Relationships between zooplankton abundance and trophic state in seven New Zealand lakes

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Keywords: New Zealand, zooplankton, *Calamoecia lucasi*, populations, multivariate analyses, trophic levels

Abstract

The zooplankton communities of seven Rotorua, New Zealand, lakes of different trophic status were studied in 1977–78. They were generally dominated by the calanoid copepod, *Calamoecia lucasi*. *Bosmina meridionalis* occurred in all the lakes and *Ceriodaphnia dubia* in most. Only small numbers of *Macrocyclops albidus* ever occurred. Rotifers were not studied in detail. Community composition was similar to that in other northern New Zealand lakes. No well defined patterns of seasonal change in abundance were found and the timing of changes, which were of low magnitude, was different in each lake. Clutch sizes in all species were small. *Calamoecia* population parameters were analysed using multivariate methods and shown to be related to lake trophic level. Population densities were higher in more productive lakes whereas breeding levels were inversely related to indices of trophic status and population abundance. It is suggested that the populations, as in other northern New Zealand lakes, are food-limited, probably as a consequence of a lack of marked climatic seasonality and the absence of major predation pressures. Groupings of the lakes based on the *Calamoecia* data are in general agreement with those derived from parallel studies of water chemistry, phytoplankton and macrobenthos.

Introduction

Because of their relatively long lifespans, their presence throughout the year and their role as grazers of algae and bacteria, zooplankton, particularly crustacean species, act as integrators of a variety of physico-chemical and biological conditions in lakes and their abundance should be a measure of lake productivity.

A number of recent studies have thus examined the relationship between zooplankton abundance and trophic status of lakes (Pedersen *et al.*, 1976; Gannon & Stenberger, 1978; Nilssen, 1978; Morgan *et al.*, 1980). New Zealand plankton communities offer particularly interesting opportunities for such investigations because of the simplicity of their structure and the apparent lack of influence of either vertebrate or invertebrate predators on them (Chapman *et al.*, 1975). Populations appear to be food limited (Chapman, 1973; Green, 1976b) which should mean a closer linkage between trophic change and zooplankton response. The communities considered here are those studied by the late V. H. Jolly as part of a collaborative study of eutrophication processes in seven lakes in the Rotorua district in the central North Island, New Zealand (Fig. 1) considered to range from oligotrophic to eutrophic.

Most other studies have used only gross population measures such as total numbers and/or biomass but we believed that in addition, detailed consideration of life history and population parameters of species populations should be undertaken. We attempt this with the dominant zooplankter, the calanoid copepod *Calamoecia lucasi* Brady. Multivariate analyses have proved sensitive in discerning patterns in zooplankton communities and asso-

Hydrobiologia 123, 119–136 (1985).

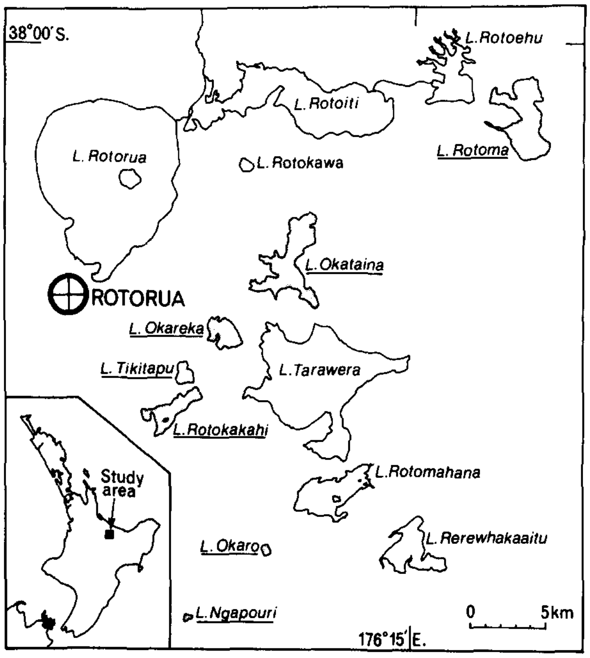

Fig. 1. Location of the study lakes (underlined) in the Rotorua district.

ciating them with subtle changes along limnological gradients (Sprules, 1977; Gannon, 1981). We used them to elucidate patterns in the *Calamoecia* populations between the lakes and to associate these with the simultaneous studies of the limnology (McColl, 1972), phytoplankton (Flint, 1977) and benthos (Forsyth, 1978) of the lakes.

Some morphometric and other data are given in Table 1. The lakes, all of volcanic origin (Healy, 1975), are small but they differ in their shoreline development and in their mean and maximum depths. They are all of sufficient size and depth to develop persistent temperature stratification throughout the warmer months of the year (McColl, 1972). Their catchments, which were originally forested, have been subjected to varying degrees of modification for agricultural and urban development. Lakes Okaro and Ngapouri are the smallest and shallowest and have had nearly all of their catchments converted to agricultural land. Their waters are of low transparency and in summer their hypolimnia become extensively depleted of oxygen. The other lakes all have considerably less modified catchments, lower nutrient and chlorophyll concentrations, clearer waters, and higher hypolimnetic oxygen concentrations. The least modified lake is Lake Tikitapu.

Table 1. Morphometric and other data for the study lakes. Mean values are for April 1970–April 1971. Data from McColl 1972.

	Ngapouri	Okaro	Okareka	Okataina	Rotokakahi	Rotoma	Tikitapu
Area (ha)	19	33	340	1089	436	1190	145
Volume (10^6 m^3)	2.57	3.81	62.47	477.3	77.1	458.9	27.65
Shoreline development	1.60	1.08	1.57	2.68	1.93	2.35	1.18
Percentage of catchment left with native forest	1	2	38	80	33	53	79
Maximum depth (m)	23.5	15	31	80	30	80	26
Mean depth (m)	13.5	11.5	18.0	44.0	17.5	38.5	19.0
Thermocline mean depth (m)	8.8	6.5	12.3	22.7	11.6	23.8	13.3
Mean Secchi disc reading (m)	1.6	2.0	7.7	11.9	7.9	11.0	11.1
Alkalinity: difference between summer mean surface and bottom values ($g \cdot HCO_3 \cdot m^{-3}$)	24.7	20.5	2.38	1.31	2.82	0.21	0.86
% O_2 saturation in summer bottom water	35.2	31.7	54.5	76.9	51.8	68.8	68.0
Mean NO_3 in surface water ($mg \cdot m^{-3}$)	5.8	5.7	2.2	1.4	1.1	1.5	1.3
Mean NH_4 in bottom water ($mg \cdot m^{-3}$)	284	432	19.3	7.9	13.3	8.3	4.4
Mean total P in surface and bottom water ($mg \cdot m^{-3}$)	70.5	116	14.6	19.1	32.1	10.8	6.2
Mean total plant pigments ($mg \cdot m^{-3}$)	18.0	32.8	3.7	2.6	5.1	3.0	2.7
Mean total dissolved solids ($g \cdot m^{-3}$)	49.7	66.8	61.0	78.7	50.3	104.6	21.7

Methods

The lakes were visited each month between April 1970 and April 1971. Zooplankton samples were taken by vertical net hauls through the water column at the deepest part of each lake. The zooplankton samples were initially collected with a 20 cm diameter net, 93 cm long, with a mesh size of 0.100 mm, but from May 1970 onwards, with a net of 30 cm mouth diameter and 100 cm length tapering to a diameter of 6 cm and of 0.158 mm mesh size. Two hauls from each station were combined and preserved immediately in 4% formalin. Chapman (1973) and Burns (1979a) assessed the variability found between replicate samples with such nets and concluded that it was acceptable. The samples were all collected and counted in a uniform way by V.H.J. and all the lakes were visited within a three day period each month. Phytoplankton samples and water for chemical analyses were collected at the same time, and water transparency, temperature and dissolved oxygen measured (see Flint, 1977; McColl, 1972).

The animals in five 2 ml aliquots from each sample were counted in a squared plastic counting cell using a stereoscopic microscope, and all samples were checked for any animals not numerous enough to appear in the sub-samples.

Male and female adult calanoid and cyclopoid copepods were counted separately and the ovigerous females and the number of eggs per egg sac were recorded, so the percentage of egg-bearing females in the samples, and the mean number of eggs in a clutch could be calculated. If the number of calanoid females was less than 50 in the aliquots counted, more were included from a random sample to make the number up to/over 50. Copepodite stages were not distinguished nor were calanoid and cyclopoid nauplii separated since the cyclopoid populations were so small.

For the cladoceran species the percentage of ovigerous females and the mean and maximum numbers of eggs per pouch were also calculated from a subsample of at least 50 females.

The counts were converted from numbers per 2 vertical hauls to numbers per m^2 by multiplying them by 15.9 for the April-May 1970 samples collected with the smaller net, and 7.07 for the remaining months. They were also expressed as numbers per litre by dividing by an appropriate depth factor representing the populated depth zones of the lakes. Information on the vertical distribution of zooplankton (not reported here) was determined by closing net samples on 2–6 dates (most frequently in summer) from each lake. The deeper layers of the lakes often had very few animals present, particularly if their hypolimnia became de-oxygenated. The factors were: Lake Ngapouri, 8 m in November-April, 24 m otherwise; Lake Okaro, 14 m except in December (6 m), January-February (5 m), March-April (8 m); Lake Okataina 40 m; Lake Rotokakahi 30 m, except in January-February (20 m), and March (17 m); Lake Tikitapu 25 m.

In order to determine the rate of recruitment of new individuals into the *Calamoecia* populations the development times in each phase of the life cycle were calculated. We used the equations derived from laboratory rearing experiments by Green (1976b), which have the general form – Development time (in days) = $a(T - 4.1)^{-2.05}$ – where T is temperature and the constant a is 1317 for eggs, 5936 for nauplii and 13646 for copepodites. The mean water temperatures in the populated depth zones were used. The resulting times were then divided into the total number of eggs, nauplii or copepodites to give the numbers of eggs hatching per day, or nauplii becoming copepodites or copepodites maturing as adults (the daily recruitment).

Multivariate analysis

In an attempt to more objectively detect any affinities between the lakes we have followed the approaches used by Sprules (1977), Janicki & DeCosta (1979), Janicki *et al.* (1979) and Roff *et al.* (1981), and analysed the *Calamoecia* population data by multivariate statistical techniques. Patterns in the *Calamoecia* population in the seven lakes were summarised by a principal components analysis (PCA) of the population parameter: lake and month correlation matrix. The resulting patterns were related to limnological characteristics of the lakes (McColl, 1972) by calculating the Spearman rank correlations between the score of each month in each lake on the principal components and the limnological data. Cluster analysis, using Euclidean distance as a measure of similarity, was used as an adjunct to PCA, and to help identify lake groupings.

With both methods, the data were first transformed to natural logarithms and six different analyses made. Firstly the whole year's data were considered together, and then the 'summer' (November-April) and 'winter' (May-October) months were considered separately. In each case analyses were made with the data expressed on both an areal and a volumetric basis, the latter obtained by dividing the areal figure by the depth zone inhabited by *Calamoecia*. Analyses were carried out at the Waikato University Computer Centre using BMDP programmes 4M and 2M (Dixon & Brown, 1979) for PCA and cluster analyses respectively and SPSS for rank correlation analysis (Nie, *et al.* 1975).

Results

The species found are listed in Table 2 which shows the close similarity in limnetic community composition between the lakes.

The percentages contributed to the total populations by each species are shown in Figure 2. For most of the year *Calamoecia* was the dominant species in each lake, replaced only occasionally by Cladocera, except in Lake Tikitapu. There, in sharp contrast, *Calamoecia* rarely formed more than 50% of the population and *Bosmina* was frequently the dominant. Rotifers appeared to be of very minor importance except in Lakes Rotokakahi and Tikitapu, though they were probably not adequately sampled because of the mesh size of the nets.

Cladocera

Limnetic species

Only three species of limnetic Cladocera were found in this survey: *Daphnia carinata* King, *Ceriodaphnia dubia* Richard, and *Bosmina meridionalis* Sars. These species all occur in lakes throughout New Zealand, and are the only cladocerans in the New Zealand freshwater plankton (Chapman *et al.*, 1975).

Daphnia carinata was found only in Lake Rotoma where it appeared in very small numbers in January 1971.

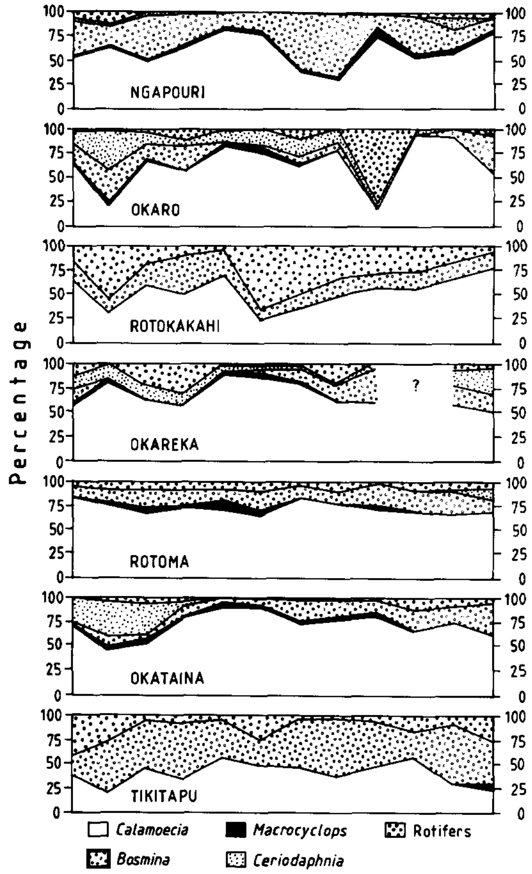

Fig. 2. The percentages of each zooplankton taxon found in monthly samples from the study lakes.

Ceriodaphnia dubia occurred in all the lakes except Lake Tititapu (Fig. 3), although in Lake Rotokakahi it was found in only three of the samples, in very low numbers. Lake Okareka was the only lake in which it was recorded in all months of the year, and in Lakes Rotoma and Ngapouri it appeared only spasmodically. Breeding females were always present in the populations although they usually formed less than 10% of them, and both the mean and maximum clutch sizes were low (Table 2). Clutches of ten eggs have been recorded in laboratory cultures of *C. dubia* (Jolly, unpublished).

Ephippial females occurred only in Lake Ngapouri, where in May 1970 approximately 30% of the females carried ephippia, though no males were observed. After May the population disappeared until the next summer.

Bosmina meridionalis was present throughout the year in all of the lakes (Fig. 3), although there

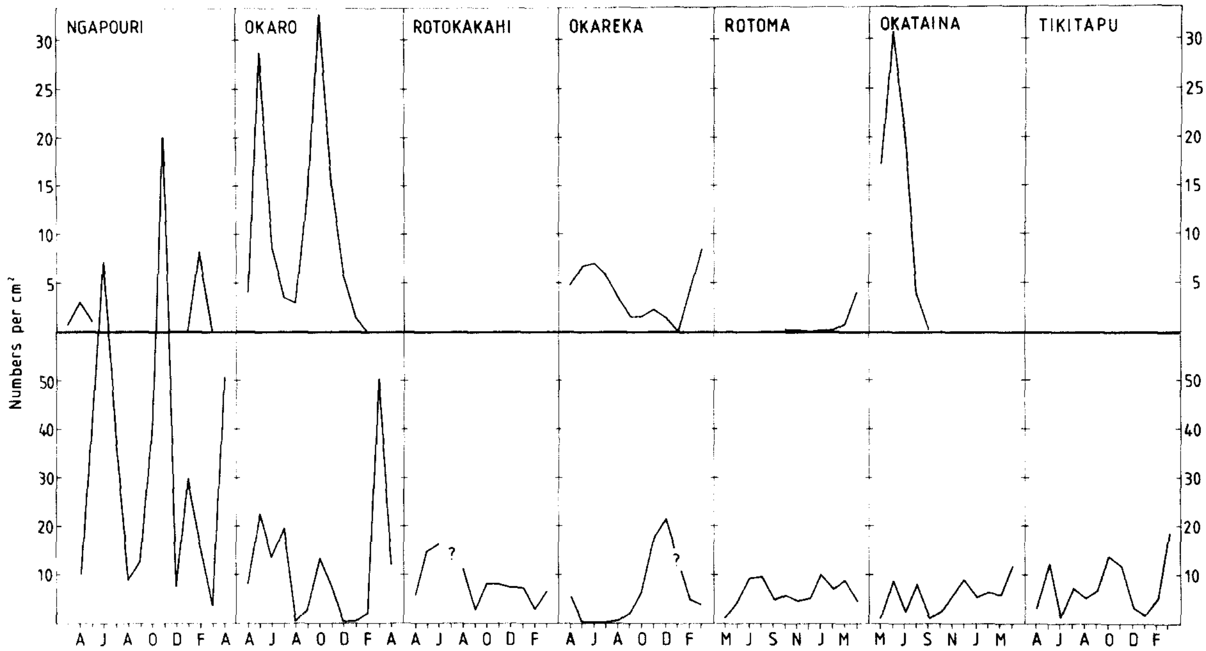

Fig. 3. Seasonal changes in abundance of *Ceriodaphnia dubia* (upper panel) and *Bosmina meridionalis* (lower panel).

Table 2. Animals recorded from monthy plankton hauls in the study lakes, April 1970 to May 1971. p = present.

	Ngapouri	Okareka	Okaro	Okataina	Rotokakahi	Rotoma	Tikitapu
Copepoda							
Macrocyclops albidus Jurine	p	p	p	p	p	p	p
Calamoecia lucasi Brady	p	p	p	p	p	p	p
Cladocera							
Bosmina (Neobosmina) meridionalis Sars	p	p	p	p	p	p	p
Ceriodaphnia dubia Richard	p	p	p	p	p	p	-
Daphnia carinata King	-	-	-	-	-	p	-
* *Alona guttata* Sars	p	-	-	p	p	p	-
* *Biapertura affinis* (Leydig)	-	p	-	-	-	-	-
* *Chydorus sphaericus* (O.F. Muller)	-	p	p	p	p	-	p
* *Neothrix armata* Gurney	-	-	-	-	p	p	-
* *Streblocerus serricaudatus* Fischer	-	-	-	-	-	-	p
Hydracarina							
* *Piona uncata exigua* Viets	-	-	p	-	-	-	-
Rotifera							
Asplanchna brightwelli Gosse	p	-	p	-	-	-	-
Asplanchna priodonta Gosse	p	p	p	p	p	p	p
Filinia terminalis (Plate)	p	p	p	-	p	-	-
Gastropus	p	p	p	p	p	p	-
Hexarthra	p	-	p	-	-	-	p
Keratella	p	p	p	-	-	-	-
Polyarthra	-	p	-	p	p	-	p
Synchaeta	-	p	-	p	-	-	-
Coelenterata							
Craspedacusta sowerbyi Lankaster	p	p	-	p	p	-	-

* Littoral or benthic.

Table 3. Mean annual population sizes and annual ranges of breeding parameters of *Ceriodaphnia dubia*.

Lake	Mean No. m^{-2}	Mean clutch size	Max. clutch size	% ovigerous females
Ngapouri	11101	1-1.4	1-2	1-21
Okaro	96652	1-2.9	2-4	3-37
Okareka	39042	1-1.7	1-3	1-38
Okataina	59794	1-1.4	1-2	2-10
Rotoma	4288		Too few animals	

was no common pattern of seasonal variation amongst them. It was particularly abundant at times in Lake Ngapouri. Although *B. meridionalis* can produce clutches of up to eight eggs when well fed in cultures (Jolly, unpublished) the largest clutch size noted in this study was four, and mean monthly clutch sizes were usually less than two (Fig. 4); often only one egg was present in the brood pouch. Breeding occurred throughout the year, except in May and June in Lake Okareka. The percentages of egg-bearing females in the populations were generally low, the annual means ranging from 17-34% (Table 4, Fig. 4). A distinctive feature of the Lake Rotokakahi population, which had the highest annual mean, was that the percentage was less than 20 only once, whereas this was frequently the case in all the other lakes. No males were observed but females with the ephippial development noted by Donovan (1970) were common, particularly in Lakes Ngapouri and Okaro.

Other species

Neothrix armata Gurney is an Australasian benthic species, previously known in New Zealand only from Lake Rotoiti (Chapman & Lewis, 1976). It was found in Lake Rotoma and Lake Rotokakahi.

Table 4. Annual means of populations sizes and breeding parameters of *Bosmina meridionalis*.

Lake	Mean No. m^{-2}	Mean clutch size	% ovigerous
Ngapouri	320060	1.05	18.9
Okaro	118861	1.29	21.4
Rotokakahi	99182	1.13	34.0
Okareka	58060	0.96	14.4
Rotoma	64393	1.03	19.0
Okataina	58581	1.07	16.9
Tikitapu	78205	1.05	21.4

The rare *Streblocerus serricaudatus* Fischer was found in plankton samples from Lake Tikitapu. *Chydorus sphaericus* (O.F. Muller), a cosmopolitan species, occurred in many samples in small numbers, but in Lake Rotokakahi it was sufficiently common at times to form 3.5% of the Cladocera. *Alona guttata* Sars and *Biapertura affinis* (Leydig) are littoral-benthic species and their presence in occasional plankton hauls was probably fortuitous.

Copepods

The same two species of copepods occurred in all lakes. *Macrocyclops albidus* Jurine, a cosmopoli-

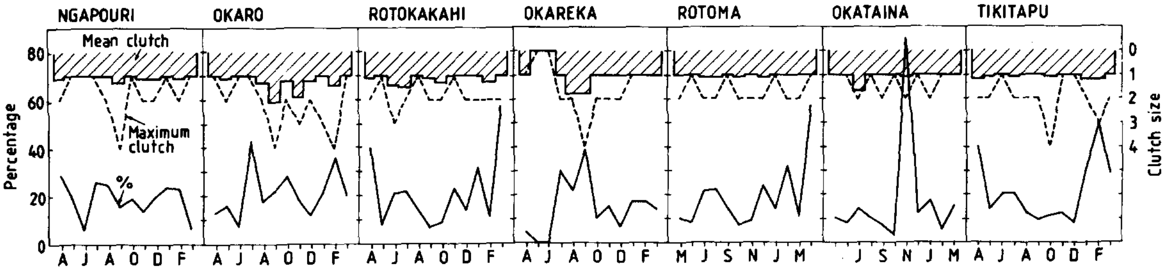

Fig. 4. Seasonal changes in breeding parameters of *Bosmina meridionalis*, showing the mean and maximum clutches and percentage of egg-bearing females.

tan cyclopoid, is generally considered littoral, but Chapman (1973) also found it to be planktonic in Lakes Rotorua and Rotoiti as did Forsyth & McCallum (1980) in Lake Taupo. The adults were rarely taken, except in the shallow Lakes Ngapouri and Okaro (Fig. 5). Copepodites occurred all through the year, but cyclopoids never formed more than 10% of a sample (Fig. 2).

The calanoid copepod *Calamoecia lucasi* Brady is common in lakes in northern New Zealand, and also in parts of Australia (Bayly, 1961; Jolly, 1955). Bayly (1961) considers it sub-tropical, and it has not been recorded further south than latitude 40° in New Zealand. The population dynamics and production of *C. lucasi* have been studied in Lakes Rotorua and Rotoiti by Chapman (1973), and in Lake Ototoa by Green (1976b).

There were considerable differences between the seven lakes in both the size and structure of their *Calamoecia* populations as well as in the timing of seasonal changes (Fig. 6). The highest densities occurred in Lakes Okaro and Ngapouri and the lowest in Lake Tikitapu, but the populations of these three lakes had coefficients of variation about their annual means which were distinctly higher than those in other lakes. That in Lake Rotoma was particularly stable.

There was often little direct relationship between the fluctuations in the numbers of nauplii, copepodites and adults in each lake (Fig. 7). This is not surprising since in these lakes breeding is continuous and relatively mild winters do not impose a strong seasonality on the populations. In Lakes Okaro and Ngapouri adults were almost always more abundant than copepodites, but in Lakes Rotoma and Okataina copepodites were the most numerous. In Lakes Tikitapu, Okareka and Rotokakahi there were usually more adults between March and September, but more copepodites in the warmer months. Nauplii (because of their faster development times and because of the early stages may not have been retained by the sampling net), were usually the least abundant stage. Table 5 includes the mean annual composition of the populations. The

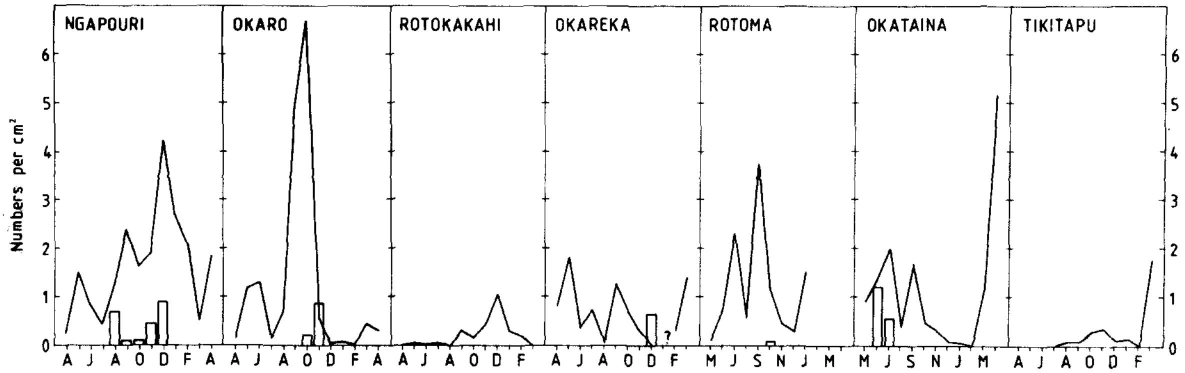

Fig. 5. Seasonal changes in numbers of copepodites (lines) and adults (boxes) of *Macrocyclops albidus.*

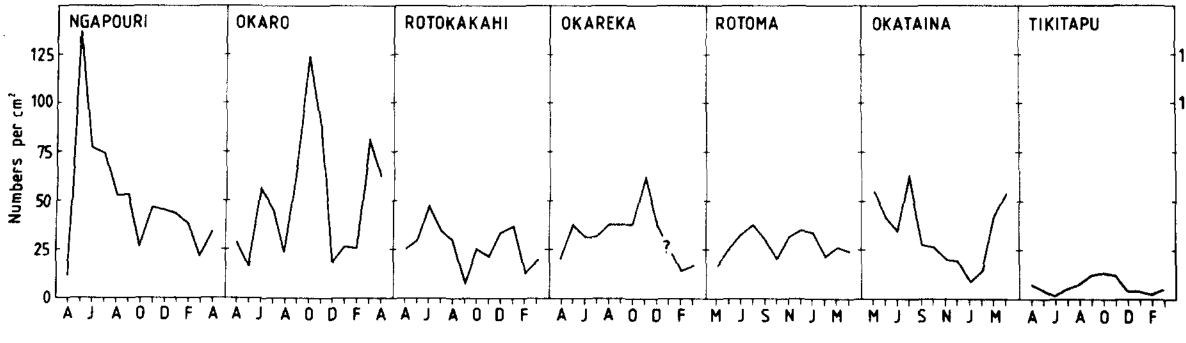

Fig. 6. Seasonal changes in total numbers of *Calamoecia lucasi.*

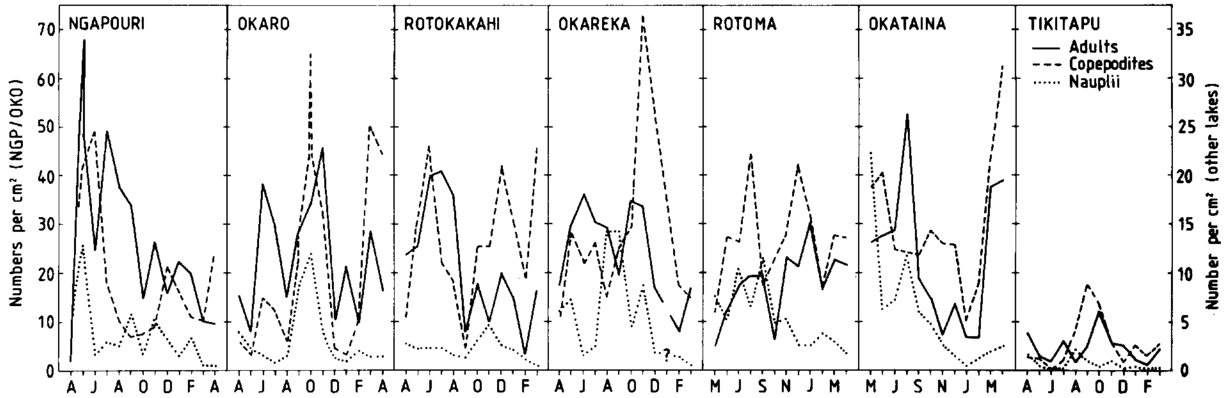

Fig. 7. Seasonal changes in the numbers of each lifecycle stage of *Calamoecia lucasi*. Scale on left axis applied only to Lakes Ngapouri and Okaro.

Table 5. Annual means of the *Calamoecia* populations. The mean percentage in each active life cycle stage is also given.

Lake	Mean clutch size	Mean % ovigerous females	Mean no. m^{-2}				
			Eggs	Nauplii	Copepodites	Adults	Total
Ngapouri	2.37	37.9	38267	78350	172381	271886	522619
				15%	33%	52%	
Okaro	2.17	30.4	18424	67052	172474	239065	498597
				13%	39%	48%	
Rotokakahi	2.94	55.6	117650	21232	134104	106972	262254
				8%	51%	41%	
Okareka	2.44	43.2	84633	57290	143785	125116	326191
				18%	44%	38%	
Rotoma	1.89	47.2	88421	54150	135700	86580	276431
				20%	49%	31%	
Okataina	1.88	44.6	42500	58050	163686	117981	339727
				17%	48%	35%	
Tikitapu	2.92	52.9	82708	6835	30120	25125	62080
				11%	49%	40%	

breeding parameters are shown in Fig. 8. Clutch sizes were always low, the maximum found in any of the lakes being 7. They were generally smallest between March-April and August-September, but the seasonal range was not great although the timing of changes differed between lakes. The percentage of egg-bearing females in the populations were variable but were particularly low in Lakes Okaro and Ngapouri where they rarely exceeded 50% (Fig. 8). In Lakes Rotokakahi and Tikitapu they were less than 50% on two or three dates only.

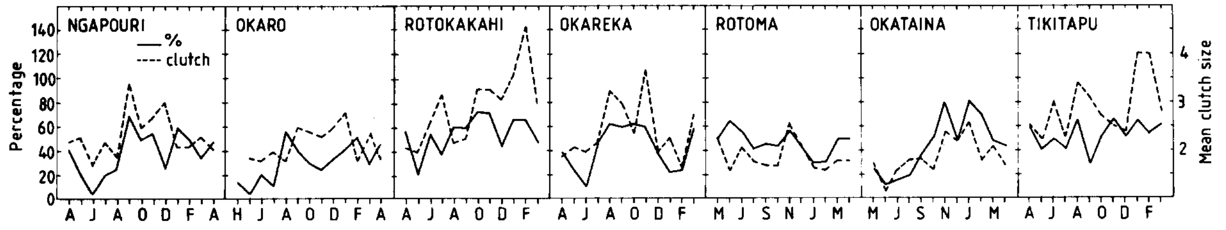

Fig. 8. Seasonal changes in the percentage of egg-bearing females and in mean clutch size of *Calamoecia lucasi*.

Daily recruitment

The recruitment rates are approximations since their calculations used only the mean temperature of the populated water column, and we had to use laboratory determined development rates for well-fed animals since our data was not sufficiently detailed to determine the true rates in the lakes. Recruitment rates are summarised in Table 6. Their seasonal changes are similar to those in numerical abundance and are not presented here. Duncan's new multiple range test of the data (Table 7) showed that the Lake Tikitapu population was the most different, with very low recruitment rates. This reflects low stock numbers since the annual temperature range (9.8°-17.7°) was similar to those in the other deeper lakes: Rotoma (10.8°-17.8°), Okataina (11.0°-16.4°), Okareka (9.8°-16.3°), Rotokakahi (10.3°-17.8°). The range was greater in Lakes Okaro (8.8°-22.8°) and Ngapouri (8.5°-20.0°) which accounts for the differences between the lake groupings in Duncan's tests on their egg and naupliar numbers and their daily recruitment rates (Table 7).

Multivariate analyses of the *Calamoecia* data

In the PCA of the areal data, the first two principal components accounted for 72.7% of the variance in the data, the first component (PC1) accounting for 51.2% and the second (PC2) accounting for 21.5% of the variance (Table 8). PCA of the volumetric data gave very similar results. Total stock, adult, copepodite, naupliar, egg stocks and

Table 6. The annual means and ranges (min.-max.) of the daily recruitment of eggs, nauplii and copepodites of *Calamoecia* (numbers per m^2 d^{-1}).

Lake	Eggs	Nauplii	Copepodites
Ngapouri	40490	8736	4580
	1370-86053	1267-20791	2724-18088
Okaro	30054	4273	5732
	1332-93401	594-7110	845-20470
Rotokakahi	22724	1308	3986
	7937-42966	346-2908	446-9794
Okareka	19576	2893	3371
	3232-66381	478-6675	304-10270
Rotoma	12529	3058	3873
	4347-30424	1502-5382	1545-7333
Okataina	11733	3281	4463
	806-38212	467-14276	1831-10838
Tikitapu	5178	290	723
	1607-9061	75-860	30-1705

Table 7. Groupings derived from Duncan's new multiple range tests of the monthly *Calamoecia* data ($\log_e$ transformed; $p = 0.05$). NP = Ngapouri, OO = Okaro, OT = Okataina, OK = Okareka, RK = Rotokakahi, RM = Rotoma, TT = Tikitapu.

Variable	Groups			
	A	B	C	D
Egg numbers	NP	NP	TT	
	OO	OT	OT	
			RM	
			OK	
			RK	
Naupliar numbers	NP			
	OO			
	RM	RK	TT	
	OT	OT		
	OK	OK		
Copepodite numbers	NP			
	OO			
	OK	TT		
	OT			
	RM			
	RK			
Adult numbers	NP	RM	TT	
	OO	RK		
		OT		
		OK		
Total population	NP	RK	TT	
	OO	RM		
	OT	OT		
	OK	OK		
Percentage ovigerous females	NP	NP	TT	
	OO	RM	RK	
	OT	OT	OT	
	OK	OK	OK	
Mean clutch size	NP	OT	TT	
	OO	OO	RK	
	OK	RM		
Daily egg hatching rate	NP	RM	RM	TT
	OO	OO	OT	OT
	OK	OK	OK	
	RK	RK		
Daily naupliar hatching rate	NP	OO	RK	TT
		OK	OK	
		OT		
		RM		
Daily copepodite hatching rate	NP			
	OO			
	OK	TT		
	OT			
	RK			
	RM			

Table 8. Eigenvectors and correlations of areally based *Calamoecia* population parameters for the whole year with components 1 and 2 for seven Rotorua lakes. ns = not significant.

	Principal Component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Total stock	0.188	0.972	-0.050	-0.107 ns
Copepodite stock	0.169	0.875	-0.057	-0.122 ns
Adult stock	0.163	0.841	-0.012	-0.025 ns
Copepodite recruitment	0.156	0.808	0.012	0.027 ns
Nauplius recruitment	0.156	0.809	-0.044	-0.094 ns
Nauplius stock	0.150	0.776	-0.083	-0.178 ns
% ovigerous	-0.051	-0.264	0.359	0.772
Egg turnover	0.111	0.574	0.344	0.738
Clutch size	-0.050	-0.264	0.338	0.727
Egg stock	0.119	0.614	0.298	0.641
% of variance explained by component	51.7		21.5	

the recruitments (all of which are parameters associated with the size of the population, or segments of it), have significant correlations with PC1. Thus lakes and months with relatively large populations will have high scores of PC1 and will lie to the right of the origin in Figure 9. Since PC1 accounts for the largest proportion of the variance in the data the major differences amongst the lakes are associated with population size and the subsections of the population vary in the same way as total population size between lakes. Percentage of ovigerous females, clutch size, egg stock and egg turnover are positively correlated with PC2, which thus summarizes variations in breeding parameters. Other population parameters (with the exception of copepodite recruitment rates) show weak negative relationships with PC2, indicating that breeding activity is inversely related to population size, which would occur if the populations were food limited.

Similar patterns resulted from the separate PCAs of the data from the 'summer' and 'winter' months (Table 9). In both monthly groupings, PC1 accounted for most of the variance and was associated with indices of population size, with PC2 being related to breeding parameters. PC1 accounted for less, and PC2 more, of the variability in the data during the winter than the summer months, i.e. breeding variations between the lakes were least in the summer, when population sizes were most variable. This could result from greater food limitation in summer, depressing reproduction and resulting in higher mortality.

The ordination plot of areal PCA (Fig. 9) shows fairly continuous variation along both components and no very distinct groupings of points. Along PC1 Tikitapu is separated to the left of the other lakes, while Okaro and Ngapouri (which are clearly eutrophic (McColl, 1972)) are located well to the right of the origin.

Cluster analysis (Fig. 10) was used to gain a better indication of possible groupings of the lakes. The most distinct groupings emerging from the cluster analysis of the areal data (Fig. 10) are shown in Figure 9. The analysis shows 3 major groups and 2 subsidiary ones. The two main clusters A and B differ largely on the basis of population size parameters, cluster B, which consists largely of Tikitapu data points, having low population indices. There is little separation of the lakes in cluster A although there is a suggestion that Okaro and Ngapouri are located more to the right of the cluster thus having larger populations. Cluster C is one data point only (Tikitapu June) with very low numbers. These groupings fall closely in line with McColl's eutrophic and mesotrophic (cluster A), and oligotrophic (clusters B and C), categories. It is clear, though, that the groups are not very distinct; because of seasonal variations none of the lakes are found exclusively in a single cluster, and there is obviously in reality a continuous gradation from one cluster to the next. Clusters D and E separate out a few data points of medium population levels

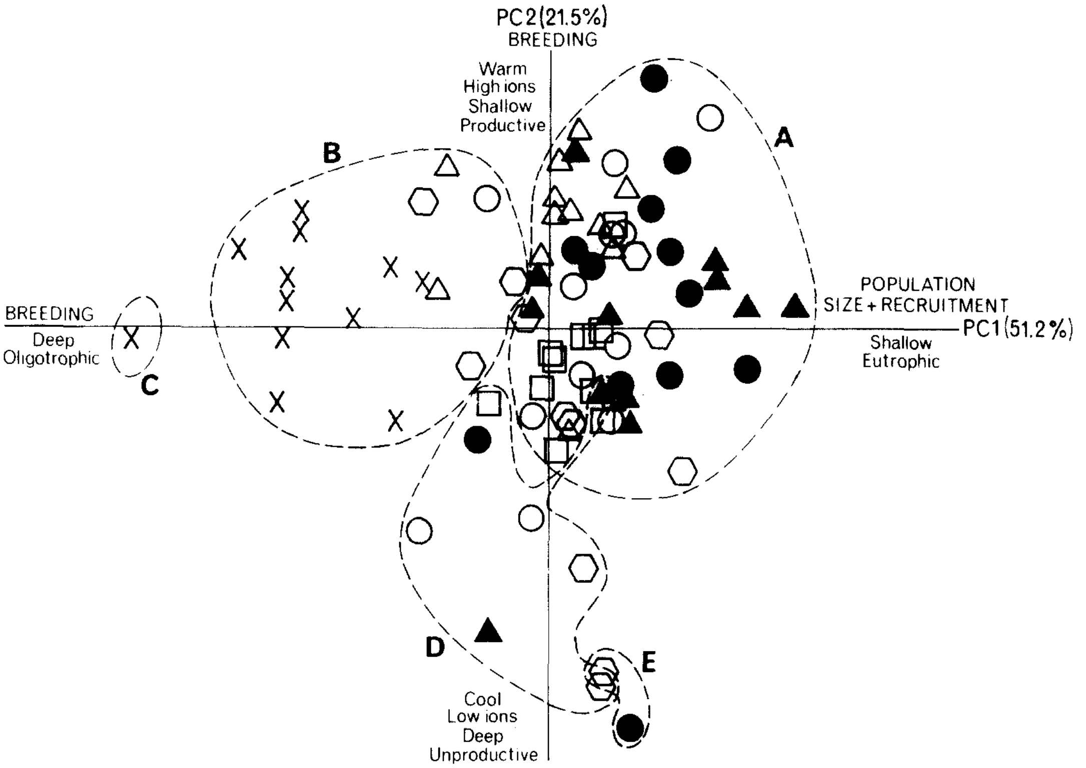

Fig. 9. Principal component ordinations of monthly samples from seven Rotorua lakes based on *Calamoecia lucasi* population parameters using data calculated on an areal basis. Dotted lines enclose groups determined by cluster analysis (Fig. 10) and variables included on the axes are from tables 9–12.
NP = L. Ngapouri; OO = L. Okaro; OK = L. Okareka; RK = L. Rotokakahi; RM = L. Rotoma; OT = L. Okataina; TT = L. Tikitapu.

but which have low breeding indices.

Cluster analyses of the volumetric data, and of the summer and winter data separately (not figured here), in general showed similar patterns to those indicated in Figures 9–10. In the summer analysis there was rather greater separation of groups than in the winter and the lakes with higher population levels (i.e. high scores on PC1) were rather more distinctly separated.

The rank correlation coefficients between the individual monthly PC scores and monthly values of various limnological parameters (McColl, pers. commun.) are shown in Table 10. Table 11 shows the correlations between the component scores and yearly mean values of these parameters, catchment ratio (ratio of grass + residential land + exotic forest area: catchment area), mean depth and a morphoedaphic index (Yearly mean surface TDS: mean depth) which McColl (1972) showed were indices of trophic status in the lakes.

PC1 scores are significantly correlated with most of the indices of trophic state. Lakes with high scores on PC1 are relatively shallow, have low Secchi transparency and bottom water oxygen concentrations; and have high levels of chlorophyll, pH, surface ion concentrations, bottom water concentrations of NH4 and TP, catchment ratios and MEI. Lakes with low scores on PC1 show opposite tendencies. PC1 is thus associated with a trophic status or productivity gradient. PC2 is less clearly related to the measured parameters than PC1, but in general, PC2 scores are significantly correlated with epilimnetic temperatures, surface ion levels (particularly Na and HCO_3), mean depth and pigment concentrations. Lakes with high scores on PC2 are thus relatively warm, shallow and with high ionic concentrations; and so are probably also relatively productive. The positive correlation with temperature is as expected because of the dependence of egg development rate on temperature (Green, 1976b), but the reasons for the relationship between PC2, salinity and mean depth are not clear,

Table 9. Eigenvectors and correlatons of *Calamoecia* areal population parameters with components 1 and 2 for seven Rotorua lakes. ns = not significant.

(a) For 'summer' months

	Principal Component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Total stock	0.167	0.972	0.053	-0.088 ns
Adult stock	0.158	0.919	0.027	-0.046 ns
Copepodite stock	0.143	0.828	-0.040	0.067 ns
Nauplius recruitment	0.142	0.824	-0.078	-0.130 ns
Copepodite recruitment	0.136	0.789	0.105	0.175 ns
Egg stock	0.135	0.785	0.306	0.513
Egg recruitment	0.134	0.776	0.291	0.487
Nauplius stock	0.129	0.748	-0.111	-0.186 ns
Clutch size	-0.044	-0.253	0.469	0.785
% ovigerous	-0.074	-0.428	0.406	0.679
% of variance explained by component	58.0		16.7	

(b) For 'winter' months.

	Principal Component			
	1		2	
	Eigenvector	Correlation	Eigenvector	Correlation
Total stock	0.188	0.977	-0.022	-0.051 ns
Copepodite stock	0.176	0.914	-0.071	-0.170 ns
Copepodite recruitment	0.172	0.896	-0.089	-0.215 ns
Nauplius stock	0.162	0.842	-0.025	-0.061 ns
Nauplius recruitment	0.155	0.806	0.045	-0.110 ns
Adult stock	0.151	0.782	0.045	0.108 ns
Egg recruitment	0.102	0.529	0.334	0.805
% ovigerous	-0.040	-0.207 ns	0.313	0.756
Egg stock	0.095	0.494	0.311	0.751
Clutch size	-0.050	-0.257	0.300	0.724
% of variance explained by component	52.0		24.1	

although that with mean depth may simply result from shallow lakes having high temperatures. The relationship with salinity is interesting since it may underly, if only partly, the very low clutch sizes of *C. lucasi* in L. Ototoa (Green, 1976b) which lies close to the sea and has a high salinity of 149 mg l^{-1} (Green, 1975).

Hydracarina

A mite, *Piona uncata exigua* Viets, was numerous in Lake Okaro plankton, particularly in the spring. It customarily lives in weed beds but may occur, sometimes in large numbers, in open water samples (Stout, 1975; Burns & Mitchell, 1980; Chapman, Jolly & Flint, 1981).

Rotifera

The rotifers found in the lakes are listed in Table 2. The most common rotifer was *Asplanchna priodonta* Gosse. *A. brightwelli* Gosse was recorded from Lakes Ngapouri and Okaro but not in large numbers. *Asplanchna* was perennial in all the lakes

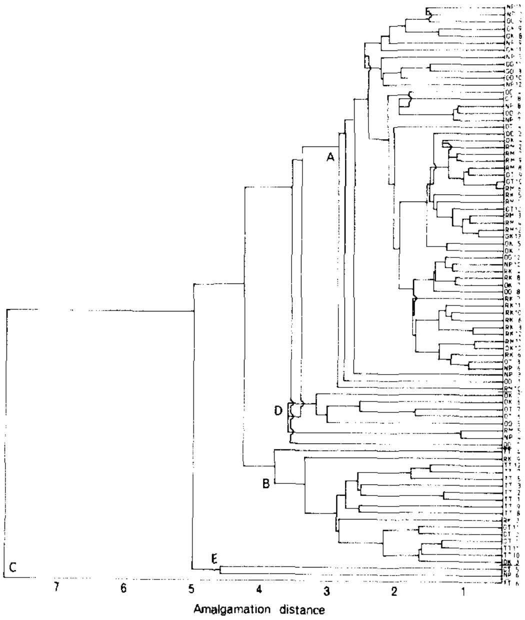

Fig. 10. Cluster analyses of seven Rotorua lakes based on *Calamoecia lucasi* population parameters using data calculated on an areal basis. Similarity is measured by euclidean distance. NP = L. Ngapouri; OO = L. Okaro; OK = L. Okareka; RK = L. Rotokakahi; RM = L. Rotoma; OT = L. Okataina; TT = L. Tikitapu.

Table 10. Rank correlation coefficients of areally based PC1 and PC2 scores of *Calamoecia lucasi* populations in seven Rotorua lakes with monthly values of a variety of environmental variables (McColl, pers. comm.).

	Principal Component	
	1	2
Temperature	-0.04	0.19*
Secchi	-0.42**	-0.12
Chlorophyll	0.40***	0.03
pH	0.33***	0.25*
Summer Hypolimnetic O_2	-0.12	0.00
TDS	0.27**	-0.27**
Ca	0.51***	-0.12
Mg	0.36***	-0.17
Na	0.22*	-0.42***
K	0.51***	-0.10
SO_4	0.58***	0.01
Cl	0.27**	-0.14
HCO_3	0.33***	-0.26**
Hypolimnetic TP	0.27***	0.00
Hypolimnetic NH_4	0.41***	0.05

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Table 11. Rank correlation coefficients of areally based PC1 and PC2 scores of *Calamoecia* populations with yearly mean values of a variety of environmental variables in Table 1. Catchment ratio is the ratio of area cleared of native forest to total catchment areas.

	Principal Component	
Variable	1	2
Catchment ratio	0.60***	-0.06
Mean depth	-0.32**	-0.25**
Morpho-edaphic index	0.56***	0.10
Alkalinity difference	0.46***	0.22*
O_2 in bottom waters in summer	-0.23*	-0.28**
Salinity	0.35***	-0.37***
Mean Secchi depth	-0.48***	-0.17
Total pigment	0.43***	0.21*
Total phosphorus	0.55**	0.11
NO_3 in surface waters	0.54***	-0.15
NH_4 in bottom waters	0.39***	0.11

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

except Okaro and Ngapouri (Fig. 11). The largest populations were found in Lakes Okaro, Rotokakahi and Okareka. It may be an important predator on plankton, since the bodies of *Bosmina, Ceriodaphnia*, nauplii and of other rotifers, as well as *Volvox* and *Staurastrum*, were seen through its clear body wall. The occurrences of other species of rotifer were not studied in detail (and the mesh size of the sampling net was too coarse to retain smaller rotifers), but collectively they were almost always considerably less numerous than *Asplanchna* and were recorded more spasmodically (Fig. 11). They were most frequent and most abundant in Lakes Ngapouri, Rotokakahi and Okareka.

Coelenterata

Medusae appeared in summer samples from Lakes Ngapouri, Okareka and Rotokakahi. The specimens were immature and therefore not readily identifiable but mature *Craspedacusta sowerbyi* Lankaster were identified from Lake Ohakuri (Fish, 1971), which receives water from Lake Ngapouri via the Waikato River system.

Discussion

The primary aim of this study was to compare the abundance and species composition of the zoo-

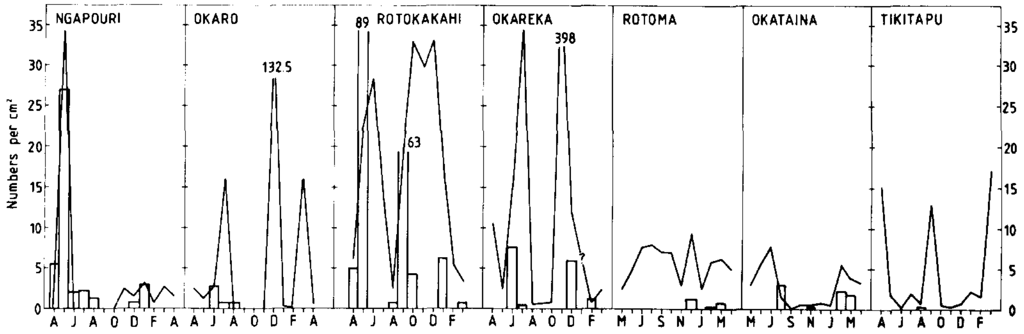

Fig. 11. Seasonal changes in abundance of *Asplanchna* (lines) and other rotifers (boxes).

plankton in lakes known to be of different trophic status. Such comparisons ideally are made on the basis of production rather than standing stock, but the determination of productions in these lakes would have required more frequent sampling to obtain adequate information on growth rates and population structure. Standing stock comparisons can be misleading since large numbers of zooplankton may be found in a lake where food availability is limiting growth rates, and predators on zooplankton may also depress population sizes to lower levels than the carrying capacity of a lake. Data on zooplankton numbers must therefore be interpreted with caution, particularly in view of the extensive variations in abundance which may occur between different years in the same lake.

New Zealand zooplankton communities contain a limited number of crustacean species, too ubiquitous in their occurrence to act as trophic indicators (Stout, 1970; Chapman *et al.*, 1975; Burns, 1979b). The study lakes all contained the same crustacean species except for Lake Tikitapu, which lacked *Ceriodaphnia*. This species is less universal in its occurrence in New Zealand than *Bosmina* (Chapman *et al.*, 1975), though both have been found in a wide range of habitats.

The only major change in species composition which is known to have occurred in recent decades has been the establishment of *Ceriodaphnia* in Lake Okataina. This was not found in the earliest zooplankton survey of the lakes in 1955–56 (12 monthly samples; Jolly, 1977) but now occurs there in moderate numbers (Fig. 3). *Ceriodaphnia* may also not have been in Lake Rotoma at that time since Jolly did not find it on her two visits, but even now it is rare in this lake and was often not recorded in the 1974–75 samples. The presence of *Daphnia* in Rotorua lakes requires further confirmation. In 1955–56 it was recorded as 'very few' on one or two sampling dates in Lake Okareka and one individual was found in two samples from Lake Rotoma (Jolly, unpublished 1959). In the latter lake the recent records are of 1–6 animals per sample on only three dates. It has thus not become more abundant in spite of considerable changes in the trophic state of the lakes as a result of agricultural and urban development. It is not present in many North Island lakes (Chapman *et al.*, 1975), though its distribution is apparently not limited by fish predation since it occurs in Lakes Taupo and Waikaremoana (Jolly, 1977), both of which contain introduced trout (*Salmo gairdneri* and *S. trutta*) and smelt (*Retropinna retropinna*) which has planktivorous fry. These fish also occur in the Rotorua lakes.

In six of the study lakes the zooplankton was usually dominated by calanoid copepods but even in Lake Tikitapu calanoids were of similar abundance to cladocerans (Fig. 2). Such a predominance of calanoid copepods is typical of many New Zealand lakes though cladocerans may be seasonally more abundant in some cases. There does not seem to be a clear-cut relationship between trophic status and the type of community. Calanoids dominate in some oligotrophic lakes, e.g. Lakes Taupo (Forsyth & McCallum, 1980) and Ototoa (Green, 1976a) and were almost always dominant in the more productive North Island Lake Rotoiti, but in Lake Rotorua Cladocera were often dominant (Chapman, 1973) as in eutrophic Lakes Hayes and Johnson (Burns & Mitchell, 1980). Stout (1970) noted that Cladocera were dominant in some eutrophic South Island lakes. Mitchell (1975), in comparing the zooplankton in Lake Mahinerangi in 1965 and again in 1969 when a three-fold increase in primary productivity had occurred, found no major changes in the numbers of the three most abundant species, *Boeckella hamata, Ceriodaphnia dubia* and *Bosmina meridionalis* though there had been increases in cyclopoids and in *Daphnia carinata.*

Despite the similarities in species composition in the study lakes they clearly differed in the abundance of zooplankton with the greatest contrasts between Lakes Okaro and Ngapouri, where numbers were generally highest, and Lake Tikitapu in which populations were very much smaller. However, certain features were common to all. Population sizes varied during the year by less than an order of magnitude in contrast to fluctuations over two or three orders in perennial species in northern hemisphere temperature lakes (Morgan *et al.*, 1980). The fluctuations that did occur (which are emphasised in our figures) varied between the lakes with no common pattern. A third feature was the continuously low clutch sizes (considerably less than in well-fed experimental females) and often low percentages of breeding females found in all the crustacean species. Breeding occurred throughout the year in all cases, except for an apparent two month period in Lake Okareka *Bosmina* population. These features have been noted in other North Island lakes (Chapman, 1973; Green, 1976b; Forsyth & McCallum, 1980).

In northern hemisphere temperature lakes it is common to find that the structure and functioning of zooplankton communities are altered by eutrophication (Gannon, 1981), with typically an increasing predominance of cyclopoids and in particular of smaller cladoceran species (e.g. Gliwicz, 1969, 1974; Winberg *et al.*, 1972; Patalas, 1975). A variety of explanations has been offered for these changes but the extent to which they are caused by alterations in the type and magnitude of predation (Brooks and Dodson, 1965; Kerfoot, 1980) and/or by changes in bacterial abundance and in the relative and absolute abundances of different algae remain to be fully clarified (e.g. Gliwicz, 1977; Nilssen, 1978; Webster & Peters, 1978; Kerfoot & Pastorok, 1978; De Mott, 1982). It is thus of interest that *Calamoecia* was dominant in all our lakes despite their range of trophic states, since a greater predominance of smaller Cladocera might have been predicted in the more productive lakes.

It seems likely that this lack of change in community structure with increasing productivity may be a consequence of the unusual characteristics of New Zealand zooplankton communities. As a result of New Zealand's depauperate fauna there are few major predators. There are no large invertebrate predators such as *Chaoborus* or carnivorous Cladocera, nor are there adult fish which are planktivorous. Also, because of the oceanic climate, there is a lack of seasonality, particularly in the North Island. Winters are mild, and breeding and development occur throughout the year. As a result of these factors the populations of the herbivorous zooplankton species are maintained throughout the year at such high levels that apparently most or all of the available food production is utilised (Chapman *et al.*, 1975). The populations are thus probably regulated mainly by competition for food, and this is true in both eutrophic (Chapman, 1973) and oligotrophic (Green, 1976b) lakes. In the study lakes food limitation also occurred as indicated by the low fecundities and the generally inverse relationship between population size and breeding parameters in the PCA.

Calanoid copepods could be expected to dominate in such food limited communities since they are more K-selected than are cladocerans (Allan, 1978). Their relatively slow development rates, ability to survive for long periods on stored food, and their possibly superior ability to compete for food at low food densities (McNaught, 1975) are all characteristics which might give calanoids a competitive edge under conditions of food shortage. Indeed *C. lucasi* may be particularly fitted to outcompete *Bosmina* and *Ceriodaphnia* since it is very small for a calanoid (females are about 0.8 mm long), which implies relatively lower absolute food requirements, and also it is known to feed on bacteria (Forsyth, pers. commun.).

Clearly, in such food limited populations, there should be a particularly close correlation between simple indices of population size and trophic status. For this reason and because of its predominance in the communities, *Calamoecia* was used to further examine the differences between the lakes. Visual inspection of the data in Figures 3–8, 11 and the results of Duncan's multiple range tests (Table 7) suggested that the lakes could be separated into three groups based on the abundance of *Calamoecia.* The Lake Tikitapu population was the most different, with the smallest total population, having low numbers and recruitment rates of all stages other than eggs, though the mean clutch size and the percentage of breeding females were amongst the highest found. Lakes Okaro and Ngapouri often had much larger populations than in the other lakes, but their breeding parameters were not particularly high: the ranges of clutch sizes found were low, as often were the percentages of breeding females. In most months Lakes Okareka, Rotokakahi, Rotoma and Okataina formed an intermediate group with medium population densities and breeding parameters. Lake Rotokakahi often had larger clutch sizes and a greater percentage of breeding females resulting in a large egg stock since adult numbers were also relatively high. The populations in Lakes Rotoma and Okataina had low mean (and maximum) clutch sizes, though *Calamoecia* was generally more numerous in the latter.

The more objective techniques of multivariate analyses also supported these suggested groupings. In the PCA, parameters associated with the size of parts or all of each population formed the first principal component which accounted for a major proportion of the variance, and the second component, associated with breeding parameters, was always much less important. The clear relation between the PC1 scores and the indices of trophic condition used by McColl (1972) supports the hypothesis that copepod population sizes might be related in a fairly direct way to lake productivity. Larger population sizes were associated with features such as higher nutrient levels and chlorophyll concentrations which indicate more productive lakes. The significance of the variations in breeding parameters which determined ordinations along PC2 cannot yet be explained, though a variety of factors may have caused them. They may be sensitive indicators of fluctuations in food availability caused by factors such as temporary increases in predation pressure, fluctuations in nutrient levels or climatic effects on primary production. When breeding parameters are low density dependent population regulation may be inferred and this appeared to be the case in our lakes.

In both the cluster analyses and the PCA the differences between the lakes were most marked in the warmer months particularly when the volumetric data were tested. The greater sensitivity of these data presumably reflects the importance of nutrient dilution in relation to plankton productivity. None of the lakes fell into an isolated cluster and they were almost always grouped with some of the monthly data points in at least one other cluster indicating that the lakes fell along a continuum between the most productive and the least.

Our groupings of the lakes, based on the *Calamoecia* analysis, differ somewhat from those of other workers (Table 12). McColl (1972), using mainly typological criteria, grouped Lake Tikitapu with Okataina and Rotoma in his oligotrophic series, whereas Flint (1977) included it with Okareka and Rotoma on the basis of phytoplankton. In a comparison of the macrobenthos of five of the lakes Forsyth (1978) found no significant differences between Lakes Tikitapu, Okareka and Rotokakahi.

Table 12. Trophic groupings of the study lakes using various criteria.

<table>
<tr><th>Grouping criteria</th><th>Eutrophic</th><th>Mesotrophic</th><th>Oligotrophic</th></tr>
<tr><td>Chemistry & Morphometry (McColl, 1972)</td><td>Okaro
Ngapouri</td><td>Rotokakahi
Okareka</td><td>Okataina
Rotoma
Tikitapu</td></tr>
<tr><td>Phytoplankton (Flint, 1977)</td><td>Okaro
Ngapouri</td><td>Rotokakahi
Okataina</td><td>Okareka
Rotoma
Tikitapu</td></tr>
<tr><td>Benthos (Forsyth, 1978)</td><td>Okaro
Ngapouri</td><td colspan="2">Tikitapu
Okareka
Rotokakahi</td></tr>
<tr><td>Zooplankton (This study)</td><td>Okaro
Ngapouri</td><td>Rotokakahi
Okareka
Okataina
Rotoma</td><td>Tikitapu</td></tr>
</table>

All these workers placed Lakes Okaro and Ngapouri in their eutrophic group. The use of zooplankton as integrators of biological conditions avoids the problems of interpreting data influenced by morphometric features of lakes such as hypolimnetic oxygen deficits or macrobenthos standing crops, whilst the long generation times of copepods in particular enable less frequent sampling than is required for phytoplankton.

Acknowledgements

The investigation was organised by Dr R. D. Thornton and his unstinted help in the initial field work was a great stimulation. The assistance of Miss C. Finlayson, Dr D. J. Forsyth and Dr R. M. S. McColl in the field work is gratefully acknowledged.

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Received 25 May 1983; in revised form 5 September 1984; accepted 6 September 1984.