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The Distribution and Dynamics of Planktonic Rotifera in the North Island, New Zealand

A thesis
submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy
at
The University of Waikato

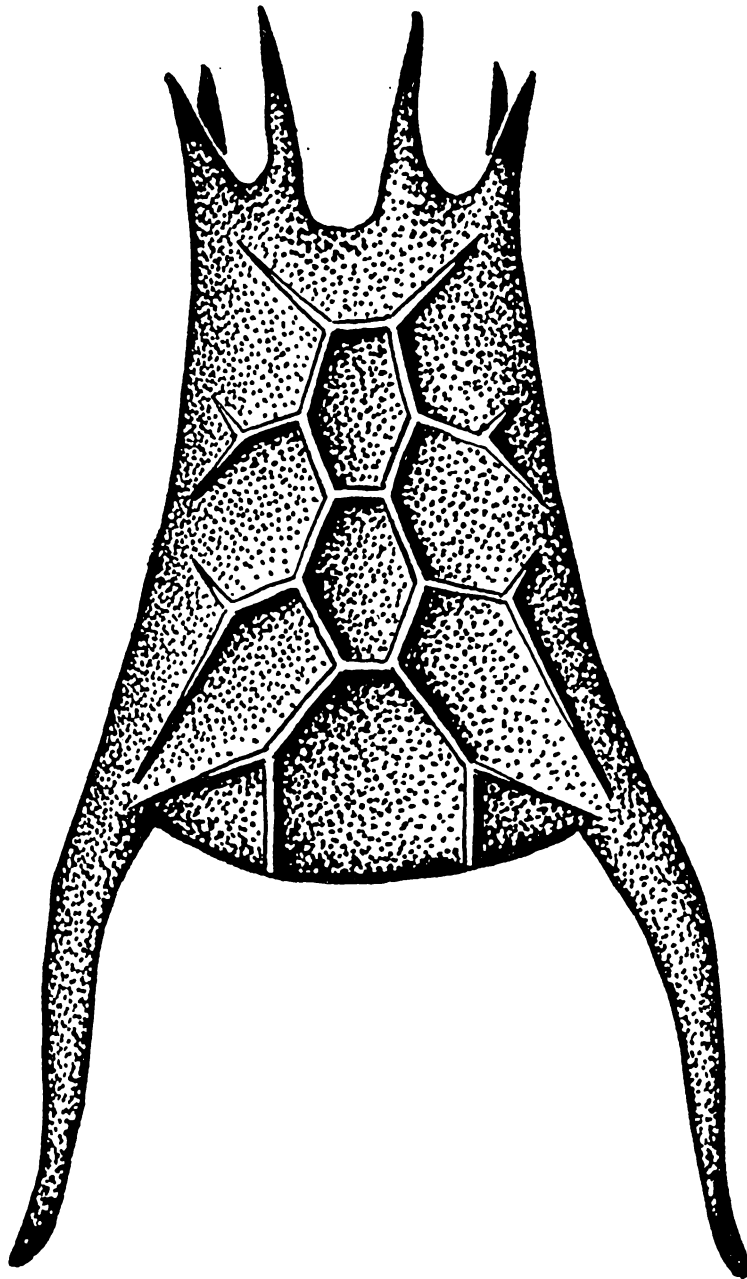
by
Ian Charles Duggan



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1999



Keratella australis (Berzins 1963) as figured in Parr (1949). This species has been recorded from a limited number of sites in New Zealand, and is currently known only from New Zealand and Australia. It was identified by Parr (1949) as the cosmopolitan *Keratella quadrata*, although later described as an Australian “endemic”.

Abstract

The distribution and dynamics of planktonic rotifers, at various spatial and temporal scales, were investigated in lakes of the North Island, New Zealand. The overall aim was to provide a better understanding of the relative influence of various environmental gradients in determining the composition of planktonic rotifer communities in New Zealand.

Potential methods for collection and concentration of samples were assessed. For investigating seasonal and vertical distributions in lakes, sedimentation provided significantly greater ($P > 0.01$) estimates of total and abundant rotifer densities than filtration with 40 μm mesh. For collection of depth integrated samples, various net designs and a tube sampler gave differing estimates of the proportions of species. Overall nets were preferred because they required less time and effort than tubes, and nets with reducing cones provided results more similar to tubes than those without.

The seasonal and vertical dynamics of rotifer communities were investigated in four central North Island lakes of contrasting trophic state and mixing regime: Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Total rotifer abundances were consistently lowest in winter. The temporal occurrence of species assemblages within lakes related to mixing pattern, with different communities in stratified (or relatively stable) and holomictic periods. Multivariate techniques (Cluster analysis, MDS, CCA) indicated that species distributions were most strongly associated with temperature. The predominant warm monomictic mixing pattern in New Zealand is likely to have prevented the occurrence of truly cold-water assemblages. No distinct hypolimnetic community was recognised in any lake, indicating that New Zealand's frequently strong winds are likely to prevent persistence of winter species in the hypolimnion. Rotifer densities were lower in the hypolimnion. Total rotifer abundance was generally greater in lakes of higher trophic state.

The geographical distribution of rotifer species in 42 North Island lakes was investigated using multivariate techniques. Distribution patterns were most strongly associated with trophic state gradients. Based on this relationship, bioindicator indices were developed using Weighted Averaging techniques using rotifer communities for inferring trophic state. Some species, for example *Keratella australis* and *Conochilus exiguus*, appear to be limited in distribution by poor dispersal abilities. Rotifer diversity within lakes, previously thought to be low in New Zealand, was found to be comparable with that of northern temperate lakes.

The methods for estimating rotifer resting egg densities from lake sediment, and the use of emergence for determining community composition from lakes, were investigated in Lakes Tikitapu and Okaro. Significantly lower ($P < 0.01$) estimates of resting egg densities were obtained by incubation of sediments than egg counts. Significantly higher ($P < 0.01$) densities of resting eggs were found from the eutrophic Lake Okaro sediments. Incubation of sediments did not result in the emergence of all the planktonic species found in the seasonal study.

The taxonomy and biogeography of North Island and New Zealand species were investigated based on the species recorded from the current study and from New Zealand to date. The level of endemism in New Zealand appears to be low. Fewer species have been recorded from the North Island than the South Island, and fewer in New Zealand than Australia. This variation can be largely explained by differences in sampling effort or biogeographical processes. No typically cold-water species, e.g., *Notholca* species, are known from the North Island. New Zealand species records have affinities with the Australian fauna.

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Chapter 1: General Introduction

The Rotifera is a phylum of predominantly freshwater microscopic animals encompassing approximately 2000 species. They are found in a wide range of habitats, being abundant and diverse in interstitial sediments and in association with the benthos and littoral macrophytes. Along with the protozoans and microcrustaceans, rotifers are also one of the predominant groups in the freshwater pelagic zooplankton in terms of diversity and biomass. In New Zealand, over 400 rotifer species have been recorded to date, from a wide array of habitats (Shiel & Green 1996, Duggan *et al.* 1998). The earliest studies of rotifers in New Zealand generally involved compiling lists of species distribution records, e.g., Schmarda (1859), Hamilton (1879), Stock (1892), Hilgendorf (1902), Hutton (1904), Murray (1911, 1913), Morris (1912, 1913) and Brehm (1928). The most comprehensive investigations of rotifers to date have been by Russell (1944-1962), who produced a number of species lists, described the endemic taxa *Keratella ahlstromi* Russell and *Notholca pacifica* Russell, and developed methodologies for collecting and photographing rotifers. Following Russell, Haigh (1963-1970) provided species lists and the descriptions of ten endemic bdelloid species. The ecology of New Zealand pelagic rotifers, however, has been little studied. In reviewing the ecology of New Zealand zooplankton, Chapman & Green (1987) felt no general statements could be made about the rotifers, except for an indication that their diversity in lakes may be low. Most studies in New Zealand to date have recorded fewer than ten species in the plankton over a year (e.g., Forsyth & McCallum 1980, Forsyth & James 1991), although greater than twenty species are typically recorded in northern temperate lakes (e.g., Elliott 1977, Berner-Fankhauser 1983, Vasconcelos 1990). Recently, Sanoamuang (1992) has made a detailed study of the seasonal dynamics of species in relation to temperature in Lake Grasmere, South Island and Sanoamuang & Stout

(1993) surveyed the rotifer distribution from 35 South Island lakes. Sanoamuang (1993) also detailed the taxonomic features of New Zealand *Filinia* species and Shiel & Sanoamuang (1993) described a new species of *Filinia* from Lake Okaro. James (1995) examined the seasonal abundances and grazing impacts of microzooplankton, including rotifers, on nanoplankton and flagellates.

Having the ability to reproduce rapidly, rotifers may account for 50% or more of the zooplankton production, depending on prevailing conditions (Herzig 1987). They are thus important components of freshwater food webs, largely as conduits for the conversion of organisms from the microbial web and nanoplankton to higher levels (e.g., Starkweather 1980, Arndt 1993). Rotifers are sensitive to gradients in abiotic (e.g., temperature, pH, oxygen), and biotic (e.g., food quality and quantity, competition, predators and parasites) conditions. The combination of these factors is primarily responsible for the variability in rotifer distribution patterns at various spatial and temporal scales, for example seasonally and vertically within water bodies, between lakes, and at a biogeographic scale (e.g., Green 1972, Ruttner-Kolisko 1974, Herzig 1987, Deimling *et al.* 1997).

Seasonal and vertical dynamics

Many studies have documented and explored the seasonal and vertical dynamics of rotifers within lakes. In temperate water bodies there are marked and predictable seasonal changes in rotifer biomass and species composition (Herzig 1987), termed succession. Most study of seasonal dynamics, however, has been undertaken on assemblages in either dimictic or shallow isothermal northern temperate lakes, where seasonal temperature cycles have commonly been considered to be the predominant factor affecting these changes (e.g., Elliott 1977, Berner-Fankhauser 1983, May 1983, Mischki 1989, Andrew & Fitzsimons 1992). Based on the timing of their occurrence, species are commonly classified as either cold or warm stenotherms based

on their temperature preferences (Hutchinson 1967, Ruttner-Kolisko 1974). Physical changes, such as the formation of stratification and mixing events, also are considered to be the important factors in controlling the seasonal succession of plankton (e.g., Reynolds 1984, Sommer *et al.* 1986, Lampert & Sommer 1997). However, the importance of these in affecting the seasonal variation in rotifer abundance and community structure, by altering density gradients and providing pulses in phytoplankton production, are only recently becoming recognised (e.g., Mengestou *et al.* 1991, Fussmann 1993, Eckert & Walz 1998).

Of the few New Zealand rotifer studies focussing on seasonal distribution to date, the majority have involved communities or populations from non-lake habitats. For example, Parr (1949) examined the seasonal distribution and temporal variation in morphology of species from some Otago ponds, and Tolich (1988) the population dynamics of species from the Mangere oxidation ponds. Both of these studies remain unpublished. Others have focused on non-planktonic lake species, for example, Duggan *et al.* (1998) examined the spatial and temporal distribution of littoral rotifers from Lake Rotomanuka. Ecological study on pelagic species has focussed primarily on recording seasonal changes in abundance, for example, by Forsyth & McCallum (1980) on Lake Taupo, Forsyth & James (1991) on Lake Okaro, Sanoamuang (1992) on Lake Grasmere, and James (1995) on Lakes Taupo, Okaro and geothermal Lake Rotowhero. Only the study of Sanoamuang (1992) focussed specifically on rotifers, and in the others they were studied incidentally, with Crustacea (Forsyth & McCallum 1980, Forsyth & James 1991) or ciliates (James 1995) as the main focus. All these studies, except for those of Forsyth & McCallum (1980) and Forsyth & James (1991), remain unpublished. A number of studies on planktonic Crustacea also have reported changes in numbers of larger rotifer species only, including Chapman (1973), Green (1974, 1976), Jolly (1977), Burns & Mitchell (1980) and Stout (1981, 1984). The value of many New Zealand studies, however, is hampered by inadequate

sampling methods and poor taxonomic resolution. For example, some studies have used nets with mesh sizes that are too coarse to retain the smaller-bodied species. Other studies lack power simply because the taxonomic resolution employed was inadequate. The need for attention to these facets in future New Zealand rotifer studies must therefore be stressed.

Studies in New Zealand to date suggest that the marked seasonality imposed on rotifers in northern temperate lakes by the annual temperature cycle is not apparent. Timings of the peak total abundance of rotifers, and those of dominant species, vary between studies. The lack of a marked seasonality in New Zealand crustacean zooplankton populations has been attributed to a mild climate, which is strongly influenced by an oceanic geographical location, providing comparatively warmer winter and cooler summer temperatures than northern temperate localities of similar latitude (Chapman & Green 1987). Because of these factors, crustacean populations are generally thought to be food limited (Chapman *et al.* 1985). Similarly, recent rotifer studies by Forsyth & James (1991) and Sanoamuang (1992) also have postulated that the abundance and composition of food may be more important than temperature in limiting the seasonal distribution of rotifer species also, although this has yet to be assessed. The mild climate is also a major determinant of a relative uniformity in mixing regime, with deeper lakes being warm monomictic and shallower lakes being generally polymictic. This pattern is different from that found in continental lakes of similar latitudes in the northern hemisphere (Green *et al.* 1987). Since the seasonality of rotifers in northern temperate lakes is associated primarily with temperature and mixing regime, New Zealand's climate is likely to lead to different patterns of seasonality in rotifers. There has generally been little effort to link rotifer species distribution or community dynamics with environmental conditions (other than season) in New Zealand, except for the study of Sanoamuang (1992) which investigated the distributions of South Island species in relation to temperature

preferences. Knowledge of the environmental factors, for example the effects of mixing and food levels, affecting the seasonal dynamics of rotifer species and communities in New Zealand is limited, particularly in the North Island.

In northern temperate lakes rotifers are often the target of intense predation, particularly by invertebrate taxa, and also by fish (e.g., Gilbert & Stemberger 1985, Williamson & Butler 1986, Moore & Gilbert 1987, Hewitt & George 1987). The seasonal cycles and species composition of New Zealand crustacean zooplankton, however, has long been thought to have no obvious impact from invertebrate or vertebrate predators. In New Zealand there are no carnivorous Cladocera, e.g., *Leptodora*, or other large invertebrate predators such as *Chaoborus*, which are commonly found in northern temperate lakes (Chapman *et al.* 1985). Burns & Mitchell (1980) provide evidence of predation on rotifers by *Asplanchna*, and Couch *et al.* (1999) by omnivorous calanoid copepods. Jeppesen *et al.* (1997) have recently argued that larval fish may play a more important role in structuring New Zealand crustacean zooplankton than was hitherto thought, particularly with respect to the lack of large bodied species in many lakes. However, Greenwood *et al.* (1999) have shown food limitation in eutrophic Lake Mangakaware is the likely cause of small-bodied cladocerans dominating New Zealand lakes, due to these having a competitive advantage over larger species under these conditions. New Zealand lacks any obligate planktivorous fish species, and the larvae of most limnetic species develop outside of the pelagic zone. Fish are therefore unlikely to have any significant direct impact on planktonic rotifer populations. However, Cryer (1988) found that smelt (*Retropinna retropinna*) preyed on *Asplanchna* in Lake Tarawera, and Mansfield & McArdle (1998) found the introduced western mosquitofish (*Gambusia affinis*) to utilise rotifers in the margins of some small northern New Zealand lakes. It appears likely, however, that predation by invertebrates and fish has a lesser effect on New Zealand planktonic rotifer communities compared with those in the northern hemisphere. The

seasonal distribution and composition of New Zealand rotifer species are likely therefore to be largely determined by variability in environmental conditions, such as climate and food concentrations. Consequently, competitive interactions between species are likely to be of great importance in structuring New Zealand rotifer communities.

Rotifers often show marked differences in vertical distribution within the water column, a factor that has important implications for niche differentiation, and thereby allowing coexistence of closely related species (e.g., Hofmann 1982, Makarewicz & Likens 1975, 1979). Such vertical distribution patterns are determined predominantly by thermal and chemical gradients (e.g., Hofmann 1982, Miracle & Vicente 1983, Miracle & Alfonso 1993, Armengol *et al.* 1998). Most of the study of rotifer vertical distributions has been carried out in northern temperate lakes with sharp gradients in physical and chemical conditions. This variability is most apparent when cold stenothermous species are found to persist through the warmer seasons in the cool hypolimnion (Herzig 1987). Stemberger (1995) found the duration of persistence of species in the hypolimnion to relate to climatic and morphometric characteristics, with mixing eliminating these refugia. The vertical distribution of rotifers should, therefore, be analysed over the course of a year, within the context of seasonality. Thermal stratification is largely determined by basin morphometry, temperature, and the strength of surface winds. Trophic state, with the presence of thermal stratification, is a major determinant of the vertical variations of many abiotic and biotic variables. Climate and trophic state are therefore often the major determinants in the vertical distribution of rotifers within lakes.

New Zealand seasonal studies of rotifers have generally involved taking vertically integrated water column samples (e.g., Forsyth & McCallum 1980, Forsyth & James 1991). However, vertically integrated samples are likely to give misleading results regarding species seasonal responses to environmental gradients, particularly at

times of stratification. Burns & Mitchell (1980) examined vertical distributions of *Asplanchna* in Lake Johnson, and James (1995) of rotifer species in Lakes Taupo and Okaro. Both studies found vertical variation in the abundances of species, particularly in summer when highest rotifer densities were confined to the epilimnion. James' (1995) study was based on samples taken from a limited number of occasions only, and analysed separately from the seasonal distribution, so no study exists of the seasonal and vertical distributions of rotifer assemblages simultaneously in New Zealand. In contrast to the sharp thermal and chemical gradients found in northern temperate lakes, vertical gradients in temperature and oxygen in New Zealand lakes are generally much weaker, with sharp gradients occurring only at depth in very large lakes (Green *et al.* 1987). Also, New Zealand's latitudinal position provides frequent strong winds from the prevailing westerlies. High wind speeds are common in summer and tropical cyclones are frequent. These winds may reduce the possibility of vertical segregation of species, prevent the persistence of cold water refugia, and therefore affect the depth distributions of New Zealand rotifer communities. These factors need to be assessed.

Distribution of species between lakes

There are commonly considerable differences in the species composition of rotifer communities between lakes, even when in close proximity to one another (e.g., MacIsaac *et al.* 1987, Ejsmont-Karabin 1995, Deimling *et al.* 1997). Variation in rotifer community composition between lakes in a given area is generally a result of local scale factors, such as the suitability of the physical, chemical or biological characteristics of the water bodies. In many rotifer studies, lake trophic state is found to have a major influence on rotifer community structure (e.g., Mäemets 1983, Ejsmont-Karabin 1995). The pH of a water body also has a significant influence on rotifer community structure (e.g., MacIsaac *et al.* 1987, Brett 1989). Geographical

factors are sometimes important also, for example latitudinal variation in Australian or Arctic rotifer communities (Shiel & Koste 1986, Chengalath & Koste 1989), and disjunct distributions are becoming more well known, for example species differences between Tasmania and mainland Australia (Shiel & Koste 1986, Koste & Shiel 1987b). Knowledge of variability in rotifer community composition between New Zealand lakes is sparse, generally coming from the spatially restricted seasonal dynamics studies. Sanoamuang & Stout (1993), however, provided species lists from a survey of 35 South Island lakes. In that study 31 new distribution records were identified, and considerable variation in species composition between lakes was apparent. However, these authors made no attempt to determine the patterns in community composition or the factors that affected distribution between lakes. No comparative study of this scale yet exists for North Island localities. In the only study of factors affecting New Zealand rotifer community composition to date, Duggan *et al.* (in press) (see Appendix 1) found the distribution of rotifers in ten Rotorua lakes to be associated with lake trophic state. This analysis was, however, based on a very restricted data set made up of single samples from each lake. It is not known if trophic state determines distribution when a wider range of seasonal variability, or a wider geographical area, is considered. New Zealand crustacean zooplankton communities contain a limited number of species that are generally ubiquitous in their distribution (Chapman *et al.* 1985, Chapman & Green 1987), although calanoid copepods are known to have disjunct patterns in their distributions over New Zealand (Jamieson 1998). These are thought to be brought about by the geological history of the New Zealand landmass, in which three geographical structures of more or less independent history have come together (Cooper 1989, Heads 1989, Jamieson 1998). It is not known if these patterns affect rotifer species in New Zealand.

Due to the wide variability of environmental conditions within lakes, particularly temporally, periods of unfavorable conditions are often encountered by

species. These conditions are avoided in many rotifers by the formation of resting eggs, which settle on the lake sediment and hatch on return to favorable conditions (Pourriot & Snell 1983). May (1986, 1987) devised methods for obtaining complete yearly rotifer species lists, and obtaining resting egg densities, from Loch Leven, Scotland by hatching resting eggs from incubated sediments. These methods may aid in community analysis by providing a useful tool for obtaining species lists and estimates of resting egg densities from widely dispersed lakes from single visits. Such methods may aid in the analysis of spatial distribution of diversity and community composition of rotifer species over a broad geographical range. However, it is noted by May (1987) that comparison has not been made between the estimates of rotifer densities obtained from hatching and those obtained from direct counts of eggs from the sediment. This aspect needs assessment, as it currently inhibits the use of this potential method. Knowledge of the effects that environmental gradients, such as trophic state, have on the distribution of resting eggs also is unknown. However, it may be expected that densities will be higher in more eutrophic conditions because of the higher abundances of rotifers which can be sustained in the plankton due to higher food levels during the year (Pourriot & Snell 1983). No studies have yet been made of rotifer resting eggs from the sediments of New Zealand lakes.

Biogeography

On a larger temporal and spatial scale, biogeographical patterns of species become apparent. Rotifer species have, in the past, commonly been thought to be widely distributed, or cosmopolitan, mainly due to their ability for passive dispersal. It was, therefore, thought that species distribution patterns, even at this large scale, were determined by ecological rather than historical factors, for example, from the effects of altitude and latitude (e.g., Green 1972). However, there is an emerging acceptance that many taxa are more restricted in their distributions. Examples of this include the

high levels of endemism of the Brachionidae in Australia and South America (Dumont 1983), and in a recent taxonomic revision of the *Lecane*, Segers (1996) found all the major zoogeographical regions to contain endemic species representatives. Segers (1996) believes that questionable taxonomy or insufficient taxonomic resolution in many published studies has been a major constraint on zoogeographical analysis, increasing the belief in cosmopolitanism in this phylum.

Shiel & Green (1996) reviewed the rotifer fauna recorded from New Zealand and noted that most species recorded to date are widely distributed or cosmopolitan taxa, although a small proportion (<5 %) are restricted to New Zealand or the Australasian region. A high degree of cosmopolitanism of New Zealand rotifer species is surprising, because endemism is a characteristic of other New Zealand freshwater animals (Forsyth & Lewis 1987). Shiel & Green (1996) were therefore suspicious of the degree of cosmopolitanism, and believed it may be partly an artefact of the lack of attention given to the group, and also because of anomalies of identification apparent in many early studies. For example, the species lists of Russell (1944 - 1962) brought the study of New Zealand's rotifers to the taxonomic standards of the time, although recent re-examination of some of Russell's taxonomy (Segers 1995) indicates that a modern reappraisal is necessary. Shiel & Sanoamuang (1993) described a new species of *Filinia* from Lake Okaro, and suggested that species from this genera may be more restricted than current records indicate. They argue that use of European identification texts outside of Europe is a contributing factor in the apparent cosmopolitanism of the Rotifera.

A recent survey of 35 lakes in the South Island of New Zealand by Sanoamuang & Stout (1993) added 31 new records to the New Zealand rotifer fauna. This included four species previously regarded as endemic forms to Australia, and two species, *Lecane eylesi* Russell and *L. herzigi* Koste & Shiel, found to occur in Tasmania and New Zealand only. Based on these findings, the New Zealand rotifer

fauna appears to have Australian affinities. However, there still remains a paucity of data on which to base zoogeographical comparison. A survey of lakes from the North Island, similar to that of Sanoamuang & Stout's (1993) South Island study, should presumably reveal more new records and allow further biogeographical comparisons of the New Zealand rotifer fauna. The hypothesis that endemism in New Zealand rotifers is higher than currently recorded needs further testing by paying closer attention to taxonomy than has previously been given. Other than historical biogeographic factors, environmental conditions are also likely to affect the species occurrence of rotifers in New Zealand. New Zealand's mild climate might also be expected to affect the species pool, particularly in winter, due to the absence of freezing which occurs in the dimictic lakes prevalent in the Northern hemisphere.

Bioindicators

Biological monitoring involves the use of biological responses to evaluate changes in the environment. This is commonly done by the development of score systems, such as the Biological Monitoring Working Party (BMWP) Score and Macroinvertebrate Community Index (MCI) (Armitage *et al.* 1983, Stark 1985, 1998), which use benthic macroinvertebrates as indicators of disturbance in lotic systems. These schemes assign scores to taxa based on knowledge of their preferences or sensitivity to environmental conditions. Using these scores, environmental conditions can then be assessed by examining community composition, generally with the advantage of lower costs than traditional methods. The use of rotifers as bioindicators of lake trophic state has been suggested elsewhere, with several authors providing lists of species indicative of lake trophic state (e.g., Mäemets 1983, Berzins & Pejler 1989a, Matveeva 1991). Inference of trophic state based on these lists relies simply on comparison of taxa. No quantitative score system has yet been developed based on community composition. Duggan *et al.* (in press), concluded that the distribution of rotifers in the Rotorua area

of New Zealand appeared to be associated with lake trophic state, and suggested that they may have potential as trophic state bioindicators (Appendix 1). Trophic state in New Zealand is commonly assessed by measurements of total phosphorus, chlorophyll *a* and Secchi transparency. A trophic state is assigned based on the OECD (1982) criteria, and more recently using the New Zealand Trophic Lake Index (TLI) system (Burns & Rutherford 1998). No bioindicator scheme based on responses of taxa to trophic state is currently used.

Study aims and objectives

The overall aim of the current study is to provide a better understanding of the relative influence of various environmental gradients, at different temporal and spatial scales, in determining the composition and distribution of planktonic rotifer communities in North Island, New Zealand lakes. The objectives are to:

- Assess the adequacy of sampling methods for use in this thesis (Chapter 2).
- Examine the temporal and spatial (vertical) distribution of rotifers in lakes of contrasting trophic state and mixing regime, to determine whether New Zealand rotifer communities exhibit patterns in species distribution within lakes, for example seasonality and vertically, and to examine the relationships between species distributions and environmental variables (Chapter 3).
- Examine the distribution of rotifer communities in a number of North Island lakes to explore patterns in species distribution, and examine the relationships between species distributions and environmental variables (Chapter 4).
- Attempt to develop a bioindicator scheme using rotifer communities for determining lake trophic state (Chapter 5).
- Assess the methods for determining rotifer resting egg densities from lake sediments, by counting of eggs removed from sediment and those emerging from incubated sediments. A comparison of densities will be made from lakes of

different trophic state, and the use of emergence for collecting complete species lists for use in community analysis will be assessed (Chapter 6).

- Examine the taxonomy and biogeography of North Island and New Zealand rotifer species, based on the species recorded from the seasonal, between lake, and hatching components of this study, and from previous studies (Chapter 7).

Chapter 2: Investigation of the adequacy of rotifer sampling techniques for collecting quantitative depth samples and qualitative depth integrated samples.

Introduction

At the onset of any investigation of rotifer communities, it is necessary to assess the adequacy of the potential sampling methods. The choice of the most suitable method must consider the advantages and errors involved compared with other methods. Various methods are commonly used for collection of zooplankton samples, including plankton nets, plankton traps, pumps and tube samplers (Bottrell *et al.* 1976). For discrete depth sampling, plankton traps and pumps are the most commonly used methods. Both collect known volumes of water, that are generally filtered through mesh screens after collection to concentrate the zooplankton. However, the concentration of samples by filtering can be problematic. Mesh size needs to be fine enough to retain small bodied species, but coarse enough to allow a reasonable volume of water to pass through to obtain an adequate sample without clogging (Likens & Gilbert 1970, Bottrell *et al.* 1976). An alternative approach, which is used less frequently but often gives superior abundance estimates, is to use sedimentation to concentrate samples (e.g., Likens & Gilbert 1970, Bottrell *et al.* 1976, May 1983, James 1995, May & Bass 1998).

Vertical net hauls and tube samplers are the most commonly used methods for collection of integrated depth samples. Net hauls are commonly criticised, however, because of changing filtration efficiency through the course of a tow, net avoidance by some taxa, and plankton loss through the mesh (Tranter & Smith 1968, Vannucci 1968, De Vries & Stein 1991). Filtration efficiency can be improved by altering the net design, for example, by the addition of cones to reduce the volume of water entering the net, thereby increasing the effective filtration area (Tranter & Heron 1967, Fraser 1968, Tranter & Smith 1968). However, it is generally accepted that nets can provide only qualitative

samples of zooplankton (Green 1977). Tube samplers on the other hand provide a quantitative method, taking a known volume of water through the water column (De Vries & Stein 1991).

This chapter considers the potential methods for use in this project. Firstly, for a quantitative estimation of rotifer densities in water samples of known volumes from discrete depths, sedimentation is compared with the filtration of the samples. Secondly, for the collection of depth integrated samples, for comparative studies of rotifer community composition between lakes, a tube sampler is compared with various net designs.

Methods

Sedimentation of samples versus the use of filtration through mesh screens was assessed as a method for determining rotifer densities from discrete depth samples. For this purpose, Lakes Rotoroa and Rotomanuka were sampled in August and September 1996, respectively. Samples were taken from each lake at a depth of 1 m using a modified 10.45 L Schindler-Patalas trap, in which the net opening at the side of the trap was closed off by a sliding flap. From ten samples, water was filtered through a 40 μ m mesh screen, and rotifers backwashed from this screen into a 120 ml container. A further ten samples were taken, and each placed unfiltered into a 20 L bucket, from which 3 L for sedimentation was removed using a measuring jug into 4 L plastic sealable containers. Samples were immediately preserved in *ca.* 4 % formalin. On return to the laboratory, samples for sedimentation were placed in a sedimentor (Fig. 2.1). This was constructed from P.V.C. piping (8 cm internal diameter, 1 m length) attached to a plastic funnel. A small plastic tube (4 mm internal diameter) was inserted into the bottom of the P.V.C. piping as an outflow for supernatant, with rubber tubing (4 mm internal diameter) and an aquarium tubing clamp attached to control flow. Rubber tubing (8 mm internal diameter) and an aquarium clamp were attached to the funnel for removal of the sedimented sample. Samples were poured

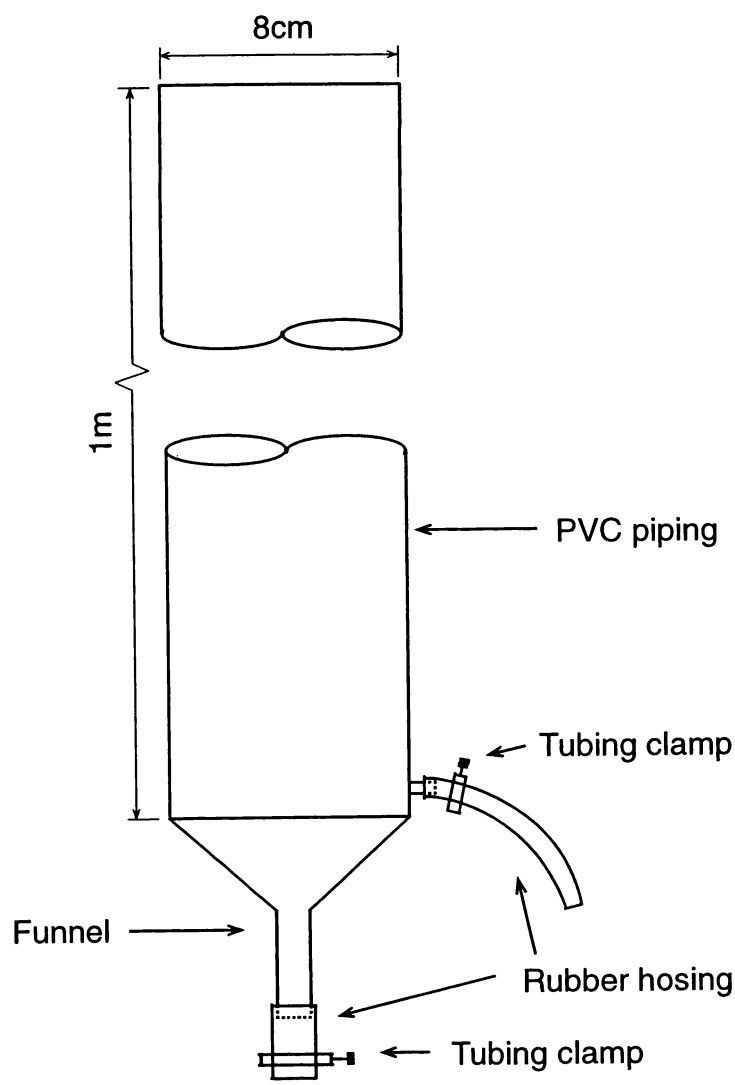


Figure 2.1. Sedimentor for settling of rotifer samples.

into the top of the sedimentor, and left to settle for at least 24 hours. Supernatant was then removed slowly from the side outflow into the 4 L container. The funnel release was then opened for removal of the sample and the sides of the sampler rinsed with de-ionised water (reverse osmosis) to ensure any animals adhering to the side of the sampler were removed. Supernatant was passed through a 40 μm mesh screen and material retained on the mesh re-added to the sample. Samples, reduced to approximately 100 ml, were stored and settled until ready for counting. At this time, excess water was removed from the surface of samples using a 5 ml autopipette, taking care not to disturb the sedimented matter on the bottom of the container, until a final volume of approximately 20 to 30 ml was obtained. Samples were made up to a known volume for counting. All samples were enumerated in 5 ml aliquots taken from the well stirred sample until at least 300 counts were obtained.

The variations in total rotifer abundances and those of dominant species between sedimented and filtered samples were assessed using *t*-tests on raw or log transformed abundance data. Analysis was carried out using InStat (Graphpad software 1993). The number of samples required to achieve adequate sampling variability (< 20 %) was determined following the procedures described by Elliott (1971).

A simple, rapid method was required for obtaining depth integrated samples of rotifer communities from lakes over a wide range of trophic state. This was needed for use both by the author and by regional councils, for whom sampling devices were to be provided for use during their regular monitoring programmes. Tube and net sampling methods were examined because single samples could be taken with minimal time and effort relative to, for example, multiple discrete samples using traps or pumps, thus ensuring the participation of regional councils. The two techniques were compared in oligotrophic Lake Taupo and eutrophic Lake Okaro, using samples taken from two depth ranges, 0-5 m and 0-15 m.

The tube sampler was similar in design to those commonly used for phytoplankton sampling (e.g., Lund *et al.* 1958) and Pennak's "littoral sampling tube" for zooplankton

(Pennak 1962). It was made from 38 mm (internal diameter) flexible plastic tubing, with lead weights and a recovery line (rope) attached to the bottom end to aid in lowering and retrieval respectively. The tube and recovery line were lowered slowly into the water column until reaching the desired depth, thereby taking a sample of the vertical profile. The top of the tube was blocked with a rubber bung, and the bottom of the hose brought to the surface by pulling up the recovery line. The bung was removed from the top of the tube and water emptied through a 40 μ m mesh screen. Rotifers retained were backwashed into a sample container.

Two designs of 40 μ m mesh nets were used: a simple conical design, and the same design with a mesh reducing cone (Fig. 2.2). Ten samples were taken using each net lowered to 5 or 15 m, and raised to the surface at approximately one metre per second. The sides of the net were rinsed so that material retained was washed into the bucket at the bottom of the sampler. A 40 μ m mesh window in the bucket was used to remove excess water, and the material retained washed into a sampling container. All samples were immediately preserved in 4 % formalin.

The variations in percentage contribution of dominant species between tube and net samples were assessed using one-way ANOVA followed by Bonferroni multiple comparisons tests on raw or log transformed percentage data. Analysis was carried out using InStat (Graphpad software 1993).

Results

Planktonic samples concentrated by the sedimentation technique from Lakes Rotoroa and Rotomanuka gave significantly higher total rotifer counts than samples that were concentrated by filtration (Table 2.1). Total rotifer counts on filtered samples were only 55 and 61 % respectively of counts obtained by sedimentation. The number of samples required to attain an acceptable coefficient of variation (SD/mean of < 20 %) (Elliott 1971) of total rotifer numbers using sedimentation for Lakes Rotoroa and Rotomanuka was 0.45

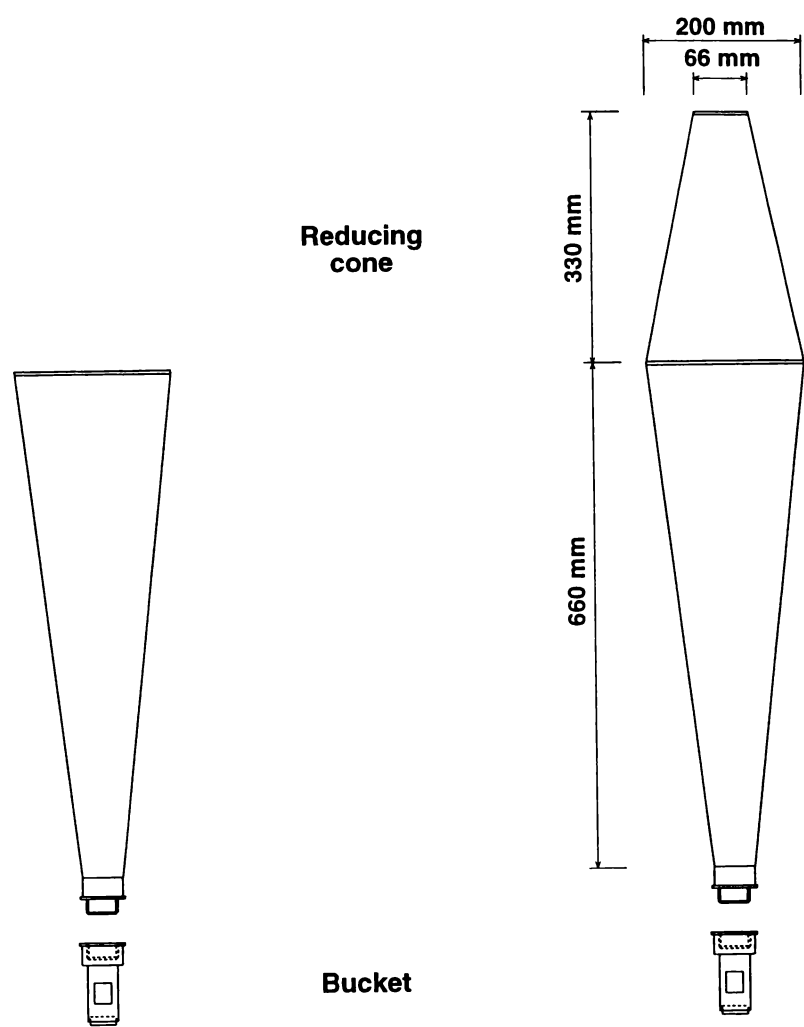


Figure 2.2. Design of plankton nets with and without reducing cones

Table 2.1. Mean counts of total rotifers ($\pm$ 1 SEM) and dominant species abundances (numbers/ L) in Lakes Rotoroa and Rotomanuka assessed from filtered and sedimented samples, and probability of differences in the means (P).

	Filtered samples	Sedimented samples	P
Lake Rotoroa			
Total abundance	520.8 (20.2)	951.5 (40.5)	< 0.0001
<i>Pompholyx complanata</i>	146.7 (6.2)	331.2 (15.2)	< 0.0001
<i>Keratella cochlearis</i>	244.0 (11.2)	355.2 (20.7)	< 0.001
<i>Asplanchna priodonta</i>	98.1 (8.3)	128.3 (5.4)	< 0.01
Lake Rotomanuka			
Total abundance	332.7 (14.0)	549.5 (21.5)	< 0.0001
<i>Ascomorpha ovalis</i>	95.6 (8.2)	174.4 (9.7)	< 0.0001
<i>Trichocerca similis</i>	89.5 (4.1)	160.8 (11.0)	< 0.0001
<i>Synchaeta pectinata</i>	65.1 (4.9)	107.3 (8.7)	< 0.005
<i>Asplanchna priodonta</i>	28.5 (2.5)	44.1 (2.8)	< 0.001

and 0.31 respectively. The number of samples required for the dominant species ranged between 0.44 - 0.84 and 0.62 - 1.33, respectively.

For 0-5 m depth integrated samples from Lake Taupo, the mean percentage contributions of the two dominant species (Table 2.2) were not significantly different ($P>0.05$) between the tube sampler and net with a reducing cone, but proportions of both species were significantly different between these methods and the net without the reducing cone ($P<0.01$). In the 0-15 m samples, the proportion of *Polyarthra dolichoptera* was significantly higher ($P<0.01$) in samples from the tube sampler than in those taken with nets, but proportions of *Conochilus dossuarius* were not significantly different ($P>0.05$) between any method. In Lake Okaro 0-5 m samples, the percentage contribution of *Trichocerca similis*, was not significantly different between the tube sampler and net with reducing cone, but significantly lower in the net without the reducing cone ($P<0.05$). *Asplanchna priodonta* was significantly greater in net samples than the tube, and *Hexarthra intermedia* lower ($P<0.05$). The percentage contribution of *Pompholyx complanata* were significantly different ($P<0.05$) between all methods. In Lake Okaro 0-15 m, *T. similis*

Table 2.2. Mean percentage composition (± 1 SEM) of dominant species in Lakes Taupo and Okaro assessed from tube samples, and nets with and without reducing cones.

	Tube sampler	Net with reducing cone	Net without reducing cone
Lake Taupo 5 m			
<i>Polyarthra dolichoptera</i>	72.23 (2.6)	65.08 (3.2)	35.58 (3.8)
<i>Conochilus dossuarius</i>	19.57 (3.5)	21.46 (1.9)	38.65 (2.8)
Lake Taupo 15 m			
<i>Polyarthra dolichoptera</i>	72.28 (1.9)	62.11 (1.8)	60.99 (1.8)
<i>Conochilus dossuarius</i>	19.13 (2.0)	22.17 (0.7)	20.30 (2.2)
Lake Okaro 5 m			
<i>Trichocerca similis</i>	47.19 (2.7)	43.73 (2.1)	34.16 (4.2)
<i>Asplanchna priodonta</i>	19.71 (2.3)	31.32 (2.3)	36.14 (3.2)
<i>Hexarthra intermedia</i>	21.50 (1.5)	6.26 (0.9)	4.37 (0.5)
<i>Pompholyx complanata</i>	9.64 (1.2)	17.17 (1.7)	23.03 (1.8)
Lake Okaro 15 m			
<i>Trichocerca similis</i>	48.55 (1.5)	51.02 (2.0)	41.85 (2.9)
<i>Asplanchna priodonta</i>	14.41 (1.0)	20.56 (1.4)	22.99 (2.8)
<i>Pompholyx complanata</i>	22.45 (2.9)	20.69 (1.5)	31.00 (5.3)

was significantly different between nets with and without reducing cones only, and *A. priodonta* between the tube sampler and net without the reducing cone only. For *P. complanata* there were no significant differences between the methods ($P > 0.05$).

Discussion

Methodology had significant effects on the assessed densities or proportions of rotifers in the comparisons of both discrete depth and depth integrating samplers. Sedimentation provided significantly greater densities of rotifers than those from filtered samples. Filter clogging was not a factor involved in this comparison, since all water was passed through the sieve, so it is likely that rotifers were lost by passing through the 40 μm mesh screen. Sedimentation is therefore the preferable method. Likens & Gilbert (1970), Bottrell *et al.* (1976), James (1995), and May & Baas (1998) have compared the use of filtration with sedimentation as a method for concentration of rotifer samples. Likens & Gilbert (1970),

Bottrell *et al.* (1976), and May & Baas (1998) all found significant numbers of rotifers were lost, particularly small or soft bodied species, through 75 μm , 70 μm and 63 μm mesh sieves respectively. However, James (1995) found no significant differences in rotifer numbers between sedimentation and filtration with a 20 μm mesh, and Likens & Gilbert (1970) found either no significant differences, or that numbers were higher in those filtered, using 35 or 48 μm mesh screens. Likens & Gilbert (1970) attributed the lower numbers in their sedimented samples to rotifers lost in the supernatant. A modification in the current study, to re-add material removed in the supernatant by passing through a 40 μm mesh, is likely to have lead to a greater efficiency in this method. It seems likely, therefore, that mesh as fine as 20 μm may be needed for the adequate filtration of rotifer samples, although is likely to be too fine to prevent mesh clogging except where very small volumes, such as the 150-200 mL used by James (1995), are used. However, from estimates of the volumes required to attain an acceptable coefficient of variation in the present study, at least 1.5 L is required for total rotifer counts, and more than 3 L for some of the dominant species.

Disadvantages of the sedimentation technique include the volumes of sample that must be returned to the laboratory, and also therefore the volume of preservative used. On return to the laboratory, samples also require further time consuming processing before counting, and as the preservative (formalin) cannot be removed without filtration, sedimentation and enumeration must be carried out in well ventilated areas. A relatively large amount of debris also was found within the sedimented samples making counting more difficult. However, these difficulties are not insurmountable, and in view of the greater estimates of rotifers found using this method it was used in preference to filtering for assessing rotifer spatial and temporal distributions (Chapter 3). Based on the means and variances of rotifer counts, two samples (6 L) were adequate for assessing total numbers and all of the dominant taxa.

The comparison of tubes versus nets for taking integrated depth samples found differences in species proportions between methodologies. The net with the reducing cone, in general, provided data that compared better with the tube sampler than the net without the reducing cone. If it is assumed that the tube sampler is the most quantitative of the three methods used, then the net with the reducing cone is more efficient than the net without the reducing cone. Tranter & Heron (1967) found net efficiency to be greater in nets with reducing cones, as these enable a greater area for filtration per volume of water filtered. The greatest differences between nets and tubes were the apparent over-sampling of *Asplanchna priodonta* using nets, or under-sampling of other animals, particularly *Hexarthra intermedia*, in Lake Okaro samples. This is likely a result of the larger body size of *Asplanchna* being preferentially retained by the mesh, with smaller bodied animals passing through the mesh to a greater degree (e.g., Tranter & Smith 1968, Vannucci 1968, De Vries & Stein 1991). The proportions of *H. intermedia* might be particularly low because they may be able to jump clear of the nets using their appendages (e.g., Gilbert & Williamson 1978). De Vries & Stein (1991) found no significant difference between total rotifer numbers collected using a tube and those estimated using nets, both filtered through 54 µm mesh, although tubes sampled greater abundances of calanoid copepods, copepod nauplii and *Bosmina*. Karjalainen *et al.* (1996) found significantly higher rotifer abundances using a tube sampler than nets, indicating a better efficiency, although the tube sampler used 48 µm mesh, and the net used 120 µm mesh only. The tube sampler, although likely providing a more accurate, and quantitative, measure of rotifer densities through the water column than the nets, was very bulky, especially when samples from increased depths were desired. The method also was relatively inefficient in the time and effort taken to collect the samples. Because this method was required to be used by regional councils during regular monitoring, consideration needed to be made regarding the time and effort involved, and this method was therefore unsuitable for this purpose. However, although not feasible for the needs of the current study, it provided a good comparison for

the results of the net samples. For sampling of rotifers from a variety of New Zealand lakes, it was therefore decided to use nets with reducing cones because of their greater efficiency than nets without cones.

Chapter 3.

The temporal and spatial dynamics of rotifers in four North Island, New Zealand lakes of contrasting trophic state.

Introduction

In lakes, the temporal and spatial distribution of rotifer species is governed by the dynamics of physical, chemical and biological factors within each lake. In temperate water bodies there are marked seasonal changes in biomass and species composition, influenced by physical and chemical limitations, competition, predation, and parasitism (Herzig 1987). Seasonal temperature cycles are often considered to be the predominant factor affecting this distribution, and more recently the influence of mixing patterns in demarcating change in community structure is becoming increasingly recognised (e.g., Fussmann 1993, Stemberger 1995, Eckert & Walz 1998). On this basis species can be divided into either cold or warm stenotherms based on the timing of their occurrence through temperature preferences (Hutchinson 1967).

In contrast to northern temperate lakes, New Zealand's oceanic climate leads to a depression in seasonal lake temperature ranges, with North Island lake ranges averaging 13.1 °C ($\pm$ 3.1) and South Island 14.0 °C ($\pm$ 4.0) (Green *et al.* 1987). Summer temperatures are relatively cool, and winter temperatures relatively high, rarely dropping below 8 °C. This mild climate is also a major determinant of a relative uniformity in mixing regime, with deeper lakes being generally warm monomictic and shallower lakes polymictic, as opposed to the predominantly dimictic pattern found in northern hemisphere continental lakes at similar latitudes (Green *et al.* 1987). Such features are likely to lead to differing patterns of seasonality in rotifers. There have, however, been few studies of the seasonal variability in rotifer community structure or species dynamics, and the factors which control them, in New Zealand. Only two studies documenting the temporal distribution of planktonic rotifers, using appropriate sampling methods, have been

published: Forsyth & McCallum (1980) from oligotrophic Lake Taupo, and Forsyth & James (1991) from eutrophic Lake Okaro. Theses by Parr (1949) from some Otago ponds, Tolich (1988) from Mangare oxidation ponds, Sanoamuang (1992) from Lake Grasmere, and James (1995) from Lakes Taupo, Okaro and geothermal Rotowhero, remain unpublished. A number of studies on planktonic Crustacea also have examined rotifers incidentally, including Chapman (1973), Green (1974, 1976), Jolly (1977), Stout (1981, 1984), and Burns & Mitchell (1980). The value of these is hampered by inadequate sampling methods for rotifers and poor taxonomic resolution. From the results of these studies, however, it appears that there is no consistency in the timing of rotifer seasonality. A lack of marked seasonality in New Zealand crustacean zooplankton populations is attributed to the mild climate, and populations are therefore thought to be food limited (Chapman *et al.* 1985). Recent studies by Forsyth & James (1991) and Sanoamuang (1993), have thus postulated that the abundance and composition of food may be more important than temperature in limiting the seasonal distribution of rotifer species, although this has not yet been assessed. Predation has long been thought to have only a limited impact on the seasonal cycles of New Zealand zooplankton compared with that of northern hemisphere lakes, due to the lack of many types of predators (Chapman & Green 1987). Jeppesen *et al.* (1997) have argued recently that larval fish may play a more important role in structuring New Zealand crustacean zooplankton than was hitherto thought, in particular by the removal of large bodied *Daphnia* which is only infrequently found. In the northern hemisphere, however, planktivorous fish generally prefer larger microcrustaceans (e.g., *Daphnia*) over rotifers as food (Herzig 1987). Also, Greenwood *et al.* (1999) have shown food limitation in eutrophic Lake Mangakaware is the likely cause of small bodied cladocerans dominating, due to having a competitive advantage over larger species under these conditions. Invertebrate predators are known to concentrate on smaller prey such as rotifers, and Couch *et al.* (1999) have shown that rotifers contribute to the diet of New Zealand calanoid copepods. Cyclopoid copepods on the other hand have very sparse

populations in New Zealand (Chapman & Green 1987). Other important invertebrate predators commonly found in the northern hemisphere are absent, such as carnivorous Cladocera, e.g., *Leptodora*, or large invertebrate predators, e.g., *Chaoborus* (Chapman *et al.* 1985), likely reducing the predation pressure on New Zealand rotifer communities compared with elsewhere.

The vertical distribution of rotifers within northern temperate lakes is affected by stratification and its consequent effects (e.g., Hofmann 1985, Miracle & Vicente 1983, Miracle & Alfonso 1993). Thermal stratification is determined by temperature and the strength of surface winds, and trophic state (with the presence of thermal stratification) is a major determinant of the spatial variability of many physico-chemical variables, oxygen in particular. New Zealand lakes have a wide range of trophic state, largely determined by the intensity of agriculture in their catchments (McColl 1972, White 1982, 1983). New Zealand rotifer studies, however, have so far generally ignored the effects of seasonal spatial variability of physico-chemical and biological variables, usually examining only vertically integrated samples.

The seasonal and spatial dynamics of rotifers were investigated in four central North Island, New Zealand lakes of contrasting trophic state and mixing regime, to characterise in detail the seasonal dynamics of various rotifer species, to examine the influence of the physical, chemical and biotic variables on the temporal and spatial distribution of diversity, community composition, and abundance of rotifers: Lakes Tikitapu (oligo – mesotrophic, warm monomictic), Rotoiti (mesotrophic, warm monomictic), Okaro (eutrophic, warm monomictic) and Ngaroto (eutrophic, polymictic) (Fig. 3.1) (BOPRC 1993, Etheredge 1987). These lakes have been subjected to varying degrees of modification for agricultural development. The catchments of Lakes Okaro and Ngaroto have been nearly entirely converted to agricultural land, with the other two relatively less modified. Some morphometric and other data for the lakes are given in Table 3.1.

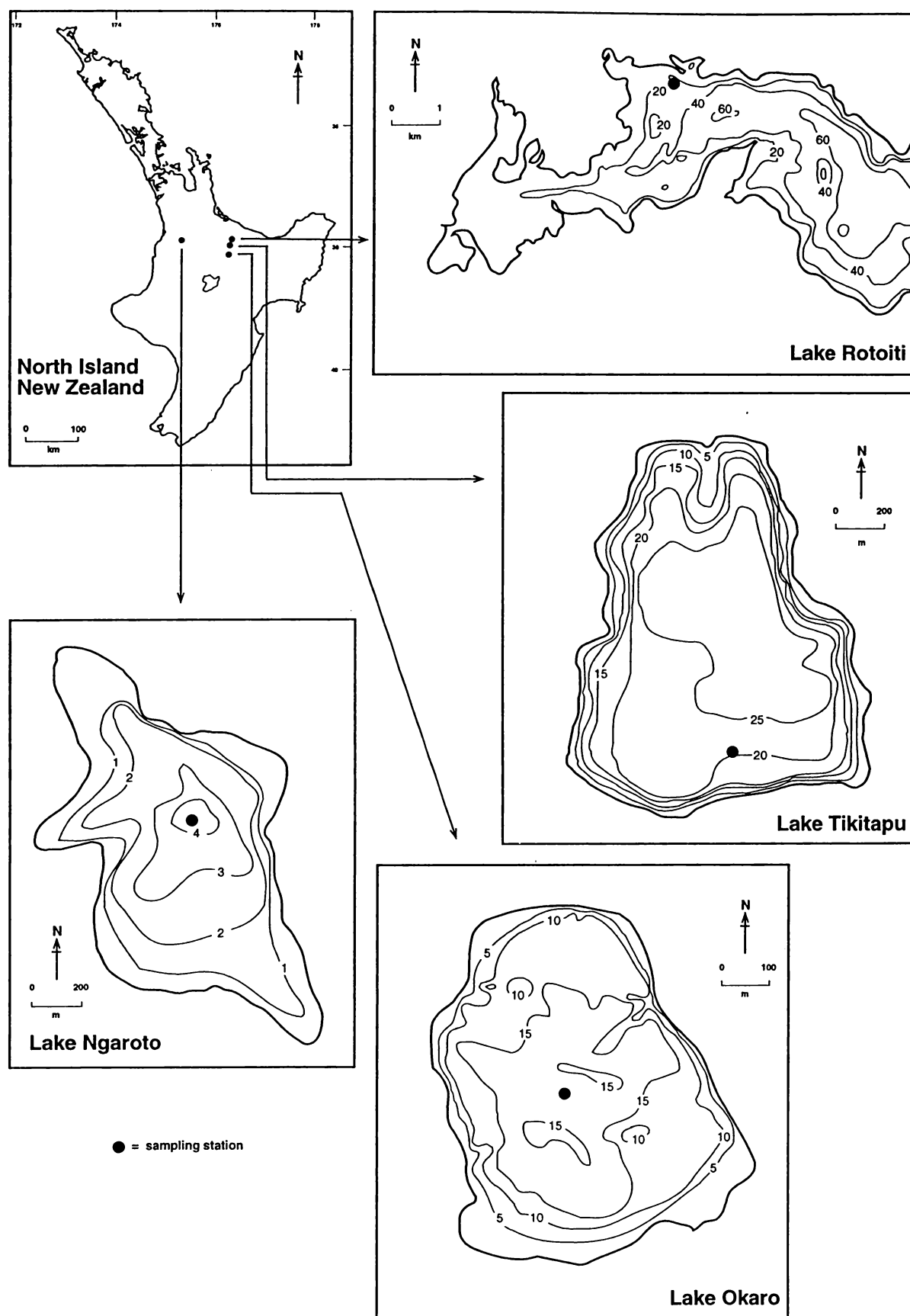


Fig. 3.1. Location map of the study lakes, showing bathymetry (m) and sampling locations.

Table 3.1. Morphometric and related data for the study lakes. Data from Irwin (1975), Livingston *et al.* (1986), BOPRC (1993) and Environment Waikato (unpublished data). – indicates that data is not available.

	Lake Tikitapu	Lake Rotoiti	Lake Okaro	Lake Ngaroto
Lake origin	volcanic	volcanic	volcanic	riverine
Latitude	38.20	28.02	38.30	37.95
Longitude	176.33	176.36	176.39	175.26
Altitude (m)	418	279	413	35
Lake area (km ²)	1.40	33.48	0.28	1.30
Max. depth (m)	27.5	93.5	18	3.5
Mean depth (m)	18.0	31.5	12.1	2.0
Secchi (m)	7.07	5.59	1.32	0.62
Chlorophyll	3.2	4.8	21.4	46.2
TP (mg/m ³)	8	19	84	105
TN (mg/m ³)	224.0	280.7	1276.0	-

Methods

Lakes were visited at two or three weekly intervals between 20 March 1997 and 16 April 1998, except Lake Ngaroto for which sampling began on April 2 1997. Sampling locations are given in Fig. 3.1. Lake Okaro was not sampled in early April 1998 due to high winds. Rotifers and physico-chemical parameters were sampled by boat in Lakes Tikitapu and Rotoiti from surface to 18 m at 3 m intervals, Lake Okaro from surface to 15 m at 3 m intervals, and Lake Ngaroto from surface to 3 m at 1 m intervals. Temperature (°C), dissolved oxygen concentration (DO, mg/L), oxygen saturation (%O), conductivity (μS), pH, and whole and size fractionated chlorophyll *a* concentrations (mg/L) were determined from each depth on each occasion. Temperature, DO, and %O were measured *in situ* using a YSI Model 50 meter. Where stratification occurred, intermediate readings of these variables were taken, generally at 1 m intervals. Conductivity and pH were measured using YSI Model 30 and Meterlab PHM210 meters respectively from water collected using a 10.45 L Schindler- Patalas trap at each depth. Water from each depth was returned to the laboratory on ice for chlorophyll *a* analysis. Secchi depth was measured on each occasion with a 20 cm diameter disc divided into black and white quadrants.

Phytoplankton biomass was determined as a surrogate measure of food concentration, assessed by determining whole and size fractionated chlorophyll *a* concentrations. Samples were size fractionated by prefiltering through a 20 µm nylon mesh, with phytoplankton thus partitioned into < 20 µm (nanoplankton) and > 20 µm (microplankton) size fractions (determined as the difference between the whole and < 20 µm results). Duplicate 25 or 50 mL samples of whole or size fractionated water were filtered onto Whatman GF/C filters (nominal pore size 1.2 µm), stored frozen for no longer than one month. The filters were homogenised, and chlorophyll *a* extracted overnight at 4 °C using 10 mL of 90 % acetone. The homogenate was centrifuged, and fluorescence of the supernatant measured before and after acidification (2 drops 2M HCl) using an Aminco SPF-500 spectrofluorometer set to 430 nm (excitation) and 665 nm (emission) (Strickland & Parsons 1972).

Daily wind strength data recorded from Rotorua airport were supplied by NIWA. Water stability was calculated as the Brunt-Vaisala frequency. This measure was chosen because it can be easily calculated from temperature profiles (Viner 1985), given by:

$$N^2 = - \frac{g}{\rho} \frac{d\rho}{dz}$$

where ρ = water density
 z = depth
 g = acceleration of gravity

Rotifers were sampled using a 10.45 L Schindler-Patalas trap fixed with a sliding flap to close the usual net aperture. The sample was emptied unfiltered into a 20 L bucket and 3 L removed and preserved with 120 mL of formalin. This procedure was done in duplicate at each depth. On return to the laboratory, samples were concentrated by sedimentation (see Chapter 2) to a final volume of *ca.* 30 mL, and stored until processed.

For counting, a known volume of sample was enumerated in 5 mL aliquots in a gridded perspex tray using a Leica MZ12 stereo microscope at *ca.* 30x magnification. Aliquots were enumerated until 300 counts were obtained, or until the entire sample was counted. Unknown animals were examined with an Olympus BX50 compound microscope and identified from body morphology, and/or trophus structure after eroding the rotifer tissue with 10 % sodium hypochlorite (Koste & Shiel 1991). Species were identified using Koste (1978), Shiel (1995), Shiel & Koste (1993), and references therein.

Physico-chemical and rotifer temporal and spatial distributions were plotted using Spyglass Transform v. 3.3.0 (Fortner 1996), a computer program that produces greyscale and/ or contour plots from 3D arrays of numbers (i.e., animal density x space and time). Any missing values were filled by interpolation from true data values using the 'weighted fill' method in which each missing data value is replaced by a weighted combination of all the true values surrounding the missing value.

Cluster Analysis, Multidimensional Scaling (MDS) and Canonical Correspondence Analysis (CCA) were used to elucidate patterns in the data sets for each lake. Cluster analysis was based on the Bray-Curtis similarity coefficient calculated on the densities ($\sqrt{\sqrt{\cdot}}$ -transformation) of abundant rotifer species and group average sorting. Abundant species (excluding bdelloids) were selected as those achieving ≥ 4 % of any sample from each lake. MDS, an ordination technique, was performed based on the ranked Bray-Curtis similarity matrix. Analyses were carried out using the Plymouth Routines in Multivariate Research statistical package (PRIMER) (Clarke & Warwick 1994). CCA was used to examine species environmental relationships and to determine important physical and chemical variables associated with groupings found in cluster analysis. The results of the CCA ordinations are presented as biplots onto which the sample, species and environmental loadings on the two major axes are graphed together (Ter Braak & Smilauer 1998). The sample scores are plotted as points and the species and environmental loadings are represented by arrows located at the intersection of the loading for that species on each

axis. The direction of the arrows thus indicates the association between samples, species and environmental variables and the length of the arrows indicate the strength of the associations. Only Axis 1 and Axis 2, the two most important axes are used in the biplots. Species data were $\ln(x+1)$ transformed prior to analysis because of their skewed distributions, and environmental variables standardised to zero mean and unit variance because of their differing units of measurement. Any missing environmental variables were interpolated from true data values using the Spyglass Transform ‘weighted fill’ method prior to being standardised (Fortner 1996). Total chlorophyll *a* and %O were removed from all CCA ordinations because of high covariability with nanoplankton chlorophyll *a* and microplankton chlorophyll *a* or DO and temperature respectively (variance inflation factor > 20) in exploratory ordinations (Ter Braak & Smilauer 1998). Forward selection and Monte Carlo permutation tests (using 99 unrestricted permutations) were performed to identify the environmental variables that were statistically significant in determining the variations in rotifer species. CCA and associated analyses were performed using CANOCO v. 4.0. (Ter Braak 1998).

Optimal environmental conditions for abundant species were estimated by taking weighted averages of physico-chemical variables, in which environmental variables are weighted proportional to the species abundances (Jongman *et al.* 1987), i.e.

$$u^* = (y_1x_1 + y_2x_2 + \dots + y_nx_n) / (y_1 + y_2 + \dots + y_n)$$

where

u^* is the weighted average

$y_1, y_2, \dots, y_n$ are the abundances of species

$x_1, x_2, \dots, x_n$ are the values of the environmental variable at sites 1, 2...n

Weighted average optima were calculated using CALIBRATE v. 0.8.2 (Juggins & Ter Braak 1997).

Results

Environmental conditions

Minimum lake temperatures occurred in all lakes between July and September 1997 (mid-winter to early spring), and maxima occurred from December to February 1998 (summer) (Fig. 3.2). Seasonal temperature ranges (STR) of the epilimnetic waters were evaluated from the top 6 m in Lakes Tikitapu, Rotoiti and Okaro, and from both the whole water column and from 1 m to 3 m in Lake Ngaroto. The STRs for the monomictic lakes were 13.2 °C in Lake Tikitapu, 11.8 °C in Lake Rotoiti, and 14.0 °C in Lake Okaro. The STR of Lake Ngaroto was 17.1 °C over the whole water column, or 16.2 °C from 1 to 3 m, removing the influence of occasional very high temperatures at the very surface. Thermal stratification occurred in Lake Okaro from the beginning of the study until May 1997. All lakes were holomictic through winter and early spring. Stratification developed in Lakes Okaro and Tikitapu from November 1997 until the end of the study. Stratification was observed in Lake Rotoiti from November at greater depths than the other lakes, and in Lake Ngaroto gradients in temperature developed from October to April 1998. Several storm events were marked by deepening of the thermocline in Lakes Tikitapu, Rotoiti and Okaro, or by periodic mixing in Lake Ngaroto. Three-day averages were calculated on the daily wind speed data, by taking a mean of each days wind speed with those either side of it, to aid in elucidating seasonal patterns (Fig. 3.3). Winter wind speeds varied widely, although they were often amongst the lowest speeds recorded in my study. Wind speed steadily increased from winter through spring. In late spring, summer and autumn, wind speeds periodically increased and decreased cyclically. Wind peaks in June, November, January, March and April correlate with mixing events identified in the temperature profiles (Fig. 3.2). Marked surface heating periodically occurred between mixing events, particularly in Lakes Okaro and Ngaroto (Fig. 3.2). Brunt-Vaisala frequency (Fig. 3.4), calculated based

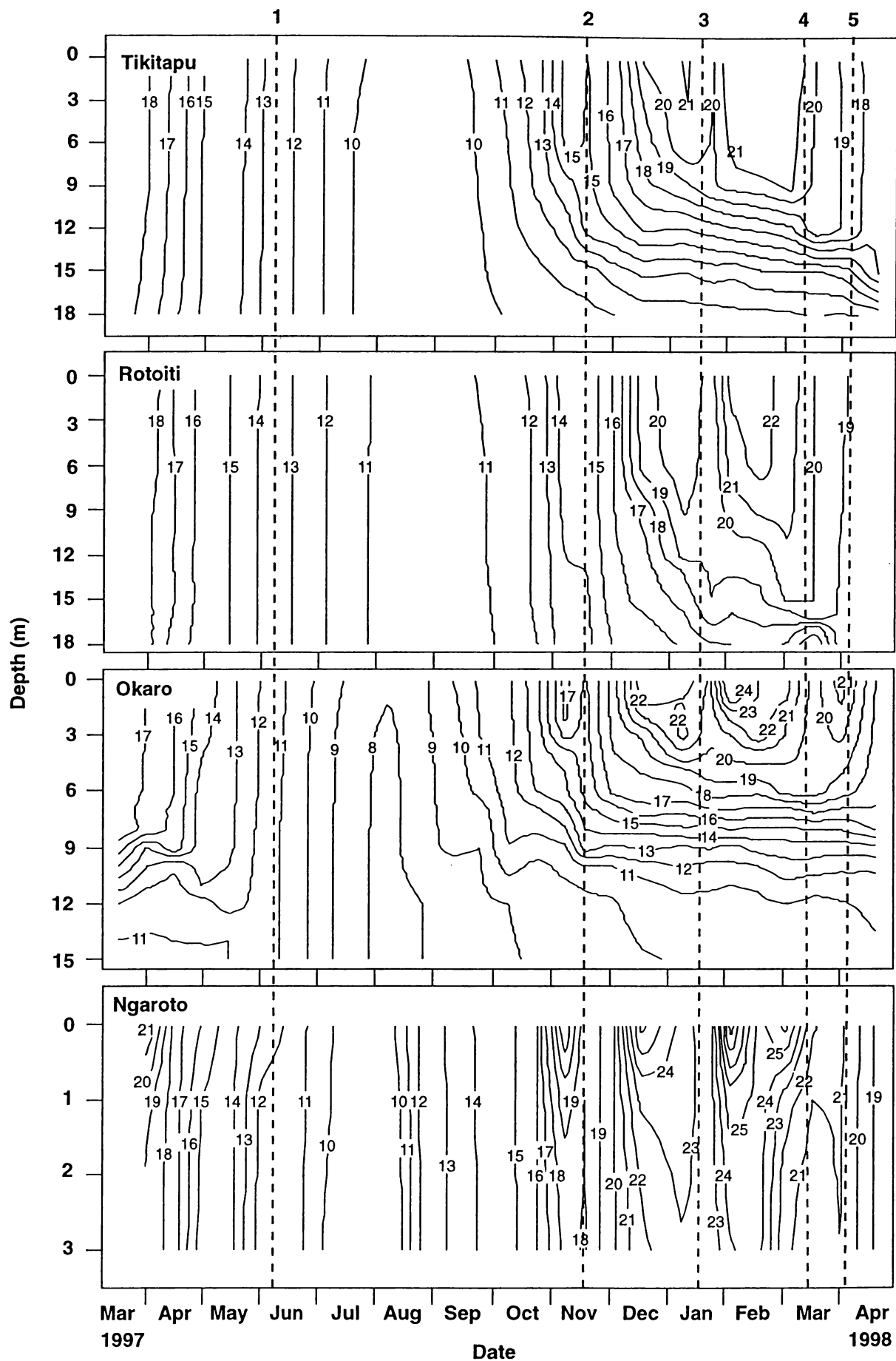


Fig. 3.2. Spatial and temporal distribution of temperature ($^{\circ}\text{C}$) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm or mixing events.

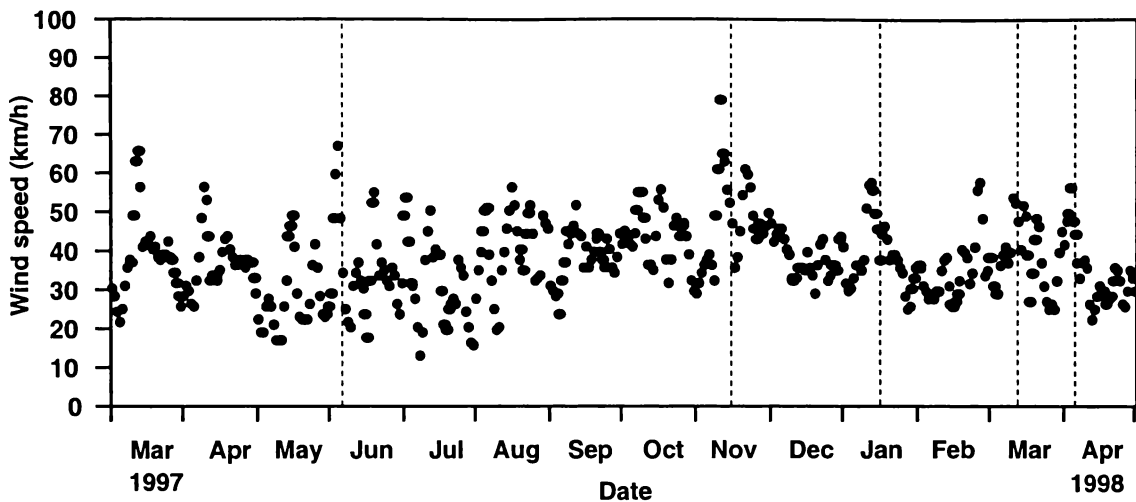


Fig. 3.3. Three day means of daily wind speeds (km/h) recorded from Rotorua airport. Dashed lines indicate storm or mixing events (cf. Fig 3.2).

on the temperature profiles, was highest (most stable) at times of thermal stratification (see above for timing). Highest stabilities occurred at the thermocline in the monomictic lakes, and at the surface in polymictic Lake Ngaroto.

DO and %O had similar temporal and spatial patterns (Fig. 3.5 and 3.6), and were generally related to periods of thermal stratification and mixing events. Lakes Tikitapu and Rotoiti were spatially fairly uniform until December when deoxygenation began to occur at depth. In Lake Tikitapu, oxygen commonly had a mild positive heterograde distribution above the thermocline from December until the end of the study. Deoxygenation occurred in Lake Okaro from the beginning of the study until mid-May, and gradients again began to develop from September, with deficits occurring from November. Sharp negative heterograde distributions occurred above the thermocline in April and December 1997. Lake Ngaroto had periodic oxygen gradients from the beginning of the study until mid-May, and again from November until the end of the study. Gradients in oxygen were occasionally weakened by mixing events, particularly in Lakes Ngaroto and Okaro (cf. Fig. 3.2).

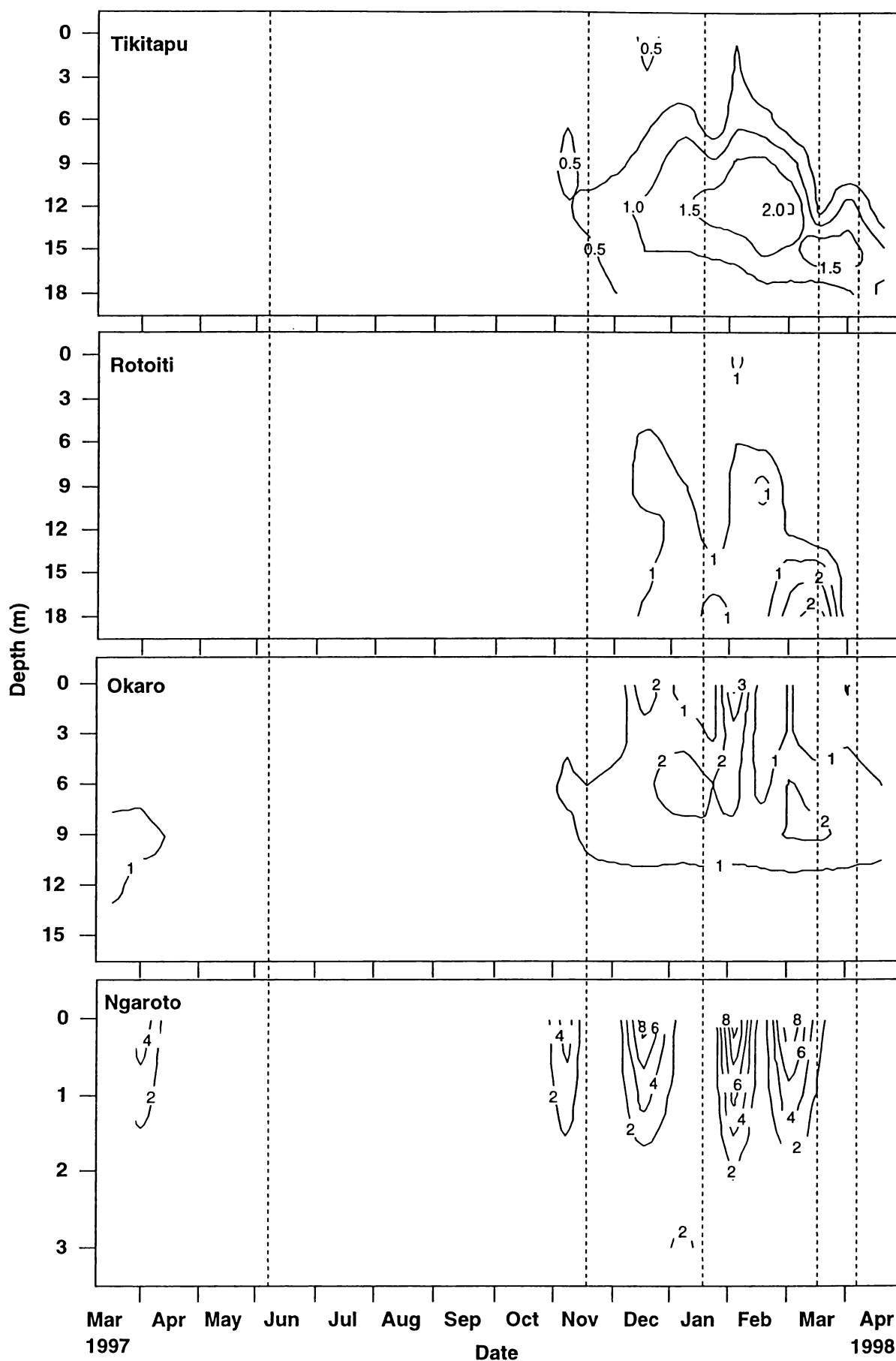


Fig. 3.4. Spatial and temporal distribution of stability (Brunt-Vaisala frequency) ($N^2 \times 10^3$) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

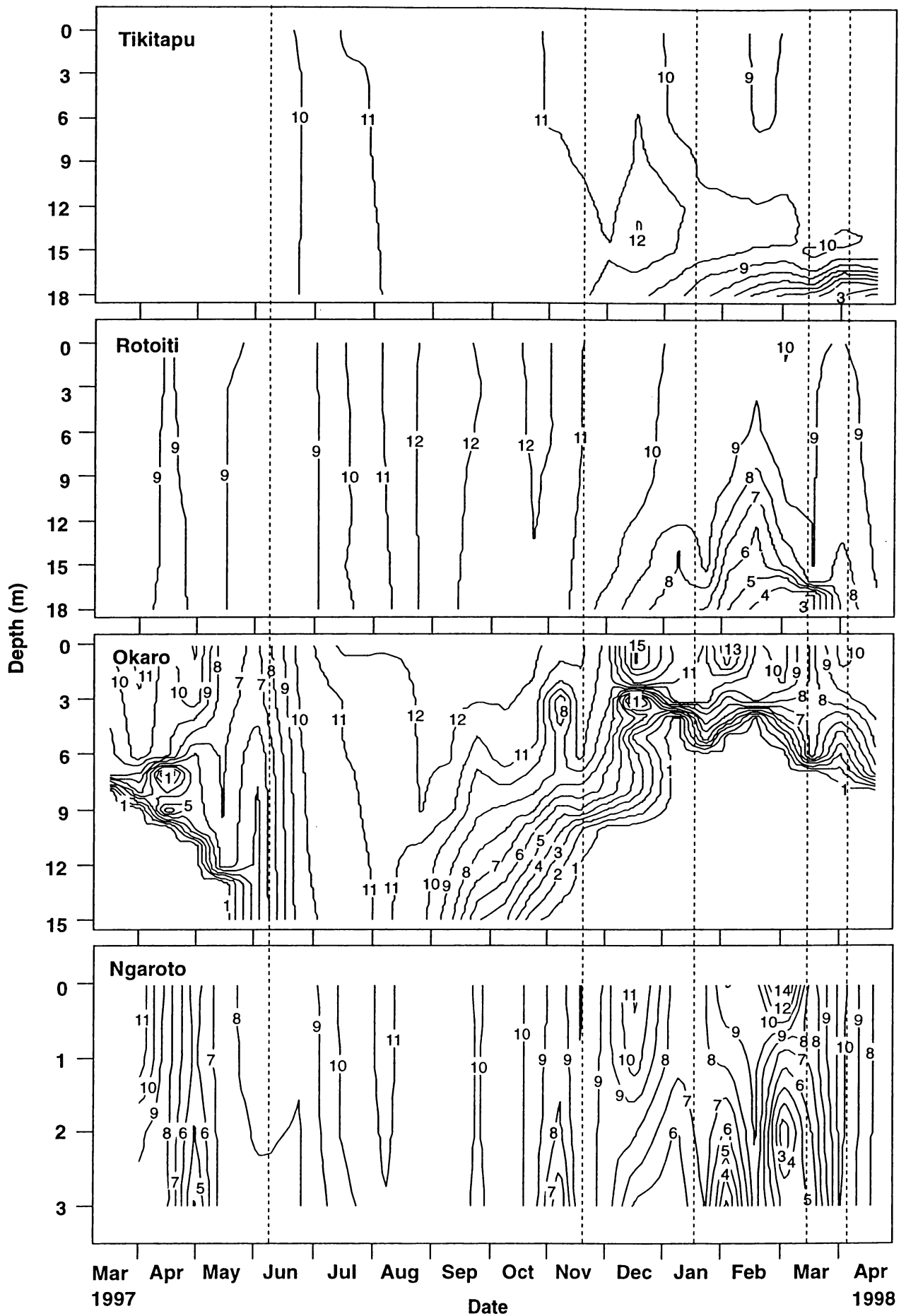


Fig. 3.5. Spatial and temporal distribution of DO (mg/L) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

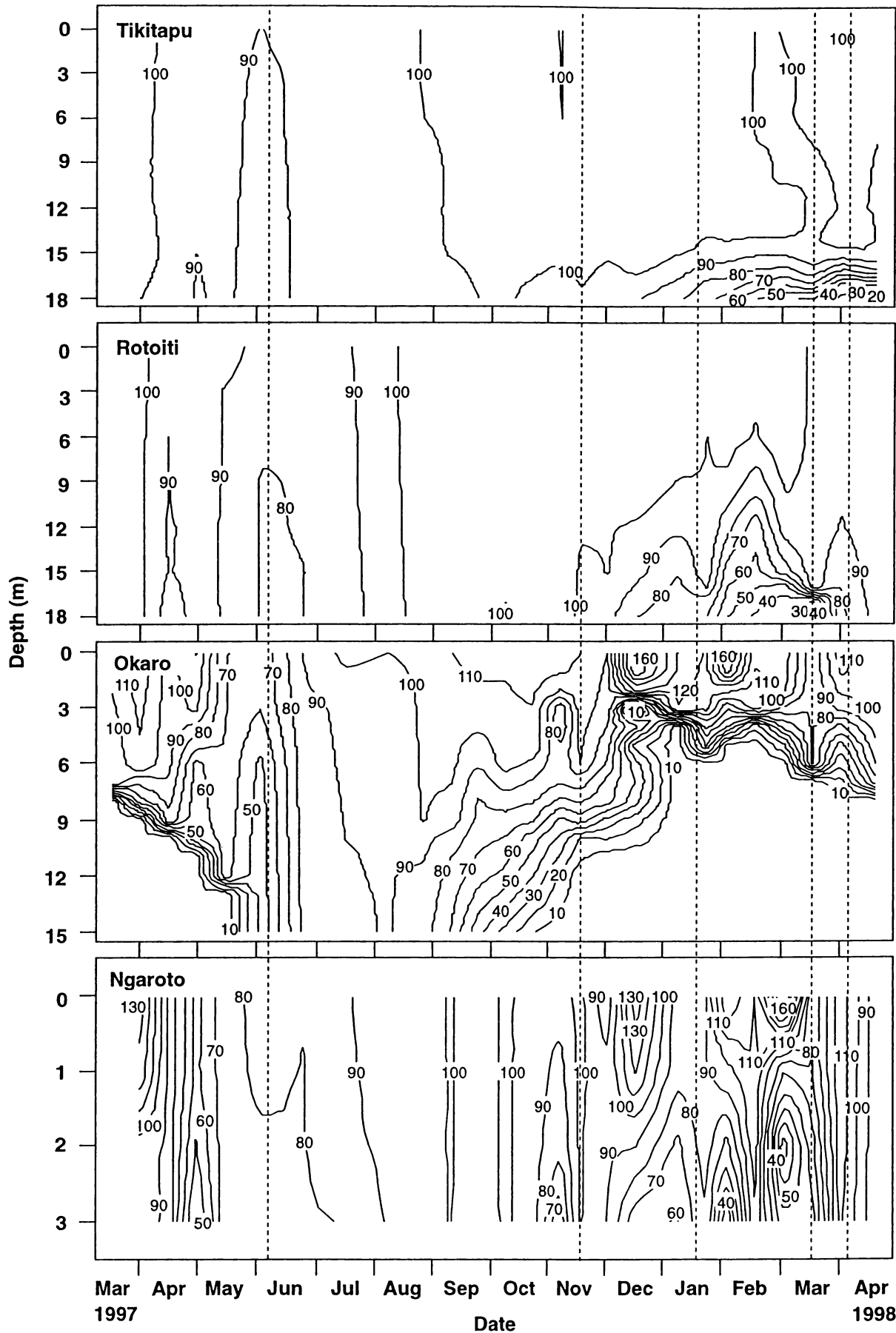


Fig. 3.6. Spatial and temporal distribution of %O in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

Levels of pH were generally lowest in winter, and highest in summer (Fig. 3.7). Lake Okaro had the highest spatial variability, with especially high values found in the epilimnion during periods of thermal and oxygen stratification. Gradients were generally broken down at times of mixing (cf. Fig. 3.2). In general, lower pH levels were found in the lower trophic state lakes.

Conductivity (Fig. 3.8) was lower in Lake Tikitapu, and higher in Rotoiti than the other lakes. Highest levels generally occurred in late winter to early spring, and also summer in Lake Ngaroto. Temporal variability was greater than spatial variability.

Total chlorophyll *a* (Fig. 3.9) was generally lowest in Lake Tikitapu, increasing in Lakes Rotoiti, Ngaroto and Okaro respectively. Lakes Tikitapu and Rotoiti had highest concentrations in August and September (late winter to early spring), with Tikitapu also having high levels at depth during thermal stratification and high stability. Lake Okaro chlorophyll *a* levels were highest from spring to mid-summer, with highest values occurring throughout the water column when the lake was well mixed (winter), or close to the surface when stratification of temperature and oxygen occurred (spring and summer). In Lake Ngaroto peak chlorophyll *a* levels occurred from late summer to early spring. In all lakes, the microplankton fraction was generally more important than the nanoplankton fraction, and peak levels of microplankton and whole chlorophyll *a* generally coincided (cf. Fig. 3.10 and 3.11). Spatial variability of chlorophyll *a* during periods of thermal stratification, in particular the nanoplankton fraction, was generally reduced by mixing events (Fig. 3.2). Maximum and mean values of chlorophyll *a* are given in Table 3.2.

Secchi depth was generally greatest in Lake Tikitapu, decreasing in Lakes Rotoiti, Okaro and Ngaroto (Fig. 3.12). Lakes generally had greatest Secchi transparencies in winter or autumn (June to August 1997, and March and April 1998). Lowest Secchi

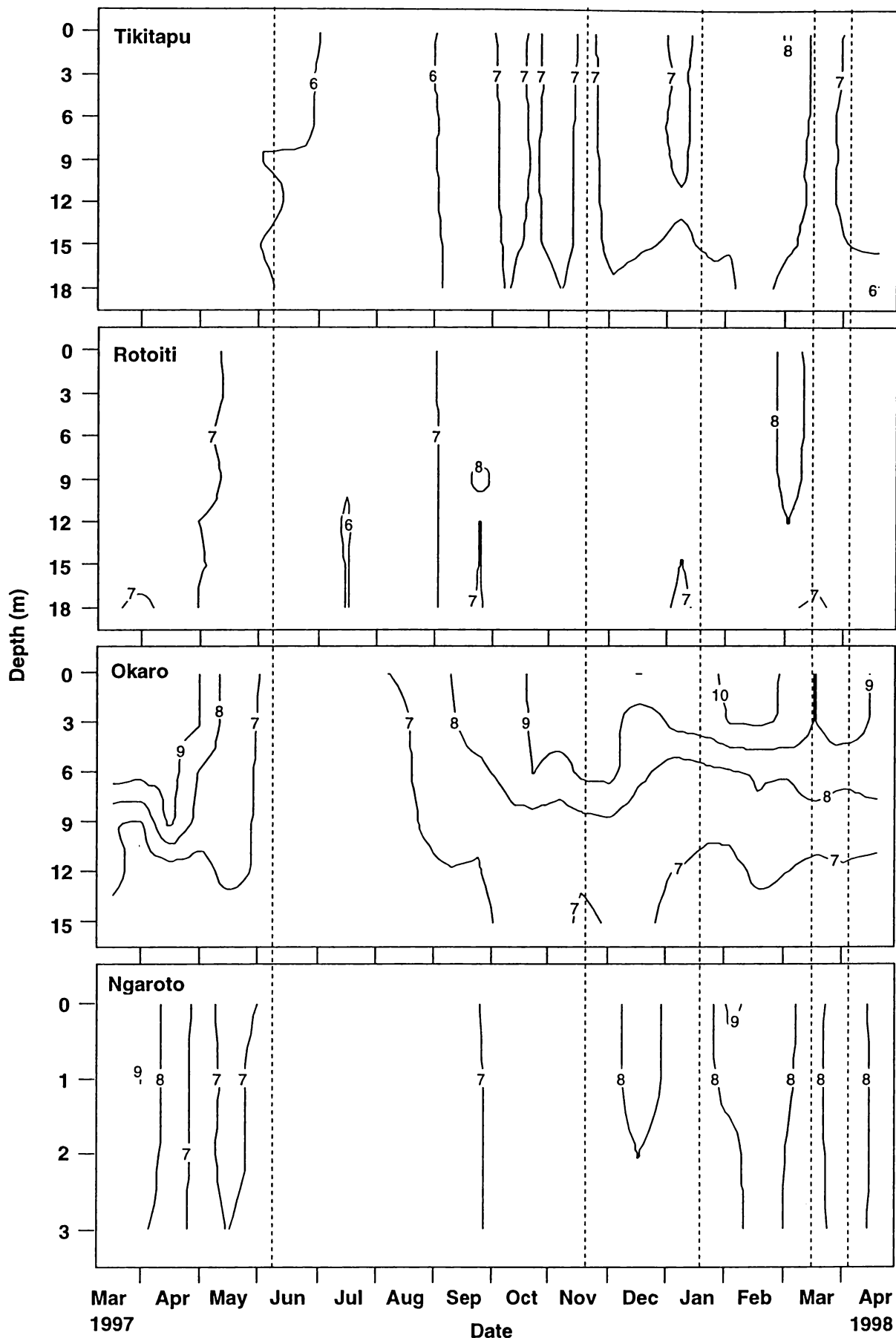


Fig. 3.7. Spatial and temporal distribution of pH in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

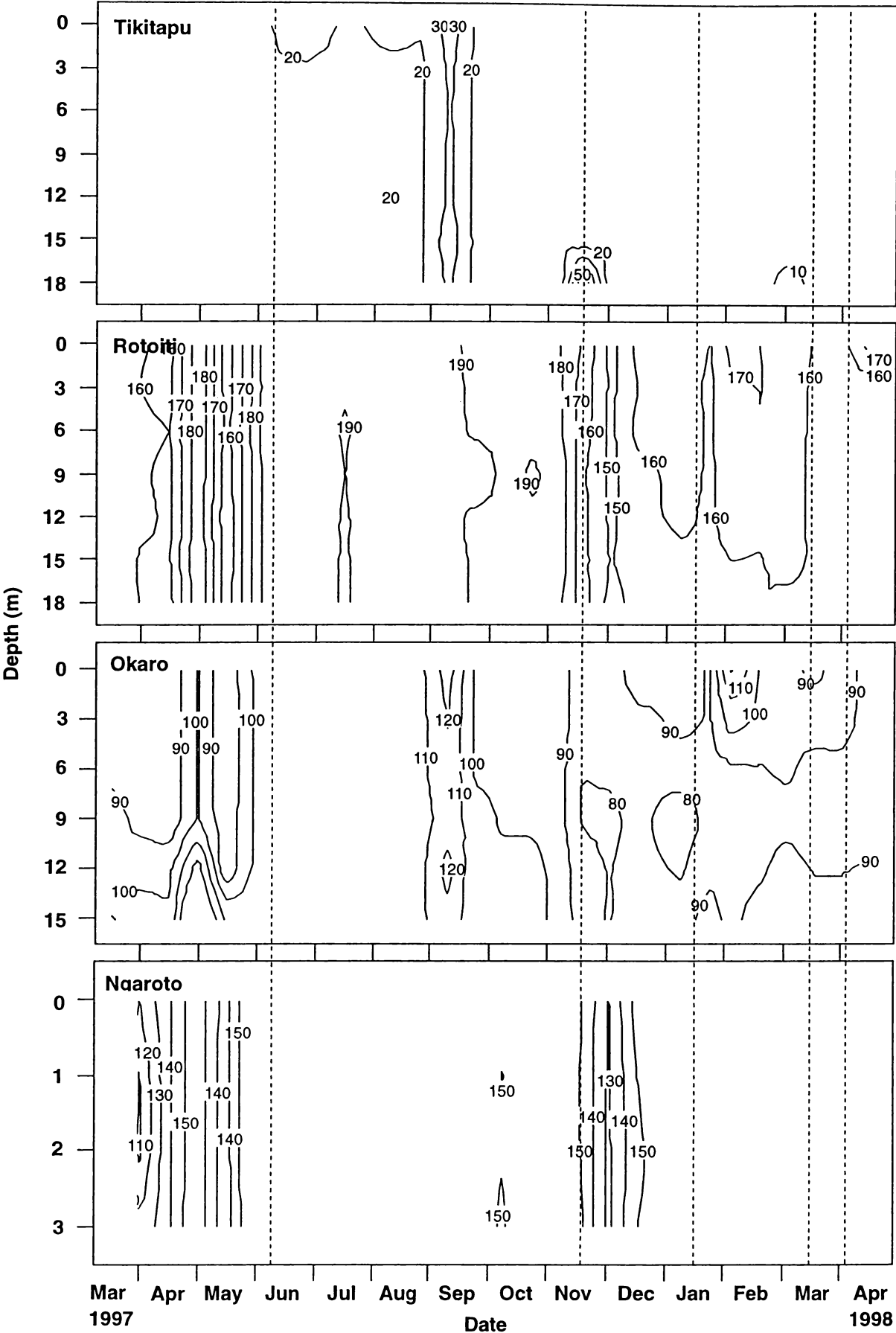


Fig. 3.8. Spatial and temporal distribution of conductivity (μs) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

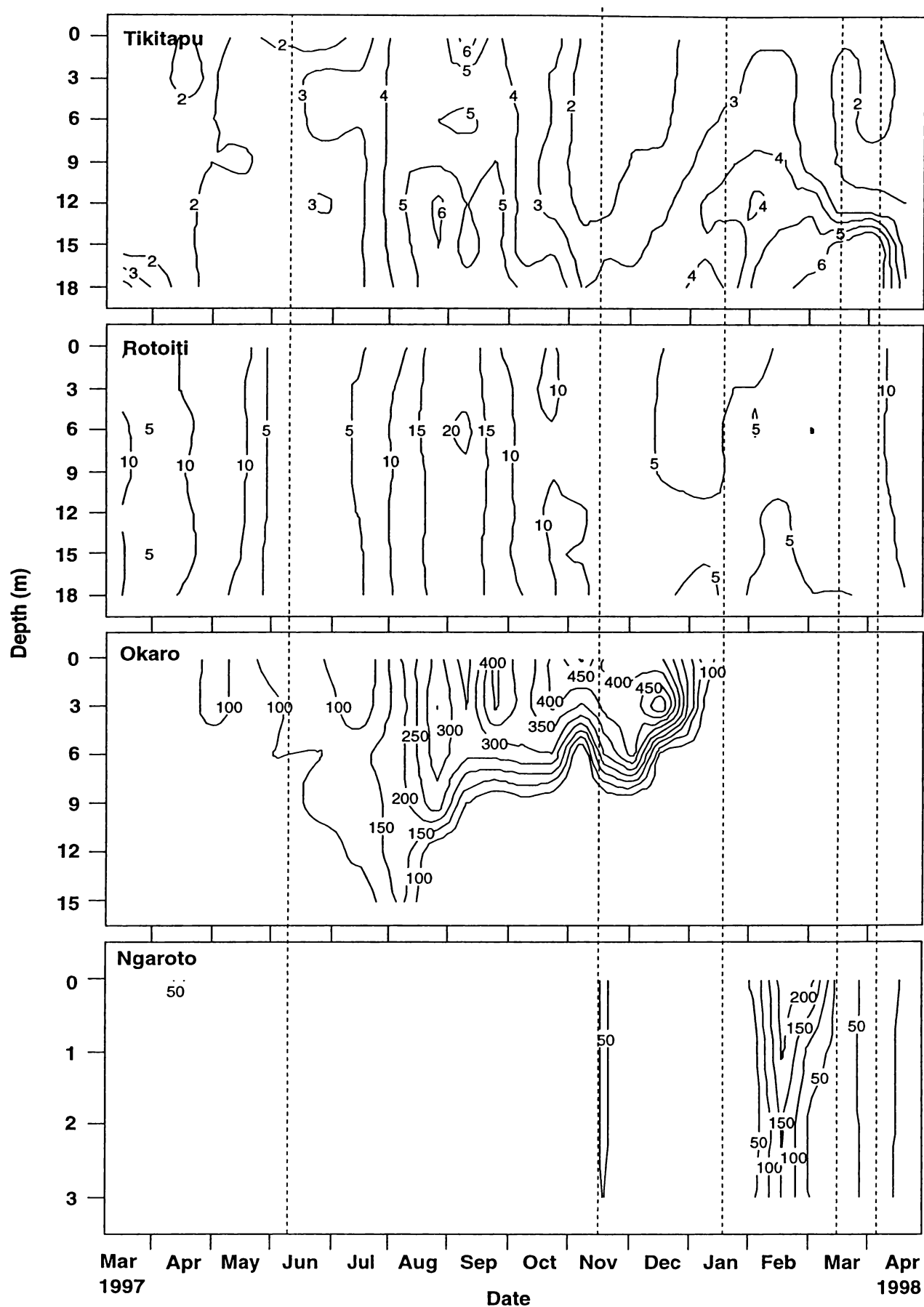


Fig. 3.9. Spatial and temporal distribution of total chlorophyll *a* (mg/L) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

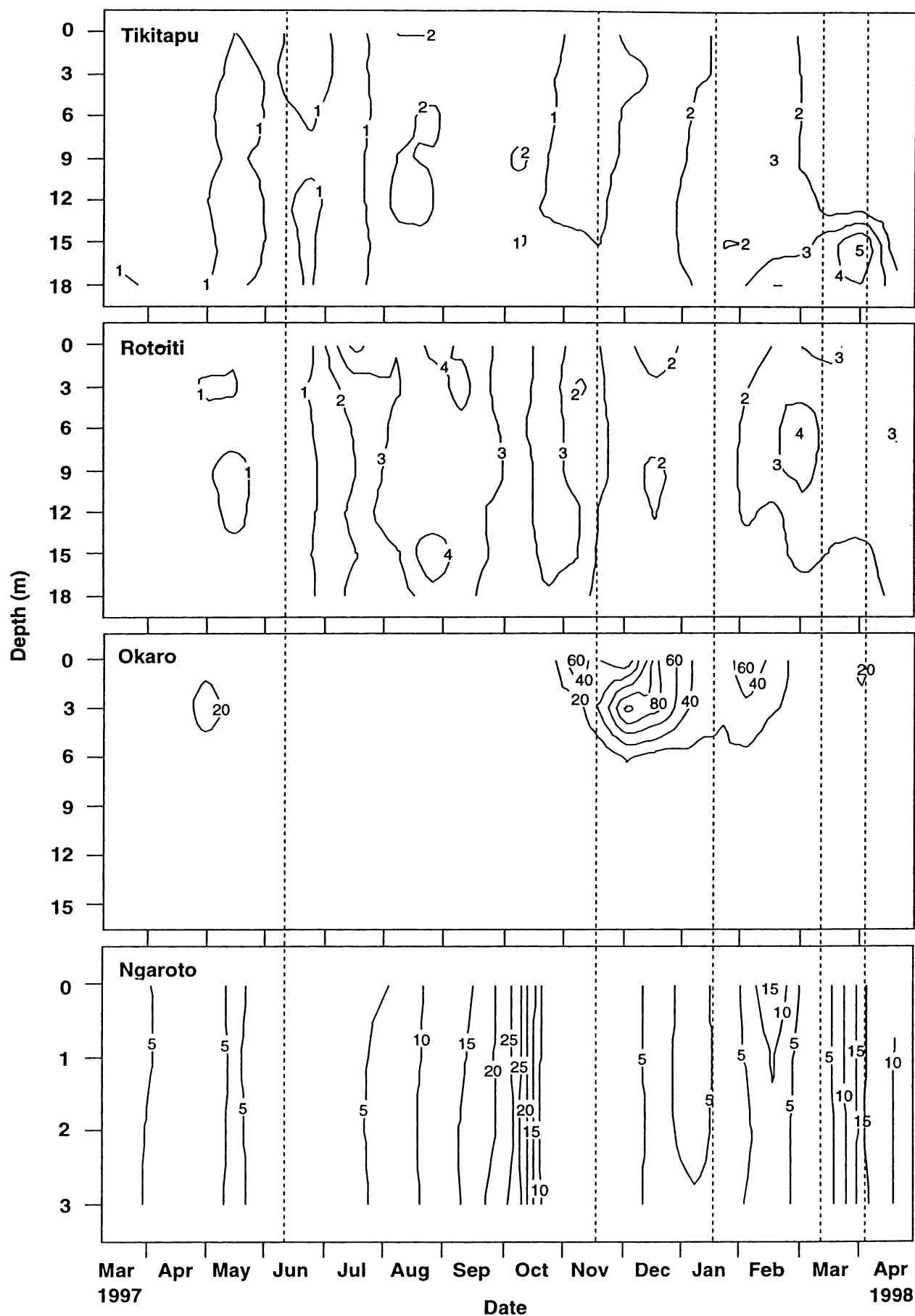


Fig. 3.10. Spatial and temporal distribution of nanoplankton (<20 μm size fraction) (mg/L) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

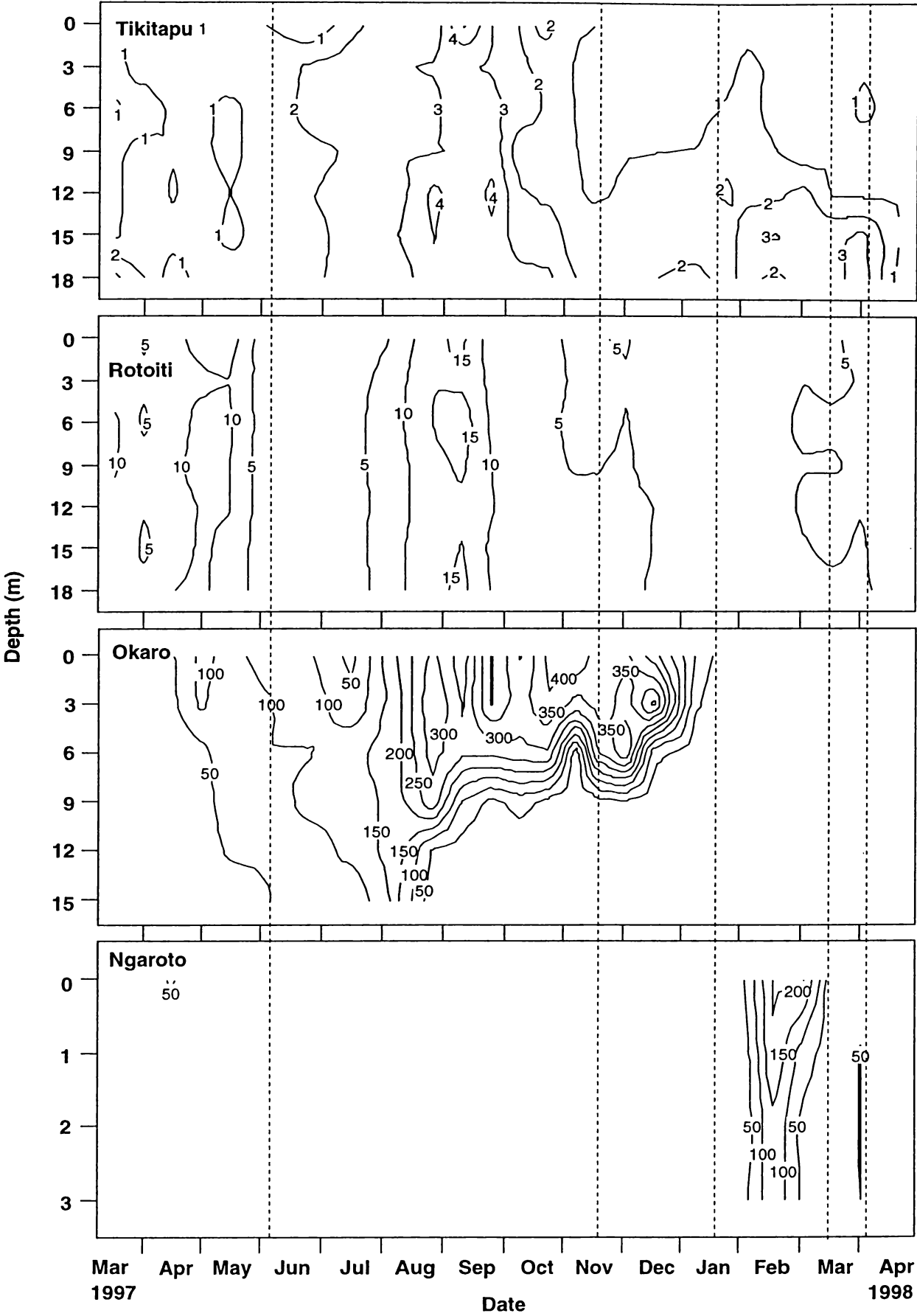


Fig. 3.11. Spatial and temporal distribution of microplankton (>20 μm size fraction) (mg/L) in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

Table 3.2. Chlorophyll *a* concentrations (mean 0-9 m) and Secchi depths recorded for Lakes Tikitapu, Rotoiti, Okaro and Ngaroto.

	Tikitapu	Rotoiti	Okaro	Ngaroto
Maximum chlorophyll <i>a</i> (mg/L)	5.25 (11/9/97)	18.04 (28/8/97)	322.71 (28/8/97)	182.99 (18/2/98)
Mean chlorophyll <i>a</i> (mg/L)	2.71	8.43	134.35	34.51
Minimum Secchi depth (m)	3.5 (4/2/98)	3.3 (11/9&22/10/97)	0.6 (4/2&19/2/98)	0.25 (4/3/98)
Mean Secchi depth (m)	5.03	4.46	1.25	0.68

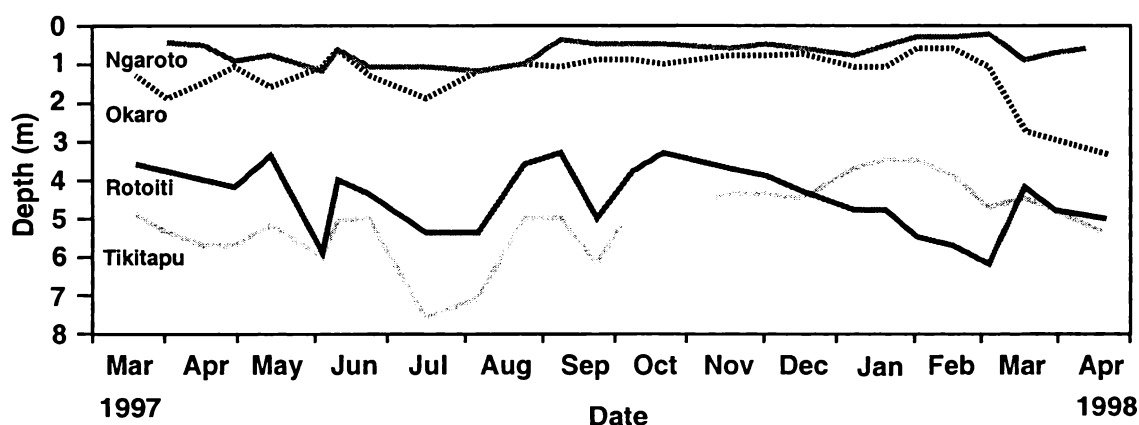


Fig. 3.12. Temporal variability of secchi depth in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto.

transparencies generally occurred in summer (December to February 1998), except in Lake Rotoiti in September. Lowest Secchi generally coincided with peak chlorophyll *a* concentrations in all lakes (cf. Fig 3.9).

Rotifer diversity

A total of 54 species of monogonont rotifer was recorded: 38 from Lake Tikitapu, 43 from Lake Rotoiti, 42 from Lake Okaro and 39 from Lake Ngaroto (Table 3.3). α diversity (total number of species) was generally greatest in Lake Rotoiti, intermediate in

Table 3.3. List of rotifer species from the four study lakes. An asterisk (*) marks presence. Species comprising > 4 % in any sample and therefore used in further analysis indicated by two asterisks (**).

	Tikitapu	Rotoiti	Okaro	Ngaroto
<i>Anuraeopsis fissa</i> (Gosse)		*	*	*
<i>A. navicula</i> Rousselet	**			
<i>Ascomorpha ovalis</i> (Bergendal)	**	**	**	*
<i>Ascomorphella volvocola</i> (Plate)	*	*		
<i>Asplanchna priodonta</i> Gosse	**	**	**	**
<i>A. sieboldi</i> (Leydig)	**	**	**	**
<i>Brachionus angularis</i> Gosse	*	*	*	*
<i>B. budapestinensis</i> Daday				*
<i>B. calyciflorus</i> Pallas	*	*	*	**
<i>B. quadridentatus</i> Hermann			*	
<i>Cephalodella biungulata</i> (Wulfert)	*			
<i>C. catellina</i> (Müller)	*	**	**	*
<i>C. exigua</i> (Gosse)			*	
<i>C. gibba</i> (Ehrenberg)	*	*	*	*
<i>Colurella uncinata</i> (Müller)		*	*	*
<i>Collotheca</i> sp.	**	**	**	*
<i>Conochilus coenobasis</i> (Skorikov)	**	**	*	**
<i>C. unicornis</i> Rousselet		**		
? <i>Eothinia</i> sp.	*			
<i>Epiphanes macrourus</i> (Barrois & Daday)				*
<i>Euchlanis dilatata</i> Ehrenberg		*	*	*
<i>Filinia longiseta</i> (Ehrenberg)	**	*	**	**
<i>F. novaezealandiae</i> Shiel & Sanoamuang	**	**	**	*
<i>F. cf. pejeri</i> Hutchinson	*	**	**	*
<i>F. terminalis</i> (Plate)		**	**	
<i>Hexarthra intermedia</i> (Wiszniewski)		**	**	**
<i>H. mira</i> (Hudson)	**			
<i>Keratella cochlearis</i> (Gosse)	**	**	**	**
<i>K. procurva</i> (Thorpe)	**	**	**	*
<i>K. slacki</i> (Berzins)	**	**	**	*
<i>K. tecta</i> (Gosse)	*	*	**	**
<i>K. tropica</i> (Apstein)	*	*	**	**
<i>Lecane bulla</i> (Gosse)	*			*
<i>L. closterocerca</i> (Schmarda)	*	*	*	*
<i>L. flexilis</i> (Gosse)	*	*	*	*
<i>L. hamata</i> (Stokes)	*	*	*	
<i>L. luna</i> (Müller)	*	*		
<i>L. lunaris</i> (Ehrenberg)	*	*	*	*
<i>Lepadella acuminata</i> (Ehrenberg)	*		*	
<i>L. patella</i> (Müller)		*	*	
<i>Pompholyx complanata</i> Gosse	**	**	**	**
<i>Polyarthra dolichoptera</i> Idelson	**	**	**	**
<i>Monommata</i> sp.		*		
<i>Mytilina bisulcata</i> (Lucks)			*	
<i>Synchaeta oblonga</i> Ehrenberg	**	**	**	**
<i>S. pectinata</i> Ehrenberg	**	**	**	**
<i>Testudinella patina</i> (Hermann)	*			
<i>Trichocerca longiseta</i> (Schränk)	**	**	*	*
<i>T. porcellus</i> (Gosse)		*		
<i>T. pusilla</i> (Jennings)	**	**	**	**
<i>T. rattus</i> (Müller)			*	*
<i>T. similis</i> (Wiszniewski)	**	**	**	**
<i>T. stylata</i> (Gosse)	*	**	*	*
<i>T. tenuior</i> (Gosse)		*	*	**
<i>Trichotria tetractis</i> (Ehrenberg)		*		*
indet. Bdelloids	*	*	*	*

Lakes Ngaroto, Okaro, and least in Lake Tikitapu (Fig. 3.13). There appeared to be no general spatial or temporal trends in α . Spatial and temporal variability of Shannon-Wiener diversity (Fig. 3.14) was similar to α , although greater variation was apparent temporally than spatially. Equitability (Fig. 3.15) was generally greater in Lake Rotoiti than in Lakes Tikitapu, Okaro and least in Lake Ngaroto, indicating that abundance in Lakes Okaro and Ngaroto was often the result of a few species, as opposed to the lakes with lower trophic state where abundance was more evenly spread between species.

Seasonal and spatial dynamics

(i) Total numbers

Total abundance of rotifers appeared to be related to lake trophic state, with abundances generally greatest in Lakes Ngaroto and Okaro, and lower in Rotoiti and Tikitapu (Fig. 3.16). Abundances were generally high in autumn (March-May), declining into winter (June-August) when the lowest abundances were found in all lakes. In Lakes Rotoiti, Okaro and Ngaroto total densities increased in late spring, reaching peak levels in late spring and summer. The spring increase in abundance occurred later in Lake Tikitapu than the other lakes, and peak abundances occurred in late summer. The timings in peak abundances in general coincided with high water column stability (summer and autumn), with densities lessening in this period during storm events (cf. Figs 3.2-3.4). Summer and autumn abundances were generally between 100 and 300 ind/L in Lake Tikitapu, 200 and 400 ind/L in Lake Rotoiti, 300 and 600 ind/L in Lake Okaro, and 500 and 1500 ind/L in Lake Ngaroto, and were therefore apparently related to lake trophic state. Lake Tikitapu peak abundances generally occurred between 6 and 12 m depth, and occasionally 18 m. In Lake Rotoiti peak abundances generally occurred between 6 and 15 m. In Lakes Tikitapu and Rotoiti the lowest abundances generally occurred in the surface waters. In Lake Okaro

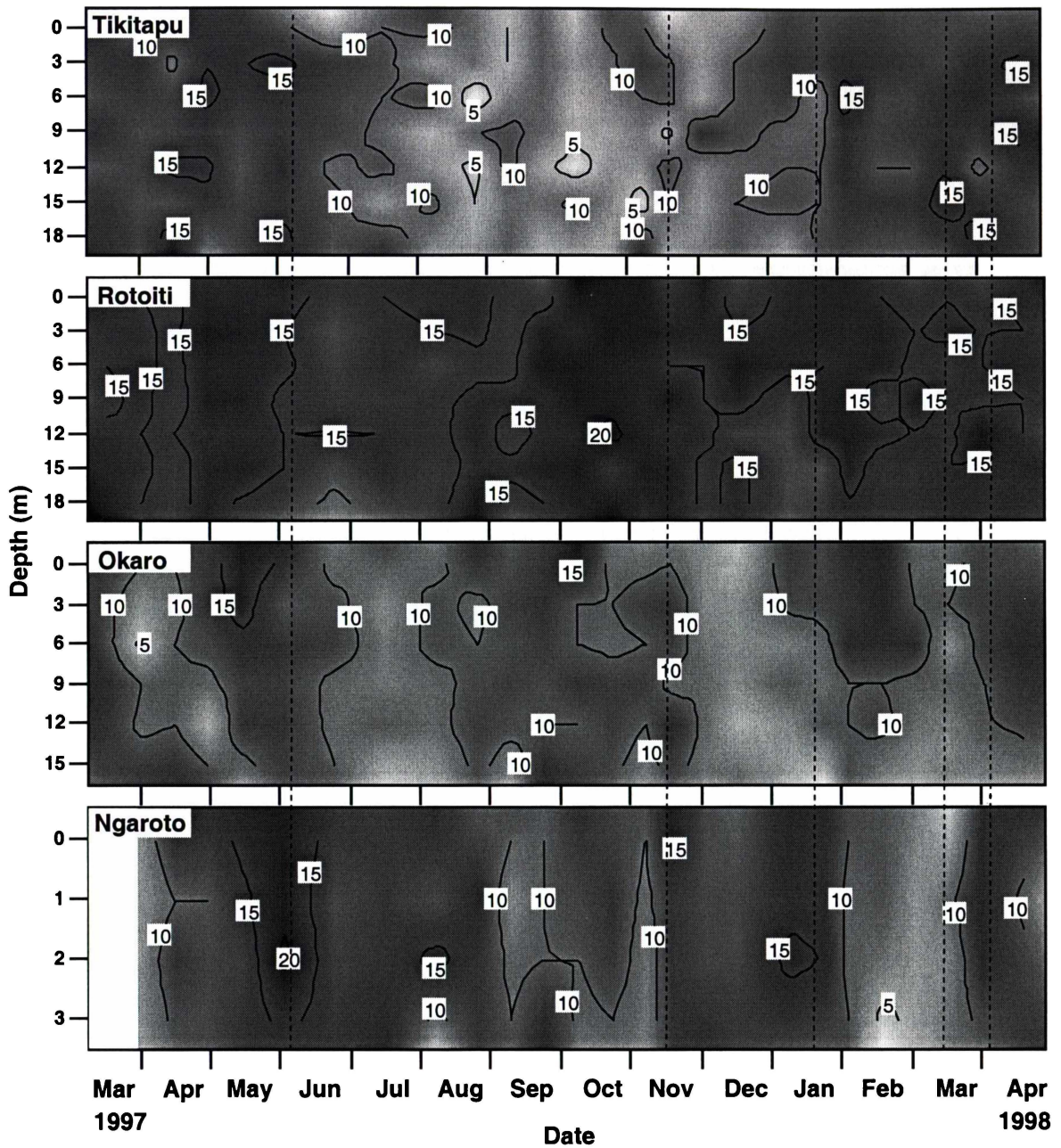


Fig. 3.13. Spatial and temporal distribution of α diversity of rotifers in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

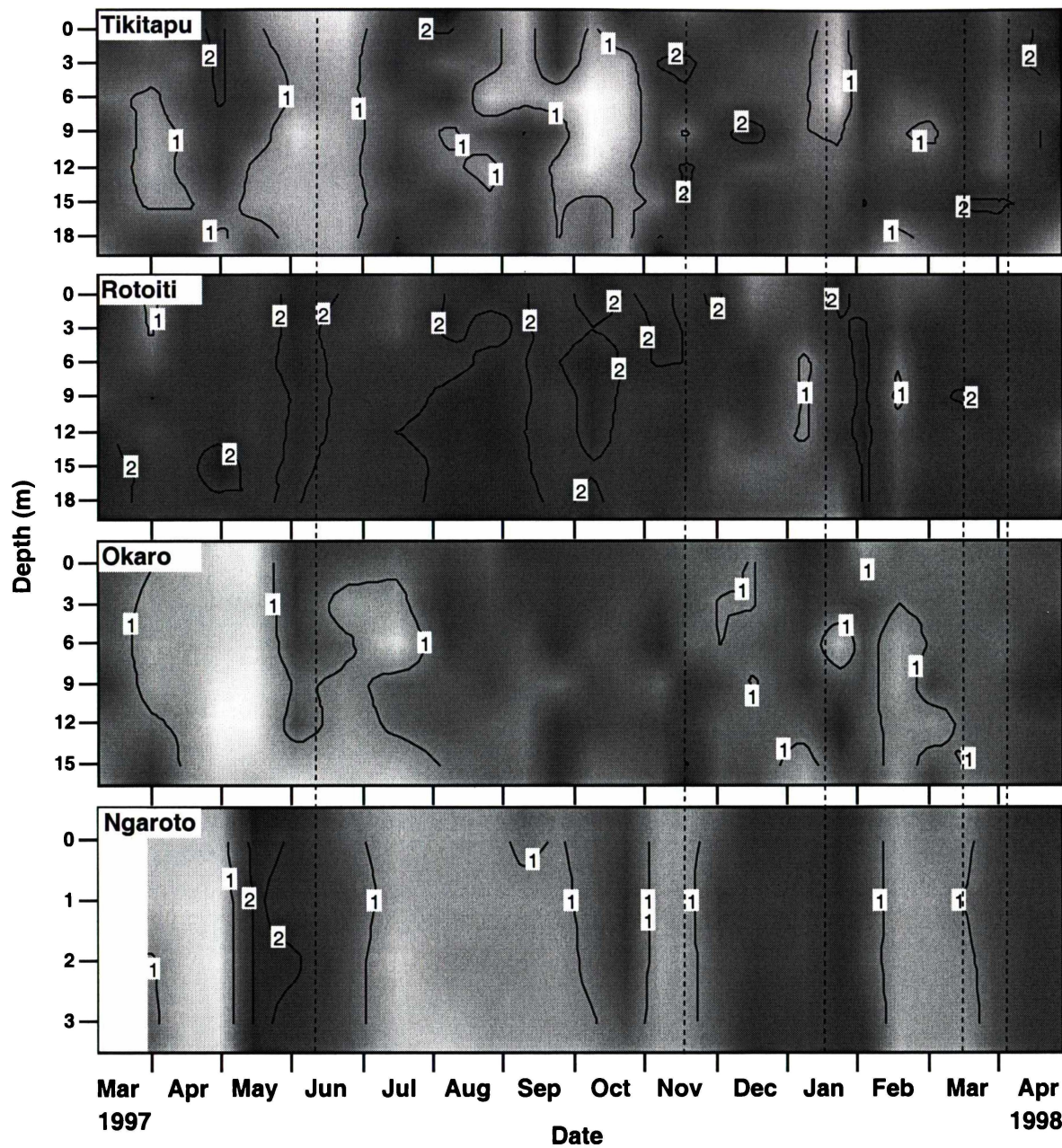


Fig. 3.14. Spatial and temporal distribution of Shannon-Wiener diversity in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

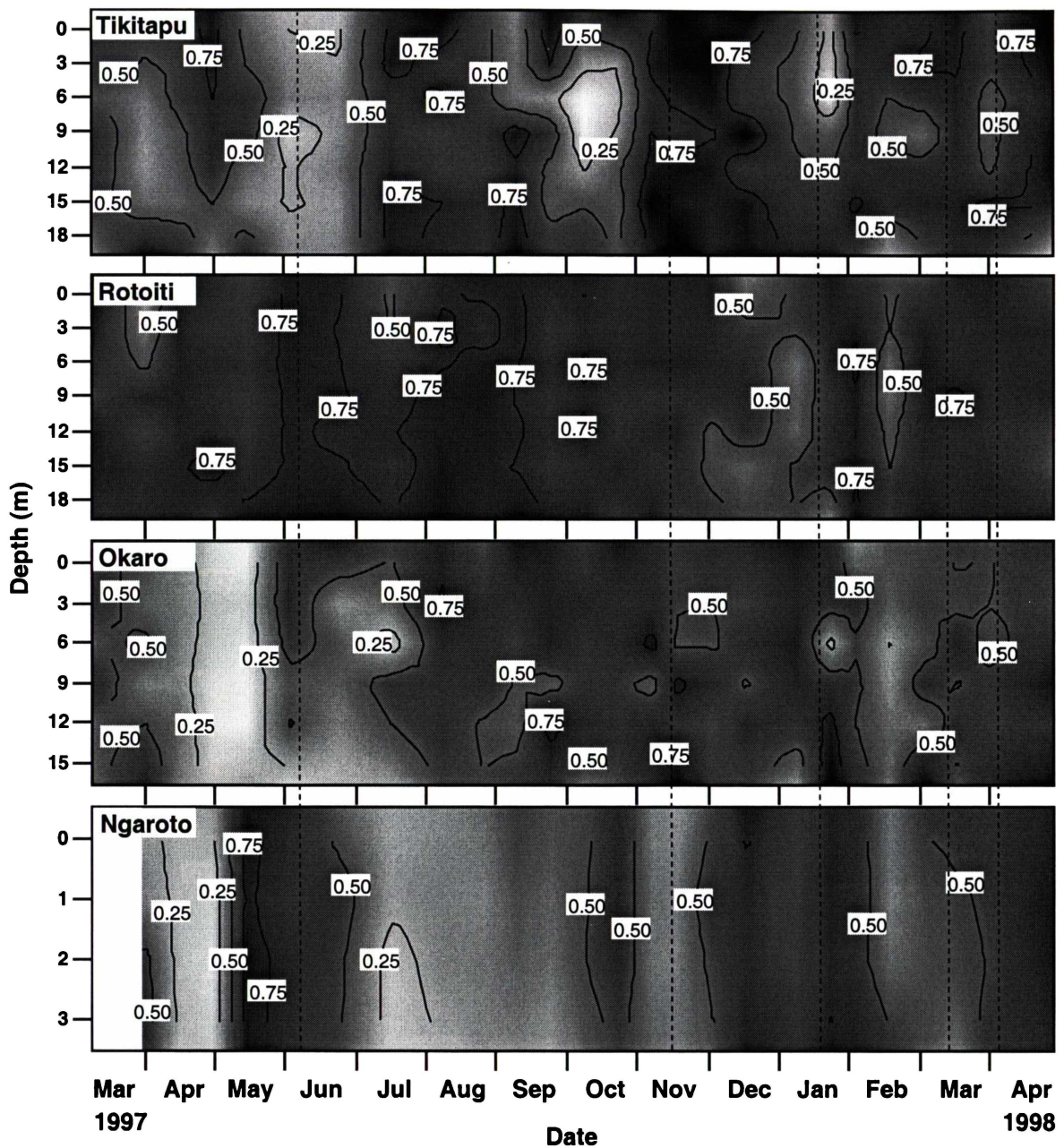


Fig. 3.15. Spatial and temporal distribution of equitability of rotifers in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

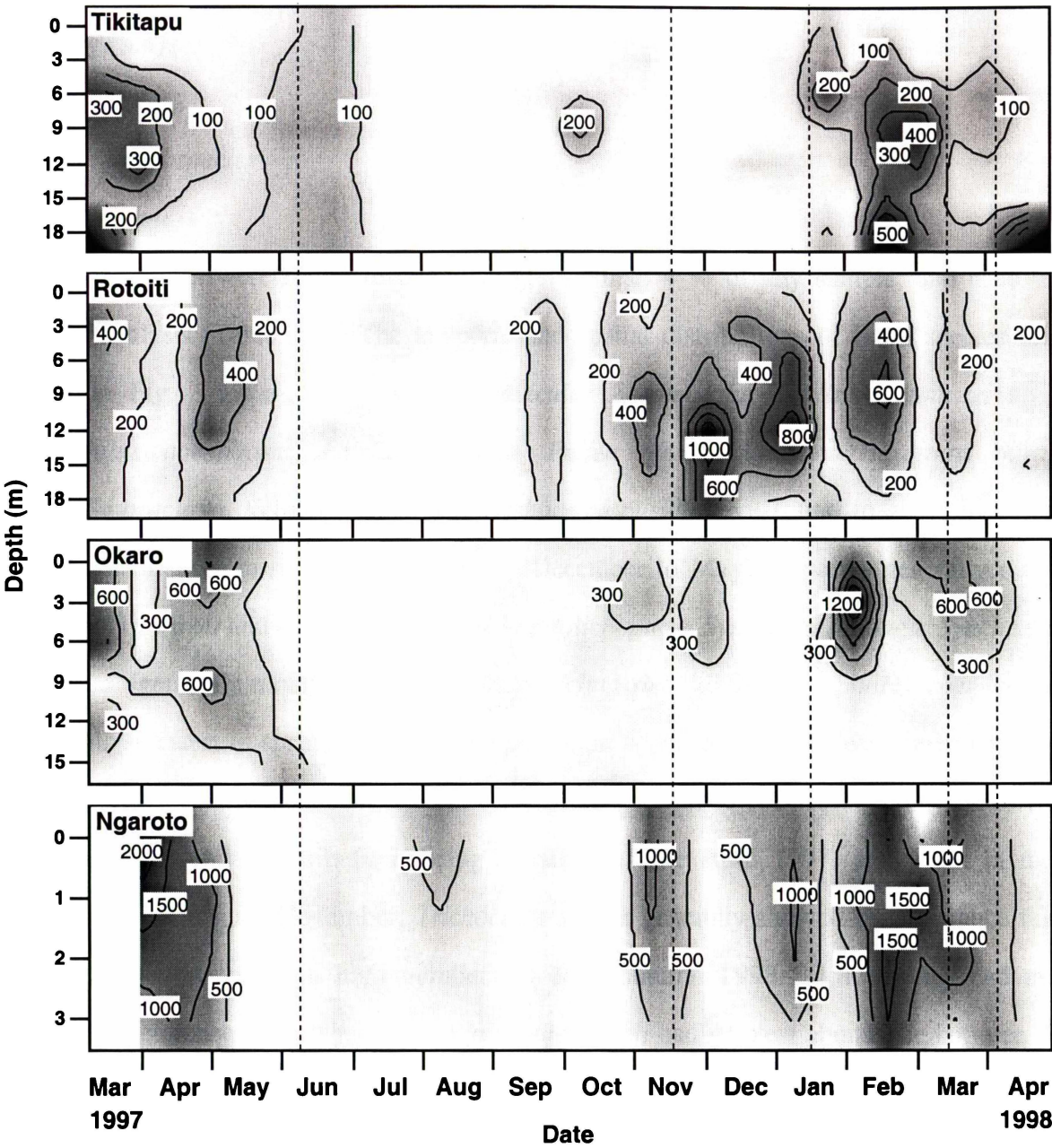


Fig. 3.16. Spatial and temporal distribution of total abundance (ind/L) of rotifers in Lakes Tikitapu, Rotoiti, Okaro and Ngaroto. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

and Ngaroto higher densities were generally near the surface. In all lakes the spatial distribution in total abundance was therefore generally associated with the greatest stability (cf. Fig. 3.4).

(ii) *Individual species*

Lake Tikitapu

Nineteen species were found to comprise greater than 4 % of any sample, and used in further analysis (Table 3.3). The temporal and spatial distributions of these species are given in Fig. 3.17 a-c. *Anuraeopsis navicula*, *Ascomorpha ovalis*, *Collotheca* sp., *Conochilus coenobasis*, *Filinia longiseta*, *Filinia novaezealandiae*, *Hexarthra mira*, *Keratella procurva*, *Keratella slacki* and *Trichocerca pusilla* were found to generally have greatest abundance in summer and autumn (December to May). Species generally most abundant in winter and spring were *Polyarthra dolichoptera*, *Synchaeta oblonga*, *Synchaeta pectinata*, (generally more so in winter), *Asplanchna sieboldi* and *Pompholyx complanata* (generally greatest in spring). *Asplanchna priodonta* appeared to have less preference for season, although was abundant once in early March. *Keratella cochlearis* and *Trichocerca longiseta* had similar distributions being abundant in late April 1997, and again in the surface waters in early November. *Trichocerca similis* generally showed no preference for season, but was found in high numbers in early autumn 1998. Most species had no apparent preference for depth, except *A. navicula* which had greatest abundance between 6 and 15 m, *Polyarthra dolichoptera* between 6 and 9 m, and *Filinia novaezealandiae* greater than 12 m.

Lake Rotoiti

Twenty-two species were found to comprise greater than 4 % of any sample, and used in further analysis (Table 3.3). The temporal and spatial distributions of these species are

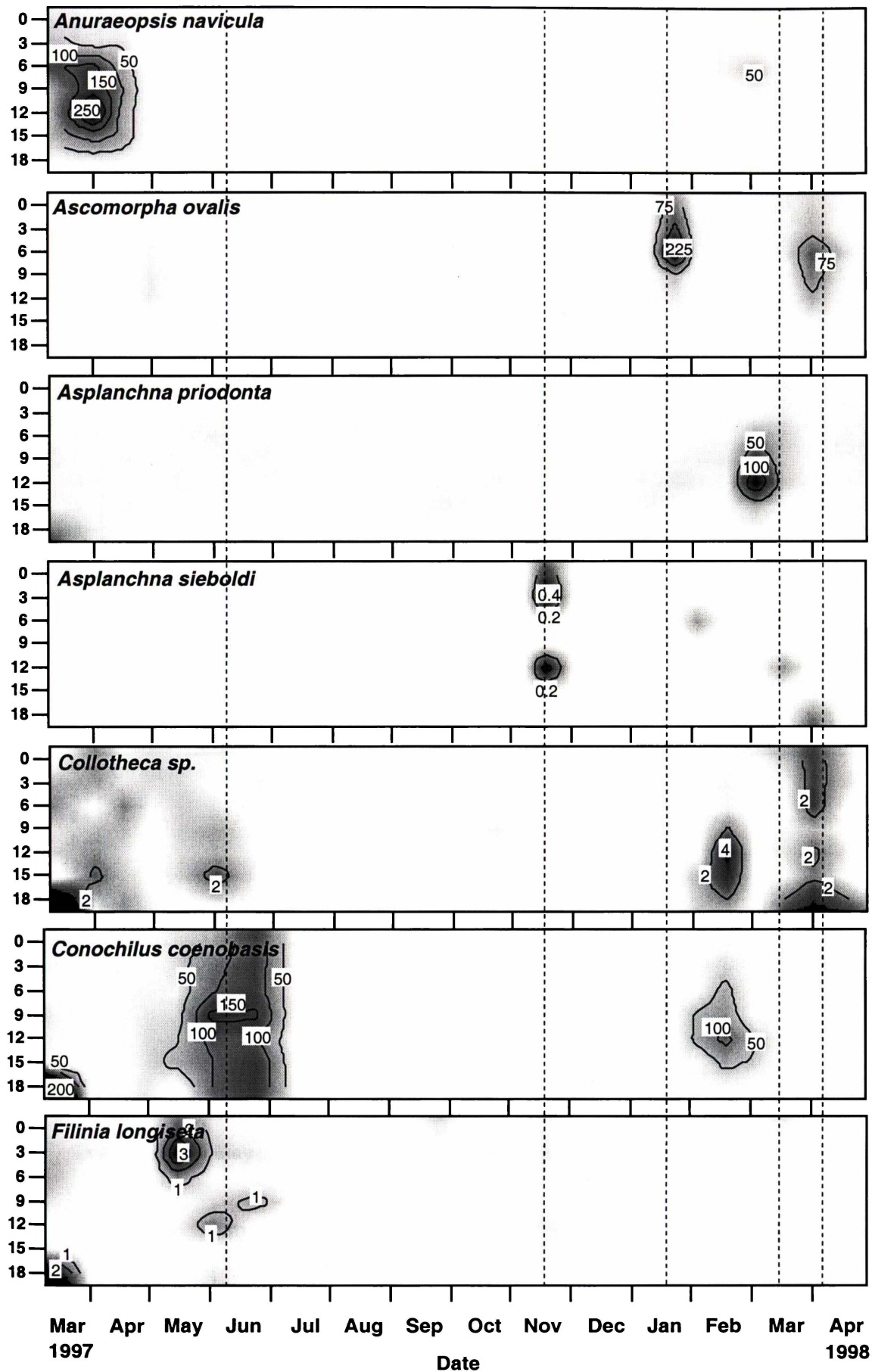


Figure 3.17 a. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Tikitapu rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

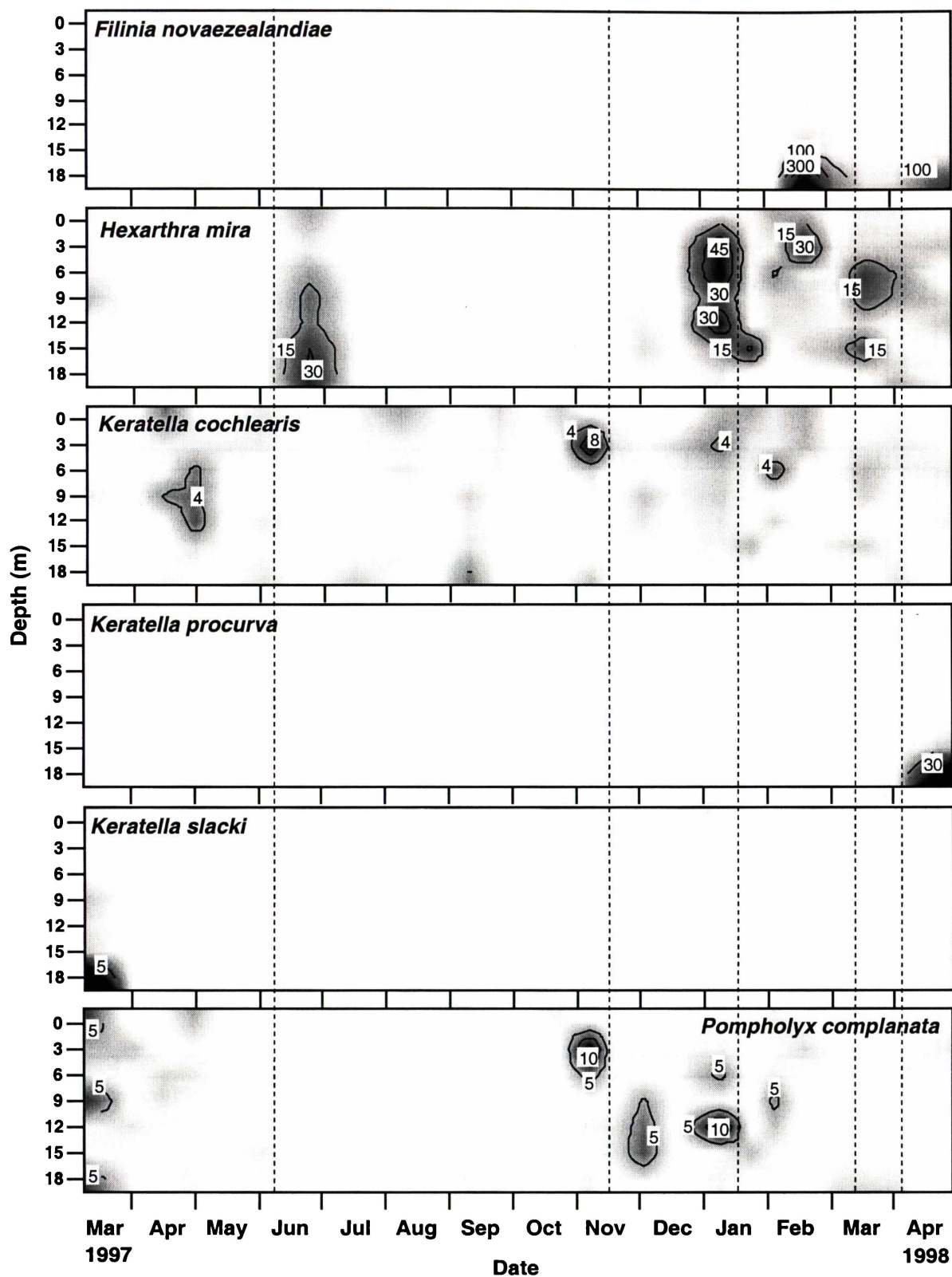


Figure 3.17 b. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Tikitapu rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

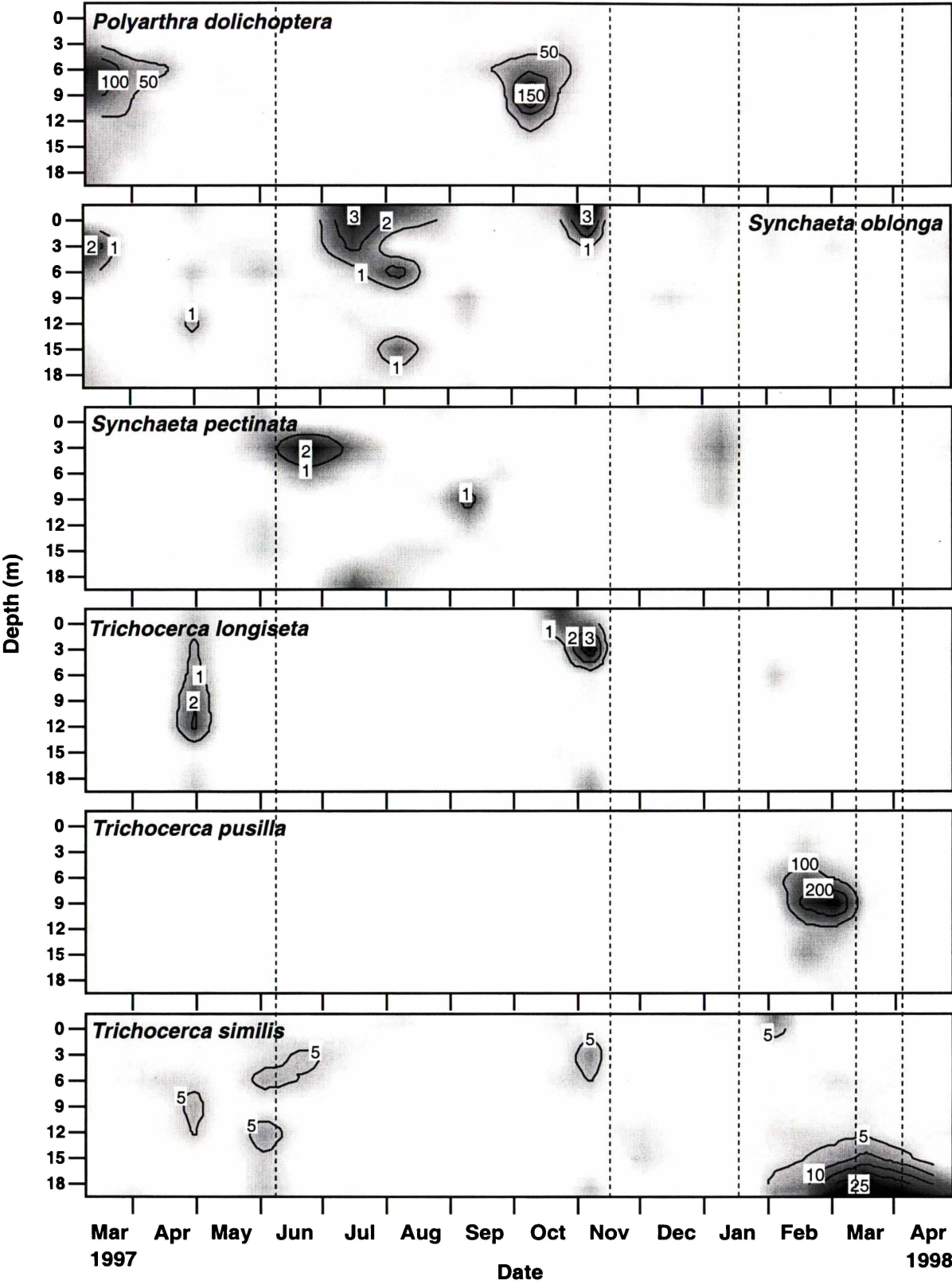


Figure 3.17 c. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Tikitapu rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

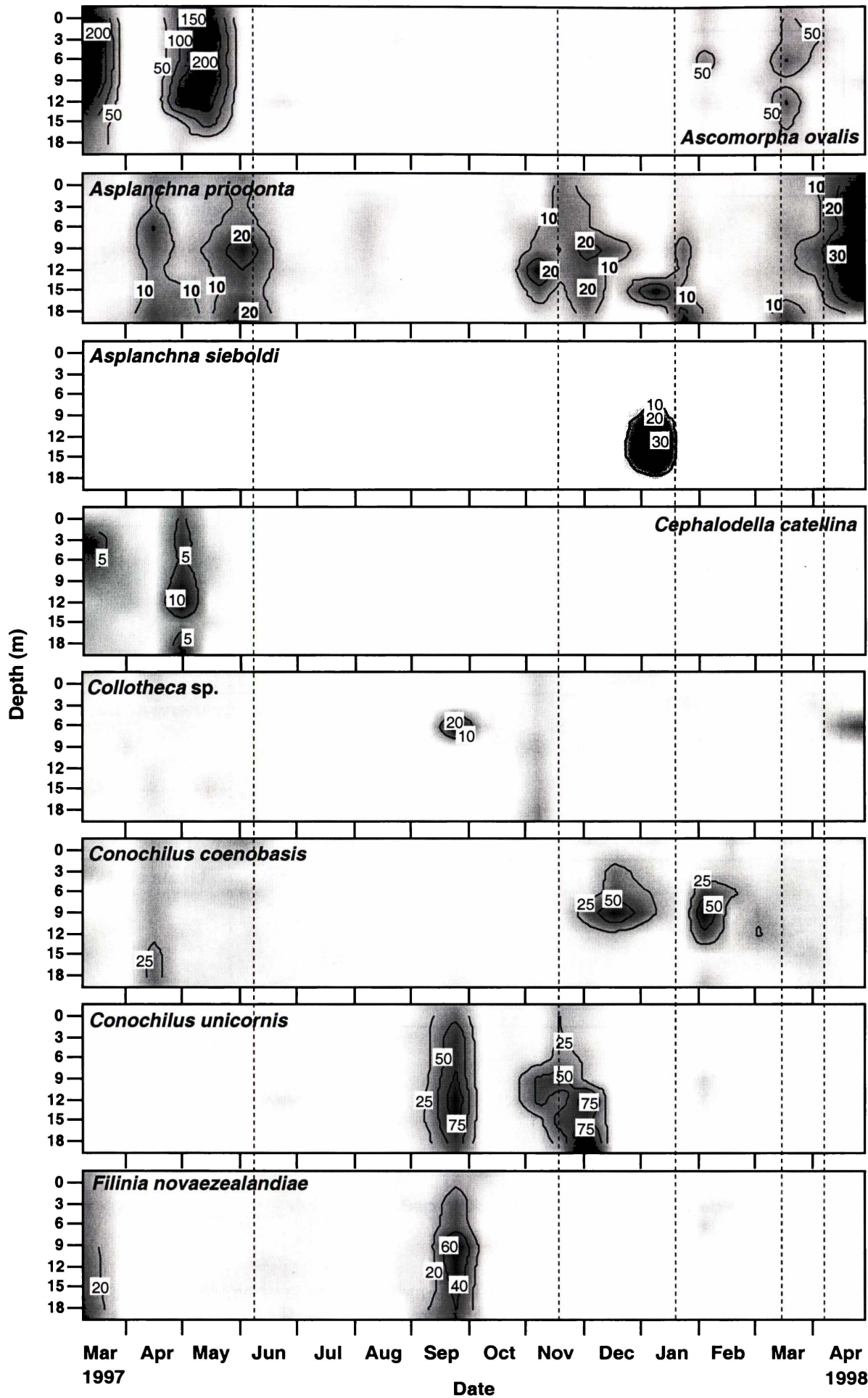


Figure 3.18 a. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Rotoiti rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

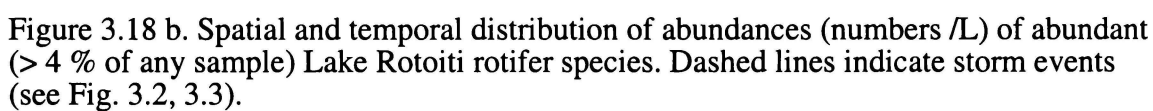


Figure 3.18 b. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Rotoiti rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

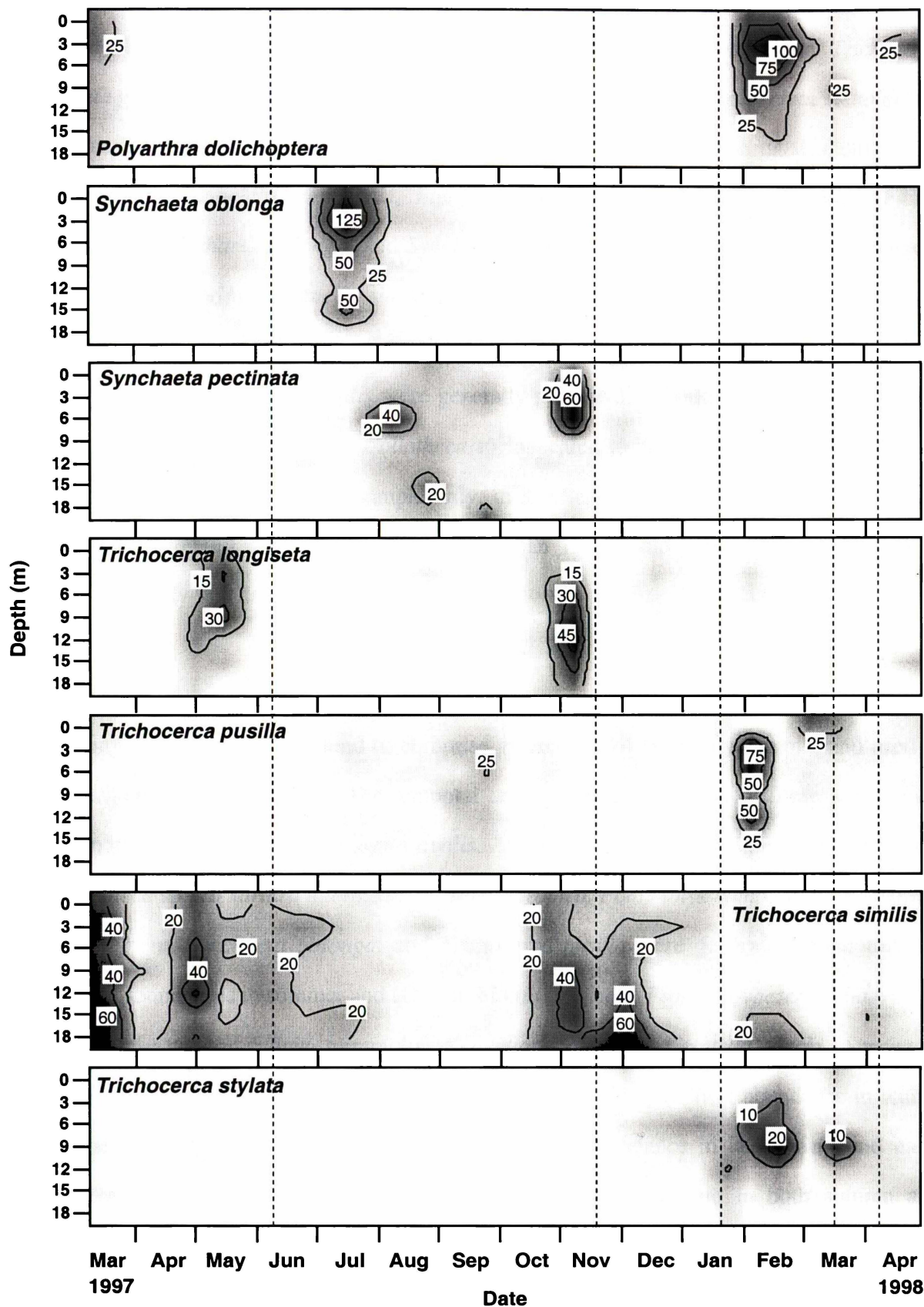


Figure 3.18 c. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Rotoiti rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

given in Fig. 3.18 a-c. *Ascomorpha ovalis*, *Asplanchna priodonta*, *Cephalodella catellina*, *Conochilus coenobasis*, *Hexarthra intermedia*, *Polyarthra dolichoptera* and *Trichocerca stylata* generally had highest abundances in summer and autumn. *Asplanchna sieboldi* and *Keratella procurva* also peaked in summer, although had more limited distributions temporally. *Conochilus unicornis*, *Filinia novaezealandiae*, *Filinia* cf. *pejleri*, *Filinia terminalis*, *Synchaeta oblonga*, and *Synchaeta pectinata* generally had highest abundances in winter or spring. *Keratella slacki* was found mainly in spring, although was also abundant in early April 1998. *Keratella cochlearis*, *Pompholyx complanata*, *Trichocerca longiseta* and *Trichocerca similis* were generally perennial, although had highest densities in both autumn and late spring. *Collotheca* sp. appeared to have no preference for season, having high abundance in one sample only, in late September at 6 m depth. *Ascomorpha ovalis* had greatest densities in samples less than 15 m, and *Conochilus coenobasis* at approximately 9 m depth.

Lake Okaro

Twenty-one species were found to comprise greater than 4 % of any sample, and used in further analysis (Table 3.3). The temporal and spatial distributions of these species are given in Fig. 3.19 a-c. *Ascomorpha ovalis*, *Asplanchna priodonta*, *Cephalodella catellina*, *Collotheca* sp., *Hexarthra intermedia*, *Keratella tropica*, *Pompholyx complanata*, *Polyarthra dolichoptera*, *Synchaeta oblonga*, and *Trichocerca pusilla* were generally found to have highest abundances in summer and autumn. *Filinia longiseta*, *Filinia novaezealandiae*, *Filinia* cf. *pejleri*, *Filinia terminalis*, *Keratella cochlearis*, *Keratella slacki*, *Synchaeta pectinata* and *Trichocerca similis* were generally found to have highest abundance in winter and spring. *Asplanchna sieboldi* was found in high abundance in late spring and early summer only. *Keratella procurva* was found to be most abundant in both autumn and spring, and *Keratella tecta* generally in winter and spring, but also in high abundance in mid-summer. *Asplanchna priodonta*, *Asplanchna sieboldi*, *Cephalodella catellina*,

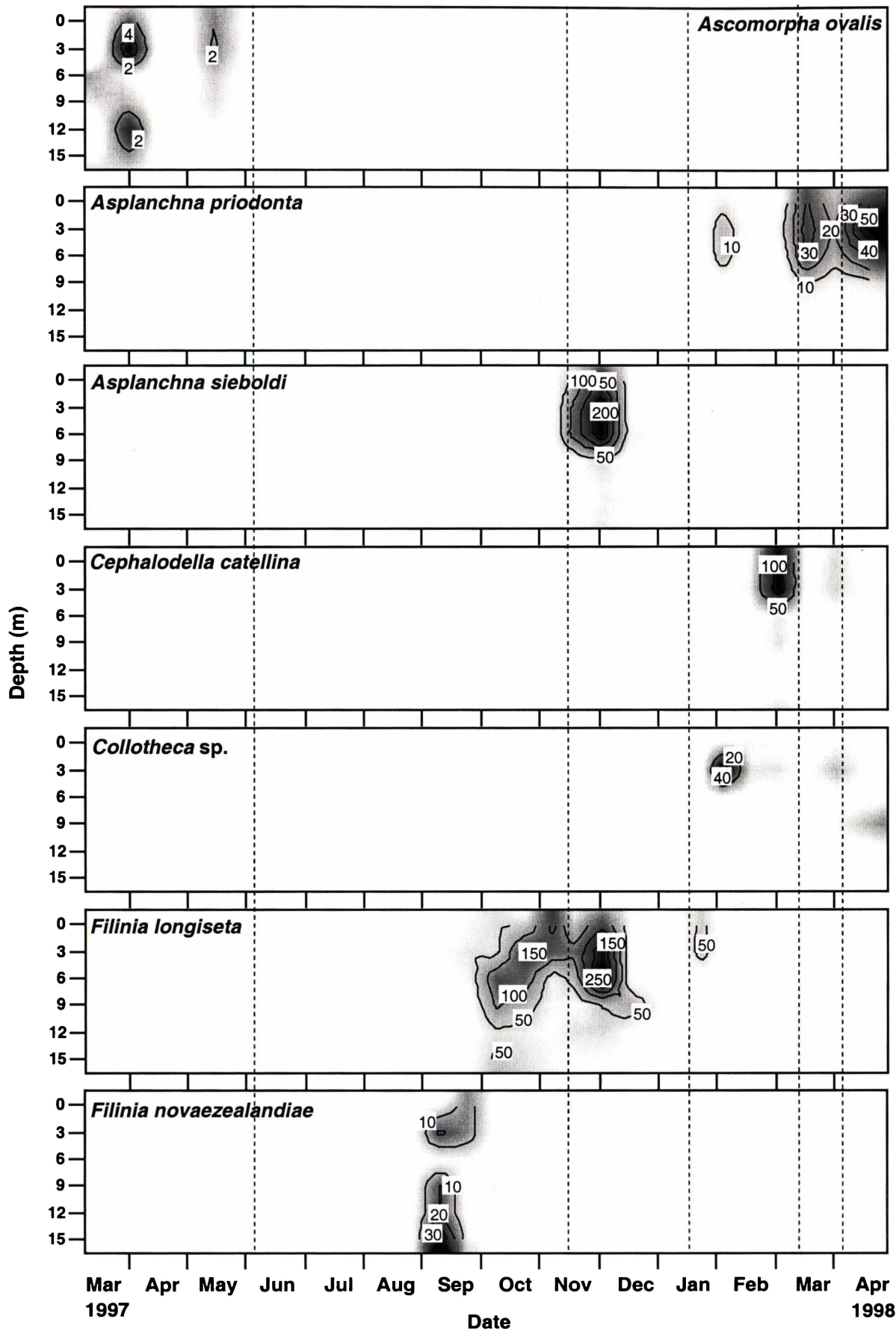


Figure 3.19 a. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Okaro rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

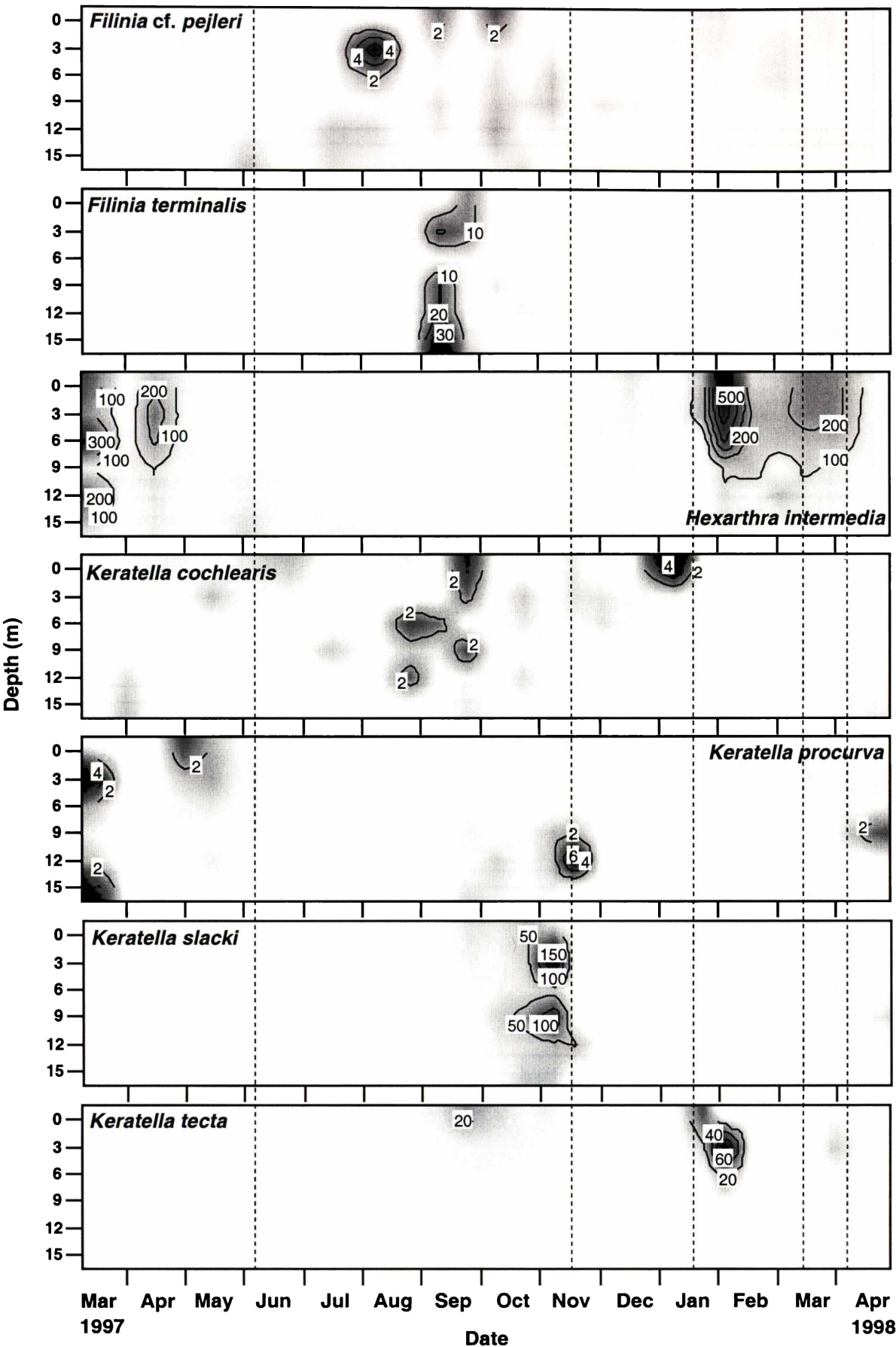


Figure 3.19 b. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Okaro rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

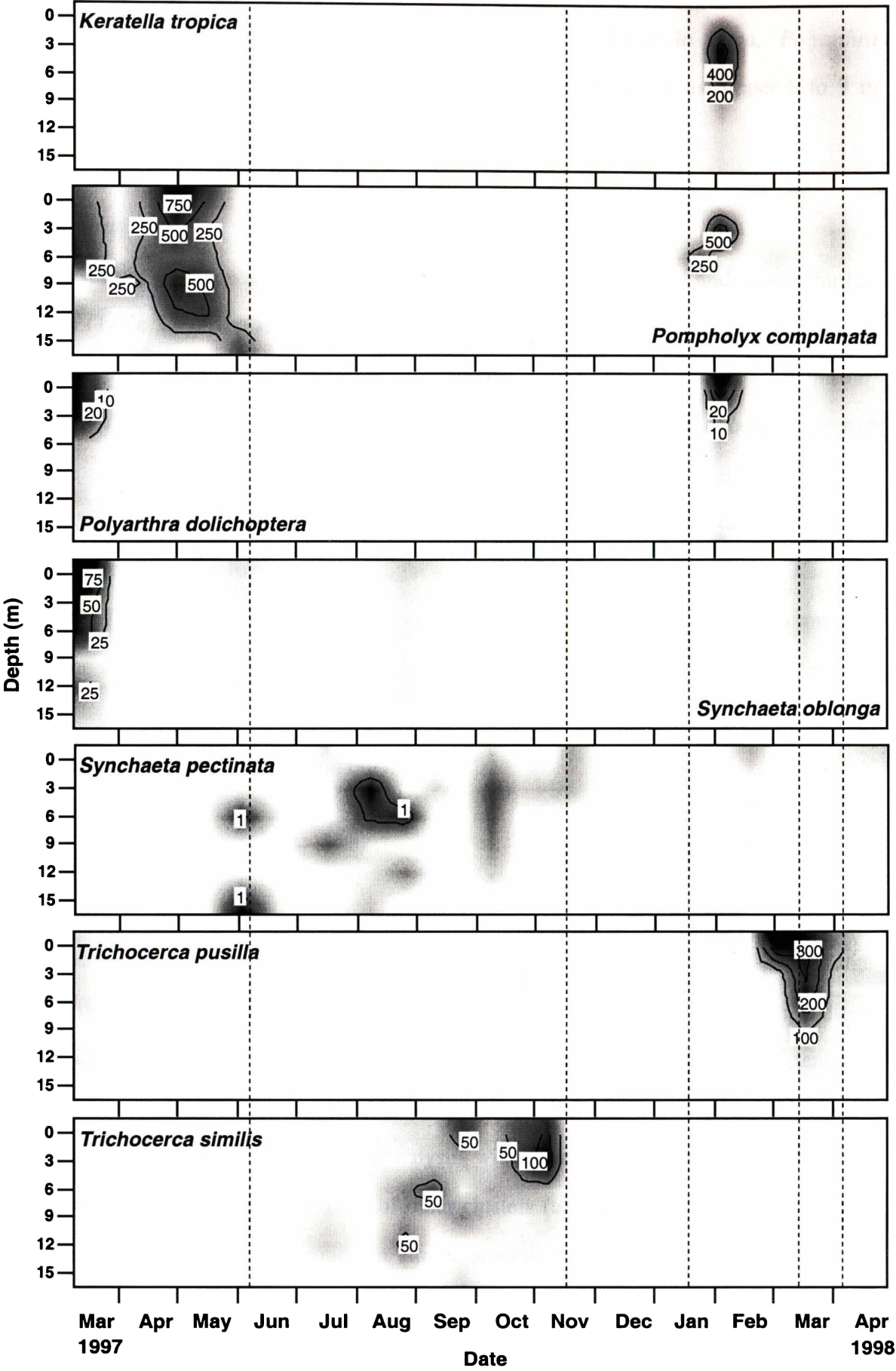


Figure 3.19 c. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Okaro rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).

Collotheca sp., *Filinia longiseta*, *Hexarthra intermedia*, *Keratella tecta*, *Polyarthra dolichoptera* and *Trichocerca pusilla* all showed some preference for the upper 6 to 9 m depth.

Lake Ngaroto

Sixteen species were found to comprise greater than 4 % of any sample, and used in further analysis (Table 3.3). The temporal and spatial distributions of these species are given in Fig. 3.20 a-b. *Asplanchna priodonta*, *Brachionus calyciflorus*, *Hexarthra intermedia*, *Keratella tecta*, *Keratella tropica*, *Pompholyx complanata*, *Polyarthra dolichoptera*, and *Trichocerca pusilla* were generally found to have highest abundances in summer and autumn. *Asplanchna sieboldi*, *Synchaeta oblonga*, *Synchaeta pectinata* and *Trichocerca similis* were generally found to have highest abundances in winter or spring. *Keratella cochlearis*, *Trichocerca pusilla* and *Trichocerca tenuior* were found to occur most commonly in winter and spring, although had highest abundances in early summer. These three species were most abundant in samples near the surface. *Conochilus coenobasis* had highest abundances in early autumn only.

(iii) Multivariate analyses

Lake Tikitapu

In Cluster analysis, division of clusters was made at levels of similarity where several large distinct groupings of samples could be discriminated. Cluster analysis of Lake Tikitapu (Fig. 3.21) revealed three major groupings of samples, plus several smaller clusters and individual samples, at the 55 % similarity level. The MDS ordination (Fig. 3.22) shows a similar distribution of data to the cluster analysis, with samples from the three main cluster groups generally separated from those of other clusters (although not distinctly). Samples not found in the main cluster groups in cluster analysis were generally peripheral to the

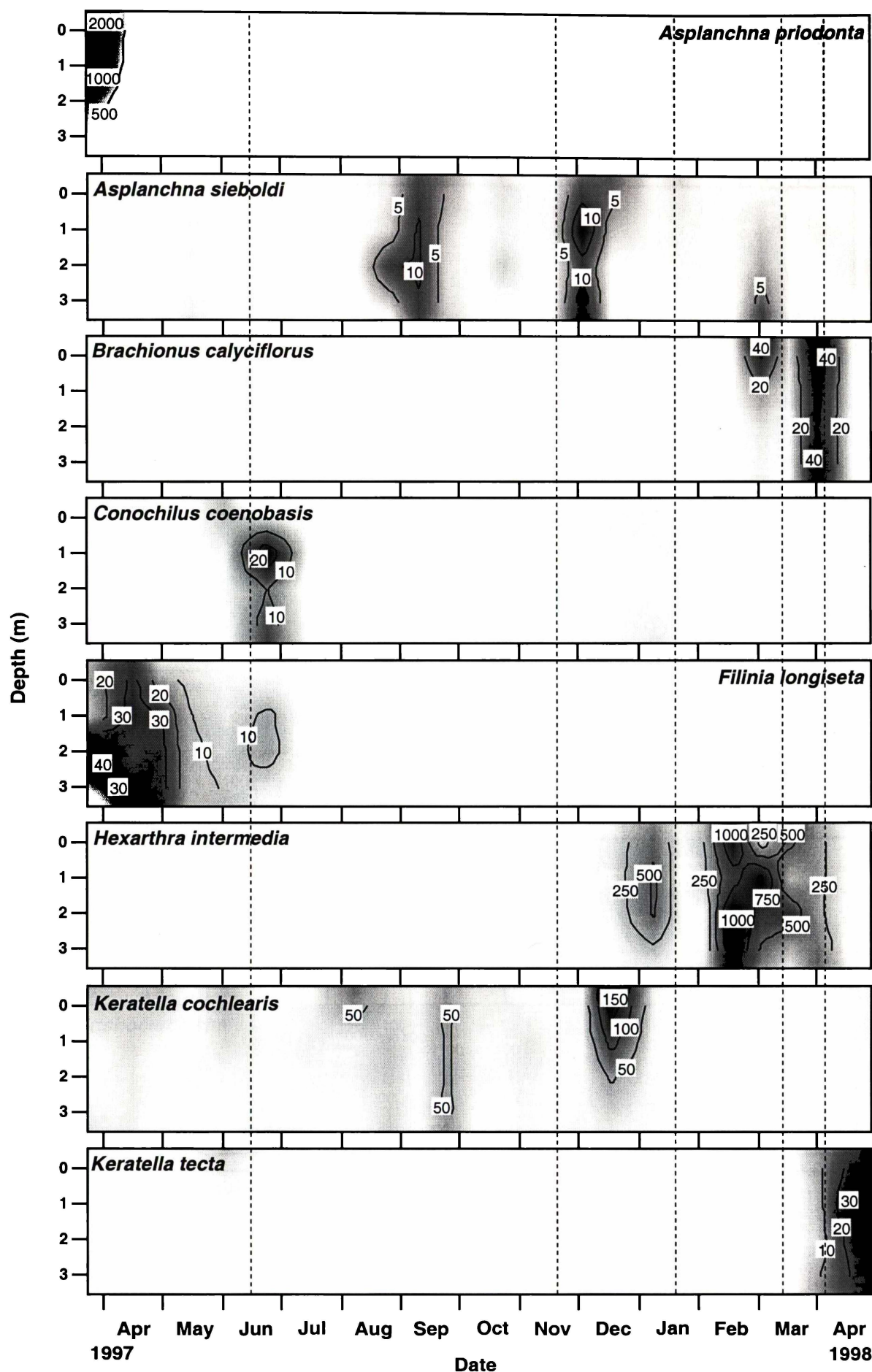
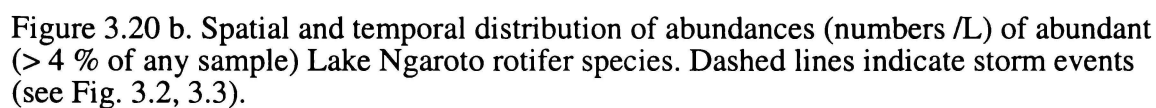


Figure 3.20 a. Spatial and temporal distribution of abundances (numbers /L) of abundant (> 4 % of any sample) Lake Ngaroto rotifer species. Dashed lines indicate storm events (see Fig. 3.2, 3.3).



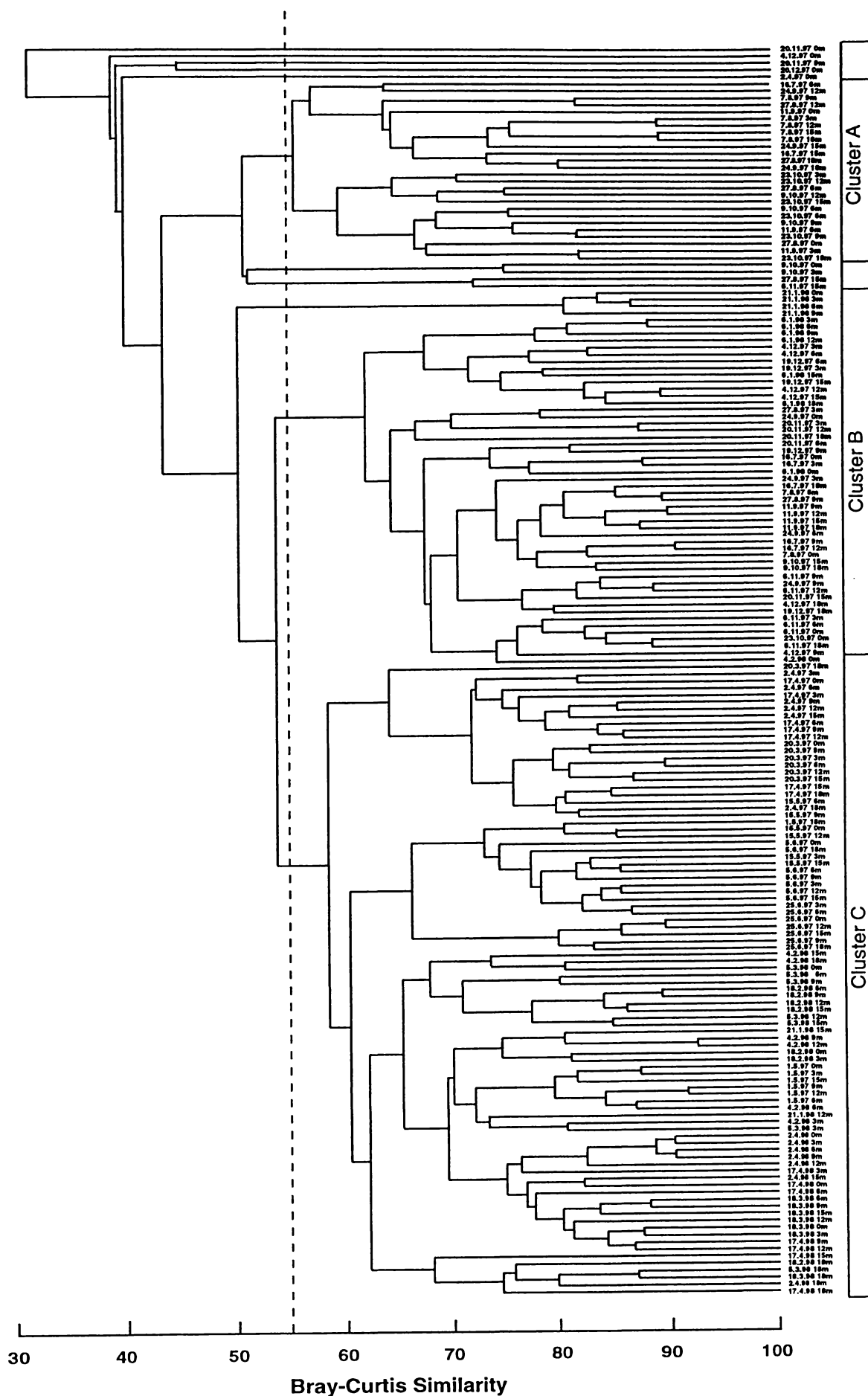


Fig. 3.21. Cluster analysis of abundant rotifer species from Lake Tikitapu. Dashed line indicates 55% similarity level.

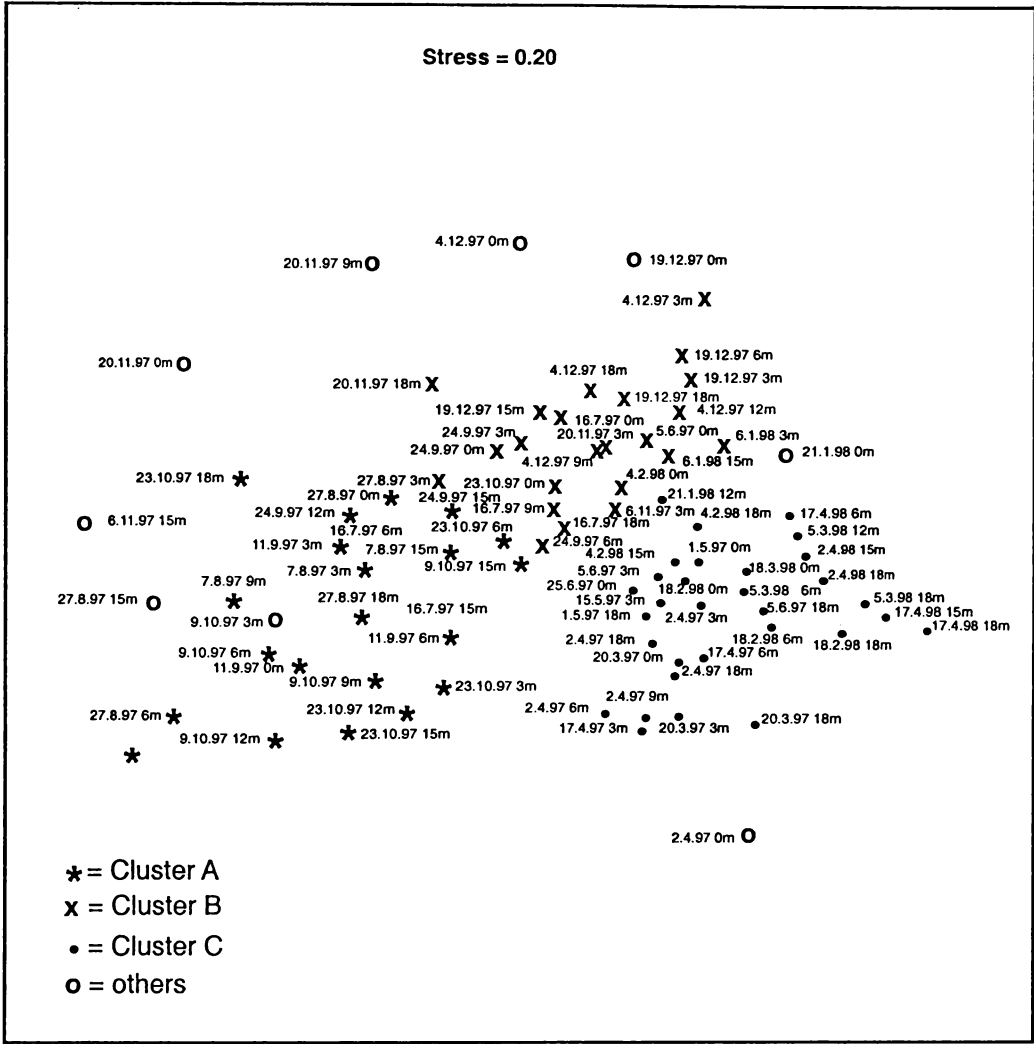


Fig. 3.22. MDS plot of samples from Lake Tikitapu based on abundant rotifer species.

Table 3.4. Summary of CCA variables for each lake.

	Tikitapu	Rotoiti	Okaro	Ngaroto
Axis 1 eigenvalues	0.160	0.215	0.342	0.282
Axis 2 eigenvalues	0.110	0.060	0.096	0.105
Species environment correlation (Axis 1)	0.827	0.957	0.849	0.888
Species environment correlation (Axis 2)	0.824	0.759	0.673	0.828
Cumulative % variance of species data explained by axes 1 and 2	18.9	28.2	24.3	32.8

main cluster samples in MDS, and were generally found to be samples from the surface water during periods of stratification. Cluster C comprises samples from the beginning of sampling, from March to late June 1997. This cluster reappeared in January 1998 at the appearance of sharp stratification, and lasted until the end of sampling in late April 1998. Cluster A comprised mainly samples from July to mid-October, while Cluster B comprised samples from July to early January. Samples from these clusters therefore overlapped temporally. Both Clusters A and B are therefore present during the holomictic period, with division of groups generally found at depth, and Cluster A coinciding with greater levels of chlorophyll *a* (cf. Fig. 3.9). The cessation of Cluster A samples coincided with the onset of thermal stratification, and Cluster B when temperature stratification became marked and oxygen depletion became apparent at depth (cf. Fig. 3.2, 3.5). Overall, temporal rather than spatial variability appears to be most important in determining cluster groupings, with the appearance or erosion of stratification apparently demarcating species groupings between predominantly summer-autumn (Cluster C) and winter-spring (Clusters A and B) assemblages.

The eigenvalues and species environmental correlations for Axis 1 and 2, and the percentage of variance of rotifer abundance accounted for by the first two axes in the CCA for each lake, are given in Table 3.4. The spread of sample scores in the Lake Tikitapu CCA ordination (Fig. 3.23, Table 3.5) correspond in general with the groups found in cluster analysis and MDS, except Cluster A and B samples are grouped more closely together, both generally positively associated with Axis 1. Cluster C (summer-autumn) samples were generally negatively associated with Axis 1, with samples from depth

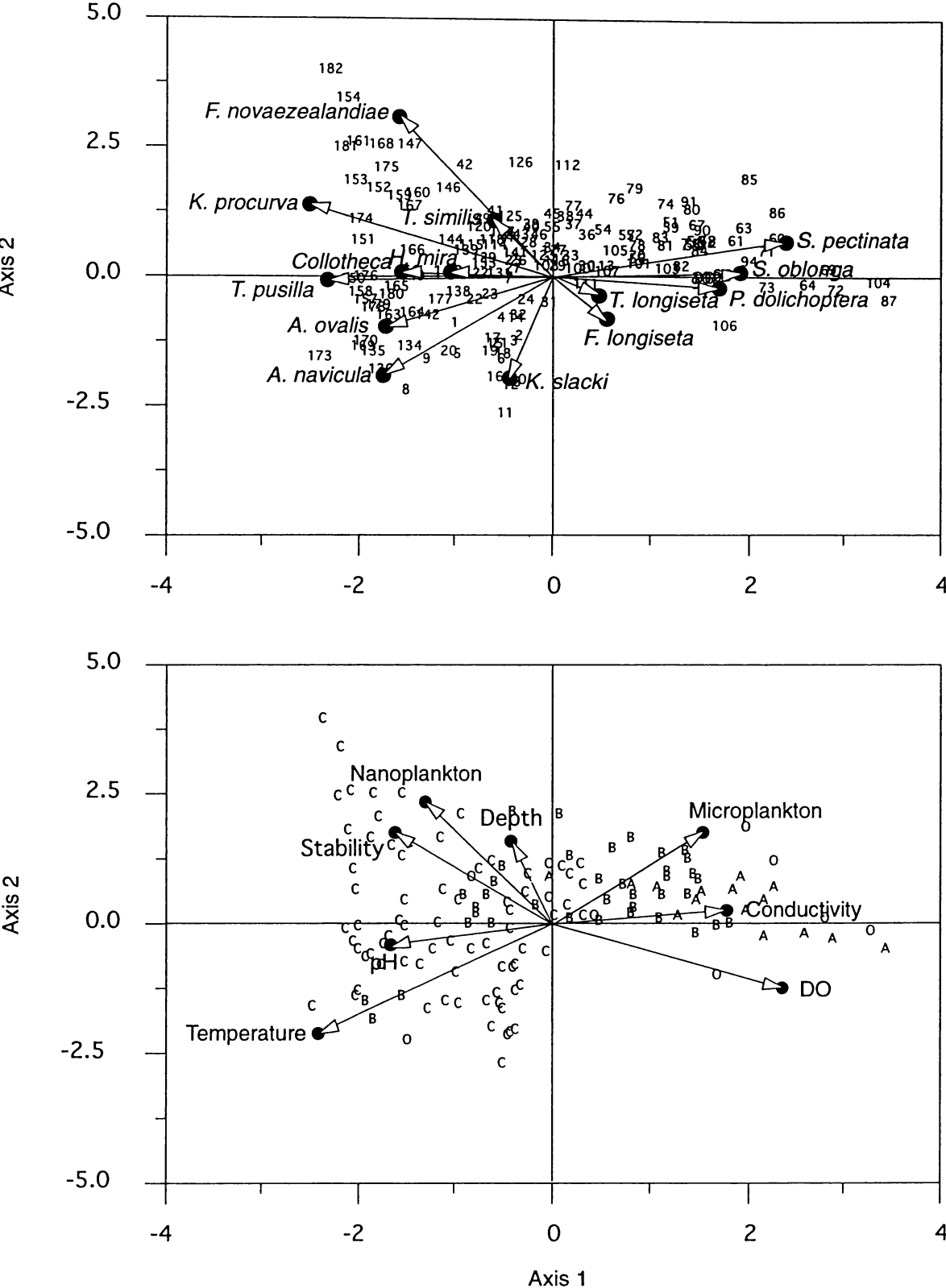


Figure 3.23. Ordination diagram based on canonical correspondence analysis (CCA) of Lake Tikitapu rotifer species with respect to environmental variables. Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers. The date and depth of each sample number is given in Table 3.5. Some sample numbers have been omitted from the ordination for clarity. Cluster groupings are superimposed on the environmental biplot.

Table 3.5. Key to sample numbers (dates (d:m:y) and depths) for Lake Tikitapu and Rotoiti CCA ordinations

n	date	depth	n	date	depth	n	date	depth	n	date	depth
1	20/3/97	0m	47	25/6/97	12m	93	23/10/97	3m	139	21/1/98	15m
2	20/3/97	3m	48	25/6/97	15m	94	23/10/97	6m	140	21/1/98	18m
3	20/3/97	6m	49	25/6/97	18m	95	23/10/97	9m	141	4/2/98	0m
4	20/3/97	9m	50	16/7/97	0m	96	23/10/97	12m	142	4/2/98	3m
5	20/3/97	12m	51	16/7/97	3m	97	23/10/97	15m	143	4/2/98	6m
6	20/3/97	15m	52	16/7/97	6m	98	23/10/97	18m	144	4/2/98	9m
7	20/3/97	18m	53	16/7/97	9m	99	6/11/97	0m	145	4/2/98	12m
8	2/4/97	0m	54	16/7/97	12m	100	6/11/97	3m	146	4/2/98	15m
9	2/4/97	3m	55	16/7/97	15m	101	6/11/97	6m	147	4/2/98	18m
10	2/4/97	6m	56	16/7/97	18m	102	6/11/97	9m	148	18/2/98	0m
11	2/4/97	9m	57	7/8/97	0m	103	6/11/97	12m	149	18/2/98	3m
12	2/4/97	12m	58	7/8/97	3m	104	6/11/97	15m	150	18/2/98	6m
13	2/4/97	15m	59	7/8/97	6m	105	6/11/97	18m	151	18/2/98	9m
14	2/4/97	18m	60	7/8/97	9m	106	20/11/97	0m	152	18/2/98	12m
15	17/4/97	0m	61	7/8/97	12m	107	20/11/97	3m	153	18/2/98	15m
16	17/4/97	3m	62	7/8/97	15m	108	20/11/97	6m	154	18/2/98	18m
17	17/4/97	6m	63	7/8/97	18m	109	20/11/97	9m	155	5/3/98	0m
18	17/4/97	9m	64	28/8/97	0m	110	20/11/97	12m	156	5/3/98	3m
19	17/4/97	12m	65	28/8/97	3m	111	20/11/97	15m	157	5/3/98	6m
20	17/4/97	15m	66	28/8/97	6m	112	20/11/97	18m	158	5/3/98	9m
21	17/4/97	18m	67	28/8/97	9m	113	4/12/97	0m	159	5/3/98	12m
22	1/5/97	0m	68	28/8/97	12m	114	4/12/97	3m	160	5/3/98	15m
23	1/5/97	3m	69	28/8/97	15m	115	4/12/97	6m	161	5/3/98	18m
24	1/5/97	6m	70	28/8/97	18m	116	4/12/97	9m	162	18/3/98	0m
25	1/5/97	9m	71	11/9/97	0m	117	4/12/97	12m	163	18/3/98	3m
26	1/5/97	12m	72	11/9/97	3m	118	4/12/97	15m	164	18/3/98	6m
27	1/5/97	15m	73	11/9/97	6m	119	4/12/97	18m	165	18/3/98	9m
28	1/5/97	18m	74	11/9/97	9m	120	20/12/97	0m	166	18/3/98	12m
29	17/5/97	0m	75	11/9/97	12m	121	20/12/97	3m	167	18/3/98	15m
30	17/5/97	3m	76	11/9/97	15m	122	20/12/97	6m	168	18/3/98	18m
31	17/5/97	6m	77	11/9/97	18m	123	20/12/97	9m	169	2/4/98	0m
32	17/5/97	9m	78	25/9/97	0m	124	20/12/97	12m	170	2/4/98	3m
33	17/5/97	12m	79	25/9/97	3m	125	20/12/97	15m	171	2/4/98	6m
34	17/5/97	15m	80	25/9/97	6m	126	20/12/97	18m	172	2/4/98	9m
35	17/5/97	18m	81	25/9/97	9m	127	6/1/98	0m	173	2/4/98	12m
36	5/6/97	0m	82	25/9/97	12m	128	6/1/98	3m	174	2/4/98	15m
37	5/6/97	3m	83	25/9/97	15m	129	6/1/98	6m	175	2/4/98	18m
38	5/6/97	6m	84	25/9/97	18m	130	6/1/98	9m	176	16/4/98	0m
39	5/6/97	9m	85	9/10/97	0m	131	6/1/98	12m	177	16/4/98	3m
40	5/6/97	12m	86	9/10/97	3m	132	6/1/98	15m	178	16/4/98	6m
41	5/6/97	15m	87	9/10/97	6m	133	6/1/98	18m	179	16/4/98	9m
42	5/6/97	18m	88	9/10/97	9m	134	21/1/98	0m	180	16/4/98	12m
43	25/6/97	0m	89	9/10/97	12m	135	21/1/98	3m	181	16/4/98	15m
44	25/6/97	3m	90	9/10/97	15m	136	21/1/98	6m	182	16/4/98	18m
45	25/6/97	6m	91	9/10/97	18m	137	21/1/98	9m			
46	25/6/97	9m	92	23/10/97	0m	138	21/1/98	12m			

generally associating more positively with Axis 2. *Keratella procurva*, *Trichocerca pusilla*, *Collotheca* sp., *Ascomorpha ovalis*, and *Anuraeopsis navicula* are strongly negatively associated with Axis 1, and therefore associated with Cluster C (summer-autumn) samples. *Synchaeta pectinata*, *Synchaeta oblonga* and *Polyarthra dolichoptera* are strongly positively associated with Axis 1, and therefore associated with Cluster A and B (winter-spring) samples. *Anuraeopsis navicula* and *Keratella slacki*, strongly negatively associated with Axis 2, and *Filinia novaezealandiae*, strongly positively associated, are also found to associate with Cluster C samples, although *Filinia novaezealandiae* is generally found associated with samples from depth (generally *ca.* 18 m).

The results of forward selection and associated Monte Carlo permutation tests of the significance of the explanatory variables are shown in Table 3.6a. The lambda-1 column lists the environmental variables and variance they explain singly, i.e., when that particular variable is used as the only environmental variable. The lambda-A column indicates the environmental variables in order of their inclusion in the CCA model, the additional variance each explains at the time of inclusion, and its significance at that time (P-value). This column is therefore ordered by including the most important variable first, with the remaining variables successively repermuted to find the most important in explaining the remaining variation not accounted for by the previous variable or variables. The first axis (Axis 1) will therefore be most strongly constrained by the first variable in the lambda-A column, and the second axis (Axis 2) most strongly by the second unrelated variable (Ter Braak & Smilauer 1998). In Lake Tikitapu, temperature was the variable found to have the greatest correlation with distribution of rotifer species, with DO and nanoplankton also each able to account for >10 % of the variation when explored by themselves (Table 3.6a). Temperature, pH and water stability are strongly negatively associated with Axis 1, and DO, conductivity and microplankton are strongly positively associated. On Axis 2, temperature is strongly negatively associated, and nanoplankton strongly positively associated.

Table 3.6 a-d. Results of forward selection and Monte Carlo permutation tests. The lambda-1 column lists the environmental variables and variance they explain singly, i.e. when that particular variable is used as the only environmental variable. The lambda-A column indicates the environmental variables in order of their inclusion in the CCA model, the additional variance each explains at the time of inclusion, and its significance at that time (P-value). Environmental variables are listed by the order of their inclusion in the model (lambda-A).

a: Tikitapu

Variable	Marginal effects	Conditional effects	
	lambda-1	lambda-A	P
Temperature	0.13	0.13	0.005
Nanoplankton	0.10	0.10	0.005
DO	0.11	0.07	0.005
Depth	0.05	0.04	0.005
pH	0.07	0.02	0.005
Microplankton	0.08	0.03	0.005
Brunt-Vaisala	0.08	0.01	0.005
Conductivity	0.05	0.01	0.11

c: Okaro

Variable	Marginal effects	Conditional effects	
	lambda-1	lambda-A	P
Temperature	0.18	0.18	0.005
Microplankton	0.18	0.15	0.005
Conductivity	0.11	0.07	0.005
pH	0.05	0.04	0.005
Nanoplankton	0.04	0.03	0.01
DO	0.09	0.03	0.005
Brunt-Vaisala	0.08	0.02	0.01
Depth	0.02	0.01	0.07

b: Rotoiti

Variable	Marginal effects	Conditional effects	
	lambda-1	lambda-A	P
Temperature	0.19	0.19	0.005
Nanoplankton	0.09	0.05	0.005
pH	0.06	0.05	0.005
Microplankton	0.05	0.03	0.005
Conductivity	0.11	0.02	0.005
DO	0.13	0.02	0.005
Brunt-Vaisala	0.05	0.02	0.005
Depth	0.01	0.01	0.005

d: Ngaroto

Variable	Marginal effects	Conditional effects	
	lambda-1	lambda-A	P
Temperature	0.22	0.22	0.005
pH	0.21	0.07	0.005
DO	0.05	0.07	0.005
Conductivity	0.06	0.07	0.005
Microplankton	0.13	0.07	0.005
Nanoplankton	0.06	0.04	0.005
Brunt-Vaisala	0.04	0.02	0.015
Depth	0.00	0.01	0.385

Comparing the rotifer groupings with the ordinations of physical and chemical variables, rotifer species associated with Cluster A and B samples (winter-spring; *Synchaeta pectinata*, *Synchaeta oblonga* and *Polyarthra dolichoptera*) are associated with low temperature, pH and water stability, and high DO, conductivity and microplankton. Rotifer species associated with Cluster C (summer-autumn; *Trichocerca pusilla*, *Collotheca* sp., *Ascomorpha ovalis*, *Anuraeopsis navicula*) were generally found at low levels of DO, conductivity and microplankton, and high temperature, pH and water stability. Comparison with graphs of species that are negatively (e.g., *A. ovalis* and *A. navicula*) or positively (e.g., *S. pectinata* and *S. oblonga*) associated with Axis 1 with graphs of temperature, pH, water stability, DO, conductivity and microplankton (cf. Fig. 3.2-3.11) confirm these relationships. Species negatively associated with Axis 2 (*A. navicula*, *Keratella slacki* and *Filinia longiseta*) correlated with high temperature and low levels of nanoplankton. Species strongly positively associated with Axis 2 (e.g., *Filinia novaezealandiae* and *Keratella procurva*) correlate with low temperature and high levels of nanoplankton. Comparison of graphs of abundances of *Filinia novaezealandiae* (Fig. 3.17) and temperature and nanoplankton (cf. Figs 3.2-3.11) confirm this relationship.

Weighted average species optima and tolerances for environmental variables, summarising the relationships of species, concur with distributions found in CCA (Fig. 3.24). In the graph of temperature optima, the environmental variable most strongly correlated with rotifer distribution in the CCA, Cluster A and B species (winter-spring; *Synchaeta pectinata*, *Synchaeta oblonga*, *P. dolichoptera*) are generally found with the lowest optima, and Cluster C species (summer-autumn; *Trichocerca pusilla*, *Ascomorpha ovalis*, *Anuraeopsis navicula*, *Collotheca* sp.) with the highest. The exceptions to this are, in particular, *Filinia novaezealandiae* and *Keratella procurva*, found at depth during summer and therefore found with optima similar to winter-spring species. Species from each cluster group were generally found to have similar optima for other physico-chemical variables (e.g., pH, DO) to those of other species in the same cluster group.

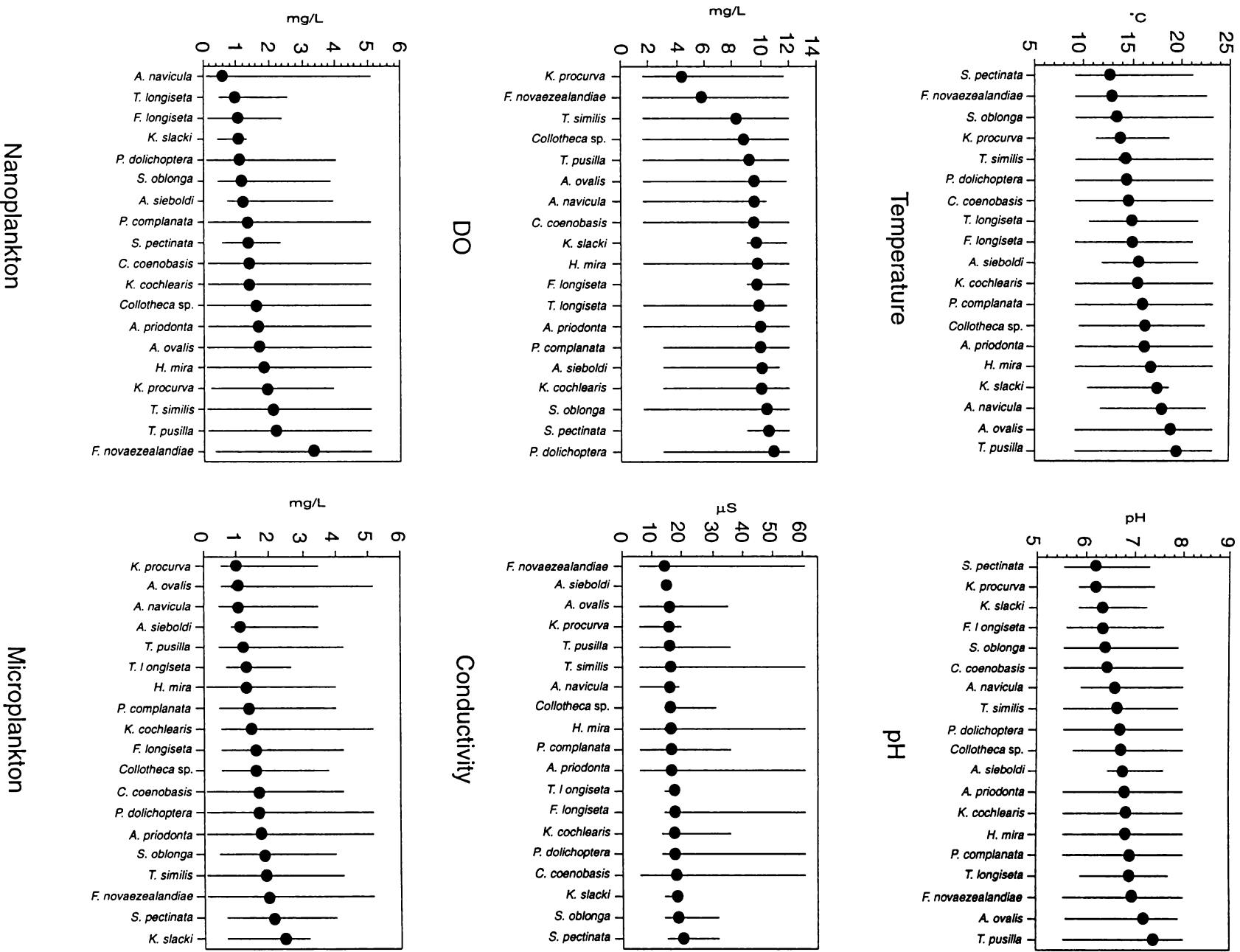


Fig. 3.24. Weighted average optima, and tolerances of Lake Tikitapu abundant species for temperature, pH, DO, conductivity, nanoplankton and microplankton. ● shows the weighted average optimum, and whiskers show the range over which a species was recorded.

Lake Rotoiti

Cluster analysis of Lake Rotoiti (Fig. 3.25) revealed two major clusters at the 58 % similarity level. Cluster B occurred from the beginning of the study to late June, and again from late January until the end of the study (summer-autumn). Cluster A occurred in the intermediate period from July to early-January (winter-spring). The transition between clusters in late January coincides with storm event 3, identified in Fig. 3.2 and 3.3. A small additional cluster was identified comprising samples from within the thermocline in early January (cf. Fig. 3.2). The MDS ordination (Fig. 3.26) shows a similar distribution of the data to the cluster analysis, with samples from the two major cluster groups separated from each other. A general temporal gradient is apparent clockwise in the ordination with samples most related temporally found close to one another, including at the division between clusters. Division of major groups appears to be determined by temporal rather than spatial distribution of species.

The spread of sample scores in the Lake Rotoiti CCA ordination (Fig. 3.27, Table 3.5) correspond in general with groups found in cluster analysis. Cluster A (winter-spring) samples were mainly positively associated with Axis 1, and Cluster B (summer-autumn) mainly negatively associated. Samples not in these clusters were found to be strongly negatively associated with Axis 2. *Ascomorpha ovalis*, *Asplanchna sieboldi*, *Cephalodella catellina*, *Keratella procurva*, *Polyarthra dolichoptera* and *Trichocerca stylata* were all strongly negatively associated with Axis 1, and therefore associate with Cluster B (summer-autumn) samples. *Conochilus unicornis*, *Filinia terminalis*, *Synchaeta pectinata* and *Filinia* cf. *pejleri* are strongly positively associated with Axis 1, and are therefore associated with Cluster A (winter-spring) samples. *Asplanchna sieboldi* and *Keratella procurva* were strongly negatively associated with Axis 2, and *Cephalodella catellina* was strongly positively associated. These were all associated with Cluster B samples.

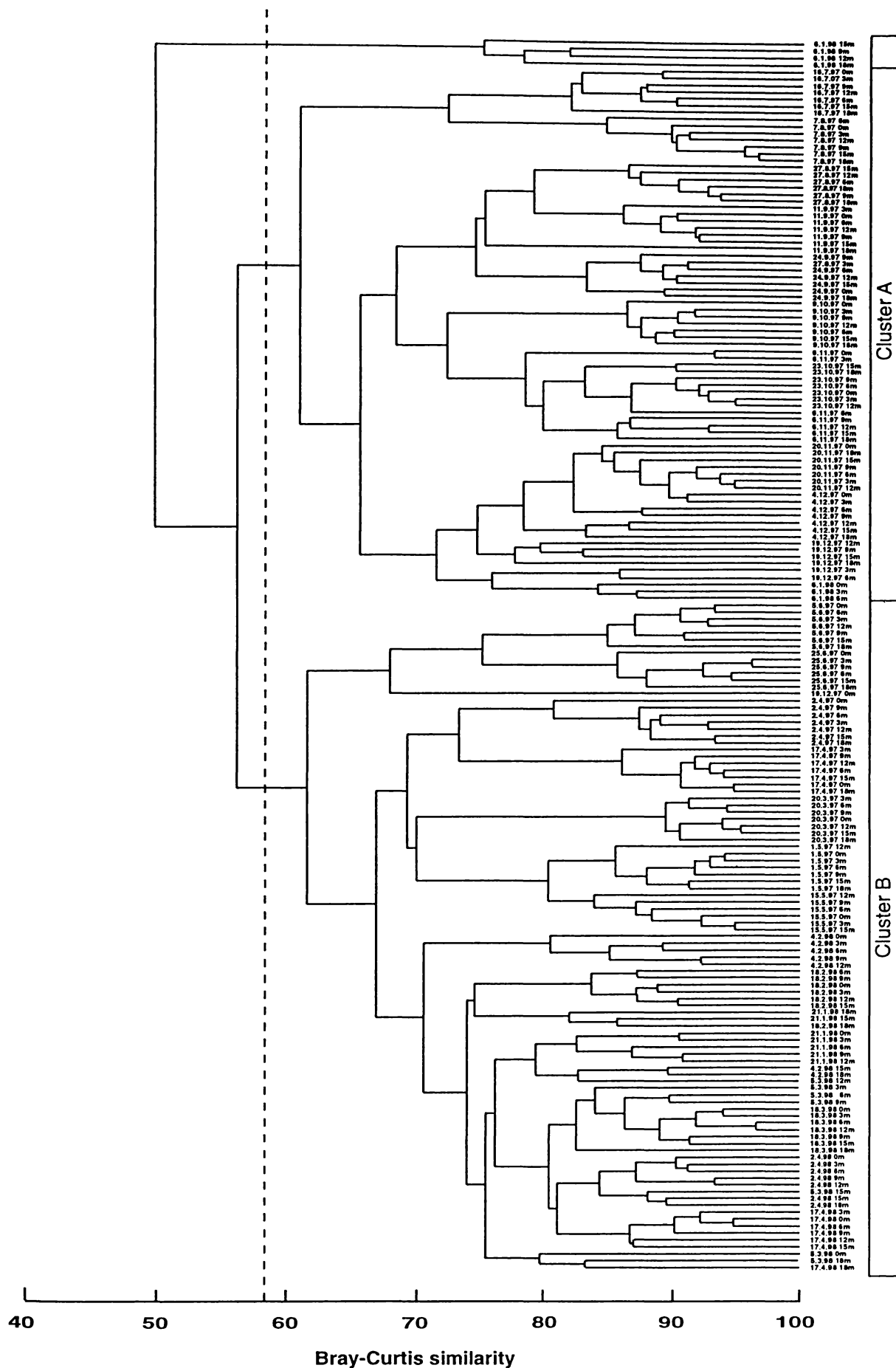


Fig. 3.25. Cluster analysis of abundant rotifer species from Lake Rotoiti. Dashed line indicates 58% level of similarity

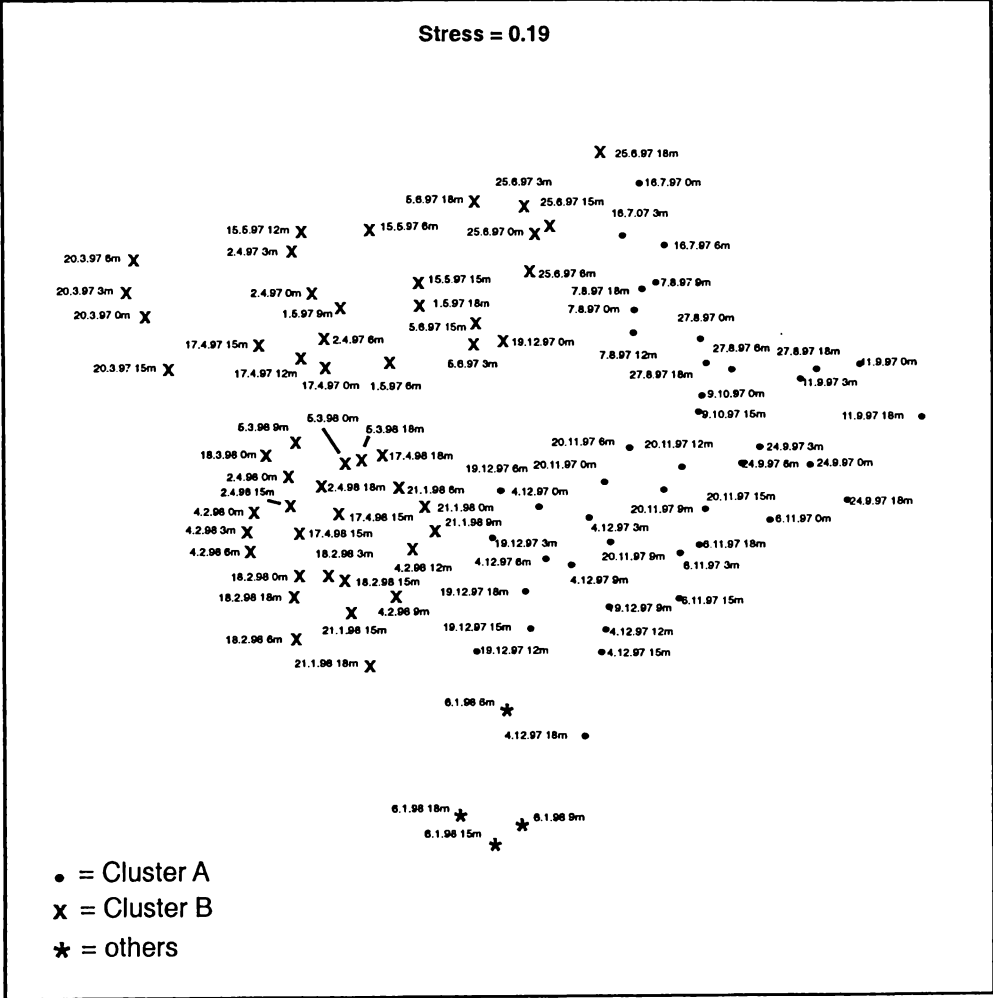


Fig. 3.26. MDS plot of samples from Lake Rotoiti based on abundant rotifer species.

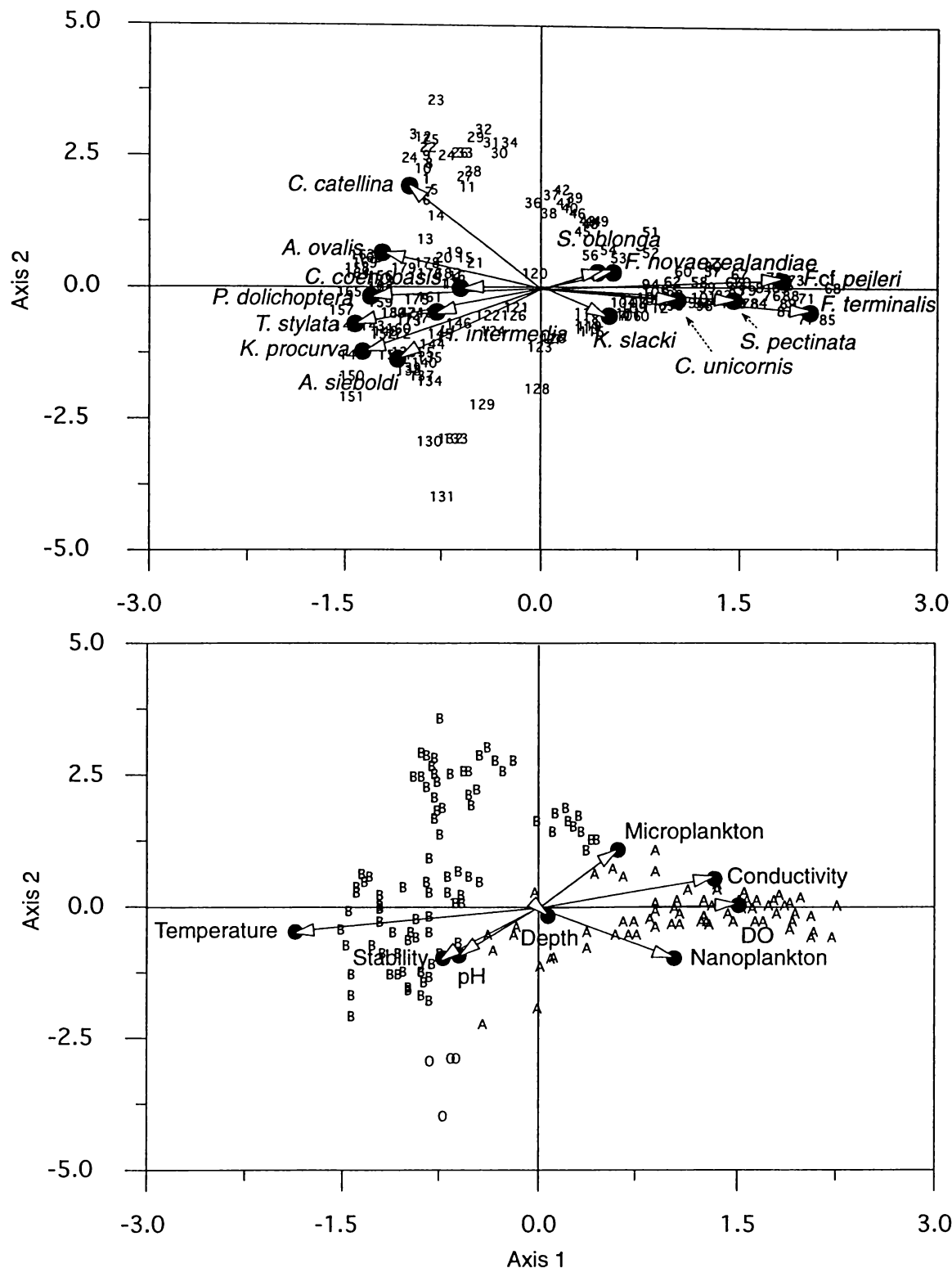


Figure 3.27. Ordination diagram based on canonical correspondence analysis (CCA) of Lake Rotoiti rotifer species with respect to environmental variables. Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers. The date and depth of each sample number is given in Table 3.5. Some sample numbers have been omitted from the ordination for clarity. Cluster groupings have been superimposed on the environmental biplot.

Forward selection and associated Monte Carlo permutation tests of the significance of the environmental variables indicated temperature had the highest explanatory power, with DO and conductivity also able to account for >10 % of the species variation when explored by themselves (Table 3.6b). In the ordination of environmental variables, temperature was found to be strongly negatively associated with Axis 1, and conductivity, DO and nanoplankton strongly positively associated. Species strongly negatively associated with Axis 1 (Cluster B species; *Ascomorpha ovalis*, *Asplanchna sieboldi*, *Cephalodella catellina*, *Keratella procurva*, *Polyarthra dolichoptera* and *Trichocerca stylata*) are therefore associated with high temperature, and low conductivity, DO and nanoplankton. Species strongly positively associated with Axis 1 (Cluster A species; *Conochilus unicornis*, *Filinia terminalis*, *Synchaeta pectinata* and *Filinia cf. pejlerei*) are associated with low temperature, and high levels of nanoplankton, conductivity and DO. Comparison of graphs of abundance of species strongly negatively (e.g., *Trichocerca stylata* and *Asplanchna sieboldi*) or positively (e.g., *Filinia terminalis*, *Filinia cf. pejlerei*) associated with Axis 1 (Fig. 3.18) with those of temperature, conductivity, DO and nanoplankton (cf. Fig. 3.2-3.11) confirm these relationships. Microplankton was positively associated with Axis 2, and pH, water stability and nanoplankton negatively associated. This axis explained a low proportion of the variability of rotifer species after addition of temperature on the first axis (Table 3.6b). On this axis, *Cephalodella catellina* is associated with low levels of nanoplankton, and *Asplanchna sieboldi* and *Keratella procurva* associated with high pH and water stability. Comparison of graphs of *Cephalodella catellina* (positively associated with Axis 2) and *Asplanchna sieboldi* (negatively associated) (Fig. 3.19) with pH, water stability and nanoplankton (cf. Figs 3.2-3.11) confirm these relationships.

Weighted average species optima for environmental variables concur with distributions found in CCA (Fig. 3.28). Cluster A (winter-spring) species (*Conochilus unicornis*, *Filinia terminalis*, *Synchaeta pectinata* and *Filinia cf. pejlerei*) are found to have

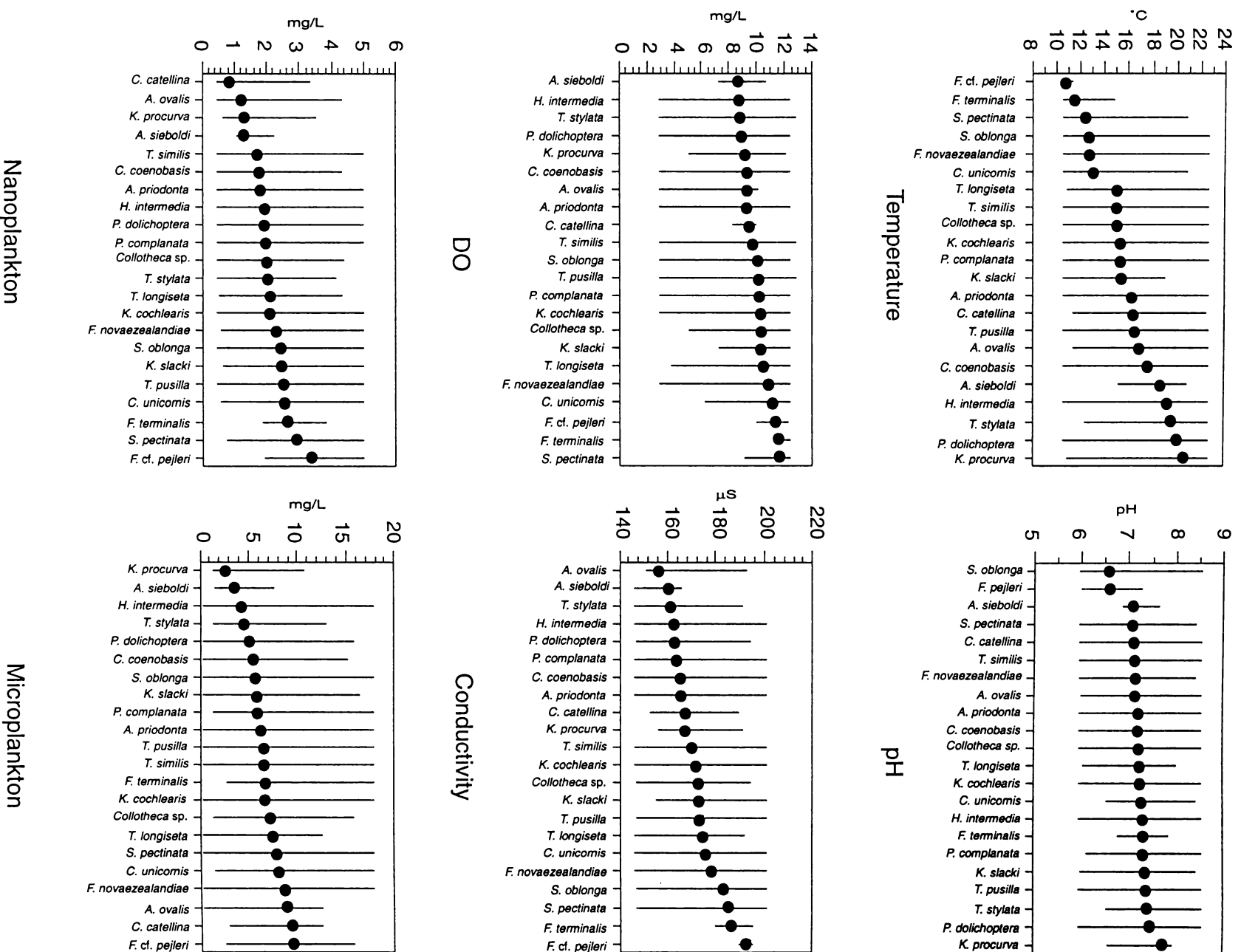


Fig. 3.28. Weighted average optima, and tolerances of Lake Rotoiti abundant species for temperature, pH, DO, conductivity, nanoplankton and microplankton. ● shows the weighted average optimum, and whiskers show the range over which a species was recorded.

low temperature optima, and Cluster B (summer-autumn) species (*Ascomorpha ovalis*, *Asplanchna sieboldi*, *Cephalodella catellina*, *Keratella procurva*, *Polyarthra dolichoptera* and *Trichocerca stylata*) are found to have high optima. Species from each cluster group were generally found to have optima for other physico-chemical variables (e.g., DO and conductivity) similar to those of other species associated with the same cluster group.

Lake Okaro

Cluster analysis of the Lake Okaro data revealed four major groupings of species at the 50 % similarity level (Fig. 3.29). The MDS ordination (Fig. 3.30) shows a similar distribution of the data to the cluster analysis, with samples from each cluster group separated from those of other clusters. Cluster A samples generally occurred early in the study during stratification of temperature and oxygen until early June when stratification broke down (cf. Fig. 3.2, 3.5), except for the appearance of Cluster B briefly in early April. Cluster C comprised samples from June to November 1997 during the winter-spring mixed period, and were found to clearly separate from Cluster A samples in the MDS ordination. Cluster B reappeared from November until January, being present at a time of stable stratification and high surface heating until mixing event 3, when it was replaced briefly by Cluster A, and then by Cluster D in February until the end of the study. Cluster C is therefore a winter-spring community present when lake water is holomictic, and Clusters A, B and D are assemblages occurring during the stratified period (summer and autumn), apparently delineated by storm events.

The spread of sample scores in the Lake Okaro CCA (Fig. 3.31, Table 3.7) correspond in general with the groupings found in cluster analysis and MDS. Cluster C (winter-spring) samples generally positively associated with Axis 1, Cluster A weakly negatively associated with Axis 1, Cluster B all positively associated with Axis 2, and Cluster D samples all strongly negatively associated with Axis 1. *Asplanchna priodonta*,

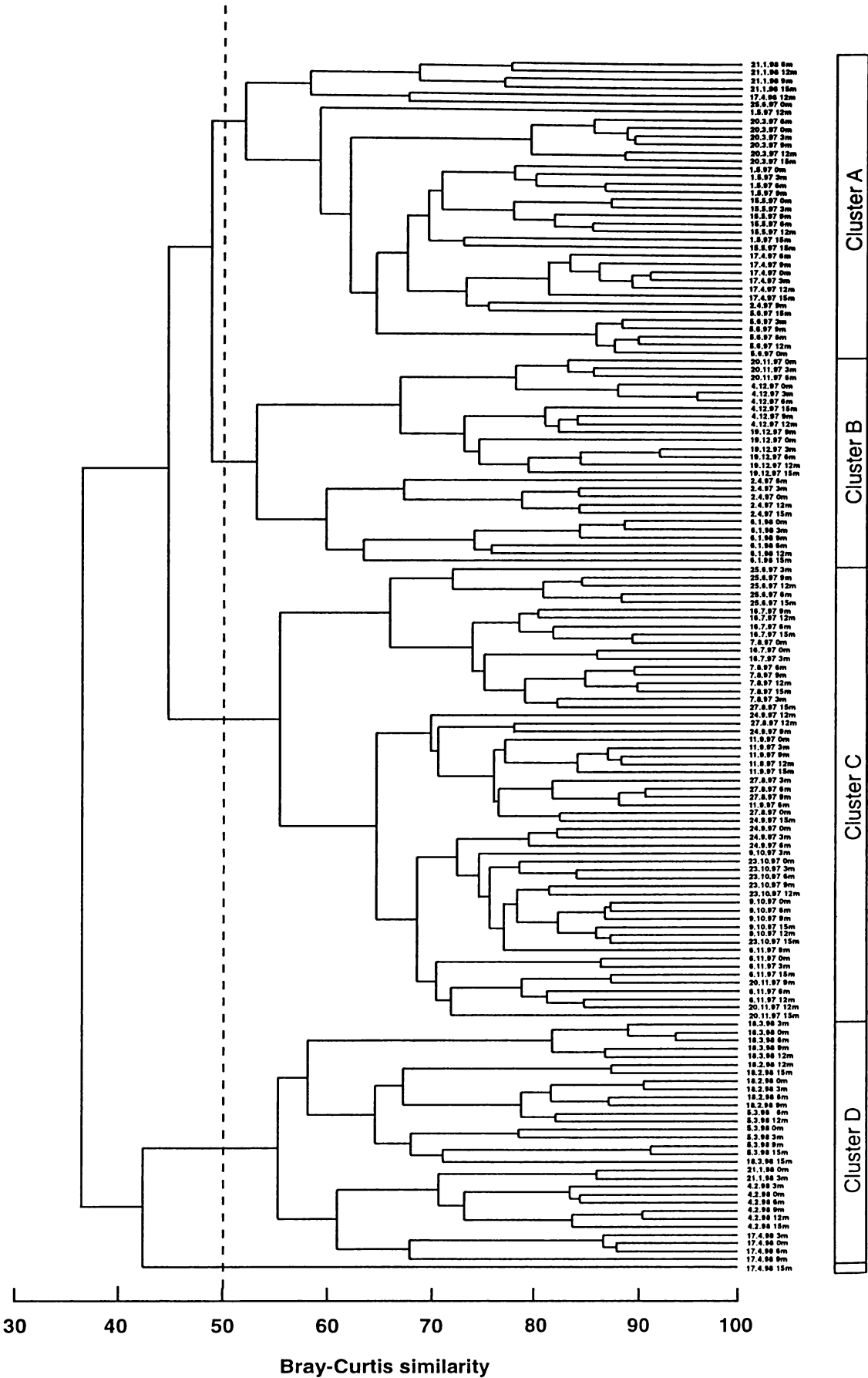


Fig. 3.29. Cluster analysis of abundant rotifer species from Lake Okaro. Dashed line indicates 50% level of similarity



Fig. 3.30. MDS plot of samples from Lake Okaro based on abundant rotifer species.

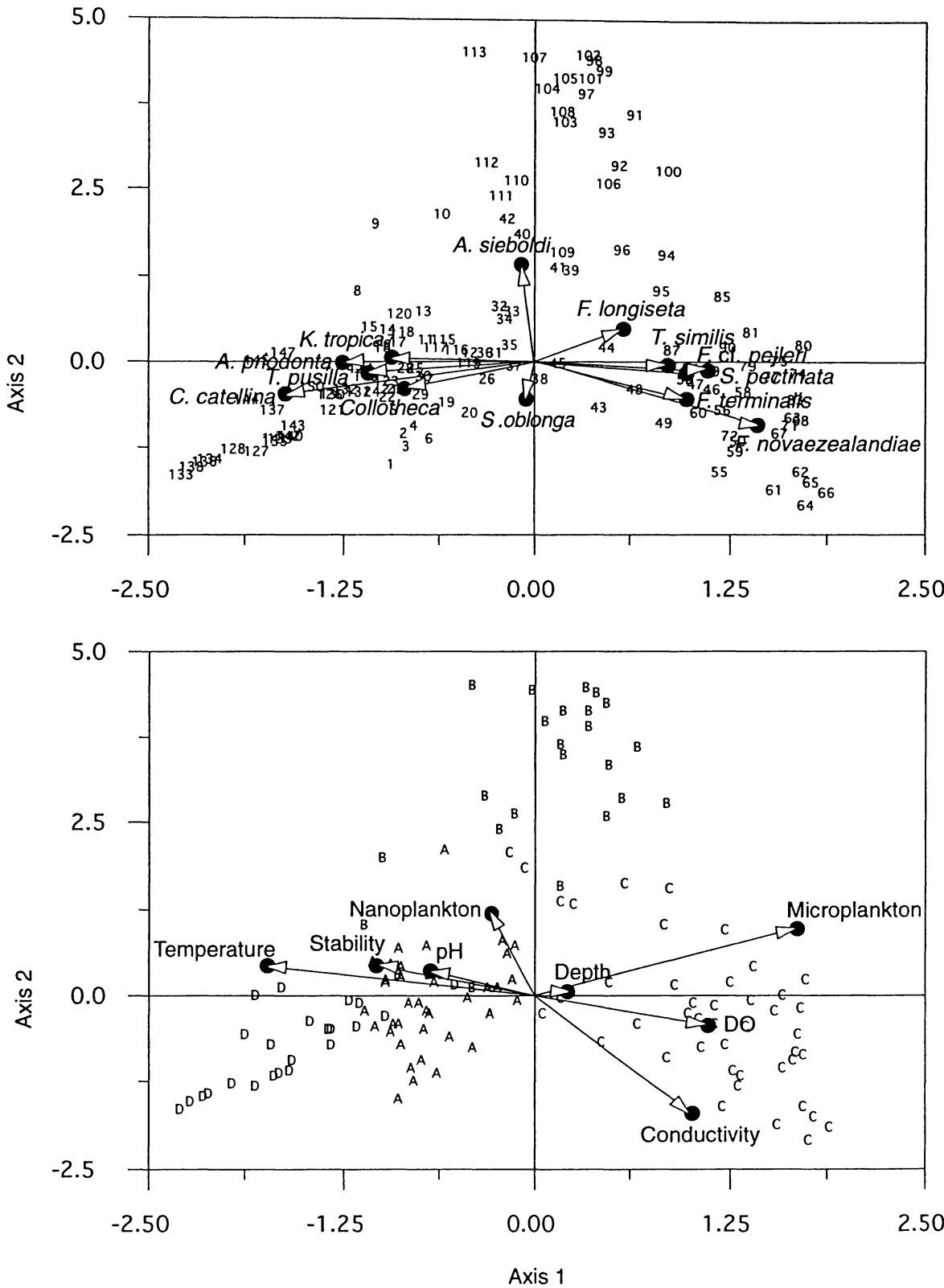


Figure 3.31. Ordination diagram based on canonical correspondence analysis (CCA) of Lake Okaro rotifer species with respect to environmental variables. Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers. The date and depth of each sample number is given in Table 3.7. Some sample numbers have been omitted from the ordination for clarity. Cluster groupings are superimposed on the environmental biplot.

Table 3.7. Key to sample numbers (dates (d:m:y) and depths) for the Lake Okaro CCA ordination.

n	date	depth	n	date	depth	n	date	depth	n	date	depth
1	20/3/97	0m	39	25/6/97	6m	77	9/10/97	12m	115	21/1/98	0m
2	20/3/97	3m	40	25/6/97	9m	78	9/10/97	15m	116	21/1/98	3m
3	20/3/97	6m	41	25/6/97	12m	79	23/10/97	0m	117	21/1/98	6m
4	20/3/97	9m	42	25/6/97	15m	80	23/10/97	3m	118	21/1/98	9m
5	20/3/97	12m	43	16/7/97	0m	81	23/10/97	6m	119	21/1/98	12m
6	20/3/97	15m	44	16/7/97	3m	82	23/10/97	9m	120	21/1/98	15m
7	2/4/97	0m	45	16/7/97	6m	83	23/10/97	12m	121	4/2/98	0m
8	2/4/97	3m	46	16/7/97	9m	84	23/10/97	15m	122	4/2/98	3m
9	2/4/97	6m	47	16/7/97	12m	85	6/11/97	0m	123	4/2/98	6m
10	2/4/97	9m	48	16/7/97	15m	86	6/11/97	3m	124	4/2/98	9m
11	2/4/97	12m	49	7/8/97	0m	87	6/11/97	6m	125	4/2/98	12m
12	2/4/97	15m	50	7/8/97	3m	88	6/11/97	9m	126	4/2/98	15m
13	17/4/97	0m	51	7/8/97	6m	89	6/11/97	12m	127	18/2/98	0m
14	17/4/97	3m	52	7/8/97	9m	90	6/11/97	15m	128	18/2/98	3m
15	17/4/97	6m	53	7/8/97	12m	91	20/11/97	0m	129	18/2/98	6m
16	17/4/97	9m	54	7/8/97	15m	92	20/11/97	3m	130	18/2/98	9m
17	17/4/97	12m	55	27/8/97	0m	93	20/11/97	6m	131	18/2/98	12m
18	17/4/97	15m	56	27/8/97	3m	94	20/11/97	9m	132	18/2/98	15m
19	1/5/97	0m	57	27/8/97	6m	95	20/11/97	12m	133	5/3/98	0m
20	1/5/97	3m	58	27/8/97	9m	96	20/11/97	15m	134	5/3/98	3m
21	1/5/97	6m	59	27/8/97	12m	97	4/12/97	0m	135	5/3/98	6m
22	1/5/97	9m	60	27/8/97	15m	98	4/12/97	3m	136	5/3/98	9m
23	1/5/97	12m	61	11/9/97	0m	99	4/12/97	6m	137	5/3/98	12m
24	1/5/97	15m	62	11/9/97	3m	100	4/12/97	9m	138	5/3/98	15m
25	15/5/97	0m	63	11/9/97	6m	101	4/12/97	12m	139	18/3/98	0m
26	15/5/97	3m	64	11/9/97	9m	102	4/12/97	15m	140	18/3/98	3m
27	15/5/97	6m	65	11/9/97	12m	103	19/12/97	0m	141	18/3/98	6m
28	15/5/97	9m	66	11/9/97	15m	104	19/12/97	3m	142	18/3/98	9m
29	15/5/97	12m	67	24/9/97	0m	105	19/12/97	6m	143	18/3/98	12m
30	15/5/97	15m	68	24/9/97	3m	106	19/12/97	9m	144	18/3/98	15m
31	5/6/98	0m	69	24/9/97	6m	107	19/12/97	12m	145	17/4/98	0m
32	5/6/97	3m	70	24/9/97	9m	108	19/12/97	15m	146	17/4/98	3m
33	5/6/97	6m	71	24/9/97	12m	109	6/1/98	0m	147	17/4/98	6m
34	5/6/97	9m	72	24/9/97	15m	110	6/1/98	3m	148	17/4/98	9m
35	5/6/97	12m	73	9/10/97	0m	111	6/1/98	6m	149	17/4/98	12m
36	5/6/97	15m	74	9/10/97	3m	112	6/1/98	9m	150	17/4/98	15m
37	25/6/97	0m	75	9/10/97	6m	113	6/1/98	12m			
38	25/6/97	3m	76	9/10/97	9m	114	6/1/98	15m			

Cephalodella catellina, *Keratella tropica* and *Trichocerca pusilla* are all strongly negatively associated with Axis 1, and are therefore associated with Clusters A and D samples. *Filinia novaezealandiae*, *Filinia terminalis*, *Filinia* cf. *pejleri*, *Synchaeta pectinata* and *Trichocerca similis* are all strongly positively correlated with Axis 1, and are therefore associated with Cluster C (winter-spring) samples. *Filinia novaezealandiae* is strongly negatively correlated with Axis 2, although is associated with Cluster C samples. *Asplanchna sieboldi* is strongly positively correlated with Axis 2, associated mainly with B samples.

Forward selection and associated Monte Carlo permutation tests of the significance of the environmental variables in determining rotifer distribution indicated temperature had the greatest explanatory power, with microplankton and conductivity also each able to account for >10 % of the species variation when explored by themselves (Table 3.6c). In the ordination of environmental variables, temperature and water stability are strongly negatively associated with Axis 1, DO, conductivity and microplankton are all strongly positively associated. Conductivity is strongly negatively associated with Axis 2, and nanoplankton and microplankton were moderately positively associated. Species associated with Clusters A and D (*Asplanchna priodonta*, *Cephalodella catellina*, *Keratella tropica* and *Trichocerca pusilla*), strongly negative on Axis 1, were therefore associated with high temperature and water stability and low DO, conductivity and microplankton. Species associated with Cluster C (*Filinia novaezealandiae*, *Filinia terminalis*, *Filinia* cf. *pejleri*, *Synchaeta pectinata* and *Trichocerca similis*), strongly positive on Axis 1, associate with low temperature and water stability, and high DO, conductivity and microplankton. Comparisons of graphs of selected species strongly positively (e.g., *Cephalodella catellina*, *Asplanchna priodonta*) or negatively (e.g., *Filinia novaezealandiae*, *Synchaeta pectinata*) associated with Axis 1 (Fig. 3.19) with those of temperature, water stability, conductivity, and microplankton (cf. Figs 3.2-3.11) confirm these relationships. *Asplanchna sieboldi*, strongly positive on Axis 2 (Fig. 3.19) associated with high nanoplankton and low conductivity (cf. Figs 3.2-11).

Weighted average species optima for environmental variables concur with distributions found in CCA (Fig. 3.32). Species associated with Clusters A and D (*Asplanchna priodonta*, *Cephalodella catellina*, *Keratella tropica* and *Trichocerca pusilla*) were generally found to have high temperature optima, and Cluster C species (*Filinia novaezealandiae*, *Filinia terminalis*, *Filinia* cf. *pejleri*, *Synchaeta pectinata* and *Trichocerca similis*) to have low temperature optima. *Asplanchna sieboldi*, associated with Cluster B, was found to have the highest microplankton and nanoplankton optima. Species from each cluster group were generally found to have optima for other environmental variables (e.g., pH, DO, microplankton) similar to those of other species associated with the same cluster group.

Lake Ngaroto

Cluster analysis of Lake Ngaroto revealed four clusters at the 55 % similarity level (Fig. 3.33). The MDS ordination (Fig. 3.34) shows a similar distribution of samples to the cluster analysis, with samples from the four cluster groups separated from those of the other clusters. Cluster A occurred from the beginning of the study to mid-May when the water column was relatively stable, and then reappeared in November to early February during a period of brief gradients in temperature and oxygen (cf. Figs 3.2, 3.5). Cluster B samples occurred in the intermediate period, winter and spring, when the water column was continually well mixed. Clusters C and D occurred from mid-February 1998, appearing after mixing and persisting through brief sharp gradations in oxygen and stability. Clusters A and C were separated by mixing that occurred between storm events 3 and 4, and C and D by storm event 4. Variation in community structure was largely temporal, and mixing events apparently played a major part in changing community structure, with separation of communities apparently separated by stratified and non-stratified periods, or storm events.

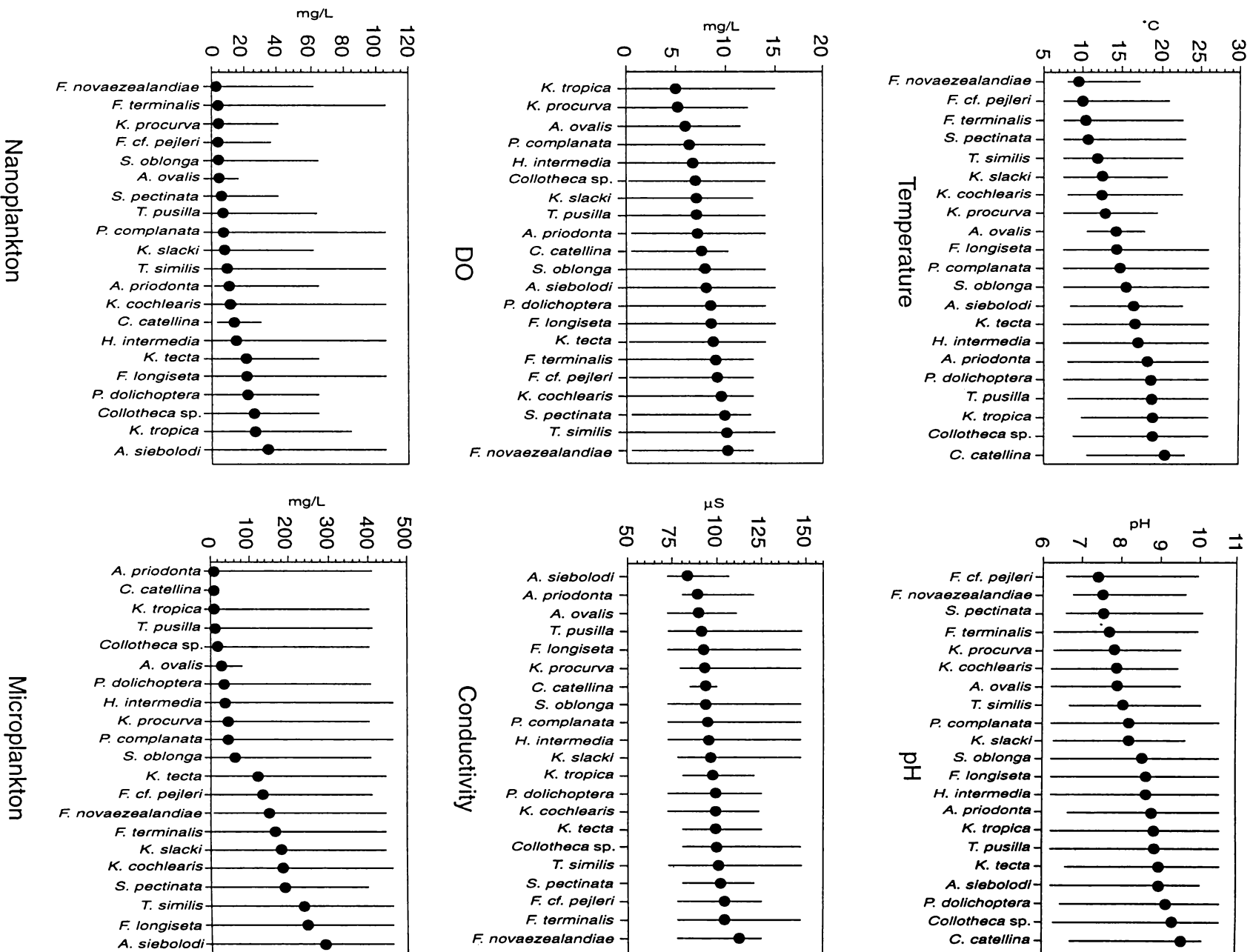


Fig. 3.32. Weighted average optima, and tolerances of Lake Okaro abundant species for temperature, pH, DO, conductivity, nanoplankton and microplankton. ● shows the weighted average optimum, and whiskers show the range over which a species was recorded.

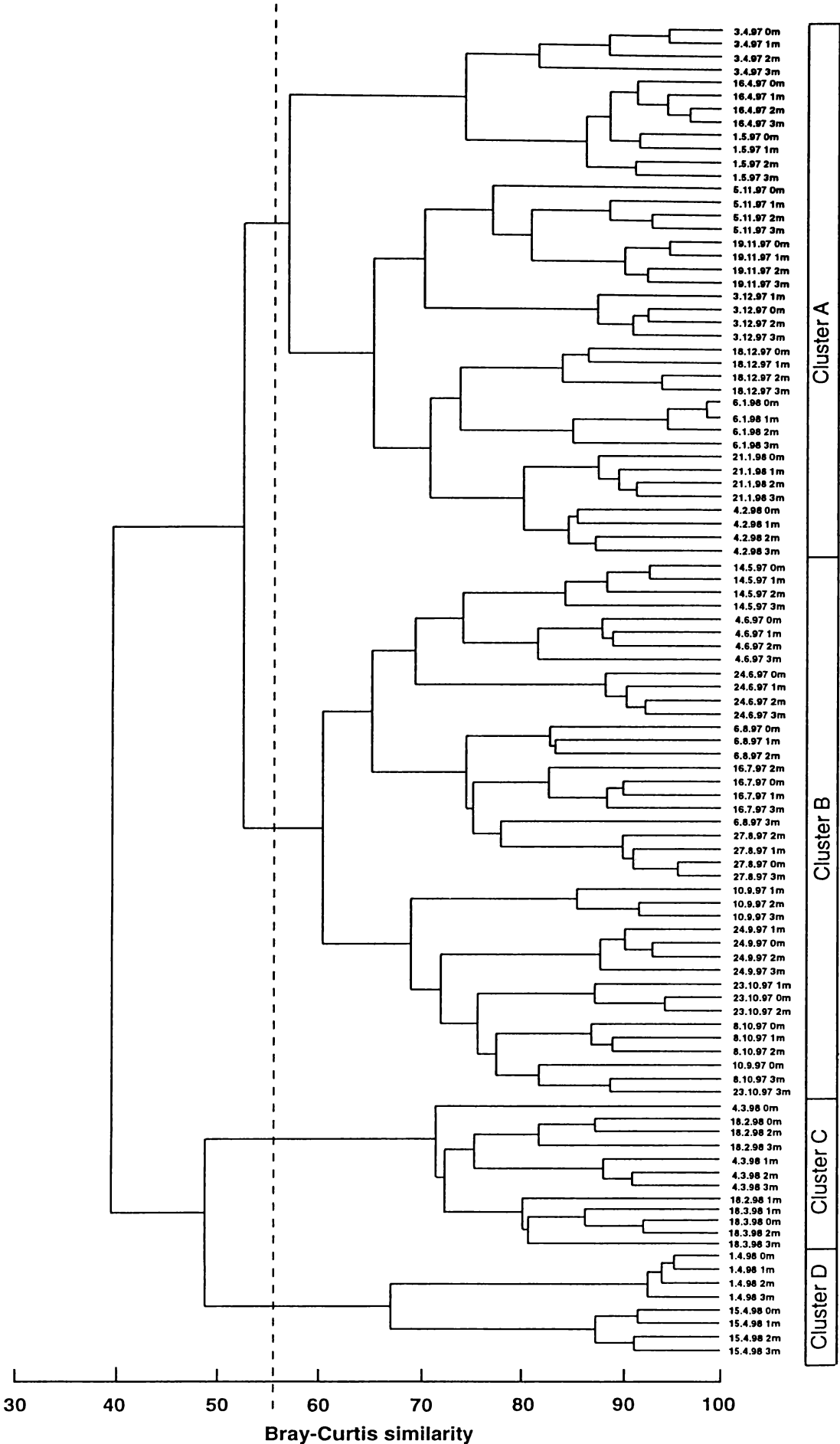


Fig. 3.33. Cluster analysis of abundant rotifer species from Lake Ngaroto. Dashed line indicates 55% similarity level.

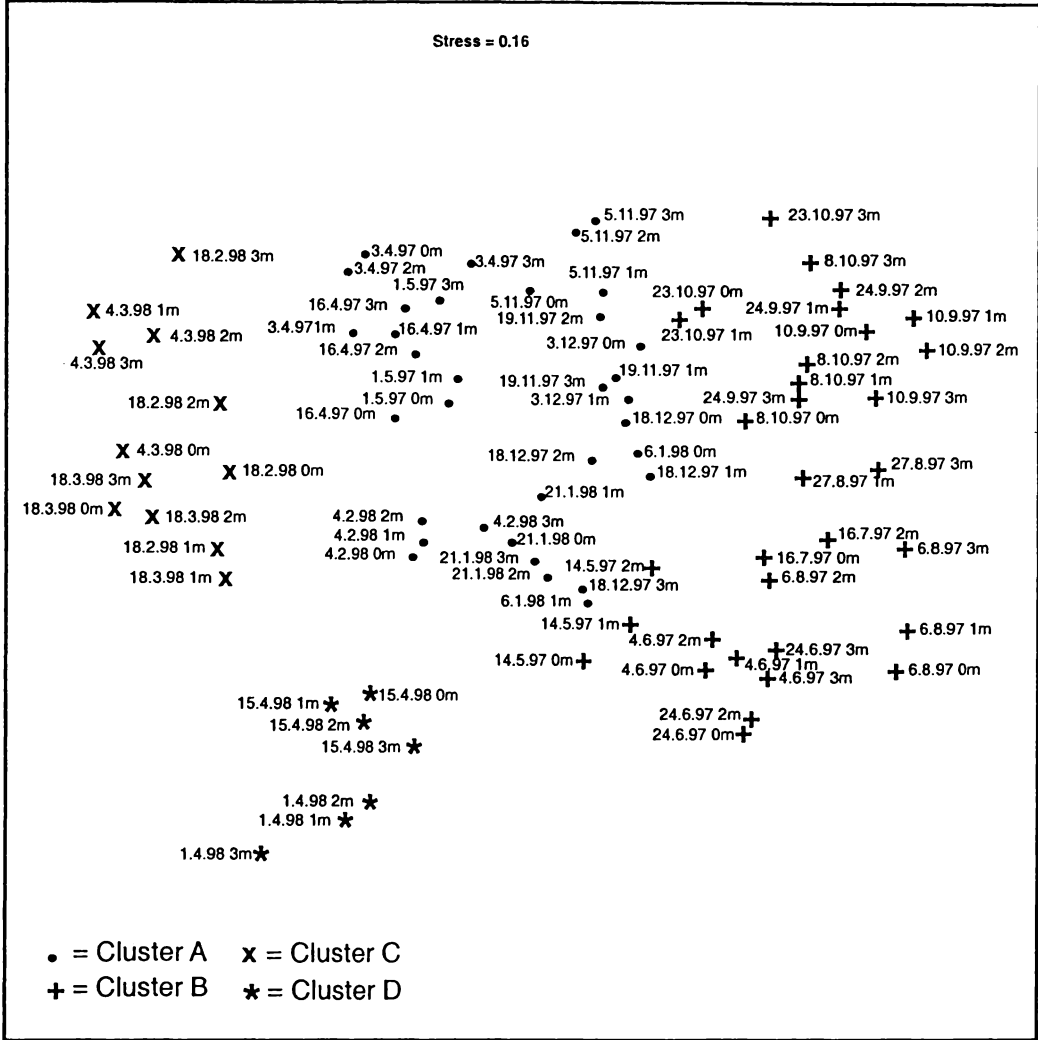


Fig. 3.34. MDS plot of samples from Lake Ngaroto based on abundant rotifer species.

The spread of sample scores in the Lake Ngaroto CCA ordination (Fig. 3.35, Table 3.8) correspond in general with groups found in the cluster analysis and MDS. Cluster B (winter-spring) samples were all found negatively associated with Axis 1. Cluster A samples were found to be generally positively associated with Axis 1, but also moderately negatively associated with this axis at the bottom of the ordination. Cluster C and D samples were all strongly positively associated with Axis 1. *Asplanchna sieboldi*, *Conochilus coenobasis*, *Keratella cochlearis*, *Synchaeta oblonga*, *Synchaeta pectinata* and *Trichocerca similis* were all strongly negatively associated with Axis 1, and therefore associated with Cluster B (winter-spring) samples. *Asplanchna priodonta*, *Brachionus calyciflorus*, *Hexarthra intermedia*, *Keratella tecta*, *Polyarthra dolichoptera* and *Pompholyx complanata* were strongly positively associated with Axis 1, and therefore associate with Clusters A, C and D (summer-autumn) samples. Of these, *Brachionus calyciflorus* most strongly associated with samples from Clusters C and D. *Trichocerca tenuior* and *Trichocerca pusilla* were strongly negatively associated with Axis 2, and *Conochilus coenobasis*, *Filinia longiseta*, and *Keratella tecta*, were all strongly positively associated. Species associated with Axis 2 were found to associate with either Cluster A or B, and Axis 2 was therefore not well related to cluster analysis groupings.

Forward selection and associated Monte Carlo permutation tests of the significance of the environmental variables indicated that temperature was the variable most highly correlated with variance in rotifer distribution, with pH and microplankton also able to account for >10 % of the species variation when explored by themselves (Table 3.6d). In the environmental ordination, temperature, pH and microplankton were found to strongly positively associate with Axis 1. Temperature also was found to be strongly negatively associated with Axis 2. This axis was found to explain little additional variability in rotifer species distribution after temperature was initially added to the model. Species associating negatively with Axis 1 (*Asplanchna sieboldi*, *Conochilus coenobasis*, *Keratella cochlearis*,

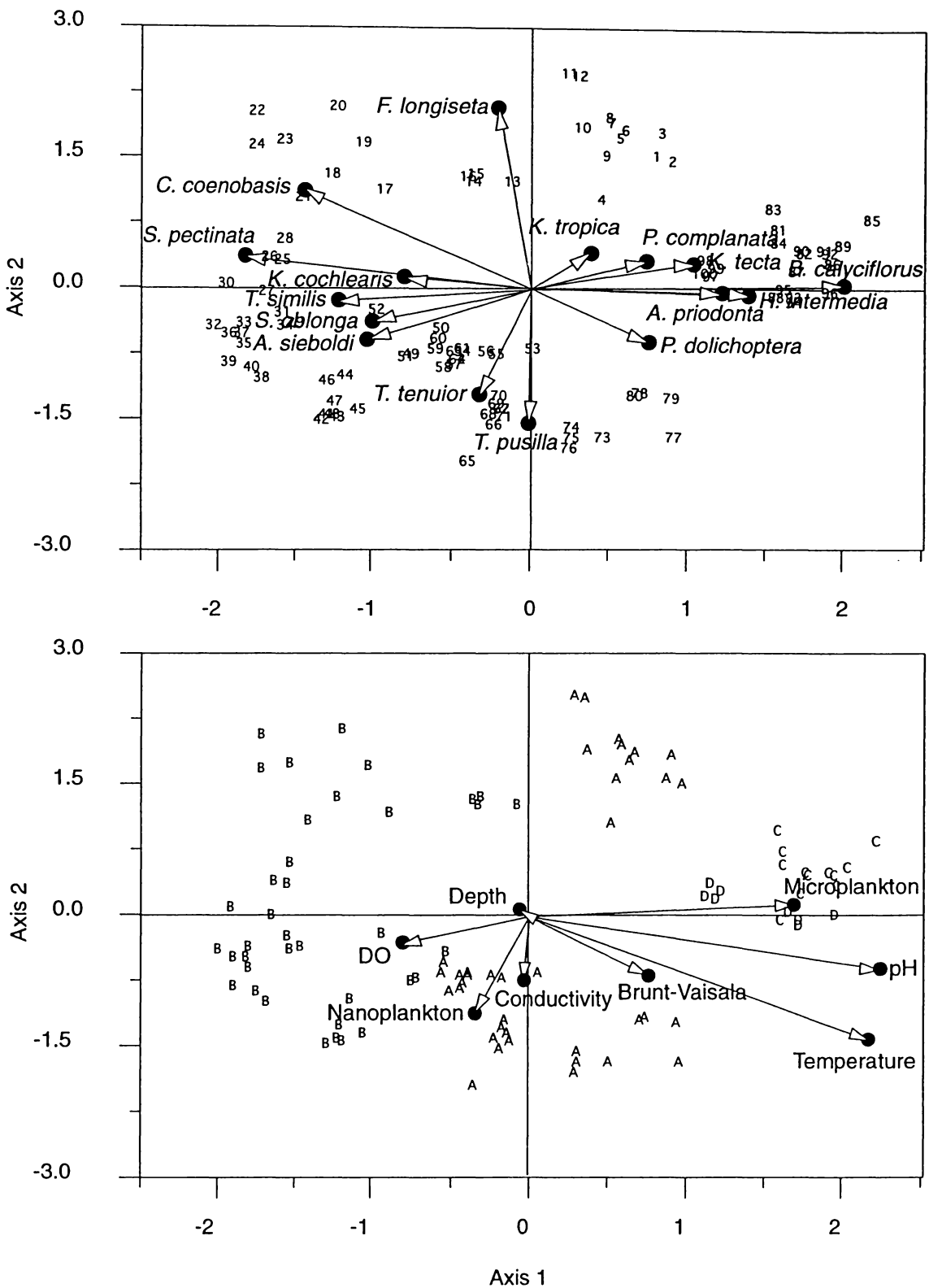


Figure 3.35. Ordination diagram based on canonical correspondence analysis (CCA) of Lake Ngaroto rotifer species with respect to environmental variables. Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers. The date and depth of each sample number is given in Table 3.8. Some sample numbers have been omitted from the ordination for clarity. Cluster groups are superimposed on the environmental biplot.

Table 3.8. Key to sample numbers (dates (d:m:y) and depths) for the Lake Ngaroto CCA ordination.

n	date	depth	n	date	depth	n	date	depth	n	date	depth
1	3/4/97	0m	26	16/7/97	1m	51	23/10/97	2m	76	21/1/98	3m
2	3/4/97	1m	27	16/7/97	2m	52	23/10/97	3m	77	4/2/98	0m
3	3/4/97	2m	28	16/7/97	3m	53	5/11/97	0m	78	4/2/98	1m
4	3/4/97	3m	29	6/8/97	0m	54	5/11/97	1m	79	4/2/98	2m
5	16/4/97	0m	30	6/8/97	1m	55	5/11/97	2m	80	4/2/98	3m
6	16/4/97	1m	31	6/8/97	2m	56	5/11/97	3m	81	18/2/98	0m
7	16/4/97	2m	32	6/8/97	3m	57	19/11/97	0m	82	18/2/98	1m
8	16/4/97	3m	33	27/8/97	0m	58	19/11/97	1m	83	18/2/98	2m
9	1/5/97	0m	34	27/8/97	1m	59	19/11/97	2m	84	18/2/98	3m
10	1/5/97	1m	35	27/8/97	2m	60	19/11/97	3m	85	4/3/98	0m
11	1/5/97	2m	36	27/8/97	3m	61	3/12/97	0m	86	4/3/98	1m
12	1/5/97	3m	37	10/9/97	0m	62	3/12/97	1m	87	4/3/98	2m
13	14/5/97	0m	38	10/9/97	1m	63	3/12/97	2m	88	4/3/98	3m
14	14/5/97	1m	39	10/9/97	2m	64	3/12/97	3m	89	18/3/98	0m
15	14/5/97	2m	40	10/9/97	3m	65	18/12/97	0m	90	18/3/98	1m
16	14/5/97	3m	41	24/9/97	0m	66	18/12/97	1m	91	18/3/98	2m
17	4/6/97	0m	42	24/9/97	1m	67	18/12/97	2m	92	18/3/98	3m
18	4/6/97	1m	43	24/9/97	2m	68	18/12/97	3m	93	1/4/98	0m
19	4/6/97	2m	44	24/9/97	3m	69	6/1/98	0m	94	1/4/98	1m
20	4/6/97	3m	45	8/10/97	0m	70	6/1/98	1m	95	1/4/98	2m
21	24/6/97	0m	46	8/10/97	1m	71	6/1/98	2m	96	1/4/98	3m
22	24/6/97	1m	47	8/10/97	2m	72	6/1/98	3m	97	15/4/98	0m
23	24/6/97	2m	48	8/10/97	3m	73	21/1/98	0m	98	15/4/98	1m
24	24/6/97	3m	49	23/10/97	0m	74	21/1/98	1m	99	15/4/98	2m
25	16/7/97	0m	50	23/10/97	1m	75	21/1/98	2m	100	15/4/98	3m

Synchaeta oblonga, *Synchaeta pectinata* and *Trichocerca similis*) were therefore associated with low temperature, pH and microplankton, and those positively associating with Axis 1 (*Asplanchna priodonta*, *Brachionus calyciflorus*, *Hexarthra intermedia*, *Keratella tecta*, and *Pompholyx complanata*) were found at high temperature, pH and microplankton. Clusters C and D, and associated *Brachionus calyciflorus*, are associated with high levels of microplankton. Comparing graphs of *Synchaeta pectinata*, *Conochilus coenobasis* (negatively associating with Axis 1), *Brachionus calyciflorus* and *Hexarthra intermedia* (positively associating) (Fig. 3.20) with those of temperature, pH and microplankton (Figs 3.2-3.11) confirm these relationships. *Filinia longiseta* and *Trichocerca pusilla*, strongly positively and negatively associating with Axis 2 respectively, due to the low level of additional explanatory power of variables after the addition of temperature, had similar distributions to rotifers from the clusters to which they belonged (B and A respectively).

Weighted average species optima for environmental variables concur with distributions found in CCA (Fig. 3.36). Cluster B (winter-spring) species (*Asplanchna sieboldi*, *Conochilus coenobasis*, *Keratella cochlearis*, *Synchaeta oblonga*, *Synchaeta pectinata* and *Trichocerca similis*) were found to be grouped at low temperatures, and Clusters A, C and D (summer-autumn) species (*Asplanchna priodonta*, *Brachionus calyciflorus*, *Hexarthra intermedia*, *Keratella tecta*, *Polyarthra dolichoptera* and *Pompholyx complanata*) associated with high temperatures. Species from each cluster group were generally found to have optima for other physico-chemical variables (e.g., pH and microplankton) similar to those of other species associated with the same cluster group.

Comparison of species dynamics between lakes

Several species were found to be abundant in more than one lake, and their comparative dynamics are therefore considered (cf. Figs 3.17-3.20). *Ascomorpha ovalis*, *Asplanchna priodonta*, *Conochilus coenobasis*, *Hexarthra intermedia*, *Collotheca* sp., *Keratella*

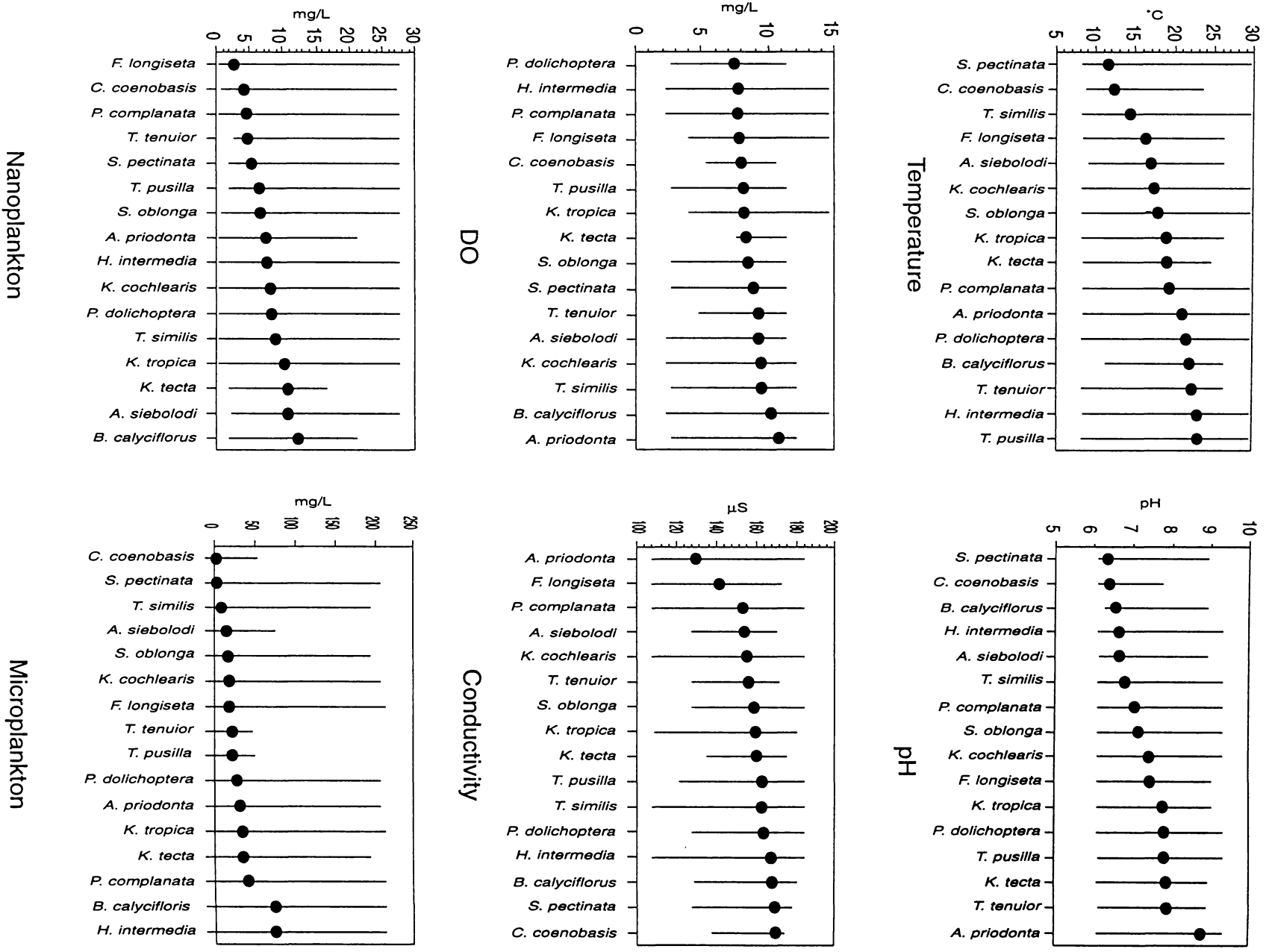


Fig. 3.36. Weighted average optima, and tolerances of Lake Ngaroto abundant species for temperature, pH, DO, conductivity, nanoplankton and microplankton. ● shows the weighted average optimum, and whiskers show the range over which a species was recorded.

procurva, *Keratella tecta*, *Keratella tropica*, *Pompholyx complanata*, *Polyarthra dolichoptera* and *Trichocerca pusilla* were generally found to have summer and autumn distributions in lakes where they were abundant. However, timings in peak abundances within this period often were found to vary, as for example in *Conochilus coenobasis*, *Keratella tecta* and *Keratella tropica*. Others were found frequently to have additional peaks outside of these periods, for example *Collotheca* sp. and *Polyarthra dolichoptera*. *Synchaeta oblonga*, *Synchaeta pectinata* and *Trichocerca similis* were generally found to have winter and spring distributions, although *Synchaeta oblonga* also peaked in early autumn 1997 in Lake Okaro, and *Trichocerca similis* had autumn peaks in Lake Rotoiti, and in Tikitapu at depth. *Filinia* cf. *pejleri* and *Filinia terminalis* were both found to have winter peaks, with *F. terminalis* peaks generally occurring immediately after those of *Filinia* cf. *pejleri*. *Asplanchna sieboldi* peaked in spring in Lake Tikitapu, summer in Lakes Rotoiti and Ngaroto, and both spring and summer in Lake Okaro. *Filinia longiseta* was most abundant in autumn 1997 in Lakes Tikitapu and Ngaroto, but in Lake Okaro was most abundant in spring. *Keratella slacki* had autumn peaks in Lake Tikitapu, autumn and spring peaks in Lake Rotoiti, and spring only in Lake Okaro. *Trichocerca longiseta* had small peaks in autumn and spring in both Lakes Tikitapu and Rotoiti. *Filinia novaezealandiae* had inconsistent dynamics between lakes. In Lake Tikitapu this species was found in autumn at depth, in Lake Okaro to peak early spring, and in Lake Rotoiti to be perennial, but most abundant in late autumn and early spring. *Keratella cochlearis* was perennial in all lakes, although peak abundances also occurred at different times in each lake. In Tikitapu this species had no particular period of great abundance, peaked in spring and summer in Lake Rotoiti, spring in Lake Okaro, and in early summer in Lake Ngaroto. These results suggest that there was much inconsistency in the seasonality of species between lakes, and also between years with some species abundant in autumn at the beginning of the study, but not at the end. Comparison with temperature preferences of species between lakes, the most important variable correlating with seasonal species

distribution within each lake, shows that although many species have wide tolerances, species generally have similar optima between lakes, e.g., *Synchaeta pectinata*, *Synchaeta oblonga*, *Filinia* cf. *pejleri*, and *Trichocerca similis* generally have low temperature optima (generally <15 °C), and *Trichocerca pusilla*, *Hexarthra intermedia*, *Asplanchna priodonta*, and *Polyarthra dolichoptera* generally have high temperature optima (>15 °C). Species with the most inconsistent timings in abundance, for example *Filinia novaezealandiae* and *Keratella cochlearis*, were found to have widely varying temperature preferences between lakes.

Discussion

Environmental conditions

The lakes displayed a wide range of trophic state and contrasting mixing patterns. Based on the observed chlorophyll *a* and Secchi depth measurements, Lake Tikitapu can be classed as oligo-mesotrophic, Rotoiti as meso-eutrophic, and Lakes Okaro and Ngaroto hyper-eutrophic using the OECD (1982) fixed boundary system. Despite both Lakes Ngaroto and Okaro being classed as hyper-eutrophic, Lake Okaro had very much higher chlorophyll *a* levels. Secchi transparency was generally lower in Lake Ngaroto, probably due to resuspension of bottom sediments in this shallow lake.

The mixing patterns of Lakes Tikitapu, Rotoiti, and Okaro are warm monomictic, and Lake Ngaroto polymictic. Lakes Tikitapu, Rotoiti and Okaro appear typical of New Zealand monomictic lakes in that stratification lasted six to seven months, from October to April or May (Green *et al.* 1987). Differences in the overall depth and duration of stratification are likely to be influenced by the differing morphometries of these lakes. New Zealand lakes have a wide range of morphometry in a small area, so these variations are likely to reflect the variety of timings in stratification and destratification.

Seasonal temperature ranges (STR) for the monomictic lakes (Lake Tikitapu 13.2 °C, Lake Rotoiti 11.8 °C, Lake Okaro 14.0 °C) are within the expected ranges ($13.0 \pm$

3.1 °C) for North Island lakes (Green *et al.* 1987), and therefore have lower STRs than lakes of similar latitudes in the northern hemisphere (Green *et al.* 1987). Lake Ngaroto, however, had a STR of 17.1 °C when the whole water column was considered, although this was affected by periods of marked surface heating. An assessment made from 1-3 m depth gave a STR of 16.2 °C, slightly above the range for North Island monomictic lakes as assessed by Green *et al.* (1987), due to the shallow nature of the lake. No temperatures were recorded lower than 7 °C during the study in any lake, which are high winter temperatures compared with northern hemisphere lakes of similar latitudes. Conversion of the temperature profiles to stability gradients (Brunt-Vaisala frequency) showed that the monomictic lakes had high stability at the base of the epilimnion during stratification, and polymictic Lake Ngaroto in the upper part of the water column during stratification, which are typical stability patterns for these mixing types (Green *et al.* 1987).

Daily wind speeds were commonly low in winter, increasing on average in spring, and had several high peaks in summer and autumn. This is markedly different from patterns generally found in North America, for example, where winds are highest in winter, declining markedly in spring, and are lowest in summer (Green *et al.* 1987). High wind speeds in the current study coincided, therefore, with thermal stratification. This is the general pattern in New Zealand, and is not commonly encountered in northern temperate lakes (Green *et al.* 1987). The timings of disturbance on the thermocline during summer and autumn were found to correlate with high wind speeds during these periods.

Mild temperatures are likely to have contributed to high epilimnetic chlorophyll *a* levels in winter in the monomictic lakes. This pattern of high winter epilimnetic chlorophyll *a* levels, when the water column is still mixed, is a general occurrence in lakes that stratify in New Zealand (Viner & White 1987). This pattern is in contrast with the annual changes expected in northern hemisphere lakes of similar latitude, which typically produce single spring peaks of biomass (Viner & White 1987). Lake Tikitapu also had peak chlorophyll *a* densities at depth during stratification, which is a common occurrence where stability

occurs in the metalimnion (Viner 1985). The contrasting summer chlorophyll *a* maxima in polymictic Lake Ngaroto is similar to patterns in other shallow, well mixed New Zealand lakes (e.g., Lakes Mahinerangi and Waipori), due to high temperatures and regular nutrient cycling during this time. High stability in the surface waters of polymictic lakes is also commonly found to promote growths of buoyant blue-green algae (Viner 1985). Microplankton chlorophyll *a* levels were in general higher than nanoplankton chlorophyll *a* levels both temporally and spatially in all lakes. This reflects the tendency of New Zealand lakes to be dominated by large algae, even in oligotrophic systems (Malthus & Mitchell 1990).

Rotifer diversity

The diversity of planktonic rotifer species found in the present study, ranging from 38 to 43, is high compared with diversities commonly recorded from New Zealand lakes. Many past studies have given the impression of a low species diversity compared with elsewhere. Of those that have used suitable sampling methods, Forsyth & McCallum (1980) and James (1995) found totals of eight and ten species, respectively, from Lake Taupo. Forsyth & James (1991) and James (1995) found twelve and eleven species, respectively, from Lake Okaro. These diversities appear remarkably low compared with my findings. In contrast Sanoamuang (1992), however, found 44 species from Lake Grasmere, South Island, a diversity similar to what was found in this study. Such species numbers are likely to be more typical of New Zealand lakes, and are comparable also with northern temperate lakes (e.g., Elliott 1977, Berner-Fankhauser 1983, Mikschi 1989, Vasconcelos 1990). Many previous diversity estimates from New Zealand lakes therefore are possibly inaccurate due to inadequate taxonomic resolution. Many species encountered in the current study are benthic-littoral taxa, for example the *Lecane* and *Lepadella* species, although these were generally found to make up only a small percentage of the total rotifer densities. In Lake Grasmere, Sanoamuang (1992) attributed a large number of benthic-

littoral taxa to the shallowness and well mixed water of this lake. Although Lakes Rotoiti and Tikitapu are significantly larger than Lake Grasmere (area 0.63 km², maximum depth 12 m), it seems likely that this may apply to them also because of the general impacts of high winds in New Zealand, and therefore the greater force of mixing (Green *et al.* 1987). Such mixing may contribute to a high number of rotifers entering the pelagic from the littoral or benthos where a high diversity is known (e.g., Duggan *et al.* 1998). This may occur even in these relatively large lakes. There were no apparent trends in the temporal and spatial patterns in the diversity of rotifers within the lakes.

Seasonal and spatial dynamics

(i) Total numbers

Total rotifer abundances in summer and autumn were generally between 100 and 300 ind/L in Lake Tikitapu, 200 and 400 ind/L in Lake Rotoiti, 300 and 600 ind/L in Lake Okaro, and 500 and 1500 ind/L in Lake Ngaroto. Greater total rotifer abundances were therefore generally found in lakes of higher trophic status, likely due to greater levels of suitable food – a correlation has been made elsewhere also (e.g., Herzig 1979, Orcutt & Pace 1984, Andrew & Fitzsimons 1992). This is reflected in the present study by the densities of the nanoplankton fraction of chlorophyll *a* which shows an increase with trophic state, and thus the increased abundance of potential food. Peak rotifer densities appear comparable with those found in northern temperate lakes, which commonly have between 200 and 500 ind/L in oligotrophic waters, and 1000 and 2000 ind/L in eutrophic waters (Ruttner-Kolisko 1979). Equitability was lower in lakes with higher trophic status, indicating that although greater abundances were found in higher trophic state lakes, only a few species were likely to dominate at any time.

There was a fairly consistent seasonal pattern of low rotifer abundances occurring in the winter months. Despite higher rotifer densities in lakes of higher trophic state, there appeared to be little correlation between the spatial and temporal distribution of the total

rotifer numbers and nanoplankton densities. In winter, peaks in nanoplankton levels in Lakes Tikitapu and Rotoiti had no noticeable correlation with total rotifer densities. However, the use of chlorophyll *a*, or the nanoplankton fraction of chlorophyll *a*, is perhaps not a true measure of food densities for rotifers due to the specificity in diet of many species (e.g., Bogdan & Gilbert 1987). There was, however, a good correlation between rotifer densities and water column stability and mixing events, with highest rotifer densities found in summer and autumn when stability was highest, and rotifer densities (and stability) reduced during mixing events during this time. Abundance also is probably restricted by cooler temperatures in winter, despite warmer winter temperatures than would be expected in equivalent northern latitudes. Low winter rotifer abundances also have been found in other New Zealand lakes (e.g., Parr 1949, Sanoamuang 1992, and James 1995), and are common in crustacean zooplankton (Chapman & Green 1987, Burns 1991). As well, there is inconsistency in the timings of peak total abundances. This was found in the present study in summer and autumn, although with variable timing. Timings in peak abundances are similar to those of James (1995) in mid summer and autumn in Lakes Okaro and Taupo, although Sanoamuang (1992) found autumn and spring maxima in Lake Grasmere. Inconsistency in the timings of peak abundance of crustacean zooplankton also is common in New Zealand. In the current study, peak rotifer densities generally coincided with peaks in stability and chlorophyll *a* concentrations. The variable timing of peak rotifer densities between lakes both in this study, and compared with others, is therefore likely to reflect the variability of stability and algal production brought about by morphometric and yearly climatic variability in New Zealand.

(ii) Community composition and species distributions

A seasonal succession was observed in rotifer community composition in all of the lakes. Distinct species assemblages generally occurred in lakes during the holomictic periods (winter and spring), and one or more during the stratified or stable periods (summer and

autumn). The predominant factor determining succession therefore appeared to be the mixing pattern, with the onset and erosion of thermal stratification in monomictic Lakes Tikitapu, Rotoiti, and Okaro, or the difference between the mixed and relatively stable seasons in polymictic Lake Ngaroto, apparently demarcating species distributions between relatively warm and cold water assemblages. Reynolds (1984) and Lampert & Sommer (1997) emphasise that mixing pattern and the degree of environmental stability are the most important factors controlling plankton (phytoplankton or zooplankton) succession. In the phytoplankton, species are randomised at times of mixing, but in more stable density gradients species buoyancy and behaviour become increasingly important (Reynolds 1984). Individuals may therefore sink or float depending on the intrinsic density of each species, or if they are motile they may make compensatory movements. In this sense, rotifer composition may be dependent on stability selecting for rotifer species with appropriate morphological or behavioural adaptations, or composition may be affected indirectly by changes in phytoplankton composition. Mixing also has been linked with rotifer succession elsewhere. Fussmann (1993) investigated the late summer and autumn breakdown of the thermocline in Heiligensee, Germany. In that study, decrease in temperature and the erosion of the hypolimnion due to storms was interrupted by periods of fine weather and temporary restratification. This sequence of physical events may have allowed mass production of algae and rotifers due to exploitation of newly available nutrients. But along with this was a progressive loss in the abundance of warm stenotherms. Similarly, Eckert & Walz (1998) in Muggelsee, Germany, found species composition to be different between summer (when water was strongly stratified and frequencies of strong wind events were low) and autumn (when intervals between strong winds were shorter). Breakdown of the summer stratification by mixing in northern hemisphere lakes, however, is generally restricted to the autumn period because of a change to more regular stronger winds (e.g., Fussmann 1993, Eckert & Walz 1998). This is in contrast with New Zealand, however, where winds are continually strong, and mixing

is likely to occur more often, including summer (Green *et al.* 1987). Several peaks in daily wind speed were found to occur during the stratified period, and correlated with an increase in the depth of the mixed layer. Erosion of the hypolimnion due to storm events and subsequent restratification (or mixing and restratification in Lake Ngaroto), generally coincided with high algal levels. Two or more species assemblages were found during the stratified period in Lakes Okaro and Ngaroto, which appeared to be demarcated by these additional allogenic events. New Zealand's windiness and unpredictable climate therefore appear to be important throughout summer and autumn, with storm events at irregular intervals at this time causing not only thermocline erosion, but probably also providing pulses of nutrients washed in from the catchments. Such features result in pulses of phytoplankton productivity and food availability (Viner & White 1987, Chapman & Green 1987), so re-setting the successional events of rotifer communities.

Multivariate analyses have proven sensitive in discerning patterns in zooplankton communities along environmental gradients, and there should be particularly close correlations between species abundances and the environmental variables that limit them. Temperature was determined as the most important factor correlating with variations in abundances of rotifer species in all four lakes, although most variables measured were found important to some degree. Temperature is commonly a key factor in restricting the occurrence of rotifer species, and it is therefore not surprising that species appeared to have temporally restricted periods of presence and abundance despite the reduced seasonal temperature range found in New Zealand. Species found to have highest densities (and optima) in warm (e.g., *Asplanchna priodonta*, *Conochilus coenobasis*, *Hexarthra intermedia*, *Trichocerca pusilla*, *Polyarthra dolichoptera*) or cold (e.g., *Synchaeta oblonga*, *Synchaeta pectinata*, and *Trichocerca similis*) water commonly showed similar trends between lakes. Temperature preferences of species in general concur with those found elsewhere. For example, *Ascomorpha ovalis*, *Keratella tropica* and *Trichocerca pusilla* are generally considered to be warm stenotherms, and *Synchaeta oblonga* and *Synchaeta*

pectinata are generally considered to be cold stenotherms (e.g., Ruttner- Kolisko 1974, Herzig 1987, Shiel & Koste 1993, Berzins & Pejler 1989b). *Conochilus coenobasis*, *Hexarthra intermedia*, *Keratella tecta* and *Pompholyx complanata* were found with summer and autumn distributions in the current study, and have been found with similar distributions in New Zealand previously (Forsyth & McCallum 1980, Forsyth & James 1991). However, some species were found to have temperature optima contrasting with other studies. *Asplanchna priodonta* was found predominantly in warm water, as reported by Sanoamuang (1992) in Lake Grasmere, although it is generally considered a true eurytherm elsewhere (e.g., Berner-Fankhauser 1983, Herzig 1987). *Polyarthra dolichoptera* was commonly found to have high thermal preferences in the current study, but is generally considered a cold stenotherm elsewhere (Ruttner-Kolisko 1974, Herzig 1987, Berzins & Pejler 1989b). Sanoamuang (1992), however, found this species to be eurythermal in Lake Grasmere, reaching peaks in abundance at any time of the year, possibly when conditions other than temperature are favorable. Thermal preference of some species in New Zealand may therefore not be as specific as some northern hemisphere studies have reported. This is possibly because the thermal tolerances of many species are sufficiently wide that they commonly at least equal the seasonal temperature range of New Zealand lakes (Forsyth & James 1991). Alternatively, the lack of consistency in temporal distributions for some species may be due to these not being the nominate taxa, but species closely resembling those of the northern hemisphere (e.g., Shiel & Sanoamuang 1993). Such species therefore deserve closer taxonomic attention. No consistent seasonal pattern was apparent for *Keratella cochlearis* and *Filinia novaezealandiae* between lakes. In the current study, *Keratella cochlearis* was generally perennial with peaks in spring, summer, or both, and in Lake Grasmere was found by Sanoamuang (1992) to have autumn and spring peaks. This lack of consistency concurs with the temporal distribution of this species in northern temperate lakes where it is considered a true eurytherm (e.g., May 1983, Herzig 1987, Mikshi 1989). *Filinia novaezealandiae* was found in autumn at depth in

Lake Tikitapu, to peak early spring in Lake Okaro, and to be perennial with peaks in late autumn and early spring in Lake Rotoiti. The seasonal preferences found in the current study are in contrast with those from which the original species was described, from spring and summer in Lake Okaro, at temperatures greater than 20 °C (Shiel & Sanoamuang 1993). This species may therefore be either eurythermal, or the thermal preferences in the initial description may be incorrect due to samples being collected using vertical hauls and not therefore taking account of vertical distribution of both rotifers and temperature. Rotifer species that are eurythermal are likely to have peaks in response to factors other than temperature.

In New Zealand crustacean communities, food levels are often regarded as being the major factor limiting populations (Chapman & Green 1987). Nanoplankton densities were highly correlated with rotifer species densities in the CCAs from Lakes Tikitapu and Rotoiti, likely because food is, to a certain degree, limiting because of the lower trophic state of these lakes. By comparison, in Lakes Okaro and Ngaroto nanoplankton densities were apparently relatively unimportant. Food, however, may be even more important than is presented here. Palatable and non-palatable forms were not separated, so reducing the effectiveness of nanoplankton as a measure. Similarly, some rotifers within a community may have specialisation in diet (e.g., Bogdan & Gilbert 1987). The variations in these species may be dependent not on the densities of nanoplankton *per se*, but on the presence of particular phytoplankton species, and therefore the seasonal succession of phytoplankton species within the nanoplankton size range. For example, *Anuraeopsis*, *Keratella*, *Filinia* and *Pompholyx* species feed on very fine particles (10-12 µm), and *Ascomorpha* species specialise on *Ceratium* and *Peridinium* (Pourriot 1977, Clément 1987, Bogdan & Gilbert 1987). Alternatively, some rotifer distribution may be independent of algal development, instead correlating with levels of bacteria, detritus or prey densities (i.e. other rotifers or ciliates), or with other competitors or predators (e.g., cladocerans or copepods).

Within each lake, individual rotifer species appeared to have differences in the timings of peak abundances, even when compared with species from the same assemblages recognised by multivariate analyses. It appears therefore that there is a great deal of habitat partitioning within the assemblages, particularly temporally, so as to avoid negative interactions between co-occurring species (Markawicz & Likens 1975, 1979). This is also apparent in the examination of species optima for different physico-chemical conditions, and the distribution of species in the CCAs, with species responding differently from one another to gradients in environmental conditions. This fine scale temporal segregation in peak abundances of New Zealand rotifer species is in contrast to patterns commonly found in New Zealand crustacean zooplankton species which generally show little seasonality and no clear relationships to patterns of temperature change. Diversity of New Zealand crustacean zooplankton is low in comparison with northern temperate lakes. These species are often thought of as generalists, adapted to cope with a wide variety of conditions and are thus not highly adapted for particular combinations of temperature and food levels (Chapman & Green 1987, Burns 1991). Greenwood *et al.* (1999), however, found competition for food resources did impose a seasonality of sorts on small bodied cladocerans in Lake Mangakaware, with timings of species abundance governed by differences in each species ability to take advantage of the unpredictable and infrequent pulses of available food. A higher diversity of Crustacea in continental regions is assumed to lead to a higher degree of specialisation and tighter species packing that may help impose seasonality, and this is likely to be the case for the more diverse rotifers in New Zealand. The timing of rotifer species succession, however, is apparently inconsistent between years and lakes. On a broad scale, the windy and unpredictable climate, combined with an increased potential for lakes to mix, are likely predisposing factors to a less predictable timing in stratification, destratification, and other mixing events, and therefore succession of rotifer communities, between years. The varying effects of topography and lake morphometry are likely to have led to the differences in the timings of the onset and erosion

of stratification between lakes in the present study, even though the lakes were studied concurrently and are in relatively close proximity to one another. This, combined with the varying effects of the morphometry on lake temperature cycles are likely to have led to much of the more subtle variation in species occurrence and abundance between lakes within each season.

Based on the apparent correlations between mixing and stratification on rotifer community dynamics, the predominance of warm monomictic lakes and mild winter temperatures in New Zealand is likely to result in a fundamental difference in succession from that seen in predominantly northern hemisphere dimictic lakes. Northern temperate lakes commonly have winter stratification “under-ice” and associated distinct cold water communities. For example, Stemberger (1995), in a study of 42 Michigan, U.S.A. lakes found *Synchaeta asymetrica*, *Notholca foliacea*, *N. squamala* and *N. michiganensis* only at temperatures below 5 °C, and Mikschi (1989) in Lunzer Obersee, Austria, found populations of *Keratella hiemalis*, *Filinia hofmanni*, *N. squamala* and *Synchaeta lakowitziana* to have greatest abundances either under ice cover or immediately after ice breakup, at temperatures below 7.5 °C. In my study, however, no temperatures were recorded lower than 7 °C. New Zealand lake temperatures are rarely recorded lower than this, so such communities never have the chance to become established.

Vertical distribution of rotifers

The spatial distribution of environmental variables was generally unimportant in determining variability in rotifer community distribution, such as the existence of a summer hypolimnetic community distinct from that in the epilimnion as occasionally found in some northern hemisphere lakes. For example Hofmann (1985) found distinct communities above and below the thermocline in summer in the Plußsee, with *Keratella quadrata*, *Keratella cochlearis*, *Kellicottia longispina* and *Conochilis unicornis* distributed almost exclusively above, and *Filinia terminalis*, *Keratella hiemalis* and *Filinia hofmanni* below the

thermocline. In the current study, a lack of segregation in rotifer communities between the epilimnion and hypolimnion was apparent in both the cluster analysis and ordinations, in which samples from similar sampling dates were usually always grouped despite marked vertical variation in physico-chemical variables. It was important, however, in affecting the total densities of rotifers vertically during periods of stratification. Low densities in the hypolimnion are presumably due to low food densities, temperature and oxygen levels being unsuitable for species. The appearance of animals in the hypolimnion, despite the unfavourable conditions, may be due to periodic strong winds forcing animals into the hypolimnion from the surface waters. Therefore, this periodic disturbance of the hypolimnion is likely to ensure that cold water species are unable to persist there. In a study of the seasonal changes in rotifer communities in 42 Michigan lakes, Stemberger (1995) found rotifer composition during stratified periods to relate to the ability of lakes to retain winter assemblages into spring, summer and autumn, with mixing events removing these refugia. Alternative reasons for the occurrence of epilimnetic species in the hypolimnion may be that weak temperature gradients in the thermoclines of New Zealand lakes (Green *et al.* 1987) may not form strong barriers to migration. It also may be that appearances in the hypolimnion are the result of recent emergence from the sediment, with the animals subsequently migrating into the epilimnion. However, because low oxygen levels in the hypolimnion were not particularly important in affecting community composition, the degree of deoxygenation caused by trophic state differences is unlikely to be an important factor in affecting distribution of rotifers between lakes. The variability of community composition between lakes relating to trophic state from the Rotorua area found by Duggan *et al.* (in press) is therefore likely to be predominantly a result of species responses to the quantity and quality of food.

Although a great deal of the variability in the distribution of rotifers could be attributed to the measured environmental variables in this study, greater variation may be accounted for by taking into account the possible impacts of predation on rotifers by

omnivorous copepods, or possibly small fish (e.g., Jeppesen *et al.* 1987, Couch *et al.* 1999). Overall, it appears that allogenic factors associated with mixing and temperature apparently have a greater influence on temporal and spatial rotifer community dynamics within lakes than factors imposed by trophic state. Trophic state appears to govern abundances, and possibly composition between different lakes as found by Duggan *et al.* (in press). This will be investigated in the following chapter.

Chapter 4:

Distribution of rotifer communities in the North Island of New Zealand

Introduction

On a regional scale, species occurrence patterns can be associated with dispersal or movement of organisms across the landscape. Once organisms have arrived within a habitat, local scale factors, such as the suitability of the abiotic environment and biotic interactions with established species, determine community composition (Ricklefs 1987, Ricklefs & Schluter 1993). Rotifer species are generally thought to have high dispersal abilities (e.g., Pennak 1978), and should therefore not be limited by dispersal at a regional scale. The species composition of rotifers in lakes therefore is generally considered to be the result of local influences, such as physical, chemical and biological factors within each lake. Variation in rotifer composition in a region is most commonly found to be associated with gradients in trophic state (e.g., Mäemets 1983, Radwan & Popiolek 1989 and Ejsmont-Karabin 1995), or pH where this factor varies widely (e.g., MacIsaac *et al.* 1987 and Brett 1989). Geographical factors are sometimes important also, for example latitudinal variation in Australian or Arctic rotifer communities (Shiel & Koste 1986, Chengalath & Koste 1989). Disjunct distributions of species are becoming more apparent, however, for example between Tasmania and mainland Australia (Shiel & Koste 1986, Koste & Shiel 1987b), and the idea that the distribution of many species is limited by poor dispersal abilities is increasingly gaining acceptance (e.g., Jenkins 1995).

Greater than 400 species of rotifer have been recorded from New Zealand to date, and these have been recorded from a wide array of lakes. Many earlier studies focused on documenting new records of species from the country, rather than recording and exploring the distribution of species within and between individual lakes (see Shiel & Green 1996, and references therein). Sanoamuang & Stout (1993) surveyed the distribution of species

from 35 lakes in the South Island of New Zealand, the most widespread survey to date, although no attempt was made to infer the factors involved in determining the distribution of species between lake habitats. In the only study of factors affecting New Zealand rotifer community composition, Duggan *et al.* (in press) found the distribution of rotifers in ten Rotorua lakes to be associated with lake trophic state. However, this study was based on single samples from each lake, and it is therefore not known if trophic state determines distribution when a wider range of seasonal variability, or a wider geographical area, is considered. In the North Island of New Zealand, there is a wide array of lake types and a corresponding range of environmental conditions (e.g., lake trophic state) within a relatively small area (e.g., McColl 1972, Lowe & Green 1987). In addition, New Zealand is geologically complex. It is made up of three different geological structures of more or less independent history and geographical affinities which have come together (Cooper 1989, Heads 1989). New Zealand calanoid copepod distribution is thought to relate to these geographical features, although it is unknown if there are any dispersal limited rotifer species that are related similarly. Here I document baseline information on the planktonic rotifer community composition of many North Island lakes, and explore the factors that may affect compositional variations.

Methods

Sampling localities and dates are shown in Fig. 4.1 and Table 4.1. Rotifer samples were collected by vertical hauls using a 40 µm mesh net with a reducing cone (see Chapter 2). Sampling was carried out between 1997 and 1999 either by the author or by Regional Councils and the National Institute of Water and Atmospheric Research (NIWA) during regular monitoring of lakes. Where possible, samples were taken once each season. Samples were preserved in 4 % formalin. NIWA and Regional councils were provided

Table 4.1. List of lakes and dates of sampling during this study.

	Summer	Autumn	Winter	Spring
Northland Dune Lakes				
1. L. Waiparera		14.5.98		
2. L. Ngatu		12.5.98		
3. L. Waimimiha		12.5.98		
4. L. Waikare (Northland)		21.5.97		
5. L. Taharoa		21.5.98		
6. L. Kai-iwi		21.5.98		
7. L. Parawanui		21.5.98		
8. L. Ototoa	16.2.98	21.5.97	26.8.97	19.11.97
9. L. Kareta		21.5.97	26.8.97	
10. L. Kuwakatai	16.2.98	21.5.97	26.8.97	19.11.97
11. L. Spectacle	16.2.98	21.5.97	26.8.97	19.11.97
12. L. Tomarata	16.2.98	21.5.97	26.8.97	19.11.97
13. L. Wainamu	16.2.98	21.5.97	26.8.97	19.11.97
Auckland Volcanic Lakes				
14. L. Pupuke	16.2.98	21.5.97	26.8.97	19.11.97
Waikato Riverine Lakes				
15. L. Waikare	28.1.99	24.3.98	30.7.98	25.11.98
16. L. Waahi	28.1.99	24.3.98	28.8.97	25.11.98
17. L. Rotokauri	29.1.99	24.3.98	23.6.98	24.9.97
18. L. Rotorua	27.1.98	28.4.98	28.7.97	8.10.97
19. L. Rotomanuka	29.1.99	30.4.98	24.7.97	25.9.97
20. L. Rotomanuka South	29.1.99	24.3.98	24.7.97	25.9.97
21. L. Ngaroto	29.1.99	24.3.98	24.7.97	25.9.97
Waikato Hydroelectric Lakes				
22. L. Karapiro	27.1.98	28.4.98	22.7.97	8.10.97
23. L. Maraetai	27.1.98	28.4.98	25.7.97	8.10.97
Rotorua Volcanic Lakes				
24. L. Rotoehu		6.5.98	18.8.97	
25. L. Rotoiti	28.1.99	3.4.98	18.8.97	22.10.97
26. L. Rotoma	28.1.98	22.4.98	23.7.97	14.10.97
27. L. Rotorua		26.3.98	22.6.98	1.9.97
28. L. Okataina	28.1.98	22.4.98	23.7.97	14.10.97
29. L. Okareka	28.1.99	26.3.98	22.6.98	1.9.97
30. L. Tikitapu	3.2.98	16.4.98	23.6.97	22.10.97
31. L. Tarawera	28.1.98	22.4.98	23.7.97	14.10.97
32. L. Rotomahana				6.10.98
33. L. Rerewhakaaitu				6.10.98
34. L. Okaro	18.12.97	17.4.97	18.7.97	6.10.98
35. L. Taupo	21.1.98	7.4.98	7.7.97 29.7.97	29.10.97
Wairoa Landslide Lakes				
36. L. Waikaremoana	29.1.98	29.4.98	24.7.97	15.10.97
37. L. Tutira	29.1.98	29.4.98	24.7.97	15.10.97
Taranaki Hydroelectric Lakes				
38. L. Rotorangi (2 sites)	19.2.98	18.3.98	19.6.97	23.10.97 (1 site)
Wanganui Dune Lakes				
39. L. Horowhenua	18.12.97	18.4.98	5.6.97 7.8.97	26.11.97
Ruamahanga Lakes				
40. L. Wairarapa (4 sites)		4.3.98 18.5.98	16.7.97 (3 sites)	11.11.98
41. Matthews lagoon				3.11.98
42. Boggy pond lagoon				3.11.98

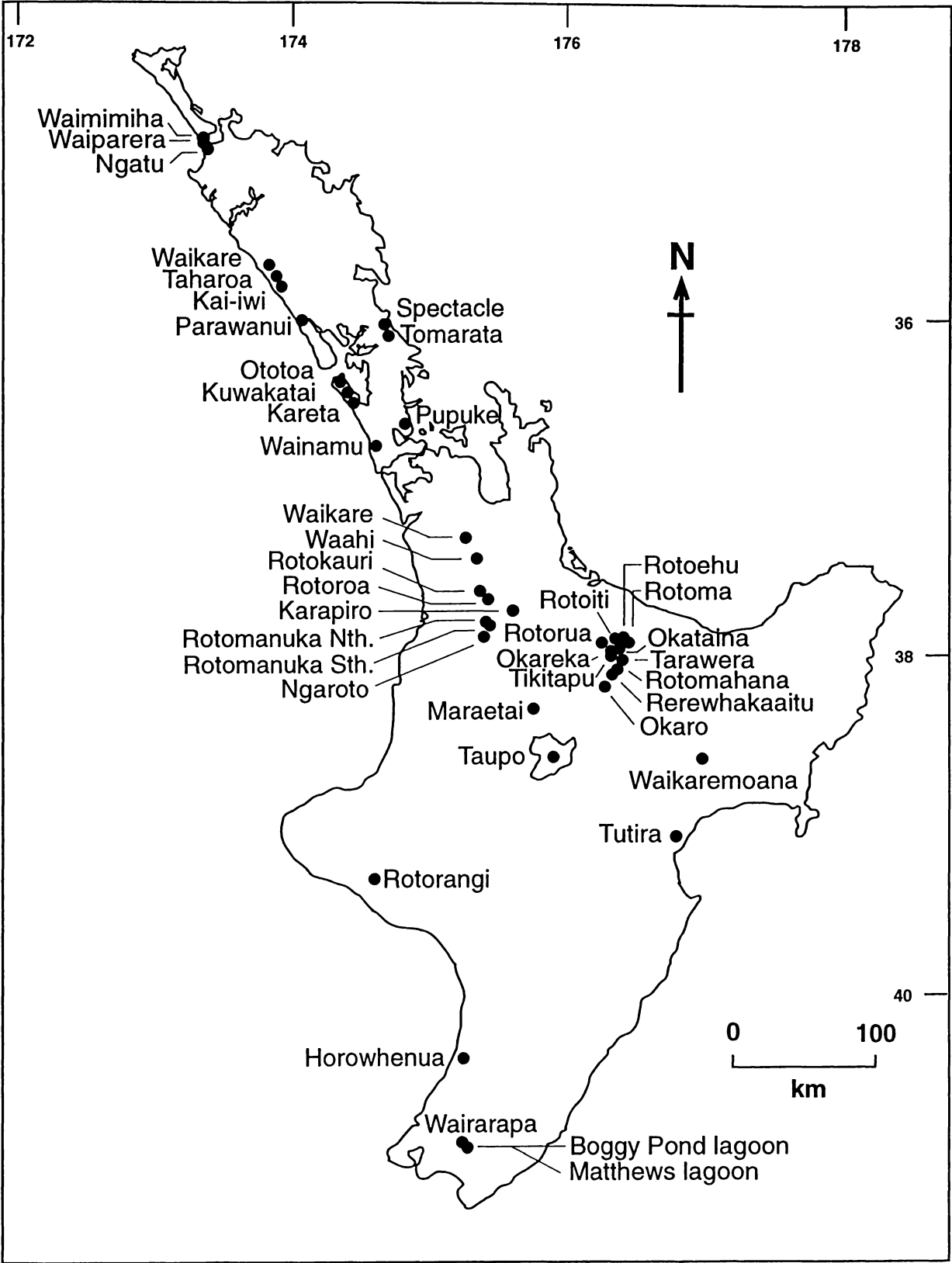


Fig. 4.1. Sampled lakes in the North Island, New Zealand.

with nets, preservative and sample bottles by the author. Surface temperature, dissolved oxygen (DO), oxygen saturation (%O), pH, total phosphorus (TP), chlorophyll *a* and Secchi depth were determined by the author, or supplied by the sources of the remaining samples. In general, samples were taken from single sites in each lake, except Lakes Rotorangi (2 sites) and Wairarapa (4 sites), and are assessed as separate entities.

For counting, samples were made up to a known volume, well stirred, and rotifers enumerated in 5 ml aliquots in a gridded perspex tray using a Leica MZ12 stereo microscope at *ca.* 30x magnification. Aliquots were enumerated until at least 1000 individuals were encountered, or until the entire sample was counted. Unknown animals were examined on an Olympus BX50 compound microscope and identified from body morphology or trophus structure after eroding the rotifer tissue with 10% sodium hypochlorite (Koste & Shiel 1991). Taxonomic literature used included Koste (1978) and Shiel (1995).

Cluster Analysis, Multidimensional Scaling (MDS) and Canonical Correspondence Analysis (CCA) were used to detect and classify groupings of species and to detect important physical, chemical or geographical variables associated with underlying trends. Cluster Analysis was based on the Bray-Curtis similarity coefficient calculated on the cube root of relative abundances (percentages) of abundant rotifer species (comprising > 4 % in any two samples from different lakes) and was initially performed on all 146 samples from 42 lakes, using 30 species. MDS was performed on 124 samples, reduced from the original data set to satisfy program restrictions by averaging samples with > 80 % similarity in cluster analysis. MDS was based on the ranked Bray-Curtis similarity matrix. In order to indicate which species were principally responsible for the observed patterns in cluster analysis and MDS, a shade diagram was constructed by re-sorting the original data matrix. On one axis the lakes were ordered by the cluster analysis of lakes based on species, and on the other axis the species were ordered by a cluster analysis of species based on lake. On the re-ordered matrix, the increasing percentage contribution of each species is plotted

as a greyscale using Spyglass Transform v. 3.3.0 (Fortner 1996), a computer program that produces greyscale plots from 3D arrays of numbers. For CCA, samples with missing environmental variables were removed from the analysis, and species again removed where not comprising > 4 % in any two of the remaining samples, leaving a total of 108 samples from 29 lakes, and 24 species. O% was removed from the CCA because of covariance with DO and temperature (variance inflation factor > 20) in an exploratory ordination (Ter Braak & Smilauer 1998). CCA was performed using species composition data (%), log (x+1) transformed to downweight dominant species, and environmental data log (x+1) transformed to remove skew and subsequently standardised to zero mean and unit variance to remove the influence of differing scales of measurement.

Optimal environmental conditions of abundant species were estimated by taking weighted averages of each environmental variable for each species, in which environmental variables are weighted proportional to the species abundances (Jongman *et al.* 1987), i.e.,

$$u^* = (y_1x_1 + y_2x_2 + \dots + y_nx_n) / (y_1 + y_2 + \dots + y_n)$$

where

u^* is the weighted average

$y_1, y_2, \dots, y_n$ are the abundances of species

$x_1, x_2, \dots, x_n$ are the values of the environmental variable at sites 1, 2...n

Weighted average optima were calculated using CALIBRATE v. 0.8.2 (Juggins & Ter Braak 1997).

To further examine the spatial variability of rotifer communities between lakes, separate from the temporal variability, lakes were removed from the initial data set where fewer than two samples were taken, and the remaining data (species and environmental) were averaged for each lake. This resulted in 35 samples from 31 lakes, with 27 species comprising greater than 4 % in any sample from two lakes before averaging. Cluster analysis was performed on this data based on the Bray-Curtis similarity coefficient

calculated on the averaged relative abundances (cube root transformed) of abundant rotifer species. MDS was performed on the same data set based on the ranked Bray-Curtis similarity matrix. A shade diagram was constructed for the data set. CCA was performed on the averaged species composition data ($\log(x+1)$ transformed) from these lakes. Missing temperature, DO and pH values were replaced with average values from all lakes allowing examination of some lakes not examined initially. Measured environmental data were log transformed and standardised (zero mean and unit variance). Standardised latitude, longitude and (log) mean lake depth data were also included in this analysis, generally taken from data published by Irwin (1971), Livingston *et al.* (1986) and Lowe & Green (1987). O% was removed from the CCA because it covaried highly with DO and temperature (variance inflation factor > 20) in an exploratory ordination (Ter Braak & Smilauer 1998).

Cluster analysis and MDS were performed using the Plymouth Routines in Multivariate Research statistical package (PRIMER 1994, Clarke & Warwick 1994), and CCA using CANOCO 4.0 (Ter Braak & Smilauer 1998).

Results

A total of 82 species of monogonont rotifer was found during this study (Table 4.2). Lake species diversity, estimated from lakes with two or more samples, indicated that greater than 21 species of rotifer are found per lake on average (Table 4.3). Lakes Taupo and Wairarapa contained the lowest diversities with nine and ten species respectively, and Lake Karapiro and Maraetai the greatest with 34 and 35 species.

Thirty-nine species were present in five or more (i.e., > 10 %) of the localities (Table 4.2). The remaining species were generally found in low abundances (comprising < 4 % composition in all samples) and are likely to either generally occur at low abundances in the plankton, or be typically benthic or littoral species sampled by chance. There were

Table 4.2 Monogonont rotifers recorded from North Island, New Zealand during this study. Locality numbers refer to Table 4.1.

<i>Anuraeopsis fissa</i> (Gosse):	11, 13, 14, 15, 16, 19, 22, 23, 38
<i>A. navicula</i> Rousselet:	1, 2, 3, 6, 10, 12, 39
<i>Ascomorpha ecaudis</i> (Perty):	21, 31
<i>A. ovalis</i> (Bergendal):	1, 2, 4, 5, 6, 7, 8, 10, 12, 13, 18, 19, 20, 22, 23, 25, 26, 27, 28, 29, 30, 31, 36
<i>A. saltans</i> Bartch:	29
<i>Ascomorphella volvocicola</i> (Plate):	23
<i>Aspelta angusta</i> Haring & Myers:	26
<i>Asplanchna brightwelli</i> Gosse:	3, 14, 16, 17, 20, 24, 42
<i>A. priodonta</i> Gosse:	1, 2, 4, 5, 6, 8, 9, 10, 12, 18, 21, 11, 13, 14, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39
<i>A. sieboldi</i> (Leydig):	21, 23, 25, 31, 34, 37, 38
<i>Brachionus angularis</i> Gosse:	11, 15, 16, 17, 21, 24, 25, 38, 39
<i>B. budapestinensis</i> Daday:	16, 17, 21, 39
<i>B. calyciflorus</i> Pallas:	17, 20, 21, 32, 39, 42
<i>B. caudatus</i> Barrois & Daday:	17, 40
<i>B. cf. lyratus</i> Shephard:	40
<i>B. quadridentatus</i> Hermann:	2, 3, 15, 16, 22, 23, 42
<i>Cephalodella catellina</i> (Müller):	16, 18, 27, 31
<i>C. gibba</i> (Ehrenberg):	10, 18, 20, 22, 29
<i>C. ventripes</i> (Dixon-Nuttal):	23
<i>Collotheca</i> sp.:	1, 2, 3, 5, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 25, 26, 27, 28, 29, 30, 31, 32, 33, 35, 36, 37, 38, 39
<i>Colurella uncinata</i> f. <i>bicuspidata</i> (Ehrenberg):	12, 19, 22
<i>Conochilus coenobasis</i> (Skorikov):	4, 5, 6, 8, 9, 10, 11, 12, 13, 18, 25, 27, 29, 30, 33, 34, 39
<i>C. dossuarius</i> Hudson:	8, 10, 18, 22, 23, 25, 26, 28, 31, 35, 36
<i>C. exiguus</i> (Ahlstrom):	19, 20
<i>C. unicornis</i> Rousselet:	4, 8, 10, 12, 17, 18, 19, 20, 22, 23, 25, 26, 27, 28, 29, 30, 33, 35
<i>Dicranophoroides caudatus</i> Ehrenberg:	42
<i>Eothinia elongata</i> (Ehrenberg):	8
<i>Epiphanes macrourus</i> (Barrois & Daday):	39
<i>Euchlanis dilatata</i> Ehrenberg:	17, 22, 23, 29, 31, 37
<i>Filinia longiseta</i> (Ehrenberg):	3, 7, 11, 15, 17, 19, 20, 21, 22, 25, 34, 37, 38, 39, 42
<i>F. novaezealandiae</i> Shiel & Sanoamuang:	8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 26, 27, 28, 29, 30, 31, 34, 36, 37, 38, 39
<i>F. cf. pejleri</i> Hutchinson:	2, 3, 4, 6, 10, 12, 18, 20, 24, 25, 29, 30, 33, 37
<i>F. terminalis</i> (Plate):	22, 24, 36, 37
<i>Gastropus hyptopus</i> (Ehrenberg):	22, 23, 25, 28, 32, 34
<i>G. minor</i> (Rousselet):	19, 38
<i>Hexarthra intermedia</i> (Wiszniewski):	2, 3, 5, 6, 8, 10, 15, 16, 17, 19, 20, 21, 24, 25, 26, 27, 28, 29, 31, 34, 39, 40, 42
<i>H. mira</i> (Hudson):	7, 9, 11, 12, 13, 14, 17, 18, 22, 23, 25, 31, 36, 37, 38
<i>Keratella australis</i> Berzins:	22, 23, 35
<i>K. cochlearis</i> (Gosse):	8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 40
<i>K. procurva</i> Thorpe:	8, 9, 10, 11, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, 28, 30, 32, 33, 37, 38
<i>K. slacki</i> (Berzins):	11, 15, 16, 17, 19, 20, 21, 22, 23, 27, 33, 34, 37, 38
<i>K. tecta</i> (Gosse):	2, 3, 8, 9, 10, 11, 13, 15, 16, 17, 19, 20, 21, 22, 23, 24, 32, 34, 37, 38, 39, 40
<i>K. tropica</i> (Apstein):	1, 2, 3, 7, 8, 9, 10, 11, 13, 15, 16, 17, 19, 20, 21, 23, 32, 34, 38, 39, 40

Table 4.2 (Continued)

<i>Lecane bulla</i> (Gosse): 1, 3, 6, 8, 10, 14, 17, 29, 38
<i>L. closterocerca</i> (Schmarda): 7, 9, 10, 14, 16, 23, 24, 29, 38
<i>L. flexilis</i> (Gosse): 2, 19, 23, 28, 37
<i>L. hamata</i> (Stokes): 3, 39
<i>L. hornemanni</i> (Ehrenberg): 1, 2, 6, 8, 9, 13, 29
<i>L. luna</i> (Müller): 1, 8, 16, 22, 29, 31, 36, 37
<i>L. lunaris</i> (Ehrenberg): 1, 2, 3, 5, 6, 7, 9, 10, 14, 18, 19, 22, 23, 25, 27, 30, 32, 33, 36, 39
<i>Lepadella acuminata</i> (Ehrenberg): 9, 33
<i>Lindia torulosa</i> Dujardin: 1, 38
<i>Lophocharis salpina</i> (Ehrenberg): 9, 19
<i>Macrochaetus altamira i</i> (Arevalo): 8, 14
<i>Monommata</i> sp.: 1, 37
<i>Mytilina bisulcata</i> (Lucks): 38
<i>M. ventralis</i> (Ehrenberg): 36, 38
<i>Notommata ?falcinella</i> Harring & Myers: 5
<i>Platyas quadricornis</i> (Ehrenberg): 2, 9
<i>Pleurotrocha petromyzon</i> Ehrenberg: 2, 14
<i>Polyarthra dolichoptera</i> Idelson: 1, 2, 5, 6, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 22, 23, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39, 40, 42
<i>Pompholyx complanata</i> Gosse: 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39, 40
<i>P. sulcata</i> Hudson: 9, 11
<i>Proales doliaris</i> (Rousselet): 15, 16
<i>Synchaeta longipes</i> Gosse: 12, 25, 26, 27, 29, 33
<i>S. oblonga</i> Ehrenberg: 9, 11, 12, 13, 15, 16, 17, 21, 22, 23, 24, 25, 27, 28, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40
<i>S. pectinata</i> Ehrenberg: 6, 9, 10, 12, 13, 14, 15, 17, 18, 19, 20, 21, 22, 23, 24, 25, 27, 28, 29, 31, 37, 38
<i>S. stylata</i> Wierzejski: 6, 12, 19, 39, 40
<i>Testudinella patina</i> (Hermann): 9, 15, 20, 22, 23, 36, 38
<i>T. parva</i> (Ternetz): 2, 19, 23
<i>Trichocerca agnatha</i> Wulfert : 32
<i>T. longiseta</i> (Schrank): 14, 21, 23, 25, 27, 30, 31, 34, 37
<i>T. porcellus</i> (Gosse): 18, 22, 23, 24, 39
<i>T. pusilla</i> (Jennings): 3, 8, 9, 10, 11, 12, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 30, 34, 36, 37, 38, 39
<i>T. rattus</i> (Müller): 14, 18
<i>T. similis</i> (Wierzejski): 1, 5, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 36, 37, 38
<i>T. stylata</i> (Gosse): 2, 4, 5, 6, 8, 15, 17, 22, 23, 25, 26, 28, 29, 31, 33, 39,
<i>T. tenuior</i> (Gosse): 9, 13, 14, 22, 23, 37, 38
<i>T. tigris</i> (Müller): 22
<i>Trichotria tetractis</i> (Ehrenberg): 22, 23, 32
Unknown 1: 36
Unknown 2: 1

Table 4.3 Cumulative α diversity from lakes with two or more samples. The table is ordered from highest to lowest diversity.

Lake	α	Lake	α	Lake	α
Maraetai	35	Okareka	22	Waikaremoana	18
Karapiro	34	Ototoa	22	Okaro	17
Rotorangi	28	Waahi	22	Rotoehu	17
Rotokauri	26	Tarawera	21	Tikitapu	17
Rotoiti	26	Rotomanuka South	21	Tomarata	17
Rotomanuka	26	Rotoroa	21	Wainamu	17
Kareta	24	Pupuke	20	Rotoma	16
Tutira	24	Waikare	20	Wairarapa	10
Kuwakatai	23	Rotorua	19	Taupo	9
Ngaroto	23	Spectacle	19		
Horowhenua	22	Okataina	18	Average	21.1

exceptions to this, with some species occurring in high relative abundance in a sample (> 4 %) but only from a limited number of lakes (< 5 in total). These were *Brachionus budapestinensis* in high relative abundance in Lakes Rotokauri and Horowhenua, *Brachionus caudatus* in Lake Wairarapa, *Conochilus exiguus* in Lakes Rotomanuka and Rotomanuka South, *Filinia terminalis* in Lakes Rotoehu and Tutira, *Gastropus minor* in Lake Rotorangi, *Keratella australis* in Lake Maraetai, *Lindia torulosa* in Lake Waiparera and *Trichotria tetractis* in Lake Karapiro.

In Cluster analysis, division of clusters was made at a level of similarity where several large distinct groupings of samples could be discriminated. Cluster analysis of all lakes and sites revealed 15 clusters of samples at a 42 % similarity level (Fig. 4.2). Within clusters, it was common for samples from single lakes to be grouped together, indicating that seasonal variability in the composition of rotifer species within lakes was often less marked than inter-lake differences (e.g., Lakes Taupo and Waikaremoana in Cluster A, Maraetai and Kuwakatai in Cluster C, and Rotorangi and Horowhenua in Cluster F). However, there was also seasonal variation between groups with samples from many lakes being divided between two or more clusters (e.g., Lakes Ngaroto and Rotokauri samples in

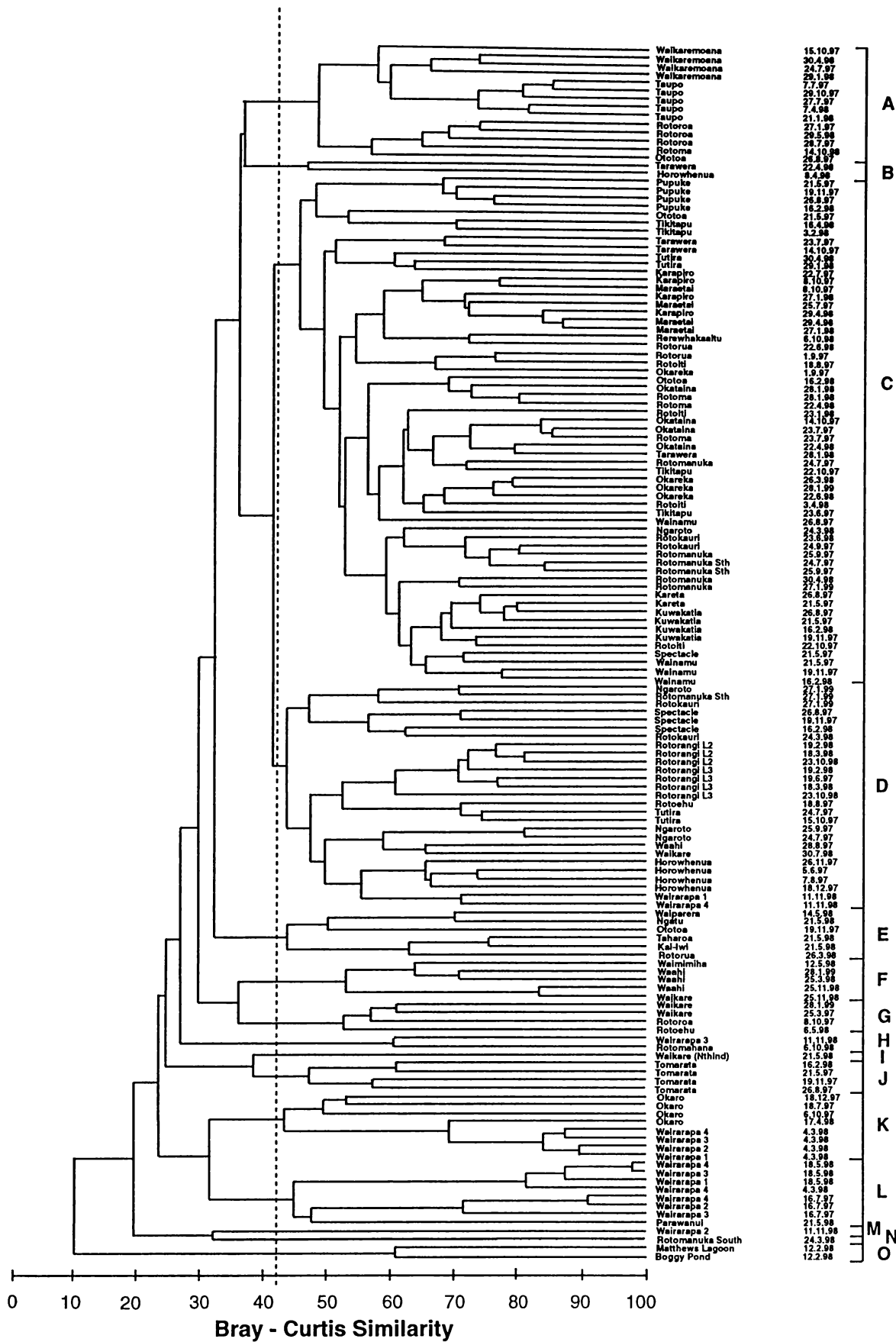


Figure 4.2. Cluster analysis of samples from lakes based on relative abundances of species present. Dashed line indicates 42 % level of similarity.

Clusters C & D). However, samples in general did not form distinct cluster groupings, with many smaller clusters forming at progressively lower similarity levels. This pattern indicates that the species composition of samples is not separated into distinct species groupings (or communities) in response to environmental conditions, but there is a gradation in community structure in response to environmental gradients. Ordination is preferable in these situations. The MDS ordination (Fig. 4.3, Table 4.4) indicates no distinct differentiation of species assemblages between the groups of samples found at the 42 % level of similarity in cluster analysis (see cluster groups superimposed on the ordination). The superimposed cluster groupings do, however, indicate a general consistency of sample distributions between classification and ordination techniques, and the lack of differentiation between groups suggest that, in general, assemblages are responding gradually to gradients in environmental conditions rather than forming distinct assemblages in response to them. The samples from the largest sample groupings from cluster analysis (Clusters C and D), however, appear central in the ordination, with remaining clusters generally surrounding them. The remaining cluster groups are generally equally related to the central groupings, a feature not apparent in the cluster analysis. These groups are therefore likely to be communities that diverge from the norm along differing environmental gradients. The samples showing the most extreme divergence from the central groupings in general are from Matthews Lagoon and Boggy Pond (Cluster O), Lake Wairarapa (Clusters K and L), Lake Tomarata (Cluster J), and the Northland lakes samples (Clusters E and M).

The shade diagram (Fig. 4.4) shows many species to be associated to greater or lesser degrees with the lake groupings determined by cluster analysis and MDS. Cluster A lakes were distinguished by having particularly high relative abundances of *Conochilus dossuarius*, *Conochilus unicornis*, *Asplanchna priodonta*, *Collotheca* sp. and *Polyarthra dolichoptera*, Cluster B of *Hexarthra intermedia*, *A. priodonta*, *Collotheca* sp. and *P.*

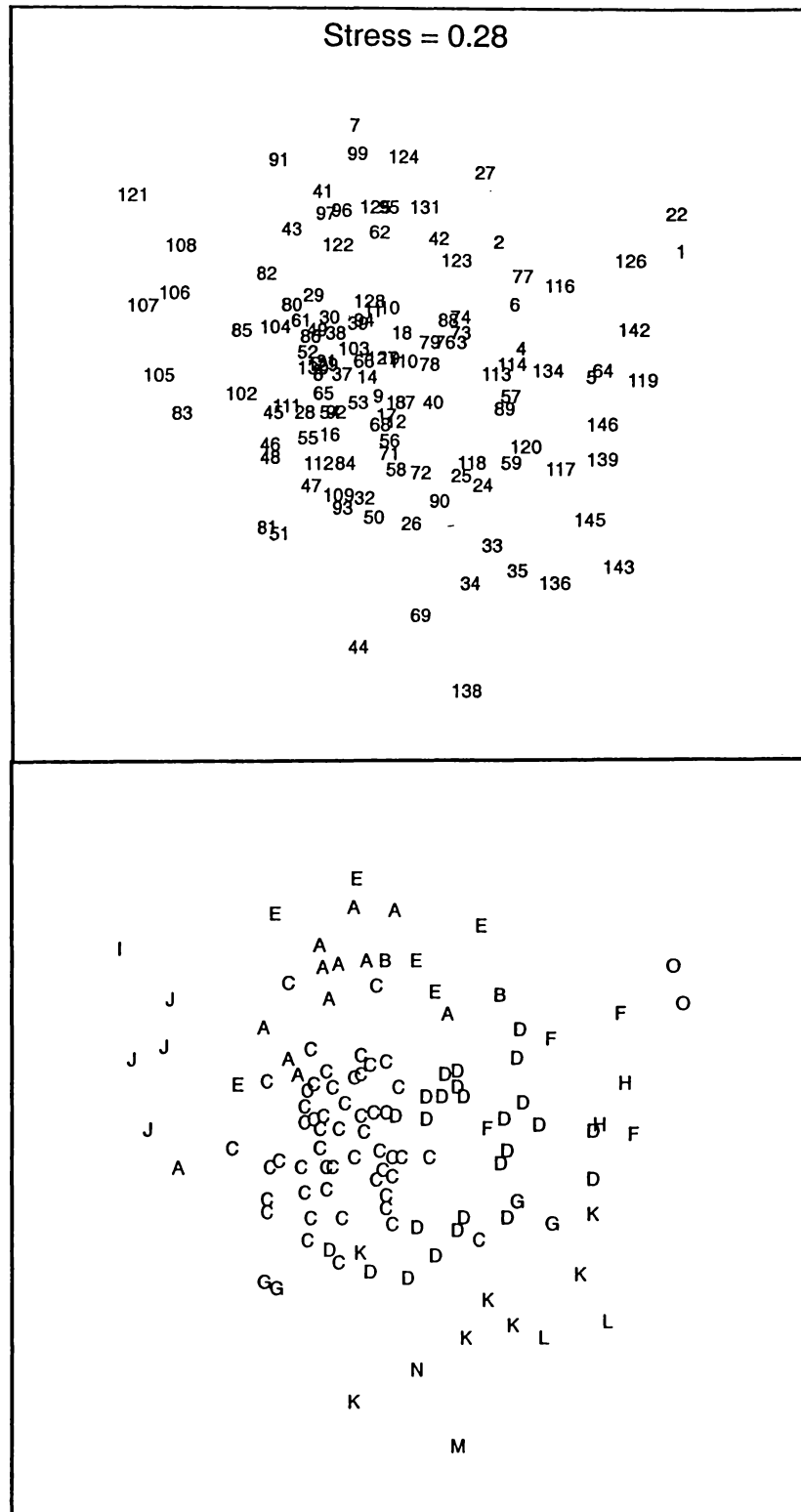


Fig. 4.3. Non-metric multidimensional scaling (MDS) plot of lake samples based on relative abundances of dominant rotifer species (above), and the same MDS plot with superimposed cluster analysis groupings (below). Key to sample numbers is given in Table 4.4.

Table 4.4. Key to sample numbers (lake and date (d:m:y)) for MDS and CCA ordinations.

n Lake	Date	n Lake	Date	n Lake	Date
1 Boggy Pond	12.2.98	50 Rotoehu	18.8.97	99 Taupo	7.4.98
2 Horowhenua	8.4.98	51 Rotoehu	6.5.98	100 Taupo	7.7.97
3 Horowhenua	5.6.97	52 Rotoiti	3.4.98	101 Tikitapu	16.4.98
4 Horowhenua	7.8.97	53 Rotoiti	23.1.99	102 Tikitapu	3.2.98
5 Horowhenua	26.11.97	54 Rotoiti	22.10.97	103 Tikitapu	22.10.97
6 Horowhenua	18.12.97	55 Rotoiti	18.8.97	104 Tikitapu	23.6.97
7 Kai-iwi	21.5.98	56 Rotokauri	24.9.97	105 Tomarata	21.5.97
8 Karapiro	22.7.97	57 Rotokauri	24.3.98	106 Tomarata	26.8.97
9 Karapiro	8.10.97	58 Rotokauri	23.6.98	107 Tomarata	19.11.97
10 Karapiro	27.1.98	59 Rotokauri	27.1.99	108 Tomarata	16.2.98
11 Karapiro	29.4.98	60 Rotoma	23.7.97	109 Tutira	24.7.97
12 Kareta	21.5.97	61 Rotoma	14.10.98	110 Tutira	15.10.97
13 Kareta	26.8.97	62 Rotoma	28.1.98	111 Tutira	29.1.98
14 Kuwakatai	21.5.97	63 Rotoma	22.4.98	112 Tutira	30.4.98
15 Kuwakatai	26.8.97	64 Rotomahana	6.10.98	113 Waahi	25.3.98
16 Kuwakatai	19.11.97	65 Rotomanuka	30.4.98	114 Waahi	28.8.97
17 Kuwakatai	16.2.98	66 Rotomanuka	24.7.97	115 Waahi	25.11.98
18 Maraetai	25.7.97	67 Rotomanuka	25.9.97	116 Waahi	28.1.99
19 Maraetai	8.10.97	68 Rotomanuka	27.1.99	117 Waikare	25.3.97
20 Maraetai	29.4.98	69 Rotomanuka Sth	24.3.98	118 Waikare	30.7.98
21 Maraetai	27.1.98	70 Rotomanuka Sth	24.7.97	119 Waikare	25.11.98
22 Matthews lagoon	12.2.98	71 Rotomanuka Sth	25.9.97	120 Waikare	28.1.99
23 Ngaroto	24.7.97	72 Rotomanuka Sth	27.1.99	121 Waikare (Northland)	21.5.98
24 Ngaroto	24.3.98	73 Rotorangi(L2)	23.10.97	122 Waikaremoana	24.7.97
25 Ngaroto	27.1.99	74 Rotorangi(L2)	19.2.98	123 Waikaremoana	15.10.97
26 Ngaroto	25.9.97	75 Rotorangi(L2)	18.3.98	124 Waikaremoana	29.1.98
27 Ngatu	21.5.98	76 Rotorangi(L3)	19.6.97	125 Waikaremoana	30.4.98
28 Okareka	1.9.97	77 Rotorangi(L3)	23.10.97	126 Waimimiha	12.5.98
29 Okareka	26.3.98	78 Rotorangi(L3)	19.2.98	127 Wainamu	21.5.97
30 Okareka	28.1.99	79 Rotorangi(L3)	18.3.98	128 Wainamu	26.8.97
31 Okareka	22.6.98	80 Rotoroa	28.7.97	129 Wainamu	19.11.97
32 Okaro	6.10.97	81 Rotoroa	8.10.97	130 Wainamu	16.2.98
33 Okaro	18.7.97	82 Rotoroa	29.5.98	131 Waiparera	14.5.98
34 Okaro	17.4.98	83 Rotoroa	27.1.98	132 Wairarapa1	18.5.98
35 Okaro	18.12.97	84 Rotorua	1.9.97	133 Wairarapa1	4.3.98
36 Okataina	23.7.97	85 Rotorua	26.3.98	134 Wairarapa1	11.11.98
37 Okataina	14.10.97	86 Rotorua	22.6.98	135 Wairarapa2	16.7.97
38 Okataina	28.1.98	87 Spectacle	21.5.97	136 Wairarapa2	18.5.98
39 Okataina	22.4.98	88 Spectacle	26.8.97	137 Wairarapa2	4.3.98
40 Ototoa	21.5.97	89 Spectacle	19.11.97	138 Wairarapa2	11.11.98
41 Ototoa	26.8.97	90 Spectacle	16.2.98	139 Wairarapa3	16.7.97
42 Ototoa	19.11.97	91 Taharoa	21.5.98	140 Wairarapa3	18.5.98
43 Ototoa	16.2.98	92 Tarawera	23.7.97	141 Wairarapa3	4.3.98
44 Parawanui	21.5.98	93 Tarawera	14.10.97	142 Wairarapa3	11.11.98
45 Pupuke	21.5.97	94 Tarawera	28.1.98	143 Wairarapa4	16.7.97
46 Pupuke	26.8.97	95 Tarawera	22.4.98	144 Wairarapa4	18.5.98
47 Pupuke	19.11.97	96 Taupo	27.7.97	145 Wairarapa4	4.3.98
48 Pupuke	16.2.98	97 Taupo	29.10.97	146 Wairarapa4	11.11.98
49 Rerewhakaaitu	6.10.98	98 Taupo	21.1.98		

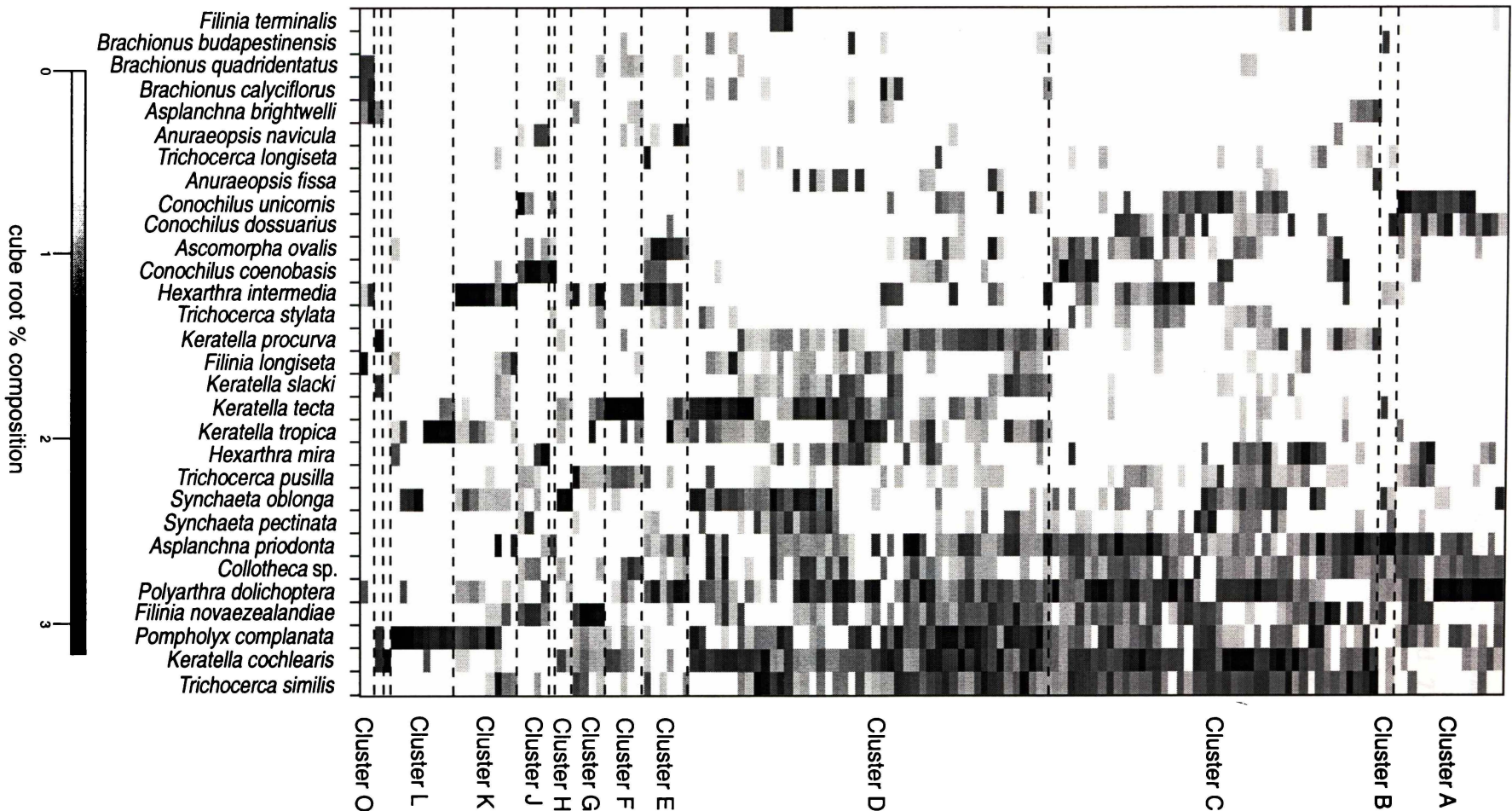


Fig. 4.4. Shade diagram of the distribution of rotifer species from North Island samples. Relative abundances (cube root) are represented by grey scale. Rows and columns of the array are ordered on the basis of cluster analysis of species and lakes. Lake groupings determined from cluster analysis are superimposed on the diagram. Some cluster labels are omitted for clarity.

P. dolichoptera, Cluster C of *A. priodonta*, *Collotheca* sp., *P. dolichoptera*, *Filinia novaezealandiae*, *Pompholyx complanata*, *Keratella cochlearis* and *Trichocerca similis*, Cluster D of *Keratella procurva*, *Keratella tecta*, and *K. cochlearis*, and Cluster E of *Ascomorpha ovalis*, *H. intermedia*, *A. priodonta* and *P. dolichoptera*. The remaining smaller clusters were generally dominated by one or two species only, with Cluster F dominated by *K. tecta*, Cluster G by *F. novaezealandiae*, Cluster H by *Synchaeta oblonga*, Clusters I and J by *Conochilus coenobasis*, Cluster K by *H. intermedia*, Cluster L by *Keratella tropica* and *P. complanata*, Cluster M by *K. cochlearis*, Cluster N by *K. procurva*, and Cluster O by *Brachionus quadridentatus*, *Brachionus calyciflorus* and *Asplanchna brightwelli*. Distinct species assemblages were not identified between clusters, with many species being important in two or more clusters. Even species apparently important in determining cluster groupings were often found present in other clusters, although were more frequently found in adjoining clusters indicating a gradient in species composition.

In general the distribution of sample scores in the CCA ordination (Fig. 4.5, Table 4.4) corresponds with that found in Cluster Analysis and MDS. Cluster A and B samples were generally found to be negatively associated with Axis 1 and 2. Cluster C samples were generally moderately negatively associated with Axis 1, and positively associated with Axis 2. Cluster D samples were generally positively associated with Axis 1. Cluster E samples were weakly positively associated with Axis 1, and weakly negatively associated with Axis 2. Cluster F, G and K were generally strongly positively related to Axis 1, with Clusters F and K generally negatively associated with Axis 2. Cluster J samples were negatively associated with Axis 1. *Conochilus dossuarius* was strongly negatively associated with Axis 1, and *Filinia terminalis*, *Ascomorpha ovalis* and *Trichocerca stylata* moderately so. *Keratella tropica*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Brachionus quadridentatus* and *Keratella tecta* were strongly positively related to Axis 1, and *Keratella slacki*, *Filinia longiseta* and *Hexarthra intermedia* moderately so. *Trichocerca*

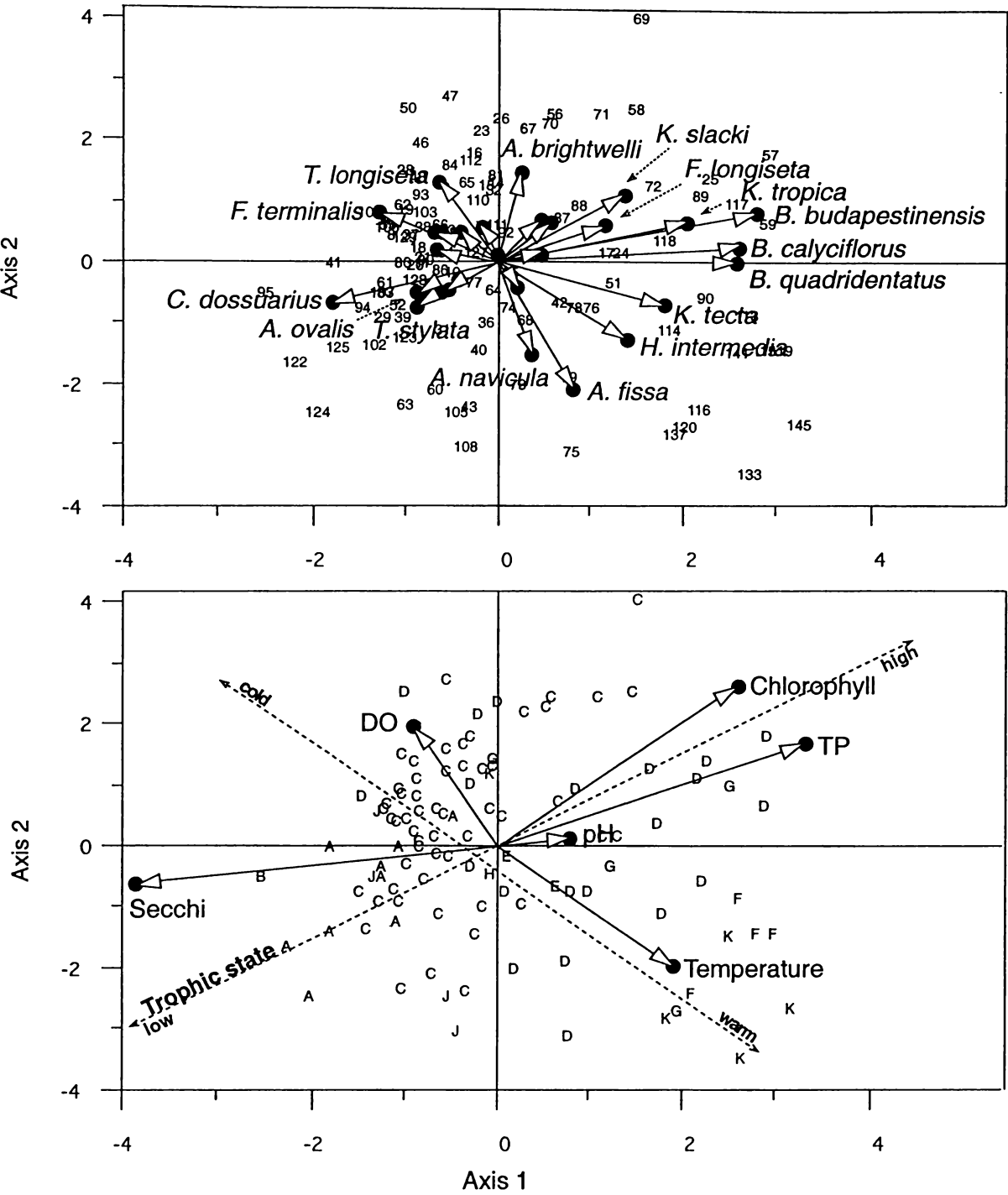


Fig. 4.5. Ordination diagram based on canonical correspondence analysis (CCA) of North Island rotifer species with respect to environmental variables. Eigenvalues for first two axes = 0.187 and 0.099. Dashed lines indicate suggested important environmental gradients based on measured variables. Cluster analysis groupings are superimposed on the environmental biplot. Scores of rotifer species and environmental variables were scaled to fit the ordination. Numbers correspond to sample numbers (Table 4.4). Species weakly associating with both Axis 1 and 2 have been omitted from the ordination for clarity.

Table 4.5. Results of forward selection and Monte Carlo permutation tests from CCA of all samples. Environmental variables are listed by the order of their inclusion in the model (lambda-A).

	lambda-1	lambda-A	P
Secchi	0.18	0.18	0.005
Chlorophyll <i>a</i>	0.13	0.08	0.005
Temperature	0.10	0.08	0.005
DO	0.08	0.06	0.005
TP	0.15	0.05	0.025
pH	0.05	0.03	0.245

longiseta, *Asplanchna brightwelli*, and *Keratella slacki* were moderately positively associated with Axis 2, and *Anuraeopsis fissa* strongly, and *Anuraeopsis navicula* and *Hexarthra intermedia* moderately negatively associated with Axis 2. Forward selection and associated Monte Carlo permutation tests of the significance of environmental variables (Table 4.5) show that Secchi transparency explained the largest proportion of the variability in rotifer community composition. After addition of Secchi transparency to the ordination, the subsequent additions of temperature, chlorophyll *a* and TP also made significant ($P < 0.05$) contributions to explaining the additional variation in rotifer species composition, indicating co-variability between the measures of lake trophic state were not strong. Secchi transparency is strongly negatively associating with Axis 1, and TP and chlorophyll *a* most strongly positively associated. Chlorophyll *a* is most strongly associated with Axis 2. Since Axis 1 is most strongly associated Secchi transparency, with significant additional variation being explained by both TP and chlorophyll *a*, Axis 1 is likely to relate to turbidity in addition to trophic state. A balance between Axis 1 and 2 is therefore likely to be the most reflective of biological trophic state (superimposed on the ordination diagram, Fig. 4.5). Samples and species positively associating with both Axis 1 and 2 are therefore related to high trophic state (e.g., many Cluster D samples; *Brachionus calyciflorus*, *Brachionus budapestinensis*, *Filinia longiseta*, *Keratella tropica*), and those negatively associated with Axis 1 and 2 are related to low trophic state (e.g., Cluster A samples; *Conochilus dossuarius*, *Ascomorpha ovalis*). Species positively associated with Axis 1 but less

strongly positively, or negatively, associating with Axis 2 (and therefore with low Secchi transparency and low chlorophyll *a* concentrations) are also likely to be associated with high turbidity (e.g., Clusters F and K samples; *Keratella tecta*, *Hexarthra intermedia*). Temperature is strongly associated with Axis 1 and 2 also, probably indicating seasonal variation amongst the samples (superimposed on the ordination). Samples and species positively associating with Axis 1 and negatively associating with Axis 2 (e.g., Cluster K and F samples; *Keratella tecta*, *Hexarthra intermedia*, *Anuraeopsis fissa*) are generally related to high temperature, and samples and species negatively associating with Axis 1 and positively associated with Axis 1 (e.g., mainly Cluster C samples; *Filinia terminalis*, *Trichocerca longiseta*) are generally related to low temperature. Weighted average species optima concur with distributions found in CCA (Fig. 4.6). Species related to high trophic state in CCA (e.g., *B. calyciflorus*, *B. budapestinensis*, *F. longiseta*, *K. tropica*) all had high optima for TP, chlorophyll *a* and low optima for Secchi transparency. Species related to low trophic state in CCA (e.g., *C. dossuarius*, *A. ovalis*) had low optima for TP, chlorophyll *a* and high optima for Secchi transparency. Species related to high (*K. tecta*, *H. intermedia* and *A. fissa*) and low (*F. terminalis*, *T. longiseta*) temperature in CCA had high and low weighted average optima also.

Cluster analysis (Fig. 4.7) of the rotifer communities averaged seasonally for each lake revealed eight groupings of lakes at a 58 % similarity level. The majority of samples were found in two clusters only (Clusters B and C). The remaining samples generally did not form distinct cluster groupings, again indicating a gradation in community structure. Rotifer distribution appears to broadly relate to lake trophic state. Clusters A and B comprised mainly oligotrophic to mesotrophic lakes, Cluster C mesotrophic to eutrophic lakes, and Clusters D, E, F and G eutrophic to hypereutrophic lakes. Samples from

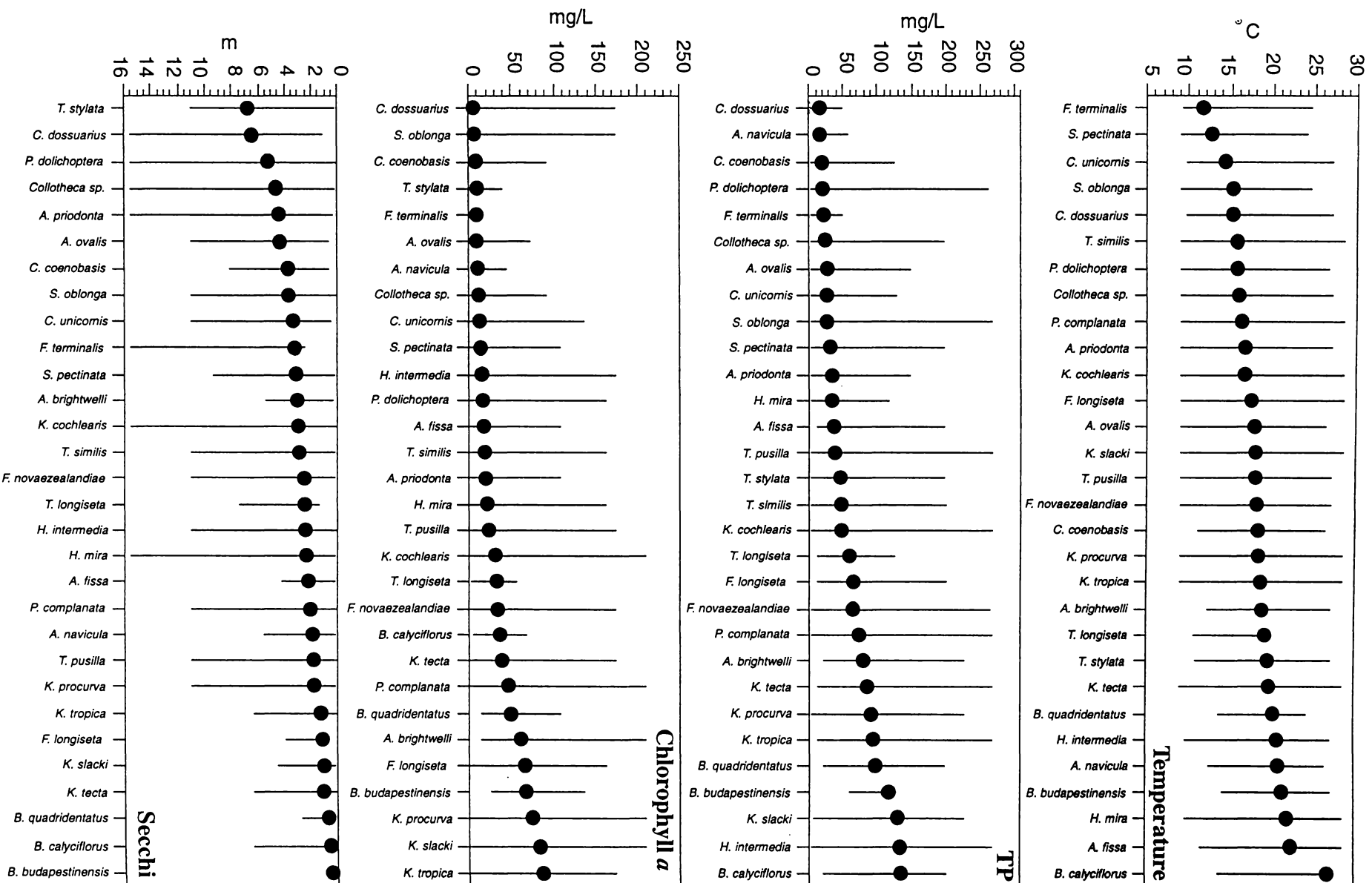


Fig 4.6. Weighted average optima (circles) and tolerances (whiskers) of abundant North Island rotifer species for temperature, TP, chlorophyll *a* and secchi depth.

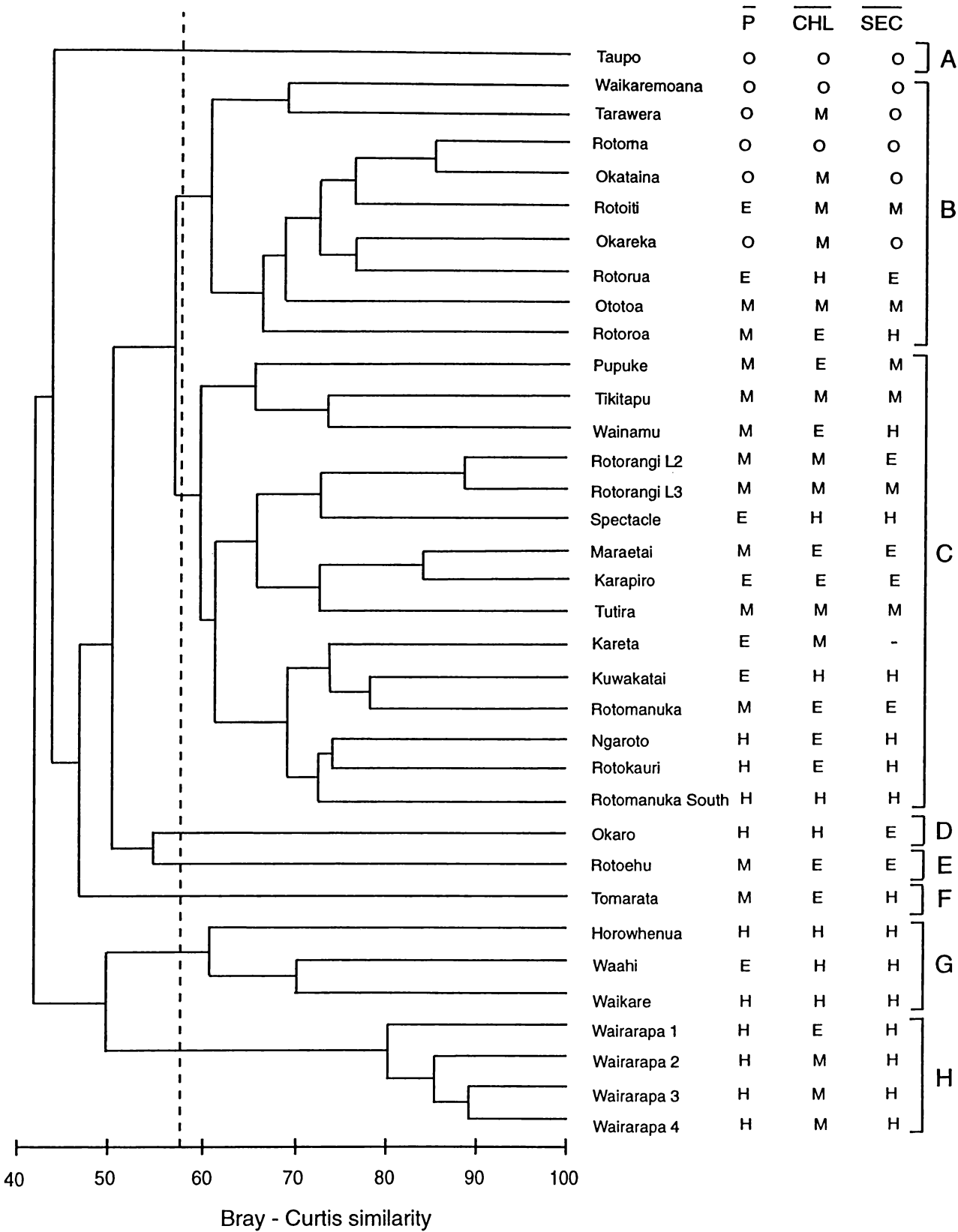


Fig. 4.7. Cluster analysis of lakes based on mean percentage rotifer species composition, and inferred trophic states, using mean total phosphorus, mean chlorophyll *a* concentration, and mean secchi transparency, based on the OECD (1982) fixed boundary system. Dashed line indicates 58 % level of similarity.

Table 4.6. Key to sample numbers for MDS and CCA ordinations of lake rotifer communities.

n	Lake	n	Lake	n	Lake
1	Horowhenua	13	Rotoiti	25	Tikitapu
2	Karapiro	14	Rotokauri	26	Tomarata
3	Kareta	15	Rotoma	27	Tutira
4	Kuwakatai	16	Rotomanuka	28	Waahi
5	Maraetai	17	Rotomanuka South	29	Waikare
6	Ngaroto	18	Rotorangi (L2)	30	Waikaremoana
7	Okareka	19	Rotorangi (L3)	31	Wainamu
8	Okaro	20	Rotoroa	32	Wairarapa 1
9	Okataina	21	Rotorua	33	Wairarapa 2
10	Ototoa	22	Spectacle	34	Wairarapa 3
11	Pupuke	23	Tarawera	35	Wairarapa 4
12	Rotoehu	24	Taupo		

different positions of the same water body were generally closely related to one another, e.g., the samples from the two sites in Lake Rotorangi, the four sites in Lake Wairarapa, and the connected hydroelectric reservoirs, Lakes Karapiro and Maraetai. There appeared to be some geographical basis to the distribution of communities, with many of the Waikato riverine lakes (e.g., Lakes Ngaroto, Rotokauri and Rotomanuka South) or Rotorua volcanic lakes (e.g., Lakes Rotoma, Okataina and Okareka) being closely related to one another, although these lakes generally had similar trophic states.

The MDS of these lakes shows a general gradation in species composition based on trophic state (Fig. 4.8, Table 4.6). Lakes with relatively low trophic state appear at the bottom of the ordination, medium trophic state lakes central, and more highly trophic state lakes near the top and top left of the ordination. This distribution was reflected within clusters also, with the more oligotrophic lakes in Cluster B (e.g., Waikaremoana and Rotoma) distributed nearer to Cluster A, and more mesotrophic lakes (e.g., Rotoiti, Rotoroa and Rotorua) closer to Cluster C. The higher trophic state lakes in Cluster C (e.g., Ngaroto, Rotokauri and Rotomanuka South) distributed nearer to Clusters D, E, H and G. Lake Tomarata (Cluster F) was found to separate from the other clusters, with distribution perhaps determined by an environmental forcing factor other than trophic state.

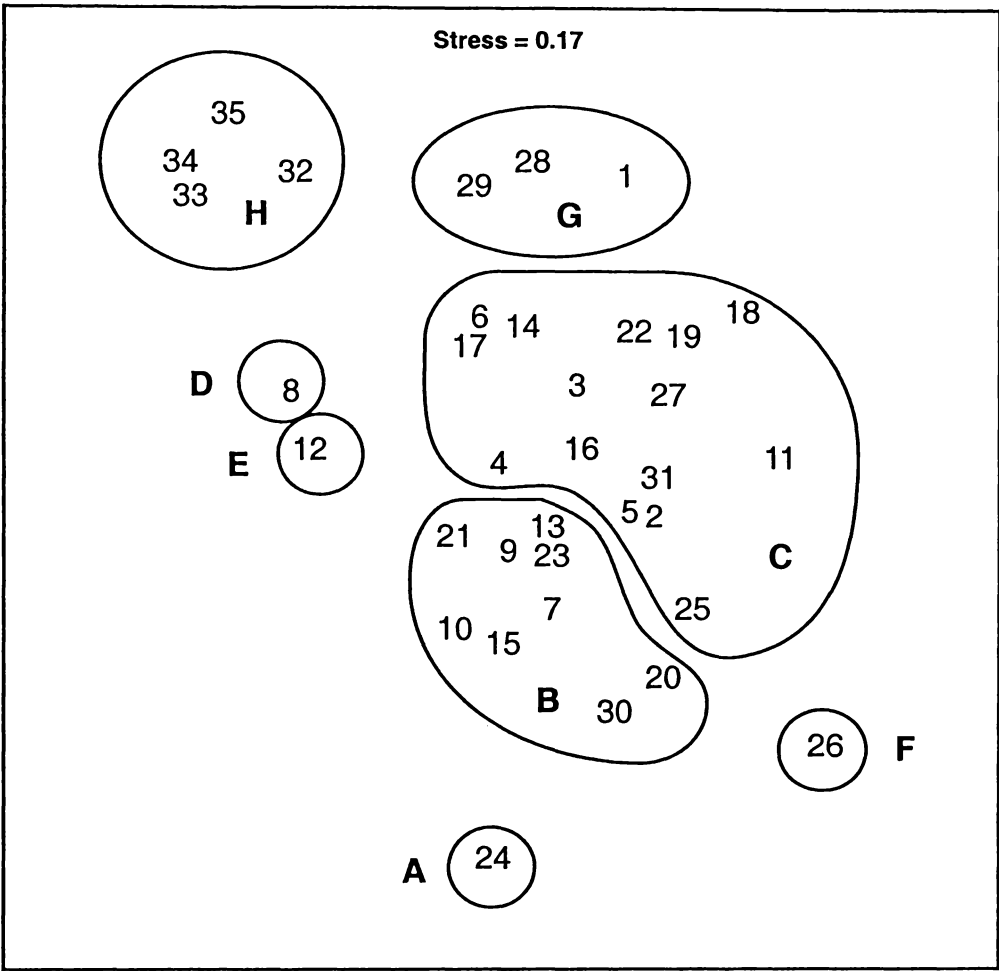


Fig. 4.8. Non-metric multidimensional scaling (MDS) plot of lakes based on mean % rotifer species composition (cube root transformation). Numbers correspond to sample numbers (Table 4.6). MDS overlaid with groupings found in cluster analysis.

The shade diagram (Fig. 4.9) shows many species to be associated to greater or lesser degrees with the lake groupings determined by cluster analysis and MDS. Cluster A and B (oligotrophic to mesotrophic) lakes were found to generally comprise *Conochilus dossuarius*, *Ascomorpha ovalis*, *Conochilus unicornis*, *Conochilus coenobasis*, *Filinia novaezealandiae*, *Asplanchna priodonta*, *Collotheca* sp. *Polyarthra dolichoptera*, *Trichocerca similis*, *Pompholyx complanata*, and *Keratella cochlearis*, Cluster C (mesotrophic to eutrophic) *F. novaezealandiae*, *A. priodonta*, *Collotheca* sp., *P. dolichoptera*, *T. similis*, *P. complanata*, *K. cochlearis*, *Keratella procurva* and *Keratella tecta*, and Clusters D, E, G and H (eutrophic to hypereutrophic) lakes *P. dolichoptera*, *P. complanata*, *K. cochlearis*, *Synchaeta oblonga*, *Hexarthra intermedia*, *Keratella tecta* and *Keratella tropica*. Lake Tomarata (Cluster F) had high relative abundances of *C. unicornis* and *C. coenobasis*, and was the only lake to lack *P. complanata* and *K. cochlearis*.

CCA (Fig. 4.10, Table 4.6) revealed a distribution of lakes that was similar to those shown by cluster analysis and MDS. Lower trophic state (Cluster A and B) samples were negatively associated with Axis 1, and mesotrophic to eutrophic (Cluster C) samples were generally found central in the ordination. Clusters D, E, G and H samples were positively associated with Axis 1, with Cluster E (Lake Rotoehu) strongly positively associating with Axis 2. *Conochilus dossuarius*, *Conochilus unicornis*, *Ascomorpha ovalis* and *Conochilus coenobasis* strongly negatively associated with Axis 1, and *Keratella tropica*, *Keratella tecta*, *Brachionus budapestinensis*, *Synchaeta oblonga* and *Hexarthra intermedia* were strongly positively associated. *Filinia terminalis*, *Trichocerca pusilla*, *Trichocerca longiseta*, *H. intermedia* and *C. dossuarius* were strongly positively associated with Axis 2, and *Anuraeopsis fissa*, *Keratella slacki*, *B. budapestinensis* and *K. tecta* strongly negatively associated. Forward selection and associated Monte Carlo permutation tests of the significance of environmental variables (Table 4.7) indicate that Secchi transparency, TP, average depth and chlorophyll *a* explain most of the variation in species distribution when considered by themselves. After the addition of Secchi transparency, only temperature and

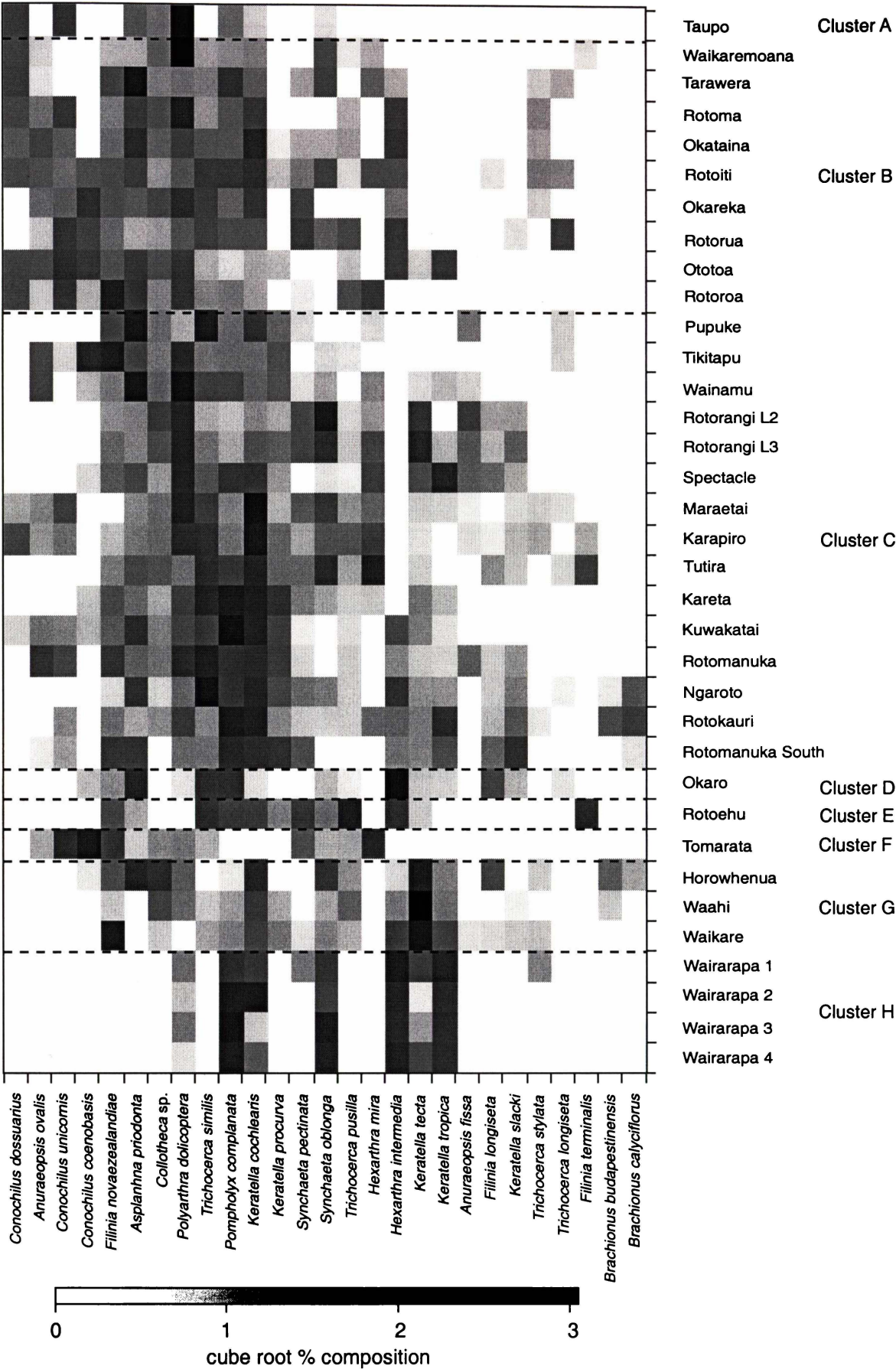


Fig. 4.9. Shade diagram of the distribution of North Island rotifer species. The cube root of relative abundances are represented by grey scale. Rows and columns of the array are ordered on the basis of cluster analyses of species and lakes. Lake groupings determined from cluster analysis are superimposed on the diagram.

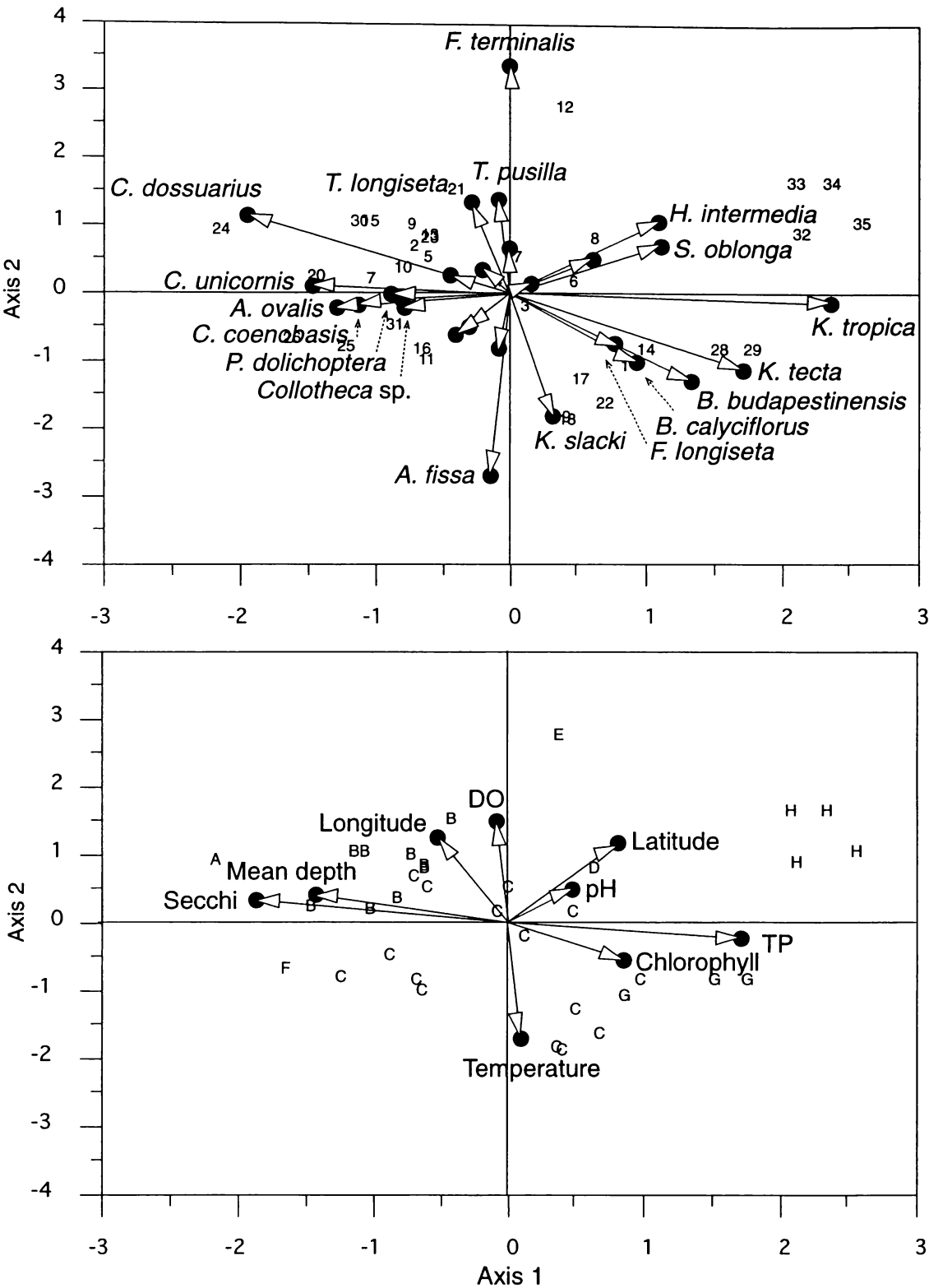


Figure 4.10. Ordination diagram based on canonical correspondence analysis (CCA) of North Island rotifer species with respect to environmental variables. Eigenvalues for the first two axes = 0.243 and 0.125. Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers (Table 4.6). Species weakly associating with both Axes 1 and 2 have been omitted from the ordination for clarity.

Table 4.7. Results of forward selection and Monte Carlo permutation tests from CCA of North Island rotifer species. Environmental variables are listed by the order of their inclusion in the model (lambda-A).

	lambda-1	lambda-A	P
Secchi	0.21	0.21	0.005
Temperature	0.10	0.11	0.005
Chlorophyll <i>a</i>	0.12	0.09	0.005
DO	0.09	0.06	0.080
Mean lake depth	0.16	0.04	0.200
Latitude	0.09	0.04	0.290
TP	0.20	0.04	0.420
Longitude	0.08	0.03	0.375
pH	0.05	0.05	0.215

chlorophyll *a* explained any significant amount of the remaining variation ($P<0.05$). TP and chlorophyll *a* were most strongly positively associated with Axis 1, and Secchi and mean lake depth most strongly negatively associated, indicating this axis was mainly related to lake trophic state and lake depth. Temperature was strongly negatively associated with Axis 2 and DO strongly positively associated. This axis is therefore likely to reflect warm and cold water assemblages caused by seasonal, latitudinal or altitude variation, e.g., *Filinia terminalis* and *Trichocerca pusilla* in colder water and *Anuraeopsis fissa* and *Keratella slacki* in warmer water.

Comparing rotifer distributions with measured environmental variables, species associated with Cluster A and B samples (*Conochilus dossuarius*, *Conochilus unicornis*, *Ascomorpha ovalis* and *Conochilus coenobasis*) are associated with high Secchi transparency, and low TP and chlorophyll *a* levels. Species associated with Cluster D, E, G and H samples (e.g., *Keratella tropica*, *Keratella tecta* and *Brachionus budapestinensis*) were associated with low Secchi transparency and high TP and chlorophyll *a* levels. Weighted average species optima and tolerances for these variables confirm these relationships (cf. Fig. 4.6). Cluster A and B species (e.g., *C. dossuarius*, *C. unicornis*, *A. ovalis* and *C. coenobasis*) were generally found to have low optima for TP, chlorophyll *a* and high Secchi transparency. Species associated with Clusters D, E, G and H (e.g., *K.*

tropica, *K. tecta* and *B. budapestinensis*) were generally found to have high optima for TP, chlorophyll *a* and low Secchi transparency. Comparison with the distributions of average TP, chlorophyll *a* and Secchi transparencies for the lakes (Fig. 4.11) most positively associated with Axis 1, and also axis 2 (Cluster H lakes, Lake Wairarapa) show that these lakes have extremely low Secchi transparencies without corresponding high rankings based on average chlorophyll *a* levels, and are therefore likely to be lakes in which inorganic suspendoids are major determinants of turbidity. Lake Rotoehu, found to associate positively with Axis 2, was sampled only in autumn and winter and was therefore found to associate with low temperatures, and is likely to have unusual distributions in ordinations due to absence of warmer water species.

Discussion

A total of 82 species of monogonont rotifer was found in the current survey. Diversities varied widely between lakes. The average of 21.1 species per lake found here is high in comparison with previous New Zealand studies (Chapman & Green 1987, see also discussion in Chapter 3), especially when assessed from such a small number of samples from each lake. The lowest diversity recorded, nine species, was in Lake Taupo. This is in agreement with the extremely low diversities reported by Forsyth & McCallum (1980) and James (1995), who respectively found totals of eight and ten species in this lake. It appears, therefore, that diversity in the pelagic of this lake is indeed low. Previous conclusions that species diversity in New Zealand may be low, based in part on study of this lake (Forsyth & McCallum 1980), now appear spurious. In fact, my study shows rotifer diversity in the open waters of New Zealand lakes appears to be comparable with, or even greater than, diversity generally found in the plankton in the northern temperate lakes (cf. Elliott 1977, Berner-Fankhauser 1983, Mikschi 1989, Vasconcelos 1990). Although it is difficult to make definite conclusions on diversity differences among these lakes due to the differences in sample sizes, some tentative conclusions may be drawn. The lowest

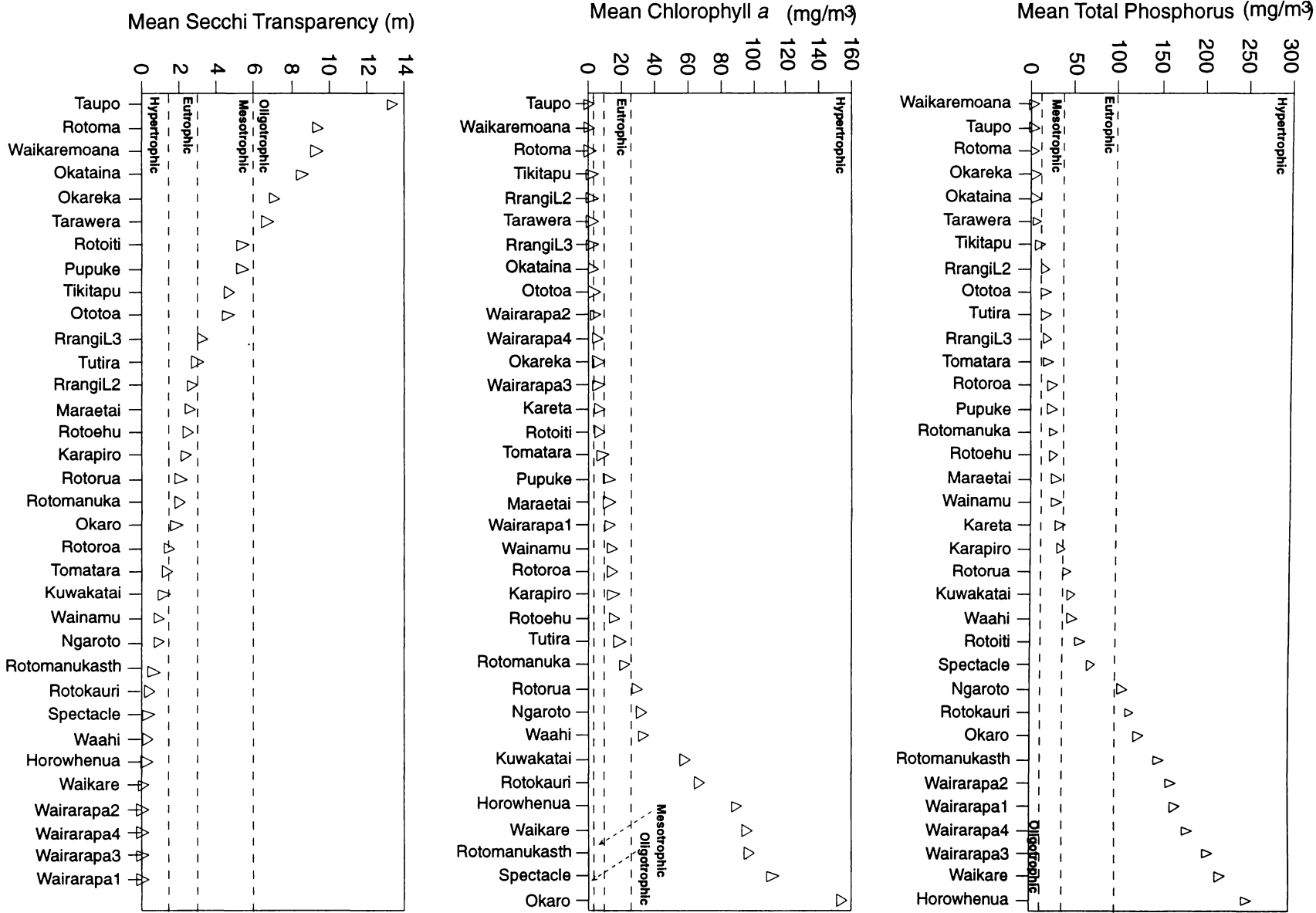


Fig. 4.11. Ranked inferred trophic status of North Island lakes using mean TP, mean chlorophyll a and mean secchi. Trophic boundary levels based on OECD (1982) fixed boundary system.

diversities recorded in the study were in the largest lakes, Lake Taupo (mean depth 98 m, area 623 km²) and Lake Waikaremoana (mean lake depth 93 m, area 56 km²). The large size of these lakes is likely to lead to greater temporal and spatial habitat stability, and their low trophic state to a low level of resources, both factors commonly associated with low diversity in communities (e.g., Rosenzweig 1995). Seasonal samples of rotifers from these lakes were grouped closely to one another in cluster analysis and MDS, indicating that rotifer community composition in these lakes did not change greatly over the year. Such low seasonality is likely to have contributed to a low overall estimate of diversity in these lakes. Lakes Taupo and Waikaremoana, and many other large lakes in New Zealand, also are known to each support only a single species of calanoid copepod, with co-occurrence of species restricted to relatively small, shallow lakes. Chapman & Green (1987) suggest that these large lakes have less niche diversification because the greater volumes of water buffer them against marked temporal changes, and this also may be the case for the rotifers. The low trophic state is likely to lead to a low level of food resources, and therefore low densities of rotifers. In such cases elimination of rare species is likely to occur (Rosenzweig 1995). Another factor could be a higher proportion of calanoid copepods in oligotrophic lakes, and in Lakes Taupo and Waikaremoana large boeckellids, which could prey on rotifers (Chapman & Green 1987, Forsyth & McCallum 1988, Jamieson 1998). In contrast, the three waterbodies with the greatest diversity, Lakes Maraetai, Karapiro and Rotorangi, are all artificial reservoirs. This is likely to be because disturbance from flowing water resulted in a high number of incursions from the littoral, where a high diversity is known, compared with the less turbulent lakes. Shiel *et al.* (1987), similarly, found reservoirs with short retention times had higher diversity than those with longer retention times.

From the examination of rotifer community distribution patterns in the North Island, it appears that species were affected by a variety of environmental gradients. Distribution was associated most strongly with measures of trophic state, as found on a

smaller scale in Rotorua lakes by Duggan *et al.* (in press). This is probably due to rotifer species being, in general, suspension feeders of algae and bacteria, so that they are likely to be sensitive to variations in food type and density caused by, for example, changing nutrient levels along a trophic gradient. Pejler (1983) found rotifer species associated with eutrophic conditions to be feeders on small particles (in particular bacteria). Species more indicative of mesotrophic and oligotrophic lakes were filtrators of coarser particles, and those in ultraoligotrophic conditions feeders on minute particles. Species in the present study found to be related to low (e.g., *Conochilus unicornis*, *Ascomorpha ovalis*, *Conochilus dossuarius*, *Conochilus coenobasis*) or high (e.g., *Keratella tropica*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Keratella tecta*) trophic state also have been found to show similar relationships elsewhere (e.g., Mäemets 1983, Sládacek 1983, Pejler 1983, and Berzins & Pejler 1989a). However, as with phytoplankton communities, distribution of rotifer species along the trophic gradient is likely to be caused not by competition for a single factor, e.g., food type (or nutrients in the case of phytoplankton), but by the combined impacts of a variety of factors with increasing trophic state (Reynolds 1998). Such factors are likely to include the appearance of toxic cyanobacteria (Snell 1980, Starkweather & Kellar 1987), the increased importance of predation on rotifers by *Asplanchna* (Ejsmont-Karabin 1974, Pejler 1983) and the degree of oxygen depletion (e.g., Berzins & Pejler 1989c, Mikschi 1989). These effects will weight in favour of the growth and survival of particular rotifer species, with the realised niches of species dependent on the variability of several of these factors along the trophic gradient.

The apparent importance of Secchi transparency in explaining rotifer distribution over the other two indicators may indicate that inorganic turbidity has a large role in determining species distributions in some lakes rather than trophic state. High average winds in New Zealand (e.g., Green *et al.* 1987) may lead to an increased turbidity in some lakes, leading to light extinction and a lowering in Secchi readings, and a subsequent

reduction in phytoplankton biomass (OECD 1982, Hamilton & Mitchell 1988). Lake Wairarapa samples, in particular, generally separated from samples of other lakes in ordinations. This lake had very low Secchi transparencies, but also low chlorophyll *a* levels compared with lakes of similar transparency, indicating a comparatively high inorganic turbidity. Some rotifer species in these environments may be favoured by exploiting unconventional food resources such as silt which has adsorbed dissolved organic matter, as found in crustacean zooplankton by Hart (1986). Other species, however, are likely to have growth inhibited by high suspended sediment loads, that only species with appropriate adaptations persist (Hart 1992). Hart (1992), however, believes the predominant factor responsible for limiting species distribution in highly turbid lakes is not the condition of high turbidity *per se*, but the associated light limitation of food resources. In the current study, inhibitory effects of turbidity on species composition are likely to have predominated over other factors. This is supported by the fact that the species dominating these environments (e.g., *Polyarthra dolichoptera*, *Keratella cochlearis*, *Synchaeta oblonga*, *Hexarthra intermedia*, *Keratella tecta* and *Keratella tropica*) were commonly found in many other lakes also. The communities are, therefore, probably distinguished more by those species that were absent rather than the presence of specialists. Possible exceptions to this generalisation are *Brachionus budapestinensis* and *Brachionus calyciflorus* which were found only in the small turbid lakes (e.g., Ngaroto, Rotokauri, Rotomanuka South, Horowhenua and Waahi). These species perhaps have superior abilities for discriminating and selecting out non-food particles (e.g., Gilbert & Starkweather 1977, 1978).

Another reason for the apparently weak coupling between trophic state indicators in the CCA ordinations may be that in some North Island lakes (particularly in the Rotorua area) nitrogen is the limiting factor to algal growth due to low N:P ratios compared with northern temperate lakes (White 1983, White *et al.* 1985). Empirical relationships relating chlorophyll *a* to TP derived from northern hemisphere phosphorus deficient lakes therefore do not apply to some lakes in New Zealand which are nitrogen deficient (White 1983).

Indeed, the fact that all three measures of lake trophic state assessed (Secchi transparency, TP and chlorophyll *a*) explained significant variations in species distribution in addition to the trophic indicators already added to the CCA models, emphasises a low correlation between these three variables, on average, in New Zealand lakes. The use of rotifers as bioindicators of lake trophic state, as suggested by Duggan *et al.* (in press), may therefore require initial screening of lakes or species, particularly the removal of highly turbid samples, or of species which prefer turbid conditions, to obtain better relationships between rotifer communities and actual lake trophic state.

A lower proportion of rotifer community variability was explained by temperature than measures of trophic state when examining all samples. From cluster analysis, in particular, it was apparent that communities from many lakes are more similar to one another in different seasons than to those between lakes at similar times. The composition of rotifer communities in many lakes may therefore be determined largely by trophic state, with a lack of marked temporal change in community composition in these lakes perhaps due to the muted seasonal temperature ranges of New Zealand lakes (Green *et al.* 1987). However, seasonal variability was apparent in some lakes in the cluster analysis of samples, and CCA indicated temperature was an important factor in determining community composition independent of the variation caused by trophic state. This variation was likely therefore to be due to seasonal succession of species (e.g., Chapter 3). Species found to have the lowest (*Filinia terminalis*, *Trichocerca longiseta*) or highest (*Brachionus calyciflorus*, *Anuraeopsis fissa*, *Anuraeopsis navicula*) temperature optima concur with those from northern hemisphere studies (e.g., Ruttner- Kolisko 1974, Berzins & Pejler 1989b). When the seasonal samples were averaged for each lake, however, temperature was still found to be a significant factor in affecting species distribution, although this is likely an artefact in the timing of collection of some samples used in the ordination. The rotifer communities from Lake Rotoehu, for example, found to strongly positively associate with Axis 2 (and therefore with low temperature) in the CCA ordination of

species in North Island lakes, comprised samples collected in autumn and winter only. Changes in communities through latitudinal variations in temperature, such as those found by Shiel & Koste (1986) and Chengalath & Koste (1989b), appeared to be of limited importance in determining the distribution of rotifers at this scale, although may be important when a wider range of latitude in New Zealand is considered, for example with the addition of South Island lakes.

One factor, which was of little importance in determining rotifer community composition in the current study, was pH. This variable had a relatively narrow range (6.8 – 8.5, average 7.6) in the current study compared with, for example, North American lakes affected by acidic atmospheric deposition, where acidity is commonly found to be important in affecting community composition (e.g., MacIsaac *et al.* 1987, Siegfried *et al.* 1989, Brett 1989). MacIsaac *et al.* (1987), Siegfried *et al.* (1989) and Brett (1989) found many species common in waters of pH above 6, for example *K. cochlearis* and *Asplanchna* species, to become rare below a pH of 5.0, and for *Keratella taurocephala* Myers to dominate in acidic lakes, particularly those with a pH below 5. Such extreme acid stress was not apparent in the current study. However, naturally acid stressed lakes do occur in the North Island, particularly in the Taupo volcanic zone through geothermal activity, although these are generally temperature stressed also. James (1995) investigated Lake Rotowhero (pH 2.98 – 3.10, temperature 29.5 – 37.5 °C) over one year and found a single rotifer species only, *Lecane* cf. *rhytida*, which was not observed in the current study.

Most species reported here are likely to be limited in their distributions by their tolerances to environmental conditions and their preferences for food quality and quantity, with passive dispersal of resting eggs sufficient to ensure species are potentially widely distributed. Species found to have restricted distributions were in general recorded only in low densities. These species also may be widespread, but may commonly occur only at low densities in the pelagic or they may have had greater abundance at times outside of those sampled. Alternatively, these species may be littoral or benthic species that have

entered the pelagic and have been sampled by chance. Species found at higher abundance but which have restricted geographical distribution (e.g., those found to contribute > 4% of the rotifers in a sample, but in less than five lakes examined) are likely to be limited in distribution by factors other than their tolerances to environmental conditions. This was particularly apparent in the brachionids. These species may be limited by regional processes, i.e. by dispersal (e.g., Jenkins 1995) or by panbiogeographic processes (e.g., Jamieson 1998). *Keratella australis*, a species limited in distribution to Australasia, was found in three waterbodies in the North Island, all of which are interconnected: Lake Taupo, and the downstream hydroelectric reservoirs Lake Maraetai and Lake Karapiro. This species also was found in only two lakes in the South Island by Sanoamuang & Stout (1993). This species therefore apparently has a restricted distribution in New Zealand, although it is pancontinental in Australia (Shiel & Koste 1986). Based on the distribution of this species in New Zealand, it is possible that it is dispersal limited, perhaps having been a recent immigrant from Australia. However, *Keratella slacki*, a species also limited to Australasia, was found in numerous locations in the North Island, although is apparently restricted in distribution in the South Island. There it was found in only one locality by Sanoamuang & Stout (1993). *Brachionus budapestinensis* and *Brachionus caudatus* also were found to have a restricted distribution, with the former being absent from the South Island (cf. Sanoamuang & Stout 1993). The endemic *Keratella ahlstromi* Russell was not found in the current study, and may therefore be restricted to the South Island, or to habitats different from those studied, e.g., wetlands. Brachionid species in general appear to have more limited distributions globally compared with most other genera (Dumont 1983), and it appears that even at a finer scale these species also are restricted. *Conochilus exiguus* was recorded only from Lakes Rotomanuka and Rotomanuka South. The distribution of this species is unusual because it has not been recorded elsewhere in New Zealand, or in Australia, and is considered to be a North American species (Ruttner-Kolisko 1974). Therefore, arrival from Australia by dispersal or other panbiogeographic

processes is unlikely for this species. Thus, its distribution is probably due to an accidental introduction. Dispersal limitation in these species may be tested by experimentally transferring these species into lakes where they do not already occur (e.g., Jamieson 1995, Lukaszewski *et al.* 1999). Distribution patterns of species, even those that were more restricted, do not appear to be in accord with the panbiogeographic patterns found in calanoid copepods (Jamieson 1998).

Recently, larval fish and omnivorous copepods have been suggested to be more important predators of crustacean or rotifer zooplankton species in New Zealand than previously thought (Jeppesen *et al.* 1997, Couch *et al.* 1999). Restricted distributions of copepod or fish species (e.g., Jamieson 1988, McDowell 1996) may account for some additional variation in rotifer species distributions in the current study.

Although the most widespread survey of North Island lakes to date, my study is still limited in the array of sites sampled and in the temporal variation covered by those samples. It is likely, therefore, that more intensive study of the pelagic rotifers in these lakes will lead to the documentation of further species, and wider distributions of many others than found in current study. This will in turn lead to a greater understanding of the factors that control the distribution of these species.

Chapter 5:

The development and assessment of a potential rotifer community index for determining lake trophic state.

Introduction

Lake trophic state is generally assessed by measuring several diverse criteria, most commonly total phosphorus (TP), chlorophyll *a* and Secchi depth (e.g., Carlson 1977, OECD 1982, Burns & Rutherford 1998). These are not direct measures of trophic state but rather are indicators of it, and confident assessment generally relies on there being good correlations between these indicators. However, these measures can vary independently of one another, particularly where factors other than phosphorus limit algal growth, and erroneous conclusions may be drawn if only a single indicator is used. This is often true in New Zealand lakes, where environmental conditions commonly differ from those where the OECD (1982) classifications of lake trophic state were developed. For example, New Zealand lakes are subject to stronger and more constant winds than are northern temperate lakes (Green *et al.* 1987). Such winds act to lower Secchi transparency by increasing abiotic turbidity and also reduce algal abundance (chlorophyll *a*) from the expected state as determined by nutrient concentrations such as TP (e.g., Hamilton & Mitchell 1988). Nitrogen limitation of algal growth, rather than phosphorus limitation, also is common in New Zealand lakes (White *et al.* 1985, 1986). In the development of the OECD (1982) classification schemes, lakes were omitted that had poor relationships between TP and chlorophyll *a*. These measures can therefore be unreliable for assessing trophic state in lakes that deviate from these relationships, as different results will be obtained using different methodologies. Despite lake trophic state being fundamentally a biological problem, biological monitoring of trophic state has generally been neglected in favour of physical and chemical methods. Biological monitoring involves the use of biological responses to evaluate changes in the environment. These practices have been developed and

utilised successfully employing benthic macroinvertebrates as indicators of organic enrichment or eutrophication of lotic systems. Examples include the Biological Monitoring Working Party (BMWP) Score (Armitage *et al.* 1983), the Belgian Biotic Index (BBI) (De Pauw & Vanhooren 1983) and the New Zealand Macroinvertebrate Community Index (MCI) (Stark 1985) and Semi-Quantitative Macroinvertebrate Community Index (SQMCI) (Stark 1998). In lakes, phytoplankton (e.g., Thunmark 1945, Rawson 1956) and chironomid or oligochaete (e.g., the Benthic Quality Index (BQI) (Wiederholm 1976) and that of Sæther (1979)) indices have been used in lake trophic state classification. The major advantage of using bioindicators is that they integrate physical, chemical and biological factors over time, and therefore assessment can be made of environmental conditions from relatively few samples at a lower cost. A common argument against the use of biological methods is that they are insensitive in distinguishing environmental conditions. However, biomonitors of lake trophic state should provide a measure of the actual biological response to increased nutrient levels, rather than any response being insensitive. Rejection of the use of biological indicators serves to perpetuate a belief in the importance of chemical measures (i.e. nutrients), even though these may be inadequate in some situations, as noted above. Based on the assessment of a historic data set from the Rotorua area, Duggan *et al.* (in press) concluded that rotifers may have potential as bioindicators of lake trophic state. On a broader scale, trophic state appears to be a predominant factor determining rotifer community composition in New Zealand lakes (see previous chapter) and commonly has been found to be important in determining distribution of rotifer communities elsewhere (e.g., Siegfried *et al.* 1989, Kaushik & Saxena 1995, Ejsmont-Karabin 1995). Several conducted studies elsewhere have provided lists of rotifer species indicative of different trophic states (e.g., Mäemets 1983, Berzins & Pejler 1989a, Matveeva 1991), although no quantitative community index has yet been developed based on these responses. This chapter will assess the potential of rotifer communities as bioindicators of lake trophic status using a set of lakes spanning a wider geographical and temporal range than that used

by Duggan *et al.* (in press), develop indices which may potentially be utilised in the assessment of lake trophic state, and report on the usefulness of these methods.

Methods

The data set detailed in Chapter 4 was used in this analysis, but samples from additional sites in Lakes Wairarapa and Rotorangi were omitted so as not to have over representation in the analyses and in development of the bioindicator schemes. Samples from the Northland lakes, Boggy pond, Matthew's lagoon and Lake Kareta also were omitted due to lack of some trophic state data. Species comprising > 1 % of any one sample, and present in five or more samples, were selected for analyses to ensure a large initial species data set.

Bioindicator schemes are developed in relation to a single environmental gradient. The OECD scheme relies on separate assessment using TP, chlorophyll *a* and Secchi transparency measurements. The Trophic Lake Index (TLI) (Burns & Rutherford 1998), developed for New Zealand conditions to enable easy comparison of trophic level of different lakes, provides an absolute indicator of lake trophic level by taking into account all of these three factors, plus total nitrogen (TN), to give a single numerical value of trophic state. On average, equivalent trophic levels are assigned using each indicator based on regression equations used in development, with the TLI value a single number which is an average of the four indicators. In the current study, TLI values were calculated only with the available data (generally four samples), without TN. In all analyses, TP, chlorophyll *a* and Secchi depth data were averaged for each lake to obtain a deseasonalised assessment of trophic state based on each variable for each lake, primarily to assess the value of using rotifer species to assess yearly average trophic state from single samples. The inference of lake trophic state using relative abundances of rotifer species in a sample requires a good statistical relation between the variable of interest (e.g., TP, TLI) and the rotifer taxa. To develop rotifer inference models for lake trophic state, the relative strengths of different trophic state indicators were estimated by running a series of Canonical Correspondence

Analyses (CCA) constrained to single environmental variables (i.e. TLI, TP, chlorophyll *a* and Secchi transparency). In this type of analysis, there is one constrained axis related to each variable, and a series of unconstrained axes. The ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) indicates the relative importance of that environmental variable in explaining the species data (Ter Braak 1988), and variables with high λ_1/λ_2 ratios are potential candidates for developing predictive models. Dixit *et al.* (1991) suggest using only those variables with λ_1/λ_2 ratios greater than 0.5 to develop inference models, with variables with lower ratios likely to be less robust. CCA was performed using untransformed species composition data (%) and raw (TLI) or log transformed (others) environmental data, averaged for each lake.

Several approaches were used to construct indices for assessing lake trophic state from rotifer community composition based on the trophic indicators with the strongest relationships with rotifer communities. Firstly, Weighted Averaging regression (WA) and tolerance downweighted Weighted Averaging (WA-tol) methods, as commonly used in paleolimnological studies for inferring past environmental conditions from the responses of modern taxa (Ter Braak & van Dam 1989, Birks *et al.* 1990). Secondly, two methods similar to those used in the development of the Biological Monitoring Working Party (BMWP) Score (Armitage *et al.* 1983), Macroinvertebrate Community Index (MCI) and Quantitative MCI (QMCI) (Stark 1985) indices for stream macroinvertebrates.

In the first approach, WA regression and calibration (with classical deshrinking) models were developed to infer trophic state from rotifer communities. This approach involves both regression (Ter Braak & Looman 1987) and calibration (Ter Braak 1987) steps. WA regression is used to estimate species indicator values, which are equivalent to the optima of a species unimodal response curve to the variable of interest. A weighted average is taken of the environmental data, in which values are weighted proportional to the species relative abundance, i.e.:

$$u^* = (y_1x_1 + y_2x_2 + \dots + y_nx_n) / (y_1 + y_2 + \dots + y_n)$$

where

u^* is the weighted average (= the species indicator value)

$y_1, y_2, \dots, y_n$ are the relative abundances of species at sites 1, 2 ... n.

$x_1, x_2, \dots, x_n$ are values of environmental variables at sites 1, 2 ... n.

In the calibration step, the estimates of optima of taxa are used to infer environmental conditions based on the taxonomic composition of the sample. A WA estimate for a sample is the average of the optima of taxa in that sample, weighted with respect to their relative abundances, i.e.:

$$x_o = (y_1u_1 + y_2u_2 + \dots + y_nu_n) / (y_1 + y_2 + \dots + y_n)$$

where

x_o is the assessed environmental variable

$y_1, y_2, \dots, y_n$ are the responses (relative abundances) of species (1, 2 ... n) at the sites.

$u_1, u_2, \dots, u_n$ are the indicator values of species (1, 2 ... n).

The tolerances of taxa also can be considered in WA models by downweighting each taxon by their respective variances, known as WA with tolerance downweighting (WA-tol), i.e.:

$$x_o = [(y_1u_1/t_1^2) + (y_2u_2/t_2^2) + \dots + (y_nu_n/t_n^2)] / [(y_1/t_1^2) + (y_2/t_2^2) + \dots + (y_n/t_n^2)]$$

In WA and WA-tol reconstructions, averages are taken twice, once in the development of indicator values and again in the inference of environmental conditions. The resulting

“shrinkage” of the inferred environmental variables is corrected for using a deshrinking regression equation (Birks *et al.* 1990). Classical deshrinking was used as it provided more reliable estimates than inverse deshrinking. Weighted averaging regression and calibration (both with and without tolerance downweighting) and calculation of deshrinking equations were performed using CALIBRATE v. 0.8.2 (Juggins & Ter Braak 1998).

Regressions were calculated between assessed WA and WA-tol values versus observed values of samples. Regression analysis was repeated on deseasonalised WA and WA-tol values for each lake having greater than two samples, obtained as an average of each lakes sample WA or WA-tol values.

In the second approach, lakes initially were divided into trophic state classes *a priori* based on TLI trophic levels assessed using each trophic indicator (Burns & Rutherford 1998). The relative abundance data of rotifer species were used to obtain index scores for individual species by calculating for each the mean percentage contribution to total rotifer numbers in each of the trophic levels, and weighting these by a nominal factor towards a high or low trophic state to provide a species score. The nominal weighting factors using TLI were: oligotrophic 2, mesotrophic 3, eutrophic 4, supertrophic 5 and hypertrophic 6. The species index score was obtained by multiplying the resulting number by ten. For example, the species score for *Conochilus dossuarius* is calculated as follows:

Trophic state (TLI)	O	M	E	S	H	
Mean % representation	6.99%	3.16%	1.18%	0.02%	0.00%	Σ=11.35
Approximate score	=	$\frac{6.99 \times 2}{11.35}$	$\frac{3.16 \times 3}{11.35}$	$\frac{1.18 \times 4}{11.35}$	$\frac{0.02 \times 5}{11.35}$	$\frac{0.00 \times 6}{11.35}$
		1.23	+ 0.84	+ 0.41	+ 0.01	+ 0.00
				= 2.49		
Species index score		= (2.49 x 10)	= 24.9			
round off				-> 25		

With this approach, an index score of '20' represents a low score and is indicative of a low trophic state species, and '60' a high score indicative of high trophic state species. *C. dossuarius* is therefore a species which is indicative of low trophic state.

Rotifer Community Index (RCI) sample values were then calculated by summing the species index scores for all species present in a sample, and dividing by the number of scoring taxa in the sample,

$$\text{i.e. RCI} = \frac{\text{site score}}{\text{no. of scoring taxa}}$$

A semi-quantitative variant (SQRCI) was also examined, modelled on Stark's (1995) QMCI approach, by taking into account the percentage contribution of each indicator species to the community. The SQRCI was calculated by taking the sum of the percentage contributions of each indicator species (i) to the total percentage of indicator taxa, multiplied by the species score,

$$\text{i.e. SQRCI} = \sum_{i=1}^n \left(\frac{\% \text{ species}_i}{\text{sum of } \% \text{ of indicator taxa}} \right) \times \text{species score}_i$$

The assessed RCI and SQRCI values were regressed against observed TP and TLI values of samples. Regression analysis was repeated on deseasonalised RCI and SQRCI values, obtained as an average of each lakes sample RCI or SQRCI values, for those lakes for which there were greater than two samples.

First, methods were developed and assessed using 44 abundant species present in 121 samples. However, the use of this number of species may not be useful for end users, for example regional councils or other lake management authorities, because of the time required to process samples and the associated costs compared with traditional schemes. The number of rotifer taxa that may be encountered in samples also will preclude use of schemes without the use of trained rotifer specialists. In recent years, rapid assessment approaches have been a focus of biomonitoring techniques (Resh & Jackson 1993). This is

Table 5.1. CCA results from tests of the strength of environmental variables based on all samples and species.

Variable included	λ_1	λ_1/λ_2	P
TLI	0.310	0.505	0.005
TP	0.304	0.490	0.005
Secchi	0.275	0.465	0.005
Chl. <i>a</i>	0.267	0.427	0.005

commonly achieved by reducing the number of taxa considered by determining only those species which are relevant, for example those with narrow tolerances to the variable of interest. A subset of potential species indicators were therefore identified, utilising methods similar to those by Dixit *et al.* (1993) and references therein. The following criteria were applied to potential indicator species: (i) more than 2 % of the variance of the taxon must be explained by the environmental variable of interest in the constrained CCA; and (ii) the WA tolerance of the taxon must be less than 1.2 units for TLI or < 0.5 for log TP.

To identify lakes in which factors other than TP were limiting algal abundance, a regression was performed of TP versus chlorophyll *a*. Lakes with large standardised residuals, as identified by Minitab 12.1 (Minitab Inc. 1998), were removed, and analyses repeated. These lakes were removed so as to compare lakes which have good relationships between trophic indicators.

Regressions were calculated between assessed environmental values of samples versus observed values for schemes using reduced taxa and with lakes removed, and on deseasonalised values for each lake having greater than two samples, obtained as an average of each lakes sample values. Regression analysis were performed using Minitab 12.1 (Minitab Inc. 1998).

Results

TLI was identified as the measure of lake trophic state most highly associated with rotifer distribution, followed by TP, both of which were significant (Table 5.1). TLI is the only variable whose first constrained eigenvalue can be considered large (> 0.5) compared to the

other unconstrained eigenvalues (cf. Dixit *et al.* 1991). Variables with lower λ_1/λ_2 ratios may still be used for calibration purposes, but with less confidence than a calibration with a high ratio (ibid). In the constrained CCA for TLI, high TLI was negatively associated with Axis 1 (Fig. 5.1, Table 5.2). Samples most strongly negatively associated with this axis therefore belong to the more eutrophic lakes (e.g., Lakes Waahi, Horowhenua and Rotokauri) and those most positively associated belong to the more oligotrophic lakes (e.g., Lakes Taupo and Waikaremoana). *Brachionus budapestinensis*, *Filinia longiseta*, *Brachionus calyciflorus*, *Keratella slacki*, *Keratella tropica*, *Keratella tecta*, *Brachionus quadridentatus* and *Asplanchna sieboldi* were all strongly negatively associated with Axis 1, and are therefore species associated with high trophic state. *Conochilus dossuarius*, *Synchaeta longipes*, *Polyarthra dolichoptera*, *Filinia novaezealandiae*, *Gastropus hyptopus*, *Trichocerca stylata*, *Conochilus coenobasis* and *Ascomorpha ovalis* were all strongly positively associated with Axis 1, and are therefore species associated with low trophic state. Bioindicator schemes were developed for TLI and TP.

The predictive ability of inference models was assessed by comparison of the coefficients of determination (R^2) between the observed and the rotifer inferred TLI or RCI values, and the deviation between observed and inferred values of samples. In the models using all species and samples, WA-tol and RCI approaches gave the highest predictive abilities, although all were similarly performed (Fig. 5.2, Table 5.2). In the WA and WA-tol methods, the majority of samples were assessed within 2 TLI values of the observed value. The coefficients of determination and distribution of samples around the line indicate rotifers can provide useful information about trophic state in North Island lakes. With the species reduced to twelve indicator taxa, *Ascomorpha ovalis*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Brachionus quadridentatus*, *Conochilus coenobasis*, *Conochilus dossuarius*, *Conochilus unicornis*, *Filinia longiseta*, *Keratella slacki*, *Keratella tecta*, *Keratella tropica*, and *Pompoholyx complanata*, all coefficients of determination decreased

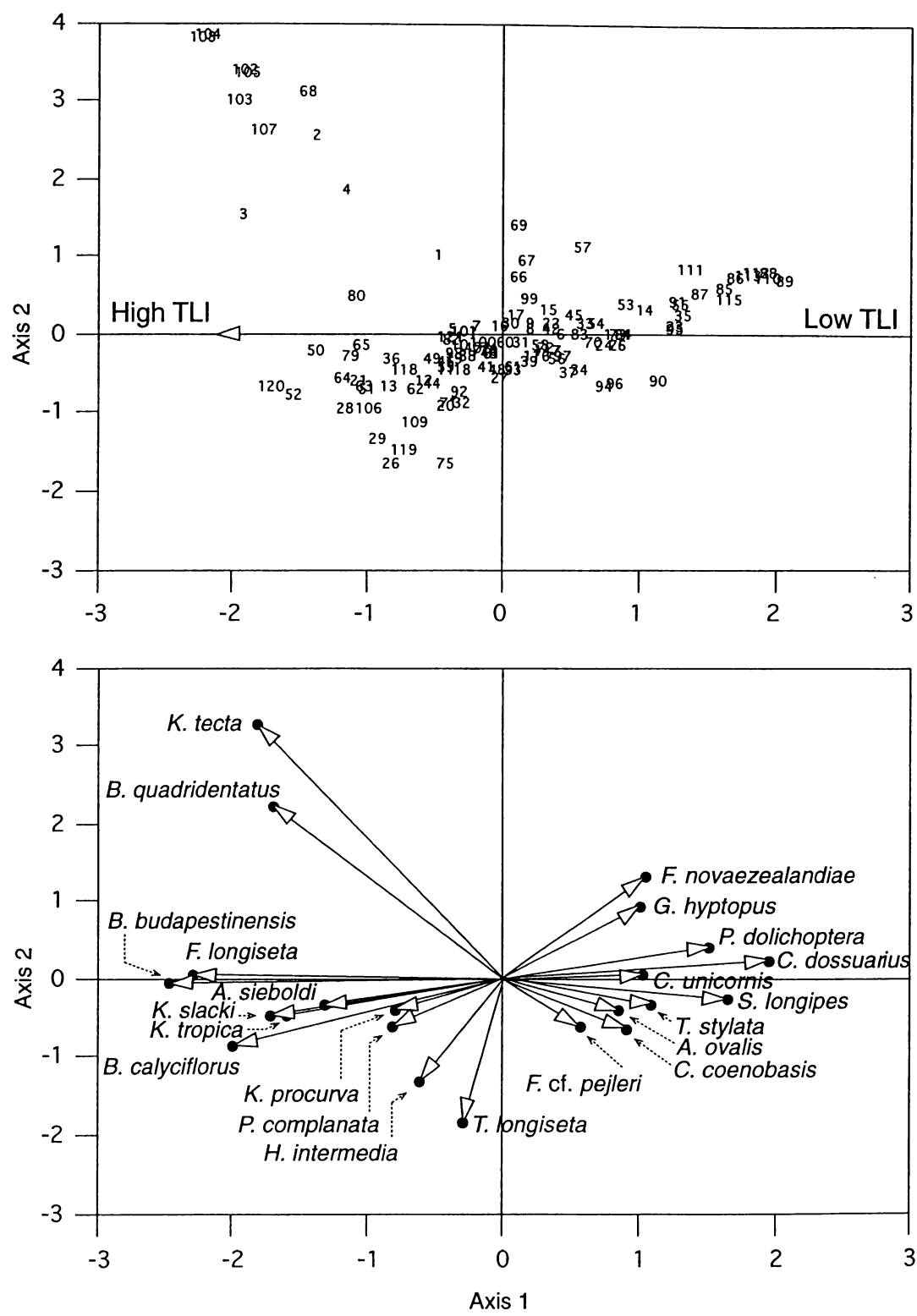
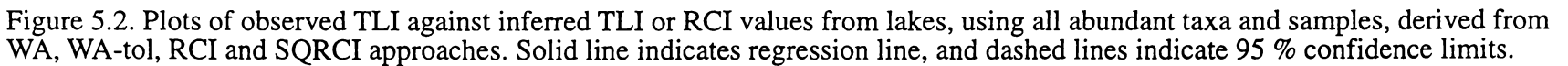


Figure 5.1. Ordination diagram based on CCA of 44 North Island rotifer species with respect to TLI. Eigenvalues for first two axes = 0.31 (constrained) and 0.61 (unconstrained). Scores of rotifer species and environmental variables were scaled to fit the sample ordination. Numbers correspond to sample numbers (Table 5.2). Some species have been omitted from the ordination for clarity.

Table 5.2. Key to sample numbers (lake and date (d:m:y)) for CCA ordination and inferred vs. observed WA and RCI graphs.

n Lake	Date	n Lake	Date	n Lake	Date
1 Horowhenua	8.4.98	42 Rerewhakaaitu	6.10.98	83 Tarawera	28.1.98
2 Horowhenua	5.6.97	43 Rotoehu	18.8.97	84 Tarawera	22.4.98
3 Horowhenua	7.8.97	44 Rotoehu	6.5.98	85 Taupo	27.7.97
4 Horowhenua	26.11.97	45 Rotoiti	3.4.98	86 Taupo	29.10.97
5 Horowhenua	18.12.97	46 Rotoiti	23.1.99	87 Taupo	21.1.98
6 Karapiro	22.7.97	47 Rotoiti	22.10.97	88 Taupo	7.4.98
7 Karapiro	8.10.97	48 Rotoiti	18.8.97	89 Taupo	7.7.97
8 Karapiro	27.1.98	49 Rotokauri	24.9.97	90 Tikitapu	16.4.98
9 Karapiro	29.4.98	50 Rotokauri	24.3.98	91 Tikitapu	3.2.98
10 Kuwakatai	21.5.97	51 Rotokauri	23.6.98	92 Tikitapu	22.10.97
11 Kuwakatai	26.8.97	52 Rotokauri	27.1.99	93 Tikitapu	23.6.97
12 Kuwakatai	19.11.97	53 Rotoma	23.7.97	94 Tomarata	21.5.97
13 Kuwakatai	16.2.98	54 Rotoma	14.10.98	95 Tomarata	26.8.97
14 Maraetai	25.7.97	55 Rotoma	28.1.98	96 Tomarata	19.11.97
15 Maraetai	8.10.97	56 Rotoma	22.4.98	97 Tomarata	16.2.98
16 Maraetai	29.4.98	57 Rotomahana	6.10.98	98 Tutira	24.7.97
17 Maraetai	27.1.98	58 Rotomanuka	30.4.98	99 Tutira	15.10.97
18 Ngaroto	24.7.97	59 Rotomanuka	24.7.97	100 Tutira	21.9.98
19 Ngaroto	24.3.98	60 Rotomanuka	25.9.97	101 Tutira	30.4.98
20 Ngaroto	27.1.99	61 Rotomanuka	27.1.99	102 Waahi	25.3.98
21 Ngaroto	25.9.97	62 RotomanukaSth	24.3.98	103 Waahi	28.8.97
22 Okareka	1.9.97	63 RotomanukaSth	24.7.97	104 Waahi	25.11.98
23 Okareka	26.3.98	64 RotomanukaSth	25.9.97	105 Waahi	28.1.99
24 Okareka	28.1.99	65 RotomanukaSth	27.1.99	106 Waikare	25.3.97
25 Okareka	22.6.98	66 Rotorangi(L3)	19.6.97	107 Waikare	30.7.98
26 Okaro	6.10.97	67 Rotorangi(L3)	23.10.97	108 Waikare	25.11.98
27 Okaro	18.7.97	68 Rotorangi(L3)	19.2.98	109 Waikare	28.1.99
28 Okaro	17.4.98	69 Rotorangi(L3)	18.3.98	110 Waikaremoana	24.7.97
29 Okaro	18.12.97	70 Rotoroa	28.7.97	111 Waikaremoana	15.10.97
30 Okataina	23.7.97	71 Rotoroa	8.10.97	112 Waikaremoana	29.1.98
31 Okataina	14.10.97	72 Rotoroa	29.5.98	113 Waikaremoana	30.4.98
32 Okataina	28.1.98	73 Rotoroa	27.1.98	114 Wainamu	21.5.97
33 Okataina	22.4.98	74 Rotorua	1.9.97	115 Wainamu	26.8.97
34 Ototoa	21.5.97	75 Rotorua	26.3.98	116 Wainamu	19.11.97
35 Ototoa	26.8.97	76 Rotorua	22.6.98	117 Wainamu	16.2.98
36 Ototoa	19.11.97	77 Spectacle	21.5.97	118 Wairarapa3	16.7.97
37 Ototoa	16.2.98	78 Spectacle	26.8.97	119 Wairarapa3	18.5.98
38 Pupuke	21.5.97	79 Spectacle	19.11.97	120 Wairarapa3	4.3.98
39 Pupuke	26.8.97	80 Spectacle	16.2.98	121 Wairarapa3	11.11.98
40 Pupuke	19.11.97	81 Tarawera	23.7.97		
41 Pupuke	16.2.98	82 Tarawera	14.10.97		



(Fig. 5.3, Table 5.2). The spread of samples increases around the line from that using all species, however, with a far greater proportion of samples assessed greater than 2 TLI units higher or lower than the observed value. This occurred between 2 and 5 observed TLI units in particular, reducing the predictive abilities in this region. The coefficients of determination increased when samples were deseasonalised to give a single value for each lake, compared with those using all samples (Fig 5.4, Table 5.3). Only Lake Waahi was assessed as having TLI levels greater than 2 TLI units different from the observed. Using the deseasonalised lake data using and only the twelve indicator taxa improved coefficients of determination to those using all samples with twelve indicator taxa, but performed more poorly than deseasonalised estimates using all rotifer species (Fig. 5.5, Table 5.3). The spread of samples around the line also increases, showing predictive abilities are reduced using only the 12 indicator taxa. WA-tol generally provided better results than the other methods.

Lakes Kuwakatai, Okareka, Rerewhakaaitu, Rotorangi, Spectacle, Tutira and Wairarapa samples were removed since they had large residuals in a TP: chlorophyll *a* regression. This left 96 samples having 41 species present in five or more samples for inference models. Removal of these lakes provided contrasting results to the schemes using all lakes. Using all species with selected lakes provided better results than those with all species and lakes (Fig. 5.6, cf. Fig. 5.2, Table 5.2). In all cases, coefficients of determination increased, and the spread of samples around the line was also greatly reduced, with Lake Waahi samples the most notable outliers. When using only 10 species (*Asplanchna sieboldi*, *Ascomorpha ovalis*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Brachionus quadridentatus*, *Conochilus dossuarius*, *Conochilus unicornis*, *Filinia longiseta*, *Keratella slacki*, and *Keratella tecta*), coefficients of determination either did not reduce greatly or were improved (Fig 5.7, Table 5.2). However, examination of the distribution of observed and inferred values show that samples generally grouped into

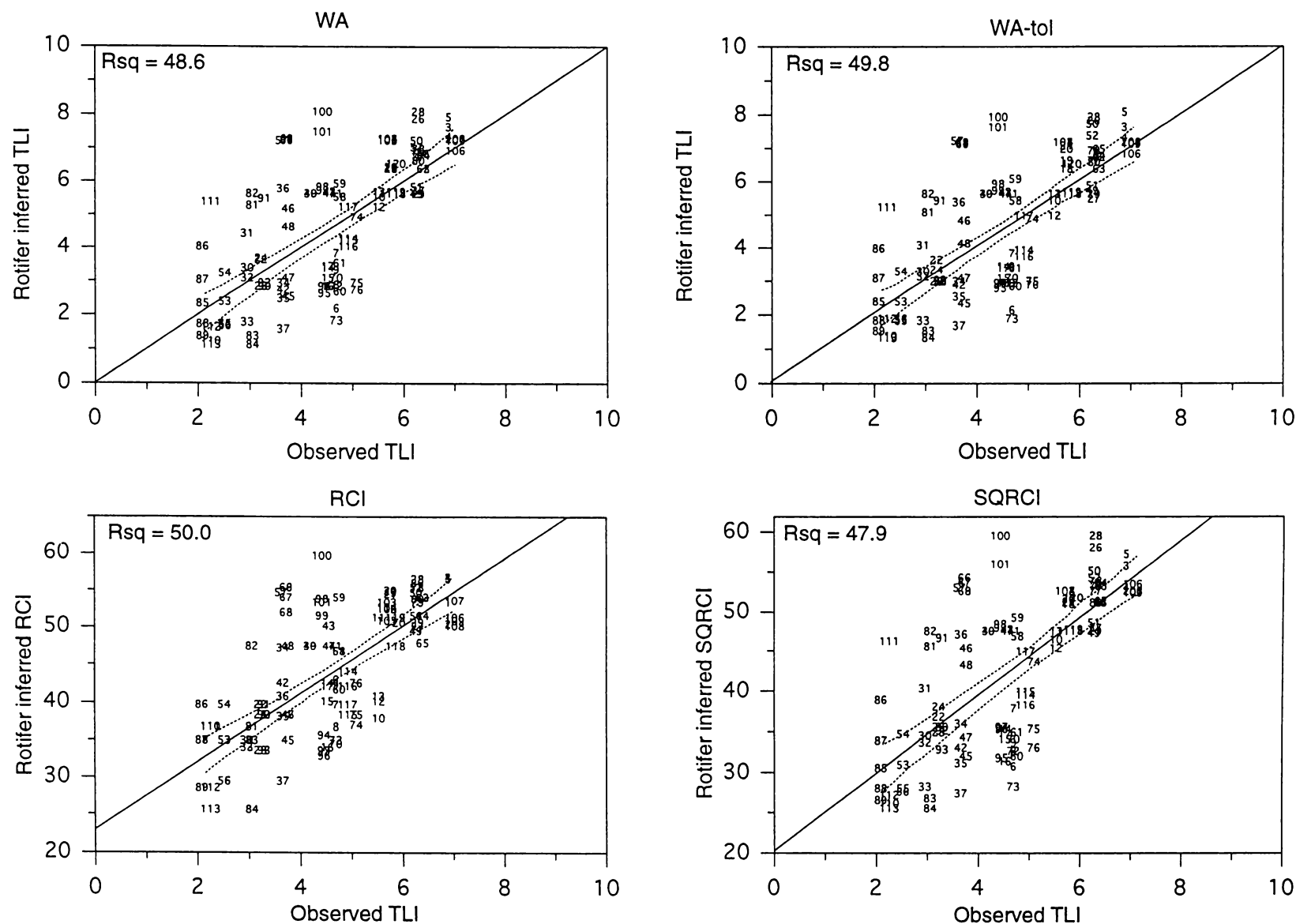


Figure 5.3. Plots of observed TLI against inferred TLI or RCI values from lakes, using 12 indicator taxa and all samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

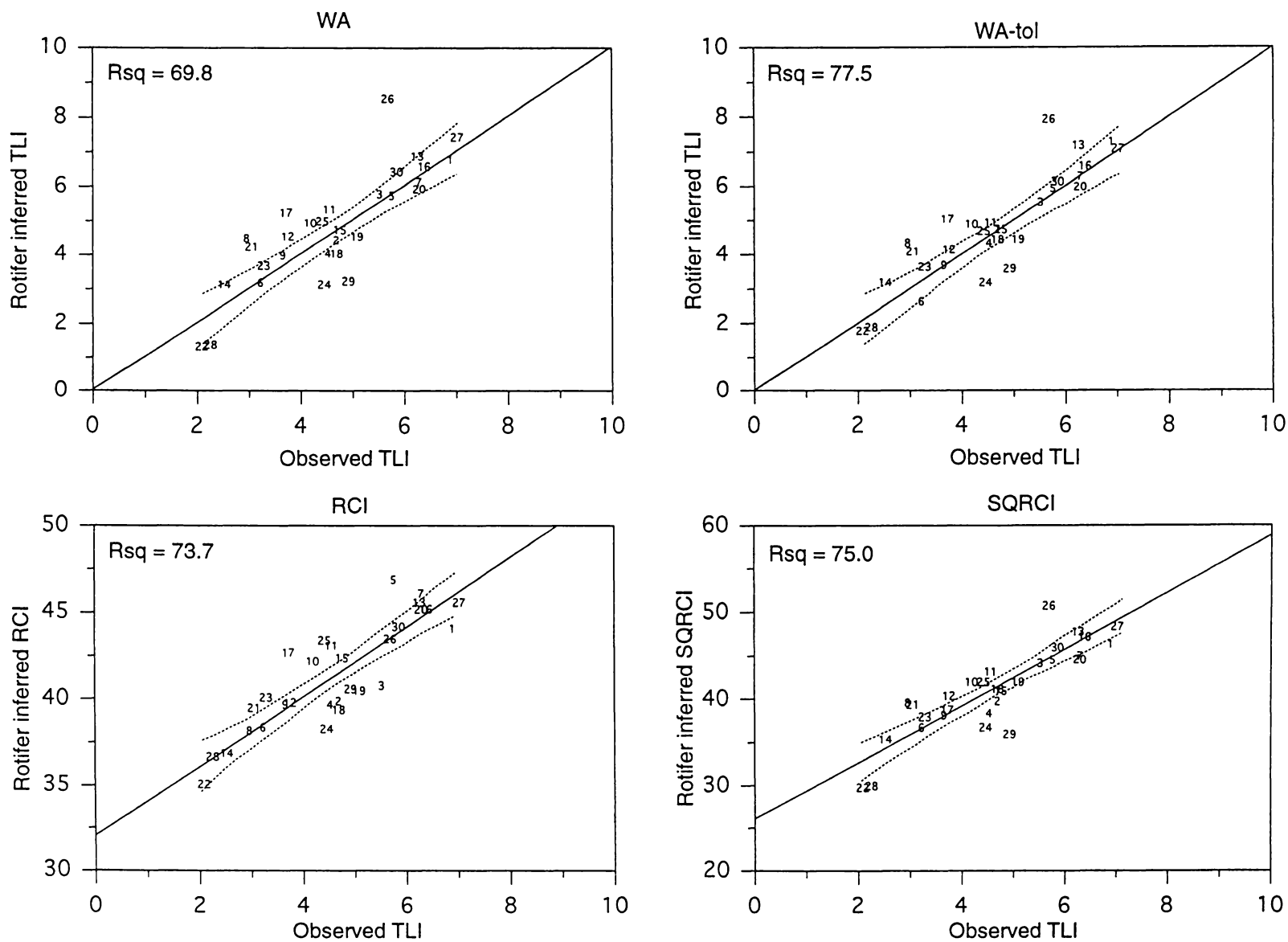


Figure 5.4. Plots of observed TLI against inferred TLI or RCI values from lakes, using all abundant species and deseasonalised samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

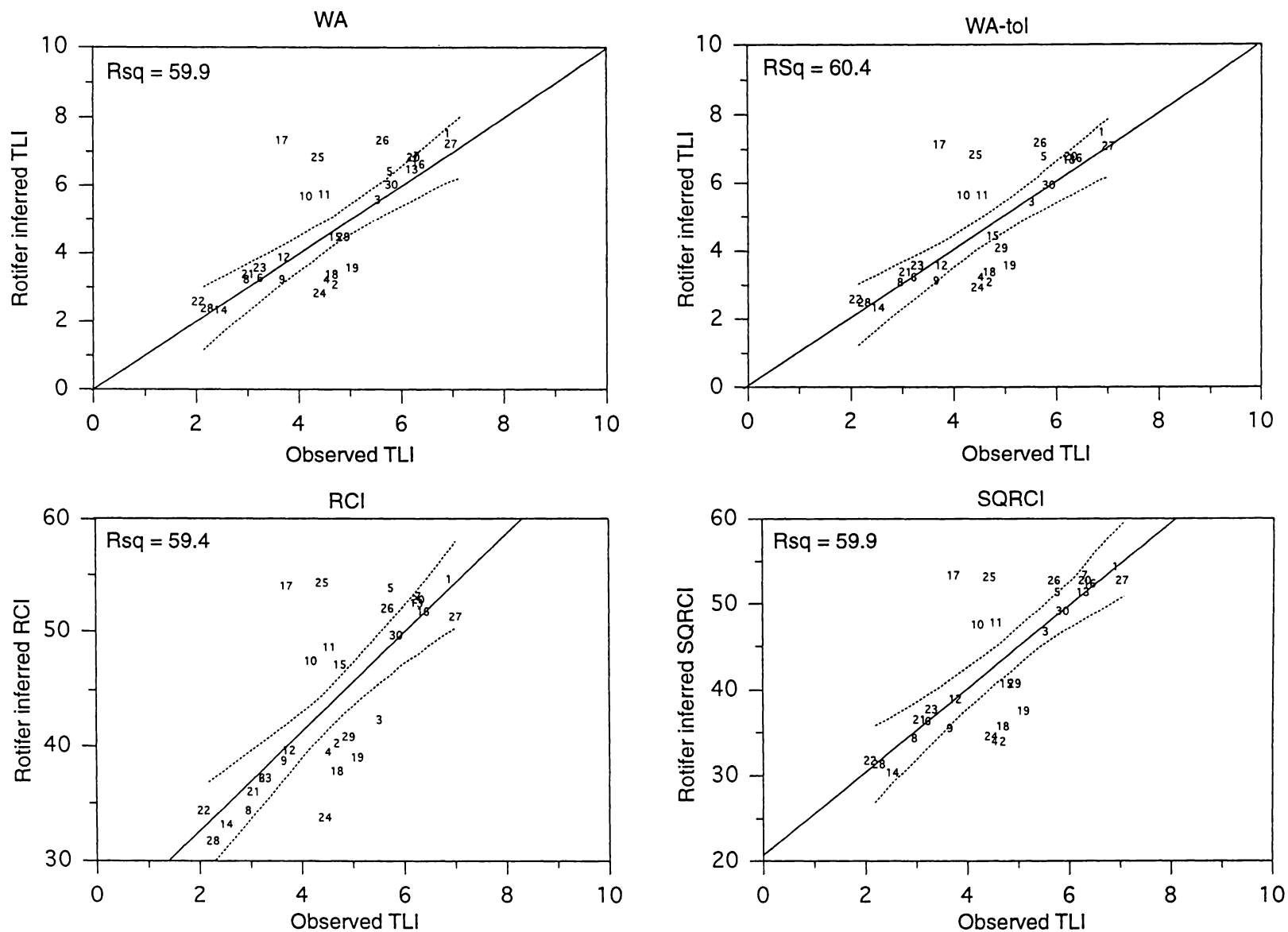


Figure 5.5. Plots of observed TLI against inferred TLI or RCI values from lakes, using 12 indicator taxa and deseasonalised samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

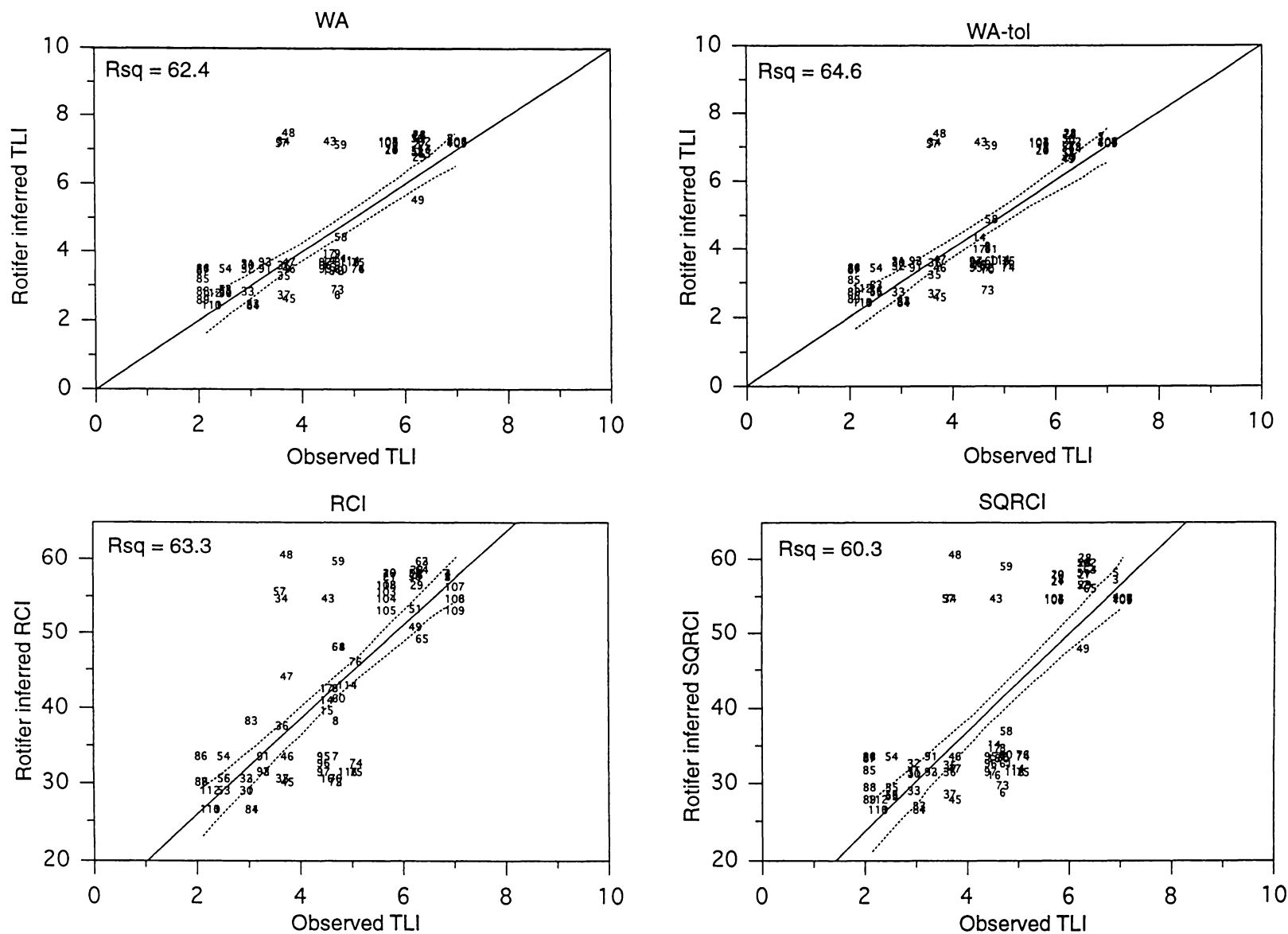


Figure 5.7. Plots of observed TLI against inferred TLI or RCI values from lakes, using 10 indicator taxa and with selected lakes removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

Table 5.3. Key to sample numbers for deseasonalised inferred versus observed TLI and TP graphs.

n	Lake	n	Lake	n	Lake
1	Horowhenua	11	Rotoehu	21	Tarawera
2	Karapiro	12	Rotoiti	22	Taupo
3	Kuwakatai	13	Rotokauri	23	Tikitapu
4	Maraetai	14	Rotoma	24	Tomarata
5	Ngaroto	15	Rotomanuka	25	Tutira
6	Okareka	16	Rotomanuka South	26	Waahi
7	Okaro	17	Rotorangi	27	Waikare
8	Okataina	18	Rotoroa	28	Waikaremoana
9	Ototoa	19	Rotorua	29	Wainamu
10	Pupuke	20	Spectacle	30	Wairarapa

clusters at either high or low trophic state, with poor predictive ability between 3 and 5 TLI units. Using deseasonalised data and all samples again improved predictive ability from that using all samples (Fig. 5.8, Table 5.3). The WA-tol coefficients of determination improved on those using all lakes, and samples were generally more closely associated with the line. Using only 10 species either did not greatly reduce, or even improved, coefficients of determination from those using all species (Fig 5.9, Table 5.3). Samples between 4 and 6 TLI units performed the most poorly.

Indices based on TP in general provided similar coefficients of determination to TLI based schemes. WA-tol and RCI provided the best results using all samples and abundant taxa (Fig. 5.10, Table 5.2). Using 15 indicator taxa, coefficients of determination were reduced (Fig 5.11, Table 5.2). The use of deseasonalised lake data provided superior results to assessment using all samples (Fig. 5.12, Table 5.3). The use of deseasonalised samples and 15 indicator taxa (*Ascomorpha ovalis*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Brachionus quadridentatus*, *Conochilus coenobasis*, *Conochilus dossuarius*, *Conochilus unicornis*, *Filinia longiseta*, *Keratella slacki*, *Keratella tecta*, *Keratella tropica*, *Synchaeta longipes*, *Trichocerca stylata*, *Pompholyx complanata* and *Polyarthra dolichoptera*), provided poorer results than using all taxa, but was superior to the use of all species and single samples (Fig. 5.13, Table 5.3).

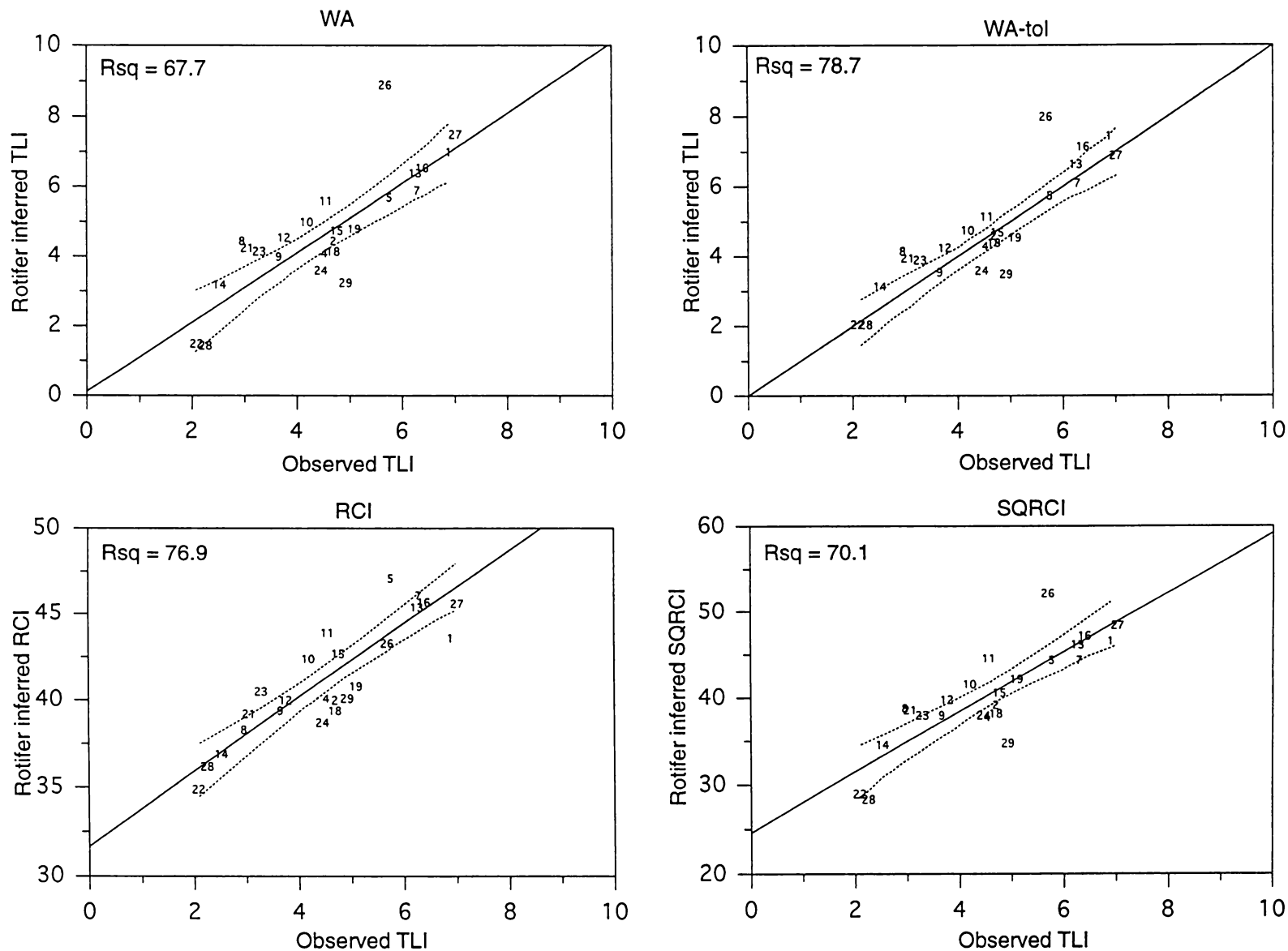


Figure 5.8. Plots of observed TLI against inferred TLI or RCI values from lakes, using all abundant taxa, deseasonalised, and with turbid selected removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

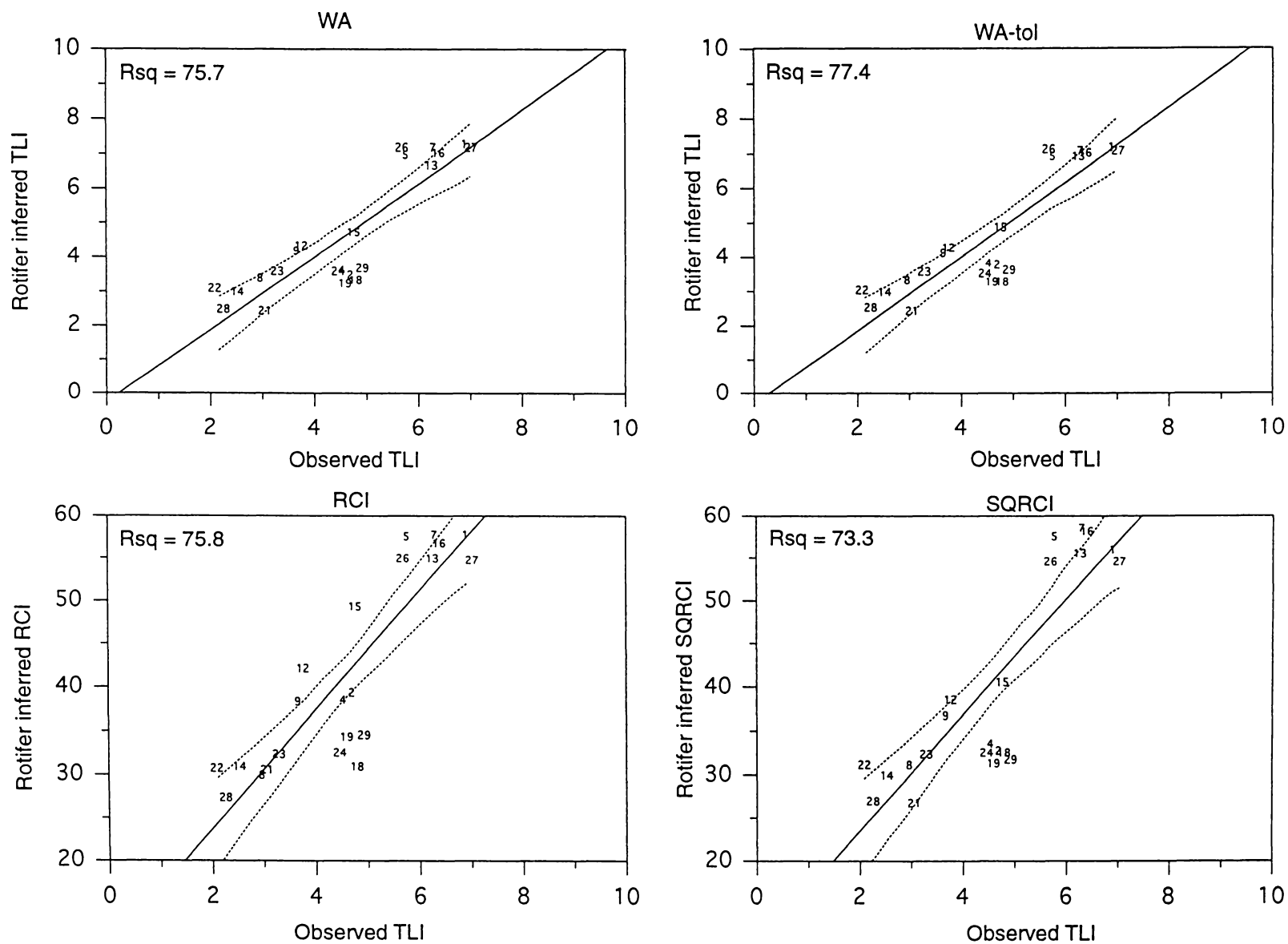


Figure 5.9. Plots of observed TLI against inferred TLI or RCI values from lakes, using 10 indicator taxa, deseasonalised, and with selected lakes removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

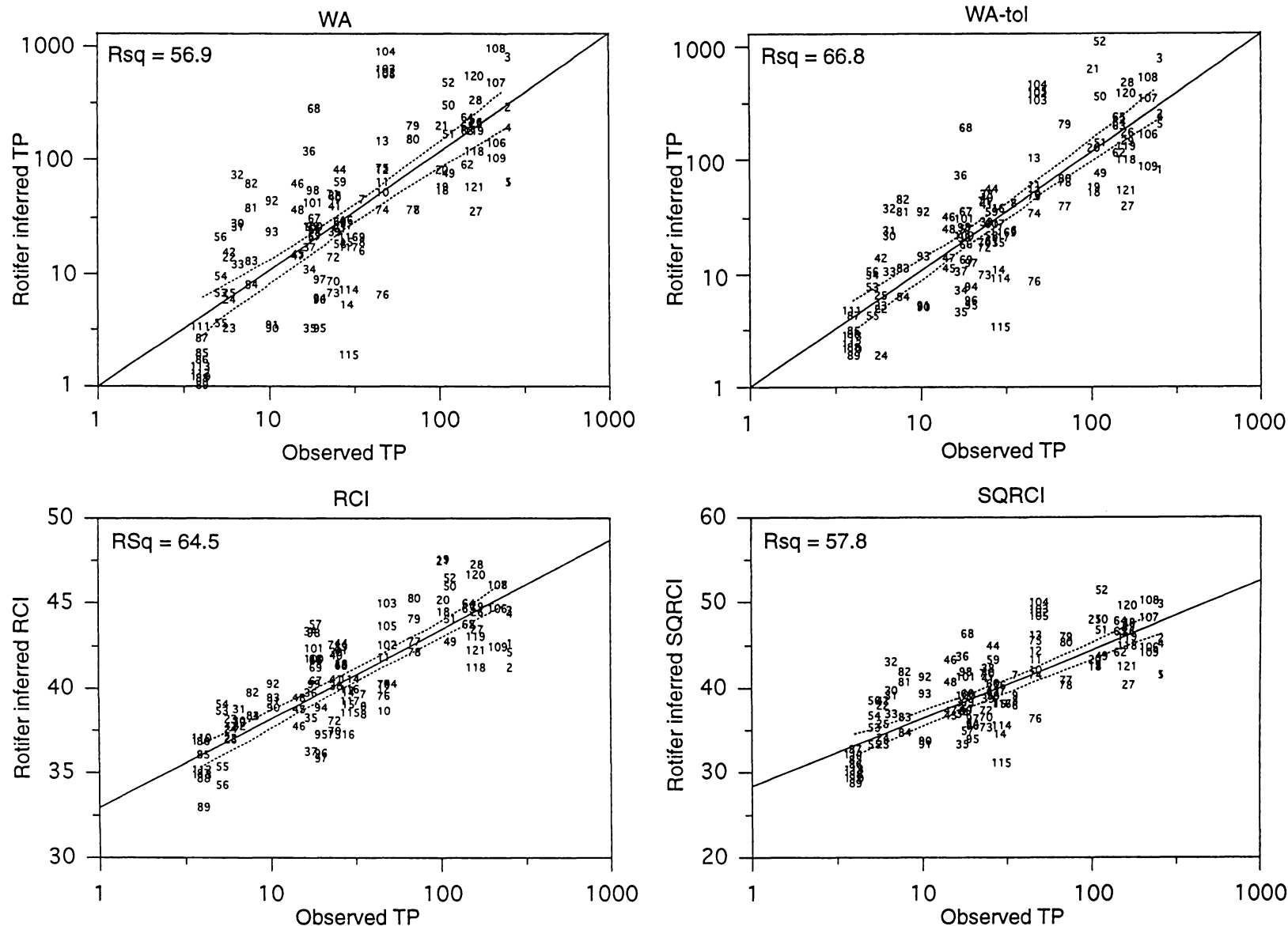


Figure 5.10. Plots of observed TP against inferred TP or RCI values from lakes, using all abundant taxa and samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

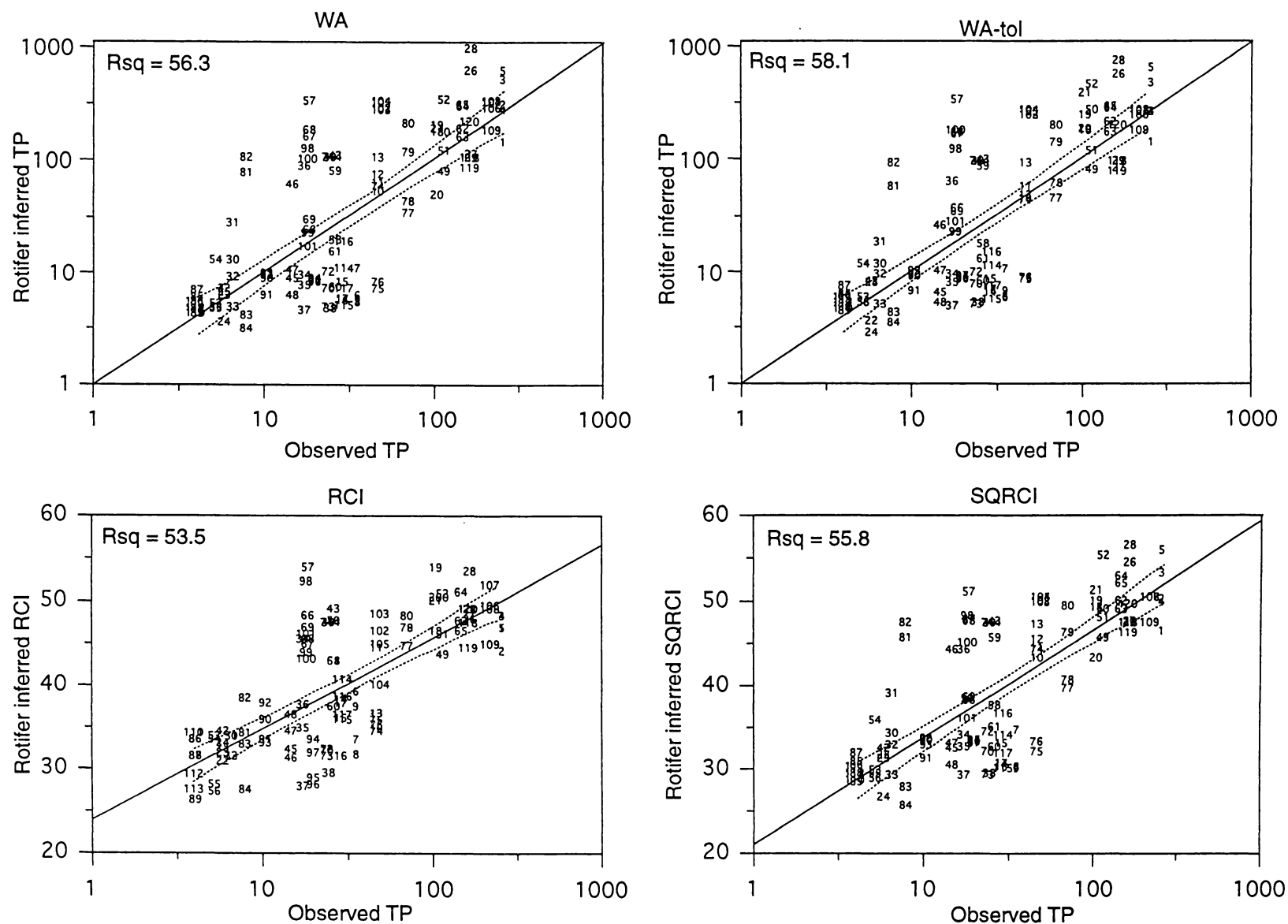


Figure 5.11. Plots of observed TP against inferred TP or RCI values from lakes, using 15 indicator taxa and all samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

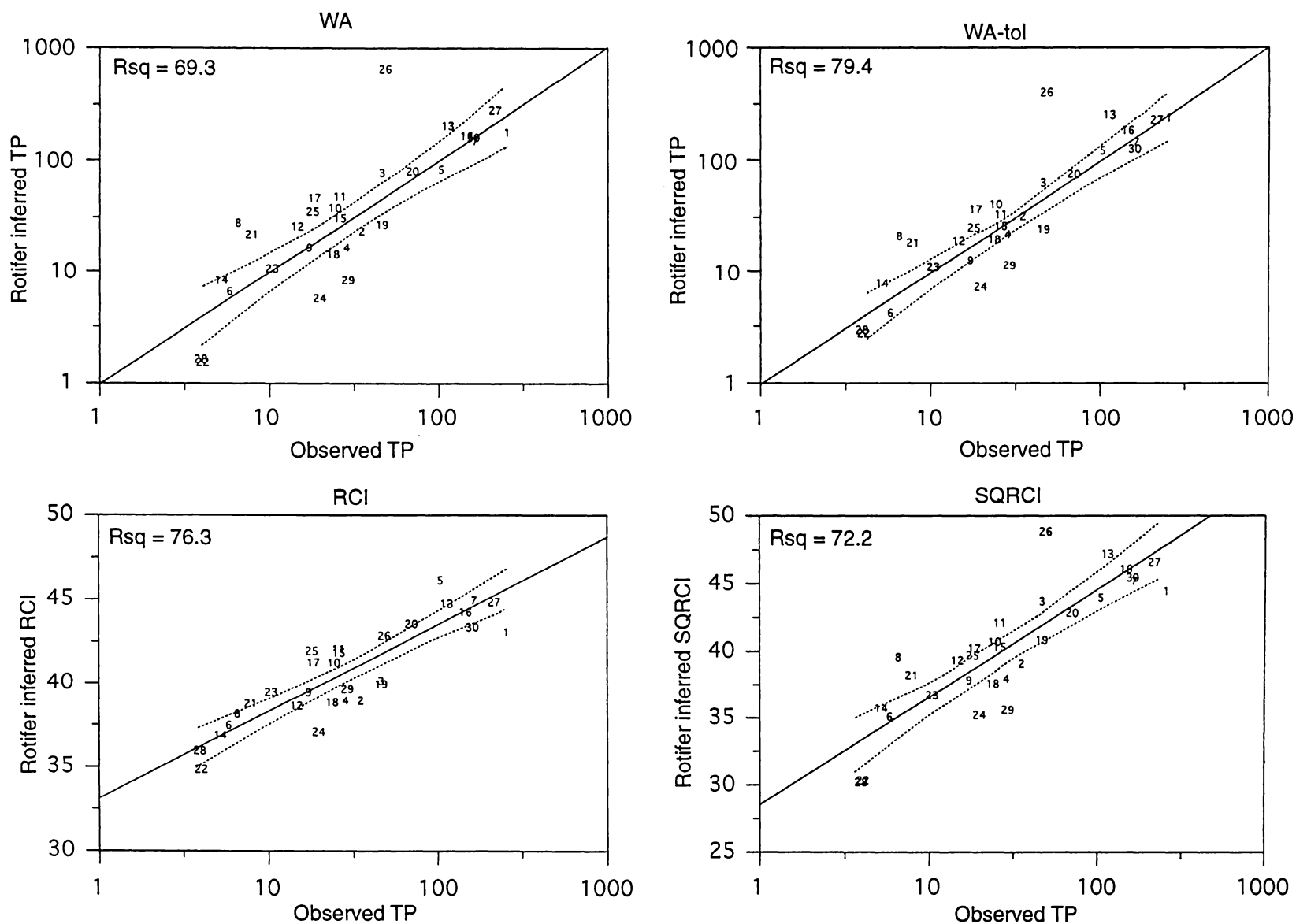


Figure 5.12. Plots of observed TP against inferred TP or RCI values from lakes, using all abundant species and deseasonalised samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

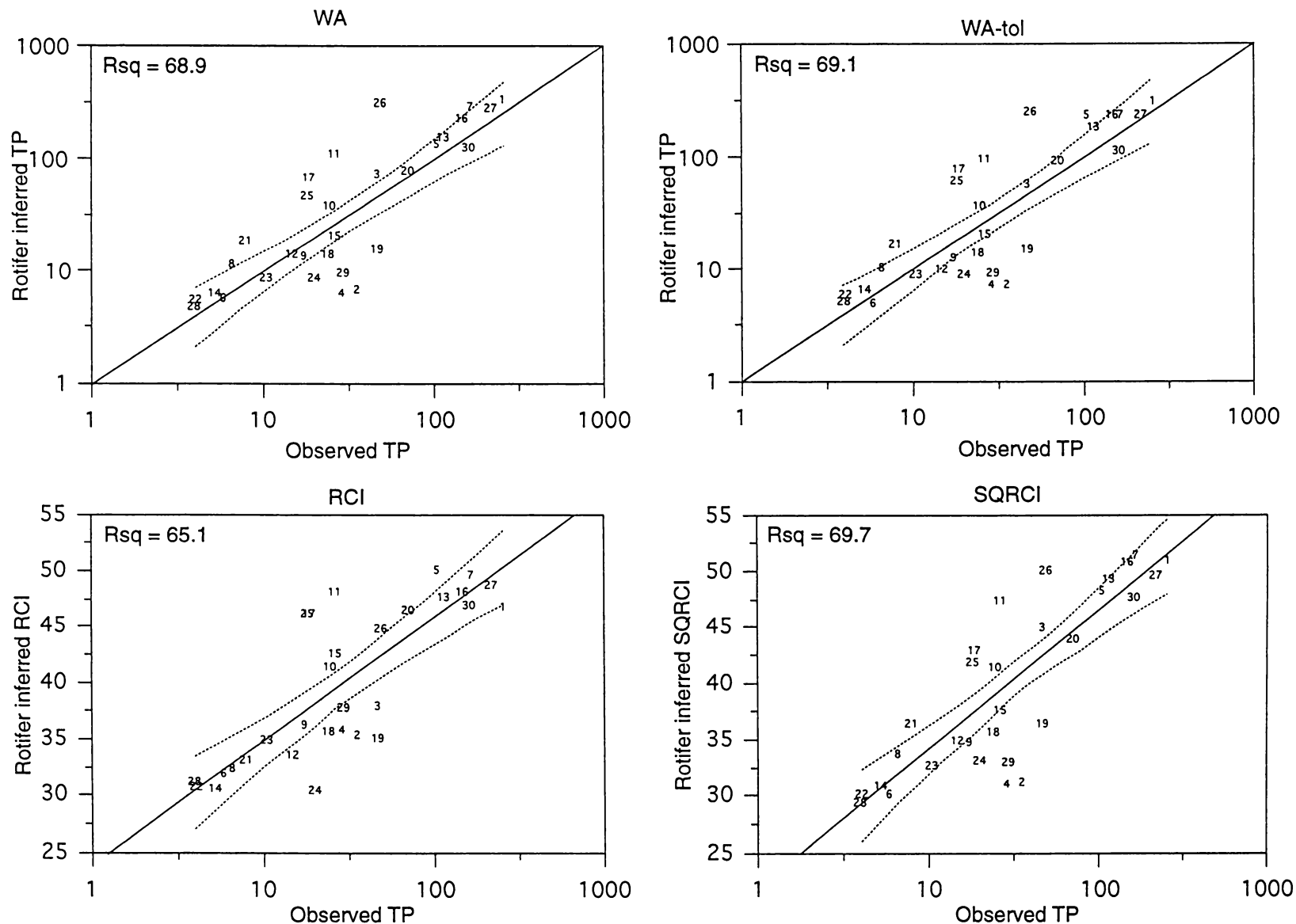


Figure 5.13. Plots of observed TP against inferred TP or RCI values from lakes, using 15 indicator taxa and deseasonalised samples, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

Removal of lakes that had poor TP: chlorophyll *a* ratios in general provided better results than the use of all samples (Fig. 5.14, Table 5.2). Using 14 indicator taxa (*Asplanchna sieboldi*, *Ascomorpha ovalis*, *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Brachionus quadridentatus*, *Conochilus dossuarius*, *Conochilus unicornis*, *Filinia longiseta*, *Keratella procurva*, *Keratella slacki*, *Keratella tecta*, *Keratella tropica*, *Polyarthra dolichoptera*, and *Trichocerca stylata*) decreased the RCI and WA-tol coefficients of determination, but increased WA and SQRCI correlations (Fig. 5.15, Table 5.2). Using deseasonalised samples also improved correlations (Fig 5.16, Fig 5.17, Table 5.3)

WA and WA-tol provided advantages over the RCI and SQRCI approaches because they give an inferred value which is more meaningful to the end user, i.e., an estimate of TLI or TP, with WA-tol generally providing superior coefficients of determination and predictive abilities than simple WA and other methods. Therefore, these results suggest WA-tol of rotifer communities provides an important avenue for determining lake trophic status. Weighted TLI and TP optima and tolerances for all rotifer species found in the present study are given in Table 5.4. Deshrinking equations are given in Table 5.5.

Discussion

In Chapter 4, trophic state was the environmental factor that was most strongly associated with the distribution of North Island rotifer species, as found on a smaller scale by Duggan *et al.* (in press) from the Rotorua area. TLI was the trophic state indicator found to most strongly associate with rotifer community composition. This is possibly because none of the single component indicators of this scheme (TP, chlorophyll *a* or Secchi transparency) accurately define trophic state alone, but the combination provided by TLI is a more reliable measure. This correlation between rotifers and TLI therefore perhaps gives confidence that the TLI scheme is a more reliable indicator of the trophic gradient than the individual indicators by themselves.

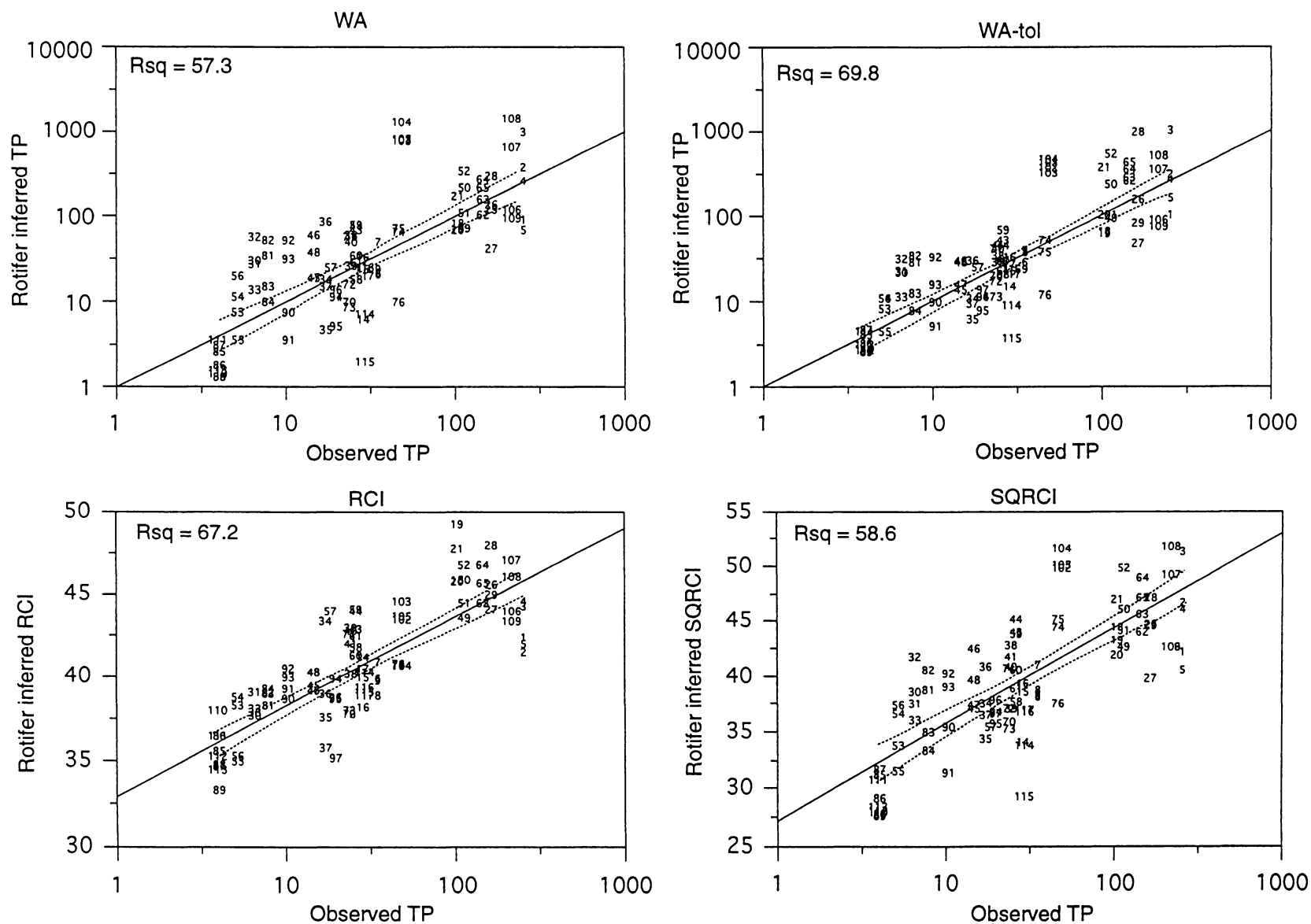


Figure 5.14. Plots of observed TP against inferred TP or RCI values from lakes, using all abundant species and with selected lakes removed derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

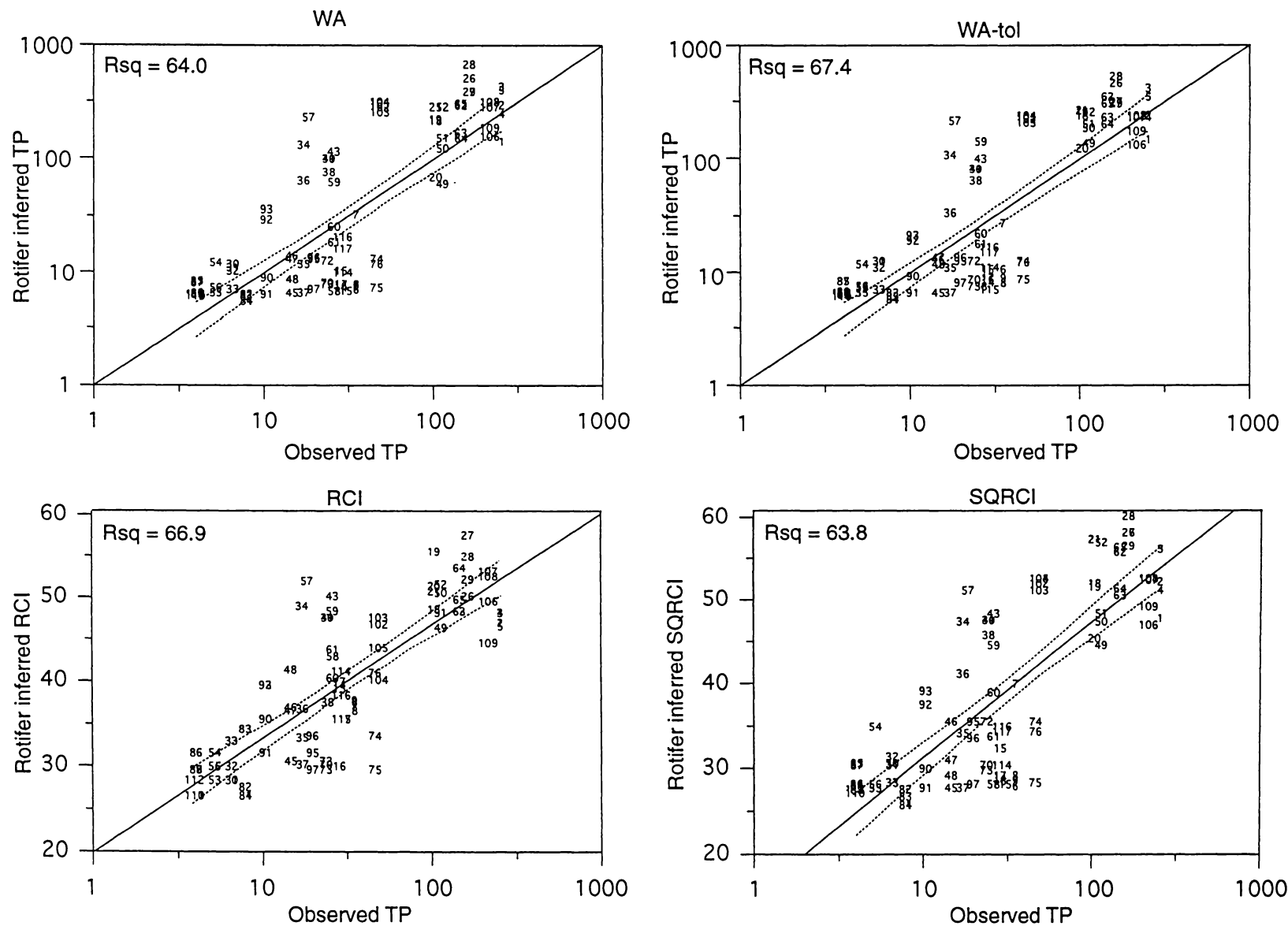


Figure 5.15. Plots of observed TP against inferred TP or RCI values from lakes, using 14 indicator taxa and with selected lakes removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

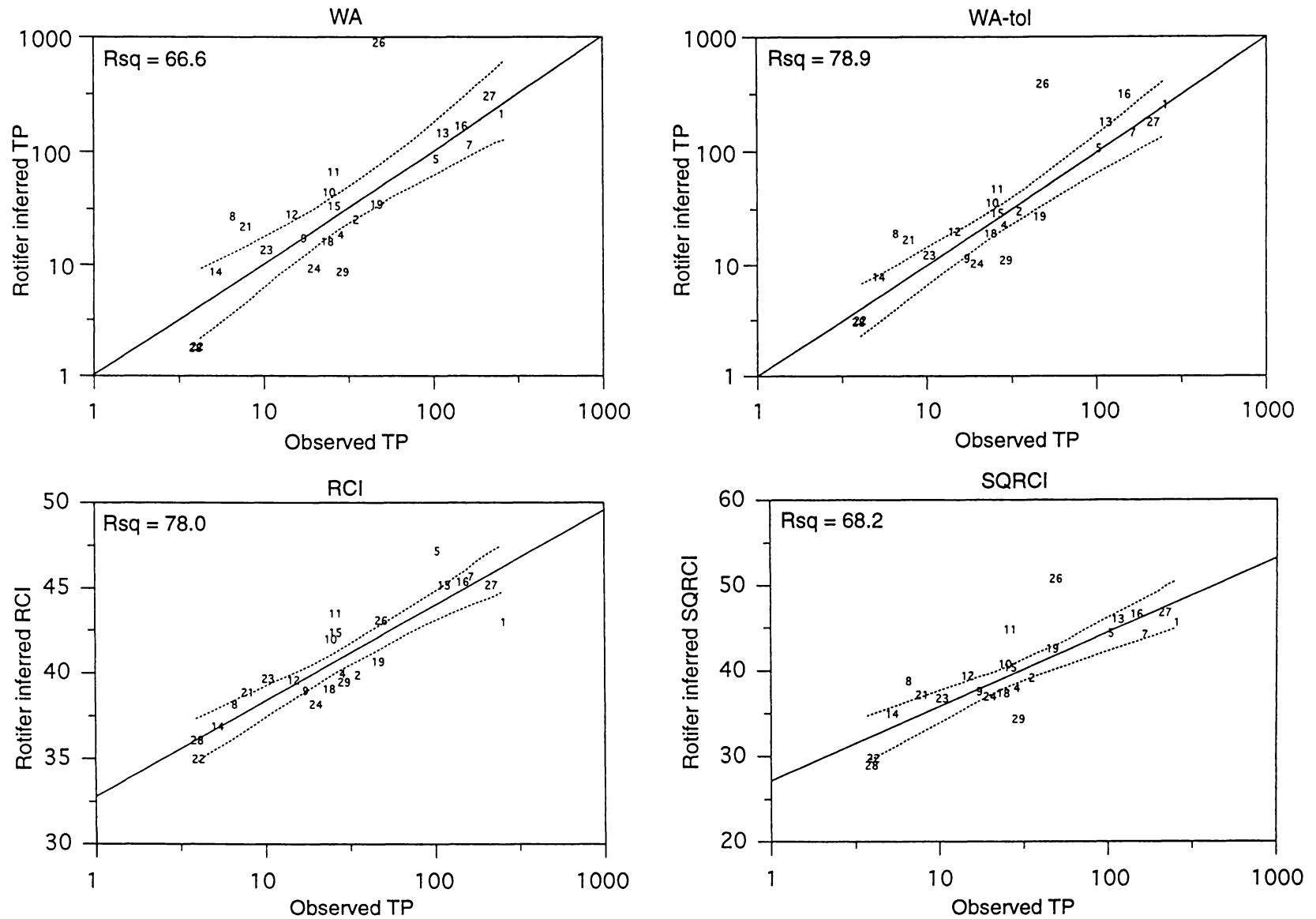


Figure 5.16. Plots of observed TP against inferred TP or RCI values from lakes, using all abundant species, deseasonalised, and with selected lakes removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

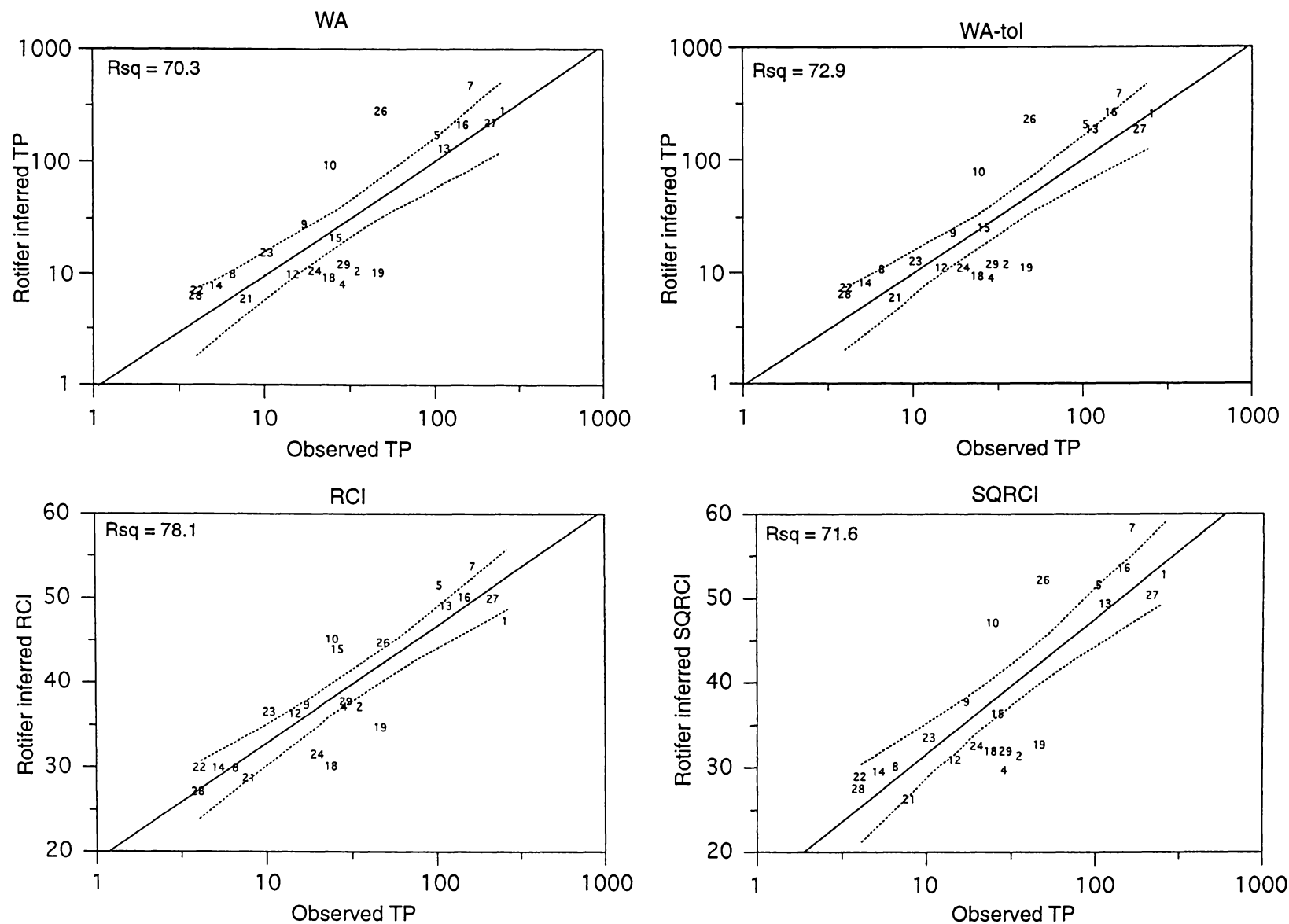


Figure 5.17. Plots of observed TP against inferred TP or RCI values from lakes, using 14 indicator taxa, deseasonalised, and with selected lakes removed, derived from WA, WA-tol, RCI and SQRCI approaches. Solid line indicates regression line, and dashed lines indicate 95 % confidence limits.

Table 5.4. Weighted average (WA) optima and tolerance data for TLI and log TP for abundant North Island rotifer species. Species are ordered by TLI optima.

Species	TLI optimum	TLI tolerance	log TP optimum	log TP tolerance
<i>C. dossuarius</i>	3.0989	0.9545	0.9298	0.3367
<i>S. longipes</i>	3.3232	0.3942	0.8248	0.1959
<i>P. dolichoptera</i>	3.4396	1.3568	1.0209	0.4582
<i>T. stylata</i>	3.7553	1.2586	1.1576	0.4779
<i>G. minor</i>	3.7921	0.3662	1.2863	0.0494
<i>C. unicornis</i>	3.8036	1.1211	1.1468	0.3838
<i>G. hyptopus</i>	3.8248	1.0634	1.3077	0.4117
<i>C. coenobasis</i>	3.9056	0.6608	1.1537	0.2498
<i>A. ovalis</i>	3.9558	0.8746	1.1930	0.2887
<i>L. closterocerca</i>	4.1376	0.5969	1.3155	0.2484
<i>L. bulla</i>	4.1650	0.7413	1.3663	0.3113
<i>T. patina</i>	4.3055	1.1250	1.4393	0.3850
<i>S. oblonga</i>	4.3875	1.2897	1.4413	0.5088
<i>A. priodonta</i>	4.4042	1.3888	1.3963	0.5336
<i>A. navicula</i>	4.4189	0.5391	1.2926	0.1438
<i>S. pectinata</i>	4.5011	0.9830	1.4084	0.4191
<i>Collotheca</i> sp.	4.5186	1.6649	1.4302	0.6438
<i>F. cf. pejlери</i>	4.5193	0.9545	1.3661	0.3989
<i>F. terminalis</i>	4.5290	0.1414	1.3582	0.1119
<i>H. mira</i>	4.6060	0.7787	1.3797	0.2433
<i>E. dilatata</i>	4.6508	0.5745	1.5075	0.2440
<i>T. tetractis</i>	4.6885	0.1556	1.5379	0.0588
<i>S. stylata</i>	4.6926	0.5304	1.4094	0.1623
<i>C. catellina</i>	4.6947	0.4421	1.3902	0.1501
<i>A. brightwelli</i>	4.6949	0.9757	1.5505	0.3346
<i>T. tenuior</i>	4.6982	0.1236	1.4110	0.1060
<i>T. porcellus</i>	4.7448	0.3732	1.5129	0.1748
<i>T. similis</i>	4.7747	0.9012	1.5281	0.3936
<i>A. fissa</i>	4.8205	1.1542	1.5031	0.2626
<i>K. cochlearis</i>	4.8324	1.1914	1.5409	0.4922
<i>F. novaezealandiae</i>	4.8392	1.4754	1.522	0.5400
<i>T. longipes</i>	4.8412	1.0207	1.5687	0.3820
<i>T. pusilla</i>	4.8556	0.7896	1.5177	0.3006
<i>H. intermedia</i>	5.0850	1.4825	1.7172	0.6057
<i>K. procurva</i>	5.2296	1.1108	1.6848	0.4185
<i>P. complanata</i>	5.2315	1.1958	1.6966	0.4811
<i>A. sieboldi</i>	5.6245	1.3073	1.9633	0.5067
<i>K. tropica</i>	5.8483	1.0890	1.9146	0.3702
<i>B. quadridentatus</i>	5.9200	0.9669	1.8585	0.3732
<i>K. slacki</i>	5.9414	0.9749	1.9917	0.3416
<i>K. tecta</i>	6.0166	1.1050	1.9384	0.4241
<i>B. calyciflorus</i>	6.1631	0.4242	2.0708	0.1229
<i>F. longiseta</i>	6.3957	0.7238	2.1733	0.3390
<i>B. budapestinensis</i>	6.5324	0.4540	2.2023	0.2498

Table 5.5. Coefficients for WA-tol classical deshrinking equations ($[x_{\text{final}} = (x_{\text{initial}} - \text{bo})/b1]$) for TLI and log TP.

	b0	b1
All species, all samples		
WA-tol TLI	2.932	0.371
WA-tol log TP	0.905	0.376
Reduced species, all samples		
WA-tol TLI	2.080	0.499
WA-tol log TP	0.660	0.534
All species, reduced samples		
WA-tol TLI	2.494	0.479
WA-tol log TP	0.810	0.456
Reduced species, reduced samples		
WA-tol TLI	2.508	0.499
WA-tol log TP	0.439	0.689

Many rotifer species were found to have preferences for either particular ranges or extremes in trophic state. For example, *Ascomorpha ovalis*, *Conochilus coenobasis*, *Conochilus dossuarius*, *Conochilus unicornis*, *Polyarthra dolichoptera* and *Synchaeta longipes* were found associated with low trophic state, and *Brachionus budapestinensis*, *Brachionus calyciflorus*, *Filinia longiseta*, *Keratella slacki*, *Keratella tecta* and *Keratella tropica* with high trophic state. Species found with poor statistical associations with trophic state in the current study may, however, also have distributions more indicative of trophic state that probably will become apparent once a larger data set is obtained. Species found to be indicative of high and low trophic state in general correspond with those found in studies elsewhere, e.g., Mäemets (1983), Sládecek (1983), Pejler (1983), and Berzins & Pejler (1989a). Pejler (1983) attributed species preferences along a trophic gradient to the size and nature of the particulate food present, with ultraoligotrophic rotifer species, e.g., *Conochilus*, predominantly feeders of minute algal particles, hypereutrophic species, e.g., *Brachionus*, predominantly feeders of bacteria, and those between these ranges feeders on coarser particles. However, as with phytoplankton communities, distribution of rotifer species along the trophic gradient is likely to be caused not by competition for a single factor, e.g., food type (or nutrients in the case of phytoplankton), but by the combined impacts of a variety of factors along the gradient (Reynolds 1998). Examples of this are

likely to include the appearance of toxic cyanobacteria (Snell 1980, Starkweather & Kellar 1987), the increased importance of predation on rotifers by *Asplanchna* (Ejsmont-Karabin 1974, Pejler 1983) and the degree of oxygen depletion (e.g., Berzins & Pejler 1989c, Mikschi 1989) with increasing trophic state. The sum of these factors will weigh in favour of the growth and survival of a particular suite of rotifer species.

Based on the relationships between rotifer species composition and lake trophic state, rotifers have previously been suggested as bioindicators, although trophic state inference in these studies has generally been fairly coarse (e.g., Mäemets 1983, Matveeva 1991). These studies relied on the simple comparison of rotifer composition with species lists of indicative taxa. Sládecek (1983) suggested a more quantitative method that used the ratio of the number of species of *Brachionus* to *Trichocerca*, based on his findings that *Brachionus* are associated with eutrophic waters and *Trichocerca* with oligotrophic waters. However, because this relationship will generally be based on a limited number of species, it too is likely to provide only a very coarse measure. Further, *Trichocerca* species were, in general, not found to be indicative of oligotrophic conditions in my study. Another problem with Sládecek's method is that *Brachionus* species are known to be limited in their global distribution (e.g., Dumont 1983). This is very likely to affect the relationship from place to place. Biotic score systems, based on community composition, have generally been preferred over indices based on either single indicator taxon or diversity measures in freshwater biomonitoring (e.g., Armitage et al. 1983, De Pauw & Vanhooren 1983, Stark 1985). Score systems are based on the responses of a number of species to environmental gradients, with inferred conditions based on those present in a sample, but not affected by species absence. Rotifer species are in general cosmopolitan in distribution, and there is a similarity between species – trophic state relations shown in this and other studies. The development of a score system for assessing lake trophic state based on North Island rotifer species may be relevant not only in the geographical area of development, but also possibly elsewhere with little or no modification. This provides advantages over bioindicator

schemes using macroinvertebrates as these species, and therefore indices, are generally regionally specific (cf. Armitage *et al.* 1983, Stark 1985).

Based on the distribution of species documented in this study, models using the WA-tol method generally provided the highest coefficients of determination and had superior predictive abilities compared with the other schemes. WA-tol gives better results because, without the removal of rare species, those with narrow tolerances are given a greater weighting than those with wider tolerances. Ideally, indicator species need to have narrow tolerances to the variable of interest (Rosenberg & Resh 1993), and WA-tol gives preference to these. This scheme also results in a numerical value of more use to freshwater managers than results obtained from the RCI or SQRCI approaches, because it provides inferences of commonly used measures of trophic state such as TP and TLI. This therefore appears to be the best useable method for inferring trophic state from rotifer community composition.

For biomonitoring schemes to provide advantages over the traditional methods of assessment, the time required for processing samples, and therefore the cost, must be comparatively low while still providing an acceptably reliable assessment of the variable of interest. The identification of a subset of species which best indicate the trophic gradient was explored as a method of rapid assessment to attempt to overcome the time consuming requirement to identify and enumerate many species of rotifer. In doing this, however, the predictive abilities of schemes were generally reduced, perhaps because too few species were recognised as being indicative of environmental conditions (between 10 and 14 only in different schemes), perhaps because models were being developed from a relatively small number of samples. A greater knowledge of the optimal conditions and tolerances of North Island rotifer species, obtained from more intensive sampling from a larger number of lakes at finer temporal intervals than in the current study, is likely to lead to a greater number of species which may be considered as indicative of trophic state. Increasing the number of indicator taxa in this way will provide a greater compromise between having too

many species to be of practical use, or too few for reliable assessment of trophic state. If a balance can be achieved, rotifers have the potential to provide good bioindicators of lake trophic state.

As stated in Chapter 4, it was found that rotifer communities within lakes from different seasons are usually more similar than communities between lakes. Bioindicator schemes might thus be expected to provide similar assessments of trophic state from both a single sample and combined seasonal samples. However, better relationships were found between deseasonalised rotifer inferred and observed TLI or TP values than models using single samples. The short life cycles, seasonal variability, and sensitivity to environmental conditions of rotifer species are therefore perhaps too great to allow adequate or confident assessment of trophic state from single samples alone. A practical bioindicator technique is likely to find favour if it requires assessment from single or few samples, so reducing effort and cost (Hellawell 1986, Johnson *et al.* 1993). The need for enumeration of samples at various times of the year may therefore lead to the technique being time consuming and costly without providing the advantage of reliable rapid assessment. However, trophic state assessment using TP and chlorophyll *a* should be generally assessed from at least twelve measurements throughout a year, so the need for collection of rotifer samples only once from each season still may be advantageous. The use of bulked rotifer samples may be a practical option also, although the accuracy of this needs to be assessed.

Despite the discrepancies between the rotifer-inferred and observed values of trophic state, these differences were often not large. Some inferred values were, however, found to deviate markedly from those observed, and these deviations are a disadvantage to the scheme at this point of development. Such deviations presumably can result because variations in rotifer community composition along a trophic gradient are caused by a multitude of factors, not only nutrient concentrations or the other factors involved in the TLI. For example, these changes in rotifer composition may reflect variations in DO,

bacteria and phytoplankton composition, zooplankton composition, etc, along the trophic gradient. Such aspects are not apparent when assessing trophic state by the traditional trophic classification schemes (and to a lesser extent TLI), with rotifer indices, for example, likely being better indicators of the biological response. The rotifer indices in general performed best at the high and low ends of the trophic gradient, and more poorly in between. Extreme ends of the trophic gradient may have communities made up of rotifer species with narrow preferences for the various trophic state variables, and because in these water bodies food is the most distinctive with a predominance of either small algal particles or bacteria (e.g., Pejler 1983). As a result, the inferred trophic state values are most accurate in these areas. However, within the meso-eutrophic states, the indices performed more poorly, perhaps because most species had broader distribution ranges. This may be because rotifer feeding is in general not specific to certain species of phytoplankton, and species can therefore obtain their nutritional requirements over a range of trophic state in which, for example, phytoplankton is of a similar size (e.g., Pejler 1983). The distribution of such species may therefore be affected only by substantial variations in trophic state, providing poorer indicators in the mesotrophic to eutrophic range. The current scheme may thus provide a useful indicator only where large changes in trophic state produce observable changes in rotifer composition. From a management perspective, where it is preferable to assess small changes or variances in trophic state, this scheme will be most reliable only at the upper and lower ends of the trophic state spectrum.

As with Stark's (1985) MCI index, development of the rotifer indices are based on relative species abundances. The current approach could be improved by basing the indices on truly quantitative samples. Total rotifer abundance is known to increase with trophic state (e.g., Orcutt & Pace 1984, Andrew & Fitzsimons 1992, and see Chapter 3), and is suggested by Matveeva (1991) to be more indicative of trophic state than lists of species indicators (e.g., those of Mäemets 1983 and Berzins & Pejler 1989a). Perhaps because the composition and relative abundance changes documented in this study were not marked

enough in mesotrophic to eutrophic ranges, the incorporation of true abundances is more likely to detect subtle changes in trophic state. Some of the variability in the inferred values also may be attributed to the small number of samples upon which these were calibrated. Pridmore (1987) suggests assessment of trophic state should be made using at least twelve measurements of TP or chlorophyll *a* over a year. Generally only four were used in the present study, and this is likely to have affected both development of the rotifer indices and the interpretation of relationships derived from them. A greater number of rotifer samples and associated trophic state variables are therefore likely required to provide better correlations and a more reliable index. However, although deviation was apparent between observed and rotifer inferred environmental variables, for some lakes there were found to be poor relationships between the traditional trophic indicators (TP and chlorophyll *a*). Better relationships between the observed and rotifer inferred environmental variables were found when lakes with poorly related TP and chlorophyll *a* concentrations were removed. Poor coupling of these variables in some lakes may be due to nitrogen rather than phosphorus limitation (e.g., Pridmore 1987, White *et al.* 1985, 1986), and/or through increased turbidity due to mineral seston (Hamilton & Mitchell 1988).

The close relationship between the rotifer indices and trophic state variables indicates that rotifers have potential as bioindicators of lake trophic state in the North Island of New Zealand. The advantage of rotifer indices developed here over the TLI is that they require the measure of a single factor, compared with the TLI, which requires assessment of four components measured a number of times over a year. Thus there is a saving in both time and cost. I suggest that the WA-tol method be used for determining lake trophic state from rotifer samples, with samples taken from different seasons over a year. Determination of rotifer inferred TLI and TP should be based on that assessed from each of these samples, averaged to provide a single value for the lake. However, the index still needs refinement because of its lack of precision in the mesotrophic to eutrophic range. To develop this protocol further a greater number of samples from a wider number of lakes

need to be assessed so as to provide the best estimates of the optima and tolerances of as many species as possible. In this way the best possible subset of species can be ascertained that will result in a workable, inexpensive assessment method.

Chapter 6:

Comparative resting egg densities in lakes of different trophic state, and their assessment using emergence and egg counts.

Introduction

Fluctuating environments can lead to the periodic occurrences of conditions detrimental or lethal to the organisms that inhabit them. Rotifers overcome these times by the production of resting eggs, which fall onto the bottom sediments of lakes and hatch on return to favourable conditions. Cues for hatching vary between species but in freshwater rotifers hatching is generally thought to be influenced by light and temperature. Few studies have documented the densities of rotifer resting eggs in lakes. They have generally been assessed by directly counting eggs, and have been found to range widely between studies (Pourriot & Snell 1983). By incubating sediment samples, May (1987) was able to infer resting egg densities from the number of rotifers emerged and, similarly, May (1986) obtained species lists equivalent to those found from four years study of the populations in Loch Leven, Scotland. To date, however, studies on rotifer egg banks have been from a limited array of sites, making results rather site-specific. Variation in egg densities caused by environmental gradients such as trophic state, for example, is unknown.

This chapter compares the results of using different methodologies for the assessment of resting egg densities, and reports on the variability of resting egg densities in lakes of different trophic state. The examination of resting eggs, and species recorded from incubation of sediments, are also assessed as tools for documenting rotifer community composition from single sampling visits.

Materials and methods

Sampling was conducted on 5 January 1999 from single sampling sites in eutrophic Lake Okaro and oligo - mesotrophic Lake Tikitapu, from depths of approximately 12 m and 25 m respectively. Sediment was collected using a 155 × 160 mm Ekman grab, and the top 5 cm of sediment was carefully removed from the grab. 20 L of surface water was taken for culture media in hatching experiments, with an additional 20 L water collected on 14 February.

On return to the laboratory, the sediment collected from each lake was mixed thoroughly. Using a syringe 30 mL subsamples were removed into twelve 250 mL Ehrlenmeyer flasks for incubation for hatching, and an additional twelve were placed in 120 mL containers and stored in a refrigerator (< 4 °C) until required for counting (no longer than two weeks).

Sediment for hatching was treated similarly to that in studies by May (1986, 1987). Surface water collected from the lakes was glass-fibre filtered (G/FC) and added to sediment in the Ehrlenmeyer flasks to give a final volume of 250 mL. Four flasks were placed in each of three temperature controlled water baths at 10, 15 and 20 °C under artificial light (fluorescent and incandescent, L:D = 12:12). At three day intervals (four on one occasion) the water in each flask was carefully decanted and passed through a 40 µm mesh screen to collect rotifers. Water in flasks was replaced alternately with fresh filtered lake water or by re-adding the water from the previous incubation. Rotifers emerging from each sample were counted and identified using stereo and compound microscopes (see Chapter 3 for details of enumeration and identification).

For assessment of resting egg densities in sediment, eggs were separated by sugar flotation (Onbe 1978). Samples were shaken in the 120 mL container with some added water, and filtered through a 20 µm mesh screen until excess water was removed. The material remaining was washed into centrifuge tubes using a 1:1 mixture (w:v) of table sugar with RO water, and spun in a clinical centrifuge for 4 minutes at the #3 setting

(approximately 2500–3000 RPM). The material remaining suspended in the sugar was washed thoroughly through a 20 µm mesh with RO water and transferred to a counting tray for immediate enumeration under the stereo microscope. Eggs were grouped according to size and morphology. Representatives of each were removed to an Olympus BX50 compound microscope, and images were captured and transferred to computer using a COHU high performance CCD camera and Perceptics Pixelbuffer grabber board, manipulated using IPLab Spectrum 3.1 software. For identification, eggs of each type (20–50 eggs where possible) were separated into small vials (10–20 mL) and incubated as above, or by comparison with diagrams from the published literature.

The variations in abundances of rotifers between lakes or methodologies were assessed using two-sample *t* tests or one-way ANOVA followed by Bonferroni multiple comparisons tests on log or cuberoot transformed abundance data. Statistical analysis was carried out using the program InStat (Graphpad software 1993).

Results

Hatching

The hatching experiment was terminated after 82 days of incubation. Thirteen species in total emerged from Lake Tikitapu, and 25 from Lake Okaro (Table 6.1). These include two species from Lake Tikitapu, *Cephalodella mucronata* and *Dicranophorus edestes*, and two from Lake Okaro, *L. luna* and *Cephalodella ventripes*, not found from these lakes in the seasonal study (Chapter 3). A number of species found to be abundant in the seasonal study (comprising > 4 % of any sample) were not found to emerge in this study, including *Ascomorpha ovalis* and *Synchaeta pectinata* from both lakes. In addition to rotifers, gastrotrichs were found in both lakes, but commonly in great abundance in Lake Tikitapu samples. Cladocera, copepod nauplii, and individual tardigrades also were found from each lake.

Table 6.1. Rotifer species hatched from incubated sediments from; a. Lake Tikitapu, and b. Lake Okaro.

a.

<i>Cephalodella catellina</i> (Müller, 1786)	<i>Lepadella patella</i> (Müller)
<i>C. mucronata</i> Myers	<i>Pompholyx complanata</i> Gosse
<i>Coleurella uncinata bicuspidata</i> (Ehrenberg)	<i>Polyarthra dolichoptera</i> Idelson
<i>Dicranophorus edestes</i> Harring & Myers	<i>Synchaeta oblonga</i> Ehrenberg
<i>Filinia</i> cf. <i>pejleri</i> Hutchinson	<i>Trichocerca similis</i> (Wiszniewski)
<i>Hexarthra mira</i> (Hudson)	<i>T. pusilla</i> (Jennings)
<i>Keratella cochlearis</i> (Gosse)	<i>T. stylata</i> (Gosse)
<i>Lecane lunaris</i> (Ehrenberg)	

b.

<i>Asplanchna priodonta</i> Gosse	<i>Keratella slacki</i> (Berzins)
<i>A. sieboldi</i> (Leydig)	<i>K. procurva</i> (Thorpe)
<i>Brachionus angularis</i> Gosse	<i>K. tropica</i> (Apstein)
<i>Cephalodella gibba</i> (Ehrenberg)	<i>Lecane luna</i> (Müller)
<i>C. ventripes</i> (Dixon-Nuttall)	<i>Lepadella patella</i> (Müller)
<i>Collotheca</i> sp.	<i>Pompholyx complanata</i> Gosse
<i>Filinia longiseta</i> (Ehrenberg)	<i>Polyarthra dolichoptera</i> Idelson
<i>F.</i> cf. <i>pejleri</i> Hutchinson	<i>Synchaeta oblonga</i> Ehrenberg
<i>F. terminalis</i> (Plate)	<i>Trichocerca similis</i> (Wiszniewski)
<i>F. novaezealandiae</i> Shiel & Sanoamuang	<i>T. pusilla</i> (Jennings)
<i>Hexarthra intermedia</i> (Wiszniewski)	<i>T. stylata</i> (Gosse)
<i>Keratella cochlearis</i> (Gosse)	

Temperature affected total abundances and emergence patterns of rotifers in Lakes Tikitapu and Okaro (Figs 6.1 & 6.2). In Lake Okaro, there was a lag in hatching at all temperatures until days 21–30 when the emergence began to increase dramatically at all temperatures. Emergence rates generally increased until days 40–43, then slowed until few hatchings were recorded after day 67 until termination. In Lake Okaro, no more than 4 % of the cumulative totals hatched from any replicate over the last 18 days of incubation. Emergence was generally greatest at 15 °C and lowest at 20 °C. At termination of the experiment, there were significantly greater ($P < 0.01$) rotifers hatched from 15 °C samples, than 20 °C (total densities of 161.62 eggs cm⁻³ and 100.13 eggs cm⁻³ respectively). Assuming that the sediment sample was 5 cm thick, these densities equate to surface area measures of 6.60 and 4.13 mm⁻² respectively. Total numbers emerging were lower from Lake Tikitapu samples than Lake Okaro samples. In Lake Tikitapu peaks in emergence

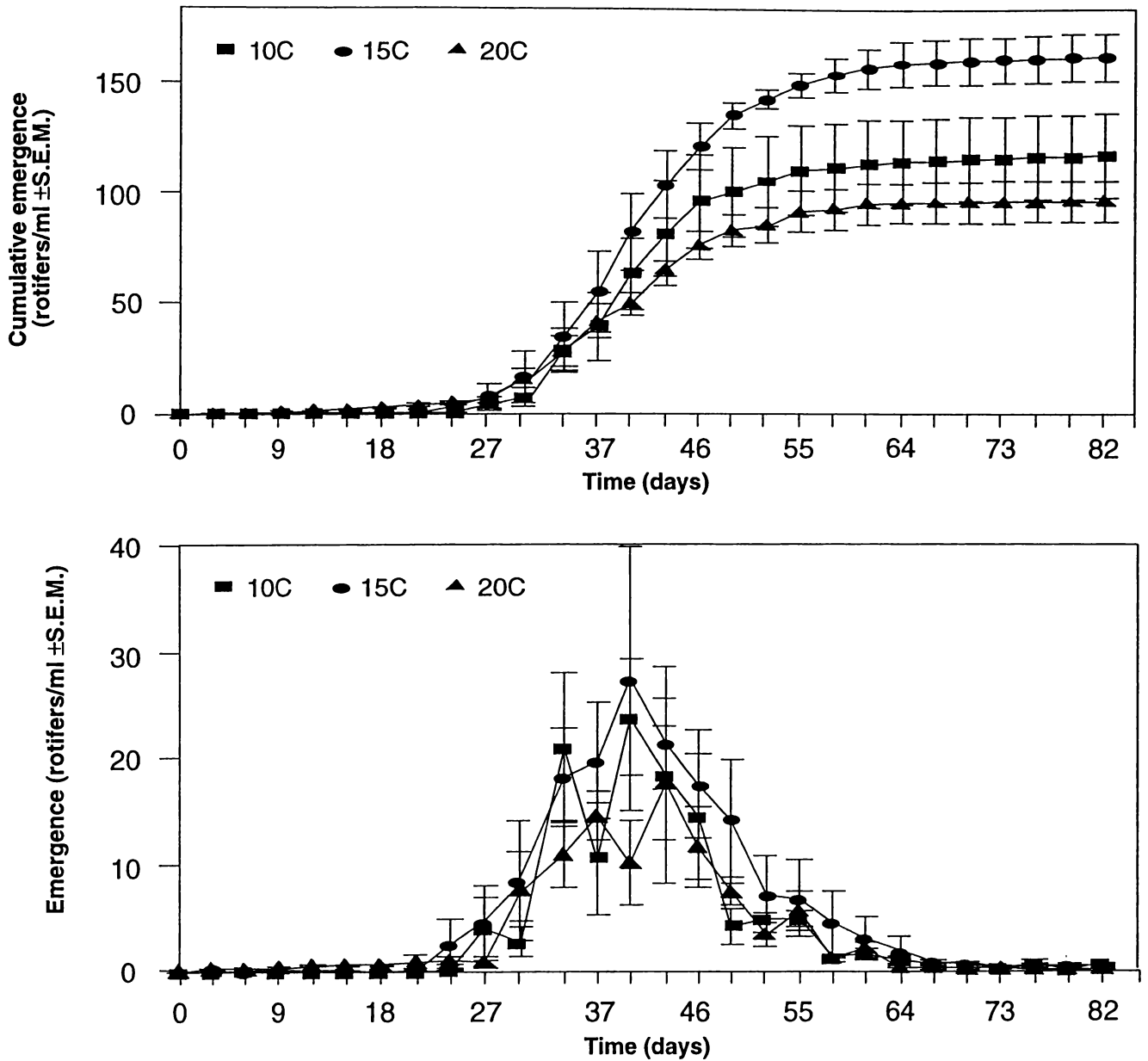


Fig. 6.1. Cumulative total emergence, and total emergence from each examination of rotifers from Lake Okaro sediment.

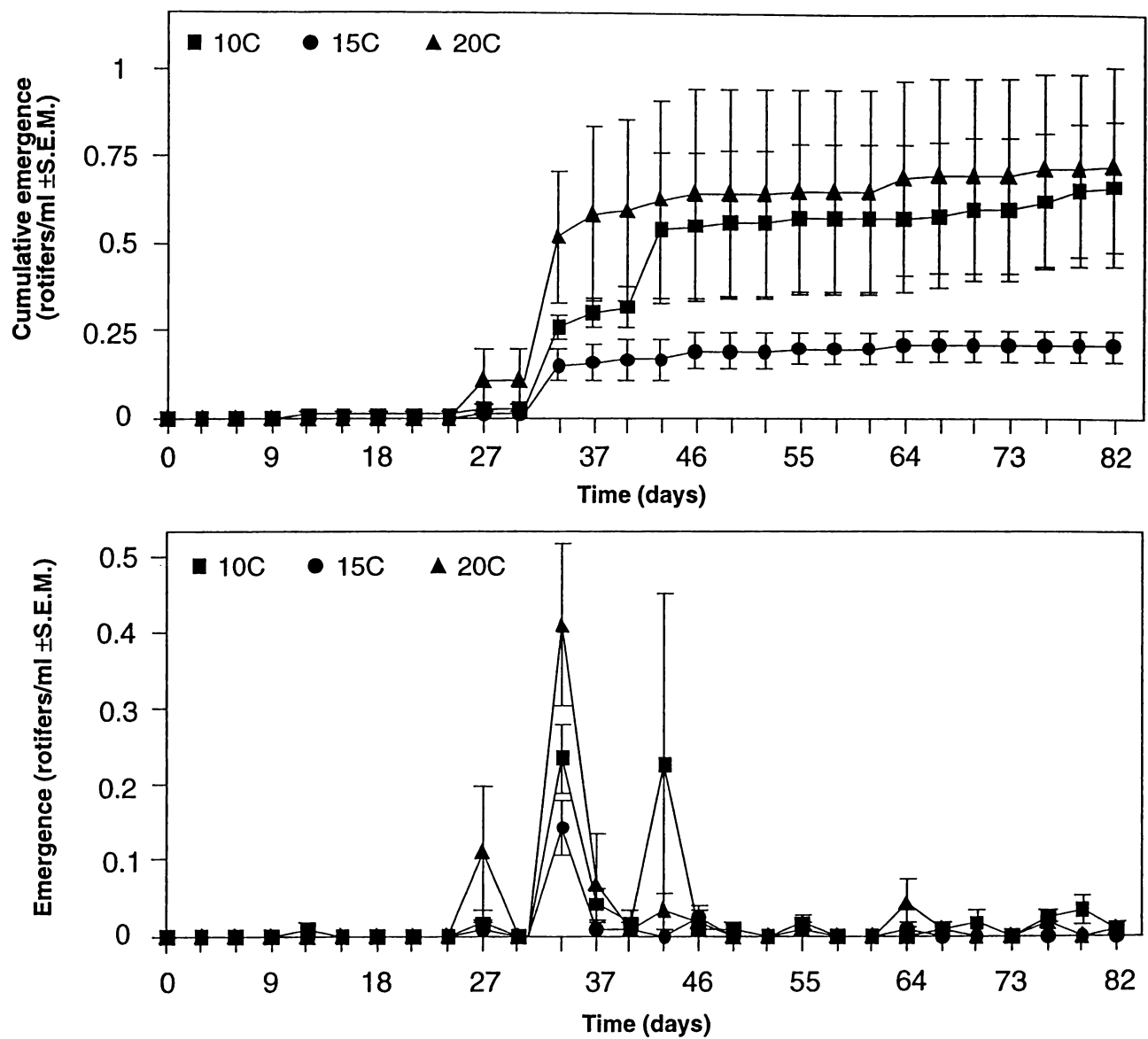


Fig. 6.2. Cumulative emergence, and total emergence from each examination of rotifers from Lake Tikitapu sediment.

occurred between days 27 and 43 (Fig. 6.2). In contrast to Lake Okaro, greatest hatching occurred in the 20 °C samples (average 0.73 eggs cm⁻³) and lowest at 15 °C (0.21 eggs cm⁻³). At termination, the total abundance in the 15 °C samples were significantly lower ($P<0.05$) than in the other two incubation temperatures.

The effect of temperature on the emergence of abundant rotifer species (i.e. those attaining total average densities greater than 4 eggs cm⁻³ at any temperature at termination) in Lake Okaro only, are shown in Fig. 6.3. The effect of temperature on the emergence of rotifers varied from species to species. *Synchaeta oblonga* constituted the vast majority of the total hatchings, and emergence patterns of this species are therefore similar to those of total Lake Okaro rotifer emergence. The total numbers of *S. oblonga* at termination were significantly greater ($P<0.05$) at 15 than 20 °C. *Pompholyx complanata* showed similar trends to *S. oblonga*, although differences between incubation temperatures were not significant. *Hexarthra intermedia* did not have the long lag period shown by the other species, emerging from the beginning of the experiment at 20 °C. Emergence in the 10 and 15 °C samples increased after day 40. The 20 °C samples had the greatest emergence until day 55 when 15 °C became greater. The 10 °C samples were significantly lower ($P<0.05$) than the other two incubation temperatures at termination.

Egg Counts

A variety of organic material was separated from the sediments using sugar flotation. Lake Tikitapu sediments contained many pollen grains, oligochaetes, nematodes, charophyte oospores, cladoceran ephippia and copepod eggs. Lake Okaro contained oligochaetes and nematodes (though far fewer than did Lake Tikitapu), cladoceran ephippia and copepod eggs. All other eggs were assumed to be rotifer resting eggs.

Total counts of rotifer eggs were significantly higher ($P<0.01$) in Lake Okaro (311.32 eggs cm⁻³) than Lake Tikitapu (2.03 eggs cm⁻³). Nine eggs from Lake Tikitapu

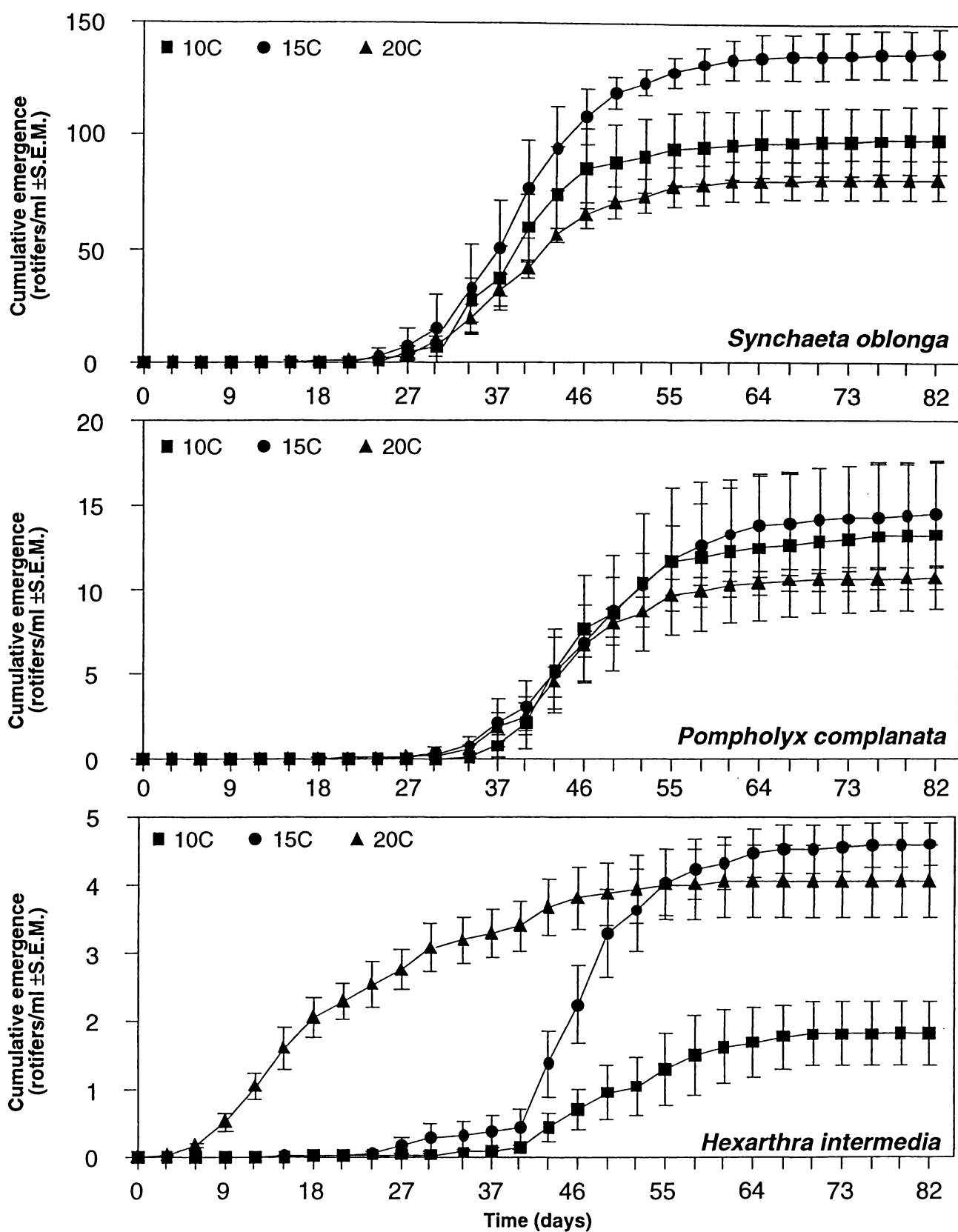


Fig 6.3. Cumulative emergence of abundant species from Lake Okaro sediment.

and seven from Lake Okaro were grouped according to size and general morphology (Fig. 6.4 a-c). Fewer egg types were therefore distinguished than species were hatched for either lake. In an attempt to hatch eggs separated into vials based on morphology, only egg 5 from Lake Okaro hatched, and was identified as *Hexarthra intermedia*. Examination of specimens from the seasonal study positively identified egg 1 from Lake Tikitapu and two eggs from Lake Okaro (not figured) as belonging to *Filinia* species, and egg 5 from Lake Okaro as a *Hexarthra* species (as hatched). Comparison of the morphology of the remaining eggs with diagrams from the published literature, indicated that eggs 4 and 9 from Lake Tikitapu are likely to be from *Conochilus* and *Ptygura* species, respectively, and egg 7 possibly from an *Encentrum* species (Koste 1978). However, no species from these genera were found in the hatching experiment. Egg 3 from Lake Okaro is likely to be from an *Asplanchna* species. The remaining eggs could not be ascribed to taxa with any confidence, due to the published illustrations of many eggs showing considerable variations in morphology within and between genera and species. Intra-species egg variation appears to be large in *Synchaeta oblonga*, for example, which have been illustrated shaped from round to oval or irregular (e.g., Nipkow 1961, Koste 1978, Pontin 1978). Between genera, the short spined Egg 3 from Lake Tikitapu appears similar to illustrations of, for example, *Rhinoglena frontalis* by Varga (1929), *Brachionus leydigi* by Rousselet (1907), and *Proales parisi* by Budde (1925). However, this egg also appears dissimilar to illustrations of those from any species known from this lake (from emergence or sampling).

Significantly greater eggs densities were obtained when assessed using sugar flotation and counting of eggs than from hatching at any temperature ($P < 0.01$) (Fig. 6.5).

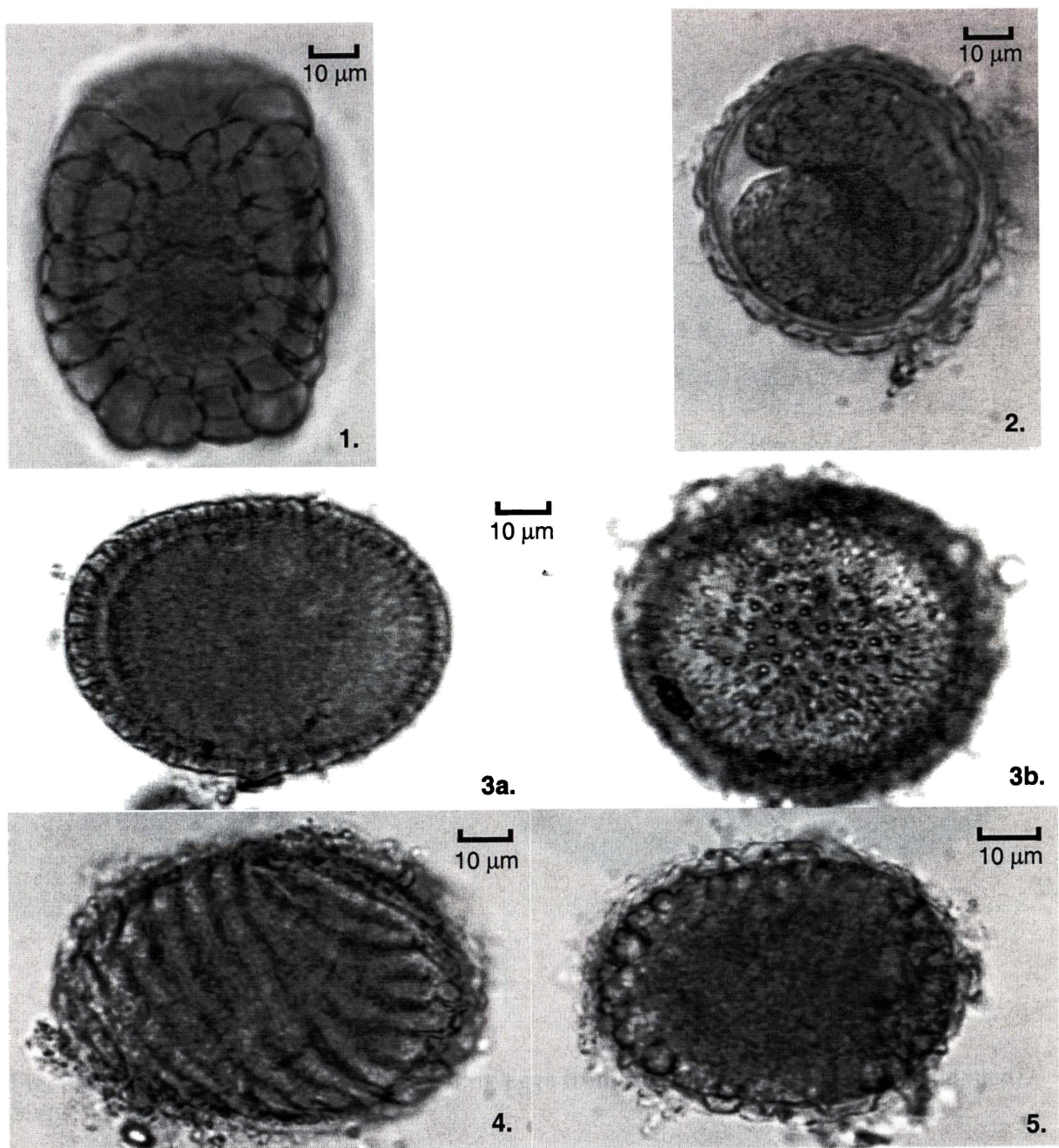


Fig. 6.4 a. Variety of morphology in resting eggs from Lake Tikitapu sediment. Suggested species are given in text.

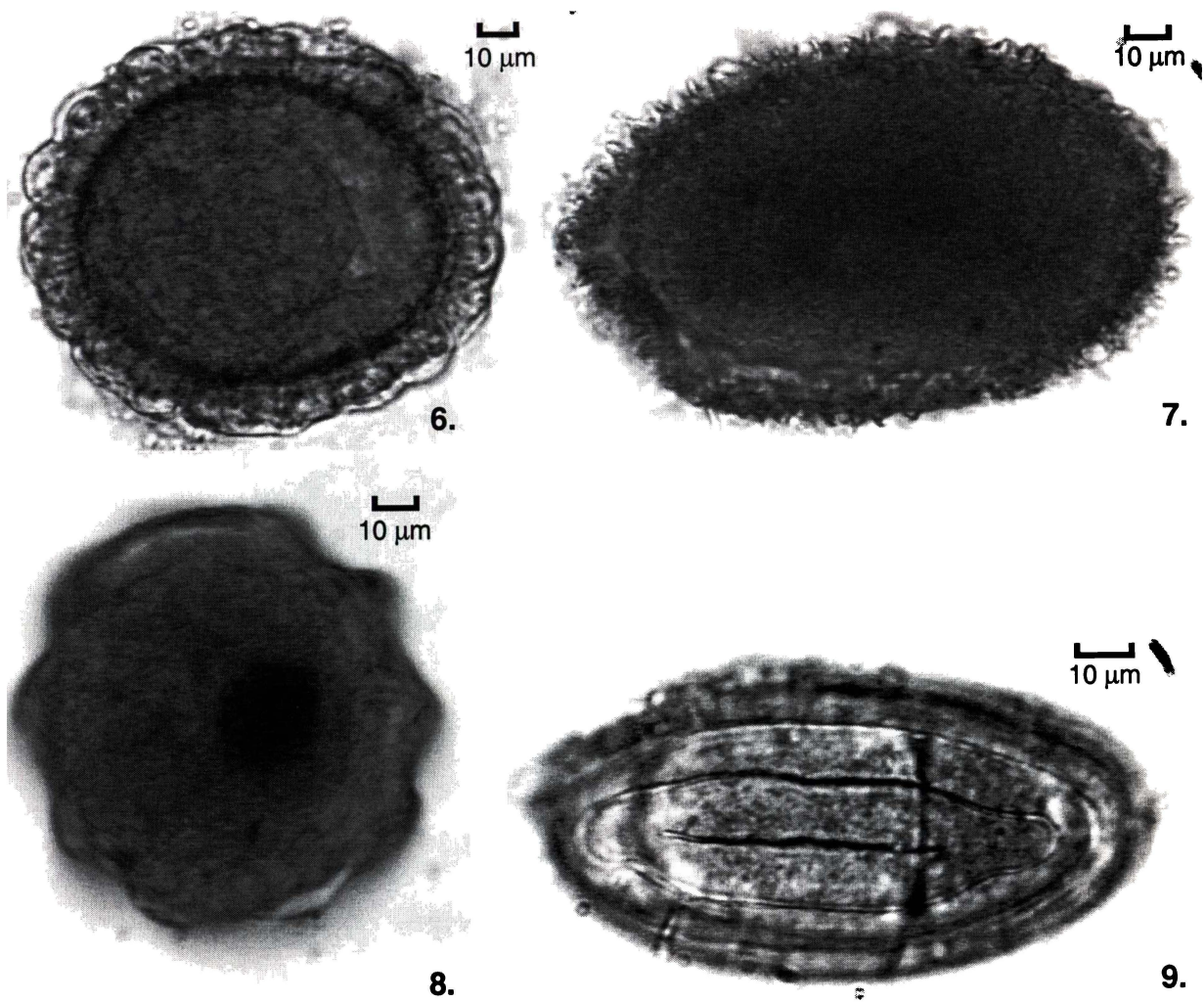


Fig. 6.4 b. Variety of morphology in resting eggs from Lake Tikitapu sediment (continued). Suggested species are given in text.

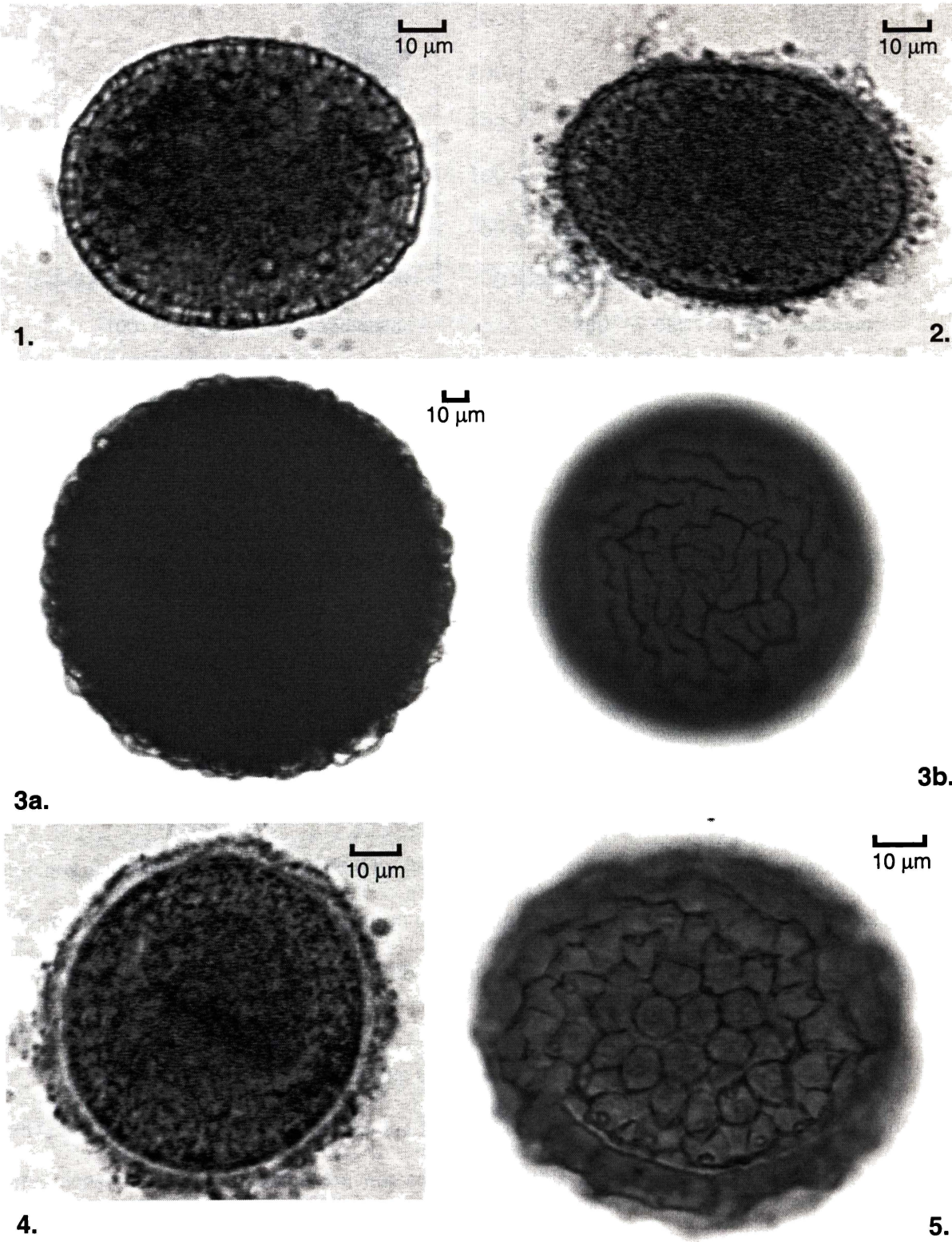


Fig. 6.4 c. Variety of morphology in resting eggs from Lake Okaro sediment. Suggested species are given in text.

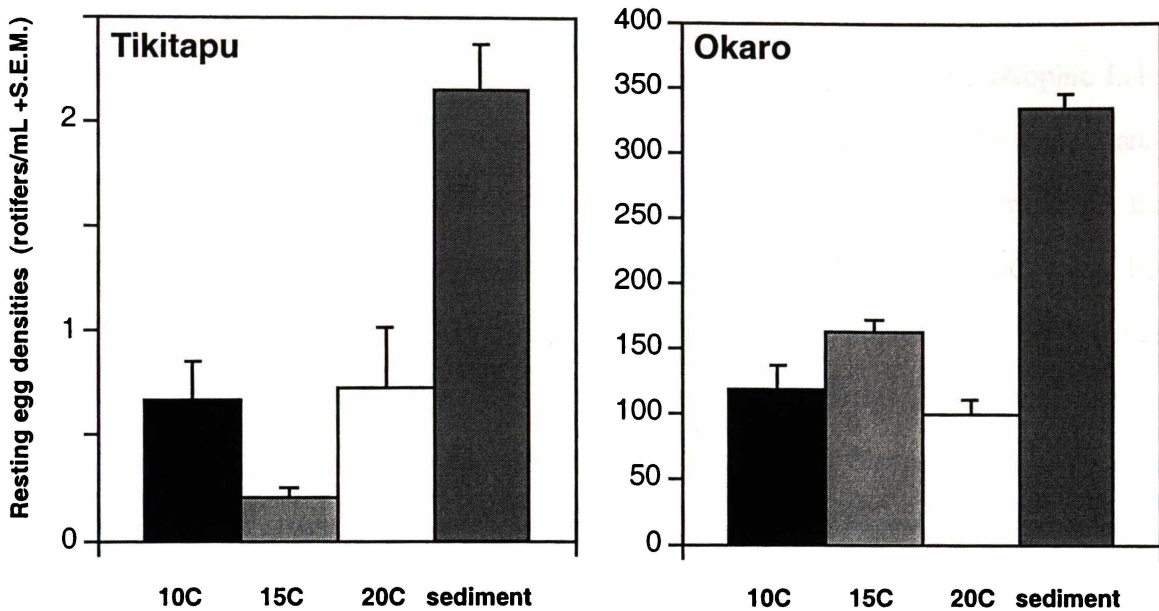


Fig. 6.5. Comparative total resting egg densities estimated by hatching at different temperatures versus counts from sediments from Lake Tikitapu and Okaro.

Discussion

There was a large difference in the densities of resting eggs between oligo - mesotrophic Lake Tikitapu and eutrophic Lake Okaro, with densities in Lake Okaro generally greater than two orders of magnitude higher. This is no doubt largely due to the higher densities of rotifers which can be sustained in Lake Okaro because of higher food levels associated with higher lake trophic state (Chapter 3), and therefore greater numbers of individuals are able to produce resting eggs at the onset of unfavourable conditions (Pourriot & Snell 1983). Densities also may have been affected by the differential effect of predation on resting eggs in the sediment. No evidence of predation on resting eggs by, for example, oligochaetes or nematodes, which were found higher in abundance in Lake Tikitapu compared than in Lake Okaro, could be found in the literature.

Total rotifer emergence from Lake Okaro was far higher than those hatched by May (1987) from eutrophic Loch Leven ($2.2\text{--}13.9\text{ cm}^{-3}$). This may be because factors limiting rotifer densities in Loch Leven are not apparent in this lake, for example lower trophic

state, lower temperatures or perhaps predation by planktivorous fish or invertebrates. Densities in Loch Leven are however higher than those found in oligo – mesotrophic Lake Tikitapu. Although densities of resting eggs could not be accurately related to surface area because of the methodology used in sediment collection, estimates can be made on the assumption that samples were taken from 0 to 5 cm depth. The values obtained, $8.7 \times 10^3 \text{ mm}^{-2}$ in Lake Tikitapu and 13.42 mm^{-2} in Lake Okaro, are comparable with densities ranging from trace to $9.66 \text{ eggs mm}^{-2}$ obtained by Ito (1958) from 15 Japanese ponds. Highest densities of a single species estimated by hatching in the present study were of *Synchaeta oblonga*, ranging between 3.30 and $5.59 \text{ eggs mm}^{-2}$ at 20 and 15°C respectively (although the actual egg count for this species may have been substantially higher), far lower than densities of the same species of $30\text{--}40 \text{ mm}^{-2}$ found by Nipkow (1961).

May (1987) thought one reason for differences between densities found in her study and those using counts from sediment were methodological, and stated the need for comparison. In my study, significantly higher estimates of resting egg numbers were made by counting resting eggs removed using sugar flotation than were found in counts of rotifers emerging from incubated sediment at any temperature. Lower density estimates may be obtained from hatching of eggs because not all eggs may be viable in the sediment, the stimulus for hatching may vary from species to species and optimal conditions for many may not have been met, or there may be a minimum duration of dormancy required for some species which has not been provided (Pourriot & Snell 1983). Conversely, estimates of egg densities may be higher than actual counts due to an inability to recognise differences between rotifer resting stages and those of other microfauna such as tardigrades and gastrotrichs, which also have ornamented resting eggs (see Strayer & Hummon 1991, Nelson 1991 and references therein). A major advantage of the hatching technique, although yielding lower estimates of resting eggs, is that it does not require the ability to recognise species solely on the basis of resting egg morphology (Nogrady *et al.* 1993). This proved difficult in the present study because fewer types of eggs were distinguished

than species were hatched. Morphological differences between resting eggs of species, although apparently species specific, may not necessarily be useful in egg count studies until more taxonomic work becomes available and is less scattered than is currently the case, including the use of scanning electron micrographs such as those of *Asplanchna* by Gilbert & Wurdack (1978).

Complete rotifer species lists for Lake Okaro and Tikitapu from incubated sediments were not obtained as they were by May (1986) from Loch Leven. For example, some species were found in the seasonal study but were not found to emerge from either lake in the hatching experiment (e.g., *Ascomorpha ovalis* and *Synchaeta pectinata* in both lakes). This may be because the conditions necessary for hatching of resting eggs were not duplicated in the experimental conditions of my study. Alternatively, minimum requirements for dormancy of eggs of these species may not have been met (Pourriot & Snell 1983). Those species that emerged which were not found in the seasonal study were either littoral-benthic species or, as in the case of *Dicranophorus edestes*, a member of the limnopsammon, and are therefore not commonly encountered in the plankton. The patterns of emergence found in this study, with synchronous hatching of large numbers of eggs over a short period of time followed by a period of inhibition is a commonly observed pattern of emergence found in other studies (e.g. Pourriot & Snell 1983, May 1987).

Chapter 7:

Taxonomy and zoogeography of rotifers of North Island, New Zealand.

Introduction

The rotifer fauna of New Zealand has been previously documented by a number of publications, reviewed by Shiel & Green (1996). These authors provide a checklist of 390 species recorded in the literature between 1859, when rotifers were first recorded from New Zealand, and 1995. Most of the named taxa are widely distributed or are considered cosmopolitan, with only a small proportion ($< 5\%$) apparently restricted to New Zealand or the Australasian region. Most of these records were the result of the work of C. R. Russell in a series of papers consisting mainly of species lists (see Russell 1944 – 1962). However, the status of these identifications has been brought into doubt with re-examination of some of Russell's original specimens (Segers 1995) indicating that a modern reappraisal of New Zealand rotifer species is necessary. Since the work of Russell, a survey of 35 lakes in the South Island of New Zealand by Sanoamuang & Stout (1993), using modern methods, added 30 new records to the New Zealand rotifer fauna. Until this study, however, taxonomic workers generally failed to give figures of the new distribution records from which to confirm the similarity, or otherwise, to nominate taxa. This has greatly inhibited comparison of these new species with those recorded elsewhere once new taxonomic literature has become available. This chapter examines the taxonomy of species from samples collected from the seasonal studies (Chapter 3), the North Island community distribution (Chapter 4) and the hatching of sediment from Lakes Okaro and Tikitapu (Chapter 7). Particular reference is made to new distribution records and unusual specimens, with comments on biogeographical aspects of New Zealand's rotifer fauna.

Results

Species Record

A total of 84 taxa was identified to at least generic level in the study (Table 7.1). 67 of these were cosmopolitan taxa previously recorded from New Zealand. The remaining 17 have not previously been recorded, either in Green & Shiel 1996, or more recently in Duggan *et al.* 1998. Three of the new records, *Conochilus exiguus*, *Dicranophorus edestes* and *Notommata* cf. *falcinella*, are not known from Australia. The majority of species morphologies conformed to those of the nominate taxa (e.g., Koste 1978, Nogrady *et al.* 1995, de Smet & Pourriot 1997). However, *Monommata* sp. is apparently a new species, as recorded by Duggan *et al.* (1998) from the Lake Rotomanuka littoral, and has yet to be described (R. J. Shiel *pers. comm.*). *Brachionus* cf. *lyratus* also may be a new species, although only a single individual was found. Ten of the new records were found in low numbers only (less than five individuals recorded in total).

Table 7.2 compiles the numbers of monogonont rotifer species recorded from North Island, South Island, New Zealand, Australia, and the number of shared taxa between Australia and New Zealand from the literature (and from an unpublished species list of Australian taxa; R. J. Shiel, *pers. comm.*). *Kellicottia longispina*, recorded in Duggan *et al.* (in press), is omitted from the record as it was noted by K. Thomasson only from the initial observations of the sample, but not on re-examination. This species has not been recorded otherwise in New Zealand, including re-examination of Lake Tikitapu from where it was originally recorded, or Australia. Therefore, this record may have been a contaminant from a northern hemisphere collection, and is treated as a spurious record. 291 species of monogonont rotifer have been recorded from New Zealand to date, with 150 species recorded from North Island, and 229 species from South Island. Only 87 taxa have been recorded from both islands. Comparison is made with the known Australian taxa

Table 7.1. Monogonont Rotifera recorded from North Island, New Zealand, during this study. An asterisk (*) indicates a new New Zealand distribution record.

<i>Anuraeopsis fissa</i> (Gosse)	<i>K. procurva</i> Thorpe
* <i>A. navicula</i> Rousselet	<i>K. slacki</i> (Berzins)
<i>Ascomorpha ecaudis</i> (Perty)	<i>K. tecta</i> (Gosse)
<i>A. ovalis</i> (Bergendal)	* <i>K. tropica</i> (Apstein)
<i>A. saltans</i> Bartsch	<i>Lecane bulla</i> (Gosse)
<i>Ascomorphella volvocola</i> (Plate)	<i>L. closterocerca</i> (Schmarda)
<i>Aspelta angusta</i> Haring & Myers	<i>L. flexilis</i> (Gosse)
<i>Asplanchna brightwelli</i> Gosse	<i>L. hamata</i> (Stokes)
<i>A. priodonta</i> Gosse	<i>L. hornemanni</i> (Ehrenberg)
<i>A. sieboldi</i> (Leydig)	<i>L. luna</i> (Müller)
<i>Brachionus angularis</i> Gosse	<i>L. lunaris</i> (Ehrenberg)
* <i>B. budapestinensis</i> Daday	<i>Lepadella acuminata</i> (Ehrenberg)
<i>B. calyciflorus</i> Pallas	<i>Lepadella patella</i> (Müller)
<i>B. caudatus</i> Barrois & Daday	<i>Lindia torulosa</i> Dujardin
* <i>B. cf. lyratus</i> Shephard	<i>Lophocharis salpina</i> (Ehrenberg)
<i>B. quadridentatus</i> Hermann	* <i>Macrochaetus altamirai</i> (Arevalo)
* <i>Cephalodella biungulata</i> (Wulfert)	<i>Monommata</i> sp.
<i>Cephalodella catellina</i> (Müller)	<i>Mytilina bisulcata</i> (Lucks)
<i>C. exigua</i> (Gosse)	<i>M. ventralis</i> (Ehrenberg)
<i>C. gibba</i> (Ehrenberg)	* <i>Notommata falcinella</i> Haring & Myers
<i>C. mucronata</i> Myers	<i>Platytas quadricornis</i> (Ehrenberg)
<i>C. ventripes</i> (Dixon-Nuttall)	* <i>Pleurotrocha petromyzon</i> Ehrenberg
<i>Collotheca</i> sp.	<i>Polyarthra dolichoptera</i> Idelson
<i>Colurella uncinata bicuspidata</i> (Ehrenberg)	<i>Pompholyx complanata</i> Gosse
<i>Conochilus coenobasis</i> (Skorikov)	<i>P. sulcata</i> Hudson
* <i>C. dossuarius</i> Hudson	<i>Proales doliaris</i> (Rousselet)
* <i>C. exiguus</i> (Ahlstrom)	<i>Synchaeta longipes</i> Gosse
* <i>C. unicornis</i> Rousselet	<i>S. oblonga</i> Ehrenberg
* <i>Dicranophoroides caudatus</i> Ehrenberg	<i>S. pectinata</i> Ehrenberg
* <i>Dicranophorus edestes</i> Haring & Myers	* <i>S. stylata</i> Wierzejski
* <i>Eothinia elongata</i> (Ehrenberg)	<i>Testudinella patina</i> (Hermann)
* <i>Epiphanes macrourus</i> (Barrois & Daday)	<i>T. parva</i> (Ternetz)
<i>Euchlanis dilatata</i> Ehrenberg	* <i>Trichocerca agnatha</i> Wulfert
<i>Filinia longiseta</i> (Ehrenberg)	<i>T. longiseta</i> (Schrank)
<i>F. novaezealandiae</i> Shiel & Sanoamuang	<i>T. porcellus</i> (Gosse)
<i>F. cf. pejlери</i> Hutchinson	<i>T. pusilla</i> (Jennings)
<i>F. terminalis</i> (Plate)	<i>T. rattus</i> (Müller)
<i>Gastropus hyptopus</i> (Ehrenberg)	<i>T. similis</i> (Wierzejski)
<i>G. minor</i> (Rousselet)	<i>T. stylata</i> (Gosse)
<i>Hexarthra intermedia</i> (Wiszniewski)	<i>T. tenuior</i> (Gosse)
<i>H. mira</i> (Hudson)	<i>T. tigris</i> (Müller)
<i>Keratella australis</i> Berzins	<i>Trichotria tetractis</i> (Ehrenberg)
<i>K. cochlearis</i> (Gosse)	

Table 7.2 Monogonont rotifer classes, families and genera (numbers of species) recorded from North Island, South Island, New Zealand and Australia (from Shiel, unpublished list), and number of New Zealand - Australian shared taxa. Marine species, and Chatham Island and Campbell Island species are not included in the New Zealand records (Russell 1953a, 1953b, 1956a, 1958).

	North Island	South Island	New Zealand	Australia	Shared
Collothecacea					
Atrochidae					
<i>Cupelopagis</i>	1	1	1	1	1
Collothecidae					
<i>Collotheca</i>	4	3	7	13	6
<i>Stephanoceros</i>	0	0	0	2	0
Flosculariacea					
Conochilidae					
<i>Conochilus</i>	6	4	7	6	5
Filiniidae					
<i>Filinia</i>	5	6	8	12	8
Flosculariidae					
<i>Beauchampia</i>	0	0	0	1	0
<i>Floscularia</i>	1	1	2	4	2
<i>Lacinularia</i>	0	0	0	8	0
<i>Limnias</i>	0	1	1	2	1
<i>Octotrocha</i>	0	0	0	1	0
<i>Ptygura</i>	0	3	3	14	2
<i>Sinantherina</i>	0	0	0	5	0
Hexarthridae					
<i>Hexarthra</i>	3	2	4	7	3
Testudinellidae					
<i>Pompholyx</i>	2	2	2	2	2
<i>Testudinella</i>	3	5	6	20	4
Trochosphaeridae					
<i>Trochosphaera</i>	0	0	0	1	0
<i>Horaëlla</i>	0	0	0	1	0
Ploimida					
Asplanhidae					
<i>Asplanchna</i>	5	4	6	7	4
<i>Asplanchnopus</i>	1	1	1	2	1
Brachionidae					
<i>Anuraeopsis</i>	2	1	2	3	2
<i>Brachionus</i>	7	10	13	27	12
<i>Keratella</i>	9	11	13	13	9
<i>Notholca</i>	0	4	4	2	1
<i>Plationus</i>	0	0	0	1	0
<i>Platyias</i>	1	0	1	1	1
Colurellidae					
<i>Colurella</i>	3	7	7	6	5
<i>Lepadella</i>	5	11	11	36	10
<i>Squatinella</i>	1	2	3	5	2
Dicranophoridae					
<i>Albertia</i>	0	0	0	1	0
<i>Aspelta</i>	2	0	2	6	2
<i>Balatro</i>	0	0	0	1	0
<i>Dicranophorus</i>	2	3	5	12	3
<i>Dicranophoroides</i>	1	0	1	2	1
<i>Encentrum</i>	0	3	3	11	1
<i>Dorria</i>	0	0	0	1	0
<i>Erignatha</i>	0	0	0	1	0
<i>Wierzejskiella</i>	0	0	0	1	0

Epiphanidae					
<i>Cyrtonia</i>	0	0	0	1	0
<i>Epiphanes</i>	1	2	3	4	3
<i>Liliferotrocha</i>	0	0	0	1	0
<i>Microcodides</i>	0	0	0	2	0
<i>Proalides</i>	0	1	1	2	1
<i>Rhinoglena</i>	0	1	1	1	1
Euchlanidae					
<i>Dipleuchlanis</i>	0	0	0	2	0
<i>Diplois</i>	0	1	1	1	1
<i>Euchlanis</i>	5	12	13	11	8
<i>Manfredium</i>	0	1	1	1	1
<i>Tripleuchlanis</i>	0	0	0	1	0
Gastropodidae					
<i>Ascomorpha</i>	3	3	3	3	3
<i>Gastropus</i>	2	2	2	3	2
Ituridae					
<i>Itura</i>	1	0	1	3	1
Lecanidae					
<i>Lecane</i>	15	25	34	71	29
Lindiidae					
<i>Lindia</i>	2	4	5	5	2
Microcodonidae					
<i>Microcodon</i>	0	1	1	1	1
Mytilinidae					
<i>Lophocharis</i>	1	1	1	3	1
<i>Mytilina</i>	3	4	4	7	4
Notommatidae					
<i>Cephalodella</i>	10	18	24	28	16
<i>Dorystoma</i>	0	0	0	1	0
<i>Drilophaga</i>	0	0	0	1	0
<i>Enteroplea</i>	0	0	0	1	0
<i>Eospora</i>	0	3	3	5	3
<i>Eothinia</i>	1	0	1	1	1
<i>Monommata</i>	2	4	5	11	2
<i>Notommata</i>	3	3	4	15	2
<i>Pleutrocha</i>	1	0	1	1	1
<i>Resticula</i>	0	0	0	4	0
<i>Rousseletia</i>	0	0	0	1	0
<i>Scaridium</i>	0	1	1	2	1
<i>Taphrocampa</i>	0	2	2	2	2
<i>Tetrasiphon</i>	0	0	0	1	0
Proalidae					
<i>Bryceella</i>	1	0	1	1	0
<i>Proales</i>	2	5	7	11	5
<i>Proalinopsis</i>	0	2	2	2	2
Synchaetidae					
<i>Ploesoma</i>	0	0	0	2	0
<i>Polyarthra</i>	4	4	4	6	4
<i>Synchaeta</i>	5	7	8	11	6
Trichocercidae					
<i>Ascomorphella</i>	1	1	1	1	1
<i>Elosa</i>	0	1	1	1	1
<i>Trichocerca</i>	19	32	39	44	30
Trichotridae					
<i>Macrochaetus</i>	2	1	2	4	2
<i>Trichotria</i>	1	2	2	5	2
<i>Wolga</i>	0	0	0	1	0
Total Monogonont Rotifera	150	229	291	525	227

because it is the closest large body of land to New Zealand, and it is likely to be a source of new species (Shiel & Green 1996). The total number of New Zealand taxa recorded to date is lower, and for all families is equal to or lower, than those recorded from Australia. Of the 291 monogonont rotifer species recorded from New Zealand, 227 (78 %) of these also are known from Australia. Only 43 % of species recorded from Australia have been recorded in New Zealand.

Representatives of new species were removed to an Olympus BX50 compound microscope, and images were captured and transferred to computer using a COHU high performance CCD video camera and Perceptics Pixelbuffer grabber board, manipulated using IPLab Spectrum 3.1 software. Temperature, DO, pH, and chlorophyll *a* ranges are provided for taxa from the data collected during the North Island distribution study, where applicable.

Notes on selected species

***Anuraeopsis navicula* Rousselet (Fig. 7.1)**

Specimens were found only from Lake Horowhenua, Lake Tikitapu and the Northland Dune lakes. The length (85 – 87.5 µm) conformed to Australian populations, and the serrated anterior margin is typical for this species, although the widths of some specimens (37.5 - 45 µm) are narrower than recorded from Australia by Koste & Shiel (1987a). 12.5 – 26.5 °C, pH 6.6 – 8.8, DO 8.0 – 12.7 mg l⁻¹, chl. *a* 2.5 – 45 µg l⁻¹. This species is cosmopolitan in warm tropical and subtropical waters, including Australia (Koste & Shiel 1987a). New record in New Zealand.

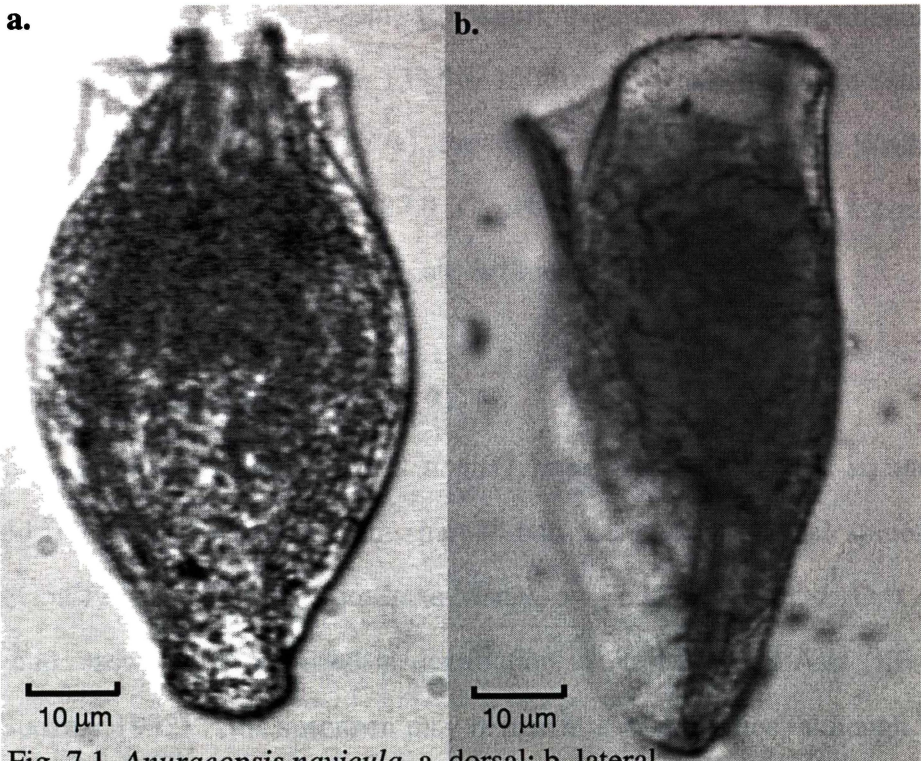


Fig. 7.1. *Anuraeopsis navicula*, a, dorsal; b, lateral

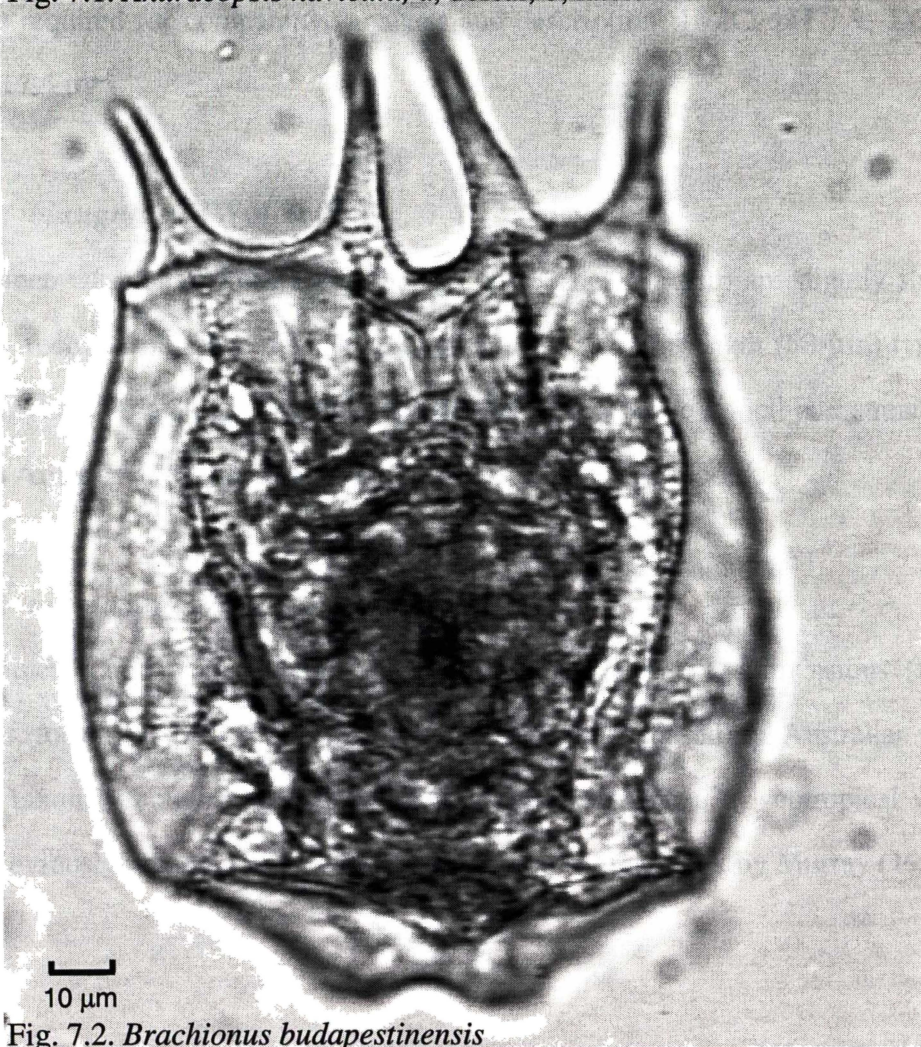


Fig. 7.2. *Brachionus budapestinensis*

***Brachionus budapestinensis* Daday** (Fig. 7.2)

Specimens were found from Lakes Waahi, Rotokauri, Ngaroto, and Horowhenua, all shallow, highly eutrophic habitats. Length 137.5 – 150 μm is within the range found in Australian populations (Koste & Shiel 1987a). Previously recorded from Lake Waahi (R. J. Shiel, J. D. Green, pers. comm). 14.1 – 27.0 °C, pH 6.8 – 8.0, DO 7.6 – 11.2 mg l^{-1} , chl. *a* 26 – 136 $\mu\text{g l}^{-1}$. Cosmopolitan taxon (Koste & Shiel 1987a).

***Brachionus cf. lyratus* Shephard** (Fig. 7.3)

A single specimen was found resembling *Brachionus lyratus* Shephard. This is an unusual morph recorded from Lake Wairarapa with sharply outward curving caudal spines. *B. lyratus* has previously been recorded from Lake Mangakaware (R. J. Shiel, J. D. Green, pers. comm), and elsewhere is restricted in distribution to Australia and Asia (Koste & Shiel 1987a, Sudzuki 1992). This specimen may represent a new species, although more individuals are required for comparative analysis and description. 18 °C, pH 7.9, DO 9.7 mg l^{-1} , chl. *a* 17.5 $\mu\text{g l}^{-1}$.

***Cephalodella biungulata* (Wulfert)** (Fig. 7.4)

A single specimen was found from Lake Tikitapu only. Toes (85 μm) are slightly shorter than Australian records, but have distinctive bifurcate tips. Trophi length (50 μm) typical. Fulcrum 30 μm , manubria 30 μm (Koste & Shiel 1991). Rare in the littoral and streams of Europe, South America and Australia (Nogrady *et al.* 1995). New record.

***Cephalodella mucronata* Myers** (Fig. 7.5)

A single specimen found from hatching of Lake Tikitapu sediment. Dimensions (Body length 190 μm , toes 130 μm , trophi 32.5 μm) appear typical based on Australian taxa. Cosmopolitan taxon, although is generally recorded as a pantropical to subtropical warm stenotherm. Previously recorded by in New Zealand from Mount Cook by Murray (1911).

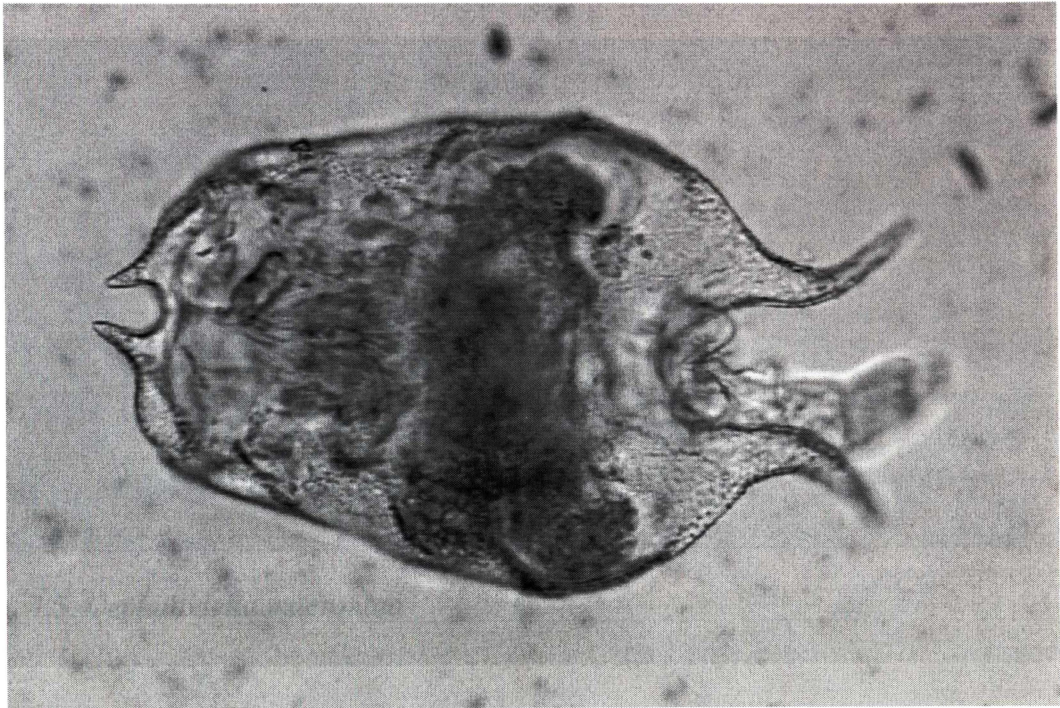


Fig. 7.3. *Brachionus* cf. *lyratus*

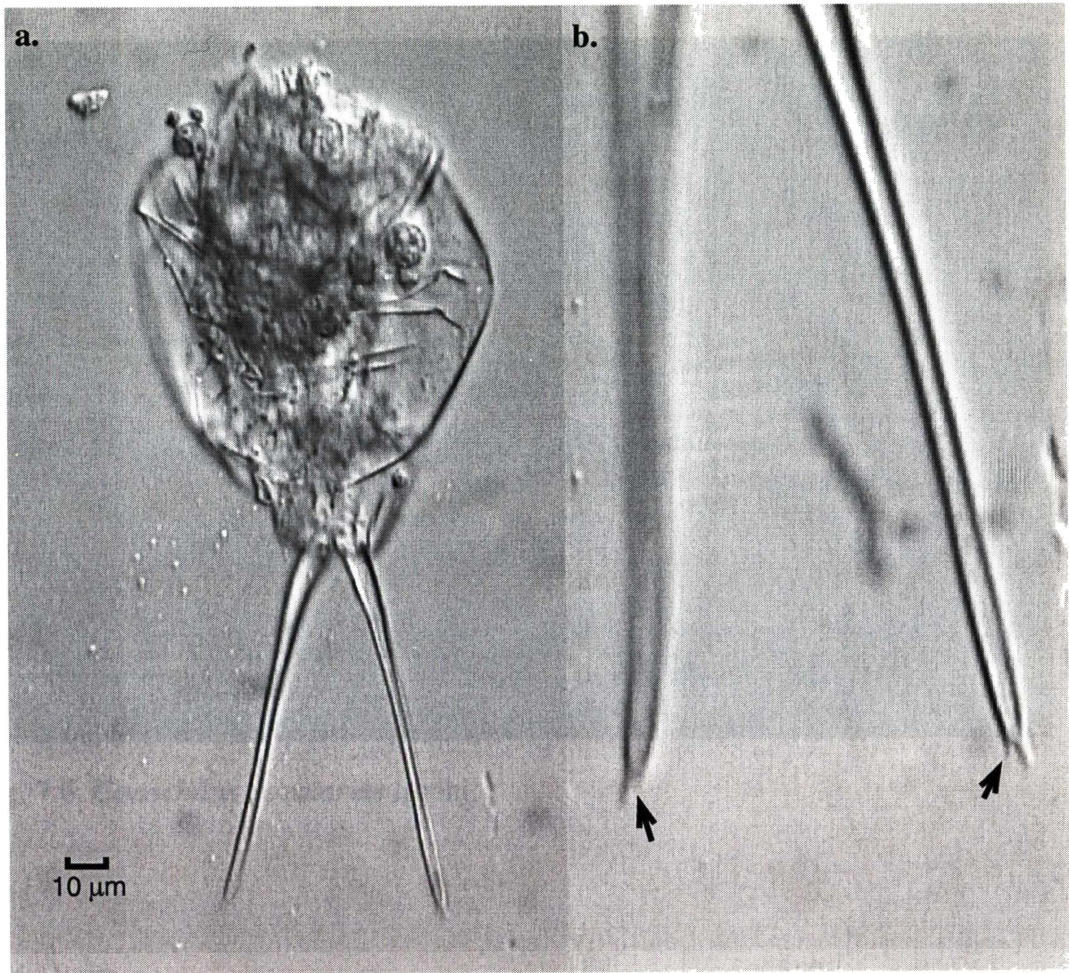


Fig. 7.4. *Cephalodella biungulata*, a, body; b, toes with bifurcate tips (indicated by arrows).

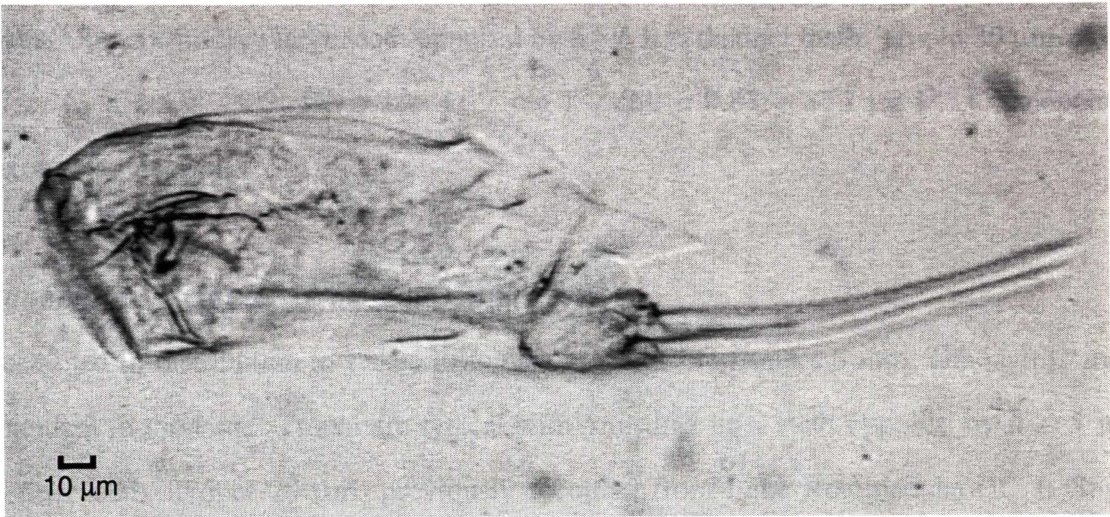


Fig. 7.5. *Cephalodella mucronata*

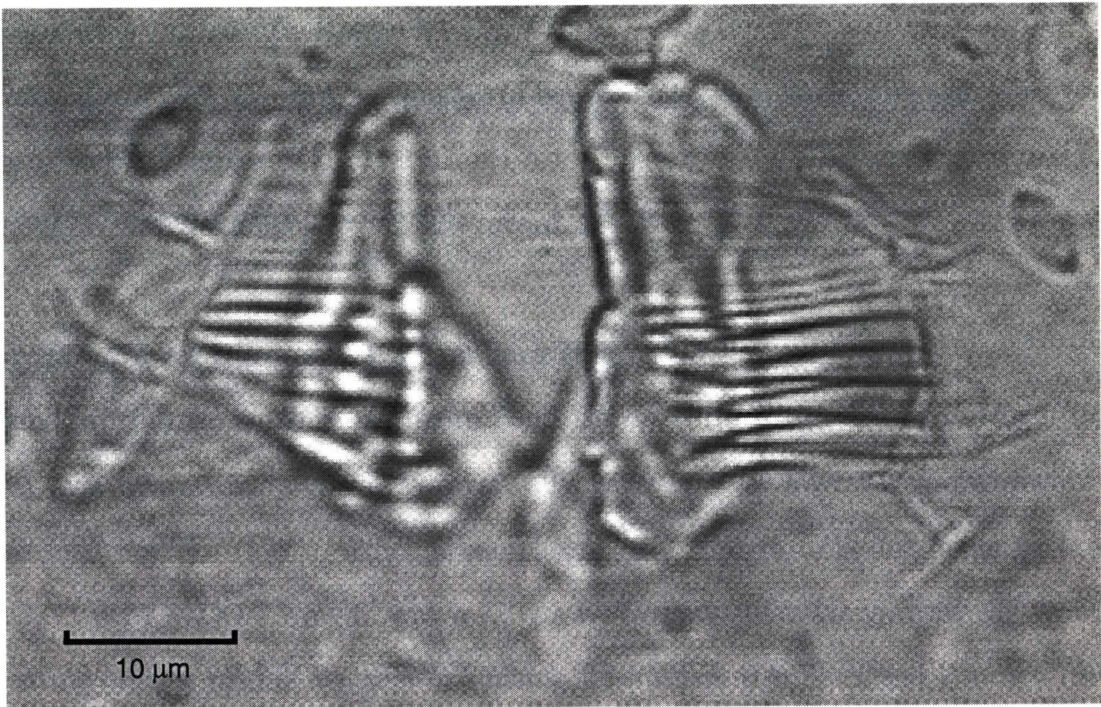


Fig. 7.6. *Conochilus dossuarius* trophi.

***Conochilus dossuarius* Hudson** (Fig. 7.6)

Widely distributed in New Zealand, although typically found in oligotrophic to mesotrophic lakes. Uncus with five large teeth opposed by 5 – 6 less distinct teeth. Trophi 30 μm . 9.7 – 27.2 °C, pH 5.9 – 8.3, DO 8.1 – 11.9 mg l^{-1} , chl. *a* 0.87 – 173 $\mu\text{g l}^{-1}$. Cosmopolitan taxon. New record.

***Conochilus exiguus* (Ahlstrom)** (Fig. 7.7)

Restricted in distribution to Lakes Rotomanuka and Rotomanuka South, although is most abundant in the latter. Trophi are typical with 4 distinct unci teeth opposed by 4 – 5 less distinct teeth. Trophi 20 μm . previously recorded from Lake Rotomanuka (R. J. Shiel, J. D. Green, pers. comm.). 13.3 – 23.2 °C, pH 7.4 – 8.6, DO 7.6 – 10.7 mg l^{-1} , chl. *a* 4.6 – 46 $\mu\text{g l}^{-1}$. This species is otherwise known from North America only (Ruttner-Kolisko 1974).

***Conochilus unicornis* Rousselet** (Fig. 7.8)

Widely distributed. Typically in colonies of between 6 to 14 animals, although often found dissociated in samples. 9.7 – 27.2 °C, pH 5.4 – 8.9, DO 6.9 – 12.5 mg l^{-1} , chl. *a* 0.83 – 91.3 $\mu\text{g l}^{-1}$. Cosmopolitan taxon. New record.

***Dicranophoroides caudatus* Ehrenberg** (Fig. 7.9)

Found in moderate numbers in Boggy Pond lagoon only. Contracted body length (92.5 μm), toes (60 μm), and trophi (25 μm) are all smaller than the lowest measurements of De Smet and Pourriot (1997), although morphologically appears to be the nominate taxon. 22.3 °C, pH 7.8, DO 7.7 mg l^{-1} , chl. *a* 220 $\mu\text{g l}^{-1}$. Cosmopolitan taxon, generally found in decaying organic mud of stagnant or running freshwaters (De Smet and Pourriot 1997). New record.

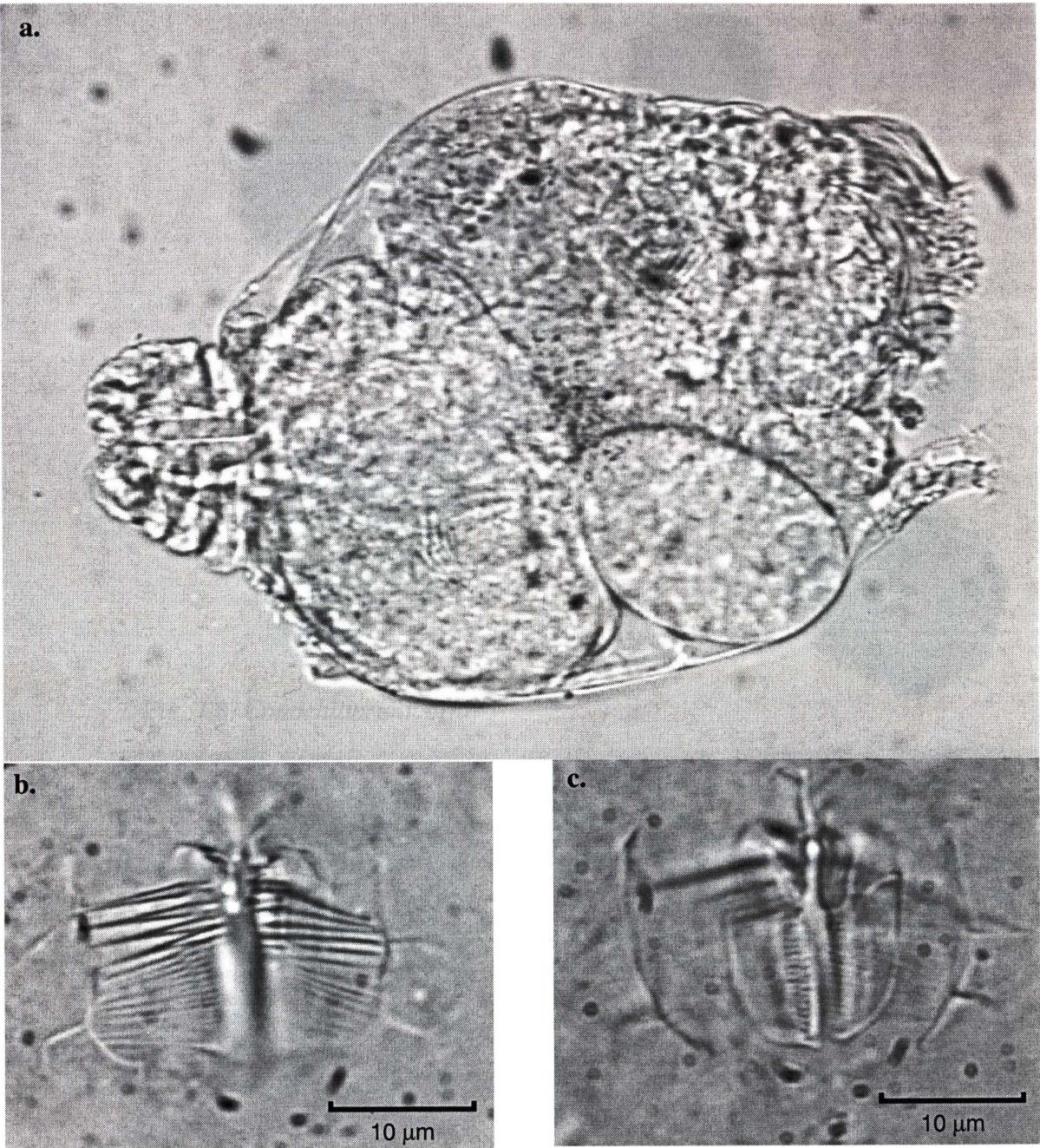


Fig. 7.7. *Conochilus exiguus*, a, body; b, trophi showing unci; c, trophi showing rami.

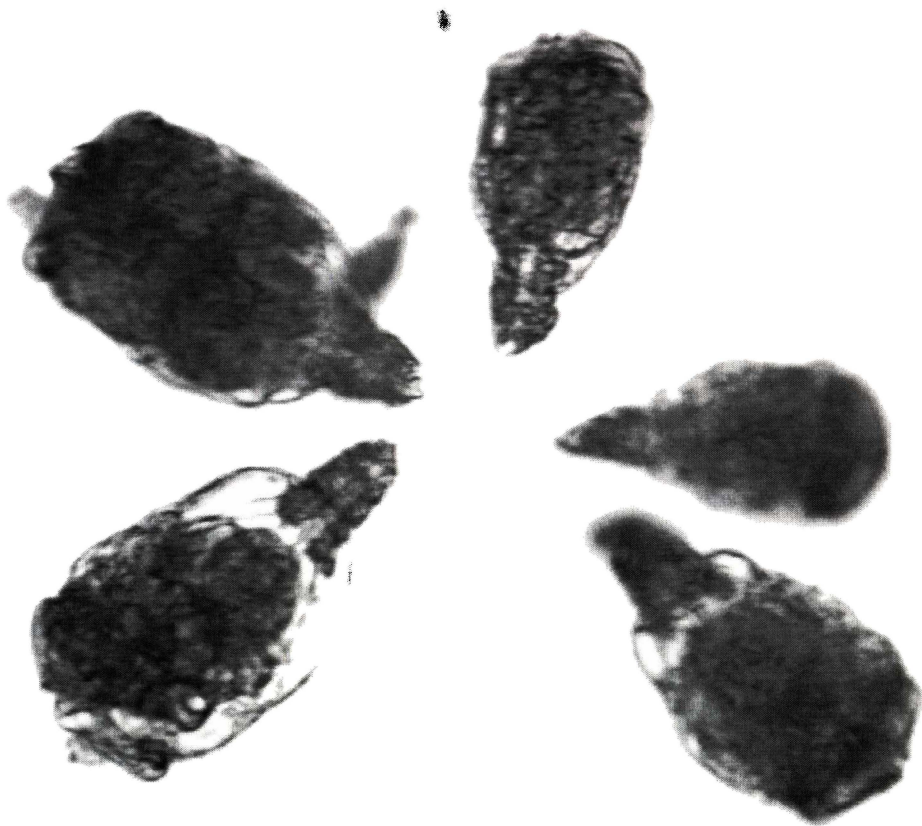


Fig. 7.8. *Conochilus unicornis*

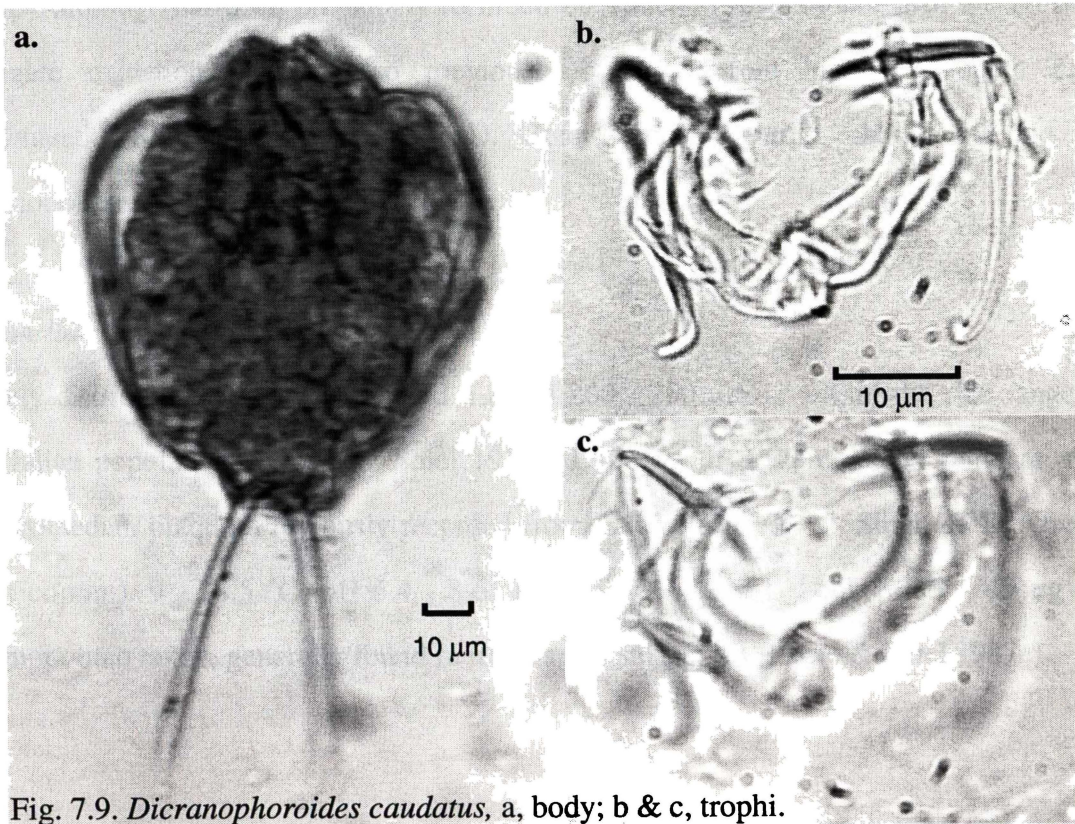


Fig. 7.9. *Dicranophoroides caudatus*, a, body; b & c, trophi.

***Dicranophorus edestes* Harring & Myers** (Fig. 7.10)

Specimens were found from hatching of Lake Tikitapu sediment only. Contracted body length (125 μm), toes (30 - 35 μm) and trophi (27.5 μm) are all smaller than the measurements of De Smet and Pourriot (1997), although morphologically appears to be the nominate taxon. Previously known from the limnopsammon of Europe, North America and Africa. Not known from Australia. New record.

***Eothinia elongata* Ehrenberg** (Fig. 7.11)

Single individual found from Lake Ototoa. Contracted body length 200 μm . Toes (30 μm) and trophi (57.5 μm) are within the size ranges of De Smet and Pourriot (1997). 16.0 °C, pH 7.7, DO 10.2 mg l^{-1} , chl. *a* 3.8 $\mu\text{g l}^{-1}$. Cosmopolitan, but rare (De Smet and Pourriot 1997). New record.

***Epiphanes macrourus* (Barrois & Daday)** (Fig. 7.12)

Found in highly eutrophic Lakes Horowhenua and Ngaroto. Not noted in Shiel & Green (1996), although has been previously recorded by Tolich (1988, unpublished thesis) from Mangare oxidation ponds. Also previously recorded from highly eutrophic Lake Rotomanuka South (R. J. Shiel, J. D. Green, pers. comm.). chl *a*. 113 $\mu\text{g l}^{-1}$. Cosmopolitan taxon (Koste & Shiel 1987a).

***Keratella tropica* (Apstein)** (Fig. 7.13)

Widely distributed in the North Island. Length 200 - 250 μm is within the size range of Australian populations (Koste & Shiel 1986). Lorica with posteromedian remnant after posteromedian plaque. Previously recorded from Lake Waahi (R. J. Shiel, J. D. Green, pers. comm.). 9 - 28.5 °C, pH 6.4 - 8.6, DO 7.5 - 13.4 mg l^{-1} , chl. *a* 2.5 - 45 $\mu\text{g l}^{-1}$. Cosmopolitan taxon, generally found in tropics and subtropics (Koste & Shiel 1987a).

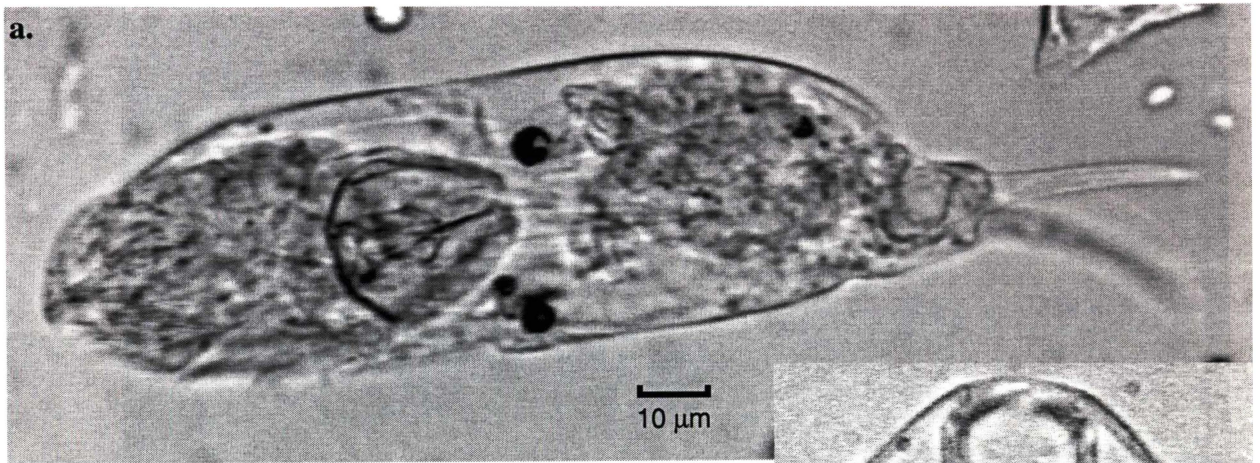
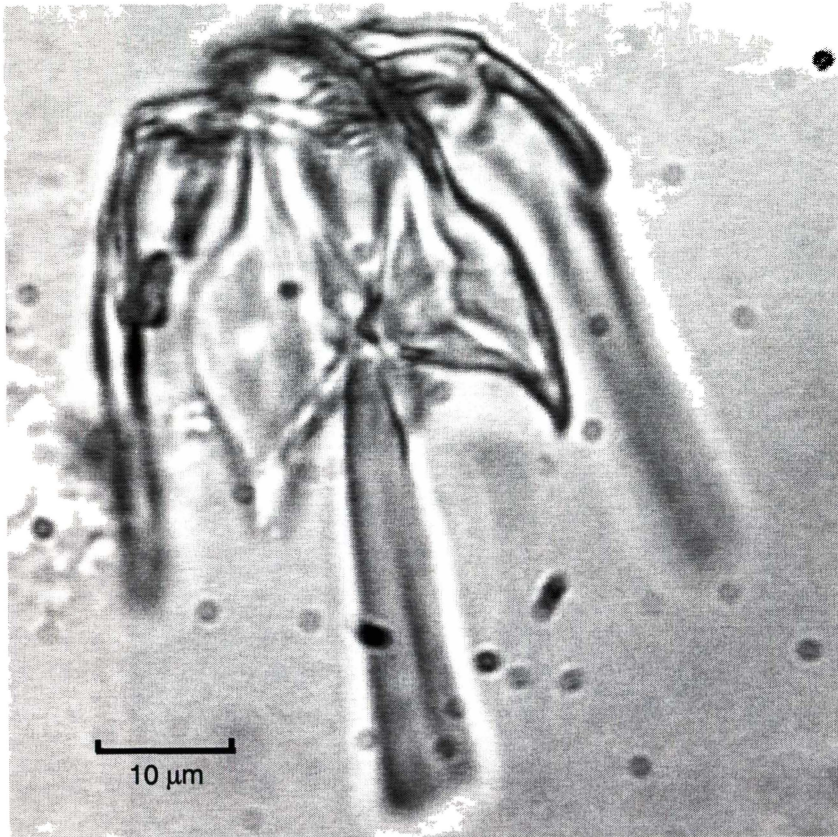


Fig. 7.10. *Dicranophorus edestes*, a, body; b, trophi.

Fig. 7.11. *Eothinia elongata* trophi.



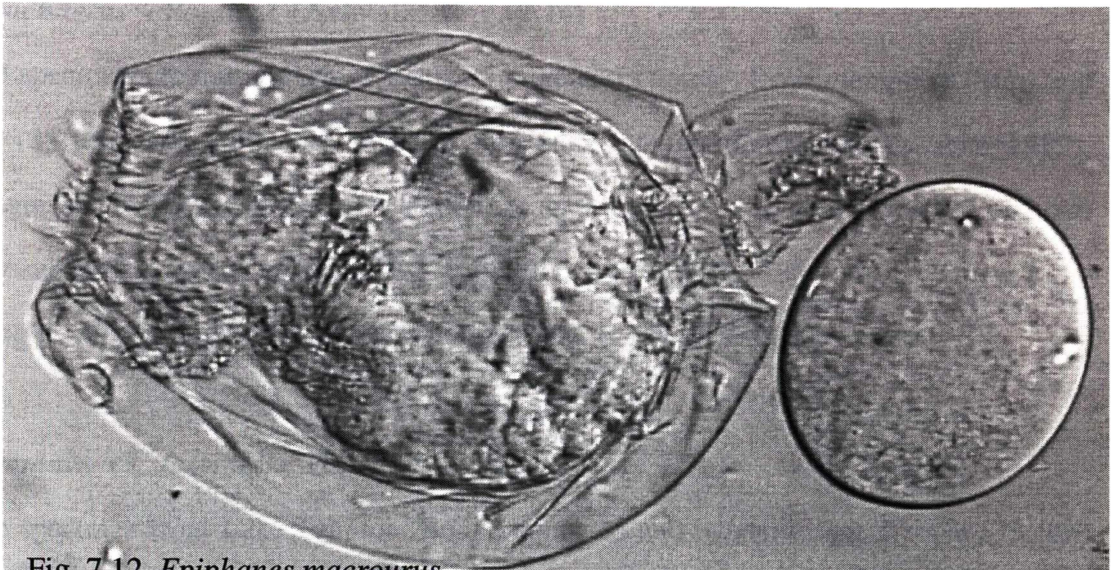


Fig. 7.12. *Epiphanes macrourus*

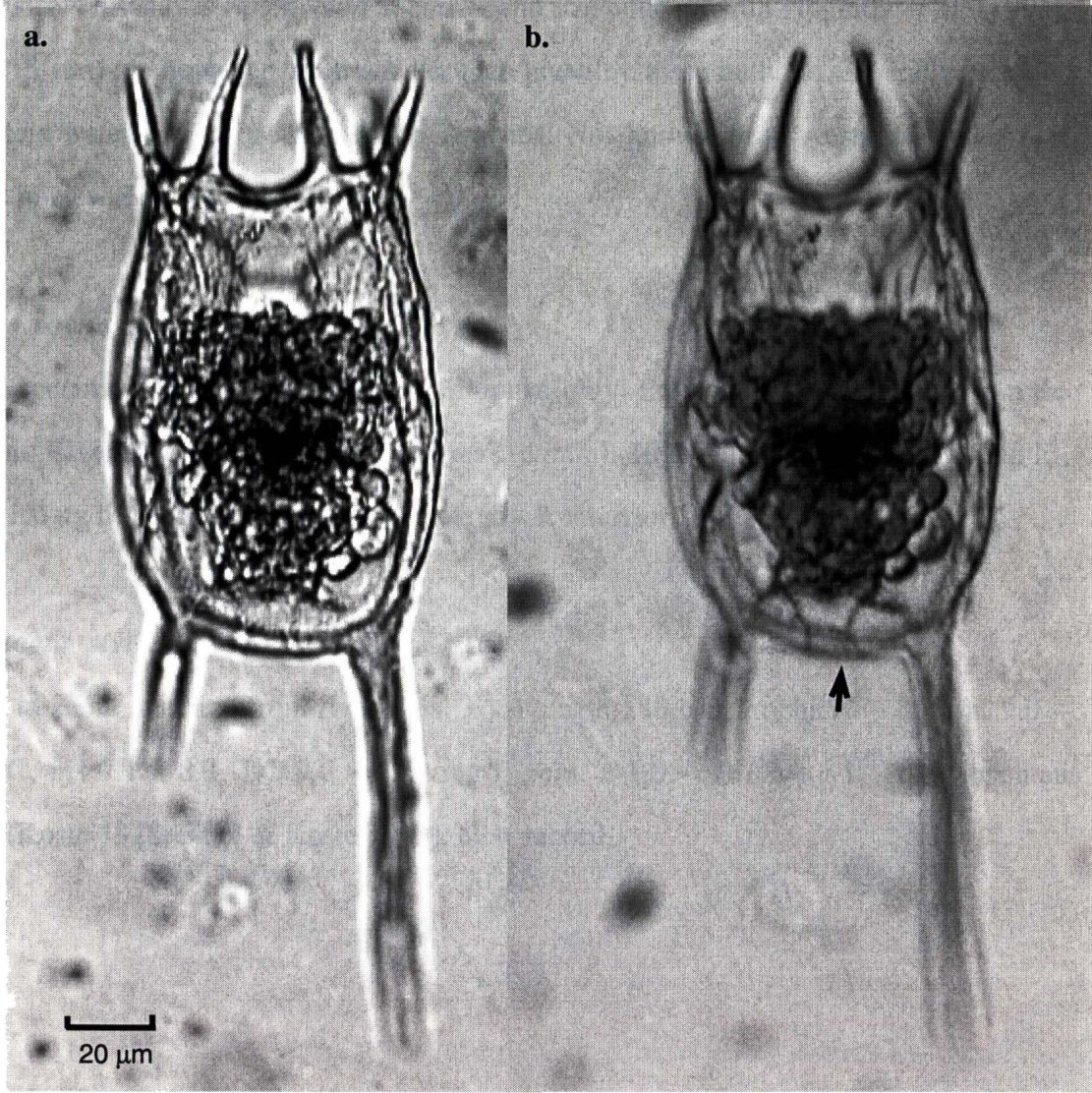


Fig 7.13. *Keratella tropica*, a, body; b, body showing posteromedian remnant (indicated by arrow).

***Macrochaetus altamirai* (Arevalo) (Fig. 7.14)**

Single specimens found in each of Lakes Pupuke and Ototoa. Lorica length (87 μm) and width (85 μm) are within the ranges of Australian populations (Koste & Shiel 1989). Distinguished by having two anteriolateral, two anteriomedian, two central median and two anterosubmedian spines present. 25.5 °C, pH 8.2 – 9.4, DO 8.3 – 8.7 mg l^{-1} , chl. *a* 2.1 – 19.9 $\mu\text{g l}^{-1}$. Cosmopolitan warm stenotherm (Koste & Shiel 1989). New record.

***Notommata cf. falcinella* Harring & Myers (Fig. 7.15)**

Single specimen from Lake Taharoa. Body contracted and indeterminate. Trophi (75 μm) most closely resembles *Notommata falcinella* and size concurs with Nogrady *et al.* (1995). Toes (15 μm) are however much smaller than given by these authors. Generally recorded from acid waters in Europe and North America. Not known from Australia, and a new record in New Zealand.

***Pleurotrocha petromyzon* Ehrenberg**

Single specimens from Lakes Ngatu and Pupuke only. Previously recorded also from the Waikato River (R. J. Shiel, J. D. Green, pers. comm). 16.3 °C, pH 7.5, DO 9.24 mg l^{-1} , chl. *a* 1.0 $\mu\text{g l}^{-1}$. Cosmopolitan taxon (Nogrady & Pourriot 1995).

***Synchaeta stylata* Wierzejski (Fig. 7.16)**

Found in small numbers from five lakes. Total length 180 μm , trophi 70 – 80 μm . 9.0 – 19.6 °C, pH 7.1 – 8.3, DO 9.6 – 12.7 mg l^{-1} , chl. *a* 7.0 – 161.3 $\mu\text{g l}^{-1}$. Cosmopolitan taxon (Koste 1978, Shiel & Koste 1993). New record.

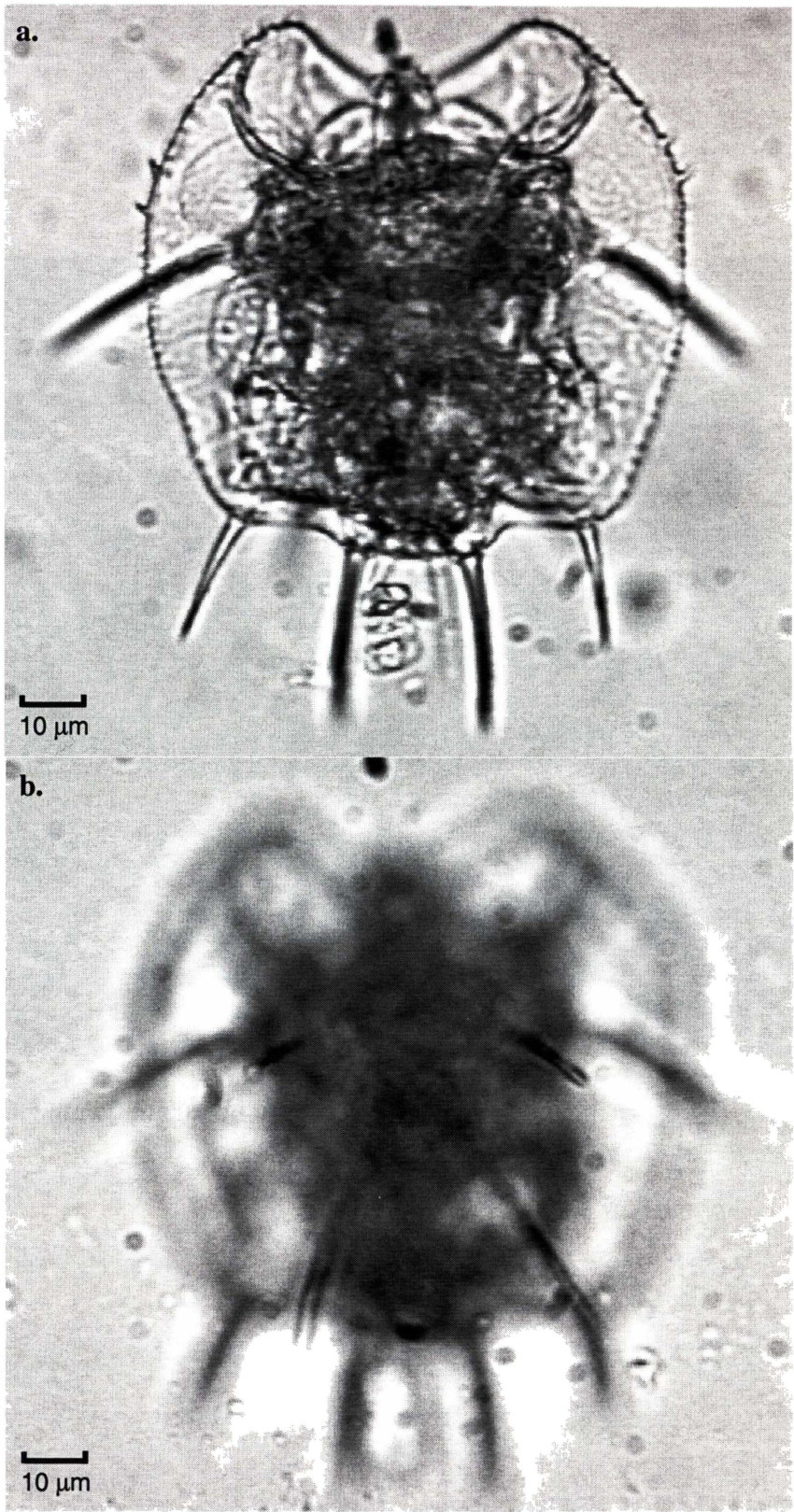


Fig. 7.14. *Macrochaetus altamirai*, a & b show different planes of focus.

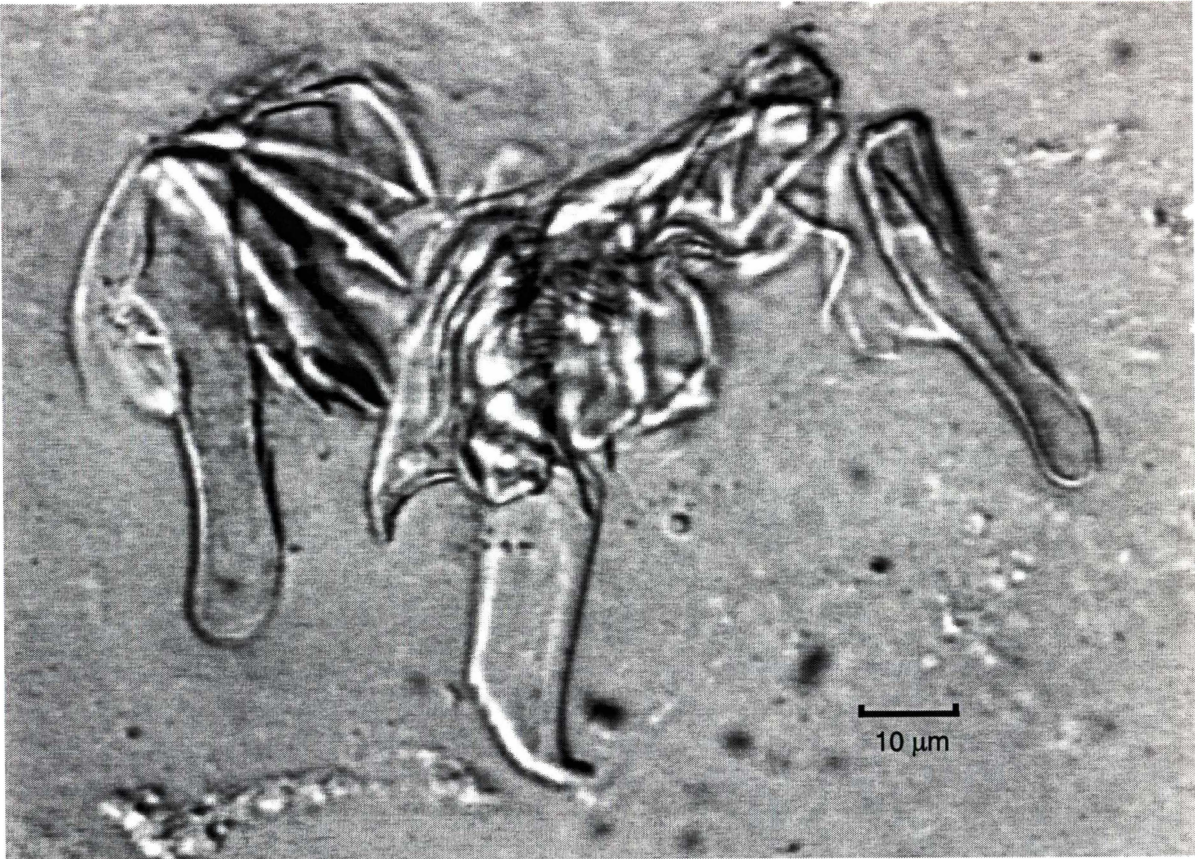


Fig. 7.15. *Notommata* cf. *falcinella* trophi.

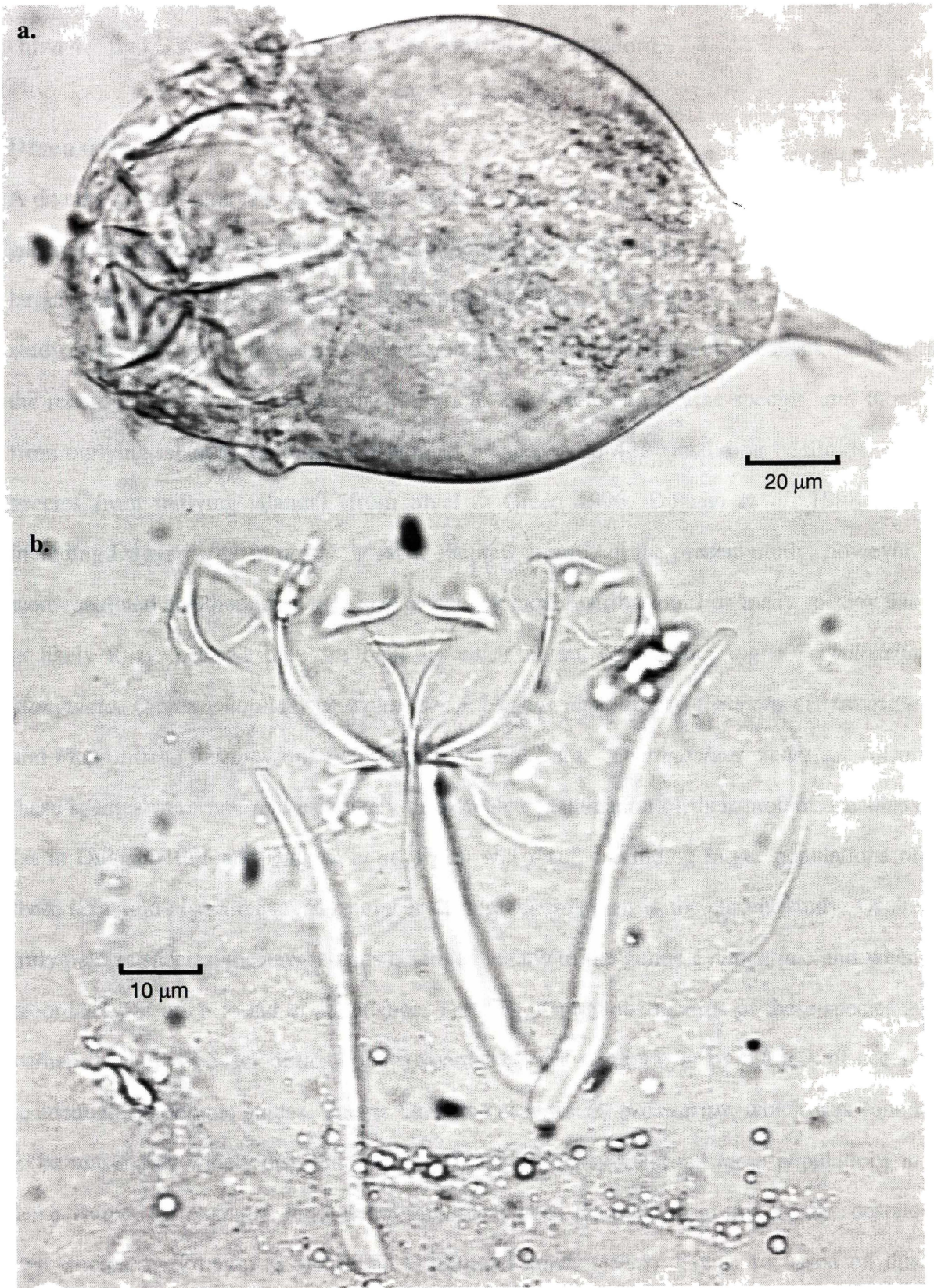


Fig. 7.16. *Synchaeta stylata*, a, body; b, trophi.

***Trichocerca agnatha* Wulfert (Fig. 7.17)**

Single specimen recorded from Lake Rotomahana only. 15.1 °C, pH 6.9, DO 10.5 mg l⁻¹, chl. *a* 4.7 µg l⁻¹. Known from Europe and Australia. New record.

Discussion

A diverse rotifer fauna was found in the current study. The majority of taxa were found to generally conform to nominate species (although size differences often existed), which largely comprised widely distributed or cosmopolitan taxa. 17 of the 84 taxa in the current study were previously unrecorded in the published literature from New Zealand, bringing the recorded number of monogonont rotifers to 291 (excluding marine species, and those from outlying islands), and the total number of species to 422 (including bdelloids, and species from outlying islands) (from Shiel & Green 1996, Duggan *et al.* 1998, and including Duggan *et al.* in press). Most of the new records in the present study, however, were restricted in either population size or geographical distribution. For many species this is likely to be because they are typically either littoral or benthic, e.g., *Cephalodella biungulata*, *Dicranophoroides caudatus*, *Macrochaetus altamirai*, *Notommata* cf. *falcinella* and *Pleurotrocha petromyzon*, or psammic in habit, e.g., *Dicranophorus edestes*. All of these species were rare and it is likely that detailed examination of their preferred habitats (as in Duggan 1995 and Duggan *et al.* 1998) will result in finding larger populations of these taxa, and also a far greater number of new records than in the current study. Of the truly pelagic species, the new records belonged mainly to the genus *Conochilus*, and when recorded were often found in abundance. The lack of previous records of these species is perhaps because of a lack of taxonomic expertise by past workers, or by the lack of access to adequate taxonomic guides. This is likely the case for *C. dossuarius*, which was found to be reasonably widely distributed geographically. This species had large populations in Lake Taupo, for example, but has not previously been recorded from this locality despite two studies, by Forsyth & McCallum (1980) and James (1995), having focussed on this

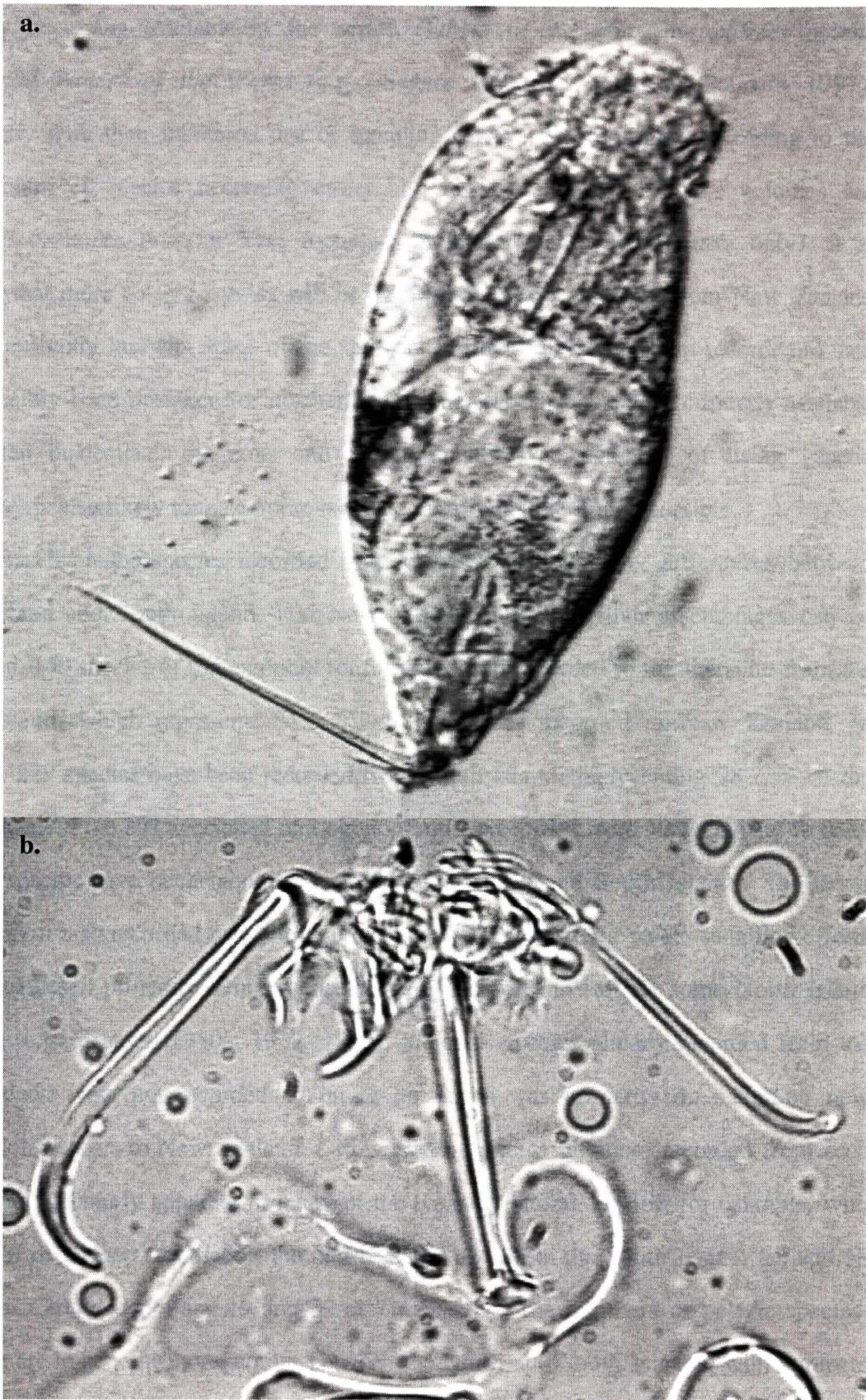


Fig. 7.17. *Trichocerca agnatha*, a, body; b, trophi.

lake. A global revision of rotifer taxa in progress, and the associated taxonomic literature currently becoming available in the series *Guides to the Microinvertebrates of the Continental Waters of the World* (e.g., Segers 1995, De Smet & Pourriot 1997), particularly with their increased use of scanning electron micrographs, is leading to the identification of species becoming easier and more precise. As further volumes are produced (volumes thus far have focussed on predominantly littoral taxa only), it is possible that more pelagic species will be discriminated and recorded from New Zealand than are currently known. Some of the apparently widely distributed taxa recorded to date have possibly been mistaken for northern hemisphere species based on currently available (and often inadequate) diagrams and measurements. The potential of using genetic techniques is also likely to make more accurate discrimination of taxa possible.

Based on the species recorded from New Zealand to date, differences between North Island and South Island, and New Zealand and Australian assemblages can be examined. 150 species of monogonont rotifer have been recorded in the literature from the North Island, which represents 51.5 % of the species recorded in New Zealand. In contrast, 229 species have been recorded from South Island, representing 78.7 % of the taxa known. Of the 291 species of monogonont rotifer recorded from New Zealand to date, only 88 species have been recorded from both the North and South Islands. The larger proportion of taxa recorded from the South Island is likely to be due to the sampling efforts of C. R. Russell primarily being focussed there. Russell did sample some North Island localities (e.g., Russell 1950a, 1952, 1959), although species already recorded from the South Island were not recorded again, as his focus was primarily on recording new distribution records to New Zealand. Differences in species numbers recorded from each genus are particularly apparent in many of the typically littoral species, for example, with 15 species of *Lecane* recorded in the North Island and 25 in the South Island, ten and 18 species of *Cephalodella*, and 19 and 32 of *Trichocerca*. The numbers of pelagic species, however, are in general more similar between the North and South Islands, with numbers

of species in many North Island genera commonly exceeding those found in the South Island, for example *Collotheca*, *Conochilus*, *Hexarthra*, *Asplanchna* and *Polyarthra* species. This is likely to reflect the greater sampling effort of planktonic environments in the North Island (e.g., Forsyth & McCallum 1980, Forsyth & James 1991, and Chapter 4). It is therefore likely that greater sampling effort focussed on, for example, vegetated habitats in the North Island will lead to greater similarity in the species records between the two islands.

Some variation in the species recorded between the North and South Islands may come about through latitudinal variation, as is known to exist in Australia (e.g., Shiel & Koste 1986), rather than through sampling artefact. A notable feature of the species composition found from lakes in the survey of North Island localities was the absence of typically coldwater forms, e.g., *Notholca* and *Kellicottia* species (Green 1972, Green 1994). This is perhaps due to New Zealand's mild oceanic climate, particularly in the warmer North Island (Green *et al.* 1987). *Notholca* is noteworthy because it is known to have numerous species in cold temperate regions, including Antarctica (Green 1994, Dartnall & Hollowday 1985), and four species have been recorded from the South Island of New Zealand to date (Hilgendorf 1898, Parr 1949, Russell 1962). However, Sanoamuang & Stout (1993) recorded only a single species, *Notholca squamula* (Müller), from only two of 35 lakes surveyed in the South Island (including many at high altitude), and distribution therefore may be restricted to particular waterbodies or habitats not sampled in the current study. *Kellicottia* has been recorded only once from New Zealand, by Duggan *et al.* (in press), although this record is treated as spurious (as noted earlier). It seems likely, however, that a reduced temperature range with particularly mild winters in New Zealand (Green *et al.* 1987) leads to an absence of many truly cold water forms, particularly in the North Island, with presence of *Notholca* species in South Island lakes possibly evidence of a latitudinal gradient of species.

Only two species of New Zealand monogonont rotifer are recorded as endemic to date (*Keratella ahlstromi* Russell and *Notholca pacifica* (Müller)), and endemism therefore comprises < 1 % of the known assemblage only. Both of these species, however, have not been recorded from the North Island, with this area therefore containing no described endemic species. Bdelloid rotifers show greater endemism in New Zealand, with 16 taxa (ca. 12 %) apparently indigenous (Shiel & Green 1996). Endemism is low in comparison with Australia where approximately 15 % of the taxa are indigenous at the species or subspecies level (Shiel & Koste 1993). However, it may be that New Zealand has endemics which are to be found in habitats other than those well studied, e.g., the littoral or wetlands of the North Island and the psammon of both islands, or that the estimation of endemics is lowered by unusual specimens recorded not yet described as new species. For example, the *Monommata* species recorded here is apparently new, as it does not conform to any of De Smet and Pourriot's (1997) species descriptions or figures. This species also was recorded by Duggan *et al.* (1998) from the Lake Rotomanuka littoral, as well as two species of *Euchlanis* and one of *Trichocerca* denoted with a "?" or "cf.", indicating that New Zealand may contain more endemics than are currently described. *Brachionus* cf. *lyratus* recorded in the current study also may be a new taxon, although further individuals need to be found before a description can be made.

The number of monogonont rotifers recorded from Australia to date is much higher than that from New Zealand. This is likely to reflect both the larger size of Australia, and also the greater sampling effort there. Based on the current knowledge of New Zealand species, there appears to be some affinities with Australian communities (e.g., Shiel 1995). In particular, the distributions of *Keratella australis*, *Keratella slacki*, *Lecane eylesi* and *Lecane herzigii*, thought until Sanoamuang & Stout's (1993) survey of South Island lakes to be endemic to Australia, are confined only to these two countries. In the survey of North Island lakes in the current study, *K. australis* and *K. slacki* are found to be more widely distributed in New Zealand than was previously known. However, *K. australis* is found in

only a limited number of sites on both islands, and *K. slacki*, although widely distributed in the North Island, is limited in distribution in South Island localities (Sanoamuang & Stout 1993, Chapter 4). These species are widely distributed in Australia (Koste & Shiel 1987a), perhaps suggesting that they are more recent arrivals in New Zealand. The presence of a specimen resembling *Brachionus lyratus* further supports the affinity between New Zealand and Australian rotifer assemblages, although the true designation of this specimen should remain in doubt until the global revision of the Brachionidae is completed. *Lacinularia* species are notably absent in New Zealand, although eight have been recorded in Australia, some of which are common components of the plankton of reservoirs and billabongs (Koste & Shiel 1987a). However, these species are also absent in Tasmania (Shiel & Green 1996). New Zealand and Tasmanian faunas also have other affinities, such as a paucity of Brachionids, absence of *Sinantherina*, and high diversity of the lecanids (Shiel & Green 1996).

It is generally accepted that dispersal plays the predominant role in determining the global distribution of Rotifera, although vicariance can be important also (e.g., Segers 1995). Dumont (1983) speculated that high levels of endemism in the genus *Brachionus* in Australia and South America are likely due to vicariance, with this genera having a Gondwanan origin, with species in Eurasia and North America only more recent arrivals by dispersal from Africa and India. New Zealand was part of Gondwana until the mid-late Cretaceous (ca. 80 mya) when the Tasman Sea formed separating New Zealand from Australia and Antarctica (Stevens *et al.* 1995). However, in New Zealand no endemic *Brachionus* are known, although *B. cf. lyratus* found in the current study may be a new species. The 13 species of *Brachionus* recorded from New Zealand to date are generally the most widely distributed species only, e.g., *B. angularis*, *B. bidentatus*, *B. budapestinensis*, *B. calyciflorus*, *B. caudatus*, *B. leydigi*, *B. plicatilis*, *B. quadridentatus*, *B. rubens* and *B. urceolaris* (Dumont 1983). Only the presence of *B. cf. lyratus* shows any

suggestion of a Gondwanan relationship, with *B. lyratus* restricted to Australia and Asia (Koste & Shiel 1987a, Sudzuki 1992).

The general lack of affinity between the New Zealand and Australian or South American *Brachionus* species, and the apparent high degree of cosmopolitanism in New Zealand, may be due to its geological history subsequent to the break-up of Gondwana. After separation from Gondwana, the New Zealand landmass eroded until the Oligocene (35 MYA), when virtually the entire land was worn down to a very low level. During this period, two-thirds of the area of modern New Zealand was submerged, with the remaining land consisting of an elongated narrow archipelago and a few scattered islands only (Stevens *et al.* 1995). At this time much of the rotifer fauna, and therefore the affinities with the Gondwanan fauna, may have been lost. The present form of New Zealand developed largely in the last 2–5 million years only, as a result of mountain building and volcanism, and the high degree of cosmopolitanism is thus perhaps due to more recent “sweepstakes” dispersal of resting eggs from Australia as a result of strong constant westerly winds (Stevens *et al.* 1995). The high proportion (78 %) of the New Zealand taxa also recorded from Australia supports this view. Shiel & Green (1996) were suspicious of the apparent high degree of cosmopolitanism of New Zealand rotifers, particularly in view of the high degree of endemism in many other New Zealand freshwater taxa. However, although endemism is high in many stream and river invertebrate groups, it is generally found to be lacking in limnetic taxa, for example lake dwelling macroinvertebrates and pelagic crustacea (Forsyth & Lewis 1987). The geological history of New Zealand, in particular the widespread submergence of the landmass, therefore may have worked against the development of a distinctive limnetic taxa, including rotifers. The higher levels of endemism in bdelloid rotifers in New Zealand (*ca.* 12 %) compared with the monogononts (< 1 %) may reflect such features, with endemic New Zealand rotifer taxa, including monogononts, perhaps more likely to be found with the examination of non-pelagic habitats including the littoral, rivers and wetlands. The majority of taxa that are recorded

from New Zealand but not from Australia are littoral species also (e.g., *Cephalodella*, *Euchlanis*, *Lecane* and *Trichocerca* species), perhaps supporting the view. Examination of these habitats rather than the pelagic is therefore likely to lead to a better understanding of the biogeographical affinities of North Island and New Zealand taxa.

Chapter 8: General Conclusions

In reviewing the ecology of New Zealand zooplankton, Chapman & Green (1987) believed that it was not possible to make general statements regarding the ecology of the rotifer communities. However, the present study has made it clear that major contrasts exist between northern hemisphere rotifer community dynamics and those of New Zealand, most of which result from the effects of New Zealand's mild oceanic climate at various temporal and spatial scales. This final chapter will therefore synthesise the discussions from the previous chapters, reviewing aspects of the current knowledge of New Zealand planktonic rotifer communities, particularly with regards to the diversity, seasonality, distribution between lakes and species associations, and biogeographical affinities.

Rotifer Species Diversity

In Chapman & Green's (1987) review of New Zealand zooplankton ecology, a tentative conclusion was made, from the few studies in which adequate attention had been given to their identification, that rotifer diversity in lakes may be low. However, this statement now appears spurious. In the present study approximately 40 species were found per lake when examined seasonally, a diversity similar to that recorded from Lake Grasmere, South Island, by Sanoamuang (1992). When only between two and four vertically integrated samples were taken in different seasons, between 9 and 35 (mean 21.1) species were recorded. These diversities are comparable with those of northern temperate lakes (e.g., Elliott 1977, Berner-Fankhauser 1983, Mikschi 1989, Vasconcelos 1990). Diversities found in many previous seasonal studies (e.g., Forsyth & James 1991, James 1995) were generally less than ten per lake, which appear remarkably low compared with the current findings and those of Sanoamuang

(1992). This raises concerns over the value of the previous rotifer work in New Zealand, much of which is likely to have been affected by either poor sampling methods or poor taxonomic resolution, and conclusions drawn from these studies should therefore be treated with caution. The importance of the adequacy of sampling methods must therefore be stressed in future studies, with the use of nets with adequate mesh sizes or the use of sedimentation, necessary for the concentration of samples. Greater attention must also be placed on species discrimination. The global revision of taxa in progress, and the associated taxonomic literature currently becoming available in the *Guides to the Microinvertebrates of the Continental Waters of the World* (e.g., Segers 1995, De Smet & Pourriot 1997) is likely, in part, to overcome this problem in the future.

Seasonal and vertical distribution

In the present study patterns of seasonality of total rotifer numbers appear to be fairly consistent between lakes, with lower total rotifer abundances occurring in the winter months. Seasonal succession in rotifer community composition also was observed in all lakes. Patterns of low total abundance in winter appear to be a general pattern of the seasonal distribution of New Zealand plankton rotifers (e.g., Sanoamuang 1992, James 1995). Distinct species assemblages generally occurred in lakes during the holomictic periods (winter and spring), and one or more during the stratified or stable periods (summer and autumn). The predominant factor determining the succession therefore appears to be the mixing pattern, with the onset and erosion of thermal stratification in monomictic lakes, or the mixed and relatively stable seasons in polymictic lakes, demarcating species distribution between relatively warm and cold water assemblages. These are factors that have not been regarded as important in rotifer communities of northern temperate lakes until recently (e.g., Fussmann 1993, Eckert & Walz 1998). However, community succession, which is fairly predictable in

northern temperate lakes, appears to be less so in New Zealand, due to the unpredictable timing in mixing events and a wide variability of lake morphometry in a small area. Additional successional events during summer and autumn were also apparently caused by additional storm events in the current study. These mixing events are likely to occur more frequently in New Zealand, including summer, than in northern temperate lakes, leading to more variable zooplankton cycles. The need for long-term (i.e., greater than one year) study is needed to investigate the repeatability of these correlations with mixing. In New Zealand, the timing of species occurrence or abundance is often inconsistent between lakes (e.g., Sanoamuang 1992, James 1995), and compared with northern temperate lakes (e.g., Ruttner-Kolisko 1974, Herzig 1987, Berzins & Pejler 1989b), although temperature appears to be the predominant factor associated with occurrence. This appears to be in common with northern temperate lakes. However, the lack of winter stratification, and an associated “under-ice” rotifer community commonly found in northern hemisphere dimictic lakes, provides a contrast with New Zealand. Typically coldwater forms, for example *Notholca* species, were therefore not found in the current survey of North Island lakes. These species may perhaps occur in the high altitude lakes in the Tongariro National Park (central North Island), e.g., Blue Lake and the Tama lakes, which are known to freeze over in winter (Healy 1975).

The importance of trophic interactions in determining the seasonal distribution of species needs further exploration. Food, in particular, may be even more important than has been presented in the current study, as palatable and non-palatable biota or food quality were not assessed, so reducing the effectiveness of size fractionated chlorophyll *a* as a measure of food availability. The possible impacts of predation on rotifers by copepods and larval fish (e.g., Jeppesen *et al.* 1987, Couch *et al.* 1999), and competition with crustacea also need to be assessed. The lack of seasonal patterns of Crustacean species may indicate a lack of competition between rotifers and

Crustacea, possibly due to the use of different food resources. Seasonal studies of rotifer species simultaneously with phytoplankton species will be invaluable in determining the influence of diet in these distribution patterns. Studies of species population parameters and related processes (e.g., comparison of clutch sizes, birth rates and death rates) may also be invaluable in determining the impacts of trophic interactions.

Vertical distribution of environmental variables generally appeared to be unimportant in determining variability in rotifer community distribution, and there was no evidence for existence of a distinct hypolimnetic community in summer (e.g. Hofmann 1982). Again, this is probably largely due to the occurrence of strong winds in summer, disturbing the cold water hypolimnetic refugia. Persistence of cold-water species in the hypolimnion may thus be unlikely to occur in New Zealand, except perhaps in deep lakes with more stable stratification (Green *et al.* 1987). However, there were great differences in total densities between the epilimnion and hypolimnion, which were likely due to the variability in temperature, oxygen and food levels.

Distribution between lakes

Greater total rotifer abundances generally were found in lakes of higher trophic state. This is likely due to greater levels of suitable food. Trophic state was the environmental gradient which was most strongly associated with the distribution of rotifer species among lakes. This finding is similar to studies from the northern hemisphere (e.g., Siegfried *et al.* 1989, Radwan & Popiolek 1989, Ejsmont-Karabin 1995), and to Duggan *et al.* (in press) from the Rotorua area. This is likely to be largely a response to variations in food type, and also the appearance of toxic cyanobacteria, the increased importance of predation on rotifers by *Asplanchna*, and the greater degree of oxygen depletion, with increased trophic state. However, the apparent importance of secchi transparency in explaining rotifer distribution over TP

and chlorophyll *a* indicated that inorganic turbidity has a large role in determining species distributions in some lakes, rather than trophic state. High turbidity brought about by inorganic suspendoids is likely to favour those rotifer species that can most efficiently discriminate and select out non-food particles. This importance of turbidity in affecting rotifer distribution is likely to have been partially a result of the high average winds in New Zealand compared with northern temperate lakes.

Based on the strong relationships between rotifers and trophic state, community bioindicator score indices were developed for inferring lake trophic state from the composition of rotifer samples. The best models for development of these were using Weighted Averaging with tolerance downweighting (WA-tol), which provided the greatest coefficients of determination, the lowest differences between observed and inferred values, and provided inferences which relate directly to the trophic state variable that they were based (e.g., TP, TLI). As many rotifer species are widely distributed, these bioindicator schemes may have the potential to be used in South Island lakes, and elsewhere, although this needs to be assessed.

Most rotifer species discussed here were apparently limited in their distributions by their preferences or tolerances to environmental conditions, particularly trophic state. For example, *Conochilus dossuarius* and *Conochilus unicornis* were generally found in lakes of low trophic status and *Filinia longiseta* and *Brachionus calyciflorus* in high trophic state lakes. This implies that passive dispersal of resting eggs is sufficient to ensure species are widely distributed. Some species, for example *Keratella australis*, *Keratella slacki* and *Conochilus exiguus*, also appear to be limited in their distributions by their dispersal abilities. This is particularly the case for some of the Brachionidae, perhaps because they are more recent arrivals from Australia. These species may be ideal candidates for investigation of dispersal limitation in New Zealand rotifer species.

Densities of resting eggs in eutrophic Lake Okaro were greater than two orders of magnitude higher than those from oligo-mesotrophic Lake Tikitapu. This is no doubt largely due to the higher densities of rotifers which can be sustained in Lake Okaro because of higher food levels associated with higher lake trophic state, and therefore greater numbers of individuals are able to produce resting eggs at the onset of unfavourable conditions. In the current study, incubation of sediments did not appear to be a useful tool for determining species composition from lakes, or for determining resting egg densities from sediments (cf. May 1986, 1987). Cues for hatching may differ in New Zealand from those in northern temperate lakes, perhaps due to the narrow seasonal temperature range. Globally, there appears to be great scope for future research on the densities and dynamics of rotifer resting.

Biogeography

A diverse rotifer fauna is known from New Zealand, with a total number of 422 species recorded in the literature to date (from Shiel & Green 1996, Duggan *et al.* 1998, Duggan *et al.* in press, and the present study). The level of endemism in New Zealand rotifers, however, appears to be low. I suggested that this lack of endemism in New Zealand rotifers is due to the geological history of New Zealand, having lost its Gondwanan affinities (e.g., endemic *Brachionus* species) during the widespread submergence of the land mass which reached its peak in the Oligocene (35 MYA). Based on the currently available species lists of North and South Island taxa, there appear to be large differences in the species compositions between the islands. These, however, appear to be mainly due to the greater sampling effort which has taken place in the South Island, particularly in vegetated habitats by C. R. Russell (1944-1962). A greater sampling effort in both islands will likely lead to a similar known composition between the two. However, latitudinal variations in community composition caused by temperature may also exist, for example cold-water species such as *Notholca* are

found in South Island lakes but not in the North Island. The New Zealand fauna appears to have affinities with the Australian fauna, with 78 % of the species recorded from New Zealand known from Australia, and the presence of some species (e.g., *Keratella australis*, *Keratella slacki*, *Lecane eylerii*, *Lecane herzigii*) known only from these two countries. The greatest similarity in species recorded appears to be in the planktonic taxa, and this is possibly because Australia has provided a source of these species for colonisation since the present form of New Zealand has developed. The greatest levels of endemism, and the greatest dissimilarities in species recorded between the Australian and New Zealand faunas, appears to be with the non-planktonic taxa. This is possibly because suitable habitats still existed for these taxa during the partial submergence of New Zealand. I suggest that endemic taxa are most likely to be found, and a greater distinctiveness of the New Zealand rotifer fauna is likely to become apparent, with more study in non-pelagic habitats.

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Appendix I

Do rotifers have potential as bioindicators of lake trophic state?

Introduction

The biological productivity of a lake is a major determinant of its suitability for many uses, and there is thus a need by different management authorities to monitor this productivity. The determination of lake trophic state is usually made by measuring several diverse criteria (e.g. OECD 1982), which are not direct measures of trophic state but are rather indicators of it, and erroneous conclusions may be drawn if only a single indicator is used (PRIDMORE 1987). Many commonly used indicators, however, may be expensive to monitor (e.g. nutrients) and/or require specialized equipment (e.g. chlorophyll *a*), making their use unavailable for some workers. The bioindicator approach, using the responses of organisms to evaluate environmental conditions, has often been neglected in favour of chemical and physical techniques. Biological methods have, however, been successfully developed and utilised using benthic macroinvertebrates, for example, as indicators of organic enrichment or eutrophication of lotic systems, e.g. the Biological Monitoring Working Party (BMWP) (ARMITAGE et al. 1983), the Belgian Biotic Index (BBI) (DE PAUW & VANHOOREN 1983) and the New Zealand Macroinvertebrate Community Index (MCI) (STARK 1985) and Semi-Quantitative Macroinvertebrate Community Index (SQMCI) (STARK 1998). In lakes, phytoplankton (e.g. THUNMARK 1945, RAWSON 1956) and chironomid or oligochaete indices have been used in lake trophic state classification, e.g. the Benthic Quality Index (BQI) (WIEDERHOLM 1976) and that of SÆTHER (1979). The community composition or abundance of rotifers may have the potential to provide useful bioindicators of trophic status as species are discriminating in their responses to the

environment and are likely to integrate physical, chemical and biological factors over time. Rotifers have the potential to make good indicators because species are widely distributed, numerically abundant within lakes, and are easily identifiable at little cost.

A preliminary data set of rotifer community composition from several lakes is considered with the aim to assess if there is potential for using rotifers as indicators of lake trophic conditions.

Materials and methods

Analysis was carried out on a data set of rotifer species collected in March 1968 from 10 lakes in the Rotorua - Taupo area of the central North Island, New Zealand: Lakes Okareka, Okataina, Rotoiti, Rotokawau, Rotoma, Rotomahana, Rotorua, Tarawera, Taupo and Tikitapu. Samples were taken for the purpose of examining phytoplankton communities (THOMASSON 1974), with rotifers collected incidentally. Samples were taken by making at least three vertical hauls with each of three nets of different mesh sizes (10, 20 and 63 μm respectively), and preserved with formalin. Sampling and identification of rotifers was done by K. THOMASSON, and the resulting data set provided to the co- authors of this paper. Species identifications used are those in the original data set, except where subsequent changes in nomenclature have occurred.

Values for mean total phosphorus (TP), mean secchi, minimum secchi, mean chlorophyll *a*, and maximum chlorophyll *a* for the studied lakes were obtained from the literature with a preference for data close to 1968, and trophic state inferred from these data using the guidelines for the fixed boundary system given by OECD (1982).

Two multivariate methods were used to elucidate patterns in the data set: Cluster analysis based on the Bray-Curtis similarity coefficient calculated on the presence-absence (no transformation) of rotifer species, employing group average sorting, and ordination by non-metric multi-dimensional scaling (MDS) (KRUSKAL & WISH 1978) based on the ranked Bray-Curtis similarity matrix. In order to indicate which species were principally responsible for the observed patterns, a shade matrix was constructed by sorting the original data matrix to show on one axis the lakes ordered by a cluster analysis

of lakes based on species present, and the other axis the species ordered by a cluster analysis of species based on lake. Analyses were carried out using the Plymouth Routines in Multivariate Research statistical package (PRIMER 1994, CLARKE & WARWICK 1994). The resulting patterns in the multivariate analyses were then compared with the inferred trophic states.

Results

61 rotifer species were found, 9 of which have not previously been recorded from New Zealand (SHIEL & GREEN 1996). *Kellicottia longispina*, noted initially from Lake Tikitapu but not found in samples when re-examined, is included in the analysis.

Table 1 lists data on TP, mean and minimum secchi depth, and mean and maximum chlorophyll *a* compiled from the literature, and inferred trophic states. Published data could not be found for TP or secchi depth from Lake Rotokawau, while chlorophyll *a* data were available only from December 1983 (JAMES 1987). However, this lake is generally considered to be oligotrophic (e.g. JAMES 1987, CLAYTON et al. 1989). Only Lakes Tikitapu (oligotrophic) and Rotoiti (mesotrophic) had the same designated trophic state when assessed by all five criteria. Inferred trophic state for Rotomahana varied between oligotrophic and eutrophic. The remaining lakes overlapped between either oligotrophic (including ultra-oligotrophic) and mesotrophic or eutrophic and mesotrophic. In most cases, TP gave higher inferred trophic states than the other parameters, likely an overestimation due to analyses not including a step eliminating interference by arsenic and silica (DOWNES 1978).

The cluster analysis based on species (Fig. 1), separated four lake groups at a 30% dissimilarity level: a) Lake Rotomahana, b) Lakes Rotoma, Okareka, Okataina, Rotoiti, Rotorua and Tarawera, c) Lakes Rotokawau and Taupo, and d) Lake Tikitapu. These groupings broadly align with the trophic state groupings. Group a was most commonly found to be mesotrophic, Group b mesotrophic or oligotrophic, except Rotorua which was mesotrophic-eutrophic, and Groups c and d were in general oligotrophic or ultra-oligotrophic.

The MDS ordination (Fig. 2a) shows a similar distribution of the data to the cluster analysis, with the four lake groups separated from each other. The inferred trophic ratings using the five criteria are superimposed on the distribution of the lakes in Figs. 2b-f. Lakes of similar productivity were grouped together, with higher productive lakes generally found on the left side of the ordination, and lower productive ones on the right.

The shade matrix (Fig. 3) shows many species to be associated to greater or lesser degrees with the lake groupings determined by classification and MDS, and therefore groupings or gradual changes in species composition appeared to be based on lake productivity. Species near the top of the matrix were therefore more typical of oligotrophic conditions, species in the middle were either more indicative of mesotrophic conditions or had no apparent preference, and those near the bottom were more indicative of eutrophic conditions.

Discussion

Although species of rotifer are commonly widespread in their distribution, our data showed that community composition varies among lakes, even when in close proximity to each other, and that this distribution seemed to be related to lake trophic state. The majority of planktonic rotifer species are filter or suspension feeders of algae and bacteria, and are likely to be sensitive indicators of variations in food type and density caused by, for example, changing nutrient levels along a trophic gradient. Trophic state has thus been found important in affecting the distribution of species between lakes by several authors elsewhere, e.g. SIEGFRIED et al. (1989), KAUSHIK & SAKSENA (1995) and EJSMONT - KARABIN (1995).

Species data from the present study were expressed as presence or absence, giving equal weighting to all species in multivariate analysis, whether rare or abundant (CLARKE & WARWICK 1994). Abundance data may provide more information, and better correlations to trophic condition. However, from the patterns elucidated by our analyses and the shade diagram, species presence or absence may be adequate for indicating trophic condition, perhaps due to narrow ranges in preferences by species.

By comparison, planktonic crustacean species are more universal in their occurrence in New Zealand lakes than rotifers, and are therefore of limited value as indicators of trophic status (CHAPMAN et al. 1985). Another limitation of crustacea is their low species diversity (CHAPMAN et al. 1985), with New Zealand communities mostly consisting of only one species of calanoid copepod and one to three species of cladocera over a year (CHAPMAN & GREEN 1987). Rotifers, however, are often the most abundant and diverse metazoans in lakes. In the present study, between 6 and 26 (average 12.4) species of rotifer were found per lake from a single sampling date, therefore a limitation in diversity is unlikely to be a problem in their value as bioindicators. It is unknown if predation by crustaceans, for example, can significantly depress rotifer abundances in New Zealand, though due to the ubiquitous nature of the crustacean zooplankton and the apparent trends shown in the present study this may not be a significant factor in determining rotifer community composition. Rotifer species are seasonal in occurrence so it is not possible to fully assess community composition from occasional samples. It is likely to be better to use community composition assessed from a number of samples taken throughout the year.

The use of rotifers as indicators of trophic state may provide advantages over physical, chemical and other bioindicator methods. Sampling, identification and enumeration can be done using simple and inexpensive equipment, rotifers have simpler communities than, for example, phytoplankton, and the identification of species is relatively simple and precise. Once a better knowledge of the relationships between rotifer community composition and trophic state is obtained, sampling of rotifers may be a useful complement or alternative to some of the methods currently used. Possible approaches include the development of an index similar to the BMWP, BBI or MCI, or by developing transfer functions such as those used for inferring, for example, acidification in paleolimnological work (e.g. DIXIT et al. 1988, STEVENSON et al. 1989, TER BRAAK & VAN DAM 1989).

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Table 1: Collated data and inferred trophic states for the 10 lakes. Trophic boundary levels are estimated from guidelines given by the OECD (1982).

Lake	Total Phosphorus (mg/m ³)	Mean Secchi depth (m)	Minimum Secchi depth (m)	Mean surface chlorophyll <i>a</i> (mg/m ³)	Maximum surface chlorophyll <i>a</i> (mg/m ³)
Okareka	14.1 a Mesotrophic	7.7 a Oligotrophic	6.0 a Ultra-Oligotrophic	2.1 a Oligotrophic	8.5 a Mesotrophic
Okataina	17.5 a Mesotrophic	11.9 a Oligotrophic	8.0 a Ultra-Oligotrophic	1.1 a Oligotrophic	4.0 a Oligotrophic
Rotoiti	15.0 a Mesotrophic	5 b Mesotrophic	2.2 d Mesotrophic	4.4 d Mesotrophic	11 d Mesotrophic
Rotokawau	? ?Oligotrophic	? ?Oligotrophic	? ?Oligotrophic	0.76 e Oligotrophic	1.89 e Oligotrophic
Rotoma	11.0 a Mesotrophic	11.0 a Oligotrophic	8.8 d Oligotrophic	1.6 a Oligotrophic	4.5 a Oligotrophic
Rotomahana	74.5 a Eutrophic	4.5 d Mesotrophic	3.2 d Oligotrophic	6.6 d Mesotrophic	14.8 d Mesotrophic
Rotorua	51.5 a Eutrophic	2.5 b Eutrophic	1.5 b Meso/ Eutrophic	5.2 d Mesotrophic	14 d Mesotrophic
Tarawera	19.0 a Mesotrophic	9 d Oligotrophic	7 d Oligotrophic	2.6 d Mesotrophic	5.5 d Oligotrophic
Taupo	~11 c Mesotrophic	15.9 c Ultra-Oligotrophic	11.83 c Ultra-Oligotrophic	1.4 c Oligotrophic	~3 c Oligotrophic
Tikitapu	6.4 a Oligotrophic	11.1 a Oligotrophic	5.5 d Oligotrophic	1.3 a Oligotrophic	5.5 a Oligotrophic

a. McCOLL (1972) from period 1970-1971, b. LIVINGSTON et al. (1986) from period 1967-1970, c. WHITE et al. (1980) from period 1974-1976, d. BOPRC (1993) from period 1991-1992, and e. JAMES (1987) from December 1983 only.

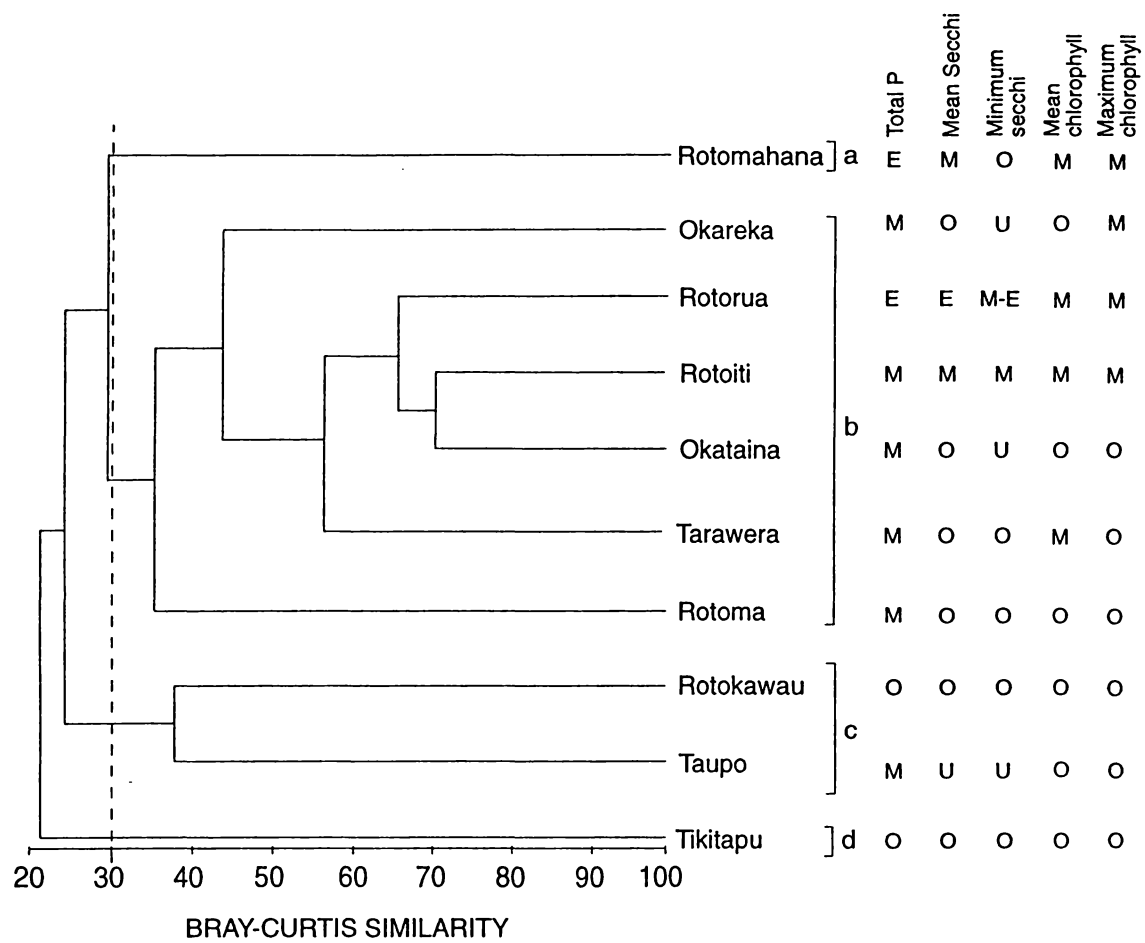


Fig. 1. Cluster analysis of 10 lakes based on rotifer species present. The dashed line indicates the 30% level of dissimilarity, and letters a-d show lake groupings at this level. Inferred trophic states for each criterion are on the right of the figure: O = oligotrophic, M = mesotrophic, E = eutrophic, U = ultra-oligotrophic.

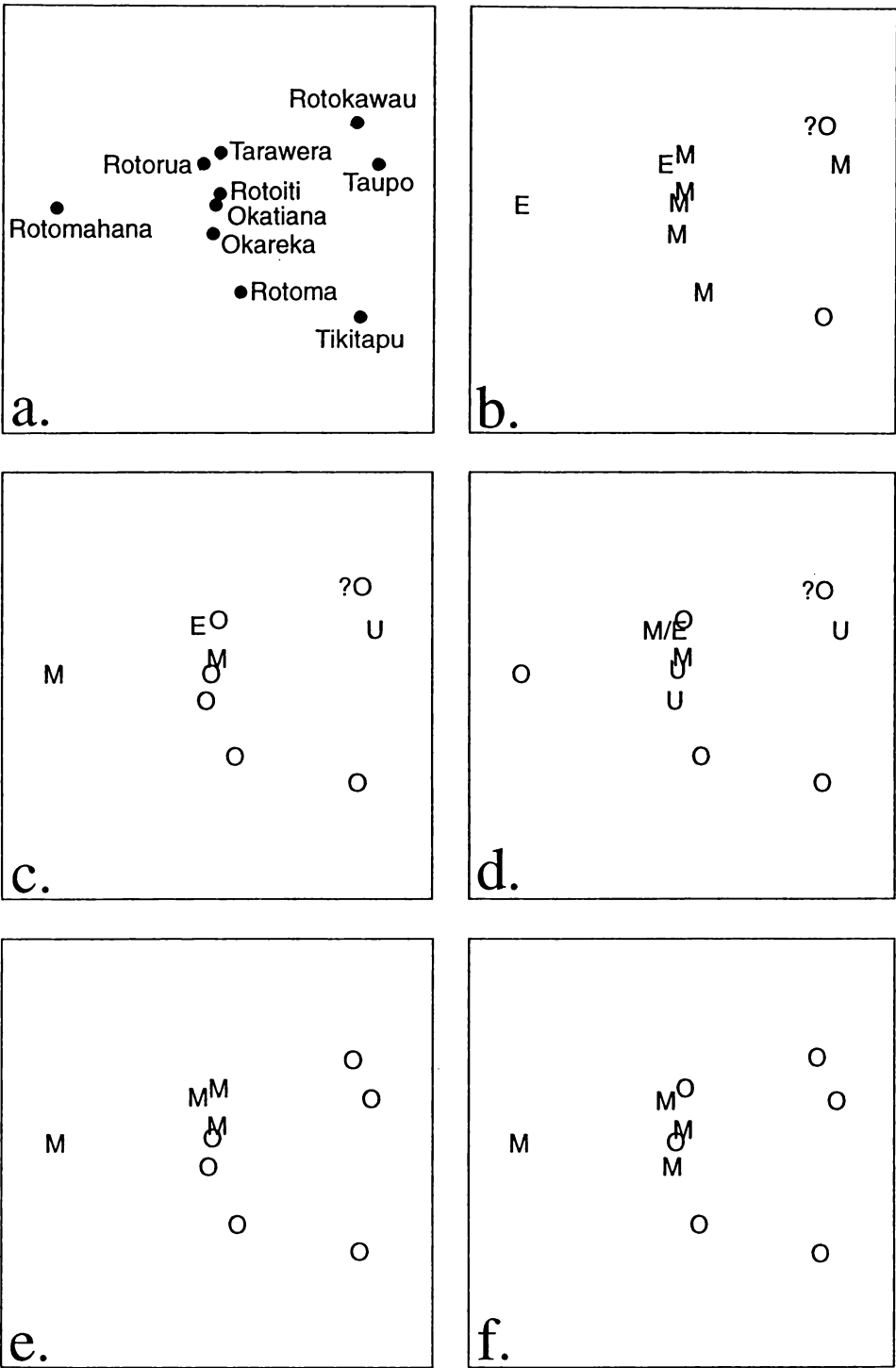


Fig. 2a. Non metric multi-dimentional scaling (MDS) plot with the least stress (0.08) from ten iterations, of ten lakes based on rotifer species present. MDS overlaid with inferred trophic state using b. total phosphorus, c. mean secchi, d. minimum secchi, e. mean chlorophyll *a*, and f. maximum chlorophyll *a*: O = oligotrophic, M = mesotrophic, E = eutrophic, U = ultra-oligotrophic.

	Rotomahana	Okareka	Rotorua	Rotoiti	Okataina	Tarawera	Rotoma	Rotokawau	Taupo	Tikitapu
GROUP	a	b						c	d	
<i>Colurella</i> sp.								•		
<i>Euchlanis dilatata</i>								•		
<i>Lepadella acuminata</i>								•		
<i>Trichocerca tenuior</i>								•		
<i>Colurella adriatica</i>								•	•	
<i>Lecane luna</i>									•	•
<i>Colurella obtusa</i>										•
<i>Kellicottia longispina</i>										•
<i>Lecane hornemanni</i>										•
<i>Macrochaetus collinsi</i>										•
<i>Trichocerca tigris</i>										•
<i>Collotheca pelagica</i>						•				
<i>Trichocerca birostris</i>						•				
<i>Cephalodella</i> sp.			•							
<i>Conochilus hippocrepis</i>			•							
<i>Conochilus</i> sp.							•			
<i>Lecane closterocerca</i>							•			
<i>Testudinella incisa</i> v. <i>emarginula</i>							•			
<i>Trichocerca dixon-nutalli</i>							•			
<i>Lecane lunaris</i>					•				•	
<i>Trichocerca stylata</i>					•					
<i>Asplanchna</i> sp.				•		•				
<i>Asplanchnopus multiceps</i>				•						
<i>Trichocerca ruttneri</i>				•						
<i>Trichocerca similis</i>				•						
<i>Keratella cochlearis</i>	•	•	•	•	•	•	•			•
<i>Conochilus coenobasis</i>		•	•	•	•	•	•	•	•	
<i>Polyarthra vulgaris</i>		•	•	•	•	•	•	•	•	•
<i>Ascomorpha ecaudis</i>	•	•	•	•	•		•			
<i>Hexarthra intermedia</i>	•	•	•	•	•	•				
<i>Pompholyx sulcata</i>	•	•	•	•	•	•				
<i>Synchaeta</i> sp.		•	•	•	•	•		•		
<i>Trichocerca longisetula</i>		•	•	•	•	•			•	
<i>Philodina</i> sp.		•		•			•	•		•
<i>Trichocerca pusilla</i>		•		•				•		
<i>Collotheca libera</i>				•	•					•
<i>Collotheca</i> sp.				•	•		•			
<i>Keratella valga</i>	•			•	•					
<i>Filinia terminalis</i>			•	•	•					
<i>Trichocerca</i> sp.			•	•	•					
<i>Asplanchna priodonta</i>		•			•		•			
<i>Hexarthra</i> sp.		•					•			
<i>Lecane bulla</i>		•					•			•
<i>Conochilus unicornis</i>		•			•					
<i>Trichocerca mus</i>		•			•					
<i>Euchlanis triquetra</i>		•								
<i>Lecane arcuata</i>		•								
<i>Lecane aspasia</i>		•								
<i>Polyarthra dolichoptera</i>		•								
<i>Polyarthra minor</i>		•								
<i>Polyarthra remata</i>		•								
<i>Synchaeta pectinata</i>		•								
<i>Testudinella patina</i> f. <i>aspis</i>		•								
<i>Testudinella</i> sp.		•								
<i>Trichocerca cylindrica</i>		•								
<i>Trichotria tetractis</i>		•								
<i>Asplanchna brightwelli</i>	•									
<i>Brachionus caudatus</i> f. <i>vulgatus</i>	•									
<i>Brachionus quadridentatus</i>	•									
<i>Filinia longisetula</i> v. <i>limnetica</i>	•									
<i>Filinia opoliensis</i>	•									

Fig. 3. Shade matrix for the rotifer species and lake groupings. Rows and columns of the array are re-ordered on the basis of classifications of species and lakes.