THE BIOLOGY OF BENTHIC CLADOCERANS IN FLOWING FRESHWATERS

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Doctor of Philosophy

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by

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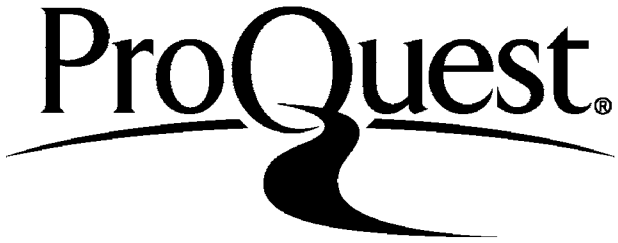

For my Mother.

ABSTRACT

A community of benthic cladocerans (Crustacea) from the River Thames at Twickenham, comprising seven chydorid and two macrothricid species, was studied. The species present were *Alona affinis, A. quadrangularis, A. rectangula, Disparalona rostrata, Leydigia leydigi, Pleuroxus uncinatus, P. trigonellus, Iliocryptus sordidus* and *Macrothrix laticornis*.

A general trend, among the chydorid species, of a midsummer peak in abundance followed by a rapid decline was noted. *Alona affinis, A. rectangula* and *Pleuroxus uncinatus* also exhibited an autumn peak in abundance. The *Iliocryptus sordidus* (Macrothricidae) population did not follow this pattern. Birth and death rates were calculated for the populations of *Alona affinis, Disparalona rostrata* and *Leydigia leydigi*.

Results obtained from qualitative sampling of rivers in Southeast England, and from a survey of the literature, indicated the presence of a taxocene of benthic cladocerans characteristic of the unvegetated substrate of lakes and rivers.

The life histories of *Disparalona rostrata* and *Leydigia leydigi* were examined in detail. The number and duration of adult and juvenile instars, duration of egg development and mean length of life were determined at four temperatures. A study of the relationship between egg volume and parent length for *Alona affinis, Disparalona rostrata* and *Leydigia leydigi* revealed a highly significant positive regression of egg volume on parent length.

The life cycle strategy of the Chydoridae as a whole was examined and found to differ from that of both the large and small planktonic Cladocera. Like the small planktonic cladocerans, the Chydoridae produce large young relative to their size at maturity. However, unlike these, the Chydoridae exhibit curtailment of growth after maturity and in this resemble the large planktonic Cladocera.

The annual production of the benthic chydorid community in the River Thames, Twickenham was calculated and was found to be 0.876g C m^{-2} in 1982.

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CHAPTER 1 : General Introduction

The Order Cladocera has been the subject of much ecological research. The majority of early studies concentrated on the largely planktonic Daphnidae. However, in the last two or three decades increasing attention has been directed towards the Chydoridae, the largest family of the Order, and the Macrothricidae. The species of these families are abundant in the littoral of freshwater bodies.

Research on the Chydoridae and Macrothricidae began with mainly taxonomic studies (Baird, 1850; Leydig, 1860; Lilljeborg, 1887) and progressed with the compilation of species lists for various water bodies (Scott, 1891, 1899; Lowndes, 1931; Galliford, 1948, 1949, 1953, 1960; Fryer, 1955; Smyly, 1958a).

Fryer (1968, 1974) determined the ecological niches of many species by reason of a detailed study of their functional morphology and workers have also used chydorid exoskeletons as guides to the history of lakes (Frey, 1958, 1959, 1960; Whiteside, 1970; Beales, 1976).

Increasing awareness of the importance of the trophic link that the littoral Chydoridae form between detritus and vertebrate and invertebrate predators in the aquatic ecosystem has resulted in a number of studies aimed at elucidating the temporal patterns of abundance and population dynamics of chydorids (Goulden, 1971; Keen, 1973, 1976;

Whiteside, 1974; Bottrell, 1977; Whiteside, Williams and White, 1978). The life histories and growth of many species of Chydoridae have also been examined (Smirnov, 1962, 1964, 1974; Keen, 1967; Shan, 1969; Bottrell, 1975b; Murugan and Job, 1982).

During the 1960's the International Biological Programme was initiated and one of its central aims was to investigate all stages of biological productivity in ecosystems. This was instrumental in stimulating research into ways of calculating the production of microcrustacea (Edmondson and Winberg, 1971; Winberg, 1971). Production studies of the Cladocera have been mainly limited to planktonic species (George and Edwards, 1974; Duncan, 1975), however, Bottrell (1977) has calculated the annual production of several chydorid species populations.

Most of the studies mentioned above have been concerned with the chydorid communities of lakes. Although qualitative surveys of rivers and streams have noted the presence of chydorid and macrothricid species (Jónassen, 1948; Larsen, 1959; Jolly and Chapman, 1966; Smirnov, 1974; Ham, 1982), the community of benthic cladocerans present in the substrate of flowing freshwaters has not been the subject of a detailed quantitative study. This may be because of the technical difficulties in collecting from this type of habitat. The sampling gear generally used in this environment will collect benthic microcrustacea but the mesh size of the screens and sieves used to wash

the samples are usually too coarse to retain the smallest organisms.

The work reported in this thesis was undertaken in an attempt partially to fill this gap in the literature. I have made detailed observations on the composition, abundance, population dynamics, life histories, growth and production of a community of benthic cladocerans in the River Thames at Twickenham. I have also attempted to define the community of cladocerans present in the benthos of flowing and standing freshwater by compiling species lists for a number of streams and rivers and by a survey of the literature.

P A R T I

Detailed observations on a community of benthic cladocerans in the River Thames, Twickenham.

CHAPTER 2 : Introduction

One of the objectives of studying a community of benthic cladocerans in the mud substrate of flowing waters was to determine the degree to which it differed from that in the mud substrate of still waters. A major difference between the two habitats is the presence of current in the former. This may influence a number of environmental factors and may thus affect the abundance and species composition of the benthic cladoceran community. Furthermore, the occurrence of benthic animals above the bottom is a familiar phenomonen in streams (Waters, 1972) and is frequently attributed to disturbance of the sediments by currents. Evans and Stewart (1977) found several species of benthic cladocerans in the water column of Lake Michigan indicating that benthic cladocerans may undergo some form of migration out of the sediments. If migration of this kind or removal from the sediment by the action of currents occurred with any frequency in a cladoceran community in a riverine environment, then large numbers of individuals would be washed downstream, possibly resulting in lowered and shifting populations of benthic cladocerans.

The number and type of species and abundance, composition and dynamics of the constituent species populations were therefore examined for a community of benthic cladocerans in flowing water. Differences in the abundance of cladoceran populations in the benthos of

lakes and rivers may merely reflect variances in the quality and quantity of the detritus present. However, analyses of the population dynamics of the species present will indicate whether observed changes in the population were the result of changes in natality or mortality, enhancing the possibility of identifying the causal factors. A considerable number of quantitative studies on the benthic cladoceran communities present in the mud of lakes have been published and are available for comparison. These include studies on the abundance (Goulden, 1971; Evans and Stewart, 1977; Whiteside *et al.*, 1978; Adalsteinsson, 1979), composition and population dynamics (Keen, 1973) of the species populations.

Fryer (1968) suggests that many benthic cladocerans may be tolerant of a wide range of physical and chemical parameters providing substrate requirements are met. In the present study the cladoceran species present in the benthos of a number of rivers and streams were determined and compared with those of lakes to explore the possibility of a benthic cladoceran community common to both lakes and rivers.

CHAPTER 3 : Description of Sampling Site and Introduction to the Cladocera

SECTION 3.1. Description of sampling site

The main sampling site had to fulfil several requirements:-

a) the river or stream must have a discernible rate of flow.

b) several species of benthic Cladocera must be present in abundance.

c) there must be easy access to the site.

The site chosen was on the Middlesex bank of the River Thames at East Twickenham. Grid reference TQ 172 734.

The site is approximately midway between Richmond lock downstream, which is the first lock on the Thames as one moves from estuary to source, and Teddington lock upstream, the limit of the tidal range. Below Richmond lock the Thames is fully tidal. Adjacent to the lock a series of sluice gates spans the river. These are lowered for four hours of every tidal cycle (two hours either side of low tide) forming a barrier which greatly reduces downstream flow and retains water above the sluice. Thus, during the sampling period there was always at least 40-50cm of water covering the river bed. Between Richmond and Teddington locks the Thames is semi-tidal: when the sluices are down there is a period of slack water, when they are raised a normal tidal cycle is resumed. Annual maintenance of the sluice gates occurs in November and

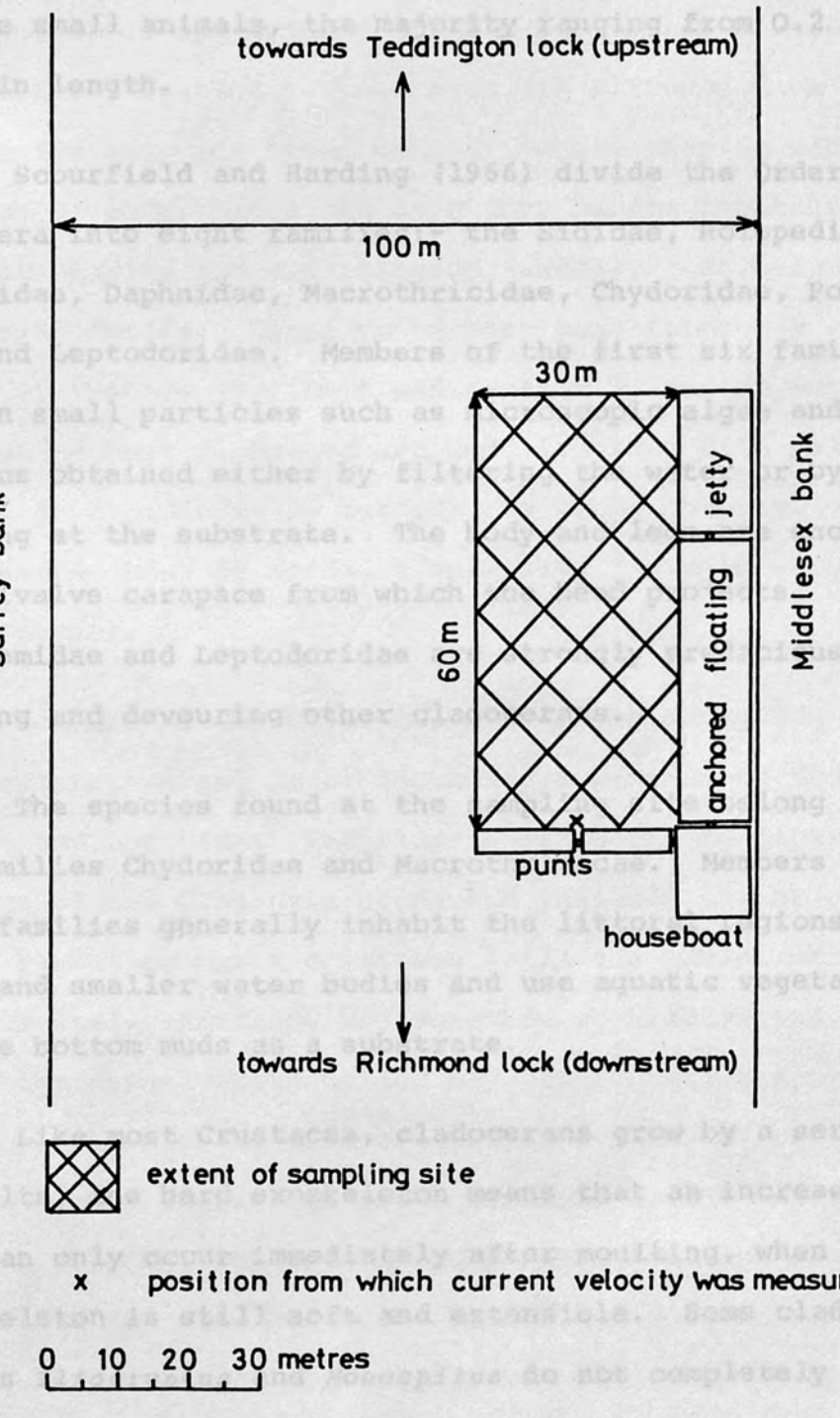
December, and at this time the sluices are permanently raised, so the river downstream of Teddington lock becomes fully tidal.

The sampling site is 60m long and 30m wide. An anchored floating jetty, 10m wide, extends from the Middlesex bank along the entire length of the sampling site. The upstream and downstream ends of the jetty mark the length boundaries of the site (Fig. 1). The width of the site is measured from the river side of the jetty towards the centre of the river. Two floating punts extend at right angles to the bank at the downstream end of the site (Fig. 1). The river is 100m wide at this point and thus the sampling site extends approximately one third of the way across. A small boat was kept on the jetty for use in sampling.

At the sampling site the substrate comprises an upper layer of apparently homogeneous loosely packed brown mud, interspersed with small fragments of leaves and other debris. This layer extends to a depth of 5-7cm and below this there is a deep layer of black anoxic mud.

Gravel, pebbles and larger stones were absent from the site as were rooted or floating aquatic macrophytes and algae such as *Cladophora*. The tidal range is approximately 6m and the depth of water over the site ranges from 40-50cm to 7.5m.

FIGURE 1. The sampling site at the River Thames, Twickenham.



SECTION 3.2. Introduction to the Cladocera

The Cladocera form an order in the Branchiopoda, a subclass of the Class Crustacea. They are found almost exclusively in freshwater, only three genera being marine, and are small animals, the majority ranging from 0.2 to 3.0mm in length.

Scourfield and Harding (1966) divide the Order Cladocera into eight families:- the Sididae, Holopedidae, Bosminidae, Daphnidae, Macrothricidae, Chydoridae, Polyphemidae and Leptodoridae. Members of the first six families feed on small particles such as microscopic algae and fine detritus obtained either by filtering the water or by scraping at the substrate. The body and legs are enclosed in a bivalve carapace from which the head projects. The Polyphemidae and Leptodoridae are strongly predacious, catching and devouring other cladocerans.

The species found at the sampling site belong to the families Chydoridae and Macrothricidae. Members of these families generally inhabit the littoral regions of lakes and smaller water bodies and use aquatic vegetation and the bottom muds as a substrate.

Like most Crustacea, cladocerans grow by a series of moults, the hard exoskeleton means that an increase in size can only occur immediately after moulting, when the new skeleton is still soft and extensible. Some cladocerans such as *Iliocryptus* and *Monospilus* do not completely cast

the carapace at each moult and so accumulate a series of carapaces on their backs, which are thought to be of survival value (Green, 1961).

During most of the year female cladocerans are parthenogenetic and produce diploid eggs which develop without fertilisation. These eggs are extruded from the ovaries into the brood chamber, where they at once begin to develop. In a few days they become immature miniature adults and are released, usually just before the parent moults. These young then pass through a series of instars (p. 29) and eventually become mature. The eggs of most Cladocera are well provided with yolk and can develop normally outside the brood chamber. In some genera, such as *Moina*, a nutritive fluid is supplied by the parent.

Members of the Chydoridae, with the exception of the Eurycercinae and Saycinae, carry a maximum of two eggs at any one time. Individuals belonging to other families of the Cladocera produce a variable number of eggs. Parthenogenesis continues until the advent of environmental conditions unfavourable to cladocerans, at which time sexual reproduction may occur. Males appear in the population followed by females capable of producing haploid eggs. These eggs are fertilised by the male and released into the female's brood pouch. When the female next moults the eggs become enclosed in a specialised part of her carapace, the ephippium. The early embryo

into which the eggs have developed will lie dormant, often withstanding freezing and drying, until the return of conditions suitable for the continuation of development.

The Macrothricidae and the two most primitive subfamilies of the Chydoridae, the Eurycercinae and Saycinae, produce an ephippium that contains a variable number of resting eggs. Most other Chydoridae produce a one-egged ephippium (Scourfield, 1899, 1902), although Fryer and Frey (1981) found that two species, *Chydorus ovalis* and a species currently listed as *Chydorus* cf. *sphaericus* consistently produce two-egged ephippia.

Cladocerans were identified using the publications of Scourfield and Harding (1966) and Fryer (1968). A total of nine species was recovered from the sampling site sediments.

Class Crustacea,
Subclass Branchiopoda,
Order Cladocera,
Tribe Anomopoda,
Family Macrothricidae.

Iliocryptus sordidus (Liéven)

Macrothrix laticornis (Jurine)

Family Chydoridae.

Subfamily Aloninae after Frey (1966)

Alona affinis Leydig

A. quadrangularis (O.F. Müller)

A. rectangula Sars

Leydigia leydigi Schödler

Subfamily Chydorinae after Frey (1966)

Disparalona rostrata (Koch 1841)

Pleuroxus uncinatus Baird

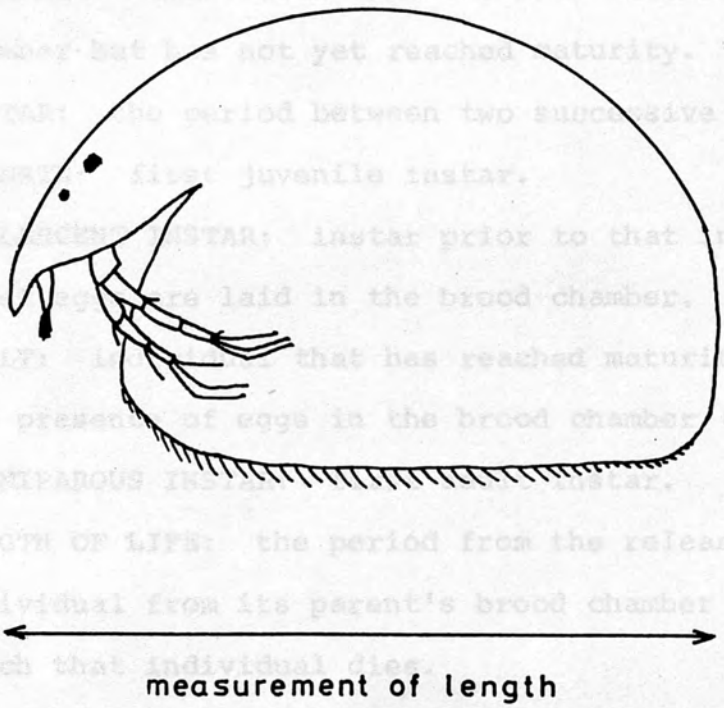
P. trigonellus (O.F. Müller)

Three of the above species, *Alona quadrangularis*, *Pleuroxus trigonellus* and *Macrothrix laticornis* were found only rarely.

The only difficulty in identification occurred while differentiating between *Alona affinis* and *A. quadrangularis*. Morphologically, these species are separated by the presence or absence of spinules on the basal spine of the post-abdominal claw (Scourfield and Harding, 1966), a feature which can be difficult to ascertain. Preliminary surveys in 1981 indicated that *Alona affinis*, *A. quadrangularis* and *A. rectangula* were the only members of the genus *Alona* found at the site and that *A. quadrangularis* occurred very rarely. Therefore, in 1982, all *Alona* species other than *A. rectangula* (easily identified by its small size), were classified as *Alona affinis*.

Fryer (1968) has shown the *Rhynchotalona rostrata* (Koch) of Scourfield and Harding (1966) differs markedly from the other member of the genus *R. falcata*, a fact also noted by Frey (1959) and Smirnov (1966). Frey (1959) placed this species in the genus *Alonella* on the basis of similarities in head pore arrangement. However, Fryer (1968) has shown that in more fundamental aspects of

FIGURE 2. A chydorid cladoceran together with an indication of how length was measured.



anatomy it differs substantially from *Alonella* spp. and he assigns it to a new genus *Disparalona*. The species becomes *Disparalona rostrata* (Koch 1841).

Definition of Terms

EGG: unless otherwise stated, this term is taken to mean parthenogenetically produced eggs.
DURATION OF EGG DEVELOPMENT: from the first appearance of an egg in the brood pouch to the moment of its liberation from the brood pouch.
BIRTH: liberation of an embryo from the parent brood pouch.
JUVENILE: individual that has been released from the brood chamber but has not yet reached maturity.
INSTAR: the period between two successive moults.
NEONATE: first juvenile instar.
ADOLESCENT INSTAR: instar prior to that in which the first eggs are laid in the brood chamber.
ADULT: individual that has reached maturity as shown by the presence of eggs in the brood chamber (cf. below).
PRIMIPAROUS INSTAR: first adult instar.
LENGTH OF LIFE: the period from the release of an individual from its parent's brood chamber to the time at which that individual dies.

With individuals collected in the field, difficulties can arise when differentiating between a juvenile and an adult without eggs. Galbraith (1967) and Allan (1973) considered all individuals larger than the smallest size at which eggs were present to be adults, this procedure

was adopted. The size at first reproduction remained constant throughout the study.

CHAPTER 4 : Methods

SECTION 4.1. Introduction to methods for sampling benthic cladocerans

The sampling programme had to be designed to give information on the cladoceran species present, and the abundance, composition and distribution of the populations. Most traditional methods for the quantitative sampling of benthic invertebrates involve the collection of substrata from which the animals are then removed. The separation of animals from substrate can be very time consuming. If, however, a trap-like sampler were used, which collects live animals but no sediment, it would save the time and labour involved in separation.

To obtain the information required both types of sampling techniques have been employed, a core-sampler for the quantitative sampling of sediment and a pattern sampler for the quantitative trapping of live animals free of sediment. These are described in detail below.

Section 4.1.1. Core sampler and flotation technique

Core Sampler: Elliott and Tullett (1978) describe many types of quantitative samplers for benthic invertebrates. Grabs, dredges and airlift samplers were considered but not employed: core type samplers seemed more appropriate. At slack water the sampling substrate is covered by a shallow depth of water and is easily reached from a flat bottomed dinghy. By sampling at this time, therefore, a

hand operated corer could be used. These have an advantage over remote control corers in that there is greater flexibility and control over the positioning of the sampler.

Holme and McIntyre (1971) suggest that, in inter-tidal areas of shallow water where the apparatus can be operated by hand, a tube or pipe may be adapted for use. Elliott (1977) states that many small sampling units are preferable to a few large ones, therefore, since the cladocerans had to be separated from the sediment, a corer of small dimensions was required. Rees (1940) used a simple brass tube of diameter 1.8cm to sample a mud flat and Goulden (1971) collected quantitative sediment samples from Lake Lacawac with a pipe corer of 1.64cm diameter. A similar corer was constructed for the present study.

The corer designed consisted of a tube of clear plastic, of internal diameter 1.5cm and length 9cm, which sampled a surface area of $1.7cm^2$.

When taking a core, the tube was slowly pushed vertically into the sediment taking care not to impede the displacement of water up the tube. When the top of the tube was approximately 1cm above the mud-water interface, the top and bottom openings were sealed and the whole lifted to the surface, thus any cladocerans present on the surface of the mud were also collected. The core of sediment was retained in the tube until processed in the laboratory, cores were stored at $5^{o}C$ and always processed

within forty-eight hours of collection (p. 35). It is well known that some benthic organisms can penetrate deeply into sediments: Cole (1955) and Stańczykowska (1966) found microbenthos at a depth of 15cm in muddy sediments. The corer described above only samples to a depth of 8cm. However, the bottom 2cm of each core always consisted of anoxic black mud (p. 8) in which it is unlikely that any cladocerans could survive. To test this assumption, the bottom 2cm of a number of cores in two separate samples were examined. No animals were found.

Flotation Technique: A method of separating the cladocerans from the mud, other than sorting under a binocular microscope, was essential. The latter method is tedious and inefficient, although it has been used by Cole (1955) and is recommended by Stańczykowska (1966). For the present study, a method of separation was required which would remove all instars of all cladocerans with equal efficiency.

Sieving the mud and examining the residue is a method employed by Whiteside and Lindegaard (1980, 1982) and Quade (1973). It is not feasible in this study because the first instars of *Disparalona rostrata*, the smallest cladocerans collected, have a minimum height of 0.13mm and length of 0.3mm. The mesh size of a sieve capable of retaining these animals (100μm) is such that much of the mud is also retained.

Separation of sediment from cladocerans by differential density centrifugation, as employed by Goulden

(1971), and decantation, as used by Evans and Stewart (1977), was considered but not employed as the time taken to process each sample unit was too long.

The technique finally chosen to separate the animals from the sediment was that of flotation: this method was found to be relatively quick and efficient. The basis of this technique is that a liquid medium is provided in which animals float while the undesirable materials sink to the bottom. Ladell (1936), Beak (1938) and Lyman (1943) were among the first to employ this method. Solutions of $MgSO_4$, NaCl, $CaCl_2$ or sucrose can be used as the flotation medium. Sucrose was used in the present study. Kajak, Dusoge and Prejs (1968) stress that the ratio of depth of sediment layer to depth of flotation solution is important and recommend that the layer of flotation solution should be seven to ten times deeper than the layer of sediment.

PROCEDURE: Each core was washed into a 500ml beaker with sucrose solution of specific gravity 1.14. The sediment formed a layer of approximately 0.5cm depth at the bottom of the beaker and enough sucrose solution was added to form a layer 8cm deep above this (ratio of depth of sediment : depth of flotation solution was 1 : 16). The contents of the beaker were stirred vigorously for fifteen seconds and then allowed to settle. After five minutes, the supernatent (sucrose and cladocerans) was filtered through a net of mesh size 80µm, and the latter rinsed out into a petri dish.

The sediment was then refloated with fresh sucrose solution and the process repeated. Initially, three flotations were carried out on each core, but cladocerans were rarely obtained from the third flotation and this was abandoned. The contents of each petri dish were examined under a binocular dissecting microscope.

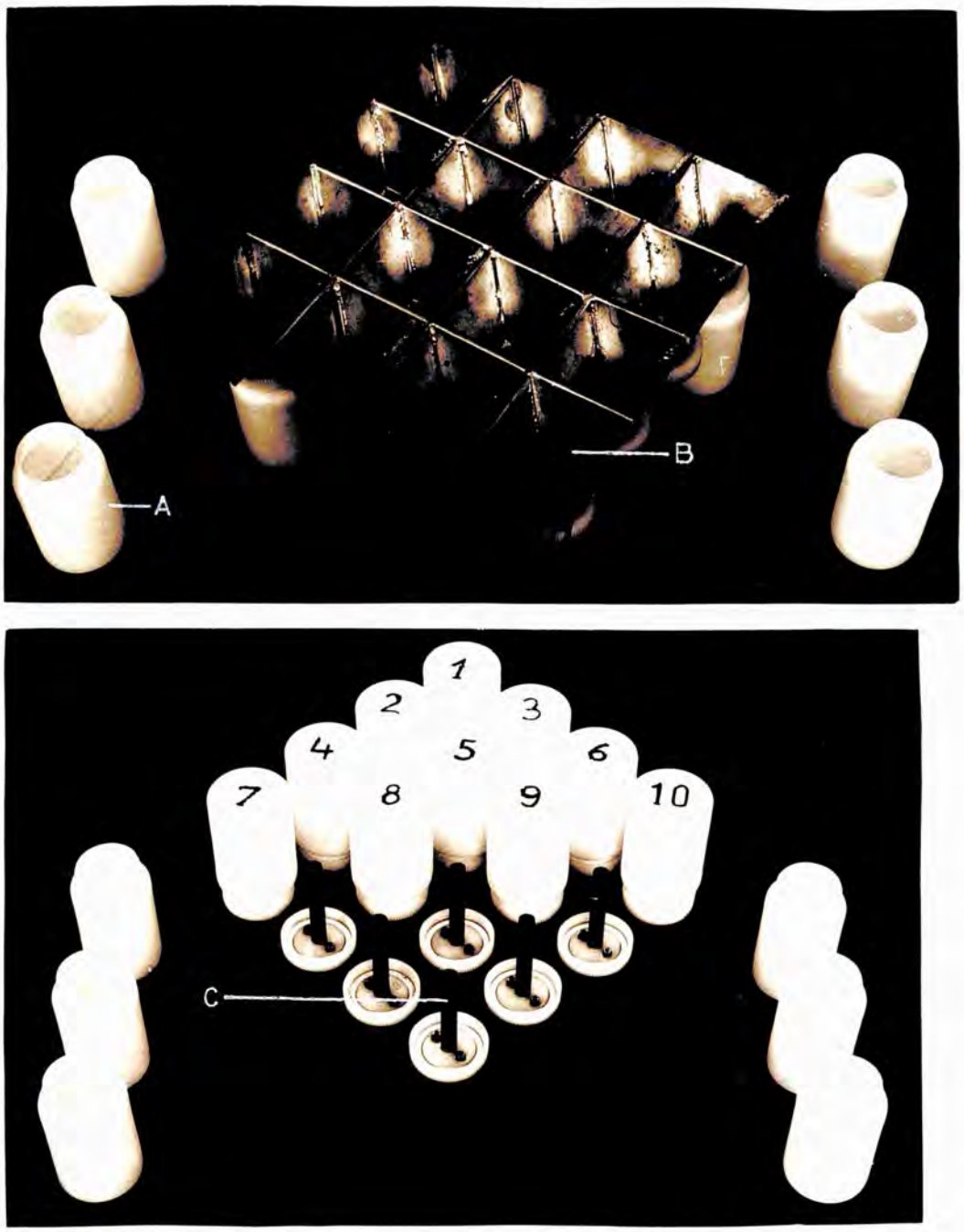
Kajak *et al.* (1968) and Anderson (1959) showed that the effectiveness of flotation of live material was several times greater than that of preserved materials and Stańczykowska (1966) found that for samples kept at 8°C alterations in the numbers of microbenthos present only became significant after forty-eight hours storage. Therefore, in this study the cores were not preserved but stored at 5°C and processed within forty-eight hours of removal from the sampling site.

The efficiency of this extraction technique was determined by hand sorting the mud remaining after flotation from a number of cores. It was found to be 95% efficient.

Section 4.1.2. Pattern sampler

The pattern sampler was originally developed by Whiteside and Williams (1975) to obtain quantitative information on the population dynamics and spatial patterns of littoral Chydoridae in Lake Itasca. The success of the sampler depends on the fact that chydorids move vertically through the surface sediment (Whiteside, 1974).

FIGURE 3. Two views of the pattern sampler. The upper photograph shows the collecting surface of sixteen square funnels. The lower photograph shows ten collecting bottles screwed into the body of the sampler.



A - collecting bottles

B - square funnel

C - tube extending from the body of the sampler into the bottles

The pattern sampler designed by Whiteside and Williams (1975) has been modified slightly for use in the present study. It is now a 4 x 4 matrix of square funnels (Fig. 3), each sampling 64cm^2 of substrate. The smaller matrix increases the manoeuverability of the sampler. The sixteen funnels lead upward through tubes into plastic collecting bottles (volume 300cm^3) which are screwed into the body of the sampler (Fig. 3). To be trapped by the sampler, an animal must move upwards from the sediment through the distance of the funnel and tube (14.5cm) into the collecting bottle and fail to escape by the tube opening. The body of the sampler was constructed from brass, thus ensuring that the sampler remained firmly in contact with the substrate and did not drift with the tide. Rings were welded to each corner for the attachment of ropes.

Whiteside and Williams (1975) found that maximum efficiency was obtained if the sampler was set down at about 2000 hours and lifted at 0800 hours. This procedure was adopted in the present study. The sampler was suspended in the water while each bottle was filled with river water (see p. 63) and screwed into place. It was then gently lowered into position. The combined weight of filled bottles and brass matrix causes the sampler partially to sink into the mud, ensuring that each funnel is completely in contact with the substrate. This is essential for successful sampling. Whiteside (1974) states that most chydorids "probably require the presence

of substrate for creeping vertically. Their upward creeping accounts for recovery of most chydorid species when the pattern sampler was in contact with the chydorid substrate". On lifting the sampler the contents of each bottle were immediately screened through a net of mesh size 80μm and washed into separate vials with absolute alcohol (see p. 65 for affects of preservation on length). These were then labelled with the date, the number of the sampler and the position of the bottle in the sampler matrix.

Animals were identified and counted under the low power of a binocular microscope. For length measurements, individuals were placed on a slide and measured to the nearest 0.007mm (Fig. 2) using a binocular microscope with a calibrated eyepiece micrometer.

The corer samples a small surface area of substrate and relatively few cladocerans are obtained per sample. Thus it is not possible to collect sufficient data on length distributions for each species using the cores alone. Each sample unit of the pattern sampler samples a much larger surface area, many chydorids are obtained and these provide ample information on length distributions. However, unlike the corer, the pattern sampler does not sample the non-swimming macrothricid *Iliocryptus sordidus* which is abundant at the site. The pattern sampler does not appear to have been used by other research groups since its development and has not been used in a lotic environment.

Its use in this study, in conjunction with the corer, will provide further information on its performance.

Section 4.1.3. Parameters measured

Two objectives of this study were to build up a detailed picture of the population abundance, composition and dynamics of the species of benthic cladocerans in the River Thames at Twickenham and obtain an estimate of production for the three most abundant species, namely *Disparalona rostrata, Alona affinis* and *Leydigia leydigi*. To fulfil these objectives the numbers of individuals in each of the following categories were determined from the field samples, at weekly intervals, for all species present :- (i) juveniles, (ii) adult females, (iii) adult females with eggs, (iv) ephippial females, (v) males and (vi) total numbers. These categories were determined for both the core and pattern sampler series.

Birth and death rates: the analysis of birth rates and death rates in natural populations allows the quantitative analysis of the mechanisms controlling population development. If the population rate of reproduction is known for a given time, the population increase for that time can be calculated. If this calculated population increase is compared with the population actually observed at the later time, then mortality in the population can be evaluated.

To carry out this comparison the exponential equation for population growth was adopted (Edmondson, 1960).

Continuous reproduction and a steady-state population were assumed. These are large assumptions, but it has been shown that this equation adequately describes the growth of many populations (Cole, 1954).

(a) $Nt = Noe^{rt}$

No and Nt denote initial population size and size t time units later.
e = base of natural logarithms
t = time interval between No and Nt
r = observed rate of population increase.

Formula (a) may be re-arranged to give the observed rate of population increase (r). Continuous reproduction, stable age distribution and no immigration or emigration between the two periods are assumed.

(b) $r = \dfrac{\log_e Nt - \log_e No}{t}$

letters as in (a)

Several methods based on the exponential model of population growth have been used to calculate the instantaneous birth rate b, the predicted rate of population increase.

Edmondson (1960) derived a formula relating the finite daily per capita birth rate (B) to an approximation of the instantaneous birth rate b. The assumptions of no

deaths, constant birth rate and a fixed development time are made.

(c) $b = \log_e (B+1)$ $\quad B = E/D$

E = number of eggs per female

D = duration of egg development.

This formula has been widely used, for example by Hall (1964), Wright (1965), George and Edwards (1974) and Smyly (1979). However Caswell (1972) found that the relationship between the finite rate and the instantaneous rate as expressed by this formula was not correct and Paloheimo (1974) noted that it underestimated b when $D < I$ and overestimated b when $D > I$.

Paloheimo (1974), assuming constant birth and death rate and fixed development time, derived the following formula:-

(d) $b = \log_e [(E^o/N^o) + 1] / D$

E^o = number of eggs in sample

N^o = number of individuals in sample

D = duration of egg development.

Polishchuk (1980) compared three formulae for the calculation of instantaneous birth rates by estimating

birth and death rates in a computer constructed population. The formulae were: Elster's (1954), Leslie's (1948) modified by Polishchuk (1980) and Paloheimo's (1974). He found that the lowest error in both birth and death rates was given by Paloheimo's method and this was used in the present study.

The estimated death rate *d* was calculated as follows:

(e) $d = b-r$

d = estimated instantaneous death rate

b = estimated instantaneous rate of population increase

r = observed instantaneous rate of population increase.

Weekly values of *r*, *b* and *d* were calculated for *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi*. Calculations were made separately for the core and pattern samplers.

The sampling season was divided into four three monthly periods each with an average temperature (p. 159) at which egg development (D) for *D. rostrata* and *L. leydigi* was determined (Table 13). The appropriate value was used in the weekly calculation of *b* for these species.

For *A. affinis* the duration of egg development at

the average temperature of each of the four three monthly periods was calculated from data given by Bottrell (1975a).

The species diversity of the cladoceran community at the River Thames, Twickenham was calculated on a weekly basis during 1982 using the Shannon - Wiener information statistic (H') (Pielou, 1969).

$$H' = -C \sum_{J} P_j \log P_j .$$

where H' = the Shannon - Wiener information statistic calculated for an indefinitely large population.

P_j = the probability that a randomly selected individual will belong to species j.

$\log = \log_2$

C = I

This is a heterogeneity index (Peet, 1974) and combines the richness of the habitat, in terms of numbers of species, and the equitability or evenness with which total abundance is distributed amongst the species. Thus, the greater the number of species present in the habitat and the more equitable the distribution of total abundance among them, the higher will be the species diversity H'.

A weekly measurement of the "evenness" (J^1) of the cladoceran community was obtained using the formula:

$$J^1 = \frac{H^1}{\log_2 S} \qquad \text{(Pielou, 1969)}$$

where H^1 = Shannon - Wiener information statistic.

S = the number of species present in the cladoceran community.

J^1 = "evenness" of the cladoceran community.

Species diversity and evenness were calculated using data from the pattern sampler series, excepting *Iliocryptus sordidus*, for which data from the core sampler series had to be used (P. 38).

The weekly length distributions in the populations of *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi* were determined: this information was required for production estimates. The range of length for a given species was divided into size classes of 0.05mm (Appendix XIII, Tables i, ii and iii). For each sample one hundred individuals of each of the three species were measured and placed in the relevant length class. Figure 2 shows the method of measuring length. This classification was carried out on individuals collected with the pattern sampler only.

SECTION 4.2. Sampling programme

In 1981 a preliminary study was initiated at the sampling site to determine:-

(i) cladoceran species present

(ii) approximate numbers that might be expected to occur

(iii) spatial distributions of the cladoceran population

Knowledge of these was required before a sampling programme could be planned.

Each action of the corer or of each funnel in the pattern sampler removes a sample unit from the substrate. A sample comprises a group of sample units. These are of equal size and have been taken within a short period of time.

In 1981 sixteen samples were taken with the pattern sampler at intervals from May through to October, and ten samples with the corer at intervals from July through to November. These indicated that the populations of benthic cladocerans had contagious distributions, the variances of the samples being significantly greater than the means (Elliott, 1977) (see Appendix I).

Elliott (1977) suggests several points which should be considered when planning a sampling programme:-

1. Dimensions of the sampling unit

Finney (1946) states that when a contagious distribution is present there are several reasons why

a small sample unit is more efficient than a larger one. More sample units can be taken for the same amount of labour in dealing with the catch and a sample of many small units has more degrees of freedom than a sample of a few large units, the statistical error is thus reduced. Many small units cover a wider range of the habitat than a few large units and, therefore, are more representative. However, with small sample units, the sampling error at the edge of the unit is proportionately greater (Elliott, 1977).

A sample unit in the core sample series sampled a surface area of substrate of $1.76cm^2$.

A sample unit in the pattern sample series sampled a surface area of substrate of $64cm^2$.

2. Number of sampling units in each sample

Elliott (1977) suggests that for contagious distributions small samples are statistically inaccurate and that, where possible, sample size (n) should be greater than fifty. This is possible with core samples since only a small amount of mud is obtained per core but with the pattern sampler, a sample of this size would take too long to count and identify. Sample size (number of sample units) can be calculated for a specified degree of precision using a formula given by Elliott (1977). He considers that a standard error equal to 20% of the mean is reasonable for most bottom samples and this value was adopted. Thus the ratio of standard error to arithmetic

mean, the index of precision, D, is 0.2 and the number of sample units in a random sample needed to give this degree of precision is:-

$$n = \frac{s^2}{D^2\bar{x}^2} = \frac{s^2}{0.2^2\bar{x}^2} = \frac{25s^2}{\bar{x}^2}$$ for a 20% standard error (Elliott, 1977)

s^2 = variance

$\bar{x}$ = mean

n = number of sampling units required to obtain the necessary degree of precision

D = index of precision

Using data obtained with the pattern sampler from the preliminary study, it was found that n for the pattern sampler varied from two to thirty-six throughout the year, being at a minimum during periods of peak abundance. A value of n = 36 occurred only once, the remaining values were all under twenty-five. To allow for losses during sampling and the possibility that maximum n may vary from season to season, thirty-two sample units were taken per sample with the pattern sample. Fifty-one sample units were taken per sample with the corer.

3. Location of sampling units in the sampling area

Random sampling was employed for both the core and pattern sampler series as this was a prerequisite for many of the statistical methods used. To take a random sample, the sample area must be divided into quadrats each of

which is the area of a sample unit. From this large number of sample units a small number is selected to form the sample. Selection must take place without bias using a table of random numbers. In the present study, it was clearly impracticable to divide the sample area into quadrats the size of a sample unit of the core sampler series. Instead the study area was divided into a two-dimensional grid, each square being equal to $1m^2$. The squares on two adjacent sides of the grid were numbered and so each square in the grid could be located by a pair of coordinates. Random numbers from Fisher and Yates (1963) were taken in pairs and these were used as coordinates to locate the square within which a sample unit of the core sample or pattern sampler series was then taken. Permanent numbered markers were placed at metre intervals along the floating jetty lying parallel to the river bank and along the punts lying at right angles to the bank to facilitate locating the desired squares (Fig. 1).

Each pattern sampler contains sixteen funnels, each of which constitutes a sample unit. However, each funnel is attached to fifteen other functional sample units and therefore each sample unit in the sample cannot be placed randomly within the sample area. To determine whether the funnels in the pattern sampler could be considered independent of each other, a sample was collected consisting of sixteen sample units from a complete pattern sampler (that is, each sample unit was attached to fifteen functional

others). A second sample of sixteen sample units was taken, in which each sample unit was collected using a pattern sampler with only one functional funnel placed at random in the matrix. On both occasions the pattern sampler was placed randomly in the sample area. Appendix II shows the results of a comparison of the variances (F-test) and means (t-test) of the two samples. Differences were not significant at the 5% level, thus the sample units taken from the complete pattern sampler can be considered to be independent of each other.

To collect a sample of the pattern sample series, four pattern samplers, each with eight functional funnels, thirty-two in total, were placed randomly in the sample area as described above. They were set down at 2000 hours and lifted at 0800 hours.

Sampling with the corer always took place at slack water (p. 21), when the water was shallow enough for samples to be collected. The state of the tidal cycle was not taken into account when placing the pattern samplers.

4. Frequency of sampling

The objectives of the present study are such that the site must be sampled as frequently as is practicable. Thus from May to mid-October inclusive, the corer and pattern samplers were used to take samples at weekly intervals. Before and after these dates sampling occurred less frequently, temperatures were lower and thus cladoceran

rates of development were slower. Qualitative samples were taken in December 1981 and January 1982 to determine the presence or absence of species belonging to the cladoceran community.

SECTION 4.3. Measurements of food available to the benthic cladoceran community

Initially it was intended to measure the seasonal changes in the abundance of food available to the benthic cladocerans at the sampling site. Examination of live animals showed that guts were full of a light brown material with an occasional greenish tinge. Fryer (1968) has shown that the guts of many Chydoridae are full of detritus, algae, diatoms and inorganic matter. Smirnov (1962), Keen (1967) and Bottrell (1977) also state that chydorids feed on detritus. However, the nutritional value of the various components in the ingested mass is not known. Smirnov (1962) suggests that bacteria associated with the detritus may be important in the diet of *Eurycercus lamellatus* and thus an attempt was made to estimate microbial numbers (p. 52). As it is not known which components are assimilated, the changes in abundance of assimilated materials throughout the sampling season cannot be measured and related to chydorid abundance.

A crude estimate of fluctuations in total organic matter present in the habitat can be obtained by weekly measurements of percentage organic content of the sediment. A significant positive correlation between this and chydorid abundance might indicate that food present in the detritus could become limited. Goulden (1971) suggests that only the sediment fraction comprising particles of diameter less than 72μm serves as food for benthic cladocerans. I have,

however, frequently seen chydorids, especially *Pleuroxus* spp., settle and apparently feed on large aggregates of particles and so it was decided to include the whole range of particle sizes, apart from macrodebris such as leaves and twigs, in the percentage organic content determinations.

An indication of the abundance of epipelic algae (associations present on and in the surface sediment) and diatoms throughout the year can be obtained by weekly measurements of chlorophyll a. Dead and dying algae may also be an important food source and their abundance can be estimated by measurement of the degredation products of chlorophyll, the phaeopigments. A significant positive correlation between fluctuations in abundance of chlorophyll a or phaeopigments and in chydorids may suggest that epipelic algae and diatoms are a limiting food source.

MICROBIAL NUMBERS

Estimates of the microbial numbers in the sampling site substrate were made during the beginning of the 1982 season to see if there was a significant correlation between these and chydorid abundance. The plate count method of Sorokin and Kadota (1972) was used. In this, the number of micro-organisms in a sample is derived from the number of colonies which ultimately grow on a plate. This technique has several limitations and essentially gives a relative number of limited groups of heterotrophic micro-organisms.

Samples of substrate were taken using sterilised

glass corers. Each corer sampled a volume of sediment of $7cm^3$ and three such cores comprised one sample. A series of dilutions were made with each core using sterilised river water as the diluent (Sorokin and Kadota 1972). Aliquots of the 10^{-4}, 10^{-5} and 10^{-6} dilutions were spread over pre- dried nutrient broth agar using the techniques described by Sorokin and Kadota (1972). For each dilution nine plates were innoculated, three plates were incubated at each of three temperatures (15^{o}, 20^{o} and $25^{o}C$). Three control plates were spread with aliquots of sterile diluent and incubated at $15^{o}C$. The plates were examined after two and five days and the number of colonies growing on and in the agar counted. Based on these counts the number of viable cells is calculated per unit volume of sediment.

Despite repeated attempts, consistent results with this method were never obtained and as it proved very time-consuming the attempt to estimate microbial numbers was abandoned.

PERCENTAGE ORGANIC CONTENT OF THE SUBSTRATE

Six samples of detritus were collected at the same time as the core sample. Approximately 30 - $50ml^3$ of mud was obtained by scooping a plastic bag through the top 2cm of the substrate. Each sample was passed through a 2mm sieve to remove macrodebris: the remaining detritus was dried overnight at $105^{o}C$ and weighed (dry weight). It was then burned at $500^{o}C$ for two hours, cooled in a desiccator and reweighed (ash free dry weight). Subtracting the latter

from the former value and multiplying by a hundred gave the percentage organic content of the sample. Mean weekly values were calculated.

CHOROPHYLL A AND PHAEOPIGMENT

Degredation products, phaeopigments, arising from dead and moribund algae, are usually present in extracts of chlorophyll derived from epipelic algae (Vollenweider, 1969). Lorenzen (1967) described a method which corrects for the presence of these products by measuring the absorbance of an algal extract before and after acidification, which converts chlorophylls to phaeopigments.

Using this method Vollenweider (1969) derives the following equations:-

(i) μg chlorophyll *a* per sample = 11.9 [2.43(Db-Da)]. (V/L)

(ii) μg phaeopigment per sample = 11.9 (V/L). (1.7Da)-chlorophyll *a*

da = optical density of extract after acidification (at 665nm)

Db = optical density of extract before acidification (at 665nm)

V = volume of solvent used to extract sample in ml.

L = path length of spectrophotometer cell in cm (1cm).

Vollenweider (1969) recommends the use of 90% aqueous acetone shaken up with $MgCo_3$ for pigment extractions, as the spectral properties of the solutions of most of the chlorophylls and their degredation products are well known for this solvent. The use of $MgCo_3$ prevents degredation of the pigments during extraction. A quantity of acetone is used such that the resulting absorbancies are below 0.6.

Accuracy is improved if the absorbance of the initial reading at 665nm is above 0.2 (Vollenweider, 1969).

Five mud cores were collected each week during the 1982 sampling season, using the same corer as described on P. 32 for cladocerans. The contents of each core were washed into a conical flask with 15cm^3 of 90% aqueous acetone (with $MgCO_3$). The flasks were stoppered and shaken mechanically overnight in a cool dark place to assist in extraction of the pigments. The acetone and extracted pigments were then centrifuged to remove any $MgCO_3$ and other suspended particles. Aliquots were taken for spectrophotometric analysis in a PYE UNICAM (SP8100 UV) spectrophotometer.

Absorbance was recorded at 750nm (measure of "background" absorption by other materials) and 665nm. The sample was acidified by adding one to two drops of 1N HCl to the cuvette. This was then shaken and the absorbance at 750nm and 665nm again determined.

The readings obtained at 665nm before and after acidification (corrected by subtracting the relevant 750nm reading) were substituted into equation (i) to find µg chlorophyll *a* per sample. The concentration of phaeopigment per sample was determined using equation (ii).

The mean of the five samples was calculated and the results expressed as mg chlorophyll *a* and mg phaeopigment under a square metre of substrate.

SECTION 4.4. Physico-chemical determinations at the sampling site

TEMPERATURE

Temperature was measured twice weekly throughout the 1982 sampling season using a mercury thermometer accurate to $\pm$ 0.5°C. Readings were taken the evening of one day and the following morning.

One reading was always taken at slack water, that is, when the substrate was most exposed to the influence of air temperature and the other when there was some depth of water over the substrate. Both readings were taken with the tip of the thermometer touching the substrate surface.

CHLORIDE

The River Thames is semi-tidal at Twickenham (p. 21), thus it is possible that a layer of heavier saline water underlies the freshwater and that this might affect the community of benthic cladocerans at the site.

On three occasions in 1983, the chloride concentration of the water at the sampling site was analysed. Chloride was measured to enable direct comparison with data supplied for Teddington weir by the Thames Water Authority.

Samples were taken on 23.2.83, 21.4.83 (neap tides) and 12.7.83 (spring tide) at hourly intervals throughout a tidal cycle. Water samples were taken in 500ml stoppered

bottles from different areas of the site and, unless otherwise stated, one sample comprised 3 x 500ml. Each bottle was weighted and lowered to just above the surface of the substrate, the stopper was removed and the bottle allowed to fill with water before retrieval. In the laboratory, the contents of each bottle were filtered through a membrane filter (0.5µm pores) to remove particulate matter (Golterman, 1969). Samples were analysed within 24 hours of collection.

100ml from each of the three 500ml bottles comprising a sample were analysed for chloride concentration using the method described by Golterman (1969) (see Appendix III for details of method). The mean chloride concentration for each hour was then calculated.

CURRENT VELOCITY

Current velocity was determined on two separate occasions using an OTT current meter, type "10.152".

Velocity was measured at a depth of 0.5 metres halfway along the punts lying at right-angles to the bank (Fig. 1). Measurements were taken at half hourly intervals for one hour either side of the high tide. Three measurements were taken at each sampling time and the average recorded.

PARTICLE SIZE ANALYSIS OF THE SUBSTRATE

It has long been recognised that the nature of the substrate is of the greatest importance in determining the

composition of the bottom flora and fauna (Morgans, 1956). The range of particle size of the sediment at the site was analysed for comparison with other studies.

Pretreatment of the sediment sample, to break down aggregates (crumbs) of substrate into their constituent particles, is inappropriate for ecological studies (Morgans, 1956). These studies require information on the substrate as it is experienced by the benthos. Lenhard (1966) supports this view although Holme and McIntyre (1971) give details of pretreatment methods.

An initial splitting of the sediment, by wet sieving, into a sand fraction (particles greater than 62μm and less than 2mm diameter) and a silt/clay subsieve fraction (particles less than 62μm diameter), is recommended by Morgans (1956). Lenhard (1966), however, suggests that a certain amount of crumb breakdown will occur even when conventional wet sieving, without pretreatment, is applied.

Following wet sieving, the sand fraction was analysed by mechanical sieving through a bank of sieves as recommended by Morgans (1956) and Holme and McIntyre (1971). The subsieve fraction (silt/clay) can then be graded by pipette analysis which is a method of sedimentation analysis (Holme and McIntyre, 1971). This method depends on the principle that, in a given time, large particles will fall faster through a column of distilled water than small ones. Holme and McIntyre (1971) give a table of settling times at 20°C (Table 1).

TABLE 1 : Time taken for particles of known diameter to fall through a given distance in a column of distilled water at 20°C (from Holme and McIntyre, 1971)

Particle diameter (mm)	Settling distance (cm) through a column of distilled water	Time taken for a particle of a given size to fall through a given distance		
		Hours	Minutes	Seconds
0.0625	20	-	-	58
0.0312	10	-	1	56
0.0156	10	-	7	44
0.0078	10	-	31	0
0.0039	10	2	3	0

In this study the following procedure was adopted:-

Five sediment cores were taken on 16.5.83, each sampling a surface area of 62.3cm^2 and penetrating the sediment to a depth of 4cm. Processing of the samples began within 2 hours of collection. The substrate from each core was processed separately and mean values calculated at the end of the analysis. There was no pre-treatment. The sediment from each core was split into a sand fraction and a silt/clay fraction by wet sieving through a 62μm sieve (Morgans, 1956).

The sand fraction retained by the sieve was oven dried at 100°C, again sieved through a 62μm sieve, and any

materials passing through added to the silt/clay fraction. Material retained on the sieve (sand fraction) was passed through a bank of Endecott squaremeshed test sieves with appertures 1000, 500, 250, 125 and 62μm (equivalent to 0, 1, 2, 3 and 4 on the phi scale) using an Endecott test sieve shaker for twenty minutes. The various sand fractions were gently brushed into clean dry containers and later weighed.

The subsieve, silt/clay fraction was divided into three grades, namely coarse silt (particles with 62μm - 15.6μm diameter), fine silt (15.6μm - 3.9μm) and clay (below 3.9μm) using the method of pipette analysis described by Holme and McIntyre (1971). The entire fraction was transfered to a 1 litre stoppered measuring cylinder and made up to 1 litre with distilled water. This was placed in a water bath at 20°C and left to equilibrate, since variations in temperature can lead to serious errors in pipette analysis (Holme and McIntyre, 1971). The cylinder was shaken until the particles were judged to be uniformly distributed, and then placed upright in the waterbath and a stopwatch started. At this moment, all the particles start to fall through the water column under the influence of gravity and at the settling velocities appropriate to their individual diameters. Three samples were then withdrawn at precise time intervals, and from precise depths in the column, using a 20ml pipette whose stem was clearly marked at 10 and 20cm from the tip. Approximately 30cm of flexible rubber tubing was attached to the other end and

the pipette was lowered very gently into the cylinder, to the appropriate mark on the stem, just before the precise moment of sampling. At the precise time, an even suction was applied by the mouth through the rubber tubing until the pipette was full. The tube was pinched shut and the pipette removed from the cylinder. The 20ml sample was transfered to a preweighed dish, dried at 100°C and accurately weighed. The material in the measuring cylinder was then resuspended, replaced in the water bath and the stopwatch restarted.

The time intervals between samples and the depth in the column at which they were taken were as follows:-

Sample	Particle diameter (μm)	Settling distance (cm)	Time		
			Hours	Minutes	Seconds
I	62	20	0	0	0
II	15.6	10	0	7	44
III	3.9	10	2	3	0

The weight of each of the three grades can be found by subtraction, for example Sample I - Sample II (corrected to 1 litre) = weight of coarse silt grade.

Finally, the results of the pipette analyses were combined with the sieve analyses and the weights in each grade expressed as a percentage of the dry weight of the total sample.

The data were analysed using the cumulative frequency curves recommended by Morgans (1956) and Holme and McIntyre (1971).

A graph is constructed with the size of the particle grades (using the phi notation) along the horizontal axis; by convention, the phi values increase positively to the right. The percent cumulative frequency for each grade is plotted.

Three attributes of the curve are considered:-

1. A measure of central tendency - the median diameter MdØ. This is determined by reading the phi value corresponding to the point where the 50% line crosses the cumulative curve.

2. A measure of degree of scatter - the phi quartile deviation QDØ. This measures the number of phi units lying between the first and third quartile diameters, that is, between the 25% and 75% points on the cumulative curve. $QD\emptyset = (Q_3\emptyset - Q_1\emptyset)/2$. A sediment with a small spread between the quartiles is regarded as well sorted.

3. A measure of the degree of assymmetry - the phi quartile skewness $Skq\emptyset = [(Q_1\emptyset + Q_3\emptyset)/2] - Md\emptyset$. Negative values suggest that small particles are better sorted than large ones while positive values suggest that the reverse is true.

SECTION 4.5. Biotic determinations at the sampling site

PLANKTON SAMPLES

Plankton samples were taken within the sampling site to determine whether cladocerans characteristic of the benthos also occurred in large numbers in the water column. The plankton samples also indicated whether the river water used to fill the collecting bottles on the pattern samplers (p. 37) contained benthic cladocerans.

Samples were taken at monthly intervals throughout the sampling season. A Hydro-bios 1 litre water sampler was used to take 10 x 1 litre samples just above the substrate at the sampling site. On retrieval, the sample was screened through an 80µm mesh net, the contents of which were preserved in 4% formalin and later examined under a dissecting microscope.

A total of 90 x 1 litre water samples were examined and from these a total of six chydorid cladocerans were obtained (two *Leydigia leydigi*, three *Disparalona rostrata* and one *Alona affinis*). Planktonic cladocerans belonging to the Daphnidae and Bosminidae were also occasionally found. Thus it may be said that the benthic cladocerans found at the sampling site very rarely occur in the water column and that the results from the pattern sampler will not be affected by the use of river water to fill the collecting bottles.

FISH GUTS

Studies on the River Thames at Reading have shown that chydorid cladocerans are an important source of energy for young fish (Berrie, 1972). During the summer months, young fish were frequently seen at the sampling site and were examined at intervals to determine whether cladocerans formed part of their diet and if so:-

a) which species were taken and in what numbers.
b) species of fish.
c) size group of fish.

Fish were caught using a 2mm or 5mm mesh net and placed in 40% formalin immediately after capture. This kills rapidly and, as the fish gasp several times before death, formalin is drawn into the gut thus preserving its contents. No regurgitation or defaecation was observed. For each sample of fish, a few were examined live and identified using keys by Bracken and Kennedy (1967), Bagenal (1973) and Maitland (1972). This was necessary, as the keys used made considerable use of pigment distribution as a diagnostic factor. Fork lengths were measured to the nearest 0.5mm except in the case of fry (caudal fins unforked) when total length was measured. The gut was removed, slit open and the contents washed into a dish and examined under a dissecting microscope. All cladocerans and cladoceran carapaces were identified and counted.

SECTION 4.6. Affect of preservation on the length of chydorid cladocerans

Absolute alcohol was used to preserve chydorids collected by the pattern sampler (p. 38) and three or four months frequently elapsed before chydorids thus preserved were finally identified and measured. Absolute alcohol is known to have a 'ballooning' effect on the carapaces of some planktonic cladocerans resulting in loss of eggs from the brood chamber and difficulty in making adequate length measurements.

In order to determine whether 'ballooning' and shrinkage of the carapace took place in chydorid cladocerans, the following test was initiated. Populations of each of the three major species (*Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi*) were cultured in the laboratory (Chapter 9). An individual selected from such a population was categorised and measured to the nearest 0.007mm, it was then preserved in absolute alcohol and stored in a separate vial on which was recorded the date of preservation, species, live length and whether eggs were present in the brood chamber. After four to six months (the maximum time for which pattern sampler collections were stored) the vial was opened and the individual re-measured and the presence or absence of eggs noted.

Thirty individuals (ten juveniles and twenty adults) of each of the three species were examined in this way.

A t-test (as in Appendix IX) was computed for each species to determine whether live measurements for length were significantly different from measurements of length after preservation, the results (*A. affinis* t = 0.5143, *L. leydigi* t = 0.0394 and *D. rostrata* t = 0.2147 with 58 degrees of freedom in each case) show that no significant difference occurred at the 5% level of significance. Out of a total of ninety chydorids examined, only two individuals lost their eggs on preservation and thus the chydorid species studied are not generally subject to shrinkage or egg loss when preserved for four to six months in absolute alcohol.

SECTION 4.7. Rivers in southeast England sampled in 1983

Throughout the summer of 1983, a number of rivers in the southeast of England were qualitatively sampled to determine whether any benthic cladocerans were present and, if so, which species. Species lists were then compared to determine whether the riverine benthic association of invertebrates contained a characteristic community of cladocerans.

The samples taken were strictly qualitative, using a small net of mesh size 80µm to collect substrate. At each site the depth of water and type of substrate was noted and every effort was made to sample different types of substrate. The collections from each type of substrate were kept separate. Samples were washed through a 2mm sieve, to remove any macrodebris, and cladocerans extracted using the flotation technique described in Section 4.1.1. and identified to species level.

The following rivers were examined in this way:-

River Chess - Hertfordshire
River Crane - Greater London
River Wey - Surrey
River Cray - Greater London
River Darent - Kent
River Lee - Hertfordshire
River Roding - Essex
River Rother - East Sussex

River Limden - East Sussex

Nunningham Stream - East Sussex

Hugletts Stream - East Sussex

River Cuckmere - East Sussex

At the River Chess, *Cottus gobio* and *Noemacheilus barbatulus* were collected and examined in the same way as the fish from the River Thames (p. 64).

CHAPTER 5 : Comparison of Core and Pattern Samplers

The substrate of the sampling site in the River Thames at Twickenham was an apparently homogenous mud, the river in this area is semi-tidal resulting in one or two feet of water covering the substrate at certain times of the day. Both features of the sampling site are essential for the successful operation of the core sampler, the diameter of the corer is such that it must be used on a substrate of small particle size as the presence of small pebbles would result in it becoming jammed. A shallow depth of water during sampling is essential as the corer is hand operated. The pattern sampler also requires a substrate such as that at the sampling site or dense beds of aquatic vegetation for successful operation. All the edges of each sample unit in the sampler must be in complete contact with the substrate if chydorids are to be sampled effectively (p. 37). The pattern sampler would be unreliable on a substrate such as mud with scattered pebbles. An edge of the sampler might rest on one of these resulting in a gap between sampler and substrate by which chydorids could escape or be prevented from crawling up the sides of the sampler.

Both samplers require a substrate of small particle size and the corer additionally needs a shallow depth of water. They therefore have a limited general application. The pattern sampler could, presumably, be used in waters of far greater depth although a thorough preliminary

examination of the substrate would be necessary and the sampler would have to be placed by a diver to ensure that it was correctly positioned.

One of the reasons for employing the pattern sampler at the Twickenham site was to test its performance in a lotic environment compared to that of the core sampler. To study the chydorid community effectively, samples from the pattern sampler must:-

a) accurately reflect the total number of chydorids present under a unit area of substrate

b) be unbiased regarding chydorid species, that is, the relative abundance of chydorid species found in the sample must reflect that present in the field

c) be unbiased regarding age/size of individuals of a given chydorid species, for example, the percentage of juveniles in a given species population as determined by the pattern sampler must reflect that present in the field.

To determine whether the pattern sampler fulfilled the requirements set out above, the pattern sampler results were compared with those of the core sampler. The latter removed an undisturbed core of mud from the sampling site, therefore, all the cladocerans within that core of mud were also removed and the method of removal was 100% efficient. The efficiency of the method of separating the chydorids from the mud was found to be 95% (p. 35). From 5.5.82 to 24.8.82 inclusive the mean numbers of *Disparalona rostrata, Alona affinis* and *Leydigia leydigi*

obtained by the core and pattern samplers were compared using a t-test preceded by an F test.

The results of this analysis showed clearly that on the majority of sampling dates there is no significant difference, at the 1% level, in the mean numbers of the three major species obtained by the two sampling methods (Appendix IV). This suggests that the pattern sampler adequately samples the chydorid community in terms of total chydorids and relative abundance of individual species.

If the percentage of juveniles and percentage of adult females with eggs in a species population for the core and pattern sampler series from June to October are compared (Appendix VII Tables viii to x) values can be seen to agree to a large extent. The pattern sampler does not seem to select for or against specific stages in a species population.

The comparison of the two sampling methods also reveals a general trend in significant differences in mean numbers of chydorids occurring at periods of low abundance (Appendices IV and VII). On many dates where significant differences were present, the numbers of chydorids under a square metre obtained from the pattern sampler were greater than those from the core sampler (Appendix VII Tables ii to iv). The efficiency of the core sampler, in terms of removing chydorids from the sampling site, is known to be high. This suggests that during periods of low abundance

it must remove too small a surface area of mud, in relation to the size and distribution of the chydorid populations to be a consistently reliable sampler. This failing could be rectified by increasing the number of sample units taken with the core sampler at these times. However, this presupposes a knowledge of patterns of chydorid abundance at a particular sampling site. Alternatively, the diameter of the core sampler could be increased so that a larger area is sampled per core. In either case, the time involved in processing the extra mud would become prohibitive.

The small sampling area of the corer caused a number of problems. At times of low chydorid abundance an entire core sample may yield no more than four or five individuals of a given species. The percentage composition of the given population was then calculated from this very small sample resulting in wide fluctuations from week to week. In the samples from the pattern sampler the chydorids are already separated from the substrate, thus it is possible to make use of a large number of sample units with a larger surface area than those of the corer without involving a prohibitive amount of time and labour. A larger number of individuals are collected resulting in smoother and perhaps more reliable estimates of percentage composition. This was also found to be so for the population dynamics results. The seasonal changes in the observed instantaneous rate of population increase (r) of the *Leydigia leydigi* population calculated using the results

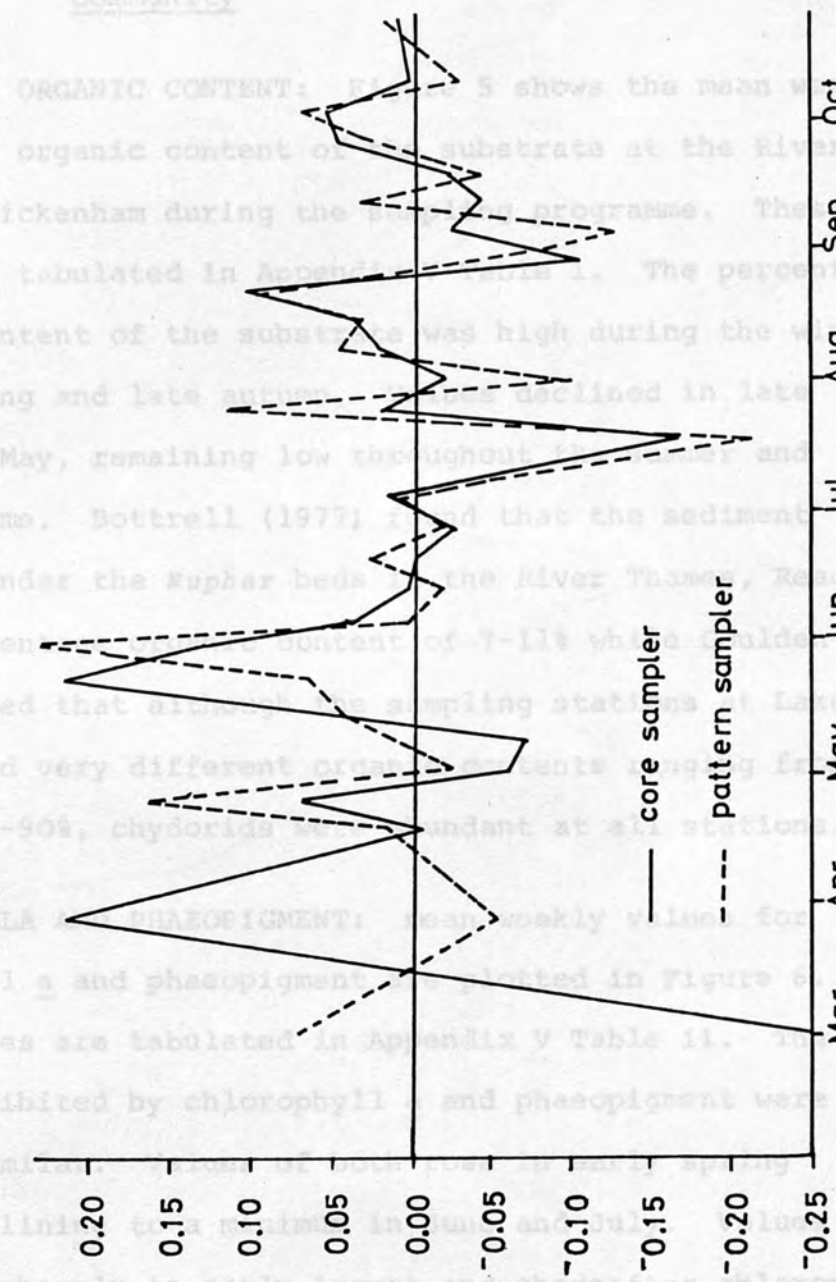
from the core and pattern sampler series are plotted together in Figure 4. This shows the wide fluctuations in the core results and the smoother variations in those from the pattern sampler during the spring when abundance was low. Closer agreement is found during periods of greater abundance.

Thus the results from the pattern and core sampler series agreed well, except during periods of low chydorid abundance when the core sampler series tended to be unreliable. The performance of the pattern sampler was good, it reliably sampled the chydorid community in the River Thames at Twickenham. However, it does not sample the macrothricid *Iliocryptus sordidus* and therefore if the benthic cladoceran community is being studied it must be used in conjunction with a conventional sampler such as a corer.

For the chydorid species, it was decided to present only the results from the pattern sampler series in graphical form in Chapter 6. Results from the core sampler series had to be used for *Iliocryptus sordidus*. Results from both series are tabulated in Appendix VII.

FIGURE 4.

Seasonal changes in the observed instantaneous rate of population increase (r) of the Leydigia leydigi population in the River Thames, Twickenham. Values plotted are obtained from the core and pattern sample series.



CHAPTER 6 : Results

SECTION 6.1. Food available to the benthic cladoceran community

PERCENTAGE ORGANIC CONTENT: Figure 5 shows the mean weekly percentage organic content of the substrate at the River Thames, Twickenham during the sampling programme. These values are tabulated in Appendix V Table i. The percentage organic content of the substrate was high during the winter, early spring and late autumn. Values declined in late April and May, remaining low throughout the summer and early autumn. Bottrell (1977) found that the sediment directly under the *Nuphar* beds in the River Thames, Reading, had a percentage organic content of 7-11% while Goulden (1971) noted that although the sampling stations at Lake Lacawac had very different organic contents ranging from 2-3% to 55-90%, chydorids were abundant at all stations.

CHLOROPHYLLA AND PHAEOPIGMENT: mean weekly values for chlorophyll a and phaeopigment are plotted in Figure 6. These values are tabulated in Appendix V Table ii. The trends exhibited by chlorophyll a and phaeopigment were broadly similar. Values of both rose in early spring before declining to a minimum in June and July. Values increased sharply in early August and thereafter chlorophyll a increased to a maximum in late October while phaeopigment abundance underwent considerable fluctuations before peaking at this time. In the first half of the year phaeopigment was always more abundant than chlorophyll a.

FIGURE 5. Seasonal changes in the percentage organic content of the substrate in the River Thames, Twickenham.

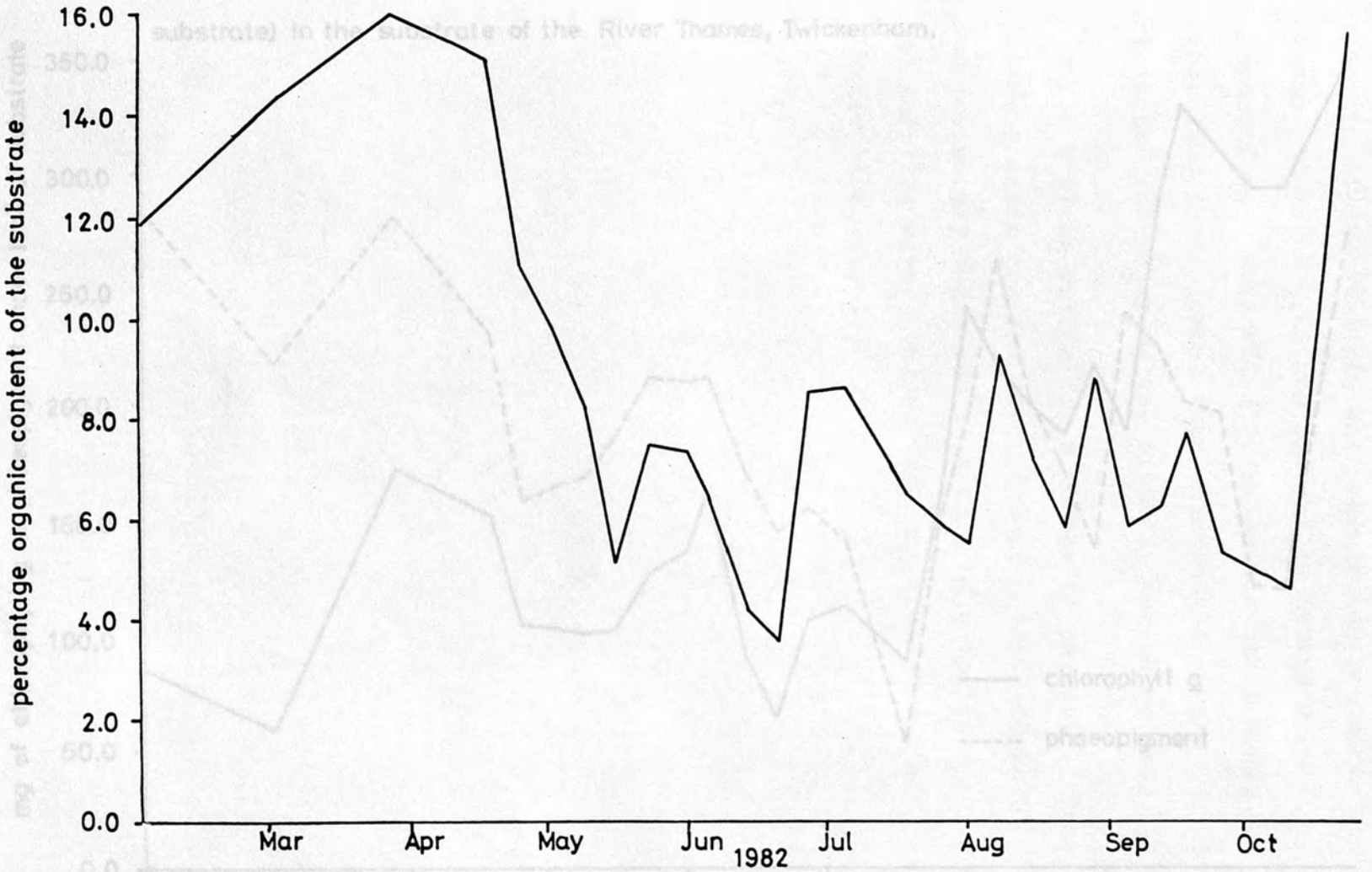
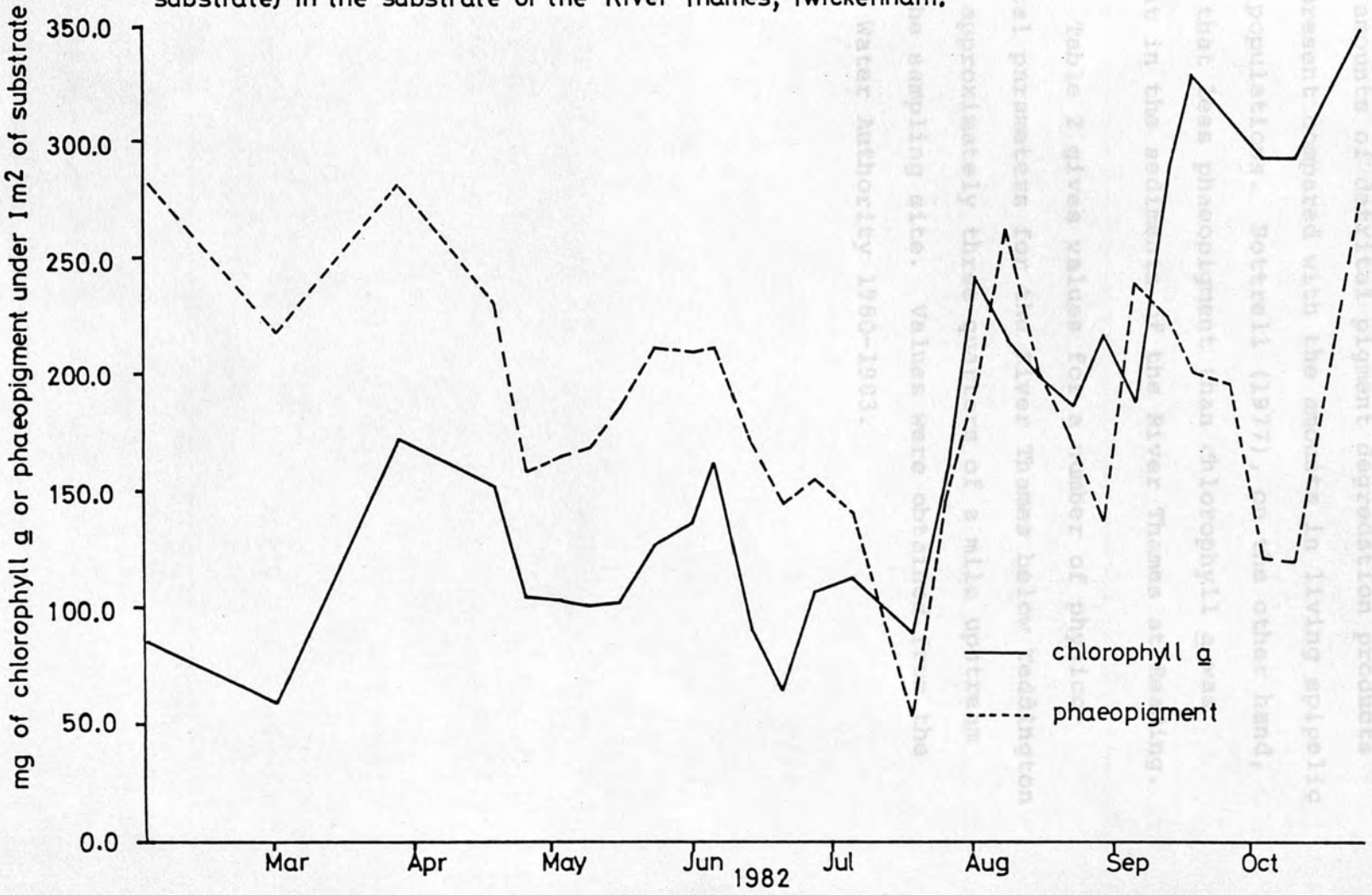


FIGURE 6. Seasonal changes in chlorophyll a (mg under $1 m^2$ of substrate) and phaeopigment (mg under $1 m^2$ of substrate) in the substrate of the River Thames, Twickenham.



Holme and McIntyre (1971) noted that in many sediments large amounts of detrital pigment degredation products were present compared with the amounts in living epipelic algal populations. Bottrell (1977), on the other hand, found that less phaeopigment than chlorophyll a was present in the sediments of the River Thames at Reading.

Table 2 gives values for a number of physico-chemical parameters for the River Thames below Teddington weir, approximately three-quarters of a mile upstream from the sampling site. Values were obtained from the Thames Water Authority 1980-1983.

TABLE 2 : Physico-chemical Parameters of the River Thames at Teddington Weir. (Samples taken downstream of Weir).

Parameter	Number of Observations	Mean	Range
pH	21	8	7.3- 9
Conductivity µS	17	612.941	359 -713
Suspended solids at 105°C	17	16.823	4 - 59
BOD 5 days	17	3	0.3- 6.2
Chloride Mg/l	22	43.9	4.9- 8.8
Alkalinity as * Mg/l $CaCO_3$	52	189.231	137.0-252.0
Phosphate as * Mg/l P	52	1.219	0.44- 2.68

Values for 1980-1983 except those marked with an asterisk where they are for 1982.

Data kindly supplied by the Thames Water Authority.

SECTION 6.2. Physico-chemical determinations at the River Thames, Twickenham

WATER TEMPERATURE: the mean weekly water temperatures for the River Thames at Twickenham are shown in Figure 7 and weekly temperatures in Appendix V Table i. Water temperatures were low in winter rising to a peak in early June (23^{o}C), thereafter temperatures remained high throughout the summer before declining in the autumn. The River Thames rarely ices over in the winter.

CHLORIDE: the results of the determination of chloride concentrations at the sampling site on 23,2.83, 21.4.83 and 12.7.83 are given in Appendix V Table iii. On all occasions values were well below the mean found for the River Thames at Teddington weir (Table 2) and are similar to, or lower than, values found for the Rivers Ray, Coln and Windrush (Table 1A, Thames Water Statistics, 1979). Samples taken just above the substrate and just below the surface on 21.4.83 indicate that for this date at least a layer of heavier saline water was not present over the substrate.

CURRENT VELOCITY: this was determined on two occasions at the River Thames, Twickenham, mean values are shown in Table 3. Results indicate that there is a considerable movement of water over the sampling site.

FIGURE 7. Seasonal changes in mean temperature (°C) at the mud surface in the River Thames, Twickenham.

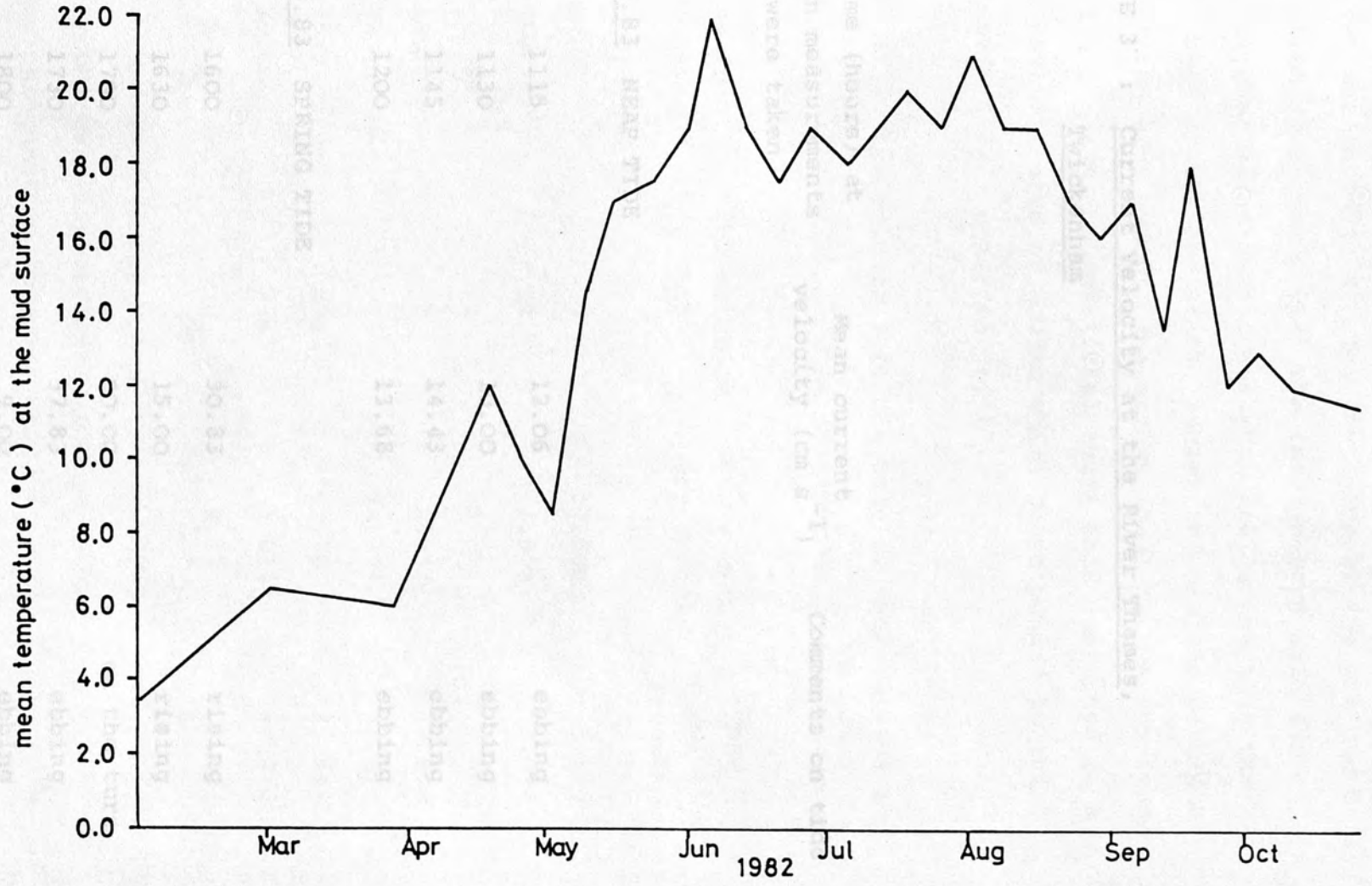


TABLE 3 : Current Velocity at the River Thames, Twickenham

Time (hours) at which measurements were taken	Mean current velocity ($cm\ s^{-1}$)	Comments on tide
24.3.83 NEAP TIDE		
1115	12.06	ebbing
1130	10.00	ebbing
1145	14.43	ebbing
1200	13.68	ebbing
30.3.83 SPRING TIDE		
1600	30.83	rising
1630	15.00	rising
1700	00.00	on the turn
1730	37.83	ebbing
1800	9.00	ebbing
1830	10.66	ebbing

SEDIMENT PARTICLE SIZE ANALYSIS: results of this analysis are set out in Table 4. The low value of the phi quartile deviation (QDØ) shows that the samples were well sorted, the phi quartile skewness was $^{-}$0.3 indicating that the efficiency of sorting of the larger and smaller particles was of the same order. The median (MdØ) of the substrate was 4.43, using Morgans (1956) chart this converted to a mean particle size of 0.05mm which corresponded to the Wentworth (1922) grade of "silt".

TABLE 4 : Analysis of Particle Size of the Sediment at the River Thames, Twickenham.

Particle diameter	Phi notation Ø	Mean % total dry weight	Mean % cumulative frequency
1-2mm	0	0.939	0.939
0.5-1mm	1	1.939	2.878
0.25-0.5mm	2	5.572	8.45
0.125-0.25mm	3	12.054	20.504
0.062-0.125mm	4	14.374	34.878
0.0156-0.062mm	5-6	60.58	95.548
3.9-15.6µm	7-8	1.816	97.274
< 3.9µm	9	2.72	99.994

Median diameter MdØ = 4.43

phi quartile deviation QDØ = 0.7

phi quartile skewness SkqØ = $^{-}$0.3

SECTION 6.3 Biotic determinations at the River Thames, Twickenham.

FISHGUTS: a summary of the results of the River Thames fish gut analysis is presented in Table 5. Fuller details are given in Appendix VI Table i.

All the fry examined live from the River Thames were found to be *Rutilus rutilus* (Roach) and preserved specimens also appeared to belong to this species. Results indicate that fish fry consume considerable numbers of benthic cladocerans. Other major prey items included rotifers (among the smaller fry), copepods, tubificids, small Ephemeroptera nymphs and chironomid larvae. Detritus was also ingested in large amounts. The majority of cladocerans eaten were adults.

The first fry (lengths 1.1-1.3cm) appeared over the sampling site sediments in early June. Gut contents consisted entirely of rotifers and detritus, despite the fact that benthic cladocerans had reached an approximate density of $17{,}000m^{-2}$, suggesting that the cladocerans were too large for fry of this size. At the end of June and in July larger fry were seen over the sampling site (1.5-2.1cm in length). The guts of fry of lengths 1.4-1.8cm contained considerable numbers of *Alona affinis*, *Leydigia leydigi* and *Disparalona rostrata*. Fry over 1.8cm appeared to consume detritus and larger invertebrates such as Ephemeroptera. Cladocerans and copepods were never found.

TABLE 5 : Benthic Cladocerans found in the Guts of *Rutilus rutilus* from the River Thames, Twickenham.

Size group of fish (cm). Number of fish examined in parentheses	Cladoceran species found with the average number found per fish in parentheses
1.1-1.3 (20)	NONE
1.4-1.6 (15)	*Alona affinis* (7.3)
	Leydigia leydigi (0.7)
	Disparalona rostrata (2)
1.7-1.8 (16)	*A. affinis* (5.7)
	L. leydigi (0.5)
> 1.8 (6)	NONE

Two *Gasterosteus aculeatus* (Three-spined sticklebacks) were caught in late July and these had also consumed individuals of the three benthic cladocerans mentioned above.

Towards the end of August the shoals of young fish moved out into the deeper parts of the river and were no longer seen over the sampling site.

The guts of fish occurring in the River Chess, Hertfordshire, were also examined, Appendix VI Table ii. *Noemacheilus barbatulus* (the Stone loach) was found to ingest benthic cladocerans. The number of cladocerans found in the gut decreased with increasing fork length. Guts of *Cottus gobio* (Bullhead) and *Phoxinus phoxinus* (Minnow) were also examined but no cladocerans were found, in the former, invertebrates such as *Gammarus*, chironomids and Ephemeroptera were taken while guts of the latter contained mainly plant material.

SECTION 6.4. Abundance of the benthic cladoceran community in the River Thames, Twickenham

Seasonal changes in the abundance of total chydorids, *Disparalona rostrata, Alona affinis, Leydigia leydigi, Pleuroxus uncinatus* and *Alona rectangula* in the River Thames, Twickenham are shown in Figures 8 to 13. Values are tabulated in Appendix VII, Tables i to vi.

Numbers of total chydorids were low throughout the winter and remained so during the early spring, then increased rapidly in late May and early June resulting in a maximum in late June and early July. This was followed by a sharp fall in numbers to a minimum at the beginning of August. Numbers remained low throughout the late summer and early autumn before increasing to a small peak at the end of October. Winter populations of chydorid species were monitored by qualitative sampling (p. 50).

Disparalona rostrata was absent from the site during the winter and very low numbers were found in the spring. The population increased rapidly in early June to a maximum in late June and early July. A sharp population decline then occurred and numbers reached a minimum in early August. This was followed by an increase in numbers to a much smaller peak in late August. Numbers remained low throughout the autumn.

Numbers of *Alona affinis* were low throughout the winter and early spring. Two population maxima occurred, the first, in early July, was followed by a sharp drop in numbers to a minimum in early August. The second took place in late October.

Numbers in the *Leydigia leydigi* population remained low throughout the winter and early spring. A diffuse population maximum occurred in June and early July, followed by a rapid population decline and thereafter numbers remained low.

The populations of *Pleuroxus uncinatus* and *Alona rectangula* showed similar seasonal trends, both were found sporadically and in very low numbers throughout the winter, spring and summer, the populations began to increase in early autumn. The *A. rectangula* population peaked in mid-October while the population of *P. uncinatus* reached a maximum at the end of October.

Throughout the winter and spring the total chydorid population consisted largely of *Alona affinis* and *Leydigia leydigi* (66% and 26% of the total chydorid population respectively). However, during June, numbers of *Disparalona rostrata* increased rapidly and this species was the largest contributor to the total chydorid midsummer maximum (67%). *D. rostrata* continued to predominate in the chydorid population throughout July, August and early September until the total chydorid

autumn maximum for which population peaks by *Alona affinis* (41% of total population), *A. rectangula* (12%) and *Pleuroxus uncinatus* (11%) were responsible.

Seasonal changes in the abundance of *Iliocryptus sordidus*, the only member of the Macrothricidae occurring in any numbers at the sampling site, are shown in Figure 14 and tabulated in Appendix VII Table vii. As *I. sordidus* cannot be sampled with the pattern sampler (p. 38) data were obtained solely from the series of core samples.

The pattern of seasonal abundance for this species differed considerably from that found among the chydorids at the sampling site. The population oscillated in the first half of the year with small peaks in mid-April and June. Beginning in August the population increased slowly to reach a peak in mid-October before declining.

FIGURE 8. Seasonal changes in the numbers of total chydorids under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

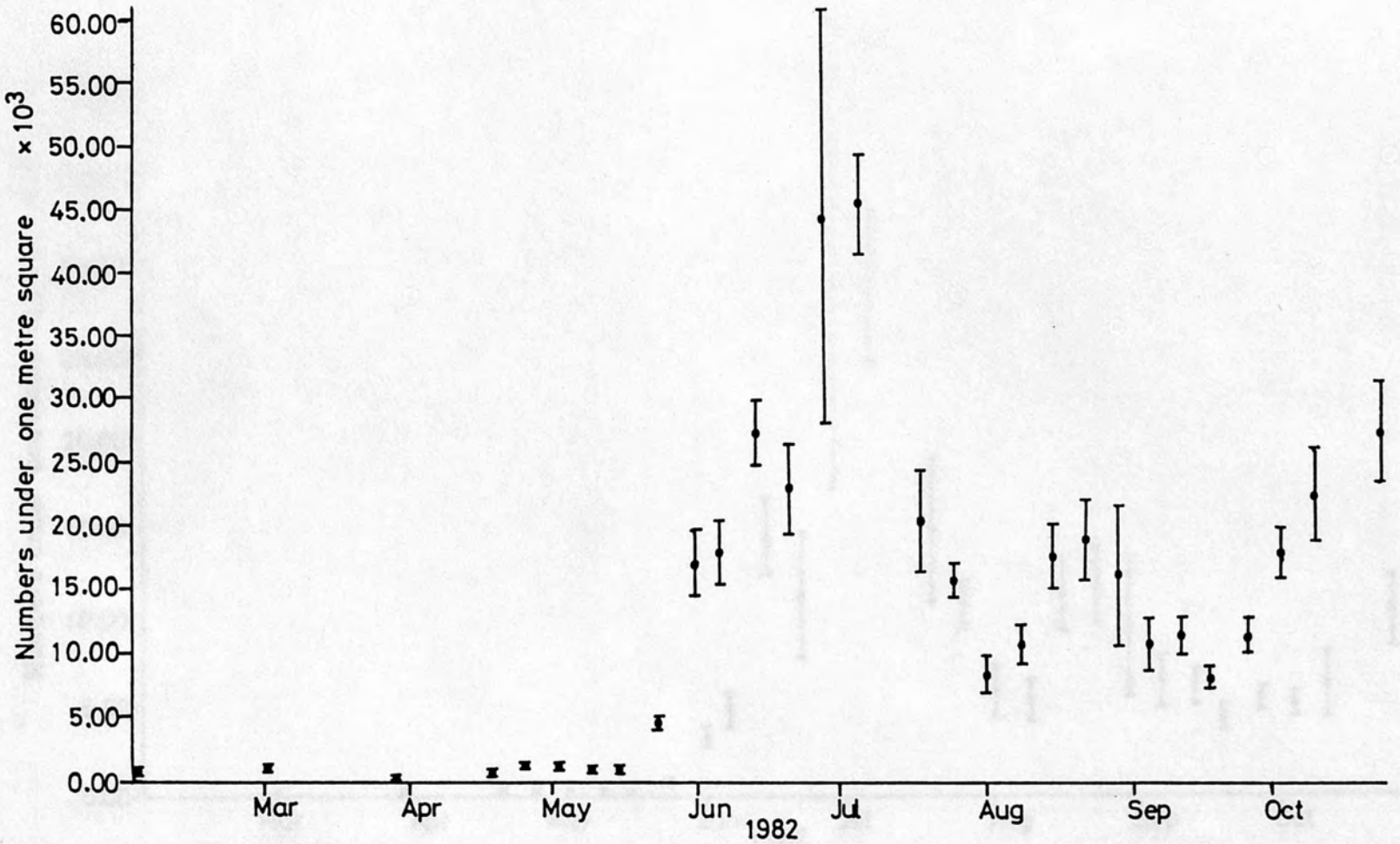


FIGURE 9. Seasonal changes in the numbers of Disparalona rostrata under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

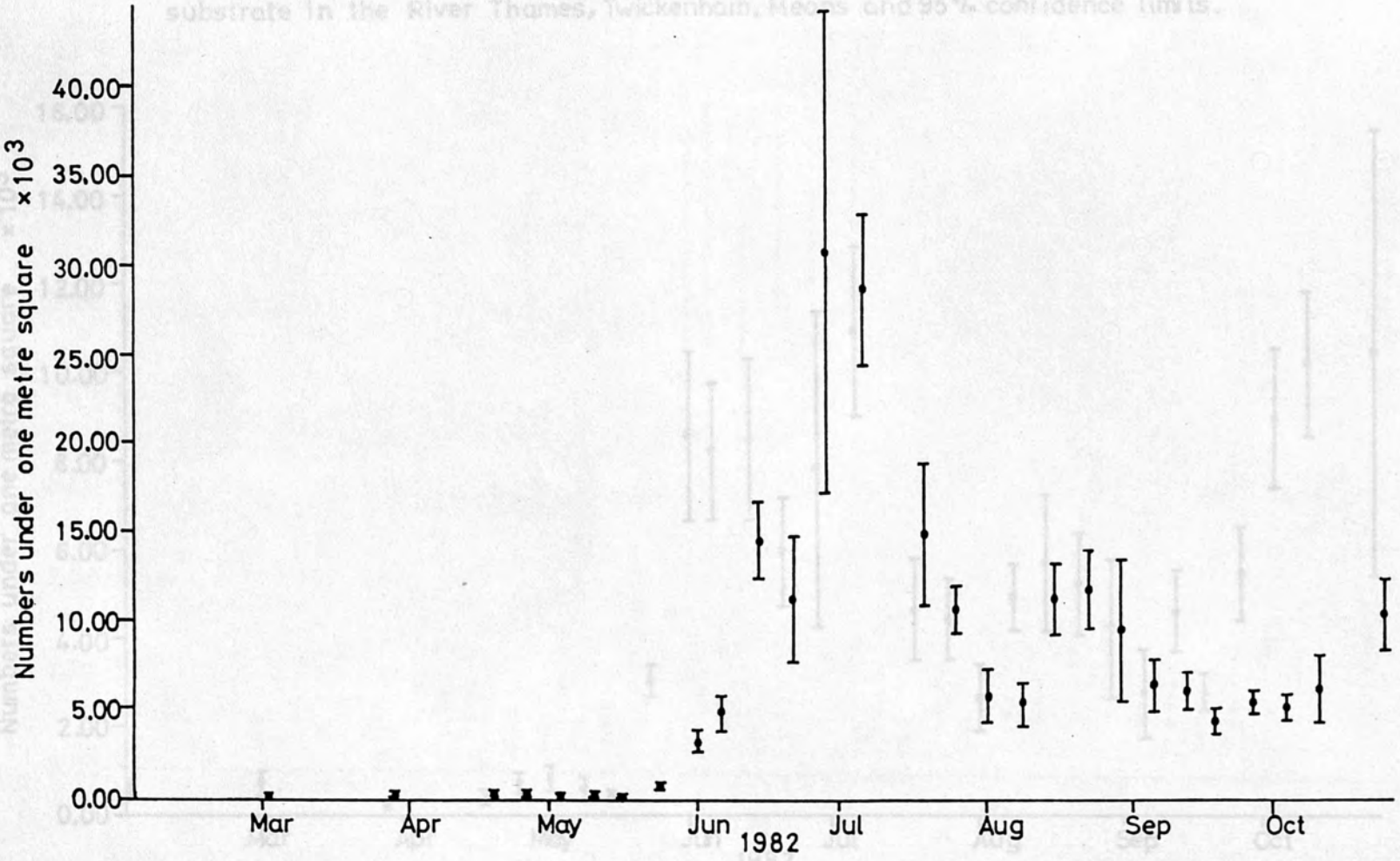


FIGURE 10. Seasonal changes in the numbers of Alona affinis under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

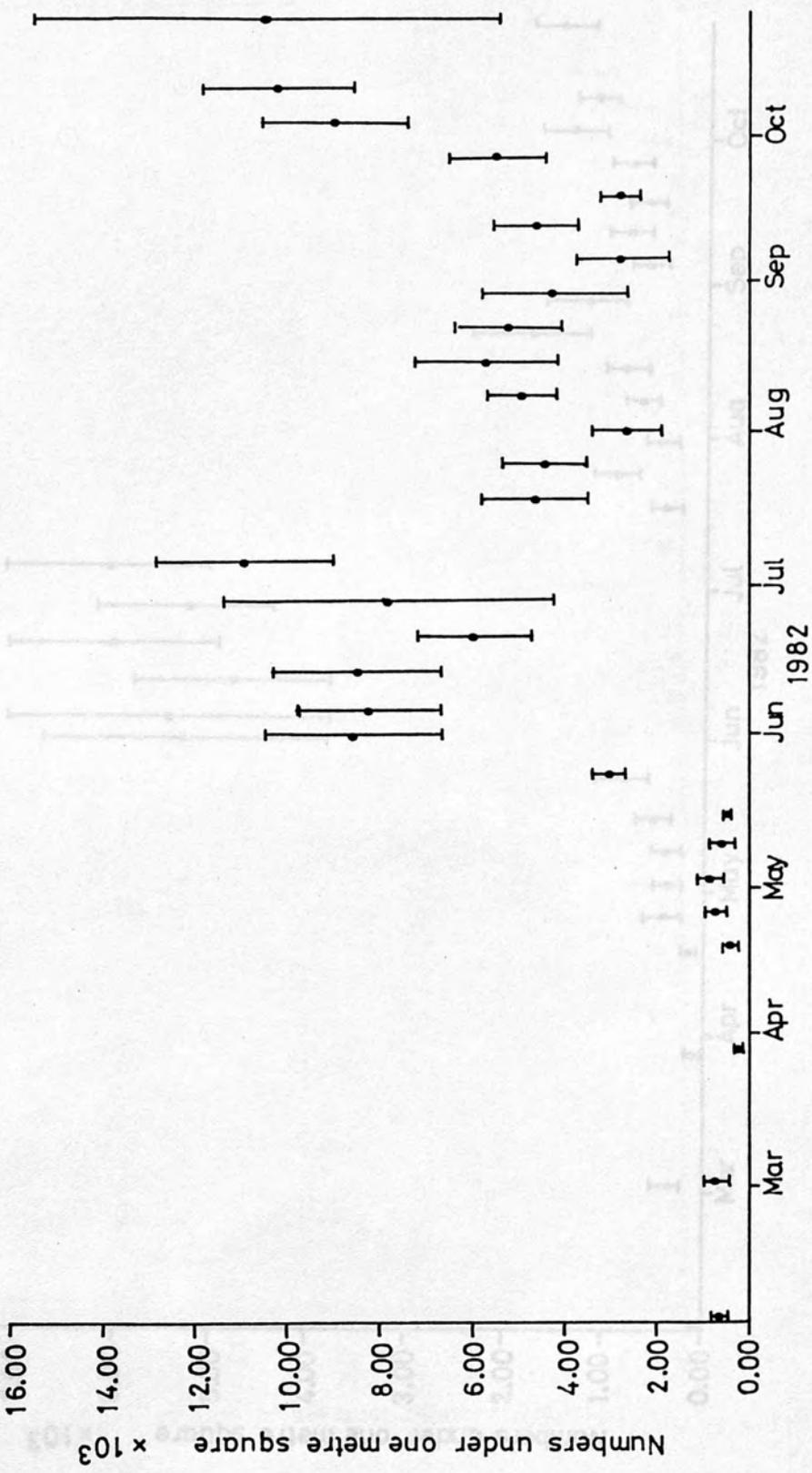


FIGURE 11. Seasonal changes in the numbers of Leydigia leydigi under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

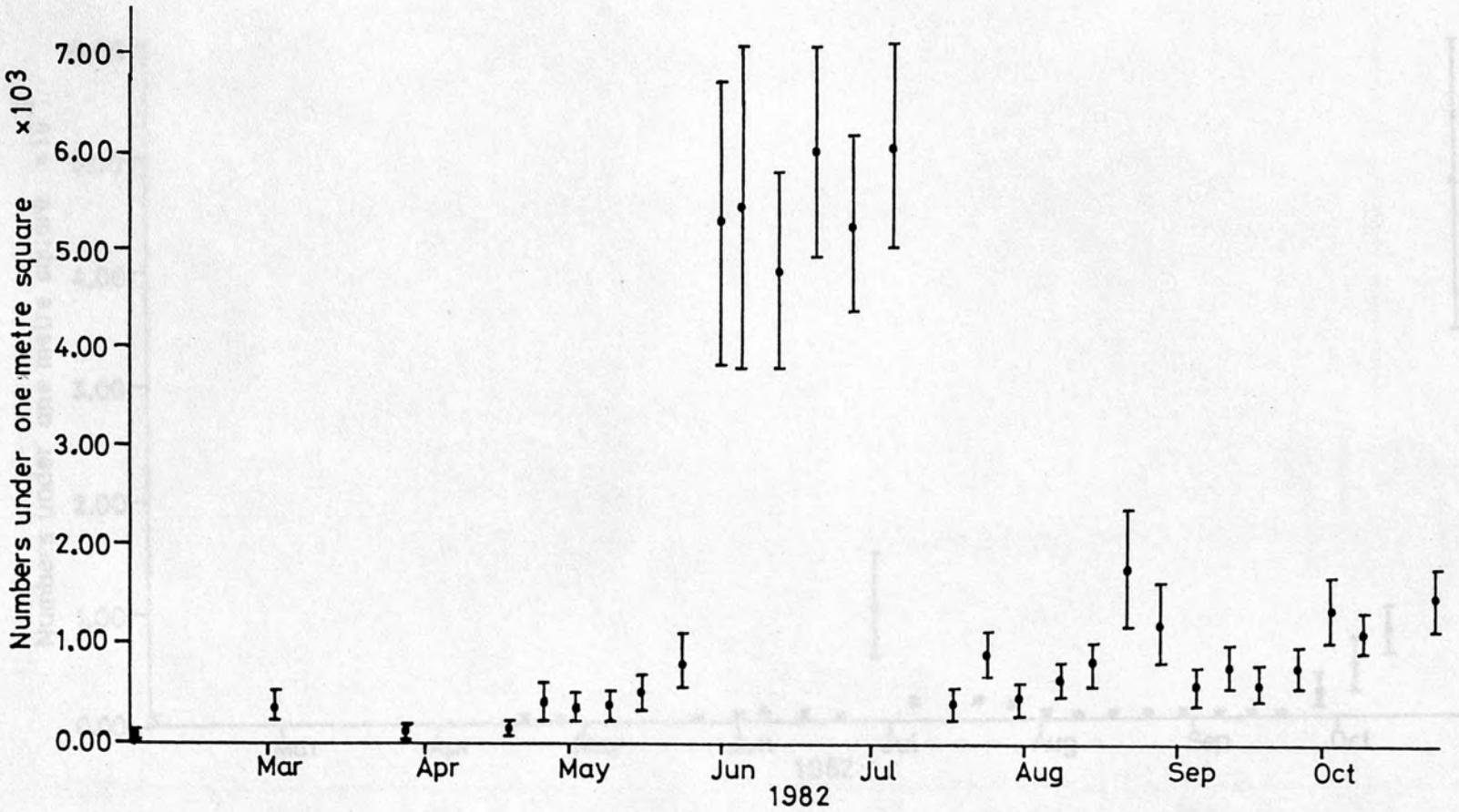


FIGURE 12. Seasonal changes in the numbers of Pleuroxus uncinatus under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

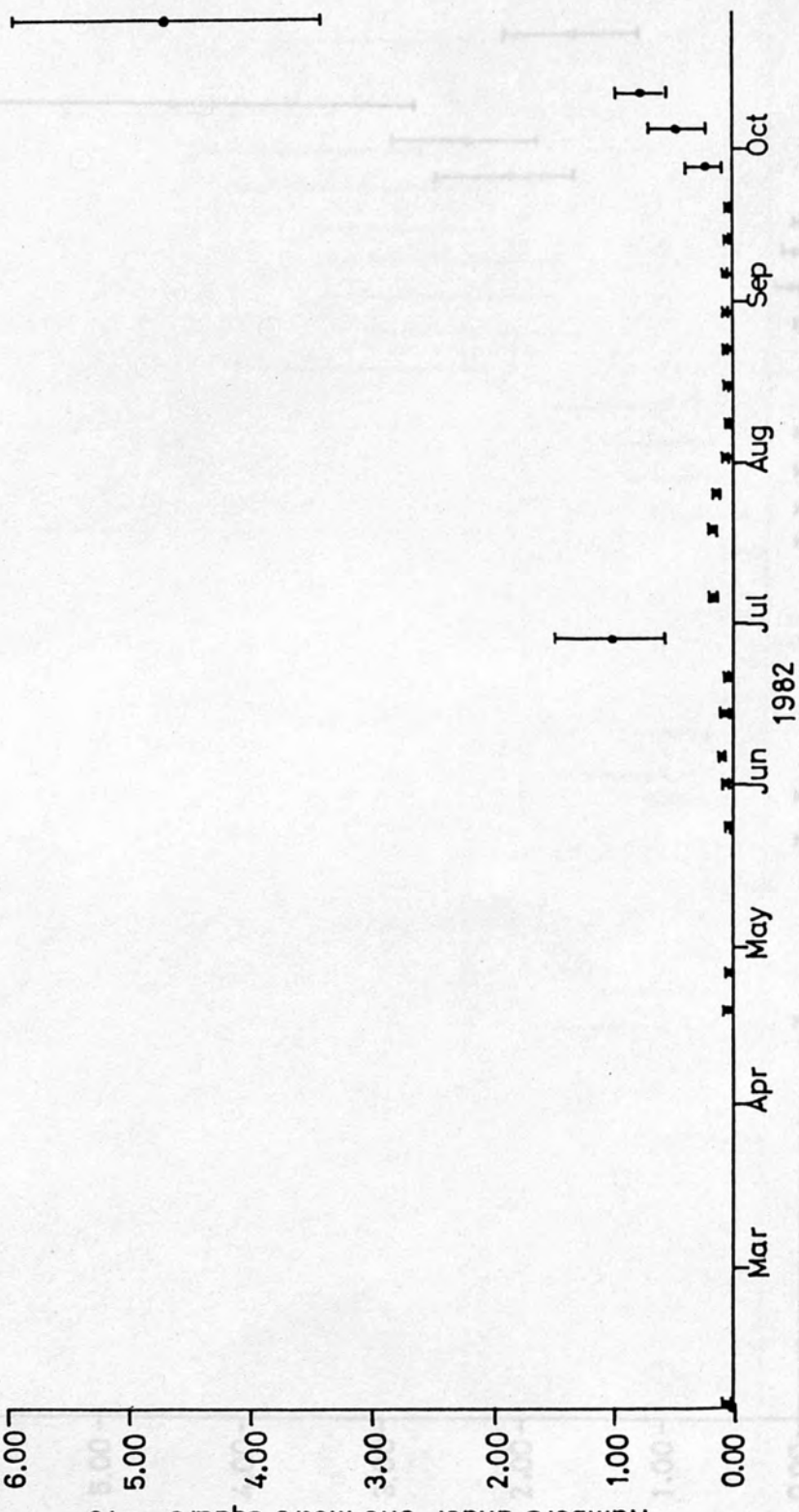
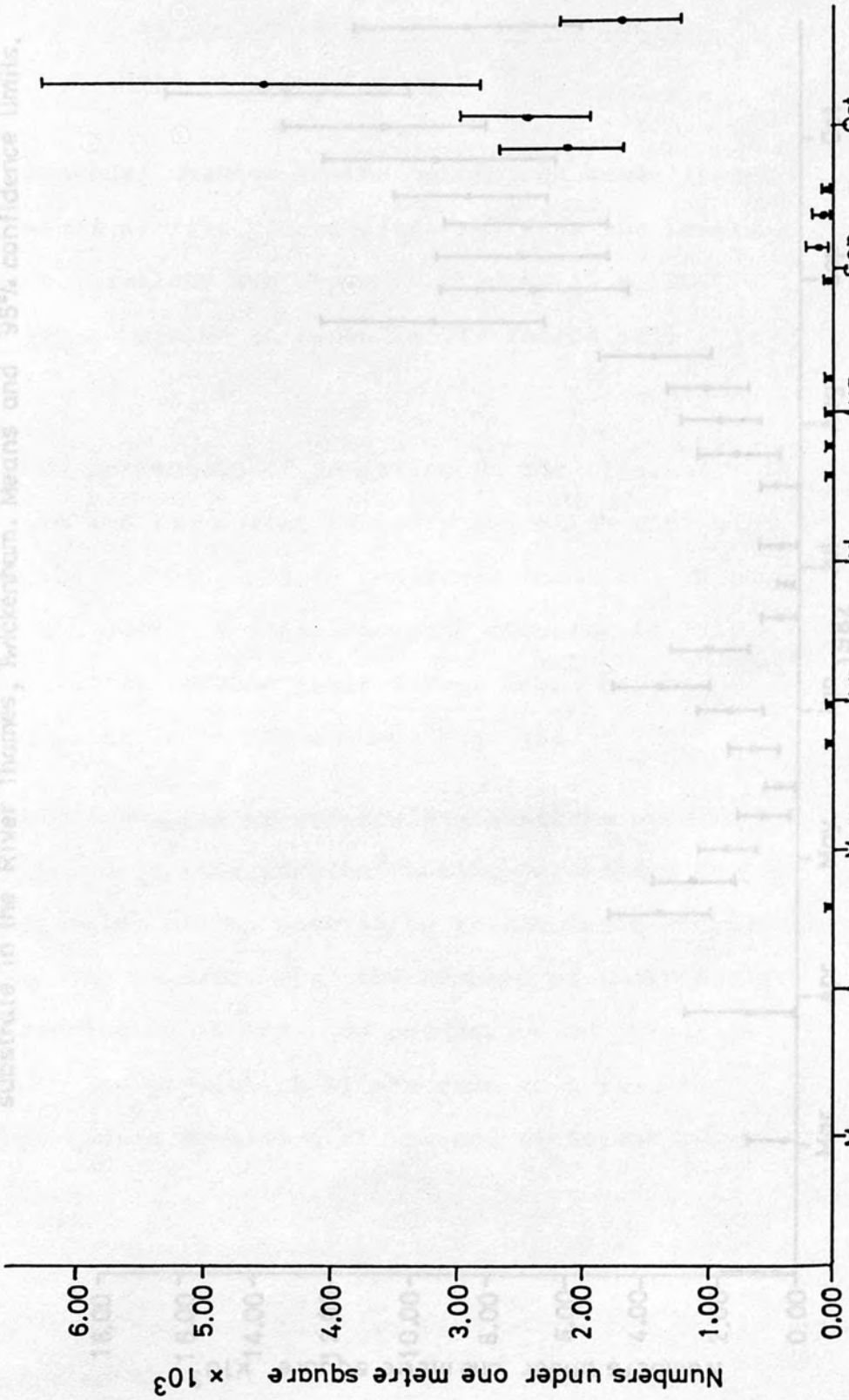


FIGURE 13. Seasonal changes in the numbers of Alona rectangula under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.



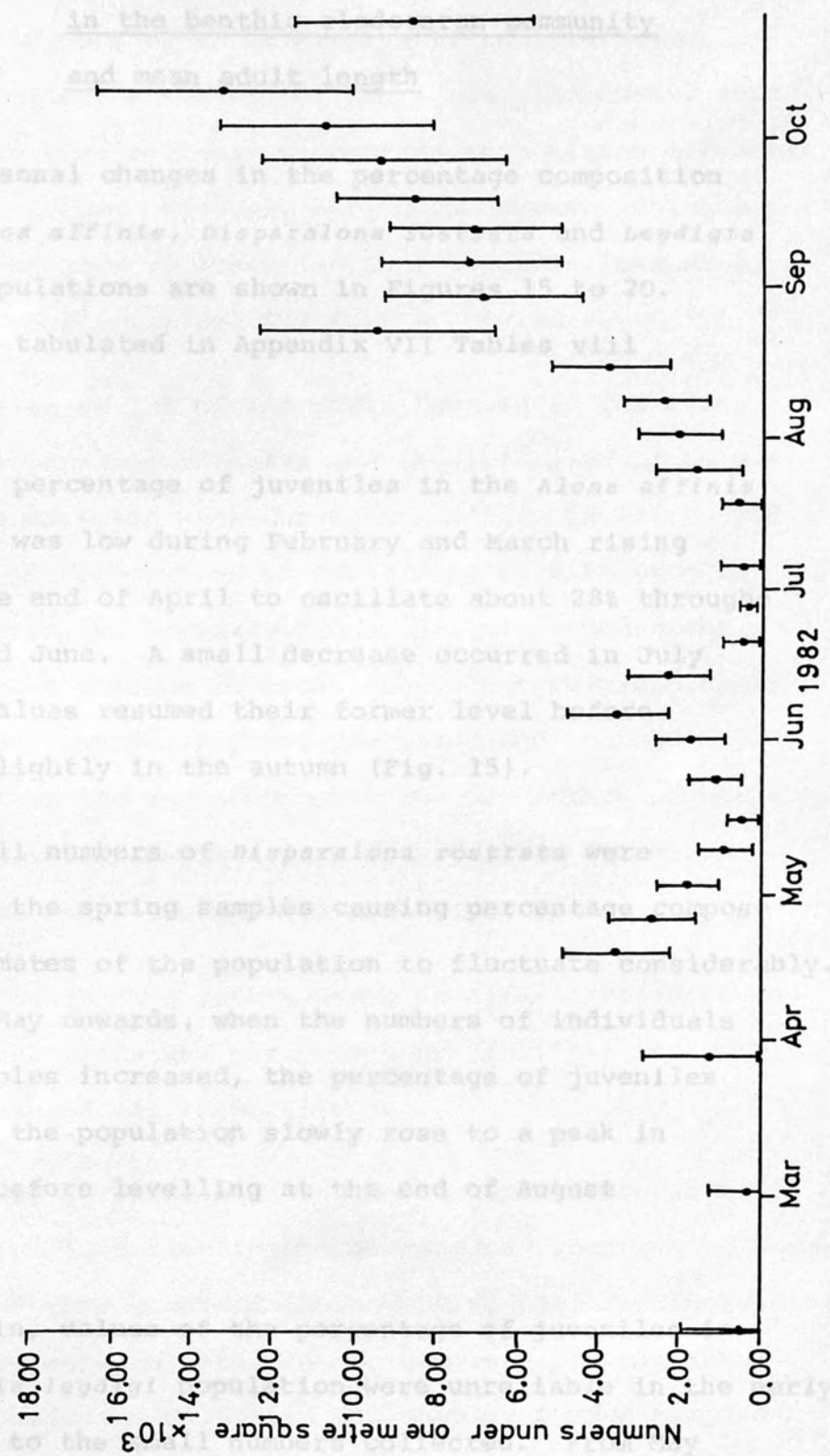


FIGURE 14. Seasonal changes in the numbers of Iliocryptus sordidus under one metre square of substrate in the River Thames, Twickenham. Means and 95% confidence limits.

SECTION 6.5. Composition of the species populations in the benthic cladoceran community and mean adult length

Seasonal changes in the percentage composition of the *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi* populations are shown in Figures 15 to 20. Values are tabulated in Appendix VII Tables viii to x.

The percentage of juveniles in the *Alona affinis* population was low during February and March rising towards the end of April to oscillate about 28% throughout May and June. A small decrease occurred in July and then values resumed their former level before dropping slightly in the autumn (Fig. 15).

Small numbers of *Disparalona rostrata* were present in the spring samples causing percentage composition estimates of the population to fluctuate considerably. From late May onwards, when the numbers of individuals in the samples increased, the percentage of juveniles present in the population slowly rose to a peak in late July before levelling at the end of August (Fig. 17).

Again, values of the percentage of juveniles in the *Leydigia leydigi* population were unreliable in the early spring due to the small numbers collected. From May onwards the percentage of juveniles levelled at about 20%

apart from a small peak in late June (Fig. 19).

The numbers of *Alona rectangula* and *Pleuroxus uncinatus* collected throughout the spring and summer were too small to give reliable percentage composition estimates of the population. However, during the autumn peak the average percentage of juveniles in the populations were 21% for *A. rectangula* and 62% for *P. uncinatus*.

On average 93% of the adult females in the *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi* populations were carrying eggs during May (Figs. 16,18 and 20). Thereafter the percentage of adult females with eggs in the *L. leydigi*, *D. rostrata* and *A. affinis* populations decreased to a minimum in early July, late July and early August respectively. Percentages increased in August and September. At the end of October the percentage of adult female *D. rostrata* females with eggs fell to 45% while those of the other two species remained high.

Throughout the autumn peaks of *Alona rectangula* and *Pleuroxus uncinatus* the percentage of adult females with eggs was 90% and 64% respectively.

Figure 17 shows that on one occasion there were apparently no juveniles in the *Disparalona rostrata* population. This occurred in the spring when few individuals of this species were obtained per sample. If only three or four animals are collected per sample, random sampling will sometimes yield a sample with no juveniles or no adult

females.

Alona affinis, A. rectangula, Leydigia leydigi and *Pleuroxus uncinatus* overwintered solely as parthenogenetic populations. The *Disparalona rostrata* population produced males and ephippial females in the autumn (Figs. 17 and 18), at the same time the numbers of females with parthenogenetic eggs decreased and the population overwintered in the form of resting eggs.

The mean adult lengths (M.A.L.) of *A. affinis, D. rostrata* and *L. leydigi* are plotted in Figures 21 to 23 and tabulated in Appendix VII Tables viii to x. Although mean adult lengths underwent considerable fluctuations throughout the course of the year, a general trend towards high values in the winter and spring and low values in the summer was noted for the three species. The high M.A.L. in late March for the *Disparalona rostrata* population was perplexing. Free-swimming individuals were absent during the winter months and thus it cannot represent old and large overwintering females. It is unlikely that individuals hatching from ephippial eggs in the early spring could have grown to these lengths given the low water temperatures in late March. It is possible that the high M.A.L. at this time was an artefact as the sample from which it was calculated consisted of two *D. rostrata* individuals.

Figures 24 and 25 show the percentage composition of

the *Iliocryptus sordidus* population and values are tabulated in Appendix VII Table xi. On average, the population possessed a higher percentage of juveniles than those of the chydorids, weekly values were also more variable. The percentage of juveniles was relatively low in the spring, rising sharply in late May/early June and thereafter oscillating about 68% before decreasing in the autumn.

The percentage of the adult population with eggs fell from a high winter level to less than 20% in the spring, although a small peak coinciding with the April peak in population density did occur. In late May the percentage of the adult female population with eggs rose and despite some very large fluctuations (for a period of three weeks in late June/July no adult females with eggs were found), tended to remain high until the autumn when it fell, reaching a minimum of 2% by the end of October. Sexual reproduction was not observed in this population of *Iliocryptus sordidus*.

Figures 26 and 27 show seasonal changes in the mean adult length and mean clutch size of those *Iliocryptus sordidus* adults with eggs. Values are tabulated in Appendix VII Table xi. In the first half of the year mean adult length (M.A.L.) fluctuated widely, peaks occurred in March, late April and early June, the last two coinciding with peaks in population density. Following a minimum in late June and early July, the M.A.L. increased to form a plateau through August and September before declining in

the autumn. The trends described above were also found in the seasonal changes of the mean clutch size. The three week gap in late June/early July found in both figures results from an absence of adult females with eggs in the samples collected at this time.

Thus an examination of Figures 25, 26 and 27 revealed that the late April and June peaks in M.A.L. of the *Iliocryptus sordidus* population coincided with peaks in mean clutch size. At the same time, the percentage of adult females with eggs increased resulting in an increase in population density.

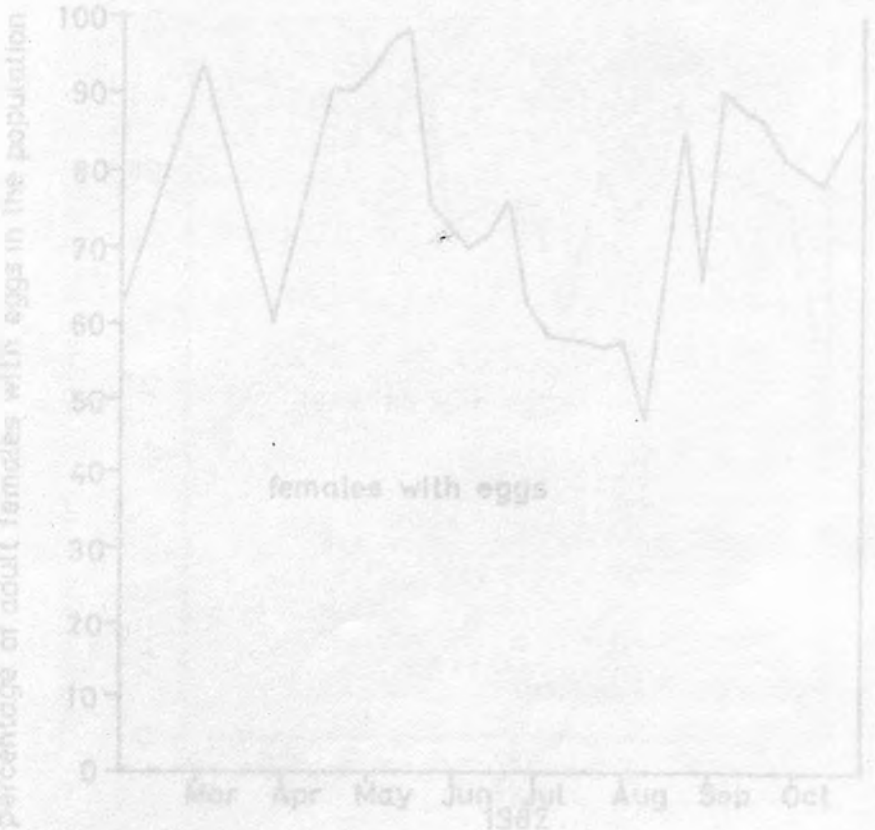


FIGURE 15. Seasonal changes in the percentage of iuveniles and adult females in the Alona affinis population in the River Thames, Twickenham.

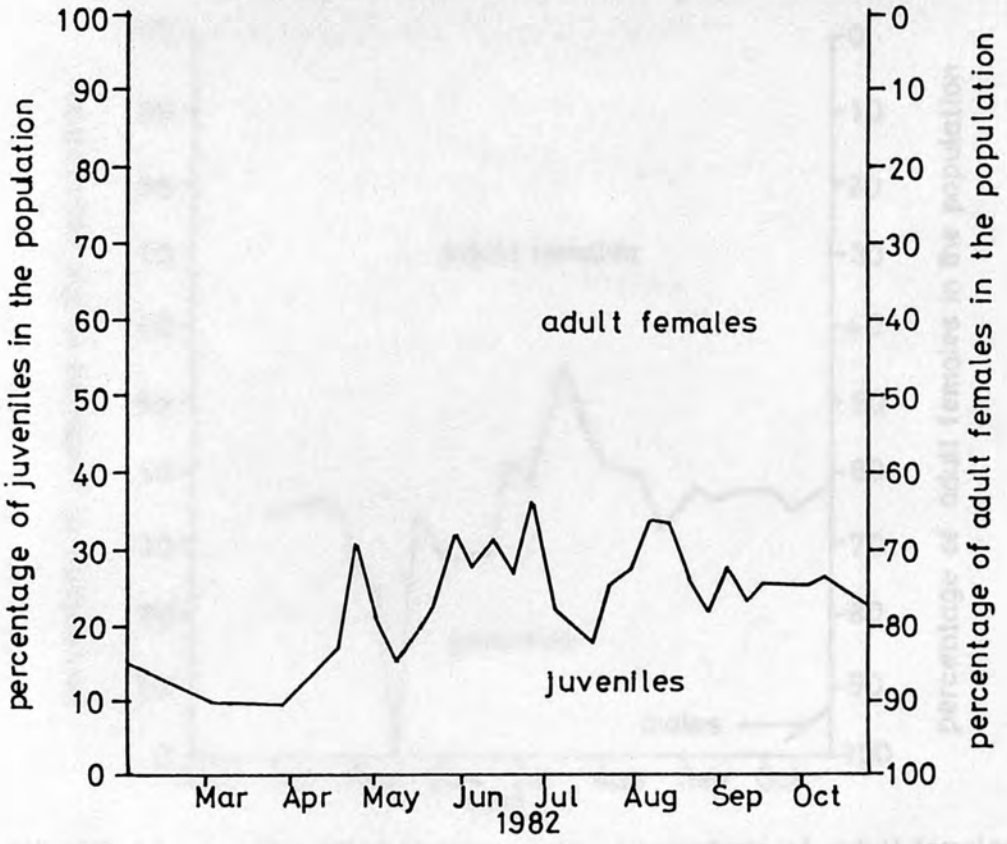


FIGURE 16. Seasonal changes in the percentage of adult females with eggs in the Alona affinis population in the River Thames, Twickenham.

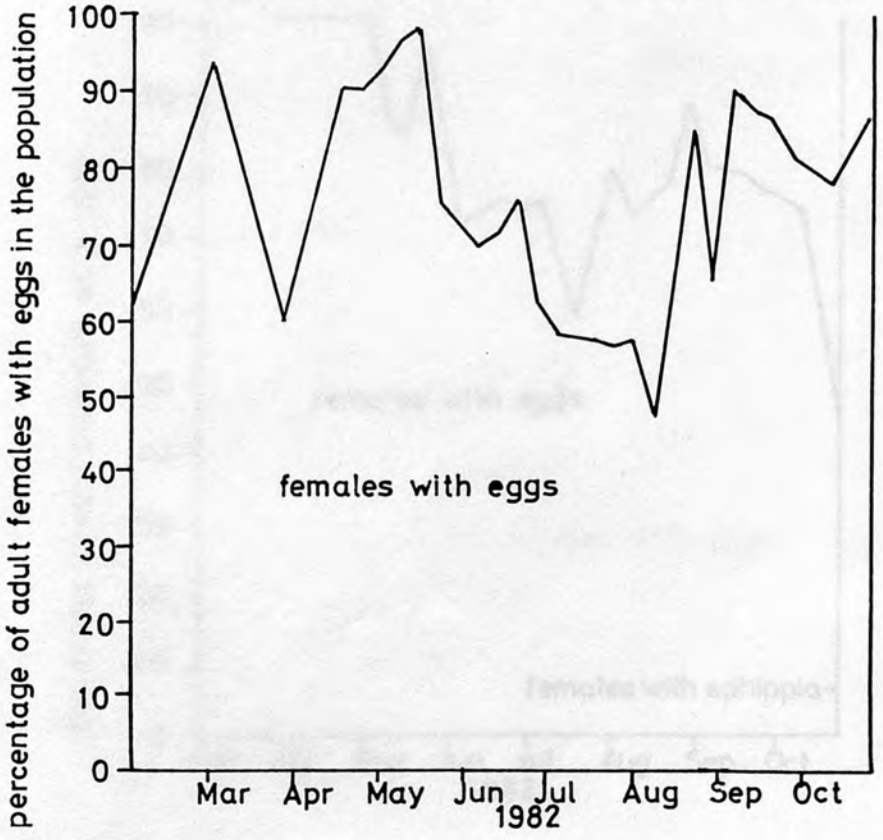


FIGURE 17. Seasonal changes in the percentage of juveniles, adult females and males in the Disparalona rostrata population in the River Thames, Twickenham.

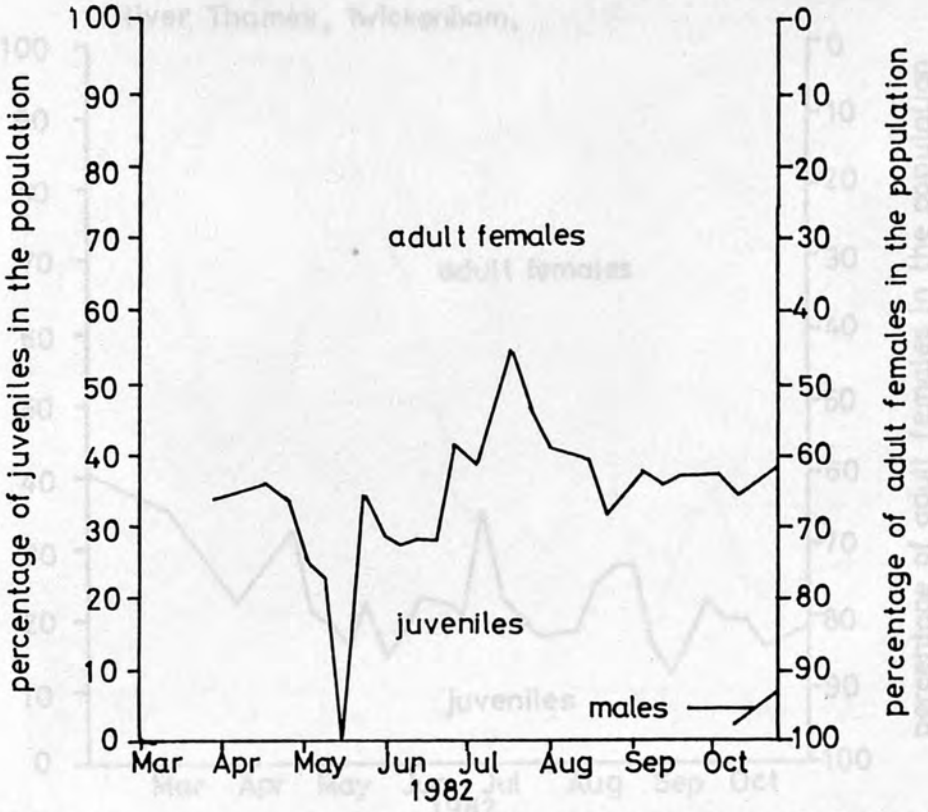


FIGURE 18. Seasonal changes in the percentage of adult females with eggs or ephippia in the Disparalona rostrata population in the River Thames, Twickenham.

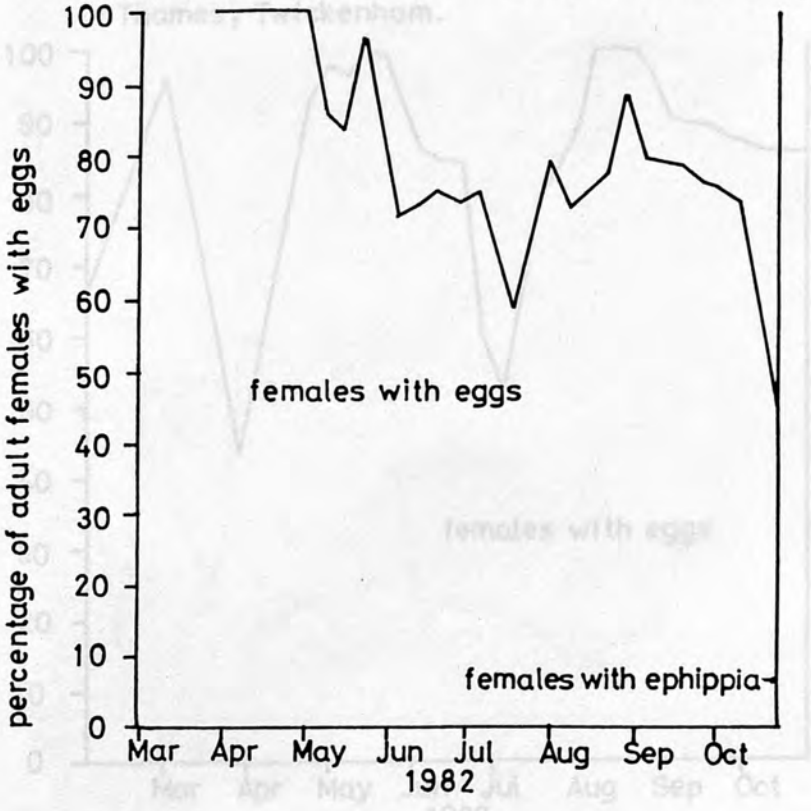


FIGURE 19. Seasonal changes in the percentage of juveniles and adult females in the Leydigia leydigi population in the River Thames, Twickenham.

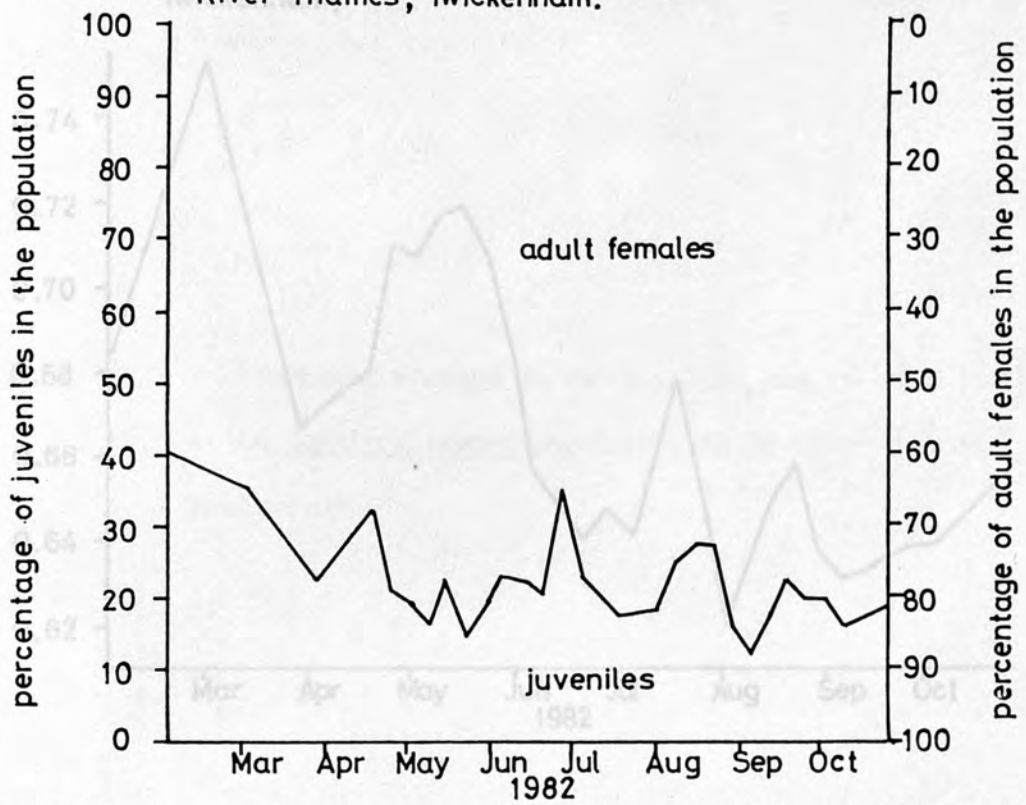


FIGURE 20. Seasonal changes in the percentage of adult females with eggs in the Leydigia leydigi population in the River Thames, Twickenham.

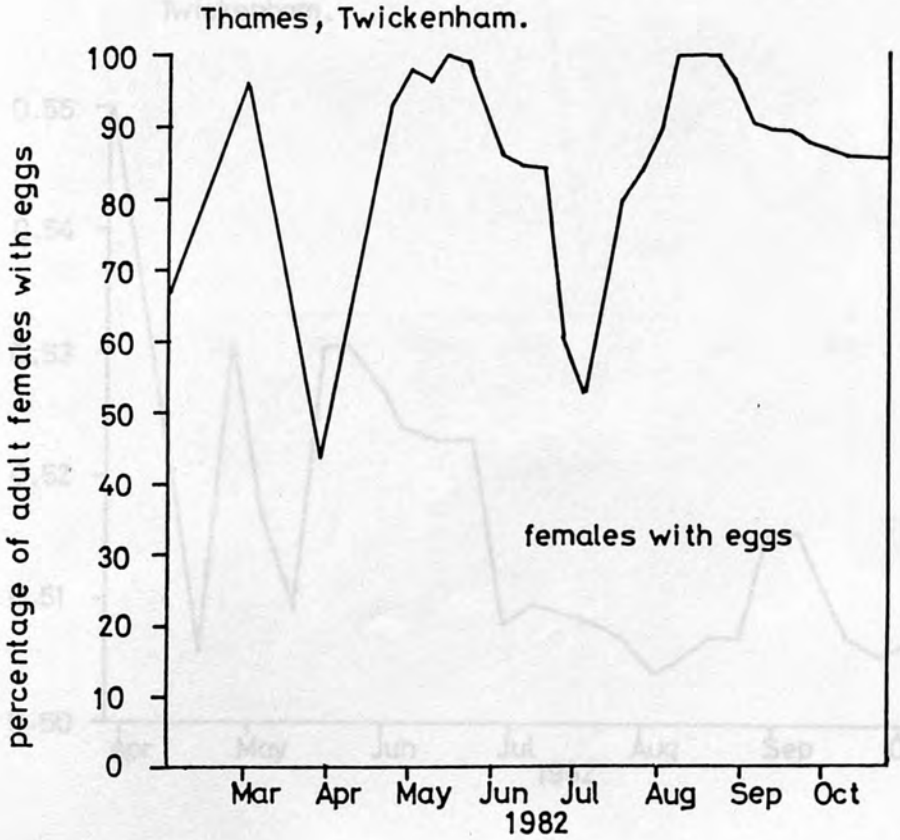


FIGURE 21. Seasonal changes in mean length, mm, of adult females in the Alona affinis population in the River Thames, Twickenham.

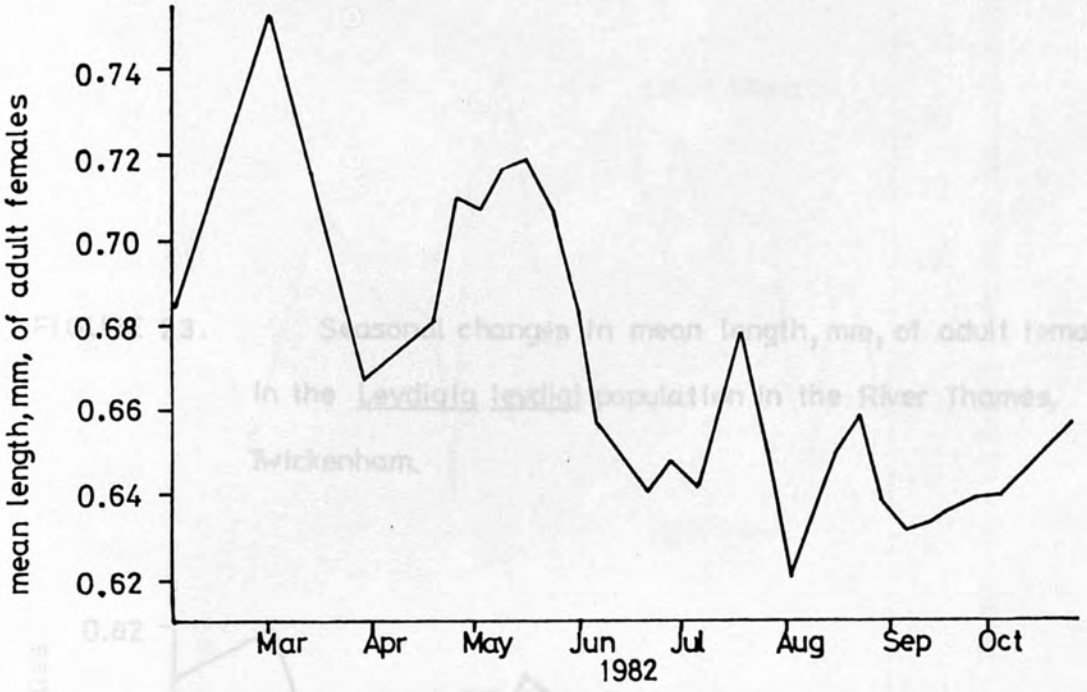


FIGURE 22. Seasonal changes in mean length, mm, of adult females in the Disparalona rostrata population in the River Thames, Twickenham.

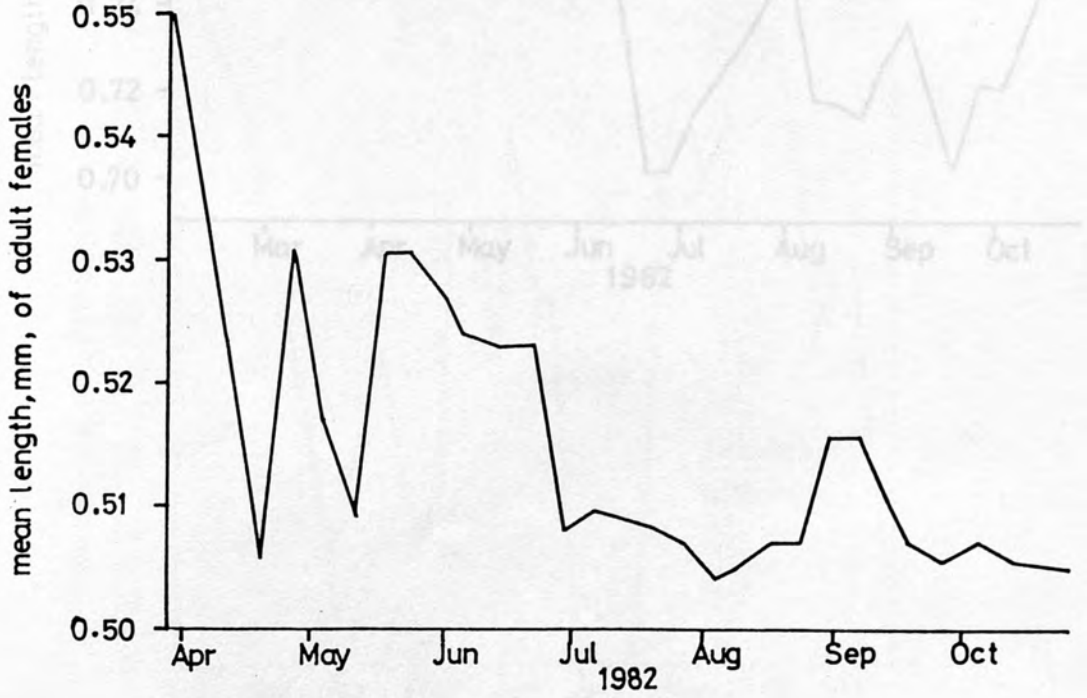


FIGURE 23. Seasonal changes in mean length, mm, of adult females in the Leydigia leydigi population in the River Thames, Twickenham.

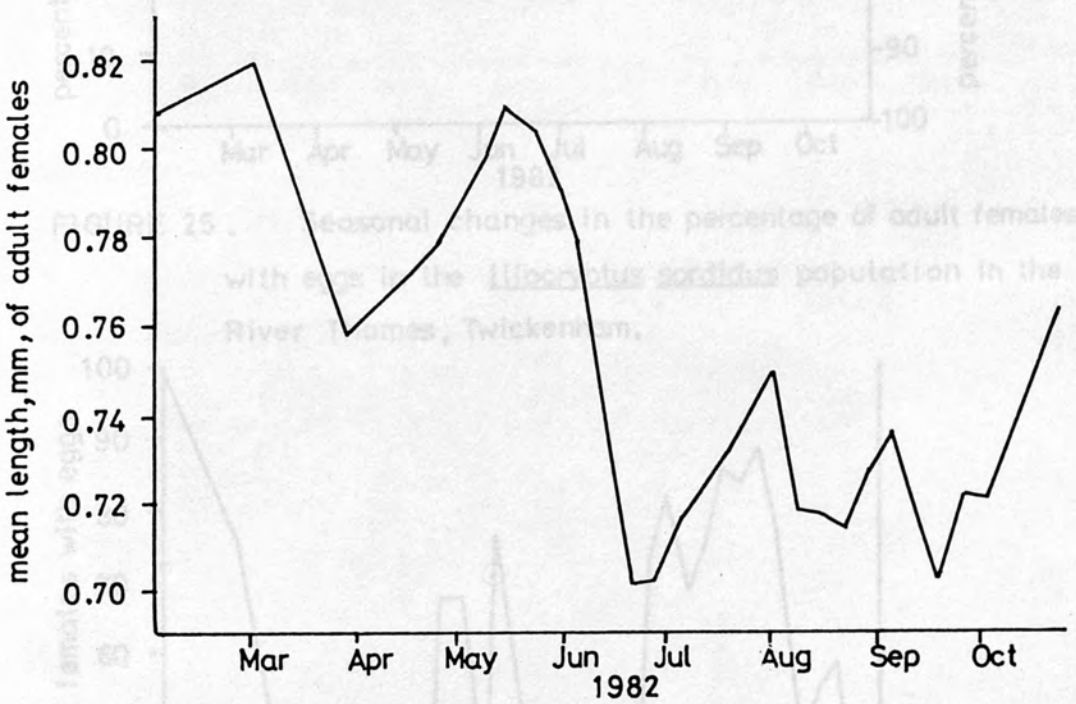


FIGURE 24. Seasonal changes in the percentage of juveniles and adult females in the Iliocryptus sordidus population in the River Thames, Twickenham.

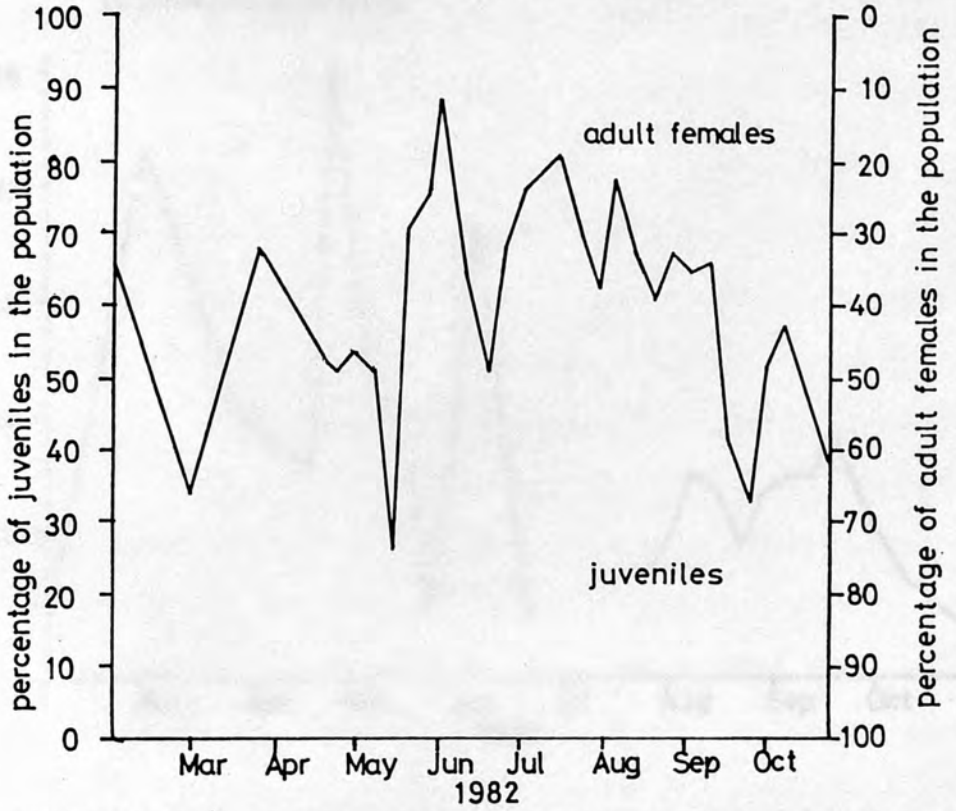


FIGURE 25. Seasonal changes in the percentage of adult females with eggs in the Iliocryptus sordidus population in the River Thames, Twickenham.

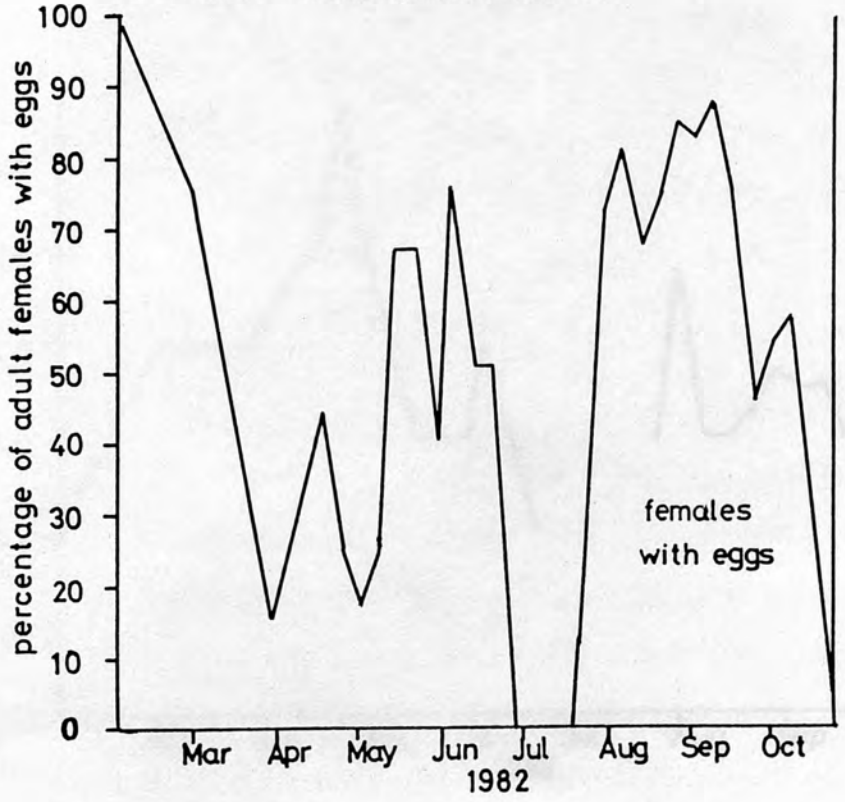


FIGURE 26. Seasonal changes in mean length, mm, of females with eggs in the Iliocryptus sordidus population in the River Thames, Twickenham.

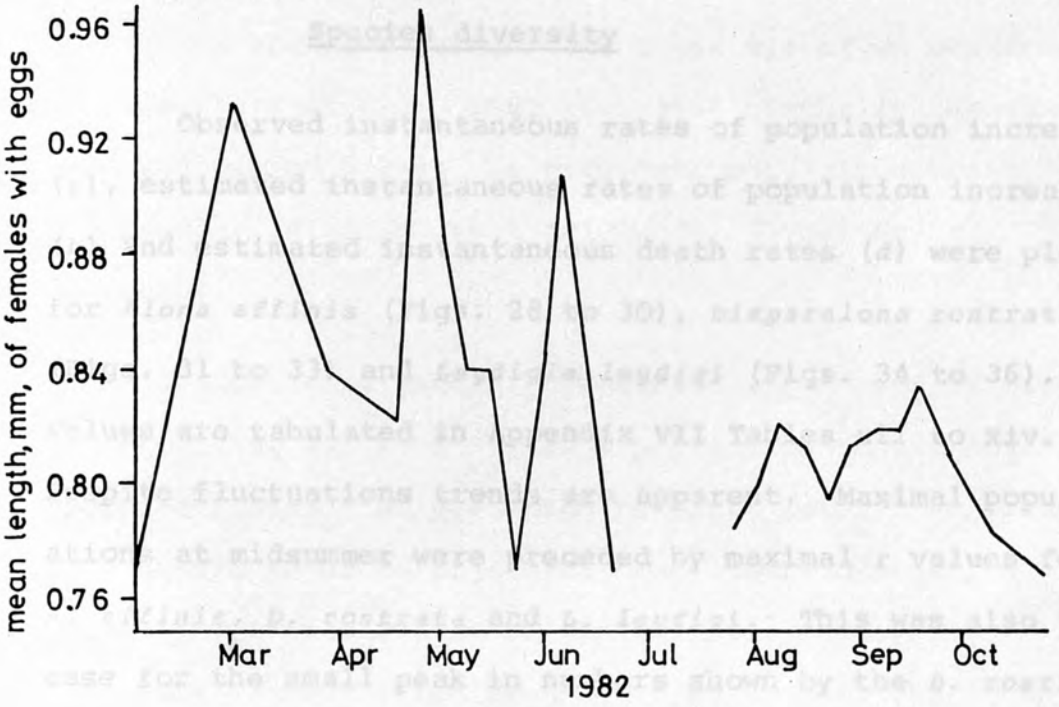
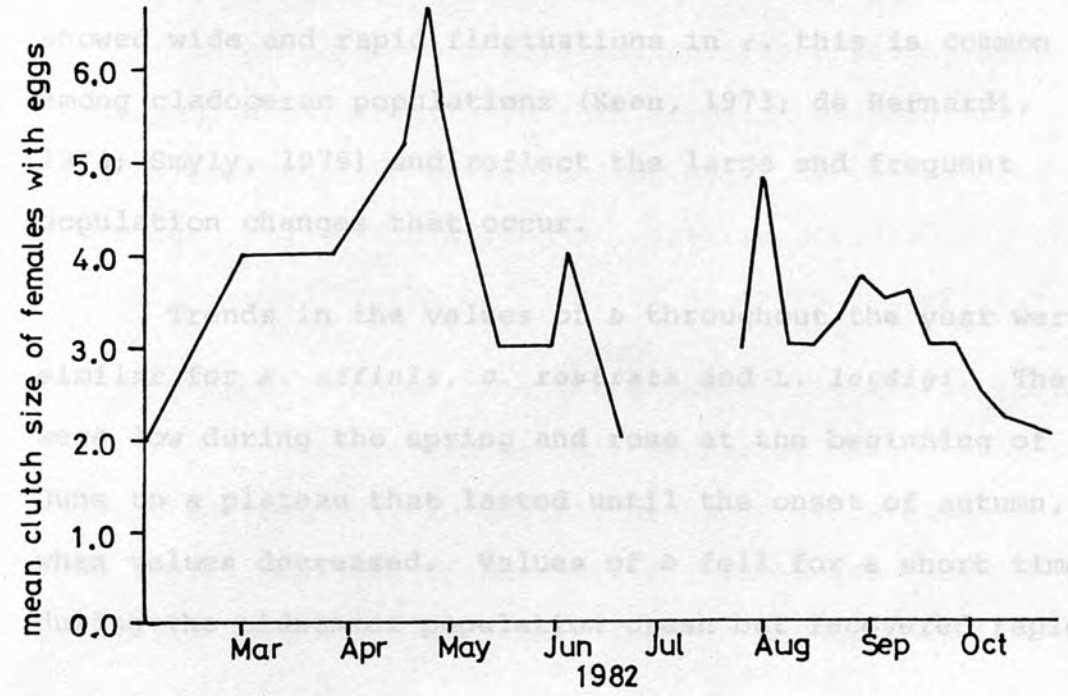


FIGURE 27. Seasonal changes in mean clutch size of females with eggs in the Iliocryptus sordidus population in the River Thames, Twickenham.



SECTION 6.6. Population dynamics of the species populations. Species diversity

Observed instantaneous rates of population increase (r), estimated instantaneous rates of population increase (b) and estimated instantaneous death rates (d) were plotted for *Alona affinis* (Figs. 28 to 30), *Disparalona rostrata*, (Figs. 31 to 33) and *Leydigia leydigi* (Figs. 34 to 36). Values are tabulated in Appendix VII Tables xii to xiv. Despite fluctuations trends are apparent. Maximal populations at midsummer were preceded by maximal r values for *A. affinis*, *D. rostrata* and *L. leydigi*. This was also the case for the small peak in numbers shown by the *D. rostrata* population in August. However the autumn peak of *A. affinis* was not preceded by maximal r values. Negative values of r were observed frequently showing decreases in population density: population minima in July and August were accompanied by minimal values of r in all cases. All species showed wide and rapid fluctuations in r, this is common among cladoceran populations (Keen, 1973; de Bernardi, 1974; Smyly, 1979) and reflect the large and frequent population changes that occur.

Trends in the values of b throughout the year were similar for *A. affinis*, *D. rostrata* and *L. leydigi*. They were low during the spring and rose at the beginning of June to a plateau that lasted until the onset of autumn, when values decreased. Values of b fell for a short time during the midsummer population crash but recovered rapidly.

Values for *d* for the three species tended to be low during the spring although this trend was often obscured by wide fluctuations. They increased gradually throughout June and peaked during the midsummer population crash and the population minima that followed. Therafter, *d* decreased.

Values of *b* should, theoretically, exceed or equal corresponding values of *r*, as a population should not increase faster than predicted by birth rate. The value of *d* should never be negative. The observed negative values may be the result of immigration, errors in estimates of population or numbers of eggs or due to an increase in the survival of non-reproductive instars (Cummins, Costa, Rowe, Moshiri, Scanlon and Zajdel, 1969). Negative values of *d* generally occurred in the spring when the counts from which the values were calculated were very low. This suggests that, in most cases, errors in the estimation of population size may have been responsible for negative values of *d* in this study. However, the high values of *r* and corresponding negative values of *d* which occurred in the spring *D. rostrata* population were probably caused by the hatching of ephippia (p. 99).

Figure 37 shows that the seasonal changes in species diversity (H') and evenness (J') occurring in the benthic cladoceran community in the River Thames at Twickenham. Values are tabulated in Appendix VII Table xv. The numerical domination of the cladoceran populations by

Iliocryptus sordidus was largely responsible for the early spring fall in values of H' and this was also reflected by lowered values of J'. Throughout May and early June expanding populations of chydorid cladocerans, induced by rising water temperatures (p. 80), coupled with a decline in the abundance of *Iliocryptus sordidus*, resulted in higher values of H' and J'.

Disparalona rostrata was numerically dominant in late June and throughout July, leading to lower values of H' and J'. In August and September the chydorid populations began to recover from the midsummer population crash. No one species was dominant and this, together with an extended population peak of *I. sordidus*, resulted in a rise of species diversity and evenness.

In the autumn, when the previously rare *Alona rectangula* and *Pleuroxus uncinatus* became numerically abundant, values of H' and J' increased further.

The mean species diversity of the benthic cladoceran community in 1982 was 1.636.

FIGURE 28.

Seasonal changes in the observed instantaneous rate of population increase (r) of the Alona affinis population in the River Thames, Twickenham.

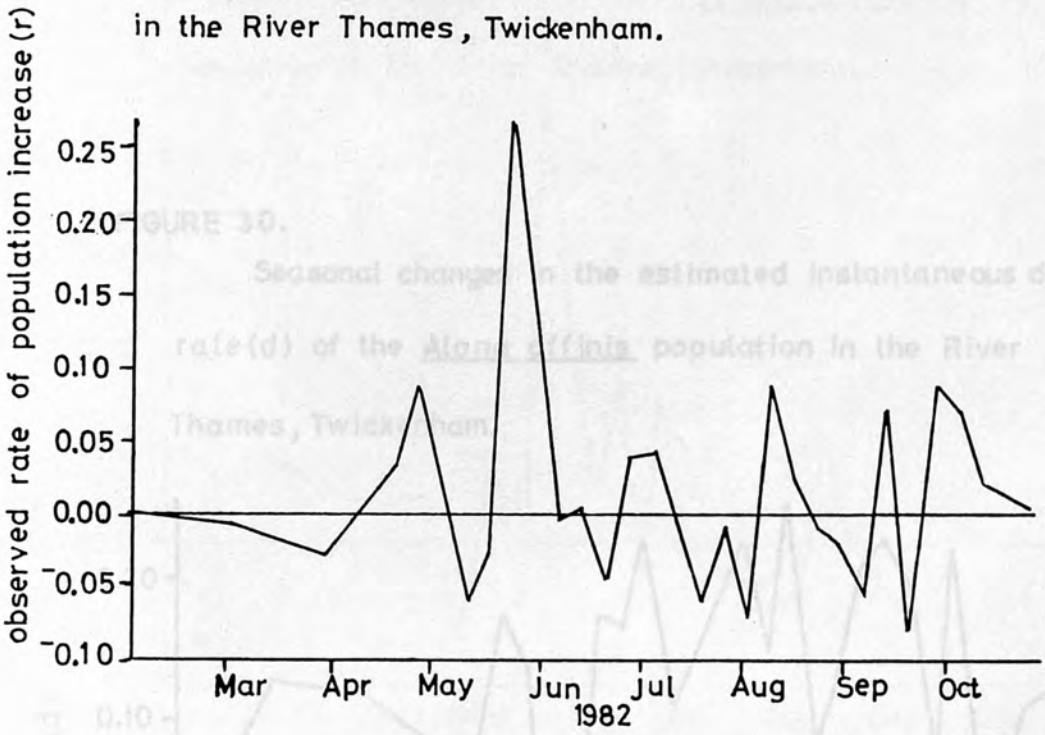


FIGURE 29.

Seasonal changes in the estimated instantaneous rate of population increase (b) of the Alona affinis population in the River Thames, Twickenham.

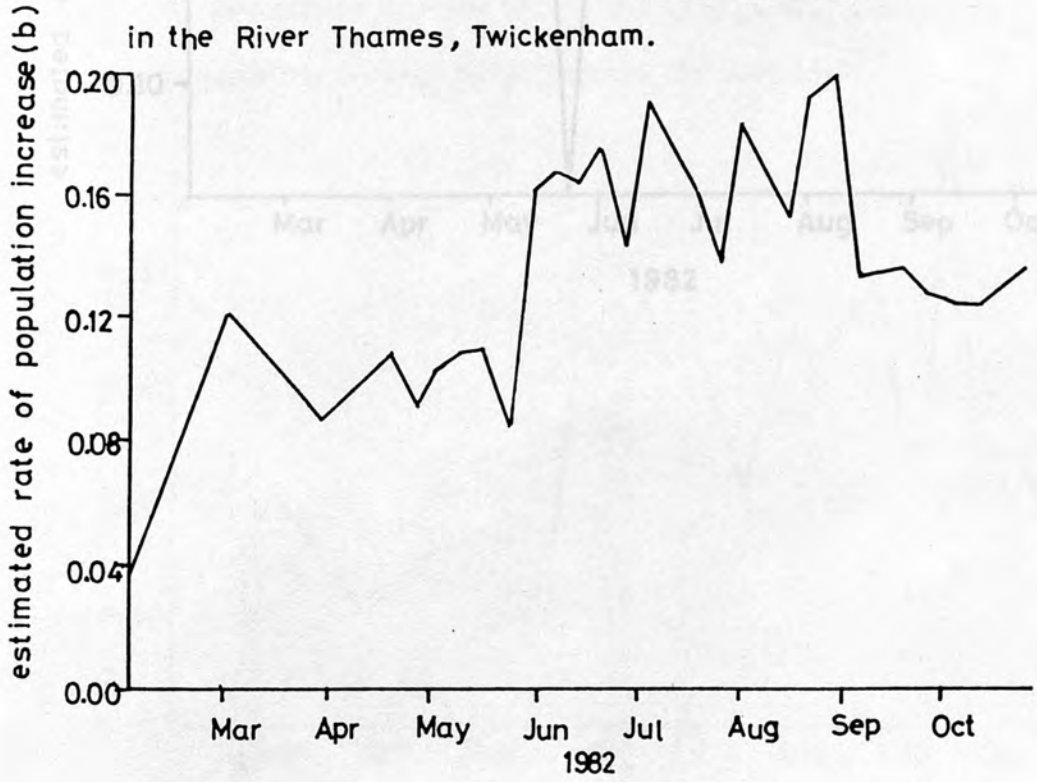


FIGURE 30.

Seasonal changes in the estimated instantaneous death rate(d) of the Alona affinis population in the River Thames, Twickenham.

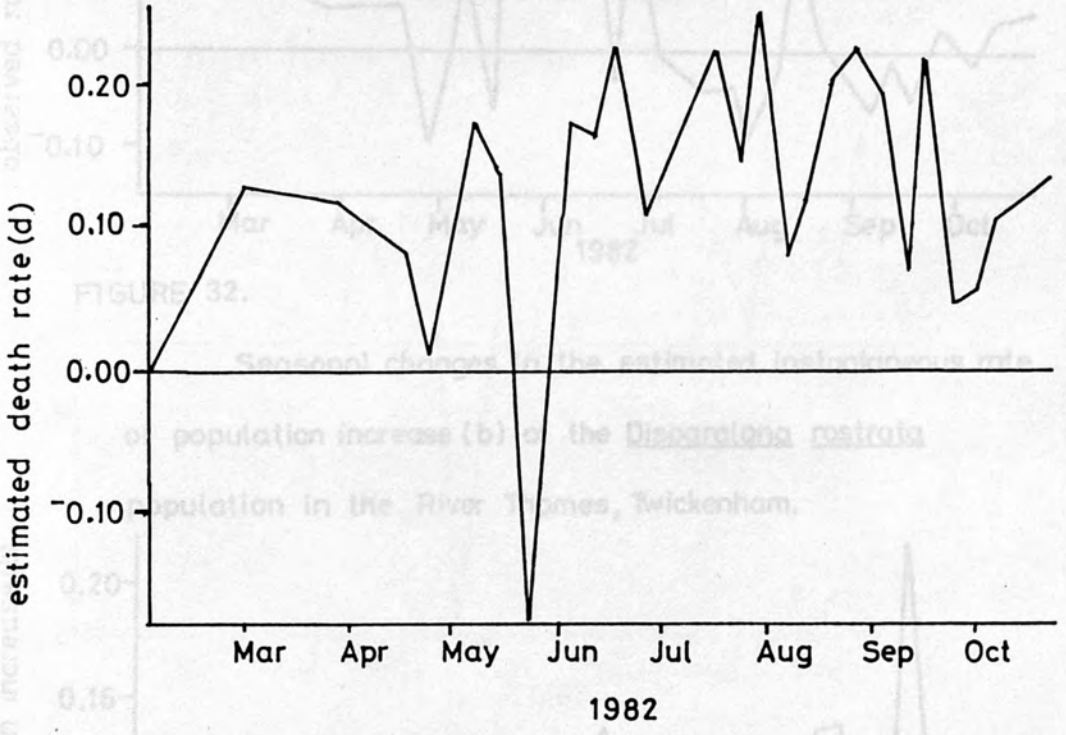


FIGURE 31.

Seasonal changes in the observed instantaneous rate of population increase (r) of the Disparalona rostrata population in the River Thames, Twickenham.

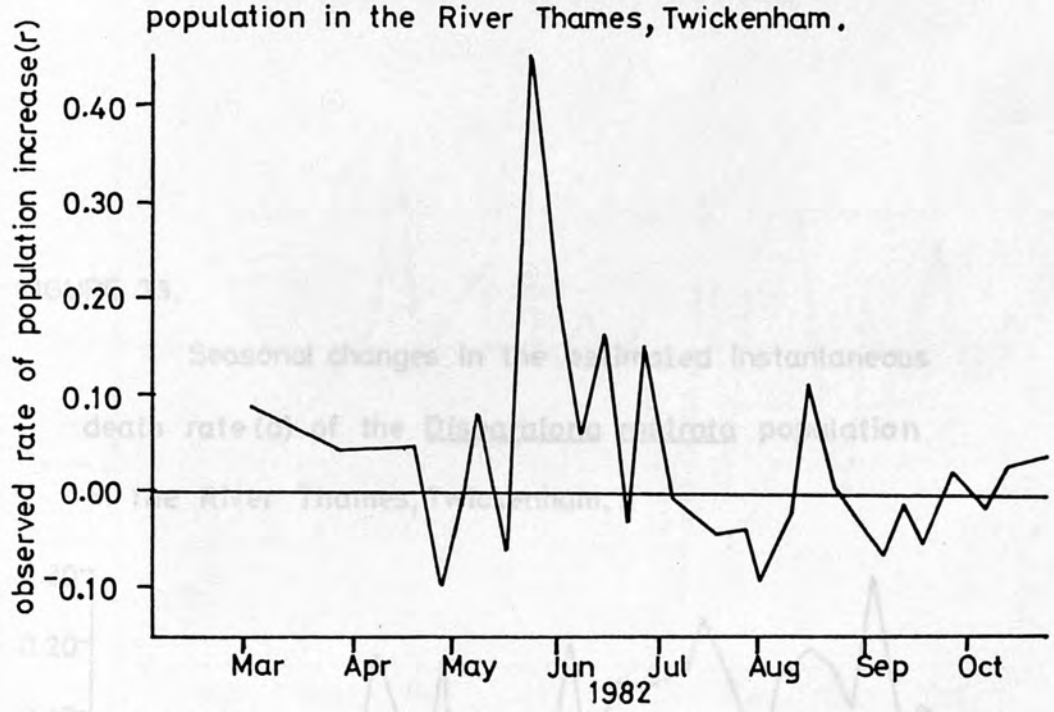


FIGURE 32.

Seasonal changes in the estimated instantaneous rate of population increase (b) of the Disparalona rostrata population in the River Thames, Twickenham.

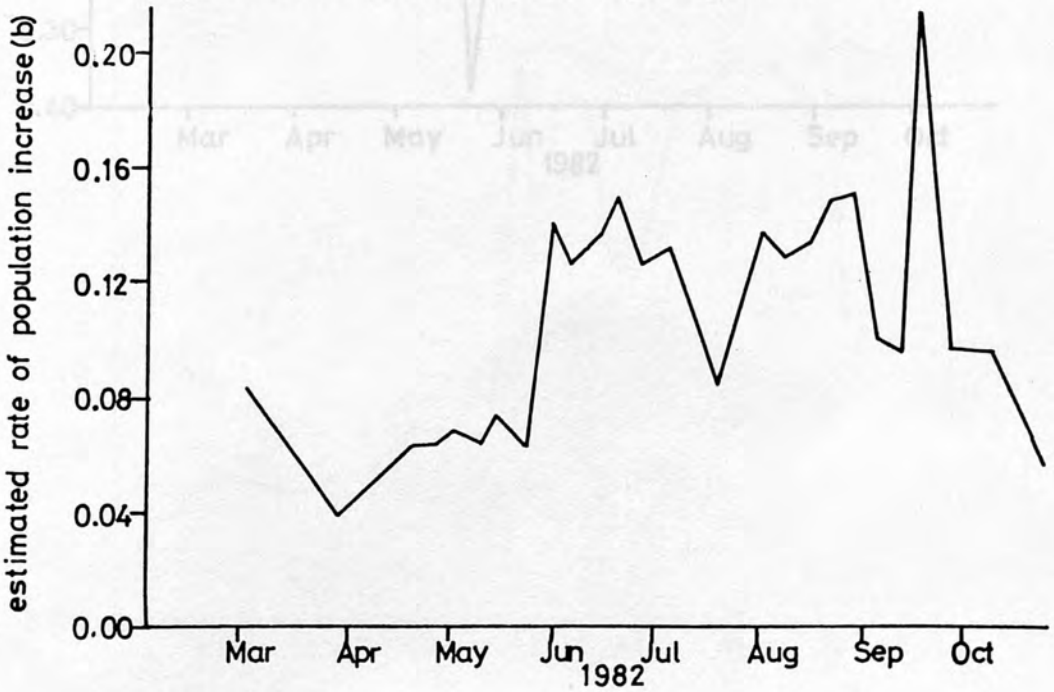


FIGURE 33.

Seasonal changes in the estimated instantaneous death rate (d) of the Disparalona rostrata population in the River Thames, Twickenham.

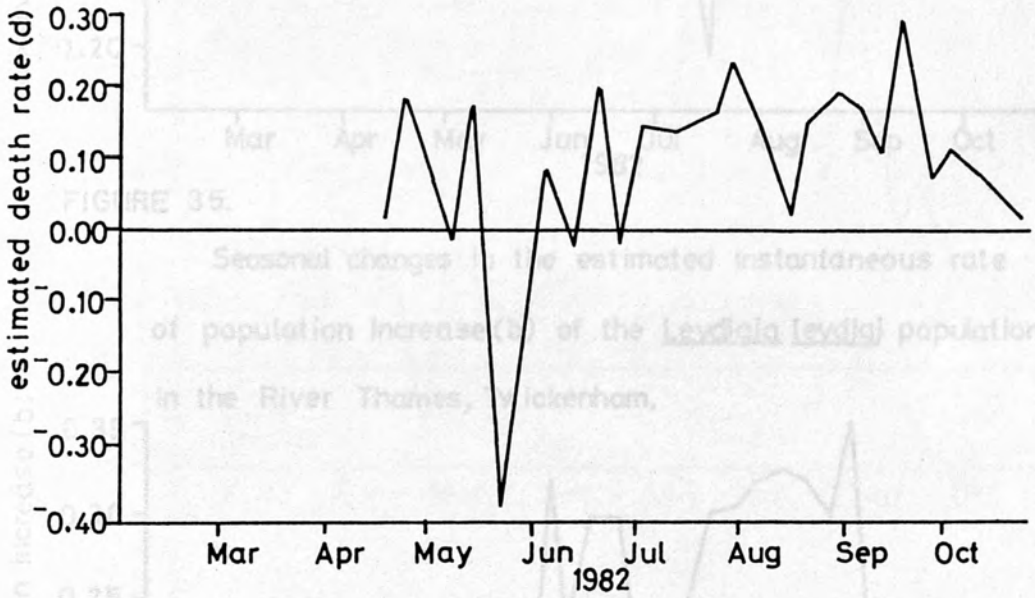


FIGURE 34.

Seasonal changes in the observed instantaneous rate of population increase (r) of the Leydigia leydigi population in the River Thames, Twickenham.

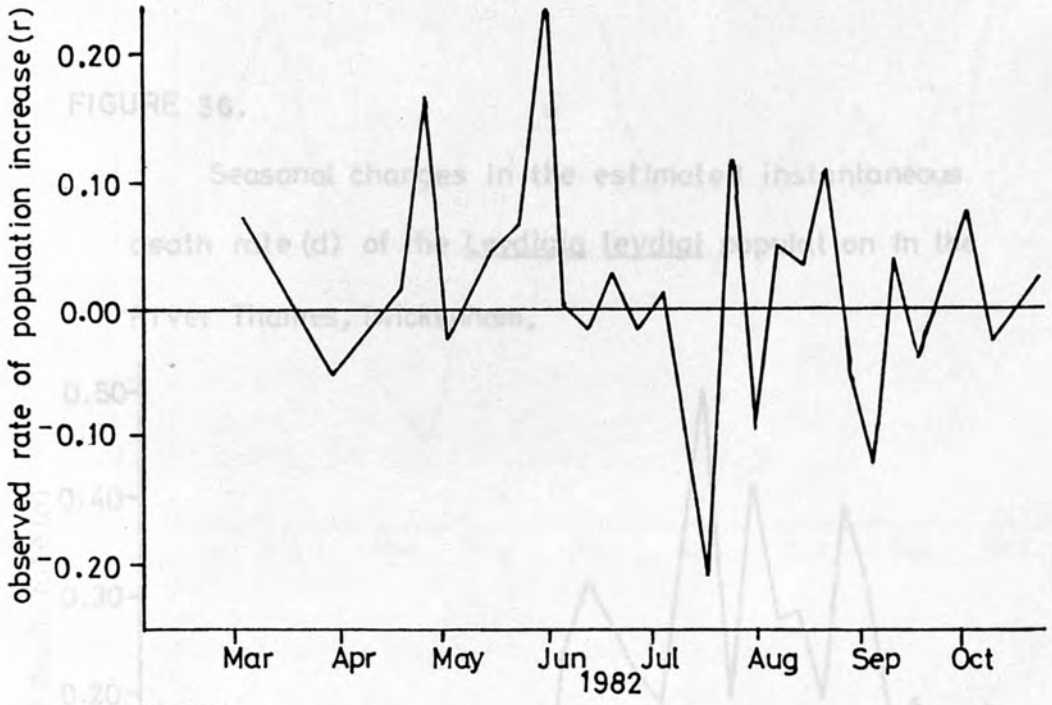


FIGURE 35.

Seasonal changes in the estimated instantaneous rate of population increase (b) of the Leydigia leydigi population in the River Thames, Twickenham.

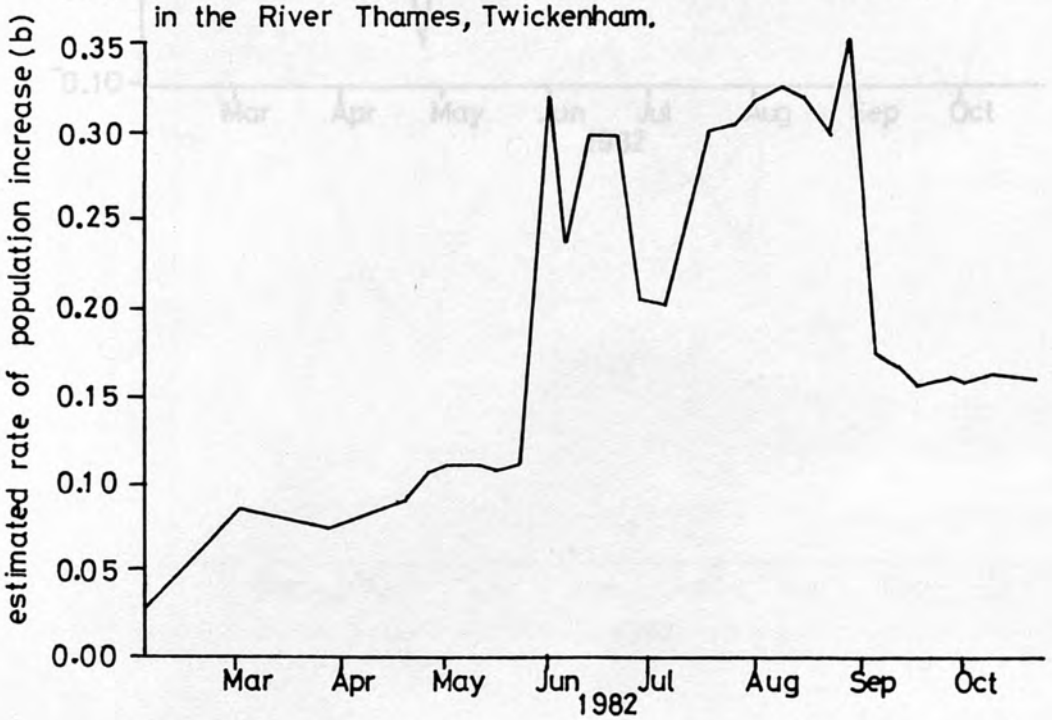


FIGURE 36.

Seasonal changes in the estimated instantaneous death rate (d) of the Leydigia leydigi population in the River Thames, Twickenham.

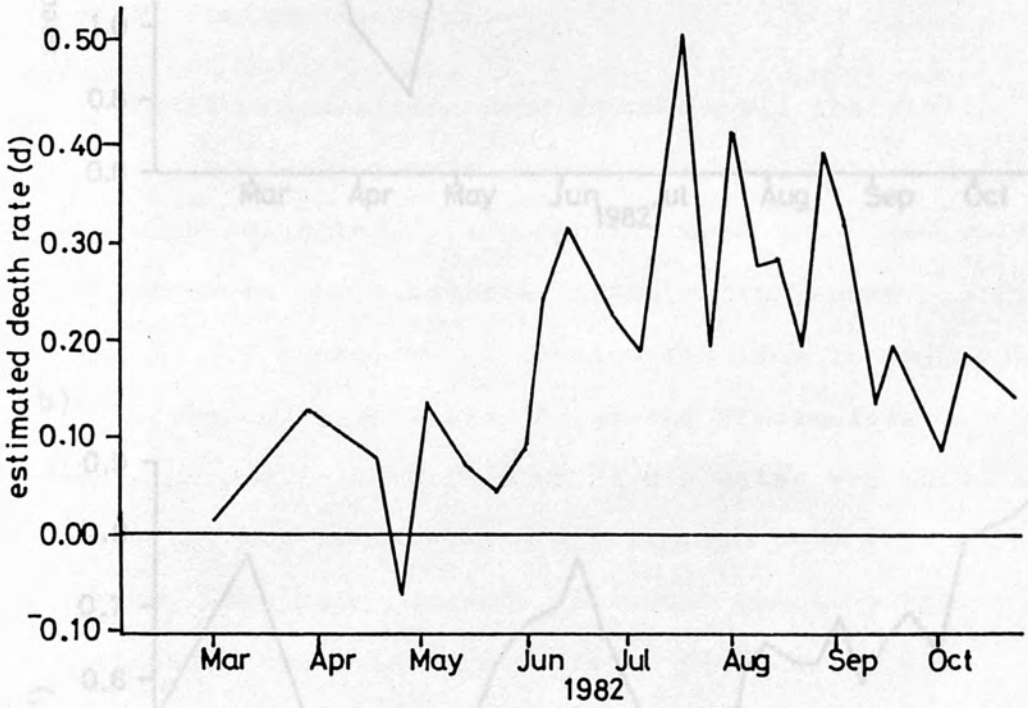
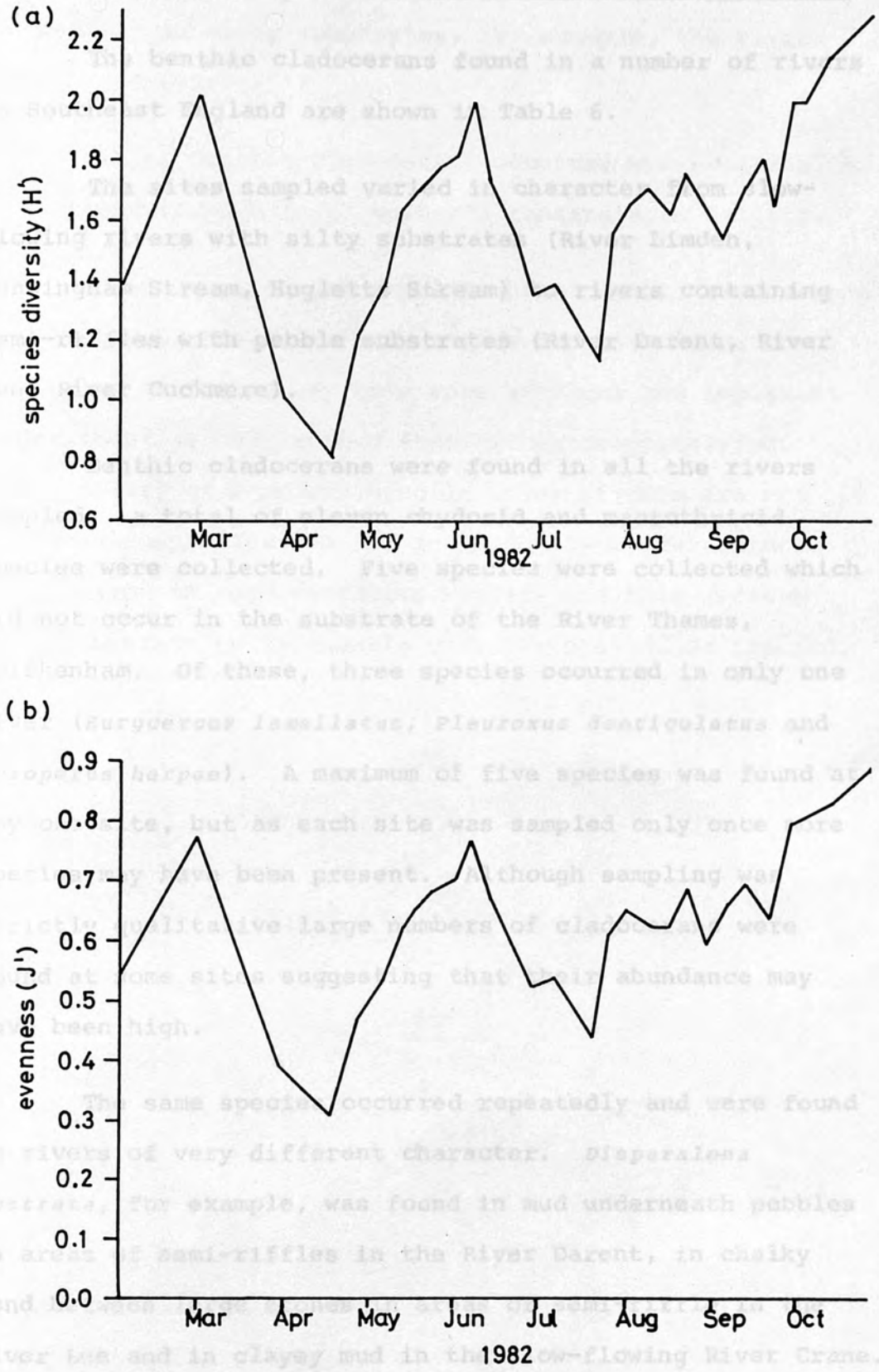


FIGURE 37. Seasonal changes in (a) species diversity (H') and (b) evenness (J') of the benthic cladoceran community in the River Thames, Twickenham.



SECTION 6.7. Rivers in Southeast England sampled in 1983

The benthic cladocerans found in a number of rivers in Southeast England are shown in Table 6.

The sites sampled varied in character from slow-flowing rivers with silty substrates (River Limden, Nunningham Stream, Hugletts Stream) to rivers containing semi-riffles with pebble substrates (River Darent, River Lee, River Cuckmere).

Benthic cladocerans were found in all the rivers sampled: a total of eleven chydorid and macrothricid species were collected. Five species were collected which did not occur in the substrate of the River Thames, Twickenham. Of these, three species occurred in only one river (*Eurycercus lamellatus*, *Pleuroxus denticulatus* and *Acroperus harpae*). A maximum of five species was found at any one site, but as each site was sampled only once more species may have been present. Although sampling was strictly qualitative large numbers of cladocerans were found at some sites suggesting that their abundance may have been high.

The same species occurred repeatedly and were found in rivers of very different character. *Disparalona rostrata*, for example, was found in mud underneath pebbles in areas of semi-riffles in the River Darent, in chalky sand between large stones in areas of semi-riffle in the River Lee and in clayey mud in the slow-flowing River Crane.

Leydigia leydigi was found in chalky sand in the River Lee as well as in muddy substrates, for example, the rivers Rother and Cray.

Thus, benthic cladocerans occurred wherever shelter from the current allowed suitable substrate to collect.

The occurrence of populations of benthic cladocerans in flowing waters, over such a wide range of conditions, indicates that they may be a more numerous and important constituent of the benthos than hitherto appreciated. The majority of samplers used in river studies are not designed to provide samples in which the microcrustacea are present in representative numbers and this section of the benthos is frequently underrepresented or ignored.

TABLE 6 : Rivers in Southeast England sampled for benthic Cladocerans in 1983

RIVER	GRID REFERENCE	DATE SAMPLE TAKEN	COMMENTS ON RIVER	COMMENTS ON SUBSTRATE	CLADOCERA
CHESS	TQ 064 955	6.6.83	Depth 70cm. Swift flowing stands of *Rannunculus* sp.	Varying from mud and macrodetritus to fine gravel/silt to coarse gravel.	*Alona affinis* Leydig *A. quadrangularis* (O.F Müller) *A. rectangula* Sars *Iliocryptus sordidus* (Liévin)
CRANE	TQ 101 771 and TQ 132 728 and TQ 154 756	14.6.83	Tributary of River Thames, slow flowing. Stands of *Potomageton* and *Cladophora*.	Varying from clayey mud to gravel and large stones with mud in between	*Acroperus harpae* Baird *Alona rectangula* Sars *Chydorus sphaericus* (O.F Müller) *Disparalona rostrata* (Koch 1841) *Eurycercus lamellatus* (O.F Müller) *Pleuroxus trigonellus* (O.F. Müller) *Iliocryptus sordidus* (Liévin)
CRAY	TQ 497 735	20.7.83	Depth 80cm. Medium flow.	Silt overlying pebbles. No weed.	*Leydigia leydigi* (Schodler) *Iliocryptus sordidus* (Liévin)
CUCKMERE	TQ 582 122	4.7.83	Depth 30cm. Swift flow trout present	Stony bottom. *Rannunculus* stands.	*Alona affinis* Leydig
DARENT	TQ 546 670 and TQ 542 656	20.7.83	Depth 6-12cm. Swift flow. Semi-riffle.	Small and large pebbles. Mud underneath and between.	*Alona affinis* Leydig *A. quadrangularis* (O.F Müller) *Disparalona rostrata* (Koch 1841) *Leydigia leydigi* Schodler *Pleuroxus uncinatus* Baird
HUGLETTS STREAM	TQ 672 138	4.7.83	Depth 70cm. Slow flow.	Clay bottom overlain with mud.	*Leydigia leydigi* Schodler
LEE	TL 276 098 and TL 220 124	26.7.83	Depth 1-1.5m. fast flow. Semi-riffle.	Mud, chalky sand and gravel in between large stones.	*Alona affinis* Leydig *Disparalona rostrata* (Koch 1841) *Leydigia leydigi* Schodler *Iliocryptus sordidus* (Liévin)
LIMDEN	TQ 707 277	20.6.83	Depth 1m. Slow flow.	Fine gravel and mud.	*Alona quadrangularis* (O.F Müller)
NUNNINGHAM STREAM	TQ 662 128	4.7.83	Depth 50cm. Slow flow.	Clay bottom overlain with mud.	*Leydigia leydigi* Schodler
RODING	TQ 467 969 and TQ 508 975	9.8.83	Depth 30cm. Medium flow.	Muddy gravel.	*Alona rectangula* Sars *Pleuroxus uncinatus* Baird *P. denticulatus* Birge *P. trigonellus* (O.F Müller) *Iliocryptus sordidus* (Liévin)
ROTHER	TQ 737 240	20.6.83	Agricultural catchment. Deeply channelled. 2m depth. Swift flowing.	Clayey mud and gravel.	*Alona guttata* Sars *A. quadrangularis* (O.F Müller) *Leydigia leydigi* Schodler *Iliocryptus sordidus* (Liévin)
WEY	TQ 070 613	5.7.83	Depth 20cm. Rapid flow-riffles in places.	Sand, gravel, pebbles.	*Alona affinis* Leydig *A. guttata* Sars

CHAPTER 7 : Discussion of Detailed Observations on a Community of Benthic Cladocerans in the River Thames, Twickenham

Examination of the results obtained from the detailed study of a community of benthic cladocerans in the River Thames and comparison of these with studies of communities in lakes revealed a number of interesting similarities and differences.

NUMBER AND ABUNDANCE OF SPECIES IN THE BENTHIC CLADOCERAN COMMUNITY

A comparison of the benthic cladocerans occurring in the vegetation covered and the benthos of the unvegetated littoral of lakes shows that many studies have found the unvegetated littoral to support a lower number of species and a lower numerical abundance of those species (Table 7).

The benthic Cladocera of flowing waters are not well documented and the data presented below were largely obtained from qualitative surveys. Jónassen (1948) found four chydorids and two macrothricid species in the mud habitat of the River Susaa, Bottrell (1977) found ten chydorid and two macrothricid species in the substrate of the River Thames at Reading while Ham (1982) found one macrothricid species and between one and three chydorid species in eleven chalk streams in southern England. In the present study seven chydorid and two macrothricid

TABLE 7 : Numbers of Benthic Cladoceran Species and their Abundance in the Vegetation Covered and Unvegetated Littoral Substrate of some Lakes and Rivers

LAKE	VEGETATION COVERED LITTORAL	UNVEGETATED LITTORAL	SOURCE
Crooked Lake U.S.A.	23 chydorid and macrothricid species	10 chydorid and macrothricid species	Quade (1973)
Elk Lake U.S.A.	21 chydorid species	------	Whiteside (1974)
Lake Balaton Hungary	------	7 chydorid and macrothricid species	Sebestyén (1947)
Lake Myvatn Iceland	------	11 chydorid and macrothricid species	Adalsteinsson (1979)
Lago di Mergozzo Italy	------	8 chydorid and macrothicid species	Smyly (1964)
Lake Itasca U.S.A.	max. abundance of total chydorids 4×10^{5} m^{-2}	max. abundance of total chydorids 7.5×10^{4} m^{-2}	Whiteside *et al.* (1978)
Ivan'kovo reservoir U.S.S.R.	average biomass of total chydorids 339mg m^{-3}	average biomass of total chydorids 47mg m^{-3}	Smirnov (1974)
River Il'd U.S.S.R.	average biomass total chydorids 455mg m^{-3}	average biomass total chydorids 30mg m^{-3}	Smirnov (1974)

species were found in the River Thames at Twickenham. If the above numbers are compared with those of Table 7 it would seem that a similar number of species are present in the benthos of the unvegetated littoral of lakes and the mud substrate of flowing waters.

Quade (1973) suggests that numbers of benthic Cladocera occur in the sediments in an inverse relationship to the presence of plant substrate. This is supported by the findings of Goulden (1971) who recorded high total chydorid abundances of approximately 307,500 m^{-2} from the benthos of the unvegetated littoral of Lake Lacawac, which does not have well-developed macrophyte beds. However, the maximum abundance of total chydorids from the River Thames at Twickenham, in which there are no aquatic macrophytes, was approximately 50,000 m^{-2}, considerably lower than that for the unvegetated littoral of lakes. The sediment at the sampling site belongs to the Wentworth grade "silt" (p. 83) and thus the comparatively low numbers of benthic cladocerans obtained may support Quade's (1973) suggestion that benthic cladocerans associate preferentially with coarse-grained organic sediments.

Whiteside (1970) suggests that chydorid species diversity is governed primarily by the diversity of the available habitat, as is the case for some other animal groups (MacArthur and MacArthur, 1961; Pianka, 1967). Macrophytes offer a spatially and temporally diverse habitat (Smirnov, 1963; Fryer and Forshaw, 1979) and this may explain the

high numbers of species and abundance found in the vegetation covered littoral of lakes.

In the River Thames at Twickenham the available habitat was one of low structural complexity and thus the mean species diversity might be expected to be lower than that of habitats in which aquatic macrophytes are present with a concommitant increase in structural complexity and niche differentiation. In a study of the chydorid cladocerans in Danish lakes Whiteside (1970) divided the lakes into two groups, the polluted and clear-water lakes. The first group had a mean species diversity of 1.50. In this group a low variety of aquatic macrophytes was present, thus decreasing the available habitat for the chydorid species. The mean species diversity for the clear water group, which had a wider variety of aquatic macrophytes, was 2.72. The mean species diversity for the benthic community at the River Thames, Twickenham was 1.63, being, as might be expected, closer to the polluted lakes group of Whiteside (1970).

TAXOCENE OF CLADOCERANS

If the benthic cladocerans found in the mud habitats of lakes and rivers are examined, the same species are found to occur repeatedly (Table 8), within the limits imposed by geographical distribution. *Alona rectangula* and *Pleuroxus uncinatus* are not found in North America (Smirnov, 1974) although the former is otherwise cosmopolitan in its distribution.

TABLE 8: Cladoceran Species occurring in the Mud Substrate of a Number of Lakes and Rivers

SPECIES / LOCATION	Lake Balaton, Hungary Sebestyén (1947)	Lago Maggiore, Italy Smyly (1964)	Lago di Mergozzo, Italy Smyly (1964)	Lago di Varese, Italy Smyly (1964)	Crooked Lake, USA Quade (1973)	Lake Itasca, USA Whiteside *et al.* (1978)	Lake Michigan, USA Evans and Stewart (1977)	Douglas Lake, USA Moore (1939)	Lake Myvatn, Iceland Adalsteinsson (1979)	River Susaa, Denmark Jónassen (1948)	River Colne, UK Ham (1982)	River Kennet, UK Ham (1982)	River Lambourn, UK Ham (1982)	River Test, UK Ham (1982)	River Thames, Reading, UK Bottrell (1977)	River Thames, Twickenham, UK Present work	River Chess, UK Present work	River Crane, UK Present work	River Rother, UK Present work	River Wey, UK Present work	River Cray, UK Present work	River Darent, UK Present work	River Lee, UK Present work	River Roding, UK Present work	River Shumarovka, USSR Smirnov (1974)	River Sunozhka, USSR Smirnov (1974)	River Il'd, USSR Smirnov (1974)	Species included in the littoral benthic taxocene of Cladocerans
Alona affinis	x	x	x		x	x	x		x		x	x	x	x		x	x			x		x	x		x	x	x	*
A. quadrangularis	x	x	x			x		x	x	x		x	x		x	x	x		x			x			x	x		*
A. rectangula			x						x						x	x	x	x						x				*
A. guttata								x							x				x									
Alonella excisa					x	x			x																			
Allonella nana					x	x			x																			
Camptocercus rectirostris					x	x		x							x													
Chydorus sphaericus			x	x	x	x			x	x					x			x							x	x	x	*
Acroperus harpae					x	x			x	x					x			x										*
Disparalona rostrata	x														x	x		x				x	x		x		x	*
Kurzia lattisima					x	x																						
Graptoleberis testudinaria						x			x																			
Leydigia leydigi				x		x	x	x		x					x	x			x		x	x	x		x		x	*
Monospilus dispar	x				x										x													
Eurycercus lamellatus		x				x	x		x		x	x	x	x	x			x										*
Pleuroxus uncinatus	x										x	x	x		x	x						x		x				*
P. trigonellus						x									x	x		x						x				
P. denticulatus					x	x																						
Iliocryptus sordidus			x	x			x	x	x	x		x	x		x	x	x	x	x		x		x	x				*
I. acutifrons		x	x																									
Macrothrix laticornis	x									x					x	x												

The following species occurred at only one of the locations listed above and were, therefore, not included in the Table:-
Alona barbulata, A. circumfibriata, A. Costata, Alonella exigua, Chydorus gibbus, C. piger, Leydigia acanthocercoides, Macrothrix hirsuticornis, Pleuroxus aduncus, P. procurvus, Pseudochydorus globosus.

The littoral benthic association, that is, that assemblage of species that is characteristically found in the benthos of the unvegetated littoral of lakes (Whiteside, 1970) and in the substrate of rivers, can be seen to include a taxocene* of cladocerans. A species was included in the taxocene if it occurred in six or more (that is, at least 20%) of the lakes and rivers in Table 8.

Littoral Benthic Taxocene of Cladocerans:-

Chydoridae	Macrothricidae
Acroperus harpae	*Iliocryptus sordidus*
Alona affinis	
A. quadrangularis	
A. rectangula	
Chydorus sphaericus	
Disparalona rostrata	
Eurycercus lamellatus	
Leydigia leydigi	
Pleuroxus uncinatus	

Although *Acroperus harpae* and *Eurycercus lamellatus* occurred frequently in the benthos of the lakes and rivers of Table 8 and were included in the littoral benthic taxocene, many workers have found them to be particularly associated with aquatic macrophytes (Sebestyén, 1948;

* A taxocene refers to a group of species, all members of a supra-specific taxon and occurring together in the same association (Chodorowski, 1959).

Smyly, 1958b; Smirnov, 1962, 1974; Fryer, 1963, 1968; Czeczuga, Golębiewski and Kossacka, 1970; Keen, 1973). Flössner (1964) states that *A. harpae* may be found in the benthos within plant beds and closer examination of Table 8 showed that *E. lamellatus* and *A. harpae* occurred most frequently in habitats where the mud substrate from which samples were taken was closely associated with beds of littoral plants (for example, Lake Itasca and the River Thames at Reading).

Many members of the taxocene are well-known inhabitants of the sediment. Flössner (1964) and Fryer (1968) found that *Alona affinis* associated preferentially with the bottom sediments and state that it frequently occurred in situations where there were no higher plants. However, Whiteside *et al* (1978) considered it to be a weed species and found the morphologically similar *A. quadrangularis* in mud habitats. Fryer (1968) noted that *Pleuroxus uncinatus* occurred on muddy substrates. *Leydigia leydigi* and *Iliocryptus sordidus* are truly benthic species and possess a number of relevant adaptations (Fryer, 1968, 1974).

Many of the studies referred to in Table 8 do not record *Disparalona rostrata*. Goulden (1971) found this species in the vegetation covered littoral of Lake Lacawac, and Jónnassen (1948) noted its presence in the vegetation covered areas of the River Susaa but not in the mud habitat. However, Sebestyén (1947) obtained a few individuals from

the mud of Lake Balaton and Fryer (1953) noted that it was very abundant in the thin layer of detritus covering stones in the Huddersfield-Ashton Canal. Bottrell (1977) found it to be common in the mud of the River Thames at Reading. Whiteside (1970) and Smirnov (1974) considered it to be characteristic of the unvegetated littoral substrate of lakes and Smirnov (1974) found it in the substrate of the River Il'd and Shumorovka. It was also obtained from the mud of several rivers in the present study.

Whiteside (1970) recognised that *Alona affinis, A. quadrangularis, Leydigia leydigi* and *Disparalona rostrata* were characteristic of the littoral benthic association of Danish lakes. Furthermore, in palaeolimnological studies of Grane Langsø he noted that members of the taxocene, namely *Chydorus sphaericus, Alona affinis, A. quadrangularis* and *A. rectangula* were true pioneer species occurring very early in the history of the lake at a time when aquatic macrophytes were probably absent.

Many species belonging to the littoral benthic taxocene are not confined to this habitat and are frequently abundant in others. *Chydorus sphaericus* and *Alona rectangula*, for example, are cosmopolitan, being found in the vegetation covered littoral and the limnetic regions of lakes. In the latter region they probably use planktonic algae as a feeding substrate (Whiteside, 1970).

Many members of the taxocene may be tolerant of a wide range of physical and chemical parameters providing

requirements of food and substrate are met (Fryer, 1968). *Alona affinis, Pleuroxus uncinatus* and *Iliocryptus sordidus* are within their known pH range (Lowndes, 1952) in the River Thames at Twickenham (Table 2). However, Lowndes (1952) states that *Alona rectangula* is found in waters of pH 4.2 to 8.4 while Røen (1962) found that this species generally occurred in waters of pH 5 to 7.5. Thus its presence at the Twickenham site extends its previously recorded limits. Many species in the taxocene occur at a wide range of temperatures. *Acroperus harpae, Alona affinis* and *Chydorus sphaericus* have been found at temperatures ranging from 3°C to 27°C. *Alona quadrangularis* and *Pleuroxus uncinatus* occur at temperatures up to 31°C, while *Alona rectangula, A. quadrangularis* and *Leydigia leydigi* have been found under the ice (Smirnov, 1974). The temperature range at the River Thames, Twickenham was 3° to 23°C and therefore the species present were within their known temperature ranges.

Crisman (1980), in a study of the distribution of chydorids in Florida, found that *Alona affinis* was largely restricted to soft-water lakes, with low phosphorus, alkalinity and conductivity values. Whiteside (1970), in his study on the distribution of Danish chydorids, noted that this species was one of the most common chydorids and found no significant correlations with phosphorus, alkalinity and conductivity.

Whiteside (1970) found that although *Acroperus*

harpae was a common component of the Danish chydorid fauna it occurred most abundantly at those localities characterised by low productivity, pH, conductivity and alkalinity. This species also tended to favour soft-water lakes in Florida (Crisman, 1980) and thus its absence from the Twickehham site was perhaps to be expected, although Bottrell (1977) found this species in the benthos of the River Thames at Reading.

These examples demonstrate that it is inadvisable to attempt a wider application of physico-chemical preferences observed for a particular species in a given locality. If chydorid distribution is related to the physico-chemical parameters of the environment it is quite possible that the relationship will only be indirect. The most important factor controlling the distribution of chydorids is probably the habitat availability for each species. Thus correlation between distribution and water chemistry may be a response to substrate type or may reflect the needs of aquatic macrophytes, whose presence, abundance and composition is one of the major determinants of littoral habitat diversity. Smyly (1958b) stresses that the distribution of species in lake district tarns was correlated more closely with the character of the bottom than with the altitude or water chemistry.

The absence of *Eurycercus lamellatus* from the Twickenham site was, initially, surprising especially as it was abundant in the River Thames at Reading (Bottrell,

1977). This species has a size at first reproduction of 1.8mm (Table 18) and this large size results in heavy losses from predation when fish are present (p.134). In the vegetation covered littoral of lakes and in rivers where aquatic plants are present the species is able to withstand this decimation because they become reproductive when quite small relative to their maximum size and have a high reproductive potential (Frey, 1973). They also show a preference for dense weed stands among which they spend much time resting motionless on plants or on their sides on the bottom (Frey, 1973). Several studies have found this species to be particularly associated with vegetation (Sebestyén, 1948; Smirnov, 1962; Fryer, 1963; Czeczuga *et al.*, 1970).

Thus the absence of *Eurycercus lamellatus* from the River Thames at Twickenham might be expected. Predation by fish is probably high and the absence of weed cover would result in the large *Eurycercus* being easily seen by fish. Predation by fish is also high in the River Thames at Reading but the dense stands of *Nuphar* allow *Eurycercus* to reach high levels of abundance (Bottrell, 1977).

PREDATION

The gut contents of fish collected from the River Thames at Twickenham are in accordance with those obtained from other more detailed studies. Hartley (1947), in a study of *Rutilus rutilus* (Roach) in the Norfolk Broads,

found that 5-15% of the diet of young fish consisted of cladocerans, including the genera *Eurycercus, Chydorus, Bosmina* and *Daphnia*. Britton (1968), working on fish in the River Thames found that the diet of Roach in the first three months of life was largely zooplankton while Mann (1973), who studied Roach in the Rivers Stour and Frome, noted that microcrustacea comprised 12% of their diet in July.

Hynes (1950), working on *Gasterosteus aculeatus* in Lake Windermere, found that 32% of the gut contents of fish of 6mm length were cladocerans including the genera *Alona, Chydorus, Eurycercus* and *Alonopsis*. He also noted that as fish size increased the percentage of cladocerans in the diet decreased.

Smyly (1955) found that *Noemacheilus barbatulus* (Stone loach) in Esthwaite water consumed *Chydorus* spp., *Alona affinis, Eurycercus* sp., *Peracantha truncata* and *Sida crystallina* and that 21% of the food of Stone loaches in the River Kent consisted of *Alona affinis*.

Phoxinus phoxinus (Minnow) from the River Chess did not prey on cladocerans although these were present in some abundance, however Frost (1943) found that littoral cladocerans were the major source of food for Minnows in Lake Windermere, she also noted that as fish length increased the percentage of cladocerans in their diet decreased.

The results of fish gut analyses from the River Thames and the River Chess support the often-stated fact that the Chydoridae, and cladocerans generally, are preyed upon by both fish and invertebrates (Fryer, 1968; Goulden, 1971; Berrie, 1972). Fish feed visually, removing the most conspicuous items (Werner and Hall, 1974; Zaret and Kerfoot, 1975). Thus the adults of any cladoceran species should be more vulnerable to fish predation than the juveniles and the results of the present study tentatively suggest that this was the case for the cladoceran species at the Twickenham site. Within a group of cladocerans the larger species are generally more visible and therefore should be subjected to heavier predation. In planktonic cladoceran communities large species, such as *Daphnia magna* and *D. pulex*, generally occur in very low abundance when fish are present in the habitat (Lynch, 1980). These species do not become mature until they reach 2.2mm and 1.4mm respectively (Lynch, 1980) and thus fish predation could eliminate all large individuals before they become reproductive. Frey (1973) noted that *Eurycercus glacialis* (mature at 3mm) was largely restricted to water bodies in which vertebrate predators were absent and Straškraba (1963, 1967) has shown that the removal of fish from littoral areas results in the replacement of small genera, such as *Chydorus* and *Pleuroxus*, by large ones such as *Eurycercus* and *Sida*.

The results of the present study show that, of the three predominant species *Alona affinis*, *Disparalona*

rostrata and *Leydigia leydigi* occurring at the Twickenham site, *Disparalona rostrata*, the smallest, is consumed by fish less frequently than might be expected from the relative abundance of the three species at this time. However, this may merely reflect differences in microhabitat preferences or behavioural adaptations.

In the absence of fish, invertebrates such as tanypod larvae are the major predators of cladocerans. Although these prey on cladocerans up to 1.5mm in length they prey most intensively on smaller individuals (Kerfoot, 1977). Fish also prey on tanypod larvae and these in turn prey on the smaller invertebrate predators (Anderson, 1970). The latter include cyclopoid copepods, *Chaetogaster* spp. and predatory rotifers and these prey on the smallest cladocerans (less than 0.5mm in length). When fish are present these smaller invertebrate predators become numerically more abundant and pressure on the smallest cladocerans may become intense.

Thus when fish are present, predation by fish increases with increasing cladoceran body size while that by small and large invertebrates decreases as the cladoceran body size increases.

When fish are absent, predation decreases with increasing cladoceran body size up to a length of about 1.5mm, beyond which individuals are relatively free from predation. Large invertebrates such as dragon fly larvae

are frequently present in the littoral environment and are known to prey on cladocerans. *Daphnia* as large as 3mm have been killed by dragon fly larvae (Johnson, Akre and Crowley, 1975; Thompson, 1975). However these were absent from the Twickenham site.

POPULATION DYNAMICS

Seasonal changes in the abundance of chydorid species found at the Twickenham site may be considered in conjunction with environmental factors. The midsummer maxima of the *Disparalona rostrata, Alona affinis* and *Leydigia leydigi* populations were the result of an increase in natality in response to the rise in water temperature that occurred in late May. Values of *b* showed a highly significant correlation with water temperature (Appendix VIII).

The duration of adult and juvenile instars and of egg development was less for *Leydigia leydigi* than for *Disparalona rostrata* at all temperatures (Tables 10 and 13). This being so, it is perhaps surprising that *L. leydigi* does not form a greater percentage of the midsummer peak in total chydorids. An examination of the birth rates indicates that those of *L. leydigi* are approximately double those of *A. affinis* and *D. rostrata*, as might be expected from the faster rates of development, yet this population potential was not realised and so high death rates were obtained. This suggests that *L. leydigi* may be subject to

heavier mortality than *D. rostrata* and *A. affinis* or that the rates of development determined in the laboratory are not realised in the field.

The most striking feature of the seasonal abundance pattern exhibited by numbers of total chydorids and the populations of chydorid species, is the sharp decrease in numbers after the midsummer peak and the subsequent low summer populations. This pattern is common among chydorid populations (Goulden, 1971; Keen, 1973; Whiteside, 1974; Williams, 1982).

The conjoint examination of the percentage of adult females with eggs, birth rate, death rate and abundance for each species population at this time may reveal the cause of the decline.

The percentage of adult females with eggs and the birth rate of the *Disparalona rostrata* population fell in mid-July, returning to their former levels in the course of the next fortnight. Abundance fell in mid-July remaining low until mid-August. Death rates peaked throughout July and early August.

The percentage of females with eggs in the *Alona affinis* population declined in late June, remaining relatively low throughout the population minimum and rising in mid-August. Numbers fell in mid-July and also remained low until mid-August. Birth rates also declined at this time for a period of two weeks. Although the fluctuations

in death rate were considerable a peak did occur from mid-July to early August.

The percentage of adult females with eggs and the birth rate of the *Leydigia leydigi* population declined in late June rising again in mid July. Numbers fell in mid-July. Although death rates fluctuated considerably a peak occurred at this time.

For the three species populations discussed, a fall in the percentage of adult females with eggs occurred at or before the time of the population crash. This was generally matched by a fall in the birth rate for the space of one or two weeks. Death rates peaked at this time and continued at a generally high level. Thus, the decline of the chydorid populations would appear to be the result of both a decrease in natality and an increase in mortality. The former must result from a fall in the number of eggs, that is, the percentage of adult females with eggs, as the water temperature and thus the rate of egg development continued high at this time. Although the birth rates of the chydorid populations suffered only a momentary decline, the fall in numbers was more permanent and was related to increased mortality.

Goulden (1971) lists several factors which may be associated with the midsummer decline in chydorid populations, including food limitation, high summer temperatures and biotic factors such as predation and parasitism. These are discussed in detail below.

1. Food limitation

An estimate of the food available to the cladoceran community was made in terms of the percentage organic content of the substrate. No significant correlation was found between this and abundance and birth rate of *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi* (Appendix VIII). This would suggest either that food is not limiting or that the measurement made was too crude to detect variations in the components of the mud that the cladocerans assimilated. A positive correlation, significant at the 5% level, was found between chlorophyll a concentration (a measure of algal abundance) and some chydorid abundances and birth rates but none was found between these and phaeopigments (Appendix VIII). If seasonal changes in chlorophyll a and chydorid abundance are compared there does not appear to be a common trend of increase or decrease in abundance. This suggests that the covariance of chlorophyll a and chydorid numbers and birth rates was probably due to the influence of an unknown factor on both variables.

If food is limited at this time then it is most likely to result in a decrease in natality. It is possible that food limitation may become so severe as to result in increased mortality (individuals starving to death) although live chydorids examined at this time appeared healthy and large numbers of recently dead individuals did not occur in the core samples.

Space is another resource that may become limited, resulting in overcrowding. However, Goulden (1971) and Whiteside *et. al.* (1978) have reported much denser populations of chydorids from the benthos of the unvegetated littoral of lakes and so this appears unlikely.

2. High summer temperatures

Maximum water temperatures occurred at the beginning of June at a time when the chydorid populations were increasing rapidly and thus the decline in numbers a month later cannot be attributed to a single peak of high temperature. At the time of the populations decline, temperatures had been consistently high for a month (average temperature 19.3^{o}C for June) and it is possible that prolonged high temperatures may have adversly affected the chydorid populations. However, stocks of *Disparalona rostrata* and *Leydigia leydigi* were maintained in the laboratory at 19^{o}C for long periods of time without excessive mortality occurring.

3. Biotic factors

The decline of the chydorid populations was partly caused by an increase in mortality for which emigration, death due to old age ('natural' mortality), parasitism or predation may have been responsible.

River rates of flow are low at this time of year ($22.6m^3\ s^{-1}$ at Teddington weir, from T.W.A. statistics 1979) and no flooding occurred during this period. Thus,

it is unlikely that the decline in numbers was due to enforced emigration resulting from large numbers of chydorids being 'flushed' out of the substrate by fast rates of flow. Voluntary emigration on a large scale also appears unlikely as chydorid counts from the plankton samples remained at very low levels during this period.

Chydorids cultured in the laboratory have life spans that are measured in weeks, even at high summer temperatures. Therefore 'natural' mortality cannot significantly account for such a high rate of mortality.

Peritricha were found attached to some chydorid species but their numbers did not noticeably increase during the summer, endo- and ectoparasites were not visible and live chydorids observed at this time seemed healthy.

It would appear from the foregoing discussion that predation must be a major causal factor of the increased mortality observed in the chydorid populations. Young fish are known to feed on chydorids (Smirnov, 1962; Keen, 1973; Bottrell, 1977; Adalsteinsson, 1979) and from late June until the end of August, large shoals of young fish were seen over the Twickenham sampling site. An examination of their gut contents showed that chydorids were consumed in considerable numbers. *Iliocryptus sordidus* was never found in fish guts, probably because this species lives deep in the sediment. The sharp population decline and subsequent low summer abundance exhibited by the chydorid species was not shown by *I. sordidus* whose numbers increased from mid-

summer onwards. This would seem to uphold the supposition that predation by young fish is a major factor in the pattern of abundance shown by the chydorid populations during the summer months. Goulden (1971), Keen (1973) and Williams (1982) also found that the summer crash in chydorid populations was caused by predation and several studies on planktonic cladocerans (Hall, 1964; Wright, 1965; de Bernardi, 1974) have related the low summer populations of *Daphnia* spp. to an increase in mortality due to predation.

Thus the midsummer decline of the chydorid populations resulted from both a decrease in natality and an increase in mortality in the populations. The decrease in natality was transient and may have been brought about by food limitation. The increase in mortality was more permanent and appears to have been caused by an increase in predation on the chydorid populations.

Bottrell (1977) found that the death rate (d) in populations of *Sida crystallina* and *Chydorus sphaericus* in the River Thames at Reading was greatest when population density was at a maximum. Mortality was largely due to predation by *Perca fluviatilis* in the first species and by *Hydra* and *Chaetogaster* in the second, and was density dependent, becoming greater when the population density increased and less as it decreased. This was not the case for the chydorid species in the River Thames at Twickenham. Although death rates increased throughout June and early July, maximum values did not occur until late July and

early August when population densities were at a minimum, implying that mortality was not density dependent in this study. De Bernardi (1974) also noted that values of *d* for *Daphnia hyalina* in Lago Maggiore did not reach a maximum until after the population density maximum had passed.

The mean adult lengths (M.A.L.) of *Disparalona rostrata, Alona affinis* and *Leydigia leydigi* fluctuated considerably in the course of the season, tending to be higher in the winter and spring than in summer for all three species. Results from the growth studies on *D. rostrata* and *L. leydigi* (Section 10.1.) indicate that, at low temperatures in culture, females of these species increase in size more slowly but reach a larger final size than females cultured at higher temperatures. Green (1956) found the same for *Daphnia magna*. Thus, the higher winter and spring M.A.L's reflect the influence of low water temperatures and, in *A. affinis* and *L. leydigi* the presence of large and overwintering females in the population. In June, as the water temperature rises and the cladoceran populations increase, large numbers of young individuals are recruited to the adult populations and the M.A.L's decrease and remain low throughout the summer. During the autumn M.A.L's of *A. affinis* and *L. leydigi* again increase reflecting the falling water temperatures. Predation on the chydorid populations by fish also affects the M.A.L. as these predators select the most conspicuous individuals,

thus during the summer months when this type of predation is high (p. 84) the M.A.L's are at a minimum.

M.A.L's also reflect the survivorship of adults. Periods of high average size correspond to periods of low mortality and therefore increased life expectancy in each of the three species.

Culver (1980) found that for *Chydorus sphaericus* the size at first reproduction (SFR) and the size of neonates varied throughout the season, being typically low in summer and high in spring and autumn, that is, they tend to decrease with increasing temperature. He suggested that this might ultimately be caused by a pronounced seasonality in predation although the immediate cause was probably one or more environmental cues, such as temperature. In the present study, although the size of eggs and neonates tended to decrease with increasing temperature for each of the three most common chydorid species in both field and laboratory (pp 190 and 191), the SFR remained constant.

Results from the core sampling series revealed that *Iliocryptus sordidus* possessed an extremely clumped distribution. During population maxima some cores contained several individuals resulting in a projected population density of $50{,}000m^{-2}$ while other cores had none. This is explained by the studies of Chirkova (from Fryer, 1974). She found that neonates just emerged from the parent brood pouch could swim and therefore those shed at the mud

surface could effect some dispersal. However, young shed within the mud did not disperse at all, resulting in aggregations of individuals. This condition is aggravated by the fact that when food is abundant females are essentially sedentary moving less than 1cm in twenty-four hours (Chirkova, from Fryer, 1974).

The seasonal abundance pattern of *I. sordidus* differed considerably from those of the chydorid populations, the midsummer peak and subsequent population crash, found among all the abundant chydorid species, was absent and the major population peak occurred in the autumn. Population density was still high at the end of the sampling season but the composition of the population (decreasing percentage of juveniles and a low percentage of adults carrying eggs together with a small mean clutch size) indicated that density would shortly decrease.

Although many studies have noted the presence of *I. sordidus* (Table 8) few have made a detailed study of its seasonal abundance. Smyly (1958) did so, in a three year study of two moorland pools. His results broadly agree with those of the present study. In both, population maxima tended to occur in the late summer and autumn with population minima in the spring and early summer.

The population of *Iliocryptus sordidus* overwintered as large parthenogenetic females at the Twickenham sampling site. Although sexual reproduction has been observed in

this species (Scourfield and Harding, 1966) it did not occur in the River Thames at Twickenham or the River Thames at Reading (Bottrell, 1977). This species was also unique among the benthic cladocerans in Lake Port-Bielh, a high mountain lake in the central Pyrenees, in overwintering as parthenogenetic females (Rey and Dupin, 1973).

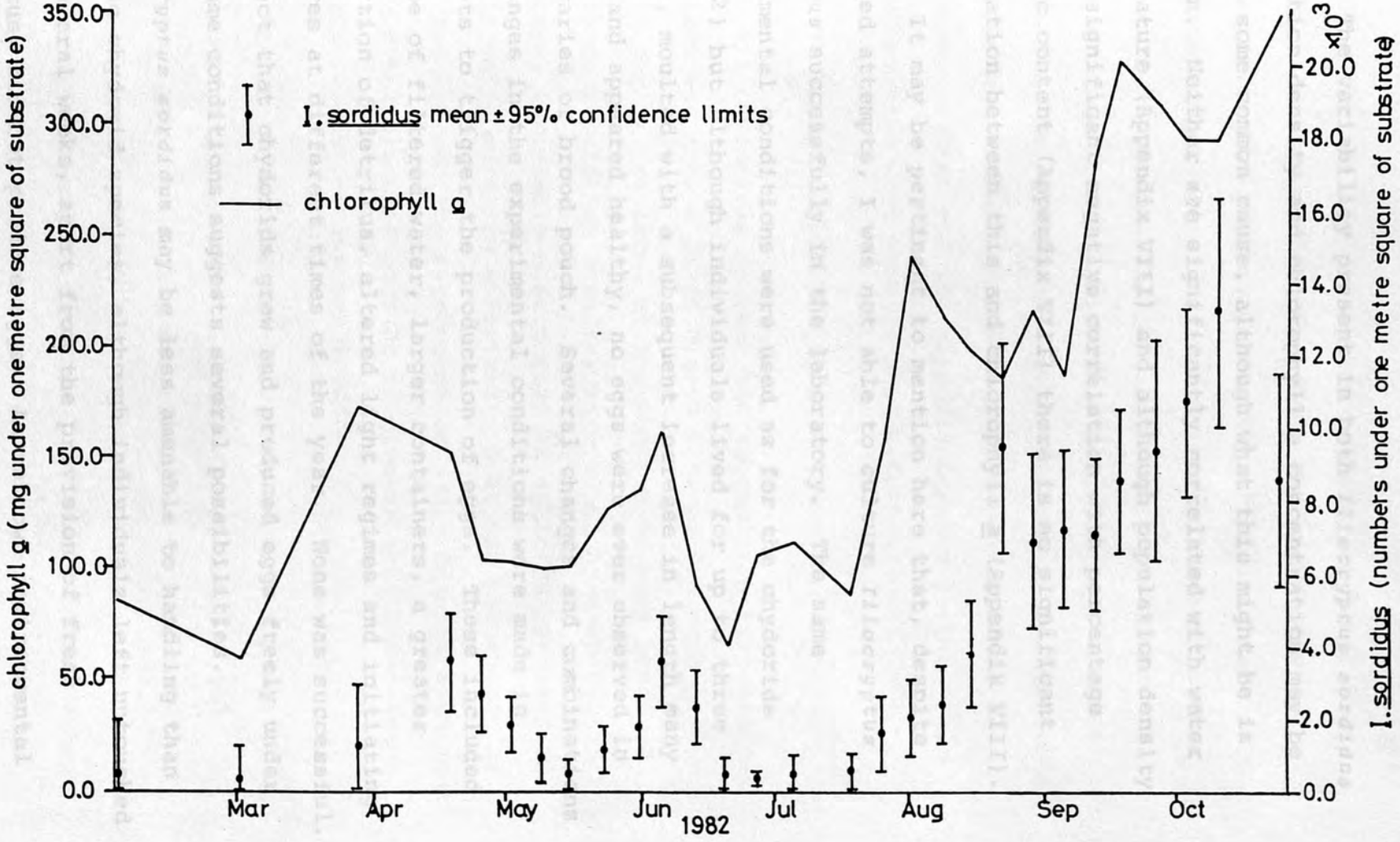
Adult *Iliocryptus sordidus* are comparatively large, body lengths ranging from 0.77-1.2mm at the Twickenham site. When the long posterior and ventral spines and the detrital masses attached to the carapace are considered, the actual size is much larger and must discourage the majority of invertebrate predators (p.135). Vertebrate and invertebrate predation seems unlikely to be a major direct factor in the regulation of adult *I. sordidus* population numbers. Juveniles are much smaller (neonates approximately 0.35mm in length) and in the early instars the detrital camouflage so characteristic of the adults is not present, thus invertebrate predation may have a significant effect on the juvenile population.

The sharp decline in the percentage of egg-bearing females in the adult population and the mean clutch size in late June and early July strongly suggests that the population is limited by an environmental factor or combination of factors at this time. This change in the population composition is frequently associated with food shortage (p. 142), but numbers of *Iliocryptus sordidus* did not give a significant positive correlation with

percentage organic content of the substrate although this may merely mean that this measurement of "available food" was insufficiently sensitive (p.139).

A significant positive correlation was found at the 1% level of significance between chlorophyll a and *Iliocryptus sordidus* population density (Appendix VIII). When plotted together (Fig. 38) peaks in chlorophyll a were frequently found to correspond to, or just precede, those of *I. sordidus*. A similar trend was noted for phaeopigment and population density although this was partially masked by wide phaeopigment fluctuations in the autumn. In this case there was no significant correlation between the two variables. The biological significance of the correlation, if it esists, is difficult to determine. That the two variables are interdependant is indisputible, but, statistically it cannot be assumed that chlorophyll a concentration is the cause of variation in population density and biologically it is perplexing to see how this could be so. *I. sordidus* density was not significantly correlated with phaeopigment concentration and yet it is this degredation product, via dead and dying phytobenthos and detritus, with which the burrowing *I. sordidus* would largely come into contact. The epipelic phytobenthos association (chlorophyll a) is largely restricted to the surface sediments, phytobenthic associations living within the sediment are virtually unknown (Holme and Mc Intyre, 1971).

FIGURE 38. Seasonal changes in mg chlorophyll a and numbers of Iliocryptus sordidus under one metre square of substrate in the River Thames, Twickenham.



The variability present in both *Iliocryptus sordidus* population density and chlorophyll a concentration may be due to some common cause, although what this might be is unknown. Neither are significantly correlated with water temperature (Appendix VIII) and although population density has a significant negative correlation with percentage organic content (Appendix VIII) there is no significant correlation between this and chlorophyll a (Appendix VIII).

It may be pertinent to mention here that, despite repeated attempts, I was not able to culture *Iliocryptus sordidus* successfully in the laboratory. The same experimental conditions were used as for the chydorids (p. 162) but although individuals lived for up to three months, moulted with a subsequent increase in length many times and appeared healthy, no eggs were ever observed in the ovaries or brood pouch. Several changes and combinations of changes in the experimental conditions were made in attempts to trigger the production of eggs. These included the use of filtered water, larger containers, a greater proportion of detritus, altered light regimes and initiating cultures at different times of the year. None was successful. The fact that chydorids grew and produced eggs freely under the same conditions suggests several possibilities. *Iliocryptus sordidus* may be less amenable to handling than are the chydorid species, although individuals left untouched for several weeks, apart from the provision of fresh detritus, did not produce eggs. An unknown environmental factor or combination of factors not present or not

reproduced in the laboratory and not effective, or less important, for chydorids may affect the egg production and therefore the population density of *I. sordidus*. The population density of *I. sordidus* may be limited in the first half of the year by the high densities of the chydorid populations. This would not, however, account for the failure of the laboratory cultures as no chydorids were present in the detritus and experiments initiated at periods of high and low chydorid density at the Twickenham site were equally unsuccessful.

FIXED AND VARIABLE CLUTCH SIZE SPECIES

All Chydoridae (except the subfamilies Eurycercinae and Saycinae) have a fixed clutch size of two eggs per brood. Parity, in terms of the numbers of eggs produced at a given population density, with cladoceran species possessing a variable clutch size is achieved by means of a different population structure. Both the percentage of adult females and the percentage of adult females with eggs in the fixed clutch chydorids is greater than those found in variable clutch size populations.

In the River Thames, Twickenham, adult females of the chydorids *Disparalona rostrata, Alona affinis* and *Leydigia leydigi* generally comprise more than 60% of their respective populations while adult females with eggs were nearly always more numerous than those without eggs, at times forming 90% of the adult populations. Bottrell

(1977) found a similar population structure among the fixed clutch chydorids in the River Thames at Reading. However, he found that cladoceran populations with a variable clutch size usually consisted of 60-80% juveniles while egg-bearing females averaged 20-30% of the adult female population. In the present study, an average of 60% of the *Iliocryptus sordidus* population (variable clutch size) was juvenile while females with eggs averaged 50% of the adult population.

Populations of chydorid species have a lower percentage of the population in the juvenile stage than medium and large size planktonic cladocerans because relatively larger young are produced (Chapter 12). These are closer to the species size at maturity and so mature early, thereby decreasing the length of time spent in the juvenile phase. This is thought to be an adaptation to minimise the effect of invertebrate predation (p. 222).

Species with a variable clutch size respond to food limiting conditions by reducing the number of eggs per clutch (de Bernardi, 1974). Fixed clutch species presumably respond by reducing the number of egg bearing females in the population, or by reducing the clutch size to one egg, or both. Nauwerck (1963) observed limnetic individuals of *Chydorus sphaericus* carrying one egg and attributed it to low food conditions while Keen (1973) noted that the percentage of one egg females increased when populations of *Graptoleberis testudinaria* and

Camptocercus rectirostris reached their maximum density. In the present study chydorids carrying one egg were never observed.

SEXUAL REPRODUCTION

In the River Thames at Twickenham sexual reproduction was found to occur in only one chydorid species, *Disparalona rostrata*, although it has been observed in other populations, *Alona affinis, A. quadrangularis* (Rey and Dupin, 1973), *A. rectangula* and *Leydigia leydigi* (Smirnov, 1974).

The causes of the shift in the mode of reproduction from parthenogenetic to sexual in cladocerans are still not clearly understood but are undoubtedly environmental (Hutchinson, 1967). The production of ephippial females is related to a rapid decrease in available food (Slobodkin, 1954), short day photoperiod and population density (Stross and Hill, 1965). Male production is thought to be influenced by food supply and temperature (Banta, 1939) and possibly photoperiod and light intensity (Shan, 1974).

The occurrence of sexual reproduction in the Chydoridae is variable indicating that a complex of stimuli may be involved. Goulden (1971) and Smirnov (1974) found that all the chydorid populations in Lake Lacawac and the Upper Volga reservoirs, respectively, underwent a sexual phase in the autumn while Keen (1973) noted that although this was the case for most species in Lawrence Lake, *Chydorus*

sphaericus overwintered as parthenogenetic females. Bottrell (1977) found that sexual reproduction occurred only in *Sida crystallina* in the River Thames at Reading and that all the chydorid species retained populations of parthenogenetic females throughout the winter.

In those instances where the chydorid community is associated with aquatic macrophytes, the decline of the latter in autumn, with a subsequent decrease in shelter and food availability might be expected to trigger sexual reproduction. This may have been so in Lake Lawrence (Keen, 1973) but it did not occur in the chydorid community associated with the *Nuphar* beds in the River Thames at Reading (Bottrell, 1977).

In Lake Balaton (Sebestyén, 1947) and in the River Thames at Twickenham, some species belonging to the benthic cladoceran community underwent sexual reproduction in the autumn while others did not. This suggests that various chydorid species utilise different components of the ingested detritus and that shortages of some of these occur in the autumn. Alternatively, the degree of influence of the various environmental factors may vary from species to species resulting in the triggering of sexual reproduction in some species in the community but not in others.

Two types of cladoceran life history are represented in the River Thames at Twickenham. *Disparalona rostrata* is an aestival species. Individuals appear sporadically in

the late spring and multiply to produce a large population. In the autumn, males appear and resting eggs are produced from which the population is recruited in the following spring. The population of *Disparalona rostrata* is monocyclic (that is, the mode of reproduction is altered once from parthenogenetic to sexual during the annual cycle). The other cladoceran species present are perennial, overwintering as adults rather than resting eggs and the populations are acyclic (no change in the mode of reproduction). Population numbers increase greatly in the spring and decline in the late autumn, only a small part of the population overwinters.

The life history exhibited by a given species may vary from location to location, thus in the River Thames at Reading, *Disparalona rostrata* is a perennial species (Bottrell, 1977) while Goulden (1971) found it to be aestival in Lake Lawrence. Berg (1931) found that, in Denmark, *Daphnia longispina* was perennial in some localities and aestival in others. Hutchinson (1967) noted that this variation was common among the Cladocera.

P A R T I I

Studies on life histories, growth and production of some chydorid species.

CHAPTER 8 : Introduction

The standing crop data obtained by quantitative sampling of the chydorid community is of limited application to the interpretation of the dynamics of the community. The life histories and development times of the constituent species must also be determined. When these are combined in various ways with data on density and individual weight they provide the time element necessary for the calculation of instantaneous birth, death and growth rates and the production of continuously reproducing species.

The life histories and rates of embryonic and post-embryonic development of several chydorid species have been published in the literature (Smirnov, 1964; Shan, 1969; Keen, 1973; Bottrell, 1975a, b; Murugan and Job, 1982). However, the duration of development and life histories of two of the three most abundant chydorids at the Twickenham site (*Disparalona rostrata* and *Leydigia leydigi*) have not yet been examined.

Bottrell (1975a, b) found significant differences between regression lines of temperature and duration of development plotted for individual chydorid species. Thus it is necessary to calculate the duration of development for each species rather than obtain data from a generalised regression line plotted for the Cladocera as a whole.

The duration of embryonic and post-embryonic

development in the Cladocera differs fundamentally in that the duration of the former is a significant function of temperature, whereas the duration of the latter is a function of both temperature and food (Bottrell *et al.*, 1976). Previous investigations on post-embryonic development have considered either the effects of various food concentrations at one temperature (Weglénska, 1971) or the effect of various temperatures under conditions of excess food (Bottrell, 1975b). Rocha (1983), however, considered both the effects of food and temperature on planktonic cladocerans.

Mann, Britton, Kowalczewski, Lack, Matthews and McDonald (1972) and Berrie (1976) have shown that the pattern of energy flow in the River Thames is dominated by the detritus food chain. The main food of most Chydoridae and Macrothricidae is detritus (Smirnov, 1974), a major exception being *Anchistropus emarginatus*, which is parasitic on *Hydra* spp. Studies by many authors, including Hartley (1947), Britton (1968) and Mann (1973) have indicated that benthic and epiphytic Cladocera are an important source of energy for young fish. Fryer (1968), Goulden (1971) and Berrie (1972) state that they are also fed upon by predatory invertebrates. Thus, benthic Cladocera, by reason of the high levels of abundance that they can attain, form an important trophic link between detritus and predatory invertebrates and young fish. As the cladocerans die and decompose they also form an important

source of detritus. Calculation of the production of the species populations within the benthic cladoceran community thus provides important information on the ecosystem as a whole. Knowledge of production, initially at the level of species populations within the ecosystem and then for the ecosystem as a whole, is basic to an understanding of the organisation of natural communities and of the ability of different kinds of waters to produce and maintain populations of particular abundance and composition (Edmondson and Winberg, 1971).

Unlike primary production, for which the rate of radiocarbon uptake provides a simple and direct measurement of the basic photosynthetic process, no single measurement can be used effectively to characterise the secondary production of a community. Values are calculated indirectly from population size and physiological data.

Winberg (1971) defines the production of a species population as the sum total of growth increments of all the individuals forming that population, including growth due to sexual products and other organic products (for example, exuviae) which become separated from the body during the period under consideration. Individual growth is defined as a process of increase in mass in a developing organism (Winberg, 1971). These definitions have been adopted in the present study.

CHAPTER 9 : Methods

SECTION 9.1. Life histories and growth of *Disparalona rostrata* and *Leydigia leydigi*

Information on the life histories and growth of *Disparalona rostrata* and *Leydigia leydigi* is not available in the literature. As growth curves for each species corresponding to the four seasons of the year were required for production calculations (p.170), the mean water temperature at the Twickenham site for each of the four three monthly periods was calculated during 1982:

	mean water temperature ^{o}C
(1) December, January and February	5
(2) March, April and May	10
(3) June, July and August	19
(4) September, October and November	14

The life histories and growth of *D. rostrata* and *L. leydigi* were examined in detail at these temperatures. It proved impossible to culture *D. rostrata* at $5^{o}C$: the stock females at this temperature rarely produced eggs and the young resulting from these died before maturity. In an attempt to overcome this problem, $5^{o}C$ cultures were initiated in the summer in case the winter mud inhibited growth, these were equally unsuccessful. The growth of *D. rostrata* was, therefore, studied at three temperatures (10, 14 and $19^{o}C$) only.

Animals were collected from the sampling site when the water temperature was $\pm$ 1°C of that at which they were to be cultured in the laboratory. After collection, they were grown through two generations under experimental conditions (see below) to eliminate any possible effects of changes in environmental conditions which may be passed from parent to offspring (Agar, 1913; Hall, 1964; Keen, 1967). *Disparalona rostrata* females from the sampling site could not be collected at the correct temperature for the 5°C cultures as free-swimming individuals were absent at this time of year (p. 99). Instead, an attempt was made to culture individuals from a stock of females originally collected at 10°C and gradually lowered to 5°C.

In preliminary experiments algae were used as a food source with the intention of estimating food consumption. Animals were first given *Chlorella* sp. CCAP 211/8P which had been cultured on agar slopes at room temperature in front of a continuously operating fluorescent lamp. *Chlorella* cultures approximately four weeks old were always used, as it has been shown that the nutritional quality of the alga changes with age (Pearsall and Loose, 1937). The chydorids grew very poorly on this alga resulting in 100% mortality by the end of the second juvenile instar. *Chlorella* was ingested, as it could be seen in the gut, but it was excreted apparently unchanged since the faeces consisted almost entirely of discrete algal cells. Smirnov (1974) found that *Chydorus sphaericus* and *Eurycercus*

lamellatus died within a few days when cultured on green planktonic algae. Two filamentous algae, *Phoridium* and *Mastigocladium*, were also used but similar rates of mortality occurred.

Smirnov (1962, 1964), Keen (1967) and Bottrell (1975a, b) successfully used detritus as a food source during their experiments with Chydoridae and it was decided to do likewise in this study. The use of detritus meant that it was not possible to quantify the amount of food added to the culture (p.51). However, it is the natural food source of the chydorids studied and thus possible adverse effects on growth and reproduction, due to feeding on an artificial source of food, are eliminated. Surface mud was collected weekly from the sampling site and kept aerated in a tank at the experimental temperature. Before it was used in chydorid cultures, it was examined under a dissecting microscope and any cladocerans and possible predators removed.

Detritus was given in excess (see below), but to ensure that this was the case the following experiment was initiated. Eighteen neonatae of *Leydigia leydigi* were isolated from a stock culture of females which had been grown through two generations at 19^{o}C. The neonatae were supplied with twice the usual amount of detritus and water (p. 162) but, apart from this, normal experimental conditions were maintained (P. 162). Individuals were examined in the same way as the other cultures (p. 163).

The results were then compared with those from *Leydigia leydigi* cultured at 19°C on the usual quantity of detritus, no significant differences were found and it was concluded that excess detritus was indeed being provided.

Cultures were set up at the beginning of each of the four, three-monthly periods, at the temperature appropriate to each period. The animals were cultured in tap water which had been aerated at the experimental temperature for at least forty-eight hours before use.

For the given temperature, a stock of twenty second generation adult females of each of the two species was isolated, placed individually in 150ml crystallising dishes and provided with 25ml of water and sufficient detritus to form a layer 2-3mm deep at the bottom of the dish; food and water were changed thrice weekly. The dishes were then covered, to reduce evaporation and protect against dust, and placed in constant temperature rooms at $\pm$ 0.5°C of the experimental temperature. A light regime of twelve hours fluorescent illumination and twelve hours darkness was maintained (these will in future be known as experimental conditions). These females were examined daily and as young were produced they were isolated under experimental conditions. Eighteen neonatae were thus obtained and these became the experimental sample.

Keen (1967) used a sample size of twenty-five when studying life histories of *Chydorus sphaericus* and *Pleuroxus*

denticulatus, Smirnov (1964) used seventeen *Pleuroxus aduncus* and sixteen *P. striatus* while Hall (1964) used ten individuals at each experimental condition for his studies on *Daphnia galeata mendotae*. In the present study, the sample size for each species at each temperature was eighteen, the sample size could not be increased further as the time involved each day in examining the cultures would have been too great. Any replacements required were obtained from the same stock of females.

Juveniles were measured daily, to the nearest 0.007mm, under a binocular microscope using a calibrated micrometer eyepiece. The method of measuring juveniles was the same as that of adults (Fig. 2). Adults carrying eggs were examined daily but only measured when new eggs were laid. This reduced the handling of the animals and thus the likelyhood of damage. Any young produced were measured. Adults without eggs were treated as juveniles.

The following characters were determined for each species and temperature:-

a) duration of juvenile and adult instars
b) number of juvenile and adult instars
c) initial length of individuals becoming mature in the third and fourth instars, percentage of individuals maturing at each of these instars
d) duration of egg development
e) length of life
f) increase in length of individuals at each moult

g) number of young produced in total by each individual and the length of each young so produced.

The relationship between body length (mm) and body weight in terms of µg of carbon was determined using the wet dichromate oxidation procedure described by Golterman (1969) and Mackereth, Heron and Talling (1978). Full details of the method are given in Appendix XII. Growth in terms of increase in length can thus be converted to growth in terms of increase in µg carbon. As the duration of development, growth increment (in µg C) at each moult, number of young produced and the weight (µg C) of these young are known, average growth curves for each species at each of the four temperatures can be constructed. For adults the mean weights of young produced in that and previous instars were added to the mean weight of the adult to provide the total weight.

A number of cultures of *Alona affinis* and *Leydigia leydigi* were established (using parthenogenetically reproducing females) in the hope of observing males which were not found at the Twickenham site. Cultures were kept at 5 and 10°C and a little fresh detritus was added every other week. It was hoped that the small amount of detritus added would result in the cultures becoming semi-starved. They were examined for males at fortnightly intervals.

SECTION 9.2. Relationship between egg volume/size of young and parent size/age for some chydorid species

Agar (1914) has shown for a monoclonal population of *Simocephalus expinosus* that " ..... when the size of the parent is constant, the size of the eggs, as estimated by the size of the young developing from them, varies inversely as their numbers. Given the number of eggs to be the same, their size varies as the size of the animal which laid them."

The Chydoridae (except the subfamilies Eurycercinae and Saycinae) produce a maximum of two eggs per brood and are thus suitable species to use for examining the latter part of the above statement. For such a study to be valid all females must be taken from one place at one time (Green, 1956). A sample of mixed chydorids was taken from the River Thames at Twickenham in August (water temperature 19°C). Females were measured to the nearest 0.007mm and the eggs teased out. These were floated in river water, the greatest and least diameter of each egg was measured and the volume found using the formula:

$$V = {}^{1}/_{6}\ \pi\ g l^{2}$$

V = egg volume

g = greatest egg diameter

l = least egg diameter.

from Green (1956) and Burgis (1967). Eggs were measured while the outer membrane was still intact, that is during the second stage of development using the categories described by Green (1956). Newly laid eggs, identified

by their opacity and transparent edges, were avoided as eggs tend to swell when first laid and do not attain their maximum size until a few hours after laying (Green, 1956). *Alona affinis*, *Leydigia leydigi* and *Disparalona rostrata* were examined in this way.

A number of measurements were made of eggs obtained from the Twickenham site at different water temperatures (10° and 14°C) to determine whether the size of eggs produced by individuals of the same species and size varies with temperature.

Green (1954) found that, for *Daphnia magna*, the size of the young also varied with the age of the mother. To determine whether this was so for *Disparalona rostrata* and *Leydigia leydigi*, data were collected for each species at 5°C (*L. leydigi* only), 10°, 14° and 19°C concerning the size of the young liberated in the first, second, third, fourth, fifth, seventh and ninth broods. The data were obtained from females used in the growth experiments (p. 162). For the first brood the number of young in each of a series of length classes was noted, the percent frequency of young in each length class was then calculated. This was repeated for the remaining broods.

SECTION 9.3. Production of three chydorid species in the River Thames, Twickenham

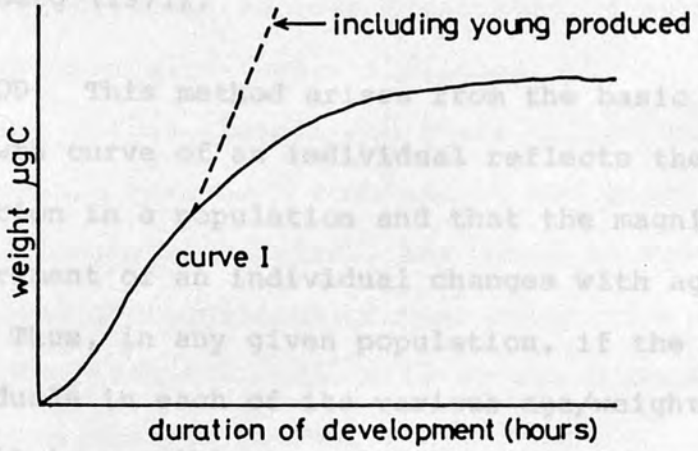
Edmondson and Winberg (1971) identify two general approaches to the determination of production. The first approach is via the birth and death rates and the structure of a population in terms of age and size, that is the dynamics of the population. The second investigates rates of feeding, assimilation and respiration in individuals of the population. The first approach was used in this study as much of the data needed had already been collected in connection with the determination of the dynamics of the species populations in the chydorid community and the life histories and growth of *Disparalona rostrata* and *Leydigia leydigi*.

The annual production of each of the three most abundant species, namely, *Alona affinis*, *Disparalona rostrata* and *Leydigia leydigi* was estimated. As these species comprised, on average, 97% of the benthic chydorid community, the results were summed to provide an annual production estimate for the whole chydorid community.

Reproduction and the recruitment of young to the populations of benthic chydorids was continuous and thus methods of calculating production which were based on cohort recognition could not be used. Instead, production was estimated using a graphical method for populations with continuous reproduction developed by Greze and Baldina

FIGURE 39. Stages in the estimation of daily production in a species population.

(a) Average growth curve.



(b) Relationship of daily growth increment to size class (curve II). Size frequency of the population (curve III).

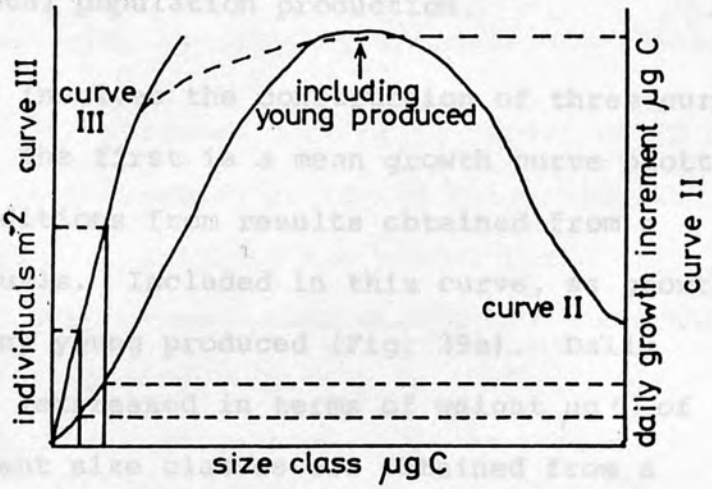


TABLE 9 Stages in the estimation of daily production in a species population.

weight class µg C	daily growth increment µg C	number of individuals m^{-2}	daily production µg C m^{-2}
			total daily production

(1964) and Winberg, Pechen and Shushkina (1965) and summarised by Winberg (1971).

PRINCIPLE OF METHOD: This method arises from the basic idea that the growth curve of an individual reflects the process of production in a population and that the magnitude of the growth increment of an individual changes with age (Winberg, 1971). Thus, in any given population, if the numbers of individuals in each of its various age/weight groups are known it is possible to calculate the combined growth increments for a defined period of time, which represents the total population production.

The method involves the construction of three curves (Winberg, 1971). The first is a mean growth curve plotted for specified conditions from results obtained from a number of individuals. Included in this curve, as growth increments, are any young produced (Fig. 39a). Daily growth increments (expressed in terms of weight µg C) of animals of different size classes are obtained from a series of points along the curve. These values are plotted as a second curve (Fig. 39b) relating daily growth increment to size class (also expressed in terms of weight µg C). The third curve, also plotted in Figure 39b, reflects the size (weight µg C) frequency of the population using data obtained from field observations. The data for Curve III are plotted cumulatively so that the highest point corresponds to the total number of individuals in the population sample. Egg production represents a further increment in individual

weight and the dotted part of Curve III portrays mature individuals who have produced various quantities of eggs and so belong to various size (weight) classes. The frequency of various weight classes and their corresponding daily growth increments have been combined in one graph and production can now be calculated. The graph is subdivided into vertical sections each corresponding to a weight category. For each the mean daily growth increment and the number of individuals present in the weight category are determined and tabulated. Daily production for the population is obtained by multiplying these figures for each weight category and summing the products (Table 9).

Winberg (1971) stresses that it is important to build up reliable data on production estimates throughout the year. He suggests that dividing the annual cycle of observations into four seasons each with a known average temperature will provide sufficiently reliable values for the estimation of annual production and this procedure has been followed.

Of the three species for which production was to be calculated in the present study, the life history and growth of *Disparalona rostrata* and *Leydigia leydigi* had already been studied in considerable detail (Section 9.1.). The mean length per instar and the duration of juvenile and adult instars for both species at each of the four temperatures had already been determined, as had the mean length of young produced in a given instar. Likewise, the

averaged growth curves had already been plotted (Fig. 40 and 41). Although the life history of *Alona affinis* has been studied by Bottrell (1975a, b) details of growth were not available. *Alona affinis* was, therefore, cultured at 19°C using the same number of individuals and methods described in Section 9.1. The growth data thus obtained was used, in conjunction with details of the duration of juvenile and adult instars determined by Bottrell (1975b) to construct average growth curves at the four experimental temperatures (Fig. 42). As *Alona affinis* was cultured only at 19°C the growth increments per instar determined for this temperature are shown in all the growth curves, thus reducing their accuracy. However, the time required to culture *A. affinis* at all four temperatures was not available.

Greze and Baldina (1964), working on copepods, stated that the growth curve should reflect the growth characteristics of both male and female individuals. However, reproduction in the benthic cladocerans studied was largely parthenogenetic: *Disparalona rostrata* was the only species where males occurred in the field and then only for two or three weeks of the year. Males were not incorporated in the growth curve.

The size frequencies in terms of numbers per square metre in each length class of the three species populations had already been determined as part of the weekly sampling programme in 1982 (p. 44). The maximum lengths of each

length class for each species were converted to µg carbon using the regressions in Appendix XII and the numbers in each length class were plotted cumulatively against these weights. The production of young represents a further increment in individual weight and this must be expressed in the curve. Considerable growth curtailment (in terms of length) occurs after maturity in *Disparalona rostrata* and *Leydigia leydigi* and thus the number of young that an individual in a given length/weight class has produced can only be estimated. If individuals of the maximum size in a given length class are considered, an examination of the data used to construct the growth curve appropriate to that season will give an indication of the minimum number of young these individuals could have produced (provided barren adult instars did not occur). The maximum weight of the class and weight of these young were then summed and the total number of individuals so far plotted against this summed value (curve III). Daily production was then calculated. The graph on which curves II and III were plotted was divided into vertical sections, each of which corresponded to a weight category. The size of these categories depended on the nature of changes in the two curves; when they showed large changes the weight categories were narrow but where less change occurred the categories were wider.

The *Disparalona rostrata* graphs were divided into five weight categories: 0-1, 1-2, 2-3, 3-6, and 6-10µg C.

The *Leydigia leydigi* graphs were divided into eight weight categories: 0-2, 2-3, 3-4, 4-10, 10-16, 16-22, 22-28 and 28-32µg C.
The *Alona affinis* graphs were divided into six weight categories: 0-1, 1-2, 2-3, 3-5, 5-10 and 10-14µg C.

Daily production for each of the three species populations was calculated each time a sample was taken from the Twickenham site, that is, weekly from mid-April to mid-October. On each date the growth curve appropriate to the season was used to construct curve II. The number of days to the next sample or to the end of the season, whichever was applicable, was determined and the daily production multiplied by this. Totals were progressively added to give the production per species for each season, the annual production per species and finally the annual production for the benthic chydorid community.

CHAPTER 10 : Results

SECTION 10.1. Life histories and growth of *Disparalona rostrata* and *Leydigia leydigi*

The means and 95% confidence limits for the duration of juvenile and adult instars of *Leydigia leydigi* and *Disparalona rostrata* are given in Table 10. In both species the duration of juvenile and adult instars decreased as temperatures increased. Juveniles moulted at shorter intervals than adults and consequently, at a given temperature, the duration of a juvenile instar was less than that of an adult.

The mean number of juvenile and adult instars for *Leydigia leydigi* and *Disparalona rostrata* at four and three temperatures respectively are given in Table 11, while the percentage and mean length at birth of *L. leydigi* and *D. rostrata* primiparous at the third and fourth instars are shown in Table 12. Individuals of both species had either two or three juvenile instars. As temperature increased the percentage of individuals primiparous at the third instar tended to increase. The length at birth of a *Leydigia leydigi* individual and number of juvenile instars showed a significant positive correlation at 5^{o}, 14^{o} and 19^{o}C but not at 10^{o}C (Appendix IX). For *Disparalona rostrata* the length at birth and number of juvenile instars showed a significant positive correlation at 10^{o}C but not at 14^{o} and 19^{o}C (Appendix IX). The mean number of adult

TABLE 10: Duration of Juvenile and Adult Instars (in days) of *Leydigia leydigi* and *Disparalona rostrata* at Four Temperatures. Means ± 95% Confidence Limits

STAGE	SPECIES	TEMPERATURE °C			
		5	10	14	19
Juveniles	*Leydigia leydigi*	11.8 ± 0.476	6.3 ± 0.518	4.0 ±0.168	2.7 ±0.239
	Disparalona rostrata	-	9.0 ± 0.495	4.8 ±0.31	4.1 ±0.25
Adults	*Leydigia leydigi*	24.9 ± 0.394	8.6 ± 0.319	5.3 ±0.243	2.8 ±0.121
	Disparalona rostrata	-	13.7 ± 0.22	6.9 ±0.256	4.8 ±0.192

TABLE 11: Mean Number of Juvenile and Adult Instars of *Leydigia leydigi* and *Disparalona rostrata* at four Temperatures

STAGE	SPECIES	TEMPERATURE °C			
		5	10	14	19
Juveniles	*Leydigia leydigi*	2.5	2.2	2.4	2.2
	Disparalona rostrata	-	2.5	2.1	2.7
Adults	*Leydigia leydigi*	4	5	5	5
	Disparalona rostrata	-	4.5	4.5	4.5

TABLE 12 : Percentage and Mean Length (mm) of *Leydigia leydigi* and *Disparalona rostrata* Primiparous at the Third and Fourth Instars at Four Temperatures. The Sample Size was Eighteen in all cases

SPECIES	INSTAR	TEMPERATURE							
		5°C		10°C		14°C		19°C	
		% primiparous	length at birth (mm)	% primiparous	length at birth (mm)	% primiparous	length at birth (mm)	% primiparous	length at birth (mm)
Leydigia leydigi	3	50	0.49	83.3	0.466	61.1	0.425	83.3	0.437
	4	50	0.434	16.6	0.462	38.8	0.408	16.6	0.401
Disparalona rostrata	3	-	-	50	0.35	88.8	0.343	66.6	0.338
	4	-	-	50	0.364	11.1	0.336	44.4	0.324

TABLE 13: Mean Length of Life in Days and Duration of Egg Development in Days (mean ± 95% Confidence Limits) of *Leydigia leydigi* and *Disparalona rostrata* at Four Temperatures

	SPECIES	TEMPERATURE			
		5°C	10°C	14°C	19°C
Mean length of life (in days)	*Leydigia leydigi*	120	54	32	21
	Disparalona rostrata	-	80	42	30
Duration of egg development (in days)	*Leydigia leydigi*	21.9 ± 0.439	8.6 ± 0.28	5.4 ± 0.238	2.8 ± 0.105
	Disparalona rostrata	-	13.0 ± 0.228	6.9 ± 0.256	4.8 ± 0.274

instars for *L. leydigi* and *D. rostrata* remained almost constant at all temperatures.

The mean length of life and duration of egg development for *Leydigia leydigi* and *Disparalona rostrata* at four and three temperatures respectively are given in Table 13. The mean length of life decreased with increasing temperature for both species as did the duration of egg development. The adult instars of both species passed through the same cycle of events, that is, development of eggs and release of fully developed young from the brood chamber, moulting accompanied by an increase in body size and release of a new set of eggs from the ovaries into the brood chamber. The time between release of the young and replacement by the next set of eggs increased as the temperature fell. For *L. leydigi* it could be one to three days at 5°C while at higher temperatures it was always less than a day. For *D. rostrata* this time could be one to four days at 10°C but was always under one day at higher temperatures. Thus the duration of an adult instar was longer than the duration of egg development at 5°C for *L. leydigi* and 10°C for *D. rostrata*.

Tables 14 to 16 show the mean weight per animal obtained for each sample of *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata* using the wet dichromate oxidation procedure (Appendix XII).

A regression relating body weight (µg C) to body length (mm) was fitted to the data. For each species the

logarithm of weight (µg C) was directly related to the logarithm of body length (mm) by a linear regression. The regression equation was written as:

$$\log W = \log a + b \log L$$

where W = mean weight in µg carbon

L = length in mm

b = regression coefficient

a = intercept

Appendix XII Figures i to iii show the regression lines relating body length to body weight for *L. leydigi*, *A. affinis* and *D. rostrata*. Appendix XII Table i gives the values of log a and b for the various regression lines.

Figures 40, 41 and 42 show the averaged growth curves for *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* at 5°C (excluding *D. rostrata*) 10°, 14° and 19°C. The growth curve data for *D. rostrata*, *L. leydigi* and *Alona affinis* is tabulated in Appendix XIII Tables i to iii. The dotted parts of the curve represent adult growth when the numbers of young produced are taken into account. For both *D. rostrata* and *L. leydigi* daily growth in the juvenile instars increased with increasing temperature.

From Figures 40 and 41 it can be seen that *D. rostrata* and *L. leydigi* undergo considerable growth curtailment after maturity (in terms of increase in length/weight of the adult only). This appears to be a common feature of the growth pattern of the Chydoridae (p. 223).

TABLE 14: Mean Weight per Animal (µg C) Obtained from a Number of Samples in each Size Class of *Leydigia leydigi*

Leydigia leydigi

Size Class (mm)	Size Class midpoint (mm)	log size class midpoint	Number of animals per sample	Mean weight µg C	log mean weight
I			50	0.75	$\bar{0}$.1249
			50	0.704	$\bar{0}$.1524
0.375-0.425	0.4	$\bar{0}$.3979	50	0.826	$\bar{0}$.083
			50	0.717	$\bar{0}$.1444
II			35	1.02	$\bar{0}$.0086
			35	0.89	$\bar{0}$.0506
0.426-0.476	0.451	$\bar{0}$.3458	35	0.95	0.0222
			35	1.2	0.0791
			35	1.14	0.0569
III			30	1.3	0.1139
			30	1.21	0.0827
0.477-0.527	0.502	$\bar{0}$.2992	30	1.27	0.1038
			30	1.35	0.1335
			30	1.4	0.1461
			30	1.44	0.1583
IV			25	1.7	0.2304
			25	1.65	0.2174
0.528-0.578	0.553	$\bar{0}$.2572	25	1.57	0.1958
			25	1.76	0.2455
			25	1.81	0.2576
V			20	2.0	0.301
			20	2.12	0.3263
0.579-0.629	0.604	$\bar{0}$.2189	20	2.26	0.3541
			20	1.91	0.2810
VI			15	2.513	0.4001
			15	2.61	0.4166
0.63-0.68	0.655	$\bar{0}$.1837	15	2.72	0.4345
			15	2.43	0.3856
			15	2.39	0.3783
VII			12	3	0.4771
			12	2.89	0.4608
0.681-0.731	0.706	$\bar{0}$.1511	12	2.92	0.4653
			12	3.14	0.4969
			12	3.201	0.5052
			12	3.01	0.4785
VIII			10	3.7	0.5682
			10	3.61	0.5575
0.732-0.782	0.757	$\bar{0}$.1209	10	3.65	0.5622
			10	3.77	0.5763
IX			8	4.4	0.6434
			8	4.29	0.6324
0.783-0.833	0.808	0.0925	8	4.27	0.6304
			8	4.51	0.6541
			8	4.45	0.6483

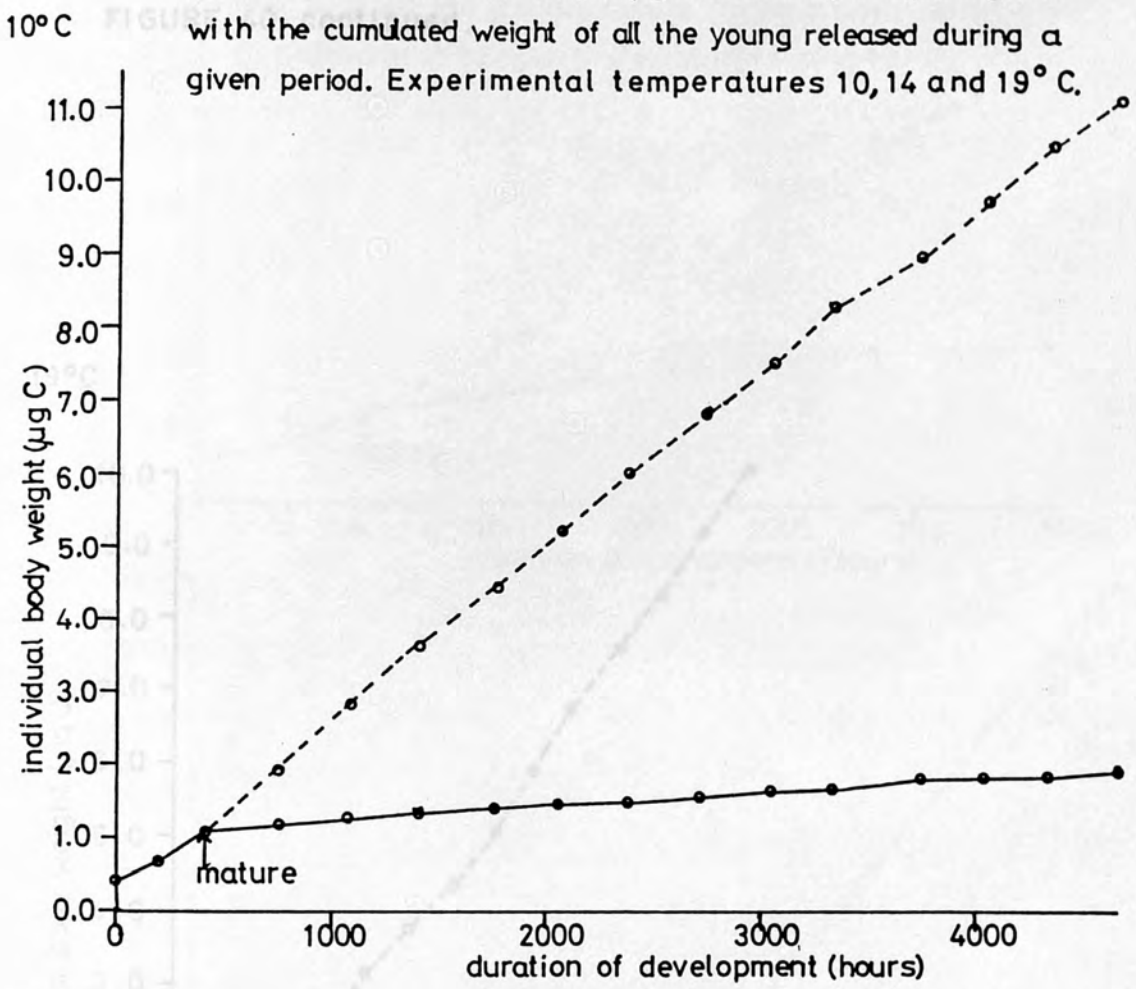
TABLE 15: Mean Weight per animal (µg C) Obtained from a Number of Samples in each Size Class of *Alona affinis*

Size Class (mm)	Size Class midpoint (mm)	log size class midpoint	Number of animals per sample	Mean weight µg C	log mean weight
II			70	0.5	$\bar{}$0.301
			70	0.48	$\bar{}$0.3187
0.356-0.406	0.381	$\bar{}$0.419	70	0.41	$\bar{}$0.3872
			70	0.56	$\bar{}$0.2518
			70	0.6	$\bar{}$0.2218
			55	0.68	$\bar{}$0.1674
III			55	0.74	$\bar{}$0.1307
			55	0.769	$\bar{}$0.114
0.407-0.457	0.432	$\bar{}$0.3645	55	0.612	$\bar{}$0.2132
			55	0.647	$\bar{}$0.189
			55	0.696	$\bar{}$0.1573
			45	0.8	$\bar{}$0.0969
IV			45	0.768	$\bar{}$0.1146
0.458-0.508	0.483	$\bar{}$0.3160	45	0.781	$\bar{}$0.1073
			45	0.89	$\bar{}$0.0506
			35	1.11	$\bar{}$0.0453
V			35	0.958	$\bar{}$0.0186
0.509-0.559	0.534	$\bar{}$0.2724	35	0.924	$\bar{}$0.0343
			35	1.24	0.0934
			35	1.19	0.0755
			25	1.58	0.1986
VI			25	1.47	0.1673
			25	1.425	0.1538
0.56-0.610	0.585	$\bar{}$0.2328	25	1.61	0.2068
			25	1.64	0.2148
			25	1.554	0.1914
			20	2.01	0.3031
VII			20	1.948	0.2895
			20	1.892	0.2769
0.611-0.661	0.636	$\bar{}$0.1965	20	2.26	0.3541
			20	2.15	0.3324
			15	2.47	0.3926
VIII			15	2.32	0.3654
			15	2.36	0.3729
0.662-0.712	0.687	$\bar{}$0.163	15	2.54	0.4048
			12	2.95	0.4698
IX			12	2.78	0.444
			12	2.74	0.4377
0.713-0.763	0.738	$\bar{}$0.1319	12	3.01	0.4785
			12	3.16	0.4996
			10	3.32	0.5211
X			10	3.16	0.4996
			10	3.11	0.4927
0.764-0.814	0.789	$\bar{}$0.1029	10	3.29	0.5171
			10	3.47	0.5403
			10	3.62	0.5587
			8	3.8	0.5797
XI			8	3.69	0.567
			8	3.725	0.5711
0.815-0.865	0.84	$\bar{}$0.0757	8	3.94	0.5954
			8	4.4	0.6434
XII			8	4.21	0.6242
			8	4.195	0.6227
0.866-0.916	0.891	$\bar{}$0.050	8	4.546	0.6576
			8	4.61	0.6637
			8	4.45	0.6483

TABLE 16: Mean Weight per Animal (µg C) Obtained from a Number of Samples in each Size Class of *Disparalona rostrata*

Size class (mm)	Size class midpoint (mm)	log size class midpoint	Number of animals per sample	Mean weight µg C	log mean weight
I			85	0.4	$\bar{0}.3979$
			85	0.425	$\bar{0}.3716$
0.323-0.373	0.348	$\bar{0}.4584$	85	0.35	$\bar{0}.4559$
			85	0.45	$\bar{0}.3467$
			85	0.44	$\bar{0}.3565$
II			55	0.625	$\bar{0}.2041$
			55	0.66	$\bar{0}.1804$
0.374-0.424	0.399	$\bar{0}.399$	55	0.602	$\bar{0}.2204$
			55	0.587	$\bar{0}.2313$
III			45	0.8	$\bar{0}.0969$
			45	0.78	$\bar{0}.1079$
0.425-0.475	0.45	$\bar{0}.3467$	45	0.892	$\bar{0}.0496$
			45	0.94	$\bar{0}.0268$
			45	0.926	$\bar{0}.0333$
			45	0.941	$\bar{0}.0264$
IV			30	1.15	0.0606
			30	1.32	0.1205
o.476-0.526	0.501	$\bar{0}.3001$	30	1.24	0.0934
			30	1.4	0.1461
			30	1.47	0.1673

FIGURE 40. Average growth curves of Disparalona rostrata at three temperatures. o—o Body weight (µg C). o--o Body weight together with the cumulated weight of all the young released during a given period. Experimental temperatures 10, 14 and 19° C.



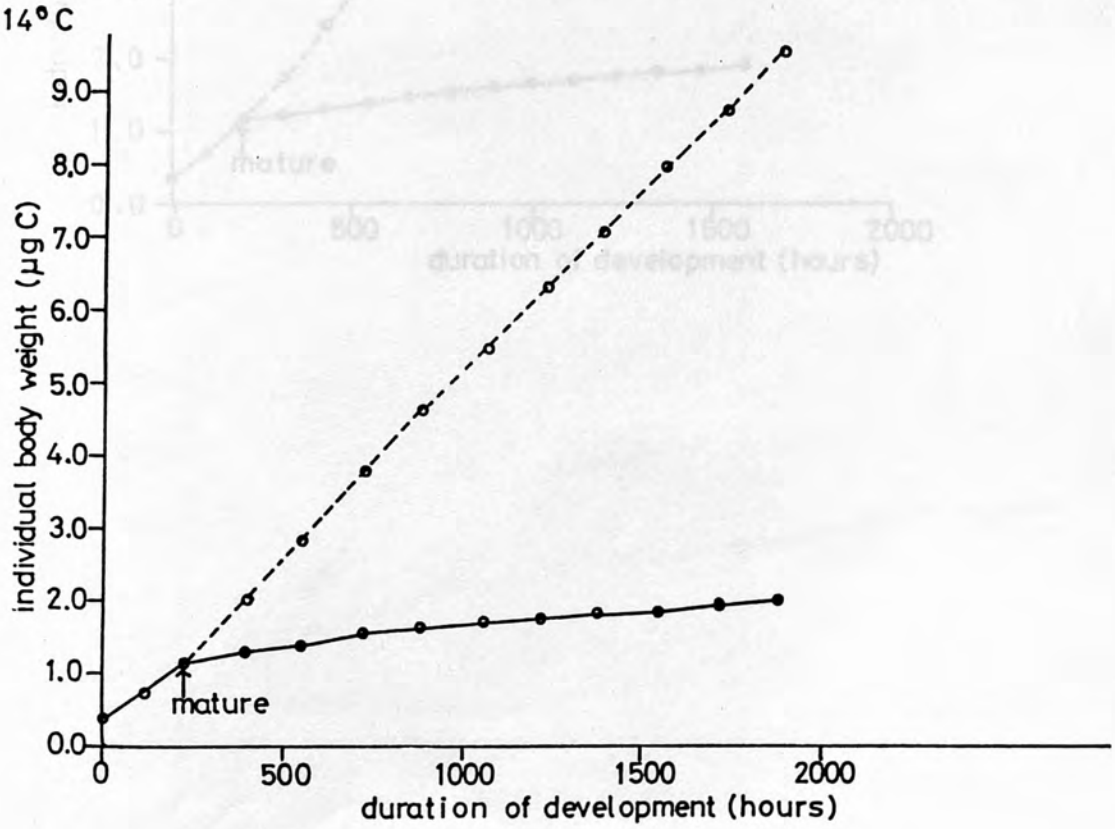


FIGURE 40 continued.

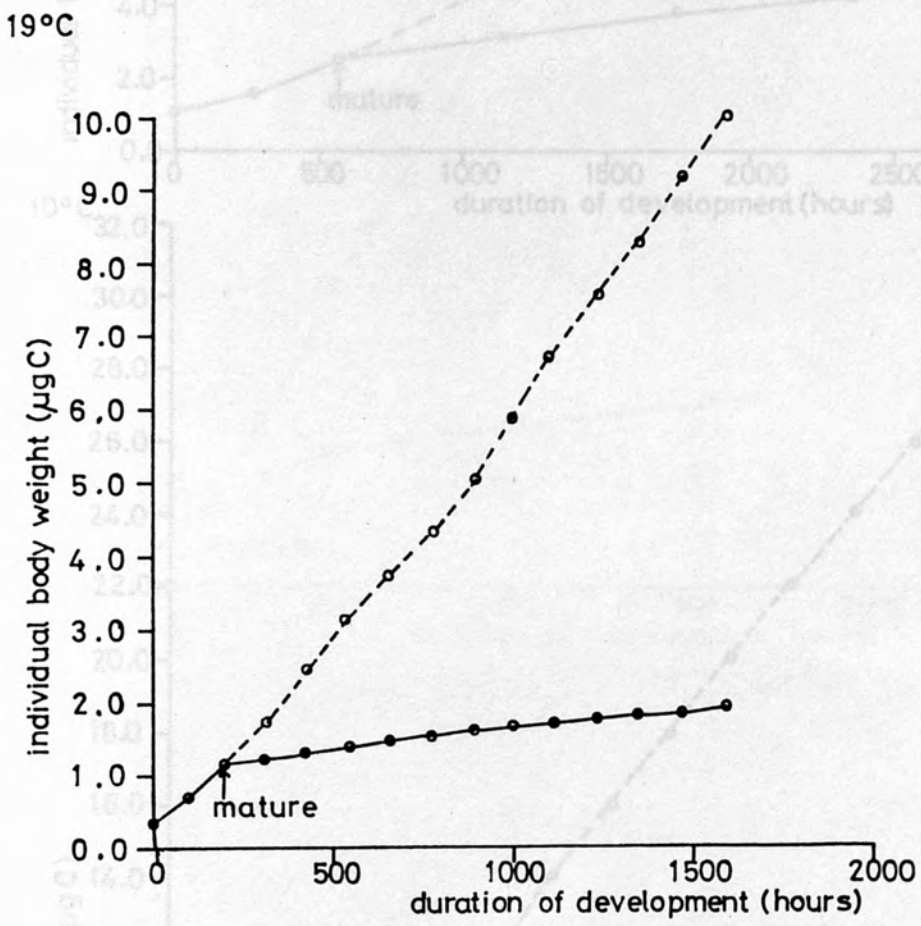


FIGURE 41. Average growth curves of Leydigia leydigi at four temperatures. ⊶⊷ Body weight. ⊶-⊷ Body weight together with the cumulated weight of all the young released during a given period. Experimental temperatures 5, 10, 14 and 19° C.

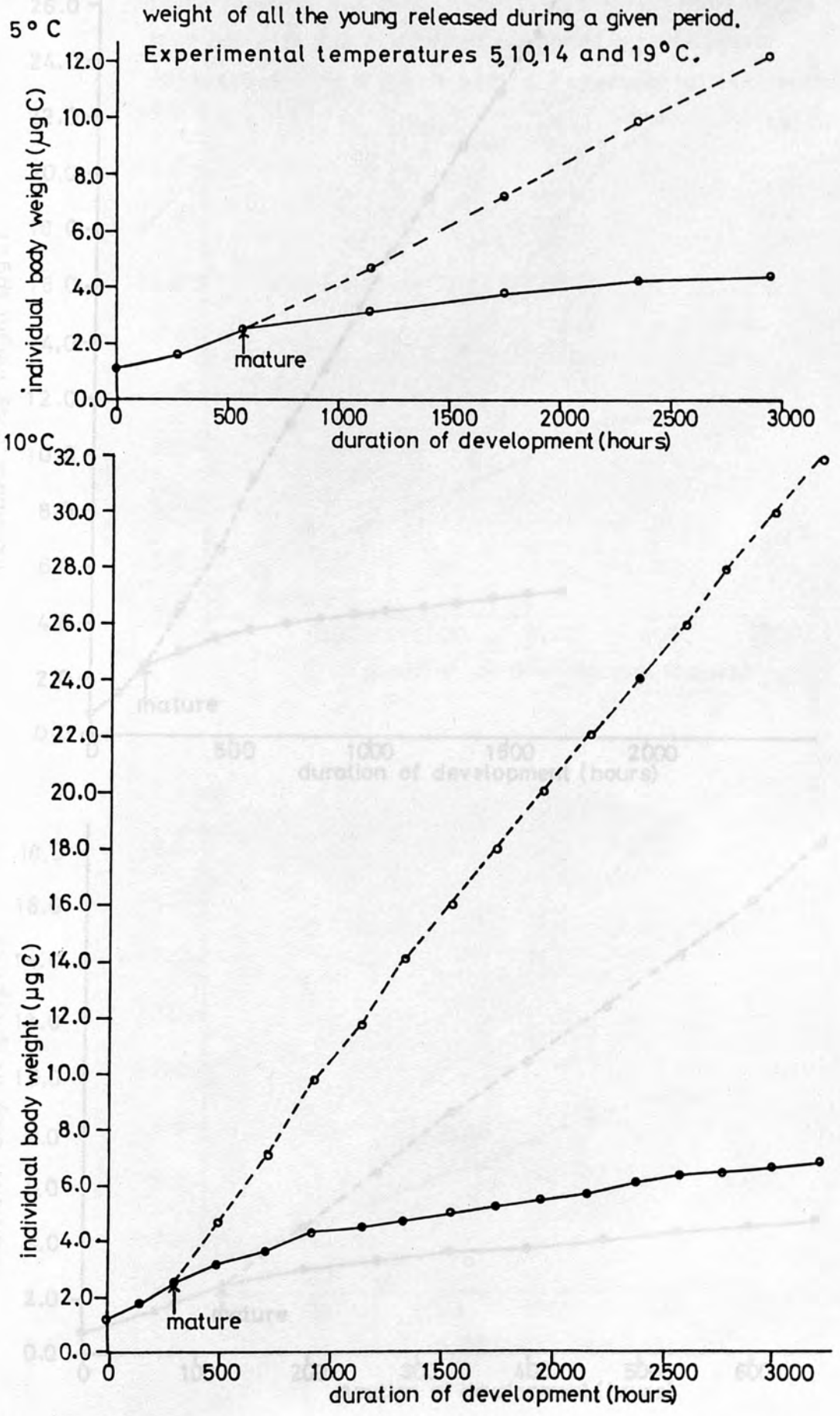


FIGURE 41 continued.

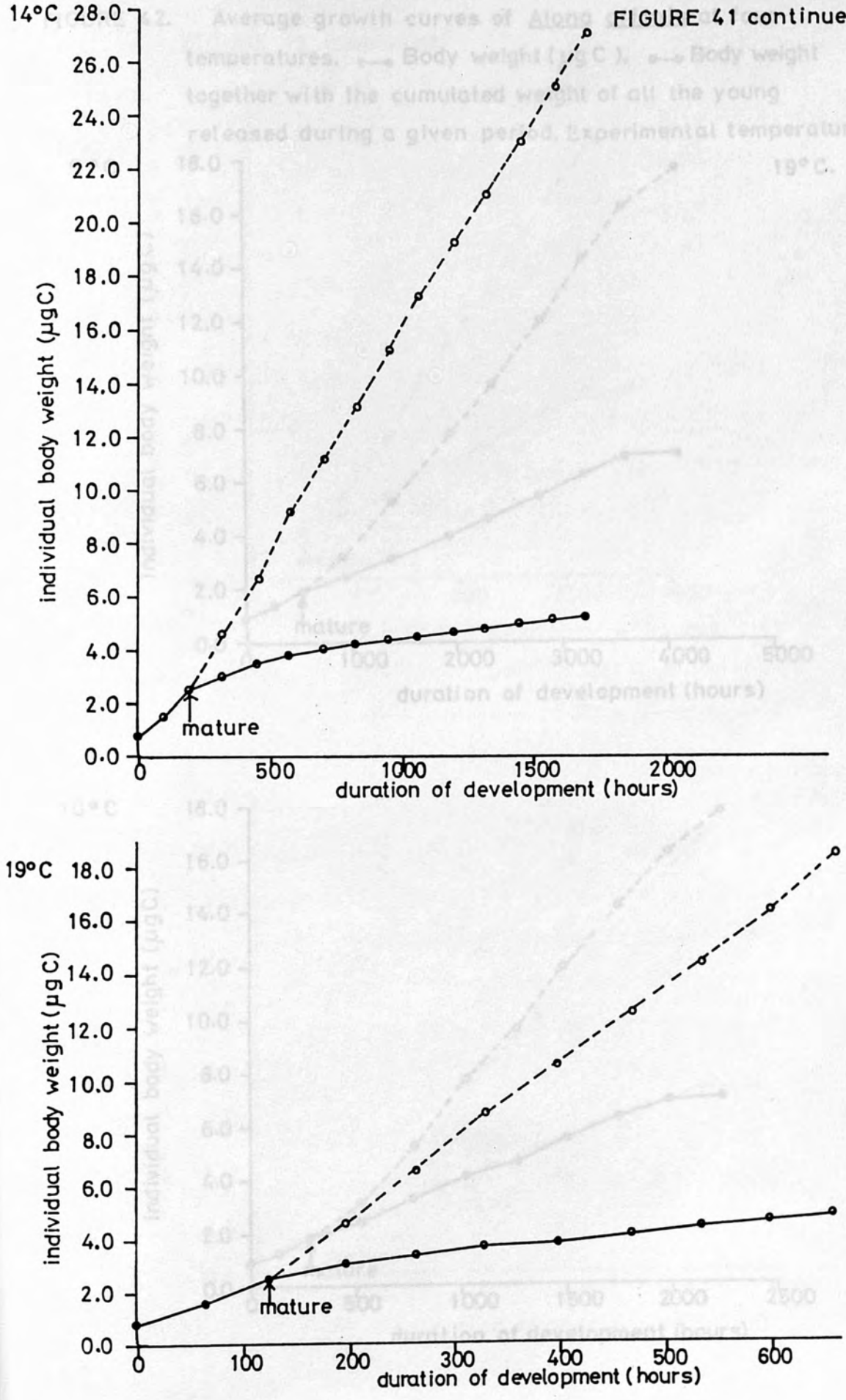
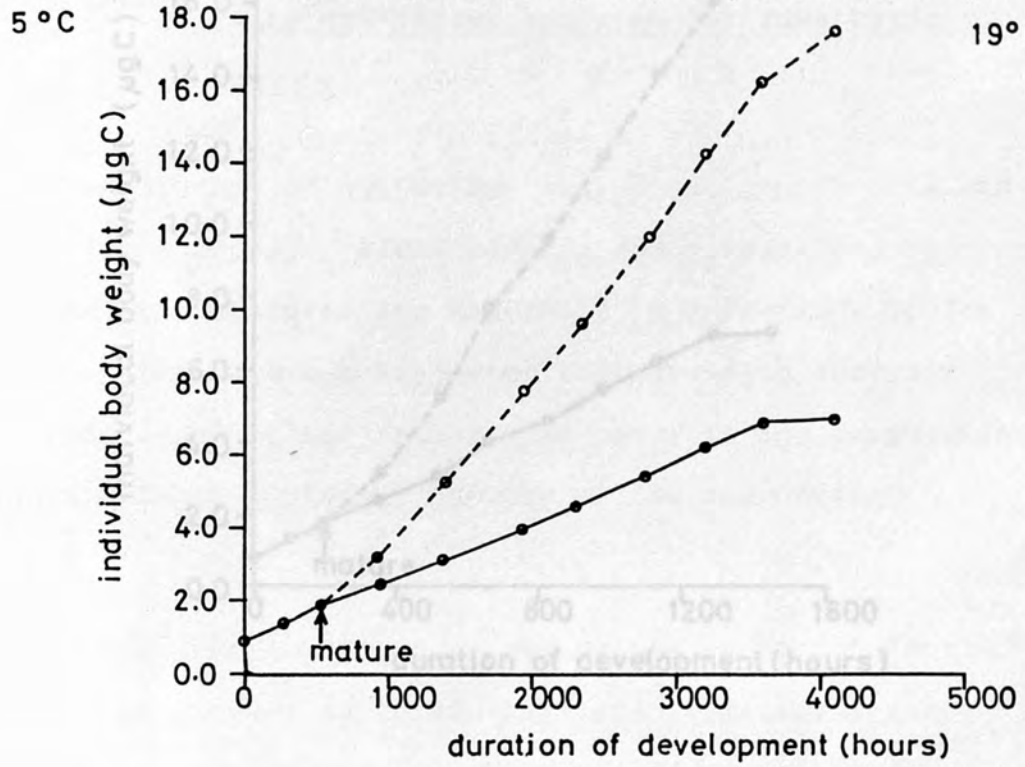


FIGURE 42. Average growth curves of Alona affinis at four temperatures. Body weight (µg C). Body weight together with the cumulated weight of all the young released during a given period. Experimental temperature



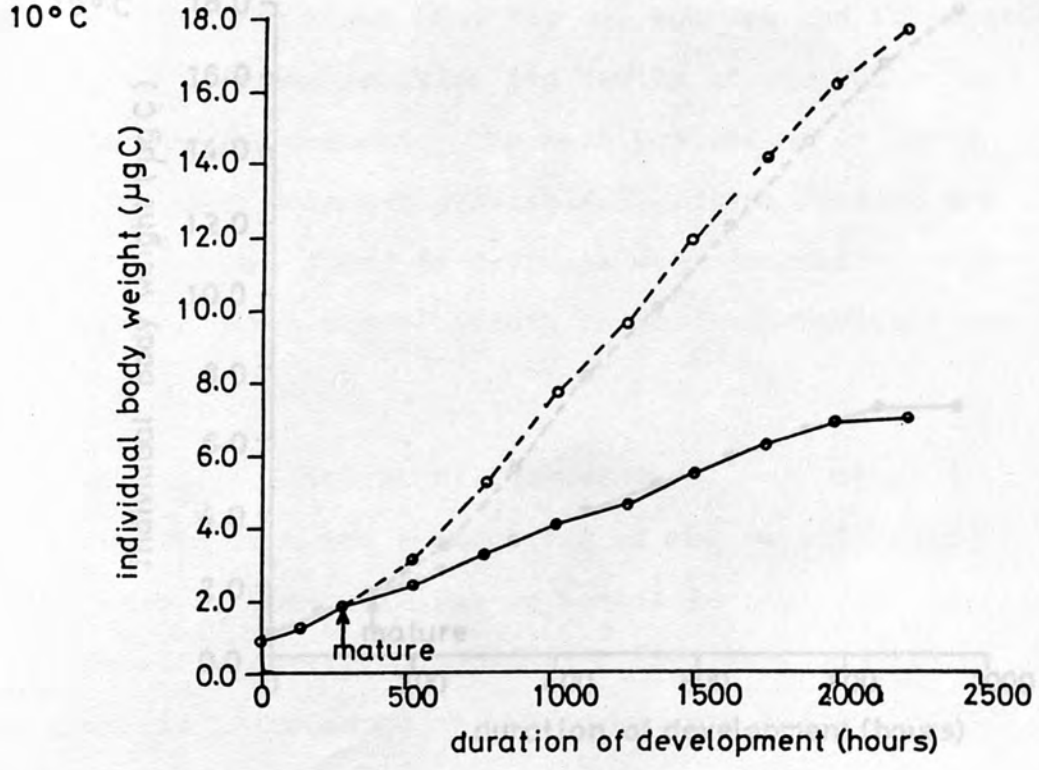
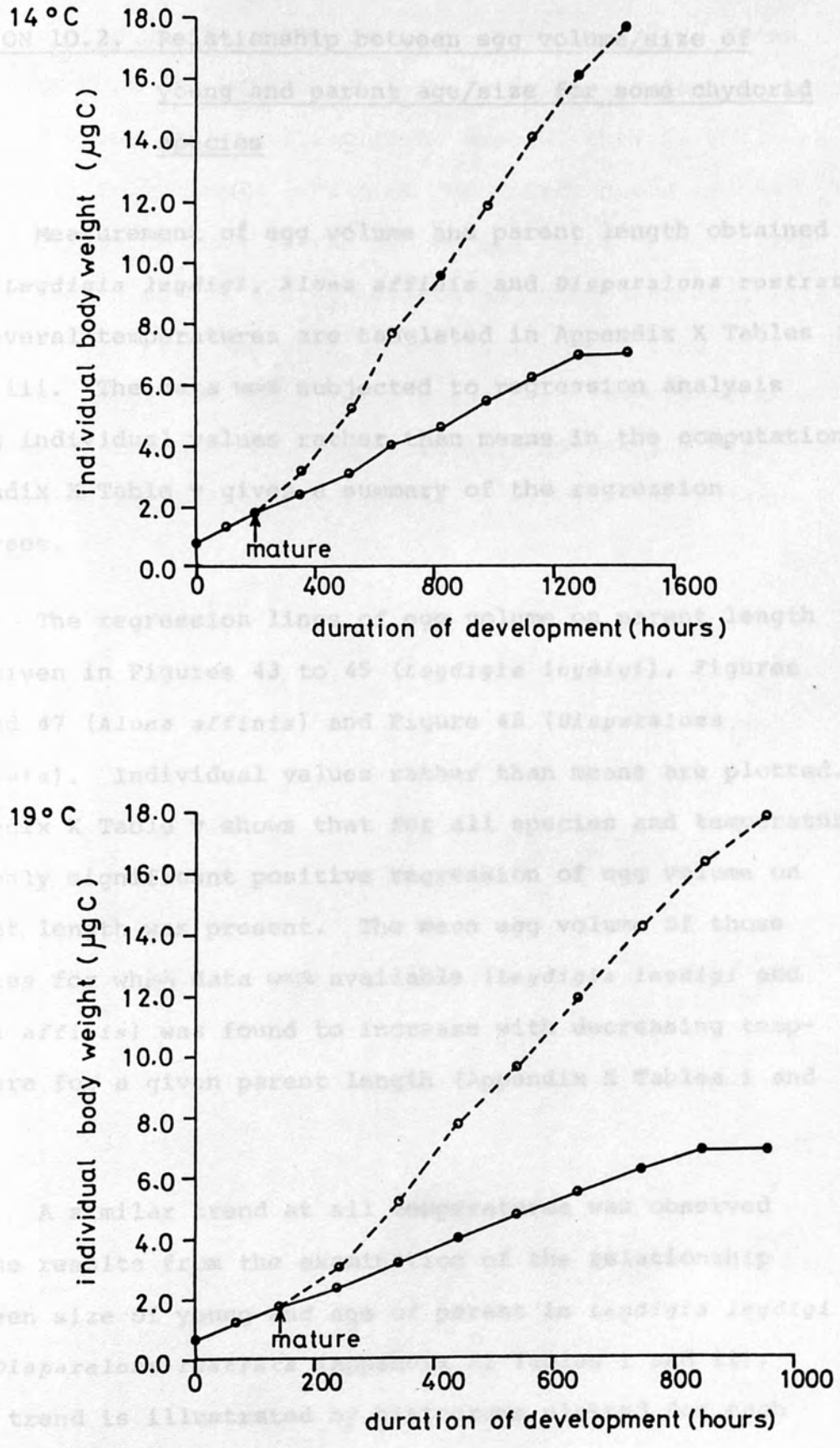


FIGURE 42 continued.



SECTION 10.2. Relationship between egg volume/size of young and parent age/size for some chydorid species

Measurement of egg volume and parent length obtained from *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata* at several temperatures are tabulated in Appendix X Tables i to iii. The data were subjected to regression analysis using individual values rather than means in the computations. Appendix X Table v gives a summary of the regression analyses.

The regression lines of egg volume on parent length are given in Figures 43 to 45 (*Leydigia leydigi*), Figures 46 and 47 (*Alona affinis*) and Figure 48 (*Disparalona rostrata*). Individual values rather than means are plotted. Appendix X Table v shows that for all species and temperatures a highly significant positive regression of egg volume on parent length was present. The mean egg volume of those species for which data were available (*Leydigia leydigi* and *Alona affinis*) was found to increase with decreasing temperature for a given parent length (Appendix X Tables i and ii).

A similar trend at all temperatures was observed in the results from the examination of the relationship between size of young and age of parent in *Leydigia leydigi* and *Disparalona rostrata* (Appendix XI Tables i and ii). This trend is illustrated by histograms plotted for each

species at a single temperature (Figs 49 and 50). These indicate that for both species there is an increase in mean size of young for the first three broods, this is followed by a fall in the mean length of the fourth brood to one intermediate to that of the second and third broods. The mean lengths of the fifth, seventh and ninth broods remain fairly constant. Appendix XI Tables i and ii show that the mean length of young for a given brood increased with decreasing temperature, complementing the results obtained for egg volume and parent length.

FIGURE 43. Linear regression of egg volume ($10^6 \mu m^3$) on parent length (mm) for Leydigia leydigi, River temperature 10°C.

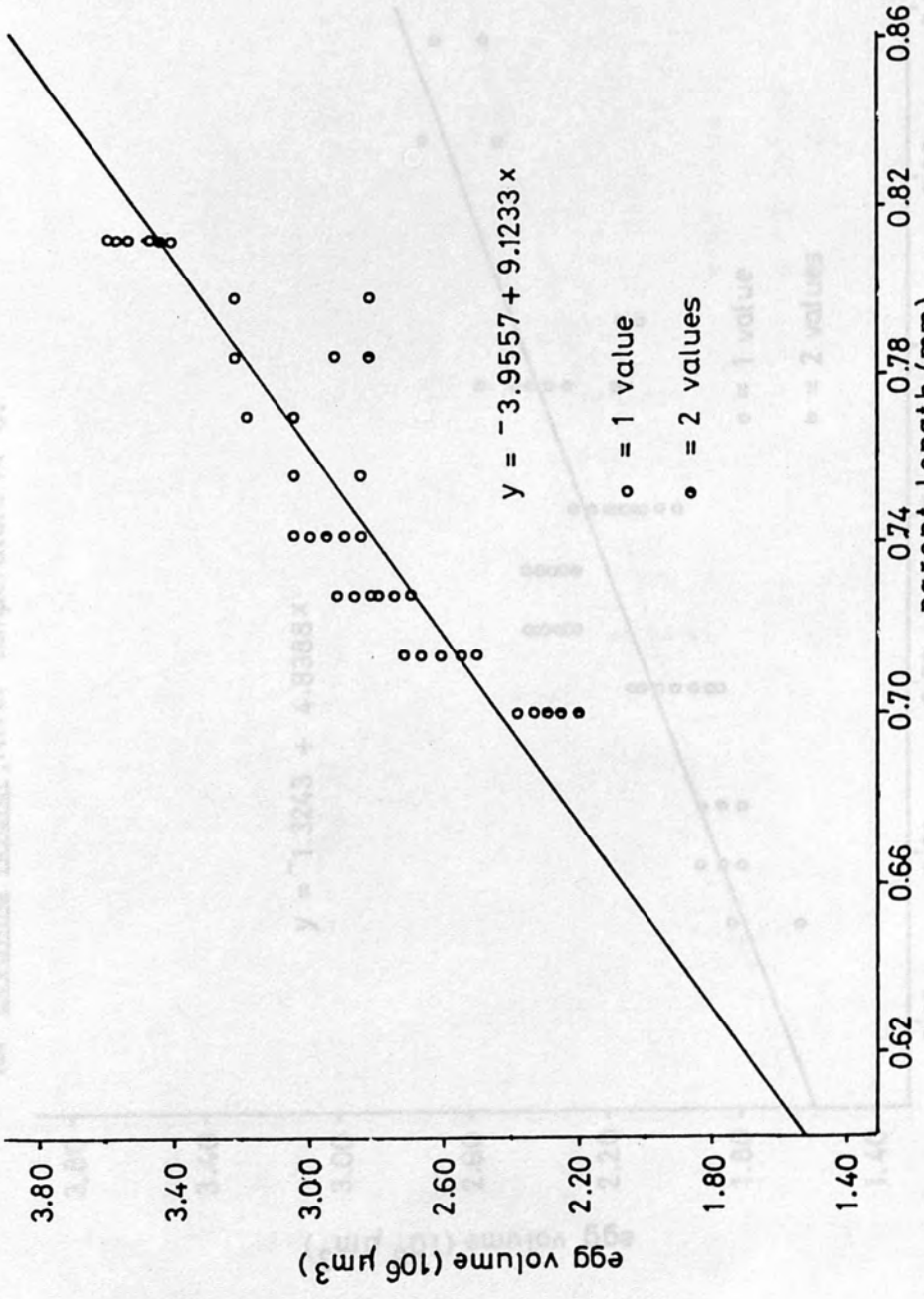


FIGURE 44. Linear regression of egg volume ($10^6 \mu m^3$) on parent length (mm) for Leydigia leydigi, River temperature 14°C.

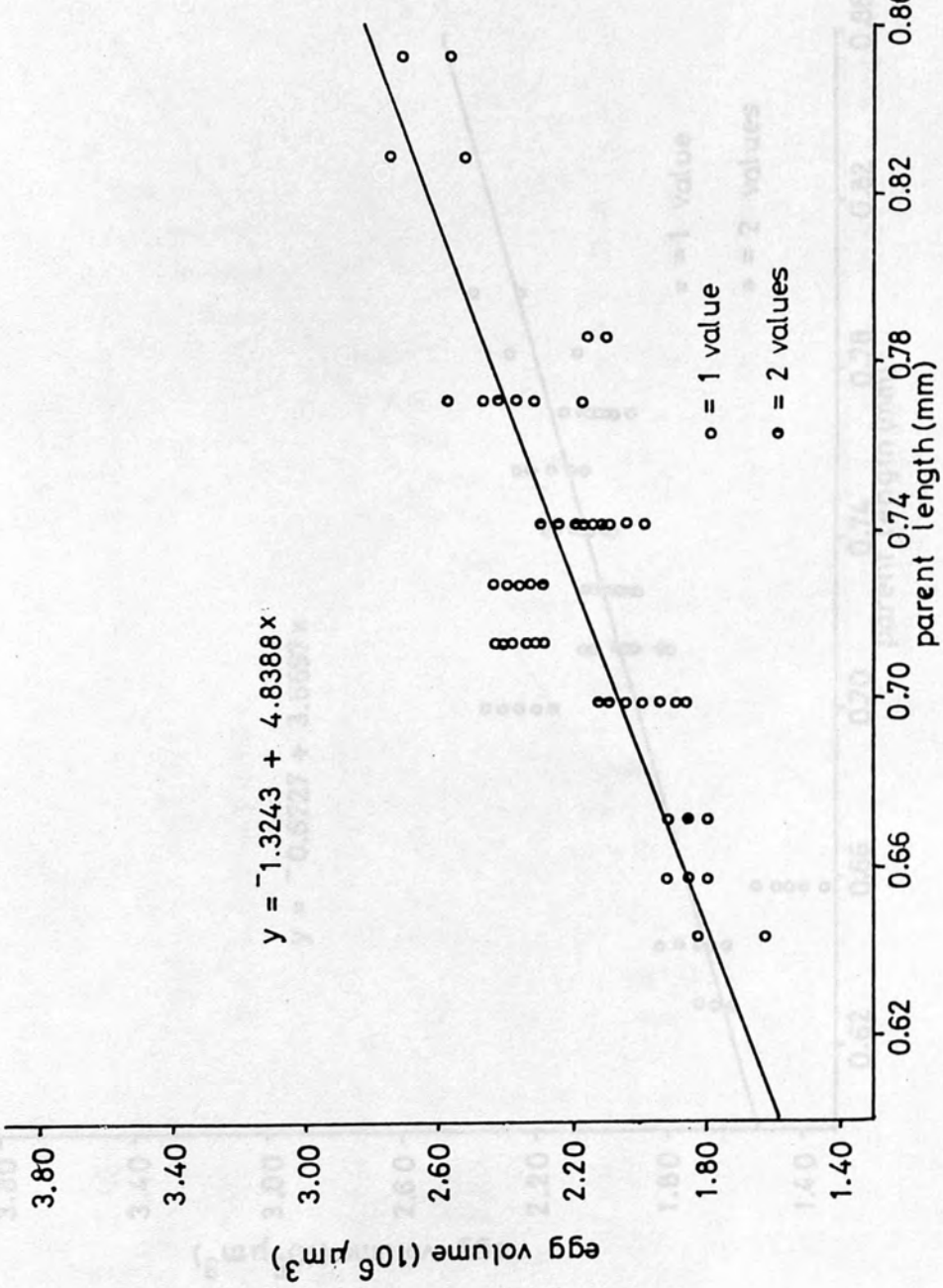


FIGURE 45. Linear regression of egg volume ($10^6 \mu m^3$) on parent length (mm) for Leydigia leydigi, River temperature 19° C.

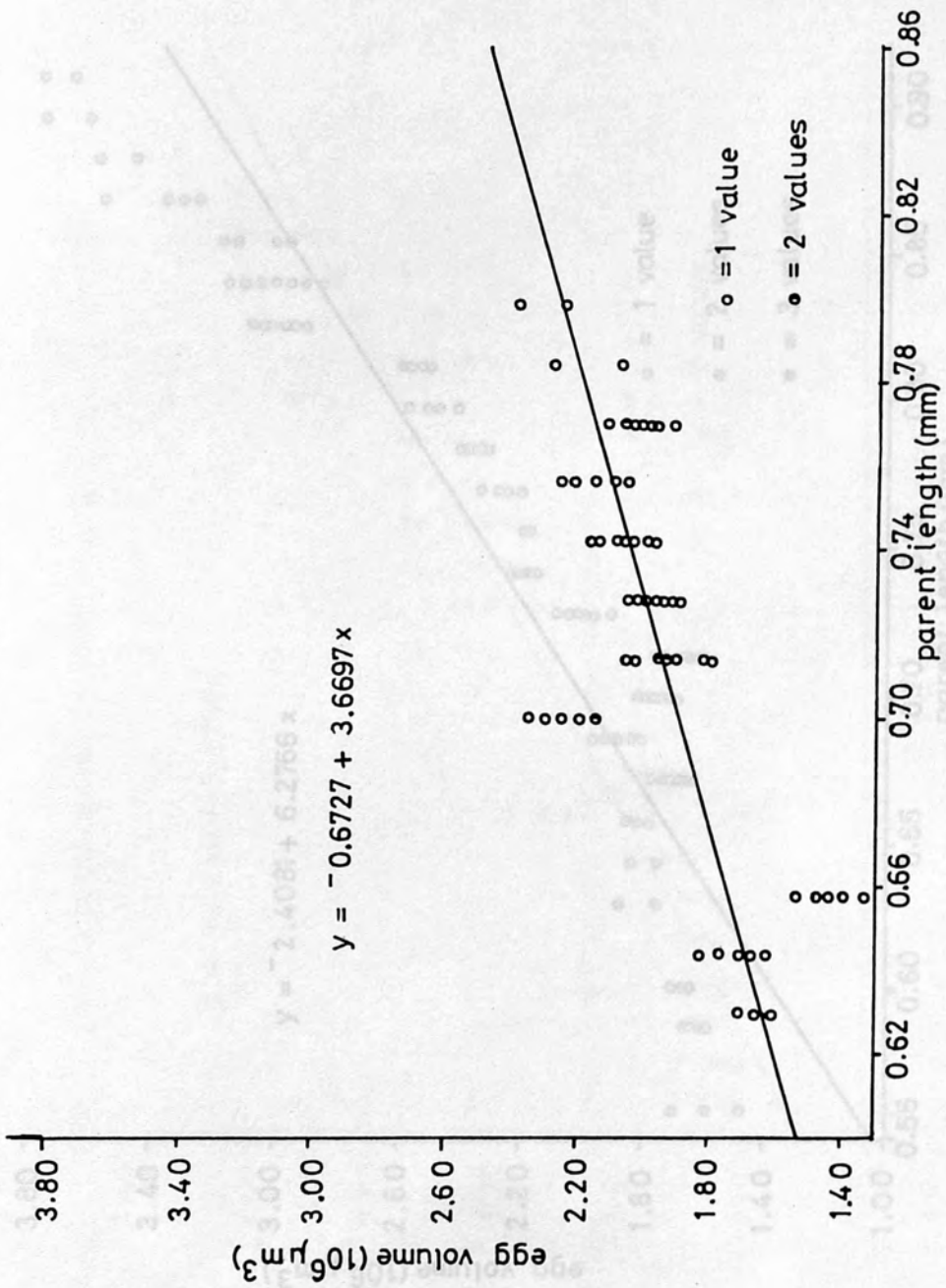


FIGURE 46. Linear regression of egg volume ($10^6 \mu m^3$) on parent length (mm) for Alona affinis . River temperature 14 °C.

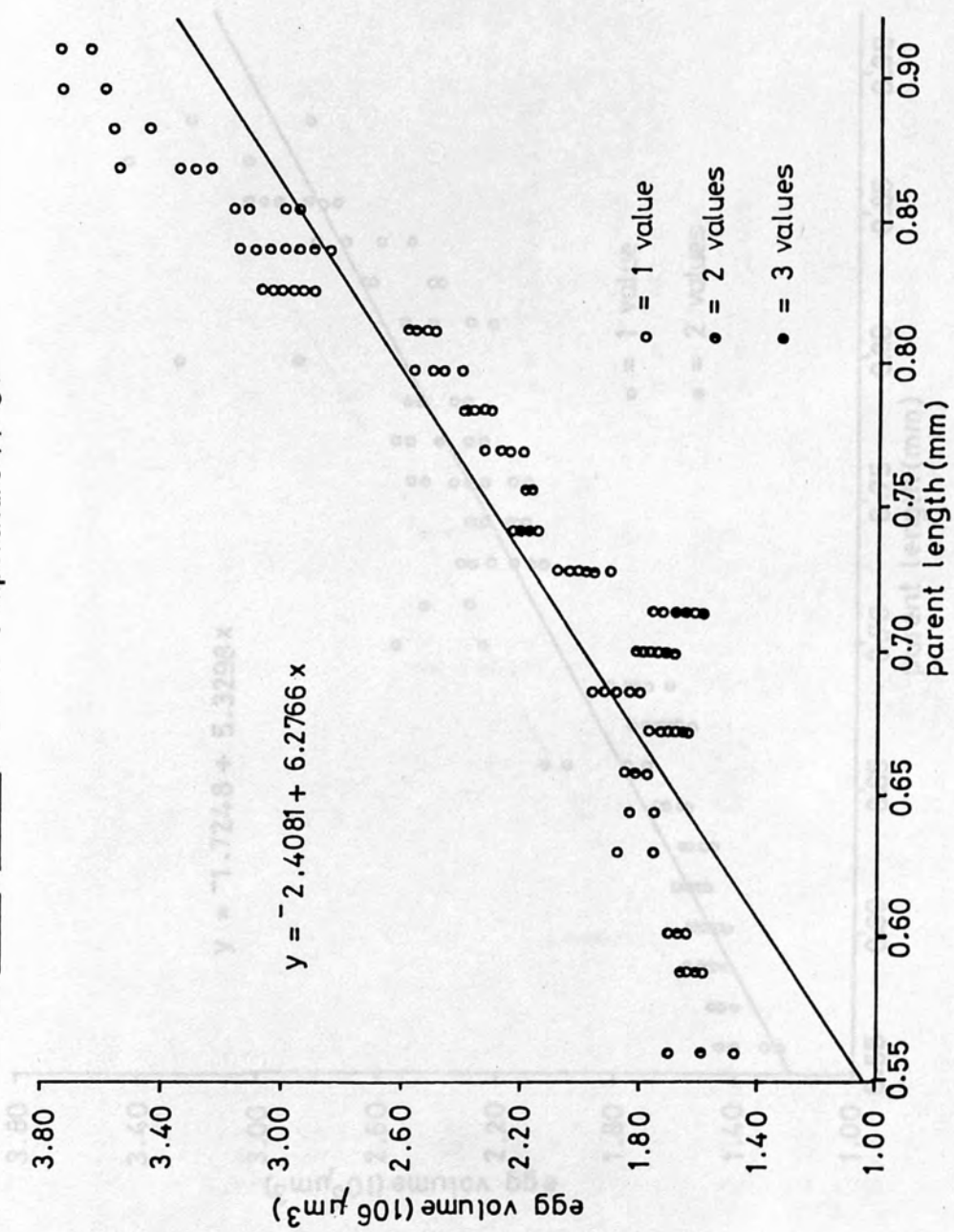
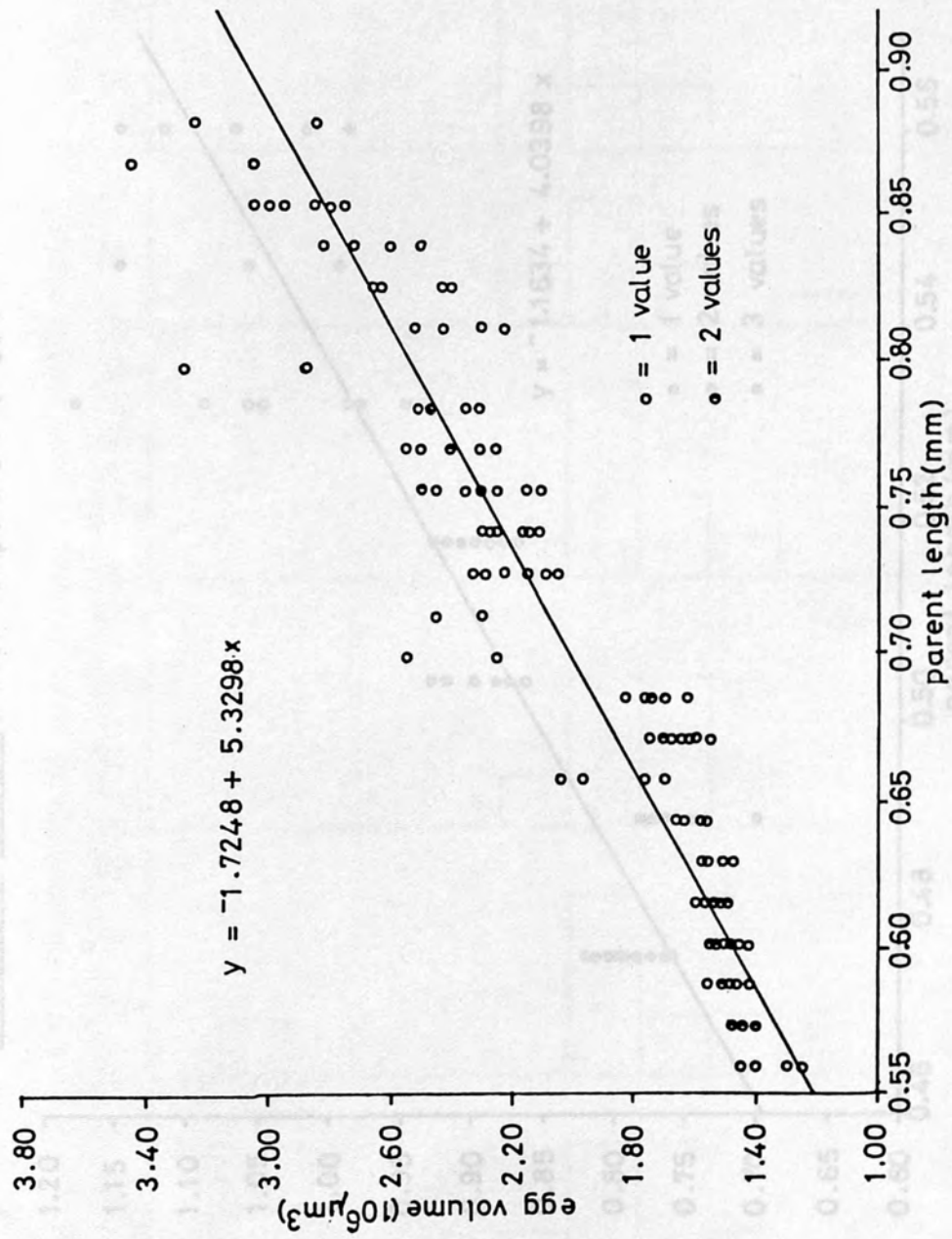


FIGURE 47. Linear regression of egg volume($10^6 \mu m^3$) on parent length(mm) for Alona affinis . River temperature 19°C.



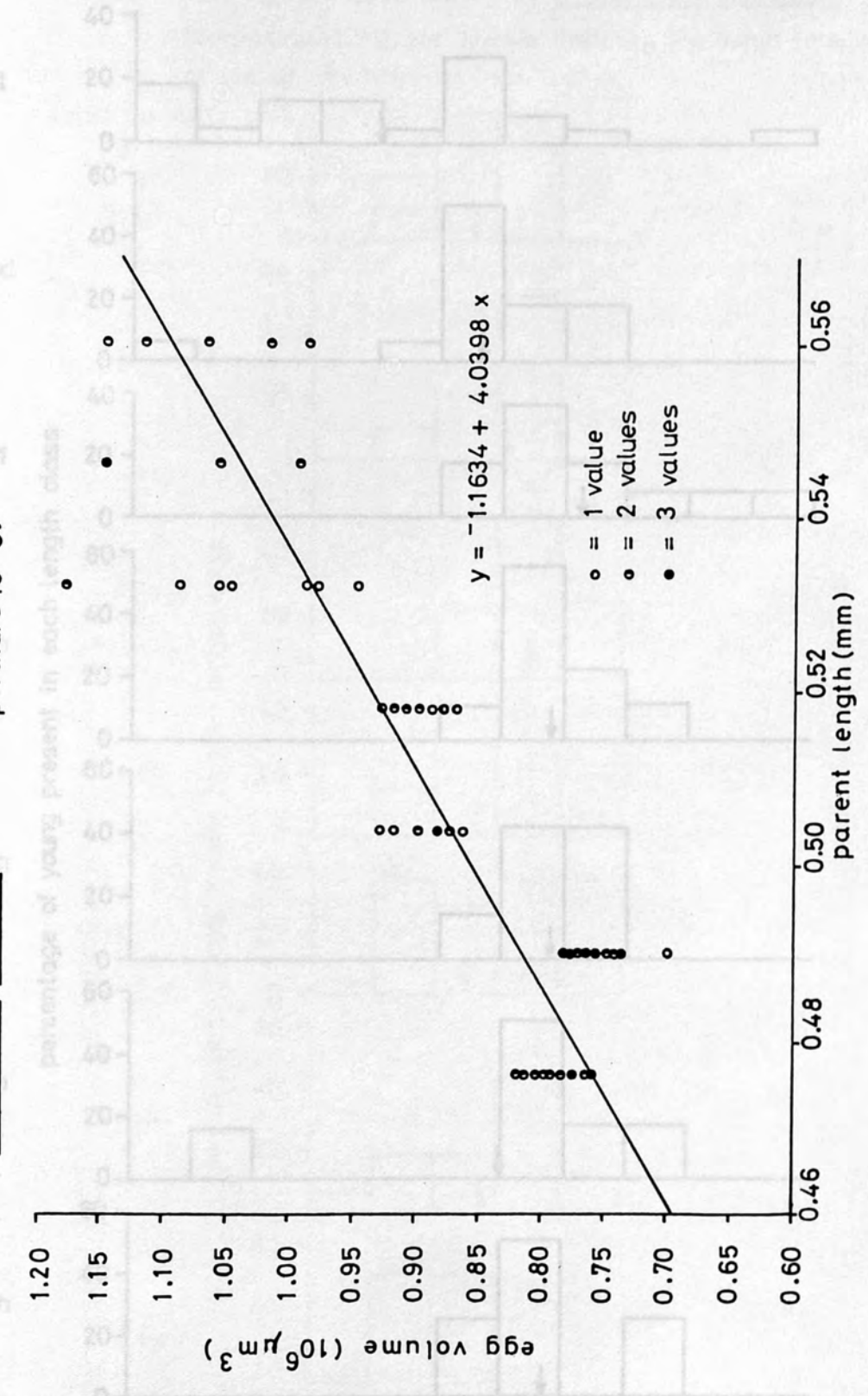
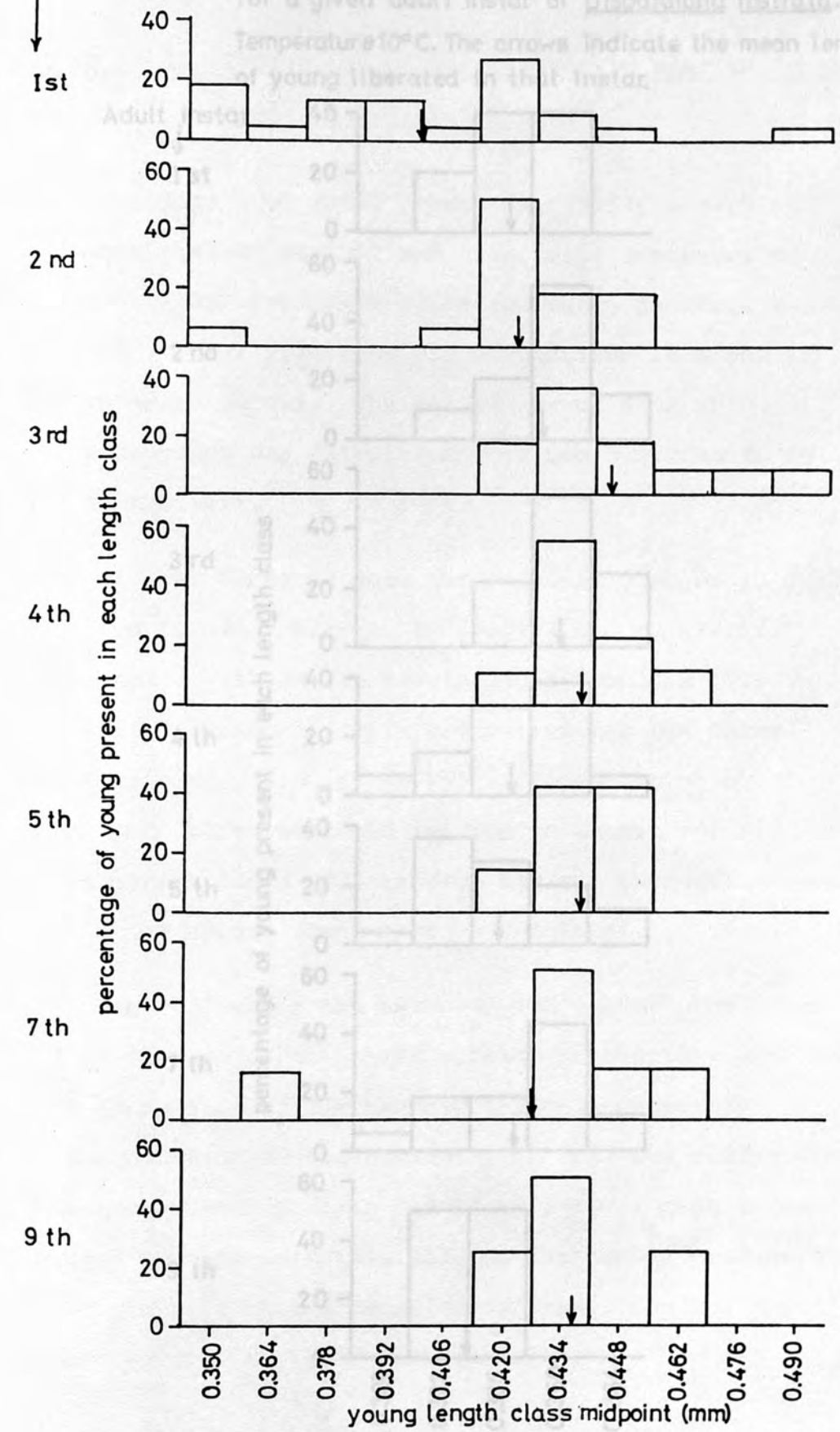


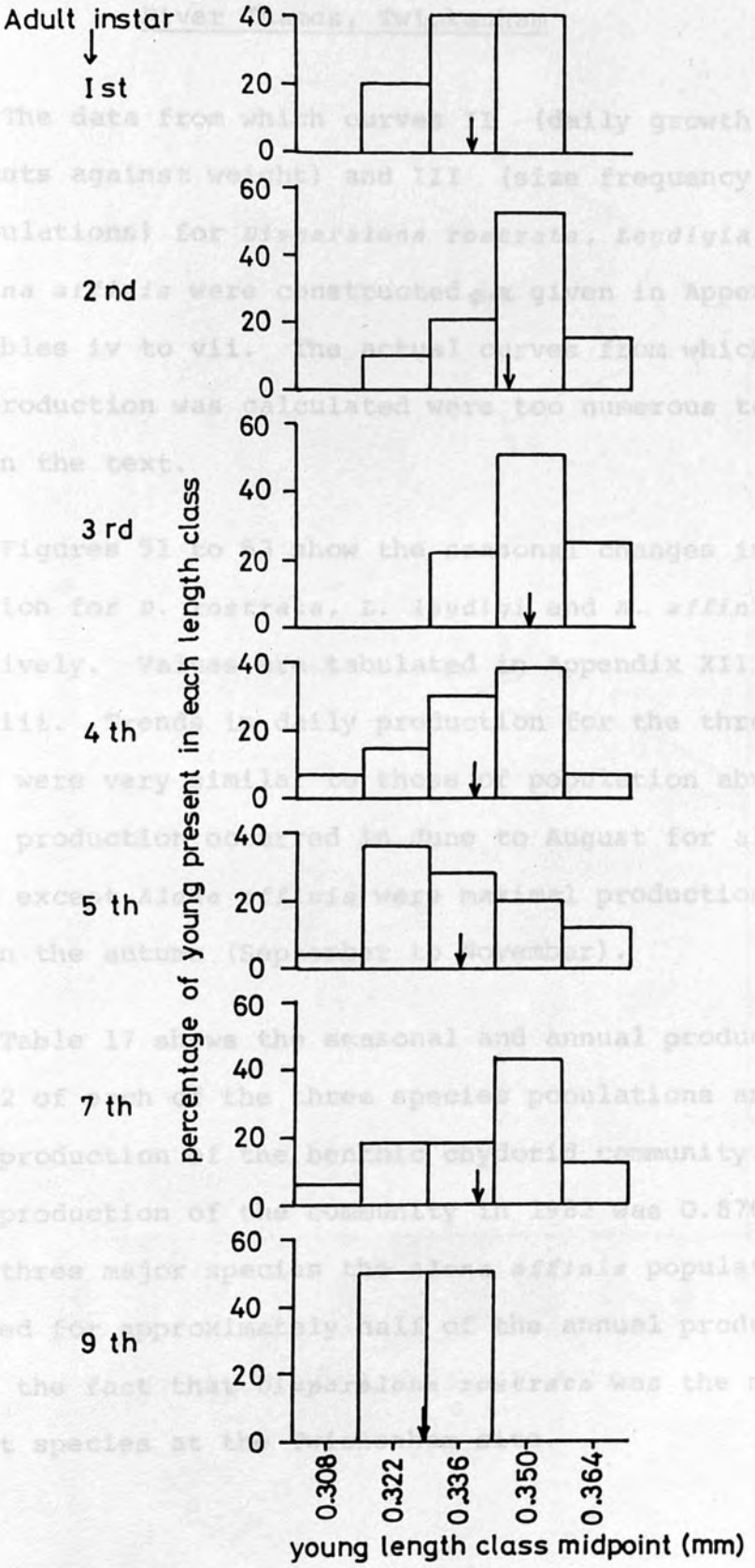
FIGURE 48. Linear regression of egg volume ($10^6 \mu m^3$) on parent length (mm) for Disparalona rostrata. River temperature 19°C.

FIGURE 49. Percentage of young present in each length class for a given adult instar of Leydigia leydigi. Temperature 14°C.



The arrows indicate the mean length of young liberated in that instar.

FIGURE 50. Percentage of young present in each length class for a given adult instar of Disparalona rostrata. Temperature 10° C. The arrows indicate the mean length of young liberated in that instar.



SECTION 10.3. Production of three chydorid species in the River Thames, Twickenham

The data from which curves II (daily growth increments against weight) and III (size frequency of the populations) for *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* were constructed are given in Appendix XIII Tables iv to vii. The actual curves from which daily production was calculated were too numerous to be shown in the text.

Figures 51 to 53 show the seasonal changes in daily production for *D. rostrata*, *L. leydigi* and *A. affinis* respectively. Values are tabulated in Appendix XIII Table viii. Trends in daily production for the three species were very similar to those of population abundance. Maximal production occurred in June to August for all species except *Alona affinis* were maximal production took place in the autumn (September to November).

Table 17 shows the seasonal and annual production for 1982 of each of the three species populations and the annual production of the benthic chydorid community. Annual production of the community in 1982 was 0.876g C m^{-2}. Of the three major species the *Alona affinis* population accounted for approximately half of the annual production despite the fact that *Disparalona rostrata* was the most abundant species at the Twickenham site.

FIGURE 51. Seasonal changes in the daily production ($\mu g\ C\ m^{-2}$) of the Disparalona rostrata population in the River Thames, Twickenham.

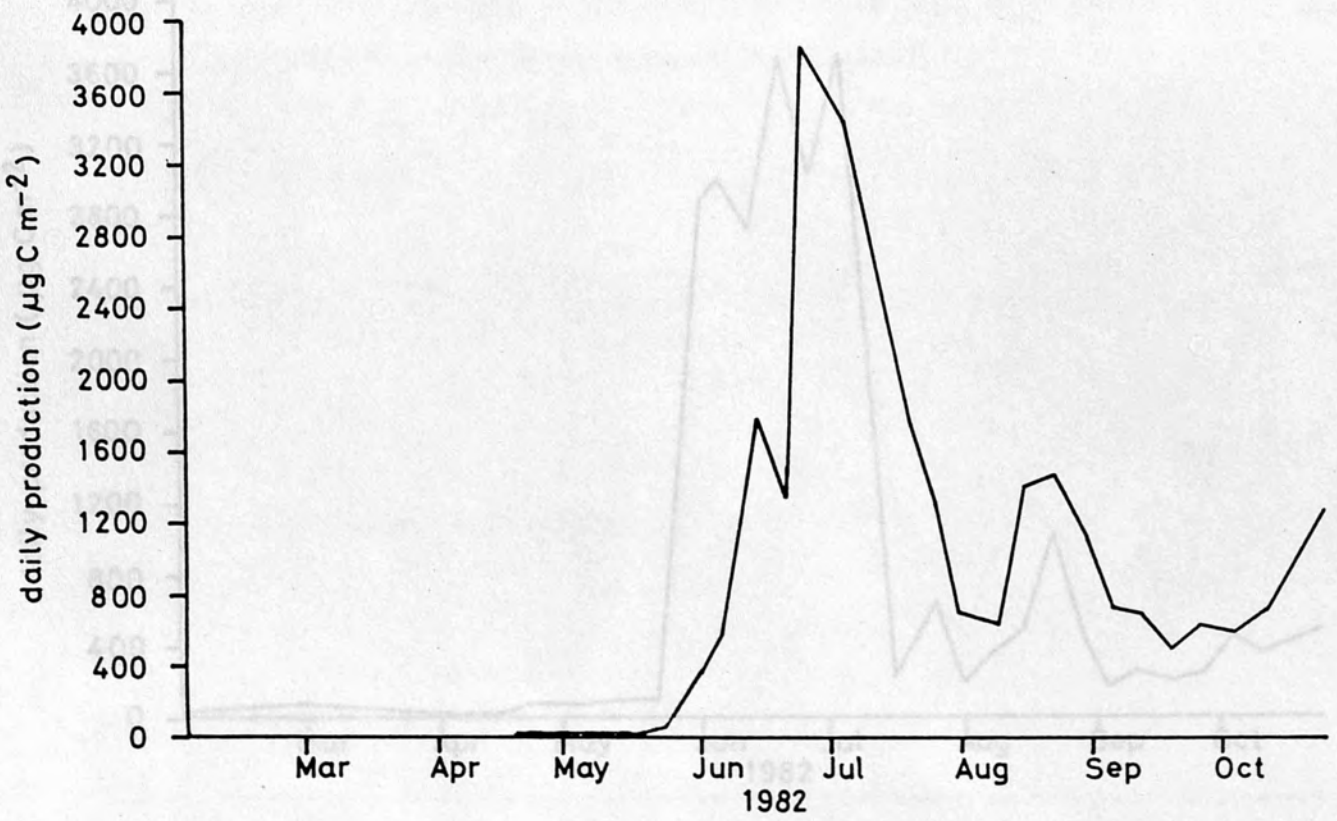


FIGURE 52. Seasonal changes in the daily production ($\mu g\, C\, m^{-2}$) of the Leydigia leydigi population in the River Thames, Twickenham.

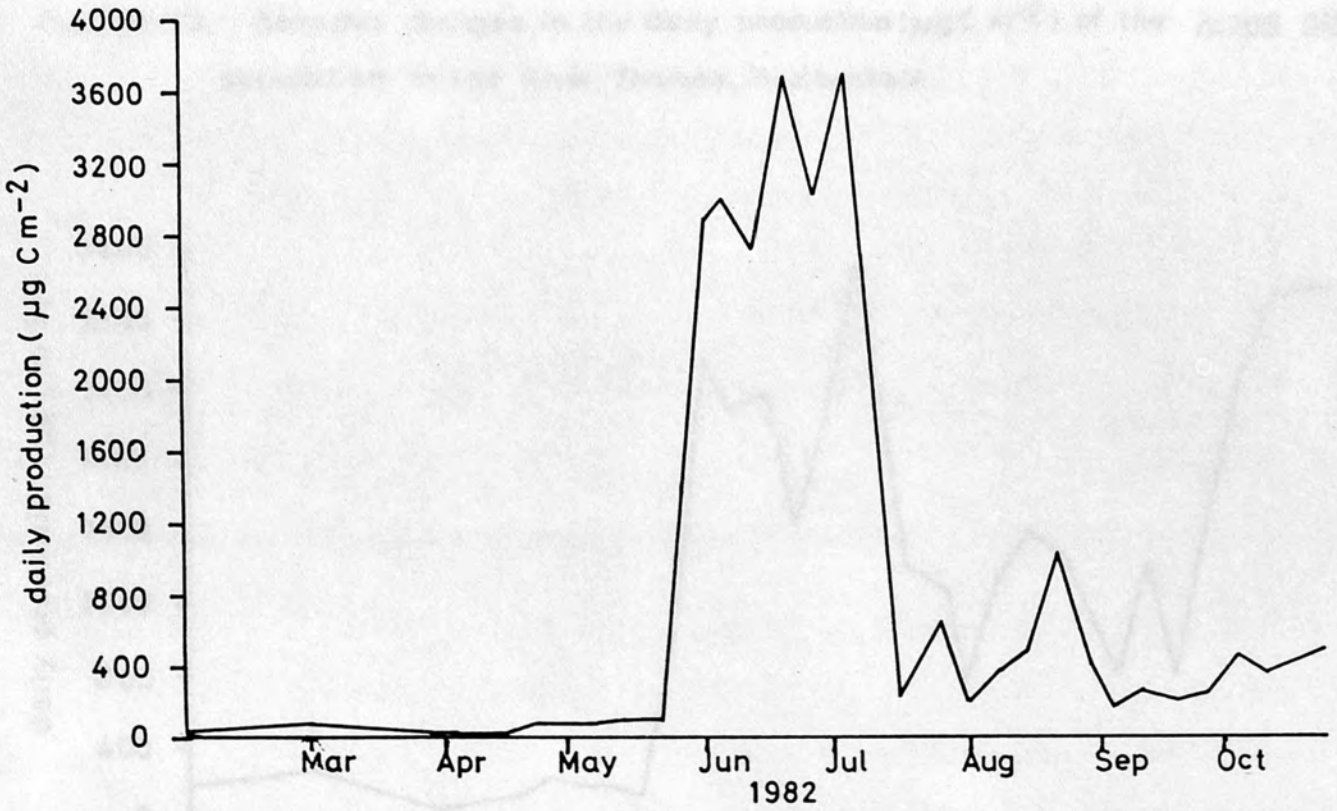


FIGURE 53. Seasonal changes in the daily production ($\mu g\ C\ m^{-2}$) of the Alona affinis population in the River Thames, Twickenham.

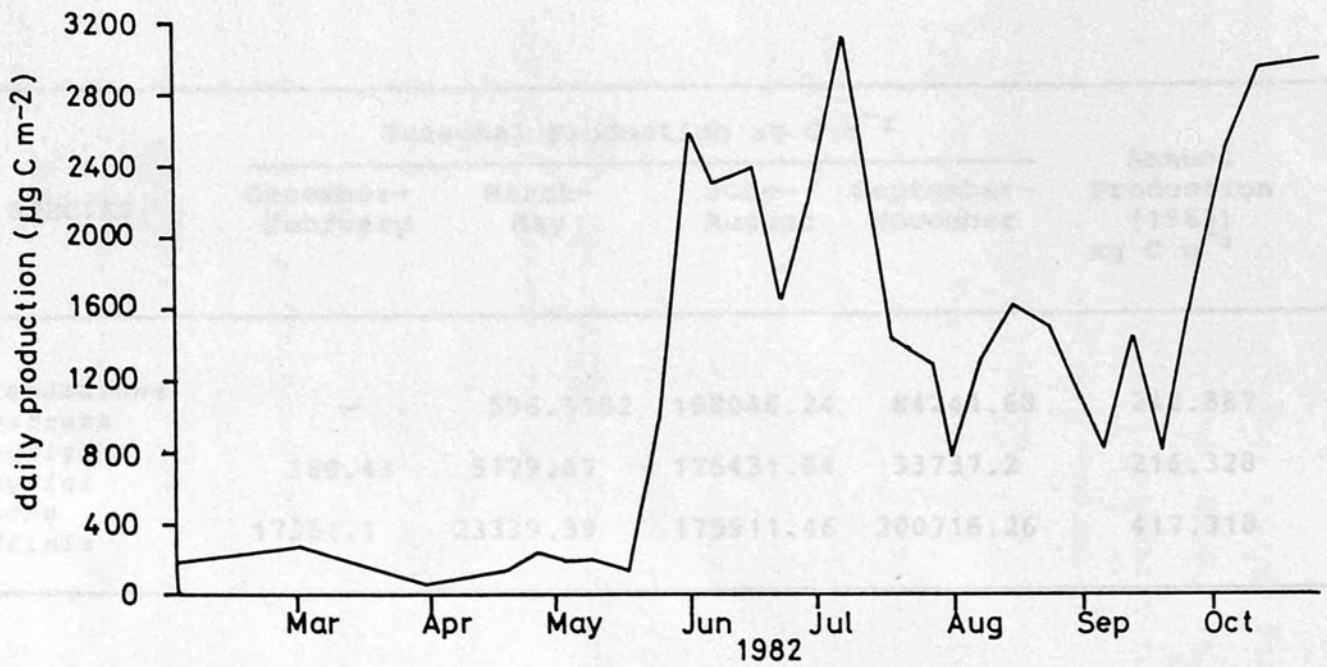


TABLE 17: Seasonal and Annual Production of *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* and Annual Production for the Benthic Chydorid Community at the River Thames, Twickenham

SPECIES	Seasonal Production µg C m^{-2}				Annual Production (1982) mg C m^{-2}	Annual Production for Benthic Chydorid Community mg C m^{-2}
	December-February	March-May	June-August	September-November		
Disparalona rostrata	—	596.1182	158046.24	84244.68	242.887	
Leydigia leydigi	380.43	5779.67	176431.54	33737.2	216.328	876.533
Alona affinis	17351.1	23339.39	175911.46	200716.26	417.318	

CHAPTER 11 : Discussion of Life Histories, Growth and Production of some Chydorid Species

LIFE HISTORIES

Several early studies on the Daphniidae showed that the duration of successive instars increased rapidly in the juvenile phase but more slowly and less regularly in the adult phase (Banta, 1939; Anderson and Jenkins, 1942; Green, 1956). In the present study, however, the duration of neither juvenile nor adult instars in *Leydigia leydigi* and *Disparalona rostrata* increased with age. This is in accordance with the results of Murugan and Sivaramakrishnan (1973, 1976) and Murugan and Job (1982) who found that for *Simocephalus acutirostratus*, *Scapholeberis kingi* and *L. acanthocercoides*, respectively, the duration of a juvenile instar remained constant with age. Murugan and Sivaramakrishnan (1976) also noted that although the duration of an adult instar of *Scapholeberis kingi* was more variable than that of a juvenile instar, there was no clear trend towards an increase of duration with age. Bottrell (1975b) found that in eight species of Cladocera the duration of an adult instar, for a given species and temperature, remained constant with age and the results of Keen (1967) show that this is also the case for *Chydorus sphaericus* and *Pleuroxus denticulatus*.

In the present study the duration of the primiparous instar (and of subsequent adult instars) in *Leydigia leydigi*

and *Disparalona rostrata* was always longer than that of a juvenile instar at the same temperature. This has been noted for many species including *Chydorus sphaericus, Pleuroxus uncinatus, Alona affinis, Eurycercus lamellatus, Acroperus harpae* (Bottrell, 1975b) *Leydigia acanthocercoides* (Murugan and Job, 1982) among the Chydoridae and for *Daphnia longispina* (Banta, 1939), *Simocephalus acutirostratus* (Murugan and Sivaramakrishnan, 1973) and *S. vetulus* (Bottrell, 1975b) among the Daphnidae. However, the primiparous instars of *Moina micrura* (Murugan, 1975) and *Scapholeberis kingi* (Murugan and Sivaramakrishnan, 1976) were found to be of the same duration as those of the preceding juvenile instars.

The duration of an adult instar and length of life in *L. leydigi* and *D. rostrata* decreased with increasing temperature in the present study and this concurs with the results of Bottrell (1975b). The lengths of life of both species were shorter than those of comparable sized chydorids studied by Bottrell (1975b) and did not fit the trend of increasing length of life with species size suggested by this author. However, *Chydorus sphaericus*, originally collected from Lake Lansing, Michigan, and cultured on detritus at 15^{o}C was found to have a mean lifespan of 102 days (Keen, 1967). The same species collected from the River Thames, Reading, and cultured on detritus at the same temperature had a mean lifespan of 32 days (Bottrell, 1975b). Thus substantial differences between different populations of the same species and of

closely related species may occur.

The mean number of adult instars for *L. leydigi* and *D. rostrata* determined in the present study are similar to those found by Bottrell (1975b) for five species of Chydoridae. Considerable variation between studies may, however, exist. Bottrell (1975b) found *Chydorus sphaericus* to have six adult instars at 15°C while Cheremisova from Smirnov (1974) found this species to have more than thirty adult instars.

Leydigia leydigi and *Disparalona rostrata* passed through two or three juvenile instars, the majority having two. Many studies on the Chydorinae and Aloninae have found them to have two juvenile instars (Werner, 1924; Smirnov, 1962, 1974; Shan, 1969), although Bottrell (1975b) found that those he studied passed through a greater number. Murugan and Job (1982) found that *L. acanthocercoides* had three juvenile instars.

Variation in the number of juvenile instars that a given cladoceran species passes through has frequently been ascribed to varying quality of the food provided (Anderson, 1932; Bottrell, 1975b). However, the chydorids of the present study and those studied by Bottrell (1975b) were all fed on fresh detritus from the site of collection and yet I obtained a variable and Bottrell a constant number of juvenile instars.

Green (1956) found that the number of juvenile instars

was frequently related to the size of the neonate in some species of Daphnidae. Appendix IX Table i shows that this was also the case for *L. leydigi* and *D. rostrata*. Results have shown that the size at which a species becomes mature is relatively constant (p. 30). Thus, assuming a constant growth rate in the juvenile stage, it is reasonable to suppose that a small neonate would have to pass through more juvenile instars to reach maturity than a larger one.

At some temperatures the number of juvenile instars is not related to size of the neonate (Appendix IX Table i). Banta (1939) also found that the size of *Daphnia longispina* neonatae which ranged from 0.59-0.71mm, had no effect on the number of juvenile instars. Given this evidence it would appear that other factors apart from neonatal size must influence the number of juvenile instars that occur. It may be that constancy and variability in the numbers of juvenile instars represent two strategies which different species, or the same species in different situations, employ to maximise their chances of survival.

Results from *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata* collected in the field (Figs. 43 to 48) and bred in the laboratory (Appendix X) suggest that the size of eggs and, therefore, the size of the neonatae, decreases with increasing temperature, Thus, if the number of juvenile instars is related to initial size one would expect the proportion of individuals with three juvenile instars to tend to increase with temperature. In fact the

reverse appears to be true. However, it can be seen from Figures 40 and 41 that, for the species studied, the juvenile daily growth does not remain constant but increases with temperature allowing a larger increase in length at each moult at higher temperatures. This may compensate for the smaller initial size at these temperatures and explain the observed decrease in variability in the number of juvenile instars with increasing temperatures.

In the present study although the daily growth in the adolescent instar of *L. leydigi* was less than that of the previous juvenile instars at all temperatures the differences were only significant at 14^{o} and 19^{o}C. Murugan and Job (1982) found that the length increment at the end of the adolescent instar of *Leydigia acanthocercoides* was only half that obtained for the other juvenile instars while Green (1956) noted that for the genus *Daphnia* the greatest length increment was generally found at the end of the adolescent instar.

EGG VOLUME AND PARENT SIZE

My results indicate that the statement made by Agar (1914), for *Simocephalus vetulus*, also applies to the chydorids *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata*, namely, that for a given temperature and egg number, egg volume increases with increasing parent length.

None of the species under discussion secrete a nutritive fluid into the brood pouch and therefore the size of eggs and the size of young may be considered together, the size of young being proportional to the size of egg (Green, 1956). Thus, for a given temperature, larger sized individuals produce larger young: this has been found for *Chydorus sphaericus* (Green, 1956). Why this should be so is not clear. It is possible that the brood chamber capacity of an individual limits the size of eggs it can produce, with smaller individuals having smaller brood chambers and therefore smaller eggs. Frey (1973) noted that the reproductive potential of *Eurycercus glaciacilis* seemed to be considerably restricted by the capacity of its brood chamber. There is also a tentative relationship between the size of neonate and the instar in which they become mature (p.174 and Green, 1956), larger neonatae tending to become a mature instar earlier than smaller ones. Juveniles of small cladoceran species are subjected to heavy invertebrate predation and so there is a premium on the production of large young and early

maturation (p.223). Thus it would appear that large-sized adults, who have managed to survive and reproduce for a considerable time and so produce larger young, are able to confer a distinct advantage upon their offspring over those of smaller-sized parents.

For a given parent size, mean egg volume increases with decreasing temperature for *Leydigia leydigi* and *Alona affinis*. Green (1966) found that mean egg volumes of *Simocephalus vetulus* and *Scapholeberis mucronata*, from the Long Water, Hampton Court, also increased with decreasing temperature although it is not clear whether the eggs were collected from parents of the same length. He also found that, for a given species, the mean egg volume for a particular temperature varied with latitude, larger eggs being produced at higher latitudes. Burgis (1967) determined that for *Ceriodaphnia pulchella* eggs measured in October (13^{o}C) had a higher mean volume than those measured at 20^{o}C from the same habitat.

Green (1966) reasoned that the production of large eggs in cold water by *Simocephalus vetulus* and *Scapholeberis mucronata* would ensure the maximum speed of maturation at these low temperatures while in warm water the greater number of smaller eggs would ensure the maximum rate of increase of the population. Unlike daphnids, however, both *Leydigia leydigi* and *Alona affinis* are fixed clutch species, producing a maximum of two eggs per brood and thus the argument presented by Green (1966) for smaller eggs cannot

apply to these species.

At low temperatures the exposure of individuals in the juvenile stage to possibly intense invertebrate predation is longer than at higher temperatures because the duration of a juvenile instar increases with decreasing temperature (Table 10). The higher allocation of energy to reproduction in the *Leydigia leydigi* and *Alona affinis* populations at low temperatures, which results in the production of larger young, may be an adaptation to counteract this increased susceptibility to invertebrate predation. The intensity of invertebrate predation decreases with increasing prey size (Lynch, 1980). At higher temperatures, higher growth rates result in individuals spending less time in the juvenile stage with a resultant decrease in exposure time to intensive invertebrate predation. At these temperatures the allocation of energy to reproduction per instar in the two populations is reduced, resulting in the production of smaller young.

The variation of the mean length of young with age of parent broadly complements that of egg volume with parent length. Although *Leydigia leydigi* and *Disparalona rostrata* exhibit growth curtailment after maturity, the growth of *L. leydigi* in the first three adult instars, although much less than in the juvenile instars, is still substantially greater than in the remaining adult instars (Fig. 41). Thus one might expect an increase in the length of young produced in the first three instars because of increasing

parent length, followed by the production of young with relatively constant mean lengths in the remaining adult instars.

Growth in *D. rostrata* practically ceases after the first adult moult (Fig. 40) and this is reflected in the fact that although the mean length of young produced increases for the first three broods, the increase between the second and third broods is very small.

For both species the decrease in mean length of young produced in the fourth brood as compared to that in the third brood was unexpected. Although parent growth has been curtailed, parent length has not decreased and thus one would have expected a mean length of young similar to that produced in the third brood. It may be that with increasing age the ability of the parent to allocate energy to reproduction decreases, although, in this case, one might expect successively decreasing mean lengths from the remaining broods and this does not occur.

Green (1954), working on *Daphnia magna*, obtained very similar results including a drop in mean length of young at the fourth brood. This species is a large planktonic daphnid which also exhibits curtailment of growth after maturity. However, it has a variable clutch size and he found that under laboratory conditions the number of young per brood increased for the first six broods and then steadied for the next six before declining. The combination of increasing brood size and reduction in the

increase in parent length, with a concommitant reduction in the increase in size of brood chamber, probably caused the drop in the mean length of young produced in the fourth adult instar. Following this the mean number of young per brood remained steady as did the mean length of young produced.

PRODUCTION

Three assumptions were made when calculating chydorid production at the Twickenham site.

When the growth curves of *Leydigia leydigi*, *Disparalona rostrata* and *Alona affinis* were constructed it was assumed, in order to simplify calculations, that all individuals became mature at the third instar. That this is not the case can be seen from Tables 11 and 12. Thus the production of individuals of a given length maturing at the fourth instar was overestimated.

Bottrell (1977) constructed regression lines of dry weight-body length for a number of cladocerans. He calculated regression for juveniles and adults without eggs for each species separately from those of adults with eggs and noted substantial differences between the two. In the present study, as the majority of adults possessed eggs and it was difficult to remove eggs from females without damaging the latter, a common regression was calculated for all stages of each species, all adult females were assumed to be carrying two eggs. These were included in the basic weight of the female. Thus the production of females without eggs was overestimated.

Although Bottrell (1975b) has stated that chydorid exuviae can account for up to 30% of the body weight, the contribution of exuviae to chydorid production was ignored in this study. As chydorids moult every two to four days

at higher temperatures, this must result in a considerable underestimation of chydorid production. George and Edwards (1974) and Duncan (1975) also disregard the contribution of exuviae although, as these studies were concerned with planktonic cladocerans which possess less substantial carapaces, the resultant error was probably lower.

The production of the species populations was calculated for four, three monthly periods, the autumn period comprising September, October and November. However, sampling was terminated at the end of October and thus production of the species populations for November was based on the relevant daily production for the 25.10.82 sampling date. In all cases this is the autumn maximum, associated with the late autumn population peaks. An examination of the composition of the three species populations indicated that abundance was about to fall and thus November production of the chydorid community based on this maximum is undoubtably overestimated resulting in artificially high autumn values.

The estimation of chydorid production eventually obtained using the graphical method of Winberg (1971) was probably very approximate. However, it was felt that, given the limited time available, this method, resulting in a rough estimate of production, was the most appropriate as much of the data required for the calculations had already been collected during the course of studies on population dynamics and life histories.

Winberg *et al.* (1972) found that the production of the planktonic cladoceran populations in three lakes in Belorussia during the summer ranged from 21.0K cal m^{-2} (mesotrophic lake) to 87.1K cal m^{-2} (highly eutrophic lake). Winberg *et al.* (1972) assumed that the average annual calorific value of net plankton was 5.5K cal g^{-1} dry weight. Using this figure and taking zooplankton dry weight to be 44% carbon (Duncan, 1975), it was estimated that production during the summer ranged from 1.6 to 6.9g C m^{-2}. George and Edwards (1974) found that the maximum daily production estimate for a population of *Daphnia hyalina*, the dominant cladoceran in a shallow eutrophic lake, was 0.6g C m^{-2} with annual production for 1970 calculated at 18.25g C m^{-2}. At the Twickenham site the benthic chydorid populations had a maximal daily production of 0.010g C m^{-2} and an annual production of 0.876g C m^{-2} for 1982. A comparison of these estimates indicates that the annual production of the two planktonic cladoceran communities is greater by a factor of at least ten than that of the benthic chydorid community at the River Thames, Twickenham.

The determination of production of the three species populations in the present study may be viewed as a first step from which further work, aimed at defining the functional role of these populations in the ecosystem may be carried out. For example, it would be useful to assess the fraction of this production that goes to satisfy the food requirements of the next trophic level. It is known

that chydorids are important food items for both vertebrate and invertebrate predators. However, neither a quantitative estimate of mortality from predation nor an estimate of the proportion of this mortality that was due to invertebrate or vertebrate predators was made.

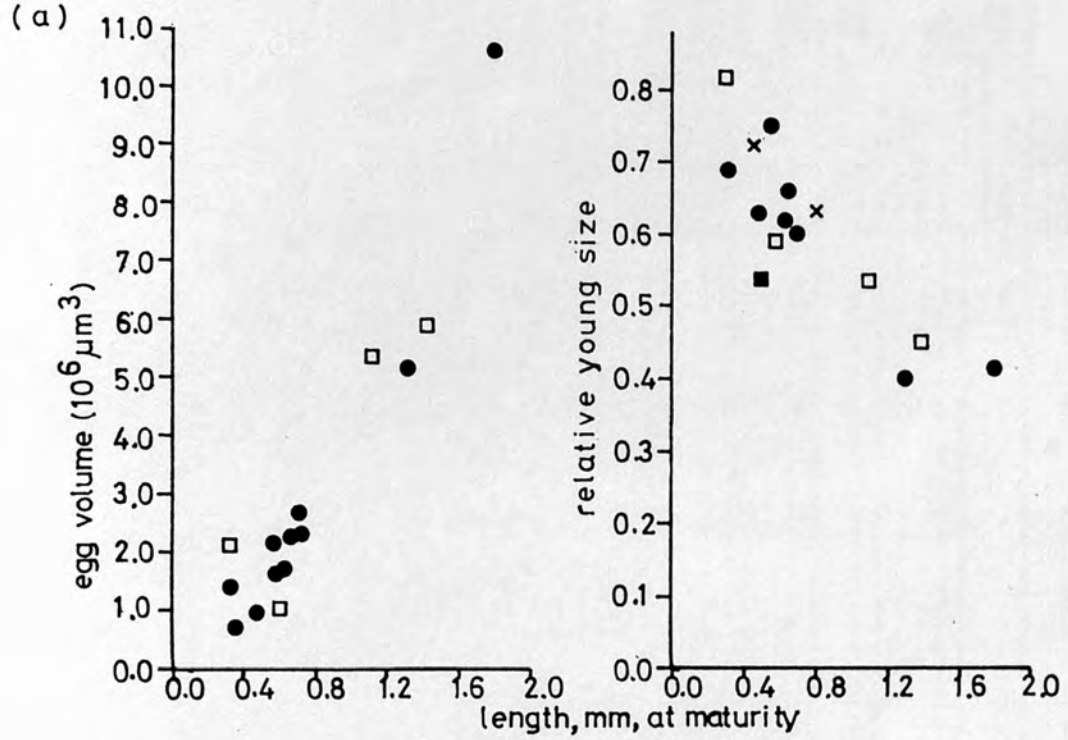
CHAPTER 12 : General Discussion

Throughout the Chydoridae and among the Cladocera generally, small species tend to produce smaller eggs than do large species (Lynch, 1980). However, when egg volumes or the size of the young produced are related to the length at maturity for the Cladocera as a whole, it becomes clear that species which mature at relatively small sizes tend to produce offspring which, at hatching, are much closer to their adult size than those of large species. This implies that less growth is required to reach the length at maturity, and thus there is a negative relationship between relative size of young and age at first reproduction (Figure 54a, b Table 18).

Species which produce relatively large eggs and mature early tend to have a shorter lifespan and thus produce fewer clutches than species with smaller eggs and later maturation (Figure 54b Table 18). This suggests that for these cladocerans the advantage gained by early maturation outweighs the disadvantages of a shorter life-span.

Iteroparity (breeding more than once) is thought to be of selective value wherever juvenile survival is poor or unpredictable (Schaffer, 1974; Bell, 1976). All cladocerans exhibit iteroparity and their offspring are highly susceptible to invertebrate predation. However, iteroparity alone may not ensure juvenile survival and

FIGURE 54 Relation of life history characters to (a) length, mm, at maturity and (b) relative young size (length of young/length at maturity) for well fed laboratory populations of cladocerans. Data from Table 15. ● Chydoridae □ limnetic Daphnidae ■ littoral Daphnidae × Sididae.



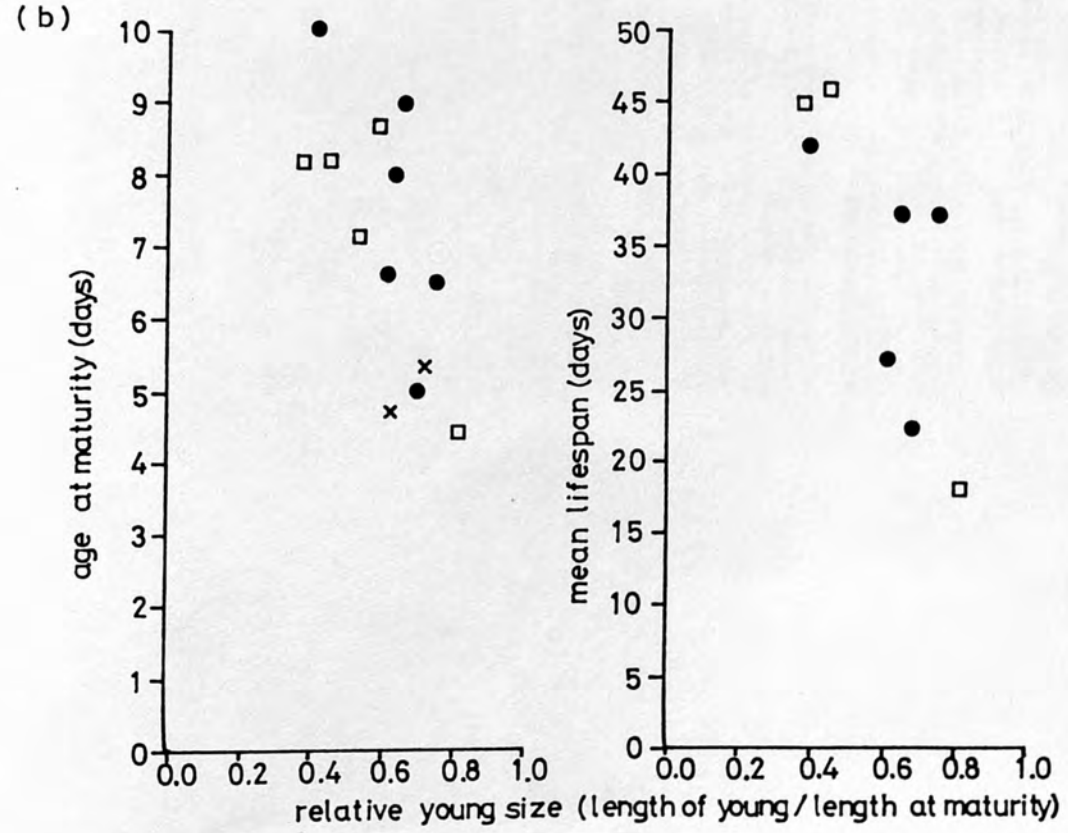


TABLE 18: Life History Characteristics of Some Well Fed Laboratory Populations of Cladocerans

SPECIES	Habitat	Length at Maturity (mm)	Egg Volume $10^6 \mu m^3$	Age at[1] Maturity (days)	Mean[2] Lifespan (days)	Relative[3] Young Size	SOURCE
CHYDORIDAE							
Chydorus sphaericus	littoral benthic	0.32	1.4	5	24	0.687	Bottrell (1975b)
Alona rectangula	"	0.35	0.67	-	-	-	Present work
Disparalona rostrata	"	0.48	0.91	8	37	0.63	Present work
Pleuroxus uncinatus	"	0.56	1.65	-	31	-	Present work Bottrell (1975b)
Alona affinis	"	0.56	2.18	6.5	37	0.75	Present work Bottrell (1975b)
Pleuroxus trigonellus	"	0.6	1.7	-	-	-	Green (1956)
Leydigia leydigi	"	0.63	2.26	6.8	27	0.615	Present work
Peracantha truncata	"	0.63	-	9	-	0.66	Lynch (1980)
Acroperus harpae	"	0.7	2.3	-	-	0.6	Green (1956) Smirnov (1974)
Alonopsis elongatus	"	0.7	2.6	-	-	-	Green (1956)
Eurycercus macrocanthus	"	1.3	5.1	-	-	0.4	Frey (1973)
Eurycercus lamellatus	"	1.8	10.7	10	42	0.411	Bottrell (1975a, b), Frey (1973), Green (1956), Smirnov (1964)
Eurycercus glacialis	"	2.8	23.1	-	-	0.314	Green (1956) Frey (1973)
DAPHNIDAE							
Ceriodaphnia cornuta	limnetic planktonic	0.32	2.05	4.4	18	0.812	Green (1971) Zaret (1972)
Scapholeberis kingi	littoral planktonic	0.52	-	-	-	0.538	Lynch (1980), Murugan and Sivaramakrishnan (1976)
Ceriodaphnia quadrangula	limnetic planktonic	0.61	1.0	8.7	-	0.59	Bottrell (1976), Dumont (1975), Kwik and Carter (1975).
Daphnia longispina	"	1.12	5.4	7.2	-	0.535	Bottrell (1975), Green (1956), Węgleńska (1971)
Daphnia hyalina	"	1.42	5.9	8.2	46	0.457	Bottrell (1976), Green (1956), Jacobs (1978), Vijuerberg (1976)
Daphnia magna	"	2.2	22.9	8.4	45	0.372	Anderson (1932), Anderson and Jenkins (1942), Duncan (1975), Green (1956)
SIDIDAE							
Latonopsis breviremis	littoral planktonic	0.48	-	5.3	-	0.729	Montu (1973)
Pseudosida bidentata	"	0.81	-	4.7	-	0.629	Montu (1973)

1 mean age at maturity for cultures of cladocerans maintained at 20°C except for those determined in the present work (19°C)

2 mean lifespan for cultures of cladocerans maintained at 20°C except for those determined in the present work (19°C)

3 relative young size = $\frac{\text{mean length of young}}{\text{length at maturity}}$

the large and small planktonic Cladocera have evolved different life history strategies to minimise juvenile mortality (Lynch, 1980).

The larger planktonic cladocerans, for example *Daphnia magna* and *D. pulex*, are capable of growing to a size where they are relatively invulnerable to most invertebrate predators that occur in the plankton (Lynch, 1980). The juveniles of these species maximise energy input into growth and postpone reproduction until they have reached such a size: after the onset of reproduction, growth is curtailed and maximum energy is alloted to reproduction. However, juvenile growth beyond the reach of invertebrate predators increases susceptibility to vertebrate predation.

Smaller planktonic cladocerans, for example *Ceriodaphnia cornuta*, that remain vulnerable to invertebrate predators throughout their life cycles have little use for such a strategy. They minimise the impact of invertebrate predation by producing young closer to the maturation length and initiating reproduction at an early age. Following the onset of reproduction they continue to grow. This continuation of growth, which simultaneously decreases susceptibility to invertebrate predation and increases exposure to vertebrate predation, suggests that the former type of predation has been of greater evolutionary significance for these species (Lynch, 1980).

The life history strategy employed by the Chydoridae

(except the Eurycercinae and Saycinae), and other small cladocerans inhabiting the littoral region, appears to lie somewhere between the two discussed above. Data is available for a number of species (Figures 40, 41, 54a, b Table 18). These littoral Cladocera produce large young relative to their size at maturity and mature early but, unlike the small planktonic cladocerans, growth is curtailed after the onset of reproduction. The combination of selection pressures which have led to the adoption of this life history strategy is unknown.

Predatory invertebrates are abundant in the littoral region (p. 135) and the small littoral benthic cladocerans have responded to this pressure by producing relatively large young and maturing quickly, in the same manner as the small planktonic Cladocera. However, in spite of the fact that the lengths at maturity of most Chydoridae (except the Eurycercinae and the Saycinae) are well within the size range of invertebrate predators, growth is curtailed after maturity. This may be due to a number of factors including vertebrate predation and the presence of vegetation in the habitat. Fish feed visually, selecting the individuals that appear largest. If fish predation is heavier, or has a more significant impact on the cladoceran populations in the littoral than in the limnetic regions, then the littoral cladocerans may have responded by curtailing growth to a size that minimises the impact of this predation. Fish predation can have a substantial

impact on large littoral cladocerans, as can be seen from the distribution of *Eurycercus glacialis* (Frey, 1973). The littoral Cladocera are frequently associated with the sediments and the aquatic plants found in these regions. The degree of protection that these offer to cladocerans, in terms of shelter from predators and buffering from wave action, may be size dependant and so may select for smaller sized cladocerans, resulting in a curtailment of growth after the initiation of reproduction.

The Eurycercinae and Saycinae are anomalies among the Chydoridae. Considerable information is available for *Eurycercus lamellatus* (Table 18). This species is large, maturing at 1.8mm, the relative young size is small and it has a larger number of juvenile instars than is usual among the Chydoridae (Frey, 1973; Bottrell, 1975b). In these respects *E. lamellatus* resembles the large planktonic cladocerans but information on the degree of growth after maturity is not available.

The results of field work and a survey of the literature has shown that a taxocene of cladocerans exists which is characteristic of the mud substrate of both lakes and rivers. The same cladoceran species are found both in the substrate of rivers, where the flow rate is fast enough to produce areas of semi-riffle, and of lakes (Table 8). Thus the species composition of a benthic cladoceran community does not appear to be affected by the presence or absence of current. The number of cladoceran

species present in the benthos of the unvegetated littoral in lotic and lentic environments was also similar. The absence of members of the taxocene from a particular site may be due to the superposition of physical and chemical preferences on substrate requirements, although many species belonging to the taxocene are considered to be eurytopic (Fryer, 1968; Smirnov, 1974). It may also be caused by biotic factors (cf. the absence of *Eurycercus lamellatus* from the Twickenham site). The chloride content of the water at the Teddington site was similar to that above Teddington weir and it appears that saline water does not extend this far upstream. It would be most interesting to determine the degree to which the benthic cladoceran community altered in composition and abundance downstream as the salinity of the water increased.

The maximum abundance of the benthic chydorids present at the Twickenham site was lower than that of the chydorids from the benthos of the unvegetated littoral of a number of lakes. The possibility that large numbers of individuals were lost from the river populations due to vertical migration or disturbance of the sediment by currents was rejected by reason of the results from the plankton samples. It is possible that the nature of the detritus present in the habitat and thus the quality of the food available to the benthic cladoceran communities, or the degree of predation is responsible for these differences in maximum abundance.

The structural complexity of the substrate at the Twickenham site is low and it has been suggested that niche differentiation may be limited. However, six cladoceran species were abundant at the site and coexisted for at least three years, apparently occupying the same habitat and utilising the same food source. This poses questions as to the mechanisms by which this can occur. It is probable that their separation is largely the result of spatial distribution. *Iliocryptus sordidus* and *Leydigia leydigi* are members of the infauna, penetrating deeply into the substrate. *Disparalona rostrata* burrows into the surface mud while *Alona affinis* crawls over the surface. It is also possible that they utilise different food resources in the habitat. For example, one cladoceran may be able to digest a particular type of micro-organism while others cannot. Brinkhurst and Chua (1969) have presented evidence that this mechanism may occur in three species of tubificid worms.

The study of the population dynamics of the benthic chydorid community at the Twickenham site indicated that the midsummer decline in population numbers resulted largely from mortality and that predation was likely to be a major cause of this. However, identification of possible invertebrate predators and examination of their gut contents was not carried out. The abundance of invertebrate predators and fish fry was not estimated. Thus the relative importance of predation by invertebrates and fish and the degree of

mortality resulting from predation could not be ascertained.

If time had been available for research into these areas then the causes of the chydorid midsummer population decline could have been evaluated in greater detail. These results would have been useful in production studies and may also have helped to clarify the combination of selection pressures that led to the life cycle strategy adopted by the Chydoridae.

The trophic interrelationships of organisms, resulting in the transfer of quantities of matter and energy from one trophic level to another, is the basis of production in ecosystems. Thus, although it is a useful first step to calculate the production of species populations, as has been done in the present study, it is of fundamental importance to know the characteristics of individual organisms which determine their interaction with organisms from adjacent trophic levels, for example, to know their food requirements.

The benthic chydorids found in the River Thames at Twickenham may be broadly classed as detritivores. Detritus contains energy and nutrients which are particularly exploited by micro-organisms: it appears, however, to be a low quality food for animals. They pass it rapidly through their guts and are only able to assimilate a small proportion of the material ingested (Berrie, 1976). There are three possibilities as to how animals utilise ingested detritus. They may digest part of the detritus particles,

they may strip off the micro-organisms coating the particles leaving the latter almost unchanged or they may use a combination of both. Brinkhurst and Chua (1969), Calow (1974) and Hargreave (1970) have found evidence that tubificid worms, snails and amphipods can ingest bacterial tissue from detritus.

Determination of the degree to which benthic chydorids rely on the detritus itself and on the associated micro-organisms would be extremely valuable in production studies. A major problem encountered in the life history and growth studies of *Disparalona rostrata* and *Leydigia leydigi* was lack of knowledge as to the precise diet of the chydorids. Without this information, attempts to standardise and quantify food given to the cultures could not be made and it was, therefore, not possible to study the interaction of food and temperature on the growth of the chydorids.

This study of the biology of benthic cladocerans in flowing freshwaters has yielded detailed quantitative information on the species composition, population dynamics and production of the benthic cladoceran community in the River Thames at Twickenham. Evidence for the existence of a taxocene of cladocerans characteristic of the unvegetated littoral benthos of lakes and rivers has been presented. Data has also been collected on the life histories of two chydorid species. However, determination of the components of ingested detritus that the benthic chydorids utilise and elucidation of the relative importance of invertebrates

and fish as predators requires further research. Investigation of these problems would clarify the position of benthic cladocerans in the trophic relationships of the riverine ecosystem.

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Appendix I

Data from preliminary study at the River Thames, Twickenham in 1981.

Individuals of a population can follow three basic types of spatial distribution (Elliott, 1977).

1. A random distribution (variance equal to the mean).
2. A regular distribution (variance less than the mean).
3. A contagious distribution (variance greater than mean).

Elliott (1977) recommends that a chi-squared (χ^2) test be undertaken to determine the type of spatial distribution present and gives the following formula:-

$$\chi^2 = \frac{s^2(n-1)}{\bar{x}}$$

s^2 = variance
n = number of sample units
$\bar{x}$ = mean

Agreement with a random distribution (Poisson series) is accepted at the 99% probability level if the χ^2 value lies between the appropriate 1% significance levels for n-1 degrees of freedom. Significance levels are given in Rohlf and Sokal (1969).

If the χ^2 value is less than expected then a regular distribution is suspected.

If the χ^2 value is greater than expected then a contagious distribution is suspected.

It can be seen from the following tables that the

Appendix I

χ^2 values for total chydorids and each of the three most abundant species lie well above the values for $\alpha = 0.005$ for n-1 degrees of freedom, this is also the case for the chydorids and *Iliocryptus sordidus* of the core sample series. Therefore agreement with a Poisson series is rejected at the 99% probability level. The high values of χ^2 indicate that the cladoceran populations have a contagious dispersion.

Appendix I

Critical values for the χ^2 distribution.* From Rohlf and Sokal (1969).

Degrees of freedom	α = 0.995	α = 0.005
8	1.344	21.955
9	1.735	23.589
10	2.156	25.188
11	2.603	26.757
13	3.565	29.819
14	4.075	31.319
15	4.601	32.801
16	5.142	34.367
17	5.697	35.718

* Values for the 1% significance level only are given, thus, with a random distribution and 15 degrees of freedom the probability that a value of χ^2 is greater than 32.801 is 0.05%.

Appendix I

PATTERN SAMPLER (1981)

TOTAL CHYDORIDS			*Alona affinis*		
DATE	χ^2	Degrees of freedom (n-1)	DATE	χ^2	Degrees of freedom (n-1)
15. 5.81*	44699	15	15. 5.81	31402	14
27. 5.81	156966	15	27. 5.81	91439	15
3. 6.81	80435	15	3. 6.81	56046	15
10. 6.81	73691	15	10. 6.81	41686	15
17. 6.81	64183	15	17. 6.81	30599	15
1. 7.81	60176	15	1. 7.81	33739	15
14. 7.81	66323	15	14. 7.81	23223	14
21. 7.81	213545	15	21. 7.81	47494	15
4. 8.81	64021	15	4. 8.81	24104	15
11. 8.81	108382	15	11. 8.81	51542	15
25. 8.81	104032	15	25. 8.81	55121	15
9. 9.81	41480	15	9. 9.81	31463	15
16. 9.81	14837	15	16. 9.81	9458	15
6.10.81	14514	15	6.10.81	13453	15
12.10.81	72932	15	12.10.81	34368	14
19.10.81	8312	15	19.10.81	3771	15

* only the date on which the pattern sampler was set down is given.

Appendix I

Disparalona rostrata			*Leydigia leydigi*		
DATE	χ^2	Degrees of freedom (n-1)	DATE	χ^2	Degrees of freedom (n-1)
15. 5.81	14894	15	15. 5.81	12645	15
27. 5.81	30568	15	27. 5.81	35296	15
3. 6.81	14857	15	3. 6.8.	12023	15
10. 6.81	9992	15	10. 6.81	32236	15
17. 6.81	4631	15	17. 6.81	34014	15
1. 7.81	24258	15	1. 7.81	27761	15
14. 7.81	37460	14	14. 7.81	5867	14
21. 7.81	163212	14	21. 7.81	11256	14
4. 8.81	48801	13	4. 8.81	10814	13
11. 8.81	40089	13	11. 8.81	19789	13
25. 8.81	55225	15	25. 8.81	24167	15
9. 9.81	27959	15	9. 9.81	5635	15
16. 9.81	8055	14	16. 9.81	6783	14
6.10.81	4939	15	6.10.81	3407	15
12.10.81	32348	14	12.10.81	4761	15
19.10.81	5611	14	19.10.81	2277	14

Appendix I

CORE SAMPLER SERIES (1981)

TOTAL CHYDORIDS			*Alona affinis*		
DATE	χ^2	Degrees of freedom (n-1)	DATE	χ^2	Degrees of freedom (n-1)
15. 7.81	104631	9	15. 7.81	114645	9
22. 7.81	247225	11	22. 7.81	75683	11
5. 8.81	274864	9	5. 8.81	99403	9
12. 8.81	542387	16	12. 8.81	253896	16
10. 9.81	150101	11	10. 9.81	124231	11
17. 9.81	75549	9	17. 9.81	66227	9
13.10.81	246614	15	13.10.81	166823	15
19.10.81	132287	15	19.10.81	168237	15
28.10.81	67203	10	28.10.81	69669	10
10.11.81	100954	17	10.11.81	130103	17
Disparalona rostrata			*Leydigia leydigi*		
15. 7.81	94201	9	15. 7.81	7488	9
22. 7.81	208463	11	22. 7.81	39369	11
5. 8.81	204229	9	5. 8.81	50973	9
12. 8.81	476692	16	12. 8.81	163282	15
10. 9.81	81804	11	10. 9.81	-	NONE
17. 9.81	35427	9	17. 9.81	39563	9
13.10.81	189233	15	13.10.81	112937	15
19.10.81	106052	15	19.10.81	116635	15
28.10.81	58709	10	28.10.81	86195	10
10.11.81	-	NONE	10.11.81	95828	17

Appendix I

Iliocryptus sordidus

DATE	χ^2	Degrees of freedom (n-1)
15. 7.81	52667	9
22. 7.81	117378	11
5. 8.81	79042	9
12. 8.81	68615	16
10. 9.81	-	NONE
17. 9.81	33891	8
12.10.81	173327	15
19.10.81	90137	15
28.10.81	39572	10
10.11.81	95828	17

Appendix II

Calculations to determine whether the Sample Units in the Pattern Sampler Matrix may be considered independant of each other.

Two samples were taken, one comprising sixteen sample units taken in a matrix and the other sixteen sample units taken separately (p. 48). The samples were compared using a t-test preceded by an F-test (Appendix IX). Chydorid distribution is contagious (Appendix I), and therefore the counts must be transformed before normal distribution tests such as the F- and t-tests can be applied (Elliott, 1977). There were no zero counts and therefore the log x transformation was used.

Sample with sample units in a matrix	Sample with sample units taken separately
$n_1 = 16$	$n_2 = 16$
$\bar{y}_1 = 3.3152$	$\bar{y}_2 = 3.4525$
$y_1 = 53.0438$	$y_2 = 55.2402$
$y_1^2 = 180.0667$	$y_2^2 = 194.6857$
$s_1^2 = 0.2810$	$s_2^2 = 0.2645$

where y and $\bar{y}$ are the transformed counts and mean respectively, s^2 is the variance and n is the number of sample units.

Appendix II

F-test

$F = 1.0623$ degrees of freedom $f_1 = 15$

$f_2 = 15$

The tabulated value of F was 2.40 at the 5% level of significance. As the calculated value of F was below this, the variances of the two samples were not significantly different at the 5% level.

t-test

$t = 0.7437$ degrees of freedom = 30

The tabulated value of t was 2.042 at the 5% level of significance. As the calculated value of t was below this, the means of the two samples were not significantly different at the 5% level.

Therefore the sample units in a pattern sampler matrix may be considered independant of each other.

Appendix III

Analysis of Chloride (Golterman, 1969)

PRINCIPLE: An excess of $AgNO_3$ in acid solution is added to the chloride - this prevents the co-precipitation of the Ag-salts of CO_3^{2-}, PO_4^{3-} etc. The excess Ag^+ is titrated with CNS^- in the presence of Fe^{3+} and nitrobenzene. I^-, Br^- and S^{2-} are measured as equivalents of Cl^-. Precision and accuracy are both limited by the accuracy of the end point detection which is better than 0.1mg Cl^-.

REAGENTS:

1. $AgNO_3$ 0.1N (analytical reagent grade) - commercially available standardised solution.

2. HNO_3 - mix equal volumes of HNO_3 (S.G. = 1.42) and H_2O. Boil until colourless and store in a glass stoppered brown bottle.

3. $Fe_2(SO_4)_3$ 25% - dissolve 25g $NH_4Fe(SO_4)_3.12H_2O$ in about 100ml H_2O to which 5 drops of HNO_3 (2) have been added.

4. KCNS 0.02N - commercially available standardised solution.

5. Nitrobenzene, pure.

PROCEDURE:

100ml of the sample is mixed with 5ml HNO_3 (2). $AgNO_3$(1) is added from a burette mixing vigorously until the approximate endpoint is reached, identified by the

Appendix III

absence of precipitation near the $AgNO_3$ drops. A further 2ml, that is excess, is added and the volume of $AgNO_3$ recorded. 3ml of nitrobenzene (5) and 1ml of $Fe(SO_4)_3$ (3) was added and the whole shaken vigorously. The excess Ag^+ is then titrated against standardised KCNS (4) using a piston microburette with an automatic zero adjustment and reservoir of titrant. The end point can be determined by the appearance of a permanent reddish colour which does not fade in one minute of intensive shaking.

For the standardisation of the KCNS, 100ml of H_2O and 10.0ml of $AgNO_3$ were used.

CALCULATION:

$$Cl^-meq = Ag^+meq - CNSmeq$$

$$Cl^-meq = \frac{[(ml \times normality) \text{ of } 1 - (ml \times normality) \text{ of } 4] \times 1000}{ml \text{ sample}}$$

Appendix IV : Comparison of Pattern and Core Samplers, in Sampling Numbers of *Disparalona rostrata*, *Alona affinis* and *Leydigia leydigi*, under $1m^2$ of substrate, using F- and t-tests (see Appendix IX)

	DATE	F	Degrees of Freedom F_1	Degrees of Freedom F_2	Tabulated value of F, 1% level of significance	t-test t	t-test d	Degrees of Freedom	Tabulated value of t, 1% level of significance
	5.5.82	478.8 *	30	50	2.11	-	2.642	30	2.750
	11.5.82	-	-	-	-	-	-	-	"
	17.5.82	4.1 *	30	50	2.11	-	2.00	51	"
	24.5.82	2.7 *	49	21	2.72	-	2.56	66	"
	1.6.82	107.6 *	51	26	2.50	-	6.37*	38	"
	8.6.82	122.8 *	51	23	2.62	-	3.88*	47	"
	14.6.82	99.5 *	51	28	2.44	-	4.35*	52	"
Disparalona	21.6.82	20.0 *	49	26	2.50	-	1.149	58	"
rostrata	28.6.82	5.1 *	49	30	2.39	-	2.129	74	"
	6.7.82	16.6 *	49	29	2.41	-	0.644	50	"
	19.7.82	5.1 *	49	30	2.39	-	0.09	72	"
	26.7.82	42.6 *	49	30	2.39	-	1.29	52	"
	2.8.82	27.0 *	47	30	2.39	-	8.47*	52	"
	10.8.82	31.0 *	49	30	2.39	-	4.01*	55	"
	16.8.82	52.0 *	50	30	2.39	-	2.6	52	"
	24.8.82	24.0 *	48	30	2.39	-	1.81	52	"

* significant difference at the 1% level.

Appendix IV

	DATE	F	Degrees of Freedom F_1	Degrees of Freedom F_2	Tabulated value of F, 1% level of significance	t-test t	t-test d	Degrees of Freedom	Tabulated value of t, 1% level of significance
	5.5.82	1.6	30	49	2.11	7.19*	-	79	2.75
	11.5.82	2.6*	28	50	2.11	-	6.95*	40	"
	17.5.82	1.1	30	50	2.11	1.95	-	80	"
	24.5.82	2.0	49	20	2.78	1.87	-	69	"
	1.6.82	30.0*	51	26	2.50	-	2.15	52	"
	8.6.82	30.0*	52	23	2.62	-	2.09	58	"
	14.6.82	35.0*	51	28	2.44	-	1.93	58	"
Leydigia	21.6.82	65.0*	50	26	2.50	-	2.10	52	"
leydigi	28.6.82	58.0*	51	31	2.37	-	2.16	55	"
	6.7.82	50.0*	49	29	2.41	-	2.20	52	"
	19.7.82	0.2	49	30	2.39	2.24	-	79	"
	26.7.82	9.4*	49	30	2.39	-	2.67	66	"
	2.8.82	9.3*	49	30	2.39	-	10.69*	66	"
	10.8.82	6.9*	49	30	2.39	-	13.88*	71	"
	16.8.82	1.8	50	31	2.37	6.48*	-	81	"
	24.8.82	9.0*	48	30	2.39	-	8.46*	62	"

* significant difference at the 1% level.

Appendix IV

	DATE	F	Degrees of Freedom F_1	Degrees of Freedom F_2	Tabulated value of F, 1% level of significance	t-test t	t-test d	Degrees of Freedom	Tabulated value of t, 1% level of significance
	5.5.82	5.2*	49	30	2.39	-	14.07*	72	2.75
	11.5.82	1.6	50	28	2.11	2.54	-	78	"
	17.5.82	27.0*	49	30	2.39	-	10.83*	55	"
	24.5.82	208 *	50	20	2.78	-	2.72	52	"
	1.6.82	61.0*	51	26	2.50	-	2.54	55	"
	8.6.82	73.0*	51	23	2.62	-	2.4	53	"
	14.6.82	61.0*	51	28	2.44	-	2.18	53	"
Alona	21.6.82	44.0*	46	25	2.54	-	2.69	50	"
affinis	28.6.82	7.0*	50	31	2.37	-	2.40	71	"
	6.7.82	29.0*	49	29	2.41	-	2.30	50	"
	19.7.82	66.0*	49	30	2.39	-	2.67	52	"
	26.7.82	51.0*	49	30	2.39	-	2.53	52	"
	2.8.82	32.0*	50	30	2.39	-	6.7 *	55	"
	10.8.82	103.0*	50	30	2.39	-	7.21*	52	"
	16.8.82	16.0*	50	31	2.37	-	6.8 *	58	"
	24.8.82	54.0*	49	30	2.39	-	5.25*	52	"

* significant difference at the 1% level.

Appendix V : Physico-chemical parameters of the River Thames at Twickenham

Table i - Seasonal changes in Temperature (^{o}C), morning and evening values are given with the mean in parentheses, and the percentage organic content of the substrate of the River Thames at Twickenham 1982.

DATE	TEMPERATURE (^{o}C) am	pm	DATE	% ORGANIC CONTENT
2- 3. 2.82	4	3 (3.5)	2. 2.82*	11.90
2- 3. 3.82	7	6 (6.5)	2. 3.82	14.21
29-30. 3.82	7	5 (6)	29. 3.82	15.99
19-20. 4.82	12	12 (12)	20. 4.82	15.09
26-27. 4.82	10	10 (10)	26. 4.82	11.08
4- 5. 5.82	9	8 (8.5)	5. 5.82	9.8
10-11. 5.82	14	15 (14.5)	11. 5.82	8.25
17-18. 5.82	17	17 (17)	17. 5.82	5.04
24-25. 5.82	17	18 (17.5)	24. 5.82	7.46
1- 2. 6.82	19	19 (19)	1. 6.82	7.32
7- 8. 6.82	21	23 (22)	8. 6.82	6.37
14-15. 6.82	19	19 (19)	14. 6.82	4.2
21-22. 6.82	18	17 (17.5)	21. 6.82	3.55
28-29. 6.82	19	19 (19)	28. 6.82	8.53
6- 7. 7.82	18	18 (18)	6. 7.82	8.62
19-20. 7.82	20	20 (20)	19. 7.82	6.56
26-27. 7.82	19	19 (19)	26. 7.82	5.95
2- 3. 8.82	21	21 (21)	2. 8.82	5.51
9-10. 8.82	18	20 (19)	10. 8.82	9.29
16-17. 8.82	19	19 (19)	16. 8.82	7.24
23-24. 8.82	17	17 (17)	24. 8.82	5.81
31.8-1.9.82	16	16 (16)	31. 8.82	8.83
6- 7. 9.82	17	17 (17)	7. 9.82	5.82
13-14. 9.82	14	13 (13.5)	13. 9.82	6.22
19-20. 9.82	18	18 (18)	20. 9.82	7.73
27-28. 9.82	12	12 (12)	27. 9.82	5.32
4- 5.10.82	13	13 (13)	5.10.82	4.97
11-12.10.82	12	12 (12)	11.10.82	4.62
25-26.10.82	11	12 (11.5)	25.10.82	15.68

* The date given is that on which the physico-chemical measurements and the core sampler series were collected. This was either the evening on which the pattern sampler was set down or the morning on which it was lifted.

Appendix V

Table ii - Seasonal changes in chlorophyll *a* (mg under $1m^2$ substrate) and phaeopigment (mg under $1m^2$ of substrate) present in the substrate of the River Thames, Twickenham 1982.

DATE	chlorophyll *a* (mg under $1m^2$)	phaeopigment (mg under $1m^2$)
2. 2.82	84.65	281.76
2. 3.82	58.34	216.62
29. 3.82	171.75	281.13
20. 4.82	150.7	229.48
26. 4.82	103.55	157.03
5. 5.82	102.31	163.33
11. 5.82	99.59	168.88
17. 5.82	101.06	183.91
24. 5.82	126.13	211.42
1. 6.82	135.46	209.11
8. 6.82	161.96	210.96
14. 6.82	92.45	170.10
21. 6.82	64.28	143.79
28. 6.82	105.99	155.28
6. 7.82	111.42	140.51
19. 7.82	87.31	53.02
26. 7.82	152.56	144.23
2. 8.82	241.01	191.67
10. 8.82	213.96	263.31
16. 8.82	197.78	201.10
24. 8.82	185.05	170.73
31. 8.82	216.45	136.21
7. 9.82	186.01	240.05
13. 9.82	281.81	225.34
20. 9.82	328.84	200.78
27. 9.82	310.87	195.67
5.10.82	292.45	120.91
11.10.82	292.57	119.51
25.10.82	348.02	272.87

Appendix V

Table iii - Chloride concentration of water samples taken from the River Thames at Twickenham 1983.

23.2.83

Time of low and high water	height of water (m)	
0555	1.6	LW
1024	5.9	HW
1854	1.5	LW

Time (hours) at which samples were removed from the site	Mean Chloride concentration (mg/l)	Comments on tide
0900	18.08	rising
1000	28.36	rising
1100	10.63	ebbing
1200	18.08	ebbing
1300	20.09	slack
1400	19.02	slack

21.4.83

Time of low and high water	height of water (m)	
0507	1.2	LW
0940	6.1	HW
1738	1.7	LW

All collections were made on an ebbing tide.

Time (hours) at which samples were removed from the site	Mean Chloride concentration (mg/l)	
	Just above substrate	Just below surface
0930	28.54	29.76
1000	27.38	32.99
1030	24.07	26.21

Appendix V

Table iii (continued)

12.7.83

Time of low and high water	height of water (m)	
0447	7.3	HW
1335	0.6	LW

Six 500ml bottles were filled at 1000 hours, i.e. on an ebbing tide.

Mean Chloride concentration (mg/l) - 38.46.

Appendix VI : Benthic Chydorids found in Fish from the River Thames and River Chess

Table i - Benthic chydorids found in the guts of *Rutilus rutilus* and *Gasterosteus aculeatus* from the River Thames at Twickenham 1982.

Fish Species	Date caught	Length of fish (cm). Number examined in parentheses.	Chydorid species found. Average number found per fish in parentheses.
Rutilus rutilus	2.6.82	1.1 (5)	NONE
"		1.2 (10)	NONE
"		1.3 (5)	NONE
Rutilus rutilus	29.6.82	1.5 (1)	NONE
"		1.6 (1)	NONE
"		1.7 (2)	*Alona affinis* (5)
			Leydigia leydigi (1)
"		1.8 (8)	*Alona affinis* (2)
"		1.9 (4)	NONE
"		2.0 (1)	NONE
"		2.1 (1)	NONE
Rutilus rutilus	26.7.82	1.4 (5)	*Alona affinis* (4)
"			*Leydigia leydigi* (1)
"		1.5 (6)	*Alona affinis* (14)
			Leydigia leydigi (1)
			Disparalona rostrata (5)
"		1.6 (2)	*Alona affinis* (3)
"		1.7 (6)	*Alona affinis* (11)
			Leydigia leydigi (1)
Gasterosteus aculeatus	26.7.82	2.0 (2)	*Alona affinis* (6)
			Leydigia leydigi (2)
			Disparalona rostrata (10)

The total number of chydorids found in fish of a given length were fairly evenly distributed among the individual fish.

Appendix VI

Table ii - Benthic chydorids found in the guts of *Cottus gobio*, *Noemacheilus barbatulus* and *Phoxinus phoxinus* from the River Chess 1983.

Fish Species	Length of fish (cm) Number examined in parentheses	Chydorid species found. Average number found per fish in parentheses
Cottus gobio	1.7 (1)	NONE
(bullhead)	2.0 (7)	"
	2.2 (2)	"
	2.5 (6)	"
	3.0 (3)	"
	6.5 (5)	"
	7.0 (1)	"
	8.0 (1)	"
Noemacheilus barbatulus	1.7 (1)	*Alona affinis* (13)
(stone loach)		*Alona rectangula* (1)
	1.8 (1)	*Alona affinis* (1)
	2.0 (3)	*Alona affinis* (8)
		Alona rectangula (9)
		Alona quadrangularis (7)
	2.2 (1)	*Alona rectangula* (4)
	2.3 (3)	*Alona affinis* (5)
		Alona rectangula (1)
		Alona quadrangularis (3)
	2.5 (2)	*Alona affinis* (1)
	3.2 (2)	*Alona affinis* (1)
	5.5 (1)	*Alona affinis* (1)
	6.5 (2)	NONE
	10 (3)	"
Phoxinus phoxinus	2.0 (7)	NONE
(minnow)		

The total number of chydorids found in fish of a given length were fairly evenly distributed among the individual fish.

APPENDIX VII : Population Parameters of the Benthic Cladocerans at the River Thames, Twickenham

Table i - Seasonal changes in numbers of total chydorids from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82*	689 ± 186	82 ± 1434
2. 3.82	954 ± 282	0.05 ± 4.95
29. 3.82	145 ± 111	7 ± 76
20. 4.82	599 ± 247	1131 ± 722
26. 4.82	1184 ± 373	1220 ± 1017
5. 5.82	1189 ± 345	1018 ± 1004
11. 5.82	969 ± 399	766 ± 550
17. 5.82	1017 ± 254	1358 ± 690
24. 5.82	4566 ± 503	7017 ± 2227
1. 6.82	17129 ± 2709	17085 ± 7479
8. 6.82	18033 ± 2573	24194 ± 5485
14. 6.82	27427 ± 2707	25030 ± 6851
21. 6.82	23089 ± 3545	26484 ± 5410
28. 6.82	44545 ± 16470	27296 ± 6627
6. 7.82	45650 ± 4050	52549 ± 8378
19. 7.82	20473 ± 3984	24483 ± 4462
26. 7.82	15851 ± 1345	13242 ± 1952
2. 8.82	8452 ± 1460	6837 ± 2587
10. 8.82	10745 ± 1525	13468 ± 5100
16. 8.82	17777 ± 2528	18308 ± 5164
24. 8.82	19057 ± 3173	21277 ± 5485
31. 8.82	16263 ± 5564	15011 ± 3879
7. 9.82	10749 ± 2179	11428 ± 2485
13. 9.82	11452 ± 1475	11535 ± 3259
20. 9.82	8009 ± 834	9846 ± 3137
27. 9.82	11452 ± 1451	15392 ± 5292
5.10.82	17968 ± 2064	17542 ± 4464
11.10.82	22539 ± 3680	23428 ± 4924
25.10.82	27562 ± 4111	25805 ± 7301

*The date given is that on which the physico-chemical measurements and the core sampler series were collected. This was either the evening on which the pattern sampler was set down or the morning on which it was lifted.

APPENDIX VII

Table ii - Seasonal changes in the numbers of *Disparalona rostrata* from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82	0 ± 0	0
2. 3.82	10 ± 15	0
29. 3.82	30 ± 31	0
20. 4.82	70 ± 40	0
26. 4.82	32 ± 24	111 ± 223
5. 5.82	35 ± 28	111 ± 223
11. 5.82	48 ± 38	0
17. 5.82	30 ± 22	226 ± 316
24. 5.82	702 ± 306	1358 ± 943
1. 6.82	3182 ± 600	5223 ± 2520
8. 6.82	4849 ± 912	8923 ± 2949
14. 6.82	14557 ± 2108	14909 ± 4118
21. 6.82	11278 ± 3520	18108 ± 5012
28. 6.82	30715 ± 13537	16863 ± 4648
6. 7.82	28683 ± 4291	34972 ± 6694
19. 7.82	14939 ± 3933	18561 ± 1903
26. 7.82	10710 ± 1286	13242 ± 1952
2. 8.82	5720 ± 1414	3183 ± 5694
10. 8.82	5424 ± 1380	8148 ± 3899
16. 8.82	11283 ± 2004	12649 ± 3169
24. 8.82	11743 ± 2209	14677 ± 3726
31. 8.82	9463 ± 4015	9507 ± 1167
7. 9.82	6354 ± 1466	7767 ± 1900
13. 9.82	6015 ± 1061	6529 ± 1434
20. 9.82	4285 ± 740	5772 ± 2251
27. 9.82	5367 ± 652	6338 ± 2156
5.10.82	5090 ± 736	6790 ± 2309
11.10.82	6098 ± 1864	6790 ± 2040
25.10.82	10374 ± 2069	12110 ± 3213

APPENDIX VII

Table iii - Seasonal changes in the numbers of *Alona affinis* from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82	605 ± 178	2357 ± 2591
2. 3.82	702 ± 270	283 ± 563
29. 3.82	214 ± 121	1131 ± 1000
20. 4.82	387 ± 167	998 ± 687
26. 4.82	718 ± 240	332 ± 375
5. 5.82	816 ± 308	565 ± 582
11. 5.82	560 ± 282	554 ± 475
17. 5.82	463 ± 97	808 ± 571
24. 5.82	3012 ± 358	4327 ± 1765
1. 6.82	8604 ± 1878	7944 ± 2133
8. 6.82	8235 ± 1550	8488 ± 2354
14. 6.82	8464 ± 1778	7509 ± 2339
21. 6.82	5937 ± 1241	6140 ± 2352
28. 6.82	7827 ± 3535	5548 ± 1503
6. 7.82	10905 ± 1933	10865 ± 2763
19. 7.82	4601 ± 1130	5093 ± 1714
26. 7.82	4409 ± 919	4640 ± 2434
2. 8.82	2641 ± 770	2995 ± 1240
10. 8.82	4923 ± 783	4549 ± 1953
16. 8.82	5689 ± 1550	4438 ± 2010
24. 8.82	5196 ± 1176	4640 ± 1534
31. 8.82	4218 ± 1588	4414 ± 1688
7. 9.82	2739 ± 1028	4105 ± 1555
13. 9.82	4588 ± 929	3700 ± 1382
20. 9.82	2763 ± 412	3169 ± 1256
27. 9.82	5463 ± 1047	4866 ± 1940
5.10.82	8991 ± 1583	6903 ± 2551
11.10.82	10216 ± 1651	10412 ± 2748
25.10.82	10458 ± 5100	10525 ± 3418

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Table iv - Seasonal changes in the numbers of *Leydigia leydigi* from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82	48 ± 46	1414 ± 50
2. 3.82	361 ± 156	0
29. 3.82	87 ± 85	377 ± 87
20. 4.82	122 ± 74	332 ± 375
26. 4.82	403 ± 185	554 ± 238
5. 5.82	337 ± 153	339 ± 383
11. 5.82	366 ± 159	221 ± 309
17. 5.82	498 ± 200	332 ± 375
24. 5.82	803 ± 298	1584 ± 1016
1. 6.82	5271 ± 1471	4461 ± 2136
8. 6.82	5429 ± 1639	5659 ± 1552
14. 6.82	4790 ± 969	5767 ± 1504
21. 6.82	5971 ± 1087	5659 ± 1879
28. 6.82	5264 ± 883	4897 ± 1672
6. 7.82	6041 ± 1040	5545 ± 1785
19. 7.82	383 ± 159	679 ± 614
26. 7.82	901 ± 225	792 ± 647
2. 8.82	443 ± 162	679 ± 525
10. 8.82	629 ± 187	792 ± 967
16. 8.82	800 ± 245	998 ± 688
24. 8.82	1778 ± 608	2122 ± 1412
31. 8.82	1202 ± 400	1018 ± 836
7. 9.82	567 ± 192	887 ± 663
13. 9.82	760 ± 224	652 ± 507
20. 9.82	594 ± 190	566 ± 485
27. 9.82	735 ± 201	792 ± 724
5.10.82	1345 ± 318	1244 ± 984
11.10.82	1123 ± 241	1270 ± 741
25.10.82	1484 ± 316	1471 ± 1012

APPENDIX VII

Table v - Seasonal changes in the numbers of *Pleuroxus uncinatus* from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	'Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82	48 ± 37	0
2. 3.82	0	0
29. 3.82	0	0
20. 4.82	15 ± 16	0
26. 4.82	5 ± 11	0
5. 5.82	0	0
11. 5.82	0	0
17. 5.82	0	0
24. 5.82	14 ± 11	0
1. 6.82	46 ± 37	0
8. 6.82	84 ± 46	0
14. 6.82	59 ± 45	108 ± 217
21. 6.82	34 ± 30	123 ± 245
28. 6.82	1002 ± 452	332 ± 375
6. 7.82	146 ± 56	0
19. 7.82	146 ± 56	0
26. 7.82	115 ± 44	0
2. 8.82	40 ± 35	0
10. 8.82	5 ± 10	0
16. 8.82	14 ± 16	0
24. 8.82	20 ± 24	0
31. 8.82	13 ± 19	0
7. 9.82	31 ± 24	0
13. 9.82	20 ± 19	0
20. 9.82	15 ± 17	0
27. 9.82	226 ± 152	679 ± 617
5.10.82	458 ± 244	1131 ± 913
11.10.82	750 ± 207	1244 ± 872
25.10.82	4679 ± 1265	1616 ± 986

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Table vi - Seasonal changes in the numbers of *Alona rectangula* from the River Thames, Twickenham in 1982

DATE	Pattern sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits	Core sampler: Numbers under $1m^2$ of substrate Means ± 95% Confidence limits
2. 2.82	0	0
2. 3.82	0	353 ± 707
29. 3.82	0	0
20. 4.82	4 ± 5	0
26. 4.82	0	0
5. 5.82	0	0
11. 5.82	0	0
17. 5.82	0	0
24. 5.82	22 ± 24	0
1. 6.82	23 ± 23	0
8. 6.82	0	0
14. 6.82	0	108 ± 217
21. 6.82	0	113 ± 226
28. 6.82	0	0
6. 7.82	0	0
19. 7.82	20 ± 19	0
26. 7.82	15 ± 16	0
2. 8.82	10 ± 14	0
10. 8.82	10 ± 20	0
16. 8.82	0	0
24. 8.82	0	0
31. 8.82	13 ± 21	0
7. 9.82	140 ± 78	221 ± 309
13. 9.82	119 ± 63	326 ± 368
20. 9.82	88 ± 56	339 ± 383
27. 9.82	2161 ± 486	1471 ± 899
5.10.82	2454 ± 505	2376 ± 1294
11.10.82	4562 ± 1748	3508 ± 1418
25.10.82	1702 ± 470	792 ± 561

APPENDIX VII

Table vii - Seasonal changes in the numbers of *Iliocryptus sordidus* from the River Thames, Twickenham in 1982

DATE	Core sampler Numbers under $1m^2$ of substrate Means $\pm$ 95% Confidence limits
2. 2.82	426 $\pm$ 424
2. 3.82	293 $\pm$ 290
29. 3.82	1223 $\pm$ 916
20. 4.82	3550 $\pm$ 1343
26. 4.82	2663 $\pm$ 1060
5. 5.82	1810 $\pm$ 754
11. 5.82	887 $\pm$ 662
17. 5.82	452 $\pm$ 419
24. 5.82	1131 $\pm$ 644
1. 6.82	1741 $\pm$ 853
8. 6.82	3550 $\pm$ 1262
14. 6.82	2285 $\pm$ 993
21. 6.82	471 $\pm$ 440
28. 6.82	339 $\pm$ 190
6. 7.82	452 $\pm$ 544
19. 7.82	565 $\pm$ 485
26. 7.82	1584 $\pm$ 1024
2. 8.82	2037 $\pm$ 1059
10. 8.82	2376 $\pm$ 1074
16. 8.82	3772 $\pm$ 1472
24. 8.82	9507 $\pm$ 2899
31. 8.82	6863 $\pm$ 2424
7. 9.82	7212 $\pm$ 2218
13. 9.82	7073 $\pm$ 2105
20. 9.82	8541 $\pm$ 1987
27. 9.82	9393 $\pm$ 3047
5.10.82	10752 $\pm$ 2625
11.10.82	13268 $\pm$ 3169
25.10.82	8601 $\pm$ 2940

APPENDIX VII

Table viii - Seasonal changes in (i) % of juveniles, (ii) % of adult females with eggs and (iii) mean length, mm, of adult females of the *Alona affinis* population in the River Thames, Twickenham 1982

DATE	PATTERN SAMPLER SERIES			CORE SAMPLER SERIES	
	i	ii	iii	i	ii
2. 2.82	14.51	62.26	0.684	0	100
2. 3.82	9.72	93.84	0.753	0	100
29. 3.82	9.09	60.00	0.667	16.66	100
20. 4.82	16.88	90.62	0.681	0	77.77
26. 4.82	30.88	90.42	0.710	33.33	100
5. 5.82	20.9	93.00	0.707	25.00	75.00
11. 5.82	15.30	96.85	0.717	20.00	75.00
17. 5.82	17.97	98.63	0.719	28.00	75.00
24. 5.82	22.96	75.48	0.707	17.14	75.86
1. 6.82	32.20	72.00	0.683	30.13	64.70
8. 6.82	27.59	69.95	0.657	44.87	65.11
14. 6.82	31.20	72.00	0.648	53.96	65.51
21. 6.82	26.83	76.45	0.640	45.00	64.28
28. 6.82	36.55	63.02	0.648	34.00	60.60
6. 7.82	21.96	58.54	0.641	32.29	61.53
19. 7.82	17.55	57.63	0.679	35.55	6.89
26. 7.82	25.50	57.00	0.652	29.26	31.03
2. 8.82	27.46	57.93	0.620	25.92	45.00
10. 8.82	34.02	47.13	0.636	34.14	40.74
16. 8.82	33.50	67.00	0.650	34.14	51.85
24. 8.82	26.18	85.46	0.659	36.58	69.23
31. 8.82	21.73	66.02	0.638	28.30	71.42
7. 9.82	27.89	90.52	0.631	27.02	77.71
13. 9.82	23.10	88.00	0.633	23.52	76.92
20. 9.82	25.67	86.81	0.636	21.42	77.27
27. 9.82	25.50	82.00	0.639	20.93	73.52
5.10.82	25.20	80.00	0.640	19.67	75.51
11.10.82	26.56	78.41	0.646	19.56	74.32
25.10.82	22.82	87.11	0.657	29.03	83.30

APPENDIX VII

Table ix - Seasonal changes in (i) % of juveniles, (ii) % of adult females with eggs, (iii) % of adult females with ephippia, (iv) % of males and (v) mean length, mm, of adult females of the *Disparalona rostrata* population in the River Thames, Twickenham 1982

DATE	Pattern sampler series					Core sampler series			
	i	ii	iii	iv	v	i	ii	iii	iv
2. 2.82	-	-	-	-	-	-	-	-	-
2. 3.82	-	-	-	-	-	-	-	-	-
29. 3.82	33.33	100.0	0.00	0.00	0.550	-	-	-	-
20. 4.82	35.71	100.0	0.00	0.00	0.506	-	-	-	-
26. 4.82	33.33	100.0	0.00	0.00	0.531	0.00	100.0	0.00	0.00
5. 5.82	25.00	100.0	0.00	0.00	0.517	100.0	0.00	0.00	0.00
11. 5.82	22.22	85.71	0.00	0.00	0.509	-	-	-	-
17. 5.82	0.00	83.33	0.00	0.00	0.530	100.0	0.00	0.00	0.00
24. 5.82	34.34	96.92	0.00	0.00	0.530	33.33	87.50	0.00	0.00
1. 6.82	28.00	82.00	0.00	0.00	0.526	20.83	86.80	0.00	0.00
8. 6.82	26.85	71.35	0.00	0.00	0.524	25.60	73.77	0.00	0.00
14. 6.82	28.00	73.00	0.00	0.00	0.523	32.84	75.00	0.00	0.00
21. 6.82	27.75	75.06	0.00	0.00	0.523	30.62	62.82	0.00	0.00
28. 6.82	41.25	73.32	0.00	0.00	0.508	32.87	64.20	0.00	0.00
6. 7.82	38.27	74.67	0.00	0.00	0.510	35.27	70.00	0.00	0.00
19. 7.82	54.31	58.27	0.00	0.00	0.508	42.07	52.62	0.00	0.00
26. 7.82	46.00	68.00	0.00	0.00	0.506	41.88	70.58	0.00	0.00
2. 8.82	40.52	78.96	0.00	0.00	0.504	33.33	72.20	0.00	0.00
10. 8.82	39.57	72.81	0.00	0.00	0.505	34.77	70.21	0.00	0.00
16. 8.82	39.00	75.00	0.00	0.00	0.507	30.00	71.42	0.00	0.00
24. 8.82	31.44	77.55	0.00	0.00	0.507	25.58	75.00	0.00	0.00
31. 8.92	33.99	88.25	0.00	0.00	0.516	33.33	82.00	0.00	0.00
7. 9.82	37.45	79.43	0.00	0.00	0.516	28.57	76.00	0.00	0.00
13. 9.82	35.50	75.00	0.00	0.00	0.511	30.50	73.00	0.00	0.00
20. 9.82	36.85	78.36	0.00	0.00	0.507	33.33	79.00	0.00	0.00
27. 9.82	37.00	76.00	0.00	0.00	0.506	32.75	76.9	0.00	0.00
5.10.82	37.00	75.00	0.00	0.00	0.507	35.08	80.00	0.00	0.00
11.10.82	33.80	73.11	0.00	1.65	0.506	30.00	66.66	0.00	0.00
25.10.82	37.45	44.80	5.92	4.52	0.505	31.77	34.27	12.16	7.47

APPENDIX VII

Table x - Seasonal changes in (i) % of juveniles, (ii) % of adult females with eggs and (iii) mean length, mm, of adult females of the *Leydigia leydigi* population in the River Thames, Twickenham 1982

DATE	Pattern sampler series			Core sampler series	
	i	ii	iii	i	ii
2. 2.82	40.00	66.66	0.808	0.00	66.66
2. 3.82	35.28	95.83	0.819	-	-
29. 3.82	22.20	42.85	0.757	0.00	100.00
20. 4.82	32.00	82.35	0.772	0.00	66.66
26. 4.82	20.75	93.33	0.778	20.00	75.00
5. 5.82	19.10	98.18	0.788	33.33	100.00
11. 5.82	16.17	96.49	0.797	0.00	100.00
17. 5.82	22.44	100.00	0.809	33.30	100.00
24. 5.82	14.63	98.92	0.804	21.42	81.81
1. 6.82	19.30	91.00	0.790	21.95	84.37
8. 6.82	23.04	85.40	0.778	28.30	79.00
14. 6.82	22.10	84.00	0.740	26.41	82.05
21. 6.82	20.37	83.62	0.701	29.40	70.37
28. 6.82	35.00	60.08	0.702	35.55	51.72
6. 7.82	22.44	51.75	0.716	22.44	60.52
19. 7.82	17.55	79.36	0.731	16.66	80.00
26. 7.82	18.00	83.00	0.741	14.28	83.33
2. 8.82	18.18	88.88	0.750	16.60	80.00
10. 8.82	24.98	100.00	0.718	14.28	83.33
16. 8.82	27.40	100.00	0.717	22.22	85.71
24. 8.82	26.92	100.00	0.714	27.70	92.30
31. 8.82	16.13	96.15	0.727	22.22	85.71
7. 9.82	11.88	90.00	0.736	12.50	85.71
13. 9.82	17.30	89.00	0.719	16.66	80.00
20. 9.82	22.71	88.88	0.702	20.00	75.00
27. 9.82	19.70	87.00	0.722	28.57	80.00
5.10.82	19.70	86.00	0.721	18.18	77.77
11.10.82	15.70	85.18	0.737	18.18	77.77
25.10.82	18.41	84.90	0.763	25.00	77.77

APPENDIX VII

Table xi - Seasonal changes in (i) % of juveniles, (ii) % of adult females with eggs, (iii) mean length, mm, of adult females with eggs and (iv) mean clutch size of adult females with eggs of the *Iliocryptus sordidus* population in the River Thames, Twickenham 1982

	Core Sampler Series			
DATE	i	ii	iii	iv
2. 2.82	66.66	100.00	0.77	2
2. 3.82	33.33	75.00	0.933	4
29. 3.82	66.66	14.28	0.84	4
20. 4.82	52.94	43.75	0.822	5.14
26. 4.82	50.00	25.00	0.966	6.66
5. 5.82	52.94	16.66	0.822	5
11. 5.82	50.00	25.00	0.84	4
17. 5.82	25.00	66.66	0.84	3
24. 5.82	70.00	66.66	0.77	3
1. 6.82	75.00	40.00	0.84	3
8. 6.82	87.09	75.00	0.909	4
14. 6.82	62.50	50.00	0.84	3
21. 6.82	50.00	50.00	0.77	2
28. 6.82	66.66	0.00	-	-
6. 7.82	75.00	0.00	-	-
19. 7.82	80.00	0.00	-	-
26. 7.82	69.23	25.00	0.784	3
2. 8.82	61.11	71.42	0.798	4.8
10. 8.82	76.19	80.00	0.822	3
16. 8.82	66.03	66.66	0.814	3
24. 8.82	59.52	73.52	0.795	3.28
31. 8.82	66.07	84.21	0.815	3.75
7. 9.82	63.33	81.81	0.82	3.5
13. 9.82	64.61	86.95	0.82	3.5
20. 9.82	39.72	75.00	0.836	3.57
27. 9.82	31.57	44.61	0.814	3
5.10.82	50.00	52.72	0.798	2.5
11.10.82	55.83	56.60	0.784	2.2
25.10.82	38.66	2.17	0.77	2

APPENDIX VII

Table xii - Seasonal changes in the observed (*r*) and estimated (*b*) instantaneous rates of population increase and the estimated instantaneous death rate (*d*) of the *Alona affinis* population in the River Thames, Twickenham 1982

DATE	Pattern Sampler Series			Core Sampler Series		
	r	*b*	*d*	*r*	*b*	*d*
2. 2.82	-	0.038	-	-	0.061	-
2. 3.82	0.008	0.12	0.128	0.067	0.127	0.194
29. 3.82	0.03	0.085	0.115	0.044	0.033	0.011
20. 4.82	0.03	0.108	0.078	0.008	0.118	0.126
26. 4.82	0.008	0.156	0.002	0.156	0.098	0.256
5. 5.82	0.015	0.104	0.089	0.059	0.067	0.008
11. 5.82	0.062	0.108	0.17	0.003	0.068	0.071
17. 5.82	0.027	0.109	0.136	0.054	0.072	0.018
24. 5.82	0.267	0.083	0.184	0.24	0.087	0.15
1. 6.82	0.131	0.162	0.031	0.075	0.094	0.019
8. 6.82	0.007	0.167	0.174	0.011	0.068	0.057
14. 6.82	0.003	0.163	0.16	0.017	0.073	0.09
21. 6.82	0.05	0.175	0.225	0.028	0.085	0.113
28. 6.82	0.039	0.141	0.102	0.014	0.099	0.113
6. 7.82	0.041	0.19	0.149	0.084	0.141	0.057
19. 7.82	0.066	0.161	0.227	0.062	0.08	0.142
26. 7.82	0.006	0.136	0.142	0.015	0.101	0.116
2. 8.82	0.073	0.183	0.256	0.062	0.16	0.222
10. 8.82	0.088	0.165	0.077	0.059	0.094	0.035
16. 8.82	0.020	0.152	0.132	0.003	0.107	0.11
24. 8.82	0.012	0.193	0.205	0.006	0.13	0.124
31. 8.82	0.026	0.20	0.226	0.007	0.168	0.175
7. 9.82	0.061	0.133	0.194	0.01	0.106	0.116
13. 9.82	0.073	0.135	0.062	0.017	0.099	0.116
20. 9.82	0.084	0.136	0.22	0.025	0.11	0.135
27. 9.82	0.085	0.126	0.041	0.053	0.131	0.078
5.10.82	0.071	0.124	0.053	0.038	0.123	0.085
11.10.82	0.018	0.124	0.053	0.058	0.106	0.048
25.10.82	0.001	0.135	0.131	0.001	0.093	0.092

APPENDIX VII

Table xiii - Seasonal changes in the observed (*r*) and estimated (*b*) instantaneous rates of population increase and the estimated instantaneous death rate (*d*) of the *Disparalona rostrata* population in the River Thames, Twickenham 1982

DATE	Pattern Sampler Series			Core Sampler Series		
	r	*b*	*d*	*r*	*b*	*d*
2. 2.82	0	0	0	0	0	0
2. 3.82	0.082	0.084	-0.002	0	0	0
29. 3.82	0.040	0.039	0.003	0	0	0
20. 4.82	-0.042	0.063	0.021	0	0	0
26. 4.82	-0.11	0.064	0.174	0.672	0.084	0.588
5. 5.82	0.003	0.069	-0.072	0	0	0
11. 5.82	-0.072	0.064	0.008	-0	0	0
17. 5.82	0.067	0.075	-0.142	0.77	0	-0.77
24. 5.82	0.45	0.062	-0.388	0.25	0.059	0.191
1. 6.82	0.188	0.143	0.045	0.168	0.179	0.011
8. 6.82	0.060	0.126	-0.066	-0.089	0.112	0.023
14. 6.82	-0.157	0.136	0.021	0.09	0.102	0.192
21. 6.82	0.036	0.152	-0.188	-0.027	0.082	0.055
28. 6.82	-0.143	0.127	0.016	0.01	0.12	0.13
6. 7.82	-0.008	0.133	0.141	-0.091	0.108	0.017
19. 7.82	-0.05	0.088	0.138	-0.052	0.08	0.132
26. 7.82	-0.047	0.113	0.16	-0.048	0.12	0.168
2. 8.82	-0.089	0.137	0.226	0.203	0.143	-0.346
10. 8.82	0.012	0.129	0.141	0.134	0.109	0.025
16. 8.82	0.109	0.134	0.025	0.062	0.115	0.053
24.8. 82	-0.005	0.15	0.145	0.018	0.123	0.105
31. 8.82	-0.026	0.152	0.178	-0.06	0.105	0.165
7. 9.82	-0.067	0.101	0.168	-0.033	0.07	0.103
13. 9.82	-0.007	0.096	0.103	-0.024	0.031	0.055
20. 9.82	0.056	0.216	0.272	0.02	0.009	0.029
27. 9.82	-0.028	0.097	0.069	0.011	0.015	0.004
5.10.82	0.007	0.096	0.103	0.009	0.052	0.043
11.10.82	0.025	0.096	0.071	0	0.079	-0.079
25.10.82	0.037	0.055	0.018	0.041	0.033	0.008

APPENDIX VII

Table xiv - Seasonal changes in the observed (*r*) and estimated (*b*) instantaneous rates of population increase and the estimated instantaneous death rate (*d*) of the *Leydigia leydigi* population in the River Thames, Twickenham 1982

DATE	Pattern Sampler Series			Core Sampler Series		
	r	*b*	*d*	*r*	*b*	*d*
2. 2.82	0	0.027	0	0	0	0
2. 3.82	0.072	0.085	0.013	0.25	0	0.25
29. 3.82	0.052	0.073	0.125	0.22	0	0.22
20. 4.82	0.016	0.089	0.073	0.006	0.098	0.104
26. 4.82	0.17	0.104	0.066	0.073	0.039	0.034
5. 5.82	0.025	0.11	0.135	0.061	0.082	0.143
11. 5.82	0.013	0.110	0.097	0.071	0.127	0.198
17. 5.82	0.044	0.108	0.064	0.059	0.06	0.001
24. 5.82	0.068	0.111	0.043	0.22	0.108	0.112
1. 6.82	0.235	0.323	0.088	0.129	0.115	0.014
8. 6.82	0.004	0.234	0.23	0.039	0.128	0.089
14. 6.82	0.017	0.299	0.316	0.002	0.132	0.13
21. 6.82	0.031	0.299	0.268	0.002	0.14	0.142
28. 6.82	0.018	0.205	0.223	0.027	0.168	0.195
6. 7.82	0.017	0.203	0.186	0.016	0.236	0.22
19. 7.82	0.212	0.303	0.515	0.17	0.247	0.417
26. 7.82	0.122	0.306	0.184	0.021	0.275	0.254
2. 8.82	0.101	0.32	0.421	0.021	0.302	0.323
10. 8.82	0.05	0.327	0.277	0.022	0.161	0.139
16. 8.82	0.034	0.32	0.286	0.038	0.2	0.162
24. 8.82	0.114	0.298	0.184	0.107	0.259	0.152
31. 8.82	0.048	0.352	0.4	0.104	0.116	0.22
7. 9.82	0.125	0.174	0.299	0.022	0.101	0.123
13. 9.82	0.041	0.166	0.125	0.043	0.087	0.13
20. 9.82	0.041	0.156	0.197	0.023	0.061	0.084
27. 9.82	0.03	0.159	0.129	0.047	0.072	0.025
5.10.82	0.075	0.159	0.084	0.056	0.085	0.029
11.10.82	0.025	0.163	0.188	0.002	0.098	0.096
25.10.82	0.021	0.159	0.138	0.01	0.087	0.077

APPENDIX VII

Table xv - Seasonal changes in the species diversity (H') and evenness (J') of the cladoceran taxocene in the River Thames, Twickenham 1982

DATE	H'	J'
2. 2.82	1.3995	0.541
2. 3.82	1.9949	0.7717
29. 3.82	1.0082	0.3900
20. 4.82	0.7980	0.3087
26. 4.82	1.2280	0.4750
5. 5.82	1.3793	0.5335
11. 5.82	1.6278	0.6297
17. 5.82	1.6960	0.6561
24. 5.82	1.7714	0.6852
1. 6.82	1.8128	0.7012
8. 6.82	1.9899	0.7697
14. 6.82	1.7420	0.6738
21. 6.82	1.5580	0.6027
28. 6.82	1.3515	0.5228
6. 7.82	1.3928	0.5388
19. 7.82	1.1280	0.4363
26. 7.82	1.5529	0.6007
2. 8.82	1.6608	0.6425
10. 8.82	1.7196	0.6261
16. 8.82	1.6186	0.6261
24. 8.82	1.7626	0.6818
31. 8.82	1.5385	0.5951
7. 9.82	1.7149	0.6634
13. 9.82	1.7995	0.6961
20. 9.92	1.6530	0.6394
27. 9.82	2.0451	0.7911
5.10.82	2.0938	0.8099
11.10.82	2.1294	0.8237
25.10.82	2.2791	0.8816

APPENDIX VIII

Correlation coefficients (r) calculated between abundance (number under a square metre) and birth rates (b) of cladocerans present in the River Thames, Twickenham and various environmental factors

Variable 2 / Variable 1	Temperature °C	% organic content	Chloro-phyll *a*	Phaeo-pigment	*Iliocryptus sordidus* no. under $1m^2$
Total chydorids no. under $1m^2$	-	-	0.388*	-0.093	0.538**
Disparalona rostrata no. under $1m^2$	-	-0.424*	0.45*	-0.212	-
Disparalona rostrata birth rate (b)	0.745**	-0.39*	0.294	-0.155	-
Alona affinis no. under $1m^2$	-	-0.23	0.435*	0.006	-
Alona affinis birth rate (b)	0.782**	-0.275	0.233	-0.165	-
Leydigia leydigi no. under $1m^2$	-	-0.275	0.145	-0.075	-
Leydigia leydigi birth rate (b)	0.782**	-0.416*	0.129	-0.231	-
Iliocryptus sordidus no. under $1m^2$	0.25	-0.619*	0.784**	0.289	-
Chlorophyll *a*	0.109	-0.0027	-	-	-

Degrees of freedom (v) = 27 in all cases.

All counts (x) of cladocerans were transformed to log x + 1. This was necessary before correlation coefficients (which require a normal distribution) could be computed (Elliott, 1977).

* significant at the 5% level

** significant at the 1% level

APPENDIX IX

Relationship between initial size and instar in which maturity is reached for two chydorid species

t-tests were computed for *Leydigia leydigi* and *Disparalona rostrata* at each of the four experimental temperatures to determine whether the differences between initial lengths of animals maturing in the third and fourth instars were significant. The null hypothesis (H^o) was that the two samples were drawn from populations with the same means and variances.

Bailey's (1959) formula for the comparison of the means of two small samples was used, this assumes an underlying normal distribution.

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} \qquad \text{where } s^2 = \frac{[\,x^2_1 - \bar{x}_1 \Sigma x] + [\Sigma x^2_2 - \bar{x}_2 \Sigma x_2]}{n_1 + n_2 - 2}$$

where the counts (x), arithmetic mean ($\bar{x}$) and number of sampling units (n) are x_1, $\bar{x}_1$, n_1 for the first sample and x_2, $\bar{x}_2$, n_2 for the second sample. s^2 is the joint variance.

In all cases the t-test was preceded by an F-test to determine whether the assumption of equal variances implied in the above formula is justified.

$$F = \frac{s_1^2}{s_2^2}$$

s_1^2 = variance of first sample

s_2^2 = varance of second sample

The tabulated value of F is found from Bailey (1959) for the chosen level of significance ($p = 0.05$) corresponding to $f_1 = n_1 - 1$ degrees of freedom in the numerator and $f_2 = n_2 - 1$ degrees of freedom in the denominator. If the calculated value of F exceeds this tabulated value then the result is significant and the variances cannot be considered equal. When this is the case the following formula is used:

$$d = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{s_1^2/n_1 + s_2^2/n_2}} \qquad \text{from Bailey (1959)}$$

where d is the ratio of the difference in means of the two samples to the standard deviation of the difference. This is considered to be distributed approximately like students 't' with 'f' degrees of freedom:

$$f = \frac{1}{\frac{v^2}{n_1 - 1} + \frac{(1 - v)^2}{n_2 - 1}} \qquad \text{where} \qquad v = \frac{s_1^2/n_1}{s_1^2/n_1 + s_2^2/n_2}$$

APPENDIX IX

Table i - Results of t-test undertaken to determine whether differences between neonatal lengths of individuals maturing in the third and fourth instars are significant at the 5% level

Leydigia leydigi

Experimental temperature °C	Calculated t or d		degrees of freedom (f)	Tabulated t at 5% level of significance	Significant difference (p=0.05) found between neonatal lengths
	t	d			
5	7.62	-	16	2.12	+
10	0.276	-	16	2.12	-
14	-	2.96	5	2.57	+
19	2.58	-	16	2.12	+

Disparalona rostrata

Experimental temperature °C	Calculated t or d		degrees of freedom (f)	Tabulated t at 5% level of significance	Significant difference (p=0.05) found between neonatal lengths
	t	d			
10	2.78	-	16	2.12	+
14	1.16	-	16	2.12	-
19	-	0.765	6	2.447	-

APPENDIX X : Relationship between Egg Volume and Parent Length for some Chydorid Species

Table i - Egg volume and parent length in *Leydigia leydigi* at three temperatures (10°, 14° and 19°C)

10°C	Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^{6}\ \mu m^{3}$
			greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
	0.7	8	0.224	0.14	1.6	2.29
	0.714	5	0.231	0.147	1.57	2.61
	0.728	6	0.252	0.147	1.71	2.81
	0.742	6	0.238	0.154	1.54	2.95
	0.756	2	0.238	0.154	1.54	2.95
	0.77	2	0.252	0.154	1.63	3.12
	0.784	4	0.245	0.154	1.59	3.03
	0.798	2	0.245	0.154	1.59	3.03
	0.812	6	0.259	0.161	1.6	3.51

14°C	Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^{6}\ \mu m^{3}$
			greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
	0.644	2	0.199	0.129	1.54	1.73
	0.658	3	0.224	0.126	1.77	1.86
	0.672	4	0.224	0.126	1.77	1.86
	0.686	-	-	-	-	-
	0.7	9	0.21	0.133	1.57	2.00
	0.714	6	0.231	0.14	1.65	2.37
	0.728	6	0.231	0.14	1.65	2.37
	0.742	13	0.21	0.14	1.5	2.15
	0.756	-	-	-	-	-
	0.77	7	0.231	0.14	1.65	2.37
	0.784	2	0.231	0.133	1.73	2.13
	0.812	-	-	-	-	-
	0.826	2	0.231	0.147	1.57	2.61
	0.84	-	-	-	-	-
	0.854	2	0.231	0.147	1.57	2.61

19°C	Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^{6}\ \mu m^{3}$
			greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
	0.63	3	0.2	0.126	1.58	1.66
	0.644	5	0.202	0.128	1.57	1.73
	0.658	5	0.182	0.123	1.48	1.44
	0.672	-	-	-	-	-
	0.686	-	-	-	-	-
	0.7	6	0.208	0.144	1.44	2.25
	0.714	9	0.215	0.131	1.64	1.93
	0.728	7	0.211	0.134	1.57	1.98
	0.742	7	0.217	0.135	1.60	2.07
	0.756	5	0.217	0.138	1.57	2.16
	0.77	8	0.219	0.133	1.64	2.02
	0.784	2	0.213	0.14	1.52	2.18
	0.798	2	0.227	0.14	1.62	2.32

APPENDIX X

Table ii - Egg volume and parent length in *Alona affinis* at two temperatures (14° and 19°C)

14°C	Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^6 \mu m^3$
			greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
	0.56	4	0.192	0.126	1.52	1.59
	0.574	-	-	-	-	-
	0.588	6	0.196	0.126	1.55	1.62
	0.602	4	0.195	0.128	1.52	1.67
	0.616	-	-	-	-	-
	0.63	2	0.212	0.128	1.65	1.81
	0.644	2	0.203	0.13	1.56	1.79
	0.658	4	0.205	0.13	1.57	1.81
	0.672	8	0.22	0.122	1.8	1.71
	0.686	5	0.23	0.125	1.84	1.88
	0.7	10	0.221	0.123	1.79	1.75
	0.714	12	0.223	0.12	1.85	1.68
	0.728	8	0.225	0.13	1.73	1.99
	0.742	8	0.23	0.135	1.7	2.19
	0.756	4	0.229	0.135	1.69	2.18
	0.77	4	0.234	0.136	1.72	2.26
	0.784	5	0.235	0.138	1.7	2.34
	0.798	4	0.239	0.141	1.69	2.48
	0.812	6	0.241	0.142	1.69	2.54
	0.826	6	0.254	0.15	1.69	2.99
	0.84	8	0.255	0.15	1.7	3.00
	0.854	4	0.26	0.15	1.73	3.06
	0.868	4	0.263	0.155	1.69	3.30
	0.882	2	0.262	0.16	1.63	3.51
	0.896	2	0.274	0.16	1.71	3.67
	0.91	2	0.273	0.161	1.69	3.70

19°C	Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^6 \mu m^3$
			greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
	0.56	4	0.196	0.115	1.7	1.35
	0.574	6	0.195	0.119	1.63	1.44
	0.588	6	0.198	0.12	1.65	1.49
	0.602	8	0.198	0.12	1.65	1.49
	0.616	8	0.199	0.122	1.63	1.55
	0.63	4	0.204	0.12	1.7	1.53
	0.644	4	0.211	0.121	1.74	1.61
	0.658	4	0.215	0.129	1.66	1.87
	0.672	8	0.213	0.122	1.74	1.65
	0.686	6	0.212	0.125	1.69	1.73
	0.7	2	0.234	0.14	1.67	2.4
	0.714	2	0.231	0.14	1.65	2.37
	0.728	6	0.23	0.135	1.7	2.19
	0.742	6	0.232	0.135	1.71	2.21
	0.756	8	0.235	0.137	1.71	2.3
	0.77	6	0.234	0.14	1.67	2.4
	0.784	4	0.235	0.14	1.67	2.41
	0.798	2	0.273	0.147	1.85	3.08
	0.812	4	0.235	0.139	1.69	2.37
	0.826	4	0.24	0.142	1.69	2.53
	0.84	4	0.242	0.145	1.66	2.66
	0.854	6	0.247	0.15	1.64	2.9
	0.868	2	0.262	0.154	1.7	3.25
	0.882	2	0.269	0.147	1.82	3.04

APPENDIX X

Table iii - Egg volume and parent length in *Disparalona rostrata* at 19°C

Parent length (mm)	Number of eggs examined	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^6 \mu m^3$
		greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
0.476	20	0.172	0.094	1.82	0.795
0.49	22	0.164	0.0945	1.73	0.766
0.504	10	0.178	0.098	1.81	0.895
0.518	10	0.179	0.098	1.82	0.900
0.532	8	0.185	0.105	1.76	1.06
0.546	7	0.185	0.105	1.76	1.06
0.56	10	0.186	0.105	1.77	1.07

Table iv - Mean egg volume determined for five chydorid species

SPECIES	Adult length range (mm)	Mean egg diameter		Ratio of greatest : least diameter	Mean egg volume $10^6 \mu m^3$
		greatest $\times 10^{-3}$ m	least $\times 10^{-3}$ m		
Alona affinis	0.56 - 0.98	0.229	0.135	1.69	2.18
Leydigia leydigi	0.63 - 0.868	0.224	0.139	1.61	2.26
Pleuroxus uncinatus	0.56 - 0.77	0.224	0.119	1.88	1.65
Disparalona rostrata	0.476 - 0.56	0.178	0.099	1.79	0.912
Alona rectangula	0.35 - 0.49	0.142	0.095	1.49	0.673

APPENDIX X

Table v - Linear regressions relating egg volume ($10^6 \mu m^3$) to parent length (mm) for *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata*

Regression equation : $Y = a + b \times \chi$

SPECIES	Temperature °C	a	b ± 95% Cl	df	F	P
Leydigia leydigi	10	−3.9557	9.1233 ±1.318	1 ; 39	195.50	0.001
	14	−1.3243	4.8388 ±1.5869	1 ; 41	37.89	0.001
	19	−0.6727	3.6697 ±0.9627	1 ; 57	58.24	0.001
Alona affinis	14	−2.4081	6.2766 ±0.5131	1 ; 121	586.54	0.001
	19	−1.7248	5.3298 ±0.3527	1 ; 114	895.09	0.001
Disparalona rostrata	19	−1.1634	4.0398 ±0.4344	1 ; 85	342.84	0.001

cl = confidence limits; df = degrees of freedom; F = Variance ratio; P = level of significance; Y = egg volume; χ = parent length

APPENDIX XI : Lengths of Young released in a given Adult Instar of *Leydigia leydigi* and *Disparalona rostrata*

Table i - percentage of young present in each length class for a given adult instar of *Leydigia leydigi* at four temperatures (5°, 10°, 14° and 19°C)

5°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th
0.35	-	-	-	-	-	-
0.364	-	-	-	-	-	-
0.378	10.0	-	-	-	-	-
0.392	37.5	8.5	-	-	-	-
0.406	37.5	-	-	-	-	-
0.42	15.0	14.3	-	-	-	-
0.434	-	14.3	-	25.0	20.0	13.3
0.448	-	14.3	17.9	35.0	33.3	26.6
0.462	-	28.5	21.4	35.0	33.3	40.0
0.476	-	20.0	42.8	5.0	13.3	20.0
0.49	-	-	17.8	-	-	-
Mean length of young for instar (mm)	0.4	0.446	0.47	0.45	0.454	0.46
Total young measured	40	35	28	20	15	15

10°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th
0.35	10.0	-	-	-	-	-
0.364	-	-	-	-	-	-
0.378	4.0	-	-	-	-	-
0.392	36.0	-	-	-	33.3	-
0.406	30.0	-	-	33.3	-	-
0.42	20.0	34.0	-	33.3	-	-
0.434	-	16.0	25.0	-	-	-
0.448	-	50.0	25.0	33.3	33.3	50.0
0.462	-	-	-	-	-	50.0
0.476	-	-	25.0	-	-	-
0.49	-	-	25.0	-	-	-
Mean length of young for instar (mm)	0.396	0.436	0.462	0.424	0.443	0.455
Total young measured	50	38	20	18	18	6

APPENDIX XI : Table - i (continued)

14°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th	9th
0.35	18.1	6.2	-	-	-	-	-
0.364	4.5	-	-	-	-	16.6	-
0.378	13.6	-	-	-	-	-	-
0.392	13.6	-	-	-	-	-	-
0.406	4.5	6.2	-	-	-	-	-
0.42	27.2	50.0	18.1	11.1	14.3	-	25.0
0.434	9.1	19.0	36.4	55.5	43.0	50.0	50.0
0.448	4.5	19.0	18.1	22.2	43.0	16.6	-
0.462	-	-	9.1	11.1	-	16.6	25.0
0.476	-	-	9.1	-	-	-	-
0.49	4.5	-	9.1	-	-	-	-
Mean length of young for instar (mm)	0.4	0.422	0.445	0.438	0.438	0.427	0.437
Total young measured	44	32	22	18	14	12	8

19°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th
0.35	8.3	12.5	-	-	-	-
0.364	-	-	-	-	-	-
0.378	10.0	12.5	-	20.0	-	-
0.392	8.3	-	16.6	-	40.0	-
0.406	20.0	12.5	-	-	-	-
0.42	28.3	12.5	16.6	60.0	60.0	50.0
0.434	16.6	25.0	16.6	-	-	-
0.448	8.3	12.50	33.3	-	-	50.0
0.462	-	-	-	20.0	-	-
0.476	-	12.50	-	-	-	-
0.49	-	-	16.6	-	-	-
Mean length of young for instar (mm)	0.389	0.418	0.438	0.42	0.408	0.427
Total young measured	60	32	24	20	15	4

APPENDIX XI

Table ii - percentage of young present in each length class for a given adult instar of *Disparalona rostrata* at three temperatures (10°, 14° and 19°C)

10°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th	9th
0.308	-	-	-	7.7	4.0	6.2	-
0.322	20.0	10.5	-	15.4	36.0	18.7	50.0
0.336	40.0	21.0	22.2	30.8	28.0	18.7	50.0
0.35	40.0	52.6	51.8	38.4	20.0	43.7	-
0.364	-	15.8	25.9	7.7	12.0	12.5	-
Mean length of young for instar (mm)	0.338	0.346	0.35	0.339	0.336	0.34	0.329
Total young measured	20	19	27	26	25	16	2

14°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th	9th
0.322	36.8	-	-	-	-	25.0	-
0.336	57.8	88.8	20.0	36.3	33.3	-	50.0
0.35	5.2	11.1	80.0	63.6	66.6	75.0	50.0
0.364	-	-	-	-	-	-	-
Mean length of young for instar (mm)	0.331	0.337	0.347	0.344	0.345	0.343	0.343
Total young measured	20	19	27	26	25	16	2

19°C

Young length class midpoint (mm)	ADULT INSTAR 1st	2nd	3rd	4th	5th	7th
0.28	22.7	-	-	-	-	-
0.294	31.8	37.5	7.7	25.0	25.0	-
0.308	-	12.5	61.5	50.0	50.0	-
0.322	31.8	25.0	15.4	25.0	-	-
0.336	13.6	25.0	15.4	-	-	50.0
0.35	-	-	-	-	-	50.0
Mean length of young for instar (mm)	0.305	0.313	0.313	0.308	0.308	0.343
Total young measured	44	32	26	16	16	4

APPENDIX XII : The Wet Dichromate Oxidation Procedure described by Mackereth *et al* (1978)

PRINCIPLE : The organic matter reacts at 100°C with a strong oxidising mixture (dichromate and sulphuric acid) and the decrease in oxidant (dichromate) is then determined by titration with a ferrous salt. The end point is determined amperometrically.

REAGENTS :

- stock potassium dichromate solution, 1.0N :
  dissolve 49.035g of $K_2Cr_7O_4$ (analytical grade, dried for two hours at 105°C) in double distilled water from which dust has been excluded and dilute to 1000ml.
- sulphuric acid-silver sulphate :
  dissolve 0.24g of Ag_2SO_4 in 20ml of conc. H_2SO_4 (analytical grade). Make up fresh on each occasion.
- ferrous ammonium sulphate (FAS), $FeSO_4.(NH_4)_2SO_4.6H_2O$:
  prepare 0.1N stock solution by dissolving 3.94g of analytical grade reagent in 100ml distilled water, add 5ml of conc. H_2SO_4.
  0.01N solution is obtained by dilution to 1000ml.

PROCEDURE :

1. Preparation of sample

   A large supply of pyrex crystallising dishes was thoroughly cleansed with hot chromic acid, rinsed and stored in closed plastic bags to exclude dust. Chydorids were sorted according to species and length class (the same as those given in Appendix XIII). Individuals were washed in distilled water, dried and accumulated in the crystallising dishes until there were sufficient animals to yield approximately

30µg carbon (Mackereth *et al*, 1978). In practice this meant 30-85 animals, depending on species, for the immature size classes and 10-30 animals per sample for the mature size classes. Between four and six samples were collected for each size class and stored in a desiccator until used.

2. Oxidation of sample

1.0ml of 0.25N potassium dichromate solution was added to the crystallising dish containing the sample. 2.0ml of sulphuric acid-silver sulphate was then added and the reaction vessel was covered with a watch glass and placed on a hot plate, where it was left to digest for two hours at 100°C. Replacement of the yellow colour by green meant that the dichromate was almost exhausted, if this occured a further addition of the same reagents was made and the oxidation repeated.

The reaction vessel was cooled and the contents diluted with 5ml of distilled water in order to cover a platinum-calomel combination electrode during titration. It was then placed on a magnetic stirrer and positioned so that a constant stirring speed was obtained. The electrode (connected with a 1 volt d.c. potential source and a millivoltmeter to form a circuit, as shown by Mackereth *et al*, 1978) was lowered into the solution which was then titrated with FAS 0.01N. The approach of the endpoint was marked by a sudden increase in current, indicated by "flickering" of the millivoltmeter needle. More FAS was added until a steady millivolt reading was obtained, this was recorded.

Titrations were performed for samples and several blanks. For the latter, just the reagents were placed in the reaction vessel and the procedure carried out as usual. The difference between the mean

blank value and a sample was used to assess the quantity of dichromate consumed in oxidation of the organic matter. The normality of the titrant was determined by titration of a known quantity of cold acidified dichromate solution.

CALCULATION :

If V_B and V_S are the titrant volumes in mls of normality n corresponding to the mean blank and sample respectively, then the oxidant consumed by the sample

$$= (V_B - V_S)n \times 10^3 \text{ (as } \mu \text{ eq reducing material)}$$

$$= (V_B - V_S)n \times 10^3 \times 3 \text{ (as } \mu\text{g carbon)}$$

Knowing the number of animals used in the sample, µg carbon per animal can be calculated.

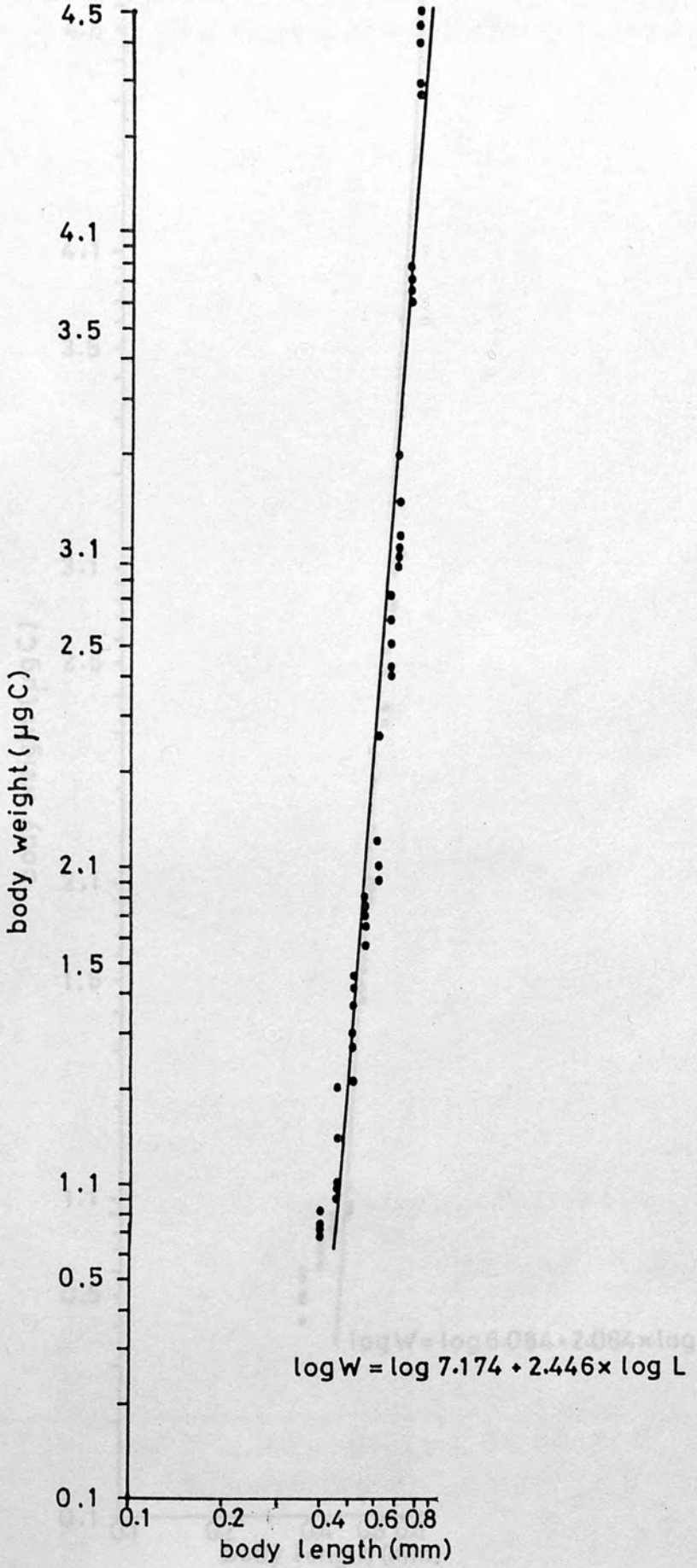
The carbon factor (3µg per µ eq) is strictly valid only for the complete oxidation of a hexose, however, tests have shown it to be approximately applicable to seston and filtrates from lakes and rivers (Mackereth *et al.*, 1978).

APPENDIX XII

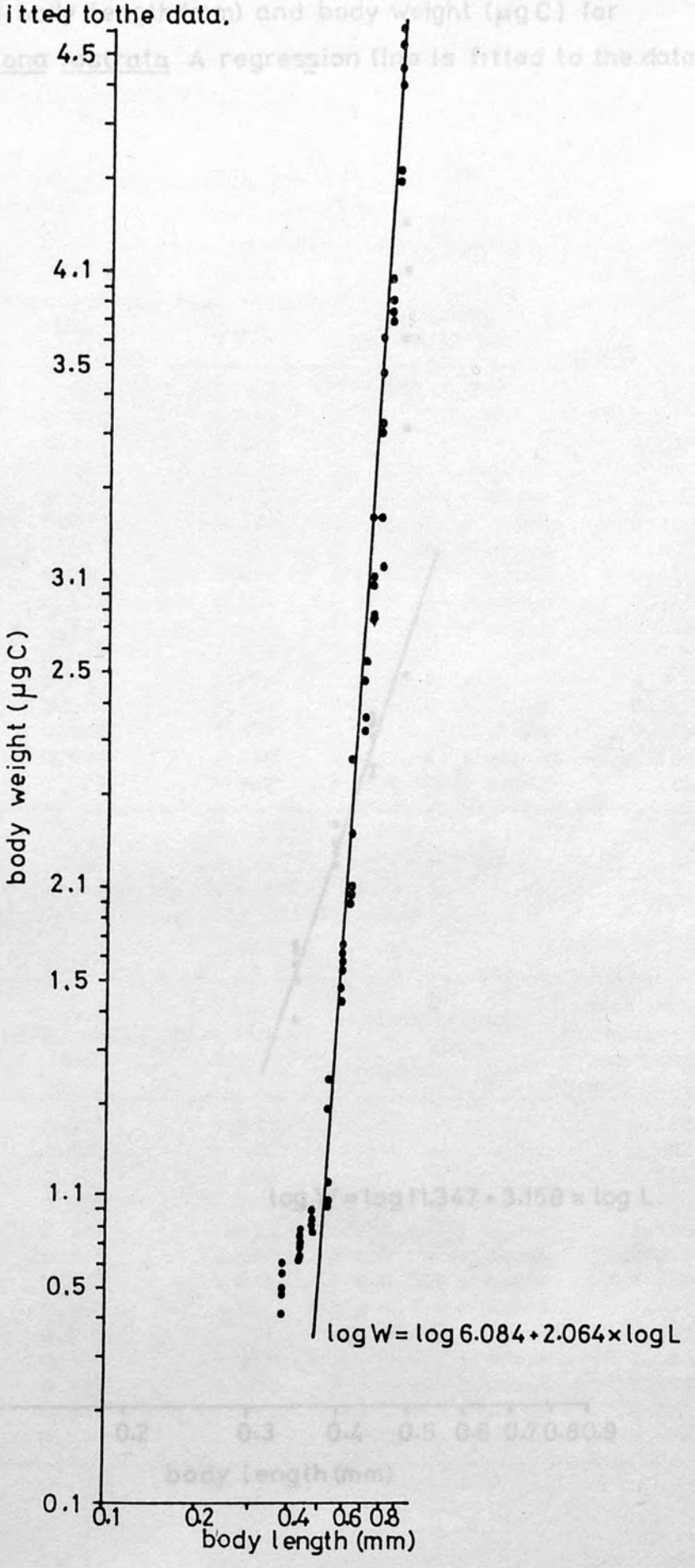
Table i - Values of log *a* (intercept) and *b* (regression coefficient) in the regression relating body length (mm) to body weight (µg C) for *Leydigia leydigi*, *Alona affinis* and *Disparalona rostrata*

SPECIES	log *a*	*b*
Leydigia leydigi	0.8558	2.4468
Alona affinis	0.7842	2.6000
Disparalona rostrata	1.0549	3.1587

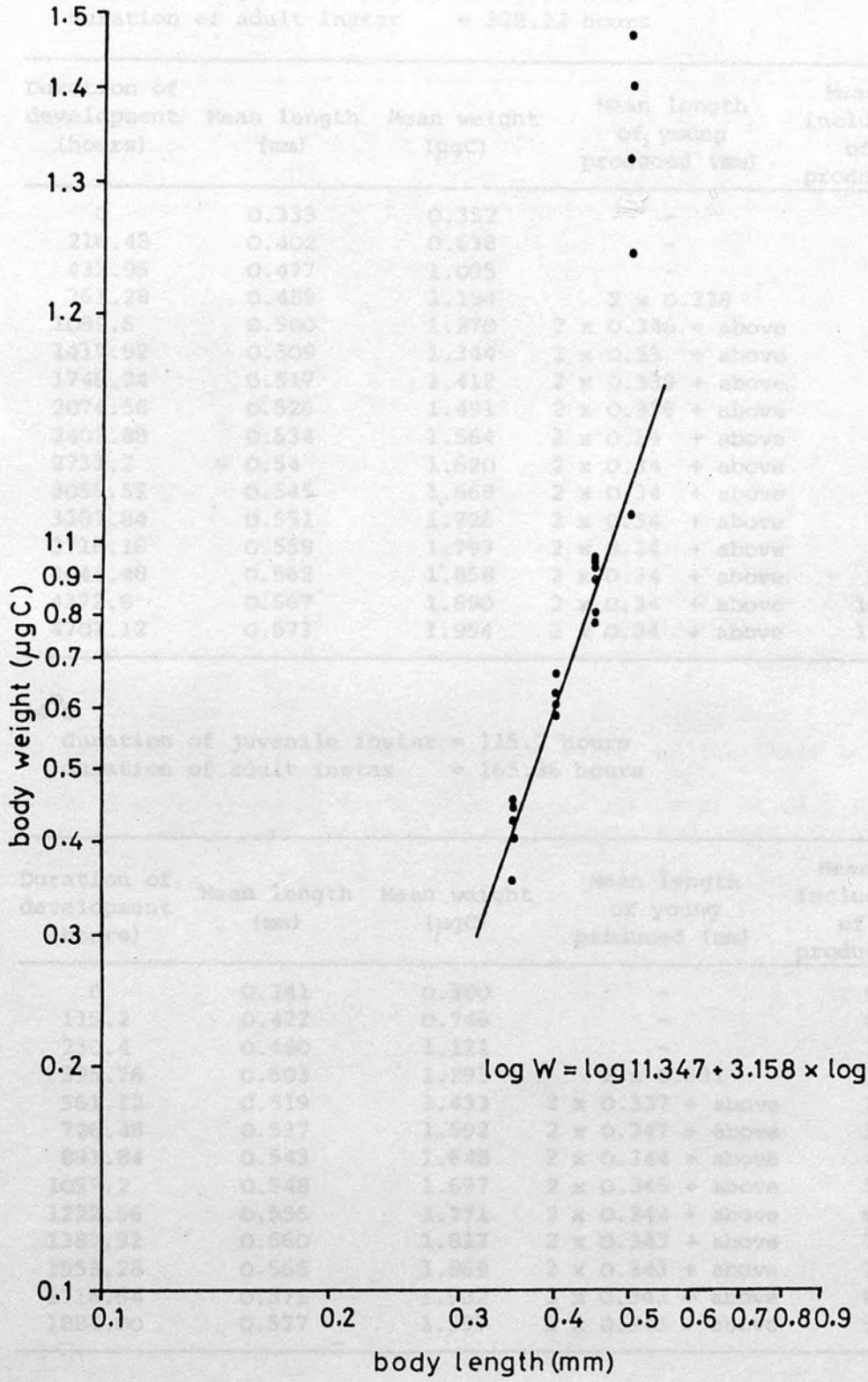
APPENDIX XII, FIGURE i. Log-log plot of the relationship between body length (mm) and body weight (µg C) for Leydigia leydigi. A regression line is fitted to the data.



APPENDIX XII, FIGURE ii. Log-log plot of the relationship between body length (mm) and body weight (µg C) for Alona affinis. A regression line is fitted to the data.



APPENDIX XII, FIGURE iii. Log-log plot of the relationship between body length (mm) and body weight (µg C) for Disparalona rostrata A regression line is fitted to the data.



APPENDIX XIII : Data from which the Daily Production of *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* were calculated

Table i - Data from which the averaged growth curves of *Disparalona rostrata* at three temperatures were plotted (10°, 14° and 19°C)

10°C
duration of juvenile instar = 216.48 hours
duration of adult instar = 328.32 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.333	0.352	-	0.352
216.48	0.402	0.638	-	0.638
432.96	0.477	1.095	-	1.095
761.28	0.489	1.184	2 x 0.338	1.922
1089.6	0.500	1.270	2 x 0.346 + above	2.803
1417.92	0.509	1.344	2 x 0.35 + above	3.700
1746.24	0.517	1.412	2 x 0.339 + above	4.512
2074.56	0.526	1.491	2 x 0.336 + above	5.316
2402.88	0.534	1.564	2 x 0.34 + above	6.140
2731.2	0.54	1.620	2 x 0.34 + above	6.948
3059.52	0.545	1.668	2 x 0.34 + above	7.673
3387.84	0.551	1.726	2 x 0.34 + above	8.409
3716.16	0.558	1.797	2 x 0.34 + above	9.157
4044.48	0.562	1.858	2 x 0.34 + above	9.875
4372.8	0.567	1.890	2 x 0.34 + above	10.605
4701.12	0.573	1.954	2 x 0.34 + above	11.346

14°C
duration of juvenile instar = 115.2 hours
duration of adult instar = 165.36 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.341	0.380	-	0.380
115.2	0.422	0.746	-	0.746
230.4	0.480	1.121	-	1.121
395.76	0.503	1.293	2 x 0.331	1.984
561.12	0.519	1.433	2 x 0.337 + above	2.854
726.48	0.537	1.592	2 x 0.347 + above	3.815
891.84	0.543	1.648	2 x 0.344 + above	4.652
1057.2	0.548	1.697	2 x 0.345 + above	5.487
1222.56	0.556	1.771	2 x 0.344 + above	6.347
1387.92	0.560	1.817	2 x 0.343 + above	7.160
1553.28	0.565	1.869	2 x 0.343 + above	7.984
1718.64	0.571	1.932	2 x 0.343 + above	8.820
1884.00	0.577	1.997	2 x 0.343 + above	9.658

APPENDIX XIII : Table i - (continued)

19°C

duration of juvenile instar = 98.64 hours
duration of adult instar = 115.92 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.330	0.343	-	0.343
98.64	0.412	0.690	-	0.690
197.28	0.482	1.132	-	1.132
313.28	0.492	1.205	2 x 0.305	1.738
429.12	0.508	1.336	2 x 0.313 + above	2.448
545.04	0.518	1.420	2 x 0.313 + above	3.111
660.96	0.525	1.482	2 x 0.308 + above	3.723
776.88	0.533	1.554	2 x 0.308 + above	4.345
891.92	0.541	1.629	2 x 0.325 + above	5.075
1007.84	0.548	1.697	2 x 0.343 + above	5.915
1123.76	0.550	1.717	2 x 0.343 + above	6.708
1239.68	0.560	1.817	2 x 0.343 + above	7.581
1355.6	0.561	1.820	2 x 0.343 + above	8.364
1471.52	0.568	1.900	2 x 0.343 + above	9.210
1587.44	0.574	1.965	2 x 0.343 + above	10.046

All individuals are assumed to become mature in the third instar.

Mean lengths of young for a given instar are obtained from Appendix XI Tables i and ii, and the duration of juvenile and adult instars from Table 10.

APPENDIX XIII

Table ii - Data from which the averaged growth curves of *Leydigia leydigi* at four temperatures were plotted (5°, 10°, 14° and 19°C)

5°C

duration of juvenile instar = 280.80 hours
duration of adult instar = 597.84 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.466	1.108	-	1.108
282	0.544	1.617	-	1.617
565	0.651	2.510	-	2.510
1163	0.720	3.212	2 x 0.4	4.737
1760	0.771	3.801	2 x 0.446 + above	7.316
2358	0.813	4.324	2 x 0.470 + above	10.073
2956	0.830	4.547	2 x 0.450 + above	12.326

10°C

duration of juvenile instar = 151.20 hours
duration of adult instar = 207.60 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.476	1.167	-	1.167
151	0.557	1.714	-	1.714
302	0.656	2.557	-	2.557
509	0.710	3.108	2 x 0.396	4.596
716	0.762	3.684	2 x 0.436 + above	7.055
923	0.803	4.189	2 x 0.462 + above	9.728
1130	0.821	4.432	2 x 0.424 + above	11.729
1337	0.840	4.683	2 x 0.443 + above	13.937
1544	0.858	4.932	2 x 0.424 + above	15.944
1752	0.876	5.189	2 x 0.424 + above	17.959
1959	0.894	5.450	2 x 0.424 + above	19.982
2167	0.912	5.720	2 x 0.424 + above	22.012
2375	0.930	6.007	2 x 0.424 + above	24.051
2582	0.944	6.230	2 x 0.424 + above	26.033
2790	0.956	6.426	2 x 0.424 + above	27.986
2997	0.970	6.659	2 x 0.424 + above	29.976
3203	0.980	6.870	2 x 0.424 + above	31.953

APPENDIX XIII : Table ii - (continued)

14°C
duration of juvenile instar = 96.48 hours
duration of adult instar = 126.24 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.418	0.850	-	0.850
96	0.535	1.554	-	1.554
192	0.653	2.528	-	2.528
318	0.706	3.060	2 x 0.400	4.585
444	0.742	3.457	2 x 0.422 + above	6.719
570	0.777	3.869	2 x 0.445 + above	9.111
696	0.789	4.020	2 x 0.438 + above	11.165
822	0.798	4.130	2 x 0.438 + above	13.179
948	0.824	4.460	2 x 0.430 + above	15.335
1074	0.838	4.655	2 x 0.427 + above	17.313
1200	0.845	4.750	2 x 0.437 + above	19.301
1326	0.852	4.848	2 x 0.437 + above	21.291
1452	0.859	4.946	2 x 0.437 + above	23.281
1578	0.866	5.045	2 x 0.437 + above	25.274
1704	0.873	5.146	2 x 0.437 + above	27.267

19°C
duration of juvenile instar = 64.56 hours
duration of adult instar = 67.92 hours

Duration of development (hours)	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0.431	0.914	-	0.914
64.5	0.552	1.675	-	1.675
129	0.655	2.550	-	2.550
197	0.708	3.079	2 x 0.389	4.503
265	0.742	3.457	2 x 0.418 + above	6.579
333	0.768	3.760	2 x 0.438 + above	8.786
401	0.778	3.880	2 x 0.420 + above	10.504
469	0.798	4.130	2 x 0.408 + above	12.474
536	0.822	4.440	2 x 0.407 + above	14.373
603	0.838	4.650	2 x 0.427 + above	16.379
671	0.855	4.890	2 x 0.427 + above	18.402

All individuals are assumed to become mature in the third instar.

Mean lengths of young for a given instar are obtained from Appendix XI Tables i and ii, and the duration of juvenile and adult instars from Table 10.

APPENDIX XIII

Table iii - Data from which the averaged growth curves of *Alona affinis* at four temperatures were plotted

Duration of development (hours) *				Growth determined at 19°C **			
5°C	10°C	14°C	19°C	Mean length (mm)	Mean weight (µgC)	Mean length of young produced (mm)	Mean weight including that of young produced (µgC)
0	0	0	0	0.469	0.849	-	0.849
261.12	142.08	100.32	68.88	0.554	1.310	-	1.310
522.24	284.16	200.64	137.76	0.630	1.830	-	1.830
971.28	528.96	355.92	239.04	0.700	2.400	2 x 0.340	3.143
1420.32	773.76	511.20	340.32	0.780	3.180	2 x 0.420 + above	5.200
1869.93	1018.56	666.48	441.60	0.854	4.000	2 x 0.464 + above	7.700
2318.4	1263.36	821.76	542.88	0.901	4.600	2 x 0.432 + above	9.673
2767.44	1508.16	977.04	644.16	0.961	5.480	2 x 0.440 + above	11.962
3216.48	1752.96	1132.32	745.44	1.011	6.240	2 x 0.440 + above	14.175
3665.52	1997.76	1287.60	846.72	1.051	6.924	2 x 0.440 + above	16.278
4114.56	2242.56	1442.88	948.00	1.051	6.924	2 x 0.440 + above	17.720

All individuals are assumed to become mature in the third instar

	Temperature (°C)				
	5	10	14	19	
duration of juvenile instar (hours)	261.12	142.08	100.32	68.88)	From Bottrell (1975b)
duration of adult instar (hours)	449.04	244.80	155.28	101.28)	

* Calculated from data given by Bottrell (1975b)

** Calculated from results of the present study

APPENDIX XIII

Table iv - Data for *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* from which curves of daily growth increments against weight at each of four temperatures were constructed

Disparalona rostrata

TEMPERATURE 10°C		TEMPERATURE 14°C		TEMPERATURE 19°C	
daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC
0.04	0.6	0.0857	0.5	0.0872	0.65
0.0514	1.8	0.12	1	0.12	1.4
0.0666	2.7	0.126	2	0.1466	2
0.053	4.2	0.125	3.5	0.1309	2.75
0.053	5.2	0.12	5	0.13	3.5
0.05	6.5	0.12	6	0.128	5.5
0.048	8	0.118	7	0.125	7
0.047	9	0.112	8.5	0.122	8.5

Leydigia leydigi

TEMPERATURE 5°C		TEMPERATURE 10°C		TEMPERATURE 14°C		TEMPERATURE 19°C	
daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC
0.032	1.25	0.184	2	0.2057	1.5	0.2743	1.5
0.075	2	0.272	4.6	0.32	2.5	0.624	3
0.0953	3.5	0.2526	10	0.342	4	0.6858	5
0.0988	6	0.213	14.6	0.393	6.7	0.72	8
0.1157	8	0.2	20	0.3507	11.11	0.72	11
0.9	10.25	0.18	26	0.35	14	0.6515	14
0.0818	11.5	-	-	0.308	17.3	0.5908	16
-	-	-	-	0.305	17.6	-	-

APPENDIX XIII : Table iv - (continued)

Alona affinis

TEMPERATURE 5°C		TEMPERATURE 10°C		TEMPERATURE 14°C		TEMPERATURE 19°C	
daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC	daily growth increment µgC	individual weight µgC
0.045	1	0.096	1	0.12	1	0.16	1
0.10	3	0.13	2	0.25	2	0.274	2
0.13	6	0.21	4	0.256	3.2	0.445	4
0.132	10	0.274	6	0.369	6	0.448	8
0.109	14	0.203	13	0.288	8	0.48	11
0.084	16	0.168	16.2	0.256	16.2	0.336	16.4

APPENDIX XIII

Table v - Numbers of *Disparalona rostrata* under a square metre in each length class. Data from which curve showing weekly size frequency of the population was constructed

DATE	LENGTH CLASSES*				
	I	II	III	IV	V
20. 4.82	9.99	9.99	4.99	39.99	4.99
26. 4.82	-	-	9.14	9.14	13.71
5. 5.82	-	-	9.45	17.5	8.05
11. 5.82	-	-	12	30	6
17. 5.82	-	-	-	12.85	17.14
24. 5.82	93.08	50.12	122	222	214
1. 6.82	302	203	748	1085	842
8. 6.82	242	242	1333	1854	1187
14. 6.82	1310	1456	2504	5459	3827
21. 6.82	1253	1565	834	4385	3244
28. 6.82	1972	6198	2251	17750	2558
6. 7.82	6052	5524	2102	12628	2389
19. 7.82	1831	4087	2114	6059	852
26. 7.82	1467	2752	739	5226	524
2. 8.82	817	1417	57	3214	217
10. 8.82	1055	1055	250	2763	299
16. 8.82	1783	1953	744	5957	835
24. 8.82	1600	1921	747	6511	960
31. 8.82	568	1135	568	5015	2176
7. 9.82	624	1361	737	2552	1077
13. 9.82	666	1161	589	2839	770
20. 9.82	535	769	302	2343	335
27. 9.82	483	1100	434	2957	392
5.10.82	432	1023	412	2840	382
11.10.82	246	1416	554	3449	431
25.10.82	220	1324	2648	5628	551

* Length class	Length (mm)	Maximal weight µgC	Maximal weight including young produced µgC		
			10°C	14°C	19°C
I	0.323 - 0.373	0.5035	-	-	-
II	0.374 - 0.424	0.7548	-	-	-
III	0.425 - 0.475	1.0806	-	-	-
IV	0.476 - 0.526	1.4913	5.3156	2.926	3.7317
V	0.527 - 0.577	1.9976	11.3895	9.657	10.079

APPENDIX XIII

Table vi - Numbers of *Alona affinis* under a square metre in each length class.
Data from which curve showing weekly size frequency of the population was constructed.

DATE	LENGTH CLASSES *													
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
2. 2.82	-	10.04	20.14	20.14	30.25	90.75	161	141	40.29	60.5	-	-	20.14	10.14
2. 3.82	-	19.72	19.72	-	19.72	39.52	59.31	128	148	118	59	49	9.82	29.62
29. 3.82	-	-	18.59	-	-	37.21	93.02	9.28	18.59	27.82	9.28	-	-	-
20. 4.82	-	5.06	10.17	20.35	30.53	35.64	76.31	71.28	45.82	71.28	15.24	5.06	-	-
26. 4.82	5.74	-	62.96	88.17	81.85	50.33	100	75.33	119	88.17	25.13	12.56	5.74	-
5. 5.82	3.26	3.26	30.19	56.3	77.52	67.72	153	100	146	127	28.56	8.16	3.26	8.16
11. 5.82	-	5.04	10.84	16.29	43.45	48.88	114	81.53	108	108	18.08	-	-	9.52
17. 5.82	5.13	-	25.69	30.83	35.97	25.69	56.57	87.4	87.4	82.27	-	15.41	5.13	5.13
24. 5.82	27.1	82.82	193.7	441	138	442	497	221	442	138	138	138	55	55
1. 6.82	68.8	215	731	1127	628	1789	1462	680	877	266	258	193	120	185
8. 6.82	61.76	185	928	992	742	2105	1485	680	495	185	123	-	62	185
14. 6.82	68	178	762	948	753	2448	1515	762	431	152	144	42.3	76.1	144
21. 6.82	53.4	115	403	633	518	2017	1037	633	230	53.4	115	-	-	115
28. 6.82	391	-	469	782	548	1722	2504	548	156	548	156	-	-	-
6. 7.82	-	197	296	1288	1090	2974	2477	1387	1090	-	98	-	-	-
19. 7.82	108	108	290	362	435	797	942	543	543	253	72	108	-	46
26. 7.82	83.77	123	330	264	322	1045	1190	516	282	114	53	62	-	22
2. 8.82	28.2	85	255	113	142	738	880	312	28.25	-	28.25	-	-	-
10. 8.82	234	422	328	609	328	1312	1031	281	234	95	-	-	49.2	-
16. 8.82	131	296	398	574	506	394	1291	523	244	113	-	170	45	-
24. 8.82	-	52	364	415	571	1195	1299	675	208	104	-	311	-	-
31. 8.82	-	41	620	703	206	992	868	537	165	41.3	41.3	-	-	-
7. 9.82	-	65.18	65.18	391	173	804	848	239	65	86	-	-	-	-
13. 9.82	-	82.58	133	532	312	1372	1431	431	160	115	-	18.35	-	-
20. 9.82	-	23	92	230	184	829	875	299	161	46	-	23	-	-
27. 9.82	81.94	191	246	431	442	1366	1590	737	279	76	-	22	-	-
5.10.82	144	279	404	692	746	2248	2598	1142	557	126	-	54	-	-
11.10.82	317	526	631	736	1052	1890	2632	1597	736	107	-	-	-	-
25.10.82	-	104	523	1464	941	2196	2510	1255	836	209	314	104	-	-

* length class	length (mm)	maximal weight µgC	maximal weight including young produced µgC			
			5°C	10°C	14°C	19°C
I	0.305 - 0.355	0.412	-			
II	0.356 - 0.406	0.584	-			
III	0.407 - 0.457	0.794	-			
IV	0.458 - 0.508	1.045	-			
V	0.509 - 0.559	1.34	-			
VI	0.56 - 0.610	1.68	-			
VII	0.611 - 0.661	2.07	-			
VIII	0.662 - 0.712	2.515	3.25			
IX	0.713 - 0.763	3.011	-			
X	0.764 - 0.814	3.563	5.574			
XI	0.815 - 0.865	4.172	7.837			
XII	0.866 - 0.916	4.843	9.88			
XIII	0.917 - 0.967	5.575	12.05			
XIV	0.968 - 1.018	6.373	14.28			

APPENDIX XIII

Table vii - Numbers of *Leydigia leydigi* under a square metre in each length class.
Data from which curve showing weekly size frequency of the population was constructed.

DATE	LENGTH CLASSES *											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
2. 2.82	9.6	-	-	9.6	-	-	9.6	-	19.2	-	-	-
2. 3.82	-	31.84	31.84	42.45	21.22	21.22	21.22	31.84	42.45	63.68	31.84	21.22
29. 3.82	-	-	9.65	-	9.65	9.65	19.31	19.31	-	19.31	-	-
20. 4.82	-	-	14.64	19.52	4.88	14.64	14.64	24.4	9.76	4.88	9.76	4.88
26. 4.82	5.19	5.19	31.39	36.63	5.19	47.07	47.07	73.26	68.02	52.3	20.91	10.43
5. 5.82	5.89	4.54	12.63	26.62	14.65	34.03	37.07	54.93	58.3	55.26	26.28	6.74
11. 5.82	5.38	5.38	5.38	21.52	21.52	32.28	37.66	53.8	69.94	69.94	37.66	5.38
17. 5.82	-	15.23	40.63	35.55	20.31	25.39	66.03	60.95	55.87	96.51	60.95	20.31
24. 5.82	7.22	7.22	29.38	51.55	22.08	58.85	66.24	162.04	132	132	110	22.08
1. 6.82	44.8	142	211	398	221	311	854	896	802	812	443	137
8. 6.82	43.43	224	269	403	314	269	1211	762	807	807	179	134
14. 6.82	287	96	163	282	230	828	1259	646	469	373	86	67
21. 6.82	463	58	174	289	231	1854	1796	753	347	-	-	-
28. 6.82	263	-	421	737	421	1421	1105	631	210	52.64	-	-
6. 7.82	123	-	308	431	493	1479	1164	986	185	370	-	-
19. 7.82	5.17	15.51	-	15.51	31.02	56.91	124	77.63	31.02	25.85	-	-
26. 7.82	47.75	19.82	-	18.02	76.58	108	308	172	76.58	33.33	-	40.54
2. 8.82	40.26	-	-	-	40.26	40.26	161	80.53	40.26	-	-	40.26
10. 8.82	-	42.83	57.17	14.27	42.83	157	143	85.73	71.45	14.27	-	-
16. 8.82	-	40	101	50.4	272	181	191	120	80	8.8	-	-
24. 8.82	-	73.96	296	148	-	370	444	296	148	-	-	-
31. 8.82	-	-	77.52	77.52	38.7	232	310	348	38.7	77.52	-	-
7. 9.82	-	-	17.01	33.33	17.01	50	250	133	-	67	-	-
13. 9.82	-	-	28.88	74.1	28.5	68.02	425	93.1	-	44.4	-	-
20. 9.82	-	-	26.96	80.96	26.96	53.99	377	26.96	-	-	-	-
27. 9.82	-	-	27.19	80.11	37.48	70.56	333	136	25.72	24.99	-	-
5.10.82	-	-	45.73	149	69.94	128	632	228	45.7	45.7	-	-
11.10.82	-	-	15.94	96.24	64.12	112.3	385	289	80.18	80.18	-	-
25.10.82	-	39.02	-	156	178	39.02	351	390	273	156	-	-

* length class	length (mm)	maximal weight µgC	maximal weight including young produced µgC			
			5°C	10°C	14°C	19°C
I	0.375 - 0.425	0.8841	-	-	-	-
II	0.426 - 0.476	1.1667	-	-	-	-
III	0.477 - 0.527	1.4966	-	-	-	-
IV	0.528 - 0.578	1.8603	-	-	-	-
V	0.579 - 0.629	2.3070	-	-	-	-
VI	0.630 - 0.680	2.7924	-	-	-	-
VII	0.681 - 0.731	3.3329	4.737	4.82	4.857	4.756
VIII	0.732 - 0.782	3.9309	10.07	7.3	9.172	10.67
IX	0.783 - 0.833	4.5881	12.365	11.885	15.456	14.522
X	0.834 - 0.884	5.3061	-	18.076	27.42	22.39
XI	0.885 - 0.935	6.0866	-	24.051	-	-
XII	0.936 - 0.986	6.9313	-	32.007	-	29.96

APPENDIX XIII

Table viii - Total daily production at each sampling date for *Disparalona rostrata*, *Leydigia leydigi* and *Alona affinis* at the River Thames, Twickenham

Disparalona rostrata			*Leydigia leydigi*			*Alona affinis*		
DATE	Total daily production $\mu gC\ m^{-2}$	No of days	DATE	Total daily production $\mu gC\ m^{-2}$	No of days	DATE	Total daily production $\mu gC\ m^{-2}$	No of days
20. 4.82	3.598	12	2. 2.82	4.227	90	2. 2.82	192.79	90
26. 4.82	1.9494	9	2. 3.82	75.09	28	2. 3.82	271.08	28
5. 5.82	1.7456	6	29. 3.82	19.91	22	29. 3.82	67.14	22
11. 5.82	1.47	6	20. 4.82	26.25	6	20. 4.82	135.64	6
17. 5.82	1.48	7	26. 4.82	65.12	9	26. 4.82	238.75	9
24. 5.82	63.218	8	5. 5.82	75.04	6	5. 5.82	198.24	6
1. 6.82	385.9	7	11. 5.82	80.21	6	11. 5.82	209.24	6
8. 6.82	602.45	6	17. 5.82	107.15	7	17. 5.82	167.56	7
14. 6.82	1787.75	7	24. 5.82	101.75	8	24. 5.82	961.46	8
21. 6.82	1362.7	7	1. 6.82	2885.95	7	1. 6.82	2579	7
28. 6.82	3858	8	8. 6.82	2993.05	6	8. 6.82	2310.1	6
6. 7.82	3448.55	13	14. 6.82	2747.75	7	14. 6.82	2384.6	7
19. 7.82	1767.25	7	21. 6.82	3669.62	7	21. 6.82	1645.3	7
26. 7.82	1298.39	7	28. 6.82	3014.95	8	28. 6.82	2194.49	8
2. 8.82	703.08	8	6. 7.82	3673.17	13	6. 7.82	3116.84	13
10. 8.82	657.09	6	19. 7.82	241.92	7	19. 7.82	1418.2	7
16. 8.82	1398	8	26. 7.82	545.07	7	26. 7.82	1264.9	7
24. 8.82	1471.41	8	2. 8.82	200.12	8	2. 8.82	777.26	8
31. 8.82	1123.28	6	10. 8.82	386.95	6	10. 8.82	1301.79	6
7. 9.82	743.28	6	16. 8.82	477.2	8	16. 8.82	1599	8
13. 9.82	707.72	7	24. 8.82	1028.75	8	24. 8.82	1513.9	8
20. 9.82	508.2	7	31. 8.82	397.83	6	31. 8.82	1105	6
27. 9.82	640.73	8	7. 9.82	189.58	6	7. 9.82	816.59	6
5.10.82	609.07	6	13. 9.82	250.56	7	13. 9.82	1324.78	7
11.10.82	736.77	14	20. 9.82	194.12	7	20. 9.82	809.48	7
25.10.82	1262.19	36	27. 9.82	241.02	8	27. 9.82	1564.38	8
			5.10.82	437.69	6	5.10.82	2507.76	6
			11.10.82	376.48	14	11.10.82	2892.63	14
			25.10.82	479.86	36	25.10.82	2949.68	36