CYCLE CHARACTERISTICS OF PLANKTONIC CLADOCERANS IN A TROPICAL LAKE, CENTRAL AMAZON : FIELD AND EXPERIMENTAL WORK

EFFECT OF TEMPERATURE, FOOD CONCENTRATION AND TURBIDITY ON THE LIFE CYCLE CHARACTERISTICS OF PLANKTONIC CLADOCERANS IN A TROPICAL LAKE, CENTRAL AMAZON: FIELD AND EXPERIMENTAL WORK.

by

Elsa Rodrigues HARDY

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Department of Zoology,
Royal Holloway and Bedford New College.

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DEDICATION

This thesis is dedicated to my husband Paul, and my sons Anthony, Allan and Andre, for the love and understanding shown to me despite so much of my time taking up on this research.

ABSTRACT

This thesis is concerned with an investigation into the effects of food concentration, temperature and turbidity on the life cycle characteristics such as growth, body size, development and reproduction of species of planktonic Cladocera brought to the U.K. from a shallow turbid Lake Jacaretinga, Amazonia. The species studied were Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi. Long term growth experiments were performed using both batch and continuous flow culture under controlled laboratory conditions using various combinations of temperature (22°, 27°, and 32°C), concentration of algal food Scenedesmus acutus (0.03, 0.05, 0.1, 0.25, 0.5, and 1.0mgC.l^{-1}) and turbidity (10, 20, and 50 NTU). Animals were examined daily throughout their cycle from the newborn (neonate) to 3rd adult instars.

The ecology of planktonic animals in Lake Jacaretinga was studied intensively during a three month period (February, March and April 1986). This period of study included two ecologically/limnologically important periods, namely, before the flooding of the River Amazon and after the river flooding, when the lake became more turbid due to suspended particles. Weekly samples of zooplankton provided information on the species composition and numerical density of the cladoceran populations as well as their horizontal distribution in five stations. Information was also obtained on environmental condition in the lake (Temperature, dissolved oxygen concentration, Secchi disc transparency, chlorophyll-a and particulate carbon concentration.

Population of Diaphanosoma sarsi, Ceriodaphnia cornuta and Daphnia gessneri, decreased during the flood, and populations of Moina reticulata increased and became a dominant species.

Life cycle experiments shows that growth and reproduction are greatly influenced by food concentration and turbidity. Consistent differences were found between Daphnia gessneri and Moina reticulata,

being Moina reticulata more successful in survival, growth and reproduction .

Application of the experimental results on the effects of food, temperature and turbidity on the life cycle characteristics of the planktonic cladocerans are used to interpret the changes in the cladoceran population in Lake Jacaretinga during this period of floading. This is a significant contribution to our knowledge since Lake Jacaretinga is one of the characteristic varzea lakes in Central Amazonia whose limnology is largely determined by the annual flooding of Amazon River.

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CHAPTER 1

INTRODUCTION

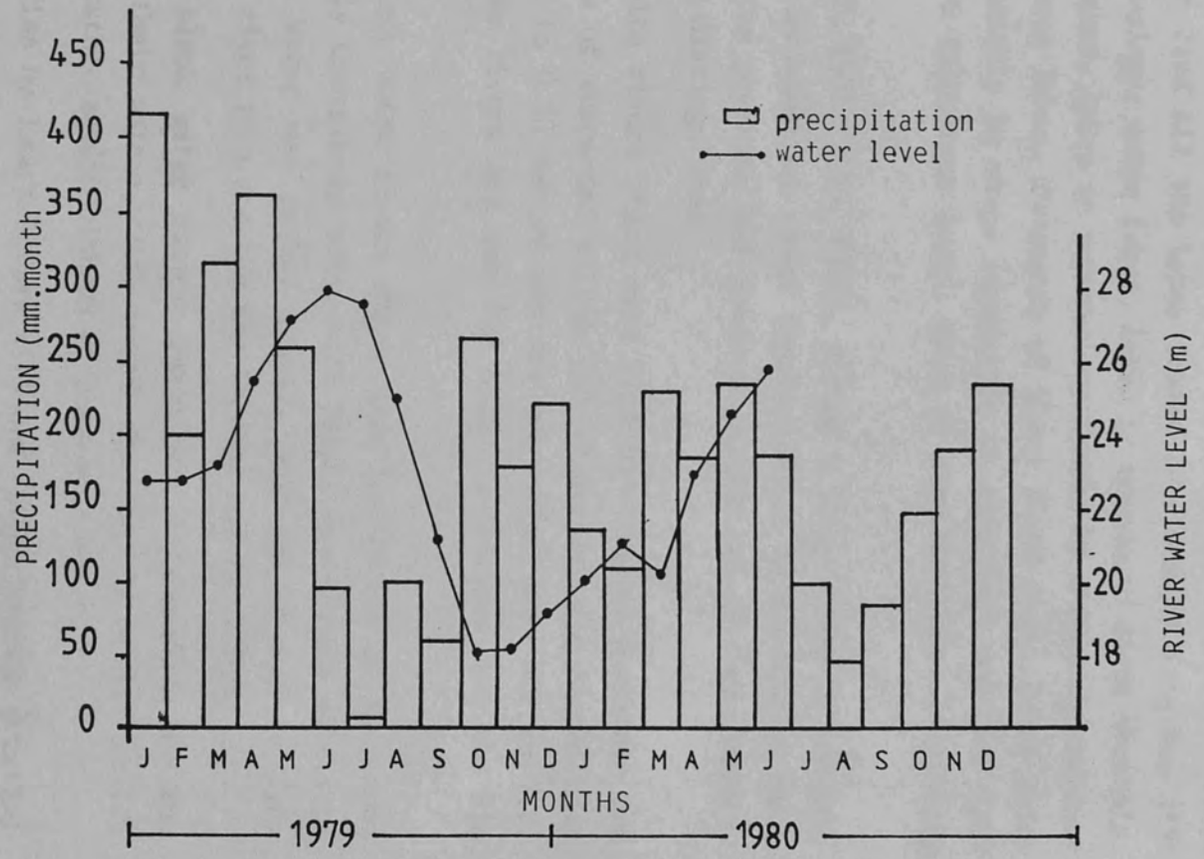
1.1 The distinctive features of the tropical lakes of Central Amazonia

The River Amazon is one of the world's largest river systems. Its hydrographic basin covers about 6.5 million square kilometres and occupies more than one third of the South American continent. The river discharges $20.10^5 m^3.s^{-1}$, which represents 18 % of all the freshwaters flowing into the world's oceans (Sioli, 1975). Some tributaries arising in the Andes or its foothills transport large quantities of sediments eroded as it passes along its course. The transportation and subsequent deposition of this material causes a continuous sequence of changes to the river beds and banks. The finer organic and inorganic particles remaining in suspension make the river water very turbid and yellow in colour. The most recent estimate of the annual loading of suspended material of the River Amazon is 9.10^8 tons (Meade et al. in Sioli, 1984).

The quantitative composition of the suspension loads of the Amazon area is characterized by extremely strong discrepancies. In addition, only a few measurements of the suspension material of these rivers have been conducted. Gibbs (1967) analysing the Ucayali mentions a mean value of 350 mg/l, which decreases to a value of 80 mg/l when reaching the Amazon estuary. However,(Irion in Sioli, 1984) found the mean suspension load in the lower course of Rio Jurua and the Rio Purus amounts to 70 mg/l; but in upper courses they might be twice or four times as much.

The large scale flooding which results from the high annual rainfall (3000 mm) is unequally distributed over the course of the year and drastically raises the water levels of all the rivers in Central Amazon. At Manaus, the river water level can increase by 10-12 metres as is shown in Figure 1.1 This annual flood inundates the vast floodplain of the middle and lower Amazon (called "varzea") which occupies 50000 60000 kilometres square for several months. Here, a

FIGURE 1.1 Monthly rainfall and the level of the River Amazon at Manaus (Manaus Harbour and station of Meteorology of INPA)



complex series of lakes called "ria" and "varzea" are formed in the lowlands of Amazonia. In fact, all standing water bodies in Central Amazonia are floodplain lakes created by the flooding of the rivers and are products of its activities. There are no examples of the well-studied temperate lake type which is a permanent water body with a closed basin. The origins of these floodplain lakes are rather diverse so that one can find all the types listed by Hutchinson in his 1957 Treatise of Limnology: oxbow lakes, lakes in abandoned river channels, lateral levee lakes, lakes in depressions formed by uneven aggradation and crescent levee lakes. Thousands of these flood plain lakes exist and vary considerably in shape (dendritic to circular) and size (100 metre long to 50 kilometres long). Most of them have been completely unstudied.

Sioli (1950, 1951, 1956, 1965), during a long series of studies, has established an Amazonian river typology which is based upon their morphology and the physical and chemical properties of their waters. Three types were distinguished:

1. The white rivers which were rich in chemical nutrients and with high levels of suspended solids. The characteristic Secchi disc depths were 0.1 to 0.50 metres and the pH varied from 6.2 to 7.2. Examples of these rivers are the Rio Solimoes-Amazonas and the Rio Madeira.

2. The clear water rivers which have low levels of suspended solids and highly transparent water with Secchi disc depths of 1.1 to 4.3 metres. The water was rather acidic, with pH of 4.5 to 7.8. Examples of this river type are the Rio Tapajos and Rio Xingu.

3. The black water rivers which are intermediate in the transparency of their waters, with Secchi disc depths of 1.3 to 2.9 metres but also rather acidic with pH of between 3.8-4.8.

Recent studies by Junk & Howard-Williams (1984) provide detailed information about the chemical characteristics of these three types of Amazonian river (Table 1.1). The mean conductivity values of the Amazonian water bodies show very clearly the low eletrolyte concentrations with highest values in white waters. Rio Solimoes have

TABLE 1.1 Chemical characteristics of rivers representing the three Amazonian water types (Junk & Howard-Williams, 1984)

	White water Rio Solimoes	Black water Rio Negro	Clear water Rio Tapajos
Colour (mgPt/l	39.3	159	11
Conductivity ($us.cm^{-1}$)	57	9	13.9
pH	6.9	5.1	5.15
Hardness (dH)	125.9	0.055	0.256
Total N (µg/l)	603	394	335
Kjeldahl N (ug/l)	551	354	331
NO_3-N (µg/l)	48	36	4.1
NO_2-N (µg/l)	1.8	0.7	1.4
Total P (µg/l)	105	25	13.4
PO_4-P (µg/l	11.6	5.8	1
HCO_3 (mg/l)	34.1	8.6	8.3
Cl (mg/l)	3.1	1.7	1.7
Si (mg/l)	4.0	2.0	2.5
Na (µg/l)	2300	380	
K (µg/l)	900	330	
Mg (µg/l)	1100	110	400
Ca (µg/l)	7200	210	1170

the highest ion content with particularly marked differences in the concentrations of HCO_3, Ca, Mg, and Na compared with the other two. These waters are neutral with respect to pH (6.5-6.9) and are significantly different (P>0.1%) from the low pH values (4.5-5.1). The total phosphorous of the water of the Solimoes is about 5 times higher than that of the Rio Negro and about 8 times higher than that of the Rio Tapajos. No clear distinction can be made between water types on the basis of their chloride contents.

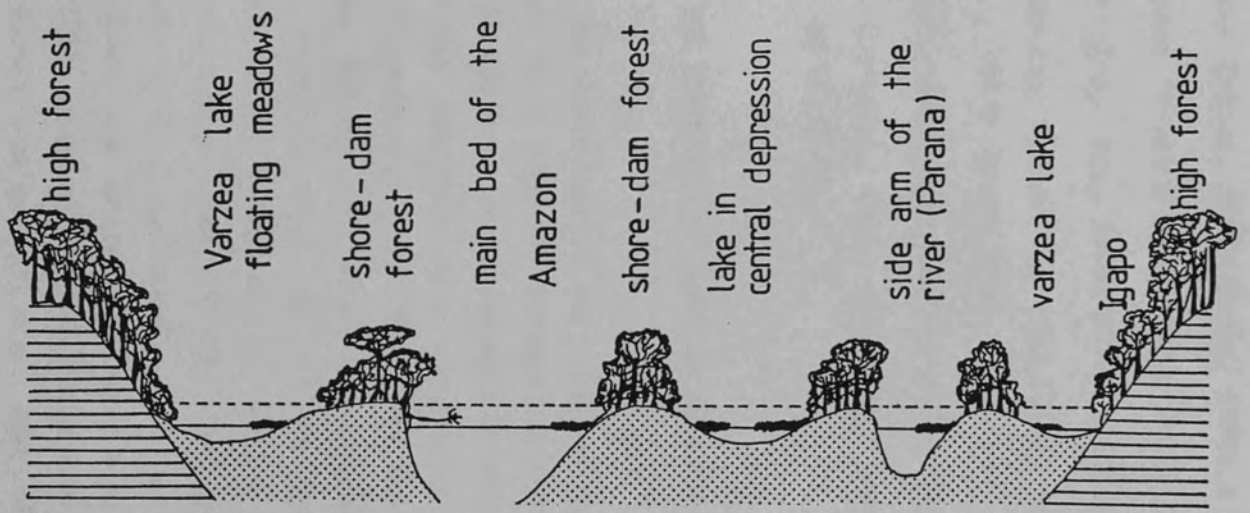
These river types influence the nature of the lakes in their localities so that there are black water lakes, white water lakes or lakes whose water is a mixture of both types of water. The clear and black water rivers from the shields of Guiana and Central Brazil carry low sediment loads.

Another characteristic feature of the River Amazon is the formation of "parana" where the main river channel divides into several side arms which sub-divide into many smaller channels. These channels may be permanent or temporary and some connect the "varzea" lake to the main river channel. Thus, during the flood periods, the lakes form part of the river itself whereas, at low water, they are isolated from the river, are often very shallow (about 1 m) and may even dry up almost completely. On the other hand, some lakes remain permanently connected to the river, only being isolated from river influence during the severest lowering of the water level. Overall, the most characteristic feature of these "ria" and "varzea" lakes is that their water level fluctuates and the fluctuations are mediated by the changes in the river level (Schmidt, 1973; Sioli, 1964; Junk, 1970; Rai & Hill, 1982a; Robertson & Hardy, 1984) as shown in Figure 1.2

The consequences to their biology of these very distinctive features of the "varzea" lakes is of great interest and has been studied to some extent. There are now numerous publications on the limnology of the water bodies lying within a radius of about 150 km from Manaus. These are listed below:

Morphology : Melack, 1984

FIGURE 1.2- Schematic cross-section through the valley of the lower Amazon (Sioli, 1964)



------ high water level

——— low water level

Physics and Chemistry: Devol et al., 1984; Fittkau, 1964; Forsberg, 1984; Furch, 1976; Furch & Junk, 1980; Schmidt, 1972, 1973a; Sioli 1954b, 1968a

Phytoplankton and Primary production: Forster, 1969; Fittkau et al. 1975; Martins, 1970; Ribeiro, 1978; Tundisi & Tundisi, 1984.

Aquatic macrophytes: Howard-Williams & Junk, 1976, 1977; Junk, 1970, 1982.

Benthos: Irmler, 1976; Reiss, 1976a,b

Perizoon: Irmler & Junk, 1982; Junk, 1973

Microbiology: Rai, 1978, 1979; Rai & Hill, 1980; 1981

Zooplankton: Brandorff, 1977, 1978; Brandorff & Andrade, 1978; Fisher et al., 1983; Hardy, 1980

Rotifers: Robertson & Hardy, 1984; Koste, 1972; Koste et al., 1984

Fish: Carvalho, 1981; Goulding, 1980; Junk et al., 1983; Marlier, 1968; Zaret, 1984.

1.2 THE LIMNOLOGY OF LAKE JACARETINGA

The limnology of lago Jacaretinga, a floodplain lake whose main feature is a periodic connection with the Rio Solimoes, has for the last decade been of increased interest to limnologists. However, there is little concrete data concerning the complexity of the system, mainly concerned with the question of the productivity of these waters. The earliest study of this nature was that of Ribeiro (1978, 1983), who reported on physico-chemical, primary production and biomass of phytoplankton. Rai & Hill (1980) investigated the basis of microbiological and physico-chemical characteristics. Tundisi & Tundisi (1984) and Tundisi et al., (1984) studied environmental variables and primary productivity of phytoplankton. Zaret et al.,(1981) and Devol et al.,(1984) performed some preliminary bioassay experiments which indicated that the primary productivity may be limited by nutrients since bioassay experiments suggest a consistent

pattern of nitrogen limitation. The general pattern of nutrient limitation and its influence on nutrient dynamics, however, is still poorly understood.

Table 1.2 provides a summary of the physico-chemical properties of the Lake Jacaretinga and give mean values or ranges of the individual chemical parameters (Hardy, 1980; Ribeiro, 1983; Furch, 1984). The high Ca and HCO_3 content of the water allows the lake to be classified as a carbonate water (Furch, 1984).

The limnology of Lake Jacaretinga is strongly influenced by the great fluctuations in water-level caused by Amazon river's annual flood which normally occurs in February-March (figure 1.3). These fluctuations have a strong influence on the seasonal cycle of events reflected in levels of light penetration and concentrations of chlorophyll a and dissolved nutrients (Tundisi et al.,1984). The diurnal pattern of mixing are effective throughout the whole water column during the period when the lake is shallow. There is, therefore, a diurnal pattern of thermal stratification during the day and a complete mixing at night (Tundisi et al., 1984).Oxygen depletion is a common feature in Lake Jacaretinga; the surface values of oxygen were always below 100% saturation and anoxic conditions were generally found below 2.0 metres (Ribeiro, 1983). The same author considered that during its low water period the lake is rather eutrophic and, at its high water phase it exhibits oligotrophic characteristics.

1.3 THE ECOLOGY OF THE CLADOCERAN SPECIES OF LAKE JACARETINGA

Ecological information about the cladoceran species in Lake Jacaretinga is rather fragmentary, although there are some investigations which have been published qualitative and quantitative information on its zooplankton.

In the earliest paper , Brandorff & Andrade (1978) observed many important aspects during a short period of study from February to April 1975 co-inciding with the flood period . They found a) changes in species composition, strongly fluctuating density pattern, c) increased egg production, d) decline and disappearence of the

Table 1.2 Mean values for the different physico-chemical parameters in Lake Jacaretinga.

PARAMETERS	L.JACARETINGA	REFERENCE
Depth (m)	0.70 - 6.0	Hardy,1980
Secchi disc (m)	0.50 - 2.0	Hardy,1980
Temperature C	25 - 32	Hardy,1980
Dissolved oxygen (mg/l)	0.5 - 6.30	Hardy,1980
Winds (km/h)	1.0 - 31.10	Ribeiro,1983
pH	5.1 - 7.7	Hardy,1980
Conductivity ($\mu S.cm^{-1}$)	60.0	Hardy,1980
Na (mg/l)	2.5	Furch,1984
K (mg/l)	1.4	" "
Mg (mg/l)	1.4	" "
Ca (mg/l)	8.6	" "
Total P (µg/l)	57.0	" "
Total C (mg/l)	16.2	" "
Cl (mg/l)	2.9	" "
Si (mg/l)	4.3	" "
Sr (µg/l)	39.7	" "
Ba (µg/l)	21.7	" "
Al (µg/l)	20.0	" "
Fe (µg/l)	123.0	" "
Mn (µg/l)	3.0	" "
Cu (µg/l)	1.6	" "
Zn (µg/l	2.2	" "
HCO_3-C (mg/l)	8.5	" "

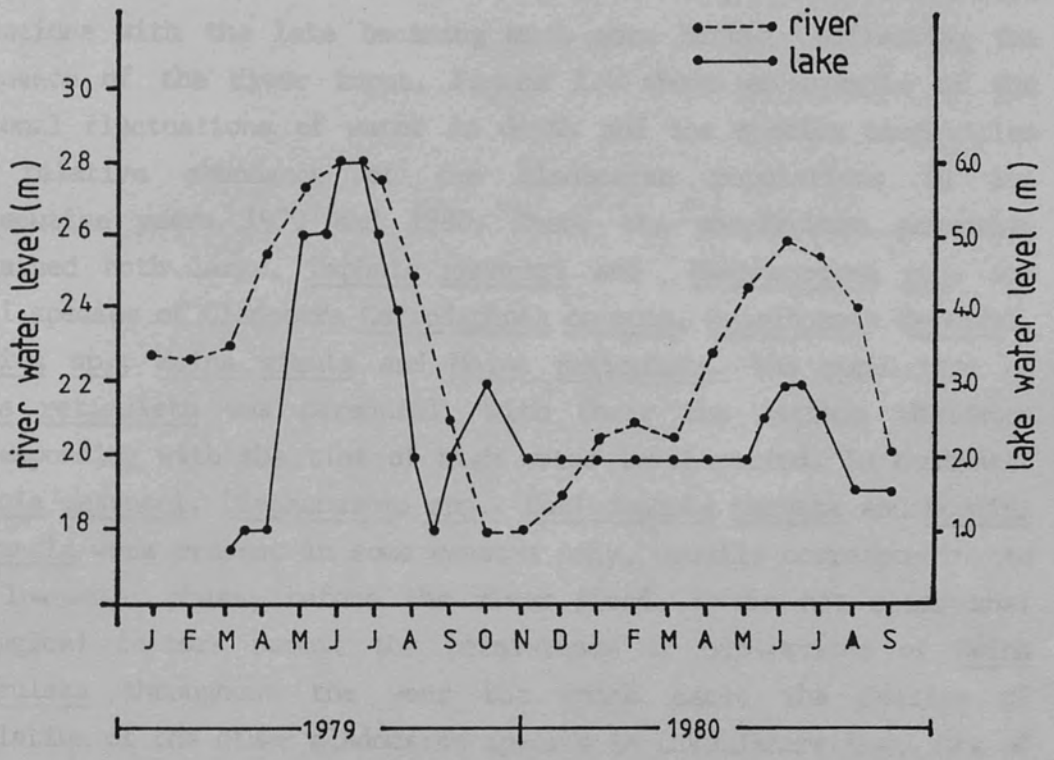


FIGURE 1.3 The Solimoes River and Lake Jacaretinga water levels during two consecutive years 1979, 1980 (In Robertson and Hardy 1984)

zooplankton fauna. The structure of zooplankton community in Lake Jacaretinga was discussed in this paper as well the effects that suspended matter of Amazon River may have on the zooplankton community structure. Possible reasons for the decline of cladocerans were discussed: these being a dilution effect due to a flushing out of the plankton by the current and predation by planktivorous fish. While the data is somewhat sparse, a pattern of events emerges which suggests that the highest densities of planktonic cladocerans coincide with the low water phase of Lake Jacaretinga and the lowest densities following the entry of the river water resulting in the high water phase. This co-incides with the lake becaming much more turbid, reflecting the influence of the river input. Figure 1.4 shows an example of the seasonal fluctuations of water in depth and the species composition and relative abundance of the cladoceran populations in two consecutive years 1979 and 1980. Then, the zooplankton community contained both large, Daphnia gessneri and Diaphanosoma spp. and small species of Cladocera Ceriodaphnia cornuta, Bosminopsis deitersi, Bosmina sp., Moina minuta and Moina reticulata. The population of Moina reticulata was perennial, with their the maximun abundance corresponding with the time of high water level period. In contrast, Daphnia gessneri, Diaphanosoma spp.. Ceriodaphnia cornuta and Bosmina chilensis were present in some seasons only, usually corresponding to the low-water phase, before the river flood. It is not clear what ecological factors permit the persistence of populations of Moina reticulata throughout the year but which cause the decline of population of the other cladoceran species in Lake Jacaretinga. One of the aims of this thesis was to study these questions.

1.4 TURBIDITY AS AN ECOLOGICAL FACTOR

Turbidity is an expression of the optical property that causes light to be scattered and absorbed rather than transmitted through the water. From the point of view of their effect upon the aquatic environment, substances causing turbidity may be divided into two groups: a) the settling suspended material and b) non-settling suspended material. Both a) and b) consist of inorganic and organic

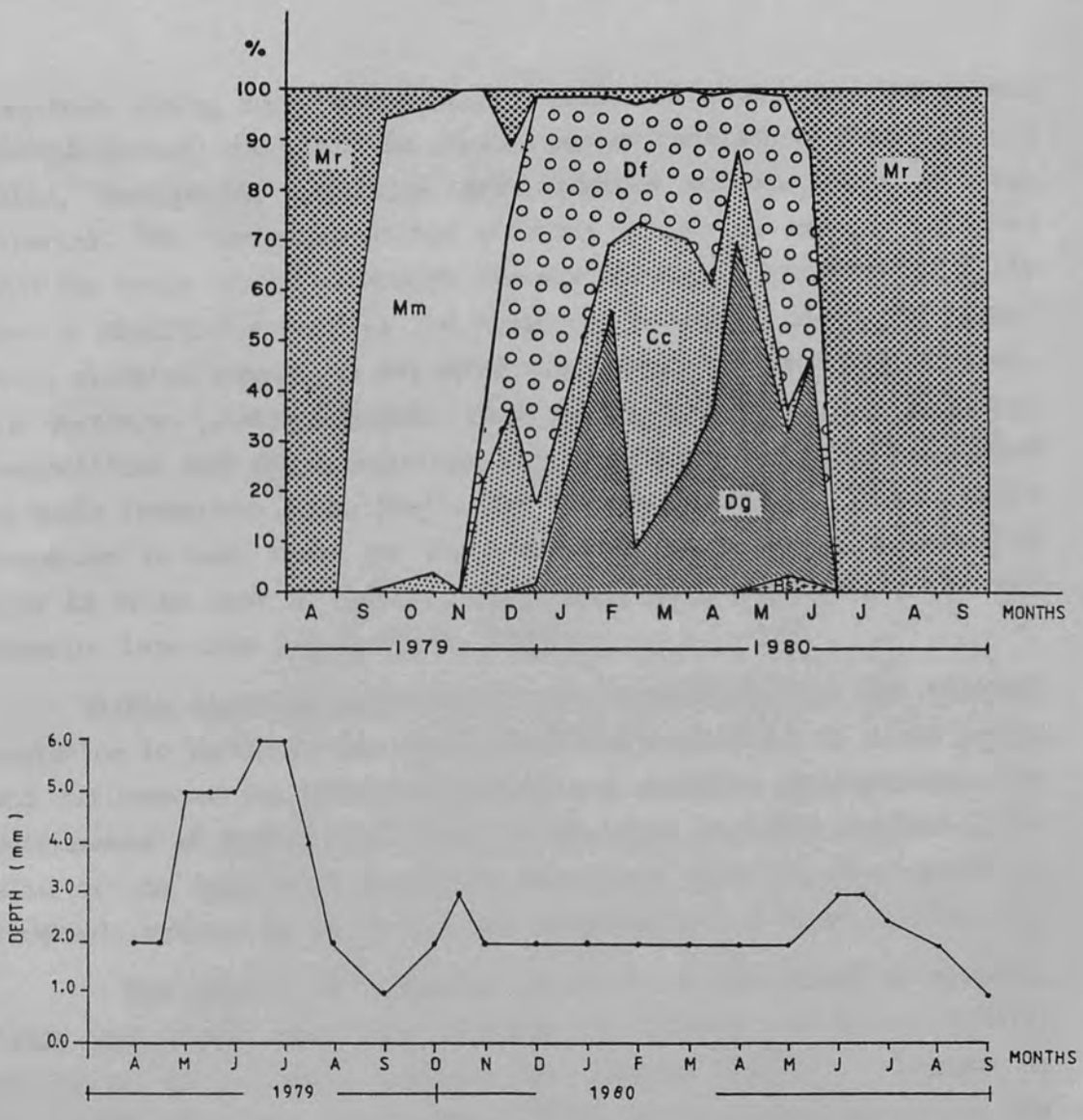


FIGURE 1.4 Composition and abundance relative of cladocerans (top) compared with the water level of L.Jacaretinga. Mr = Moina reticulata, Mn = Moina minuta, Df = Diaphanosoma spp, Cc = Ceriodaphnia cornuta, Dg = Daphnia gessneri, Bs = Bosmina chilensis. (Hardy unpublished data).

compounds coming from sources both outside (allochthonous) and within (autochthonous) the lake. The organic matter consists of phytoplankton cells, macrophytes particles and detritus derived from decaying material. The inorganic matter consists mainly of erosion products from the rocks in the watershed. The weathered products from the soils form a significant part of the suspended material. Since the parent rock, climate, topography and other conditions vary from area to area, the weathered products reflect these variations. These have different compositions and characteristics depending upon the place and method of their formation (Grim, 1968). The two materials most commonly found suspended in most lakes are algal cells and clay particles. the term clay is often used to define a particular size, usually the smallest fraction less than 2-4 um (Grim, 1968).

Within standing water bodies considerable spatial and temporal variation in turbidity can result from the seasonality of river inputs and differences in turbulent mixing and sediment resuspension. The maintenance of turbid conditions is dependent on water movements, the size of the suspended particles and their settling rate which is inversely related to their size and mass (Akhurst & Breen, 1988).

The effects of suspended materials on the biota in streams, lakes and rivers have been reviewed by Cordone and Kelley (1961), Hollis et al., (1964), Everhart and Duchrow (1970), Ivanoto et al.,(1978) and Stern and Stickle (1978). Cairns (1968) summarized the roles of suspended sediments into four categories: 1) they have an abrasive action, 2) can reduce the light penetration, 3) can serve as a substrate for bacterial or fungal growth and 4) can adsorb chemicals. High concentrations of suspended material redically alter the degree of light penetration and primary production (Jewson & Wood, 1975; Schwartzkopf & Hergenrader, 1978; Gloss et al., 1980). The ability of sediment to adsorb and transport nutrients (Green et al., 1978; Gloss et al., 1980) and heavy metals (De Groot, 1976, Forstner, 1976; Litherathy & Laszlo, 1976) has been well-documented. They therefore play a fundamental role in the productivity of turbid aquatic ecosystems, controlling the form of the productivity-depth profile, and influencing growth and

composition of phytoplankton (Cheng & Tyler 1974; Wang, 1974; Stegmann, 1978; Murphy, 1962; Brylinsky, 1980). Turbidity also affects the survival, reproduction, and behavior of sport fishes (Wallen, 1951; Hemistra et al., 1969) and influences aquatic predator-prey interactions (Vinyard & O'Brien, 1976; Confer et al., 1977). Vinyard and O'Brien (1976) and Wright (1981) showed that increasing turbidity impairs the ability of planktivorous fish to locate their prey. Buck (1956) reported that the production of sunfish (Lepomis microlophus) in low turbidity ponds was 300 times greater than in ponds with high turbidity.

The actions of turbidity as an environmental influence may at times be obvious, but at other times may be quite inconspicuous. Many descriptive observations have been made on turbid waters and many effects of turbidity have been suggested, although quantitative studies on its direct or indirect effects, especially on animals like cladocerans, are sparse. Nevertheless, the importance of suspended matter to the structure of freshwater plankton communities is receiving increasing attention in field and laboratory studies (Geddes, 1984; Carvalho, 1981; Arruda et al., 1983; Dirnberger & Threlkeld 1987, 1988; Threlkeld & Choinski 1986; Gliwicz, 1986; Hart, 1986a,b; McCabe & O'Brien, 1983). Some investigations have shown that the abundance of zooplankton was positively related to water transparency; daphnids were virtually absent in periods when high levels of inorganic turbidity prevailed (Hart, 1987; Threlkeld, 1986; Brandorff & Andrade, 1978). In laboratory studies, Robinson (1957) showed that low concentrations of clay particles increased the egg production of Daphina magna, but that concentrations from 100 to 200 mg/l dry weight diminished its egg production. Reeve (1963) demonstrated that the ingestion rate of Artemia fed on the alga Plaeodactylum increased in the presence of low concentrations of sand (0.007 mm diameter), but decreased with higher concentrations. The ability of the copepod Calanus helgolandicus to molt was reduced at concentrations of 10 mg/l of a fine-grained residue resulting from an aluminium-extraction process (Paffenhofer, 1976). Sherk et al. (1976) demonstrated a reduction in ingestion of phytoplankton cells by marine

copepods in the presence of sand or natural sediments. Thus, the concentration of particles at which ingestion rates of Acartia tonsa were reduced was 50 mg/l and was 250 mg/l for Eurytemora affinis. It has been demonstrated experimentally that concentrations of suspended sediments between 0.0 to 2451 mg/l decreased by 95% ingestion rate of ^{14}C labelled Chlorella vulgaris by Daphnia parvula and Daphnia pulex and decreased their incorporation rates by 99% (Arruda et al.,1983). McCabe & O'Brien (1983) showed that it is quite likely that high concentrations of silts and clays reduce energy transfers in food chains. It seems that levels of silts and clays can reduce zooplankton feeding rate and assimilation efficiency. The combined effect of reduced feeding and assimilation can depress zooplankton production by perhaps as much as 16 times that possible in non-turbid water. These effects, combined with the fact that high levels of suspended silts and clays also affect the depth of the euphotic zone and thus the potential primary productivity of the ecosystem, also impair the ability of planktivorous fish to find their prey. Thus turbidity may greatly reduce the trophic efficiency and productivity of affected lakes and reservoirs. However the role played by suspended material in natural waters appears to be imperfectly understood and the evidence concerning its effect on life in these waters is still conflicting. Little experimental work has been done on the relationship of turbidity and turbidity levels to planktonic animals and much less is understood about the direct interactions of living plankton organisms and the suspended matter. Another of the aims of this thesis was to work experimentally on some of these questions.

1.5 THE EFFECTS OF FOOD CONCENTRATION AND TEMPERATURE ON THE LIFE CYCLE CHARACTERISTICS OF TROPICAL AND TEMPERATE ZOOPLANKTON SPECIES.

Temperate or tropical lakes are characterized by considerable seasonal variation in biotic and abiotic components and the population inhabiting these water bodies need to display genetic, physiological and behavioral adaptations to the seasonally changing environment. The

physical and biological conditions suitable for growth, development and reproduction prevail only during particular seasons and in the case of a population that has several short-lived generations, like Cladocera, each generation exists in a different environment (Herzig, 1984).

Concepts on seasonal variation developed for aquatic systems are mainly based upon the annual changes in levels of solar radiation and temperature in the temperate region or upon monsoonal patterns in the tropics and do not appear to be applicable to the floodplain lakes of tropical Amazonia. In the Central Amazonian lakes, seasonal variations in biotic and abiotic parameters are influenced mainly by fluctuations in river levels during the flooding periods when the water river arises. These floods are regular annual events resulting in two well defined periods, a high-water and a low-water period each year (Figure 1.2). Previous works by Braun (1952), Sioli (1964,1975), Marlier (1967), Junk (1970), Schmidt (1973), Rai (1979) and Rai & Hill (1981a, 1981c) have indicated that the changing water levels were the dominating forces driving the biological events in the Central Amazonian lakes. This section attempts to review what is known so far about some environmental parameters that influences the growth and reproductive characteristics of Cladocera inhabiting such water bodies.

Temperature and food resources are major environmental factors, amongst many others such as light and oxygen content of the water, which influence the life cycle characteristics of aquatic invertebrates.

Herbivorous species of zooplankton, belonging to the same genera or sometimes the same species, may experience wide ranges of temperature conditions or food concentrations across latitudinal gradients or seasonal changes but to understand the importance of these two variables upon the seasonal dynamics and production of zooplankton requires detailed investigations on a few species only or confined to one or two water bodies. The usual approach in such investigations is to study the effects of either temperature or food conditions based upon either field observations or on laboratory

experimentation. Thus, one variable is normally held constant whilst the other is manipulated experimentally. Most investigations of this kind have been conducted in the temperate region, and their findings will be reviewed below. As will be shown, such studies have been very rare in the tropical regions.

Since, both temperature and food quality and quantity as separate factors affect the life history properties of zooplankton species, a study combining these as interacting variables is likely to give a more realistic picture of what occurs in the natural environment where the zooplankton is subjected to variation in both these factors and many more. However, these parameters have seldom been considered simultaneously in temperate regions and much less in the tropics. The present work attempts to analyse the simultaneous effect of temperature and food concentration on body size, duration of development, growth and reproduction of three species of Cladocera from Lake Jacaretinga, a shallow lake in Central Amazonian.

The growth, reproduction and, in the final analysis, the production of crustaceans is largely dependent on the nature of the feeding of the crustaceans, on the amount of food present and/ or the availability to them. Growth, whether somatic or reproductive, is the end point of a variety of metabolic processes as well as the evolutionary desirable outcome for the species's survival. All environmental factors influencing metabolic and activity rates may therefore indirectly affect growth and need to be examined.

Food resources

The quality as well as quantity of food is known to be an important factor controlling the growth and reproduction of zooplankton. Zooplankton nutrition has been reviewed by Edmondson (1957) and Jorgensen (1966). These papers provide and summarize evidence that any particulate matter that is filterable and assimilable is available as food for filter-feeding zooplankton. This particulate matter includes the living and dead parts of algae,

bacteria, and protozoans as well as animal detritus. A number of factors is responsible for the nutritional adequacy of a certain food species, e.g. ingestibility, digestibility and chemical content. There are evidence in the literaure that Daphnia spp. can digest the main biochemical components of particulate matter in the water (Dehn 1930, Hasler 1935, 1937 in Lampert, 1987) studied the digestive enzymes of Daphnia magna and they found proteinases, peptidases, amylase and lipase in the gut. There are, however, pronounced differences in the digestibility of different cells. This may be determined to a large extent by their physical characteristics, such as size, shape, thick cells walls or gelatinuous sheaths. A considerable amount of information on the filter feeding mechanism of freshwater zooplankton is available in the literature and it seems well established that, although many animals are able to collect particles of a wide range of sizes, all them have an upper and lower limit

Brooks and Dodson (1965), in developing their "size-efficiency hypothesis", have assumed that the upper size limit of particles that can be taken by large cladocerans probably is determined by the animals's size. Large and small-bodied cladoceran species differ widely in their life-history characteristics (Lynch 1980). Thus, it might be expected that populations of these cladoceran species would respond differentially to changes in their food supply. Burns (1968 b) determined experimentally the maximum sizes of spherical beads ranging in diameter from 1 to 80 μ that could be ingested by Bosmina longirostris and six species of daphnids of various sizes. Natural particles are often not spherical, thus, an upper size limit for natural food particles is difficult to define.

For the study of food selection, gut analyses can provide useful information on maximum particle size, on fragmentation and on utilization of cells or colonies (Infante 1973; Nadin-Hurley & Duncan 1976; Horn 1981; Infante and Edmondson 1985). Long listings of items found in the gut of the cladocerans are given in these studies.

Recent studies using electron microscopes have added useful contributions on the filter feeding mechanism of cladoceran. Measurements of the intersetular distance have shown that it differs

in different species, within different populations of the same species, and in different body sizes of the same species (Korinek & Machacek, 1980; Korinek et al. 1981; Geller & Muller, 1981; Porter et. al., 1983; Brendelberger & Geller. 1985; Hessen, 1985; Ganf & Shiel, 1985 a,b,; Jayatunga, 1986).

Geller & Muller (1981) used the size of their filter meshes to classify cladocerans into three feeding group:

1) Those with filter meshes from 0.24 µm-1.6 um, presumed to be highly efficient bacterial feeders.

2) Those with filter meshes from 1.0 µm-1.6 um, presumed to be low efficiency bacterial feeders.

3) Presumed macrofiltrators with meshes finer than 2 um in only a small part of their filtering areas, which would be unable to feed on suspended bacteria.

Jayatunga (1986), using a scanning electron microscope carried out measurements on the inter-setular distance of the filtering limbs of four tropical cladoceran species including their whole size ranges. She proposes that Daphnia lumholzi, Diaphanosoma excisum, Moina micrura and Ceriodaphnia cornuta can be classified as micro filtrators that can feed on particles less than 1 µm in diameter, according to the classification of Geller (1981).

According to the degree of digestion and the survival, reproduction and growth success or not of Daphnia reared with several different algae species, Lefere (1942) qualified them as good, intermediate, or poor foods. Great differences were observed between closely related food species;; for example, while Scenedesmus expinosos was considered a good food, Scenedesmus quadricauda was qualified as an intermediate food. Horn (1981) also pointed out that resistant and non-resistant forms can exist in the same genus(Scenedesmus). Rocha (1983) tested Scenedesmus acutus and Monodus subterraneus in her studies and both proved to be a good quality foods. However S.acutus seemed to be slightly better food supporting high growth rate and large reproductive output in the three species of

Daphnia. Later, Jayatunga (1986) and in the present study used S.acutus growing exponentially in the same culture conditions.

In their study of Daphnia in Lake Washington, Edmondson and Litt (1982) hypothesized that Oscillatoria may have delayed the re-appearance of Daphnia in the lake. Infante (1985) measured the effect of Oscillatoria on Daphnia pulicaria and Daphnia thorata in L. Washington. She found that both growth and reproduction were affected. There was a clear trend toward a decrease in body size as the filaments became more numerous. The number of embryos produced was also affected by the presence of filamentous Cyanobacterium; the causes of this inhibition are less clear. It is possible that the filaments interfere with the feeding process, as has been observed repeatedly in other experiments (Webster and Peters 1978; Gliwicz 1981; Porter and Mc Donough 1983). Cladoceran populations can decline or disappear when some kinds of blue-green algae, especially filamentous forms, predominate (Burns 1968a; Keating 1976; Infante 1982).

In an extensive work about the utilization of algae by rotifers Pourriot (1957) found that size and shape were the major factor determining the ingestibility of algal cell. It is known that, in the field, eggs numbers and production of daphnids in lakes are maximal during periods of high abundance of particulate matter smaller than 30 µm (Lampert 1978; Sarnelle 1986).

Blue-greens are usually an inadequate food for Daphnia (Bogotová 1965). They cause rejection of collected food and interrupt appendage movement (Burns 1968a). Growth and reproduction of D.pulicaria were reduced in the presence of Oscillatoria agardhii (Infante & Abella 1985. Aphanizomenon flos-aquae blooms are often associated with high densities of Daphnia (Hrbáček 1964). Ingested Aphanizomenon is not toxic, but if the blue-green is the only food of Daphnia pulicaria, growth is poor (Lampert, 1981). Anabaena filaments have similar effects to those of Aphanizomenon. They increase rejection and respiration in Daphnia magna (Porter & McDonough 1984) as well as lower filtering and feeding rates.

Gut analyses also show that certain algal remain undigested in the intestine, although they are swallowed. Gelatinous green algae and the blue green Chroococcus limneticus have been found still intact in the gut of D.pulex five days after ingestion (Porter 1975). Since they are ingested but not digested, these items in high abundance are disavantageous for the animal.

Food quality can also be related to the nutritional value of the diet itself, as determined by the chemical or caloric content of the food such algae or other elements in the water (bacteria, protozoa, detritus, and mineral particles). Yesipova (1969) reported shorter developmental duration, higher growth rates and greater fecundity of daphnids fed on fresh algal detritus compared with those fed on old detritus from the bottom of a pond. She concludes that the caloric value, rather than the bacterial content, was the major factor determining the difference in the quality of the food. Many studies investigated the detrital food chain in lakes (Gliwicz 1969; Gliwicz and Hillbricht-Ilkowska 1975) but results are variable. Schindler (1968) observed lower feeding and assimilation rates of D.magna when fed on detritus and nitrogen deficient algae than those feeding on healthy algae. Rodina (1963) reported reduced growth of D. magna fed detritus, compared with controls.

Since cladoceran filters rather unselectively below a certain upper size limit, the kinds of detritus, and mineral particles available and usable by zooplankton is varied. This is important in shallow lakes with a high load of suspended silt as Lake Jacaretinga studied in the present work. The interactions of mineral particles and cladocerans have been shown in section 1.4.

From the investigations mentioned up to now the importance of food quality is unquestioned in affecting the responses of the life cycle of cladocerans. However, the quantity of food is also important.

Many studies have dealt with the effect of increasing food concentration (quantity) on the life cycle of Cladocera and they all show essentially similar results, indicating a strong food dependence on filtering and ingestion rates. Feeding rates (Rigler, 1961) and

assimilation rates (Lampert, 1977a) of filtering zooplankton exhibit a characteristic dependence on food concentration. At low concentration the rated of energy input increase proportionally up to the "incipient limiting level concentration" and above that they reach a plateau. Rigler (1961) studying the feeding behaviour of D. magna stated: It appears that, below 10^5 yeast cell/ml, the feeding rate is limited by the amount of water the animal can filter, but above 10^5 cell/ml it is limited by some other factor. As a result, ingestion rate increases with increasing food concentration until an "incipient limiting level (ILL)" is reached (McMahon and Rigler, 1965). This is the food level at which dependency on food concentration ceases and the feeding rate remains maximal. Below the ILL, daphnids exhibit the maximum filtering rate while the maximum ingestion rate is found above the ILL. This type of curve has been frequently described in the literature (McMahon and Rigler 1965; Burns and Rigler 1967; Kersting and v.d. Leeuw 1976; Hayward and Gallup 1976). Although there is no disagreement about the general shape of the ingestion curve with food concentration, different mathematical models can be fitted to the data: a rectilinear form consisting of two straight lines. One line describes the increase of the ingestion rate at low food concentrations and the second one lies parallel to the x-axis and indicates the maximum ingestion rate. Both lines intersect at the ILL (Muck & Lampert 1984). The other models are the Ivlev saturation curve (Ivlev 1961) and the commonly used Michaelis-Menten curve (Holling 1966). Attempts to decide statistically which model describes the functional response best failed for Daphnia (Lampert 1977b; Porter et al.,1982). Therefore, different investigators favour different models for their own data sets, which, of course, introduces incomparability.

Food conditions in the field fluctuate very widely, so it can be assumed that there are periods when the animals have very little food and other periods when they have sufficient food. Since in filter feeders the amount of food ingested is dependent on the food concentration, it is ecologically useful to know the critical concentration of food level below which the animal will starve

It has proved more difficult to define the lowest food concentration at which feeding occurs, despite its obvious ecological importance, particularly in oligotrophic waters.

On an individual basis Lampert & Schober (1980) defined the threshold food concentration as that at which an animal is just able to balance its metabolic losses with its assimilation so that it does not grow, yet does not lose weight either. This is the food concentration that is derived graphically from the intersection of the plots for assimilation rate and rate of metabolic losses on food concentration.

Unlike some marine copepods, Daphnia does not show a feeding threshold at very low food concentrations, as proposed by the optimal foraging model of Lehman (1976). The feeding curve passes through the origin if alinear model is applied (Muck and Lampert 1980) and the fit of a non-linear is better without a threshold (Porter et al. 1982). A slight depression of the appendage beat rate (Burns 1980, 1984) has been observed at very low food concentration. Muck & Lampert (1984) attribute this effect to exhaustion during the period of acclimation to low food, as it parallels the weight loss during this period.

In adult Daphnia pulex, if Scenedesmus acutus is used as food, the threshold concentration ranges from 0.04 to 0.12 $mgC.l^{-1}$ (Lampert & Schober, 1980). In an other experiment involving the simultaneous measurement of assimilation and respiration, Bohrer & Lampert (1988) found a threshold concentration of 0.075 $mgC.l^{-1}$ for adult D. magna fed on Scenedesmus acutus.

Another approach to threshold food concentration was introduced by Frost (1985) defining food limitation as a condition in which a particular physiological rate is constrained by food availability and, for grazing rates in copepods, he calls this the upper limit of constraint, the critical food concentration. The lower level, where the rate is zero, he termed the threshold food concentration. Between these two concentrations of food lies the range of limiting food levels for the species. The determination of the threshold value is very difficult, demanding a large number of food levels and

considerable care. The Michaelis-Monod function, introduced by Hrbacek et al., (1978) in their work on Daphnia spp., is rather useful. The function provides two ecological parameters: umax or the maximal rate at non-limiting by food quantity and K_s or the food concentration at which half u_{max} is attained.

Rocha (1983) using the Monod model compared the primipara female absolute growth rates for D. hyalina at 20°C which had the lowest K_s (0.02 $mgC.l^{-1}$), for D. magna (0.12 $mgC.l^{-1}$) and for D. pulicaria which had the highest value for K_s (0.23-0.24 $mgC.l^{-1}$). The comparative pattern of response changed at the lower temperatures. The values for μ_{max} were also different in the three species. Such specific differences in the growth rates in relation to food and temperature are clearly relevant to the outcome of inter-specific competition between the three co-existing species living in a temperate habitat where both food concentration and temperature changes.

Threshold food concentration are virtually unknown for tropical species of cladocerans. Jayatunga (1986) was the first to conduct studies on growth and life cycle characteristics of tropical cladocerans which involved life cycle experiments where the development of a neonate is followed throughout its life history to the reproducing adult. She recorded the threshold for growth for Daphnia lumholzi to be between 0.03-0.05 $mgC.l^{-1}$ at higher temperatures (27°C and 32°C) but to be higher at 22°C where it lies between 0.05 and 0.1 $mgC.l^{-1}$. This result is comparable to that of Rocha (1983) mainly because both experiments were conducted under same procedures (well defined food concentrations and temperature controlled conditions). Rocha's results shows that the temperate daphnids, D. magna, D. pulicaria and D. hyalina, can grow at 0.01 $mgC.l^{-1}$ in temperatures of 10-20°C which are lower than any of the threshold levels for the tropical cladoceran reared at 22°C but in both temperate and tropical species, the threshold food level for reproduction decreased with increase in temperature.

Other authors have investigated how food availability affects growth rates. Generally, limiting the amount of available food caused

a distinct reduction in rates of growth and reproduction. Ingle et. al.,(1937) also found in D. longispina fed on low food an increase duration of instars so that a longer period of time was required for effecting smaller growth increments and for the production of smaller broods of young than in the case of normal well-fed mothers. In fact, prolongation of post-embryonic development (D_j) and reduction in size at maturity, is a well-known physiological response of cladocerans to reduced food supply (e.g. Richman 1958; Hkbáčková-Esslová 1963, Hall 1964, Weglenska 1971, Hrbáčkova and Hrbáček 1978, Neill 1981).

Another observed effect of food concentration is on the reproductive capacity of the adults. The number of eggs produced by an adult female depends upon food intake. If the food supplies only enough energy to meet maintenance requirements, no eggs are produced. Numerous experimental studies (Ingle et al.1937, Green 1954, 1956, Richman, 1958, Hall, 1964, Kerfoot 1974; Rocha 1983; Jayatunga 1986, amongst others) have shown that there is a direct relationship between food supply and the number of progeny produced by a female during her life time.

Other parameters of zooplankton life history may also respond to changes in food supply. Decrease in the size at maturity associated with low food levels has also been observed in laboratory experiment. Green (1954), Hrbáčková (1963, 1974) and Kerfoot (1974) have found larger primiparas when the food was enriched than in natural food.

Rocha (1983) studied three daphnids under well defined food concentrations. Her results showed that the length of the primipara female of all daphnids is also reduced as food conditions are decreased to limiting levels (0.01 $mgC.l^{-1}$). Variation in sizes is very difficult to detect in cladocerans, particularly with the smaller tropical species, bearing in mind that live animals which must not be damaged and/or stressed are being measured.

Decreased in the size of primipara has been also observed in the field (Brambilla, 1980). It was observed that spring daphnids matured at 1.5-1.6 mm, produced 30-40 eggs per female. In the summer, there was a dramatic decline in the size of primipara to 0.80-1.0 mm,

with 5-6 eggs. These variations were interpreted by the author as adaptations to alternated invertebrate and vertebrate predators. Food limitation and temperature were rejected as causal factors, probably due to his unsuccess in defining food levels either in field enclosures or in the laboratory.

In addition, the response to fluctuating concentrations of food may be another mechanism controlling the composition and relative abundance of different species. Goulden et al.(1982) examined experimentally the competitive abilities between daphnids and bosminids; he found species with the largest body size were the competitive dominants in the high food cultures. The larger species, Daphnia galeata (0.7-2.4 mm) was subsequently displaced by the smaller species, Bosmina longirostris (0.9-4.5 mm). This has also been noted for other Cladocera (Orcutt and Pierce, 1985). The larger sized species Daphnia ambigua is favoured over the smaller Diaphanosoma brachyurum when food is abundant. However, D. brachyurum is favoured over Daphnia ambigua when food is sufficiently limited. Studies of this kind require precise information on the nature food available, bearing in mind that in the field changes continuously occur.

Temperature

It is well established that rates of various biological and physiological processes of poikilotherm animals are dependent on temperature: this is known to be so in zooplankton for processes such as development and life cycle duration, feeding, respiration and growth . In general, increasing temperature promotes an increase in the rates of metabolism and activity within the tolerance range of each species. Differences have been observed between species or between biological processes in the temperature-induced rates of increase. Most studies measuring the effect of temperature on the rate of food uptake of Daphnia spp found optimum curves. The largest range of temperatures (5-35°C) was tested by McMahon(1965) with Daphnia magna. The filtering rate increase up to 24°C and decreased slowly above this value until a sharp drop occurred above 33°C. The

optimum is often found at about 20°C or slightly higher, but this may simply reflect the temperature at which the animals had been culture

A number of mathematical equations have been used by biologists to describe the relationship between temperature and development time (D_e). Among these the Krogh's "normal curve" (Krogh,1914), the Belehradek function (Belehradek, 1929, 1935) and the Van't Hoff-Arrhenius function, have been widely used. Others authors adopted the recommendation of Edmondson & Winberg (1971) and Winberg(1971) to use the reciprocal of duration (1/D) as the rate of development in order to quantify the temperature effect on egg development duration. However, as Bottrell (1975) points out, the reciprocal transformation of duration is only useful if it produces a linear relationship. He found a curvilinear relationship in eight out of nine species of cladoceran from the River Thames. Thus, he suggested that curvilinear functions which can be easily linearized and statistically compared are more adequate. He used Polynomial regressions which usually gave best fits by introducing more terms. However, as Sutcliffe and Carrick (1981) pointed out "they do not necessarily provide better predictions for the dependent variable than predictions based on simple two-parameter equations".

The Van't Hoff-Arrhenius function came from two commonly used temperature functions originally developed by chemists to relate the rate of chemical reactions and temperature and taken over by biologists for the temperature relations for whole organisms. One of these, the Vant' Hoff law which implies a constant ratio of increase produced by a given difference of 10°C in temperature is expressed by:

$$Q_{10} = \left(\frac{V_1}{V_2}\right)^{10/(t1 - t2)}$$

where V is the rate of development (1/D) at the given temperature in degress centigrades, and Q_{10} is a constant usually 2-3 indicating the increase in rate over a 10°C rise in temperature. This equation can be re-arranged as follows:

$$V_2 = V_1 \cdot Q_{10}^{(t1 - t2/10)}$$

generalised as:

$$V = a\, b^{T}$$

and transformed to a linear equation as:

$$\log V = \log a + T \log b$$

If Q_{10} is found to be constant in biological data, then a plot of the logarithm of duration rate against temperature °C will be linear, and its slope (b) will be log Q_1 from which Q_{10} can be calculated. The other temperature function is the Arrhenius equation which represents a further development of the Van't Hoff formula is based on thermodynanic considerations of the frequency of molecular collision as a function of temperature and can be expressed as:

$$V_2 = V_1 \cdot e^{0.5(1/T3-1/T2}$$

where V is the rate of development (1/D), T is temperature (absolute, in Kelvin), e is the base of natural logarithms and Arrhenius u is a constant.

This equation can be generalised as:

$$V = a.e^{\,b(1/T)}$$

and transformed to a linear equation as

$$\ln V = \ln a + b\,(1/T)$$

if u is found to be constant in biological data, then a plot of the logarithm of duration against reciprocal temperature will be linear.

It is evident in the literature that neither Q_{10} nor the Arrhenius u appear to be constant over the biological range of of temperatures. To demonstrate this Bottrell (1975a) found that the

relationship between the logarithm of development rate and temperature is curvilinear in eight of out of nine species of cladoceran from River Thames. A quadratic term added to the equation, reduced significantly the residual mean square.

$$\log V = \log a + T \log b + T^2 \log b$$

Thus, Bottrell advocated the use of D rather than its reciprocal (1/D or V) and that should be transformed logarithmically to ensure the normality of data which is necessary in regression analysis.

Belehradek's equation (1935) has been used to relate the duration of development to temperature:

$$D = a /(t - b)^c$$

where D is duration of development, t is temperature, and a, b, and c are constants. Herzig (1983) did a set of experiments for six species of planktonic copepods at constant temperatures in a wide range from 1.4°C to 27.3°C at short intervals. He concludes that the curvilinear relationship between the duration of embryonic development and inverse of temperature in these freshwater copepods was most adequately described by the Belehradek's equation because a high proportion of the total variance of development duration was explained. Later, Herzig (1984) studied the duration of embryonic development in Diaphanosoma brachyurum at fifteen different constant temperatures (between 8.2 -29.7°C) and the post-embryonic development time at nine different constant temperatures (between 8.2-26.0°C). His results showed that the curvilinear relationships are well described by Belehradek's function, since 97.29% and 99.27% of the total variance of development duration are explained.

The general findings by many authors related to what equation is best for the biological interpretation of their data set is still controversial: McLaren (1963) demonstrated the usefulness of Belahradek's function for predicting the effects of temperature on development rates of marine copepods. Bottrell (1975a) found Krogh's curve and van't Hoff-arrhenius function to be inadequate for expressing the relationship between (De) to temperature in cladocerans from the River Thames and used polynomial regression. Lei and Armitage

(1980) also found Krogh's curve unreliable for predicting the time of embryonic development in Daphnia ambigua; instead, they found curvilinear logarithmic functions describe the relationships most apropriately. This kind of function was also used in the present work. However, as Heip (1974) emphasize, there is no theoretical justification for choosing one rather another.

Very few experimental information is available from tropical zooplankton in relation to the effects of temperature on duration of development. Earlier studies are from Lake Chad (Africa) on copepods and cladocerans(Gras & Saint-Jean, 1969, 1976, 1978, 1981; Gras, 1970; Leveque & Saint-Jean, 1983). The studies by Burgis (1971) on estimated development periods and productivity in Thermocyclops hyalinus from Lake George, Uganda, of Hart and Allanson (1975) on Pseudodiaptomus hessei of Magadza (1977) on Moina dubia from Zambia and of Magadza and Mukwena (1979) on Thermocyclops neglectus from Lake Mcllwaine, Rhodesia comprise the major contributions in this field in tropical Africa.

Since the early 1960's, there have been several contributions on the duration of development and growth of tropical species from Indian water bodies. Michael (1962) observed in Ceriodaphnia cornuta reared with pond water at 28° and 31°C that a rapid growth took place during the early period and the juveniles moult once or twice to reach the first adult instar. Murugan (1975) found that the rate of egg production in Ceriodaphnia cornuta is comparatively lower than in allied tropical cladocerans such as Simocephalus acutirostratus (Murugan and Sivaramakrishan, 1973), Daphnia carinata (Navaneethakrishnan and Michael, 1971, Scapholeberis kingi (Murugan and Sivaramakrishnan, 1974) and slightly higher than for the Moina micrura (Murugan. 1975). However, their results are not comparable for various methodological reasons, mainly among others, undefined food levels.

The duration of embryonic development of tropical rotifers Brachionus caudatus and B.calyciflorus (Sri Lanka) was determined at several temperatures by Duncan, 1983 who presents the exponential regressions of egg duration on temperature. Egg size versus duration

was an important combination in this. Long term growth experiments were carried out on the tropical cladoceran species, Diaphanosoma excisum, Moina micrura, Daphnia lumholzi and Ceriodaphnia cornuta from Kalawewa Reservoir in Sri Lanka by Jayatunga (1986). In all these species she found a decrease in embryonic duration (De) with increasing temperature at all food levels and post-embryonic duration (Dj) is influenced by food concentration as well as temperature. The Dj decreased as temperature and food concentration increased.

From the examples mentioned so far in tropical zooplankton only the latter investigation by Jayatunga (1986) has dealt with life cycle long-term experiments examining the effects of food concentration and temperature simultaneously. This represents a pioneering work in examine the influence of these environmental factors upon the reproductive parameters of tropical species.

1.6 AIMS OF THIS STUDY

This thesis is concerned with the effect of temperature , food concentration and turbidity upon the life cycles of species of Cladocera that are ecologically important components of the zooplankton of an Amazonian Lake Jacaretinga.

These effects were studied both experimentally in the laboratory and by field investigation in the lake, since it was hoped that the experimental results would aid in the interpretation of the changes that occurred in the lake in terms of species composition in the zooplankton community and the population dynamics of individual cladoceran species.

The aims were therefore:

(1) To examine the effects of temperature, concentration of available food and turbidity on the growth and reproduction of three species of Cladocera, Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata, under defined and controlled conditions.

(2) To study the population dynamics of the cladoceran species-populations and the species composition of the zooplankton community in Lake Jacaretinga before, during and after the period when the lake was subjected to flooding by the River Amazon and when both abiotic and biotic environmental conditions for the cladocerans changed considerably.

(3) To interpret, if possible, the ecological changes in the cladoceran populations of Lake Jacaretinga on the basis of how the life cycles of the different species of Cladocera responded to experimentally controlled changes in temperature, food and turbidity.

CHAPTER 2

2. THE STUDY SITE AND SPECIES

Lake Jacareringa (3°14'S and 59°45'W), located approximately 25 km East of Manaus in the Central Amazon of Brazil, is a small floodplain lake with an area of 0.10 km^2 and is connected periodically for about six months with the Rio Solimoes (as the Rio Amazon is called above its junction with the Rio Negro (Figure 2.1). As the level of the Amazon rises from February-September, water from the Parana do Careiro flows over the embankment and through the varzea forest into the lake via a very narrow canal about 150 meters long to the west of the lake. During the period when river water flows in, the lake is highly turbid with a Secchi disc depth of 0.5 m. The reduced light penetration favours the development of floating macrophytes, which cover more than 30 % of the lake surface (Junk,1973). As the influence of the river declines, the suspended sediment drops out of the water column and phytoplankton production increases (Schmidt,1973 a,b,).

The relative composition of the zooplankton fauna was studied by Hardy(1980) who recorded a marked change from a rotiferan-cladoceran fauna during the low water phase in February to a calanoid-cyclopoid copepod fauna in July during the period of the high water level. The relative proportions changed from Rotifera 56%, Cladocera 23%, Calanoida 11%, Cyclopoida 10% in February to Rotifera 31%, Cladocera 9%, Calanoida 34% and Cyclopoida 26% in July. The planktonic cladoceran species living in the lake during February to April 1986 were: Diaphanosoma sarsi Richard,1894, Daphnia gessneri Herbst,1965, Ceriodaphnia cornuta Sars,1886, Moina reticulata (Daday,1905), Moina minuta Hansen,1899. Of these, Moina reticulata, Diaphanosoma sarsi and Daphnia gessneri (Plates 2 (a,b,c)) were studied experimentally for this thesis used in the experiments reported here.

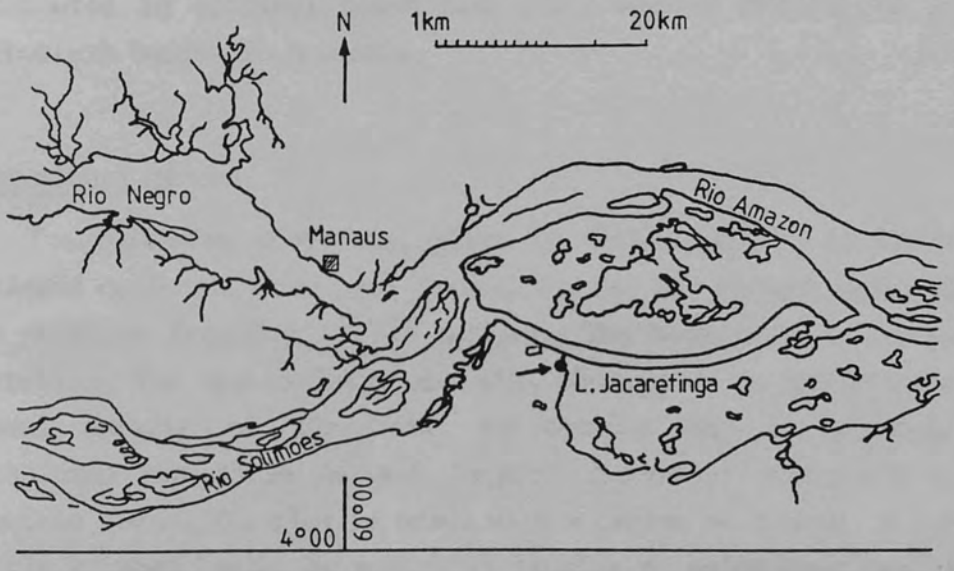


FIGURE 2.1 Map of South America showing the River Amazon basin and geographical position of the study area. (Above). Central Amazon region showing the lake studied (Below).

Ceriodaphnia cornuta Sars

This species was originally described by Sars(1885). Recently, Korinek(1984) who examined material from lakes in Brazil, including Lake Jacaretinga, found that the Ceriodaphnia cornuta agreed with Sars's description. The main diagnostic characters for the female are: head small, rounded on top, with supraocular depression, sometimes with a small projection or horn with a large compound eye and an ocellus present. There has been a long dispute over the difference between Ceriodaphnia cornuta Sars and Ceriodaphnia rigaudi Richard,1894 where the latter lacks the projection on the head. Kořinek(1984) examined the variations in structure of this species from different parts of the world and suggested that at least two distinct species are included under the species Ceriodaphnia cornuta Sars. As the specimens collected in the present study were horn-carrying females with ephippia as described by Kořinek(1984), the species was considered to be Ceriodaphnia cornuta. No males were found.

The distribution is considered to be tropico-cosmopolitan, according to Brandorff's classification (Brandorff 1977). It is widely distributed in tropical ponds and lakes and is present in various freshwaters bodies in Amazonia.

Moina minuta Hansen

The following diagnosis, given by Goulden(1899), is based upon specimens collected from Lago Isabal, Guatemala. It is a small species that measures from 0.5 to 0.7 mm long. The head bears a supraocular depression. The eye is large and lies contiguous to the anterior and ventral margins of the head. An ocellus may be present. The postabdomen has three to six lateral feathered teeth and a long bidentate tooth. The claw is armed with a pecten of eleven to fourteen sharply pointed teeth. No ephippial females or males have been found, but there can be no doubt that Moina minuta is a distinct species, owing to the very characteristic first leg and the long sensory setae of the second antennae.

This species has a neotropical distribution. Specimens were collected from the open water and littoral areas of Lago Izabal in Guatemala where it was very commonly present in the littoral collections. Robertson & Hardy(1984) collected Moina minuta in differents types of lakes such as those influenced by Rio Solimoes, Rio Negro, Rio Tocantins, Rio Japura, Rio Aripuana and Curua-Una reservoir.

Moina reticulata (Daday)

The original description is based on Daday's type material. The body is rounded and has a depressed head. The surface of the shell and head is reticulated, but there are no hairs. The compound eye is large and fills the tip of the head. An ocellus is present. Moina reticulata has been reported by Daday from several pools in Paraguai. He placed this species in the genus Moinodaphnia because it possessed the ocellus and a well-developed abdominal fold. In the present work this species has been placed in the genus Moina based upon two characters given by Goulden(1969). First, the presence of an ocellus and of an abdominal fold are not infallible characters since it is possible that one species of Moina, namely Moina minuta, has an ocellus while several other species possess an abdominal fold. Secondly, the species lacks the characteristic pattern of setae on the shell and second antennae. Moina reticulata may be distinguished from Moina micrura by the presence of an ocellus, a well-developed abdominal fold and a long bidentate tooth on the postabdomen bearing spines of equal length. Moina reticulata is a distinct species and should not be confused with other species of the family.

Distribution. Subsequent to Daday's publication, this species has been found in the plankton of many freshwater lakes in the Amazonia Region (Robertson & Hardy,1984). It was classified by Brandorff 1977, as tropical-cosmopolitan in distribution. In the present study, males and sexual females were found quite often.

Daphnia gessneri Herbst

This species was originally described from South America. Kořinek(1984) found that samples collected from different localities in Amazonia agreed with Herbst's description.However, he found two distinct populations in the material studied from Lake Mweru (E.Africa). The only difference between them was the presence of helmet-like shaped heads and an ocellus situated close to the optic vesicle. The population in Lake Jacaretinga resembles the species Daphnia gessneri, but the helmet is regarded as an unreliable character as its presence is regulated by external factors. Possibly several species with a set of similar characters have been confused; these are Daphnia laevis Daphnia gessneri and Daphnia dubia Herrick,1895 as well as other laevis-like populations from Africa. During the present study period, only populations with helmet-like shape were collected and these agreed with Herbst's description for Daphnia gessneri.

Distribution. According to Brandorff(1977), Daphnia gessneri together with Diaphanosoma sarsi and Ceriodaphnia cornuta are the most numerous Cladocera in Lake Castanho. Within his classification, Daphnia gessneri is an neotropical species present in South America and Southern United States.

PLATE 2(a) Photograph of Moina reticulata

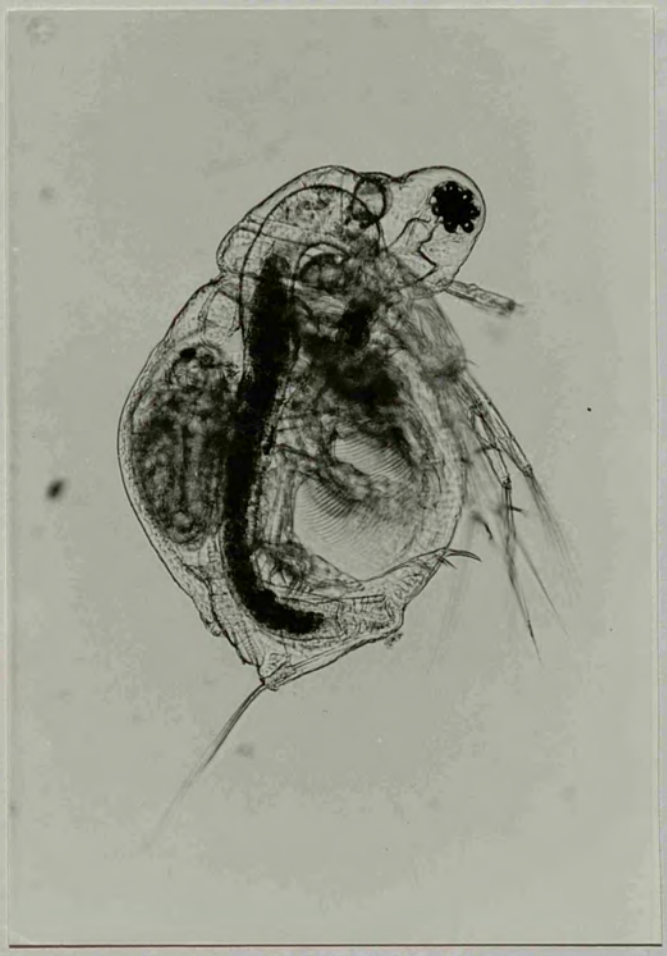


PLATE 2(b) Photograph of Diaphanosoma sarsi

PLATE 2(c) Photograph of *Daphnia gessneri*

CHAPTER 3

MATERIAL AND METHODS

3.1 Field investigations in Lake Jacaretinga, Brazil

Outline plan of work

The field studies on the cladoceran populations were carried out weekly from February to April 1986. To analyse their horizontal distribution, the lake was sampled at 5 locations (Figure 3.1), where at the same time determined the depth of water, water transparency, temperature, and the concentrations of chlorophyll a and particulate organic carbon. The sampling dates and measurements made are summarised in Table 3.1. In addition, qualitative net samples were taken at weekly intervals for size frequency analysis of the cladoceran population and for length-carbon weight relationships.

Weekly sampling at five stations

The zooplankton was collected using a 12-litre Patalas-Schindler volume sampler which had a net with a mesh pore size of 55 µm. Bearing in mind that the volume sampler had a height of 30 cm, it was possible to take integrated samples from top to bottom at the following depth intervals: 0.3, 0.9, 1.2, 1.5, 2.0 and 3.0 metres. Usually the sampling began at 12 noon and took approximately 30 minutes at each station, finishing 2½ hours later.

Physico-chemical characteristics of Lake Jacaretinga

Vertical profiles of temperature and dissolved oxygen concentration were taken with an oxygen sensor, the Termoeletrico Model WTW OX1 91, which was calibrated in air before each profile and taken at every 0.2 meters between the surface and lake bed. Transparency and depth of

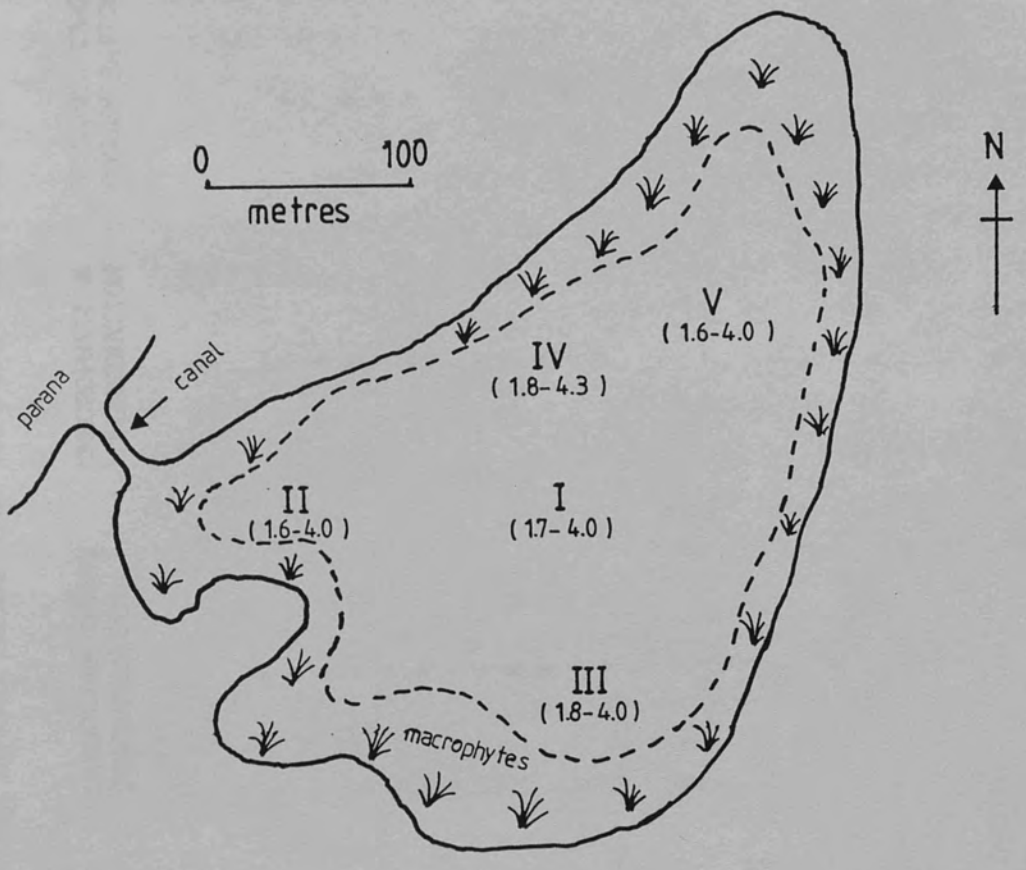


FIGURE 3.1 A schematic diagram of the lake showing the position of the sampling stations. (dots line represent the level of the lowest phase) I,II,III,IV,V are stations.

TABLE 3.1 FIELD INVESTIGATIONS AT LAKE JACARETINGA (February, March and April 1986)

DATES	TEMPERATURE °C	DISSOLVED OXYGEN CONCENTRATION	CHLOROPHYLL-A CONCENTRATION	SESTONIC CARBON CONCENTRATION	TRANSPARENCY Secchi disc
Feb 20th	+	+			+
Feb 24th	+	+		+	+
Mar 4th	+	+	+		+
Mar 11th	+	+	+	+	+
Mar 19th	+	+	+	+	+
Mar 26th	+	+	+	+	+
Apr 1st	+	+	+	+	+
Apr 8th	+	+	+	+	+
Apr 15th	+	+	+		+
Apr 22nd	+	+	+	+	+
Apr 29th	+	+			+

water were both measured with a 20 cm white Secchi disc and a line marked at 5 cm interval. It was hoped that the Secchi disc depth would provide some measure of turbidity.

Chlorophyll a

Water samples were collected using a 1-litre transparent Ruttner volume sampler at 1.0, 2.0 and 3.0 meter depths and bulked to provide an integrated column sample. The water was stored in plastic bottles and kept in an ice box for the journey back to Manaus. In the laboratory of Institute National of Research of Amazonia(INPA), this bulked sample was fractioned by filtration through 55 µm netting and 20 um netting to provide samples of different sizes of algae.These fractions were kept refrigerated for subsequent analyses within 48 hours. A known volume of water was filtered onto a GF/F pad of 0.7 µm. The filter was ground up and the pigment extracted by adding 2.0 ml of 90% acetone which was then made up to 10 ml. The extract was centrifuged 10 minutes at 3000 rpm, and the supernatant was used to fill a 1.0 cm path length cuvette. Its absorption at 665 and 750 nm wave length was determined using a spectrophotometer Spectronic 100, digital Bausch & Lomb. The calculation was made according to Golterman(1970) as follows:

$$\text{Chl-a mg/l} = \frac{11.23(A665-A750) \times \text{extracted vol.(ml)}}{\text{filtered vol(l)} \times \text{cell length(cm)}}$$

Sestonic particulate organic carbon

The same bulked Ruttner samples provided water for estimation of the sestonic particulate organic carbon in the water column. These too were filtered through the same series of nettings as for chlorophyll a but in the field and finally onto 45 mm GF/F pads, previously pre-combusted at 500°C to remove background carbon. The pads were transported to the laboratory in a desiccator to avoid carbon contamination. They were then dried at 60°C, stored individually in

cleaned, labelled glass vials and kept in a desiccator for transport to England. In England, the determinations of particulate organic carbon were made by the wet dichromate oxidation method according to Mackereth et al.(1978). The principle of the method consists of oxidising the organic matter at 100°C with a known volume of dichromate and sulphuric acid. The decrease in dichromate was determined by titration against a ferrous salt. The end-point is detected amperometrically. The procedure and method are given in Appendix 1.

Handling procedures for the zooplankton samples

The quantitative samples of zooplankton were collected from between four and six depths and then bulked to give 48-72 liters of water. This bulked sample was concentrated to a small volume of about 70 ml in a labelled plastic bottle, immediately killed and preserved by addition of concentrated formaldehyde to allow a final concentration of 6%. The samples were transported to England by ship where the counting was carried out about one year later.

Only Cladocera were counted. Whenever possible a total count of animals in each sample, which consisted of three replicates was made. On occasions when the density of a dominant cladoceran was high and a total count was not practicable, the sample was brought to a constant volume (200 ml), agitated and sub-sampled with a 5 ml Stempel-pipette. This was filled and emptied several times prior to sub-sampling in order to disperse the specimens in the sample. Three sub-samples were always counted for any species or stage. A minimum of 100 organisms was counted for 80% of the samples but this number could not be attained for males and sexual females, even if the whole sample was counted. The counting was made with the aid of a Petri dish 8.7 cm of diameter, divided into 20 parts, under an Olympus microscope with a X20 magnification. As the taxonomy of planktonic Cladocera from Lake Jacaretinga is well known, the identification of each species in this study was not difficult.

Procedures for determination of the carbon weight and length relationships of the field population

Zooplankton collected by a series of horizontal and vertical net hauls, using 55 μm mesh netting, were kept in 20 litres of filtered natural water. The container was immersed in an ice box during the journey back to Manaus. At INPA, cladocerans were sorted, measured while alive on a glass slide with a drop of water, under a Zeiss microscope with a calibrated eye piece. Figures of the cladocerans and the positions of measurements taken are given in Figure 3.2. Size categories of 0.05 mm intervals were measured, sorted, washed in distilled water and transferred carefully into nickel pans stored in numbered cavities bored in an aluminium block which had previouly been muffled at 500°C. Finally, when a reasonable number of Cladocera had been collected, the blocks were wrapped with muffled aluminium foil, dried at 60°C and stored in a disiccator with silica gel. In this conditions, the samples were brought back to England where the carbon determinations were carried out using high temperature dry combustion method described by Salonen(1979). This technique is quick and analyses could be performed very rapidly, with a sensitivity of 0.01 μgC. The concentration of carbon dioxide from the combusted Cladocera was detected by the attenuation of infra-red in a Hartmann & Braun infra-red carbon dioxide analyser, as describe in Appendix 2. The peak height was measured and converted to carbon weight using the calibration curve in Figure 3.3., determined with known concentrations of oxalic acid. This calibration curve agreed with those of Carlos dos Santos who was responsable for bringing Salonen technique into operation in the Department.There were no difficulties during the analyses since the technique of the method had been well developed. As the method was sensitive, only one or a few individual animals of the same size were needed to obtain a result.

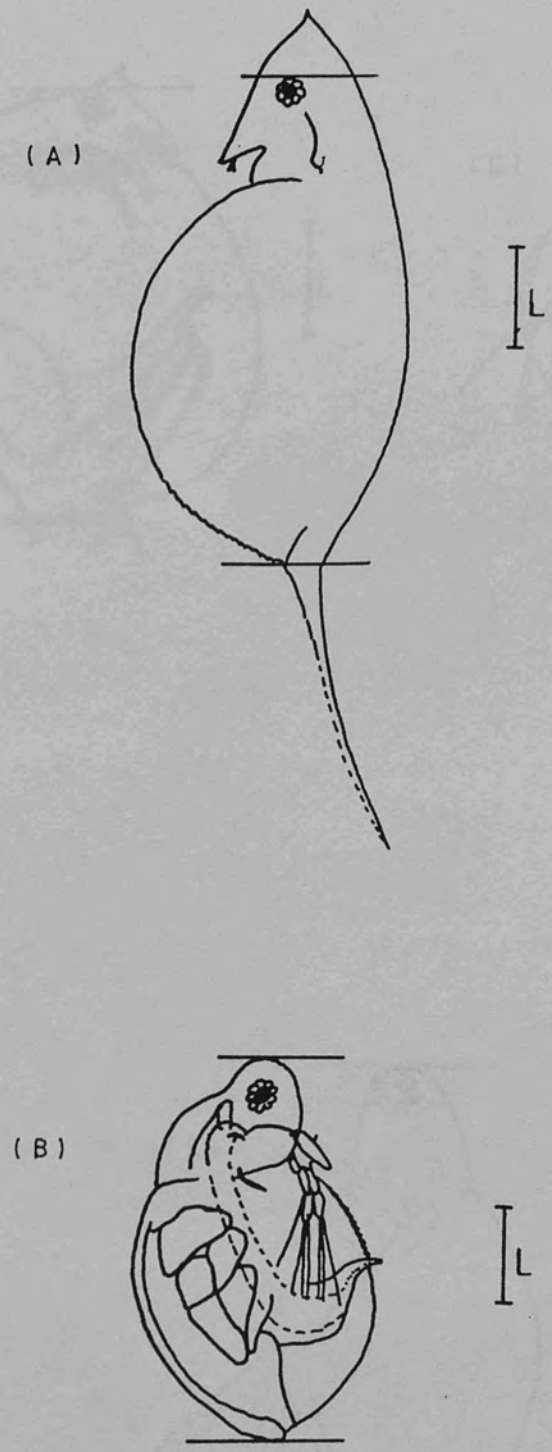


FIGURE 3.2 (A) Daphnia gessneri, (B) Moina reticulata, (C) Ceriodaphnia cornuta, (D) Moina minuta, (E) Diaphanosoma sarsi, showing schematically the positions where the measurements were taken.

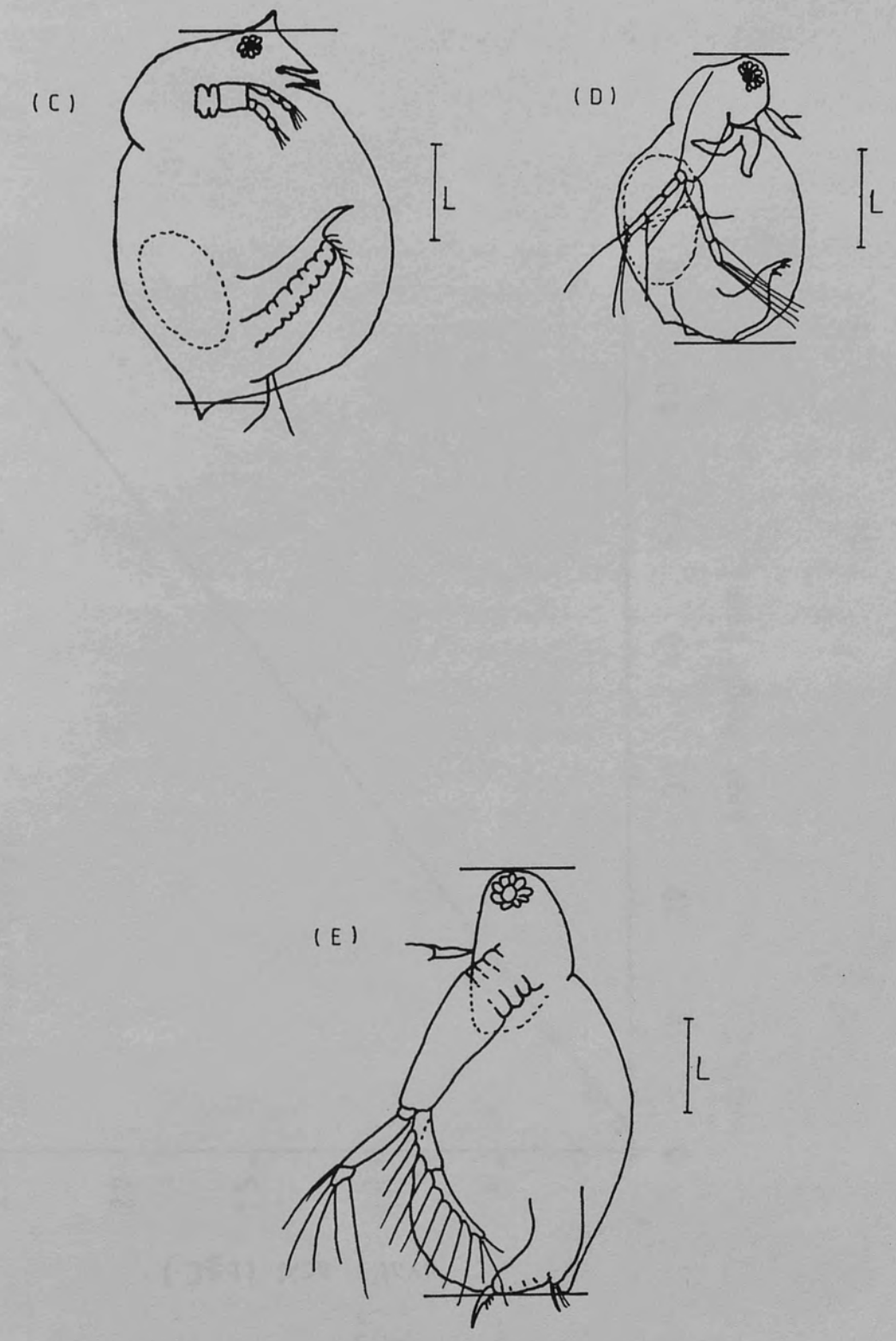


FIGURE 3.2 continued.

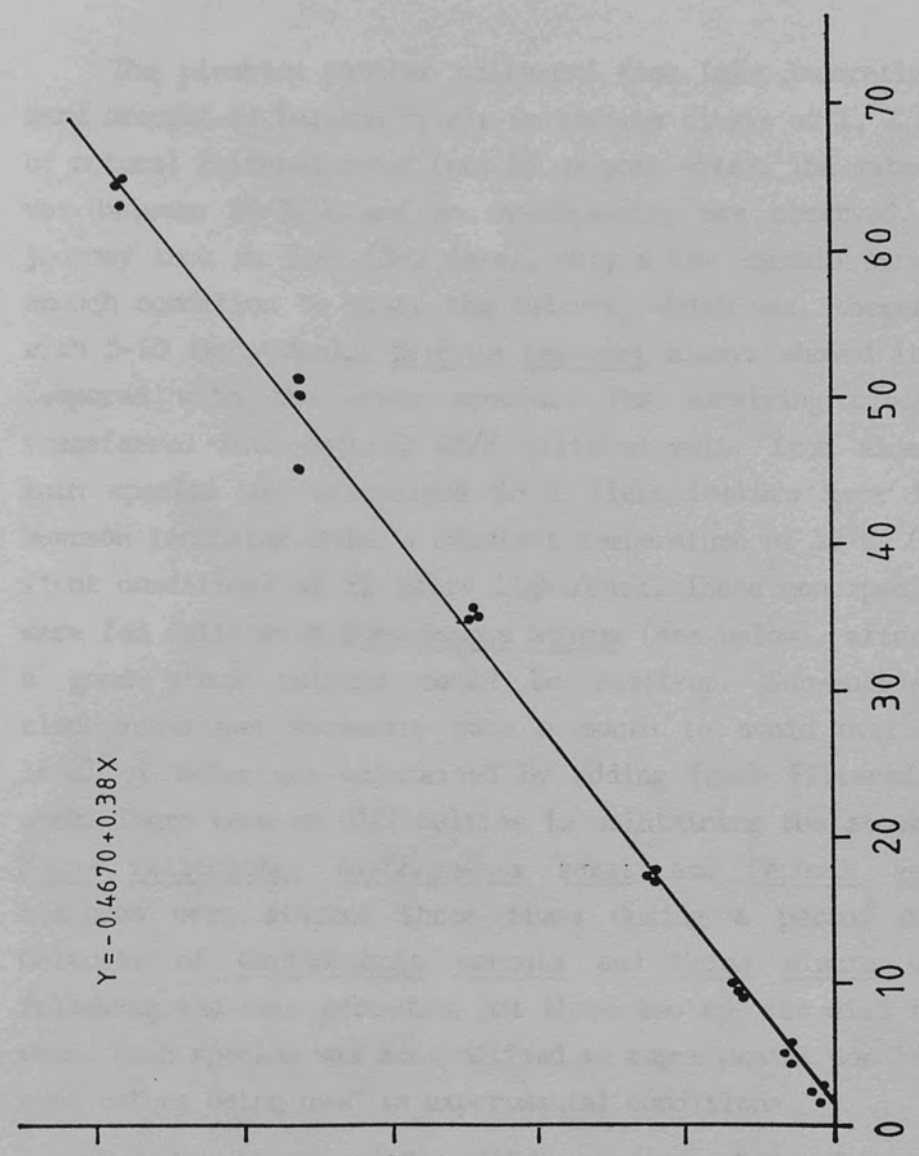


FIGURE 3.3 Calibration curve obtained using Oxalic acid for the high temperature dry combustion technique

3.2 EXPERIMENTAL INVESTIGATIONS AT RHBNC

Sources and stocks: Transportation, maintenance of Cladocera stocks

CLADOCERA CULTURE

The plankton samples collected from Lake Jacaretinga, Amazonia were brought to England by air in thermos flasks of 1, 2 and 10 litres of natural filtered water (net 55 µm pore size). The water temperature was between 28-30°C and no overcrowding was observed. Because the journey took so long (3-5 days), only a few animals survived in good enough condition to start the culture, which was, therefore, started with 5-10 individuals. Daphnia gessneri always showed lower survival compared with the other species. The surviving cladocerans were transferred into natural GF/F filtered water from Alderhurst pond. Each species was maintained in 1 litre beakers kept in an Astell Hearson incubator under a constant temperature of 27°C 0.5°C and day light conditions of 12 hours light/dark. These monospecific cultures were fed daily with Scenedesmus acutus (see below). after three weeks a good stock culture could be built-up. Sub-culturing of the cladocerans was necessary once a month to avoid overcrowding; the level of water was maintained by adding fresh filtered water every week. There were no difficulties in maintaining the stock cultures of Moina reticulata, Diaphanosoma sarsi and Daphnia gessneri. New cultures were started three times during a period of 1½ years. Cultures of Ceriodaphnia cornuta and Moina minuta were started following the same procedure but these two species died in the second week. Each species was acclimatized to experimental conditions for 3/4 week before being used in experimental conditions.

Scenedesmus acutus, Class Chlorophyceae, Order Chlorococcales, is a single elongated fusiform cell, without mucilage or a thick cell wall. Its physical and chemical characteristics were determined by Rocha(1983) to be as follows: cell length, 10.34 µm ±2.44; cell width, 4.68 µm ±1.36; cell volume, 102.39 µm; ash free weight,19.74 ±4.86; chlorophyll a, 0.49 µg/cell; total organic carbon, 11.78 ±0.30

pgC/cell. These physical and chemical characteristics were assumed applicable to this study since the culture conditions followed the same procedures as reported by Rocha(1983).

MAINTENANCE OF THE ALGA IN THE EXPERIMENTAL PHASE OF GROWTH

Scenedesmus acutus was maintained in stock culture at RHBNC in petri dishes with an agar-Chu12 medium (Appendix 3), and kept at 13°C in an Astell Hearson incubator. When experimental work was started, new cultures were set up and maintained by two methods; A) using agar plates for the experimental food stock and B) using liquid cultures in Chu12 medium for preparation of the experimental food.

The stock agar Chu12 cultures were sub-cultured monthly. To 1 litre of distilled water, 1 ml of each of the chemical solution was added and approximately 10 grams of agar was dissolved by gentle heating. This medium was poured into sterile petri dishes, covered and allowed to cool. Scenedesmus acutus, resuspended in distilled water from an agar plate of known age, was inoculated onto the new agar plate using a sterilized Pasteur pipette. These plated were kept in the conditions describe above, to be used in the preparation of experimental food 8-10 days later. Only rarely contamination by fungi was observed in some agar plates, which were immediately rejected. Only uncontaminated plated were used. These plates could only be used once and were therefore prepared in batches usually of 20, which was enough for 3-4 weeks.

Chu12 liquid medium was prepared three times a week in a series of flat-bottom flask (500 ml), following the same procedure as described above but without the addition of agar. Scenedesmus acutus, from recently inoculated agar plated was suspended in distilled water and a few drops transferred with a sterilized pipette into the flasks of sterilized liquid medium. These flasks were kept in a culture room at approximately 20°C, under continuous illumination of fluorescent

lamps. The medium was gently and continually aerated with Whisper 300 aerators which were attached to clean vinyl tubing on end of which an air-stone was immersed in the medium liquid. It should be noted that these liquid cultures were not bacteria free but contamination with other algal species did not occur. Liquid culture medium from one flask was used twice.

The period of exponential growth of Scenedesmus acutus in liquid medium was well defined under these conditions by Rocha(1983) and Jayatunga(1986) as continuing for between 5-9 days old. This was confirmed in July 1985 by taking 1.0 ml sub-samples from a flask of liquid culture daily for 10 days. These samples were fixed with lugol's iodine, sedimented in an Utermohl sedimentation chamber and counted using a Wild Orthoplan inverted microscope. A minimum of 100 cells were counted. The cell concentration plotted against time is shown in Figure 3.4. For feeding the experimental animals, the algae were therefore harvested from liquid medium between 5-9 days after innoculation, to ensure the cells were still dividing exponentially.

SOURCE AND IDENTIFICATION OF INORGANIC PARTICLES FOR TURBIDITY

A series of sediment samples was taken from the bottom of Lake Jacaretinga with an Ekman grab during the last visit to the lake (29.04.1986). At INPA, they were air-dried and transported by air to England where a preliminary size fractionation was carried out using a mortar and pestle to break the large particles which were then sieved through a series of meshes from 500 μm to 60 μm. A 20 gram sample of the final powder was then prepared to provide a 2 micron fraction for X-ray diffraction technique (Whittig,1965) in the Geology Dapartment of RHBNC.

This technique is based on the fact that soil clays contain crystalline mineral components that yield x-ray diffraction patterns. Crystalline structures are characterized by a systematic and periodic arrangement of atoms, or ions in a three dimensional array. Because crystals are composed of regularly spaced atoms, each crystal contains

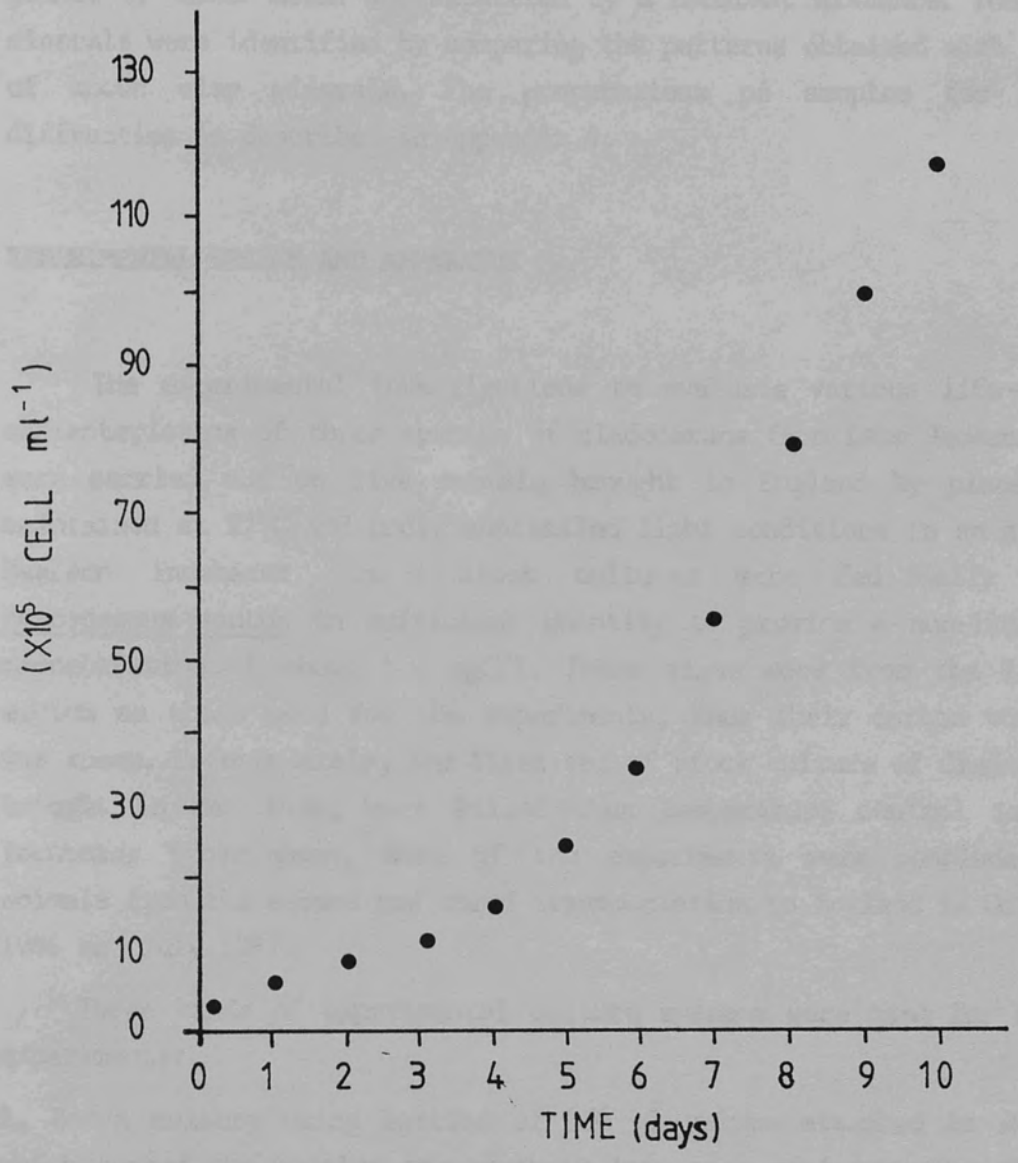


FIGURE 3.4 Growth of Scenedesmus acutus in CHU 12 liquid culture medium.

planes of atoms which are separated by a constant distance. The clay minerals were identified by comparing the patterns obtained with those of known clay minerals. The preparations of samples for x-ray diffraction is described in Appendix 4.

EXPERIMENTAL DESIGN AND APPARATUS

The experimental investigations to evaluate various life-cycle characteristics of three species of cladocerans from Lake Jacaretinga were carried out on live animals brought to England by plane and maintained at 27°C and under controlled light conditions in an Astell Hearson incubator. These stock cultures were fed daily with Scenedesmus acutus in sufficient quantity to provide a non-limiting concentration of about 1.0 mgC/l. These algae were from the liquid medium as those used for the experiments, thus their carbon content was known. Unfortunately, the first set of stock culture of Cladocera, brought in May 1986, were killed when temperature control in the incubator broke down. Most of the experiments were concluded in animals from the second and third transportation to England in October 1986 and July 1987.

Three kinds of experimental culture systems were used for these experiments:

1. Batch culture using bottles of 250 ml volume attached to wheels which turned the bottles around their long axes at 1 rpm. The wheels were kept in temperature-controlled water tanks and under a controlled light-dark regime. Each bottle contained one individual animal.

2. Batch culture using bottles which were turned on their short axes by rollers turning at 1 rpm inside an Astell Hearson incubator with light and temperature control shown in Plate 3.1. Only one individual animal grew in each bottle.

In both these batch systems, the food concentration was kept more or less constant by replacing the food medium in the bottles every 24 hours. By adjusting the volume of the bottle to the size of the

PLATE **3.1** Experimental set-up. Astell Hearson incubator with bottles rotating in rollers.

growing animal,the food concentration was not allowed to decrease by more than 20% during 24 hours.

3. A continuous flow-through system designed by Lampert(1976) in which food is maintained at a constant concentration by slow replacement at a rate controlled by a peristaltic pump. Up to 15 individual animal were kept in each vessel. The experimental system is shown in Plate 3.2.

BATCH CULTURE EXPERIMENTS

A . Bottles rotated in wheels in constant temperature water baths.

Experiments were carried out in 250 ml polystop bottles. According to Jayatunga(1986), this size of bottle provides a large enough volume of even the lowest concentration of food medium such that a cladoceran as large as an adult Diaphanosoma excisum cannot reduce the food concentration by more than 20% in 24 hours. This was accepted since tha Amazonian cladoceran species were of similar body size (1.3 mm).

There were four replicate bottles each with one individual animal for each combination of temperature and food concentration and all five food concentrations were studied at the same time. The twenty bottles were attached to the wheels which were rotated at one revolution per minute in order to maintain the cells of Scenedesmus acutus homogeneously in suspension. The temperature in the bottles was kept constant ±0.5°C by immersing the rotating wheels in a water bath of about 200 litres whose temperature was controlled by Beta-tech CU 400 heater-chiller. Daylight conditions were provided by fluorescent light timed to switch on/off every 12 hours.

Three species of cladocerans, Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata were grown at three temperature and five food concentration as shown in Table 3.2

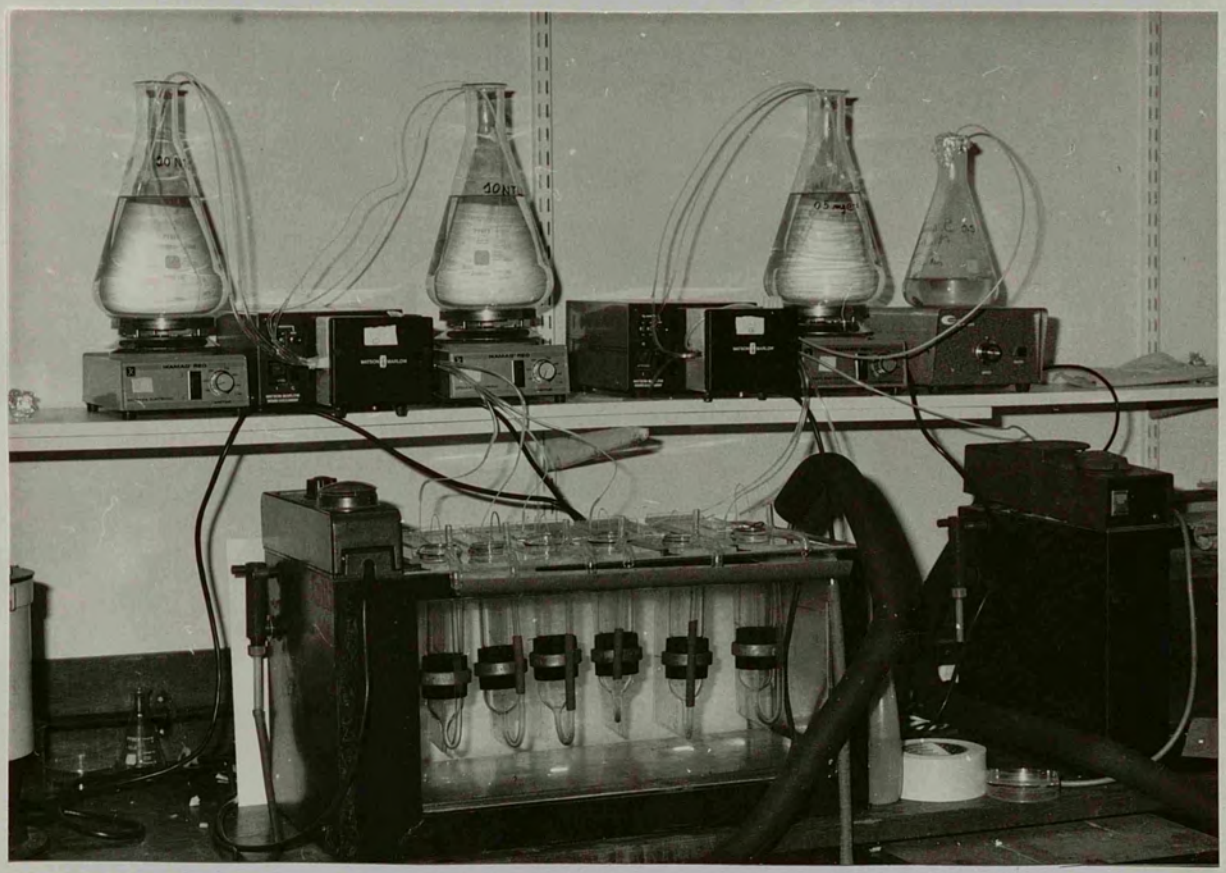


PLATE **3.2** Experimental set-up. Lampert's Flow-through system

TABLE 3.2 Experimental design using rotating bottles on wheels in water baths. Each bottle contained one individual. Species: Daphnia gessneri, Diaphanosoma sarsi, Moina reticulata.

TEMPERATURE °C	FOOD CONCENTRATION mgC.l^{-1}					
	0.03 *	0.05	0.10	0.25	0.50	1.0
22	-	+	+	+	+	+
		+	+	+	+	+
		+	+	+	+	+
		+	+	+	+	+
27	+	+	+	+	+	+
	+	+	+	+	+	+
	+	+	+	+	+	+
	+	+	+	+	+	+
32	-	+	+	+	+	+
		+	+	+	+	+
		+	+	+	+	+
		+	+	+	+	+

TABLE 3.3 Experimental design using rotating bottles and rollers in an Astell Hearson incubator. Each bottle contained one individual. Species: Daphnia gessneri, Moina reticulata

TEMPERATURE °C	FOOD CONCENTRATION mgC.l^{-1}	TURBIDITY NTU			
		0	10	20	50
27	0.05	+	+	+	+
		+	+	+	+
		+	+	+	+
		+	+	+	+
27	0.50	+	+	+	+
		+	+	+	+
		+	+	+	+
		+	+	+	+

\+ represents one bottle with one individuals
* Only Moina reticulata

B . Bottles rotated on rollers in an Astell Hearson Incubator

These experiments were conducted at one temperature only as they were designed to test the effect of turbidity at two food concentrations on the life-cycles of two cladoceran species, Daphnia gessneri and Moina reticulata. There were four replicate bottles for each treatment of temperature-food-turbidity, each containing 1 individual animal. The botlles were kept in an incubator in which a roller drive rotated the horizontal bottles at 1 rpm. Temperature and light could be set to the desired level, 27°C and 12 hours dark/light. The experiments that were carried out in this system are summarized in Table 3.3.

C . Lampert's continuous flow through system in constant temperature water baths.

This system was based in that described by Lampert(1976). Figure 3.5 shows the main vessel consisted of two parts separable at a glass junction with a combined capacity of 100 ml. Animals were confined to the upper part by netting of 300 µm pore size which prevented the animals escaping. The screen was kept in place by rubber washers and allowed the junction to be screwed tightly to prevent leakage. The lower part was connected to a U-shaped outlet tube which siphoned out the excess volume of medium. The vessels were suspended in a water bath at a constant temperature of 27°C. A multi-channel Watson Marlow peristaltic pump, whose flow rate was set at 0.84 ml/minute, provided the experimental vessels with the food suspension from a 2 litre reservoir, via a glass capillary submerged in the water bath to adjust its temperature to that of the experimental vessel in which the animals were feeding. The food in the reservoirs was continuously stirred by a magnetic follower to keep the cells in suspension. Experimental conditions of temperature, food and turbidity are

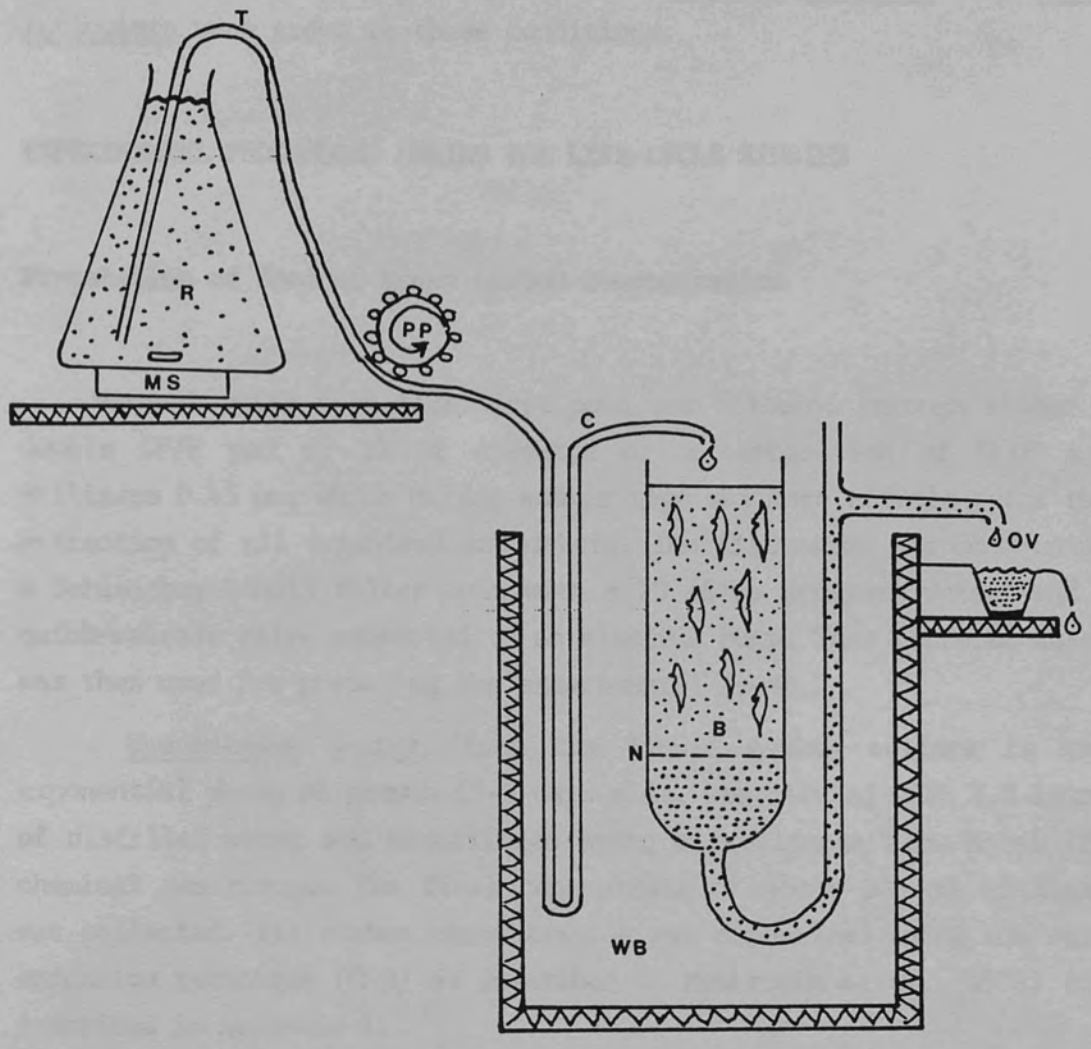


FIGURE 3.5 Schematic drawing of the Flow-through system

MS - magnetic stirrer
R - reservoir containing food suspension
T - Vinyl tubing
PP - peristaltic pump
C - glass capillary
WB - temperature-controlled water bath
N - Mesh net
B - Vessel containing the animals
OV - Over-flow

summarized in Table 3.4. The species Daphnia gessneri and Moina reticulata were grown in these conditions.

EXPERIMENTAL PROCEDURES DURING THE LIFE-CYCLE STUDIES

Preparation of food of known carbon concentration

Natural water from Alderhurst pond was filtered through either a double GF/F pad of 15 cm diametre or a combination of GF/F and millipore 0.45 μm, which during summer time was more efficient for the extraction of all organisms and debris. The filtration was done using a Schleicher-Schull filter unit with a 20 litre pressure vessel and a quick-release valve connected to an electric pump. This filtered water was then used for preparing the experimental food.

Scenedesmus acutus, from the liquid medium culture in the exponential phase of growth (5-9 days old), was diluted with 2.0 litre of distilled water and centrifuged using a continuous flow Model IEC chemical centrifuge. The final concentrate of about 300 ml of algae was collected. Its carbon concentration was determined using the wet-oxidation technique (COD) as described in Mackereth et al.,(1978) and described in Appendix 1.

This algal concentration was then diluted as appropriate to give 0.03, 0.05, 0.1, 0.25, 0.5, and 1.0 mg C/l by adding known volumes of natural filtered water. The daily preparation of known concentration experimental food was always a crucial point in determining the accuracy and time available of the growth experiments.

TABLE **3.4** Experimental design using Lampert's Flow-through system. Each vessel contained 15-20 individuals. Species: Daphnia gessneri, Moina reticulata

TEMPERATURE	FOOD CONCENTRATION	TURBIDITY			
^{o}C	$mgC.l^{-1}$	NTU			
27	0.05	0	10	20	50
		+	+	+	+
		+	+	+	+
27	0.5	+	+	+	+
		+	+	+	+

+ represents one vessel with 15-20 individuals

PREPARATION OF SUSPENSIONS OF KNOWN TURBIDITY AND FOOD

The natural particles used to provide a suspension of known turbidity came from the bottom sediments of Lake Jacaretinga which were transported to England after being air-dried at INPA in Brazil.

The following procedure was used to obtain a sample of mineral particles of reasonably uniform size. The air-dried material was suspended in distilled water, sieved through a series of meshes from 500 µm to 60 µm and wet-fractionated in glass settling columns. The final material still remaining in suspension after 24 hours consisted of fine particles between 0.7 and 2.0 µm diameter. Their size was determined by means of a Model TA II Coulter Counter, using a 70 µm orifice tube, calibrated with 9.7 µm latex beads. About 200-300 ml of concentrated particles was prepared and kept as a stock for experimental use. This stock was stored in a refrigerator at 5°C and was used within 5-7 days. Arruda(1983) reports that no bacterial growth occured under these circumstances. Checks for bacterial growth were made on days 0, 3 and 7 using the epifluorescence microscopic technique. The absence of green fluorescence confirmed that no bacterial growth was occuring. (Mansour Galal, pers. comm.).

The concentrations of suspended inorganic particles used experimentally were determined daily with a turbidimeter Great Lakes model. Each concentration was prepared by adding volumetrically known amounts of stock to an alga suspension of previous determined carbon concentration. The final feeding suspension (Scenedesmus acutus and inorganic particles) had the following concentrations in turbidity: 10, 20 and 50 NTU (Nephelometric turbidity unit), with range of variation about 1.0 NTU.

Dry weights and number of particles in a natural water sample brought back from Lake Jacaretinga kept under cool condition for about two weeks were also determined in relation to the concentration of particles. The counts were done by a TAII Coulter Counter, using a 140 µm tube. The results obtained are given as follows(Table 3.5).

Dry weight	Turbidity	Total n° of particles
mg/l	NTU	10^6 n°/ml
10	6.5	1.6
20	12.8	3.0
40	25.0	5.9
50	31.7	8.3
100	63.5	18.5

PREPARATION AND HANDLING OF EXPERIMENTAL ANIMALS IN THE BATCH AND FLOW-THROUGH SYSTEMS.

Cladocerans were adapted to the experimental conditions of light, temperature and food concentration for at least 3 weeks before each set of experiments. The evening before an experiment was started, several egg-carrying females were isolated in a beaker with enough food. By morning, the newborns, not older than 12 hours and considered to be first instars, were sorted out and measured using an Olimpus microscope with a calibrated eye piece and a magnification of X40 (1 eye piece division= 0.025 mm). Each replicate individual in the batch experiments and in the flow-through vessels was followed throughout the life cycle and up to the appearance of the third brood of eggs. Daily observation was made of their length, their instar stage by the appearance of an ecdysed carapace and the number of eggs or embryos in the brood pouch. It was important to handle the live animals carefully as each individual was removed from the bottle or vessel using a large bore pipette and placed on a glass slide with a drop of water. All the observations and measurements were made as quickly as possible to avoid stressing the animal. Some cladocerans were especially sensitive to disturbance, in particular, Daphnia gessneri and Diaphanosoma sarsi tend to release the eggs or embryos from the brood pouch when disturbed and care was taken to avoid this happening.

BATCH EXPERIMENTS

Neonates from the experimental stock were used to start each experiment. One individual was added to each bottle filled with previously prepared experimental food medium. With four replicate animals and the various treatments involved, about 20-24 bottles were used in each set at one experimental temperature. The bottles were attached to the wheels in a water bath for 24 hours. After their daily examinations, the animals were transferred to a clean set of bottles filled with daily freshly prepared food medium. The empty bottles and all glassware were washed daily, using hot water and soap, rinsed with distilled water and oven dried.

Each experiment lasted longer than the actual duration from neonate to third instar because, when accidental deaths and losses occurred it was necessary to replace lost individuals by a new neonate from the stock culture, and the new animal was studied from the first day so that the replicate animals in the experiments were always of known age.

FLOW-THROUGH CULTURE SYSTEM

In this system, each of 6-8 vessels which were used simultaneously at one temperature were started with 15-20 neonate animals. Each turbidity-food concentration combination had replicates. The vessels were each connected by the peristaltic pump to 2 litre flat-based flask containing freshly prepared food medium sufficient for a period of 24 hours.

As a large number of neonates (120-160) were required to start the eight vessels necessary for one experiment, it needed two days of preparation to get an experiment started using this system. Nevertheless, the starting age of each neonate was known.

Daily observations were made. The contents of each vessel were poured gently in a glass vessel through a net mesh which retained the animals. The animals were then poured into a small petri dish from

which they were removed by means of a large-bore pipette for examination. After observation and measurement of their size, the animals were returned to a clean flow-through vessel filled with freshly prepared food medium. Any accidental deaths and losses of animals in this set of experiments were not replaced as in the batch cultures. The level of mortality in all three systems was higher in the first two days of experiments, when the animals were still in their first instars.

DETERMINATION OF THE CARBON WEIGHT AND LENGTH RELATIONSHIPS OF EXPERIMENTAL ANIMALS.

The carbon weight of experimental animals of known length which had been reared under known conditions of temperature, food concentration and turbidity was determined by high temperature dry combustion as has been described earlier. Fewer experimental animals than field ones were available so that the sensitivity on the Salonen technique was important.

3.3 Analysis of data

A number of statistical methods were used to analyse the data obtained in this study. Computer facilities and statistical packages were available at RHBNC for processing the data.

Regression analysis (Sokal and Rohlf, 1969)

An elementary statistical computer program (ESP) was used to assess the effect of an independent variable on a dependent variable to evaluate whether there is any significant relationship between the two parameters. The F value was employed in judging the level of significance. The exponential and power relationship were linearized by natural log transformation. Reciprocal transformation was required for linearization of the Michaelis-Monod function.

Multiple regression analysis (Sokal and Rohlf, 1969)

The Minitab statistical package was used to evaluate the contribution of a set of independent variables on a dependent variable. The program combines stepwise analysis, which provides control over the inclusion of independent variables in the regression equation. This test predicts the F value due to the interacting effect of the independent variables employed as well as the F value due to each independent variable separately, providing a means of judging which of the independent variables had the greatest effect on the dependent variable.

Covariance analysis (Steel and Torrie, 1980)

The analysis of covariance is concerned with two or more measured variables where any measurable independent variable is not at predetermined levels as in a factorial experiment. It makes use of the concepts of both analysis of variance and of regression. This technique was used for comparing regression lines and predicting

whether there were significant differences between them. Two tests were combined in the covariance analysis: SS-STP (The Sum of Squares Simultaneous Test Procedure, Sokal and Rohlf, 1969) predicts the difference between the slopes (regression coefficients) and the S-N-K (Student-Newman-Keuls test, Steel and Torrie, 1980) predicts the differences between the elevations of the regressions. Both test were available in the ESP-Elementary Statistical Program.

Analysis of variance (ANOVA-one way classification).(Steel and Torrie, 1980.

A procedure used for testing the equality of means. This technique was used for comparing densities between five stations on one date. Differences between pair of groups were performed by the S-N-K test. Available in the elementary statistical computer program.

Kolmogorov-Smirnov test for normality (Steel and Torrie, 1980)

Is suitable for assessing goodness of fit of an observed to an expected cumulative frequency distribution. This technique was used to test normality of the densities for each species of cladoceran in five stations collected from Lake Jacaretinga.

GROFIT (Wroot, 1984)

A computer program written by Wroot (1984) based on Schnute's model (1981) was used for fitting the Richard's growth function to a series of growth curves obtained from the experiments at different temperature, food and turbidity conditions.

CHAPTER 4

The effect of food concentration and temperature on growth of cladocerans.

The success of cladoceran crustaceans in colonizing different waterbodies may be determined to a great extent by their ability to survive at low food concentrations. Such important individual and population parameters as the rate of individual growth, body weight at maturity, maximum clutch size are correlated with this ability (Romanovsky, 1984).

Growth is a measure of increase in body weight, but has been described in terms of length as well as weight. Any measure of growth must be referred to some definite interval of time, either expressed or implied. Since only lengths and ages of live animals are available from long-term experimental studies some relationships between length and weight must be measured so that measured length can be converted to individual weights for animals of known age in order to derive growth curves and growth rates.

4.1 THRESHOLDS FOR GROWTH

Daphnia gessneri

During the life cycle experiments, Daphnia gessneri was tested at three temperature (22, 27 and 32°C) and five food concentrations (1.0, 0.5, 0.25, 0.1 and 0.05 $mgC.l^{-1}$). At the lowest temperature of 22°C in all food levels, the animals did grow to maturity and successfully produce three broods. At 27°C in 1.0, 0.5 and 0.25 $mgC.l^{-1}$ the animals attained the third brood too, but at the lowest food levels of 0.1 and 0.05 $mgC.l^{-1}$ juveniles died in the 3rd instar and only two Daphnia managed to grow and reproduce. At 32°C the animals attained maturity at all food levels but at low food (0.05 $mgC.l^{-1}$ they died after the second brood. At this temperature the animals were observed to have abnormal reproduction, such abortion

and degeneration of eggs. In addition, mortality was high in the adult stage, particularly during the process of ecdysis. Daphnia gessneri has a threshold food concentration for growth between 0.1 and 0.05 $mgC.l^{-1}$ only at 27°C.

Diaphanosoma sarsi

Only one experimental temperature (27°C) was used for Diaphanosoma sarsi. While carrying out the life cycle experiments at high food levels the animals reached maturity but the juveniles died below 0.1 $mgC.l^{-1}$; out of the four replicates, two did not mature. Therefore, the threshold food concentration for this species at 27°C is also between 0.1 and 0.05 $mgC.l^{-1}$.

Moina reticulata

The life cycle experiments for this species was also carried out at 27°C but an extra food concentration of 0.03 $mgC.l^{-1}$ was added. The animals did grow at very low food levels of 0.1 and 0.05 $mgC.l^{-1}$, but Moina reticulata did not thrive for more than three days at 0.03 $mgC.l^{-1}$. This species has a threshold food concentration for growth at the lowest food level tested (0.03 $mgC.l^{-1}$). Therefore, Moina reticulata requires less food for metabolism and growth than Daphnia gessneri and Diaphanosoma sarsi.

4.2 GROWTH CURVES

When followed throughout the life cycle, the growth in weight of many animals follows a sigmoid or S-shaped curve and that this is so in cladocerans. Such life cycle growth curves provide important information on the influence of environmental factors such as temperature and nutritional conditions, particularly if studied experimentally and provided that they can be described/expressed by a mathematical equation. Several such equations exist in the literature which have been used to describe the curvilinear response of body weight to age in different animals species:

(1) Logistic

$$W_t = W_{max}/1 + \exp(-g(t-t_o))$$

(2) Von Bertalanffy

$$W_t = W_{max}\ (1 - \exp(-g(t - t_o))^P$$

(3) Gompertz

$$W_t = W_{max}\ (\exp(\exp(-g(t-t_o)))$$

(4) Richards

$$W_t = W_{max}\ (1 - (b)\exp(-g(t-t_o)))^P$$

which are rather similar in describing the growth curve in terms of the asynptotic weight, the shape of the curve, the steepness of the initial exponential growth period and the time of inflection at which the growth starts to reduce. All of these may be influenced by experimental conditions and the equation tries to express the whole life cycle pattern of growth. The problem lies in deciding which of these growth models provides the best fit to the experimental/empiracle raw data of weights and ages. Fortunately, a computer programme called GROWTH exists at Royal Holloway Bedford New College which permits the interative fitting of data to any one of these equations until a best fit is found with the least residual mean squares. This programme was written by Wroot (1984) and is based upon Schnute (1981). The programme also includes Schnute's own model which is different from the above theoretical equations in being based upon growth acceleration. In the event, the Richard's growth model was found to provide the best fit for all the species and for all combinations of treatments.

In Richard's model:

$$W_t = W_{max}\ (1 - (b)\ \exp(-g(t-t_o))^P$$

where:

W_t = weight at time t ($\mu gC.ind^{-1}$)

W_{max} = assymptotic weight ($\mu gC.ind^{-1}$)

g = growth constant

t_o = the time of inflection (days)

b = model parameter

p = the exponent and equal to reciprocal of b

In this section therefore a series of Richard's growth curves are analysed which represent the changes in the three cladoceran body size related with time under various combinations of food concentration and temperature.

Growth curves for Daphnia gessneri were obtained for fifteen treatments consisting of combining three temperature and five food concentrations. For Moina reticulata and Diaphanosoma sarsi only one temperature (27°C) was investigated, giving five treatments. For each species of cladoceran a Richard's growth curve was obtained for each treatment studied and these are all presented in Figure 4.1, 4.2, 4.3, 4.4 and 4.5. In these figures, the empiracle data for each studied individual is plotted and the arrow on each growth curve indicates the size and time of appearance of the primiparous female which gives a visual picture of whether or not the curve inflects before the onset of maturity. The parameters of the Richard's growth equations are given in Table 4.2 and the value of the residual mean square gives some estimate of the goodness of fit.

Daphnia gessneri at all three temperatures and five food combinations shows exponential growth at early stages of development (Figure 4.1(a)-(o). Under non-limiting food conditions the exponential phase goes up to, or beyond the onset of maturity, as indicated by t_o (time of inflection of the curve). This can be seen by comparing the time to in Table 4.2 with the age indicated by the arrows in Figure 4.1. For example, at the highest food of 1.0 mgC.l-1 and 32°C, t_o was seven days and the age of the primipara female was four days. The same trend was obtained for 0.5 and 0.25 $mgC.l^{-1}$, 7.2 and 6.9 days for t_o and 6.0 days for the primipara age. For 32°C and 0.1, 0.05 $mgC.l^{-1}$ t_o and age were very similar, primipara female matured at point of inflection. At 27°C, it seems exponential growth extended beyond time of maturity at all food concentrations. At 22°C and 1.0 $mgC.l^{-1}$ t_o was 8.7 days and and age 5.0; t_o and age of

primipara female were also similar, but a different response was obtained with low food concentrations (0.1 ,0.05 mgC.l^{-1}).In these case the t_o values were very low.

Food level has a major effect on the final size attained by individuals as can be seen in Table 4.2 and Figures 4.1 in which the values of W_{max} directly reflect the large variation in the final adult body size with food level.There were also very clear differences in the primipara body size as well as age affected by food concentration.

The highest values for W_{max} was obtained in 1.0 mgC.l^{-1} and the lowest values were in 0.1 and 0.05 mgC.l^{-1} for all three temperature. For 32 °C and 1.0 mgC.l, W_{max} was 20.62, with 0.05 mgC.l^{-1} was 8.5. For 27 °C and 1.0 mgC.l^{-1} W_{max} was 20.27 but in 0.05 mgC.l^{-1} was 6.68. For 22 °C with 1.0 mgC.l^{-1} the value for W_{max} was 10.09 and in 0.05 mgC.l^{-1} the value was 0.90 the lowest.

The effect of food concentration is illustrated in Figure 4.2 where body growth at different food levels and at one temperature are plotted together.

It is clear that at the two lowest food level (0.1 and 0.05 mgC.l^{-1}) at 32 °C, Daphnia gessneri took 8-9 days, twice the time to attain the primipara stage as in high food concentration (1.0 mgC.l^{-1}), 4-5 days. This prolongation of the primipara age also occurs at the lower temperatures: 8.0 days in 0.1 and 0.05 mgC.l^{-1} while in 1.0, 0.5 and 0.25 mgC.l^{-1} at 22 °C the female animals took 5-6 days to reach maturity (Figure 4.2 (c). Also, at 22 °C in limiting food level (0.05 mgC.l^{-1}) no exponential growth was observed as indicated by the negative values obtained for t_o (Table 4.2). The combination of low temperature and low food concentration seems to be very stressful.

Figure 4.3 illustrates the effect of temperature on growth curves at each particular food concentration but at different temperatures.

At 27 °C and 32 °C with non-limiting food level the growth curves were very similar and it would seems that temperature does not affect the body size of Daphnia gessneri of the third adult instar. At low

food level (0.1 and 0.05 mgC.l^{-1}) the effect of temperature became more evident, mainly on duration with a very pronounced prolongation in time as temperature decrease. The effect of temperature on the body size at 22 °C is also evident and more pronounced at the two lowest food level (0.1 and 0.05 mgC.l^{-1}).

The growth curves for Diaphanosoma sarsi and Moina reticulata are illustrated in Figures 4.4 and 4.5. and the parameters of the Richard's equations are given in Table 4.2.

Figure 4.4 and Table 4.2 for Diaphanosoma sarsi shows that at 27 °C the trends are very similar with those of Daphnia gessneri in that body growth is directly related to the amount of food available. The final adult body size W_{max} declines clearly from 5.9 ugC in 1.0 mgC.l^{-1} to 1.5 µgC in 0.05 mgC.l-1.

The time of inflection of the curve and age of the primipara female of Diaphanosoma sarsi were very similar in higher food level. In 1.0 mgC.l^{-1} t_o was 3.0 days and age of primipara was 3.0 days. In 0.5 mgC.l^{-1} t_o was 4.0 and age was also 4.0 days. At lower food concentration of 0.25 and 0.1 mgC.l^{-1} the exponential growth was slightly shorter (1.0 day) than the age on onset of reproduction. At limiting food level of 0.05 mgC.l^{-1} the t_o was markedly shorter than age of primipara female.

Figure 4.5 shows for Moina reticulata at 27 °C a visual effect on body length of adult animals when less food is available as occurred with the other two species, but the shape of the curves is different been almost straight in high food level. The sharply increased slope (b) about 0.7 in high food concentration indicates that food level might operates mainly upon the duration of the life cycle of Moina reticulata. The maximum values for W_{max} (7.7 and 4.7 ugC) occurs in the higher food level of 1.0 and 0.5 mgC.l^{-1} as given in Table 4.2. W_{max} declines drastically to 2.0-1.1µgC in lower food level of 0.05 and 0.03 mgC.l^{-1}.

Body growths at the five different food levels but one temperature (27 °C) are plotted together in Figures 4.6 for Diaphanosoma sarsi and Moina reticulata.

For Diaphanosoma sarsi, the Richard's growth curves for 1.0 and 0.5 mgC.l^{-1} are very similar almost lie on top each other. For 0.25 and 0.1 mgC.l^{-1} the growth curves were also similar but lower than those in higher food level. An effect of shortage of food affecting body growth of the adult and also primiparous female is more clear at 0.05 mgC.l^{-1}.

In Moina reticulata , the shape and steepness of the curves were also very similar at 1.0 and 0.5 mgC.l^{-1} but a gradual lower curves occur with shortage of food available mainly in 0.03 mgC.l-1. The time taken to attain the primipara size is well illustrated by the arrows in the diagrams for both species. At the lower food level is always prolonged, taken twice the time of those in higher food concentration.(See Table 4.2).

4.3 EXPONENTIAL GROWTH RATES

Since we do not know how to test for significant differences between a series of curvilinear equations the growth curves in Figures 4.1-4.6 can only provide the possibility of visual comparison.

Exponential growth rates for the appropriete period in the life cycle are calculated as linear regression of log transformed weight on age and linear regressions can be tested for significant difference of slope, which is the instantaneous growth rate in particular treatments.This is useful as the growth rates under different treatment can be compared, either as the fraction of the body weight per day or converted to absolute growth per individual. The instantaneous growth rate, (g), can be calculated from the equation:

$$W_t = W_o \, e^{g(t-t_o)}$$

where,

W_t = weight at time t (μgC.ind^{-1})

W_o = initial weight ($\mu gC.ind^{-1}$)

t = final time (days)

t_o = initial time (days)

g = daily instantaneous growth rate, for that period in the life cycle that is exponential. This can be seen in the semi-logarithmic plots of the Figures 4.1-4.5 as the initial straight partion.

This relationship can be linearized by transformation of weight to natural logarithms, resulting in:

$$\ln W_t = \ln W_o + g \quad t$$

where:

$$t = t - t_o$$

in which the regression relating $\ln W_t$ with Δ t has a slope which corresponds to the instantaneous growth rate.

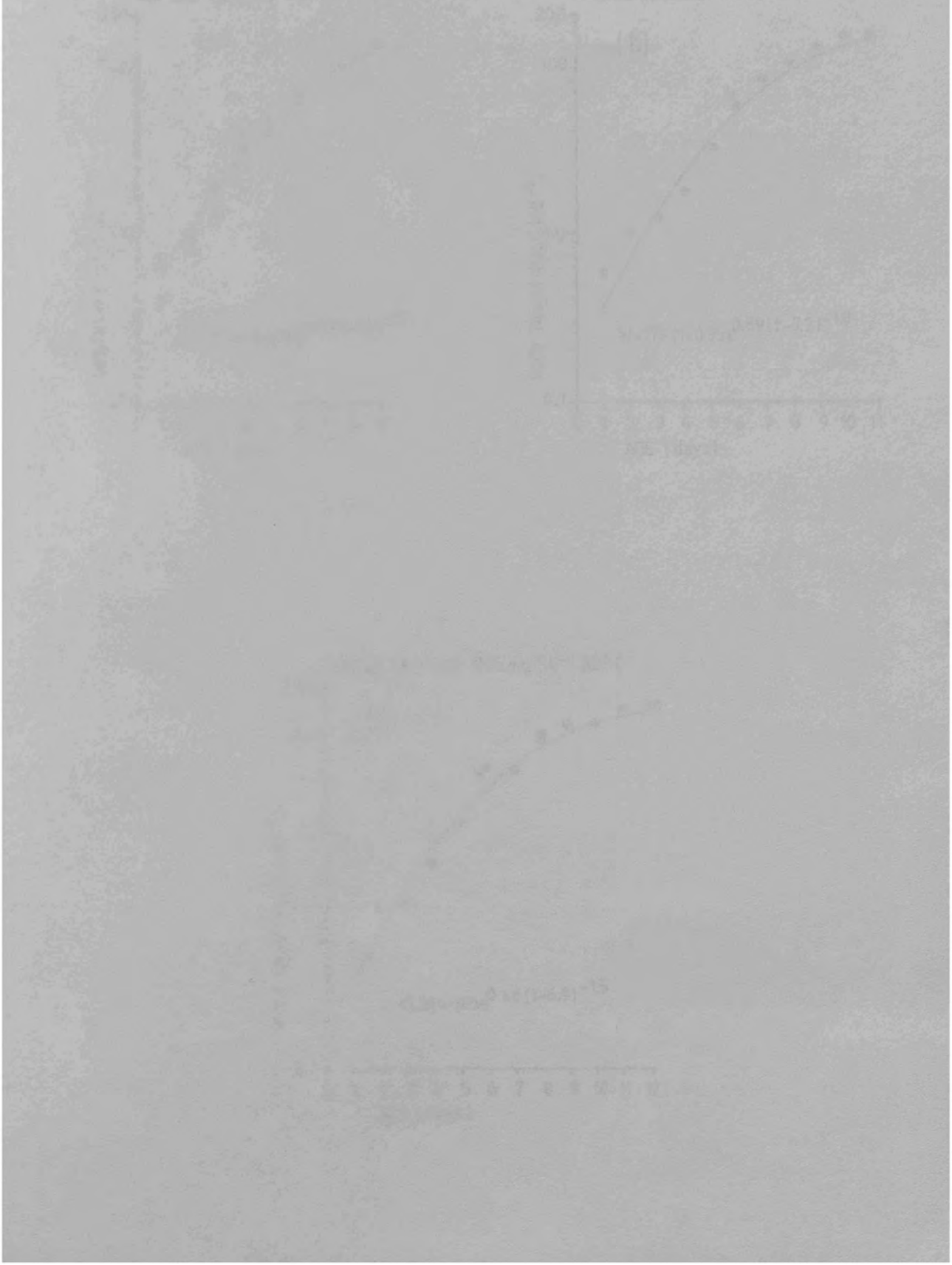
Table 4.1 presents the regressions of weight on age for the different treatments to which the three cladoceran species were subjected.

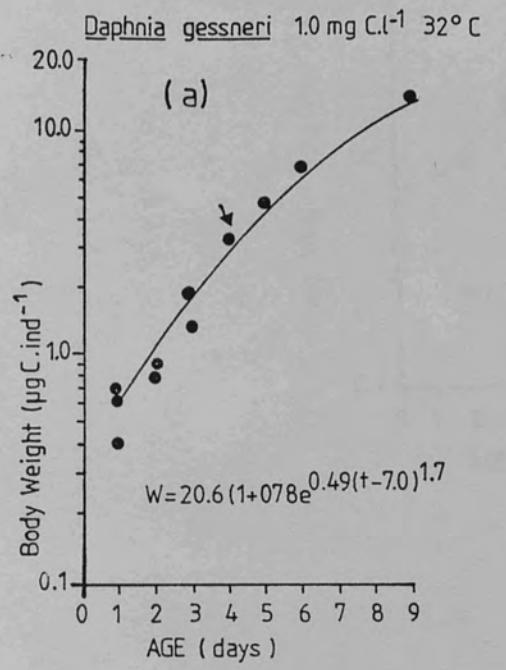
All regressions are statistically significant. From this table is clear that the regression coefficients (b) which represent the daily instantaneous growth rate (g) for this periods of exponential growth are strongly influenced by food concentration in all three species. The higher values were obtained in the three non-limiting food level (1.0, 0.5 and 0.25 $mgC.l^{-1}$) to drop markedly below 0.25 $mgC.l^{-1}$ Temperature effect for Daphnia gessneri has also an influence, but in a lesser extent as can be seen from the values of (b) in table 4.1. Figure 4.7 illustrates the values in Table 4.1 as three dimensional diagrams of juvenile instantaneous growth rates in different treatments. The values at 32 °C and 27 °C are quite similar with a range of 0.44 to 0.20 µg/day and 0.48 to 0.23 µg/day respectively. But the values at 22 °C decreased from 0.33 to 0.06 µg/day the lowest value obtained in limiting food level (0.05 $mgC.l^{-1}$).

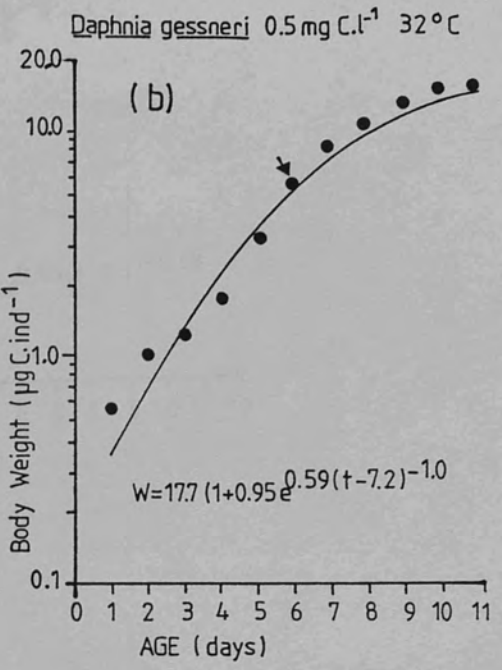
In Diaphanosoma sarsi, at only one temperature (27°C) and five food level, there is a tendency for juvenile instantaneous growth rate (b) to decrease with decreasing food concentration. The values for Diaphanosoma sarsi were quite the same for Daphnia gessneri. The higher value was 0.35 µg/day in 1.0 $mgC.l^{-1}$ and the lower was 0.15 µg/day in 0.05 mgC.l-1.

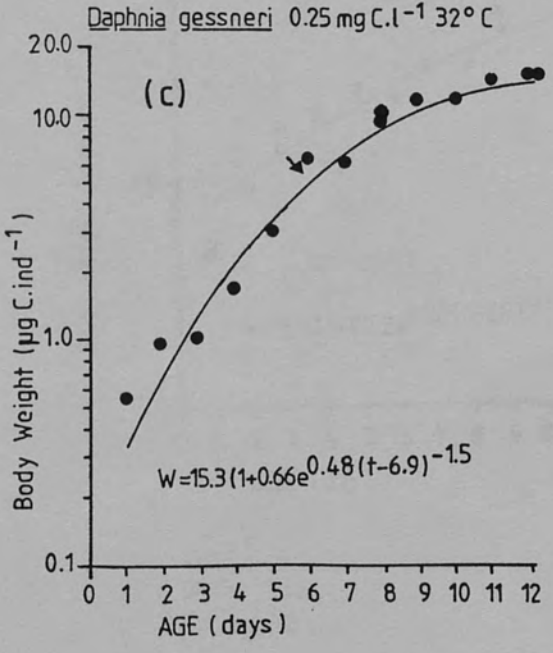
In Moina reticulata, the values of (b) obtained were very high particularly in non-limiting food levels which range was 0.75 to 0.46 µg/day. In the two lowest food level (0.05 and 0.03 $mgC.l^{-1}$) the daily instantaneous growth drops to 0.37 and 0.23 ug/day. The values for Moina reticulata were usually 1 ½ times higher than those for Daphnia gessneri, and Diaphanosoma sarsi under the same experimental conditions, indicating that this species has a very high instantaneous growth rates.

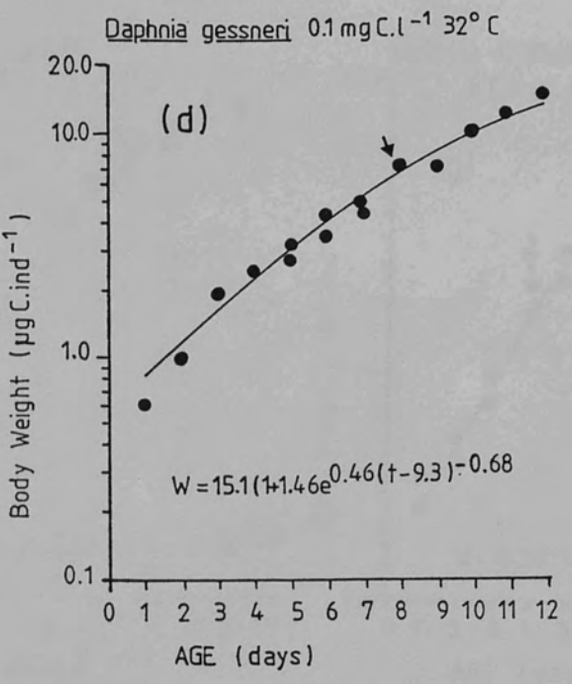
FIGURE 4.1 Richard's growth curves for Daphnia gessneri in various temperature-food concentration treatments. The original individual body weights and ages are also plotted. The arrow indicates the size and age of the primiparous female.

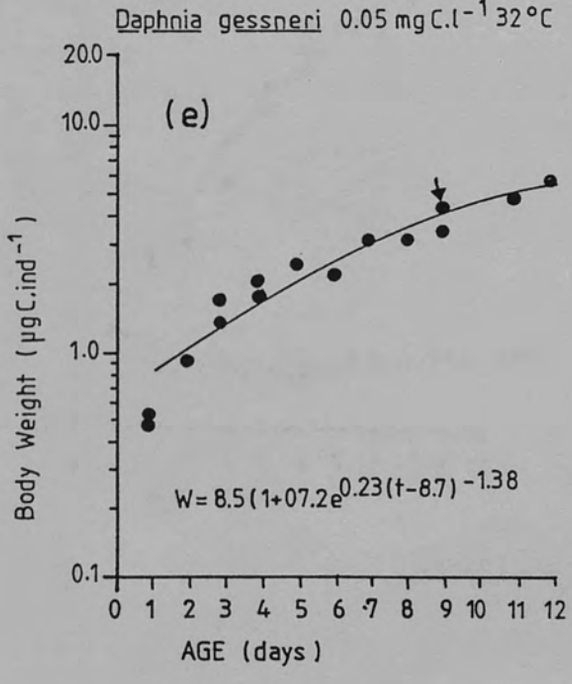


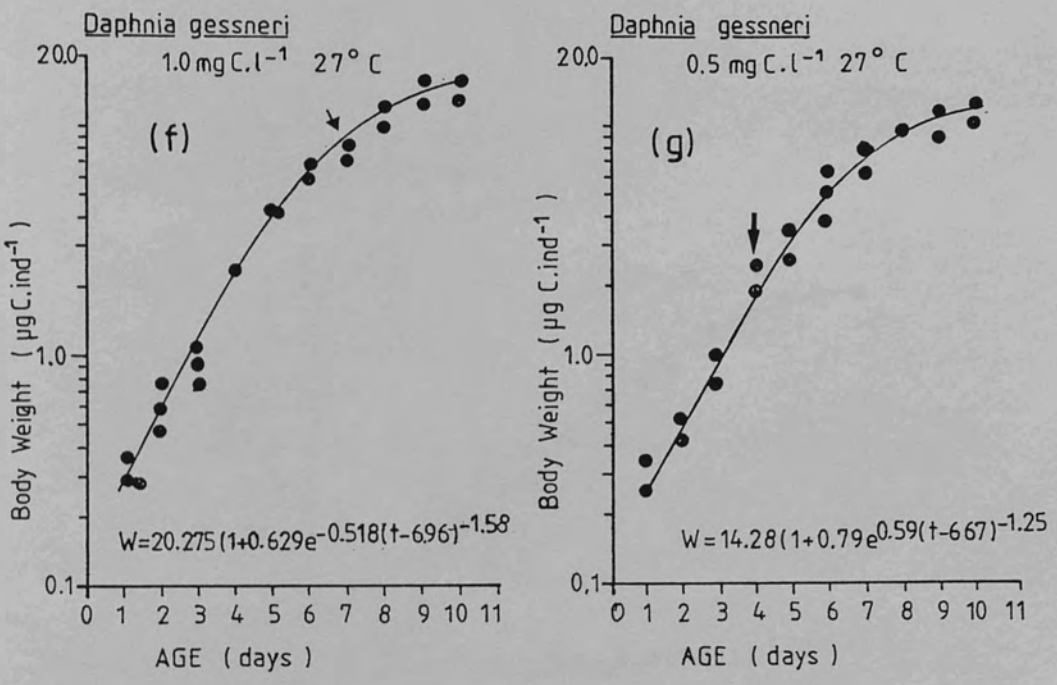

Daphnia gessneri 1.0 mg C.l-1 32° C
(a)
20.0
10.0
1.0
0.1
Body Weight (µg C.ind-1)
W=20.6 (1+078e0.49(t-7.0)1.7
0 1 2 3 4 5 6 7 8 9
AGE (days)

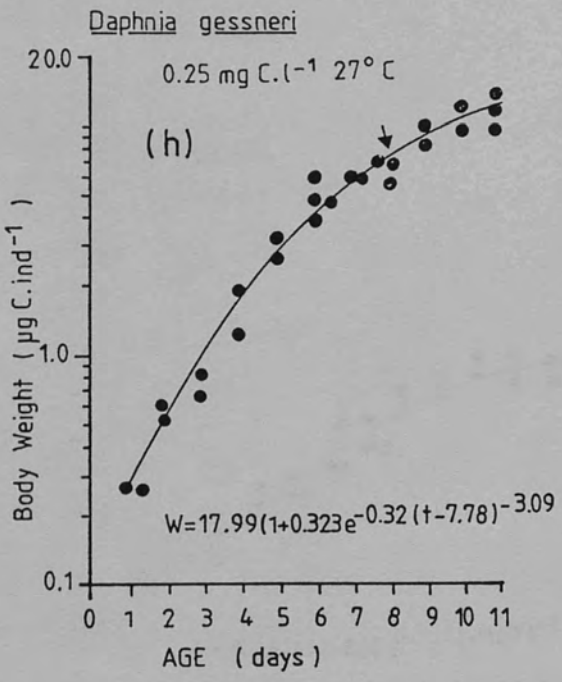

Daphnia gessneri 0.5 mg C.l-1 32° C
(b)
20.0
10.0
1.0
0.1
Body Weight (µg C.ind-1)
W=17.7 (1+0.95e0.59(t-7.2)-1.0
0 1 2 3 4 5 6 7 8 9 10 11
AGE (days)

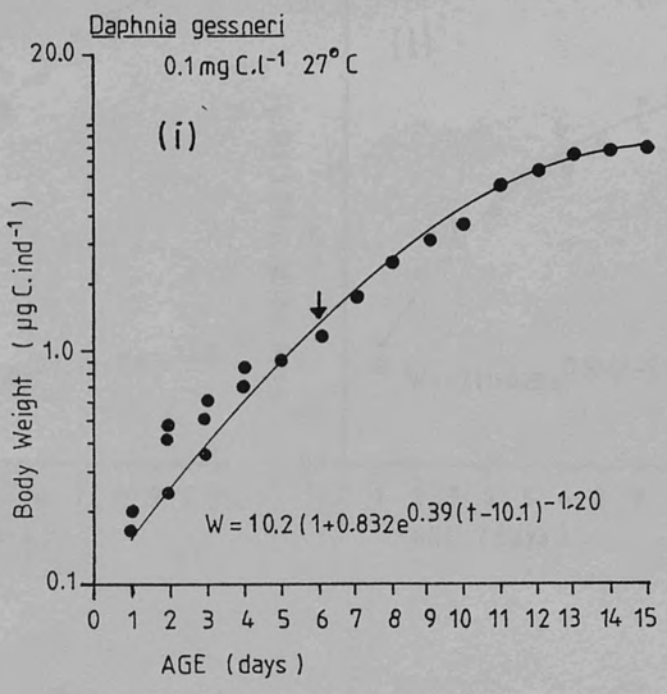

Daphnia gessneri 0.25 mg C.l-1 32° C
(c)
20.0
10.0
1.0
0.1
Body Weight (µg C.ind-1)
W=15.3 (1+0.66e0.48 (t-6.9)-1.5
0 1 2 3 4 5 6 7 8 9 10 11 12
AGE (days)

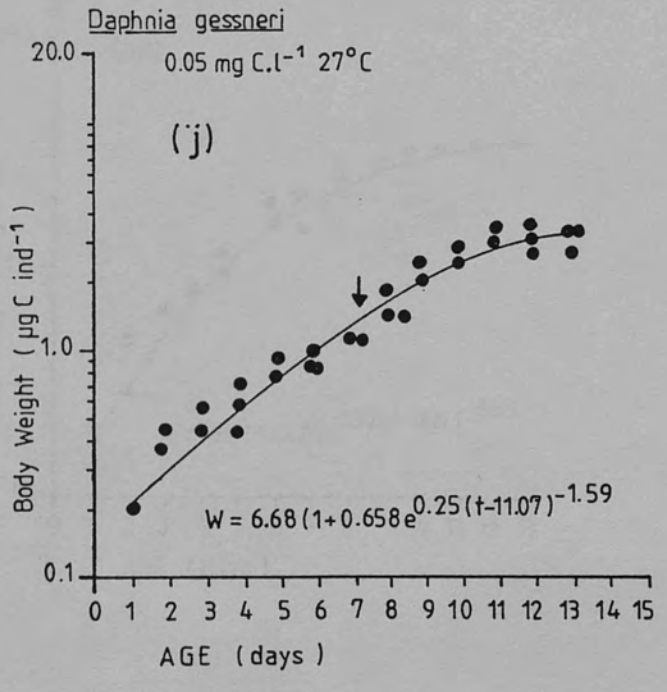

Daphnia gessneri 0.1 mg C.l⁻¹ 32° C
(d)
Body Weight (µg C.ind⁻¹)
20.0
10.0
1.0
0.1
W = 15.1 (1+1.46e^0.46(t-9.3))^-0.68
0 1 2 3 4 5 6 7 8 9 10 11 12
AGE (days)

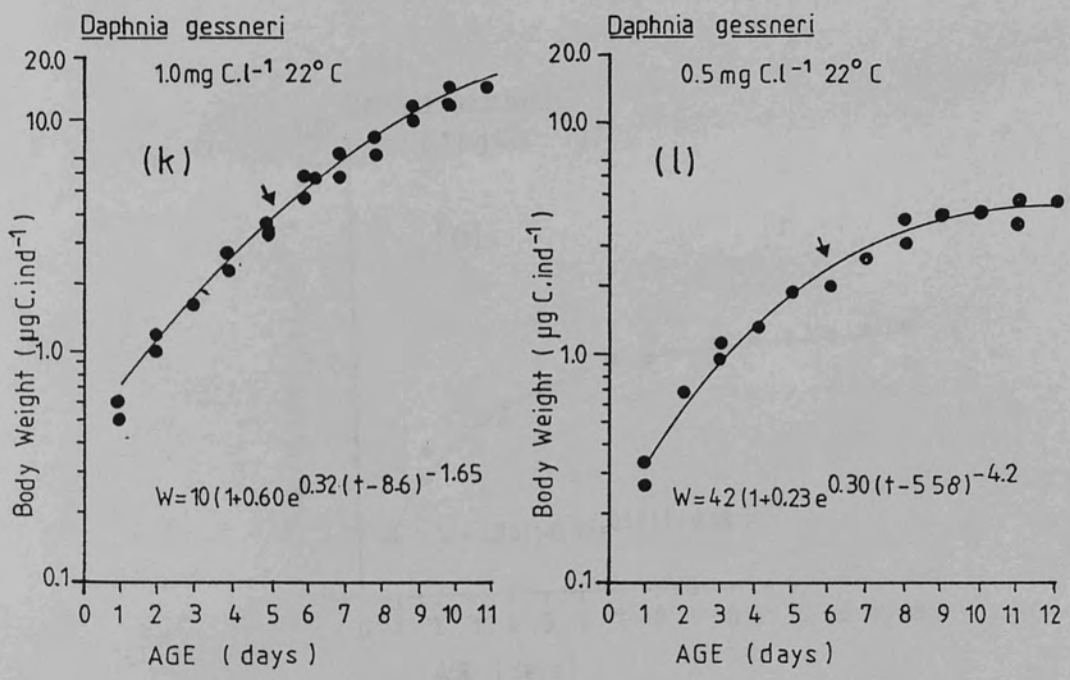

Daphnia gessneri 0.05 mg C.l⁻¹ 32°C
(e)
Body Weight (µg C.ind⁻¹)
20.0
10.0
1.0
0.1
W = 8.5 (1+07.2e^0.23(t-8.7))^-1.38
0 1 2 3 4 5 6 7 8 9 10 11 12
AGE (days)

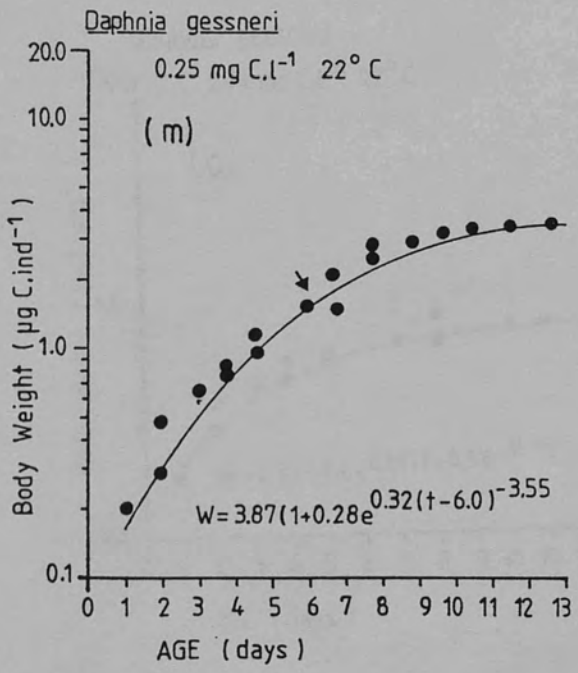

Daphnia gessneri
1.0 mg C.l⁻¹ 27° C
(f)
Body Weight (µg C.ind⁻¹)
20.0
1.0
0.1
W=20.275(1+0.629e^-0.518(t-6.96))^-1.58
0 1 2 3 4 5 6 7 8 9 10 11
AGE (days)
Daphnia gessneri
0.5 mg C.l⁻¹ 27° C
(g)
Body Weight (µg C.ind⁻¹)
20.0
1.0
0,1
W = 14.28(1+0.79e^0.59(t-6.67))^-1.25
0 1 2 3 4 5 6 7 8 9 10 11
AGE (days)

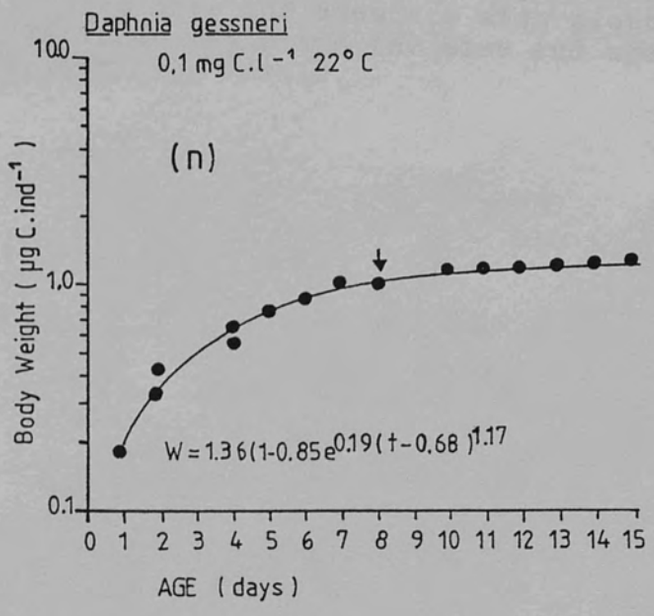

Daphnia gessneri
0.25 mg C.l⁻¹ 27° C
(h)
Body Weight (µg C.ind⁻¹)
20.0
1.0
0.1
W=17.99(1+0.323e^-0.32(t-7.78))^-3.09
0 1 2 3 4 5 6 7 8 9 10 11
AGE (days)


Daphnia gessneri
0.1 mg C.l-1 27° C
(i)
20.0
1.0
0.1
Body Weight (µg C.ind-1)
W = 10.2 (1+0.832e0.39(t-10.1))-1.20
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE (days)


Daphnia gessneri
0.05 mg C.l-1 27°C
(j)
20.0
1.0
0.1
Body Weight (µg C ind-1)
W = 6.68 (1+0.658e0.25(t-11.07))-1.59
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE (days)


Daphnia gessneri
1.0 mg C.l-1 22° C
(k)
Body Weight (µg C.ind-1)
20.0
10.0
1.0
0.1
W=10(1+0.60e0.32(t-8.6)-1.65
0 1 2 3 4 5 6 7 8 9 10 11
AGE (days)
Daphnia gessneri
0.5 mg C.l-1 22° C
(l)
Body Weight (µg C.ind-1)
W=42(1+0.23e0.30(t-5.58)-4.2
0 1 2 3 4 5 6 7 8 9 10 11 12
AGE (days)


Daphnia gessneri
0.25 mg C.l-1 22° C
(m)
Body Weight (µg C.ind-1)
20.0
10.0
1.0
0.1
W=3.87(1+0.28e0.32(t-6.0)-3.55
0 1 2 3 4 5 6 7 8 9 10 11 12 13
AGE (days)


Daphnia gessneri
0,1 mg C.l⁻¹ 22° C
(n)
Body Weight (µg C.ind⁻¹)
10.0
1,0
0.1
W = 1.36(1-0.85e^0.19(t-0.68))^1.17
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE (days)

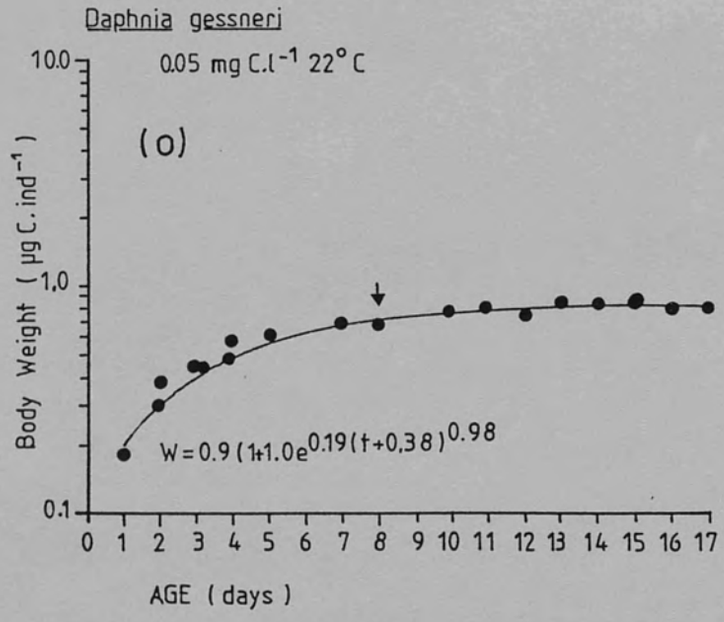
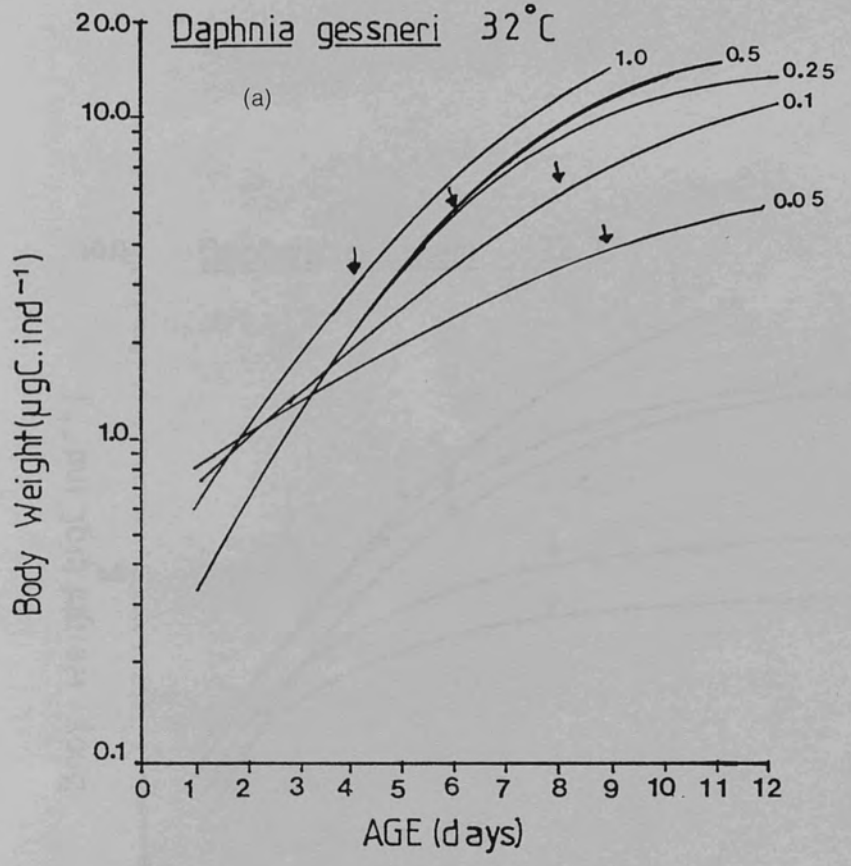
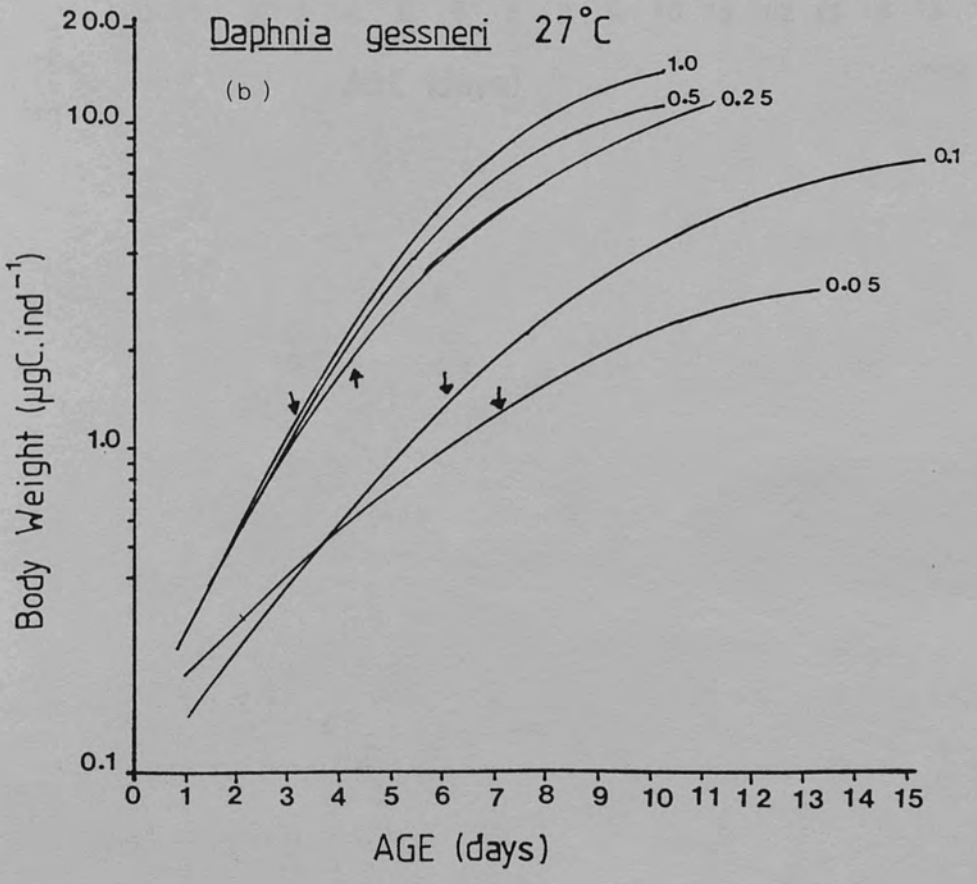
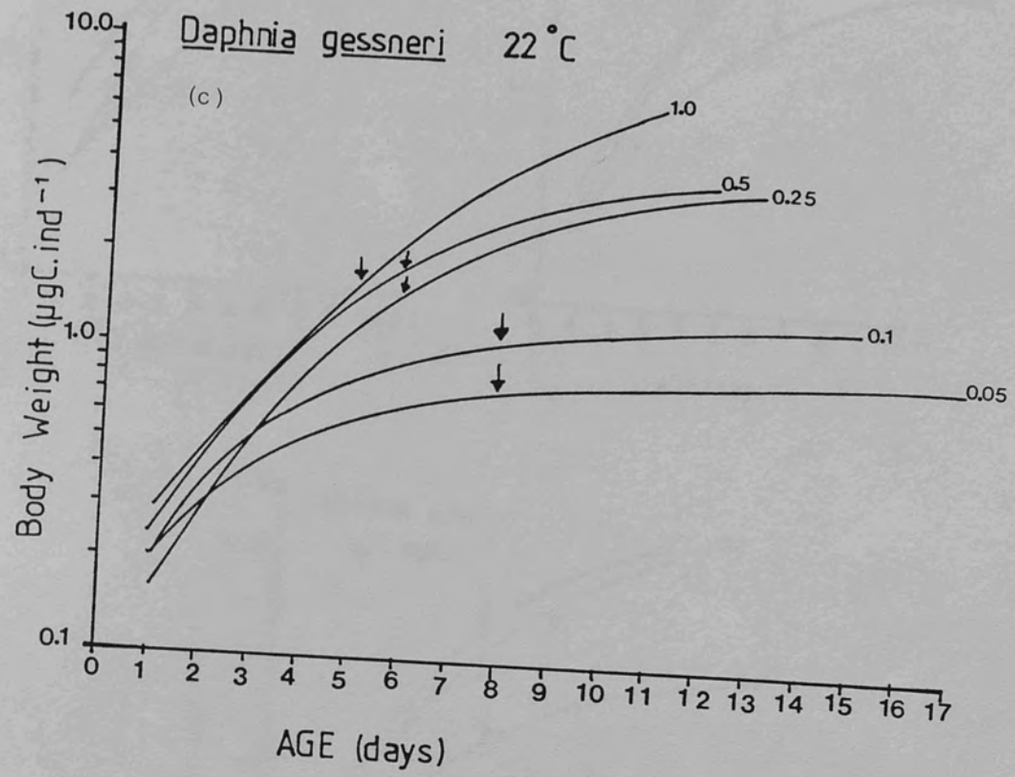

Daphnia gessneri
0.05 mg C.l⁻¹ 22° C
(o)
Body Weight (µg C.ind⁻¹)
10.0
1,0
0.1
W = 0.9 (1+1.0e^0.19(t+0.38))^0.98
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
AGE (days)

FIGURE 4.2 Richard's growth curves for Daphnia gessneri in different food concentration, at each constant temperature.The original individual body weights and ages are also plotted. The arrow indicates the size and age of the primiparous female.


Daphnia gessneri 32°C
(a)
1.0
0.5
0.25
0.1
0.05
20.0
10.0
1.0
0.1
Body Weight(µgC.ind⁻¹)
0 1 2 3 4 5 6 7 8 9 10 11 12
AGE (days)


Daphnia gessneri 27°C
(b)
1.0
0.5
0.25
0.1
0.05
20.0
10.0
1.0
0.1
Body Weight (µgC.ind⁻¹)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
AGE (days)


Daphnia gessneri 22 °C
(c)
10.0
1.0
0.1
Body Weight (µgC.ind⁻¹)
1.0
0.5
0.25
0.1
0.05
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
AGE (days)

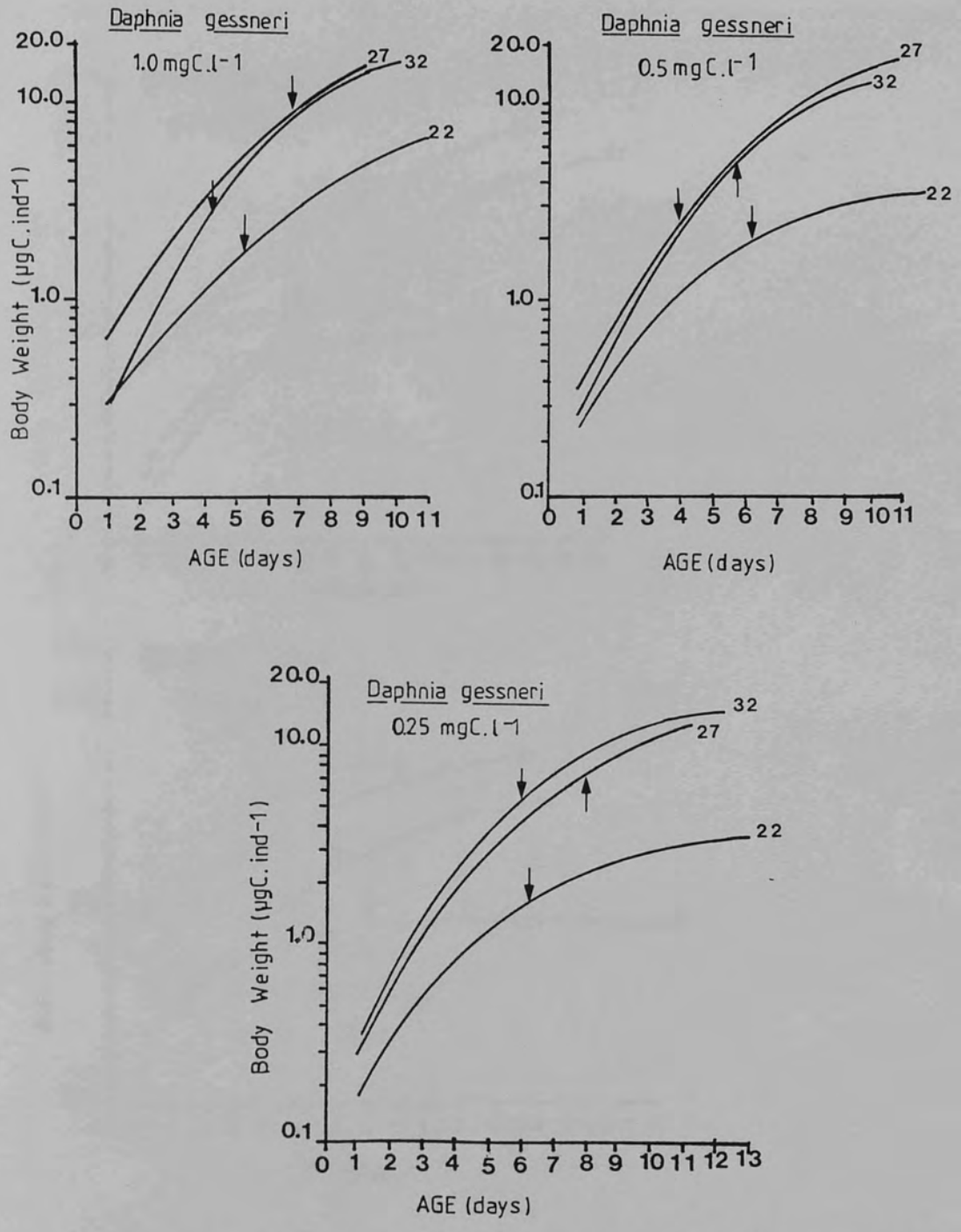
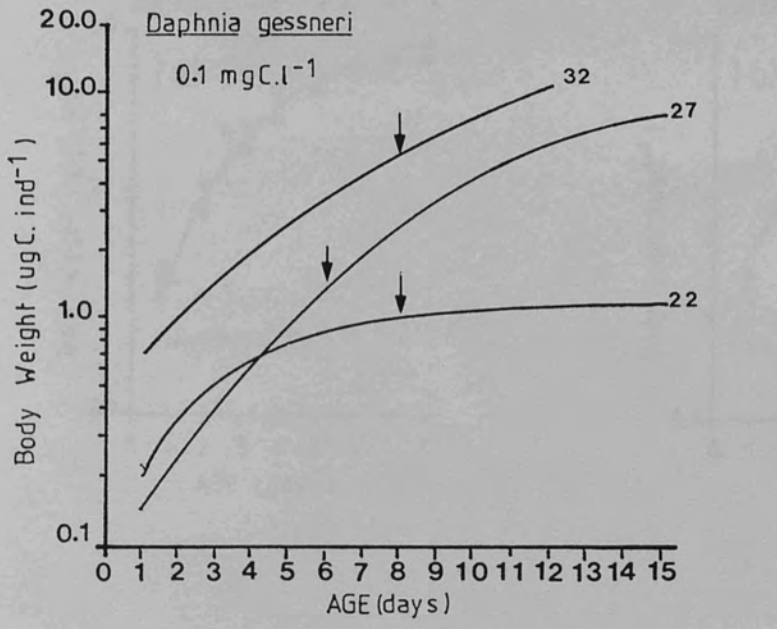


FIGURE 4.3 Richard's growth curves for Daphnia gessneri in different temperature, at each constant food concentration. The arrow indicates the size and age of the primiparous female.



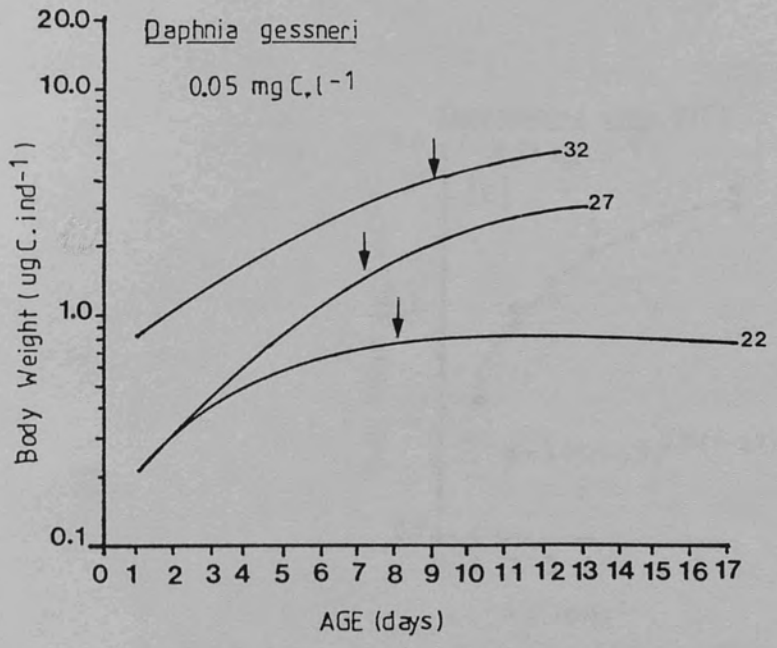


FIGURE 4.3 continued.

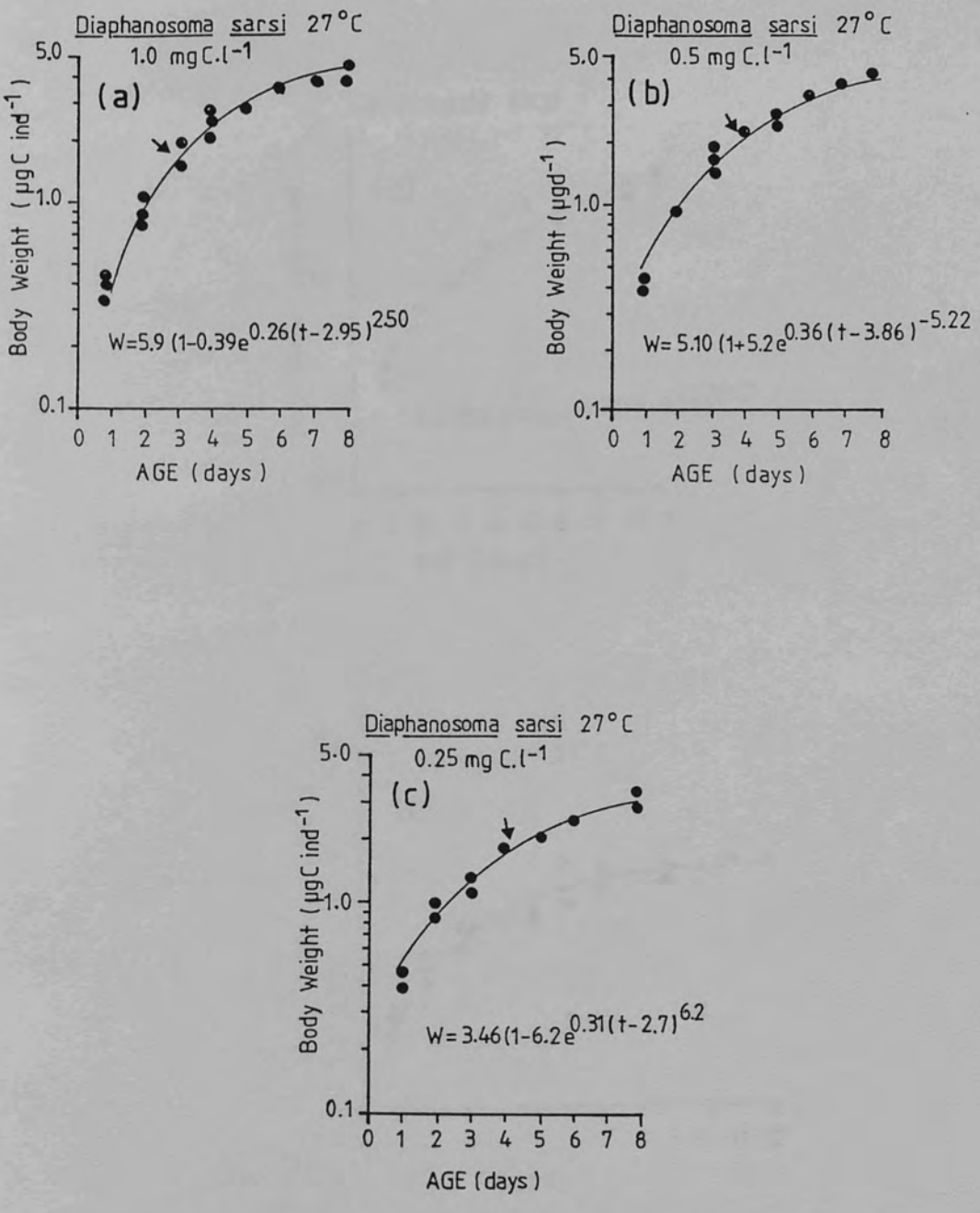
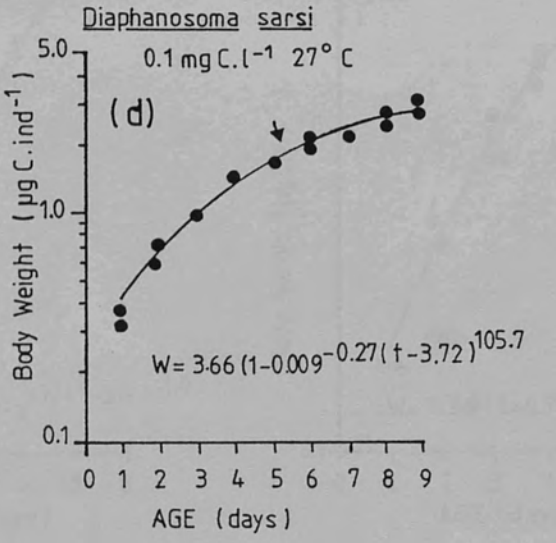


FIGURE 4.4 Richard's growth curves for Diaphanosoma sarsi in various food concentration at 27°C. The original individual body weights and ages are also plotted. The arrow indicates the size and age of the primiparous female.



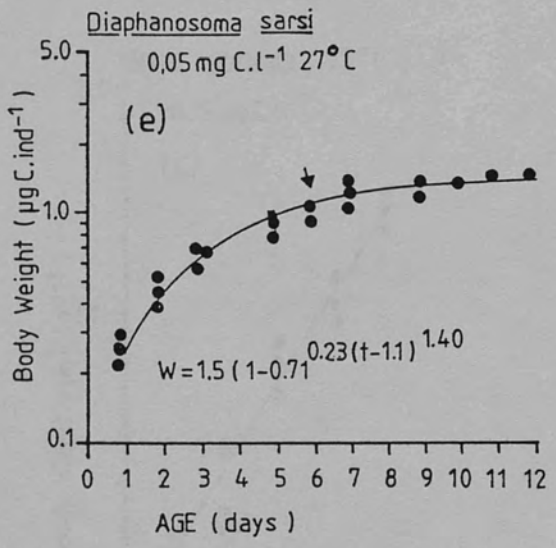


FIGURE 4.4 continued.

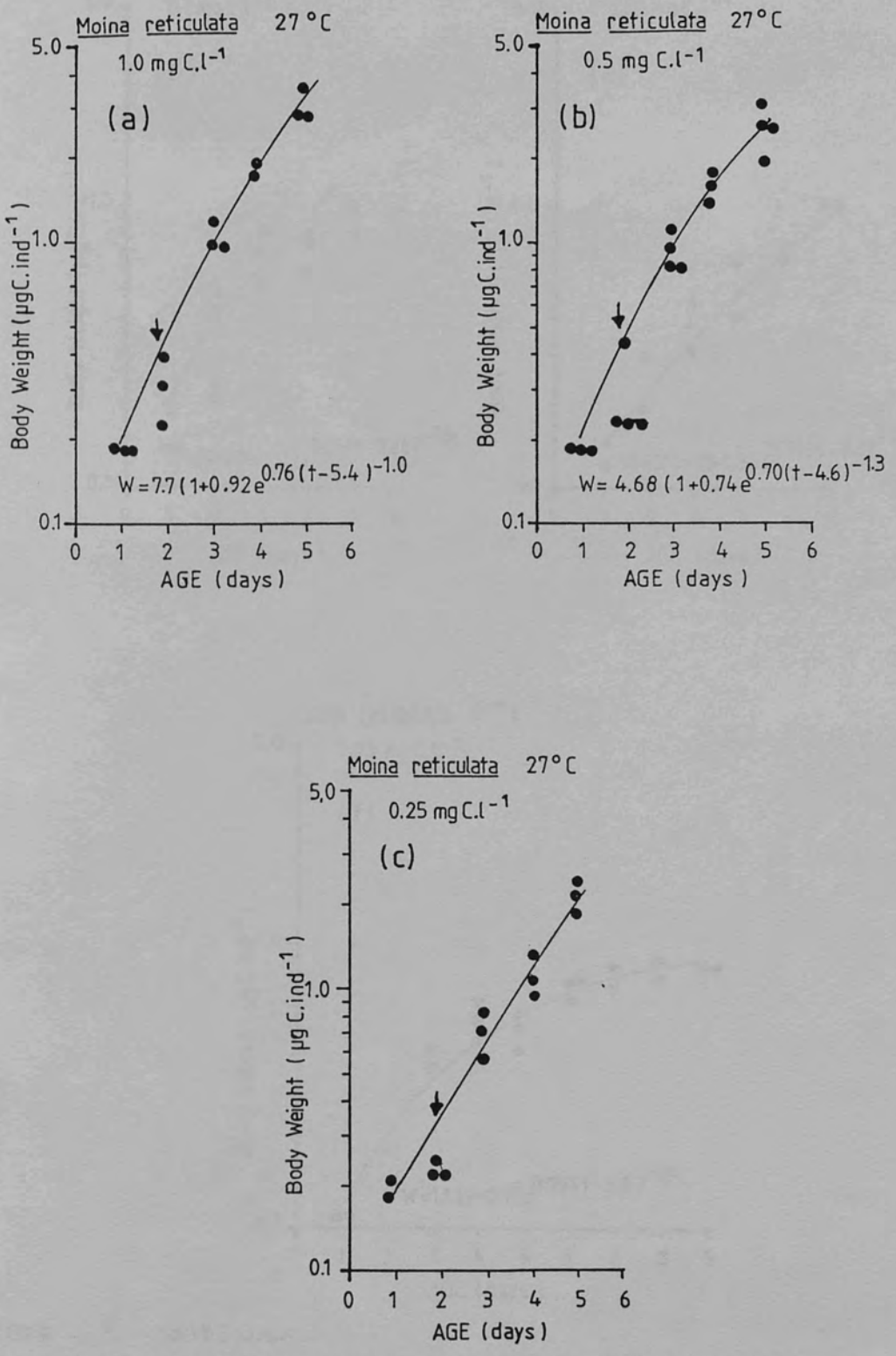
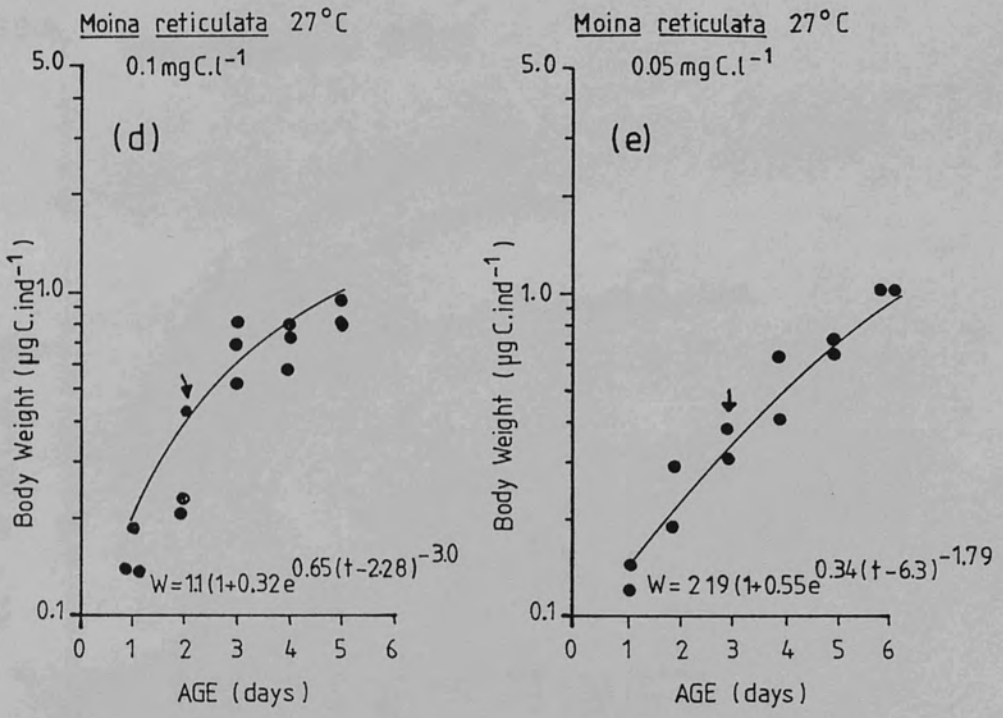


FIGURE 4.5 Richard's growth curves for Moina reticulata in various food concentration at 27°C. The original individual body weights and ages are also plotted. The arrow indicates the size and age of the primiparous female.



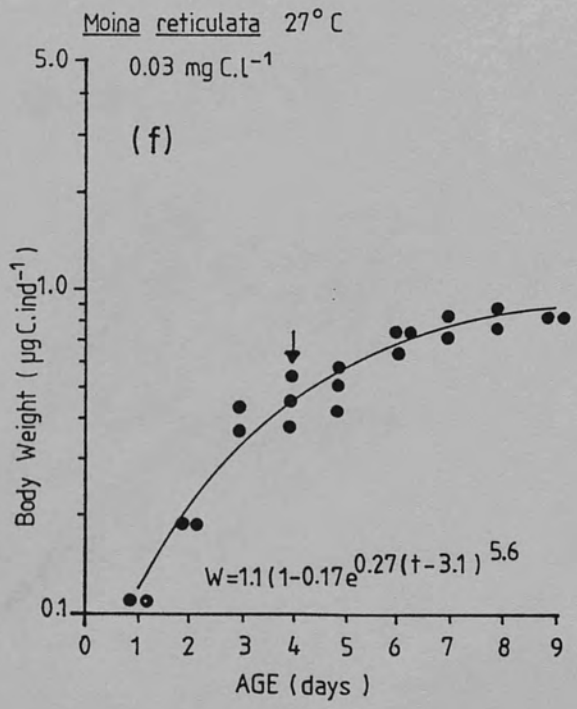
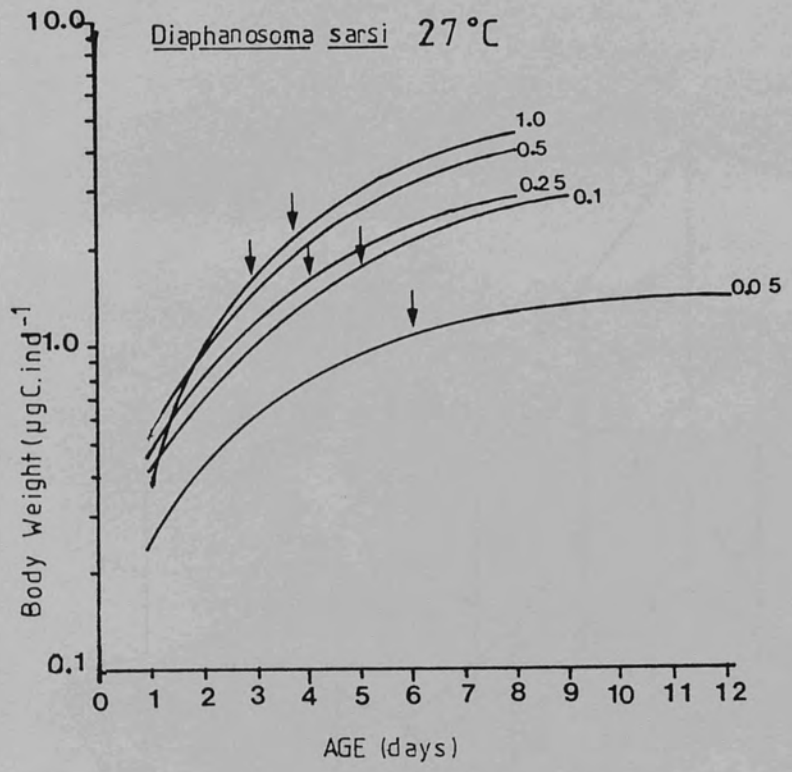


FIGURE 4.5 continued.



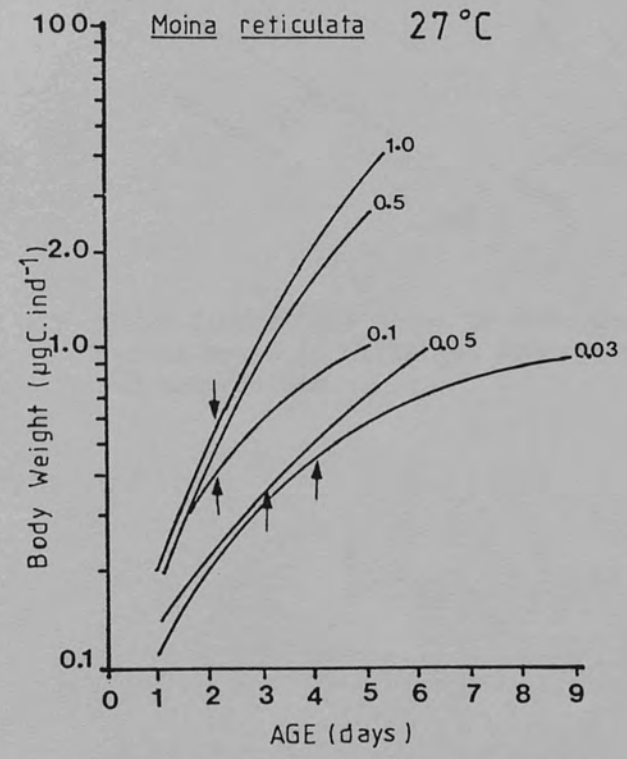


FIGURE 4.6 Richard's growth curves for Diaphanosoma sarsi and Moina reticulata, in different food concentration but at the same temperature. The arrow indicates the size and age of the primiparous female.

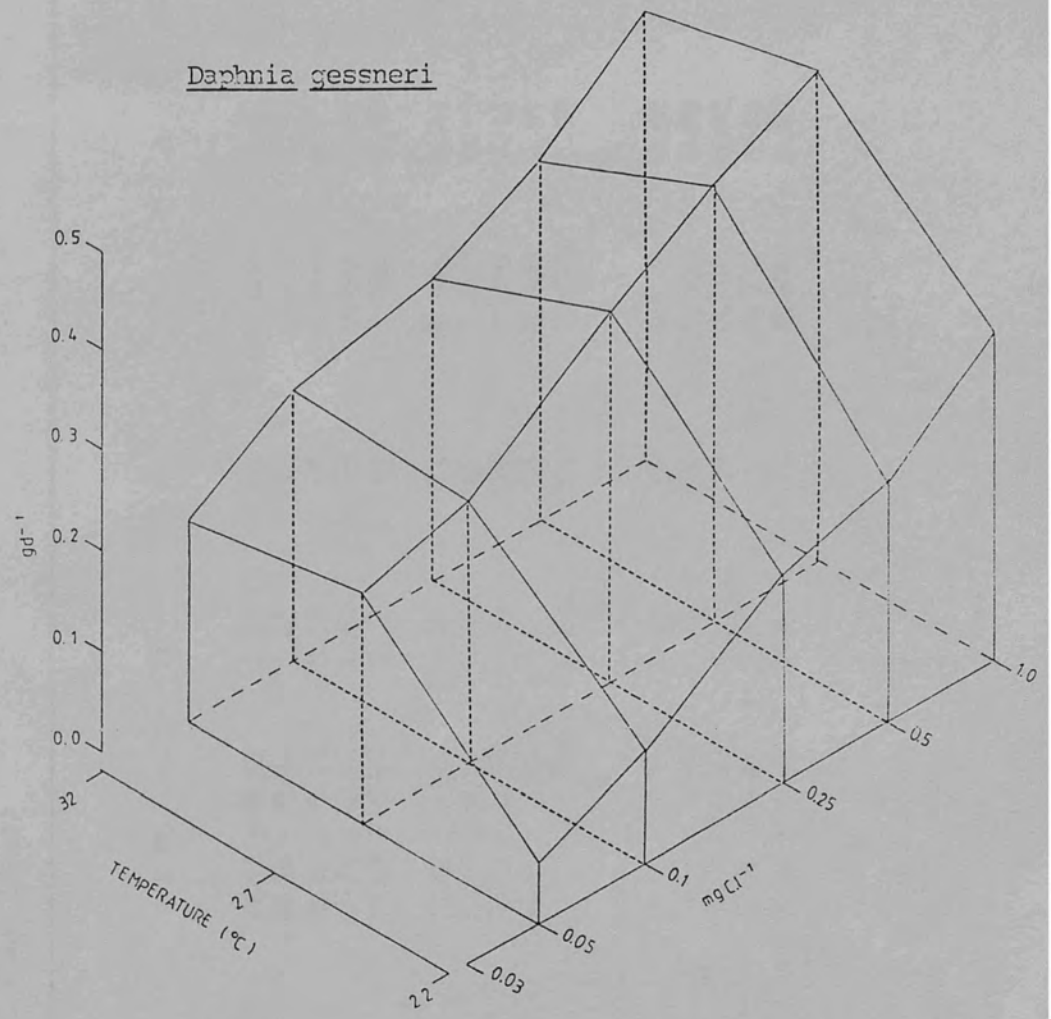


FIGURE 4.7 Three-dimensional plots to show the juvenile instantaneous growth rates in different treatments of food concentration and temperature.

TABLE **4.1** Parameters of the linear regression equations relating weight to age during the period of exponential growth at different temperature and food combinations.

Equation $\ln W_t = \ln W_0 + g\ t = \ln W \ln a + bX$
W = weight ($\mu gC.ind^{-1}$); X = age (days)

Daphnia gessneri

TEMPERATURE °C	FOOD LEVEL $mgC.l^{-1}$	ln a	b ± SE d^{-1}	df	F	P	r
32	1.0	- 0.837	0.44 ± 0.02	1,14	292	0.000	0.95
	0.5	- 0.686	0.36 ± 0.02	1,12	194	0.000	0.96
	0.25	- 0.624	0.31 ± 0.02	1,10	136	0.000	0.93
	0.1	- 0.506	0.27 ± 0.01	1,11	199	0.000	0.95
	0.05	- 0.490	0.20 ± 0.02	1,12	85	0.000	0.88
27	1.0	- 1.39	0.48 ± 0.02	1,26	419	0.000	0.94
	0.5	- 1.36	0.44 ± 0.02	1,20	280	0.000	0.93
	0.25	- 1.16	0.37 ± 0.02	1,28	328	0.000	0.92
	0.1	- 1.23	0.26 ± 0.01	1,19	407	0.000	0.97
	0.05	- 1.45	0.23 ± 0.008	1,32	894	0.000	0.98
22	1.0	- 1.39	0.33 ± 0.01	1,17	313	0.000	0.97
	0.5	- 1.19	0.24 ± 0.02	1,12	83	0.000	0.94
	0.25	- 1.13	0.21 ± 0.02	1,12	78	0.000	0.93
	0.1	- 1.12	0.11 ± 0.01	1,16	43	0.000	0.86
	0.05	- 1.04	0.06 ± 0.01	1,15	31	0.000	0.83

TABLE **4.1** continued

TEMPERATURE °C	FOOD LEVEL mgC.l^{-1}	ln a	b ± SE d^{-1}	df	F	P	r
Diaphanosoma sarsi							
27	1.0	- 0.95	0.35 ± 0.03	1,15	85	0.000	0.92
	0.5	- 0.85	0.33 ± 0.04	1,10	52	0.000	0.92
	0.25	- 0.78	0.26 ± 0.03	1,12	65	0.000	0.92
	0.1	- 0.89	0.24 ± 0.02	1,11	88	0.000	0.94
	0.05	- 1.10	0.15 ± 0.01	1,19	76	0.000	0.89
Moina reticulata							
27	1.0	- 2.51	0.75 ± 0.04	1,15	243	0.000	0.97
	0.5	- 2.21	0.59 ± 0.04	1,23	206	0.000	0.95
	0.25	- 2.41	0.64 ± 0.04	1,12	224	0.000	0.97
	0.1	- 2.18	0.46 ± 0.05	1,13	67	0.000	0.92
	0.05	- 2.23	0.37 ± 0.03	1,11	136	0.000	0.96
	0.03	- 1.95	0.23 ± 0.02	1,21	98	0.000	0.91

TABLE **4.2** Parameters of the Richard's growth model equation for fitting growth curves to Daphnia gessneri Diaphanosoma sarsi and Moina reticulata.

Equation : $W_t = W_{max}[1- b \exp (- g(t - t_0)]^p$
W_t = weight ($ugC.ind^{-1}$) ; W_{max} = maximum weight attained; t_o = time of inflection of the curve; g = growth constant; p = exponent.

TEMPERATURE °C	FOOD LEVEL $mgC.l^{-1}$	W_{max} µgC	g d^{-1}	t_o days	b	p	RSS	pp(age)* days
Daphnia gessneri								
32	1.0	20.62	0.49	7.0	- 0.78	- 1.27	0.70	4.0
	0.5	17.69	0.59	7.2	- 0.95	- 1.05	0.56	6.0
	0.25	15.34	0.48	6.9	- 0.66	- 1.50	1.28	6.0
	0.1	15.15	0.46	9.3	- 1.46	- 0.68	1.24	8.0
	0.05	8.50	0.23	8.7	- 0.72	- 1.38	0.83	9.0
27	1.0	20.27	0.51	6.9	- 0.63	- 1.59	6.73	3.0
	0.5	14.28	0.59	6.6	- 0.79	- 1.25	8.09	4.0
	0.25	17.99	0.32	7.8	- 0.32	- 3.09	8.70	4.0
	0.1	10.20	0.39	10.16	- 0.83	- 1.20	1.33	6.0
	0.05	6.68	0.25	11.0	- 0.65	- 1.51	1.27	7.0
22	1.0	10.09	0.32	8.67	- 0.60	- 1.65	1.10	5.0
	0.5	4.24	0.30	5.58	- 0.23	- 4.21	0.42	6.0
	0.25	3.87	0.32	6.06	- 0.28	- 3.55	0.85	6.0
	0.1	1.36	0.19	0.68	0.85	1.17	0.01	8.0
	0.05	0.90	0.19	- 0.38	1.01	0.98	0.01	8.0

*pp= primipara female

TABLE **4.2** continued

TEMPERATURE °C	FOOD LEVEL mgC.l^{-1}	W_{max} µgC	g d^{-1}	t_o days	b	p	RSS	pp(age) days
Diaphanosoma sarsi								
27	1.0	5.91	0.26	2.95	0.39	2.50	0.28	3.0
	0.5	5.10	0.36	3.86	- 0.19	- 5.22	0.27	4.0
	0.25	3.46	0.31	2.71	0.16	6.21	0.10	4.0
	0.1	3.66	0.27	3.72	0.00	105.70	0.09	5.0
	0.05	1.51	0.23	1.13	0.71	1.40	0.04	6.0
Moina reticulata								
27	1.0	7.72	0.76	5.42	- 0.92	-1.08	0.47	2.0
	0.5	4.68	0.70	4.62	- 0.74	-1.34	0.99	2.0
	0.25	*	0.66	*	- 1.06	-0.93	0.26	2.0
	0.05	2.19	0.34	6.36	- 0.55	-1.79	0.04	3.0
	0.03	1.11	0.27	3.17	0.17	5.62	0.07	4.0

* undefined in these data set

CHAPTER 5

The effect of food concentration and temperature on the duration of development: Embryonic and Post-embryonic.

The duration of embryonic development (D_e) is the duration of egg development in the brood pouch. It comprises the time since the eggs were released from the ovary into the brood pouch until the fully developed embryos are released into environment.

The duration of post-embryonic development (D_j) is the duration of the juvenile or immature phase, and includes all juvenile or immature instars, including the last juvenile instar will carry an ovary.

It has frequently been shown in the literature that the duration of embryonic development in Cladocera is temperature dependent but whilst the embryonic development time is a function of temperature only, the duration of the post-embryonic development is influenced by both temperature and food. Cultured Cladocera provided with high food concentrations have a shorter duration of post-embryonic development than those cultured at low food levels (Lei & Armitage, 1980; Vijverberg, 1980; Kankaala & Wulf, 1981; Rocha, 1983; Jayatunga, 1986. Most of the information published so far is derived from temperate species and much more investigation is needed on tropical zooplanktonic species in order to understand the effect of food quality and quantity and temperature upon their duration of post-embryonic development. In this study, an attempt was made to examine the effects of three temperatures (22, 27, 32°C), and five food concentrations using Scenedesmus acutus as the food organism (1.0, o.5, 0.25, 0.1, 0.05 $mgC.l^{-1}$) on both embryonic and post-embryonic duration of Daphnia gessneri, a tropical cladoceran commonly found in Amazonian "varzea" lakes. Moina reticulata and Diaphanosoma sarsi were also investigated at the same food concentration but only at one temperature (27°C).

5.1 Duration of embryonic development (D_e)

Table 5.1 summarizes the data on embryonic development in all three species at different combinations of temperature and food. In Daphnia gessneri, there is an increase in duration as either temperature or food concentration decreases, although the effect of temperature is much greater, doubling compared with 30% by food concentration. The shortest development time was obtained with a combination of the highest temperature (32°C) and highest food concentration (1.0mgC.l^{-1}). Food concentration has less effect but duration also increases as food concentration declines, at least down to 0.25 mgC.l^{-1}. Below this, at least at 22°C, duration starts to decline again. In Moina reticulata and Diaphanosoma sarsi, the effect of decreasing food concentration is similarly noticeable (Table 5.1) In Moina reticulata, the development time (24 hours) did not vary in the three higher food concentration but it started increase at 0.1 mgC.l^{-1} doubling with the lowest food concentration. In Diaphanosoma sarsi at 27°C duration of development increased clearly as food concentration declined also doubling the time.

The relationships between temperature and embryonic development time for each food level can be described by a power function, $D = a.T^{-b}$, where D is embryonic duration in hours, T is temperature in degrees centigrades and "a" and "b" are constants. Transformations of both variables to natural logarithms permitted the calculation of linear regressions together with regression statistics which are given in Table 5.2. The regressions of duration of egg development time on temperature were statistically significant for Daphnia gessneri grown in the following food levels 1.0, 0.5 and 0.25 mgC.l^{-1}, but not significant at 0.1 mgC.l^{-1}. It was not possible to obtain a regression at 0.05 mgC.l^{-1} since data were available for one temperature only; either animals died prior to reproduction or did not complete three broods.

The significant regressions given in Table 5.2 were compared by covariance analysis in order to detect any differences between then

and this is presented in Table 5.3. The differences in the slopes (b) of the regressions of egg development time on temperature at different food levels were not significant with respect to food concentration. A comparison of the elevations of the regressions showed that those for the two upper food concentrations (1.0 and 0.5 $mgC.l^{-1}$) were not significantly different, but did differ from that at the lowest food level 0.25 $mgC.l^{-1}$. The regression for 0.25 $mgC.l^{-1}$ also had the highest elevation of all three (Figure 5.1). This indicates that, in Daphnia gessneri, embryonic development was prolonged at all temperatures when grown in the food of 0.25 $mgC.l^{-1}$ but not in 0.5 and 1.0 $mgC.l^{-1}$.

The relationship between embryonic duration and food concentration can be also described by the same power function $D=a.F^{-b}$, where D is embryonic duration in hours and F is food concentration in $mgC.l^{-1}$, "a" and "b" are constants. As given in Table 5.4 these show no significant relationship between egg development time and food concentration except in Diaphanosoma sarsi, where duration increased steadily as food concentration decreased. At 27°C the duration of embryonic development for Moina reticulata did not vary in the three upper food level (1.0, 0.5 and 0.25 $mgC.l^{-1}$) remaining constant at about 24 hours, but at the low food level the variation became greater. At 0.03 $mgC.l^{-1}$ the embryonic development was found to be 51 ± 2.53 hours, more than twice the value found for any of the high food levels. However, visually there is a tendency for embryonic development of these species to increase in duration with reduced food supplies to the mother at 27°(Figure 5.2). In Moina reticulata the response is different from all the other species, as it is curvilinear on a log-log plot whereas it is possible to force a log-linear on the other. So, these results must be interpreted carefully.

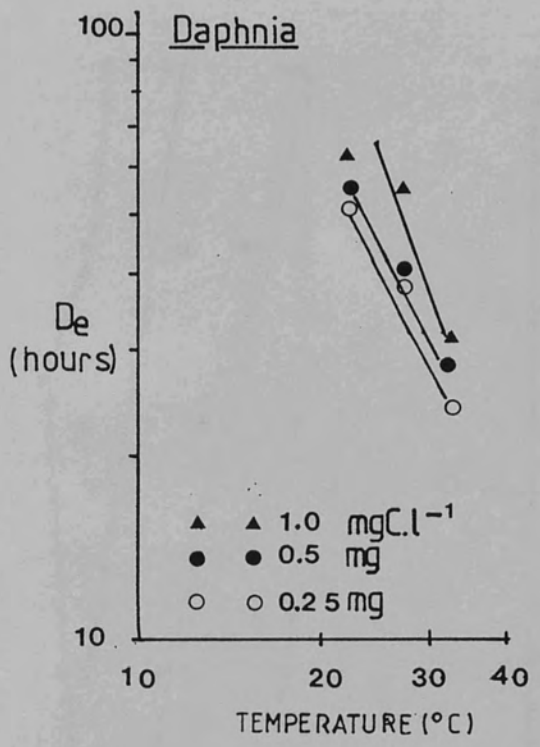


FIGURE 5.1 Duration of embryonic development on temperature at three food concentrations for D.gessneri

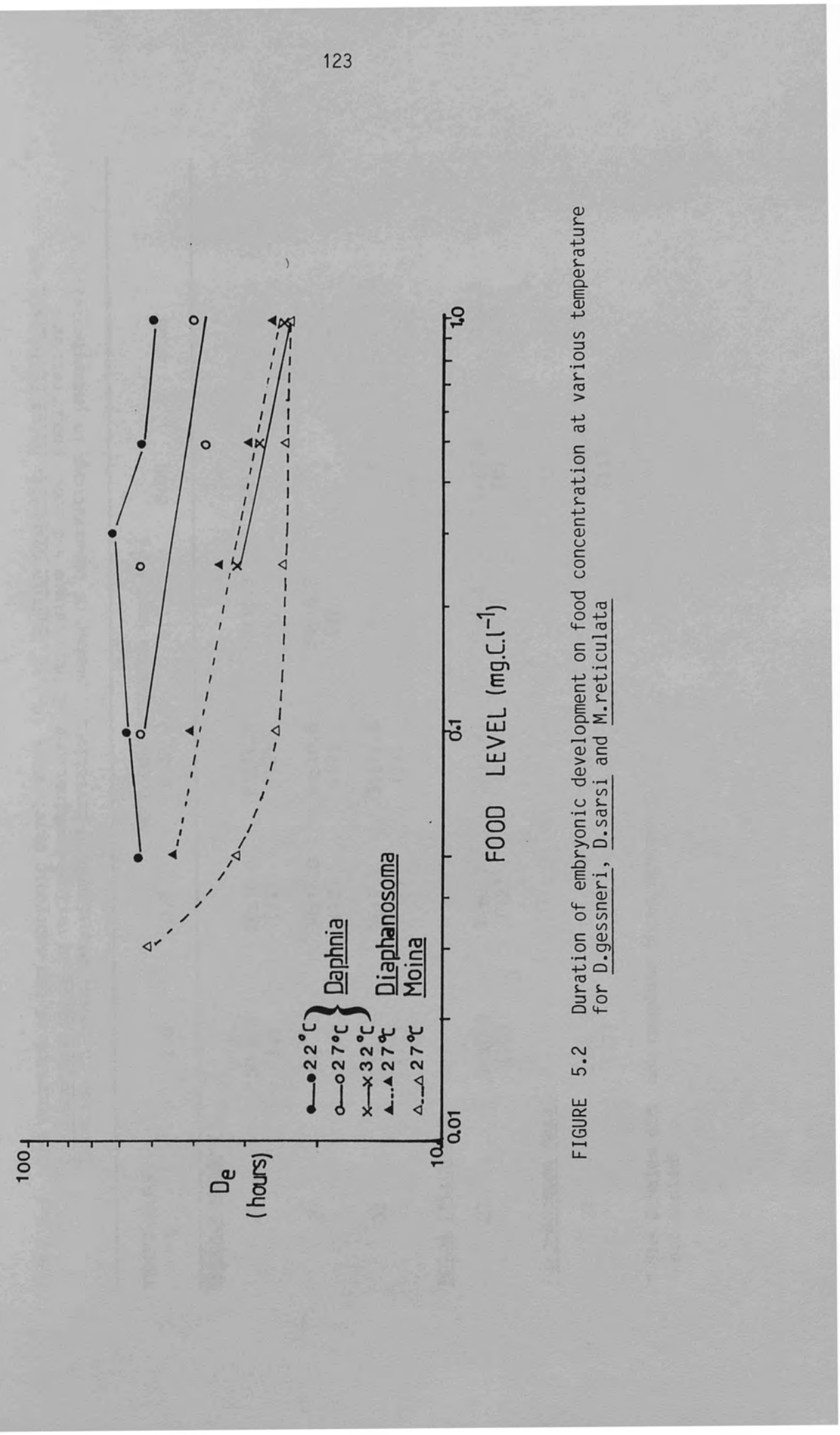


FIGURE 5.2 Duration of embryonic development on food concentration at various temperature for D.gessneri, D.sarsi and M.reticulata

TABLE 5.1 The duration of the embryonic development (D_e) of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi in various combinations of temperature and food concentrations. Duration in hours; mean±Standard deviation; (number of observations in parenthesis).

TEMPERATURE °C	FOOD CONCENTRATION ($mgC.l^{-1}$) 1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	50±4.6 (12)	56±10.6 (12)	63±11.5 (12)	58±16.3 (9)	54±10.0 (7)	-
27	40±14.7 (12)	38±16.0 (12)	54±10.8 (12)	54±16.9 (8)	* *	- -
32	24±0.0 (12)	28±9.7 (12)	31±11.5 (12)	*	*	-
Moina reticulata						
27	24±0.0 (12)	24±0.4 (12)	24±0.4 (12)	25±3.4 (12)	31±7.0 (8)	51±2.5 (7)
Diaphanosoma sarsi						
27	24±0.0 (12)	29±10.4 (9)	34±12.4 (9)	40±11.4 (6)	44±20.4 (11)	

* The females did not complete three broods
- not tested

TABLE 5.2 Curvilinear regressions relating the duration of embryonic development to temperature at various food concentrations for Daphnia gessneri.

Regression equation $\ln Y = \ln a - b \ln X$
Y = duration of embryonic development in hours; X = temperature in ^{o}C
df = degress of freedom; F = variance ratio; P = level of significance

FOOD LEVEL ($mgC.l^{-1}$)	ln a	b	df	F	P
Daphnia gessneri					
1.0	9.76	- 1.88	1,29	27.9	0.11
0.5	9.86	- 1.90	1,32	87.6	0.06
0.25	10.03	- 1.88	1,31	5.7	0.25
0.1	8,87	- 1.54	1,18	2.6	0.35
0.05	*				

* regression could not be calculated

TABLE 5.3 Covariance analysis of the significant regressions of duration of embryonic development on temperature at various food levels for Daphnia gessneri. The regression coefficients were compared by the SS-STP tes and the differences between elevations by the S-N-K test. Regression coefficients and means underlined are not significantly different at P = 0.05 level; Group numbers are given in ascending order of magnitude.

		Comparisons of slopes				
FOOD LEVEL $mgC.l^{-1}$	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
1.0	1	- 1.88±0.30	2,95	0.001	0.99	1 2 3
0.5	2	- 1.90±0.33				
0.25	3	- 1.88±0.33				

		Comparison of elevations				
$mgC.l^{-1}$	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
1.0	1	3.59±0.15	2,98	8.61	0.000	1 2 3
0.5	2	3.64±0.15				
0.25	3	3.85±0.15				

TABLE 5.4 Curvilinear regressions relating the duration of embryonic development to food concentration at various temperature for Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi.

Regression equation $\ln Y = \ln a - b \ln X$
Y = duration of embryonic development in hours; X = food concentration in $mgC.l^{-1}$;
df = degrees of freedom; F = variance ratio; P = level of significance

TEMPERATURE °C	lna	b	df	F	P
Daphnia gessneri					
22	3.97	- 0.026	1,47	0.41	0.56
27	3.55	- 0.196	1,41	3.35	0.20
32	3.21	- 0.091	1,29	4.85	0.15
Moina reticulata					
27	3.07	- 0.136	1,57	6.19	0.06
Diaphanosoma sarsi					
27	3.19	- 0.179	1,42	130.02	0.001

5.2 Duration of post-embryonic development (D_j)

The duration of post-embryonic development taken to extend from the time at which the neonate was release from the brood pouch to the end of the juvenile instar prior to the appearance of the primiparous female.The duration determined at different temperature and food combinations for the three species of Cladocera are summarized in Table 5.5 and illustrated in Figure 5.3. The pattern in Daphnia gessneri is similar in the three temperatures: At 32°C the post-embryonic duration shows a steady increase with declining food concentration. The shortest D_j occurs from 1.0 $mgC.l^{-1}$ down to 0.25 $mgC.l^{-1}$, then at 0.1 and even more at 0.05 $mgC.l^{-1}$, the D_j prolongs and changes sharply with further decrease in food concentration. At 27°C a, perhaps, anomalously long duration was recorded with 1.0 $mgC.l^{-1}$ food but at lower food concentrations the pattern of increase was very close at first to that at 32 and 22°C. Similar pattern was obtained in Diaphanosoma sarsi. The shape of the curve is basically similar but the steep increase starting at 0.25 $mgC.l^{-1}$. Moina reticulata is very different compared with the other two species. Very little changes occurs in D_j from 1.0 $mgC.l^{-1}$ down to 0.1 $mgC.l^{-1}$ then at 0.05 and 0.03 $mgC.l^{-1}$ the post-embryonic time increase clearly. It is striking that the development time of Diaphanosoma sarsi and particularly, Moina reticulata at 27°C are much shorter than those of Daphnia gessneri at any of the three temperatures.

Table 5.5 also shows that in all three species there is an increase in the number of instars within the juvenile period as the food concentration decreases on the two top levels and this is much more marked at the lowest food levels. Thus, in the highest food levels at 22°C, Daphnia gessneri became primiparous at the V to VIII instar but this was delayed to the IX to X instar at the lowest food concentration. At the same time, the onset of reproduction occurred at a much older age, from 177 hours to 240 hours or from 7.4 to 10 days. This pattern of the onset of reproduction taking place at a later instar and at an older age also occurs at 27 and 32°C (Table 5.5).A similar pattern of development and age response to food concentration

is seen in Moina reticulata and Diaphanosoma sarsi at 27°C. In this respect too Moina reticulata appears to be much more fixed in its response but this may simply be a consequence of its ability to complete this stage of its development as rapidly at 0.1 $mgC.l^{-1}$ as at 0.5 $mgC.l^{-1}$.

The relationship between the duration of post-embryonic development and temperature at various food concentrations can be only be calculated for Daphnia gessneri and it was found that it could be fitted to the power function, $Y = a X^b$.

The regressions for Daphnia gessneri, are given in Table 5.6 and illustrated in Figure 5.4. Table 5.6 indicates that statistically significant regressions could be obtained only for the three upper food levels (1.0, 0.5, 0.25 $mgC.l^{-1}$) but not for the two lowest food levels (0.1 and 0.05 $mgC.l^{-1}$).

Covariance analysis was performed on these regressions for Daphnia gessneri which related the post-embryonic duration to temperature at different food levels. The results of this analysis are given in Table 5.7 and reveal that neither slopes ($P = 0.24$) nor the elevations ($P = 0.26$) are significantly different and thus there is no significant effect of temperature at these food concentrations. Because no significant relationship between temperature and post-embryonic duration could be obtained for Daphnia gessneri at 0.1 and 0.05 $mgC.l^{-1}$, these food levels were not included in the covariance analysis. Nevertheless, these results are important in showing, as it is evident from Table 5.5, how juvenile duration is prolonged when food concentration decrease to these low levels although there is no apparent systematic effect of temperature.

Table 5.8 presents all the regressions for Daphnia gessneri which relate post-embryonic duration to food concentration at each of the three experimental temperatures. All three regressions are statistically significant and are plotted on an arithmetic scale in Figure 5.5. Covariance analysis of the regressions was undertaken and the results are given in Table 5.9. The slopes of the lines at 22°C and 27°C are not significant;y different, nor are those of 22°C and

32°C but there is a significant difference between 32°C and 27°C and the elevation of the line at 22°C is significantly higher than that of the other two which are not significantly different from each other. Thus the effect of change in food concentration on duration is much the same at all three temperature but at any one food concentration the duration is significantly longer at 22°C than at the higher temperatures.

Table 5.8 shows that the regressions for Diaphanosoma sarsi at 27°C is statistically significant, with a high F value and $P<0.0001$. The plot of this regression is shown in Figure 5.5 and lies well below those for Daphnia gessneri because this species has a much shorter juvenile phase. On the other hand, no significant regression was obtained for Moina reticulata at 27°C ($P=0.14$) probably because of the rather constant juvenile duration of 48 hours shown by this species from 1.0 down to 0.1 $mgC.l^{-1}$ (Table 5.5). When the regression was performed using data from the three lowest food concentration only (0.1, 0.05 and 0.03 $mgC.l^{-1}$), a significant relationship was obtained (Table 5.8). It seems that the onset on limiting food conditions occurs in Moina reticulata at much lower food levels than for the other two species.

This section has shown that, in all three cladoceran, the duration of juvenile development becames prolonged when the food concentration falls below a certain level. It has also shown that the food level at which this prolongation starts is lower in Moina reticulata (0.05 $mgC.l^{-1}$) than in the other two species (0.1 $mgC.l^{-1}$). A visual comparison of the regression, plotted in an arithmetic scale, is given in Figure 5.5 and shows how much longer is the juvenile phase in Daphnia gessneri than in the smaller species, Diaphanosoma sarsi and Moina reticulata.

An attempt was made to examine the relationship of post-embryonic duration to both temperature and food concentration, by means of multiple regression analysis in which both of these were independent variables. Various types of transformations were tested for the multiple regressions analysis and the best fit with highest F values ($P<0.001$) were obtained using the reciprocal of the post-embryonic

duration, the reciprocal of temperature and the logarithm of the food concentration. The results of this relationship are given in Table 5.10; the F and P values given separately allocate the probability of the variance due to food concentration and due to temperature. Table 5.10 shows that the effect of food concentration on D_j is three times greater than the effect of temperature on juvenile duration of Daphnia gessneri.

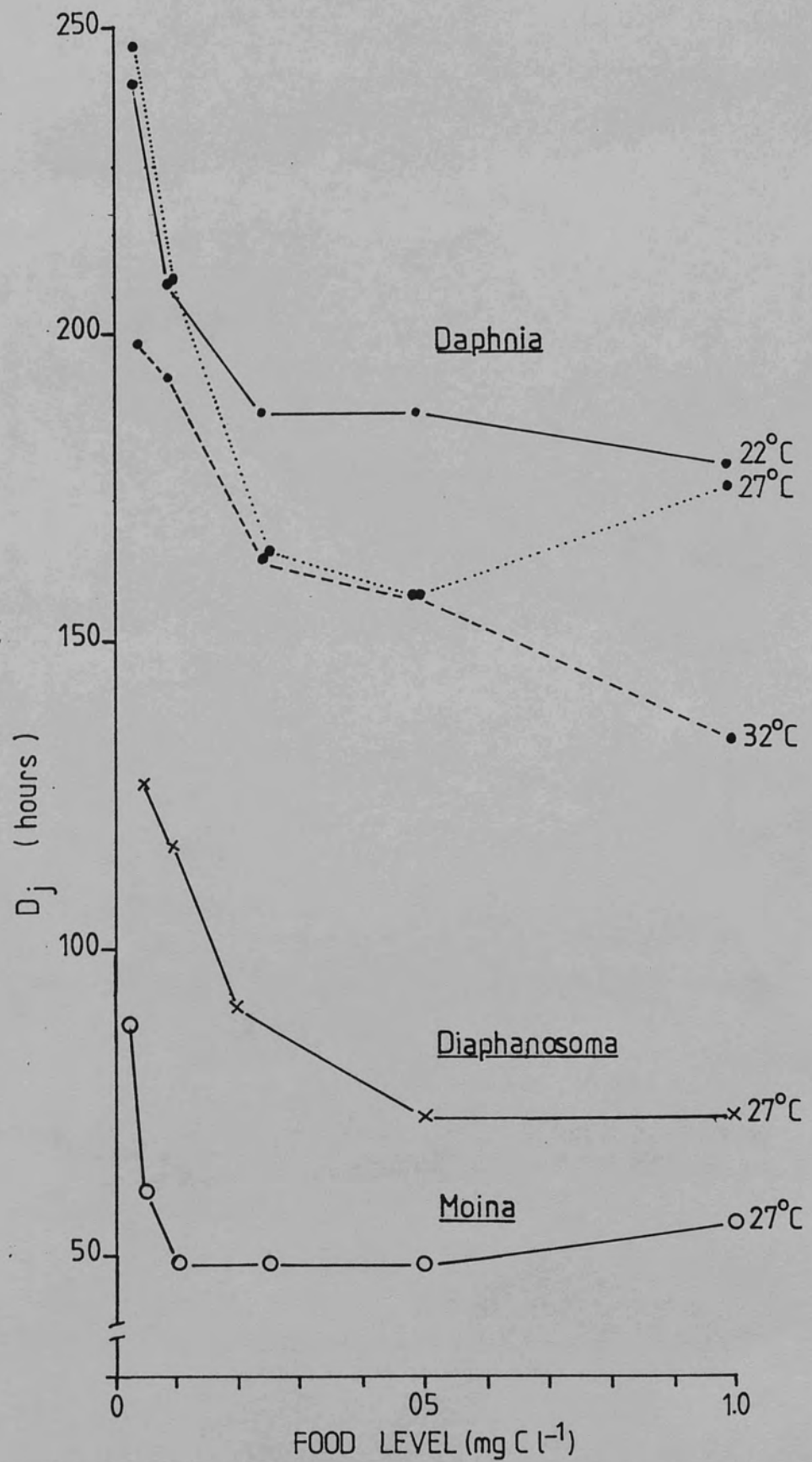


FIGURE 5.3 The effect of food concentration on the mean duration of post-embryonic development of D.gessneri, D.sarsi and M.reticulata at various temperatures.

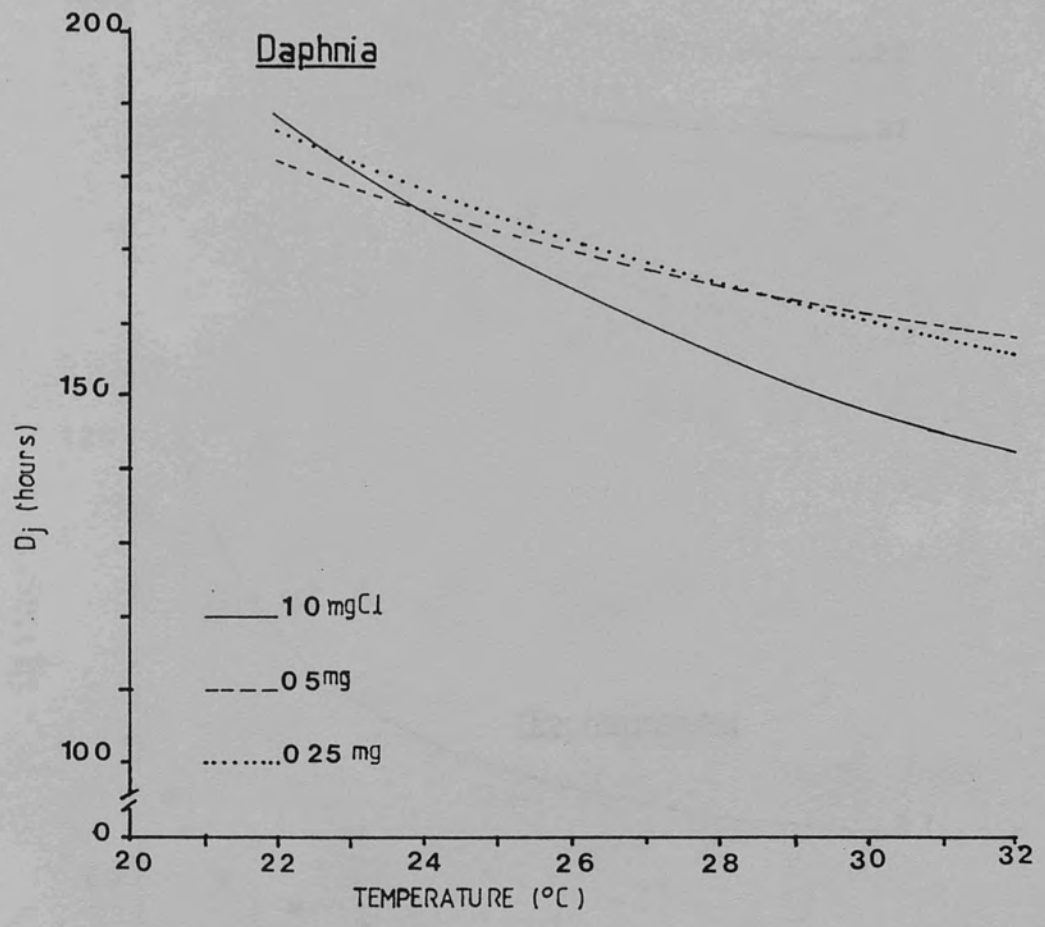


FIGURE 5.4 Significant regressions of post-embryonic duration on temperature in Daphnia gessneri at three food concentrations.

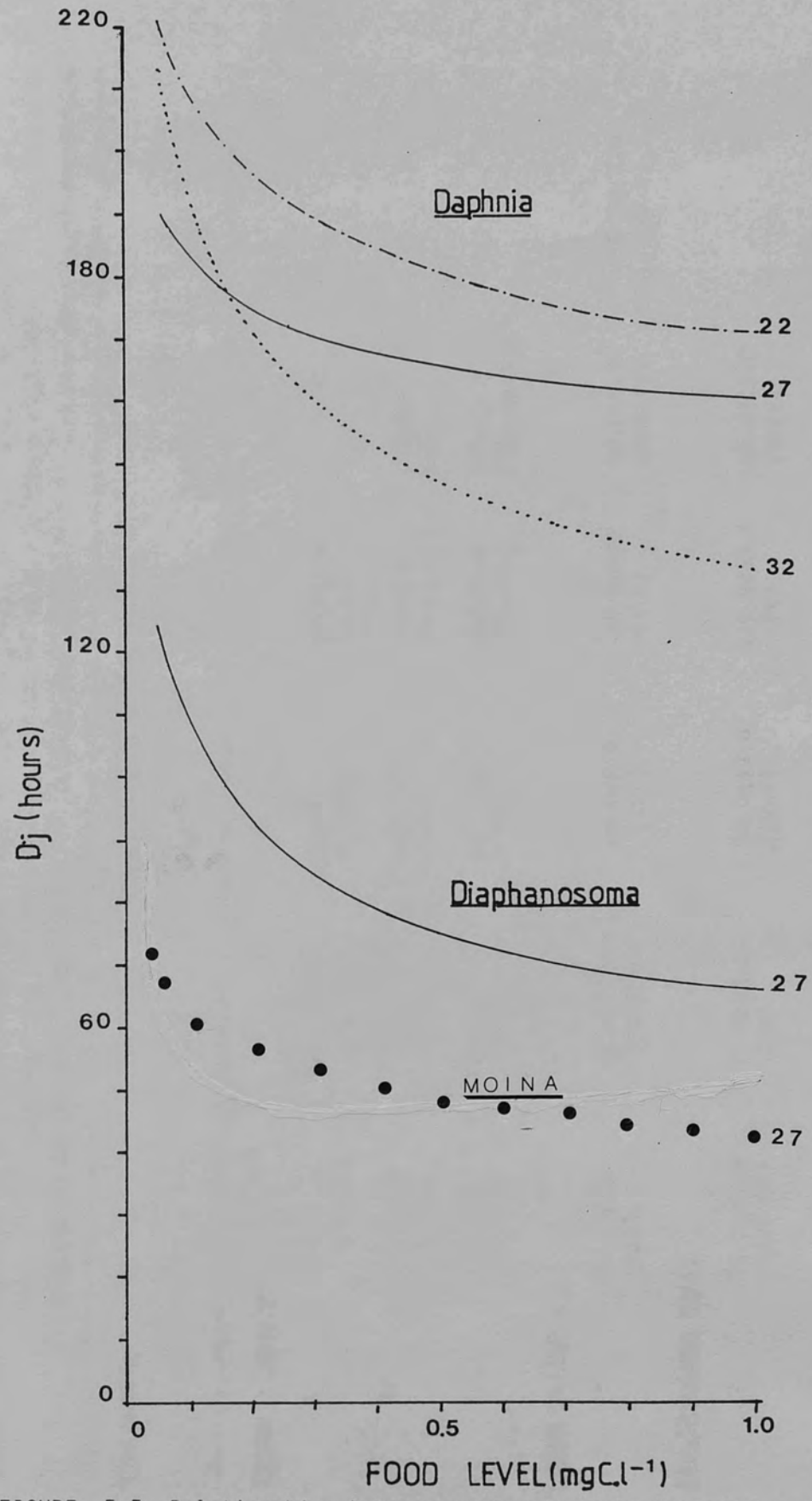


FIGURE 5.5 Relationships between post-embryonic duration and food concentration for D.gessneri, D.sarsi and M.reticulata at different temperature. The statistics of the curvilinear regressions are given in Table 5.8

TABLE 5.5 Duration of post-embryonic development (hours) to primipara and numbers of instars (in parenthesis) attained in various combinations of food and temperature in Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi. N = 4 | SD = standard deviation

TEMPERATURE °C	FOOD CONCENTRATION ($mgC.l^{-1}$)					
	1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	177±11.4 (V-VII)	186±12.0 (VI-VII)	186±20.7 (VI-VIII)	207±35.8 (VIII)	240±56.7 (VII-X)	-
27	174±12.0 (V-VII)	156±16.9 (V-VII)	162±12.0 (VI-VII)	192±0.0 (VIII-IX)	198±22.8 (IX)	-
32	132±0.0 (IV-VI)	156±0.0 (V-VI)	162±12.0 (V-VI)	207±18.0 (VI-VII)	246±53.2 (VII-VIII)	-
Moina reticulata						
27	54.0±0.0 (III)	48.0±0.0 (III)	48.0±0.0 (III)	48.0±0.0 (III)	60.0±0.0 (III-IV)	90.0±12.0 (IV-V)
Diaphanosoma sarsi						
27	72.0±13.8 (III-IV)	72.0±13.8 (IV)	90.0±12.0 (IV-V)	116.0±13.8 (V)	126.0±12.0 (V-VI)	-

- not tested

TABLE 5.6 Curvilinear regressions relating the duration of post-embryonic development to temperature at various food concentration for Daphnia gessneri.

Regression equation $\ln Y = \ln a - b \ln X$
Y = post-embryonic development in hours; X = temperature in °C
df = degrees of freedom; F = variance ratio; P = level of significance

FOOD CONCENTRATION ($mgC.l^{-1}$)	ln a	b	df	F	P
Daphnia gessneri					
1.0	7.55	- 0.75	1,10	19.75	0.001
0.5	6.67	- 0.47	1,10	9.96	0.010
0.25	6.34	- 0.37	1,10	4.72	0.05
0.1	5.25	0.01	1,8	0.006	0.94
0.05	5.01	0.09	1,10	0.059	0.81

TABLE 5.7 Covariance analysis of the regressions comparing the duration of post-embryonic development on temperature at different food concentrations for Daphnia gessneri. The regression coefficient were compared by the SS-STP test and the difference between elevations by the S-N-K test. Regression coefficients and means underlined are not significantly different at P = 0.05 level.

Regression equation $\ln Y = \ln a - b \ln X$
Y = duration of post-embryonic development in hours; X = food concentration in $mgC.l^{-1}$;
df = degrees of freedom; F = variance ratio; P = level of significance

		COMPARISON OF SLOPES				
FOOD LEVEL $mgC.l^{-1}$	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
1.0	1	- 0.75±0.17	2,30	1.45	0.24	3 2 1
0.5	2	- 0.47±0.15				
0.25	3	- 0.37±0.17				
		COMPARISON OF ELEVATIONS				
$mgC.l^{-1}$	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
1.0	1	5.07±0.05	2,33	1.39	0.26	1 2 3
0.5	2	5.10±0.05				
0.25	3	5.13±0.05				

TABLE 5.8 Curvilinear regressions relating the duration of post-embryonic development to food concentration at various temperature for *Daphnia gessneri*, *Moina reticulata* and *Diaphanosoma sarsi*

Regression equation $\ln Y = \ln a - b \ln X$
Y = post-embryonic development in hours; X = food concentration in $mgC.l^{-1}$

TEMPERATURE °C	ln a	b	df	F	P
Daphnia gessneri					
22	5.14	- 0.087	1,18	8.63	0.008
27	5.07	- 0.060	1,16	6.89	0.018
32	4.89	- 0.160	1,18	50.70	0.000
Moina reticulata					
27	43.38	- 8.05	1,18	3.22	0.14
Diaphanosoma sarsi					
27	4.20	- 0.21	1,17	45.1	0.000

TABLE 5.9 Covariance analysis of the regressions comparing the duration of post-embryonic development on food concentration at different temperature for Daphnia gessneri. The regression coefficient were comoared by the SS-STP test and the difference between elevations by the S-N-K test. Regression coefficients and means underlined are not significantly different at P = 0.05

Regression equation $\ln Y = \ln a - b \ln X$
Y = duration of post-embryonic development in hours; X = temperature in ^{o}C
df = degrees of freedom; F = variance ratio; P = level of significance

		COMPARISON OF SLOPES				
TEMPERATURE(^{o}C)	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
22	1	- 0.087±0.02	2,52	4.76	0.012	3 1 2
27	2	- 0.060±0.02				
32	3	- 0.168±0.02				
		COMPARISON OF ELEVATIONS				
		ADJUSTED MEAN±SE	df	F	P	S-N-K
22	1	5.28±0.08	1,35	9.18	0.005	1 2
27	2	5.15±0.08				
22	1	5.27±0.094	1,38	9.94	0.003	1 2
32	3	5.14±0.094				

TABLE 5.10 Parameters of the multiple regressions relating the effect of food concentration and temperature on the duration of post-embryonic development of Daphnia gessneri.

Regression equation: $1/D_j = a - b.\ 1/T + \ln F$
D_j = juvenile duration in hours; T = temperature in ^oC; F = food concentration in $mgC.l^{-1}$
df = degress of freedom; F = variance ratio; P = level of significance.

Daphnia gessneri

a	b	c	df	F	P
0.0087	- 0.0611	0.00054	2,55	24.37	0.001
Due to food concentration				36.39	0.001
Due to temperature				12.31	0.001

CHAPTER 6

The effect of food concentration and temperature on reproduction

The onset of reproduction in the life cycle occurs in the primiparous female, which is the first developmental stage in the life cycle at which assimilated food energy goes into reproduction. The primiparous female can be defined by her age, by her size and / or by her developmental stage or instar.

The number of eggs produced by Daphnia is known to be influenced by a variety of factors, such as the age and size of the mother, available food and temperature (Green,1956). It is our purpose here to explore the influence of various combinations of temperature and food concentration on reproductive characteristics of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi under controlled laboratory conditions.

6.1 Food threshold for reproduction

Fecundity was defined as the total number of eggs per female in the first three broods. Four replicates were obtained in almost of all the food concentrations each at three temperatures (22, 27, 32°C) in Daphnia gessneri and at one temperature, 27° C in Diaphanosoma sarsi and Moina reticulata as set out in Table 6.1. This table also provides some information on juvenile mortality and the inability of animals to complete their life cycle to the third brood.

In the lowest experimental food concentrations (0.05 $mgC.l^{-1}$), the individual animals died and had to be replaced more frequently than in higher food concentration (0.5 and 0.25 $mgC.l^{-1}$).

In Daphnia gessneri, at 0.05 $mgC.l^{-1}$ and at 32°C all four animals reached reproductive stage but died during the second brood. At 27 °C and 0.1 $mgC.l^{-1}$, out of four replicates, only two Daphnia reached the reproductive stage; one produced two neonates and the

other only one young, and died in the following day with an empty brood pouch. At 22° C and 27°C with 0.5 mgC.l^{-1} all four animals produced three broods but at 32°C two animals out of four died after six days. At higher food concentration (1.0 and 0.5 mgC.l^{-1}) at all three temperatures the animals completed three successive broods, although it was noticeable that at 32°C new eggs started to appear in the ovary while the embryos were still developing. At this temperature mortality of adults occurred, during the process of ecdysis on several occasions. Another feature noted in Daphnia at 32° C and 1.0 mgC.l^{-1} was that a yellow-brown body colour developed, due to the presence of oil globules which may be easily confused with a developing ovary. Probably 32°C was too warm for this species and the optimum was between 22-27°C

In Diaphanosoma sarsi, which were reared only at 27° C all the animals managed to produce eggs in all three broods in the higher food concentrations but did not always managed to produce eggs in the 0.1 and 0.05 mgC.l^{-1} food level(Table 6.1). At 0.05mgC.l^{-1} one individual died before it reached the reproductive size and the others died before completing three broods.

Moina reticulata was also only reared at 27° C and all four replicate animals completed three successive broods in almost all food concentrations. The only exception was in the lowest food level, 0.03 mgC.l^{-1}, in which one juvenile died and the other three juveniles did manage to attain sexual maturity and hatch neonates, but these adults died before reaching the second brood. Moina reticulata, always managed to produce eggs; an empty brood was never observed (Table 6.1).

The results in Table 6.1 suggest that there is a threshold food concentration for reproduction in Daphnia gessneri rather below 0.05 mgC.l^{-1} that this is the same threshold food concentration for all three temperatures. In Diaphanosoma sarsi, the threshold food concentration for reproduction, at 27° C was approximately at 0.05 mgC.l^{-1} but, for Moina reticulata probably also below 0.05 mgC.l^{-1} since at 0.03 mgC.l^{-1} 3/4 of the animals did reproduce but they did not reach the third brood. Thus this species is able to reproduce at

very low food conditions and lower than Daphnia gessneri and Diaphanosoma and would probably have an advantage over the other two in conditions of food shortage, at least at 27°C. In all three species, the fecundity generally increased with increasing food concentration. In Daphnia gessneri at 27 and 32°C there was litlle difference in fecundity at 0.5 and 1.0 mgC.l^{-1} but at 22° C the fecundity was higher at 1.0 that at 0.5 mgC.l^{-1} . In Moina reticulata, fecundity was actually lower at 1.0 than that at 0.5 MgC.l^{-1} suggesting that the optimum food level had been surpassed at 1.0 mgC.l^{-1}.

6.2 Fecundity and temperature

Since only Daphnia gessneri was reared at three temperatures, this is the only species in which the influence of temperature upon fecundity can be examined. In general, the number of eggs produced per female declined as temperature increased for any one food concentration. This result is illustrated in Figure 6.1(a-f) which shows relationships that appear linear. Linear regressions of fecundity on temperature for each experimental food level were calculated and are given in Table 6.2. These regressions were statistically significant ($P<0.05$) for the three highest food levels (1.0,0.5 and 0.25 mgC.l^{-1}) and for the lowest (0.05 mgC.l^{-1}) but were not statistically significant at the food level of 0.1 mgC.l^{-1}) as can be seen in Table 6.2. This food level was therefore omitted from covariance analysis, which is given in Table 6.3. The results indicated that the regressions for 1.0 and 0.5 mgC.l^{-1} were not significantly different in either their slopes or elevations. The regressions for 0.25 and 0.05 mgC.l^{-1} had lower slopes which were not significantly different from each other. Their elevations also were the lowest and were significantly different from the elevations of the higher food concentrations. Thus, with food concentrations of 0.5 and 1.0 mgC.l^{-1}, temperature had the same effect on fecundity (Figure 6.1(f). Below these food concentration the effect of temperature was

less marked and at 0.1 mgC.l^{-1} surprisingly temperature had no effect on fecundity.

6.3 Fecundity and food concentration

The relationship between fecundity, defined as the mean sum of eggs for three broods, per female and food concentration at 22°C, 27°C and 32°C in Daphnia gessneri, and 27°C in Diaphanosoma sarsi and Moina reticulata is illustrated in Figure 6.2(a-f). These figures show that the relatioship is curvilinear. It proved possible to fit a logarithmic expression (Y=a+lnX) to the empirical data and statistically significant logarithmic regressions were computed, the results for which are given in Table 6.4. The analysis of covariance of these, given in Table 6.5, indicates that, in Daphnia gessneri, the regressions coefficient for 22, 27 and 32°C are significantly different compared by SS-STP test. The regression for 32°C has a lower slope and for 22°C the regression has a higher slope indicating in this temperature a rapid increase in fecundity as food concentration increases. The effect of food on fecundity is moderated by the environmental temperature, visually illustrated in figure 6.2(a)(b)(c).

For Diaphanosoma sarsi and Moina reticulata the effect of food concentration on fecundity was determined at one temperature only (27°C). The curvilinear relationship between fecundity and food concentration at 27°C in Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata is illustrated in Figure 6.2(f). The analysis of covariance of the regressions, given in Table 6.6, indicates that the regressions coefficients compared by SS-STP test for Daphnia gessneri and Moina reticulata are not significantly different from each other, but the regressions of the elevations compared by S-N-K test indicates different elevations. Moina reticulata has the higher elevation. The regression coefficient for Diaphanosoma sarsi shows a significant different slope. Visually, it is clear that, for all three species, total fecundity is strongly influenced by food level.(Figure 6.2(f)

A multiple regression analysis was attempted in order to examine the combined effects of temperature and food concentration upon fecundity of Daphnia gessneri; this is given in Table 6.7. The regression was significant with high values of the variance ratio F, confirming that both temperature and food concentration effect fecundity and the effects can be quantified. An analysis of the components of the variance shows that the effect of food concentration on fecundity was six time greater than that of temperature. The magnitude of the variance ratio F was 67.02 (P=0.005) due to food concentration and 10.68 (P=0.0025) due to temperature.

In Diaphanosoma sarsi at 27°C, the average brood size was lowest at the lower food concentration (0.1, 0.05 $mgC.l^{-1}$). Animals raised in food concentrations of 1.0, 0.5 and 0.25 $mgC.l^{-1}$) showed the highest fecundity. In Moina reticulata at the same temperature, the number of eggs increased up to 0.5 $mgC.l^{-1}$ and then declined slightly in 1.0 $mgC.l^{-1}$ as can be seen in Table 6.1. This table also shows that Diaphanosoma sarsi has the lower fecundity compared with the other two species.

6.4 The primiparous female: Fecundity, size and age

Table 6.8 and Figure 6.3 illustrate for the three species of Cladocera studied the mean number of eggs per brood carried by the first reproductive female (primipara) for each experimental combination of temperature and food concentration. In the food levels of 0.05 and 0.1 $mgC.l^{-1}$, there is a tendency for the brood size to be constantly high in all three temperatures for Daphnia gessneri and at 27°C for Diaphanosoma sarsi and Moina reticulata. At 22°C, the fecundity of Daphnia gessneri increases with food concentration and flattens out at about 7 eggs per brood at 0.5 and 1.0 $mgC.l^{-1}$. At 27°C and 32°C the plateau at 4-5 eggs per brood is attained both at a lower fecundity level and starts at the lower food concentration of 0.25 $mgC.l^{-1}$.

Figure 6.3(b) illustrates at 27°C that Moina reticulata and Daphnia gessneri increased fecundity with the increase in food concentration while for Diaphanosoma sarsi the effect on fecundity when food level increased seems to be very little.

It can be seen in Table 6.9 that, in general, it took longer for the females to reach first reproduction as the availability of food declined and this was true for all three species. The age at which first reproduction occurred in Daphnia gessneri was prolonged from 4.0-5.5 days at 1.0 $mgC.l^{-1}$ to 7.7-8.1 days at 0.05 $mgC.l^{-1}$ at all temperatures; that is appears to be independent of temperature. The difference in the primipara age of Diaphanosoma sarsi and Moina reticulata at 27°C was only two days between high and low food levels. These two species were small compared with Daphnia gessneri (Table 6.10. These results suggest that daily observation is not sufficient for following the life cycles of small tropical Cladocera, particularly at high temperatures as was done here.

The mean size reached by the primiparous females of Daphnia gessneri, Diaphanosoma sarsi, and Moina reticulata, under the various experimental conditions are given in Table 6.10. The average body length of primipara of Daphnia gessneri did not change greatly with temperature at any one food concentration but, at 22°C and 27°C, showed some decrease in length as food became less available. The decline in size of the primipara when grown for her whole life in low food concentration was much more pronounced in Daphnia gessneri than in Diaphanosoma sarsi and Moina reticulata at the same temperature, probably again because of their small body size. The decrease in length is more difficult to measure, especially with live animals.

An attempt to assess the relative importance of temperature and food concentration as influences on the size of the Daphnia gessneri primipara by multiple regression analysis is presented in Table 6.11. An analysis of variance associated with the regression shows that a larger variance ratio (F= 9.95) arises from food concentration than from temperature (F= 2.88). This indicates that food concentration

influenced the size of the primiparous female to a greater extent than temperature.

Three reproductive parameters were measured during these experiments: size of primiparous female, her fecundity and her age. To assess the relative importance of the influence of temperature and food concentration upon these and also the interaction between them, a partial multiple regression analysis was performed. Table 6.12 shows the resulting simple correlation coefficients for all combinations of variables for Daphnia gessneri. Temperature shows a significant correlation only with size of primipara. On the other hand food concentration, which is strongly and positively correlated with fecundity and body size has a significant negative effect on the age of the primipara of Daphnia gessneri, but there is a correlative link between food concentration and primipara body size. Fecundity has a positive correlation with length of primipara but a negative one with age; length too is negatively correlated with age. So, the more food there is the younger and larger the primipara is and the more eggs she can carry. Food concentration, fecundity and the primipara length are closely inter-correlated.

6.5 Fecundity and body size

The importance of size in relation to various biological processes is becoming increasingly recognized. Increased egg production with an increase in body size within a species has been found (Green 1956). This section attempts to analyse the relations between size and fecundity in three cladoceran species grown under experimental conditions of different combinations of food concentration and temperature. The species studied in this investigation were: Daphnia gessneri at three temperatures (22°, 27° and 32°C); Moina reticulata and Diaphanosoma sarsi, both at 27°C.

The number of eggs produced per female was both quite variable and depended mainly upon food concentration. Figures 6.4-6.9 illustrated how the number of eggs per female in the first three

broods vary with female size in all three species in relation to temperature and food concentration. The reproductive response of all the species to the changes in food concentration at one temperature was similar and characterized by a decrease in fecundity as food concentration decreases until the concentration of food falls below that of the threshold food concentration for reproduction. It was possible to quantify this relationship between fecundity and adult length at any one temperature-food concentration by means of simple linear regressions whose statistical significance could be tested and which are given in Table 6.13.

Table 6.13 and Figure 6.4 show that, in Daphnia gessneri at 22°C, significant relationships between fecundity and female body size were found for all tested food concentration, except for 0.05 $mgC.l^{-1}$. At 27°C, Figure 6.5 significant regressions were obtained for all food levels above 0.1 $mgC.l^{-1}$. At 0.1 $mgC.l^{-1}$, there is a tendency for the fecundity to increase with body size from 1 to 3-4 eggs per female but the variability was too high to obtain a significant relationship (P=0.065 Table 6.13). This food concentration seems to be near the threshold food concentration at this temperature since no reproduction was observed at 0.05 $mgC.l^{-1}$. The same table shows that results were more variable at 32°C than the other two temperature; significant relationship were obtained only in 1.0 and 0.1 $mgC.l^{-1}$ and not in 0.5, 0.25 and 0.05 $mgC.l^{-1}$. The main cause of this in 0.5 and 0.25 $mgC.l^{-1}$ can be seen in Figures 6.6. Fecundity was very variable for to narrow span of length and a small number of experimental results at this combination resulted in non-significance, despite the clear tendency, in Figure 6.6(b) for example, of increasing fecundity with body size. Data for a fourth brood might have retrieved this regressions. The food concentration of 0.05 $mgC.l^{-1}$ at 32°C was probably near the threshold for reproduction as the females did not manage to complete three broods so that the data are few. For the same reason a significant relationship was accepted at (P=0.10) for the regression of Daphnia gessneri at 22°C with 0.25 $mgC.l^{-1}$ (Figure 6.4(c).

The relationship between food and temperature is evident in Figure 6.7 which is a compilation of three temperatures and various

food concentrations, showing a general trend that a maximum fecundity occurred at 22°C in non-limiting food concentrations of 1.0 and 0.5 $mgC.l^{-1}$. On the other hand, the interaction between food and temperature results in a maximum body size reached by the females at the intermediate temperature of 27°C, in the three higher food level (1.0,0.5 and 0.25 $mgC.l^{-1}$, pooled), as is illustrated in figure 6.7.

In Moina reticulata, which was studied at 27°C only,(Figure 6.8) the size of female strongly influenced the level of fecundity, there being a significant linear relationship between number of eggs per female and adult carapace length in all food levels except 0.03 $mgC.l^{-1}$. The highest fecundity was reached at the food concentration of 0.5 $mgC.l^{-1}$ and 0.25 $mgC.l^{-1}$ as illustrated in Figure 6.8(b)(c). Despite a narrow life span Moina reticulata get significant regressions and very steep slopes compared with Daphnia gessneri. The values of (b) are given in Table 6.13. It is very clear that the threshold for reproduction lies between 0.05 and 0.03 $mgC.l^{-1}$

In Diaphanosoma sarsi at 27°C there were significant linear relationships at the higher food levels of 1.0, 0.5 and 0.25 $mgC.l^{-1}$ whereas the relationships were not significant at the lower food levels of 0.1 and 0.05 $mgC.l^{-1}$ (Table 6.13). A general trend suggest that the smaller reproductive size (0.80 mm) was also reached in the lowest food level(0.05 $mgC.l^{-1}$) as illustrated in Figure 6.9(e). The maximum fecundity was reached in the higher food concentration 1.0 $mgC.l^{-1}$. At this food level there is a tendency for the fecundity to increase with body length from 2 to 5 eggs per female. The increase in number of eggs as body size increases was observed to a lesser extent at 0.5 and 0.25 $mgC.l^{-1}$ and in these two food concentration the animals did not grow bigger compared with 1.0 $mgC.l^{-1}$(Figure 6.9(a).

Covariance analysis was used in order to compare the significant linear regressions of fecundity on body length under various combinations of food concentration and temperature. The results for covariance analysis in order to see whether differ or not are given in Table 6.14 for each species. Multiple comparison tests S-N-K (Student-Newman-Keuls) test and SS-STP (Sum of Squares Simultaneous Test

Procedure) were applied to detect possible differences between elevations and slopes of the curves, as explained in section 3.3.

In Daphnia gessneri at 22°C, the slopes of all the significant regressions differed between each other and the regressions for the high food levels (1.0 and 0.5 $mgC.l^{-1}$) were much higher or exhibiting a greater fecundity when compared to the slopes of the low food levels. At 27°C none of the regression coefficients (b) were significantly different, so that the slopes of the relationships can be considered to lie parallel and it is possible to test whether the regression elevations differ. Table 6.14 shows that none of the adjusted means of the regressions differed significantly between themselves. However, when the regressions for Daphnia gessneri at 32°C were compared these were significantly different but that for the higher food level (1.0$mgC.l^{-1}$) was much higher than that for the low food level (0.1 $mgC.l^{-1}$).

In Moina reticulata, at 27°C the coefficient regressions were not significantly differents except at 0.5 $mgC.l^{-1}$. Comparison between the elevations shows that those for the higher food levels (1.0 and 0.25 $mgC.l^{-1}$) were not significantly different from each other but were significantly different from those for the low food levels (0.1 and 0.05 $mgC.l^{-1}$). The results for this species, suggested clearly the influence of body size on fecundity despite her small size and short life span. The higher and steeper slopes obtained with 0.5 $mgC.l^{-1}$ was anomalous and its causes are unknown.

In Diaphanosoma sarsi, the regressions for 1.0 and 0.25 $mgC.l^{-1}$ were not significantly different in slopes or in elevations, so the relationships can be considered to lie parallel and we can conclude that there were an effect of body size on fecundity. The steepness of the slopes for 0.5 $mgC.l^{-1}$ again seems unusual.

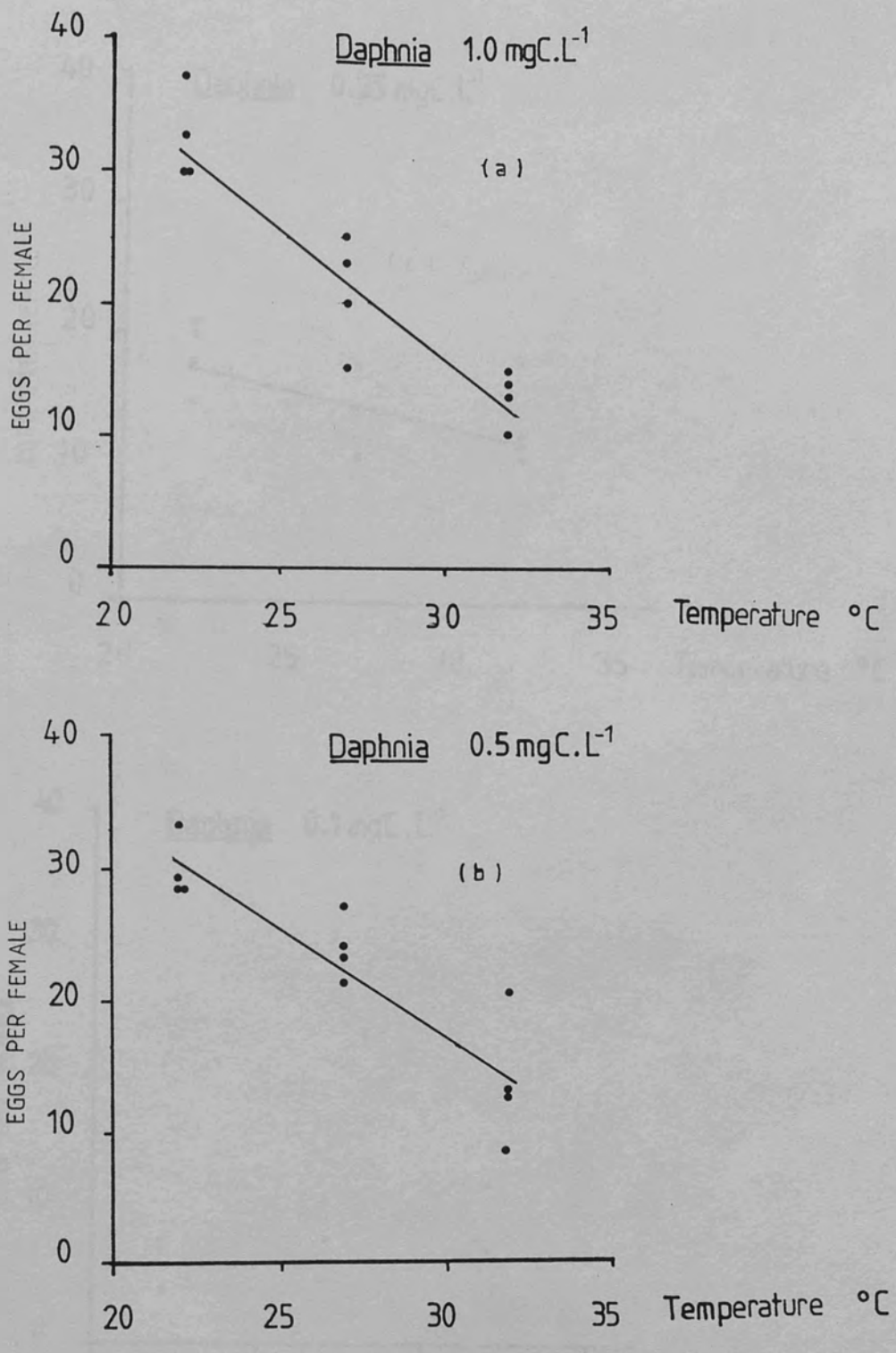
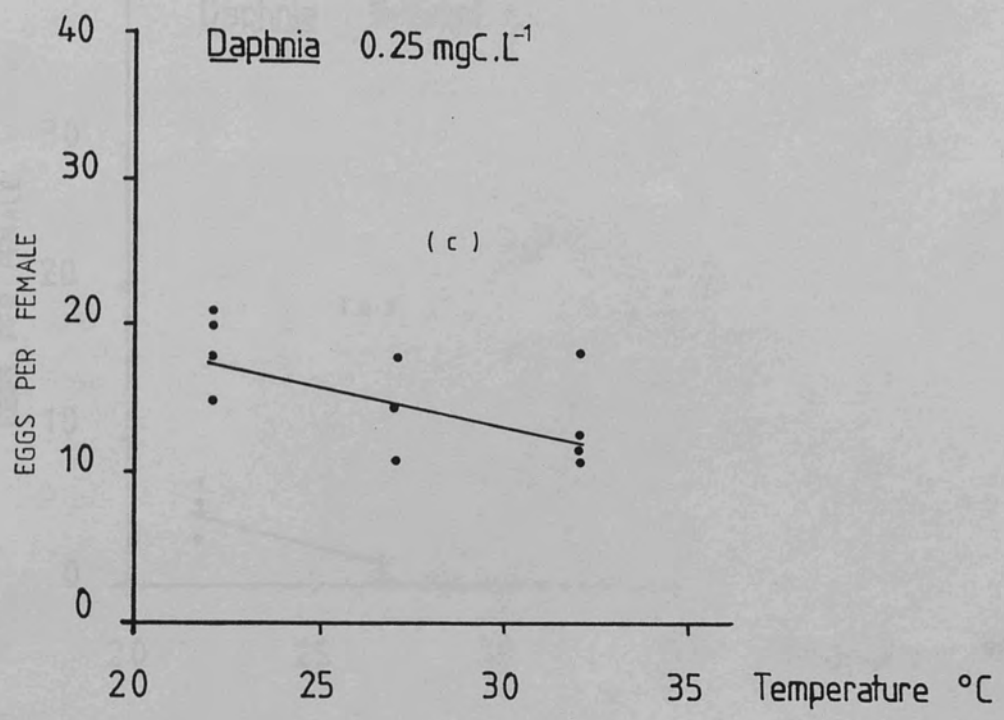


FIGURE 6.1 Linear relationships of fecundity on temperature for different food concentration in Daphnia gessneri Regression equation given in Table 6.2



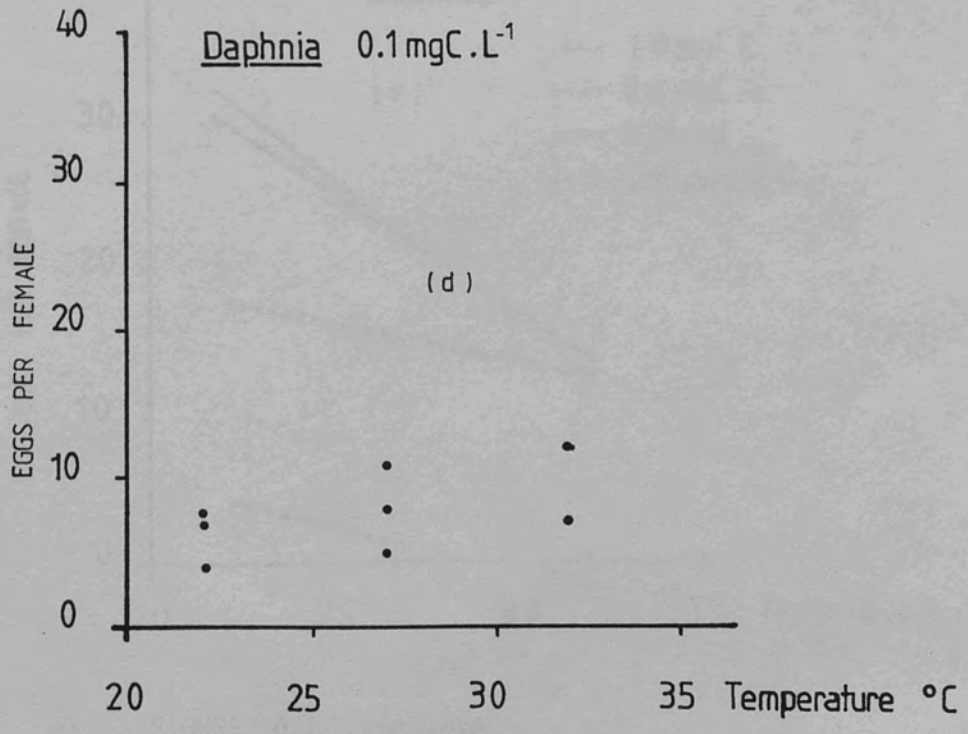
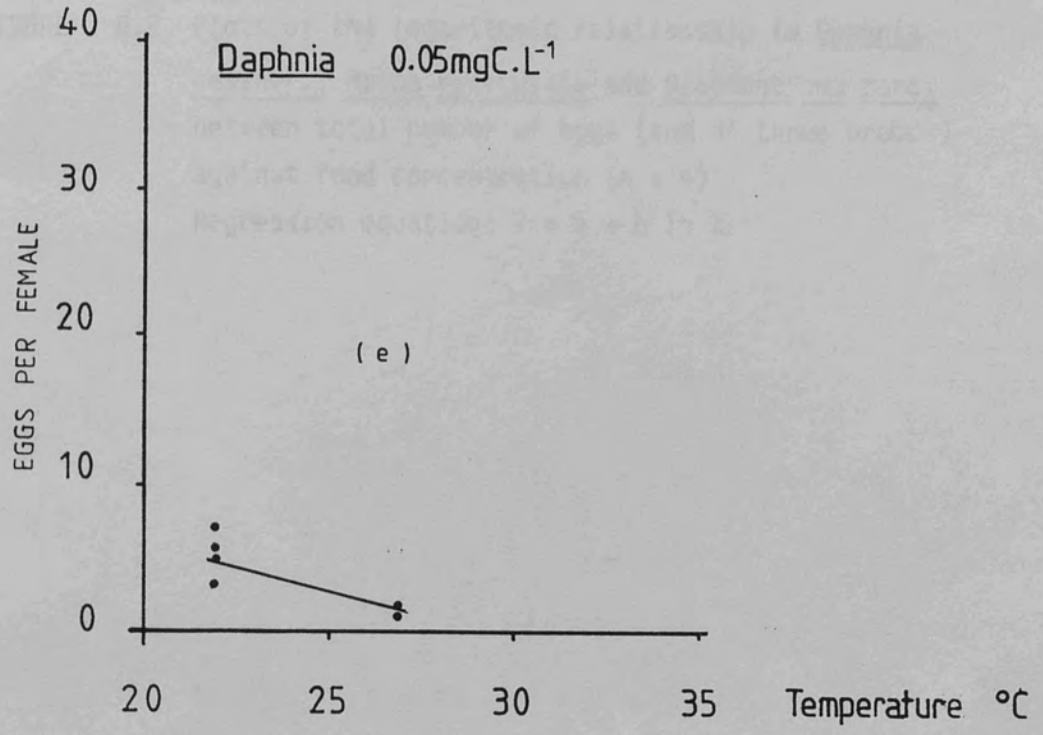


FIGURE 6.1 continued.



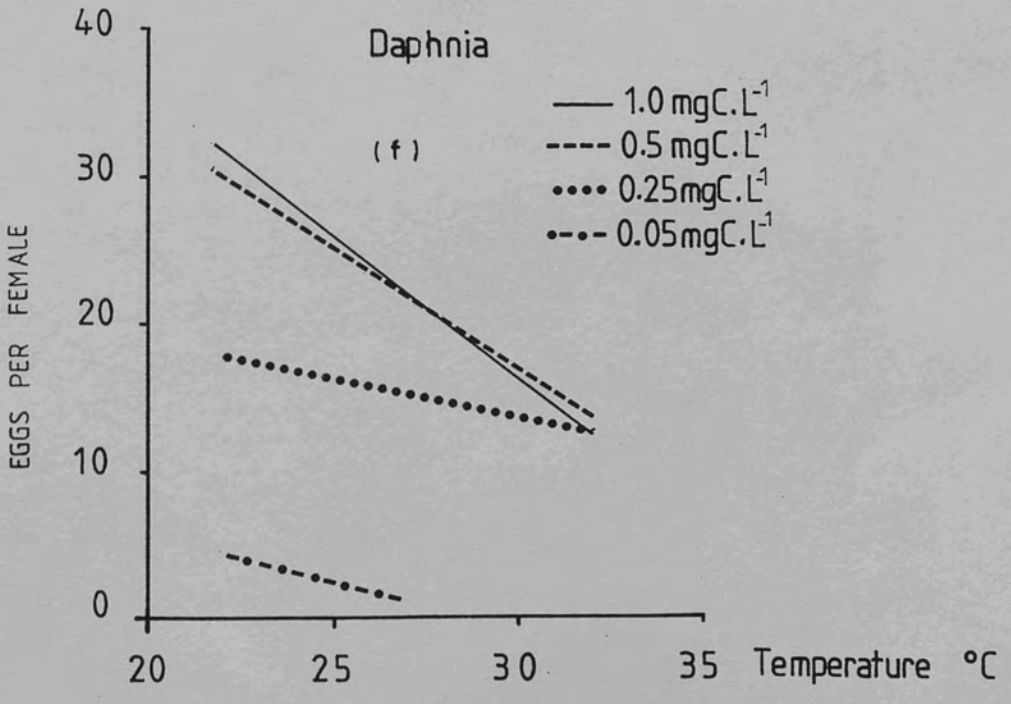


FIGURE 6.1 continued

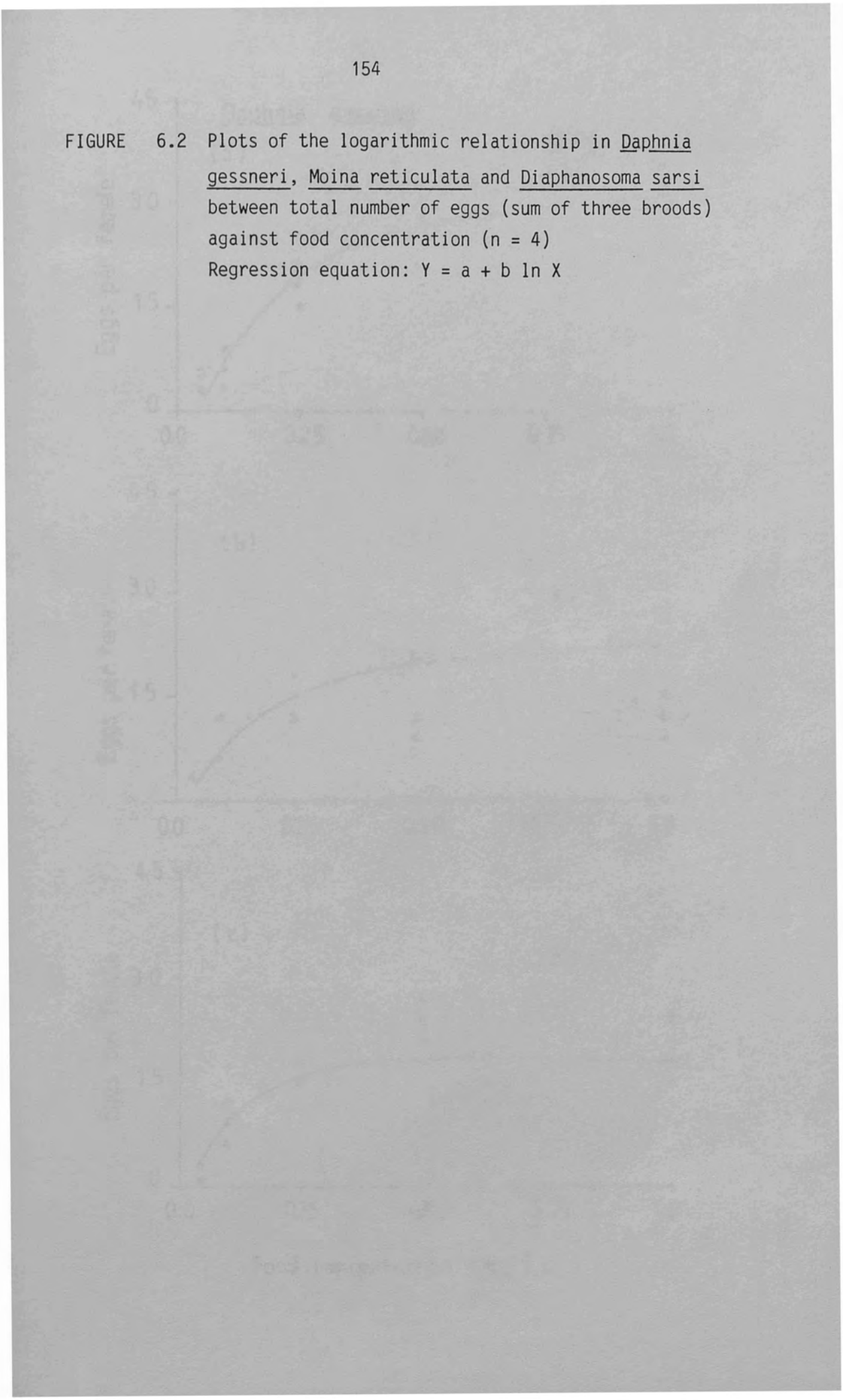
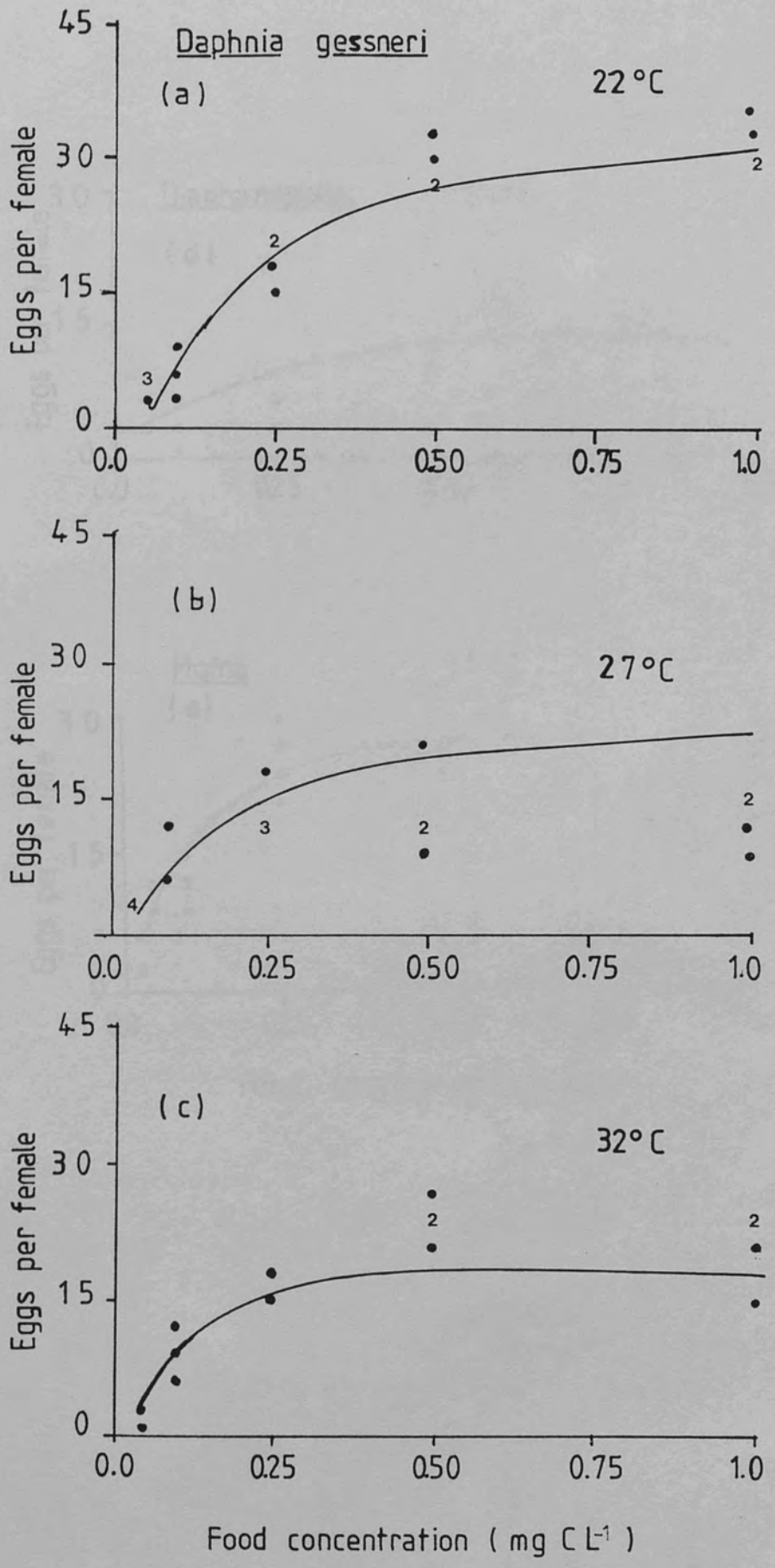
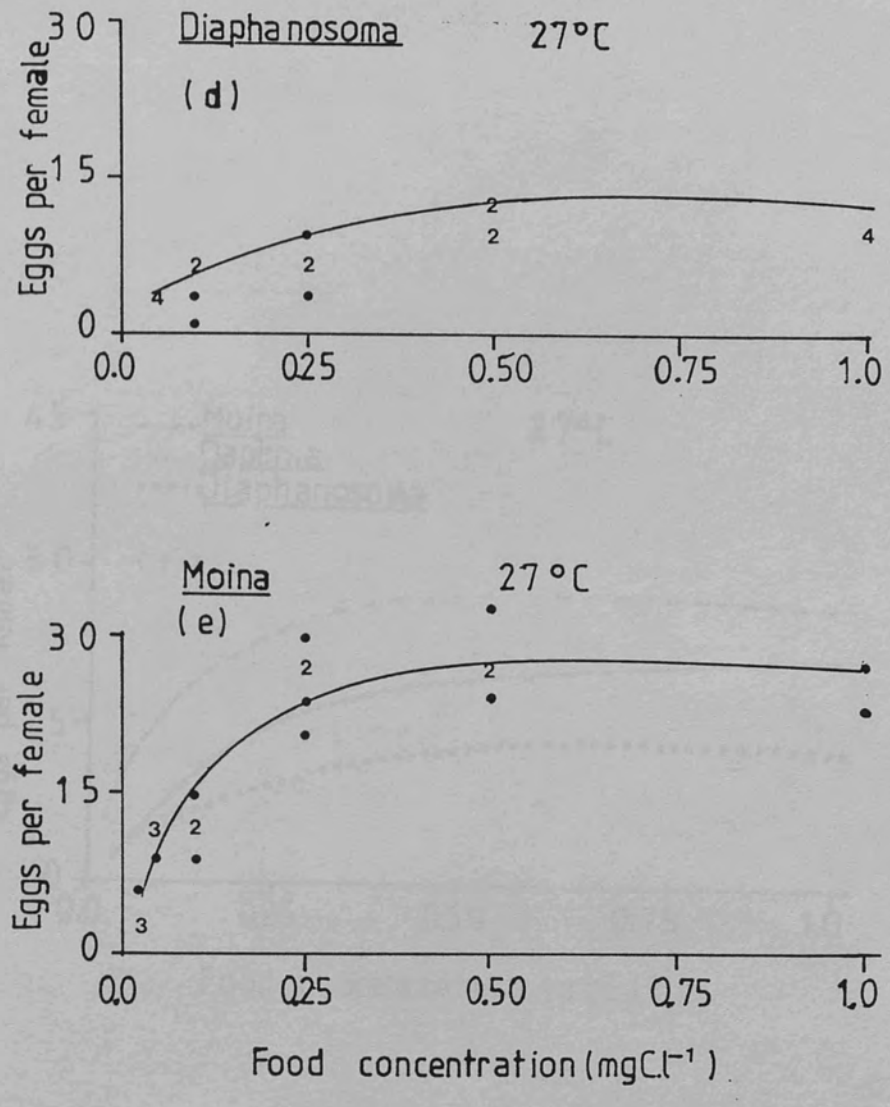
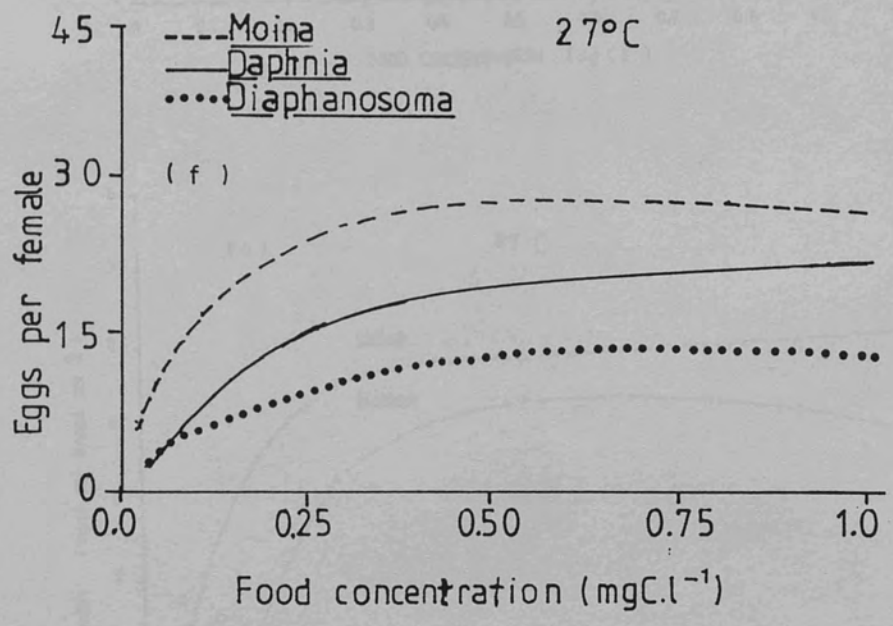


FIGURE 6.2 Plots of the logarithmic relationship in Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi between total number of eggs (sum of three broods) against food concentration (n = 4)
Regression equation: $Y = a + b \ln X$


Daphnia gessneri
(a)
22 °C
(b)
27 °C
(c)
32 °C
Eggs per female
45
30
15
0
0.0
0.25
0.50
0.75
1.0
Food concentration (mg C L-1)


Diaphanosoma
27°C
(d)
Eggs per female
30
15
0
0.0
0.25
0.50
0.75
1.0
Moina
27°C
(e)
Eggs per female
30
15
0
0.0
0.25
0.50
0.75
1.0
Food concentration (mgC.l⁻¹)


45
30
15
0
Eggs per female
----Moina
——Daphnia
••••Diaphanosoma
27°C
(f)
0.0
0.25
0.50
0.75
1.0
Food concentration (mgC.l⁻¹)

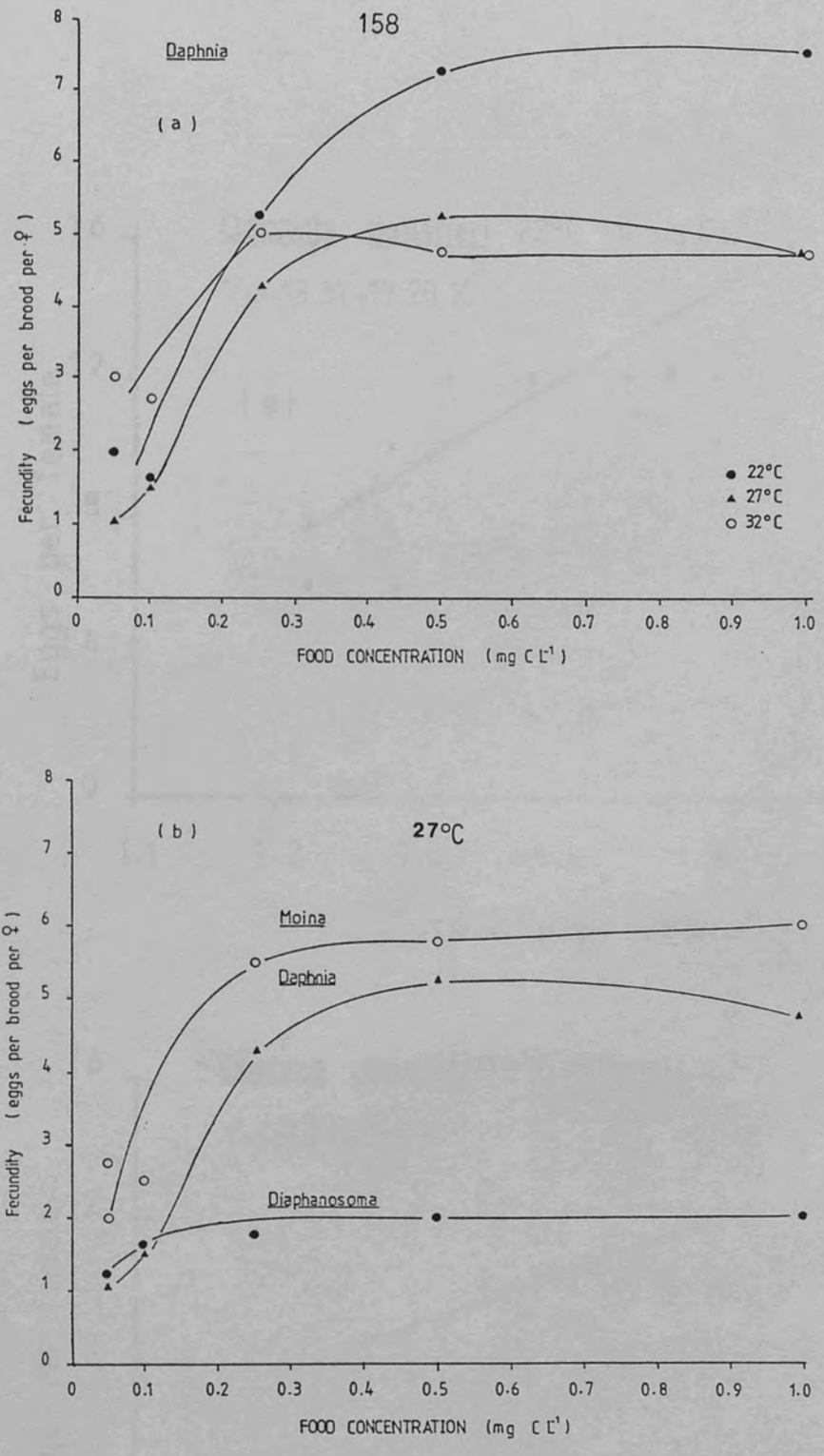
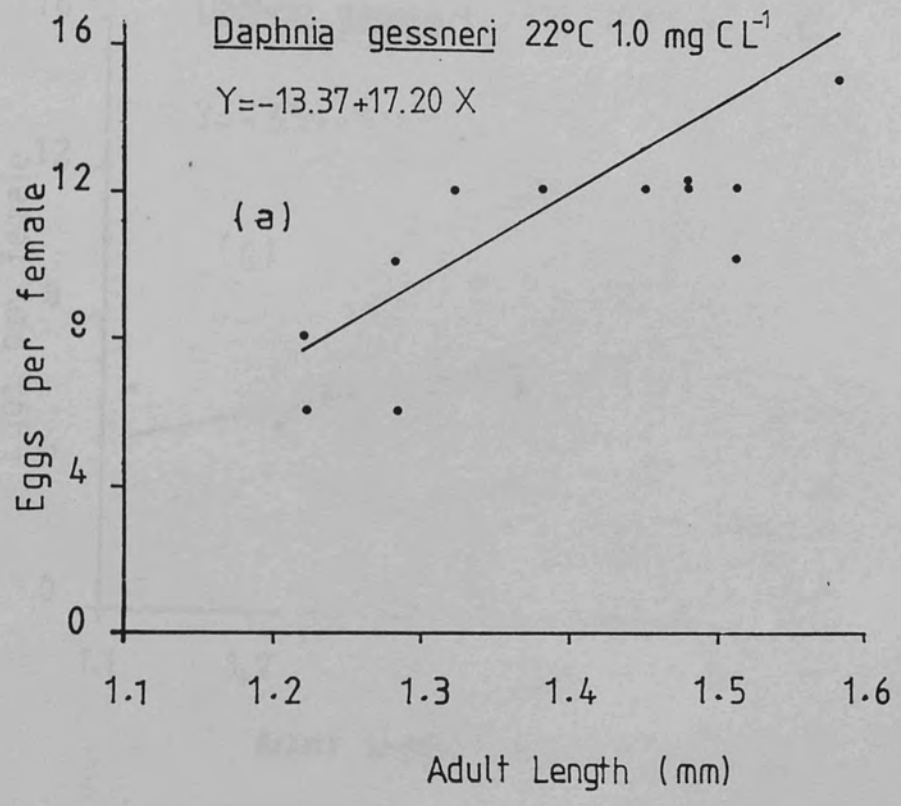


FIGURE 6.3 The influence of food concentration on fecundiy of of the primiparous female in three cladoceran (fitted by eye).



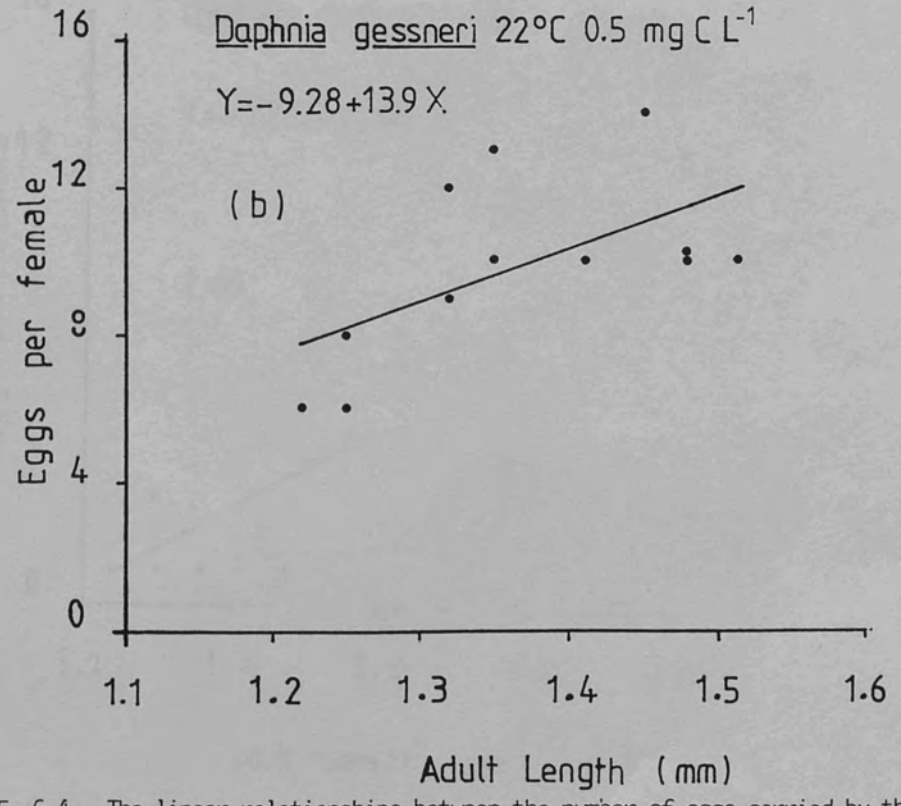
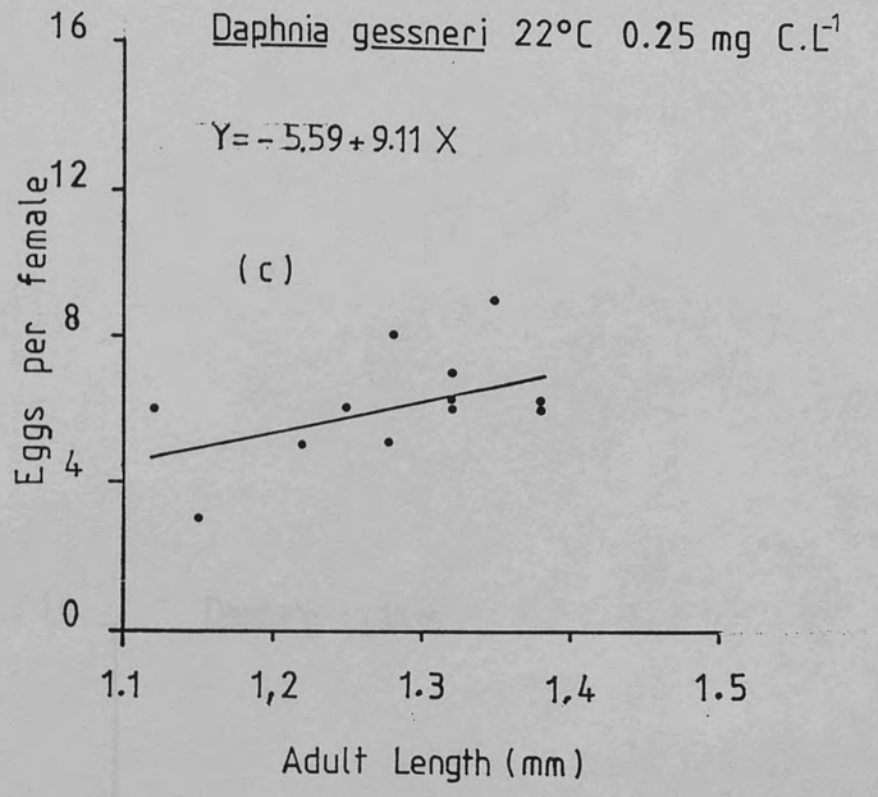


FIGURE 6.4 The linear relationships between the number of eggs carried by the female in relation to their body length at 22°C and various food levels.



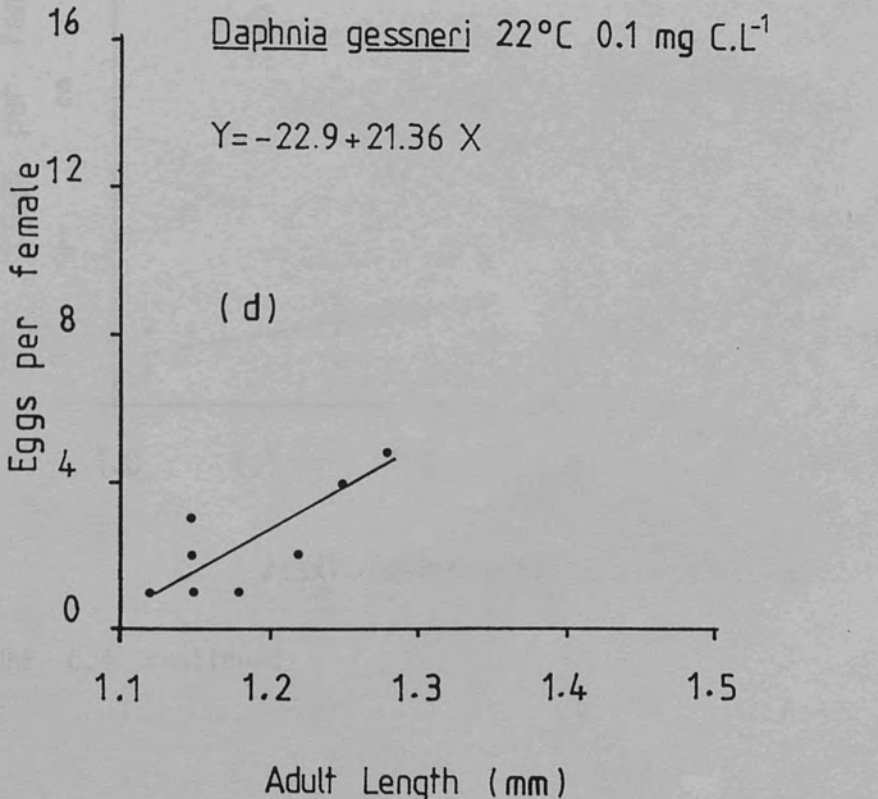


FIGURE 6.4 continued.

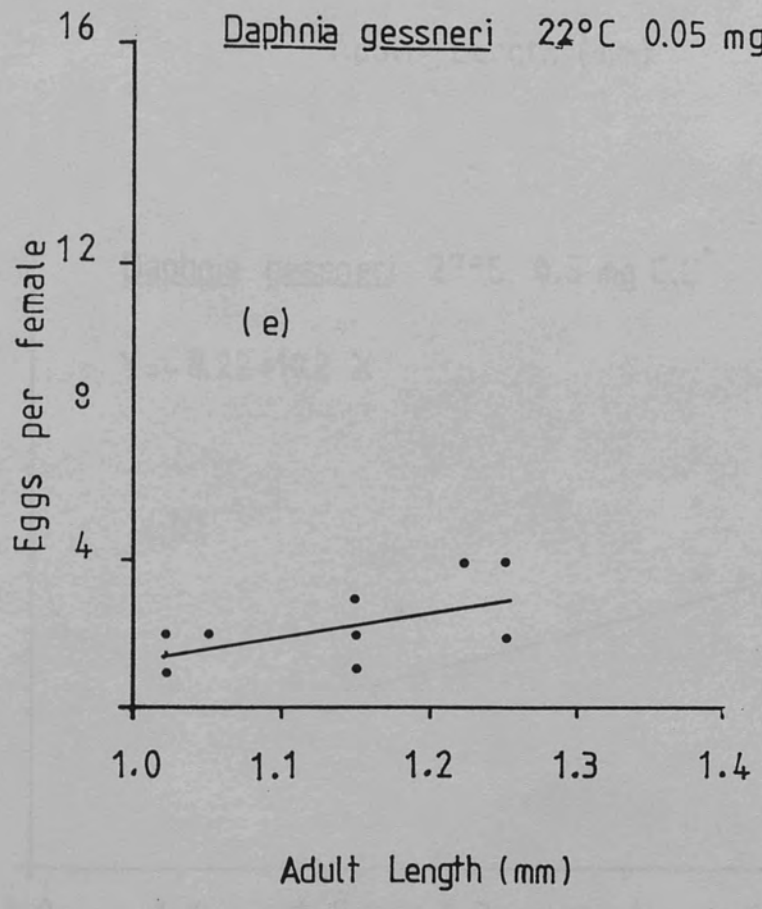
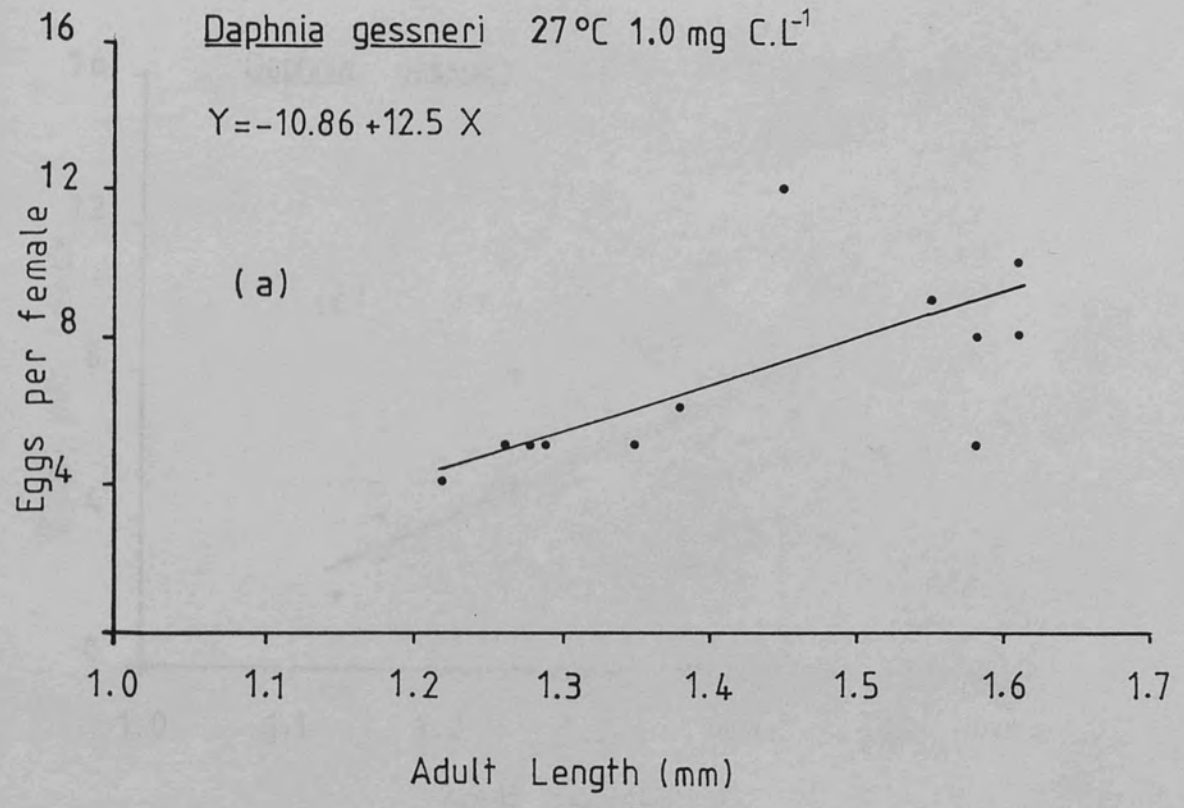


FIGURE 6.4 continued.



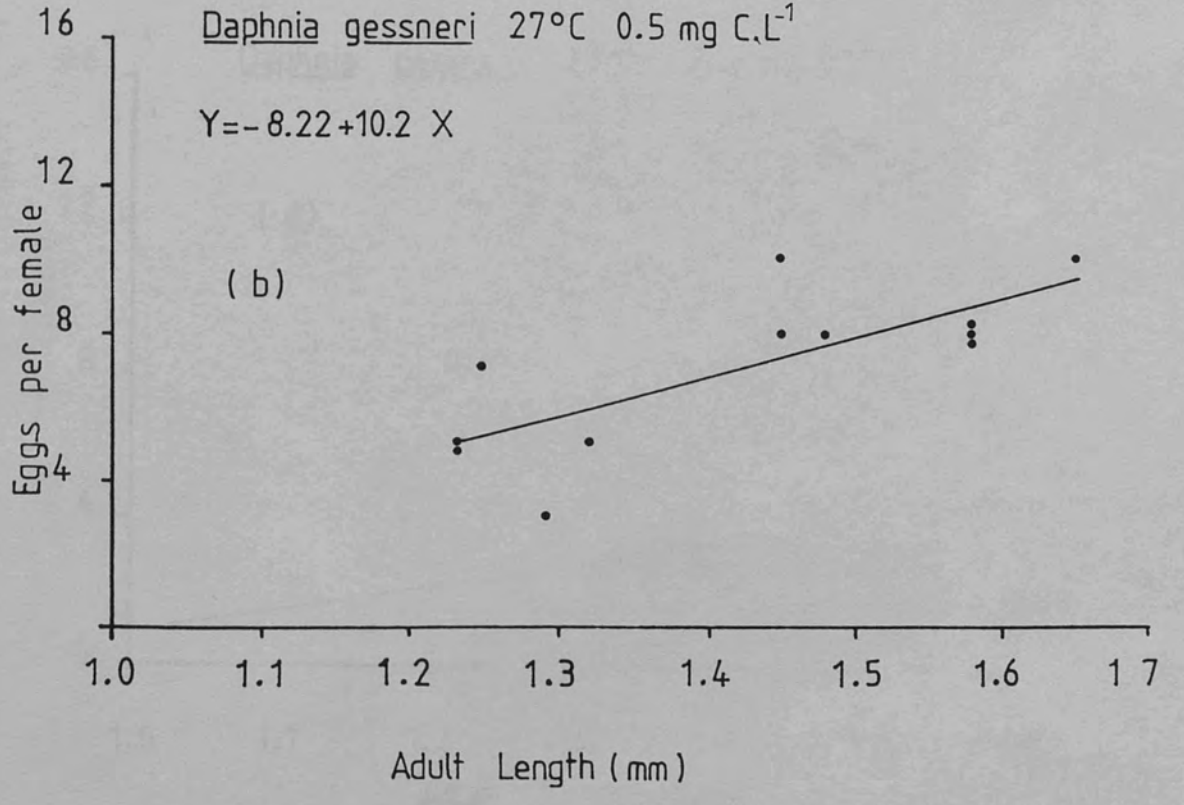
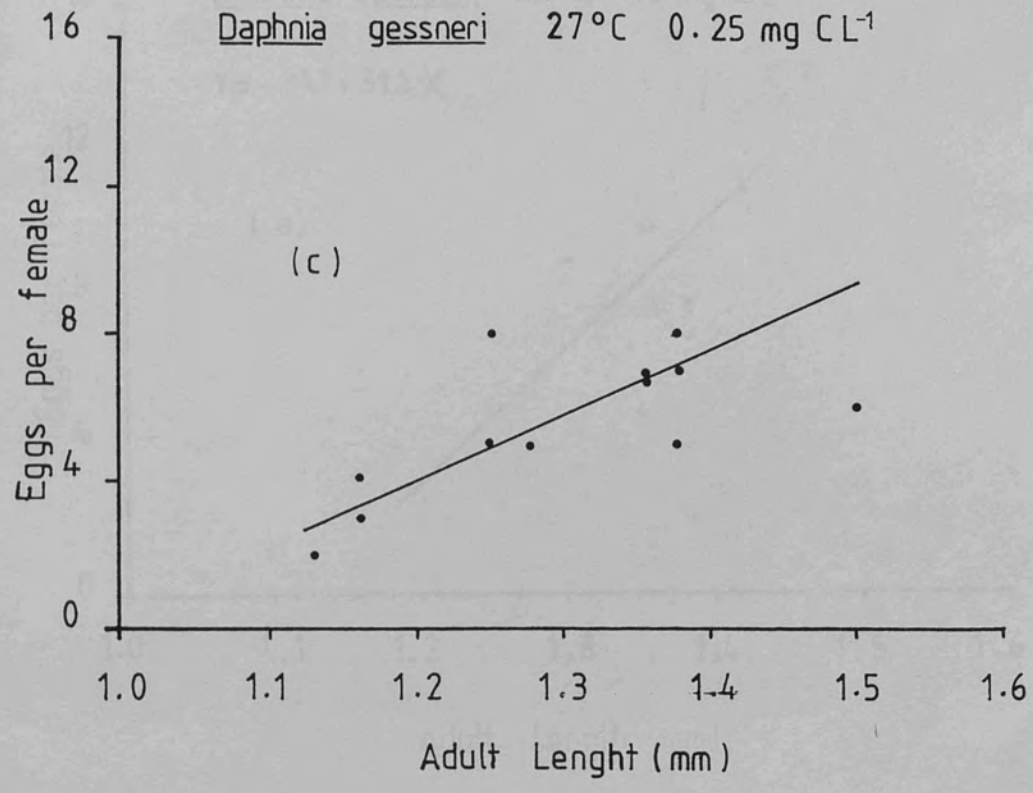


FIGURE 6.5 The linear relationships between the number of eggs carried by the female in relation to their body length at 27°C and various food levels.



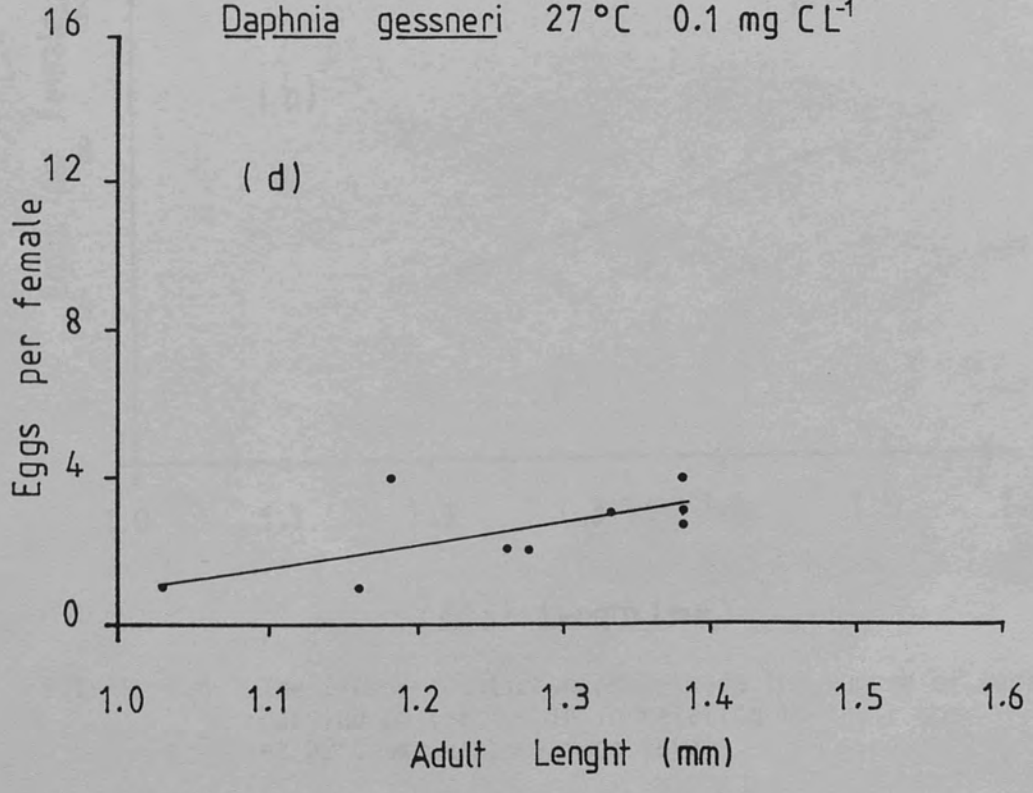


FIGURE 6.5 continued.

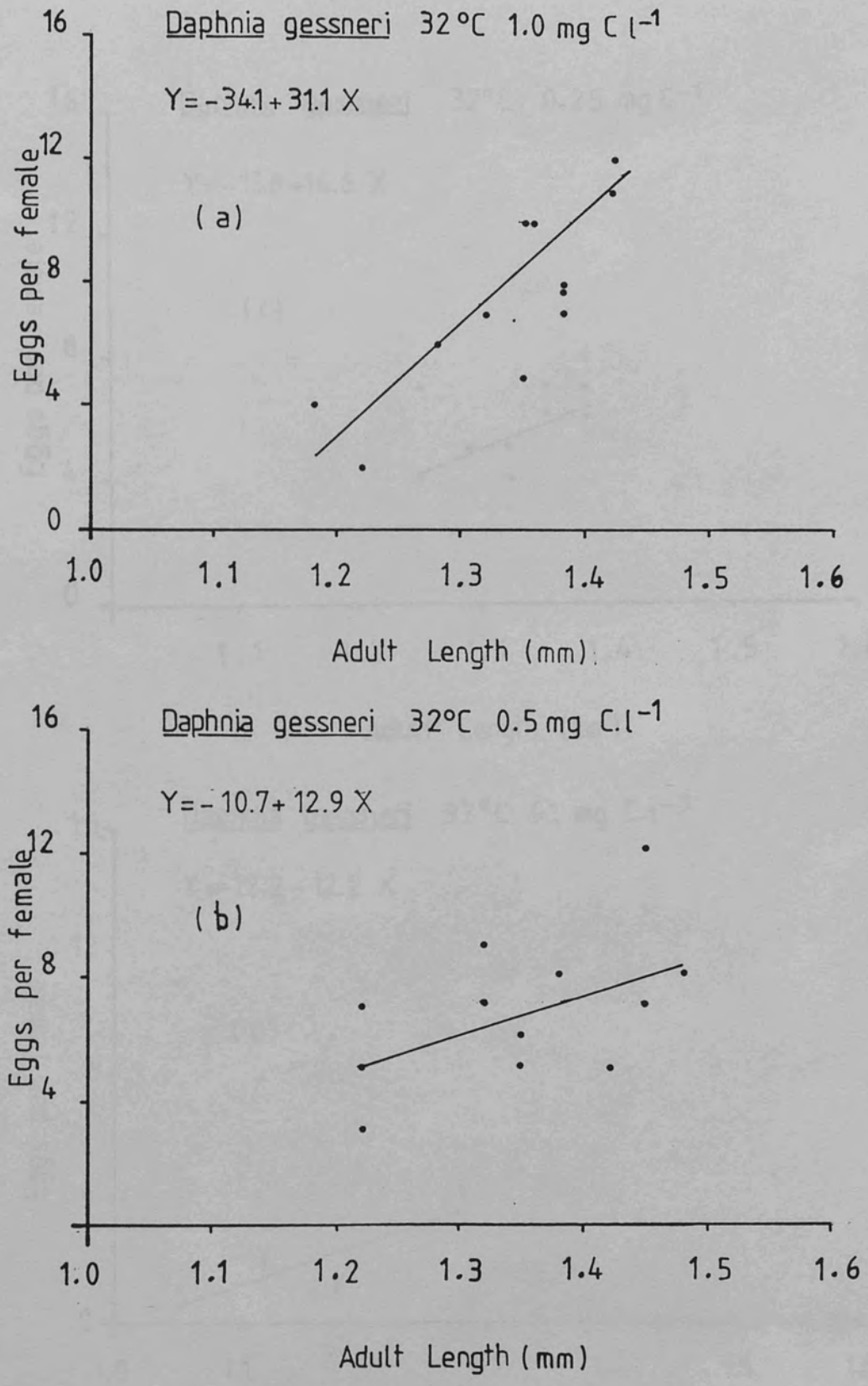
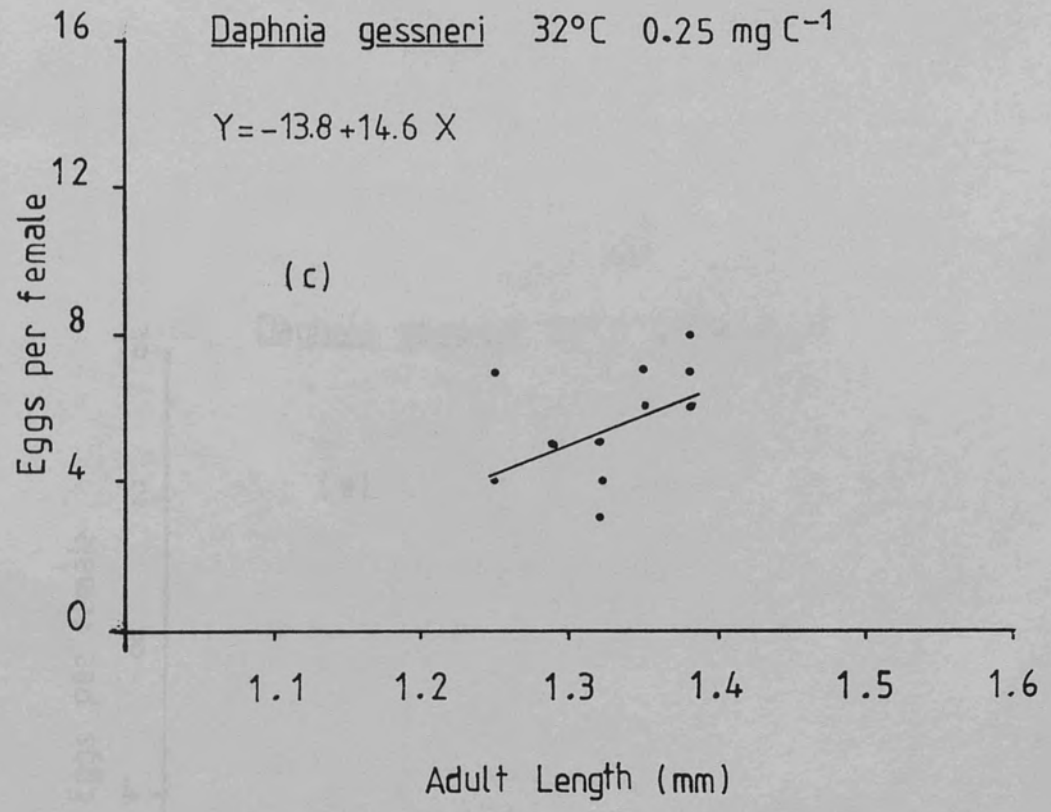


FIGURE 6.6 The linear relationshios between the number of eggs carried by the female in relation to their body at 32°C and various food levels.



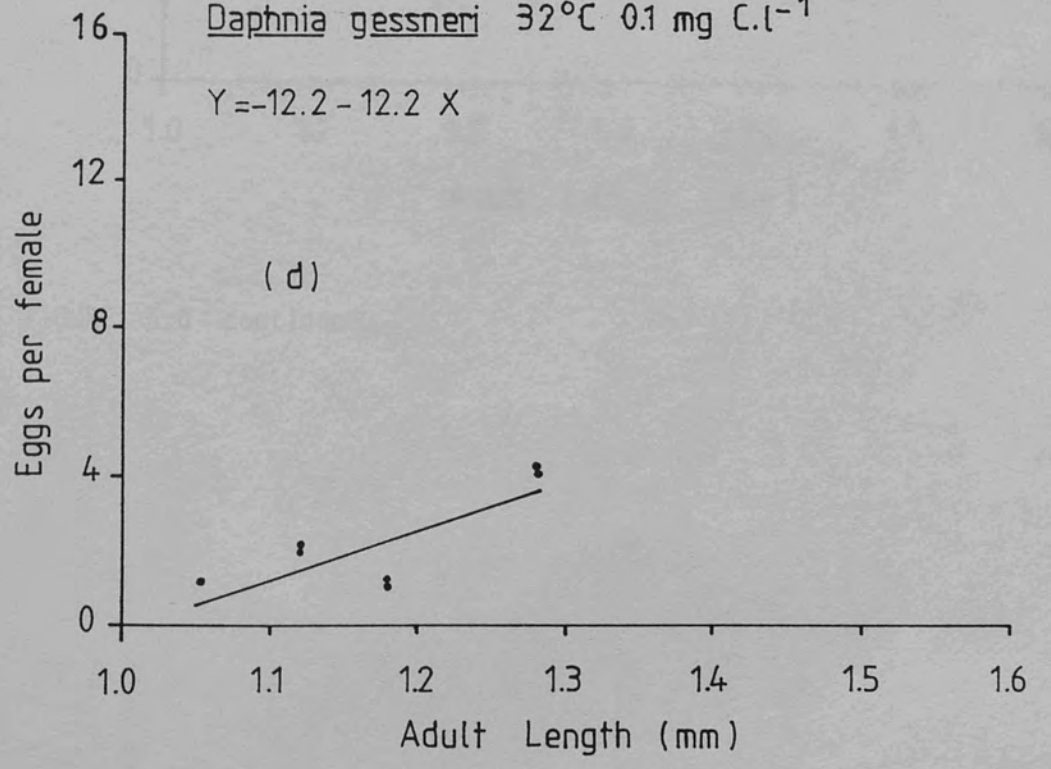


FIGURE 6.6 continued

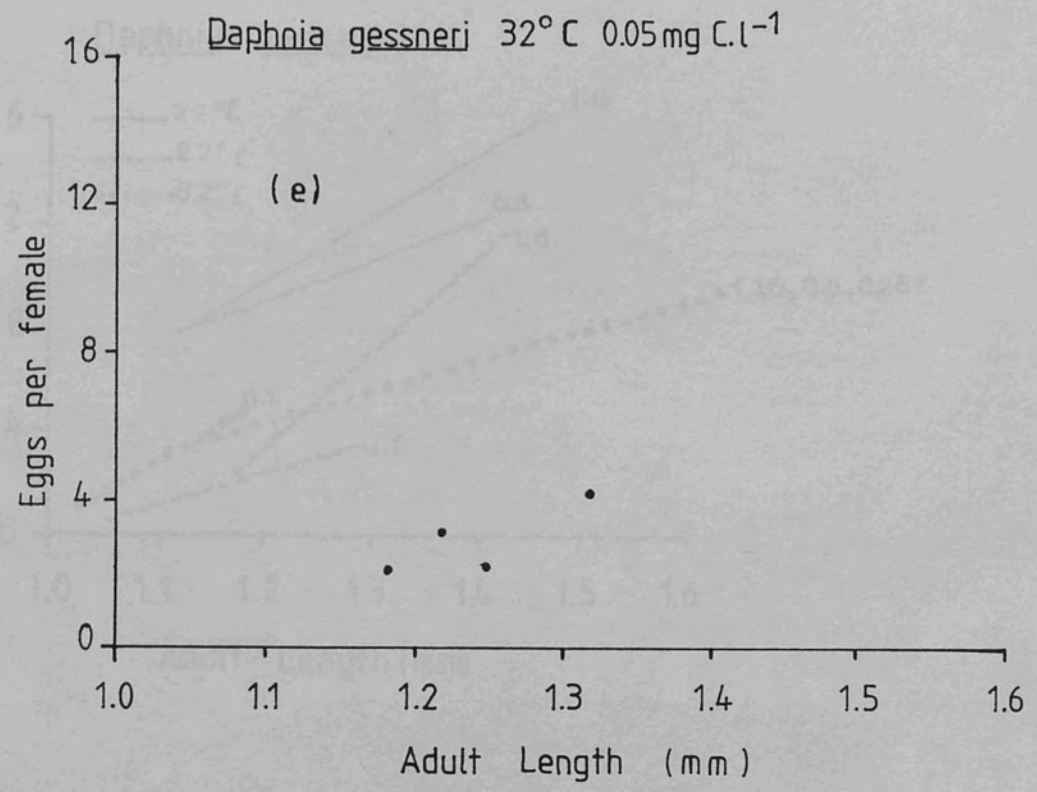


FIGURE 6.6 continued

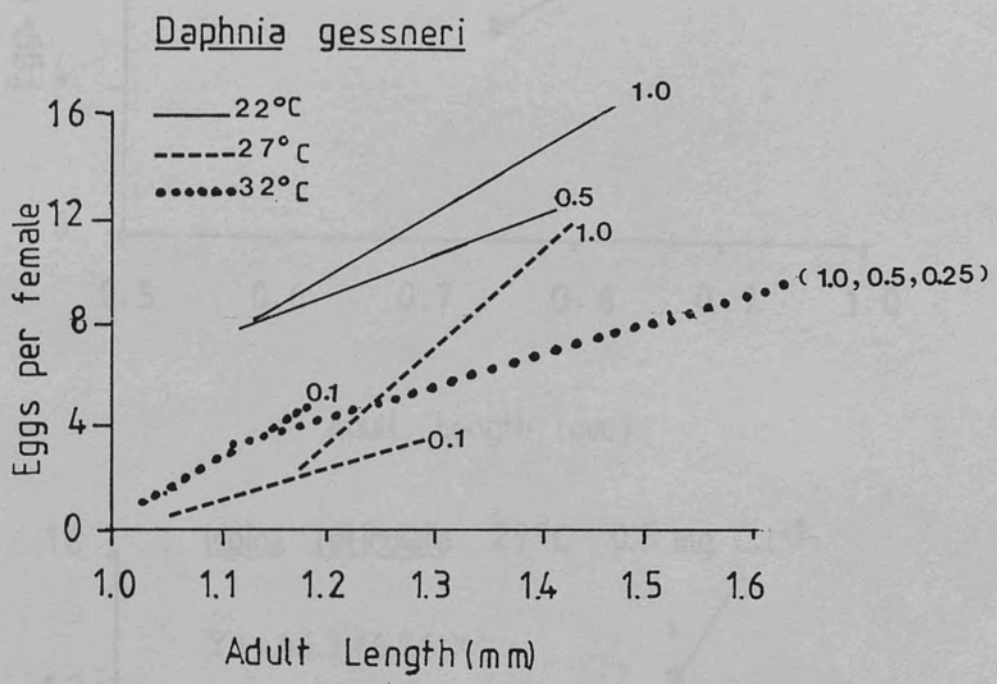
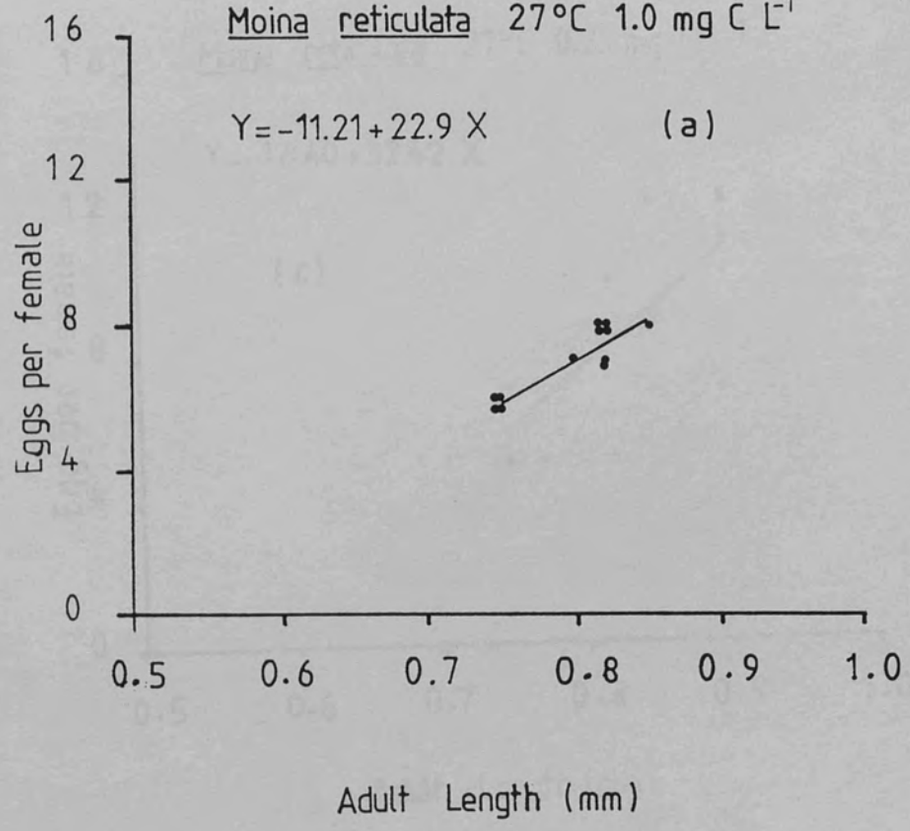


FIGURE 6.7 The significant linear relationships between the number of eggs carried by the females Daphnia gessneri in three broods in relation to their body length (Batch).



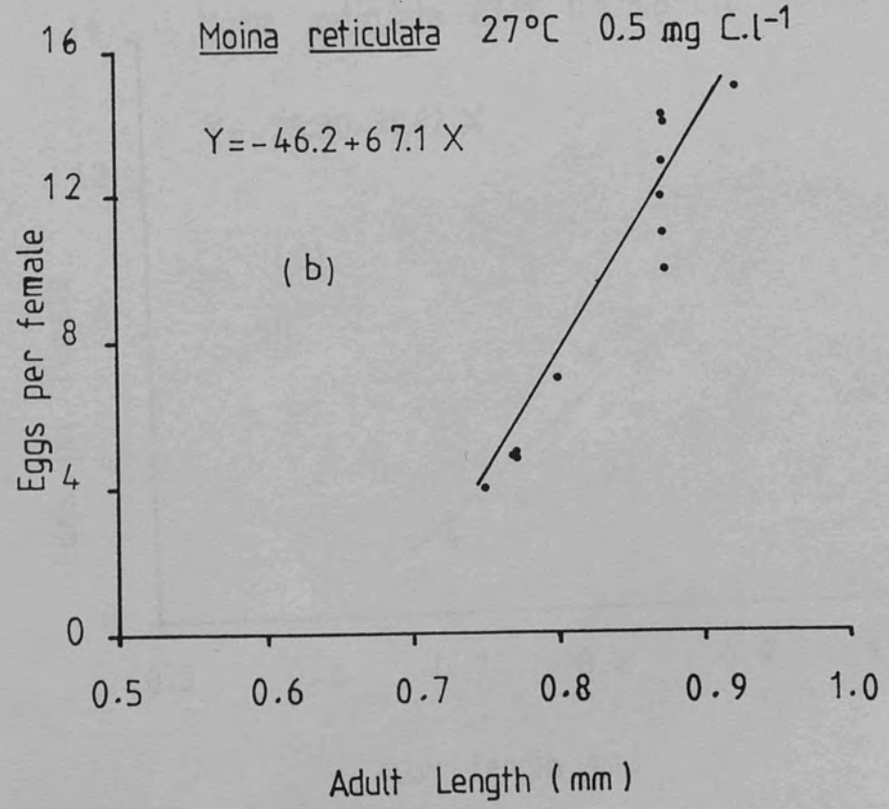
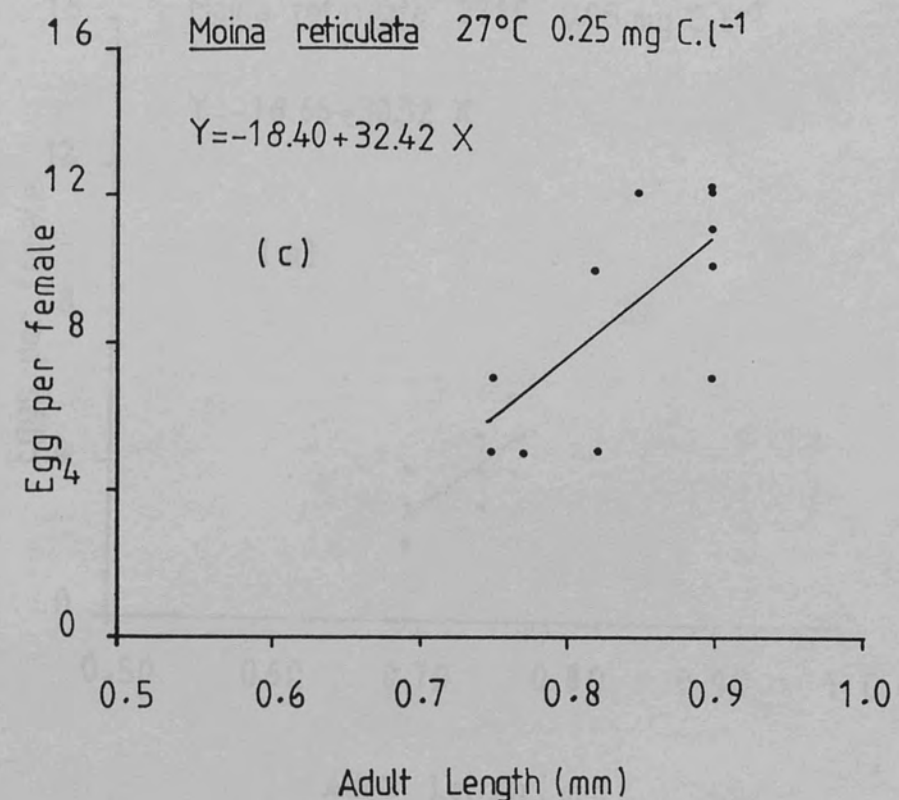


FIGURE 6.8 The linear relationships between the number of eggs carried by the female Moina reticulata, in relation to their body length at at 27°C and various food levels.



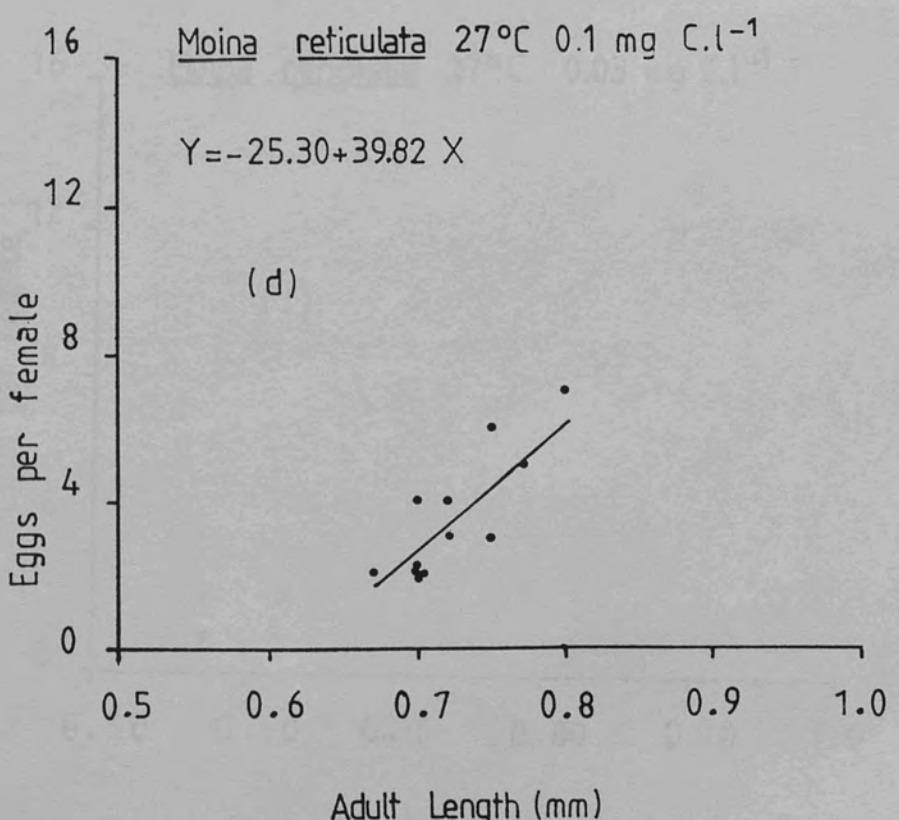
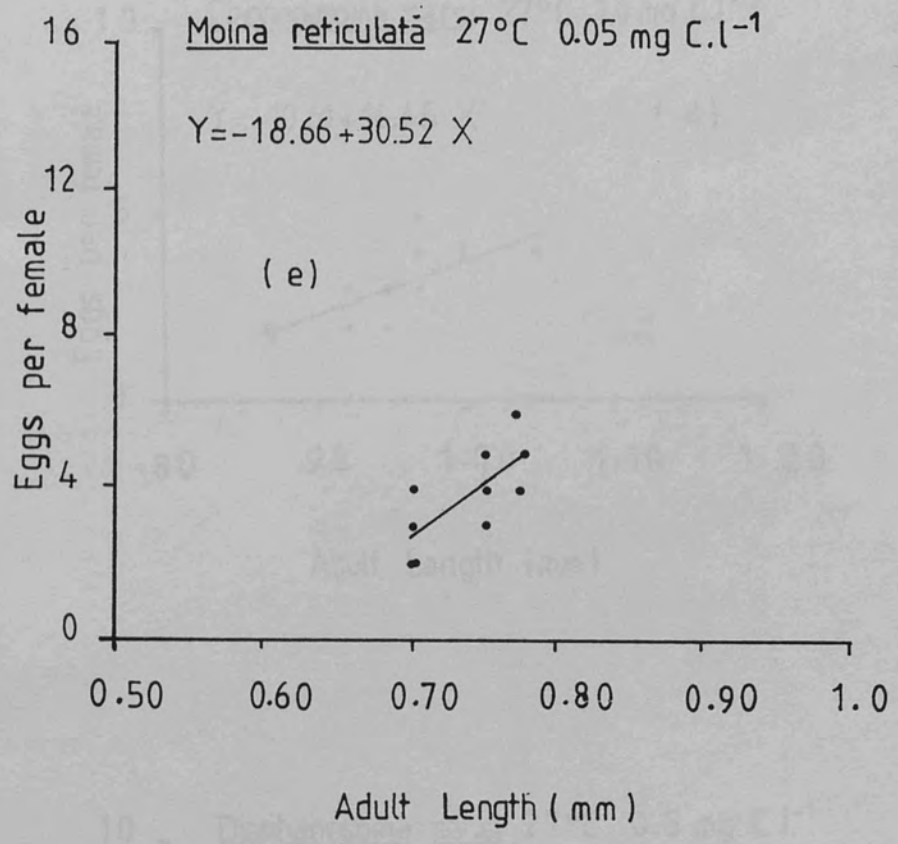


FIGURE 6.8 continued.



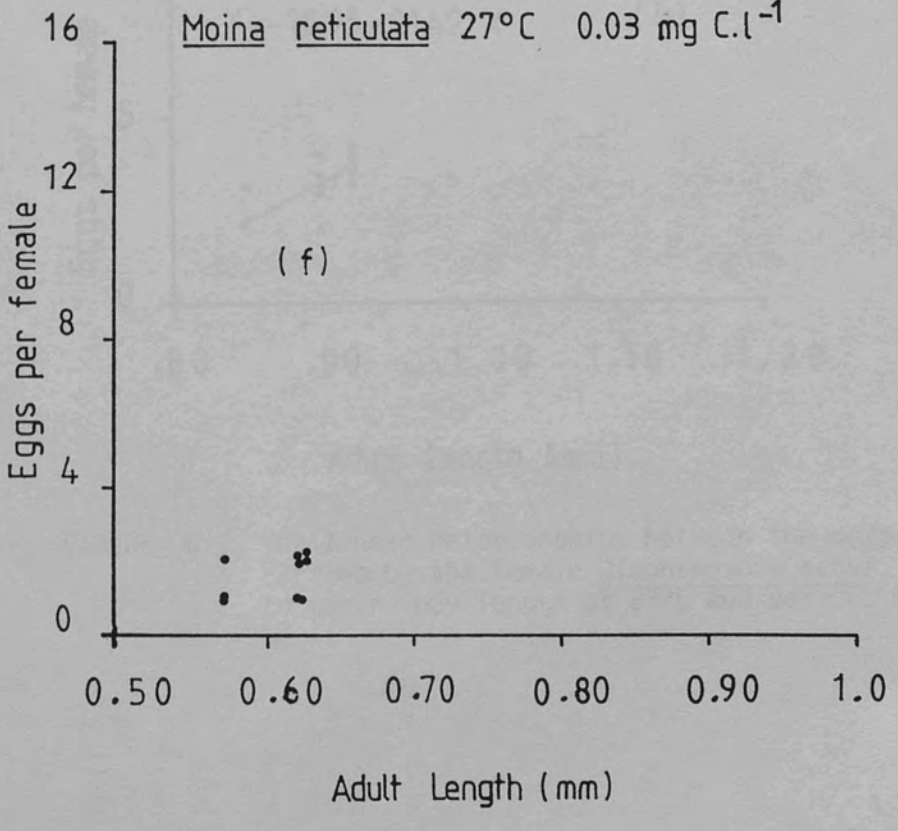
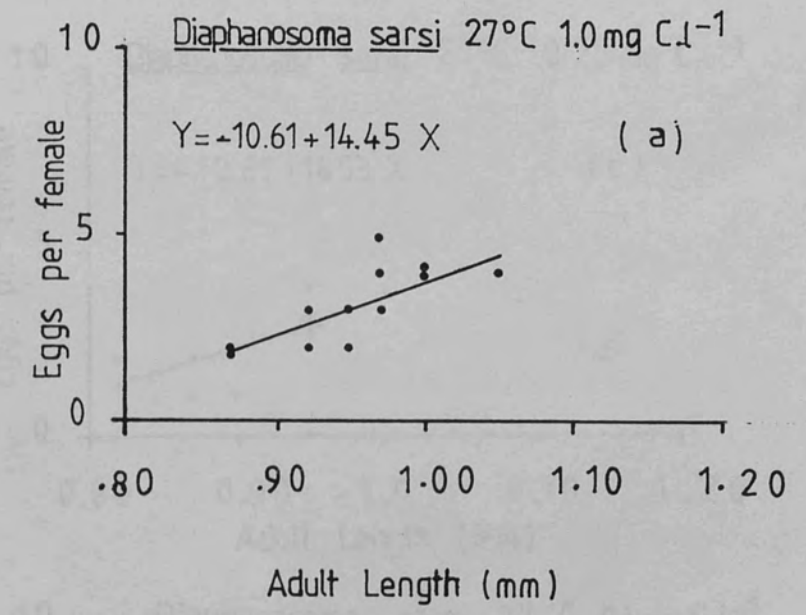


FIGURE 6.8 continued.



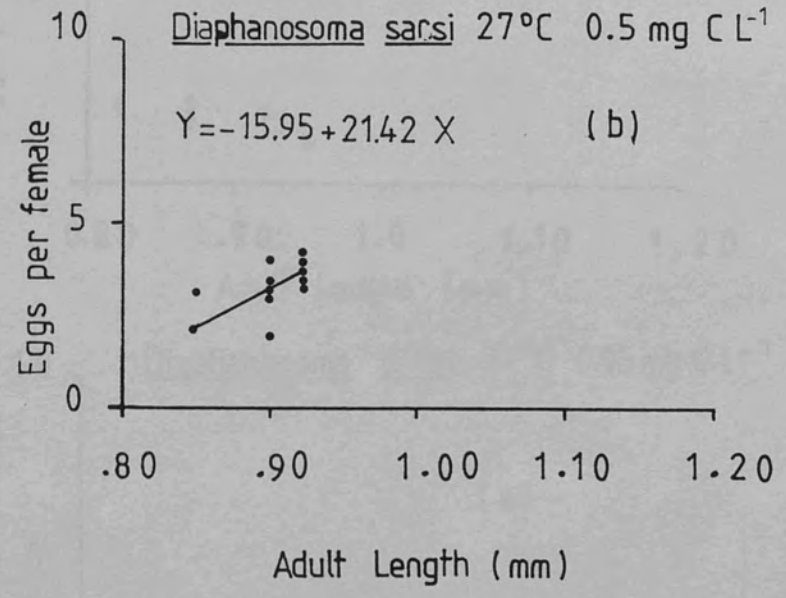


FIGURE 6.9 The linear relationships between the number of eggs carried by the female Diaphanosoma sarsi, in relation to their body length at 27°C and various food levels.

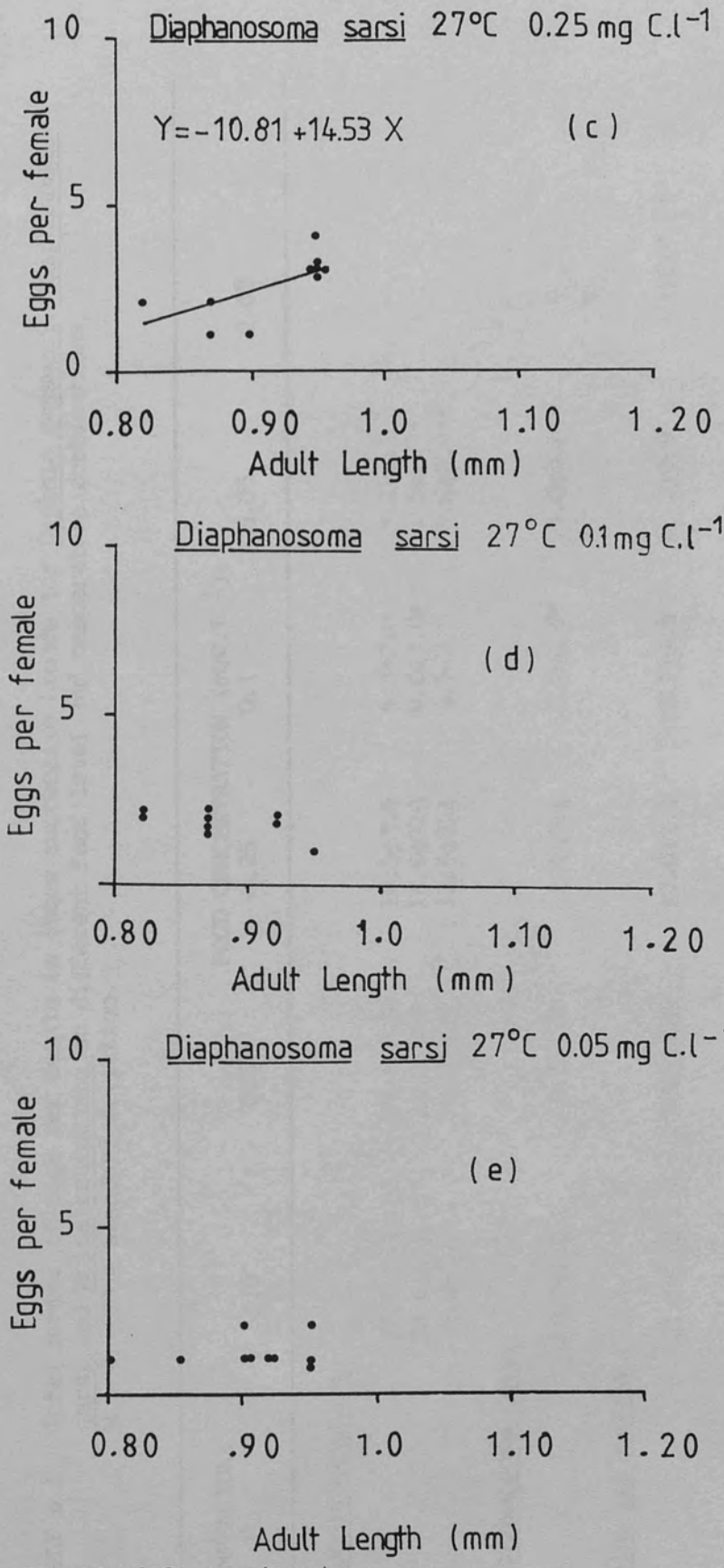


FIGURE 6.9 continued

TABLE 6.1 Total number of eggs per female in three successive broods for Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata at different food level and temperature combinations. N = 4; ±SD = standard deviation.

TEMPERATURE °C	FOOD CONCENTRATION (mgC.l^{-1}) 1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	32.5±3.3	29.5±2.3	18.5±2.6	6.3±2.0	5.2±1.7	-
27	20.0±4.1	21.5±3.9	14.6±3.6	8.0±3.0*	1.5±0.7*	
32	13.0±2.1	13.2±4.9	13.5±3.1	9.5±3.5	3.0±0.8**	
Diaphanosoma sarsi						
27	10.2±1.8	9.5±1.7	8.0±0.8	5.0±1.0*	3.0±0.8**	-
Moina reticulata						
27	21.5±1.2	28.5±3.3	27.0±2.1	12.2±2.8	11.2±0.9	4.0±0.9**

* juveniles died
** animals died before reached the third brood
- not tested

TABLE 6.2 Linear regression relationships between fecundity and temperature at different food level ($mgC.l^{-1}$). Regression equation $Y = a+bX$
Y = total number of eggs per female (sum of three broods); X = temperature ^{o}C
df = degrees of freedom; F = variance ratio; P = level of significance; r = correalation coeff.

Daphnia gessneri FOOD LEVEL ($mgC.l^{-1}$)	a	b	df	F	P	r
1.0	74.81	- 1.95	1,10	64.90	0.000	- 0.93
0.5	66.04	- 1.62	1,10	42.06	0.000	- 0.89
0.25	29.13	- 0.50	1,9	5.72	0.040	- 0.62
0.1	- 0.63	0.31	1,6	1.88	0.21	0.48 *
0.05	21.75	- 0.75	1,4	8.10	0.04	- 0.81

TABLE 6.3 Covariance analysis comparing the significant regressions of the number of eggs per female on temperature at different food concentrations. The regressions are given in ascending order of regression coeff. (STP test) and the differences between the elevations by the SS-STP test. Any regression not joined by the underline are significantly different at P = 0.05 level. (df = degrees of freedom; F = variance ratio; P = level of significance).

FOOD LEVEL $mgC.l^{-1}$	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
1.0	1	- 1.95±0.24	3,36	12.0	0.000	1 2 4 3
0.5	2	- 1.62±0.25				
0.25	3	- 0.50±0.20				
0.05	4	- 0.75±0.26				
		Comparison between elevations				
		ADJUSTED MEAN±SE	df	F	P	S-N-K
1.0	1	23.30±1.97	2,27	111.0	0.000	4 1 2
0.5	2	23.30±1.97				
0.05	4	- 0.55±2.01				

TABLE 6.4 Logarithmic regressions between fecundity (sum of eggs in the first three broods per female of the three species of Cladocera against food concentration ($mgC.l^{-1}$) at various temperatures. Regression equation $Y = a + b \ln X$
Y = fecundity; X = food concentration; df = degrees of freedom; F = variance ratio; P = level ofsignificance; r = correlation coefficient.

TEMPERATURE °C	a	b	df	F	P	r
Daphnia gessneri						
22	33.55	10.12	1,17	201.3	0.000	0.73
27	24.30	7.00	1,14	46.8	0.000	0.87
32	15.15	3.62	1,18	21.1	0.000	0.73
Diaphanosoma sarsi						
27	10.86	2.51	1,17	80.9	0.000	0.90
Moina reticulata						
27	28.36	5.95	1,21	42.6	0.000	0.81

TABLE 6.5 Covariance analysis comparing the regressions of fecundity against food concentration for three species of Cladocera reared at different temperatures. The regressions are given in ascending order of regression coefficients (STP test) and mean values (S-N-K test. Any regression number not joined by the underline are significantly different.(df = degrees of freedom; F = variance ratio; P = level of significance).

Daphnia gessneri TEMPERATURE °C	GROUP	REGRESSION COEFF.±SE	df	F	P	SS- STP
22	1	10.12±0.78	2,49	11.55	0.000	3 2 1
27	2	7.00±1.02				
32	3	3.62±0.78				

TABLE 6.6 Covariance analysis compar ing the regressions of fecundity against food concentration for three species of Cladocera reared at 27°C.

TEMPERATURE °C						
Daphnia gessneri	1	7.00±1.02	2,52	7.06	0.001	2 3 1
Diaphanosoma sarsi	2	2.51±0.27				
Moina reticulata	3	5.95±0.91				
		Comparison between elevations				
		ADJUSTED MEAN±SE	df	F	P	S-N-K
Daphnia gessneri	1	14.27±2.59	2,55	38.93	0.000	1 3
Moina reticulata	3	19.23±2.59				

TABLE 6.7 Multiple regression analysis of the effect of temperature and food concentration upon the fecundity of *Daphnia gessneri*.

Regression equation $Y = - a + bT + c \ln S$
Y = fecundity (total number of eggs per female in three broods; T = temperature ^{o}C; S = food concentration($mgC.l^{-1}$); df = degrees of freedom; F = variance ratio; P = level of significance; r = correlation coefficient.

a	b	c	df	F	P	r
45.6	- 0.79	7.08	2,52	68.95	0.000	0.85
Due to temperature				10.68	0.002	
Due to food concentration				67.02	0.000	

TABLE 6.8 Mean number of eggs per brood carried by the primiparous female of the three species of Cladocera at different temperature and food combinations. (N = 4±SD; Food concentration $mgC.l^{-1}$).

TEMPERATURE °C	FOOD CONCENTRATION $mgC.l^{-1}$					
	1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	7.5±1.9	7.2±1.5	5.2±1.5	1.6±1.5	2.0±0.8	-
27	4.7±0.5	5.2±1.7	4.2±0.9	1.5±1.0	1.0±0.0	-
32	4.7±1.6	4.7±2.3	5.0±0.8	2.7±1.7	3.0±0.8	-
Diaphanosoma sarsi						
27	2.0±0.0	2.0±0.0	1.7±0.6	1.6±0.6	1.2±0.5	-
Moina reticulata						
	6.0±0.0	5.7±0.5	5.5±1.0	2.5±1.0	2.7±1.0	2.0±0.0

- not tested

TABLE 6.9 Average age at first reproduction (days) of the three species of Cladocera reared in different food concentration and temperature conditions.
N = 4 ; Food concentration ($mgC.l^{-1}$)
SD= standard deviation

TEMPERATURE	FOOD CONCENTRATION ($mgC.l^{-1}$)					
°C	1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	5.5±0.0	5.8±0.5	6.0±0.0	7.5±0.5	8.0±0.0	-
27	4.0±0.0	4.3±0.5	5.0±0.0	7.0±0.0	7.7+_0.5	-
32	5.0±0.0	5.5±0.5	5.8±0.5	8.2±0.9	8.1±0.9	-
Diaphanosoma sarsi						
27	3.6±0.5	4.0±0.0	4.2±0.5	5.6±0.5	6.2+_0.5	-
Moina reticulata						
27	2.5±0.5	2.0±0.0	2.0±0.0	2.0±0.0	3.0±0.0	4.2±0.5

- not tested

TABLE 6.10 Length (mm) of the primiparous females of three Cladocera species reared in different temperature and food concentrations.
X = mean of four replicates; ±SD = standard deviation; food concentration($mgC.l^{-1}$).

TEMPERATURE ^{0}C	FOOD CONCENTRATION ($mgC.l^{-1}$) 1.0	0.5	0.25	0.1	0.05	0.03
Daphnia gessneri						
22	1.25±0.03	1.26±0.04	1.20±0.07	1.14±0.01	1.09±0.06	-
27	1.25±0.03	1.25±0.03	1.14±0.13	1.13±0.04	*	-
32	1.25±0.04	1.24±0.08	1.27±0.03	1.18±0.12	1.24±0.05	-
Diaphanosoma sarsi						
27	0.84±0.03	0.84±0.04	0.78±0.06	0.77±0.0	0.80±0.05	-
Moina reticulata						
27	0.58±0.02	0.60±0.03	0.67±0.0	0.62±0.03	0.60±0.04	0.54±0.03

* juveniles died
- not tested

TABLE 6.11 Parameters of the multiple regression of the size of primiparous female in relation to temperature and food concentration for Daphnia gessneri
Regression equation $Y = -a + bT + C \ln S$
Y = body length(mm) of primiparous; T = temperature ^{o}C; S = food concentration($mgC.l^{-1}$)
df = degrees of freedom; F = variance ratio; P = level of significance; r = correlation coefficient.

a	b	c	df	F	P	r
1.03	0.0048	0.096	2,52	6.90	0.002	21.0
Due to temperature				2.88	0.000	
Due to food concentration				9.95	0.000	

TABLE 6.12 Simple correlation coefficient between reproductive parameters of Daphnia gessneri reared at different temperature and food combinations.
Temperature ^{o}C; Food concentration($mgC.l^{-1}$);Length(mm); Eggs = eggs per female

VARIABLE	TEMPERATURE	FOOD	EGGS	LENGTH
FOOD	- 0.000			
EGGS	- 0.158	0.682***		
LENGTH	0.329*	0.620***	0.752***	
AGE	- 0.009	- 0.758***	- 0.667***	- 0.543***

Significant levels * 0.05
** 0.01
*** 0.001

TABLE 6.13 Parameters of linear regressions relating fecundity (number of eggs per female) to the body length(mm) of the adult mother at different temperature and food concentrations for Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata .In each case, the first three broods were used to obtain this relationship.
Regression equation Y = a + bX
Y = number of eggs per female up to third brood; X = adult length in mm;
df = degrees of freedom; F = variance ratio; P = level of significance

Daphnia gessneri

TEMPERATURE	FOOD LEVEL					
^0C	$mgC.l^{-1}$	a	b	df	F	P
22	1.0	- 13.37	17.20	1,10	16.86	0.002
	0.5	- 9.28	13.99	1,10	4.80	0.053
	0.25	- 5.59	9.11	1,10	3.43	0.093
	0.1	- 22.99	21.36	1,6	10.79	0.016
	0.05	- 6.07	7.37	1,7	4.08	0.082 *
27	1.0	- 10.86	12.55	1,10	14.10	0.003
	0.5	- 8.22	10.22	1,10	14.78	0.003
	0.25	- 9.51	11.62	1,10	8.58	0.015
	0.1	- 4.94	5.93	1,7	4.76	0.065*
32	1.0	- 34.17	31.13	1,10	19.22	0.001
	0.5	- 10.68	12.99	1,10	3.68	0.683*
	0.25	- 13.83	14.67	1,9	2.25	0.167*
	0.1	- 12.25	12.27	1,5	7.74	0.038
	0.05	- 12.96	12.65	1,2	3.12	0.210*

* not significant

TABLE 6.13 continued

TEMPERATURE °C	FOOD LEVEL mgC.l^{-1}	a	b	df	F	P
Moina reticulata						
27	1.0	- 11.21	22.99	1,10	51.22	0.000
	0.5	- 46.25	67.10	1,10	80.0	0.000
	0.25	- 18.40	32.42	1,10	9.00	0.013
	0.1	- 25.30	39.82	1,10	26.24	0.000
	0.05	- 18.66	30.52	1,8	9.84	0.013
	0.03	- 2.46	6.66	1,7	0.77	0.407*
Diaphanosoma sarsi						
27	1.0	- 10.81	14.45	1,8	8.42	0.019
	0.5	- 15.95	21.42	1,10	9.30	0.012
	0.25	- 10.81	14.53	1,8	8.42	0.019
	0.1	5.87	- 4.53	1,7	3.98	0.086
	0.05	- 0.63	2.03	1,8	0.45	0.520*

* not significant

TABLE 6.14 Covariance analysis comparing the significant regressions of fecundity against adult length at different food concentrations and temperature for Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi. The regressions are given in ascending order of regression coefficients (STP test) and mean values (S-N-K test). Any regression number not joined by the underline are significantly different.

Daphnia gessneri			Comparison between slopes				
TEMPERATURE °C	FOOD LEVEL mgC.l^{-1}	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
22	1.0	1	17.20±4.18	2,16	33.16	0.812	2 1 3
	0.5	2	13.99±6.38				
	0.1	3	21.36±6.50				
			Comparison between slopes				
27	1.0	1	12.55±3.34	2,29	2.09	0.139	2 3 1
	0.5	2	10.75±3.20				
	0.25	3	11.62±3.96				
			Comparison between elevations ADJUSTED MEAN±SE				
27	1.0	1	6.60±0.86	2,32	0.004	0.996	1 3 2
	0.5	2	6.65±0.86				
	0.25	3	6.63±0.87				
			Comparison between slopes				
32	1.0	1	31.13±7.1	1,15	3.85	0.068	2 1
	0.1	2	12.27±4.4				

TABLE 6.14 continued

Moina reticulata

TEMPERATURE	FOOD LEVEL	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
°C	$mgC.l^{-1}$						
27	1.0	1	22.99±3.21	4,48	4.65	0.003	1 5 3 4 2
	0.5	2	67.10±7.50				
	0.25	3	32.42±10.80				
	0.1	4	39.82± 7.77				
	0.05	5	30.52± 9.72				
			Comparison between elevations				
			ADJUSTED MEAN±SE	df	F	P	S-N-K
27	1.0	1	6.43±0.63	3,42	2.48	0.073	5 4 1 3
	0.25	3	6.80±0.69				
	0.1	4	5.18±0.67				
	0.05	5	5.08±0.65				

Diaphanosoma sarsi

TEMPERATURE	FOOD LEVEL	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
27	1.0	1	14.45±4.14	2,28	0.325	0.726	1 3 2
	0.5	2	21.42±7.02				
	0.25	3	14.53±5.00				
			Comparison of elevations				
			ADJUSTED MEAN±SE	df	F	P	S-N-K
	1.0	1	2.92±0.48	1,20	0.169	0.694	3 1
	0.25	3	2.79+0.48				

CHAPTER 7

The effect of food concentration and turbidity on life cycle, reproduction and growth of Daphnia gessneri and Moina reticulata

In this part of the experimental study, two culture techniques were used, namely, batch (one individual per 250 ml in each bottle and a continuous system (15-20 individuals in each vessel).See details in chapter 3, section 3.5). Turbidity was produced by introducing a suspension of natural sediments of fine particles between 0.7 um and 2.0 um in diameter which originated from Lake Jacaretinga (procedure in chapter 3). The level of turbidity was measured in nephelometric turbidity units (NTU). Three experimental concentrations were tested, namely 10, 20 and 50 NTUs, which were representative of the turbid inflows in Lake Jacaretinga. The inorganic particles were added to two food concentrations; these were 0.5 and 0.05 $mgC.l^{-1}$, where the former was considered to be an optimal food level and the latter 0.05 $mgC.l^{-1}$ a limiting food levels.(See chapter 6). Scenedesmus acutus was the food organism used for both the experimental food levels and the control, with zero turbidity in NTU. Two species, Daphnia gessneri and Moina reticulata, were grown at the constant temperature of 27° C, which is the average temperature in Lake Jacaretinga where these two species are representative and common zooplankters. Neonates from stock cultures not older than 12 hours were used to start all these experiments.

The aim of these experiments was to evaluate the effect of suspended sediments on the survival, reproduction,fecundity of adults up to their third brood, growth, size and age of the primiparous female.

7.1 Survivorship

Table 7.1 summarizes the survival of Daphnia gessneri and Moina reticulata under experimental conditions in batch culture system.

In Daphnia gessneri with 0.5 $mgC.l^{-1}$ and no turbidity, all four animals reached the third brood adult instars. With 0.5 $mgC.l^{-1}$ and low turbidity of 10 NTU of natural sediment, the survival was 100 % too. With the treatment combination of 0.5 $mgC.l^{-1}$ and 20 NTU, the four animals reached the primipara stage, but all died after their eggs hatched and at 0.5 $mgC.l^{-1}$ with 50 NTU the four initial neonates died at age of three days. Turning to the experiments with 0.05 mg $C.l^{-1}$ which is considered to be a limiting food concentration for Daphnia gessneri (chapter 6), Table 7.1 shows that, with (0) NTU, three out of four animals died as juveniles and only one individual managed to attain sexual maturity; this individual, however did not complete three broods and died at the age of 5 days. On the other hand, in the combination of 0.05 $mgC.l^{-1}$ plus 10 NTU, only one animal died at the primipara stage, immediately after hatching their eggs, whereas the other three managed to reach the third adult instars and to produce three broods. The survival of the animals at the two highest concentrations of turbidity (20 and 50 NTUs) in limiting food was zero and all the juveniles died between 2-3 days, both the initial neonates and the replacement individuals.

In Moina reticulata, grow in batch culture at the high food level of 0.5 $mgC.l^{-1}$ and zero turbidity, no mortality did occurred. A similar response was recorded when inorganic particles producing turbidity of 10 and 50 NTUs were present. However, at 0.5 $mgC.l^{-1}$ with 20 NTU, 100 % mortality was recorded for the animals at primipara stage that died after managing to hatch their eggs.This seems an anomalous result and the causes of the mortality which occurred at this food-turbidity treatment of 0.5 $mgC.l^{-1}$ and 20 NTU is not known. In the lower food level of 0.05 $mgC.l^{-1}$ with zero turbidity as well as with turbidity of 20 and 50 NTUs, Moina reticulata showed 100 % survival. This species seemed to have all the physiological requirements needed to grow and reproduce under these conditions. A low mortality of 25% did occur at 0.05 $mgC.l^{-1}$ with 10 NTU; the cause

for this is also unknown and anomalous since the all the other survivors reached the third adult instars (75%).

The results of these experiments, which are presented in Table 7.1, show that there was a distinct difference between Daphnia gessneri and Moina reticulata in their response to the presence of inorganic particles amongst their food. Daphnia gessneri exhibits two distinct but opposite reactions to turbid conditions. First, there is the deleterious effect of 100% mortality in high turbidity (20 and 50 NTU) and optimal food (0.5 $mgC.l^{-1}$). Second, there is the apparently beneficial effect of better survival in limiting food (0.05 $mgC.l^{-1}$) when is slightly turbid conditions of 10 NTU compared with the control. As many as 75% of the animals in 10 NTU managed to survive to the third adult instar (Table 7.1). In contrast, the addition of inorganic particles to the food of Moina reticulata was apparently not harmful. The two sets of mortalities recorded in Table 7.1 seem rather anomalous with no causal explanation other than, maybe, handling. Due to lack of time it was impossible to repeat this particular food-turbidity treatment.

Table 7.2 gives a summary of the survival of Daphnia gessneri and Moina reticulata under the experimental conditions of the continuous flow system, with the same food concentrations and turbidity levels as in the batch cultures.

Under a continuous supply of 0.5 $mgC.l^{-1}$ food medium, some individuals of Daphnia gessneri were able to survive to the third instar in all turbidities as well as in the control. The survival to the third instar was 100% in both the control and 10 NTU but dropped to 86% in 20 NTU and to 40% in 50 NTU. It is striking that 33% of the 60% mortality in 50 NTU were due to deaths of the juveniles, mostly at an age not more than three days.The rest of the mortalities were due to death of primiparous females (20%) and adults in their second instar (7%).

The harmful effect of turbid conditions when the food medium is at a limiting concentration is clearly shown in Table 7.2. About 66%-70% were able to survive to a third adult instar in 10 NTU and 0 NTU

but none survived to this stage in 20 and 50 NTU. It was the juveniles that died when 2-3 days old in the higher turbidities whereas some reproduction occurred at the lower levels.

As in the batch culture experiments, Moina reticulata survived better than Daphnia gessneri in turbid conditions. More than 7% of the animals attained their third adult instar, irrespective of level of turbidity when grown in the optimal food level of 0.5 $mgC.l^{-1}$. The survival rate was also high in the limiting food level of 0.05 $mgC.l^{-1}$, ranging from 31-60%. However, for both food levels, it is clear that 50 NTU is stressful, since the mortalities that did occur took place in the second adult instar. However, Moina reticulata survived better in batch culture than in continuous flow condition, if tables 7.1 and 7.2 are compared.

To sum up for both species in continuous flow system, the results presented in Table 7.2 show that there was a slight difference between the two species in their response when turbidity were added to the food source. Daphnia gessneri could not reach the third adult instars in low food level with turbidity but Moina reticulata could do so. To summarize from the results described in Table 7.1 and 7.2, in batch and in continuous flow culture, mortality increased with increasing turbidity, except that in low food level (0.05 $mgC.l^{-1}$) mortality was greater than when a low level of sediment (10 NTU) was also present.

7.2 Fecundity and body size of the adult instars

That fecundity is closely related to body size in Cladocera is well known in the literature for temperate and tropical species. it is well documented that larger females carry more eggs in their brood pouch than smaller ones. The relationship has been expressed as fecundity-body length regressions.

It proved possible to calculate significant linear regressions of clutch size versus female body length for Daphnia gessneri reared in batch culture at two food levels and three sets of turbid conditions.

These regressions are illustrated in Figure 7.1 and the regressional statistics are given in Table 7.3.

Table 7.3 and Figure 7.1 show that a significant regression of fecundity on length was obtained only in the high food level (0.5 $mgC.l^{-1}$) without inorganic particles (zero NTU). In this food-turbidity treatment, the number of eggs per female increased from 3-4 at a body length of 1.2 mm to 10 or more at a length of 1.7 mm. Significant regressions could not be obtained in the other two experimental situations where a reasonable number of animals produced eggs; this can be seen in Table 7.3 and Figure 7.1 for 0.5 $mgC.l^{-1}$ and 10 NTU and for 0.05 $mgC.l^{-1}$ and 10 NTU. In the former, fecundity varied from 3 to 10 eggs per female over a very small range in length, from 1.1 to 1.3 mm, giving an impression of size-independence of fecundity in turbid conditions. In the latter situation of the same turbidity but much lower food levels (0.05 $mgC.l^{-1}$), similar sized females were able to produce up to 4-6 eggs, suggesting again some beneficial effect. No regressions were calculable in other experimental combinations because too few females were able to reproduce (Figure 7.1).

Table 7.3 also presents the significant regressions of fecundity on body length for Daphnia gessneri when reared in a continuous flow of medium with the same two food levels and three levels of turbidity. These results are illustrated in Figure 7.2 (a-g) together with the original data and the significant linear regressions. All four regressions for animals cultured at the high food level of 0.5 $mgC.l^{-1}$ are statisticaly significant but the slope of the regression for 50 NTU (Figure 7.2(d) is markedly less steep than those for the lower turbid levels (a)-(c). There is also a tendency for an opposite effect of increasing steepness in slope as the turbidity increases from zero to 10 NTU and to 20 NTU, that is, more evidence for the apparently beneficial effect of low turbid levels. At the lower food concentration of 0.05 $mgC.l^{-1}$, a significant regression of fecundity on body length was obtained for Daphnia gessneri grown in zero NTU but not in 10 NTU (Figure 7.2 (g) illustrates the very striking result that the regression for 0.05 $mgC.l^{-1}$ and zero NTU lies on top of that

for 0.5 mgc.l^{-1} and 50 NTU. It was necessary to determine whether any of these regressions from the continuous flow experiments were different. The covariance analysis performed on the significant regressions in Table 7.3 are presented in Table 7.4. This shows the existence of three pairs of regressions which do not differ between themselves but which, as pairs, do have significantly different slopes. When testing the adjusted means for these is confirmation that the regression for 0.5 mgC.l^{-1} and 50 NTU is not statistically different in elevation from the regression for 0.05 mgC.l^{-1} and zero NTU, which is a very revealing result. The other pair, for 10 and 20 NTU and 0.5 mgC.l^{-1}, also did not differ in elevation but the regression for 0.5 mgC.l^{-1} and zero NTU was found to be significantly lower in elevation than that for 10 NTU.

Table 7.5 provides a summary of the experimental results from the turbidity experiments and also a useful comparison of the batch and flow system of culture. In the continuous flow system, the level of fecundity of Daphnia gessneri was rather constant,at about 6 eggs per female in 0.5 mgC.l^{-1} and turbidity from zero-20 NTU but halved, to 3.5 eggs per female, when the turbidity was increased to 50 NTU. At the same food level in batch culture, there was a decreasing fecundity from 7.8 to 4.2 egg per female, with increasing turbidity and no reproduction occurred at 50 NTU. The results for the 0.05 mgC.l^{-1} gave lowered fecundities compared with 0.5 mgC.l^{-1} food but slightly better levels in flow culture. No reproduction occurred in 20 NTU as well as in 50 NTU.

The relationship between fecundity and body size was studied in Moina reticulata, a much smaller species than Daphnia gessneri. How this relationship changed under the experimental conditions of different concentrations of natural inorganic particles was determined by linear regression, given in Table 7.6 and these are illustrated in Figure 7.3 and 7.4.

In batch culture with high food levels 0.5 mgC.l^{-1}, Table 7.6 shows that the relationship between fecundity and body size was significant at three levels of turbidity and that there was too little data (n = 4) in 20 NTU for a regression. All the experiments with

turbid conditions at low food levels resulted in non-significant regression compared with the control. When the high food level regressions were tested by covariance analysis (Table 7.7), it is clear that the slopes of all three significant regressions are different as is shown in Figure 7.3 (i).

Table 7.8 and figure 4 (a-i)shows that very similar results were obtained for Moina reticulata when grown under different turbidities and high and low food in continuous flow conditions. In 0.5 $mgC.l^{-1}$ food, there were significant relationships between fecundity and body size at all tested levels of turbidity but in 0.05 $mgC.l^{-1}$ such a relationship could be obtained only in the control. The results of covariance analysis, given in Table 7.9, reveals that none of the regressional slopes were different at the high food condition and that all the regressions had similar elevations except for that for 50 NTU, which was lower than the others.

A summary of these results on how turbidity affects the fecundity of Moina reticulata is given in Table 7.10 and offers the opportunity to compare the effects of batch and continuous flow culture. As with Daphnia gessneri, the fecundities obtained with high food concentrations of 0.5 $mgC.l^{-1}$ are very uniform, about 6 eggs per female,in the continuous flow vessel compared with batch culture they where both more variable and can attain higher levels (e.g. 9.6 and 9.8 eggs per female at zero or 10 NTU). A similar result is demonstrated for the limiting food level of 0.05 $mgC.l^{-1}$, with lowerred fecundities which are more constant in flow conditions but able to attain higher fecundities at zero NTU in batch culture.

From the results in Table 7.10 we conclude that fecundity for Moina reticulata was dependent mainly upon food concentration and that this was not affected by turbidity. Also, for this species fecundity was quite similar in both systems, continuous flow and in batch.

Both species, Moina reticulata and Daphnia gessneri showed that the differences in fecundity are closely related to the differences in body size.

7.3 Primiparous female; size, fecundity, age, instars

The primiparous female or first egg-bearing adult instar represents an important phase during the development of the cladoceran life cycle. At this stage, whilst still growing at a juvenile rate, the female has to produce an ovary for both of which food must be available. Any lack of resources could delay or even limit the physiological process like growth and or reproduction. In order to understand how food resources are allocated it is important to know the level of fecundity, body length, age and instar of the individuals at which reproduction starts when the animals are reared in limiting and non-limiting food levels and in various concentrations of natural inorganic particles.

Table 7.11 gives some information about the primipara female of Dapnia gessneri when reared in batch and flow culture. In a non-limiting food level, the number of eggs carried per primiparous female varied only from 4.0 to 5.0 eggs at 10 and 20 NTU. There is no influence of inorganic particles upon the age or instar stage of the primiparous female in any combination of high food (0.5 $mgc.l^{-1}$) and various turbidities. The reproductive stage was attained in four days for all experimental treatments with 0.5 $mgC.l^{-1}$. Results obtained with animals cultured in batch and in continuous flow did not show strong differences except in the case of 0.5 mgc,l^{-1} and 50 NTU. In batch, all four Daphnia died before reached the primiparous stage, but they were able to reproduce in these food-turbidity conditions when cultured in continuous flow. At low food concentration (0.05 $mgC.l^{-1}$) and 20 and 50 NTUs, the animals died whilst juveniles, but surprisingly they did reach maturity and produced eggs at 0.05 $mgc.l^{-1}$ and in the combined food and inorganic particles (0.05 $mgC.l^{-1}$ and 10 NTU) in both batch and continuous flow system. This primiparous stage was attained with 4-5 days in flow system and within 5-6 days in batch.

The mean sizes of the primipara female Daphnia gessneri and Moina reticulata are presented in Table 7.12 for both systems, batch and

flow culture. These results did not show any noticeable influence of turbidity upon the body length of the primiparous female in any combination of food and turbidities except that in batch in high food (0.5 mgC.l^{-1}) and zero turbidity the animals reached the bigger body size (1.25 mm) compared with 1.10 mm under similar food conditions but with 20 NTU. In limiting food (0.05 mgC.l^{-1}) with zero and 10 NTU the body sizes attained by the primiparous female were very similar (1.05 and 1.11 mm respectively). The body sizes of the animals cultured in continuous flow under the same experimental conditions did not vary. In non-limiting food level with 0,10 and 20 NTU the body sizes were similar,only a slight decrease in size was recorded in the higher turbidity condition (50 NTU), when the animal had 1.06 mm (Table 7.12).

The results for Moina reticulata as given in Table 7.12 did not show any strong tendency for a change in body size with change in concentrations of turbidity. In batch the body length range at high food level and various turbities was 0.60-0.66 mm. Smaller sizes were attained by the animals under 0.05 mgC.l^{-1} and various turbidities ranging between 0.54-0.58. In continuous flow the body sizes did not show any apparent change in any of food-turbidity experimental conditions. Due to the small size of this species,our ability to detect such small size differences is rather doubtful.

Table 7.13 gives the results of fecundity of the primiparous female of Moina reticulata at different food-turbidity conditions reared in batch and in continuous flow. The highest fecundity occurred at high food concentrations, but surprisingly at the lower food and various turbidities the animals produced eggs in both systems, although the response was much bigger in batch than in the continuous flow system. The maximum fecundity was 8.0 eggs per female with high food and lower turbidity.

At low food level (0.05 mgC.l^{-1}) the number of eggs were quite similar varying only from 1.5 to 2.7 eggs per female. Even the age and instars of the primiparous female did not show any strong influence in

any of the experimental condition. The age ranged between 2.2 to 3.0 days.

To sum up for both species, food concentration influences fecundity, very markedly in Moina reticulata compared with Daphnia gessneri. On the other hand, turbidity did not affect fecundity on Moina reticulata, even in the high concentrations of turbidity (50 NTU) which were deletereous for Daphnia gessneri. The main difference between the two species is that Moina reticulata, under these experimental conditions, is more successful at growing and producing eggs than Daphnia gessneri is.

7.4 Length-carbon relationships

Length-carbon relationship for Daphnia gessneri and Moina reticulata reared in continuous flow culture were obtained for known concentrations of food (0.5 and 0.05 $mgC.l^{-1}$) and turbidity(0,10,20 and 50 NTUs) under constant temperature (27°C). Body carbon content was measured from known length animals as described in Chapter 3.

Table 7.14 gives for Daphnia gessneri the parameters of the linear regressions for these relationships which were statistically significant, except for the limiting food level of 0.05 $mgC.l^{-1}$. Those significant regressions were compared by analysis of covariance which results are given in Table 7.15. There were no significant differences between the slopes of the carbon-length of Daphnia gessneri reared at 0.5 $mgC.l^{-1}$ with 0,10,20 and 50 NTUs and 0.05 $mgC.l^{-1}$ with 10 NTU, but significant differences were find between the elevations of the regression lines. In the limiting food level 0.05 $mgC.l^{-1}$ with 10 NTU the adjusted mean (elevation of the curve) was very low and differed from all other regressions. The higher elevations was found for non-limiting food level (0.5 $mgC.l^{-1}$) with low turbidity (10 NTU), whose adjusted mean was not significantly different from those for non-limiting food with zero and 20 NTU. Figure 7.5 illustrates the statistically significant length-carbon weight on double logarithmic regressions for Daphnia gessneri reared throughout its life cycle under constant but different concentrations of food and turbidities.

The four regressions lie on top of one another, but each one has an individual elevation, which is statistically significant. The pooled regression 0.05 mgC.l^{-1} zero and 10 NTU has the lowered elevation compared with the others. It seems that this food level and turbidity has similar response with non-limiting food level and high turbidity (0.5 mgC.l^{-1} , 50 NTU); both regression lines showed the lowered elevation indicating that the carbon weight of individuals per unit length is limited. Length-carbon relationships was not obtained in the lowest food level (0.05 mgC.l^{-1} with 0,20 and 50 NTU), suggesting that the effect of turbidity was much more marked in the limiting food concentration than in the non-limiting food.

The length-carbon relationship obtained for Moina reticulata at two food levels and various turbidities levels are given in Table 7.16. In high food (0.5 mgC.l^{-1}) all the regressions were statistically significant; the same response occurred in low food with 10 and 50 NTU. but a non-significant regression was obtained with 20 NTU. Table 7.17 gives the results of the analysis of covariance which shows that the regression coefficients were not significantly different and the elevation of the curve in non-limiting food was significantly higher compared with the others, as has been illustrated in Figure 7.6. Like Daphnia gessneri, also Moina reticulata, shows that the lowered elevation occurs in any food level when turbidity is added, resulting in less carbon weight of individuals per unit length throughout the life cycle.

7.5 Growth curves of cladocerans at different turbidities

In this part of the study, growth curves were obtained to provide information on how the size of the Daphnia gessneri and Moina reticulata varies with time (days) under various concentrations of turbidity and two food levels (0.5 and 0.05 mgC.l^{-1}, but at a constant temperature(27°C).

The growth curves for each food-turbidity combination was obtained using Richard's model following the same procedure previously accept for other set of data (chapter 4).

The parameters of the Richard's growth equations for Daphnia gessneri are given in Table 7.18 and illustrated in Figures 7.7(a-d) On each growth curve, the time and size of the primipara, is indicated by an arrow which gives a visual picture of whether or not the curve inflects before the onset of maturity.

In Daphnia gessneri, it is clear from the initial straight part of the growth curve that the early stage of development shows exponential growth under all experimental cconditions. As can be seen from the age of primipara related with the time of inflection (t_o) in table 7.18 and figure 7.7 it is apparent that the exponential growth occurs just after the primipara stage in all food and turbidity conditions.

The turbidity effect is mainly on duration but it is evident only in non-limiting food level with the higher turbidity (50 NTU). In this condition the time taken to attain the primipara stage took two days longer in the turbidity than in the control. There were a very clear evidence that the maximum weight attained by the 3rd adult instars given by W_{max} was influenced by turbidity levels; the values declined as turbidity increases, in the range of 14.28 to 6.6 in non-limiting food levelsand from 6.68 to 2.63 in limiting food levels. Daphnia gessneri did not grow at 0.05 mgC.l^{-1} with 20 and 50 NTUs.

Figure 7.8 combines the two food levels and various turbidities at 27°C to illustrate the effect of food and turbidity on growth of Daphnia gessneri It is clear that at non-limiting food levels with inorganic particles of 50 NTU the animals tend to have a lesser carbon content very close to those obtained for limiting food level (0.05 mgC.l^{-1}, 0.0 NTU.

For Moina reticulata the growth curves at various turbidities an two food levels are plotted in Figures 7.9(a-h). The effect of turbidity is mainly noticed at 0.5 mgC.l^{-1} food on the carbon content of the animals. The final maximum weight reached by the animals under higher turbidity condition (50 NTU) is 2½ times less than those reared only with food zero turbidity (table 7.18). The effect of turbidity was less extent in 0.05 mgC.l^{-1} food, but even the W_{max} values in the control was almost twice the values found in the turbidity conditions.

There were no differences in the maximum weight between various turbidities in none of the food levels. Body growth for Moina reticulata combined food and turbidity are plotted together in Figure 7.10. The effect considered here is prolongation. It is clear that the time taken to the animals attain the 3rd adult instar was prolonged one day under turbidity conditions at both food concentration.

7.6 Growth rates

The daily instantaneous growth rates at different turbidity and two food level were calculated by regressing natural log body weight on age of Daphnia gessneri and Moina reticulata. The procedures and equation considered have previously been described in chapter 4.

Table 7.19 gives the results of this regressions and all are statistically significant for both cladoceran. The (b) value which represents the daily instantaneous growth rate (g) obtained for Daphnia gessneri did not vary that much in the food control (0.5mgC.l^{-1}) and with low turbidity (10 NTU), but clearly the (d^{-1}) declines above 20 NTU reaching the minimum rate in the higher turbidity (50 NTU) and, for limiting food level the minimum (d^{-1}) was observed in 10 NTU and grow did not occur above this turbidity level.

The values of (d-1) for Moina reticulata in 0.5 mgC.l-1 with 10,20 anf 50 NTU were clearly similar (Figure 7.10) but this three differ in approximately half the rate of the control food. In 0.05 mgC.l^{-1} food the daily growth rates did not show any strong difference, suggesting that in this experimental conditions turbidity did not affect the (d^{-1}). Also the values obtained for Moina reticulata were higher than those for Daphnia gessneri, particularly at in the lower food level.

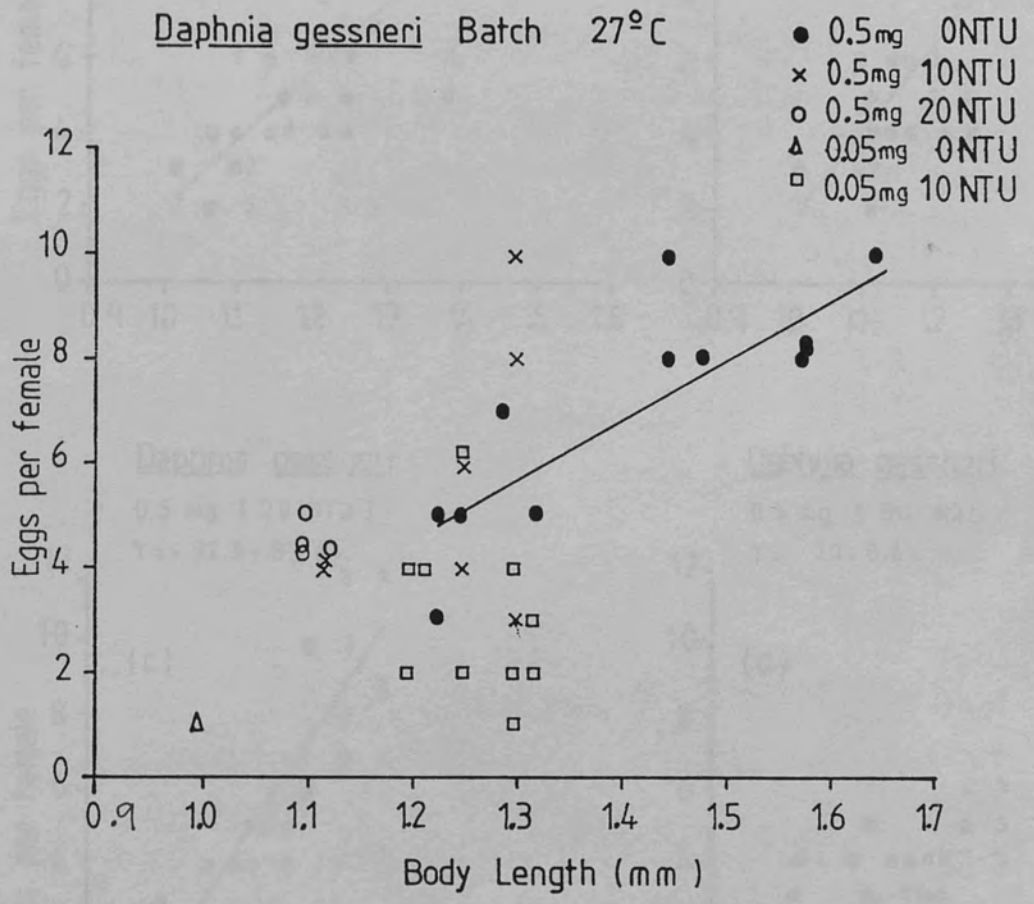


FIGURE 7.1 The fecundity of females of known length when grown under different conditions of food concentration and turbidity. The statistics for the one significant regression are given in Table 7.3. Each point means one animal

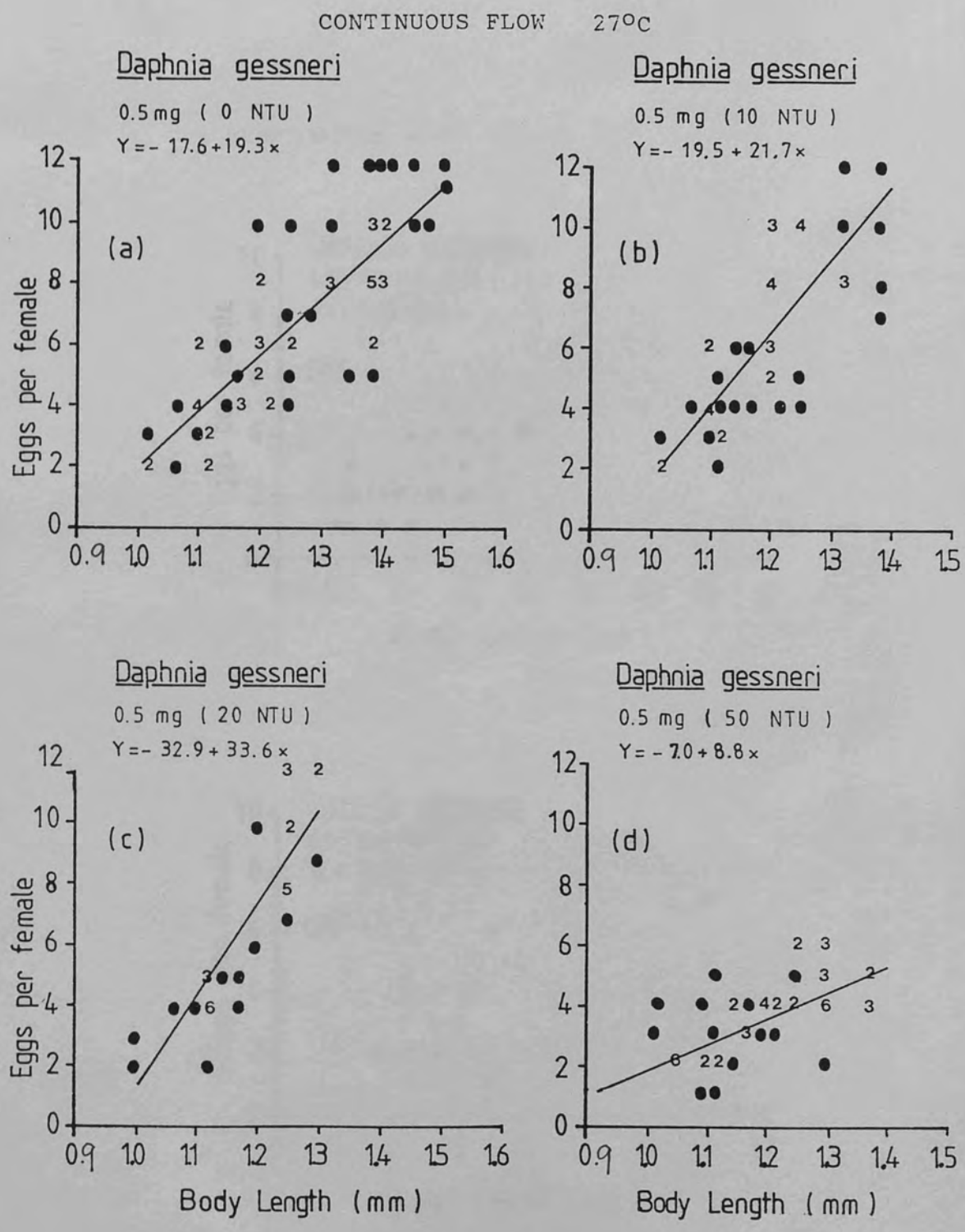
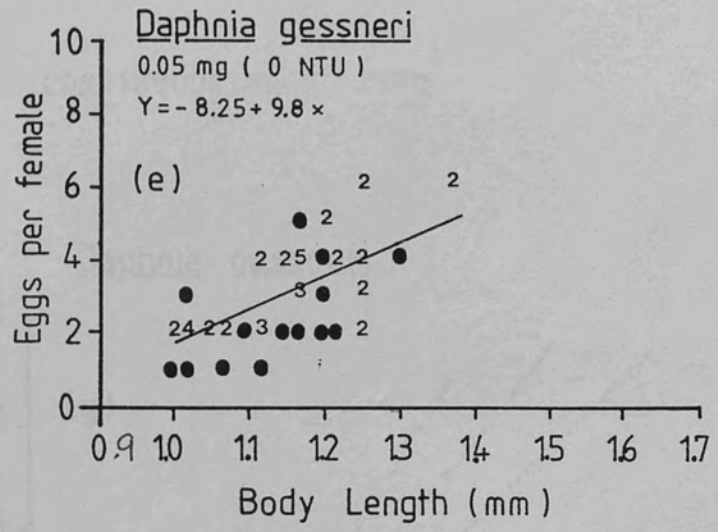


FIGURE 7.2 The fecundity of females of known length when grown under different conditions of food concentration and turbidity. The statistics for the significant regressions are given in Table 7.3 Numbers represents animals observed.

CONTINUOUS FLOW 27 °C



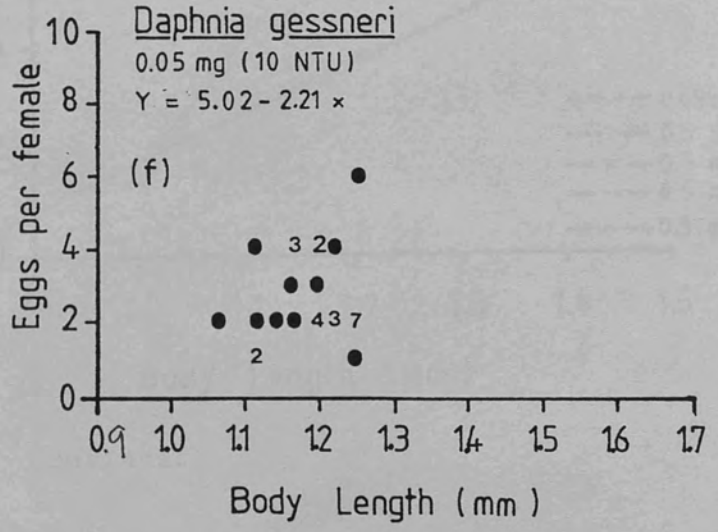


FIGURE 7.2 continued

CONTINUOUS FLOW 27°C

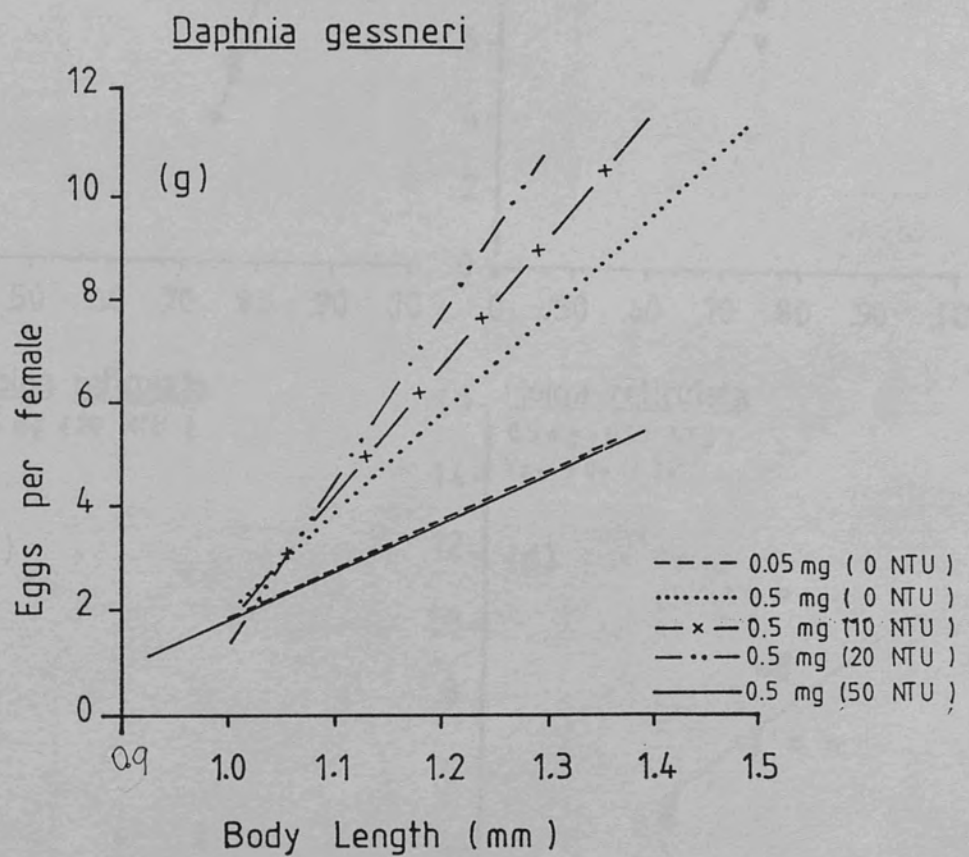


FIGURE 7.2 continued

BATCH 27°C

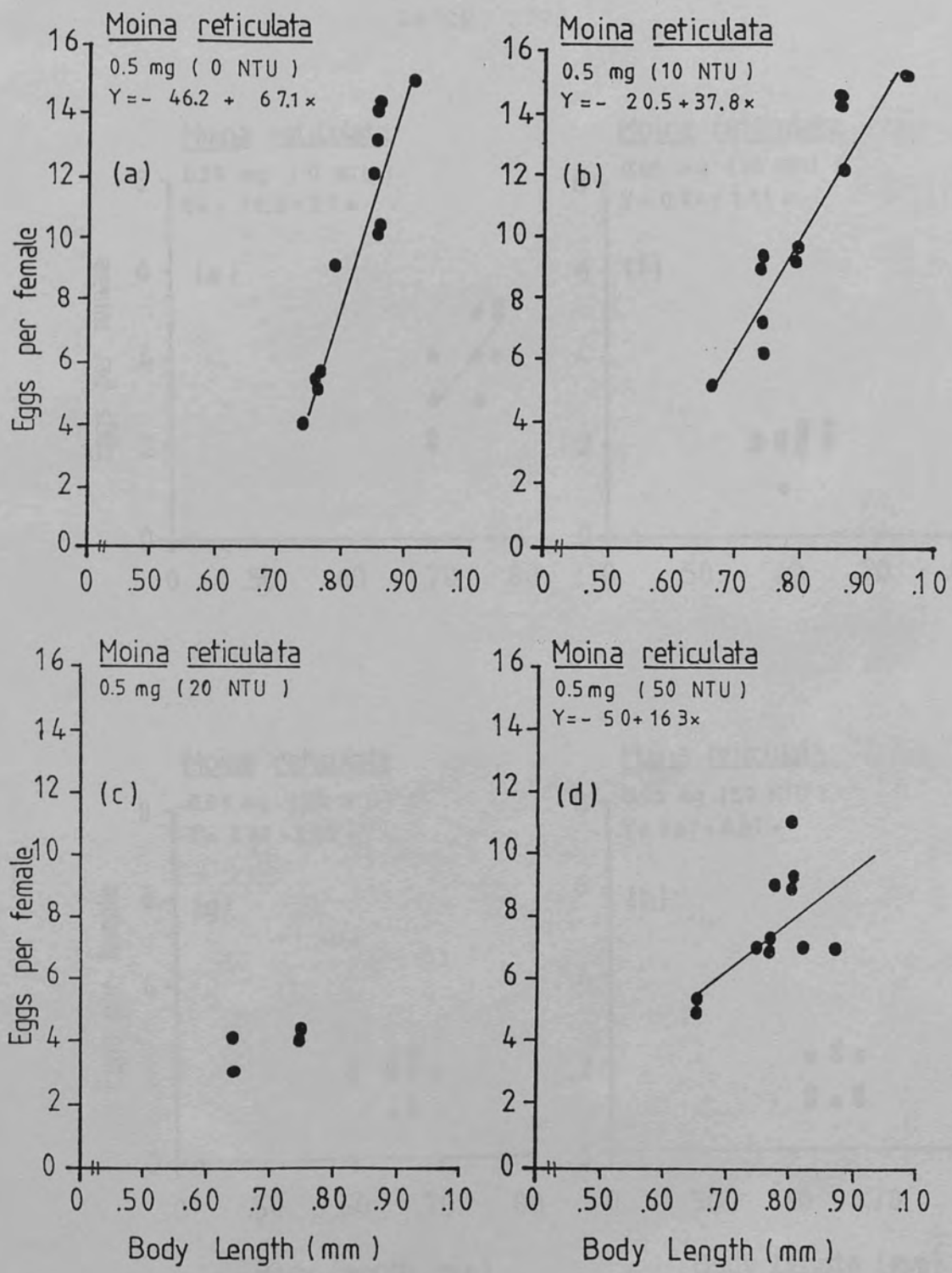


FIGURE 7.3 The fecundity of females of known length when grown under different conditions of food concentration and turbidity. The statistics for the significant regressions are given in Table 7.6

BATCH 27°C

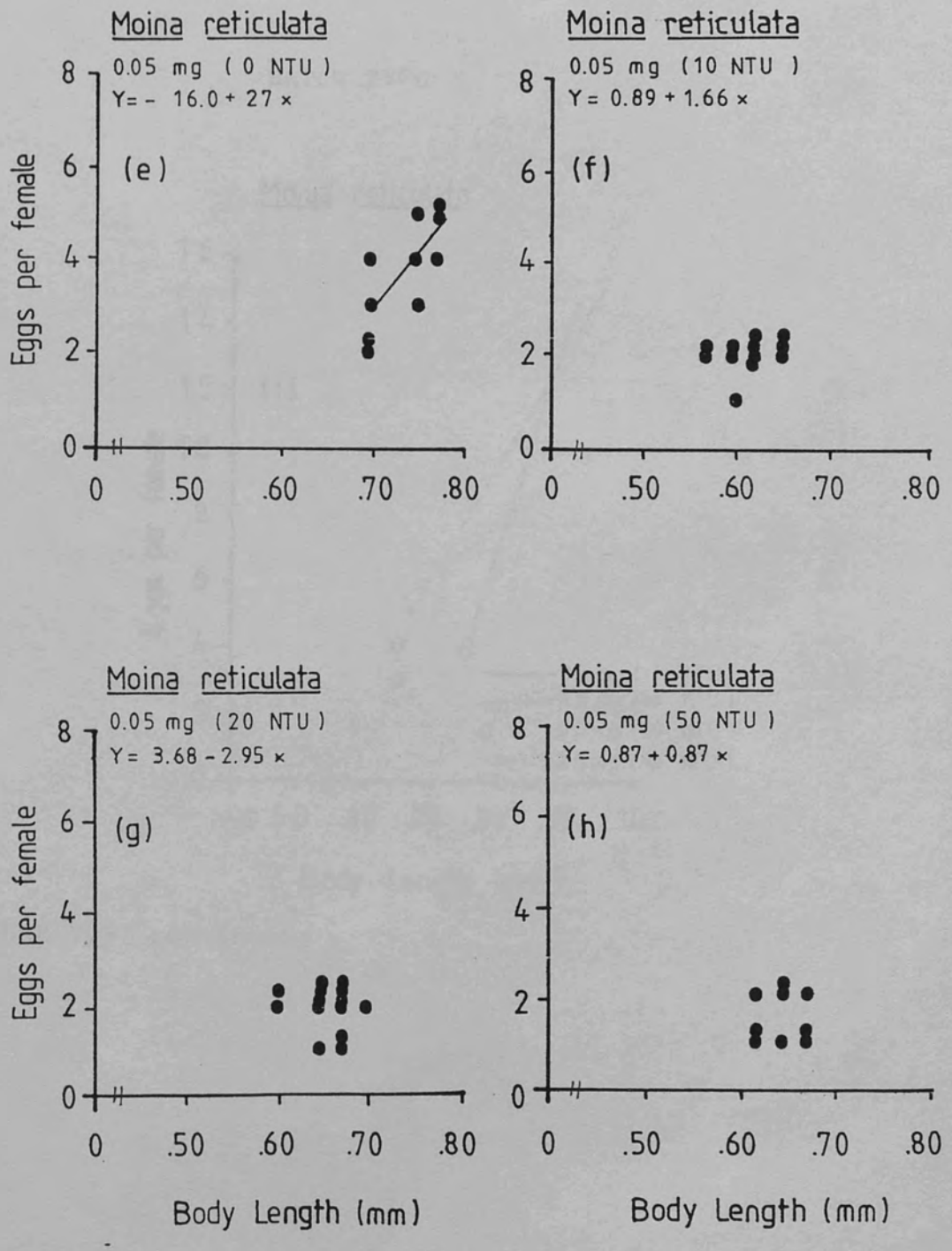


FIGURE 7.3 continued

BATCH 27°C

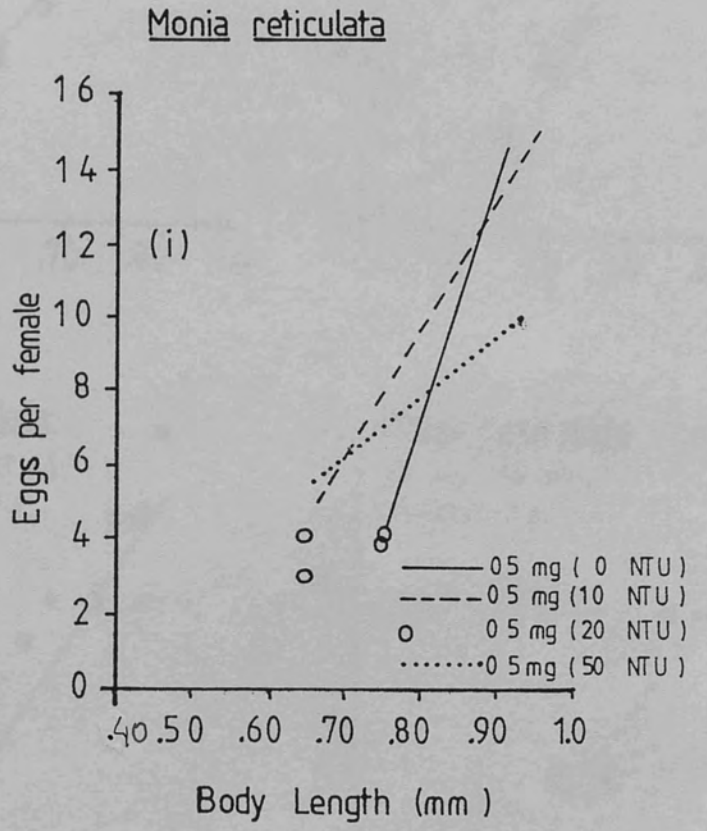


FIGURE 7.3 continued

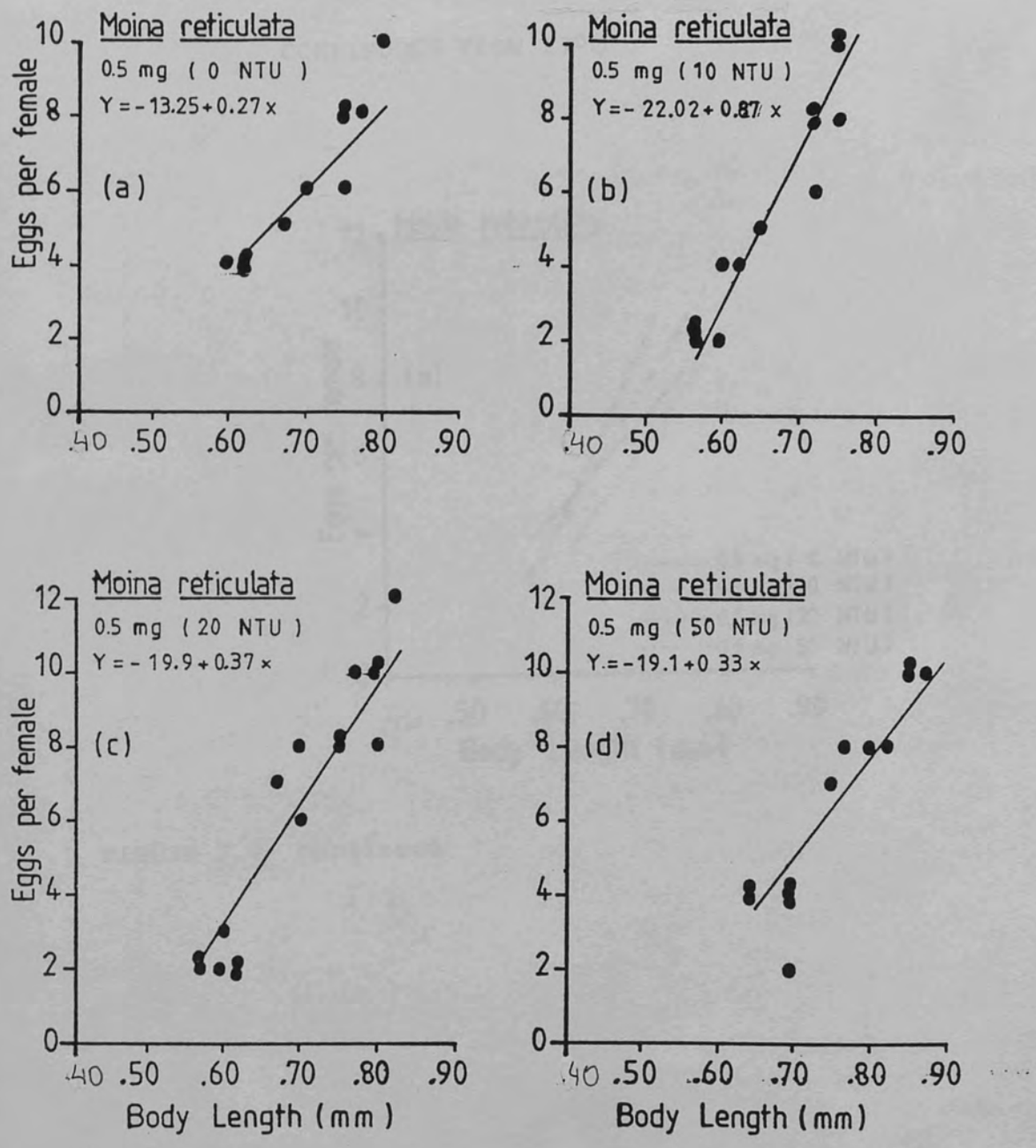


Figure 7.4 Fecundity of females of known length when grown under different conditions of food concentration and turbidity. Each point means one animal.

CONTINUOUS FLOW 27°C

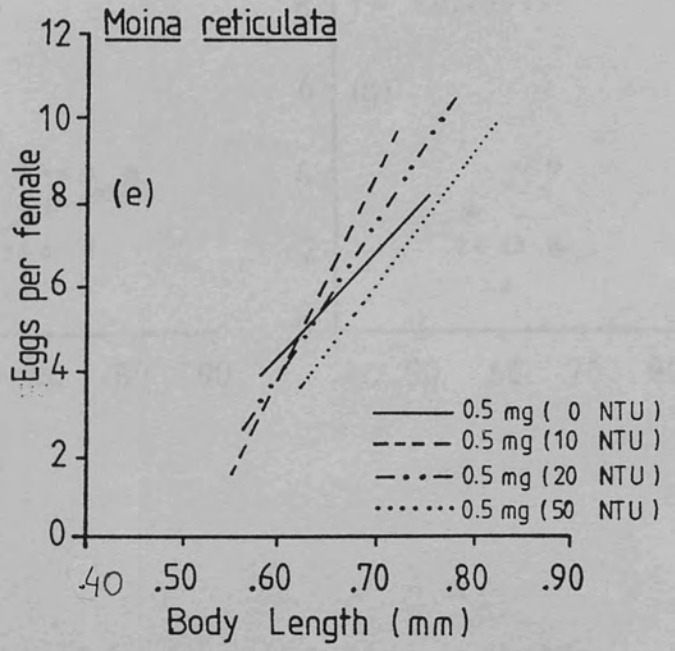


FIGURE 7.4 continued

CONTINUOUS FLOW 27°C

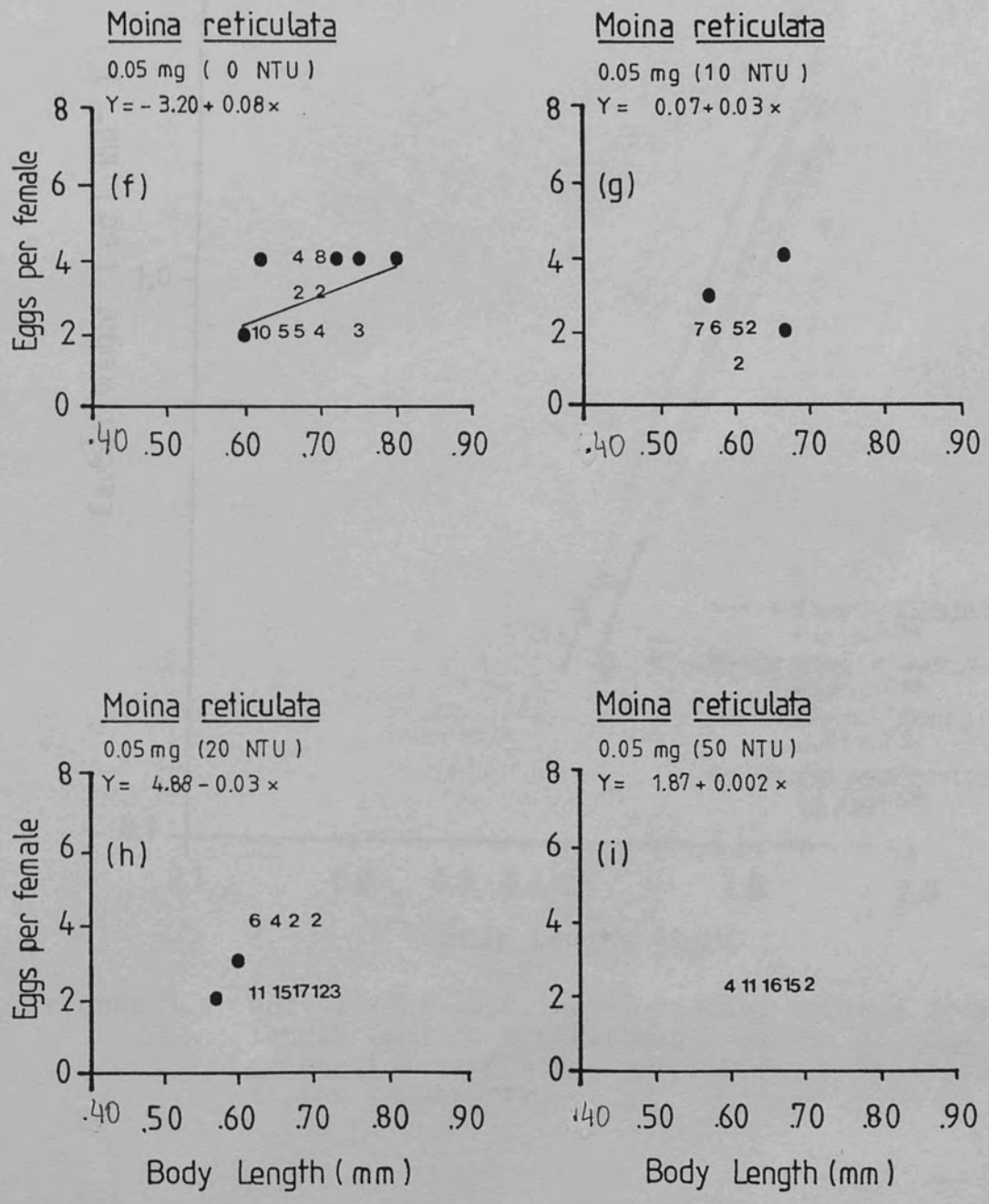


FIGURE 7.4 continued

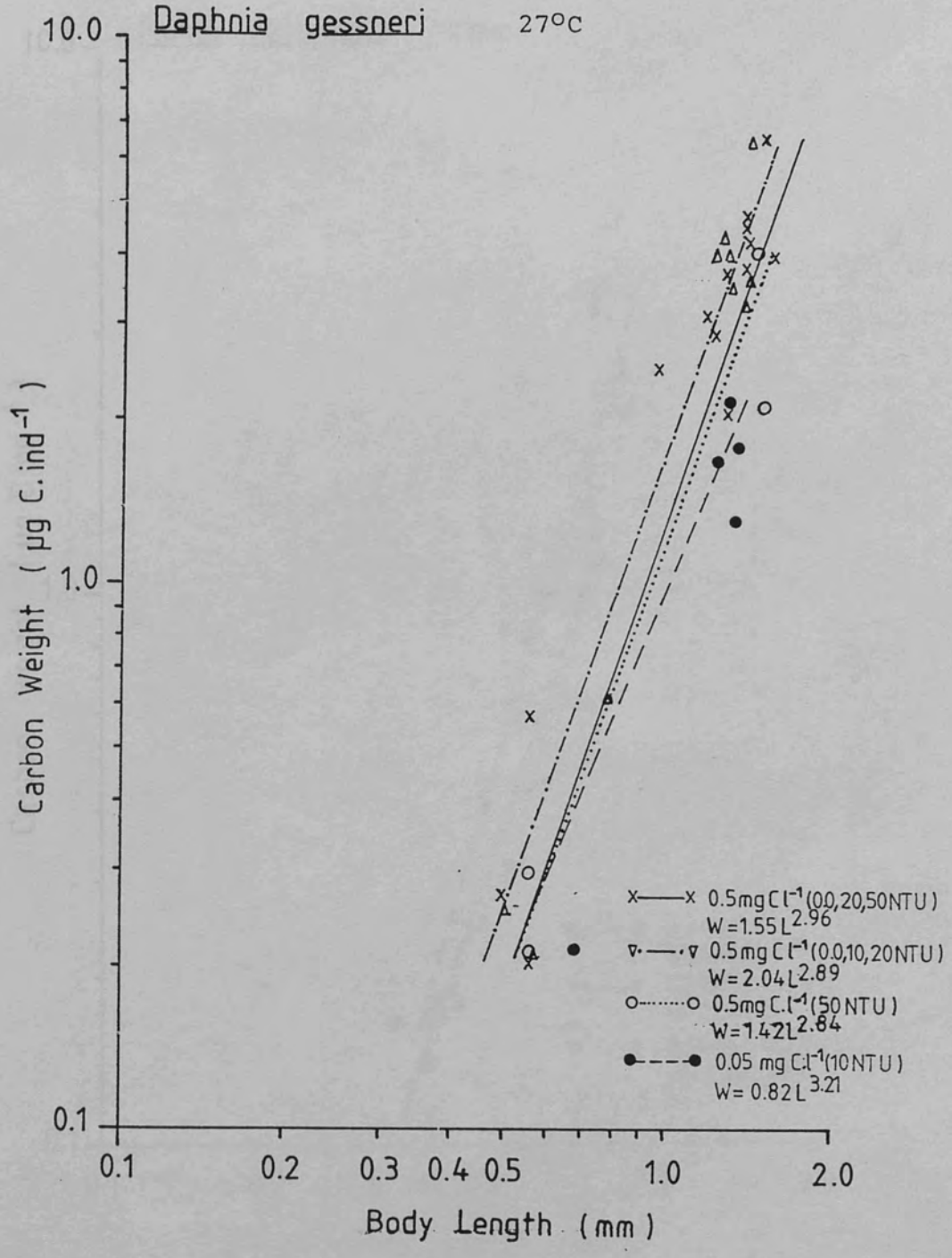


FIGURE 7.5 Body weight (ugC.ind^{-1}) plotted against body length (mm) on logarithmic axes for Daphnia gessneri reared under experimental conditions in the laboratory.

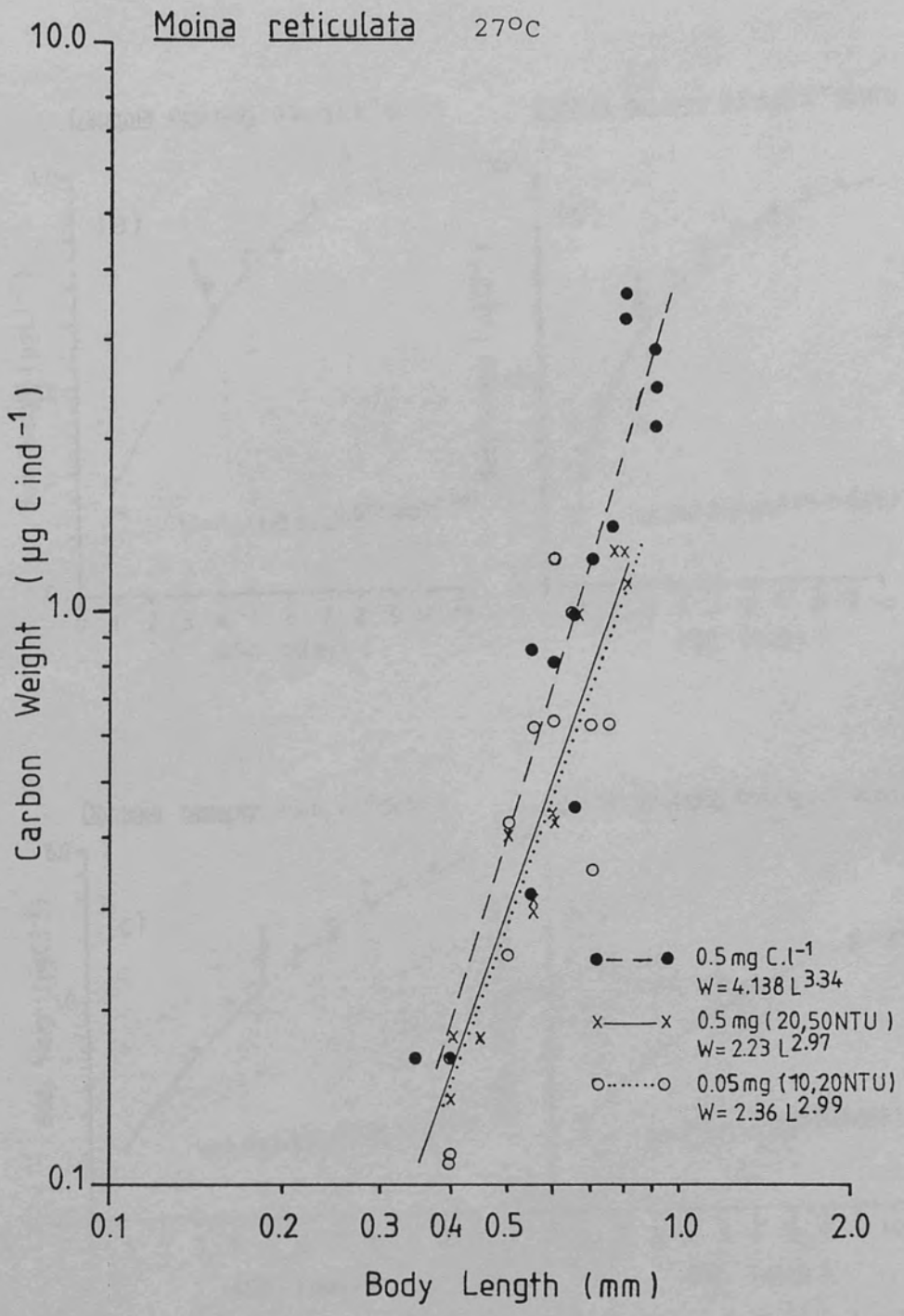


Figure 7.6 Body weight (ugC.l^{-1}) plotted against body length (mm) on logathmic axes for Moina reticulata, reared under experimental conditions in the laboratory.

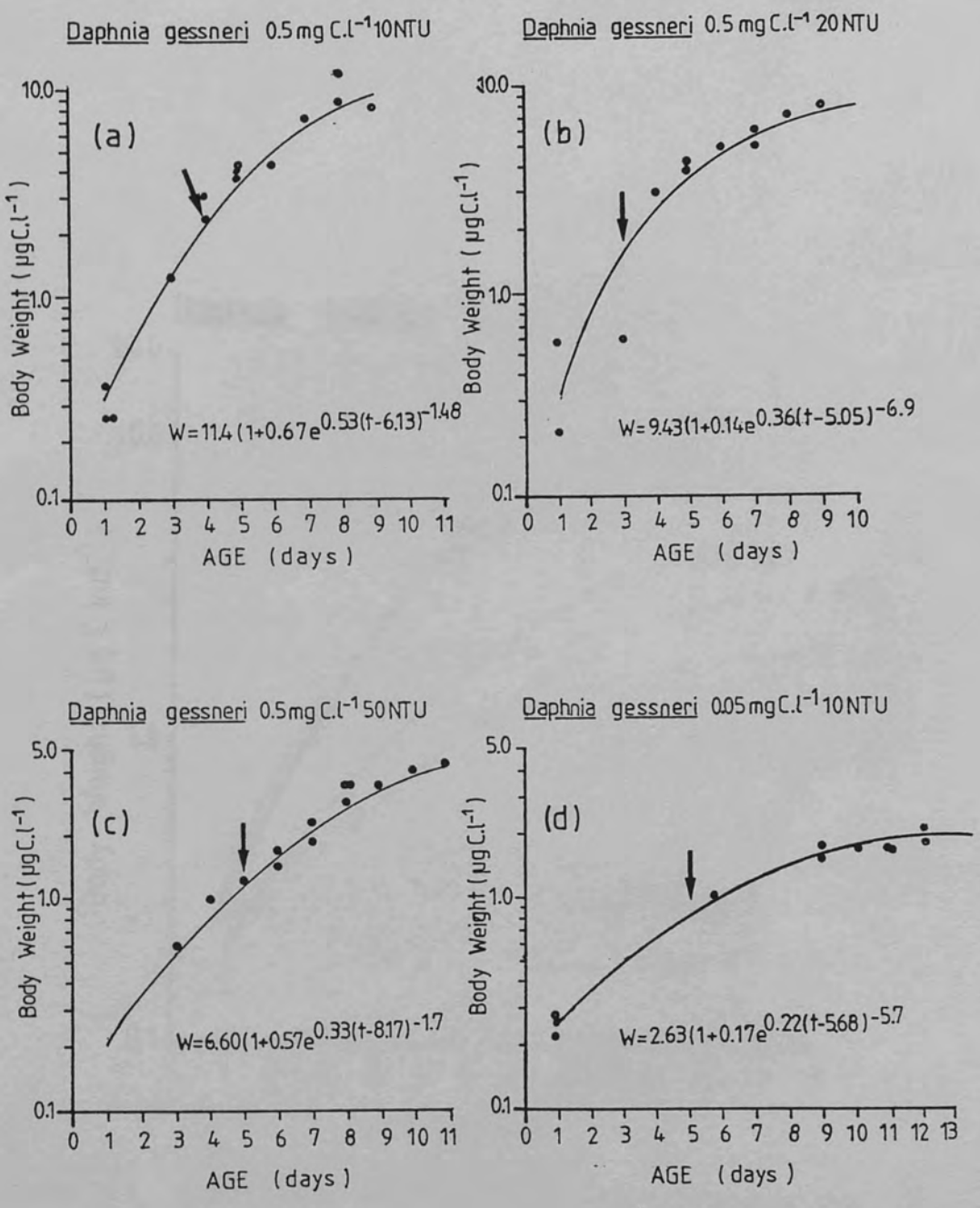


FIGURE 7.7 Richard's growth curves for Daphnia gessneri at various combinations of turbidity(NTU) and two food level, under constant temperature(27°C) The arrow indicates the size and age of the primiparous female.

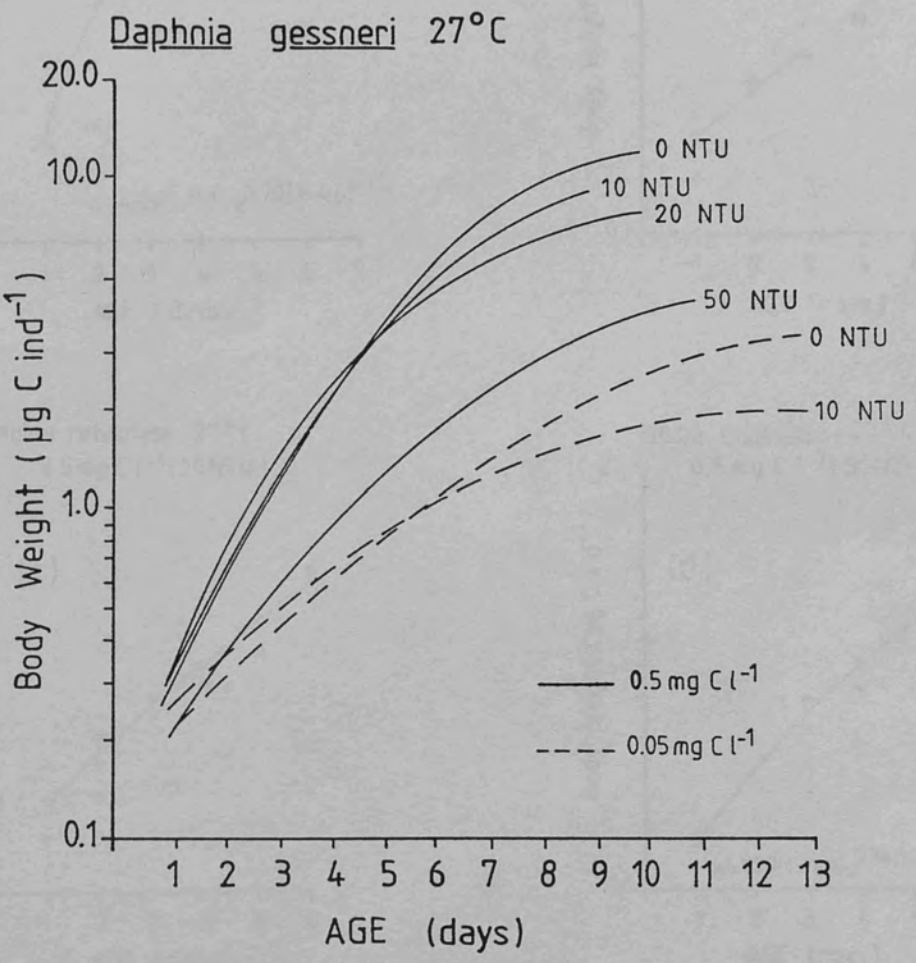


FIGURE 7.8 Comparison of Richard's growth curves for Daphnia gessneri at various turbidity and food treatments.

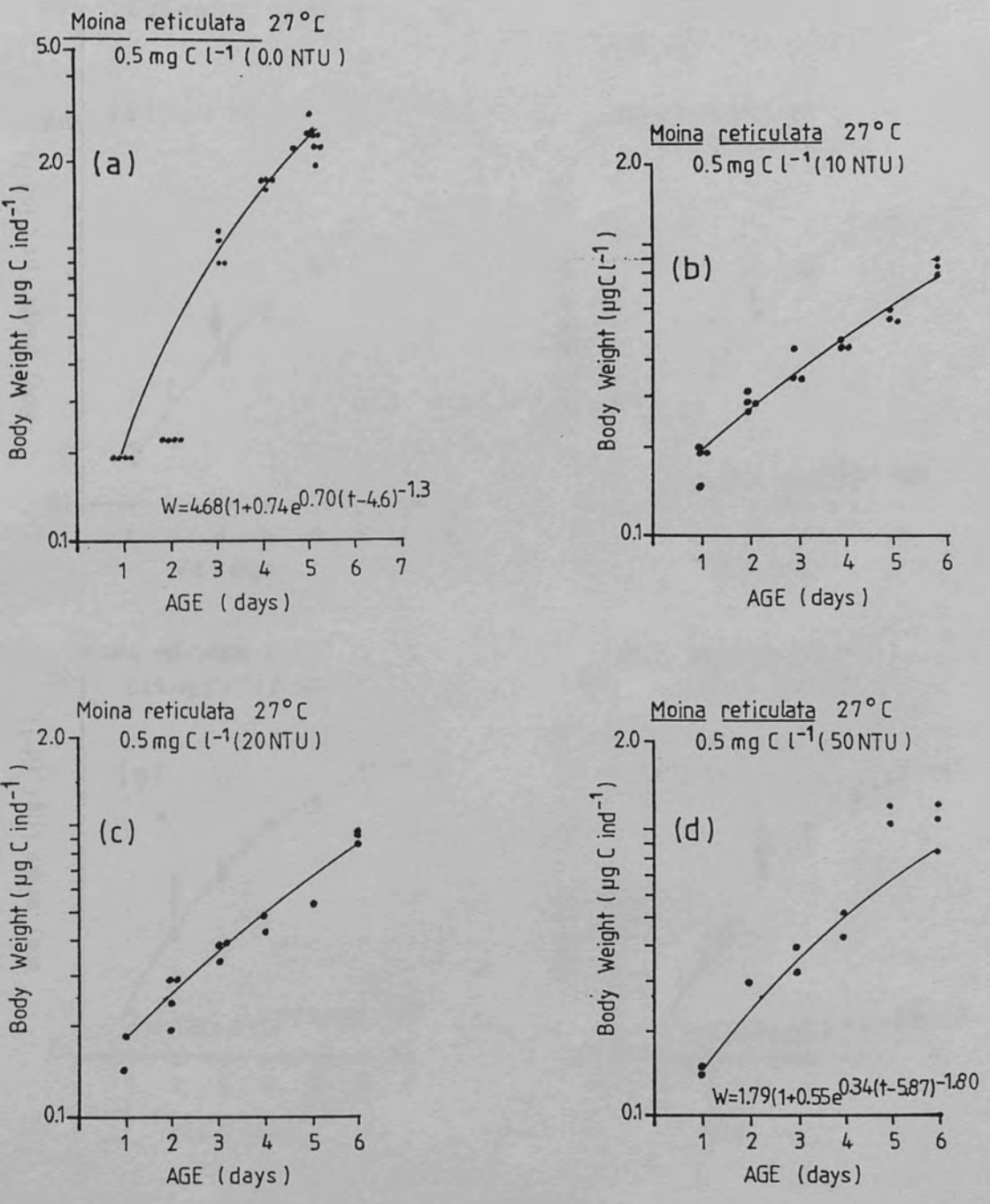


FIGURE 7.9 Richard's growth curves for Moina reticulata at various combinations of turbidity (NTU) and two food level, under constant temperature(27°C). The arrow indicates the size and age of the primiparous female.

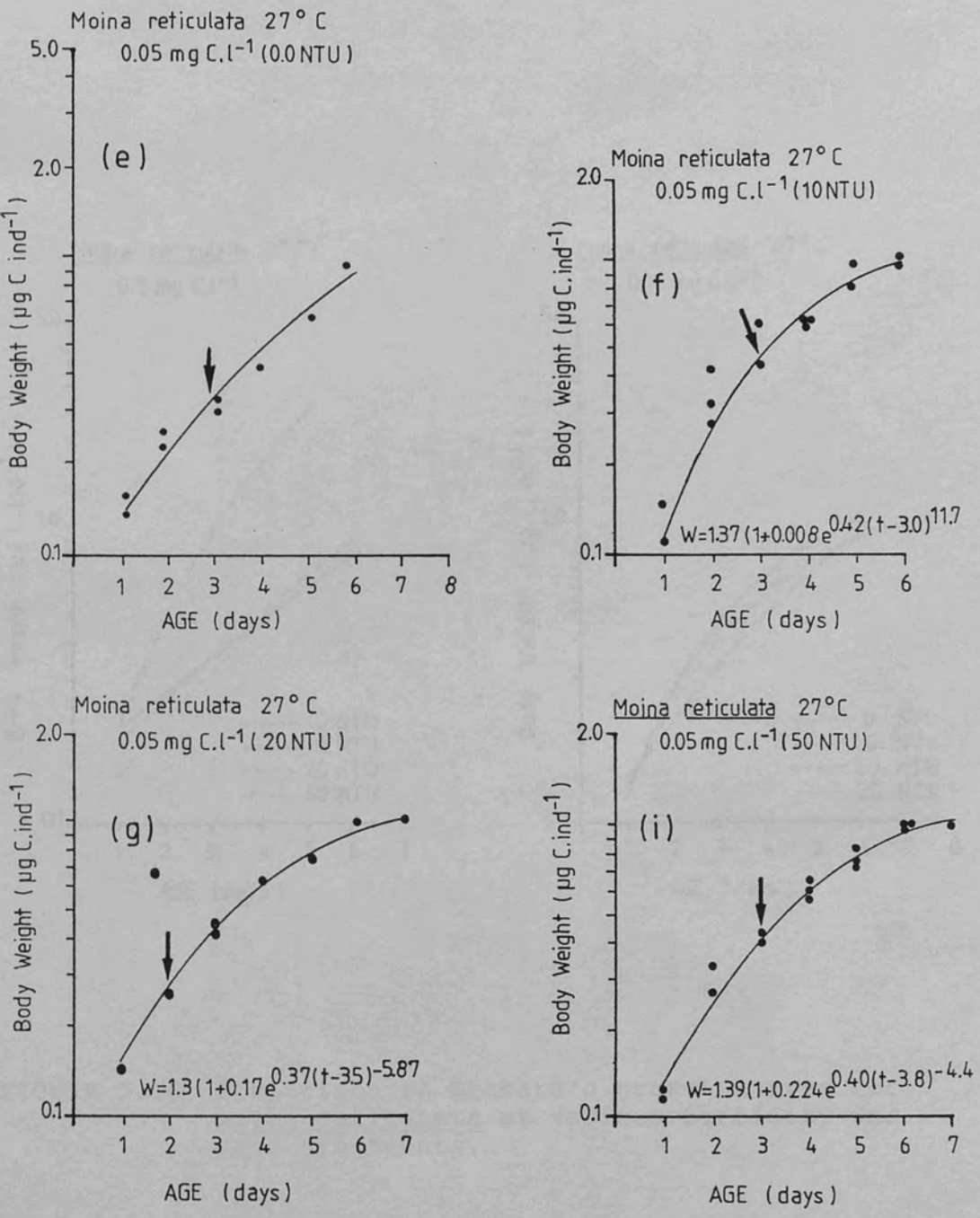


Figure 7.9 continued.

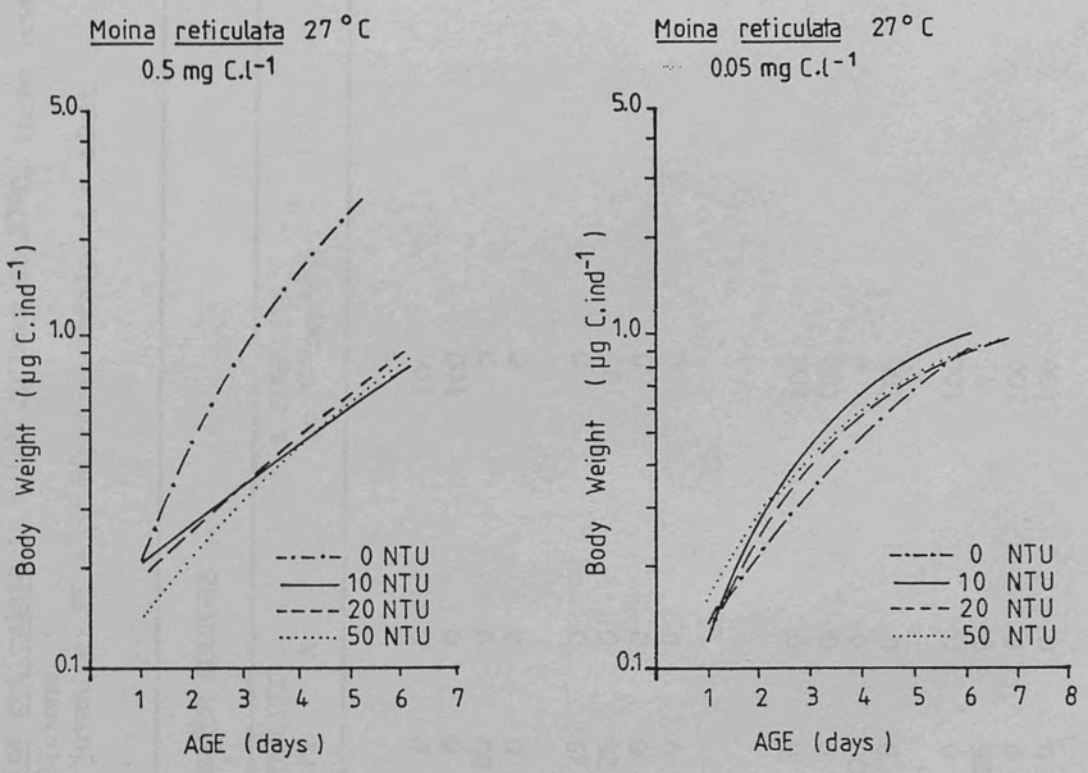


FIGURE 7.10 Comparison of Richard's growth curves for Moina reticulata at various turbidity and food treatments.

TABLE 7.1 Survival of *Daphnia gessneri* and *Moina reticulata* in batch culture at 27°C, three levels of turbidity and high and low food conditions.
N = 4 (number of observations); J = juvenile; PP = primiparous female; A = adult

BATCH CULTURE					
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	% MORTALITY J	PP	A	% SURVIVAL to 3rd brood
Daphnia gessneri					
0.5	0	0	0	0	100
0.5	10	0	0	0	100
0.5	20	0	100	0	0
0.5	50	100	0	0	0
0.05	0	75	25	0	0
0.05	10	0	25	0	75
0.05	20	100	0	0	0
0.05	50	100	0	0	0
Moina reticulata					
0.5	0	0	0	0	100
0.5	10	0	0	0	100
0.5	20	0	100	0	0
0.5	50	0	0	0	100
0.05	0	0	0	0	100
0.05	10	0	25	0	75
0.05	20	0	0	0	100
0.05	50	0	0	0	100

TABLE 7.2 Survival of *Daphnia gessneri* and *Moina reticulata* in continuous flow culture at 27°C and three levels of turbidity and high and low food conditions. N = number of observations; J = juvenile; PP = primiparous female; A = adult

CONTINUOUS FLOW CULTURE						
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	% MORTALITY J	PP	A	% SURVIVAL to 3rd brood	N
Daphnia gessneri						
0.5	0	0	0	0	100	15
0.5	10	0	0	0	100	15
0.5	20	7	0	7	86	15
0.5	50	33	20	7	40	15
0.05	0	10	5	15	70	20
0.05	10	0	0	34	66	15
0.05	20	100	0	0	0	15
0.05	50	100	0	0	0	20
Moina reticulata						
0.5	0	0	0	0	100	15
0.5	10	6	14	0	80	18
0.5	20	0	8	0	92	19
0.5	50	0	0	21	79	19
0.05	0	20	20	0	60	15
0.05	10	40	0	0	60	15
0.05	20	0	7	62	31	15
0.05	50	10	0	50	40	15

TABLE 7.3 Parameters of the linear regressions relating eggs per female to body length (mm) of Daphnia gessneri reared at 27°C in different concentrations of food and turbidity (NTU) in batch culture.
Regression equation: Y = a + bx
X = body length (mm); Y = number of eggs per female

BATCH CULTURE						
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	a	b	df	F	P
0.5	0	- 9.3	11.50	1,10	21.6	0.000
0.5	10	-17.0	18.67	1,5	3.79	0.090
0.05	10	12.6	- 7.84	1,8	0.48	0.500

FLOW CULTURE						
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	a	b	df	F	P
0.5	0	- 17,6	19.34	1,48	80.31	0.000
0.5	10	- 19.5	21.71	1,37	47.08	0.000
0.5	20	- 32.9	33.58	1,24	83.13	0.000
0.5	50	- 7.0	8.87	1,44	48.44	0.000
0.05	0	- 8.2	9.85	1,40	66.25	0.000
0.05	10	5.0	- 2.21	1,22	0.28	0.660 NS

TABLE 7.4 Covariance analysis of the significant regressions of fecundity against adult length (mm) at two food concentrations and three concentrations of turbidity in continuous flow culture at 27°C for Daphnia gessneri. The regression coefficients are compared by the SS-STP test and the differences between the elevations by the S-N-K test. Regression coefficients at P = 0.05 or the adjusted means underlined are not significantly different. df = degress of freedom; F = variance ratio; P =level of significance.

			Comparison of the regression coefficients				
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
0.5	0	1	19.34±1.75	2,244	15.48	0.004	4 5 1 2 3
0.5	10	2	21.71±2.85				
0.5	20	3	33.58±3.42				
0.5	50	4	8.87±1.23				
0.05	0	5	9.85±1.57				
			Comparison of the regression elevations				
$mgC.l^{-1}$	NTU	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
0.5	0	1	6.13±1.30	1,119	5.73	0.018	1 2
0.5	10	2	7.00±1.30				
0.5	10	2	6.19±1.29	1,79	2.79	0.090	2 3
0.5	20	3	6.89±1.29				
0.5	50	4	3.36±0.69	1,107	0.03	0.85	4 5
0.5	0	5	3.33±0.69				

TABLE 7.5 Summary of the results of batch and flow experiments giving the mean fecundity (eggs per three broods per female) for Daphnia gessneri reared at two food concentrations and three concentrations of turbidity(NTU) at constant temperature (27°C).
SD = Standard deviation

BATCH CULTURE

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	MEAN FECUNDITY eggs per female		
		X	±SD	N
0.5	0	7.8	2.1	12
0.5	10	5.8	2.7	9
0.5	20	4.2	0.5	4
0.5	50	no reproduction		
0.05	0	1.0	0.0	1
0.05	10	2.7	1.5	10
0.05	20	no reproduction		
0.05	50	no reproduction		

Continuous flow culture

mgC.l^{-1}	NTU	MEAN FECUNDITY		
		X	±SD	N
0.5	0	6.6	2.9	65
0.5	10	6.3	2.8	48
0.5	20	6.6	3.1	33
0.5	50	3.5	1.3	55
0.05	0	3.1	1.3	53
0.05	10	2.3	0.9	29
0.05	20	no reproduction		
0.05	50	no reproduction		

TABLE 7.6 Parameters of linear regressions relating fecundity (eggs per three broods per female) to the size of the mother at different combinations of food and turbidity at 27^{0}C for Moina reticulata in batch culture .

Regression equation: Y = a + bx
(Y = number of eggs per three broods per female; X = adult length in mm); df = degrees of freedom; F = variance ratio; P = level of significance; NS = not significant.

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	a	b	df	F	P
0.5	0	- 46.25	67.1	1,10	80	0.000
0.5	10	- 20.57	37.8	1,10	66	0.000
0.5	20	0.25	5.0	1,2	1	NS
0.5	50	- 5.00	16.3	1,10	8.5	0.001
0.05	0	- 16.0	26.8	1,8	9.7	0.01
0.05	10	0.89	1.6	1,10	0.26	NS
0.05	20	3.68	- 2.9	1,10	0.37	NS
0.05	50	0.87	0.87	1,7	0.09	NS

TABLE 7.7 Covariance analysis of the significant regressions of fecundity against adult length (mm) at two food concentrations and three concentrations of turbidity in batch culture at 27°C for Moina reticulata. The regression coefficients are compared by the SS-STP test and the difference between the elevations by the S-N-K test. Regression coefficients at P = 0.05 or the adjusted means underlined are not significantly different.

df = degrees of freedom; F = variance ratio; P = levels of significance.

FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	GROUP	Comparison of the regression coefficients REGRESSION COEFF.±SE	df	F	P	SS-STP
0.5	0	1	67.1±7.5	2,30	16.0	0.000	3 2 1
0.5	10	2	37.8±4.6				
0.5	50	3	16.3±5.6				

TABLE 7.8 Parameters of linear regressions relating fecundity (eggs per three broods per female) to the size of the mother at different combinations of food and turbidity at 27°C for Moina reticulata in a continuous flow culture.

Regression equation: $Y = a + bx$
Y = number of eggs per three broods per female; X = adult length im mm; df = degrees of freedom; F = variance ratio; P = level of significance; NS = not significant

FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	a	b	df	F	P
0.5	0	-13.25	0.278	1,10	100.2	0.000
0.5	10	-22.02	0.418	1,13	160.4	0.000
0.5	20	-19.89	0.375	1,14	136.4	0.000
0.5	50	-19.18	0.338	1,11	72.6	0.000
0.05	0	- 3.20	0.008	1,45	9.6	0.000
0.05	10	0.07	0.033	1,24	1.2	0.27 NS
0.05	20	4.88	- 0.037	1,73	1.9	0.17 NS
0.05	50	1.08	0.015	1,52	0.62	0.43 NS

TABLE 7.9 Covariance analysis of the significant regressions of body size and fecundity of Moina reticulata reared in continuous flow culture at 27°C at different levels of food-turbidity concentrations. The regression coefficients are compared by the SS-STP test and the differences between the elevations by the S-N-K test. Regression coefficients or adjusted means underlined are not significantly different at P = 0.05. Group numbers are given in ascending order of magnitude.

df = degrees of freedom; F = variance ratio; P = level of significance

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
0.5	0	1	0.27±0.02	3,48	2.5	0.067	1 2 3 4
0.5	10	2	0.41±0.03				
0.5	20	3	0.37±0.03				
0.5	50	4	0.33±0.03				

Comparison of the regression elevations

mgC.l^{-1}	NTU	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
0.5	0	1	6.27±0.51	3,52	14.1	0.000	4 1 3 2
0.5	10	2	7.01±0.51				
0.5	20	3	6.35±0.51				
0.5	50	4	4.37±0.52				

TABLE 7.10 The mean fecundity (eggs per three broods per female) of Moina reticulata when reared at high and low food levels and three concentrations of turbidity in a constant temperature(27°C). A summary of experiments with batch and continuous flow cultures.

SD = Standard deviation

BATCH CULTURE

FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	MEAN FECUNDITY eggs per female		
		X	±SD	N
0.5	0	9.6	4.0	12
0.5	10	9.8	3.2	12
0.5	20	3.7	0.5	4
0.5	50	7.7	1.8	12
0.05	0	3.7	1.1	10
0.05	10	1.0	0.2	12
0.05	20	1.7	0.4	12
0.05	50	1.3	0.5	11

CONTINUOUS FLOW CULTURE

$mgC.l^{-1}$	NTU	X	±SD	N
0.5	0	5.9	2.1	12
0.5	10	5.6	3.4	15
0.5	20	6.2	3.5	16
0.5	50	6.3	2.8	13
0.05	0	2.7	0.9	47
0.05	10	2.0	0.5	26
0.05	20	2.3	0.8	81
0.05	50	2.0	0.3	55

TABLE 7.11 The age in days, the instar stage and mean fecundity of the primiparous female Daphnia gessneri when reared at 27°C in batch and continuous flow cultures at different concentration of food and turbidity
SD = Standard deviation

BATCH CULTURE

FOOD LEVEL mg C.l^{-1}	TURBIDITY NTU	AGE days	INSTAR	FECUNDITY eggs per female X	±SD
0.5	0	4	V	5.0	1.6
0.5	10	4	V	4.0	0.0
0.5	20	4	V	4.2	0.5
0.5	50			juveniles died	
0.05	0	5	V	1.0	
0.05	10	5-6	VI	4.6	1.1
0.05	20	3		juveniles died	
0.05	50	3		juveniles died	

CONTINUOUS FLOW CULTURE

MgC.l^{-1}	NTU	AGE days	INSTAR	FECUNDITY eggs per female X	±SD
0.5	0	4	V	3.9	1.4
0.5	10	4	V	3.6	1.2
0.5	20	4	IV-V	3.9	0.9
0.5	50	4	IV	2.3	1.0
0.05	0	4-5	V	1.9	0.4
0.05	10	4	V	2.0	1.0
0.05	20			juveniles died	
0.05	50			juveniles died	

TABLE 7.12 The mean length (mm) of the primiparous females of Daphnia gessneri and Moina reticulata when reared at 27°C in batch and in continuous flow cultures at different concentrations of food and turbidity.

Sd = Standard deviation

Daphnia gessneri — BATCH CULTURE

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	BODY LENGTH(mm) X	±SD	N
0.5	0	1.25	0.02	4
0.5	10	1.07	0.05	4
0.5	20	1.10	0.01	4
0.5	50	no reproduction		
0.05	0	1.05	0.0	1
0.05	10	1.11	0.08	4
0.05	20	no reproduction		
0.05	50	no reproduction		

CONTINUOUS FLOW CULTURE

mgC.l^{-1}	NTU	X	±SD	N
0.5	0	1.11	0.04	15
0.5	10	1.12	0.05	19
0.5	20	1.10	0.05	15
0.5	50	1.06	0.05	13
0.05	0	1.01	0.01	8
0.05	10	1.10	0.03	7
0.05	20	no reproduction		
0.05	50	no reproduction		

TABLE 7.12 continued.

Moina reticulata	BATCH CULTURE			
FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	BODY LENGTH (mm) X	±SD	N
0.5	0	0.63	0.02	4
0.5	10	0.61	0.04	4
0.5	20	0.60	0.03	4
0.5	50	0.66	0.02	4
0.05	0	0.58	0.02	4
0.05	10	0.54	0.01	4
0.05	20	0.58	0.02	4
0.05	50	0.57	0.02	4
	CONTINUOUS FLOW CULTURE			
$MgC.l^{-1}$	NTU	X	±SD	N
0.5	0	0.60	4.1	14
0.5	10	0.59	2.3	13
0.5	20	0.60	3.5	21
0.5	50	0.67	2.9	10
0.05	0	0.61	0.02	10
0.05	10	0.56	0.02	9
0.05	20	0.62	0.01	8
0.05	50	0.62	0.02	11

TABLE 7.13 The age in days, the instar stage and mean fecundity of the primiparous female Moina reticulata when reared at 27°C in batch and continuous flow cultures at different concentration of food and turbidity.

SD = Standard deviation

Moina reticulata		BATCH CULTURE			
FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	AGE days	INSTAR	FECUNDITY eggs per female X	±SD
0.5	0	2-3	III-IV	5.5	0.5
0.5	10	2-3	III-IV	8.0	2.0
0.5	20	2-3	III	6.4	2.2
0.5	50	2-3	III-IV	6.2	0.9
0.05	0	3	III	2.7	0.5
0.05	10	3	III	2.0	0.0
0.05	20	3	III	1.7	0.5
0.05	50	3	III-IV	1.5	0.5
		CONTINUOUS FLOW CULTURE			
mgC.l^{-1}	NTU	days	INSTAR	eggs per female X	±SD
0.5	0	2	III	2.5	4.0
0.5	10	2-3	III-IV	2.5	4.0
0.5	20	3	III	4.0	0.0
0.5	50	3	III	4.2	0.6
0.05	0	3	III	2.0	0.0
0.05	10	3	III	2.0	0.0
0.05	20	3	III	2.0	0.0
0.05	50	3	III	2.0	0.0

TABLE 7.14 Parameters of the linear regressions relating organic carbon content (ugC.ind^{-1}) to length(mm) of Daphnia gessneri reared in continuous flow culture at 27°C in different food and turbidity concentrations.
Regression equation: lnY = lna + b lnX
X = body length; Y = ugC.ind^{-1}

FOOD LEVEL	TURBIDITY	ln a	b	df	F	P	
mgC.l^{-1}	NTU						
0.05	0	1.39	2.97	1,5	5.7	0.07	NS
0.05	10	- 0.19	3.21	1,4	46.8	0.006	
0.5	0	0.59	2.80	1,3	62.3	0.01	
0.5	10	0.89	2.45	1,7	21.2	0.003	
0.5	20	0.51	3.46	1,2	195.8	0.014	
0.5	50	0.35	2.84	1,7	164.0	0.000	

TABLE 7.15 Covariance analysis of the significant regressions of organic carbon (ugC.ind^{-1}) against length (mm) at two food concentrations and three concentrations of turbidity in continuous flow culture at 27°C for Daphnia gessneri. The regression coefficients are compared by the SS-STP test and the differences between the elevations by the S-N-K test. Regression coefficients at P = 0.05 or the adjusted means underlined are not significantly different. df = degrees of freedom; F = variance ratio; P = level of significance.

Comparison of the regression coefficients

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
0.05	10	1	3.21±0.46	4,22	0.75	0.56	3 2 5 1 4
0.5	0	2	2.80±0.35				
0.5	10	3	2.46±0.53				
0.5	20	4	3.45±0.07				
0.5	50	5	2.84±0.22				

Comparison of the regression elevations

mgC.l^{-1}	NTU	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
0.05	10	1	0.008±0.14	4,27	8.40	0.000	1 5 4 2 3
0.5	0	2	0.75 ±0.14				
0.5	10	3	1.02 ±0.14				
0.5	20	4	0.67 ±0.14				
0.5	50	5	0.52 ±0.14				

TABLE 7.16 Parameters of the linear regressions relating organic carbon content ($ugC.l^{-1}$) to length (mm) of Moina reticulata reared in continuous flow culture at 27°C in different food and turbidity concentrations.
Regression equation: $\ln Y = \ln a + b \ln X$
X = body length ; Y = Organic carbon ($ugC.ind^{-1}$)

FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	lna	b	df	F	P
0.5	0	1.42	3.34	1,11	70.18	0.000
0.5	20	0.63	2.78	1,4	47.09	0.002
0.5	50	0.87	2.99	1,5	86.71	0.000
0.05	10	1.34	3.55	1,4	16.31	0.001
0.05	20	0.50	2.65	1,3	3.31	0.166 NS

TABLE 7.17 Covariance analysis of the significant regressions of organic carbon (ugC.ind^{-1}) against length (mm) at two food concentrations and three concentrations of turbidity in continuous flow culture at 27°C for Moina reticulata. The regression coefficients are compared by the SS-STP test and the differences between the elevations by the S-N-K test. Regression coefficients at P = 0.05 or the adjusted means underlined are not significantly different. df = degrees of freedom; F = variance ratio; P = level of significance

Comparison of the regression coefficients

FOOD LEVEL mgC.1^{-1}	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
0.5	0	1	3.34±0.39	3,27	0.32	0.81	2 3 1 4
0.5	20	2	2.78±0.40				
0.5	50	3	2.99±0.32				
0.05	10	4	3.56±0.88				

Comparison of the regression elevations

mgC.1^{-1}	NTU	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
0.5	0	1	- 0.21±0.17	3,31	3.67	0.023	2 3 4 1
0.5	20	2	- 0.70±0.17				
0.5	50	3	- 0.60±0.17				
0.05	10	4	- 0.44±0.17				

Table 7.18 Parameters of the Richard's growth equation for fitting growth curves to Daphnia gessneri and Moina reticulata under constant temperature and different food and turbidity concentrations.

Equation: $Wt = W_{max}(1 - b \exp (-g(t-t_o)))^p$

Wt = weight ($ugC.ind^{-1}$) and time t; Wmax = maximum weight attained; to = time of inflection of the curve; g = growth constant; p =exponent; RSS = residual mean square; pp = primipara age in days.

FOOD LEVEL ($mgC.l^{-1}$)	TURBIDITY (NTU)	W_{max}	g	t_o	b	P	RSS	pp
Daphnia gessneri								
0.5	0	14.28	0.59	6.67	-0.79	-1.25	8.00	4
0.5	10	11.46	0.53	6.13	-0.67	-1.48	31.00	4
0.5	20	9.43	0.36	5.05	-0.14	-6.92	2.60	4
0.5	50	6.60	0.33	8.17	-0.57	-1.73	0.64	4
0.05	0	6.68	0.25	11.07	-0.65	-1.51	1.27	4-5
0.05	10	2.63	0.22	5.68	-0.17	-5.67	0.05	4
0.05	20	*	*	*	*	*	*	*
0.05	50	*	*	*	*	*	*	*
Moina reticulata								
0.5	0	4.68	0.70	4.62	-0.74	-1.34	0.99	2-3
0.5	10	**	0.28	**	-1.12	-0.89	0.03	2-3
0.5	20	**	0.33	**	-1.14	-0.87	0.04	3
0.5	50	1.79	0.34	5.87	-0.55	-1.80	0.01	3
0.05	0	2.19	0.34	6.36	-0.55	-1.79	0.08	3
0.05	10	1.37	0.42	3.04	0.008	117.51	0.04	3
0.05	20	1.36	0.37	3.49	-0.17	-5.87	0.01	3
0.05	50	1.39	0.40	3.77	-0.22	-4.46	0.02	3

* no growth
** undefinable in this data set

7.19 Parameters of the linear regressions relating carbon weight (ugC.ind^{-1}) to length (days) of Daphnia gessneri and Moina reticulata during the period of exponential growth when reared at two food levels and three turbidities. at 27°C.

Equation: lnW = lna + bX
W = weight (ug.ind^{-1}); X = age (days)

Daphnia gessneri

FOOD LEVEL mgC.l^{-1}	TURBIDITY NTU	RANGE OF WEIGHT ugC.ind^{01}	ln a	b±SE	df	F	P	r
0.5	0	0.26-12.8	- 1.36	0.44±0.02	1,20	280	0.000	0.93
0.5	10	0.26-12.8	- 1.44	0.46±0.04	1,13	109	0.000	0.95
0.5	20	0.21- 7.8	- 1.05	0.37±0.05	1,10	40	0.000	0.90
0.5	50	0.22- 4.5	- 1.44	0.29±0.01	1,10	251	0.000	0.98
0.05	0	0.20-3.5	- 1.45	0.23±0.0008	1,32	894	0.000	0.98
0.05	10	0.22-2.2	- 1.58	0.20±0.02	1,5	73	0.001	0.97
0.05	20	*						
0.05	50	*						

* no growth

TABLE 7.19 continued.

Moina reticulata

FOOD LEVEL $mgC.l^{-1}$	TURBIDITY NTU	RANGE OF WEIGHT $ugC.ind^{-1}$	ln a	b±SE	df	F	P	r
0.5	0	0.19-3.13	- 2.21	0.59±0.04	1,23	206	0.000	0.95
0.5	10	0.14-0.90	- 1.89	0.28±0.01	1,17	255	0.000	0.97
0.5	20	0.14-1.00	- 2.07	0.33±0.04	1,9	60	0.000	0.93
0.5	50	0.15-0.90	- 2.11	0.33±0.02	1,10	196	0.000	0.97
0.05	0	0.12-1.00	- 2.23	0.37±0.03	1,11	136	0.000	0.96
0.05	10	0.10-1.00	- 2.05	0.38±0.05	1,12	59	0.000	0.91
0.05	20	0.14-1.00	- 1.99	0.32±0.04	1,6	61	0.000	0.96
0.05	50	0.12-1.00	- 2.16	0.36±0.03	1,13	112	0.000	0.95

CHAPTER 8

THE ECOLOGY OF PLANKTONIC CLADOCERA IN LAKE JACARETINGA

Lake Jacaretinga is a shallow varzea lake which is subjected to great variation in its depth and area during each year. In 1986, the limnology of the lake was studied more intensively than it had ever been done before by weekly sampling from February to April, a period which included the end of the low water season and the beginning of the river flooding. The aim of the study was to follow the fate of the populations of planktonic cladocerans during the natural perturbations of the flooding and with the arrival of flood waters carrying the highly turbid waters of the River Solimoes-Amazon, which started between 19^{th}-26^{th} March 1986. This chapter deals with the species composition of the cladocerans, their density and horizontal distribution and considers the effects that high turbidity may have on the structure of the zooplankton community. Details of methodology are provided in chapter 3.

8.1 The limnology of Lake Jacaretinga

A range of physical and chemical environmental factors were measured at weekly intervals and simultaneously with chlorophyll a and sestonic carbon levels and more detailed sampling of the zooplankton. These environmental measurements were carried out only at Station 1 (Chapter 2), which represented the central point of the lake. Figure 8.1 (a,b,c,d,) presents the results of these measurements.

Figure 8.1 shows that the depth of the lake fluctuate from 1.8 m at the end of February to 4.0 m by the end of April, as a result of the entry of the river water from the end of March onwards. Thus, the water depth doubled in two months. The same figure shows that the water transparency of the lake water declined with the influx of water from the white water river. The Secchi disc depth decreased from 1.40 m at the beginning to 0.7 m towards the end largely due to the increased presence of large quantities of inorganic particles in

suspension. In order to quantify the amount of particles in the water, samples were collected in April 26th and kept refrigerated for approximately two weeks before beginning the analysis at RHBNC using a Coulter Counter with 140 um tube. Results indicated the following: Amazon River ($16.180.10^6$ μm^3 ml^{-1}) and Lake Jacaretinga ($3.220.10^6 \mu m^3$ ml^{-1}). It is clear that the river contains a much higher level of particles than the lake (about 7 times more). There is some information about these in chapter 1.

The water temperature of the lake was measured at two depths and the mean temperature of these varied very little with time, between 27.5°C and 30.8°C. As is to be expected, the surface temperature was more variable than the bottom one, as can be seen in figure 8.1b. Although the thermal pattern was rather unvarying throughout the study period, with an overall average of 28°C, there were large differences in the concentration of dissolved oxygen, both between the surface and bottom samples and with time between the low and high water phases. Figure 8.1c shows that the highest oxygen concentrations was 3.0 $mg.l^{-1}$ in the surface water when the depth of the lake was only 1.80 m. As water depth increased, the oxygen content of the water declined to 1.0 $mg.l^{-1}$ and there appeared a zone of anoxia at the bottom from mid-March onwards. Even at these high temperatures, the level of dissolved oxygen is very low in the lake; at 28°C, 3 $mg.l^{-1}$ represents 36% saturation and 1.0 $mg.l^{-1}$, only 11%.

In order to obtain some idea of the level of food available to the cladoceran populations in Lake Jacaretinga, the chlorophyll a and sestonic carbon were measured at weekly intervals as the concentrations of the fractions which passed through a 55 µm and a 20 um mesh. On some occasions, the fraction passing through 10 µm mesh was also determined but this proved to be not different from the less than 20 µm fraction and is therefore not used. Figure 8.1d illustrates how the concentrations of the less than 55 µm fractions of chlorophyll a and particulate organic carbon (POC) changed with time and less than 20 µm fraction will be dealt with in more detail in the next section. The chlorophyll a concentration became very low and minimal immediately on the onset of the high water phase but reached a maximal

value of 14 $\mu g.l^{-1}$ by the middle of April. A similar changeover from low values in the low water phase to higher values in the high water phase was also recorded for the particulate sestonic carbon. The highest value of 3.4 $mgC.l^{-1}$ was reached in mid-April, a week earlier than the chlorophyll a. This pattern suggests that the reduced water transparency [illegible] of this period is associated with organic as well as mineral particles transported by the river into the lake.

8.2 The species composition, population densities and succession of the Cladocera.

Seven species of Cladocera and four species of Copepoda were recorded from the limnetic zone of Lake Jacaretinga during February, march and April 1986. The scientific names of these species are listed in Table 8.1. Other animals present in the zooplankton were rotifers and the predatory Chaoborus sp. Only the cladoceran species were considered in any detail.

The zooplankton was sampled by mean of three replicate samples at five satations in the lake, using a technique which provided an integrated sample for the whole water column. The mean density and percentage abundance of each of the five species of cladocerans on ten sampling dates are presented in table 8.2 and illustrated in figure 8.2. These show a strong pattern of succession of species. As can be seen in figure 8.2, Diaphanosoma sarsi was dominant in the early samples, followed by Ceriodaphnia cornuta and Daphnia gessneri, each species declining as the next one took over. Moina reticulata contributed only 10% of the individuals during this low water phase but, in sharp contrast, became the dominant species immediately after the flood and during the whole of the high water phase. Moina minuta, on the other hand, rarely contributed more than 5% of the animals and appeared to be of minor importance although it was present throughout. Bosminopsis deitersi and Bosmina sp. were both recorded but were always rare (less than 1%) and were not considered further in these studies.

When the species are considered in the other of their appearance in the sucession, table 8.2 shows that Diaphanosoma sarsi was the first to achieve a maximal mean density of 15 ind.l^{-1} on February 25th and then rapidly declined to less than 1 ind.l^{-1} before the end of the low water phase. Although there was a second small peak abundance of about 4 ind.l^{-1} immediately after the flood, this did not last long and the species disapeared during the high water phase. Table 8.3 shows that male Diaphanosoma sarsi appeared throughout the low water phase but only one epphipial female was recorded on March 26th 1986.

Ceriodaphnia cornuta built up its population densities during February and March to peak at 29 ind.l^{-1} on March 11th, two weeks after Diaphanosoma sarsi. Its densities declined to 2 ind. l^{-1} or less with the onset of the flooding of the river from March 19th-26th and disappeared during the whole of the high water phase. Table 8.3 shows that no males were recorded for the Ceriodaphnia population but epphippial females appeared during the period of high population densities.

Individuals of Daphnia gessneri were present on most sampling dates but in variable densities (0-30 ind.l^{-1}). Table 8.2 shows two peak abundances, 31.5 ind .l^{-1} on March 4th before the flood dates and 19.7 ind.l^{-1} on March 26th which coincided with the influx of the white water. During its second peak, Daphnia gessneri contributed the highest percentage (50%) of the cladoceran fauna but immmediately afterwards declined to less than 1 ind.l^{-1}, which formed only 4% of the cladocerans. Male and ephippial individuals were recorded on three occasions between March 11th and April 8th which include the periods of high densities.(Table 8.3).

The population of Moina reticulata was present throughout the period of study but with widely fluctuating densities, from 1-79 ind.l^{-1}. Densities were low during the low water phase, 1-3 ind.$^{-1}$ and less than 10% of all the animals. However, the influx of white water was followed by a period of increasing densities of this species until it attained a density of 79 ind.l^{-1} on April 15th 1986. From April 1st onwards and during the whole high water phase, this species contributed 88% or more of the cladocerans. Sexual individuals, males

and ephippial females, were present throughout but were particularly abundant during the full flood phase in April and during population peak densities. Up to 20 males per litre were recorded on April 15th.

As in Moina reticulata, Moina minuta was present throughout the period of study but in much lower densities. Its peak abundance of 10.38 ind.l^{-1} also occurred on April 15th during the flood but did not last long and densities soon declined to less than 1 ind.l^{-1}. Unlike Moina reticulata, male and ephippial female Moina minuta were recorded only during the high water phase, from April 8th onwards

Table 8.4 presents the percentage of adult females with eggs or embryos in each of the five cladoceran species during the field study. It seems that only the two species of Moina reticulata produced eggs throughout the whole duration of the study, notably in the flood period after March 26th, when up to 35% of the Moina minuta was breeding. In contrast to this situation, egg-bearing females of Daphnia gessneri were more abundant only before and immediately after the flood, comprising 3% of the population. Ceriodaphnia cornuta carrying egg/embryos were found only before the flood. The highest abundance occurred in February 25th (4%). The same pattern was observed for Diaphanosoma sarsi, except that 2% of the egg-bearing females were found immediately after the influx of the white water.

The number of eggs or embryos per gravid female could be calculated reliably only for Moina reticulata and Daphnia gessneri and these values for fecundity are given in Table 8.5. The fecundity of Moina reticulata varied between 2-5 eggs per gravid female throughout the period of study and appears to differ very little. However, calculation of the 95% confidence limits shows that the fecundity was higher after the onset of and during the flood than before (Figure 8.3). Daphnia gessneri was able to produce similar numbers of eggs per gravid female before and after the flood, at about 5 eggs per female, but only for a very short time, although the fecundity was somewhat lower on March 11th which was the date for peak densities of Ceriodaphnia cornuta.

8.3 Horizontal distribution of cladoceran species

Table 8.6 gives the population density of the cladoceran in five stations of the Lake Jacaretinga (map given in chapter 2). Samples were taken by integrating the whole column of water from bottom to surface using Patalas-Schindler (detail in chapter 3). The results given by numbers of individuals per litre are means of three replicates for each species.

Comparisons between stations for the horizontal distribution of each cladoceran are illustrated in Figure 8.4. From the results in Table 8.6 and figure 8.4 can be seen that there is no consistent pattern of density for any species in a single station.

Diaphanosoma sarsi was recorded at all stations during the period before the flood with the highest densities at station I (mid-lake) and station III on February 25th. The lowest densities in general occurred at stations II (canal) and V. After the flood phase D.sarsi was not recorded at any station.

Ceriodaphnia cornuta , also recorded in all 5 stations did vary in density between stations but changes were much more extent in time. Stations II and V had the lowest densities. Just before the flood the peak density was observed in stations I and III for a very short time as given in Figure 8.4 then this species declined drastically to disappear completely after the flood-phase.

Daphnia gessneri was present throughout the low-water phase in highest densities, but did not occur in station II and V on February 25th. Its peak density was coinciding with the flood on March 26th particularly in stations II and V. The minimum density during this time occurs in station IV. As can be seen from the Table 8.6 and Figure 8.4 this species also declined severely in the high-water phase.

Moina reticulata, was present throughout the whole period of the study in all staions. The highest density was recorded during the high-water phase particularly in station V, on April 15th (note different values in the scale of figure 8.4), with a peak density of

185.0 ind.l^{-1}. There was a general trend to low densities before the flood (<1 to 7.0 ind.l^{-1}).

As present in Figure 8.4., Moina minuta was find in very small numbers. At the low-water phase the maximum density observed was in station III with 7.0 ind.l^{-1}, then in high-water phase a short increase was recorded in stations I and V respectively with 16.0 and 23.0 ind.l^{-1}.

In order to compare stations statistically analyses of the densities for each species were tested. Kolmogorov-Smirnov test was used to test normality and the results showed to have normal distribution. Also comparisons of the horizontal distribution were computed by ANOVA -one way classification with Student-New-Keuls test (SNK). The results are given in Appendix 8.1 , showing that there is no consistent pattern of similarities between stations although it seems that during the low-water phase, stations II and V were not significantly different from each other showing in general the lowest densities. No clear pattern has been seen during the high water-phase.

8.4 Length-carbon weight regression of the cladoceran species

There are evidence in the literature that the nutricional condition due to seasonal variation of temperate Daphnia species affects their carbon weight-length relationship (Rocha,1983; Duncan,1985). Seasonal variation in carbon weight-length relationships within a tropical species were obtained by Jayatunga (1986) from Kalawewa reservoir, Sri Lanka for Diaphanosoma excisum, Moina micrura, Moina micrura, Daphnia lumholtzi and Ceriodaphnia cornuta.

Considering that L.Jacaretinga is subjected to seasonal variation during the year (section 8.1) an attempt was made in the present section to establish carbon-length relationship for some species during the period of February-April 1986 for further comparisons with the species reared at laboratory conditions.

The animals were collected weekly and at INPA sorted out into different size classes, trying to obtain whole range of sizes for each possible species. Their body carbon content was then measured using the dry combustion method (Salonen, 1979). Detail of the procedure is given in chapter 3.

The length carbon-weight relationship computed for three out of five species occurring in the lake include eggs or embryos when they were present. Regressions could be estimated for four dates for Daphnia gessneri and Moina reticulata and only one date for Diaphanosoma sarsi. As given in Table 8.7 all regressions of length on carbon weight for the three species were statistically significant. Plots of these regressions lines and parameters are illustrated in figures 8.5. In order to detect any differences between the regressions of Daphnia gessneri and Moina reticulata at four occasions for the field population, a covariance analysis was performed. From the results given in Table 8.8 it is evident that for Daphnia gessneri there are no significant differences between the slopes and elevations of the February 25th, March 4th and March 15th field regressions, but the April 1st regression shows a significant different slope when compared with the March 4th regression. However in this date Daphnia gessneri was present in the lake in very low numbers thus N=5 is smaller than the other three regressions, and could not be reliable for comparative purposes.

The significant relationship between length and carbon weight of the Moina reticulata from field collected in four occasions is given in Table 8.7. All regressions were statistically significant. The covariance analysis comparing these regressions (Table 8.8) shows that there were no significant differences between the slopes and elevations of the regressions lines for the February and April field populations. However, there is a significant difference for March 4th population with a flatter slope than that for the others. but March 4th regression has a very narrow range of sizes which might account for this result. The lack of significant differences between the

length-carbon relationship, for the field population of Moina reticulata suggest that this species was able to keep the same carbon content per unit of length at the time of sampling. Also, for Moina reticulata a significant pooled regression was undertaken, (figure 8.5e).

Diaphanosoma sarsi, was present in the lake in February 25th and March, but it was only possible to obtain a length-carbon weight relationship on February 25th whose regression was statistically significant.(Table 8.7).

Figure 8.6 compares carbon-length relationship of the three cladocerans, from Lake Jacaretinga. The regressions for Daphnia gessneri were pooled for February 25th and March 5th,15th. For Moina reticulata the pooled regressions were February 25th and April 15th. In order to examine interspecific differences the significant relationships of the three species in the field population given in Table 8.9 were compared by analysis of covariance (Table 8.10). There were no significant differences between the slopes (b) of the regression for Daphnia gessneri and Moina reticulata but they had significant different elevations. The former cladoceran has both flatten slope and lower elevation, indicating that Daphnia gessneri field population has less body carbon weight than Moina reticulata sampled at the same time. The third species Diaphanosoma sarsi did show to have a significant different coefficient regression which is compared with the two other cladoceran.

An attempt was made to compare the field regressions for these species with those obtained experimentally under temperature and food turbidity controlled conditions as given in chapter 7, by analysis of covariance.

Comparison of the February 25th and March 5th,15th pooled regressions with the experimental regressions for Daphnia gessneri obtained when grown at in food concentration of 0.05 mgC.l^{-1} with 10 NTU and 0.5 mgC.L^{-1} with 0; 20 and 50 NTU (pooled) is given in Table 8.11. There are significant differences between the slopes of the carbon-length regression of the animals under experimental conditions

and those of the February-March field regressions; the latter regression has a lower slope. The two regressions (0.05 $mgC.l^{-1}$ with 10 NTU and 0.5 $mgC.l^{-1}$ with 0, 20 and 50 NTU has a similar slope but the former regression has a much lower elevation which is statistically significant. (Figure 8.7). It appears that food levels 0.05 $mgC.l^{-1}$ with 10NTU limit the carbon weight of individuals per unit length.

Carbon-length relationship for Moina reticulata reared at the laboratory under constant conditions of food concentration and turbidity and those field animals are shown in Figure 8.8. Table 8.11 gives the parameters of the linear regressions for these relationships and Table 8.12 gives the results of the analysis of covariance comparing these lines and those from field regressions (February, March and April) pooled. There were no significant differences between the slopes of the carbon-length regressions of Moina reticulata reared at 0.5 $mgC.l^{-1}$ and 0.5 $mgC.l^{-1}$ with turbidity, but there were significant differences between these laboratory relationship and that obtained from field animals. Regressions belonging to the animals under experimental conditions demonstrate the lowered elevation in 0.5 $mgC.l^{-1}$ with turbidity compared with 0.5 $mgC.l^{-1}$ food concentration.

8.5 Food availability for the cladoceran population in L.Jacaretinga

This section presents the results obtained over the same period of two months of weekly sampling on the availability of edible particles, as chlorophyll a or as sestonic carbon, to the cladoceran populations in Lake Jacaretinga. For this purpose, the particles passing through a mesh size of less than 20 um was chosen to represent the particle sizes that the species of Cladocera in the lake could ingest in relation to their body sizes. This decision was based upon the relationship established by Burns (1969) for temperate daphnid species which is supported by Jayatunga's (1986) results for tropical species which appear to be similar to temperate species in their filter structure and filter area despite their smaller body size.

In order to convert the measured less than 20 um chlorophyll a fractions to algal carbon, a conversion factor of 40:1 was used. According to Reynolds (1984), this is an appropriate factor for phytoplankton consisting or diatoms or cyano-bacteria, such as in Lake Jacaretinga. As is demonstrated in Table 8.13 the edible algal carbon concentration can be otained by multiplying the less than 20 um chlorophyll a fraction by 40. The edible non-algal component of the particular organic carbon could then be obtained by subtraction from the measured values of sestonic carbon.

Table 8.13 present the results for each stage in the calculation and the time course for edible chlorophyll a, edible sestonic carbon and the two expressed in carbon weight per litre are illustrated in Figure 8.9a,b,c. Figure 8.9a shows that edible chlorophyll a concentration in Lake Jacaretinga ranged from 3.6 to 17.0 $ug.L^{-1}$ during the period of study. The lowest values occurred in March, when the water levels was also at its lowest and at the beginning of April. The highest values, up to 17 $ug.l^{-1}$, occurred later in April and were associated with higher water levels.

The time course of POC in figure 8.9b shows a gradual increase with the entry water river (indicated by an arrow). Lowest levels were obtained in April (2.7 $mgC.l^{-1}$). As given in Figure 8.9c, edible algal carbon did not vary markedly. Values ranged from 0.15 to 0.7 $mgC.l^{-1}$ with the average of 0.35 $mgC.L^{-1}$ 0.18. The maximum values were observed by the end of April when this fraction exceeded 0.5 $mgC.l^{-1}$. On the other hand, the carbon levels of the edible non-algal fraction in relation to sestonic carbon, given in Figure 8.9c and Table 8.13 is much higher and more variable ranging from 0.5 to 1.83 $mgC.l^{-1}$ throughout the period of study, with a clear increase during the entering of water from the river. It is evident that the non-algal contribution to the sestonic carbon content was greater than algal carbon by about 10 times. The results might be interpreted as showing that non-algal particulate carbon accounts for the large amount of total particulate organic carbon (POC) in Lake Jacaretinga. Nevertheless, there is not a condition of food limitation in the lake because the algal carbon always attained above 0.1 $mgC.l^{-1}$.

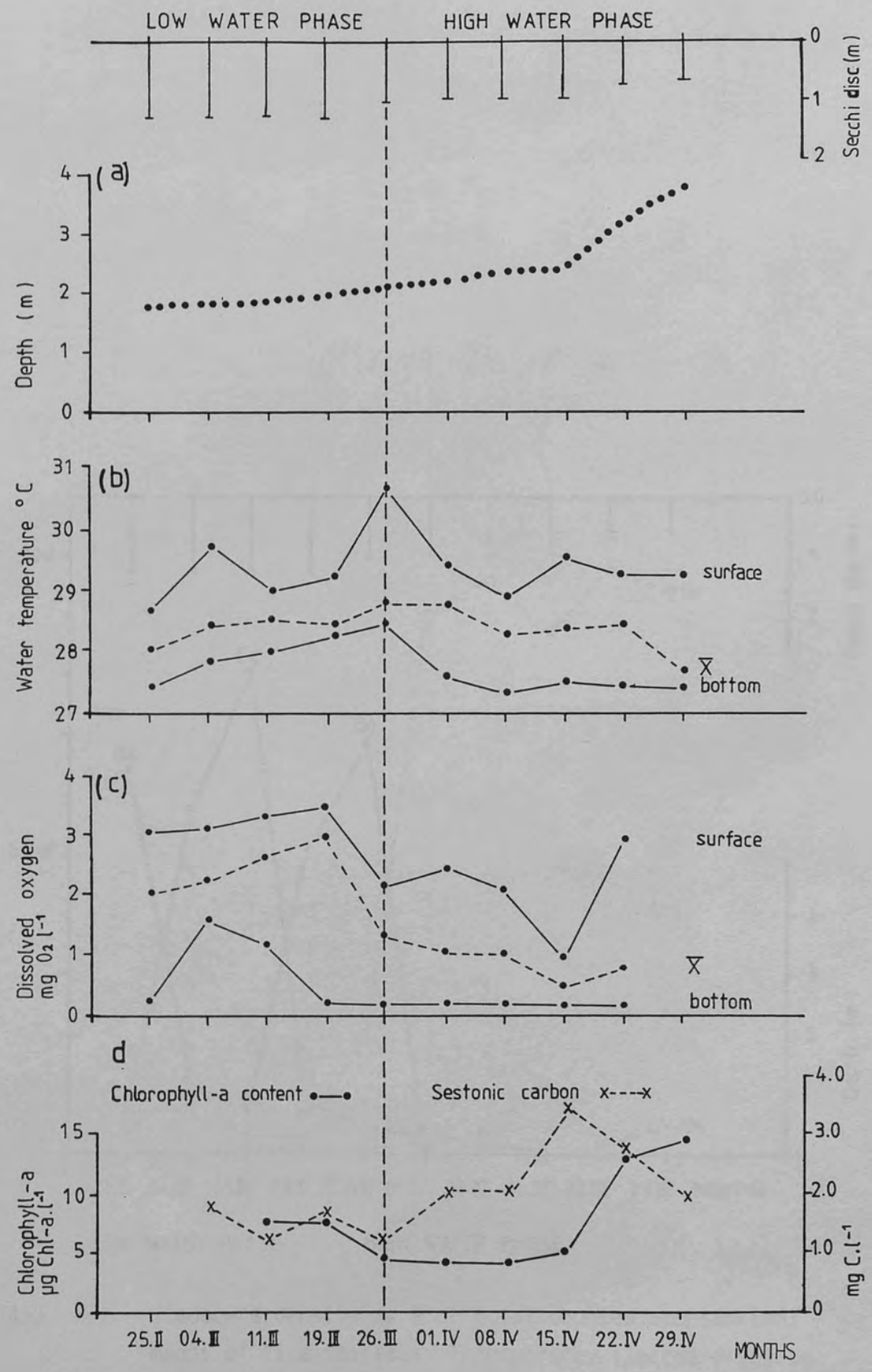


FIGURE 8.1 Physico-chemical and biological characteristics at station I, Lake Jacaretinga (February-April 1986). The vertical broken line indicates when flood began in the lake.

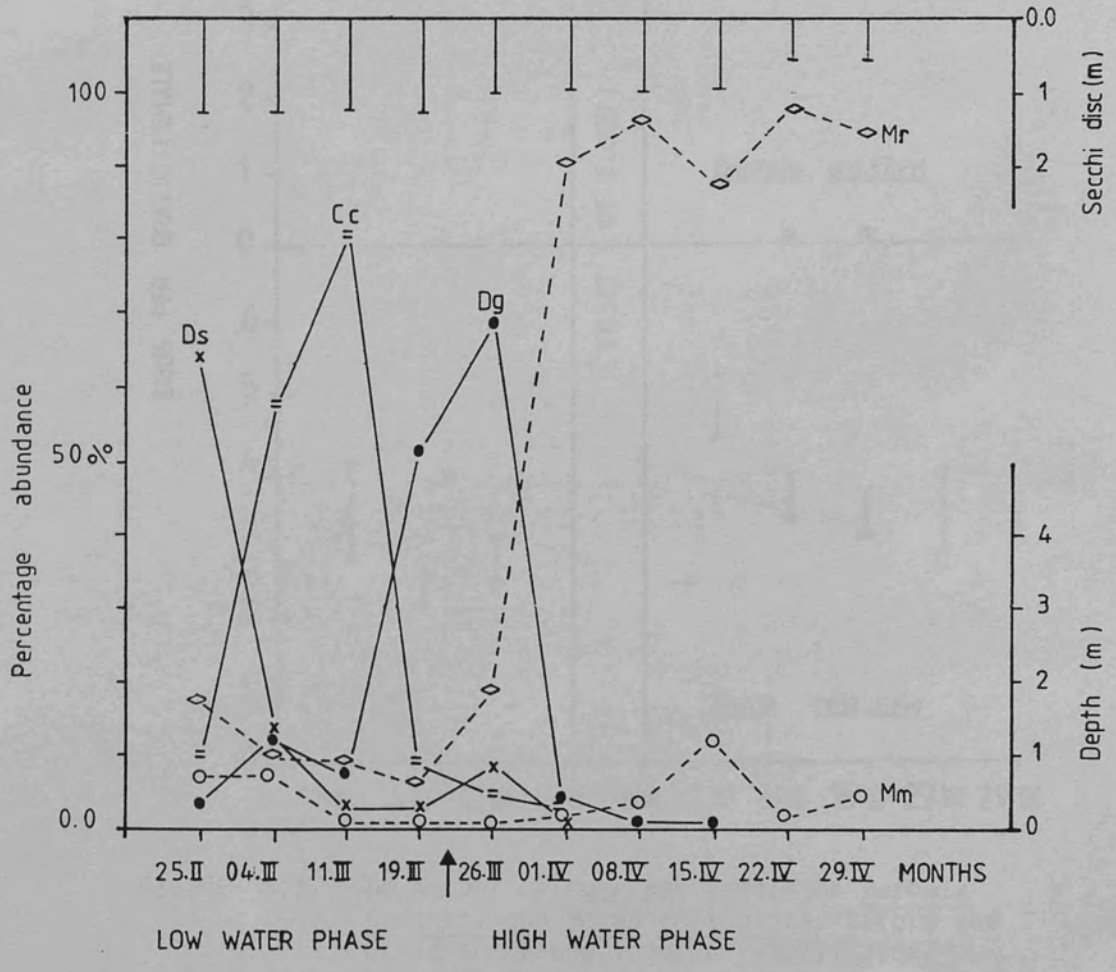


FIGURE 8.2 Cladocera density as % of total counted zooplankton; means of five stations. Transparency (Secchi disc) in Lake Jacaretinga. Ds = Diaphanosoma sarsi, Cc = Ceriodaphnia cornuta, Dg = Daphnia gessneri, Mn = Moina reticulata, Mn = Moina minuta .

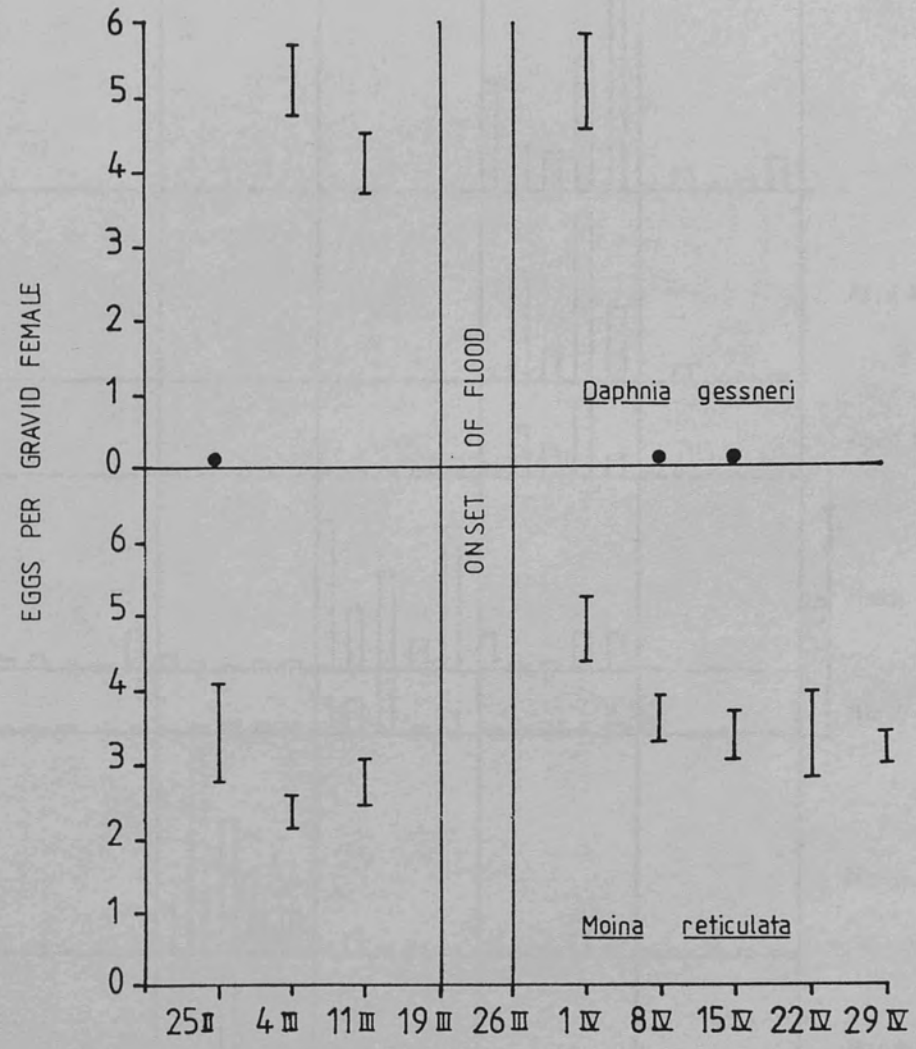


FIGURE 8.3 The number of eggs per female of Daphnia gessneri and Moina reticulata before and after the flood (February-April 1986)

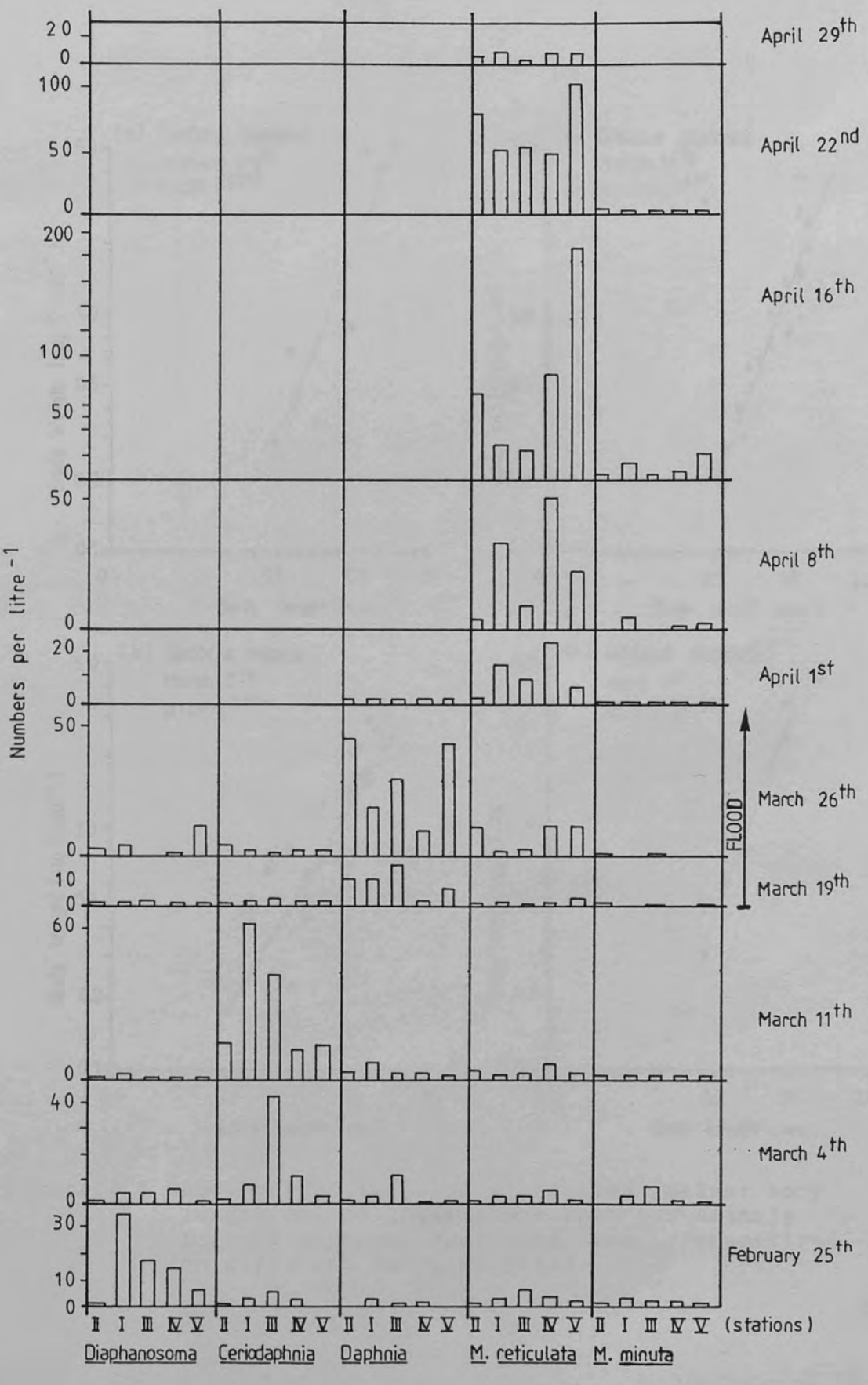


FIGURE 8.4 Horizontal distribution (numbers per litre) of cladoceran at five stations during February-April 1986 in Lake Jacaretinga.

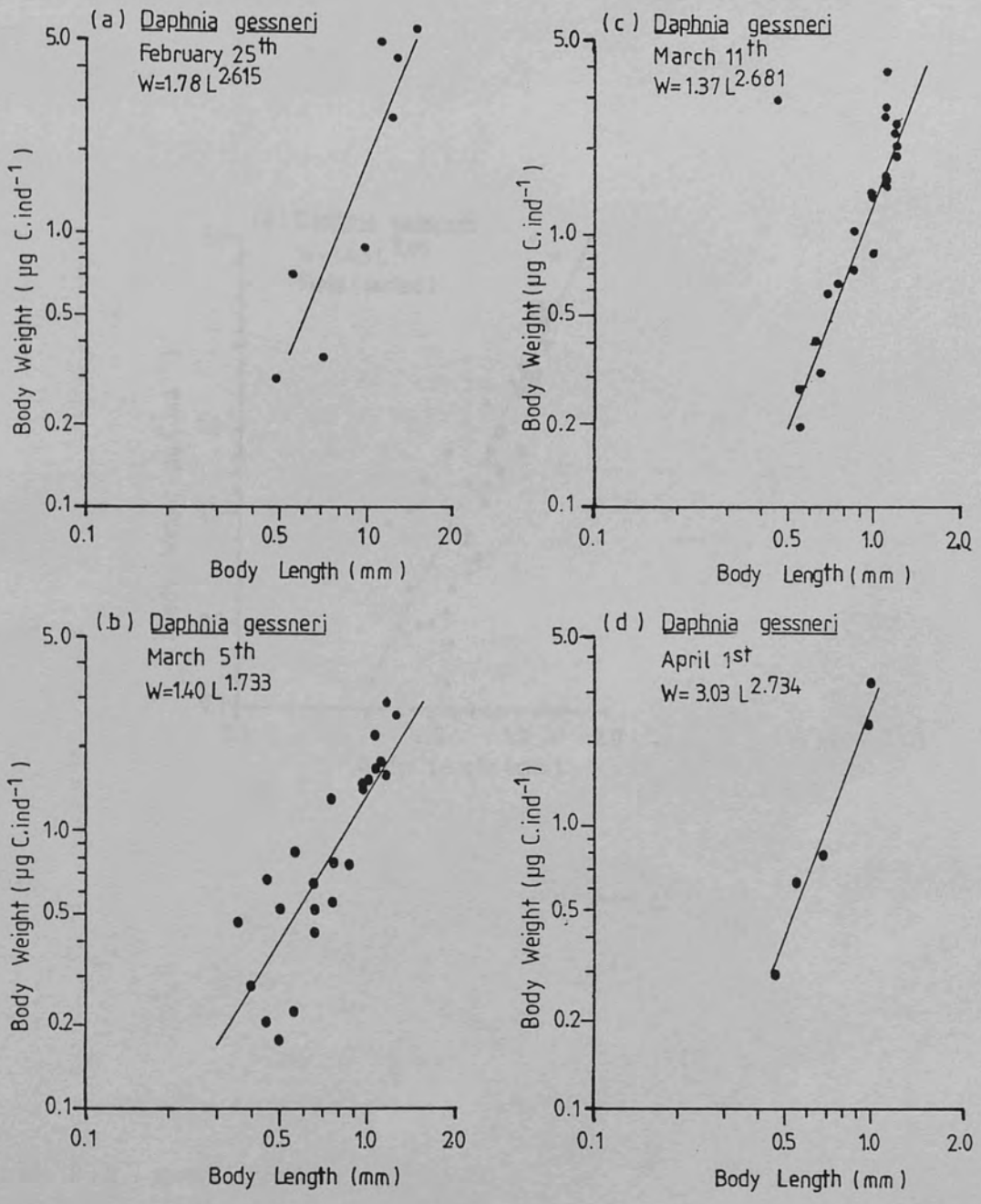


Figure 8.5 Body weight (ugC.ind^{-1}) plotted against body length(mm) on logarithmic axes for animals Daphnia gessneri collected from L.Jacaretinga on different sampling dates.

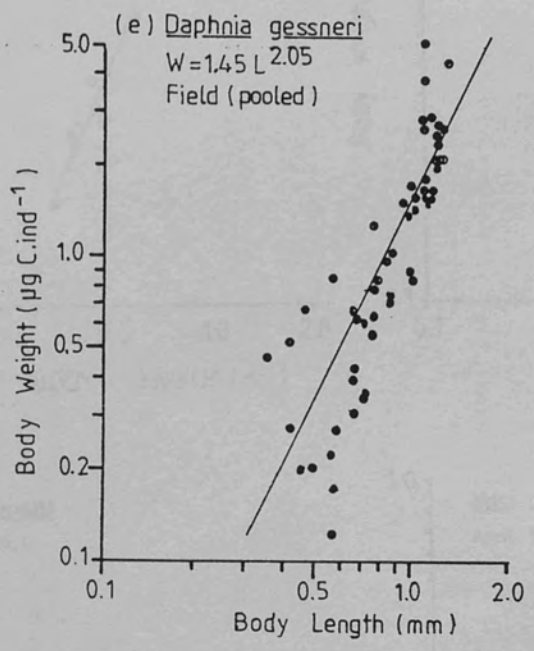


Figure 8.5 continued.

(Pooled regression for Feb.25th, Mar.5th, Mar.15th

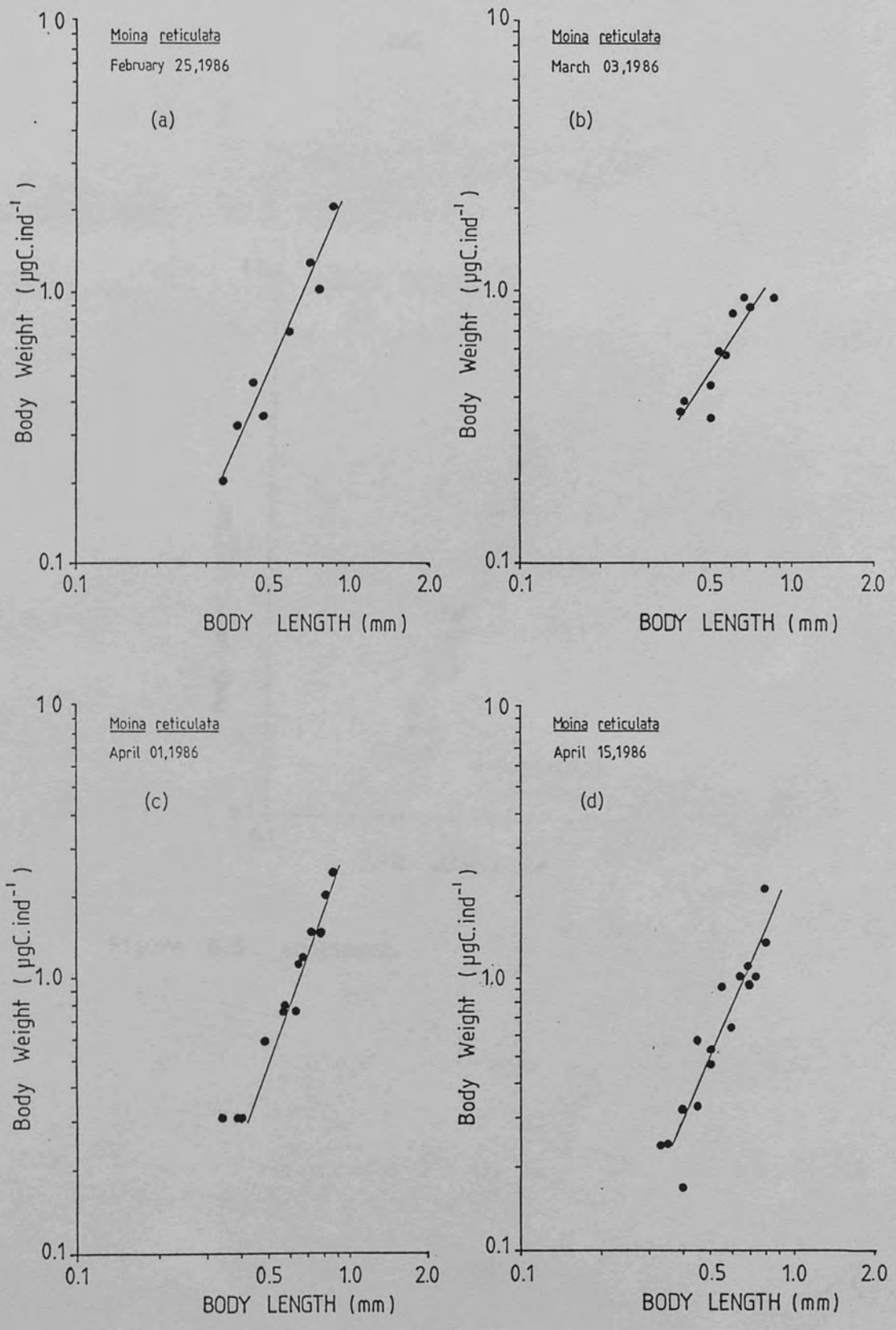


Figure 8.5 Body weight ($\mu gC.ind^{-1}$) plotted against body length (mm) on logarithmic axes for animals Moina reticulata collected from L.Jacaretinga on different sampling dates.

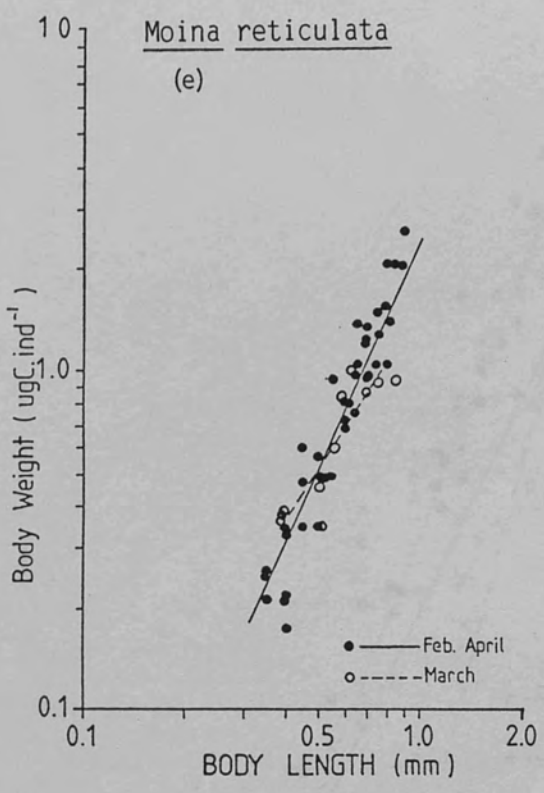


Figure 8.5 continued.

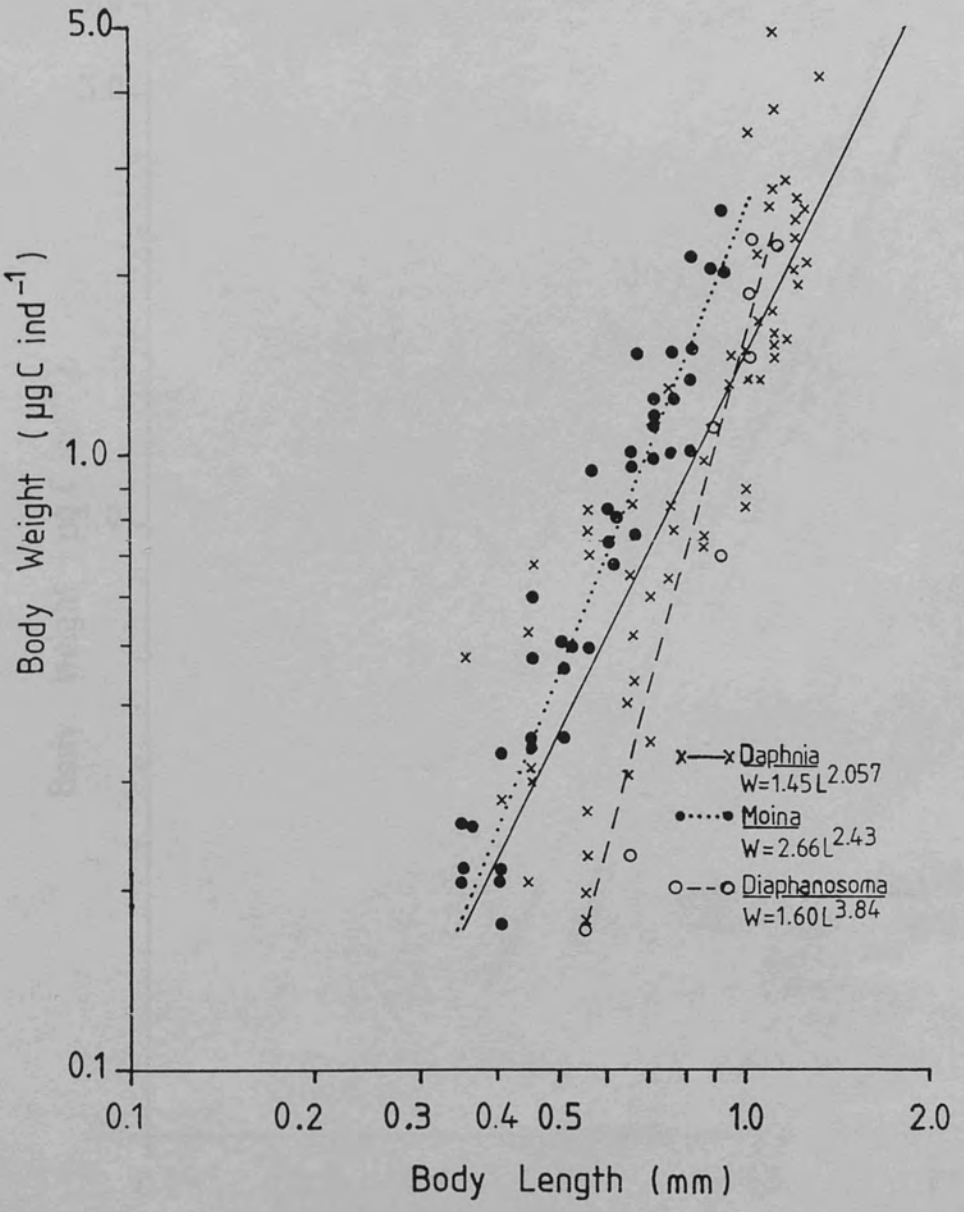


Figure 8.6 Body weight (µgC.ind^{-1}) plotted against body length (mm) on logarithmic axes for Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi collected from Lake Jacaretinga.

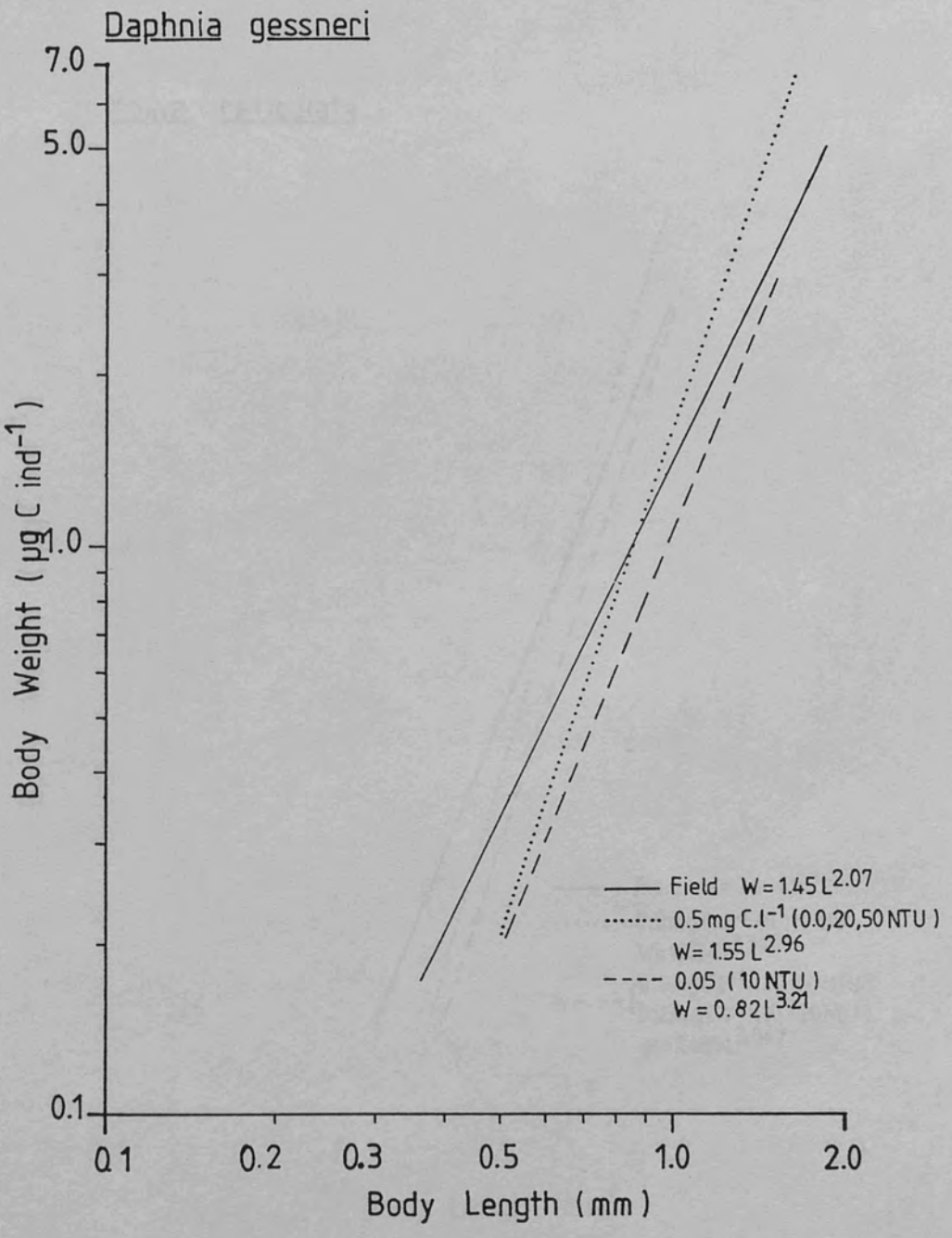


Figure 8.7 Body weight ($\mu gC.ind^{-1}$) plotted against body length (mm) on logarithmic axes for Daphnia gessneri from field and those reared at laboratory in the turbidity experiments.

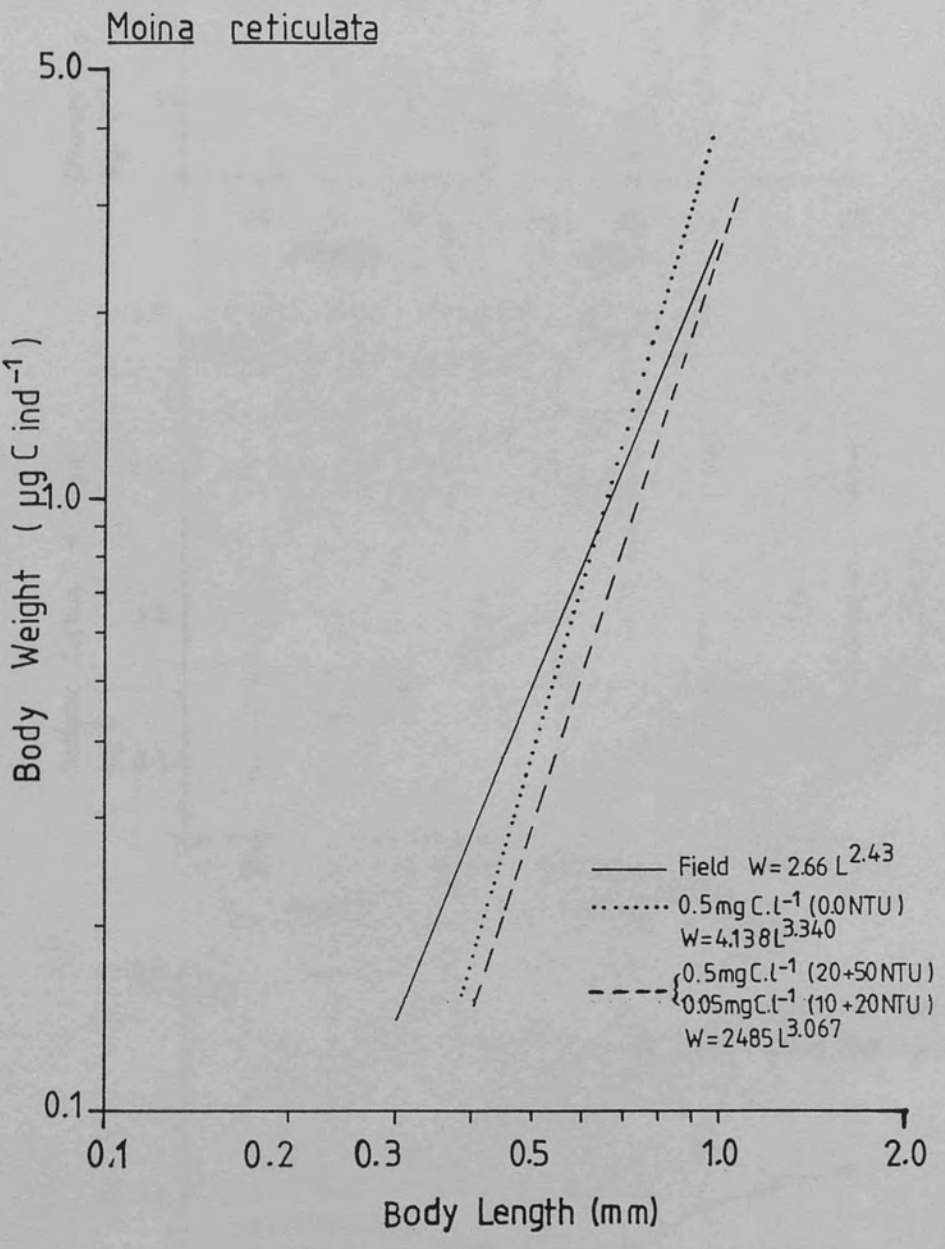


Figure 8.8 Body weight ($\mu gC.ind^{-1}$) plotted against body length on logarithmic axes for Moina reticulata from field and those reared at laboratory i n the turbidity experiments.

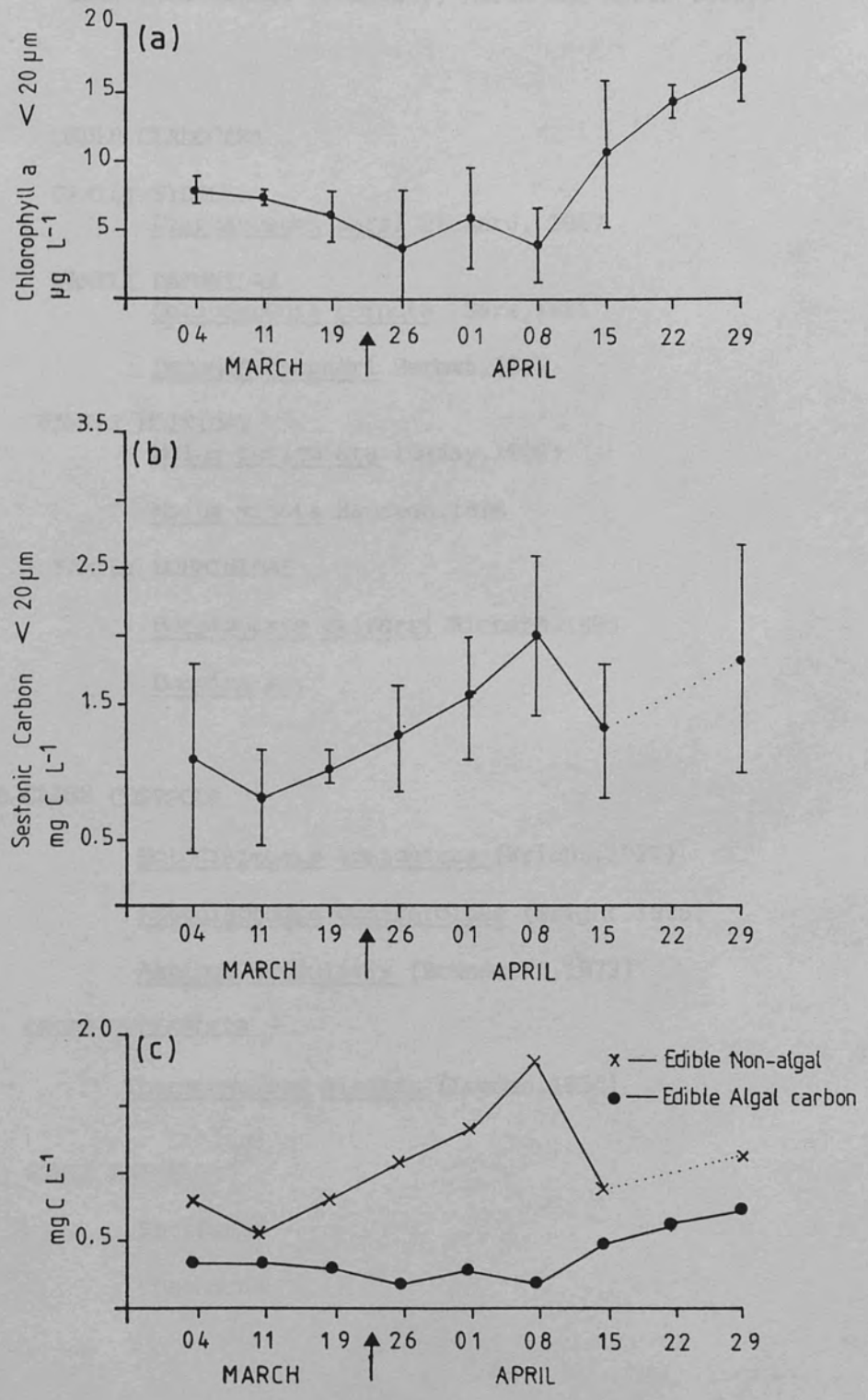


Figure 8.9 Edible chlorophyll a (a), edible sestonic carbon(POC) (b) and carbon-chlorophyll a (c) relationship in L.Jacaretinga during March-April 1986.

TABLE 8.1 List of planktonic crustacean species and other animals in Lake Jacaretinga (February, March and April 1986).

ORDER CLADOCERA

FAMILY SIDIDAE

Diaphanosoma sarsi Richard, 1967

FAMILY DAPHNIDAE

Ceriodaphnia cornuta Sars,1886

Daphnia gessneri Herbst,1967

FAMILY MOINIDAE

Moina reticulata (Daday,1905)

Moina minuta Hanseen,1899

FAMILY BOSMINIDAE

Bosminopsis deitersi,Richard,1895

Bosmina sp.

SUB-CLASS COPEPODA

Notodiaptomus amazonicus (Wright,1927)

Notodiaptomus coniferoides (Wright,1925)

Aspinus acicularis (Brandorff,1973)

ORDER CYCLOPOIDA

Thermocyclops minutus (Lowdes,1934)

OTHER ANIMALS

Rotifera

Chaoborus

Table 8.2 The Cladocera species of Lake Jacaretinga, their density (number per litre) during February-April 1986. Means of five stations and three replicates. Number between brackets are percentages. N = 15; $\bar{x}$ = mean value; SD = standard deviation; 95% CL = 95 per cent confidence limits.

DATES	D.sarsi		C.cornuta		D.gessneri		M.reticulata		M.minuta	
	$\bar{x} \pm$ SD	$\pm$95%CL	$\bar{x} \pm$ SD	$\pm$95%CL	$\bar{x} \pm$ SD	$\pm$95%CL	$\bar{x} \pm$ SD	$\pm$95%CL	$\bar{x} \pm$ SD	$\pm$95%CL
Feb 25th	15.1±13.5 (64.5)	±7.0	2.3±2.3 (9.8)	±1.0	0.7±0.8 (2.98)	±0.47	3.3±2.4 (14.3)	±1.3	1.98±1.2 (8.45)	±0.66
Mar 4th	3.0± 2.7 (13.4)	±1.5	13.4±16.9 (54.2)	±9.5	3.1±5.0 (12.5)	±2.64	2.8±2.0 (11.1)	±1.2	2.34±2.8 (9.48)	±1.40
Mar 11th	0.7±0.6 (1.98)	±0.5	78.9±22.9 (78.9)	±11.6	3.0±2.3 (8.4)	±1.25	3.4±1.7 (9.3)	±0.9	0.49±0.3 (1.33)	±0.20
Mar 19th	0.9±0.7 (6.8)	±0.4	1.3±1.1 (9.5)	±5.6	9.6±5.5 (74.3)	±2.98	1.0±0.9 (8.3)	±0.5	0.13±0.2 (1.0)	±0.10
FLOOD ↓ Mar 26th	4.2±4.6 (12.2)	±2.5	2.2±1.0 (6.4)	±0.5	19.7±15.3 (57.3)	±8.41	8.2±5.1 (23.8)	±2.7	0.1±0.1 (0.3)	±0.1
Apr 1st	0		0.5±0.4 (3.4)	±0.2	0.7±0.4 (5.8)	±0.24	11.5±8.6 (88.2)	±4.5	0.32±0.2 (2.45)	±0.11
Apr 8th	0		0		0		23.5±19.2 (94.4)	±10.0	1.38±1.73 (5.54)	±0.80
Apr 15th	0		0		0		79.0±64.7 (88.5)	±34.0	10.26±9.0 (11.5)	±4.8
Apr 22nd	0		0		0		67.2±24.0 (97.8)	±55.0	1.48±0.6 (2.1)	±0.4
Apr 29th	0		0		0		6.6±3.1 (95.3)	±1.9	0.32±0.2 (4.6)	±0.1

TABLE 8.3 Occurrence of males and ephippial females of Cladocera in numbers of ind.L^{-1} at Lake Jacaretinga. The values represent mean of five station and three replicates

DATES	Diaphanosoma sarsi		Daphnia gessneri		Ceriodaphnia cornuta		Moina reticulata		Moina minuta	
th	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Feb.th	1	0	0	0	0	1	1	0	0	0
Mar.4th	1	0	0	0	0	1	2	1	0	0
Mar.11th	1	0	0	1	0	1	2	1	0	0
FLOOD Mar.19th	1	0	1	1	0	0	0	0	0	0
Mar.26Th	1	1	1	1	0	0	0	0	0	0
Apr. 1st	0	0	0	0	0	0	0	0	0	0
Apr. 8th	0	0	1	1	0	0	4	1	1	2
Apr.15th	0	0	0	0	0	0	20	3	1	1
Apr.22sd	0	0	0	0	0	0	5	1	1	2
Apr.29th	0	0	0	0	0	0	2	1	1	2

TABLE 8.4 The percentage of species ofegg-bearing Cladocera in Lake Jacaretinga during February-April 1986. Means of five stations and three replicates.

DATES	C. cornuta	D.gessneri	D. sarsi	M. reticulata	M. minuta
Feb.25th	4.0	0	1.5	1.6	3.0
Mar.4th	0.5	3.5	1.5	4.5	8.0
Mar.11th	0.6	3.0	0.5	2.0	2.0
FLOOD Mar.19th	0.4	0.5	1.0	1.7	7.0
Mar.26th	0	3.0	2.0	5.2	5.0
Apr. 1st	0	3.5	0	2.0	36.0
Apr. 8th	0	0	0	8.0	35.0
Apr.15th	0	0	0	3.6	11.0
Apr.22nd	0	0	0	3.0	4.5
Apr.29th	0	0	0	15.0	2.0

Table 8.5 The number of eggs per female of Moina reticulata and Daphnia gessneri during February-April 1986. N = number of females with eggs; $\bar{x}$ = mean value; SD =standard deviation; 95%CL = 95 per cent confidence limit.

DATES	EGGS PER FEMALE					
	Daphnia gessneri			Moina reticulata		
	N	$\bar{x} \pm$ SD	$\pm$95%CL	N	$\bar{x} \pm$ SD	$\pm$95%CL
Feb 25th	no egg-bearing female			15	3.4±1.20	±0.68
Mar 4th	55	5.2±1.80	±0.49	41	2.3±0.77	±0.24
Mar 11th	22	4.1±0.90	±0.42	36	2.7±1.00	±0.34
Apr 1st	10	5.2±0.95	±0.67	36	4.8±1.30	±0.45
FLOOD						
Apr 8th	no egg-bearing female			56	3.6±1.10	±0.31
Apr 15th	no egg-bearing female			32	3.4±0.90	±0.34
Apr 22nd	no egg-bearing female			15	3.4±1.20	±0.68
Apr 29th	no egg-bearing female			18	3.2±0.80	±0.24

TABLE 8.6 The horizontal distribution of Cladocera density (number per litre) at integrated depth in Lake Jacaretinga during February -April 1986. N = 3

Diaphanosoma sarsi NUMBER OF IND.L^{-1}

DATE	SITE 1		SITE 2		SITE 3		SITE 4		SITE 5	
	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
FEB 25th	36.0	5.0	1.0	0.25	18.0	1.0	15.0	0.87	5.7	2.4
MAR 4th	4.0	2.0	0.1	0	4.5	0.8	6.4	2.6	0.3	0.1
MAR 11th	2.0	0.65	0.4	0.46	0.7	0.25	0.7	0.4	0.2	0.1
MAR 19th	0.1	0.09	0.3	0.02	2.0	0.95	1.0	1.15	1.0	1.0
FLOOD ↓ MAR 26th	4.5	1.40	3.0	0.50	0	0	1.0	0	12.5	0.5
APR 1st	0	0	0	0	0	0	0		0	0
APR 8th	0	0	0	0	0	0	0		0	0
APR 15th	0	0	0	0	0	0	0		0	0
APR 22sd	0	0	0	0	0	0	0		0	0
APR 29th	0	0	0	0	0	0	0		0	0

TABLE 8.6 continued.

Daphnia gessneri NUMBER OF IND .L-1

DATE	SITE 1		SITE 2		SITE 3		SITE 4		SITE 5	
	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
FEB 25th	2.0	0.34	0	0	0.5	0.5	1.0	1.0	0	0
MAR 4th	2.0	0.57	0.6	0.42	12.0	2.8	0.6	0.25	0.3	0.03
MAR 11th	7.0	0.98	2.7	1.29	2.4	0.58	2.3	0	1.0	0.43
FLOOD ↓ MAR 19th	11.0	2.55	11.2	1.95	17.0	0	2.0	0.95	7.0	1.90
MAR 26th	19.0	4.3	46.0	11.0	30.0	5.13	10.0	0.57	44.0	3.10
APR 1st	1.0	0.26	0.03	0.02	0.8	0.10	1.0	0.05	1.0	0.4
APR 8th	0	0	0	0	0	0	0	0	0	0
APR 15th	0.4	0.32	0.13	0.12	0.5	0.3	0	0	0.5	0.5
APR 22sd	0.3	0.1	0	0	0.4	0.35	0	0	0	0
APR 29th	0	0	0	0	0	0	0	0	0	0

TABLE 8.6 continued

Ceriodaphnhia cornuta NUMBER OF IND .L-1

DATE	SITE 1		SITE 2		SITE 3		SITE 4		SITE 5	
	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
FEB 25th	3.0	0	0.01	0.01	6.0	0	2.0	0.84	0.5	0.12
MAR 4th	7.7	1.5	1.5	0.42	43.0	18.0	11.0	0.58	3.7	1.53
MAR 11th	63.0	7.5	15.0	3.6	42.0	11.4	12.0	0.58	13.0	2.0
MAR 19th	1.7	0.56	0.14	0.23	3.0	0.21	0.4	0.37	1.0	0.65
FLOOD ↓ MAR 26th	2.0	0.70	4.0	0	1.0	0.32	2.0	0	2.0	0.76
APR 1st	1.0	0.26	0.6	0.59	0.14	0.10	0	0	0.5	0.4
APR 8th	0	0	0	0	0	0	0	0	0	0
APR 15th	0	0	0	0	0	0	0	0	0	0
APR 22sd	0	0	0	0	0	0	0	0	0	0
APR 29th	0	0	0	0	0	0	0	0	0	0

TABLE 8.6 continued.

Moina reticulata NUMBER OF IND .L-1

DATE	SITE 1		SITE 2		SITE 3		SITE 4		SITE 5	
	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
FEB 25th	3.2	0.49	0.7	0.21	7.0	1.77	4.2	1.13	1.6	1.0
MAR 4th	2.9	1.42	0.4	0.12	4.0	1.75	5.5	1.50	1.1	0.1
MAR 11th	1.7	0.06	3.2	1.04	2.9	0.99	6.3	0.25	3.0	0.55
MAR 19th	0.9	0.06	1.0	0.40	0.3	0.1	0.6	0.2	2.6	0.68
MAR 26th	2.3	0.3	11.0	4.0	3.0	1.0	12.6	0.85	12.1	0.60
APR 1st	15.6	0.2	1.3	0.35	9.6	0	24.0	1.0	7.0	2.43
APR 8th	30.4	2.75	3.0	0.30	9.2	2.2	52.0	8.3	23.0	1.70
APR 15th	29.0	8.0	70.0	8.0	25.0	3.9	86.0	8.2	185.0	37.5
APR 22sd	52.0	7.4	79.0	28.0	54.0	10.3	47.0	4.1	104.0	6.35
APR 29 th	9.5	2.3	5.0	0.58	1.8	0.29	8.3	3.2	8.4	2.52

FLOOD

TABLE 8.6 continued

Moina minuta NUMBER OF IND. L^{-1}

DATE	SITE 1		SITE 2		SITE 3		SITE 4		SITE 5	
	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
FEB 25th	3.0	1.0	0.1	0.05	3.0	0.33	2.3	0.33	1.5	0.57
MAR 4th	3.0	0.39	0.1	0.06	7.0	0.85	1.0	0.1	0.6	0.32
MAR 11th	0.3	0.25	0.05	0.01	1.0	0.82	0.7	0.18	0.4	0.13
MAR 19th	0	0	0.15	0.08	0.5	0.13	0	0	0.02	0.03
FLOOD → MAR 26th	0	0	0.4	0.03	0.1	0.1	0	0	0	0
APR 1 st	0.3	0.02	0.03	0.03	0.3	0.14	0.4	0.17	0.6	0.1
APR 8th	4.0	1.0	0.0	0.0	0.0	0.0	0.63	0.25	2.3	1.7
APR 15th	16.0	6.5	1.6	0.8	2.7	1.3	8.0	1.45	23.0	1.4
APR 22sd	1.4	0.4	2.4	0.8	1.7	0.4	0.8	0.24	1.0	0.15
APR 29th	0.3	0.2	0.7	0.03	0.3	0.3	0.3	0.14	0.0	0.0

TABLE 8.7 Parameters of the linear regressions relating organic carbon conten ($\mu gC.ind^{-1}$) to length (mm) of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi, collected from the L. Jacaretinga at various occasions of the year.
Regression equation: lnY = lna + b lnX
Y = organic carbon conten; X = length (mm)

DATE	ln a	b	df	F	P
Daphnia gessneri					
FEBRUARY 25th	0.576	2.614	1,4	7.89	0.04
MARCH 5th	0.336	1.733	1,24	56.13	0.000
MARCH 11th	0.319	2.681	1,20	138.76	0.000
APRIL 1st	1.114	2.734	1,3	120.58	0.001
Moina reticulata					
FEBRUARY 25th	0.845	2.23	1,7	65.1	0.000
MARCH 5th	0.356	1.52	1,8	38.8	0.000
APRIL 1st	1.117	2.76	1,12	490.2	0.000
APRIL 15th	0.938	2.30	1,15	101.7	0.000
Diaphanosoma sarsi					
FEBRUARY 25th	0.474	3.83	1,6	112.2	0.000

TABLE 8.8 Results of the covariance analysis comparing the carbon-weight length regressions of Daphnia gessneri obtained from the L. Jacaretinga. The regressions are given in ascending order of regression coefficients (STP test) and mean values (S-N-K test). Any regression number not joined by the underline are not significantly different.
df = degrees of freedom; F = variance ratio; P = level of significance; SE = standard error

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Daphnia gessneri — Comparisons between slopes

DATE	GROUP	REGRESSION COEFF. ±SE	df	F	P	SS-STP
FEBRUARY 25th	1	2.614± 0.93	3.54	2.83	0.047	2 1 3 4
MARCH 5th	2	1.733±0.23				
MARCH 15th	3	2.681±0.22				
APRIL 1st	4	2.734±0.24				

Comparisons between elevations

		ADJUSTED MEAN ± SE	df	F	P	S-N-K
FEBRUARY 25th	1	0.074±0.21	3,58	3.16	0.031	3 2 1 4
MARCH 5th	2	-0.034±0.21				
MARCH 15th	3	- 0.211±0.21				
APRIL 1st	4	0.425±0.21				

TABLE 8.8 CONTINUED

Moina reticulata			Comparisons between slopes			
DATE	GROUP	REGRESSION COEFF. ± SE	df	F	P	SS-STP
FEBRUARY 25th	1	2.23±0.27	3,42	6.84	0.000	2 1 4 3
MARCH 5th	2	1.52±0.24				
APRIL 1st	3	2.76±0.12				
APRIL 15th	4	2.30±0.22				
			Comparisons between elevations			
FEBRUARY 25th	1	- 0.41±0.32	3,46	1.52	0.221	1 3 4
APRIL 1st	3	- 0.39±0.32				
APRIL 15th	4	- 0.38±0.32				

TABLE 8.9 Parameters of the pooled regressions relating individual weight in carbon content ($\mu gC.ind^{-1}$) to length(mm) of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi from the field.
Regression equation: $\ln Y = \ln a + b \ln X$
Y = organic carbon content; X = length (mm)

DATE	Ln a	b	df	F	P
Daphnia gessneri					
FEB.25th-MAR.5th15th	0.371	2.05	1,53	140.0	<0.0001
Moina reticulata					
FEB.25th APR.15th	0.978	2.43	1,39	399.3	<0.0001
Diaphanosoma sarsi					
FEB. 25th	0.474	3.83	1,7	112.2	<0.0001

Table 8.10 Analysis of covariance comparing significant regressions of organic carbon content and length of Daphnia gessneri, Moina reticulata and Diaphanosoma sarsi from the field. The regression coefficients are compared by the SS-STP test and the differences between the elevations by the SNK test. Regression coefficients, or adjusted means underlined are not significantly different at P =0.05. Group numbers are given in ascending order of magnitude.

Comparison between the slopes

	GROUP	REGRESSION COEFF±SE	DF	F	P	SS-STP
Daphnia gessneri (pooled)	1	2.057±0.17	2,98	6.12	0.003	1 2 3
Moina reticulata (pooled)	2	2.430±0.12				
Diaphanosoma sarsi	3	3.838±0.42				

Comparison between the elevations

Daphnia gessneri	1	-0.354±0.22	2,101	16.40	<0.0001	1 2
Moina reticulata	2	0.114±0.22				

TABLE 8.11 Parameters of linear regressions relating organic carbon content (ugC.ind.$^{-1}$) to length (mm) of Moina reticulata from the field and those reared at laboratory conditions.

FOOD LEVEL mgC.L^{-1}	TURBIDITY NTU	ln a	b	df	F	P
0.5	0	1.42	3.34	1,11	70.1	<0.0001
0.5	(20,50)	0.79	2.95	1,12	159.7	<0.0001
FIELD (pooled)		2.66	2.43	1,38	399.3	<0.0001

TABLE 8.12 Analysis of covariance comparing significant regressions of organic carbon content and length of Moina reticulata from the field and those reared at laboratory conditions. The regression coefficients are compared by the SS-STP tes and the differences between the elevations by the S-N-K test. Regression coefficients, or adjusted means underlined are not significantly different at P = 0.05.

Comparisons between the slopes

FOOD LEVEL mgC.L^{-1}	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
0.5	0	1	3.34±0.39	2,60	6.45	0.002	3 2 1
0.5	(20,50)	2	2.95±0.23				
FIELD (pooled)		3	2.43±0.12				

Comparisons between the elevations

FOOD LEVEL mgC.L^{-1}	TURBIDITY NTU	GROUP	ADJUSTED MEAN±SE	df	F	P	S-N-K
				2,63	16.6	0.000	2 1
0.5	0	1	0.76±0.16				
0.5	(20,50)	2	0.44±0.16				

TABLE 8.12 Analysis of covariance comparing significant regressions of organic carbon content and length of Daphnia gessneri from the field and two food level with various concentrations of turbidity. The regression coefficients are compared by the SS-STP tes and the differences between the elevations by the S-N-K test. Regression coefficients, or adjusted means underlined are not significantly different at P = 0.05. Group numbers are given in ascending order of magnitude

FOOD LEVEL $mgC.L^{-1}$	TURBIDITY NTU	GROUP	REGRESSION COEFF.±SE	df	F	P	SS-STP
			Comparisons between the slopes				
0.05	10	1	3.21±0.47	2,70	5.22	0.007	3 2 1
0.5	(0,20,50)	2	2.96±0.16				
FIELD	(pooled)	3	2.07±0.17				
			Comparisons between the elevations				
0.05	10	1	-0.41±0.25	2,73	3.47	0.036	1 2
0.5	(0,20,50)	2	0.14±0.25				

Table 8.13 Chlorophyll a, algal carbon, total sestonic carbon (POC) and non-algal carbon content of Lake Jacaretinga during March-April 1986. The results are expressed in mg^{-1} ± SD. A conversion factor of 40:1 chlorophyll a was used.

DATE	Chlorophyll a, <20 um ($mg.l^{-1}$) measured	Algal carbon $mg.l^{-1}$ (column 1x40)	Sestonic carbon $mgC.l^{-1}$ (<20um) (mesured)	Non-algal carbon $mgC.l^{-1}$ (<20um)
Mar 4th	0.0080±0.008	0.320	1.118±0.004	0.798
Mar 11th	0.0072±0.003	0.288	0.813±0.002	0.533
Mar 19th	0.0062±0.001	0.248	1.046±0.001	0.798
Mar 26th	0.0036±0.017	0.144	1.250±0.004	1.106
Apr 1st	0.0061±0.023	0.244	1.582±0.004	1.338
Apr 8th	0.0040±0.022	0.160	2.005±0.004	1.845
Apr 15th	0.0109±0.034	0.436	1.309±0.004	0.873
Apr 22nd	0.0147±0.010	0.588	*	*
Apr 29th	0.0171±0.019	0.684	1.856±0.002	1.172

* undetermined

CHAPTER 9

DISCUSSION

9.1 Changes in species composition: Abiotic and biotic determinants

The results of this study have shown (Figure 8.2) that, during the period from February 25th to April 29th 1986, the cladoceran community in Lake Jacaretinga, a shallow tropical lake, shifted from a complete dominance by Diaphanosoma sarsi, Ceriodaphnia cornuta, and Daphnia gessneri to dominance and density by Moina reticulata a smaller-bodied cladocera (0.40-0.80 mm). This shift was associated with the annual floading of the River Amazon, when water carrying large ammount of fine suspended particles entered into the lake. Attempts to explain seasonal succession in a natural zooplankton community often suggest that one species has certain genetic, morphological, physiological or ecological features which temporarily enable it to utilize its habitat to greater advantage.

Many authors have investigated the possibility that water renewal (dilution, currents, transparency), temperature, dissolved oxygen, predation (vertebrate and invertebrate), and food (quality and quantity) are the major factors. There is no doubt that a variety of factors contribute to the seasonality of the cladocerans and play an important role in life cycle characteristics. However, which factors are exactly more important and how they operate are rarely demonstrated. Allan (1977) found that seasonal succession in Frain Lake, Michigan, was correlated with temperature, while De Mott (1983) found that food composition influenced the relative advantage of each Daphnia species more than temperature, pH or dissolved oxygen. Brooks & Dodson (1965) have implicated the influence of predation and Edmondson & Litt (1982) discussed the combined effects of predation and nutrition.

The effect of dilution and flushing out of the plankton could be easily accepted in Lake Jacaretinga on account of the intensity and duration of the flood. During heavy floods, Lake Jacaretinga is connected by a narrow "furo" to another lake, Lago Redondo, although

such connection was not observed during the present field studies. The magnitude of throughflow, especially during 1986 (measured by water depth, Figure 8.1 (a), seems inadequate to reduce zooplankton by dilution significantly. In spite of strong current generated by the inflow as was seen in the mouth of the canal, it does not occur in the lake, since natural barriers such as inundated forest and aquatic macrophytes diminish the current effect.

Temperature has long been known to influence rates of activity of different animals. The general positive effect of temperaure on secondary production is a result of the reproductive biology of zooplankton. Therefore, temperature variation has been invoked to explain why some species populations are present or absent at certain seasons. In particular, previous workers have noted correspondence between temperature and Daphnia successions (Allan 1977, Hebert 1977). In evaluating this possibility, it should be remembered that the water temperature in Lake Jacaretinga varies very little with time, between 27.5°C and 30.8°C with an overall average of 28°C. It would be naive, however, to postulate that temperature is the direct cause of changes in composition at least in tropical aquatic environments. Even the indirect effects of temperature via food type, feeding, efficiency, and fecundity are unlikely to occur in such a narrow range of temperature fluctuation.

The dependence of the the distribution of aquatic invertebrate upon availability of oxygen is thought to be critical and is described by several authors. Brylinsky (1980), has found that carnivorous zooplankton production in a wide range of lakes is influenced by oxygen concentration in the epilimnion. Jonasson (1978) suggests that sufficent oxygen is important to benthos production because food cannot be metabolized efficiently at low oxygen levels. Fox, Gilchrist & Phear (1951), has reported that when the oxygen content of the water falls below 2 or 3 ml/l, the number of eggs produced by Daphnia obtusa decreases in proportion to any further decrease in oxygen content. The effect of oxygen on the growth of Daphnia magna was reported by Green (1956). His results suggest that lack of oxygen retards growth.

The rate of oxygen consumption by cladocerans has been measured many times. Carbon dioxide release is usually represented as the respiratory quotient (RQ), because this provides a clue to the substrate used to fuel respiration (Peters, in Peters and De Bernardi, 1987). Richaman (1958) induced a decline in RQ from 1.1 to 0.7 by starving Daphnia pulex and interpreted this as a shift from carbohydrate metabolism in well-fed animals to consumption of fat reserves in starving animals. Lampert and Bohrer (1984) induced similar changes in the RQ of Daphnia magna by varying food level.

The level of dissolved oxygen in lake Jacaretinga is often very low, particularly during high water (1.0 $mg/1^{-1}$), since large quantities of organic material and detritus from the flooded terrestrial vegetation become available for decomposition. Therefore, oxygen concentrations, even near the surface, are in general low (Figure 8.1 (c). In the present study the maximum oxygen concentration observed was 3.0 $mg/1^{-1}$ which represents 36% saturation and the minimum was 1.0 $mg/1^{-1}$ which represents 11% saturation at temperature of 27°C. Dependence of the distribution of aquatic invertebrate upon oxygen concentration is described by several authors in Amazonia lakes and reservoirs. Junk (1973) shows that the numbers and total biomass of periphyton colonizing the floating macrophyte vegetation diminishes strongly under hypoxic conditions. Brandorff (1977) observed Daphnia gessneri inhabiting only the oxygenated layers of Lake Castanho. Fisher et al. (1983), found, in Lake Calado (Amazonia), the zooplankton confined to the epilimnion in the top 4 meters of the water column where the O_2 saturation was less than 30%. The hypolimnion was anoxic and contained H_2S (detected by odor), a very commum feature in such kinds of lake, including Lake Jacaretinga. The authors invoked the lack of oxygen and the presence of reducing substances as possible environmental clues that enable the zooplankters to avoid the hypolimnion.

A two-year study on the composition and abundance of the zooplankton was conducted in an Amazonia varzea, Lake Camaleao, by Hardy et al. (1984). This provided some evidence that the poor oxygen conditions may be harmful enough to cause changes in the

structure population of aquatic organisms. One of the striking features of this lake is the rich rotifer fauna and the poor crustacean fauna, particularly, during the period of low oxygen content. Daphnia gessneri was not observed during this study. Other cladocerans Ceriodaphnia cornuta, Moina reticulata and Diaphanosoma spp. were present in low numbers. Their increased density was associated to better oxygen conditions.

The rarity and absence of Daphnia gessneri, Diaphanosoma sarsi and Ceriodaphnia cornuta after the flood and in contrast to the dominant presence of Moina reticulata, as demonstrated in this field investigation in Lake Jacaretinga ,did correspond with changes in dissolved oxygen amongst others environmental factors. Unfortunately no experimental investigation has been done relating to oxygen tolerance in these species, although it seems that Moina reticulata is more tolerant than the other cladoceran. Based on available evidence, it appears that the confinement of cladoceran, especially Daphnia gessneri, within the shallow, oxygenated upper layers is not an unusual phenomena, particularly in the Amazonia lakes. How far changing oxygen concentrations lead to shift or death of cladoceran species cannot yet be shown.

The importance of mineral in various kind of aquatic environment is also receiving increasing attention. Arruda et al. (1983) and McCabe and O'Brien (1983) have discussed the importance of suspended sediments on the ecology of cladoceran in reservoirs. Deleterious effects of suspended clays on Daphnia have been recorded. According to Moghraby (1977), large quantities of suspended particles in the water act directly on zooplankton by obstructing their respiratory and swimming structures. Gliwicz & Rybak (1976) state that a large quantity of suspended material interferes with filtration processes of Daphnia, killing them. Carvalho (1984) noted that fluctuations in Daphnia gessneri populations in a floodplain lake in Amazonia correlated most with intense predation by fish and with water turbidity, although though reduction of light penetration during periods of flooding and high turbidity may help Daphnia to avoid visual predators (McCabe and O'Brien 1983, Geddes 1984). Scholtz S.

et al.(1988) suggested that visual predation by fish rather than turbidity 'per se' probably influenced the seasonality of Daphnia species . During the warmer months, selective removal of Daphnia pulex by visually foraging fishes may allow Daphnia barbata to gain dominance. The authors also mentioned the effects of temperature and nutrition as possible cause of the species changeover. It likely that in Lake Jacaretinga predation plays an important role as well, but until now there is little reported evidence. The possible influence of fish predation in Lake Jacaretinga was reported only by Zaret (1984). Analysis of stomach contents on the two most abundant plankton-feeding fishes Moenkhausia dichroura and Ctenobrycon spilurus in Lake jacaretinga, show that the fishes are feeding selectively on cladocerans over copepods and consuming as many as 1800 individuals per meal . Diaphanosoma sarsi was found in the highest proportion, followed by Bosmina, Daphnia gessneri, Ceriodaphnia cornuta and Moina reticulata. Zaret's findings are unique in Lake Jacaretinga and, unfortunately, there is no comparable studies to confirm his findings. Also, his studies did not cover a the whole year but only the low water phase. The relationship zooplankton-predators was not investigated in this study.

The greater success of Moina reticulata and poor performance of the others cladoceran during the flood period in Lake Jacaretinga corresponds to the presence of low transparency associated with the quantity of suspended food and silt particles .

Threlkeld (1986) have studied the dynamic population of four cladocerans in a turbid reservoir (Secchi depth usually <1 m), (Lake Texoma, Texas).He found that mean recruitment and longevity of Ceriodaphnia lacustris and Daphnia parvula in life table experiments were reduced during the flood when abundant silt particles and picoplankton (<2 um) replaced algal particles in the water column. Field collections revealed that Ceriodaphnia and Daphnia populations declined immediately after the arrival of turbid water, and remaining females carried fewer eggs. Conversely, populations of Moina micrura and Diaphanosoma leuchtenbergianum increased during the flood, and life table experiments showed that these species were able to grow

well in silt-laden water. According to the author the strong life table responses of Moina and Diaphanosoma to environments high in suspended sediments suggest a potent reason for their increased densities during the flood period. Hart (1986a) investigated on population dynamic and production of crustacean zooplankton on lake le Roux, a sub-tropical reservoir, and his findings showed that the abundance of zooplankton was positively related to water transparency; daphnids were virtually absent in years when high levels of inorganic turbidity prevailed. The present results partially supported the findings of Threlkeld and Hart and suggest that there a highly specific responses of individual populations to turbid inflow. The principal effect of high turbidity might be upon food availability and interference with mechanical acquisition of food particles may be a compound influence, although turbid water fauna like Moina reticulata may have evolved appropriate morphological or behavioral compensations. Measurements of food availability in Lake Jacaretinga as presented in Figure 8.9 shows that there is no condition of food limitation during the period of study. However, mineral particles can be ingested by cladocerans and occupy the gut space with no nutritive food. In Lake Jacaretinga the algal carbon was always more than 0.1 $mgC.l^{-1}$, higher than the threshold food level found in the experimental work carried out in this investigation (0.05-0.03 $mgC.l^{-1}$ using unialgal Scenedesmus acutus as food. Therefore, the values found in Lake Jacaretinga are higher than those obtained experimentally bearing in mind that under natural conditions the animals will be exposed to a variety of food. It is evident from the literature that it is not possible to apply the experimentally defined threshold levels directly to the field conditions since food quality also matters in the determination of food tresholds. This is evident from the results of Lampert (1978) in which he found the minimum food concentration for reproduction in Daphnia longispina to be 0.1 $mgC.l^{-1}$ under laboratory conditions, with unialgal food, but the threshold shifted to 0.2 $mgC.l^{-1}$ for field populations. He suggested that the higher value in the field might be due to a number of reasons: the size of particles (<60) that he considered to be food might have been greater than the preferred size range; the field food

might also have included non-consumable particles; and the food quality of the natural seston may not have been as good as that provided in the experiments.Thus it is important to evaluate the quantity of edible food available in the field for each species. Duncan (1985) put forward an indirect method for evaluating this by means of length-carbon regressions. The availability of food resources is reflected in the presence of egg-bearing female and number of eggs in the brood pouch. The results presented in Table 8.4 show that a greater change in the percentage of egg-bearing female occurred only to the species of Moina corresponding to the increase of edible non-algal carbon during the flood period.The number of eggs per female was kept constant for Moina reticulata and no egg bearing female was found for Daphnia gessneri, Diaphanosoma sarsi and Ceriodaphnia cornuta. Differential ingestion and assimilation of suspended silts may partially mediate species composition among those cladoceran. Suspended silt reduces filtering rate, assimilation efficiency and the rate of population increase in Daphnia (Zurek 1982; McCabe and O'Brien 1983. High concentration of suspended silt (2.4 g/1) decreased the ingestion rate of Daphnia pulex and Daphnia parvula for Chlorella by 95% and reduced the incorporation rate for carbon by 99%; 50-100 mg/liter were sufficient to reduce the algal carbon ingested to potential starvation levels (Arruda et al. 1983). The same authors concluded that ingestion rates of mineral particles by daphnids began to be limited at particle concentration of 5.0 X 10^6 particles / ml and were dependent on particle size, daphnid species and body size. Thus the differential ability to ingest particles suggest a mechanism of regulating daphnid species composition if the organic matter adsorbed to the mineral sediment particles is useful as food. There is no comparable studies to test the possibility that Moina reticulata and the other cladoceran assemblage in Lake Jacaretinga differ in their abilities to capture, ingest, or assimilate natural food items. However, long-term life cycle experiments using natural silt particles and Scenedesmus acutus as food source in this investigation, provide evidence against high concentration of silt particles (50 NTU) particularly for Daphnia gessneri. Moina reticulata may exploit more efficiently non-

conventional food resources such as silt-adsorbed dissolved organic matter in Lake Jacaretinga turbid waters.

9.2 Comparison of species responses to turbid conditions

The field investigation during February-May 1986 in Lake Jacaretinga, described in chapter 8, provided clear results, namely, that Daphnia gessneri was the dominant species during the pre-flood low-water phase of the lake, when its turbidity was low, but was replaced by another dominant, Moina reticulata, during the post-flood high-water phase with greatly increased levels of turbidity. Earlier research in 1979 and 1980 (figure 1.4) showed that Moina reticulata was a perennial species whose maximal abundance coincided with the high-water phase of the lake whereas Daphnia gessneri, along with less abundant Diaphanosoma spp, Ceriodaphnia cornuta and Bosmina chilensis, were present in some seasons only, usually during the low-water phase before the river flood. Brandorff & Andrade (1975) suggested that one of the causes for this decline in cladocerans populations might be an increased turbidity of the lake water associated with the river input.

The turbidity of the water of Lake Jacaretinga has not been studied in any systematic manner but a water sample collected on May 9th 1986, after the river flood, was brought back to England in order to count and size its suspended particles by a TAII Coulter Counter, using a 140 μm tube. This was used to determine the concentration and total volume of the particles recorded in the channel counting the smallest particles (less than 25 μm^3 volume and less than 3.6 um equivalent spherical diameter) as well as the total numbers of particles. These values were determined for the river, the channel and stations I to V within the lake (Figure 3.1) and given as follows:

Sampling site	Total n°of particles	Numbers of particles 3.6 µm	% of particles 3.6 µm	Volume of particles 3.6 µm
	10^6n°/l	10^6n°/ml	?	mm^3/ml
River	0.441	0.229	52	16.18
Channel	0.109	0.062	56	4.02
Station I	0.068	0.032	47	3.22
Station II	0.072	0.037	51	2.02
Station III	0.066	0.039	59	2.54
Station IV	0.058	0.035	60	2.50
Station V	0.073	0.039	53	3.66
Mean (Lake)	0.067	0.036	54	2.79

This table shows that the smallest (less than 3.6 µm) particles formed slightly more than 50% of the total particles and that both the smallest particles and the total particles declined in abundance as the water passed from the river to the lake via the channel. As a result, the concentration of the particles in the lake was about one sixth that in the river both numerically and by volume.

It would be useful for comparative purposes to be able to convert these particle counts of Lake Jacaretinga water into units of turbidity, such as NTU and or mg/l of suspended sediment. This can be done very roughly using the values in Table 3.5 (chapter 1) which lists the numbers and weight of particles used to produce the various experimental values of NTU for the turbidity experiments, assuming that the less the 3.6 um particles recorded by the Coulter Counter are equivalent to the particles (0.7-2.0 µm) used for the turbidity regimes. An examination of the values in table 3.5 shows that there is a linear relationship between particle concentration and weight between the NTU values of 10 and 40; in this range, the dry weight of one particle is 6.57 pgDW/particle. This is very similar to the value

of 10 pgDW/particle given by Arruda et al. (1983) which comes from his "suspended sediment concentrations of 50 mg/l represent 5.10^6 particles/ml". Table 3.5 also provides a relationship of Y = 0.63 X, where Y is NTU and X is mg/l.

Applying these two relationships (6.57 pg/particles and Y = 0.63 X) to $0.229.10^6$ particles/ml for the river gives a weight of suspended sediment of 1.50 mg/l and a turbidity of 0.94 NTU; doing the same for the $0.036.10^6$ particles/ml for the lake gives a weight of suspended sediment of 0.24 mg/l and a turbidity of 0.15 NTU. These are both much lower values than expected. Brandorff & Andrade (1975) recorded a weight of 55 mg/l for Lake Jacaretinga after the influx of white water and commented that this did not differ from what was measured before the influx. Iron (1984) gives the mean values of 70 mg/l for some white water Amazonian rivers. The water samples were kept under cool conditions for about two weeks though such procedures are not recommended in analysis of water particles . The main conclusion from this major discrepancy of result is that it is an urgent matter for there to be a systematic study of the variation in natural turbidity in this lake.

The above relationship between turbidity measured as mg/l, numbers of particles per ml and NTUs can also used to establish the weight and number of mineral particles contained in the experimental turbid suspensions measured as 10, 20, and 50 NTU. These are give below:

Turbidity	Weight	Numbers
NTU	mg/l	$n°.10^6$/ml
10	16.0	2.5
20	31.5	4.7
50	79.0	?

In the restricted enviroment of laboratory batch and flow cultures, Moina reticulata was equally successful at all the experimental levels of turbidity from 0 to 50 NTU. On the other hand, Daphnia gessneri was less successful in 20 and 50 NTU compared with

its performance in 0 and 10 NTU. Success was measured in terms of survival, growth and reproductive performance. The presence of a suspension of inorganic particles used to simulate natural turbid conditions resulted in two distinct responses from Daphnia gessneri: firstly, the species did not perform as well as expected in high, non-limiting food concentrations (0.5 mgC.l) combined with high turbidities of 20 and 50 NTU; secondly, the species' performance was better than expected in low limiting food levels (0.05 mgC.l) combined with a low turbidity (10 NTU).

Similar findings of both deleterious and beneficial effects of suspended solids upon Daphnia magna have also been reported by Robinson (1957). She even went on to state that Daphnia magna was unable to survive well or reproduce optimally without the presence of some inorganic material in the water. This beneficial effect of low concentrations of suspended (13-39 ppm) upon the survival and reproduction of this species was found for all the materials she tested, when compared with the controls without turbidity. The range of materials used by Robinson included, montmorillonite, illite and kaolinite, presented together with yeast cells as food. The concentrations of inorganic particles were reported in parts per million (ppm = about mg/l), not an inappropriate measure and comparable to the nephelometric turbidity units (NTU) used in this study (Table 3.5). Her ranges of turbidity were 13 - 1458 ppm.

The important differences between her study and this one were the food species provided and how the food was quantified. In this study, the green alga Scenedesmus acutus was used as a food source and quantitatively determined in carbon weight per litre. There is no doubt that algal food and the use of natural sediments from the lake itself gave more ecologically representative experimental conditions than in Robinson's experiments.

McCabe and O'Brien (1983) also investigated the effect of suspended silt and clay upon Daphnia pulex. They measured turbidity as NTU, using a Hach 2100Å turbidimeter metre. The filtering rates of

Daphnia pulex fed on low concentrations of Ankistrodesmus falcatus and increasing amounts of silt (2, 9 and 33 NTU) were greatly diminished compared with their maximal filtering rates in the absence of turbidity. They also found that quite low concentrations of suspended particles were sufficient to depress the assimilation efficiency of the species. Compared with the controls, the efficiencies were 65% and 25% in turbid suspensions of 2 and 33 NTU, respectively. This indicates that even at a low turbidity of 2 NTU, there is a detectible worsing of the species' ability to exploit its food. Unlike with Robinson's and my own results.

Life cycle studies on Daphnia pulex, Daphnia galeata mendotae, Ceriodaphnia cornuta, showed that their growth rates were significantly reduced in 2, 9 and 33 NTU.

In the long-term life cycle studies carried out with eight combinations of turbidity and food concentration (0.5 and 0.05 mgC.l; 0. 10, 20 and 50 NTU), there was little difference in the survival of Moina reticulata. Adding inorganic particles to high food (0.5 mgC.l) was apparently not harmful. The only exception was the occurrence of high mortalities with 0.5 mgC.l and 20 NTU in batch culture but this is considered to be an anomalous result which might not have been significant with more replication. Even at low food concentrations (0.05 mgC.l), there were no marked differences in the survival of Moina reticulata with turbidity, although the greatest percentage survival occurred in the controls (0 NTU) and the least in 20 and 50 NTU. On the other hand, all tested levels of turbidity were harmful to Daphnia gessneri. Mortality increased with turbidity and was greatest at low food levels (0.05 mgC.l) and higher turbidities (20 and 50 NTU). At low turbidity (10 NTU) and low food, the effect was beneficial for survival. A very striking difference between the two species was that, in 0.05 mgC.l and 20-50 NTU, Daphnia could not but Moina could manage to survive to the third adult instar.

One possible explanation for these differences in response to turbid suspensions between the two species might lies in the structure of the 'filtering' limbs, which are the thoracic limbs III and IV in both cases. Although there is no published information on

the structure of the limbs of Daphnia gessneri and Moina reticulata, Jayatunga (1986) has studied the limbs of the related species Daphnia lumholzi and Moina micrura from Sri Lanka. From the relationships of filter comb area to body length, she found that the comb area per unit length was slightly greater in Daphnia compared with Moina. In both species, the intersetular distance increased with stage in the life cycle but the range of intersetular distances was very similar for the two species (Daphnia lumholzi, 0.181 - 0.416 um; Moina reticulata, 0.189 - 0.345 um). Therefore, both species could capture the inorganic particles of 0.7 - 2.0 um and, in unselective filtering, would be forced to collect them. There is no possibility that the inorganic particles could pass through the limbs of Moina and thus not be ingested.(Photographs of guts in 50 NTU and 10 NTU Moina reticulata (a), Daphnia gessneri (b)).

Arruda et al. (1983) also found a difference in response to turbid suspensions in two species of Daphnia. In a series of careful experiments, these authors reported that the addition of seven concentrations of suspended particles from sediments (0.0, 0.0245, 0.245, 2.45, 24.5, 245 and 2450 mg/l) to Chlorella vulgarus var. viridis Chodat as food (5.10^4 cells/ml = about 0.17 mgC/l) substantially decreased the ingestion rates of Daphnia parvula (1.2 mm) and Daphnia pulex Leydig (1.68 mm). In both species the decrease started in 24.5 mg/l (= about 15 NTU) and became very marked in 2450 mg/l, although more in Daphnia pulex than in Daphnia parvula. That is, the two species differed in their response to the higher turbidities. No such species difference occurred with assimilation which decreased similarly over the same range of turbidities. Compared with the control, the decrease in assimilation efficiency was very marked, from 70% in 24.5 mg/l to as low as 10% in 2450 mg/l

The mean diameter of the sediment particles used above was 10 µm, which is larger than those used in this thesis (0.7 - 2.0 µm). In a subsequent experiment, Arruda et al. (1983) compared the ingestion of suspensions of coarse (4.65 µm) and fine (1.88 µm) particles when offered in different concentrations and without algal food. The ingestion rates per individual were higher in fine than coarse

suspensions in both species and ingestion per unit body weight was greater in Daphnia pulex than in Daphnia parvula within each suspension. However, in both species, ingestion rates of both fine and coarse clay particles reached a plateau at the same incipient limiting concentration of 5.10^6 particles/ml; in the fine suspension, this probably represents about 35 NTU. If this is so, then Daphnia parvula is much more tolerant of fine turbid suspensions than Daphnia gessneri, a daphnid of similar size.

In another extremely interesting experiment, Arruda et al.(1983) tested the effect upon the two species of a suspension of 'amended' sediment particles to which a bacto-peptone had been adsorbed to give a carbon concentration of 0.67 mgC/l in a turbidity of about 6 NTU. Compared with a non-turbid yeast suspension of 2.33 mgC/l, the duration of the life span and growth rate in length was not very different in the 'amended' suspension but the fecundity of Daphnia pulex decreased from 6.21 to 0.08 egg/female and Daphnia parvula was unable to reproduce. For daphnids, a food level of 0.67 mgC/l is quite high and might be expected to support a greater fecundity than 0.08 egg/female. However, the ability to reproduce at all on sediments with attached organic carbon compounds supports the findings in this thesis that cladocerans find low levels of turbidity beneficial at low food concentrations.

That high concentrations of suspended particles can reduce the availability of edible food to filtering cladocerans seems undoubted. The turbidity at which this starts may be quite low, about 15 NTU, from the results of Arruda et al.(1983). The precise concentration of this turbid suspension probably varies with species of cladoceran and the individual's body size, age or reproductive state. For example, in general most mortality in Daphnia geeneri was due to the death of juveniles younger than 3 days old or due to the deaths of the primiparous female carrying her first brood.(Table 7.1). A common cause of death in the primiparous female was the stress of ecdysis and/or the release of the embryos which was additional to the stress of turbidity. Prepas & Rigler (1978) comment that most mortality in Daphnia rosea occurred in the embryonic stage or during their release

from the brood pouch. Neill (1975) suggests that newly born Daphnia magna were more likely to die of starvation than the adults.

The inability of Daphnia gessneri to reproduce in high turbidity and low food (20 - 50 NTU; 0.05 mgC.l) whereas it did reproduce but with low fecundity in 20 NTU and 0.5 mgC.l lends further support to the idea that highly turbid suspensions affect the species adversely. This result agrees with the findings of McCabe and O'Brien (1983) on the fecundity of Daphnia pulex. A comparison of the reproduction of Daphnia gessneri and Moina reticulata shows that the two species responded differently. Moina reticulata was the better reproducer in all food-turbidity treatments in both batch and flow cultures, indicating its great tolerance of turbid conditions. In contrast, the reproduction of Daphnia gessneri did not proceed well. Most of her eggs never hatched because they were either resorbed, lost during the next moult or died with the mother. This was most noticeable in the flow cultures in which Daphnia gessneri did manage to produce eggs in 50 NTU and 0.5 mgC.l food. Arruda et al. (1983) also reported on the degeneration of the eggs of Daphnia pulex which were being fed on the 'amended' sediment particles with adsorbed organic compounds.

In neither Daphnia gessneri nor Moina reticulata was there any noticeable effect of turbidity on the body length of the primiparous female. Daphnia gessneri did produce smaller primipara in turbid batch cultures but with no consistent pattern. Since one effect of turbidity is to reduce the available concentration of food to the animal, there might have been a detectible reduction in the carbon weight but this was not measured. McCabe and O'Brien (1983) have reported on an opposite effect, namely, a smaller mean length in control Daphnia pulex compared with those from high turbidity but there is no indication that these measurements are comparable.

This study was the first to determine growth rates in cladocerans in terms of weight and under turbid conditions, although Arruda et al.(1983) have compared the growth in length of Daphnia pulex fed on 'amended' sediment particles with those on yeast cells. The turbidity experiments show that Moina reticulata could grow in conditions where Daphnia gessneri could not: 0.05 mgC.l and 20-50 NTU. The level of

turbidity affected the size of adults of both species, but with greater effect on Daphnia gessneri, compared with the control animals which were the biggest (Table 7.18). In Moina, the effect of turbidity on the maximal length attained by females in their third adult instar was not significant in low food concentrations but was markedly noticeable in high food levels.

That high sediment concentrations added to food must constrain severely the energy acquisition of planktonic cladocerans is well illustrated by Figures 7.8 and 7.10. This shows the growth curves of Daphnia gessneri and Moina reticulata in two quite different situations of high food-high turbidity (0.5 mgC.l and 50 NTU) and of low food-no turbidity (0.05 mgC.l and 0 NTU). In these two quite different conditions, the two growth curves are practically the same. Table 7.19 provides additional evidence in terms of the instantaneous daily growth rates. The rate at high food-turbidity is not significantly different from the rate at low food-no turbidity.

It seems clear that one effect of turbid suspensions is to reduce the availability of food levels to cladocerans. How or why this happens needs more investigation. However, one effect must be to overwhelm the food cells with mineral particles, given the assumption of unselective feeding. This can be shown by a simple calculation. According to Rocha (1983), the carbon weight of Scenedesmus acutus is 11.78 pgC/cell. Thus, the cell densities for 0.5 and 0.05 mgC.l food media is $0.042.10^6$ and $0.0042.10^6$cells/ml. The particle concentrations for turbid suspensions of 10, 20 and 50 NTU was given earlier in this section as $2.5.10^6$, $4.7.10^6$ and probably about 14.10^6 particles per ml, respectively. Assuming that Daphnia gessneri responds similarly to Daphnia parvula, the incipient limiting concentration for ingestion of sediment particles was found to be about 5.10^6 particles/ml by Arruda et al. (1983). One effect of 50 NTU would be to depress the daphnid's filtering rate but not at 10 NTU and probably not at 20 NTU. Another effect would be to 'dilute' the number of algal cells reaching the intestine for digestion. At high food levels of 0.5 mgC.l, the ratio of algal cell:mineral particles would be 1:60 in 10 NTU, 1:112 in 20 NTU and 1:333 in 50

NTU. The situation would be ten times worse in the low food level of 0.05 mgC.l, thus giving a ratio of 1:595 at 10 NTU which is rather similar to the ratio of 0.5 mgC.l and 50 NTU.

Further literature comparisons with the present study cannot be made due to the lack of investigations which test the effect of turbidity on planktonic cladoceras by long-term life cycle experiments, whether from the temperate or tropical regions. However, according to the hypothesis stated at the beginning of this section, consistent differences in life history characteristics were found between the two main dominant species of Lake Jacaretinga. If Moina reticulata is more successful at growing and producing eggs than Daphnia gessneri in the presence of naturally turbid suspensions, then this could explain the species succession which was observed in the lake before and after the flooding of the river. The main causative factor may be due to the increased sediment loading brought in by the river water but this has yet to be established and quantified. At present there are no measurements of the turbidity of the lake other than Brandorff and Andrade's two or three values. It is possible that the changeover in species could be caused by other environmental changes, such as dissolved oxygen concentration, concentration of food or increased predation pressure by incoming riverine fish species.

In relation to the present study, we cannot explain why Moina is more tolerant of turbid suspensions than Daphnia. Nevertheless, it is clear that differences do exist between the cladoceran species and that the presence of turbid conditions does severely affect uptake of food, growth and reproduction of some but not other species of cladocerans. There does exist the possibility that the species changeover in Lake Jacaretinga is due to the differing abilities of Moina reticulata and Daphnia gessneri to capture, ingest or assimilate the natural food items existing in the lake but this is still not known and needs more research. We still have much to learn about the effects of suspensoids on cladocerans. However, we can speculate that it is Moina's tolerance of silt and clay particles

that enables the species to exist perennially in the lake and to be the dominant species after the flood.

That suspended silt may provide and additional source of food for freshwater filter-feeders by an adsorptive mechanism involving clay suspensions may be important in oligotrophic conditions with highly abundant suspended material, as in reservoirs (Arruda et al, 1983) or floodplains (Gibbs, 1967; Schimidt, 1973). Thus the adaptive value of specializing on an alternative food resource could be the reason for the great advantage experienced by Moina reticulata in Lake Jacaretinga where suspended particles are abundant.

9.3 The influence of food-temperature combinations on the life cycle of tropical cladocerans.

Knowledge of temperature and food level on life cycle parameters of zooplankton is basic to understanding the mechanisms which regulate the production and seasonal dynamics of zooplankton populations. In this study we present data on temperature and food concentration upon growth and reproduction of three Cladocera species. Each individual was followed throughout the life cycle from newborn (neonates) until adult 3rd brood, kept under defined and controlled experimental conditions.

Life cycle threshold food concentration.

These experiments illustrate the threshold food concentration and reproduction of Daphnia gessneri and Diaphanosoma sarsi to be between 0.1 and 0.05 mgC.l^{-1}, higher than the threshold found for Moina reticulata, which lies at 0.03 mgC.l^{-1} at 27°C. Lampert (1977a) suggested that the threshold food concentration for a cladoceran with a dry weight of 50 ug feeding on Scenedesmus acutus at 20°C should be about 0.05 mgC.l^{-1}. Rocha (1983) reports that temperate daphnids, Daphnia magna, Daphnia pulicaria and Daphnia hyalina grow and reproduce at an even lower threshold food concentration of 0.01

$mgC.l^{-1}$ in temperatures of 15°C and 20°C. Jayatunga (1986) records the occurrence of reproduction in tropical Diaphanosoma excisum and Moina micrura in 0.05 $mgC.l^{-1}$, but not in 0.03 $mgC.l^{-1}$ at 27 and 32°C, and for Daphnia lumholtzi at 22°C is 0.1 $mgC.l^{-1}$, the same concentration found in this work for Daphnia gessneri at 27°C. These findings for tropical cladocerans would be considered quite high since threshold values for reproduction in temperate species of Daphnia are as low as 0.05 $\mu gC.l^{-1}$ (Lampert 1977a) and 0.01 $mgC.l^{-1}$ (Rocha, 1983). However, Moina reticulata in the present study was able to reproduce with two broods in 0.03 $mgC.l^{-1}$, the lowest food concentration tested at 27°C, but studies to test the possibility that Moina reticulata and Daphnia gessneri and Diaphanosoma sarsi differ in their abilities to capture, ingest, or assimilate natural food items are lacking. Since in the field, cladocerans will be exposed to a variety of different food items; algae, bacteria, detritus, mineral particles and food concentration can change drastically in a fluctuating environment, slight differences in the ability of resource utilization may be important for the success of a species. These differences might be caused by structural differences such filtering area and intersetular distance in the filtering combs. Jayatunga (1986) has provided some information on tropical species of cladocerans, included Daphnia lumholtz, Diaphanosoma excisum and Moina micrura. According to her findings it seems that the range of intersetular distance in these cladocerans are very similar in Moina micrura with values between 0.189-0.345 um and in Daphnia lumholtzi with values between 0.181-0.416 um, smaller intersetular distances were found in Diaphanosoma excisum (0.179-0.227 um). It is striking that in spite of its smaller size Moina micrura (0.50-0.70 mm in length) has such high values compared with those obtained for Daphnia and Diaphanosoma (0.57-1.90 mm) and (0.50-0.96 mm), respectively.

Romanovsky (1985) believes that species of the genus Moina can be considered ("explerents" or "ruderals"), a life-history strategies analogous to the primary strategies in vascular plants proposed by Ramensky (1938) and Grime (1979). This strategy is associated with a short life-span, high rates of individual growth and has evolved in

severely disturbed and productive environments of pronounced seasonal fluctuations in biomass and production of edible seston frequently observed in eutrophic environments. If Moina reticulata has such a strategy and if its juveniles have high rates of individual growth, this implies that this species may be better adapted for pronounced changes in biotic and abiotic parameters caused by flooding in Lake Jacaretinga than other crustacean cladocerans. The threshold food concentration of 0.03 $mgC.l^{-1}$ recorded experimentally in this study for Moina reticulata is lower than the average of the POC in the field measured for edible non-algal organic particles where values lies between 0.5-1.83 $mgC.l^{-1}$, and in edible algal carbon (0.15-0.7 $mgC.l^{-1}$). However, we cannot compare defined threshold levels in laboratory using unigal cells directly to the field conditions since in nature the food composition is more conplex. Nevertheless, resource limitation in Lake Jacaretinga appears to be more a result of changes in resource quality than simple resource depression.

Effects of food limitation on growth and reproduction

GROWTH

The results of laboratory experiments presented in this paper show that the concentration of the food available is a factor as important for the growth and reproduction of cladocerans as temperature. In this study, growth curves of the three species of cladocerans were strongly influenced by the food concentration. In all three species, an initial period of exponential growth was observed, and then grows progressively more slowly after having reached sexual maturity and then reach an asymptotic adult size. Comparing graphically these results with those obtained by Rocha (1983) with temperate daphnids, and Jayatunga (1986) on tropical cladocerans, it is evident, on the whole, the shape of the growth response to food concentration is very similar. As has been demonstrated previously, the maximum size attained by cladoceran species being those from non-limiting food concentrations (Lampert, 1984; Rocha, 1983; Jayatunga, 1986). This

was confirmed for Daphnia gessneri, Diaphanosoma sarsi and Moina reticulata, the largest animals being those from cultures at high food levels (1.0, 0.5, 0.25 $mgC.l^{-1}$). Growth is poorest when food was limited (0.1, 0.05 $mgC.l^{-1}$) for Daphnia and Diaphanosoma and 0.03 $mgC.l^{-1}$ for Moina. At 27°C, for all three species the influence of food level on the growth rate was very strong. This was evident in the instantaneous growth rates of juveniles (Table 4.1). There is however, a substancial difference between species. Moina reticulata, as expected, revealed higher growth rates (approx. 1½ times) than those for Daphnia gessneri and Diaphanosoma sarsi even in limiting food levels. The two larger species Daphnia gessneri and Diaphanosoma sarsi have similar growth rates. Thus, this species utilized the available food resources for growth with more efficiency. This is in accordance with the results of Jayatunga (1986), who found almost double values of growth rates for Moina micrura compared with those for Diaphanosoma excisum, under the same experimental conditions. Such differences might have important ecological implications. The relatively lower food requirements per individual of the smaller species provides a competitive advantage in a food-oscillating environments. This factor may explain, in part, the dominance of Moina reticulata and the poor performance of Daphnia gessneri and Diaphanosoma sarsi in Lake Jacaretinga a variable environment during the flood.

It has been shown from several experimental field studies on competition that small species outcompete larger species under near natural conditions. For example, both Neill (1975) and Lynch (1978) showed that Ceriodaphnia could out compete large Daphnia because, according to Neill (1975) juvenile Daphnia were particularly sensitive to resource depression. DeMott and Kerfoot (1982) suggest that competitive interactions between Daphnia rosea and Bosmina longirostris were related to fundamental differences in their filtering pattern. In Bosmina, the thoracic limbs are clearly modified for dual purposes of large-particle grasping or small-particle filtering. This specific feeding strategy of being able to handle two sizes of particles does not seem to be the causal factor

in Moina's success, however very little information is available on how Moina feeds although something is known about their morphology of the filterstructure (Jayatunga, 1986).

REPRODUCTION

It is generally accepted that the number of eggs produced by an adult Cladocera depends upon different biotic and abiotic factors. Among them, food intake, temperature, age and size of the mother are recognized to play important roles in regulating reproduction. (Green, 1956; Hall, 1964; Kerfoot, 1974). Development times usually decreased with increasing temperatures, retardation in development occurring close to the upper lethal range (Herzig, 1983).

In this study, reproductive output in the tropical cladocerans was influenced in a systematic way with size, food supply and temperature. The food concentrations tested spanned the range from near threshold to optimal conditions and the temperatures from the rather low one of 22°C to the very high one of 32°C. All three cladocerans responded to a decrease food concentration by reducing fecundity, delaying the time to attain maturation, and reaching maturity at a smaller body size. In all the species, the primipara female has the smallest length in most severely limiting food concentrations and her largest length in the non-limiting concentrations. In Daphnia gessneri and Diaphanosoma sarsi, the degree of reduction in length is more marked than in Moina reticulata, probably due the greater difficulty of detecting small differences in size in small-bodied cladocerans. The results of these experiments agree with the data of many other authors who showed the existence of a positive correlation between the changes of individual fecundity and food concentrations. However, most of these authors did not quantify the food levels at which this occurred, as did Rocha (1983) who found a similar response in three temperate daphnids and as did Jayatunga (1986) who also described the same trend with her tropical cladocerans. Both results from these two authors are

extremely relevant to this study, bearing in mind that the same methodology was used to quantify food levels, that Scenedesmus acutus was the common food resource and so entirely comparable with the present work.

Since only Daphnia gessneri was tested at three temperatures, in this work, this is the only species in which the influence of temperature upon fecundity can be examined. In the present study, fecundity was reduced when temperature increased in all food whether food limited and non-limited, although the general trend was for fecundity to decrease with temperature. The tropical cladocerans examined by Jayatunga (1986) showed that above the threshold food concentrations (0.05 $mgC.l^{-1}$) fecundity increased with temperature. Orcutt and Porter (1984) found that temperature had a reducing effect on fecundity of Daphnia parvula raised at various temperature (10, 15 and 25°C) and food (0.02, 0.2 and 2.0 $mgC.l^{-1}$). Fecundity increase from 10°C to 15°C and decrease from 15°C to 20°C at all experimental food levels.

Based on a field investigation, Green (1966) invoked temperature as a causal factor in reduced fecundity of Simocephalus vetulus, and he suggested that at higher temperatures the cladocerans matured at a smaller size which reduced the egg carrying capacity. Culver (1980) also observed that as the temperature increased from spring to summer, there occurred a pronounced decrease in size of primipara, fecundity and size of neonates of seven species of cladocerans at Bay of Quinte, Lake Ontario. By comparing samples taken from the open water where cladocerans were exposed to fish predation and samples from enclosures without fish, the same pattern was observed. The author invoked temperature as the main factor responsible for the seasonal variation in the reproductive characteristics and not predation. Changes in body size and reproductive traits of cladocerans have also been interpreted solely as adaptive responses to size predation (Brambilla, 1980, 1982). The present study provide evidence that fecundity and body size are strongly dependent on food concentration and less dependent in temperature. Among the other tropical species examined by Jayatunga (1986), Diaphanosoma excisum

did not show any variation in the size of the primipara with temperature but did respond to low temperature and low concentration by delaying maturity. Smaller size associate with high temperature occurred in Moina micrura.

As mentioned elsewhere, the highest temperature of 32°C used in the present experiments, produced a series of abnormal responses like eggs degeneration and abortion, and any interpretation in this temperature must be made with caution. It is evident from this investigation that Daphnia gessneri has its optimal temperature for reproduction between 22 and 27°C.

Duration of Development - Embryonic and Postembryonic Development

It has frequently been shown that the duration of embryonic development of Cladocera is purely temperature dependent (Ingle et al. 1937; Esslova 1959; Hrbackova-Esslova 1963; Hall 1964; Korinek 1970; Munro & White 1975; Bottrel 1975; Magdza 1977; Leveque & Saint-Jean, 1983, Herzig 1984). However, it seems now recognized that both temperature and food concentration has effects on developmental duration. This fact probably was denied before, probably due to difficulties in quantify food and and experimenting with simultaneous food-temperature combinations.

Temperature was the main factor controlling embryonic duration in Daphnia gessneri on non-limiting food levels. There is an increase in duration as either temperature or food level decreases (Table 5.1). Only a few published data is comparable for Daphnia gessneri, a tropical cladoceran reared at 22, 27 and 32°C. Jayatunga (1986) found the embryonic development time for Daphnia lumholzi at 22°C (the only temperature available) to be 60 13.16 hours and 51.04 8.6 hours at non-limiting food level, and 64 13.8 hours at 0.1 $mgC.l^{-1}$, very similar to those obtained in the present work for Daphnia gessneri. The effect of food concentration on duration of embryonic development of Moina reticulata and Diaphanosoma sarsi was also observed although more extensively in limiting food levels than in non-

limiting food levels as Jayatunga's data set for Moina micrura. Magadza (1977) shows that development period of Moina dubia, another tropical cladocera followed inverse exponential relationship with temperatures tested between 14°C-30°C, but unfortunatly food levels were not assessed by the author. Orcutt and Porter (1984) conducted a set of experiments in which they raised Daphnia parvula at three food levels of Chlamydomonas reinhardi at 10, 15 and 25°C. Similar to the results of this study, they found that food concentration may have a substantial effect on embryonic development. The duration of embryonic development decrease with increase in food concentration at all temperatures, but, the greatest prolongation occurred at the lowest food level, and temperature had no effect. Herzig (1984) has analysed the duration of embryonic development of Diaphanosoma brachyurum at temperatures between 8.2°C and 29.7°C. Clear differences were found between spring and summer generations. A comparison of the D_e at 27°C of Diaphanosoma brachyurum (29.0 0.22 hours) is very similar with D_e of Diaphanosoma sarsi reared at non-limiting food levels (1.0 and 0.5 $mgC.l^{-1}$) respectivelly 24 0.0 and 29±10.4 hours. Again, food concentration eas not assessed, since the algal source was not adequately quantified. Rocha (1983) also gives evidence that duration of D_e in temperate species of daphnids increases as either temperature or food concentration decreases although the effect of temperature is much greater. Thhe species studied were Daphnia magna, D.pulicaria and D.hyalina. D.magna significantly prolongs D_e below 0.1 $mgC.l^{-1}$.

A weak point in many investigations which results in incomparability of results is due to differences in the range of food concentrations used. In fact, results of this study suggests that food concentration may have a substantial effect on D_e and particularly attention must be drawn to assess low food levels. Again, differences between the three species of cladoceran is evident. Moina reticulata takes a shorter time to complete development than Daphnia gessneri and Diaphanosoma sarsi under the same food-temperature combinations.

As in embryonic development, food concentration and temperature are the factors that determine the duration of postembryonic development (D_j). In these experiments, the D_j in cladocerans starts from the release of the young from the females and ending by the appearance of the first eggs in the brood pouch, determined in the primiparous female.

The dependence of the duration of D_j on trophic conditions is obvious in Daphnia gessneri and Diaphanosoma sarsi, in all food concentrations, but the prolongation in D_j for Moina reticulata occurred only at low food levels, and remained constant (48 0.0 hours) at non-limiting food levels. The increase in D_j could result from an increase in the duration of juvenile instars with the number of juvenile instars unchanged or from an increase in the number of juvenile instars with instar duration unchanged, or from the increase of both the duration and number of juvenile instars (Bottrell et al. 1976). The results in this study suggests that prolongation of juveniles duration occurred by both increase in the duration of the juvenile instars and an increase in the number of juvenile instars (Table 5.5).

Although the D_j of cladocerans has been determined either under various food concentration at one temperature (Wegleska, 1971) or under various temperatures with excess food (Bottrell 1975b, Herzig 1985) it is now generally accepted that food and temperature should be investigated simultaneously as has been carried out by Rocha (1983) on temperate species, Jayatunga (1986) and the present study. Here it is evident that Moina reticulata can develop to maturity faster than Diaphanosoma sarsi and Daphnia gessneri at all food concentrations and under similar conditions (Figures 5.3 and 5.4). At 27°C development was faster at non-limiting food concentration compared with the drastic slow down in limiting food levels (0.05 and 0.03 $mgC.l^{-1}$).

The smaller-bodied Moina reticulata shows a faster maturation time, which in fact, provides supporting evidence for the hypothesis of a positive relationship between body size and duration of

postembryonic development among cladocerans, suggested by Hall et al. (1976) and Allan and Goulden (1980).

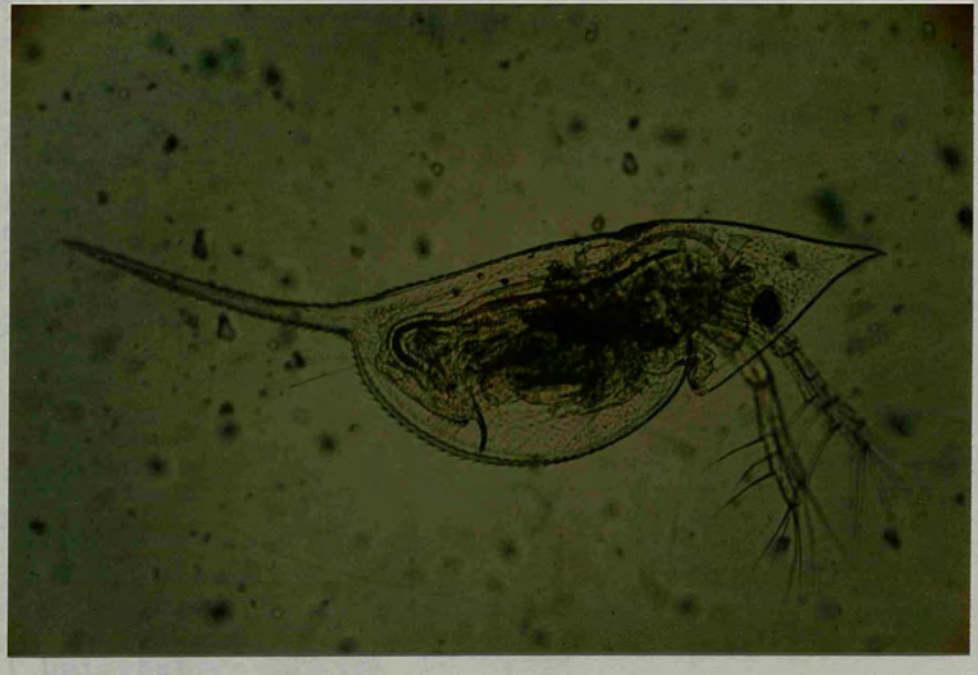
Similar results were reported by Jayatunga (1983) in tropical cladoceran species and by Rocha (1986) in three temperate daphnids, although some variations on the duration of juvenile were observed between species of the same genera. Diaphanosoma sarsi reaches maturity at 27°C in non-limiting food level between 2.9 to 3.75 days, and in limiting food between 4.8 to 5.25 days, while Jayatunga (1986) gives a duration of juvenile for Diapahnosoma excisum of 3.3 to 4.3 days in non-limiting food and 5.4 days to 7.25 days in limiting food levels. Herzig (1984) gives juvenile duration for Diaphanosoma brachyurum at 26°C of 3.19 days. In Herzig's work the animals were reared under non-limiting food only. Thus effect of food was not taken into consideration but our results enables us to. However, from the present results it is very clear that the prolongation of juvenile duration is stronger in the lowest food resource. The same pattern can be seen in the other tropical species. Obviously more research on the duration, number of juvenile instars and body size is needed in order to see whether populations changed their developemnt time.

In conclusion, the reproductive characteristics of Moina reticulata show that it is comparatively more fit organism than Daphnia gessneri at low food levels even in the presence of mineral particles thus turbidity could influence the seasonal succesion of these cladocerans in Lake Jacaretinga by interacting with other factors. Simultaneous field and experimental studies with particularly small-bodied cladocerans like Moina must be encouraged to stablish the response of these animals to environmental parameters like dissolved oxygen content, food resource and turbidity.

Plate 9.1. Photographs showing the gut of (a) Moina reticulata and (b) Daphnia gessneri.

(a)

(b)



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APPENDIX 1

The wet combustion technique for determination of the algal concentration of Scenedesmus acutus and of the sestonic organic carbon from Lake Jacaretinga

The carbon content of Scenedesmus acutus from liquid medium and also sestonic carbon from Lake Jacaretinga were determined by the wet dichromate oxidation procedure, as described in Mackereth et al.,(1978). The method employs relatively strong dichromate solution as oxidant, acting on solid material obtained by filtration.

Principle

Organic matter is oxidised to yield its original inorganic constituents and the amount of carbon present can be calculated from the amount of oxygen used in the reaction:

$$C_xH_2yO_z + (x + {}^{y-z}) O_2 = x\ CO_2 + y\ H_2O$$

The values of x, y and z can be determined if the composition of the organic matter is known. In most cases, this is not known but many authors consider the oxidation of a hexose

$$C_6H_{12}O_6 \text{ -- } 6CO_2 + 6H_2O$$

where 1 mg oxygen is equivalent to 0.375 mg carbon. here, the oxidising agent used is $K_2Cr_2O_7$ where, 1 ml of 0.125N $K_2Cr_2O_7$ is equivalent to 1 mg O_2 and so :

1 ml of 0.125N $H_2Cr_2O_7$ is equivalent to 0.375 mg C; thus in the titration,

1 ml of 0.01 $K_2Cr_2O_7$ is equivalent to 0.030 mg C as

1 ml of 0.01 $K_2Cr_2O_7$ is equivalent to 1.0 ml of 0.01N FAS (Ferrous ammonium sulphate),

1 ml of 0.01N FAS is equivalent to 0.030 mgC or 30 µgC

Reaction

The organic matter is heated (100 C/2 hours) with excess $K_2Cr_2O_7$ in the presence of concentrated sulphuric acid + a silver catalyst.

The dichromate remaining unreduced is determined by titrating with ferrous ammonium sulphate (FAS) to an end point detect amperometrically using a platinum-calomel combination eletrode and millivoltmeter.

Reagents

a) Potassium dichromate solution 0.2N $K_2Cr_2O_7$

0.98 g dried to constant weight was dissolved in 100 ml distilled water.

b) Ferrous ammonium sulphate 0.01N($FeSO_4.(NH_4)_2SO_4.6H_2O$

The stock solution 0.1N was prepared by dissolving 9.8 g in 100 ml of distilled water, add 5 ml of concentrated H_2SO_4 and dilute to 250 ml. 0.01N solution was made from this stock solution

c) Sulphuric acid-silver sulphate (Ag_2SO_4 + H_2SO_4)

0.24g was dissolved in 20 ml of sulphuric acid, made up fresh every week.

Apparatus

a) small beakers (50 ml) covered with watch glass

b)) dry-block heating unit

c) volumetric pippetes (2.0 and 1.0 ml)

d) narrow stemmed platinum-calonel eletrode (Type EA 234 of Metrohm)

e) 1 volt (d.c) potential source (1.5V dry battery and 10k potentiometer

f) Automatic piston burette

g) Fluke Digital Multimeter (8022A) magnetic stirrer and follower

The glassware must be throughly cleaned, rinsed and stored with precautions to exclude dust. Titrations were performed on filtered algal samples and two blank pads. The difference in the volume of FAS used for the blanks and for the samples represents the quantity of dichromate consumed to oxidise the algal sample. The normality of the

titrant was found by separate titration of 1.0 ml of 0.2N $K_2Cr_2O_7$ and 2.0 ml of H_2SO_4/Ag_2SO_4 without heating.

Calculations

$$ugC.ml^{-1} = (B - A) \times \frac{20}{S} \times 1 \times 30$$

where, B is the volume of FAS in ml required in the blank; A is the volume of FAS in ml required in algal sample. The volume of 0.01N FAS required to oxidise 1.0 ml of 0.2N $K_2Cr_2O_7$; S is the volume of algal sample; 30 is the carbon equivalent in µg of 1.0 ml of 0.01N FAS

The sensitivity of the method was tested by using different concentrations of analar grade glucose in addition to using the relationship of 1 ml 0.01N ferrous ammonium sulphate geing equivalent to 30 µgC

Procedure

Analar grade glucose solution containing 600 µgC was prepared by dissolving 1.285 mg glucose in a 1 litre of distilled water. By dilution with distilled water a series of solutions which contained 300, 150, 75, and 37.5 $\mu gC.ml^{-1}$ were prepared. 1 ml of each solution (three replicates) was taken and titration was carried out according to the procedure described above. At each concentration µgC equivalent to 1 ml of 0.01N ferrous ammonium sulphate was calculated as in the following table

Concentration of ugC in solution = µgC in 1 ml of 0.01N FAS

600.0 = 30.670

300.0 = 29.720

150.0 = 30.800

75.0 = 30.784

37.5 = 31.565

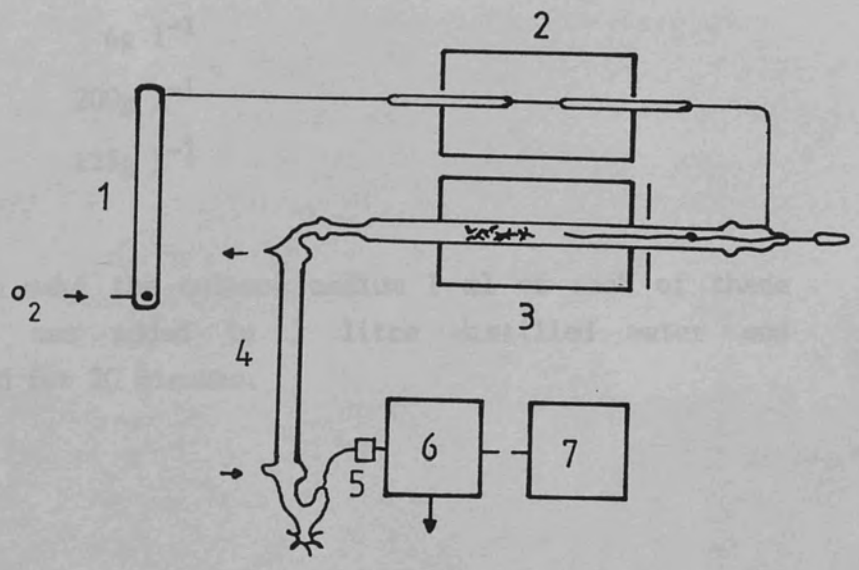
Where, mean value ugC equivalent to 1 ml of 0.01N FAS is = 30.71.

Procedure

Each pre-muflled nickel cup, which contained a known number of known length Cladocera was introduced carefully using clean forceps into the platinum cup in the combustion tube through a side opening closed by a slightly conical Teflon plug which fits into a Teflon collar fixed onto the tube with epoxy. The sample was transferred into the furnace at 920° C by steadily pushing the rod into the tube until it is wholly inside. The dried carbon dioxide was carried through the 22 cm cuvette and determined by the attenuation of infra-red in an Infra-Red gas analyser of Hartmann & Braun whose output was recorded on a BBC model Servogor 120 chart, with a pen recorder which gave a peak height in proportion to the carbon dioxide content of the sample. The peak height was measured in proportion to the carbon dioxide content of the sample. The peak height was measured in mm and converted to carbon weigth in µgC using the calibration curve determined with several known concentrations of oxalic acid.

APPENDIX 2

The high temperature dry combustion technique for determining the carbon weight of cladoceran specimens, using the Hartmann & Braun Infra Carbon dioxide analyser Schematic diagram (Salonen, 1976).



1. Oxygen is passed through the tube (Flow-meter)
2. Pre combustion furnace
3. Sample combustion furnace 1000°C
4. Condenser
5. Dust filter
6. Infra red gas analyser
7. Recorder

APPENDIX 3

Algal culture medium CHU 12 (Stein, 1973)

Stock solution

$KaHPO_4$	50g l^{-1}
$MgSO_4$	50g l^{-1}
Na_2CO_3	20g l^{-1}
$FeCl_3$	4g l^{-1}
$Ca(NO_3)_2$	200g l^{-1}
Na_2SiO_4	125g l^{-1}

To make the culture medium 1 ml of each of these solutions was added to 1 litre distilled water and autoclaved for 20 minutes.

APPENDIX 4

Preparation of clay specimens for x-ray diffraction less than 2 um fraction (from class schedule kindly supplied by Dr.G. Marriner from Geology department RHBNC).

PRINCIPLE: Laue, in 1912 reasoned that if crystals were composed of regularly spaced atoms, these might act as centres of scattering for x-rays. If x-rays were eletromagnetic waves of wavelength about equal to the interatomic distances in crystals, then it should be possible to diffract x-rays with crystals. Since no two minerals have exactly the same interatomic distances in three dimensions, the angles at which diffraction occurs will be distinctive for a particular mineral. The interatomic distances within a mineral crystal then result in a unique array of diffraction maxima which serves to identify that mineral, (Whittig 1965).

PROCEDURE: 20 grams of sample were weighed into a 500 ml beaker to which 100 ml of 6% hydrogen peroxide was added. The beaker was placed on a steam bath for 45 minutes. This oxidises any carbonaceous material to CO_2. 20 ml of 2M HCl was added to 250 ml distilled water replaced on a steam bath for 50 mins. This stage breaks down any carbonate present. It was made up to 1 litre with distilled water and left overnight to settle. The supernatant liquid was removed approximately 2 cm above the sludge and discarded. The pH of the slurry mixture was adjusted to 4 by adding 2N Na_2CO_3. The slurry was then dispersed in 20 ml of Calgon (100 gms of sodium hexa-meta-phosphate and 25 gms of Na_2CO_3) in a litre cylinder, diluted to volume with distilled water, mixed throughly and left to stand for 24 hrs. The supernatant suspension was siphoned off to 8.0 cm above the setlled slurry, and the residual slurry discarded. The suspension contained the 2 micron fraction of the clay. The suspension was centrifuged and the precipitate split into 2 portions. To the first portion was added 10-20 ml of satured $MgCl_2$ solution and mixed. The suspension was centrifuged again and

two 1 ½ inch square glass slides coated with the resultant slurry left to dry in air. To the second portion was added 10-20 ml of saturated KCl solution, mixed and centrifuged as before, but because of excess KCl on the slide, it was advisible to wash the precipitate with methanol or acetone and recentrifuge. Again two 1 ½ inch slides were coated with the slurry and left to air dry. When the slides were dry, one of each was run through the x-ray diffractometer from 2-30 20 if using CuK radiation. The second $MgCl_2$ saturated sample was heated for 1 hour in an oven at 60 C. A glass jar was prepared with a lid with a central support surrounded by glycol. The slide was placed on the support so that it was above the surface of the glycol, the lid was replaced and left for 1 hour before heating in the oven at 60 C again for 1 hour, and the sample run on the diffractometer immediately. The second KCl satured slide was heated in an oven at 500 C for 1 hour and run on the diffractometer immediately. The 4 resulting traces were compared and the constituent clay mineral identified by comparing the patterns obtained with those of known clay minerals.

A diffraction spacing of approximately 14 A. obtained from a Mg-saturated, air dried sample may be contributed by montmorillonite, vermiculite, or chloride, or by a mixture of these species. Solvation with glycerol allows separation and positive identification of montmorillonite. Saturation with K similarly allows separation of vermiculate from chlorite, which does not collapse. Heating of a sample to 500 C, serves two functions. It effects collapse of vermiculite which contains nonexchangeable interlayer aluminium hydroxy complexes, and it destroys the kaolin minerals. When chlorite is present in a sample, it normally yields a second-order maximum at nearly the same position as the first-order maximum kaolinite (7.15A.). If a 7.15A. spacing, obtained from an unheated sample, disapears or decreases in intensity after heating at 500 C, the presence of kaolinite is confirmed.

APPENDIX 8.1 Analyses of varianace: One way classification comparing densities between 5 stations on one date. S-N-K test, (Group of means underlined are not significantly different. Treatments = 5 stations; Error = 3 replicates.

SPECIES : Ceriodaphnia cornuta

DATES	SOURCE	SS	DF	MS	F	P	S-N-K
25.II	Treatments	68.61	4	17.15	119.6	< 0.0001	2 5 4 1 3
	Error	1.43	10	0.14			
04.III	Treatments	3510.74	4	877.68	13.3	0.0005	2 5 1 4 3
	Error	659.01	10	65.90			
11.III	Treatments	6122.93	4	1530.7	37.7	0.0001	4 5 2 3 1
	Error	406.00	10	40.60			
19.III	Treatments	27.05	4	6.76	13.75	0.0007	4 5 2 1 3
	Error	4.43	9	0.49			
26.III	Treatments	15.30	4	3.82	16.24	0.0002	3 1 4 5 2
	Error	2.35	10	0.24			
01.IV	Treatments	2.51	4	0.63	11.69	0.0008	2 4 3 5 1
	Error	0.54	10	0.05			

APPENDIX 8.1 continued

SPECIES: Daphnia gessneri

DATES	SOURCE	SS	DF	MS	F	P	S-N-K
25.II	Treatments	8.37	4	2.09	8.39	0.003	5 2 3 4 1
	Error	2.49	10	0.25			
04.III	Treatments	303.58	4	75.89	44.09	<0.001	5 2 4 1 3
	Error	17.21	10	1.72			
11.III	Treatments	68.12	4	17.03	27.15	0.0002	5 2 3 4 1
	Error	6.27	10	0. 63			
19.III	Treatments	378.05	4	94.51	31.83	<0.0001	4 5 2 1 3
	Error	29.69	10	2.97			
26.III	Treatments	2875.08	4	718.77	21.23	0.0007	4 1 3 5 2
	Error	338.53	10	33.85			
01.IV	Treatments	2.22	4	0.55	13.66	0.0004	2 3 4 5 1
	Error	0.41	10	0.04			

APPENDIX 8.1 continued

SPECIES: Diaphanosoma sarsi

DATES	SOURCE	SS	DF	MS	F	P	S-N-K
25.II	Treatmensts	2287.4	4	571.8	86.3	<0.0001	1 2 3 4 5
	Error	66.2	10				
04.III	Treatments	90.36	4	22.59	9.8	0.001	2 5 1 3 4
	Error	22.88	10				
11.III	Treatments	6.44	4	1.61	9.0	0.002	5 2 4 3 1
	Error	1.78	10	0.18			
19.III	Treatments	7.52	4	1.88	3.8	0.037	1 4 2 5 3
	Error	4.83	10	0.84			
26.III	Treatments	294.90	4	73.72	162.8	<0.0001	3 4 2 1 5
	Error	4.5	10	0.45			

APPENDIX 8.1 continued

SPECIES: Moina reticulata

DATES	SOURCE	SS	DF	MS	F	P	S-N-K
25.II	Treatments	73.74	4	18.43	16.1	0.0002	2 5 1 4 3
	Error	11.38	10	1.14			
04.III	Treatments	51.59	4	12.90	8.8	0.0025	2 5 1 3 4
	Error	14.61	10	1.46			
11.III	Treatments	34.32	4	8.58	17.6	0.0001	1 3 5 2 4
	Error	4.85	10	0.49			
19.III	Treatments	9.94	4	2.49	18.8	0.0001	3 4 1 2 5
	Error	1.32	10	0.13			
26.III	Treatments	313.34	4	78.34	20.9	<0.0001	1 3 2 5 4
	Error	37.39	10	3.74			
01.IV	Treatmenst	904.92	4	226.23	160.3	<0.0001	2 5 3 1 4
	Error	14.11	10	1.41			
08.IV	Treatments	4453.38	4	1113.35	66.5	<0.0001	2 3 5 1 4
	Error	167.27	10	16.73			
15.IV	Treatments	50132.20	4	1253.05	38.7	<0.0001	3 1 2 4 5
	Error	3230.56	10	323.06			
22.IV	Treatments	6935.59	4	1733.90	8.6	0.0027	4 1 3 2 5
	Error	2005.34	10	200.53			
26.IV	Treatments	122.57	4	30.64	6.8	0.0063	3 2 4 5 1
	Error	44.67	10	4.47			

APPENDIX 8.1 continued

SPECIES: Moina minuta

DATES	SOURCE	SS	DF	MS	F	P	S-N-K
25.II	Treatmensts	16.83	4	4.21	11.9	0.001	2 5 4 3 1
	Error	3.17	9	0.35			
04.III	Treatments	91.04	4	22.76	113.3	<0.0001	2 5 4 1 3
	Error	2.01	10	0.20			
11.III	Treatments	1.73	4	0.43	2.7	0.089	*
	Error	1.58	10				
19.III	Treatments	0.40	4	0.10	21.61	<0.0001	1 4 5 2 3
	Error	0.05	10	0.0			
26.III	Treatments	0.40	4	0.10	39.48	<0.0001	1 4 5 3 2
	Error	0.03	10				
01.IV	Treatments	0.54	4	0.14	11.80	0.0008	2 1 3 4 5
	Error	0.12	10	0.01			
08.IV	Treatments	27.91	4	6.98	9.23	0.0021	2 3 4 5 1
	Error	7.56	10	0.76			
15.14	Treatments	950.22	4	237.56	24.31	0.0004	2 3 4 1 5
	Error	97.69	10	9.77			
22.IV	Treatments	4.87	4	1.22	6.33	0.0083	4 5 1 3 2
	Error	6.79	10				
26.IV	Treatments	0.54	4	0.14	5.16	0.0161	5 4 1 3 2
	Error	0.26	10				

* not signifficant