more teeth 15

15. Larva an obligate commensal of the freshwater mussel *(Hyridella menziesi* (Gray)); labial plate variable, in the 4th instar with 5-8 small similar medial teeth forming a nearly straight line flanked by a smaller separate tooth, then a large tooth beginning a descending series of 7 smaller teeth. Teeth of the 3rd instar variable in number and disposition .... *Xenochironomus canterburyensis* (Freeman)
  [Probably widely distributed in lakes inhabited by the molluscan host. Forsyth 1979, Forsyth & McCallum 1978a & b, Freeman 1959]
- Larva free-living; labial plate with 15 teeth 16

16. Paralabial plates with coarsely serrated anterior margin and recurved striations (Fig. 6.7n) .... *Parachironomus cylindricus* (Freeman)
  [This is the larva of Freeman's *Chironomus (Cryptochironomus) cylindricus* which Saether (1977) assigned tentatively to the genus *Parachironomus*. This, relatively uncommon, species is found in lakes. Freeman 1959]
- Paralabial plate without serrated anterior margin; median and second lateral teeth of similar size, first laterals smaller (Fig. 6.7k) ..... *Chironomus* sp.a
  [This species is the "salinarius" type of *C. zealandicus* Hudson and is found in many fresh-brackish-polluted water habitats. Forsyth 1971, Hudson 1892, Hutton 1902]

Orthocladiinae

Wise (1973) recorded 12 species in 10 genera from New Zealand but recent collecting indicates that there are many more species yet to be described. Of those in Wise's list, *Camptocladius stercorarius* (De Geer) is unlikely to have aquatic larvae as its immature stages occur in cow dung in Britain and parts of Europe (De Geer 1776) while the larvae of *Smittia verna* (Hutton) (Hutton 1902) are likely to be terrestrial like those of most other species in the genus. The larvae of only three of the other species listed by Wise are known. Those of *Corynoneura donovani* Forsyth (Fig. 6.7v) and *Lymnophyes vestitus* (Skuse) have been adequately described (Forsyth 1971, Edward & Colless 1968) but the description of *Syncricotopus pluriserialis* (Freeman) (Forsyth 1971) is insufficiently detailed to separate it from very similar *Cricotopus* species.

Because it deals with such a small proportion of the fauna and does not use generic or specific diagnostic characters to separate taxa, Forsyth's (1971) key is of limited value. Keys written for use in other countries also have little utility in this country and it is not uncommon to find the same specimen will key to different genera in different keys. If overseas keys are used, the user should qualify his identification with a statement such as, "keys to *Cricotopus* sp. in Mason (1973)".

Adult chironomids, like larvae, almost always need to be mounted on slides for microscopic examination and identification. Methods for preparing and mounting specimens for examination are given by Edwards (1929), Schlee (1966), Saether (1969) and Pinder (1978).

The following key to adult male chironomids is based on the works of Pagast (1947), Freeman (1959, 1961), Beck & Beck (1966), Brundin (1966), Forsyth (1971, 1975b), Coffman (1978), Pinder (1978) and Sublette & Wirth (1980) as well as additional taxonomic investigations of my own. The key includes 26 genera and 52 species of chironomids from the subfamilies Tanypodinae, Podonominae, Diamesinae and Chironominae (including all the described species known from New Zealand). Eight further species (of the genus *Parochlus* (Podonominae)) are included but can be identified to species only as pupae (Brundin 1966). No attempt has been made to key to genera or species within the subfamilies Telmatogetoninae (marine) and the difficult Orthocladiinae.

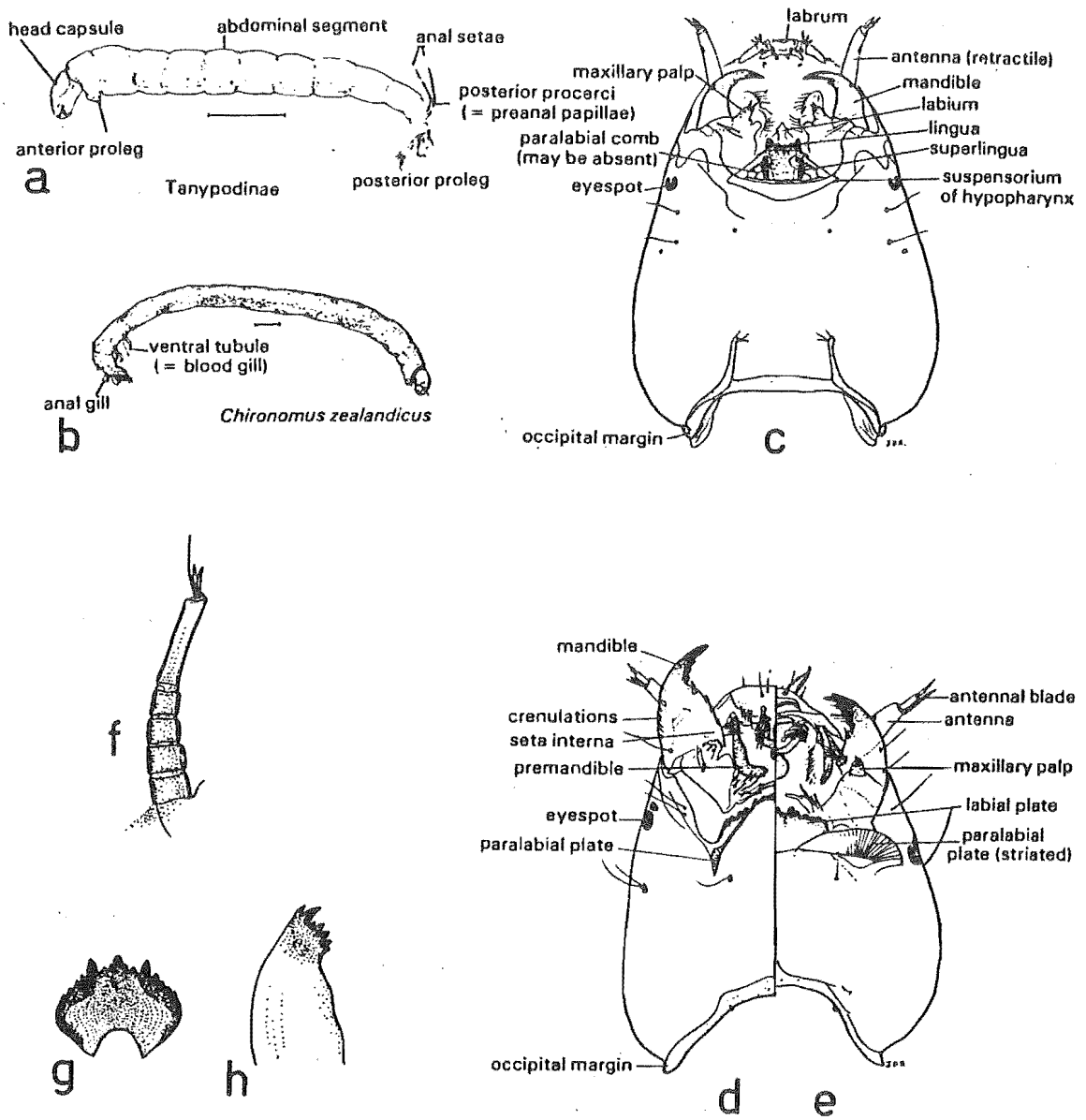


Fig. 6.6 a. Tanypodinae, larva. b. *Chironomus zealandicus*, larva. c. Tanypodinae head capsule (ventral). d. Orthocladiinae head capsule (ventral). e. Chironominae head capsule (ventral). f. *Ablabesmyia mala*, labial palp. g. *Parochlus* sp., labial plate. h. *Parochlus* sp., mandible. Scale bar = 1 mm.

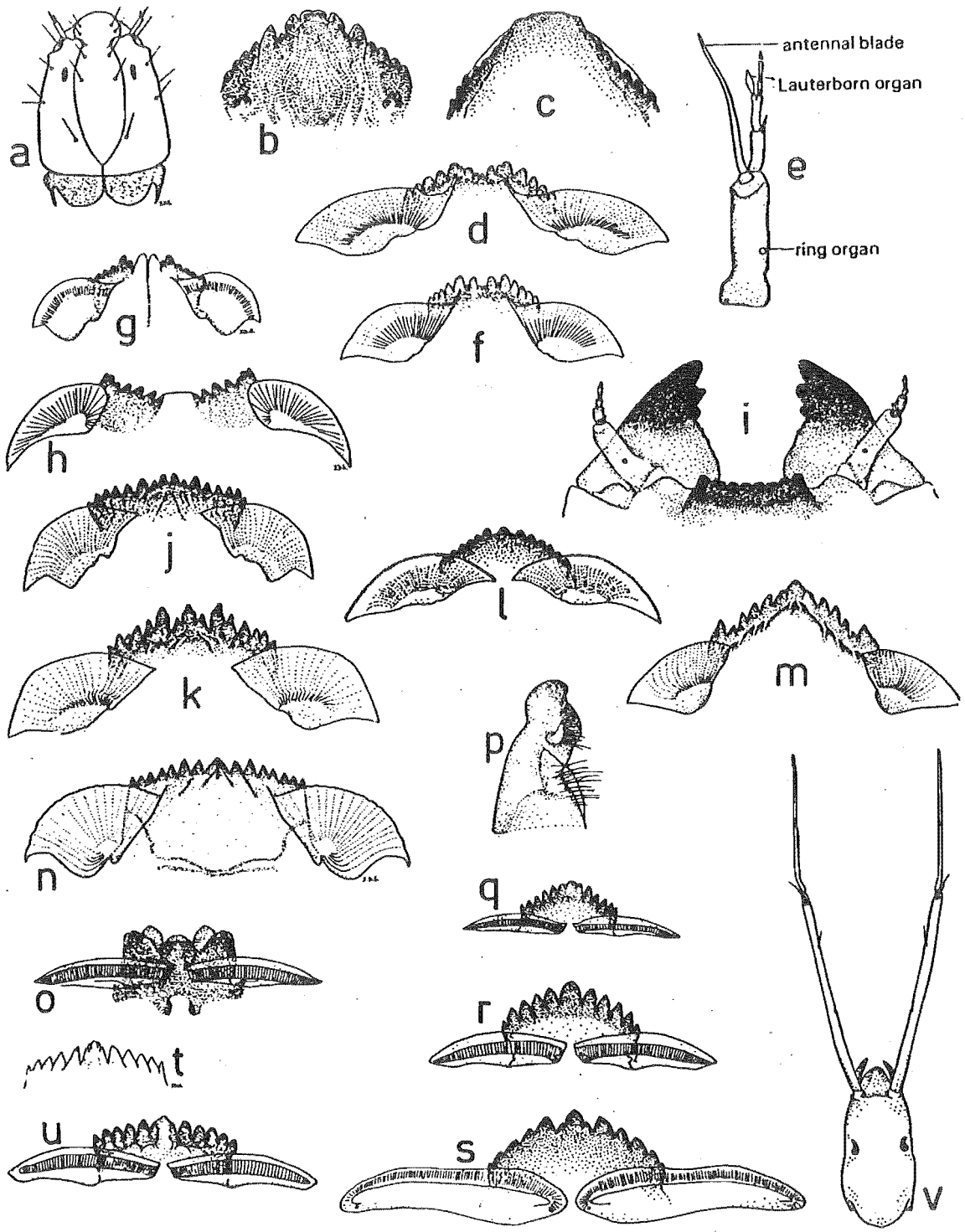


Fig. 6.7 All figures show labial and paralabial plates unless otherwise indicated. a. *Maoridiamesa* sp. head capsule, dorsal (after Brundin 1966). b. *M. stouti* labial plate (after Brundin 1966). c. *Lobodiamesa campbelli* labial plate (after Brundin 1966). d. *Paucispinigera approximata*. e. *P. approximata* antenna. f. *Paucispinigera* sp. g. *?Microtendipes* (after Mason 1973). h. *Cryptochironomus* sp. i. *Harrisius pallidus* labial plate, antennae and mandibles. j. *Polypedilum* sp. k. *Chironomus zealandicus, C. analis* and *C.* sp.a. l. *Kiefferulus opalensis* (after Forsyth 1975). m. *Cladopelma curtivalva*. n. *Parachironomus cylindricus*. o. *Corynocera* sp. p. *Corynocera* sp. mandible. q. *Calopsectra* sp. r. *Tanytarsus vespertinus*. s. *Paratanytarsus agameta* (after Forsyth 1971). t. *Calopsectra funebris* newly moulted larva showing details of "middle tooth" (after Sublette & Wirth 1980). u. *Calopsectra funebris*. v. *Corynoneura* sp. head capsule dorsal.

6.3.2 Key to Adult Male Chironomidae of New Zealand

* = Tribes not known from New Zealand.

Reference should be made to Fig. 6.8 for morphological terminology, and to figures given in published adult descriptions (referenced, where appropriate, below) to assist in the interpretation of this key.

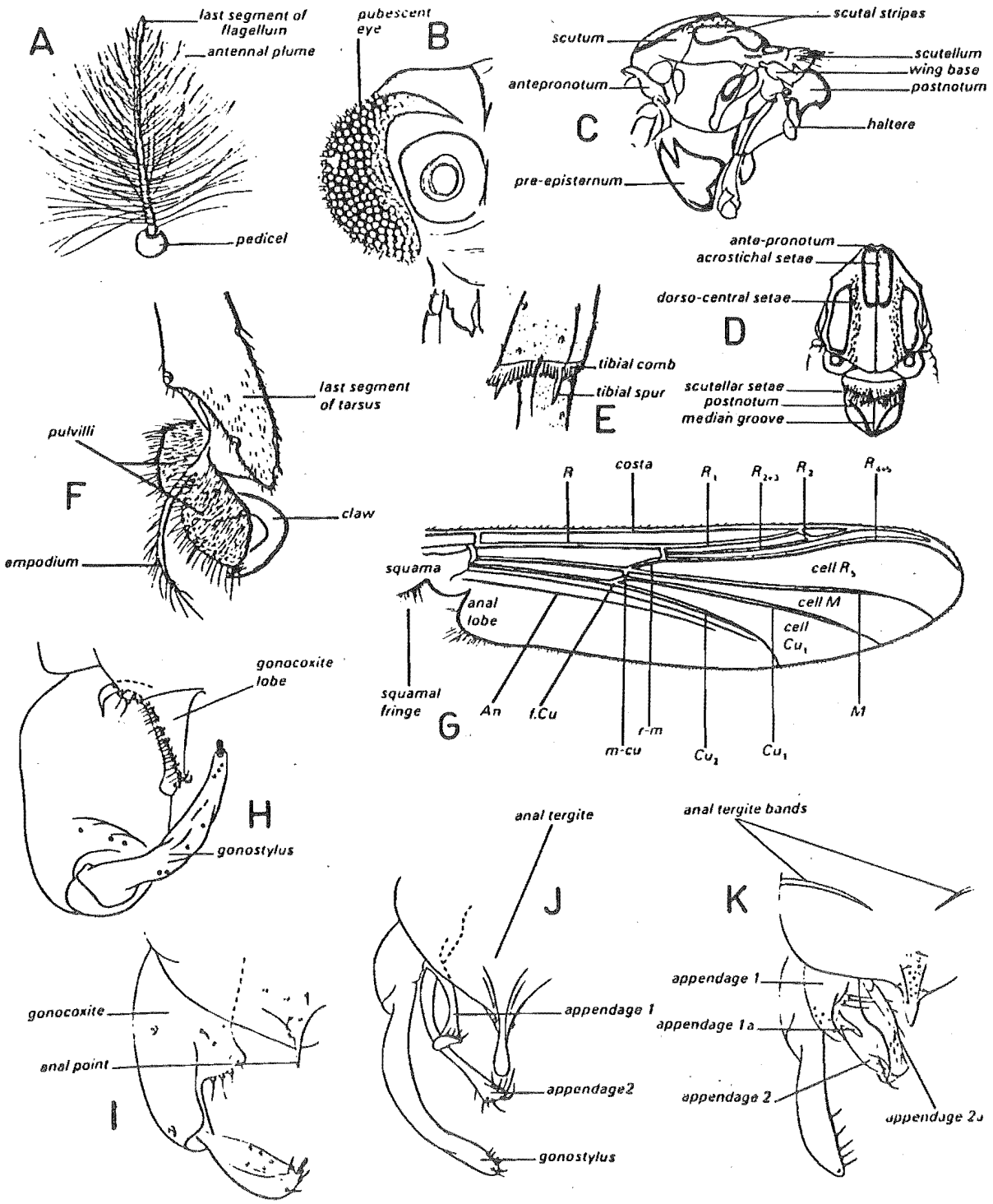


Fig. 6.8 A. Male antenna. B. Part of the head of a chironomid showing its pubescent eye. C. Lateral and D. dorsal views of the thorax of an adult chironomid. E. Tibial combs and spurs of a Chironominae adult. F. Foot of a chironomid showing large pulvilli. G. Wing of a tanypodinid showing terminology applied to veins. Dorsal views of male hypopygia of H. Tanypodinae, I. Orthocladiinae, J. Chironomini and K. Tanytarsini. (Figures from Pinder 1978)

1. Postnotum without a median groove or keel; antennal filament consisting of 4-6 segments (marine) ..... Telmatogetoninae (not keyed)

- Postnotum usually with a median groove or keel (except Tribe Clunionini, an exclusively marine tribe of Orthocladiinae); antennal filament consisting of at least 10 segments 2

2. X - vein M-Cu present 3
- X - vein M-Cu absent 5

3. R_{2+3} present 4
- R_{2+3} absent ..... Podonominae 6

4. R_{2+3} simple ..... Diamesinae 7
   R_{2+3} forked ..... Tanypodinae 13

5. Gonostylus directed rigidly backwards ..... Chironominae 20
- Gonostylus directed inwards ..... Orthocladiinae ... (not keyed)

6. Gonystylus with two lobes ..... Podonomini 22
- Gonostylus simple ..... Boreochlini*

7. f-Cu distal to M-Cu X-vein 8
- f-Cu proximal to M-Cu X-vein, OR M-Cu X-vein runs into f-Cu 10

8. Antepronotal lobes prolonged and strongly curved outwards; mesothorax with large expanse of short, suberect hairs arising from large pits ..... Lobodiamesini
   [One species known: *Lobodiamesa campbelli* Pagast 1947. Pagast 1947, p. 443, Fig. 1; Brundin 1966, p.417, Figs 603-608.]
- Antepronotum normal; mesothorax with single, double or triple row of bristles 9

9. Eye fuscous (= 'hairy')..... Heptagyini (in part) *Maoridiamesa*... 32
- Eye bare ..... Prodiamesini*

10. Gonostylus narrow, simple and attached mesally one third the way up from the distal end of gonocoxite ..... Protanypiini*
- Gonostylus attached at distal end of gonocoxite 11

11. Gonostylus short and robust ..... Boreoheptagyini*
- Gonostylus longer and narrower 12

12. M-Cu X-vein runs into f-Cu ..... Heptagyini (in part)*
- f-Cu proximal to M-Cu ..... Diamesini*

13. 4th tarsal segment cordiform (= heart-shaped)... Coelotanypodini*
- 4th tarsal segment cylindrical 14

14. f-Cu sessile .....(i.e. proximal or opposite M-Cu X-vein) 15
- f-Cu stalked .....(i.e. distal to M-Cu X-vein) 19

15. Costa not, or only slightly, produced beyond the end of R_{4+5} ... . Pentaneurini in part (except *Natarsia*) 35
- Costa produced beyond the end of R_{4+5} by 2× length of r-m 16

16. Wings with macrotrichia (larger hair-like structures on wing surface, cf. microtrichia) at distal end only; no rows of proximal spines on tibial spurs ..... Anatopyniini*
- Wings with dense macrotrichia; tibial spurs with rows of proximal spines 17

17. Eyes irridescent ..... Macropelopiini in part *(Psectrotanypus & Apsectrotanypus)*?..... 36
- Eyes not irridescent 17

18. Mesonotal tubercle (= hump-like plate lying in middle of mesonotum) present; claws pointed .... Macropelopiini in part (*Macropelopia*) 36
- Mesonotal tubercles absent; claws much split at apices .... Pentaneurini in part (*Natarsia*)*

19. Stalk of f-Cu less than one third as long as Cu_2; eyes irridescent; mesonotal tubercle present ..... Tanypodini*
- Stalk of f-Cu more than half as long as Cu_2; eyes black; mesonotal tubercle absent ..... Macropelopiini in part *(Procladius & Psilotanypus)**

20. Wing with macrotrichia on membrane and X-vein r-m parallel to and practically continuous with R_{4+5}; squama bare .... Tanytarsini 45
[N.B. Adult of *Corynocera* sp. not known]
- Wing usually without macrotrichia on membrane, when present then r-m transverse; squama usually fringed 21

21. Anterior tibia with well-formed black spur with enlarged base ..... Pseudochironomini
[One described species: *Riethia zeylandica* Freeman 1959 Freeman 1959, p. 423, Figs 3a and 3a']
- Anterior tibia without spurs or with only a small spur or scale ..... Chironomini 48

22. 4th tarsal segment with wide membranous sole extending from distal margin ..... *Podonomus* 25
- 4th tarsal segment without sole 23

23. Gonostylus ventrally with small separate lobe; segment 15 of antenna longer than 14; eyes densely fuscous .... *Podochlus* 27

\- Gonostylus not as above; segment 15 of antenna shorter than 14; eyes bare 24

24. Last palpal segment strongly swollen; outer spur of hind tibia nearly as long as inner; wings very strongly reduced .... *Zelandochlus*
[One described species: *Z. latipalpis* Brundin 1966
Brundin 1966, p. 105, Fig. 35, p. 107, Figs 36-39.]

\- Last palpal segment not swollen; outer spur much shorter than inner or lacking; wings not reduced ..... *Parochlus* 30

25. Apical lobe of gonostylus long and slender, situated in a distinctly ventral position relative to the subapical lobe; basal part of gonostylus strongly swollen .... *Podonomus parochloides* Brundin 1966
[Brundin 1966, p. 201, Fig. 173]

\- Apical lobe of gonostylus short, situated on level of subapical lobe 26

26. Apical lobe widened terminally...*Podonomus waikukupae* Brundin 1966
[Brundin 1966, p. 201, Fig. 172]

\- Apical lobe not widened terminally .... *Podonomus pygmaeus* Brundin 1966
[Brundin 1966, p. 201, Fig. 174]

27. Inner lobe of gonostylus with long and slender terminal tooth.. 28

\- Inner lobe of gonostylus with short and broad terminal tooth... 29

28. Antennal segment 14 1.5× longer than 13, segments 10-13 cylindrical ..... *Podochlus grandis* Brundin 1966
[Brundin 1966, p. 249, Fig. 289]

\- Antennal segment 14 somewhat shorter than 13, segments 10-13 bottle-shaped ..... *Podochlus stouti* Brundin 1966
[Brundin 1966, p. 249, Fig. 290]

29. Inner lobe of gonostylus parallel-sided .... *Podochlus cockaynei* Brundin 1966
[Brundin 1966, p. 249, Fig. 291]

\- Inner lobe of gonostylus with marked swelling subterminally ... *Podochlus knoxi* Brundin 1966
[Brundin 1966, p. 249, Fig. 292]

30. Cell R_1 of wing of normal width (i.e., maximum width of cell R_1 approximately equal to length of r-m X-vein) .... *Parochlus conjungens* Brundin 1966 [Brundin 1966, p.129, Fig. 52]

\- Cell R_1 narrow (i.e., maximum width of cell R_1 approximately half length of r-m X-vein) 31

31. Mesonotum well arched; wings and legs of normal type; subapical lobe of gonostylus rather slender, 2-3× longer than broad .... 8 spp. of *Parochlus* recognisable only as pupae. [*P. aotearoae* Brundin 1966, *P. spinosus* Brundin 1966, *P. maorii* Brundin 1966, *P. ohakunensis* (Freeman 1959) (Freeman 1959, p. 403, Fig. 1c), *P. carinatus* Brundin 1966, *P. pauperatus* Brundin 1966, *P. novaezelandiae* Brundin 1966, *P. longicornis* Brundin 1966]

\- Mesonotum only slightly arched; wings very narrow; legs conspicuously long; subapical lobes of gonostylus very large, only a little longer than broad...*Parochlus glacialis* Brundin 1966 [Brundin 1966, p. 157, Fig. 113]

32. Legs with hair of normal length; male antennae 11-14 segments.. 33

\- Legs with very short hair; body light coloured; male antennae 7-segmented; gonostylus very large, much longer than gonocoxite ..... *Maoridiamesa insularis* Brundin 1966 [Brundin 1966, p. 397, Fig. 551]

33. Gonostylus compact, little more than 2× longer than broad .... *Maoridiamesa harrisi* Brundin 1966 [Brundin 1966, p.395, Fig. 549]

\- Gonostylus slender, 3.5 - 4× longer than broad 34

34. Male antennae 14-segmented with normal plume .... *Maoridiamesa stouti* Brundin 1966 [Brundin 1966, p. 397, Fig. 550]

\- Male antennae 11-segmented, reduced plume .... *Maoridiamesa glacialis* Brundin 1966 [Brundin 1966, p. 414]

35. Tibiae with 3 or 4 well-defined black rings; prescutellar area well-defined, more or less circular with acrostichal bristles diverging around it ..... *Ablabesmyia mala* (Hutton 1902) [Freeman 1959, p. 400; Sublette & Wirth 1980, p.303-304, p. 338, Fig. 4]

- Tibiae without black rings; prescutellar area not well-defined and with acrostichal bristles running across it ..... *Pentaneura*
[One described species *P. harrisi* Freeman 1959 although more are known to exist. Freeman 1959, p. 400]

36. Dark femoral markings when present, confined to an apical or subapical ring; pulvilli absent 37
- Femora with central as well as one or two subapical dark rings; small pulvilli present 44

37. Wings with a discrete dark spot on centre of stem of posterior fork (= vein Cu proximal to f-Cu); a dark species; wings heavily marbled; postnotum bare .... *Gressittius antarcticus* (Hudson 1892)
[Freeman 1959, p. 402 & Plate II, Fig. a; Sublette & Wirth 1980, p.302 & p.335, Fig. 1]
- Wings without a dark spot on centre stem of posterior fork; postnotum with a group of 6-10 hairs 38

38. Tarsal segments lacking dark tips .....
..... *Macropelopia flavipes* (Freeman 1959)
[Freeman 1959, p. 405, Fig. 1b]
- Tarsal segments with dark tips 39

39. Wings with obvious pale spots near wing margin in cells M_1 and M_3 40
- Wings without pale spots in cells M_1 and M_3, often uniformly clouded or more or less clear, or with discrete dark spots at apices of veins 42

40 Dark markings on anterior margin of abdominal segments (in dorsal view) ..... *Macropelopia apicincta* (Freeman 1959)
[Freeman 1959, p. 403 & Plate II, Fig. b]
- Dark markings either basally or centrally placed on dorsal surface of abdominal segments 41

41. M_{3+4} with an elongate dark cloud along most of its length; anal cell with a single large rectangular dark patch .....
..... *Macropelopia debilis* (Hutton 1902)
[Freeman 1959, p. 404 & Plate II, Fig. d]
- M_{3+4} dark at tip; anal cell with two separate dark patches ....
..... *Macropelopia languidus* (Hutton 1902)
[Freeman 1959, p. 403 & Plate II, Fig. c]

42. Wing with five distinct dark spots .....
..... *Macropelopia quinquepunctata* (Freeman 1959)

[Freeman 1959, p. 405, Fig. 1a]

- Wing without distinct dark spots at apices of veins M_{3+4} and Cu_1 43

43. Wing apex with broad cloud containing a dark spot near middle of cell R_5; abdominal pattern formed of a row of three spots on each segment ..... *Macropelopia umbrosa* (Freeman 1959)
[Freeman 1959, p. 406 & Plate II, Fig. e]

- Wing apex less distinctly clouded, no darker spot in cell R_5, abdominal pattern formed of a basal or sub-basal band on each segment, usually absent from segments 1 and 2 .... *Macropelopia apicinella* (Freeman 1959)
[Freeman 1959, p. 406]

44. Mesonotum pruinose (with dull surface) between the stripes; anal cell with a pale area within the dark at the tip; wing pattern darker; femur dark at base with two subapical rings ... . ?*Apsectrotanypus quadricincta* (Freeman 1959)
[Freeman 1959, p. 407 & Plate II, Fig. f]

- Mesonotum with whitish pruinosity all over; anal cell dark at apex and without included pale area, wing pattern paler; femur pale at base and with only one subapical ring .... ?*Apsectrotanypus cana* (Freeman 1959)
[Freeman 1959, p. 408]

45. Combs of posterior tibiae well separated, at least one bearing a longish spur 46

- Combs of posterior tibiae usually contiguous, with or without spurs; if clearly separated, spurs are absent 48

46. Anal point with 16 irregularly arranged spinulae (small spines or thorn-like projections), appendage 1a present .... *Tanytarsus albanyensis* Forsyth 1971
[It is possible that this species should be placed in the genus *Calopsectra* but I have not seen any specimens. Forsyth 1971, p. 138, Fig. 14d]

- Anal point with fewer spinulae arranged in a single/double row, appendage 1a absent 47

47. Wing length 2.0 - 2.5 mm; anal point with a single row of 3 to (perhaps) 6 spinulae ..... *Calopsectra funebris* (Freeman 1959)
[Freeman 1959, p. 436, Fig. 6b; Sublette & Wirth 1980, p. 374, Fig. 40c]

- Wing length about 1.6 mm; anal point with only one or two spinulae ..... *Calopsectra* undescribed sp.
  [This undescribed species is known from the Hurunui River hot springs area (= *Micropsectra* in Stark, Fordyce & Winterbourn 1976) and morphologically is very similar to *C. funebris*.**
  C. funebris however, is a much larger species and has dark brown thoracic markings whereas the undescribed species is smaller and paler (light yellow-brown). Associated larvae differ in the form of the labial plate (see larval key). Adults of both species resemble the Australian *Tanytarsus fuscithorax* Skuse 1889 and *T. inextentus* Skuse 1889.]

Footnote

** Selected measurements from the undescribed *Calopsectra* and *C. funebris*. Number examined given in brackets.

Palp ratios	0.038:0.084:0.099:0.176 mm	0.039:0.110:0.117:0.214 mm
AR*	0.91 - 0.92 (2)	0.67 - 1.14 (5)
WL* (mm)	1.59 - 1.63 (3)	2.00 - 2.18 (3) – Freeman 1959 gave WL = 2.5 mm
VR*	1.13 - 1.15 (2)	1.06 - 1.19 (3)
Macrotrichia on wing veins		
R with	16 - 18 (2)	22 - 27 (3)
R_1 with	12 - 15 (2)	21 - 25 (3)
R_{4+5} with	15 - 16 (2)	21 - 26 (3)
Leg ratios (LR*)		
Fore	1.88 - 1.90 (4)	1.71 - 1.89 (3)
Mid	0.49 - 0.53 (8)	0.53 - 0.54 (3)
Hind	0.61 - 0.64 (4)	0.61 - 0.63 (3)
Total body length (mm)	2.10	3.28

* AR = antennal ratio = the ratio of the length of the last two segments (Tanypodinae) or last one (other subfamilies) of the antennal flagellum to the short basal segments of the flagellum taken together.

WL = wing length.

Cont'd

VR = venarum ratio = a ratio obtained by dividing the length of Cu, measured from its base (at the arculus) up to the cubital fork (f-Cu) by the length of M, measured from its base (at the arculus) up to r-m.

LR = leg ratio = the ratio of the basitarsus (i.e., the basal or proximal segment of the tarsus) to the tibia. Unless otherwise stated, this ratio applies only to the front legs.

---

48. Combs on hind tibiae fused and armed with one or two spurs .... *Paratanytarsus agameta* (Forsyth 1971)
[Female only known. Forsyth 1971, pp.137-141]

\- Combs separated and unarmed... *Tanytarsus vespertinus* Freeman 1959
[Freeman 1959, p. 436, Fig. 6a]

49. Posterior tibiae with two spurs (i.e., each comb with a spur).. 50

\- One spur on small outer comb, large inner comb unarmed 58

50. Pronotum much reduced; mesonotum projects as a cone over the head 51

\- Pronotum reaching up to front of mesothorax, sometimes collar-like, sometimes closely applied to mesonotum 52

51. Wing membrane thickly clothed with macrotrichia .... *Harrisius pallidus* Freeman 1959
[Freeman 1959, p. 427, Fig. 4a]

\- Wing membrane without macrotrichia .... *Ophryophorus ramiferus* Freeman 1959
[Freeman 1959, p. 427, Fig. 4b]

52. Appendage 2 in male genitalia extremely broad and bulbous apically (i.e. tennis racquet-shaped) .... *Kiefferulus opalensis* Forsyth 1975
[Forsyth 1975b, p. 216, Fig. 1a]

\- Appendage 2 more slender, not or scarcely enlarged distally ... 53

53. Appendage 2 reaching well beyond tip of gonocoxite 54

\- Appendage 2 very much reduced or absent 56

54. Anal point very broad at distal end, not tapering to a point; appendage 1 short, broadly ovate and pubescent .... *Xenochironomus canterburyensis* (Freeman 1959)
[Freeman 1959, p. 425; Forsyth 1971, p. 126, Fig. 7c]

\- Anal point narrower, tapering to a point; appendage 1 well developed, chitinised and bare except for a few setae basally ..... *Chironomus* spp. 55

55. Anal point of male narrow, not much wider basally than near tip ..... *Chironomus zealandicus* Hudson 1892 [Freeman 1959, p. 423, Fig. 3b]

\- Anal point stout, much wider basally than near tip .... *Chironomus analis* Freeman 1959 [Freeman 1959, p. 423, Fig. 3c]

56. Appendage 1 rod-like and bearing a few apical setae .... *Parachironomus cylindricus* (Freeman 1959) [2 apical setae. Freeman 1959, p. 423, Fig. 3d]

\- Appendage 1 reduced 57

57. Appendage 1 reduced and bearing 3 apical setae; gonostylus long and curved ..... *Cladopelma curtivalva* (Kieffer 1917) [Freeman 1961, p. 697, Fig. 21f]

\- Appendage 1 short, broad and pubescent; gonostylus short and broad ..... ?*Cryptochironomus* sp. [Adult of N.Z. larva keying to this genus not known]

58. Squama bare ..... *Microtendipes/Paralauterborniella*? [Adult of N.Z. larva keying to this generic complex not known]

\- Squama fringed 59

59. Pulvilli easily visible and divided longitudinally; anterior tibial scale (≡ tibial comb with 'teeth' fused) usually with small spur; 8th abdominal segment of male constricted basally ..... *Polypedilum* spp. 60

\- Pulvilli only visible on slide mounts, not divided; anterior tibiae without either scale or spur; 8th tergite not constricted basally ..... *Paucispinigera* spp. 68

60. Wings with dark markings and clouds 61

\- Wings unmarked 63

61. R_{4+5} strongly curved; veins Cu_1 and M with macrotrichia .... *Polypedilum opimus* (Hutton 1902) [Freeman 1959, Plate III]

\- R_{4+5} practically straight; veins Cu_1 and M bare 62

62. Wing length 1.3 - 1.5 mm; wing markings more definite and including a dark spot basal to the X-vein .... *Polypedilum longicrus* Kieffer 1921 [Freeman 1959, p. 431, Fig. 5b, Plate IIk]

- Wing length 3.5 - 4.0 mm; markings ill-defined, dark spot basal to X-vein absent ..... *Podypedilum pavidus* (Hutton 1902) [Freeman 1959, p. 431, Fig. 5a, Plate IIj]

63. Abdomen dark with pale markings or pale with dark markings; costal cell rounded at tip 64
- Abdomen dark brown or black without pale markings; costal cell pointed 67

64. Cylindrical finger-like process between bases of gonocoxites of male ..... *Polypedilum digitulus* Freeman 1959 [Freeman 1959, p. 431, Fig. 5e]
- Finger-like process absent 65

65. Abdominal segments dark with pale markings along anterior margins ..... *Polypedilum harrisi* Freeman 1959 [Freeman 1959, p. 431, Fig. 5d]
- Abdomen pale (yellow) or pale with dark markings (yellow/brown) 66

66. Wing length 1.4 mm; anterior tibial scale with short spur .... *Polypedilum luteum* Forsyth 1971 [Forsyth 1971, p. 135, Figs. 12a & 12b]
- Wing length 1.8 - 2.0 mm; anterior tibial scale without obvious spur ..... *Polypedilum alternans* Forsyth 1971 [Forsyth 1971, p. 138, Figs. 14a & 14c]

67. Abdomen blackish and without pruinose bands ..... *Polypedilum cumberi* Freeman 1959 [Freeman 1959, p. 431, Fig. 5f]
- Abdomen dark brown or blackish with pruinose bands at apices of segments ..... *Polypedilum canum* Freeman 1959 [*P. ignavus* (Hutton) may be a synonym of *P. canum*, Freeman 1959, p. 431, Fig. 5g]

68. Appendage 1 blunt-ended .. *Paucispinigera approximata* Freeman 1959 [Freeman 1959, p. 427, Figs 4c & 4d]
- Appendage 1 pointed apically ..... *Paucispinigera* undescribed sp. [See Fig. 6.9. Adult known only from male pupa collected from L. Gault, South Island.]

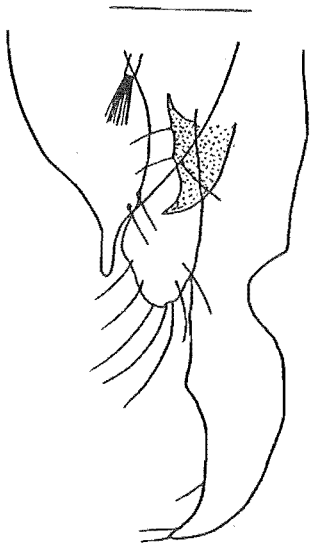


Fig. 6.9

Male hypopygium of undescribed *Paucispinigera* sp. (one side only shown).

(Scale bar = 0.05 mm)

6.3.3 Description of the Adult Male of *Eukiefferiella* sp. (Chironomidae: Orthocladiinae)

Head dark brown, palps lighter, similar to legs. Thorax dark, scuta and pre-epipisternum shining dark brown-black. Legs uniform mid-brown. Abdomen brown and hairy, somewhat darker on distal margins of segments.

Eyes bare and without dorsal extension. Antenna with 13 flagellomeres, its apex distinctively shaped (Fig. 6.10B). AR = 1.00 - 1.06, mean 1.02 (n = 3).

Wing (Fig. 6.10A) with very fine microtrichia, WL = 1.97 - 2.13 mm, mean 2.05 mm (5), VR = 1.37 - 1.40, mean 1.39 (4). Squama fringed with approximately 8 setae. Costa not produced, R_{4+5} reaches wing margin proximal to wing tip. R_{4+5} nearly straight. R with macrotrichia (approximately 6 - 8). R_{2+3} feint and lying close to R_{4+5} but without clear ending in costa. M reaches wing margin at wing tip. Cu_2 almost straight but curved close to wing margin and not distinctly reaching wing margin. R_{4+5} ending above the end of Cu_1. Anal vein short and curved down near tip, not quite reaching f-Cu. F-Cu well beyond r-m. Anal lobe well developed.

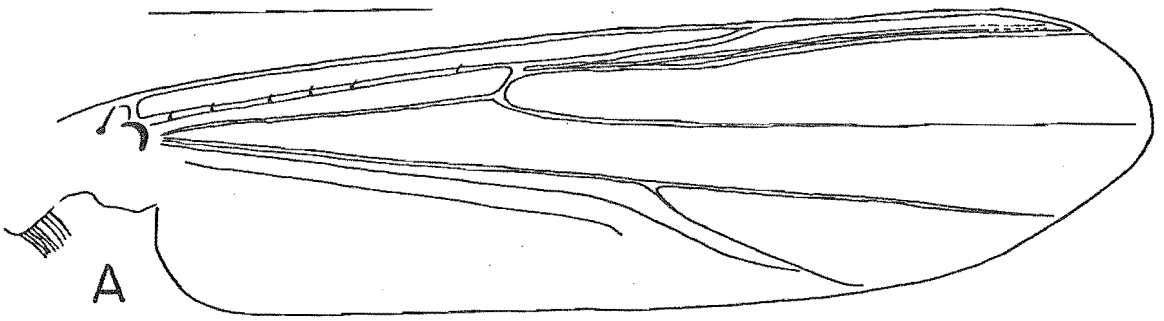
Thorax. Scutellum with a single transverse row of 8 setae. Scutal stripes fused, dorsocentral (= dorso-lateral setae of some authors) setae (approximately 8) erect and uniserial. Mesonotum without visible acrostichal setae.

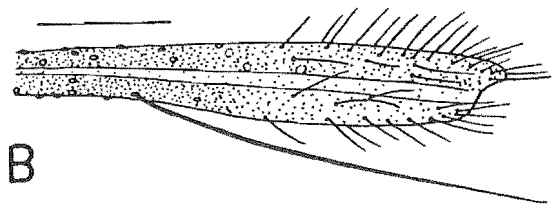
Legs. LR = 0.50 - 0.53, mean 0.52 (5). Distal end of hind tibiae expanded, outer spine of hind tibiae less than half as long as

inner, 5th tarsal segment slightly dorsoventrally flattened, small pulvilli present and empodium (e.g. Fig. 6.8F) well developed. Legs with distinct hairs (up to 0.20 mm long).

Abdomen covered with hairs, segments 7 and 8 constricted basally.

Hypopygium (Fig. 6.10C). Anal point absent. Gonocoxite lobe free and well developed, gonostylus expanded medially with a terminal triangular point and strong subterminal tooth, prominent seta distal to base of medial expansion. A second prominent seta arises from end of gonostylus just distal to terminal triangular point.





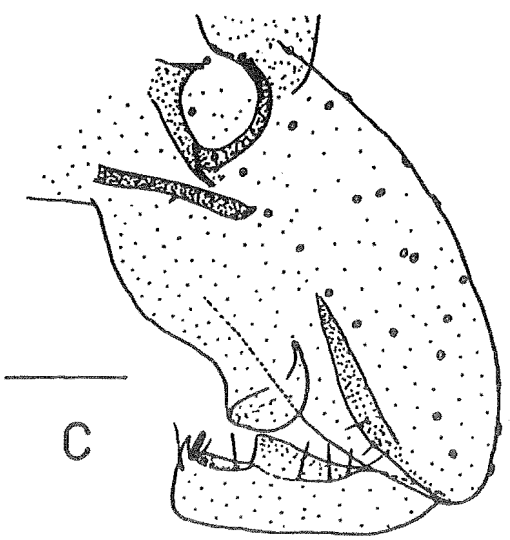


Fig. 6.10

Eukiefferiella sp. male -

A. Wing

B. Terminal of antenna (large hairs arise from the distinct pits - only one is shown).

C. Hypopygium (large hairs, which arise from the distinct pits, and fine hairs found on gonocoxite lobe are not shown).

Scale bars are 0.05 mm (B & C) and 0.5 mm (A).

Specimen localities

South Island. BR - Lake Rotoiti, Nelson, 21 November 1978, B.V. Timms 2♂♂; MC - Lake Grasmere, 1976 - 1980 9♂♂; Kenwyn Avenue, Christchurch, 7 November 1979 1♂; Avon River near junction with Okeover Stream, Christchurch, 22 November 1979, V.M. Stout 1♂.

Diagnosis

This species fits the diagnoses of *Eukiefferiella* Thienemann 1926 as given by Coe (1950) and Sublette & Wirth (1980) which are broader than the diagnosis given by Brundin (1966) who stated that *Eukiefferiella* never had pulvilli and that R_{4+5} ended proximal to Cu_1. As now recognised, this genus is an artificial group of heterogeneous species (Sublette & Wirth 1980). The combination of a normally developed antepronotum, weakly bowed Cu_2, R_{2+3} usually lying near R_{4+5} or completely fused with it, the end of R_{4+5} over or proximal to the end of Cu_1, outer spur of hind tibia weakly developed or absent, weak or absent dorsomedial (= acrostichal) setae, and genitalia usually without an anal point and with a glossiform (= tongue-shaped) medial lobe to the gonocoxite, differentiates most species of the genus.

The species described here keys to *Psectrocladius* Kieffer in Brundin (1956) and Pinder (1978) *unless* the pulvilli are considered 'small and difficult to see'. They are small but distinct. Further, this species would be referred to the subgenus *Mesopsectrocladius* Laville since it possesses dorsoventrally flattened fifth tarsal segments and lacks an anal point (Langton 1980). The above keys separate *Psectrocladius* and *Eukiefferiella* on the presence or absence, respectively, of *distinct* pulvilli (a rather unsatisfactory couplet). However, this New Zealand species differs from the *Psectrocladius* diagnosis (Brundin 1956) in that R_{2+3} does not end about midway between the ends of R_1 and R_{4+5} and f-Cu is markedly distal to r-m, and is, therefore, more properly placed in the genus *Eukiefferiella*.

6.3.4 Chironomid Larvae and Pupae from Lake Grasmere

The purpose of this section is to document the 'types' of chironomid larvae (and some pupae) collected from Lake Grasmere and to outline briefly the bases for their recognition. Figure 6.11 shows diagnostic features of the chironomids that presented problems.

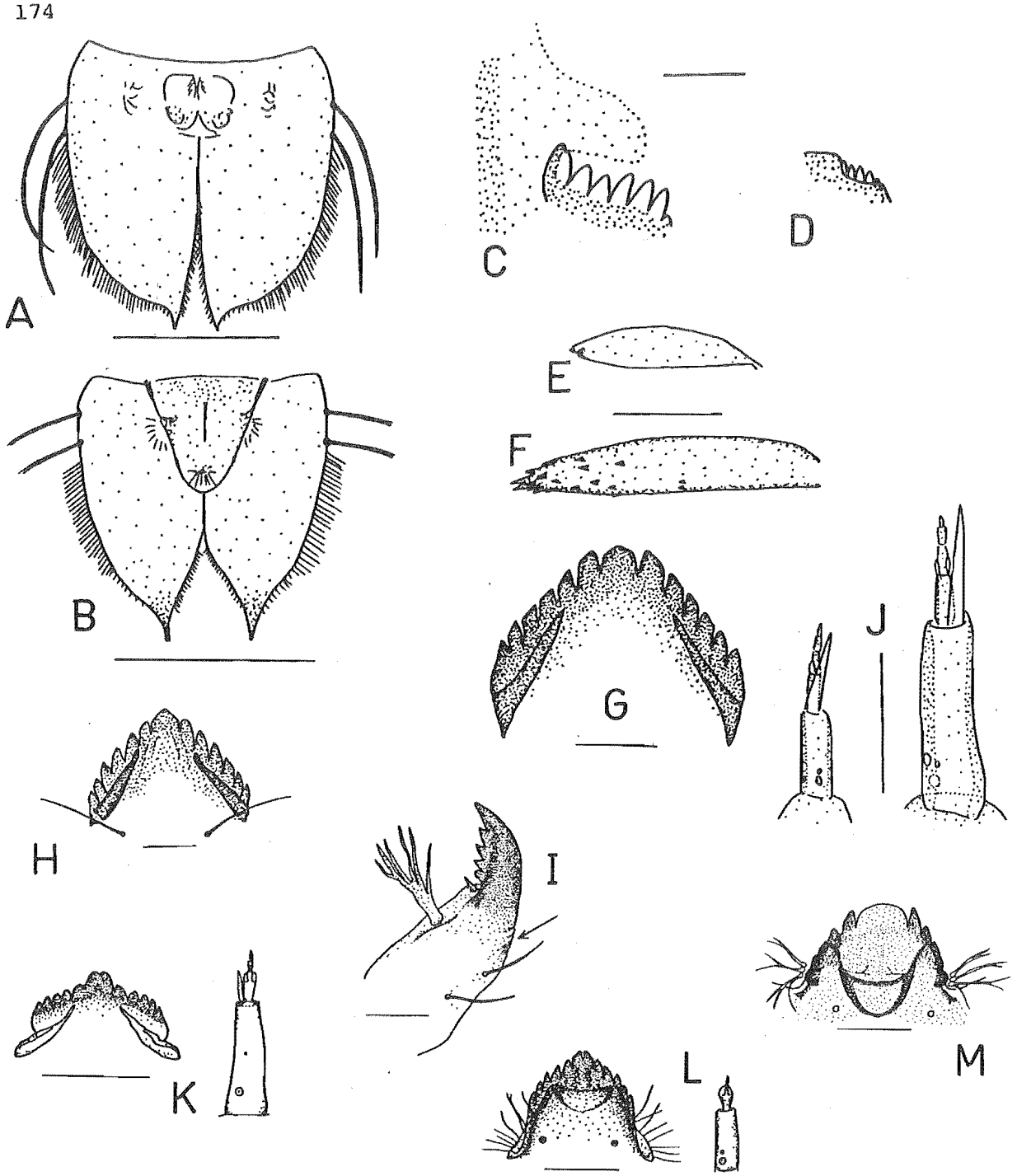


Fig. 6.11 Morphological features of some Chironomidae larvae and pupae from Lake Grasmere. Caudal swim fins of pupal (A) *Macropelopia languidus* and (B) *M. umbrosa*; paralabial combs of pupal (C) *Gressittius antarcticus*-type and (D) ? *M. umbrosa*; pupal respiratory trumpets of (E) *Syncricotopus pluriserialis* and (F) *Cricotopus zealandicus*; labial plates of (G) *S. pluriserialis* and (H) *Cricotopus* sp.; (I) mandible and (J) antennae of *Cricotopus* sp.; labial plates and antennae of (K) Orthocladiinae A and (L) Orthocladiinae B = ?*Rheocricotopus* sp.; (M) labial plate of Orthocladiinae C. [Scale bars 0.05 mm except for A and B (0.5 mm) and C and D (0.02 mm).]

(1) Tanypodinae

Three kinds of tanypodine larvae were recognised in quantitative samples from Lake Grasmere: *Ablabesmyia mala, Pentaneura* sp. and *Macropelopia/Gressittius* (two species).

A. mala did not present problems of specific identification. Larvae were recorded from Lake Grasmere (Appendix 3) and adults were collected in light-trap and hand-net samples from the lake shore (Appendices 5.1 and 5.2).

Only one species of *Pentaneura* (*P. harrisi* Freeman) has been recorded from New Zealand (Freeman 1959, Forsyth 1971). Adults of this species are known from the Cass area (checklist in Burrows 1977) but, in the absence of a positive adult association, I hesitate to identify the two larval specimens collected further than to genus. The genus *Pentaneura* (*sensu* Freeman 1961) is now considered to be a composite group of genera (Martin 1974) and there is some doubt as to the correct generic placement of Australasian *Pentaneura* (Dr J. Martin pers. comm.). I know of the existence of adults of an undescribed New Zealand species of 'Pentaneura' and I have also seen larvae and pupae (different from the Grasmere types and *P. harrisi*) from the Reefton area of the South Island (see Cowie 1980).

New Zealand larvae keying to the tribe Macropelopiini also present problems of identification. Ten species have been described as adults (Hudson 1892, Hutton 1902, Freeman 1959, Sublette & Wirth 1980) but the larva of only one (*Gressittius antarcticus* (Hudson)) has been described (Forsyth 1971), and since larvae of most of the other species are unrecognised, it is not known whether this description adequately distinguishes this species from congenerics.

Three species of adult Tanypodinae in the tribe Macropelopiinae were recorded from Lake Grasmere and surrounding areas (Appendix 5.2) but only two pupal types were collected from the lake. The most common pupa was that of *Gressittius antarcticus* (established from reared association) (see Forsyth 1971, pp.116-117, Fig. 2; Sublette & Wirth 1980, pp. 303 & 335-336, Figs 1 & 2). The respiratory trumpet of this species, with its wide and convoluted trachea, is very distinctive (see Sublette & Wirth 1980, p. 335, Fig. 1E). Adults of *G. antarcticus* were also the most common Macropelopiini collected (Appendices 5.1 & 5.2).

Adults of two further species of *Macropelopia (M. umbrosa* and *M. languidus)* were found in light-trap samples from the southern end of Lake Grasmere (Appendix 5.2). However, the absence of *M. languidus* in hand-net collections from the lake shore (Appendix 5.1) and the low numbers caught in light-traps (Appendix 5.2) suggests that larvae and pupae were the least likely to be present in the lake. They may have been present in nearby Lake Pearson or in streams.

Fig. 6.11 shows the caudal swim fins of the pupae of *M. languidus* (reared from the Avon River, Christchurch) and *M. umbrosa* (reared from Lake Grasmere). The caudal region of the pupa of *M. languidus* (Fig. 6.11A) is similar to that of *G. antarcticus* (cf. Sublette & Wirth 1980, Fig. 2E) but is much smaller (Table 6.1) and the respiratory trumpet is of the *M. apicinella*-type (cf. Forsyth 1971, p. 118, Fig. 3b) with broad, apically-directed spinules on the external surface. Pupae of the *M. languidus* type have not been collected from Lake Grasmere.

Table 6.1 Maximum lengths and widths of respiratory trumpets and caudal swim fins of pupae of *Gressittius antarcticus*, *Macropelopia languidus* and *M. umbrosa*.

	G. antarcticus	*M. languidus*	*M. umbrosa*
Respiratory trumpet length × width (mm)	0.75 × 0.22	0.48 × 0.22	0.36 × 0.17
Caudal swim fin length × width (both fins together) (mm)	1.31 × 1.37	0.89 × 0.80	0.69 × 0.62

The caudal region of the pupa of *M. umbrosa* (Fig. 6.11B) differs from those of *G. antarcticus* and *M. languidus* in that the swim fins taper to a more acute point, but the respiratory trumpet is similar in shape to the *apicinella*-type although the apically directed spinules are minute. Pupae of *M. umbrosa* were collected from Lake Grasmere.

Two separate types of Macropelopiini larvae were distinguished from material collected during the quantitative sampling program. They differed in the number of teeth in the paralabial comb (Fig. 6.11C & D). The paralabial comb of *G. antarcticus* (Forsyth 1971, p. 117, Fig. 2b) is not unlike that depicted in Fig. 6.11C. Although pupae of

G. antarcticus and *M. umbrosa* have been collected and reared to adults from Lake Grasmere, positive associations with larvae have not been made. As these two species were common in light-trap and hand-net collected samples of adults (Appendices 5.1 & 5.2), it is possible that the two larval types recognised are *M. umbrosa* (Fig. 6.11D) and *G. antarcticus* (Fig. 6.11C). However, in the absence of reared associations with adult material, the two larval morphs were not separated in the analyses.

(2) Podonominae

Adults of *Parochlus*, belonging to the Araucanus group (see Brundin 1966), were found in light-trap and hand-net collections from the shores of Lake Grasmere (Appendices 5.1 & 5.2). Eight species in New Zealand belong in this group but are recognised clearly only in the pupal stage (Brundin 1966). No work has been done in an attempt to separate adults, but those collected from Lake Grasmere were most likely of one species since no characters could be found to separate them. Larvae and pupae of *Parochlus* were not found in quantitative samples from the macrophyte zones of Lake Grasmere but pupae of *P. spinosus* Brundin 1966 were collected from the stony shore at the southern end of the lake. This species is in the Araucanus group (in the *spinosus* subgroup) so it is likely that the adults collected were of this species also.

(3) Orthocladiinae

Orthocladiinae presented the greatest problems of generic and specific identification and many of the difficulties could not be overcome.

The *Syncricotopus/Cricotopus* complex

Positively identified adults of *Syncricotopus pluriserialis* and *Cricotopus zealandicus* were recorded in hand-net and light-trap collections from the lake shore (Appendices 5.1 & 5.2) and pupae of these species were found in the lake. The respiratory trumpets of *S. pluriserialis* and *C. zealandicus* differ in size and ornamentation (Fig. 6.11E,F). *S. pluriserialis* larvae (from ponds near the main entrance of the James Hight Library at the University of Canterbury) (labial plate, Fig. 6.11G) have been reared to adults to confirm specific identity and several *Cricotopus*-type larvae from Lake Grasmere

(labial plate, Fig. 6.11H; mandible, Fig. 6.11I) were reared and shown to be *C. zealandicus*. However, there was much variation in the form of the labial plate (for example, in the width and shape of the middle tooth) in larvae from Lake Grasmere keying to the genus *Cricotopus* and it is uncertain whether this variation is inter- or intraspecific. There was also variation in the relative lengths of the antennal segments (Fig. 6.11J) but this was probably inter-instar variability.

Larvae of the *Cricotopus*-type were the most common chironomids on macrophytes in Lake Grasmere (Appendix 3) but only a single individual of *S. pluriserialis* (a pupa) was recorded on macrophytes. The tube-dwelling larvae of *S. pluriserialis* were present, however, amongst filamentous algae and diatoms on the upper surface of rocks on the stony shore at the southern end of the lake, although still outnumbered by larvae of *Cricotopus* sp. (at least during summer). It was somewhat anomalous, therefore, that adults of *S. pluriserialis* were much more common than those of *C. zealandicus* in light-trap and hand-net collections (Appendices 5.1 & 5.2). But this may be explained by the fact that *S. pluriserialis* is a multivoltine species (Forsyth 1971) whereas *C. zealandicus* is probably univoltine. The peak of *C. zealandicus* emergence was probably not recorded by the relatively infrequent hand-net sampling of adults (Appendix 5.1) and this species did not seem to be attracted appreciably to light (Appendix 5.2).

Hirvenoja (1973), in a revision of the genus *Cricotopus* and its closest relatives, synonymised the Australasian *Syncricotopus* Brundin 1956 with the genus *Paratrichocladius* Santos Abreu 1918. Whereas the adults of New Zealand *Syncricotopus* agree with this diagnosis of *Paratrichocladius*, the larvae do not. *S. pluriserialis* larvae from New Zealand have a seta interna on the inner margin of the mandible, a feature that is absent in *Paratrichocladius*. Because of this, it is my belief that *Syncricotopus* and *Paratrichocladius* are not synonyms and, therefore, I consider that the New Zealand (and Australian) species should be retained in *Syncricotopus*.

Orthocladiinae A

The larva of Orthocladiinae A (Fig. 6.11K) keyed to *Psectrocladius* in Mason (1973) but did not key satisfactorily using the more regionalised keys of Bryce & Hobart (1972) and Oliver, McClymont & Roussel (1978). It is possible that this larva is the immature stage of the adult *Eukiefferiella* sp. described previously (see p. 171).

Orthocladiinae B

The larva of Orthocladiinae B (labial plate and antenna Fig. 6.11L) keyed to *Rheocricotopus* in Oliver, McClymont & Roussel (1978); *Trichocladius* in Mason (1973); and *Rheocricotopus (Trichocladius)* in Bryce & Hobart (1972). I did not manage to associate this larval type positively with an adult, and could not find any adults in hand-net or light-trap collections that possessed the required features (see the generic diagnosis of *Rheocricotopus* in Brundin (1956). Larvae of this type have been recorded from the benthos of Lake Grasmere (and several other South Island lakes) by Timms (1980, in prep).

Orthocladiinae C

I tentatively attribute this unusual larva (labial plate Fig. 6.11M) to the subfamily Orthocladiinae, but it could represent a new subfamily. Superficially, the dark pigmentation of the head is reminiscent of *Maoridiamesa* (although it lacks the pronounced black occipital margin) but the labial plate is not of the *Maoridiamesa*-type (see the larval key, p. 149). The flattened, forked 'hairs' comprising the beard on the paralabial plates are unlike those of any known chironomid larvae. Overseas keys to larvae were of no value in identifying this species.

The unidentified 'black orthoclad' (Appendix 5.1) with a patterned wing may be the adult of Orthocladiinae C (presumptive association), and, as with the larva, overseas keys were of no use for its identification. For example, it keyed to *Eukiefferiella* in Pinder (1978) but then did not agree with the generic diagnosis given by Coe (1950), Brundin (1956) or Sublette & Wirth (1980). The pupa of this adult (positive association) differed from the normal orthoclad type in lacking stout bristles on the caudal fins (or anywhere on the abdomen) and was more like a diamesid in this respect.

Description of the adult male of the 'black orthoclad'

WL = 1.6 - 1.7 mm, AR = 0.4, LR = 0.5 - 0.6
Antenna 13-segmented, plume sparse; eyes hairy.
Dorsocentrals (5) uniserial, erect and arising from distinct pits.
Wing without macrotrichia but with very obscure black markings across middle, in anal cell and nearer wing tip; squama bare; Costa not produced and ending on a level with Cu_1, R_{2+3} close to R_{4+5} and ending

in Costa near the end of R_{4+5}, f-Cu well beyond r-m, Cu_2 gently curved (but not straight), M straight and ending at wing-tip.
Legs. All tarsi of normal shape, the 5th perhaps slightly flattened dorsoventrally, pulvilli absent and small empodium present.
Hypopygium. Anal point distinct, sharp and bare, gonocoxite without a medial lobe but with a slight ridge with prominent setation, peg on gonostylus appears continuous with gonostylus (i.e., seems to be made of the same material and not articulated).

(4) Chironominae

Larvae of two species of Chironominae, *Chironomus zealandicus* (Tribe Chironomini) and *Tanytarsus vespertinus* (Tribe Tanytarsini) were recorded in quantitative samples. All life history stages of both species were recognised easily.

CHAPTER VII

GENERAL DISCUSSION

Few studies have been made on the macrophyte-associated macroinvertebrates in New Zealand lakes, although the species characteristic of this habitat have been documented in general surveys (see for example, Stout 1975b, Winterbourn & Lewis 1975). Taxonomic limitations in past years make comparisons of species lists difficult (Table 7.1), however, allowing for this, it appears that the number of invertebrate taxa recorded from the survey of Lake Grasmere is the greatest recorded from any New Zealand lake. About 113 macroinvertebrate species were collected from the lake and its immediate environs, of which about 87 were associated with macrophytes. Of these, 49 were insects, with species of Chironomidae (17) and Trichoptera (12) best represented. Thirty invertebrate species were new records for the Cass district (c.f. checklist in Burrows 1977). In New Zealand lakes, species of Crustacea and Trichoptera are represented at least as well as in many overseas lakes but Ephemeroptera, Odonata, Hemiptera, Coleoptera, Acarina, and Mollusca are poorly represented (Table 7.1). Comparisons of chironomid species richness are hampered by taxonomic difficulties, but in the Nearctic and Palearctic, where midge faunas are relatively well known, the littoral zone of a mesotrophic (= moderately productive) lake may be inhabited by some 50 chironomid species (see Saether 1979). In contrast, the total New Zealand freshwater chironomid fauna comprises approximately 70 described species (Wise 1973, Stark in press) with perhaps another 10 - 15 species undescribed (mostly Orthocladiinae) (Stark in press and unpublished records). Of these, perhaps 40% may live in standing waters. The 17 species recorded from Lake Grasmere (easily the largest number recorded from a New Zealand lake) may be close to the maximum species richness for such a habitat.

Stout (1975b) noted that the freshwater fauna of Canterbury (and New Zealand as a whole) comprised fewer species than would be found in comparable geographic regions in the northern hemisphere, and that several groups (e.g., freshwater Anostraca and Conchostraca, Polyphemidae, *Leptodora, Diaptomus, Asellus,* and insects living on the water surface such as the hemipterans *Nepa, and Ranatra* and Gyrinidae) are absent or poorly represented. Similarly, Winterbourn (1980) noted that ponds and

Table 7.1 Taxonomic comparisons of macrophyte-associated macroinvertebrate faunas of Lake Grasmere, New Zealand and other lakes in New Zealand and overseas. Also given is the taxonomic composition of the benthos of Lake Grasmere (Timms pers. comm.). * = not recorded, - = not present.

Species composition by taxa	L. Grasmere, N.Z.	benthos	L. Waitaki, N.Z. (Greig 1973)	L. Aviemore, N.Z. (Greig 1973)	Three Dubs Tarn, England (Macan 1949)	Hodson's Tarn, England (Macan 1963)	Great Grebe L., Sweden (Berg & Petersen 1956)	L. Erken, Sweden (Nyman 1971)	Goczalkowice Reservoir, Poland (Kuflikowski 1974)	12 lakes in Snowdonia, Wales (Liddle *et al.* 1979)
Coelenterata	1	-	-	-	-	-	1	1	2	-
Platyhelminthes	1	1	1	-	2	1	3	1	-	2
Ectoprocta	1	-	-	-	-	-	2	1	1	-
Nematoda	2+	-	1+	-	-	-	-	1+	1	1
Annelida	7	4	7	7	5	4+	2+	13	21	3
Crustacea	16	-	2	8	9	1	1	3	9	1
Ephemeroptera	1	-	1	1	3	4	1	7	9	4
Odonata	3	1	1	1	5	7	9	2	5	6
Plecoptera	3	-	-	-	1	1	-	-	-	1
Hemiptera	2	-	-	-	10	8	-	2	3	6
Coleoptera	4	-	2+	2+	7	8	6	4	12	2
All Diptera	23	4	5+	4+	3+	1+	2+	4+	29	*
Chironomidae	17	4	3+	2+	1+	*	*	*	22	*
Neuroptera	-	-	-	-	-	-	-	2	-	-
Trichoptera	12	4	5	6	6	4	9	23	12	5
Lepidoptera	1	1	1	-	-	1	-	1	3	1
Acarina	5	1	1	1	16	13	12	*	10	1
Mollusca	5	3	6	4	2	1	-	15	15	3
Total all species	87+	19	32+	33+	69+	43+	48+	80+	132	36+
Total insects	49+	10	15+	14+	35+	33+	25+	45+	85	26+

lakes in New Zealand are geologically young habitats that support an impoverished fauna. Thus, in some northern European eutrophic (= nutrient-rich) lakes it is not uncommon to find 155 invertebrate species on wave-exposed stony shores (Ehrenberg 1957), 300 species in the macrophyte zone (Müller-Liebenau 1956), 50 species in the sublittoral, and up to 20 species in the profundal (Jonasson 1978) (cf. Lake Grasmere, Table 7.1).

As noted for other lakes (by, for example, Müller-Liebenau 1956, Gerking 1957, Soszka 1975a, Wetzel 1975, Jonasson 1978, Higler 1980, and Morgan 1980), the invertebrate fauna of the macrophyte zone of Lake Grasmere was more diverse than that of the benthos (Table 7.1) and all species found in the bottom mud (Dr B.V. Timms pers. comm.) were present also on aquatic plants. The species richness of the benthos of seven Rotorua lakes (North Island) (a mean of 12 taxa per lake including eight insects, but Annelida were not differentiated) studied by Forsyth and McColl (1974) and Forsyth (1975a, 1978) was similar to that recorded for Lake Grasmere (Dr B.V. Timms pers. comm. and Table 7.1). Timms (1980) also studied the benthos of the Nelson lakes (South Island) where the community composition was similar to that of Lake Grasmere benthos (except that more species of Chironomidae were present).

In addition to differences in the taxonomic representation of lacustrine invertebrates between New Zealand and the northern hemisphere, there are differences in the groups that are numerically dominant. Mollusca (55.4%), primarily *P. antipodarum*, Coelenterata (16.1%) and Crustacea (15.5%) were best represented in the macrophyte-associated invertebrate communities in Lake Grasmere. Insecta (4.2%), including Trichoptera (2.1%) and Chironomidae (2.0%), Acarina (3.8%), and Annelida (4.4%) comprised most of the remainder. Dominance of macrophyte-associated invertebrate communities by Mollusca (principally *P. antipodarum*) has been noted also for other lakes in New Zealand by, for example, Greig (1973) (Lakes Aviemore and Waitaki) and Stout (1975b) (Canterbury lakes). In contrast, invertebrate communities associated with macrophytes in northern hemisphere lakes usually are dominated by Diptera (especially Chironomidae), Annelida (especially Oligochaeta), and sometimes Ephemeroptera (Table 7.2, Gak *et al.* 1972, Morgan 1980). Only a few overseas lakes (e.g., Lakes Chad and Léré in Africa and some warm temperate lakes in the Soviet Union) are dominated by Mollusca (Morgan 1980).

Table 7.2 Dominant invertebrate groups in macrophyte zones of some northern hemisphere lakes.

Lake Erie, U.S.A. (Krecker 1939)	Annelida 39.4%, Chironomidae 23.9%
Goczalkowice Res., Poland (Kuflikowski 1974)	Chironomidae 64-82%, Oligochaeta 9-12%
Lake Velence, Hungary (Andrikovics 1975)	Chironomidae 80-87%, Ephemeroptera 4-12%
Mikolajske Lake, Poland (Soszka 1975a)	Diptera 50%, Oligochaeta 35%
Dubh Lochan, Scotland (Minto 1977)	Ephemeroptera 40-45%, Oligochaeta 33-36%, Chironomidae 13-18%

Differences in invertebrate abundance were observed on different macrophyte species in Lake Grasmere. Of the plants examined (*Elodea canadensis, Myriophyllum propinquum, Isoetes alpinus* and *Ranunculus fluitans*) only the last named could be considered a relatively poor habitat, with invertebrate densities usually less than half those on the other plants (in terms of numbers per g dry weight of plant or numbers per m^2 of lake bottom). *I. alpinus* supported a relatively abundant fauna including many animals (e.g., Ostracoda and some Chironomidae) that were not actually on the plants but were living in the silty substrate that collects in the root zone and around stem bases. It was impossible to separate these animals from those living on the plant itself. On all plants the principal features of their associated animal communities were the high contributions made by molluscs (59-86% by numbers) and the greater contribution of insects to the faunas on native (*M. propinquum* 9.5%, *I. alpinus* 8.4%) compared with adventive (*E. canadensis* 2.4%, *R. fluitans* 2.9%) macrophytes. However, all of the species that comprised greater than 0.1% (by numbers) of total invertebrates collected were present on all four plants. The apparent macrophyte-substrate specificity of less common taxa was probably a function of their rarity rather than an expression of their niche specificity.

Invertebrate population densities on different macrophytes have been found to bear some relationship to morphological features of the plants (Krecker 1939, Andrews & Hasler 1943, Entz 1947, Rosine 1955, Gerking 1957, Greig 1973, Cattaneo & Kalff 1980), or they may be related to water chemistry (Frost 1942), chemical composition of plants, or difference in plant periphyton (Harrod 1964, Wolnomiejski pers. comm. *in*

Soszka 1975a, Cattaneo & Kalff 1980). In Lake Grasmere, the macrophytes with the most finely divided leaves (*M. propinquum* and *E. canadensis*), perhaps by providing increased protection and surface area for periphyton growth and invertebrate grazing, facilitated the presence of a more diverse and abundant fauna than did *R. fluitans*. Cattaneo & Kalff (1980) found, by experiment, that plants with finely dissected leaves (e.g., *Myriophyllum*) accumulated significantly more periphyton biomass than plants with relatively simple leaves (e.g., *Potamogeton*) and that this was reflected in the densities of their associated invertebrate populations. However, many authors (e.g., Godward 1937, Flint 1950, Macan 1963, Pieczynska & Spodnieska 1963, Macan & Kitching 1972, 1976, Soszka 1975b, Wetzel 1975, Hodgkiss & Tai 1976, Bowker & Denny 1978) have noted marked similarity in periphyton community composition on different species of macrophyte, artificial plants and stony substrates, and often a marked similarity in species composition of the associated invertebrate fauna. Therefore, differences in composition of periphyton-browsing invertebrate communities on different macrophyte species and between macrophytes and stony/rocky substrates are probably due primarily to factors other than food availability (e.g., wave action, oxygen saturation, water depth). In Lake Grasmere, most of the macrophyte-associated invertebrates were found also on stony or rocky substrates. Notable exceptions included *Chlorohydra viridissima* and *Nymphula nitens* (almost exclusively on macrophytes) and *Procordulia grayi* (in silty substrates). However, a number of species were virtually restricted to the stony shore zone (although some of these were collected rarely from plants) (e.g., *Deleatidium* sp., *Stenoperla prasina, Austroperla cyrene, Zelandobius furcillatus, Polyplectropus puerilis, Psilochorema nemorale*). These mayfly, stonefly and caddisfly species are more commonly found in running waters but are present on exposed shores in lakes (see Winterbourn & Lewis 1975).

The introduced macrophyte *E. canadensis*, a native of North America, has been in New Zealand for over 100 years (Mason 1975, Hughes 1976). It is not known when it was introduced into Lake Grasmere although it was present in nearby Lake Sarah in 1934-1935 (Flint 1938). *E. canadensis* formed a dense monoculture in mesotrophic Lake Grasmere and excluded all other macrophyte species at depths ranging from about 0.5 - 1.2 m to 7 m. The lower limit is within the photic zone and compares with a maximum Secchi disc visibility of 8.2 m recorded by Stout (1977). Brown (1975) stated that the upper depth limit of *E. canadensis* is determined by the wave exposure pattern of a lake and

the lower limit is related to light penetration or, perhaps, temperature. Coffey (1975) contended that when *E. canadensis* competes with native submerged macrophytes it coexists with, rather than displaces, them in oligotrophic (= nutrient poor) and eutrophic waters, whereas in mesotrophic waters it displaces the natives completely within its depth range (as in Lake Grasmere). Further spread in this lake is unlikely unless land-use changes lead to eutrophication or environmental conditions change dramatically (e.g., long periods of calm conditions allowing *E. canadensis* to colonise shallow water).

It is difficult to determine the precise effects that the displacement of native macrophytes by *E. canadensis* has had in Lake Grasmere since no macrophyte or invertebrate surveys had been undertaken prior to its introduction. Coffey (1975), from an intensive study of macrophyte communities in the Waikato lakes (North Island), suggested that the dominant elements of the native, submerged macrophyte floras were *Myriophyllum* and *Potamogeton* spp. and charophyte algae in oligotrophic waters, with *Potamogeton* becoming increasingly dominant in more mesotrophic conditions. Brown (1975) noted that the widespread occurrence of comparable species throughout New Zealand suggests that a similar native species association might be a common feature of lakes not markedly affected by adventives. Therefore, charophytes and *Potamogeton* may have been the original deep-water vegetation in Lake Grasmere, with mixed native species of *Myriophyllum*, *Potamogeton* and *Isoetes* in shallow water (see Stout 1975b and references therein). Native communities of tall-growing *Potamogeton* and *Myriophyllum* species have fewer stems per unit area of lake bottom than adventives like *E. canadensis* (Brown 1975), and *Potamogeton* in particular, may exhibit pronounced die-back during winter (Stout 1975a). Since almost all invertebrate species collected from *E. canadensis* in Lake Grasmere were present on the other macrophytes studied and on other substrates (e.g., sand, stones or rocks), it is probable that invertebrate species richness has not been reduced by displacement of the native plants. Furthermore, since invertebrate densities per m^2 of lake bottom were higher on *E. canadensis* than on the native plants, the total invertebrate population of the lake may now be greater.

The invertebrates associated with aquatic macrophytes in Lake Grasmere exhibit a range of feeding strategies. It is often impractical or impossible to separate species into rigid trophic levels (Morgan 1980) since most aquatic invertebrate species are generalist (polyphagous) rather than specialist feeders (Cummins 1973, Merrit &

Cummins 1978, Cummins & Klug 1979, Mackay & Wiggins 1979), and food habits may be subject to considerable intraspecific variation such as age-specific or habitat-specific differences (Cummins 1973, Anderson & Cummins 1979, present study). Despite this, most species can be assigned to "most probable feeding categories" and this enables invertebrate community composition of macrophytic and benthic habitats of some New Zealand lakes to be considered in terms of functional feeding groups (modified from Cummins 1973) as in Table 7.3. Species, or higher taxa, were assigned to functional feeding groups on the basis of their predominant food type and feeding mechanisms. For example, *Hudsonema amabilis* was termed an herbivorous browser since, although it was strictly omnivorous, most of its food was diatoms, macrophyte tissue and filamentous algae. On the other hand, *Nymphula nitens* and *Triplectides cephalotes* fed primarily on macrophyte tissue and were classed as shredders, even though other food types were recorded in their faeces. The common snail *Potamopyrgus antipodarum*, was considered an herbivorous browser when living on plants or stones but a detritivorous browser when on the benthic mud in the profundal zone.

Table 7.3 Feeding types (% by numbers) in relation to habitat in some New Zealand lakes.

	L. Grasmere	L. Waikaremoana[1]	L. Rotoiti[2]	L. Rotoroa[2]
	Macrophyte zone		Benthos	
Shredders	0.2	-	0.1	0.2
Browsers				
Detritivores	17.4	94.6	76.5	76.5
Herbivores	77.5	2.3	10.4	4.7
Predators	4.6	0.3	5.0	9.8
Filterers	0.3	2.8	0.1	8.8

(Data from Main (1976)[1], Timms (1980)[2] and present study)

Living macrophytes seem to be little used as food in running waters (Westlake 1975, Anderson & Sedell 1979) or lakes (Entz 1947, Rosine 1955, Soszka 1975b, Jonasson 1978, Cattaneo & Kalff 1980) and this is attributed to their high C/N ratios, large quantities of relatively indigestible cellulose and lignin, and low digestibility of their proteins (Boyd 1970). In the macrophyte zone of Lake Grasmere, shredders of aquatic macrophytes (viz., *N. nitens* and *T. cephalotes*)

comprised only 0.2% of the invertebrate community (Table 7.3). They were poorly represented also in the benthos (Dr B.V. Timms pers. comm.) and in the benthos of other New Zealand lakes (Table 7.3, Forsyth 1975). Herbivorous browsers dominated the macrophyte zone of Lake Grasmere (Table 7.3) and included gastropod molluscs, hydroptilid caddisflies, *H. amabilis, Eucyclops serrulatus,* and most orthocladine chironomids. Detritivorous browsers (mostly oligochaetes and oribatid mites) were next in abundance (Table 7.3). Since most of the browsing invertebrates recorded on macrophytes in Lake Grasmere were found in other habitats as well (e.g., on stones and/or mud), it seems that macrophytes are used mainly as a substrate from which periphyton is grazed. Predators (the swimming mites, tanypodine chironomids, some Trichoptera e.g., *Oecetis* spp., *Antiporus strigosulus,* and Odonata) comprised 4.6% of the macrophyte-associated invertebrate community in Lake Grasmere, and filterers (bivalve molluscs) only 0.3% (Table 7.3). In the profundal benthos of New Zealand lakes, communities are dominated by detritivorous browsers (mainly Oligochaeta), and filterers tend to be better represented than in macrophytic habitats (Table 7.3, Forsyth 1978). Although quantitative data on the composition of the benthos of Lake Grasmere is not immediately available, semiquantitative information (Dr B.V. Timms pers. comm.) indicates that detritivorous browsers (Oligochaeta, *P. antipodarum,* and Chironomidae) dominate the fauna, as in the benthos of other lakes (Table 7.3, Jonasson 1978).

Proportions of different feeding groups (e.g., detritivores, shredders, predators, filterers) may vary at different depths within a lake (Jonasson 1978, Table 7.3). In macrophyte-rich localities the accumulated remains of plants are decomposed through a detritus food chain (Wetzel & Allen 1972) since utilisers of fresh macrophyte tissue are rare (Cummins & Klug 1979, Cattaneo & Kalff 1980). On the rocky shore of a lake where wave action prevents the growth of aquatic macrophytes but diatoms and other algae may grow on the rocks, grazing food chains predominate (see Jonasson 1978). In the profundal benthos, invertebrate communities are dominated by detritivorous deposit feeders (e.g., most oligochaetes and some chironomids) and filter-feeders (bivalve molluscs) that feed on accumulated fine particulate organic matter (Jonasson 1978).

In Lake Grasmere, detritus, living macrophytes, filamentous algae, diatoms and animal tissues probably represent an increasing nutritional gradient (Anderson & Cummins 1979), and the food habits of most invertebrates studied were characterised by ingestion of food

of increasing quality with increasing age. For example, the major changes in the food habits of *H. amabilis* with age were the reduction in detritus intake and increased consumption of macrophyte tissue and animal prey items. *T. cephalotes* and *N. nitens* also showed relatively less ingestion of detritus and increased ingestion of macrophyte tissue in later instars. *N. nitens* was observed to feed mainly on the young shoot tips which would have had rather limited exposure to colonisation by diatoms and microorganisms. However, growing tips are more nutritious than older growth since they have greater nitrogen and protein content and less indigestible lignin (Feeny 1970, 1976). The other shredder studied (*T. cephalotes*), preferred older leaves and did not eat fresh growth (see also Babington 1967). Like many other shredders, it may derive its nutritional requirements from ingested microorganisms and macrophyte tissues that have already been partially hydrolysed by periphytic communities present on decomposing macrophytes (Cummins & Klug 1979).

A notable feature of the food habits of three of the species studied was their predation upon Mollusca (viz., *P. antipodarum*). The feeding of *X. zealandica* on *P. antipodarum* is the only instance of dragonfly predation upon a mollusc that I have found, and the incidence of predation on *P. antipodarum* by the two trichopterans (*H. amabilis* and *T. cephalotes*) also appears to be the highest recorded. Slack (1936) noted that two of 12 *Molanna angustata* (Trichoptera: Molannidae) examined had fed upon *Lymnaea* sp. in a Scottish lake, and Winterbourn (1978b) found a radula of *P. antipodarum* in the gut of one (of 17) *Psilochorema bidens* (Trichoptera: Rhyacophilidae) in a New Zealand stream. Experimental studies have shown that living *P. antipodarum* are preyed upon actively by *H. amabilis* (Wilson 1980) and *Neolimnia* spp. (Diptera: Sciomyzidae) (Barnes 1979) both of which enter the shell aperture and can prise aside the operculum. This seems to be a very effective feeding strategy and, considering the marked dominance of molluscs in many New Zealand freshwater habitats (Winterbourn & Lewis 1975, present study), makes available an abundant food resource.

In the macrophyte zones of Lake Grasmere, the fauna at all sites was dominated by browsers, mainly those feeding on periphyton growing on plant surfaces, but a number of species' populations had their primary representation in different areas of the lake. For example, although *P. hendersoni* was the most common hydroptilid caddisfly on plants in most parts of the lake, *P. tillyardi* was the most common

species on *E. canadensis* in the eastern sampling area, and *O. albiceps*, although sometimes recorded on plants, was most abundant on algal covered stony substrates. On plants, spatial separation may occur also at the microhabitat level. For instance, some species (like *P. antipodarum*) may browse predominantly on macrophyte surfaces close to the lake bottom, whereas other macrophyte-associated invertebrates may be distributed more evenly over the plants (e.g., the hydroptilids), or are present mainly on shoot tips (e.g., *N. nitens*).

Fig. 7.1 is a generalised food web for invertebrates in the macrophyte zone of Lake Grasmere summarising the interrelationships between functional feeding groups of invertebrates. The shredder and filterer based pathways are relatively unimportant compared with the detritus and periphyton browsing food chains in the macrophyte zone. Most macrophyte tissue is degraded via microbial and fungal decay and enters the detritus food chain (Wetzel & Allen 1972).

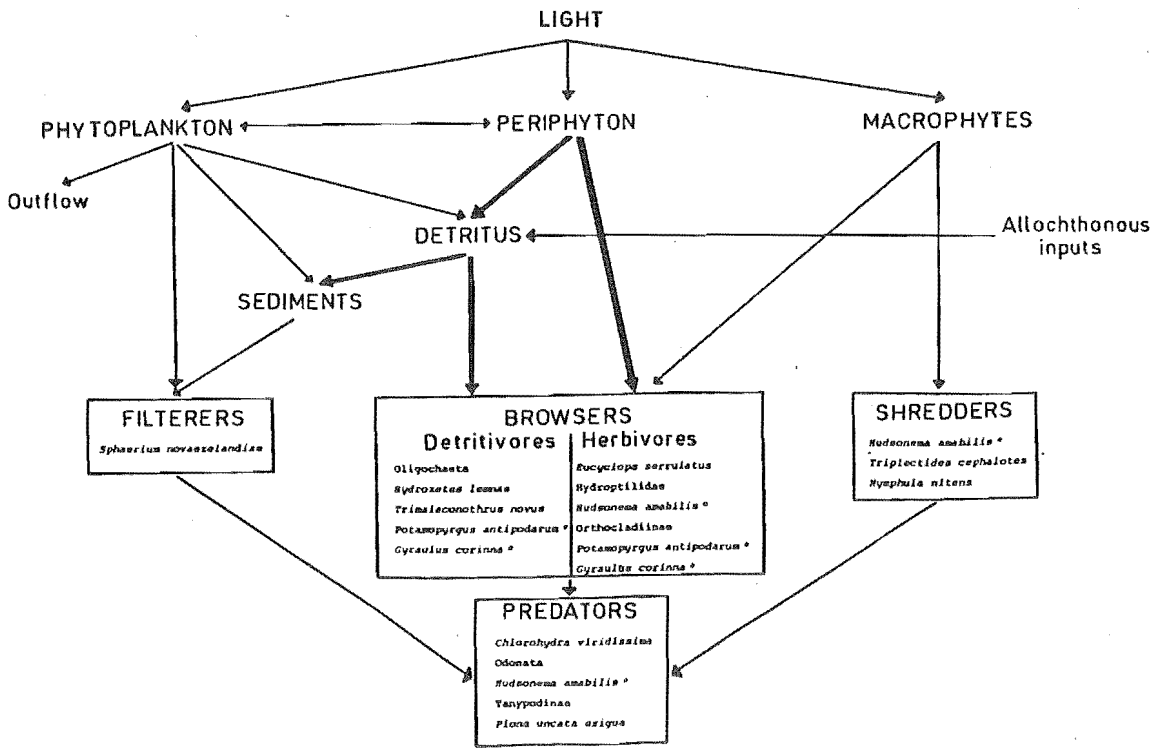


Fig. 7.1 Food web for invertebrates in the macrophyte zones of Lake Grasmere showing the importance of browsing invertebrates and the periphyton and detritus-based food chains. Prominent examples of invertebrates in each of the functional feeding groups are shown. (* denotes invertebrates that belong in more than one functional group.)

Highly seasonal life-history patterns are characteristic of most holarctic invertebrate species (Hynes 1970 and references therein). In contrast, in New Zealand (and other temperate regions of the southern hemisphere) many freshwater insects have weakly synchronised life-histories characterised by poorly-defined cohort growth and long flight periods (see Babington 1967, Norrie 1969, Winterbourn 1974, Towns 1976, McFarlane 1977, Crumpton 1979, Deacon 1979, Cowie 1980, present study). Only a few examples of freshwater insects with well-synchronised life-histories have been recorded in New Zealand (e.g., *Rakiura vernale*, Michaelis 1973; *P. tillyardi*, present study). The life-histories of only a few non-insectan freshwater invertebrates have been studied in New Zealand. Winterbourn (1970b) investigated the population dynamics of *P. antipodarum*, Towns (1976) the life-history of the amphipod *Paracalliope fluviatilis*, and there have been a number of studies of planktonic crustaceans (e.g., Green 1974, Chapman, Green & Jolly 1975, Burns 1979). Complete life-histories are known for only a few mites (viz., *Eylais waikawae, Piona uncata exigua, Hydrachna maramauensis*, Stout 1953a & b). Most freshwater mites probably have annual cycles with adults present from late spring until autumn (Stout 1976).

The life-histories of most insects studied in Lake Grasmere (*P. tillyardi, H. amabilis, T. cephalotes, P. aureola, O. unicolor, N. nitens*) were univoltine, fitting Hynes' (1970) slow seasonal cycle category. Larvae recruited in late summer/autumn and emerged in spring and summer and some (e.g., *H. amabilis, T. cephalotes* and *N. nitens* especially) exhibited little or no growth during winter. On the other hand, *O. albiceps* and *P. hendersoni* may belong more properly in Hynes' (1970) non-seasonal category since individuals of all stages may be present at all times of year. Hopkins (1976) found that *O. albiceps* was bivoltine (with pupae in October and June), but it may be that this species and *P. hendersoni* have multiple overlapping flexible generations depending upon prevailing environmental conditions (especially temperature which is related to latitude). *X. zealandica*, since it can have a two or three-year life-history and a summer diapause in the F-2 to F instar larvae (Deacon 1979, present study) also fits Hynes' (1970) non-seasonal category.

Most work on the life-histories of New Zealand freshwater invertebrates has concerned stream insects (see Chapter V) and several explanations have been put forward to explain their observed aseasonality or poorly-synchronised life cycles. Devonport and

Winterbourn (1976) considered that New Zealand's relatively mild climate could be responsible, but Towns (1976) suggested that the long period of isolation of the fauna (together with severe long-term climatic variations) and the lack of pronounced autumnal leaf fall were key factors (cf. Anderson & Cummins 1979). Cowie (1980) considered various arguments in some detail and concluded with respect to stream insects that "severe and unpredictable climatic conditions would favour selection for opportunism, and consequent spreading of the risks of emergence through poorly synchronised life histories".

In Lake Grasmere, seasonality of life-histories is probably not keyed to food availability since there are no obvious periods of food shortage or pulses of abundance during the year. Rather, the relatively buffered lacustrine environment (with respect to climatic influences, especially temperature) which would not exert any selective pressure for marked seasonality, could be involved in the relatively aseasonal life-history patterns seen in most New Zealand lacustrine insects. The resultant long adult flight periods spread the risks of emergence so that there is a reduced likelihood of bad weather affecting emergence success, adult abundance, survival and mating, and consequent recruitment to the next generation. Nevertheless, marked changes in population densities may occur between years (e.g., *N. nitens* and *X. zealandica*, present study), changes that may well be related to the influences of climate on the adult stage of the life-history.

Finally I would like to emphasise the importance of sound taxonomic knowledge to ecological investigations. As Watt (1979) stated "The increasingly recognised need for accurate identifications in applied research thus often had to be met by the applied research worker first undertaking a taxonomic revision of whatever group of pests or beneficial organisms he was studying, before he could make further progress." In the present work, deficiencies in taxonomic knowledge of many species (notably Chironomidae) were a limitation until late in the study when taxonomic investigations were undertaken and 'difficult' species were identified. Much important information on, for example, habitat preferences may be overlooked if species cannot be distinguished. Further necessary taxonomic work remains to be done, especially on chironomids in the subfamily Orthocladiinae and will enable more refined ecological work to be done.

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Appendix 1. Numbers of invertebrates per sample (= 0.008 m^2) collected from Lake Grasmere during the pilot survey (14 April 1976) using the cylinder-sampler. (*E* = *Elodea canadensis*, *I* = *Isoetes alpinus*, *R* = *Ranunculus fluitans*)

Sampling area	NORTH								SOUTH				EAST												WEST							
Lake depth (m)	2	2	2	1	1	1	1	1	1	1	2	2	2	2	2	2	1	1	1	1	0.6	0.5	0.7	0.6	2	2	2	2	1	1	1	1	1
Macrophyte	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*I*	*I*	*E*	*E*	*E*	*E*	*E*	*E*	*R*	*R*	*R*	*R*	*I*	*I*	*I*	*I*	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*I*	*I*
Dry wt macrophyte (g)	0.87	2.19	2.09	1.82	1.13	1.16	1.82	0.90	0.40	0.83	0.95	2.03	2.02	2.23	1.96	2.74	1.08	1.45	0.81	0.76	0.26	0.35	0.23	0.16	0.59	0.82	0.97	1.25	0.51	0.57	0.32	1.30	1.25
Invertebrate taxon																																	
Chlorohydra viridissima	3	10	24				1	6	7	1	100	3	31	44	23	12						2	1		11	37	1		5	1	12	4	2
Cura pinguis		2	1	1		1	8	1					4	1		3		1							4				1			
Plumatella repens	P	P	P	P	P		P	P	P		P	P	P	P	P	P	P	P	P	P					P	P	P	P					
Chaetogaster sp.	5	38	19	28		6					14		13	6	6											11	6	1	38		13		1
Other OLIGOCHAETA	1		3	4			61	12					130	1		57	1			8				1	209	2	3			20	1	5	
NEMATODA									1		1	1							1						1								1
Glossiphonia sp.					1		1																		1								
unident. CLADOCERA		45	17	8	62	7	28	27	6		17	57		6	5	24	10	10	3	2	1	4	27	63	9	2	51	28	27	16	7	7	20
OSTRACODA							2					1	2	1		2	7	9		6		9	19	96	2		8		2	5			4
Eucyclops serrulatus		5	13	7	5	4		15		1	3	12	1	5			10		3	4	3	36	135	148	1		9	2	12			2	3
Xanthocnemis zealandica			1	1	11	3	5	2	1	1			1							1				1	1			1	1	1	1	2
Diaprepocoris zealandiae																				1						1						
Antiporus strigosulus								1													1		1	1								
Oxyethira albiceps																											1		1		1	
Paroxyethira hendersoni	1		2	21	13	10	12	1	4	10	14	22	4	4	2	1	3	2	2	1						1	2	2	4	1		1	6
P. tillyardi														2	3	9													3			3	
precase HYDROPTILIDAE		2	1	62	44	9	19		6	6	27	86	3	15	7		4	4	5	2		8	76	16	1	1	12	2	33	10	9	24	82
Triplectides cephalotes																											1				1	1
Hudsonema amabilis																			4	1	1	8	13	27								
Nymphula nitens	1											1	1	2	1	2	1		1													
CHIRONOMIDAE				2			2	1		6		18	7	1			1	7			1		2	8	8		6		5	2		5	10
HYDRACARINA	8	32	7	31	16	10	39	9	11	9	1	66	33	30	49	66	37	43	17	14	1	7	33	64	13	15	5	4	4	4	7	20	48
Gyraulus corinna	138	367	292	219	88	45	288	51	3	3	13	75	26	30	13	31	7	3	16	1	3	6	5	10	37	42	45	58		20	38	21	50
Potamopyrgus antipodarum	168	506	373	838	834	455	627	230	116	460	317	294	1012	2360	665	1893	794	1540	708	604	144	739	1603	1435	92	140	444	130	506	379	201	283	1602
Sphaerium novaezelandiae	1												11			17	9	7		11		1		12							1		1

Appendix 2.1 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the northern sampling area (water depth = 2 m) Sept. 1976 - Oct. 1977.

NE2m

Date	2/9/76			2/11/76			2/12/76			20/1/77			2/3/77			8/4/77			10/5/77			20/6/77			13/7/77			3/10/77		
Dry wt macrophyte (g)	0.58	3.03	0.92	0.52	0.68	0.35	0.27	0.22	0.18	0.26	0.28	0.20	0.34	0.22	0.45	1.26	1.04	1.29	1.01	1.61	0.30	0.72	0.37	0.66	0.11	0.32	0.35	0.40	0.34	0.49
Invertebrate taxon																														
Chlorohydra viridissima		3	1	1	11		19		4	35	48	46	4	4	9	17	37	39	5	37	14	11	3	8						3
Cura pinguis					1								1		1	3	1	2	1		1		1		1					
Plumatella repens	P	P								P	P	P	P	P	P	P	P	P	P	P	P	P			P	P				P
Chaetogaster sp.			10		1		13	1	1	13	19	6	5	1	1	11	5	2	4	4	7	5	1	5	9	5	8	5	1	8
other OLIGOCHAETA	3	114					70		57	10	17	5	33	27	8	21	1	33	17	11	94	4	1	9	4	2	1	4	1	1
Glossiphonia sp.													1		5		1	1												
Placobdella maorica										1																				
Bosmina meridionalis																1				2		44		4	167	195	55	29		2
Graptoleberis testudinaria																8	23	7		10	2	5			1	6	20	1		1
Chydorus sphaericus																		2												1
Ceriodaphnia dubia																1	1				1									
unident. CLADOCERA	7					1	8		6	61	72	52		53	7															
OSTRACODA																										1				
Eucyclops serrulatus	2	3	1	12	11	1	28	6	24	54	127	109	94	25	27	402	316	409	45	77	49	9	39	10	5	5	8	27	17	18
Procordulia grayi																1														
Xanthocnemis zealandica			2															1												
Diaprepocoris (A)									1																					
zealandiae (L)																				1										
Sigara arguta (A)							1																							
Paroxyethira (L)	3			7	1		1						1		1	2	7	2	2	6	4		5	3	2	2	1			1
hendersoni (P)				2				1																						
Paroxyethira (L)																				1	1					1				
tillyardi (P)																													1	
precase HYDROPTILIDAE						1	3	1			2		1			4	8	3	3	3		2		1		5		1	1	2
Triplectides (L)				1					1								1									1				
cephalotes																														
Hudsonema amabilis (L)		1																												
CHIRONOMIDAE				9	1	1					1				1	3	1	1	5	5	2	4		2	2	24	8	3	4	4
Piona uncata exigua		3		10	4	7	3	5	3	6	2	1	22	17	19	8	14	10	6	8	15	4	5					10	3	5
Hydrozetes lemnae		4		3	3	6	5	8		4	4	2	4	8	1	4	1	16	2	3	2	3		3		1		4	1	1
Trimalaconothrus (A)				1						5	8	2	4	5	5	1			1	1										
novus (L)																														
Gyraulus corinna	27	54	5	54	34	27	42	42	8	34	36	20	41	34	79	106	113	83	107	69	18	15	2	37	6	21	14	10	4	7
Potamopyrgus antipodarum	79	249	89	159	172	106	74	74	57	63	69	32	118	38	218	540	411	452	350	495	135	122	83	64	58	126	39	130	171	304
NEMATODA										1			1	1					1		14	1			4	3	4			

(A) = Adult, (L) = Larva, (P) = Pupa. For *Plumatella repens*, P = present.

Appendix 2.2 Numbers of invertebrates per sample (= 0.008 m^2) of *Isoetes alpinus* collected from the southern sampling area (water depth 0 - 1 m), September 1976 - October 1977.

SI

Date		2/9/76	2/11/76		2/12/76	20/1/77	2/3/77		8/4/77		10/5/77	20/6/77	13/7/77		3/10/77
Dry wt macrophyte (g)		0.28	0.28	0.39	0.19	0.20	0.11	0.26	0.17	0.19		0.03	0.12	0.03	
Invertebrate Taxon															
Chlorohydra viridissima			2	2	11	19	10	7	2	1		8		1	
Cura pinguis			1		1	2	2	4		1		1	1		
Plumatella repens			P	P		P		P				P			
Chaetogaster sp.			2		13	15	3	4	2	3		12		4	
other OLIGOCHAETA		3	1	64		101	2		5	7		15	1	2	
Glossiphonia sp.							1								
Bosmina meridionalis												12	3	11	
Alona guttata										24		52	10	17	
Graptoleberis testudinaria									13	3			2	3	
Chydorus sphaericus									1			3			
unident. CLADOCERA				1	13	24	4	14							
OSTRACODA						1	4	1		1					
Eucyclops serrulatus		4	4	3	7	14	5	8	1	10		16	12	20	
Deleatidium sp.							1								
Zelandobius furcillatus					1									1	
Diaprepocoris zealandiae	(A)								1	1					
Oxyethira albiceps	(L)											3			
Paroxyethira hendersoni	(L)	1	10	8	4	9				2		9	4	1	
	(P)		1				1								
Paroxyethira tillyardi	(L)					1									
	(P)														
precase HYDROPTILIDAE		2	1		23	11	7					11			
Triplectides cephalotes	(L)				1							2			
Oecetis unicolor	(L)						2								
Oecetis iti	(L)						1								
Nymphula nitens		1													
CHIRONOMIDAE	(L)	2	2	9	2	30	3	6	20	22		37	4	2	
	(P)					1									
Piona uncata exigua			2			3	8	6	1	3		1			
Hydrozetes lemnae		11	26	28	20	12	6	7	6	4		4	1		
Trimalaconothrus novus	(A)	1					1								
	(L)			1			1								
Gyraulus corinna		1	6	8	6	20	28	28	57	43		10	10	3	
Potamopyrgus antipodarum		69	62	69	85	17	129	128	241	133		368	42	23	
Sphaerium novaezelandiae		1					3					11			
NEMATODA			1			12	6					12		1	

Appendix 2.3 Numbers of invertebrates per sample (= 0.008 m^2) of *Myriophyllum propinquum* collected from the southern sampling area (water depth = 0 - 1 m), September 1976 - October 1977.

SM

Date		2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		0.67	0.37	0.47	0.24	0.27	0.36	0.53	0.59	0.18	
Invertebrate taxon											
Chlorohydra viridissima			9	4	5		6		4		
Cura pinguis								4			
Plumatella repens			P		P	P	P		P		
Chaetogaster sp.			11		12		6	7	7	4	
other OLIGOCHAETA		3		3	2	9	12	4	3		
Bosmina meridionalis									3	1	
Alona guttata							3	31		2	
Graptoleberis testudinaria							9	5	22	1	
Chydorus sphaericus							12	33			
Ilyocryptus sordidus										2	
Neothrix armata										1	
unident. CLADOCERA		21	1		19	1					
OSTRACODA				6			14	12			
Eucyclops serrulatus		14	8	3	1	1	32	26	31	1	
Zelandobius furcillatus		1									
Diaprepocoris zealandiae	(A)										
	(L)						1	1			
Sigara arguta	(L)						1				
Paroxyethira hendersoni	(L)	7	19	3	11		2	4	5	2	
	(P)	1	1	1							
precase HYDROPTILIDAE		5	1	5	20		10	3	4	1	
Pycnocentrodes aureola	(L)					1	6	1			
Triplectides cephalotes	(L)			5			2	3		1	
T. obsoleta	(L)						1				
Hudsonema amabilis	(L)			1			1		2		
Nymphula nitens	(L)	1		1	1		2		2	1	
	(P)			1							
CHIRONOMIDAE	(L)	4	1	12	22	8	8	78	55	8	
	(P)				1	1					
Piona uncata exigua			5	1	4	5	5				
Hydrozetes lemnae			18	17	2	9	15	12	3		
Trimalaconothrus novus	(A)		1	3		2	2	3	4		
	(L)			1		1	8	5			
Gyraulus corinna			14	24	27	5	11	101	12	5	
Potamopyrgus antipodarum		43	79	95	9	109	1699	166	67	97	
Sphaerium novaezelandiae							5				
NEMATODA				2	3		1	6	3	1	

Appendix 2.4 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the eastern sampling area (water depth = 1 m), September 1976 - October 1977.

EE 1m

Date		2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		0.55	1.09	0.64		0.27	0.84	0.41			
Invertebrate taxon											
Chlorohydra viridissima				2		51	191	12			
Cura pinguis						1	10	1			
Plumatella repens		P				P	P	P			
Chaetogaster sp.						1	5				
other OLIGOCHAETA		15	3					6			
Glossiphonia sp.							1				
Alona guttata								4			
Graptoleberis testudinaria								1			
unident. CLADOCERA		9		4		1					
OSTRACODA			4								
Eucyclops serrulatus			52	3		1	54	86			
Diaprepocoris zealandiae	(A)		1								
Antiporus strigosulus	(A)										
	(L)						1				
Paroxyethira hendersoni	(L)						6				
P. tillyardi	(L)	3	11				2	9			
precase HYDROPTILIDAE				1		5	3	1			
Pycnocentrodes aureola	(L)	1									
Hudsonema amabilis	(L)	1									
Nymphula nitens								2			
CHIRONOMIDAE			2	1		2		6			
Piona uncata exigua		1	17	2		10	4	20			
Hydrozetes lemnae		20	24	2		8	18				
Trimalaconothrus novus	(A)					3	3	1			
	(L)					1		1			
Gyraulus corinna		4	1			2	6	9			
Potamopyrgus antipodarum		109	712	81		135	827	526			
Sphaerium novaezelandiae		1						13			
NEMATODA								3			

Appendix 2.5 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the eastern sampling area (water depth = 2 m), September 1976 - October 1977.

EE2m

Date	2/9/76			2/11/76			2/12/76			20/1/77			2/3/77			8/4/77			10/5/77			20/6/77			13/7/77	3/10/77			
Dry wt macrophyte (g)	0.88	0.92	0.89	0.74	0.81	0.74	0.44	0.50	0.79	0.47	0.77	0.55	0.25	0.53	0.30	1.10	0.72	0.68	0.63	0.63	0.50	0.62	0.69	0.24		0.16	0.49	0.38	0.40
Invertebrate taxon																													
Chlorohydra viridissima			1	1	5		8	13	9	58	76	127	13	64	18	209	103	85	27	7	53	1	13	2		5	13	69	8
Cura pinguis										5	2	1		3	3	1	3		1	3									
Plumatella repens	P			P	P	P				P	P	P	P	P	P	P	P	P	P	P	P	P	P	P			P		P
Chaetogaster sp.							1			2		2	2	3	1		1	1	4		4		1	3		2		1	
other OLIGOCHAETA		53	1	7			6	4	1	13	2	3	3	10	10		9	2	18	5		8	19	30				1	2
Glossiphonia sp.				1		1																							
Bosmina meridionalis																							1	10					
Alona guttata																								1					
Graptoleberis testudinaria																1	1		1									1	
Chydorus sphaericus																			3										
unident. CLADOCERA	13	14	18				6	2	3	2	3	11	8	8	6														
OSTRACODA		1		2		2	4	4	2	1	5		1	10	13				7	2	1	1	3	16					
Eucyclops serrulatus	3	4	11	5		1	8		3	11	23	3	12	24	7	113	238	71	41	3	28	14	45	10		11	11	11	2
Diaprepocoris (A)															1		4	4											
zealandiae (L)															1						1								
Paroxyethira (L)						1	1		1		2						1	1	1		1								
hendersoni (P)																													
P. tillyardi (L)	3			2	2	1	5	1	1	5						1		1	6	4	3	1	6	1		3	6	2	7
precase HYDROPTILIDAE	1							1			1			1		1	3	2								2			
Pycnocentrodes aureola (L)			1																			2							
Triplectides obsoleta (L)															1														
Hudsonema amabilis (L)	1	2											1	2	1	2	2			1		12		1					
Nymphula nitens		1													1	1											1		
CHIRONOMIDAE		5	1	1		1	2	3	2	4	3	1		5	1			3	12	1		2	1	8			1		
Arrenurus sp.									1																				
Piona uncata exigua			5	12	8	9	4	5	2	17	32	8	7	15	7	4	7	3	23	4	4	5	2	6		8	4	9	13
Hydrozetes lemnae (A)	2	21	10	13	6	9	7	12	14	4	8		4	8	3	1	4	3	4		1		2	1		1	5	1	8
(L)																										1			
Trimalaconothrus (A)										4			1	2					1										
novus (L)		1																											
Gyraulus corinna		5	4	2					3		12	1	9	13	3	9	12	12	21	15	35	8	13	7		2	9	3	5
Physastra variabilis											1			1		1	1				2								1
Potamopyrgus antipodarum	385	359	145	372	175	370	130	85	96	114	137	147	116	565	392	503	681	304	515	346	407	376	329	195		178	148	108	245
Sphaerium novaezelandiae		8		2		1	2	2						3	6				7	4		2		6					
NEMATODA								1		1	1	2	1	1				1								1			

Appendix 2.6 Numbers of invertebrates per sample (=0.008 m^2) of *Isoetes alpinus* collected from the eastern sampling area (water depth = 0 - 1 m), September 1976 - October 1977.

E1

Date		2/9/76		2/11/76		2/12/76		20/1/77	2/3/77		8/4/77	10/5/77	20/6/77		13/7/77	3/10/77
Dry wt macrophyte (g)		0.42	0.50	0.25	0.19	0.14	0.06		0.05	0.10	0.12	0.20	0.03	0.05		0.05
Invertebrate taxon																
Chlorohydra viridissima			1						7	22	12	2	2			1
Cura pinguis										2	3	1	1			1
Chaetogaster sp.										2	1	3				
other OLIGOCHAETA						2						2	1	2		
Bosmina meridionalis														5		
Alona guttata												2	8			1
Graptoleberis testudinaria											6		15	16		
Chydorus sphaericus													1			
unident. CLADOCERA			18	2	3	5			1	13						
Gomphocythere duffi			2							2						1
other OSTRACODA			1	1					3	3		21				1
Eucyclops serrulatus		6	34	2	13	42	23		3	103	54	86	114	49		
Deleatidium sp.					1											
Zelandobius furcillatus			4													
Diaprepocoris zealandiae	(A)															
	(L)												1			
Antiporus strigosulus	(A)					1										
	(L)															
Paroxyethira hendersoni	(L)						2					1		1		
	(P)					1										
P. tillyardi	(L)										2					1
	(P)					1										
precase HYDROPTILIDAE		1	5		2	27	7			3	3	1	1	3		1
Pycnocentrodes aureola	(L)												1	1		
	(P)															
Hudsonema amabilis	(L)				1					1			1	3		
	(P)															
Nymphula nitens	(L)					1										
CHIRONOMIDAE			2		2		1		1	15	6	17	2	10		2
Piona uncata exigua	(A)		1	1	2	1	2			9	2					
Hydrozetes lemnae		3	15		11	20	14		1	4	1	4				2
Trimalaconothrus novus	(A)		35	1		4	1			1				4		
	(L)		8			2				1				1		
Gyraulus corinna			2			3	3			7	1	3				7
Physastra variabilis												1				
Potamopyrgus antipodarum		12	106	16	41	48	4		40	234	169	18	57	54		62
Sphaerium novaezelandiae														1		
NEMATODA						1				3				1		1

Appendix 2.7 Numbers of invertebrates per sample (= 0.008 m^2) of *Myriophyllum propinquum* collected from the eastern sampling area (water depth = 1 - 2 m), September 1976 - October 1977.

EM

Date		2/9/76	2/11/76		2/12/76		20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)			0.57	0.44	0.48	0.33	0.38	0.26	0.19	0.41	0.45		0.26
Invertebrate taxon													
Chlorohydra viridissima			1		5	11	109	21	13	2	1		
Cura pinguis					1			1	3	1			
Plumatella repens								P	P	P			P
Chaetogaster sp.							9	1		9	1		3
other OLIGOCHAETA					2								1
Graptoleberis testudinaria									2				
Chydorus sphaericus										1	2		
unident. CLADOCERA					6	3	31	3					
OSTRACODA								1					
Eucyclops serrulatus				5	24	28	1	1	14	9	5		
Sigara arguta	(A)					1							
Paroxyethira hendersoni	(L)				2	3	3			2			
	(P)							1					
P. tillyardi	(L)			2					2	2			1
precase HYDROPTILIDAE					15	25	6	1	4	9			1
Hudsonema amabilis	(L)		2	1		1		1			5		
Triplectides cephalotes	(L)												
	(P)				1								
Nymphula nitens	(L)			1	1		1		3	2	2		
	(P)				1								
CHIRONOMIDAE					2		4	10	2	6			1
Piona uncata exigua			5	1	5	2	13	5	2				
Hydrozetes lemnae			1	4	24	29	14	7	1				2
Trimalaconothrus novus	(A)			1				1	2				1
	(L)												
Gyraulus corinna			1	2	2		4	1	2	1			
Physastra variabilis								1					
Potamopyrgus antipodarum			59	45	313	155	113	118	241	49	19		27
NEMATODA					1								

Appendix 2.8 Numbers of invertebrates per sample (= 0.008 m^2) of *Ranunculus fluitans* collected from the eastern sampling area (water depth = 1 - 2 m), September 1976 - October 1977.

ER

Date		2/9/76	2/11/76	2/12/76		20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		0.66	0.47	0.26	0.24		0.40	0.25				
Invertebrate taxon												
Chlorohydra viridissima					1		5	6				
Cura pinguis								1				
Plumatella repens		P						P				
Chaetogaster sp.			1		1							
other OLIGOCHAETA				2	1							
Graptoleberis testudinaria								7				
unident. CLADOCERA		2	1									
OSTRACODA		2										
Eucyclops serrulatus		9	1	9	9		2	19				
Sigara arguta	(A)			1								
Paroxyethira hendersoni	(L)											
	(P)		2									
P. tillyardi	(L)				1			1				
precase HYDROPTILIDAE				8	11			8				
Hudsonema amabilis	(L)	2	1		1		1					
CHIRONOMIDAE		2			1			9				
Piona uncata exigua		1	1	2	2		12	4				
Hydrozetes lemnae		3	8	19	23			1				
Trimalaconothrus novus	(A)	1					2					
	(L)				1							
Gyraulus corinna			1		1		1	6				
Potamopyrgus antipodarum		12	26	143	84		70	392				
Sphaerium novaezelandiae								1				
NEMATODA								1				

Appendix 2.9 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the western sampling area (water depth = 1 m), September 1976 - October 1977.

WE 1m

Date		2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		0.63	0.92	0.66	0.41	0.39	0.65	0.58	0.61	0.27	
Invertebrate taxon											
Chlorohydra viridissima					7	4	14	18	12		
Cura pinguis						4		1			
Plumatella repens		P	P				P	P	P	P	
Chaetogaster sp.					67	9	11	130	17	12	
other OLIGOCHAETA			3	71	21	3	3	6	6	201	
Bosmina meridionalis								3		10	
Alona guttata							1	12			
Graptoleberis testudinaria							1	65	67	5	
Chydorus sphaericus								5			
unident. CLADOCERA				4	126	11					
OSTRACODA			7		13	15	2			2	
Eucyclops serrulatus		3	3	2	12	17	25	130	140	9	
Deleatidium sp.						1					
Xanthocnemis zealandica			3	2	1			1			
Oxyethira albiceps	(L)					1				1	
Paroxyethira hendersoni	(L)	16	9	3			5	4	5	2	
	(P)	25	1								
P. tillyardi	(L)		2								
precase HYDROPTILIDAE		4		1		1	6	10		1	
Pycnocentrodes aureola	(L)						1				
Triplectides cephalotes	(L)		1	1				1			
Oecetis unicolor	(L)		1								
Hudsonema amabilis	(L)	1									
CHIRONOMIDAE			2	2	2	1	3	76	6	11	
Arrenurus sp.									1		
Piona uncata exigua			2	2	1	11	4	1		1	
Hydrozetes lemnae		1	9	6		2	1	2			
Trimalaconothrus novus	(A)				1	3		1			
	(L)										
Gyraulus corinna		9	34	18	20	24	67	129	59	21	
Potamopyrgus antipodarum		212	722	191	258	209	247	80	114	129	
Sphaerium novaezelandiae									6		
NEMATODA					4	9		2		5	

Appendix 2.10 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the western sampling area (water depth = 2 m), September 1976 - October 1977.

WE2m

Date	2/9/76			2/11/76			2/12/76			20/1/77			2/3/77			8/4/77			10/5/77			20/6/77			13/7/77			3/10/77		
Dry wt macrophyte (g)	0.77	0.75	1.63	0.32	0.42	0.54	0.18	0.22	0.33	0.40	0.78	0.33	0.58	0.48	0.57	1.27	0.88	0.53	0.77	0.76	0.76	0.59	0.47	0.50	0.25	0.22	0.66	0.14	0.73	0.17
Invertebrate taxon																														
Chlorohydra viridissima	1		4	13	6	23				294	195	308	13	36	21	141	190	54	383	62	66	87	240	180	59	1		11	5	14
Cura pinguis																			3	2	7									
Plumatella repens				P		P				P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P		P	P
Chaetogaster sp.	13		6	3	1	4				29	9	9	1	8	3	3	20	13	16	1	8	19	3	7	12	10	6	5	4	2
other OLIGOCHAETA		13	2			3			9	46	41	27	24	14	12	56	3	2	20	21	255		15	5	2		67	3	6	1
Bosmina meridionalis																						8	15	6	61	69	15	6		2
Alona guttata																			6	3		1								
Graptoleberis testudinaria														19	4	92	73	16	30	53	8	10	11	17	5	28	12	2		1
Chydorus sphaericus														1		3	6	2				6	3	5				3		
unident. CLADOCERA	3	3	3	1			26	73	2	57	104	23	3																	
OSTRACODA						1						1																		
Eucyclops serrulatus	4	3	3	12	32	3	3	29	5	46	41	27	10	7	4	83	30	40	229	88	107	35	56	21	26	72	38	26	14	9
Xanthocnemis zealandica	1	1					1	2		1						1	1				1							1		
Diaprepocoris zealandiae (A)																														
(L)																					1		1	1						
Paroxyethira hendersoni (L)			3			2		1		2	3	1	4	2		1		3	4	5	1	1			1		4			
(P)						1				1																				
P. tillyardi (L)													3		3															
precase HYDROPTILIDAE	12	3	9					1		1		2				1	2	1	5	5	1						1	1		
Triplectides cephalotes (L)															1							1					1			
CHIRONOMIDAE							1			10	2	2		4	2	4	5	6	52		7	1	3		21	1	3	11	1	4
Piona uncata exigua (A)				1	8	1	2		2	32	3	2	4	1	4	17	14	12	35	13	13			1	6		2		28	2
(L)														3											1		4			
Hydrozetes lemnae	1		3	10	10	5	7	6	3			1	3	2		7	4	3		2	8		1					1		
Trimalaconothrus novus (A)										11		8		2	1			2					1							
(L)																														
Arrenurus sp.																					1									
Gyraulus corinna	10	3	29	4	2	9	12	2	18	27	39	14	15	16	18	90	79	74	56	104	71	6	5	15	14	21	24	3	1	1
Potamopyrgus antipodarum	34	43	44	32	46	91	35	31	65	99	176	110	60	73	87	258	221	250	404	299	551	143	154	216	97	60	129	41	136	64
Sphaerium novaezelandiae												1							1		3									
NEMATODA													1				1					2			1				2	

Appendix 2.11 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* from the western sampling area (water depth = 3 m), September 1976 - October 1977.

WE 3m

Date		2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		1.32	0.85	0.40	0.24	0.16	0.46	0.40	0.31	0.19	
Invertebrate taxon											
Chlorohydra viridissima		22	9	22	55	143	2000	89	92	276	
Cura pinguis				1			1			6	
Plumatella repens		P	P	P	P		P	P	P	P	
Chaetogaster sp.		42	5				5	60	7		
other OLIGOCHAETA			34	2	4	2		3	2	3	
Glossiphonia sp.					1						
Bosmina meridionalis									15	370	
Alona guttata							1	2	1	2	
Graptoleberis testudinaria							2	2	3	8	
Chydorus sphaericus							1	1			
unident. CLADOCERA		10		8	43	38					
OSTRACODA				1	2						
Eucyclops serrulatus		10	5	66	21	65	160	60	46	42	
Xanthocnemis zealandica		2									
Sigara arguta	(A)			1							
Paroxyethira hendersoni	(L)	2	2							1	
	(P)		2	2							
precase HYDROPTILIDAE		10	1								
CHIRONOMIDAE	(L)	2					4	40		18	
	(P)						1				
Piona uncata exigua			7	8	2	15	4		9		
Hydrozetes lemnae			34	16	5	6	3		2		
Trimalaconothrus novus	(A)		2			4					
	(L)										
Gyraulus corinna		4	6	13	6	15	59	65	5	29	
Potamopyrgus antipodarum		98	121	65	36	71	179	183	116	188	
Sphaerium novaezelandiae				1						1	

Appendix 2.12 Numbers of invertebrates per sample (= 0.008 m^2) of *Elodea canadensis* collected from the western sampling area (water depth = 4 m), September 1976 - October 1977.

WE 4m

Date	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)	3.41	0.52	0.47	0.40	0.53	0.36	0.86	0.28	0.09	
Invertebrate taxon										
Chlorohydra viridissima	8	1	30	251	440	389	1147	53	86	
Cura pinguis				1			4		1	
Plumatella repens	P	P	P		P	P	P	P	P	
Chaetogaster sp.		5	5		6	9	125	9	9	
other OLIGOCHAETA			4	6	8	2		2		
Bosmina meridionalis								10	47	
Alona guttata							2	1		
Graptoleberis testudinaria						6	16	2	6	
Chydorus sphaericus							3	1		
Ceriodaphnia dubia								1		
unident. CLADOCERA	6		4	47	2					
OSTRACODA				3				1		
Eucyclops serrulatus	1	23	26	102	14	52	125	29	7	
Procordulia grayi					1					
Paroxyethira hendersoni (L)	2			1		2			1	
(P)	1									
P. tillyardi (L)			1							
precase HYDROPTILIDAE			2			1				
CHIRONOMIDAE					1		[illegible]		17	
Piona uncata exigua		1	3	16	7	4		4		
Hydrozetes lemnae	3	2	16	19	15	3				
Trimalaconothrus novus (A)			1	20	13					
Gyraulus corinna	7		3	18	41	58	108	4	10	
Potamopyrgus antipodarum	48	40	72	41	110	333	435	103	27	

Appendix 2.13 Numbers of invertebrates per sample (= 0.008 m^2) of *Isoetes alpinus* collected from the western sampling area (water depth = 0 - 1 m), September 1976 - October 1977.

WI

Date		2/9/76	2/11/76		2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt macrophyte (g)		1.40	0.14	0.09	0.23	0.11	0.12		0.18	0.12	0.11	
Invertebrate taxon												
Chlorohydra viridissima			1	1	3	10	7		16	3	2	
Cura pinguis		1			2		14		22	2	3	
Plumatella repens						P			P			
Chaetogaster sp.			8		1		1		2	28	20	
other OLIGOCHAETA				3		1	3		30	7		
Bosmina meridionalis										2	4	
Alona guttata									18	22	16	
Graptoleberis testudinaria									7	16	6	
Chydorus sphaericus									1			
Ceriodaphnia dubia										5		
unident. CLADOCERA		20		1	2	50	71					
OSTRACODA		46	12	80	1	1	6		80	27	2	
Eucyclops serrulatus			4	46	27		134		30	230	33	
Xanthocnemis zealandica		1				1						
Oxyethira albiceps	(P)			1								
Paroxyethira hendersoni	(L)	11	2	7			1		23	7	16	
	(P)	115	3	2								
P. tillyardi	(L)	3			4					1		
precase HYDROPTILIDAE		16	1		5		7		7	6	1	
Triplectides cephalotes	(L)			3		2				2		
Oecetis unicolor	(L)	2		1			2		3	1		
Oecetis iti	(L)						1					
Nymphula nitens						3						
CHIRONOMIDAE			2	10		1	4		26	51	43	
Arrenurus sp.							1					
Piona uncata exigua		1	2	3	1	1	8		2			
Hydrozetes lemnae		32	13	62	12	2	9		4	4		
Trimalaconothrus novus	(A)	25		19	24		5		1	44	2	
	(L)	3	1	9	2		10		9	9	1	
Gyraulus corinna		5	2	2	10	15	31		83	39	20	
Potamopyrgus antipodarum		440	22	219	98	57	280		317	288	149	
Sphaerium novaezelandiae				8			3		26	16	4	
NEMATODA				1		1	6		16	25	10	

Appendix 3 Chironomids collected during the quantitative sampling program (see Appendix 2 for numbers of samples collected).

	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77	TOTAL
N*E* 2 m											
Ablabesmyia mala						1					1
Macropelopia/Gressittius spp.		4				1	2		1	1	9
Cricotopus spp.		7			1	3	10	6	34	10	71
Chironomus zealandicus				1							1
S*I* 1 m											
Ablabesmyia mala		8				1					9
Macropelopia/Gressittius spp.				4	3			3	2		12
Cricotopus spp.	2	3		7/1 pupa	6	27		23	1		69/1 pupa
Orthocladiinae A				4		5		3			12
Orthocladiinae B						1		3			4
Orthocladiinae C			1								1
Chironomus zealandicus								1			1
Tanytarsus vespertinus			1	15		8		4	3		31

Cont'd

	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77	TOTAL
S *M* 1 m											
Ablabesmyia mala		1			1 pupa						1/1 pupa
Macropelopia/Gressittius spp.	1					1	3		1		6
Cricotopus spp.	2			21/1 pupa	6		47	33	4		113/1 pupa
Orthocladiinae A				1		4	3	4	3		15
Orthocladiinae B	1							4			5
Orthocladiinae C			2		1						3
Tanytarsus vespertinus			10		1	3	25	14			53
E *E* 1 m											
Macropelopia/Gressittius spp.		2					6				8
Cricotopus spp.					2						2
Chironomus zealandicus			1								1
E *E* 2 m											
Ablabesmyia mala	2										2
Macropelopia/Gressittius spp.	4	2	7	5	6	2	9	11		1	47
Cricotopus spp.				3		1	4				8

Cont'd

	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77	TOTAL
WE 2 m											
Macropelopia/Gressittius spp.				9		2	4	1	3	5	24
Cricotopus spp.			1	4	6	13	56	2	22	11	115
Chironomus zealandicus				1				1			2
WE 3 m											
Macropelopia/Gressittius spp.									2		2
Cricotopus spp.	2					4	40		16		62
Syncricotopus pluriserialis						1 pupa					1 pupa
WE 4 m											
Cricotopus spp.					1			34	16		51
Chironomus zealandicus									1		1
WI 1 m											
Macropelopia/Gressittius spp.		12					2	11	4		29
Cricotopus spp.				1	4		20	33	37		95
Tanytarsus vespertinus							4	7	2		13

	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77	TOTAL
E *I* 1 m											
Pentaneura sp.										2	2
Ablabesmyia mala	2	2	1		2			2			9
Macropelopia/Gressittius spp.								2			2
Cricotopus spp.					14	6	17	8			45
E *M*											
Ablabesmyia mala			2								2
Cricotopus spp.				4	10	2	6			1	23
E *R*											
Cricotopus spp.	1		1			9					11
Orthocladiinae B	1										1
W *E* 1 m											
Macropelopia/Gressittius spp.		2	2	1	1		1		1		8
Cricotopus spp.						3	75	6	10		94
Tanytarsus vespertinus				1							1

Cont'd

Appendix 4.1 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from triplicate (n = 3) samples from *NE 2* during the quantitative sampling program (2 September 1976 - 3 October 1977, Appendix 2.1) and the pilot survey (14 April 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g dry wt of macrophyte).

	Pilot 14/4/76	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt	0.21	0.51	0.19	0.12	0.10	0.20	0.07	0.15	0.18	0.29	0.11
COELENTERATA	0.87(0.72)	0.66(0.50)	0.88(0.85)	0.75(0.67)	0.09(0.16)	0.29(0.15)	0.23(0.25)	0.51(0.48)	0.32(0.17)	-	1.00(1.00)
ANNELIDA	0.56(0.47)	0.85(0.56)	1.00(1.00)	0.52(0.49)	0.31(0.23)	0.26(0.32)	0.36(0.32)	0.60(0.88)	0.37(0.28)	0.21(0.82)	0.35(0.32)
CRUSTACEA	0.42(0.53)	0.55(0.82)	0.38(0.34)	0.38(0.39)	0.15(0.17)	0.27(0.35)	0.06(0.003)	0.22(0.45)	0.34(0.36)	0.24(0.48)	0.39(0.40)
INSECTA	0.67(0.66)	0.29(0.55)	0.74(0.71)	0.33(0.22)	1.00(1.00)	0.50(0.51)	0.26(0.33)	0.24(0.31)	0.06(0.16)	0.56(0.40)	0.16(0.16)
ACARINA	0.39(0.27)	1.00(1.00)	0.19(0.32)	0.36(0.36)	0.28(0.23)	0.06(0.47)	0.22(0.19)	0.18(0.77)	0.23(0.28)	1.00(1.00)	0.38(0.39)
MOLLUSCA	0.25(0.21)	0.40(0.21)	0.14(0.09)	0.17(0.11)	0.19(0.11)	0.37(0.20)	0.07(0.07)	0.31(0.11)	0.14(0.12)	0.34(0.32)	0.09(0.17)
Total Invertebrates	0.25(0.22)	0.48(0.17)	0.16(0.10)	0.21(0.13)	0.13(0.08)	0.16(0.04)	0.05(0.03)	0.20(0.32)	0.17(0.15)	0.25(0.41)	0.19(0.08)

Appendix 4.2 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from duplicate (n = 2) samples from *SI* during the quantitative sampling program (2 September 1976 - 3 October 1977, Appendix 2.2) and the pilot survey (14 April 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g wt of macrophyte).

	Pilot 14/4/76	2/11/76	2/3/77	8/4/77	13/7/77
Dry wt	0.35	0.16	0.41	0.06	0.60
COELENTERATA	0.75(0.87)	0(0.16)	0.18(0.84)	0.33(0.38)	1.00(1.00)
ANNELIDA	-	0.88(0.84)	0(0.41)	0.22(0.17)	0.50(0.85)
CRUSTACEA	0.71(0.85)	0(0.16)	0.28(0.14)	0.43(0.39)	0.31(0.77)
INSECTA	0.35(0.004)	0.10(0.07)	0.43(0.71)	0.09(0.03)	0.33(0.33)
ACARINA	0.10(0.43)	0.02(0.15)	0.10(0.49)	0(0.06)	1.00(1.00)
MOLLUSCA	0.59(0.30)	0.06(0.10)	0.01(0.42)	0.26(0.31)	0.33(0.33)
Total Invertebrates	0.53(0.21)	0.23(0.07)	0.03(0.43)	0.15(0.21)	0.006(0.60)

Appendix 4.3 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from triplicate (n = 3) samples from *EE* 2 m during the quantitative sampling program (2 September 1976 - 3 October 1977, Appendix 2.5) and the pilot survey (14 april 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g dry wt of macrophyte).

	Pilot 14/4/76	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	3/10/77
Dry wt	0.08	0.01	0.03	0.19	0.15	0.24	0.16	0.08	0.27	0.20
COELENTERATA	0.45(0.42)	1.00(1.00)	0.76(0.75)	0.15(0.23)	0.24(0.42)	0.51(0.28)	0.29(0.16)	0.46(0.52)	0.70(0.52)	0.64(0.60)
ANNELIDA	0.81(1.01)	0.97(0.97)	0.84(0.84)	0.43(0,50)	0.50(0.75)	0.29(0.24)	0.66(0.67)	0.50(0.46)	0.35(0.65)	0.33(0.45)
CRUSTACEA	0.43(0.54)	0.18(0.19)	0.61(0.61)	0.35(0.58)	0.29(0.22)	0.21(0.03)	0.36(0.42)	0.47(0.44)	0.29(0.46)	0.26(0.42)
INSECTA	0.18(0.12)	0.13(0.34)	0.13(0.15)	0.14(0.50)	0.44(0.69)	0.42(0.36)	0.21(0.31)	0.42(0.41)	0.26(0.35)	0.24(0.30)
ACARINA	0.19(0.43)	0.45(0.44)	0.17(0.19)	0.13(0.30)	0.38(0.45)	0.30(0.11)	0.25(0.33)	0.64(0.60)	0.17(0.52)	0.23(0.26)
MOLLUSCA	0.26(0.29)	0.25(0.25)	0.22(0.24)	0.12(0.27)	0.09(0.25)	0.36(0.25)	0.21(0.26)	0.11(0.13)	0.17(0.17)	0.17(0.33)
Total Invertebrates	0.24(0.26)	0.23(0.23)	0.21(0.23)	0.11(0.25)	0.08(0.26)	0.35(0.22)	0.21(0.25)	0.16(0.16)	0.12(0.23)	0.10(0.27)

Appendix 4.4 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from duplicate (n = 2) samples from *EI* during the quantitative sampling program (2 September 1976 - 3 October 1977, Appendix 2.6) and the pilot survey (14 April 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g dry wt of macrophyte).

	Pilot 14/4/76	2/9/76	2/11/76	2/12/76	2/3/77	20/6/77
Dry wt	0.22	0.09	0.14	0.40	0.33	0.25
COELENTERATA	0.90(0.83)	1.00(1.00)	-	-	0.52(0.22)	1.00(1.00)
ANNELIDA	1.00(1.00)	-	-	1.00(1.00)	1.00(1.00)	0(0.25)
CRUSTACEA	0.72(0.86)	0.80(0.77)	0.52(0.62)	0.34(0.07)	0.90(0.81)	0.33(0.53)
INSECTA	0.58(0.70)	0.83(0.81)	1.00(1.00)	0.51(0.14)	0.90(0.81)	0.50(0.29)
ACARINA	0.77(0.91)	0.90(0.89)	0.73(0.79)	0.23(0.19)	0.71(0.50)	1.00(1.00)
MOLLUSCA	0.48(0.60)	0.80(0.77)	0.44(0.54)	0.85(0.67)	0.71(0.49)	0.02(0.27)
Total Invertebrates	0.51(0.64)	0.83(0.80)	0.54(0.63)	0.49(0.11)	0.76(0.58)	0.15(0.39)

Appendix 4.5 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from replicate (n = 3) samples from *WE* 2 m during the quantitative sampling program (2 September 1976 - 3 October 1977, Appendix 2.10) and the pilot survey (14 April 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g dry wt of macrophyte).

	Pilot 14/4/76	2/9/76	2/11/76	2/12/76	20/1/77	2/3/77	8/4/77	10/5/77	20/6/77	13/7/77	3/10/77
Dry wt	0.15	0.28	0.15	0.18	0.28	0.06	0.15	0.004	0.07	0.38	0.55
COELENTERATA	0.81(0.75)	0.72(0.57)	0.35(0.28)	-	0.13(0.32)	0.29(0.35)	0.31(0.26)	0.62(0.62)	0.26(0.31)	0.98(0.97)	0.27(0.44)
ANNELIDA	1.00(1.05)	0.15(0.31)	0.48(0.38)	1.00(1.00)	0.21(0.30)	0.21(0.26)	0.42(0.19)	0.72(0.72)	0.13(0.13)	0.63(0.29)	0.30(0.47)
CRUSTACEA	0.60(0.57)	0.05(0.24)	0.51(0.48)	0.62(0.61)	0.27(0.15)	0.36(0.42)	0.30(0.07)	0.26(0.26)	0.17(0.21)	0.31(0.49)	0.38(0.77)
INSECTA	0.59(0.60)	0.29(0.36)	1.00(1.00)	0.58(0.54)	0.40(0.47)	0.05(0.05)	0.11(0.36)	0.62(0.61)	0.33(0.36)	0.57(0.75)	0.60(0.70)
ACARINA	0.35(0.45)	0.66(0.52)	0.30(0.32)	0.18(0.33)	0.64(0.64)	0.13(0.18)	0.11(0.18)	0.26(0.26)	0.58(0.59)	0.50(0.67)	0.86(0.51)
MOLLUSCA	0.38(0.33)	0.17(0.09)	0.32(0.17)	0.27(0.16)	0.19(0.09)	0.14(0.15)	0.04(0.25)	0.13(0.14)	0.14(0.17)	0.18(0.18)	0.34(0.19)
Total Invertebrates	0.26(0.36)	0.13(0.13)	0.18(0.03)	0.15(0.20)	0.06(0.21)	0.12(0.18)	0.13(0.12)	0.18(0.17)	0.13(0.19)	0.04(0.26)	0.22(0.28)

Appendix 4.6 Indices of precision (D) for macrophyte dry weight and invertebrate density obtained from duplicate (n = 2) samples from *EM*, *ER* and *WI* from the quantitative sampling program (2 September 1976 - 3 October 1977, Appendices 2.7, 2.8 and 2.13) and the pilot survey (14 April 1976, Appendix 1) with densities expressed as numbers/sample (numbers/g dry wt of macrophyte).

	EM 2/11/76	*EM* 2/12/76	*ER* 14/4/76	*ER* 2/12/76	*WI* 2/11/76
Dry wt	0.13	0.19	0.22	0.04	0.22
COELENTERATA	1.00(1.00)	0.38(0.52)	-	1.00(1.00)	0(0.22)
ANNELIDA	-	1.00(1.00)	1.05(1.17)	0(0.04)	0.45(0.26)
CRUSTACEA	1.00(1.00)	0.02(0.20)	0.40(0.34)	0(0.04)	0.78(0.85)
INSECTA	0.33(0.44)	0.15(0.33)	0.22(0.05)	0.22(0.26)	0.43(0.59)
ACARINA	0(0.13)	0.03(0.22)	0.37(0.20)	0.11(0.15)	0.71(0.80)
MOLLUSCA	0.12(0.007)	0.34(0.17)	0.33(0.11)	0.25(0.22)	0.81(0.87)
Total Invertebrates	0.05(0.08)	0.22(0.04)	0.32(0.10)	0.15(0.11)	0.73(0.82)

Appendix 5.1 Adult Chironomidae collected by hand-net sweeps adjacent to Lake Grasmere, 2 November 1976 - 7 December 1978. All collections from the southern end of the lake *except* 14-20/1/77 (north and east), 27/10/78 (north and south), 17/11/78 and 7/12/78 (north). (males, females)

	1976		1977							1978				
	2/11	2/12	14-20/1	2/3	8/4	10/5	3/10	29/11	26/12	11/4	9/10	27/10	17/11	7/12
TANYPODINAE														
Ablabesmyia mala		0,1											0,2	0,1
Gressittius antarcticus			7,1						0,1				1,2	0,1
Macropelopia umbrosa		2,1	2,7						3,0					2,14
PODONOMINAE														
Parochlus sp.		0,1	0,2										2,13	0,3
ORTHOCLADIINAE														
Syncricotopus pluriserialis	0,1	0,4	1,0	0,1	0,2	1,1			1,3	0,11		30,18	9,5	2,3
Cricotopus zealandicus													0,2	
Metriocnemis lobifer												3,0	1,0	
Eukiefferiella sp.				1,0			2,7					70,31	24,10	
"black species"												1,0		9,29
CHIRONOMINAE														
Chironomus zealandicus		5,5	3,2		4,4	1,1	1,1	3,1	9,7	3,2	9,2	23,7	8,1	19,23
Xenochironomus canterburyensis					2,0				5,0	1,0	1,0		1,0	5,3
Cladopelma curtivalva			3,5						2,1					
Polypedilum canum													10,0	1,2
Tanytarsus vespertinus			5,0	1,0		2,0	114,6					1,0		
Calopsectra funebris											1,0			

Appendix 5.2 Adult Chironomidae collected by light trapping at the southern end of Lake Grasmere. (males,females)
* = generator-powered mercury discharge lamp (160W)
** = battery-powered (12V) fluorescent tube (white light)
All times given are N.Z.D.T.

	29/11/77			26/12/77				25/1/78	7/12/78
	2045-2245h	2245-2345h	2345-0045h	2200-2300h		2300-2400h		1h between 2300 & 0300h	
	*	*	*	**	*	**	*	**	*
TANYPODINAE									
Ablabesmyia mala			1,2		0,1				0,1
Gressittius antarcticus		0,1	0,235	0,13	1,24	0,5	0,7	0,15	0,47
Macropelopia languidus				0,1	0,2				
M. umbrosa				0,11	0,5	0,2	0,1		0,41
PODONOMINAE									
Parochlus sp.						0,1	1,1		
ORTHOCLADIINAE									
Syncricotopus pluriserialis	0,2	0,3	0,99	0,51	0,15	0,10	0,15	0,46	0,11
Cricotopus zealandicus								0,1	
CHIRONOMINAE									
Chironomus zealandicus	5,3	1,2	7,383	0,11	0,1	5,1	2,4	0,2	18,40
Xenochironomus canterburyensis			2,7					0,1	10,2
Cladopelma curtivalva								0,1	
Polypedilum pavidus					0,1				1,12
Tanytarsus vespertinus						1,0		0,1	2,0

Appendix 5.3 Adult Trichoptera collected by hand-net sweeps adjacent to Lake Grasmere, 2 November 1976 - 7 December 1978. Collection site details given in Appendix 5.1 (males,females).

	1976		1977							1978				
	2/11	2/12	14-20/1	2/3	8/4	10/5	3/10	29/11	26/12	11/4	9/10	27/10	17/11	7/12
HYDROPSYCHIDAE														
Aoteapsyche colonica		2,2												1,0
A. tepoka		1,0												
CONOESUCIDAE														
Pycnocentrodes aureola	8,4	0,1	8,1					9,0	0,1				1,0	15,0
HYDROPTILIDAE														
Oxyethira albiceps		0,1	0,1	0,2		0,1		0,1				2,1	5,1	4,1
Paroxyethira hendersoni	1,0	17,27	5,7	65,9	10,3	6,2	37,4	90,18	8,3	9,18	53,5	83,4	9,3	0,2
P. tillyardi			44,24	0,2					0,1					3,1
LEPTOCERIDAE														
Oecetis unicolor			10,12											
Hudsonema amabilis		2,15	6,33					0,1	1,4				4,0	10,1
Triplectides cephalotes			0,1											
T. obsoleta		0,1		1,3					1,0					

Appendix 5.4 Adult Trichoptera collected by light trapping at the southern end of Lake Grasmere. (males,females)
* = generator-powered mercury discharge lamp (160W)
** = battery-powered (12V) fluorescent tube (white light)
All times given are N.Z.D.T.

	29/11/77			26/12/77				25/1/78	7/12/78
	2045-2245h	2245-2345h	2345-0045h	2200-2300h		2300-2400h		1h between 2300 & 0300h	
	*	*	*	**	*	**	*	**	*
HYDROPSYCHIDAE									
Aoteapsyche colonica		1,0					2,0	2,0	1,0
A. tepoka	6,1		13,0		3,0		7,0	9,1	4,0
POLYCENTROPODIDAE									
Polyplectropus puerilis							2,0	1,0	18,9
RHYACOPHILIDAE									
Hydrobiosis umbripennis		1,2	10,17		3,6		1,6	1,0	
H. parumbripennis					0,6				
H. harpidiosa			4,0						1,0
H. frater		2,0	11,0		3,0		5,1		0,1
H. clavigera			3,0		1,0	1,0			
Psilochorema bidens		1,0	2,0						
Ps. leptoharpax	2,1	1,0	17,0		1,0		1,0	0,2	
Costachorema xanthoptera	0,2	4,0	15,17		2,0	1,0	1,1		1,0
C. callistum							1,0		
CONOESUCIDAE									
Pycnocentrodes aureola	1,3				2,3	5,2	8,10	4,8	111,329
HYDROPTILIDAE									
Oxyethira albiceps	0,3	0,1	21,45	4,22	30,62	19,24	150,183	0,11	38,36
Paroxyethira hendersoni	21,2	17,2	93,160[s]	20,13	134,40	6,37	63,28	4,22	24,16
P. tillyardi								1,1	
LEPTOCERIDAE									
Oecetis unicolor				4,0	5,0		5,0	16,3	21,2
Hudsonema amabilis		1,1	2,0	1,0	4,2	3,1	15,12	4,8	202,57
Triplectides cephalotes							4,0	1,0	2,0

s = subsample

Appendix 5.5 Adult Tipulidae collected by hand-net sweeps adjacent to Lake Grasmere, 2 December 1976 - 2 February 1979. (Collection site details given in Appendix 5.1.)

	2/12/76	20/1/77	2/3/77	3/10/77	26/12/77	11/4/78	9/10/78	27/10/78	17/11/78	7/12/78	2/2/79
Zelandotipula sp.			1								1
Leptotarsus (Macromastix) minutissima											1
Limonia (Dicranomyia) otagensis	1										
L. (D.) sp. A									1		
L. (D.) sp. C		1									
?Metalimnophila										1	
Aphrophila neozelandica	1										
Erioptera (Trimicra) pilipes		20+		1	1	1	1	9	1		1
Amphineurus 4 spp.	1	1			1			1	1		1
Molophilus sp.						1		1	1		1

Appendix 5.6 Adult Tipulidae collected by light trapping at the southern end of Lake Grasmere.
* = generator-powered mercury discharge lamp (160W)
** = battery-powered (12V) fluorescent tube (white light)
All times given are N.Z.D.T.

	26/12/77		25/1/78	7/12/78
	2200-2300h	2300-2400h	1h between 2300 & 0300h	
	*	*	**	*
Limonia (Dicranomyia) ? vicarians				1
Aphrophila neozelandica	1		1	
Erioptera pilipes	1	1		1
Amphineurus 2 sp.	2	1	1	

Appendix 5.7 Adults of Odonata, Plecoptera and Ephemeroptera collected by hand-net sweeps adjacent to Lake Grasmere, 2 November 1976 - 7 December 1978. (Collection site details given in Appendix 5.1) (males,females)

	1976			1977				1978			
	2/11	2/12	14-20/1	2/3	8/4	3/10	29/11	9/10	27/10	17/11	7/12
ODONATA											
Xanthocnemis zealandica		2,0	16,13	7,6	1,0			5,4			
PLECOPTERA											
Zelandobius furcillatus		3,0	1,0			1,0		4,1	5,4	7,0	4,0
EPHEMEROPTERA											
Deleatidium sp.	0,2	0,6				0,1	44,1				

1♀ *Deleatidium* light trapped 26/12/77, 2200-2300h NZDT in mercury vapour trap.

Appendix 6.1

(a) Percentage composition of the faecal material of final instar *Paroxyethira hendersoni*, in terms of major food categories, on a projected area basis; and

(b) generic composition (% by numbers) of the diatom category. * = <0.1%.

(September 1976 - November 1977 and overall)

	1976			1977				Over-
	2/9	2/11	2/12	20/1	8/4	20/6	18/8	21/11	all
(a)									
Diatoms	54.8	37.5	53.1	49.9	41.0	48.6	67.5	52.0	50.0
Detritus	19.5	30.6	14.3	22.5	18.0	11.3	14.5	24.4	18.9
Macrophyte	7.9	5.9	4.4	9.4	4.7	14.8	2.4	13.5	7.2
Filamentous algae	17.8	26.0	28.2	17.3	26.2	16.1	15.6	10.1	21.3
S.R.T's	-	-	-	0.9	10.1	9.2	-	-	2.7
Number of larvae examined	12	11	10	10	10	9	7	4	72
(b)									
Cocconeis	34.7	57.6	73.8	59.1	93.9	82.3	68.9	28.1	63.0
Gomphonema	27.9	13.6	4.4	0.9	1.6	0.3	14.1	62.9	15.8
Epithemia	6.6	15.7	17.0	34.8	1.1	5.4	1.5	0.4	7.9
Synedra	11.2	-	0.3	-	0.3	1.3	5.0	2.7	3.5
Asterionella	6.2	-	-	-	-	3.8	6.2	-	2.6
Fragilaria	2.7	5.8	-	-	2.1	3.8	1.5	5.8	2.6
Rhoicosphenia	4.2	7.3	4.4	4.3	0.3	-	-	-	2.3
Cymbella	5.2	-	-	-	-	0.3	0.3	-	1.1
Cyclotella	1.2	-	-	0.9	0.8	1.4	2.6	-	0.7
Melosira	-	-	-	-	-	0.7	2.1	-	0.7
Navicula	-	-	-	-	-	0.7	-	-	*

Appendix 6.2

(a) Percentage composition of the faecal material of final instar *Paroxyethira tillyardi*, in terms of major food categories, on a projected area basis; and

(b) generic composition (% by numbers) of the diatom category.

(September 1976 - November 1977 and overall)

	1976			1977				
	2/9	2/11	2/12	8/4	20/6	18/8	21/11	Overall
(a)								
Diatoms	58.1	40.5	57.0	31.7	23.5	45.0	31.3	41.0
Detritus	17.2	33.5	21.5	21.1	23.5	33.9	33.9	26.4
Macrophyte	4.5	2.2	9.1	11.9	13.1	7.3	7.5	8.0
Filamentous algae	20.2	23.8	12.4	25.2	39.2	13.8	27.3	23.1
S.R.T's	-	-	-	10.1	0.7	-	-	1.5
Number of larvae examined	12	10	10	9	10	7	16	74
(b)								
Cocconeis	75.3	61.6	74.6	82.0	95.5	91.3	76.4	77.8
Epithemia	5.8	21.2	8.5	4.6	0.9	1.0	3.6	7.3
Rhoicosphenia	3.5	3.4	12.3	9.3	1.8	3.8	-	6.2
Gomphonema	13.1	10.3	2.9	0.7	-	2.9	12.7	6.1
Fragilaria	-	-	0.7	2.7	0.9	1.0	5.5	1.0
Synedra	1.2	2.7	-	-	-	-	-	0.7
Cyclotella	0.4	-	0.7	-	0.9	-	-	0.4
Navicula	0.8	-	-	0.7	-	-	-	0.3
Cymbella	-	0.7	-	-	-	-	-	0.1
Pinnularia	-	-	0.4	-	-	-	-	0.1

Appendix 6.3 Percentage composition of the faecal material of *Hudsonema amabilis*, in terms of major food categories, on a projected area basis (2 September 1976 - 21 November 1977 and overall) for instars 2 - 5.

	2nd instar				3rd instar					
	8 Apr.	20 Jun.	18 Aug.	OVERALL	2 Sep.	2 Nov.	8 Apr.	20 Jun.	18 Aug.	OVERALL
Diatoms	27.2	26.2	33.9	28.8	10.8	42.3	40.1	23.6	27.3	36.3
Detritus	50.6	40.3	52.3	46.3	32.9	27.5	34.9	20.9	28.3	25.9
Macrophyte	9.2	4.0	2.0	4.4	28.8	13.8	13.2	19.6	3.4	14.1
Filamentous algae	12.3	10.1	11.8	11.1	11.0	16.5	11.0	23.4	11.9	16.6
Animal	-	0.4	-	0.2	16.5	-	0.7	2.5	0.8	2.6
S.R.T's	0.7	19.0	-	9.1	-	-	-	9.9	28.3	4.5
Number of larvae examined	2	3	6	11	3	1	2	5	7	18

	4th instar								5th instar							
	2 Sep.	2 Nov.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL	2 Sep.	2 Nov.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Diatoms	56.2	30.6	35.5	39.0	30.9	48.4	32.2	42.4	42.5	32.3	32.8	22.4	32.6	38.7	24.9	33.5
Detritus	17.8	25.7	21.3	19.8	24.2	21.8	23.3	20.9	17.4	18.4	19.8	13.5	24.0	22.2	20.8	16.8
Macrophyte	20.2	21.2	14.9	20.9	12.2	12.0	13.5	16.6	34.5	29.5	21.3	55.2	19.9	22.1	19.1	29.0
Filamentous algae	4.3	9.1	4.3	5.7	15.9	12.7	15.6	9.4	6.1	8.3	6.4	5.0	10.3	3.1	14.3	8.2
Animal	1.5	13.4	21.3	19.4	10.3	4.8	12.7	9.2	9.5	10.4	19.5	4.0	11.4	8.8	19.6	12.4
S.R.T's	-	-	2.7	-	6.5	0.3	2.8	1.5	-	-	0.2	-	1.9	0.1	1.4	0.4
Number of larvae examined	10	4	1	10	10	10	5	50	10	10	10	6	10	10	10	66

Appendix 6.4 Generic composition (% by numbers) of diatoms in the faeces of *Hudsonema amabilis* (2 September 1976 - 21 November 1977) * = < 0.1%. (See Appendix 6.3 for number of larvae examined.)

	2nd instar				3rd instar					
	8 Apr.	20 Jun.	18 Aug.	OVERALL	2 Sep.	2 Nov.	8 Apr.	20 Jun.	18 Aug.	OVERALL
Cocconeis	76.9	65.4	95.5	81.2	66.7	36.6	84.8	60.5	63.9	63.6
Asterionella	-	3.8	-	1.4	6.8	2.4	-	12.8	16.5	9.3
Rhoicosphenia	11.5	9.6	-	5.6	8.6	12.2	2.2	9.3	4.1	7.2
Epithemia	7.7	7.7	-	4.2	6.8	24.4	10.9	7.0	6.2	9.0
Cyclotella	-	3.8	-	1.4	-	-	2.2	1.2	-	0.5
Gomphonema	-	3.8	1.5	2.1	6.8	-	-	-	2.1	2.6
Fragilaria	3.9	1.9	-	1.4	0.9	17.1	-	2.3	3.1	3.4
Navicula	-	-	-	-	0.9	4.9	-	3.5	2.1	2.1
Synedra	-	1.9	-	0.7	1.7	2.4	-	-	2.1	1.3
Cymbella	-	1.9	-	0.7	-	-	-	2.3	-	0.5
Diatoma	-	-	-	-	0.9	-	-	-	-	0.3
Rhopalodia	-	-	3.0	1.4	-	-	-	-	-	-
Pinnularia	-	-	-	-	-	-	-	1.2	-	0.3

	4th instar								5th instar							
	2 Sep.	2 Nov.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL	2 Sep.	2 Nov.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Cocconeis	66.5	47.8	65.2	67.8	43.0	59.7	84.0	62.9	69.4	69.9	49.6	85.2	68.5	53.3	77.9	65.8
Asterionella	5.0	-	-	-	32.3	14.5	-	9.2	9.2	0.7	0.8	1.7	11.1	18.3	-	6.2
Rhoicosphenia	3.3	18.5	21.7	5.3	13.3	6.6	2.7	6.5	7.1	15.4	9.8	2.9	2.7	2.4	2.3	7.0
Epithemia	5.8	13.0	8.7	17.4	2.5	4.5	4.8	7.1	5.0	8.9	3.9	5.3	4.4	4.2	5.8	5.3
Cyclotella	0.8	-	-	1.6	0.4	0.5	3.2	1.2	-	0.2	29.7	-	4.1	1.1	0.3	6.3
Gomphonema	9.8	9.8	-	3.9	1.8	4.0	1.6	5.8	3.9	2.8	2.3	0.8	1.6	2.1	2.9	2.7
Fragilaria	4.0	2.2	-	-	1.4	5.9	1.1	3.1	2.3	0.4	2.3	0.8	3.8	7.2	1.2	2.5
Navicula	3.0	5.4	-	1.3	0.4	1.4	0.5	1.9	0.8	0.9	1.5	-	1.6	1.6	4.1	1.4
Synedra	1.7	3.3	-	0.3	1.1	2.1	-	1.4	0.9	-	0.3	0.4	1.6	6.1	0.6	1.2
Cymbella	0.8	-	-	1.6	0.4	0.7	0.5	0.8	0.4	0.2	-	0.4	-	1.6	0.3	0.4
Eunotia	-	-	-	0.7	-	-	1.6	0.2	-	0.7	-	-	-	1.6	3.2	0.6
Diatoma	-	-	-	0.7	-	-	-	*	1.0	-	-	2.5	-	-	-	0.5
Melosira	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	1.5	0.2
Rhopalodia	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	*
Pinnularia	-	-	-	-	-	-	-	-	-	-	-	-	0.3	0.3	-	*

Appendix 6.5 Percentage composition of the faecal material of *Triplectides cephalotes*, in terms of major food categories, on a projected area basis (2 September 1976 - 21 November 1977 and overall) for instars 2 - 5.

	2nd instar	3rd instar				4th instar						
	8 Apr. = OVERALL	2 Nov.	8 Apr.	18 Aug.	OVERALL	2 Nov.	2 Dec.	20 Jan.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Diatoms	17.5	22.3	9.7	21.5	20.0	28.0	35.5	21.6	24.9	18.8	25.3	29.1
Detritus	24.0	32.5	23.7	17.1	19.7	12.0	11.8	4.6	21.0	16.1	12.0	12.1
Macrophyte	38.1	25.4	23.7	38.9	35.5	54.1	36.4	68.3	40.3	47.2	51.2	47.4
Filamentous algae	10.0	-	23.7	11.4	11.8	5.9	3.6	4.6	12.4	17.2	11.5	6.4
Animal	5.0	19.8	11.8	4.9	7.4	-	7.7	-	-	-	-	2.6
S.R.T's	5.4	-	7.5	6.1	5.6	-	6.8	0.9	1.4	0.8	-	2.4
Number of larvae examined	2	1	1	6	8	8	8	1	2	2	2	23

	5th instar								
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Diatoms	62.3	16.3	22.2	22.8	15.1	17.5	41.0	8.1	22.1
Detritus	12.7	5.7	12.9	7.4	11.1	11.2	14.6	11.2	9.6
Macrophyte	21.7	71.9	58.9	55.4	43.7	59.8	31.7	76.1	57.9
Filamentous algae	2.3	1.4	5.0	5.4	26.6	4.8	11.2	-	5.3
Animal	1.0	4.6	0.3	9.0	-	1.2	-	4.1	4.1
S.R.T's	-	-	0.7	0.1	3.6	5.6	1.5	0.5	1.0
Number of larvae examined	4	5	4	6	3	4	2	3	31

Appendix 6.6 Generic composition (% by numbers) of diatoms in the faeces of *Triplectides cephalotes* (2 September 1976 - 21 November 1977) * = < 0.1%. (See Appendix 6.5 for number of larvae examined.)

	2nd instar	3rd instar				4th instar						
	8 Apr. = OVERALL	2 Nov.	8 Apr.	18 Aug.	OVERALL	2 Nov.	2 Dec.	20 Jan.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Cocconeis	76.7	82.6	81.2	34.5	43.2	74.4	80.5	80.0	79.6	21.7	45.2	74.4
Gomphonema	-	4.4	6.3	17.8	15.5	9.4	5.1	-	3.7	30.0	-	7.6
Rhoicosphenia	3.3	-	6.3	5.8	5.2	4.9	3.0	1.8	1.9	3.3	-	3.6
Epithemia	6.7	13.0	-	3.4	4.2	4.3	5.5	5.5	7.4	5.0	48.4	6.1
Fragilaria	-	-	6.3	26.4	22.1	1.5	2.6	3.6	1.9	13.3	-	2.6
Asterionella	3.3	-	-	2.9	2.3	2.3	0.2	-	1.9	5.0	-	1.3
Cyclotella	-	-	-	-	-	-	0.4	7.3	1.9	5.0	6.5	0.9
Synedra	6.7	-	-	5.8	4.7	0.8	-	-	1.9	-	-	0.4
Cymbella	3.3	-	-	1.1	0.9	2.1	0.4	-	-	3.3	-	1.2
Navicula	-	-	-	1.1	0.9	0.2	-	1.8	-	13.3	-	0.8
Melosira	-	-	-	-	-	-	2.3	-	-	-	-	1.0
Opephora	-	-	-	-	-	-	0.2	-	-	-	-	*
Pinnularia	-	-	-	0.6	0.5	0.2	-	-	-	-	-	*
Achnanthes	-	-	-	0.6	0.5	-	-	-	-	-	-	-

	5th instar								
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	18 Aug.	21 Nov.	OVERALL
Cocconeis	27.0	84.3	79.5	74.9	72.8	57.9	36.8	74.2	63.2
Gomphonema	20.4	1.8	1.8	1.5	2.5	2.9	27.1	3.1	7.5
Rhoicosphenia	31.8	-	6.4	0.9	3.7	5.0	4.2	2.1	8.1
Epithemia	5.1	2.2	2.7	9.4	6.2	5.7	2.8	7.2	5.5
Fragilaria	2.7	0.7	2.3	-	8.6	5.7	6.2	1.0	2.3
Asterionella	6.3	9.9	5.0	1.1	-	18.6	-	7.2	5.5
Cyclotella	0.9	-	-	12.2	-	2.9	2.1	5.2	4.1
Synedra	0.9	0.7	-	-	3.7	0.7	13.9	-	1.7
Cymbella	3.0	0.4	1.4	-	-	-	4.2	-	1.1
Navicula	0.9	-	0.5	-	1.2	-	2.8	-	0.5
Opephora	0.3	-	0.5	-	1.2	0.7	-	-	0.2
Diatoma	0.3	-	-	-	-	-	-	-	*
Tabellaria	0.3	-	-	-	-	-	-	-	*

Appendix 6.7 (a) Percentage composition of the faecal material of *Nymphula nitens*, in terms of major food categories, on a projected area basis (25 July 1976 - 18 August 1977 and overall), for each of three size classes; and
(b) Generic composition (% by numbers) of the diatom category.

	Size group 1					Size group 2							Size group 3				
	25 Jul.	2 Sep.	2 Nov.	18 Aug.	OVERALL	25 Jul.	2 Sep.	2 Nov.	8 Apr.	20 Jun.	18 Aug.	OVERALL	2 Nov.	20 Jan.	20 Jun.	18 Aug.	OVERALL
(a)																	
Diatoms	28.7	6.9	6.8	7.3	11.4	14.1	16.3	10.2	14.5	13.9	12.6	13.5	9.9	17.6	20.5	3.8	14.4
Detritus	36.8	53.8	22.2	30.0	40.7	15.5	20.5	22.3	5.3	35.7	22.4	21.4	18.6	3.2	31.6	13.0	10.7
Macrophyte	32.9	23.5	66.6	51.8	38.0	69.4	51.5	60.0	75.7	45.5	60.5	57.4	65.0	76.5	47.9	75.4	71.0
Filamentous algae	1.6	15.9	4.4	10.9	9.9	0.9	11.7	7.5	4.5	5.0	4.5	7.7	6.5	2.7	-	7.9	3.7
Number of larvae examined	3	3	1	1	8	2	6	9	2	6	3	28	3	2	1	1	7
(b)																	
Cocconeis	68.8	62.5	55.6	100.0	68.4	92.4	41.4	82.1	89.3	85.4	77.8	68.2	96.6	99.1	90.5	54.5	96.5
Diatoma	-	-	-	-	-	-	25.4	-	1.2	-	-	10.2	-	-	-	-	-
Gomphonema	16.9	10.0	-	-	12.5	-	9.0	1.7	2.4	0.8	-	4.4	1.7	0.3	-	-	0.4
Epithemia	2.6	5.0	11.1	-	3.7	3.8	2.1	8.5	3.6	4.1	14.8	4.5	1.7	0.3	2.7	27.3	1.5
Asterionella	-	-	-	-	-	-	14.4	0.9	-	1.6	-	6.1	-	-	2.7	-	0.4
Fragilaria	9.1	15.0	-	-	9.6	-	0.8	1.7	-	6.5	-	1.6	-	-	-	-	-
Synedra	-	2.5	11.1	-	1.5	3.8	3.7	1.7	-	-	7.4	2.3	-	-	-	18.2	0.4
Rhoicosphenia	2.6	2.5	11.1	-	2.9	-	1.2	0.9	2.4	-	-	1.0	-	-	2.7	-	0.4
Cymbella	-	-	11.1	-	0.7	-	0.8	1.7	1.2	0.8	-	1.0	-	0.3	1.3	-	0.4
Navicula	-	-	-	-	-	-	0.8	0.9	-	-	-	0.5	-	-	-	-	-
Cyclotella	-	2.5	-	-	0.7	-	-	-	-	0.8	-	0.2	-	-	-	-	-
Stephanodiscus	-	-	-	-	-	-	0.4	-	-	-	-	0.2	-	-	-	-	-

Appendix 6.8 Percentage composition of the faecal material of *Xanthocnemis zealandica*, in terms of major food categories, on a projected area basis (2 September 1976 - 21 November 1977 and overall) for three size classes.

	Size class 1						Size class 2						
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	20 Jun.	OVERALL	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	OVERALL
Diatoms	19.7	18.6	17.5	14.6	24.2	20.3	35.1	21.8	21.9	6.0	12.5	15.1	21.1
Detritus	11.6	9.1	12.1	24.9	17.1	10.1	9.1	12.8	8.7	16.8	12.5	12.7	11.3
Macrophyte	7.6	3.9	4.2	5.0	7.3	5.1	6.9	4.9	3.3	6.9	7.3	6.0	5.6
Filamentous algae	8.6	4.4	5.0	0.3	3.7	5.9	3.5	5.8	3.7	5.2	6.4	6.1	5.0
Animal	52.6	64.0	61.2	54.7	47.5	58.5	45.4	54.7	62.1	65.0	56.0	58.7	55.9
S.R.T's	-	-	-	0.5	0.2	0.1	-	-	0.3	0.1	5.4	1.4	1.1
Number of larvae examined	10	3	7	2	4	26	10	10	10	3	10	10	53

	Size class 3							
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	21 Nov.	OVERALL
Diatoms	36.5	26.0	18.5	11.1	6.4	12.6	17.1	16.7
Detritus	17.8	13.5	12.4	19.1	6.9	12.7	12.7	14.9
Macrophyte	1.8	2.4	5.6	5.1	1.2	6.6	4.3	4.8
Filamentous algae	2.1	2.0	3.1	3.5	9.2	7.4	4.5	4.0
Animal	41.9	56.1	59.7	61.0	76.3	60.1	61.2	59.4
S.R.T's	-	-	0.7	0.2	-	0.6	0.1	0.3
Number of larvae examined	2	8	10	10	1	8	8	47

Appendix 6.9 Generic composition (% by numbers) of diatoms in the faeces of *Xanthocnemis zealandica* (2 September 1976 - 21 November 1977) * = < 0.1%. (See Appendix 6.8 for number of larvae examined.)

	Size class 1						Size class 2						
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	20 Jun.	OVERALL	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	OVERALL
Cocconeis	53.4	91.2	83.0	79.6	69.9	72.4	51.3	72.0	86.4	87.1	73.5	64.8	69.3
Fragilaria	6.4	1.8	4.0	10.2	5.8	5.1	9.5	6.4	5.5	-	3.4	10.9	7.3
Epithemia	6.8	0.9	4.5	4.1	11.5	6.0	2.5	5.6	4.1	9.7	8.8	8.8	5.1
Synedra	17.4	2.7	0.9	-	-	5.9	13.1	4.6	1.0	-	3.4	3.1	5.7
Asterionella	5.1	-	1.8	-	2.6	2.6	12.0	2.3	0.5	-	5.4	1.7	4.8
Cymbella	4.2	0.9	0.5	-	3.2	2.2	6.6	4.1	0.7	-	0.5	1.4	3.1
Cyclotella	-	-	0.9	-	1.9	0.6	1.3	0.3	0.7	-	2.5	5.8	1.6
Gomphonema	4.2	2.7	2.2	-	0.6	2.4	1.6	2.8	0.7	3.2	1.5	2.7	1.7
Rhoicosphenia	1.3	-	0.9	6.1	-	1.0	0.5	1.5	0.3	-	1.0	-	0.6
Navicula	1.3	-	-	-	-	0.4	0.3	0.5	-	-	-	-	0.2
Melosira	-	-	-	-	-	-	1.1	-	-	-	-	-	0.3
Pinnularia	-	-	0.5	-	-	0.1	-	-	0.2	-	-	1.0	0.2
Tabellaria	-	-	0.9	-	4.5	1.2	0.2	-	-	-	-	-	*

	Size class 3							
	2 Sep.	2 Nov.	2 Dec.	20 Jan.	8 Apr.	20 Jun.	21 Nov.	OVERALL
Cocconeis	55.9	66.3	82.9	81.3	88.9	67.6	65.9	73.3
Fragilaria	3.2	8.0	4.8	2.8	-	5.9	6.2	5.2
Epithemia	14.0	4.4	6.5	5.7	11.1	7.1	7.0	6.5
Synedra	4.3	3.6	0.5	1.4	-	1.6	4.0	2.2
Asterionella	2.2	9.2	-	0.5	-	3.2	-	2.4
Cymbella	10.8	5.3	1.2	0.7	-	0.4	-	2.1
Cyclotella	1.1	0.3	1.9	5.5	-	8.7	4.8	3.8
Gomphonema	3.2	1.5	0.5	0.5	-	2.4	6.2	1.9
Rhoicosphenia	-	0.9	0.5	1.2	-	-	0.7	0.7
Navicula	1.1	-	-	0.5	-	1.6	5.1	1.2
Melosira	4.3	0.3	-	-	-	-	-	0.3
Pinnularia	-	0.3	0.2	-	-	-	-	0.1
Opephora	-	-	1.0	-	-	1.2	-	0.4

Appendix 6.10

(a) Percentage composition of the faecal material of *Potamopyrgus antipodarum*, in terms of major food categories, on a projected area basis; and

(b) generic composition (% by numbers) of the diatom category. * = <0.1%.

(2 September 1976 - 21 November 1977)

	1976			1977				
	2/9	2/11	2/12	20/1	8/4	20/6	21/11	Overall
(a)								
Diatoms	44.9	52.1	67.8	47.6	15.8	64.3	68.6	50.8
Detritus	19.0	21.5	18.9	24.5	25.6	15.1	11.1	18.8
Macrophyte	24.1	16.0	5.2	19.3	36.2	12.2	16.8	19.7
Filamentous algae	11.9	10.4	7.8	6.0	22.4	4.1	3.6	9.5
S.R.T's	-	0.1	0.3	2.6	-	4.4	-	1.2
Number of snails examined	12	6	6	6	6	6	6	48
(b)								
Rhoicosphenia	21.8	4.0	12.1	47.4	3.3	43.9	78.1	39.0
Cocconeis	38.5	63.4	50.8	36.8	80.3	37.3	14.0	38.3
Epithemia	13.2	19.8	26.1	6.9	13.9	5.6	6.3	10.6
Fragilaria	-	2.0	1.0	1.0	0.8	9.6	0.8	3.2
Asterionella	9.8	1.5	4.5	0.3	-	0.8	-	2.5
Gomphonema	2.9	5.4	2.5	3.1	-	0.3	-	1.7
Synedra	6.3	1.5	1.5	-	1.6	0.3	-	1.6
Cyclotella	-	2.0	1.0	2.7	-	1.7	-	1.1
Melosira	4.8	-	-	-	-	-	0.8	1.1
Cymbella	1.6	-	0.5	1.4	-	0.5	-	0.6
Navicula	0.5	0.5	-	-	-	-	-	0.1
Diatoma	0.7	-	-	-	-	-	-	0.1
Opephora	-	-	-	0.3	-	-	-	*
Pinnularia	-	-	-	-	-	0.2	-	*