Life History Strategies Of New Zealand *Ceriodaphnia* (Crustacea:Cladocera): A Comparative Study

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Tracey Greenwood

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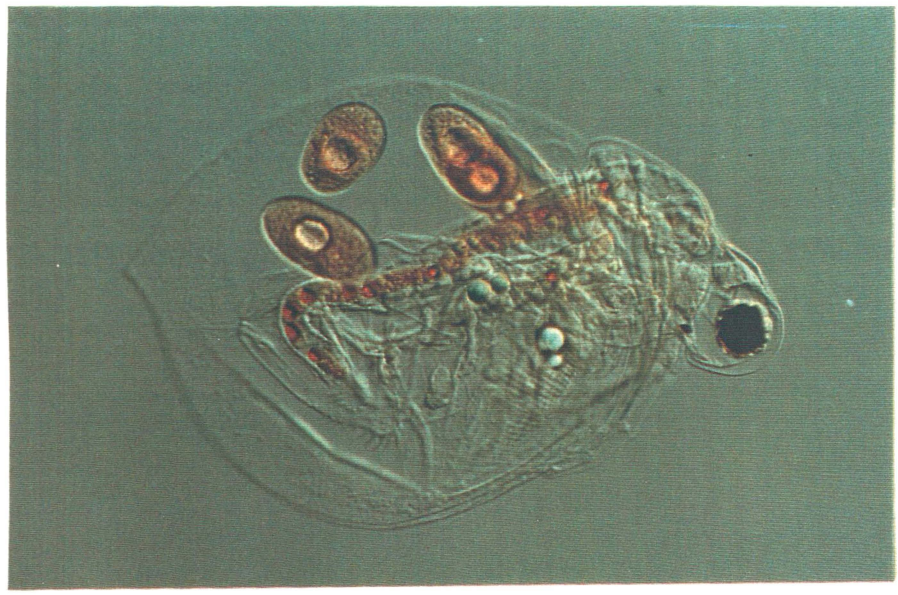
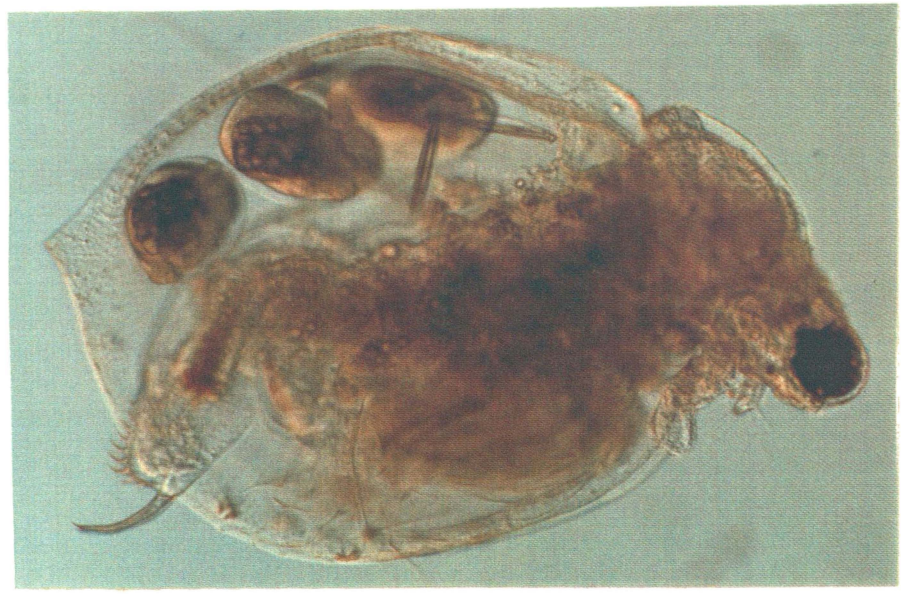


Ceriodaphnia pulchella (X140)



Ceriodaphnia dubia (X100)

"All animals are equal but
some animals are more
equal than others"

George Orwell
Animal Farm

ABSTRACT

The seasonal changes in the plankton communities, and the dynamics and life histories of the Cladocera of Lake Mangakaware, were studied over a period of 19 months, during which time populations were sampled at weekly or two weekly intervals. Lake Mangakaware, a small, polymictic lake in the North Island of New Zealand, is characterised by a high nutrient status, low Secchi transparencies, and an unstable thermal regime. In the algal community, small euchlorophycean genera and diatoms predominated. Peak abundances occurred in autumn and late spring and were due almost exclusively to *Tetrastrum triangulare* and *Aulacosira distans* respectively. The frequent mixing events precluded the prolonged abundance of any one species and species replacements were rapid. Small species (< 30 μm) predominated amongst the dominant class (Euchlorophyceae), but there were frequent occurrences of large, unpalatable and/or nutritionally poor genera (*Aulacosira, Closterium, Trachelomonas*).

Amongst the zooplankton, the Copepoda and Rotifera predominated. The rotifer community exhibited a pattern of sharp sequential peaks in the abundance of different species. Maximum density occurred in summer (1989) due almost entirely to *Keratella cochlearis*. The Copepoda were generally low in abundance in winter, but increased in summer and autumn periods.

The four cladoceran species: *Bosmina meridionalis; Ceriodaphnia pulchella; C. dubia;* and *B. longirostris*; exhibited disjunct population maxima, with peak abundances occurring in mid summer (1987), autumn (1988), spring (1988), and summer (1989). Only *B. longirostris* was perennially present.

The Cladocera of Lake Mangakaware have life histories which predispose them to success at particular times of the year. All species exhibited low fecundities and lipid scores, indicating that resource availability was low and competitive interactions and starvation resistance were probably important in determining species success. Increases in body size in cooler seasons were correlated with higher egg volumes, but not with higher clutch sizes, giving further support for the view that available food was limited. *B. longirostris* appears to be the most successful planktonic cladoceran in Lake

Mangakaware. It is a small species, but produces relatively large neonates which mature quickly. It appears able to maintain populations for prolonged periods with low fecundity, produces ephippia as a means of persistence, and is not particularly vulnerable to predation from *Mesocyclops leuckarti* . Its selective feeding mode is probably favoured in Lake Mangakaware, where palatable algal species are in low density or difficult to obtain. *B. meridionalis* is a less able competitor than its congener and is apparently disadvantaged by long development times at low temperatures.

The seasonal success of each of the two species of *Ceriodaphnia* appears to be partly determined by temperature. *C. pulchella* was the more abundant species but was restricted to warmer seasons and, like *B. meridionalis*, has a prolonged development time at low temperature. In contrast *C. dubia* grows quickly at low temperature. The life history responses of *C. pulchella* and *C. dubia* to different food and temperature regimes were examined using two way ANOVA for the treatments: 23°C-high food; 23°C-low food; 13°C-high food; 13°C-low food. Growth, fecundity, and resource allocation were examined and the two species found to be different in critical aspects of their life history. At high resource levels, *C. dubia* had a higher fecundity than *C. pulchella* and increased its reproductive effort with age while maintaining a high growth rate. However, at low food levels, *C. dubia* lost most of this advantage and development times were also considerably prolonged. *C. dubia* neonates were larger than those of *C. pulchella,* yet possessed the same amount of lipid for any given regime. *C. pulchella*, although the smaller of the two species, with generally lower fecundity and longer development times, produced relatively larger neonates than *C. dubia*. *C. pulchella* was less responsive to low food level, curtailed growth after maturity, and maintained a rather constant clutch size regardless of food availability. Offspring were quite resistant to starvation and were able to reproduce without provided food, regardless of maternal history. The results suggest that subtle differences in life history can determine seasonal success and competitive outcome between similar species. Very large differences in life history strategy or selection pressure need not be invoked.

ACKNOWLEDGEMENTS

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PART ONE

INTRODUCTION:

SOME HISTORICAL PERSPECTIVES AND THE CURRENT STATUS AND DIRECTION OF CLADOCERAN RESEARCH

A perennial endeavour in zooplankton ecology is to determine the relative importance of physical and biotic factors in governing community structure and species distribution and abundance. It has long been widely recognized that the composition and structure of communities comprising mainly herbivorous zooplankton is greatly dependent on biotic interactions, namely exploitative resource competition and predation (Bernardi *et al.* 1987). The central role of such interactions arises as a result of the unstructured and relatively uniform nature of the pelagic environment of lakes. In such environments, refuges are few and competition and predation are severe.

The first attempt to combine these two kinds of interactions in a mechanistic theory of zooplankton community structure was made in the size-efficiency hypothesis (SEH) proposed by Brooks and Dodson (1965). In this, they provided support for the view that competition has played an important role in determining the species composition of zooplankton communities. Specifically, they argued that the predominance of large zooplankton species in habitats lacking visual planktivores was a consequence of their competitive superiority over small species, an advantage that accrues to them due to their greater efficiency in food collection and lower metabolic demand per unit mass. When visual predation is intense, these larger, more visible, species are very vulnerable, and small species can predominate. Therefore the distribution and abundance of small species should be directly related to the abundance of vertebrate planktivores.

Independent support for the importance of competition in structuring zooplankton communities has also been obtained from niche analysis studies (e.g. Makarewicz and Likens 1975) which have shown that spatial or temporal separation of abundance peaks is one way in which co-occurring species may avoid competition. Such studies have the

major failing that they cannot show that disjunct distributions are the result of competition, or even that competition is completely avoided.

These two lines of work: community composition and niche analysis, supported the idea that, in natural habitats, zooplankton species occupy different niches and, when forced to compete, competitive exclusion of one species (the competitive inferior) is the result.

The SEH generated a great number of field, experimental, and theoretical investigations, aimed at determining the validity of its assumptions (e.g. Allan 1974; Hall *et al.* 1976; Threlkeld 1976; Lynch 1977; Smith and Cooper 1982). Much attention has also been given to the various strategies adopted by different species to counteract or minimise the detrimental effects of predation. The significance of vertical migration as a means of avoiding predators has been examined in detail, most often for large *Daphnia* species which suffer heavily from the impact of visual planktivores (e.g. Zaret and Suffern 1976; de Bernardi 1981; Stich and Lampert 1981, 1984). Other workers have examined the role of body size and visibility in determining the risk of mortality from predation (e.g. Dodson 1974; Kerfoot 1974; Zaret and Kerfoot 1975; Gophen 1985).

Generally, the view that vertebrate predators are important in determining the size structure of zooplankton communities containing large cladoceran species is one that has been strongly supported by the available data (de Bernardi *et al.* 1987). Highly visible prey have virtually no chance of escape and each predator is capable of consuming a very large number of prey per day. Moreover, because planktivores also consume the eggs of fecund adults, their impact on population growth rates is considerable. However, the data on competitive interactions have been less supportive of the SEH. Experimental studies provided examples where small species could outcompete larger ones under near natural conditions. For example, both Neill (1975) and Lynch (1978) showed that *Ceriodaphnia* could outcompete large *Daphnia* because juvenile *Daphnia* were particularly sensitive to resource depression.

These studies have shown that the essential shortcoming of the SEH was its failure to consider the age structure of competing populations (Goulden *et al.* 1982b), or account for complicated but weak interactions that take place between distantly related genera (De

Mott and Kerfoot 1982). The relative importance attributed to competition and size-selective predation in structuring zooplankton communities changed with the recognition of the importance of size selective feeding by invertebrate predators. In contrast to vertebrate planktivores, invertebrate predators feed mainly on small zooplankton (Dodson 1974). Thus the dominance of large bodied prey species in the absence of vertebrate predators can be due not only to their 'competitive superiority' but also to their lower vulnerability to predation by invertebrates (Romanovsky 1984a). The role of competition was thus downplayed and, for a long period, the major focus was placed on predation (vertebrate and invertebrate) as the dominant mechanism structuring microcrustacean communities (Hoenicke and Goldman 1987).

In the 'balanced predation' hypothesis Dodson (1974) suggested that size selective predation alone is the organizing factor in zooplankton communities. Quite apart from influencing community structure, invertebrate predators are also considered to be responsible for the cyclomorphic adaptations observed in planktonic cladocerans (Brooks 1965; Jacobs 1980; Kerfoot 1980; O'Brien *et al.* 1980; Havel 1985).

Cladoceran workers have since moved towards a more balanced view, recognising that the comparison between competition and predation is misdirected and that together these two factors act to affect zooplankton communities in a multitude of frequently interacting ways. Moreover, the relative importance of each of these factors may appear in different ways in different lakes. This is not to negate the role of size selective predation, at least for the north temperate communities to which most of the studies apply. For example, on the basis of data collected from a large number of studies, Lynch (1980a) suggested that the selective pressures imposed by predators are the most important ones in the evolution of cladoceran life histories. Competition was viewed as important in the success of similar species, but only within the framework provided by a predator induced community structure.

In 1986, the Plankton Ecology Group (Sommer *et al.* 1986) proposed 'a model of seasonal succession' to account for observed successional events in freshwater plankton. Based on empirical evidence from a wide range of water bodies (lakes, reservoirs, and

ponds) the model was an attempt to integrate the ideas of phytoplankton succession with those regarding the roles of resource competition and predation in zooplankton communities. Although simplistic, the model acknowledged the importance of life cycle adaptations (e.g. the production of ephippia and persistence under starvation) and the mechanisms for their evolution: physiological constraints; resource competition; and predation. More recent research has elaborated on these ideas by emphasising the evolutionary perspective (e.g. Perrin *et al.* 1990; Ebert 1991), an approach developed earlier by Lynch (1980a,b).

Herbivorous zooplankton, occupying a middle position in the aquatic food web, clearly experience both resource competition and predation, and individual fitness will be made up by the joint effects of resource utilization and mortality. For herbivorous species, predation pressure will determine the resource level required for population persistence, whereas the supply of available food will influence the degree of predation that can be tolerated (Rothhaupt 1990).

The adoption of a life history approach to the investigation of zooplankton community structure has enabled a more realistic view of the important factors governing the dynamics of natural populations. The theoretical 'optimal life histories' for organisms exposed to different selective pressures have been reviewed by Stearns (1976), and are based on the assumption that individual success will depend on the relative apportionment of energy to reproduction and survival. Key life history characteristics are: brood (clutch) size; offspring size; the age distribution of the reproductive effort; the interaction of that reproductive effort with adult mortality; and the variation in these traits among progeny (Stearns 1976). The theoretical difficulty lies in attempting to predict which combination of characteristics will evolve in different situations. This task is made more difficult because organisms can solve the ecological 'problems' they face (resource competition and predation for example) in different ways. For this and other reasons, associated with physiological and morphological limitations, 'optimal' life history strategies may never evolve in real organisms (Stearns 1977).

It is appropriate, however, to consider the adaptive value of different life histories between species exposed to different selective pressures. As outlined by Lynch (1980b) and later by Dorazio and Lehman (1983) cladoceran species should be expected to follow the following strategies:

(1) In the absence of predation, or when exposed to vertebrate predators which prefer large prey, species should hatch from small eggs and grow quickly to a small size (i.e., initiate reproduction early at a small size);

(2) Populations exposed to invertebrate predators which prefer small prey may increase juvenile survivorship by hatching from large eggs and shortening the juvenile period. Alternatively they can hatch from small eggs and postpone maturity until they grow beyond the size range available to their predators. Which of these two strategies is adopted will depend on the dynamics of resource availability;

(3) When exposed to both vertebrate and invertebrate predators, small adult size, and large offspring size may simultaneously be favoured; and

(4) When the nutritional status of the environment declines small bodied individuals will be favoured.

It is on the analysis of life history features such as these that cladoceran research has been focused in recent years. Indeed, life history theory has provided the framework within which a multitude of different approaches can be accommodated. Most of this work has involved either the experimental investigation of the life history characteristics of co-occurring species (e.g. Tessier and Consolatti 1989, 1991; Foran 1986a,b) and/or an examination of these characteristics in natural populations, where the selective pressures are known or can be assessed (e.g. Brambilla 1982; Tessier 1986a,b). These studies have progressed in concert with a continued interest in the resource dynamics of cladoceran communities (e.g. Pace *et al.* 1983) and the role of grazer selectivity in the community structure of both producers and consumers (e.g. Bleiwas and Stokes 1985; De Mott 1986; Balseiro *et al.* 1992). Moreover, analyses of the dynamics of natural populations have become increasingly more realistic with the incorporation of time lag responses (e.g.

Matveev 1985) and the recognition of the importance of threshold food concentrations to competing species (Rothhaupt 1990).

The most recent work in the experimental investigation of cladoceran life histories has been associated with the role of food depletion in altering the way in which resources are allocated to growth and reproduction. Some of these studies have examined the response of a single species to changes in resource level or quality (e.g. Lynch and Ennis 1983: *Daphnia pulex*; Perrin *et al.* 1990: *Daphnia magna*; Groeger *et al.* 1991: *Daphnia pulex*; Stuchlíková 1991: *Daphnia pulicaria*; Urabe 1991: *Bosmina longirostris*; Mitchell *et al.* 1992: *Daphnia magna*).

Other workers have looked for clonal differences in patterns of energy allocation in an attempt to explain or predict the adaptive success of different life history characteristics (e.g. Weider 1987: *Daphnia pulex*; Ebert 1991: *Daphnia magna*; Yampolsky and Kalabushkin 1991: *Daphnia magna*). The above studies have shown that differences in life history traits can be inherited and are expressed largely through differences in neonate size, number of preadult instars, clutch size, and growth rate. The results also suggest that, because of the heritability of life history traits and the importance of clonal succession in zooplankton communities, under field conditions the outcome of competition will often be unpredictable. Moreover, key life history features, such as the threshold size at maturation, will not be stable either, but will change according to the selective pressures acting at the time (Ebert 1991).

While studies of clones have illustrated the potential importance of clonal succession in cladoceran communities, there is ample evidence that differences in critical life history characteristics such as clutch and egg size are direct environmental responses (e.g. to temperature or resource level) and are not simply the result of genetic change (e.g. Gliwicz and Guisande 1991). A promising approach, that has become increasingly popular in recent years, is seen in the efforts to examine, experimentally, the life history features of two or more competing species, and to better integrate the findings with the current ideas of resource competition and size selective predation (e.g. Foran 1986a,b; Robertson 1988; Lynch 1989, 1992; Tessier and Consolatti 1989, 1991; Gliwicz and

Guisande 1992). In particular, as with single species studies, attention has been paid to the significance of resource depression in shaping life history responses. It is becoming clear from these more recent studies that, in terms of life history strategies, cladocerans behave in a manner consistent with two general notions which have been commonplace in the ecological literature for decades (Smith and Fretwell 1974; Stearns 1976). Firstly, that there is a trade-off between offspring size and number and secondly, that at low resource levels, per-offspring investment should be higher than at high or non-fluctuating food levels, even though the offspring number would be reduced because of delayed maturation, lower clutch sizes, and increased time between clutches. A recognition of the differences in life history between species has lead to a greater understanding of the way in which coexistence between species, or competitive dominance of one species over another, might be achieved. Continued emphasis on the importance of life history evolution in cladoceran community ecology, particularly with regard to starvation resistance and population response to fluctuating food levels, will further this understanding.

It is within the context of such current research that this study is placed. New Zealand cladoceran communities are interesting from a worldwide perspective because: (1) large bodied species are rare and limited in their distribution; (2) the efficient invertebrate predators of north temperate regions are absent, and the only invertebrate predators of significance to limnetic populations are rather inefficient (e.g. omnivorous cyclopoids and predatory mite species); and (3) vertebrate planktivores are absent from many lakes, or restricted in the plankton to particular seasons (e.g. larval *Gobiomorphus cotidianus*).

In New Zealand, the mild, oceanic climate and predominance of warm monomictic or polymictic lakes has led to multivoltine zooplankton species and communities where resource competition appears to be the predominant structuring force (Burns 1991). New Zealand lacustrine environments therefore represent ideal systems in which to investigate variations in cladoceran life history in response to resource competition. The species are all quite small, yet two or more species frequently co-occur despite seemingly rather similar life histories. In Lake Mangakaware, the presence of four small cladoceran

species (*Bosmina longirostris, Ceriodaphnia pulchella, B. meridionalis* and *C. dubia*), the latter two of which are quite restricted in their temporal distribution and all of which show disjunct population maxima, suggests that their life histories are sufficiently different to permit coexistence but predispose each to a particular season. Thus, the aims of this study were:

(1) To establish the particular characteristics of each species in the field i.e., examine their demography in some detail;

(2) To test experimentally the life history responses of two of these species, *C. pulchella* and *C. dubia*, to temperature and resource level; and

(3) To place these findings in the context of current life history theory.

I hope that this study will add to the current thinking on the role of life history evolution and resource competition in structuring cladoceran communities. Certainly, the situation in New Zealand is very different to that in north temperate regions where most of the current ideas on cladoceran community ecology have been developed.

The examination of a community where the cladoceran species are probably not much different from each other in terms of the selective pressures shaping their life histories, serves as a valuable opportunity to test the global validity of life history theory as it pertains to cladoceran species.

PART TWO

Field Studies on the Zooplankton of Lake Mangakaware (New Zealand) with Particular Emphasis on the Cladocera

PART TWO
CHAPTER ONE:
LAKE MANGAKAWARE

1.1 LAKE MANGAKAWARE

Lake Mangakaware (37°55'S, 175°13'E) is a small, crown owned lake, situated approximately 20 kilometres from Hamilton (Fig. 1). The lake was formed c.17,000 years B.P., as a result of the damming of a small valley by Hinuera Formation alluvium, deposited by the ancestral Waikato River. Later peat accumulation contributed to the present form of the lake basin (Green and Lowe 1985). A bathymetric map of Lake Mangakaware, (NZMS1 N65 Ref. 730293), is given in Figure 2, and morphometric and physiographic data are given in Table 1.

Surrounded by an extensive area of reserve land, and currently a wildlife reserve, the lake is quite shallow and very productive. The input of humic compounds from localised pockets of peat development makes the lake water moderately dark and, as in many of the small peat stained Waikato lakes, Secchi depths and pHs are relatively low. Summer and winter ranges for these, and other physicochemical parameters, are given in Table 2. According to the boundaries suggested by White (1983), these indicate a eutrophic status for Lake Mangakaware. Although reserve, the surrounding land is mainly in pasture with only narrow broken margins of willows (*Salix fragilis*), flax (*Phormium tenax*) and raupo (*Typha orientalis*). Consequently, runoff and drainage from the surrounding farmland are extensive and account for a major part of Lake Mangakaware's high nutrient status. Water-lilies (*Nymphaea* sp.), planted by the tenant farmer, are also now spreading rapidly around the lake and, in summer, there are quite extensive marginal areas of submerged macrophytes (*Elodea canadensis*, *Potamogeton ochreatus*) and floating plants (*Azolla rubra*).

High rates of runoff, and frequent, often considerable, fluctuations in water level (as a result of periodic blocking of the outlet channel at the south end of the lake), together

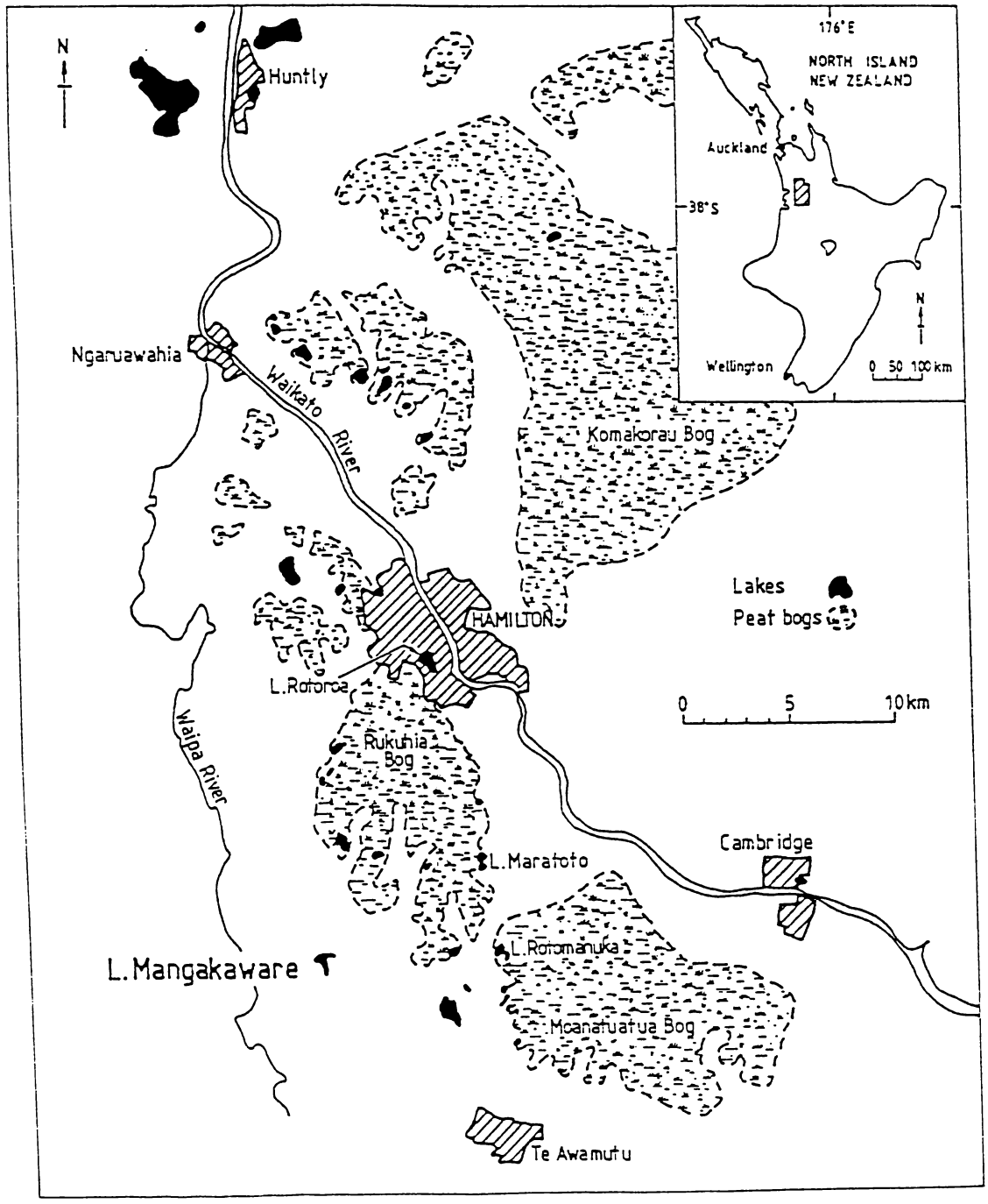

Figure 1. Location of Lake Mangakaware, and some other Waipa lakes referred to in this study.

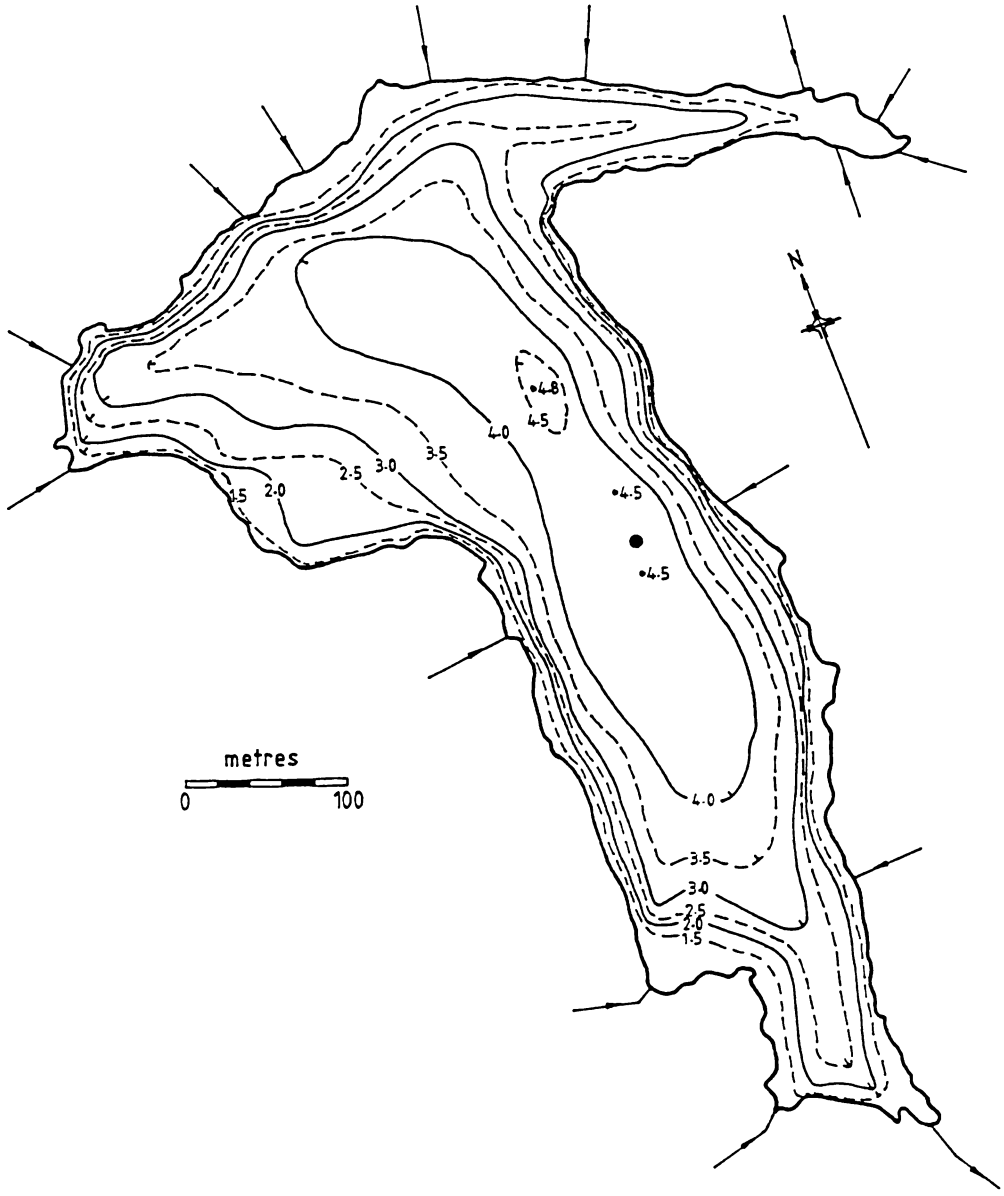

Figure 2. Bathymetric map of Lake Mangakaware. Arrows represent inlet and outlet drains. The central sampling site is marked with a circle. Isobaths in metres.

Table 1: Some morphometric and physiographic parameters of Lake Mangakaware (J.D. Green *unpublished data*).

Stratum (m)	**Area (m^2)**
0	133032
0.5	*
1.0	*
1.5	115769
2.0	104160
2.5	86997
3.0	71980
3.5	52090
4.0	29794
4.5	1805
Maximum length	0.68 km
Maximum width	0.32 km
Maximum depth	4.80 m
Mean depth	2.93 m
Relative depth	1.17%
Direction of main axis	N-S
Length of shoreline	2425 m
Shoreline development	1.88
Volume	39050m^3
Volume development	0.61

*** = No contour line**

Table 2: Physicochemical data from Lake Mangakaware during summer and winter. Data are compiled from this study, Chapman and Boubeé (1977), Boswell *et al.* (1985), Greenwood (1987), and J.D. Green (*unpublished data*).

Parameters		Summer (range)	Winter (range)
Temperature (°C)			
- surface		20.7 - 27.2	9.4 - 15.1
- bottom		18.8 - 24.4	8.5 - 14.4
Dissolved oxygen (gm^{-3})			
- surface		4.5 - 12	6.2 - 10.8
- bottom		0.0 - 0.4	5.7 - 9.8
Secchi depth (m)		0.5 - 1.5	0.8 - 2.5
pH		6.0 - 8.4	*5.8 - 6.7
Suspended solids (gm^{-3})		2.2 - 10.8	*2.8
T.P.	$mg\ m^{-3}$	36 - 116	26 - 39.5
T.D.P.	$mg\ m^{-3}$	13 - 38	16 - 19
D.R.P.	$mg\ m^{-3}$	0 - 5	*0
NO_3-N	$mg\ m^{-3}$	BDL - 351	1283 - 1974
NH_4-N	$mg\ m^{-3}$	6 - 110	84 - 112
T.K.N.	$mg\ m^{-3}$	798 - 1400	480 - 775
SO_4	$mg\ m^{-3}$	3.7 - 18.1	0 - 13
Cl	$mg\ m^{-3}$	16 - 17.6	13 - 14
Ca	$mg\ m^{-3}$	5.88 - 11.4	5.7 - 6.9
Mg	$mg\ m^{-3}$	2.56 - 2.9	2.2 - 2.3
Na	$mg\ m^{-3}$	10.1 - 12.5	10 - 10.4
K	$mg\ m^{-3}$	4.9 - 15.6	7.2 - 7.45
Total Mn	$mg\ m^{-3}$	0.03 - 0.25	0.06 - 0.07
Total Fe	$mg\ m^{-3}$	0.33 - 1.49	0.54 - 0.64
Electrical Conductivity (µS/cm)		110 - 151	108 - 114
**% oxygen saturation (surface)		73 - 140 ($\bar{x}$ = 105.4)	62 - 88 ($\bar{x}$ = 73.8)

***** = **mean value**
****** = **calculated from this study - pooled result of two seasons' data in each case (1988 & 1989)**
BDL = **below detectable limits**

with an exposed aspect and strong south-westerly winds, result in a high degree of water column disturbance, with large amounts of suspended material often visible.

Scientifically, the planktonic fauna of Lake Mangakaware is notable. Two species of calanoid copepods (*Boeckella delicata* and *Calamoecia lucasi*) are present in the lake, a relatively uncommon occurrence in New Zealand (Chapman *et al.* 1975). In addition, four cladoceran species, in two genera (*Ceriodaphnia* and *Bosmina*), are present. Two of these, *C. dubia* and *B. meridionalis,* are widespread throughout New Zealand (Chapman *et al.* 1975). The remaining two species, *C. pulchella* and *B. longirostris* s.l., have been noted only recently (1985 and 1987 respectively). The taxonomy of *Ceriodaphnia pulchella* and *C. dubia* is discussed in Greenwood *et al.* 1991. The identification of *Bosmina longirostris* s.l. is still somewhat tentative, but specimens have been examined by V. Korinek and identified as belonging to a "longirostris group" (V. Korinek *pers. comm.*).

The remainder of the planktonic zooplankton comprises the cyclopoid copepod cf. *Mesocyclops leuckarti,* and at least seventeen rotifer species. A variety of primarily littoral cladocerans, arachnids, and insect species are occasionally found in the plankton but their occurrences are sporadic and they are never very abundant.

Very few fish species are present in the lake. Both smelt (*Retropinna retropinna*) and mosquitofish (*Gambusia affinis*), which are present in nearby Lake Rotomanuka (Fig. 1), are absent, although there are small, restricted, littoral populations of *Gobiomorphus cotidianus* (Chapman and Boubée 1977; J.D. Green *pers. comm.*). The lake does, however, support large eel populations (*Anguilla* spp.) which are fished commercially on a small scale (J.A. Krippner *pers. comm.*).

1.2 CLIMATE

The topography and geographic position of the Hamilton Basin result in characteristically mild winters and warm summers with constant, high humidity (de Lisle 1967). Rainfall is high and regular, occurring on between 130 and 150 days per year, and varying between 1200 and 1400 mm annually. Westerly winds predominate, although the

Hamilton Basin is regarded as being one of the least gusty regions of New Zealand (de Lisle 1967).

1.3 SAMPLING

Dissolved oxygen and temperature measurements, and samples of phytoplankton and zooplankton, were taken between November 1987 and September 1989 at weekly (November 1987 - May 1988) or two-weekly (June 1988 - September 1989) intervals, at a mid lake station. Occasional periods of bad weather (most notably Cyclone Bola in early March 1988) meant the sampling interval was not always a uniform seven or fourteen days, although these intervals were maintained whenever possible.

It was assumed that because of the small size of the lake and the frequent mixing episodes, a sample taken from a single station at the deepest area of the lake was adequate to describe seasonal trends. Sample precision from two sites (one being the central site sampled here) was assessed in an earlier study of Lake Mangakaware (Greenwood 1987), and found to be acceptable (standard error < 20% of the mean, after Cryer 1983). Both sites showed the same trends and the shallower site (not sampled here) was the most variable of the two.

PART TWO
CHAPTER TWO
PHYSICOCHEMICAL CONDITIONS

2.1 INTRODUCTION

The annual cycles of heat and oxygen distribution in a lake are fundamental to its ecology. In shallow, polymictic lakes, such as Mangakaware, the dynamics of mixing events are pivotal to the understanding of plankton seasonality, and to patterns of nutrient regeneration. Similarly, mixing events alter the distribution of dissolved oxygen in lakes, important not only for its consequences for the lake biota, but also because the distribution of oxygen affects the solubility of inorganic nutrients, which can govern the timing of seasonal shifts in nutrient availability. The pattern of seasonal change in these physical parameters is discussed below.

2.2 FIELD METHODOLOGY

Measurements of temperature and dissolved oxygen concentration were made with a Yellow Springs Instruments meter (Model 57). Readings were made from the surface to the bottom at 0.5 metre intervals. Water transparency was measured with a standard, 20 cm diameter, Secchi disc.

2.3 RESULTS

2.3.1 Temperature

The changes in thermal conditions in Lake Mangakaware during the sampling period are shown in Figure 3. Surface temperatures ranged between a maximum of 27.2°C (16.2.88) and a minimum of 9.4°C (9.7.88) giving a seasonal temperature range, or STR, (Green *et al.* 1987), of 17.8°C, and an annual (1988) mean value of 19.2°C. The mixing patterns recorded during the sampling period were complex, typified by autumnal-winter holomixis, and by the transient development of summer stratification, often interrupted by brief periods of mixing.

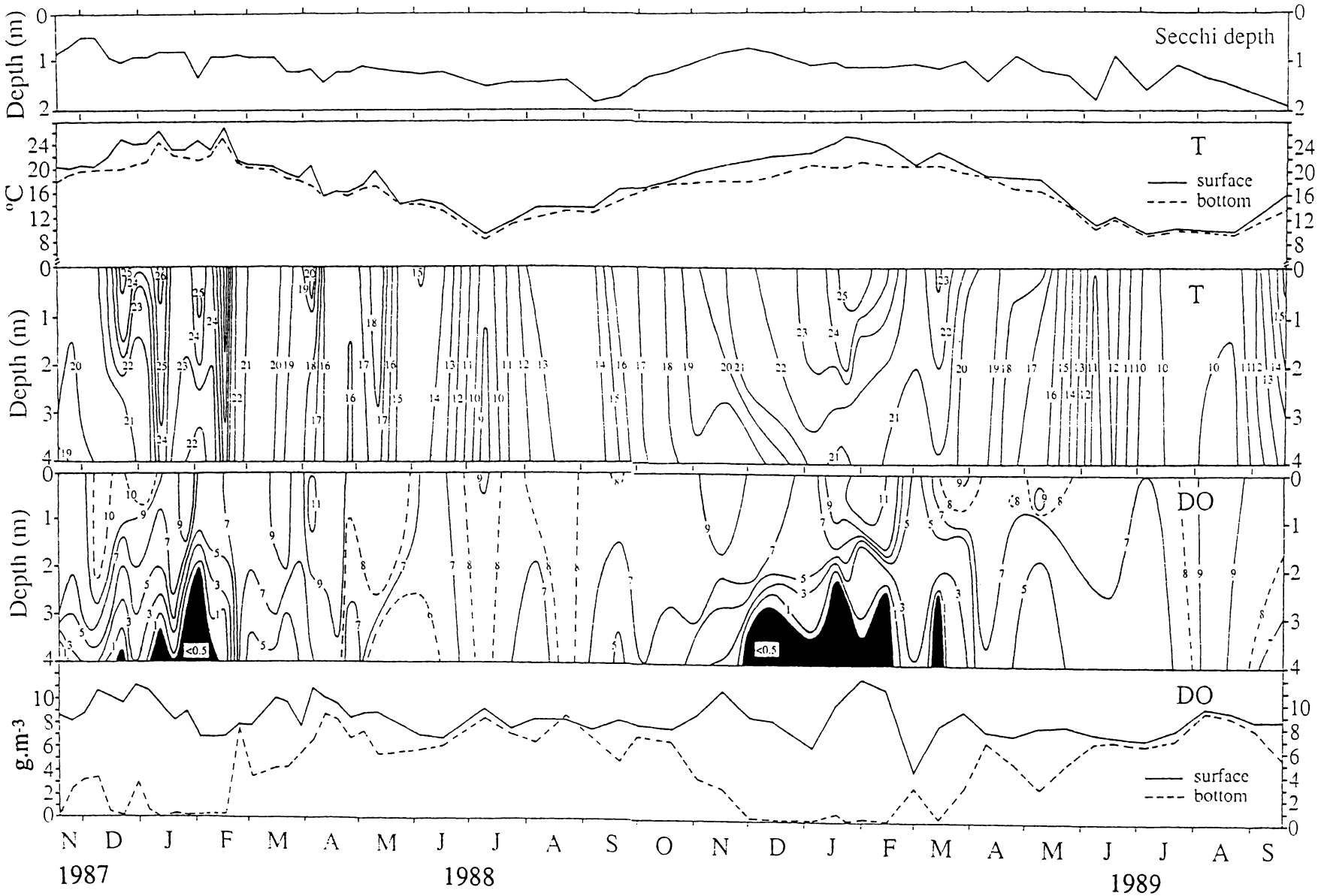

Figure 3. Seasonal changes in temperature (^{0}C), oxygen (g.m^{-3}), and Secchi transparency in Lake Mangakaware November 1987 - September 1989.

The pattern during the summer of 1988 was particularly influenced by windy conditions. Notably, Cyclone Bola, in early March, contributed to the early, rapid breakdown of stratification, and a period of mixing that lasted until early April when the lake developed a weak and transient thermal stability. The lake was essentially mixed from June through until mid November, when a weak stratification developed. This gradually strengthened as temperatures warmed through December 1988 and January 1989. During February of 1989 thermal stability declined and the lake was almost completely holomictic again. A weak stratification reestablished during March, but this was brief and the lake became homothermal again by April, remaining essentially so until the end of sampling.

2.3.2 Oxygen

Figure 3 shows the changes in dissolved oxygen during the sampling period. The patterns of oxygen distribution were strongly influenced by thermal conditions and were similarly complex. Even brief periods of thermal instability and mixing, such as in March 1988 and February 1989, resulted in marked increases in the oxygen content of bottom waters, and an almost uniform distribution of oxygen in the water column. Similarly, any brief periods of stability following surface heating (as on 14.3.89) were marked by a decline in the oxygen content of the hypolimnion. Oxygen depletion in the hypolimnion to levels below 0.5 gm^{-3} was typical of the summer periods, although in both 1988 and 1989 this was alleviated by mixing episodes. The highest overall oxygen levels occurred during winter holomixis, when concentrations ranged from 5.5 - 9 gm^{-3} and, apart from small declines above the sediments, were almost constant with depth. Surface dissolved oxygen levels were, however, highest during the summer of 1989, coincident with high algal productivity.

The percentage surface saturation levels (Table 2) ranged between 6.2% (4.7.89) and 140% (31.1.89) with values commonly exceeding 100% during the summer period. For much of the rest of year though, surface waters were slightly undersaturated, with increases in percentage saturation being broadly associated with peaks in algal abundance.

2.3.3 Secchi Transparency

Annual variations in the depth of Secchi transparency are plotted in Figure 3, and ranged between 0.5 metres (December 1987) and 1.8 metres (6.9.88). Typically, Secchi depths were lower during periods of warmer weather, high thermal stability, and/or increased phytoplankton abundance, and higher during the winter months when phytoplankton densities were low. This relationship was, however, neither consistent nor predictable. For example, Secchi transparencies during April 1988, when phytoplankton numbers were high, were considerably greater (1.4 m) than in November-December 1988 (0.7 m) when algal densities were similar. Notably though, the lower Secchi depths during the last two months of 1988 were associated with low lake levels, a pronounced bloom of *Closterium*, and a large amount of suspended material in the water column.

2.4 DISCUSSION

New Zealand lakes which develop thermal stratification have been variously classified as warm monomictic, thereimictic, or cheimomictic (Green *et al.* 1987). The thermal regime in Lake Mangakaware, which clearly fits none of these classifications, is best described as a discontinuous, warm polymictic system, characterised by a summer period punctuated by intervals of partial or complete mixing of the water column. The 1987 - 1989 period was in no way atypical, despite the considerable influence of Cyclone Bola in early March 1988. Intermittent episodes of mixing and stratification were recorded for Lake Mangakaware in 1985 - 1986 (Greenwood 1987) and in 1983 - 1984 (Etheredge 1987) also.

New Zealand's oceanic climate and characteristically strong winds have been associated with deep epilimnia and the late onset of summer stratification (Green *et al.* 1987). The impact of strong winds on relatively shallow lakes, such as Mangakaware, is significant. The characteristically unstable nature of the thermal conditions here can be related both to the windy conditions and the low mean depth of the lake (2.9 metres). Similar periodic disruption of summer stratification, attributable to strong winds, has been recorded in Lake Maratoto (Fig. 1) (Boubée 1983; Etheredge 1983, 1987), and in Lakes

Mangahia, Kainui, Ngaroto and Rotoroa (Etheredge 1987). The seasonal temperature range (STR) of surface waters in Lake Mangakaware, at 17.8°C, is higher than that given by Green *et al.* (1987) for North Island lakes (mean 13.0 ± 3.1°C). This was more the result of elevated temperatures in summer, than lower winter temperatures, the latter being well within the range typical for lakes in this region (Green *et al.* 1987). However, the high STR recorded for Lake Mangakaware in 1988 may have been atypical. STRs of 14°C and 15°C were recorded by Etheredge (1987) and Greenwood (1987) respectively, and these may be more typical values for this lake. More importantly, these values for STR are low in comparison with those recorded in lakes of similar latitude within continental regions (refer Green *et al.* 1987; Fig. 8). The lower STRs of New Zealand lakes relative to those in the Northern Hemisphere (Green *et al.* 1987; Burns 1991), particularly with respect to the higher winter temperatures, may have significant consequences for lake communities, encouraging year round primary production, and uninterrupted reproduction amongst zooplankton. Elevated winter temperatures may also result in high summer hypolimnetic temperatures (Green *et al.* 1987) thereby increasing the probability of deep and/or shifting epilimnia, and thermal instability. This in turn maximises the opportunities for short-lived pulsed episodes in the seasonality of phytoplankton, and may contribute to a dynamic pattern of shifting dominance amongst both primary and secondary producers.

The levels of surface oxygen saturation, which ranged between 62% and 140%, and were for most of the year below 100%, are in contrast to those found in other New Zealand lakes (e.g. Jolly 1968; Green 1975), where levels in the surface waters markedly exceed 100% saturation throughout summer, and during periods of low temperature also if phytoplankton productivity is high. Relatively lower saturation levels are frequently the result of high humic levels and accompanying chemical and photochemical oxidations (Gjessing and Gjerdahl 1970; Etheredge 1987). However, high loads of suspended particulate matter in Lake Mangakaware, both as a result of inflow, and of resuspension of bottom sediments during frequent mixing events, are likely to increase oxygen demand in the epilimnion also.

High oxygen demands in hypolimnetic waters, particularly as a result of increased development of the catchment, are often associated with increased eutrophy (Burns 1991). Certainly, according to the boundaries suggested by White (1983), nutrient levels in Mangakaware (Table 2) indicate a eutrophic status for this lake, and are in keeping with the oxygen depletion observed for hypolimnetic waters during summer. The high incidence of mixing episodes is significant in this respect also, as entrainment of bottom waters promotes nutrient regeneration, and thus internal loading (Wetzel 1983).

Secchi depths in Lake Mangakaware also reflect its high nutrient status, humic component, and high level of suspended organic material. Levels recorded were comparable with these in Lake Rotongaio (Forsyth *et al.* 1983), and in many of the small Waikato lakes (Chapman and Boubèe 1977) which, like Lake Mangakaware, are very productive. The unstable thermal regime of Lake Mangakaware, in combination with its high nutrient status, characterise a dynamic system, the ecology of which appears to be governed by frequent episodic events and successive replacement of species dominance. Aspects of this will be discussed in the following chapters.

PART TWO
CHAPTER THREE
PHYTOPLANKTON

3.1 INTRODUCTION

Patterns of phytoplankton seasonality are governed both by physical (allogenic) factors, such as temperature, light and the frequency of mixing events, and by autogenic or self regulating mechanisms, generated by the component species themselves (Reynolds 1984). These have been examined in detail for the Waikato lakes in Etheredge (1987), and the discussion of phytoplankton cycles here is restricted mainly to periodicity, in relation to the consequences it holds for the zooplankton community, in particular the Cladocera, which are the topic of this thesis.

3.2 DATA COLLECTION AND ANALYSIS

3.2.1 Field Methodology

Phytoplankton samples were taken with a rubber phytoplankton tube, 4 metres long and with an inside diameter of 10 mm. This delivered an integrated water sample of 314 ml, from which a 120 ml subsample was taken and fixed with Lugol's iodine, to a pale straw colour.

3.2.2 Laboratory Methodology

Phytoplankton were counted, with assistance from J. Baas, using the sedimentation technique of Utermöhl (1958), as recommended by Wetzel and Likens (1979) and discussed in Etheredge (1985). The sample to be counted was gently but thoroughly mixed and a known volume (4-25 ml) removed and settled for 24 hours (Etheredge 1985), before enumeration with a model M2 Olympus inverted microscope.

Only the 10-12 most dominant phytoplankton species were counted, with rarer species being noted but not enumerated. Counting continued until approximately 100 of each of the dominant species had been recorded (Lund *et al.* 1958). Counts were generally made at three magnifications: 200X, 400X, and 800X, and species were recorded as

plankton units or p.u. (Lewis 1978; Etheredge 1985). Thus, colonial species such as *Actinastrum, Dictyosphaerium,* and *Sphaerocystis*, and filamentous types (e.g. *Aulacosira*) were not counted as cells, but as discrete entities. The total number of each taxon per aliquot was obtained by multiplying the number occurring in the counts by the ratio of the chamber area to the area covered by the number of fields of view counted. This value was converted to numbers per ml by dividing by the subsample volume sedimented. 'Dead' cells, i.e., those with less than one half of the usual cellular contents, (Etheredge 1985) were not counted. Algal identification and taxonomic arrangement to the familial level (Table 3) follows Bourrelly (1966, 1968, 1970). Additional texts consulted for identification were those of Huber-Pestalozzi (1938, 1941, 1942, 1955, 1961, 1968) and Prescott (1962). Mean GALD (greatest axial linear dimension) values for the dominant species (Table 4) were taken from a previous study (Greenwood 1987), obtained following the method described in Etheredge (1983).

3.2.3 Sample Precision

The precision of the methodology (and equipment) used in algal enumeration has been discussed fully in earlier works based on the Waikato Lakes (Etheredge 1985, 1987). Using Fisher's Index of dispersion (Fisher 1948), Etheredge (1987) tested for both the randomness of phytoplankton distribution on the basal plate of the sedimentation chamber, and for randomness in the drawing of subsamples. She found that, provided the recommended technique was adhered to, it produced a random distribution for all taxa, except *Dinobryon cylindricum* and *Synura uvella*, both representatives of genera largely absent from Mangakaware during the sampling period. She also found no significant 'edge-effects', i.e., non-random settling patterns, when comparing the densities of the common taxa in peripheral and central areas of the chamber. Based on these assessments, no further tests of the methodology were done for this study.

3.3 RESULTS

3.3.1 Phytoplankton Composition

A total of 61 species (including varieties) in eight major taxonomic groupings, were recorded (Table 3). The percentage contribution of each of the major taxa to total numbers is given in Table 5 and a complete record of counts in Appendix 1, Table 1. Numerically, the phytoplankton were dominated by the Euchlorophyceae and the Diatomophyceae, and within each of these by only a single species, *Tetrastrum triangulare*, (mean density = 1978 p.u.ml^{-1}) and *Aulacosira distans* (mean density = 2115 p.u.ml^{-1}) respectively. The most diverse taxon was the Euchlorophyceae, with 34.4% of the total number of species recorded, although, with the exception of *T. triangulare*, none of these were among the ten most abundant. The desmids (21.3% of the total species), and euglenophytes (9.8% of the total species) were the next most diverse taxa, with the remaining 21.4% of species being distributed among other minor groups.

Small species (< 30 µm GALD) predominated among the chlorophytes, comprising 78.4% of the total green algal abundance and 98.9% of the euchlorophycean numbers. Of the 61 species recorded, only 30 could be considered to be major species (mean density ≥ 1.0 p.u.ml^{-1}), as defined by Etheredge (1983). Of these, nine species (30%) were in the Euchlorophyceae, six (20%) were desmids, and four species (13.5%) were diatoms.

3.3.2 Periodicity

In terms of abundance, the phytoplankton community was characterised by irregular episodes of species abundance, and marked fluctuations throughout the sampling period (Figs 4 and 5). Total density ranged from 149 p.u.ml^{-1} (4.7.89) to 30620 p.u.ml^{-1} (1.12.87) with a mean value of 5915 p.u.ml^{-1} (n = 57). Typically the phytoplankton community exhibited low numbers through winter and summer, with pronounced autumnal (1988) and late spring - early summer (in 1988 & 1989) peaks due almost exclusively to *Tetrastrum triangulare* and *Aulacosira distans* respectively.

The Euchlorophyceae had one major peak of abundance in autumn (April-May 1987) due almost entirely to the major dominant at the time, *Tetrastrum triangulare*, with

Table 3: List of phytoplankton species

TAXON

Chlorophyta

Euchlorophyceae

Volvocales

Volvocaceae

Volvox aureus

Chlorococcales

Chlorococcaceae

Tetraedron regulare
T. planktonicum
T. limneticum

Palmellaceae

Sphaerocystis sp.

Oocystaceae

Kirchneriella contorta
K. lunaris
Monoraphidium contortum
M. irregulare
Nephrocytium limneticum
Oocystis sp.

Micractiniaceae

Micractinium pusillum

Dictyosphaeriaceae

Botryococcus braunii
Dictyosphaerium pulchellum

Scenedesmaceae

Actinastrum hantzschii
Coelastrum microporum
C. reticulatum
Scenedesmus sp.
Tetrastrum triangulare

Hydrodictyaceae

Pediastrum duplex
P. tetras

Zygophyceae

Zygnematales

Chlorophyta (continued)

Desmidiaceae

Closterium aciculare
C. acutum
C. acutum var. *variabile*
C. gracile
C. setaceum
Closterium sp.
Staurastrum angulum var. *obesum*
S. leptocladum var. *insigne*
Staurastrum sp. 1
Staurastrum sp. 2
Staurastrum sp. 3
Staurodesmus triangularis
Staurodesmus sp.

Chromophyta

Xanthophyceae

Mischococcales

Pleurochloridaceae

Pseudostaurastrum sp.

Sciadaceae

Centritractus belanophorus

Diatomophyceae

Coscinodiscales

Coscinodiscaceae

Aulacosira distans
A. granulata var. *angustissima*
Cyclotella sp.

Diatomales

Diatomaceae

Tabellaria sp.

Naviculales

Nitzschiaceae

Nitzschia acicularis

Cyanophyta

Cyanophyceae

Chroococcales

Chroococceae

Aphanocapsa sp.
Coelosphaerium hutzingianum
Microcystis aeruginosa
M. flos-aquae
M. minutissima

Cyanophyta (continued)

Nostocales

Nostocaceae

Anabaena circinalis
Aphanizomenon sp.

Oscillatoriaceae

Lyngbya limnetica sp.

Euglenophyta

Euglenophyceae

Euglenales

Euglenaceae

Euglena oxyuris
Phacus suecicus
Phacus sp.
Trachelomonas planktonica
T. volvocina
Trachelomonas sp.

Pyrrohphyta

Cryptophyceae

Cryptomonadales

Cryptomonadaceae

Cryptomonas sp. 1
Cryptomonas sp. 2

Dinophyceae

Peridiniales

Peridiniaceae

Peridinium cinctum
P. contortum

Ceratiaceae

Ceratium sp.

Chloromonadophyta

Chloromonadaceae

Vacuolaria sp.

Table 4: Sizes (GALD) of dominant phytoplankton species recorded in Lake Mangakware (December 1987 - September 1989)

Taxon	GALD µm
Actinastrum hantzschii	22
Anabaena circinalis	85
Aulacosira distans	*22/7
Aulacosira granulata var. angustissima	*116/29
Botyrococcus braunii	232.60
Centritractus belanophorus	158
Ceratium sp.	190
Closterium aciculare	319.12
Closterium acutum var. *variable*	46.25
Cryptomonas sp. 1	12.5
Cyclotella sp.	10.8
Dictyosphaerium pulchellum	35
Microcystis minutissima	60
Monoraphidium contortum	20
Nitzschia acicularis	85
Peridinium cinctum	53.76
Scenedesmus sp.	9.0
Sphaerocystis sp.	32
Staurastrum leptocladum var. *insigne*	54.25
Tetastrum triangulare	5.49
Trachelomonas volvocina	14
Vacuolaria sp.	12.8

* **Both p.u. GALD and cell GALDs are included as cells sometimes occurred singularly.**

Table 5: Percentage contribution of the main phytoplankton taxonomic groups to total phytoplankton density in Lake Mangakaware, December 1987 - September 1989.

	percentage of total
Chlorophyta	
Euchlorophyceae	35.19
Zygophyceae	9.19
Chromophyta	
Xanthophyceae	0.06
Diatomophyceae	40.87
Cyanophyta	
Cyanophyceae	3.75
Euglenophyta	
Euglenophyceae	9.49
Pyrrophyta	
Cryptophyceae	0.93
Dinophyceae	1.37
Chloromonadophyta	
Chloromonadaceae	0.16

a very small contribution from *Botryococcus braunii*, the latter species having a rather broad period of abundance from March through to July 1988.

Of the small, numerically less important greens, *Monoraphidium* spp. and *Actinastrum hantzschii* had coincident peaks of abundance in December 1987, with *Actinastrum* peaking again, just two months later, in February-March. Most of the remaining small euchlorophycean species exhibited rather sharp abundance peaks, with species replacing each other sequentially throughout the period spanning December 1988 (*Tetraedron* spp, *Kirchneriella* spp.) through January - March 1989 (*Kirchneriella* spp., *Scenedesmus* sp. and *Coelastrum* spp.). Of the larger Euchlorophyceae, *Sphaerocystis* and *Dictyosphaerium pulchellum* also peaked during this general period, in late spring

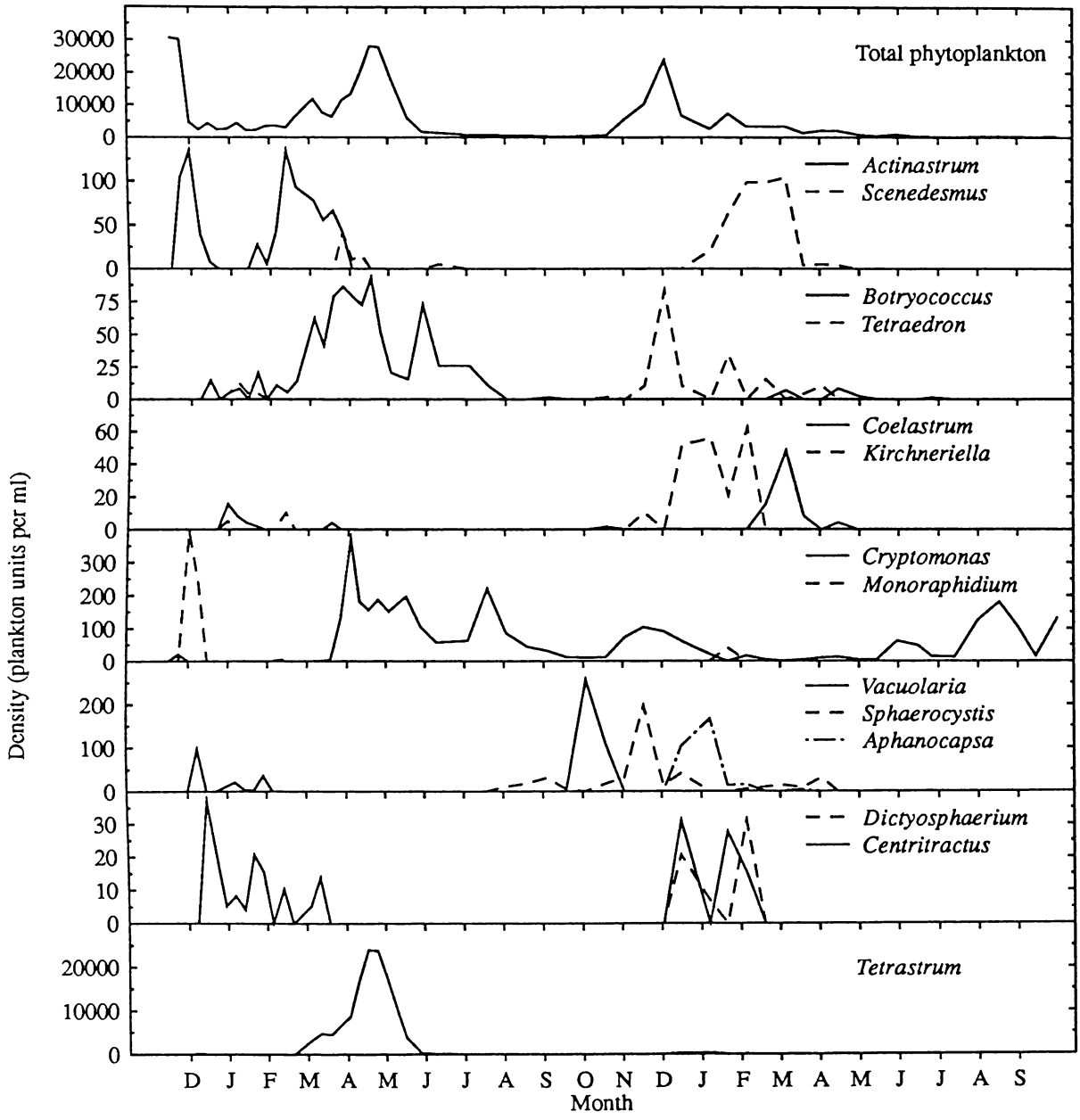

Figure 4.

Seasonal variation in total numbers of phytoplankton plus individual species (*Actinastrum hantzschii*, *Scenedesmus* spp., *Botryococcus braunii*, *Tetraedron* spp., *Coelastrum* spp., *Kirchneriella* spp., *Monoraphidium* spp., *Cryptomonas* spp., *Aphanocapsa* sp., *Sphaerocystis* sp., *Vacuolaria* sp., *Dictyosphaerium pulchellum*, *Centritractus belanophorus*, and *Tetrastrum triangulare*) in Lake Mangakaware during November 1987-September 1989.

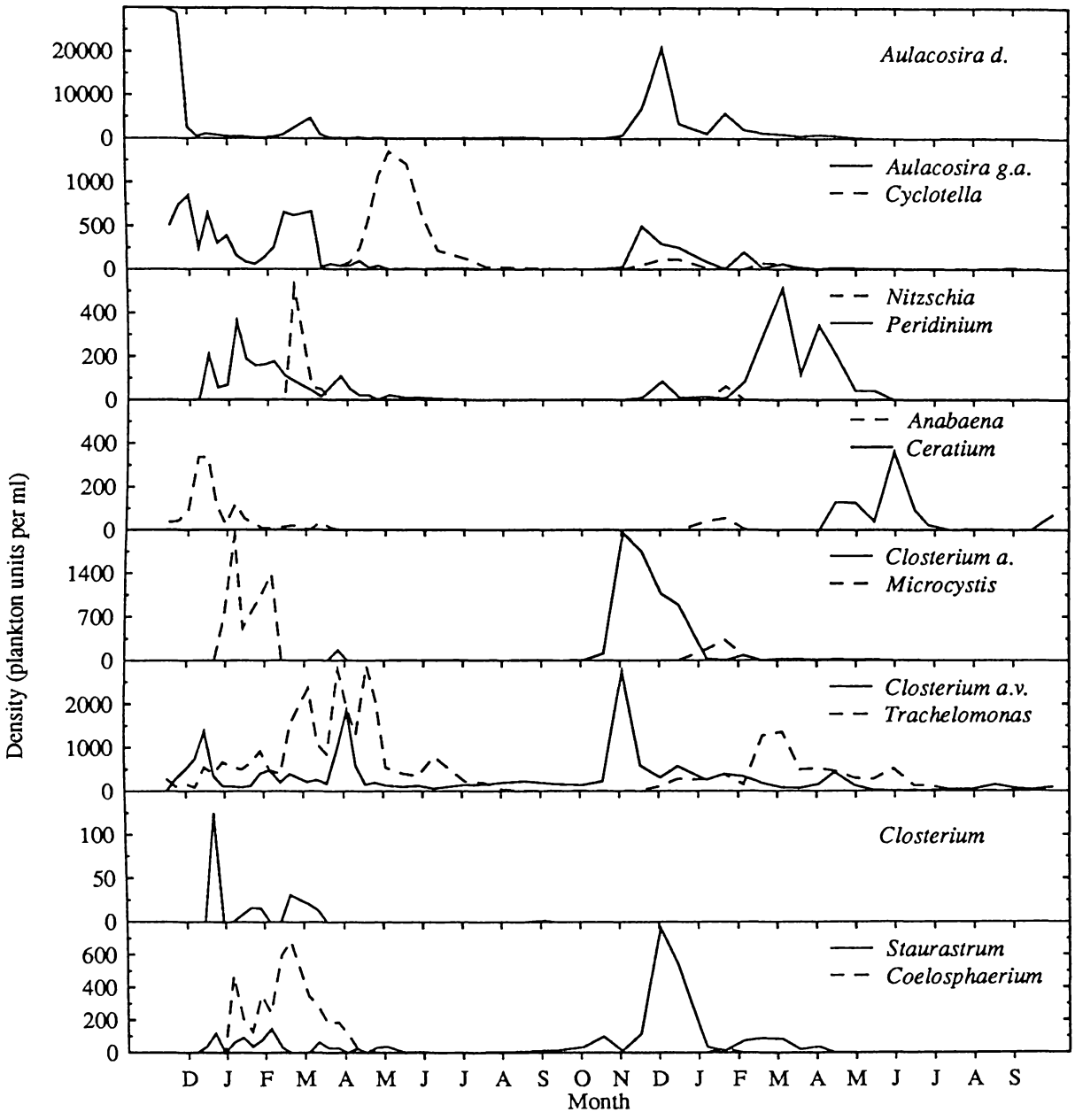

Figure 5.

Seasonal variation in numbers of *Aulacosira distans*; *Aulacosira granulata* var. *angustissima*; *Cyclotella* sp.; *Nitzschia acicularis*; *Peridinium cinctum*; *Anabaena circinalis*; *Ceratium* sp.; *Closterium aciculare*; *Microcystis* spp., (*M. aeruginosa*, *M. minutissima*, *M. flos-aquae*); *Closterium aciculare*; *Closterium acutum* var. *variabile*; *Trachelomonas* spp. (includes *T. planktonica* and *T. volvocina*); *Closterium* spp. (*C. acutum*, *C. gracile*, *C. cetaceum*); *Coelosphaerium hutzingianum*, and *Staurastrum* spp. in Lake Mangakaware during November 1987 -September 1989.

(November 1988) and late summer (mid February 1989) respectively. The desmids, dominated by *Closterium aciculare*, *Cl. acutum* var. *variabile* and *Staurastrum*, were also most abundant during late spring, peaking in October-November 1988, just prior to the rise in diatom numbers, and the broader period of small euchlorophycean abundance. The chloromonads, represented by *Vacuolaria*, showed their only peak of abundance at this time also.

The diatom community, of which *Aulacosira distans* was numerically the most important, predominated in late spring - early summer in both 1987 and 1988, in the latter year peaking immediately after the decline in desmid abundance. Brief, sequential peaks in the abundance of *A. granulata* var. *angustissima* and *Nitzschia* (February 1988), and *Cyclotella* (April-May 1988) coincided with a period of reduced thermal stability that extended sporadically from mid February through to early May.

The cryptophyceaeans, represented by two species of *Cryptomonas*, were the least marked by sharp peaks of abundance, being present, albeit in quite low numbers (maximum 373 p.u.ml^{-1}), throughout most of the year, generally being in greater abundance during autumn, following periods of reduced thermal stability.

The dinophyceans were generally not very abundant, *Peridinium* being notable during only one period (February-April 1989), and *Ceratium* following with a peak in May. When present however, their large size made them a conspicuous feature of the phytoplankton community.

Of the remaining taxa, the cyanophytes were most abundant in summer (December 1987 - March 1988), with *Anabaena circinalis* (December) being replaced by *Microcystis* spp. (January) and *Coelosphaerium* (February). However, numerically the cyanophytes were never a major part of the summer phytoplankton, although their larger size meant their contribution to the biomass was probably quite significant.

Trachelomonas (various species but mainly *T. volvocina*) were the predominant euglenophytes, peaking sporadically throughout late summer and autumn in both 1988 and 1989.

3.4 DISCUSSION

In contrast to the situation in the Northern Hemisphere, the seasonal cycles of phytoplankton in New Zealand tend not to fit any obvious successional pattern, and the timing of peak algal abundance varies widely between lakes. For example, abundance peaks were recorded in late winter and summer in Lake Ototoa (Donovan 1970; Green 1976b) and Lake Rerewhakaaitu (Chapman *et al.* 1987), in late spring and summer in Lake Maratoto (Etheredge 1983, 1987) and in autumn and late winter in Lake Pounui (Lawless 1983). Differences in seasonality can be related to differences in availability of light and nutrients, and to different mixing patterns, which, as discussed in Chapter Two, are themselves a reflection of New Zealand's mild, windy, oceanic climate. While most temperate Northern Hemisphere lakes exhibit low phytoplankton productivity in winter, this is not the case in Lake Taupo and other central North Island lakes, where mixing increases the availability of nutrients and allows algal biomass to develop (Viner and White 1987). Although the phytoplankton community in Lake Mangakaware exhibited high species density and abundance in late spring and autumn rather than in winter, a similar rationale probably holds. Mixing episodes during these seasons were coincident with increased phytoplankton growth, and shifted peaks away from the early spring abundance period that is typical of Northern Hemisphere phytoplankton communities following winter holomixis.

In terms of species dominance in Lake Mangakaware, this too is unpredictable year to year. In both 1983 - 1984 (Etheredge 1987) and 1985 - 1986 (Greenwood 1987) the dominant classes were the Euchlorophyceae and the Diatomophyceae, as in this study, but the species responsible for this dominance were different each year. In 1983 - 1986, the dominant euchlorophycean genus was *Monoraphidium* (*M. contortum* in 1983 - 1984; *M. tortile* in 1985 - 1986), whereas in 1988 - 1989 this position was occupied by *Tetrastrum triangulare*. Similarly, *Acanthoceras zachariasi* was overwhelmingly the dominant diatom in 1983 - 1986 but was absent from the lake in 1988 -1989, when *Aulacosira* predominated.

If there was any pattern at all in the phytoplankton periodicity in Lake Mangakaware during 1988 - 1989 it was one of a series of unpredictable and brief abundance peaks, with the predominance of a single species at each of the two times of peak abundance. Some trends were in keeping with those found for phytoplankton communities both in New Zealand and in Northern Hemisphere lakes. For example, the cryptophyceans (*Cryptomonas* spp.) were most abundant in autumn and early winter, continuing to flourish after the peak of euchlorophycean abundance. Moreover, they were perennially present in low to moderate numbers between the pulses of other algae. These features are typical of species in cryptophyte-microflagellate complex (Stewart and Wetzel 1986) many of which, being facultative heterotrophs, and auxotrophic, benefit from the increase in dissolved organic matter arising after the decomposition of other taxa. Similarly, as is typical for the Cyanophyta (Reynolds 1982, 1984), representatives of this class were only present in summer periods when thermal stability increased. Both *Closterium* and *Aulacosira* were abundant in late spring - early summer, which is a little earlier than is typical for these genera in the Northern Hemisphere (Reynolds 1982), but not dissimilar to the pattern recorded in New Zealand, although the latter genus is often a winter bloomer in central North Island eutrophic lakes (Viner and White 1987).

The predominance of small (< 30 μm) species in the dominant classes in Lake Mangakaware is unusual for lakes of eutrophic status, although amongst the less abundant taxa, (e.g. the Zygophyceae) large species predominated (e.g. *Closterium*). It is difficult to assign a trophic status to Lake Mangakaware on the basis of phytoplankton assemblage alone. The large numbers of *Trachelomonas* indicate eutrophy, but some of the species classed by Flint (1975) as typical of eutrophic waters (*Actinastrum hantzschii, Micractinium pusillum*, and *Centritractus* spp.) were not very abundant. In particular, the cyanophytes, which are typical bloom formers in nutrient rich waters, were only of minor importance, and some other summer dominants typical of eutrophy such as *Dinobyon* (Viner and White 1987) were not found at all during 1988 - 1989 although they were present from 1983 - 1986 (Etheredge 1987, Greenwood 1987).

The pattern of species replacement in Lake Mangakaware appeared to be closely related to the unstable thermal regime, where periods of stability alternated with short periods of holomixis or weakly developed stratification, and there were rapid shifts in species assemblage and dominance. For example, the unstable stratification/mixing regime through February and March 1988 was coincidental with increases in the abundance of sub-dominant diatom species. Similarly, maximal *Aulacosira* densities occurred in late November - early December of that year, at the end of winter holomixis, but declined rapidly when stratification reestablished in January 1989. Typically diatoms are associated with periods of lake turnover (Stewart and Wetzel 1986), and in polymictic systems such as in Lake Mangakaware periodic mixing enables species with potentially high settling rates, such as diatoms, to take advantage of the nutrient regeneration occurring at such times. Conversely taxa, such as the cyanophytes, with the physiological adaptations to exploit periods of high stability, low nutrient availability, and high temperatures, predictably exhibit a summer abundance. In Mangakaware, there were no very prolonged periods of thermal stability and thus the cyanophytes were probably unable to achieve the bloom proportions they reach in other eutrophic lakes (Viner and White 1987).

Given its high nutrient status, the predominance of small euchlorophycean genera in Lake Mangakaware (rather than cyanophytes, desmids and chrysophytes) may seem unusual. However Reynolds (1984) suggests that an abundance of small euchlorophycean species such as *Ankistrodesmus* and *Scenedesmus* may not be uncommon in shallow lakes subject to very high nutrient loading. Padisák *et al.* (1988) have also demonstrated that wind-induced mixing is important in phytoplankton succession, with smaller algal species showing synchronous development after storms.

The governing factors in the autogenic succession of species within the rather more broad seasonal periodicity is difficult to explain without the benefit of nutrient analyses. Clearly the patterns of community change in Lake Mangakaware are complex, and physical (e.g. mixing) and biotic (e.g. grazing) factors will both be important. The fact that species dominance is not consistent from year to year is evidence of the unpredictability of

the lake, and the ability of species to rapidly exploit transient periods of favourable conditions must be pivotal in governing the composition and periodicity of the phytoplankton community in this lake.

PART TWO
CHAPTER FOUR
ZOOPLANKTON - GENERAL CYCLES

4.1 INTRODUCTION

The animal components of the freshwater plankton community are dominated by three taxa: rotifers, and two classes of crustaceans (copepods and cladocerans). In New Zealand these communities are distinctive both in their (apparently) low species diversity, and in the paucity of many predators typical of Northern Hemisphere lakes (Chapman and Green 1987). Here, the structure and seasonality of the three predominant taxa, the Rotifera, the Copepoda, and the Cladocera are discussed.

4.2 DATA COLLECTION AND ANALYSIS

4.2.1 Field Methodology

Zooplankton was sampled using a PAR electric peristaltic pump at 1 metre depth intervals from the surface to the bottom (4 m). The hose end was fitted with a four-way split piece, projecting horizontally from the base of the hose. This had the effect of drawing in water from all directions at the desired depth and helped to reduce problems of intake avoidance by the more agile copepod species. At each of the five depths, 20 litres was pumped through a specially constructed, short cone net, fitted with 47 μm plankton mesh. The zooplankton from each 20 litre volume was washed into a sample container, before the next depth sample was taken. All five samples were then combined and preserved with cold sucrose-formalin (final concentration c. 4%) (Prepas 1978). Samples were refrigerated after collection to minimise the fading of visible lipid in the cladocerans.

The zooplankton was also sampled by two vertical net hauls, from the bottom to the surface, using a 0.92 metre long Nansen type net (mouth diameter 215 mm) fitted with 0.47 μm mesh, modified after the design of Currie and Foxton (1967). Severe clogging of fine meshed nets makes net hauls an unreliable sampling method for quantitative work in Lake Mangakaware (Greenwood 1987). Therefore, these samples were used solely for the

purpose of obtaining extra animals for use in determining the reproductive parameters and age structure of the cladoceran populations.

4.2.2 Laboratory Methodology

For counting, the entire plankton sample was searched for species occurring in very low numbers (particularly *Piona* and *Anisops* species which occurred in the plankton only sporadically). For most species, high densities meant that enumeration of the entire sample was not practicable and subsampling was necessary.

The sample was diluted to a known volume in an appropriately sized pyrex beaker. Beaker volumes were checked for accuracy and the same beakers used throughout (Greenwood 1987). The sample was stirred using a figure of eight motion and a 5 ml subsample withdrawn using a wide mouthed automatic pipette. This method minimises any vortices in the sample which could lead to unrepresentative subsamples being withdrawn (Cryer 1983).

The subsample was then transferred to a squared, perspex counting tray, and mounted on the movable stage of an Olympus X-2 stereomicroscope. Counts were made at 31.5X magnification and recorded on a Denominator double bank counter. The wide variation in the abundance of different species meant that different dilutions were required for the enumeration of a single sample. Generally, 30-150 individuals of each taxon were counted per subsample, and the subsampling was repeated until the results were reproducible. The mean count was then multiplied by the appropriate dilution factor to give the number per 100 litre sample.

4.2.3 Taxonomic Identification

Taxonomic identification followed Chapman and Lewis (1976) (for Copepoda and Arachnida); Ruttner-Kolisko (1974) and Koste (1978) for Rotifera; Smirnov and Timms (1983) for the Chydoridae; and my own work for *Ceriodaphnia* (but see also Greenwood *et al.* 1991). Specimens of both *Bosmina* species were identified by V. Korinek (*pers. comm.*), but for *B. longirostris* s.l. at least, these identifications are tentative. Calanoid and cyclopoid nauplii were not distinguished but were enumerated together. Rotifers were identified to specific level wherever possible, but to generic level only when the taxonomy was unclear.

4.2.4 Sample Precision

Three factors contribute to the variability of final plankton counts: the non-random distribution of animals in the lake; the efficiency of the sampling equipment; and the accuracy of the subsampling technique (Green 1973; de Nie and Vijverberg 1985). Total sampling precision (including site variability) was estimated in Greenwood (1987) for Schindler-Patalas trap samples from two sampling stations. Those counts indicated that the zooplankton populations in Lake Mangakaware are non-randomly distributed and described by the negative binomial distribution where $\sigma^2>\mu$ (Elliot 1977). Here, two factors: pump efficiency, and subsampling and counting accuracy, were assessed jointly for their contribution to total sample variability. A set of five replicate 100 litre pump samples from the sampling station were taken on 24 November 1987. An estimate of the population mean and variance for each taxon was derived from the replicates and the standard error of the samples estimated, using Elliott's (1977) formula for determining the precision of a given number of samples.

$$Ds = \sqrt{\frac{1}{n\bar{x}} + \frac{1}{n\hat{k}}}$$

where $\hat{k}$ is estimated by:

$$\hat{k} = \frac{\bar{x}^2}{s^2 - \bar{x}}$$

Ds = precision (S.E. /$\bar{x}$) $\bar{x}$ = sample mean

s^2 = sample variance n = number of samples

$\hat{k}$ = the exponent in the negative binomial equation.

In none of the taxa sampled did the predicted standard error of the 100 litre samples exceed 20% of the mean, (Appendix 2), an acceptable level of precision for zooplankton population studies (Cryer 1983).

4.3 RESULTS

4.3.1 Compositional Analysis

A list of the planktonic zooplankton species recorded during the sampling period is given in Table 6 and a complete record of all zooplankton counts in Appendix 1, Table 2. The Cladocera account for approximately one fifth of the total zooplankton numbers recorded, with the remainder being divided similarly between the copepods and rotifers (Table 7). *Bosmina longirostris* was the major contributor (59.2%) to total cladoceran abundance, being present throughout most of the sampling period, and often in high numbers (maximum 112200 per 100 litres).

Calamoecia lucasi was the predominant copepod present throughout the sampling period, remaining reasonably abundant even during winter when numbers of *Boeckella* and *Mesocyclops* were very low.

The rotifer population was dominated by *Keratella cochlearis*, which accounted for 34.3% of the total rotifer numbers. The rest of the rotifer community comprised mainly *Pompholyx* cf. *sulcata* (18.7%), *Keratella tropica* (11.6%), *Conochilus* sp. (10.8%), and *Asplanchna* (9.9%), with the remaining 10 species being numerically far less important (less than 5% of total rotifer numbers each).

4.3.2 Periodicity

Copepoda

Changes in the seasonal abundance of the Copepoda are plotted in Figure 6. *Mesocyclops leuckarti* was primarily a summer-autumnal species during 1987 - 1989, with pronounced increases in population density in February, March, and April of 1988 and in January and March-April of 1989. In contrast, numbers were very low throughout the winter and early spring period (June to October).

Both calanoid species (but particularly *Boeckella delicata*) followed a similar pattern to that of *Mesocyclops*, with increased summer and autumnal abundance. *B. delicata* numbers were generally much lower than those of *Calamoecia lucasi* with the latter species showing only one very pronounced summer peak in January 1989, and a pattern of rather less dramatic fluctuation throughout the rest of the sampling period.

Table 6: List of planktonic zooplankton species found in Lake Mangakaware, November 1987 - September 1989.

ARTHROPODA

Arachnida

Acarina

Pionidae

Piona (Tetrapiona) pseudouncata (Piersig, 1906)
Piona spp.

Crustacea

Copepoda

Calanoida

Centropagidae

Boeckella delicata Percival, 1937
Calamoecia lucasi Brady, 1906

Cyclopoida

Cyclopidae

Cyclopinae

cf. *Mesocyclops leuckarti* (Claus, 1857)

Branchiopoda

Diplostraca

Cladocera

Bosminidae

Bosmina meridionalis Sars, 1904
B. longirostris s.l.

Chydoridae

**Alona (Biapetura) affinis* (Leydig, 1860)
**Alona guttata* Sars, 1862
**Chydorus sphaericus?*

Daphniidae

Ceriodaphnia dubia Richard, 1895
C. cf. *pulchella* Sars, 1862
**Simocephalus vetulus* (Schødler, 1858)

Macrothricidae

**Ilyocryptus sordidus* (Lieven, 1848)

Insecta

Hemiptera

Notonectidae

**Anisops* sp.

ROTIFERA

Monogononta

Ploima

Brachionidae

Brachionus sp. L*
Brachionus angularis Gosse, 1851
Epiphanes clavulata Ehrenberg, 1832
Euchlanis dilata Ehrenberg, 1832
Keratella cochlearis Gosse, 1851
K. tropica (Apstein)

Trichocercidae

Trichocerca similis (Wierzejski, 1893)
Trichocerca (Diurella) gracilis (Tessin, 1890)

Gastropodidae

Gastropus sp.

Asplanchnidae

Asplanchna brightwelli Gosse, 1850
A. priodonta Gosse, 1850

Synchaetidae

Polyarthra cf. *remata* (Skorikow, 1896)
Synchaeta (stylata-pectinata group)

Floscullariacea

Testudinellidae

Filinia cf. *pejleri* Hutchinson, 1964
Pompholyx cf. *sulcata* Hudson, 1885

Hexarthridae

Hexarthra mira (Hudson, 1871)

Conochilidae

Conochilus sp.

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* **Mainly littoral species**
L* **Large species**

Table 7: Percentage contribution of the major (>0.5%) zooplankton species and taxonomic groups to total zooplankton density in Lake Mangakaware, November 1987-September 1989.

Taxonomic Group	percentage of total zooplankton
Cladocera	21.7
Copepoda	40.1
Rotifera	38.2
Cladocera	
Ceriodaphnia pulchella	5.37
Ceriodaphnia dubia	0.57
Bosmina longirostris	12.81
Bosmina meridionalis	2.90
Copepoda	
*cf. *Mesocyclops leuckarti*	5.79
**Boeckella delicata*	2.17
**Calamoecia lucasi*	7.55
Total copepod nauplii	24.59
Rotifera	
Keratella cochlearis	11.94
Keratella tropica	4.05
Conochilus sp.	3.75
Polyarthra remata	1.03
Filinia cf. *pejleri*	1.76
Synchaeta sp.	1.30
Brachionus angularis	0.36
Pompholyx cf. *sulcata*	6.52
Trichocerca similis	1.70
Hexarthra mira	2.02
Asplanchna spp.	3.43

***adults and copepodites**

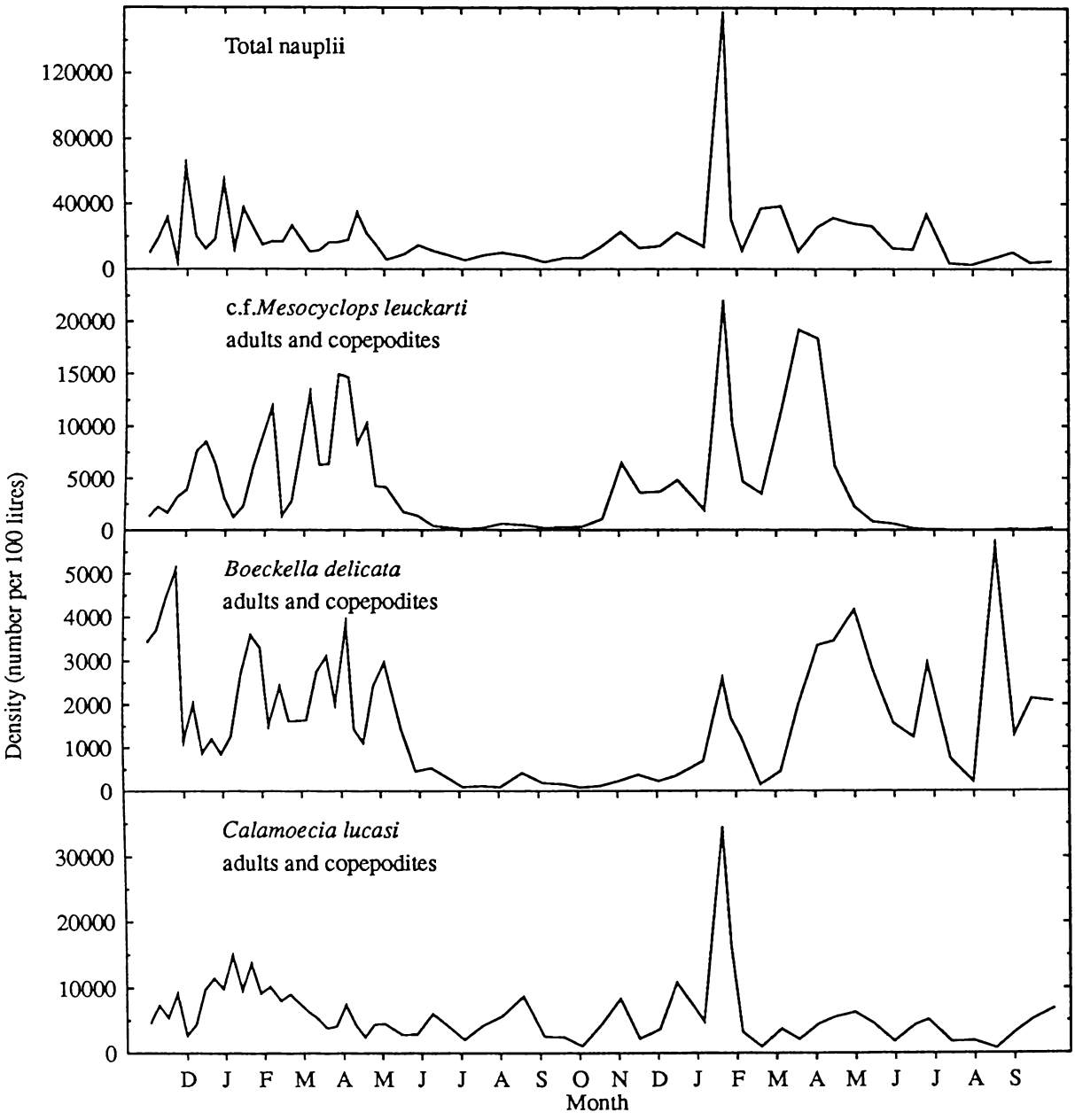

Figure 6.

Seasonal variation in numbers of total nauplii, c.f. *Mesocyclops leuckarti*, *Boeckella delicata*, and *Calamoecia lucasi* in Lake Mangakaware during November 1987-September 1989.

Not unexpectedly, naupliar abundance showed similar fluctuations with generally low numbers throughout the winter periods and a single very large population increase in mid January 1989, corresponding to peaks in *Mesocyclops* and *Calamoecia* density.

Cladocera

Of all the taxa, the Cladocera exhibited the most pronounced pattern of seasonal replacement of species (Figure 7). Although maximal densities achieved by each species varied widely (112200 per 100 litres for *Bosmina longirostris* and 4700 per 100 litres for *Ceriodaphnia dubia*), each had a quite restricted period during which it was the dominant cladoceran. For *Bosmina meridionalis* this period was extremely short, with a sharp period of peak abundance in December of 1987, followed by a rapid decline and disappearance from the plankton by mid June 1988. *B. meridionalis* reappeared briefly in April 1989 in low numbers and on only two occasions.

The peak in abundance of *B. meridionalis* was followed in February by the appearance of *Ceriodaphnia pulchella*, the numbers of which reached a sharp peak in March 1988, then generally declined in a fluctuating manner and remained rather low and stable through winter and spring. *C. pulchella* had disappeared from the plankton by December 1988, not reappearing again until the following winter.

Coincident with the decline in peak *C. pulchella* abundance was an increase in the abundance of *C. dubia* throughout the winter and spring of 1988 reaching a peak at the beginning of November, just before *C. pulchella's* disappearance. Following this peak in abundance, *C. dubia* disappeared from the plankton entirely for almost five months, not being recorded again until May 1989 when it increased dramatically through winter to an early spring peak at the end of the sampling period, during which time it was the predominant cladoceran.

Of all four cladoceran species, *Bosmina longirostris* was the most persistent species, being present, with the exception of the first three months, throughout the entire sampling period. Relative to the maximal density achieved, low numbers of *B. longirostris* were evident from the time of its appearance at the beginning of March until it increased sharply in early summer 1989. There followed a sharp decline and somewhat

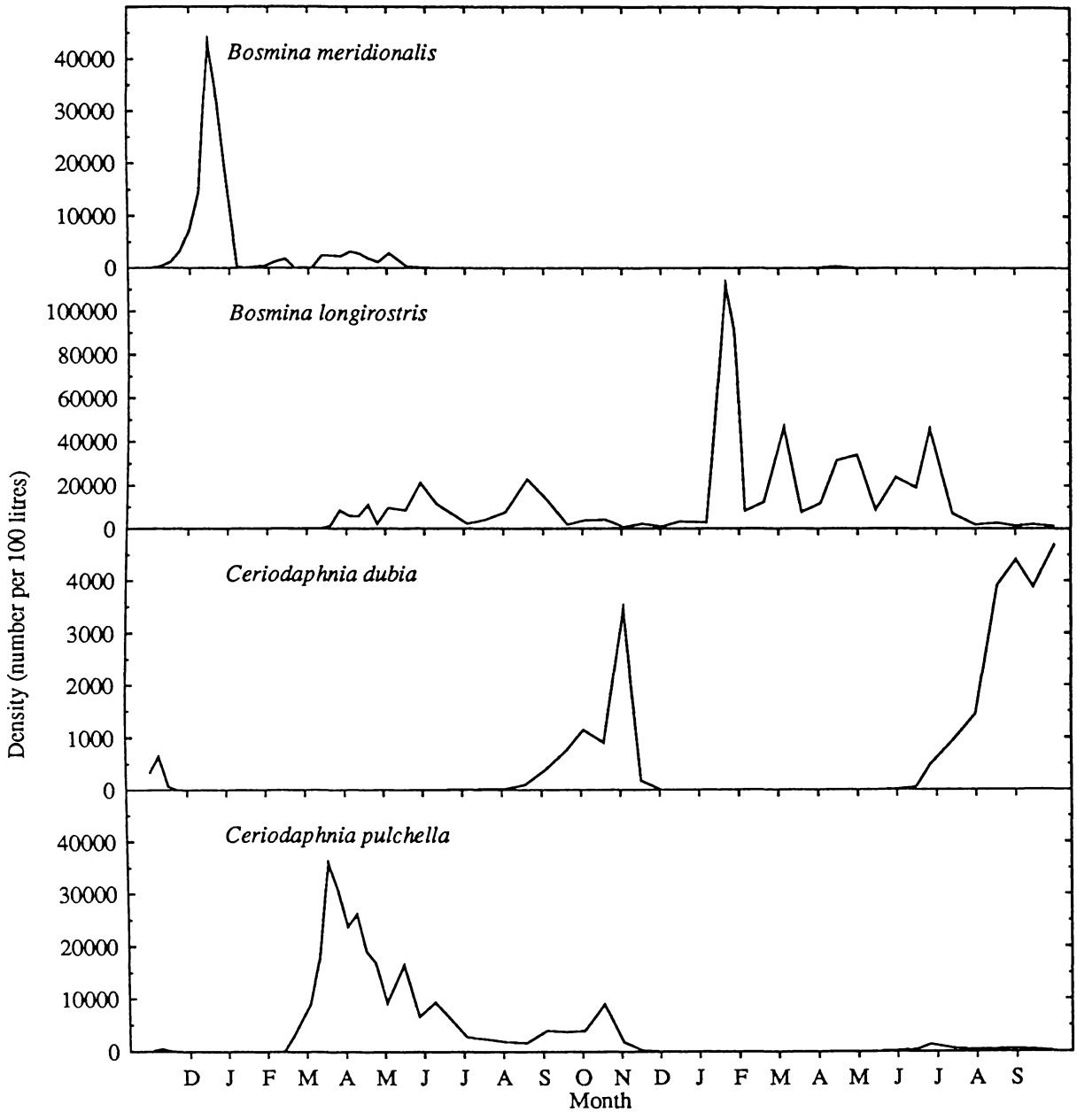

Figure 7.

Seasonal variation in numbers of *Bosmina meridionalis*, *Bosmina longirostris*, *Ceriodaphnia dubia*, and *Ceriodaphnia pulchella* in Lake Mangakaware during November 1987-September 1989.

lower but variable numbers throughout the summer and early winter. At the time of *C. dubia's* dramatic increase in July 1989, the numbers of *B. longirostris* were already low, remaining so until the end of sampling.

The seasonal replacement of Cladocera was thus quite clearly defined, with *B. meridionalis* (December 1987) being followed by a peak in *C. pulchella* density (March-April 1988), a brief increase in *C. dubia* (October-November 1988), and a 1989 cycle where the Cladocera were dominated first by *B. longirostris* and then by *C. dubia.* Interestingly, although *B. longirostris* did maintain a reasonably high population abundance throughout most of 1988, there was a clear spring decline in 1988 coincident with the peak in *C. dubia* density.

Rotifera

The pattern of species abundance in the Mangakaware rotifer community (Figs 8 and 9) was one of sequential sharp peaks, with most species (the exceptions being *Filinia* cf. *pejleri, Keratella tropica* and *Conochilus*) having only a brief period during which they were significant contributors to the plankton. The seasonality of total rotifer abundance was, however, marked by a very large increase in summer densities in 1989 that was almost entirely due to the increased numbers of *Keratella cochlearis.* Smaller increases in total rotifers were recorded during the summer of 1987 - 1988 and again in winter 1989.

Eight species (*F.* cf. *pejleri, Polyarthra* cf. *remata, K. tropica, K. cochlearis, Trichocerca gracilis, Hexarthra mira, Epiphanes clavulata* and *Pompholyx* cf. *sulcata*), exhibited peaks of abundance in summer (late November - February). Of these, only *H. mira* and *K. tropica* peaked during both of the summers covered by the sampling period. *F.* cf. *pejleri, P.* cf. *sulcata,* and *H. mira* were the predominant species during 1987 - 1988, while the following summer was dominated almost exclusively by *K. cochlearis*, the density peak of which was very large, but restricted only to January 1989.

Rotifer populations in autumnal and winter periods were generally very sparse during 1988, with only a small contribution from a large *Brachionus* species, and rather low and steady numbers of *Trichocerca similis.* The latter species reached a peak in spring 1988, together with *Synchaeta* which also peaked during this period

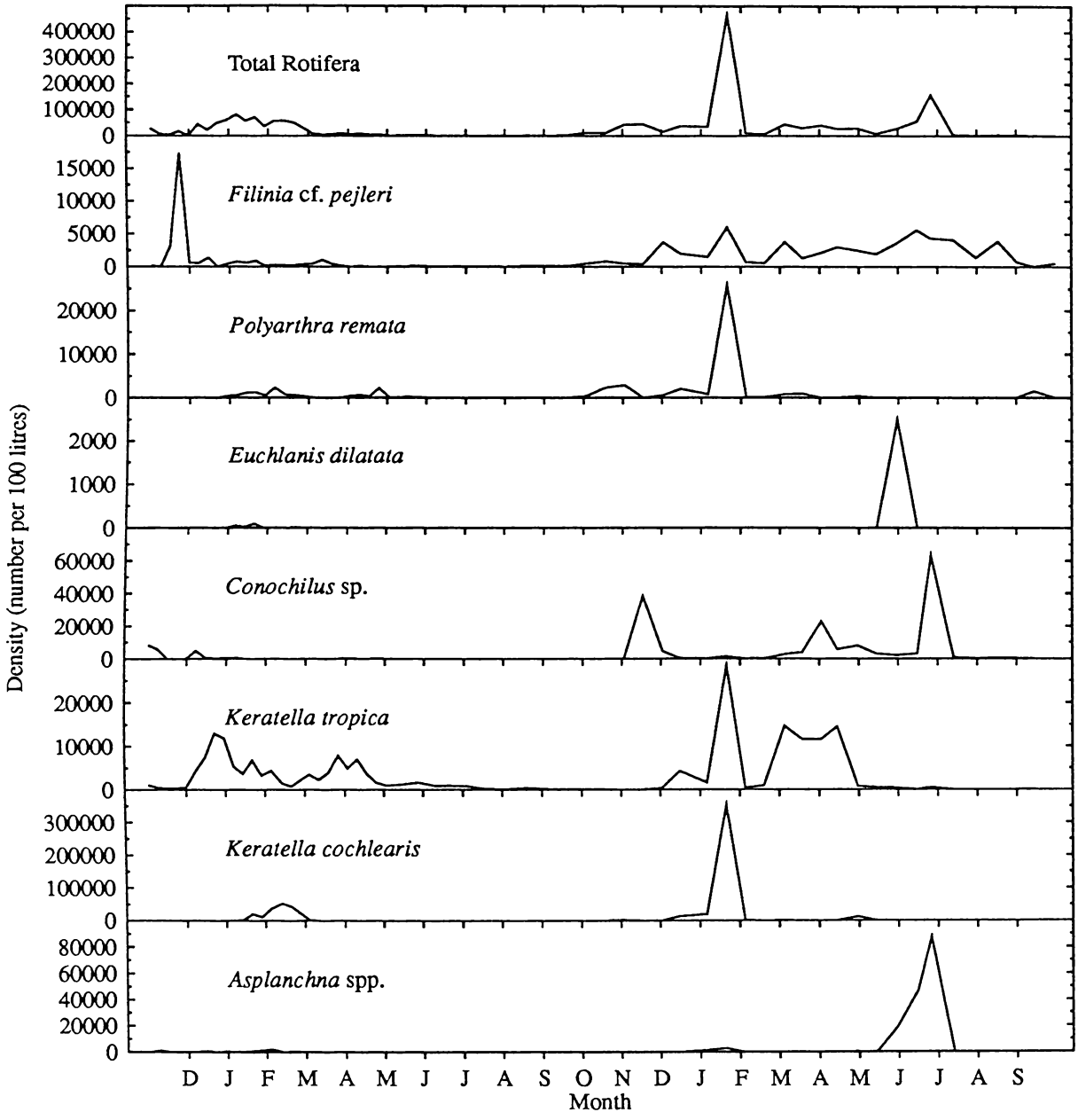

Figure 8.

Seasonal variation in total rotifer abundance and in the numbers of *Filinia* cf. *pejleri*; *Polyarthra remata*; *Euchlanis dilatata*; *Conochilus* sp.; *Keratella tropica*; *K. cochlearis*; and *Asplanchna* spp. (*A. priodonta*, *A. brightwelli*) in Lake Mangakaware during November 1987-September 1989.

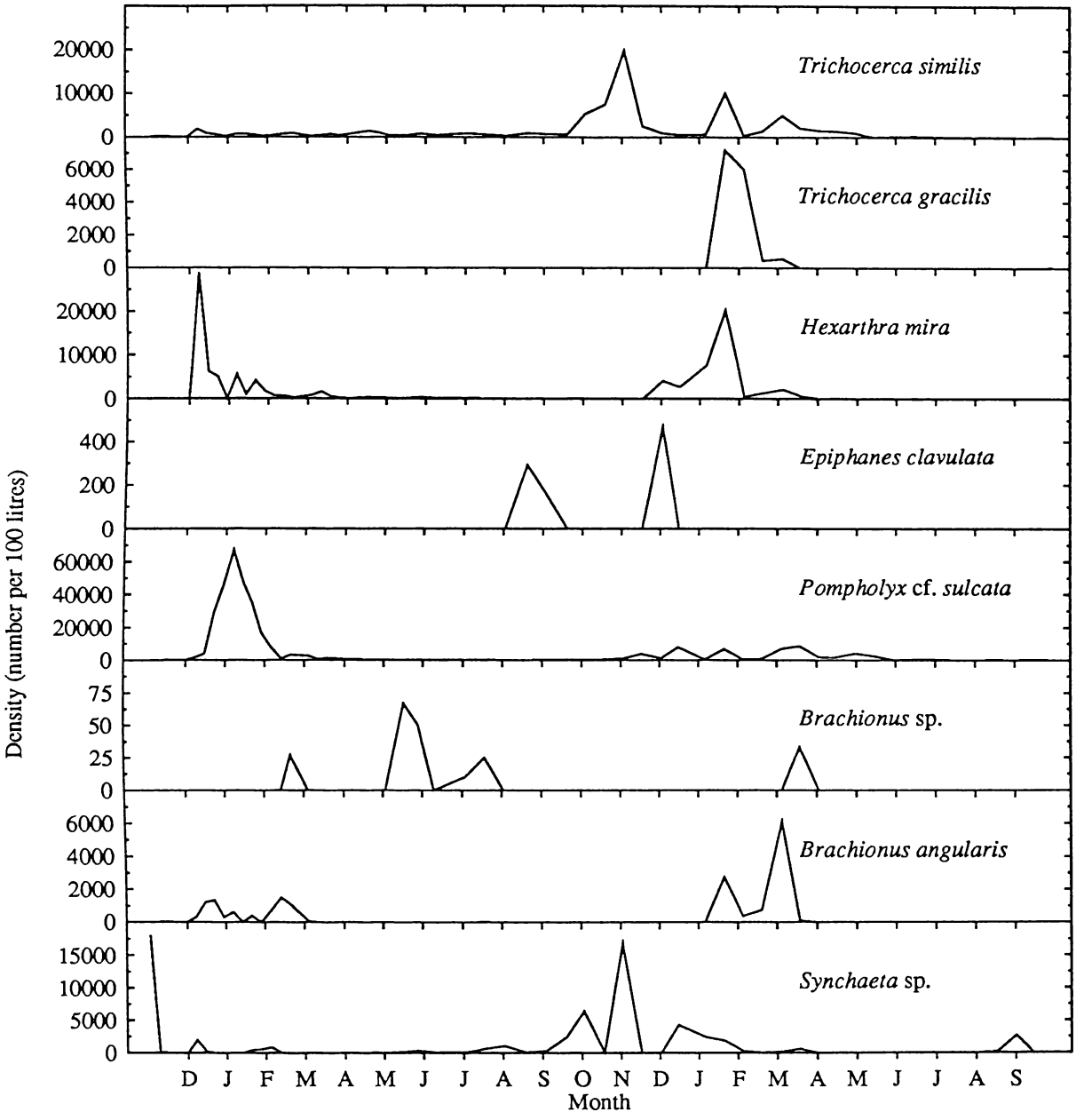

Figure 9.

Seasonal variation in numbers of *Trichocerca similis*, *T. gracilis*, *Hexarthra mira*, *Epiphanes clavulata*, *Pompholyx* cf. *sulcata*, *Brachionus* spp., and *Synchaeta* sp. in Lake Mangakaware during November 1988-September 1989.

(September - November). During the second winter period of sampling, rotifers were generally much more abundant with major contributions from two genera of large rotifers, *Euchlanis (E. dilata)* and *Asplanchna* (*A. priodonta* and *A. brightwelli)*. These followed the decline of an autumn population of *Brachionus angularis*, which reached its peak abundance in March 1989. The colonial rotifer *Conochilus* also peaked during this period, after a period of general abundance that extended from the beginning of October. *Filinia*, which had virtually disappeared from the plankton after a summer peak in 1987, reappeared in late spring 1988 and continued to make a significant contribution to the rotifer numbers until the end of sampling.

4.4 DISCUSSION

Numerically, the dominant taxa in Lake Mangakaware during 1987 - 1989 were calanoid copepods and rotifers, the Cladocera comprising a much smaller proportion of the total zooplankton. A predominance of calanoid copepods in the limnetic Crustacea is well documented in New Zealand (Barker 1967; Green 1976b; Forsyth and McCallum 1980; Lawless 1983; Chapman and Green 1987; Burns 1991), but rotifers have been little studied and generalisations about their numerical importance (or taxonomy) are not possible. Forsyth *et al.* (1983) recorded a numerical dominance by rotifers in Lake Rotongaio, with their seasonality being characterised by a succession of abundance peaks, each dominated by particular species. This was similar to the pattern in Lake Mangakaware, with density increases in the rotifer community being dominated by only a few species at a time.

Total zooplankton densities in Lake Mangakaware were very high compared with those recorded from other New Zealand lakes, where rotifers have been enumerated. The maximum total density in Lake Mangakaware during 1988 - 1989 (7.96×10^5 m^{-3}) was four times that found by Lawless (1983) in Lake Pounui (1.9×10^5 m^{-3}), and twelve times the maximum recorded by Green (1976b) in Lake Ototoa (5.75×10^4 m^{-3}). The cyclopoid populations, in particular, reached much higher densities (maximum = 2.2×10^4 $100l^{-1}$) than is typical for this taxon in New Zealand, where populations are often sparse and numbers are generally lower than those of other taxa (Chapman *et al.* 1975; Chapman and Green 1987). The seasonal cycle of cf. *M. leuckarti* in Lake Mangakaware, where winter

populations are typically low (Greenwood 1987), was similar to that described for this species in Lakes Pupuke (Barker 1967) and Ototoa (Green 1973, 1976b). Green (1976b) suggested that *M. leuckarti* populations in northern New Zealand lakes exhibit a pattern of year round breeding, with increases in spring and summer. Since adults, copepodites and nauplii of *M. leuckarti* were never completely absent from the plankton, such a pattern seems true for this species in Lake Mangakaware also. Moreover, littoral populations were often extremely high (*pers. obs.*) particularly during summer when peak planktonic densities were recorded.

The pattern of seasonal abundance of *Calamoecia lucasi*, with a very sharp increase in density in January, is unlike that recorded for this species in Lakes Ngapouri, Okaro, Rotokakahi, Okareka, Rotoma, Okataina, or Tikitapu (Chapman *et al.* 1985), where autumn and/or spring abundance is more typical. Similarly, Green (1976a) and Lawless (1983) recorded peak densities in March for this species in Lakes Ototoa and Pounui respectively. *Calamoecia* always predominated over *Boeckella* in Lake Mangakaware, although the two species were similar in their pattern of seasonality. Chapman and Green (1987) suggest that *C. lucasi* is an ecologically tolerant species, and may be advantaged by its smaller size and lower food requirements during periods of resource depletion. Its coexistence with *Boeckella* on the other hand, may be a function of frequent changes in the food base and mixing regimes in Lake Mangakaware, which may allow the requirements of each species to be met (Hutchinson 1967; Chapman and Green 1987). There is evidence, for example, that *Boeckella* and *Calamoecia* may utilise different size fractions of the phytoplankton. Forsyth and James (1991) showed that *C. lucasi* preferentially selected particles in the 0-3 μm range, in a system where the predominant size fraction was greater than 20 μm, and, in an earlier study, enclosure experiments to assess grazing effects demonstrated the ability of *Boeckella* to feed raptorially on long filamentous algae (James and Forsyth 1990).

The seasonal fluctuations in the densities of the Cladocera in Lake Mangakaware during 1987 - 1989 were almost identical in pattern (particularly for *Ceriodaphnia*) to those in 1985 - 1986 (Greenwood 1987), although, in this study, the absolute density changes were an order of magnitude higher for both species of *Ceriodaphnia*, and five

times higher for *Bosmina*. Unfortunately, the two *Bosmina* species were not distinguished in this previous study (Greenwood 1987) and the two abundance peaks observed for this genus in 1987 - 1986 were not due just to the one species, *B. meridionalis*. If the magnitude and timing of the peaks in *Bosmina* abundance is an indication, then the autumn peak recorded in 1985 was probably due to *B. longirostris* and the smaller summer (1986) peak to *B. meridionalis*. Interestingly, although *C. dubia* showed similar timing in its peak abundance in both 1988 and 1989, neither *B. meridionalis* nor *C. pulchella* repeated their 1988 patterns the following year. The high densities of *B. longirostris* and rotifers (see below) through summer and autumn may have been influential in this, acting to depress the levels of available food sufficiently to prevent successful breeding by other Cladocera. It was not until the numbers of *B. longirostris* fell in 1989 that other cladocerans showed any significant increase.

The repetition of a predictable seasonal pattern of species replacement appears to be unusual for New Zealand Cladocera, which are generally thought to exhibit irregular fluctuations in the timing of abundance peaks, both between adjacent lakes, and from year to year (Chapman and Green 1987). However, previous workers have identified only *C. dubia* and *B. meridionalis* in their seasonal studies, and there is now some question as to which of four (or more!) species were examined. The apparent unpredictability of cladoceran cycles in New Zealand may simply reflect the rather poorly established taxonomy of the genera here.

The most striking feature of the seasonality of the Lake Mangakaware Cladocera is the clear separation of peak densities, and the predominance of only one species at a time. Inverse relationships in the abundance of *Ceriodaphnia* and *Bosmina* have been recorded in Lakes Rotorua and Rotoiti (Chapman 1973), Lake Johnson (Burns and Mitchell 1980), Lake Taupo (Forsyth and McCallum 1980), Lake Pounui (Lawless 1983), and Lake Rerewhakaaitu (Chapman *et al.* 1981). This pattern is not consistent though, and coincidence in the timing of peak abundance has been recorded also, as in Lake Hayes (Burns and Mitchell 1980).

A single late autumn period of *Ceriodaphnia* abundance, similar to that of *C. pulchella* in Lake Mangakaware, has been recorded in Lake Okataina (Chapman *et al.*

1985) but seems to be unusual for this genus in New Zealand, where spring and/or summer abundance is more common (e.g. the Auxiliary Nihotupu Reservoir, Green 1968; Lakes Rotorua and Rotoiti, Chapman 1973; Lakes Taupo, Rotorua, and Rotoiti, Jolly 1977; Lake Taupo, Forsyth and McCallum 1980; Lake Rerewhakaaitu, Chapman *et al.* 1981; Lake Pounui, Lawless 1983; Lake Grasmere, Staples 1984).

The potential for competitive exclusion and, conversely, niche diversification to avoid competitors, are much debated topics. Earlier studies (e.g. Allan 1973, 1977; Neill 1975a, b; Jacobs 1977; Lynch 1978, 1979; Gliwicz 1980) have concentrated on niche partitioning and the efficiency of resource use. More recently, the emphasis has been not just on resource partitioning, but on the particular aspects of life histories that enable niche specialisation (e.g. Goulden *et al.* 1982b; Tessier 1986b; Mort 1990; Rothhaupt 1990; Tessier and Consolatti 1991; Lynch 1992). The clear separation of the cladoceran population peaks, and the failure of *C. pulchella* and *B. meridionalis* to repeat their 1988 pattern the following year, suggests that competition may be forcing different species to occupy different seasonal positions. However, it is likely that the seasonal dynamics may be constrained not only by competition, but also by genetically determined life history adaptations that predispose different species to particular seasonalities (adaptation to lower temperatures for example). This topic will be addressed more fully in the following chapter on Cladocera.

The pattern of rotifer seasonality during 1987 - 1989 was dominated by the large peak in numbers in the second summer of sampling. Smaller peaks of abundance reflected successive sharp peaks in the density of different species. Most New Zealand studies have paid scant attention to the rotifers, and their taxonomy and seasonality is little studied here. However, this study indicates that the communities may be more diverse than first thought. *Asplanchna* is probably the best studied member of the phylum in New Zealand, and a summer or autumn abundance appears to be characteristic of the genus in New Zealand (e.g. Lakes Rotorua and Rotoiti, Chapman 1973; Lake Rerewhakaaitu, Chapman *et al.* 1981; Lake Benmore, Stout 1981). The *Asplanchna* population in Lake Mangakaware did not fit this pattern in 1987 - 1989, although a summer/autumn abundance was recorded in 1985 - 1986 (Greenwood 1987). *Filinia* cf. *pejleri* was one of the most uniformly

abundant species over the sampling period and was not restricted to only one season, although it was absent throughout the winter of 1988. This pattern differs from that found in Lake Rotongaio (Forsyth *et al.* 1983) where peaks in abundance were restricted quite clearly to spring and autumn, although in this lake *Filinia* was the dominant rotifer genus.

The pattern of seasonal abundance of two of the larger species, *Epiphanes clavulata* and *Euchlanis dilata*, was somewhat contrary to what might be expected on the basis of what is known about these species. *Epiphanes* was sporadically abundant in winter and spring of 1988, its numbers declining as stratification patterns stabilised in early summer. *E. clavulata* is typically a warm, stenothermous species (Koste and Shiel 1987), and is often found in small, oxygen depleted ponds, or in the hypolimnion of small lakes when oxygen depletion is severe (J.D. Green *pers. comm.*). Its disappearance just before hypolimnetic oxygen levels fell (Fig. 3) is therefore rather at odds with its known ecology and, indeed, is in contrast to the pattern it exhibited in 1985 - 1986 (Greenwood 1987). Similarly, *Euchlanis dilata*, a species known for its association with the cyanophyte blooms on which it feeds (Ruttner-Kolisko 1974), was most abundant in early winter, when cyanophytes were virtually absent.

It appears the rotifers do not conform to any well defined seasonality. Most of the species recorded in Lake Mangakaware are tolerant of a wide range of temperatures and salinities (Ruttner-Kolisko 1974), and their seasonal patterns more probably reflect their differing abilities in exploiting rapid changes in the food base (see Chapter Three). Certainly, there were times during the sampling period when large inputs of flocculent organic material, following heavy rain, were noted (e.g. in late September 1988), and many rotifers (e.g. *Brachionus*) are preferentially detrital feeders (Ruttner-Kolisko 1974). Such inputs represent a readily available and exploitable food source, to which a population may rapidly respond if other conditions are favourable. In this respect, the rotifer community in Lake Mangakaware appears to be influenced by allogenic events, in a similar manner to the phytoplankton.

The seasonal cycles of different rotifer genera can be compared between lakes, and, in some cases, the patterns of abundance coincide. *Asplanchna* is a good example of this. However, there are more cases where the seasonalities are markedly different. For

example, *Keratella* appears to be a summer genus in Lake Mangakaware (Greenwood 1987, this study) but peaked in autumn and winter in Lake Rotongaio (Forsyth *et al.* 1983). Similarly, *Hexarthra* occurred only in autumn and winter in Lake Ototoa (Green 1976b), but is clearly a summer genus in Lake Mangakaware (Greenwood 1987; this study). Until the taxonomy of New Zealand rotifers is better clarified, and the populations studied more carefully, it is unwise to offer generalisations about community structure and species abundance.

The paucity of large bodied daphnids in New Zealand may be an important factor in the determining rotifer abundance in some lakes in this country. MacIssac and Gilbert (1991), for example, examined the competitive abilities of rotifers in the presence and absence of large and small bodied Cladocera, and found that competitive dominance of cladocerans over rotifers decreased markedly with increasing cladoceran body size, and that rotifers and small cladocerans could coexist, although these situations were always accompanied by suppression of one or both populations. Interestingly, the species used for these studies were *Keratella cochlearis, B. longirostris,* and *C. dubia*, all of which coexist in Lake Mangakaware. In addition, in an earlier study (MacIssac and Gilbert 1989), the competitive ability of *K. cochlearis,* in culture with the small bodied *Daphnia ambigua,* was greater when food levels were chronically low.

The influential factors in the seasonal dynamics of the zooplankton community can be broadly classified into those that are largely physical, for example temperature and patterns of mixing, and those that are biotic - competition, predation, and resource utilisation, for example. The rotifer community, characterised by a pattern of successive species replacements, appears to respond rapidly to abrupt changes in the physical environment and resource base. The paucity of rotifers through winter supports this, in view of the fact that the species present are typically thermophilic (Ruttner-Kolisko 1974). The Copepoda, too, exhibit a strong, apparently temperature related, seasonal response, maintaining low populations during winter, when development times are prolonged. Peak copepod abundances also coincided broadly with peak algal densities, suggesting a close dependence on an algal food base for this group.

The Cladocera, in contrast, do not appear to exhibit seasonal patterns clearly related only to temperature or algal abundance. At lower temperatures *C. dubia* has a two to three day advantage over *C. pulchella* and *B. meridionalis* in embryonic development time (Greenwood 1987; Appendix 4), and is well suited to rapid population expansion at cooler temperatures. At higher temperatures though, the development times of *Bosmina* and *Ceriodaphnia* are similar, and that developmental advantage is lost. Thus, while temperature appears to be influential in cladoceran seasonality, clearly other factors must be important, at least in the dynamics of *Bosmina* and *C. pulchella.*

Varying preferences in the use of the available food base may also be pivotal in governing cladoceran seasonality. For example, peak densities of both species of *Bosmina* were generally associated with increased abundance of *Aulacosira* spp. (primarily *A. distans)*, suggesting that this cladoceran is at least not inhibited by the presence of filamentous species. The "specialised collector" mode of feeding is well documented for *Bosmina* (Balseiro *et al.* 1991). This genus has been shown to feed preferentially on large particles (De Mott 1982; Bleiwas and Stokes 1985), and is also an efficient feeder at low concentrations of preferred algae (De Mott 1982; De Mott and Kerfoot 1982). Similarly Fulton (1988) showed that *B. longirostris*, of all the (various) taxa tested, had the highest selectivity for *Melosira (Aulacosira) granulata angustissima.* The potentially large contribution of bacteria and picoplankton (0.2 - 2 μm) to the food base cannot be discounted either. Although neither of these fractions was assessed in this study, their importance as food sources is likely to be paramount (e.g. Pace *et al.* 1983; Porter *et al.* 1983; Stockner 1991). The input of detritus and dissolved organic matter is also likely to be of particular significance to zooplankton, particularly in more humic systems (Salonen and Hammar 1986).

Wylie and Currie (1991) suggest that where copepods dominate the crustacean community, bacteria and picoplankton contribute insignificantly to the food base, but that this is not the case when cladoceran densities are high. Etheredge (1987) found that bacteria were rapidly and significantly depleted within limnocorrals containing zooplankton in Lake Maratoto, suggesting that they may have been providing a valuable carbon source in this lake. This is likely to be the case for Mangakaware also. The

competitive advantage of bacterial feeding in a stained lake such as Mangakaware, is obvious, considering that in such lakes bacteria often make up 50% of the biomass available to herbivore zooplankton (Hessen 1985). Certainly, studies of the filter mesh sizes of Cladocera (Geller and Müller 1981) suggest that size selectivity may be critical in the seasonal dynamics of filter feeding zooplankton, and that species composition is strongly influenced by the abundance of bacterial cells available to species, like *Ceriodaphnia*, with fine filter meshes. Laboratory studies by Schoenberg (1989) also indicate high capture efficiency for bacteria by *Ceriodaphnia*, whereas *B. longirostris* was a "dual-option" species, whose selectivity shifted with different food concentrations but was generally not inclined toward bacteria.

The contribution of picoplankton to the food base has not been assessed for the Waikato lakes, but Burns and Stockner (1991) and Peterson (1991) suggest that picoplankton is less important as a contributor to primary productivity in eutrophic waters than in oligotrophic systems. This was supported by negative correlations between picoplankton density and chlorophyll *a* levels in the lakes studied (Burns and Stockner 1991).

The potential for specialisation in feeding habit, and genetic adaptation to predictable physical parameters, such as day length and seasonal temperature, certainly exists for the Cladocera of Lake Mangakaware. Life history adaptations should be evident in parameters such as body size, clutch size, and development time, and differences in these, in turn, will be reflected in the relative abilities of different species to compete at different times of the year. These aspects of cladoceran life histories, and others, will be examined in the following chapter.

PART TWO
CHAPTER FIVE
CLADOCERA

5.1 INTRODUCTION

The marked separation of abundance peaks of the four planktonic cladoceran species in Lake Mangakaware indicates that the factors governing their temporal distribution, and their niche preferences must be different. These differences should be reflected in their patterns of growth and reproduction, i.e., in the suite of adaptations collectively termed life history tactics (Stearns 1976). In comparing the similarities and differences amongst the cladoceran life histories, two questions seem appropriate. Firstly, what are the observable interspecific differences between demographic and growth variables that result in given life history patterns? Secondly, how do these life history patterns relate to temporal and geographical distribution? These questions will be addressed below.

5.2 METHODOLOGY

5.2.1 Age Structure and Reproductive Parameters of *Ceriodaphnia* and *Bosmina*

The population age structure, body lengths, and breeding parameters of *Bosmina* and *Ceriodaphnia* were assessed from successive subsamples removed from the concentrated samples from 100 litres (see Chapter 4, 4.2.1). When the abundance of any species was low, the pump samples were supplemented by the net hauls which were treated in the same way.

Measurements were made with a stereomicroscope using an eyepiece micrometer at x 80 magnification. Body lengths of *Ceriodaphnia* were made from the front of the head to the dorso-posterior of the carapace. Those of *Bosmina* were from the front of the head to the midpoint on the posterior margin of the carapace, excluding the mucro. Measurements of both genera were made to within 0.01 mm, except on occasions when carapace ballooning reduced the accuracy of measurement to approximately 0.025 mm.

At least 70-100 animals of each species were measured to determine the proportions of juveniles and adults, ovigerous and ephippial females, and males. The adult females and juveniles of both *Bosmina* and *Ceriodaphnia* were separated on the basis of body shape, the adults having a pronounced brood pouch (with or without eggs) that is absent in the juveniles (Frey and Hann 1985).

Ephippial females of *Bosmina* were recognised by the ridged and thickened carapace (Appendix 3, Figure 1A, Plate 1), and those of *Ceriodaphnia* by the dark, sculptured appearance of the ephippium (Greenwood *et al.* 1991). Males of *Bosmina* were easily distinguished from females by a blunter thicker rostrum and larger antennules (Appendix 2, Figure 1B). The males of *Ceriodaphnia* were obvious from the different body shape, larger antennules and long flagellum arising from the first trunk limb (Greenwood *et al.* 1991). Males of both genera were recorded separately as a group, regardless of age, because of the difficulty in determining "maleness" in juveniles. This difficulty was also recorded by Staples (1984) for *Ceriodaphnia dubia.* Since the males of both *Ceriodaphnia* and *Bosmina* recorded from Lake Mangakaware were always at least of adult (*Bosmina*), or third instar (*Ceriodaphnia*) size, the number recorded does not reflect those animals unrecognised within the juvenile section of the population. Data from age/sex analyses (as proportions) were multiplied by the counts to give numbers per 100 litres.

In addition to these measurements, for each species, at least 50 ovigerous females were measured, and the number of eggs per female recorded to give an estimate of population mean clutch size. All loose eggs and embryos were counted, and the number of females losing clutches, as a result of preservation, calculated as the number of loose eggs divided by the mean clutch size. Females losing only part of a clutch (where some eggs were retained but the carapace valves were well parted) were recorded as losing eggs, and the remainder of their clutch was added to the total count of loose eggs. Stray eggs of *Bosmina* and *Ceriodaphnia* were easily distinguished on the basis of morphology (size and shape). Within each genus, stray eggs were not easily assigned to a species, and were divided according to the proportion of ovigerous females and the mean clutch size in each

species. Fortunately, this was seldom a problem. Egg loss was greatly reduced by the use of sucrose-formalin (Prepas 1978) and was minimal when there were two species of the same genus present together. Egg stocks were calculated by multiplying the mean clutch size by the number of ovigerous females present.

The minimum size at first reproduction, a life history parameter that may vary in response to changing juvenile mortality (Lynch 1980a), was defined as the smallest size at which at least ten percent of the adult population reproduced (Culver 1980).

Egg (and clutch) volumes, and mean and maximum body size, were measured on a monthly basis, from the pooled results of weekly or fortnightly samples. This enabled major trends in reproductive and growth parameters to be identified, and overcame some of the problems of small sample sizes associated with low animal and/or egg numbers.

Egg volumes were measured for all species at x 80 magnification. Both egg lengths and widths were recorded for every egg in the clutch. In most cases this was possible to do by simply manipulating the whole animal until the eggs were in the right plane for measurement. However, sometimes, particularly with larger clutch sizes, dissection of the eggs from the brood pouch was required. Egg volumes were then calculated using the formula for volume of an ovoid, after Burgis (1967):

$$EV = \frac{1}{6} \Pi \, gl^2$$

Where: EV = egg volume

g = greatest linear dimension

l = least linear dimension

Clutch volume was calculated simply as the sum of all the egg volumes in one clutch. Because of the reliance of egg volume calculation on egg shape, only eggs in stage II (*Bosmina*: Table 8), or stage II, III, and IV (*Ceriodaphnia*: Table 9) were measured. This reduced the total number of eggs available for measurement, but usually at least 50 eggs could be obtained without difficulty.

Animals measured for egg and clutch volumes were also assessed for clutch size. Thus mean clutch size was established on both a sample date, and monthly basis. The animals used for determining egg sizes were assumed to be representative of the reproductive population generally and the trends were therefore expected to be exactly the same for unpooled and pooled results.

5.2.2 Lipid Scores of *Ceriodaphnia* and *Bosmina*

Lipid score (Lipid-Ovary Index or LOI) was used as an indication of the level of food limitation in the cladoceran populations, as described by Tessier and Goulden (1982). Clutch size, or any other parameter based on reproductive state, (egg volume, for example), provides information only on the adult section of the population. Lipid scoring provides a direct and simple way of assessing the degree of feeding success and is useful for all age classes (Tessier and Goulden, 1982). At the same time as body sizes and reproductive data were recorded, animals from the field samples were scored for the amount of accumulated visible lipid.

The Lipid-Ovary Index is based on visual indexing of the accumulated lipid. A rank score (0 - 3) is given, based on the size and number of lipid droplets within the body cavity. Each animal is also scored (0 - 3) for the size and opacity of the ovaries. The LOI is simply the sum of these two. For juveniles where ovaries are immature, scoring was only possible for body cavity lipid (0 - 3) and scores were recorded as a Lipid Index or LI. Thus, scores ranged from 0 - 3 (juveniles) or 0 - 6 (adults). Tessier and Goulden (1982) described how the visible lipid in cladocerans varies according to the stage of moult cycle. In early egg stages, energy reserves have only recently been allocated to reproduction, and even well nourished animals appear low in lipid. For this reason, only animals with eggs in stages III - IV (*Bosmina*: Table 8) or V - X (*Ceriodaphnia*: Table 9) were used in calculating LOI values in adult ovigerous females. These egg stages correspond to Threlkeld's (1979a) egg stages 2,3 and 4, but a more detailed staging description was required here, to accommodate egg measurement, and to correspond to stages used in laboratory work. For non-fecund females no egg stage adjustment could be made.

Table 8: Stages of embryonic development defined for *Bosmina* spp. (modified after Kankaala and Wulff 1981).

Stage	Description
I	Egg elongated, dark and opaque (egg membrane intact)
II	Egg oval, paler and opaque (egg membrane intact)
III	Embryo with barely visible rostrum and antennae: eyespots not visible
IV	Embryo with two distinct red eyespots, fused together
V	Embryo with one large black eye

Table 9: Stages of embryonic development defined for *Ceriodaphnia* (after Staples 1984).

Stage	Description
I	Egg elongate, dark and opaque, with central translucent oil globule
II	Egg oval, paler and opaque
III	Periphery of egg transparent
IV	Periphery of egg transparent and granular, fat cells forming in cytoplasm
V	Egg membrane cast off; embryo headless
VI	Embryo with small head and short antennal buds
VII	Embryo with pronounced head and longer antennae
VIII	Second membrane shed; embryo with two small pink eyes
IX	Embryo with two red eyes
X	Embryo with two black eyes
XI	Embryo with one black eye

Whenever possible, refrigerated samples were processed within 48 hours of collection to minimise lipid fading. However, in samples older than this, staining before analysis proved an acceptable method of determining lipid scores. Samples to be analysed were treated in 5 ml subsample volumes to 1-3 minutes staining in Sudan (IV) red following the methods described in Bjorkman and Shapiro (1986). Using this technique samples may be processed for up to six months after staining but, generally, processing was completed within one month of collection.

An illustration of the lipid and ovary indices, as used in this study, is given in Figure 10. These were modified very slightly from Tessier and Goulden (1982) for use with *Ceriodaphnia* and *Bosmina,* and were based on the range of values observed in laboratory cultures (Part Three).

5.2.3 Population Dynamics of *Ceriodaphnia* and *Bosmina*

The estimations of the instantaneous rates of population birth, death, and growth were made using the egg ratio method proposed by Edmondson (1960) for rotifers and later widely applied to Cladocera (e.g. Hall 1964; Wright 1965; Keen 1973; Smyly 1979; Mitchell and Williams 1982). The egg ratio method combines the egg stock data from field samples with the egg development times determined at controlled temperatures, and assumes that population growth is modelled by the exponential growth equation:

$N_t = N_0 e^{rt}$

where N_0 = initial population size at time 0

N_t = population size after some time interval t

e = the base of natural logarithms

r = the instantaneous coefficient of population increase which, assuming no immigration or emigration, is given by:

$r = b - d$

where b and d are the instantaneous rates of population birth and death respectively.

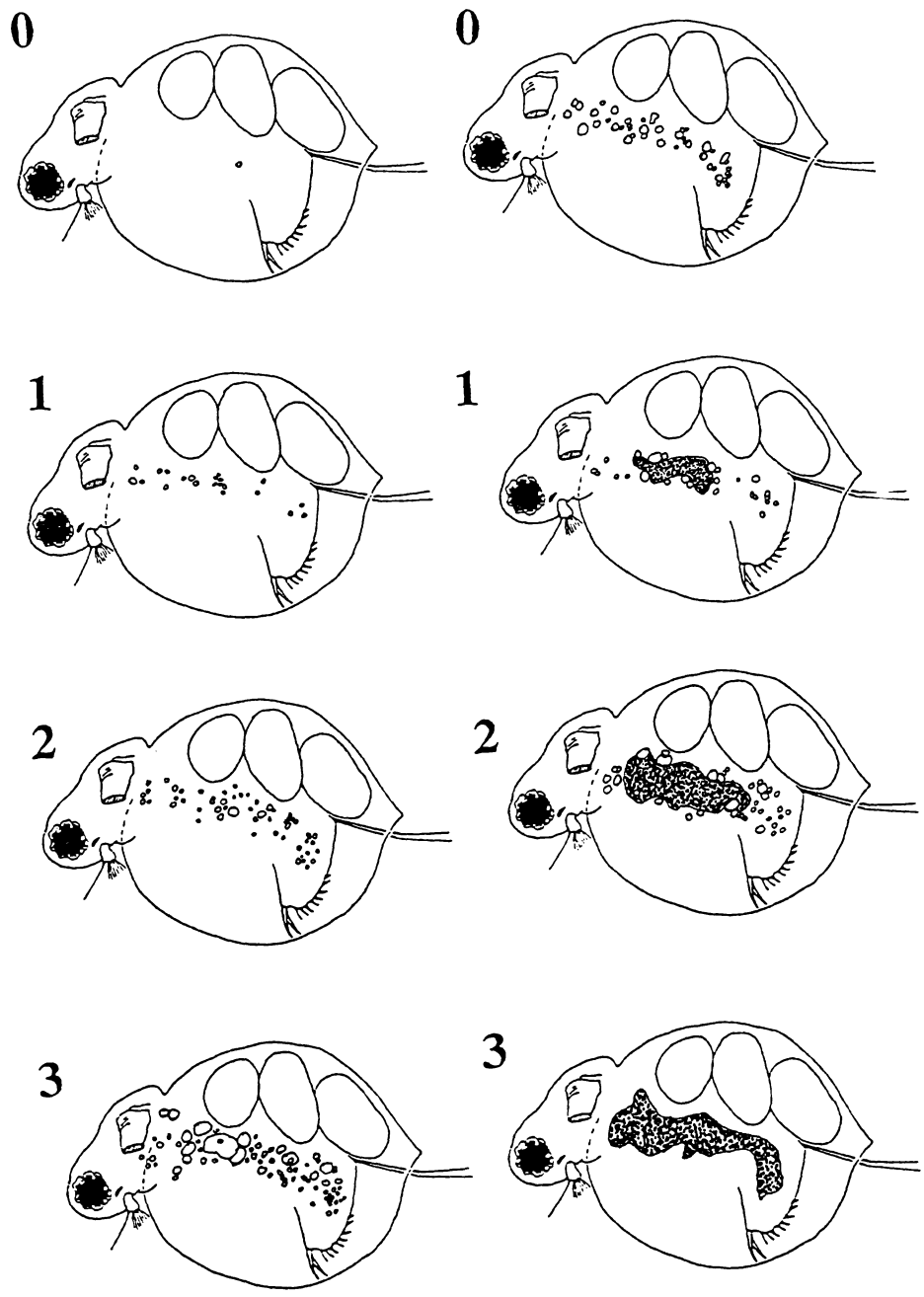

Figure 10. Lipid (left) and Ovary (right) Indices for *Ceriodaphnia* and *Bosmina* from Lake Mangakaware. The Lipid Ovary Index is given by the sum of scores for each parameter. Scores are illustrated for *Ceriodaphnia pulchella* but are applicable to *C. dubia* and *Bosmina* also.

The instantaneous rate of population increase, r, was calculated from successive pairs of estimates of population density:

$$r' = \frac{\log_e N_t - \log_e N_0}{t}$$

and the finite birth rate, B (= the number of births per individual per day) from the equation:

$$B = \frac{1}{D} \times \frac{\dot{E}}{N_0}$$

where: $\dot{E}$ = the egg stock (number of ovigerous females x mean clutch size)

and $\frac{\dot{E}}{N_0}$ = the egg ratio of the population

and D = the development time of the eggs in days (see below).

From the value of B, the instantaneous birth rate, b', was then calculated by: $b' = \log_e (1 + B)$, and the instantaneous death rate by: $d' = b' - r'$.

The egg ratio method for estimating b', d', and r', assumes that the population in question is characterised by continuous growth, zero egg mortality, and a stable age distribution of eggs. Knowing the accuracy of estimates made using the egg-ratio method is essential to proper use of this technique. Errors in estimates arise from violations of any of the above population characteristics, from violations of the assumption that mortality is independent of age, from sampling error, from errors in the determination of egg development time, from immigration and emigration, and from the hatching of ephippial (resting) eggs (Brett *et al.* 1992).

A number of refinements to the egg-ratio model have been made to counter the biases introduced by these assumptions and inherent errors (Edmondson 1968; Caswell 1972; Paloheimo 1974). Some workers have suggested improvements to the model by accounting for the age distribution of eggs (Threlkeld 1979a), by instar analysis (Seitz 1979), by estimating the variance of the calculated rates (De Mott 1980; Keen and Nassar 1981), by introducing time lags (Matveev 1985), or by pooling samples from several sites, to minimise the effects of zooplankton patchiness on sampling accuracy (Taylor 1988).

Approaches involving the assessment of egg age distribution may seem to be advances on the Edmondson-Paloheimo model, but the additional work they entail may not

be justified if a variance in b' of about 0.003 can be tolerated (Lynch 1982). Brett *et al.* also argue against egg aging, on the basis of the increased sample sizes required for analysis, and suggest that the unmodified egg-ratio method gives a better estimate of average birth rate, as it takes into account the whole egg population, which may be unevenly distributed.

Taylor and Slatkin (1981) suggest that birth rate estimates, using the egg ratio method in its simple form, will be more accurate for taxa such as cladocerans and rotifers, in which short juvenile periods, high birth rates, and simple life histories lessen the sensitivity of birth rate estimates to deviations from the assumption of stable age structure. Moreover, the accuracy of b', d' and r' will be improved if the sampling interval is short relative to the duration of the juvenile period, and if efforts are made to improve the accuracy of population density estimates (Lynch 1982). Shorter sampling intervals increase the error in estimates (Taylor 1988; Brett *et al.* 1992) but are preferred, as longer intervals can obscure real, short term dynamics. Here, a summer sampling interval of one week during summer (1987-1988) and two weeks during winter, was considered a compromise between loss of episodic detail in the calculation of b', and sample processing time.

Obtaining an accurate assessment of egg development times is one of the most restrictive problems associated with the egg-ratio method (Brett *et al.* 1992), and realistic estimates of these can greatly improve the accuracy of estimates of b' (see below). In a shallow lake such as Lake Mangakaware, individuals are not subjected to large variations in diel temperature, and vertical migration is negligible anyway. Thus, development times based on mean lake temperature are likely to be more accurate than is the case in deep lakes.

As d' is determined by difference from the estimated values of b' and r' it is the most subject to error. In particular, negative death rates can quite commonly be produced (Brett *et al.* 1992), particularly when the sampling interval is short. In Lake Mangakaware, where all of the four cladocerans under study produced ephippia, the hatching of resting eggs is likely to be a significant cause of negative death rates.

5.2.4 Determination of Egg Development Times

In this study the egg development times (EDTs) used for *Bosmina meridionalis*, *Ceriodaphnia pulchella* and *C. dubia* were those established in Greenwood (1987). For *Bosmina longirostris*, EDTs were estimated, as for the other three species, at 2°C intervals from 11-25°C, from individuals reared in the laboratory. Lake water from 0.5 m depth (as an organic base and food source) was collected, filtered through 50 μm plankton mesh, and aerated under constant fluorescent illumination (spectral range 30 - 1100 nm). Lake water was discarded after one week and replaced. This base was supplemented with 1.3 μg $Cml^{-1}day^{-1}$ *Chlamydomonas* suspension (see Part Three, Chapter Three for details of algal culture). Animals (approximately 20 - 50 per temperature) were collected from the field, and reared individually in 4 ml, conically based autoanalyser tubes (Greenwood 1987). These were cheap and could be discarded daily when the food suspension was renewed. The tubes were placed in polystyrene floats in Julabo water baths set at the appropriate temperature (see Part Three, Fig. 35). Animals were maintained on a 14:10 hour, light:dark cycle and examined once (11-15°C) or twice (17-25°C) daily. Assessment of the times of egg deposition and neonate release were made on the basis of the number of embryonic stages (Table 8) passed in the time elapsed since the last observation.

Polynomial regressions relating the duration of egg development (in hours) to temperature (°C) were fitted to the data for each species using SYSTAT (1989) statistical software. The general form of the regression was that of Bottrell's (1975a) equation 4:

$$\ln D = \ln a + b\ln T + c(\ln T)^2$$

where D = development time in hours

T = temperature (°C)

and a, b, and c are fixed constants.

The regression equations and their corresponding ANOVA tables, are given in Appendix 4. The egg development data are provided on floppy disk at the back of this volume.

5.3 RESULTS

Data on population structure, dynamics, and reproductive parameters for *Ceriodaphnia* and *Bosmina* are given in Appendix 5, Tables 1-6.

5.3.1 Population Structure

Bosmina longirostris

The seasonal variation in the proportions of adults and juveniles of *B. longirostris* are shown in Figure 11. Despite large fluctuations in density the *B. longirostris* population typically had a high proportion of juveniles. During the period of *B. longirostris* abundance juveniles comprised at least half of the total population, except at the beginning of August 1988 (45%), mid December 1988 (30.9%), and late July (36.7%). The corresponding increase in adult females at these times preceded major population increases in August 1988 and January 1989, although not in August 1989. Not unexpectedly, the fluctuations in the numbers of juveniles and adult females reflected quite closely the trends in total population abundance, although the January density peak, during which juveniles comprised 78% of the total population, was sharper for this section of the population than for adults. Ephippial females were recorded on one date during the sampling period, in August 1988, when they accounted for 3% of the adult females. Interestingly, this peak occurred four months before the peak in population density, which was not the case for *B. meridionalis* (see below).

Bosmina meridionalis

Seasonal trends in population age structure, and in the number of males and ephippial females, in *B. meridionalis* are shown in Figure 12. For much of the period during which *B. meridionalis* was present (November 1987 - June 1988) adult females comprised a high proportion of the total population, particularly when numbers were relatively low, as they were throughout the first few months of 1988. Juveniles predominated (57.9%) at the time of peak population abundance (December 1987) but this was generally uncommon and not a consistent trend until May 1988, just before *B. meridionalis* disappeared from the plankton. Males and ephippial females were recorded

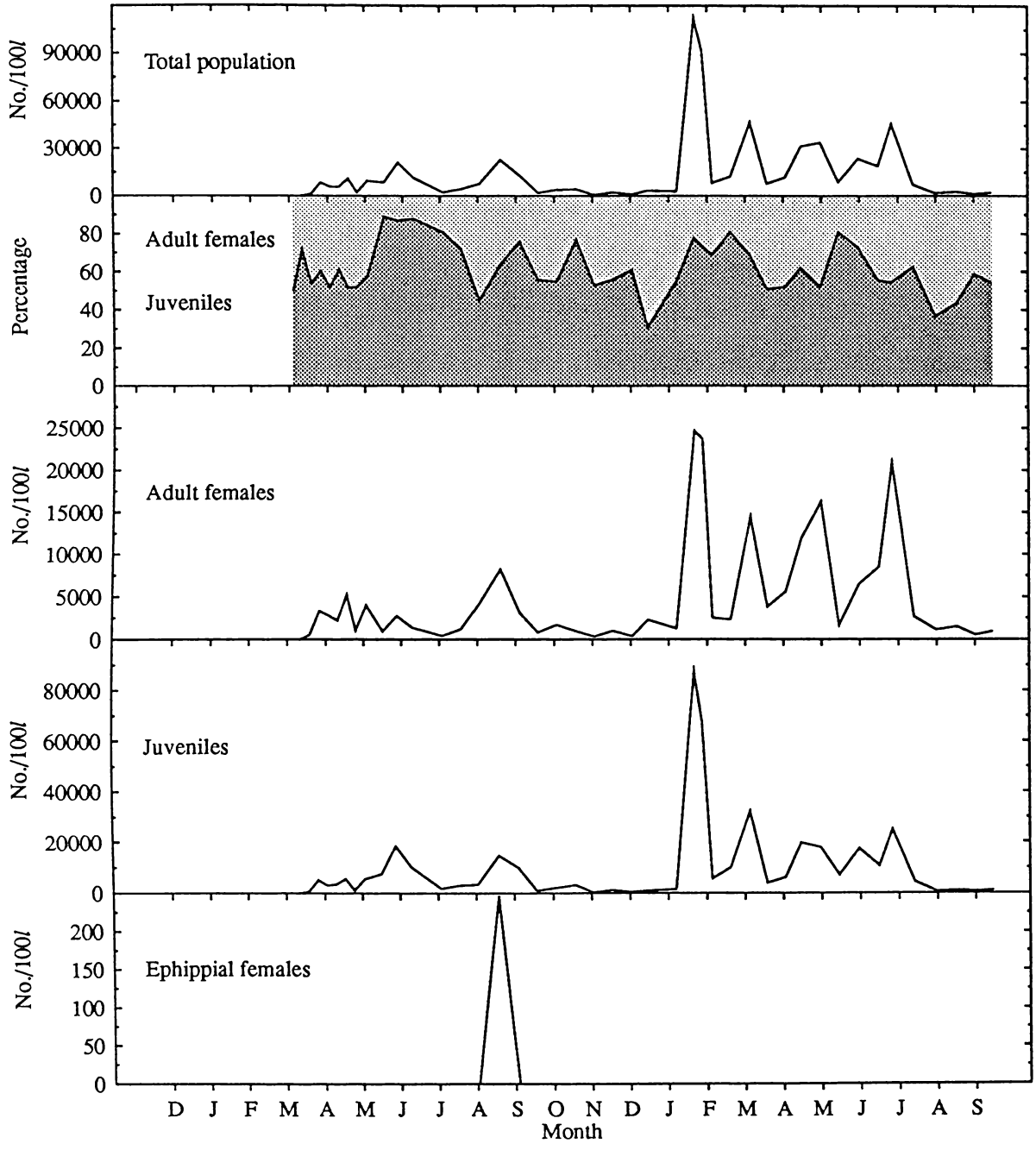

Figure 11.

Seasonal variation in total population numbers, percentage and numbers of adult females and juveniles, and numbers of ephippial females of *Bosmina longirostris* in Lake Mangakaware during November 1987-September 1989.

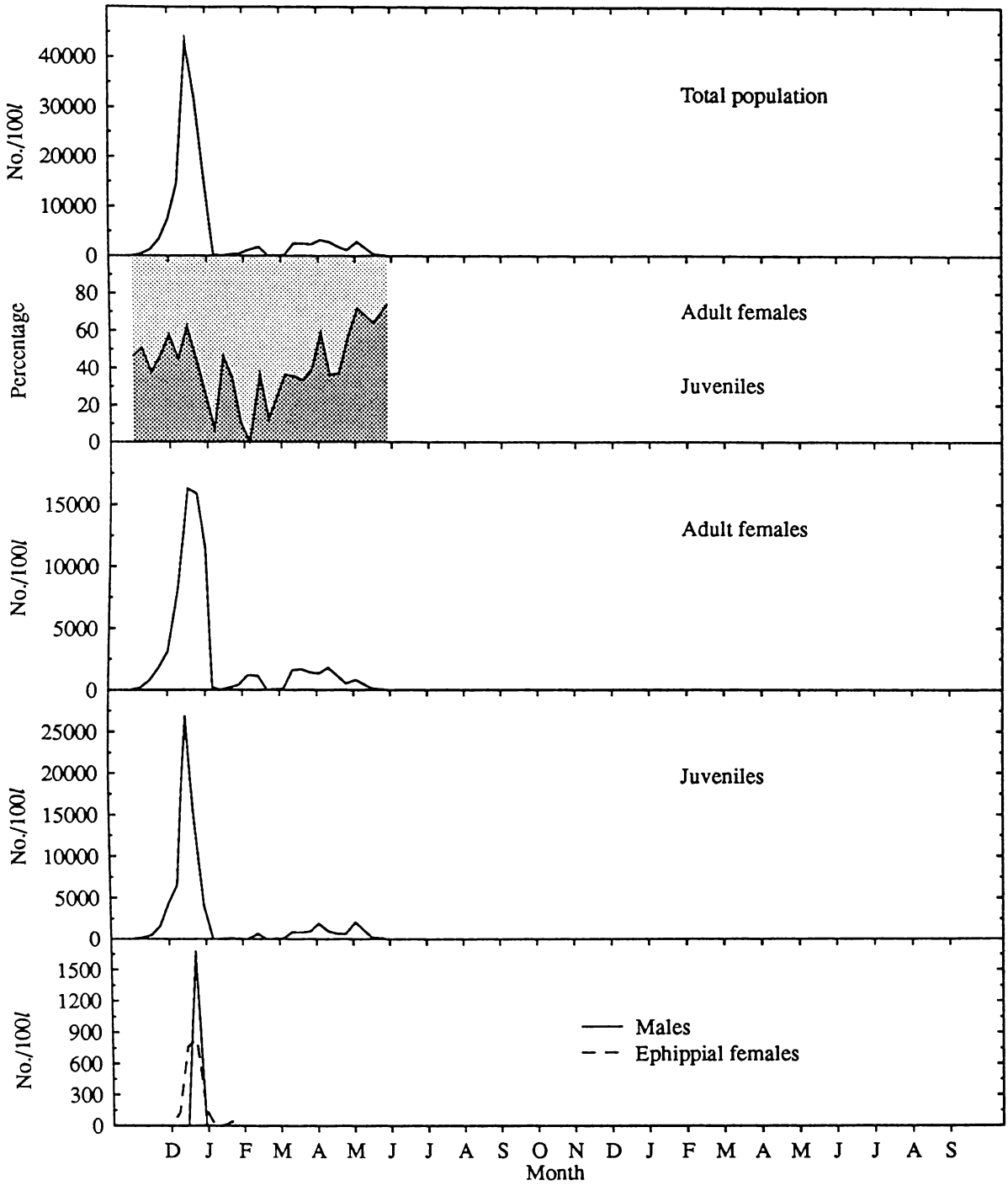

Figure 12.

Seasonal variation in total population numbers, percentage and numbers of adult females and juveniles, and numbers of males and ephippial females of *Bosmina meridionalis* in Lake Mangakaware during November 1987-September 1989.

for a brief period at the time of peak abundance, accounting for approximately one twentieth of the total population, or adult females respectively.

Ceriodaphnia pulchella

Seasonal variations in the proportions and numbers of juveniles and adult females, and in the number of sexual (ephippial) females of *C. pulchella* are plotted in Figure 13.

For most of the period during which *C. pulchella* was present (the major exception being mid December 1987), juveniles comprised a relatively constant high proportion of the population. Fluctuations in the numbers of adults and juveniles were similar to those in total numbers, except in mid October 1988, when juveniles were largely responsible for the small peak in total population density.

Ephippial females were recorded on two occasions, in early August, and again in early October. Although obvious by their morphology, even at their peak in August 1989, ephippial females accounted for only 1.8% of the adult females present. A single male was noted in August 1989 but this identification was tentative as the animal was distorted by preservation. More probably it was a male of *C. dubia*, since these were present at this time.

Ceriodaphnia dubia

C. dubia appeared sporadically throughout the sampling period, and low numbers at some times during their presence hampered the accurate assessment of population age structure. The most notable trend, as illustrated in Figure 14, was the change from an adult dominated population in July and August of 1988, to a juvenile dominance in spring. This trend was repeated almost exactly the following year. During both periods of peak abundance, (October - November 1988 and August - September 1989), males and ephippial females were recorded, the former reaching a maximum 12% of the population on 19.10.88 and a maximum density of 207 per 100 litres on 2.11.88.

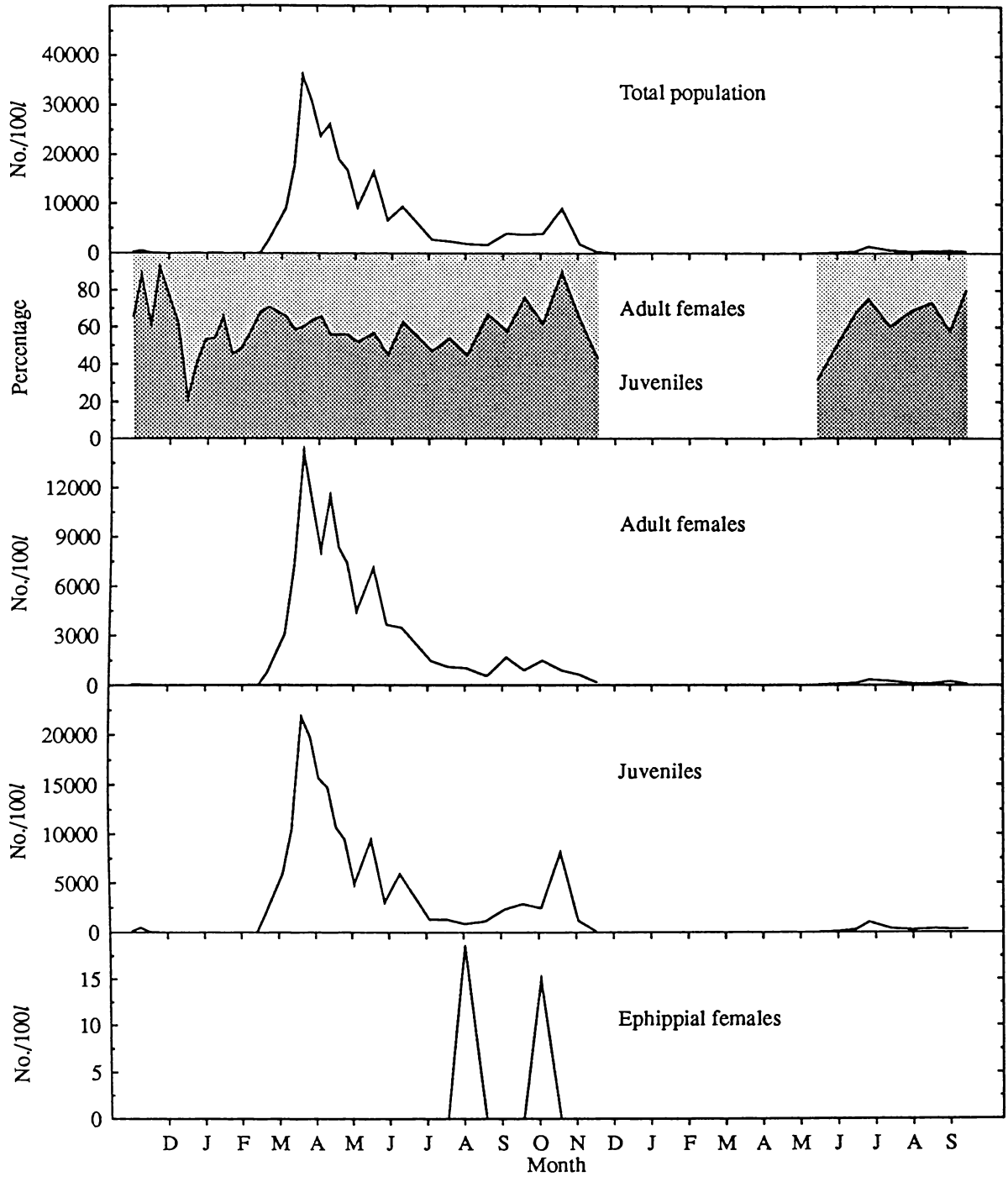

Figure 13.

Seasonal variation in total population numbers, percentage and numbers of adult females and juveniles, and numbers of ephippial females of *Ceriodaphnia pulchella* in Lake Mangakaware during November 1987-September 1989.

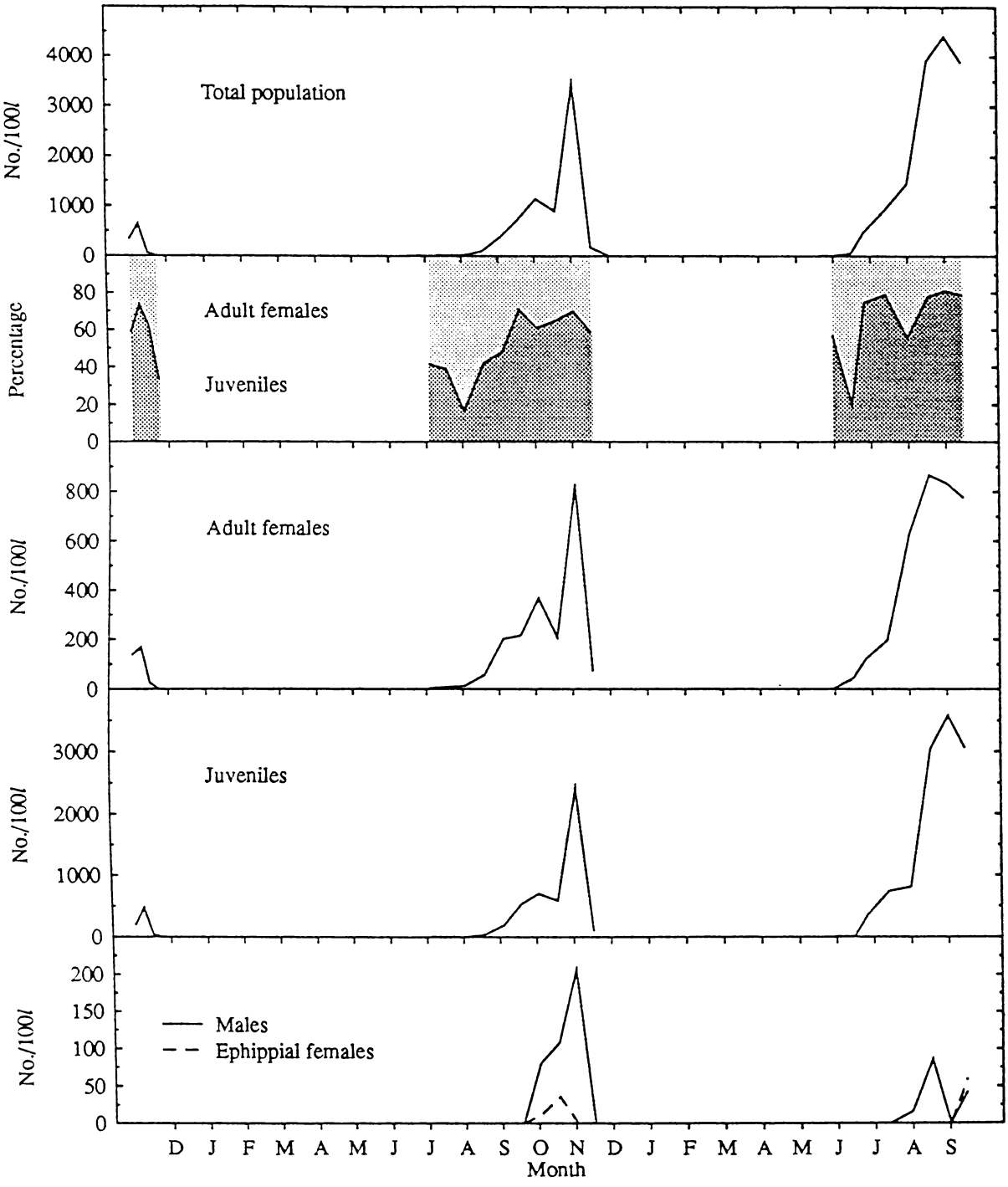

Figure 14.

Seasonal variation in total population numbers, percentage and numbers of adult females and juveniles, and numbers of males and ephippial females of *Ceriodaphnia dubia* in Lake Mangakaware during November 1987-September 1989.

5.3.2 Reproductive parameters

Bosmina longirostris

The pattern of fluctuation in the proportion of females ovigerous at any one time (Fig. 15) was generally similar to that of the proportion of total adult females (Fig. 11), falling when the adult females were scarce (e.g. May and October 1988) and increasing when adults in the population predominated (December 1988). Although a high proportion of the adult population was egg bearing during summer and autumn, there were only two occasions (15.3.88 and 22.3.88) on which all females found were ovigerous, and low numbers generally on these dates probably contributed to greater error in this assessment. There were marked declines in the proportion of egg bearing females in October 1988 and June - July 1989, both periods being associated with low population numbers generally.

Fluctuations in mean clutch size (Fig. 15) were similarly variable. For much of the sampling period, clutch sizes (calculated only from egg bearing females) remained at a minimum of one, with fluctuations around a clutch size of 1.5 eggs per female being more common during the period from late winter 1988 to early summer 1989. The high clutch sizes recorded at the time of *B. longirostris*' appearance in the plankton were quite probably atypical, and a result of the small sample sizes available at this time.

Egg stock (Fig. 15), the product of the number of ovigerous females present and their mean clutch size, exhibited a pattern consistent with the number of ovigerous females. This was the result of a rather low and constant mean clutch size, as is typical for *Bosmina* in Lake Mangakaware (Greenwood 1987).

The seasonal pattern in size of first reproduction (Fig. 15) was generally one of larger body sizes during autumn, winter, and spring, with a noticeable decrease over the summer period. Although the magnitude of this decrease was only in the range 0.05 - 0.1 mm (mean: April - October 1988 = 0.40 mm; mean: November 1988 - April 1989 = 0.34 mm), as a proportion of annual (April 1988 - April 1989) mean first reproductive body size (0.36 mm) it represents a 15-20% decrease within a period of less than two months.

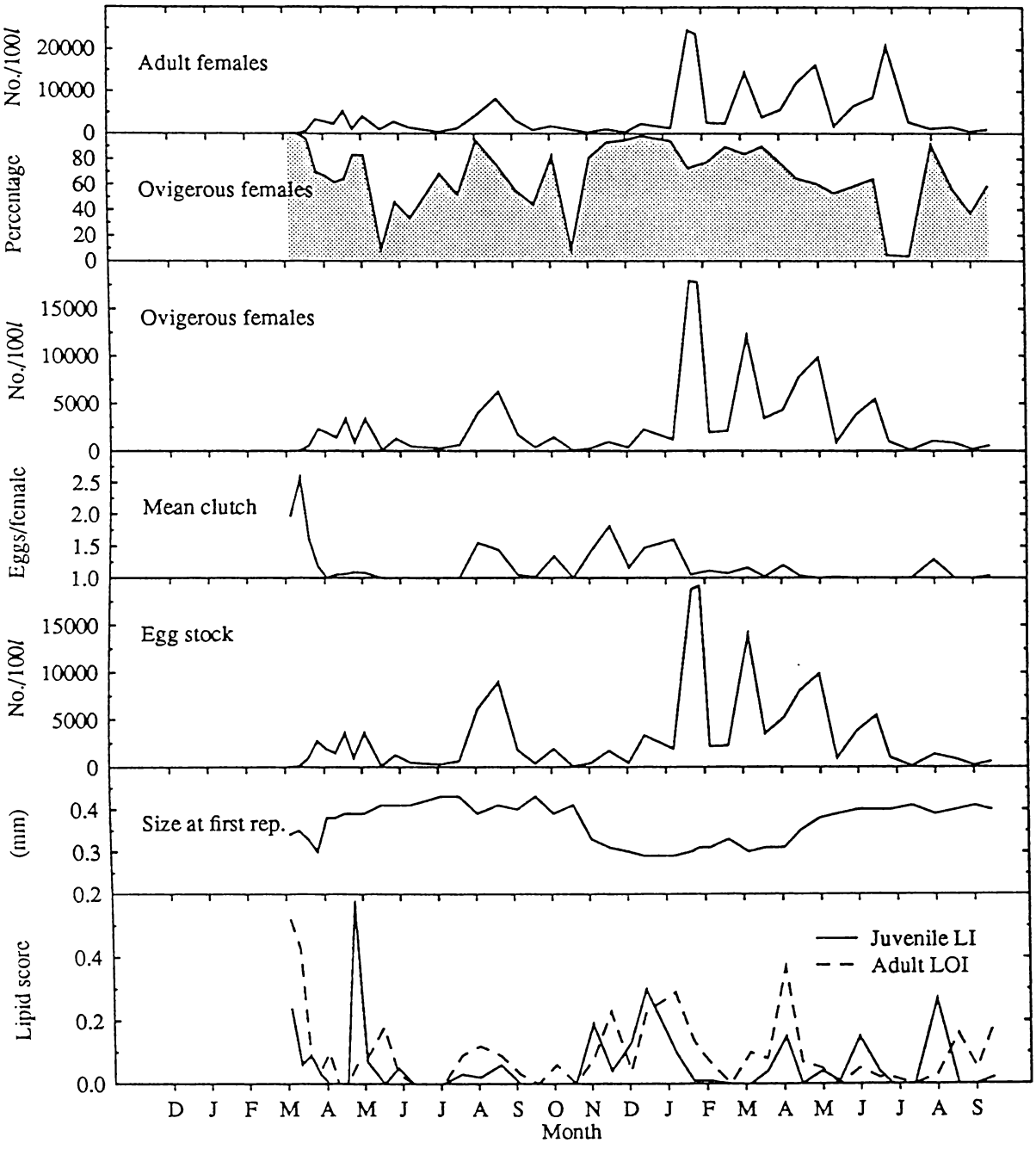

Figure 15.

Seasonal variation in total number of adult females, percentage and number of adult females ovigerous, mean clutch size, egg stock, minimum body size at first reproduction, and adult and juvenile lipid scores in *Bosmina longirostris* in Lake Mangakaware during November 1987-September 1989. LOI= Lipid Ovary Index. LI= Body Lipid Index.

Bosmina meridionalis

The general trends in the proportions and numbers of females ovigerous, the egg stock, and the mean clutch size in *B. meridionalis* were similar (Fig. 16). Large increases in the number of egg bearing females during November - December 1987 combined with a maximum mean clutch size to produce a sharp peak in the egg stock. Increases in these parameters in late summer and autumn in 1988 were less pronounced but the coincidence of the patterns remained, with higher mean clutches being associated with increases in the proportion of females bearing eggs. As for *B. longirostris*, body size at first reproduction increased during cooler periods from a mean of 0.265 mm in December 1987 to a mean of 0.323 mm in May 1988, an increase of almost 0.06 mm, representing a change of 20% from the mean (0.295 mm) recorded for the period during which this species was present.

Ceriodaphnia pulchella

Seasonal variations in the parameters of *C. pulchella* reproduction are shown in Figure 17. Peak population (and adult female) abundance was associated with a sharp decline in the proportion of the adult population bearing eggs. When population numbers were lower, as they were in summer 1987 - 1988, and in winter and spring periods, the proportion of egg bearers was high, particularly during May - August 1989. Similarly mean clutch sizes were lowest just after the autumnal density peak and declines in mean clutch size were always coincident with increases in total population density (Fig. 13), as in mid October 1988 and late June 1989. Not unexpectedly, the total egg stock was greatest at the time of peak abundance (March 1988), despite a near minimal mean clutch size and a rapid decline in the proportion of females ovigerous.

As with *Bosmina,* larger body sizes were associated with cooler autumnal and winter periods, with marked declines during summer. Interestingly, larger body sizes were clearly associated with low clutch sizes, and animals were at their most fecund when body sizes were small.

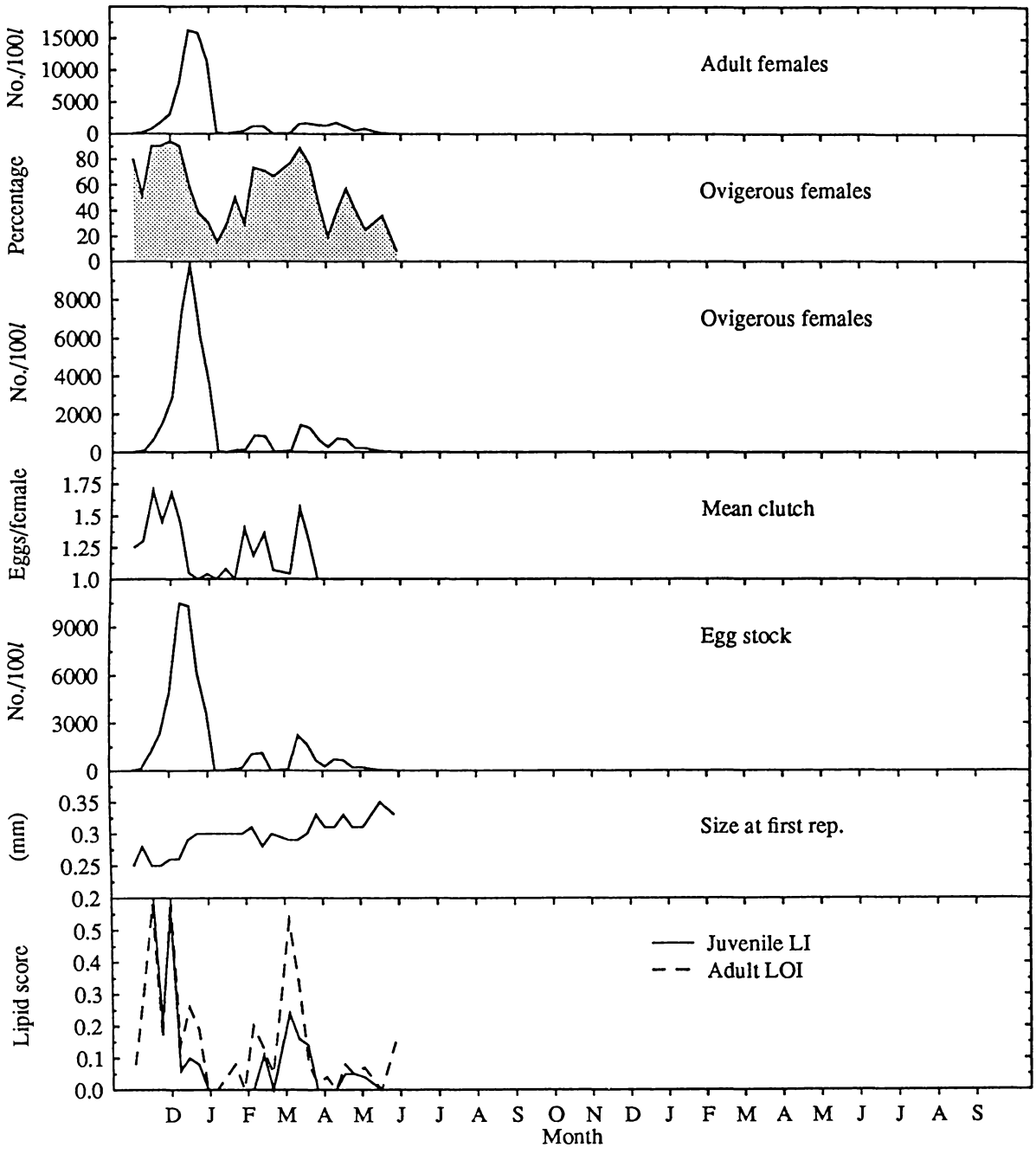

Figure 16.

Seasonal variation in total number of adult females, percentage and number of adult females ovigerous, mean clutch size, egg stock, minimum body size at first reproduction, and adult and juvenile lipid scores in *Bosmina meridionalis* in Lake Mangakaware during November 1987-September 1989. LOI= Lipid Ovary Index. LI= Body Lipid Index.

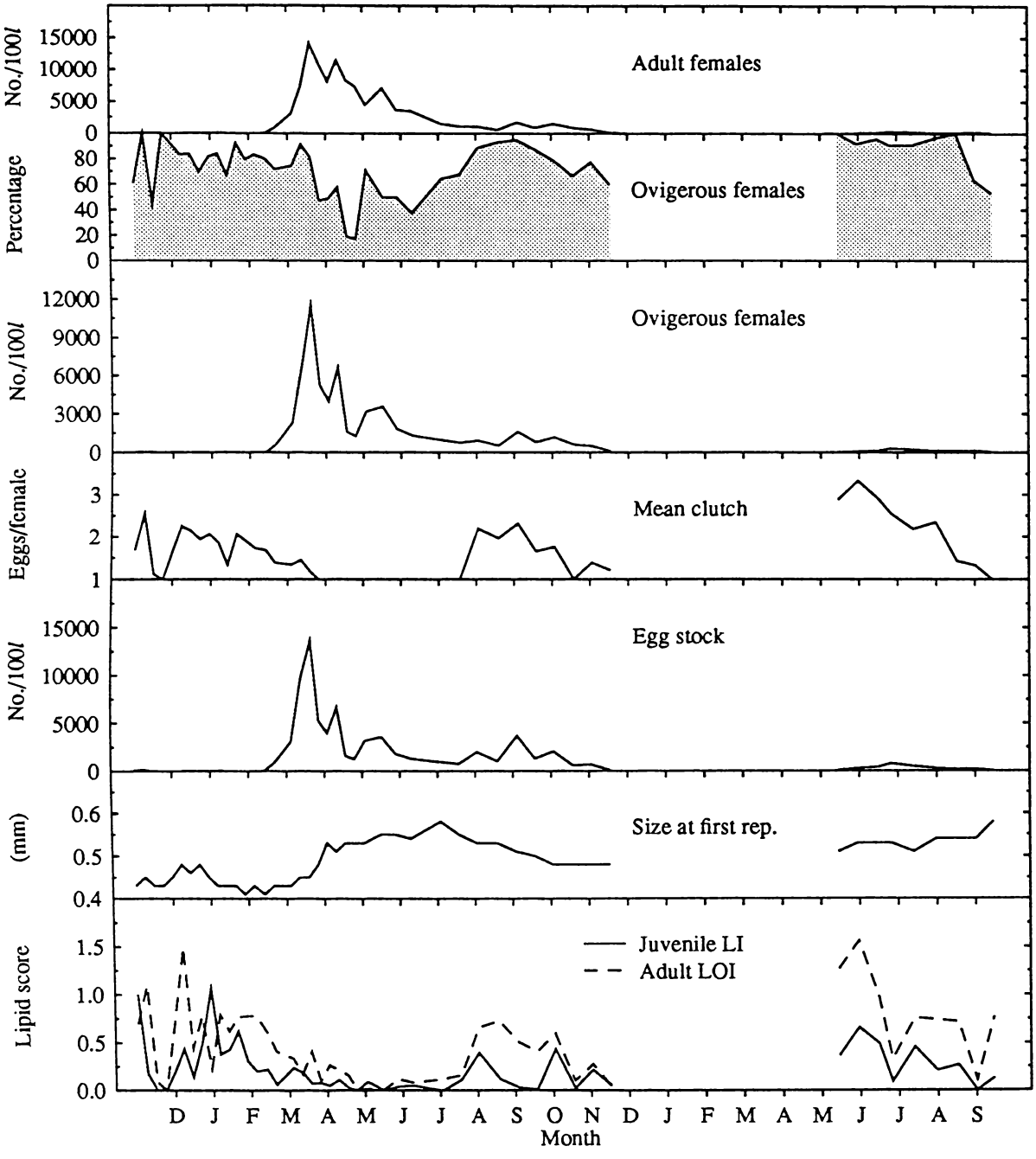

Figure 17.

Seasonal variation in total number of adult females, percentage and number of adult females ovigerous, mean clutch size, egg stock, minimum body size at first reproduction, and adult and juvenile lipid scores in *Ceriodaphnia pulchella* in Lake Mangakaware during November 1987-September 1989. LOI= Lipid Ovary Index. LI= Body Lipid Index.

Ceriodaphnia dubia

Analysis of the *C. dubia* population for reproductive parameters such as mean clutch size was often hampered by low numbers of this less abundant species. *C. dubia* was unusual amongst the planktonic Cladocera in Lake Mangakaware in that a high proportion (> 90%) of the females were ovigerous for much of the time they were present (Fig. 18). Only during one period (October - November 1988) did the proportion of ovigerous females fall significantly. This decline just preceded the rise in total population numbers, and as for *C. pulchella* was associated with a sharp decline in mean clutch size (Fig. 18).

In 1988 changes in the egg stock (Fig. 18) reflected the overall pattern of abundance in ovigerous females, but was influenced considerably by the low mean clutch size. This flattened the peak in egg density and brought the absolute change down to levels not dissimilar to those recorded just prior to the peak in population numbers, when both the proportion of females ovigerous and the mean clutch size had been higher. In 1989, higher overall mean clutch sizes and a high proportion of egg bearing females, resulted in an egg stock that more closely resembled the pattern of total population change.

Trends in body size at first reproduction (Fig. 18) were more difficult to discern than in *C. pulchella* or *B. longirostris*, particularly as *C. dubia* occurred over a restricted seasonal range. Low densities in July 1988 and June 1989 may account for the apparently large mean body sizes recorded for primiparous females at these times. Discounting these periods, body size changes over the period during which *C. dubia* was abundant, were minimal, although, as with *Bosmina* and *C. pulchella,* there was a tendency for animals to be larger during cooler months.

5.3.3 Lipid Scores

Bosmina longirostris

With the exception of the period from mid April to mid May 1988, both juveniles and adults of *B. longirostris* exhibited similar patterns of lipid storage (Fig. 15). Mean scores were consistently low (< 0.6) and generally fluctuated around levels of about

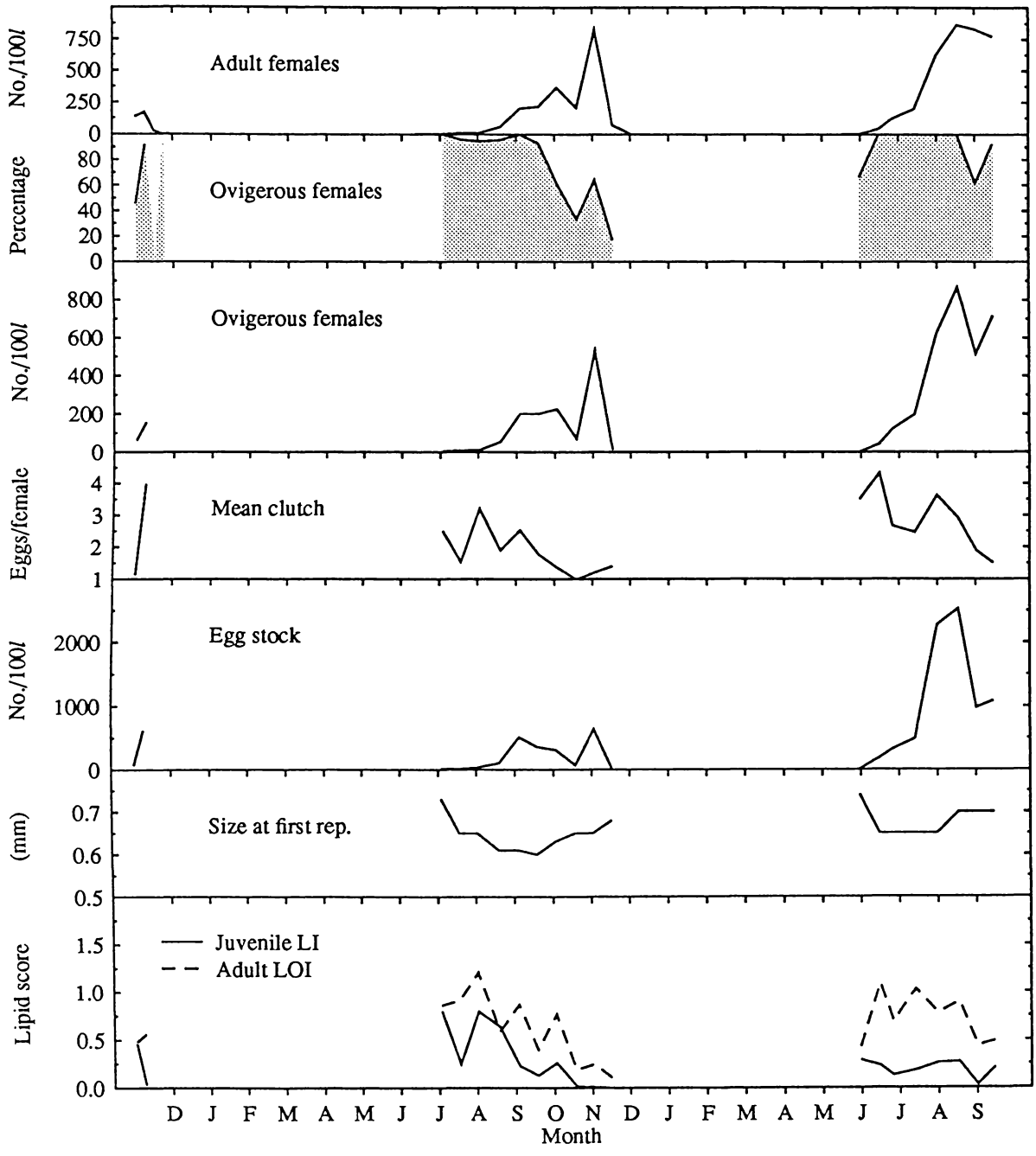

Figure 18.

Seasonal variation in total number of adult females, percentage and number of adult females ovigerous, mean clutch size, egg stock, minimum body size at first reproduction, and adult and juvenile lipid scores in *Ceriodaphnia dubia* in Lake Mangakaware during November 1987-September 1989. LOI= Lipid Ovary Index. LI= Body Lipid Index.

0.1 - 0.15. The only noticeable increase in visible lipid was recorded in autumn (April - May) 1988, when the mean lipid score for juveniles peaked at just below 0.6. Smaller peaks occurred the following summer and during the autumn of 1989, but apart from this being a time when *B. longirostris* was generally abundant, these were not clearly associated with any peaks in density. There was, however, a general tendency for scores to increase at the same time as the mean clutch size and the proportion of egg bearing females. This relationship was particularly close for the second half of 1988.

Bosmina meridionalis

As for *B. longirostris*, the mean lipid scores for *B. meridionalis* were consistently low at less than 0.6 (Fig. 16). Peaks in lipid score, of just below 0.5, were recorded for both juveniles and adults during the period of maximum population density in November - December 1987. However, later increases in lipid storage, particularly for adults (in March 1988), were not associated with pronounced changes in population density, although they were coincident with increases in the proportion of ovigerous females and the mean clutch size.

Ceriodaphnia pulchella

Lipid scores in *C. pulchella* were generally higher and more variable than those in *Bosmina*, fluctuating between values at, or close to, 0, and just above 1.5 (Fig. 17). Not unexpectedly, juveniles, which could be scored only for body lipid, had scores that were consistently lower than those of the adults. The most notable feature of the seasonal variability in visible lipid was that minimum lipid scores, for both juveniles and adults were recorded at the times of highest population density i.e., through autumn and winter 1988. Scores were higher when population density was lower and more stable. As for *Bosmina,* higher lipid scores were associated with higher mean clutch sizes and increases in the proportion of egg bearing females.

Ceriodaphnia dubia

As for *C. pulchella* scores were higher and more variable for *C. dubia* than for either species of *Bosmina*, fluctuating between 0 and 1.25 (Fig. 18). Similarly, adult scores were consistently higher than those recorded for juveniles. Scores for *C. dubia*

were highest when the population was low (but increasing) in late winter 1988, and began declining as the population density increased during spring of that year. Minimum lipid scores were coincident with maximal population abundance in early November. A similar pattern held during 1989, although the trend was less apparent in that year. As was the case for other cladoceran species, declining lipid scores were closely associated with declining clutch sizes and a fall in the proportion of females bearing eggs.

5.3.4 Monthly Analysis of Body Size, and Parameters of Egg Production

Mean and maximum adult body size

The monthly trends in the mean and maximum adult body size in *Ceriodaphnia* and *Bosmina* (Figs 19 and 20) were similar to those recorded for size at first reproduction. All four species showed a tendency toward larger body size during winter periods, with a general decline in size in the spring and/or summer. This trend was most pronounced in *B. longirostris*, for which a complete annual cycle was recorded. A paucity of complete seasonal data for *B. meridionalis, C. pulchella,* and *C. dubia* made it difficult to establish whether or not small body sizes were typical of these species at very high (e.g. summer) temperatures, although the trends in the data indicate this.

When maximum body size is considered, the trend for large winter body size is more pronounced for all species, except *B. longirostris*. For this species, the decline in body size was less noticeable when the maximum value was taken as an indication of trends in growth.

Mean and maximum clutch sizes

As was expected, pooling data sets to achieve monthly values for mean clutch size (Fig. 21) did not affect the general trends observed in this parameter. However, short term fluctuations were smoothed and general trends clearer, except perhaps for *C. dubia*, where the smaller sample sizes used in assessing monthly clutch size data in this species reduced the confidence of the measures. For *Ceriodaphnia*, mean clutch sizes were highest during the early winter, with minimum mean clutch sizes being recorded for each species at the time of their respective peak abundancies. For *B. longirostris* the pattern of fluctuation in mean clutch size was similar, with minimal clutch sizes occurring at peak

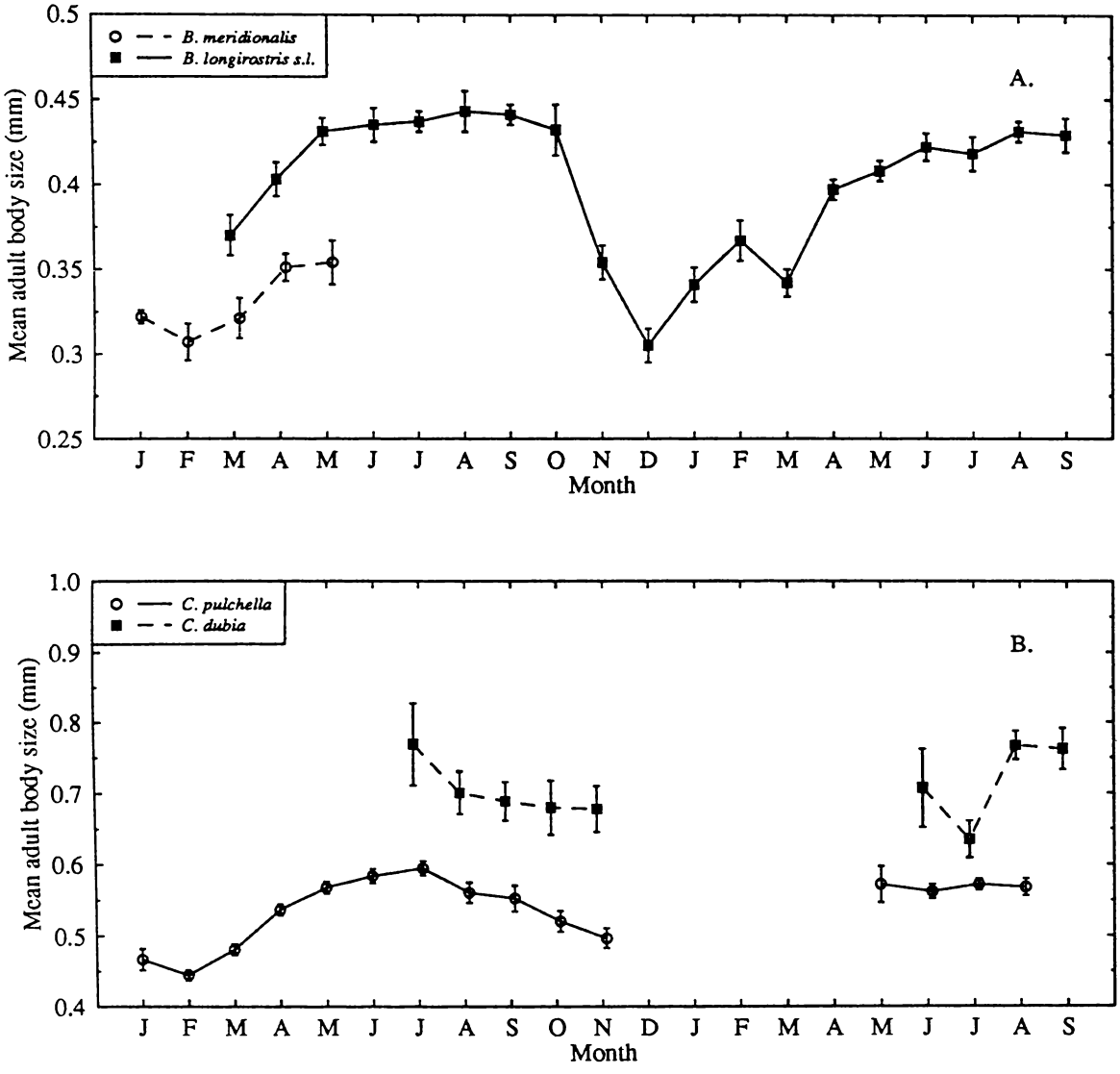

Figure 19.

Variation in mean adult body size in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989. Vertical bars are 95% confidence intervals.

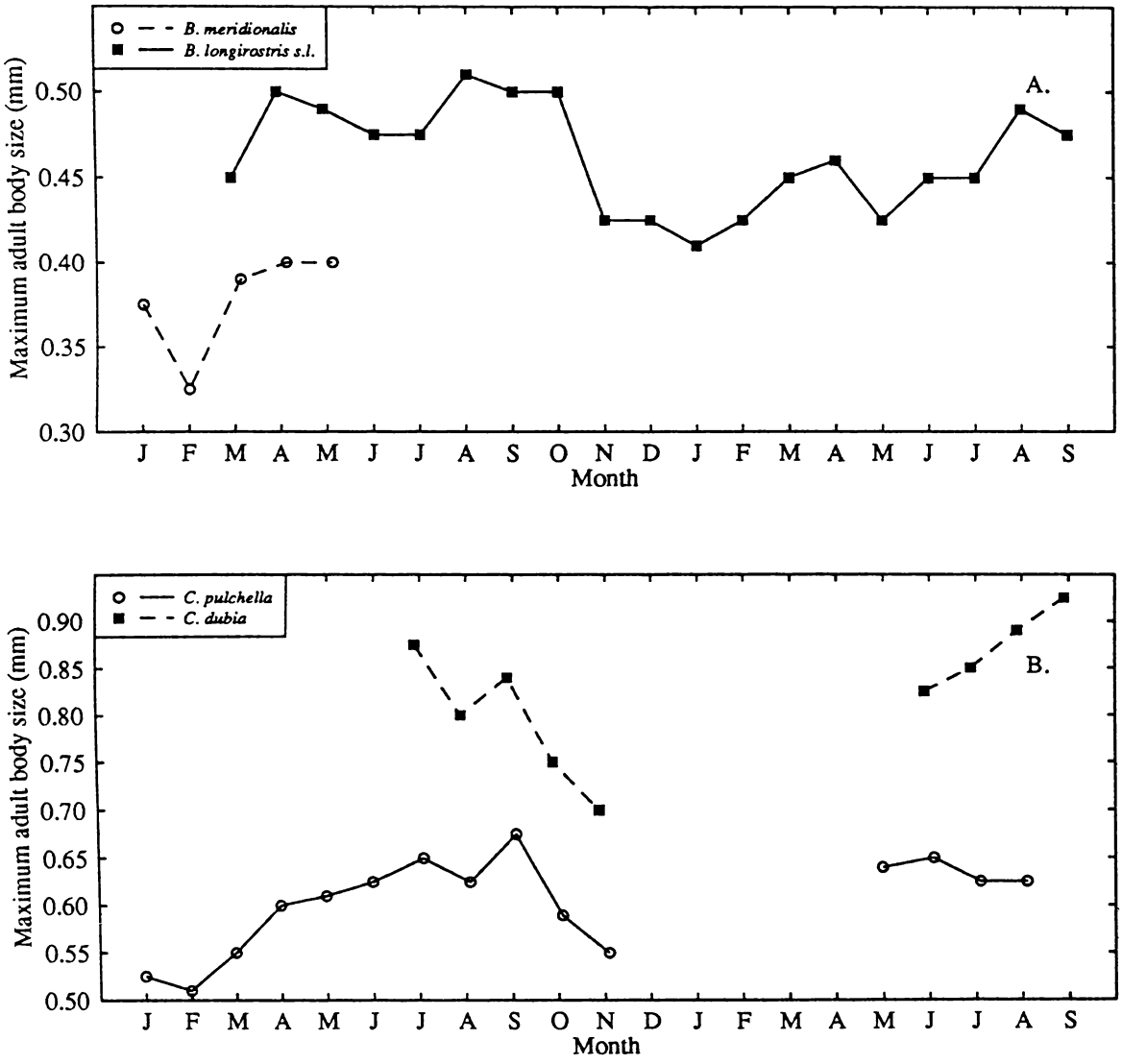

Figure 20.

Variation in maximum adult body size in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989.

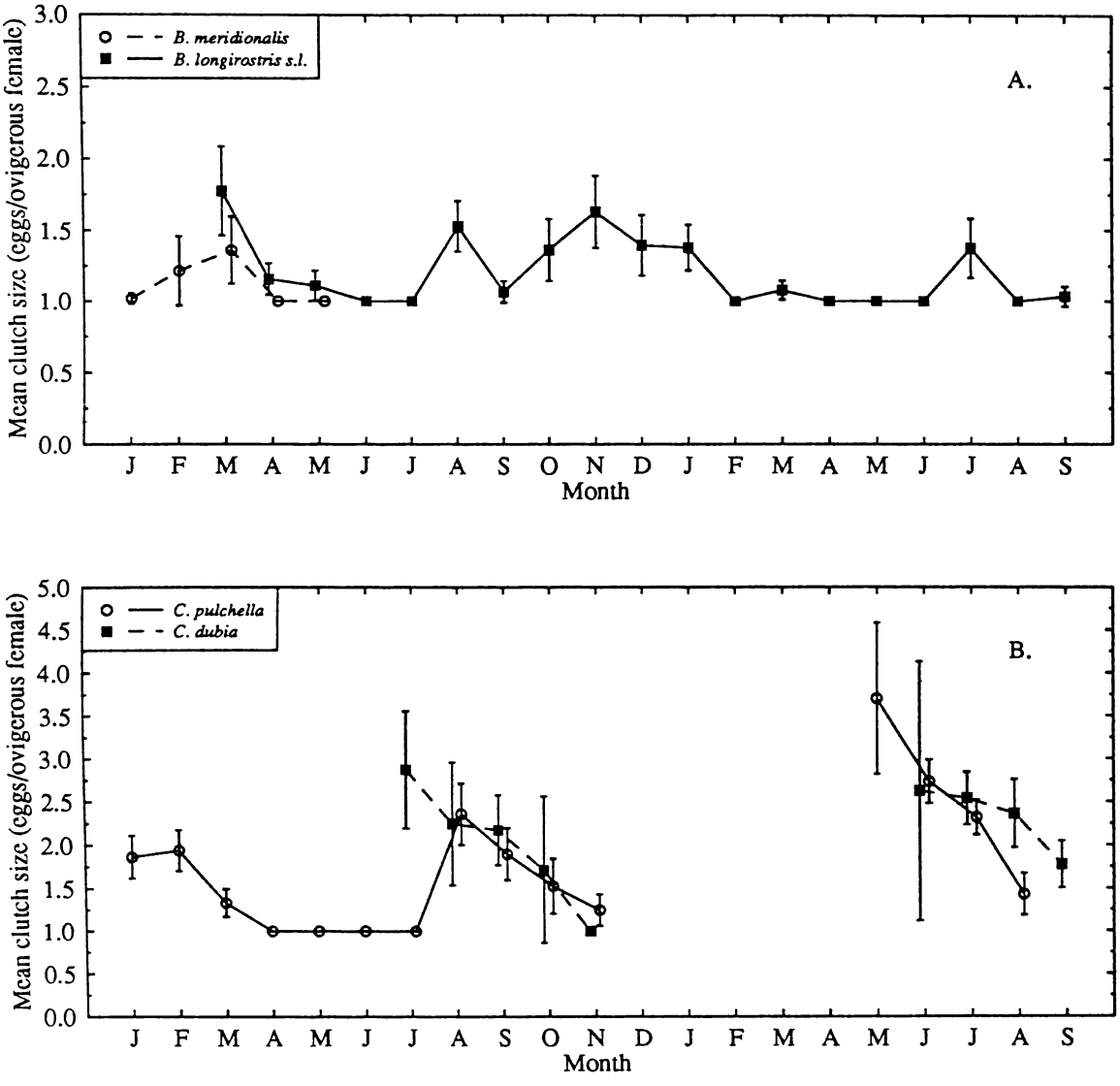

Figure 21.

Variation in mean clutch size in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989. Vertical bars are 95% confidence intervals.

population densities. This was not true for *B. meridionalis* though, in which clutch sizes were maximal when the population density was highest (December 1987). No monthly data were calculated before January 1988, and those for *B. meridionalis* are limited in extent anyway. The December 1987 period is not plotted here but see Figure 16 for mean clutch sizes over that month.

Patterns of fluctuation in maximum clutch size (Fig. 22) were similar to those for mean clutch size, but the trends were clearer and more pronounced for all species. Maximum clutch sizes recorded over the January 1988 - September 1989 period, for all species, ranged between three (*B. meridionalis* in March 1987) and seven (*C. dubia* in June 1989). However, all species had times when the maximum clutch size also equalled the minimum i.e. one, and, with the exception of *B. meridionalis* (maximum clutch size, December 1987 = 3) maximum clutch sizes were highest when densities were low.

Mean egg volume

The seasonal trends in mean egg volume (Fig. 23) in *Bosmina* during the sampling period, were, for the most part, in contrast to the patterns observed for mean clutch size, with egg volumes tending to be higher when clutch sizes were falling or static. There were exceptions to this pattern for *B. longirostris*, in August 1988 and July 1989 (both parameters high), but there was a strong seasonal tendency for higher egg volumes to be associated with lower clutch sizes. However, the coincidence in the patterns between egg volume and mean body size is remarkable. In both species of *Bosmina*, fluctuations in these two parameters were closely matched throughout the entire sampling period.

For *Ceriodaphnia*, the patterns of seasonal change in egg volume were somewhat similar to those recorded for *Bosmina*. For *C. pulchella* minimum clutch sizes in autumn of 1988 were clearly associated with increasing egg volumes, although during winter and spring both parameters declined. In 1989, egg volume increased again, while clutch sizes fell dramatically. The pattern for *C. dubia* in 1988 was the same as for *C. pulchella* in that year, at least for the winter - spring period when it was present. Both clutch sizes and egg volumes fell steadily over that period, both parameters reaching a minimum in the month of peak density. In 1989 however, this pattern was reversed and declining clutch sizes

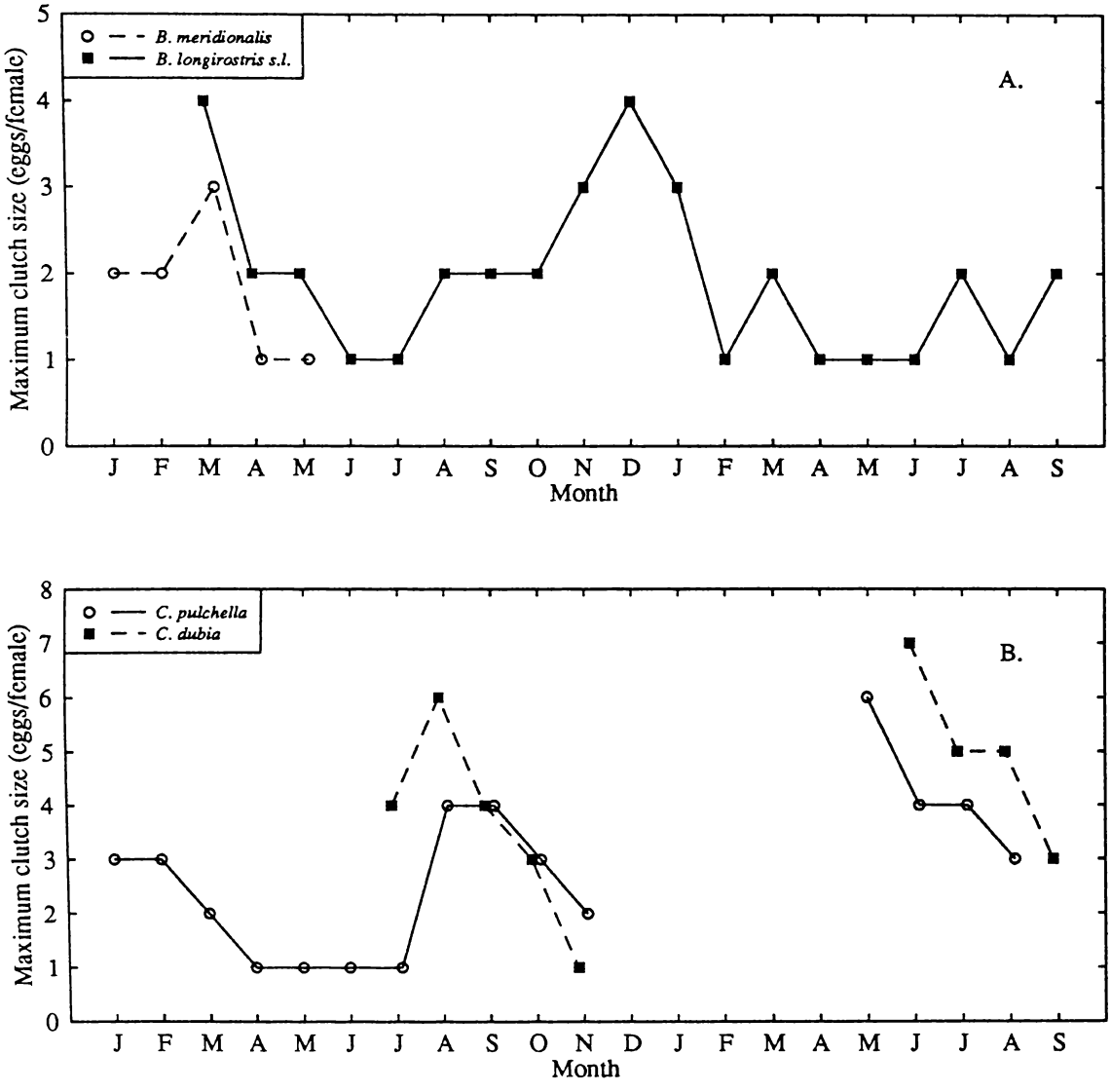

Figure 22.

Variation in maximum clutch size in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989.

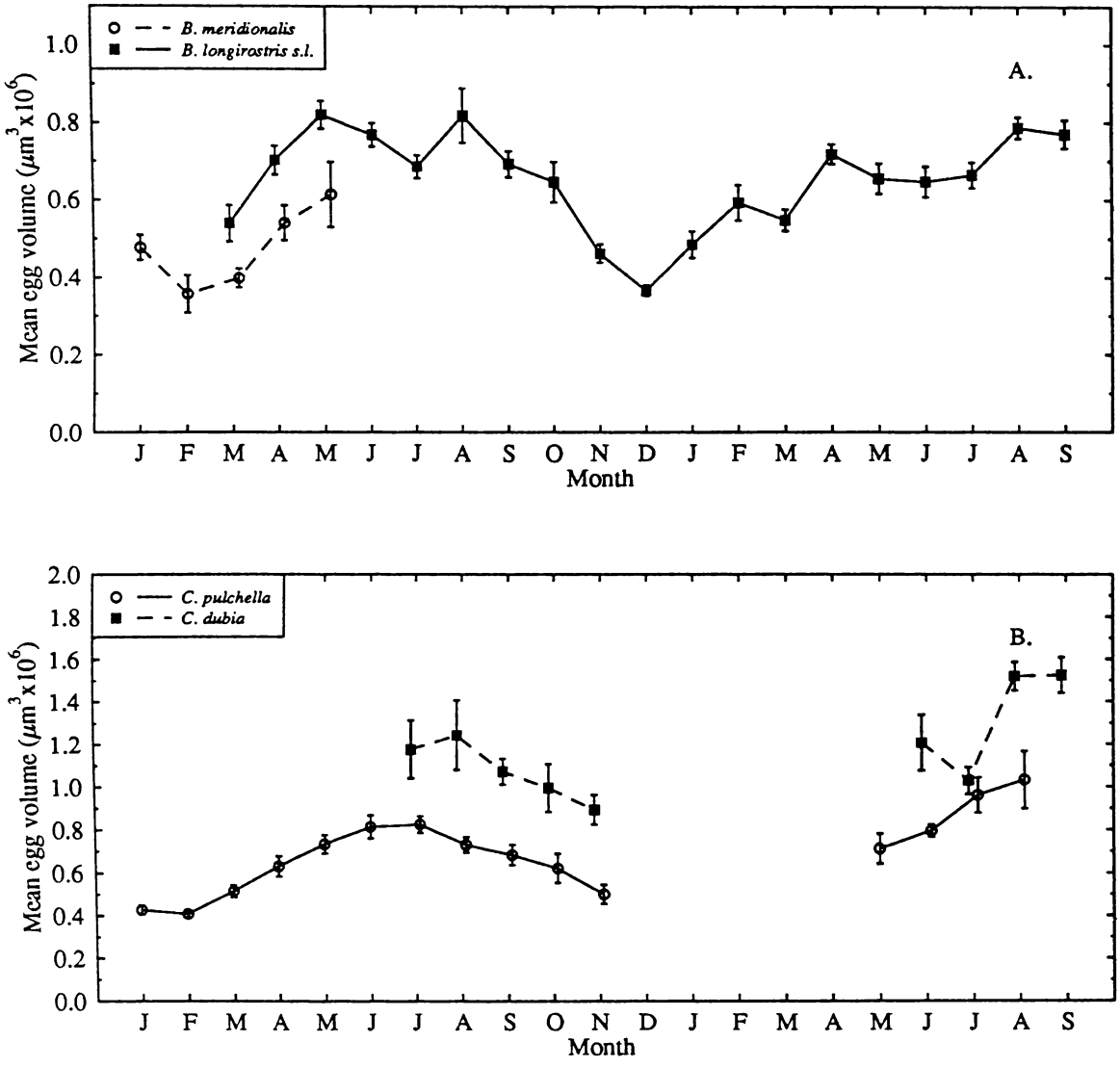

Figure 23.

Variation in mean egg volume in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989. Vertical bars are 95% confidence intervals.

were associated with increasing egg volumes. As in *Bosmina*, the matching of trends in egg volume and body size was extremely close. This suggests that the positive relationship between egg volume and body size is much stronger than the negative one between this parameter and clutch size, at least for *Ceriodaphnia*.

When all four species are considered collectively, egg volumes in *Ceriodaphnia* were generally higher than those in *Bosmina*. Within genera, egg volumes for *C. pulchella* were significantly lower than for *C. dubia*, and greater for *Bosmina longirostris* than for *B. meridionalis*, at least over the seasonal range when comparison is possible.

Mean clutch volume

Changes in mean clutch volume (Fig. 24) reflected the dependence of this parameter on both clutch size and egg volume. For *Bosmina*, the contrasting patterns of change in the latter two parameters, for the most part, combined to flatten out marked changes and result in a more uniform seasonal pattern of clutch volume variation. The exceptions to this were seen in *B. longirostris* in August 1988, and July 1989, when higher egg volumes and clutch sizes resulted in peaks in clutch volume.

For *Ceriodaphnia*, there was a quite different pattern of clutch volume variation. Low clutch sizes and increasing egg volumes combined to result in rather uniform clutch volume changes in *C. pulchella* in the first half of 1988, but this was not the case later that year. For both *C. pulchella* and *C. dubia* the winter and spring of 1988 were marked by dramatic declines in clutch volume, especially for the latter species. This pattern was the result of decreases in both clutch size and egg volume during this period, and was repeated in 1989 for *C. pulchella*. By contrast, clutch volumes in *C. dubia* in 1989 were relatively high and variable, with the effects of declining clutch sizes being somewhat offset by high egg volumes.

5.3.5 Instantaneous Rates of Population Birth, Death, and Growth

Maximum, minimum and mean values of b', d', and r' for *Ceriodaphnia* and *Bosmina* over the sampling period are summarised in Table 10. The seasonal variations these parameters is discussed for each species below.

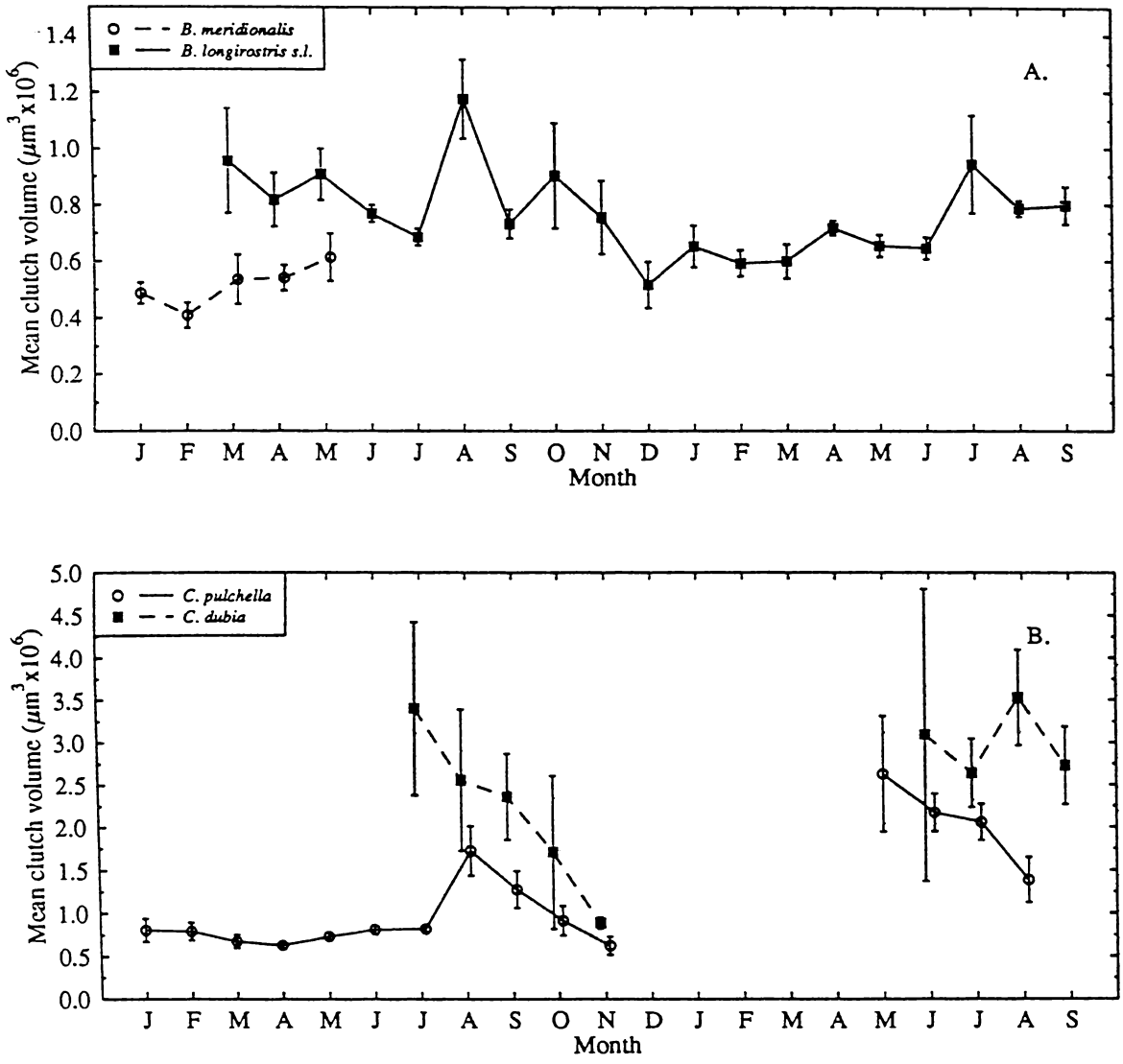

Figure 24.

Variation in mean clutch volume in (A) *Bosmina* and (B) *Ceriodaphnia* in Lake Mangakaware during 1988-1989. Vertical bars are 95% confidence intervals.

Table 10: Minimum, maximum, and mean values of b', d', and r' for *Bosmina* and *Ceriodaphnia* in Lake Mangakaware over the sampling period.

	b'			d'			r'		
Species	min	max	$\bar{x}$	min	max	$\bar{x}$	min	max	$\bar{x}$
B. longirostris	0.003	0.440	0.129	-0.118	0.454	0.116	-0.303	0.398	0.014
B. meridionalis	0.005	0.411	0.145	-0.229	0.892	0.147	-0.675	0.268	0.004
C. pulchella	0.02	0.414	0.149	-0.493	0.372	0.145	-0.25	0.658	0.008
C. dubia	0	0.555	0.215	-0.064	0.508	0.244	-0.508	0.219	-0.002

Bosmina longirostris

Seasonal fluctuations in total population abundance, and in the instantaneous rates of population growth (r'), birth (b') and death (d') in *B. longirostris* are illustrated in Figure 25. b' showed marked seasonal change, with birth rates being generally lower through autumn and winter and increasing markedly during the summer period. Death rates exhibited similar tendencies and were of the same magnitude, but were generally much more variable. As a consequence, population growth rates, for the most part, fluctuated around zero (± 0.1). Exceptions to this pattern occurred in late March 1988 and mid January 1989 (when high b's and very low d's resulted in maximal r' values), and in late April 1988 and late January 1989, when the reverse was the case (low b's, high d's and negative r's). In 1989, these sharp changes in the magnitude of birth and death rates produced the very dramatic peak and then decline in population density in January and February.

Bosmina meridionalis

The fluctuations in b', d', and r' in *B. meridionalis* are plotted in Figure 26. For this species there were very marked fluctuations in all three parameters. An exponential increase in the population at the beginning of December 1987 was the result of high birth rates, accompanied by low d's. Peak densities were reached in the middle of that month

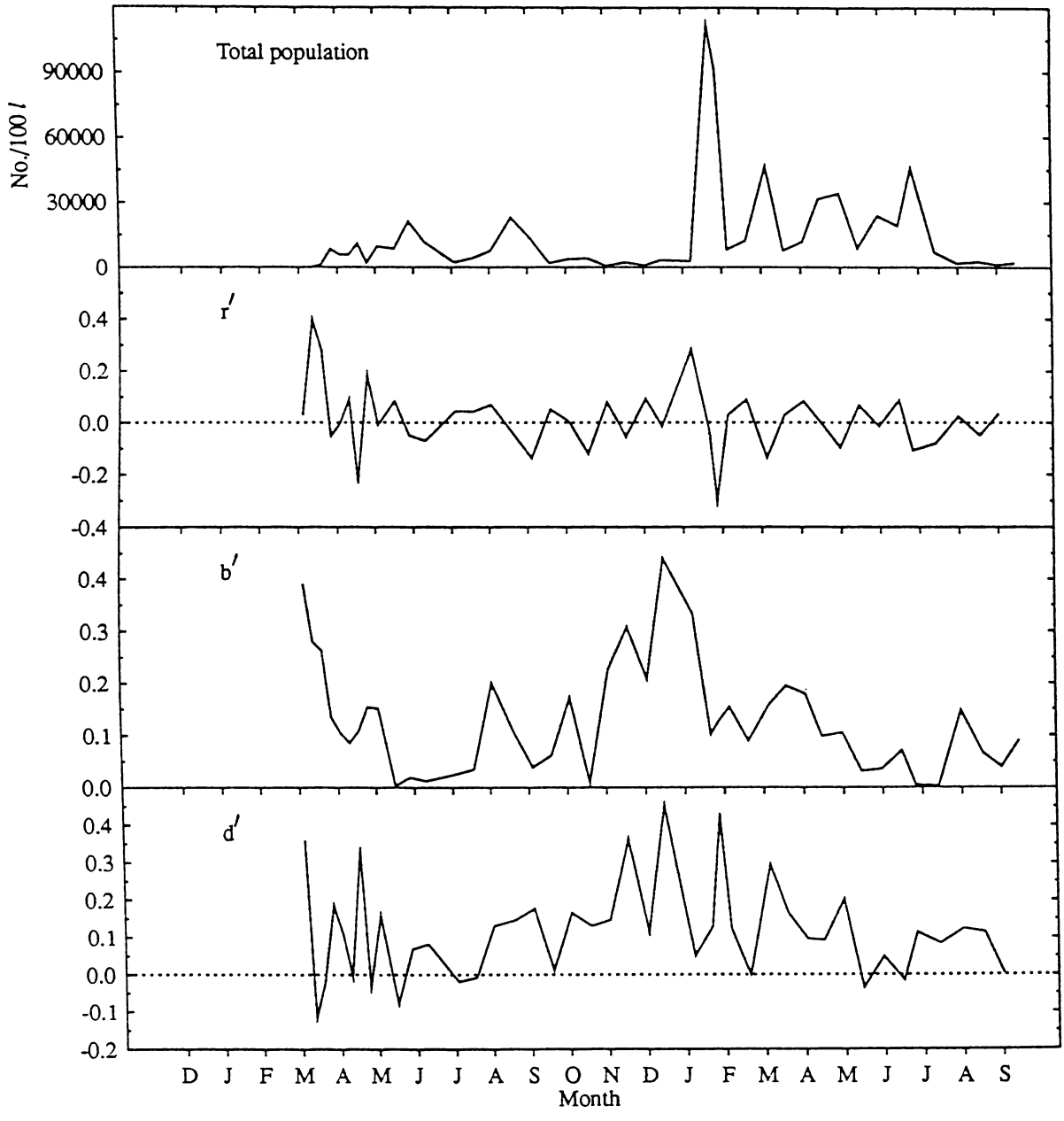

Figure 25.
Seasonal variation in total abundance, r′, b′, and d′ of *Bosmina longirostris* in Lake Mangakaware during November 1987-September 1989.

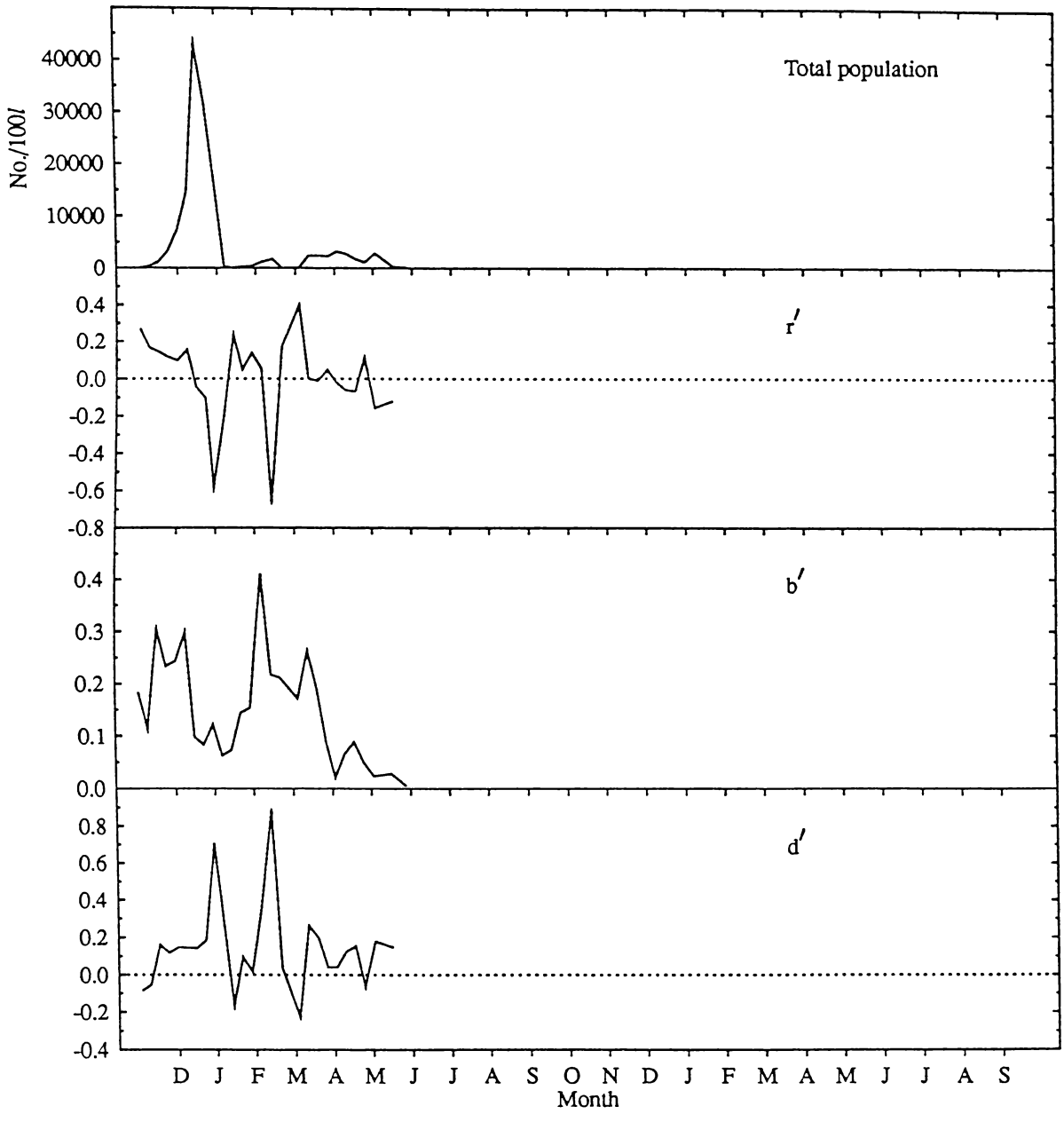

Figure 26.
Seasonal variation in total abundance, r′, b′, and d′ of *Bosmina meridionalis* in Lake Mangakaware during November 1987-September 1989.

but were not sustained, as sharply declining b's and increasing d's resulted in very negative rates of population growth. Values for r' were positive throughout most of January 1988, a consequence of increasing b's and low d's, but, as numbers were very low, the changes in population density were not large. Very high death rates (0.892) again in mid February were largely responsible for the very negative rates of population growth in this month, and it was not until March when values of d' fell that there was any significant rise in population density.

Ceriodaphnia pulchella

Fluctuations, in b', d', and r' for *C. pulchella* are shown in Figure 27. The pattern of variation in b', d', and r' accounts for *C. pulchella*'s single large abundance peak in autumn 1988, as the only period when population growth was significantly above zero was in mid February, just prior to the sharp increase in population density. The high values of r' in this month were a consequence of high birth rates and rapidly declining d's. For most of the remaining period when *C. pulchella* was present in the lake, death rates were rather low and steady, and moderate increases in b' resulted in positive values of r' and rather small increases in population density. High values of b' recorded in mid December 1987 and again in mid May 1989 may not be realistic, as the numbers of animals at these times were low enough to introduce considerable error into estimates of b' (and therefore d' also).

Ceriodaphnia dubia

Fluctuations of b', d', and r' in *C. dubia* are plotted in Figure 28. In contrast to the pattern observed for *C. pulchella*, birth and death rates in *C. dubia* varied similarly, with birth rates generally remaining a little higher than death rates. As a consequence, changes in population growth reflected subtle changes in the balance between those two parameters. Because of the rather low and steady rates of population growth, absolute changes in population density were not as dramatic as those observed for *C. pulchella*. The main peaks in population density of *C. dubia*, in November 1988 and August - September 1989, were the result of r' values of just below 0.1, when neither b's nor d's were high. The accurate estimation of b', d', and r' in November 1987 was hampered by low numbers of animals, and thus the values of these are liable to large error.

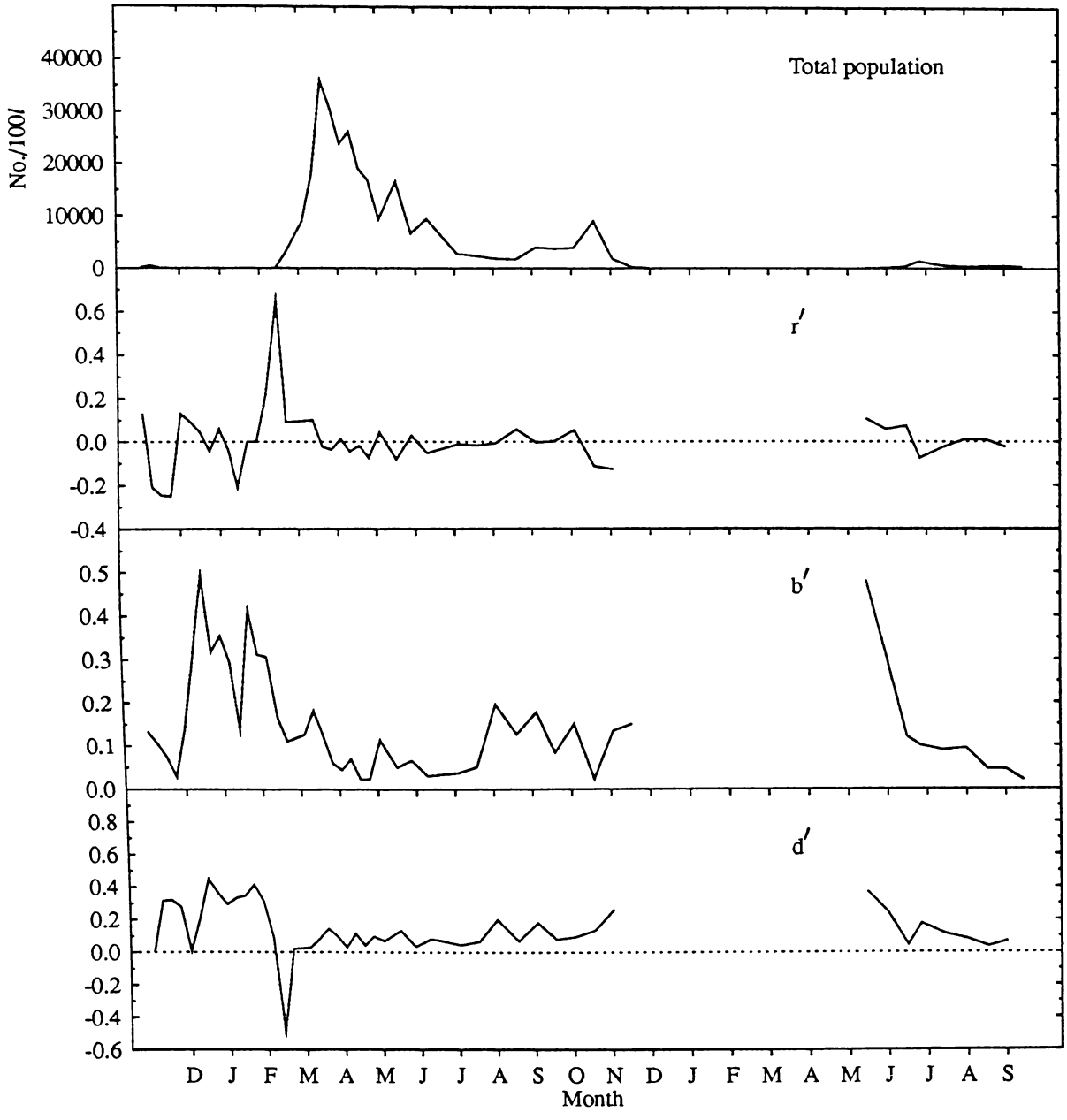

Figure 27.
Seasonal variation in total abundance, r′, b′, and d′ of *Ceriodaphnia pulchella* in Lake Mangakaware during November 1987-September 1989.

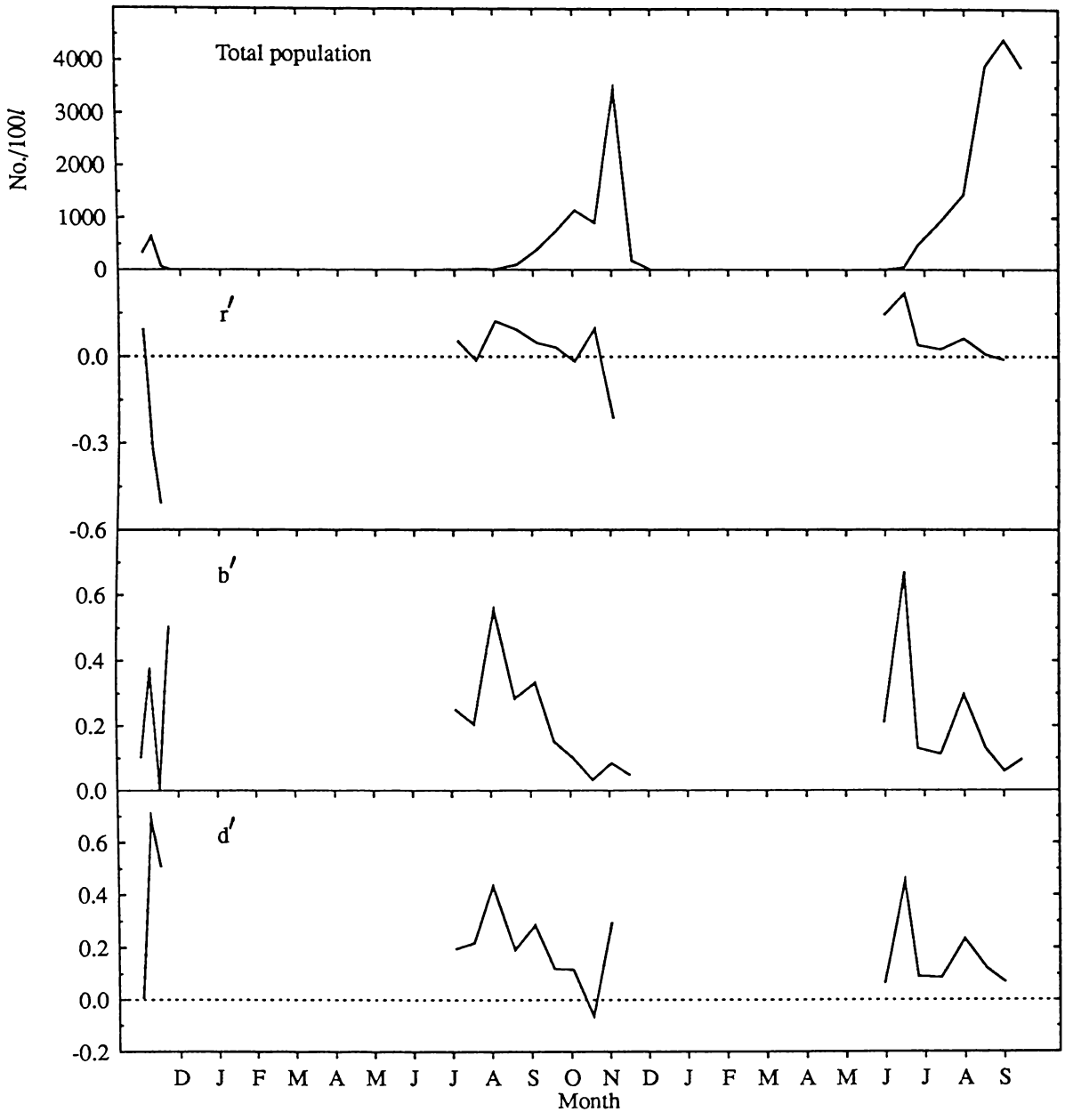

Figure 28.
Seasonal variation in total abundance, r′, b′, and d′ of *Ceriodaphnia dubia* in Lake Mangakaware during November 1987-September 1989.

5.4 STATISTICAL ANALYSES OF FIELD DATA

5.4.1 Correlation Analyses

In an attempt to establish the significance of potentially important controlling factors in the seasonal dynamics and reproductive biology of the Cladocera, a series of partial correlations was performed using SYSTAT statistical software (Wilkinson 1989). Potentially important correlations were chosen on the basis of their known relationship to, or influence on, parameters of interest (see Discussion). Where necessary, data were transformed to achieve normality. Direct counts were log transformed, while proportions were arcsine normal. The data were then tested and corrected for autocorrelation using series analysis transformation by difference (SYSTAT: Wilkinson 1989).

A number of confounding factors, such as temperature and body size, can influence the correlation between parameters of interest, if they are interdependent (see Discussion). The influence of these factors was first assessed using Pearson correlations with Bartlett's chi-square test for significance. These factors were then held constant (as independent variables) during the partial correlation to remove their influence from the relationship of interest.

Pearson Correlations

1. Influencing factor = temperature

   Parameter of interest = body size

   Pearson correlations between temperature and mean body size were performed for *Bosmina* and *Ceriodaphnia* for the monthly data collected over 1988-1989. Only for *C. pulchella* was there a significant (negative) correlation between mean body size and temperature (Table 11,A). For *C. dubia, B. longirostris,* and *B. meridionalis*, probability, p = 0.489, 0.158, and 0.272 respectively, although for all these the correlation was negative.

2. Influencing factor = temperature

   Parameter of interest = density of small (< 30 μm) phytoplankton

   Pearson correlations between temperature and phytoplankton density were not significant (p = 0.460, n = 20).

3. Influencing factor = temperature

   Parameter of interest = body size at first reproduction (SFR)

   The correlation between temperature and SFR was significant only for *B. longirostris* (Table 11,B). For *B. meridionalis, C. pulchella,* and *C. dubia* p = 0.802, 0.273, and 0.080 respectively. For all species except *B. meridionalis*, the correlation was negative as with mean body size and temperature.

4. Influencing factor = temperature

   Parameter of interest = adult Lipid Ovary Index

   The relationship between lipid-ovary score and temperature was not significant for any of the cladoceran species.

5. Influencing factor = temperature

   Parameter of interest = egg volume

   An inverse relationship between egg volume and temperature existed for all species, but was significant only for *C. pulchella* (Table 11,C).

The complete results of the Pearson correlations are given on floppy disk at the back of this volume.

Partial Correlation Analyses

The complete results of all significant and non significant partial correlations are given on floppy disk at the back of this volume.

1. Body size, clutch size, and egg volume

The correlations between body size, clutch size, and egg volume were performed for all four cladoceran species, holding temperature constant. For every species, there was a significant positive correlation between egg volume and body size (Table 12,A). For both *Ceriodaphnia* species there was also a positive, although not significant, relationship between clutch size and body size, whereas for *Bosmina*, this relationship was negative. However, the correlation was significant only for *B. meridionalis.*

Table 11: Matrices of Pearson correlation coefficients and associated probabilities for significant correlations of **A.** mean body size with temperature (monthly data), **B.** body size at first reproduction and temperature, and **C.** egg volume with temperature. TEMP=temperature; BSZ=mean body size; SZR1=size at first reproduction; EV=egg volume; CP=*Ceriodaphnia pulchella*; BL=*Bosmina longirostris*. See text for details of data transformation and non-significant correlations.

A.

	BSZCP	TEMP
BSZCP	1.000	
TEMP	-0.679	1.000
Bartlett chi-square statistic:		10.207
Probability:		<.001
n = 19		

B.

	SZR1BL	TEMP
SZR1BL	1.000	
TEMP	-0.446	1.000
Bartlett chi-square statistic:		8.743
Probability:		<.01
n = 42		

C.

	EVCP	TEMP
EVCP	1.000	
TEMP	0.001	1.000
Bartlett chi-square statistic:		11.524
Probability:		<.001
n = 19		

2. Body size; clutch size; or egg volume, and density of small phytoplankton

For all these analyses the influence of either temperature, or both temperature and body size, was removed by treating these as constants.

B. longirostris was the only species to show a significant correlation (negative) between body size and phytoplankton (Table 12,B). Although not significant, correlations between these parameters were positive for *Ceriodaphnia* but negative for *B. meridionalis*.

Both *B. meridionalis* and *C. dubia* showed significant correlations between clutch size and small phytoplankton, but the relationship was positive only for *B. meridionalis* (Table 12,B).

In both species of *Bosmina* there was a significant positive correlation between egg volume and the density of small phytoplankton (Table 12,B). For *Ceriodaphnia*, the partial correlation coefficient was negative, although not significant.

3. Lipid ovary score and the densities of potential competitors and small (<30 μm) phytoplankton.

For three of the four Cladoceran species (*B. meridionalis, C. pulchella* and *C. dubia*) there were significant negative correlations between the adult Lipid Ovary Index (LOI) and the density of potential competitors (Table 13). For *B. meridionalis*, there was a strong ($p < 0.001$) negative correlation between LOI and the density of *C. pulchella*, a species that became abundant following the summer demise of *B. meridionalis*. For both species of *Ceriodaphnia*, declines in LOI were associated with increases in the density of each species. This finding supports that obtained from the plots of reproductive parameters and LOI, where high densities were associated with minimal clutch sizes and low lipid score. Surprisingly, none of the species showed any correlation of lipid score with phytoplankton density.

4. Proportion of adult females ovigerous, population density, and the number of small phytoplankton.

For both species of *Ceriodaphnia*, the proportion of females ovigerous was negatively correlated with their population density (Table 14). As with lipid score (see above) this reflects the decline in population fecundity associated with high densities. For

Table 12: Results of partial correlations of A. body size with the reproductive parameters, clutch size and egg volume, and B. each of these parameters with the numbers of small (< 30 μm) phytoplankton. Results in each case are displayed as the matrix of partial correlation coefficients, and significant ($p < 0.05$) correlations between variables are bolded. Variables held constant (= independent) in each case are given on the right, together with the probabilities of the partial correlation coefficients where these are significant. BSZ=body size; CLSZ=clutch size; EV=egg volume; TEMP=temperature; PHY=small phytoplankton. See text for details of data transformation and non-significant correlations.

A. *Ceriodaphnia pulchella:*

	BSZ	CLSZ	EV	df	Independent(s)	p
BSZ	1.000					
CLSZ	0.158	1.000				
EV	**0.564**	-0.207	1.000	17	TEMP	< .01

Ceriodaphnia dubia:

	BSZ	CLSZ	EV	df	Independent(s)	p
BSZ	1.000					
CLSZ	0.114	1.000				
EV	**0.803**	0.065	1.000	12	TEMP	< .001

Bosmina longirostris:

	BSZ	CLSZ	EV	df	Independent(s)	p
BSZ	1.000					
CLSZ	-0.245	1.000				
EV	**0.833**	**-1.172**	1.000	16	TEMP	< .001

Bosmina meridionalis:

	BSZ	CLSZ	EV	df	Independent(s)	p
BSZ	1.000					
CLSZ	**-0.961**	1.000				
EV	**0.944**	-0.816	1.000	2	TEMP	< .05

B. *Bosmina longirostris:*

	BSZ	PHY	df	Independent(s)	p
BSZ	1.000				
PHY	**-0.544**	1.000	16	TEMP	< .01

Bosmina meridionalis:

	CLSZ	PHY	df	Independent(s)	p
CLSZ	1.000				
PHY	**1.000**	1.000	1	TEMP, BSZ	< .001

Ceriodaphnia dubia

	CLSZ	PHY	df	Independent(s)	p
CLSZ	1.000				
PHY	**-0.605**	1.000	11	TEMP, BSZ	< .05

B. longirostris

	EV	PHY	df	Independent(s)	p
EV	1.000				
PHY	**0.616**	1.000	15	TEMP, BSZ	< .01

B. meridionalis

	EV	PHY	df	Independent(s)	p
EV	1.000				
PHY	**1.000**	1.000	1	TEMP, BSZ	< .001

Table 13: Results of partial correlations of adult lipid-ovary score, with numbers of potential competitors and the density of small (< 30μm) phytoplankton. Results in each case are displayed as the matrix of partial correlation coefficients, and significant ($p < 0.05$) correlations between the variables of interest are bolded. Variables held constant (= independent) in each case are given on the right, together with the probabilities of the partial correlation coefficients where these are significant. LO=lipid-ovary score; CP=density of *C. pulchella*; CD=density of *C. dubia*; BL=density of *B. longirostris*; BM=density of *B. meridionalis*; COP=total copepod density; ROT=total rotifer density; PHY=small phytoplankton; TEMP=temperature. See text for details of data transformation and non-significant correlations.

Bosmina meridionalis

	CP	CD	BL	BM	ROT	PHY	LO	COP	df	Independent	p
CP	1.000										
CD	-0.318	1.000									
BL	-0.100	0.022	1.000								
BM	0.403	-0.487	-0.240	1.000							
ROT	0.134	-0.190	-0.004	-0.565	1.000						
PHY	0.252	-0.468	-0.269	0.263	-0.019	1.000					
LO	**-0.944**	0.312	0.048	-0.474	-0.036	-0.245	1.000				
COP	-0.150	-0.120	0.093	-0.205	0.583	0.075	0.019	1.000	9	TEMP	< .001

Ceriodaphnia pulchella

	CP	CD	BL	BM	ROT	PHY	LO	COP	df	Independent	p
CP	1.000										
CD	0.320	1.000									
BL	0.136	-0.059	1.000								
BM	0.078	-0.156	-0.033	1.000							
ROT	0.280	0.145	0.491	-0.090	1.000						
PHY	-0.527	-0.390	-0.026	0.049	-0.058	1.000					
LO	**-0.300**	0.046	0.075	0.008	-0.051	0.002	1.000				
COP	0.160	0.067	0.474	-0.004	0.689	0.166	0.167	1.000	37	TEMP	< .05

Ceriodaphnia dubia

	CP	CD	BL	BM	ROT	PHY	LO	COP	df	Independent	p
CP	1.000										
CD	0.320	1.000									
BL	0.136	-0.059	1.000								
BM	0.078	-0.156	-0.033	1.000							
ROT	0.280	0.145	0.491	-0.090	1.000						
PHY	-0.527	-0.390	-0.026	0.049	-0.058	1.000					
LO	0.237	**-0.354**	-0.023	0.110	-0.072	0.050	1.000				
COP	0.160	0.067	0.474	-0.004	0.689	0.166	-0.139	1.000	37	TEMP	< .05

Bosmina, the correlation was not significant, and although it was positive for *B. meridionalis*, *B. longirostris* showed a similar relationship to *Ceriodaphnia* between proportion ovigerous and population density. As was the case with lipid score, in none of the species was the proportion of ovigerous females correlated significantly with phytoplankton density.

5. Birth rate, and the densities of small phytoplankton and potential competitors.

b' was significantly correlated with competitors only for *Bosmina* (Table 15). For *B longirostris*, significant correlates were the numbers of Cladocera (negative) and the numbers of Copepoda (positive). For *B. meridionalis*, b' was negatively correlated with rotifer density. Birth rates were not significantly correlated with phytoplankton density in any species.

6. Death rates and the density of predators, and competitors.

The partial correlations between death rates and (1) the numbers of potential predators (*Mesocyclops* and *Asplanchna*), and (2) the numbers of potential competitors (Cladocera, Copepoda, and Rotifera) were performed, holding constant the density of the population being tested. None of the species had death rates that were significantly correlated with potential predators, and the values of the partial correlation coefficients were not consistently positive or negative. The correlation of d' with the numbers of competitors was similar, with no significant relationship being found between death rates and competitor density for any of the four species.

5.4.2 Regression of Clutch Volume on Body Size

The relationship between body size and clutch volume can serve to illustrate differences in size specific reproductive effort. Differences between the slopes of the regression lines, for the clutch volume - body length relationship, indicate differences in the rate of change in volume of egg material carried, in proportion to body length (Burgis 1967). The relationship of total egg volume carried by parthenogenetic females of *B. meridionalis, B. longirostris, C. pulchella*, and *C. dubia* was investigated using linear regression on log transformed data (SYSTAT statistical package, Wilkinson 1989).

Table 14: Results of partial correlations of proportion of adult females ovigerous with population density and numbers of small (< 30μm) phytoplankton. Results in each case are displayed as the matrix of partial correlation coefficients, and significant ($p < 0.05$) correlation values are bolded. Variables held constant (= independent) are given on the right, together with the probabilities of the partial correlation coefficients where these are significant. OV=proportion ovigerous. Other abbreviations as for Table 13. See text for details of data transformation and non-significant correlations.

Ceriodaphnia pulchella:

	CP	OV	PHY	df	Independent(s)	p
CP	1.000					
OV	**-0.227**	1.000				
PHY	-0.080	-0.020	1.000	53	TEMP	< .05

Ceriodaphnia dubia:

	CD	OV	PHY	df	Independent(s)	p
CD	1.000					
OV	**-0.383**	1.000				
PHY	-0.214	0.055	1.000	54	TEMP	< .01

Table 15: Results of partial correlations of birth rate (b') with densities of potential competitors and numbers of small (< 30μm) phytoplankton. Results are displayed as the matrix of partial correlation coefficients, and significant correlations between variables of interest are bolded. Variables held constant (= independent) are given on the right, together with the probabilities of the partial correlation coefficients where these are significant. Abbreviations as for Table 13. See text for details of data transformation and non-significant correlations.

Bosmina longirostris

	ROT	b'	PHY	CLAD	COP	df	Independent(s)	p
ROT	1.000							
b'	-0.029	1.000						
PHY	-0.070	-0.052	1.000					
CLAD	0.492	**-0.434**	-0.286	1.000				
COP	0.608	**0.315**	0.150	0.543	1000	39	BL, TEMP	< .05

Bosmina meridionalis

	ROT	b'	PHY	CLAD	COP	df	Independent(s)	p
ROT	1.000							
b'	**-0.433**	1.000						
PHY	-0.058	0.259	1.000					
CLAD	0.028	-0.154	0.122	1000				
COP	-0.555	0.141	-0.167	0.254	1000	20	BM, TEMP	< .05

The data and fitted regression lines are plotted in Figure 29, and the corresponding regression equations and ANOVAs given in Table 16.

The overlap in the 95% confidence intervals of the regression coefficients, indicates no significant difference between *C. dubia* and *B. meridionalis* , between the two species of *Ceriodaphnia*, or between *B. meridionalis* and *B. longirostris* in the rate at which clutch volume increases in proportion to body length. However, *B. longirostris*, with a lower b value, is significantly different from both species of *Ceriodaphnia* in this respect (Table 16). *Ceriodaphnia* , therefore, increases the volume of egg material carried, in proportion to body length, more rapidly than does *B. longirostris*. On the basis of the 95% confidence intervals of b, the clutch volume-body size relationship is significantly different between *C. pulchella* and *B. meridionalis* also. However, there is a good deal of scatter in the data and such a conclusion should be regarded cautiously.

As would be expected given the strong correlation between body size and egg volume (Table 12), and the inherent effect of body length on clutch size, maximum clutch volumes were greatest in the largest species, *C. dubia*. Similarly *C. pulchella* > *B. longirostris* > *B. meridionalis* in terms of maximum clutch volume achieved.

5.5 DISCUSSION

5.5.1 Population Structure and Gamogenesis

The breakdown of cladoceran communities into age or instar classes by length-frequency analysis is a difficult task, requiring a very short sampling interval, equal to, or less than, the development time of a single instar. Such analyses have rarely been attempted for Cladocera and most studies that investigate age distributions have dealt with theoretical models which incorporate adjustments to the assumption of a stable age distribution (e.g. Seitz 1979; Taylor and Slatkin 1981). The sampling interval in this study was too long to attempt any kind of cohort analysis, therefore only adult and juvenile groups were distinguished in the field samples. As is characteristic of cladocerans, which typically exhibit rapid and continuous development with generational overlap (Taylor and Slatkin 1981), both juvenile and adult sections of the population tended to fluctuate

Table 16: Regression equations relating clutch volume (cl.vol.) to body size (bs) in *Bosmina* and *Ceriodaphnia* as shown in Figure 29. The general form of the regression is given by log cl.vol. = a + b logbs. The standard error (SE) and 95% confidence interval (CI) for the regression coefficient b, is given in each case, together with R^2. The ANOVA for each regression is given below. SOURCE=source of variation; SS=sum of squares; DF=degrees of freedom; MS=mean square.

1. ***Bosmina longirostris***

log cl.vol. = 1.111 + 1.560 log bs
SE of b = 0.080 R^2 = 0.351
CI of b = 0.132

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	31.279	1	31.279	383.470	0.001
Residual	57.506	705	0.082		

2. ***Bosmina meridionalis***

log cl.vol. = 1.211 + 1.723 log bs
SE of b = 0.261 R^2 = 0.241
CI of b = 0.432

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	2.681	1	2.681	43.521	0.001
Residual	8.194	133	0.062		

3. ***Ceriodaphnia dubia***

log cl.vol. = 1.763 + 2.498 log bs
SE of b = 0.303 R^2 = 0.304
CI of b = 0.501

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	13.356	1	13.356	68.213	0.001
Residual	30.545	156	0.196		

4. ***Ceriodaphnia pulchella***

log cl.vol. = 1.637 + 2.614 log bs
SE of b = 0.230 R^2 = 0.228
CI of b = 0.379

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	31.939	1	31.939	129.130	0.001
Residual	107.841	436	0.247		

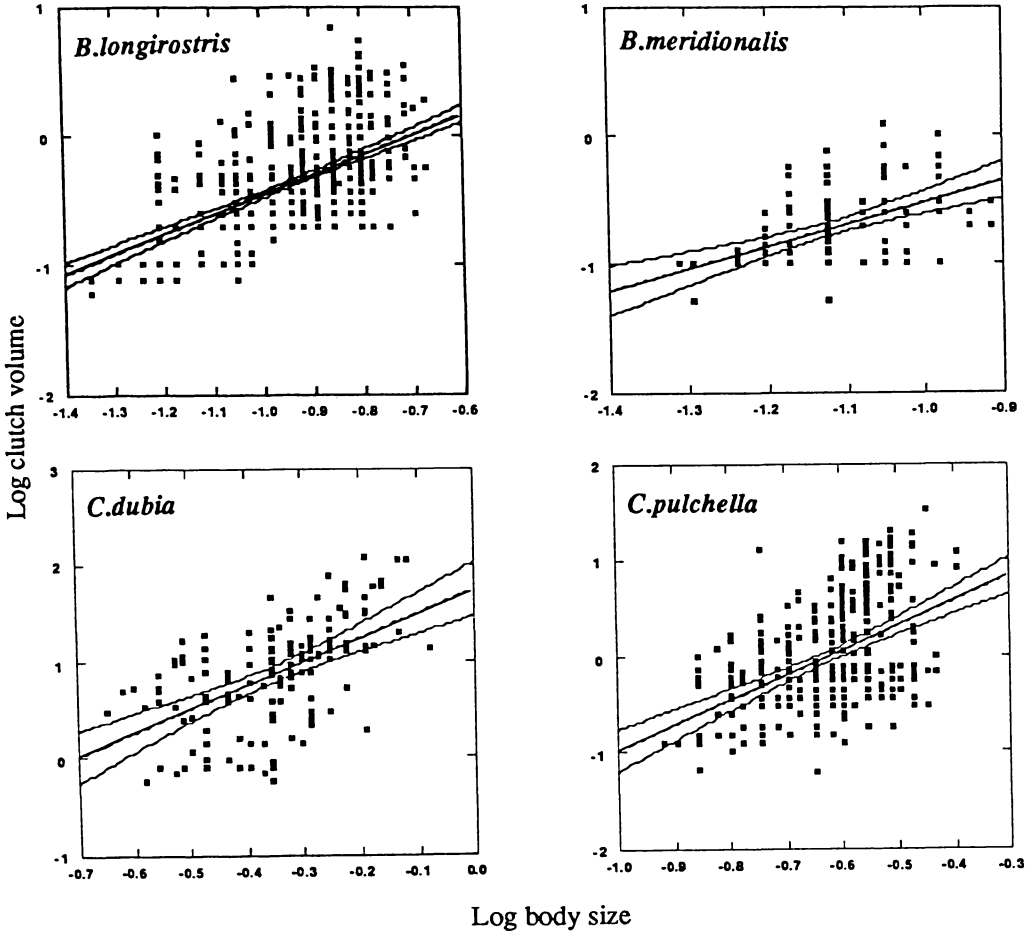

Figure 29.
The log-log relationship of clutch volume to body length in *Ceriodaphnia* and *Bosmina* from Lake Mangakaware, January 1988 - September 1989.

together. There was some variability in the proportion of adults and juveniles seasonally, particularly for *B. meridionalis*, where adults showed a marked proportional increase at the time of steep population decline, following peak abundance. Adults also tended to predominate in populations early in their seasonal development, i.e., shortly after their first appearance in the plankton, as was the case for both species of *Ceriodaphnia*. This is not unexpected very early in the development of a population, when the number of hatched juveniles is still very low. For the most part though, the proportions of juveniles and adults, while not stable, fluctuated uniformly about some relatively constant value.

The occurrence of gamogenetic individuals was common in the cladoceran community, and was recorded for *C. pulchella* and *Bosmina* in 1985 also (Greenwood 1987). Sexual reproduction in Cladocera is well documented (Hutchinson 1967) and is a strategy for persistence in a fluctuating, often unfavourable, environment. Records of sexual reproduction in New Zealand cladoceran populations, however, are sparse. Ephippial *Ceriodaphnia* have been recorded in Lake Ngapouri (Chapman *et al.* 1985), the Auxiliary Nihotupu Reservoir (Green 1968) and Lake Grasmere (Staples 1984), and Donovan (1970) recorded ephippial *Bosmina* in Lake Ototoa, although males were not found. In these studies, ephippial production was associated with high population densities, rather than with a requirement for an overwintering stage (e.g. Smyly 1974, 1979), or as a survival mechanism through drought, as occurs in temporary water bodies (Stirling and McQueen 1986).

For *B. meridionalis* and *C. dubia* both males and ephippial females occurred at the time of peak population density. However this was not the case for *B. longirostris* and *C. pulchella*, where ephippial females were recorded respectively four months before, and four months after, peak densities. Interestingly, neither of these two species appeared to produce males during 1987 - 1989. This is in contrast to the situation for *C. pulchella* in 1985 (Greenwood 1987) where gamogenetic animals occurred at the highest population density, and both males and ephippial females were recorded. This suggests that the cues for the production of males and ephippia are different for *B. longirostris* and *C. pulchella* than for *C. dubia* and *B. meridionalis*.

Governing factors in the control of gamogenesis in Cladocera have been much studied, but are still relatively poorly understood, perhaps because the causal factors in the onset of sexual reproduction appear to vary depending on the species. Moreover, it is difficult to separately evaluate the effects of physical and biological cues when identifying factors involved in triggering sexual reproduction. Some of those implicated include photoperiod, temperature, crowding and starvation, and the type and quality of food (e.g. Stross and Hill 1965, 1968; D'Abramo 1980). Stirling and McQueen (1986) found the production of both ephippia and males to be associated with increasing temperatures before summer drought, while lower temperature provided the cue for the hatching of ephippia and the production of a large bodied parthenogenetic population. Other studies have implicated crowding factors in the induction of gamogenesis (e.g. Banta and Brown 1929), although crowding itself is frequently concomitant with high competition and starvation, both of which have been associated with sexual induction (Helgen 1987). More recent work has provided evidence for the importance of threshold feeding levels in triggering sexual reproduction in cladocerans. D'Abramo (1980), for example, found that ephippial egg production in *Moina macrocopa* was related to decreased particle ingestion rates under crowded conditions, and suggested that anything reducing feeding rate will stimulate sexual reproduction. Probably a combination of cues is important. For *B. meridionalis* and *C. dubia*, crowding, or its associated effects, was almost certainly important and, given the timing of occurrence, increasing day length may also have been a factor. Carvalho and Hughes (1983), for example, induced resting eggs in *Daphnia magna* with low food, high culture densities, and short-day photoperiods, and suggested that this species has a degree of plasticity in its response to the stimuli inducing the production of ephippia.

For *B. longirostris* and *C. pulchella* no obvious crowding factors appeared to be involved in 1988, since zooplankton densities generally were quite low at the times of ephippia production. Interestingly, both these species, newly recorded in New Zealand, are more typical of the Northern Hemisphere, where overwintering phases in Cladocera are common. In Lake Mangakaware, the switch to sexual reproduction was similarly

associated with cooler temperatures, although not convincingly with shorter day lengths. Berner *et al.* (1991) found differences in the responsiveness of seasonal clones to inducing factors and suggested that such variability in response may be the basis for differences observed in the timing of gamogenesis. This may be the case for Cladocera in Lake Mangakaware also. Certainly, ephippial production has been associated with peak densities for *B. longirostris* and *C. pulchella* in earlier years (Greenwood 1987). Chemical cues and shorter day lengths have been implicated in the production of males (Hobáek and Larsson 1990) and chemical mediation ("autoallelopathy") has been known to depress feeding response also (Helgen 1987). Most workers agree that the environmental cues for the production of ephippia and males are likely to be subtly different, and more recent work has suggested that it is the response of the female to environmental stimuli which elicits sex-ratio regulation and determines the production of male or female offspring (Hobáek and Larsson 1990).

5.5.2 Growth and Reproduction

When viewed overall, a number of general trends in the patterns of growth and reproduction appear to be shared by the four cladocerans in Lake Mangakaware. Firstly, all species showed a very strong positive correlation between egg volume and body size, so much so that the seasonalities of these two parameters were almost identical. Secondly, increases in body size were generally associated with decreases in temperature.

Reproductive effort

The positive correlation between egg size and adult body size in Cladocera is well documented (Green 1956; Burgis 1967; Kerfoot 1974; Allan and Goulden 1980) as is the positive correlation between this parameter and size of the primiparous adult (Green 1956, 1966). Green (1966) also found that egg size correlates positively with maternal nutrition but inversely with temperature (see also Burgis, 1967; Brambilla 1982). The relationship between egg volume and adult LOI was not consistent for the Cladocera in Lake Mangakaware. For *C. pulchella* , the pattern of fluctuation in egg size was consistently contrary to that shown by the LOI. In *C. dubia* both parameters declined together in 1988, but there was no obvious relationship in 1989. For *Bosmina*, the relationship between lipid

score and egg size was similarly weak. Clearly, for the cladocerans in Lake Mangakaware, egg size is correlated primarily with body size, and does not appear to be greatly influenced by maternal nutrition (as assessed by LOI). Consistent with this, between species too, the volume of egg material carried was greater for larger species than for smaller ones (see above).

The monthly data for all species do indicate an inverse relationship between egg volume and temperature, but this was significant only for *C. pulchella.* The restricted seasonal range of both *C. dubia* and *B. meridionalis* precludes any generalisations about the lack of a significant correlation between these variables for these species. Had they been present over the full seasonal temperature range the data may have been more conclusive.

Increasing egg size is not necessarily associated with increasing clutch size in Cladocera. Indeed, there is an adaptive "choice" that can be made in the way that the reproductive effort is packaged. Burgis (1967) points out that *C. pulchella* produces more eggs, but a lower clutch volume, than *C. reticulata* of the same size. In other words, the eggs of *C. pulchella* are packaged into more, smaller units than those of its cogener. It is difficult to determine, from the field data, if this is true of *C. pulchella* relative to *C. dubia* in Lake Mangakaware, since these two species were similar with respect to mean clutch size. However, *C. dubia* is capable of producing more eggs than *C. pulchella* for any given body size in the laboratory (Greenwood 1987) and this relationship will be examined further in Part Three.

Invariably, the packaging of reproductive effort involves a trade-off between the production of fewer, larger young that achieve maturity earlier, and a large number of smaller neonates. *Bosmina longirostris* typically produces eggs that are large relative to adult body weight (Lynch 1980a), and this is supported by the study of this species in Lake Mangakaware. Typical values of relative egg size (egg length ÷ body length) for *B. longirostris* and *B. meridionalis* are similar, and range from 0.35 - 0.43. Relative egg sizes in *C. pulchella* are somewhat lower (0.26 - 0.35), and those of *C. dubia* lower again (0.20 - 0.29). This has implications for breeding success. For example, Lynch (1980a) points out

the negative relationship between large relative egg size and age at first reproduction. Species producing relatively large young which mature at an early age will be advantaged in a system where short term fluctuations in the physical environment and the food base are typical, since early maturation will better allow rapid exploitation of transient resources.

Variation in body size and feeding success

As described earlier, seasonal increases in body size were generally associated with decreasing temperature for both *Ceriodaphnia* and *Bosmina* . When the probabilities of the partial correlation coefficients were tested however, the size-temperature relationship was significant only for *B. longirostris* (size at first reproduction), and *C. pulchella* (mean adult body size). The inverse relationship between body size and temperature in Cladocera is well recognised (e.g. Burgis 1967; Kerfoot 1974; Culver 1980) and much attention has been given to seasonal variations in the size at first reproduction in particular. Vijverberg (1980) recorded a general trend for cladocerans at high temperature to mature at a small size, and Green (1956) noted that both starvation and increasing temperature reduced body size in *Daphnia.* In a review of the effects of food limitation on the life history characteristics of rotifers and cladocerans, Duncan (1989) noted that, in the Cladocera for which data were examined, limiting food reduced body size and increased the age of maturation. These effects were attributed to the high cumulative costs of respiration through a protracted juvenile period. Similarly, Gophen (1976) found that increasing temperature affected body size in *C. reticulata* through increased rates of respiration causing an energy deficit and a decline in both body size and egg production. Temperature increases thus preceded a progressive decline in the population.

Declines in body size with temperature have been recorded for New Zealand *Bosmina* and *Ceriodaphnia* in both laboratory and field studies (Greenwood 1987), but the role of food limitation in those declines was not investigated. Bhajan and Hynes (1972) recorded increases in the body size of *B. longirostris* at low temperatures, similar in magnitude to those found for *Bosmina* in this study, and Brambilla (1982) found that while temperature affected body size and egg production in *Daphnia*, the response varied

according to whether the animals were from early or late season populations. It may be that food limitation at particular times during a seasonal cycle enhances the negative effect of temperature on body size. Under conditions of limited food it may be advantageous to reduce body size anyway, given that fewer resources will be required to reach maturity. Moreover, smaller bodied individuals are more resistant to protracted periods of food depletion, since their requirements for maintenance are lower (Romanovsky and Feniova 1985).

Partial correlations between body size and indicators of available food for Lake Mangkaware Cladocera were somewhat contradictory with respect to what might be expected from the literature. There was no significant correlation between body size and small phytoplankton density in *Ceriodaphnia*, although the relationship was positive, indicating that larger body sizes were at least associated with increases in potentially available food. For *Bosmina* though, the results are more confusing. Body sizes were generally smaller, but egg volumes larger, with increased phytoplankton abundance, although the body size relationship was significant only for *B. longirostris*. This is despite the strong positive correlation between egg volume and body size, and suggests that the dependence of egg volume on size and available food is greater than that of size on nutrition. Similarly, for *C. pulchella,* clutch size, as a measure of reproductive effort, was lower when body size was largest, suggesting that different factors govern the fluctuations in these two parameters.

Thus, while temperature appears to exert a considerable influence on body size, larger clutch sizes are not necessarily associated with larger body sizes, but seem to be determined by some other factor, probably food availability. This is supported by the declines observed in mean clutch size and lipid score during or just after peak population densities in all species. Similarly, for *B. meridionalis* and *C. pulchella*, the proportion of females ovigerous generally increased with mean clutch size and LOI, suggesting a dependence of population fecundity on nutrition. For *C. dubia*, the proportion of females ovigerous was high and constant for most of the year, except at peak densities. The lack of any correlation between small phytoplankton density and indices of feeding success, such

as LOI, may be because palatable types are heavily grazed, and the algal species that are abundant are so because they are not contributing much to the base of nutritionally suitable food.

Correlations of both proportion of egg bearing females and LOI indicate that, for both species of *Ceriodaphnia,* high population densities had a negative effect on population fecundity and feeding success. For *B. meridionalis,* feeding success (as measured by LOI) was negatively affected by high densities of *C. pulchella,* suggesting that there was at least the potential for competitive displacement of the former species by the latter in the autumn. *Bosmina* probably has more chance for rapid population expansion and feeding success during summer periods when larger algal species are more abundant, and its more selective mode of feeding is favoured (see Chapter Four).

Of the four species, absolute changes in body size were greater for *C. dubia* than for *C. pulchella* or *Bosmina,* which are smaller species and thus less flexible in the degree to which they can vary body size when environmental conditions change. In agreement with this, maximum mean clutch sizes were greatest for the largest species (1.68, 2.57, 3.33, 4.33 for *B. meridionalis, B. longirostris, C. pulchella,* and *C. dubia* respectively), although clearly, since body size places limits on the number of eggs that can be carried (Green 1956), both *C. pulchella* and *Bosmina* are potentially more limited in their fecundity anyway, simply because they are smaller. Notably though, the fecundities of all species were reduced below those recorded in laboratory cultures (Donovan 1970; Staples 1984; Greenwood 1987; Urabe 1991) giving further support for the conclusion that resource depletion has limiting effects on clutch size in Lake Mangakaware.

This raises the question not just of food limitation *per se* but of food quality. Numerous studies have explored the effects of food quality on cladoceran growth and fecundity (e.g. Vijverberg 1976; Goulden *et al.* 1982a; Matveev and Balseiro 1990; Groeger *et al.* 1991), and more recently much emphasis has been placed on the role of cyanophytes as food sources for Cladocera (e.g. Fulton and Paerl 1987; Fulton 1988 a, b; Benndorf and Henning 1989; Forsyth *et al.* 1990; Fulton and Jones 1991). As discussed, *Bosmina* is known to be selective in its feeding mode, with a marked preference for small

flagellated cells and less efficient selection for bacteria (Geller and Muller 1981) and large phytoplankton (Burns 1968). However some findings are conflicting. Sarnelle (1986) for example found that cryptomonads were probably of low food value to cladocerans, even though they are small naked flagellates. In contrast, Ahlgren *et al.* (1990) found cryptomonads were the most suitable food for three species of cladocerans (including *Eubosmina*).

The nutritional quality of the small algal species available to *Ceriodaphnia* and *Bosmina* seasonally was not assessed here. However, many of the species that can reasonably be assumed to be palatable (e.g. *Scenedesmus, Actinastrum, Coelastrum, Kirchneriella, Vacuolaria, Cryptomonas,* and *Monoraphidium*) were found at low densities relative to other less palatable phytoplankton, such as *Aulacosira.* This suggests that they were being heavily grazed. Selective mode feeding, such as that shown by *Bosmina*, would then be advantageous especially when large and/or unpalatable species (eg. *Closterium*) were present in large numbers. Certainly, the predominance of *Bosmina*, both temporally, and in terms of total abundance, suggests that this genus is not disadvantaged by high densities of phytoplankton species that might present handling difficulties for *Ceriodaphnia*, (*Aulacosira* being the best example).

5.5.3 Predation, Competition and Demography

Although food limitation and the potential competitive advantages afforded to *Bosmina* in view of its feeding mode have been considered in some detail above, predation is likely to be of at least some importance in Lake Mangakaware. Size selective predation has long been implicated as a primary factor in the size structuring, seasonality and life history modification of Cladocera (e.g. Allan 1974; Gliwicz and Biesiadka 1975; de Bernardi *et al.* 1987; Ketola and Vuorinen 1989; Hovencamp 1990; Matveev and Martinez 1990). However, in New Zealand zooplankton communities, there are few invertebrate predators, and zooplanktivorous fish are often restricted in their distribution (Chapman and Green 1987; Malthus and Mitchell 1990).

In Lake Mangakaware the main invertebrate predators are *Mesocyclops leuckarti* and, to a lesser extent, *Asplanchna*, although small numbers of *Piona* spp. and *Anisops* are

occasionally found in the plankton. *Mesocyclops* has been found to prey successfully on *Ceriodaphnia* but can not easily attack *Bosmina* because of its rounded shape and harder cuticle (Jamieson 1980). The high densities of *Mesocyclops* in Lake Mangakaware during summer and autumn, when *Bosmina* species were present, supports the view that *Mesocyclops* is not a successful predator on this genus. *Ceriodaphnia dubia*, in contrast, was abundant only when *Mesocyclops* densities were low, and although *C. pulchella* was abundant at the same time as *Mesocyclops* in 1988, this was not the case in 1989.

Asplanchna will successfully consume both *Ceriodaphnia* and *Bosmina* (Chapman and Green 1987), and the latter genus was sometimes recorded in the guts of *Asplanchna*. However, death rates in *Ceriodaphnia* and *Bosmina* were not significantly correlated with either of the above predators, supporting the view expressed by Chapman and Green (1987) that food limitation and competitive interactions are more important than predation in regulating zooplankton seasonality in New Zealand. Partial correlations of b' with competitor density also suggest this. Birth rates are dependent on population fecundity, and so although *B. longirostris* was the only species to show a significant inverse relationship of b' with the density of other Cladocera, all species, except *B. meridionalis*, showed the negative effects of competition on at least some measure of performance associated with high birth rate (e.g. proportion of ovigerous females). Certainly, declines in *B. longirostris* density were broadly coincident with increases in other cladocerans, particularly *C. dubia*. Although birth rates in *B. longirostris* were also positively correlated with copepod density, this is not unexpected, since this species and copepods generally were abundant throughout most of the year.

For *B. meridionalis* seasonal data were rather limited in extent and so are inconclusive. However, birth rates in this species were negatively correlated with rotifer density, and some kind of competitive interaction between this small cladoceran and *Filinia* and *Hexarthra* in early summer seems likely. Certainly, rotifers, often present in very high densities, are potentially important as competitors for small algal species in Lake Mangakaware and the importance of this large and diverse phylum in depleting available food sources must be considered. Larger cladoceran species have been known to adversely

affect susceptible rotifer species through interference (e.g. Gilbert 1988), but the reverse situation, in the case of smaller Cladocera, has not been examined to my knowledge. Exploitative competition at high densities is likely anyway, even if interference is relatively unimportant.

As is characteristic of New Zealand populations (Chapman and Green 1987), fecundities of Lake Mangakaware Cladocera are low, and birth rates are affected primarily by changes in the proportion of egg bearing females, rather than by large changes in clutch size. Chapman and Green (1987) also note that the Cladocera in New Zealand tend to have low birth rates and low percentages of egg bearing females. While this is the case for *Bosmina* in Lake Mangakaware (Table 10), it is not true for *Ceriodaphnia* in this lake, where mean annual birth rates were two to three times higher than those recorded in Lakes Pounui (Lawless 1983) and Grasmere (Staples 1984), and the proportions of egg bearing females were relatively high. However, it does seem that major population increases in Lake Mangakaware *Ceriodaphnia* are governed by decreases in death rates, rather than by very high birth rates. For *C. dubia* in particular, death rates were high, and for this species the mean death rate over the sampling period was considerably higher than the mean b', resulting in a mean r' that was slightly negative (Table 10). In this respect, the demography of *Ceriodaphnia*, particularly *C. dubia*, suggests some loss not attributable to poor population performance. The most likely cause of loss is, of course, predation.

The influence of zooplanktivorous juvenile bullies (*Gobiomorphus cotidianus*) was not assessed and was assumed not to be of much importance in Lake Mangakaware, where there are only small littoral populations, and repeated drop-net fishing revealed no planktonic occurrences (own data). However, limnetic *Gobiomorphus* larvae may make some impact on cladoceran populations, particularly if adult breeding in the littoral region is protracted, as it is in Lake Waahi (Chapman and Green 1987).

The demography of *Bosmina* in Lake Mangakaware, like that of *Ceriodaphnia*, is governed largely by changes in d', but for this genus, marked increases in b' were also very important in achieving the positive growth rates associated with rapid population expansion. Sharp reversals in the relative importance of these two parameters contributed

to the very pronounced pattern of peaks and declines in population abundance. This sort of pattern, seen to an extent in *C. pulchella* also, where high birth rates are followed by increased density, then by low fecundity and population decline, is typical of populations that overexploit the available resources and suffer a concomitant fall off in reproductive success.

5.5.4 Synthesis

In Lake Managakaware, the seasonality and demography of the four cladoceran species appears to be governed, not only by changes in temperature and food availability *per se*, but by different patterns of growth and reproduction in the face of a sharply fluctuating resource base, and changing sources of mortality (e.g. predation or starvation).

There is much evidence to suggest that food limitation affects different cladoceran species in different ways and, in particular, emphasis has rightly been placed on the importance of juvenile starvation as a competitive bottleneck in the dynamics of food limited populations (Romanovsky 1984a, b; Romanovsky and Feniova 1985). Although Lake Mangakaware is very productive, this does not necessarily imply high food availability or quality, particularly as zooplankton densities are high, and palatable phytoplankton species may be subjected to heavy grazing pressure and be swamped by larger inedible types. While disjunct patterns in the timing of peak abundances do not necessarily imply competitive displacement, the generally low fecundities and lipid scores of the Cladocera in Lake Mangakaware suggest that resource depletion is important in the seasonality of species replacement in this lake.

Lynch (1980b) suggests that under conditions of low resource availability, one might expect smaller bodied species to predominate, since the energetic advantage of large species is reduced, and their pre-reproductive period prolonged, at low food levels. However, it is difficult to translate assumptions made on the basis of Northern Hemisphere populations to the New Zealand situation. Whilst both vertebrate and large invertebrate predators are important in structuring the cladoceran communities in north temperate regions (Lynch 1980b), predation appears to be much less pivotal here (Chapman and Green 1987). New Zealand lacks the large invertebrate predators of Northern Hemisphere

lacustrine systems, and the number of fish species with zooplanktivorous stages is low (Chapman and Green 1987). Moreover, the low fecundities and population birth rates of zooplankton in New Zealand argue against an important role for predation in determining zooplankton cycles and life histories. Large bodied cladocerans occur only infrequently in New Zealand lakes and are not widespread in their distribution and, in most New Zealand situations, as in this study, the cladoceran species under consideration are all quite small. The differences in their life history patterns and the factors governing their seasonality are therefore likely to be more subtle than is the case for Northern Hemisphere communities.

A large number of studies have been devoted to examining the seasonal succession and coexistence of cladoceran species in natural systems (e.g. Allan 1973, 1977; Jacobs 1977; Lynch 1978, 1979; Threlkeld 1979b; Kerfoot and De Mott 1980; De Mott 1983; Tessier 1986b) and many of these have dealt with the way in which species partition resources or respond to fluctuating food levels. Much of the frequent success of large bodied daphnids (over small ones) has been attributed to their ability to feed efficiently on a wide range of particle sizes. However, implicit in the consideration of relative feeding efficiencies is the assumption that preferences do not vary much between species. Yet food preferences involve more factors than dietary breadth alone. De Mott and Kerfoot (1982) for example, found that *Bosmina*'s coexistence with *Daphnia* was related to its efficient feeding mode on highly edible algal species, especially when these occurred in low densities. Similarly Neill (1975b) stressed the importance of resource specialisation in the coexistence of different species, and Romanovsky and Feniova (1985) suggested that oscillating food levels may allow large and small bodied cladocerans to persist together, with the latter becoming abundant when food levels are depressed. The temporal separation of abundance peaks may also provide a means of avoiding intense resource competition in species which co-occur (Makarewicz and Likens 1975), and may arise through differential responses to temperature, in addition to resource preferences (Jacobs 1977).

The success (as measured by numerical dominance) of a species at any time will depend on it achieving a growth rate (r) that surpasses that of competing species.

Population growth rate will itself depend on population fecundity and embryonic development time which in turn are affected by food availability and temperature. Higher food levels and increased temperatures act to increase birth rate by, respectively, increasing clutch size and decreasing development time. However, species specific responses to food availability and temperature are not uniform. Slight differences in the magnitude of a response to food level, or shifts in the way a species allocates its available resources, will alter the competitive balance so that different life history schedules will be favoured in different temporal and spatial environments.

B. longirostris could be considered the most successful cladoceran species in Lake Mangakaware, being both more abundant, and more persistent than the other species. The life history pattern of *B. longirostris*, I believe, predisposes it to success in this lake. It is a small species, which produces relatively large eggs (therefore neonates), which develop quickly (Appendix 4). Like *B. meridionalis*, it is relatively resistant to predation from *Mesocyclops*, which is probably the only invertebrate predator to be of much importance throughout most of the year. Although fecundities are lower than for *Ceriodaphnia*, juveniles probably have a high survival rates and, being smaller, are less susceptible to the detrimental effects of resource depletion.

Bosmina's feeding mode is also well suited to the selection of palatable algal species from the available resource base. To an extent, both species of *Bosmina*, but particularly *B. meridionalis,* exhibited a 'boom and bust' pattern of population change, with rapid growth followed by sharp declines in fecundity and density. Given that a similar pattern exists for the phytoplankton in Lake Mangakaware this is not a disadvantageous strategy. However, *B. longirostris* also maintained a reproductively active population throughout the year, even when, at times, a high proportion of adults ceased to breed. The persistence of non-ovigerous females in the population, through periods unfavourable for breeding, enables rapid reproduction once environmental conditions improve. This then avoids the lag associated with the hatching of resting eggs and development of juveniles to reproductive age.

Like the cessation of breeding, the switch to sexual reproduction is a strategy for persistence in a fluctuating environment. However, while the production of ephippia in *B. meridionalis, C. pulchella* and *C. dubia* was associated with their disappearance from the plankton, this was not the case for *B. longirostris*. Clearly, in this species, sexual induction is not necessarily associated with environmental conditions unfavourable enough to result in population extinction. Rather, for *B. longirostris*, ephippial production is another method for ensuring the persistence of this more perennial species.

The success of *B. meridionalis* during summer may depend on *B. longirostris* abundance, since these two species both appear to maximise population growth during summer. Notably though, *B. longirostris* does not suffer the same developmental disadvantage as *B. meridionalis* at low temperature (Appendix 4), which may account for the more perennial presence of the former species.

In contrast to *B. longirostris*, the seasonality of *C. dubia* appears to involve a strong temperature response. This species has a marked developmental advantage over *C. pulchella* and *B. meridionalis* at low temperatures (Greenwood 1987; Appendix 4), and appears to maximise this advantage by reproducing quickly when temperatures are low. Increased food availability during spring, quite probably in the form of bacteria, picoplankton, or small ciliates, as well as small phytoplankton, is probably critical also. *C. dubia* produces relatively smaller neonates than *C. pulchella* and, as such, they are more likely to be adversely affected by time spent before maturity at low food levels. *C. dubia* also suffered the highest mean death rates, despite having the highest maximum b', suggesting that this species might also be highly vulnerable to predation or juvenile starvation.

C. pulchella could be regarded as intermediate in its life history between the 'boom and bust', small bodied *B. longirostris,* and the larger, potentially more fecund *C. dubia. C. pulchella* has proved an extremely difficult species to rear in the laboratory (personal observation; C. Hickey *pers. comm.*) and its exact food requirements appear to be very specific. Clearly, resources other than algae are important to its seasonality, for although *C. pulchella* was maximally abundant during the autumn algal bloom (*Tetrastrum*), the

decline in fecundity and lipid score at this time, together with the very fact that *Tetrastrum* densities were extremely high, suggests that this alga was not a major food source.

C, pulchella's appearance, after *B. meridionalis* numbers had declined, also points to the use of a different resource base for these two species. *C. pulchella* does, however, appear to be fairly resistant to starvation and, like *B. longirostris,* high proportions of the adults were non-fecund at times. Personal observations of populations from Lake Rotoroa (Hamilton) show that this is the case in this lake also, except that the occurrence of starving non-fecund animals, in very large numbers, is much higher.

5.6 CONCLUSION

The different patterns of seasonal abundance exhibited by the four species of planktonic Cladocera in Lake Mangakaware appear to be related to different life history characteristics that favour each species at different times of the year. For example, although peak abundances are disjunct the sequence of species replacement appears to be quite predictable from year to year. Rapid fluctuations in the resource base in Lake Mangakaware may allow competitive advantages to alter quite quickly away from one species, in favour of another. The adaptive features of *B. longirostris* are well suited to this type of environment and both temporally, and in terms of abundance, it could be regarded as the most successful cladoceran in this lake.

The factors governing the relative successes of the two *Ceriodaphnia* species seasonally are less easily pinpointed. Both species have potentially higher fecundities than *Bosmina*, but this does not seem to advantage them particularly in Lake Mangakaware, and their temporal distributions are more restricted. Subtle differences in the allocation of resources to growth and reproduction, when resource levels and mixing (therefore temperature) patterns are not predictable, may help to explain why, of the two *Ceriodaphnia* species present, *C. pulchella* is seemingly the most able competitor in Lake Mangakaware. These potential differences were explored in a controlled context in the laboratory. The results are presented in the following chapters.

PART THREE

Experimental Investigations of the Life Histories of *Ceriodaphnia*

"Science. Is truth for life

Discovery

Dissolved all illusion

Mystery

Destroyed with conclusion"

Natalie Merchant
10,000 Maniacs

PART THREE:
CHAPTER ONE
INTRODUCTION

Field studies of the cladoceran populations in Lake Mangakaware (Greenwood 1987; this study, Part Two), have indicated that different seasonal patterns of abundance in two *Ceriodaphnia* species may have a root in the different responses of each to particular seasonal changes. Potentially, *C. dubia* and *C. pulchella* are co-exploiters, being similar in appearance, habit and, presumably, also in feeding mode. Indeed, they have been confused taxonomically in most New Zealand studies to date (Greenwood *et al.* 1991). While they coexist for a large part of the year, the two species differ in how successful they are seasonally. Moreover, these differences appear to be quite predictable, at least in the sequence of species' appearance. It seems likely that their coexistence, and their different temporal abundance patterns, are based on underlying differences in features of their life histories, which predispose them to success at a particular time.

Life history features have been used to examine, and attempt to explain, cladoceran seasonality and community structure (e.g., Lynch 1977, 1980; Foran 1986, a,b; Tessier and Consolatti 1989), but many such studies have concentrated on *Daphnia*, often with only interclonal comparisons between a single species (e.g. Lei and Armitage 1980; Foran 1986a, b; Perrin *et al.* 1990; Ebert 1991; Ebert and Jacobs 1991). Where species from two or more genera have been compared, the attention has focused on the competitive abilities of species that differ markedly in size, as is the case with *Daphnia* and *Ceriodaphnia*, or *Daphnia* and *Bosmina* (e.g. Goulden and Hornig 1980; Goulden *et al.* 1982b; Lynch 1992) There have been relatively fewer studies that compare the life history features of small bodied species from a single genus as, for example, did Burgis (1967) with *Ceriodaphnia*. In New Zealand, *Ceriodaphnia* is often a common component of the planktonic community, yet co-occurrences of *C. dubia* and *C. pulchella* are still largely unstudied, on account of the very recent recognition of the latter species in this country (Greenwood *et al.* 1991). However, it is likely that co-occurrences are quite common, since even a

restricted survey of species distribution has indicated the presence of both *C. pulchella* and *C. dubia* in a number of New Zealand lakes (Greenwood *et al.* 1991). The adaptations that define the life history strategies of *C. pulchella* and *C. dubia* are worthy of investigation as potential indicators of the causative factors in the distribution patterns of these species in New Zealand. *C. pulchella* is the smaller of the two species and, in Lake Mangakaware, is also the most seasonally persistent, despite the fact that *C. dubia* has potentially higher fecundity and growth rates (Greenwood 1987).

In the following two chapters I report the outcome of experiments performed to compare the life history characteristics of these two closely related species. The data generated from these experiments are used to describe the growth and reproductive responses of laboratory populations of *C. pulchella* and *C. dubia* to different food types, and to high and low food levels at two temperatures. Temperatures were chosen to represent those encountered in Lake Mangakaware annually (23°C and 13°C). A comparison of the species specific responses of *C. dubia* and *C. pulchella* to different nutritional and temperature conditions, should enable a clearer assessment of the nature of the competitive balance between them.

PART THREE
CHAPTER TWO:
SELECTION OF A NUTRITIONALLY SOUND REGIME FOR THE CULTURE OF *CERIODAPHNIA*

2.1 INTRODUCTION

As the primary aim of the experimental study of growth and reproduction in *Ceriodaphnia dubia* and *C. pulchella* was to compare and contrast species specific responses to high and low food levels, at high and low temperature, preliminary trials were required in order to establish a food regime that provided adequate nutrition for both species. The criteria for nutritional adequacy in Cladocera generally includes indices of fecundity, such as clutch and egg size and volume, and particular life cycle characteristics that are important ecologically, such as the duration of development and body size at maturity. The food provided to experimental animals must be in quantities adequate to supply energy requirements, and be of a quality that is able to support successful reproduction (Taub and Dollar 1968; Goulden *et al.* 1982a; Mitchell *et al.* 1992). Groeger *et al.* for example, found that *Daphnia* grown on nitrogen deficient algal cells accumulated more lipid than those fed on algae grown on N-sufficient media, but this extra lipid did not equate with better growth and reproduction. Only after nutritional requirements are met can the response to food limitation be tested. The preliminary trials to determine a diet suitable for successfully rearing *Ceriodaphnia* are described in this chapter.

2.2 SELECTION OF A FOOD TYPE FOR *CERIODAPHNIA*: 1

Initial feeding trials were attempted to investigate the nutritional suitability, for *Ceriodaphnia*, of a broad range of food types generally found to be suitable as foods for daphnids (*Daphnia* in particular). It was thought that such foods might also prove suitable for *Ceriodaphnia* , although some modifications, either to food type or concentration, or to culture medium, might be required. The protocol followed was that of elimination, whereby media and/or foods that were poorly tolerated were discarded.

Three early trials were based on culture media of either aged, aerated tap water; membrane filtered (0.45 μm) surface water from Lake Mangakaware; or daphnid dilution water (Appendix 7: Table 2). The food to be tested was then added to each medium as required. These early trials were largely unsuccessful and, at best, inconclusive. A full description of the methodology and results of these trials is given in Appendix 6. The main findings from these early trials are summarised as follows:

(i) Yeast was an unsuitable food for the culture of *Ceriodaphnia* and even in combination with algal food gave variable results in terms of growth and fecundity.

(ii) Survival and growth in single food media (yeast alone; *Scenedesmus* alone; *Chlamydomonas* alone; Banta's (1921) medium) was generally poor, particularly for *C. pulchella*.

(iii) Banta's medium, in combination with *Scenedesmus*, appeared to be a more suitable food for *Ceriodaphnia*, but attempts to maintain stock cultures on this preparation were unsuccessful, and populations often suffered unexplained sharp declines in fecundity and density. For controlled experiments stock cultures should be raised on the same basic food medium as that used for test animals. Banta's medium did not seem reliable in this respect. Since one of the aims of this study was to investigate longevity under different conditions, cultures also needed to be maintained over a long period of time.

The poor results in these early trials can, I think, be related mainly to the condition of the animals collected from the field for use in the trials. The presence of males and ephippial females of *C. dubia* in the trials was not encouraging, and there was much difficulty in maintaining viable cultures (see Appendix 6). Trials were thus abandoned, and attempted in a following year with different animals. On the basis of the general consistency of results regarding the unsuitability of yeast as a food, and the variability of Banta's medium, the decision was made to retrial single and mixed algal diets, natural food (lake water), and an artificial food mix. This retrial is discussed below.

2.3 SELECTION OF A FOOD TYPE FOR *CERIODAPHNIA*: 2

This experiment involved the use of two mixed media (artificial food suspension, and *Chlamydomonas* + *Cryptomonas* cells), one unialgal culture (*Chlamydomonas*), and one naturally variable food source (lake water, filtered through 50 μm mesh). This experiment had two main aims: (1) To establish which of four food types provided the best diet for both *C. pulchella* and *C. dubia*, so that, given adequate nutrition, response to food level and temperature could later be tested. Thus, a food inadequate for one species was discarded, regardless of its suitability for the other. (2) To decide which of a number of measurable variables would provide useful information for the assessment of food quality in *Ceriodaphnia*. These variables could then be used, in a later experiment, to assess the relative performances of *C. dubia* and *C. pulchella* in different food and temperature regimes.

2.3.1 Methodology

Stock cultures

All test animals were removed from stock populations cultured in the laboratory from animals collected from Lake Mangakaware. Stocks were maintained in static culture in 2 litre beakers containing daphnid dilution water (Appendix 7, Table 2). Animals were fed daily with 5-8 x 10^4 cells ml^{-1} *Chlamydomonas* (see 'Algal culture' below), and stirred gently twice daily. Oxygen levels in the cultures were checked regularly with a YSI oxygen probe and never fell below 7 gm^{-3} DO. The medium was changed, and culture density reduced, every three days. To do this, animals were removed by gentle filtration through a 50 μm mesh and transferred to a large petri dish, before sorting under X 12.5 magnification (Olympus X 2 stereomicroscope). Densities were generally reduced by half and animals returned to fresh medium as required. Culture vessels were thoroughly cleaned in hot water at each water change. Discarded animals were preserved and checked for fecundity and stores of visible lipid (as for field samples, Part Two, Chapters Four and Five). Cultures were maintained at 20°C under ambient laboratory lighting.

Algal culture

The algae used throughout the course of this experiment consisted of two flagellated taxa: *Cryptomonas* and *Chlamydomonas*. The early, unsuccessful, trials used *Scenedesmus* as a food source, and the culture techniques employed for this genus were the same, except in some minor details which are outlined below. Algae were identified only to the generic level, but cultures appeared to be monospecific. Approximate cell sizes ranged from 10 µm (*Scenedesmus*) to 20 µm (*Chlamydomonas*) GALD.

Scenedesmus and *Chlamydomonas* cultures were obtained from stocks held in the University of Waikato, Department of Biological Sciences. A culture of *Cryptomonas* was obtained from the University of Otago. All cultures were maintained in 1 litre Erlenmeyer flasks in modified MBL medium with added buffer (Appendix 7, Table 1), and kept under constant fluorescent illumination with natural lighting during the day also. Every three days, counts were made using a haemocytometer, to determine cell density, and cultures were diluted by about half, to maintain log-phase growth.

Scenedesmus cultures were kept on a mechanical shaker (50 rpm) to maintain cells in suspension. Cultures of *Chlamydomonas* and *Cryptomonas* were kept in water baths at 20°C and agitated gently approximately three times daily. Percentage carbon content of *Chlamydomonas* and *Cryptomonas* cultures was determined by The University of Waikato Stable Isotope Unit, on dried samples of a known volume and cell density. Before use in feeding, measured volumes of algae were centrifuged at 200 rpm for 5 minutes, the supernatant removed, and the cells resuspended in the medium appropriate to the test animals. Required volumes were calculated on the basis of cell density (see above).

Preparation of artificial food suspension

A synthetic food consisting of a mix of bacteria, yeast, and powdered cereal was prepared as per Appendix 6, Table 1C. The final carbon content of this food varied between 38 and 42% (University of Waikato, Stable Isotope Unit).

Test animals

Except in the case of regime 1 (filtered lake water) the culture medium for *Ceriodaphnia* was a synthetic water (Appendix 7, Table 2) modified by the addition of filtered river water and vitamins. Test animals (10 per food regime) were reared individually in 12 ml glass vials containing 10 ml of the appropriate culture medium and

food type. Vials were inverted gently, twice daily, to resuspend any settling material, in addition to the daily renewal of medium and replenishment of food. Clean vials were used at each change of medium and all vials were thoroughly cleaned with hot water before reuse. Vials were suspended in polystyrene floats in a thermostatically controlled water bath maintained at 20°C, under a 14:10 hour light:dark cycle of fluorescent illumination (see Fig. 35 for general design). Experiments were run at 20°C because, at this temperature, the developmental rates of *C. pulchella* and *C. dubia* are similar (Greenwood 1987; Appendix 4). Any major differences observed in development time would thus be the result of differences in food regime.

As one of the purposes of this study was to obtain realistic comparisons with field populations, monoclonal cultures were avoided. A total of 40 ovigerous females were taken from stock cultures and, from the combined pool of young produced, 10 neonates were assigned at random to each food regime. Animals were then acclimatised to the appropriate experimental conditions by two generations of culture, as illustrated in Figure 30. This also effectively removed the effects of pre-experimental maternal history (Lynch and Ennis 1983; Vijverberg 1989). Neonates from first broods were not selected as test animals because, in Cladocera, first brood neonates are often smaller than those from later broods, regardless of nutritional history (Goulden *et al.* 1982a; Ebert 1991).

The food regimes used are described in Table 17. For regime 1, lake water was centrifuged at low speed, cell concentration established with a haemocytometer, and density then adjusted to the appropriate level.

Table 17: Description of food regimes used in a trial of food suitability for *Ceriodaphnia*.

Regime number	Food	Vol.10ml^{-1}.d^{-1}	Final food concentration
1	Filtered (50 µm) lake surface water	NA	Naturally variable between 1-3 x 10^4 cells ml^{-1}
2	Artificial food suspension	0.1 ml	1.5 µg C ml d^{-1}
3 (=2)	*Chlamydomonas*	1.8 ml	1.3 µg C ml d^{-1}
4 (=3)	*Chlamydomonas* + *Cryptomonas*	1.0 ml	0.74 µg C ml d^{-1} + 0.68 µg C ml d^{-1}

See Appendix 6, Table 1C for preparation of artificial food suspension, and text for details of algal culture. Numbers in brackets indicate new regime number after Food 2 was discarded because of unsuitability. All food types were added to daphnid dilution water (Appendix 7, Table 2) except for food regime 1.

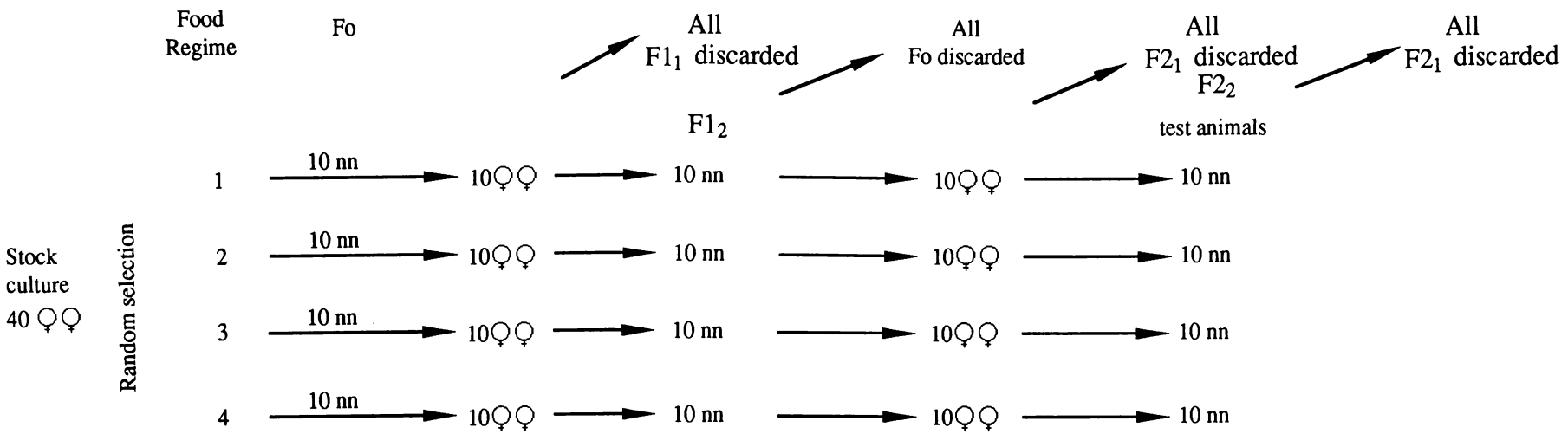

Figure 30.

Acclimation procedure for test animals used in food suitability experiment. Subscripts refer to brood number. nn = neonates; ♀♀ = adult females. Temperature = 20°C throughout.

Handling and assessment of performance

To assess growth and reproductive performance in *Ceriodaphnia* it was necessary to make measurements of live animals. To do this, animals were removed from vials in turn using a pasteur pipette, placed in a depression slide, and examined under X 80 magnification. Water was quickly drawn from the animal, measurements taken as appropriate, and the animals returned to their vial. *Ceriodaphnia* were not damaged at all with this technique and did not appear to suffer any ill effects from the treatment. However, to avoid undue stress, handling was reduced at times when animals were vulnerable: in early instars, especially instar one; in later egg stages when animals were preparing to moult; and just before egg deposition.

Measurements of body length, egg size and lipid ovary scores were made following the methods described for field samples, with the following adjustments:

(i) It was not usually possible to measure every egg in a clutch. Generally, eggs in the correct orientation were measured and an average egg volume obtained. This value was then multiplied by the clutch size to obtain clutch volume.

(ii) Because of the need to avoid overhandling, especially at high temperatures, lipid scores were assessed for animals in egg stages IV-VIII, rather than V-X as in field samples. This slightly underestimates scores relative to those in the field samples since ovary opacity increases quite noticeably in stages X and XI. However, the underestimate would be consistent for all animals.

Animals were raised in each regime from birth to the time just after the deposition of clutch five (usually the eighth instar). The neonates produced from broods 1-4 were collected soon after their release from the brood pouch, preserved, measured for body length, and scored for lipid. Measures of body size, egg volume, clutch size, clutch volume, and lipid score were taken at each of the first five adult instars.

In a repeated measures experiment such as this, autocorrelation creates difficulties for the statistical analysis and interpretation of results. To correct for this, the raw data were used to calculate general measures of performance, so that for each variable of interest, there was only one value per animal. Table 18 describes the variables used for

assessment of growth and reproduction in this experiment. These were chosen on the basis of their potential to illustrate similarities and differences between *C. pulchella* and *C. dubia* in patterns of development.

Table 18: Variables used in the assessment of growth and reproductive performance in *Ceriodaphnia* grown at different food regimes.

1.	**Indices of development**
	Time taken to first reproduction (= age at maturity)
	Time taken to reach clutch five
	Body size at first reproduction (mm)
	Body size at clutch five (mm)
2.	**Indices of reproductive effort and growth**
	Neonate body size (at time 0)
	Ratio of body size at clutch two to size at birth
	Egg length at first reproduction
	Relative egg size (egg length ÷ body length) at first reproduction
	Total egg production to clutch five
	Mean egg volume (clutches 1-5)
	Mean clutch volume (clutches 1-5)
	Offspring size relative to size of the primiparous adult
3.	**Lipid score**
	Mean Lipid-Ovary Index (clutches 1-5)
4.	**Offspring body size and lipid**
	Body size of offspring produced over clutches 1-4
	Mean lipid score of offspring produced over clutches 1-4

2.3.2 Assessment of Methodology

Static culture

Static, as opposed to flow-through cultures, suffer inherent problems of settling food and concomitant decrease in the food cell concentration in suspension (e.g. Pace *et al.* 1983). In addition, algal and other food debris may accumulate at the bottom of the culture vessel and result in fouling of the medium by the breakdown products of bacterial decomposition (Vijverberg 1989). These problems are reduced somewhat in individual static culture because increasing animal density is not a factor.

The limitations of static culture were minimised in this study by: (1) frequent renewal of the medium and the use of clean vials daily; (2) by inversion of vials twice daily to resuspend settling material; and (3) by use of motile algal species. Viable cell counts were performed on algal foods after centrifugation and, in addition, residual counts, i.e., cell counts after feeding, were also performed on occasion, as a check against excessive food depletion. Vijverberg (1989) suggests that cryptomonads, in particular, are susceptible to centrifugation damage, but this appeared not to be the case here, and no difference was observed between cells spun and resuspended and those directly from culture.

Water quality and nutrition

A number of studies have reviewed the suitability of different culture conditions in the laboratory rearing of daphnids (e.g. Goulden *et al.* 1982a; Vijverberg 1989), particularly with reference to the problems associated with the use of *Daphnia* for ecotoxicological work (e.g. Baird *et al.* 1989). Water quality and nutrition (food quantity and quality) are the most important variables in the culture of Cladocera. Frequently, water from natural habitats is used (Vijverberg 1989), often after membrane or glass fibre filtration. Synthetic waters have been used less frequently (e.g. Cowgill *et al.* 1985; Elendt 1989), despite the obvious advantages in terms of providing a standardised, defined medium for toxicological and other studies. However, cladocerans are often quite sensitive to water hardness (Cowgill and Milazzo 1990), and growth and fecundity on synthetic media can sometimes be poor, with high mortality rates (Cowgill *et al.* 1985; Vijverberg 1989).

A synthetic culture medium was chosen for these studies primarily because of ease of preparation. Although lake water was readily available, filtering productive water through a 0.45 μm membrane filter was very time consuming in view of the quantities required to maintain stock and test populations. To provide a medium that better approximated the dissolved organic content of natural water, 20% membrane filtered river water was added to the synthetic medium. Reproduction and growth, for the most part, appeared normal on this mixture. There were a few cases of egg degeneration, but usually

only in animals in later reproductive instars. Egg degeneration was also observed in *C. dubia* by Staples (1984) and appears to be related, at least in part, to deficiency of vitamin B12, a cofactor which Keating (1985) found to be critical for normal reproduction and development in this species reared in synthetic media. To counter egg abnormalities a solution containing vitamin B12 was added to the medium later in the experiment and for subsequent studies (Chapter Three).

The main types of diets used in cladoceran cultures have been uni- or mixed algal diets, synthetic diets (such as the one used here) or non defined diets, the most popular of which is Banta's medium (Vijverberg 1989). Unfortunately, the synthetic diet proved completely unsuitable as a nutritional source for *C. pulchella*, and this species failed even to survive for long on this food. It was therefore discarded and only three food regimes (two algal and one undefined) were compared. For cladocerans, green algae represent a high quality food (Goulden *et al.* 1982a; Vijverberg 1989), although a number of studies have demonstrated the inadequacy of unialgal diets for daphnids (e.g. Taub and Dollar 1968; Smyly and Collins 1975). Microbial food sources appear to be quite important for nutrition in species of *Ceriodaphnia* (Smyly and Collins 1975; Pace *et al.* 1983; Staples 1984; Cowgill *et al.* 1985), and were to be provided in this experiment as a component in the artificial food suspension.

The failure of *C. pulchella* to survive on the synthetic diet is surprising, in view of the wide use of this food for daphnid culture (Goulden *et al.* 1982a). Mount and Norberg (1984) reared *C. reticulata* more successfully on a trout chow medium than on a unialgal diet. Similarly Cowgill *et al.* (1984) reported good growth and reproduction in *Daphnia* on this diet, although Goulden *et al.* (1982a) found it to be inadequate. Using an undefined bacterial culture as food creates a problem in that pathogenic and/or nutritionally unsuitable species may replace the original microbial population (Cowgill *et al.* 1985). This may explain the sudden declines observed in cladoceran populations maintained for long periods on undefined bacterial media (Vijverberg 1989; this study). Cowgill *et al.* (1985), in a test of 17 potentially suitable foods for *C. dubia*, found the best nutritive sources to be chlorophyceans (e.g. *Chlamydomonas*), whereas *Cryptomonas* was a poor

food, which did not support reproduction. This is in contrast to other studies which have found cryptomonads to be of very high nutritional quality for daphnids (Ahlgren *et al.* 1990).

The diets provided for *Ceriodaphnia* in this experiment were thus chosen on the basis of their potential suitability in providing adequate nutrition. Food densities were judged to be non limiting, based on food levels provided by other workers for *Ceriodaphnia* (Cowgill *et al.* 1985; Keating 1985), and a filtration rate of approximately 6 ml per individual per day at 20°C (Mourelatus and Lacroix 1990). The criteria for assessing growth and reproductive performance are explained below.

Assessment of growth and reproduction in *Ceriodaphnia*

A number of life history characteristics can be used to assess the growth and reproductive success of cladocerans. Among the most commonly used are measurements of body length or weight (e.g. Tessier 1986), egg size and clutch size (e.g. Guisande and Gliwicz 1992), and lipid score (e.g. Goulden and Hornig 1980; Tessier and Goulden 1982; Cowgill *et al.* 1984; Sterner *et al.* 1992). Other important life history traits include the time taken to reach maturity (e.g. Romanovsky 1984b), and the size at which that is achieved (Lynch 1980a; Tessier 1986). The calculated parameter, relative egg size (Lynch 1980a; Tessier 1986), although less commonly used than clutch size, is a good indicator of the amount of reproductive effort invested in each offspring.

The above are all variables which are useful, not only for interspecific comparison, but also as indicators of a species' response to resource depletion or starvation. Resource limitation is known to prolong the time spent in juvenile stages (e.g. Romanovsky 1984b; Taylor 1985), reduce fecundity, and result in a decline in the body size at which individuals first reproduce (Guisande and Gliwicz 1992).

Not surprisingly, body fat levels are also reduced under food limitation, or when nutrition is otherwise poor (e.g. Guisande and Gliwicz 1992; Sterner *et al.* 1992). Moreover, indices of fat storage are useful in the study of cladocerans because, unlike variables based on reproductive maturity, lipid scores can be applied to the juveniles in a population (Tessier and Goulden 1982). The main difficulty with the use of lipid score in

assessing fat stores has been with scorer bias, as the score is somewhat subjective and individuals score differently. This was not a problem here because scoring was performed by only one person.

There has recently been some debate about the use of mean lipid score (and statistical tests based on normal distributions), in the analysis of feeding success in cladoceran populations, as LO indices are considered to be rank variables and therefore do not display normality (Sterner *et al.* 1992). While this is true, lipid scores simply reflect an underlying normal distribution, with actual lipid densities ranging continuously from nil to some maximal value (R. Littler *pers. comm.*). The limitation is in being able to reflect this in a subjective score. Certainly, mean LO indices have been used to assess visible lipid in field populations (Tessier and Goulden 1982), and the derived values then tend to show a normal distribution (see 2.3.3 Statistical Analyses, below).

The indices used in this study for the assessment of performance in different food regimes, (Table 18), were compiled from the above studies, and from Lynch (1980a), who reviewed the reproductive and growth characteristics of the Cladocera, and examined interspecific differences in these as indicators of variation in life history strategies. Total egg production to clutch five (end of trial) was used in preference to mean clutch size, so that negative responses to food regime, that might not be detected by mean clutch size (as by early death, for example), could be accounted for. Many of the variables measured or calculated in this experiment were the same as, or similar to, those used in a later examination of species specific response to temperature and food limitation (Chapter Three). The rationale for their use follows that outlined above.

2.3.3 Statistical Analyses

The differences between the three food regimes were tested for significance ($p < 0.05$) by one way analyses of variance, followed by Tukey multiple comparison tests of means differences, using SYSTAT statistical software (Wilkinson 1989). Statistically, species were assessed separately for their response to food regime, as the differences between the species (in size for example) were generally so large that they masked food

effects in two way ANOVAs. The two species were then compared graphically, using the 95% confidence interval as an indication of significant difference.

As described, the variables chosen for assessing food suitability were calculated values that gave some measure of general performance. This removed the complication of autocorrelation and reduced what would otherwise have been a large error term resulting from unaccounted for variance. For each species, the null hypothesis, Ho, was for no difference in measures of growth and reproductive performance between food regimes.

In order to be properly applied, ANOVA requires that data are normally distributed and that variances are equal. Calculated variables were tested for both normality and homoscedasticity. Not unexpectedly, considering the derived nature of the variables, all data were normal or nearly normal in their distributions in a normal probability plot. The plot of studentised residuals (errors) against their estimated (predicted) data values, indicated that errors were independent and, with the exception of a few outliers in some cases, displayed constant variance.

As discussed in Zar (1984) ANOVA is fairly insensitive to departures from normality, with the validity of the test being only slightly affected by even quite large deviations from the normal distribution. It is also quite robust against considerable variance heterogeneity, as long as all the n_i are equal or nearly equal.

Obvious outliers were removed when they occurred, and analyses rerun without them. In almost every case where outliers were excluded, the F values were lowered and hence the possibility of a Type I error (rejection of Ho when it is true) was reduced, i.e., the applied test became more rigorous. For some variables that depended on animals reaching a certain (relatively old) age, for example, body size and age at clutch number five, data were missing if individuals did not live that long. Similarly, if animals died in their early reproductive instars, the calculated values of variables reliant on continued reproduction (e.g. accumulated clutch volume), were inconsistent with those of animals that lived longer. In the above cases, missing data resulted in unequal n values among treatments, and one should be somewhat more circumspect in the interpretation of results for these variables. Zar (1984) has suggested the replacement of missing data with means

or values otherwise calculated on the basis of the nonmissing data. I decided against this primarily because the death of animals is a result in itself, and increasing the central tendency of the data by replacing missing values was unrealistic in terms of the experimental aims.

2.4 RESULTS

Full results (data files, ANOVA and means tables, and Tukey probability matrices) are given on floppy disk at the back of this volume.

2.4.1 General Comments on the Growth and Reproduction of *Ceriodaphnia*

Both *C. pulchella* and *C. dubia* showed the greatest growth increments in early instars, with the rate of growth tapering in later life (see Chapter Three). Most often, animals reached maturity in their fourth instar, but extra preadult instars were observed on one occasion in *C. dubia* in the unialgal regime. One ephippial *C. pulchella* occurred on the lake filtrate diet, although no egg was laid into the ephippium. The incidences of egg degeneration were not very high (8 cases in 150 clutches), but were lowest (one case) in the lake filtrate, and highest in the unialgal diet.

2.4.2 Indices of Development: TABLE 19, FIGURE 31

Time to first reproduction

Time to first reproduction (= age at maturity) was generally not very different between the two species or for each species, between regimes. For *C. pulchella,* time to maturation was significantly longer at regime 1 than it was at regime 3 ($p < 0.01$), indicating some prolongation of the juvenile period in animals fed on lake filtrate.

Time to clutch number five

When development with time was considered to the fifth, rather than just the first, adult instar, the differences between the three food regimes became more apparent, for both species. For *C. pulchella,* time to clutch five was longest at regime 1 and shortest at regime 3. For *C. dubia,* there was no difference between regimes 2 and 3, but in regime 1 animals took significantly longer to reach clutch five. However, even at regime 1, *C. dubia* reached its fifth adult instar approximately two days before *C. pulchella.*

Table 19: Results of one way ANOVA followed by Tukey multiple comparison tests of data in Figure 31, to show the effects of food regime on **A.** time to first reproduction, **B.** time to clutch five, **C.**body size at first reproduction, and **D.** body size at clutch five in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (i.e., across food regimes) are indicated by the same letter. Abbreviations: Source = source of variation; SS = sums of squares; MS = mean square. See Table 17 for details of food regimes.

A. TIME TO FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	4.098	2	2.049	6.205	0.006
	Error	8.915	27	0.330		
C. dubia	Regime	0.366	2	0.183	0.534	0.593
	Error	9.260	27	0.343		

Table of differences

	Regime Number			
	1	2	3	p
C. pulchella	a	ab	b	< .01
C. dubia	a	a	a	> 0.6 NS

B. TIME TO CLUTCH NUMBER FIVE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	65.945	2	32.972	25.586	0.001
	Error	29.640	23	1.289		
C. dubia	Regime	14.036	2	7.018	10.738	0.001
	Error	15.686	24	0.654		

Table of differences

	Regime Number			
	1	2	3	p
C. pulchella	a	b	c	< .01
C. dubia	a	b	b	.001 < p < .01

C. BODY SIZE AT FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.007	2	0.003	19.520	0.001
	Error	0.005	27	0.000		
C. dubia	Regime	0.016	2	0.008	7.553	0.002
	Error	0.028	27	0.001		

Table of differences

	Regime Number			
	1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .01

D. BODY SIZE AT CLUTCH FIVE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.017	2	0.008	65.425	0.001
	Error	0.003	22	0.000		
C. dubia	Regime	0.161	2	0.081	141.592	0.001
	Error	0.013	23	0.001		

Table of differences

	Regime Number			
	1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .001

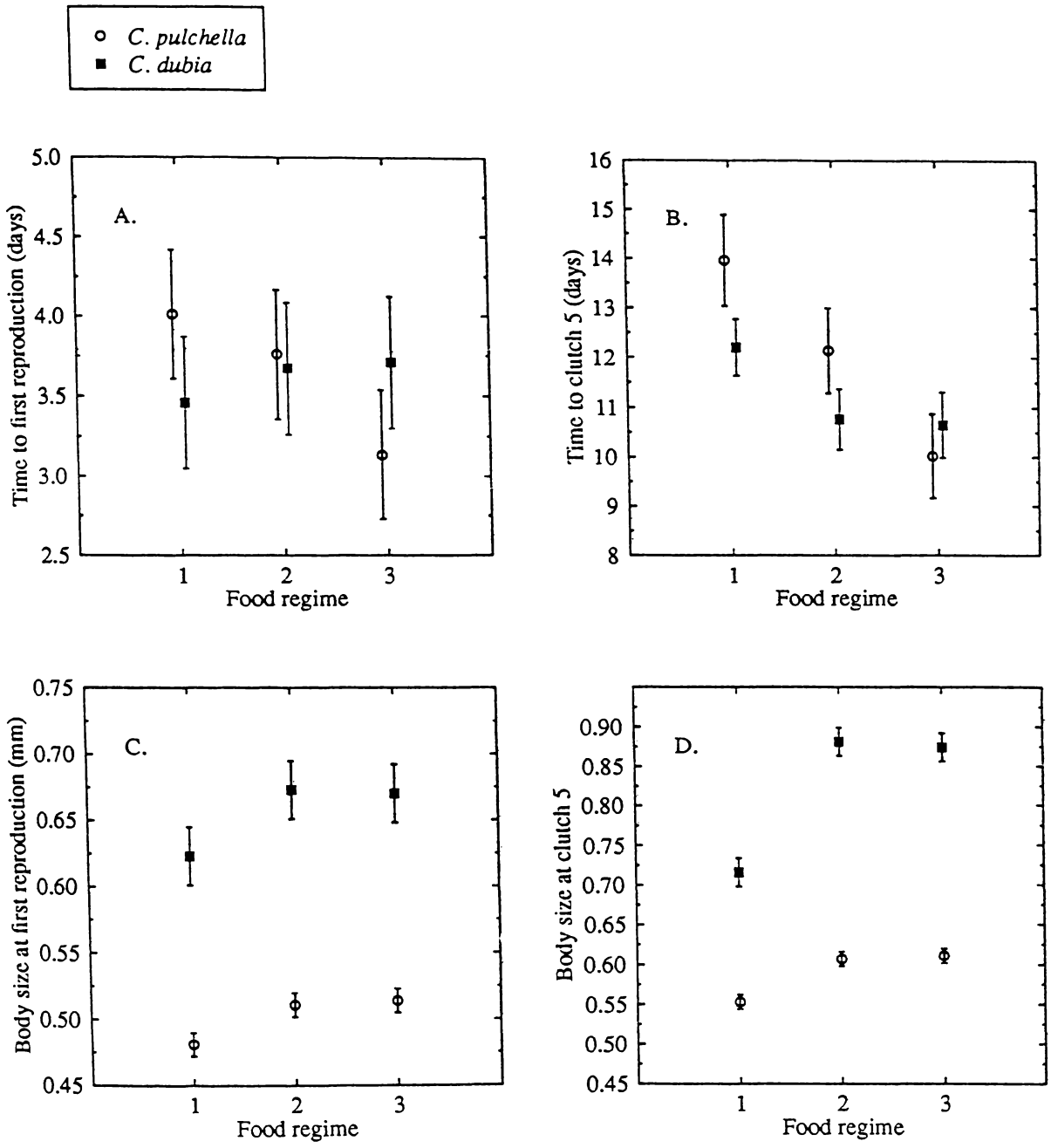

Figure 31.

Indices of development in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at three different food regimes at 20°C. (A) Time taken to first reproduction, (B) time taken to reach clutch five, C) body size at first reproduction, (D) body size at clutch five. Regimes: 1 = Lake filtrate; 2 = *Chlamydomonas*; 3 = *Chlamydomonas* + *Cryptomonas*. Vertical bars are 95% confidence intervals.

Body size at first reproduction

For both species, primiparous adults were significantly smaller when reared in lake filtrate than when grown on defined algal diets. The genetic differences in body size between *C. pulchella* and *C. dubia* are clearly apparent in these data, with the latter being the larger of the two species by approximately 30%.

Body size at clutch number five

The differences observed in body size between regime 1, and regimes 2 and 3, were even more pronounced at clutch five than they were at first reproduction, particularly for *C. dubia*, which made relatively small growth increments when reared on lake filtrate. For both species though, there was no difference between the two algal diets in fifth adult instar body size.

2.4.3 Indices of Reproductive Investment and Relative Growth: TABLE 20, FIGURE 32

Neonate size

For *C. pulchella* there was no difference in initial neonate size between regimes, despite lengthy preconditioning. For *C. dubia*, neonates were significantly smaller at regime 2 than at regimes 1 and 3.

Ratio of adult body size to neonate size

The size of the adult compared to its size as a neonate gives an indication of the amount of growth since birth. For both species, there were significant differences in this ratio between regimes, (regime $1 < 3 < 2$, $p < 0.05$). The low ratios of regime 1, in particular, are indicative of the small growth increments made by both species reared in lake water, compared to those reared on defined algal diets. Consistent with the much larger adult body size of *C. dubia*, the ratio of adult size to neonate size in this species was much higher on all regimes than in *C. pulchella*.

Egg length at first reproduction

In keeping with its larger body size egg lengths in *C. dubia* were greater over all regimes than in *C. pulchella*. Within species though there were no significant differences between egg lengths at different regimes.

Table 20: Results of one way ANOVA followed by Tukey multiple comparison tests of data in Figure 32, to show the effects of food regime on **A.** neonate size, **B.** ratio of body size at clutch two to neonate size, **C.**egg length at first reproduction, and **D.** relative egg size in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (i.e., across food regimes) are indicated by the same letter. Abbreviations as for Table 19. See Table 17 for details of food levels.

A. NEONATE SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.000	2	0.000	1.132	0.338
	Error	0.001	25	0.000		
C. dubia	Regime	0.001	2	0.001	7.069	0.004
	Error	0.003	25	0.000		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	a	a	> 0.3 NS
C. dubia	a	b	a	.001 < p < .05

B. RATIO OF BODY SIZE TO NEONATE SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.218	2	0.109	75.556	0.001
	Error	0.035	24	0.001		
C. dubia	Regime	0.649	2	0.324	80.540	0.001
	Error	0.101	25	0.004		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	b	c	< .05
C. dubia	a	b	c	< .05

C. EGG LENGTH AT FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	166.667	2	83.333	0.706	0.503
	Error	3187.500	27	118.056		
C. dubia	Regime	2648.985	2	1324.492	2.024	0.152
	Error	17012.222	26	654.316		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	a	a	> 0.5 NS
C. dubia	a	a	a	> 0.1 NS

D. RELATIVE EGG SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.003	2	0.002	4.284	0.025
	Error	0.010	26	0.000		
C. dubia	Regime	0.008	2	0.004	2.737	0.083
	Error	0.038	26	0.001		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	b	ab	< .05
C. dubia	a	a	a	> 0.1 NS

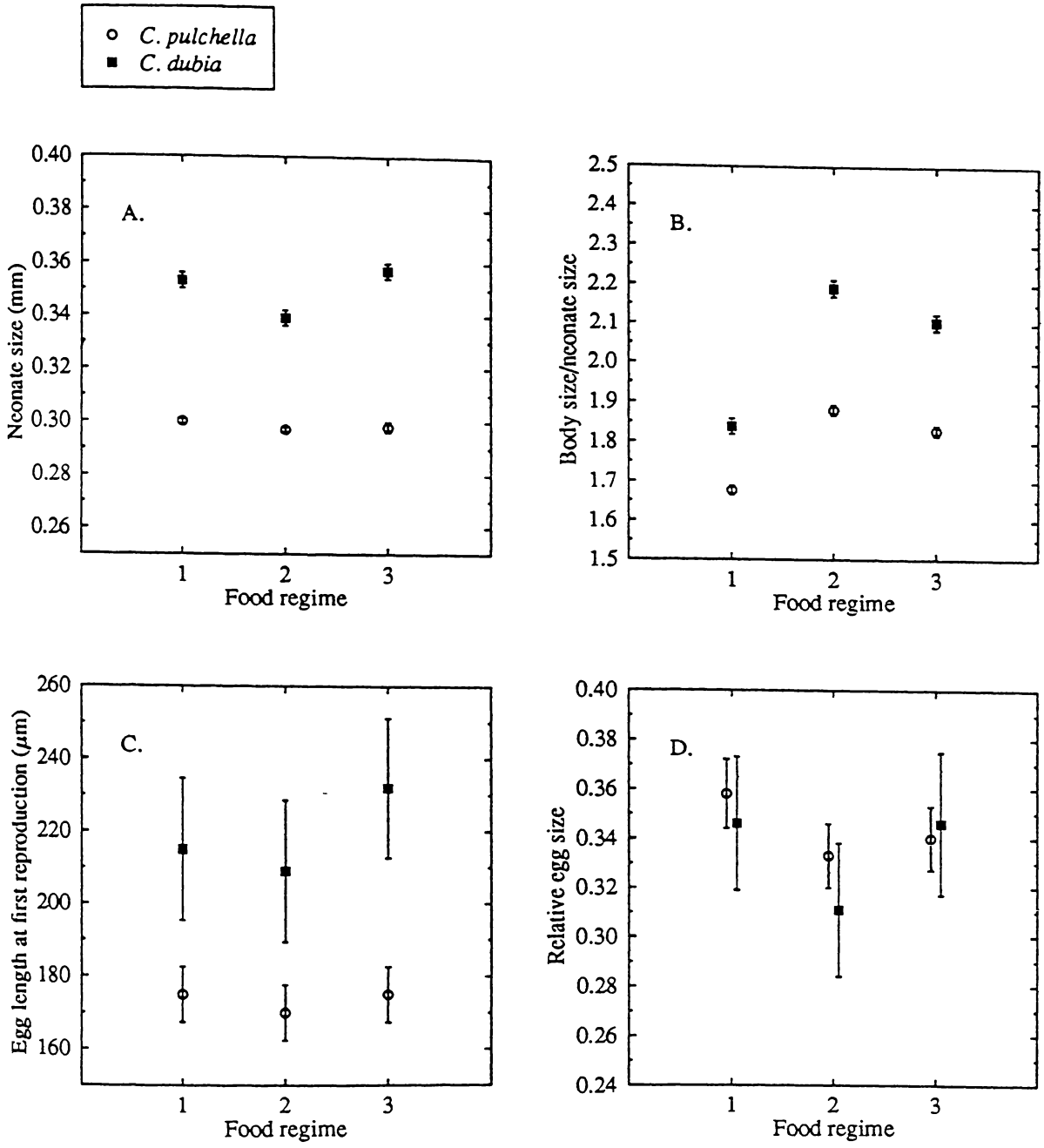

Figure 32.

Some aspects of egg size and body size in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at three different food regimes at 20°C. (A) Neonate size at the start of the experiment, (B) ratio of body size at clutch two to neonate size, (C) egg length at first reproduction, (D) relative egg size (egg length/body length) at first reproduction. Regimes: 1 = Lake filtrate; 2 = *Chlamydomonas*; 3 = *Chlamydomonas* + *Cryptomonas*. Vertical bars are 95% confidence intervals.

Relative egg size (at first reproduction)

There was no significant difference in relative egg size between regimes for *C. dubia*. Thus, although the size of the primiparous adult was significantly smaller at regime 1 in this species (Fig. 31), egg size also decreased, and the relative investment in each egg was similar across all regimes. For *C. pulchella*, relative egg size was significantly lower in regime 2 ($p < 0.05$), indicating that eggs were smaller, relative to the size of the primiparous adult, on this food than on either lake water or a mixed algal diet.

2.4.4 Egg Production and Lipid Score: TABLE 21, FIGURE 33

Total egg production to clutch five

Total egg production was higher (by 10 eggs) in *C. dubia* than in *C. pulchella* at regimes 2 and 3, but at regime 1 there was no significant difference between the two species in this parameter. For both species, egg production was much lower in filtered lake water than in regimes 2 and 3, but there were no significant differences between the two algal diets.

Lipid-ovary score

Lipid scores were at, or close to, 0 for both species reared in lake water and, on this regime, differences between the species were not significant. For regimes 2 and 3 however, lipid scores were significantly higher in *C. dubia* than in *C. pulchella*, although, for each species, there was no difference between the two algal diets in the amount of visible lipid.

Mean egg volume

Mean egg volume in *C. pulchella* was not significantly affected by food regime, despite the lower clutch sizes observed in regime 1 for this species. For *C. dubia* though, eggs were significantly smaller in animals reared on lake water, although there was no difference observed in egg size between the two algal diets.

Mean clutch volume

Differences in mean clutch volume reflect the combined differences in clutch size (egg production) and egg size. For *C. pulchella*, clutch volumes were significantly lower at regime 1, than at regimes 2 and 3. This reflects the influence of clutch size, rather than

Table 21: Results of one way ANOVA followed by Tukey multiple comparison tests of data in Figure 33, to show the effects of food regime on **A.** total egg production to clutch five, **B.** mean lipid-ovary score, **C.**mean egg volume (clutches 1-5), and **D.** mean clutch volume (clutches 1-5) in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (i.e., across food regimes) are indicated by the same letter. Abbreviations as for Table 19. See Table 17 for details of food levels.

A. TOTAL EGG PRODUCTION TO CLUTCH FIVE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	563.444	2	281.722	104.917	0.001
	Error	56.389	21	2.685		
C. dubia	Regime	3132.171	2	1566.086	401.427	0.001
	Error	85.829	22	3.901		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .001

B. MEAN LIPID-OVARY SCORE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	41.814	2	20.107	820.608	0.001
	Error	0.662	26	0.025		
C. dubia	Regime	71.380	2	35.690	528.860	0.001
	Error	1.687	25	0.067		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .001

C. MEAN EGG VOLUME:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.048	2	0.024	2.043	0.149
	Error	0.316	27	0.012		
C. dubia	Regime	1.000	2	0.500	21.537	0.000
	Error	0.603	26	0.023		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	a	a	> 0.141 NS
C. dubia	a	b	b	< .001

D. MEAN CLUTCH VOLUME:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	43.197	2	21.598	96.332	0.001
	Error	5.605	25	0.224		
C. dubia	Regime	765.238	2	382.619	185.531	0.001
	Error	51.557	25	2.062		

Table of differences

	Regime Number 1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .001

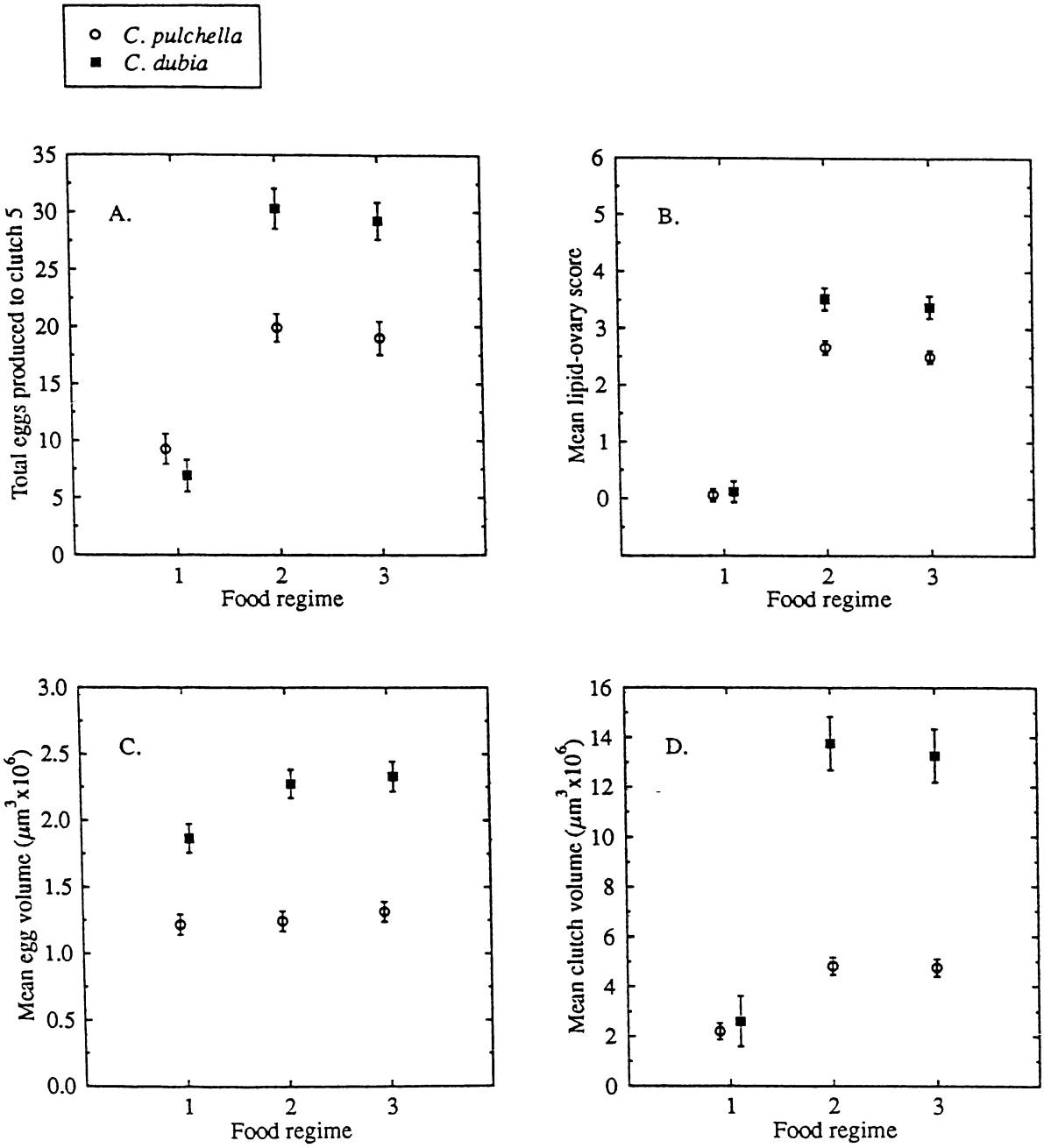

Figure 33.

Egg production and lipid score in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at three different food regimes at 20°C. (A) Total number of eggs produced to clutch five, (B) mean lipid-ovary score (clutches 1-5), (C) mean egg volume (clutches 1 - 5), (D) mean clutch volume (clutches 1-5). Regimes: 1 = Lake filtrate; 2 = *Chlamydomonas*; 3 = *Chlamydomonas* + *Cryptomonas*. Vertical bars are 95% confidence intervals.

egg volume, on clutch volume in this species, since the latter did not vary significantly between regimes.

In regime 1, significantly lower clutch and egg sizes combined to result in very low clutch volumes in *C. dubia*, and the differences in this parameter between regime 1 and regimes 2 and 3 were accentuated. For each species, there was no significant difference in clutch volume between regimes 2 and 3 and, as was the case with total egg production, no difference between the two species at regime 1.

2.4.5 Offspring Body Size and Lipid: TABLE 22, FIGURE 34

At regimes 2 and 3, there were no significant differences in offspring lipid score between species, or between regime. At regime 1, offspring of *C. pulchella* had significantly less visible lipid than offspring of *C. dubia* and, for both species, lipid levels were significantly lower at regime 1 than at regimes 2 and 3.

As was the case for neonate size, offspring size in *C. dubia* was much greater than in *C. pulchella*. For *C. pulchella*, the offspring produced from animals reared in lake water were larger than those from regimes 2 and 3, with no significant difference between the latter two diets. This was not the case for *C. dubia*, where the offspring from both regimes 1 and 2 were significantly larger than those from regime 3.

The size of offspring relative to the size of their primiparous mothers also differed between species, and within species between regimes, with both species having relatively larger offspring at regime 1 than at regimes 2 and 3. There was, however, no significant difference in relative offspring size between the two algal diets. Of the two species, the relative offspring size of *C. pulchella* was larger over all regimes than that of *C. dubia*. This reflects a trend that was apparent for relative egg size, although for this parameter the differences between the two species were not significant.

Table 22: Results of one way ANOVA followed by Tukey multiple comparison tests of data in Figure 34 to show the effects of food regime on **A.** offspring body size, and **B.** offspring lipid score, and **C.** the ratio of offspring body size to size of the primiparous adult in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (i.e., across food regimes) are indicated by the same letter. Abbreviations as for Table 19. See Table 17 for details of food levels.

A. OFFSPRING BODY SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.000	2	0.000	8.542	0.001
	Error	0.001	27	0.000		
C. dubia	Regime	0.001	2	0.000	8.923	0.001
	Error	0.001	27	0.000		

Table of differences

Regime Number

	1	2	3	p
C. pulchella	a	b	b	< .01
C. dubia	a	a	b	.001 < p < .05

B. OFFSPRING LIPID SCORE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	5.255	2	2.628	772.269	0.001
	Error	0.082	24	0.003		
C. dubia	Regime	4.053	2	2.027	160.859	0.001
	Error	0.328	26	0.013		

Table of differences

Regime Number

	1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .001

C. OFFSPRING BODY SIZE/SIZE OF PRIMIPAROUS ADULT:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Regime	0.016	2	0.008	18.369	0.001
	Error	0.012	27	0.000		
C. dubia	Regime	0.015	2	0.007	5.526	0.010
	Error	0.036	27	0.001		

Table of differences

Regime Number

	1	2	3	p
C. pulchella	a	b	b	< .001
C. dubia	a	b	b	< .05

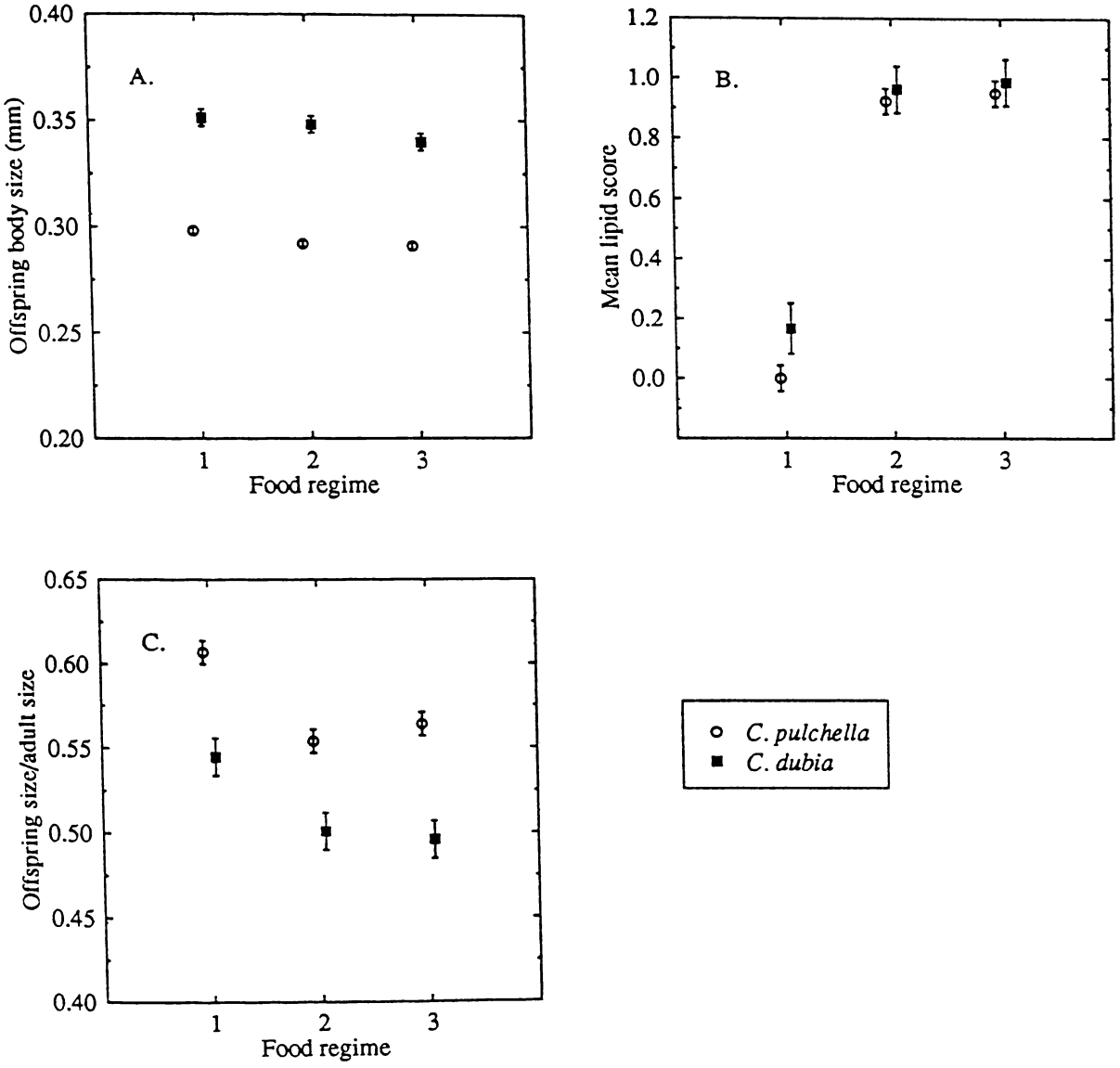

Figure 34.

Aspects of body size and nutrition in offspring of *Ceriodaphnia pulchella* and *Ceriodaphnia dubia*, grown at three different food regimes at 20°C. (A) Offspring body size at birth, (B) offspring lipid score, (C) ratio of offspring size to size of the primaparous adult. Regimes: 1 = Lake filtrate; 2 = *Chlamydomonas*; 3 = *Chlamydomonas* + *Cryptomonas*. Vertical bars are 95% confidence intervals.

2.4.6 Summary

From the results of these food suitability trials a number of clear responses emerge:

1. Lake filtrate even when concentrated, is a poor food for *Ceriodaphnia*, relative to the algal diets tested. On this regime, fecundities and lipid scores in both species were reduced, body sizes were smaller, and time to reach the fifth adult instar was significantly prolonged.
2. When reared on either of the two algal diets, fecundities and lipid scores in *C. dubia* were markedly higher than in *C. pulchella*. When reared on lake filtrate however, the differences between the two species in these parameters were not significant.
3. On the lake filtrate diet, relative neonate size was significantly larger, and adult growth from birth significantly lower, than on the defined algal diets, for both species. Thus, reduced body sizes on the lake filtrate diet were not concomitant with smaller neonates.
4. At all regimes, *C. dubia* was larger, and produced significantly larger eggs and neonates than *C. pulchella*. However relative neonate size was greater in the smaller species.
5. While the lake filtrate is clearly the least suitable as a food source for *Ceriodaphnia*, on first appearance there appears to be little difference between the two algal diets in nutritional adequacy. The mixed algal diet was finally selected as the most suitable on the basis of three features:
   (i) Development times to the fifth adult instar were significantly shorter in *C. pulchella* on this food regime.
   (ii) There were no incidences of reproduction being delayed to the fifth instar on this diet in either species, and
   (iii) In both species, the incidences of clutch degeneration or egg abnormality were lower when fed a mixture of algae.

2.5 DISCUSSION

Not unexpectedly, given the low fecundities of the Lake Mangakaware cladoceran community, lake water as a food source did not support very high growth or reproductive rates in laboratory reared *Ceriodaphnia*. The low clutch sizes of animals reared on lake water, compared with those on defined algal diets, suggests that animals were food limited on this nutritional regime. This suggestion is supported by the significantly longer time taken by both species to reach the fifth adult instar when reared on lake water, although this prolongation was not evident in the age at maturity. In addition, the body sizes and lipid levels of lake water fed animals were significantly reduced below those of algal fed animals, as is typical of Cladocera when food limited (Hrbáčková 1974; Vijverberg 1976; Hrbáčková and Hrbáček 1979; Taylor 1985; Duncan 1989). The close agreement between adult body sizes, lipid scores, and fecundities, in laboratory animals reared in lake water and those in Lake Mangakaware itself, (Figs 17, 18, 19, 21, 22, 24), is further evidence that food availability, rather than predation, governs these parameters in field populations.

Even though, in the laboratory trials, the cell concentration of the lake water was increased by centrifugation, clearly the level of nutritionally suitable algal species was still too low for optimal growth and reproduction. In contrast to adult body size however, neonate body sizes (at time 0), were not significantly different between regimes, except for *C. dubia* on the unialgal medium. This may be because the accuracy of live neonate measurement is lower than for preserved animals, due to the need for minimal handling and manipulation. However, when the offspring of mothers from different regimes are compared, the first instar juveniles of mothers reared in lake water were significantly larger than those from the unialgal diet (*C. pulchella*) or the mixed algal diet (*C. pulchella* and *C. dubia*). These differences may simply be the result of the higher accuracy gained by measuring preserved animals, but may also reflect a time dependent response, i.e., neonate size differences may not become evident until mothers have been cultured for a considerable time at a particular regime.

A larger neonate under food limited conditions is not necessarily an expected response in Cladocera. Hrbáčková (1974) for example, found that neonates of *Daphnia*

hyalina were smaller, in broods subsequent to the first, when reared under food limited conditions, although, as in this study, relative neonate size increased in non enriched food conditions. In contrast, other studies have shown the neonates from poorly fed mothers to be larger and more resistant to starvation than those from well fed cultures (Tessier *et al.* 1983; Tessier and Consolatti 1989; Guisande and Gliwicz 1992).

Larger body sizes in the offspring of the mothers reared on lake water were not the result of larger eggs *per se*. Although relative neonate size in both species (and relative egg size also in *C. pulchella*), was higher in the lake water regime, this was a function of smaller body size in the primiparous adult. This apparently contradictory result may be due to the use of body length (rather than mass) as a measure of neonate size. Tessier and Consolatti (1989) for example, found that neonates of *Daphnia pulex* and *D. pulicaria*, produced at low food concentration, were lowest in mass, but body lengths in these offspring were equal to, or greater than, those in neonates produced at high food.

This disparity in body size between *C. pulchella* and *C. dubia* is reflected in reproductive parameters such as clutch size and egg volume. As shown in Part Two, Chapter Five, there is a strong positive relationship between egg volume and body size, both within and between species, and between clutch size and body size between, but not within, species. *C. dubia* is a larger species than *C. pulchella* and, not unexpectedly, has the highest overall clutch sizes and egg volumes. However, on a regime of lake water (= low food?) the species are not significantly different in fecundity (clutch size or volume) or in stored lipid, although *C. dubia* always has the largest eggs, regardless of food regime. This supports the findings of the field studies, (Part Two), which showed that while egg volume was strongly associated with body size, clutch size was related to some other (unrecognised) variable (probably food availability). Further discussion of specific life history features in *Ceriodaphnia* is restricted to the next chapter, where the influence of temperature and food level is assessed.

Interestingly, although lake water was clearly not an optimal food, the incidences of egg abnormality and egg degeneration were the lowest on this regime. Keating (1985) has stressed the importance of vitamin B12 to reproduction in *C. dubia*, and the problems

associated with the use of defined media have been discussed already. The addition of a vitamin solution to the culture greatly reduced the incidence of egg abnormality and was a methodology adopted throughout the latter half of this experiment. Clearly lake water provides the dissolved organic compounds necessary for normal, although not necessarily high, egg production.

While the results point to lake water being inadequate in providing nutrition for *Ceriodaphnia*, there was little to choose between the two defined algal diets in terms of growth and reproductive response. Certainly, the instances of egg degeneration and prolonged development were lower on the mixed regime, but fecundities and lipid levels were not significantly different between mono- and mixed-algal diets. A number of workers have warned against the use of monocultures of algal in culturing daphnids. Taub and Dollar (1968) found that reproduction was submaximal on a monoculture of either *Chlamydomonas* or *Chlorella*, and abnormal as well when defined inorganic media were used. Lundstedt and Brett (1991) also found monocultures of *Scenedesmus* and *Chlorella* to be poorer foods than mixed cultures representative of spring bloom populations, although it is worth noting that the use of static cultures in their study may have biased the findings in favour of the mixed culture, which comprised a high proportion of flagellates. Vijverberg (1989) does not specifically recommend the use of mixed algal diets for cladoceran culture, but notes that reproduction is often enhanced when two or more algal species are provided. Similarly Goulden *et al.* (1982a) found a mixed diet to be superior to a monoculture when rearing *Daphnia magna.*

Given the above recommendations, a mixed algal diet was deemed the most suitable for the rearing of *C. pulchella* and *C. dubia.* This diet was then used in the culture of these two species at high and low food levels, at 23°C and 13°C. This experiment is the topic of the next chapter.

PART THREE

CHAPTER THREE:

RESPONSES OF *CERIODAPHNIA* TO DIFFERENT FOOD LEVELS AND TO HIGH AND LOW TEMPERATURES

3.1 INTRODUCTION

This chapter examines the effects of food limitation and temperature on the growth and reproductive characteristics of *Ceriodaphnia pulchella* and *C. dubia,* and considers the life history implications of resource depression to these two species.

In most New Zealand limnetic systems, food limitation appears to govern seasonality in zooplankton to a greater extent than does predation (Chapman and Green 1987; Burns 1991). In Lake Mangawakare, the fecundities of the planktonic Cladocera are well below what they are able to achieve when in well fed laboratory cultures and, in this respect, the populations in this lake appear to be no exception to the above generalisation.

In Cladocera, limiting food conditions can affect a number of ecologically important life cycle characteristics:

1. Adult body size is often reduced (e.g. Weglenska 1971);
2. The duration of development, particularly in juvenile stages, is prolonged (e.g. Romanovsky 1984b; Foran 1986a).
3. The number of instars to critical stages in the life cycle e.g. maturity, increases (e.g. Staples 1984).
4. Fecundity is reduced (e.g. Foran 1986a)

While these aspects of reproduction and growth under food limited conditions are generally true, the quantitative response of these variables may vary substantially between different species (Lynch 1992). For example, while two species might both reduce clutch size at some level of food depletion, the rate of the decline in fecundity is likely to be different for each. Moreover, different species allocate available energy to reproduction in different ways. Thus the fecundity of a species that produces a few, relatively large, eggs may be more adversely affected by resource depression than a species that divides its

reproductive effort into smaller packages, and can therefore reduce clutch size while continuing to reproduce.

The effects of temperature on life cycle characteristics have been extensively studied in the Cladocera (e.g. Bottrell 1975, a, b), and the inverse relationship between development time and temperature is well established. Knowledge of the specific response to high and low temperature can be useful in explaining seasonal abundance patterns. In *C. dubia*, development time at low temperature is substantially shorter than in *C. pulchella* (Greenwood 1987; Appendix 4), affording the former species a strong population growth advantage at temperatures below about 18°C. However, it is not known if this response is altered by food limitation. It is the nature of the species specific responses to food level and temperature, and to the interaction between these two variables, that I wish to explore in this chapter.

3.2 METHODOLOGY

The experimental investigation of the growth and reproductive responses of *Ceriodaphnia* to different food and temperature levels involved the use of a mixed algal diet, *Chlamydomonas* plus *Cryptomonas*. This diet, already established as being the most nutritionally suitable of the foods trialed (Chapter Two), was provided at two levels, one an order of magnitude lower than the other. Details of food levels are provided in Table 23, and were determined on the basis of the range of values given in other studies of cladoceran life histories (Lynch and Ennis 1983; Cowgill *et al.* 1985; Keating 1985; Lynch 1989; Hessen 1990).

The methodologies employed for maintaining stock populations of *Ceriodaphnia*, and algal cultures, were identical to those described in Chapter Two. Test animals were reared in 12 ml vials containing 10 ml each of daphnid dilution water (Appendix 7, Table 2). Vials were floated in polystyrene holders in thermostatically controlled insulated water baths, maintained at 23°C (high temperature) or 13°C (low temperature) as shown in Figure 35. Both baths were shielded from ambient lighting by black cloth, with overhead lighting being provided by a 14:10 hour light:dark cycle of fluorescent illumination.

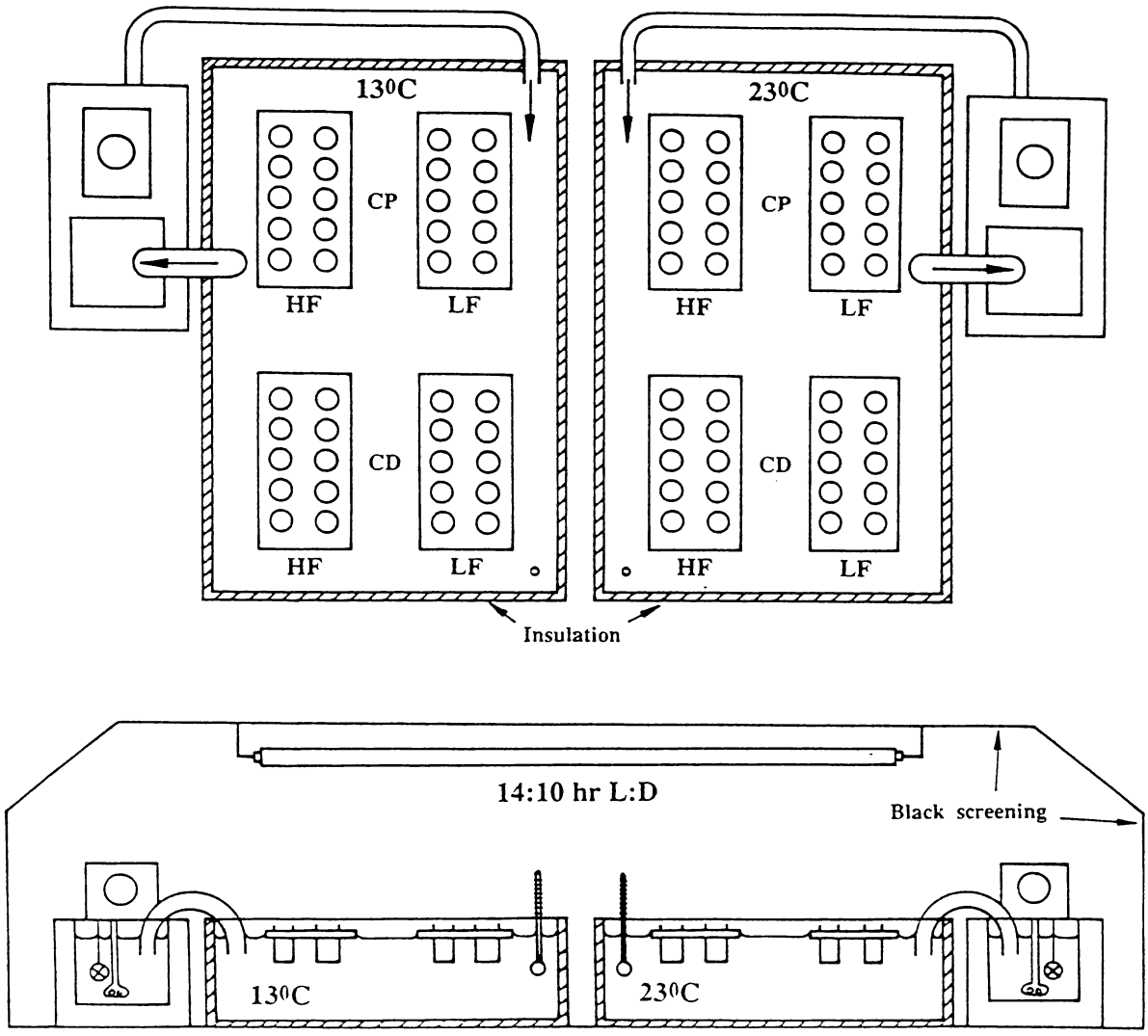

Figure 35. Experimental design for food/temperature studies on *Ceriodaphnia*. Both plan and side views are shown. The design for earlier food trials (Chapter Two) was similar but only one temperature was used (20°C). For initial feeding trials in mass culture (Chapter Two), 500 ml beakers were placed directly in the bath.

Table 23: Description of food regimes used in a test of the effects of food and temperature level on reproduction and growth in *Ceriodaphnia.*

	Range of Values		
Food level	***Chlamydomonas***	***Cryptomonas***	**Total**
HIGH (HF)			
µg C ml^{-1} d^{-1}	0.62 - 0.92	0.43 - 0.51	1.1 - 1.43
cells ml^{-1} d^{-1}	3.2 - 4.4 x 10^4	2.5 - 3.0 x 10^4	5.7 - 7.4 x 10^4
LOW (LF)			
µg C ml^{-1} d^{-1}	0.067 - 0.09	0.043 - 0.05	0.11 - 0.143
cells ml^{-1} d^{-1}	3.2 - 4.4 x 10^3	2.5 - 3.0 x 10^3	5.7 - 7.4 x 10^3

Ten animals from stock populations were assigned to each of four temperature-food regimes: high temperature, high food (HH); low temperature, high food (LH); high temperature, low food (HL); low temperature, low food (LL). They were acclimated to experimental conditions over two generations, following the procedure outlined in Figure 36. Total food ration was delivered by micropipette, in two (am and pm) pulses daily. Together with daily vial inversion, this reduced the problem of food settling. As in food trials, food was provided in quantities determined according to cell densities established by haemocytometer counts. All post-feeding residual cell counts and tests for cell viability after centrifugation were as for Chapter Two.

Test animals were reared from birth until they died. However, measurement of egg and clutch volumes ended after the deposition of clutch six. Offspring of the first five broods were collected soon after their release from the brood pouch, preserved, measured, and scored for lipid. As in the food trials, raw data were used to calculate general measures of performance, so that for each variable of interest, there was one only value per animal. The variables used in assessing growth and reproductive performance were the same as those outlined in Chapter Two, except that clutch six, rather than clutch five, was taken as the end point for most measures. The rationale for the use of these parameters follows that given in Chapter Two. In addition to these, longevity, total number of adult

instars, and maximum body size were also recorded, since these are often affected by both temperature and resource depression (Lynch and Ennis 1983; Duncan 1989). As well as egg production to clutch six, total egg production to day 30 was also included as a variable of interest. This measure effectively accounted both for differences in development time at different temperatures, and for variations in the time between neonate release and egg deposition, which may be prolonged at low food levels (Romanovsky 1984b). Clutch dependent measures of egg production cannot account for these variations because they are independent of time.

The assessment of all other methods is as described in Chapter Two. The complete list of measured, or calculated variables is given in Table 24.

Starvation

In addition to other data collected, some of the neonates of mothers from each regime were starved to determine their longevity given a particular maternal environment. One neonate was removed from eight of the ten individual test animals at each regime. These were then maintained in 4 ml autoanalyser tubes containing daphnid dilution water, at the temperature to which they had been acclimatised. The percentage survival after each day of starvation was then recorded.

Statistical analyses

The differences between animals reared at each of the four temperature-food regimes were tested for significance ($p < 0.05$) by two way ANOVA (temperature x food effects), followed by Tukey multiple comparison tests of mean differences, using SYSTAT statistical software (Wilkinson 1989). As was the case for the earlier food trials, experimental effects were tested for significance on each species separately, as for most variables the large differences between the two species masked the effects of regime in three way ANOVAs. In other words, the differences between the species, in most cases, were so large that statistics were generally not required to compare them. Moreoever, the primary aim of the experiment was to determine the responses of each species to differences in food and temperature level, not to establish whether or not the two species were different *per se*.

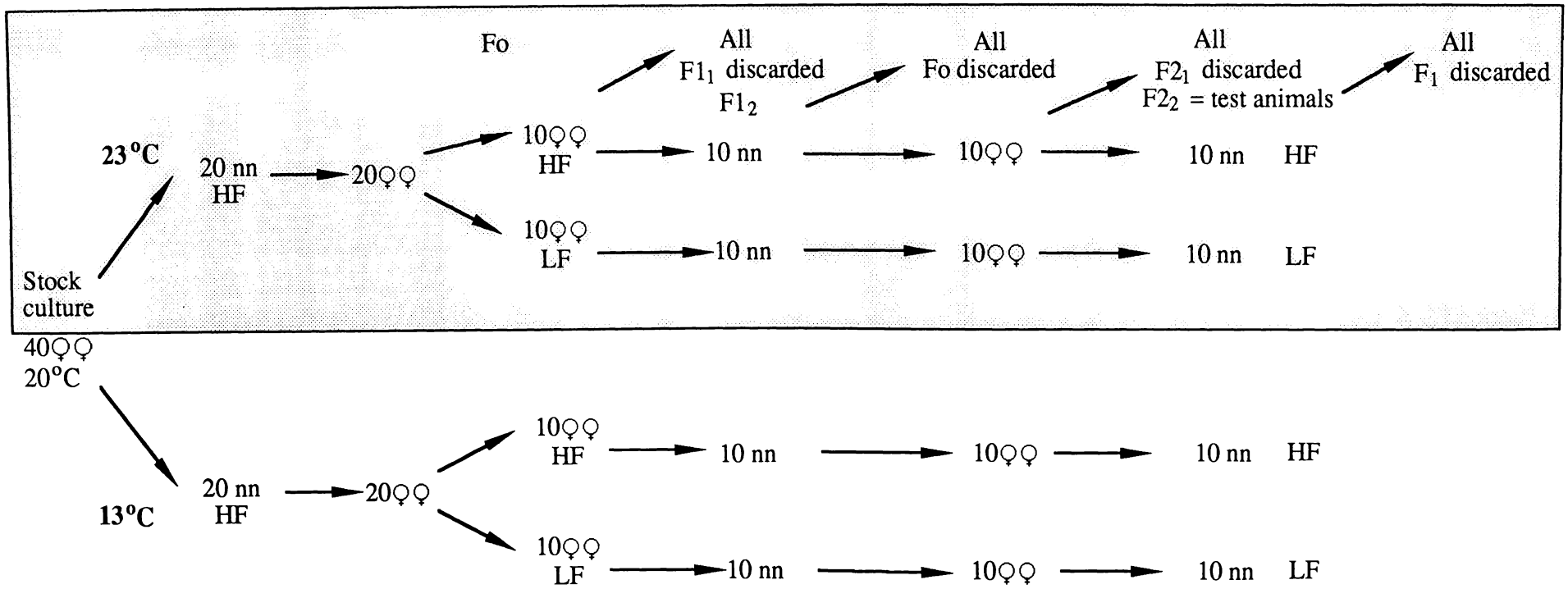

Figure 36.
Acclimation procedure for test animals used in food-temperature experiment. HF = high food; LF = low food; nn = neonates; ♀♀ = adult females. High temperature region shaded.

Table 24: Variables used in the assessment of growth and reproduction in *Ceriodaphnia* under different temperature-food regimes.

1.	**Developmental responses with time**
	Time taken to first reproduction (= age at maturity)
	Time taken to clutch six
	Length of life
	Number of adult instars
2.	**Growth responses**
	Maximum body size
	Neonate body size (at time 0)
	Body size at clutch six
	Ratio of adult body size at clutch two to size at birth
	Size at first reproduction
3.	**Indices of reproductive effort**
	Egg length at first reproduction
	Relative egg size (egg length ÷ body length) at first reproduction
	Mean egg volume (clutches 1-6)
	Mean clutch volume (clutches 1-6)
	Total egg production to day 30
	Total egg production to clutch 6
	Offspring size relative to size of the primiparous adult
4.	**Lipid score**
	Mean lipid-ovary score (clutches 1-6)
5.	**Offspring body size and lipid**
	Body size of offspring produced over clutches 1-5
	Mean lipid score of offspring produced over clutches 1-5

For each species, the null hypothesis, Ho, was for no difference in measures of growth and reproductive performance between temperature-food regimes. Data were tested for normality and homoscedasticity, as in Chapter Two, and conformed to the assumptions of the model in these respects.

In addition to ANOVAs, linear regression analyses relating clutch volume to body length were performed on log transformed data, for each species separately for regime and then pooled on regime, and then pooled for both regime and species. Differences between regimes in the clutch volume - body length relationship for each species were assessed on the basis of the 95% confidence interval of the regression coefficient, b, in the regression

equation: clutch volume = a + b logbodylength. The difference in the clutch volume - body length relationship between species, disregarding regime, was determined using the equation provided by Neter *et al.* (1989) for the comparison of regression slopes:

$$F = \frac{SSE_{(R)} - SSE_{(F)}}{df_{(R)} - df_{(F)}} \div \frac{SSE_{(F)}}{df_{(F)}}$$

where $df_{(F)} = n - 2$

and $df_{(R)} = n - 1$

This method uses the error sums of squares (SSE) of full (F) and reduced (R) (pooled for species) models to determine an F statistic, which can then be used to assess the significance of slope differences . All statistical methodology and assessment is otherwise as described in initial food trials (Chapter Two).

3.3 RESULTS

Full results (data files, ANOVA and means tables, and Tukey probability matrices) are given on floppy disk at the back of this volume.

3.3.1 Growth at Different Food and Temperature Levels

Instar growth (increment in body length per instar), and increase in mean adult body size with time are shown in Figures 37 and 38 respectively.

As in the food suitability trials, the first reproductive instar was usually the fourth. *C. pulchella* was never observed to include extra juvenile instars (except under starvation), but this was not uncommon in *C. dubia* at low food levels (5 occurrences at low food and 23°C, 3 occurrences at low food and 13°C). *C. dubia* individuals which reproduced at the fifth instar were not necessarily larger than those reproducing in their fourth instar but, rather, seemed to have a preadult history of smaller growth increments per moult. They then appeared to require an extra moult to achieve a size and/or lipid level similar to that at which others, in their fourth instar, were first reproducing.

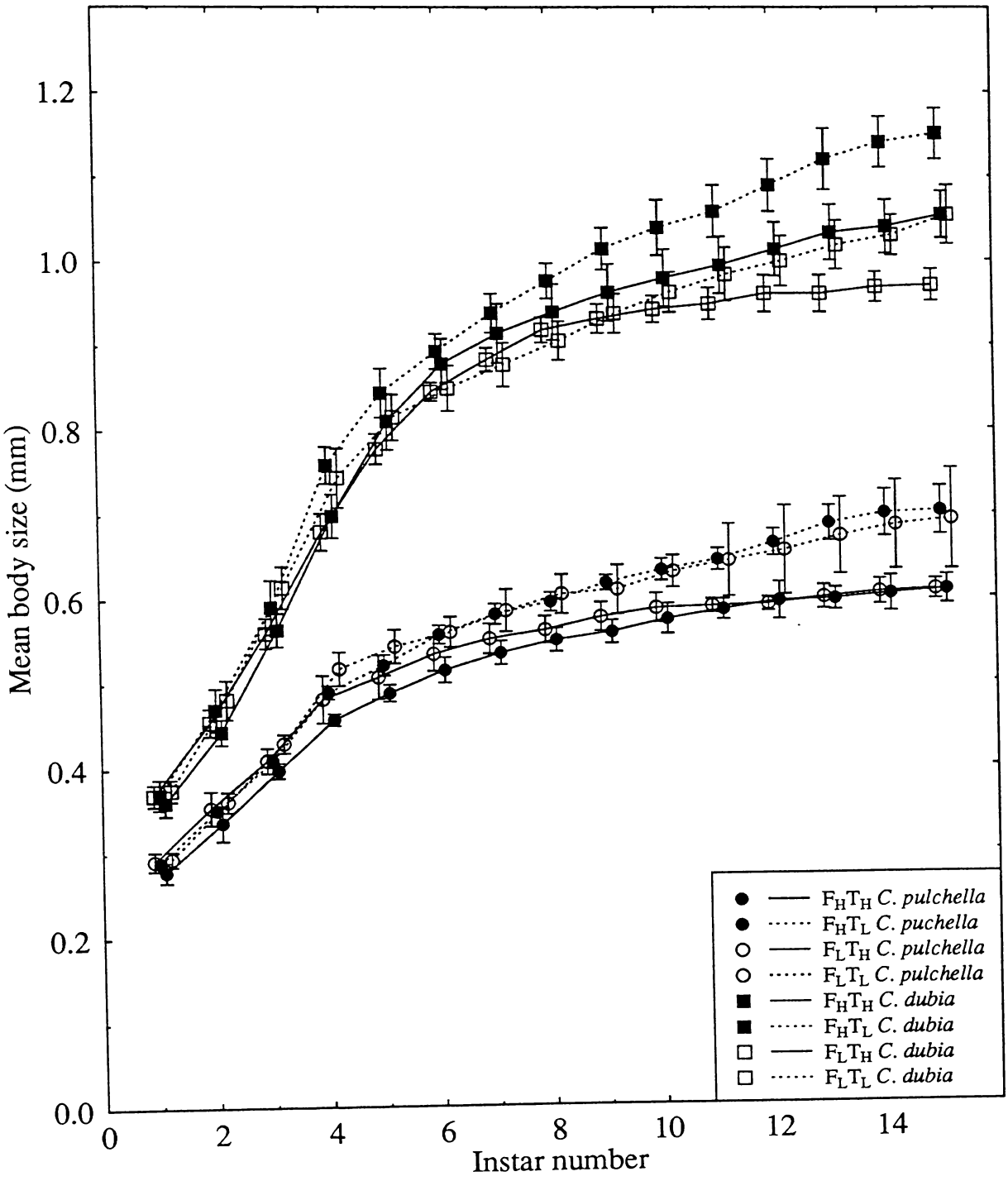

Figure 37.
Instar growth (expressed as mean body size) in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* grown at high food (F_H) and low food (F_L) levels at high (T_H) = 23°C and low (T_L) = 13°C temperatures. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

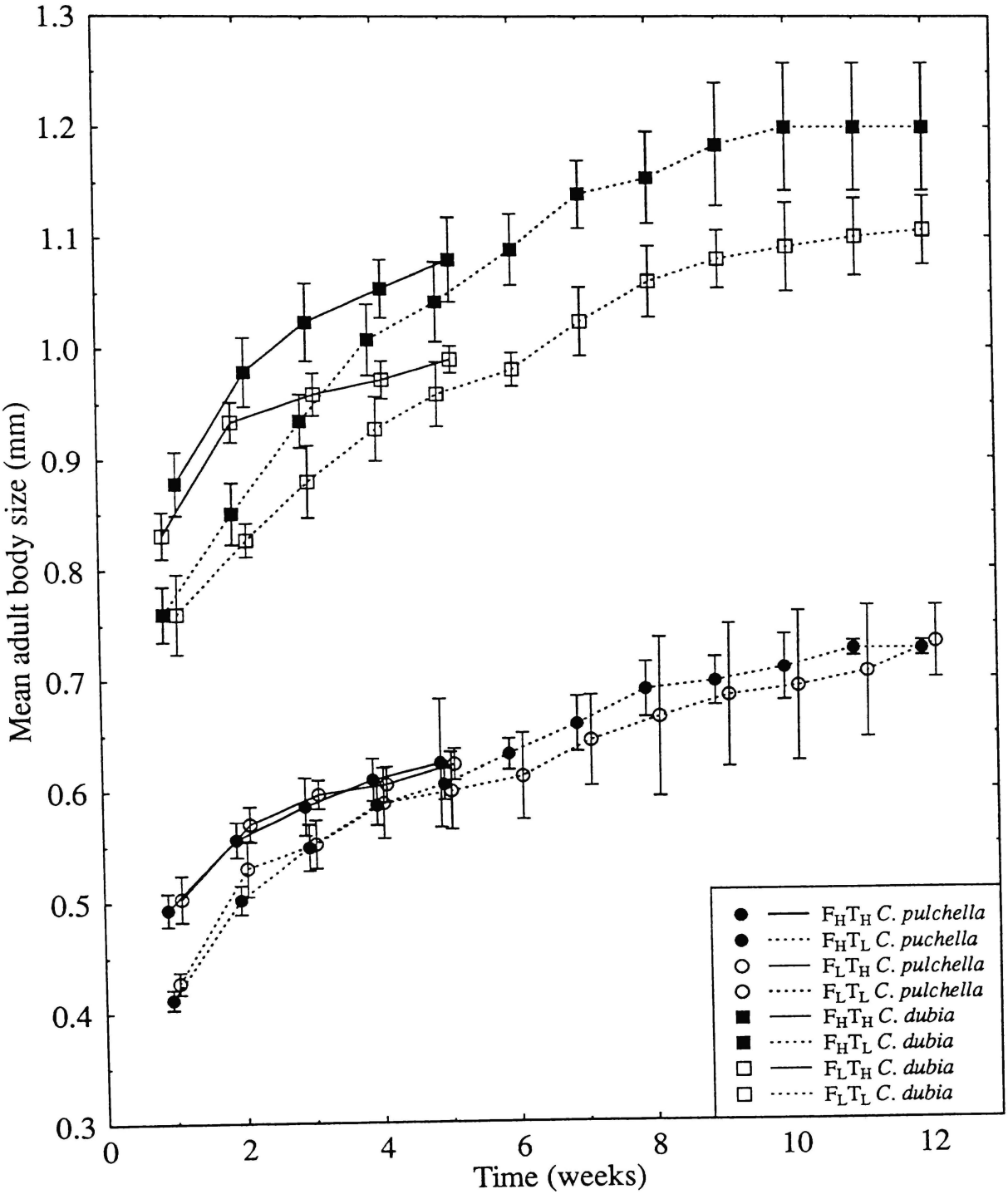

Figure 38.
Increase in mean adult body size with time in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* grown at high food (F_H) and low food (F_L) levels at high (T_H) = 23°C and low (T_L) = 13°C temperatures. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

In both growth curves the most striking feature is the disparate sizes of the two *Ceriodaphnia* species. Neonates of *C. dubia* were significantly larger than those of *C. pulchella* at all food regimes (Fig. 37) but the absolute value of the difference was less than 0.1 mm. By the fourth instar however, the size differential had increased to twice that value (regime for regime).

Comparing the slopes in Figure 37, *C dubia's* rate of increment in early instars was approximately 1.5 times that in *C. pulchella*. Moreover, the reduction in growth rate after the fourth instar (i.e., after maturity) was more rapid in *C. pulchella* than in *C. dubia*, particularly at high temperature, although growth in the latter species was severely curtailed after the eighth instar at the HL regime. Notably, for both species, temperature effects on body size became more pronounced late in adult life, with the growth curves diverging markedly after the tenth instar.

Both species showed a marked reduction in body size at high temperature but in *C. pulchella* this temperature response was not significantly affected by food level. In *C. dubia* however, high food levels enhanced the effect of low temperature on body size, and the difference in curves was greatest between high and low temperatures at low and high food levels respectively.

The effect of time on the form of the growth curve (Fig. 38) was to compress the high temperature response, and accentuate the effects noticeable in the per instar growth curves. In other words, at high temperatures, curves appear steeper initially, at least for *C. dubia*, because animals pass through several moults at 23°C for every one moult at 13°C.

3.3.2 Cumulative Egg Production at Different Food and Temperature Levels

Most obvious from the curve of cumulative egg production (Fig. 39) is the significant positive effect of food level on egg production, particularly at high temperature, when the number of moults per unit time is greater. For *C. dubia*, total egg production was greatest at high food level and low temperature, primarily because at lower temperature animals lived longer. For any given time period up to five weeks however, the cumulative egg production was highest at the HH regime, and differences between low and high food levels at high and low temperature respectively were not significant. *C. dubia,* at the LL

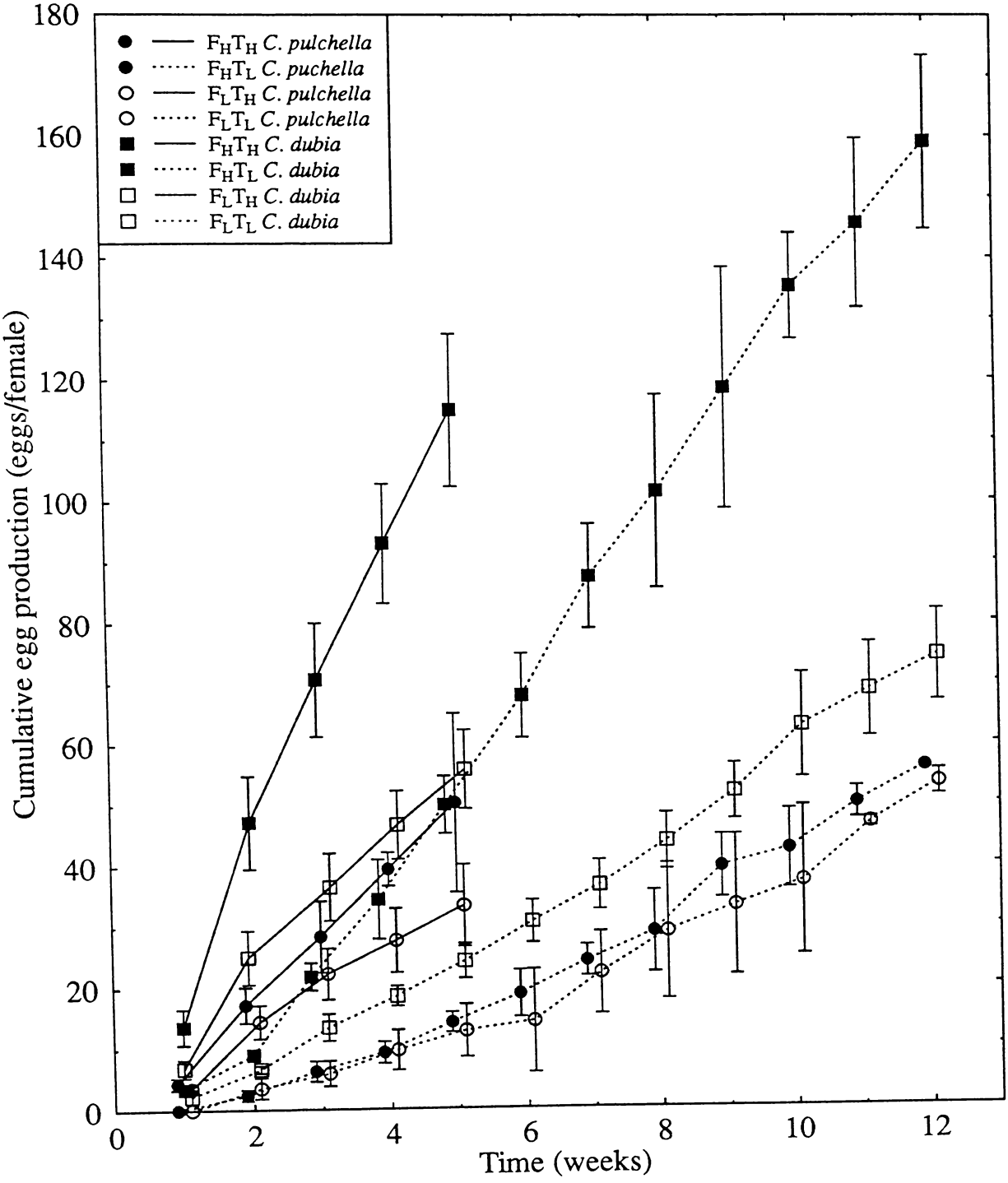

Figure 39.

Cumulative egg production in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* grown at high food (F_H) and low food (F_L) levels at high (T_H) = 23°C and low (T_L) = 13°C temperatures. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

regime, had the slowest rate of cumulative egg production but, by virtue of a longer life, produced more eggs in total than those at low food levels and 23°C. The response of *C. pulchella* to food and temperature level was less clear. Temperature appeared to have the most significant effect on total egg production, but the differences between food levels were generally not great, although the data at high temperature are quite variable. Per unit time, egg production was greater at the higher temperatures regardless of food level, but even at high food concentration, total egg production at 23°C was not significantly different from either food level at low temperature.

Notably, egg production, both in total and per unit time, was lower in *C. pulchella* than in *C. dubia* when compared regime for regime.

3.3.3 Developmental Responses with Time: TABLE 25, FIGURE 40

Number of adult instars and length of life

There was no significant difference in the number of adult instars either between food-temperature regimes, or between species, although there was a tendency for *C. dubia* to have a greater number of adult instars than *C. pulchella*, particularly at the lower temperature. When the length of life is considered, however, the effect of increased instar duration at low temperature is apparent. There was no significant difference between high temperature regimes in length of life in *C. dubia*, but longevity was increased considerably at low temperature, and within low temperature regimes by low food levels.

For *C. pulchella*, animals reared at high food levels and low temperature lived significantly longer than those at high food and high temperature but there were no significant temperature effects between animals at low food levels.

Time to first reproduction

Not unexpectedly, temperature effects predominated in determining the time to first reproduction in both species. However, food effects were negligible. Between species, *C. dubia*'s developmental advantage over *C. pulchella* is evident even by first reproduction, with the latter species' age at maturity being significantly greater at lower temperature than *C. dubia*'s. At 23°C the species were more similar and the differences between them were not significant.

Table 25: Results of 2 way ANOVA followed by Tukey multiple comparison tests on data in Figure 40, to show the effects of food and temperature level on **A.** number of adult instars **B.** length of life, **C.** time to first reproduction, and **D.** time to clutch six in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (i.e., across temperature-food regimes) are indicated by the same letter. Abbreviations: HH = 23°C, high food; HL = 23°C, low food; LH = 13°C, high food; LL = 13°C, low food. See Table 23 for details of food levels. Source = source of variation, SS = sum of square, DF = degrees of freedom, MS = mean square.

A. NUMBER OF ADULT INSTARS

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	55.225	1	55.225	1.248	0.271
	Food	27.225	1	27.225	0.615	0.438
	Temp x Food	87.025	1	87.025	1.966	0.169
	Error	1593.300	36	44.258		
C. dubia	Temp	21.025	1	21.025	0.487	0.490
	Food	2.025	1	2.025	0.047	0.830
	Temp x Food	2.025	1	2.025	0.047	0.830
	Error	1554.700	36	43.186		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.20 NS
C. dubia	a	a	a	a	> 0.90 NS

B. LENGTH OF LIFE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	6047.542	1	6047.542	7.544	0.009
	Food	219.891	1	219.891	0.274	0.604
	Temp x Food	1176.954	1	1176.954	1.468	0.234
	Error	28858.968	36	801.638		
C. dubia	Temp	21888.111	1	21888.111	45.270	0.001
	Food	4404.983	1	4404.983	9.111	0.005
	Temp x Food	1564.480	1	1564.480	3.236	0.081
	Error	15471.939	32	483.498		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	ab	b	ab	< .05
C. dubia	a	a	b	c	< .05

C. TIME TO FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	182.088	1	182.088	435.591	0.001
	Food	0.019	1	0.019	0.045	0.833
	Temp x Food	0.233	1	0.233	0.558	0.460
	Error	14.213	34	0.418		
C. dubia	Temp	136.995	1	136.995	446.386	0.001
	Food	0.860	1	0.860	2.803	0.103
	Temp x Food	0.373	1	0.373	1.214	0.278
	Error	10.741	35	0.307		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	b	b	< .001
C. dubia	a	a	b	b	< .001

D. TIME TO CLUTCH SIX:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	2356.762	1	2356.762	2544.111	0.001
	Food	7.249	1	7.249	7.826	0.001
	Temp x Food	0.845	1	0.845	0.913	0.349
	Error	21.306	23	0.926		
C. dubia	Temp	2635.071	1	2635.071	3272.610	0.001
	Food	22.031	1	22.031	27.361	0.001
	Temp x Food	0.847	1	0.847	1.051	0.312
	Error	27.376	34	0.805		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	b	b	< .001
C. dubia	a	b	c	d	< .05

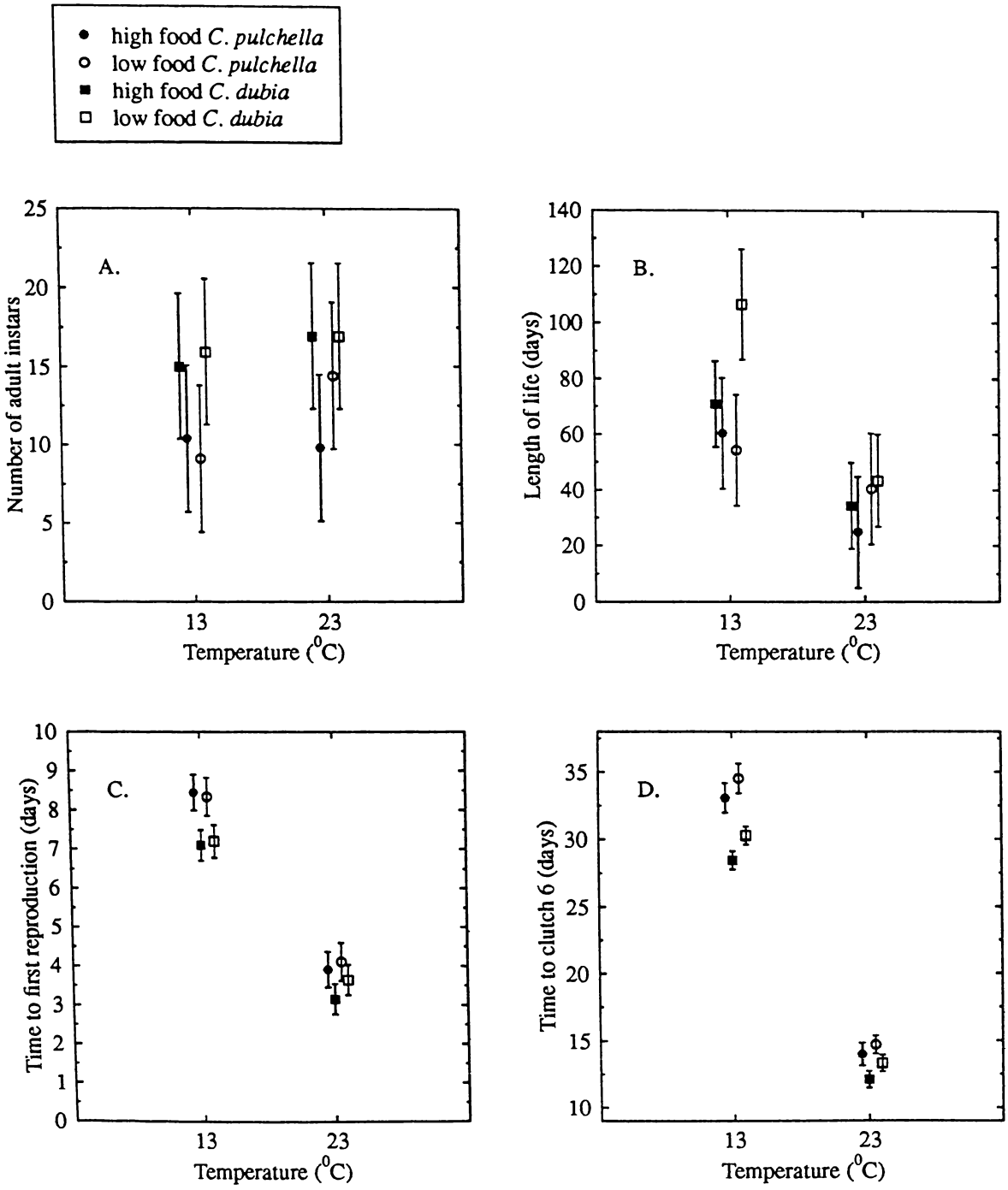

Figure 40.

Developmental responses with time in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at high and low food levels at 13°C and 23°C. (A) Number of adult instars, (B) total length of life, (C) time to first reproduction, (D) time taken to reach clutch six. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

Time to clutch six

The differences evident between regimes in development time were even more pronounced in time to clutch six than in age at maturity. Again, temperature effects predominated but, over the longer time period, food effects became more apparent for the larger species, *C. dubia*. In this species, time to clutch six was markedly longer at lower temperatures but, within each temperature regime, low food prolonged development time significantly ($p < 0.05$).

For *C. pulchella* food effects were significant (animals took longer to reach clutch six), but these effects were masked by the very large effect of temperature in prolonging development time. Notably, the development time disadvantage expressed by this species at low temperature in the age at maturity was also evident after six clutches at 23°C.

3.3.4 Growth Responses: TABLE 26, FIGURE 41

Maximum body size

For this variable, the large differences between the two *Ceriodaphnia* species were apparent, with maximal body sizes of *C. dubia* being 0.3 mm - 0.6 mm larger than those of *C. pulchella*. For *C. pulchella* the ANOVA indicated a significant temperature effect on maximum body size ($p = 0.022$), with animals being larger at the lower temperature. When food level is considered as well however, the effect of temperature is reduced, and there were no significant differences in maximum body size between food-temperature regimes. For *C. dubia* though, both temperature and food effects were highly significant. *C. dubia* was larger at high food and at low temperature, although the mean maximum size at the high temperature - high food regime was not significantly different from that at low food and low temperature.

Neonate size

Neonate size at the start of the experiment (following two generations of preconditioning) was significantly different between species, but not between regimes. There was a tendency for neonates to be smaller at high food regardless of temperature, but this food effect was significant for *C. pulchella* ($p = 0.041$) and not for *C. dubia* ($p = 0.094$).

Table 26: Results of 2 way ANOVA followed by Tukey multiple comparison tests on data in Figure 41 to show the effects of food and temperature level on **A.** maximum body size, **B.** neonate size, **C.**body size at clutch six, and **D.** ratio of body size at clutch two to neonate size in *Ceriodaphnia*. Means that are not significantly different at $p< 0.05$ within rows (ie. across temperature-food regimes) are indicated by the same letter. Abbreviations as for Table 25. See Table 23 for details of food levels.

A. MAXIMUM BODY SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.029	1	0.029	5.702	0.022
	Food	0.007	1	0.007	1.465	0.234
	Temp x Food	0.004	1	0.004	0.694	0.410
	Error	0.182	36	0.005		
C. dubia	Temp	0.107	1	0.107	54.722	0.001
	Food	0.055	1	0.055	28.411	0.001
	Temp x Food	0.000	1	0.000	0.092	0.764
	Error	0.062	32	0.002		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.05 NS
C. dubia	a	b	c	a	< .01

B. NEONATE SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.000	1	0.000	2.338	0.135
	Food	0.000	1	0.000	4.483	0.041
	Temp x Food	0.000	1	0.000	0.885	0.353
	Error	0.007	36	0.000		
C. dubia	Temp	0.000	1	0.000	0.927	0.342
	Food	0.001	1	0.001	2.962	0.094
	Temp x Food	0.000	1	0.000	0.001	0.973
	Error	0.014	35	0.000		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.05 NS
C. dubia	a	a	a	a	> 0.2 NS

C. BODY SIZE AT CLUTCH SIX:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.017	1	0.017	73.304	0.001
	Food	0.000	1	0.000	1.373	0.254
	Temp x Food	0.000	1	0.000	0.812	0.377
	Error	0.005	22	0.000		
C. dubia	Temp	0.009	1	0.009	9.551	0.004
	Food	0.025	1	0.025	26.120	0.001
	Temp x Food	0.005	1	0.005	5.110	0.031
	Error	0.032	32	0.001		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	b	b	< .001
C. dubia	a	a	b	a	< .01

D. RATIO OF BODY SIZE TO NEONATE SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.037	1	0.037	4.798	0.035
	Food	0.007	1	0.007	0.849	0.363
	Temp x Food	0.003	1	0.003	0.360	0.552
	Error	0.266	34	0.008		
C. dubia	Temp	0.001	1	0.001	0.040	0.842
	Food	0.027	1	0.027	0.935	0.340
	Temp x Food	0.002	1	0.002	0.062	0.805
	Error	1.035	36	0.029		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.1 NS
C. dubia	a	a	a	a	> 0.8 NS

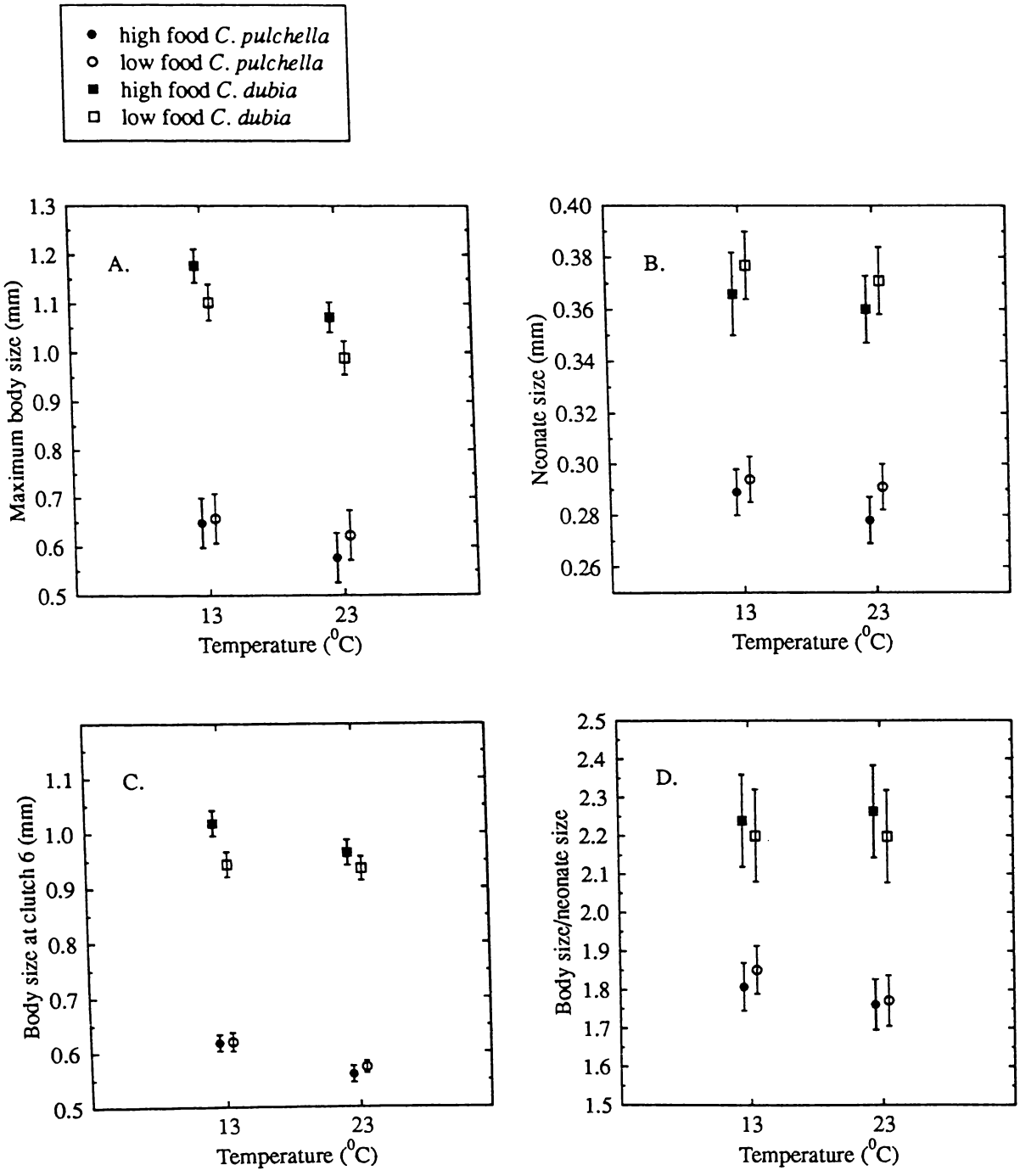

Figure 41.

Growth responses in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at high and low food levels at 13°C and 23°C. (A) Maximum body size reached, (B) neonate size at the start of the experiment, (C) body size at clutch six, (D) ratio of body size at clutch two to neonate size. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

Body size at clutch six

For *C. pulchella*, body size at clutch six was affected primarily by temperature, with animals at low temperature being significantly larger than those at the higher temperature. Food effects were negligible ($p = 0.254$). For *C. dubia* however, food effects were more influential than temperature on body size at clutch six, although both were highly significant. Animals were larger at low temperatures but only significantly so when at the high food regime.

Ratio of body size at clutch two to size at birth

As an indication of the amount of growth since birth, the body size/neonate size ratio was not significantly affected by regime in either species. *C. pulchella* showed a significant temperature response in this ratio ($p = 0.035$), with the amount of growth since birth being greater at 13°C than at 23°C. The effects of different food levels however, reduced the impact of temperature so that regime differences were non-significant. *C. dubia* show no significant response to temperature in body size/neonate size ratio, although, when compared to *C. pulchella*, it is clear that this species achieved a much greater body size, relative to its size at birth than did its cogener.

3.3.5 Indices of Growth, Reproduction, & Resource Allocation: TABLE 27, FIGURE 42

Relative egg size at first reproduction

Relative egg size was significantly influenced by both food and temperature in *C. pulchella*, but only by temperature in *C. dubia*. For *C. pulchella*, relative egg size was greater both at higher temperature and, within temperature regimes, at higher food levels (Table 27). However, regime differences were only significant at the 13°C:low food combination. For *C. dubia*, temperature had the same effect as in *C. pulchella*, i.e., relative egg size declined at low temperature, the effect being even more pronounced than in *C. pulchella*. Between species, the relative egg sizes of *C. pulchella* were significantly greater than those of *C. dubia*, at all food and temperature combinations.

Table 27: Results of 2 way ANOVA followed by Tukey multiple comparison tests on data in Figure 42 to show the effects of food and temperature level on **A.** relative egg size, **B.** egg length at first reproduction, **C.** body size at first reproduction, and **D.** mean lipid-ovary score in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (ie. across temperature-food regimes) are indicated by the same letter. Abbreviations as for Table 25. See Table 23 for details of food levels.

A. RELATIVE EGG SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.014	1	0.014	21.313	0.001
	Food	0.003	1	0.003	4.362	0.044
	Temp x Food	0.001	1	0.001	2.112	0.155
	Error	0.024	36	0.001		
C. dubia	Temp	0.020	1	0.020	36.888	0.001
	Food	0.000	1	0.000	0.003	0.954
	Temp x Food	0.000	1	0.000	0.315	0.578
	Error	0.019	35	0.001		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	ab	b	< .001
C. dubia	a	a	b	b	< .01

B. EGG LENGTH AT FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	464.539	1	464.539	3.876	0.057
	Food	62.512	1	62.512	0.522	0.475
	Temp x Food	552.377	1	552.377	4.609	0.039
	Error	4194.878	35	119.854		
C. dubia	Temp	3918.966	1	3918.966	21.73	0.001
	Food	250.047	1	250.047	1.387	0.247
	Temp x Food	64.236	1	64.236	0.356	0.554
	Error	6310.764	35	180.308		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	ab	abc	ac	< .05
C. dubia	a	a	b	ab	.001 < p < .05

C. SIZE AT FIRST REPRODUCTION:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.014	1	0.014	26.326	0.001
	Food	0.005	1	0.005	9.157	0.005
	Temp x Food	0.000	1	0.000	0.561	0.459
	Error	0.019	35	0.001		
C. dubia	Temp	0.016	1	0.016	12.905	0.001
	Food	0.008	1	0.008	6.323	0.017
	Temp x Food	0.000	1	0.000	0.341	0.563
	Error	0.045	36	0.001		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	ab	b	c	< .05
C. dubia	a	ab	b	b	.001 < p < 0.05

D. MEAN LIPID-OVARY SCORE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.588	1	0.588	11.901	0.001
	Food	5.249	1	5.249	106.225	0.001
	Temp x Food	0.007	1	0.007	0.132	0.719
	Error	1.779	36	0.049		
C. dubia	Temp	4.211	1	4.211	38.730	0.001
	Food	24.163	1	24.163	22.227	0.001
	Temp x Food	0.017	1	0.017	0.159	0.693
	Error	3.806	35	0.109		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	b	a	c	< .05
C. dubia	a	b	c	d	.001 < p = 0.05

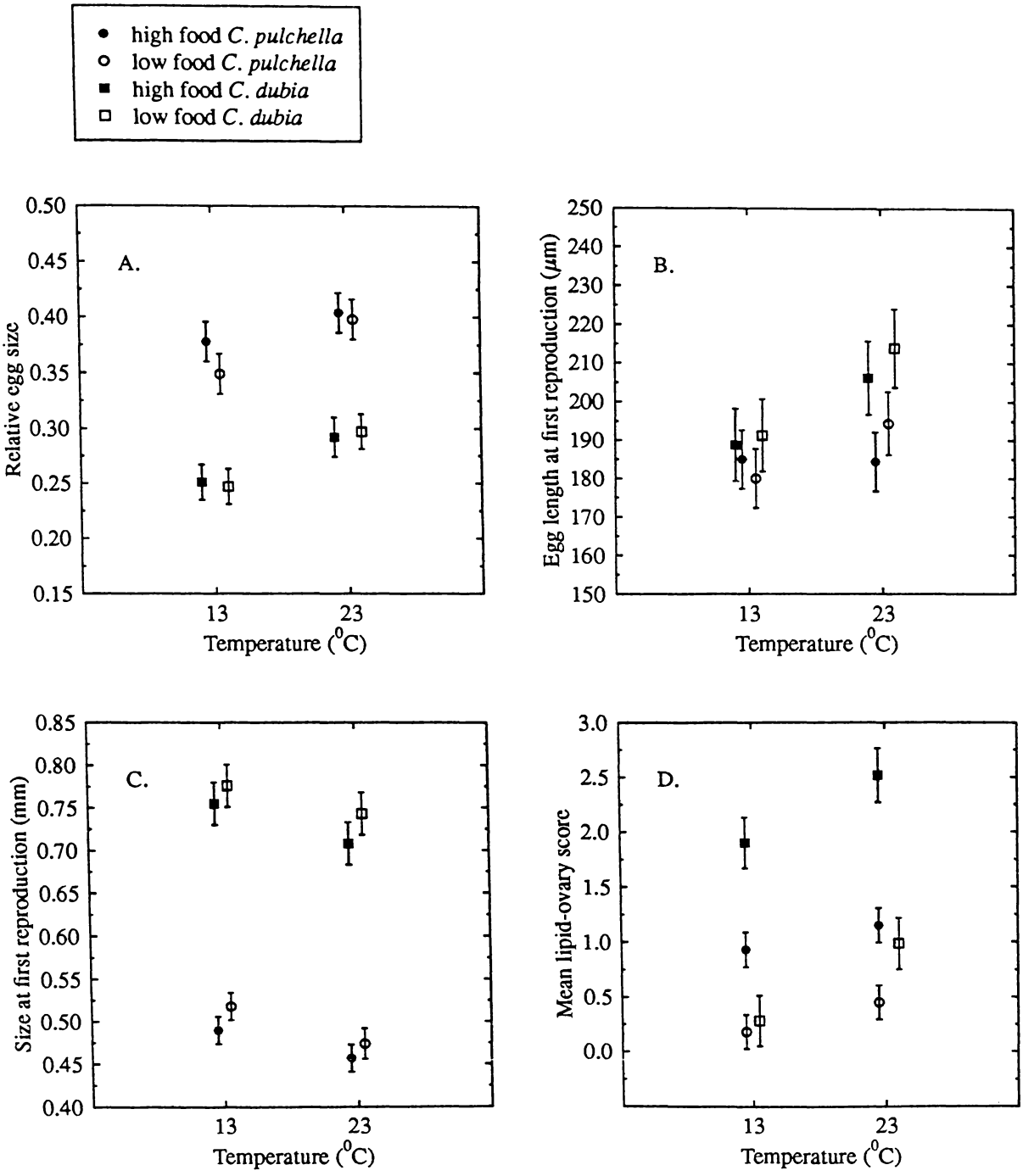

Figure 42.

Indices of reproductive performance and resource allocation in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at high and low food levels at 13°C and 23°C. (A) Relative egg size (egg length/body length) at first reproduction (B) egg length at first reproduction, (C) body size at first reproduction, (D) mean lipid-ovary score. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

Egg length at first reproduction

The response of first reproductive egg length was quite different for each species. In *C. pulchella*, regime (i.e., food x temperature) effects were significant, whereas in *C. dubia*, temperature was the only significant influence on egg length. In *C. pulchella,* the high temperature:low food regime was significantly different from the low temperature: low food regime, with eggs being smaller in the latter regime. However, neither food nor temperature effects alone were significant.

In *C. dubia*, animals at the low temperature also produced smaller eggs but the effect of food alone was significant. There were no significant differences between the two species in egg length at low temperature regimes but, at 23°C, *C. dubia* egg lengths were greater than those of *C. pulchella.*

Size at first reproduction

Both temperature and food had significant effects on body size at maturity in *C. pulchella*, with animals being significantly smaller at high temperature and, within temperature regimes, at high food. For *C. dubia*, the same result was obtained. Interestingly, low food levels at 23°C had much the same effect on size at first reproduction as high food levels at low temperature, and the difference between these two regimes was not significant. This was the case for *C. pulchella* also.

As with other size, or size dependent, variables, the differences between the two species were marked.

Lipid-Ovary Index

For both species LOI was significantly affected by both food and temperature, with low temperature and low food causing a marked reductions in lipid score. In *C. pulchella*, high food levels reduced the effect of low temperature to the extent that HH and LH regimes were not significantly different. At low food levels however, the effects of temperature were enhanced, so that HL and LL regimes were (just) significantly different ($p = 0.05$).

In *C. dubia*, the effects of temperature and food level were even more pronounced than for *C. pulchella*, with 23°C:high food producing the highest lipid scores and

13°C:low food the lowest. Between species, lipid scores in *C. dubia* reared at low food levels were generally similar to those of *C. pulchella* at all food levels. At high food levels though, *C. dubia* stored much more visible lipid than did *C. pulchella.*

3.3.6 Indices of Egg Production: TABLE 28, FIGURE 43

Total number of eggs to day 30

For both species egg production at low temperature was significantly reduced below that at 23°C, a consequence of the extended intermoult period at 13°C. For *C. pulchella*, whilst temperature effects were highly significant ($p < 0.001$), food effects were negligible. For *C. dubia* though, both food and temperature effects were highly significant ($p < 0.001$), and egg production was lower both at low temperature and, within each temperature regime, at low food. As was the case with size at first reproduction, egg production at low food levels at 23°C was much the same as at the high food level and 13°C.

Total egg production to clutch six

When the effect of temperature on development time was accounted for by taking clutch six (rather than day 30) as an end point for total egg production, temperature was no longer a significant influence on total fecundity in *C. pulchella.* For this species, food effects were also non-significant and there was no difference between regimes in egg production.

For *C. dubia* however, temperature had a significant effect ($p < 0.02$) on egg production, even after accounting for prolongation of development time at low temperature (mean at 13°C = 29.8 eggs; mean at 23°C = 34.5 eggs). Food effects, however, were highly significant, so that at high and low temperature, animals produced more eggs at the high food than at the low food level. Differences between the same food level at different temperatures were, however, not significant.

Between species, egg production in *C. dubia* was significantly higher than in *C. pulchella,* at all temperatures and food levels.

Table 28: Results of 2 way ANOVA followed by Tukey multiple comparison tests on data in Figure 43, to show the effects of food and temperature level on **A.** total number of eggs produced to day 30, **B.** total number of eggs produced to clutch six, **C.**mean egg volume (clutches 1-6), and **D.** mean clutch volume in *Ceriodaphnia*. Means that are not significantly different at $p < 0.05$ within rows (ie. across temperature-food regimes) are indicated by the same letter. Abbreviations as for Table 25. See Table 23 for details of food levels.

A. TOTAL NUMBER OF EGGS TO DAY 30:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	1800.000	1	1800.000	44.905	0.001
	Food	2.469	1	2.469	0.062	0.806
	Temp x Food	0.099	1	0.099	0.002	0.961
	Error	1162.444	29	40.084		
C. dubia	Temp	16421.063	1	16421.063	216.459	0.001
	Food	9566.784	1	9566.784	126.108	0.001
	Temp x Food	2415.168	1	2415.168	31.836	0.001
	Error	2579.311	34	75.862		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	b	b	< .001
C. dubia	a	b	b	c	< .01

B. TOTAL NUMBER OF EGGS PRODUCED TO CLUTCH SIX:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	11.025	1	11.025	0.398	0.532
	Food	34.225	1	34.225	1.236	0.274
	Temp x Food	11.025	1	11.025	0.398	0.532
	Error	996.700	36	27.686		
C. dubia	Temp	215.947	1	215.947	6.259	0.017
	Food	2652.488	1	2652.488	76.880	0.001
	Temp x Food	8.077	1	8.077	0.234	0.632
	Error	1207.556	35	34.502		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.6 NS
C. dubia	a	b	a	b	< .001

C. MEAN EGG VOLUME:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.022	1	0.022	1.443	0.238
	Food	0.001	1	0.001	0.086	0.771
	Temp x Food	0.096	1	0.096	6.272	0.017
	Error	0.554	36	0.015		
C. dubia	Temp	0.002	1	0.002	0.027	0.871
	Food	0.040	1	0.040	0.580	0.451
	Temp x Food	0.064	1	0.064	0.924	0.343
	Error	2.513	36	0.070		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> .06 NS
C. dubia	a	a	a	a	> .62 NS

D. MEAN CLUTCH VOLUME:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.291	1	0.291	0.505	0.482
	Food	0.184	1	0.184	0.320	0.575
	Temp x Food	0.751	1	0.751	1.306	0.261
	Error	20.709	36	0.575		
C. dubia	Temp	29.148	1	29.148	3.950	0.055
	Food	358.708	1	358.708	48.605	0.001
	Temp x Food	0.036	1	0.036	0.005	0.944
	Error	258.301	35	7.380		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.5 NS
C. dubia	a	b	a	b	< .01

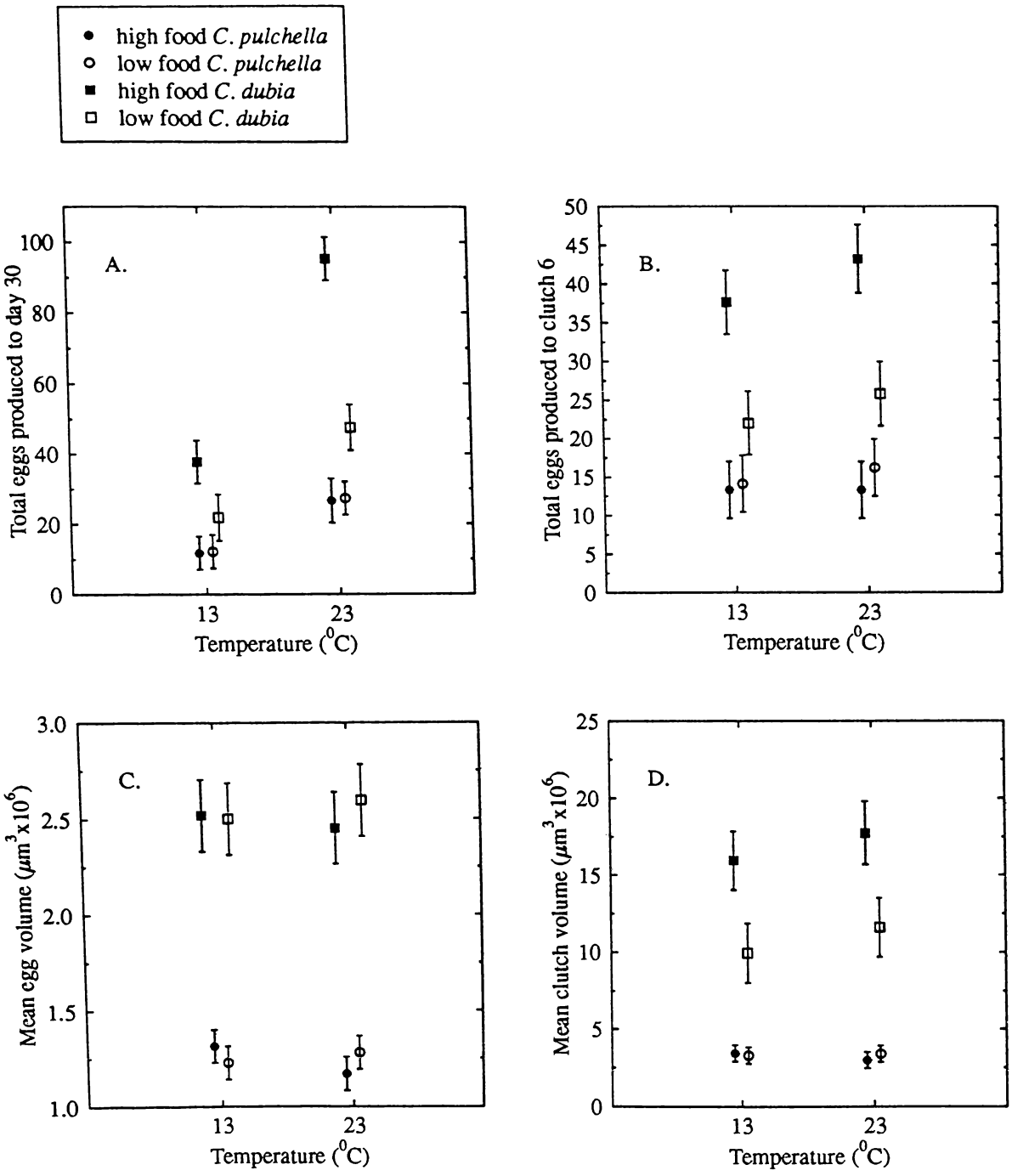

Figure 43.

Egg production in *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at high and low food levels at 13°C and 23°C. (A) Total number of eggs produced to day 30, (B) total number of eggs produced to clutch six, (C) mean egg volume (clutches 1 - 6), (D) mean clutch volume (clutches 1-6). Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

Mean egg volume

Neither food nor temperature had any significant effect on egg volume, in either species. However, egg volumes in *C. dubia* were approximately twice as large as those in *C. pulchella*. There was a tendency for eggs to be larger at the high temperature:low food regime in *C. dubia* and at the low temperature:high food regime in *C. pulchella*.

Mean clutch volume

Mean clutch volume, which incorporates both mean clutch size and egg volume, was significantly affected by food level in *C. dubia*, but not in *C. pulchella*. For both species, temperature effects were not significant. In *C. dubia*, the highest clutch volumes were associated with the highest food levels. There was also a tendency for larger clutch volumes at the higher temperature ($p = 0.055$). As differences in egg volume were nonsignificant in this species, regardless of regime, the observed variations in clutch volume primarily reflect the effects of food level on clutch size.

3.3.7 Aspects of Body Size and Nutrition in Offspring of *Ceriodaphnia*: TABLE 29, FIGURE 44

Body size

Offspring size at birth was significantly affected by both food and temperature in *C. dubia* ($p < 0.001$), with neonates being smaller both at high temperature and, within a temperature regime, at high food. This was similar to the tendency observed in maternal size at birth (Fig. 41). For *C. pulchella*, the response was much the same, and neonates were significantly smaller at high temperature (mean at 23°C = 0.279; mean at 13°C = 0.292, $p < 0.01$) and larger at low food (at least at 23°C). This contrasting effect meant that only the HH regime was significantly different from other regimes in neonate body size produced.

Mean lipid score

For both species the lipid score of offspring was signicantly affected by food level, with animals from mothers reared at low food having significantly less lipid than those from mothers at high food levels. For *C. pulchella*, temperature effects were also significant, with animals at 13°C being better supplied with lipid than those at 23°C. For

Table 29: Results of 2 way ANOVA followed by Tukey multiple comparison tests on data in Figure 44 to show the effects of food and temperature level on **A.** offspring body size (clutches 1-5), **B.** offspring lipid score (clutches 1-5) and C. ratio of offspring size to size of the primiparous adult in *Ceriodaphnia*, Means that are not significantly different at $p < 0.05$ within rows (ie. across temperature-food regimes) are indicated by the same letter. Abbreviations as for Table 25. See Table 23 for details of food levels.

A. BODY SIZE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.001	1	0.001	23.623	0.001
	Food	0.000	1	0.000	6.719	0.014
	Temp x Food	0.000	1	0.000	7.292	0.011
	Error	0.002	32	0.000		
C. dubia	Temp	0.004	1	0.004	104.274	0.001
	Food	0.001	1	0.001	40.754	0.001
	Temp x Food	0.000	1	0.000	3.990	0.054
	Error	0.001	33	0.000		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	b	b	b	< .01
C. dubia	a	b	c	d	< .05

B. MEAN LIPID SCORE:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.365	1	0.365	15.195	0.001
	Food	3.219	1	3.219	134.130	0.001
	Temp x Food	0.001	1	0.001	0.062	0.806
	Error	0.768	32	0.024		
C. dubia	Temp	0.098	1	0.098	3.175	0.083
	Food	2.037	1	2.037	66.254	0.001
	Temp x Food	0.027	1	0.027	0.873	0.356
	Error	1.107	36	0.031		

Table of differences

	HH	HL	LH	LL	p
C. pulchella	a	b	c	b	< .05
C. dubia	a	b	a	b	< .001

C. OFFSPRING BODY SIZE/SIZE OF PRIMIPAROUS ADULT:

Analysis of Variance

	Source	SS	DF	MS	F	p
C. pulchella	Temp	0.005	1	0.005	4.717	0.037
	Food	0.000	1	0.000	0.000	0.985
	Temp x Food	0.000	1	0.000	0.040	0.843
	Error	0.040	36	0.001		
C. dubia	Temp	0.001	1	0.001	0.967	0.332
	Food	0.000	1	0.000	0.560	0.459
	Temp x Food	0.001	1	0.001	0.819	0.371
	Error	0.029	36	0.001		

Probability Table

	HH	HL	LH	LL	p
C. pulchella	a	a	a	a	> 0.350 NS
C. dubia	a	a	a	a	> 0.550 NS

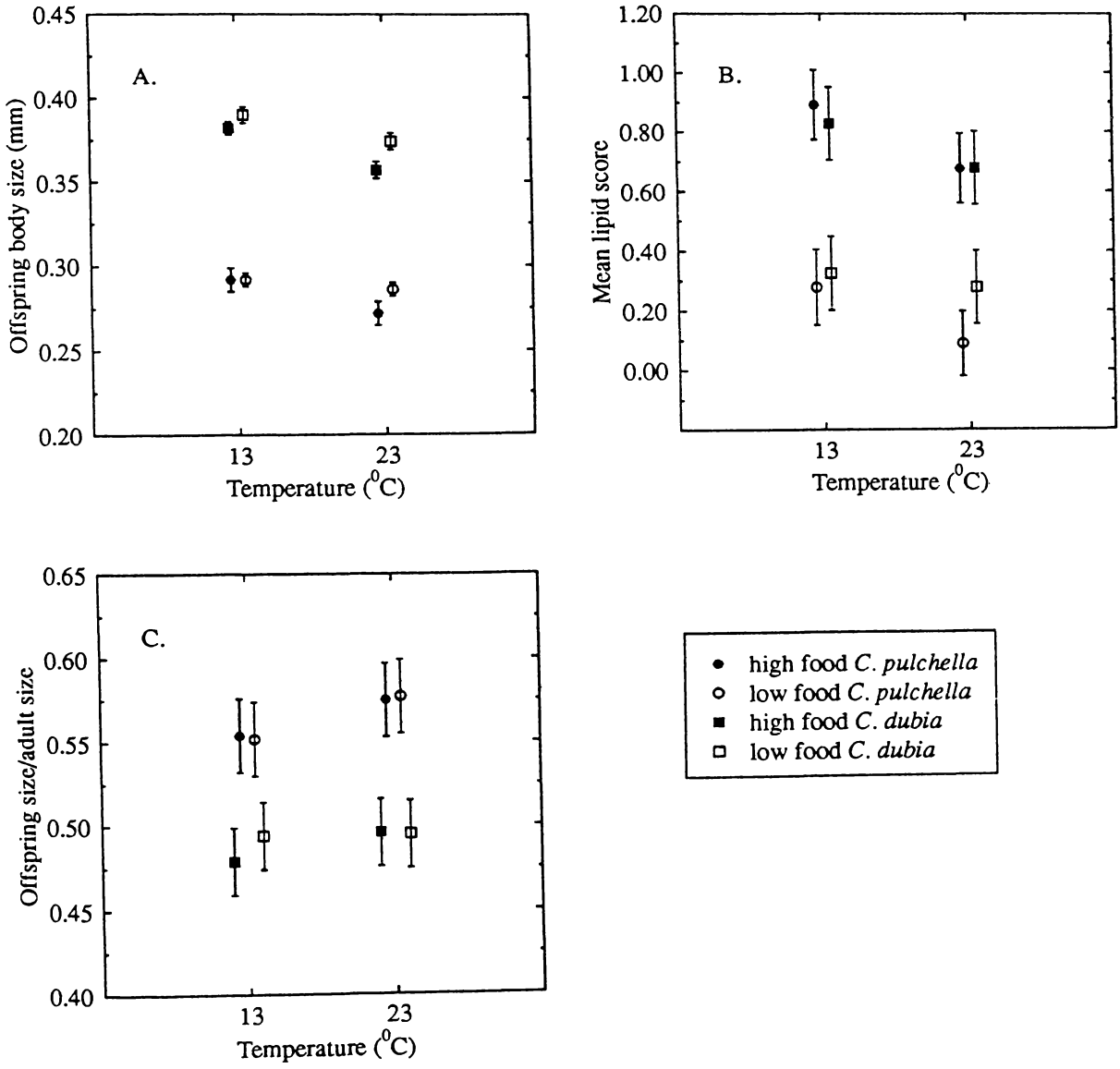

Figure 44.

Aspects of body size and nutrition in offspring of *Ceriodaphnia pulchella* and *Ceriodaphnia dubia*, grown at high and low food levels at 13°C and 23°C. (A) Offspring body size, (B) offspring lipid score, (C) ratio of offspring size to size of the primaparous adult. Vertical bars are 95% confidence intervals. See Table 23 for details of food regimes.

this species, low food appeared to be the predominant influence on neonate lipid, since the differences between high and low temperature low food regimes were not significant. For *C. dubia* at a single food level, temperature differences were not significant.

Within each temperature-food regime, species differences in neonate lipid were not significant.

Ratio of offspring body size to size of the primiparous adult

The ratio of offspring body size to maternal size was largely unaffected by food or temperature. *C. pulchella* produced relatively larger neonates at high temperature ($p = 0.037$) but regime effects were not significant.

For *C. dubia,* neither temperature nor food effects were significant and, for this species also, regime effects were not significant.

3.3.8 Relationship of Clutch Volume to Body Length

On the basis of the overlap in the 95% confidence interval of the regression coefficient, the slope of the regression line relating clutch volume and body length did not vary significantly between regimes in *C. pulchella* (Table 30, Fig. 45). In *C. dubia* however, the rate at which clutch volume increased with increasing body length was significantly lower in the 13°C:low food regime than in animals reared at 23°C and high food. When the data for each species are pooled on regime (Table 31, Fig. 46), and the regression slopes then compared (Neter *et al.* 1989), the rate of clutch volume increase is significantly higher in *C. dubia* than in *C. pulchella* ($F = 21.45$, $p < 0.001$). In other words; *C. dubia* increases the amount of egg material carried, proportional to body length, more rapidly than does *C. pulchella.*

3.3.9 Survival of Offspring from Different Temperature-Food Regimes

There was a marked difference between species in the response of offspring from different regimes to starvation (Fig. 47). When removed to a non-enriched medium (daphnid dilution water) percentage survival of *C. pulchella* neonates was higher at both HH and LL regimes, whereas neonates from HL and LH regimes had much the same survival success, regardless of species. High temperature reduced percentage survival markedly in both species, with no neonates surviving past the 27th day of starvation. At

Table 30: Regression equations relating clutch volume (cl.vol.) to body size (bs) in *Ceriodaphnia* grown at different temperature-food regimes. The general form of the regression is given by log cl.vol. = a + b logbs. The standard error and 95% confidence interval (CI) for the regression coefficient, b, is given in each case, together with values of F, p, and R^2. See Table 23 for details of food regimes. Complete results are given on floppy disk at the back of this volume.

C. pulchella

1. **High food, 23°C**

log cl.vol. = 3.406 + 3.404 log bs
SE of b = 0.459 CI of b = 0.770 R^2 = 0.540
n = 47 F = 54.957 p < 0.001

2. **High food, 13°C**

log cl.vol. = 3.497 + 3.875 log bs
SE of b = 0.552 CI of b = 0.925 R^2 = 0.502
n = 49 F = 49.355 p < 0.001

3. **Low food, 23°C**

log cl.vol. = 3.032 + 3.034 log bs
SE of b = 0.562 CI of b = 0.939 R^2 = 0.323
n = 60 F = 29.109 p < 0.001

4. **Low food, 13°C**

log cl.vol. = 2.968 + 3.299 log bs
SE of b = 0.779 CI of b = 1.305 R^2 = 0.245
n = 53 F = 6.610 p < 0.001

C. dubia

1. **High food, 23°C**

log cl.vol. = 3.412 + 4.657log bs
SE of b = 0.341 CI of b = 0.570 R^2 = 0.761
n = 59 F = 186.178 p < 0.001

2. **High food, 13°C**

log cl.vol. = 3.082 + 3.701 log bs
SE of b = 0.310 CI of b = 0.518 R^2 = 0.709
n = 59 F = 142.444 p < 0.001

3. **Low food, 23°C**

log cl.vol. = 2.920 + 4.123log bs
SE of b = 0.646 CI of b = 1.079 R^2 = 0.406
n = 59 F = 40.676 p < 0.001

4. **Low food, 23°C**

log cl.vol. = 2.602 + 3.998 log bs
SE of b = 0.506 CI of b = 0.847 R^2 = 0.292
n = 56 F = 23.699 p < 0.001

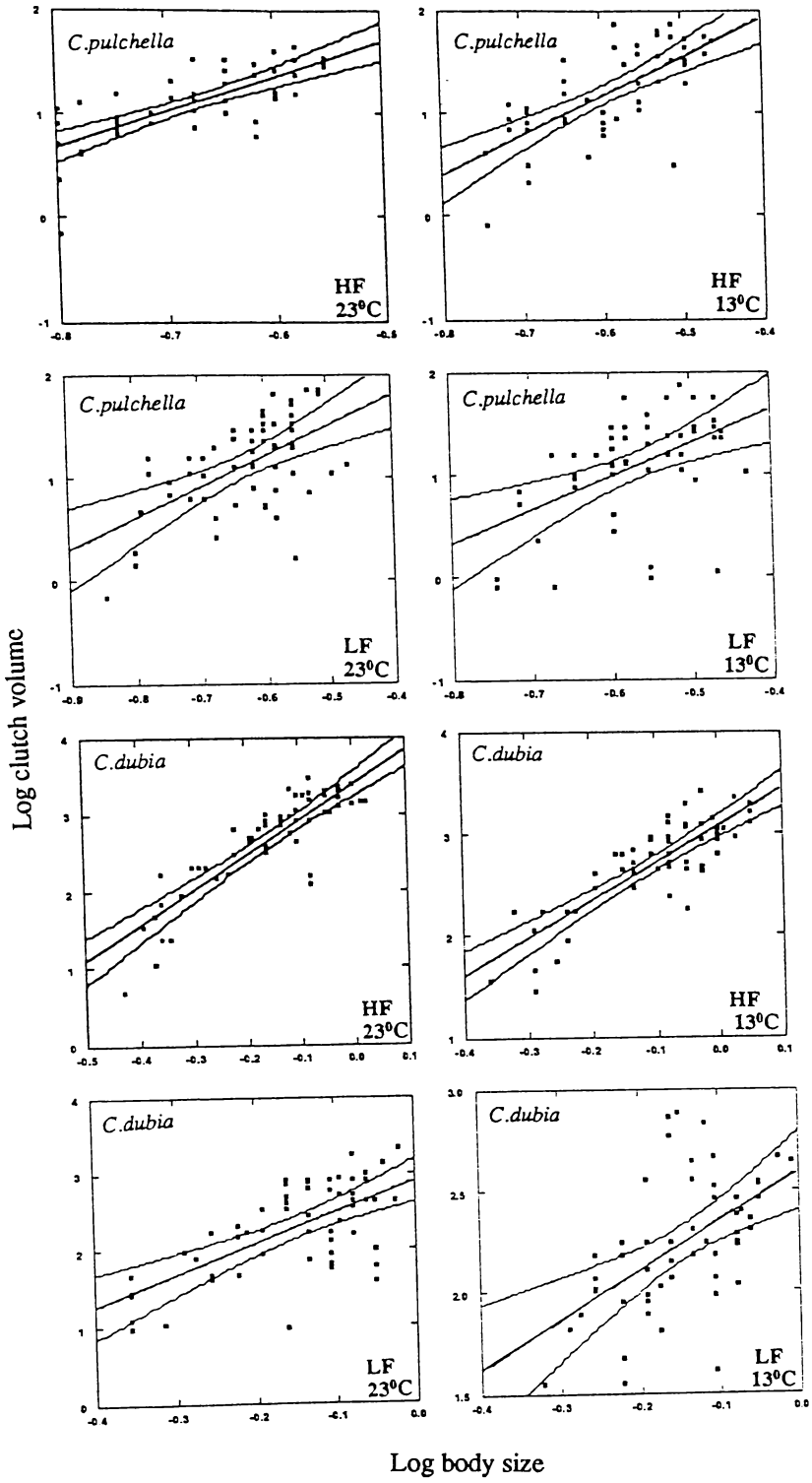

Figure 45.
The log - log relationship of clutch volume to body length in *Ceriodaphnia* grown at different food-temperature regimes . HF=high food. LF = low food. See table 23 for details of food levels.

Table 31: Regression equations relating clutch volume (cl.vol.) to body size (bs) in *Ceriodaphnia* grown at different temperature-food regimes, but pooled for regime. The general form of the regression is given by log cl.vol. = a + b logbs. The standard error and 95% confidence interval (CI) for the regression coefficient, b, is given in each case, together with values of R^2, and the ANOVA for each regression. Abbreviations as for Table 25. Complete results are given on floppy disk at the back of this volume.

1. ***C. pulchella***

log cl.vol. = 2.848 + 2.792 log bs
SE of b = 0.289 CI of b = 0.478 R^2 = 0.308

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	12.749	1	12.749	93.618	< 0.001
Residual (error)	28.191	207	0.136		

2. ***C. dubia***

log cl.vol. = 3.046 + 4.036 log bs
SE of b = 0.253 CI of b = 0.418 R^2 = 0.521

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	37.228	1	37.228	253.840	< 0.001
Residual (error)	33.878	231	0.147		

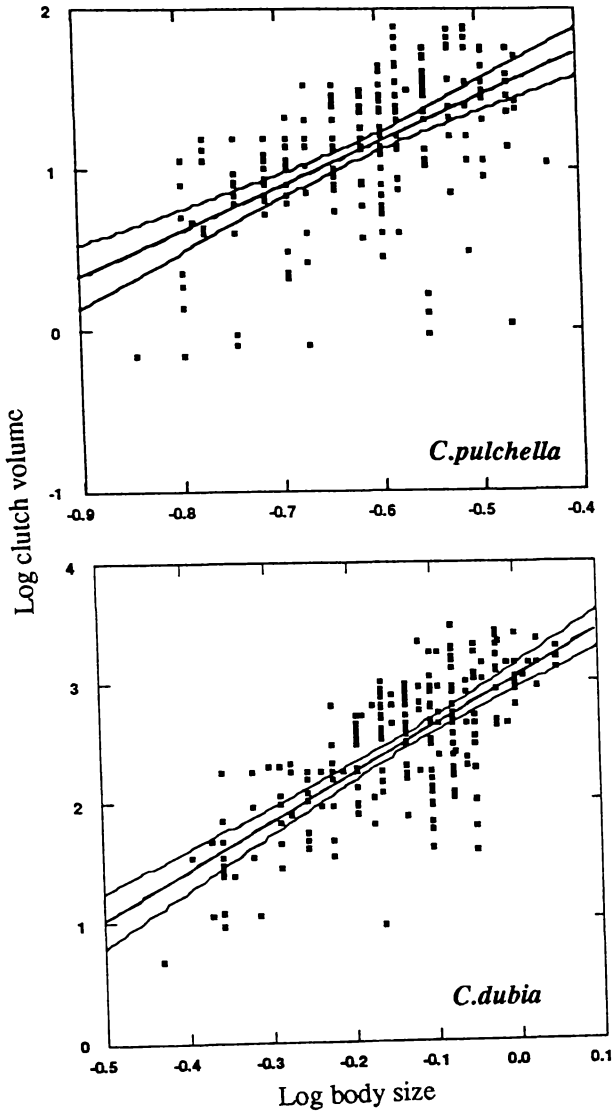

Figure 46.
The log - log relationship of clutch volume to body length in *Ceriodaphnia*. Pooled data from four food-temperature regimes.

low temperature, survival of offspring was more than doubled, except for *C. dubia* from low food levels, where all offspring were dead by day 51.

Regardless of maternal history some *C. pulchella* offspring went on to produce eggs despite starvation (Table 32). Time taken to produce the first clutch was, however, very much longer when starved than otherwise (Table 32). In addition, a number of animals also moulted into the adult body form but failed to produce eggs. From those that produced an egg (clutch size consistently = 1), viable neonates were released in all cases at low temperature, although not always at high temperature (Table 32). *C. pulchella* produced an extra juvenile instar on only one occasion (maternal history of HH).

The response of *C. dubia* to starvation was much different. No starved offspring produced eggs or moulted into an adult body form. Of those that lived past the third instar, all produced a fourth (extra) juvenile stage.

Table 32: Reproductive and growth characteristics of *Ceriodaphnia* offspring under starvation conditions. Age at maturity for non starved animals is given as a comparison. Temperature-food regimes are as defined in Table 25.

Species	Maternal Regime	No reaching adult instar*	No. producing eggs	No. producing viable young	Percentage with 4 pre-adult instars**	Mean no. of days to adult: starved	Mean no. of days to adult: not starved
C. pulchella	HH	4	4	1	20	14	3.91
	HL	7	5	4	0	14	4.11
	LH	7	1	1	0	33	8.45
	LL	5	2	2	0	35.5	8.34
C. dubia	HH	0	-	-	100	-	3.15
	HL	0	-	-	100	-	3.65
	LH	0	-	-	100	-	7.10
	LL	0	-	-	100	-	7.20

* As defined by body shape with brood pouch
** of those living long enough to do so
n = 8 in each case

3.3.10 Summary

When examining the differences in species specific response in growth and reproduction to different food and temperature levels, the principal findings were as follows:

1. In both species, temperature was the primary influence on development time, but *C. dubia* was also influenced by low food level, which significantly prolonged time to the sixth adult instar at low temperature.
2. Both the maximum adult body size and the size at the sixth adult instar were significantly reduced by high temperature in both species, but *C. dubia* was also sensitive to low food levels which acted similarly to high temperature. In contrast, the size of the primiparae was significantly larger at low food levels in both species.
3. Adult lipid stores were significantly reduced by low food and low temperature, but both the absolute and the percentage reduction was far greater in *C. dubia.*
4. Fecundity was significantly affected by food level in *C. dubia* but not in *C. pulchella* (low food = lower fecundity). However, in both species, neither temperature nor food had any effect on egg size.
5. In both species low temperature increased longevity. However, within the 13°C regime, length of life was increased by low food in *C. dubia*, and by high food in *C. pulchella.*
6. In both species, offspring body size was generally reduced at high temperature but increased at low food levels. Low food also acted to reduce offspring lipid.
7. As a consequence of rather static egg volumes and a lack of response to regime in the size at first reproduction, relative neonate size was similar across all food-temperature combinations.
8. *C. dubia* increased clutch volume with body size more rapidly than did *C. pulchella*, but this rate was significantly reduced by low food and low temperature.

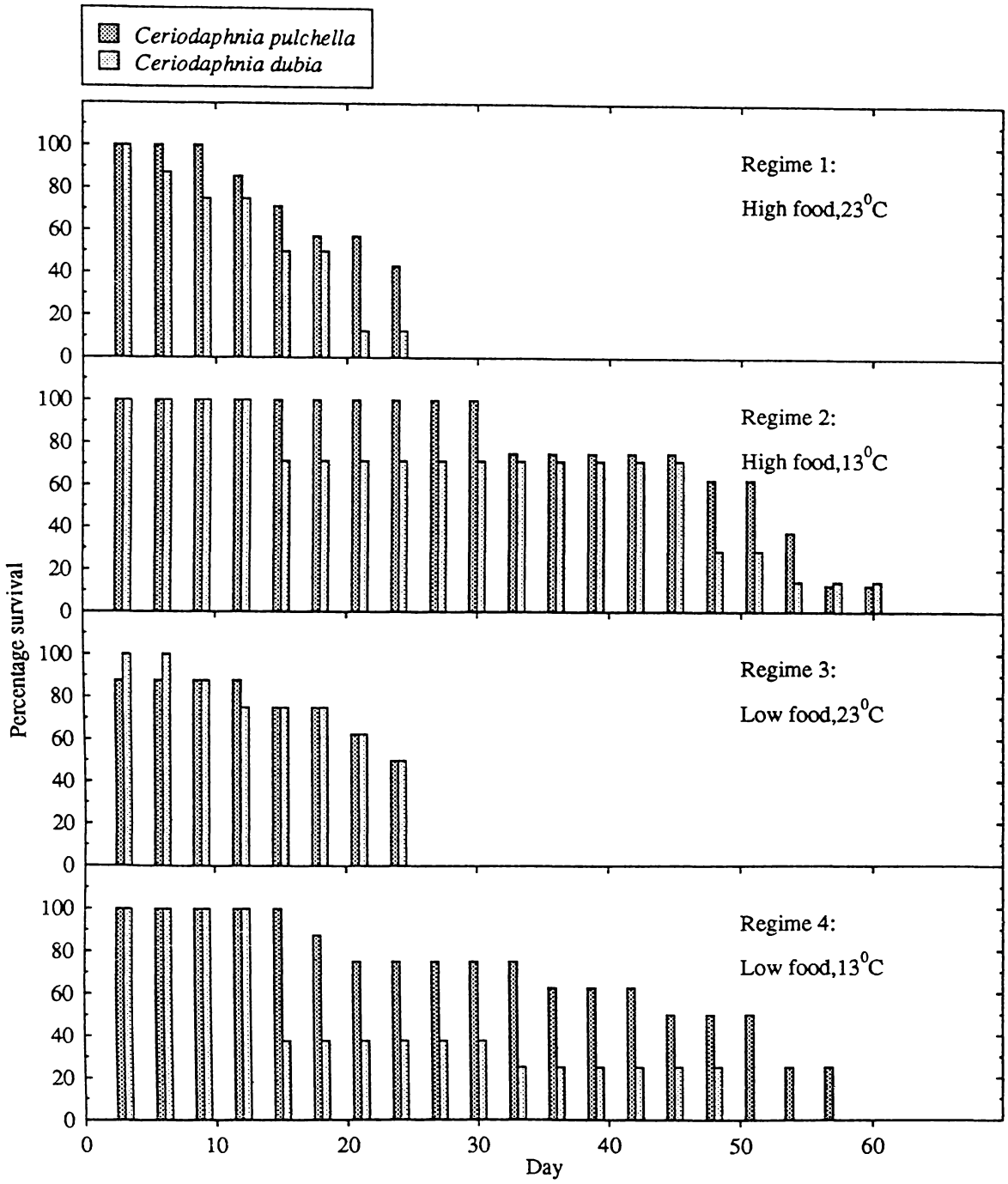

Figure 47.

Survival of offspring of *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* grown at different food and temperature regimes and maintained with no provided food (at the acclimated temperature in each case). See Table 23 for details of food regimes.

3.4 DISCUSSION

Before considering the effect of food level or temperature on the life history features of *C. pulchella* and *C. dubia* it is worth firstly considering the obvious morphological differences between the two species. As shown by this and previous laboratory studies (Greenwood 1987), the adult body sizes of *C. dubia* are more variable, but generally larger, than those of *C. pulchella*. *C. dubia* can vary from being equal in length to intermediate sized *C. pulchella*, to almost twice the latter species' maximum body size of about 0.7 mm. This genetically determined disparity has ecological implications for these species. As discussed in the previous chapter, *C. dubia*, by virtue of its large size, produced larger eggs and neonates, and potentially has a much higher fecundity than its smaller congener. Moreover, its growth rates are higher, and its development times at lower temperature shorter, than those of *C. pulchella*.

In the absence of strong size selective predation, these features could be expected to favour *C. dubia* ecologically when it coexists with *C. pulchella*. However, as is shown by the results in this Chapter, increases in food and temperature affect growth and development in these species quite differently. In *C. dubia*, high food increased the growth increment made per instar, while high temperature had the opposite effect. For *C. pulchella*, food effects were negligible (Fig. 37).

As was suggested by the field studies, body size (at maturity, clutch six and maximum) was strongly influenced by temperature and, in both species, animals were smaller at 23°C than at 13°C, regardless of instar number. As discussed in Part Two, Chapter Five, temperature has frequently been associated with a decline in body size, both in field and laboratory populations of Cladocera (Green 1966; Gophen 1976; Culver 1980; Stirling and McQueen 1986). However, the effects of food level were not assessed in these studies, even though food limitation has also been shown to reduce adult body size in Cladocera, in addition to prolonging the time to maturity (as reviewed by Duncan 1989).

While the effects of temperature on body size appear to be consistent with animal age, and between species, this was not the case for food level. In both species body size at maturity was larger at lower food levels, so that animals were longest when reared in

colder, more food limited, conditions. The body size response in later instars was not in accordance with that in the primiparae however. Food effects on body size at the sixth and final adult instars were not significant for *C. pulchella,* but *C. dubia* were significantly larger at high food levels. This apparent incongruity may be explained by two other body size aspects.

Firstly, there was a tendency for neonates to be larger at low food levels, and this effect may continue through until the first reproductive instar. It may be that low food levels act to reduce body size only with increasing age and time spent under food limiting conditions, and then only for the larger species *C. dubia.* Secondly, as discussed in Chapter Two, apparent increases in body 'size' at low food levels may reflect the use of body length rather than mass to assess this parameter, and animals may be longer but, in fact, lighter when reared under food limiting conditions (Tessier and Consolatti 1991). While this may have been the case, the response to food level of *C. dubia* body size at the sixth and final adult instar was typical of that expected from what is known of Cladocera (i.e., larger body size at higher food). Either the neonates and primiparous adults of both species are longer but lighter at low food (as suggested by Tessier and Consolatti (1991) for *Daphnia*), and body length only later accords with mass, or the production of larger neonates at low food is a real phenomenon, and the body length-food level response is reversed quite late in life.

The measurements of body length of the offspring from animals at different regimes support the view that, in both *C. dubia* and *C. pulchella*, the production of larger neonates at low food is a characteristic of their respective life histories. Thus, the results here indicate that although low food levels promote the production of larger neonates, food limited animals 'lose ground' over a period of time, so that by later adult instars they are smaller than individuals reared under more favourable nutritional conditions. These smaller food limited adults continue to produce larger neonates. However, it is clear that, at least for *C. dubia*, the production of a smaller neonate does not preclude its later rapid growth to a larger body size.

Curiously, given the relationship between offspring body size and low food, neither egg lengths, nor egg volumes, were significantly larger under food limited conditions, although there was a tendency for eggs to be larger at low food, particularly at high temperature. The production of larger neonates when food resources are limited is a life history response that appears to be typical of many Cladocera (Gliwicz and Guisande 1992; Guisande and Gliwicz 1992), and is seen as one solution in a trade-off between offspring size and number. Tessier and Consolatti (1989), for example, found that at both high and low resource levels, fitness increases with size at birth but this fitness advantage is greater at low food. Lynch and Ennis (1983) came to a similar conclusion in their investigation of maternal inheritance effects in *Daphnia pulex*. Both *C. pulchella* and *C. dubia*, but particularly the latter, appear to shift maternal investment toward the production of fewer, larger, young at low food levels, and this shift is enhanced by high temperatures. Gliwicz and Guisande (1992) found a similar shift in *Daphnia*, giving evidence that this response is environmental, and not the result of genetic change, as may occur with clonal succession.

The production of larger young in response to declining resources is likely to be advantageous with respect to starvation resistance, since larger neonates should be better supplied with maternal reserves (Tessier *et al.* 1983; Tessier and Consolatti 1989). However, in my study the indices of visible lipid in offspring did not necessarily support this, since neonates from low food regimes had significantly lower lipid scores than those from high food levels. Gliwicz and Guisande (1992) suggest that there is a critical food level at which individuals must make a 'choice' about how best to divide their reproductive allocation or, indeed, whether to reproduce at all. The largest species, *C. dubia*, certainly seems to shift maternal investment towards the production of fewer, larger, young at low food levels, at least at 23°C, but it seems that the magnitude of the response may not be large enough to endow the young with a greater absolute energy store. An investigation of maternal investment at an intermediate food level might shed more light on the true nature of this response.

Temperature also appears to be a strong influence on lipid storage in adults of both species and may alter the pattern of response in allocation of energy reserves to offspring. Both adults and offspring of *C. pulchella* have greater lipid reserves at high food but, in adults, less lipid is stored at lower temperature for any given food level. In neonates, the pattern is different, and neonates from low temperature have the highest lipid levels. Thus, at low temperature, *C. pulchella* adults have less lipid than at high temperature but apparently allocate relatively more of it to the neonate. A similar response was observed for *C. dubia*, but in this species the temperature effect on neonates was not significant. To my knowledge, this temperature response in maternal - offspring lipid allocation has not been recorded before in Cladocera. It may be related to the production, at low temperature, of a larger neonate which demands a greater relative investment, even if the absolute amount of maternal fat passed to the young is lower than for well fed animals.

C. pulchella was much less variable in total fecundity than *C. dubia*, and for most life history features, particularly those associated with fecundity or body size, *C. pulchella* was much less influenced by low food than *C. dubia*. This partly reflects the fact that body sizes in *C. pulchella* vary over a much more restricted range than in *C. dubia*, and its potential fecundity is therefore lower. However, even with this constraint, *C. pulchella* appears to maintain a rather more constant reproductive effort regardless of food or temperature level. In *C. dubia*, a high degree of variability in fecundity was the result of strong responses to both changing temperature and food level, the former acting through body size (larger at low temperature).

Thus, while *C. dubia,* in terms of potential fecundity, is far the superior at high food levels, under food limited conditions the two species are not very different, despite the fact that there is always a large size differential between them. This applies to reserves of lipid also. *C. dubia* has larger stores of energy in the form of lipid at high food levels, but when food levels decline the two species are similar, particularly at low temperature. Decreasing food concentrations and increasing body size have been found to increase the proportion of assimilated carbon lost to respiration in *Bosmina* (Urabe 1991), and this seems likely to be the case for *Ceriodaphnia* in this study also. This has implications for

C. dubia's ability to compete under resource limited conditions, as appear to occur in Lake Mangakaware. Certainly, *C. dubia* has the ability to achieve higher population growth rates (r) than *C. pulchella*, given its greater fecundity and shorter development times, but it loses most of this advantage when food levels are low. Moreover, it has a larger body size and thus a higher absolute metabolic requirement than the smaller *C. pulchella*. In addition, in *C. dubia*, development time is prolonged more by low food than in *C. pulchella*, although the former species still retains a clear developmental advantage at 13°C.

The view that smaller bodied cladoceran species are favoured under food limited conditions is widely held (Threlkeld 1976; Lynch 1980a; De Mott and Kerfoot 1982; Romanovsky and Feniova 1985; De Mott 1989). Tessier and Goulden (1987), for example, found that net production amongst five daphnid species (including *C. reticulata*) depended on food level, and that while larger bodied animals had greater exploitative ability at high food, production rates were depressed more severely at low food than those of smaller species. Thus, under chronic food limitation, small species are not exploitatively inferior. Tessier and Goulden (1987) also suggest that the more food resources fluctuate, the more difficult it becomes to predict the relative success of a species based on size. With significant temporal and spatial patchiness, other factors, such as the speed of response to increased food level, and the ability to persist when starved, determine the ultimate competitive outcome between morphologically similar species.

The response of *Ceriodaphnia* neonates to starvation in this study supports the view that the smaller of the two species is the most resistant to decreases in food level. Regardless of maternal history, the offspring of *C. pulchella* females performed better under starvation conditions than the offspring of *C. dubia*, not only with respect to survival, but in their ability to grow and, in some cases, to produce eggs. In contrast, no *C. dubia* neonates managed to reach adulthood when starved, and all that lived long enough produced an extra juvenile instar. For both species, relatively long starvation times seem to suggest that true food deprivation had not occurred. Non-sterile water with a high content of dissolved organic compounds is a suitable environment for the growth of

bacteria and small heterotrophic flagellates (Salonen and Hammar 1986) which are a potential source of food. Moreover, organic compounds may be utilized directly (Porter *et al.* 1982). Differences in the abilities of these two species to utilise 'foreign' food sources may account for some of the differences observed between them under 'starvation' conditions.

A maternal history of high food did not seem to ensure better survival in starved neonates. Rather, high temperature reduced starvation resistance much more noticeably, presumably as a result of the higher respiratory costs incurred at 23°C. This is contrary to the findings of Stuchlíková (1991), who recorded better starvation resistance amongst *Daphnia* neonates previously exposed to low levels of resource availability, and of Gliwicz and Guisande (1992), who found that the larger neonates of food limited mothers were better able to survive periods of starvation.

The production of additional juvenile instars in Cladocera has the effect of considerably prolonging the length of time in pre-reproductive stages (Taylor 1985). Staples (1984) found that in *C. dubia*, this phenomenon appeared to be associated with the smaller growth increments made per moult in the first three instars of life. Well fed animals made greater growth increments per instar and reached a larger body size sooner than when food limited. She related this delay in reproduction to a requirement for a certain body size in the adolescent instar. The results here indicate that, in *C. dubia*, temperature appears to be critical also, with animals at higher temperature reproducing at a smaller size regardless of food level. Because of the temperature effect on body size, extra juvenile moults result in larger first reproductive body size at low, but not at high, temperature. In fact, the incidence of fourth instar juveniles was slightly higher in the high temperature:low food regime than at low temperature and low food, despite the fact that animals tended to be larger at 13°C.

The prolongation of the juvenile period at low food, so that primiparae reach some (undetermined) critical body size, may be more closely related to longer time taken to accumulate energy reserves sufficient for reproduction, than to body size *per se*. As shown by Kryuchkova (1973) and Bottrell (1975a,b), moulting rate in Cladocera is influenced

mainly by temperature, and only secondarily by food level. Although cladocerans appear to prolong instar duration at low food levels (Romanovsky 1984b), presumably, given the dependence of moulting rate on temperature, they cannot do so indefinitely. It follows, therefore, that food limited animals must undergo additional moults before reproducing. Alternatively, the 'critical' body size that must be reached before reproducing may be reduced at high temperature i.e., all body sizes are shifted down with increasing temperature. Most of the few studies that have considered size specific reproductive effort in Cladocera (Frey and Hann 1985; Taylor 1985; Robertson 1988; Lynch 1989) are generally consistent with the notion that reproductive onset is more closely related to size than to age. However, these two explanations need not be mutually exclusive. Critical body size may simply be a function of growth sufficient to achieve some level of energy reserve adequate for egg production.

Both the growth curves and the ratios of adult body size to size at birth of the two *Ceriodaphnia* species, give an indication of the amount of growth since the first instar. Neonates of *C. pulchella* and *C. dubia* are significantly different in size, the latter being larger, but this differential increases with age. In particular, the growth increments made by *C. dubia* juveniles are much greater, both in absolute and relative terms, than those made by *C. pulchella*. Consequently, the ratio of adult size to neonate size is significantly higher in *C. dubia* than in *C. pulchella*.

Both species did reduce growth rate in adult instars compared to their juvenile stages, as is typical in Cladocera (Lei and Armitage 1980; Lynch 1992). Moreoever, while *C. pulchella* very quickly reduces the rate of size increment on maturity, *C. dubia* does so more slowly, except when food limited at 23°C. Lynch (1992) attributes this fall off in growth rate to a plateau in the net rate of energy intake that occurs shortly after maturity. Together with the increased cost of moulting as animals age this accounts for the levelling off in the age specific reproduction frequently observed in Cladocera. At high food levels in this study, the rate of cumulative egg production was not noticeably lower in older animals, but was apparent at low food, particularly for *C. pulchella* at high temperature. Lynch (1992) suggests that the maximum net energy intake is lower, and the cost of

moulting higher, for smaller species, and that this places an upper limit on body size (and so egg production) that is lower than is attainable by larger species.

Interestingly, the growth pattern of *C. dubia* (curtailment of growth versus continued high growth rate) varies depending on food level, whereas this is not the case for *C. pulchella*. Apparently, *C. dubia* opts for continuing to make relatively large body length increments only at high food levels. Lynch (1980a) suggests that the continuation of high growth rates is typical of many, but not all, smaller species (< 1 mm). *C. dubia*, although the larger of the two species here, is still only small to intermediate sized, relative to larger species such as *Daphnia pulex* or *D. carinata*. At low food levels *C. dubia*'s rates of increment are more severely curtailed after the onset of maturity, and growth curves are more similar in form to those of *C. pulchella*.

Curtailment of growth after the onset of reproduction appears to be associated with a relatively constant clutch size throughout life (Lynch 1980a), and this is supported here, both by the data for *C. pulchella*, and for *C. dubia* at low food. As suggested by Lynch (1980a,b), growth increments beyond a certain size seem not to provide any energetic advantage to species exhibiting this pattern. In contrast, species that maintain high growth rates after maturity generally seem to increase clutch size as they grow (Lynch 1980a), and this seems to be the case for *C. dubia* at high food levels also. Thus, it appears that whilst *C. pulchella* exhibits a pattern of relatively slow growth rate and rather constant investment in reproduction, *C. dubia*'s response is variable depending on the environment. Again, this has implications for both species in the natural situation.

Clearly, the ability to curtail growth at low food would be advantageous when food is limiting. Conversely, rapid growth to a larger size would be beneficial when responding to transient increases in food availability, since rapid attainment of a larger size increases fecundity and reduces per unit body mass metabolic costs. If one considers the size specific allocation of available reserves to reproduction, clearly *C. pulchella* is the more conservative of the two species. When all food-temperature regimes are considered together, the rate at which *C. dubia* increases its total reproductive effort (clutch volume) with increasing body size is greater than for *C. pulchella*. At lower food levels though, the

clutch volume - body length relationship is similar for the both species, as it is in the field situation. In terms of relative egg size in the primiparous adult, *C. pulchella* makes a bigger reproductive investment, relative to maternal body size, than does *C. dubia.* This is a feature that appears to be typical for smaller species of Cladocera (Lynch 1980a). For both species though, relative egg size declined at low temperature, primarily as a consequence of static egg sizes and larger first reproductive body size. Brambilla (1982), in a study of pond *Daphnia pulex*, also found temperature to be of minor influence on absolute (not relative) egg size. However, the role of temperature on egg size remains unclear. Kerfoot (1974) for example, found egg size to be negatively correlated with temperature in *Bosmina,* but not in other cladocerans in the same lake.

Lynch (1980a) compared different cladoceran species in the relationship between relative egg size and age at first reproduction and found these to be inversely related. Although *C. pulchella* does not mature at an earlier age than *C. dubia*, despite its larger relative egg size, both species have short maturation times and relatively large eggs compared to other daphnids (Lynch 1980a; Fig. 2). Lynch (1980a) also concluded that, for the species he examined, larger relative egg size is associated with short lifespan. He then suggested that cladocerans maturing early must therefore give priority to demands for energy that ensure early survival at the expense of a longer life. I found this not to be the case for *C. pulchella* and *C. dubia.* Longevity was prolonged by low temperature and, in *C. dubia,* also by low food, but, even at 23°C, mean lifespsans (depending on food level) ranged between 25 and 41 days in *C. pulchella*, and 34 and 43 days in *C. dubia.* This puts them within the range of values for mean lifespan noted by Lynch (1980a) as being typical of species with small relative egg sizes, that curtail reproduction and prolong life. Similarly, with respect to the number of adult instars, well fed *C. pulchella* and *C. dubia* produced a maximum of 12 and 24 respectively - more than appears to be typical for species with large relative egg size.

The longevity of *Ceriodaphnia* in this study was increased more by low temperature than by high food. This is contrary to the response in *Daphnia ambigua* (Lei and Armitage 1980) where, although longevity was increased at low temperature, lower

nutrition shortened life span. Staples (1984) also found longevity to be inversely related to temperature in *C. dubia*, but the median lifespan of 12 days at 22°C is shorter that that recorded for *C. dubia* at 23°C in this study (17 days), although much the same as that recorded for *C. pulchella* (13 days). Like Lei and Armitage (1980), Staples (1984) also found that higher food levels provided the optimal conditions for survival.

The significantly longer mean lifespan of *C. dubia* when food limited at 13°C may seem counter-intuitive, since well nourished animals might reasonably be expected to live longer than poorly nourished ones. However, there is no a priori reason to expect this if food limitation is not too severe and the energy requirements for metabolic functions are met. The larger body size of *C. dubia* at low temperatures may enable this species to survive for an extended period as long as metabolic expenditure is reduced, as it is at low temperature. Mean lifespan was slightly longer at high food in *C. pulchella* but not significantly so and, as with other measures of performance discussed earlier, food effects on longevity were minimal for this species.

Of course, a longer life at low food levels may not increase reproductive fitness in animals if much of the extended lifespan is spent in a non-fecund state. As dicussed, moulting rate (i.e., instar duration) in Cladocera is dependent on temperature rather than food (Kryuchkova 1973; Bottrell 1975a,b). The prolongation of the time taken to reach certain life stages (e.g. the sixth adult instar) comes as a result of a longer time between brood releases. Orcutt and Porter (1984) recorded a nearly four-fold increase in this period in food limited *Daphnia parvula* at 25°C. Similarly Brandl and Wittingerová (1991) found that *Daphnia galeata* populations from lakes of different trophic status exhibited differences in the between-brood period, with animals from highly eutrophic ponds exhibiting little lag between the hatching of one brood and the deposition of the next clutch. For *Ceriodaphnia* in this study, a lag response was noted at low food, particularly at low temperature. However the effects of reduced food only became significant with increasing animal age, and then only for *C. dubia*. Thus, the effects of low resource levels appear to be cumulative, resulting in a gradual increment in the between-brood period. Presumably, as animals become larger and their absolute metabolic requirement (for

moulting and maintenance) increases, the time lag between releasing one brood and laying the next is extended. Ultimately, this lag will be governed by the rate at which animals can accumulate reserves sufficient for reproduction.

Summary

C. pulchella and *C. dubia*, although both morphologically very similar species, are quite different in some important aspects of their life histories, particularly with respect to their responses under food limitation. As is usual for Cladocera, development times are governed largely by temperature, but low food levels prolong development by increasing the period between broods, particularly for *C. dubia*. At high levels of resource availability, *C. dubia* has a much higher fecundity than *C. pulchella* and increases its reproductive effort with age while maintaining a high growth rate. However, *C. dubia* is relatively more affected by low food levels than is *C. pulchella* and, when resource limited, the two species are much closer in terms of total egg production and lipid reserve. *C. pulchella*, in contrast to *C. dubia*, appears to alter its patterns of growth and reproduction very little at low food. Growth rate is severely reduced at the onset of reproduction, regardless of food level, and a relatively constant clutch size is maintained throughout life. However, the ability of this smaller species to continue to grow and reproduce when starved is far superior to that of *C. dubia*.

Curtailment of growth after the onset of reproduction is an indication that growth after maturity provides little, if any, energetic advantage. For *C. dubia*, growth rates after maturity were severely reduced only at the high temperature-low food regime, suggesting a flexibility in life history response to fluctuating food levels. When resource availability declines markedly it is not a bad strategy to curtail growth and divert available resources into reproduction. At high resource levels though, the ability to maximise growth to a large size and thereby increase fecundity must be advantageous.

The larger relative egg and neonate sizes of *C. pulchella* indicate that this species makes a larger reproductive investment in its young than does *C. dubia*. However, while *C. dubia* neonates are larger in absolute terms and would have higher absolute energy requirements, their lipid endowment at birth is not significantly different from that

provided to *C. pulchella* neonates. Thus, under conditions of chronic food depletion these neonates appear to be more disadvantaged than *C. pulchella* offspring.

From this examination of life history variation in *C. pulchella* and *C. dubia* it seems reasonable to expect *C. pulchella* to be the superior competitor when the levels of resource availability are low or fluctuating. In the concluding chapter, I review these findings both in the context of the field situation, and generally.

PART FOUR

SYNTHESIS AND CONCLUDING DISCUSSION

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A life history approach to the factors governing cladoceran distribution and community structure has arisen following more than two decades of research. During this time the focus has shifted somewhat, away from the role of predation as the dominant mechanism structuring microcrustacean communities (Brooks and Dodson 1965; Zaret and Kerfoot 1975), towards a recognition of the importance of competitive interactions in many systems (Lynch 1978; De Mott and Kerfoot 1982; De Mott 1983).

Concerted efforts have been made to experimentally examine mechanisms of species coexistence which are independent of predation (Neill 1975a,b; Goulden and Hornig 1980; De Mott 1982; Goulden *et al.* 1982a; Smith and Cooper 1982; Matveev 1987). This research has supported the view that predation, although very important in many systems, may not have deserved the emphasis it often received. Moreover, experimental studies have provided the foundation for a burgeoning interest in the role of life history evolution in zooplankton community ecology.

In contrast to the effects of vertebrate and invertebrate predation on zooplankton communities, the effects of food limitation and resource competition are less well understood (Rothhaupt 1990). While predation is a direct interaction and therefore not difficult to assess, competitors affect each other indirectly via the exploitation of common food sources, and empirical evidence of resource competition is more difficult to obtain. Field analysis of the role of resource dynamics in cladoceran competition is difficult, due to the paucity of accurate techniques to measure the severity of food limitation. Individual growth rate and fecundity have been the major parameters for assessing feeding success, yet these are both profoundly influenced by the interplay of other factors, such as temperature and body size (Allan and Goulden 1980).

The manipulation of communities within enclosures enables the assessment of growth and, indirectly, competition, under 'natural' conditions (e.g. Kerfoot and De Mott 1980), but the difficulty in controlling enclosure effects reduces the long term explanatory

power of such investigations. Recent use of lipid indices to assess food limitation has solved some of these problems, since lipid scores depend not only on food availability, but on nutritional history, food quality, and the degree of environmental stress (Tessier and Goulden 1982). Widening the range of variables to include measures weighted for adult body size (such as relative egg and neonate size) allows reproductive allocation among species to be meaningfully compared. Such variables have the advantage of being easily applied to natural populations. These improvements made to the methods used to assess feeding success in the field have allowed the performance of species in natural populations to be interpreted more realistically.

The success of a species in any environment is ultimately determined by its relative apportionment of resources to reproduction, growth, and survival, given certain levels of resource depletion and predator pressure. The recognition of this basic premise has been central to much of the recent work on the Cladocera. Some of these studies have been attempts to theoretically define optimal life histories for organisms exposed to different selection pressures (Lynch 1980b; Dorazio and Lehman 1983), while others have examined real situations and have attempted to explain the observed characteristics of populations on the basis of optimal life history theory (Jacobs 1977; Lynch 1980a; Foran 1986a,b; Tessier 1986a; Robertson 1988; Brandl and Wittingerovâ 1991).

Despite a wealth of detailed information on the life history characteristics of many cladoceran species, prior to 1980 there had been no attempt to interpret the success of different cladocerans on the basis of their life history attributes. Lynch (1980a), by examining the interspecific variation in patterns of cladoceran reproduction and growth, offered the first attempts at providing a broad life history based interpretation of cladoceran distribution and abundance. Later workers have developed this approach and have examined not only how life history patterns can vary between different species at different food concentrations (Tessier and Consolatti 1989; Gliwicz and Guisande 1992), and temperatures (Foran 1986a,b), but how they can vary even within clonal assemblages (Vanni 1987; Weider 1987; Ebert and Jacobs 1991). These studies illustrate the complexity of life history variation that exists among the Cladocera, and should serve as a

caution against the wanton application of broad brush predictive models (e.g. Lynch 1980b; Dorazio and Lehman 1983), that seek to provide a mechanistic basis for the interpretation of species success in different environments. Such models are valuable in that they provide a framework for evaluating the impact of competition and predation on real populations, but they are often speculative, as Lynch (1980b) himself admits.

The general agreement between observations of life history variation in cladocerans, and what is expected on the basis of the 'optimal' strategy, given certain selective pressures, is encouraging. Thus, when subjected to vertebrate predation, cladoceran body sizes are small, and when mortality declines with increasing size (as with invertebrate predation), animals are large at birth and maturity, and produce small clutches. On the other hand, energetic constraints appear to be behind the fact that small bodied genotypes and species are increasingly favoured under conditions of resource depletion, since the energetic advantage of large species is reduced, and their pre-reproductive period prolonged, in food depleted environments. The interpretation of the adaptive significance of cladoceran life histories therefore requires that both feeding success and vulnerability to predators be assessed (Lynch 1980b).

It is within this framework that this study has examined the life histories of four, small bodied, cladoceran species: *Bosmina longirostris, B. meridionalis, Ceriodaphnia dubia*, and *C. pulchella*. The apparently long term coexistence of these species in Lake Mangakaware is not easily interpreted by analogy with the north temperate communities on which the predictive models of zooplankton life history strategy are based. Lake Mangakaware is virtually free of planktivorous vertebrates, and although large populations of omnivorous cyclopoids are present, their ability to exert strong selective pressure on cladocerans is probably small compared to the effects of chaoborid larvae and predatory calanoids elsewhere (Burns 1991).

As appears to be typical for New Zealand limnetic communities (Chapman and Green 1987; Burns 1991) the low fecundities of the Lake Mangakaware cladocerans indicate that their populations are probably regulated by the quantity and quality of available food. The relative success of each species, both in terms of abundance and

persistence, will therefore be determined by how effectively foraging ability translates to reproductive performance and population growth rate.

Of the four planktonic cladoceran species present in Lake Mangakaware, *Bosmina longirostris* is arguably the most successful. Although a small species, it produces relatively large eggs and neonates, which mature quickly. It is relatively invulnerable to predation from *Mesocyclops* (Jamieson 1980) and is able to feed selectively on palatable algal species even when the density of unpalatable or nutritionally poor taxa is high (Geller and Muller 1981). Although it had the lowest mean birth rates of the four cladoceran species, *B. longirostris* also suffered the lowest death rates and, over the entire sampling period, showed the highest mean rate of population growth. Moreover, unlike *B. meridionalis*, which could be regarded as its life history equivalent in any predictive model, *B. longirostris* is not disadvantaged by having excessively long development times at low temperatures. During cooler periods, *B. meridionalis* is clearly less able to maintain the high population growth rates required to persist in competition with its more able congener.

The seasonal changes observed in parameters of body size and fecundity where the highest clutch sizes and lipid scores were associated with the smallest body sizes, suggest that fecundity is more closely tied to feeding success in *B. longirostris* (and the other three species studied) than to body size *per se*. Increases in the latter variable are closely associated with the seasonal onset of cooler temperatures, a view supported by Culver (1980), but not Brambilla (1980), who found declines in the size of some pond *Daphnia* to be an adaptation to food limitation. However, most workers agree that seasonal declines in size (particularly size at maturity) are often the result of growth limitation through environmental deterioration (Brambilla 1980). It is possible that, as found by Kerfoot (1974), winter increases in body size and egg size are an adaptive response to counter invertebrate predation, but this theory does not accord with the pattern of *Mesocyclops* abundance, which was lowest during winter, or with the association of large body size with indications of poor feeding success. In fact, at least for *B. longirostris* and *Ceriodaphnia*, the data lend further support for the unimportance of invertebrate predation as a selective

force in structuring New Zealand cladoceran communities. While there is no question that *Mesocyclops* is a predator of small cladocerans, particularly *Ceriodaphnia*, the life history characteristics of these small cladoceran species have probably evolved in response to other stronger selective pressures such as food limitation and temperature.

Romanovsky (1984a) suggests that small species are able to minimise individual growth rate as a consequence of large relative egg size, i.e., the neonates hatch at a size that is close to their size at maturity. However, because small body size restricts clutch size, smaller species cannot invest maximum energy in reproduction and hence they maintain somatic growth after maturation. This suggestion is supported by Lynch (1980a) who cites data from a number of different studies that show that *B. longirostris* produces relatively large neonates from small clutches, and maintains growth throughout life in an effort to achieve optimal foraging size.

Romanovsky (1984a) also suggests that smaller species are slow growing, but this view is not substantiated by Lynch (1980a) or this study, in which the data are supportive of an early maturation among smaller species. In contrast with lakes of low trophy, Lake Mangakaware represents a productive system where the supply of nutritionally adequate food is unpredictable and in high demand. Protracted periods of resource depletion will favour smaller species with strategies for persistence through periods of starvation. These include the production of gamogenetic individuals (a feature of all the four cladoceran species in Lake Mangakaware), and the production of relatively large neonates which spend less time in vulnerable pre-adult stages. Indeed, the supposed competitive advantage of large species (Brooks and Dodson 1965) really applies only to adult instars, since at low food levels the larger juveniles of these species starve before they ever reach maturity (Romanovsky 1984a).

Given that the cladoceran populations in Lake Mangakaware are food limited (low fecundities and lipid scores), the success of the small bodied *Bosmina longirostris* might easily be predicted on the basis of its life history characteristics. However, the term 'small species' can be regarded as a relative rather than absolute description when the Lake Mangakaware populations are discussed, since, as described, all are quite small by

temperate standards. With the possible exception of *B. meridionalis,* for which there are limited data, these species coexist, although their peak abundances are disjunct. Disjunct temporal maxima arising as a result of large differences in reproductive and growth strategies, as between north temperature 'large' and 'small' species, will not be evident in cladoceran communities where all the species are small. Indeed, in New Zealand communities, species distribution and abundance are more likely to be related to quite subtle differences in a suite of life history characteristics that collectively tip the balance in favour of different (small) species seasonally. This is in marked contrast to the northern temperate situation where the debate as to the significance of a 'large' versus 'small' species strategy continues.

The differences observed in this study between *C. pulchella* and *C. dubia* in their responses to food limitation and temperature illustrate how the seasonal distributions of two superficially very similar species might be governed by what could be regarded as quite minor differences in life history.

The use of experimental studies to elucidate differences in patterns of growth and energy allocation between similar species is an approach that has become increasingly popular in recent years, particularly with regard to explaining clonal succession (e.g. Lynch and Ennis 1983; Yampolsky and Kalabushkin 1991; Ebert 1991; Ebert and Jacobs 1991), and changes in maternal reproductive effort (Robertson 1988; Perrin *et al.* 1990; Groeger *et al.* 1991; Tessier and Consolatti 1991). Such studies give better insight as to the role of factors such as temperature and food depletion in shaping the life history characteristics of different species. In natural populations the effects of food and temperature are not separable and 'food limitation' effects (as evidence of competition) may simply be the result of temperature acting on body size.

Clearly, advantages gained by controlling these two variables is great when attempting to explain the observed responses of natural populations to environmental or autogenic change. Together with patterns of reproductive allocation *per se.*, the trade off between the number and size of offspring produced by an individual is central to life history theory (Smith and Fretwell 1974; Winkler and Wallin 1987). Changing the way in

which reproductive effort is packaged is one way in which Cladocera can respond to the vagaries of resource depletion and size selective predation. Another is through changes in body size. Often the responses are concomitant and inexorably linked as part of a species specific life history strategy. In searching for patterns of energy allocation by parents to their offspring two relationships are intuitive. As the per offspring energy investment increases, (1) the number of young that can be produced declines, and (2) the fitness of individual offspring increases. In addition, offspring fitness may alter after birth, depending on the strength and type of selective forces acting on the neonate.

For organisms in a variable environment, resource acquisition by the parent is an indicator of the expected level of resources available to the offspring and, if offspring fitness and size change as a function of resource availability, then optimal neonate size might also change (Tessier and Consolatti 1991). Superimposed on the effort per offspring - clutch size trade off are other features of life history that, for cladocerans, may dictate seasonal success: survivability when starved; ability to produce persistent resting stages; patterns of individual growth; size dependent foraging ability; and vulnerability to size selective predators.

The flexibility, or otherwise, of a species in critical features of its life history might then predispose it to seasons or environments where its success is more likely. I believe this is so for the two species of *Ceriodaphnia* in Lake Mangakaware. The seasonal distribution and abundance of *C. pulchella* and *C. dubia* appears to be related primarily to temperature and to resource availability, and less so to predator pressure. As described, the principal zooplanktivorous predator in Lake Mangakaware is the omnivorous *Mesocyclops leuckarti*, to which *Ceriodaphnia* is quite vulnerable, especially in the juveniles stages (Jamieson 1980). However, of the two species, the smaller *C. pulchella* might be expected to be the most vulnerable to *Mesocyclops* predation, yet this species was maximally abundant during the period of high *Mesocyclops* density. Even if vertebrate predation from larval *Gobiomorphus cotidianus* was important (and I do not believe it is in Lake Mangakaware), then the overlapping size ranges of these two cladoceran species would make both equally vulnerable as prey.

The selective advantage to small bodied species in food limited environments, especially when they also produce relatively large young, has been discussed in some detail earlier (see also Part Three, Chapter Three). Both species of *Ceriodaphnia* in Lake Mangakaware, conform to this expected life history feature (as do the two species of *Bosmina*). However other features of their life history, made clear only by examining their responses to changes in food and temperature, are evidently critical to their seasonal distribution in Lake Mangakaware. The salient features of each, with respect to the other, are summarised below (Table 33).

Table 33: Summary of some important life history features of *Ceriodaphnia* from Lake Mangakaware, in relation to food and temperature level. Comparisons are between the two species. HT=23°C; LT=13°C; HF=high food; LF=low food; EDT=egg development time; Cp=*C. pulchella*; Cd=*C. dubia*.

Life History Characteristics	*C. pulchella*	*C. dubia*
Mean EDT at LT	8.6 days	5.0 days
Mean EDT at HT	2.2 days	1.8 days
Time to maturity	Both spp: Longer at LT. No food effect.	
	Significantly longer than Cd at LT	Significantly shorter than Cp at LT
Time to sixth clutch	Both spp: Longer at LT	
	Significantly longer than Cd at both HT and LT	Significantly shorter than Cp at both HT and LT but relatively greater prolongation at LF
Adult body size (field and experimental)	Smaller: 0.45 - 0.7 mm	Larger: 0.65 - 1.10 mm
Mean offspring body size (experimental)	Smaller:0.272 - 0.292 mm	Larger: 0.37 - 0.39 mm
	Both spp: Smaller at HT. Larger at LF	
Relative egg size	Larger than Cd. Larger at HT or HF	Smaller than Cp. Larger at HT. No food effect.
Absolute egg size	Smaller than Cd. Tend to be larger at LT-HF regime	Larger than Cp. No temperature-food effect
Survival of starved offspring	Good survival regardless of maternal history. Many produce eggs under starvation	No juveniles reach adulthood.
Growth and fecundity with time	Curtails growth after maturity. Maintains rather constant clutch size.	Curtails growth less. Maintains high growth rates at LT when well fed.
Relationship of clutch volume to body length	Increases amount of egg material with body length only slowly	Increases amount of egg material with body length at greater rate.
Length of life	No significant food effect. Longer at LT.	Prolonged at LT and at LF.
Lipid Score (adult)	Both spp: Higher at HF and at HT	
	Lower than Cd except at LT:LF	Higher than Cp except at LT:LF
Lipid score (neonate)	Both spp: Higher at HF and at LT. No difference between spp.	

It is clear from this summary that, with the exception of egg size, for most life history characteristics, *C. pulchella* is much less responsive to changes in food availability than is *C. dubia*, especially with respect to starvation resistance. Among the Cladocera, starvation resistance usually increases with increasing body size (Threlkeld 1976), but while this appears to hold for adults, juvenile stages are more vulnerable to low food supply and it is more advantageous to be small (Lynch 1978). Indeed it appears that the ability of *C. pulchella* to complete growth to maturity and reproduce under severe food deprivation may be the critical feature of its life history that makes it the more successful species of *Ceriodaphnia* in Lake Mangakaware. The slightly smaller body size and relatively larger neonates of *C. pulchella* compared with its congener are features well suited to maintaining populations through unfavourable periods. *C. pulchella* juveniles need to make much smaller growth increments to reach maturity than do juveniles of *C. dubia*. The latter are severely disadvantaged when, at low food, their growth rates are reduced, and they must prolong juvenile development by the incorporation of extra pre-adult instars. This exposes the juveniles to a 'competitive bottleneck' (Romanovsky 1984b), where they no longer have the resources to reach maturity and are less able to compete with adult *C. pulchella*.

However, at temperatures below about 18°C *C. pulchella* becomes severely disadvantaged by long development times, regardless of the amount of food available. The ability of *C. dubia* to grow rapidly at low temperature is consistent with its winter appearance in the plankton and late spring population expansion. During summer and autumn periods, when the density of other zooplankters is high, the greater sensitivity of this species to food depletion precludes its success. A number of workers have discussed the important role of different life-histories in the competitive interactions of herbivorous zooplankton (Neill 1975; Lynch 1978; Goulden *et al* 1982; Romanovsky and Feniova 1985). Size or age dependent competitive bottlenecks, caused by low or fluctuating food levels, can shift the competitive balance toward species with lower resource requirements and better starvation resistance.

Population time-lags (i.e. delay in response to changes in resource level) also appear to be important in determining the relative success of competing species. This suggestion is made on the basis of the view that time-lags are causative to population oscillations in Cladocera (Goulden and Hornig 1980; Matveev 1985; 1987), and these oscillations may allow species coexistence, with differential success, in situations where resources are alternately over- and under-exploited.

Variability of resource availability is emerging as one of the most important factors influencing zooplankton competition (De Mott 1989). Changing biotic and abiotic conditions may prevent steady state conditions and reverse or shift competitive superiority at a speed determined by the time-lag response (Hebert 1982). This then can lead to prolonged coexistence, primarily because competitive superiority is determined by the conditions at the time, and these are not static (Rothhaupt 1990). This appears to be the case in Lake Mangakaware, not only for the Cladocera, but for other zooplankton taxa also. In this lake, limnetic resource levels fluctuate on different time scales, and probably for different reasons. Mixing events during summer stratification e.g. by storms, lead to enhanced phytoplankton growth and changes in algal community composition. Presumably, such events also alter the abundance and composition of non-algal food sources (bacteria and detritus). The effect of this resource variation on the cycles of the Cladocera (and the zooplankton generally) will depend on both its magnitude and time scale. Very short term variations are probably of little importance in determining competitive outcomes, but variations over time periods long enough to require some starvation resistance are likely to have important consequences for competing species. Unlike the north temperate systems where 'low resource availability' is usually associated with oligotrophy, in Lake Mangakaware and in other eutrophic waters, low resource availability may be associated more with the presence of large and/or unpalatable algal species than with low algal abundance *per se*.

In this lake, and others of its type, periods of food deprivation may be quite prolonged. Different species, and different age classes of the same species, may experience fluctuating food supply/suitability in different ways. Then, subtle differences

in life history characteristics: the ability to store energy (e.g. as lipid), and differential energy allocation into maintenance, somatic growth and reproduction, will clearly be pivotal to competitive success.

In the context of the predictions of optimal life history theory (Stearns 1976; Lynch 1980b; Dorazio and Lehman 1983), the Cladocera of Lake Mangakaware adhere to certain expected patterns. Compared with many of cladoceran species of north temperate zones they are small, produce relatively large young, and their development rates are quite high, all features of a life history strategy which is predicted to be favoured in an environment where resources are limited and competition is relatively more important than susceptibility to predation. The apparently long term coexistence of the Lake Mangakaware cladocerans, and their different patterns of seasonal abundance, can be attributed to relatively small differences in their abilities firstly to take advantage of pulses in the availability of suitable food (which includes the advantage of rapid development time) and, secondly, to persist when these food pulses are infrequent or unpredictable. The concept of food thresholds for growth and reproduction in different species (Rothhaupt 1990) may be applicable here. *C. dubia* for example, requires a higher food level for the successful growth of offspring than does *C. pulchella* (and presumably also *Bosmina*).

Bosmina longirostris and *Ceriodaphnia dubia* are both advantaged by more rapid development times at low temperature, but the selective feeding mode of the former (Geller and Muller 1981) is favoured during summer periods when large or unpalatable algal types are abundant. Indeed, differences in resource use have often been used to explain abundance patterns in herbivorous zooplankton (e.g., De Mott and Kerfoot 1982; Hoenicke and Goldman 1987), although the evidence for a dependence of competitive ability on food composition has not always been conclusive (Rothhaupt 1990). *B. meridionalis* and *B. longirostris* probably utilise the same food base and it is likely that their feeding modes are similar (Matveev 1985). However, like *C. pulchella*, *B. meridionalis* is limited by long development times at low temperature. During colder periods its abundance and persistence appears to be determined by the presence of other

cladocerans. Certainly, it disappeared from the plankton as the abundance of *C. pulchella* and *B. longirostris* increased.

The value of this study, as an addition to the current literature on cladoceran life histories, lies in its examination of a cladoceran community populated by four small species, which exhibit differences in life history that, while subtle, are large enough to permit coexistence and govern seasonal distribution. In New Zealand, the geographical distribution of *C. pulchella* and *C. dubia* may be determined by the selective value of their different life history features in different environments. *C. dubia* certainly appears to exhibit a general distribution pattern associated with larger and more oligotrophic lakes than Lake Mangakaware. For example, *C. dubia* appears to be the only species of *Ceriodaphnia* in Lakes Taupo and Ototoa (Greenwood *et al.* 1991). In more oligotrophic systems of this type, the abundance of unpalatable algae is usually lower and the role of picoplankton as a food source is likely to be more important than in eutrophic systems (Burns and Stockner 1991). Moreover, *C. dubia* seems to be the predominant species of *Ceriodaphnia* in the South Island where winter temperatures are lower (Greenwood *et al.* 1991). In contrast, *C. pulchella*'s distribution appears to be largely restricted to small North Island lakes of high trophy. This suggests that the differences observed here between the life history features of these two species are not peculiar to Lake Mangakaware populations, but represent quite stable strategies which are just as distinctive as those exhibited by north temperate large and small species.

The approach taken here in experimentally examining the life histories of two congeneric species raises further questions that need to be addressed, particularly with respect to how different time scales and amplitudes of resource variance affect competitive outcomes in species which differ only in small details of their life histories. The comparative experimental approach is a promising one, made more valuable by application to real field situations. The current recognition of competition as a multifaceted phenomenon will no doubt result in the development and extension of this approach, in order to better incorporate the observations of experimental and field trends into an integrated picture of cladoceran life history evolution.

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APPENDIX ONE

Counts of phytoplankton and planktonic zooplankton from Lake Mangakaware November 1987 - September 1989

Table 1: Counts of phytoplankton (p.u./ml)

Day	*Vacuolaria*	*Actinastrum hantzschii*	*Botryococcus braunii*	*Coelastrum microporum*	*Coelastrum reticulatum*	*Pediastrum duplex*	*Monoraphidium contortum*	*Tetrastrum triangulare*	*Coelosphaerium hutzingianum*	*Kirchneriella lunaris*	*Tetraedron regulare*	*Tetraedron planktonicum*	*Tetraedron limneticum*
15	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	103.68	0	0	0	6.91	0	0	0	0	0	0	0
29	0	134.78	0	0	0	0	393.97	0	0	0	0	0	0
36	97.2	38.88	0	0	0	0	239.75	194.39	0	0	0	0	0
43	0	7.41	14.81	0	0	0	0	29.62	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0
57	10.36	0	5.18	15.55	0	0	0	5.18	0	5.18	5.18	0	0
64	20.74	0	8.29	8.29	0	0	0	0	472.76	0	12.44	0	0
71	4.15	0	0	0	4.15	0	0	0	207.35	0	4.15	0	0
78	2.3	27.65	20.74	0	2.3	0	0	0	128.15	0	2.3	2.3	0
85	36.29	5.15	0	0	0	0	0	0	352.5	0	0	0	0
92	0	41.47	10.83	0	0	0	0	15.55	243.64	0	0	0	0
100	0	134.78	5.41	0	0	0	5.18	0	596.14	10.36	0	0	0
107	0	93.31	14.21	0	0	0	0	82.94	684.26	0	0	0	0
120	0	77.76	62.21	0	0	0	0	3250.5	347.31	0	0	0	0
127	0	55.29	41.47	0	0	0	0	4750.78	283.38	0	0	0	0
134	0	66.35	78.79	4.15	0	0	0	4472.96	174.18	0	0	0	0
141	0	41.47	86.4	0	0	0	0	6626	188.17	0	0	0	0
148	0	0	79	0	0	0	0	8668	116.8	0	0	0	0
155	0	0	72.6	0	0	0	0	17169.5	25.92	0	0	0	0
162	0	0	93.3	0	0	0	0	24004	20.74	0	0	0	0
169	0	0	51.8	0	0	0	0	23837	0	0	0	0	0
177	0	0	20.74	0	0	0	0	16503	0	0	0	0	0
190	0	0	15.55	0	0	0	0	3896.5	0	0	0	0	0
201	0	0	72.6	0	0	0	0	300.7	0	0	0	0	0
213	0	0	26	0	0	0	0	165.9	0	0	0	0	0
236	0	0	26	0	0	0	0	10.4	0	0	0	0	0
250	0	0	10.4	0	0	0	0	0	0	0	0	0	0
264	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1: Continued

Day	*Pediastrum tetras*	*Monoraphidium irregulare*	*Kirchneriella contorta*	*Dictyosphaerium pulchellum*	*Sphaerocystis*	*Closterium acutum var. variabile*	*Closterium aciculare*	*Scenedesmus* sp.	*Aulacosira distans*	*Aulacosira granulata var. angustissima*	*Cyclotella*	*Nitzschia acicularis*	*Tabellaria* sp.
15	0	0	0	0	0	0	0	0	29796.6	504.86	0	0	0
22	0	0	0	0	0	283.38	0	0	28858.95	744.11	0	0	0
29	0	0	0	0	0	497.64	0	0	2571.16	850.14	0	0	0
36	0	0	0	0	0	738.69	0	0	460.06	239.75	0	0	0
43	0	0	0	0	0	1370	0	0	1066.38	644.27	0	0	0
50	0	0	0	0	0	352.5	0	0	815.58	299.63	0	0	0
57	0	0	0	0	0	119.23	0	0	585.77	388.78	0	0	0
64	0	0	0	0	0	111.97	0	0	443.73	161.73	0	0	0
71	0	0	0	0	0	87.09	0	0	414.7	87.09	0	0	0
78	0	0	0	0	0	117.49	0	0	188.92	59.9	0	0	0
85	0	0	0	0	0	399.15	0	0	233.27	134.78	0	0	0
92	0	0	0	0	0	476.91	0	0	331.76	248.82	0	0	0
100	0	0	0	0	0	196.98	0	0	834.59	658.34	0	0	0
107	0	0	0	0	0	393.97	0	0	2270.45	622.05	0	518.38	0
120	0	0	0	0	0	207.35	0	0	4625.77	665.6	0	57.02	0
127	0	0	0	0	0	255.73	0	0	981.46	27.65	0	48.38	0
134	0	0	0	0	0	170.03	0	0	298.59	62.21	8.3	0	0
141	0	0	0	0	0	947	166.7	41.7	165.9	41.7	41.7	0	0
148	0	0	0	0	0	1845.4	0	10.4	103.7	41.5	83	0	0
155	0	0	0	0	0	585.8	0	15.6	326.6	98.5	243.6	0	0
162	0	0	0	0	0	155.5	0	0	114	20.74	611.7	0	0
169	0	0	0	0	0	197	0	0	207.4	41.5	1078.2	0	0
177	0	0	0	0	0	129.6	0	0	103.7	0	1353	0	0
190	0	0	0	0	0	103.7	5.18	0	83	10.36	1213	0	0
201	0	0	0	0	0	124.4	0	0	51.8	0	642.8	0	0
213	0	0	0	0	0	62.2	5.18	5.18	62.2	10.36	217.7	0	0
236	0	0	0	0	0	142.6	7.78	0	173.7	15.55	114	0	0
250	0	0	0	0	0	150.3	2.6	0	168.5	0	26	0	0
264	0	0	0	0	10.4	193.5	0	0	324.8	0	24.2	0	0

Table 1: Continued

Day	*Centritractus belanophorus*	*Anabaena circinalis*	*Microcysis* spp.	*Aphanocapsa*	*Trachelomonas planktonica*	*T. volvocina*	*Trachelomonas* sp.	*Phacus* spp.	*Cryptomonas* spp.	*Peridinium cinctum*	*Ceratium* sp.	*Closterium* spp.	*Staurastrum* spp.	Total phytoplankton
15	0	36.29	0	0	0	282.52	0	0	0	0	0	0	0	30620.27
22	0	41.47	0	0	0	103.68	0	0	20.74	0	0	0	0	30162.92
29	0	93.31	0	0	0	165.88	0	0	0	0	0	0	0	4706.88
36	0	336.95	0	0	0	84.24	0	0	0	0	0	0	0	2429.91
43	37.03	335.08	0	0	0	548	0	7.41	0	207.35	0	0	37.03	4304.39
50	20.74	119.75	0	0	0	400.88	0	0	0	56.23	0	124.41	117.5	2431.63
57	5.18	25.92	699.81	0	0	658.34	5.18	0	0	67.39	0	0	0	2617.78
64	8.29	120.26	2015.46	0	0	564	4.15	8.29	0	360.79	0	0	62.21	4387.55
71	4.15	54.15	514.23	0	0	489.35	4.15	0	0	188.17	0	8.3	91.23	2162.41
78	20.74	28.88	793.12	0	0	649.7	0	0	0	157.03	0	16.13	36.86	2256.81
85	15.55	7.74	1062	0	0	912.35	0	0	0	160.9	0	15.55	77.76	3412.99
92	0	8.66	1389.25	0	0	482.1	0	0	0	175.44	0	0	145.15	3569.58
100	10.36	13.54	0	0	0	393.97	0	0	0	111	0	0	31.1	3001.75
107	0	20.31	0	0	0	1544.77	0	0	0	85.29	0	31.1	0	6361.04
120	5.18	0	0	0	0	2354.5	0	0	0	41.47	0	20.74	0	11715.41
127	13.82	34.56	0	0	0	1078.23	0	6.91	0	13.82	0	13.82	62.21	7667.51
134	0	12.44	0	0	0	833.55	0	4.15	4.15	62.21	0	0	29.03	6281.09
141	0	0	0	0	0	2778.5	0	0	131.3	108.3	0	0	27.7	11392.54
148	0	0	0	0	0	1928.4	0	0	373.2	49	0	0	0	13298.4
155	0	0	0	0	0	1290.8	0	0	181.44	20.74	0	0	25.92	20057.02
162	0	0	0	0	0	2882	0	0	155.5	20.74	0	0	0	28078.22
169	0	0	0	0	0	2094.2	0	0	186.6	0	0	0	31.1	27724.8
177	0	0	0	0	0	539.1	0	0	150.3	20.74	0	0	36.3	18856.48
190	0	0	0	0	0	404.3	0	0	196.9	10.36	0	0	5.18	5944.03
201	0	0	0	0	0	347.3	0	0	103.66	10.36	0	0	5.18	1658.8
213	0	0	0	0	0	793	0	0	57.06	5.18	0	0	0	1409.96
236	0	0	0	0	0	217.7	0	0	62.2	0	0	0	0	769.93
250	0	0	0	0	0	197	0	0	220.4	0	0	0	2.6	777.8
264	0	0	0	0	0	38	0	0	86.35	0	0	0	3.5	680.75

Table 1: Continued

Day	*Vacuolaria*	*Actinastrum hantzschii*	*Botryococcus braunii*	*Coelastrum microporum*	*Coelastrum reticulatum*	*Pediastrum duplex*	*Monoraphidium contortum*	*Tetrastrum triangulare*	*Coelosphaerium hutzingianum*	*Kirchneriella lunaris*	*Tetraedron regulare*	*Tetraedron planktonicum*	*Tetraedron limneticum*
280	0	0	0	0	0	0	0	0	0	0	0	0	0
295	0	0	1.7	0	0	0	0	0	0	0	0	0	0
304	0	0	0	0	0	0	0	0	0	0	0	0	0
323	257.2	0	0	0	0	0	0	0	0	0	0	0	0
338	108.8	0	0	1.7	0	0	0	0	0	0	1.7	0	0
352	0	0	0	0	0	0	0	0	0	0	0	0	0
366	0	0	0	0	0	10.36	0	10.36	0	0	0	0	10.36
381	0	0	0	0	0	0	0	0	0	0	0	0	83.35
394	0	0	0	0	0	0	0	290.3	0	0	0	0	10.36
415	0	0	0	0	0	0	0	324.85	0	0	0	0	0
428	0	0	0	0	0	0	0	41.47	27.65	6.9	0	0	34.56
442	0	0	0	0	0	0	0	98.5	0	0	0	0	0
456	0	0	0	15.55	0	0	0	15.55	0	0	5.2	0	10.37
471	0	0	6.9	48	0	0	0	6.9	0	0	0	0	0
484	0	0	0	8.3	0	0	0	0	0	0	0	0	4.15
498	0	0	0	0	0	0	0	0	0	0	0	0	10.37
510	0	0	8.3	4.15	0	0	0	8.3	0	0	0	0	0
525	0	0	2.59	0	0	0	0	0	0	0	0	0	0
539	0	0	0	0	0	0	0	0	0	0	0	0	0
554	0	0	0	0	0	0	0	0	0	0	0	0	0
569	0	0	0	0	0	0	0	0	0	0	0	0	0
579	0	0	1.3	0	0	0	0	0	0	0	0	0	0
596	0	0	0	0	0	0	0	0	0	0	0	0	0
613	0	0	0	0	0	0	0	0	0	0	0	0	0
629	0	0	0	0	0	0	0	0	0	0	0	0	0
643	0	0	0	0	0	0	0	0	0	0	0	0	0
656	0	0	0	0	0	0	0	0	0	0	0	0	0
672	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1: Continued

Day	*Pediastrum tetras*	*Monoraphidium irregulare*	*Kirchneriella contorta*	*Dictyosphaerium pulchellum*	*Sphaerocystis*	*Closterium acutum var. variabile*	*Closterium aciculare*	*Scenedesmus* sp.	*Aulacosira distans angustissima*	*Aulacosira granulata var.*	*Cyclotella*	*Nitzschia acicularis*	*Tabellaria* sp.
280	0	0	0	0	18.1	228	2.6	0	282.5	0	15.6	0	0
295	0	0	0	0	31.1	184.9	3.5	0	74.3	3.5	10.4	0	0
304	0	0	0	0	5.2	164	0	0	34.6	0	5.2	0	6.9
323	0	0	0	0	0	140	1.7	0	32.8	0	1.7	0	5.2
338	0	0	0	0	17.3	224.6	108.8	0	69	5.2	0	0	0
352	0	0	0	0	31.1	2747.4	2052.8	0	746.5	31.1	0	0	0
366	0	0	10.36	0	197	591	1752.1	0	6792.8	497.6	51.84	0	10.36
381	0	0	0	0	13.82	311	1071.32	0	20836.78	290.3	110.59	0	0
394	20.72	0	51.84	20.72	41.47	570.22	891.6	0	3421.3	248.8	114.04	0	0
415	0	0	55.3	6.9	0	255.73	27.65	20.74	1078.2	82.94	13.8	0	0
428	0	41.47	13.8	0	0	394	0	62.2	5778.7	6.9	0	62.2	0
442	0	0	62.2	31.1	5.2	336.95	82.9	98.49	1985.4	197	0	0	0
456	0	0	0	0	10.37	186.6	0	98.54	1270.03	15.55	72.57	0	0
471	0	0	0	0	13.8	82.94	27.65	103.7	988.4	62.2	62.2	0	0
484	0	0	0	0	8.3	70.5	20.74	4.15	568.14	24.88	0	0	0
498	0	0	0	0	31.1	155.5	10.36	5.2	891.6	5.2	0	0	0
510	0	0	0	0	0	435.4	20.74	4.15	688.4	20.74	0	0	0
525	0	0	0	0	0	129.6	15.6	0	269.6	15.6	2.59	0	0
539	0	0	0	0	0	27	14.5	0	16.6	6.22	0	0	0
554	0	0	0	0	0	8.3	0	0	8.3	4.15	0	0	0
569	0	0	0	0	0	19	1.73	0	3.46	3.46	0	0	0
579	0	0	0	0	0	10.36	0	0	5.18	3.9	0	0	0
596	0	0	0	0	0	45.6	0	0	41.5	2.07	6.2	0	0
613	0	0	0	0	0	49.8	0	0	31.1	2.07	2.07	0	0
629	0	0	0	0	0	149.3	0	0	24.9	4.14	6.2	0	0
643	0	0	0	0	0	72.57	0	0	53.9	4.14	18.66	0	0
656	0	0	0	0	0	39.96	0	0	41.5	1.48	7.4	0	0
672	0	0	0	0	0	91.96	0	0	3.5	0	0	0	0

Table 1: Continued

Day	*Centritractus belanophorus*	*Anabaena circinalis*	*Microcysis* spp.	*Aphanocapsa*	*Trachelomonas planktonica*	*T. volvocina*	*Trachelomonas* sp.	*Phacus* spp.	*Cryptomonas* spp.	*Peridinium cinctum*	*Ceratium* sp.	*Closterium* spp.	*Staurastrum* spp.	Total phytoplankton
280	0	0	0	0	0	15.6	0	0	44.1	0	0	0	7.8	614.3
295	0	0	0	0	0	8.6	0	0	31.1	0	0	1.7	13.8	364.6
304	0	0	0	0	0	13.8	0	0	12.1	0	0	0	15.55	257.35
323	0	0	0	0	0	10.4	0	0	10.3	1.7	0	0	33	494
338	0	0	0	0	0	5.2	0	0	12.1	0	0	0	98.5	654.6
352	0	0	0	0	0	0	0	10.36	72.56	0	0	0	10.36	5702.18
366	0	0	0	0	0	20.74	0	0	103.7	10.36	0	0	114	10182.94
381	0	0	0	0	0	110.59	0	0	90.26	83.35	0	0	763.95	23765.31
394	31.1	0	0	103.68	0	269.56	10.36	10.36	62.2	10.36	0	0	539.12	6718.11
415	0	41.47	179.7	165.88	0	255.73	6.9	6.9	20.74	13.8	0	0	34.54	2591.77
428	27.65	55.3	331.76	13.8	0	387.06	0	13.8	0	6.9	0	0	13.8	7319.92
442	15.55	5.2	77.76	15.55	0	150.3	0	0	15.55	82.9	0	0	72.6	3333.15
456	0	0	0	0	0	1270.03	0	5.2	5.2	295.5	0	0	88.09	3369.55
471	0	0	0	0	0	1354.7	0	6.9	0	511.5	0	0	82.94	3365.63
484	0	0	0	4.15	0	501.8	0	0	4.15	116.1	0	0	20.74	1364.4
498	0	0	0	0	0	523.6	0	5.2	10.36	342.1	0	0	36.3	2078.79
510	0	0	0	0	0	452	16.6	0	12.5	215.6	128.6	0	0	2015.48
525	0	0	0	0	0	300.7	0	0	5.18	41.5	127	0	0	912.55
539	0	0	0	0	0	280	0	0	4.15	41.5	39.4	0	0	429.37
554	0	0	0	0	0	505.9	8.3	0	62.25	0	360.8	0	0	958
569	0	0	0	0	0	122.7	1.73	0	48.4	0	93.3	0	0	295.51
579	0	0	0	0	0	131.3	0	0	14.3	1.3	23.3	0	0	190.94
596	0	0	0	0	0	41.5	0	0	12.44	0	0	0	0	149.31
613	0	0	0	0	0	18.66	0	0	124.4	0	4.14	0	0	232.24
629	0	0	0	0	0	8.28	0	0	180.39	0	2.07	0	0	375.28
643	0	0	0	0	0	8.28	0	0	103.66	0	0	0	0	261.21
656	0	0	0	0	0	14.8	0	0	14.8	0	0	0	0	119.94
672	0	0	0	0	0	20.74	0	0	133.1	0	69.1	0	0	318.4

Table 2: Zooplankton counts (numbers per 100 litres)

Day	*C.pulchella*	*C.dubia*	*Bosmina longirostris*	*Bosmina meridionalis*	*Mesocyclops*	*Boeckella*	*Calamoecia*	Nauplii	*Keratella cochlearis*	*Keratella tropica*	*Conochilus*	*Polyarthra remata*	*Filinia pejleri*	*Synchaeta*	*Brachionus angularis*
1	223	330	0	57	1325	3425	4575	10100	0	1075	8225	0	175	17950	0
8	557	641	0	372	2250	3690	7298	19300	0	518	5700	0	0	150	17
15	129	70	0	1197	1675	4450	5425	31650	33	312	0	0	3100	27	39
22	23	2	0	3283	3175	5100	9150	4500	0	384	0	0	17350	0	0
29	4	0	0	7390	3888	1150	2675	63050	0	509	0	0	635	0	11
36	10	0	0	14545	7575	2007	4356	20080	189	4168	4810	0	530	1932	303
43	19	0	0	43142	8503	871	9716	12503	76	7350	682	0	1364	227	1212
50	26	0	0	31727	6370	1200	11506	18420	83	13000	250	0	0	0	1334
57	19	0	0	15491	3068	850	9872	54094	278	11947	445	417	458	0	300
64	29	0	0	259	1211	1250	14975	12377	167	5376	667	583	778	0	611
71	22	0	0	60	2278	2708	9666	37500	1900	3600	0	1133	600	0	0
78	5	0	0	319	6125	3583	13750	25700	21100	6800	0	1200	900	483	400
85	5	0	0	447	9041	3292	9208	14836	11253	3251	0	500	167	583	0
92	5	0	0	1175	11833	1500	10208	16753	36757	4334	0	2250	250	834	667
100	28	0	0	1804	1333	2417	8041	16837	52350	1500	0	667	278	0	1500
107	2806	0	4	16	2750	1611	9083	26550	42750	806	0	611	278	27	1083
120	9000	0	59	150	13133	1626	6422	10600	2200	3467	0	67	467	0	67
127	17725	0	73	2466	6275	2750	5350	11550	150	2250	0	0	1050	0	0
134	36000	0	1183	2466	6360	3100	3833	16221	350	3910	0	0	467	0	0
141	30809	0	8425	2300	14938	2000	4125	16221	525	7877	0	0	175	0	0
148	23791	0	5866	3216	14624	3833	7416	17866	267	4867	333	467	0	0	0
155	26207	0	5736	2801	8291	1417	4375	34674	500	7000	0	667	167	0	0
162	19041	0	10916	1833	10222	1111	2472	21667	208	3708	0	375	0	42	0
169	16833	0	2127	1147	4208	2417	4375	14753	208	1667	83	2167	0	83	0
177	9250	0	9583	2875	4125	2958	4500	5825	150	967	0	67	50	0	17
190	16541	0	8458	375	1722	1417	2833	9125	783	1283	0	250	117	200	17
201	6625	0	21124	100	1350	450	2875	14583	375	1650	0	117	150	350	0
213	9405	0	11539	0	400	533	6070	11000	217	967	0	0	50	100	0
236	2783	8	2266	0	94	94	2062	5469	104	896	0	83	63	94	0
250	2400	17	4200	0	225	113	4250	8475	225	250	0	25	50	650	25
264	1883	14	7566	0	611	89	5655	10125	217	67	0	0	33	1033	0

Table 2: Continued

Day	*Pompholyx sulcata*	*Trichocerca similis*	*Hexarthra mira*	*Asplanchna* spp.	*Epiphanes clavulata*	*Piona*	*Anisops*	*Euchlanis dilatata*	*Brachionus large sp.*	*Trichocerca gracilis*	Total zooplankton	Total Rotifera	Total Cladocera	Total Copepoda
1	0	100	0	0	0	0	0	0	0	0	47560	27525	610	19425
8	0	217	0	1209	0	0	0	0	0	0	41919	7811	1570	32538
15	39	173	0	33	0	0	1	0	0	0	48353	3756	1396	43200
22	50	42	25	0	0	0	0	0	0	0	43084	17851	3308	21925
29	72	161	58	6	0	0	0	0	0	0	79609	1452	7394	70763
36	1629	1894	28869	152	0	0	0	0	0	0	93049	44476	14555	34018
43	3789	909	6289	776	0	0	0	0	0	0	97428	22674	43161	31593
50	29422	667	5084	0	0	0	0	0	0	0	119089	49840	31753	37496
57	46200	223	0	400	0	0	0	0	0	0	144062	60668	15510	67884
64	67200	722	5584	176	0	0	0	53	0	0	112018	81917	288	29813
71	48100	750	933	251	0	0	0	22	0	0	109523	57289	82	52152
78	35100	600	4200	833	0	0	0	100	0	0	121198	71716	324	49158
85	16753	250	1750	1417	0	1	0	0	0	0	72754	35924	452	36377
92	8168	417	667	2120	0	0	0	8	0	0	97946	56472	1180	40294
100	834	778	667	34	0	0	0	0	0	0	89068	58608	1832	28628
107	3305	917	278	534	0	0	0	17	27	0	93453	50633	2826	39994
120	2533	200	800	0	0	0	0	0	0	0	50791	9801	9209	31781
127	550	500	1600	25	0	0	0	0	0	0	52314	6125	20264	25925
134	1400	700	584	0	0	0	0	0	0	0	76574	7411	39649	29514
141	992	408	175	0	0	0	0	0	0	0	88970	10152	41534	37284
148	400	733	0	83	0	0	0	0	0	0	83762	7150	32873	43739
155	500	1084	250	125	0	0	0	0	0	0	93794	10293	34744	48757
162	292	1417	375	42	0	0	0	0	0	0	73721	6459	31790	35472
169	333	1083	250	42	0	0	0	0	0	0	51776	5916	20107	25753
177	67	483	200	42	0	0	0	0	0	0	41159	2043	21708	17408
190	133	417	133	0	0	0	0	0	67	0	43871	3400	25374	15097
201	75	825	350	0	0	0	0	0	50	0	51049	3942	27849	19258
213	133	500	133	0	0	0	0	0	0	0	41047	2100	20944	18003
236	167	906	135	0	0	0	0	0	10	0	15234	2458	5057	7719
250	67	650	50	0	0	0	0	0	25	0	21697	2017	6617	13063
264	0	350	0	0	0	0	0	0	0	0	27643	1700	9463	16480

Table 2: Continued

Day	*C.pulchella*	*C.dubia*	*Bosmina longirostris*	*Bosmina meridionalis*	*Mesocyclops*	*Boeckella*	*Calamoecia*	Nauplii	*Keratella cochlearis*	*Keratella tropica*	*Conochilus*	*Polyarthra remata*	*Filinia pejleri*	*Synchaeta*	*Brachionus angularis*
280	1689	98	22832	0	483	417	8750	7875	500	444	0	83	167	125	0
295	4013	388	13042	0	225	188	2558	4333	63	175	0	25	138	313	0
310	3769	744	1863	0	288	156	2438	6866	100	63	0	6	125	2433	0
323	3927	1146	3791	0	326	83	1055	6900	83	125	0	375	500	6416	0
338	9009	903	4166	0	1048	115	4510	14000	167	42	0	2333	833	42	0
352	1833	3450	750	0	6470	233	8371	22800	2850	0	0	2850	500	16800	0
366	308	177	2284	0	3583	375	2208	12900	750	0	38400	0	450	0	0
381	24	2	981	0	3669	225	3635	14000	58	350	4493	584	3734	58	0
394	0	0	3333	0	4825	350	10850	22400	13700	4300	400	2000	2000	4300	0
414	0	0	2833	0	1883	683	4833	13586	19420	1584	0	750	1500	2420	0
428	0	0	112200	0	22050	2600	34500	157875	352875	28500	1500	25875	6000	1875	2750
434	0	0	91320	0	10270	1685	16370	30300	.			.	.		
442	0	0	8104	0	4669	1200	3224	11161	1434	400	0	67	700	289	367
456	0	0	12239	0	3492	142	950	37047	300	967	133	167	567	33	733
471	0	0	46700	0	11707	453	3707	38520	1500	14700	2700	800	3800	200	6100
484	0	0	7750	0	19200	2000	2100	10800	150	11600	3800	900	1300	600	100
498	0	0	11700	100	18350	3350	4450	25560	480	11640	22920	0	2160	0	0
510	0	0	31500	375	6233	3450	5500	31300	600	14500	5600	0	3000	0	0
525	0	0	34000	0	2233	4167	6267	27900	12300	800	8000	400	2500	0	0
539	40	0	8700	0	800	2800	4550	26200	200	533	3000	0	1933	0	0
554	181	6	23800	0	600	1567	1775	12800	200	400	2100	0	3600	0	0
569	440	53	19100	0	180	1240	4280	12000	300	0	3100	0	5600	0	0
579	1360	473	45900	0	75	2950	5125	33480	360	540	63540	0	4320	0	0
596	633	933	7140	20	40	747	1773	3600	0	0	800	0	4100	0	0
613	405	1448	1800	7	25	208	1867	2650	0	17	125	17	1392	0	0
629	500	3905	2650	0	45	5640	735		0	0	585	0	3885	180	0
643	580	4410	1320	0	120	1300	3260	10220	0	40	370	30	780	2660	0
656	420	3880	2050	0	40	2140	5160	3940	0	40	20	1470	50	0	0
672	120	4700	1130	0	220	2080	6860	4740	0	20	0	0	540	20	0

Table 2: Continued

Day	*Pompholyx sulcata*	*Trichocerca similis*	*Hexarthra mira*	*Asplanchna* spp.	*Epiphanes clavulata*	*Piona*	*Anisops*	*Euchlanis dilatata*	*Brachionus large sp.*	*Trichocerca gracilis*	Total zooplankton	Total Rotifera	Total Cladocera	Total Copepoda
280	0	944	83	0	0	0	0	0	0	292	44782	2638	24619	17525
295	88	763	0	0	0	0	0	0	0	150	26462	1715	17443	7304
310	50	656	0	0	0	0	0	0	0	0	19557	3433	6376	9748
323	208	5333	0	0	0	0	0	0	0	0	30268	13040	8864	8364
338	375	7541	0	56	0	0	2	0	0	0	45142	11389	14078	19673
352	900	19800	0	122	0	0	0	0	0	0	87729	43822	6033	37874
366	3750	2550	0	31	0	0	0	0	0	0	67766	45931	2769	19066
381	1109	934	4085	97	0	0	0	0	0	467	38505	15969	1007	21529
394	7900	600	2700	31	0	0	0	0	0	0	79689	37931	3333	38425
414	333	667	7585	1467	0	0	1	0	0	0	59545	35726	2833	20985
428	6750	10125	20250	2900	7200	0	0	0	0	0	795825	466600	112200	217025
434	.	.	.		.	.	.	.	.		149945	.	91320	58625
442	467	334	400	0	6000	0	0	0	0	0	38816	10458	8104	20254
456	733	1333	1233	0	448	0	0	0	0	0	60517	6647	12239	41631
471	7000	5000	2100	0	560	0	0	0	0	0	145547	44460	46700	54387
484	8500	2100	600	133	0	0	0	0	33	0	71666	29816	7750	34100
498	1920	1560	0	0	0	0	0	0	0	0	104190	40680	11800	51710
510	1600	1400	0	233	0	0	0	0	0	0	105291	26933	31875	46483
525	4000	1000	0	333	0	0	0	0	0	0	103900	29333	34000	40567
539	2533	0	0	93	0	0	0	0	0	0	51382	8292	8740	34350
554	0	200	0	19050	0	0	0	2500	0	0	68779	28050	23987	16742
569	400	300	0	46800	0	0	0	0	0	0	93793	56500	19593	17700
579	540	180	0	87660	0	0	0	0	0	0	246503	157140	47733	41630
596	0	40	0	20	0	0	0	0	0	0	19846	4960	8726	6160
613	17	25	0	0	0	0	0	0	0	0	10003	1593	3660	4750
629	45	45	0	0	0	0	0	0	0	0	18215	4740	7055	.
643	10	30	0	0	0	0	0	0	0	0	25130	3920	6310	14900
656	100	0	0	0	0	0	0	0	0	0	19310	1680	6350	11280
672	0	140	0	0	20	0	0	0	0	0	20590	740	5950	13900

APPENDIX TWO

Replicate samples of zooplankton and estimates of sample precision from Lake Mangakaware on 24 November 1987

Replicate samples of zooplankton from Lake Mangakaware (24 November 1987) with estimated $\hat{k}$ and predicted coefficients of variation, SE/$\bar{x}$ (%). See text for details.

Taxon	Sample Number 1	2	3	4	5	$\bar{x}$	S^2	$\hat{k}$	SE/$\bar{x}$ (%)
Ceriodaphnia pulchella	557	480	475	380	740	526.4	1.82×10^4	15.65	11.5
C. dubia	641	630	690	550	730	648.2	4.62×10^3	105.89	4.8
Bosmina meridionalis	372	415	380	290	490	389.4	5.26×10^3	31.12	8.4
Mesocyclops leuckarti	2250	2400	2200	1900	3600	2470	4.32×10^5	14.13	11.9
Boeckella delicata	3690	3600	3550	2900	1800	3108	6.33×10^5	15.30	11.5
Calamoecia lucasi	7298	7400	7300	5900	8700	7321.6	9.82×10^5	54.98	6.05
Nauplii	19300	18900	20300	17500	22600	19720	3.6×10^6	108.62	4.3
Keratella tropica	518	560	500	480	680	547.6	6.35×10^3	51.68	6.5
Conochilus	5700	7600	5900	6100	3200	5700	2.52×10^6	12.95	1.5
Synchaeta	150	120	115	180	60	125	2.00×10^3	8.33	16.0
Trichocerca similis	217	250	190	230	140	205.4	1.81×10^3	26.29	9.3
Asplanchna	1210	1300	1150	1430	800	1194	3.40×10^4	43.5	6.9
Total	41893	33685	42740	37840	43540	39940	1.70×10^7	93.48	4.6

APPENDIX THREE

Recognition of ephippial and male *Bosmina*

Identification of ephippial females and males of *Bosmina*

The occurrence of males and ephippial females of *Bosmina* appears to be uncommon in New Zealand. Jolly (1955) recorded neither in her collections from some thirty lakes and ponds throughout New Zealand, and although Donovan (1970) recorded ephippial females in both field samples and laboratory cultures, males were not found, and it was suggested that *B. meridionalis* might produce fertile resting eggs asexually. Males and ephippial females of *B. meridionalis* occurred within a very restricted time period in Lake Mangakaware in 1987 as was the case in 1986 also (Greenwood 1987). Ephippial females were abundant in the *B. longirostris* population on only one occasion and although males were not found they did occur infrequently in cultures raised in the laboratory. The infrequent appearance of gamogenetic individuals in field populations of *Bosmina* probably explains their apparent rarity in New Zealand. In addition, males superficially resemble juveniles and could easily be missed if their numbers formed a very small proportion of the population. Moreover, gamogenetic individuals frequently occur at high population densities (Donovan 1970; Greenwood 1987; this study), and they may be rare, or absent, in the subsamples taken for enumeration.

Features of male and ephippial *B. meridionalis* are outlined below and in Figure 1. Recognition of gamogenetic *B. longirostris* is based on similar morphological characteristics. These are intended as a guide for the recognition of animals in field populations, and details of postabdomens and male claspers are not included. These are given by Smirnov and Timms (1983).

Ephippial females

The eggs of ephippial *Bosmina* are larger and darker than those of parthenogenetic individuals, only one egg is carried at a time, and the carapace is ridged and thickened (Fig. 1A, Plate 1). Under high power light microscopy the thickened carapace ridges are darkened and have a speckled appearance but, unlike the ephippia of *Ceriodaphnia*, there is no obvious sculpturing.

Males

In preserved samples, males are most easily recognised by the blunt rostrum and the large antennules (Fig. 1B). The body shape is similar to the adolescent instar.

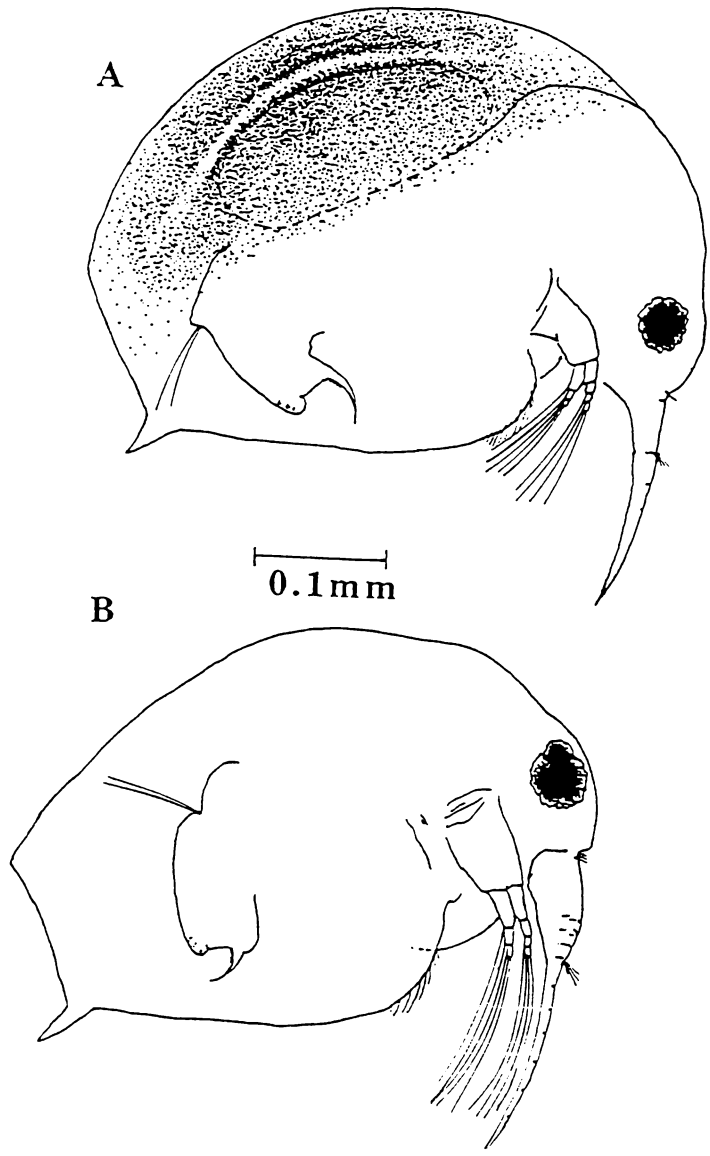
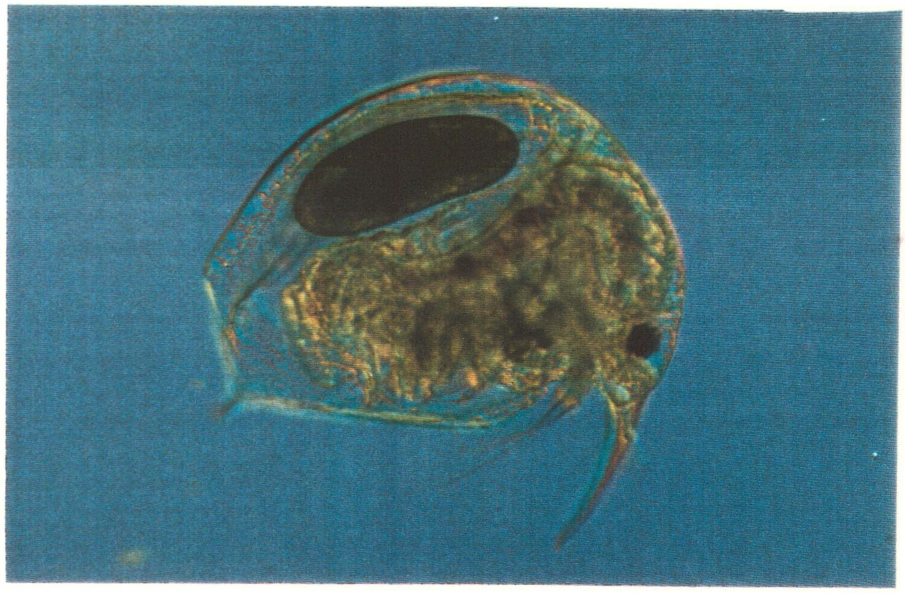


Figure 1. *Bosmina meridionalis*. A. Ephippial female and B. male. Recognition features in *B. longirostris* are similar.

PLATE 1



Bosmina meridionalis
Ephippial female (X160)

APPENDIX FOUR

Multiple linear regressions relating embryonic development time to temperature in *Ceriodaphnia* and *Bosmina*

Curvilinear regression equations relating the duration of embryonic development (EDT), in hours, to temperature (T), in °C, in *Bosmina meridionalis*, *B. longirostris*, *Ceriodaphnia pulchella*, and *C. dubia*. ANOVA tables and probabilities for each regression are given below.

	Species								n	r^2
EDT	*B. meridionalis*	ℓnEDT	=	6.069	+	0.318 lnT	-	0.313 $(\ln T)^2$	215	0.972
	B. longirostris	ℓnEDT	=	4.048	+	1.404 lnT	-	0.482 $(\ln T)^2$	277	0.948
	C. pulchella	ℓnEDT	=	10.494	-	2.839 lnT	+	0.239 $(\ln T)^2$	382	0.958
	C. dubia	ℓnEDT	=	7.245	-	1.081 lnT	-	0.009 $(\ln T)^2$	431	0.938

Analysis of variance

	Source	SS	DF	MS	F	p
B. meridionalis	Regression	46.446	2	23.223	3621.122	0.0001
	Residual	1.360	212	0.006		
B. longirostris	Regression	28.384	2	14.192	2491.704	0.0001
	Residual	1.561	274	0.006		
C. pulchella	Regression	82.706	2	41.353	4319.512	0.0001
	Residual	3.628	379	0.010		
C. dubia	Regression	40.198	2	20.099	3241.425	0.0001
	Residual	2.654	428	0.006		

APPENDIX FIVE

Population structure, dynamics, and reproductive parameters of *Ceriodaphnia* and *Bosmina* from Lake Mangakaware November 1987 - September 1989

Table 1: Reproductive parameters and population structure of *Bosmina meridionalis*

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females ovigerous	Number of adult females ovigerous	Egg stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Proportion of males	Number of males	Minimum size at first reprodn	Adult LOI	Juvenile LI
1	57	1.250	0.538	30.67	0.800	24.53	30.67	0.462	26.33	0.0000	0.00	0.000	0.00	0.250	0.080	0.700
8	372	1.304	0.491	182.65	0.516	94.25	122.90	0.509	189.35	0.0000	0.00	0.000	0.00	0.275	0.310	0.726
15	1197	1.704	0.623	745.73	0.901	671.90	1144.92	0.377	451.27	0.0000	0.00	0.000	0.00	0.250	0.581	0.648
22	3283	1.446	0.535	1756.41	0.902	1584.28	2290.86	0.465	1526.60	0.0000	0.00	0.000	0.00	0.250	0.164	0.208
29	7390	1.675	0.421	3111.19	0.938	2918.30	4888.15	0.579	4278.81	0.0000	0.00	0.000	0.00	0.260	0.602	0.561
36	14545	1.441	0.553	8043.39	0.905	7279.26	10489.42	0.447	6501.62	0.0160	128.69	0.000	0.00	0.260	0.143	0.059
43	43142	1.047	0.377	16264.53	0.605	9840.04	10302.53	0.623	26877.47	0.0470	764.43	0.000	0.00	0.290	0.256	0.100
50	31727	1.000	0.500	15863.50	0.386	6123.31	6123.31	0.447	14181.97	0.0526	834.42	0.053	1681.53	0.300	0.193	0.078
57	15491	1.040	0.740	11463.34	0.311	3565.10	3707.70	0.260	4027.66	0.0135	154.76	0.000	0.00	0.300	0.000	0.000
64	259	1.000	0.930	240.87	0.151	36.37	36.37	0.070	18.13	0.0000	0.00	0.000	0.00	0.300	0.000	0.000
71	60	1.077	0.536	32.16	0.289	9.29	10.01	0.464	27.84	0.1560	5.02	0.000	0.00	0.300	0.044	0.000
78	319	1.000	0.649	207.03	0.500	103.52	103.52	0.351	111.97	0.2080	43.06	0.000	0.00	0.300	0.080	0.000
85	447	1.400	0.895	400.07	0.294	117.62	164.67	0.105	46.94	0.0000	0.00	0.000	0.00	0.300	0.000	0.000
92	1175	1.182	1.000	1175.00	0.733	861.28	1018.03	0.000	0.00	0.0000	0.00	0.000	0.00	0.310	0.200	0.000
100	1804	1.364	0.633	1141.93	0.710	810.77	1105.89	0.367	662.07	0.0000	0.00	0.000	0.00	0.275	0.130	0.110
107	16	1.071	0.875	14.00	0.667	9.34	10.00	0.125	2.00	0.0000	0.00	0.000	0.00	0.300	0.048	0.000
120	150	1.038	0.635	95.25	0.772	73.53	76.33	0.365	54.75	0.0000	0.00	0.000	0.00	0.290	0.525	0.239
127	2466	1.563	0.645	1590.57	0.888	1412.43	2207.62	0.355	875.43	0.0000	0.00	0.000	0.00	0.290	0.338	0.159
134	2466	1.299	0.667	1644.82	0.761	1251.71	1625.97	0.333	821.18	0.0000	0.00	0.000	0.00	0.300	0.080	0.136
141	2300	1.000	0.604	1389.20	0.458	635.70	635.70	0.396	910.80	0.0000	0.00	0.000	0.00	0.325	0.016	0.000
148	3216	1.000	0.410	1318.56	0.195	257.12	257.12	0.590	1897.44	0.0000	0.00	0.000	0.00	0.310	0.038	0.000
155	2801	1.000	0.637	1784.24	0.400	713.69	713.69	0.363	1016.76	0.0000	0.00	0.000	0.00	0.310	0.000	0.000
162	1833	1.000	0.630	1154.79	0.571	659.39	659.39	0.370	678.21	0.0000	0.00	0.000	0.00	0.325	0.079	0.054
169	1147	1.000	0.440	504.68	0.409	206.41	206.41	0.560	642.32	0.0000	0.00	0.000	0.00	0.310	0.045	0.054
177	2875	1.000	0.280	805.00	0.250	201.25	201.25	0.720	2070.00	0.0000	0.00	0.000	0.00	0.310	0.071	0.038
190	375	1.000	0.360	135.00	0.361	48.74	48.74	0.640	240.00	0.0000	0.00	0.000	0.00	0.350	0.000	0.000
201	100	1.000	0.260	26.00	0.077	2.00	2.00	0.740	74.00	0.0000	0.00	0.000	0.00	0.325	0.154	0.000
213	0	0.000	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.0000	0.00	0.000	0.00	0.000	0.000	0.000

Table 2: Reproductive parameters and population structure of *Bosmina longirostris*

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females	Number of adult females ovigerous	Egg Stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Minimum size at first	Adult LOI	Juvenile LI
100	0	.												
107	0	.	.	.	.	.	.	.	.	.	.	.	.	.
120	59	1.960	0.500	29.50	1.000	29.50	57.82	0.500	29.50	0.00	0.00	0.340	0.520	0.240
127	73	2.571	0.280	20.44	1.000	20.44	52.55	0.720	52.56	0.00	0.00	0.350	0.429	0.056
134	1183	1.614	0.460	544.18	0.957	520.78	840.54	0.540	638.82	0.00	0.00	0.325	0.087	0.093
141	8425	1.180	0.395	3327.88	0.698	2321.86	2739.79	0.605	5097.13	0.00	0.00	0.300	0.040	0.030
148	5866	1.000	0.480	2815.68	0.667	1878.06	1878.06	0.520	3050.32	0.00	0.00	0.375	0.104	0.000
155	5736	1.050	0.386	2214.10	0.614	1359.45	1427.43	0.614	3521.90	0.00	0.00	0.375	0.000	0.000
162	10916	1.056	0.482	5261.51	0.642	3377.89	3567.05	0.518	5654.49	0.00	0.00	0.390	0.000	0.000
169	2127	1.094	0.480	1020.96	0.833	850.46	930.40	0.520	1106.04	0.00	0.00	0.390	0.057	0.580
177	9583	1.075	0.420	4024.86	0.829	3336.61	3586.85	0.580	5558.14	0.00	0.00	0.390	0.083	0.069
190	8458	1.000	0.110	930.38	0.091	84.66	84.66	0.890	7527.62	0.00	0.00	0.410	0.182	0.000
201	21124	1.000	0.130	2746.12	0.462	1268.71	1268.71	0.870	18377.88	0.00	0.00	0.410	0.034	0.046
213	11539	1.000	0.120	1384.68	0.333	461.10	461.10	0.880	10154.32	0.00	0.00	0.410	0.000	0.000
236	2266	1.000	0.190	430.54	0.684	294.49	294.49	0.810	1835.46	0.00	0.00	0.425	0.000	0.000
250	4200	1.000	0.280	1176.00	0.520	611.52	611.52	0.720	3024.00	0.00	0.00	0.425	0.091	0.028
264	7566	1.554	0.550	4161.30	0.945	3932.43	6110.99	0.450	3404.70	0.00	0.00	0.390	0.123	0.022
280	22832	1.440	0.360	8219.52	0.758	6230.40	8971.77	0.640	14612.48	0.03	246.59	0.410	0.086	0.063
295	13042	1.048	0.240	3130.08	0.550	1721.54	1804.18	0.760	9911.92	0.00	0.00	0.400	0.027	0.000
309	1863	1.020	0.441	821.96	0.442	363.30	370.57	0.559	1041.04	0.00	0.00	0.425	0.000	0.000
323	3791	1.340	0.450	1705.95	0.822	1402.63	1879.53	0.550	2085.05	0.00	0.00	0.390	0.060	0.000
338	4166	1.000	0.230	958.18	0.087	83.36	83.36	0.770	3207.82	0.00	0.00	0.410	0.000	0.000
352	750	1.430	0.470	352.50	0.809	285.00	407.54	0.530	397.50	0.00	0.00	0.325	0.081	0.190
366	2284	1.810	0.440	1004.96	0.930	934.81	1692.01	0.560	1279.04	0.00	0.00	0.310	0.230	0.036
381	981	1.160	0.390	382.59	0.949	362.96	421.04	0.610	598.41	0.00	0.00	0.300	0.039	0.130
393	3333	1.470	0.691	2302.44	0.981	2258.69	3320.27	0.309	1030.56	0.00	0.00	0.290	0.230	0.300
415	2833	1.600	0.447	1267.48	0.941	1192.96	1908.73	0.553	1565.52	0.00	0.00	0.290	0.290	0.095

Table 2: Reproductive parameters and population structure of *Bosmina longirostris*

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females	Number of adult females ovigerous	Egg Stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Minimum size at first	Adult LOI	Juvenile LI
428	112200	1.045	0.220	24684.00	0.727	17952.67	18760.54	0.780	87516.00	0.00	0.00	0.300	0.140	0.013
434	91320	1.076	0.260	23743.20	0.750	17807.40	19160.76	0.740	67576.80	0.00	0.00	0.310	0.100	0.013
442	8104	1.107	0.310	2512.24	0.774	1944.98	2153.09	0.690	5591.76	0.00	0.00	0.310	0.061	0.014
456	12239	1.074	0.190	2325.41	0.895	2080.54	2234.50	0.810	9913.59	0.00	0.00	0.325	0.000	0.000
471	46700	1.156	0.310	14477.00	0.839	12141.86	14035.99	0.690	32223.00	0.00	0.00	0.300	0.098	0.000
484	7750	1.021	0.490	3797.50	0.898	3410.16	3481.77	0.510	3952.50	0.00	0.00	0.310	0.080	0.039
498	11700	1.202	0.478	5590.26	0.767	4289.97	5156.54	0.522	6109.74	0.00	0.00	0.310	0.365	0.149
510	31500	1.040	0.378	11900.70	0.647	7700.94	8008.98	0.622	19599.30	0.00	0.00	0.350	0.074	0.000
525	34000	1.000	0.478	16245.20	0.605	9823.47	9823.47	0.522	17754.80	0.00	0.00	0.375	0.048	0.043
539	8700	1.023	0.189	1643.43	0.529	870.03	890.04	0.811	7056.57	0.00	0.00	0.390	0.000	0.014
554	23800	1.000	0.272	6466.46	0.583	3771.89	3771.89	0.728	17333.54	0.00	0.00	0.400	0.046	0.148
569	19100	1.000	0.444	8488.04	0.641	5440.83	5440.83	0.556	10611.96	0.00	0.00	0.400	0.020	0.040
579	45900	1.000	0.456	20912.04	0.049	1020.51	1020.51	0.544	24987.96	0.00	0.00	0.400	0.016	0.000
596	7140	1.000	0.375	2677.50	0.035	93.98	93.98	0.625	4462.50	0.00	0.00	0.410	0.000	0.000
613	1800	1.286	0.633	1139.94	0.912	1039.97	1337.40	0.367	660.06	0.00	0.00	0.390	0.026	0.273
629	2650	1.000	0.567	1501.76	0.563	844.74	844.74	0.433	1148.25	0.00	0.00	0.400	0.162	0.000
643	1320	1.000	0.411	542.65	0.371	201.54	201.54	0.589	777.35	0.00	0.00	0.410	0.050	0.000
656	2050	1.040	0.456	933.98	0.585	546.75	568.62	0.544	1116.02	0.00	0.00	0.400	0.192	0.020

Table 3: Reproductive parameters and population structure of *Ceriodaphnia pulchella*

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females ovigerous	Number of adult females ovigerous	Egg stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Minimum size at first reprodn	Adult LOI	Juvenile LI
1	223	1.692	0.345	76.94	0.609	46.85	79.28	0.655	146.07	0.000	0.0	0.425	0.700	1.000
8	557	2.545	0.114	63.50	1.000	63.50	161.60	0.886	493.50	0.000	0.0	0.45	1.100	0.170
15	129	1.125	0.386	49.79	0.441	21.96	24.70	0.614	79.21	0.000	0.0	0.425	0.090	0.000
22	23	1.000	0.071	1.63	1.000	1.63	1.63	0.929	21.37	0.000	0.0	0.425	0.000	0.000
29	4	1.625	0.223	0.89	0.917	0.82	1.33	0.777	3.11	0.000	0.0	0.45	0.700	0.200
36	10	2.250	0.375	3.75	0.833	3.12	7.03	0.625	6.25	0.000	0.0	0.475	1.500	0.438
43	19	2.143	0.781	14.84	0.840	12.46	26.71	0.219	4.16	0.000	0.0	0.46	0.440	0.143
50	26	1.940	0.590	15.34	0.696	10.68	20.71	0.410	10.66	0.000	0.0	0.475	0.780	0.500
57	19	2.060	0.466	8.85	0.815	7.22	14.86	0.534	10.15	0.000	0.0	0.45	0.230	1.070
64	29	1.860	0.460	13.34	0.840	11.21	20.84	0.540	15.66	0.000	0.0	0.425	0.793	0.382
71	22	1.330	0.342	7.52	0.667	5.02	6.67	0.658	14.48	0.000	0.0	0.425	0.615	0.427
78	5	2.060	0.546	2.73	0.924	2.52	5.20	0.454	2.27	0.000	0.0	0.425	0.771	0.623
85	5	1.900	0.513	2.57	0.795	2.04	3.87	0.487	2.44	0.000	0.0	0.41	0.782	0.311
92	5	1.733	0.430	2.15	0.833	1.79	3.10	0.570	2.85	0.000	0.0	0.425	0.782	0.200
100	28	1.680	0.316	8.85	0.800	7.08	11.89	0.684	19.15	0.000	0.0	0.41	0.608	0.218
107	2806	1.386	0.289	810.93	0.719	583.06	808.12	0.711	1995.07	0.000	0.0	0.425	0.408	0.062
120	9000	1.338	0.342	3078.00	0.744	2290.03	3064.06	0.658	5922.00	0.000	0.0	0.425	0.338	0.240
127	17725	1.452	0.412	7302.70	0.913	6667.37	9681.01	0.588	10422.30	0.000	0.0	0.45	0.170	0.194
134	36000	1.180	0.395	14220.00	0.814	11575.08	13658.59	0.605	21780.00	0.000	0.0	0.45	0.410	0.072
141	30809	1.000	0.360	11091.24	0.475	5268.34	5268.34	0.640	19717.76	0.000	0.0	0.475	0.100	0.082
148	23791	1.000	0.342	8136.52	0.487	3962.49	3962.49	0.658	15654.48	0.000	0.0	0.525	0.273	0.053
155	26207	1.000	0.439	11504.87	0.578	6649.82	6649.82	0.561	14702.13	0.000	0.0	0.51	0.205	0.109
162	19041	1.000	0.439	8359.00	0.191	1596.57	1596.57	0.561	10682.00	0.000	0.0	0.525	0.158	0.031
169	16833	1.000	0.440	7406.52	0.171	1266.51	1266.51	0.560	9426.48	0.000	0.0	0.525	0.000	0.000
177	9250	1.000	0.480	4440.00	0.711	3156.84	3156.84	0.520	4810.00	0.000	0.0	0.525	0.021	0.090
190	16541	1.000	0.430	7112.63	0.500	3556.32	3556.32	0.570	9428.37	0.000	0.0	0.55	0.010	0.000

Table 3: Continued

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females ovigerous	Number of adult females ovigerous	Egg stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Minimum size at first reprodn	Adult LOI	Juvenile LI
201	6625	1.000	0.550	3643.75	0.500	1821.88	1821.88	0.450	2981.25	0.000	0.0	0.55	0.122	0.044
213	9405	1.000	0.370	3479.85	0.375	1304.94	1304.94	0.630	5925.15	0.000	0.0	0.54	0.075	0.048
236	2783	1.000	0.530	1474.99	0.644	949.89	949.89	0.470	1308.01	0.000	0.0	0.575	0.115	0.000
250	2400	1.000	0.460	1104.00	0.676	746.30	746.30	0.540	1296.00	0.000	0.0	0.55	0.156	0.111
264	1883	2.191	0.550	1035.65	0.885	916.55	2008.16	0.450	847.35	0.018	18.6	0.525	0.658	0.400
280	1689	1.964	0.330	557.37	0.931	518.91	1019.14	0.670	1131.63	0.000	0.0	0.525	0.726	0.119
295	4013	2.313	0.420	1685.46	0.947	1596.13	3691.85	0.580	2327.54	0.000	0.0	0.51	0.505	0.034
309	3769	1.650	0.240	904.56	0.875	791.49	1305.96	0.760	2864.44	0.000	0.0	0.5	0.410	0.013
323	3927	1.760	0.380	1492.26	0.790	1178.14	2073.53	0.620	2434.74	0.010	14.9	0.475	0.600	0.440
338	9009	1.000	0.100	900.90	0.667	600.90	600.90	0.900	8108.10	0.000	0.0	0.475	0.100	0.022
352	1833	1.390	0.350	641.55	0.774	496.69	690.40	0.650	1191.45	0.000	0.0	0.475	0.275	0.215
366	308	1.210	0.566	174.24	0.600	104.54	126.50	0.434	133.76	0.000	0.0	0.475	0.036	0.047
381	0	0.000	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.0	0	0.000	0.000
525	0	0.000	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.0	0	0.000	0.000
539	40	2.890	0.683	27.33	1.000	27.33	78.99	0.317	12.67	0.000	0.0	0.51	1.268	0.368
554	181	3.330	0.500	90.50	0.920	83.26	277.26	0.500	90.50	0.000	0.0	0.525	1.560	0.660
569	440	2.910	0.322	141.77	0.957	135.60	394.60	0.678	298.23	0.000	0.0	0.525	0.972	0.492
579	1360	2.550	0.244	332.38	0.909	302.17	770.53	0.756	1027.62	0.000	0.0	0.525	0.327	0.088
596	633	2.180	0.396	250.41	0.909	227.65	496.28	0.604	382.59	0.000	0.0	0.51	0.760	0.455
613	405	2.340	0.311	126.00	0.963	121.33	283.92	0.689	279.00	0.000	0.0	0.54	0.736	0.210
629	500	1.431	0.244	122.20	1.000	122.20	174.87	0.733	366.65	0.000	0.0	0.54	0.724	0.273
643	580	1.330	0.422	244.88	0.633	155.01	206.16	0.578	335.12	0.000	0.0	0.54	0.108	0.000
656	420	1.000	0.200	84.00	0.533	44.80	44.80	0.800	336.00	0.000	0.0	0.575	0.773	0.125

Table 4: Reproductive parameters and population structure of *Ceriodaphnia dubia*

Day	Number per 100 litres	Mean clutch size	Proportion of adult females	Number of adult females	Proportion of adult females ovigerous	Number of adult females ovigerous	Egg stock	Proportion of juveniles	Number of juveniles	Proportion of adult females ephippial	Number of adult females ephippial	Proportion of males	Number of males	Minimum size at first reprodn	Adult LOI	Juvenile LI
1	330.0	1.15	0.412	135.96	0.458	62.27	71.61	0.588	194.04	0.000	0.00	0.000	0.00	0.475	0.476	0.463
8	641.0	3.98	0.263	168.58	0.920	155.10	617.28	0.737	472.42	0.000	0.00	0.000	0.00	0.500	0.560	0.025
15	70.0	0.00	0.377	26.39	0.000	0.00	0.00	0.623	43.61	0.000	0.00	0.000	0.00	.	0.000	0.000
22	2.0	2.00	0.667	1.33	1.000	1.33	2.67	0.333	0.67	0.000	0.00	0.000	0.00	0.575	2.000	0.000
29	0.0	0.00	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.00	0.000	0.00	.		
213	0.0	0.00	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.00	0.000	0.00	.		.
236	8.0	2.50	0.583	4.66	1.000	4.66	11.66	0.417	3.34	0.000	0.00	0.000	0.00	0.725	0.857	0.800
250	17.0	1.53	0.608	10.34	0.958	9.90	15.15	0.392	6.66	0.000	0.00	0.000	0.00	0.650	0.917	0.250
264	14.0	3.21	0.833	11.66	0.946	11.03	35.41	0.167	2.34	0.000	0.00	0.000	0.00	0.650	1.207	0.800
280	98.0	1.89	0.580	56.84	0.955	54.28	102.59	0.420	41.16	0.000	0.00	0.000	0.00	0.610	0.588	0.643
295	388.0	2.53	0.520	201.76	1.000	201.76	510.45	0.480	186.24	0.000	0.00	0.000	0.00	0.610	0.873	0.229
309	744.0	1.78	0.290	215.76	0.931	200.87	357.55	0.710	528.24	0.000	0.00	0.000	0.00	0.600	0.400	0.127
323	1146.0	1.37	0.320	366.72	0.613	224.80	307.98	0.610	699.06	0.031	11.37	0.070	80.22	0.625	0.774	0.262
338	903.0	1.00	0.230	207.69	0.333	69.16	69.16	0.650	586.95	0.174	36.14	0.120	108.36	0.650	0.190	0.015
352	3450.0	1.20	0.240	828.00	0.643	532.40	638.88	0.700	2415.00	0.000	0.00	0.060	207.00	0.650	0.250	0.014
366	177.0	1.40	0.414	73.28	0.172	12.60	17.65	0.586	103.72	0.000	0.00	0.000	0.00	0.675	0.103	0.000
381	0.0	0.00	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.00	0.000	0.00	.		
539	0.0	0.00	0.000	0.00	0.000	0.00	0.00	0.000	0.00	0.000	0.00	0.000	0.00	.		
554	6.0	3.50	0.429	2.57	0.667	1.72	6.01	0.571	3.43	0.000	0.00	0.000	0.00	0.740	0.429	0.286
569	53.0	4.33	0.800	42.40	1.000	42.40	183.59	0.200	10.60	0.000	0.00	0.000	0.00	0.650	1.091	0.227
579	473.0	2.67	0.254	120.14	1.000	120.14	320.78	0.746	352.86	0.000	0.00	0.000	0.00	0.650	0.690	0.128
596	933.0	2.46	0.211	196.86	1.000	196.86	484.28	0.789	736.14	0.000	0.00	0.000	0.00	0.650	1.034	0.183
613	1448.0	3.63	0.433	626.98	1.000	626.98	2275.95	0.556	805.09	0.000	0.00	0.011	15.93	0.650	0.780	0.260
629	3905.0	2.92	0.222	866.91	1.000	866.91	2531.38	0.778	3038.09	0.000	0.00	0.000	0.00	0.700	0.901	0.271
643	4410.0	1.90	0.189	833.49	0.615	512.60	973.93	0.811	3576.51	0.000	0.00	0.000	0.00	0.700	0.436	0.027
656	3880.0	1.51	0.200	776.000	0.923	716.25	1081.53	0.789	3061.32	0.077	59.75	0.011	42.68	0.700	0.494	0.211

Table 5: Estimated rates of population birth, death, and growth of *Bosmina* in Lake Mangakaware 1987-1989

Day	*Bosmina longirostris* b'	*Bosmina longirostris* d'	*Bosmina longirostris* r'	*Bosmina meridionalis* b'	*Bosmina meridionalis* d'	*Bosmina meridionalis* r'
1	.			0.183	-0.085	0.268
8	.			0.112	-0.055	0.167
15	.			0.305	0.16	0.144
22	.			0.233	0.117	0.116
29	.			0.243	0.147	0.097
36	.			0.299	0.144	0.155
43	.			0.098	0.142	-0.044
50	.			0.083	0.185	-0.102
57	.			0.122	0.707	-0.584
64	.			0.062	0.271	-0.209
71	.			0.073	-0.166	0.239
78	.			0.144	0.096	0.048
85	.			0.154	0.016	0.138
92	.			0.411	0.358	0.054
100	.			0.217	0.892	-0.675
107	.	.	.	0.211	0.038	0.172
120	0.39	0.359	0.03	0.171	-0.229	0.4
127	0.28	-0.118	0.398	0.263	0.263	0
134	0.262	-0.018	0.28	0.189	0.199	-0.01
141	0.134	0.186	-0.052	0.088	0.04	0.048
148	0.104	0.107	-0.003	0.02	0.04	-0.02
155	0.085	-0.007	0.092	0.065	0.125	-0.061
162	0.108	0.342	-0.234	0.089	0.155	-0.067
169	0.154	-0.034	0.188	0.05	-0.065	0.115
177	0.151	0.16	-0.01	0.023	0.179	-0.157
190	0.003	-0.08	0.083	0.028	0.148	-0.12
201	0.019	0.069	-0.05	0.005	.	
213	0.012	0.082	-0.071			
236	0.025	-0.019	0.044			
250	0.034	-0.008	0.042			
264	0.2	0.131	0.069			
280	0.109	0.146	-0.037			
295	0.038	0.177	-0.139			
309	0.061	0.011	0.051			
323	0.172	0.166	0.006			
338	0.008	0.131	-0.122			
352	0.227	0.147	0.08			
366	0.308	0.364	-0.056			
381	0.207	0.113	0.094			
393	0.44	0.454	-0.015			
415	0.333	0.05	0.283			
428	0.101	0.13	-0.029			
434	0.127	0.43	-0.303			
442	0.154	0.124	0.029			
456	0.089	-0.001	0.089			
471	0.157	0.295	-0.138			
484	0.195	0.166	0.029			
498	0.179	0.096	0.083			
510	0.098	0.092	0.005			
525	0.105	0.203	-0.097			
539	0.031	-0.036	0.067			
554	0.035	0.049	-0.015			
569	0.071	-0.016	0.088			
579	0.005	0.114	-0.109			
596	0.003	0.084	-0.081			
613	0.148	0.124	0.024			
629	0.066	0.115	-0.05			
643	0.039	0.005	0.034			
656	0.09	.				

Table 6: Estimated rates of population birth, death , and growth of *Ceriodaphnia* in Lake Mangakaware 1987-1989

Day	*Cerioadphnia dubia* b'	*Cerioadphnia dubia* d'	*Cerioadphnia dubia* r'	*Cerioadphnia pulchella* b'	*Cerioadphnia pulchella* d'	*Cerioadphnia pulchella* r'
1	0.101	0.006	0.095	0.133	0.002	0.131
8	0.377	0.694	-0.316	0.106	0.315	-0.209
15	0	0.508	-0.508	0.074	0.32	-0.246
22	0.505			0.028	0.278	-0.25
29				0.137	0.006	0.131
36				0.3	0.209	0.092
43				0.494	0.45	0.045
50				0.316	0.361	-0.045
57				0.355	0.294	0.06
64				0.293	0.333	-0.039
71				0.134	0.346	-0.212
78				0.414	0.414	0
85				0.311	0.311	0
92				0.306	0.091	0.215
100				0.165	-0.493	0.658
107				0.11	0.02	0.09
120				0.126	0.029	0.097
127				0.182	0.081	0.101
134				0.123	0.145	-0.022
141				0.06	0.097	-0.037
148				0.044	0.031	0.014
155				0.07	0.116	-0.046
162				0.023	0.041	-0.018
169				0.023	0.098	-0.075
177				0.114	0.07	0.045
190				0.049	0.133	-0.083
201				0.066	0.036	0.029
213				0.03	0.083	-0.053
236	0.25	0.196	0.054	0.037	0.047	-0.011
250	0.204	0.218	-0.014	0.05	0.067	-0.017
264	0.555	0.434	0.122	0.196	0.203	-0.007
280	0.283	0.192	0.092	0.126	0.069	0.058
295	0.333	0.287	0.047	0.177	0.182	-0.004
309	0.151	0.12	0.031	0.083	0.08	0.003
323	0.101	0.117	-0.016	0.15	0.095	0.055
338	0.032	-0.064	0.096	0.022	0.136	-0.114
352	0.084	0.296	-0.212	0.134	0.262	-0.127
366	0.047			0.15		
381						
394						
415						
428						
434						
442						
456						
471						
484						
498						
510						
525				0.48	0.372	0.108
539				0.309	0.249	0.059
554	0.208	0.063	0.145	0.121	0.045	0.075
569	0.67	0.452	0.219	0.1	0.177	-0.076
579	0.13	0.09	0.04	0.089	0.115	-0.026
596	0.112	0.086	0.026	0.094	0.082	0.012
613	0.296	0.234	0.062	0.045	0.036	0.009
629	0.131	0.123	0.009	0.045	0.068	-0.023
643	0.059	0.069	-0.01	0.02		
656	0.096					

APPENDIX SIX

Initial trials of the suitability of culture methods for *Ceriodaphnia*

A 6.1 INTRODUCTION

Earlier difficulties (Greenwood 1987) in rearing *Ceriodaphnia*, (particularly *C. pulchella*) successfully in the laboratory prompted an early trial period testing the suitability of a variety of different foods for growth and reproduction.

A 6.2 METHODOLOGY AND SOME COMMENTS ON CULTURING DIFFICULTIES

Trials 1 & 2

These trials were based on a culture medium of 72 hour aged and aerated tap water. Details of food preparation are given in Table 1,A and B, and treatment descriptions (1 - 5) in Table 2. A sixth treatment of *Scenedesmus* alone was trialed without any success (all *C. pulchella* died), and was abandoned. Animals were reared in 500 ml beakers with all test populations being started from 3 adult females (mean clutch = 2 - 3 eggs), and 7 juveniles. These animals were removed at random from stock populations collected from Lake Mangakaware and held at 20°C in 2 litre beakers containing daphnid dilution water (Appendix 7, Table 2) and supplemented with 5 - 8 x 10^4 cells ml^{-1} *Chlamydomonas*. For details of stock culture maintenance and algal culture see Part Three, Chapter Two.

Animals were held in static culture and fed daily. The water in the beakers was stirred gently, twice daily, to resuspend settling food. Dissolved oxygen levels were checked regularly with a YSI oxygen probe, and water was changed completely every second day (animals removed and replaced). After 9 days, animals produced in excess of 3 adult females were removed, preserved in sucrose-formalin (Prepas 1978), measured, and the clutch size of fecund females recorded. The numbers of males and ephippial females were noted separately where these were present. Measurement of body length followed the methods outlined in Part Two, Chapter Five. Trials continued for 22 (*C. dubia*) or 19 (*C. pulchella*) days in trial 1, and for 8 days in trial 2.

Table 1: Artificial foods used in initial feeding trials of *Ceriodaphnia*.

A. **Banta's Medium** (Banta 1921; modified from Staples 1984)

Constituents:

Garden soil	45.4 g
Horse manure (1-4 weeks old)	8.5 g
Aged tap water	425.0 ml

The above ingredients were mixed and left undisturbed in a glass jar at c. 15°C for 48 hours. The liquid was strained through 100 µm mesh plankton netting, allowing enough silt through to give a final strained volume of c. 400 ml. The mixture was used within 4 days.

B. **Yeast** (After Wang and Willis 1965)

80 mg dried active yeast was added to the following glucose salts medium:

Reagent	per 100 ml (g)
$(NH_4)_2 HPO_4$	0.2
KH_2PO_4	0.2
$MgSO_4.7H_2O$	0.01
Yeast extract (Vegemite®)	0.05
Glucose	2.0

The mixture was aerated gently in a 200 ml Erlenmeyer flask for 3 days before use. Cell counts were established with a haemocytometer and the suspension diluted to the appropriate concentration. The suspension was used within one week, or discarded.

C. **Artificial Food Suspension** (Modified from USEPA 1985)

The combined food is prepared from three ingredients as follows:

a) Digested cichlid pellets*:

5.0 g of cichlid pellets was added to 1 litre of deionized water, blended at high speed and aerated continuously for one week at 20-23°C (digestion). After the digestion period, the mixture was refrigerated and allowed to settle overnight. 300 ml of the supernatant was decanted and combined with equal volumes of supernatant from CEROPHYL® and yeast preparations (below). The remainder was discarded.

b) CEROPHYL® (Powdered, dried, cereal leaves):

5.0 g of CEROPHYL® powder was blended for 5 minutes with 1 litre of deionized water. The mixture was refrigerated and allowed to settle overnight. 300 ml of the supernatant was decanted and combined with equal volumes of the supernatant from the digested cichlid pellets (above) and yeast preparations (below). The remainder was discarded.

c) Yeast:

5.0 g of dried yeast was blended at low speed in 1 litre of deionized water. The mixture was refrigerated overnight, mixed thoroughly and 300 ml combined with equal volumes of the supernatant from the digested cichlid pellets and CEROPHYL® preparations (above). The remainder was discarded.

Equal (300 ml) volumes of the three foods were mixed and frozen in 100 ml aliquots. Fresh or thawed food was stored in the refrigerator between feedings and used for a maximum of 5 days.

* **USEPA recommends trout chow. In New Zealand this has proved to be an unreliable and variable food source, with concentrations of heavy metals often toxic to *Ceriodaphnia* (C. Hickey *pers. comm.*).**

Table 2: Treatment descriptions for initial feeding trials 1 & 2, based on a culture medium of aged and aerated tap water. See Table 1,A & B (above) for details of yeast and Banta's preparations, and main text (Part Three, Chapter Two) for details of algal culture and preparation.

Treatment Number	Food Regime	Amount provided per 500 ml
1	Yeast*	1.5 ml
2	Yeast + *Scenedesmus***	0.8 ml + 45 ml
3	Yeast + Banta's	0.8 ml + 45 ml
4	Banta's + *Scenedesmus*	25 ml + 25 ml
5	Banta's	90 ml

* **Approximate yeast concentration = 14 mg dry weight per 1.5 ml**
** **Approximate *Scenedesmus* concentration = 1 x 10^5 cells ml^{-1}**

Ideally, test animals should have been taken from the appropriate stock cultures maintained on each of the foods to be tested. This was not practicable here because some of the foods tested would not support the maintenance of stock populations. It was considered unwise to risk stock cultures in potentially poor conditions because, as described earlier (Part Two, Chapters Four and Five), *C. pulchella* and *C. dubia* were present only sporadically in Lake Mangakaware and not often at the same time, so the period during which both species could be collected was limited. Thus, to lose a stock culture was no small calamity. There was also a continuing problem with the capture of animals, from the field, that already seemed locked into a pattern of decline. Despite the addition of algal food to lake water, and the maintenance of low culture densities, animals still died, or produced ephippia soon after removal from the field.

I also attempted to collect animals from other lakes in the Waikato area. Unfortunately however, there are few lakes in the region where these two species coexist. *C. pulchella* appears to be the most widespread species of *Ceriodaphnia* in the Waikato (Greenwood 1987) but, as in Lake Mangakaware, seasonal distribution appears to be very sporadic, and attempts to collect animals were largely unsuccessful. The only other lake in the area where *C. pulchella* and *C. dubia* exist together, in any kind of reliable abundance, is Lake Rotoroa (Hamilton), but the populations here are invariably starving, with very few

fecund adults. Attempts to culture animals from Lake Rotoroa were fruitless and animals frequently died soon after collection. Those that appeared to recover and began to reproduce either produced sterile eggs, or developed a rather odd antennal paralysis that seemed to spread quickly through the culture, usually with no survivors. I believe this affliction was in no way related to the method of culture, or to the food provided, since a proportion of the animals examined immediately after capture were seen to behave in the same manner. Taub and Dollar (1968) noted a similar paralysis in *Daphnia* reared on the nutritionally unsound unialgal medium of *Chlorella*.

Trial 3

A third feeding trial involved using a culture medium of either filtered lake water or daphnid dilution water (Appendix 7, Table 2). Food preparations were different to those used in trials 1 & 2, and are described in Table 3. In contrast with trials 1 & 2:

(i) A nonflagellate (*Scenedesmus*) was replaced with a flagellated algal species (*Chlamydomonas*).

(ii) An artificial food suspension comprising equal proportions of yeast, bacteria, and cereal material was trialed.

Other methodologies were as for trials 1 and 2, except that trial 3 ran for 9 days.

Table 3: Treatment descriptions for feeding trial 3, based on culture medium of daphnid dilution water (DDW), or filtered lake water (FMK). See Tables 1A & C above for details of yeast preparation and artificial food suspension (AF). Details of DDW preparation are given in Appendix 7. See main text (Part Three, Chapter Two) for details of algal culture and preparation.

Treatment Number	Culture Medium	Food Regime	Concentration ($\mu g\ C\ ml^{-1}d^{-1}$)	Vol./500 µl
1	FMK	*Chlamydomonas*	1.3	90 ml
2	DDW	*Chlamydomonas*	1.3	90 ml
3	DDW	*Chlamydomonas* + AF	0.6 + 0.75	45 ml + 45 ml
4	DDW	AF	1.5	5 ml
5	DDW	Yeast	1.5	1.5 ml

A 6.3 RESULTS

Trials 1 & 2

The results of trials 1 & 2 are presented in Figure 1. Yeast was an unsuitable food for *C. pulchella* and would not support growth in this species. It was discarded as a food in the second trial, but its replacement, Banta's medium with no other food additions, was not suitable either. A combination of live yeast suspension and *Scenedesmus* (regime 2) gave much the same result for *C. pulchella* in both trials, but juvenile and egg production on this food was much better in the second trial for *C. dubia*.

The best food type appeared to be a combination of Banta's medium and *Scenedesmus* (regime 4), at least in trial 2. However, success in maintaining stock cultures on this medium was variable, and it did not appear to be a suitable food for the long term maintenance of healthy animals.

A combination of yeast and Banta's medium generally produced the best response in terms of growth and reproduction in trial 1 for both species of *Ceriodaphnia*, but this food was less suitable than Banta's and *Scenedesmus* in trial 2.

In summary, suitability of food, as measured by growth and reproduction, was variable both within and between different food types. A combination of yeast and Banta's medium gave inconsistent results; being the best food in trial 1, at least for *C. pulchella*, but not in trial 2. Banta's in combination with *Scenedesmus*, also gave variable results, and was the best food in trial 2, but not in trial 1. Simple foods, either Banta's alone, yeast alone, or *Scenedesmus* alone, gave poor results in terms of growth, reproduction, and survival, especially for *C. pulchella*. The presence of males and/or ephippial females of *C. dubia* in both trials, and in all regimes, suggests that animals were from a population that was physiologically stressed in some way. This confuses any findings from the trials.

Trial 3

Trial 3 was largely unsuccessful and was abandoned after 9 days. Growth in both species of *Ceriodaphnia* in all food regimes was poor. Soon after the trial was stopped the fecundity of all stock populations declined markedly and could not be recovered. These populations crashed soon after. The results of trial 3 are given in Table 4. *C. pulchella* fared particularly badly, and most animals died before the trial ended. *C. dubia* grew more

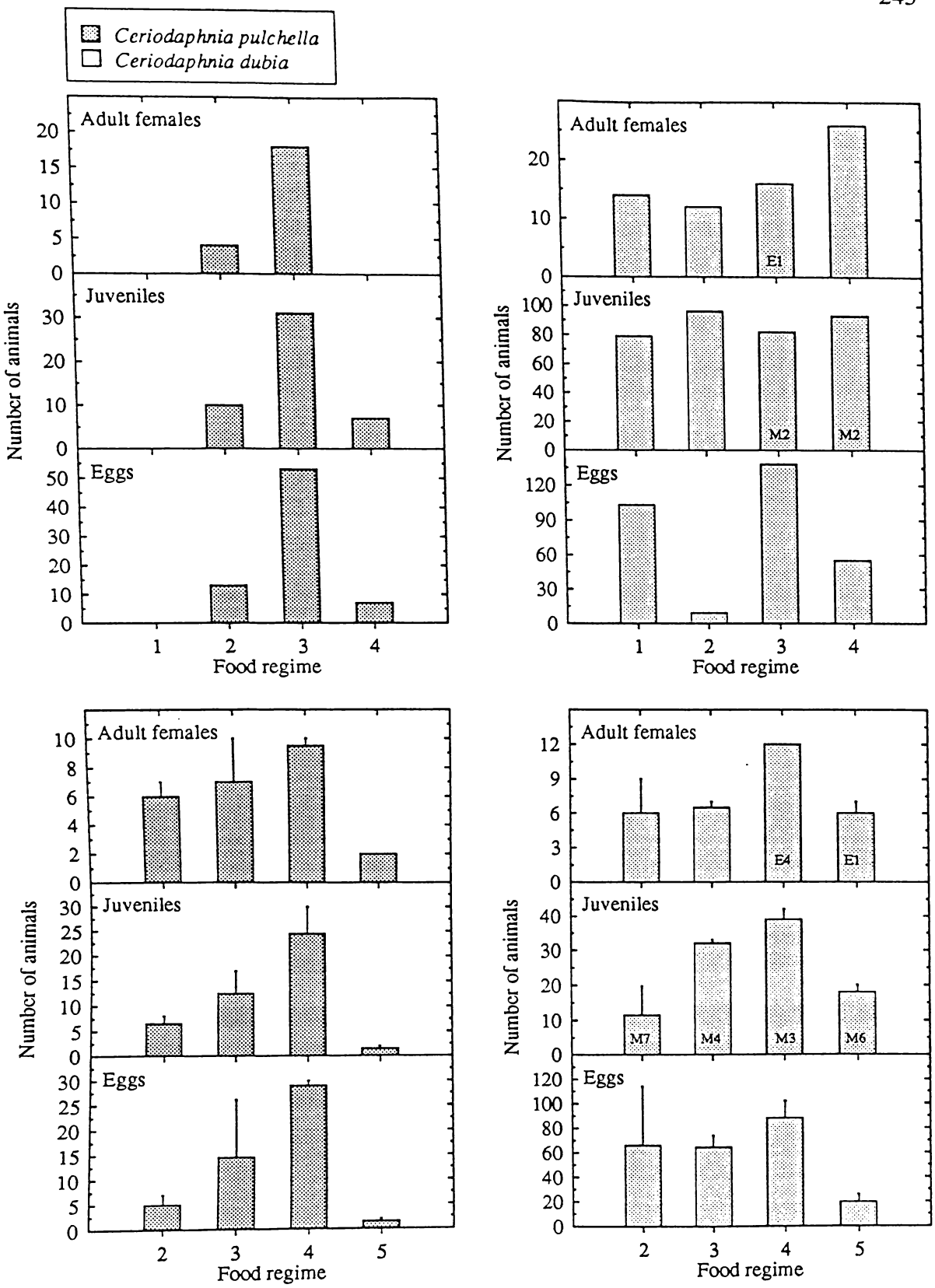


Figure 1.

Growth and reproduction in early trials of potential food regimes for *Ceriodaphnia pulchella* and *Ceriodaphnia dubia* at 20°C. Upper panels = Trial 1. Lower panels = Trial 2. Numbers refer to the net gain in animals, i.e., discounting initial densities. Refer to Table 2 in this appendix for a full description of the regimes in each trial. M(n) and E(n) = total number of males and ephippial females respectively, noted separately where they occurred. Eggs= total egg production during trial. Vertical bars are standard errors, n=2 in each case.

successfully, particularly in regimes 1-3, all of which contained the small flagellate *Chlamydomonas*. Growth on the artificial food suspension was poor, as was growth and survival on yeast, confirming the results of trials 1 and 2. No ephippial females or males were found, despite poor survival and growth. This further supports the view that it was likely to be the physiological state of animals captured from the field that determined sexual induction, and not necessarily the culture conditions themselves.

Table 4: Growth, survival, and reproduction of *Ceriodaphnia* in feeding trial 3, based on a culture medium of filtered lake water or daphnid dilution water. Treatment numbers as for Table 3. Results are given as the net gain to the culture after 9 days. Loss = net loss through the death of seed animals used to begin each test.

Species	Treatment Number	Juveniles	Adults females	Clutch size	Loss	Comments
C. dubia	1	31	0	-	0	} Dead by
	1	7	0	-	0	} day 7
	2	37	0	-	0	
	3	26	1	11	0	
	4	0	2	12	0	
	5	5	2	4	0	Dead by day 7
C. pulchella	1				3	} Dead by
	1				3	} day 5
	2	4	0		0	
	3	4	0		0	
	4	0	0		0	
	5	0	0		0	

A.6.4 Summary

Although the results of these initial trials were largely inconclusive, in that no one food appeared to consistently provide adequate nutrition for both species of *Ceriodaphnia*, a number of salient points can be summarised:

1. Yeast is not a suitable food for *Ceriodaphnia*. Staples (1984) concluded similarly for *C. dubia* from Lake Grasmere.
2. Unialgal cultures give variable and largely unsatisfactory results in terms of growth and fecundity in *Ceriodaphnia*. Staples (1984) reported a high incidence of egg sterility and degeneration in a unialgal medium, with this leading to reduced production of neonates. Poor growth and survival on unialgal food has been

reported by Taub and Dollar (1968) for *D. pulex* also. In this study one unialgal medium (*Scenedesmus*) would not even support the survival of *C. pulchella.*

3. As found by Staples (1984), Banta's medium (bacterial) combined with a green alga provided adequate nutrition for *Ceriodaphnia* in the short term. Over longer periods though, stock populations could not be successfully maintained on this food. Goulden *et al.* (1982b) also report inconsistent results with the use of Banta's medium to maintain daphnid cultures. Alone, it does not appear to be a suitable food for *Ceriodaphnia.*

APPENDIX SEVEN

Media for the culture of algae and *Ceriodaphnia*.

Table 1: Algal culture medium: (Modified MBL Medium after Stemberger 1981). Modified with the addition of buffer.

Stock Solutions (g per 500 ml)

Solution A:	$CaCl_2.2H_2O$	18.38
	$NaNO_3$	21.25
	Na_2EDTA	2.18
	$FeCl_3.6H_2O$	1.58
	$CuSO_4.5H_2O$	0.005
	$ZnSO_4.7H_2O$	0.011
	$MnCl_2.4H_2O$	0.090
	$Na_2MoO_4.2H_2O$	0.003
	$CoCl_2.6H_2O$	0.005
	H_3BO_4	0.065
Solution B:	$MgSO_4.7H_2O$	18.49
Solution C:	K_2HPO_4	2.18
Solution D:	$NaHCO_3$	6.30
Solution E:	Na_2SiO_3	14.21

Vitamin Stock Solution (mg per litre)

Solution F:	Thiamine HCl	100
	Biotin	0.5
	Cyanocobalamin (B_{12})	0.5

1 ml of each stock solution in order, A-E to approx. 950 ml deionised distilled H_2O and dilute to 1 litre. Buffer with 250 $mg.l^{-1}$ n-glycylglycine and sterilise. Add 1 ml solution F by sterile pipette. Refrigerate at 1-4°C. Note: Solution F was frozen, thawed just prior to use, and refrozen for storage.

Table 2: Daphnid dilution water, modified from USEPA (1985) synthetic freshwater.

Reagent	Stock Solution ($g.l^{-1}$)	Element	Concentration ($mg.l^{-1}$)
$CaSO_4.2H_2O$	1.5	Ca	7.0
$NaHCO_3$	2.48	Na	13.6
$MgSO_4.7H_2O$	2.93	Mg	2.9
KCl	0.10	K	0.83

20 ml of each of the above stock solutions was added to 920 ml of aged (48 hours) and aerated milli Q water. This was then modified by the addition of approximately 200 ml 0.45 µm filtered aerated Kaniwhaniwha (Mount Pirongia) stream water and 2 ml of vitamin stock solution F (see Table 1 above). Final volume, approximately 1.2 litres. Final pH 7.2 - 7.8.

APPENDIX EIGHT

Key to Diskette Abbrevations

KEY TO DISKETTE ABBREVIATIONS

SYSTAT data files have been converted to text files. Residuals have not. EXCEL data files have been converted to text files.

EXPT2CALC.ANOVASP_	=	food-temperature experiment results
FEXCALCSP_.FULL	=	data files for food-temperature experiment
FEXCALCSP_.OLOUT	=	outliers removed
ANOVA.variable	=	Analysis of variance and means tables
RES.variable	=	Residuals from ANOVA
FIRSTEXPT. CALC	=	food suitability experiment
FIRSTEXCALC.FULLSP_	=	data files for food suitability experiment
FIRSTEXCALC.OLOUTSP_	=	outliers removed
ANOVA.EXPT1Variable	=	Analysis of variance and means tables
RES.EXPT1Variable	=	Residuals from ANOVA
SP1	=	*C. pulchella*
SP2	=	*C. dubia*
TEMP1	=	23°C
TEMP2	=	13°C
FOOD1	=	High food
FOOD2	=	Low food

Variables (EXPT2CALC & FIRSTEXPT.CALC)

BS6(5)	=	Body size at clutch number six (number five)
BSNS	=	Ratio of body size at clutch two to size at birth
CLVOL6(5)	=	total accumulated clutch volume to clutch six (clutch five)
EGGS6(5)	=	egg production, clutches 1-6 (1-5) inclusive
EL(REP1)	=	egg length at first reproduction
MAXSZ	=	maximum body size
NBS	=	size of offspring produced (clutches 1-4 or 1-5)
NLOI	=	lipid score of offspring produced (clutches 1-4 or 1-5)
NOAI	=	number of adult instars
NS	=	size at birth (time 0)
RELES	=	relative egg size at first reproduction
RELNS	=	size of offspring/size of primiparous adult
SZREP1	=	size at first reproduction
TCL6(5)	=	time taken to reach clutch six (five)
TLIFE	=	length of life (days)
TREP1	=	time to first reproduction (age of maturity)
XCLVOL	=	mean clutch volume, clutches 1-6 (or 1-5)
XEGGVOL	=	mean egg volume, clutches 1-6 (or 1-5)
XLOI	=	mean lipid-ovary index, clutches 1-6 (or 1-5)

Field correlations = **Pearson and partial correlations of data from field populations**

bl	=	*Bosmina longirostris*
bm	=	*B. meridionalis*
cd	=	*Ceriodaphnia dubia*
cp	=	*C. pulchella*
bsz/t	=	Pearson correlation of mean body size with temperature
ev/t	=	Pearson correlation of mean egg volume with temperature
lo/t	=	Pearson correlation of lipid score with temperature
szr1/t	=	Pearson correlation of size at first reproduction with temperature
phy/t(/date)	=	Pearson correlation of small phytoplankton with temperature by month (by date)
CORR.DATA	=	data for field correlation (untransformed)

Partial correlations:

corr1: d' with densities of *Mesocyclops* and *Asplanchna*
corr2: d' with densities of Cladocera, Copepoda and Rotifera
corr3: b' with densities of cladocerans, copepods, rotifers, and small phytoplankton
corr4: proportion of females ovigerous with density of small phytoplankton
corr5: LOI with densities of competitors and small phytoplankton
corr6: mean body size with densities of small phytoplankton
corr7: mean clutch size with densities of small phytoplankton
corr8: egg volume with densities of small phytoplankton
corr9: egg volume, body size, and clutch size

Field Analysis/month

SP._BSCS.DAT:	Body size, clutch size, clutch volume, and egg volume for each species. BL=*B. longirostris*; BM=*B. meridionalis*; CD=*C. dubia*; CP=*C. pulchella*
logbs/cv field regress (res):	regression of body size with clutch volume for *Bosmina* and *Ceriodaphnia* from Lake Mangakaware (+ residuals)

Final Expt regressions

log cv/4 * 2 regress (res):	regression of body size with clutch volume for *Ceriodaphnia* at different food and temperature levels. 2 x species at 4 x regimes (+ residuals)
log cv/bs 2 * 1 regress (res):	as above. 2 x species, pooled for regimes (+ residuals)
SP1 + 2 log cv/bs regress (res):	as above. Pooled for species and regimes (+ residuals)