"A quantitative study of reproduction in some species of" *Ceriodaphnia* (Crustacea:Cladocera)".

A thesis submitted for the degree of
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in the University of London,
by

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Abstract:

The world distribution of species of the genus *Ceriodaphnia* has been compiled from the literature and is summarised. The nomenclature of *C. cornuta* is discussed.

The present study is based on collections of *C. pulchella*, *C. reticulata*, *C. megalops* and *C. laticaudata* from the Long Water and the Wick Pond of Hampton Court, Middlesex during the period April 1963 - July 1964. The seasonal variations in the size of parthenogenetic females and of their reproductive capacity were investigated and are recorded. The relationships of egg numbers and egg volumes to body lengths and to the temperature and chlorophyll content of the water are analysed and discussed.

The occurrence of sterile eggs in *Ceriodaphnia pulchella* and *C. reticulata* during 1963 is recorded.

A few details of body size, egg number and egg size of an unidentified species from Malta are given and compared with those of the British species.

The results of these recordings and analyses are discussed in relation to the principle of the ecological niche and the idea that size difference is a prerequisite

of cohabitation of species of the same genus. The results are also discussed in the light of those of other authors' work on other cladoceran species.

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"A quantitative study of reproduction in some species of Ceriodaphnia (Crustacea:Cladocera)"

Introduction:

Members of the genus Ceriodaphnia are small, planktonic Cladocera (Crustacea), found in bodies of freshwater throughout the world. This genus is included in the Family Daphniidae and, although a considerable amount of work, both physiological and ecological, has been done on various species of Daphnia during the last century (Banta et al. 1939; Berg 1931; Fox 1948; Green 1953, 1955, 1956), Ceriodaphnia has rarely been made the particular object of a detailed study. Various species have been mentioned in numerous general accounts and the literature has therefore been searched in order to obtain some idea of their distribution throughout the world.

The practical aspects of the present study are confined to the species Ceriodaphnia pulchella (Sars), C. reticulata (Jurine), C. megalops (Sars), and C. laticaudata P.E. Müller. Little or nothing is known of the ecology or physiology of these species. Harnisch (1949) compared limb structure and mode of feeding in Ceriodaphnia with that of

Daphnia and Fox (1945) measured the oxygen affinity of haemoglobin obtained from C. laticaudata with that from various other invertebrates. Otherwise detailed knowledge of the genus is lacking.

With this in mind it was decided to make a start by studying the occurrence and reproduction of the species known to occur in two artificial lakes near London; the Long Water and the Wick Pond in Hampton Court Park. The object was to discover similarities and differences between the species listed above, especially Ceriodaphnia pulchella and C. reticulata which are found together, over the same seasonal range, in the Long Water.

Also included in some parts is a species of Ceriodaphnia which was hatched, and subsequently cultured, from dried mud recieved from Malta. It has as yet been impossible to equate this species with any so far described and, since much further research will be necessary before it can definitely be described as a new species, it has been left unidentified for the purpose of this thesis and is referred to as "the Maltese species".

Distribution and taxonomy:

Most species of Cladocera have a wide-spread distribution throughout the world. Those of the genus Ceriodaphnia are no exception and various species have been recorded by many authors throughout the last century. A survey of these records gives some idea of the occurrence of these species and can be summarised as in Table 1. This could also be called a summary of collectors and expeditions so lack of records cannot be taken as definite evidence for the absence of a species in any particular area.

There has been considerable controversy over the nomenclature of Ceriodaphnia cornuta (Sars). The original description in 1885 was of Australian specimens which had horns on the head. In 1894 Richard described a species without horns, but very similar in every other respect, which he named C. rigaudi. Both these forms and many intermediates have since been found throughout the tropics. Jenkin (1934) discussed this problem and came to the non-commital conclusion that four forms should be recognised: horned and unhorned C. cornuta, horned and unhorned C. rigaudi. Collections made in Lake Victoria by Rzoska (1956) contained all these forms and his numerical analyses show that all four can safely be regarded as forms of C. cornuta to which name precedence must

TABLE 1.

The world distribution of Ceriodaphnia spp. as compiled from the literature. The numbers in brackets indicate the source as shown in the bibliography.

	C.pulchella	C.reticulata	C. megalops	C.laticaudata	C.dubia	C.quadrangula	C.cornuta	C.setosa	C.rotunda
EUROPE:									
Iceland (40)	-	-	-	-	-	+	-	-	-
Finland (60)	+	+	-	-	-	-	-	-	-
Sweden (8;36;39)	+	+	+	+	+	+	-	-	+
Denmark (4)	+	+	+	+	-	+	-	-	+
British Isles (16;17; 34;55;58;59)	+	+	+	+	+	+	-	+	-
Switzerland (61;63)	-	-	+	+	-	+	-	-	-
Italy (38)	+	+	-	+	+	+	-	+	-
Yugoslavia (23)	-	+	-	-	-	-	-	-	-
AFRICA:									
Ivory Coast (42)	-	-	-	-	-	-	+	-	-
Senegal (18)	-	-	-	-	-	-	+	-	-
L.Tanganyika (28)	-	-	-	-	-	-	+	-	-
L.Victoria (48)	-	-	+	+	-	-	+	-	-
Uganda (66)	-	-	-	-	-	-	+	-	-
Kenya (33)	-	-	-	-	-	-	+	-	-
Nigeria (25)	-	-	-	-	-	-	+	-	-
S.Africa (54)	-	+	-	-	-	+	-	-	-
ASIA:									
East Indies (62)	-	-	-	-	-	+	-	-	-
Central Asia (53)	+	+	+	-	-	+	-	-	-
China (43)	-	-	-	-	-	-	+	-	-
Iran (37)	-	-	-	-	-	+	-	-	-
AUSTRALASIA:									
Australia (49;50)	-	-	-	+	+	-	+	-	-
New Zealand (51)	-	+	-	-	+	-	-	-	-
Tasmania (6)	-	-	-	-	+	-	-	-	-
NORTH AMERICA:									
(11)	+	+	+	+	-	+	-	-	+
SOUTH AMERICA:									
L.Titicaca (27)	-	-	-	-	+	+	-	-	-
Patagonia (10)	-	-	-	-	+	+	-	-	-
Colombia (64)	-	+	-	-	-	+	-	-	-

be given. The size and development of the horns appear to vary from one generation to another. This may well be another example of cyclomorphosis as seen in Daphnia (Coker 1939) and some Rotifera (Green 1960). The nomenclature of the other species in Table 1. follows that of Scourfield and Harding (1958).

Ceriodaphnia cornuta, like C. pulchella, is among the smallest species of the genus but, whereas C. pulchella has only been recorded from temperate regions, C. cornuta appears to be confined to the tropics. It is possible that they fill very similar ecological niches within their respective ranges. A more exact knowledge of the ecology and distribution of both species will be necessary before any elaboration of this idea could be considered.

Ceriodaphnia reticulata and C. quadrangula appear to have no longitudinal or latitudinal restriction to their distribution. C. quadrangula is the only member of the genus found in Iceland (Poulsen 1939). C. megalops, C. laticaudata and C. dubia are not widely recorded while C. setosa and C. rotunda are even less so.

Sampling sites and methods:

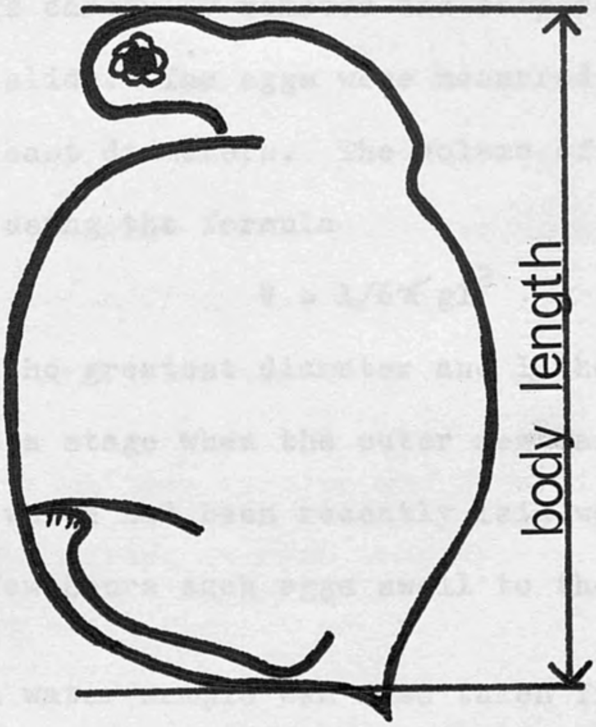
The Long Water is a rectangular, artificial lake approximately 1000m x 30m. There is a very slow flow along the long axis and the level can be maintained by means of a sluice. The greatest depth of water is probably 2 - 3m in the centre. Thick reed beds grow intermittently along the entire length of both long banks and during the summer the surface of the shallow water becomes covered with the alga Enteromorpha sp. and duck-weed, Lemna sp. Away from the bank water-lilies, Nymphaea sp. cover a good deal of the surface. The emergent vegetation is periodically cleared; one of these clearances occurred in August 1963 and for the rest of that year there was little emergent vegetation. There is always a thick layer of organic detritus on the bottom.

The Wick Pond (approx. 400m x 30m) is quite different from the Long Water despite their proximity. It is of less regular outline and the principle emergent vegetation consists of extensive beds of irises in the shallow water. Large quantities of filamentous algae are present between the iris beds and there are small patches of Potamogeton sp. The banks are sandy and much steeper than those of the Long Water with relatively few trees. On the sampling site there was little organic debris.

Other cladoceran species making up the dense populations found in the Long Water include Polyphemus pediculus, Simocephalus vetulus, Scapholeberis mucronata and Sida crystallina.

Cladocera were collected from the Long Water and the Wick Pond using a fine meshed pond net at approximately weekly intervals throughout 1963 and the first half of 1964: the same regions of the pond were sampled on each occasion. The animals were examined alive in the laboratory on the same day. Samples of 25 parthenogenetic females of each species of Ceriodaphnia were taken at random using a low power (X30) binocular microscope. Each animal was measured from the crown of the head to the posterior border of the carapace, excluding the length of the small posterior prolongation (see Fig. 1.). This was done with a calibrated micrometer eyepiece. The carapace was then opened using fine mounted needles and the number of eggs, or embryos, in the brood pouch counted. Unless otherwise stated the term egg refers to parthenogenetic eggs; ephippial eggs will be referred to as such. The term "egg number" refers to the number of eggs, or embryos, in the brood pouch of a parthenogenetic female. The stage of development of the eggs was noted and the presence of any sterile eggs recorded.

FIGURE 1.



Outline diagram of a female Ceriodaphnia reticulata to indicate the position of the body length measurement.

To estimate the volume of parthenogenetic eggs, samples of 75 - 100 eggs were taken from females of varying sizes. The length and egg number of each female was recorded and the eggs carefully removed and suspended in a film of water on a slide. The eggs were measured along their greatest and their least diameters. The volume of each egg was then calculated using the formula

$$V = 1/6\pi gl^2$$

where g is the greatest diameter and l the least. Eggs were measured at a stage when the outer membrane was still complete: those eggs which had been recently laid were avoided: during the first few hours such eggs swell to their maximum size.

A water sample was also taken from open shallow water in the Long Water about 12 cms from the bank, in the same place on each occasion. This was used to measure the chlorophyll content of any phytoplankton present, thus providing some measure of the food available to zoo-plankton at a particular time. 100ml of the sample were vacuum-filtered through a Millipore filter, size DA. The chlorophyll was then extracted with acetone and the volume made up to 5ml. After centrifugation, measurements of optical density at 665mμ and 750mμ were made using a Unicam spectrophotometer. The latter reading gives a measure of scattering and residual absorption which can be subtracted from the former to give a more accurate measure of the absorption due to chlorophyll. This difference is recorded throughout in spectrophotometer units.

The temperature of the water was measured with a total-immersion, mercury-in-glass thermometer held approximately 3 cms below the water surface in the same place as that from which the water samples were taken. The time was normally between 9.30 and 10,00 a.m.

The Maltese species was hatched by the addition of filtered lake water, at room temperature, to a small quantity of the dried mud. The two or three females thus obtained were transferred to clean water in a crystallising dish and fed on a suspension of Chlorella vulgaris. They were kept at room temperature and fed at intervals of two or three days. The culture of C. vulgaris was never used for feeding after it was four weeks old since it has been found (Ryther 1954) that senescent Chlorella has an inhibitory effect on the feeding of Daphnia magna and may have a similar effect on other Cladocera. When the culture was established, some females were removed at random and examined in the same way as those obtained from the Long Water. Their lengths and egg numbers were noted and their eggs were measured.

The other species obtained from the Long Water were also cultured in the laboratory in the way described above. It was intended to use these for studies on the growth and reproductive rates of individual females. Individual females carrying parthenogenetic eggs were placed in 2 x 1 in. tubes with 10ml of Chlorella suspension of 0.29 optical density, as measured with an M.R.C. grey-wedge photometer. These tubes were lightly plugged with non-absorbent cotton wool and kept in a thermostatic water-bath at 21°C. The Chlorella was resuspended each day with a small bulb pipette and the suspension was renewed completely on alternate days. In general this method is that of Green (1956). By examination of the animals under a microscope at regular intervals, attempts were made to determine the interval between broods, the length of time from the release of the eggs into the brood pouch to the release of the young into the water, and the length of time these young take to mature, i.e. to the laying of the first eggs into the brood pouch. For various reasons, including an infection in the Chlorella cultures, these attempts did not progress beyond the preliminary stages. The results presented in this thesis are, therefore, almost entirely confined to the field studies and future work will be concentrated on the more physiological aspects of the ecology of these species.

Seasonal variation in water temperature and chlorophyll content of the Long Water:

During 1963 the lake was covered with ice until the beginning of March, after which the temperature rose rapidly to 9°C. and then gradually increased to a maximum during June, July and August. From 1 June to 20 August the temperature remained above 16°C. In 1964 this temperature was reached by the second week in May, after only two or three days of ice cover in February. Green (in press) has shown that the average temperature in the Long Water during the Spring and Summer of 1963 was lower than that of previous years.

In 1963 there were two Spring peaks in the chlorophyll (Fig. 2.) one in the middle of April, the other towards the end of May. Subsequently the concentration dropped considerably, but not, except on one occasion, below 100 spectrophotometer units. There was a sharp rise in level during August and again in the second week in September. A low level was reached by the last week in September and it remained so until the beginning of February 1964.

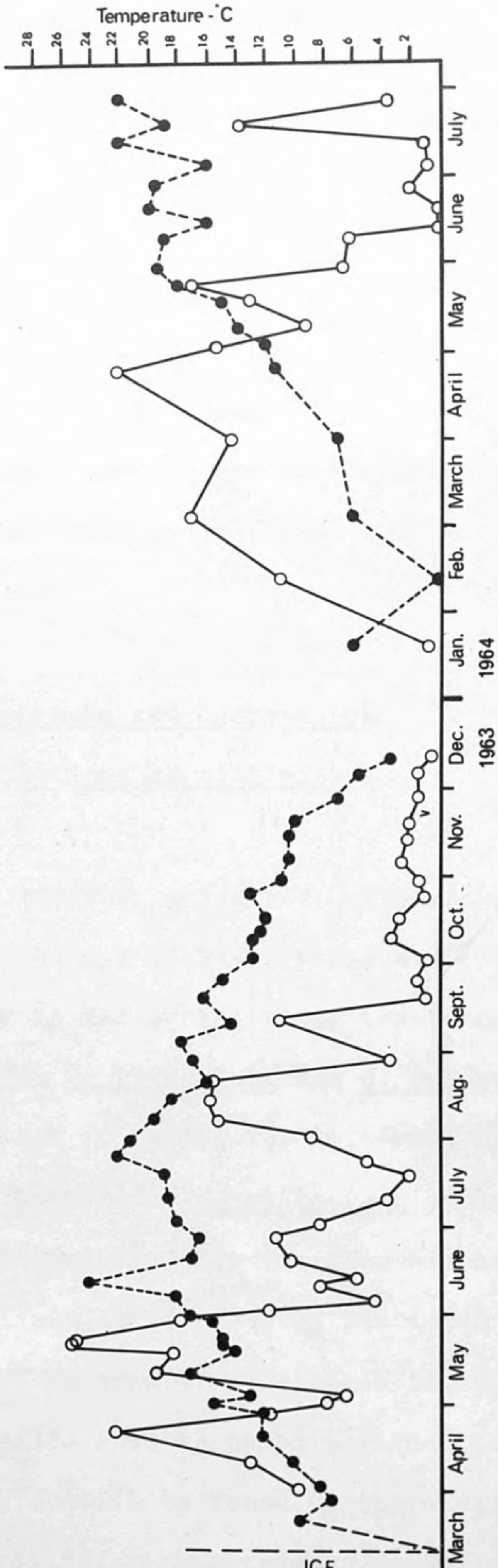
In 1964 (Fig. 2.) a relatively high concentration was reached much earlier, by the end of February, and although

Figure 2.

Seasonal variation in the temperature and chlorophyll content of the Long Water, Hampton Court - March 1963 to July 1964.

Temperature. ●

Chlorophyll. ○


Temperature - °C
28
26
24
22
20
18
16
14
12
10
8
6
4
2
Chlorophyll - spectrophotometer units
700
600
500
400
300
200
100
ICE
March
April
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
1963
Jan.
1964
Feb.
March
April
May
June
July

the April peaks were the same in both years, the second Spring peak was lower in 1964. The subsequent drop in concentration was, however, almost to zero and the level remained extremely low until the second week in July. Readings were not continued sufficiently long in 1964 to enable comparison to be made with the 1963 Autumn levels. The readings for both temperature and chlorophyll for 1963 and 1964, as illustrated in Fig. 2., are recorded in Appendix 1.

Seasonal variation in occurrence and composition of Ceriodaphnia populations at both sites:

Ceriodaphnia is a summer genus and, although specimens can be found well into the Autumn at water temperatures below 10°C it does not re-appear in the Spring until the temperature reaches about 12°C. In 1963 C. reticulata and C. pulchella appeared during the last week in April, the latter in greater numbers than the former, Numbers of C. reticulata rapidly increased, however, and predominated for the rest of the year; C. pulchella maintained itself at 30 - 40% of the total Ceriodaphnia population. Clearance of vegetation in August 1963 appeared to make no difference to numbers either then or in 1964. Both species could still be found by the middle of October 1963 but only C. reticulata was present in the collections up to the end of November. This seasonal variation in numbers of C. pulchella agrees closely with that given by Smyly (1957) for this species in some Lake District tarns and by Carlin (1943) for some lakes in Southern Sweden.

Ceriodaphnia laticaudata is fairly abundant but for a more limited season. It is principally found among the leaf litter and bottom detritus in deep water at the S.E. end. This species is easily distinguished by its red colouration due to a relatively high content of haemoglobin. Other species of Ceriodaphnia at Hampton Court are almost colourless. In 1963 this species was first found on 2 July and in 1964 on 17 June. It may however have appeared earlier than the 1963 date suggests; it was only appreciated at that time that this species is confined to lake-bottom debris. In 1964 search was made from the beginning of April and the date given above records it first appearance in the 1964 samples. Numbers of C. laticaudata dropped immediately and steeply after the clearance of the lake on 27 August and two weeks later it could not be found at all. Whether this disappearance was a direct result of the clearance of vegetation is uncertain since debris remained abundant on the bottom. The disturbance may have resulted in an increased oxygen content among the upper layers of detritus which would normally have remained undisturbed until the end of the Summer. Ceriodaphnia laticaudata has proved difficult to keep in laboratory culture without detritus and it is possible that this is due to a necessity for an environment with a relatively low oxygen concentration. Pacaud (1939) has shown that C. rotunda which is found in a similar habitat is a great deal more tolerant of decreases in the oxygen concentration of its environment than other species. Like C. laticaudata it contains a high concentration of haemoglobin (Green; personal communication), a condition possibly associated with its environment.

In the Wick Pond Ceriodaphnia megalops is the predominant cladoceran and is found principally among the irises and in the shallow water immediately surrounding the iris beds. It was abundant when first sampled on 22 May 1963 while in 1964 it appeared during the first week in May. It has been found in the Long Water only occasionally. C. reticulata was present in the Wick Pond in low numbers throughout the Summer while C. megalops was found up to the end of October 1963. Numbers fell to a low level about 23 July when swarms of young fish were seen in the shallow water at the margins of the pond. After about a week these fish moved away, possibly into the deeper water in the centre of the pond: numbers of C. megalops rose again but not to the high levels of June.

Males and ephippial females of Ceriodaphnia reticulata were first recorded in small numbers on 17 July 1963.

Ephippial females maintained their low level until the beginning of September after which numbers rose until they comprised approximately 45% of the female population by mid-October. Males were recorded intermittently from 17 July onwards and a similar pattern was evident in C.pulchella. Males of C. megalops, however, appeared on about 12 June in both 1963 and 1964 and in the latter year ephippial females were recorded one week later. Both sexes were present in small numbers thereafter alongside the parthenogenetic females.

Seasonal variation in body length:

Each point in Figure 3 (the data for which are presented in Appendixes 2A - the Long Water 1963, 2B - the Long Water 1964 and 2C - the Wick Pond 1963 and 1964) represents a mean of 25 animals except at the extremes of the season when all those animals found were measured. The vertical lines represent the standard errors of those means.

It is clear that the variation in Ceriodaphnia pulchella, C. reticulata and C. megalops followed the same basic pattern in 1963. The spring peak in all three is followed by a sharp drop during the second and third week of June. In C. pulchella and C. reticulata this follows, as can be seen

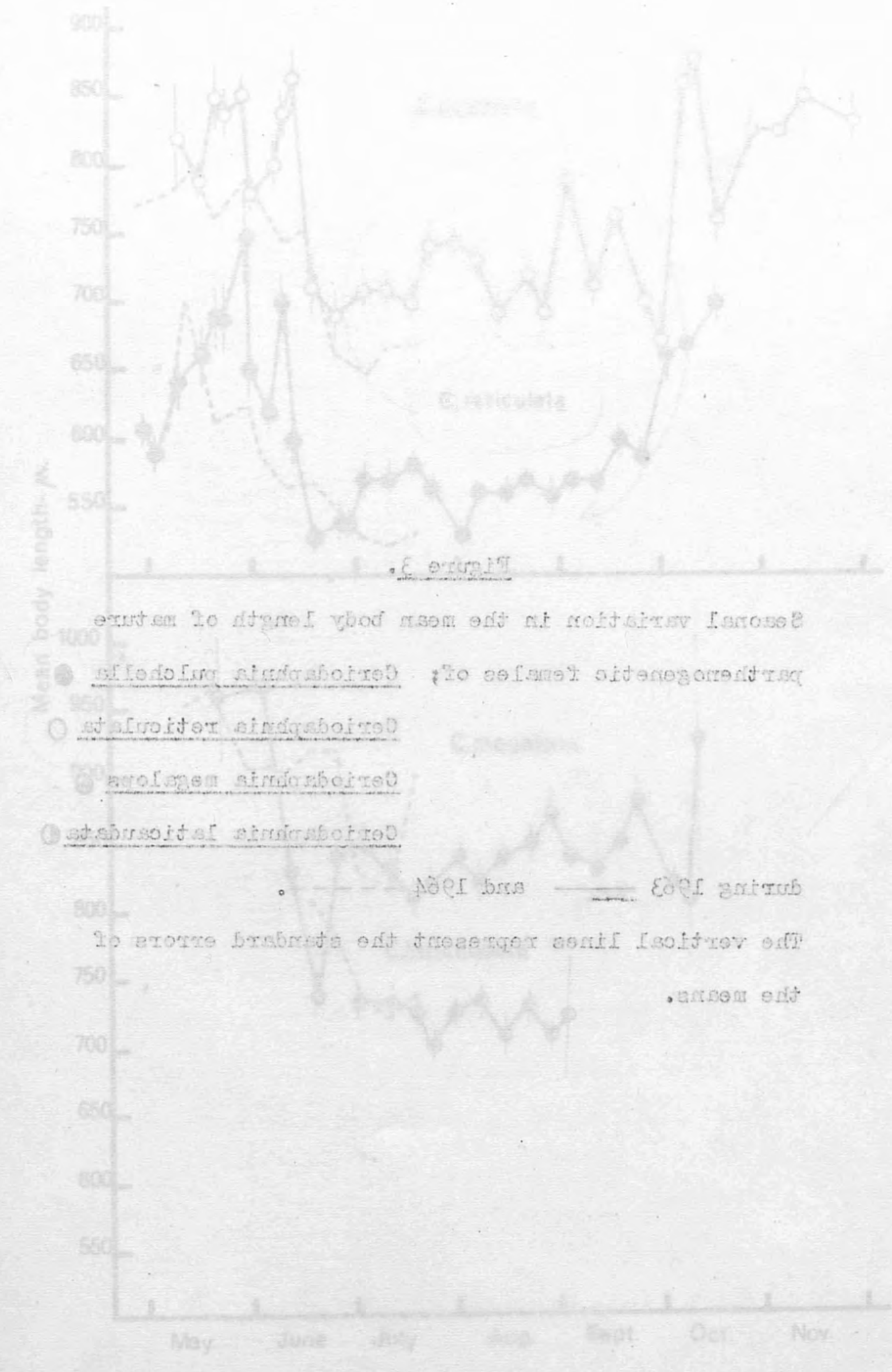

Mean body length µ
900
850
800
750
700
650
600
550
C. reticulata
1000
950
C. megalops
800
750
700
650
600
550
May
June
July
Aug.
Sept.
Oct.
Nov.

Figure 3.

Seaonal variation in the mean body length of mature parthenogenetic females of; *Ceriodaphnia pulchella* ●

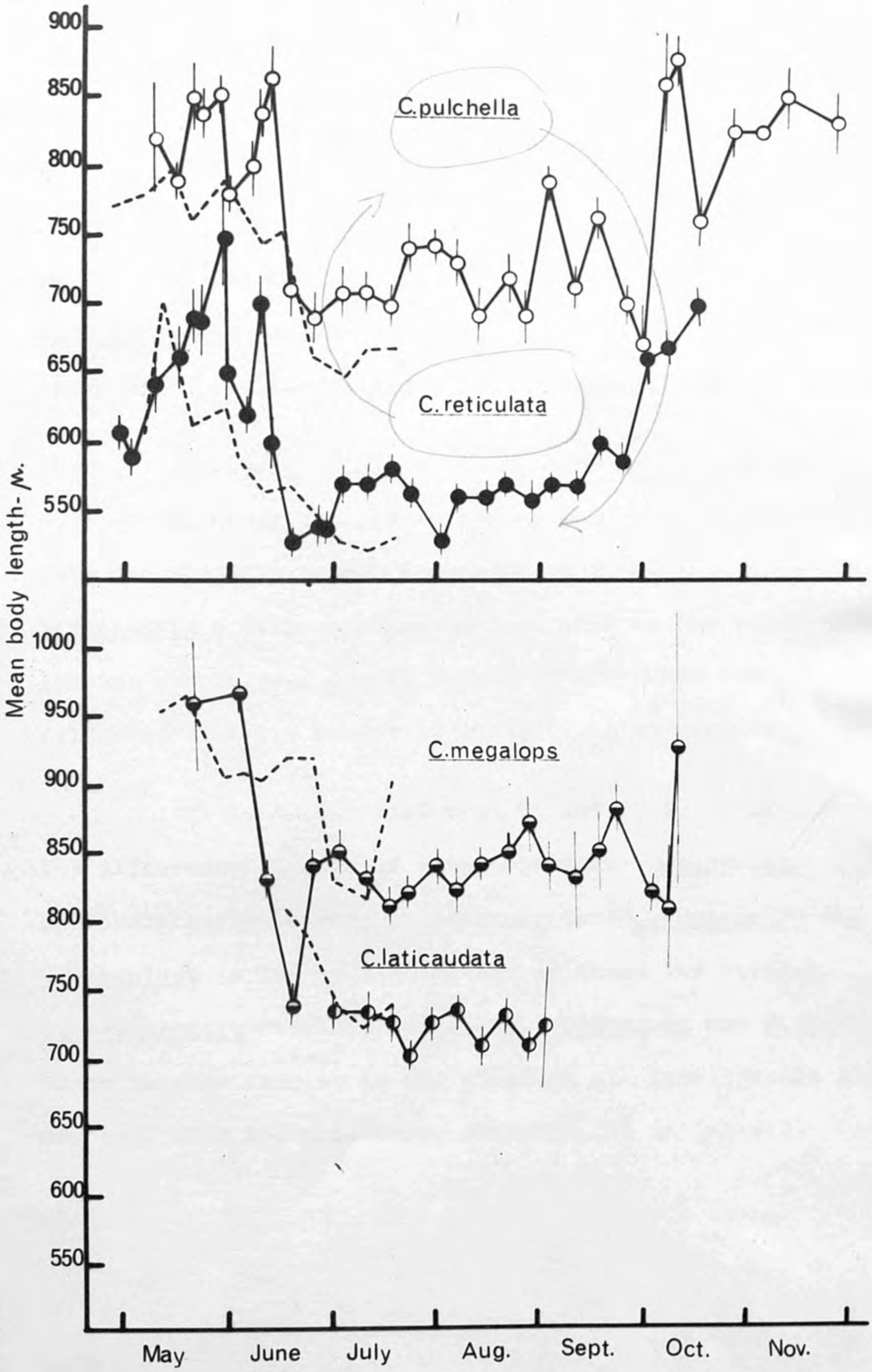
Ceriodaphnia reticulata ○

Ceriodaphnia megalops ⊖

Ceriodaphnia laticaudata ◐

during 1963 ——— and 1964 - - - - - -.

The vertical lines represent the standard errors of the means.


C.pulchella
C.reticulata
C.megalops
C.laticaudata
Mean body length- μ.
900
850
800
750
700
650
600
550
1000
950
May
June
July
Aug.
Sept.
Oct.
Nov.

by comparison with Fig. 2, a drop in the chlorophyll content of the Long Water and the beginning of the high summer temperatures. Throughout the following three months the lengths varied about a fairly constant level before rising steeply at the beginning of October, immediately prior to their disappearance. C. laticaudata was first collected in the middle of June 1963 after which the length did not show a great deal of variation.

In 1964, as shown by the broken lines on Fig. 3, none of the newly hatched spring animals were as large as in 1963 and the mean length decreased earlier. In Ceriodaphnia laticaudata a drop, similar to that seen in the other three species can be seen in the Spring of 1964 when specimens were collected from the moment of their first appearance.

An important fact brought out by these graphs is the difference in size of these species. Ceriodaphnia reticulata is consistantly larger, on average, than C. pulchella and C. megalops is larger than either of these two species. C. laticaudata overlaps between C. reticulata and C. pulchella. There is some overlap in the sizes of all four species when one considers the full range measured, as in Table 2.

TABLE 2.

Body length and egg number of four species of Ceriodaphnia collected from the Long Water and the Wick Pond, Hampton Court during 1963.

	Range of body lengths of egg bearing females measured in 1963 μ.	Grand mean body length of 1963. μ.	Grand mean egg number of 1963.	Ratio of grand mean egg number to grand mean length.
C.pulchella	410-830	597	3.83	0.0064
C.reticulata	580-1010	752	5.20	0.0069
C.megalops	720-1620	850	3.85	0.0045
C.laticaudata	590-920	725	2.76	0.0038

Seasonal variation in egg number:

Measurement of the number of eggs carried by mature females serves as an indication of the reproductive capacity of the species at that particular time and under the prevailing conditions. As can be seen in Figure 4 (Appendices 2A, 2B and 2C) the variation in mean egg number of Ceriodaphnia pulchella and C. reticulata is similar, and very like the pattern of their mean body lengths. Correlation between body length and egg number is discussed later (p. 22).

This similarity in fluctuation of mean egg number and mean body length recalls that found by Green (1955) in a population of Daphnia magna. As he suggests, it may be explained by the fact that samples taken at random include females of all ages. The size of newly matured females will be affected by the conditions in which they have developed to maturity. In Daphnia, factors favouring growth also favour egg production (Green 1954) and these, therefore, tend to fluctuate together. This may also be true of Ceriodaphnia.

In Ceriodaphnia megalops from the Wick Pond, Fig. 4, the pattern in 1964 is slightly different from the other two species and also from the pattern of variation in body length. After the rapid fall in egg number during the second week

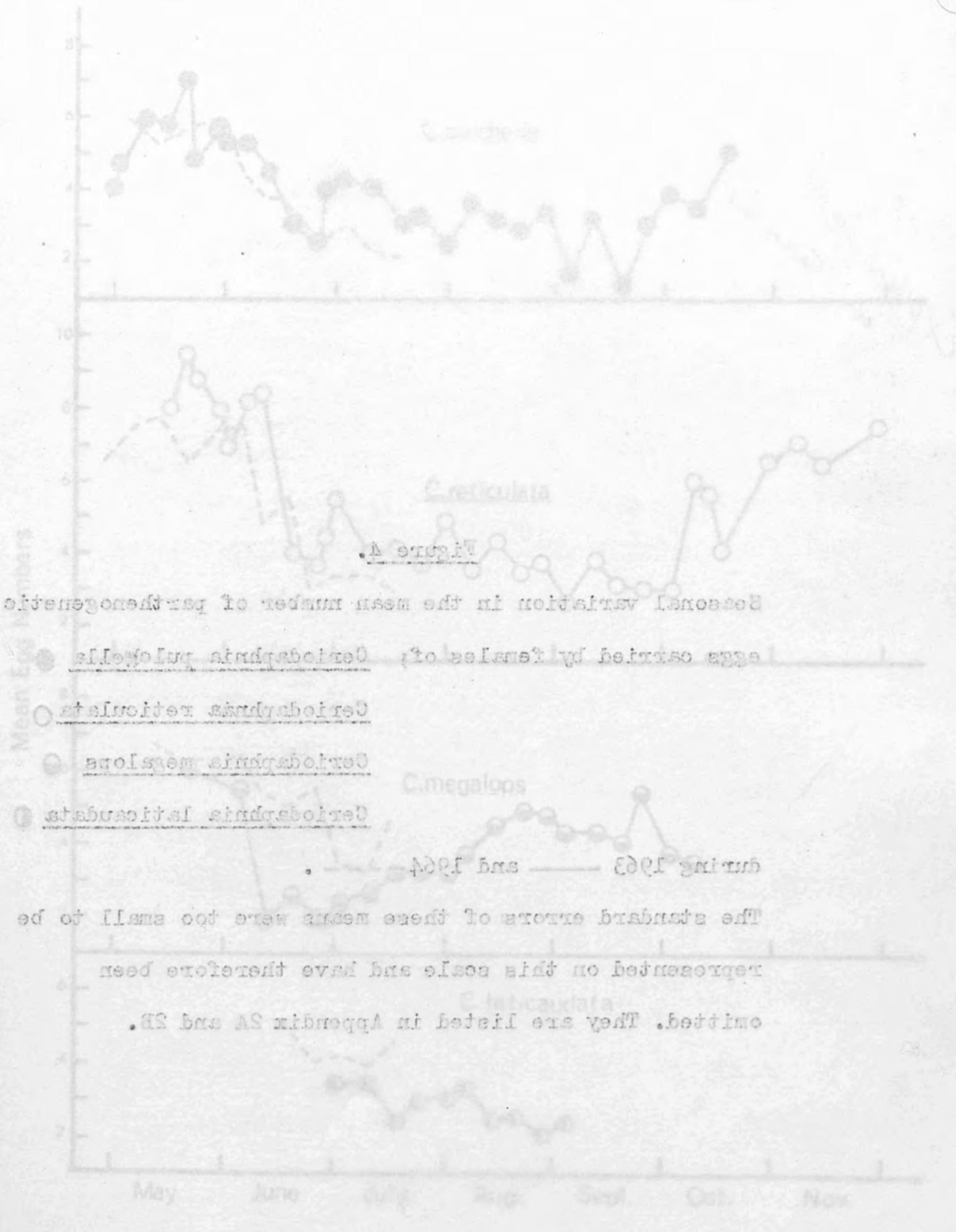


Figure 4.

Seasonal variation in the mean number of parthenogenetic eggs carried by females of; *Ceriodaphnia pulchella*, *Ceriodaphnia reticulata*, *Ceriodaphnia megalops*, *Ceriodaphnia laticaudata* during 1963 - - - and 1964 ——— .

The standard errors of these means were too small to be represented on this scale and have therefore been omitted. They are listed in Appendix 2A and 2B.

Explain fall in Summer

Figure 4.

Seasonal variation in the mean number of parthenogenetic eggs carried by females of; *Ceriodaphnia pulchella* ●

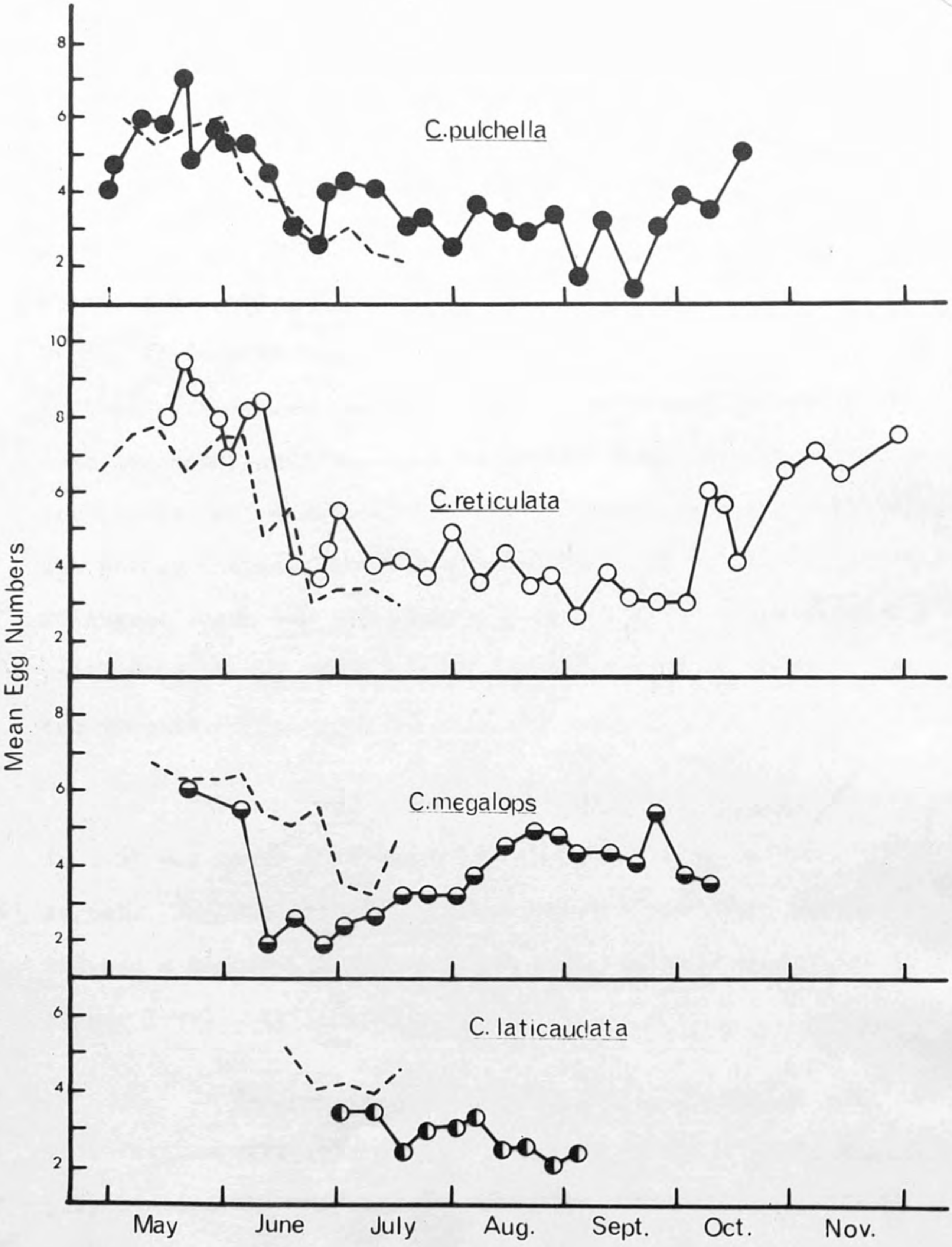
Ceriodaphnia reticulata ○

Ceriodaphnia megalops ⊖

Ceriodaphnia laticaudata ◐

during 1963 ——— and 1964 - - - - .

The standard errors of these means were too small to be represented on this scale and have therefore been omitted. They are listed in Appendix 2A and 2B.


C.pulchella
C.reticulata
C.megalops
C. laticaudata
Mean Egg Numbers
2
4
6
8
10
May
June
July
Aug.
Sept.
Oct.
Nov.

of June, the egg number remained low for only four or five weeks, after which there was a gradual rise until the end of August. A possible explanation of this difference is the presence of the swarm of young fish mentioned earlier (p. 21) which, presumably, depleted the population about 23rd July 1963. It is well known (Berg 1931) that in Cladocera, the parthenogenetic reproduction rate is frequently higher in less dense populations. The reduction in this population was very sudden and drastic. Those few females remaining originated the steady increase in mean egg number which followed. After 20 August there was a gradual decline, but for one sample, until 8 October. There was no final increase as in the other two species.

The mean egg number of *Ceriodaphnia laticaudata* in 1963 was lower than of the other species during July and August. In 1964 the first specimens were collected earlier and had a higher egg number which then declined to a slightly higher level than in 1963.

In *Ceriodaphnia reticulata* and *C. pulchella* the 1964 figures were very similar to those of 1963; in *C. megalops* they started the same but dropped less sharply and slightly later.

Relationship between egg number and body length:

In Fig. 5 (Appendices 2A and 2C) the mean egg numbers of *Ceriodaphnia pulchella*, *C. reticulata* and *C. megalops*, recorded in 1963, have been plotted against their mean body lengths. Over 60% of these points represent means of at least 25 observations. The regression of egg number on length for each species has been calculated from the individual measurements and the regression lines inserted on the graph. The slopes of these lines are not significantly different from each other (*C. pulchella* $b = 0.0081 \pm 0.0009$; *C. reticulata* $b = 0.017 \pm 0.0010$; *C. megalops* $b = 0.012 \pm 0.0012$)*. The correlation coefficients are low but are none the less significant due to the high degrees of freedom involved: *C. pulchella* 0.32 ($p < 0.001$), *C. reticulata* 0.54 ($p < 0.001$) and *C. megalops* 0.58 ($p < 0.001$).

Although the rate of increase in egg number with body length is the same in each species the larger species do not on the whole carry greater numbers of eggs than the smaller species where their length ranges overlap. This is more clearly illustrated in Fig. 6 which is based on the individual measurements.

In Fig. 6 (Appendix 3) the widths of the blocks are proportional to the number of individual females of each length class which were found to be carrying that number of eggs.

* b is the coefficient of regression with its standard error.

Figure 5.

Mean egg number and mean body length during 1963 in:

Ceriodaphnia pulchella ●

Ceriodaphnia reticulata ○

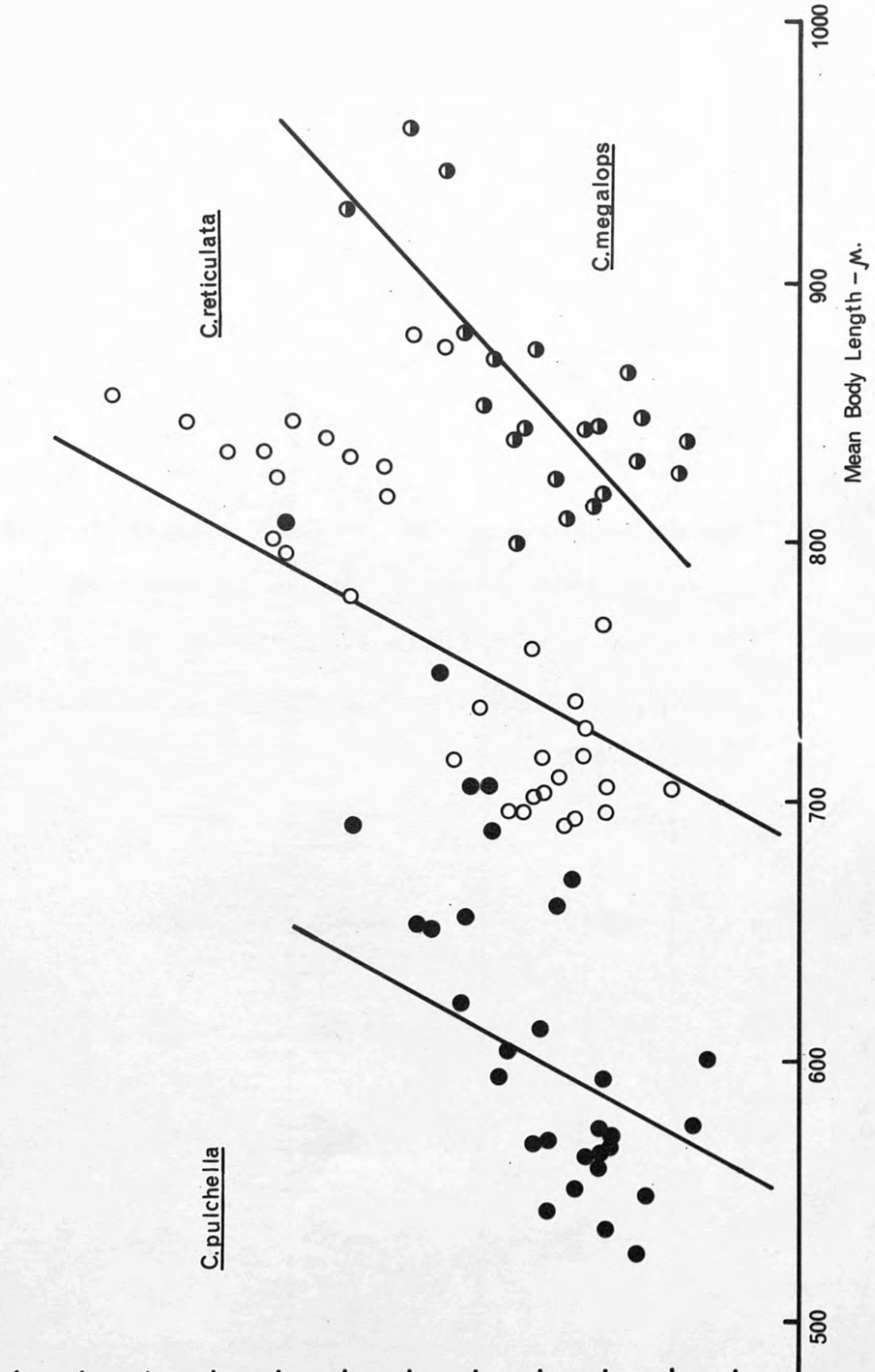
Ceriodaphnia megalops ◒

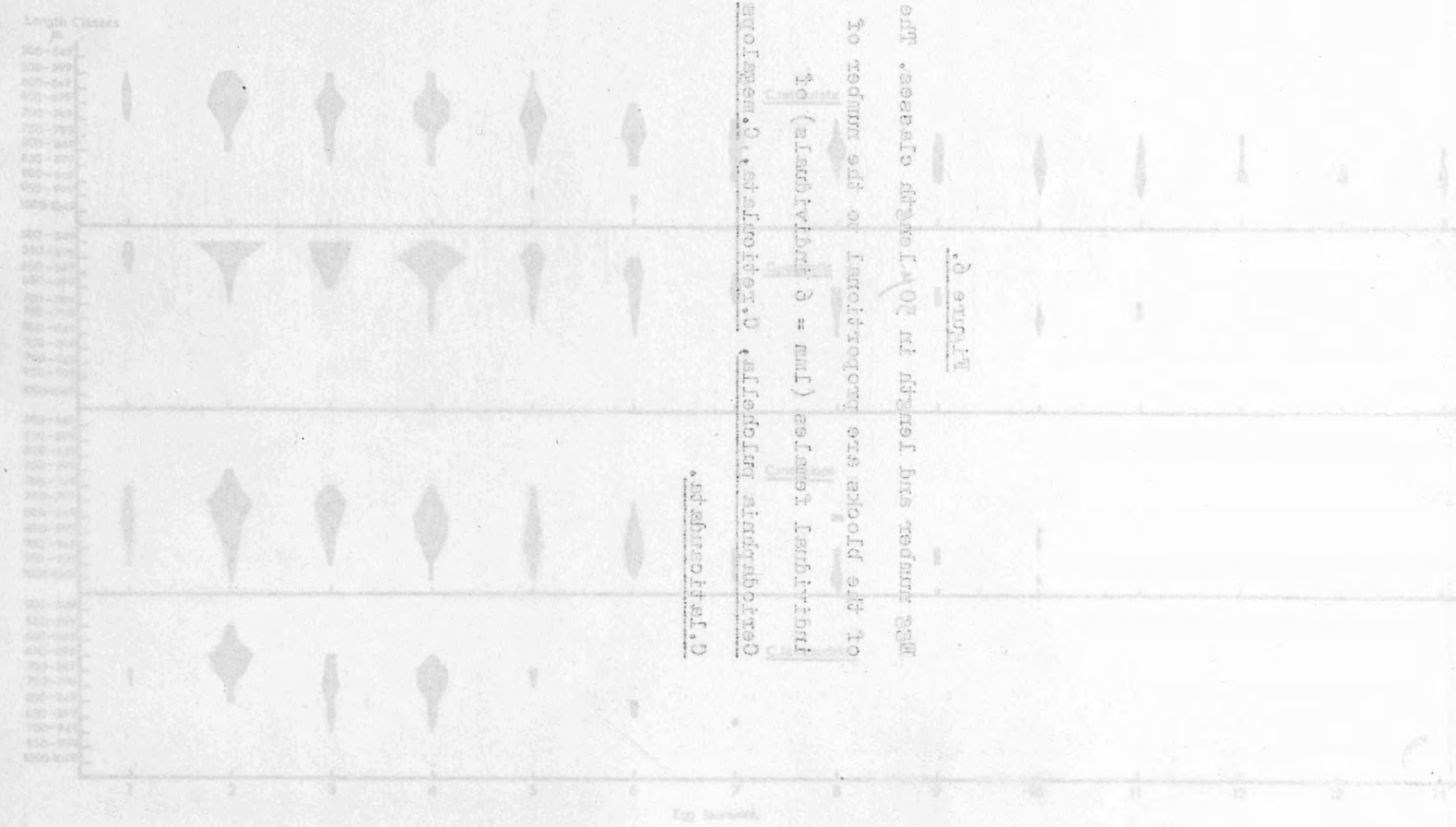
The regression coefficients of egg number on length for each species, b= 0.0081 $\pm$ 0.0009 C.pulchella

0.017 $\pm$ 0.0010 C.reticulata

0.012 $\pm$ 0.0012 C.megalops

There is no significant difference between these coefficients.

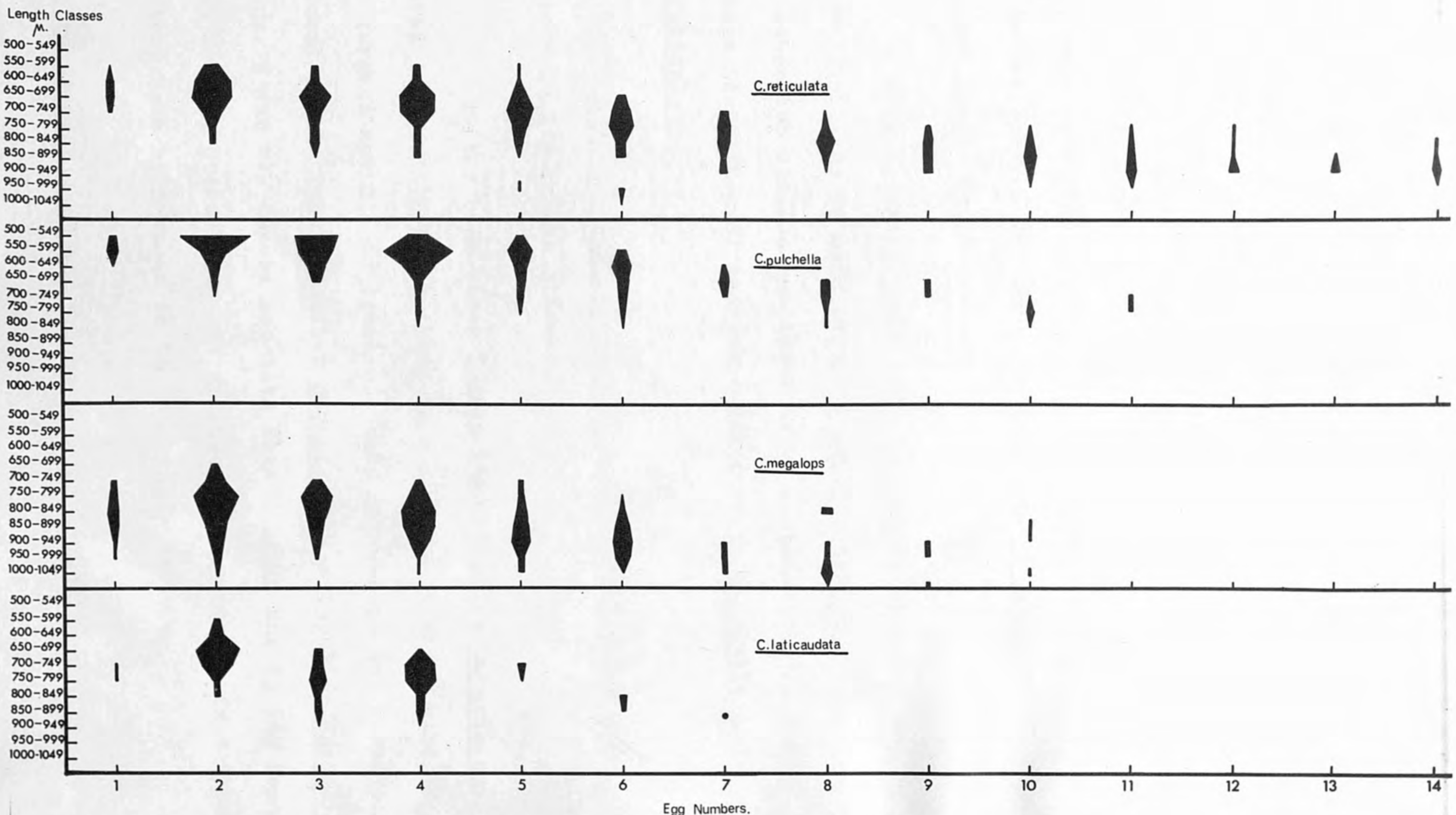

C.pulchella
C.reticulata
C.megalops
Mean Egg Number
1
2
3
4
5
6
7
8
9
10
11
12
500
600
700
800
900
1000
Mean Body Length - µ.



Length Classes
μ
Egg Number

Figure 6.

Egg number and length in 50 μ length classes. The widths of the blocks are proportional to the number of individual females (1mm = 6 individuals) of *Ceriodaphnia pulchella*, *C.reticulata*, , *C.megalops* and *C.laticaudata*.



Length Classes
μ.
500-549
550-599
600-649
650-699
700-749
750-799
800-849
850-899
900-949
950-999
1000-1049
C.reticulata
C.pulchella
C.megalops
C.laticaudata
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Egg Numbers.

All animals collected in 1963 are included in this diagram except for six specimens of Ceriodaphnia reticulata, in the 950-999μ length class, which were carrying 15-18 eggs. It is evident from this diagram that females of C. pulchella carry more eggs than C. reticulata of the same size. Similarly, the latter species carries more eggs than C. megalops of the same but larger length classes.

The ratio of grand mean egg number to grand mean length (Table 2) is much lower in Ceriodaphnia megalops than the other two species but there is no significant difference between the ratios of the grand means of C. pulchella and C. reticulata.

Ceriodaphnia laticaudata has relatively low egg numbers in its length classes.

It has been shown (Green 1954) that in Daphnia sp. reared in the laboratory there is a decline in brood size in the largest and oldest females. This however is not found in natural populations of either Daphnia (Green 1955) or Ceriodaphnia (Figs. 5 and 6). Green suggests that this is due to the fact that females probably do not survive the senescence in nature as they have been known to in laboratory culture.

The relationship of egg volume to body length:

TABLE 3.

The shape and volume of eggs from the brood pouches of females of four species of Ceriodaphnia collected from the Long Water and the Wick Pond, Hampton Court during 1963 and 1964.

	Range of body lengths of measured. μ .	Number of females measured.	Number of eggs measured.	Mean ratio g/1	Mean egg volume in millions cu. μ..
C. pulchella	500-770	37	174	1.56	1.25
C. reticulata	660-990	21	136	1.43	1.72
C. megalops	770-1030	24	104	1.41	2.56
C. laticaudata	630-880	9	33	1.85	2.28

Table 3 includes the mean egg volumes of the four species of Ceriodaphnia collected from the Long Water and the Wick Pond during 1963 and 1964. These show a progressive increase from the smallest species, C. pulchella, to the largest, C. megalops with the exception of C. laticaudata. The latter stands out; the range of lengths of this species overlaps with the largest C. pulchella and the smallest C. reticulata, and it has eggs with a relatively high mean volume, almost equal to that of C. megalops.

In Fig. 7 (Appendix 4) the total volume of egg material carried by females of C. pulchella, C. reticulata and C. megalops have been plotted against their body lengths on logarithmic scales. Log:log regressions of total egg volume on body length for the three species are not significantly different from each other. (C. pulchella $b = 2.10 \pm 0.176$; C. reticulata $b = 2.66 \pm 0.150$; C. megalops $b = 2.50 \pm 0.045$: b is the coefficient of regression with its standard error). The rate of increase in egg volume with body length is therefore the same in all three species. C. megalops do not appear to carry higher total volumes of egg material than C. pulchella and C. reticulata as might be expected from their greater size. The regression line for this species lies lower than those of the other two species when the graphs are superimposed. This confirms the evidence of Figs. 5 and 6 which show that C. megalops

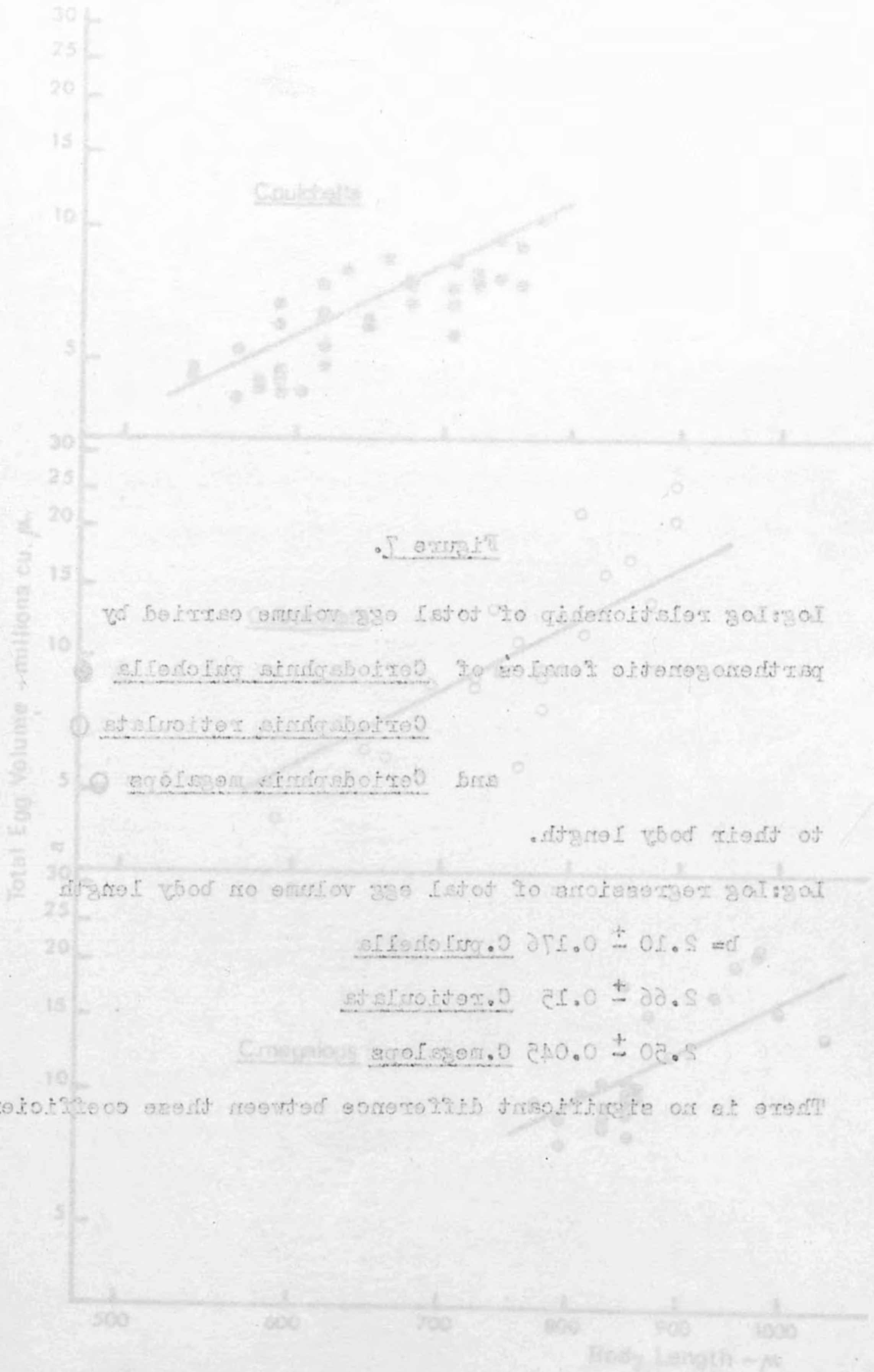

Total Egg Volume - millions cu. µ
Body Length - µ
500
600
700
800
900
1000

Figure 7.

Log:Log relationship of total egg volume carried by parthenogenetic females of *Ceriodaphnia pulchella* ●

Ceriodaphnia reticulata ○

and *Ceriodaphnia megalops* ⊖

to their body length.

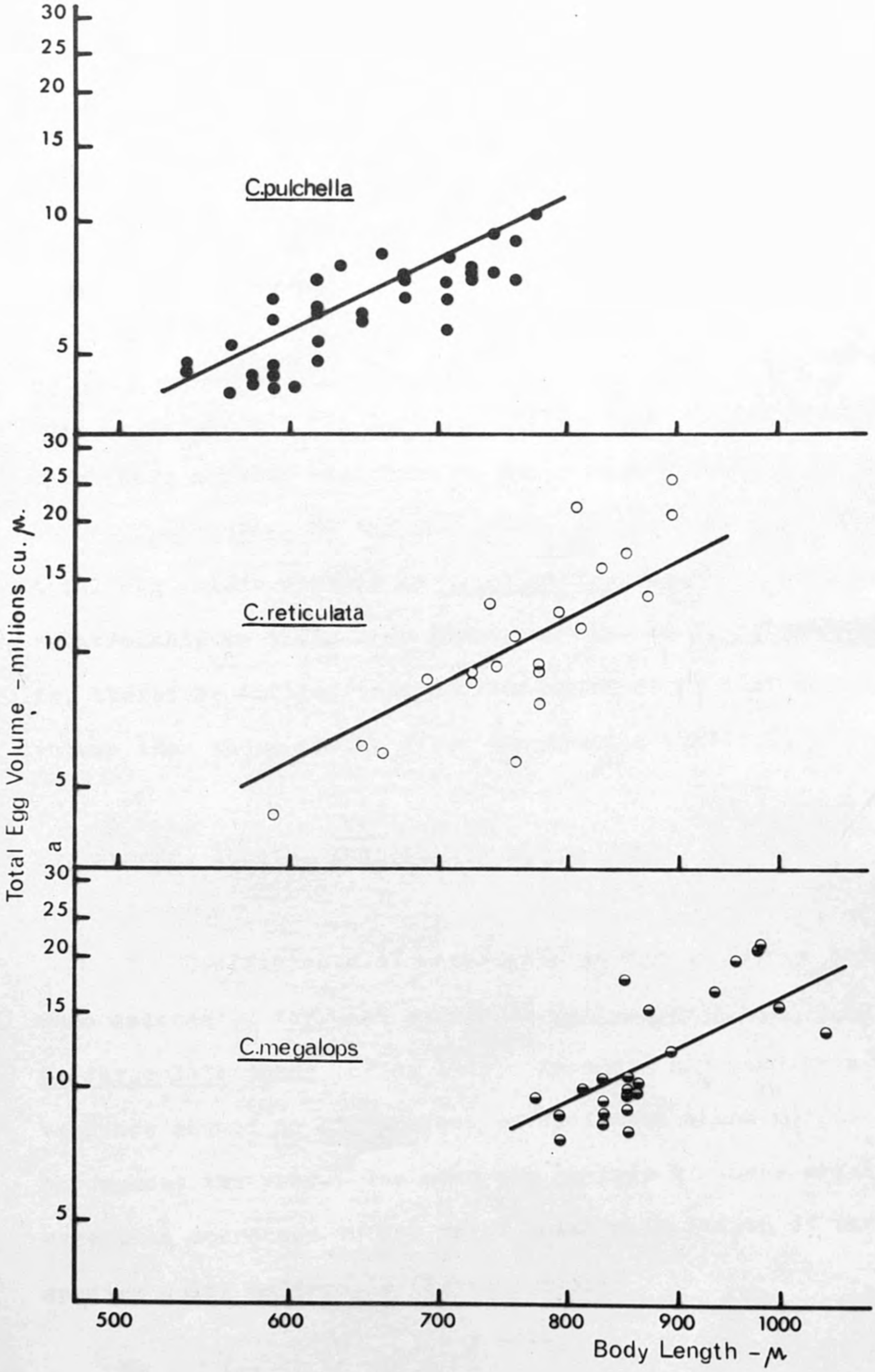
Log:Log regressions of total egg volume on body length

$b = 2.10 \pm 0.176$ *C.pulchella*

2.66 ± 0.15 *C.reticulata*

2.50 ± 0.045 *C.megalops*

There is no significant difference between these coefficients.


C.pulchella
C.reticulata
C.megalops
Total Egg Volume - millions cu. µ.
Body Length - µ
30
25
20
15
10
5
500
600
700
800
900
1000

carries smaller numbers of eggs than C. reticulata of the same size. The greater mean volume of eggs from C. megalops (Table 3.) appears to be insufficient to compensate the total volume for the relatively low numbers.

Ceriodaphnia pulchella have lower total egg volumes than C. reticulata but these are relatively smaller animals which have already been seen to carry higher numbers of eggs than C. reticulata of the same size, (Figs. 5 and 6). The total egg volume carried by C. pulchella, which bears the same relationship to their body length as that of C. reticulata, is, therefore divided into smaller units of smaller individual volume than those of the other two species (Table 3.).

Egg number, length, temperature and chlorophyll:

Coefficients of regression of egg number on body length were calculated for each sample of Ceriodaphnia pulchella and of C. reticulata taken during 1963, (Appendix 2A). Analysis of variance showed no significant variation of these coefficients throughout the year. The mean egg numbers of these samples were then corrected to the grand total mean length of the species using Snedecor's (1956) formula:

$$Y = y - bx$$

where Y is the corrected mean egg number of the sample, y the mean egg number of the sample, b the coefficient of regression of egg number on length for the sample and x is the mean length of the sample minus the grand total mean length of all the samples taken in 1963. This correction eliminates, statistically, the inherent effect of body length on the number of eggs carried in the brood pouch. Corrected mean egg numbers were then plotted against temperature and the chlorophyll content of the water.

In both species there is no correlation between corrected mean egg number and temperature.

It can be seen from Fig. 8 (Appendices 1 and 2A) however, that body length in both Ceriodaphnia pulchella and C. reticulata has an inverse relationship to temperature. On this graph each point represents a mean of at least one sample of 10-25 animals. The areas of the circles are proportional to the number of animals on which the mean is based. Only two points, those at 11 and 14°C for C. pulchella are based on less than 10 animals. The single sample of each species taken at 24°C shows a sharp rise in mean length which is difficult to explain. It is also evident that at any temperature between 10 and 24°C the mean length of C. pulchella is less than that of C. reticulata. Any decrease of mean egg number with rising temperature is therefore a factor of the decreased size of the females rather

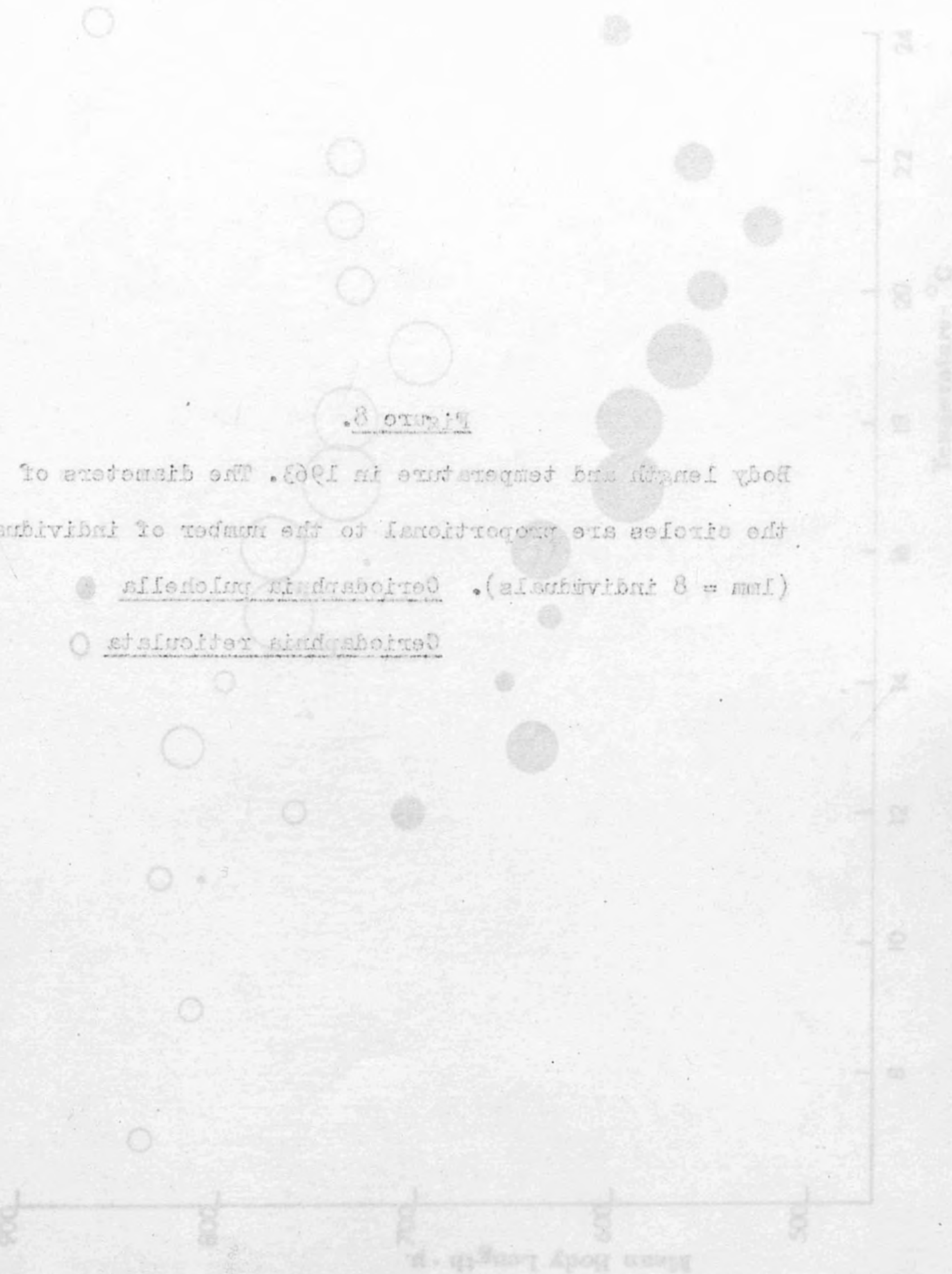

Temperature - °C
8
10
12
14
16
18
20
22
24
Mean Body Length - µ
500
600
700
800
900

Figure 8.

Body length and temperature in 1963. The diameters of the circles are proportional to the number of individuals (1mm = 8 individuals). *Ceriodaphnia pulchella* ●

Ceriodaphnia reticulata ○

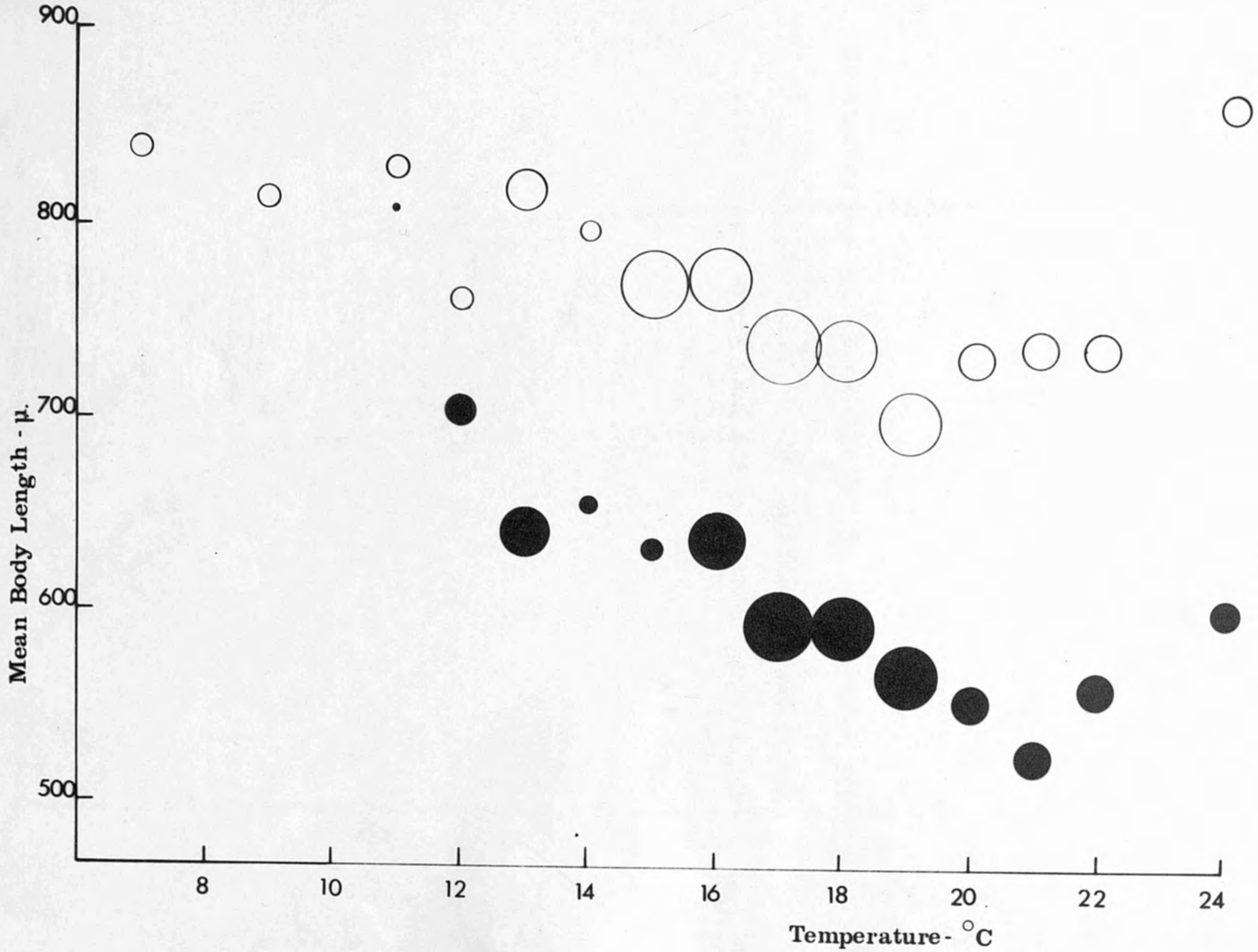
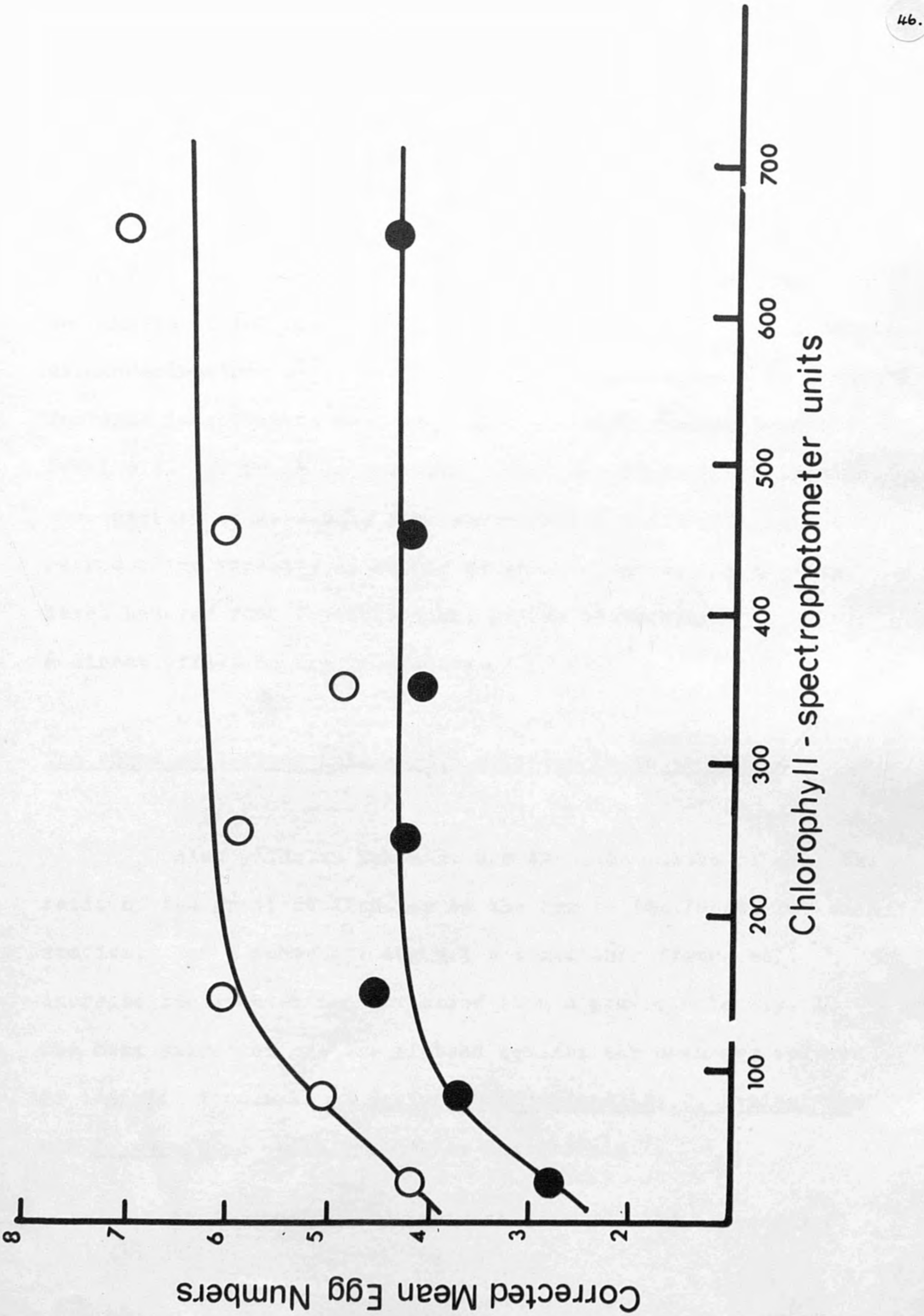

900
800
700
600
500
Mean Body Length - μ.
8
10
12
14
16
18
20
22
24
Temperature - °C

Figure 9.

The relationship of the corrected mean egg numbers of *Ceriodaphnia pulchella* ● and *C.reticulata* ○ to the chlorophyll content of the Long Water during 1963.


Corrected Mean Egg Numbers
2
3
4
5
6
7
8
100
200
300
400
500
600
700
Chlorophyll - spectrophotometer units

than a direct effect of temperature on brood size.

In Fig. 9 (Appendices 1 and 2A) corrected mean egg numbers of Ceriodaphnia reticulata and C. pulchella have been grouped in classes of 50 chlorophyll units, up to 100, and then in classes of 100 units, before being plotted against chlorophyll. At concentrations of chlorophyll below 200 units there is a marked increase in corrected mean egg number in both species before they level off. It would appear that, above a certain concentration, the quantity of available food makes little difference to the reproductive capacity of either of these species. Up to this level however food concentration, unlike temperature, does have a direct effect on egg production.

The shape of Ceriodaphnia eggs in relation to their volume:

Also given in Table 3. are the mean values of g/l, the ratio of the greatest diameter of the egg to the least, for each species. For a spherical egg g/l = 1 and this figure will increase the greater the deviation from a sphere. In Fig. 10 the mean values of g/l are plotted against the mean egg volumes of individual animals of Ceriodaphnia pulchella, C. reticulata and C. megalops. Both scales are logarithmic.

It is immediately apparent from Fig. 10 (Appendix 4)

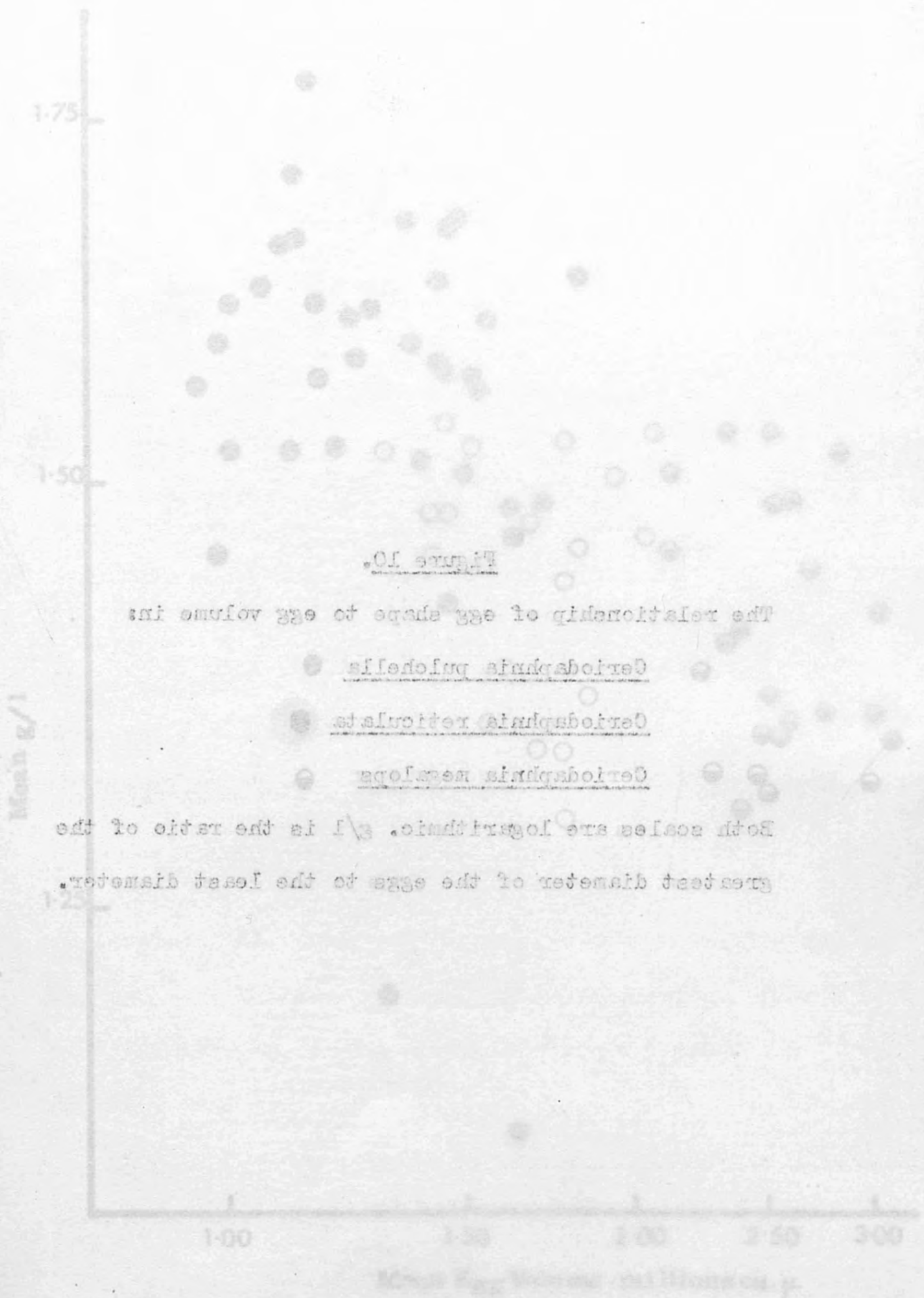

1·75
1·50
1·25
Mean g/l
1·00
3·00

Figure 10.

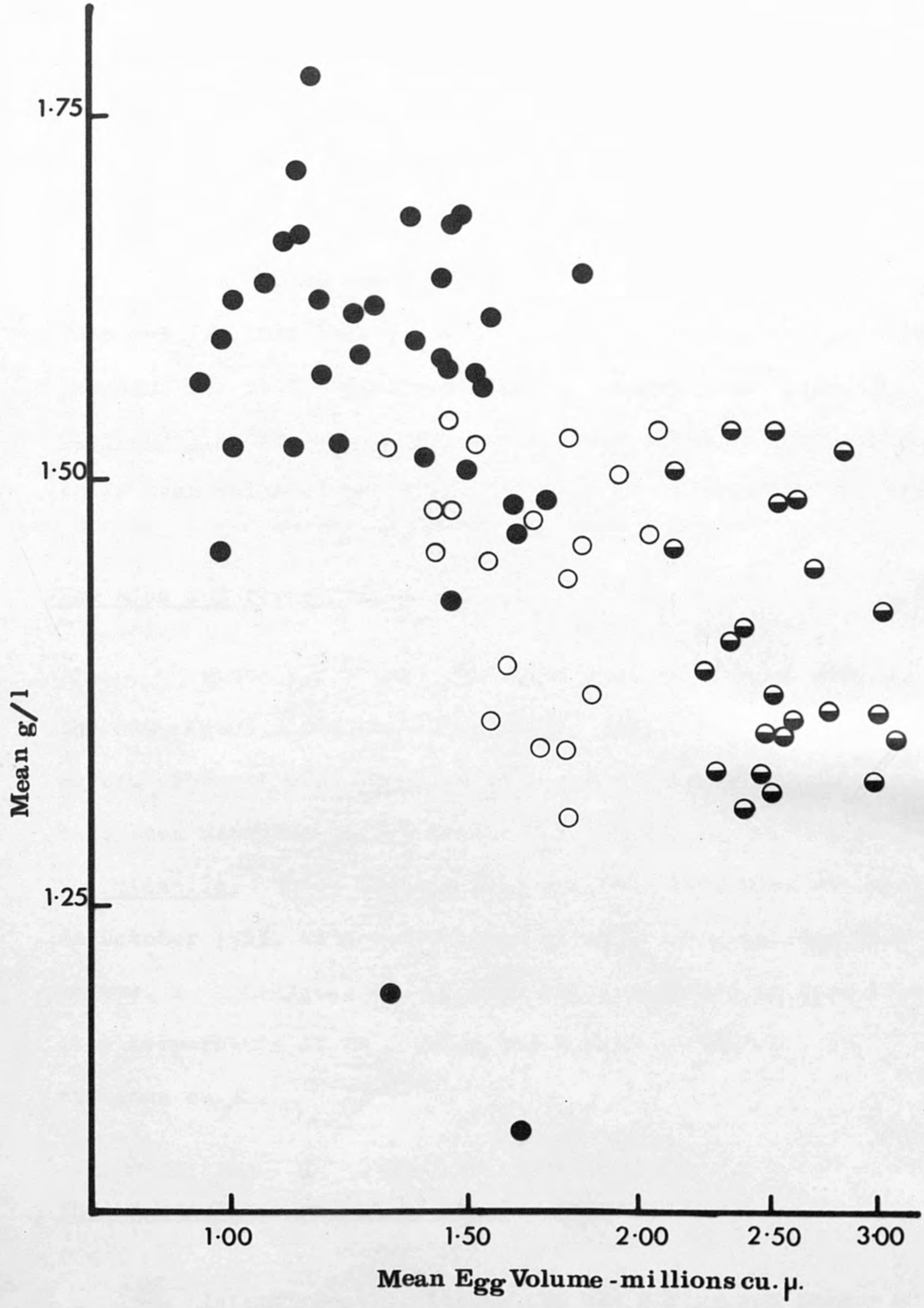
The relationship of egg shape to egg volume in:

Ceriodaphnia pulchella ●

Ceriodaphnia reticulata ○

Ceriodaphnia megalops ◒.

Both scales are logarithmic. g/l is the ratio of the greatest diameter of the eggs to the least diameter.


1·75
1·50
1·25
Mean g/1
1·00
1·50
2·00
2·50
3·00
Mean Egg Volume - millions cu. μ.

that the larger eggs approximate most nearly to a sphere. There is a negative correlation coefficient of -0.57, which, with 81 degrees of freedom has $p < 0.001$.

As can be seen from Table 3. Ceriodaphnia laticaudata does not fit into this pattern. This species carries relatively few eggs per unit length and they are larger than those of C. pulchella and C. reticulata but their shape is very elongated, their mean value of g/l being the highest of the four species.

Egg size and temperature:

Green (in press) has found that cladoceran eggs of the same species are larger in cooler waters than in warmer water. The temperature range from which eggs of Ceriodaphnia have been measured is too narrow for comparison, except in C. pulchella. Those eggs of this species which were measured in October 1963, at a temperature of 13°C had a greater mean volume, 1.42 millions cu.μ., than those measured in June 1964, at a temperature of 20°C which had a mean volume of 1.09 millions cu.μ..

The seasonal occurrence of sterile eggs:

Intermittently, throughout the Spring and Summer of

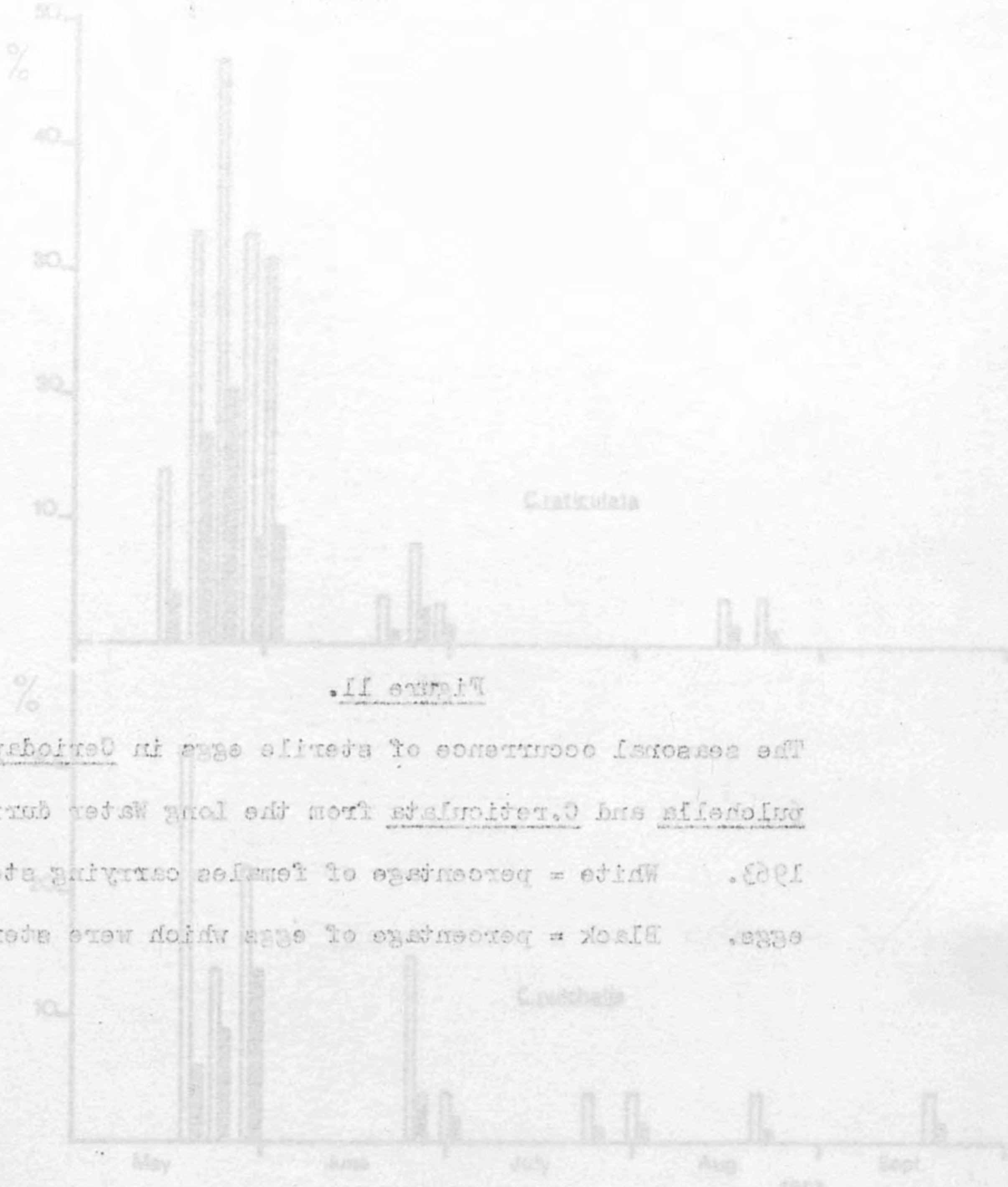
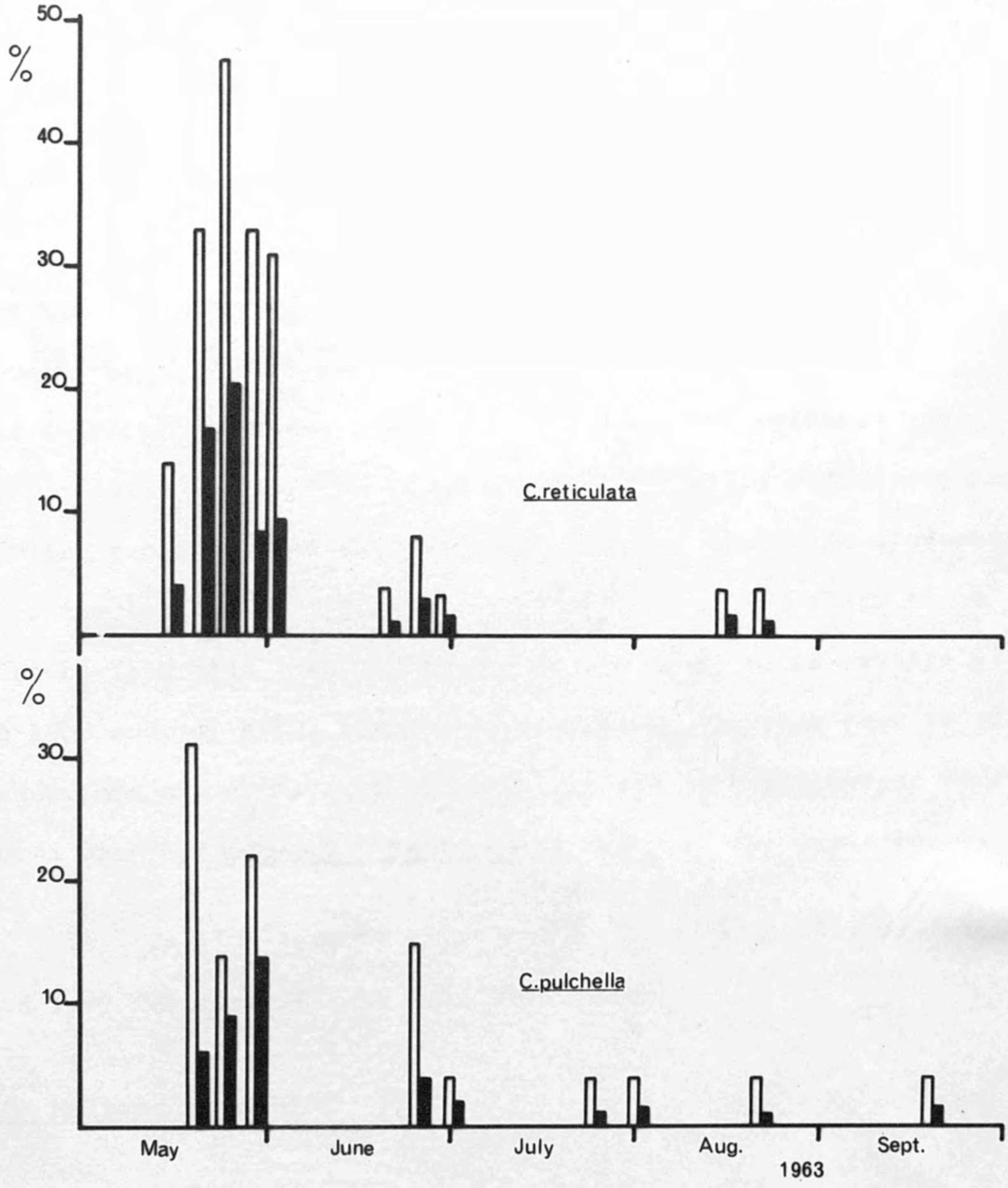

%
50
40
30
20
10
C.reticulata
%
10
C.pulchella
May
June
July
Aug
Sept
1963

Figure 11.

The seasonal occurrence of sterile eggs in *Ceriodaphnia pulchella* and *C.reticulata* from the Long Water during 1963. White = percentage of females carrying sterile eggs. Black = percentage of eggs which were sterile.


50
%
40
30
20
10
C.reticulata
%
30
20
10
C.pulchella
May
June
July
Aug.
Sept.
1963

1963, females of Ceriodaphnia pulchella and C. reticulata were found to have some underdeveloped or sterile eggs in their brood pouches. The proportion of females carrying sterile eggs and the proportion of the total eggs in a sample of twenty-five females which were sterile are shown in Fig. 11 (Appendix 5). The dates of their occurrence and the peaks of abundance are very similar to those recorded by Green (personal communication) for the occurrence of sterile eggs in other species of Cladocera from the Long Water. From his records of previous years it is also obvious that this phenomenon is confined, almost entirely, to 1963 and, although the cause is unknown, it would seem to be infectious since the only species in which no sterile eggs were found was Polyphemus pediculus which has a closed brood pouch.

In 1964 records have been kept to the middle of July and very few sterile eggs have been found.

The Maltese species:

This unidentified species is considered separately from the rest since no field observations have been made upon it. All specimens whose body length, egg number and egg size were measured were reared in the laboratory and these measurements (recorded in Appendix 6) are not, therefore, strictly comparable with those made of field samples of the other species. The body lengths of the ten specimens measured ranged from 900μ. - 1160μ. with egg numbers from 2 to 14 giving a mean length (with standard error) of 1011μ. ± 32.09 and mean egg number (with standard error) of 6.2 ± 1.49. These eggs had a mean volume of 3.49 million cu.μ. and mean length/breadth ratio of 1.34. These last two observations maintain the trend shown in C. pulchella, C. reticulata and C. megalops, that the larger the egg the more spherical its shape tends to be. The eggs of this species are, however, much larger than those of the species from Hampton Court, including the relatively large, elongate eggs of C. laticaudata (Table 2). Since the eggs measured here were developed at laboratory temperatures between 10 and 20°C it would be interesting to know the mean size of the eggs from animals of comparable body length reared in temperatures nearer to those of Malta, their natural habitat, If the trend noted on Page 29 is maintained they might reasonably be expected to be smaller.

Discussion:

It is widely believed that, in a small community, competition is most severe between species of the same genus. This has been discussed by, among others, Elton (1946) and Williams (1947; 1964). Gause's hypothesis that "no two species, having the same ecology, can persist in the same area" (Allee et al. 1949), is a logical extension of these ideas. It has been investigated by Debach and Sundby (1963) and has been examined, rather as a statement than as an attempt to prove or disprove it, by Gilbert, Reynoldson and Hobart (1952).

In the Long Water, Hampton Court, there are four species of the genus Ceriodaphnia. From May to October one can always collect C. pulchella and C. reticulata. In June, July and August C. laticaudata is also found and, at irregular intervals, one or two specimens of C. quadrangula var. hamata. This last species has not been included in this study but its occassional appearance must be borne in mind.

Ceriodaphnia laticaudata is easily separated from C. pulchella and C. reticulata by its colour and, as has already been pointed out, it occupies an obviously different niche from the other two species, in the bottom debris of the lake, Future investigation into the feeding habits and physiology of this species may yield information which will show the ways in which it is adapted to this bottom-dwelling habitat. Of particular interest is the relatively high concentration of haemoglobin seen in this species and any possible correlation with its suspected ability to withstand conditions of low oxygen ~~tension~~.

Ceriodaphnia pulchella and *C. reticulata*, as can be seen from Figs. 2 and 3, occur over the same period of the year and, therefore, at the same temperatures, and can be collected from exactly the same areas of the lake. Both species reproduce parthenogenetically throughout the season and sexually, with increasing frequency, from mid-summer onwards. In structural details these two species are quite distinct. The most obvious difference between them is the consistently smaller body lengths of *C. pulchella*. In his review of copepod studies, Hutchinson (1951) gives several examples of co-generic species, with often only minute structural differences, living together. He stresses that in nearly every case there is a difference in mean body size of the two species. He points out that, to filter feeders especially, particles which are small to a large species may be large to a small species and, therefore, the food of two different sized species will, inevitably, differ slightly.
This idea is based on the assumption that the organs of filtration of a larger species are proportionately larger than those of a smaller species. Although a greater intake of food would presumably be necessary for the maintenance of a larger animal, this could also be achieved by an increase in the extent ? of the filtration mechanism rather than in the size of the filter. Both *C. pulchella* and *C. reticulata* feed on phytoplankton but whether either or both species filter out more of one ~~sized~~

species of alga than of others has still to be investigated. This knowledge, ~~plus~~ together with measurements of the distances between the filtration setae, would throw more light on whether food differences consequent upon ~~their~~ a difference in size could separate their niches. In 1959 Hutchinson recorded the interspecific size ratio of various sympatric, co-generic species of birds and mammals and found a variation from 1.1 to 1.4 with a mean at 1.28. This figure, he estimated, is probably an indication of the minimum size difference necessary to enable two species of the same genus to live in the same habitat. It is interesting to note that the ratio of the grand mean body lengths of C. reticulata to C. pulchella is 1.26. It is doubtful if size difference alone can enable cohabitation. This is more likely to be due to some difference of feeding or physiological adaptation which may or may not be consequent upon the difference in size.

At any particular temperature in 1963 the mean body length of Ceriodaphnia pulchella was less than that of C. reticulata (Fig 8). In both species body length decreased with increasing temperature. Mean egg number increased with mean body length at the same rate in both species (Fig. 5) but when mean egg numbers were corrected to the grand mean length there was no correlation of corrected mean egg number with temperature. Any correlation of egg number with temperature is, therefore, a direct result of the effect of temperature on body length. Corrected mean egg numbers plotted against the chlorophyll content of the water, however, show a direct effect of food on egg number. The latter rises to a maximum and then levels off. It appears that over and above a certain concentration food has no further effect on egg production. Whether this is due to limitations of the filtration rate or of the animal's ability to assimilate is unknown. Ryther (1954) found an inverse relationship between the filtering rate of Daphnia magna and the concentration of the suspension of Chlorella vulgaris on which he fed them. This relationship might well be investigated in Ceriodaphnia.

Although egg number increases with body length at the same rate in Ceriodaphnia pulchella, C. reticulata and C. megalops, the regression lines of this relationship are placed increasingly further towards the right hand side of Fig. 5. Larger females of C. pulchella carry more eggs than C. reticulata of the same size and similarly with C. reticulata and C. megalops.

Ceriodaphnia megalops is the predominant species in the Wick Pond and although specimens of C. pulchella and C. reticulata can usually be found there it could not be said that they cohabit with C. megalops in the same way as they do together in the Long Water. C. megalops is the largest of the three species in

Fig. 5 but it carries relatively fewer eggs than the other two species for its size. This may be connected to the scarcity of green phytoplankton in the Wick Pond. During six weeks' samples taken from May to July 1964 the level of chlorophyll in the Wick Pond never rose above 50 spectrophotometer units even at times when several hundred units were recorded from the Long Water. Pyatokov (1956) found that, under conditions poor in food, Daphnia lays very much larger and fewer eggs than under conditions of more abundant food. As can be seen from Figs. 5 and 6 and Table 3. C. megalops lays fewer and larger eggs than those of C. pulchella and C. reticulata from the Long Water where phytoplankton as a source of food is more abundant than in the Wick Pond. That this species can still survive under these conditions, either by utilising some other source of food or by using efficiently the little that is available, may explain its predominance in the Wick Pond.

Although Fig. 7 shows that the relationship of total egg volume to body length is the same in Ceriodaphnia pulchella and C. reticulata, the eggs of the former are smaller than those of the latter (Table 2.). It has been found by Green (1956) that in Daphnia larger eggs result in larger young being released from the brood pouch. These mature after fewer instars than the smaller young from smaller eggs. However, this was an intra-specific comparison and the size of the young at release relative to the size at which they mature must be the more important factor in an inter-specific comparison. Should this be the same in both species, *C. pulchella* loses no advantage by the smaller size of its young at release and gains from the relatively high numbers produced by the larger females of the species. *C. reticulata*, however, reaches greater absolute lengths and therefore produces higher absolute numbers of eggs and young. This could explain the 10 - 20% predominance of numbers estimated for *C. reticulata* in the Long Water.

Apart from the obvious size difference between *Ceriodaphnia pulchella* and *C. reticulata* and those differences, such as absolute egg production, which are consequent upon it, this study seems to have pointed more to the similarities in their ecology than to their difference. It has also pointed out the obvious differences of *C. megalops* and *C. laticaudata* and has opened up a vista of problems for the future. Perhaps further study on more physiological lines will supplement these field studies and help to explain how *C. pulchella* and *C. reticulata* live in the same habitat and remain distinct.

Acknowledgements:

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Summary:

1. The world distribution of species of the genus Ceriodaphnia, as derived from a survey of the literature, has been summarised in Table 1. and the controversy over the nomenclature of C. cornuta and C. rigaudi discussed. It is concluded that the latter is a variety of the former.

2. An account has been given of the occurrence of Ceriodaphnia pulchella, C. reticulata, and C. laticaudata in the Long Water and of C. megalops in the Wick Pond, Hampton Court; also of their males and periods of sexual reproduction in the two habitats.

3. The seasonal variation in body size and egg number of parthenogenetic females of these species has been recorded

throughout the period March 1963 to July 1964. The mean body length of C. reticulata is consistently higher than that of C. pulchella. C. megalops is larger, on average, than both these species.

4. The relationship between egg number and body length of Ceriodaphnia pulchella, C. reticulata and C. megalops has been discussed. Egg number increases with body length at the same rate in all three species, but C. megalops, the largest species, carries relatively fewer eggs than C. reticulata of the same size. C. reticulata carry relatively fewer eggs than C. pulchella of the same size. This is confirmed by Fig. 6 in which C. laticaudata is included. The egg numbers of this latter species are relatively low although its length range overlaps those of C. pulchella and C. reticulata. This may perhaps be correlated in some way with the fact that this species occupies an obviously different niche from that of C. pulchella and C. reticulata, in the bottom debris of the Long Water.

5. Total egg volume also increases with body length at the same rate in Ceriodaphnia pulchella, C. reticulata and C. megalops. The reproductive material of C. pulchella is therefore divided into more, smaller units than that of C. reticulata and C. megalops. Absolute egg production in C. reticulata is, however, greater than in C. pulchella due

to its greater average size. The relatively low numbers of rather larger eggs found in C. megalops may possibly be correlated with the smaller amounts of phytoplankton found in the Wick Pond as compared with the Long Water.

6. Body length in Ceriodaphnia pulchella and C. reticulata varies inversely with temperature. When the mean egg numbers of these two species are corrected to the grand mean length of the species, there is no correlation between egg number and temperature. Any apparent inverse relationship between egg number and temperature is therefore a consequence of the effect of temperature on body length.

7. Corrected mean egg numbers of Ceriodaphnia pulchella and C. reticulata show an initial increase with the chlorophyll content of the water after which there is no further increase. Food, therefore, appears to have a direct effect on egg number over and above the inherent increase of egg number with body length which would result from an increase in available food. Above a certain level, increase in concentration of available food makes no difference to egg production. The animal is presumably unable to filter or assimilate more than a maximum concentration.

8. The larger eggs of Ceriodaphnia megalops are more nearly spherical than those of C. reticulata and C. pulchella.

The latter has small eggs, more elongate in shape. This is a trend found in many Cladocera: the larger the eggs the more spherical they are. *C. laticaudata* does not fit this pattern; it has larger eggs which are relatively very elongated.

9. The occurrence of sterile eggs in the brood pouches of *Ceriodaphnia pulchella* and *C. reticulata* has been recorded. The cause of this sterility is unknown and appears to have been confined to 1963.

10. The species of *Ceriodaphnia* hatched from dried mud from Malta is as yet unidentified. It is a bigger species than any of those described above and has larger, more spherical eggs.

11. General theories of the cohabitation of closely related species have been discussed in relation to the present studies on *Ceriodaphnia* and to work on other Cladocera.

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APPENDIX 1.

The seasonal variation in the temperature and chlorophyll content of the Long Water, Hampton Court during 1963 and Jan. - July 1964.

1963				1964			
Month	Day	°C	Chlorophyll in spectrophotometer units	Month	Day	°C	Chlorophyll in spectrophotometer units
				Jan.	29	8.0	30
				Feb.	12	0.0	270
March	20	9.5		March	3	6.0	435
	27	7.5			31	7.0	355
April	1	8.0	220	April	15	11.5	550
	10	10.0	325		21	12.0	480
	18	12.0	550		28	14.0	235
	26	12.0	300				
	30	15.0	127				
May	2	13.0	156	May	6	16.0	332
	9	17.0	480		12	18.0	413
	15	14.0	458		19	20.0	174
	20	15.0	625		29	19.0	156
	22	15.0	622				
	28	16.0	438				
	31	17.0	292				
June	5	18.0	119	June	4	16.0	8
	10		202		10	20.0	6
	12	24.0	121		17	20.0	51
	19	17.0	256		24	16.0	26
	26	17.0	277				

/July

APPENDIX 1 Cont'd

1963				1964			
Month	Day	°C	Chlorophyll in spectrophotometer units	Month	Day	°C	Chlorphyll in spectrophotometer units
July	2	18.0	213	July	2	22.0	38
	10	19.0	94		9	19.0	343
	17	19.0	52		16	22.0	88
	23	22.0	123				
Aug.	1	21.0	219				
	6	20.0	381				
	14	19.0	390				
	21	16.0	398				
	27	17.0	84				
Sept.	3	18.0					
	11	15.0	270				
	18	16.0	29				
	25	15.0	37				
Oct.	2	13.0	20				
	8	13.0	74				
	11	13.0					
	16	12.0	63				
	23	13.0	55				
	29	11.0	35				
Nov.	6	11.0	61				
	13	9.0	58				
	19	10.0	55				
	28	7.0	35				
Dec.	4	6.0	75				
	10	4.0	45				

APPENDIX 2A.

The seasonal variation in mean body length and mean egg number of parthenogenetic females of Ceriodaphnia pulchella collected from the Long Water, Hampton Court during 1963, with their standard errors. b is the regression coefficient of egg number on length for each sample with its standard error. N is the number of females in each sample.

Month	Day	N	Mean Length μ.	$\pm$	Mean Egg No.	$\pm$	b	$\pm$	Corrected Mean Egg Number
April	30	14	612	10.2	4.0	0.25	0.010	0.0057	3.98
May	2	11	594	19.6	4.7	0.50	0.011	0.0075	4.88
	9	8	655	19.5	5.9	0.67	0.029	0.0074	4.61
	15	5	656	22.9	5.8	0.66	0.025	0.0084	4.66
	20	16	694	17.5	7.0	0.60	0.023	0.0066	5.07
	22	7	690	23.5	4.8	0.97	0.012	0.0069	3.84
	28	9	750	30.2	5.6	0.74	0.013	0.0077	3.79
	31	15	655	19.5	5.3	0.44	0.017	0.0038	4.54
June	5	25	624	11.8	5.3	0.34	0.010	0.0056	5.17
	10	7	707	19.6	5.1		0.008		4.33

APPENDIX 2A cont'd.

Month	Day	N	Mean Length μ.	±	Mean Egg No.	±	b	±	Corrected Mean Egg Number
June	12	15	605	16.8	4.5	0.57	0.015	0.0085	4.59
	19	21	536	8.2	3.0	0.00	0.015	0.0048	4.12
	25	13	549	15.9	2.5	0.28	0.014	0.0033	3.36
	26	25	544	7.9	3.9	0.25	0.013	0.0059	4.76
July	2	25	570	10.8	4.2	0.36	0.031	0.0026	5.44
	10	25	571	11.1	4.0	0.26	0.015	0.0040	4.59
	17	25	569	8.1	3.0	0.22	0.013	0.0048	3.54
	23	25	560	8.4	3.2	0.28	0.025	0.0044	4.47
Aug.	1	25	526	9.8	2.5	0.17	0.010	0.0032	3.34
	6	25	558	9.0	3.6	0.30	0.025	0.0045	4.91
	14	25	566	8.6	3.2	0.25	0.016	0.0046	3.90
	21	25	570	6.8	3.0	0.20	0.015	0.0052	3.60
	27	25	565	13.6	3.3	0.28	0.010	0.0029	3.75
Sept.	3	25	577	8.6	1.7	0.17	0.006	0.0035	1.89
	11	25	573	9.3	3.1	0.25	0.016	0.0048	3.70

APPENDIX 2A cont'd.

Month	Day	N	Mean Length μ.	±	Mean Egg No.	±	b	±	Corrected Mean Egg Number
Sept.	18	25	602	8.6	1.5	0.14	0.008	0.0035	1.57
	25	25	595	13.4	3.0	0.37	0.020	0.0026	3.62
Oct.	2	15	662	16.1	3.8	0.94	0.010	0.0025	3.29
	8	25	672	14.7	3.6	0.31	0.010	0.0031	2.98
	16	16	706	13.3	5.0	0.46	0.010	0.0051	4.04
	29	1	810		8.0				

The seasonal variation in mean body length and mean egg number of parthenogenetic females of <u>Ceriodaphnia reticulata</u> collected from the Long Water, Hampton Court during 1963 with their standard errors. b is the regression coefficient of egg number on length for each sample with its standard error. N is the number of females in each sample.

Month	Day	N	Mean Length μ.	±	Mean Egg No.	±	b	±	Corrected Mean Egg Number
May	9	4	825	32.7	8.2		0.044	0.0114	5.75
	15	7	797	12.8	8.0	1.37	0.043	0.0446	6.81
	20	15	846	23.5	9.5	1.03	0.038	0.0058	6.59
	22	19	836	19.9	8.9	0.66	0.021	0.0064	7.51
	28	27	846	12.6	7.9	0.50	0.025	0.0060	5.98
	31	23	782	13.4	7.0	0.50	0.029	0.0049	6.64
June	5	24	802	18.1	8.2	0.77	0.038	0.0037	6.96
	10	10	837	17.2	8.4	0.23	0.038	0.0060	5.83
	12	15	858	24.4	10.7	0.23	0.039	0.0041	7.24
	19	25	715	20.3	4.0	0.49	0.022	0.0018	5.19
	25	25	694	18.5	3.6	0.28	0.012	0.0018	4.50
	26	27	697	15.3	4.5	0.39	0.023	0.0023	6.15
July	2	25	714	18.9	5.4	0.54	0.024	0.0030	6.72
	10	25	704	14.6	4.0	0.28	0.010	0.0034	4.65
	17	25	703	14.6	4.1	0.30	0.011	0.0034	4.83

APPENDIX 2A cont'd.

Month	Day	N	Mean Length µ.	±	Mean Egg No.	±	b	±	Corrected Mean Egg Number
July	23	25	742	16.3	3.6	0.30	0.011	0.0029	3.94
Aug	1	25	737	11.0	4.9	0.36	0.018	0.0055	5.48
	6	25	732	17.1	3.6	0.44	0.014	0.0043	4.08
	14	25	696	21.5	4.3	0.47	0.018	0.0024	5.61
	21	25	716	16.7	3.5	0.44	0.020	0.0033	4.57
	27	25	692	20.8	3.7	0.40	0.017	0.0023	5.02
Sept.	3	25	707	11.6	2.0	0.17	0.011	0.0020	2.68
	11	25	709	15.4	3.8	0.39	0.020	0.0028	5.01
	18	25	766	14.2	3.1	0.30	0.15	0.0033	3.16
	25	25	698	15.7	3.0	0.42	0.024	0.0025	4.72
Oct.	2	15	705	30.6	3.0	0.51	0.014	0.0024	3.89
	8	5	878	38.6	6.0	0.56	0.005	0.0089	5.46
	11	10	876	17.8	5.6	0.57	0.014	0.0110	4.11
	16	9	761	17.3	4.2	0.45	0.017	0.0077	4.34
	29	6	830	16.9	6.5	1.10	0.040	0.0294	4.08
Nov.	6	17	833	68.2	7.0	0.64	0.020	0.0073	5.91
	13	12	815	24.4	6.5	0.79	0.026	0.0061	5.32
	28	10	840	23.7	7.4	0.83	0.029	0.0076	5.35

APPENDIX 2A cont'd.

The seasonal variation in mean length and mean egg number of parthenogentic females of Ceriodaphnia laticaudata from the Long Water, Hampton Court, during 1963, with their standard errors. N. is the number of females in each sample.

Month	Day	Mean length μ.	±	Mean Egg No.	±	N.
July	2	737	12.9	3.5	0.20	25
	10	735	14.0	3.5	0.27	25
	17	726	12.5	2.4	0.11	25
	23	704	10.3	2.86	0.18	25
Aug.	1	727	13.2	3.0	0.23	25
	6	730	14.3	3.2	0.24	25
	14	710	14.0	2.4	0.15	25
	21	728	12.8	2.4	0.14	25
	27	710	10.0	2.0	0.0	2
Sept.	3	723	46.3	2.3	0.33	3

APPENDIX 2 B

The seasonal variation in mean length and mean egg number (with their standard errors) of parthenogenetic females of *Ceriodaphnia pulchella* and *C. reticulata* from the Long Water, Hampton Court during 1964. N is the number of females in each sample.

		C. pulchella					*C. reticulata*				
Month	Day	Mean Length μ.	±	Mean Egg No.	±	N	Mean Length μ.	±	Mean Egg No.	±	N
Apl.	28						770		6.5		2
May	6	610		6		1	780	31.1	7.4	1.63	5
	12	700	11.9	5.4	0.66	7	796	15.5	7.7	0.62	25
	19	617	9.7	5.6	0.41	25	761	17.0	6.4	0.59	25
	29	625	9.9	5.7	0.44	24	791	17.6	7.5	0.66	25
June	4	587	9.8	4.5	0.26	25	769	23.0	7.4	0.69	25
	10	565	8.5	3.8	0.29	25	746	19.0	4.8	0.58	25
	17	566	9.6	3.7	0.23	25	754	17.3	5.5	0.40	25
	24	548	11.3	2.5	0.19	25	664	14.5	2.9	0.26	25
July	2	528	8.0	3.0	0.25	25	649	29.7	3.3	0.21	25
	9	524	9.4	2.4	0.21	25	668	10.3	3.3	0.21	25
	16	529	9.3	2.1	0.01	25	670	11.7	2.9	0.23	25

The seasonal variation in mean body length and mean egg number (with their standard errors) in parthenogenetic females of <u>Ceriodaphnia laticaudata</u> from the Long Water, Hampton Court, during 1964. N is the number of females in each sample.

Month	Day	Mean Length μ	±	Mean Egg No.	±	N
June	17	809	18.2	5.1	0.49	16
	24	776	34.0	3.9	0.44	8
July	2	736	26.0	4.1	0.52	11
	9	722	14.1	3.9	0.33	25
	16	738	11.3	4.4	0.25	24

APPENDIX 2C.

The seasonal variation in mean body length and mean egg number of parthenogenetic females of <u>Ceriodaphnia megalops</u> from the Wick Pond, Hampton Court, during 1963, with their standard errors. N is the number of females in each sample.

Month	Day	Mean Length μ.	±	Mean Egg No.	±	N.
May	22	961	48.6	6.0	0.83	15
June	5	945	13.6	5.5	0.33	25
	12	829	13.8	1.93	0.17	15
	19	865	17.0	2.7	0.23	22
	26	841	9.9	1.8	0.11	25
July	2	848	13.8	2.4	0.19	25
	10	831	12.8	2.6	0.24	25
	17	815	10.4	3.2	0.18	25
	23	816	8.6	3.2	0.31	25
Aug.	1	844	10.1	3.2	0.23	25
	6	823	15.1	3.8	0.25	25
	14	840	13.5	4.5	0.37	25
	21	855	16.0	4.9	0.40	25
	27	872	18.8	4.8	0.47	25
Sept.	3	842	17.7	4.4	0.36	25
	11	833	17.7	4.4	0.40	24
	18	850	18.1	4.1	0.33	25
	25	888	17.7	5.3	0.31	25
Oct.	2	825	14.5	3.8	0.35	25
	8	810	45.1	3.6	1.19	3
	11	930	102.5	7.0	3.0	2

The seasonal variation in mean body length and egg number in parthenogenetic females of <u>Ceriodaphnia megalops</u> from the Wick Pond, Hampton Court, during 1964, with their standard errors. N is the number of females in each sample and Chl. the chlorophyll content of the Wick Pond in spectrophotometer units.

Month	Day	Mean Length μ.	$\pm$	Mean Egg No.	$\pm$	N.	Chl.
May	12	953	63.6	6.6	3.9	3	5
	19	960	13.4	6.3	0.42	25	30
	29	907	17.9	6.3	0.53	24	/
June	4	908	16.9	6.4	0.47	25	1
	10	904	13.9	5.4	0.27	25	4
	17	920	14.8	5.0	0.45	25	35
	24	918	11.4	5.5	0.22	25	33
July	2	829	16.7	3.5	0.26	25	49
	9	819	9.9	3.2	0.25	25	4
	16	905	11.4	4.7	0.29	25	45

APPENDIX 3.

The mean egg numbers (with their standard errors) of various length classes of *Ceriodaphnia reticulata*, *C. pulchella*, *C. megalops* and *C. laticaudata*. N. is the number of females in each length class.

Length Classes	*C. reticulata*			*C. pulchella*			*C. megalops*			*C. laticaudata*		
μ.	Mean Egg No.	±	N.	Mean Egg No.	±	N.	Mean Egg No.	±	N.	Mean Egg. No.	±	N.
500-549				2.7	0.071	138						
550-599	2.3	0.203	22	3.5	0.090	161				2.0	-	5
600-649	2.4	0.121	55	3.1	0.330	87				2.0	-	12
650-699	3.1	0.106	121	5.2	0.344	46	2.0	-	2.	2.2	0.073	49
700-749	4.2	0.143	110	6.9	0.458	24	2.4	0.183	29	3.0	0.120	70
750-799	5.5	0.141	81	7.7	0.843	11	2.8	0.101	100	3.5	0.131	47
800-849	6.6	0.260	67	8.5	1.409	6	3.2	0.260	96	3.8	0.345	17
850-899	8.0	0.555	44	9.0	-	1	4.0	0.068	97	4.6	0.531	8
900-949	10.9	0.342	40	9.0	-	1	4.8	0.226	81	3.3	0.500	2
950-999	11.2	1,586	9				5.8	0.238	33			
1000-1049	12.0	6.00	2				6.5	0.458	18			
1050-1099							8.6	0.332	3			

APPENDIX 4.

The size and shape of eggs from parthenogenetic females of four species of Ceriodaphnia from the Long Water and the Wick Pond, Hampton Court. g/l is the ratio of the greatest diameter of the egg to the least.

C. pulchella

Date	Temp. °C	Length of females μ.	No. of eggs in brood pouch	Mean egg volume in millions cu.μ.	Total egg volume in millions cu.μ.	Mean g/l
1.10.63	13	540	2	1.12	2.24	1.70
		580	3	1.46	4.39	1.57
		590	4	1.12	4.48	1.66
		610	4	1.21	4.82	1.61
		610	4	1.32	5.28	1.20
		650	4	1.50	6.00	1.42
		660	6	1.39	8.39	1.51
		680	5	1.33	6.67	1.48
		680	4	1.82	7.27	1.65
		680	6	1.25	7.50	1.58
		700	5	1.34	6.68	1.48
		700	5	1.44	7.22	1.64
		700	6	1.36	8.16	1.65
		700	4	1.39	5.57	1.59
		720	5	1.46	7.32	1.57
		720	5	1.51	7.56	1.65
		720	5	1.55	7.73	1.56
		740	5	1.53	7.63	1.60
		740	6	1.51	9.05	1.50
		760	6	1.53	9.20	1.56

C.pulchella cont'd.

Date	Temp. °C	Length of females µ	No. of eggs in brood pouch	Mean egg volume in millions cu.µ.	Total egg volume in millions cu.µ.	Mean g/l
1.10.63	13	760	5	1.47	7.36	1.67
		770	6	1.70	10.19	1.46
10.6.64	20	500	4	1.01	4.05	1.52
		540	4	1.16	4.64	1.78
		540	4	1.17	4.68	1.61
		560	4	0,99	3.98	1.61
		560	4	1.27	5.09	1.61
		580	4	1.12	4.48	1.52
		590	4	1.13	4.53	1.63
		590	5	1.18	5.90	1.57
		590	4	1.02	4.07	1.64
		590	6	1.09	6.57	1.67
		610	6	1.20	7.22	1.52
		610	6	1.06	6.38	1.63
		610	6	1.00	6.02	1.62
		630	8	0.97	7.77	1.56
		650	6	0.98	5.89	1.45

C. reticulata

Date	Temp. °C	Length of females μ.	No. of eggs in brood pouch	Mean egg volume in millions cu.μ.	Total egg volume in millions cu.μ.	Mean g/l
12.5.64	18	660	4	1.47	5.88	1.64
		700	5	1.69	8.45	1.47
		720	4	2.11	8.44	1.47
		720	6	1.49	8.94	1.47
		740	5	1.88	9.40	1.36
		770	6	1.32	7.92	1.51
		810	11	1.79	21.51	1.52
		830	9	1.78	16.03	1.43
		860	10	1.71	17.15	1.33
		900	14	1.79	25.06	1.29
		900	12	1.76	21.07	1.33
17.6.64	19.5	594	3	1.42	4.26	1.53
		648	4	1.53	6.14	1.51
		738	8	1.59	12.72	1.38
		756	4	1.43	5.73	1.45
		756	6	1.82	10.92	1.45
		774	6	1.56	9.39	1.35
		774	6	1.56	9.36	1.44
		792	6	2.06	12.36	1.46
		810	8	1.42	11.37	1.47
		864	7	1.93	13.51	1.49

C. laticaudata

Date	Temp. °C	Length of females µ.	No. of eggs in brood pouch	Mean egg volume in millions cu.µ.	Total egg volume in millions cu.µ.	Mean g/l
9.7.64	19	630	2	2.37	4.74	2.07
		650	2	2.67	5.34	1.87
		680	4	1.45	5.39	1.75
		680	4	2.44	9.76	1.94
		720	4	2.74	10.98	1.78
		740	5	2.17	10.85	1.81
		770	6	2.43	14.58	1.92
		810	5	2.62	13.10	2.00
		880	6	2.30	13.80	1.74

C. megalops

Date	Temp. °C	Length of females μ.	No. of eggs in brood pouch	Mean egg volume in millions cu.μ.	Total egg volume in millions cu.μ.	Mean g/l
4.6.64	16	770	4	2.32	9.27	1.32
		790	3	2.56	7.68	1.36
		810	4	2.49	9.98	1.34
		830	4	2.35	9.40	1.39
		850	4	2.47	9.89	1.32
		850	4	2.41	9.65	1.40
		850	4	2.26	9.04	1.38
		850	4	2.59	10.36	1.48
		860	7	2.56	17.92	1.34
		880	6	2.53	15.18	1.31
		900	5	3.00	12.02	1.35
		940	7	2.41	16.84	1.30
		950	7	2.77	19.43	1.35
		990	8	2.60	20.87	1.35
		990	7	2.99	20.93	1.31
2.7.64	22	830	3	3.00	9.01	1.41
		830	4	2.64	10.57	1.48
		840	3	2.85	8.56	1.52
		860	4	2.37	9.50	1.52
		860	4	2.53	10.12	1.53
		860	4	2.01	8.04	1.50
		900	4	2.12	8.61	1.45
		1010	5	3.08	15.39	1.34
		1030	5	2.74	13.70	1.44

APPENDIX 5.

The occurence of sterile eggs in the brood pouches of parthenogenetic females of Ceriodaphnia pulchella and C. reticulata from the Long Water, Hampton Court during 1963.

Ceriodaphnia pulchella

Date	Total	No. with sterile eggs	%	Total eggs	No. eggs sterile	%
20.5	16	5	31.2	112	7	6.2
22.5	7	1	14.3	34	3	8.2
28.5	9	2	22.2	51	7	13.7
25.6	13	2	15.3	45	2	4.4
1.7	25	1	4.0	106	2	1.8
23.7	25	1	4.0	80	1	1.2
1.8	25	1	4.0	62	1	1.6
21.8	25	1	4.0	77	1	1.3
18.9	25	1	4.0	64	1	1.6

Ceriodaphnia reticulata

Date	Total	No. with sterile eggs	%	Total eggs	No. eggs sterile	%
15.5	7	1	14.0	56	2	3.5
20.5	15	5	33.0	143	24	16.7
22.5	19	8	47.2	146	30	20.5
28.5	27	9	33.0	221	19	8.6
31.5	22	2	9.0	163	5	3.0
19.6	25	1	4.0	119	1	0.8
25.6	25	2	8.0	90	3	3.3
26.6	27	1	3.7	127	2	1.5
14.8	25	1	4.0	109	4	3.6
21.8	25	1	4.0	89	1	1.1

APPENDIX 6.

The body length, egg number and egg size and shape of parthenogenetic females of the Maltese species. g/l is the ratio of the greatest diameter of the eggs to the least.

Body length μ.	Egg No.	Mean egg volume in millions cu.μ.	Total egg volume in millions cu.μ.	Mean g/l
900	3	38.0	114.0	1.38
900	2	25.0	50.0	1.51
940	2	27.0	54.0	1.45
950	4	41.0	164.0	1.37
950	7	29.3	205.1	1.32
970	3	42.0	126.0	1.39
1100	3	40.0	120.0	1.47
1120	12	36.8	441.6	1.32
1120	12	33.8	405.6	1.32
1160	14	36.6	512.4	1.27