ECOLOGICAL STUDIES ON LAKE OTOTOA WITH SPECIAL REFERENCE TO THE COPEPOD *CALAMOECIA LUCASI*.

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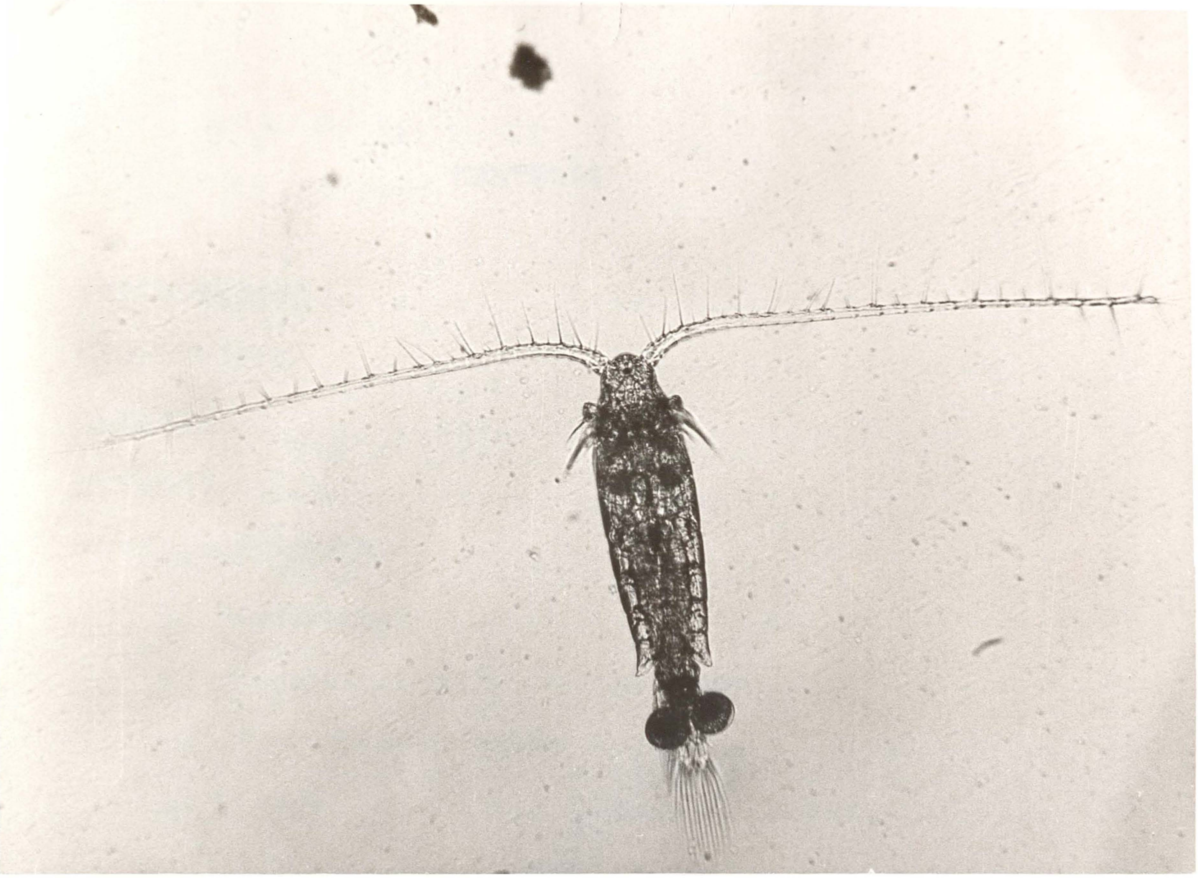
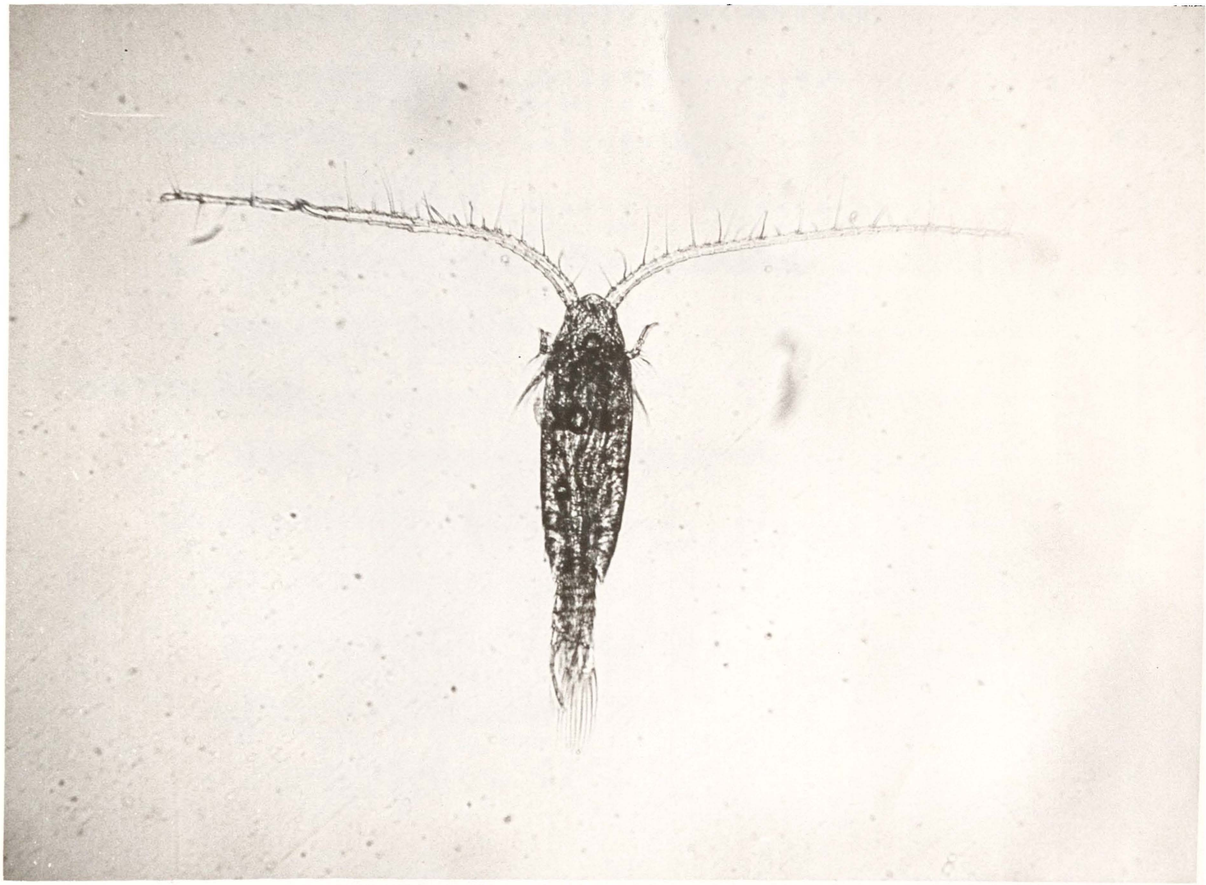
Frontispiece: *Calamoecia lucasi* adults - female above, male below (x85).





CONTENTS

SYMBOLS

Throughout this thesis the following symbols and abbreviations have been used:

* = $P > 0.05$
** = $P > 0.01$
*** = $P > 0.001$
n = number of observations
s = standard deviation
t = students t
r = value of the correlation coefficient.

"There is something fascinating about science. One gets such wholesale returns of conjecture out of such a trifling investment of fact."

Mark Twain

INTRODUCTION

New Zealand is a country richly endowed with lakes of all kinds, yet apart from some pioneering surveys (e.g. Cunningham et al 1953, Flint 1938 , Stout 1969, Jolly 1968) and a few more detailed recent studies (e.g. Fish 1970, Barker 1970, Chapman 1972) very little is known about their detailed limnology or of the biology of the plant and animal species inhabiting them. The South Island is characterised by having many large, deep glacial lakes, and a lesser number of smaller bodies of water, supporting populations of various species of the copepod genus *Boeckella*. In the North Island there are fewer larger lakes, and most of these are concentrated in the volcanic region near the centre of the Island. Elsewhere smaller bodies of water are more characteristic, and particularly in the far north and along the western coastline the most important and common of these are the sand-dune lakes. In contrast with the South Island, species of *Boeckella* are relatively less common and in most of the smaller lakes, as well as the majority of the larger central ones their place is taken by the small centropagid *Calamoecia lucasi* which is usually the dominant zooplankter whenever it occurs. However, only two studies have been made of its biology. Barker (1967) studied some aspects of its seasonal cycle in Lake Pupuke, a eutrophic lake near Auckland, and recently Chapman (1972) has made more extensive investigations of these aspects as well as of population dynamics in Lakes Rotorua and Rotoiti, two large mesotrophic lakes in the centre of the North Island.

The study upon which this thesis is based is the first of the ecology of *C. lucasi* in an oligtrophic lake, and was mainly concerned with the copepod's seasonal biology, population dynamics and production in one of the northern sand-dune lakes. As well as these aspects, the general limnology of the lake and the cycles of phytoplankton were considered in some detail, not only because of the importance of the environment in determining most limnological cycles, but also because of the lack of knowledge of the general limnology of this important class of New Zealand lake.

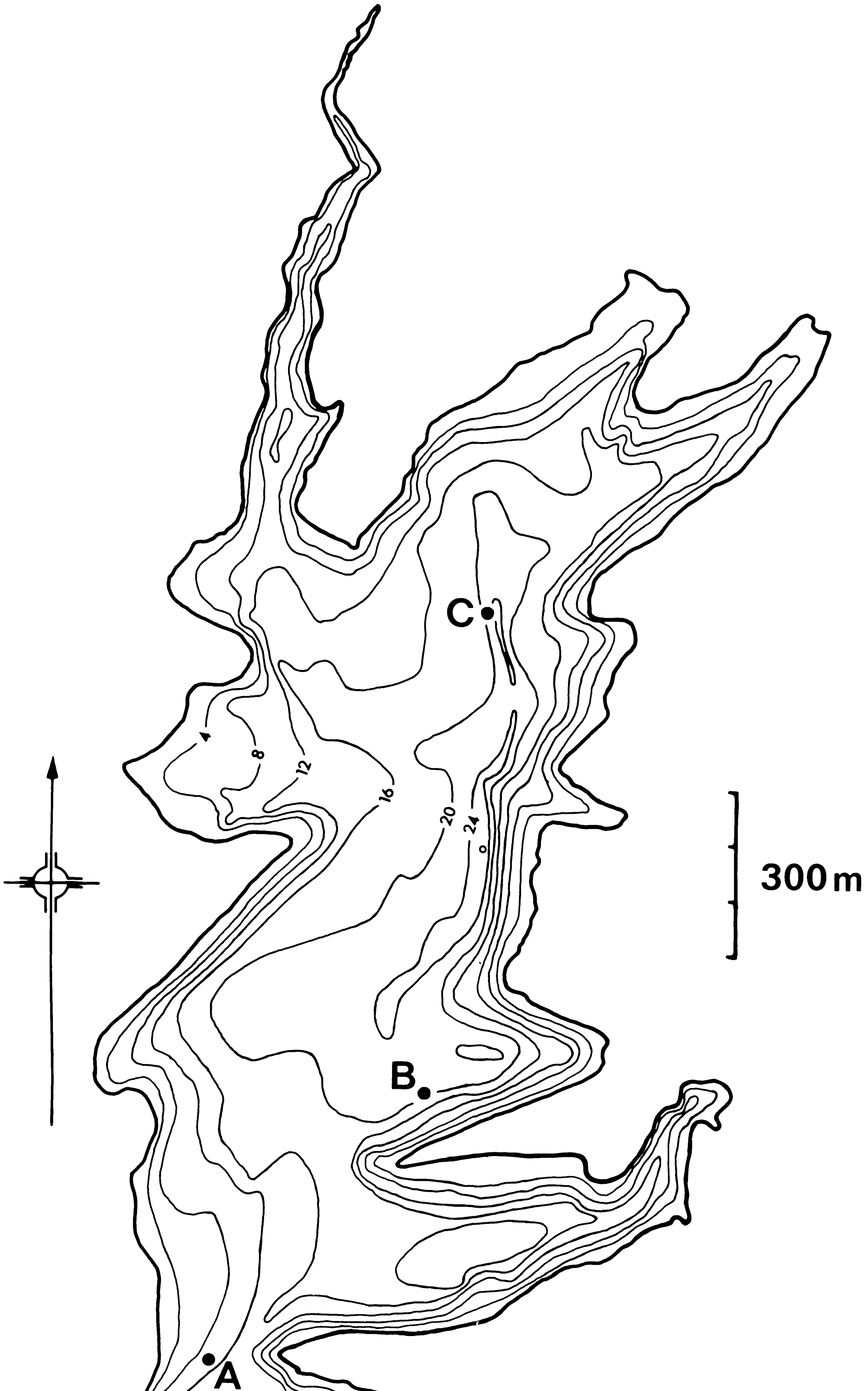
LAKE OTOTOA

Lake Ototoa lies about 50 miles north of Auckland at 30° 30' S and 174° 14' E in the extensive series of sand dunes which border much of the west coast of the North Island. It is situated on the south head of the Kaipara harbour, a peninsular of land separating the Tasman Sea from the harbour itself , and to the west, north and east the lake is never more than 5 km from the sea.

Ferrar (1934) believes that the dunes in the region of the Kaipara harbour are of two series, both formed during the Pleistocene. The older (Kaihu) series to the east have become consolidated as a yellow, sandy soil which is now extensively farmed, while the younger, darker and less consolidated series near the coast is being covered by drifting sand. Plantings of toetoe *(Cortaderia conspicua)* and spinifex *(Spinifex hirsutus)* have been made in an endeavour to consolidate the dunes, but in many places they are still constantly encroaching eastwards.

The whole coastline is characterised by the formation of lakes where the valleys of streams draining the consolidated dunes have been blocked by advancing sands. The lakes tend to be elongated and orientated with their longest axis in a north-south direction. The valley sides are steep and often there are dendritic side branches where small stream valleys have been flooded. Lake Ototoa is the largest and deepest of these lakes, many of the others being shallower because of filling by wind blown sand (Cunningham et al, 1953).

Fig. 1: Hydrographic map of Lake Ototoa showing the location of the sampling stations. Contour interval 4m.


C
4
8
12
16
20
24
300 m
B
A

A bathymetrical map of Lake Ototoa compiled in 1970 from echo sounding traverses (Irwin 1973) is shown in Fig. 1. A 4-metre contour interval has been used in this figure, but the areas enclosed by 2-metre isobaths have been calculated from the original chart with a compensating polar planimeter (Welch 1948) and these and other morphometrical parameters are given in table 1.

The lake is rectangular in shape, and the deepest regions are located to the east where the basin slopes steeply down from the Kaihu sands, while there is a much more gentle slope up towards the westward dunes. Drifting sand is encroaching along the central western shore of the lake, and the coformation of the basin probably results from gradual filling by an inflow of windborne sand from the west. The surrounding countryside is quite high with steep hills or dunes on all sides except the south and north, and this configuration funnels winds along the length of the lake. The strength and persistence of these winds is strikingly illustrated by the lopsided heads of the lakeside manuka scrub *(Leptospermum scoparium)*. The growth of these trees is severly inhibited on their southern side, yet is quite luxuriant on that facing north.

There is no outlet stream and the lake is apparently fed up by seepage and a few small seasonal rivulets. During the study period there were no large fluctuations in the lake level, but a gradual drop of about 1 metre occurred over the summer of 1969-70.

Plate 1.

Above: A view of Lake Ototoa from the western sand dunes, looking northward over station C. In the foreground are clumps of the Toe-toe, *Cortaderia conspicua*.

Below: The southern half of Lake Ototoa from the west, overlooking station B (left) and station A (centre). In the background are the consolidated Kaihu dunes.

DEPTH (m)	AREA OF CONTOUR ($m^2 \times 10^6$)	VOLUME OF STRATUM ($m^3 \times 10^6$)	(% of total)
0	1.623		
		3.072	15.39
2	1.451		
		2.791	14.99
4	1.340		
		2.574	12.90
6	1.234		
		2.339	11.72
8	1.106		
		2.092	10.49
10	0.987		
		1.857	9.31
12	0.871		
		1.629	8.17
14	0.759		
		1.362	6.83
16	0.605		
		1.021	5.12
18	0.421		
		0.673	3.37
20	0.258		
		0.368	1.85
22	0.119		
		0.140	0.70
24	0.037		
		0.033	0.16
26	0.005		
Total Volume		19.951	
Mean Depth		12.29m.	

Table 1: Some morphometrical parameters of Lake Ototoa. The volume of each stratum was calculated using the equation $V = h/3(a_1 + a_2 + \sqrt{a_1 a_2})$, where h = the depth of the stratum, a_1 = area of the upper surface, a_2 = area of lower surface. The mean depth ($\bar{z}$) was calculated using, $\bar{z} = V/A$, where V = total volume, A = surface area.

The littoral vegetation consists mainly of the sedge *Eleocharis sphacelata*, which forms narrow bands around the shore. It is moderately common in the less steeply sloping and shallower parts of the lake, in the northern and eastern arms and along the dune face to the west. The main submerged aquatic is *Chara australis* which is abundant along the southern edge to depths of between 10 and 15 metres.

The small goby *(Gobiomorphus australis)* is common, especially in the shallow bays, but skin-divers found them over the deep central basin, the floor of which is covered with a loose sandy mud. Smelt *(Retropinna retropinna)* were also seen on one occasion. Beds of the mussel *Hyridella menziesii* are common as is the freshwater crayfish *Paranephrops planifrons*.

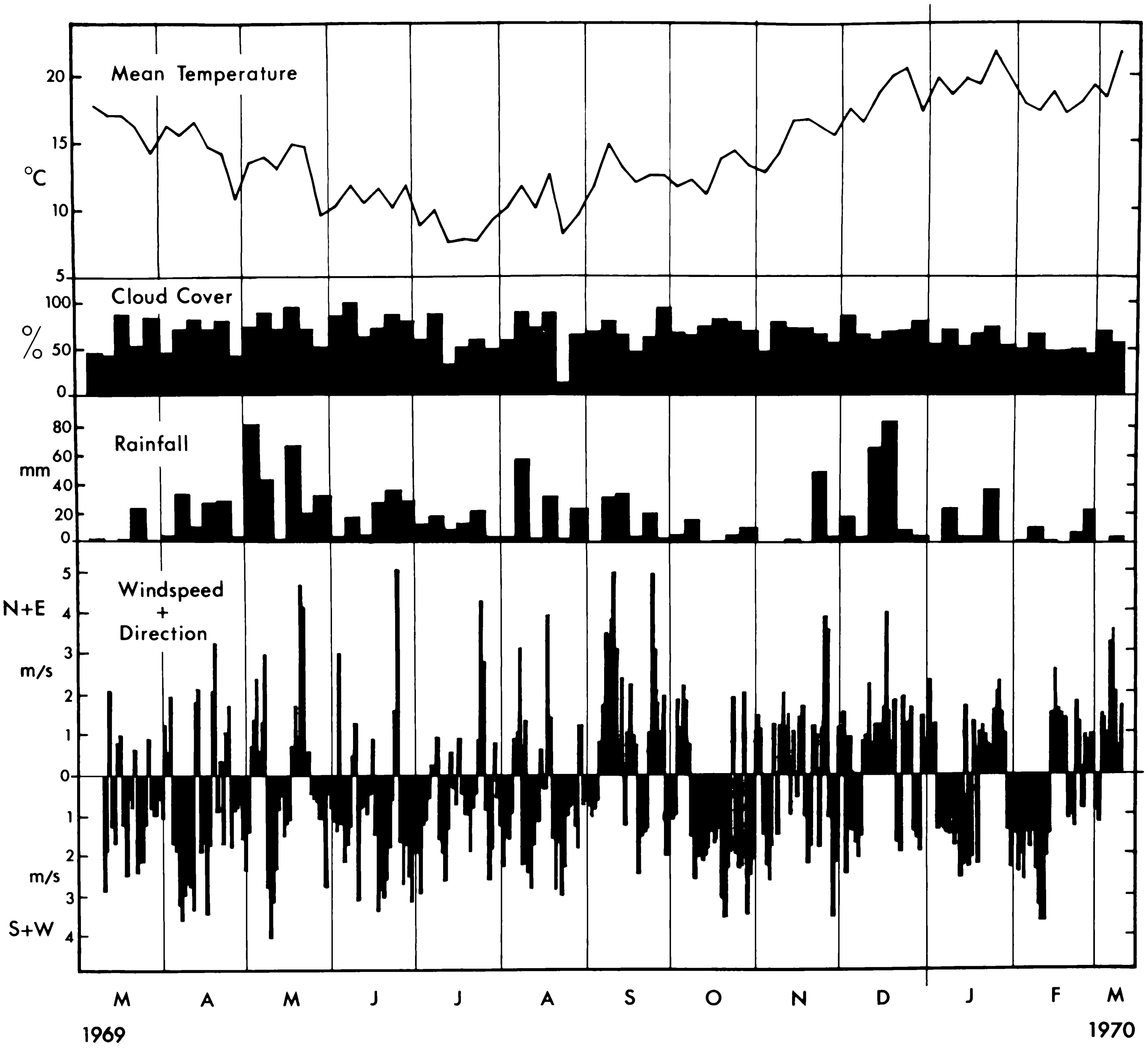
CLIMATE

Observations made at the Woodhill Forest meteorological station are summarised in Fig. 2. This station lies near the coast (36° 44'S, 174° 26'E) about 20km to the south of Lake Ototoa in the same belt of consolidated sand dunes, and the conditions are likely to closely approximate those at the lake. Oceanic influences dominate the climate in this area, temperatures are mild, winds frequent, moderately strong and variable. The islands of New Zealand are positioned in a belt of predominantly westerly airstreams that are characterised by a alternating sequence of anticyclones and low pressure troughs. The anti-cyclones may cross the country at approximately weekly intervals and the low pressure zones often give stormy weather. There is plenty of cloud, but because of the disturbed air-streams it is seldom maintained for any length of time, and the country has a high amount of sunshine (1800 - 2400 hrs. per year).

Mean temperatures, average cloud cover and total rainfall have been derived for 5-daily periods, while winds are daily averages. Mean temperatures were calculated by taking the means of the daily maxima and minima and then averaging the two.

The annual range in average air temperatures was small (14.2°C), the minimum being 7.6°C in July and the maximum 21.8°C in January and March. Average monthly temperatures from the Woodhill station over a ten-yearly period (1950 - 1960) (Gerlach 1966) are shown together with those of 1969 - 70 in table 2. It can be seen that although the autumn and winter months were a little colder than average, spring and

Fig. 2: Weather conditions, from March 1969 to March 1970, at the Woodhill Forest Meteorological station, to the south of Lake Ototoa.


Mean Temperature
20
15
°C
10
5
Cloud Cover
100
%
50
0
Rainfall
80
60
mm
40
20
0
Windspeed
+
Direction
N+E
5
4
3
m/s
2
1
0
1
2
m/s
3
S+W
4
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

	MEAN TEMPERATURES (°C)		MONTHLY RAINFALL (cm.)	
	10 yr. AVERAGE (1950-1960)	1969 - 1970	10 yr. AVERAGE (1950-1960)	1969 - 1970
Mar.	18.1	16.4	7.9	2.6
Apr.	15.8	14.8	10.7	11.0
May	13.6	13.2	13.2	17.4
Jun.	11.6	11.0	14.0	12.2
Jul.	10.1	8.6	14.2	8.3
Aug.	10.9	10.6	11.9	12.8
Sept.	12.1	12.8	9.9	9.6
Oct.	13.8	12.7	10.4	4.1
Dec.	17.1	18.3	8.4	18.7
Jan.	18.7	19.7	8.6	6.7
Feb.	19.6	17.9	10.4	3.9
Mean temp.	14.7	14.3	Tot.Fall.128.2	113.0

Table 2: Mean temperature and total monthly rainfall at Woodhill Forest between 1950 and 1960, and during 1969-70.

summer temperatures during 1969 and 70 tended to be higher. Cloud cover rarely dropped below 50% (mean 67.3%) and most rain fell in autumn and winter (between March and September 1969). However, maximum daily fall was during the early summer, in December. Average monthly rainfalls over the 10 year period are also shown in table 2 together with those of 1969-70 and it can be seen that from June 1969 to February 1970 rainfall was lower than average. The yearly rainfall between March 1969 and March 1970 was 113.1 cm as compared to the 10 year average of 128.5 cm.

In fig. 2 and table 3 the monthly frequencies of the various wind directions and speeds are shown. Although the strongest winds came from the north and east, the most notable feature is the persistence of those from the south and west . The axis of the lake is aligned in a N-S direction, so the winds sweep along the length of the lake, and the effect on the lakeside vegetation has already been noted above. No absolutely windless days were recorded. In the classification of wind velocities put forward by Yoshimura (1936) these winds are classed as weak. (Weak - av. velocity $<$ 2m/s; moderate - av. velocity 2-3 m/s; strong - av. velocity 3-5 m/s; very strong- av. velocity 5 $>$ m/s.). Nevertheless the surrounding countryside funnels the wind down the length of the lake, giving the greatest possible fetch. On occasions waves 60 - 90 cms high were experienced at the northern end of the lake.

	South and West				North and East				
Month	W	SW	S	SE	NW	N	NE	E	Calm
M	1	17	1	2	1	1	2	2	4
A	4	10	2	2	4	1	1	2	4
M	1	10	1	3	1	1	7	2	5
J	1	17	0	4	0	1	0	3	4
J	6	8	2	1	2	0	4	1	7
A	3	12	1	2	3	0	4	1	5
S	3	5	1	1	2	5	9	3	1
O	5	16	1	1	3	0	3	1	1
N	0	12	2	0	3	3	5	5	0
D	4	5	0	2	6	3	9	1	1
J	0	9	2	5	4	1	5	4	1
F	2	1	7	6	1	1	1	8	1
M	0	8	0	3	2	3	13	2	0
Total	30	130	20	32	32	20	63	35	34
Percentage	7.6	32.8	5.1	8.1	8.1	5.1	15.9	8.8	8.6
	53.6%				37.9%				8.6%

Table 3: Frequency of wind directions at the Woodhill Forest expressed as number of observations of each direction at 9 a.m. per month between March 1969 & March 1970.

METHODS

Regular sampling was carried out between March 1969 and March 1970. Visits were generally made weekly, although on a few occasions the interval was 3 to 4 weeks. Between 10 March 1969 and 28 April 1969 samples were taken from one station only (B) centrally located in one of the deepest areas of the lake. However after this two more stations (A and C) were established at the south and north ends of the lake respectively. The stations (fig. 1) were permanently marked with buoys and were chosen to take account of any variations in the distribution patterns of both physio-chemical and biological features along the lake axis.

Temperatures were measured at weekly intervals with a thermistor thermometer which could be read accurately to within 0.05°C. Readings were made at metre intervals from the surface to the bottom at each station. Transparency was measured at all stations, generally at weekly intervals, with a standard 20 cm secchi disc divided into quadrants alternately black and white (Welch 1948). Between September and November the light meter used by Barker (1970) was made available. Starting at a depth of one metre recordings of light intensity were made at metre intervals to the bottom at all stations.

Water samples were taken with a Ogawa-Seiki reversing Nansen bottle of 1.1 litres capacity. Surface samples for oxygen and pH analysis were collected at two or three weekly intervals over the whole sampling period and during the summer samples were also taken from the bottom at each station. A vertical series of samples for oxygen and pH at depths of 0, 3, 6, 9, 12, 15, 18 and 21 metres was made on 12 January 1970 during summer stratification. After June 1969 monthly samples for chemical analysis were taken from a depth of 1m at stations A and C. A one litre sample was taken and transported to the laboratory in plastic containers which had previously been treated with iodine to reduce bacterial uptake of phosphate and nitrate on their inner surfaces.

All estimations were made according to Mackereth (1963) immediately on returning to the laboratory. Oxygen was determined by unmodified Winkler's method, pH on a Radiometer model 22 pH-meter, Na and K on an E.E.L. flame photometer and Ca, NO_3 and PO_4 by spectrophotometric methods using a Beckman DB spectrophotometer. Alkalinity was determined titrimetrically using standard acid (N/100 HCl) and B.D.H. 4.5 indicator, and Mackereth's (1955) cation ion exchange methods were used to estimate total anionic concentration, chlorides and sulphate. Unfortunately Mg could not be estimated separately, but an approximate value was found by subtracting the equivalent sum of Na, K and Ca from the total anionic concentration. The amount of organic matter present was analysed by acid-dichromate oxidations after Maciolek (1962). Two determinations were made, one on 100 ml of raw lake-water, the other on a sample which had first been filtered through an 0.8 μ pore size Millipore filter.

Samples for chlorophyll analysis were taken at weekly intervals from a depth of 1m at each station. The samples were kept cool and away from the light, and were analysed immediately on returning from the field using the methods of Richards and Thompson (1952). Generally 3-5 L was filtered using a type AA Millipore filter (0.8 µ pore size). Concentrations of simple chlorophyll-a were determined according to Talling and Driver (1963).

Weekly samples were also taken from a depth of 1m for phytoplankton counts. These samples were taken from station B only between 17 March 1969 and 21 April 1969, from stations A and C between 5 May and 11 August and after this from all stations. Each of these samples was of one litre volume. Unfortunately no counts were made of phytoplankton during the last 3 weeks of June because of an accident which destroyed the samples.

A membrane filter technique mainly after De Noyelles (1968) but modified according to information supplied by the Millipore Corporation (AR81) to give permanent mounts, was used by phytoplankton counts. The sample was preserved in Lugols iodine - acetic acid (Willen 1959) immediately after collection, and then stained for 24 hours with analine blue and Eosin-Y (stock solutions - 0.7g stain/50ml of water. 6 drops of each were used per 100ml of sample). After staining the phytoplantkton was filtered off using a Swinny filter holder and a 13mm HA Millipore filter (0.45 µ) as described by De Noyelles. The filter circle was then removed and its underside blotted dry with filter paper. Initially the filter was left to air dry for 20 minutes before clearing and mounting. However, this resulted in many of the species (e.g. *Cosmarium*, *Staurastrum* and the diatoms) becoming either distorted or full of air bubbles. Because of this the method finally adopted was to dehydrate the filter (in iso-propanol) after only a few minutes of air drying. This is the method advocated by the Millipore Corporation and retains the characteristic morphology of most species very well. The danger here is that some algae may become detached from the filter surface, and although this certainly happens when a fast dehydrant such as ethyl alcohol is used, such an effect when using iso-propanol was either absent or minimal. After dehydration the filter was cleared in xylol and mounted in canada balsam.

2 or 5mls of water (depending on the algal concentration) was filtered, and the whole filter surface was examined and the algae counted. Total numbers counted were between 500 and 1300. To aid counting the filter was divided into four by etching lines onto the surface of the coverslip.

The replicability of the phytoplankton sampling and counting techniques was tested by counting two lots of 5 replicate samples, collected from Lakes Rotoroa (Hamilton) and Koutu (Cambridge). The results of these counts are set out in table 4. The numbers in these samples is similar to those found from Ototoa. Except where there were only very small numbers of cells the method gives favourable results,

SPECIES	1	2	3	4	5	Mean	S.D.	C.V.%
Trachelomonas	398	417	445	434	436	426.0	18.6	4.4
Cryptomonas	257	235	254	263	231	248.0	14.1	5.7
Dinoflagellates	116	103	147	140	167	134.6	25.4	18.9
Unident.flagellate	78	130	113	90	92	100.6	20.7	20.6
Tetrastrum	78	62	77	91	81	77.8	10.4	13.4
Nitzschia	107	81	101	80	99	93.6	12.3	13.2
Phacus	20	21	17	18	21	19.4	1.8	9.8
Scenedesmus	18	17	30	19	31	23.0	6.9	30.0
Closterium	7	3	10	8	8	7.2	2.6	36.0
Melosira 1	48	57	51	46	54	51.2	4.4	8.7
Melosira 2	29	25	25	23	22	24.8	2.7	10.8
Euglena	5	4	5	5	2	4.2	1.3	31.0
Oscillatoria	2	3	3	0	2	2.0	1.2	61.0
Ankistrodesmus	3	6	5	4	1	3.8	1.9	50.5
Gomphonema	1	1	0	1	0	0.6	0.5	91.7
TOTAL	1167	1165	1283	1222	1247	1216.8	51.2	4.2

Table 4(a): Replicate samples of phytoplankton from Lake Koutu (Cambridge).

SPECIES	1	2	3	4	5	Mean	S.D.	C.V.%
Dinobryon	236	146	133	113	103	146.2	52.9	36.2
Navicula	100	79	62	93	80	82.8	14.6	17.6
Cyclotella	36	25	19	23	23	25.2	6.4	25.4
Small flagellate	63	40	73	60	68	60.8	12.6	20.7
Chroomonas	30	14	22	21	20	21.4	5.7	26.6
Cryptomonas	12	26	21	11	16	17.2	6.3	36.6
Nephrocytium	13	15	18	16	8	14.2	3.4	23.9
Chlamydomonas	7	6	10	8	8	7.8	1.5	19.2
Dinoflagellates	7	4	2	3	4	4.0	1.9	47.5
Trachelomonas	2	2	3	3	2	2.4	0.6	25.0
Shaerocystis	2	3	2	4	5	3.2	1.3	40.6
Mallomonas	3	1	2	1	2	1.8	0.8	44.4
Ankistrodesmus	3	0	1	1	3	1.6	1.3	81.2
Oscillatoria	2	0	2	2	2	1.6	0.9	56.3
TOTAL	516	361	370	359	345	390.2	70.9	18.2

Table 4(b): Replicate samples of phytoplankton from Lake Rotoroa (Hamilton).

the co-efficient of variation generally being between 10 and 30%.

The zooplankton was sampled by a vertical net haul from the bottom to the surface at each station. A Hansen type net (based on the modified design of Currie and Foxton 1967) was used. The mouth of the net was 20 cm in diameter and behind this was a 30 cm canvas band followed by a 28cm length of 13 xx bolting silk (100 µ mesh size) and then a 40 cm long cone shaped section of silk attached to a 7 cm diameter bucket. The catches were carefully washed from the bucket and net into 1 litre containers and preserved immediately with neutralised formalin.

For counting the plankton sample was made up to a known volume in a 1 litre measuring cylinder and after thorough mixing by inversion a 5 ml subsample was withdrawn. This was then transferred into a squared perspex counting tray mounted on the moving stage of a stereoscopic microscope. A magnification of x 32.5 was used for counting and the numbers recorded on a Clay-Adams tally counter. The subsampling was repeated until 3 very similar results were obtained, and generally between 40 and 100 specimens of *Calamoecia* were aged and sexed in each subsample. For any one date 200 - 500 *Calamoecia* were aged in the subsamples from the three stations. The clutch size, percentage ovigerous and lengths of ♀ *Calamoecia* were estimated later by taking subsamples from the plankton concentrate which had been diluted and stirred. 50-60 animals were examined or counted for measurement of length, from the front of the head to the end of the metasome, these determinations being made using an eyepiece micrometer and x 100 magnification and measurements could be made to within 0.01mm.

The replicability of the net samples and subsampling was tested by taking a set of 8 replicate samples on 17 February 1970. Three factors act jointly to cause variation of plankton numbers in a set of samples: the efficiency of the sampling device, natural non-random distribution patterns of the animals in the lake and the accuracy of the subsampling process. It is not possible to determine the relative importance of each by simply taking a series of replicate samples, but an approximate indication of the range of variability in the sampling process is given by Pearson's coefficient of variation (100. Standard deviation/mean) which gives some basis for comparison between methods. The results of these samples are set out in table 5 and compare very favourably with those of 9 - 40% and 13 - 25% by Bayly (1962) and Chapman (1965) respectively both of whom used closing nets, and 19 - 20% by Barker (1967), 20 - 50% by Cassie (1963) and 10 - 30% by Green (1968) using pumps.

The dry weight, lipid, protein, organic matter and ash of ♀ *C. Lucasi* (generally from the station B samples) were also determined, the analyses being made at Waikato University. Dry weights were determined weekly, and this was generally the case with lipid also although on occasions the interval was 2 or 3 weeks. Protein estimations were made fortnightly and organic matter and ash at 2 - 4 week intervals.

	Sample Number										
Group	1	2	3	4	5	6	7	8	Mean	S.D	C.V(%)
Nauplii	4	6	8	7	4	4	8	6	5.9	1.6	26.4
Calamoecia Copepodites	106	98	97	103	112	104	91	96	100.9	6.2	6.2
Cyclopoids	1	3	1	2	3	2	3	1	2.0	0.9	43.3
Bosmina	32	27	31	35	36	25	23	32	30.1	4.4	14.5
Rotifera	9	6	6	8	8	7	9	6	7.0	1.3	18.2
Total	152	140	143	155	163	142	134	141	146.3	8.9	6.1

Table 5: Replicate samples of zooplankton from Lake Ototoa. (Station B, 17 February 1970).

The dry weights of 6 series of eggs, nauplii, copepodites and adults, chosen to correspond to actual development sequences, were also found and the samples from which the animals were taken for these weighings are given in table 6.

	Series					
Stage	1	2	3	4	5	6
Egg	17 Mar.	19 May	16 June	8 Sept.	19 Oct.	27 Jan
Nauplius	"	"	"	"	"	2 Feb.
Cop.I	31 Mar.	2 June	30 June	15 Sept.	26 Oct.	"
Cop.II	"	9 June	5 Jul.	29 Sept.	2 Nov.	9 Feb.
Cop.III	"	16 June	"	"	17 Nov.	"
Cop.IV	12 Apr.	30 June	14 Jul.	6 Oct.	14 Dec.	"
Cop.V	"	14 Jul.	28 Jul.	13 Oct.	"	17 Feb.
♂	21 Apr.	21 Jul.	28 Jul.	26 Oct.	22 Dec.	"

Table 6: Samples from which animals were taken for dry weight determinations.

An aliquot of the stirred preserved sample was run through 4xx bolting silk to separate the females, males and larger copepodites from the naupliar and young copepodite stages, and other zooplankton. While the sample was still on the gauze it was rinsed with distilled water to remove excess preservative. Such rinsing does not lead to serious errors in the analysis of biochemical components.(Platt et al1969, Omori 1970). The copepods were then placed in a petri dish of distilled water and the required number of ♀♀ separated out for analysis.

The copepods were placed on tared aluminium boats for weighing. The boats were made from domestic aluminium foil by using a cork-borer to cut out circles of foil which were then shaped into small dishes. Two sizes were used, ca 100 µg for weighing younger copepodites, nauplii and eggs and ca 1 mg for older copepodites and adults. The bottoms of the boats were then peppered with small holes using a finely eroded tungsten needle, and the boat was then placed on a circle of filter paper over self-indicating silicagel in a snap-top vial. Weights were determined on a Beckman LM 500 microbalance using the 1 mg range for the 100 µg boats and the 5 mg range for the 1 mg boats. On the 1 mg range readings could be made to within ± 0.2 µg and on the 5 mg range to within ± 1 µg. The number of animals which were used for weighing depended on their size. Generally 50 ♀♀ were sufficient, but for eggs up to 250 had to be used.

The animals to be weighed were then sorted out, and transferred into the boat which was held with watchmakers forceps over a circle of filter paper under a stereo-microscope. The copepods, contained in a drop of water, were then run into the boat with a fine pipette, and the water was sucked through the holes in the bottom of the boat by the filter paper while the animals remained. Without the holes in the base of the boat it was very difficult to transfer the copepods because the drop of water containing them was of greater volume than the boat itself, and because of the interference of water tension.

The boat plus copepods was then placed in the vial and dried in an oven at 60-70°C for 24-48 hours (Lovegrove 1966). The vial was then recapped and the animals left to cool and dessicate for 12 hours, when they were weighed on the microbalance.

To check for replicability of the weighings, two groups of 50 ♀♀ were re-weighed on successive days with the following results:

Sample µg	Day 1	2	3	4	Mean
a	3750.0	3751.5	3751.0	3751.0	3750.8 µg
b	3368.5	3368.0	3368.5		3368.3 µg

The tare weights were: a) 3707.0 µg
b) 3341.5 µg

Thus the copepods weighed: a) 43.8 µg (0.88 µg/♀)
b) 26.8 ug (0.54 µg'♀)

Therefore in (a) the variation was:

3751.5 - 3750.0
= 1.5 µg
= 1.5/43.8 = 3.4% of copepod weight

in (b) the variation was:

= 0.5 µg
= 1.9% of copepod body weight

These weights were low because fats had been extracted (see below) and so percentage variation would be expected to be less in animals not so treated.

Lipids were extracted with 1:1 chloroform-methanol solution. After the initial weighing 10-15 ml of solvent was slowly run, over a period of about 30 minutes, from a fine tipped burette into each of the aluminium boats containing the ♀♀. The boat was supported on a mat of several thicknesses of filter paper which soaked up and carried away the solvent and lipid after it had passed out through the bottom of the boat. The boats were then redried in the oven, dessicated and reweighed. The difference in weight was taken as the lipid free weight. Giese (1967) recommends extraction of lipids by chloroform-methanol solutions, and states that it is superior than the soxhlet method using ethyl-ether because it extracts both structural and stored lipids in contrast to the soxhlet method which only extracts the latter. A similar method was used by Siefkin and Armitage (1968) for determining lipids in *Diaptomus spp.*

A modified version of Lowry's method (Lowry, Rosebrough, Fair and Randall 1951), which is the method recommended by Giese (1967), and Winberg (1971), was used for protein determinations. In this method the colour developed depends on the quantity of tyrosine and tryptophan residues in the sample protein and so the determination rests on the degree of similarity in the levels of these in the sample and standard.

10-20 ♀♀ were used for protein analysis, and determinations of any one date were made in triplicate. The copepods were ground in Lowry's solution C in a tissue grinder for one minute, made up to 2 ml with solution C, allowed to extract for one hour and centrifuged. 0.2 ml of Folin and Cicalteu's phenol reagent diluted 37 ml/100 was jetted into the supernatant and the colour allowed to develop for one hour. The absorbance of the solution was then read on a Beckman DB Spectrophotometer at 660 mμ. A calibration curve was prepared in a similar way using known amounts (0-20 μg) of crystalline bovine serum albumin.

Organic matter in the copepods was analysed by quantitative dichromate oxidation using the micromethod of Maciolek (1962). Three samples of 250 ♀♀ were used from each date, and the oxidations were done in chemically clean "Discardit" (Beckton Dickinson RTU) boiling tubes with appropriate controls. As such methods probably oxidise about 90% of the organic matter present (Winberg 1971) the values obtained have been corrected by 10%. The amount of oxygen consumed in the oxidation can be used to give estimates of organic carbon and calorific content per copepod by application of appropriate conversion factors (Maciolek loc. cit;).

Ash weights were also determined for the copepods from the samples used for organic matter analyses. Because a large number of animals were needed for ashing, copepodites IV, V and oo were used as well as the ♀♀. It has been assumed that these stages have similar ash contents to the ♀♀. Enough animals to give a dry weight of ca 1.5 - 2 mg were weighed in platinum boats (of similar design to those used for dry weight determinations) and ash content determined after combusting for half an hour at 500°C in a muffle furnace.

All the above analyses were made on specimens that had been stored for up to a year in 4% neutralised formalin and such preservation is known to effect the biochemical composition of plankton. Lovegrove (1966) found that after preservation in formalin there was reduction of water content and apparent increase in organic matter and ash of mantle tissue of *Loligo*. Marked changes occurred in the first three days and there were only small changes after this. Organic matter dropped from an initial 92.6% dry weight to 86.6% after 56 days and then remained constant; ash increased from 7.4% to 13.4% in the same period. Fudge (1968) states that after formalin preservation the dry weight of *Neomysis integer* dropped slightly, ash fell from 12% to 9% dry weight, chitin remained unchanged, lipid increased from 11% to 15% dry weight and carbohydrate increased from 3% to 9%. He found that protein, as determined by the Biuret reaction, decreased markedly from 73% to 5% dry weight, but it seems that this may have been due to the method of determination rather than to such a large decrease in protein. Omori (1970) found that for *Calanus cristatus* there was a decrease in dry weight after formalin preserving to 53% of the initial value. As % of the dry weight H fell from 10.2% to 9.2%, C from 59.9% to 55.5%, while N increased from 6.7% to 7.5%. Ash was largely unchanged, but the C:N ratio decreased indicating that proportionately more C than N was lost. Lebedeva and Kozlova (1969) observed that Cladocera fixed in 4% formalin changed weight over a period of time. Some increased in weight by 30 - 60%, others lost 20 - 40% while the remainder did not change. Schindler, Clark and Gray (1971) showed that samples of *Diaptomus oregonensis* stored in formalin for 4 months had slightly, but significantly lower calorific values than frozen ones (6325 ± 147 cf 6680 ± 101 cal/gm).

However, in contrast to these observations Ostapenya, Suschenya and Khmeleva(1967) quote work by Pavlyutin which showed that neither fixation nor prolonged storage in 4% formalin affected the calorific value of aquatic animals, and Faustov and Zotin who showed that fixation in 10% formalin did not affect the caloricity of amphibian or fish eggs. Russell-Hunter, Meadows, Apley and Burky (1968) using a wet oxidation method found that values of organic carbon per unit net weight of molluscs fixed in 12% formalin were consistently higher than for those per unit live weight, and varied in the same way. This was thought to be due to loss of weight and defaecation on fixation. But these authors pointed out that if formalin is maintained at neutrality, there should be no breakdown of carbohydrates, proteins and lipids, and that only a small amount of additional C from the formalin should remain bound to the proteins after washing in distilled water. McLaren (1969) found that carbon content of fresh

Pseudocalanus minutus did not deviate significantly from those preserved in formalin.

It seems, then, that the determinations made in this study on the preserved *Calamoecia* are likely to give values that are too low for dry weight and protein, but lipid and organic determinations are probably less affected and the former may in fact be too high.

PHYSIOCHEMISTRY

1. Temperature

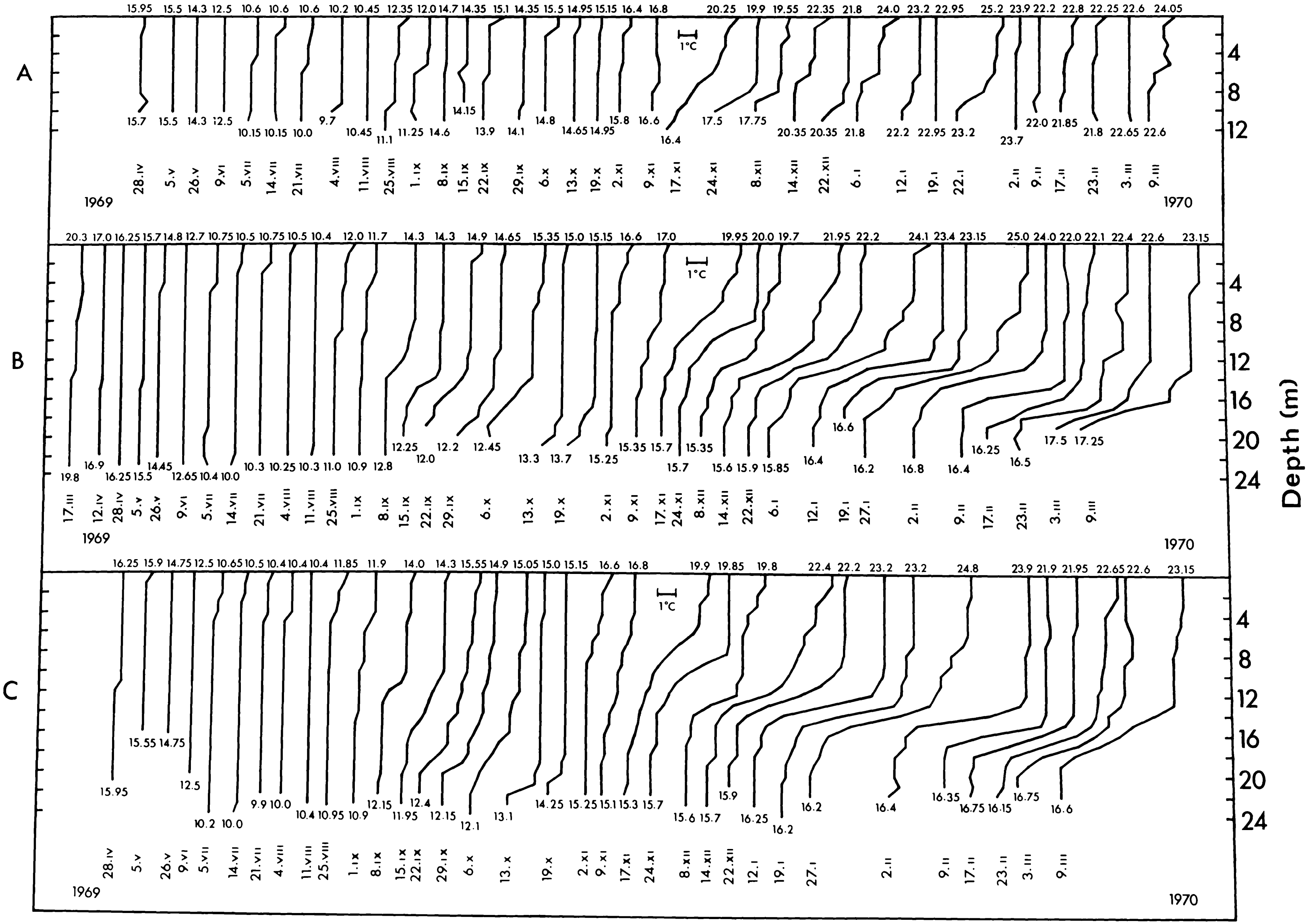
The temperature records are shown in fig. 3.

From March to early September 1969 Lake Ototoa was essentially homothermal and during this time temperatures dropped gradually to reach their lowest values in August (9.7°C on 4 August). Following warm weather in September there was considerable surface heating, and a weak themocline developed. However, although heating continued the stratification was gradually broken down by the strong north and east winds of September.

In November stratification reformed and remained strongly developed from December to the end of the sampling period. During most of December and January the epilimnion and metalimnion and hypolimnion occupied approximate depth ranges of 0-12 m, 12-16 m, and 16 - 23 m respectively; which comprise 72.8%, 15.0% and 12.2% of the total lake volume.

During January the depth of the thermocline increased slightly, and this trend became more apparent in February and March as the epilimnion cooled. By the end of sampling, the hypolimnion comprised only 5.9% of the lake volume and stratification appeared to be close to breaking down, although the thermocline was sharpened a little by the increased temperature on 9 March 1970.

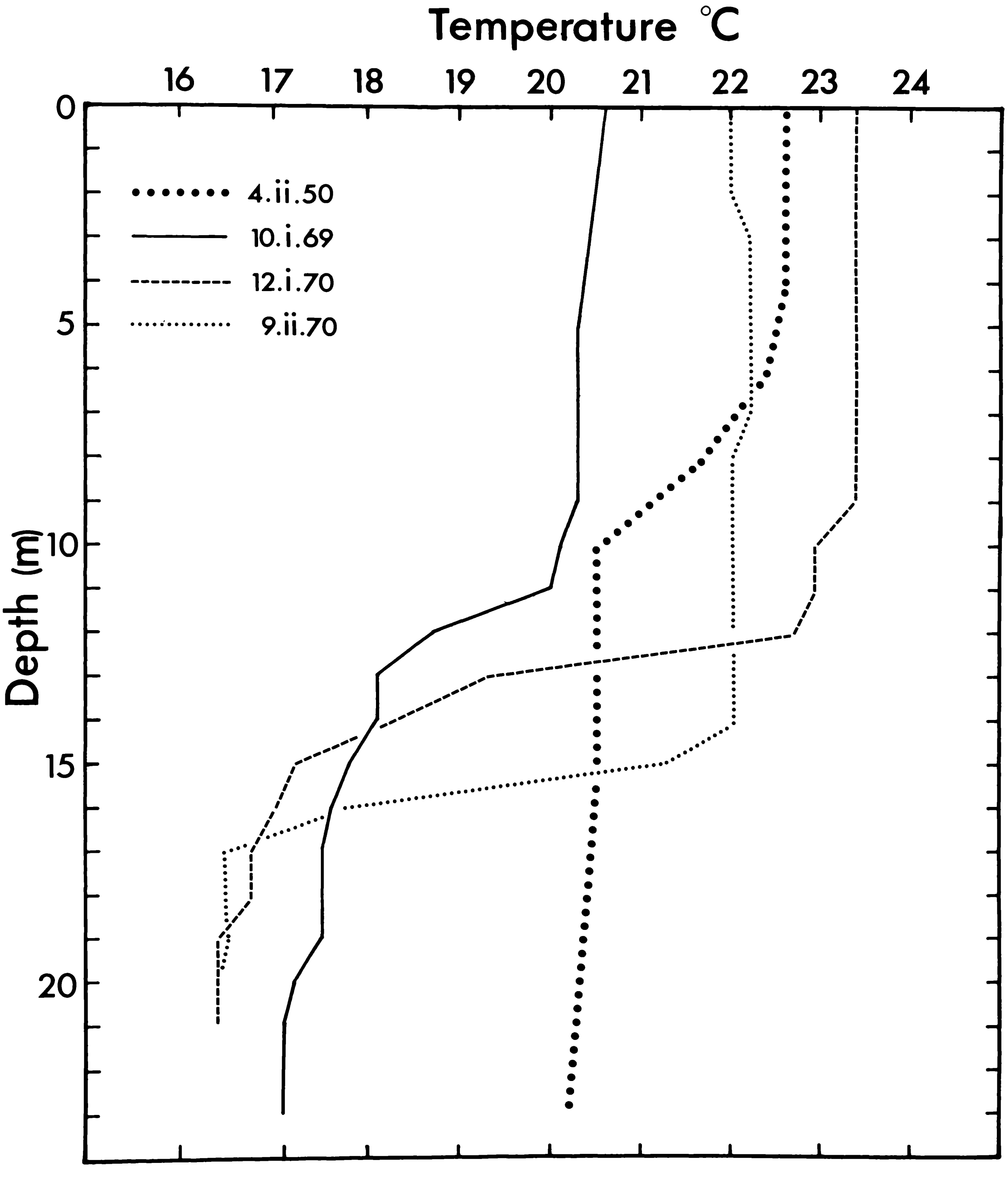
Fig. 3: The distribution of temperature with depth at stations A, B, and C during the sampling period. In each case the surface and bottom temperatures are shown. Temperatures in degrees Celcius.


A
B
C
1°C
Depth (m)
4
8
12
16
20
24
1969
1970
15.95 15.5 14.3 12.5 10.6 10.6 10.6 10.2 10.45 12.35 12.0 14.7 14.35 15.1 14.35 15.5 14.95 15.15 16.4 16.8 20.25 19.9 19.55 22.35 21.8 24.0 23.2 22.95 25.2 23.9 22.2 22.8 22.25 22.6 24.05
15.7 15.5 14.3 12.5 10.15 10.15 10.0 9.7 10.45 11.1 11.25 14.6 14.15 13.9 14.1 14.8 14.65 14.95 15.8 16.6 16.4 17.5 17.75 20.35 20.35 21.8 22.2 22.95 23.2 23.7 22.0 21.85 21.8 22.65 22.6
28.IV 5.V 26.V 9.VI 5.VII 14.VII 21.VII 4.VIII 11.VIII 25.VIII 1.IX 8.IX 15.IX 22.IX 29.IX 6.X 13.X 19.X 2.XI 9.XI 17.XI 24.XI 8.XII 14.XII 22.XII 6.I 12.I 19.I 22.I 2.II 9.II 17.II 23.II 3.III 9.III
20.3 17.0 16.25 15.7 14.8 12.7 10.75 10.5 10.75 10.5 10.4 12.0 11.7 14.3 14.3 14.9 14.65 15.35 15.0 15.15 16.6 17.0 19.95 20.0 19.7 21.95 22.2 24.1 23.4 23.15 25.0 24.0 22.0 22.1 22.4 22.6 23.15
19.8 16.9 16.25 15.5 14.45 12.65 10.4 10.0 10.3 10.25 10.3 11.0 10.9 12.8 12.25 12.0 12.2 12.45 13.3 13.7 15.25 15.35 15.7 15.7 15.35 15.6 15.9 15.85 16.4 16.6 16.2 16.8 16.4 16.25 16.5 17.5 17.25
17.III 12.IV 28.IV 5.V 26.V 9.VI 5.VII 14.VII 21.VII 4.VIII 11.VIII 25.VIII 1.IX 8.IX 15.IX 22.IX 29.IX 6.X 13.X 19.X 2.XI 9.XI 17.XI 24.XI 8.XII 14.XII 22.XII 6.I 12.I 19.I 27.I 2.II 9.II 17.II 23.II 3.III 9.III
16.25 15.9 14.75 12.5 10.65 10.5 10.4 10.4 10.4 11.85 11.9 14.0 14.3 15.55 14.9 15.05 15.0 15.15 16.6 16.8 19.9 19.85 19.8 22.4 22.2 23.2 23.2 24.8 23.9 21.9 21.95 22.65 22.6 23.15
15.95 15.55 14.75 12.5 10.2 10.0 9.9 10.0 10.4 10.95 10.9 12.15 11.95 12.4 12.15 12.1 13.1 14.25 15.25 15.1 15.3 15.7 15.6 15.7 15.9 16.25 16.2 16.2 16.4 16.35 16.75 16.15 16.75 16.6
28.IV 5.V 26.V 9.VI 5.VII 14.VII 21.VII 4.VIII 11.VIII 25.VIII 1.IX 8.IX 15.IX 22.IX 29.IX 6.X 13.X 19.X 2.XI 9.XI 17.XI 24.XI 8.XII 14.XII 22.XII 12.I 19.I 27.I 2.II 9.II 17.II 23.II 3.III 9.III

A feature of the traces in fig. 3 are the minor irregularities in the epilimnion on many occasions, which on some dates show similar patterns at all three stations (e.g. 17:xi:69, 8:xii:69, 18:xii:69 6:i:70, 19:i:70 and 27:i:70). These microstratifications are probably evidence of strongly turbulent conditions in the epilimnion and result from surface heating and subsequent mixing by the wind.

Epilimnetic temperatures generally followed trends in air temperatures and were highest in late January (maximum 24.2°C). Those at stations B and C were similar, while those at station A were often higher, probably because this station was shallower and more sheltered than the other two. During the summer the greatest drop in temperature over the metalimnion was 6.4°C which is similar to that found in other New Zealand lakes (Jolly 1968, Barker 1970, Fish 1970). The range in temperature of the bottom waters over the year was 6.5°C. Most of this increase occurred between August and November, and during stratification (between December and March) temperatures in the hypolimnion rose about 1°C. During this latter period hypolimnetic temperatures after increasing slightly in December remained fairly constant during January and February and increased once again during March 1970. This variation of bottom temperatures is somewhat greater than found for other shallow, stratified lakes in New Zealand (Jolly 1968, Fish 1970).

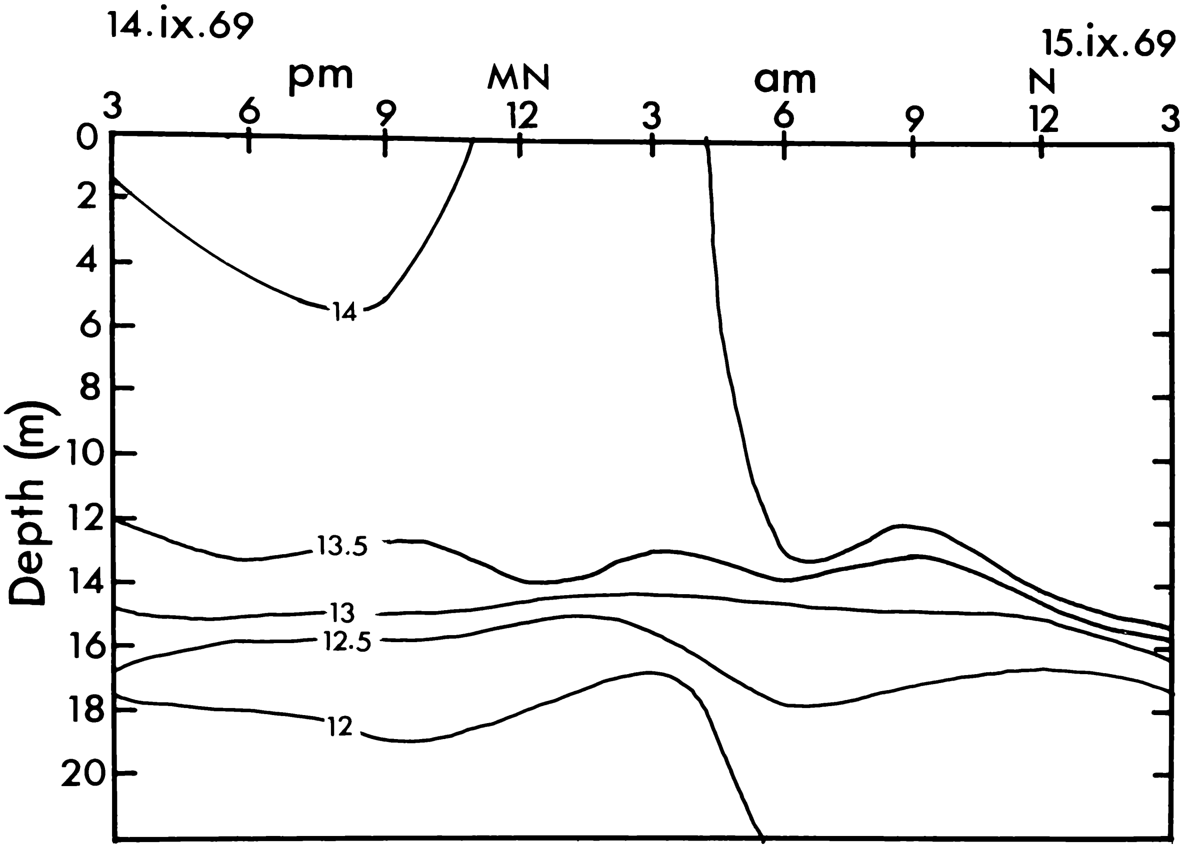
Fig. 4: Thermocline depth in Lake Ototoa during the summers of different years. 1950 from Cunningham, et. al., (1953); 1969, a preliminary visit by the author; 1970, from the present study.

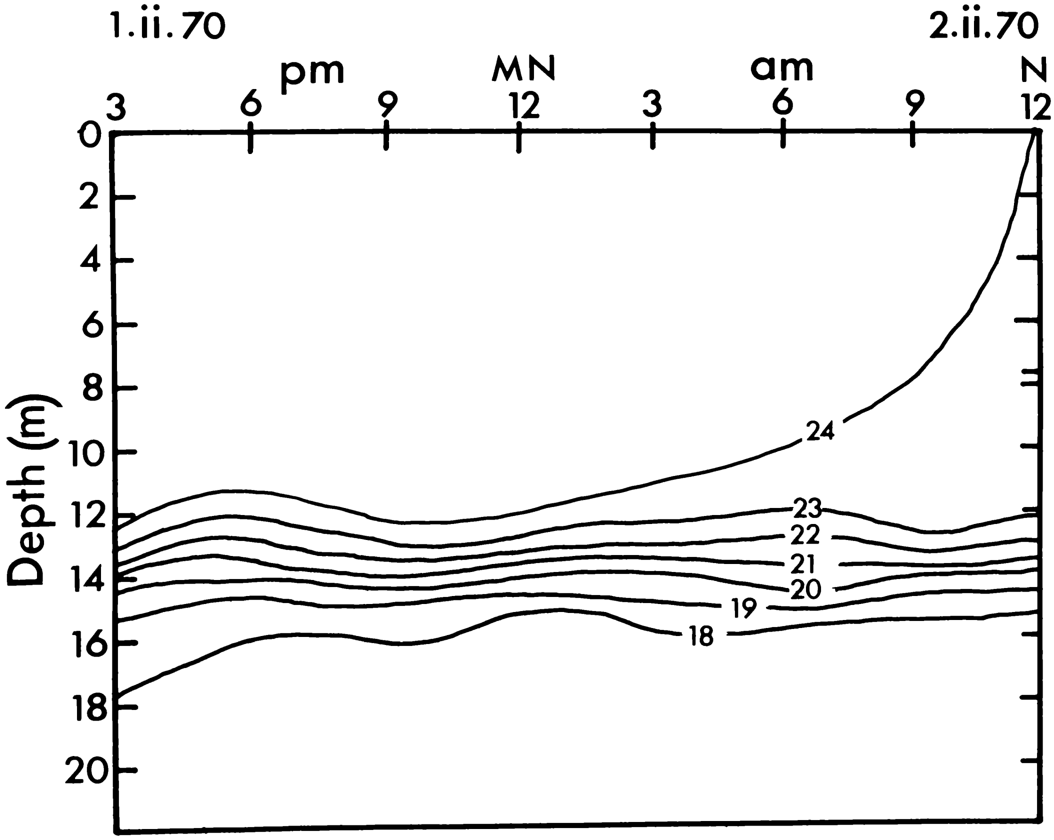

Temperature °C
16
17
18
19
20
21
22
23
24
0
5
10
15
20
Depth (m)
4.ii.50
10.i.69
12.i.70
9.ii.70

There may be considerable variation in the thermal regime of Lake Ototoa from year to year. Fig. 4 shows patterns of stratification recorded on similar dates during 1950 (Cunningham et al, 1953), 1969 (a preliminary visit by the author before beginning this study) and 1970. Cunningham et al found only weak stratification, and believed that a previous stronger stratification had been broken down a short time before their visit. In 1969 although a distinct thermocline was present it was not as deep as the present study and the temperature difference between epi- and hypolimnion was smaller. The summer of 1970 was warmer than average (see page 8). It is possible that the conditions observed in this study are not typical and that in other years stratification is less marked and perhaps more transient.

The temperature records made during diurnal samples on 14-15 September 1969 and 1-2 February 1970 are shown in Fig. 5. Lake Ototoa might be expected to develop internal seiches because of its elongate shape and orientation parallel to the prevailing wind. However, apart from minor fluctuations in the isotherms there was no distinct oscillation like that found by Green, Norrie and Chapman (1969) in Lake Rotoiti, a larger but similarly shaped lake. There was some surface heating during the day on 15 September, and the slight lowering of the thermocline is interesting because it was probably associated with the

Fig. 5: Thermal stratification at station B during two diurnal periods. Temperatures in degrees Celcius.


14.ix.69
15.ix.69
pm
MN
am
N
3
6
9
12
3
6
9
12
3
Depth (m)
0
2
4
6
8
10
12
14
16
18
20
14
13.5
13
12.5
12


1.ii.70
2.ii.70
pm
MN
am
N
3
6
9
12
3
6
9
12
Depth (m)
0
2
4
6
8
10
12
14
16
18
20
24
23
22
21
20
19
18

active disruption of the weak stratification which was taking place during this month.

As there is only one circulation period during the year, and temperatures are always well above 4°C, Lake Ototoa may be classified as a warm monomictic lake (Hutchinson, 1957).

The annual heat budget of Lake Ototoa was calculated using Birge's(1911) method. For a warm monomictic lake this value will be summer heat income only (θ_{bs}). Mean temperatures used in the calculation were : maximum - 22.7°C on 27 January 1970, and minimum - 10.1°C on 4 August 1969. The heat budget thus calculated is 15,500 $cal.cm^{-2}$. Heat budgets of other New Zealand and Australian lakes have been calculated by Bayly 1962, Timms and Midgly 1969, Barker 1970 and Fish 1970. These are shown together with the budget for Ototoa in table 7 The budget of Ototoa is similar to those of Pupuke and Okaro. That of Okataina is much greater while the rest are smaller and low by world standards.

In the first 5 lakes in the table there is a tendency for the budget to be greater as area, mean depth and volume increase as Gorham (1964) and Schindler (1971) have also found. Area affects heat intake by allowing greater wind fetch in larger lakes and thus more efficient mixing of heat into the water, and the relationships with depth and

	θ_{ba} cal/cm^2	A_o m^{2}x10^4	$\bar{z}$ m	V m^{3}x10^6
Okataina[1]	57,643	1049.4	45.5	477.25
Pupuke[2]	16,000	85.7	34.0	29.23
Ototoa	15,500	162.3	12.3	19.95
Okaro[1]	11,851	32.95	11.1	3.65
Ngapouri[1]	9,496	22.34	12.1	2.72
Borumba[3]	7,963	501	8.5	42.6
Aroarotamahine[4]	6,000	10.2	12.2	1.25
Rotoehu[1]	5,296	791.24	8.2	64.53

Table 7: The heat budgets of New Zealand and Australian lakes. Data from, 1) Fish 1970; 2)Barker 1970; 3) Timms & Midgely 1969; 4) Bayly 1962. Surface area (A_o), mean depth ($\bar{z}$) and total volume (V) are also given for each lake.

volume may arise because larger lakes will often also have greater surface areas. The other three lakes are a little atypical: Borumba is a reservoir and so may lose heat in its outflow, Aroarotamahine is very sheltered and Rotoehu does not stratify.

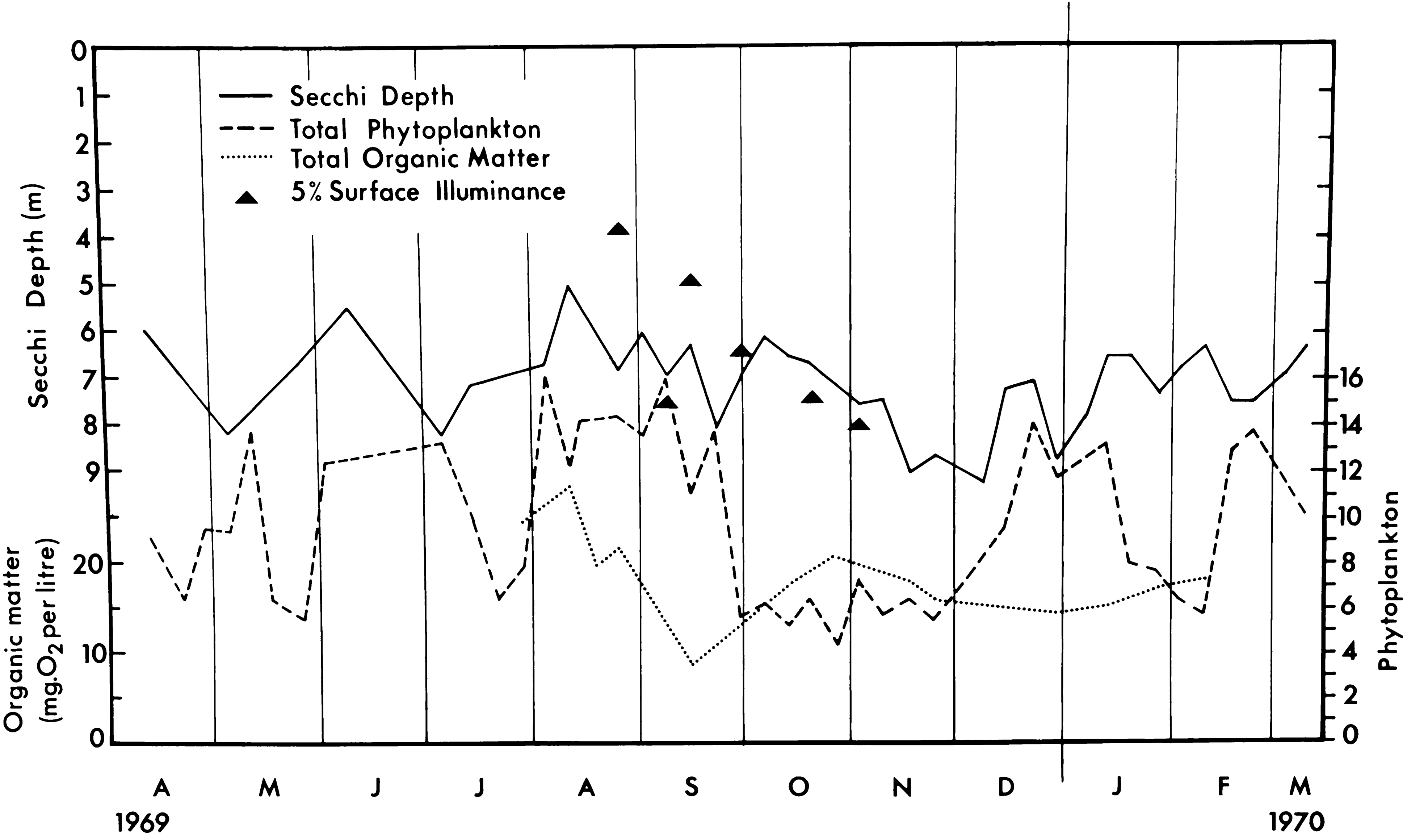
The amount of work done by the wind in distributing the heat budget was calculated for Lake Ototoa by Birge's (1916) method. The work of the wind (B) thus calculated is 1766 gmcm.cm^{-2}, and the unit work of the wind (the amount of work needed to distribute each calorie of the heat budget i.e. B/θ_{bs})is thus 0.114 gmcm.cal^{-1}. These two values have not been calculated for any other Australasian lakes, but are rather high by world standards (Hutchinson 1957) and as discussed later the wind probably has to do more work because heating takes place at relatively high temperatures.

2. Transparency by Secchi Disc.

Secchi disc transparencies over the sampling period are plotted in fig. 6. As the transparencies at the three stations were similar on any one date, the values plotted are the averages.

After sampling began, transparency increased during April and May, followed by a decrease in June. After another increase in July secchi depth decreased to the lowest value recorded in mid August (5 metres on 11 August). Between August and September transparency, although

Fig. 6: Changes in secchi depth throughout the sampling period. Total phytoplankton, organic matter and the depth of 5% illuminance are also shown.


Secchi Depth
Total Phytoplankton
Total Organic Matter
5% Surface Illuminance
Secchi Depth (m)
0
1
2
3
4
5
6
7
8
9
Organic matter (mg.O_2 per litre)
20
10
0
Phytoplankton
16
14
12
10
8
6
4
2
0
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

variable increased slightly. Following a slight decrease in early October there was a steady increase during the spring, and the greatest secchi depth was found in early December (9.2 m on 8 December). Transparency decreased again in mid-December followed by a further lowering in mid-January. Secchi depths then remained relatively constant until the end of the sampling period.

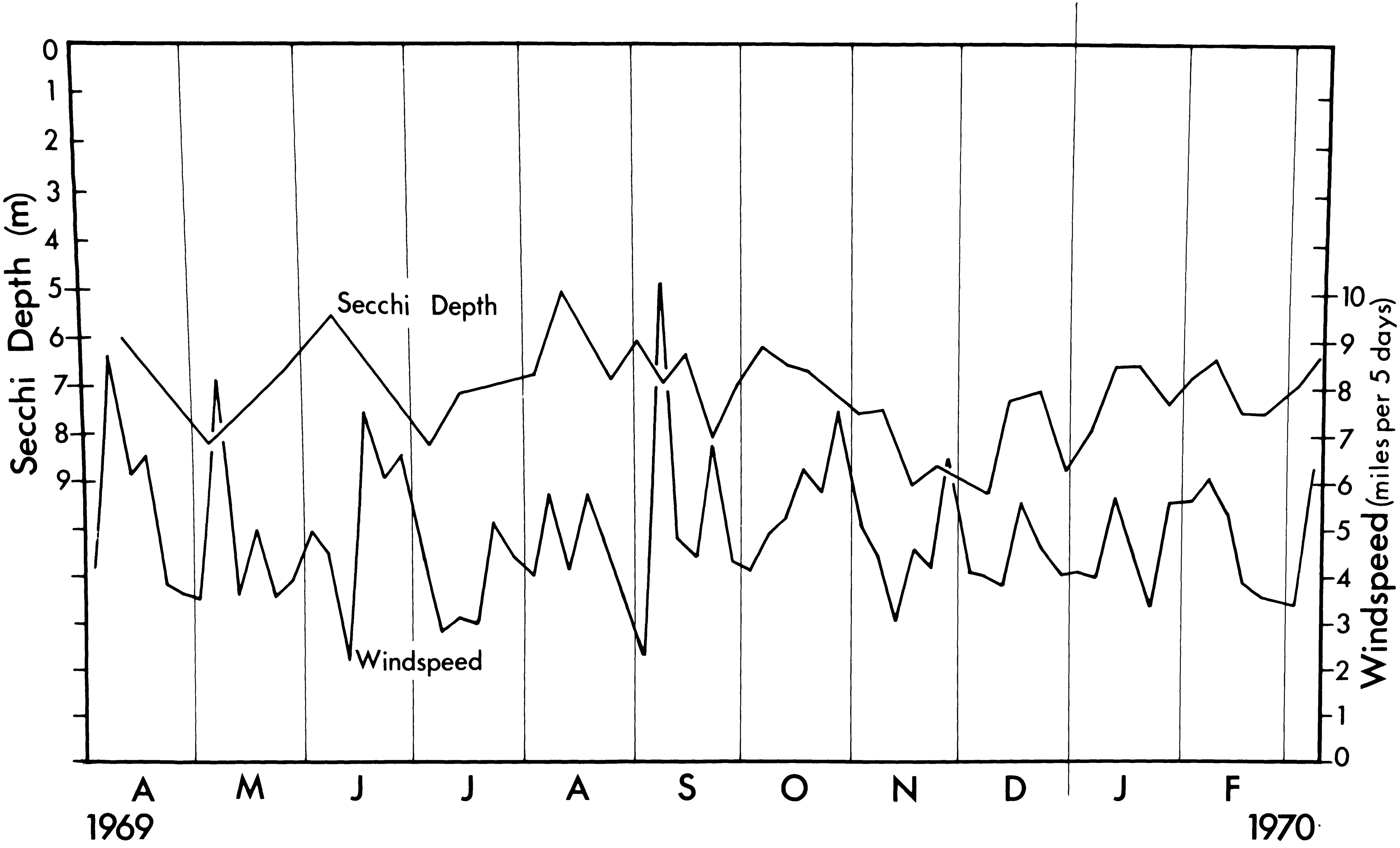
As transparency is often correlated with amounts of seston (Hutchinson 1957), the total numbers of phytoplankton and total organic matter has also been plotted in fig. 6. There was little relationship between secchi depth and either of these factors throughout the whole of the sampling period, however periods of high phytoplankton concentrations during August and September, and during late December and early January coincided with generally lower secchi depths. The increase in organic matter during October ,followed by decreasing concentrations during November, mayalso be related to the decrease in transparency in October and the gradual increase in the following two months. However, it is likely that the combined effect of these two factors is more important in determining secchi depth than either of them alone.

The high concentrations of *Botryococcus braunii* which were always present could also have affected secchi depth, and may have introduced irregular variations depending not only on the concentration and distribution but also on the surface light intensity. A secchi depth observation is a comparison of the brightness of the disc with the water around it (Hutchinson 1957). Although variations in surface light intensity should not affect the result, particles such as the large colonies of *Botryococcus* which appear much brighter in higher light intensities (especially if concentrated in the upper waters on a clear calm day) might affect the reading in an erratic manner. Small particles of wind blown sand from nearby dunes may also be important in determining secchi depths in coastal sand dune lakes such as Ototoa. This may be the reason for the correspondence between wind speed and secchi depth between December 1969 and March 1970 (fig. 7).

Yoshimura (1938) considered that the secchi disc disappeared at the level of about 5% surface illumination. These values for Lake Ototoa have also been shown in fig. 6, and on all but two occasions were closely similar to the secchi depths.

The secchi transparencies of Lake Ototoa are high compared with other relatively small New Zealand lakes, which tend to be productive and turbid with low secchi depths (Haydon 1967, Donovan 1968, Jolly 1968, Green 1968 and Mitchell 1971). Cunningham et al (1953) found a secchi transparency in Lake Ototoa of 9 m on the 4 January 1950, which is a little greater than found at the same time of the year in this study. The shallower sand dune lakes they visited had much lower transparencies which were believed to

Fig. 7: Changes in secchi depth and wind speed at the neighbouring Woodhill Forest Meteorological station throughout the sampling period. Wind speed is expressed as the number of metres run in a five day period.


Secchi Depth (m)
0
1
2
3
4
5
6
7
8
9
Secchi Depth
Windspeed
Windspeed (miles per 5 days)
10
9
8
7
6
5
4
3
2
1
0
A
M
J
J
A
S
O
N
D
J
F
1969
1970

be caused by disturbance of silt and bottom sediments by the wind. Of the lakes studied by Jolly (1968) the secchi depths of Ototoa are most like those of the large clearer lakes of the Rotorua area - Tarawera, Tikitapu, Okataina and Rotoiti.

3. Light Transmission.

The photometer readings made on those occasions when a light meter was available are shown in fig. 8. The slopes of these lines are a measure of the absorption of light by the water, and may be expressed as the vertical extinction coefficient (n"), and the transmission of light by the water column as the percentile transmission per metre (Hutchinson 1957, Barker 1970). The vertical extinction coefficient is given by:

$$n'' = \frac{\ln Ia - \ln Ib}{z_b - z_a}$$

Where Ia and Ib are light intensities at depths z_a and z_b respectively, when z_a is less than z_b

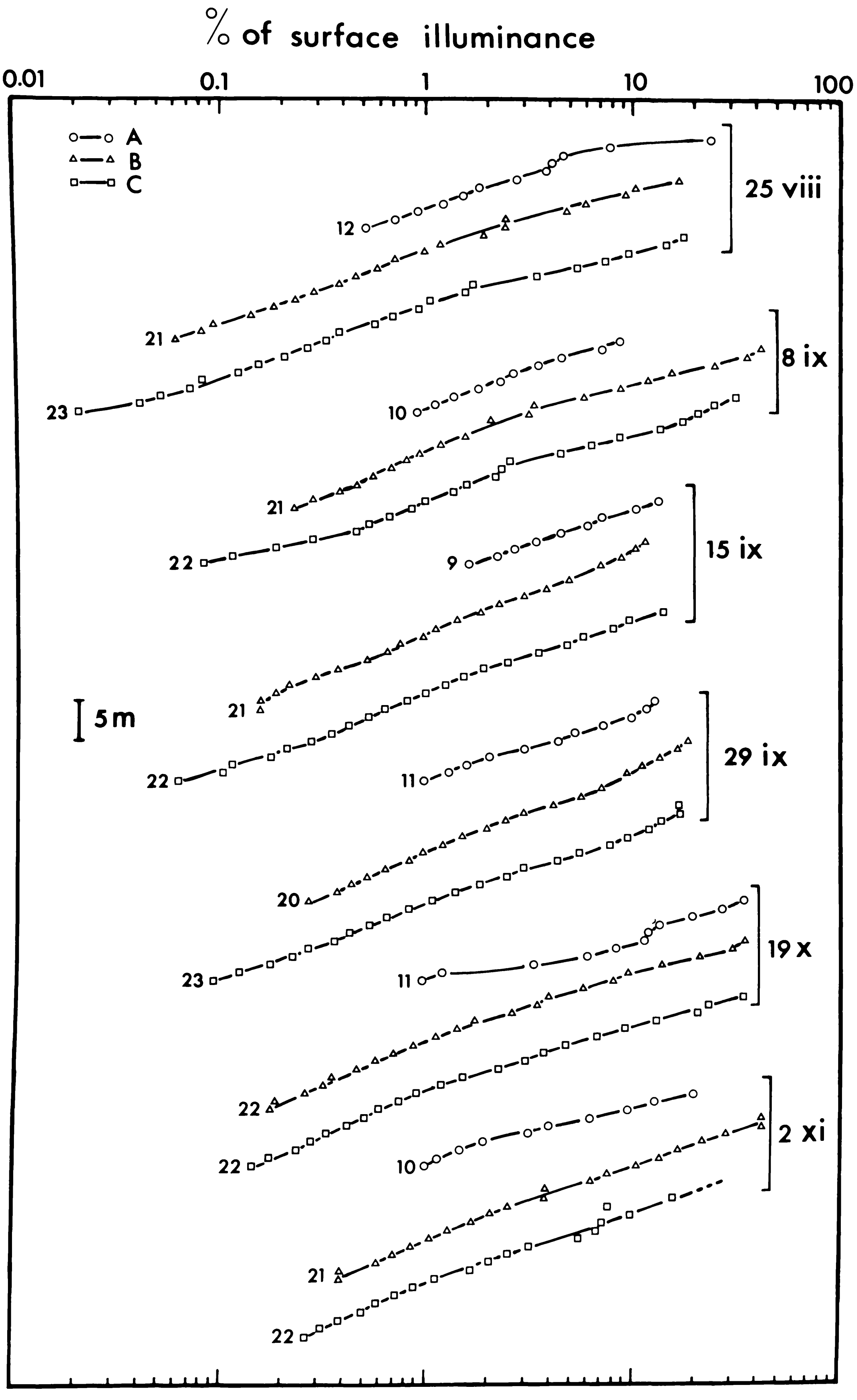
The percentile transmission (Pt/m) is given by:

$$Pt/m = 100e^{-n''}$$

These two parameters over four different depth ranges in Lake Ototoa are shown in table 8

The results emphasize the clarity of the water in Lake Ototoa. Using the same light meter Barker (1970) obtained transmissions ranging from 23%/m during the summer on Lake

Fig. 8: Transmission of light in Lake Ototoa. Light intensity at each depth has been expressed as a % of the surface illuminance. The slopes of these lines give a measure of the vertical extinction coefficient, a steeper slope indicating greater light transmission.



% of surface illuminance
0.01
0.1
1
10
100
A
B
C
25 viii
8 ix
15 ix
29 ix
19 x
2 xi
5m
12
21
23
10
21
22
9
21
22
11
20
23
11
22
22
10
21
22

DATE	Depth range (m)	Stn. A.		Stn. B.		Stn. C.	
		n"	Pt/m	n"	Pt/m	n"	Pt/m
25 August	1-6	0.445	64.07	0.392	67.6	0.333	71.7
	6-11	0.270	76.3	0.247	78.1	0.323	72.4
	11-16	-	-	0.220	80.3	0.242	78.5
	16-21	-	-	0.269	76.4	0.277	75.8
8 September	1-6	0.265	76.7	0.315	73.0	0.253	77.6
	6-11	0.239	78.8	0.372	68.9	0.278	75.8
	11-16	-	-	0.139	87.1	0.240	78.7
	16-21	-	-	0.220	80.3	0.352	70.3
15 September	1-6	0.277	75.8	0.225	79.8	0.281	75.5
	6-11	0.250	77.9	0.247	78.1	0.254	77.6
	11-16	-	-	0.222	80.1	0.208	81.3
	16-21	-	-	0.175	83.9	0.245	78.3
29 September	1-6	0.220	80.3	0.196	82.2	0.153	85.8
	6-11	0.300	74.1	0.257	77.4	0.292	74.7
	11-16	-	-	0.226	79.8	0.247	78.2
	16-21	-	-	0.213	80.8	0.220	80.3
19 October	1-6	0.226	79.8	0.298	74.2	0.328	72.1
	6-11	0.496	60.9	0.305	73.7	0.299	74.2
	11-16	-	-	0.222	80.1	0.217	80.5
	16-21	-	-	0.223	80.0	0.212	80.9
2 November	1-6	0.371	69.0	0.229	79.6	-	-
	6-11	0.285	75.2	0.255	77.5	0.268	76.5
	11-16	-	-	0.257	77.3	0.255	77.5
	16-21	-	-	0.198	82.1	0.204	81.5

Table 8 : Light extinction coefficients (n") and percentile transmissions (Pt/m) in Lake Ototoa.

Pupuke, to 75%/m in October and April and Green (1968) found values between 3 and 22%/m on the Auxiliary Nihotupu reservoir. The values for Ototoa are near those of Crystal Lake (82%/m) the clearest of the Wisconsin lakes studied by Birge and Juday (Hutchinson loc. cit.) and to lake 161 of the Canadian E.L.A. lakes (75.2%/m, Schindler, 1971).

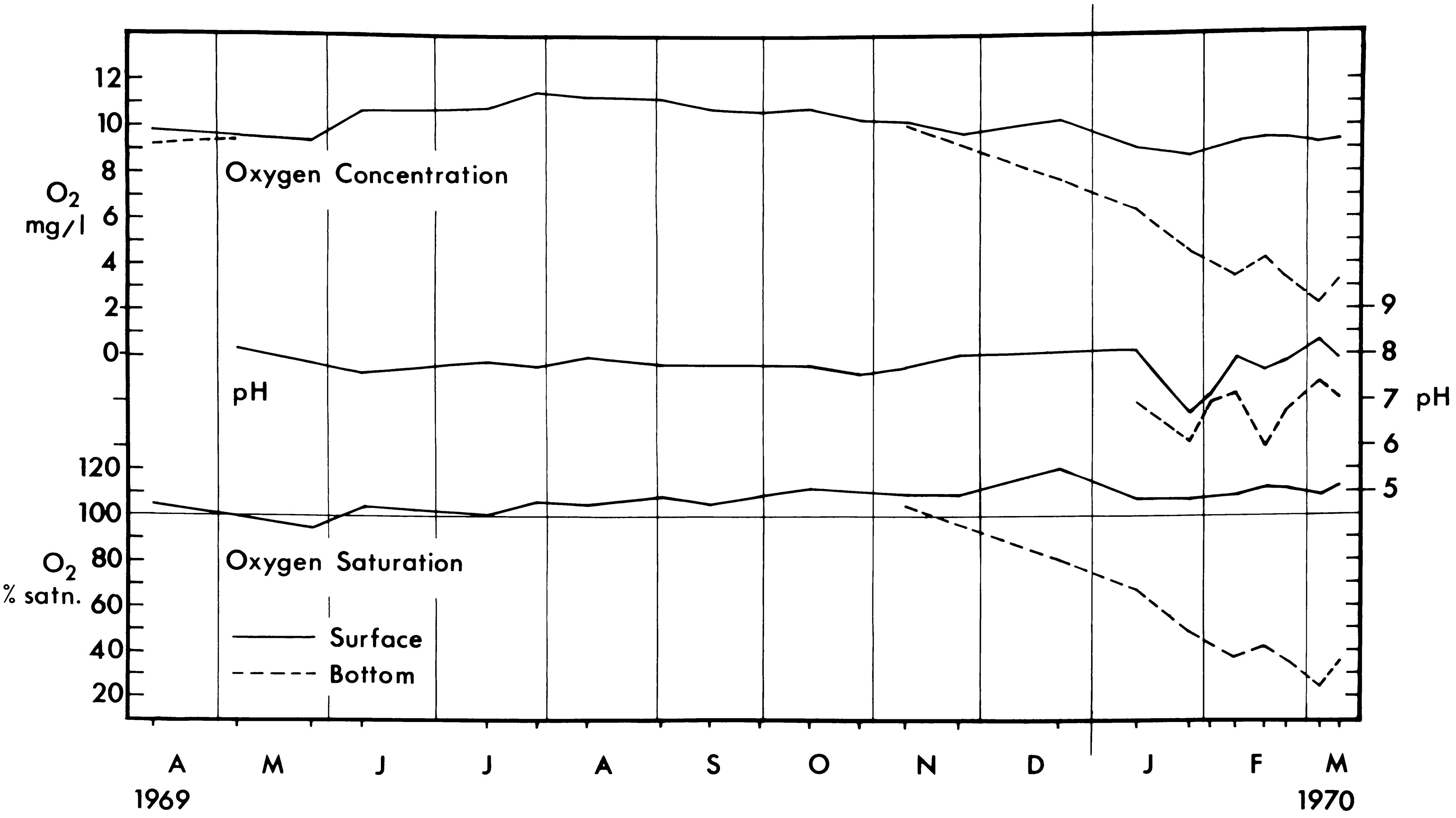
A feature of the lines in fig. 8 is the increase in slope below about 11 metres in many of them. This indicates an increase in transmission compared with the shallower depths and is further emphasised in table 8 where the percentile transmission between 6 and 11 metres is generally less than that between 11 and 16 or 11 and 21 metres depth. This suggests that detrital matter, phytoplankton or perhaps zooplankton was denser nearer the surface. Perhaps colonies of *Botryococcus* which, as noted above, were always present, were the cause of the lower transmission between 6 and 11 metres depth.

7. Oxygen.

Surface oxygen concentrations and saturations differed little between the three stations, and the average values have been plotted in fig. 9. The mean values from the bottom waters at stations B and C are also shown.

Oxygen concentrations were highest in winter and dropped gradually during spring and summer, although there

Fig. 9: Changes in oxygen concentration, % saturation and pH of the surface waters of Lake Ototoa throughout the year and of the bottom waters during the summer. The surface values are the averages of those from all stations, and the bottom values are those from stations B and C.


Oxygen Concentration
O_2 mg/l
12
10
8
6
4
2
0
pH
120
100
80
60
40
20
O_2 % satn.
Oxygen Saturation
Surface
Bottom
9
8
7
6
5
pH
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

were small increases in December and February. Surface waters were supersaturated with oxygen on all but one occasion, in May 1969. Saturation levels increased during the spring and summer to reach maximum levels in December (121% on 22nd). They then declined and there was another small increase in February. These higher saturation levels during spring and summer were probably the result of increased photosynthetic activity by phytoplankton which was more abundant in December and February.

During the summer, from November onwards, both oxygen concentrations and saturation levels gradually dropped in the bottom waters reaching minimum levels of 2.3 mg/l and 24% saturation on 3 March 1970. Concentrations were a little lower at station C than at station B during this period, and probably resulted from its greater depth (23m at station C cf 21m at station B). The small increases in February and March came at a time when the thermocline was descending and may have been caused by some mixing of well oxygenated epilimnetic waters into the hypolimnion.

A vertical series of oxygen determinations was made on 12 January 1970. Samples were taken from depths of 0,3.6,9,12,15,18 and 21 metres at station B, and the results are shown in fig. 10. Oxygen increased slightly in the lower epilimnion and upper metalimnion, followed by a reduction in the lower metalimnion and hypolimnion.

This is a weakly developed example of a positive heterograde curve. Such distributions are produced in clear lakes when light transmission is great enough to allow algal photosynthesis in the stable metalimnetic layers (Hutchinson 1957) and this seems to be the most likely explanation for the observed curve in Ototoa. On 12 January the thermocline lay between 12 and 14 metres where the illumination was probably about 1% of surface light intensity, * which is thought to be approximately the lower limit for the occurrence of photosynthesis (Clarke 1953). Positive heterograde oxygen distributions has also been recorded from Lakes Pupuke (Barker 1970), Okataina (Fish 1970) and the Lower Nihotupu reservoir (Haydon 1967).

When Lake Ototoa was sampled on the 4 January 1950 by Cunningham et al (1953), surface saturations were similar to those found in January 1970 (table 9). There was weak thermal stratification between 6 and 10 metres depth (fig. 4) and although a positive heterograde oxygen distribution was not found, oxygen saturations did drop to 55% at 25 m (3.0 ml/l) which is comparable with the results found in the present study.

---

* The secchi depth on 12 January was 6.5 m which is similar to that of 19 October when the depth of penetration of 1% of surface light was ca 13 m (fig. 8).

DEPTH (m)	4 January 1950	12 January 1970
0	110	108
2	110	-
4	-	108
6	110	-
8	109	108
9	-	111
10	105	-
12	-	114
15	93	95
18	-	83
21	-	69
24	55	-

Table 9: Profiles of oxygen saturation in Lake Ototoa during the summers of 1950 and 1970. 1950 data from Cunningham et al (1953).

LAKE	AREAL DEFICIT		VOLUMETRIC DEFICIT	
	$mg.cm^{-2}.day^{-1}$	$mg.cm^{-2}$	$gm.m^{-3}$	$gm.m^{-3}.day^{-1}$
Okataina[1]	0.042	7.6	2.3	0.013
Ngapouri[1]	0.044	8.4	9.7	0.050
Okaro[1]	0.034	6.3	10.0	0.054
Pupuke[2]	0.032	-	-	-
Auxiliary[3] Nihotupu	0.038	-	-	-
Ototoa	0.015	0.96	2.14	0.033

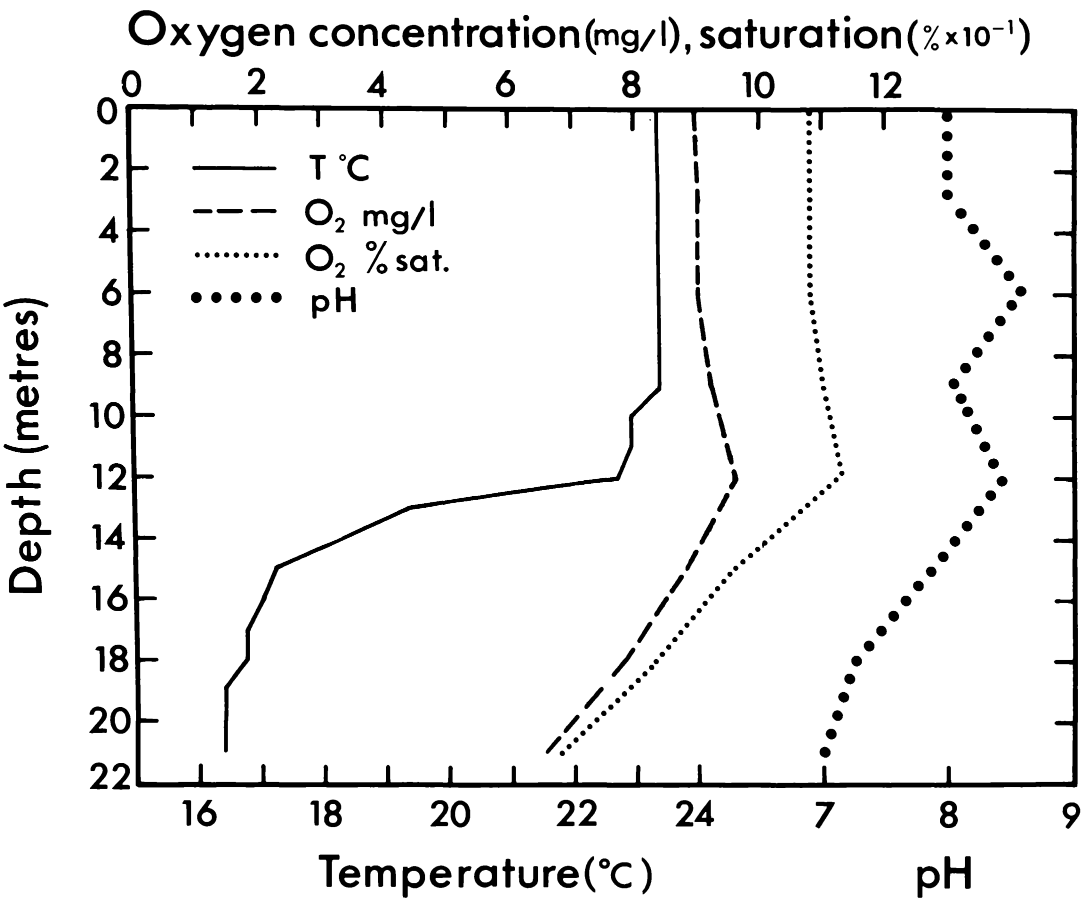
Table 10: The hypolimnetic oxygen deficits of some New Zealand lakes. Data from 1) Fish 1970; 2) Barker 1970 3) Green 1968.

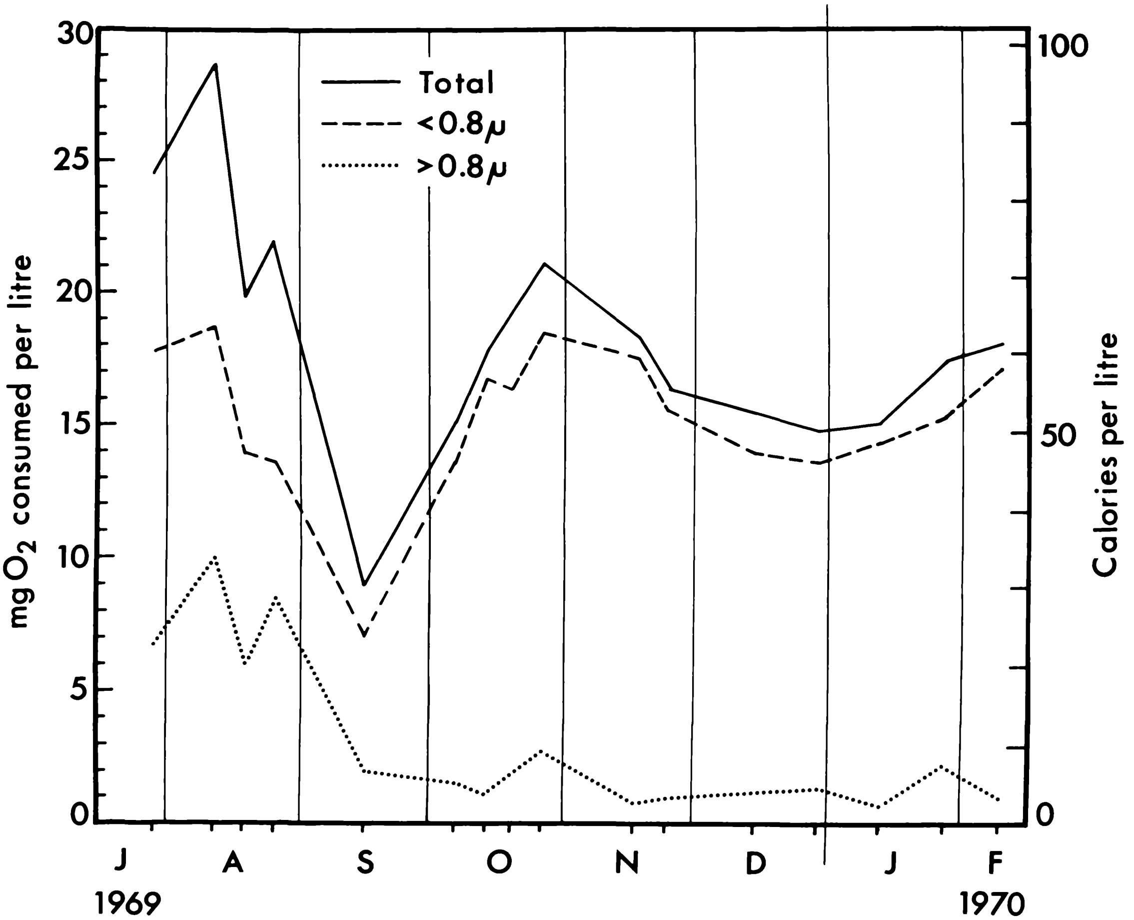
Oxygen Deficit: The relative hypolimnetic areal oxygen deficit may be defined as the difference between the amounts of oxygen dissolved in the hypolimnion during spring circulation and summer stagnation, expressed per unit area of the hypolimnetic surface (Hutchinson 1957). The data presented in fig. 10 can be used together with the oxygen concentrations determined on 9 November to calculate this deficit for Lake Ototoa. A vertical series of samples was not taken on 9 November but as stratification had only just begun to form, and the bottom waters were still supersaturated with oxygen (fig. 9) it has been assumed that the bottom value (10.2 mg/l) is a close approximation of the actual oxygen concentrations in the whole of the hypolimnion.

Using the known volumes of the layers below the thermocline, the average oxygen content of these layers and assuming lateral uniformity, the total oxygen content of the waters below 14 metres depth was calculated on these two dates (Edmondson 1966). Thus for Lake Ototoa a deficit of 0.96 $mg.cm^{-2}$ over 64 days or 0.015 $mg.cm^{-2}.day^{-1}$ was calculated, which is considerably lower than the deficits of other New Zealand lakes (table 10). Fish (1970) believed that the deficits of the lakes he studied could be meaninfully compared only when expressed on a volumetric basis (see, however, discussion), and the cubic deficits for

Fig. 10: The distribution of temperature, pH, oxygen concentration and oxygen saturation with depth at station B during mid-summer (12.1.70).

Fig. 11: Seasonal changes in the concentration of organic matter in Lake Ototoa. The total amount of organic matter is shown as well as those fractions smaller than 0.8 microns in diameter (<0.8μ) and larger than 0.8 microns in diameter (>0.8μ).


Oxygen concentration(mg/l), saturation(%×10⁻¹)
0 2 4 6 8 10 12
Depth (metres)
0 2 4 6 8 10 12 14 16 18 20 22
T °C
O₂ mg/l
O₂ %sat.
pH
16 18 20 22 24
7 8 9
Temperature(°C)
pH


Total
<0.8µ
>0.8µ
mg O₂ consumed per litre
0 5 10 15 20 25 30
Calories per litre
0 50 100
J A S O N D J F
1969
1970

Ototoa have been shown in the table as well.

The figures for Ototoa may be a little too low however, because even though 14 metres (taken as the upper limit of the hypolimnion in the calculation) was below the slight oxygen maximum on 12 January (fig. 10), oxygen produced photosynthetically in the upper metalimnion may have been transferred to some extent into the upper hypolimnion by turbulent mixing.

5. Hydrogen Ion Concentration.

In Lake Ototoa there was little seasonal variation in the pH of the surface waters (fig. 9). Slightly higher values were found in the summer and autumn (maximum 8.3; 3/3/70) than in the winter (generally 7.63 - 7.95). However the lowest values were found in late January and early February when pHs dropped to about 7.2 , a fall which may be related to lower phytoplankton stocks at this time.

Flint (1938) and Mitchell (1971) working on Lake Sarah and Waipori, Mahinerangi and Tomahawk lagoon respectively, also found seasonal trends of lower winter pH rising to higher values in the summer as did Barker (1970) in Lake Pupuke.

Taken as a whole the pHs were a little higher than those found in most of the lakes studied by Stout (1969), Fish (1970) and Mitchell (1971), and of those of Jolly (1968) which were not affected by thermal waters; a tendency which may reflect the higher alkalinity of Ototoa.

On the other hand they were not as high as in Aroarotamahine (Bayly 1962), Pupuke (Barker 1970) and a variety of volcanic lakes in southeast Australia (Bayly and Williams 1964). In these cases high pHs (over 9) are thought to be caused by large amounts of sodium carbonate in solution. In other Northland sand-dune lakes Chapman and Green (1973) recorded pHs similar to those found in this study.

As in most stratified lakes, the bottom waters had slightly lower pH values (Hutchinson 1957), which fluctuated over the summer (fig. 9). The vertical variation in pH on 12 January is shown in fig.10. High pH at 6 and 12 metres may have been related to algal photosynthesis, and the associated development of an oxygen maximum at this lower depth. Below the thermocline pHs dropped gradually to reach neutrality in the bottom waters.

Previous estimates of the pH in Ototoa by Cunningham et al (1953) were 6.6 at the surface, and 6.4 at 24 metres, which are significantly lower than the values found in the present study. However, these authors suggest that their pH measurements may contain errors, for checks on lakes in the Wellington series of dune lakes gave pHs considerably at variance with the original figures.

6. Ionic Composition.

Ionic composition varied little between stations, and the mean values of the major and minor ions are set out in tables 11 and 12.

a) Major ions: The salinity of Lake Ototoa is typical of the series of Northland lakes studied by Chapman and Green (1973). These are considerably more saline than the dilute waters of the Canterbury mountain lakes (Stout 1969), yet more dilute than Aroarotamahine (Bayly 1962), Pupuke (Barker 1970) and Tomahawk lagoon (Mitchell 1971) (table 13). The anionic concentration of 2.24 me/1 further reflects this position. The lakes studied by Jolly (1968) which were not affected by thermal waters had concentrations between 0.25 and 1.45 me/1, while Pupuke (Barker,loc.cit) had an average value of 3.30 me/1.

Between August 1969 and March 1970, values of Na, Cl, HCO_3 and SO_4 increased, which was probably due to concentration as the lake level was lowered by evaporation during the summer. However, concentrations of Ca and Mg decreased and this is difficult to account for as pHs were still below those where calcium would precipitate. It may be that the decrease was a result of biological deposition, perhaps during photosynthesis (Horie 1968).

Previous analyses of water from Lake Ototoa by Cunningham et al (1953) gave concentrations of 58.2mg/1 Cl and 4 mg/1 SiO_4. .In neighbouring Lake Kuwakatai, which is only a few

	Na		Mg		Ca		K		Cl		HCO_3		SO_4		Tot. Strong acids	Total anion	Salinity
DATE	mg/l	me/l	mg/l	me/l	mg/l	me/l	mg/l	me/l	mg/l	me/l	mg/l	me/l	mg/l	me/l	me/l	me/l	mg/l
14.7.69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.40	-	-
11.8.69	23.0	1.00	12.2	1.00	3.0	0.15	2.43	0.06	-	-	50.5	0.83	-	-	1.38	2.21	-
22.9.69	24.5	1.07	10.3	0.85	4.60	0.23	2.53	0.07	-	-	50.5	0.83	-	-	1.39	2.22	-
26.10.69	28.5	1.24	8.4	0.69	4.66	0.24	2.50	0.06	-	-	50.6	0.83	-	-	1.39	2.22	-
17.11.69	23.8	1.03	-	-	4.40	0.22	2.45	0.06	-	-	-	-	-	-	1.37	-	-
29.12.69	25.1	1.09	10.7	0.88	3.13	0.16	2.43	0.06	44.4	1.25	50.6	0.83	4.99	0.10	1.36	2.19	141.3
27.1.70	32.25	1.40	7.1	0.58	3.85	0.19	2.60	0.07	48.05	1.36	51.8	0.85	4.04	0.08	1.39	2.24	149.7
17.2.70	32.75	1.42	7.3	0.60	3.53	0.18	2.50	0.06	47.40	1.34	51.8	0.85	4.23	0.09	1.41	2.26	149.0
27.2.70	34.75	1.51	6.3	0.52	3.73	0.19	2.80	0.07	46.55	1.31	52.4	0.86	5.52	0.12	1.43	2.29	152.0
9.3.70	34.75	1.51	6.1	0.50	4.51	0.23	2.28	0.06	46.40	1.31	53.7	0.88	5.43	0.11	1.42	2.30	153.2
MEAN	28.8	1.25	7.3	0.71	3.93	0.20	2.50	0.06	46.55	1.31	51.5	0.84	4.84	0.10	1.39	2.24	149.0

Table 11: The chemical composition of Lake Ototoa. (Major ionic constituents).

DATE	NO_3(mg/l)	PO_4(µg/l)
11.viii.69	0.6	-
22.ix.69	0.5	5.95
26.x.69	0.3	1.00
17.xi.69	0.17	10.20
29.xii.69	0.37	3.15
27. i.70	0.36	3.15
17.ii.70	0.46	2.65
23.ii.70	0.31	-
9.iii.70	o.12	-
Mean		

Table 12: The chemical composition of Lake Ototoa (minor ionic constitutents).

	CONCENTRATION (mg/l)							(me/l)
LAKE	Na	Mg	Ca	K	Cl	HCO_3	SO_4	Total anion
Ototoa	28.8	7.3	3.93	2.5	46.55	51.5	4.84	2.24
Pupuke[1]	35.0	14.7	8.50	2.16	44.0	96.7	23.7	3.30
Northland[2] Dune Lakes	20.7	8.5	1.7	1.4	38.7	16.0	4.9	-
Aroarotamahine[3]	125.0	1.2	0.9	4.0	76.0	102	4.0	-
Canterbury[4] lakes	1.75- 8,1	0.33- 1.5	2.2- 13.5	0.05- 1.2	3- 8	0.33- 0.99	-	-
Tomahawk[5]	-	12.3- 24.3	30.8- 88.6	-	278 580	-	-	-
Mahinerangi[5]	-	0.2- 1.0	0.9- 2.0	-	4- 5	-	-	-
Waipori[5]	-	0.3-	0.8-	-	2.5-	-	-	-

Table 13: Comparison of the chemical composition of some New Zealand Lakes. Data from 1) Barker (1970); 2) Chapman and Green (1973); 3) Bayly (1963); 4) Stout (1969); 5) Mitchell (1971).

hundred metres to the south of Ototoa, these authors found concentrations very similar to those determined in the present study of Ototoa: their values were Na - 28.0mg/l, Mg - 7.4mg/l, Ca - 6.6mg/l, K - 3.0mg/l and also SiO_4 - 3.4mg/l. Similarly, analyses of samples from Lake Ototoa carried out by the government analyst at Auckland on 27 April 1964 gave the following results: pH - 7.6, Cl - 55mg/l, total solids - 130 mg/l, alkalinity - 50 mg/l. These only differ greatly from those of 1969 - 70 in the slightly higher chloride concentration.

Ionic ratios from Lake Ototoa are shown in table 14 together with those of typical seawater, world average freshwater and a number of New Zealand and Australian lakes, or groups of lakes. The ionic sequence in Ototoa is $Na > Mg > Ca > K$ for the cations and $Cl > HCO_3 > SO_4$ for the anions, compared with the order for typical freshwater of $Ca > Na = Mg > K$ and $HCO_3 > SO_4 > Cl$.

Such enrichment of Na, Cl and Mg is widespread in Australasian lakes, especially in those nearer the sea, e.g. the Queensland, New South Wales coastal dune lakes (Bayly 1964, Timms 1969), the SE Australian Volcanic lakes (Bayly and Williams, 1964,66), Lake Aroarotamahine (Bayly 1962), Pupuke (Barker 1970) and the Northland Dune lakes (Chapman and Green 1973), and has been explained in terms of atmospheric supply of ions from the sea, which Gorham (1961) has shown is a major source of Na, Mg, Cl and SO_4 but not Ca and K. Even in the very dilute waters studied by Stout (1969) (table 14) there is a greater proportion of sodium, which presumably also comes from the sea.

IONIC PROPORTIONS

(m-equiv. % of total cations or anions)

WATER	Na	Mg	Ca	K	Cl	HCO_3	SO_4	Na/Cl	Salinity (mg/l)
Ototoa	56.3	32.0	9.0	2.7	58.4	37.2	4.4	0.97	149
Seawater	77	18	3	2	90	(0.4)	9	0.86	35,000
Mean fresh water[1]	16	17	64	3	10	73	16	1.60	146
Pupuke[2]	49.0	35.6	13.8	1.6	36.9	48.8	14.3	1.33	225
Queensland-New South Wales dune lakes[3]	78	16	4	2	82	2	16	0.95	39
Wooli lakes[4]	80	14	5	1	75	17	8	1.07	74
Canterbury lakes[5]	31	11	55	2	-	-	-	-	-
Aroarotamahine[6]	96	2	1	2	38	62	1	2.52	-
Northland dune lakes[7]	56.1	36.7	4.9	2.4	68.5	13.9	6.1	0.82	-
Northland dune lakes[8]	60	24	13	3	-	-	-	-	147

Table 14 Comparison of mean proprotions of major ions in Lake Ototoa with those of other waters.

(1) Conway 1962; (2) Barker 1970; (3) Bayly 1964; (4) Timms 1969; (5) Stout 1969; (6) Bayly (1963); (7) Chapman & Green 1973; (8) Cunningham et al. (1953).

The relatively small enrichment in this case is probably related to the distance from the coast (80-90 km).

It can be seen from table 14 that the ionic ratios of Lake Ototoa are more similar to those of seawater than to those of standard freshwater, and there can be little doubt that oceanic ion supply via rainfall and spray is of importance in this lake.

The concentrations of Ca and bicarbonate are however higher in Ototoa than if only atmospheric supply of ions was important. These two ions, and possibly also some Mg, are most likely introduced by solution of limestones in the consolidated Kaihu dunes. High proportions of bicarbonate in Pupuke (Barker 1970) and the Wooli lakes (Timms 1969) are thought to be determined in a similar manner. In Ototoa HCO_3 is more nearly equivalent to Cl than in Pupuke or Aroarotamahine (table 13). This has also been found in a pond studied by Timms (1967) who notes that in more dilute Australian waters (below 500 mg/l salinity), Williams (1964a) has found a tendency for bicarbonate to become approximately equal to chloride.

The low Ca concentrations in Ototoa are similar to those of other New Zealand lakes (2-8 mg/l) which are characteristically soft (Fish 1969).

Ohle (1934) regards waters with less than 10 mg/l Ca as "poor", those with 10 - 25 mg/l as "medium" and those over 25 mg/l as "rich" (in relation to productivity). Ototoa is thus "poor" as were most of the Tasmanian lakes studied by Williams (1964 b).

b) Minor Ions: Nitrate concentrations were highest in mid-winter (0.6 mg/l, table 12), and decreased during spring to 0.17 mg/l. Concentrations rose again in the summer but declined in March to the lowest value found (0.12 mg/l). Phosphate tended to be highest in late winter and in spring. The high value recorded on 17 November 1969 (10.2 µg/l) is the result of the significant concentration of 16.7 µg/l at station C. This may have been caused by aerial topdressing, as superphosphate was being distributed over the farmland around the north of the lake as the sample was being collected.

Barker (1970) found similar nitrate concentrations in Lake Pupuke (0.09 - 0.27 mg/l). Lowest values were found in the summer, but the distinct seasonal cycle found in lakes elsewhere (Hutchinson ,1944) was not obvious. This was not so in the Wellington reservoirs however where there was a distinct seasonal trend for low summer values and high autumn and winter concentrations which was found to be related to the development of a phytoplankton maximum in mid-summer (Stevenson 1952). In Ototoa the opposite was true, nitrate concentrations were greatest at times of increased phytoplankton densities.

In the Wellington reservoirs nitrate varied between 0.05 and 0.6 mg/l. Cunningham et al (1953) found nitrate concentrations varying between 0 and 0.24 mg/l in the West Coast dune lakes (and a value of 0.20 mg/l in Ototoa) which are a little lower than the concentrations found in this present study. Jolly (1968) using a less sensitive method than in the present study, found only a trace in three of the lakes she studied (the rest had none), and in Lakes Waipori, Mahinerangi and Tomahawk lagoon (Mitchell 1971) nitrate was always below 0.08 mg/l.

Phosphate concentrations in Ototoa tend to be lower than many reported from other New Zealand lakes. Cunningham et al (1953) found values ranging from a trace to 30 µg/l (16 µg/l in Ototoa); Jolly (1968) found 0 - 360 µg/l in the large North Island lakes; Fish and Chapman (1969) recorded trace - 50 µg/l in Lake Rotorua and trace - 100 µg/l in Rotoiti while Mitchell (1971) found 2.1 - 133 µg/l in Tomahawk lagoon, 0.5 - 3.0 µg/l in Lake Mahinerangi and 1.7 and 8.7 µg/l in Lake Waipori.

7. Organic Matter:

Highest concentrations of total organic matter were found in August (fig. 11) but declined considerably during September to the lowest values found. Quantities increased again in October but fell gradually during the following three months. Further increases had occurred in late January and early February.

On all occasions most organic matter was contained in the fraction smaller than 0.8 microns, and so was presumably composed mainly of dissolved organic material and small nonliving detrital particles. From September onwards this fraction underwent a seasonal fluctuation which was the reverse of that of total phytoplankton (fig. 11). The increase in November and February may therefore be caused by the gradual breakdown of dead phytoplankton, and the low values during September and December may indicate the subsequent incorporation of this material into new algal stocks.

Organic matter larger than 0.8 microns was present in large amounts only during August. There was a decline to low values in September, and smaller increases occurred in late October and again in January. This fraction can be expected to correspond to most of the living phytoplankton and larger detrital particles, and the large amounts in August may be related to the Dinobryon bloom which occurred at that time. Later changes did not seem to be related to any significant changes in phytoplankton numbers.

The only other determinations of organic matter in Australasian waters by similar methods to those used in this study appear to be those of Fish (1966) and Bayly (1964). In the Queensland - New South Wales dune lakes during August and September 1963, Bayly found values between 0.5 and 39.0 mgO_2/l consumed (mean 15.7 mgO_2/l) compared with the range 8.97 to 28.7mg/l O_2 (mean 18.41) in Ototoa. A few isolated determinations from samples of water taken near weed beds in Lake Rotoiti gave values of 0.6 - 2.35 mg/l O_2 consumed (Fish 1966).

8. Discussion.

Many of the characteristics of Lake Ototoa are determined by its proximity to the sea. The direct effect on the chemical composition of the lake waters has already been discussed above, but more important because of its influence on seasonal cycles within the lake, is the damping effect of the oceanic climate. The extremes characteristic of continental regions are reduced and as far as the physical features of the lake are concerned the results of this amelioration are seen most clearly in the thermal regime.

Winter temperatures are high, the annual range of temperatures is small and when heating occurs it must take place at relatively high temperatures where distribution of heat into the lake is difficult because of the greater density differences which occur as temperature increases. Thus in Lake Ototoa a considerable amount of work must be done to distribute the heat budget, as shown by the rather high value for unit work of the wind (B/θ_{bs} = 0.114 gmcm.cm^{-2}).

Because of such factors warm monomictic lakes in oceanic regions may be expected to have heat budgets that are low in comparison with those of dimictic lakes. The budget of

Lake Ototoa and those of the other lakes shown in table 7 are rather low, (with the exception of Lake Okataina), but nevertheless it is perhaps more interesting that those of Pupuke, Ototoa and Ngapouri do at least approach the annual budgets of many of the Northern hemisphere lakes shown in table 53 of Hutchinson (1957), and are comparable with the budgets of the ELA lakes (Schindler 1971). Two factors are probably responsible for this possibility of increased heat uptake by some New Zealand lakes and both result from the oceanic milieu:

1. Opportunities for exposure to persistent, variable and moderately strong winds, which may be coupled with:
2. A slower rate of heating between maximum and minimum temperatures which facilitates the mixing of heated surface waters by the wind deeper into the lake, with the consequent development of a deeper thermocline and thus a higher summer heat income. In New Zealand heat is acquired over similar periods of time to lakes in northern and continental countries, yet the range of temperatures of the surface waters is much less: c.f. 10° - 25°C in Ototoa with 0° - 22°C in the ELA lakes (Schindler 1971).

In Lake Ototoa the large increases in bottom temperatures during the year is indicative of the efficient transfer of heat into the deeper regions of the lake by these processes. Those New Zealand lakes which are well sheltered from the wind develop shallow thermoclines and have very small heat budgets, (e.g. Aroarotamahine - heat budget 6000 cal.cm^{-2}, thermocline depth 4-8m; Auxiliary Nihotupu Reservoir Green (1968) thermocline depth 2m; small sand dune lakes (Cunningham et al 1953) - Okaihau (4m), Westmere (2.5m), Waitawa (3m)), while on the other hand slow heating and very large surface area are probably the reasons for the deep thermocline and exceptionally large heat budget of Lake Okataina (Fish 1970).

Although the reduction of climatic extremes is an important maritime influence, winds and cloudiness are variable, and storms can occur at any time, irregularly throughout the year. All these factors affect patterns of stratification and so there may be considerable variation in thermal regimes from year to year. The time of onset of stratification is thus probably subject to some variation, depending on the particular combination of wind and insolation which occurs during the period of heating between September and November. The transient stratification which developed in Lake Ototoa between August and October 1969 may well have stablised had the winds of September and October been weaker. Conversely the divergence found between the patterns of stratification of 1970, and those of the summers of 1950 and 1969, indicate that in some years stratification may be less well developed and may break down earlier than found in the present study.

Hutchinson (e.g. 1957) has shown that the areal hypolimnetic oxygen deficit gives a good measure of lake productivity. He regarded lakes which lost oxygen at a rate of up to 0.033 mg.cm^{-2}.day^{-1} as oligotrophic and those in which the rate was between 0.05 and 0.14 mg.cm^{-2}.day^{-1} as eutrophic. Mortimer (1956) has suggested slightly different values of 0.025 mg.cm^{-2}.day^{-1} as an upper limit for oligotrophy and 0.055 mg.cm^{-2}.day^{-1} as a lower limit for eutrophy. However, Fish (1970) believed that these values did not give an acceptable basis for distinguishing eutrophic from oligotrophic lakes in New Zealand. He reached this conclusion largely because he found that Lake Okataina (which has many oligotrophic features) had a similar oxygen deficit to the small eutrophic Lakes Okaro and Ngapouri (table 10).

However, when interpreting and discussing areal oxygen deficits it is important to bear in mind that they relate to actual organic productivity under unit surface area, and while this may be reflected in the typology of the lake, it is not necessarily so. Two lakes might have identical areal oxygen deficits but because of differing epilimnetic depths, hypolimnetic volumes etc., one may appear eutrophic (in the typological sense **i.e.** dense plankton, marked clinograde oxygen curve, low secchi depth etc.), the other oligotrophic. A classic example of this is provided by Lakes Mendota and Green (Hutchinson 1938). Because of the existence of such morphometrical oligotrophy it is a mistake to expect that the typology of a lake will always be able to be defined in terms of its areal oxygen deficit.

It seems possible that Fish (1970) found no apparent relationship between degree of eutrophy and areal oxygen deficit in the Rotorua lakes because he was in fact using the terms eutrophy and oligotrophy in the typological sense, and was not in fact relating the deficits to the real biological productivity of the lakes. There is no doubt that Okataina is typologically more oligotrophic than lakes Okaro and Ngapouri. However, the significance of the oxygen deficits appears to be that they show that Okataina is nearly as productive, on an areal basis, as the two shallower lakes.

Okataina has a less dense plankton, and the smaller amount of suspended solids (2.0 g/m^3 cf 10 and 14 g/m^3 in Okaro and Ngapouri) was cited by Fish as an indication of its lower production. However "... the plankton crop is an expression of the amount of solar energy converted into biochemical energy ..." (Hutchinson 1938) and thus lakes should be compared in terms of weight per unit area, since light enters only through the lake surface. Even though there was a low density of phytoplankton in Okataina, the epilimnion is very thick and the water is much clearer than in Okaro and Ngapouri, so the actual production under unit surface could well be nearly as great as in these smaller lakes.

Care must also be taken when interpretations are based on deficits calculated from lakes such as Okaro and Ngapouri, where there is complete deoxygenation in much of the bottom waters. Where the hypolimnion is small, as in these two lakes, the oxygen debt from production in the trophogenic zone may be much greater than can be supplied by the oxygen reserves of the hypolimnion, and a deficit which is uncorrected to give the "real" value (Hutchinson, 1957) will give an indication of the productivity of the lake which is too low.

It is possible therefore that some doubt may be placed on the interpretation of the oxygen deficits determined by Fish. This being the case there seems to be no adequate reason, as yet, for believing that Mortimer's standard deficit values should not apply to New Zealand lakes. Nevertheless they should be used with caution. Hypolimnetic temperatures of New Zealand lakes vary considerably. Those of the large southern lakes are low and constant (Jolly 1968), while those of many of the smaller northern lakes can be much higher, especially when under oceanic influences, as noted above. Because of these thermal differences the rate of development of the deficit would tend to be greater (independant of productivity) in lakes of this latter type. If New Zealand lakes as a group are found to have higher hypolimnetic temperatures relative to epilimnetic temperatures than do lakes in the northern hemisphere, then it may become necessary to set the limits which relate oxygen deficits to oligotrophy and eutrophy higher than recommended by Mortimer.

The oxygen deficit calculated for Lake Ototoa was 0.015 $mg.cm^{-2}.day^{-1}$, and thus on the basis of Mortimer's **classification** is to be regarded as oligotrophic, in the edaphic sense. This low deficit was developed even though there was a thick epilimnion much of which could have been trophogenic because of the clear water. The reduction of oxygen which did occur in the hypolimnion during the summer resulted from the small volume of water below the thermocline, which constituted only 12% of the lake volume (cf Okataina 47%, Okaro 44%, Ngapouri 61% (Fish 1969); Pupuke 33% (Barker 1970); Aroarotamahine ca 68% (Bayly 1962). Although the deficit may be a little too low because of metalimnetic oxygen production, it would seem that Ototoa is less productive than any other lake in the North Island which has been studied in detail. This is also suggested by the water clarity, relatively low soluble phosphate concentrations and also the small concentrations of chlorophyll and phytoplankton numbers (see later).

PHYTOPLANKTON

Few studies have been made of the seasonal cycles of phytoplankton in New Zealand lakes. Those of Flint (1938), Stevenson (1952), Cassie (1969) and Fish (in prep; pers.comm.) have been concerned with the larger diatoms, desmids and dinoflagellates, and changes in the stocks of nannoplankton likely to be of importance as food for zooplankton have been recorded only rarely (Green 1968).

In this study the phytoplankton was considered because of its possible significance as food for the zooplankton. The following section is thus concerned mainly with the overall seasonal changes in abundance, and the possible causes underlying these changes are not considered in any great detail.

Various of the collections (21 April 1969, 14 July 1969, 24 November 1969, 29 December 1969, 27 January 1970 and 17 February 1970) were kindly examined by Drs. E. A. Flint and U. V. Cassie who identified the main types present. The species list is set out in table 15 The dimensions of 10-20 individuals of the commonest species were measured at a magnification of x 800 using an eyepiece micrometer, and the average sizes calculated from this data are presented in table 16.

1. Chlorophyll a.

Concentrations of chlorophyll a throughout the sampling period are plotted in fig. 12. These values are the averages from the stations sampled on any one date.

CHLOROPHYCEAE

Ankistrodesmus falcatus (Corda) Ralfs
Ankistrodesmus sp.
Botryococcus braunii Ktz.
Coelastrum reticulatum (Daug) Sena.
Cosmarium sp. a
Cosmarium sp. b
Dictyosphaerium sp.
Gonatozygon sp.
Nephrocytium lunatum W.West
Oocystis sp.
Shaerocystis sp.
Staurastrum avicula?
S. chaetoceras? (Schroder)G.M.Smith
S. smithii? facies triradiatum
S. sagittarium Nordst.
S. planktonicum?

BACILLAROPHYCEAE

Cyclotella stelligera Cl.&Grun
Melosira sp.(islandica?)
Rhizosolenia eriensis H.L.Smith
Synedra sp.
Tabellaria flocculosa (Roth) Ktz.

DINOPHYCEAE

Ceratium hirundinella (O.F.M.)Schrank
Glenodinium sp.
Gymnodinium sp.
Peridinium sp.

Table 15 (cont. next page)

CHRYSOPHYCEAE

Dinobryon divergens Imhof.
D. sertularia Ehr.

CRYPTOPHYCEAE

Cryptomonas sp.
Cryptomonas? ("small monad")

CYANOPHYCEAE

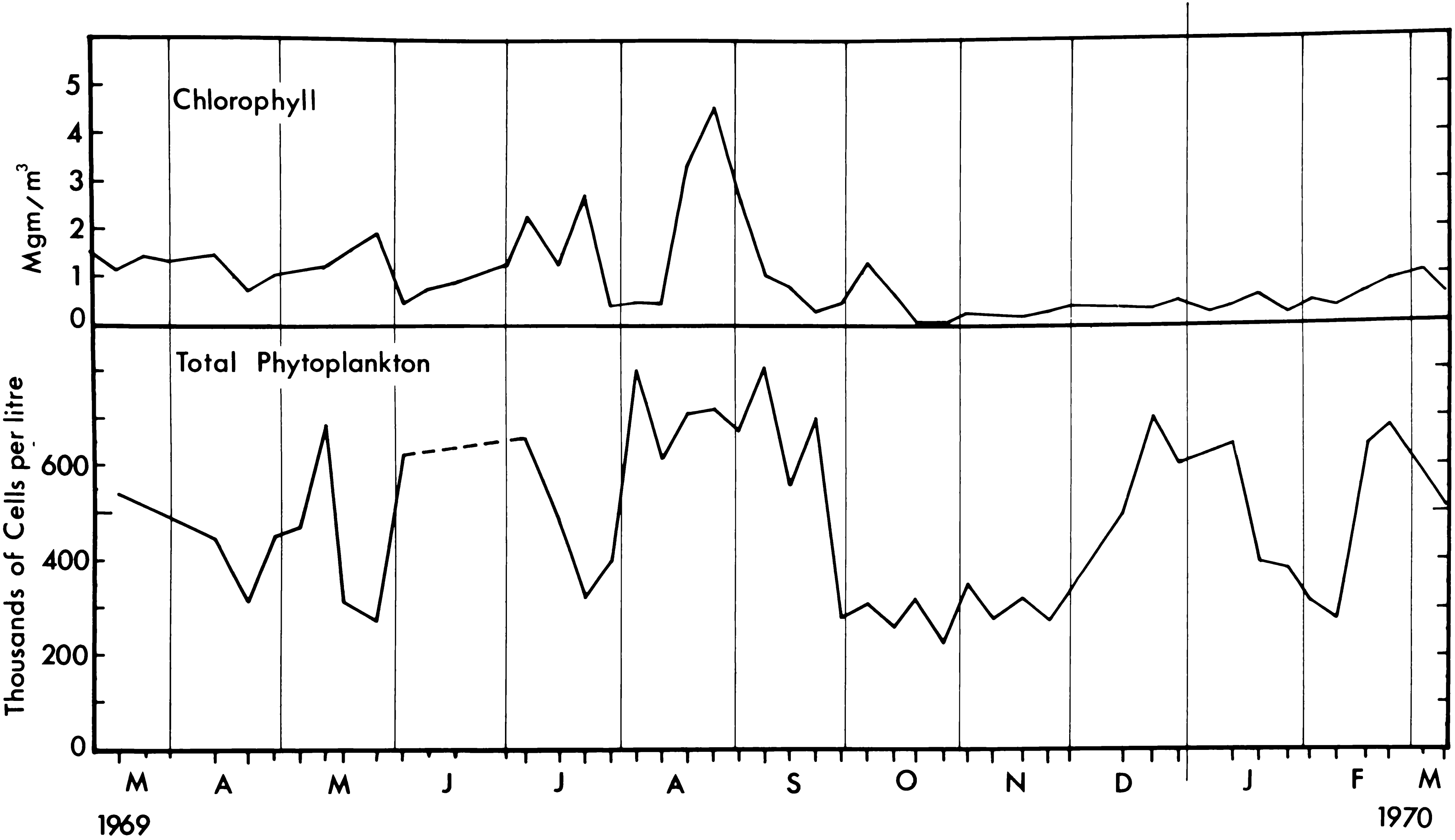
Chroococcus limneticus var?

Table 15: Planktonic algae from Lake Ototoa.

ALGA	CELL SIZE		COLONY SIZE	
	Length or Width(μ)	Breadth or Depth (μ)	Length (μ)	Breadth (μ)
Cyclotella	8.5	3.4		
Melosira	18.1	11.3		
Other Diatoms	27.3	7.0		
Rhizosolenia	40.3	8.0		
Cosmarium	15.8	9.8	19.8	16.0
Staurastrum	7.8	3.0	7.8	7.5
Gymnodinium	9.8	8.3		
Glenodinium	8.0	7.3		
Cryptomonas	18.5	10.5		
Small Monad	7.6	3.2		
Dinobryon	33.3	8.8	178	95
Botryococcus				
cells	11.5	3.8		
Shaerocystis	3.5	3.5	20.2	20.2
Coelastrum	5.0	5.0	23.8	23.8
Oocystis	8.3	4.5	13.3	7.8
Ankistrodesmus	13.3	2.2	37.5	2.2
Nephrocytium	5.0	3.0	11.8	6.2
Unicells	4.3	4.3		
Chroococcus	5.0	5.0	17.3	12.5

Table 16: Average sizes of planktonic algae from Lake Ototoa. The figures given are the means of 10 - 20 individual measurements.

Fig. 12: Seasonal changes in the concentration of chlorophyll and total numbers of phytoplankton in Lake Ototoa. Samples were taken at a depth of 1m.


Chlorophyll
Mgm/m³
5
4
3
2
1
0
Total Phytoplankton
Thousands of Cells per litre
600
400
200
0
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

Between March and May 1969 chlorophyll concentrations remained relatively constant at about 1 mg/m^3. Following a decrease in early June concentrations increased to ca 2 mg/m^3 in July. Maximum concentrations of chlorophyll were found during mid-winter - in late August - and resulted from large increases in numbers of *Dinobryon* (see later). After another small increase in early October chlorophyll fell to the lowest values later in this month (0.039 mg/m^3 on 19.10.69). Over the rest of the sampling period values remained very low, although increasing gradually to attain concentrations of ca 1 mg/m^3 in early March 1970.

Compared with chlorophyll concentrations determined from other New Zealand lakes, those from Ototoa are very low, and show less pronounced variation e.g. Stout (1969) 0.22 - 8.88 mg/m^3 in the Canterbury mountain lakes; Barker (1970), ca 2 - 145 mg/m^3 in Lake Pupuke; Mitchell (1971), ca 1 - 60 mg/m^3 in Tomahawk lagoon and ca 1.75 - 14.5 mg/m^3 in Lakes Waipori and Mahinerangi; and also Lakes Rotorua and Rotoiti (Fish, pers. comm.).

In Lakes Rotorua and Rotoiti, Fish found highest chlorophyll concentrations in late autumn and winter, with generally lower values in the spring and summer, as was also found in Ototoa. This situation contrasts with the cycles found by Mitchell (1971) in Lakes Waipori and Mahinerangi and the Tomahawk lagoon, and Barker (1970) in Lake Pupuke where concentrations were low in mid-winter and highest in late summer and early autumn.

Such a cycle is also characteristic of many lakes in other parts of the world, (Hutchinson 1967).

2. Total Numbers of Phytoplankton.

The numbers of cells per litre plotted in fig. 12 are the average numbers from all stations sampled on any one date.

Like chlorophyll concentrations total phytoplankton numbers were low, generally being between 200 x 10^3 and 800 x 10^3 cells per litre (cf Lake Rotorua,(Cassie 1969) - 300 - 5000 cells/ ml). Between March and July 1969 numbers were variable with minima in late April, late May and late July. In August and early September (late winter and early spring) total numbers were high (600 - 800 x 10^3 cells per litre). Numbers fell during September and during much of the spring (October and November) the standing stock was low (ca 300 x 10^3 cells per litre) and constant.

Numbers increased during December to mid-summer peak in late December and early January, and after a decline in late January and early February a further peak developed in late February and March.

Similar changes in total numbers have been found by Cassie (1969) and Fish (pers. comm.) in Lakes Rotorua and Rotoiti, although in these lakes the changes in numbers are much greater, and there is often a steady decline over the spring from high winter concentrations and summer increases may be absent.

3. Seasonal Cycles.

Apart from the macroscopic colonies of *Botryococcus braunii* the species most characteristic of the phytoplankton of Lake Ototoa was the centric diatom *Cyclotella stelligera* which was numerically dominant for most of the year. After decreasing in numbers between March and May 1969 it increased to maximal densities during mid-winter. Numbers then gradually dropped during the spring; and there were smaller increases in December and February 1970. The cycle of abundance exhibited by *Cyclotella* appears to be inversely related to that of the temperature of the upper 15 metres of water (fig. 13). This may imply a preference for cooler waters, although the decrease during March and May 1969 and the increases in December and February during the summer do not support this. It is possible however that turbulence is necessary to keep cells of *Cyclotella* in suspension (Hutchinson 1967) and that the decreases in spring and summer result from settling out during the period of temperature stratification when the vertical component of turbulence is reduced.

The desmids found in Lake Ototoa were two unidentified species of *Cosmarium* and four species of *Staurastrum*. *S. chaetoceras* and *S. sagittarium* were found very rarely, and Dr. Flint (pers. comm.) notes that it is unusual to find the former species in an oligotrophic lake but that it is very common in the eutrophic lakes of the Rotorua area. The most common desmids were the small *S. planktonicum* and *S. smithii* which were responsible for the greater part of the changes in stock of *Staurastrum* shown in

Fig. 13: Seasonal changes in numbers of the individual phytoplankton species in Lake Ototoa. Samples were taken at a depth of 1m.

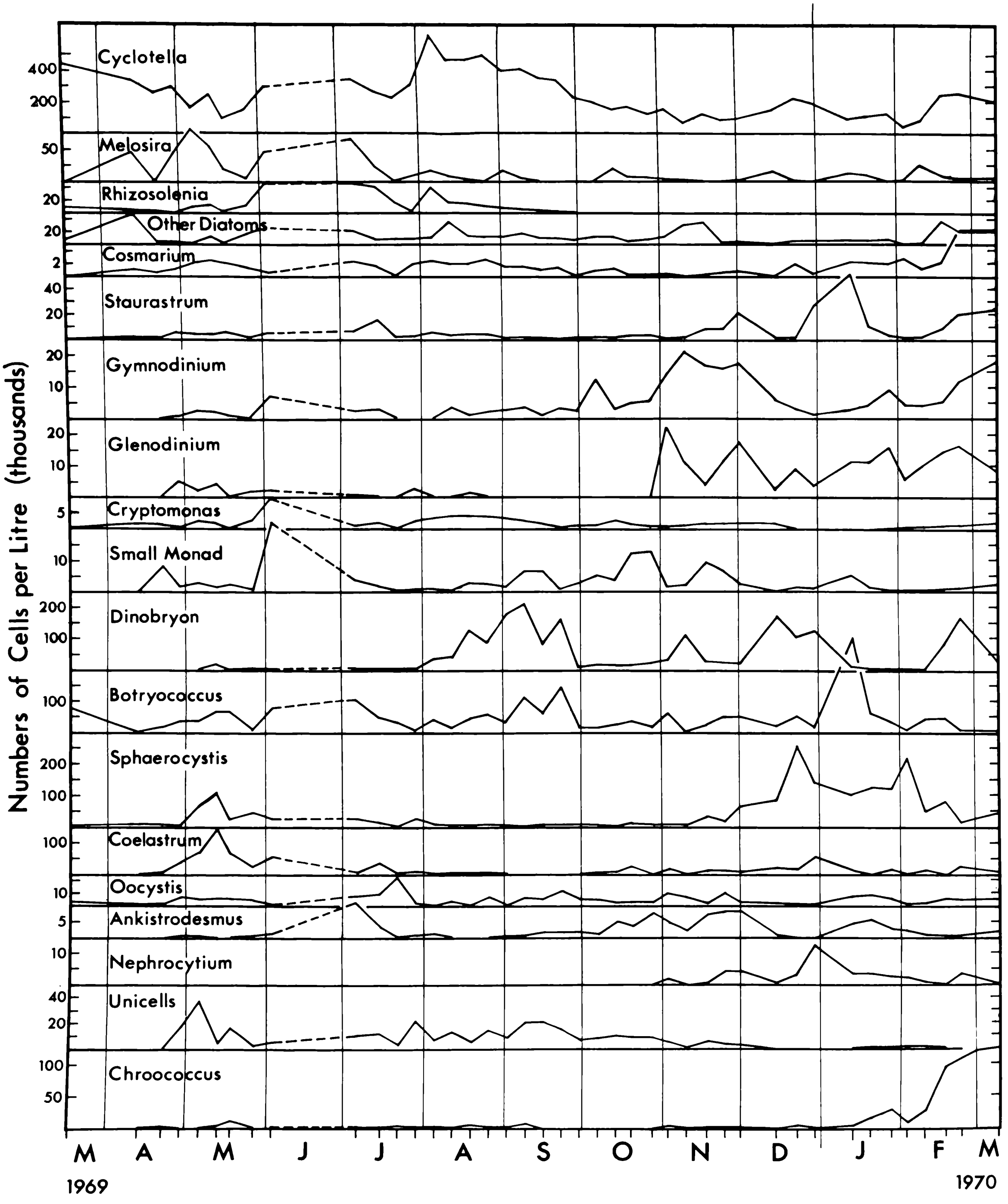

Numbers of Cells per Litre (thousands)
Cyclotella
400
200
Melosira
50
Rhizosolenia
20
Other Diatoms
20
Cosmarium
2
Staurastrum
40
20
Gymnodinium
20
10
Glenodinium
20
10
Cryptomonas
5
Small Monad
10
Dinobryon
200
100
Botryococcus
100
Sphaerocystis
200
100
Coelastrum
100
Oocystis
10
Ankistrodesmus
5
Nephrocytium
10
Unicells
40
20
Chroococcus
100
50
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

fig. 13. As found elsewhere (Hutchinson 1967) *Staurastrum* is a summer form and in Ototoa it exhibited peaks in early December, January and also further increases in February and March when *S. chaetoceras* was most abundant. Throughout the rest of the sampling period numbers were low, especially during spring and autumn. *Cosmarium* was found in low, fairly constant densities during autumn, winter and early spring, and declined to lower levels later in the spring. Numbers increased again in the summer and during late February and March 1970 there were marked increases to densities about twice those during the rest of the sampling period.

The two commonest dinoflagellates were *Gymnodinium* sp and *Glenodinium* sp, although very small numbers of *Peridinium* sp and *Ceratium hirundinella* were also found on occasions. *Gymnodinium* was most common in late spring and early summer when it was one of the most conspicuous members of the flora. After declining in numbers in December and January, it increased again at the end of the sampling period. Small numbers were also present during winter and early spring. *Glenodinium* was found in fluctuating numbers over the whole of the summer period, and in December, January and February was the most common dinoflagellate. It also occurred in small numbers during the autumn of 1969. Dinoflagellates are alloauxotrophic, requiring accessory organic substances for successful growth. The increases in the fraction of organic matter smaller than

0.8 µ which occurred in November (fig. 11) may therefore have been associated with the increases in abundance of *Gymnodinium* and *Glenodinium*.

Cryptomonas, although found in greatest abundance in late autumn was present in rather constant low numbers during most of the sampling period, except for a period of absence in late December and early January. Another small monad (probably a small *Cryptomonas* - Flint, pers.comm.) was also most abundant in late autumn, but during the spring months it underwent a number of increases and was a conspicuous member of the phytoplankton, at times when the densities were generally low.

Dinobryon spp had three main periods of abundance. The principal one during late August and September was responsible for the main peak in chlorophyll a concentrations, and together with increases in cells of *Botryococcus braunii* and *Cyclotella* caused the maxima in total phytoplankton numbers during August and September. Further major increases in numbers of *Dinobryon* occurred in December and February with a smaller increase in early November. In the Wellington reservoirs (Stevenson 1952) and in the Auxiliary Nihotupu reservoir (Green 1968) *Dinobryon* was found to occur at similar times. In lakes overseas *Dinobryon divergens* is known to increase at times of low phosphate concentrations (below 5 µg/l) following previous period of diatom abundance in spring. Flint (1938) believed that such a relationship did not explain the periodicity of

Dinobryon in Lake Sarah, in the South Island of New Zealand. In Lake Ototoa the main outburst of *Dinobryon* in August and September did follow the main period of diatom abundance, which was between May and August 1969, but unfortunately no determinations of phosphate concentrations were made before September. The concentrations of soluble phosphate in September was 5.95 µg/l, and dropped to 1.00 µg/l in October, when however *Dinobryon* had also decreased. Between November 1969 and February 1970 phosphate concentrations were constantly below 5 µg/l, and yet numbers of *Dinobryon* both increased and then declined. It seems likely then, that as in Lake Sarah, changes in phosphate concentration were not the main determinants of the seasonal cycle of *Dinobryon* in Lake Ototoa, at least in the summer.

Colonies of *Botryococcus braunii* were always obvious in the water of Lake Ototoa, however they were found only rarely on the filters during counting. The numbers plotted in fig. 13 refer to free cells which were always present, but it is not known whether these counts reflect a true abundance of free cells in the lake water. Conceivably such cells could become detached from the colonies after the sample had been fixed in Lugol's iodine following collection.

Sphaerocystis was mainly a summer form, although there was a small increase in May, and small numbers present during the winter and spring. There were two peaks of abundance, in late December and in early February. During January and February the mucous sheaths surrounding the colonies contained bacterial cells orientated at right angles to the colony surface and such infestation is thought to be characteristic of a declining population (Flint, pers. comm). *Coelastrum* was most abundant in May, but was also found in smaller numbers in spring and summer - when there was a smaller peak in late December. *Oocystis* occurred in small numbers throughout the whole of the sampling period while *Nephrocytium* was found only in the summer, with peak abundance in late December - early January. *Ankistrodesmus* had three periods of abundance, in July, October and November, and January. An unidentified unicell was moderately common between autumn and spring, but disappeared during the warmer part of the summer.

The only myxophycean recorded was *Chroococcus limneticus* and apart from some isolated occurrences in 1969 it was found only in late summer and early autumn (during February and March), when it underwent a large increase. This is a typical seasonal cycle for a blue-green alga, which are almost invariably found in abundance at the end of summer in association with increases in dissolved organic matter and lowered nutrient levels (Hutchinson, 1967).

Cunningham et al (1953) did not make any quantitative counts of the phytoplankton of Lake Ototoa during their 1952 survey. However in a similar sand dune lake near Wellington (Lake Kopureherehe) they found a phytoplankton assemblage similar to that reported from Lake Ototoa in this study, although in Kopureherehe the concentrations were a little lower. Their counts are set out in table 17.

Following the classification of phytoplankton associations advocated by Hutchinson (1967) the phytoplankton of Lake Ototoa would appear to exhibit features of types 1 - 4 i.e. an oligotrophic diatom *(Cyclotella, Rhizosolenia)*- desmid *(Staurastrum)* plankton, associated with *Botryococcus braunii*, *Dinobryon* and *Sphaerocystis*.

ALGA	No/litre
Cyclotella	216,000
Navicula	21,000
Staurastrum spp.	13,000
Ankistrodesmus	8,000
Peridinium	150
Eudorina	30
Closterium	20
Oocystis	20
TOTAL	258,220

Table 17: Phytoplankton concentrations in Lake Kopureherehe, August 26 1952. Data from Cunningham et al (1953).

ZOOPLANKTON

The zooplankton of Lake Ototoa was dominated by the small centropagid calanoid copepod *Calamoecia lucasi* Brady, which is widely distributed throughout the north of New Zealand and eastern Australia (Timms 1970 , Chapman and Green, 1973). The cosmopolitan cyclopoid copepod *Mesocyclops leuckarti* Claus was found in very small numbers, and the only limnetic cladoceran was *Bosmina meridionalis* Sars. The other New Zealand limnetic cladoceran *Ceriodaphnia dubia* Richard was absent as it is from other New Zealand coastal lakes of high alkalinity. The Rotatoria were represented by *Asplanchna priodonta* Gosse, *Conochiloides coenobasis* Skorikow, *Filinia terminalis* Plate, *Synchaeta* sp. and *Hexarthra* sp.

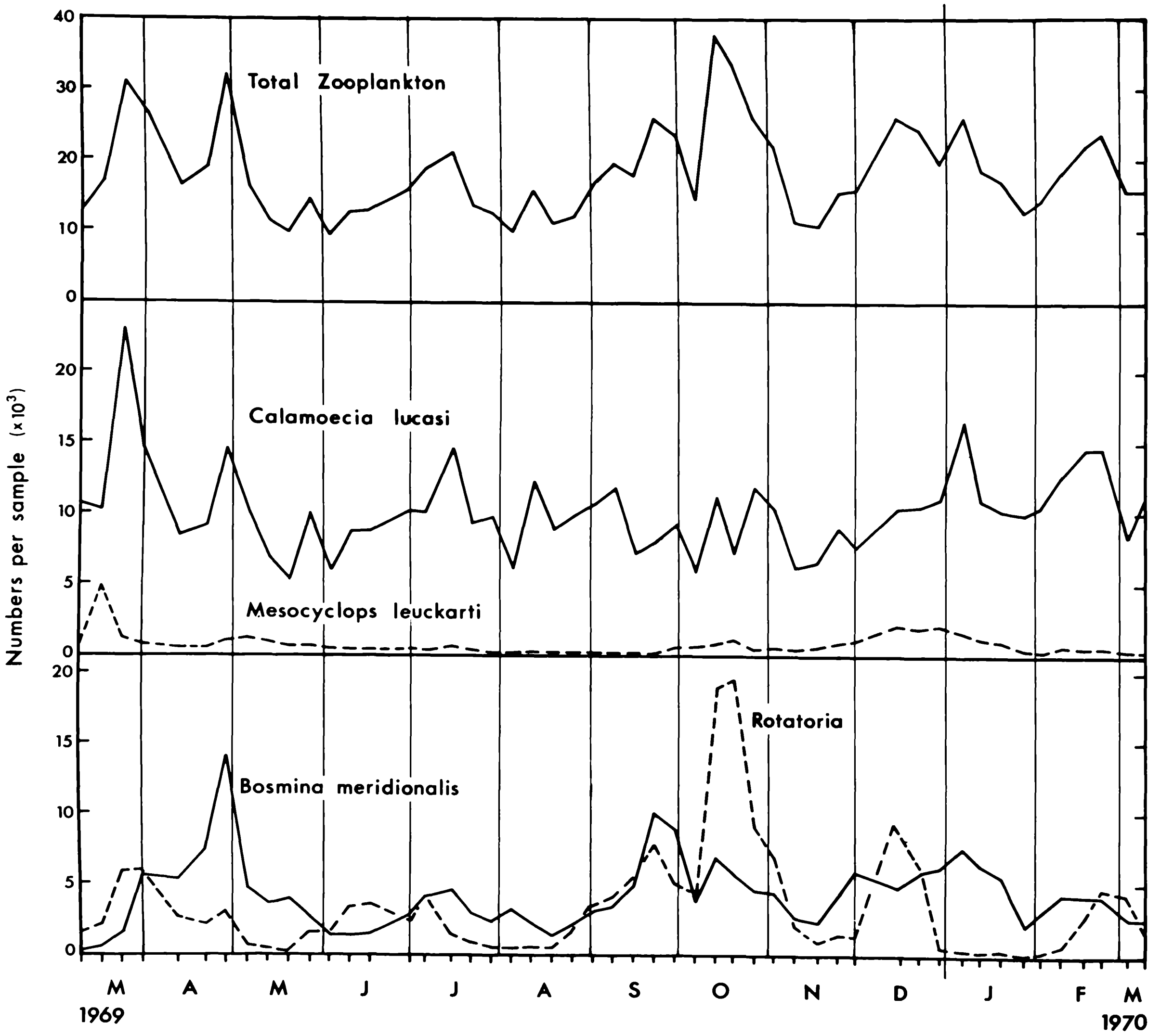
In this and following sections numbers of zooplankton refer to numbers per "standard sample." Early in the study when only station B was sampled these are the numbers found in the one sample taken. But for the remainder of the study when three stations were sampled this figure has been obtained by totalling the numbers in the samples from stations A, B and C and then dividing by three. If it is assumed that the net was 100% efficient, then the numbers per sample may be converted to numbers under 1 m^2 by multiplying by 31.8 and to numbers per

m^3 by multiplying by 1.77. While it is certainly unlikely that the net was in fact 100 % efficient, because of clogging and spillover at the net mouth, care was always taken to ensure a slow and steady net haul and because of the fairly sparse plankton in Lake Ototoa clogging was not likely to have been very important. Thus the conversion factors probably give close approximations to the true values. The numbers per sample as used in this study are fully comparable with those of Chapman (1972) who used a net of identical design in her studies of zooplankton in Lakes Rotorua and Rotoiti.

1. Total numbers of Zooplankton.

In late March and April, during the autumn of 1969, there were two large peaks in total numbers of zooplankton, after which numbers declined considerably in May. Similar autumnal falls in zooplankton numbers have been reported from Lakes Rotorua and Rotoiti (Chapman 1972). Numbers then gradually increased to an early winter peak in July, after which numbers fell again to lower values in mid-winter. During September and October there was a large spring outburst, caused mainly by increasing numbers of *Bosmina* and rotifers, followed by a decline in November. During the summer numbers again increased, and there were peaks in December, January and February. In spite of these variations compared with other New Zealand lakes the total numbers were rather constant (Chapman 1972, Barker 1967, Green 1968).

Fig. 14: Seasonal changes in the total numbers of zooplankton, and in the standing stocks of the major groups. Stock numbers are expressed as numbers per standard sample in this and following figures (see text).


Numbers per sample (x10³)
Total Zooplankton
Calamoecia lucasi
Mesocyclops leuckarti
Rotatoria
Bosmina meridionalis
40
30
20
10
0
20
15
10
5
0
20
15
10
5
0
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

2. Individual Species.

The seasonal biology of the dominant zooplankter, *Calamoecia lucasi*, is the major subject of this thesis, and the seasonal cycles of the other zooplankters will be only briefly described.

a. *Calamoecia lucasi:* Total numbers of *Calamoecia lucasi* showed little change over the sampling period and many of the minor rises and falls in fig. 14 may have resulted partly from sampling variability. The standing stock was highest during the summer of 1970 (between December 1969 and March 1970) and during early autumn 1969. From March to May 1969 numbers declined following two major peaks of abundance (in late March and late April) and during the rest of the year numbers fluctuated around a mean level of about 7-8 thousand per sample. While the mean population size in Lake Ototoa ($\bar{x}$ = 10,163, CV = 31%) was much lower and constant than in Lakes Rotorua ($\bar{x}$ = 18,228, CV = 50%) and Rotoiti ($\bar{x}$ = 25,062, CV = 38.5%) (Chapman 1972), the broad patterns of seasonal change, with high summer and autumn and lower winter numbers, is similar in all three lakes.

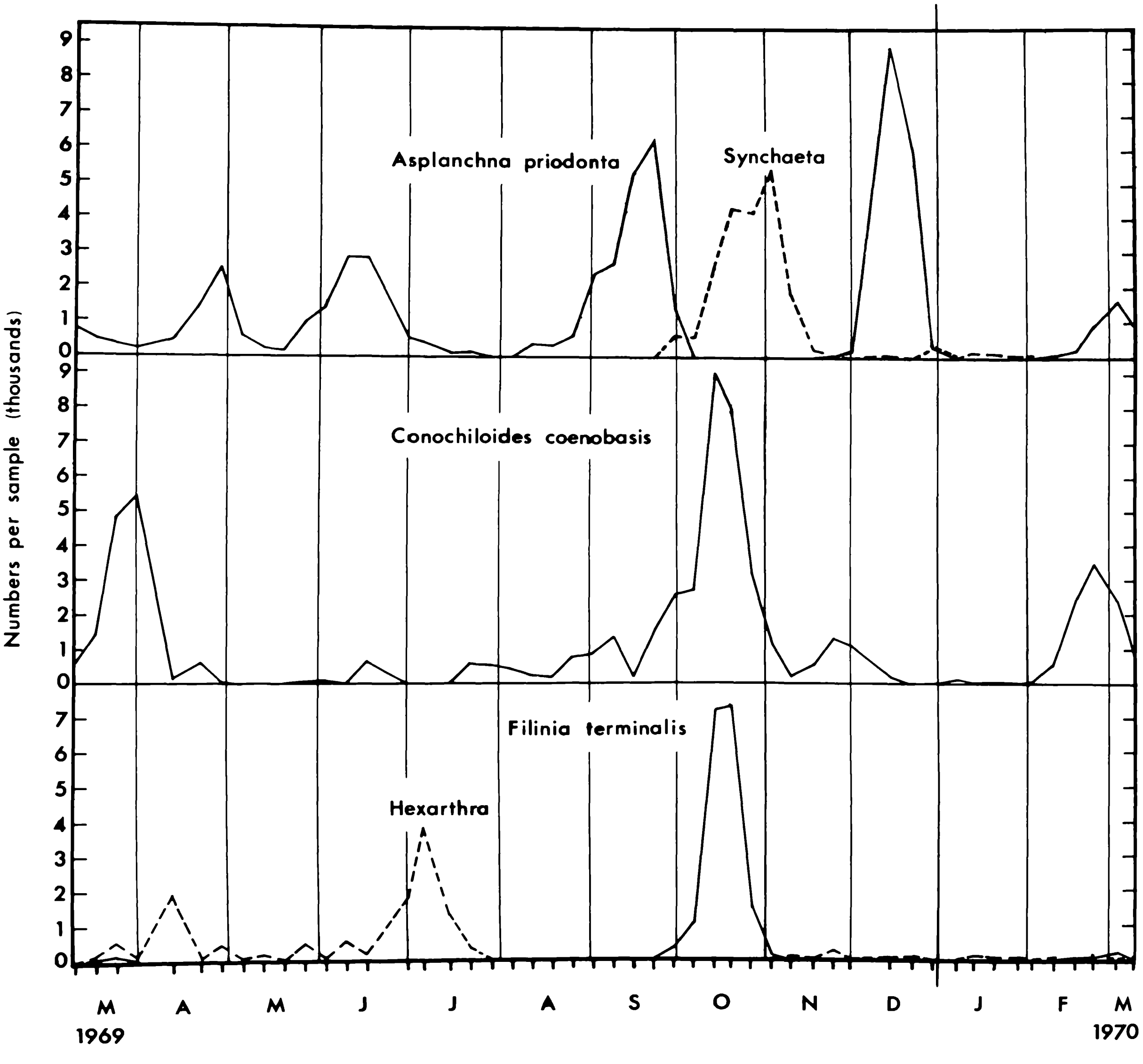
b. *Mesocyclops leuckarti:* The stock of *M. leuckarti* was much lower than that of *Calamoecia* at all times (fig. 14). Numbers were greatest during the autumn of 1969 and the early summer of 1969 - 70. This pattern of low winter and high summer numbers of *M. leuckarti* is generally similar to that found in other New Zealand lakes, although somewhat different in detail. In Lake Pupuke, Barker (1967) found that numbers of *M. leuckarti* increased in early August, declined and then increased again in September. Standing stocks then returned to low levels until a further increase occurred in February and March, followed by a decline to low winter values. Green (1968) found similar patterns in the Auxiliary Nihotupu reservoir, and suggested that in Northern New Zealand the seasonal cycle of *M. leuckarti* is like that found in Lago Maggiore by Ravera (1954) where *M. leuckarti* breeds mainly in the spring and summer but is present throughout the year with continuing slow development in the winter. Such a cycle contrasts with those found in lakes further north in Europe, where breeding occurs only in the summer with the production of two generations. The development of the second generation ceases at either copepodite IV or V which then either go into a state of diapause in the bottom mud or overwinter in the plankton without further development until the following spring. In Lake Ototoa breeding probably occurred throughout the year, because even though ovigerous ♀♀ were only very rarely found cyclopoid nauplii were always present in the samples.

c. *Bosmina meridionalis:* *Bosmina meridionalis* was the only limnetic cladoceran found in Lake Ototoa during this study. There was a large autumnal increase in the population between March and early May (fig. 14), and numbers dropped to lower levels during the winter, although there was a slight mid-winter increase during July. A large spring increase followed in September, and after a gradual decline in October and November there was a summer increase in December and January. For the rest of the sampling period numbers were a little lower.

The cycle observed in Ototoa is generally similar to that found by Chapman (1972) in Lakes Rotorua and Rotoiti. However, in these and in other lakes in the North Island of New Zealand, *Bosmina* co-occurs with *Ceriodaphnia dubia* which often increases markedly in late spring or summer and for a time may replace *Bosmina* which either disappears from the plankton or is present in much reduced numbers (Green, 1968, Chapman loc. cit.). In Lake Ototoa the absence of a potentially competitive *Ceriodaphnia* population may be one of the reasons why *Bosmina* maintained a moderately large population during the summer. *Bosmina* is known to feed on smaller particles than other cladocera (Burns, 1968) and is probably a bacterial and detritus feeder. Such material would be in high concentration from late spring to autumn. The period of maximum abundance of *Bosmina* also corresponded with times of occurrence of many small green algae, small monads and the dinoflagellates - some of which may have served as food.

d. Rotatoria: Rotifers (fig. 14) were found in greatest abundance during the spring, but there were also smaller peaks in March, June, December and February. Numbers of *Asplanchna priodonta* underwent two major increases, during early spring in September, and in December during the summer (fig. 15). Two other smaller peaks occurred in late April and June, and during the rest of the year it was either absent or present in only very low numbers. Such spasmodic, large increases are characteristic of *Asplanchna*, and the cycle of *A. priodanta* in Lake Ototoa is similar to that observed in Lakes Rotorua and Rotoiti (Chapman, loc. cit.). *Asplanchna* is a raptorial form, and it may be significant that the periods of maximum abundance either closely followed or coincided with periods of abundance of *Dinobryon*. Species of *Synchaeta*, another small raptorial form, are often most common during spring and summer. In Ototoa *Synchaeta sp* showed one pronounced period of abundance in the spring and was absent for the rest of the year except for small numbers which were found in December and January. Elsewhere in New Zealand species of *Synchaeta* have been found to develop during spring and summer in a similar manner (Byars, 1960, Barker, 1967, Green, 1968). *Conochiloides coenobasis* was present in only small numbers during summer and winter, but it became much more prominent in the autumn and especially during the spring, in October, *Conochiloides* is thought to feed on particles smaller than 12 μ (Hutchinson,1967) and such forms were becoming more abundant in Lake Ototoa during the spring.

Fig. 15: Seasonal changes in the standing stocks of the various rotifer species.


Asplanchna priodonta
Synchaeta
Conochiloides coenobasis
Filinia terminalis
Hexarthra
Numbers per sample (thousands)
9
8
7
6
5
4
3
2
1
0
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

Conochiloides has been recorded in New Zealand by Byars (loc. cit.) from a pond in Otago where it was most abundant in summer, and by Green (loc. cit.) from the Auxiliary Nihotupu reservoir in Auckland where its cycle was similar to that in Lake Ototoa, with maximum abundance in the spring. *Conochiloides* is also a spring form in South Africa (Hutchinson loc. cit.). *Filinia terminalis*, another species which probably feeds on particles smaller than 12 μ, also increased markedly in October and was not found during the rest of the year apart from a few occurrences during March of both 1969 and 1970. The only other rotifer found was a species of *Hexarthra* which occurred sporadically in very low numbers during the summer but was most abundant during late autumn and early winter of 1969, especially in July when it was the dominant rotifer. A noticeable feature of the rotifer fauna of Lake Ototoa was the absence of species of *Keratella* which are generally considered some of the most characteristic of the temperate region and which are abundant in other New Zealand lakes e.g. Pupuke (Barker, 1967).

THE BIOLOGY OF *CALAMOECIA LUCASI*

1. Introduction:

In the following sections the seasonal biology of *Calamoecia lucasi* in Lake Ototoa will first be described, and then the population dynamics and production will be considered. Throughout comparisons will be made with the populations studied by Chapman (1972) in order to bring out any similarities and differences which may occur between the ecology of *C. lucasi* in lakes of different trophic status.

2. Seasonal Changes in Numbers of Developmental Stages:

The seasonal changes in numbers of different developmental stages from nauplius to adult are shown in fig. 16 . In New Zealand *Calamoecia* breeds throughout the year and so various growth stages are always found in the plankton.

Nauplii increased to greatest numbers during winter and fell away gradully during spring and summer. Changes in naupliar numbers throughout the year are inversely related to temperature and this probably reflects a fairly constant egg production and longer naupliar development times at lower temperatures. Copepodites were found in highest densities between spring and autumn. Between late autumn and early winter, however, numbers in the successive growth stages declined sequentially to very low levels followed by gradual increases, progressing through the developmental stages, to rather constant low winter levels of abundance. Similar sequential drops in numbers of the copepodite stages occurred during the spring, in October and November followed by increases to the larger summer populations. Numbers of adults were more

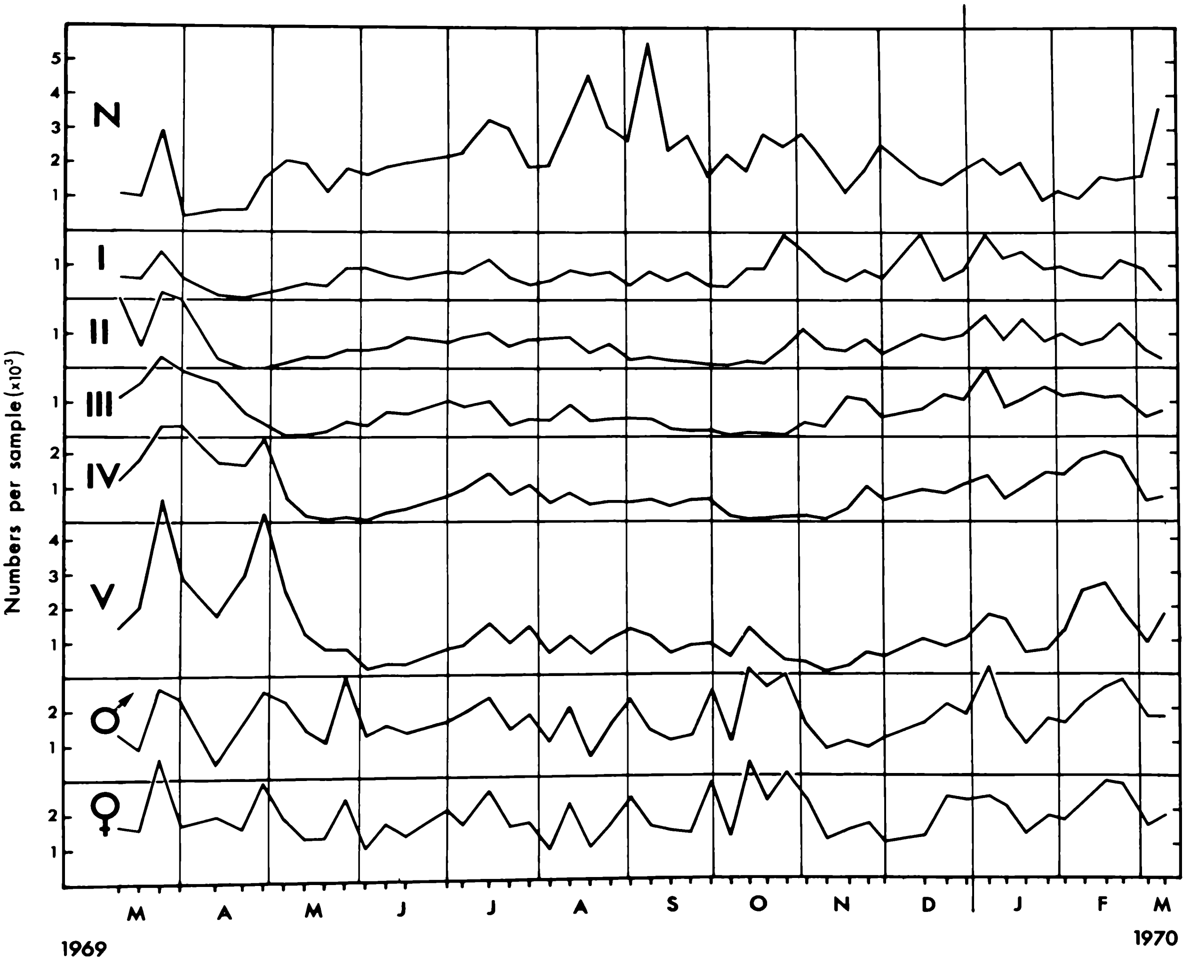
Fig. 16: Seasonal changes in the stocks of nauplii, copepodites and adults of *Calamoecia lucasi* in Lake Ototoa during the sampling period.

N = nauplii

I - V = copepodites I to V.

♂ = males

♀ = females


Numbers per sample (x10³)
N
I
II
III
IV
V
♂
♀
1
2
3
4
5
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

constant and there was little difference between the average standing stock of winter and summer. However weak (yet significant - see below) peaks of abundance did occur in the spring (October), summer (December-January; February) and autumn (March to May).

On the whole the pattern is similar to that found by Chapman (1972) for *C. lucasi* in Lakes Rotorua and Rotoiti although she found naupliar peaks in spring and autumn, rather than a gradual increase over the winter, and the numbers of copepodites, and particularly adults, showed greater variations in numbers.

The relative abundance of the various growth stages was also similar to those found by Chapman (loc. cit.) except that the numbers of nauplii formed a smaller fraction of the population in Ototoa than in Rotorua. The annual mean percentages of the total population and the range of variation for the various stages were: Eggs-6% (4% to 18%); N-19% (3% to 50%); CI-8% (1% to 18%); CII-7% (1% to 18%); CIII-7% (1% to 18%); CIV-8% (1% to 20%); CV-12% (1% to 32%); and adults - 33% (16% to 53%). Such proportions seem similar to those of Northern Hemisphere copepods that have been studied (e.g. Ravera 1954; Chapman 1969; Comita 1972) but contrast with those found in *Boeckella propinqua*, another New Zealand copepod, where nauplii generally constitue the greatest fraction of the population, with progressively smaller proportions being found in each suceeding copepodite stage, with mature adults often comprising a much smaller percentage of the standing stock than in *C. lucasi*. Thus Bayly (1962) found that in Lake Aroarotmahine the percentage of the population that was mature ranged between 10% and 37%, Green (1967) found that in the Auxiliary Nihotupu reservoir mean numbers of the different stages were:

Eggs-35%; N-32%; CI-10%; CII-7%; CIII-5%; CIV-3%; CV-2% and adults - 6%, while Jolly (pers. comm.) has found that in Lake Taupo during 1971 the proportions were N-30%; CI-40%; CII-20%; CII+IV+V-8%) and adults 3%. Such proportions have been confirmed by Chapman (pers. comm.) who also studied *B. propinqua* in Lakes Taupo and Rotoaira during 1970. Providing that the ratio of length of life of a particular stage to the total taken to grow from egg to adult is similar in both genera, then this situation may reflect different patterns of the incidence of mortality in *C. lucasi* and *Boeckella propinqua*. Unfortunately no development times for *Boeckella* are available to enable this possibility to be examined.

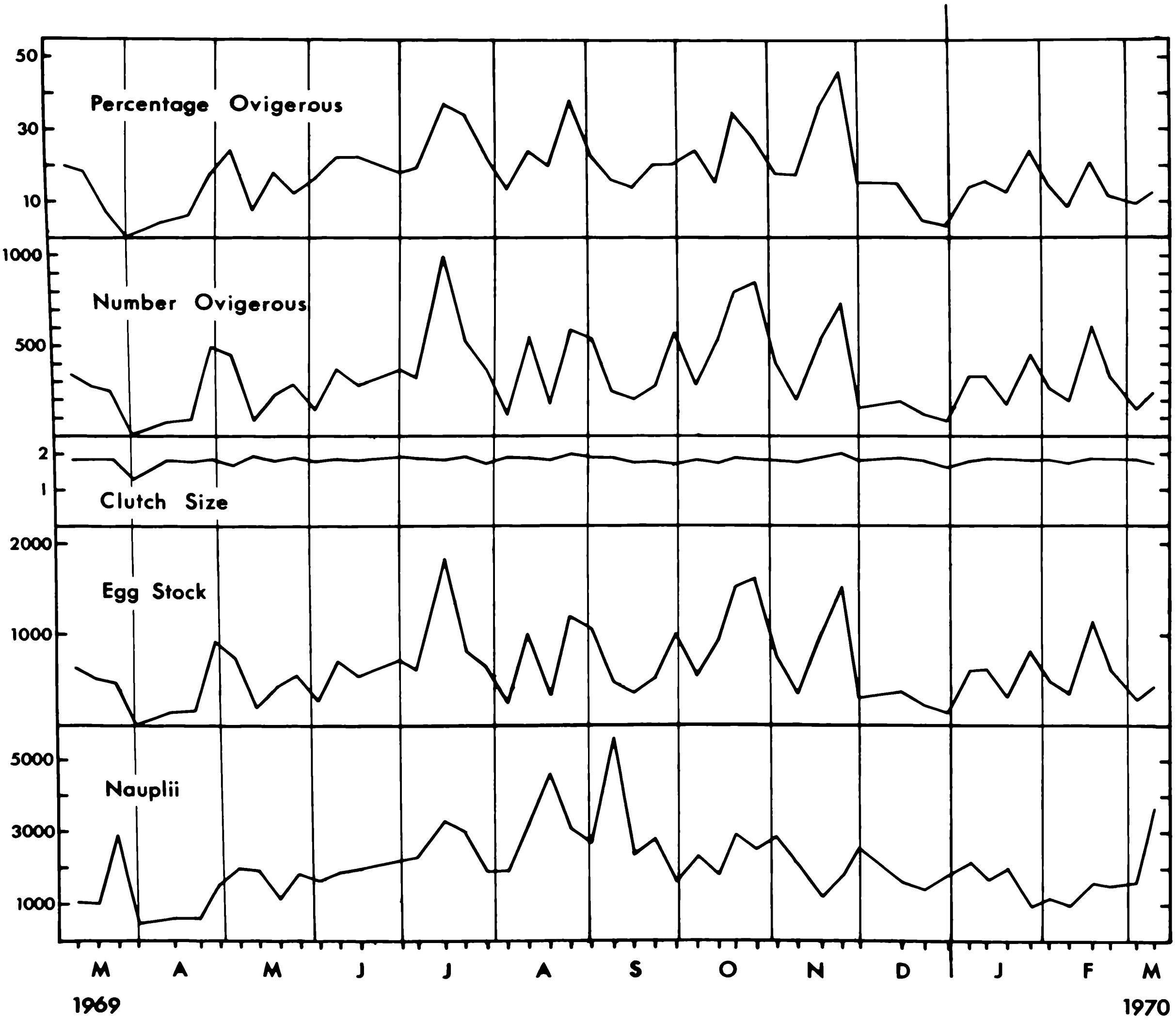
3. Breeding Parameters:

(a) Clutch size:

The mean clutch size of *C. lucasi* in Lake Ototoa (fig. 17) remained monotonously constant and low throughout the sampling period, rising above 2.00 only twice (2.01 on 25 August; 2.08 on 24 November), and generally being between 1.80 and 1.90. The minimum was 1.30 on 31 March 1969.

The other populations of *C. lucasi* that have been studied also have low clutch sizes (e.g. Chapman, 1972; Rotorua, annual mean 3.33, range 1.75 - 6.06; Rotoiti, annual mean 1.97, range 1.1 - 3.4) although none have clutches as low and unvarying as those found in Ototoa. Moreover, clutches of 3 were found only rarely in Ototoa, and a clutch of 4 found only once among some 4,000 ♀♀ which were examined, whereas in the other populations of *C. lucasi* clutch sizes between 5 and 10 are relatively common. In a pond on the campus of the University of Waikato, which contains a dense population of *C. lucasi* clutches of up to 30 eggs are often found.

Fig. 17: Seasonal changes in the breeding parameters and numbers of nauplii of *Calamoecia lucasi* in Lake Ototoa. Egg stock, nauplii and number ovigerous as numbers per sample.


Percentage Ovigerous
50
30
10
Number Ovigerous
1000
500
Clutch Size
2
1
Egg Stock
2000
1000
Nauplii
5000
3000
1000
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

C. lucasi is a small copepod and might be expected to produce smaller clutch sizes than the larger species of *Diaptomus* and *Boeckella* (where clutches of well over 100 have been reported, e.g. *B. propinqua* can bear clutches containing 80 to 130 eggs, Green 1968) solely because of physiological limitations on egg production inherent in such small size. Nevertheless, because of the clutch sizes which can be produced by some populations of *C. lucasi* those produced by the Ototoa population must be considered to be very low, even for *Calamoecia*. This may be related to the oligotrophic nature of Lake Ototoa, and consequent low food levels. The lowering of clutch sizes of a species in its more oligotrophic habitats is known for northern hemisphere copepods (Hutchinson 1967).

The constancy of clutch size in Lake Ototoa is also notable, because even in a poor lake a seasonal change in clutch size induced by temperature might be expected. This may indeed have happened to a slight extent as the highest clutch sizes were found at the time of lowest temperature in August (table 18). This effect was minimal however, and it seems that food levels in the lake were so low as to be below the level where temperature changes could effect any significant change in clutch size.

It is tempting to suggest a scheme relating clutch size to food levels and temperature in which there is some minimum food level below which eggs are not produced at all, and a second, higher food level below which the number of eggs produced is dependant on variations of both food and temperature, perhaps in a way similar to that described by Deevey (1960, 64) for copepod lengths and above which the physiological maximum number of eggs is produced, the number being dependant only on temperature (e.g. McLaren 1963).

Date	No. of ♀♀	%ovigerous	No. ovigerous	Clutch	Egg Stock
10 March 1969	1668	20.0	334	1.84	615
17 March	1534	18.0	276	1.85	511
24 March	3534	7.3	258	1.85	477
31 March	1666	0.0	0	1.30	0
12 April	1934	4.0	77	1.82	140
21 April	1532	6.0	92	1.80	166
28 April	2822	17.7	499	1.87	933
5 May	1867	24.2	452	1.70	768
12 May	1227	7.5	92	1.97	181
19 May	1267	18.0	228	1.81	413
26 May	2400	12.3	295	1.91	563
2 June	933	16.2	151	1.80	272
9 June	1645	22.7	373	1.88	701
16 June	1311	22.6	296	1.86	551
30 June	2067	18.1	374	1.95	729
5 July	1645	19.5	321	1.88	603
14 July	2667	37.5	1000	1.84	1840
21 July	1533	34.6	530	1.94	1028
28 July	1645	22.6	372	1.75	651
4 August	889	13.8	123	1.95	240
11 August	2250	24.7	556	1.94	1079
18 August	922	20.1	185	1.86	344
25 August	1561	38.4	599	2.01	1204
1 September	2400	23.3	559	1.92	1073
8 September	1511	16.4	248	1.91	474
15 September	1422	14.3	203	1.79	363
22 September	1378	20.7	285	1.84	524
29 September	2867	20.4	585	1.75	1024
6 October	1209	24.5	296	1.89	559
13 October	3445	15.5	534	1.78	951
19 October	2289	35.0	801	1.93	1546
26 October	3089	27.9	862	1.89	1629

Table 18: Contd....

Date	No.of ♀♀	%ovigerous	No Ovig.	Clutch	Egg Stock
2 November	2306	18.0	415	1.85	768
9 November	1155	17.7	204	1.78	363
17 November	1473	36.6	539	1.90	1024
24 November	1600	46.4	742	2.08	1543
30 November	1056	15.4	163	1.86	303
14 December	1267	15.7	199	1.91	380
22 December	2423	5.0	121	1.86	225
29 December	2317	3.7	86	1.67	144
6 January 1970	2400	14.0	336	1.81	608
12 January	2134	15.5	331	1.89	626
19 January	1311	12.8	168	1.85	311
27 January	1889	24.3	459	1.81	831
2 February	1755	15.2	267	1.86	497
9 February	2245	8.8	198	1.77	350
17 February	2867	21.4	614	1.89	1160
23 February	2800	11.7	328	1.87	613
3 March	1533	9.5	146	1.88	274
9 March	1867	12.8	239	1.74	416
MEAN	1891	18.8	355	1.85	664
s	653.6	9.7	221.8	0.11	424.2
CV%	34.6	51.3	62.5	5.90	63.9

Table 18 : Breeding Parameters of *Calamoecia lucasi* from Lake Ototoa 1969 - 1970.

These food levels would of course be dependant on the population density of the copepod in relation to its ability to gather food and on the replacement rate (e.g. division rates of algae) of the food which is likely to be the greatest during the warmer months of the year. A population existing in an environment providing a food level near the lower of the two would be characterised by a clutch size averaging between 1 and 2, because the ovaries are paired and a minimal possible egg production is likely to be expressed, therefore, by the production of a single egg from one, or perhaps both ovaries.

It is suggested that the low and constant clutch size indicates that the population of *Calamoecia lucasi* in Lake Ototoa may be existing near this lower food level.

(b) Percentage of Females Ovigerous:

The percentage of the female population bearing eggs is shown in fig. 17 and table 18 .

Percentage ovigerous dropped to the lowest value recorded at the end of March, just after sampling had begun. Values then increased gradually during April and May, and during much of the winter and spring, from June to November, the percentage bearing eggs fluctuated around a level of between 20% and 30%, with noticeable increases occurring in early May, June, August, October and November. Percentages fell to low levels during December (3.7% ovigerous on 29 December) and during the rest of the summer of 1970 percentage ovigerous fluctuated between 10% and 20% with peaks in early and late January, and mid-February.

The annual picture is thus one of higher winter and spring percentages of ♀♀ carrying eggs and lower summer percentages, with intervening periods of very low percentages in late autumn and early summer.

The annual mean percentage bearing eggs was 18.8%, ranging between 0% and 46.4% (table 18). This is rather lower than found for the populations in Lakes Rotorua and Rotoiti (Chapman 1972) which varied from 8-66% and 11-82% respectively. The yearly pattern was also different, with pronounced winter depressions in percentage ovigerous being found on both Rotorua and Rotoiti.

(c) Number of Ovigerous Females:

Because of the rather constant number of total ♀♀, the number of ovigerous ♀♀ largely reflected changes in the percentage bearing eggs, although because of fluctuations in total ♀♀ abundance there was greater annual variation (average yearly number of ovigerous ♀♀/sample = 355, table 18). However significant trends and peaks in the percentage ovigerous curve which were noted above remained clearly defined in the curve of numbers of ovigerous ♀♀.

In Lakes Rotorua and Rotoiti Chapman (loc. cit.) found that the numbers of breeding females of *Calamoecia lucasi* followed changes in the total ♀ numbers, rather than percentage of breeding ♀♀ as found in Ototoa - even though the variation in percentage ovigerous in the Rotorua lakes was much larger. This resulted from the greater change in total ♀ abundance in these lakes than in Ototoa and serves to illustrate that the amplitudes of yearly changes characteristic of most limnological events in Ototoa were much reduced when compared to those in more productive lakes further south in New Zealand.

(d) Egg Stock:

The egg stock of any one date has been determined by multiplying the number of ovigerous ♀♀ by the mean clutch size and so will be affected by all of the parameters discussed above. Because of the constancy of clutch size annual changes in the egg stock (fig. 17 , table 18) were practically identical to those of numbers of ovigerous ♀♀ This has also been found by Chapman (loc. cit.) but for *Boeckella propinqua* Green (1968) found that variations in clutch size usually accounted for changes in egg stock.

(e) The Number of Clutches per Female:

An estimate of the number of clutches produced by the ♀♀ during the year may be made using a method outlined by Chapman (1965). The monthly mean numbers of ovigerous ♀♀ were divided by the monthly mean egg development times (using egg development times at different temperatures presented on page 140, and the temperature of the upper 15 metres, where most animals were found) to give an estimate of the numbers of ♀♀ producing eggs per day, and thus per month (table 19). The number of ♀♀ producing eggs per month was then divided by the monthly mean stock of ♀♀ to give the number of clutches these ♀♀ could have produced.

It can be seen from table 19 that clutch production was highest in spring and summer when between 2 and 3 clutches could have been produced (maximum 3.2 in November). In other months clutch production varied between 1.3 and 1.6 ♀ $^{-1}$ and the yearly average was 1.9 clutches.

Month	No. ovig. females	Egg devel. time	No. females producing eggs.		No. of females	Clutches per female
			per day	per month		
March	189	2.10	90	2790	2101	1.3
April	224	2.63	85	2550	1964	1.3
May	286	3.13	91	2821	1753	1.6
June	302	4.33	70	2100	1667	1.3
July	453	5.53	82	2542	1741	1.5
August	399	5.25	76	2356	1611	1.5
September	396	3.79	104	3120	1764	1.8
October	582	3.10	188	5828	2534	2.3
November	446	2.45	182	5460	1707	3.2
December	181	1.87	97	3007	1893	1.6
January	275	1.62	170	5370	1968	2.7
February	335	1.60	209	5852	2182	2.7
March	238	1.60	149	4619	2067	2.2
MEAN						1.9

Table 19 : Numbers of egg clutches produced by *Calamoecia lucasi* in Lake Ototoa.

♀$^{-1}$. Animals reared in the laboratory (see below) produced similar numbers of clutches, the average numbers being produced being 1.8 at 20°C and 2.2 at 25°C (pp 143 + 144).

(f) Egg sizes:

Average egg diameters of *Calamoecia lucasi* in Lake Ototoa are shown in table 20. The yearly average of 111.9 μ is similar to that found for other freshwater calanoid copepods (e.g. Ren (1955)) found that *Diaptomus castor* bore eggs averaging 0.117 μ during April-May, and 0.138 μ during June-July; Czeczuga (1959) found that the average mean egg diameter of *D. gracilis* was 113 μ and of *D. graciloides* 120.9 μ and Comita (1964) found that the diameter of *D. siciloides* eggs varied between 100 and 120 μ), but smaller than in large marine copepods (e.g Marshall and Orr (1953) found that the diameter of *Calanus finmarchicus* eggs was 145 μ and those of *C. helgolandicus* 170 μ; Conover (1967) found that eggs of *C. hyperboreus* varied between 190 and 244 μ, and averaged 209 μ; and McLaren (1966) gives egg diameters for *Pseudocalanus minutus* ranging between 108.5 μ and 130.4 μ).

Species of *Diaptomus* bear larger eggs in the warmer months of the year, often in association with smaller clutch sizes (Hutchinson 1967). Because of this the summer batches of eggs may still contain as much egg substance as the larger clutches of smaller winter eggs. It has been suggested (Hutchinson 1967) that the larger summer eggs, by either providing more food per egg or by allowing hatching at a later

	Mean Diameter (microns)	s	CV(%)
10 March 1969	109.0	7.91	7.25
12 May	111.0	5.50	4.95
16 June	111.6	5.93	5.31
28 July	116.3	5.72	4.92
18 August	112.6	6.73	5.98
15 September	111.8	6.99	6.25
19 October	109.7	6.96	6.35
17 November	117.2	9.71	8.28
22 December	112.0	7.00	6.25
12 January 1970	109.1	6.19	5.67
9 February	111.2	5.60	5.04
9 March	110.8	4.00	3.61
AVERAGE	111.9		

Table 20 : Egg diameters of *Calamoecia lucasi* from Lake Ototoa 1969-1970.

naupliar stage, will result in higher naupliar survival at a time when conditions are not favourable. In Lake Ototoa eggs were largest in July and November, and smallest in March 1969 and January 1970. However, there was no distinct seasonal trend in egg size and this may reflect the relatively constant environmental conditions compared with those in Northern Hemisphere lakes in which egg size is more variable.

4. Female length:

The body length of copepods is affected by both temperature and food concentrations during development, negatively by temperature, positively by food (Coker 1933, Marshall and Orr 1955, Deevey 1960, McLaren 1963, Carter 1965, El Maghraby 1965). Thus copepods developing at different times of the year often have markedly different length distributions, and by following the changes in these distributions throughout the year it is possible to determine when new groups of animals enter the adult population (Tonolli 1964, Chapman 1964, Conover 1956).

(a) Mean length: Mean female metasomal lengths are presented in table 21 and fig. 22. The annual mean length of Ototoa females was 0.570 mm which is considerably shorter than lengths of *Calamoecia lucasi* in other lakes (table 22). As well as being the most oligotrophic of these bodies of water, Ototoa is also the most northerly and has the highest average annual temperature, so the shorter lengths may be a consequence of the depressing effects of low food levels coupled with higher temperatures.

DATE	Mean Length(mm)	S.D.	C.V.%
10.3.69	0.551	0.020	3.57
17.3.69	0.552	0.020	3.62
12.4.69	0.568	0.017	3.01
28.4.69	0.572	0.020	3.45
12.5.69	0.568	0.016	2.83
26.5.69	0.553	0.016	2.93
16.6.69	0.557	0.019	3.39
30.6.69	0.569	0.017	3.04
5.7.69	0.572	0.017	2.88
21.7.69	0.572	0.014	2.50
4.8.69	0.584	0.018	3.11
18.8.69	0.581	0.016	2.70
8.9.69	0.581	0.018	3.04
22.9.69	0.569	0.017	2.97
6.10.69	0.573	0.022	3.75
19.10.69	0.590	0.018	3.10
2.11.69	0.574	0.020	3.49
17.11.69	0.574	0.023	3.99
30.11.69	0.568	0.019	3.36
22.12.69	0.585	0.154	2.63
6.1.70	0.580	0.019	3.33
19.1.70	0.573	0.020	3.54
2.2.70	0.566	0.017	3.00
17.2.70	0.564	0.019	3.28
3.3.70	0.565	0.017	2.94

Table 21: Mean metasomal lengths of female *Calamoecia lucasi* from Lake Ototoa, 1969 - 70.

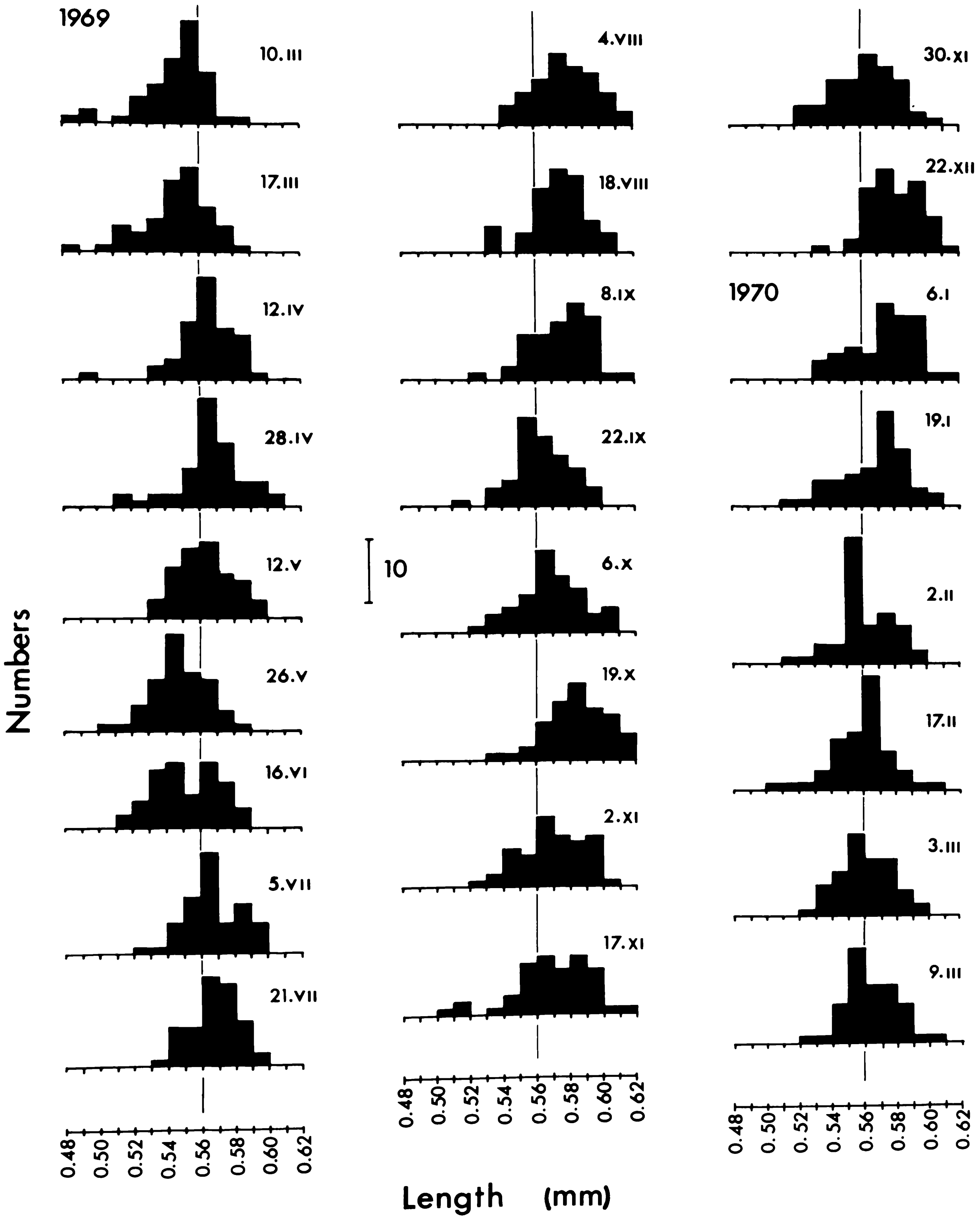
LAKE	Reference	Mean Length(mm)
Ototoa	This study (annual mean)	0.570
Piha Pond (West Auckland)	*	0.822
Waikare	*	0.616
Atiamuri	*	0.725
Rotorua	Chapman(1972) (annual mean)	0.654
Rotoiti	"	0.641

Table 22: A comparison of female lengths of *Calamoecia lucasi* from Lake Ototoa with those from other populations further south in the North Island. Those marked with an * are unpublished results from summer collections made by the author.

Mean lengths showed increases in April and May 1969, but lengths were greatest during the winter,spring and summer (from July to December), after which lengths decreased gradually. This seasonal sequence is very similar to that found in Lake Rotorua (Chapman 1972) although in Ototoa the amplitude of the changes is less marked.

(b) Length Distributions (fig. 18): At the beginning of the sampling during March lengths were centred on a mode of 0.55 mm, with a number of animals being found in the smaller categories below this length, but few in those above it. By 12 April however, a new group of larger ♀♀ had entered the population which now had a modal length of 0.56 mm and with more individuals in the larger size classes. The distribution of length remained similar during early May although smaller animals were appearing and by the end of May (26 May) the ♀ population consisted of a group of smaller animals with a modal length of 0.54 mm. This group was still present in mid-June (16 June) but on this date the length distributions was bimodal, with new animals of 0.56 mm - 0.58 mm having entered the population. From mid-June to mid-September (8 September) there was a gradual increase in the numbers of larger ♀♀ and the modal length increased during this period from 0.56 mm in July to 0.58 mm on 8 September, although there were always a considerable number of animals in the size categories between 0.56 mm and 0.59 mm. By the end of September (22 September) an abrupt decrease in modal size to 0.55 mm occurred with a positively skewed distribution, and between 22 September and 19 October the

Fig. 18: Metasomal lengths of *Calamoecia lucasi* females during the sampling period.


1969
10.III
17.III
12.IV
28.IV
12.V
26.V
16.VI
5.VII
21.VII
4.VIII
18.VIII
8.IX
22.IX
6.X
19.X
2.XI
17.XI
30.XI
22.XII
1970
6.I
19.I
2.II
17.II
3.III
9.III
10
Numbers
0.48
0.50
0.52
0.54
0.56
0.58
0.60
0.62
Length (mm)

modal size gradually increased, probably indicating a renewal of the female population by progressively larger animals. In early and mid-November lengths decreased. The modal interval dropped to 0.56 mm, but there was a more even spread of lengths between 0.55 mm and 0.59 mm which may indicate that a proportion of the larger females of late October were still surviving together with the smaller more recent recruits. By the end of November however the numbers in the larger age groups had been considerably reduced, and the length distribution was more evenly distributed around a mode of 0.56 mm, with a greater proportion of the animals falling into the categories between 0.52 mm and 0.55 mm.

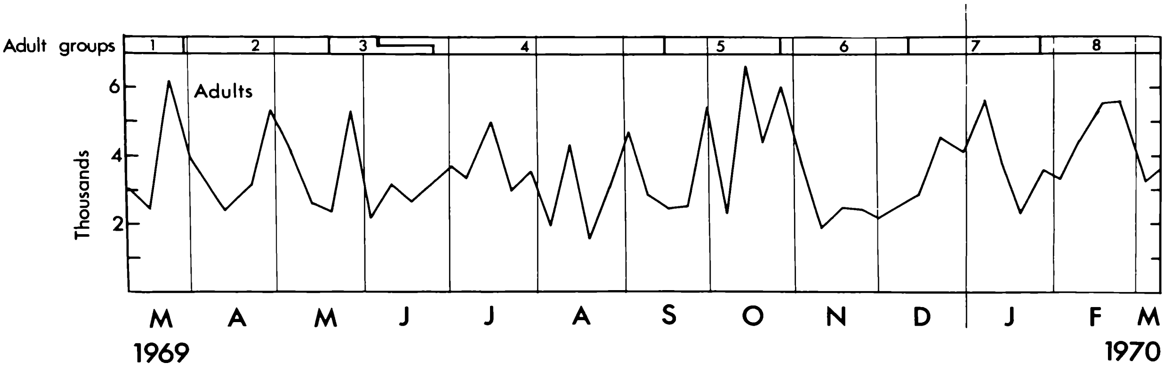
In mid-December modal size increased to between 0.57 mm and 0.59 mm and most animals were found in these size groups until mid-January 1970. However, from early January more ♀♀ began to appear in the smaller categories below 0.56 mm and by 2 February there was a distinct shift in the modal size to 0.55 mm. Apart from a change in the modal size to 0.56 mm on 17 February, the length distributions remained centred about 0.55 mm till the end of the sampling period, although in March 1970 slight increases in the 0.57 mm and 0.58 mm size groups may indicate the beginning of an influx of new adults.

These changes are very similar to those found by Chapman (1972) in Lakes Rotorua and Rotoiti, although no decreases in size comparable to those between 12 and 26 May, and between 8 and 22 September in Lake Ototoa were found. This may have been because she used a larger time interval between measurements than in the present study, or as seems more probable, because variation from year to year in different lakes makes absolute correspondance of cycles unlikely.

The changes outlined above can be used to identify a number of groups of adults, and the times when they entered the adult population. The changes of lengths observed were not great compared to those found in some Northern temperate lakes (Chapman 1969) and in other New Zealand copepods(Green 1968) and this is probably because of the small size of *C. lucasi* and the low amplitude of seasonal changes in temperature and food levels in Lake Ototoa.

The first group of adults is that present during March 1969. The second group is represented by the length distributions of 12 April, 28 April and 12 May. A third smaller group (which may represent some of the second group whose development rate became slowed down in the later copepodite stages - see section 5 page 100) may be represented by the distribution of 26 May and the left hand mode of 16 June. A fourth group, maturing slowly over the winter, and gradually increasing in size , possibly under the influence of lowering temperatures and increasing food levels, (see section 7,p 128) can be found in the histograms of 16 June (right hand mode), 5, 21 July; 4, 18 August and 8 September. A fifth group appeared on 22 September and may be represented in the following two distributions on 6 and 19 October -if this is so, the later maturing ♀♀ of this fifth group became progressively larger, and this would imply that the environment became more favourable for growth as these

Fig. 19: The probable sequence of adult groups determined from a consideration of seasonal changes in female length distributions. Seasonal changes in adult standing stock are also shown.


Adult groups
1
2
3
4
5
6
7
8
Adults
Thousands
6
4
2
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

♀♀ developed through the various growth stages. A sixth group may be represented by the distributions of 2, 11 and 30 November when smaller ♀♀ were found (although like the third group mentioned above, these may represent a later part of the fifth group which underwent development when temperatures had increased and food levels declined so that their lengths were shorter), while during the midsummer period a seventh group matured. The final eighth group appeared during February and was probably present to the end of the sampling period, although a ninth group may have begun to mature in March 1970.

This sequence of groups of adults is shown in fig. 19.

5. The Seasonal Cycle:

The seasonal cycle of *C. lucasi* in Lake Ototoa, and indeed elsewhere in New Zealand, is a multivoltine one with continuous breeding and, at least in the summer, considerable overlapping of generations. It is difficult to attempt an analysis of the yearly sequence in terms of generations, distinct groups of individuals developing to the adult stage more or less together from some clearly delimited period of egg production, as has been done for some northern temperature and subarctic species of copepods. However, by using the various groups of adults distinguished in the length analysis and the seasonal fluctuations in breeding intensity associated with these adult groups it is possible to gain some insight into the events involved in the seasonal cycles of development and maturation of *C. lucasi* in Lake Ototoa.

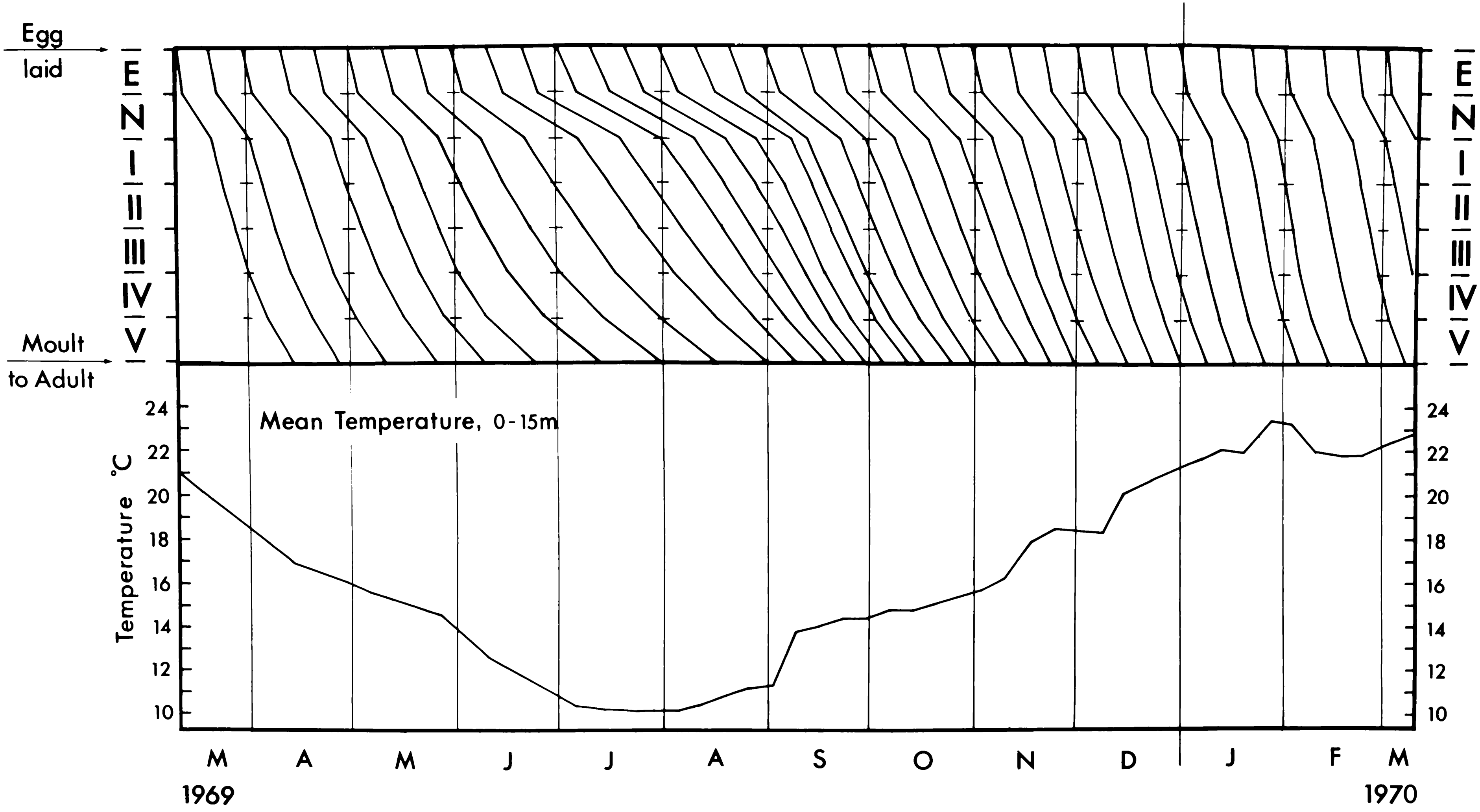
The development times of the various growth stages of *C. lucasi* were determined by rearing experiments in the laboratory, and a description of this study will be given below when the dynamics of the Ototoa population is considered. These development times proved to be useful in giving some idea when certain groups of eggs would have matured if they had developed at the rates determined in the laboratory , although it is unlikely that laboratory determined development rates can ever exactly describe rates in nature, because of variation in environmental factors other than temperature affecting development times.

However, under the influence of a maritime climate Lake Ototoa (together with other New Zealand lakes) tends to have environmental conditions that are much less variable than in equivalent sized Northern Hemisphere lakes. Furthermore it seems likely that, because of the oligotrophic nature of Ototoa, phytoplankton production throughout the year was much more even than in other New Zealand lakes. It is also thought that above a certain food level, growth rates of zooplankton reaches a certain maximum value and is not affected by changes in food concentration (e.g. McLaren 1969, Paffenhofer 1970). In Lake Ototoa there were no catastrophic declines in algal populations similar to those which are often found at the end of the spring outburst, and at the beginning of winter in northern hemisphere lakes and eggs were produced fairly evenly all year round suggesting that *C. lucasi* had at most times at least an adequate amount of food growth. It seems possible that therefore that in Lake Ototoa sudden food shortages may play a less important part in the determination of development rates of *C. lucasi* than temperature, and that the use of laboratory determined rates may be valid, and indeed it was found that there was often a pleasing correspondance between the sequence of events predicted from the laboratory rates and the development patterns that could be discerned in the population by consideration of the actual biological data.

So that the laboratory determined rates could be conveniently related to the Ototoa population fig. 20 was constructed which shows the presumptive time of maturation of eggs laid at 20 day intervals throughout the year. The time to complete successive developmental stages has been determined at the average enviornmental temperatures prevailing during the approximate period when each stage would have been developing, and these points were then joined to give the developmental sequences shown in the figure.

The flattening of the slopes of these lines from March to July shows how development times increased as temperatures dropped and the times of moult from copepodite V to adult for individuals laid in successive 20 day intervals became spaced further apart. As the lake warmed from August onwards, development quickened and the lines became steeper, so that in January development would have taken only about a month, while in winter up to 2½ months were required. A particularly interesting feature of the diagram is the way in which a large number of lines end in September and October. The hypothetical adults maturing in these two months would have resulted from egg layings of three earlier months (mid-June to mid-September) and if these had similar lifespans to adults during the rest of the year a large increase in adult standing

Fig. 20: Probable developmental sequences of eggs of *Calamoecia lucasi* laid at 20 day intervals during the sampling period. The developmental fate of each of these eggs has been calculated using the laboratory determined relationships between temperature and development time of the various stages (figs. 27 & 28), and the average temperature of the upper 15m in Lake Ototoa (also shown).


Egg laid
E
N
I
II
III
IV
V
Moult to Adult
Mean Temperature, 0-15m
Temperature °C
24
22
20
18
16
14
12
10
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

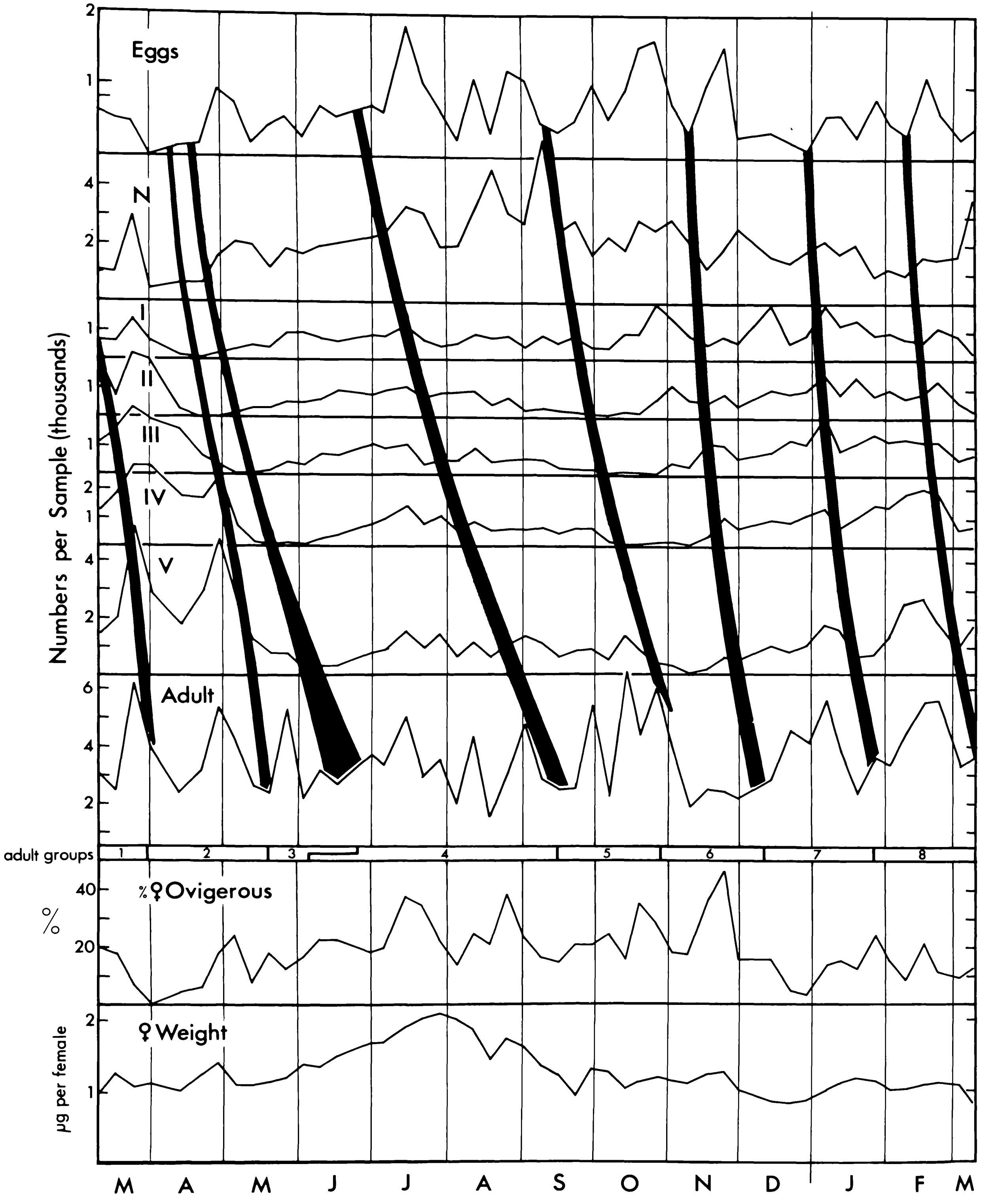
stock might be expected - and this was what in factoccurred, (see fig. 21).

Fig. 21 shows much of the data related to the following description of the seasonal cycle, and on the graph have been imposed bars which delimit periods between which the various adult groups may have developed. Although these may delimit "cohorts," especially during the winter period, it must be emphasised that during the summer the groups undoubtedly overlapped considerably and the suggested grouping is meant mainly as a basis for description, and may not represent "cohorts" in the true sense of a distinctive group of eggs or young.

The first group of adults present in March gave rise to eggs during this month, and their development can be followed through the growth stages in the series of peaks between March and May. They probably matured as the adults of group 2. These are represented by the adults present in April, particularly the peak numbers later in that month. The breeding of group 2 probably gave rise to the increases in egg stock between late April and mid-May.

The origin of the small 3rd group is very problematical. If it had developed in the normal sequence it would probably have arisen from a small number of eggs laid in early and mid-April by the group 2 females, and this is the sequence shown in the diagram. However, it is equally likely that these group 3 adults are late developing animals from group 2 whose development rate has slowed down. This interpretation is supported by the presence of "knees" on the curves of Cop III to V during the

Fig. 21: An interpretation of the seasonal cycle of *Calamoecia lucasi* in Lake Ototoa. Possible origins of the adult groups identified in the length analysis are indicated. Seasonal changes in % of females ovigerous and female weight are also shown.


Eggs
N
I
II
III
IV
V
Adult
Numbers per Sample (thousands)
2
1
4
2
1
1
1
2
1
4
2
6
4
2
adult groups
1
2
3
4
5
6
7
8
% ♀ Ovigerous
%
40
20
♀ Weight
µg per female
2
1
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

decreases from the late April maximax which may indicate when these animals broke off from the main group. This was a time of declining temperatures and algal stocks, events which are known to slow development rates in other copepods (Chapman 1969, McLaren 1969, Comita 1972) although, as noted above, it is unlikely that these changes would have been great enough in Lake Ototoa to cause catastrophic mortality. If such retardation occurred it is more likely that it would have taken the form of a gradual slowing of development which would affect certain sections of the population (perhaps the weaker ones) more than others.

In any event the later surviving adults of group 3 intermingled with the earliest animals of group 4, and this is shown in the diagram as an expansion of the base of the 3rd vertical bar. The group 4 females were found between June and September and are represented by the increasing numbers in July and the subsequent fluctuations afterwards. Although these probably result in part from sampling errors, the fluctuations may also indicate that there was variable mortality during the mid-winter period. These group 4 females probably arose from eggs, already referred to, laid by the group 2 females as well as the eggs of late May and June which were produced by the group 3 adults, and shown by small increases in the percentage ovigerous curve in early June. The development of the group 4 eggs can be clearly followed through the copepodite stages, and the gradual increase in the numbers of succeeding stages already referred to (page 79) is part of this sequence and most likely results from slowing of development times, and perhaps also lowered mortalities,in the falling temperatures so that greater stock numbers accumulate in each stage. The troughs in the curves of the development stages between April and June can be similarly interpreted. They probably resulted from both lowered recruitment as declining temperatures spread out the developing group, perhaps combined with higher mortalities brought about by changing environmental conditions.

These group 4 females underwent an initial burst of egg production as shown by the large increases in percentage ovigerous and egg stock in July. Between mid-July and mid-August there was a marked reduction in egg production, at a period when temperatures were at their lowest. This comparative cessation of breeding may have contributed towards the increase in female weight at this time. However later in August there was another burst of egg production, before the first of the 5th adult group appeared. The eggs produced between late June and early September by the group 4 females probably developed into group 5 adults between late September and early November, when there were considerable increases in adult numbers (page 80), and could have resulted because even though the timespan of group 5 adults was 1 - 2 months they resulted from 2½ - 3 months of egg production by group 4, as was expected from a consideration of probable temperature dependant development times (fig. 20). The 5th adult group can also be noted in small increases in the weight curve, as well as in the percentage ovigerous curve in late September and early October, and from this breeding resulted the large egg increases in these months.

These eggs probably developed into the group 6 adults by November, at quicker rates than the earlier groups because of the increasing temperatures, but even though there was a fairly large egg stock only a small stock of adults resulted. If this origin of the 6th adult group is correct then the stock numbers decreased considerably during the development of this group, as would result from the combined effects of decreasing development times, perhaps proportionately lower production rates and of increased mortality. This was the period the year when temperature stratification was becoming marked, when algal stocks were undergoing changes, and when certain of the other zooplankton species were increasing greatly in numbers. It may thus have been a time of greater mortality, particularly in the younger stages which may have been affected more by competition from the various rotifer and *Bosmina* populations. It is also possible that the 6th group represents a slower developing fraction of the 5th group. However the 6th group is associated with a great increase in breeding intensity that seems more typical of reproduction by newly matured and vigorous adults, rather than by animals held back in development by low food levels. There was also a noticeable increase in weight on the appearance of the 6th group, which also is more compatible with the appearance of a group of robust animals. It seems therefore that the first interpretation of the 6th adult group is to be preferred, and it is supported by the successive peaks in Nauplii, CI and CII between October and early November. However, in the stages between CII and the group 6 adults there was great reduction in the standing stocks. Increases in CIII - CV did occur later in November, and one interpretation could be that these were part of the group 6 sequence but leading, because of retarded development, to the group 7 adults. However if the group 6 adults are to be regarded as a distinct group, then these increases in CIII - CV are probably best interpreted as having resulted from the intermingling of the last of the early spring animals of group 6 with the first of later spring and summer animals, developing initially from the eggs produced by group 6, and which were to become the group 7 adults.

Stock numbers over the summer were generally high and the increases in most stages may be an indication of higher production and perhaps higher survival rates at a time when temperature determined development rates were increasing.

The group 7 adults show up as a distinct peak during December and January, and may have largely resulted from the breeding of group 6 adults. However later arriving members of group 7 could well have largely developed from eggs laid from the first group 7 females, and adult groups 6 - 8 appear to overlap considerably.

The first half of the group 7 adults were very low in weight and produced few eggs; the main breeding activity of this group came in January after a gradual weight increase, which may indicate improving nutritional conditions. These late eggs may then have developed to give group 8 adults in February. These themselves produced eggs in mid-February and if the sequences in 1970 was similar to that in 1969, these would have developed to give group 1 again.

Summary:

The Lake Ototoa population of *Calamoecia lucasi* was characterised by continuous breeding, and this is reflected in the constant high naupliar numbers. On the whole there was a very stable adult population, with copepodite numbers also being rather constant, especially during the winter and summer. However April-June and October - mid-November seem to have been times when higher mortalities and/or changed developmental rates resulted in lower copepodite numbers. The 8 groups of adults distinguished from the length analysis could also be recognised in the adult stock curve, and possible development sequences could be determined for most of these, especially those maturing in the colder part of the year. In most cases there seemed to be a close correspondance between development rates determined experimentally and those shown by the copepods in the lake.

6. Weight and Chemical Compositions:

Weight, protein, lipid and organic matter were determined in the hope that a knowledge of the gross biochemical composition of the ♀ population throughout the year might help in understanding events of the seasonal cycle. However, the results hold further interest because even though the organic composition of marine plankton and its seasonal changes have been frequently studied (e.g. Fisher, 1962; Cowey and Corner, 1962, 1963; Beers ,1966; Jawed, 1969 ; Comita, Marshall and Orr 1966; Conover and Corner 1968; Lewis, 1969; Jefferies, 1969; Raymont, Srinivasagam and Raymont, 1969; Omori, 1969, 1970), the only detailed study of organic nutrients in freshwater copepods seems to be that of Siefkin and Armitage (1968) on *Diaptomus* spp (although calorific values, carbon content and other constituents have been determined occasionally, e.g. Comita and Schindler, 1963; McLaren, 1969; Platt, Brawn and Irwin 1969; Wierzbicka and Kedzierski 1970; Kibby, 1971; Schindler, Clark and Gray, 1971), and there have been no previous studies of this sort on New Zealand copepods.

The present study is an introductory one, and only gross measures of what are probably the main organic constituents have been made. Thus carbohydrate was not determined because it is generally only a minor constituent of most copepods that have been studied, and attention was paid to protein and lipid as being the main structural and storage components, and dry weight.

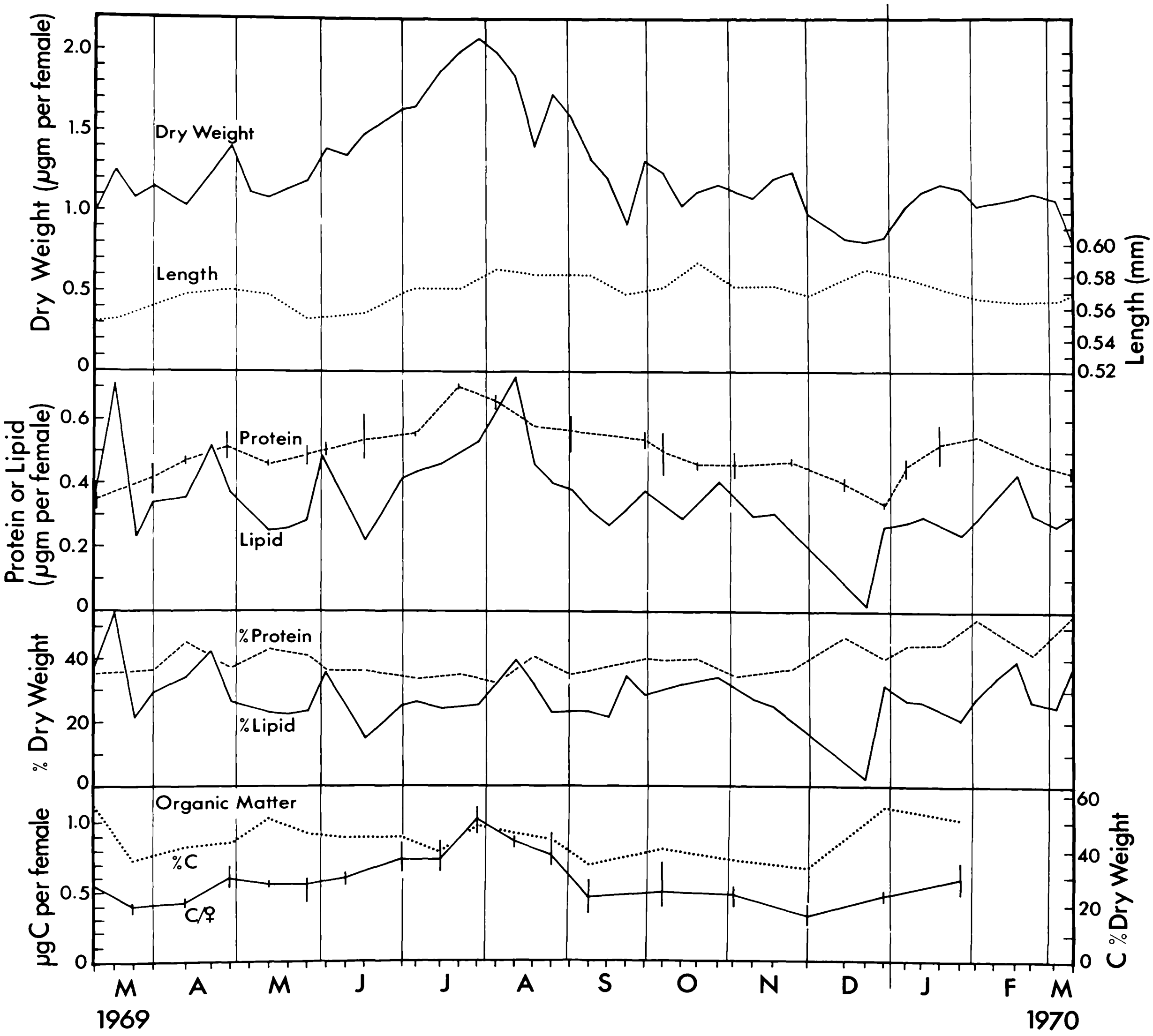
(a) Dry weight:

Seasonal changes in ♀ dry weight are shown in fig. 22 Initially, during March and early April 1969, weights were approximately 1.1 µg/♀ and during late April there was an increase to a peak of 1.40 µg/♀ . As autumn gave way to winter, during May, June and July, ♀ weight gradually increased to the maximum recorded, 2.08 µg on 28 July. During August and September the weights dropped to ca 1 µg/♀, and over the spring fluctuated between 1.0 and 1.3 µg/♀. Lowest weights were found in December (0.82 µg/♀ on 22/12/69), but in January there was a smooth increase and values generally remained between 1.0 and 1.2 µg/♀ for the rest of the sampling period.

The mean dry weight for the year was 1.23 µg/♀ which is considerably lower than the weights of other copepods that have been studied (table 23), and this is so even when allowance is made for loss of weight on preservation.

There was no consistent relationship between the seasonal trends of ♀ length and dry weight, ($r = 0.149$, $n = 26$, n.s.) thus the long animals of December weighed very little - and this was quite obvious when looking at the samples; these December ♀♀ were very transparent compared with the heavier and more opaque ones of mid-winter. Even so the increase in length between May and August associated with the main winter increase in weight, and the increase in length between March and May was associated with the peak in weight during late April.

Fig. 22: Seasonal changes in dryweight, mean length, protein, lipid, % protein, % lipid and organic matter of female *Calamoecia lucasi* during the sampling period. The range of variation in the determinations of protein, lipid and organic matter are shown.


Dry Weight (μgm per female)
2.0
1.5
1.0
0.5
0
Dry Weight
Length
0.60
0.58
0.56
0.54
0.52
Length (mm)
Protein or Lipid (μgm per female)
0.6
0.4
0.2
0
Protein
Lipid
% Dry Weight
40
20
0
% Protein
% Lipid
μgC per female
1.0
0.5
0
Organic Matter
%C
C/♀
60
40
20
0
C % Dry Weight
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

SPECIES	Reference	Measurement	Stage	Weight(μg)
Diaptomus clavipes	Siefkin & Armitage(1968)	Lipid free Dry Weight	♀ ♂	28-46 19-32
D.pallidus	"	"	♀ ♂	1.9-5.7 1.5-6.1
D.clavipes	"	"	♀ ♂	5-45 5-33
D.siciloides	"	"	♀ ♂	1.1-3.1 0.5-2.1
D.siciloides	Comita(1968)	Dry Weight	♀	3.2
D.oregonensis	"	"	♀	4.75
D.leptopus	"	"	♀	22.2
D.clavipes	"	"	♀	28.7
D.arcticus	"	"	♀	300
Boeckella triarticulata	*	"	♀ ♂	29.67 25.32
B.hamata	*	"	♀ ♂	13.86 6.73
B.delicata	*	"	♀ ♂	10.10 8.26
B.propinqua	*	"	♀ ♂	8.48 5.29
B.minuta	*	"	♀ ♂	8.33 3.49
B.tanea	*	"	♀ ♂	3.90 2.79
Calamoecia lucasi	This study	"	♀ ♂	1.23 1.06

Table 23: A comparison of the dry weights of *Calamoecia lucasi* with those of some New Zealand and North American freshwater calanoid copepods. Those marked with an * are some unpublished results of the author.

There did however seem to be some relationship between weight, sequences of adult groups, and breeding activity. Thus the increases in weight in April were associated with the maturation of the second group of adults and the small third group can be recognised as a minor peak of weight which occurred in early June during the course of the winter weight increase. The main winter bulge in the weight curve - between mid-July and mid-August - was associated with the fourth adult group, while the sudden weight increase in late September marks the maturation of the fifth group.

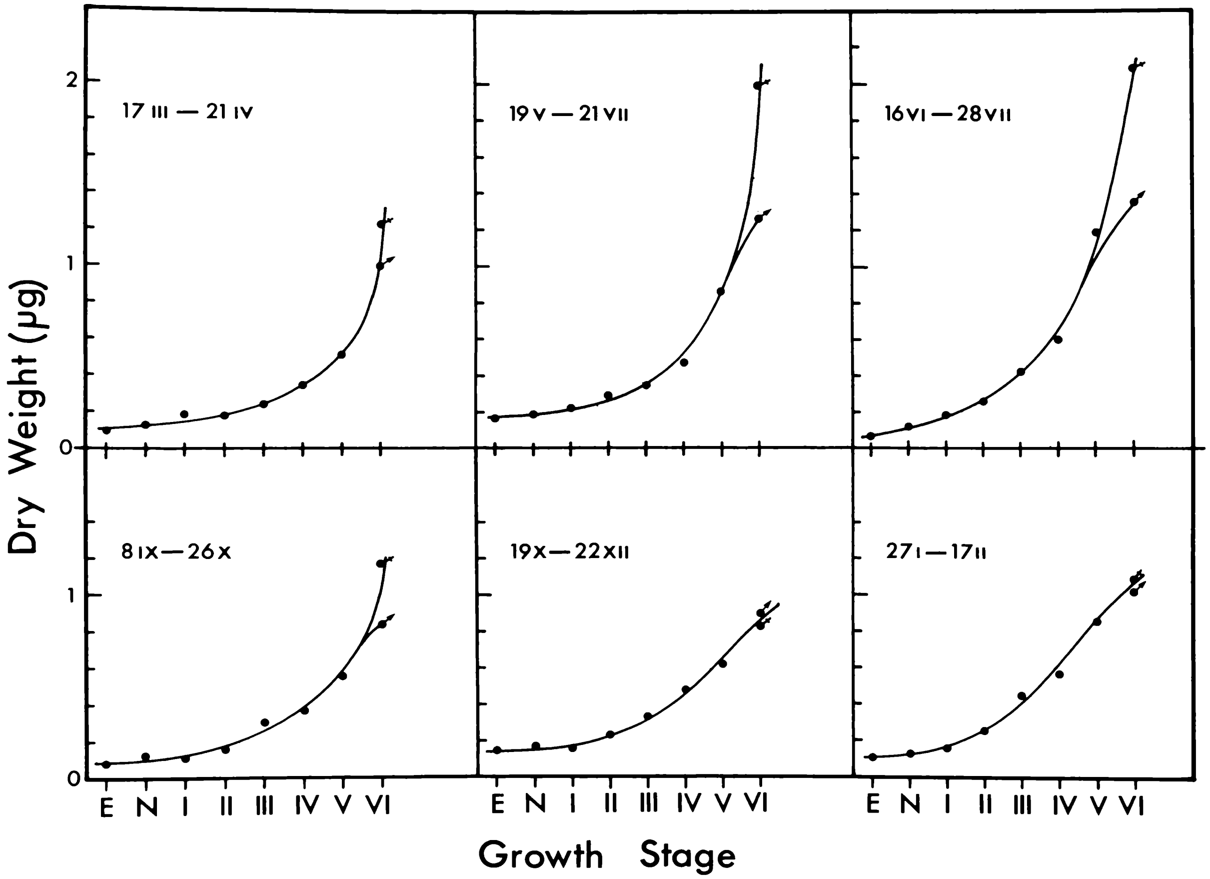
Probably because changes in weight can reflect the degree of development of the ovaries, other features of the weight curve either preceded or coincided with events in the reproductive activity of the population (as shown in the closely related percentage ovigerous and eggstock curves) and this was particularly noticeable during spring, summer and autumn. Thus the late April peak of weight is associated with an increase of eggstock and percentage ovigerous, as are the weight increases of the fourth adult group during June and July and late August, and also the smaller spring weight peaks of early October, late October and especially November. The low weights of December reflect low egg productuion and the increases in weight during January and February came at times of increases in percentage ovigerous and egg stock. The relationships show up in a significant correlation between weight and percentage ovigerous ($r = 0.460^{***}$ $n = 50$).

Dry weight was also significantly correlated with environmental temperature at the time of sampling ($r = 0.774^{***}$ $n = 50$). Siefkin and Armitage (1968) found that lipid free weight of *Diaptomus clavipes* and *D. pallidus* was correlated with temperature in a similar way, as did McLaren (1965) for *Pseudocalanus minutus*. Siefkin and Armitage found that food levels affected weight also and quote other studies showing the importance of food in determining size e.g. Comita and Anderson 1959. Such studies often consider size in terms of body length, which may not necessarily be correlated with weight (e.g. Comita, Marshall and Orr and the Ototoa data above), but Conover and Corner (1968) found that *Calamus hyperboreus* and *C. finmarchicus* did increase in weight at the time of the spring bloom in phytoplankton

In Lake Ototoa weights of *Calamoecia lucasi* were not significantly correlated with total phytoplankton numbers at the time of sampling ($r = 0.178$, $n = 42$), but there was a highly significant correlation between numbers of ingestible phytoplankton (see p.128 for discussion of ingestible phytoplankton) and weight ($r = 0.492^{***}$, $n = 42$). The introduction of a lag time into these relationships by correlating weight with phytoplankton on the previous sampling date did not improve the coefficients. However, this significant correlation is misleading because temperature and phytoplankton are themselves highly correlated ($r = 0.347^{***}$, $n = 42$), and when this relationship is removed from the reckoning by partial correlation analysis, the partial correlation coefficient between weight and ingestible phytoplankton becomes (0.316 n = 42) which is just significant at the 5% level. Thus in Lake Ototoa the dry weight of *C. lucasi* was correlated most highly with temperature, but there was also a weak relationship with ingestible phytoplankton.

As well as these ♀ weighings, weight determinations were also made on six series during the year of the growth stages, chosen to correspond approximately with actual development sequences in the lake. The results are shown in fig. 23 and the mean weights in table 24. During autumn, winter and spring growth was broadly parabolic (as has been found for many other copepods, Winberg, 1971), oo were always considerably lighter than ♀♀. During these periods of the year the larger ♀♀ appeared to lay lighter eggs. During the summer growth became more sigmoidal and there was little difference between the weights of the ♂♂ and ♀♀. Rates of egg production are greater at higher temperatures, and this lack of difference may have been because less material was accumulating in the ovaries in the summer than in the winter. It can be seen from table 24 that the ratio of maximum to minimum weight is greater for ♀♀ and older copepodite stages than for nauplii, young copepodite stages and ♂♂, and this is probably an indication that there may be greater seasonal variation in the growth of ovaries than in general body material.

Fig. 23: Mean weight of six sequences of the development stages of *Calamoecia lucasi* during the sampling period. The dates of the samples from which specimens were taken are set out in Table 6.



Dry Weight (µg)
0
1
2
0
1
17 III — 21 IV
19 V — 21 VII
16 VI — 28 VII
8 IX — 26 X
19 X — 22 XII
27 I — 17 II
E N I II III IV V VI
E N I II III IV V VI
E N I II III IV V VI
Growth Stage

Growth Stage	Mean Dry Weight (micrograms)	Range	Maximum weight / Minimum weight
EGG	0.111	0.067- 0.166	2.48
NAUPLIUS	0.146	0.124- 0.193	1.56
COP. I	0.190	0.152- 0.234	1.54
COP. II	0.250	0.185- 0.297	1.61
COP. III	0.361	0.242- 0.459	1.90
COP. IV	0.472	0.353- 0.600	1.70
COP. V	0.766	0.510- 1.190	2.33
♂	1.062	0.842- 1.350	1.60
♀	1.230	0.820- 2.080	2.54

Table 24 : Mean weights of the various growth stages of *C. lucasi* during the year.

(b) Protein:

Seasonal changes in the weight of protein per ♀ and percentage protein are shown in fig. 22.

The absolute amount of protein per ♀ showed a seasonal trend similar to that of dry weight. There was an initial rise to a minor peak in late April followed by further increases until late July when the maximum amount of protein/♀ (0.71 µgm/♀ was found. Then followed a gradual decrease to the minimum in late December (0.34 µgm/♀). A smooth increase occurred in January, paralleling that noted in the weight curve, after which values fell away during February and March.

However, protein expressed as percentage of the dry weight shows much less seasonal change, generally being between 35 and 50%. Values were lowest in midwinter (33% on 4 August, 1969) and highest during summer between December 1969 and March 1970 (54.3% on 9 March 1970). The yearly average weight of protein per ♀ was 0.50 µgm, and the corresponding proportion of dry weight was 40.5%.

As noted above the seasonal changes in protein/♀ closely follow those of dry weight ($r= 0.874^{***}$, n = 25) and the peak in dry weight in late April, the main increases in winter, the general decrease after this and the increases in January were probably largely caused by changes in the total amount of protein per ♀. However, the heavier copepods tended to contain proportionately less protein, and weight and percentage protein are negatively correlated ($r - 0.662^{**}$, n = 25). Like dry weight, protein/♀ was negatively correlated with temperature at the time of sampling ($r = 0.644^{***}$, $n = 25$), but not with phytoplankton . Percentage protein showed a positive correlation with temperature ($r = 0.662^{***}$, $n = 25$).

Raymont et al (1969) found that for some deepwater decapod mysid and euphausid zooplankton protein 53 - 71% dry weight and Fudge (1968) found a value of 75% for *Neomysis integer*; both of these are considerably higher than found for *Calamoecia lucasi*. In most zooplankton studies however total N is usually determined rather than protein, thus Beers (1966) found that in a variety of copepods N was between 9 - 11% of the dry weight, Conover and Corner (1968) gives N values ranging from 5 - 8% dry weight for *Calanus hyperboreus* and Omori (1969, 1970) found that N varied from 5.0 - 13.1% (av. 9.4%) and quotes N levels in *Calanus finmarchicus* ranging between 10.21% (Vinogradov 1933) and 4.7 - 5.9% (Curl 1962) of dry weight. He notes that there is a clear difference between copepods of subarctic and of tropic-subtropic waters; those of the former contain N as ca 6.7% dry weight while the latter are generally about 10.3% N.

For comparison the protein values from *Calamoecia lucasi* can be converted to an approximate figure for N as percentage of dry weight by dividing by 6.25 (the average conversion factor between N and protein, Winberg 1971) and the value so obtained is 6.48% of dry weight as N. This is similar to most of the figures quoted above, although less than the 10.3% given by Omori for tropic-subtropic species, to which *C. lucasi* might have been expected to show the most pronounced similarities.

(c) Lipid:

Seasonal changes in the weight of total lipid per ♀ and lipid as percentage dry weight are shown in fig. 22.

The amount of lipid showed more pronounced fluctuations than protein, but there was still a distinct winter maximum (which however occurred about three weeks later than that of protein) followed by a decline to lower summer values. This increase between July and August undoubtedly contributed in part to the winter weight increase. Three conspicuous increases in weight of lipid per ♀ between March and early June were also related to increases in the weight curve, and the increases of dry weight in late September, October, January and February were also associated with greater amounts of lipid. Thus absolute amount of lipid per ♀ was found to be correlated with dry weight ($r = 0.596^{***}$, $n = 39$). Lipid as a proportion of dry weight was generally between 20 - 40% and showed no clear seasonal trend, although lowest values were recorded in December.

The mean weight of lipid/♀ over the sampling period was 0.36 μgm/♀ over the sampling period was 0.36 μgm/♀ and the average concentration 28.7% of the dry weight, which is comparable to values found in other freshwater copepods. Siefkin and Armitage (1968) found the lipids in *Diaptomus clavipes* ranged between 5.1 - 50.1% dry weight, in *D. pallidus* from 17.0 - 39.2% and *D. siciloides* 1.9 - 55.0%. Wierzbicka and Kedzierski (1970) found up to 20.3% in *Cyclops vicinus* and quote Farkas (1958) who found lipids in planktonic cyclopoids ranging from 40 - 45% dry weight. Haq (1967) found lipid concentrations of 25.37% dry weight in *Metridia longa* but smaller values in *M. lucens* (1-5%) and Fisher (1962) gives similarly low values (15-11.0% dry weight) for some other marine copepods. Ostapenya et al (1967) give values for marine tropical plankton ranging between 2 + 10% dry weight.

Although there is a significant correlation between lipid per ♀ and temperature ($r = 0.401^{**}$, n = 39) it is not as clear as those of weight and protein. There is also a correlation between lipid per ♀ and ingestible phytoplankton ($r = 0.872^{*}$, n = 32) but there is no significant correlation between percentage lipid and either temperature or ingestible phytoplankton. Siefkin and Armitage (1968) found no consistent relationship between lipid concentration and either food or temperature in the copepods they studied, although in both *Diaptomus clavipes* and *D. siciloides* high lipid percentage tended to be associated with high chlorophyll values. In the arctic and sub-arctic species of *Calanus* lipid levels are related to available food. These species are known to lay down large stores of fat during the spring flowering of diatoms (Marshall and Orr 1955, Conover and Corner 1968, Omori 1969, 1970) and because of this percentage lipid is inversely related to percentage protein. There was no such relationship in *Calamoecia lucasi* however (r = 0.263 ns, n = 17) and on the whole both lipid and protein constitued rather constant proportions of the dry weight.

An interesting feature of the lipid curve is that most of the major peaks are clearly associated with the sequence of adult groups. The increases in March, mid-April and early June coincide with the development of adult groups 1, 2 and 3 respectively, the main winter increase occurred during the maturation of group 4, the abrupt increase to slightly higher percentages in September and October occurred on the appearance of group 5 and the decline in November and December was associated with the weak 6th group. Similarly the summer increases in January and February were associated with the 7th and 8th groups. Marshall and Orr (1955) have found that in *Calanus finmarchicus* percentage of fat is related to generations, and Siefkin and Armitage (1968) think that this might be so in *Diaptomus* spp also.

Because of the utilization of fat in egg production in copepods (e.g. Marshall and Orr 1955) it might be expected that lipid would be more closely related to events in the reproductive cycle than other biochemical constituents and in *Calamoecia lucasi* some weak relationships can be discerned between lipid /♀ and the percentage ovigerous. The overall increase in percentage ovigerous between April and July came at a time when lipid/♀ also showed some increase, the increasesin lipid/♀ in September and October were also associated with increases in the percentage ovigerous as were the increases in January and February. The correlation between these two factors is just significant at the 5% level ($r = 0.334^*$, $n = 39$). However, on many occasions increases in the percentage ovigerous were associated with sharp declines in the lipid per ♀ and percentage lipid as would be expected if lipid were utilised in egg production, e.g. the increases in percentage ovigerous in early May, mid-June, late August, late November and late January. Also peaks in percentage ovigerous (and egg stock) in July coincided with a dip in the percentage lipid curve. Schindler et al (1971) suggested that fat increases preceded rather than accompanied egg production in *Diaptomus* in contrast to Cummins (1967)) whom they state believed that highest seasonal calorific values (and thus fat concentrations) occurred during times of egg production. Thus they found that decreases in calorific value accompanied the production of eggs in *D. minutus*. Siefkin and Armitage (1968) also related fluctuations in lipids to changes in reproduction. The build up in lipids which they observed in autumn when food decreased was believed to be due to lowered reproduction as well as a differential response of activitity and metabolism to temperature. This latter point is of interest, because Schindler et al suggested that as the winter increases in fat took place in both juveniles and adults it was therefore not related solely to reproduction. They considered that it is more likely that the increase has survival value allowing the copepods to survive or even grow in periods of low food or poor food quality. The survival value of increased fat reserves would obviously be be increased if the metabolic rate per gram was also proportionately lowered as found in *Calanus* spp (Conover and Corner 1968). The increased amounts of lipid per ♀ in *Calamoecia lucasi* during the winter may also have served to aid survival, and may possibly have resulted from some seasonal metabolic change. However, the environmental conditions in Lake Ototoa are very mild compared to thos in northern hemisphere continental dimictic lakes and it seems more likely that seasonal storage in *C. lucasi* resulted from changes in the balance between intake of food and its utilisation, rather than to some inherent change in the metabolic activity of the copepods to counteract severe winter conditions. One of the main drains on the lipid reserves is probably the production of eggs. This occurs throughout the year in Lake Ototoa, although the rate of production varies (fig. 30, p. 155). The increases of lipid in winter may have come about because rates of egg production and respiration in the lower temperatures of August and preceding months utilised a proportionately smaller section of the food intake than between September and December when lipids decreased and rate of egg production rose.

(d) Organic Matter:

Total organic matter determined by the dichromate oxidations has been expressed as µg C/♀ and is shown in fig. 22

Changes in weight of organic carbon/♀ underwent similar seasonal changes to dry weight, and these two factors are significantly correlated ($r=0.898^{***}$, $n= 18$).

Carbon can also be expressed as percentage of dry weight (table 25). There was no marked seasonal change, values varying between 30.8% and 56.1%. The average value of 43.6% dry weight is similar to those of Beers (1966) who found that in marine copepods carbon constituted 35.2% to 47.6% dry weight (average 41.6%) and Omori (1969) who found an average carbon content for marine zooplankton of 45.6% (the values of copepods ranged from 39.0% - 66.6%, but the higher values were found only in the sub-arctic species). Similarly the ash content of *C. lucasi* ranged between 2.64% and 9.09% of the dry weight which is comparable to those found by Omori (loc. cit.) who gives values ranging between 1.9% and 6.4%. Schindler et al (1970) found that *Diaptomus minutus* contained 0.9 - 2.0% ash, while in their study of marine tropical zooplankton Ostapeny et al (1967) found ash contents between 1.31% and 40%. Comita and Schindler (1963) state that the copepods they combusted had no ash.

An approximate calorific value can be computed from the amount of oxygen consumed during the dichromate oxidations. The standard value of 3.4 kcal.gm^{-1} of O_2 was used as a conversion factor (Maciolek 1962). The calorific values so obtained are shown in table 25 and ranged between 3577 and 5773 cal.gm^{-1}. There was little seasonal change, and no pronounced winter increase similar to that found in

Date	μgm C.♀$^{-1}$	C as % dry wt.	Ash as % dry wt.	Calorific value cal. ash-free gm^{-1}
10.3.69	0.558	56.4	5.41	5773
24.3.69	0.398	36.9	5.14	3776
12.4.69	0.426	41.4	6.30	4294
28.4.69	0.606	43.3	7.01	4514
12.5.69	0.557	51.6	6.16	5331
26.5.69	0.552	46.4	3.78	4687
9.6.69	0.607	45.9	3.37	4521
30.6.69	0.737	44.9	6.46	4664
14.7.69	0.734	39.0	6.18	4031
28.7.69	1.032	49.6	5.68	5102
11.8.69	0.867	46.6	6.91	4859
25.8.69	0.770	44.3	9.09	4747
8.9.69	0.471	35.1	4.86	3599
6.10.69	0.504	40.3	5.58	4171
2.11.69	0.483	42.7	2.64	4272
30.11.69	0.333	33.6	8.42	3577
29.12.69	0.471	56.1	2.73	5617
27.1.70	0.354	30.8	3.86	5163
MEAN	0.581	43.6	5.53	4594
s	0.185	7.126	1.80	645
CV%	31.8	16.34	32.5	14.1

Table 25 : Organic matter in *Calamoecia lucasi* from Lake Ototoa.

Diaptomus minutus by Schindler et al (loc. cit.) although values during spring were a little lower than most of the others. The mean value over the sampling period was 4594 cal.gm^{-1} ashfree weight. This is lower than values for other freshwater and marine copepods (Ostapenya et al 1967) - 5.14 kcal.gm^{-1} ash free weight; Comita and Schindler (1963), for *Diaptomus* spp ♂ = 5400, ♀ = 5535 Schindler et al (loc. cit.) for *D. minutus* 5475 - 7375; Kibby (1971) mean values for *D. gracilis* - adults 5711, copepodites 5277, nauplii 5011 and eggs 5675) and less than might be expected from the proportions of protein and lipid (using the average values for lipid and protein of 28.7% and 40.5% dry weight respectively and assuming the remainder as carbohydrate, a calorific value of 6260 cal.gm^{-1} was calculated after Winberg 1971) although the lack of seasonal change in caloricity reflects the constancy of percentage lipid and percentage protein. This probably shows that oxidation efficiences were less than allowed for, but nevertheless the results obtained can be expected to be proportional to the real values and show the same seasonal changes. Comita, Marshall and Orr (1966) showed that in *Calanus finmarchicus* organic matter analysis by dichromate oxidations occasionally gave calorific values differing widely from those obtained by bomb calorimetry probably because all the fat was not accounted for, however, calorific values as determined by the two methods showed similar seasonal trends.

7. The food of *Calamoecia*.

All the species of phytoplankton counted are not likely to be equally important as food for *Calamoecia lucasi*. Many copepods show selectivity in their feeding, removing only certain species of algae from the water (Lowndes 1935, Fryer 1954, Malovitskaya and Sorokin, 1961, McQueen, 1970). Cell size is likely to be one of the most important factors affecting such selectivity (although other features such as shape, surface texture and chemical properties are probably also important) and some copepods select a definite size range of algae (Gliwicz 1969b, McQueen 1970). Particle size selection in *C. lucasi* was studied by the method first used by Burns (1968) which involves feeding the animals a suspension of "micronic" beads, small plastic spheres ranging in size between ca 1 µ and 100 µ in diameter. Some of these beads are eaten by the copepods and the size range selected can be determined by examining those contained in the gut. The beads are inert, smooth and spherical and are thus unlike most natural phytoplankton species. However, the method does at least give an indication of the range and maximum size of particle that *C. lucasi* is physically capable of ingesting, and the results have been used to determine which phytoplankton species may have been available as food for the copepods. As well as these studies the gut contents of the preserved animals from Lake Ototoa were also examined.

(a) Beads experiments:

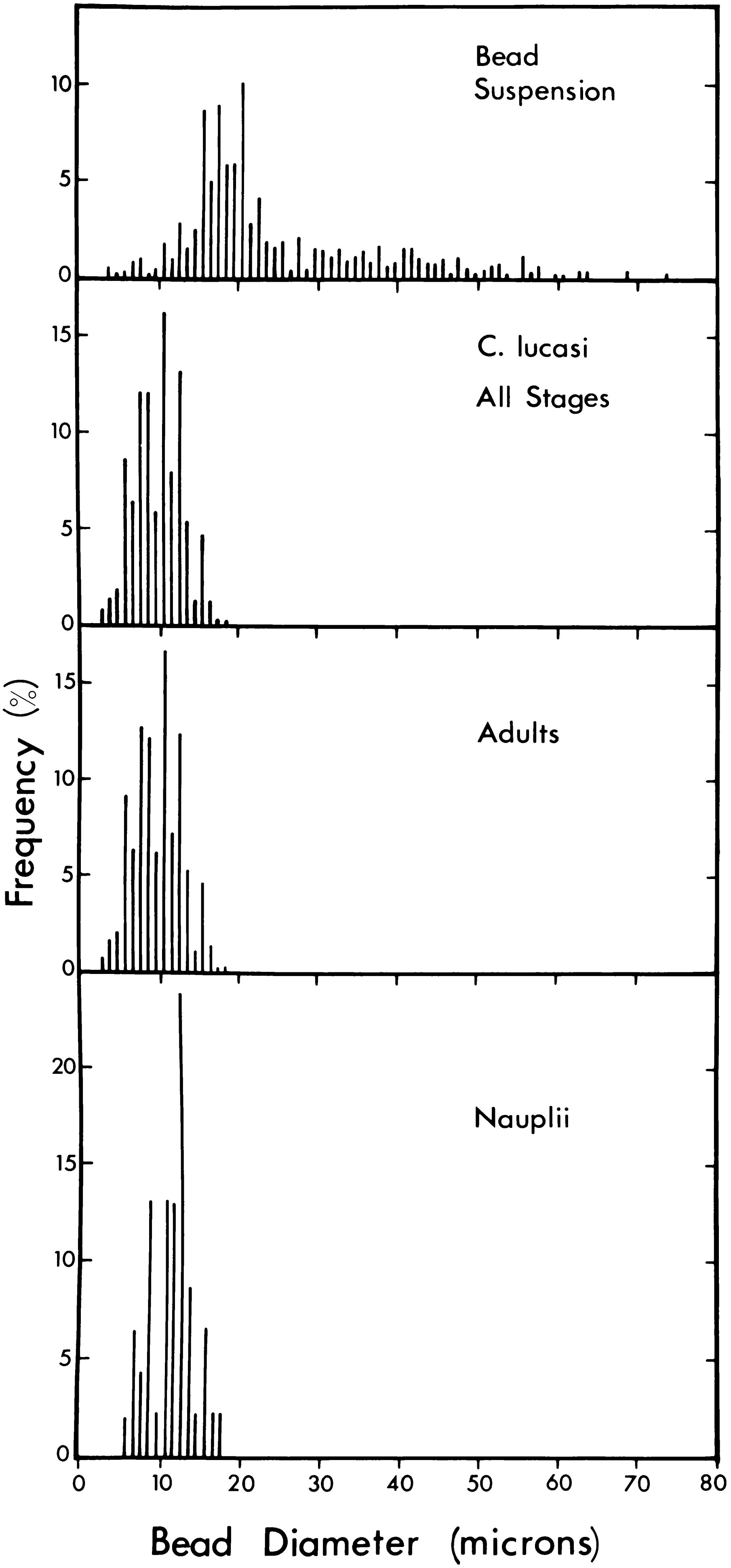
These experiments were carried out using *C. lucasi* collected from the ponds on the Waikato University campus and Lake Rotoroa.

The micronic beads were first washed three times in distilled water and a stock suspension made up. After stirring the concentration and size range of the beads in this suspension was determined by counting 1000 - 2000 beads in a haemocytometer (Spencer Bright Line), and measuring the diameters of 500 of these beads with the aid of an ocular micrometer at x800 magnification. The feeding suspension contained 2.5×10^4 beads.ml^{-1} and was made up immediately prior to use by adding the desired amount of stirred stock suspension to millipore filtered (0.8 µ pore size) water from Lake Rotoroa. As even small amounts of detergent have detrimental effects on *C. lucasi*, detergents in the filters were first removed by washing with hot water (Cahn 1967). Usually the yeast *Saccharomyces cerivisae*, added to give concentration of ca 0.5×10^4 cells.ml^{-1}, was used as a food source in the experiments, but on a few occasions *Chlorella pyrenoidosa*, *Chlamydomonas rheinhardtii*, *Pandorina morum* and natural lake water were used instead to determine whether the presence of different sized potential food particles affected particle size selection.

The feeding experiments were carried out in 80ml clear glass, stoppered reagent bottles. These were filled with the feeding suspension, and to each was added 30 - 80 *Calamoecia* (mainly adults) which had previously been kept overnight in millipore filtered water from Lake Rotoroa. The copepods were allowed to feed for 30 minutes during which time the containers were placed on a black bench under white fluorescent lighting, and inverted by hand every two minutes to keep the beads in suspension. At the end of the feeding period the copepods were fixed in formalin (a process that does not result in defaecation in *C. lucasi*), dehydrated in isopropanol, cleared in xylol and mounted in canada balsam. Using phase contrast the beads ingested were then measured at x800 magnification with an ocular micrometer. Few young stages were included in the experiments and most of the animals examined were adults. Of these ca 30% had taken in beads but only a few of the nauplii and copepodites were found containing them.

The distribution of particle size in the feeding suspension, and of the beads ingested by *C. lucasi* in all the experiments is shown in fig. 24 . It can be seen that *C. lucasi* only selected particles between 2.5 and 18.2 microns in diameter, whereas most of the beads in the feeding suspension were between 15 and 50 microns in diameter with only 12.85% being smaller than 15 microns in diameter. Considering all the experiments together the

Fig. 24: The frequency distribution of "micronic bead" diameters in the stock suspension and ingested by *Calamoecia lucasi*.


Bead Suspension
C. lucasi All Stages
Adults
Nauplii
Frequency (%)
Bead Diameter (microns)
0
5
10
15
20
0
10
20
30
40
50
60
70
80

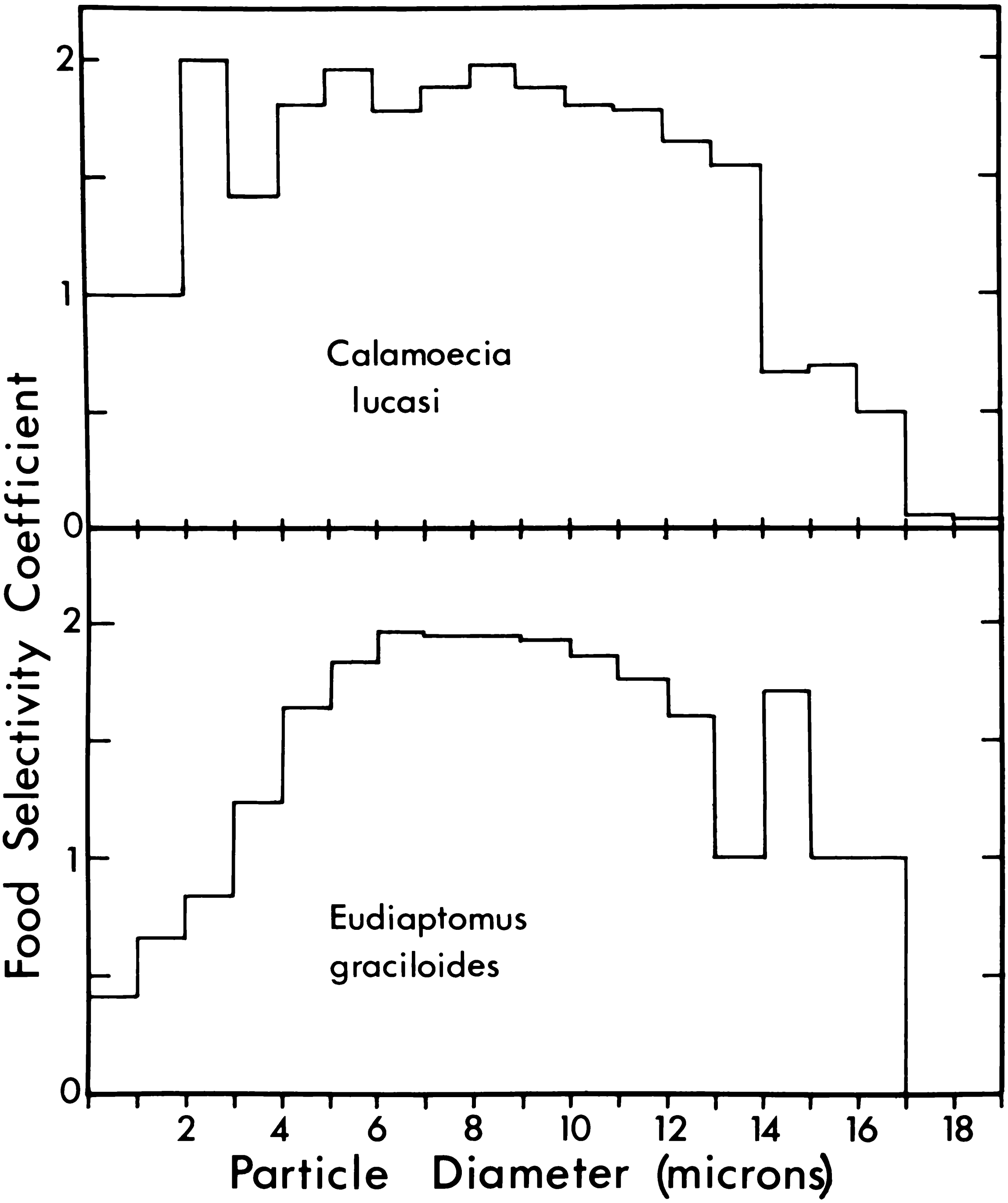
mean particle size selected was 9.6 microns. No significant difference was found between the mean size of particles ingested by oo and ♀♀ (♂♂ x 9.314 μ, $s = 3.001$ $n = 345$; ♀♀ $\bar{x} = 9.671\ \mu$, $s = 3.024$, $n = 288$; $t = 1.488$, ns). The few copepodite stages exaimed also selected beads within the adult range (CII $\bar{x}$ 3.8 μ, $n = 2$; CIII $\bar{x} = 14.3\ \mu$, $n = 1$; CIV $\bar{x} = 10.6\ \mu$, $n = 3$; CV $\bar{x} = 9.4\ \mu$, $n = 5$), and although nauplii selected beads in the same size range as the adults (fig. 24) the mean size was significantly larger ($\bar{x} = 11.239\ \mu$, $s = 2.776$, $n = 46$; $t = 3.508^{***}$). No significant difference was found between the mean particle size selected by all stages of *C. lucasi* with yeast as food ($\bar{x} = 9.822\ \mu$, $s = 3.105$) and those with *Chlamydomonas* ($\bar{x} = 9.71\ \mu$, $s = 3.40$, $t = 0.148$, 78 df ns), *Chlorella* ($\bar{x} = 11.30\ \mu$, $s = 2.91$, $t = 1.83$, df 64, ns), *Pandorina* ($\bar{x} = 10.32\ \mu$, $s = 2.98$, $t = 0.772$, 77 df ns) and natural food ($\bar{x} = 8.852\ \mu$, $s = 3.01$, $t = 1.716$, 124 df, ns).

The degree to which a certain bead size was selected can also be expressed by Ivlev's coefficient of food selectivity, S (Gliwicz 1969 b):

$$S = \frac{g - e}{g + e}$$

where: g - for any given size class of bead is the percentage frequency of that size class in the beads found in the gut of all the animals during all the experiments e - is the percentage frequency of the size class in the feeding suspension.

Fig. 25: A comparison of particle size selection in *Eudiaptomus graciloides* and *Calamoecia lucasi*. The data from *E. graciloides* is from Gliwicz (1969). Ivlev's coefficient of food selectivity (S) has been used as an expression of relative selection (see text).


Food Selectivity Coefficient
Calamoecia
lucasi
Eudiaptomus
graciloides
0
1
2
2
4
6
8
10
12
14
16
18
Particle Diameter (microns)

The results are shown in fig.25 together with similar figures for *Eudiaptomus graciloides* calculated by Gliwicz (loc. cit.). To simplify the graphical presentation of the results, negative values of the coefficient have been eliminated by adding + 1 to all of the figures. Both *C. lucasi* and *E. graciloides* select similar particle sizes, although *C. lucasi* shows relatively greater selection of particles below 5 μ, while *E. graciloides* shows a greater selection of particles larger than 14 μ in diameter. McQueen (1970) has shown that *Diaptomus oregonensis* selects particles in a similar size range.

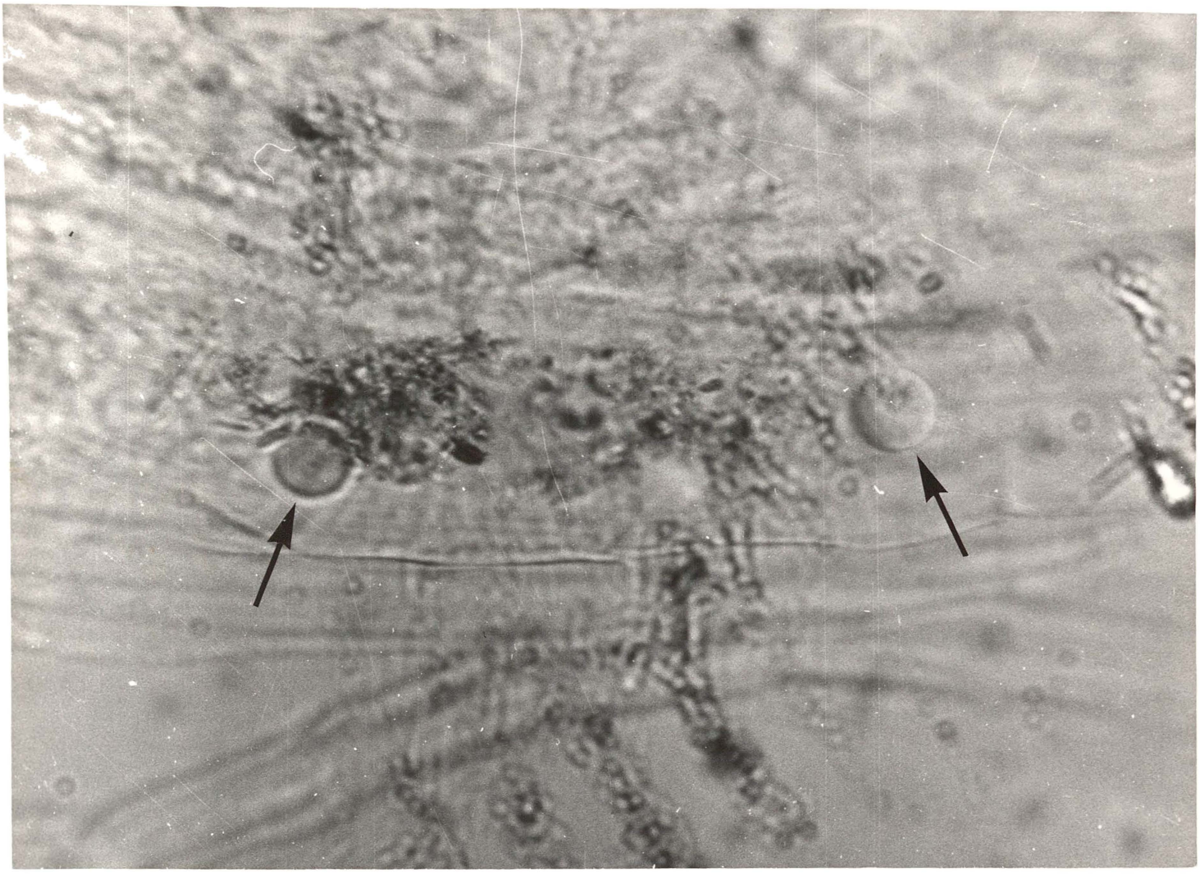
(b) Gut contents:

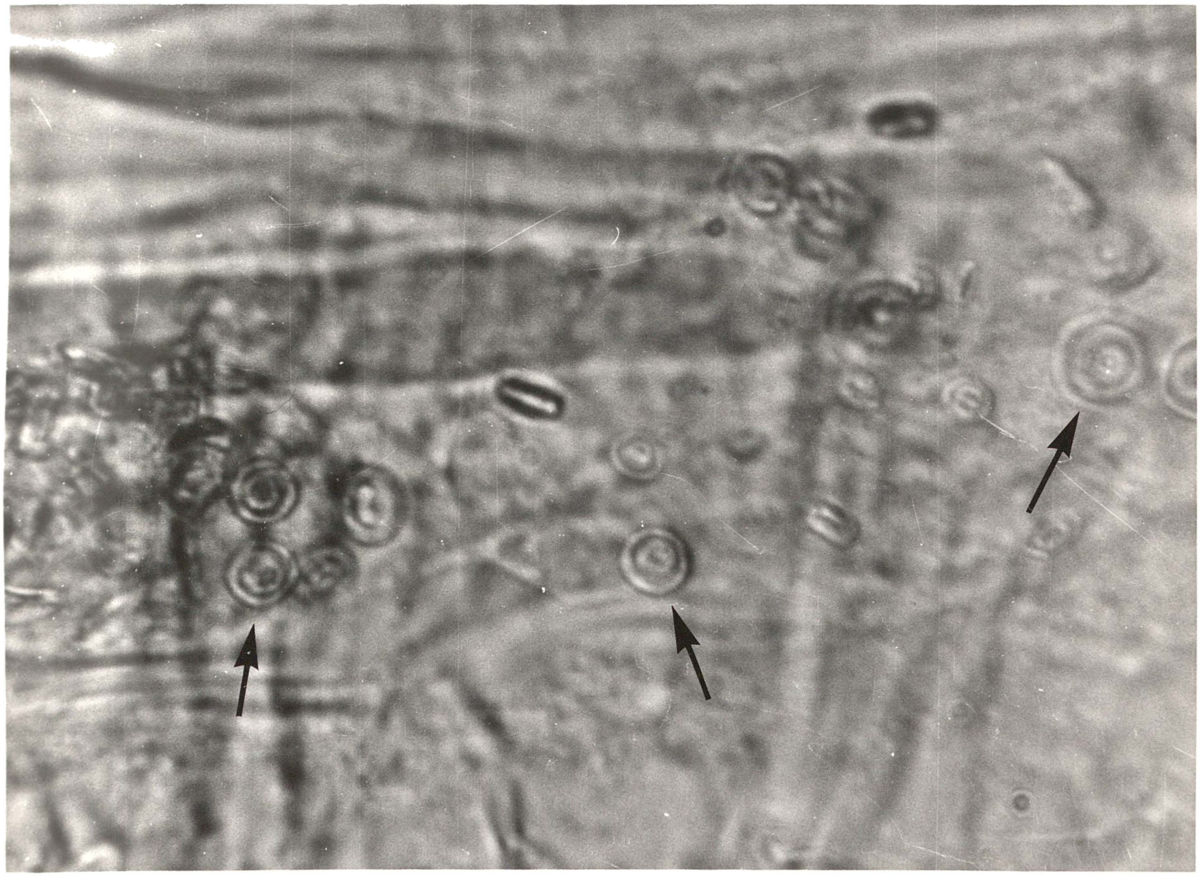
The gut contents of *C. lucasi* from Lake Ototoa were examined at approximately monthly intervals. A portion of the stirred sample was taken and the gut contents of the copepods rendered visible by the same method described above for the plastic beads. In virtually all of the samples examined *Cyclotella* was the only identifiable alga, and was found in the guts of every growth stage of *C. lucasi* in all samples, and on many occasion was present in large quantities (plate 2). The only other algae seen were single specimens of a small naviculoid diatom (found in ♀♀ on three occasions) and other material in the gut formed an unidentifiable mush, generally making up 20 - 70% of the total, although in some of the young copepodite

Plate 2.

Above: Two micronic beads (arrowed) in the gut of a female *Calamoecia lucasi* (x 1000).

Below: *Cyclotella stelligera* (arrowed) in the gut of a female *Calamoecia lucasi* from Lake Ototoa (February 1970) (x 1000).
Note the similarity in size between the naturally ingested cells and the beads.





stages between October and December this material made up the whole of the gut contents.

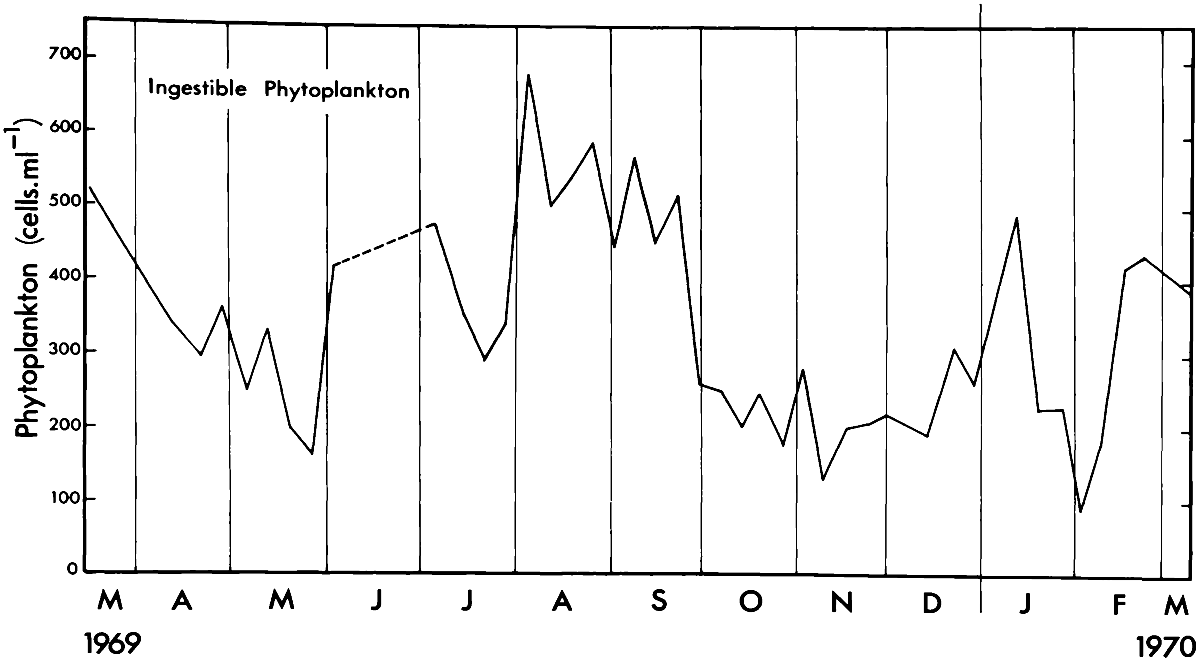
The amount of food in the gut varied during the year. and an approximate indication of this was gained by counting the number of *Cyclotella* contained in the guts of 10 ♀♀ from every month. The results are shown in table 26 and it can be seen that the numbers of *Cyclotella* /♀ fell between April and June 1969, increased thereafter to a maximum in September, dropped again until December and then increased to higher levels in late summer and autumn.

The average diameter of *Cyclotella* from Lake Ototoa (table 16) is very close to the mean size of bead ingested by *C. lucasi* and the presence of *Cyclotella* in the guts of *C. lucasi* from Lake Ototoa suggests that the results of the beads experiments may give a good indication of the size of food being eaten by the copepods in the lake. Plastic beads between 2 and 19 microns in diameter were found to be ingested, and the phytoplankton species from Lake Ototoa with maximum dimensions falling within this range are *Cyclotella stelligera*, *Staurastrum* spp, *Gymnodinium* sp "small monad", *Oocystis* sp, "Unicells" free cells of *Botryococcus braunii*, *Cryptomonas* sp, *Chroococcus limneticus* and *Cosmarium* spp (table 16). These may be called the "ingestible" phytoplankton species, and their combined numbers throughout the sampling period are shown in fig. 26 . *Cyclotella* was by far the most

	Mean number of *Cyclotella*	s	n
12 April	22.90	19.90	10
19 May	8.10	6.64	10
16 June	7.30	7.44	10
14 July	10.90	13.80	10
18 August	14.80	7.39	10
8 September	35.80	22.90	10
13 October	28.20	11.3	10
17 November	13.80	5.59	10
29 December	8.60	6.17	10
12 January	11.50	8.58	10
9 February	25.82	8.29	11
3 March	23.40	13.17	10

Table 26 : Mean number of *Cyclotella stelligera* in the gut of ♀ *Calamoecia lucasi* from Lake Ototoa, between April 1969 and March 1970. (s = standard deviation, n = number of ♀♀ examined).

Fig. 26: Seasonal changes in the numbers of "ingestible phytoplankton" during the sampling period (see text for a list of the species in this category).


Ingestible Phytoplankton
Phytoplankton (cells.ml⁻¹)
700
600
500
400
300
200
100
0
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

abundant of these comprising between 20.3% and 98.5% (mean 70.6%) of the total, and the seasonal trend in the numbers of ingestible phytoplankton largely follows that of *Cyclotella*. Numbers were highest in the coldest months of the year, although there were also peaks in numbers during the summer in January and February. The finding that the most consistently abundant of the ingestible algae, *Cyclotella*, was such an important constituent of the gut contents of *C. lucasi* throughout the year in Lake Ototoa is in contrast to the results of McQueen (1970) for *Diaptomus oregonensis*, who found that even though *Cyclotella* and *Merismopeadia* were of an ingestible size and were very common in Marion Lake, they were not utilised by the copepod.

POPULATION DYNAMICS AND PRODUCTION

A more complete understanding of the numerical changes discussed in the preceding sections requires knowledge of the recruitment and mortality occurring in the population during the year, and once these are known it is then possible to estimate the amount of organic matter produced.

To do this it is first necessary to know the rate of development of the various growth stages. Ideally these should be determined in the field in order to take into account not only the influence of temperature on development rates, but also any effects of natural variations in food levels and other environmental factors. Unfortunately field data from continuously reproducing populations with overlapping generations cannot be used to determine development rates. Development times of the eggs and copepodites of *C. lucasi* had therefore to be determined in the laboratory.

1. Development times of Eggs and Copepodites:

(a) Methods:

Egg development times of *C. lucasi* from Lake Ototoa, Chelsea pond (Auckland), Lake Rotoroa and the Waikato University pond, were determined by Edmondson's (1965) graphical method which has also been used for copepods by Taube (1966) and Burgis (1971). Only the effect of temperature on development rates was studied, because although other factors might conceivably affect development times Elster (1954) and Eckstein (1964) have shown that in other freshwater calanoids temperature is the only important environmental determinant of egg development times under natural conditions. A sample of copepods was collected (by a vertical haul through the epilimnion of Lake Ototoa and by tows from the shore at the other localities) and taken back to the laboratory in a dewar flask. The females were lightly anaesthetised with CO_2 to slow movements, and their eggs removed. 30 to 100 egg sacs were taken in this way and placed in 5 or 10 ml beakers containing 3 - 5 ml of water from the collection site. The eggs were then incubated at the desired temperature by placing the beakers in a foam plastic rack floating in a water bath the temperature of which should be kept constant to within ± 0.5°C. This temperature was generally that of the locality where the eggs were collected, although on a few occasions other temperatures were used. This practice should not invalidate the result if, as would seem reasonable, either lowering or raising the temperature has proportionately the same effect on the development times of eggs at different stages of development. The egg sacs were counted at intervals until all had hatched. The number of unhatched eggs was then plotted against time, and a straight line fitted to the results which, when extrapolated to the time axis, gave the mean development time.

Although it is probably best to leave the eggs attached to the females, it was found that *C. lucasi* females generally produced a new clutch of eggs soon after the earlier one had hatched. Thus in initial experiments with groups of egg bearing females numbers of unhatched clutches did not decrease gradually with time but instead showed an initial drop followed by constant or slightly increasing numbers of clutches as new eggs were produced. It was impractical to either keep large numbers of females in individual containers or to count the nauplii produced between observations, so the procedure outlined above was adopted. Removing the eggs from the females did not appear to affect the development times or hatching success. To test this a sample of females was taken, the eggs removed from half of them and the egg development times determined for them in the normal way. The other half were kept in individual containers at the same temperature, and the development times of these eggs determined. No significant difference was found between the development times of the eggs in these two groups. Hatching processes appeared to be normal in the detached eggs and no mortality was ever observed. Elster (1954) notes that in *Diaptomus gracilis* detached egg sacs develop normally at the same rates as eggs still attached to the female.

The development rates of the various growth stages of *C. lucasi* were found by raising them individually or in pairs from the egg. Calanoid copepods are notoriously difficult to culture in the laboratory and this was found to be the case with *C. lucasi* also. The animals were very sensitive to small amounts of contaminants remaining on the glassware used as culture vessels. In particular there was heavy mortality in vessels which had been washed in detergents, even though these had been thoroughly rinsed in distilled water. Because of this all culture vessels were first cleaned in chromic acid. The provision of an adequate food supply also posed problems. Marine copepods can be reared on diets composed of single algal species (Mullin and Brooks 1967, Corkett and Urry 1968, Corkett 1970) and initially a large number of experiments using cultured algae (*Chlorella pyrenoidosa, Chlamydomonas rheinhardtii, Tetraedon sp., Oocystis sp., Cosmarium sp.*) as food for *C. lucasi* were tried but without success. The method finally adopted was similar to that used by Eckstein (1964) for rearing *Diaptomus graciloides.*

4 - 6 ml of lake water (obtained from both Forest Lake and Lake Rotoroa, Hamilton) filtered through 18 xx (70 µ aperture) bolting silk to remove zooplankton, was placed in c. 5 or 10 ml beaker and to this was added 5 - 8 drops of Banta's medium (Needham et al 1937). Apart from the addition of bacteria and protozoans, this acted as an enrichment medium for the lake water and stimulated the development of a variety of algae, especially in thse containers kept at higher temperatures. Into each of these containers were placed one or two eggs taken off females collected from either Lake Rotoroa or the ponds on the

Campus of Waikato University. The culture vessels were then floated, as described above, in water baths maintained at 12°, 15°, 20° and 25° ± 0.5° C and kept near windows exposed to the normal cycle of day and night. 25 - 30 containers were kept at each temperature, and generally each container was examined daily (although this was not always possible) and the development stage of the animal noted. This was often difficult to accomplish because considerable time had to be spent waiting for the copepod to orientate itself so that its legs could be counted, and there were undoubtedly times when mistakes in instar determination occurred. When an animal died the vessel was discarded and replaced by a new one containing fresh medium and eggs.

Mortality was quite high in naupliar and young copepodite stages, especially in the 12° cultures (table 27). The most common cause of death was failure to moult successfully. Many failed to break clear of the exuvium, and occasionally others became caught in algal material and detritus adhering to the sides of the culture vessels. These hazards became less significant as the copepods developed, and mortality declined markedly after copepodite III (table 27).
52 *Calamoecia* were raised to the adult stage at 25°, 53 at 20° abd 7 at 15°, but because of very slow development times and higher moralities at 12° none were raised past copepodite III. At both 25° and 20° a number of males and females were mated and produced clutches of eggs which hatched into a second generation.

	12°		15°		20°		25°	
	Survival	% mortality	Survival	% mortality	Survival	% mortality	Survival	% mortality
Eggs	47	0	57	0	147	0	160	0
Nauplii	47	85	57	40	147	40	160	35
Cop. I.	7	43	34	36	82	21	104	24
Cop. II.	4	50	25	12	65	15	79	13
Cop. III.	2	-	22	27	55	0	69	17
Cop. IV.			16	0	55	4	57	2
Cop. V.			16	-	53	-	56	-

Table 27 : Survival of *Calamoecia lucasi* reared at different temperatures.

Note :- a) at 12° no animals developed past Cop. III.

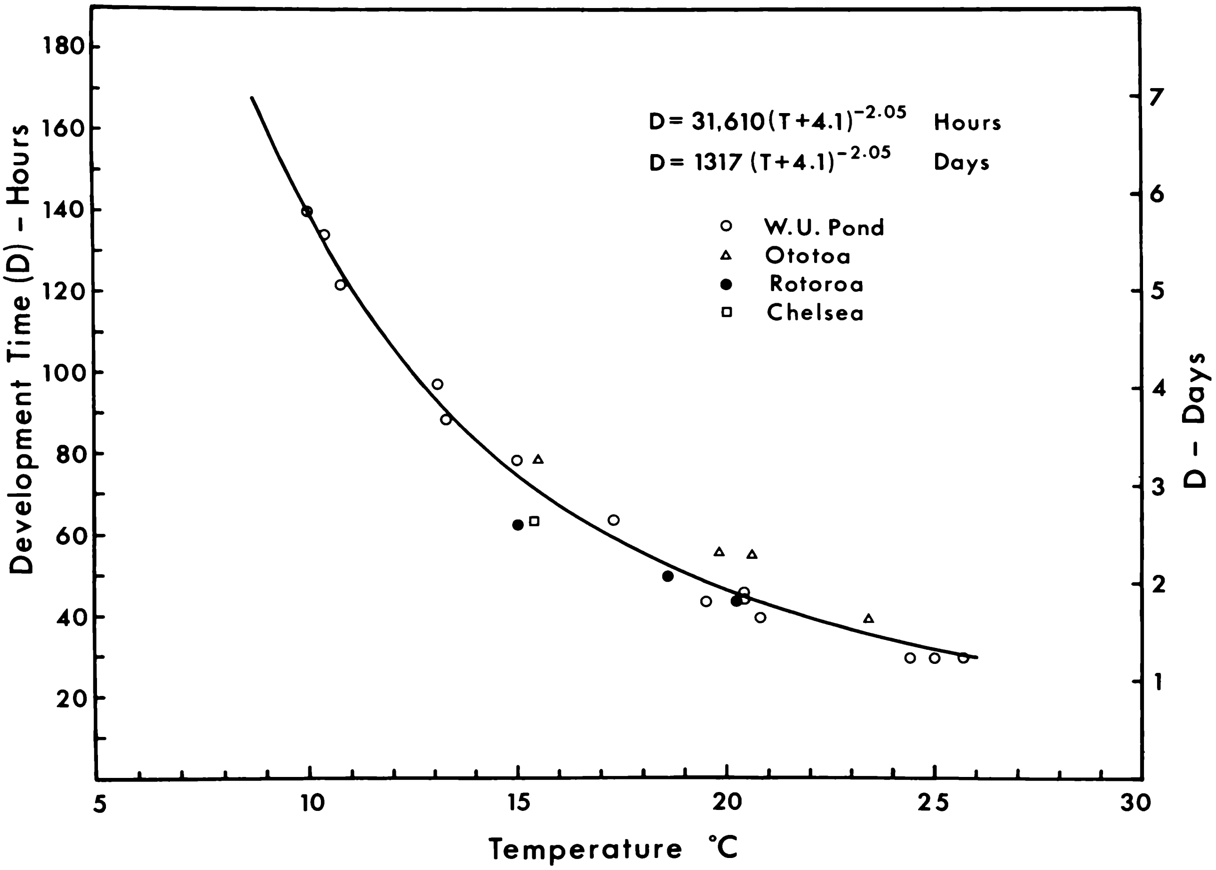
b) it is not possible to give accurate survivorship figures to the adult stage because the experiment was terminated before many of the copepods which had had developed to Cop. V had moulted to the adult. However, in 122 of such moults mortality was noted on only 4 occasions.

The method adopted for rearing the copepods was obviously not ideal because there was no exact control over the food levels in the cultures. However, the algal food supply growing in the culture vessels was supplemented at weekly intervals by additionals of Banta's medium, and the copepods can probably be regarded as at least moderately well fed, as is evidenced by the production of large clutches of eggs by many of the females (see below).

(b) Results:

The effect of temperature on the development times of the eggs and copepodites of *C. lucasi* are shown in fig. 27 and 28 . The development times of eggs from the different localities determined as described above are shown in fig. 27 . The scatter of points around the fitted line (see below) is not large, but there is a tendency for the development times of eggs from Lake Ototoa to be a little longer than those from the other localities. However, these differences are only very slight, and because there are only small numbers of observations from Ototoa the data have not been considered separately. The mean length of time spent in each instar by the individual animals in the rearing experiments was estimated by takingthe average of the maximum and minimum possible times the individual could have spent in the stage considered. The maximum was the time interval between the last observation before the animal moulted to the stage considered and the first time it was noted to have moulted to the following stage, while the minimum was the time interval

Fig. 27: The development time of eggs of *Calamoecia lucasi* at different temperatures. The fitted line is Bělehrádek's function (see text).


D= 31,610(T+4.1)^-2.05 Hours
D= 1317 (T+4.1)^-2.05 Days
○ W.U. Pond
△ Ototoa
● Rotoroa
□ Chelsea
Development Time (D) - Hours
180
160
140
120
100
80
60
40
20
D - Days
7
6
5
4
3
2
1
Temperature °C
5
10
15
20
25
30

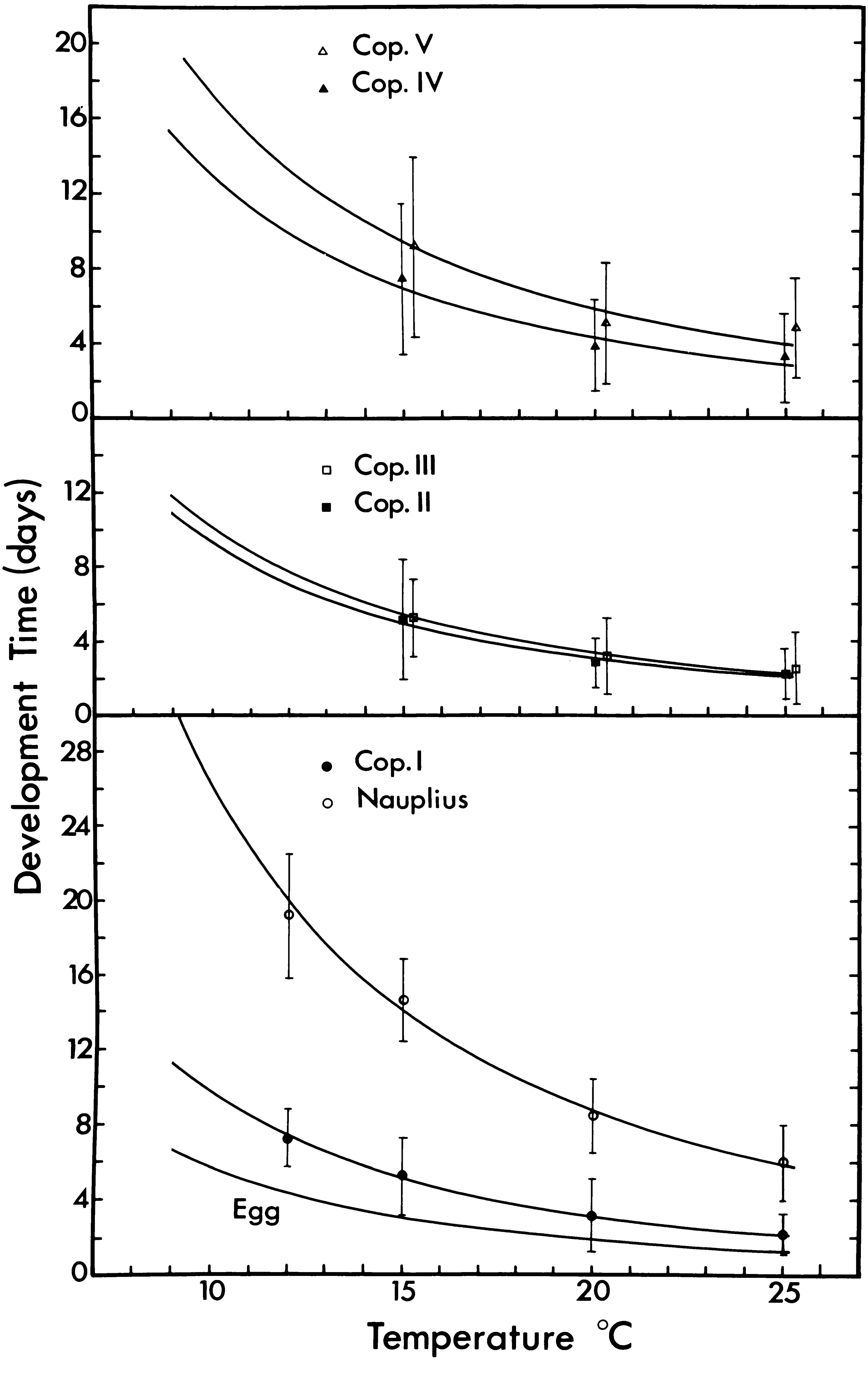
between the first observation when the animal was noted to have moulted into the stage under consideration, and the last observation before it moulted to the following stage. The mean development times of the nauplii and copepodites shown in fig. 28 are the averages of all these estimated individual development times from the rearing experiments. Bělehrádek's equation (McLaren 1963, 1965; McLaren, Corkett and Zillioux 1969; Corkett and McLaren 1970; Corkett 1970) has been used to describe the results. This equation has the form:

$$D = a\,(T - \alpha)^{b}$$

Where D is the development rate, T the temperature and a, b and α fitted constants. The use of this equation has been discussed at length by McLaren (loc. cit.). Corkett and McLaren (loc. cit.) and Corkett (loc.cit.) have found that the constants α and b are the same for all development stages of the same species of copepod. Thus once α and b have been found for one stage, e.g. the egg, then the form of the curve relating developmental time to temperature for any of the other growth stages can be predicted as long as the development time of this stage at any one temperature is known.

For *Calamoecia lucasi* the egg data was most complete. McLaren et al (loc. cit.) have shown that - 2.05 was the best estimate of b for the development times of eggs of a number of species of copepods, and this value has been used

Fig. 28: The relationship between development time of nauplii and copepodite stages of *Calamoecia lucasi* and temperature. The range of variation at each temperature is shown and the fitted line is Bělehrádek's function (see text).


△ Cop. V
▲ Cop. IV
□ Cop. III
■ Cop. II
● Cop. I
○ Nauplius
Egg
Development Time (days)
Temperature °C
0
4
8
12
16
20
0
4
8
12
0
4
8
12
16
20
24
28
10
15
20
25

for *C. lucasi* also. The equation was fitted by conversion to logarithms to give $\log D = \log a + b. \log (T-\alpha)$ and the other two constants found by successively approximating to that value of α (-4.1) which gave the required value of b in the regression equation.

Using these values of b and α, a number of separate values of a were calculated for each growth stage using the average development times found at the different experimental temperatures. A mean value of a for each stage was then obtained by averaging these separate values of a, and was used in the equation describing the relation between development time and temperature. The equations calculated in this way (table 28) describe the data very well (fig. 28) and have been used to estimate the average development times of the older copepodites at 12° and 15° where observational data is lacking.

It must be emphasised that Bělehrádek's equation has been applied to the development times of *Calanoecia lucasi* only because it provides a standardised way of describing and comparing the effect of temperature on the development times of the different growth stages, and also because it enables the data for *C. lucasi* to be directly compared with results obtained from other copepods. Other equations can describe the relationships adequately also. For instance that between egg development rate and temperature can be fitted to the power curve

$D = 5547.7\ T^{-1.50}$ ($r = 0.971$ cf $r = 0.974$ for Bělehrádek's

INSTAR	EQUATION
EGG	$D = 1317 (T + 4.1)^{-2.05}$
NAUPLIUS	$D = 5936 (T + 4.1)^{-2.05}$
COPEPODITE I	$D = 2194 (T + 4.1)^{-2.05}$
COPEPODITE II	$D = 2120 (T + 4.1)^{-2.05}$
COPEPODITE III	$D = 2322 (T + 4.1)^{-2.05}$
COPEPODITE IV	$D = 2996 (T + 4.1)^{-2.05}$
COPEPODITE V	$D = 4020 (T + 4.1)^{-2.05}$

Table 28 : The relationship between development time and temperature for *Calamoecia lucasi* reared in the laboratory.

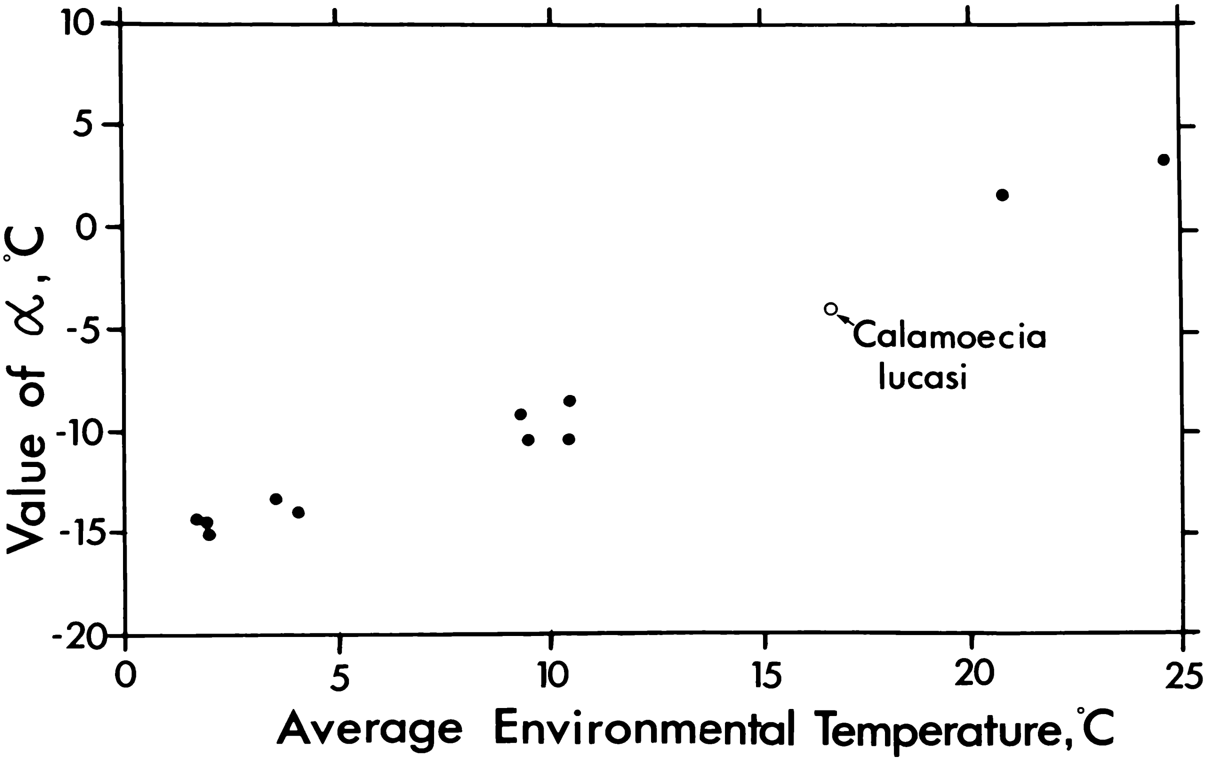
D = days. T = $^{\circ}$C

equation). McLaren et al(1969) have found that the values of α for egg development rates of a number copepod species are related to average environmental temperature, cold-water species have low values, and warm-water species high values. McLaren et al's fig. 3 is shown as figure 29. An approximate point for *C. lucasi* (using the yearly average epilimnetic temperature of Lake Ototoa 16.8 °C, and α =-4.1) has been added for comparison, and appears to fit into the general relationship.

A comparison of the times taken to develop from egg to adult, and of the time spent in copepodite V, was made between male and female *C. lucasi* reared at 15°, 20°, and 25°. The results are shown in table 29 . No significant difference was found between the development times of the two sexes.

In the 20° and 25° cultures a number of the males and females were mated and egg production of the females followed throughout their adult life. These observations are presented in tables 30 and 31 . Most females produced more than one clutch, the mean being 1.8 at 20° and 2.2 at 25°. The maximum number of clutches produced was six. Clutch size varied between 1 and 10 (mean 5.5 at 20°, 3.7 at 25°) and the total number of eggs produced per female varied from 0 to 24 (mean 16.0 at 20°, 8.3 at 25°). The production of clutches of eggs throughout the life of any one female varied greatly, although some general points emerge. Females were capable of producing eggs very soon after moulting from

Fig. 29: (Fig. 3 of McLaren, et. al., 1969). The relationship between α ("biological zero") of Bělehrádek's temperature function for eggs of eleven species of copepods and estimates of average temperature in their environmental ranges. These values for *Calamoecia lucasi* in Lake Ototoa have also been shown.


Value of α, °C
10
5
0
-5
-10
-15
-20
0
5
10
15
20
25
Average Environmental Temperature, °C
Calamoecia lucasi

Temperature	Mean Development time Egg - Adult (days)		s	n	t
25°	Male	16.6	4.9	24	1.911 (ns)
	Female	19.4	5.8	29	
20°	Male	23.7	5.69	29	0.625 (ns)
	Female	22.8	4.46	24	
15°	Male	36.8	8.82	3	0.266 (ns)
	Female	35.18	7.09	4	

Temperature	Mean Development time Copepodite V (days)		s	n	t
25°	Male	4.67	2.33	26	0.797 (ns)
	Female	5.28	3.09	25	
20°	Male	4.63	2.75	26	0.991 (ns)
	Female	5.51	3.63	26	
15°	Male	11.4	6.41	3	1.036 (ns)
	Female	7.6	3.22	4	

Table 29 : Development time of copepodite V, and total time taken to develop from egg to adult, for male and female copepods reared at 25°. 20°, and 15° C.

Day	Female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1		-	-	-	-	-	-	-	-	-	-	-	-	-*	-	-	-
2		-	-	-	-	-	-*	-	-	-*	-*	-*	-*	-	-	-	-
3		-	-	-	-	-	-	-	-*	8_{i}	7_{i}	-	-	-	-	-	2i
4		-*	-	-	-	-*	s	-	7_{i}	8	7	-	5i	4_{i}	-	-*	-
5		6_{i}	-	-	-	6i	-	-*	7	-	8_{ii}	-	-	4	-	7_{i}	-
6		6	-*	-	-	-	-	-	-	-	8	-	-	-	-	7	
7		-	s	-*	-	-	-	-	-	-	-	-	4_{ii}	-	-	-	
8		7_{ii}	-	-	-	6_{ii}	-	7_{i}	-	-	-	-	4	-	-	10_{ii}	
9		7	-	-	s	6	-	7	-	-	-	-	-	-	-*	10	
10		-	-	-	-	-	-	-	-	-	-	-	-	-	5_{i}	-	
11		-	-	-*	-	4_{iii}	-	-	-	-	-	-	-	-	5	-	
12		-	-	7	-	3	-	-	-	-	-	-	-	-	1_{i}	2_{iii}	
13		-	-	7	-	-	-	-	-	-	-	-	-	-	1	2	
14		-	-	7	-	-	-	4_{ii}	-	-	-	-	-	-	-	-	
15		-	-	7	-	-	-	4	-	-	-	-	-	-	-		
16		-	-	7	-	-	-	-	-	-	-	-	5_{iii}	-	7_{iii}		
17		6_{iii}	-	7	-	-	-	-	-	-	-	-	5	4_{ii}	7		
18		6	-	-	-	-	-	-	-	-	-	-	-	4	-		
19		-	-	-	-	-	-	-	-	-	-	-	-				
20		-	-	-	-	-	-	-	-	-	-						
21		-	-	-	-	7_{iv}	-	-	-	-	-						
22		-	-	-	-	7	-	-	-	-	-						
23		-	-	-	-	s	-	-	-	-							
24		-	-	-	-	-	-	-	-								
25		-	-	-	-	-	-	-	-								
26		-	-	-	-	-	-	-	-								
27		-	-	-	-	-	-	-									
28		4_{iv}	-	4_{ii}	-	-	-	-									
29		4	-	4	-	-	-										
30		-	-	-	-	-											
32		-	-	6_{iii}	-												
33		-	-	-	-												
34		-	-	-	-												
35		-	-	-	-												
36		-	-	-													
39		-	-	-													
43		-	-														
68		-*															
69		-															
70		s															
75		s															

Table 30 : Breeding activity of females reared at 20°C. (* = male added; - = female carrying no eggs; s = female carrying spermatophore; 1-8 = clutch size; i-iv= clutch number).

Day	Female 1	2	3	4	5	6	7	8	9	10	11	12	13
1	-	-	-*	-	-*	-*	-*	-*	-*	-	-	-	-*
2	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	2	-	3i	-	-	-	-	-	-	-	-
			i										
4	-	-	2	-	-	-	-	-	8	-	-*	-*	-
									i				
5	-	-	6	-	s	-	-	-	4	-	-	4	4i
			ii									i	
6	-	-	6	-*	-	-	-	-	-	-	-	4	-
7	-	-	-	-	-	-	-	-	6	-	-	-	-
									ii				
8	-	-	-	-	-	-	-	-	6	-*	s	3ii	-
9	-	-	-	-	-	-	-	4	6	6i	-	-	
								i	iii				
10	-*	-*	-	s	-	-	-	4	6	-	1i	-	
11	-	-	-	s	-	-	7	-	-	-	-		
							i						
12	5i	-	5	s	-	-	7	-	-	-			
			iii										
13	2ii	-	5	s	-	-	2	s	3iv	-			
							ii						
14	-	-	4	s	-	-	2	s	-				
			iv										
15	-	-	4	s	-	-	2	2ii					
							ii						
16	-	3	~~1~~	~~1~~	-	~~2~~	2						
		i											
17	-	3	3	1i	-	-							
			v										
18	-	-	3	s	-	-							
19	-	6	-	s	-	-							
		ii											
20	-	6	4	s	-*	-*							
			vi										
21	-	-	4	s	1	-							
					ii								
22	-	1iii	-	-	1	4i							
23	-	-	-	-									
24	-	-	-										
25	-	-											
26	-	-											
27	-	-											
28	-												

Table 31: Breeding activity of females reared at 25°C. (* = male added; - = female carrying no eggs; s = female carrying spermatophore; numbers = clutch size; i-vi = clutch number).

copepodite V (e.g. females 9 + 10 at 20°, table 30). Generally eggs were produced the day after the introduction of a male, although in some cases, particularly at 25°, egg production did not begin for some time. Often two or more clutches were produced in quick succession, followed by further egg production at longer intervals and often the first clutches of eggs were larger than later ones, although this was not always so. The adults lived for considerable lengths of time, the longest lived being female 1 at 20° (table 30) who survived for 75 days as an adult. This particular female produced 4 clutches of eggs in its first month. However, when a new male was added after 2 months, mating occurred but no eggs were produced, and this may indicate that fertility declines with age.

2. Population Dynamics:

The standing stock of the total population, or any part of it, represents the net result of the balance between numbers entering the population or stage, and those leaving it. Any change in the standing stock over a period of time is an indication that this balance has changed. These processes were estimated for the population of *C. lucasi* in Lake Ototoa by the widely used methods pioneered by Elster (1954) and Edmondson (1960) which have been fully discussed in a number of recent publications (Petrusewicz and McFayden 1970, Edmondson and Winberg 1971, and Winberg 1971).

The number of individuals passing from one stage of the life cycle to the next between samples (recruitment to the latter stage) was calculated by:

$$R_s = \frac{\bar{N}_{s-1}}{\bar{D}_{s-1}} \cdot T \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where R_s is the recruitment into stage s, $\bar{N}_{s-1}$ is the average of the stock of stage s-1 on two consecutive sampling dates t_1 and t_2, $\bar{D}_{s-1}$ is the average of the development rates at times t_1 and t_2, and T the time interval considered is t_2-t_1. This relationship applies to the whole population or any part of it. Thus recruitment into the population as a whole is measured by the number of eggs hatching during the interval ($\bar{H}$);

$$\bar{H} = \frac{\bar{N}_e}{\bar{D}_e} \cdot T \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

where $\bar{N}_e$ is the average of the egg stock at times t_1 and t_2, $\bar{D}_e$ the average of the egg development times at t_1 and t_2 and T the interval considered ($t_2 - t_1$). Similarly recruitment into copepodite III for example is given by:

$$R_{III} = \frac{\bar{N}_{II}}{\bar{D}_{II}} \cdot T \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

where R_{III} is the number of animals moulting into copepodite III from copepodite II, $\bar{N}_{II}$ and $\bar{D}_{II}$ the average stock and development time of copepodite II during the interval T.

The numbers leaving the population or any phase of it (n_s) is the sum of the efflux to the following stage and "losses" during the interval (loss includes all forms of mortality, due to old age, predation, failure to moult successfully etc., and when the total population is considered as a unit these constitute the whole of n_s).

Thus:

$$\dot{n}_s = \frac{\bar{N}_s}{\bar{D}_s} . T + \text{losses} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (4)$$

where $\bar{N}_s$ and $\bar{D}_s$ are respectively the average stock and development time of stage s during T. Thus for copepodite IV for example:

$$\dot{n}_{IV} = \frac{\bar{N}_{IV}}{\bar{D}_{IV}} . T + \text{losses} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (5)$$

and for the total population:

$$n_{total} = \text{losses} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6)$$

Therefore, if change in stock is designated $N_s^{t2} - N_s^{t1}$ where N_s^{t1} is the stock of stage at time t_1 and N_s^{t2} the stock at a later time t_2 then:

$$N_s^{t2} - N_s^{t1} = \frac{\bar{N}_{s-1}}{\bar{D}_{s-1}} . T - \frac{\bar{N}_s}{\bar{D}_s} .T - \text{losses} \quad \ldots\ldots \quad (7)$$

i.e. (1) minus (4).

This equation can then be rearranged to give losses:

$$\text{losses} = N_s^{t1} - N_s^{t2} + \frac{\bar{N}_{s-1}}{\bar{D}_{s-1}} \circ T - \frac{\bar{N}_s}{\bar{D}_s} \circ T \quad \ldots\ldots\ldots \quad (8)$$

If desired for comparative purposed this figure may the be converted to a specific loss rate by dividing the total losses by $\bar{N}_s$.

Thus if the total population is considered:

$$\text{loss}_{(\text{total})} = N_T^{t1} - N_T^{t2} + \frac{\bar{N}_e}{\bar{D}_e} \circ T \quad \ldots\ldots\ldots \quad (9)$$

where N_T^{t1} and N_T^{t2} are the total standing stock of the population on two successive sampling dates, and $\bar{N}_e$ and $\bar{D}_e$ are respectively the mean egg stock and egg development rate during the interval T, and in copepodite IV for example:

$$\text{loss}_{IV} = N_{IV}^{t1} - N_{IV}^{t2} + \frac{\bar{N}_{III}}{\bar{D}_{III}} \cdot T - \frac{\bar{N}_{IV}}{\bar{D}_{IV}} \cdot T \quad \ldots\ldots\ldots \quad (10)$$

The equation for adult losses has a slightly different form because there is no "efflux" to a following stage:

$$\text{loss}_{VI} = N_{VI}^{t1} - N_{VI}^{t2} + \frac{\bar{N}_V}{\bar{D}_V} \circ T \quad \ldots\ldots\ldots \quad (11)$$

Once the losses in the adult stage have been calculated it is then possible to estimate the average ecological longevity ($\bar{t}$) of the adults (Petruscewicz and McFadyen 1970):

$$\bar{t} = \frac{\bar{N}_{VI}}{\nu_E} \circ T \quad \ldots\ldots\ldots \quad (12)$$

where γ_E is the number of adults eliminated in time T, which is equal to loss_{VI} (11).

Using these methods, and the laboratory determined development times, recruitment and loss have been calculated for the population as a whole, as well as losses of nauplii, copepodites I - V and adults (table 32). Losses in the egg cannot be determined separately, and are included in the naupliar losses, but the results of the rearing experiments would suggest that egg mortality is minimal. It is realised that the average development times determined in the laboratory are unlikely to correspond exactly to the field rates, and may at times be widely different. However, it is hoped that at most times they provide at least a first approximation of the actual development rates. In all cases the temperature used in estimating the development times of the various stages in Lake Ototoa is the mean temperature of the upper 15 m, since checks on the vertical distribution of the copepods indicated that very few animals were found below 15m at any time of the year, or day and night. Recruitment and loss as calculated in this study represent mean values between sampling dates, and in graphing the results values have been plotted midway between these times.

DATE	No. days between samples (a)	D_e (b)	$\bar{D}_e$ (c)	Egg stock (ES) (d)	$\overline{ES}$ (e)	Mean H (e/c) (f)	Egg prodn. in Nov. (f.a)	Egg prodn. between each date (a.e) (g)	N_T (g)	$N_T^{t1}-N_T^{t2}$ (i)	Loss (i+g) (j)	Loss per day (j/a) (k)	Losses in Nov. (k.a)
26.10.69		2.99		1629					11851				
	6+1		2.93		1199	409	409	2863		1462	4325	618	618
2.11.69		2.86		768					10389				
	7		2.78		566	204	1428	1428		4279	5707	815	5707
9.11.69		2.70		363					6110				
	8		2.51		694	276	2208	2208		-458	1750	219	1750
17.11.69		2.31		1024					6568				
	7		2.25		1284	571	3997	3997		-2233	1764	252	1764
24.11.69		2.19		1543					8801				
	6		2.21		923	418	2508	2508		1213	3721	620	3721
30.11.69		2.23		303					7588				
							10550						13560

Table 32(a): The calculation of monthly production and loss figures, hatching rates and loss rates (Lake Ototoa, November 1969). Symbols explained in text.

DATE	No.days between samples (a)	Mean H (b)	N_T (c)	$\bar{N}_T$ (d)	$\bar{B}$ (b/d) (e)	b' $\ln(\bar{B}+1)$ (f)	$\ln N_T$ (g)	$\ln N_T^{t2} - \ln N_T^{t1}$ (h)	r' (h/a) (i)	d' (f-i) (j)	D $(1-e^{-d'})$ (k)	T (1/k) (l)
26.10.69			11851				9.2646					
	7	409		11120	0.037	0.0363		-0.0161	-0.0023	0.0386	0.0379	26.4
2.11.69			10389				9.2485					
	7	204		8250	0.025	0.0247		-0.5308	-0.0758	0.1005	0.0956	10.5
9.11.69			6110				8.7177					
	8	276		6339	0.044	0.0431		0.0723	-0.0090	0.0341	0.0335	29.9
17.11.69			6568				8.7900					
	7	571		7685	0.074	0.0714		0.2926	-0.0418	0.0296	0.0292	34.2
24.11.69			8801				9.0286					
	6	418		8195	0.051	0.0497		-0.1483	0.0247	0.0744	0.0717	13.9
30.11.69			7588				8.9343					

Table 32(b): The calculation of instantaneous birth and death rates, instantaneous rates of population change, finite birth and death rates and population turnover time. (Lake Ototoa, November 1969). Symbols explained in text.

DATE	No. days between samples	N_{III}	$\bar{N}_{III}$	D_{III} days	$\bar{D}_{III}$ days	Recruitment into CIV between dates (c/e).a	N_{IV}	$\bar{N}_{IV}$	D_{IV} days	$\bar{D}_{IV}$ days	Recruitment into CV (efflux from CIV) between dates (h/j).a	$N_{IV}^{t1} - N_{IV}^{t2}$	Loss in CIV (l+f-k)	Loss per day (m/a)
	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)	(k)	(l)	(m)	(n)
26.10.69		67		5.3			133		6.8					
	7		245		5.2	330		156		6.7	163	-45	122	17
2.11.69		422		5.1			178		6.5					
	7		356		5.0	498		134		6.3	149	89	438	63
9.11.69		289		4.8			89		6.1					
	8		717		4.5	1275		234		5.7	328	-289	658	82
17.11.69		1144		4.1			378		5.3					
	7		1095		4.0	1916		723		5.2	973	-689	254	36
24.11.69		1045		3.8			1067		5.0					
	6		814		3.9	1252		842		5.1	991	450	711	119
30.11.69		583		3.9			617		5.1					

Table 32(c): The calculation of recruitment into, and losses from, copepodite IV. (Lake Ototoa, November 1969). Symbols explained in text.

Models of population growth based on the well known exponential growth equation have also been used to estimate instantaneous birth and death rates in copepod populations (Edmondson, Comita and Anderson 1962, Cummins et al 1969 , Burgis 1971, Kibby 1972 , Chapman 1972). In such models population growth is described by:

$$N_t = N_o e^{rT}$$

where: N_o = population size at time 0.
N_t = population size at some later time, t.
r = instantaneous coefficient of population increase.
T = time between 0 and t.
e = base of natural logarithms.

When immigration and emigration into the population can be assumed to be negligible, changes in population numbers will come about only as a result of variations in birth and death rates and the instantaneous coefficient of population growth, r, may be thought of as comprising an instantaneous birth rate, b, and death rate, d. Thus:

$$r = b - d$$

and: $$N_t = N_o e^{(b-d)T}$$

In practice, b can be calculated from the finite birth rate (Edmondson 1960).

$$b' = \ln (1 + B)$$

(the prime on b', and also on following d's and r's, indicate that these are only estimates of the true values). Measurements of population size on two consecutive dates can be used to calculate r':

$$r' = \frac{\ln N_{t2} - \ln N_{t1}}{t_2 - t_1}$$

Thus having estimates of both b' and r' it is possible to calculate d':

$$d' = b' - r'$$

It is implicit in such models of population growth that individuals born into the population reproduce themselves at the same rate as those present previously, and do so within the interval between samples. This may be true when such animals as rotifers are considered which hatch, mature and begin to reproduce between sampling dates, but in the study of most copepod populations, in which the time between samplings is normally relatively short compared to the length of the life cycle it is not strictly correct to assume geometrical population growth, and the methods outlined above are not truly applicable. Nevertheless, for the purposes of comparison with other published figures, instantaneous rates of birth and death were calculated for *Calamoecia lucasi* in Lake Ototoa. B was calculated from the mean hatching rates and mean total population size between sampling dates:

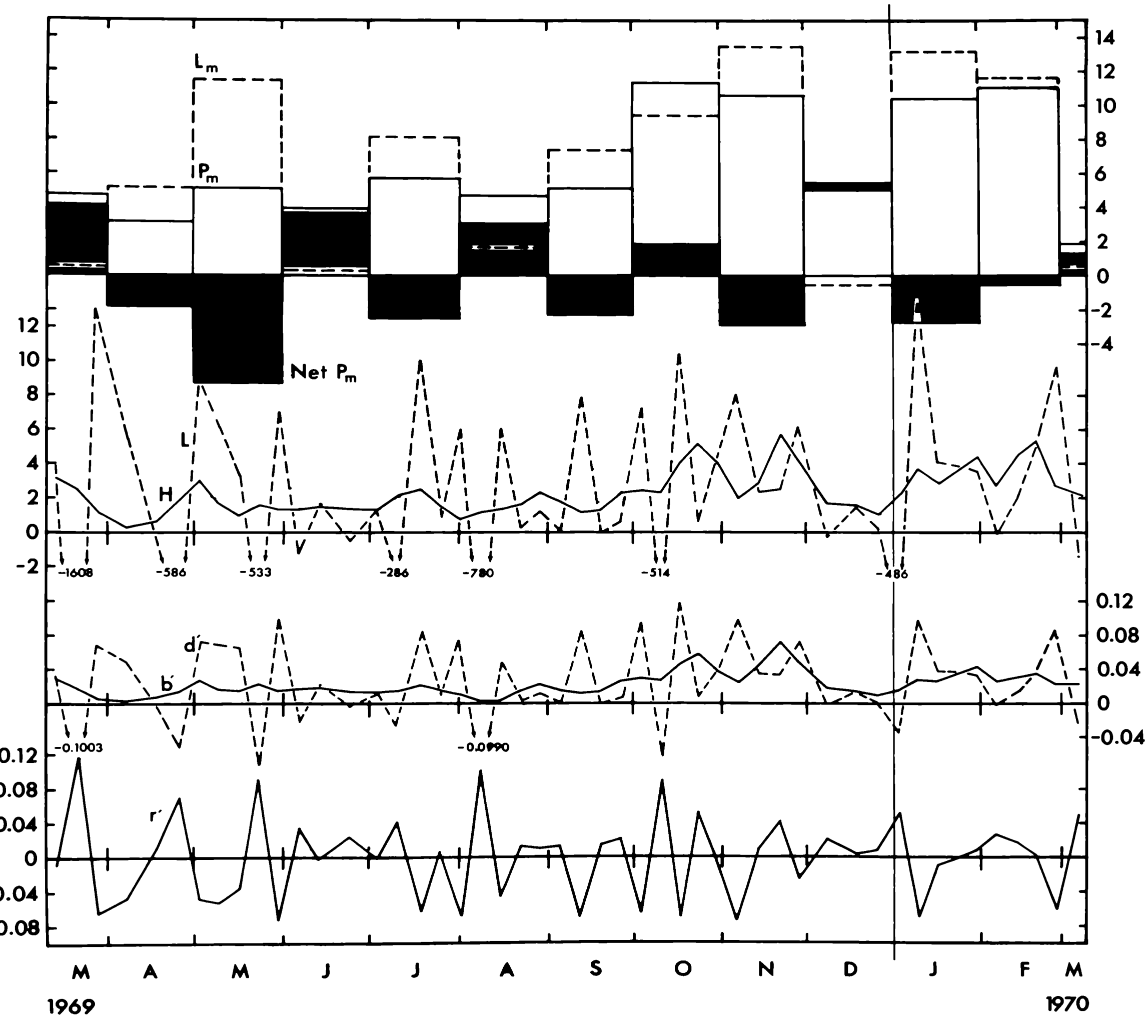
$$B = \frac{\bar{H}}{\bar{N}}$$

and the total population numbers on two consecutive sampling dates were used to calculate r' (table 32).

Mean egg hatching rates (H) and losses per day (L) for the total population and corresponding instantaneous birth and death rates are shown in fig. 30 . Using the values of H and L, estimates of total monthly egg production (P_m), total monthly loss (L_m) and net monthly production ($P_m - L_m$) have been calculated (table 32) and are also shown. Daily loss rates for the various growth stages throughout the sampling period are shown in fig. 32 . It can be seen that negative values for loss and death rates occurred on a number of occasions. This paradoxical situation results when the change in population size during a time interval is greater than the difference between numbers entering and leaving the population, and can result from sampling errors, errors in determination of breeding parameters or from the estimated development times being different from the true ones. When such negative values occurred they have merely been accepted at their face value.

Hatching rates remained rather constant from May to September, but increased to higher levels in October and November, and January and February. These increases were

Fig. 30: Parameters of egg production and total population losses in *Calamoecia lucasi* in Lake Ototoa. Upper histograms: monthly losses (dashed lines); net production (black histograms). The graphs are of: mean number of eggs hatching per day (H), losses per day (L); exponential birth and death rates (b', d'), and rates of population increase or decrease (r').



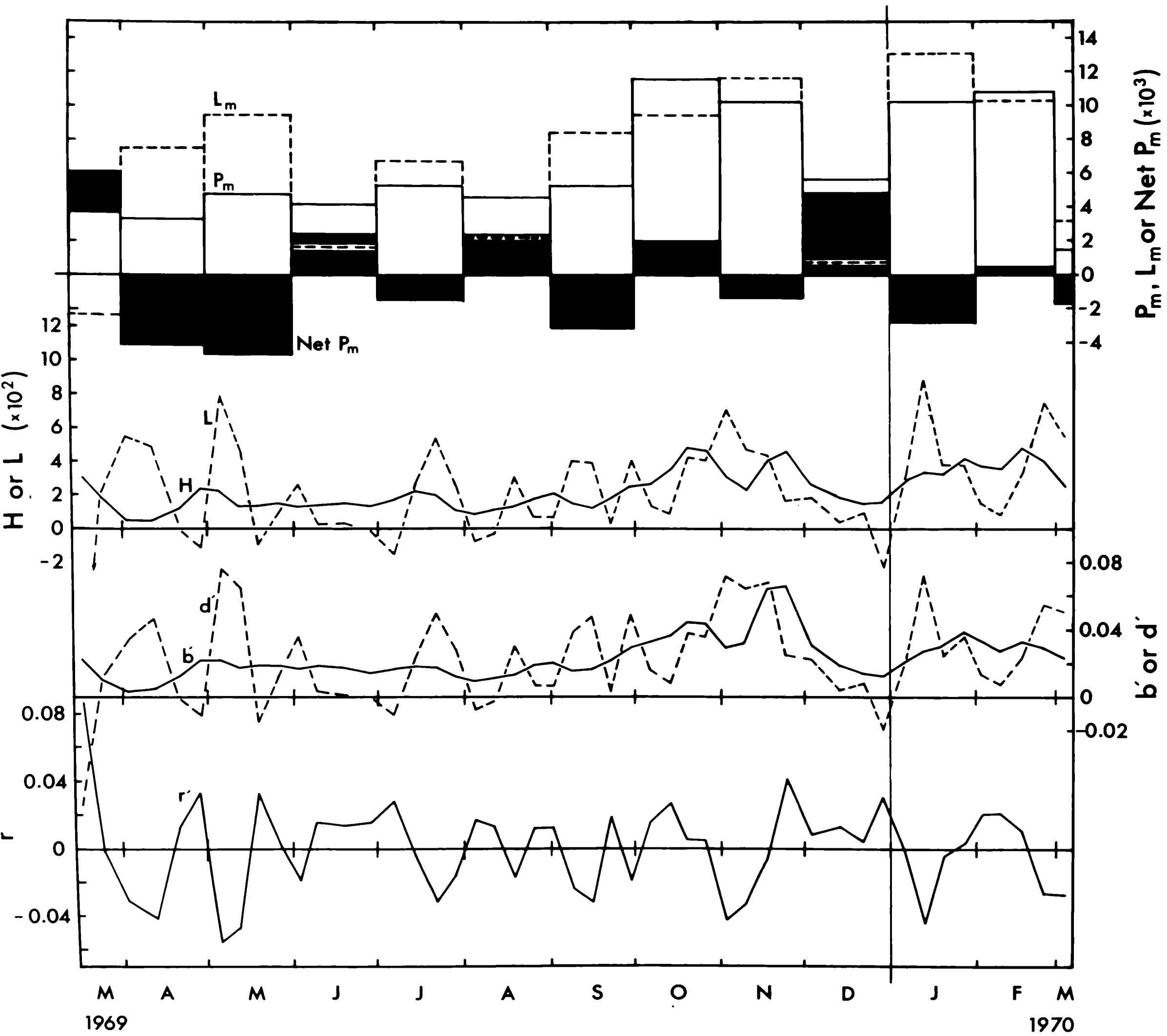
L_m
P_m
Net P_m
P_m, L_m or Net P_m ($\times 10^3$)
14
12
10
8
6
4
2
0
-2
-4
H or L ($\times 10^2$)
12
10
8
6
4
2
0
-2
L
H
V
-1608
-586
-533
-286
-780
-514
-486
d′
b′
b′ or d′
0.12
0.08
0.04
0
-0.04
-0.1003
-0.0990
r′
0.12
0.08
0.04
0
-0.04
-0.08
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

not very great however being to only about 3-4x the mean winter-early spring values. For most of the year changes in b' mirrored changes in H, and there were only slight differences arising from differences in population size at different times. Changes in hatching rates were largely dependant on variations in the percentage of ovigerous ♀♀ (percentage ovigerous ♀♀ and H are significantly correlated, $r = 0.564^{***}$, n = 50) and temperature had a less marked, but still significant effect ($r = 0.374^{**}$, n = 50), as Chapman (1972) has also found for *C. lucasi* in Lakes Rotorua and Rotoiti. There was also a significant negative correlation between mean hatching rate between samples and stock of ingestible phytoplankton on the first date ($r = -0.334^{*}$, n = 41) but the amount of ingestible phytoplankton is also significantly negatively correlated with temperature ($r = -0.397^{**}$, n = 41) and when this is taken into account by partial correlation analysis the correlation between H and ingestible phytoplankton is not significant (r = -0.218, n = 41, ns).

The curves of loss rates L and d' were also very similar and both varied considerably, generally fluctuating around the curves of H and b'. Periods when hatching rate were high were generally accompanied by higher losses, especially in spring and summer, and the only periods of consistently reduced losses were in June and December. The general features of the H, L, b', d' and also the r' curves are shown more clearly in fig. 31 where a two point moving average has been applied to the data in fig. 30 . These smoothed curves emphasis the way in which losses generally follow births, especially from July to November, and the more prolonged periods of excess of births over deaths in June, December and early February.

r' is an expression of population change; when r' is positive the population is increasing, when negative, decreasing. The curve of r' emphasises the constancy of the Ototoa population. It shows no clear seasonal trends and generally fluctuates around the zero line. The only periods when r' was positive for more than two consecutive intervals were during June and July, December and early February - times when, as noted above, losses were low rather than when births were particularly high. The longest periods of population decease were in autumn and early winter. Thus for most of the year in Lake Ototoa production of eggs was balanced by loss. There was little relationship between egg production and population size, the main determinant of which was loss, and throughout the year periods of posititive r' were always followed, within at most 2-3 weeks, by large increases in losses. Similarly, Chapman (1972) found that in Lakes Rotorua and Rotoiti egg production was generally balanced by losses and r' was never positive for long.

Fig. 31: Parameters of egg production and total population losses of *Calamoecia lucasi* in Lake Ototoa. The raw data used in preparing fig. 30 has been smoothed by averaging the values on successive dates, and the resulting figures have been plotted at the mid-point of the time interval. Abbreviations as in fig. 30.

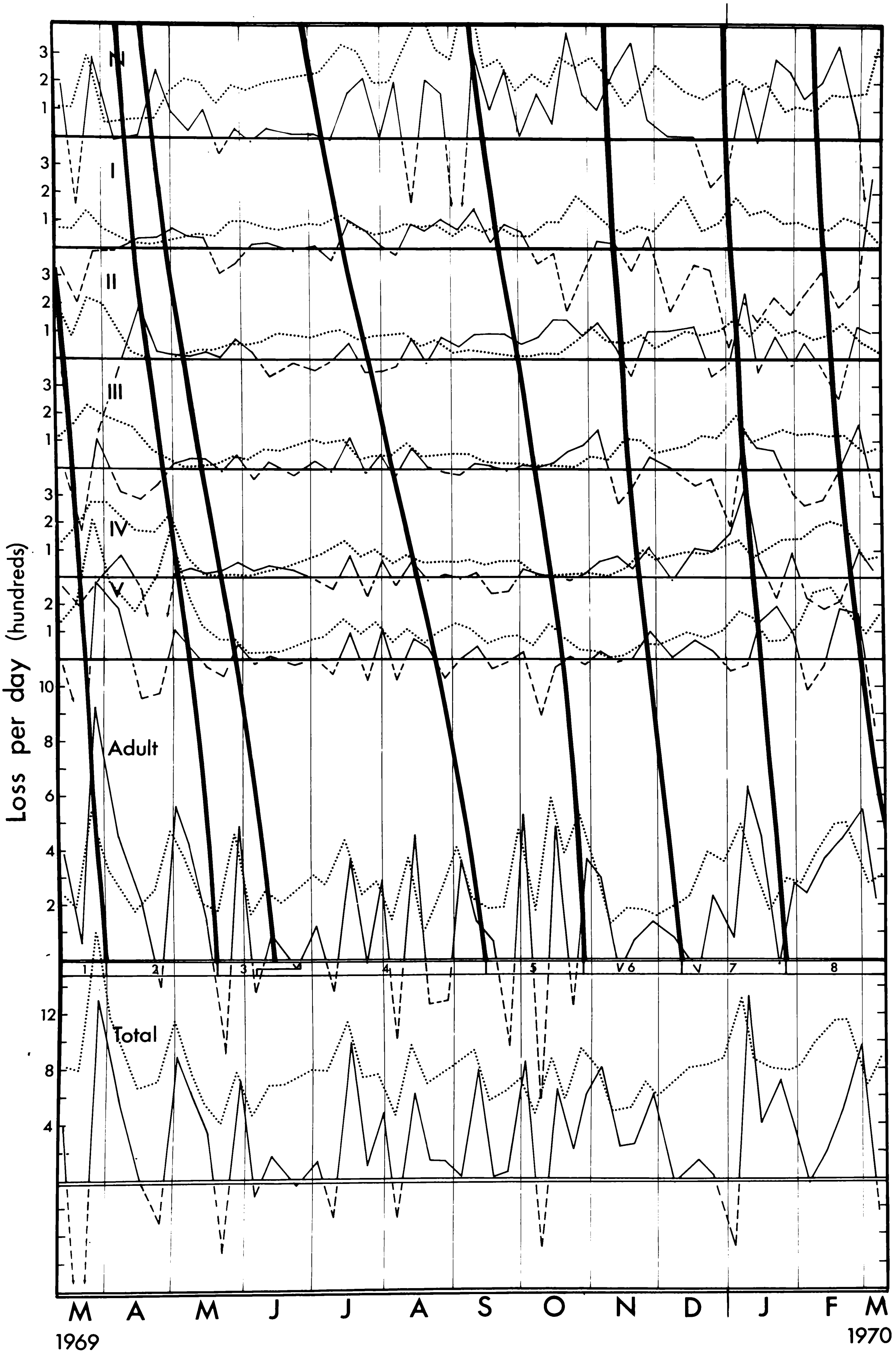

Lm
Pm
Net Pm
Pm, Lm or Net Pm (x10³)
14
12
10
8
6
4
2
0
-2
-4
H or L (x10²)
12
10
8
6
4
2
0
-2
L
H
d′
b′
b′ or d′
0.08
0.04
0
-0.02
r′
0.08
0.04
0
- 0.04
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

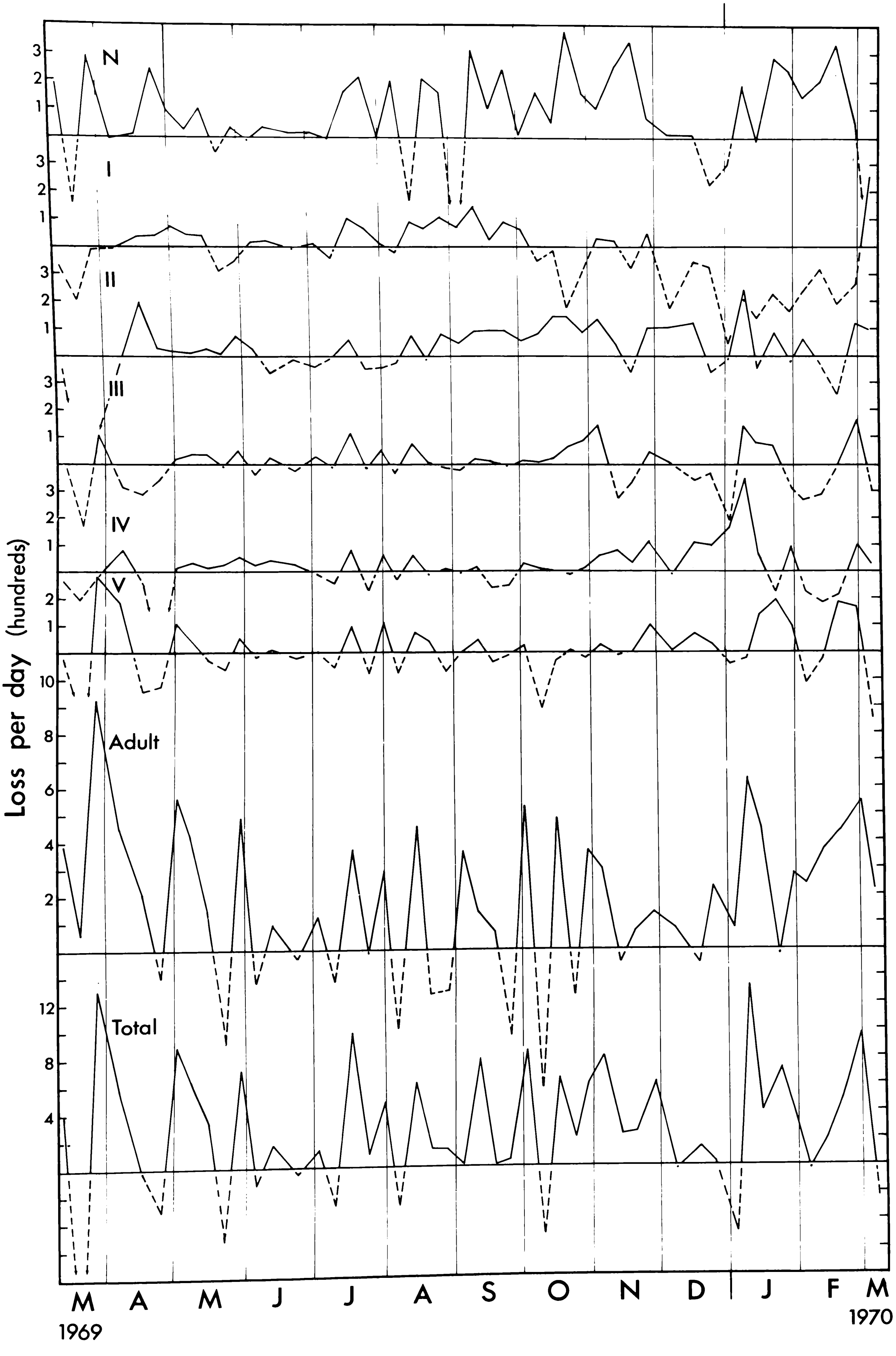
The histograms showing monthly egg production, loss and net production serve to emphasise these points. Although October, November, January and February were the months when the egg production was highest, net production was greatest in March, June and December because of lower losses in these months which were times of low egg production. The greatest negative net production was in May when losses greatly outweighed slight increases in egg production. In other months increased egg production was usually balanced by increased losses and net production was never greatly positive or negative in any one month, nor for more than one month in succession.

A figure for yearly net production can be obtained if the total yearly loss is subtracted from the total yearly egg production and expressed as the percentage of the total production which survived. Thus in Ototoa net production was 0.6% of total production which may be compared with the similar figure of -1.6% in Lake Rotorua and the considerably higher value of 16.8% for *C. lucasi* in Lake Rotoiti (Chapman loc. cit.). Also the seasonal patterns of egg production and total population loss in these two lakes are similar to that found in Lake Ototoa, except that the increase in egg production which occurred in October and November in Lake Ototoa was not until December, and this is presumably related to the more southerly latitude and slower rates of heating of these large lakes.

Loss rates in the various development stages are shown in fig. 32 which also relates the losses to the possible development sequences outlined above (p.100ff). The most noticeable feature of these data is that for much of the year most of the loss occurred in the adult stage and much less in the copepodites. In the copepodite stages, especially the later ones, loss per day generally fluctuated around the zero line, although values tended to be somewhat higher in summer and autumn. In the nauplii and copepodites I and II there was little loss early in the winter, but loss increased later in the winter and in spring and summer. During much of the late spring and summer the losses of CI were consistently negative, and this could be because either the development times used in the calculations of loss were incorrect, or because the naupliar population was undersampled. It was noted earlier that developmental group 6 may have undergone heavier mortality in spring than the groups preceding it or succeeding it, and in fig. 32 it can be seen that losses in the nauplii, CII, CIII and CIV were higher than in the other groups. Losses in the adults closely followed increases in adult standing stock and was higher in April and May (when the population was decreasing) and after the stock increases in December-January and February, while in the winter groups 4 and 5 loss generally fluctuated more.

Fig. 32: Losses per day in the developmental stages of *Calamoecia lucasi* in Lake Ototoa, and the sum of these losses. Seasonal changes in the numbers of the various developmental stages and of the total population, and the possible sequence of development groups (see fig. 21) are shown in the overlay.


N
I
II
III
IV
V
Adult
Total
Loss per day (hundreds)
3
2
1
10
8
6
4
2
12
8
4
1
2
3
4
5
V6
V
7
8
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970



N
I
II
III
IV
V
Adult
Total
1
2
3
4
6
8
10
12
Loss per day (hundreds)
M
A
M
J
J
A
S
O
N
D
J
F
M
1969
1970

The total losses in all the individual stages is also shown in fig. 32 and it is interesting that this curve is almost exactly the same as that for total losses calculated as L (fig. 30) and emphasises the way in which population increases are closely followed by increases in loss.

The total recruitment and loss for each development stage in each of the developmental groups has been found by determining the area under the appropriate regions of the daily loss curve (fig. 32) and the daily recruitment curves (not shown here) with a planimeter. The results of this analysis are shown in table 33 . An estimate of percentage survival (S) in each stage can be made as follows:

$$S = 100 \left(\frac{R - L}{R}\right)$$

where: R = total recruitment

L = total loss

In those cases where loss was negative, survival has been assumed to be 100%.

Survival in the naupliar (48-77%) and copepodite (15-100%) stages was generally high and for the year as a whole the overall survival of nauplii and copepodites was 90%. There was no trend for any of the copepodite stages to have higher percentage survival than the others, but the nauplii showed lower survival. However, the figures for their survival are of course a collective figure for the 6 naupliar stages, and if the losses for these could be calculated separately they would show a higher survival.

	NAUPLII.			COP. I.			COP. II.			COP. III.			COP. IV.			COP. V.			ADULTS.			
GROUP	R	L	%S	R	L	%S	R	L	%S	R	L	%S	R	L	%S	R	L	%S	R	L	%S	Average % Cop.+ Nauplii surviving
1	9725	2975	69	9475	-2350	100	6175	-175	100	6175	375	94	5925	-50	100	5275	-2625	100	9400	8275	12	94
2	4225	1300	69	4050	-1925	100	6625	-4375	100	11950	-2525	100	14625	-2550	100	17250	1625	91	13400	14925	-11	93
3	900	400	56	1025	625	39	800	650	19	600	175	71	500	425	15	550	-350	100	1300	900	31	50
4	11700	3475	70	8725	250	97	8400	250	97	8150	1475	82	6975	1300	81	5125	800	84	5950	7575	-27	85
5	11750	4150	65	10450	4500	57	6600	2625	60	3375	500	85	2875	75	97	3125	-1750	100	3750	925	75	77
6	16575	8600	48	9000	-1050	100	9875	4825	51	5225	1325	75	3925	1475	62	2250	400	82	2925	5650	-93	70
7	14450	3325	77	10700	-5450	100	16725	2375	86	14750	-1775	100	17025	6050	64	11550	1750	85	10325	9275	10	85
8	13525	5575	59	8950	-8400	100	17200	1375	92	16325	-1025	100	18050	-975	100	19250	3900	80	14300	13635	5	89
TOTAL	82850	29800	64	62375	-13800	100	72400	7550	90	66550	-1475	100	69900	5750	92	64375	3750	94	61350	61159	0.3	90

Table 33: Recruitment (R), loss (L) and the percentage of the recruitment surviving (%S), in the various developmental groups of *Calamoecia lucasi* in Lake Ototoa. The average % survival in the naupliar and copepodite stages is also shown. When loss was negative, survival has been assumed to be 100%.

An estimate of the average survival in each nauplius stage can be made using an approximate average recruitment $\bar{R}$:

$$\bar{R} = \frac{R + (R - L)}{2}$$

and for the yearly total this is 67950. Assuming that the total naupliar loss is spread evenly over all the naupliar stages then the survival in any one nauplius stage becomes:

$$S = 100\left(\frac{\bar{R} - L/6}{\bar{R}}\right)$$

and this value is 93%, which is very similar to the average survival of 95% in the copepodite stages throughout the year. Thus overall there seems to be relatively high and similar survival in all the immature stages and that as noted above most mortality occurs in the adult stage, in which the yearly percentage survival was only 0.3%. A very approximate estimate of the average amount of the egg production which survives to the adult was obtained by dividing the adult recruitment by the naupliar recruitment and the figure so obtained is 74%.

The pattern of survival was not the same in all of the developmental groups, however. Survival in the summer and autumn groups 1, 2, 7 and 8 was similar and high as it was in the two winter groups 4 and 5, although in these the average percentage survival was a little less than in the summer and autumn groups. However, groups 3 and 6 particularly the former, showed lower survival. Group 3 developed in the transition between autumn and winter, when the population as a whole was declining slightly, and developed when both temperature and numbers of ingestible phytoplankton were dropping. Survival was low particularly in the stages from nauplius to CIV but higher in the CVs and adults. In Lakes Rotorua and Rotoiti Chapman (1972) also found lowered survival in the autumn when the populations declined considerably. In Lake Ototoa, apart from the lower survival in group 3, at this time there were also large losses in the adults of group 2.

Group 6 on the other hand was developing during spring and early summer, when temperatures were increasing markedly, phytoplankton stocks were at low levels and other zooplankton species (especially *Bosmina meridionalis* and the rotifers) were increasing in numbers. As already noted mortality was relatively higher in the nauplii and copepodites II, III and IV of this group than in groups 4, 5, 7, 8 and 2. This slight decrease in survival in the spring animals was not found by Chapman (loc. cit.) in the Rotorua Lakes where there was higher survival in spring leading to a large population pulse at this time, a pattern not observed in Lake Ototoa.

It can be seen that recruitment was much higher in the summer and autumn groups than in the winter ones. However, this did not result in correspondingly greater stocks of the copepodites because the debit to the following stage increased in a complementary manner. Similarly, the adult stocks of the summer and autumn groups were not very much larger than in the winter ones because at most times losses balanced recruitment, except for short periods resulting in isolated stock peaks which were however immediately followed by increased losses.

Adult length of life:-

The average ecological longevities of the adults throughout the year are presented in table 34 and range between 1.1 and 76.9 days (mean 17.6 CV 90.5 %). There was no clear seasonal trend, but the greatest longevities were in the early autumn and in the late spring and early summer. The mean longevities of the various adult groups are also shown in table 34, and the spring, early summer and autumn groups (5, 6, 7 and 1) tended to have mean longevities greater than the others which may indicate more favourable conditions for the adults at these times. Although the mean ecological longevity was considerably lower than the lengths of life of many of the individuals reared in the laboratory (tables 30 and 31 pages 143-4) it is similar to estimates of 22.5 days for *Diaptomus vulgaris* in summer (Tonolli 1964), 11.5 days for *D. laciniatus* (Nauwerck 1963), ca 2 weeks for *D. gracilis* (Chapman 1969) and also ca 2 weeks for *Boeckella propinqua* (Green 1968).

DATE	Mean longevity in period (days)	Adult group	Mean longevity of group (days)	Population turnover time (T)
10.3.69	7.1			27.9
17.3.69	76.0	1	29.5	-
24.3.69	5.5			14.9
31.3.69	7.1			20.5
12.4.69	13.5			-
21.4.69	-			-
28.4.69	8.4	2	11.0	14.2
5.5.69	8.1			14.4
12.5.69	18.0			18.6
19.5.69	-			-
26.5.69	1.1	3	15.7	11.7
2.6.69	-			-
9.6.69	30.2			45.1
16.6.69	-			-
30.6.69	27.3			75.8
5.7.69	-			-
14.7.69	10.8			12.4
21.7.69	-			106.4
28.7.69	9.4	4	13.9	13.6
4.8.69	-			-
11.8.69	6.4			21.7
18.8.69	-			500.0
25.8.69	-			84.0
1.9.69	10.3			3333.3
8.9.69	19.4			12.3
15.9.69	40.3			-
22.9.69	-			181.8
29.9.69	7.2	5	19.6	10.8
6.10.69	-			-
13.10.69	11.3			8.9
19.10.69	-			142.9
26.10.69	13.6			24.8
2.11.69	9.8			10.6
9.11.69	-	6	21.4	29.2
17.11.69	33.8			31.8
24.11.69	17.0			14.1
30.11.69	32.8			-
14.12.69	-			71.4
22.12.69	18.7			384.6
29.12.69	61.5	7	23.6	-
6.1.70	7.4			10.6
12.1.70	6.9			27.0
19.1.70	-			27.1
27.1.70	12.4			29.4
2.2.70	16.1			-
9.2.70	13.4	8	13.1	71.9
17.2.70	12.8			29.7
23.2.70	8.2			12.3
3.3.70	15.5			-
9.3.70				

Table 34: Adult longevities of *Calamoecia lucasi* in Lake Ototoa, mean longevities of the various adult groups, and population turnover times (T) calculated as 1/D. (- indicates that losses were negative, and thus no longevity could be calculated).

Population turnover time.

The population turnover time, which gives an indication of the average duration of life of an individual in the population, may be calculated either as the reciprocal of the finite death rate D (Heinle 1966) where:

$$D = 1 - e^{-d'}$$

or as the reciprocal of the finite birth rate B (Cummins et al 1969). These values for the Ototoa population are shown in table 34 while the yearly average and those from Lakes Rotorua and Rotoiti (Chapman 1972) are shown in table 42 . There is little seasonal trend although the turnover times tend to be higher in winter and a little lower in spring when loss rates were higher. The values from Ototoa are somewhat greater than those of the more productive Lakes Rotorua and Rotoiti. An estimate of the population turnover rate, i.e. the number of times the population stock was replaced in the year, can be made by dividing the total annual egg production by the mean population size. The figure of 8.2 so obtained is considerably lower than values of 22.7 in Lake Rotorua and 18.3 in Lake Rotoiti (Chapman loc. cit.).

3. Production:

Production may be defined as "the increase in biomass which occurs in a given period of time, whether or not all of it survives to the end of that period" (Mann 1969) and in a population, increase in biomass is a result of growth by the individuals of different ages making up the population. At any one time each of the constituent age groups will have a characteristic absolute daily growth rate and numerical abundance, and in calculating production such differences in growth rate and numbers with age must be taken into account. This may be done by graphical methods of computation (Winberg 1971). In this study the mean production of *Calamoecia lucasi* for each month was determined by the graphical method of Winberg, Pechen and Shushkina (1965), in which changes in absolute daily growth increment and numbers with age are graphed and the production then found by multiplication of these curves. As an example, the curves used for calculating production in July are shown in fig. 33 .

To obtain the survival curve of individuals ($\bar{N}/\bar{D}$) the monthly mean numbers of each stage were divided by the mean development time in that month (fig. 20) to give the average number of individuals present in each day of their life; and these points were plotted in the centre point of the development time of that stage.

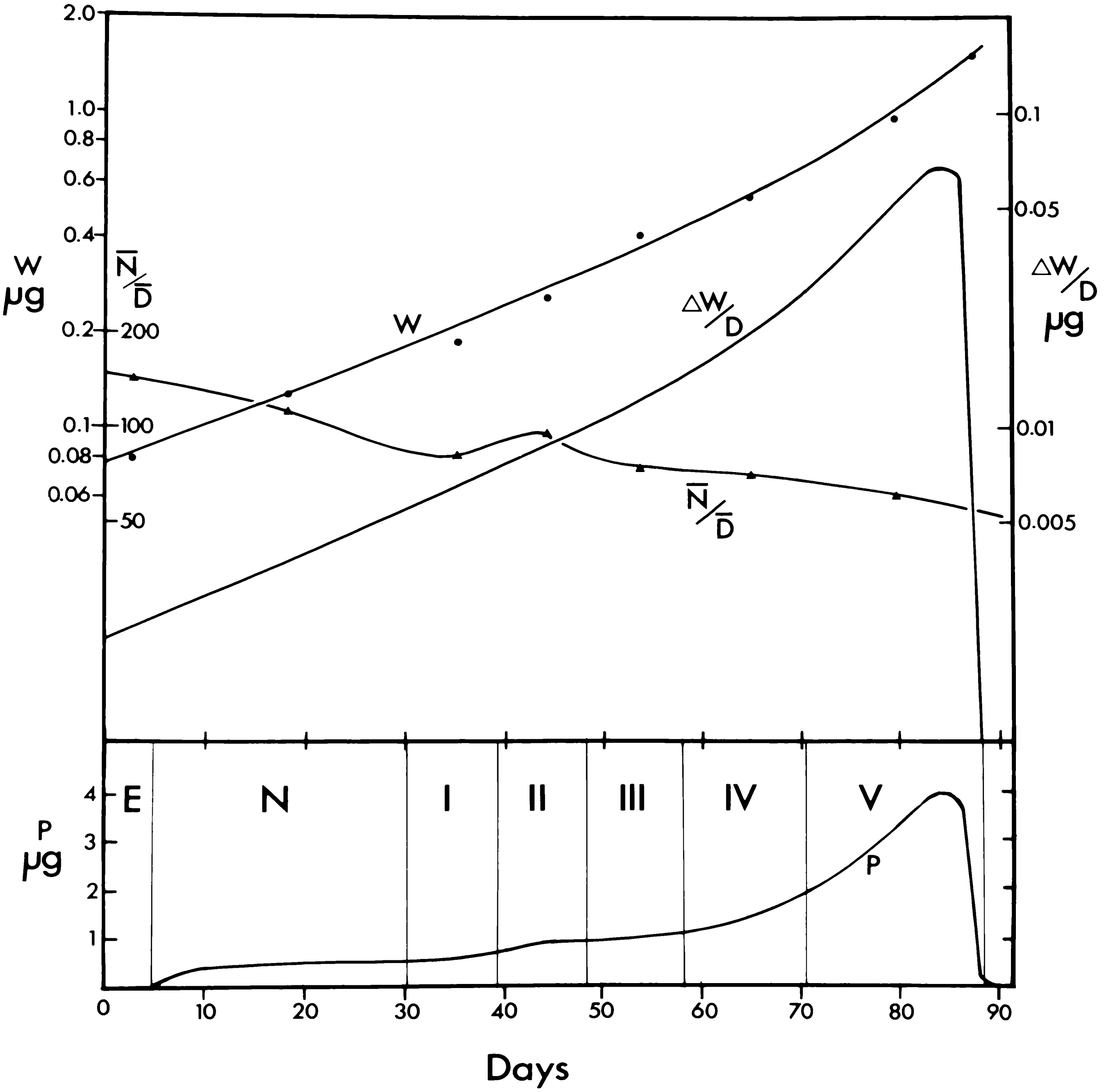
Fig. 33: The series of curves used in calculating the production of *Calamoecia lucasi* in Lake Ototoa in July.

W = daily individual growth curve.

ΔW = daily absolute weight increment.

$\bar{N}/\bar{D}$ = survivorship curve (number of the different age classes in the population).

P = daily production of the different age classes.



W μg
2.0
1.0
0.8
0.6
0.4
0.2
0.1
0.08
0.06
N̄/D̄
200
100
50
W
ΔW/D
N̄/D̄
ΔW/D μg
0.1
0.05
0.01
0.005
P μg
4
3
2
1
E
N
I
II
III
IV
V
P
0
10
20
30
40
50
60
70
80
90
Days

Using the data presented in fig. 23, the weight of each stage on each sampling date was estimated, and these figures were then used to calculate a mean monthly weight for each stage. This mean weight was then plotted in the middle point of the stage's development time,* and the points joined to give the daily growth curve (W) from which a curve showing the daily weight increment of individuals of different ages ($\Delta W/D$) was obtained. This curve of daily weight increments was then multiplied by the survival curve to give the daily production curve (P). The daily production curve was plotted on millimeter graph paper, but it was found more convenient to plot the survival, growth and weight increment curves on semi-logarithmic graph paper. The total production of all the immature individuals in the population, and of the various growth stages separately, was then found by integrating the area under the whole production curve, or the respective parts of it, with a planimeter. To this mean daily figure for naupliar and copepodite production was added the monthly mean daily production of eggs by the adults ($\bar{P}_e$):

$$\bar{P}_e = \bar{H} . \bar{w}_e$$

where : $\bar{H}$ = average monthly egg hatching rate

$\bar{w}_e$ = average monthly egg weight

and the total monthly production was found by multiplying the total daily production of all stages by the number of days in the month.

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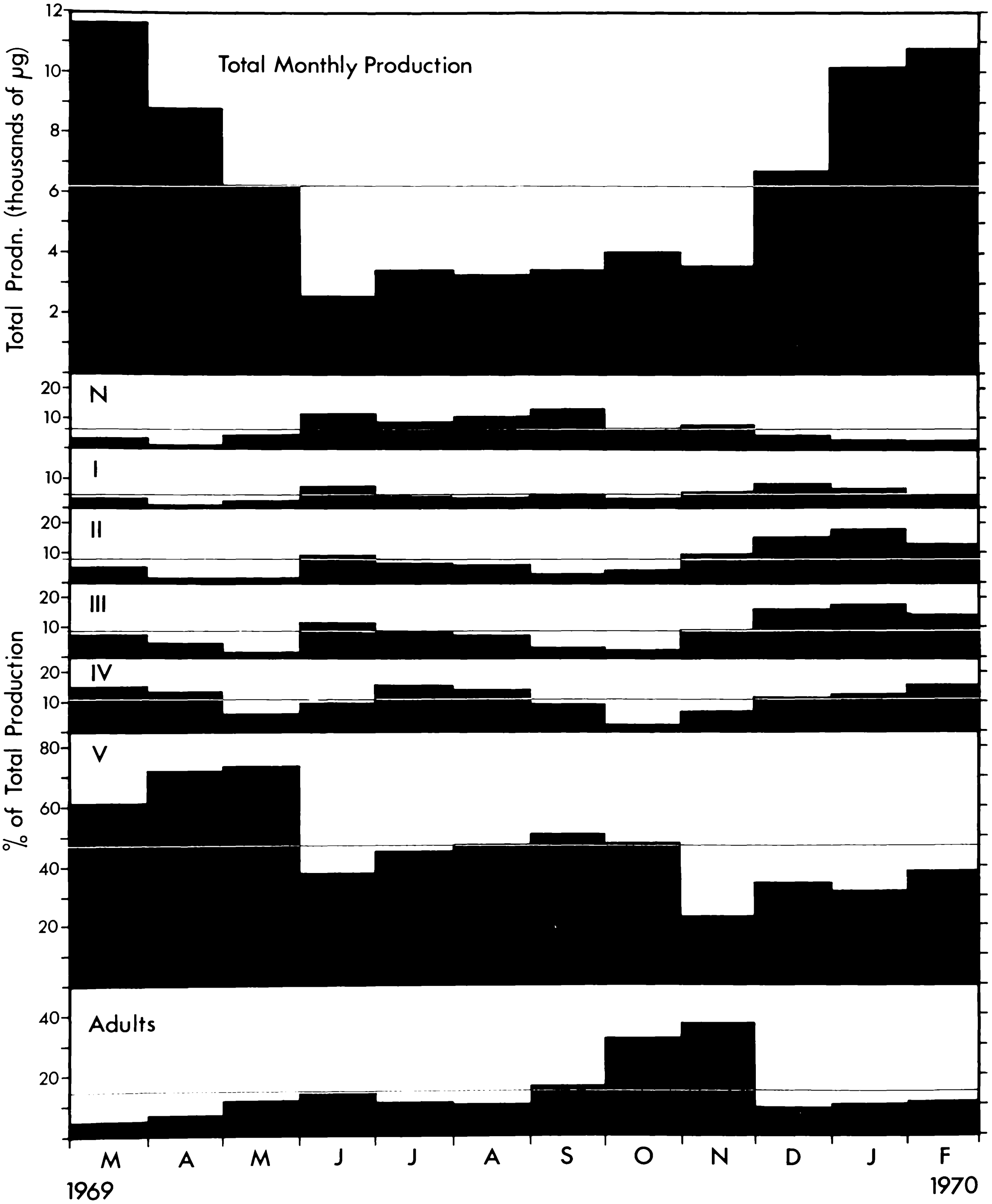
* This procedure is slightly different from that described by Winberg et al (1965) who use initial and final weights of a stage rather than the mean weight and introduces a slight error. As growth is parabolic the mean weight, of a stage determined from a random sample of individuals will in reality be applicable to an age a little greater than at the mid-point of the stage's development time, and thus should more accurately be plotted at this later time. However, the error is probably not great since the mean weights of each individual copepodite stage were used in the present study rather than those of the general categories of nauplii, copepodites, and adults that Winberg et al used.

Total production for each month calculated in this way is shown in fig. 34 and table 35 , where the average monthly population biomass (calculated by multiplying the mean monthly weight of a stage by its monthly mean numbers), daily, monthly and yearly P/B ratios, and biomass turnover times (B/P) are also presented. Some figures for the production of *C. lucasi* in Lake Rotorua have been calculated by Chapman (pers. comm.) and are given in table 36 for comparison with the Ototoa values. Monthly production, biomass and P/B ratios for the various developmental stages in Lake Ototoa are given in table 37 , and in table 38 comparative figures for Lake Rotorua are shown. Fig. 34 shows the monthly production of each stage in Lake Ototoa as a percentage of the total production, and biomass turnover times for the developmental stages in Lakes Ototoa and Rotoiti are presented in tables 39 and 40 respectively.

(a) Total Production:- Total production showed a clear seasonal trend with low, but slightly increasing values from June to November, followed by large increases during the summer (fig. 34 table 35). Maximum monthly production was in March 1969 but during the autumn production fell away rapidly to the June minimum. The period of rather low constant production in the winter and spring months was

Fig. 34: Total monthly production of organic matter by the population of *Calamoecia lucasi* in Lake Ototoa, and the % of the total produced by each development stage throughout the sampling period. Annual mean values are shown by horizontal lines.



Total Monthly Production
Total Prodn. (thousands of μg)
12
10
8
6
4
2
N
20
10
I
10
II
20
10
III
20
10
IV
20
10
V
80
60
40
20
Adults
40
20
% of Total Production
M
A
M
J
J
A
S
O
N
D
J
F
1969
1970

	PRODUCTION		MEAN BIOMASS	P/B RATIOS		B/P
Month	µg/day	µg/month	µg	daily	monthly	days
March	376.6	11675	7634	0.049	1.53	20.4
April	293.5	8805	7144	0.041	1.23	24.4
May	200.8	6225	6150	0.033	1.01	30.3
June	84.8	2544	5983	0.014	0.43	71.4
July	110.5	3426	7994	0.014	0.43	71.4
August	105.8	3280	7267	0.015	0.45	66.7
September	113.6	3408	5816	0.020	0.59	50.0
October	130.2	4036	6423	0.020	0.63	50.0
November	118.9	3567	4678	0.025	0.76	40.0
December	218.5	6774	5880	0.037	1.15	27.0
January	327.5	10153	6664	0.049	1.52	20.4
February	384.7	10772	8016	0.048	1.34	20.8
TOTAL		74665				
MEANS	205.5	6222	6637	0.030	0.92	41.1

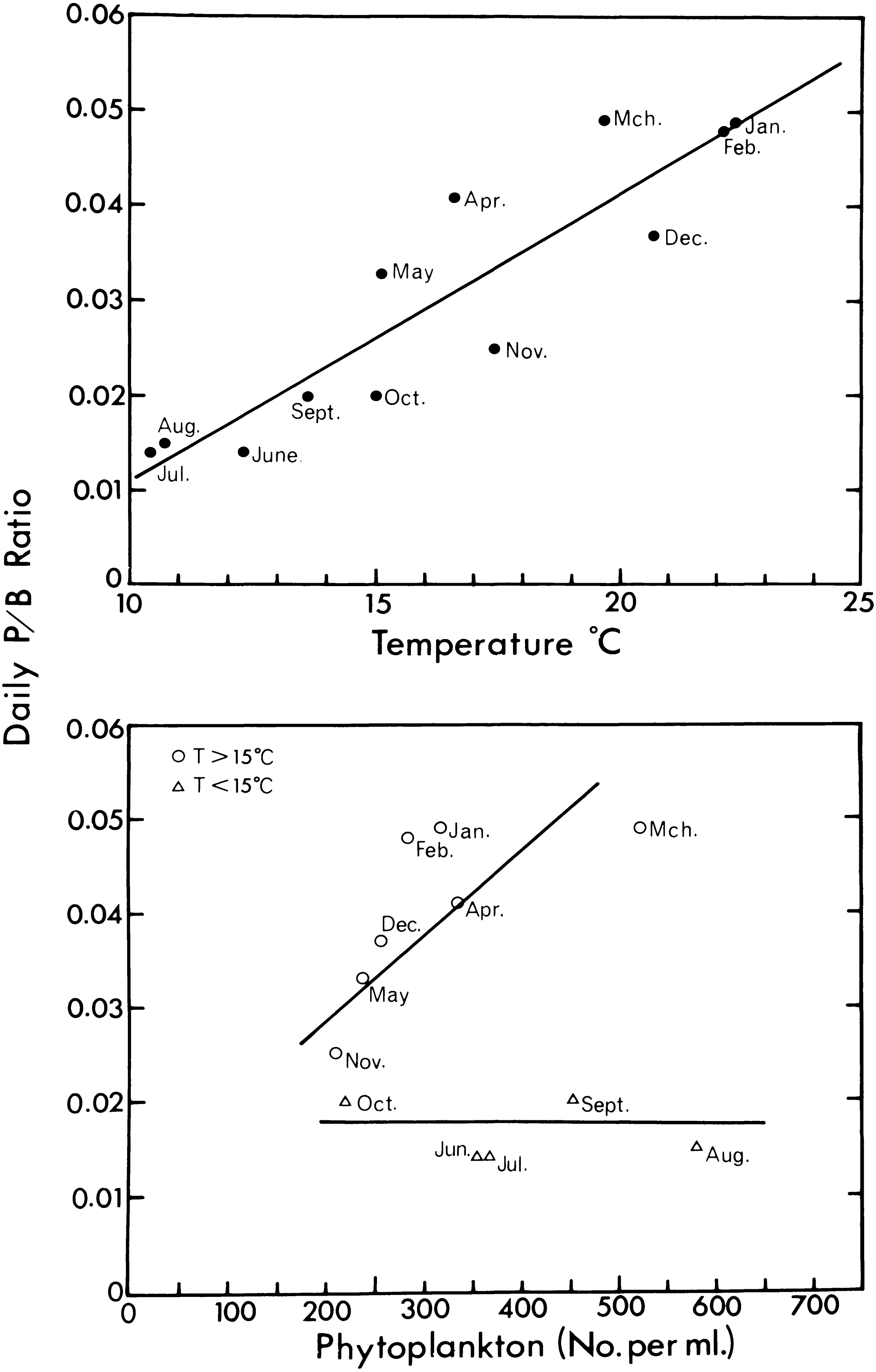
$$\text{Yearly P/B} = \frac{74665}{6637} = 11.25$$

Table 35 : Average monthly production, biomass, P/B ratios and turnover time of the biomass (B/P) of the total population of *Calamoecia lucasi* in Lake Ototoa.

associated with developmental groups 4 - 6, while the period of greater production during the summer and autumn was associated with groups 7, 8, 1, 2 and 3. Total biomass was highest in autumn and midwinter with lower values in early winter and spring, but on the whole biomass did not vary greatly. The P/B ratios showed seasonal trends similar to those of production, being low in winter and increasing to higher values in summer and autumn.

P/B ratios indicate the efficiency with which organic matter is produced by the population and can be considered a specific growth rate with the dimensions gm. gm^{-1}. day^{-1} if the daily P/B is used. Thus the trend in the P/B ratios indicates that the specific growth rate of the population increased gradually from winter to summer and decreased again in the autumn. Specific growth rate might be expected to be dependant on temperature and food availability, and there is a significant positive correlation between daily P/B and mean monthly temperature (fig. 35) ;($r = 0.904^{***}$ 10 df). The relationship between P/B and ingestible phytoplankton is less clear however, but it can be seen from fig. 35 that while increases in monthly mean phytoplankton numbers gave no apparent increase in daily P/B in months when the temperature was below about 15°C, in months when temperature was higher than this there was an apparent positive relationship. The results thus indicate that whilst above 15°C specific

Fig. 35: The relationship between monthly P/B ratios of *Calamoecia lucasi* in Lake Ototoa, mean monthly temperatures and mean monthly numbers of ingestible phytoplankton. In the upper panel a fitted regression line is shown, and in the lower panel the two lines shown have been included to guide the eye to possible relationships.


Daily P/B Ratio
0.06
0.05
0.04
0.03
0.02
0.01
0
10
15
20
25
Temperature °C
Mch.
Jan.
Feb.
Apr.
Dec.
May
Nov.
Oct.
Sept.
Aug.
Jul.
June
0.06
0.05
0.04
0.03
0.02
0.01
0
○ T > 15°C
△ T < 15°C
Jan.
Feb.
Mch.
Apr.
Dec.
May
Nov.
Oct.
Sept.
Jun.
Jul.
Aug.
0
100
200
300
400
500
600
700
Phytoplankton (No. per ml.)

growth rate appears to be influenced both by temperature and food levels, below 15°C growth rate is influenced by temperature alone. This may mean that below ca 15°C the relationship between feeding rate, assimilation efficiency and the various components of the metabolic rate are such that the animals are unable to utilise increased food levels in the environment to produce more organic matter. It would clearly be of interest to investigate these relationships in more detail, by considering the production in smaller time intervals than the monthly ones used here in conjunction with studies on feeding and metabolic rates.

The mean turnover time of the biomass of the total population was 41.1 days if the monthly turnover times are averaged (table 35) or 33.3 days if the reciprocal of the yearly mean daily P/B is used. It thus appears that on the average the biomass is replaced in a little over a month (although in midwinter the time is ca 2 months and in summer ca 0.6 months) and this is in accord with the yearly P/B ratio of 11.25 (table 35).

Production and biomass were much higher in Lake Rotorua than in Lake Ototoa in the summer (table 36) although during June the values were more similar. The most interesting feature of this data however is the close correspondance between the P/B ratios and biomass turnover times in two lakes. This is rather surprising since Lake Rotorua is considerably more eutrophic than Lake Ototoa,

	PRODUCTION				BIOMASS		P/B RATIOS				TURNOVER TIME OF BIOMASS (B/P)	
	µg/day		µg/month		µg		Daily		Monthly		Days	
	O	R	O	R	O	R	O	R	O	R	O	R
June	84.8	89.6	2544	2688	5983	6829	0.014	0.013	0.43	0.39	71.4	76.9
Oct.	130.2	169.9	4036	5267	6423	6413	0.020	0.026	0.63	0.82	50.0	38.5
Nov.	118.9	248.0	3567	7440	4678	9474	0.025	0.026	0.76	0.79	40.0	38.5
Dec.	218.5	345.5	6774	10711	5880	9131	0.037	0.038	1.15	1.17	27.0	26.3
Jan.	327.5	724.0	10153	22444	6664	14792	0.049	0.049	1.52	1.52	20.4	20.4
MEAN	176.0	315.0	5415	9710	5926	9328	0.029	0.030	0.90	0.94	41.8	40.1

Table 36 : A comparison of production, biomass, P/B ratios and biomass turnover times of the total populations of *Calamoecia lucasi* in Lakes Ototoa (O) and Rotorua (R). The Rotorua data is for 1968 and is from Chapman (pers. comm.)

and it is usually stated that P/B ratios tend to be higher in lakes of higher trophic status (e.g. Shuskina 1966). The close similarity between the P/B ratios may suggest that factors affecting the total amount of organic matter produced by the populations are similar in both lakes.

(b) Production in the Developmental Stages:- the seasonal pattern of changes in production and biomass of the nauplii (table 37) were rather different from those in the rest of the population. Naupliar production increased gradually from the seasonal minimum in April to the maximum in September, then decreased and remained rather constant from October to March. Biomass increased slowly to a maximum in September and October and then gradually declined again during the spring and summer.

In all the copepodite stages there were large summer increases in production, associated with groups 7 and 8, between November and March 1970 and rapid declines between March and May 1969. However, between July and September, along with the development of groups 4 and 5, production increased, leading to increases in biomass in these months and also to the higher female weights noted above (p 107). During September and October, the months when group 6 was developing, here were declines in the production of copepodites II - IV associated with decreases in biomass. Group 6 suffered greater relative mortality than the groups

		MARCH	APRIL	MAY	JUNE	JULY	AUGUST	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.	MEAN
	P	12.5	3.0	8.5	10.0	9.8	11.5	15.8	9.0	10.0	9.5	9.5	10.5	10.0
NAUPLII	%	3.2	1.0	4.2	11.5	8.7	10.4	13.0	6.5	7.9	4.2	2.9	2.7	6.4
	B	190	169	308	282	367	383	416	406	354	293	216	171	296
	P/B	0.066	0.018	0.028	0.035	0.027	0.030	0.038	0.022	0.028	0.032	0.044	0.061	0.036
	P	12.5	2.3	4.5	6.3	4.5	4.3	5.8	5.0	7.5	19.0	22.5	17.0	9.3
CI	%	3.2	0.8	2.2	7.2	4.0	3.9	4.8	3.6	5.9	8.4	6.8	4.4	4.6
	B	150	55	121	169	144	140	136	185	170	196	199	155	148
	P/B	0.083	0.042	0.037	0.037	0.031	0.031	0.043	0.027	0.044	0.097	0.113	0.110	0.058
	P	20.0	3.5	2.5	8.0	7.5	6.8	3.8	6.0	12.5	35.0	60.0	50.5	18.0
	%	5.1	1.2	1.2	9.2	6.7	6.1	3.1	4.3	9.9	15.4	18.0	13.0	7.8
CII	B	414	107	79	199	223	177	72	98	166	236	274	223	189
	P/B	0.048	0.033	0.032	0.040	0.034	0.038	0.053	0.061	0.075	0.148	0.219	0.226	0.084
	P	30.0	13.8	3.5	10.0	9.8	8.3	4.0	4.0	12.0	36.5	59.0	57.5	20.7
CIII	%	7.6	4.8	1.7	11.5	8.7	7.5	3.3	2.9	9.5	16.1	17.7	14.8	8.8
	B	416	245	69	249	308	220	113	52	207	450	540	509	282
	P/B	0.072	0.056	0.051	0.040	0.032	0.038	0.035	0.077	0.058	0.081	0.109	0.113	0.064
	P	58.8	38.8	12.0	8.0	17.8	15.8	10.5	3.5	9.0	26.7	41.0	60.5	25.2
CIV	%	15.0	13.5	5.9	9.2	15.8	14.2	8.6	2.5	7.1	11.8	12.3	15.6	11.0
	B	759	692	236	198	501	351	221	80	176	484	627	865	433
	P/B	0.078	0.056	0.051	0.040	0.036	0.045	0.048	0.044	0.051	0.055	0.065	0.070	0.053
	P	240.0	206.3	149.0	33.0	50.8	52.5	62.0	66.5	29.0	79.0	106.0	149.5	102.0
CV	%	61.1	71.8	73.5	37.8	45.2	47.3	51.0	47.8	22.9	34.8	31.9	38.5	47.0
	B	1466	1621	1077	406	1017	1114	746	448	231	673	890	1405	925
	P/B	0.164	0.127	0.138	0.081	0.050	0.047	0.083	0.148	0.126	0.117	0.119	0.106	0.109
	P	19.1	19.7	22.8	12.0	12.3	11.8	19.6	45.2	46.9	21.0	34.5	42.7	25.6
ADULTS	%	4.9	6.9	11.2	13.7	10.9	10.6	16.1	32.5	37.0	9.3	10.4	11.0	14.5
	B	4201	4204	4187	4429	5368	4821	4039	5013	3253	3509	3861	4620	4292
	P/B	0.005	0.005	0.005	0.003	0.002	0.002	0.005	0.009	0.013	0.006	0.009	0.009	0.006

Table 37 : Mean daily production (P), daily production as a percentage of total daily production (%), average biomass (B) and daily P/B ratios for the various growth stages of *Calamoecia lucasi* in Lake Ototoa. Production and biomass are stated in μg per standard sample .

preceding it (table 33) and this may have been the cause of the lowered reproduction. In CV however production increased in September and October, and these increases were followed by the main period of adult production during October and November. Production by the adults increased again in the summer, but during the rest of the sampling period was much lower.

Except during November when adult production was at a maximum, by far the greater part of the total production occurred in copepodite V (fig. 34), the yearly average being 47.0% ranging between 22.9% and 73.5% of the total (table 37). It is possible that the sudden increase in production between CIV and CV was due to the rapid deposition of gonadal material in CV, which was then utilised for egg production in the adult. The way in which the main period of adult production followed increases in CV production between September and October may be an example of such utilisation of previously laid down biomass.

The yearly average percentage of the total production contributed by each stage increased between CI and CV (table 37) and the proportion produced by CI, II, III and IV was greater between June and August, and November and March, than between April-May and September-October (fig. 34) although the seasonal variation was not great. In contrast the percentage of the total production occurring in the nauplius was greatest in winter and spring and lower in summer and autumn.

P/B ratios of the nauplii and CI - IV followed the same seasonal trends as P/B of the total population, being lower in winter and increasing to higher values in summer and autumn. In CV and the adults there was also a decline to lower values between March and August and an increase in September and October, but during the summer daily P/B dropped slightly. Daily P/B ratios were highest in CV reflecting the rapid growth rate in this stage and very low in the adults because of the low rate of egg production. It is also interesting to note that the mean P/B of CII was higher than either those of nauplii and CI or CIII and CIV, although it is not clear for what reason.

Table 38 shows that in Lake Rotorua the production of the individual stages was also higher in summer, and emphasises the much higher summer biomasses in Rotorua. In Lake Rotorua CV contributed a smaller percentage of the production than in Lake Ototoa, but the adults more, and this is also shown in the P/B ratios - the adult ratios for instance, being greater in Rotorua than in Ototoa. The P/B ratios in CI - IV were more comparable in the two lakes, but the naupliar P/B was much lower in Lake Rotorua. This was because naupliar biomass, but not production, was much higher in Lake Rotorua and it is possible that because of the great production of eggs by the

		JUNE		OCTOBER		NOVEMBER		DECEMBER		JANUARY		MEANS	
		O	R	O	R	O	R	O	R	O	R	O	R
NAUPLII	P	10.0	4.4	9.0	12.3	10.0	10.6	9.5	21.3	9.5	32.5	9.6	16.2
	%	11.5	4.8	6.5	8.4	7.9	4.2	4.2	6.0	2.9	4.4	6.6	5.6
	B	282	942	406	2158	354	1447	293	1547	216	1787	310	1576
	P/B	0.035	0.005	0.022	0.006	0.028	0.007	0.032	0.014	0.044	0.018	0.032	0.010
C I	P	6.3	4.4	5.0	5.3	7.5	3.1	19.0	11.3	22.5	31.3	12.1	11.1
	%	7.2	4.8	3.6	3.6	5.9	1.2	8.4	3.2	6.8	4.2	6.4	3.4
	B	169	135	185	113	170	59	196	203	199	443	184	191
	P/B	0.037	0.033	0.027	0.047	0.044	0.053	0.097	0.056	0.113	0.071	0.064	0.052
C II	P	8.0	10.1	6.0	12,8	12.5	8.8	35.0	18.8	60.0	62.5	24.3	22.6
	%	9.2	10.9	4.3	8.7	9.9	3.5	15.4	5.3	18.0	8.4	11.4	7.4
	B	199	204	98	211	166	77	236	289	274	509	195	258
	P/B	0.040	0.050	0.061	0.060	0.075	0.114	0.148	0.065	0.219	0.123	0.109	0.082
C III	P	10.0	10.5	4.0	12.5	12.0	3.5	36.5	33.8	59.0	62.5	24.3	24.6
	%	11.5	11.4	2.9	8.5	9.5	1.4	16.1	9.6	17.7	8.4	11.5	7.9
	B	249	323	52	303	207	47	450	277	540	674	300	325
	P/B	0.040	0.033	0.077	0.041	0.058	0.074	0.081	0.122	0.109	0.093	0.073	0.073
C IV	P	8.0	11.6	3.5	15.0	9.0	16.3	26.7	18.1	41.0	60.0	17.6	24.2
	%	9.2	12.5	2.5	10.2	7.1	6.4	11.8	5.1	12.3	8.1	8.6	8.5
	B	198	428	80	480	176	323	484	296	627	790	313	463
	P/B	0.040	0.027	0.044	0.031	0.051	0.050	0.055	0.061	0.065	0.076	0.051	0.049
C V	P	33.0	22.4	66.5	17.4	29.0	66.9	79.0	29.4	106.0	235.0	62.7	74.2
	%	37.8	24.2	47.8	11.9	22.9	26.3	34.8	8.3	31.9	31.8	35.0	20.5
	B	406	540	448	866	231	833	673	363	890	1835	548	887
	P/B	0.081	0.041	0.148	0.020	0.126	0.080	0.117	0.081	0.119	0.128	0.118	0.070
ADULTS	P	12.0	29.1	45.2	71.2	46.9	145.0	21.0	220.5	34.5	256.0	31.9	144.4
	%	13.7	31.5	32.5	48.6	37.0	57.0	9.3	62.4	10.4	34.6	20.6	46.8
	B	4429	4103	5013	1975	3253	6213	3509	5595	3861	8240	4013	5225
	P/B	0.003	0.007	0.009	0.035	0.013	0.023	0.006	0.039	0.009	0.031	0.008	0.027

Table 38: A comparison of daily production (P), daily production as a % of total daily production (%), average biomass (B) and daily P/B ratios for the various growth stages of *Calamoecia lucasi* in Lakes Ototoa (O) and Rotorua (R). The data for Rotorua refer to 1968 and are from Chapman (pers.comm.). Production and biomass are stated in µg per standard sample.

Month	N	CI	CII	CIII	CIV	CV	AD
March	15.2	12.0	20.8	13.9	12.8	6.1	200.0
April	55.6	23.8	30.3	17.9	17.9	7.9	200.0
May	35.7	27.0	31.3	19.6	19.6	7.2	200.0
June	28.6	27.0	25.0	25.0	25.0	12.3	333.3
July	37.0	32.3	29.4	31.3	27.8	20.0	500.0
August	33.3	32.3	26.3	26.3	22.2	21.3	500.0
September	26.3	23.3	18.9	28.6	20.8	12.0	200.0
October	45.5	37.0	16.4	13.0	22.7	6.8	111.1
November	35.7	22.7	13.3	17.2	19.6	7.9	76.9
December	31.3	10.3	6.8	12.3	18.2	8.5	166.7
January	22.7	8.8	4.6	9.2	15.4	8.4	111.1
February	16.4	9.1	4.4	8.8	14.3	9.4	111.1
MEAN	31.9	22.1	19.0	18.6	19.7	10.7	225.9

Table 39 : Turnover times (B/P) of the biomass in the developmental stages of *Calamoecia lucasi* from Lake Ototoa

	N		CI		CII		CIII		CIV		CV		AD	
	O	R	O	R	O	R	O	R	O	R	O	R	O	R
June	28.6	200.0	27.0	30.3	25.0	20.0	25.0	30.3	25.0	37.0.	12.3	24.4	333.3	142.9
Oct.	45.5	166.7	37.0	21.3	16.4	16.7	13.0	24.4	22.7	32.3	6.8	50.0	111.1	28.6
Nov.	35.7	142.9	22.7	18.9	13.3	8.8	17.2	13.5	19.6	20.0	7.9	12.5	76.9	43.5
Dec.	31.3	71.4	10.3	17.9	6.8	15.4	12.3	8.2	18.2	16.4	8.5	12.3	166.7	25.6
Jan.	22.7	55.6	8.8	14.1	4.6	8.1	9.2	10.8	15.4	13.2	8.4	7.8	111.1	32.3
MEAN	32.8	127.3	21.2	20.5	13.2	13.8	15.3	17.4	20.2	23.8	8.8	21.4	159.8	54.6

Table 40 : A comparison of turnover times (B/P) of the biomass of the various development stages of *Calamoecia lucasi* in Lakes Ototoa(O) and Rotorua (R). The data from Lake Rotorua are for 1968 and are from Chapman (pers.comm.)

Rotorua adults, competition for food in the resulting large naupliar population may have been more intense than in Lake Ototoa, thus allowing proportionately less production.

Turnover times of the biomass (table 39), which give an estimate of the time necessary for a particular stage to produce material equivalent to its mean biomass, were greatest in the colder months as might be expected. The yearly mean times for CI - CIV were rather similar, and higher than for CV, while the naupliar times were higher and the values for the adults very much larger. The turnover times for the Rotorua population (table 40) were not greatly different from those in Ototoa although there was perhaps a slight tendency for them to be higher, possibly as a result of lower temperatures in the larger lake.

(c) Comparison with other areas:- Most of the few studies in which the production of copepods has been calculated have been made on North European and North American lakes, and apart from the date from Lake Rotorua included above there is no published information on zooplankton in Australian and New Zealand lakes with which to compare the Ototoa data.

In table 41 the production, biomass and P/B ratios of *Calamoecia lucasi* in Lake Ototoa are compared with similar values obtained for some Northern Hemisphere freshwater calanoids and also with values from some of the more recent studies of marine calanoids. As well, results from Burgis' study of the tropical cyclopoid, *Thermocyclops*

					P/B		
REFERENCE	SPECIES	AREA & PERIOD	PRODUCTION	BIOMASS	DAILY	MONTHLY	GROWING SEASON
This study.	*Calamoecia lucasi*	Lake Ototoa, year 1969-70. March-March.	2.37 g/m^2 Total in 365 days 0.132 g/m^3 Total in 365 days.	0.211 g/m^2 0.012 g/m^3	0.030	0.92	11.25
Burgis (1971)	*Thermocyclops hyalinus*	Lake George, Uganda. Tufmac Bay. April 1970.	0.103gC/m^3/day	0.416 gC/m^3/ day	0.25		
Cummins et al (1969)	*Diaptomus siciloides*	Sanctuary Lake Pennsylvania. May-Nov. 1966	1.012g/m^3 Total in 191 days	0.146 g/m^3 (my calc. from fig.12 & tab.6)	0.036	0.99	6.93
		June-Nov. 1967	6.291 g/m^3Total in 167 days.	0.217 g/m^3 (my calc.)	0.174	4.83	29.0
Hillbricht-Ilkowska & Weglenska (1970).	*Eudiaptomus graciloides*	Lake Mikolajskie July-Aug. 1964	8.65 g/m^3Total in 40 days.	2.01 g/m^3	0.108		
Hillbricht-Ilkowska, Gliwicz & Spodniewska (1966).	*Eudiaptomus graciloides*	Lake Mikolajskie (E) and Lake Taltowisko (M) Annual	21.0 g/m^2 17.0 g/m^2			0.5-4.5 0.5-2.5	18

Table 41: (continued next page)

REFERENCE	SPECIES	AREA & PERIOD	PRODUCTION	BIOMASS	P/B		
					DAILY	MONTHLY	GROWING SEASON
Hillbricht-Ilkowska & Weglenska (1970)	*Eudiaptomus graciloides*	Lake Mikolajskie(E)					
		1963 (May-Oct)	25.0 g/m^2 Total	3.0 g/m^2	0.046	1.39	8.33
		1964 180 days	70.7 "	7.9 "	0.050	1.49	8.95
		Lake Taltowisko(M)					
		1963 (May-Oct)	16.1 "	1.5 "	0.060	1.79	10.7
		1964 180 days	28.2 "	3.7 "	0.042	1.27	7.6
Patalas (1970)	*Eudiaptomus graciloides*	Lake Lichenskie (heated) July-August 1966. T=26-28.5°C	0.025g/m^2/day	0.180g/m^2	0.14		
		Lake Mikorzynskie (unheated) July-August 1966. T=21-22°C.	0.226g/m^2/day	1.71g/m^2	0.13		
Petrovich et al (1961)	*Diaptomus sp*	Lake Naroch 1960 May-September obs. data	5.86g/m^3 April-Nov. = 210 days	0.62g/m^3	0.045	1.35	9.4
		April-May and Sept. - Nov.data extrapolated	4.63 g/m^3 May - Sept. = 120 days	0.49 "	0.080	2.37	9.45
Shuskina (1966)	*Diaptomids*	28 Byelorussian & Kerelian Lakes	Mean g/m^3/month	g/m^3			
		a) Eutrophic (11)	5.4	1.1	0.16	4.7	
		b) Mesotr. (10)	1.1	0.4	0.098	2.9	
		c) Oligotr.(7)	0.3	0.2	0.067	2.0	

Table 41: (continued next page)

REFERENCE	SPECIES	AREA & PERIOD	PRODUCTION	BIOMASS	P/B		
					DAILY	MONTHLY	GROWING SEASON
Winberg et al (1965)	*Eudiaptomus gracloides*	Lake Batorin(E) May-Oct. 1962	4.8g/m^{3}Total in 150 days	0.5g/m^3	0.064	1.92	9.6
		Lake Myastro (M-E) May-Oct. 1962	8.2 g/m^{3}Total in 150 days	1.0	0.055	1.64	8.2
		Lake Naroch (M) May-Oct. 1960	3.8 g/m^{3}Total in 150 days	0.5	0.050	1.52	7.6
Weglenska (1971)	*Eudiaptomus graciloides*	Lake Mikolajskie(E) July-Aug. (40 days) 1964.	14.70 g/m^{3}Total in 40 days	3.76 g/m^3	0.098	2.81	
Greze & Baldina (1964)	*Acartia clausi*	Black Sea 1960-61	0.067 g/m^{3}Total in 365 days	0.0051g/m^3	0.035		13.0
	Centropages kyoyeri	"	0.014 g/m^3 Total in 150 days	0.0012g/m^3	0.077		11.5
Greze (1970)	*Paracalanus parvus*		0.0002g/m^3/day	0.0014g/m^3	0.09		
	Pseudocalanus elongatus		0.0003 "	0.0023 "			
	Centropages ponticus	Black Sea in summer	0.00001 "	0.00013 "	0.09		
	Acartia clausi		0.00018 "	0.00146 "	0.12		
	Oithona similis		0.00001 "	0.00007 "	0.08		
	Oithona minuta		0.00012 "	0.00050 "	0.11		
Heinle (1966)	*Acartia tonsa*	Patuxent R. Estuary July-Sept.1964 Mean T = 25.5°C.	0.06 g/m^3/day	0.1275g/m^3	0.50		

Table 41: (continued next page)

					P/B		
REFERENCE	SPECIES	AREA & PERIOD	PRODUCTION	BIOMASS	DAILY	MONTHLY	GROWING SEASON
Winberg (1970)	*Diaptomus sp*	Lake Chad (26° lat)		3.5 g/m^3 wet wt.			
Yablonskaya (1962)	*Diaptomus salinus*	Aral Sea Spring, summer & autumn; 1954, 56, and 57.	4.6 g/m^2	1.8 g/m^2	0.007		2.5

Table 41: A comparison of Production, Biomass and P/B ratios of various copepod populations.

hyalinus are included.

Except for the 1966 values in Cummins' et al (1969) study of *Diaptomus siciloides* and those from Greze's studies on Black Sea copepods, production and biomass of *C. lucasi* were very much lower than for any of the other copepods listed. The mean daily P/B values were also lower than all other values except that of *Diaptomus salinus* (Yablonskaya 1962) which is too low however because egg production and the winter growth of the adults were not included (Winberg 1971). The contrast between the low Ototoa P/B values and the higher European ones is emphasised when the Ototoa data are compared with those of Shushkina (1966) who gives an equation relating the production to the biomass of Diaptomids in several Byelorussian and Karelian lakes, which has the form:

$$P = 0.39\ B^{1.3} \quad *$$

where: P = production per month

B = mean monthly biomass

If *C. lucasi* fitted this relationship then the expected production by the mean monthly biomass in Lake Ototoa of 6637 µg (table 35) would be 36,280 µg/month which is obviously very much higher than the observed mean monthly production of 6222 µg (table 35). However, because the growing season encompasses the whole year in Lake Ototoa, in contrast to the 6-7 month season in many of the northern lakes, the P/B value for the entire growing season in Ototoa

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*Note: This appears to be the correct form of the equation. In her paper Shuskina gives it in the form $P=3.9B^{1.3}$ but this does not seem to fit the data presented.

was more similar to the figures for the other species.

CONCLUDING DISCUSSION

Lake Ototoa appears to be much more oligotrophic than the larger lakes in the central North Island, and it is therefore not surprising that there are contrasts between the population of *Calamoecia lucasi* it supports and those in Lakes Rotorua and Rotoiti (Chapman 1972). Many of these have been noted above, but for convenience a comparison of some relevant population parameters of *C. lucasi* in these three lakes is given in table 42 . Lake Ototoa contains a small stable population while those in Lakes Rotorua and Rotoiti are larger and subject to greater absolute, as well as proportional changes. Not only are total population numbers, biomass and the breeding population lower and more constant in Ototoa, but also birth and death rates. As well, mean individual turnover times are longer and the population turnover rate lower. However, even though individuals live on the average longer in Ototoa. *C. lucasi* in both Ototoa and Rotorua showed virtually the same P/B ratios, and therefore specific growth rates and biomass turnover times. Thus even though the population in Lake Rotorua has been able to produce a much larger biomass, the amount of production necessary to maintain this level appears to be relatively the same as in the less productive Ototoa population. As noted above this may suggest that in all the populations the production of organic matter is limited in the same way, although this cannot be stated with certainty until the full yearly data for Rotorua and Rotoiti become available.

PARAMETER	OTOTOA	ROTORUA	ROTOITI
Mean Temperature (°C)	16.8 (24%)	14.7 (29%)	13.8 (19%)
Mean population size (N)	10163 (31%)	18228 (50%)	25062 (39%)
Mean Biomass (µg)	6637 (5926*)	(9328*)	-
Mean Percentage of ovigerous ♀♀	19 (51%)	37 (38%)	40 (29%)
Mean number of ovigerous ♀♀	355 (63%)	864 (109%)	1545 (76%)
Mean clutch size	1.85 (5%)	3.33 (30%)	1.97 (27%)
Mean egg stock (E)	664 (68%)	3063 (113%)	3516 (89%)
Total Annual Egg production (P)	83002	416664	461217
Total Annual Losses (L)	82498	423296	383638
Total net production (P-L); as a percentage of P.	0.6%	-1.6%	16.8%
Mean production (µg/day)	205.5 (176.0*)	(315.4*)	-
Mean b'	0.023 (61%)	0.057 (101%)	0.040 (88%)
Mean d'	0.046 (72%)	0.077 (89%)	0.058 (58%)
Mean B	0.024 (70%)	0.064 (100%)	0.044 (98%)
Mean r' (neglecting sign)	0.039 (78%)	0.030 (79%)	0.024 (83%)
Mean turnover time (days). Calculated from mean d'	12.5	13.6	17.9
Mean turnover time (from mean B)	41.7	15.6	22.7

Table 42: Continued over page.

PARAMETER	OTOTOA	ROTORUA	ROTOITI
Mean turnover time of biomass (days)	(41.1) (41.8*)	(40.1*)	-
Population turnover rate (P/N)	8.2	22.7	18.3
Yearly P/B	11.25 (10.84*)	(12.34*)	-
Mean daily P/B ratio	0.030 (0.024*)	(0.030)	-

Table 42 : Annual means of certain parameters in Lakes Ototoa, Rotorua and Rotoiti. Those of Ototoa 1969-1970 (this study); Rotorua 1967-1969 and Rotoiti 1968-1969 (Chapman 1972). Those values marked with an asterisk are for periods when comparable data from Ototoa and Rotorua are available only for periods of 5 months (June, October to January; see production section).

Though there were considerable differences in productive levels between the populations in Ototoa and Rotorua, there were nevertheless pronounced similarities between their population cycles, and on the whole breeding and development followed the same general seasonal patterns in all three lakes. The larger southern lakes warmed more slowly than Ototoa and were also characterised by lower temperatures (table 42), so that events in them occurred about a month later, especially during the period of warming in spring. However, there was a clear pattern in all the lakes of lower winter populations, a spring outburst of breeding, which occurred between September and November in Ototoa but generally from October onwards in the others, followed by increased population numbers, breeding and production during the summer-autumn period. It was during this latter period that the differences between the populations in the three lakes became most apparent. After the spring reproductive period numbers and biomass increased to much higher levels in the Rotorua lakes and this is presumably because their primary productive capacity was much greater resulting in the production of enough food to support larger populations of *Calamoecia*. Finally, during the autumn, generally between April and May, the larger summer stocks gave way to lower numbers again, presumably as a result of decreasing growth rates and survival as temperatures and phytoplankton stocks declined.

There were some differences in detail between the cycles however. In Lake Ototoa there appeared to be two periods, one already mentioned, in autumn (during groups 2 and 3) and another in spring (during group 6) when survival was lower and which separated the period of low winter production from the period of high summer production. In the Rotorua lakes the autumn period of loss was a regular feature, but a similar lower period of survival in spring did not always occur, and in the summer the populations fluctuated more than in Ototoa. However, only one yearly cycle was studied in Lake Ototoa and it is impossible to say whether these small differences between the lakes are maintained from year to year.

In table 43 population parameters of some species of temperate and tropical limnetic Entomostraca are presented and it is apparent that the birth and death rates in these populations are very much larger than in Lake Ototoa. This results partly because of the large proportions of immature stages in the population of *Calamoecia* and its small clutch size and breeding population. Kibby (1971) gives average values of a finite birth rate (with the dimensions eggs.♀$^{-1}$.days^{-1}, cf the finite birth rate used in this study and those in table 43 which is eggs.individuals^{-1}.days^{-1}) for comparable British populations of *Diaptomus gracilis*, in which some breeding occurs throughout the year, of 1.17

Species	Reference	Birth or death rate	Individual turnover time	Population turn-over rate
Daphnia galeata (Michigan USA)	Hall (1964)	b = 0-0.610 (mean ca 0.1)	Summer - 4 days Winter - 20-25 days	-
Daphnia schoedleri (Montana USA)	Wright (1965)(1958 data)	B = 0.01-0.80 (mean 0.171)	5-8 days	31.4 (April-Sept.)
Leptodora kindtii (Pennsylvania USA)	Cummins et al (1969) (1966 data)	B = 0.005 - 0.66) Mean B = 0.130 Mean d = 0.296	1.5-200 days 3.9 days	53.8 (May-Nov.)
Diaptomus siciloides	-ditto-	d = 0.009-1.142 Mean d = 0.220	1.5 - 111.1 days 5.05 days	41.8 (May-Nov.)
Cyclops vernalis	-ditto-	d = 0-0.771 Mean d = 0.253	1.9 - ∞ days 4.5 days	46.6
Thermocyclops hyalinus (Uganda)	Burgis (1971)	B = 0.397-0.162 0.162	2.5 - 6.1 days Mean 4.2	86.9

Table 43: Some population parameters of Northern temperate and tropical Entomostraca. B = finite birth rate; b = instantaneous birth rate; d = instantaneous death rate. Turnover times and rates have been calculated as explained in the text.

in the Queen Elizabeth Reservoir and 0.74 in the King George Reservoir. However, the comparable annual mean figure for *C. lucasi* in Lake Ototoa is 0.12 which is still considerably lower.

As might be expected from these low birth and death rates, population turnover times, the numerical equivalents of P/B ratios, were considerably larger than elsewhere. Chapman (1972) also noted this and suggested that it might relfect low absolute production of organic matter in New Zealand lakes. This indeed appears to be the case, as shown above (table 36) and the populations of *Calamoecia lucasi* in the Rotorua lakes as well as in Ototoa are very much less productive than those Northern Hemisphere and equatorial ones which have been studied. It could be suggested that New Zealand lakes are less productive because they have been largely uninfluenced by "cultural eutrophication," but while this may be true of Ototoa and perhaps Rotoiti, Lake Rotorua has shown signs of considerable enrichment of this type in recent years (Chapman and Bell, 1967). However, this observed lower productivity may also mean that New Zealand lakes are potentially less productive than those elsewhere. Although much more work need to be done before such a statement can be substantiated, it is worth noting that New Zealand soils (and hence presumably the lakes also) are characterised by severe trace element deficiencies in many areas, and Goldman (1964) has shown that the addition of Zn, Co, Mo, Fe, and chelating agents to the water of two South Island lakes greatly increased their production. Furthermore, New Zealand lakes are low in Ca and as noted earlier are classed as "poor" in Ohle's scale relating productivity to calcium levels.

The populations of *Calamoecia lucasi* so far studied in New Zealand, and especially that in Lake Ototoa, contrast further with most of their counterparts elsewhere in their stable populations, in which recruitment generally seems to be balanced by loss, and in the maintenance of breeding throughout the year. Similar cycles have been reported only for *Thermocyclops hyalinus* in Lake George, Uganda (Burgis 1971) and *Eudiaptomus vulgaris* in Lago Maggiore (Ravera 1954). Most populations of *Diaptomus* live in lakes which have a relatively severe climate when compared with the mild conditions in New Zealand lakes. The winter is very cold, often with ice cover, and the main vegetative period is in the spring and summer for a period of only 6-8 months (e.g. Hillbricht-Ilkowska et al, 1966, Chapman 1969, Comita 1972). During these months there is initially a burst of algal production in spring and the small population of copepods present at these times are able to grow in abundance of food at maximum rates. Under these conditions, especially in the higher latitudes where the growing season is very short, important determinants of the seasonal cycles are the length of the growing season and the speed with which the animals can grow and utilize the spring phytoplankton.

In many cases it appears that there is an excess of food and growth rates may be limited mainly by temperature (e.g. McLaren 1969). Growth and birth rates are high at these times and large P/B ratios are characteristic (e.g. Petrovich et al 1961). As the growing season lengthens rapidly developing predator pressure may begin to take its toll and large and sudden increases in death rates are often correlated with the incidence of predatory species such as *Leptodora kindtii*, *Chaorborus sp.* and cyclopoids (e.g. Hall 1964, Wright 1965, Cummins et al 1969, Comita 1972). This is not to say that food limitation of growth is unimportant but only that it comes into play later in the season after a period of rapid population growth and decimation by predators. Thus Chapman (1969) suggested that food shortage limited growth and led to subsequent increased mortality in late summer and autumn in *Diaptomus gracilis* in Loch Lomond, Weglenska (1971) indicates that rates of growth of *D. graciloides* are affected by food levels in the environment, and Comita (1972) believed that there was food limitation in those generations of *Diaptomus siciloides* developing later in the season, between September and November.

In these populations rate of egg production is an important determinant of population size, and is generally found to be dependant upon both environmental temperature and food levels (e.g. Edmondson, Comita and Anderson 1962, Edmondson 1965). Kibby (1971) has found that birth rates of *Diaptomus gracilis* were correlated with temperature, total phytoplankton, filamentous algae, *Anabaena*, numbers of *Diaptomus* and the combination; filamentous algae *cryptomonas Rhodomonas*.

While it is often obvious which factors are important in the control of population cycles in the Northern Hemisphere temperatue lakes, it is not at all clear what controls the seasonal cycle of *Calamoecia lucasi* in Lake Ototoa. The relationship between birth rates, ingestible phytoplankton and temperature was investigated, and as might have been expected both H and b' were positively correlated with environmental temperature ($r = 0.445^{**}$, $n = 48$ for H; $r = 0.305^{*}$, $n = 48$ for b'), but both were negatively correlated with ingestible phytoplankton ($r = -0.340^{*}$, $n = 41$ for H; $r = -0.477^{**}$, $n = 41$ for b') and the introduction of a time lag by correlating mean birth rates in an interval with numbers of phytoplankton at the beginning of the previous interval did not change the coefficients significantly. As the relationship between birth rates and ingestible phytoplankton was possibly confused by the significant relationship between ingestible phytoplankton and temperature ($r = -0.397^{**}$, $n = 42$) this latter correlation was removed from the reckoning by partial correlation analysis and when this was done only the relationship between b' and ingestible phytoplankton remained significant ($r = -0.407^{**}$ $n = 41$). The partial regression equation relating b' to both ingestible phytoplankton was also calculated and takes the form:

$$b' = 0.0287 + 0.00058T - 0.0000207IP$$

where: b' = mean specific birth rate between samples
T = temperature at the beginning of the interval
IP = numbers of ingestible phytoplankton cells per ml at the beginning of the interval.

Both regression coefficients are significant at the 0.1% level.

It is difficult to assess the meaning of the negative relationship between specific birth rate and numbers of ingestible phytoplankton, especially in the absence of data on the primary production in the lake. Turnover rates may be such that low phytoplankton numbers may not necessarily imply lower production of organic matter, which is probably a better indication of food availability than actual numbers of cells. Even if standing stocks of phytoplankton can give a measure of food availability, as Brocksen et al (1969) have suggested, phytoplankton may be low at times of high birth rates because of greater utilisation by the egg producing adults. Furthermore, phytoplankton may be only a small part of the total food spectrum of the copepods, since it is becoming increasingly realised that detritus, organic aggregates and associated bacteria are probably important food sources of zooplankton (Nauwerck 1963 Gliwicz 1969a). Unfortunately no measures of bacterial populations were made on Lake Ototoa and only a few determinations of organic matter (which increased in October and November when b' was high), and so while the numbers of ingestible phytoplankton cells have had to be used as a measure of food levels it is quite possible that food availability may have been quite different. Any apparent relationship between population attributes and ingestible phytoplankton should thus be viewed with some scepticism.

However, it is unlikely that a knowledge of such relationships between birth rates and possible causative environmental factors in Lake Ototoa will help in understanding the control of the seasonal cycle, since it was shown above that there was little apparent relationship between breeding activity and population numbers, and losses appeared to be the main determinant of population size. Apart from 'natural' mortality (i.e. that background mortality due to failure to moult, old age, etc.) the most important agents of loss might be expected to be predatory mortality and death from food shortage. In the population of *Calamoecia lucasi* in Lake Ototoa there was no evidence of predatory mortality such as that suffered by the population of

Daphnia galeata mendotae studied by Hall (1964) in which prolonged periods of negative r values were associated with heavy predation by *Leptodora kindtii*. In Lake Ototoa the r values of *C. lucasi* tended to fluctuate around zero, suggesting that predation was either constant in its effect or absent. In New Zealand there is no equivalent of *Leptodora* and the only predatory zooplankter in Lake Ototoa was *Mesocyclops leuckarti*. However, the cyclopoids were present in very low numbers and there was no significant relationship between either L or d' and numbers of cyclopoids. The fauna of planktivorous fish is also limited, the only ones in Lake Ototoa being the juvenile stages of bullies (*Gobiomorphus sp*) and a very few smelt (*Retropinna lacustris*). Although there is no data on their abundance in Lake Ototoa they never seem to be present in large numbers and it is difficult to see how they could seriously affect planktonic populations in any but the shallowest lakes. The apparent high rates of survival till the adult stage, and the similarity in percentage survival between the various growth stages in *C. lucasi* may also indicate a lack of predatory mortality. It is hard to believe that both stage V copepodites and the much smaller nauplii and CIs would be equally vulnerable to predation.

It seems likely that food limitation may have been more important than predatory limitation in controlling the population size of C. *lucasi* in Lake Ototoa and this suggestion is supported by the low clutch sizes, egg production and P/B ratios.

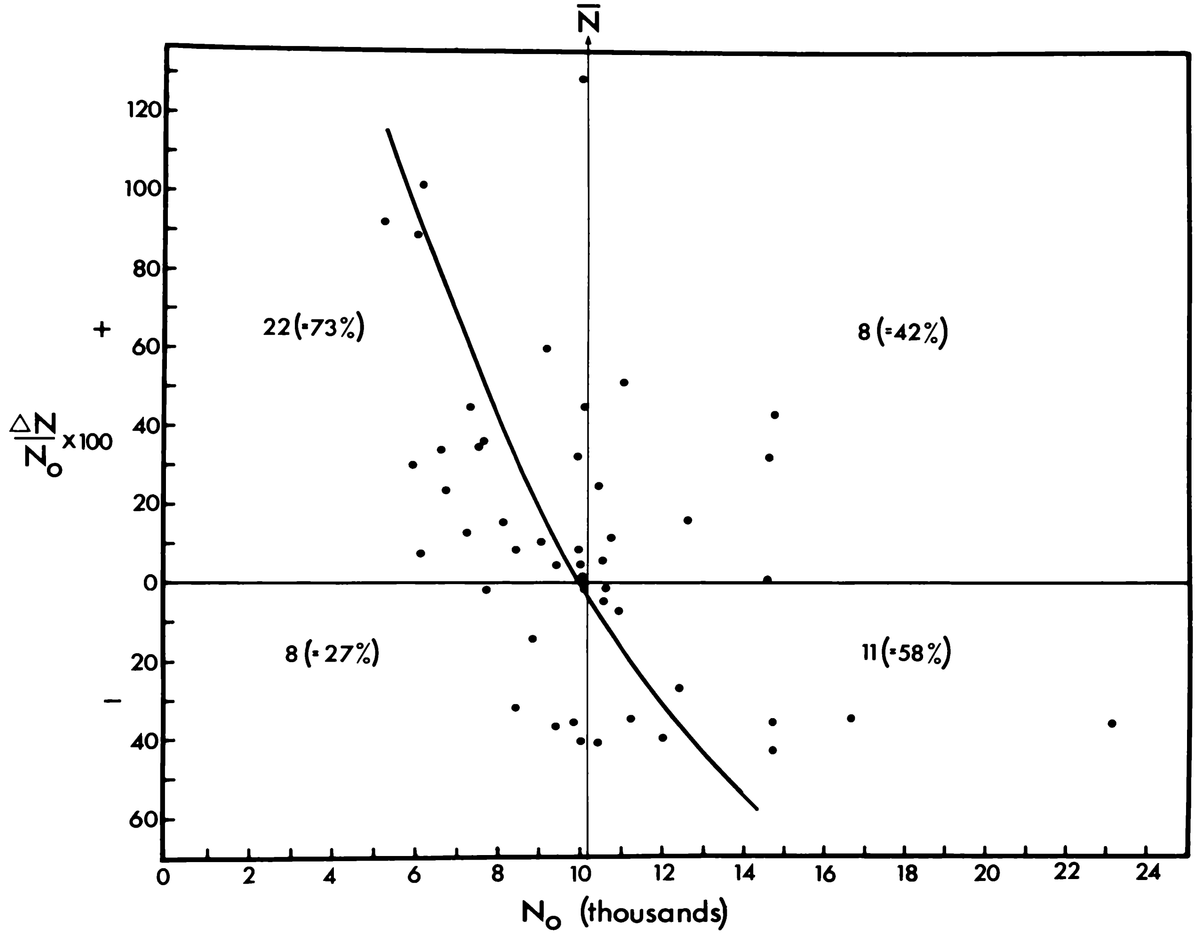
A population limited by food availability might be expected to come into a steady state with its food reserves. Such a population would tend to grow in size until the pressure on the food resource would be such that growth rates would be slowed, and where food would be scarce enough to limit breeding by the ♀♀ to the production of small numbers of eggs at any one time. Such a population would have a rather low production but a relatively high biomass since little would be being removed by predators. Presumably the population would be maintained by a low even production of eggs, and any great excess of production of individuals would be likely to be sufficient to exceed the carrying capacity of the food resource, and would result in higher mortality. Thus increases in either birth rates or population numbers would generally be followed by increases in loss.

The Ototoa population of C. *lucasi*, and indeed those of Lakes Rotorua and Rotoiti also, shows remarkable similarity to such a hypothetical food limited - non-predatory limited population and perhaps this is hardly surprising. If the presumed low predator pressure is correct then the lack of severe environmental variations brought about by the oceanic climate of New Zealand means that the populations are in a situation where they are potentially able to bring themselves into equilibrium with the environment more readily than in a highly seasonal lake. The low clutch size and breeding rates have been commented on previously as have the low P/B ratios in both Ototoa and the Rotorua Lakes. In comparison to lakes elsewhere the biomass thus turns over more slowly, and is maintained by lower birth rates, even though temperatures are on the average high. The relationships between monthly production, food levels and temperature (fig. 35) point to a degree of food limitation also. Although in the colder months production of the copepods appeared to be limited by their ability to grow fast enough at the low temperatures, as temperatures increased in spring and summer production also increased but was apparently limited by food levels also.

The low clutch sizes are of further interest since they suggest also that predation is not important as a mortality factor in Lake Ototoa. A herbivore species suffering predatory mortality might be expected to be kept below the maximum population able to be sustained by the primary production of the environment. Because in such situations of lowered density there would be more food per ♀ if algal populations remained unchanged, and as algal stocks would be liable to increase further in such conditions anyway (because of lowered grazing pressures by the herbivores) clutch size would be expected to be greater than the minimum possible, at least at certain times of the year when predation was highest and environmental conditions favourable. Thus the small and nearly constant clutch sizes that *C. lucasi* produced in Lake Ototoa seem to indicate that the population was not limited in this way.

A population limited by food is limited by a density-dependant resources and increases in numbers should be followed by increases in mortality. Increased loss rates were in fact found to follow increases in population numbers in the Ototoa population, although this is difficult to quantify. In fig. 36 the relationship between change in population size (ΔN) between samples expressed as a percentage of the population size at the beginning of the period (N_o), and N_o is shown. The yearly mean population size is also indicated. The scatter of points is great and no very clear trend in the results is discernable. However, the fact that on those occasions when the population was below the average level change was positive on 73% of these occasions, and that when above the mean level change was negative 58% of the time, perhaps suggests that some type of density dependant stabilising mechanism, perhaps food limitation, may have been operating.

Fig. 36: Change in population size between sampling dates, against population size on the first date, for the total population of *Calamoecia lucasi* in Lake Ototoa. A line has been included to guide the eye to possible trends.


N̄
120
100
80
60
40
20
0
20
40
60
+
−
$\frac{\Delta N}{N_o} \times 100$
22 (=73%)
8 (=42%)
8 (=27%)
11 (=58%)
0
2
4
6
8
10
12
14
16
18
20
22
24
N_o (thousands)

Chapman (1972) has suggested that predation is not a major factor in controlling the cycles of *C. lucasi* in Lakes Rotorua and Rotoiti also and as the P/B ratios of Lake Ototoa and Rotorua were found to show striking similarities to one another it may be that all three populations are limited mainly by the amount of food which can be produced in each lake. Thus, although the more productive Rotorua lakes support larger standing stocks and biomass of *C. lucasi* than in Lake Ototoa because of their higher potential for food production, the three lakes may form a cohesive group characterised by stable unproductive populations, maintained by low reproductive rates in comparison with those in other countries.

The difficulties encountered in endeavouring to provide explanations for these types of seasonal cycles possibly result largely because in such stable populations low level, yet significant, relationships which may exist between parameters of population change and their underlying causes are obscured by random variation brought about by errors involved in the initial sampling and counting processes. This is a recurring problem in the ecological study of plankton populations, but because of the nature of the populations in the North Island of New Zealand it seems that it is likely to set a limit to the usefulness of population studies in eliciting deeper understanding of the ecology of *C. lucasi* . Obviously it would be possible to reduce the effects of sampling variability by taking more samples more often, but this is generally impracticable.

Thus while a little is **now** known of the ecology of *C. lucasi* in a range of New Zealand lakes, it is apparent that the most pressing requirement is for more information on the biology of the individual animal. The determination of the population dynamics and production of *C. lucasi* in the present study has depended on the use of laboratory determined, temperature dependant development times. However, Weglenska (1971) has shown that natural variations in food levels can markedly affect the growth rate of copepods and if **her** findings are also true for copepods in New Zealand lakes, as they almost certainly are, then many of the values computed for *Calamoecia lucasi* in Lake Ototoa are probably inaccurate to varying degrees and more needs to be known about the relationships between environmental food levels and development times in this species before more accurate figures can be arrived at. Studies of feeding, assimilation and metabolic rates, preferably under natural conditions, are no less important, and clarification of the apparently unusual productive properties of New Zealand copepod populations, and the relationships between their cycles of both numbers and biomass, and the environment, will probably largely depend on future investigations of these aspects.

SUMMARY

Between March 1969 and March 1970 a study was made of the limnology of Lake Ototoa, a large sand-dune lake on the south head of the Kaipara harbour, north of Auckland. Particular emphasis was placed on an investigation of the seasonal biology of the calanoid copepod *Calamoecia lucasi*, and its population dynamics and production.

Lake Ototoa is a warm monomictic lake, and became thermally stratified in November and remained so until the end of the sampling period. The metalimnion was between 12m and 16m depth. Surface temperatures ranged between 10.2°C (in August) and 25.2°C (in late January), bottom temperatures between 9.7°C and 17.5°C. The annual heat budget was calculated to be 15,500 cal.cm^{-2} and the work of the wind in distributing the heat income 1766 gm.cm.cm^{-2}. The thermal features of the lake reflect the influence of the maritime climate as well as its exposed position. Thus compared with northern hemisphere continental lakes the temperature range and heat budget are low because of the damping effect of the sea, yet there is sufficient windiness to give a fairly deep thermocline and a high value for the work of the wind.

The water was clear, secchi depths ranging between 5m and 9.2m (mean 7.07m), with greatest transparencies in the summer. Percentile transmission was also high, ranging between 61 %/m and 87%/m. Variation in transparency did not seem to be correlated with changes in amount of seston.

Surface waters were supersaturated with oxygen on all but one occasion. There was some depletion in the bottom waters during summer stratification and a positive heterograde distribution of oxygen with depth was found. The oxygen deficit was calculated to be 0.015 mg.cm^{-2}.day^{-1}. This low value suggests that Lake Ototoa can be regarded as oligotrophic and is the least productive New Zealand lake for which such values have been obtained. Mean surface pH was 7.82 (range 7.25 to 8.30) and higher values were found in the summer than in the winter. pHs dropped slightly in the bottom waters during stratification.

The ionic composition of the waters was similar to that of other small New Zealand and Australian lakes located near the sea. Wind borne spray probably contributed to the ionic dominances of $Na > Mg > Ca > K$ for the cations and $Cl > HCO_3 > SO_4$ for the anions. Compared with other New Zealand lakes PO_4 concentrations (range 1.00 µg/l to 10.20 µg/l) were low and NO_3 concentrations (range 0.12 mg/l to 0.60 mg/l) high.

The seasonal cycles of both chlorophyll a concentrations and numbers of the major phytoplankton species were studied. Concentrations of chlorophyll a were low (range 0.04 mg/m^3 to 4.61 mg/m^3; mean 0.97 mg/m^3) with highest values in the winter. The phytoplankton densities were also low and the assemblage was found to be an oligotrophic diatom-desmid plankton, associated with *Botryococcus*, *Dinobryon* and *Sphaerocystis*. Examination of the gut contents of preserved *Calamoecia lucasi* and determination of size of particle selected by live specimens of *C. lucasi* showed that those species between 2.5 and 18.2 microns diameter were probably ingested.

The zooplankton was dominated by *Calamoecia lucasi* whose numbers remained fairly constant throughout the year. *Bosmina meridionalis* was the only limnetic cladoceran and was present in greatest numbers during autumn and spring. A number of rotifer species were also common. The only cyclopoid copepod was *Mesocyclops leuckarti* which was only found in very small numbers.

The biology of *C. lucasi* was examined in detail. Breeding was continuous, and clutch sizes and egg stocks were low and fairly constant. The yearly average numbers of clutches per female was calculated to be 1.9. Eggs were similar in size to those of other freshwater copepods, and there was little seasonal change. The numbers of adults and immature stages also showed little seasonal change, although numbers were higher in summer than in winter and there were periods of lower standing stocks in autumn and spring, probably as a result of greater mortalities and/or changing development rates at these times. By analysing changes in female lengths and using changes in breeding intensity and numbers of development stages throughout the year, the development of 8 possible groups could be followed. The broad aspects of the seasonal cycle in Lake Ototoa were found to be similar to those of *C. lucasi* in Lakes Rotorua and Rotoiti.

Dry weight of females was greatest in mid-winter and decreased during spring to low summer values. Weight increases were due to increases in both protein and lipid, and the proportions of these showed little seasonal variation. Analysis of organic matter gave approximate calorific values ranging between 3577 cal.gm^{-1} and 5773 cal.gm^{-1} (mean 4594 cal.gm^{-1})

with little seasonal change. The mean proportion of the dry weight as carbon was 43.6% and the yearly mean ash content was 5.53%. The weights of the developmental stages were also determined at various times during the year and growth was broadly parabolic.

The development rates of eggs, nauplii and copepodites at different temperatures were determined in the laboratory and were used to determine recruitment and loss in the various development stages, and also the population as a whole. Birth and death rates were low, the means of both linear and exponential rates varying between 0.02 and 0.05. Thus average individual turnover times were relatively long, between 21.5 and41.7 days, and the annual population turnover rate was 8.2. Losses were found to closely follow births and there was little relationship between births and population size, which was determined mainly by losses. The only periods of consistently reduced losses were in June and December, and periods of greatest losses were in autumn and spring. Losses were much lower in the naupliar and copepodite stages than in the adults. Total recruitment, loss and survival were also calculated, and survival was generally found to be similar (ca 90%) in all the immature stages. However losses were found to be greater in those groups developing in autumn and spring. Mean adult longevity was calculated to be 17.6 days. Longevity was greater in early autumn, late spring and early summer.

Production was low in winter but increased considerably in spring and summer. It was very low compared with production in other planktonic copepod populations, both in New Zealand and elsewhere, as was the mean daily P/B ratio of 0.030. This gives a mean turnover time for the biomass of 33.3 days andthe seasonal range was from ca 2 months in winter to ca 0.6 months in the summer. Average daily P/B ratios in each month were compared with those of *C. lucasi* in Lakes Rotorua and Rotoiti and found to have almost identical absolute values,and to show the same seasonal trends with low winter and high summer values. The proportion of the total production contributed by the various development stages was also examined and CV was found to be the most important, contributing on the average 47.0% of the total.

The low birth and death rates and lack of seasonal change in the New Zealand populations are emphasised as are the low production and P/B ratios. It is suggested that they may arise from lack of extreme seasonal climatic variation and a more even distribution of primary production throughout the year than in cold temperate lakes, combined with probable lack of predation on the copepod populations. It seems likely that populations of *C. lucasi* in New Zealand may be food, rather than predator limited. However it is also suggested that New Zealand lakes may be inherently less productive than many in the Northern Hemisphere.

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