THE FEEDING BIOLOGY OF TINTINNID PROTOZOA AND SOME OTHER INSHORE MICROZOOPLANKTON

by

David John Blackbourn

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Department of ZOOLOGY

The University of British Columbia
Vancouver 8, Canada

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ABSTRACT

Tintinnids are among the largest and most abundant of the marine ciliate microzooplankton but there is very little published information on their feeding rates and abilities.

The feeding of Tintinnopsis subacuta (and to a lesser extent, that of 12 other species) was investigated with three methods 1) direct observation 2) counts of accumulated food cells and 3) Coulter Counts of the particles in the experimental medium. There was reasonable qualitative agreement between the results obtained by the three methods but quantitative agreement was poor. Many of the results showed no significant differences due to very great variability in the results for a single tintinnid species within and between experiments. Much of this variability may be due to the methods used but it also reflects the variability of tintinnids in natural populations.

A wide variety of items was eaten by tintinnids, including smaller tintinnids; and the maximum food size can be related to tintinnid cell volume over a wide range but is dissimilar in tintinnid species of similar cell size. Several tintinnid species showed differential predation on various types of laboratory phytoplankton. This differential predation was based upon the ability of the predator to handle prey, or on prey size or prey type depending upon the particular tintinnid species. 'Negative' selection of some types of laboratory phytoplankton in mixed-prey samples was also shown for some tintinnid species, particularly Tintinnopsis subacuta on members of the Cryptophyceae.

Feeding rates measured with the accumulation method were equivalent

to 0.65% ml/hr/tintinnid for T. subacuta and usually much less. Feeding rates for this species measured with the Coulter Counter technique ranged from 0.33 to 3.8% ml/hr/tintinnid. Very little feeding was observed directly but feeding rates estimated with this method were somewhat higher than those estimated for the same species from accumulation experiments.

Tintinnids apparently both consumed, and caused the production of particles during experiments. Correlations between feeding rate and 9 other experimental variables were such that it would be impossible to predict the feeding rate of a tintinnid species using only the size distribution of available particulate biomass of less than 20 um diameter. There were large differences between the apparent feeding rate asymptotes of T. subacuta and S. ventricosa as measured with the Coulter Counter and the accumulation method. The latter method gave lower asymptotes than did the former. Ivlev electivity indices for T. subacuta were most consistently positive in those middle Coulter size classes which also showed the greatest growth in controls.

Increased temperature had little effect on the rate of food accumulation by four tintinnid species, but there was some evidence of a faster rate of disappearance of ingested food at very high temperatures. The relationship between the gain of new food and the loss of old food in individual T. subacuta and Stenosomella ventricosa was highly variable and may strongly reflect the physiological history of the cell. The rate of gain of new food may be largely independent of the amount of old food in a tintinnid, but the average rate of loss of old food is faster in cells given new food than in starved cells.

It was shown that natural concentrations of T. subacuta can apparently control the growth of natural populations of phytoplankton of less than 20 um dia. in under 24 hours. From a comparison with some other types of microzooplankton it was concluded that the larger species of tintinnid could probably have a potentially predominant effect upon the highly productive phytoplankton of less than 10 um diameter in English Bay and other coastal localities.

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1) INTRODUCTION

This study consists of a largely experimental investigation of the feeding abilities of the large and common ciliates, particularly the tintinnids, from the marine plankton near Vancouver.

Our knowledge of the structure and interactions of marine planktonic food webs is poor; this ignorance is unfortunate in view of the large discrepancies between various estimates of potential total oceanic fish production, such as for example those taken from data on catches of fish, and from measurements of marine primary productivity (Steele, 1965). One of the areas of greatest ignorance includes the food links to and from microzooplankton. Ciliate protozoa are the smallest and most abundant of the microzooplankton (30 - 1000 um) organisms in most oceans. In some marine areas, ciliates also form an important part of the total microzooplankton biomass, and (presumably) metabolic activity (Beers and Stewart, 1969B; Zaika and Averina, 1969; Zenkevitch, 1963). Tintinnids are among the largest of the ciliate microzooplankton, but almost nothing is known of their ecology in the sea or in freshwater.

Since much of the total mortality in a cohort in many species of fish apparently occurs from starvation at a very early age, a great increase in information on the tropho-dynamics of their potential prey (often small microzooplankton) mayybe vital to any understanding of the large natural yearly variations in survival of cohorts of fish (Korniyenko, 1971). Furthermore, LeBrasseur and Kennedy (1972) think that investigation of the feeding habits and rates of production of very small (<50 um) ciliates will be required to aid in estimating the vital winter nutrition and development

of the dominant macrozooplankters of the open subarctic Pacific Ocean. The latter are crucial to the food-webs of the adults of several species of fish of commercial importance, e.g. sockeye salmon. Similarly, Eggert (1973) states that tintinnids are very numerous in Lake Baikal and are important to the winter nutrition of copepod nauplii in that lake.

The importance of microzooplankton to their predators at least partly depends upon the rates and efficiencies with which they incorporate the nannoplankton which is unavailable to the larger organisms. Subjective field observations and estimates of microzooplankton feeding and productivity must be heavily augmented with experimental work, but the feeding mechanisms of diverse microzooplankters cannot simply be extrapolated from those more easily investigated in crustacean macrozooplankton. Although the crustacean members of the microzooplankton can be expected to feed largely by filter-feeding with a fairly rigid 'filter-basket', as do the larger and frequently studied crustacean macrozooplankton (Poulet, 1973), many of the microzooplankton including the tintinnids and other ciliates, use cilia to obtain individual food items and this specialized mode of feeding should be investigated in its own right. The papers of Strathmann (1971) and Strathmann, et. al. (1972) represent most of what is known of the feeding behaviour of some typical nearshore metazoan planktonic ciliary feeders, including echinoderm larvae.

Nothing is known of the productivity or feeding rates of tintinnids in situ. There is also no published quantitative information on the feeding abilities of tintinnids in the laboratory and little more is known of their growth rates in laboratory cultivation (Gold, 1971, 1973). Indeed, very little is known of the feeding abilities of any marine ciliate, benthic or

planktonic from which one might estimate the feeding rates to be expected from tintinnids. Pavlovskaya (1973) has discussed the feeding and growth of a few ciliates found in the littoral zone of the Black Sea, and Fenchel (1968) has studied the food contents and reproductive rates of some benthic ciliates from the Baltic Sea. Hamilton and Preslan (1969) have grown one species of a small bacteria-grazing planktonic ciliate in culture. There is rather more, but still fragmentary data on some freshwater species. For example, Klekowski et. al. (1972) gives some details of the energy budget of one species of benthic freshwater ciliate and Goulder (1972, 1973) has indirectly estimated the feeding rate of a ciliate free-swimming in a pond.

In general, the smaller the organism the smaller the absolute amount of food it removes per unit time, and the faster its reproductive rate. However, as ciliates usually greatly outnumber other microzooplankton and macrozooplankton; the total feeding effect of ciliates per unit volume of seawater may, under some circumstances, provide significant competition in removing phytoplankton, for macrozooplankton such as large copepods and euphausiids. It has been shown that some copepods and euphausiids have a lower size threshold in their feeding below which they graze phytoplankton poorly, if at all (Parsons and LeBrasseur, 1970). It is of interest to determine whether tintinnids and other ciliates would utilize these very small (2-15 um) food items.

In order to obtain initial answers to the problem of the likely effects of tintinnids as predators and competitors this study was intended to be a broad and general experimental investigation of feeding rates and preferences in the larger local species. More specifically, the intention was:

1. To investigate the range of material eaten by tintinnids and its overlap with the food of larger zooplankton.

2. To obtain measurements of the feeding rates of tintinnid ciliates and other microzooplankton on natural types of food.

3. To make such measurements with more than one technique and in such a way (e.g. by size separation of natural zooplankton samples and by using a Coulter counter) that as far as possible comparisons could be made between different species of tintinnids and between tintinnids and other microzooplankton.

4. To investigate the circumstances under which prey selection (if any) occurs in various tintinnid species.

5. To examine particularly the effect of such factors as food concentrations, prey size, hunger state and temperature upon tintinnid feeding rates.

6. If possible, to investigate the relationship between feeding rate, digestion rate, and growth rate of tintinnids on phytoplankton cultured from natural samples; and to compare this information with observations made during natural tintinnid 'blooms'.

7. To estimate the potential ability of tintinnids to control the growth of populations of small phytoplankton cells.

2) TINTINNID BIOLOGY

General

The major emphasis of this study has been on attempts to obtain qualitative and quantitative information on the feeding rates of several of the local tintinnid species. During this work, much information (often qualitative) on various aspects of tintinnid biology has accrued. Since the natural history of tintinnids is generally so poorly known, some details from the literature (with references) plus some of my observations are presented here. Various aspects of tintinnid biology have been treated in the following papers:

Systematics -- Marshall (1969); Tappan and Loeblich (1968); Zeitzschel (1969) and many others.

Distribution of species -- Many papers quoted in Zeitzschel (1969).

Distribution of numbers and biomass -- Beers and Stewart (1969B, 1971); Zeitzschel (1969); Zenkevitch (1963).

Seasonal and vertical distribution -- Beers and Stewart (1969A); Vitiello (1964); Zaika (1972).

Vertical migration -- Eggert (1973); Zaika and Ostrovskaya (1972).

Seasonal variation in numbers and size -- Burkovsky (1973).

Growth in culture -- Gold (1971, 1973).

Morphology of Lorica -- Biernacka (1965); Halme and Lukkarinen (1960); Burkovsky (1973).

Cytology -- Campbell (1926, 1927).

Ultrastructure -- Laval (1971, 1972, 1973).

Tintinnids form an Order in the Subclass Spirotricha which also includes the closely related Order Oligotrichida and others of the more highly evolved ciliates in the Subphylum Ciliophora. Most non-tintinnid marine planktonic

ciliate species are Oligotrichs. Both orders are characterized by possession of few somatic cilia and an anterior oral opening surrounded by a large complex ciliary structure which serves both to move, and provide food for the organism. Tintinnids are attached posteriorly by a thin contractile structure, to the side or bottom of an external sheath (or lorica) of carbohydrate or proteinaceous material secreted by the cell. This lorica, which may be either transparent, or nearly opaque and covered with foreign particles, normally covers the posterior four-fifths of the cell and may be many times longer than the latter. The feeding (or adoral) cilia are normally completely exposed and project at an angle laterally beyond the lorica when the organism is extended. (see Fig. 1). Oligotrich ciliates possess no lorica, but some have a tightly-fitting posterior sheath of carbohydrate material and they generally have proportionately larger oral cilia than do tintinnids.

Food items are drawn towards the ciliate by means of a vortex created by the anterior cilia, as the cell rotates and moves intermittently in a helical path of a shape characteristic for each species. Unlike some of the Oligotrichs, the local tintinnids are incapable of making large and sudden 'jumping' movements. There is some preliminary sorting of food in the anterior ciliary region and mucus may perhaps be produced to aid in the capture of food (Laval, 1972). Intracellular digestion follows the phagocytosis of individual food items. Egestion of the undigested material as either single objects or as clumps occurs at some posterior site in the cell plasma membrane. Most tintinnids must then remove the egested material from inside the lorica. This is done by a row of thin lateral cilia which pass the egesta along the narrow space between cell and lorica wall and out over the

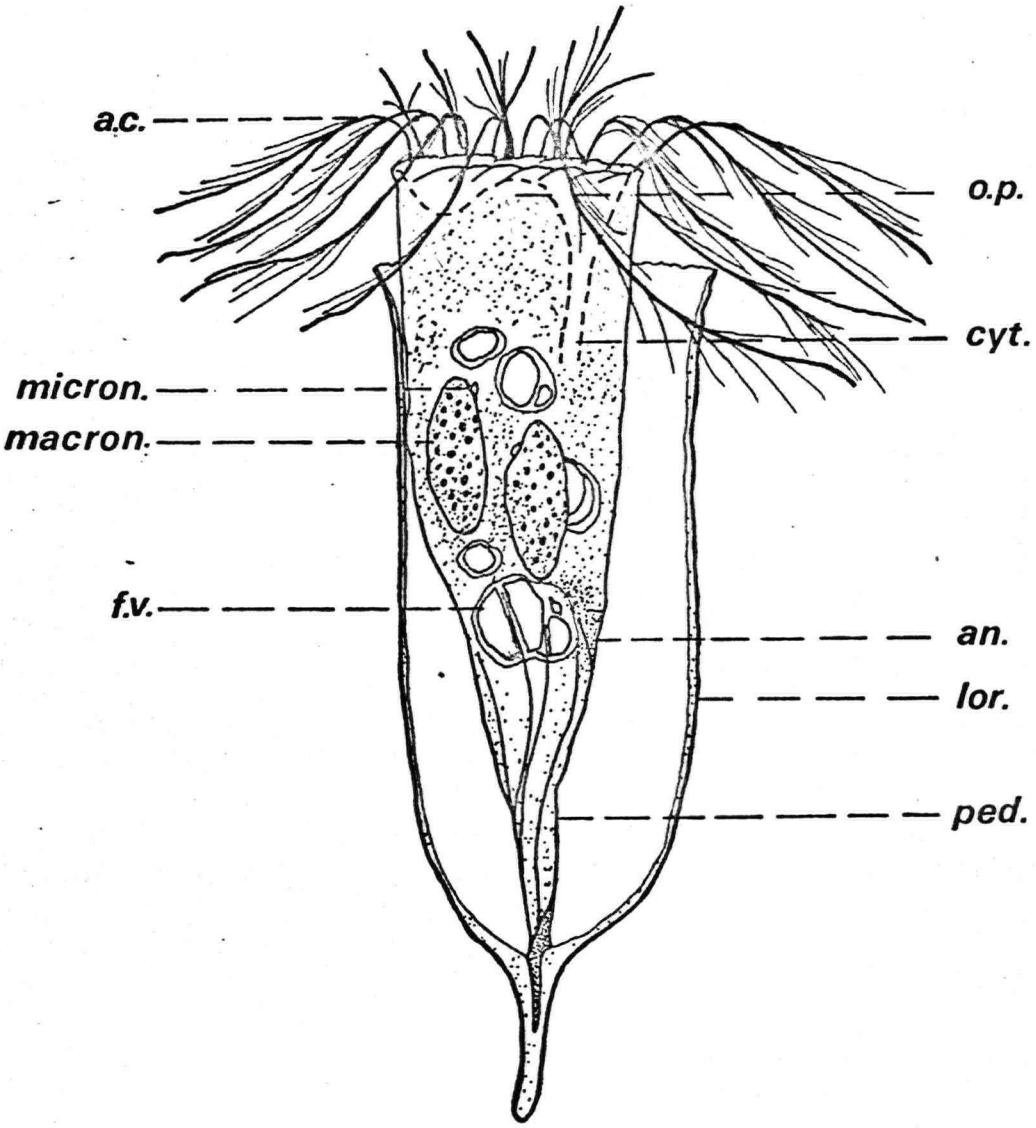


Fig. 1. Diagram of *FAVELLA sp.* (modified from Campbell, 1927) showing adoral cilia, *a.c.*, anus, *an.*, cytopharynx, *cyt.*, food vacuoles, *f.v.*, lorica, *lor.*, macronucleus, *macron.*, micronucleus, *micron.*, oral plug, *o.p.*, peduncle, *ped.*

lip of the lorica. In the genus Eutintinnus, egested material remains posterior to the cell and may eventually pass out of the lorica through the posterior opening.

Tintinnids are generally most abundant in the upper part of the euphotic zone and are nearly always more abundant in inshore waters than offshore. (Beers and Stewart 1969B, 1971; Zeitzschel 1969). There is evidence that some species make short diurnal vertical migrations away from the surface at dawn and towards the surface at dusk, (Eggert, 1973; Zaika and Ostrovskaya, 1972).

Taxonomy

The taxonomic designations of Marshall (1969) have been followed as closely as possible in this study, although even this practice has involved the arbitrary choice of specific name in some cases. This problem will be dealt with again in the comments on lorica morphology later in this Section.

Seven genera of tintinnids represented by thirteen species have been studied in the course of this project. A few other species occur in Georgia Straight but for these no data has been obtained. Ten of these species are commonly found throughout the year, often in the same sample. There is an eight-fold range of cell length and a three hundred-fold range of cell volume between the smallest species Tintinnopsis nana and the largest, Favella serrata (see Table 1).

A single inshore microzooplankton sample has been found to contain up to six species of other phagotrophic ciliates, up to three species of rotifers, and larvae and adults of three or four species of small copepods. More temporary microzooplankters include the larval forms of barnacles,

bryozoans, polychaetes, and bivalve and gastropod molluscs.

Temperature and salinity effects

The bulk of the samples were taken by sampling from shore in English Bay and Coal Harbour, Vancouver. Samples were also taken from Boundary Bay, Horseshoe Bay, central Georgia Strait, and from Departure Bay, Saanich Inlet, and from harbours at Sydney, Victoria and Tofino on Vancouver Island. No species was found to be unique to any particular area, and this would almost certainly still be true on a much broader geographic scale in inshore waters. Also, as expected in a semi-estuarine area, all species were extremely tolerant to slow changes in temperature, and to fast or slow changes over a considerable range in salinity. These abilities were checked in brief experiments. Most of the tintinnid species were found at all the various natural combinations of temperature and salinity, but large numbers or 'blooms' of for example, 2 or more individuals/ml generally occurred in water of some less extreme combination of temperature and salinity. The seasonal trends of temperature and salinity of the local surface water are inversely correlated, due to the great influence in mid-summer of the Fraser River freshet. 'Blooms' of various species occurred at any time from March to December, usually after a few days of fine weather, but were most frequent in April-May and September-November.

Those tintinnid species which occurred in large numbers ('blooms') (1-15/ml) primarily in the months March-May and September-December were Tintinnopsis subacuta, T. parvula, T. rapa, Stenosomella ventricosa and S. nivalis. In those months surface temperatures in English Bay are between 8 and 15° C and salinities are between 10 and 27‰. Helicostomella kiliensis and Eutintinnus tubulosus were numerous only between May and

September, when surface water temperatures are between 12 and 20°C. Tintinnopsis nana and Tintinnidium mucicola have been found in large numbers in every month, but January and February. Tintinnopsis cylindrica was at its most abundant from May to September, but was never as numerous as 1/ml. It is curious that T. cylindrica (frequently) and one individual of T. subacuta, were the only tintinnid species seen to contain various stages of an unidentified dinoflagellate internal parasite. The other three species in Table 1 (section 4) were never numerous. Eutintinnus latus was seen only in summer, and Favella serrata and Ptychocyclis acuta (very rare) were seen in late summer-fall in waters of a salinity exceeding 15‰. However, it is likely that all other environmental factors are of secondary importance to a good supply of suitable food in the production of large numbers of tintinnids.

Lorica morphology

One tintinnid species, Tintinnidium mucicola, appears to have a lorica to which particulate matter may adhere at any time. Others such as those in the genera Tintinnopsis and Stenosomella have loricas which appear to be 'sticky' for a short time only after formation and are less so than that of Tintinnidium mucicola even then. Species of the genera Favella, Ptychocyclis, Helicostomella and Eutintinnus in local waters never have particles adhering to their loricas even when inwater with much small detritus, although the lorica of E. tubulosus has been seen to be covered by a coating of fine detritus which could be easily discarded. Several species of the genera Tintinnopsis and Stenosomella can be kept in laboratory conditions for short periods where they usually form apparently normal loricas with no adhering detritus whatever. The function (if any) of detritus on loricas is not obvious.

Lorica 'repair' is thought to be carried out by some tintinnid species (Biernacka, 1965) and occasional irregularities in lorica morphology may be due to imperfect repair following 'accidents'. The shape of the loricas of tintinnids in laboratory cultures is occasionally abnormal (Gold, 1971; and personal observation). This may be due to the lack of suitable detritus in such cultures, but abnormalities also occur in cultures of Helicostomella kiliensis (see above).

Of more importance to the study of the taxonomy, palaeontology and population dynamics of tintinnids is the variation in the length of loricas within a species. Tintinnids are the only ciliates which appear to have left fossils (Tappan and Loeblich, 1968) due to the nature of the particles adhering to the loricas of some species. At present, the taxonomy of tintinnids is based entirely on the morphology of the lorica, and species are designated largely upon the basis of lorica length (e.g. Marshall, 1969). Marshall, in particular, recognized this state of affairs to be unsatisfactory. For example, Burkovsky (1973) has suggested from samples collected over two years that eleven species in the genus Parafavella from the White Sea are all variants of P. denticulata.

It has been observed in this study that lorica length is at least partly a function of recent environmental conditions; and that the mean length, and the greatest length, of the loricas in one apparent population of a species may differ considerably in two samples taken a few days apart. In general in this area loricas tend to be longer in conditions of plentiful food, and this is often noticeable near the end of 'blooms'. However, cells with particularly long loricas are someimes found in samples in which there are few individuals of that species. Burkovsky (1973) found a generally

inverse relationship between the lorica lengths of Parafavella denticulata and phytoplankton concentrations and temperature. The diameters of loricas are much less variable than lorica lengths (this study and Burkovsky, 1973). The only completely reliable diagnostic features in a genus of tintinnids such as Tintinnopsis appear to be those most visible in live or very carefully preserved organisms. Such features might include the average cell length and diameter, and the length of the adoral cilia. Differences in swimming and feeding behaviour are also a useful but subtle taxonomic guide (see Section 4B).

Generally the cells of most tintinnid species are approximately cylindrical for the anterior-two-thirds of their lengths, and conical for the posterior one-third. The most obvious exceptions to this rule are Stenosomella ventricosa and S. nivalis, where the cell has a short anterior cylindrical section, and is sub-spherical posteriorly, as are the loricas of these species. During starvation the shape of the cells of all species change greatly to something like that of a cone, and the cell volume may decrease by more than 50%. Cells of this shape are particularly common in winter.

The ratio of cell length to lorica length is variable within a species for several reasons. Simple transverse binary fission without sexual recombination is by far the commonest form of tintinnid reproduction. At the end of this process, the anterior daughter cell breaks off from the posterior daughter cell and moves away without a lorica. Therefore, the anterior daughter possesses the 'parental' oral cilia, the posterior daughter possesses the parental lorica, and they share the parental cytoplasm and assimilated food. The duration of the process of division is unknown but lasts at least for several hours (in most species). The daughter cells are initially half

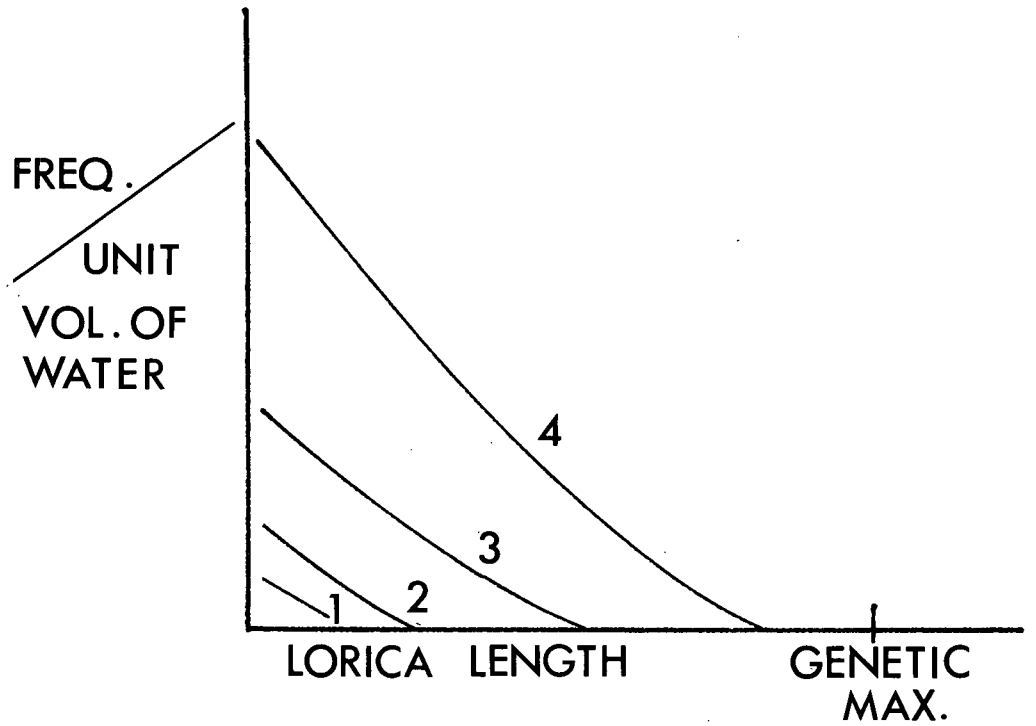
that of the maximum parental cell length, which generally seems to be a characteristic of each species, but which may vary somewhat with relatively long-term environmental conditions and with the physiological capacities of a clone of cells. Each daughter cell contains a random fraction of the recently ingested food. It is not certain to what extent the posterior daughter cell can continue to add to the length of the parental lorica. Since loricas with recent additions at the oral end are fairly common, especially on cells in laboratory cultures, lorica addition may be possible for any 'young' cell. Certainly, as the anterior daughter cell grows toward the maximum cell length, it concurrently manufactures a complete new lorica from the secretion of material held in granules in the anterior portion of the cell. The new lorica invariably hardens and grows from the posterior (or aboral) end of the new cell, often from a template consisting of a small particle of detritus. It is not known how closely the rates of growth of cell and lorica are related. The anterior daughter cell begins to feed very soon after division and forms a complete lorica rapidly, usually in a day or so. Whether the ultimate size of the new lorica is chiefly dependent on the nutritional state of (a) the growing cell, or (b) the parental cell is not certain. When cells of near maximum size are seen inside very small loricas, the cause is probably some sudden stress resulting in the detachment of the cell from its original lorica. Alternatively, this condition may result from some imbalance in the relative rates of growth of cell and accretion of lorica, perhaps over several generations. Short cells with relatively large loricas are either the result of recent cell division or, and less likely, of starvation. A newly divided cell starved since division would be both short and 'thin'. Some ciliates grown in laboratory culture can be 10 to 20 - fold larger at high growth rates than at low growth rates due to

a delay in the maximum rate of reproduction (Canale, et.al., 1973; Hamilton and Preslan, 1969). Therefore, comparisons between tintinnid cell sizes within a species should best await further data on growth rates from laboratory cultures.

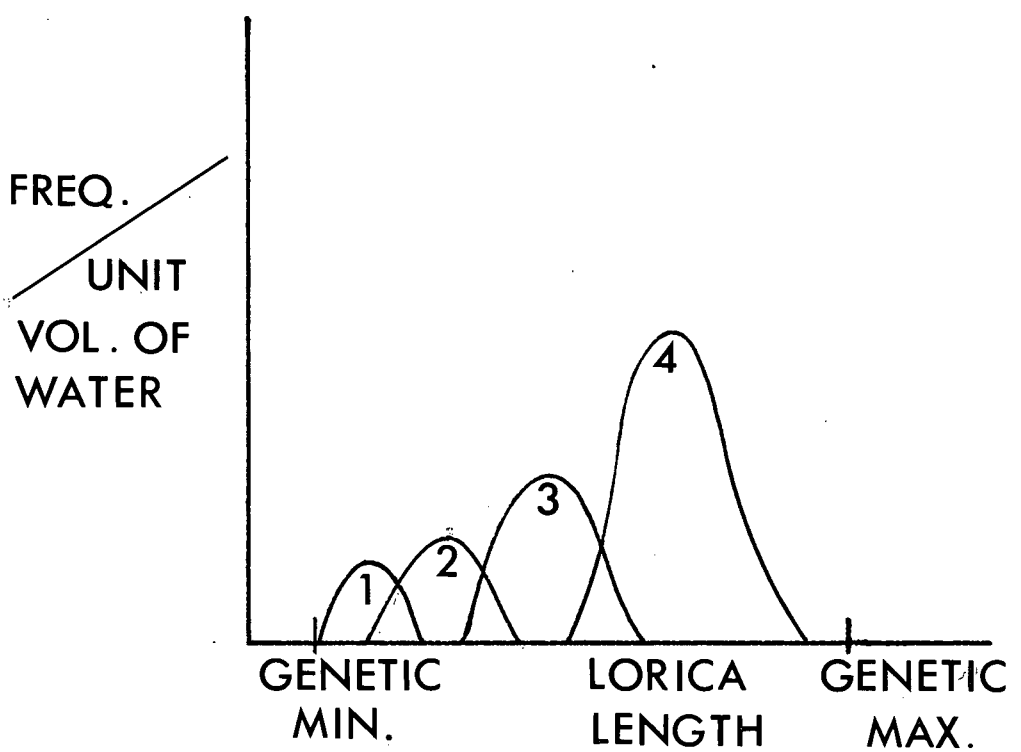
Data consisting of length-frequency distributions of tintinnid loricas taken from field samples, may give information about some aspects of the 'population dynamics' of the loricas; and perhaps on the recent history of growth of the (semi-immortal) cells themselves. This sort of information can be obtained from almost no other free-living protozoa. Halme and Lukkarinen (1960) and Burkovsky (1973) presented the two previous analyses of tintinnid lorica measurements from field samples. Lorica length-frequency data from a time-series of samples taken at very short intervals, may help to distinguish between two extreme theories of lorica accretion, assuming synchronous reproduction and given certain as yet unverifiable assumptions about lorica 'mortality'. These theories are as follows: a) Lorica accretion is continuous throughout the 'life' of the contained cell and is dependent upon the current nutritional state of that cell; and b) Lorica accretion is discontinuous and confined to new loricas, occurs only immediately following division, and is dependent upon the nutritional state of the parental cell. If theory a) holds, then length-frequency diagrams of the loricas of one population of one species from a time-series of consecutive samples 1 to 4, with conditions for growth improving in that order and no lorica mortality, would appear as in Figure 2a); and if theory b) holds, then the length-frequency diagrams would appear as in Figure 2b). Intermediate patterns are possible. Biernacka (1965) believes, and I concur, that while most lorica accretion occurs immediately after cell division, it can occur in some species

Figure 2. Possible theoretical relationships between tintinnid lorica length and frequency (see text for details).

Fig. 2 a)


FREQ.
UNIT
VOL. OF
WATER
4
3
2
1
LORICA LENGTH
GENETIC
MAX.

2 b)


FREQ.
UNIT
VOL. OF
WATER
4
3
2
1
GENETIC
MIN.
LORICA
LENGTH
GENETIC
MAX.

at any time.

Length-frequency diagrams of the loricas of one species of tintinnid from English Bay are shown in Figure 3. Data from Burkovsky (1973) are shown in Figure 4. These diagrams seem to indicate that theory b) is a better description of lorica accretion than theory a) at least under some circumstances. There have been no previous theoretical attempts at analyses of this kind.

It would be useful in some future study to check these tentative ideas and other theories of lorica growth and size and age-dependent (lorica) mortality rates, etc., with data from a much wider range of samples and environmental conditions. It is probable that a new lorica can be considered mainly as a metabolic 'cost' to the parental cell, and as such may be relatively greatest in those species which have the largest ratio of lorica length to cell length. One local species in particular, Helicostomella kiliensis, possesses a lorica with markings which may be of some future use in estimating rates of lorica accretion, etc. These markings consist of closely adjacent narrow strips of material laid down in the shape of a helix on top of the anterior portion of the lorica. These 'annuli' are invariably about 4 um apart but their number per lorica is greatly variable; and they are not always most numerous upon the longest loricas of H. kiliensis. In short, the relationships between the rates of tintinnid cell growth and division and the rate of annulus formation (if any); and between the latter and the rate of accretion of the whole lorica, are unknown.

Asexual reproduction

Tintinnid cells do not necessarily grow and divide most rapidly when they contain the largest amounts of recently ingested, or of assimilated food

Figure 3. Lorica length-frequency data for Tintinnopsis subacuta from three successive field samples.

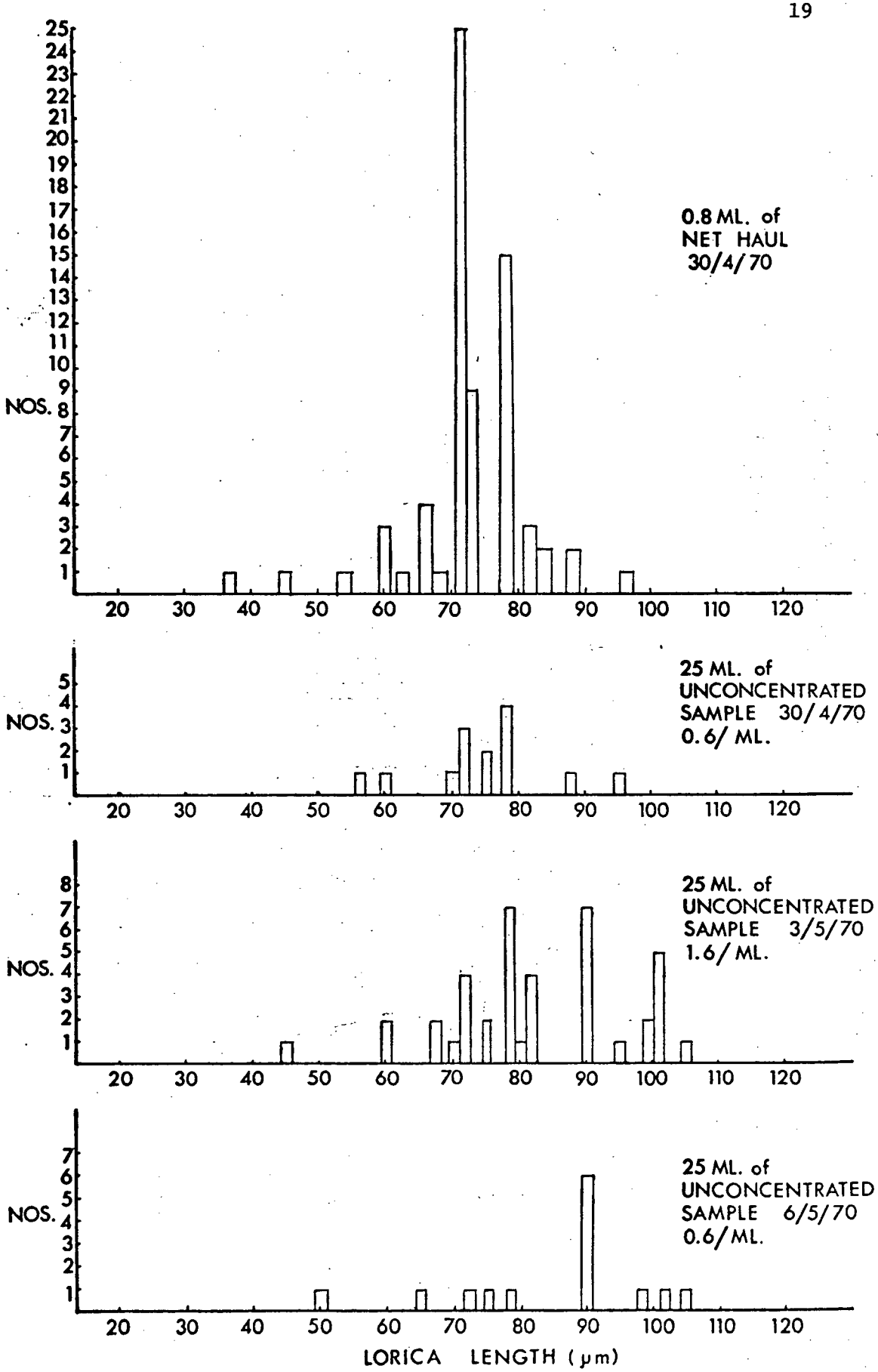
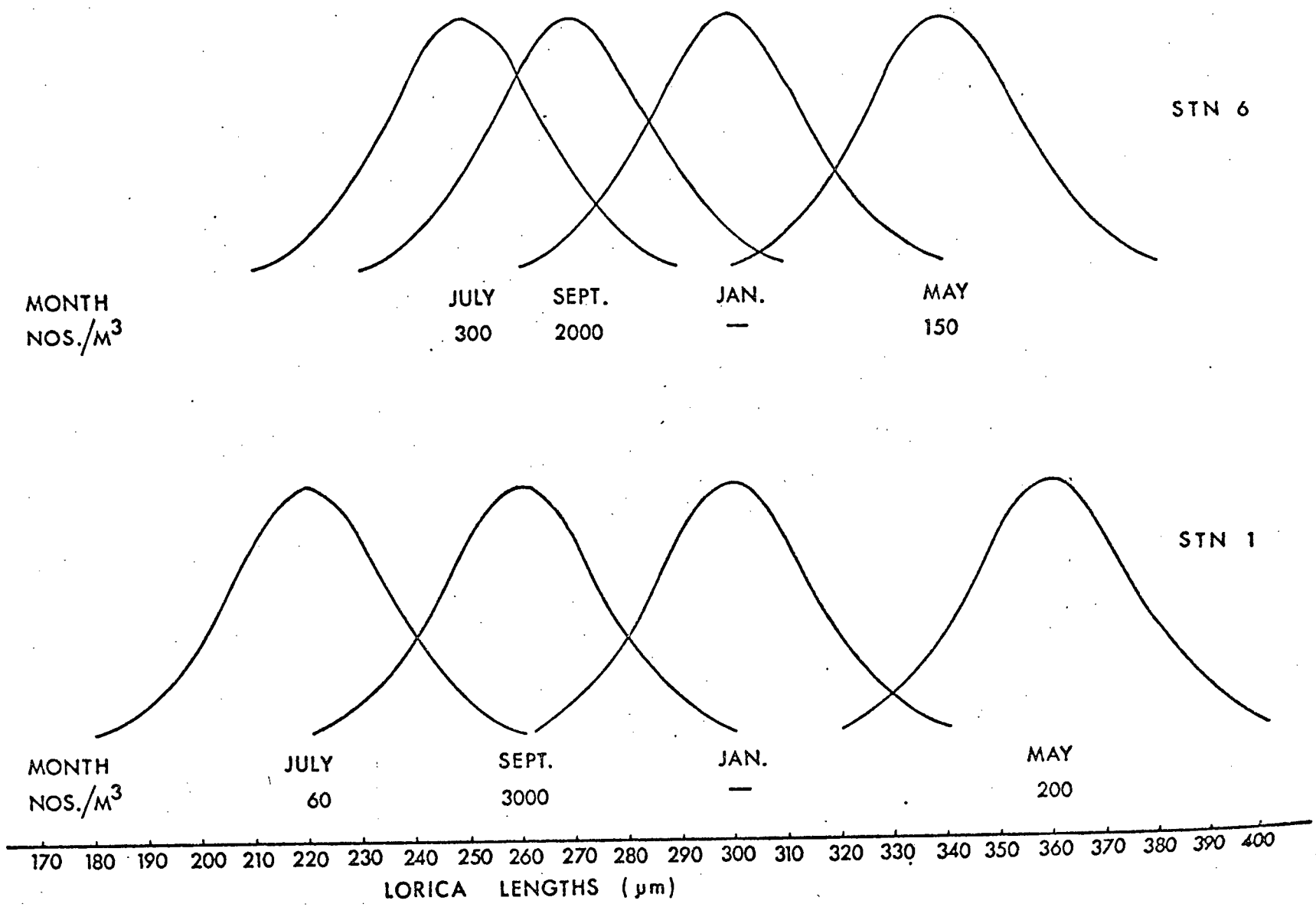

0.8 ML. of
NET HAUL
30/4/70
25 ML. of
UNCONCENTRATED
SAMPLE 30/4/70
0.6/ ML.
25 ML. of
UNCONCENTRATED
SAMPLE 3/5/70
1.6/ ML.
25 ML. of
UNCONCENTRATED
SAMPLE 6/5/70
0.6/ML.
NOS.
LORICA LENGTH (μm)

Figure 4. Seasonal abundance and lorica lengths of 100 Parafavella denticulata. Data from Burkovsky (1973).


STN 6
MONTH
NOS./M3
JULY
300
SEPT.
2000
JAN.
—
MAY
150
STN 1
MONTH
NOS./M3
JULY
60
SEPT.
3000
JAN.
—
MAY
200
170 180 190 200 210 220 230 240 250 260 270 280 290 300 310 320 330 340 350 360 370 380 390 400
LORICA LENGTHS (μm)

(see Section 4). Temperature may have a greater effect on division rate than on feeding rate. The oral structures of the posterior daughter cell develop spirally (from a primordium or anlage) over a period of several hours at a mid-point in the lateral surface of the parental cell, which is at that time probably close to its maximum length for that species (Campbell, 1926). The diameter of the new (posterior) oral region, and the length of the oral cilia around it, increase together, as the anterior daughter cell is extended forward well clear of the lorica. The latter is finally connected to the posterior daughter only by a thin strand of cytoplasm close to the new full-sized oral region. Throughout at least the first part of cell division the parental oral region remains superficially unchanged, (unlike that in many groups of ciliates) and may gather food.

The eventual decline of viability of an asexual clone (as shown by small size, slow reproductive rate, etc.) is a well known genetic phenomenon in ciliates in laboratory culture. This decline can only be arrested by sexual recombination. Presumably natural clones of tintinnids are prone to such declines, but there is no data on the subject.

Sexual Reorganization

This is a much less common phenomenon than asexual reproduction in tintinnids, as is the case in all natural populations of ciliates. Mating involves the pairing (or conjugation) of cells belonging to some of the different mating types within a morphologically defined species of ciliate for the purpose of genetic recombination through the exchange of micro nuclei. Conjugants eventually form cytoplasmic connections in the oral region for this exchange. Conjugation has been seen most commonly in this study in fairly abundant late summer-fall populations of tintinnids. For example, in one

sample in September 1973, approximately 25% of individuals of Stenosomella nivalis, about 20% of Tintinnopsis parvula and about 10% of T. subacuta were in conjugating pairs. The specific factors which stimulate this process are unknown. During a feeding experiment at that time, one pair of cells of T. subacuta remained in conjugation for at least 1½ hours and probably much longer, and did not feed. Nothing is known of the details of the mating processes nor of the possible number of 'mating types' in any species of tintinnid.

Gold and Pollingher (1971) claim to have observed an unusual type of sexual process in a laboratory culture of one species of tintinnid involving a mobile microgamete which attached itself to the posterior end of the macrogamete. Their evidence seems insufficient for their claim to be supported unreservedly. The phenomenon has not been seen in this study.

Motion and Metabolism

Throndsen (1973) has shown that in a wide variety of marine algal flagellates there is no obvious relation between cell size and swimming rate and the distances travelled per second may range from 10 to 40 cell lengths in different species. Rotation and gyration are the rule in flagellates but each species has a characteristic motion. Bullington (1925) studied the motion of ciliates and found that cell rotation and helical paths were characteristic of many species. He found that larger species were generally faster than small ones, and that the faster their speed the fewer the turns they made. Bullington also showed that most ciliate species had a speed of 5 or 6 cell lengths per second, rather slower in relation to size than the flagellates mentioned above, but much faster in μm/second. In Bullington's results the paths of the faster ciliates described fewer spirals per body

length travelled, than did the slower species. He states Prorodon marinus (200 x 100 um) as moving at about 1000 um/second. In this study, Prorodon sp. has been seen to move at between 5 and 12 cell lengths/second, with rotation but very infrequent helical motions. Bullington (loc. cit.) did not study tintinnids. It has been occasionally possible to make direct measurements of tintinnid speeds in this study. For example, the speed of Stenosomella ventricosa has been estimated at different times at four and at eight body lengths per second.

The amount of energy expended on motion by very small organisms seems to be a very small proportion of their total metabolic energy losses. Halfen and Castenholz (1971) state that the energy required to move a gliding blue-green bacterium cannot be more than 5% of the energy produced by oxidative phosphorylation. Likewise, Pavlova and Lanskaya (1969) found that in five species of Black Sea dinoflagellates the percentage of active (motion) respiration in the total metabolism was about 1%. In the case of the much larger copepods, Vlymen (1970) estimated that extensive daily vertical migrations would require the equivalent of less than 1% of the basic metabolic rate of these organisms. In all swimming organisms smaller than about 1 cm. in length energy is expended mostly to overcome the viscosity of the medium rather than the inertia of the organism. Also, turbulent flow is not created by small, slow organisms, and therefore energy need not be expended to overcome it. It is not likely that the constant motion of tintinnids will be an important part of their total metabolic activity, particularly in warm water, the viscosity of which is lower than that of cold water.

A very rough estimate of the total oxygen consumption of Tintinnopsis subacuta was made with the use of a differential microrespirometer as

described by Swift (1974). Five hundred tintinnids of one species from a net sample were placed in the respirometer in 3 ml of filtered seawater at 15 C. This was thought to be a necessary but unnaturally high degree of crowding, but Gold (1973) has grown healthy populations of tintinnids in higher concentrations than this. Since no (or very little) food was available, the respiration measured might be considered that of mobile but very crowded, slowly starving organisms. However, since only 38% of the tintinnids were alive after the 18¼ hr experimental period, the respiration measured may be partly the result of bacterial metabolism. If the latter possibility is ignored, the total oxygen consumption was the equivalent of between 1.6 and 5.9×10^{-4} ul/hr/Tintinnopsis subacuta.

This is equivalent to a mean daily consumption rate of 0.009 ul O_2/ T. subacuta. There are no comparable data for tintinnids or other planktonic ciliates and little for other microzooplankton; but Doohan (1973) states that a female Brachionus plicatilis rotifer carrying three eggs utilises about 0.14 ul O_2/rotifer/day. Petipa, and Marshall and Orr have measured the respiration of marine copepod nauplii. In their results (summarized with other work by Marshall, 1973) Acartia clausii stage V and VI nauplii used about 0.10 ul O_2/nauplius/day; and Calanus finmarchicus stage III nauplii used about 0.19 ul O^2/nauplius/day. The metabolic rates for the adults of these two copepod species were about 15 times greater than that of the quoted nauplius for A. clausii females and 50 times greater in the case of C. finmarchicus (in Marshall, 1973).

The weight of A. clausii stage V and VI nauplii can be calculated from Marshall (1973) to be about 0.10 ug dry weight. From the data given by Theilacker and McMaster (1971) a large individual of Brachionus plicatilis

would have a volume of 1 to 2 x 10^6 um^3. If a specific density of 1.0, and a wet weight to dry weight ratio of 10/1 are assumed, then a dried B. plicatilis female would weigh about 0.15 ug. Therefore the respiration rates, and dry weights are similar for A. clausii late naupliar stages and B. plicatilis females. Using the above conversions Tintinnopsis subacuta (7 x 10^4 um^3) would have addry weight of about 0.007 ug. Thus these three microzooplankton organisms have an approximately similar respiration rate per ug dry weight.

The respiration rate of T. subacuta may be calculated in terms of ug Carbon/tintinnid/day thus: --+0.009 x $\frac{12}{22.4}$ x 1.0 (respiratory quotient) = 0.0048 ugC/tintinnid/day. If a carbon/dry weight ratio of 0.5 is assumed, then the mean respiration rate given is equivalent to about 137% T. subacuta body weight/day. This figure seems a little high, but not unreasonable in view of the fact that a tintinnid may easily consume the equivalent of 2-300% of its body weight in food in a day.(seeGeneral Discussion). A respiratory quotient of 0.8 may be more suitable than one of 1.0 if lipids are the chief respiratory substrate (see Materials and Methods Section). If so then the respiration rate would be equivalent to about 110% T. subacuta body weight/day.

Feeding

This subject will be discussed in more detail in other sections. The predominant living items in the environmnet of tintinnids, which are small enough to be eaten by them, are small (3 to 30 μm) naked unicellular flagellated algae. As tintinnids are, in a general sense, unselective feeders, it is not surprising that their food content in general, reflects this preponderance of flagellates. Occasionally, small diatoms, thecate dinoflagellates,

silicoflagellates, other tintinnids, detritus particles or bacteria (usually on the latter) form part of the cell contents. Blooms of one or more species of flagellates are usually soon followed within 1 or 2 days, or are accompanied by, blooms of one or two species of tintinnids.

Blooms of food cells are not always the result of photosynthesis. For example, in late December 1972, unusually high numbers (for the time of year) of Tintinnidium mucicola were seen in samples from English Bay in which there were very high numbers of a flagellate (or coccoid bacterium) 2 - 3 µm in diameter, and not much else. During the previous ten days the cloud cover had been complete, and heavy rain had fallen almost continuously. As a result, some small landslides had added much turbid run-off to the sea in the sampling area. The short-lived flagellate (or bacterial) bloom was therefore almost certainly dependent on the uptake of allochthonous organic compounds in the surface low-salinity water. Occasionally, blooms of flagellates are not followed by large numbers of tintinnids. Except for those cases in which the flagellate was obviously too large for the available tintinnid species to ingest, as for a bloom of the dinoflagellate Prorocentrum micans in 1971, there seem no simples explanations for these 'unaccompanied' blooms of flagellates.

The opposite situation also occurred, where a sample contained relatively many tintinnids. In such cases, the tintinnids contained few food items or storage granules, as an indication of a recent low level of food intake. A sample taken the following day often contained many fewer tintinnids. Therefore the previous sample either represented a) a food-poor environment in which tintinnids had been temporarily concentrated by water movements; or b) an environment in which tintinnid reproduction had 'overshot' that of its

food, and where the food had as a result become greatly depleted causing the tintinnid population to 'crash' from starvation. Such overshoots are possible because declines in the reproductive rate of laboratory populations of ciliates and other protozoa are known to lag behind declines in feeding and growth rates; (Mitchison, 1971; Williams, 1971, 1972).

Among the microzooplankton as a whole, some of the larval forms appear to take little or no food; but otherwise (even amongst the tintinnids) there is much food 'overlap', and possibly also competition for food, if the latter is ever limiting. Although the ciliates are almost always the most numerous microzooplankters, and have the fastest reproductive rates; some of the metazoans, such as the rotifer Synchaeta littoralis contact and ingest algal cells at a faster rate than many ciliates, (see Section 4c), and also reproduce very rapidly (personal observations). Large populations of S. littoralis occur in inshore water of fairly low salinity (<10‰) and high temperature (>15°C); and as such almost certainly have a greater effect on the flagellate populations than do ciliates or any other microzooplankton. There is no published information on the feeding of this genus of rotifer, and very little further information has been added during this study (but see Section 4c). However, information on laboratory feeding, growth and energy budgets of the brackish-water rotifer Brachionus plicatilis may be found in the papers of Doohan (1973) and Theilacker and McMaster (1971).

Predation on and Among Tintinnids

Questions concerning the identities and activities of the predators of planktonic ciliates are important to an understanding of planktonic food webs but there are only the scantiest answers. Of all these ciliates, only (the loricase of) tintinnids leave recognisable remains after mastication. This

ensures that ciliates will only be found in natural samples, except by chance, inside those predators with some form of primary intracellular digestion (e.g. other protozoa), those with relatively weak powers of mastication (e.g. rotifers and chaetognaths), or those with no mastication and slow rates of extracellular digestion (e.g. some flatfish larvae). Other likely predators of tintinnids would need to be checked with the use of radioactively-labelled tracer experiments. Data on the potential ingestion of tintinnids has come from observation of the food grooves of benthic crinoids, and the mouthparts of planktonic crustacea (Bainbridge, 1958). It is improbable that planktonic ciliates have any specialized predators, and likely predators would include any fairly indiscriminate planktonic or benthic organisms well adapted for the ingestion of objects between 30 μm and 300 μm long.

Ciliates form about 90% of the diet of the larvae of three species of freshwater fish during the first four days of their exogenous mode of feeding (Korniyenko, 1971). As the motions of most ciliates are not erratic, they almost certainly do not elicit searching movements by some raptorial predators such as chaetognaths and copepods, but are probably captured and eaten as a result of random encounters. However, Pearre (1973), has shown that tintinnids can form up to 18% of the diet of young (Stage I) chaetognaths. In this study, various tintinnid species have been seen inside polychaete larvae, the rotifer Synachaeta littoralis, the large ciliates Prorodon sp. and Strombidium (Lohmaniella) spiralis, and the tintinnids Tintinnopsis subacuta, T. cylindrica and Favella serrata. As tintinnids are both primarily herbivorous and cannibalistic (personal observation); as their predators include organisms which are variously planktonic, benthic, carnivorous or predominantly herbivorous; and as some predators later become tertiary carnivores

(e.g. fish larvae), it can be seen that the microzooplankton may form the base of some (structurally) extremely complex food webs. From another point of view, omnivory, which is probably widespread in marine plankton, might be considered to have a simplifying and stabilizing effect on the dynamics of food webs.

Encystment

There is no strong evidence that tintinnids or any planktonic marine ciliates can form resistant and metabolically dormant cysts. This ability would probably be useful to tintinnids in this area, but likely cysts have not been seen during this study. However, single thick-walled objects of the appropriate shape have been seen inside the loricas of Favella serrata in a few samples taken from Georgia Strait and photographed severalyyears after preservation (F.J.R. Taylor, unpublished data). A few individual loricas of two species of tintinnids from the South-West Indian Ocean have been seen to contain plugs just inside the oral end. One of these preserved loricas also contained what appeared to be a pair of recently divided cells (F.J.R. Taylor, unpublished data). Such lorica plugs might be useful to a metabolically quiescent tintinnid whether the latter was encysted or not. Loricas with plugs have not been seen during this study.

"Photosynthetic" ciliates

Until recently it has been axiomatic to consider ciliate protozoa as heterotrophs, consuming the complex products of photosynthesis or chemosynthesis carried out by other organisms; or as the hosts of symbionts which are entire algal cells. During this study, and as a direct result of examining large numbers of field samples for tintinnids, several planktonic ciliates were found to contain chloroplasts and other 'foreign' organellesoof algal

origin which were not inside food vacuoles but 'free' and undigested in the ciliate cytoplasm. Descriptions of the ultrastructure of these organisms and a discussion of their possible ecological significance may be found in Taylor et.al. (1971) and Blackbourn et.al. (1973). Several of these ciliates also at times ingest and digest whole algal cells, so if the undigested chloroplasts prove to be functional, the host ciliates can be considered as both heterotrophs and as functional autotrophs. It is interesting and inexplicable that these undigested chloroplasts were never found inside tintinnids in this study, even in those species with transparent loricas which might allow the passage of enough light for photosynthesis. This possible semi-autotrophy amongst some members of the microzooplankton, makes a consideration of marine food-webs even more fascinating and complex.

3) MATERIALS AND METHODS

a) Sampling and initial treatment

All tintinnids and other microzooplankton used in experiments were obtained by sampling inshore surface seawater from docks or jetties as close to the time of high-tide as possible. Concurrently, temperature and salinity observations were recorded and samples were taken for examination and preservation. An unconcentrated bucket sample and a short haul with a 30 cm diameter net made of monofilament nylon mesh of 50 µm aperature were taken. The net haul was made by walking along the dock or jetty as slowly as possible (~0.5 m.p.h.) and towing the net just submerged. The net was removed from the water as gently as possible with the cod-end in a bucket of seawater, and the contents poured gently into a 4-litre insulated container which had previously been half-filled with surface seawater. More unconcentrated seawater was then added to a final quantity of 3 litres. If it was apparent that many zooplankton larger than 400 um had been netted, the partially diluted net sample was poured gently through a short perspex tube fitted at one end with nylon mesh of 75 µm aperture. The filtrate from this process was diluted and placed in a separate insulated container. About 3 litres of unconcentrated seawater was placed in a third insulated container. The trip from dock or jetty to the laboratory took from between 2 minutes and 1 hour, depending on location. The temperature of the water, and the condition of the organisms in the containers usually remained unchanged for at least 6 hours. Surface seawater temperatures were measured with an unprotected thermometer, and salinities were estimated from the specific gravity as measured with a hydrometer. The latter was checked against an Auto-Lab inductive salinometer and found to differ from it by no more than 1‰ over the temperature

range of the samples. This amount of error is unimportant given the great tolerance of tintinnids to changes in salinity. Transfers of tintinnids, other protozoa and ciliated microzooplankton were made with disposable glass Pasteur pipettes drawn out to a terminal diameter of about 150 µm and fitted with a small hard rubber bulb. Copepod adults and nauplii were transferred with pipettes with a mouth diameter of approximately 5 µm.

Approximately 100 mls of most of the unconcentrated and the netted field samples were preserved with Lugol's iodine solution. Four drops of the concentrated solution were added to screw-top glass jars, before the sample was added. This ensured the rapid fixation of microorganisms in the sample. More preservative was added if the organisms were so numerous as to absorb the initial amount of preservative. Preserved samples kept air-tight and dark for four years showed little indication of cell lysis or loss of stain. In some experiments where circumstances permitted, formaldehyde buffered with phosphate and diluted with seawater to a final concentration of 3%, was used to preserve tintinnids. Of the fixatives best suited for cytological work; gluteraldehyde buffered with phosphate proved unsatisfactory in this work as a fixative and as a preservative, and osmium tetroxide was found to be too dangerous to use in the working area.

The size 'spectrum' of particle biomass (volume) of many field samples was measured with a Model B Coulter Counter within 1 or 2 hours after the sample had been collected (see also Section 3b (iv)). The total numbers and volumes of particles (living and non-living) were estimated for several arbitrary size classes from approximately 2 µm to 30 µm diameter (Sheldon and Parsons, 1967).

The food contents of live tintinnids immobilized by coverslip pressure were estimated within one or two hours after collection of the sample. More details of these methods are given in Section 3b (ii). Estimates were made of the number, degree of 'clumping', type, colour, size and state of digestion of food items. The type of food item inside the tintinnids could be easily identified only in the case of the Bacillariophyceae, Dinophyceae, Euglenophyceae, and a small number of other organisms inoother families of algae. Detritus and protozoans (e.g. other tintinnids) could also be clearly identified as ingested food. Approximate estimates were made of the number of identifiable spherical food storage granules inside tintinnids (i.e. 'many', 'few' or 'none') and the approximate average size of such granules. The latter estimates could be considered as analogous to measurements of 'condition factor' in larger animals. Since ciliates are not known to accumulate insoluble protein or carbohydrate, these granules may well be composed largely of lipids. The total amount of lipid per cell, and the number of cells containing neutral fat granules is greatest in rapidly growing populations of Tetrahymena pyriformis (Hill, 1972). Lipids are also the major substrates for aerobic metabolism in this species (Hill, loc. cit.). The presence and size of any early signs of cell division (oral anlage) in the ciliates were noted; together with the sizes of the cells and the length of their oral cilia. Lastly, the dimensions of the tintinnid loricas (if any) were measured, and the length noted of any portions of any obviously different material, which might indicate recent lorica accretion. The approximate fullness of the gut of rotifers, the pigmentation of their food and the number of eggs (sexual and asexual) were estimated. Whenever possible, the food items were noted for at least 10 of all species of tintinnids in a sample. For reasons of scarcity of for lack of available time this was often impossible,

and then only 2 or 3 of the less abundant tintinnid species were examined.

b) Experimental Methods

(i) General comments

The feeding rates of organisms can be measured directly or indirectly. Direct methods include (i) observation and (ii) counts of the number of food items accumulated inside an organism in a period of time too short for appreciable digestion to have begun. Indirect methods include (iii) the uptake of tracers (e.g. ^{14}C-labelled algae) and (iv) counts of the number of food items in the surrounding medium (e.g. with a Coulter Counter) before and after feeding. Method (ii) can only be used in those organisms such as tintinnids which eat relatively slowly and do not masticate the food before digestion. Direct methods are very accurate and very sensitive, but must often be carried out under relatively artificial conditions and can lead to great variability of results. The best use of indirect methods requires considerable knowledge of the physiology of the organisms used; and necessitates, in the case of slow feeders, the use of relatively long experiments. However, indirect methods can be used under more natural conditions than some direct methods and usually give less variable results.

All four of the above experimental methods were used in this study: direct observation; the counting of accumulated food items; the counting of ^{14}C-labelled algal food; and Coulter counts of the particles in the medium. None was wholly satisfactory for a variety of reasons. The ^{14}C-tracer method in particular proved to be too difficult to use with tintinnids due to low rates of ingestion and this technique was soon discarded. The data obtained from direct observation was sparse and difficult to relate to other data (see Section 4b). Therefore most of the useful data has been obtained from

counts of accumulated food (Section 4a) and from Coulter Counter experiments (Section 4c).

The experimental organisms (mainly tintinnids) were fed with either: natural phytoplankton and other particles from unconcentrated seawater; with one or more laboratory phytoplankton cultures of single or mixed species composition; or with natural and synthetic inert particles such as tree pollen and polystyrene latex spheres. Many of the phytoplankton cultures were of local origin.

Some consistency in the quality of the laboratory phytoplankton food was achieved by using only one type of culture medium, and by only taking sub-samples for experimental use from cultures which were less than two weeks old and in the exponential growth phase. This practice should have ensured that the phytoplankton were of relatively high food value, with relatively larger amounts of protein and vitamins etc., than if the samples had been taken from older cultures. The culture medium used (Jowett's) was based on local seawater plus a very small amount of soil extract and a good balance of nutrients. Its composition was as follows: -

IN I LITRE

875 mls	Filtered seawater
175 mls	Distilled water
0.25 G	Tris (Hydroxymethyl)Aminomethane
0.10 G	$NaNO_3$
0.01 G	K_2HPO_4
0.03 G	Na_2SiO_3+10 mls 1N HCL
6×10^{-3}G	Na_2EDTA
2×10^{-3}G	$FeCl_3 6H_2O$

2×10^{-4}G	Mn(as SO_4)
2×10^{-5}G	Zn(as Cl)
2.5×10^{-6}G	Co(as Cl)
2.5×10^{-6}G	Cu(as Cl)
3.9×10^{-4}G	Mo(as Na)
3.0×10^{-4}G	H_3Bo_3
5×10^{-4}G	Thiamine HCL
3×10^{-5}G	Nicotinic Acid
3×10^{-5}G	Ca Pantothenate
3×10^{-6}G	P-Aminobenzoic Acid
1×10^{-6}G	Biotin
5×10^{-4}G	Inositol
6×10^{-7}G	Folic Acid
1×10^{-6}G	Cyanocobalomin
2.5 mls	Soil Extract (Supernatant from autoclaved mixture of equal volumes of soil and distilled water)

The experimental containers were normally plastic or glass beakers of 50 to 500 ml volume, and these were usuallyccovered with aluminum foil to exclude the light. The containers were rinsed and scrubbed in distilled water only. A few experiments were done with organisms in one-litre plastic stoppered bottles tied to the side of floating jetty in Saanich inlet. Most experimental containers were placed in trays in incubators held for other reasons at 9°C, 13°C or 16°C or at room temperature (about 22°C). Whenever possible, the containers were placed on a slowly-reciprocating shaker table. Experiments lasted from a few minutes to several hours. Food particles of laboratory origin were dispensed into the experimental containers from single-species stock cultures with Eppendorf micropipettes or small volume glass

pipettes. The numbers and average volumes of the cells in these stock cultures were measured with the Coulter Counter from 1/100 dilutions immediately before the experiments. In many of the experiments, tintinnids were gently pipetted onto glass slides for the examination of their food contents with a high-power microscope at intervals or at the end of the experiment. As these tintinnids were thereby killed, it was impossible to make repeated observations on the same organisms and thus each sample was taken as representative of the experimental population at that time. On occasions, sub-samples of tintinnids taken at intervals were fixed and preserved for 1 or 2 days in formaldehyde before examination, but this was limited to a minority of experiments involving food organisms that were easily distinguishable when preserved.

(ii) Counts of accumulated food

The food contents of live microzooplankton were estimated from cells immobilized by coverslip pressure in small volumes of water under thin cover slips on glass slides. Eventually ciliary beating in these cells ceased, and cell lysis began. Larger organisms such as rotifers were often squashed by this procedure, and tintinnids were often extruded from their loricas. The cell plasma membrane of extruded cells did not necessarily break, nor did cell lysis occur immediately in squashed organisms. The cell contents of tintinnids with non-transparent loricas often could not be seen clearly unless some extrusion of the cell from the lorica had taken place. Also, protozoa containing many food items could only be clearly examined after some extrusion and flattening had occurred. The estimation of the proportion of ingested food items which had undergone digestion was somewhat subjective under these circumstances. However, after considerable experience it became clear that undigested food items did not change rapidly in appearance until after tintinnid cell lysis began, and the latter followed by several seconds the

the complete cessation of motion of the tintinnid adoral cilia. Therefore, 'semi-digested' cells were considered to be those appearing distorted in shape, changed in colour, reduced in size, etc., before the ciliary organelles stopped beating. A partially digested food item can be confused with an undigested item of smaller size and different shape, and discrimination between the two was entirely subjective and based on previous experience. This problem was naturally most difficult when natural food items were examined, particularly when they were difficult to relate to identifiable items in the environment.

The cell structures most resistant to the digestive enzymes in the food vacuoles of tintinnids included the siliceous cell walls of diatoms, the cellulose thecae of dinoflagellates, and the carotenoid-lipid 'eyespots' of some flagellates. These are probably all egested eventually having undergone little digestion. Of these structures, only the reddish (and often clumped) eyespots could be sometimes confused with other small whole food items. It is interesting that one (but apparently only one) local ciliate, a species of the Oligotrich genus Strombidium, seems to retain these algal eyespots for its own use (Blackbourn et.al., 1973). These clumped eyespots might in some future work prove to be useful long term markers of the rates of ingestion and digestion of certain food items. This would be best carried out in conjunction with observations with the electron microscope, which was impossible to use in this study.

(iii) Observations of feeding behaviour

Most observations were made with a Mark III Zeiss Stereomicroscope fitted with a zoom focussing control and sub-stage illumination. The range of total magnification was x4 to x40. The tintinnids swam freely in shallow Petri

dishes placed on the microscope stage and containing 10 to 15 ml of seawater to a depth of 0.7 to 1.0 cm. The transmitted double light source was calibrated with a Lightmeter (Photovolt Corp.) equipped with neutral filter no. 3. For most observations the light intensity at the microscope stage was approximately 2,000 Lux. The light passed through a heat filter but seawater in the Petri dish would warm from about 10 C to about 20 C in about 30 minutes. Therefore, tintinnids and/or seawater were taken from insulated containers for short observation periods only.

Tintinnids showed little apparent reaction to the illumination, and at allllight intensities tended to move upwards to the water surface unless under obvious physiological stress. There is little or no difference in the food accumulated by tintinnids in strong, dim or no light. This has been shown in experiments (see Section 4a); and in samples from Coal Harbour where the food contents of tintinnids taken at dusk and again at dawn, showed essentially no differences. Goulder (1973) also found no diurnal periodicity of feeding in the freshwater planktonic ciliates Loxodes striatus and Loxodes magnus. Therefore, it is assumed that the intensity of light had no effect on tintinnid feeding behaviour during these observations (but see Results in Section 4b).

The zoom rapid focussing control was essential for closely following a particular individual tintinnid, as it changed direction frequently and rapidly and moved in shallow helices. The right hand was used to control the focus and the position of the Petri dish on the microscope stage, and the left hand controlled 2 stopwatches and a counting device. Events were recorded as follows: the total length of observation of a particular tintinnid (a 'run') was timed with stopwatch a), and the duration of one event

of interest (e.g. the 'handling' of a food item by the tintinnid) during a 'run' was timed with stopwatch b). The counter was used to record a) the number of apparent particles contacted by a tintinnid per run, and b) the number of such contacts which resulted in ingestion by the tintinnid. The smallest particle that could be detected and its fate clearly followed, was of approximately 4 µm diameter (but see Section 4a and 4 b). The stopwatch and counter records were noted at the end of each run and they were reset. When possible, 5 to 10 individuals of each species were observed one at a time until their behaviour changed drastically, e.g. by staying at the bottom or at the water surface of the dish.

Occasionally, after a 'run', the tintinnid was placed on a slide for examination of the food contents at high magnification. Where a particle was large enough to be seen during ingestion; or large enough to cause the tintinnid to stop moving or to change direction in order to handle it, whether by ingestion or eventual rejection, the event could be accurately recorded. However, some ingestion may have gone unrecorded. Very small or unfocussed items might well have been ingested with no overt behavioural change by the tintinnid; and in the opposite direction, minor changes in the angle of the path of tintinnid movement may not always have indicated ingestion or rejection.

(iv) Coulter Counter experiments

The method used is essentially similar to that described by Sheldon and Parsons (1967). A Model B electronic Coulter Counter was used with aperture tubes of 50 µm or 100 µm diameter orifices. The numbers and total volumes were calculated for particles of between 1.2 and 20.0 µm diameter. With this technique, the numbers of particles in each of a continuous series of arbitrary

size classes expanding geometrically, were multiplied by the average volumes (calculated as spheres) of each size class. Hence, the diameters corresponding to the average spheres in these size classes were as follows: 1.78, 2.24, 2.82, 3.57, 4.49, 5.66, 7.12, 8.98, 11.3, 14.3, and 18.6 µm. This total 'spectrum' covered the size range of most particles eaten by most tintinnid species in this study, but of course most natural particles are non-spherical. The use of a spherical average volume was unavoidable, but it should be noted that the actual dimensions of a food particle would be of importance to a tintinnid, particularly near the upper size limit of its feeding ability.

Counts were made on subsamples taken at the beginning and end of the experiments from both 'experimental' and 'control' containers and were designated as E_1, E_2, C_1 and C_2 respectively. Control containers were set up from field samples by passing 200 to 500 ml of the sample through nylon mesh of a size (usually 30 um for tintinnids) to exclude all predators, and incidentally also much large phytoplankton, usually diatoms. Unfiltered water, or water filtered through mesh of a size to exclude only predators larger than tintinnids, was used in the 'experimental' containers. The subsamples were slowly stirred during counting which took from 10 to 30 minutes to complete. Six replicate counts were taken in each size range, with a variance of 5 to 10% of the mean value for counts between 100 and 1000, and a variance of 10 to 20% of the mean for counts between 10 and 100. Counts were taken for 2 to 16 seconds, depending on the frequency of particles.

The accuracy of the estimation of particle volume by the counter was checked on a number of occasions by calibration with ragweed pollen of known size. The accuracy of the estimation of particle number was not checked, as all other counting methods were considered to be less accurate, and so has

been assumed to be absolute. For this reason perhaps, the Coulter Counter is best used for the estimation of relative changes in number, as in these experiments, rather than for counting the numbers of particles in a field sample. After the final Coulter count, the predators in the subsample from the experimental container were counted. The dead organisms were counted at x20 magnification on a squared Petri dish before the subsample was fixed. Immediately after fixation, all the organisms were counted, and the difference between the two counts was considered to be the livertotal. This was done for three 10 ml subsamples of the E_2 container, and the mean value calculated.

The volumes in each size class and in the total, were calculated for C_1, C_2, E_1, and E_2 with the use of a computer programme. This programme also tested the hypothesis of no difference between initial and final values in each size class ($\alpha = 0.05$). As the frequency of occurrence of a particle in seawater often decreases rapidly with increasing size, the counts in the largest size classes were relatively low and the values calculated were often not significant as a result. To count any size class for more than 16 seconds would have been unduly time-consuming, and longer counts were not made. This decision may have resulted in the underestimation of feeding rates on the largest size classes in some experiments. The total particle volumes for C_1 and E_1 never differed by more than 20%.

Two values for the feeding rate were estimated for reasons described below, but both calculations were made with an equation derived from those given by Frost (1972) and others. A combination of 3 equations in Frost (1972) (as modified by my notation) may be written as follows:

$$FR/P = \frac{E_1 \left(e^{(k-g)T} - 1\right) Vg}{T.(k-g).P} \qquad (1)$$

where FR/P = ingestion rate as cells eaten/predator/hour

P = number of predators in experimental container

V = volume of experimental container

k = algal growth coefficient in control container

g = grazing coefficient in experimental container

and T = duration of the experiment in hours.

Equation (1) can be written as:

$$FR/P = ((E_2-E_1)/(T.P.)).\ (\log 10\ (C_2/C_1)-\log 10\ (E_2/E_1))/\log 10\ (E_2/E_1)) \quad (2)$$

where FR/P = volume (μm^3) of particles eaten/predator/hour.

and P = number of predators/ml in experimental container.

It will be seen that equation (2) assumes that the grazing mortality in E, and the increase in numbers (if any) of the food organisms in both C and E is exponential. If these changes were linear in form the corresponding equation would be written as:

$$FR/P = (((C_2.E_1)/C_1)-E_2)/T.P \quad (3)$$

These two equation can give very different values for FR/P. The use of equation (2) will give lower values of FR/P than equation (3) when there is any (exponential) net increase in the control population during the experiment; equal values of FR/P when there is no net increase or decline in the control; and higher values of FR/P than equation (3) when there is a net decline in both the control and experimental containers.

Ideally, the form of the grazing mortality coefficient and the growth coefficient, should be estimated from samples taken from both C and E at frequent intervals throughout an experiment (see Frost, 1972). This is not

feasible with slowly feeding organisms such as tintinnids. Alternatively, there should exist some independent estimate of the maximum feeding rate of the organism under conditions similar to those pertaining in the experiment. Unfortunately, there was little reliable data of this type available in this study (see Section 4b). The particle concentration (number or volume/ml) at which an organism reaches its constant maximum ingestion rate at a given temperature and for a particular type of food, is termed in this study the 'optimal food concentration' (OFC). This change in rate may be abrupt or gradual.

The correct choice of the method of calculation of feeding rates relies upon a knowledge of the OFC. Most invertebrate filter-feeders are generally assumed (until behavioural or selection experiments are done) to sample their environment passively and completely, under 'normal' circumstances. That is, contact is made with food items and they are all eaten, at a characteristic constant rate at a given temperature. This leads to an exponential rate of decline of a non-growing population of food cells, and equation (2) may then be used to calculateffeeding rates. At any food concentration above the OFC below some inhibitory level, the organism will feed at its maximum rate no matter what the concentration, and the latter will decline slowly and linearly. In such circumstances, equation (3) may be used to calculate feeding rates. If the population of grazed food items decreases from a concentration above the OFC to a concentration below the OFC during the experiment, then a linear rate of decline will be followed by an exponential rate of decline.

The form of the natural rate of increase in number of a growing population of cells can be linear, exponential or hyperbolic, depending upon the environmental conditions and internal physiological state of the cells. When

cell growth is rapid, the exponential form of population increase is most likely, and has been assumed to be true in all these experiments. Hence the use of equation (2). Some of the results indicate a posteriori that the OFC had not been exceeded in these Coulter Counter experiments, and that therefore the choice of equation (2) had been correct (but see Section 4a). If any size and/or taxonomic group of phytoplankton reproduced so rapidly during the experiment so as to push the total particle volume in the experimental vessel temporarily over the OFC level for a tintinnid species, the latter may have altered its feeding behaviour in response, thus increasing the likelihood of poor correlations between the calculated feeding rate and the logmean experimental total food volume (see Section 4a and General Discussion).

The value of the total feeding rate (FR/P) for each experiment was initially calculated as the sum of negative and positive FR/P values in each size class. This calculation, 'net total consumption' (or NTC), gave anomalous positive values in several experiments. That is, in those experiments the predators appeared to make a net addition of particles to the medium relative to the control. Poulet (1974) also found positive values in some experiments using the Coulter Counter. There are a number of possible explanations for such results which include (1) contamination of the experimental container (only) with extraneous particles during the experiment; (2) the effect of predators on a) resuspending sedimented particles; b) increasing the growth of algae in some size classes by the excretion of NH_3, etc.; c) increasing the growth of algae in some size classes by selectively removing other algae which are competing with them for scarce nutrients; or d) creating larger or smaller particles by clumping or comminution from those particles that they attempt to ingest. Most of the Coulter Counter experiments were too lengthy (20 to 52 hours) to rule out any of these possibilities, although (2) b) and

(2) c) seem the most likely. In many experiments relative particle removal (consumption) was demonstrated in all or most size classes, and in the remainder no net change in total volume was seen. The possibilities mentioned above may apply even in experiments where net total consumption occurred. Also, a particular size class may have had better growth or less mortality by chance in the experimental container than in the control container.

Food selection experiments (see Section 4a) have indicated that some items may not be eaten at all by some tintinnids, and that other items may be eaten to varying degrees. This may be reflected in those size classes which show no relative change between the control and experimental containers. It must be remembered that the size classes used are arbitrary, and that natural or laboratory food items of one species may spread over several Coulter size classes. One size class may also contain several different species of food item, especially in natural samples. All in all, the calculated (NTC) values of FR/P may represent <u>minimal</u> net values of consumption by tintinnids, but reasonably reflect their overall total effects on natural phytoplankton populations. This may be true even in those experiments where all size classes show net consumption, if some food items in those size classes are at the same time unaffected by tintinnid feeding. To obtain values for FR/P close to the <u>maximum</u> possible for all experiments it was also calculated as the total of all negative (consumed) values <u>only</u>, and these values were designated as 'edible spectrum only' (or ESO). Multiple correlation coefficients were calculated separately for NTC and ESO values, for 10 variables associated with these experiments (see Section 4c).

One of the variables expected to be strongly correlated with values of FR/P was C_2/C_1, or the growth rate of the control population, which is assumed

to be also the potential growth rate of the populations of food cells in the experimental container. This assumption is least justified in the longest experiments. Also, C_2/C_1 values are the mean of the total spectrum, and these would not necessarily correlate well with total FR/P values calculated over the whole spectrum. As a check on the possibility that the 'feeding size-spectrum' of tintinnids is enlarged when less total food is available, i.e. that they become less 'selective' when 'hungry', the number of Coulter size classes showing net consumption for each experiment (ESP) was included as a variable (4) in the calculation of correlation. Variable (3) in Table 27 is 'logmean E' - which is considered to be the mean value of total food available to the predator during the experiment, adjusted to an experimental duration of 24 hours. This value is transient and for long experiments with large changes in C and E particle concentrations it is also arbitrary. It was calculated as follows:

$$\text{logmean } E = \frac{E_2 - E_1}{\text{Log}_n E_2 - \text{Log}_n E_1} \qquad (4)$$

The use of this equation gives very similar results to that of equation (3) in Frost (1972).

GLOSSARY

C_1 and C_2 - the totalainitial and final particulate volumes from 1 to 20 μm in the control vessel.

E_1 and E_2 - as above for the experimental vessel.

FR/P (or FR) - individual feeding rate in numbers of cells or μm^3/predator/hr or as equivalent ml/pred/hr.

OFC - optimum food concentration - the food concentration at which the feeding rate of a predator is at, or close to, maximum.

NTC - net total consumption - the total feeding rate (FR/P) from all size classes measured, including net additions or losses of particle volume.

ESO - edible spectrum only - the total feeding rate (FR/P) from only those size classes showing net losses of particle volume (Consumption).

C_2/C_1 - index of increase of total particle volume in the control vessel during the experiment.

ESP - edible spectrum portion - the number of size classes in an experiment which showed net losses of particle volume.

Logmean E - logarithmic mean value of particle volume available to the predator.

Electivity index - An index of proportionality of ingestion of a particular item in the diet compared with its abundance in the medium.

Differential Predation - the difference between the electivity indices of various prey types with no comparison with a single-prey situation. No selection or preference is inferred.

Negative Selection - where a food type has a neutral electivity index in one situation and a strongly negative index in another situation where more prey types are involved. However, where all prey types show a more negative index when presented together than when presented with fewer other prey types, then the cause may lie in the fact that the total prey concentration is now above the OFC for that predator. In long experiments apparent feeding selection may be the result of differences in prey digestibility.

Loss Rates - the rate of apparent disappearance of food from tintinnids in μm^3/pred/hr.

Search Rate - the theorectical rate at which the medium is thoroughly searched by a predator in ml/pred/hr.

Contact Rate (CR) - the rate at which a particular concentration of prey is contacted by a predator in nos/pred/hr or equivalent ml/pred/hr.

Control of Phytoplankton Growth - when $\frac{E_2}{E_1} < 1$ and $\frac{C_2}{C_1} > 1$ overall, as the net result of relative total particle volume changes in 24 hours.

4) RESULTS AND DISCUSSION

a) Accumulation Experiments

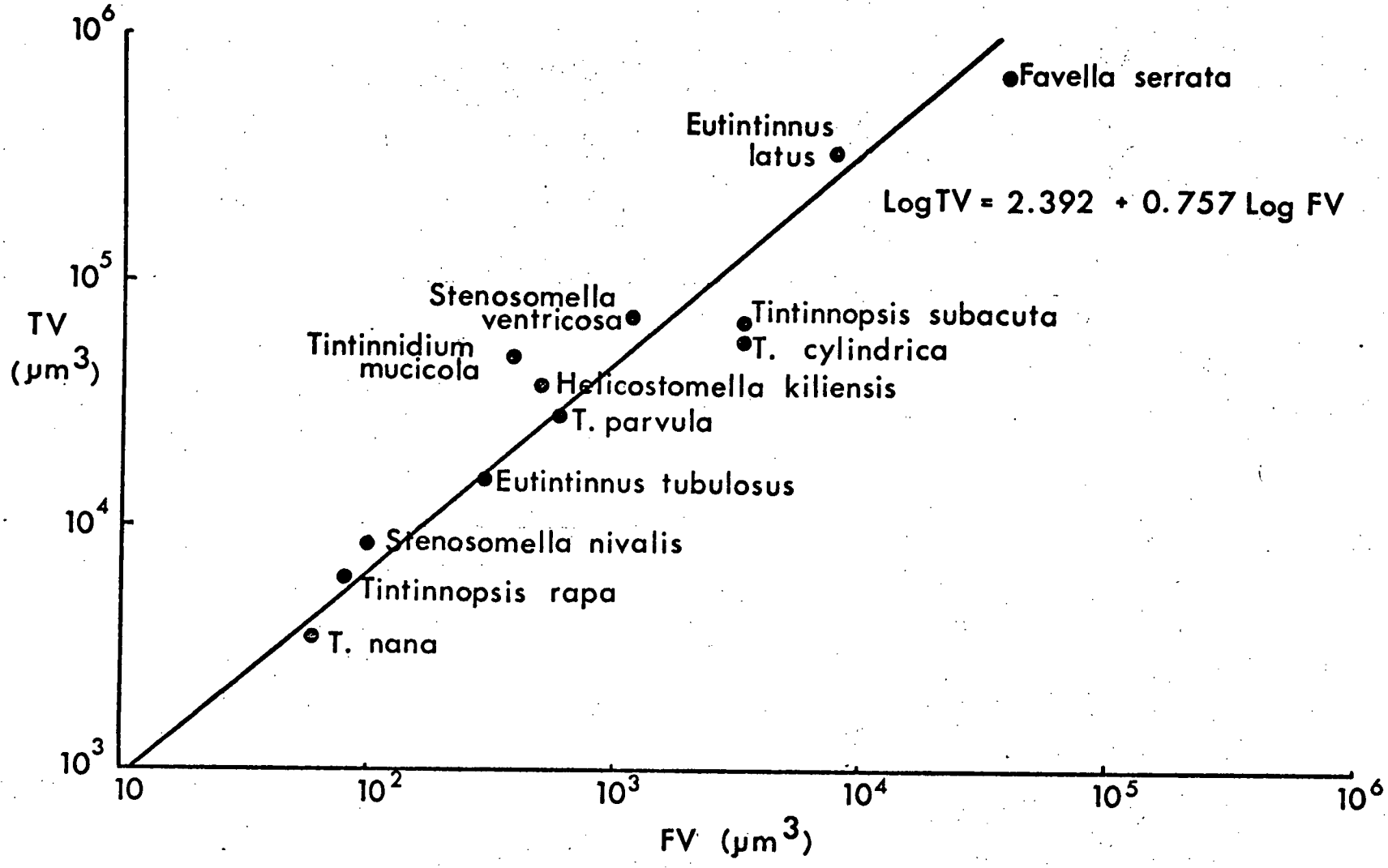
(i) Qualitative Results

Table 1 presents some of the cell measurements of the tintinnid species studied; and from this table the relationship between the volume of the largest single contained food item, whether identified or not, and the maximum estimated volume of the tintinnid cells is shown in Figure 5. In almost all cases, the maximum volume of tintinnid cells refers to the maximum size of the parental cell just before division. The minimum volume of the resulting daughter cells will be about half the volume of the parental cell. A two-fold difference in the cell volume of a species will alter Figure 5 very little. In Figure 5 the relationship is described by the equation: log tintinnid volume (in μm^3) = 2.392 + 0.757 log food volume (in μm^3). The significance of this generality is unknown. The species whose value falls furthest from the line is Tintinnidium mucicola. Other unusual features of the feeding behaviour of this species will be discussed later. There appears to be no absolute minimum food size for tintinnids (see Table 2) unlike other zooplankton (Parsons, et.al., 1967; Poûlet, 1973); but very small food items may be eaten in equal or greater proportion to their abundance much less consistently than larger items, by at least one species of tintinnid (see Section 4c). As a field sample may contain up to ten species of tintinnids, the size overlap in their feeding may be considerable. Those tintinnid species in the narrow range of volumes between 3 and 10 x 10^4 μm^3 show almost no relationship between cell volume and volume of largest food item. For example Tintinnopsis subacuta is less than twice as large as Tintinnidium mucicola, but the difference in the volume of their largest food item is almost tenfold. The largest item seen inside both Tintinnopsis subacuta and

TABLE I. List of Tintinnid species and their cell measurements.

Species	Lorica Dimensions (µm) Diam.	Length 'Ave.'	Length Max.	Maximum Cell Dimensions (µm) Diam.	Length	Cell Volume (µm)	Length of Adoral Cilia (µm)
Eutintinnus latus	75	200	250	70	200	5×10^5	35
E. tubulosus	25	100	150	20	100	2.5×10^4	20
Favella serrata	120	250	250	100	200	8×10^5	50
Helicostomella kiliensis	30	150	250	25	100	4×10^4	30
Ptychocyclis acuta	70	100	100	60	80	---	--
Stenosomella ventricosa	70	90	100	50	100	8×10^4	50
S. nivalis	30	50	50	25	30	8×10^3	30
Tintinnidium mucicola	45	150	350	35	60	5×10^4	30 (thin)
Tintinnopsis subacuta	45	100	160	40	80	7×10^4	35
T. cylindrica	40	160	220	35	90	7×10^4	35 (thin)
T. parvula	35	80	150	30	70	3×10^4	35
T. rapa	25	60	75	20	40	6×10^3	10
T. nana	20	40	60	15	25	3×10^3	10

Figure 5. Relationship between tintinnid cell volume (TV) and maximum observed volume of individual food items (FV).


10^6
10^5
10^4
10^3
TV
(μm^3)
Favella serrata
Eutintinnus
latus
LogTV = 2.392 + 0.757 Log FV
Stenosomella
ventricosa
Tintinnopsis subacuta
Tintinnidium
mucicola
T. cylindrica
Helicostomella kiliensis
T. parvula
Eutintinnus tubulosus
Stenosomella nivalis
Tintinnopsis rapa
T. nana
10
10^2
10^3
10^4
10^5
10^6
FV (μm^3)

Tintinnopsis cylindrica was Tintinnopsis nana, during a 'bloom' of the latter. These medium-large species are probably the most important of all tintinnids in their grazing effects on phytoplankton for most of the year.

The results of qualitative and quantitative tests of the feeding abilities of tintinnids on known food items are presented in Table 2. In this table also the approximate value of the upper food size boundary and the complete lack of a lower food size boundary is evident. In comparison the freshwater ciliate Stentor coeruleus ($\sim 2 \times 10^8 \mu m^3$) eats prey ranging in size from bacteria to fellow Stentors (D.J. Rapport - personal communication). Table 2 also shows the wide range in quality of the particles eaten by tintinnids. Living and inert items are ingested by all species for which they are not too large. Willow (Salix) and Yew (Taxus) pollen, wine yeast cells and corn starch granules are all at least partly digested by those tintinnids which ingest them. Latex spheres are not digested, but are compacted in large boluses in the cell after one or two hours. The only potential food items to which healthy animals show no apparent feeding reaction are the colourless flagellates and bacteria which are present in large numbers in crowded net field samples full of dead and moribund zooplankton. However, tintinnids are often seen to violently reject particles which are small enough for them to ingest and which appear innocuous to the observer. Several species of laboratory phytoplankton are shown in Table 2 as 'variably' eaten by tintinnids, particularly: Pyramimonas c.f. grossii, Pavlova gyrans, and Prymnesium parvum. In most cases these species were not eaten when used in experiments in heavy final concentrations ($>10^4$ cells/ml) or from old (about 1 month) stock cultures. 'Always' and 'never' eaten refers to at least three tests at moderate ($<10^4$/ml) concentrations. Such species as Monochrysis

TABLE 2. Food eaten by microzooplankton. E = always eaten; V = variably eaten; N = never eaten; blank = untested.

FOOD			MICROZOOPLANKTON																	
PHYTOPLANKTON			Tintinnids												Others					
SPECIES	CLASS	Vol. (μm^3)	T. nana	T. rapa	S. nivalis	E. tubulosus	T. parvula	H. kiliensis	T. mucicola	T. cylindrica	T. subacuta	S. ventricosa	E. latus	F. serrata	Prorodon sp.	Synchaeta sp.	S. littoralis	Pseudocalanus minutus N III & IV	Barnacle nauplii
Micromonas sp.	Prasinophyceae	3	V	E	E		E	E			E	E							
Unidentified	Blue-green Bacterium	20									E								
Monochrysis lutheri	Haptophyceae	50	V	V	E	E	E	E	V	E	E	E	E	V		E	E	E	E
Isochrysis galbana	Haptophyceae	50	N	V	V	E	E	E	V	E	E	E	V	E	N		E	V	E
Coccolithus huxleyi	Haptophyceae	60								E	E	E		E					
Thalassiosira pseudonana	Bacillario-phyceae	60									E		E						
Isoselmis sp.	Cryptophyceae	75	N	N	V	E	V	E	E		E	E		V					
Plagioselmis sp.	Cryptophyceae	130	N	N	N	V	V		E	V	E	E	V						
Phaeodactylum tricornutum	Bacillario-phyceae	130							N		V	V						V	E
Pyramimonas cf. grossii	Prasino	140					V		N		V	V							
Pavlova gyrans	Haptophyceae	150					V	V	N		V	V							
Prymnesium parvum	Haptophyceae	150				N	V	N	V	N	V	V	N	V	N		V		
Dunaliella tertiolecta	Chlorophyceae	200	N	N	V	E	V		N	E	E	E	E	E	N	E	E		E
Platymonas maculata	Chlorophyceae	300			N	V			N	E	E	E	E	E		E	E		
Cryptomonas minuta	Cryptophyceae	450	N			N	V	E	V	N	E	E		E	N				
Pseudopedinella pyriformis	Chrysophyceae	450	N	N		V	N	E	N	V	V	V							
Eutreptiella sp.	Euglenophyceae	500	N	N	N	N	V	E	N	N	E	E	V	E	N	N	E	V	E
Amphidinium carterae	Dinophyceae	800					V		N	V	V			E			E		E
Cryptomonas profunda	Cryptophyceae	1200					N	V	N	N	E	E	E	E					
OTHER	FOOD																		
Kaolin		1-4	E						E		E								
Polystyrene	Latex	0.5	V				E		E		E	E					E		
Polystyrene	Latex	17	N	E			E		V		E	E					E		
Polystyrene	Latex	380					E				E	E		V			E		
Polystyrene	Latex	3000									V	V					E		
Salix and Taxus	Pollen	1-3000					V				V	V	E	N			V	N	
Yeast cells		50-3000									V	V					E		
Starch grains		30-3000					E		V		E	E							

lutheri, Isochrysis galbana, Dunaliella tertiolecta and Eutreptiella sp. were eaten in almost any concentration or condition by most species; and consequently the latter were much used in the quantitative experiments on feeding and loss rates and feeding preferences, described in Section 4a (ii). Tintinnidium mucicola and Eutintinnus latus showed anomalous feeding preferences or abilities for tintinnids of their size, (see Table 2) and these abilities have been examined experimentally (see Sections 4a and 4b). In the majority of field samples Tintinnidium mucicola contained food items of 5 to 10 µm diameter which mostly had the appearance of cryptomonad cells or chloroplasts. Many of the quantitative accumulation experiments in Section 4a are concerned with the apparently selective feeding behaviour of the common group of species of middle size: Tintinnopsis subacuta, T. cylindrica, Stenosomella ventricosa and Tintinnidium mucicola.

Whether tintinnids and other zooplankton can or do ingest bacteria and/or detritus is a question of some importance to an understanding of the survival of zooplankton in food-poor situations; such as in some tropical seas, below the euphotic zone, or in winter in high latitudes. Almost all of these tintinnid species including the largest were seen to contain a few bacteria and small detrital particles, most usually in conditions where concentrations of phytoplankton were fairly low. This question requires a great deal more study. Tintinnopsis nana and T. rapa must almost certainly depend upon bacteria and phytoplankton of less than 44µm diameter for their particulate nutrition, since they appear to eat nothing much larger than this. It was unusual to find either of these species in a field sample to contain any visible food items. However, T. nana was frequently very numerous (>15/ml) in this study, but even then appeared to contain little food. It is possible that T. nana and T. rapa obtain food from organic material, either dissolved

or more likely absorbed into very small particles of detritus. Useful dissolved material may be in fairly high concentrations in this area, but since T. nana rarely contains particles, and 'contacts' a very small volume of water and number of particles in an hour (see Section 4a), this source of nutrition is also dubious. The lorica of Tintinnopsis nana is normally covered with small particles of inorganic detritus, as are the loricas of all the members of that genus. When T. nana is ingested by larger tintinnids or other predators much of the detritus inside the latter can be attributed to this source, and not to the ingestion of individual small particles.

An indication of the permeability of the plasmalemma of tintinnids to dissolved substances was obtained by adding large amounts of (a) neutral red and (b) neutral red and methylene blue dyes to a field sample. Two hours later the tintinnids Tintinnopsis subacuta, Stenosomella ventricosa and Tintinnidium mucicola were seen to have dye only inside food vacuoles containing food items. The food items and possibly also the soluble contents of the food vacuoles, were stained. The degree of staining of the Oligotrich ciliates in the sample was uncertain. Dinoflagellate cells were generally but faintly stained, and Rotifers showed staining only in the epithelial cells. Copepod adults and nauplii and gastropod larvae were generally and heavily stained. These results indicate that the cells of some tintinnid species are surprisingly and relatively impermeable to some dissolved substances. Tintinnids in this area are extremely euryhaline, but the contribution of the relative impermeability of the plasmalemma to this euryhalinity is not known. Unlike some estuarine and brackish-water ciliates, tintinnids have no apparent vacuole to aid in osmoregulation.

Centric diatoms dominate the larger phytoplankton in the Vancouver area

except in mid-summer. The only diatoms seen inside tintinnids from field samples were occasional small pennate diatoms, probably of the genus Nitzschia; and single cells of the small centric diatom Skeletonema costatum. Even small diatoms usually occur in chains of cells and consequently are too large for tintinnids to ingest. Diatoms thus form part of planktonic food chains which overlap in size those containing tintinnids, but which are independent of them. However, larger zooplankton eat both diatoms and tintinnids. The largest food items contained in Favella serrata and Eutintinnus latus are always dinoflagellates of various species. Estimates of the 'electivity' or apparent differential selection of food items of various types are given in Sections 4a and 4b. The Rotifer species (mostly of the genus Synchaeta), copepod and barnacle nauplii, and gastropod larvae were apparently similar to tintinnids in being generally unselective predators (Table 2). The large holotrich ciliate Prorodon sp. was the only non-tintinnid ciliate, which did not appear to eat laboratory phytoplankton. However, despite the fact that this species is quasisymbiotic (Blackbourn et.al., 1973), on one occasion it contained several 9.5 μm diameter polystyrene latex particles and one Tintinnopsis nanaccèll.

a) Accumulation experiments

(ii) Quantitative Results

General

Tables3 to 24 show the results of a variety of feeding experiments and associated experiments of a similar nature. In most cases experiments were done with modified natural samples. Such samples usually contained a preponderance of 1 or 2 species of tintinnid and a few individuals of several other species. Since there is no other quantitative data on tintinnid feeding, the results of all species encountered in an experiment have been given in Tables 3 to 24 however small the number of cells involved. The simplest experimental results are shown before the more complex; both in terms of objectives e.g. comparisons of the relative selection of several prey species, or estimating only uptake rates of simultaneous uptake and loss rates; and also in terms of the number of tintinnid species per experiment. In several selection experiments, the tintinnids in some sections died or were moribund, leaving the results incomplete.

The method of 'scoring' used was one in which the number of cells of a particular food type accumulated in each tintinnid cell since the start of the experiment, or since the last sub-sample of tintinnids, was counted. Unless otherwise noted, the sub-samples were not preserved and counted later (see Methods Section), so there is in most cases an unavoidable lag in the timing of sub-samples taken from otherwise comparable treatments.

For the most of the experiments, a one-way anaalysis of variance was performed together with Scheffe's test for multiple comparisons with unequal sample sizes amongst all 'levels' in the experiment. The levels are identified in each Table by a small ringed number. To obtain homogeneity of

variance amongst the mostly small and highly variable levels, a log 10 transformation was made of each food cell count, after 1.0 had been added to each value to avoid zero values. In each Table, the result of the one-way analysis of variance is represented by the F-value and its significance level. Only those (Scheffe's) comparisons between levels which had a probability of less than 0.05 of being the same, are shown in the Tables. Little emphasis has been placed on directly comparing or condensing results on the same species of tintinnid from different experiments, particularly if long periods of time separate the experiments. This is because of the apparent sensitivity of tintinnids to environmental factors other than food, and the large between- and within - experiment variability in feeding rates. The probable causes of variability in tintinnid feeding rates are discussed later in this Section. Apparently recurring phenomena are discussed although the Scheffe's comparisons in any one experiment on which they are based may not show a significant difference.

One predator type and one prey type

Tables 3 to 6 show the results of simple experiments involving only one predator type and one prey type but with more than one concentration of food used. The feeding rates (in ml/hr/tin) of Eutintinnus tubulosus and Tintinnopsis parvula were extremely low (<0.0001) in these experiments even at high food concentrations, in one case in excess of 73×10^3 cells/ml. This was probably because the experiments lasted more than 3 hours, by which time a possible 'steady-state' had been reached between food eaten and food lost or digested. The calculation: accumulated food cells/time did not then accurately represent a feeding rate.

Table 3 shows that there was no significant difference between the cells

TABLE 3. Eutintinnus tubulosus feeding on Isocrysis galbana at two concentrations. Temperature 18°C; Salinity 11.5‰.

Duration (hrs)	Numbers of prey examined	Numbers of prey/ predator	Percentage of prey digested	Volume of prey/ predator	Numbers of prey/ml.	FR nos./hr/ Tin.	FR ml/hr/ Tin.
3.7	5	15.4 ± 5.1	21	770	53, 400	4.2	0.00007
3.0	6	21.3 ± 9.0	27	1065	73, 600	7.1	0.00009

One-way ANOVA		Comparisons (Scheffés Test) with a significant difference at .05 level
F value	Significant	
1.28	No (.05)	Nil

TABLE 4. Eutintinnus tubulosus feeding on Monochrysis lutheri at two concentrations. Temperature 17°C; Salinity 9.5‰.

Duration (hrs)	Numbers of prey examined	Numbers of prey/ predator	Percentage of prey digested	Volume of prey/ predator	Numbers of prey/ml	FR nos./hr/ Tin.	FR ml/hr/ Tin.
4.0	6	16.8 ± 6.9	15	840	4, 600	4.2	0.0009
5.0	7	17.7 ± 5.9	14	885	21, 000	3.5	0.00016

One-way ANOVA		Comparisons (Scheffés test) with a significant difference at .05 level
F value	Significant	
0.02	No (.05)	Nil

accumulated per tintinnid by Eutintinnus tubulosus in 3 to 3.7 hours at two high but very different concentrations of Isochrysis galbana. Likewise, in Table 4 E. tubulosus accumulated a similar number of Monochrysis lutheri cells at two very different concentrations in an experiment lasting 4 to 5 hrs. Obviously some sort of nutritional steady-state had been reached in both the experimental results shown in Table 3 and 4, and it is also possible that 4,600 M. lutheri cells/ml is approximately an optimal food concentration (OFC- see Methods Section) for E. tubulosus. The very high food concentrations in Table 3 were probably inhibitory to the feeding of E. tubulosus. Again, in Table 5 it can be seen that E. tubuolsus accumulated its maximum prey cell number in less than 5.3 hours even at 9,000 cells/ml of M. lutheri, and that this maximum number was quite similiar to that in Tables 3 and 4. It is interesting that the percentage of prey cells undergoing digestion was fairly similar (14 to 31%) in all 3 experiments.

The number of cells of Monochrysis lutheri accumulated by Tintinnopsis parvula can be seen in Table 6 to be similar in 3 very different concentrations of food in experiments lasting 5 to 6 hours. The number accumulated at 23 to 28 hours after the start was also similar in the three food concentrations, and was much lower than at the 5 to 6 hours' check. This is probably due to reduced feeding activity caused by some physiological stress, as can be seen from the fact that T. parvula was less active in the later check. The digestion rate was apparently less affected by this possible stress. A much higher proportion of M. lutheri cells were undergoing digestion by T. parvula in the later check than in the earlier check. From Tables 5 and 6 it seems that T. parvula has an accumulated food maximum of about 20 cells of M. lutheri (at 9 or 10°C.) and that its OFC is below 7000 cells/ml of M. lutheri.

TABLE 5. Eutintinnus tubulosus feeding on Monochrysis lutheri at three concentrations. Temperature 16°C; Salinity 28‰.

Duration (hrs.)	Numbers of prey examined	Numbers of prey/ predator	Percentage of prey digested	Numbers of prey/ ml.	FR nos./hr/ Tin.	FR ml/hr/ Tin.
6.3	11	25.0 ± 6.6	20	9,000	4.0	0.00044
5.6	13	29.0 ± 10.1	28	18,000	5.2	0.00028
5.3	7	25.7 ± 10.2	31	72,000	4.9	0.00006

One-way ANOVA		Comparisons (Scheffes Test) with a significant difference at .05 level.
F-value	Significant	
0.64	No (0.05)	Nil

TABLE 6. Tintinnopsis parvula feeding on Monochrysis lutheri at three concentrations. Two samples taken from each. Temperature 9°C; Salinity 24‰.

Duration (hrs)	Numbers of prey examined	Numbers of prey/ predator	Percentage of prey digested	Numbers of prey/ml.	FR nos./hr/ Tin.	FR ml/hr/ Tin.	Tin. condition	Tin. Dividing
6.5 ①	9	21.3 ± 6.5	6	14,000	3.3	0.0002	Active	Nil
28.0 ②	3	6.7 ± 4.7	50	14,000	---	---	Slow	Nil
6.0 ③	16	18.6 ± 7.7	6	29,000	3.1	0.0001	Active	Nil
28.0 ④	10	5.4 ± 3.6	35	29,000	---	---	Slow	Nil
5.0 ⑤	10	28.7 ± 12.1	18	73,500	5.7	0.00007	Active no granules	2
23.0 ⑥	11	6.6 ± 6.2	64	73,500	---	---	No or few granules	Nil

One-way ANOVA		Comparisons (Scheffes Test) with a significant difference at .05 level
F-value	Significant	
10.10	Yes (.01)	1/4, 1/6, 3/4, 3/6, 4/5

From Tables 3 to 6 it can be seen that optimal food concentrations (i.e. optimal for maximum feeding rate) for the medium-sized tintinnids Eutintinnus tubulosus and Tintinnopsis parvula seem to be less than 4,000 cells/ml of small prey species of about 50 um^3 volume. Steady-state feeding rates under these conditions were reached in less than 3 hours and the equivalent maximum number of prey/tintinnid was about 20 to 30 or about 1,000 to 1,500 um^3.

Table 7 shows the result of the only factorial design among the accumulation experiments. It involved Tintinnopsis subacuta feeding on Dunaliella tertiolecta. Samples were taken at three times after the start; at 0.66 hrs, 1.5 hrs and 6.0 hrs; at three temperatures: 10.0, 13.2 and 19.8 C; and at three concentrations of food: 1,750, 8,700 and at 43,400 cells/ml. The sampling was staggered in the same order and for the same length of time across temperatures and food levels at each time check; and samples were immediately added to formaldehyde to a final concentration of about 2%. Adherence to this procedure made possible the removal of as much sampling bias as possible. The variance across the 3 food levels was by far the most significant, followed by that in the interaction between temperature and food level. Variance across the three levels of time and in the interactions between all 3 factors was significant at the .05 level. Variance across the levels of temperature and between time and temperature was not significant at the .05 level. It might be true to say that food level is the most important variable of these to T. subacuta, followed by temperature and time. T. subacuta would never be subjected to a temperature as high as 19.8 C in a natural situation; nor is it likely to be presented with as many as 43,400 cells/ml of one species of natural food. It is interesting that the percentage of semi-digested cells was greater at 19.8 C than at the lower temperatures, especially at the lower food levels. It will also be seen in other

TABLE 7. Tintinnopsis subacuta feeding on Dunaliella tertiolecta (210 μm^3) at three temperatures and three food levels. Formalin used. Salinity 9‰ dark.

Duration (hrs)	Predator	Number predators examined	Temp. °C	Number prey/ predator	Percentage prey digested	Volume prey/ predator	Number of prey/ml	FR nos./hr/ Tin.	FR ml/hr/ Tin.
0.66	T. subacuta	8	10.0	3.4± 2.6	Nil	714	1, 750	5.2	0.0030
1.5	T. subacuta	2	10.0	1.5± 0.7	Nil	315	1, 750	1.0	0.00057
6.0	T. subacuta	3	10.0	4.3± 3.1	62	903	1, 750	---	---
0.66	T. subacuta	12	13.2	7.5± 3.5	Nil	1, 575	1, 750	11.4	0.0065
1.5	T. subacuta	3	13.2	7.3± 4.5	Nil	1, 533	1, 750	4.9	0.0028
6.0	T. subacuta	3	13.2	3.3± 1.6	50	693	1, 750	---	---
0.66	T. subacuta	9	19.8	1.0± 1.4	Nil	210	1, 750	1.5	0.00087
1.5	T. subacuta	4	19.8	3.5± 2.9	79	735	1, 750	2.3	0.0013
6.0	T. subacuta	6	19.8	2.5± 6.1	80	525	1, 750	---	---
0.66	T. subacuta	8	10.0	6.6± 4.3	11	1, 386	8, 700	10.0	0.0012
1.5	T. subacuta	5	10.0	12.8± 4.8	13	2, 688	8, 700	8.5	0.0010
6.0	T. subacuta	7	10.0	12.0± 8.3	18	2, 520	8, 700	---	---
0.66	T. subacuta	4	13.2	7.0± 4.2	11	1, 470	8, 700	10.6	0.0012
1.5	T. subacuta	4	13.2	13.0± 7.9	Nil	2, 730	8, 700	8.7	0.0010
6.0	T. subacuta	3	13.2	8.0± 5.6	83	1, 680	8, 700	---	---
0.66	T. subacuta	6	19.8	9.3± 8.6	14	1, 953	8, 700	14.1	0.0016
1.5	T. subacuta	3	19.8	24.0± 6.9	54	5, 040	8, 700	16.0	0.0018
6.0	T. subacuta	9	19.8	15.9± 9.0	68	3, 339	8, 700	---	---
0.66	T. subacuta	5	10.0	23.4± 7.2	10	4, 914	43, 400	35.5	0.00082
1.5	T. subacuta	9	10.0	24.3± 6.6	11	5, 103	43, 400	16.2	0.00037
6.0	T. subacuta	3	10.0	16.0± 5.3	50	3, 360	43, 400	---	---
0.66	T. subacuta	9	13.2	17.6± 6.6	4	3, 696	43, 400	26.7	0.00061
1.5	T. subacuta	7	13.2	19.9± 8.3	4	4, 179	43, 400	13.3	0.00031
6.0	T. subacuta	4	13.2	32.5±14.8	45	6, 825	43, 400	---	---
0.66	T. subacuta	8	19.8	11.1± 8.0	11	2, 331	43, 400	16.8	0.00039
1.5	T. subacuta	3	19.8	19.7± 3.1	42	4, 137	43, 400	13.1	0.00030
6.0	T. subacuta	3	19.8	26.3±16.2	61	5, 523	43, 400	---	---

Analysis of Variance for 3x3x3 factorial on log-transformed values + 1.0

Interaction	F-value	Significant
Time	4.58	yes (.05)
Temperature	0.45	no
Time x Temperature	1.41	no
Food level	70.16	yes (.01)
Time x Food level	2.71	yes (.05)
Temperature x Food level	3.78	yes (.01)
Time x Temperature x Food level	2.42	yes (.05)

Tables that digestion rate appears to be more directly affected by temperature than does feeding rate.

Two or more predator types and one prey type

In Table 8 Tintinnopsis parvula and Tintinnopsis cylindrica were exposed to moderate numbers of Monochrysis lutheri at only one level (7,000 cells/ml) in dim light and also in darkness, both at 10 C. This experiment was much shorter than those shown inTable 3 to 6 and this is reflected in the small percentage of M. lutheri cells undergoing digestion (10% until after 1 hour). There was no significant difference between the accumulated cell number of T. parvula and that of T. cylindrica in darkness or in dim light (also see Methods Section). The maximum initial feeding rate of the two species in Table 8 - about 70 cells/hr/tintinnid or equivalent to about 1% ml/hr - was faster than those shown in Tables 3 to 6 and was the fastest feeding rate seen in these accumulation experiments. However, the maximum accumulation of prey cells was still only about 20 per tintinnid (see above).

In Table 9 two tintinnid species, Eutintinnus tubulosus and Helicostomella kiliensis, are compared when feeding on Monochrysis lutheri at 3 very dense concentrations. The accumulated food cell numbers are again typical of those in Table 3 to 6 in 41,400 cells/ml and in 107,000 cells/ml, and only lower and significantly different from these at 213,000 cells/ml. The contact rates (see Section 4b) of these species were concurrently observed in this experiment (Table 9), and this rate declined in H. kiliensis through a 5-fold increase in prey cell concentrations. The contact rate of E. tubulosus increased relatively less than did the prey cell concentration in the samples (Table 9). These very high levels of food cells (or their associated metabolites) were obviously close to the level at which the normal feeding

TABLE 8. *Tintinnopsis parvula* and *T. cylindrica* feeding on *Monochrysis lutheri*. in dim light and in darkness. Temperature 10°C; Salinity 23‰.

Duration (hrs)	Predator	Number predators examined	Number prey/ predator	Percentage prey digested	Volume prey/ predator	Number of prey/ml	FR nos./hr/ Tin.	FR ml/hr/ Tin.	Illumination
0.25	T. parvula	6	15.2± 6.6	Nil	760	7,000	60.8	0.0087	Dark
0.25	T. cylindrica	5	18.4± 9.2	Nil	920	7,000	73.6	0.011	Dark
0.75	T. parvula	8	13.9± 3.2	9	690	7,000	18.5	0.0026	Dark
0.75	T. cylindrica	1	11.0	Nil	550	7,000	14.6	0.0021	Dark
1.25	T. parvula	8	16.4± 6.0	5	820	7,000	13.1	0.0019	Dark
1.25	T. cylindrica	1	10.0	Nil	500	7,000	8.0	0.0011	Dark
0.50	T. parvula	5	13.0± 11.0	Nil	650	7,000	26.0	0.0037	Dim
1.0	T. parvula	6	20.8± 5.5	10	1040	7,000	20.8	0.0030	Dim
1.0	T. cylindrica	1	13.0	45	650	7,000	13.0	0.0019	Dim
1.5	T. parvula	1	19.0	58	950	7,000	13.0	0.0019	Dim
1.5	T. cylindrica	2	16.5± 7.5	28	825	7,000	11.0	0.0016	Dim

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level
F-Value	Significant	
0.98	No	Nil

TABLE 9. Eutintinnus tubulosus and Helicostomella kiliensis feeding on Monochrysis lutheri at three concentrations. Temperature 16°C; Salinity 15‰.

Duration (hrs)	Predator	Number predators examined	Number prey/ predator	Percentage prey digested	Volume prey/ predator	Number of prey/ml	FR nos./hr/ Tin.	FR ml/hr/ Tin.	Tins dividing
8.5①	E. tubulosus	3	15.0± 8.0	30	750	41,400	1.8	0.00004	Nil
8.5②	H. kiliensis	3	14.7± 2.6	34	735	41,400	1.7	0.00004	1
8.0③	E. tubulosus	6	22.0± 3.0	17	1100	107,000	2.8	0.00002	Nil
8.0	H. kiliensis	1	3.0	100	150	107,000	---	---	Nil
7.0④	E. tubulosus	1	9.0	67	450	213,000	1.3	---	Nil
7.0	H. kiliensis	8	5.5± 9.3	59	275	213,000	0.8	---	4

One-way ANOVA

F-value	Significant	Comparisons (Scheffes Test) with a significant difference at .05 level
7.36	yes (.01)	2/4, 3/4

CONTACT RATES

Predator	Number predators examined	Total Duration (secs)	Total Contacts	Ingested	Number prey/ml	Contacts/ minute	CR ml/hr/ Tin.	FR ml/hr/ Tin.
E. tubulosus	1	50	9	Nil	41,400	10	0.015	Nil
H. kiliensis	1	20	8	Nil	41,400	24	0.035	Nil
E. tubulosus	4	159	39	Nil	107,000	14.7	0.0082	Nil
H. kiliensis	3	236	62	Nil	213,000	15.8	0.0045	Nil

behaviour of these tintinnid species breaks down. These levels are probably 5 to 10 times higher than high field concentrations of food cells of this size. The low level of feeding activity in H. kiliensis in 213,000 prey cells/ml was, however, associated with a high level of reproductive activity, and 4 of the 8 sampled individuals showed early signs of cell division (oral Anlage).

In Table 10 the results are shown of an experiment in which 5 species of tintinnid were exposed to four concentrations of Dunaliella tertiolecta. The highest concentration (19,400 cells/ml) was from a month-old stock culture and the lower concentrations were from stocks less than 1 week old. The age of the culture made no difference in this experiment. The percentage of prey being digested had a similar range in all species and was 18 to 39% in Tintinnopsis subacuta, 17 to 36% in T. parvula and 9 to 40% in Stenosomella ventricosa. No prey cells were digested in S. nivalis and 100% were digested by the rare tintinnid Ptychocyclis acuta. T. subacuta and S. ventricosa had similar feeding rates (about 0.0020 ml/hr), with those of the latter being a little higher, but not significantly so. The optimal food concentration (OFC) was between 2,000 and 3,900 cell/ml for T. subacuta and S. ventricosa or 0.37 to 0.72 ppm by volume. The feeding rate of Tintinnopsis parvula was only 1/4 or 1/5 of that of the latter two species at the same food cell concentration; and the smallest of the species Stenosomella nivalis, had an accumulation of prey cells only 1/10 of that of T. subacuta in this experiment.

The results shown in Tables 8 to 10 of the accumulation and feeding rates of more than one tintinnid species, are an extension of those of Tables 3 to 6 in indicating that the average number of cells accumulated/tintinnid was about 200 M. lutheri and that optimal food concentrations of M. lutheri were about

TABLE 10. Various tintinnid species feeding on "new" and "old" cultures of Dunaliella tertiolecta at four concentrations. Temperature 14°C; Salinity 28‰.

Duration (hrs)	Predator	Number predators examined	Number prey/ predator	Volume of pred/prey (μm^3)	Percentage prey digesting	Number prey/ml	FR nos/hr/ Tin.	FR ml/hr/ Tin.	Age of prey stock culture
0 + 1.8 ①	Tintinnopsis subacuta	10	3.6± 3.4	702	39	2,000	2.1	0.0011	4 days
0 + 2.0 ②	Tintinnopsis subacuta	9	14.0± 9.8	2730	31	3,900	7.0	0.0018	4 days
0 + 2.25 ③	Tintinnopsis subacuta	9	19.9±12.3	3881	18	7,800	8.8	0.0011	4 days
0 + 2.5 ④	Tintinnopsis subacuta	12	21.9±12.3	4271	28	15,600	8.7	0.0006	4 days
0 + 2.8 ⑤	Tintinnopsis subacuta	11	25.1± 8.9	4718	17	19,400	8.9	0.0005	1 month
0 + 2.0 ⑥	Tintinnopsis parvula	2	3.0± 3.3	585	17	3,900	1.5	0.0004	4 days
0 + 2.25 ⑦	Tintinnopsis parvula	2	5.5± 6.0	1073	36	7,800	2.4	0.0003	4 days
0 + 1.8	Stenosomella ventricosa	1	18.0	3510	11	2,000	10.0	0.0051	4 days
0 + 2.0 ⑧	Stenosomella ventricosa	3	15.7± 5.9	3062	26	3,900	7.9	0.0020	4 days
0 + 2.25 ⑨	Stenosomella ventricosa	3	30.3± 9.3	5909	40	7,800	13.5	0.0017	4 days
0 + 2.5 ⑩	Stenosomella ventricosa	4	15.0± 9.9	2925	12	15,600	6.0	0.0004	4 days
0 + 2.8 ⑪	Stenosomella ventricosa	3	46.7±14.2	8780	9	19,400	16.5	0.0009	1 month
0 + 2.25	Stenosomella nivalis	2	Nil	Nil	--	7,800	--	--	4 days
0 + 2.5	Stenosomella nivalis	1	2.0	390	Nil	15,600	0.8	0.00005	4 days
0 + 2.8	Stenosomella nivalis	2	Nil	Nil	Nil	19,400	--	--	1 month
0 + 2.25	Ptychocyclis acuta	1	2.0	390	100	7,800	0.9	0.00011	4 days

One-way ANOVA		Comparisons (Scheffés Test) with a significant difference at .05 level
F-value	Significant	
7.76	yes (.01)	1/3, 1/4, 1/5, 1/9, 1/11, 6/11

2 or 3,000 per ml. It is interesting that the estimated feeding rates of tintinnids sampled at 1 hour in Table 8 were considerably lower than the initial rates at 0.25 hours, even though the number of semi-digested cells at 1 hour was still very low (<10%). Therefore, it seems that here ingestion slowed well before the digestive capacity of the cells was saturated, but the accumulated prey numbers/tintinnid at 0.25 hours were close to the maximum. It seems that the tintinnids were apparently near saturation in terms of numbers at 0.25 hours (see end of this Section). Table 10 shows that the smaller tintinnid species accumulated many fewer Dunaliella tertiolecta than did the larger species. The OFC of T. subacuta on this prey species was about 4,000/ml.

Differential predation and selection experiments

One predator type and two or more prey types

In the following Tables Ivlev's electivity index has been used as a measure of comparative 'catchability' or of differential predation and not as an index of prey selection (and see Section 4c). Tables 11 to 13 show the results of one predator exposed to 2 or more prey types simultaneously.

In the experiment shown in Table 11 Tintinnopsis parvula was exposed for about 1 hour to Isoselmis sp. singly at 9,500 cells/ml, and to Isoselmis sp. plus Monochrysis lutheri at 9,500 and at 14,000 cells/ml, respectively. The number of Isoselmis sp. accumulated/tintinnid was no different in the two situations, and was much lower than the number of M. lutheri accumulated. The electivity index indicated that a disproportionately large number of M. lutheri, and a disproportionately small number of Isoselmis sp. were accumulated from the prey food mixture, but this shows only differential predation. Although Isoselmis sp. is a little larger, and usually moves faster than

TABLE 11. Tintinnopsis parvula feeding on Isoselmis sp. and Monochrysis lutheri. Temperature 16°C; Salinity 15‰.

Duration (hrs)	Number predators examined	Prey	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR Nos/hr/ Tin	FR ml/hr/ Tin	Elec- tivity Index
0.8 ①	7	Isoselmis sp.	1.9± 1.9	140	9, 500	2.4	0.00025	
1.1 ②	4	Isoselmis sp.	1.5± 2.1	113	9, 500	1.4	0.00014	-.63
③		and M. lutheri	15.0± 7.8	750	14, 000	13.6	0.0010	+.28
		Total	16.5	863	23, 500	15.0	0.00063	

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level
F-value	Significant	
11.56	yes (.01)	1/3, 2/3

TABLE 12. Tintinnopsis subacuta feeding on Eutreptiella sp. (500 μm^3) and Isochrysis galbana (45 μm^3). Temperature 14°C; Salinity 9‰.

Duration (hrs)	Number predators examined	Prey	Number prey/ predator	Vol. prey/ predator (μm^3)	Number prey/ml	FR Nos/hr/ Tin.	FR ml/hr/ Tin.	Elec- tivity Index
11.3 ①	8	Eutreptiella only	16.4± 8.3	8, 200	4.4×10^3	1.5 ? minimal	0.0003 ? minimal	---
12.5 ②	11	I. galbana only	26.3±12.2	1, 200	66×10^3	2.1 minimal	0.00003 ? minimal	---
11.5 ③	13	Eutreptiella sp.	18.3± 7.6	9, 100	4.4×10^3	1.6 ? minimal	0.0004 minimal	+ .86
④		and I. galbana	4.5± 8.2	203	66×10^3	0.4 minimal	6×10^{-6} minimal	- .65
		Total	22.8	9, 303	70.4×10^3	2.0		

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level
F-value	Significant	
25.11	yes (.01)	1/4, 2/4, 3/4

M. lutheri its liability to predation was lower in this experiment.

Tables 12 and 13 show the results of Tintinnopsis subacuta alone exposed to Eutreptiella sp. and another prey species in relatively long experiments. In Table 12 the results are seen of an experiment lasting 11.3 to 12.5 hours with T. subacuta exposed to Eutreptiella sp. singly at 4,400 cells/ml; to Isochrysis galbana at 66,000 cells/ml; and to a dense mixture of the two species at 4,400 cells and 66,000 cells/ml respectively. There was no significant difference between the number of accumulated cells (steady-state balance) per tintinnid in Eutreptiella sp. only; in I. galbana only; or of Eutreptiella sp. in the mixed situation. As in some previous experiments the maximum of prey cells/tintinnid was on average between 16 and 25 despite a 10-fold difference in prey volume. It is also noteworthy that proportionately more Eutreptiella sp. than I. galbana were accumulated when both were presented singly. However, the number of I. galbana accumulated over 11.5 hours in the mixed situation was significantly reduced to about 1/6 of that of the number accumulated when exposed to I. galbana singly. An individual T. subacuta with a new lorica in Eutreptiella sp. contained merely 6 prey items after up to 11.3 hours, whereas in the mixed prey situation a similar individual with a new lorica contained 40 Eutreptiella sp. and 30 I. galbana in up to 11.5 hours. Therefore, it seems that the great variability in individual tintinnidd feeding performance seen in all these experiments can be found even amongst individuals with a relatively similar recent physiological history. The estimated feeding rates in Table 12 are extremely low due to the fact that after 11 to 12 hours, the tintinnids were probably in some sort of steady-state with regard to the uptake of these food items.

Table 13 shows the results of another experiment of this type, but also

TABLE 13. Tintinnopsis subacuta feeding on Eutreptiella sp. (500 μm^3), Isochrysis galbana (45 μm^3), and Dunaliella tertiolecta (210 μm^3). Temperature 14°C; Salinity 9‰.

Duration (hrs)	Number predators examined	Prey	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR Nos/hr/ Tin	FR ml/hr/ Tin	Elec-tivity Index
6.0 ①	2	Eutreptiella and	16.0 ± 2.8	8.0×10^3	1,500	2.7 min.	0.0018 min.	+.47
③		D. tertiolecta	6.6 ± 2.0	1,390	4,400	1.1 min.	0.00025	-.44
		Total	22.6	9,390	5,900			
6.3 ③	7	D. tertiolecta only	9.7 ± 1.8	2,040	4,400	1.5 min.	0.00034 min.	---
6.6 ④	9	D. tertiolecta and	2.7 ± 2.1	570	4,400	0.41 min.	0.00009 min.	-.07
⑤		I. galbana	46.7 ± 21.9	2,100	66,000	7.1 min.	0.00011 min.	+.004
		Total	49.4	2,670	70,400			

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level.
F-value	Significant	
24.24	yes (.01)	1/4, 2/5, 3/4, 3/5, 4/5

including the flagellate Dunaliella tertiolecta. Tintinnopsis subacuta was exposed to D. tertiolecta singly at 4,400 cells/ml; to Eutreptiella sp. (1,500/ml) plus D. tertiolecta (4,400/ml); or to D. tertiolecta (4,400/ml) plus Isochrysis galbana (66,000/ml). All tintinnids in the other possible single-food situations in this experiment; e.g. with Eutreptiella sp. and I. galbana, died from unknown causes during the experiment. More cells of D. tertiolecta were accumulated per tintinnid when presented singly than when presented together with I. galbana or Eutreptiella sp., although the difference was not significant in the latter case. Despite these real numerical differences, D. tertiolecta was apparently accumulated only slightly less than in the proportion in which it occurred, in the very dense mixture with I. galbana (electivity of -.07); but was accumulated much less than proportionately in the mixture with Eutreptiella sp. (electivity of -.44), but as it can be seen from Table 13, this apparent difference is due to the peculiar nature of Ivlev's formula. The slightly decreased accumulation of D. tertiolecta in either of the mixed-prey situations compared with the single-prey situation is a similar result to that of I.galbana when exposed with Eutreptiella sp. inTTable 12 and has no obvious behavioural explanation.

It seems as though T. subacuta cannot (or does not) accumulate more of the most easily caught item (e.g. Eutreptiella sp. - in Table 12), when in a mixture than it does in single-prey situations, but that it does take less of the other prey species in the mixture than singly. In Table 13 it can be seen that although about 47 I. galbana and only about 16 Eutreptiella sp. were accumulated, prey volume/predator was about 8,000 μm^3 for Eutreptiella sp. and only about 2,100 μm^3 for I. galbana. As both species are rapidly digested by T. subacuta, the tintinnid gained much more in terms of biomass by feeding on Eutreptiella sp. than on I. galbana.

TABLE 14. Tintinnopsis subacuta and Tintinnidium mucicola feeding on Eutreptiella sp. (500 μm^3) and Isoselmis sp. (75 μm^3). Temperature 13°C; Salinity 12.5‰.

Duration (hrs)	Predator	Number predators examined	Prey	Number prey/ predator	Vol. prey/ predator (μm^3)	Number prey/ml	FR Nos/hr/ Tin.	FR ml/hr/ Tin.	Elec-tivity Index
0.6	T. subacuta (1)	6	Eutreptiella and	5.3 ± 2.0	2,650	3,650	8.4	0.0023	+.71
0.6	T. subacuta (2)	6	Isoselmis	2.0 ± 2.0	150	30,000	3.2	0.00010	-.53
			Total		2,800		11.6	0.00034	
0.6	T. mucicola (3)	6	Eutreptiella and	Nil		3,650	Nil	Nil	-1.0
0.6	T. mucicola (4)	6	Isoselmis	7.2 ± 4.4	540	30,000	11.4	0.00037	+.06
			Total		540		11.4	0.00037	

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level.
F-value	Significant	
3.45	No	Nil

Two or more predators and two or more prey types

In Table 14 the results are shown of a fairly short experiment involving Tintinnopsis subacuta and the unusual species Tintinnidium mucicola. They were presented with only a mixture of Eutreptiella sp. and Isoselmis sp. (cryptophycae) at 3,650 and 30,000 cells/ml respectively. After 0.6 hours T. subacuta had accumulated disproportionately more of Eutreptiella sp. than of the much smaller and much more numerous Isoselmis sp.. On Eutreptiella sp. T. subacuta showed a fast estimated initial feeding rate of 0.0023 ml/hr/tintinnid. T. mucicola did not eat Eutreptiella sp. and accumulated more Isoselmis sp. than did T. subacuta from the mixutre of prey types. However, due to the short feeding periods and small numbers of accumulated cells, the latter were not quite significantly different at the .05 level. In Table 14 the electivity indices are indicative of real trends but only by comparison with the other predator, and not by comparison with a single-prey situation for the same predator.

In the field sample from which the tintinnids were taken for the latter experiment, the contact rate of T. mucicola on all particulate material was a little more than half that of T. subacuta. It is of similar size to the latter but moves more slowly (see Section 4b). Therefore, the fact that T. mucicola may have accumulated more Isoselmis sp. than T. subacuta cannot be ascribed to a faster contact rate. Three of the six T. subacuta shown in Table 14 showed the early signs of cell division. None of four T. subacuta taken from the same field sample as those used in the experiment showed signs of cell division, even though two of them had eaten one Tintinnopsis nana each. No T. mucicola cell showed signs of cell division in the field sample or in the experiment. It is, therefore, perhaps possible that some T. subacuta individuals in the experiment had responded to the act of ingestion or the

presence of Eutreptiella sp. in their cytoplasm (none appeared to be digested) or in the medium, and in the space of 38 minutes had begun cell division. The results in Table 14 confirmed the apparent selectivity of these two tintinnid species in a field sample taken 4 days previously. In this sample T. subacuta contained mainly many cells of a species of euglenoid (probably Eutreptiella sp.), and T. mucicola contained only small reddish cells 5-7 μm in diameter which were probably a species of cryptomonad. Similar observations were made on several other occasions.

Table 15 shows the food cells accumulated by Tintinnopsis subacuta, T. nana, T. rapa and Tintinnidium mucicola presented with Monochrysis lutheri (13,000 cells/ml) and Dunaliella tertiolecta (6,200 cells/ml) for 1 hour. Only T. subacuta ate both prey species; M. lutheri apparently rather more then proportionately compared to its abundance intthe medium, and D. tertiolecta rather less so. However no single-prey situation was available for comparison. The average feeding rate of T. subacuta on M. lutheri was 26.5 cells/hr/tintinnid or 0.002 ml/hr/tintinnid, a figure similar to that on Eutreptiella sp. in Table 14. T. rapa and T. nana accumulated less M. lutheri than did T. subacuta, and their contact rates and cell volumes (Table 1) are also much smaller than the latter's. T. rapa and T. nana ate no D. tertiolecta and they may be too small to ingest it (Table 2). Tintinnidium mucicola ate neither prey species on this occasion for unknown reasons, although most individuals did contain some old food items. Scheffé's test was not significant for most of the comparisons between levels in this experiment due to the small sample sizes.

Table 16 shows the results of an experiment in which two tintinnid species of similar size and general 'searching rate' Tintinnopsis subacuta

TABLE 15. Various tintinnid species feeding on *Monochrysis lutheri* (50 μm^3) and *Dunaliella tertiolecta* (200 μm^3). Temperature 16°C; Salinity 22‰.

Duration (hrs)	Predator	Number predators examined	Prey	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR Nos/hr/ Tin.	FR ml/hr/ Tin.	Elec-tivity Index
0 + 1.0	*Tintinnopsis subacuta* ① ②	2	*M. lutheri*	26.5± 2.2	1325	13,000	26.5	0.0020	+.16
			D. tertiolecta	2.0± 2.0	400	6,200	2.0	0.0003	-.64
0 + 1.0	*Tintinnopsis rapa* ③	2	*M. lutheri*	6.5± 0.7	325	13,000	6.5	0.0005	--
			D. tertiolecta	Nil	Nil	6, 200	Nil	Nil	--
0 + 1.0	*Tintinnopsis nana* ④	4	*M. lutheri*	1.8± 2.4	90	13,000	1.8	0.00013	--
			D. tertiolecta	Nil	Nil	6,200	Nil	Nil	--
0 + 1.0	*Tintinnidium mucicola*	4	*M. lutheri*	Nil	Nil	13,000	Nil	Nil	--
			D. tertiolecta	Nil	Nil	6,200	Nil	Nil	--

One-way ANOVA		Comparisons (Scheffé's Test) with a significant difference at .05 level.
F-value	Significant	
5.76	Yes (.05)	1/4

TABLE 16. *Tintinnopsis subacuta* and *Stenosomella ventricosa* feeding on *Eutreptiella sp.* (450 μm^3), *Monochrysis lutheri* (50 μm^3), and *Isoselmis sp.* (75 μm^3), singly and in combination.

Duration (hrs)	Predator		Number predators examined	Prey	Number prey/ predator	Percentage prey digested	Volume prey/ predator	Number prey/ml	FR nos/hr/ Tin.	FR ml/hr/ Tin.	Electivity Index (nos)
0 + 2.7	*Tintinnopsis subacuta*	1	9	*Eutreptiella sp.* (only)	16.0±3.4	58	7200	1400	5.9	0.0042	--
0 + 1.8		2	7	*M. lutheri* and	26.0±5.4	-	1300	8000	14.4	0.0018	+.10
		3		*Isoselmis sp.*	12.6±5.0	-	945	6600	7.0	0.0011	-.15
				Total	38.6		2245	14600	21.4	0.0015	
0.+ 3.5		4	9	*Eutreptiella sp.* and	11.7±3.7	75	5265	1400	3.3	0.0024	+.69
		5		*M. lutheri* and	11.0±6.0	-	550	8000	3.1	0.0004	-.10
		6		*Isoselmis sp.*	3.9±3.0	-	293	6600	1.1	0.0002	-.46
				Total	26.6		6108	16000	7.5	0.0005	
0 + 2.7	*Stenosomella ventricosa*	7	9	*Eutreptiella sp.*	5.1±3.7	72	2295	1400	1.9	0.0013	--
0 + 1.8		8	8	*M. lutheri* and	36.4±7.6	-	1820	8000	20.2	0.0025	+.15
		9		*Isoselmis sp.*	12.8±4.9	-	960	6600	7.1	0.0011	-.27
				Total	49.2		2780	14600	27.3	0.0019	
0 + 3.5		10	12	*Eutreptiella sp.* and	1.6±1.2	70	720	1400	0.46	0.0003	-.08
		11		*M. lutheri* and	17.0±6.8	-	850	8000	4.9	0.0006	+.18
		12		*Isoselmis sp.*	5.0±4.6	-	375	6600	1.4	0.0002	-.32
				Total	23.6		1945	16000	6.76	0.0004	

One-way ANOVA

F-value	Significant
26.4	Yes (.01)

Comparisons (Scheffé's Test) with a significant difference at .05 level.

1/6, 1/7, 1/10, 1/12, 2/6, 2/7, 2/10, 2/12, 3/6, 3/10, 4/6, 4/8, 4/10, 5/8, 5/10, 6/8, 6/9, 6/11, 7/8, 7/11, 8/10, 8/12, 9/10, 10/11, 11/12.

and Stenosomella ventricosa (see Section 4b), were presented with three prey types in various combinations. It is almost certain that steady-state feeding conditions were reached during this experiment despite the fairly high feeding rates estimated. Eutreptiella sp. was presented singly at 1,400 cells/ml; and together with Monochrysis lutheri at(8,000 cells/ml)and Isoselmis sp. : (6,600 cells/ml). Tintinnopsis subacuta accumulated more Eutreptiella sp. when presented singly than in the three-prey mixture, but not significantly more. There was also not quite a significant difference in the number of M. lutheri accumulated by T. subacuta in the two or three-prey mixture, but significantly fewer Isoselmis sp. were accumulated in the three-prey mixture than in the two prey mixture. The electivity index for Isoselmis sp. (cryptophyceae) was negative in bothcases. As in previous Tables the electivity index for T. subacuta feeding on Eutreptiella sp. in a mixture of prey types was highly positive. The feeding rate on the latter prey was also relatively high - about 6 Eutreptiella sp/hr/tintinnid or equivalent to 0.0042 ml/hr/tintinnid (see General Discussion).

As shown in Table 16 Stenosomella ventricosa accumulated significantly less Eutreptiella than did T. subacuta (about 1/3 as many) when it was presented singly to the tintinnids. S. ventricosa also had less Eutreptiella sp. (but not significantly less) in the 3-prey mixture than in the single-prey case, and about 7-fold fewer than did T. subacuta. Eutreptiella sp. in the 3-prey mixture had a negative electivity index in S. ventricosa. In contrast, the number of M. lutheri accumulated by S. ventricosa was larger (but not significantly so) than the number in T. subacuta in both the 2-prey and 3-prey mixtures. More M. lutheri were found inside S. ventricosa in the 2-prey than in the 3-prey mixtures, but again, the difference was not significant. S. ventricosa accumulated the same number of Isoselmis sp. as did T. subacuta

in the two-prey mixture, and a non-significantly larger number than did T. subacuta in the 3-prey mixture. The electivity index for S. ventricosa on Isoselmis sp. was also negative in both cases. In summary, these two species of tintinnid in Table 16 responded in a similar manner to M. lutheri and Isoselmis sp., and very differently to the much larger Eutreptiella sp.. It is interesting that the total number (but not the volume) of accumulated cells is similar in the 3-prey situation for both species of tintinnid.

In summary the results shown in Tables 11 to 16 indicate various complex forms of differential predation for some tintinnid species on certain prey types. In some cases this behaviour could be said to be some form of negative selection in mixed-prey situations, although its behavioural basis and adaptive value seem obscure. For example, Tintinnopsis parvula showed only differential predation in favour of Monochrysis lutheri over Isoselmis sp. in Table 11 since the number of the latter accumulated was the same in the single-prey as in the two-prey situation. However, the accumulation of M. lutheri was not enhanced because it was larger or faster than Isoselmis sp., as the reverse is true. In Table 12 differential predation is apparent by T. subacuta feeding on Eutreptiella sp. over Isochrysis galbana in single-prey situations, and negative selection is apparent against I. galbana in the 2-prey situation. It should be remembered that in long experiments (Table 12) when a feeding steady-state has been reached, that both apparent differential predation and negative selection may in fact be caused by differences in the ease with which the prey types are digested.

In another long experiment (Table 13) Dunaliella tertiolecta was accumulated less in a mixture with I. galbana than when presented to T. subacuta alone. The latter cannot be considered as either differential predation or

negative accumulation/selection since both prey types were accumulated in proportion to their abundance. In a much shorter experiment (Table 14) T. subacuta and Tintinnopsis mucicola showed opposite differential predation; T. subacuta aginst Isoselmis sp. and T. mucicola against Eutreptiella sp.. In another short experiment (Table 15) T. subacuta showed differential predation against D. tertiolecta (as in Table 13) when fed with M. lutheri. This cannot be a product of the relatively faster digestion of D. tertiolecta, as the latter is notably more difficult to digest by tintinnids than is M. lutheri. As seen in Table 15 the small tintinnids T. rapa and T. nana show the maximum differential predation against D. tertiolecta, almost certainly because it is too large for them. Stenosomella ventricosa shows differential predation on Eutreptiella sp. when compared with T. subacuta (Table 16); and both tintinnid species show negative selection against Isoselmis sp. and M. lutheri(to a lesser extent)in a 3-prey situation. To judge from the figures in Table 16 it is unlikely that the latter phenomenon is caused by the fact that the feeding rates were only then at or above their maxima.

Effects of prior starvation on feeding rates

Tables 17 and 18 show the results of the effect of prior starvation for various long periods on the feeding rate of Tintinnopsis subacuta and Stenosomella ventricosa. In the experiment shown in Table 17, a dense but unknown concentration (but certainly above the OFC level) of Dunaliella tertiolecta was presented to T. subacuta after the latter had been starved in filtered water for 0,30 or 48 hours. The non-starved cells accumulated about twice as many food cells as the starved cells which all showed about the same results. These differences were not statistically significant because of very large variance in the samples. Similarly in Table 18, tintinnids starved

TABLE 17. Tintinnopsis subacuta (etc.) starved for various periods in filtered seawater feeding on Dunaliella tertiolecta at unknown, but dense, concentrations. Salinity 26‰

Duration of prior starvation (hrs)	Duration of feeding period (hrs)	Temperature °C	Number predators examined	Number prey/ predators	Number of other food items/ Tin.	Comments
30	0.33	8	5	7.2±8.3	nil	
48	0.50	8	6	8.0±8.8	nil	
nil	1.3	17	5	17.0±8.7	3.2	
48	1.4	17	6	5.0±6.2	nil	3 had no food
			Tintinnidium mucicola			
nil	1.3	17	4	nil	4.6	

One-way ANOVA

F-value	Significant
2.98	no (.05)

TABLE 18. Tintinnopsis subacuta and other predators starved for various periods and feeding on Eutreptiella sp. Temperature 8°C; Salinity 26‰.

Duration of prior starvation (hrs)	Duration of feeding period (hrs)	Predator	Number predators examined	Number prey/ predator	Number prey/ml	FR nos/hr/ predator	FR ml/hr/ predator	Comments
72	0.4 ①	T. subacuta	3	5.0±1.0	14600	12.5	0.0009	Pred. cells thin; no storage granules
72	0.4	Synchaeta littoralis	1	21.0	14600	52.5	0.0036	Pred. 400x200µm
72	1.0 ②	T. subacuta	4	4.5±3.7	14600	4.5	0.0003	No granules
90	0.45 ③	T. subacuta	5	3.2±1.1	14600	7.1	0.00046	Pred. cells thin; no granules
90	0.45 ④	Stenosomella ventricosa	3	1.3±1.2	14600	2.9	0.0002	Cells thin; some granules
90	1.1 ⑤	T. subacuta	5	8.4±1.2	14600	7.6	0.00051	No granules
90	1.1 ⑥	S. ventricosa	3	4.3±1.6	14600	3.9	0.00026	Many granules

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level
3.72	yes (.05)	4/5

for 72 or 90 hours in filtered water were then presented with very high concentrations of Eutreptiella sp. (14,600/ml) for 0.4 or 1.0 hours. Both Tintinnopsis subacuta and Stenosomella ventricosa showed very low feeding rates on this food whether starved for 72 or 90 hours, with T. subacuta accumulating more Eutreptiella sp. than S. ventricosa (as in Table 16). One individual of the large rotifer Synchaeta littoralis contained about 4 times as many food items as did T. subacuta (and see Section 4c). Starved S. ventricosa contained some food storage granules although the cells were thin, but the cells of starved T. subacuta were thin and without obvious food reserves. S. ventricosa may be better adapted than T. subacuta to environments containing little food. The results of Tables 17 and 18 indicate that starvation for more than 48 hours can seriously reduce the ability of tintinnids to eat when food is once more provided in dense concentrations. Since the total number of cells accumulated was small, it is not only a question of an inability to digest food once eaten, because of low levels of the pools of digestive enzymes (and see discussion at the end of this Section).

Feeding and loss rates

The experiments whose results are shown in Tables 19 to 23 include estimations of the rate of 'loss' of old food items by tintinnids, as well as estimations of feeding rates on newly presented prey items. Losses are probably the result of digestion plus egestion with the rate of digestion or partial digestion as the limiting step. Most food items contain an undigestible fraction, but this fraction may very in size with changes in the physiological states of predator and prey. Therefore, in Tables 19 to 23, loss rates refer to the estimated rate of disappearance of accumulated food items. It was not possible to know whether the food was a) mostly digested and then egested at a similar rate; b) wholly digested with no residue to egest; or

c) egested before any digestion took place. As with feeding rates, losses are compared from differences between the mean values of sacrificed sub-samples.

In Tables 19 and 20 the results of a type of nutritional 'homeostasis' in tintinnids are shown. When a natural seawater sample is diluted with filtered seawater of the same origin, there is often very little change in the accumulated food cells per tintinnid. This can result from two possible causes: a) the dilution of a dense concentration of particulate matter merely reduces that concentration to (or above) the OFC or level at which the tintinnid can feed (or digest) at its fastest rate; or b) the loss rate of food is reduced by the tintinnid to match the reduced opportunities for feeding in a dilute medium, thus increasing digestive efficiency and reducing the likelihood of starvation. The latter may be a largely 'mechanical' consequence of a slower feeding rate. This problem is also discussed later in this Section,

In Table 19 it can be seen that the small tintinnid species Stenosomella nivalis lost about half of its accumulated food cells in 7 to 8 hours when a natural sample was diluted with filtered seawater, whether the dilution was 1/3 or 9/10 of the original volume. Likewise, in Table 20, the number of accumulated natural food items of Tintinnidium mucicola showed an appreciable but not statistically significant difference after 5.5 to 7.3 hours, but only when the dilution factor was as great as 7 to 1. In dilutions of 1 to 1 and 3 to 1 with filtered seawater no difference was seen from the original sample; and in all three levels of dilution, the change in the accumulated cell number over about 24 hours paralleled the change (a slight decline) in the undiluted original sample. After 26 hours the T. mucicola in the sample which had been

TABLE 19. Loss rate of Stenosomella nivalis at two levels of dilution of medium with filtered seawater. Temperature 9°C; Salinity 26‰.

Duration (hrs)	Percentage original seawater	Number predators examined	Prey	Number prey/ predator	Percentage prey digested	Tins with algal eyespots	Loss rate nos/Tin/ hr	Loss rate μm^3/Tin/ hr	Condition
0	100	9 ①	~5µm green flagellates	21.1±11.3	3	1	-	-	Active
7.25	<1	12 ②	"	10.2±8.1	51	7	1.5	~75	Active
8.0	66	17 ③	"	8.0±10.5	77	8	1.6	~80	Active

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level
7.54	Yes (.01)	1/2, 1/3

TABLE 20. Change of food contents of Tintinnidium mucicola with time at four levels of dilution of medium with filtered seawater. Temperature 9°C; Salinity 25‰.

Time since dilution (hrs)	Percentage original medium	Number predators examined	Prey	Numbers prey/ predator	Percentage prey digested	'Loss rate' from previous check nos/hr/ Tin	'Loss rate' from previous check μm^3/hr/ Tin	Nos & size of Tin. storage granules	Tins dividing
5.5	100	9	Yellow-brown cells (cryptos?)	22.3±13.8	17	-	-	Many - >3μm	nil
24.0	100	6	"	15.7± 7.6	27	0.35		---	1
6.5	50	10	"	24.1± 9.8	35	nil*	-	Many - >3μm	nil
24.5	50	7	"	12.3± 6.6	28	0.66		"	nil
7.0	25	9	"	26.7±11.3	30	nil*	-	---	nil
24.7	25	10	"	13.7± 5.6	24	0.73		Many	2
7.25	12	5	"	14.6± 9.6	18	1.1*	-	Few-low prey number; Many-high number	1
26.5	12	8	"	9.5± 4.2	32	0.26		Very few	nil

* Value for 100% medium at 5.5 hrs used as "time zero" for this calculation.

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level
3.31	yes (.01)	nil

diluted by 7 to 1 had very few food reserve storage granules. Tintinnids in the original sample and in 1 to 1 and 3 to 1 dilutions still had many storage granules. This would seem to indicate that there was still enough food to allow T. mucicola to feed and store nutrients in all samples, except in that of the 7 to 1 dilution. This experiment was carried out at 9 C. Tintinnid digestion (loss) rates may be faster at higher temperatures.

Simultaneous feeding and loss rates

Tables 21, 22 and 23 show the results of experiments in which are estimated the rates of feeding on new food types and the simultaneous rate of loss of different old food types. Feeding and loss rates were estimated from the differences between the average number of food cells/tintinnid, in various samples since the start of the experiment.

Effect of temperature

In Table 21 four tintinnid species Tintinnopsis subacuta, T. parvula; T. rapa and Tintinnidium mucicola were presented with Monochrysis lutheri at 5,000 cells/ml and Cryptomonas minuta at 2,000 cells/ml, whilst losing old natural food of various types (mostly unidentified) in an experiment lasting up to 2 1/4 hours. The tintinnids were taken from a field sample at 14.5 C and kept at one of the 4 experimental temperatures (8, 13, 17 or 22°C) for 6 hours before the experiment. One time check was made of those samples kept at 8 and 13°C and three time checks were made of samples at 17 and 22°C. Comparisons between levels (Scheffé's test) were confined within the results for one species, to avoid undue complexity.

In Table 21 the feeding rates of T. subacuta on M. lutheri are fairly high and not significantly different at all 4 temperatures, with the maximum at 10.7 cells/hr/tintinnid or equivalent to 0.0022 ml/hr/tintinnid. This

TABLE 21. Tintinnopsis subacuta, T. parvula, T. rapa and Tintinnidium mucicola feeding on new food Monochrysis lutheri (42μm^3) and Cryptomonas sp. (280μm^3), and loss rate of old food of various types at four temperatures. Salinity 23‰

Duration (hrs)	Predator	Number predators examined	Temp. °C	Numbers prey/ predator	Volume prey/ predator	Number prey/ ml	FR or Loss Rate nos/hr/Tin	FR as ml/hr/Tin	Electivity Index
0 + 2.0	T. subacuta	5	8.0	Old					
	①			2.4	-	-	-	-	-
				New: M.L.					
	②			17.4±10.0	731	5000	8.7	0.0017	+.15
				New: Cryp.					
	③			0.8±1.8	224	2000	0.4	0.0002	-.73
0 + 1.5	T. subacuta	10	13.0	Old:					
	④			1.5±1.4	-	-	-	-	-
				New: M.L.					
	⑤			16.1±6.6	676	5000	10.7	0.0022	+.15
				New: Cryp.					
	⑥			0.7±0.8	197	2000	0.5	0.0002	-.74
0	T. subacuta	6	17.0	Old:					
	⑦			6.2±1.1	-	-	-	-	-
0 + 1.6	T. subacuta	9	17.0	Old:					
	⑧			3.8±2.7	-	-	1.6	-	-
				New: M.L.					
	⑨			7.9±5.5	332	5000	4.9	0.0010	+.17
				New: Cryp.					
				nil	nil	2000	nil	nil	-1.0
0 + 2.25	T. subacuta	5	17.0	Old:					
	⑩			3.2±2.0	-	-	From 0 1.33	-	-
				New: M.L.					
	⑪			5.6±1.7	235	5000	From 0 2.5	0.0005	+.15
				New: Cryp.					
	⑫			0.2±0.4	56	2000	nil	nil	-.81
0	T. subacuta	7	22.0	Old:					
	⑬			10.1±4.3	-	-	-	-	-
0 + 1.0	T. subacuta	9	22.0	Old:					
	⑭			4.3±1.7	-	-	5.8	-	-
				New: M.L.					
	⑮			4.2±4.4	176	5000	4.2	0.0008	+.12
				New: Cryp.					
	⑯			0.4±0.4	112	2000	nil	nil	-.54
0 + 1.5	T. subacuta	3	22.0	Old:					
	⑰			5.7±0.7	-	-	From 0 2.9	-	-
				New: M.L.					
	⑱			8.0±6.9	336	5000	From 0 5.3	0.0011	+.11
				New: Cryp.					
	⑲			1.0±1.0	281	2000	0.7	0.0004	-.44

One-Way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level.
14.52	Yes (.01)	2/3, 2/4, 2/6, 2/12, 2/16, 3/5, 3/13, 4/13, 5/6, 5/12, 5/15, 5/16, 5/19, 6/9, 6/13, 7/16, 9/12, 9/16, 12/13, 13/16

TABLE 21. Continued

Duration (hrs)	Predator	Number predators examined	Temp. °C	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR or Loss Rate nos/hr/Tin	FR as ml/hr/Tin	Electivity Index
0 + 2.0	T. parvula	6	8.0	Old:	-	-	-	-	-
	①			0.3±0.8	-	-	-	-	-
				New: M.L.					
	②			14.0±6.1	588	5000	7.0	0.0014	+.11
				New: C.M.					
	③			1.6±2.2	450	2000	0.8	0.0004	-.47
0 + 1.5	T. parvula	8	13.0	Old:					
				nil	-	-	-	-	-
				New: M.L.					
	④			19.0±4.6	798	5000	12.7	0.0025	+.15
				New: C.M.					
	⑤			0.6±0.5	169	2000	0.4	0.0002	-.47
0	T. parvula	6	17.0	Old:					
	⑥			-2.7±2.4	-	-	-	-	-
0 + 1.6	T. parvula	7	17.0	Old:					
	⑦			0.6±1.1	-	-	1.3	-	-
				New: M.L.					
	⑧			12.3±3.3	517	5000	7.7	0.0015	+.17
				New: C.M.					
				nil	nil	2000	nil	nil	-1.0
0 + 2.25	T. parvula	8	17.0	Old:			From 0		
				nil	-	-	1.2	-	-
				New: M.L.					
	⑨			14.6±5.6	613	5000	6.5	0.0013	+.17
				New: C.M.					
				nil	nil	2000	nil	nil	-1.0
0	T. parvula	7	22.0	Old:					
	⑩			4.3±2.0	-	-	-	-	-
0 + 1.0	T. parvula	3	22.0	Old:					
	⑪			1.7±0.6	-	-	2.6	-	-
				New: M.L.					
	⑫			4.3±5.1	181	5000	4.3	0.0009	+.17
				New: C.M.					
				nil	nil	2000	nil	nil	-1.0
0 + 1.5	T. parvula	4	22.0	Old:			From 0		
	⑬			0.3±0.5	-	-	2.7	-	-
				New: M.L.					
	⑭			14.0±6.7	588	5000	9.3	0.0019	+.16
				New: C.M.					
	⑮			0.3±0.5	84	2000	0.2	0.0001	-.86

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level
27.22	yes (.01)	1/2, 1/4, 1/8, 1/9, 1/14, 2/3, 2/5, 2/6, 2/7, 2/13, 2/15, 3/4, 3/8, 3/9, 3/14, 4/5, 4/6, 4/7, 4/10, 4/11, 4/15, 5/8, 5/9, 5/14, 6/9, 7/8, 7/9, 7/14, 8/15, 9/13, 9/15, 13/14, 14/15.

TABLE 21. Continued

Duration (hrs)	Predator	Number predators examined	Temp. °C	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR or Loss Rate nos/hr/Tin.	FR as ml/hr/Tin	Electivity Index
0 + 2.0	T. mucicola	4	8.0	Old:					
	①			7.8±6.3	-	-	-	-	-
				New: M.L.					
	②			0.5±0.6	21	5000	0.25	0.00005	-.30
				New: C.M.					
	③			0.8±1.0	225	2000	0.40	0.0002	+.37
0 + 1.5	T. mucicola	5	13.0	Old:					
	④			11.8±5.8	-	-	-	-	-
				New: M.L.					
				nil	nil	5000	nil	nil	-1.0
				New: C.M.					
	⑤			0.6±0.6	169	2000	0.40	0.0002	+.56
0	T. mucicola	11	17.0	Old:					
	⑥			9.8±3.7	-	-	-	-	-
0 + 1.6	T. mucicola	8	17.0	Old:					
	⑦			8.0±3.6	-	-	1.1	-	-
				New: M.L.					
	⑧			0.5±1.1	21	5000	0.31	0.00006	-.44
				New: C.M.					
	⑨			1.3±1.2	365	2000	0.81	0.0004	+.01
0 + 2.25	T. mucicola	4	17.0	Old:			From 0		
	⑩			8.8±7.6	-	-	0.44	-	-
				New: M.L.					
				nil	nil	5000	nil	nil	-1.0
				New: C.M.			From 0		
	⑪			1.8±1.3	506	2000	0.8	0.0004	+.56
0	T. mucicola	6	22.0	Old:					
	⑫			7.7±2.6	-	-	-	-	-
0 + 1.0	T. mucicola	2	22.0	Old:					
	⑬			3.0±4.2	-	-	4.7	-	-
				New: M.L.					
	⑭			2.0±2.0	84	5000	2.0	0.0004	-.04
				New: C.M.					
	⑮			1.0±1.0	281	2000	1.0	0.0005	+.07
0 + 1.5	T. mucicola	3		Old:			From 0		
	⑯			2.7±2.5	-	-	3.3	-	-
				New: M.L.			From 0		
	⑰			1.3±2.3	55	5000	0.86	0.00017	-.12
				New: C.M.			From 0		
	⑱			1.0±1.7	281	2000	0.66	0.00033	+.21

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level
12.48	yes (.01)	2/4, 2/6, 2/7, 3/6, 4/5, 4/8, 4/9, 5/6, 5/7, 5/12, 6/8, 6/9, 7/8, 8/10, 8/12.

TABLE 21. Continued

Duration (hrs)	Predator	Number predators examined	Temp. °C	Number prey/ predator	Volume prey/ predator	Number prey/ml	FR or Loss rate nos/hr/Tin	FR as ml/hr/Tin	Electivity Index
0 + 2.0	T. rapa	4	8.0	Old:					
				3.0±0.8	-	-	-	-	-
				New:					
				nil	-	-	-	-	-
0 + 1.5	T. rapa	3	13.0	Old:					
				nil	-	-	-	-	-
				New: M.L.					
				1.7±1.7	71	5000	1.0	0.0002	+.17
				New: C.M.					
				nil	-	2000	-	-	-1.0
0	T. rapa	5	17.0	Old:					
				3.4±1.7	-	-	-	-	-
0 + 1.6	T. rapa	3		Old:					
				1.0±1.0	-	-	1.5	-	-
				New: M.L.					
				0.7±0.8	29	5000	0.4	0.00008	+.17
				New: C.M.					
				nil	-	2000	-	-	-1.0

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level.
3.21	No (.05)	nil

0 + 2.0	Helicostomella kiliensis	3	8.0	Old:					
				0.6±1.0	-	-	-	-	-
				New: M.L.					
				13.3±5.7	559	5000	6.7	0.0013	+.17
				New: C.M.					
				nil	nil	2000	nil	nil	-1.0
0 + 1.6	Helicostomella kiliensis	1	17.0	Old:					
				nil	-	-	-	-	-
				New: M.L.					
				5.0±5.0	210	5000	3.1	0.0006	-
0 + 2.25	Helicostomella kiliensis	1	17.0	Old:					
				nil	-	-	-	-	-
				New: M.L.					
				6.0±6.0	252	5000	2.7	0.0005	-
0	Helicostomella kiliensis	1	22.0	Old:					
				7.0	-	-	-	-	-
0 + 1.5	Helicostomella kiliensis	1	22.0	Old:					
				nil	-	-	4.7	-	-
				New: M.L.					
				9.0	378	5000	6.0	0.0012	+.07
				New: C.M.					
				2.0	562	2000	1.3	0.0007	-.22
0 + 2.0	Stenosomella ventricosa	1	8.0	New: M.L.					
				12.0	504	5000	6.0	0.0012	-
0 + 2.25	Stenosomella ventricosa	1	17.0	Old:					
				nil	-	-	-	-	-
				New: M.L.					
				15.0	630	5000	6.7	0.0013	+.17
				New: C.M.					
				nil	-	2000	-	-	-1.0

maximum was achieved at 13°C - the closest temperature of those used to that of the field sample. The greatest feeding rate on M. lutheri was at the first check (0 + 1.6 hours) at 17°C, but at the second check (0 + 1.5 hours) at 22°C. The number of C. minuta accumulated was much less than that of M. lutheri at all temperatures and nil at one check at 17°C. The electivity value for T. subacuta on C. minuta was strongly negative at all temperatures again indicating differential (negative) predation of this tintinnid species on laboratory cultures of some cryptophyceae. The estimated rate of loss of old food from T. subacuta tended to decline with time at both 17 and 22°C (and see discussion later in this Section). Loss rates could not be estimated at 8 and 13°C. The loss rate was greater at 22 than at 17°C; but again due to the small sample sizes and great individual variability, there were no significant differences between the remaining numbers of old food cells. In terms of biomass T. subacuta definitely lost a greater volume of old food than the other tintinnid species shown in Table 21. Several of the T. subacuta contained one or two T. nana (volume 3,000 μm^3) and Eutreptiella sp. (500 μm^3) at the start, whereas the largest old food cells contained by T. parvula and T. mucicola in this experiment were about 150 μm^3 or less in volume.

The feeding rate of Tintinnopsis parvula on Monochrysis lutheri (Table 21) showed no significant differences at different temperatures or times, and the feeding rates surprisingly, were similar to those of the larger T. subacuta (Table 21) at 8 and 13°C and greater than those of the latter at 17 and 22°C. As in T. subacuta the estimated feeding rate by T. parvula on M. lutheri rose to its maximum earlier at 17 C than at 22°C. Since 22°C is much higher than the highest field temperature experienced by these species, this 'lag' in the feeding rate at 22°C may reflect some problem of

physiological adaptation, but if so it does not appear in the differences between loss rates. The feeding rates of T. parvula on Cryptomonas minuta were, like those of T. subacuta, very low or nil and the electivity values were always negative.

The accumulated number of M. lutheri cells in Tintinnidium mucicola (Table 21) was very much lower than in T. subacuta and T. parvula despite a comparable contact rate. The number of C. minuta per T. mucicola was very small at all temperatures and only slightly greater than that in T. subacuta and T. parvula. However, the electivity index of T. mucicola on C. minuta was positive, unlike that for the other two tintinnid species. This result emphasizes a problem in the use of Ivlev's index, in that its magnitude and even its sign depends not only on the amount eaten of the food item in question, but also on the amount of the other items eaten. The loss rate of old food from T. mucicola at 22°C was higher than that of T. parvula and lower than that of T. subacuta. The loss rate in Table 21 was also higher at 22 C than at 17°C, and declined with time (or more likely with biomass remaining) as did the loss rates of T. parvula and T. subacuta.

Fragmentary results from a few other species of tintinnid in the same experiment as above are shown in Table 21. Tintinnopsis rapa contained very little of either new prey species at three of the experimental temperatures, but its rates of loss of old food material at 17°C were no lower than those of the larger species. The sample sizes of Helicostomella kiliensis were extremely small, but if the information can be utilised, then this species seemed to contain about as many cells of M. lutheri at 8 and 17 C as did T. subacuta and T. parvula. The rate of loss of old food material by H. kiliensis at 22°C was also in the same range as that of T. subacuta and T. parvula.

One cell of Stenosomella ventricosa in each sample at 8 and 17°C, also contained a number of M. lutheri cells in the same range as T. subacuta and T. parvula, and no Cryptomonas sp.. The incidence of the early stages of reproduction in this experiment was rather higher in Tintinnidium mucicola than in T. subacuta or T. parvula but was apparently not positively correlated with higher temperatures.

Effect of Starvation

Table 22 shows the results of an experiment in which Tintinnopsis subacuta was presented with a dense mixture of Monochrysis lutheri (16,000/ml) and Plagioselmis sp. (8,000/ml) for 3 hours, and checks were made of the number of accumulated food cells/tintinnid at 0 + 1.0 and at 0 + 3.0 hours. At 0 + 2.17 hours some of the latter T. subacuta were gently washed with a large volume of filtered water, and tintinnids in one sub-sample of these were starved in filtered water for 0.66 hours. A second sub-sample of washed T. subacuta was presented with a mixture of two new prey types: Eutreptiella sp. (3,800/ml) and Isoselmis sp. (15,000/ml) for 0.33 hours. T. subacuta accumulated both species of old food in the original mixture in the proportions in which they were presented, but rather slowly. There were no significant differences between the numbers of M. lutheri, nor between the numbers of Plagioselmis sp. per tintinnid in any of the treatments. However, if the differences between the accumulations of old food are used to estimate loss rates on an hourly basis, it is highly probable that the loss rate of old food (especially M. lutheri) was greater in the T. subacuta fed with new food than in those cells which ewere starved. The hourly loss rate of M. lutheri was 4.1 cells in the starved cells after 0.66 hours and 22.8 cells in the newly fed T. subacuta (after 0.33 hours). This comparison between samples taken at different times is also partly specious because loss rates

TABLE 22. Feeding and loss rates of Tintinnopsis subacuta; losing Monochrysis lutheri and Plagioselmis sp. and either starved, or gaining Eutreptiella sp. and Isoselmis sp.

Duration (hrs)	Number predators examined		Prey	Number prey/ predator	Number prey/ml	FR or Loss Rate nos/hr/Tin	FR or Loss Rate μm^3/hr/Tin	FR ml/hr/Tin	LR D - C nos/hr/Tin	LR D - C μm^3/hr/Tin	Gain (D) Loss (D-C) μm^3
A											
1.0	21	①	M. lutheri and	16.1±6.2	16000	16.1	805	0.0010	-	-	-
		②	Plagioselmis sp.	8.0±3.2	8000	8.0	600	0.0010	-	-	-
B											
3.0	18	③	M. lutheri and	24.2±6.0	16000	-	-	-	-	-	-
		④	Plagioselmis	13.0±4.3	8000	-	-	-	-	-	-
C											
0.66	18		Old:								
(starved		⑤	M. lutheri and	19.3±6.2	nil	4.1*	205	-	-	-	-
from		⑥	Plagioselmis	9.8±3.7	nil	3.3*	396	-	-	-	-
2.17 hrs)			New Food	nil	nil	nil	-	-	-	-	-
D											
0.33	7		Old:								
(new food		⑦	M. lutheri and	14.4±7.3	nil	22.8*	1140	-	18.7	935	4.6
after		⑧	Plagioselmis	11.0±4.0	nil	3.0*	360	-	nil	nil	-
2.17 hrs)			New:								
		⑨	Eutreptiella and	2.4±1.0	3800	7.2	3744	0.0019	-	-	-
		⑩	Isoselmis	2.4±2.4	15000	7.2	540	0.00048	-	-	-

*Loss rates calculated from interpolated values A to B of accumulated old food at 2.5 hours.

One-way ANOVA F-value	Significant	Comparisons (Scheffé's Test) with a significant difference at .05 level.
23.63	yes (.01)	1/2, 1/6, 1/9, 1/10, 2/3, 2/5, 2/9, 2/10, 3/6, 3/9, 3/10, 4/9, 4/10, 5/6, 5/9, 5/10, 6/10, 7/9, 7/10, 8/9, 8/10.

decline with time. However, a 'forcing effect' of the ingestion of new food on the digestion (or disappearance) of old food has also been observed in the ciliate Stentor coeruleus (D.J. Rapport, unpublished data) and is probably a real phenomenon (but see Table 23).

The accumulation of new food shown in Table 22 was rather slow (0.0019 and 0.00048 ml/hr/tin) and was much less than the (estimated) loss rate of old food in terms of numbers of cells, but in terms of biomass the ratio of hourly gain/loss entirely due to feeding (D-C in Table 22) was 4.6/1. This phenomenon, which will be discussed again later in this Section, was due largely to the fact that one of the new prey types, Eutreptiella sp. is much larger than the others used in this experiment.

Tables23 shows the results of a similar experiment where three species of the 'warm-water'type of tintinnids, namely Tintinnopsis cylindrica, Helicostomella kiliensis and Eutintinnus latus plus the ubiquitous Tintinnidium mucicola, were given food for several hours then washed in filtered water and either starved, or alternatively given new food of a visibly different type. The old food type used was one of either Monochrysis lutheri, Isoselmis sp. or Dunaliella tertiolecta; and if given new food, the type used was either Isoselmis sp. or D. tertiolecta. Scheffé's test of multiple comparisons was not made between the results from different tintinnid species.

The results of this experiment (Table 23) seem to be partly in direct contrast to those shown for another species of tintinnid in Table 22, in that old food cells of M. lutheri or D. tertiolecta were not lost more rapidly from those T. cylindrica cells given new food than from those starved. However, in the case of old Isoselmis sp. there were significantly more old food cells remaining in starved T. cylindrica than in those fed with new

TABLE 23. Accumulation and loss rates of Tintinnopsis cylindrica, Helicostomella kiliensis, Tintinnidium mucicola and Eutintinnus latus, feeding on Monochrysis lutheri, or Isoselmis sp.; or starved, and losing M. lutheri, Isoselmis sp., or Dunaliella tertiolecta. Temperature 16°C; Salinity 16‰.

Duration (hrs)	Predator		Number predators examined	Prey	Number prey/ predator	Percentage prey digested	Numbers prey/ml	FR or LR nos/hr/Tin	FR or LR μm^3/hr/Tin	FR ml/hr/Tin
0	Tintinnopsis cylindrica	①	10	M. lutheri	53.9±12.2	39	-	-	-	-
6.7	"	②	6	Old: M.L.	8.3±5.2	38	nil (starved)	6.8	462(L)	-
7.17	"	③	9	Old: M.L. and New	8.6±9.4	75	nil	6.3	430(L)	-
		④		Isoselmis sp.	3.9±3.9	26	13000	0.54	43(F)	0.00004
0	"	⑤	6	D. tertiolecta	16.7±6.0	50	-	-	-	-
7.17	"	⑥	7	Old: D.T.	3.4±2.6	88	nil (starved)	1.85	615(L)	-
7.66	"	⑦	11	Old: D.T. and New	2.1±3.1	100	nil	1.91	635(L)	-
		⑧		M. lutheri	24.8±11.0	6	4000	3.24	220(F)	0.0008
0	"	⑨	11	Isoselmis sp.	14.8±7.5	61	-	-	-	-
8.0	"	⑩	7	Old: Isoselmis sp.	8.6±2.5	100	nil (starved)	0.78	62(L)	-
8.33	"	⑪	5	Old Isoselmis sp. and New	1.0±1.4	100	nil	1.66	133(L)	-
		⑫		M. lutheri	41.6±19.2	40	3500	5.00	340(F)	0.0014

One-way ANOVA

F-value	Significant
29.01	yes (.01)

Comparisons (Scheffé's Test) with a significant difference at .05 level

1/2, 1/3, 1/4, 1/6, 1/7, 1/9, 1/10, 1/11, 3/8, 3/11, 3/12, 4/5, 4/8, 4/9, 4/12, 5/6, 5/7, 5/11, 6/8, 6/9, 6/12, 7/8, 7/9, 7/10, 7/12, 8/11, 9/11, 10/11, 11/12.

TABLE 23. Continued

Duration (hrs)	Predator	Number predators examined	Prey	Number prey/ predator	Percentage prey digested	Numbers prey/ml	FR or LR nos/hr/Tin	FR or LR μm^3/hr/Tin	FR ml/hr/Tin
0	Helicostomella kiliensis	3	M. lutheri	8.0±7.0	12	-	-	-	-
6.7	"	2	Old M.L.	2.0±1.4	50	nil (starved)	0.9	45	-
0	"	2	D. tertiolecta	5.5±2.1	0— 36	-	-	-	-
7.66	"	1	Old D.T. and New M. lutheri	0.0	nil	nil	0.72	239	-
				0.0	nil	4000	nil	nil	nil
0	"	2	Isoselmis sp.	6.0±1.4	50	-	-	-	-
8.33	"	2	Old Isoselmis sp. and New M. lutheri	0.0	nil	nil	0.72	58	-
				11.5±9.1	74	3500	1.38	110	0.00039

One-way ANOVA F-value	Significant
0.61	no

0	Tintinnidium mucicola	5	M. lutheri	4.0±1.9	60	-	-	-	-
0	"	4	D. tertiolecta	nil	nil	-	-	-	-
7.17	"	2	Old D.T.	nil	nil	nil (starved)	-	-	-
7.66	"	3	Old. D.T. and New M. lutheri	nil	nil	-	-	-	-
				nil	nil	-	-	-	-
0	"	4	Isoselmis sp.	18.3±13.9	40	-	-	-	-
8.0	"	1	Old Isoselmis sp.	4.0	100	nil (starved)	1.78	143	-
8.33	"	1	Old Isoselmis sp. and New M. lutheri	0.0	nil	nil	2.20	176	-
				0.0	nil	3500	nil	nil	nil

TABLE 23. Continued

Duration (hrs)	Predator	Number predators examined	Prey	Number prey/ predator	Percentage prey digested	Numbers prey/ml	FR or LR nos/hr/Tin	FR pr LR μm^3/hr/Tin	FR ml/hr/Tin
0	Eutintinnus latus	1	M. lutheri	10.0	50	-	-	-	-
6.7	"	1	M. lutheri	8.0	33	nil (starved)	0.3	20	-
7.17	"	1	Old D. tertiolectus	10.0	100	nil (starved)	-	-	-
7.66	"	1	Old D. tertiolectus and New M. lutheri	2.0	100	-	-	-	-
				6.0	100	4000	0.78	261	0.0002
0	"	1	Isoselmis sp.	8.0	88	-	-	-	-
0	E. tubulosus	1	D. tertiolecta	8.0	33	-	-	-	-

TABLE 23A. Summary of accumulation experiments with Tintinnopsis subacuta.

Table Number	Prey	Max. FR ml/hr/Tin.	Numbers prey/ml	Maximum Av. Prey Nos/Tin.	Max. Prey Volume/Tin.	Diffl. Pred.	Apparent Selection
7	D. tertiolecta	0.0065	1,750	32.5	6,825	---	---
10	D. tertiolecta	0.0018	15,600	25.1	4,718	---	---
12	Eutreptiella sp.	0.0004	4,400	18.3	9,100	Yes	No
12	I. galbana	0.00004	66,000	26.3	1,200	Yes	Yes
13	D. tertiolecta	0.00034	4,400	9.7	2,040	Yes	Yes
13	Eutreptiella sp.	0.0018	1,500	16.0	8,000	Yes	No
13	I. galbana	0.00011	66,000	46.7	2,100	Yes	No
14	Eutreptiella sp.	0.0023	3,650	5.3	2,650	Yes	No
14	Isoselmis sp.	0.00010	30,000	2.0	150	Yes	No
15	M.llutheri	0.0020	13,000	26.5	1,325	Yes	No
15	D. tertiolecta	0.0003	6,200	2.0	400	Yes	No
16	Eutreptiella sp.	0.0042	1,400	16.0	7,200	Yes	Yes
16	M. lutheri	0.0018	8,000	26.0	1,300	Yes	Yes
16	Isoselmis sp.	0.0011	6,600	12.6	945	Yes	Yes
21	M. lutheri	0.0017	5,000	17.4	730	Yes	No
21	Cryptomonas sp.	0.0004	2,000	1.0	280	Yes	No
22	M. lutheri	0.0010	16,000	24.2	---	No	No
22	Plagioselmis sp.	0.0010	8,000	13.0	---	No	No
22	Eutreptiella sp.	0.0019	3,800	2.4	---	Yes	No
22	Isoselmis sp.	0.00048	15,000	2.4	---	Yes	No

M. lutheri. This may be due to the fact that many more new food cells were accumulated in 7 to 8 hours by the T. cylindrica individuals containing old Isoselmis sp. (and thus the smallest total volume of old food) than in the other two cases. However, the difference between the accumulations of new M. lutheri in T. cylindrica containing old D. tertiolecta or old Isoselmis sp. was not significant.

Hence, the 'forcing effect' of new food on old food may depend somewhat on the amount of new food eaten. The small loss of old M. lutheri during the very small accumulation of Isoselmis sp. seems to emphasize this point. It is interesting that T. cylindrica (as T. subacuta and Stenosomella ventricosa in previous tables) shows differential (negative) predation/accumulation on Isoselmis sp. The relationship of old and new food is also discussed later in this Section. The gain/loss ratio for T. cylindrica was positive in terms of numbers when new M. lutheri followed old D. tertiolecta or old Isoselmis;; but was positive in terms of cell volumes only in the latter case. This is because M. lutheri and Isoselmis sp. are of similar size (50 and 75 μm^3) but D. tertiolecta is much larger (200 μm^3).

The sample sizes of Helicostomella kiliensis in Table 23 were too small to show significant differences between means even if they had existed, but the rates of feeding and loss in this species were lower than in the considerably larger T. cylindrica, except that old Isoselmis sp. was lost at about the same rate in the two species. Table 23 also shows again the apparent relative affinity for Cryptomonad cells by Tintinnidium mucicola. The accumulation and loss rates of this tintinnid species on Isoselmis sp. were not only much larger than on the other two food types, but were also slightly larger than the feeding or loss rates of T. cylindrica or

H. kiliensis on Isoselmis sp. The loss rate of one individual of T. mucicola given the opportunity to eat M. lutheri (although it did not do so) was greater than that of one starved T. mucicola cell. It is possible that relative 'activity' (eg. 'handling'or avoiding particles) has some effect on the rate of loss of old food material. The loss rate of old D. tertiolecta from one starved Eutintinnus latus was slower than in one E. latus cell fed with new M. lutheri (Table 23).

In summary, the results of Tables 21, 22, and 23 indicate that feeding rates in four species of tintinnid are little affected by changes in temperature after acclimation for several hours (Table 21); but that simultaneous loss rates are somewhat increased at very high temperatures. Table 21 also showed once more the apparent differential predation of T. subacuta and T. parvula against a cryptomonad prey, and of T. mucicola against a non-cryptomonad prey. The loss rates (in numbers) varied directly with the cell size of the tintinnid species, as did the feeding rates in a general sense. Loss rates (in biomass) were greatest for T. subacuta, since some of its old food items were extremely large. In Tables 22 and 23 the old food items were of known species, and parallel experiments were done with starved and fed tintinnids. T. subacuta as shown in Table 23, for once did not eat proportionately less of a cryptomonad (Plagioselmis sp.) then of M. lutheri; and when starved, T. subacuta also lost both of these prey types in proportion. However, negative differential predation was seen against the new cryptomonad food Isoselmis sp. when compared with the new Eutreptiella sp. in Table 22. In Table 22 it can be seen that old food is lost more rapidly when new food is added, than when the tintinnid is starved. An alternative (or additional) explanation for these results if that loss rates decline exponentially with time whether the tintinnid is fed or not.

Table 23 shows that the loss rates of old food from Tintinnopsis cylindrica in a long (7 - 8 hour) experiment were in some cases a function of the amount of new food eaten (or vice-versa), which in turn depended upon the type of new food presented. T. cylindrica was the fourth species in this study to show negative differential predation on the cryptomonad Isoselmis sp.

Individual variability in tintinnids losing old food and eating new food

In the previous experimental results there appeared to be a positive relationship between the average amount of new food added to, and the average amount of old food concurrently lost from tintinnids. It was not clear which of the two processes was the controlling factor in the relationship. It is probable that the process of ingestion of food in some way 'forces' the tintinnid to 'lose' food more rapidly; and starving cells or cells with relatively little food seem to lose it at a slower rate than do well-fed cells (Table 22, 23; and Rapport, unpublished data). Also Berger (1971) and Goulder (1972) have shown that old food disappears from some other ciliates at a rate which is much faster initially than later. This is also a well known phenomenon in during the egestion of solid particles and the excretion of metabolites by planktonic crustacea.

The amount of old food inside a tintinnid may also place some reciprocal upper limit on its feeding rate on new food. There may be an upper limit for the total number or volume of all contained food cells which is constant for a particular tintinnid species, and at which ingestion rate equals the maximum digestion rate. If this 'reservoir size' is approximately a constant then the total of old and new food should be very similar in different individuals in one experiment, no matter what the variability of either old or new

food per tintinnid. Also, if this theory holds the mean values of old and new food in several tintinnids in each of a successive series of samples, should lie on a negatively sloping regression line of old (x) on new (y) food; and the individual values should fall close to such a line with relatively small variance. Thirdly to fulfil the predictions of this theory, the values of the two intercepts extrapolated from a line joining the means of successive samples should be similar and be equivalent to the mean theoretical reservoir size for that species (ie. the line should have a slope of -1.0).

As an indication that the 'constant reservoir' theory is unlikely to be true, it can be calculated from Tables 21 to 23 that there is a wide range in average numbers of old plus new food cell totals for each species in various parts of those experiments. The range is 8.9 to 30.2 total food items/tintinnid for Tintinnopsis subacuta; 12.5 to 53.9 for T. cylindrica; 6.0 to 19.6 for T. parvula and 5.0 to 12.2 for Tintinnidium mucicola. The ranges of hourly gain to loss ratios for averages of these species can also be calculated from Tables 21 to 23, and these too are fairly wide. These ranges are: for Tintinnopsis subacuta 0.72 to 3.1 (number) and 2.9 to 4.6 (volume); for T. cylindrica 0.08 to 3.0 (number) and 0.1 to 2.0 (volume); for T. parvula 1.7 to 3.5 (number) and for Tintinnidium mucicola 0.46 to 1.8 (number).

The results of two experiments done 4 days apart to test this theory are shown in Figures 6 and 7. Firstly it is obvious that the variance about any regression line in Figures 6 and 7 is very large, and that the reservoir theory mentioned above does not hold in terms of volume. In fact, as the necessary conditions for normal linear regression analysis do not apply to Figures 6 and 7, a constrained linear regression analysis was performed. The line was constrained about the Y axis at a point equivalent to the mean of

Figure 6. Relationship between the volume ($\mu m^3 \times 10^2$) of old food and new food contained by individual Tintinnopsis subacuta.
new food - Dunaliella tertiolecta
old food - Isochrysis galbana and natural food items.
○ Low concentrations of I. galbana checked at 0 + 5 mins.
● Low concentrations of I. galbana checked at 0 + 57 mins.
△ High concentrations of I. galbana checked at 0 + 8 mins.
▲ High concentrations of I. galbana checked at 0 + 68 mins.

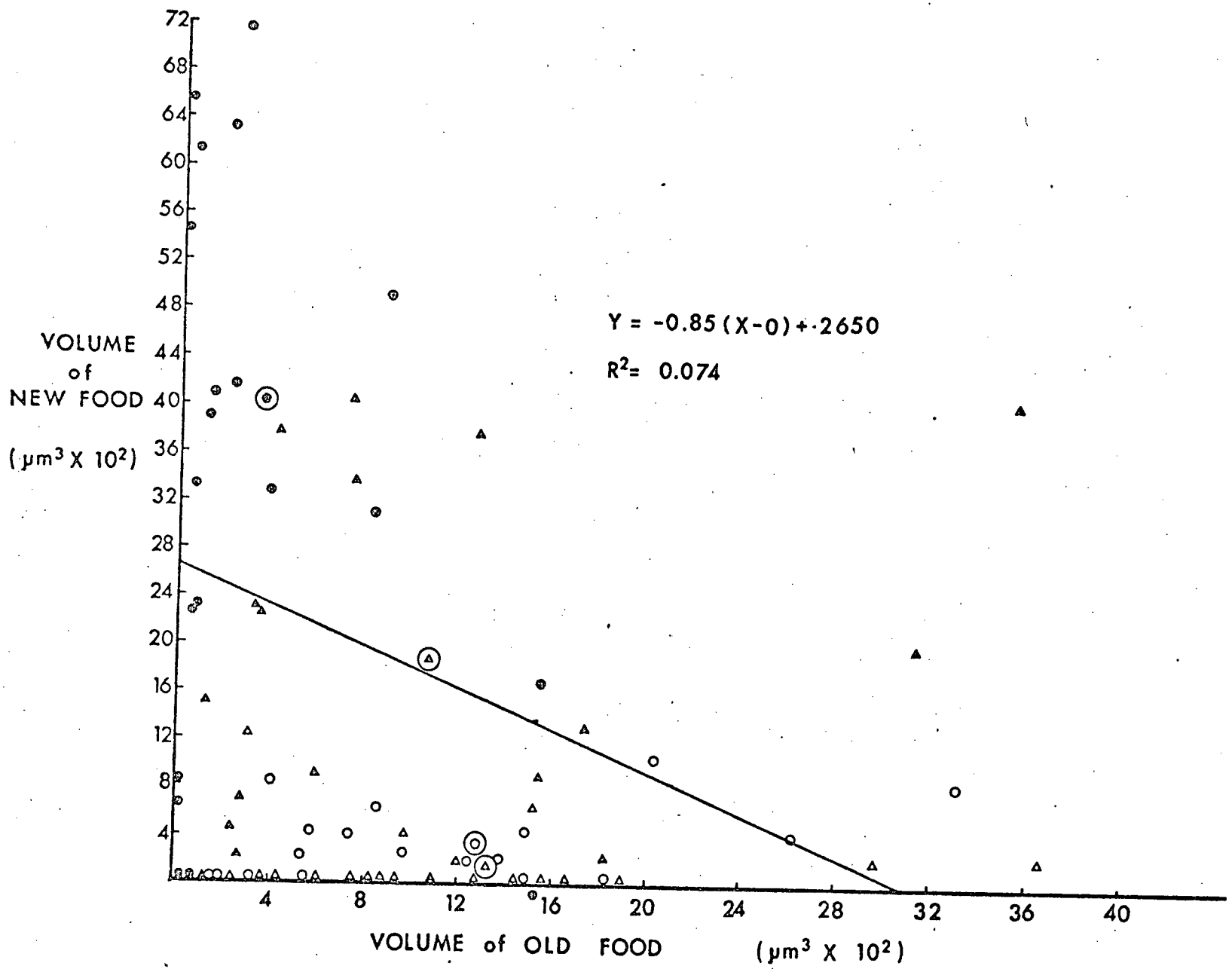
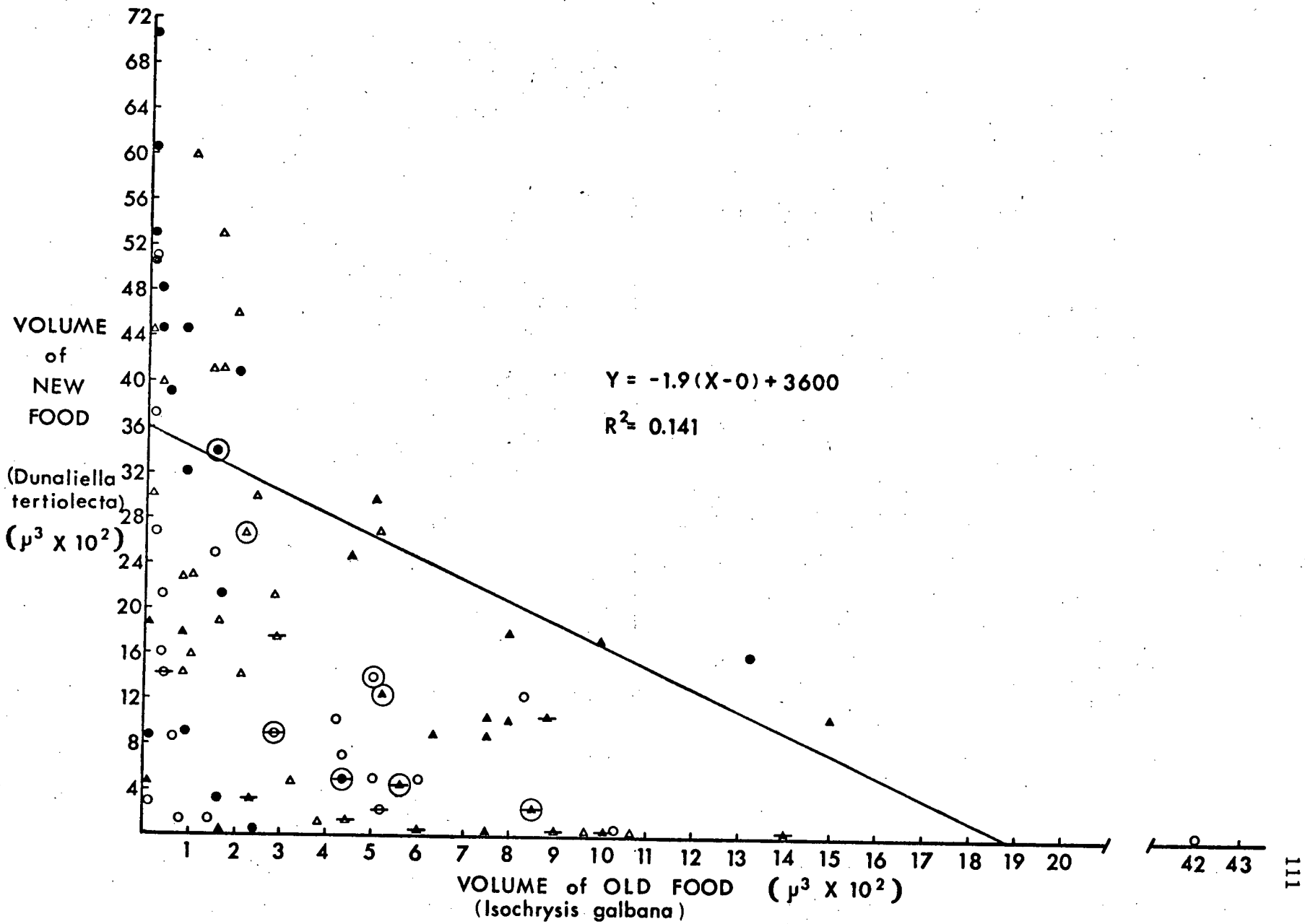

72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
VOLUME of NEW FOOD (μm³ X 10²)
Y = -0.85 (X-0) + 2650
R² = 0.074
4
8
12
16
20
24
28
32
36
40
VOLUME of OLD FOOD (μm³ X 10²)

Figure 7. Relationship between the volume ($\mu m^3 \times 10^2$) of old food and new food contained by individual Tintinnopsis subacuta and Stenosomella ventricosa.

O - T. Subacuta
⊖ - S. ventricosa
new food - Dunaliella tertiolecta
old food - various
O - Tintinnids in filtered water for 7 hours.
● - Tintinnids from field sample.
△ - Tintinnids from field sample plus high concentrations of 5 μm dia. polystyrene latex.
▲ - Tintinnids from field sample plus high concentrations of Isochrysis galbana.


72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
VOLUME of NEW FOOD (Dunaliella tertiolecta) (μ³ X 10²)
Y = -1.9(X-0) + 3600
R² = 0.141
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
42 43
VOLUME of OLD FOOD (μ³ X 10²)
(Isochrysis galbana)

all Y values when X (old food) was zero. The regression analysis shown in Figure 7 was performed only on data from Tintinnopsis subacuta. In these circumstances, the regression of X on Y would naturally be significantly different from zero. However, the regression coefficient (R^2) in both Figures 6 and 7 is very small, indicating great individual variability in the data. The values (volume) of the X and Y intercepts are very similar in Figure 6 where the old food was Dunaliella tertiolecta and the new food was Isochrysis galbana etc. However, the value of the X intercept in Figure 7 is about half that of the Y intercept value, and here the old food is either I. galbana, 5 μm latex, or small natural particles, all smaller than the new food D. tertiolecta. Therefore the intercept values of X and Y if based upon food cell numbers would not be similar in either experiment. It is curious that the mean values of the various sub-groups in Figures 6 and 7 do fall close to an imaginary straight line despite the large scatter of the individual values.

A one-to-one correlation between the intercept volumes might be expected if the limitation on feeding rate was set in some way by the total volume of food inside the tintinnid undergoing digestion. A one-to-one correlation between the intercepts in terms of numbers of old and new food items might be expected if each item is contained in a different food vacuole, as is usually the case particularly for large items, and if the formation of food vacuoles is the limiting factor in the process of ingestion. Certainly food vacuole membrane synthesis is an extremely active process in some phagotrophic protozoa (Ricketts, 1971); but recent work with the ciliate Paramecium caudatum (Allen, 1973) has indicated that the food vacuole membrane in this species is neither finally egested with the food residue nor broken down into its components, but is 'conserved' as fragments in small vesicles which

may be rapidly transported back to the oral region for reuse. On the other hand, Ricketts (1973) states that the digestive enzymes within food vacuoles in Tetrahymena pyriformis are not conserved at egestion, but are lost to the medium. Ricketts thinks that the ingestion rate of T. pyriformis is ultimately limited by the availability of digestive enzymes. An experiment with Paramecium aurelia showed that food vacuoles containing old red carmine particles were reduced in number at the same rate as vacuoles containing new black ink particles were formed by the ciliate (J.D. Berger, unpublished data). If there is any correspondence at all between the loss of old food and the gain of new food in tintinnids, it is perhaps a little more likely especially for large prey to be on a number (or food vacuole?) basis than on the basis of relative volumes or biomass of material. This is a subject about which very little is known for any protozoan.

There are several other possible explanations for the great variability in feeding rates between individual tintinnids seen in the results of these accumulation experiments. These are that variability may be due to one or more of the following: 1) Heterogenous distribution of food items in the environment; 2) the size of the unused portion of the pool of digestive enzymes in the cell, which in turn may be the product of (a) the recent feeding rate and biomass of prey, and (b) the less-recent nutritional history and the subsequent rate of synthesis of digestive enzymes; 3) differential physiological effects of the immediate environment, other than food; 4) short-term spontaneous changes in motion or feeding behaviour; 5) the age of the tintinnid cell or how recently the parent cell divided; 6) genetic variability among members of a clone or between strains or syngens within a species. Most of these possibilities have not been tested in tintinnids, nor in any protozoan.

(1) The heterogenous distribution of food items may be a factor particularly in less dense cell concentrations or when experimental vessels are not agitated. In fact, experiments with very dense cell concentrations or with stirred samples seem to contain as much individual feeding variability as any others. (2) Differential digestive enzyme synthesis and utilisation is a likely possibility which could have complex effects on the future feeding performance of a tintinnid. Theoretically, larger species should have a greater capacity for enzyme synthesis and storage than smaller species, and therefore should be less individually variable; and previously well-fed individuals of any species should be better able to recover from starvation when once re-fed, than individuals whose history has been one of poor nutrition (and see Ricketts, 1973). Feeding on 'blooms' or dense concentrations of the same species or quality of prey type, should rapidly reduce the variance in feeding performance in a tintinnid species caused by factor (2). Fenchel (1968) has shown that for many species of benthic ciliate the maximum reproductive rate decreaseswwith increasing cell volume. As this is probably also true for tintinnids it is likely that when all species are at (or near) their maximum reproductive rate, the variation between cells due to different nutritional histories will be reduced more rapidly in small species than in large ones. However, small species almost certainly need much denser concentrations of food to reach their maximum reproductive rate than do large species (see General Discussion). (3) Differential physiological effects of unknown origin are also a distinctly possible source of variation in individual feeding rates, and this is borne out by the differences in feeding behaviour sometimes observed in this study amongst individuals of the same species. This possibility could best be tested when it is possible to grow laboratory cultures of tintinnids under completely controlled conditions.

TABLE 24. The relationship between tintinnid cell length and number of accumulated food items in two species taken from different experiments.

Species	Cell Length (µm)	Cell Diameter (µm)	Lorica Length (µm)	Number of Food Items: Brown Cells 6-8µm dia.
Tintinnidium mucicola	40	35	40	3
"	40	35	100	7
"	45	35	110	6
"	45	35	125	4
"	80	35	150	11

Species	Cell Length (µm)	Cell Diameter (µm)	Lorica Length (µm)	Volumes of Food Items µm³: TYPE 1 Natural large dinos, Eutreptiella sp.	TYPE 2 Isochrysis galbana
Eutintinnus latus	100	70	nil	1450	45
"	100	70	nil	8500	800
"	100	70	250	3800	700
"	100	70	250	7850	840
"	125	70	220	7700	770
"	125	70	250	1100	420
"	200	70	250	6500	525
"	200	70	275	7000	280

(4) Spontaneous changes in feeding behaviour have not been seen in this study but Strathmann (1971) has noted them in echinoderm larvae. (5) The age of a tintinnid cell is probably not an important cause of variability in feeding rate, apart from the fact that a parental cell will probably not have fed during division so that a very newly divided cell may contain less food than do others. Table 24 shows that in two experiments involving different species of tintinnids there was no relationship between tintinnid cell length and the amount of food contained therein.

b) Observations of Tintinnid Motions and Feeding Behaviour

Many of the tintinnids studied had characteristic motions so that they could sometimes be identified even when without a lorica. All tintinnids rotate the cell and lorica on its long axis and also follow helical paths which are normally of a characteristic angle in healthy organisms. The largest species are generally the fastest and several species move at about five cell lengths per second. Stensosomella nivalis and Helicostomella kiliensis move rapidly for their size and Tintinnidium mucicola moves rather slowly for its size. The most important feature of the motion for a predator of this type is the frequency of contact with food rather than the velocity of the predator. All food items tested in this study were slower in motion than the tintinnids used, and the distribution and motion of both food items and predators can reasonably be regarded as random. There was negligible contact between predators at the concentrations used in this study. The velocity (in um/sec) of a tintinnid species may be a function of the length and number of its adoral cilia; and its 'search rate' (in ml/hr) is a function of its velocity and of the effective diameter of the vortex created by its adoral cilia. A helical path will not increase the frequency of contact with randomly dispersed prey so long as the predator's velocity remains unchanged. Larger and faster prey are contacted more frequently than smaller and slower prey at the same concentration, and this may explain some of the apparent differential predation of Tintinnopsis subacuta on Eutreptiella sp. when compared to other prey presented singly in this study. The 'contact rate' (CR - in ml/hr) is the product of the search rate of the tintinnid species and the concentration (in nos/ml) and velocity of the prey items. All particles which cause a tintinnid to interrupt its normal motion, whether the item is eaten or not, will reduce the long-term contact rate. Feeding rate

(FR) is calculated either: as the number of items observed to be successfully eaten per hour; as the number found to be accumulated in the tintinnid per hour: or as the volume of water theoretically cleared of food in ml/hr., for each type of food.

The direct measurement of tintinnid velocities and search rates by eye is made very difficult by their helical motion and frequent changes of direction. Relative and absolute contact rates of tintinnids and (if they ate) their feeding rates, have been obtained from a study of their reactions to known concentrations of identifiable food items. Unfortunately observations of 'contacts' have a subjective element. Where a tintinnid ate, or attempted to eat, or changed direction after contact - then a 'contact' could be confirmed. However, all tintinnid species apparently contacted many more particles than were eaten (see Table 26), i.e. particles would be swept towards the oral region and apparently collide with the inside of the spiral of adoral cilia and be moved out again without being eaten. It is perhaps invalid to assume that a tintinnid was "in a position" to eat such items or even that they could have eaten those particles which cause them to make sudden changes of direction.

Small particles (4 - 10 μm) were definitely seen to be eaten at times in conjunction with a slight, brief 'tremor' or 'shudder' in the motion of the tintinnid. The method used by tintinnids to retain small particles is unknown. Perhaps mucus may be secreted to form a sheet or meshwork near the oral region (Laval, 1971); or the partially overlapping insertion of the adoral cilia may act as a barrier to any particle which is intthe centre of the vortex created by the beating of those cilia. Strathmann (1971) and Strathmann, et.al., (1972) have shown that many ciliary feeders do not use

mucus, but trap particles either by (a) a local induced reversal of beat of individual cilia or (b) by the downstream entrapment of particles against a second row of cilia. Tintinnids may use one of these or other methods to obtain particles very small relative to their oral dimensions. Larger items cause a longer interruption of the normal tintinnid motion; usually with the adoral cilia bent inwards so preventing the escape of the prey, whilst the other oral cilia attempt to push it further down the cytopharynx. During this period the motionless tintinnid slowly sinks. This process takes about two seconds for Tintinnopsis subacuta feeding successfully on Eutreptiella sp; and takes 6 - 8 seconds for Eutintinnus latus feeding on the same prey unsuccessfully. Although particles smaller than about 4 µm diameter could not be seen with the stereo microscope, one aspect of tintinnid behaviour indicated that very small particles were being eaten (and see Section 4c). A unique feature of tintinnids is the possession of a region of extensile cortical cytoplasm adjacent to the oral groove/cytopharynx region and called the oral plug. (see Figure 1). This oral plug can be seen occasionally to 'pump' or move back and forth quite violently as the tintinnid swims in its normal motion. The exact function of this pumping is unknown but it is particularly obvious in Tintinnidium mucicola. The pumping motions of five individuals of this species were counted as they were observed for varying lengths of time in seawater containing many flagellates and other small particles. 'Contacts' between T. mucicola and particles visible to the observer were also counted. Both measurements were also made of five individuals placed in seawater which had been filtered a few days before but which contained some particles. The average figures for the tintinnids in the filtered water were 7.1 'pumps' and 4.5 contacts/minute; for those in the unfiltered water the averages were 17.4 'pumps' and 9.7 contacts/minute. Pumps exceeded contacts in both cases, just

as small particles usually outnumber large ones; and the ratios of pump/contact were respectively 1.67 and 1.58 in the two kinds of water. This would seem to be evidence that the rate of 'pumping' at least in T. mucicola is a direct function of the number of very small particles in the water and may be connected with the rate of feeding on them.

Unwanted particles which have definitely been observed to enter the cytopharyngeal region of a tintinnid are usually ejected by a momentary reversal of some or all of the cilia in the oral region. A very powerful or prolonged ciliary reversal of this type will cause the tintinnid to reverse direction away from the object, as also happens after contact with objects larger than the tintinnid. Rarely, a tintinnid which cannot eject an object in this way may move its aboral end through 180°, and then reverse to move away from the object. Some individual cells, particularly of Tintinnidium mucicola, may show apparent signs of stress in the form of aberrant motion, for several seconds after ejecting an unwanted object. The characteristics of certain large prey items which prevent them from being ingested by a particular tintinnid species were experimentally investigated as shown in Table 25. The predator was Eutintinnus latus (lorica 250x70 μm; cell 80-200x60 μm) and the prey were algal flagellates from laboratory cultures; Eutreptiella sp. (25x7x4 μm) and Cryptomonas profunda (30x10x4 μm). It had been noticed in a qualitative test that E. latus contained C. profunda but not Eutreptiella sp. although the latter is only about half the volume of the former.

The attempts of E. latus to ingest these flagellates when they were presented in single-prey samples, was observed with the prey in either normal, or an immobilized condition. Mild sonication for 15 seconds immobilized both prey types, but with different results. Sonicated Eutreptiella sp. lost

TABLE 25. The effect of immobilization by sonication on the successful ingestion of algal flagellates by the tintinnid, Eutintinnus latus. Temperature 18-20°C.

Prey Type	Prey Condition	Number of Tintinnids	Total Number Contacts	Successful Ingestion Events	Handling Time (Secs.)	Rate of* Contact with prey No./Min.	Number prey cells/ ml.	Contact* Rate ml/hr/Tin.	Ingestion* Rate ml/hr/Tin.
Eutrepticlla sp.	Normal	3	13	0	6-8 (Av. 7.3)	4.6	5230	0.053	0
"	Immobile	3	7	5	2-12 (Av. 4.8)	3.0	5230	0.034	0.025
Cryptomonas profunda	Normal	6	11	6	5-19 (Av. 9.3)	2.9	4630	0.038	0.021
"	Immobile	3	2?	0	0	0.82	4630?	0.011?	0?

* These rates are calculated as the total elapsed time of a "run" and include handling time.

their flagellae, became more rounded and could not swim, but were definitely alive and showed the unique euglenoid type of cell motion when supported on a glass slide. Sonicated C. profunda did not lose their flagellae, but were unable to move whether supported or not. C. profunda may have been killed by this treatment, and the results in Table 25 may reflect this. Normal Eutreptiella sp. moved at about 250 to 400 µm/second at 18-20 C, or about 10 to 16 cell lengths/second. C. profunda moved about ½ as fast as Eutreptiella sp.

'Contacts with prey' were conservatively equated with visible 'attempts at ingestion' since only then was it certain that the tintinnids were aware of a prey item. The two contacts with immobilized C. profunda were 'glancing blows' causing E. latus to change direction slightly and may not have been what they seemed, i.e. the rapid identification and rejection of probably inedible prey items. Therefore, it is doubtful whether E. latus rejected the immoblized C. profunda. However, from Table 25 it is obvious that the immobilization of Eutreptiella sp. definitely made a difference to the ability of E. latus to handle and eat it (from 0 to 71% success), and also reduced the handling time by 35%, though this may not be a significant difference. Naturally, random contact with immobilized Eutreptiella sp. was less frequent than with normal Eutreptiella sp. Normal Eutreptiella sp. were always released unharmed after attempted ingestion. The very high ingestion rate (or FR/P) of 0.025 ml/hr of E. latus on immobilized Eutreptiella sp. was very similar to that on C. profunda, but the individual handling time on the latter was longer.

It is interesting that E. latus is about seven-fold larger than Tintinnopsis subacuta (see Table 1) which ingests Eutreptiella sp. in about two seconds. Both these tintinnids and Tintinnopsis cylindrica have adoral cilia of about 35 µm length, but T. cylindrica moves a little more slowly than

T. subacuta and was not seen to ingest Eutreptiella sp. in the laboratory. Stenosomella ventricosa has exceptionally thick and powerful-looking adoral cilia (Table 1) but moves only a little faster than T. subacuta and eats Eutreptiella sp. much less frequently than the latter (see Section 4a (ii)). However, the adoral cilia of S. ventricosa are 50 µm long; as are those of Favella serrata which is about 10 times larger. Perhaps the number of cilia per tintinnid rather than their length is important in providing both higher speeds and increased ability to subdue prey. It was impossible to make definitive counts of the numbers of adoral cilia in this study, but they appeared to differ rather narrowly between species from about 16 to 24.

Tintinnid contact rates

Table 26 shows the contact rates of various tintinnid species on natural and laboratory food items in the same, and in different, experiments. Other contact rates may be seen in Table 8 and 9 (accumulation experiments). These results indicate that under the conditions of observation and with the cell concentrations used, tintinnids ate very few of the particles encountered even when the tintinnids were active and in large numbers in the environment. Therefore it is possible that the experimental conditions were not optimal for tintinnid feeding. It can also be seen in Table 26 that the activity of different species is not affected to the same extent by dense concentrations of particles. Although there is considerable variability between experiments, on the whole the values of the contact rates (and therefore probably the search rates) for Tintinnopsis subacuta and Stenosomella ventricosa are similar, with the latter perhaps a little higher. This supports the relative feeding rates estimated in the results of the Accumulation (Section 4a) and Coulter Counter (Section 4c) experiments, except when the two species were

TABLE 26. Observed contact rates of various tintinnid species on natural and laboratory food items.

Experiment Number	Prey	Predator	Average contacts/ min/Tin.	Prey Nos/ml	CR ml/hr/Tin.	Average Ingestions/ min/Tin.	FR ml/hr/Tin.	Relative CR	Comments
1A	Natural particles	T. subacuta	18.8	12,200	0.092	nil	nil	IF 1.0	Unusually sluggish
	"	T. parvula	21.8	12,200	0.107	nil	nil	1.2	--
	"	T. mucicola	3.5	12,200	0.017	nil	nil	0.2	Rejections lengthy
	"	S. nivalis	28.8	12,200	0.141	nil	nil	1.5	Very active
1B	Natural particles and Dunaliella tertiolecta	T. subacuta	22.4*	19,700	0.068	nil	nil	IF 1.0	Very slow, shallow spirals
		S. ventricosa	28.6	19,700	0.087	nil	nil	1.3	--
		T. mucicola	15.8	19,700	0.048	0.75	0.0023	0.7	Violent rejection motion
	"	S. nivalis	18.5	19,700	0.056	nil	nil	0.8	Rapid shallow spirals
1B (+ 12 hrs)	Natural particles and Dunaliella tertiolecta	T. subacuta	16.3	?	-	nil	nil	IF 1.0	--
		T. parvula	11.3	-	-	nil	nil	0.7	--
		S. ventricosa	17.7	-	-	nil	nil	1.1	--
		T. mucicola	7.0	-	-	nil	nil	0.4	--
		S. nivalis	6.3	-	-	nil	nil	0.4	--
2	Natural particles most < 10 µm	T. subacuta	36.2	9,500	0.226	nil	nil	IF 1.0	Bloom ~6/ml
		S. ventricosa	40.0	9,500	0.252	nil	nil	1.1	
		T. mucicola	22.0	9,500	?	nil	nil	0.6	
		S. nivalis	22.0	9,500	?	nil	nil	0.6	
3	Natural particles	T. cylindrica	32.0	71,000	0.027	nil	nil	IF 1.0	
		T. mucicola	18.2	71,000	0.022	2.30	0.0018	0.8	
		H. kiliensis	42.2	71,000	0.036	nil	nil	1.3	
		E. tubulosus	9.8	71,000	0.011	0.37	0.0004	0.4	
4A	Natural particles and dense Isosclmis sp.	T. cylindrica	27.0	-	-	nil	-	IF 1.0	
		T. mucicola	9.0	-	-	0.8	-	0.3	
		H. kiliensis	7.9	-	-	nil	-	0.3	
		E. latus	14.2	-	-	nil	-	0.5	

* 0.29 of contacts were with D. tertiolecta (0.37 of all particles)

TABLE 26. Continued

Experiment Number	Prey	Predator	Average contacts/ min/Tin.	Prey Nos/ml	CR ml/hr/Tin.	Average Ingestions/ min/Tin..	FR ml/hr/Tin.	Relative CR	Comments
4B	Natural particles and dense Dunaliella tertiolecta	T. cylindrica	29.0	-	-	nil	-	IF 1.0	
		T. mucicola	9.2	-	-	nil	-	0.3	
		H. kiliensis	8.2	-	-	nil	-	0.3	
		E. tubulosus	2.0	-	-	nil	-	0.1	
5	Monochrysis lutheri	T. parvula	18.4	36,000	0.030	nil	-	IF 1.0	
		T. mucicola	13.9	36,000	0.023	0.80	0.0017	0.8	

eating Eutreptiella sp.. The contact rates of Tintinnopsis parvula, Tintinnidium mucicola and Stenosomella nivalis were on the whole not very different, and were about 0.3 to 1.0 of the values for T. subacuta. This also partly supports the relative feeding rates calculated by the other methods, particularly for T. parvula.

Tintinnopsis cylindrica appeared to have a slightly lower contact rate than T. subacuta when seen in the same sample (qualitative observation) but there are no data for this comparison. T. mucicola and Helicostomella kiliensis had contact rates which were similar and equivalent to 0.3 to 1.3 of those of T. cylindrica. The contact rates of Eutintinnus tubulosus were only about 0.1 to 0.4 of those of T. cylindrica and less than those of H. kiliensis (and see Table 9). In contrast, the numbers of accumulated food items in E. tubulosus and H. kiliensis were fairly similar in one accumulation experiments (see Table 9), but there are no short-term accumulation estimations of feeding rate in these two species. The large tintinnid Eutintinnus latus in one experiment in Table 26 has a contact rate of only about half of that of T. cylindrica, although in the results seen in Table 25 E. latus had a very high feeding rate.

Table 26 shows that very few items were definitely seen to be eaten during these observations, but the feeding rates shown for T. mucicola are comparable with those seen in the results of the accumulation experiments (section 4a). Attempts were made to observe changes in contact and feeding rates during the progress of experiments and as tintinnids starved or slowed their apparent accumulation of food items, but none of these attempts was satisfactory.

c) The effect of microzooplankton on natural and laboratory phytoplankton populations (Coulter Counter Experiments)

General

The feeding rates of two species of tintinnids and the late naupliar (Stage V and VI) stages of a small copepod (probably Pseudocalanus minutus) and a barnacle are shown in Appendices 1 to 11. The regulatory effect of the feeding of Tintinnopsis subacuta on natural food particle concentrations is shown in Figs. 12, 13 and 14. The complete lists of observations; multiple correlation coefficients for 10 variables; and simple linear regression coefficients on variable (1) and plots for these Coulter Counter experiments as calculated with the University of British Columbia Computer programme STRIP may be found in Appendices 1 to 11. All results were adjusted to an experimental duration of 24 hours before analysis. Tintinnopsis subacuta was used in experiments with naturally occurring particulate material (44 observations) and laboratory phytoplankton cultures (15 observations); and Stenosomella ventricosa was used with laboratory cultures only (16 observations). Crustacean nauplii were used mainly with laboratory cultures (5 observations), but one experiment was carried out with a field sample. There is one Coulter Counter result of feeding by Tintinnopsis parvula and another by the holotrich ciliate Tiarina fusus, both on field samples. The latter three single experiments were included in the analyses of correlation and regression only in the 'all samples' category.

One experiment involving two species of rotifers has been analysed separately (Table 28). Some of the observations included in the analyses were 'replicates' in the same experiment. Where two or three pairs of control and experimental flasks were used, every possible value of feeding rate (FR/P)

was calculated from every possible combination of all values of C_1, C_2, E_1 and E_2 and included in the analyses to increase the total number of observations. Similarly, flasks within a particular experiment which were subject to manipulation such as placement in the light or dark, additional predators, etc., have all been included without distinction in the general analyses. Calculations of feeding rate as net total consumption (NTC) or as edible spectrum only (ESO) are shown separately. It is obvious from the list of observations in the Appendices that there is great variability in the food consumption rate FR/P (or variable (1)) even amongst 'replicates' in the same experiment (see General Discussion).

Multiple correlation coefficients.

Only those correlation coefficients greater than 0.5 have been included in Tables 27 a,b,c,d. The remainder of the correlation matrices may be seen in Appendices 1 to 11. Those pairs of variables which had correlation coefficients greater than 0.5 are not necessarily the same either in the NTC and ESO results for any one subset of observations (e.g. Tintinnopsis subacuta on laboratory food); nor for NTC (or ESO) results as compared between subsets of observations. Also, the sign of the correlation is often different for the same pair of variables in NTC and ESO results, and/or between subsets of observations. Coefficients for ESO results are generally higher than those for NTC results.

Very few variables are strongly correlated with the food consumption rate (variable 1), and by far the best figures are found with E_1 (variable 2) and logmean E (3) in Tintinnopsis subacuta feeding on laboratory cultures of phytoplankton (Table 27b). The greater coherence of these data may be largely explained by the fact that in most cases the same phytoplankton

TABLE 27A. Multiple correlation coefficients from Coulter Counter experiments. (only those > 0.5 are shown) Tintinnopsis subacuta on natural samples.

Variable	Net total consumption (NTC)	Edible spectrum only (ESO)
	39 observations	44 observations
(1) FR/P Feeding rate μm^3/pred/hr	Nil	2 (.59), 3(.62)
(2) E_1 Initial experimental particle volume μm^3/ml	3(.91), 9(-.81)	1(.59), 3(.98), 4(.68)
(3) Log mean E 12 hr. log mean experimental particle volume μm^3/ml	2(.91), 8(.71), 9(-.63)	1(.62), 4(.75)
(4) ESP. Number of size classes with consumption	5(.58)	2(.68), 3(.75)
(5) C_2/C_1 Increase in total control volume in 24 hrs.	4(.58)	Nil

TABLE 27B. Multiple correlation coefficients from Coulter Counter experiments. (Only those > 0.5 are shown) Tintinnopsis subacuta on laboratory food.

Variable	Net total consumption (NTC)	Edible spectrum only (ESO)
	10 observations	15 observations
(1) FR/P Feeding rate μm^3/pred/hr	6(-.67), 9(-.94)	2(.96), 3(.92), 7(.50)
(2) E_1 - Initial experimental volume μm^3/ml	3(.99), 7(.73), 8(.83)	1(.96), 3(.97), 4(.52), 7(.51)
(3) Log mean E 12 hr log mean experimental particle volume μm^3/ml	2(.99), 7(.67), 8(.81)	1(.92), 2(.97)
(4) ESP - Number of size classes with consumption	Nil	2(.52)
(5) C_2/C_1 - Increase in total control volume	7(-.61)	7(-.59)
(6) PCON - Number preds/ml	1(-.67), 9(.59)	7(-.55)
(7) Alive - Estimated live fraction of preds at 12 hrs	2(.73), 3(.67), 5(-.61) 8(.80)	1(.50), 2(.51), 5(-.59) 6(-.55), 9(-.51)
(8) Temperature ^oC	2(.83), 3(.81), 7(.80)	Nil
(9) Sal. - Salinity ‰	1(-.94), 6(.59)	7(-.51), 10(-.51)
(10) Time - Total duration of experiment	Nil	9(-.51)

TABLE 27C(i). Multiple correlation coefficients from Coulter Counter experiments. Only those > 0.5 are shown. Stenosomella ventricosa (all values) on laboratory food.

Variable	Net total consumption (NTC) 13 observations	Edible spectrum only (ESO) 16 observations
(1) FR/P - Feeding rate - μm^3/pred/hr	6(-.67)	6(-.57), 7(-.67), 10(-.51)
(2) E_1 - Initial experimental volume μm^3/ml	3(.60), 5(-.62), 7(-.50) 8(.81)	3(.90), 4(.71)
(3) Log mean E - 12 hr mean exp. vol. μm^3/ml	2(.60), 9(-.58), 10(.52)	2(.90), 4(.55), 10(.64)
(4) ESP - Number of size classes with consumption	Nil	2(.71), 3(.55)
(5) C_2/C_1 - Increase in total control volume	2(-.62), 7(.79), 8(-.90) 10(.54)	7(.64), 8(-.74)
(6) PCON - Number predators/ml	1(-.67), 9(.67)	1(-.57), 9(.62)
(7) Alive - Estimated live fraction of predators at 12 hrs	2(-.50), 5(.79), 8(-.81) 10(.68)	1(-.67), 5(.64), 8(-.77) 10(.69)
(8) Temperature °C	2(.81), 5(-.90), 7(-.81)	5(-.74), 7(-.77)
(9) Sal. - Salinity ‰	3(-.58), 6(.67), 10(-.53)	6(.62), 10(-.54)
(10) Time - Total duration of experiment	3(.52), 5(.54), 7(.68), 9(-.53)	1(-.51), 3(.64), 7(.69) 9(-.54)

TABLE 27C(ii). Stenosomella ventricosa (one high value of FR/P omitted) on laboratory food.

Variable	Edible spectrum only (ESO) 15 observations
(1) FR/P - Feeding rate - μm^3/pred/hr	2(.56), 3(.56), 6(-.61)
(2) E_1 - Initial experimental volume μm^3/ml	1(.56), 3(.92), 4(.71)
(3) Log mean E - 12 hr mean exp. vol. μm^3/ml	1(.56), 2(.92), 4(.54), 10(.58)
(4) ESP - Number of size classes with consumption	2(.71), 3(.54)
(5) C_2/C_1 - Increase in total control volume	7(.75), 8(-.72)
(6) PCON - Number predators/ml	1(-.61), 9(.68), 10(-.57)
(7) Alive - Estimated live fraction of predators at 12 hrs	5(.75), 8(-.94)
(8) Temperature °C	5(-.72), 7(-.94)
(9) Sal. - Salinity ‰	6(.68), 10(-.70)
(10) Time - Total duration of experiment	3(.58), 6(-.57), 9(-.70)

TABLE 27D. Multiple correlation coefficients from Coulter Counter experiments. (Only those > 0.5 shown)
Barnacles and copepod Nauplii on laboratory food.

Variable	Net total consumption (NTC)	Edible spectrum only (ESO)
	3 observations	5 observations
(1) FR/P - Feeding rate - μm^3/pred/hr	2(-.73), 3(-.90), 4(.84) 5(-.97), 6(-.68), 7(.98) 8(-.91), 9(-.94)	2(.82), 3(.75), 4(.78), 8(-.64) 9(-.68)
(2) E_1 - Initial experimental volume μm^3/ml	1(-.73), 3 (.96), 4(-.98), 5(.87), 7(.85) 8(.95), 10(.91)	1(.82), 3(.99), 4(.79)
(3) Log mean E - 12 hr log mean exp. vol. μm^3/ml	1(-.90), 2(.96), 4(-.99) 5(.98), 7(.97), 8(1.0) 9(.68), 10(.75)	1(.75), 2(.99), 4(.70)
(4) ESP - Number of size classes with consumption	1(-.97), 2(.87), 3(.98) 5(-.95), 7(-.93), 8(-.99) 9(-.60), 10(-.82)	1(.78), 2(.79), 3(.70), 8(-.73) 10(-.72)
(5) C_2/C_1 - Increase in total control volume	1(-.97, 2(.87), 3(.98), 4(-.94), 7(1.0), 8(.98) 9(.83), 10(.58)	6(.80), 7(.92), 9(.80)
(6) PCON - Number predators/ml	1(-.68), 7(.52), 9(.90)	5(.80), 7(.66), 9(.90)
(7) Alive - Estimated live fraction of predators at 12 hrs	1(-.98), 2(.85), 3(.97) 4(-.93), 5(1.0), 6(.52) 8(.98), 9(.85), 10(.56)	5(.92), 6(.66), 9(.61)
(8) Temperature °C	1(-.91), 2(.95), 3(1.0) 4(-.99), 5(.83), 6(.90) 7(.85), 9(.71)	1(-.64), 4(-.73), 10(.77)
(9) Sal. - Salinity ‰	1(-.94), 3(.68), 4(-.60) 5(.83), 6(.90), 7(.85) 8(.71)	1(-.68), 5(.80), 6(.90), 7(.61)
(10) Time - Total duration of experiment	2(.91), 3(.75), 4(-.82) 5(.58), 7(.56)	4(-.72), 8(.77)

species was used, namely Monochrysis lutheri either singly, or with one other species. The strong correlations seen in the results of experiments with the crustacean nauplii are non-significant (Table 27d) due to the small number of observations. Food consumption rates (variable 1) were usually most strongly correlated with E_1 values (variable 2) and Logmean E values (3) as expected. More surprisingly, correlation coefficients greater than 0.5 were found between individual feeding rate (variable 1) and predator concentration (6); fraction of predators alive after 12 hours (7); and salinity (9). There is no obvious explanation for these latter relationships. On the other hand, the expected strong correlation between feeding rate (variable 1) and the number of size classes showing net consumption or 'ESP' (variable 4) and between (1) and the growth rate of control populations (C_2/C_1 - variable 5) did not appear (but see Materials and Methods). However, variable (4) was in some cases strongly and positively correlated with E_1 values (variable 2). This implies that predators in relatively high concentrations of food did not restrict their consumption to a narrower portion of the food size spectrum than did those in relatively low concentrations of food (and see Electivity results in this Section). That is, --if one ignores the unknown prior nutritional history of the predator-- they do not become 'choosier' of the size of their food when satiation is becoming more likely or vice-versa, --at least at these levels of concentration of food, which all seem to be below the OFC (see below). There was surprisingly, no consistent relationship between temperature (variable 8), and food consumption rate (1), 'width of spectrum' eaten (4), or C_2/C_1 (5).

Linear regression coefficients

Simple linear regressions were calculated for all other variables on feeding rate (variable 1). Regression coefficients and r^2 values for all

variables and computer plots for variables 2,3 and 4 are shown in Appendices 1 to 11.

As in the case of the correlation coefficients, the r^2 values for the ESO results were generally higher than those for the NTC results. The values of the regression coefficients of variables (2) and (3) on the food consumption rate (1) were generally greater, and the regression line was more similar to the form expected, for the ESO results than for the NTC results.

This seems to confirm that the ESO method of calculating food consumption rates may be more useful for microzooplankton than the more logical NTC method. The (ESO) calculated regression lines of values of E_1 (variable 2) or Logmean E (variable 3) on feeding rate (variable 1) showed the following features:

(i) a negative intercept on (1) --i.e. when variable (1) = 0, then variable (3) > 0.

(ii) a positive slope; and

(iii) no asymptote apparent in the data.

(i) negative intercept - or threshold feeding value

'Threshold' feeding values, or the lower level of total available food at which feeding (apparently) stops, are a common feature with some planktonic crustacean filter feeders (Adams and Steele, 1966); Parsons et.al., 1967) and with some planktivorous fish (Parsons and Lebrasseur, 1970). Parsons et.al. (1967) and Poulet (1974) also utilized the Coulter Counter technique. Feeding thresholds applicable over the total size range of the biomass of food available with one feeding technique are probably useful (or essential) in enabling the predator under natural conditions to avoid wasteful effort when the energy return in feeding with that technique is negligible. Poulet (1974) found that

the small copepod Pseudocalanus minutus showed a feeding threshold for each size category and could switch its feeding emphasis away from a size class containing a low total volume of particles. Despite the insufficient detail of experimental technique, and the apparently inadequate methods of calculation as given by Poulet (1973 and 1974), any feeding behaviour of this type would be a very useful attribute for an organism reliant on a food supply highly variable in its size composition; and would aid the maintenance of ecological stability (if any) in the plankton. The mechanisms(s) used by crustacea to detect these differences in total volume between size classes is difficult to imagine. The Coulter Counter results in this study show low apparent feeding thresholds for microzooplankton which may be experimental artifacts and which are (as always) linear extrapolations from known values. They are particularly suspicious in tintinnids as it would seem impossible for tintinnids to stop feeding and yet continue swimming. It is interesting that the larvae of several species of fish which eat food items individually do not show feeding thresholds. Parsons et.al. (1967), Poulet (1974) and others have shown that planktonic crustacea also have a qualitative lower size feeding threshold. The attributes of tintinnids in this respect are dealt with in Section 4a.

Lower threshold feeding values calculated from the plots in Appendices 1 to 11, and the corresponding regression coefficients, are shown in Table 28. Over all experiments, the extrapolated threshold values of Logmean E range from 35 to 340 x 10^3 um^3/ml, with no clearcut differences in the range of values between the tintinnid species or between tintinnids and nauplii (Table 28). The threshold value for 'all samples' (ESO) is 72 x 10^3 um^3/ml -- equivalent in volume to approximately 1440 Monochrysis lutheri cells, or 144 Eutreptiella sp. cells/ml. These values are very low indeed, especially as

TABLE 28. Microzooplankton lower threshold feeding values and regression coefficients of Log mean E (variable 3) when food consumption rate (variable 1) is zero. N.S. = non significant at .05 probability level.

Species of predator	Food type	Calculation method	Lower Log mean E (3) Thresholds ($\mu m^3 \times 10^3$/ml)	Regression Coefficient of Variable (3) on Variable (1)
Tintinnopsis subacuta	Natural	NTC	35	0.0197
"	Natural	ESO	124	0.0377
"	Laboratory	NTC	Intercept Negative	0.0033 (N.S.)
"	Laboratory	ESO	101	0.0205
Stenosomella ventricosa	Laboratory	NTC	340	0.0068 (N.S.)
"	Laboratory	ESO	Regression Negative	Negative
"	Laboratory	ESO	46 (one high value omitted)	0.0089
Barnacle and copepod/ Nauplii	Natural	ESO	--	0.0093 (N.S.)
	Laboratory	NTC	Regression Negative	Negative
"	Laboratory	ESO	38	0.0238 (N.S.)
Tintinnopsis parvula	Natural	ESO	--	0.0056 (N.S.)
Tiarina fusus	Natural	ESO	--	0.231 (N.S.)
All samples	--	NTC	Intercept Negative	0.0015
"	--	ESO	72	0.0247

they represent all particles less than approximately 20 μm diameter.

Using the carbon (μg) to volume ($\mu m^3 \times 10^6$) conversion factor (.052) given by Parsons et.al. (1967), a threshold value of 72×10^3 μm^3/ml is equivalent to 0.0037μg/carbon/ml. The latter is much lower than the threshold values Poulet (1973) gives for Pseudocalanus minutus in a coastal embayment and only 1/14th the value of the lowest of those given for three species of coastal planktonic crustaceans by Parsons et.al. (1967). It is almost certainly only coincidental that the average threshold value is about equivalent to the carbon content of one Tintinnopsis subacuta (see Section 2).

(ii) positive slope of regression

Although the regression analysis used presupposes a single linear relationship between variables (1) and (3), there are few data points which obviously violate this assumption in the various sub-sets of observations. An exception to this is seen in the results of Tintinnopsis subacuta feeding on natural food, where some of the values of an experiment involving a natural 'bloom' of Eutreptiella sp. appear to be unusually high and lie perhaps on a different, or on an exponential curve (Appendix 1). However, other 'replicate' results were much lower, and there was considerable 'scatter' amongst the results in that experiment.

Several of the NTC values show no positive linearity, which lends support to the surprising utility of the ESO method of calculation, but which makes difficult any approximate prediction of the feeding rate of a species from a knowledge of merely the initial total particle volume in a sample. The values of the regression coefficients are equivalent to an unrealistically continuous and uniform individual feeding rate of between 0.33 and 3.8% of the

particle volume/ml/hour (and see Section 4a and 4b); with an exceptional single value of 23.1% for the holotrich ciliate Tiarina fusus (ESO only). Tintinnopsis parvula (1 experiment only) shows a small coefficient (0.56%/ml/hr) and this tintinnid has a cell volume and a 'search rate' both about half of that of T. subacuta (coefficient of 0.33 to 3.8%/ml/hr) and Stenosomella ventricosa (coefficient of 0.68 to 0.89%/ml/hr). The latter two species are similar to each other in both cell size and 'search rate' (see Sections 4a and 4b). However some feeding rates of T. parvula on small prey items shown in Section 4a are as high as or higher than those of T. subacuta. The crustacean nauplii show a similar range of values at 0.93 to 2.38%/ml/hour although larger than tintinnids. The coefficients calculated for tintinnids in the short-term accumulation experiments (Section 4a (ii)) are all 1.1%/ml/hr or less. All these values are about 10-fold lower than thenmaximum individual feeding coefficients given by Poulet (1973) for the much larger adult copepod Pseudocalanus minutus (17%/ml/hr) over a food size range from 2 to 114 um. Feeding coefficients of two species of planktonic rotifers (see the end of this Section) ranged from 0.29% (NTC) to 5.53%/ml/hr (ESO) (and see General Discussion).

(iii) lack of asymptote

It is obvious from the computer plots of the regression of Logmean E on feeding rate (FR/P) in Appendices 1 to 11 that there is no case of a trend in the data towards a positive curvilinear relationship or towards an asymptote. Since theoretically there must be an asymptote, or at least a curvature for each predator at some high concentration of available food, it must be concluded that these (ESO) Coulter results occur below such optimum levels of edible particulate material (OFC) (but see Section 4a (ii)). The discrepancy between the levels of the OFC shown by the two experimental methods

in this study is inexplicable. The maximum particle concentrations used (between 1 and 20 μm diameter) are equivalent to 1.92 ppm (by volume) for laboratory cultures and 0.76 ppm for natural samples (see also General Discussion). However, the feeding rate asymptote for Pseudocalanus minutus according to Parsons et.al. (1967) occurs at about 11.0 ppm of particles between 1 and 114 um diameter.

The Feeding Electivity of Tintinnids in Coulter Counter Experiments

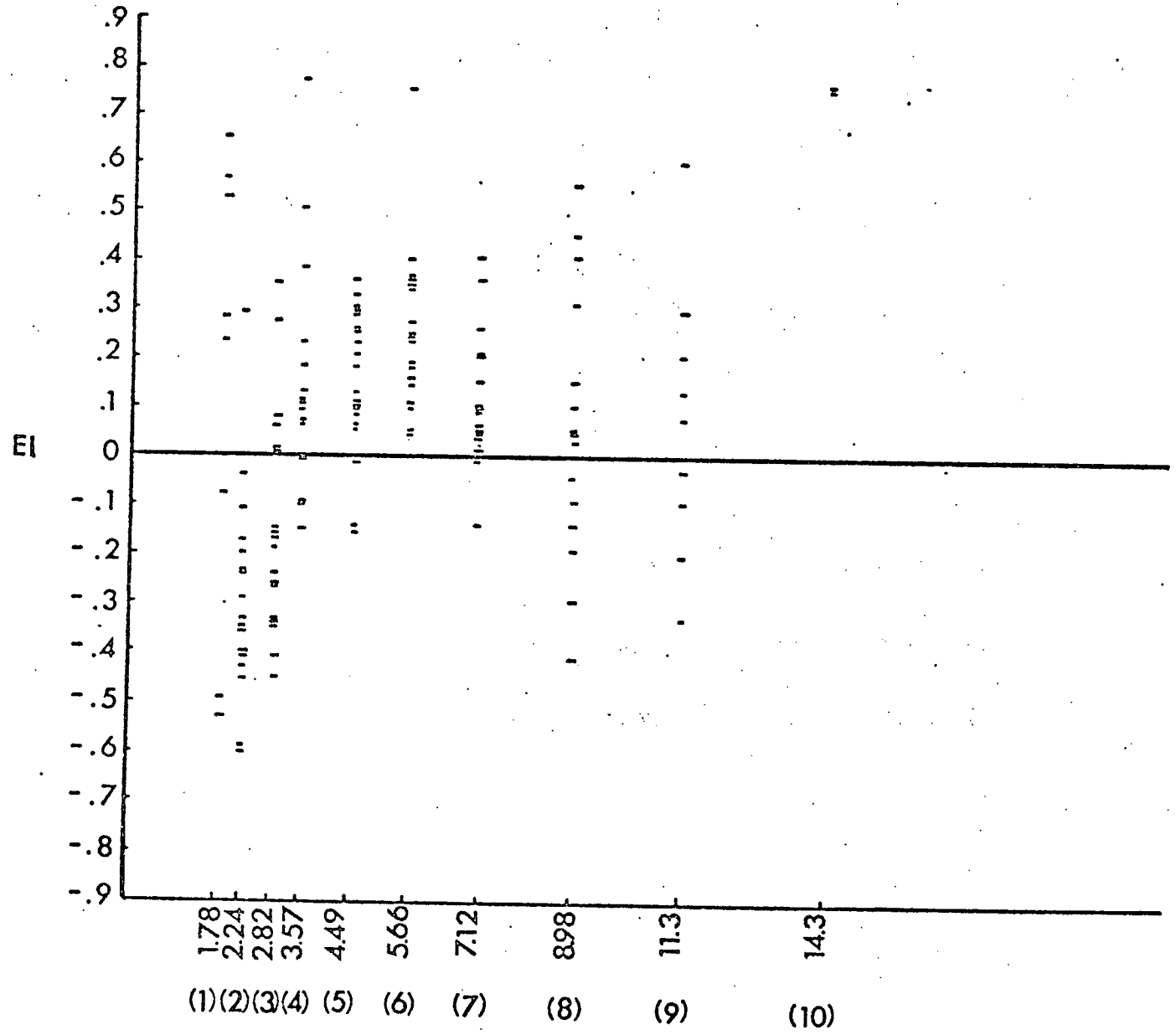
Indices of electivity or feeding preference are in most cases merely indices of the relative ease with which the food items in question are caught by a predator at any time. One measure which does not confuse catchability with preference or selection is the preference coefficient of Rapport et.al. (1972). In order to calculate this coefficient one must know the feeding rate of the predator on the food in question in single and in mixed cultures at equivalent densities. Rapport et. al. (1972) and Rapport (unpublished) have calculated preference coefficients for the ciliate Stentor coeruleus on several foods.

For the purpose of estimating the possible differential feeding rates of tintinnids on various size classes of particles in these Coulter Counter experiments, Ivlev's electivity index (here called El) has been used. Ivlev's index was chosen since there were no comparative cases of predation on single and mixed food cultures in these experiments.

$$El = \frac{ri - pi}{ri + pi} \qquad (5)$$

where ri = the proportion of item i in the diet of the predator and pi = the proportion of item i in the environment. Therefore, in this section El is a measure simply of the availability and ease of capture of an item or

Figure 8. Relationship between electivity values (El) of Tintinnopsis subacuta on natural particles and the mean diameter of Coulter Counter size classes.


.9
.8
.7
.6
.5
.4
.3
.2
.1
EI
0
-.1
-.2
-.3
-.4
-.5
-.6
-.7
-.8
-.9
1.78
2.24
2.82
3.57
4.49
5.66
7.12
8.98
11.3
14.3
(1)(2)(3)(4) (5) (6) (7) (8) (9) (10)
PARTICLE DIAMETER (um)

size class of particles and not a measure of its selection or preference by the tintinnid. E1 has the theoretical limits of -1.0 to +1.0. A zero result indicates that a size class of particles is eaten exactly in the proportion in which it occurs in the environment. A positive E1 fraction indicates that the feeding rate (in μm^3/hr/tintinnid) on a particular size class is a larger proportion of the total net feeding rate in that experimental replicate, than the logmean E value of that size class is of the total logmean E. value (also see Section 4a). Figures 8 to 11 show the relationship of the electivity indices with other factors for each of 10 size classes from that of mean diameter 1.78 μm (class 1) to that of mean diameter 14.3 μm (class 10). Only the values of Tintinnopsis subacuta feeding on natural samples have been used. Figure 8 shows the relationship between E1 and size class; Figure 9 shows the relationship between E1 and the mean total particle volume (logmean E) for each size class; Figure 10 shows the relationship between E1 and the total logmean E for all size classes in the experiment; and Figure 11 shows the relationship between the E1 values and the index of increase of particle volume in the control vessel (C_2/C_1) for each size class. In Figures 9,10 and 11 the logmean E and C_2/C_1 values have been recalculated for an experimental duration of 24 hours.

There is no simple relationship between particle size and electivity index (Figure 8). Positive and negative values are found in almost all size classes, except 6 (5.66 μm), but the values are consistently positive only in those size classes from 3.57 to 7.12 μm mean diameter. Size classes both larger and smaller than this have a wider range of E1 values, both positive and negative. Size classes 1,2 and 3 (1.78 to 2.82 μm) are more often negative than positive and the two values in class 10 (14.3 μm) are both positive. Therefore, the overall trend is for electivity values for Tintinnopsis

Figure 9. Relationship between electivity values (El) of Tintinnopsis subacuta on natural particles and the Logmean E values of each Coulter Counter size class.

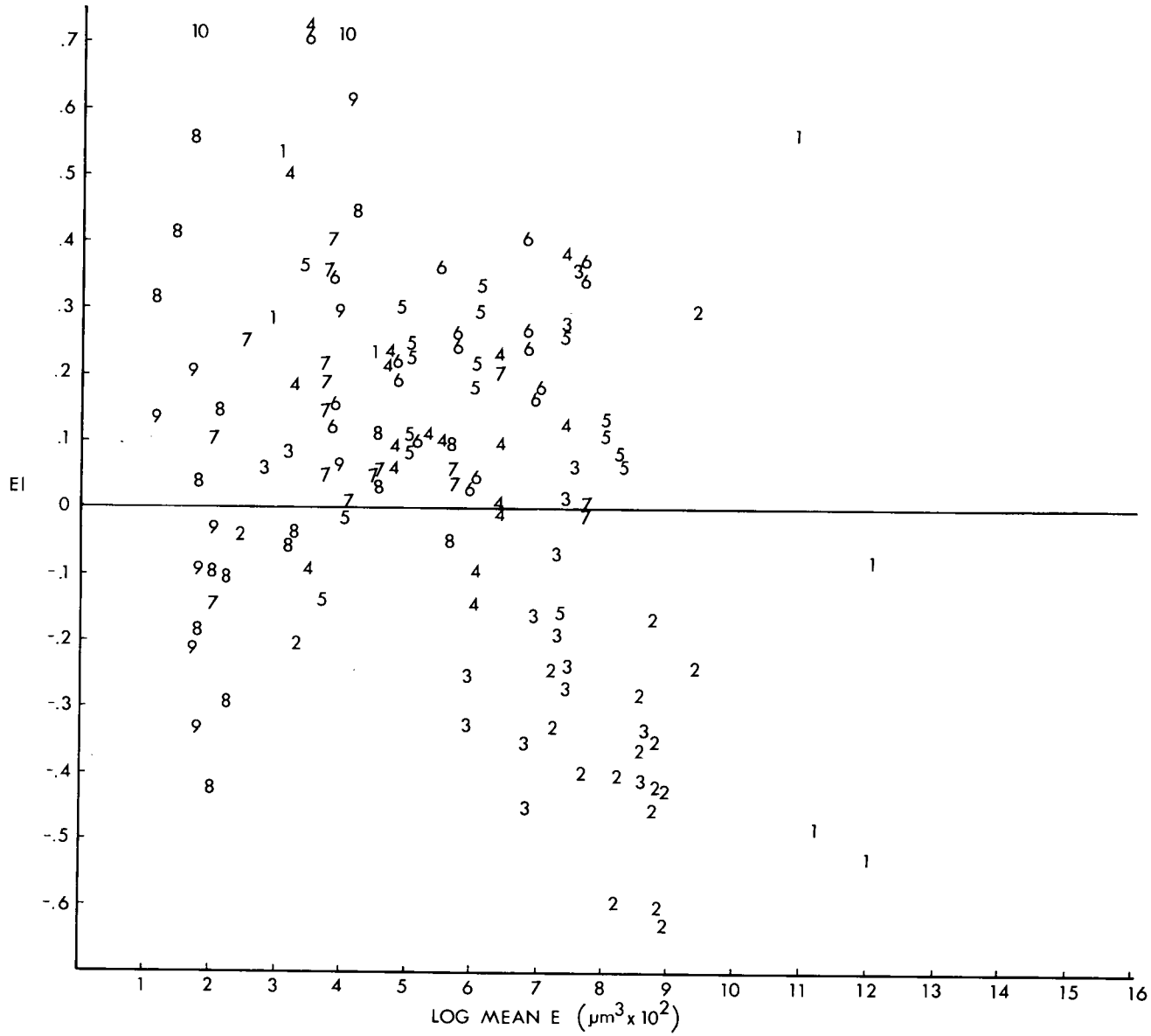
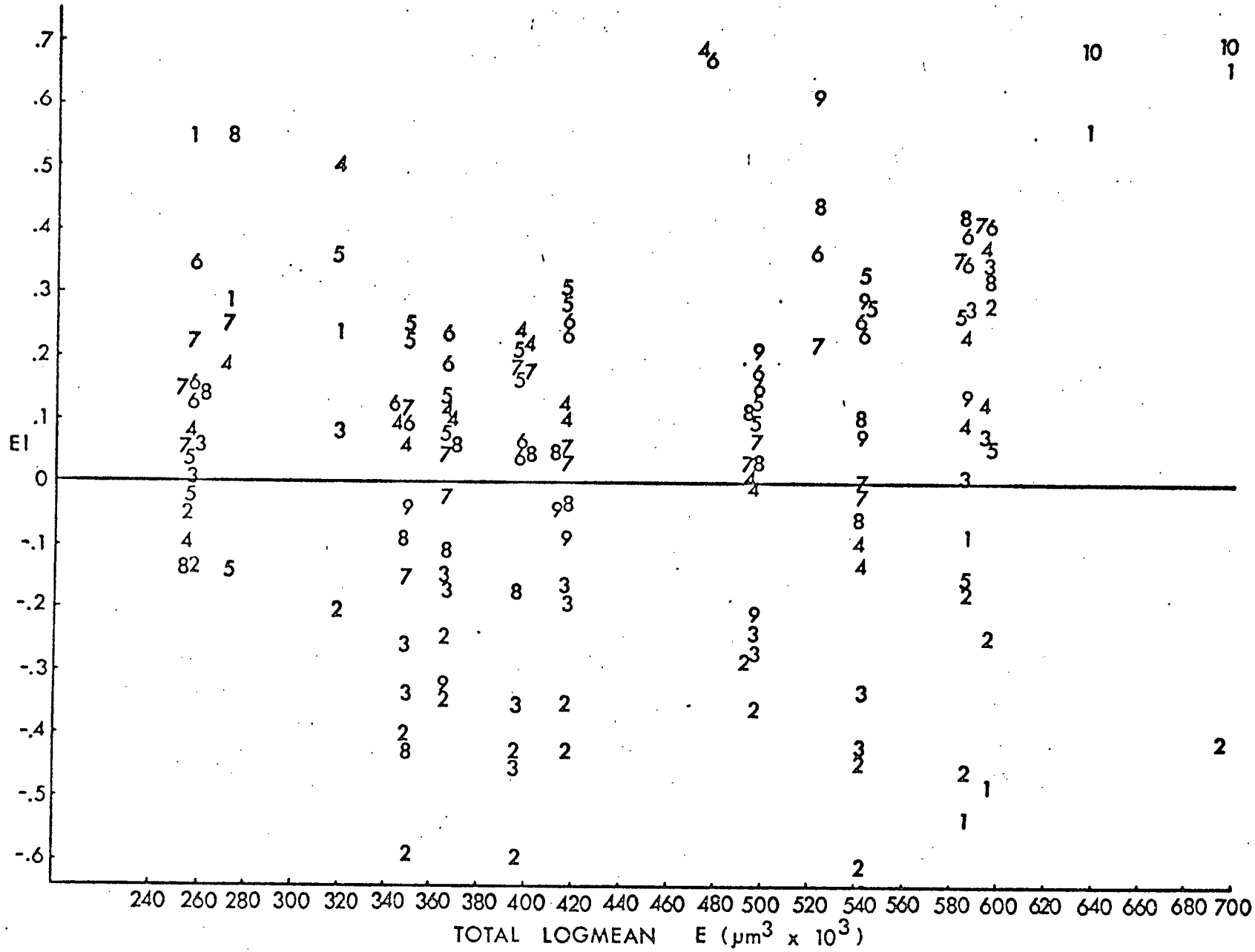
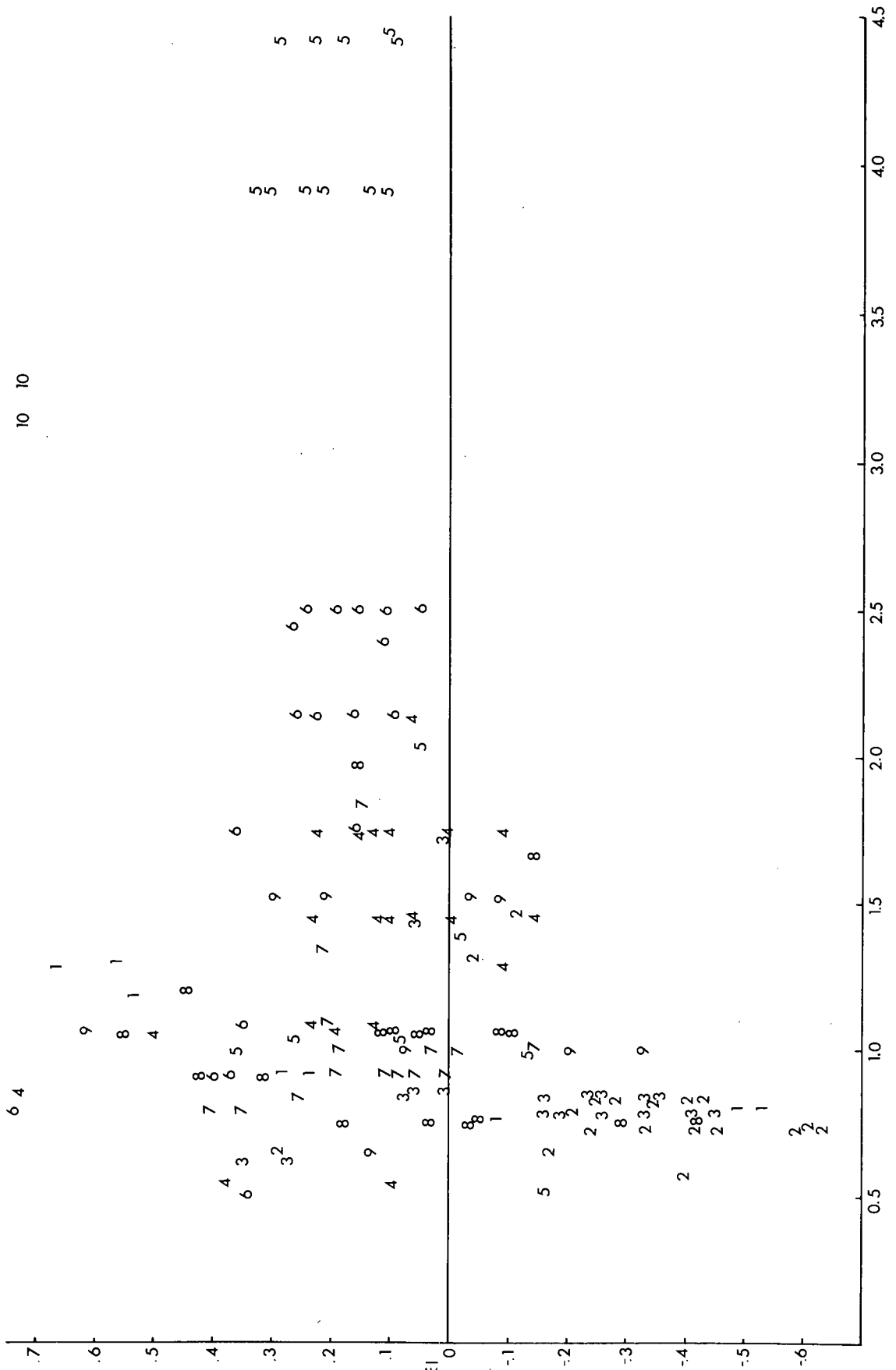

EI
.7
.6
.5
.4
.3
.2
.1
0
-.1
-.2
-.3
-.4
-.5
-.6
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
LOG MEAN E (μm³ x 10²)

Figure 10. Relationship between the electivity values (El) of Tintinnopsis subacuta on natural particles and the total Logmean E values of all Coulter Counter size classes.


.7
.6
.5
.4
.3
.2
.1
EI
0
-.1
-.2
-.3
-.4
-.5
-.6
240 260 280 300 320 340 360 380 400 420 440 460 480 500 520 540 560 580 600 620 640 660 680 700
TOTAL LOGMEAN E (μm3 x 10^3)

subacuta to be more consistently positive in Coulter size classes larger than about 3 μm, but not to increase in magnitude with size above this. Particles as small as 1.6 μm are eaten to some extent by this species. In Figure 9 it can be seen that although the mean total volume of particles is greatest in the smaller size classes, there is no tendency for electivity values to increase with the total particle volume in each size class. Figure 11 shows that the potential rate of increase in the number of particles per size class (C_2/C_1); may be related in a complex manner to the electivity index of a size class. There is no relationship between C_2/C_1 and El when C_2/C_1 is equal to or less than 1.0, i.e. when there was no change, or a decline in the total particle volume for that size class in the control vessel. In the majority of cases, total C_2/C_1 values greater than 1.0 (i.e. showing 'growth') are associated with size classes with positive El values. The greatest C_2/C_1 values occur in size classes 5 and 6 (between about 4 and 6.5 μm), but these size classes do not have the largest positive El values (see also Figure 8). There is not complete independence between these factors since the El values are based upon feeding rates; and the calculation of the latter involves the C_2/C_1 ratio, and the logmean E value for each size class (see Section 3b (iv)). In general, the sign of the electivity index is consistent only in the middle range of the size classes in these Coulter Counter experiments, and these size classes are those which show not the greatest mean particle volume, but the greatest growth rate in controls. The magnitude of the electivity index of Tintinnopsis subacuta bears no consistent relationship to the size, total volume or growth rate of natural food particles. This may be due to peculiarities in the method of calculation of the index. Figure 10 shows that there is no relationship between electivity values for any size class and the total particle volume of any experiment.

Figure 11. Relationship between the electivity values (E1) of Tintinnopsis subacuta on natural particles and the changes in control values (C_2/C_1) in each Coulter Counter size class.


EI
C_2/C_1
.7
.6
.5
.4
.3
.2
.1
0
-.1
-.2
-.3
-.4
-.5
-.6
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5

Poulet (1973, 1974) has investigated the feeding rates of the small neritic copepod Pseudocalanus minutus on natural particles with a Coulter Counter technique. Poulet also used Ivlev's electivity index, and found that although positive and negative electivity values were found in all of his five arbitrary size classes from 1.5 μm to 144 μm, the frequency of positive values increased with the size of the class to about 60 μm diameter and then decreased. Electivity values were mostly negative for Poulet's particles between 1.58 and 9 μm, except when particles of this size reached 40 - 60% of the total concentration. Poulet (1974) found that food consumption in P. minutus was strongly correlated with the total particle volume in all size classes except in the size range below 3.57 μm. Poulet therefore argued that P. minutus has a very strong opportunistic feeding behaviour and a very efficient utilization of the standing stock whatever its size distribution (and see General Discussion).

Poulet's method of calculating feeding rate and standing stock and therefore - electivity indices, comes under some suspicion primarily because he calculated feeding rate as merely the difference between final control and experimental particle concentrations. This means that he has used a linear method of calculation (see Methods Section) which may well be inappropriate for his particle concentrations and experimental periods and could lead to large over or under-estimation of the feeding rate. Nevertheless his conclusions on the feeding 'strategies' of P. minutus may well hold, but it should be remembered that this electivity index indicates changes in the proportion of items of a particular size eaten, and does not necessarily indicate selection by the predator. In the Coulter Counter experiments in this study Tintinnopsis subacuta does not appear to eat proportionately more of

a size class of natural particles when that size class contains a large total volume of particles (Figure 9), nor when the total volume in all size classes is large (Figure 10). Therefore T. subacuta does not appear to be as 'opportunistic' a feeder as P. minutus; but not all the particles in a size class may be equally available for predation nor equally edible (and see Section 4a). T. subacuta like P. minutus eats particles in all size classes in its range but takes disproportionately more from the middle size classes (3.57 to 7.12 µm mean diameter), more frequently than from the particles of less than 3.57 µm or more than 7.12 µm diameter. These middle size classes are those which show the greatest potential growth rate in these Coulter Counter experiments. The methods used by Poulet (loc.cit.) did not allow him to discuss the relationship between potential growth rate and electivity.

The effect of tintinnid feeding on the 'control' of phytoplankton populations

It is important to try to ascertain the conditions under which tintinnids and other microzooplankton may 'control' phytoplankton populations composed of relatively small organisms. Figures 12,13 and 14 show the total effect of predator feeding in these Coulter Counter experiments, and the number of predators/ml in the same experiments. General 'control' is presumed to have taken place when $\frac{E_2}{E_1} < 1$ and $\frac{C_2}{C_1} > 1$. All values have been recalculated from the data for an experimental duration of 24 hours, and the predator concentrations shown are those calculated to be alive/ml after 12 hours. The NTC values are given. The data are so variable that they support only the most tentative statements, but it is clear that natural concentrations of tintinnids (at least of T. subacuta), apparently under some circumstances, reduce the biomass of growing phytoplankton populations within 24 hours, thus exerting a controlling influence.

Figure 12. Relationship between the changes in the total particle volume of Coulter Counter control (C_2/C_1) and experimental (E_2/E_1) containers at various concentrations of tintinnids per ml.
'1.0' - Tintinnopsis subacuta on natural particles.
(1.0) - T. parvula on natural particles.

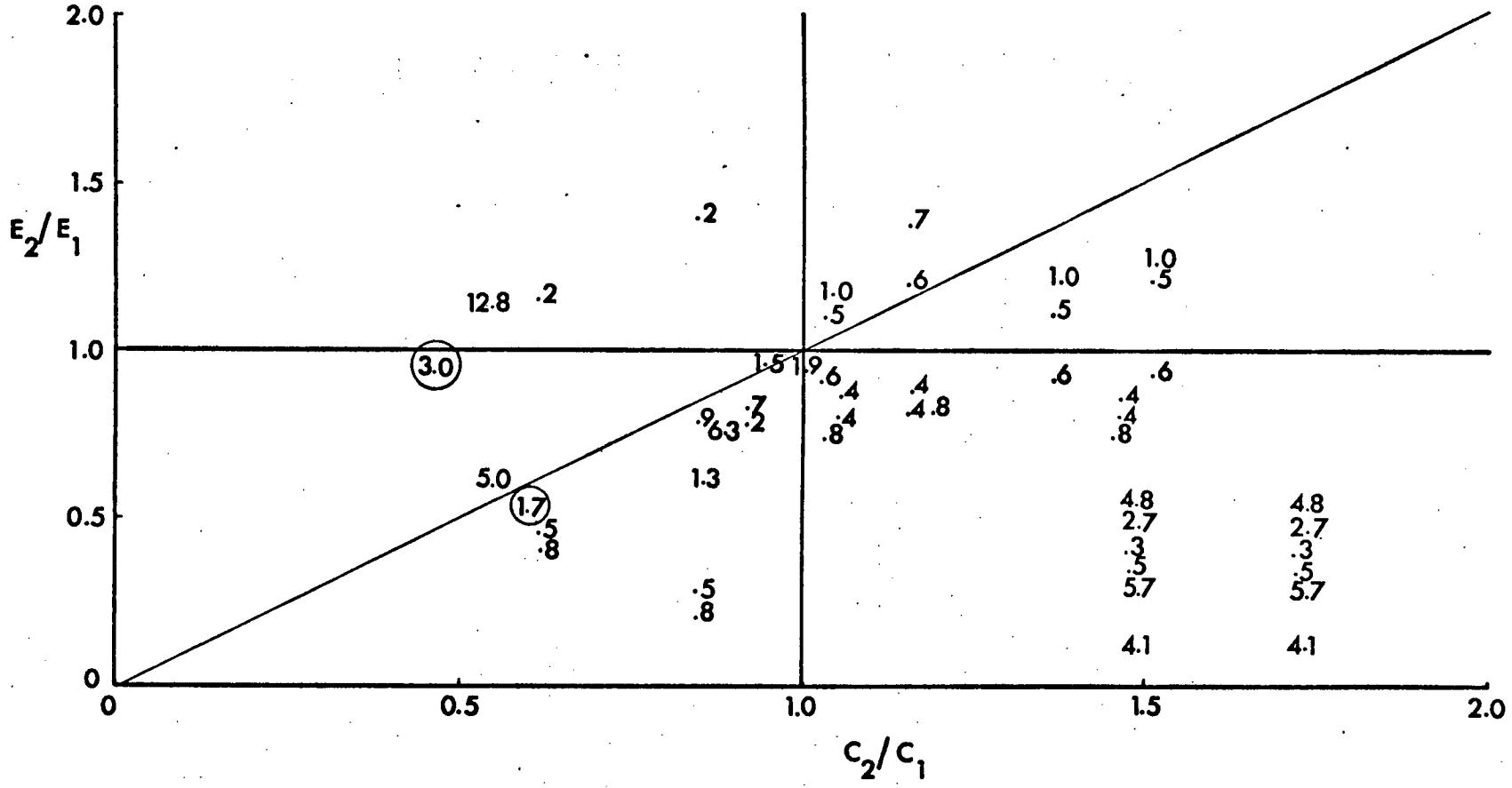

2.0
1.5
1.0
0.5
0
0
0.5
1.0
1.5
2.0
E_2/E_1
C_2/C_1
12.8
.2
.2
.7
1.0
.5
.6
1.0
.5
1.0
.5
3.0
1.5
1.9
.6
.4
.4
.4.8
.6
.6
.4
.4
.8
.9
.6
.3
.7
.2
.8
.4
5.0
1.3
1.7
.5
.8
4.8
2.7
.3
.5
5.7
4.8
2.7
.3
.5
5.7
.5
.8
4.1
4.1

Figure 13. Relationship between the changes in the total particle volume of Coulter Counter control (C_2/C_1) and experimental (E_2/E_1) containers at various concentrations of Tintinnopsis subacuta per ml. on laboratory food.

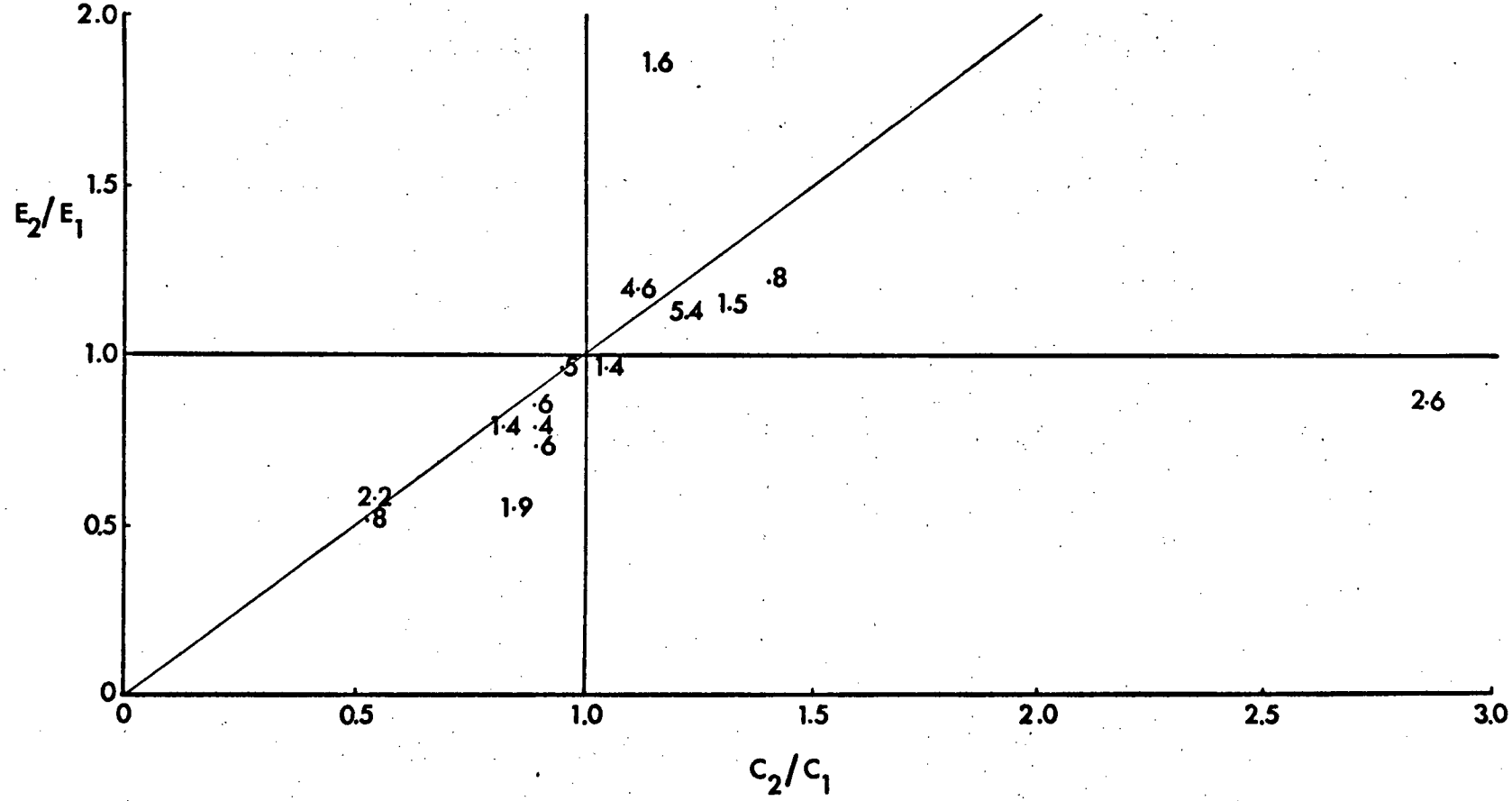
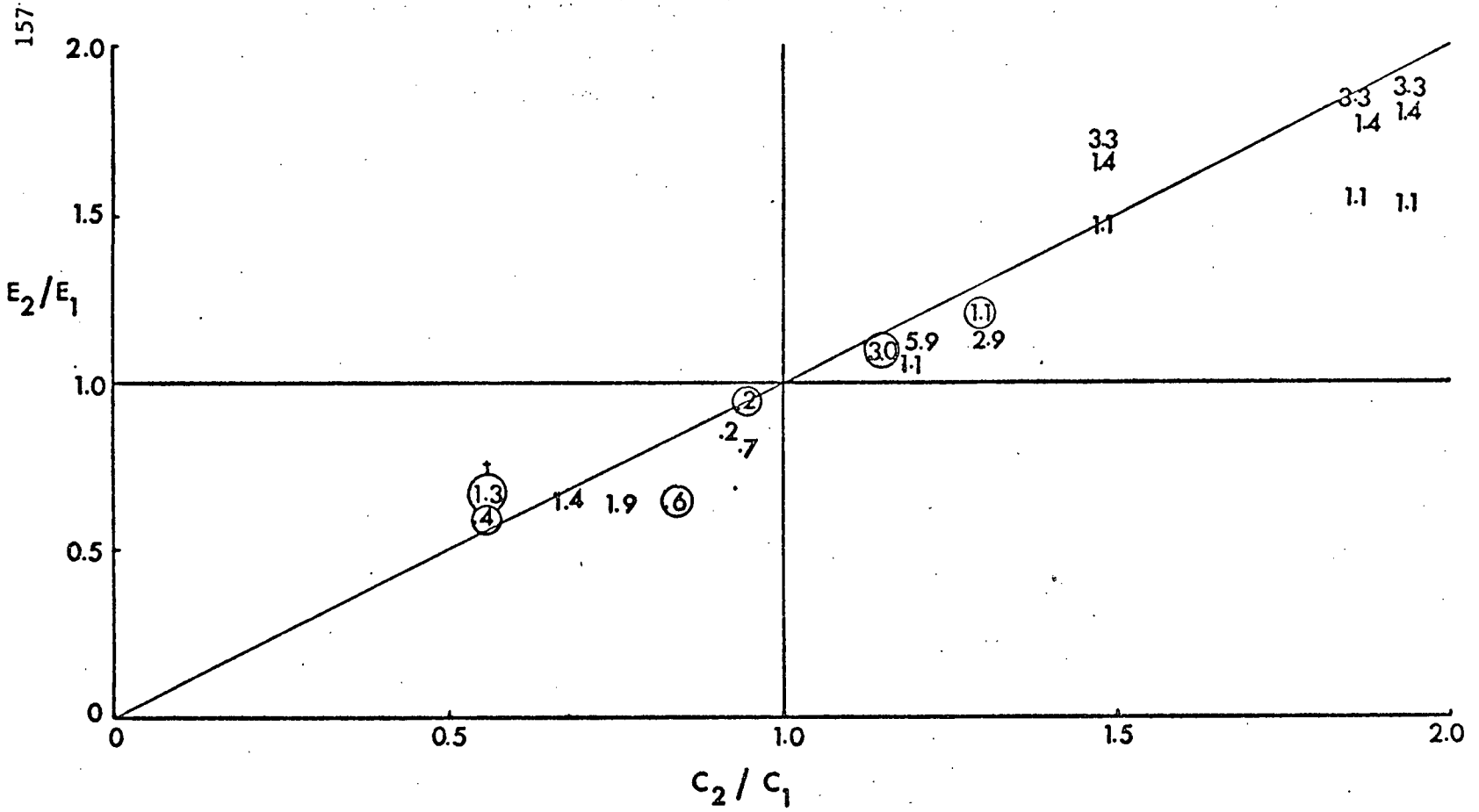

2.0
1.5
1.0
0.5
0
E_2/E_1
0
0.5
1.0
1.5
2.0
2.5
3.0
C_2/C_1
1.6
4·6
5.4
1.5
·8
·5
1·4
·6
1·4
·4
·6
2·2
·8
1·9
2·6

Figure 14. Relationship between the changes in the total particle volume of Coulter Counter control (C_2/C_1) and experimental (E_2/E_1) containers at various concentrations of predators per ml.
'1.0' - Stenosomella ventricosa on laboratory food.
(1.0) - Barnacle and copepod nauplii on laboratory food.
(1.0)+ - Barnacle and copepod nauplii on natural particles.


2.0
1.5
1.0
0.5
0
0
0.5
1.0
1.5
2.0
E_2/E_1
C_2/C_1
3.3
1.4
3.3
1.4
3.3
1.4
1.1
1.1
1.1
1.1
2.9
3.0
5.9
1.1
2
.2
.7
1.3
4
1.4
1.9
6

A Coulter Counter experiment with Rotifers

Of several attempted Coulter Counter experiments with planktonic rotifers, only one gave useful results. This was much shorter thantthe earlier experiments with tintinnids and has been analysed separately and the results shown in Table 29. Of the two species used: Synchaeta littoralis (about 500 x 200 µm) is the largest marine planktonic rotifer in the study area; and the smaller species is also probably of the genus Synchaeta and is about 250 x 100 µm in size. All animals used were females; many S. littoralis females with external eggs do not take food (personal observation), and at such times their eggs have a darker, rougher appearance than usual. The latter may be mictic (or fertilised) eggs and are possibly among the last produced by such a female. None of the S. littoralis in this experiment appeared to carry mictic eggs.

In this experiment, the same control was used for both rotifer species, and the prey was Dunaliella tertiolecta in filtered seawater. The duration of the experiment was 7.42 hours for S. littoralis and 7.17 hours for Synchaeta sp.. There were 0.65 S. littoralis/ml and 0.60 Synchaeta sp./ml. The 'exponential' equation (see Methods Section) was used to calculate the feeding rate (FR/P). In Table 29 positive values of FR/P indicate a net increase in particle volume in that size class, and negative values indicate a net loss of particle volume. The latter is interpreted here as due to consumption by rotifers. Table 29 shows that particle consumption by both species occurred in size classes of mean diameter 7.12 to 14.3 µm; and that a net increase of particles occurred in size classes 2.28 to 7.12 µm. These opposite trends were weakest in the middle size classes, and there seems to be a gradual change from production to consumption of particles with increasing particle

TABLE 29. Results of Coulter Counter experiment with *Synchaeta littoralis* and *Synchaeta* sp. eating *Dunaliella tertiolecta*.

	Mean Diameter of Size Class (µm)								
	2.82	3.57	4.49	5.66	7.12	8.98	11.3	14.3	Total
C_2/C_1	1.14	0.94	0.51	0.79	0.69	0.54	2.43	13.4	0.86
				S. littoralis					
E_1 ($\mu m^3 \times 10^3$)	87.4	88.7	109.6	88.6	132.2	238.3	64.0	25.9	834.7
E_2 ($\mu m^3 \times 10^3$)	152.7	98.9	98.0	87.7	80.7	120.6	42.6	13.0	694.2
Log mean E ($\mu m^3 \times 10^3$)	117.1	93.7	103.5	88.2	104.4	172.7	52.6	19.0	751.2
FR $\mu m^3 \times 10^3$/hr/predator	+10.4	+3.3	+12.0	+4.1	-2.7	-2.3	-14.4	-12.8	NTC -2.2 ESO -32.1
FR ml/hr/predator	--	--	--	--	0.026	0.013	0.274	0.674	NTC 0.0029 ESO 0.0427
				Synchaeta sp.					
E_1	93.8	89.0	110.0	87.5	150.7	305.0	64.6	17.3	918.0
E_2	195.5	100.8	98.1	83.4	103.1	100.5	56.0	24.5	761.9
Log Mean E	139.0	95.3	103.9	85.8	128.5	184.2	60.3	20.7	838.3
FR $\mu m^3 \times 10^3$/hr/predator	+19.4	+4.1	+13.5	+3.7	-0.2	-21.0	-14.4	-10.8	NTC -5.7 ESO -46.4
FR ml/hr/predator	--	--	--	--	0.002	0.114	0.239	0.522	NTC 0.0067 ESO 0.0553

size. In this relatively short experiment, particle production at these sizes is probably caused by the fragmentation of large particles or by the egestion of old food and not by differential particle growth. The C_2/C_1 values in Table 28 indicate that values greater than 1.0 were associated with a high feeding rate. However, the overall, C_2/C_1 value was 0.86.

As in the other Coulter Counter experiments the ESO values were higher than the NTC values;bbut in this case the latter were also negative. Feeding rates calculated as ml/hr/rotifer were, for the total particle volume:0.0029 (NTC) and 0.0427(ESO) for S. littoralis; and 0.0067(NTC) and 0.0553(ESO) for Synchaeta sp.. Those size classes which contained most of the D. tertiolecta were 7.12 to 11.3 μm diameter; and the feeding rates in ml/hr/tintinnid for the total of the latter were: 0.0586 for S. littoralis and 0.00954 for Synchaeta sp.. It is surprising that the feeding rate of Synchaeta sp. on D. tertiolecta here exceeds that of the much larger S. littoralis. At these rates 100% of the D. tertiolecta would have been eaten in 10 to 17 hours.

The feeding rates shown in Table 29 exceed those of any tintinnid species in this study by a factor of 2 (Coulter experiments) to 5 or more(accumulation experiments). Rotifers in inshore waters in this area may occasionally attain concentrations as high as 3 or 4/ml, and at such times an equivalent total feeding rate by tintinnids would require concentrations of perhaps 15 to 20 T. subacuta/ml. Concentrations such as this of large tintinnids rarely occur. Although these two rotifer species have faster feeding rates than tintinnids and rapid reproductive rates; at times they do not feed at all, and they are much less common than tintinnids in cold or high-salinity water. Tintinnopsis subacuta has a maximum cell volume of about 7×10^4 μm^3; a large female S. littoralis is about 100 times larger. Therefore, on the basis of

individual volume, the tintinnid is a considerably more effective predator than the rotifer.

Variability in feeding rates in Coulter Counter experiments

The four most likely causes of variability in these experiments were: 1) variability between replicates of control and experimental samples; 2) divergence between growth rates of prey items in control and experimental samples; 3) invalid assumptions about mortality of the predators; 4) differences in the feeding response of predators to various prey types, particularly in those experiments where one or a few prey types may have been dominant.

Variability between control replicates is not readily explicable, but ca certainly any initial differences would have been most enlarged in the longest experiments. The combination of variability in control and experimental samples would be multiplied in the calculationoof feeding rates. The assumption that the potential changes in particulate volume in each size class in the experimental vessel parallel the changes in those size classes in the control vessels, was also least valid in the longest experiments. Several of the experiments were too long, but it was often difficult to obtain significant changes in particulate volumes in more optimal periods of time such as 6 to 8 hours, particularly with low natural concentrations of tintinnids.

In order to calculate feeding rates the assumption was made that the tintinnids which died during the course of the experiments did so at a uniform rate. This assumption was not verified. If most of the dead tintinnids had died near the start, or conversely near the end of experiments; the use of the above assumption would greatly underestimate or overestimate

respectively, the feeding rate of the remainder. In any future Coulter Counter experiments with tintinnids, the number, condition and accumulated food contents of tintinnids should ideally be checked at intervals. As has been seen in results of accumulation experiments (Section 4a (ii)), some tintinnid species show apparent differential predation and selection on some types of food. This selection usually takes a negative form in that some food items are eaten disproportionately less when they are presented together with another food item which is apparently more easily caught even in low concentrations. The qualitative response of tintinnids and other microzooplankton to various prey types should also be checked if possible during Coulter Counter experiments on natural samples.

5) General Discussion

Of the 13 species of tintinnids mentioned in this study: much of the information has been gained from one common and relatively large species, Tintinnopsis subacuta; somewhat less has come from 4 or 5 other species of moderate size and frequency; and still less from 3 or 4 more species mostly found in mid-summer. Virtually no information has come from the 2 smallest, the 2 largest, and one very rare species. The two smallest species Tintinnopsis nana and Tintinnopsis rapa did not eat enough visible particulate material to give much information with the techniques used here. The largest species, Favella serrata and Eutintinnus latus were too rare to be of much practical use, although some information was obtained from them, especially from E. latus (Section 4b).

Of the other ciliate microzooplankton encountered, the holotrichs Prorodon sp. and Mesodinium rubrum were never seen to ingest particles, although the former was very occasionally seen to contain food material and may have a very rapid digestion rate. There is one Coulter Counter experimental result from the holotrich Tiarina fusus. This species occasionally occurred in large numbers but is probably primarily a histophage. Of the oligotrich ciliates which are closely related to tintinnids, several genera and species were observed during this study. The smallest species (15 to 30 μm), almost certainly ingested bacteria and/or dissolved organic material; those of a similar size range to tintinnids appeared to contain similar food to tintinnids in similar amounts, and were often very numerous; and the largest (200-300 μm) were predatory, largely upon tintinnids. Some of the non-tintinnid ciliates may be 'quasi-symbiotic' at times (Blackbourn et.al, 1973) but this does not appear to be true of tintinnids.

One Coulter Counter experiment was carried out with two species of rotifers, and their feeding rates were about 2 to 5 or more times as fast as those of Tintinnopsis subacuta. (Table 30). The feeding rates of mixtures of barnacle nauplii and small copepod nauplii (chiefly the former) when measured with the Coulter Counter method, were very similar to those of the two tintinnid species used in similar experiments. It seems likely from this fragmentary information that the potential overall feeding effect of tintinnids on natural populations of phytoplankton, isaat least as great as that of any other group of microzooplankton used in this study. It is possible that the overall effect of the feeding of oligotrichs is greater than that of tintinnids, but there is no quantitative information on the feeding rates of the former. Oligotrich populations seemed to be even more transient and variable than those of tintinnids, and the population feeding effect of either group would be extremely difficult to evaluate over periods of more than a day or two.

In comparing the results of this study with those of other authors, the great variability which has bedevilled the project makes any but the most general statements untenable. However, the following comments on some details and some general trends are probably justified. There are no other quantitative data on tintinnid or oligotrich ciliate feeding rates with which to compare this work, but the feeding rates of some free-living semi-planktonic ciliates have been examined in the papers by Goulder (1972), Hamilton and Preslan (1969) and Pavlovskaya (1973). Rapport et.al. (1972) have discussed the food preferences of the sessile ciliate species Stentor coeruleus, and Berger (1971), Curds and Cockburn (1971) and Ricketts (1971, 1973) and others have discussed feeding in the freshwater bacteria-eating species Paramecium aurelia and Tetrahymena pyriformis. Most authors who have worked with

protozoa have used methods different from those used in this study, e.g. radioactive tracers (Pavlovskaya, 1973); the estimation of weight or total cell yield, etc. (Curds and Cockburn, 1971; Hamilton and Preslan, 1969) or extrapolations from rates of loss to feeding rates (Goulder 1972). Berger (1971) made counts of food vacuoles labelled with radioactive bacteria, and Ricketts (1971) counted food vacuoles which contained latex particles. Rapport et.al. (1972) counted the accumulations of food in Stentor coeruleus after 1 hour.

Tintinnids eat almost anything of less than a certain size (Table 2), but differential predation does occur in some species on some prey types (Section 4a). For example, Tintinnopsis subacuta eats disproportionately more Eutreptiella sp. than other prey species in mixtures; and this appears to depress the ingestion of the other species compared to controls when the latter are presented singly to T. subacuta. This might be considered as negative selection, but if deliberate, its utility is not obvious. On the other hand, Cryptomonas sp. and Isoselmis sp. (Cryptophyceae) are eaten less than proportionately by T. subacuta, T. cylindrica, T. parvula and Stenosomella ventricosa when mixed with other prey items, and very little at any time. True negative selection by these tintinnids on Cryptomonads was also found in some experiments (Section 4a). On the other hand Tintinnidium mucicola accumulates all food items at a generally slower rate than the above tintinnid species, and has an apparently disproportionately negative feeding reaction to most prey species in mixtures but to Isoselmis sp. and other Cryptomonads. The feeding rate of S. ventricosa and Tintinnopsis cylindrica on most small prey items (such as Monochrysis lutheri) is fairly similar to that of T. subacuta to which they are similar in size. However, S. ventricosa eats much less Eutreptiella sp. from a similar concentration of cells, than

does T. subacuta, and T. cylindrica has never eaten Eutreptiella sp. in the laboratory although cells which resemble euglenoids have been seen inside this tintinnid species from field samples. It has been shown that Eutintinnus latus which is larger than T. subacuta, cannot subdue normal Eutreptiella sp. but can eat the larger and slower prey species Cryptomonas profunda. (Section 4c). E. latus does not seem to habituate to Eutreptiella sp. and never fails to attempt to ingest it. Tintinnids may deal differently with relatively small prey.

This kind of differential and sometimes negatively selective predation has not been identified in other groups of ciliates, but no doubt it occurs. In contrast, Rapport (Rapport, et.al. 1972; and unpublished data) has found definite but transitive positive feeding preferences in Stentor coeruleus. S. coeruleus, generally, prefers large prey to small prey and ciliates are preferred to flagellates; but the degree of preference changes with changes in the absolute and relative concentrations of prey types in mixed samples. S. coeruleus shifts its preference in the direction favouring that prey species of relatively high abundance. Feeding experiments with tintinnids over a wide range of concentrations of mixed prey were not possible with the techniques used in this study; but it is possible that the degree of prey selection seen in Section 4a may change with changes in the concentration of prey. It is important to note that whatever its effect on the mixed-prey populations, a preference for the most abundant prey item will probably be of less use to a predator than a preference for that (easily digested) prey with the largest total biomass/ml (see comparative discussion of Coulter Counter experiments below). The feeding response of microzooplankton to prey may greatly depend upon the quality of the prey, which may vary between prey species and certainly between different growth stages of the same species.

Such qualitative differences may explain some of the variability seen in this study and in the results of Rapport (unpublished data) and Strathmann (1971). However, several different species of phytoplankton have similar proportions of the major nutritional constituents, and when in the exponental growth phase (as in 'blooms' or from new laboratory cultures) should be similarly useful to a predator. Predators must respond to the behaviour or surface characteristics of prey, and therefore selection cannot be based upon its nutritional composition per se. Also it is difficult to understand the biological basis for the persistence of predation on a less-preferred prey type at very high concentrations of mixtures of prey types (this study Section 4a and Rapport, unpublished data), since most individuals of all prey species will be rejected under such circumstances.

The feeding rates of tintinnids in this study in general increase with the increase of cell volume among predator species. Also the search rates of various tintinnid species as seen in Section 4b on items which can be ingested by all, do not vary by more than a factor of 5 or 10, and the range of cell volumes among these tintinnids is also approximately 10-fold. A feeding rate of 0.0042 ml/hr/tintinnid (Table 15) from Eutreptiella sp. at 1,400 cells/ml amounts to about 6 prey cells ingested/hour, and is equivalent to about 3,000 μm^3/hr/tintinnid. To obtain this volume of food T. subacuta would have to ingest about 60 Monochrysis lutheri/hour or about 15 Dunaliella tertiolecta/hour. At a feeding rate of 0.0042 ml/hr/tintinnid this would require cell concentrations of 10 times or 22½ times that of Eutreptiella sp. for M. lutheri and D. tertiolecta respectively. From the relationships between temperature, size, and reproductive rate shown for benthic ciliates by Fenchel (1968), it can be estimated that the maximum reproductive rate of a tintinnid such as T. subacuta might be about one division per 37 hours

at 10°C and one per 15 hours at 20°C, if it could tolerate such a temperature for long. However, Gold (1971, 1973) has shown that Tintinnopsis beroidea (probably synonymous with T. subacuta) divides about once every 19 to 27 hours at 12.5°C in continuous culture. A rate of one division in 24 hours would give a maximum specific growth rate of 0.029 hr for a newly divided T. subacuta ($\sim 4 \times 10^4$ μm^3). At a growth/consumption ratio (K_1) of 0.3 (Klekowski et.al., 1972; Pavlovskaya, 1973) this would require a continuous intake of 3,880 μm^3/hr or 9.7% tintinnid cell volume/hr or about 8 Eutreptiella sp. or 80 Monochrysis lutheri/hr.

At a feeding rate of 0.0042 ml/hr, the prey cell concentration that would be necessary for the maximum growth rate of a new T. subacuta at 12.5°C would be about 1,900/ml Eutreptiella, or about 19,000/ml M. lutheri (0.95 ppm). Thus it seems plausible that T. subacuta could obtain enough food from the concentration of Eutreptiella sp. in Table 15 (0.75 ppm) to reach a reproductive rate of about 3/4 of its theoretical maximum. Blooms of T. subacuta and euglenoid and other large flagellates, and temperatures of about 12°C all occur typically in late spring in this area. However, it is almost certain that feeding by T. subacuta is not continuous; and just as the relationship between feeding rate and digestion rate is not a simple one, the relationship between digestion and growth may also be complex.

Pavlovskaya (1973) gives fairly simple models for the relationship between food concentration, feeding rate on one type of food and reproductive rates, for three species of ciliates. Her data has some unacknowledged inconsistencies, and it is not possible to judge the accuracy of the estimates of feeding rate. She gives the relationship between feeding rate (ration), maximum ration, and food concentration as:

$$R = Rmax\ (1-e^{p(k-ko)}) \qquad (5)$$

where R = ration, and p and k are constants.

The relationship between reproductive rate and ration is given by: -

$$g = a\ R^{-b} \qquad (6)$$

where g = time taken for a ciliate to double its population size (in days), and a and b are constants and are derived from the data. The values of R and g given by Pavlovskaya (loc. cit.) are as follows: -

Keronopsis rubra (wet weight 10^{-4} mg)	$R(mg/hr) = 5x10^{-6}(1-e^{-80(k-0.8x10^{-5})})$ $g(days) = 0.112\ (R)^{-0.215}$
Uroleptopsis viridis	$R(mg/hr) = 14.9x10^{-5}(1-e^{-850(k-0.2x10^{-5})})$ $g(days) = 0.205\ (R)^{-0.169}$
Condylostoma magnum (wet weight $7x10^{-3}$ mg)	$R(mg/hr) = 4.9x10^{-4}(1-e^{-0.5(k-0.5)})$

Condylostoma magnum is a very large free swimming ciliate here feeding on dinoflagellates, and the other two species are bottom feeders on diatoms and bacteria. The maximum rations shown by Pavlovskaya (loc. cit) were obtained at food concentrations equivalent to 5% of ciliate body weight/hr at 2,000 diatoms/Cm^2 for Keronopsis rubra; and equivalent to 6% of body weight/hr for Condylostoma magnum. The fastest rates were about 3 times faster than, and occurred at food concentrations of about 1/3 of, the latter. As Tintinnopsis subacuta is somewhat smaller than these two species, it seems reasonable that its feeding rate in terms of percentage of cell volume/hr as calculated above is a little higher than that of Keronopsis rubra and Condylostoma magnum.

Hamilton and Preslan (1969) showed that although the maximum specific

growth rate of the small ciliate Uronema marinum is very high (0.147 hr); it feeds sufficiently slowly that the concentration of bacteria necessary for maximum growth (0.49 ug C/ml or 10 ppm) would be very rarely found in the sea, except perhaps on the corpses of planktonic organisms. Therefore, they termed U. marinum an 'opportunistic' predator. It is likely that very small tintinnids such as Tintinnopsis nana and small oligotrich ciliates have similar trophic characteristics. An approximate estimation of the food required for maximum cell growth in T. nana similar to that made for T. subacuta (above) gives a value of about 60×10^3 Monochrysis lutheri/ml, or even more of a smaller prey. This is equivalent to about 3.0 ppm by volume, a level so high as to be rarely found among particles of less than 5 µm diameter in this area. T. nana has very transient 'blooms' in this area, in which it may become as abundant as 15 to 20/ml. Hamilton and Preslan (1969) also found that U. marinum underwent up to 20-fold changes in cell volume, which may be a consequence of a time lag in the rate of division. Canale et.al.(1973) noticed a similar phenomenon with Tetrahymena pyriformis. There was no evidence of great variation in tintinnid cell volumes in this study.

There has been considerable discussion of 'loss' rates and of the relationship between hunger, starvation, and the feeding rates of tintinnids in this section on accumulation experiments. No firm conclusions could be drawn from this discussion. Berger (1971) found that the loss rate of food vacuoles in feeding Paramecium aurelia was an exponential function; and Goulder (1972) found the same result at a much slower rate in starved individuals of the very large ciliate Loxodes magnus. Goulder (loc.cit.) equated loss rate with feeding rate and estimated the feeding rates of L. magnus by extrapolating the rate of food loss back to zero time. However, this produces a very low

feeding rate for such a large ciliate; and as there is some evidence that a feeding ciliate loses food even initially at a faster rate than a starved ciliate (Rapport, unpublished data; this study Section 4a), this method of calculation may be suspect. Canale, et.al. (1973) and Gold (1971) have found that starving ciliates suffer rapid mortality and cell lysis in laboratory culture; and in this study it was found that the feeding abilities of tintinnids were considerably reduced after complete starvation for about 30 hours, which may indicate moribundity. More data is needed on this subject.

The only other behavioural study of feeding in ciliated microzooplankton was that of Strathmann, (1971). Strathmann studied the detailed feeding behaviour and numbers of food cells accumulated by the planktonic larvae of 15 species of echinoderms. He found that these larvae regulate their feeding rate on particles with a variety of methods. Echinoderm larvae show spontaneous variability of feeding rates over short periods of time even in filtered water. Likewise the variable response of individual tintinnids to two apparently similar successive particles may spring from some purely internal physiological changes. Particles are ingested by echinoderm larvae by local induced reversals of beating by some cilia of the ciliary band, without the use of mucus. Feeding may be stopped or reduced by passing particles over the ciliated band with the water. Strathmann et.al. (1972) state that mucus is probably used by many filter feeders only in the rejection or egestion of particles and not in the process of ingestion. The details of the ingestion of very small particles by tintinnids could not be seen in this study although the oral plug may play some part in the process (Section 4c). Echinoderm larvae can sort particles inside the gut; and if necessary expel them by muscular contractions, or if they are indigestible sort them to bypass the stomach towards the anus. It is not known if tintinnids can

sort particles internally. Particles are rejected before reaching the gut by the larvae stopping or reversing the beat of all cilia in the ciliary band, and this seems analogous to the rejection behaviour of tintinnids (Section 4b).

Strathmann (1971) found that the rate of passage of food through the gut in echinoderm larvae was extremely irregular, but generally increased with an increase in the ingestion rate. This observation may be analogous to the 'forcing effect' of new food on the rate of loss of old food by tintinnids seen in the accumulation experiments in this study (Section 4a). Echinoderm larvae can ingest particles (especially 'discs' or 'spheres') of a size of up to 75 to 100% of the diameter of the oesophagus or 80 to 100 µm in most species. Tintinnids can ingest particles far larger than the undistended diameter of their cytopharynx and carnivorous ciliates are even more impressive in this regard. Planktonic crustacea rarely ingest particles which are relatively as large as this. Most echinoderm larvae can ingest large thin diatom cells (200 x 30 µm) but like tintinnids they cannot deal with long chains of cells of any size. Strathmann (loc. cit.) found that although there was no positive selection of or preference for, food items of various types by echinoderm larvae there was some differential ease of capture; and he thought that the ingestion of very large items 'interfered' with the ingestion of smaller items (apparent negative selection), though not vice versa. Differential predation and apparent negative selection in mixed-prey situations was seen in tintinnids in this study (Section 4a); but any 'interference' by one food item with another is unlikely to be a mechanical process at least in tintinnids, due to the time lag between ingestion events even at high food concentrations.

Strathmann (1971) calculated clearance (feeding) rates in two ways which were essentially similar to those used in this study in Sections 4a and 4b, except that the periods of accumulation were shorter in the more rapidly-feeding larvae than in tintinnids. Rates determined by direct observation of echinoderm larvae were higher and more variable than those determined from food accumulation. Very little ingestion was observed by tintinnids in this study; but the 'observed' feeding rate of Tintinnidium mucicola (Table 26) was somewhat greater than feeding rates calculated for this species by the accumulation method. As there can be rejection of particles from the mouth of echinoderm larvae, and as observations were made over very short periods of time in both kinds of organisms; this discrepancy in feeding rates is not too surprising. Echinoderm larvae do not feed at a rate sufficient to pack the gut with algae for long periods of time.

The optimal food concentrations (OFC) for echinoderm larvae are lower, and feeding rates decline more rapidly at high food concentrations than in some larger types of microzooplankters (e.g. see Table 30). Although little reliable information on OFC values has been obtained during this study: from some of the results in the Section on accumulation experiments (Section 4a), it seems that in tintinnids also (e.g. in Tintinnopsis subacuta) OFC levels may be as low as 1,500 cells/ml of Eutreptiella sp. or more of smaller prey. The feeding rates found in 7 species of echinoderm larvae varied with food, species and growth phase between 0.02 and 0.53 ml/hr/larva. These rates are 2 to 50 times greater than the feeding rate of Tintinnopsis subacuta (Table 30). However tintinnids are far more than 2 to 50 times more abundant than echinoderm larvae or any organism of similar size, in this area.

Some of the feeding ppeculiarities of the tintinnids in this study

correlate well with qualitative evidence from field samples. For example, relatively high natural concentrations of euglenoid flagellates are almost always accompanied by large numbers of active Tintinnopsis subacuta, many of which will be undergoing division. Relatively large numbers of cryptomonad flagellates are usually accompanied by relatively large numbers of Tintinnidium mucicola. Favella serrata is at its most abundant locally when there are fairly high numbers of dinoflagellates in field samples in late summer or fall. There is some qualitative evidence from studies of toxic 'red-tides' in Eastern Canada for the predation of Favella sp. on large dinoflagellates.

There are few data on the effect of the feeding of ciliates or other microzooplankters on natural populations of prey organisms. Goulder (1972) estimated that the fresh-water ciliate Loxodes magnus would remove a negligible fraction of the dominant algal food items in one day. His methods of calculation may have led to an under-estimate. Most of the other information comes from the work of Parsons and LeBrasseur (1970), Parsons et.al. (1967) and Poulet (1973, 1974) on the feeding rates and food webs of neritic planktonic crustacea. These authors utilised Coulter Counter techniques and some of their results have been discussed in that part of the study (Section 4c).

The feeding rates of Tintinnopsis subacuta and Stenosomella ventricosa have been measured with the Coulter Counter technique to vary between about 0.33 and 3.8% ml/hr/tintinnid depending upon the method of calculation. The overall effect of tintinnids on 'populations' of natural particles (living or inert) is sometimes to increase the volume of particles in some size classes, or overall. Similar results were found in experiments with two species of rotifers in this study, and by Poulet (1973) on Pseudocalanus

minutus. Pseudocalanus minutus appears to eat particles from 3 to 100 - 114 µm diameter, but apparently only eats those smaller than 9 um when they are relatively very abundant; and in general may eat the greatest volume/hour from those size classes which contain the greatest total volume. This is also seen in some of the results of Parsons et.al. (1967). The situation in Tintinnopsis subacuta is much less clear-cut. Natural particles as small as 1 µm are eaten, but much less in proportion to their total volume than particles from 3 to 8 µm diameter. This apparent differential size predation in the tintinnid is confused by the fact that particles of the size that is most consistently eaten are also those with the highest potential rates of increase (Section 4c). However, in those experiments showing the greatest feeding rates of T. subacuta on natural samples, and also the most consistently positive electivity values, the dominant prey item was a species of Eutreptiella. T. subacuta showed the same characteristics in the results of the accumulation experiments (Section 4a).

In addition to differential predation on various sizes of particles, several authors (Adams and Steele, 1966; Parsons, et.al. 1967) have estimated that filter-feeding by planktonic crustacea may stop in very low total concontrations of food. This phenomenon was also judged to be present by extrapolations from Coulter Counter data in T. subacuta and S. ventricosa for which it is probably not useful, but these extrapolated lower threshold values were extremely low in these two species. Bearing in mind the behaviour of tintinnids, the use of such extrapolations is probably not justified in this case.

Parsons et.al. (1967) and Poulet (1973, 1974) have demonstrated that the potential growth of natural phytoplankton populations can be controlled

in some cases by natural concentrations of small planktonic crustacea. Such potential control has also been demonstrated by Tintinnopsis subacuta in some experiments in this study (Section 4c). However, the great variability in these results do not readily allow the identification of the necessary conditions (e.g. the cell concentration of T. subacuta) for such control.

Approximate relative sizes, range of food size, and maximum feeding rates are compared in Table 30 for four very different types of marine microzooplankton. Of the three metazoan organisms, only the rotifer is numerous enough locally to have a comparable population feeding effect to the tintinnid over the size range of food common to both, despite the greater feeding rate of the individual rotifer. Certainly manyyother large and small zooplankton and benthic filter feeders will also affect phytoplankton populations in this and other coastal areas. However it seems highly likely that ciliates will have a greater effect on the biomass and diversity of the productive phytoplankton of less than 10 μm diameter than any other zooplankton organisms.

Due to considerable food size overlaps, the relative productivity and feeding impact of tintinnid and oligotrich species on small natural particles will partly depend on the prey species and biomass distribution. For example, the maximum reproductive rate of Tintinnopsis nana may be 4 or 5 times that of T. subacuta; and at such a rate T. nana would soon be so numerous as to have a greater feeding effect than larger tintinnids on particles of 5 μm diameter. However, in order to reach the maximum rate, T. nana might require 4 to 5 times as many particles of that size as would T. subacuta, because of the faster search rate of the latter. T. subacuta can also eat particles 60 times larger than is possible for T. nana including T. nana itself. Thus T. subacuta may be able to reproduce at a rate equal to or greater than that of

TABLE 30. Approximate relative sizes and feeding rates of various types of marine microzooplankton.

Organism	Relative Size	Basis of Size Comparison	Size Range of food (spheres) (μm)	Maximum FR as percentage ml/hr/pred	Optimal Food Concentration (Total) $\mu m^3 \times 10^6$/ml (ppm)	Maximum FR as percentage body vol. or wt/hr	Reference
Tintinnopsis subacuta (protozoan)	1 ($7 \times 10^4 \mu m^3$)	-	1 - 20	Av. 1.0	0.7	10.0	Present Study
Synchaeta littoralis (rotifer)	100	Estimated volume	< 5 - ?	4.3	-	0.6	Present Study
Strongylocentrotus droebachiensis (echinoderm larva)	500	$\frac{\text{Length}^3}{2}$	< 8 - 85	9.6	4	0.01 (est.)	Strathmann (1971)
Pseudocalanus minutus (copepod)	1000	μg C	3 - 100	17.0	15	2.3	Parsons and Lebrasseur (1970) and Poulet (1974)

T. nana in many natural situations. The same simplistic reasoning may apply equally well to comparisons between other species of tintinnids.

The importance of tintinnids as potential 'controllers', competitors, or valuable prey is stilliin doubt; but certainly the larger species, particularly Tintinnopsis subacuta, eat at a sufficient rate and are numerous enough at times in English Bay to fill all these categories.

(6) SUMMARY

1) General aspects of the feeding biology of 13 local species of tintinnids and some other microzooplankton were examined qualitatively and quantitatively.

2) Tintinnids and other microzooplankton ate a wide variety of items: living and inert, natural and unnatural, including other tintinnids.

3) The maximum volume of food eaten was a function of the tintinnid cell volume taken over all species. Tintinnid species of similar volume were dissimilar in the maximum size of their food.

4) There is apparently no minimum size of food for tintinnids and all the local species ate bacteria and other particles of 1.5 um diameter or less.

5) Several tintinnid species showed differential predation on laboratory cultures of phytoplankton. In various species these differences were based upon: the handling ability of the predator; prey size; or prey type.

6) Also some types of laboratory phytoplankton were selected less than others from some mixed-prey situations particularly by Tintinnopsis subacuta.

7) The rates of accumulation of prey by four species of tintinnid were little affected by temperature, but there was some evidence of a faster rate of loss of ingested food at very high temperatures.

8) The relationship between the gain of new food and the loss of old food in individual Tintinnopsis subacuta and Stenosomella ventricosa was highly variable and may be heavily dependent upon the physiological history of the individual cell. The rate of gain of new food seemed to be largely independent of the amount of old food in a tintinnid, but the rate of loss of old food was on average faster in those cells which were gaining the greatest amounts of new food.

9) The feeding rates of a tintinnid species were extremely variable within and between experiments. Much of this variability was due to the use of tintinnids from field samples and much was due to the experimental methods used.

10) Feeding rates as estimated by the three methods used showed fair qualitative agreement but poor quantitative agreement. The feeding rate of Tintinnopsis subacuta in accumulation experiments was the equivalent of 0.65% ml/hr/tintinnid or usually much less. In Coulter Counter experiments T. subacuta ate the average equivalent of 2.0% (minimum) or 3.8% (maximum) ml/hr/tintinnid on natural samples, and 0.33% (minimum) or 2.0% (maximum) ml/hr/tintinnid from cultures of laboratory phytoplankton.

11) The feeding rates of Tintinnopsis subacuta and Stenosomella ventricosa were positively correlated most consistently with the initial and estimated mean total experimental particle volume. Correlation coefficients between feeding rates and another seven variables showed largely inexplicable trends.

12) It has been shown that prediction of tintinnid feeding rates from only a knowledge of the size distribution of particle biomass in a natural sample would be impossible.

13) Feeding rates of T. subacuta and S. ventricosa in Coulter Counter experiments showed no apparent upper asymptote below 0.76 ppm on natural samples and 1.92 ppm on laboratory cultures. However, in accumulation experiments T. subacuta showed apparent asymptotes (OFC) at 0.35 ppm on Dunaliella tertiolecta and at 0.70 ppm on Eutreptiella sp. These differences were not resolved.

14) The Ivlev electivity indices of Tintinnopsis subacuta on natural samples were most consistently positive in the middle size classes (3 to 7.5 um dia.) of its food range. These size classes showed the greatest growth in controls. The magnitude of the electivity indices of tintinnids on any prey type in accumulation experiments partly depended on the amount of other prey types eaten.

15) Natural concentrations of Tintinnopsis subacuta can apparently control the growth of natural populations of phytoplankton less than 20 um dia. under some conditions. The most likely concentrations of T. subacuta necessary for such control are unknown due to the great variability of results.

16) An average feeding rate of T. subacuta was compared with those of larger microzooplankters. It was concluded that the larger species of tintinnids would probably eat enough phytoplankton of less than 10 um dia., and are often numerous enough to have a potentially predominant effect upon such phytoplankton in English Bay and perhaps other coastal localities.

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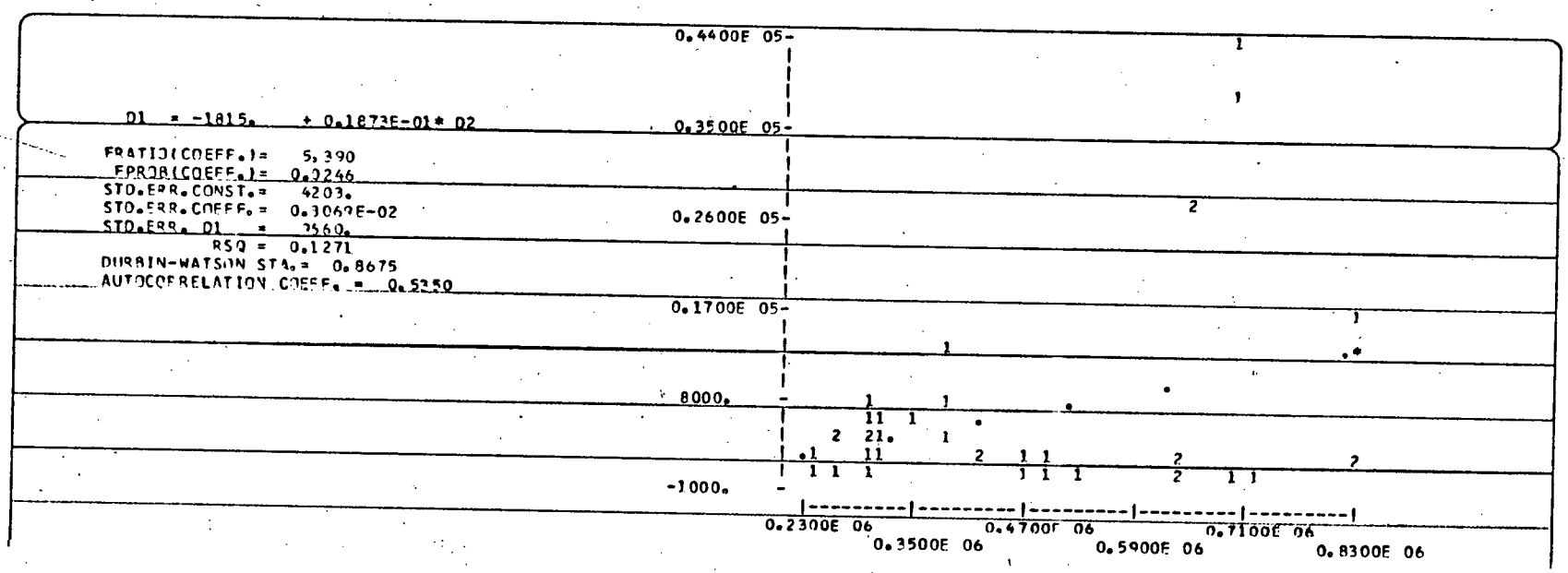
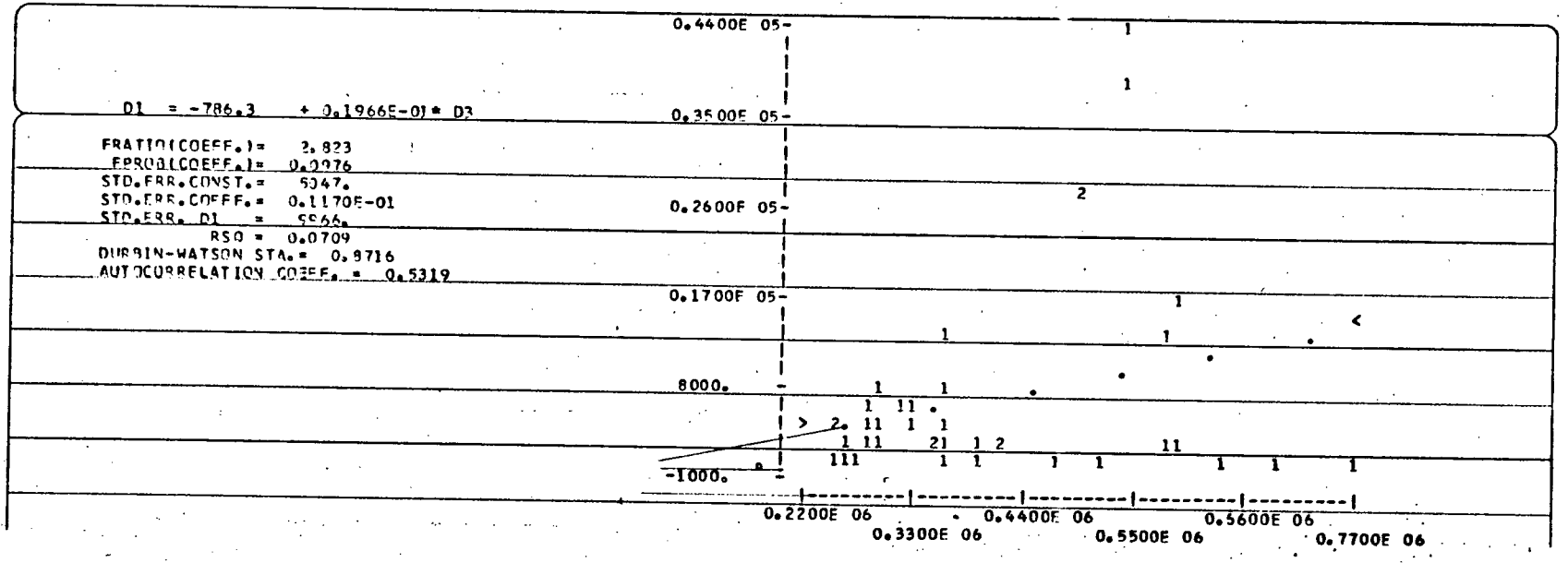
Appendix 1. Coulter Counter data. Tintinnopsis subacuta on natural particles. N.T.C. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
3334.	0.8333E 06	0.5989E 06	4.000	0.6200	0.4800	0.7700	9.000	12.50	44.00
0.1640E 05	0.8333E 06	0.5989E 06	8.000	0.8500	0.4800	0.7700	9.000	12.50	46.00
3449.	0.8316E 06	0.5865E 06	6.000	0.6200	0.7800	0.7700	9.000	12.50	46.00
0.1270E 05	0.8316E 06	0.5865E 06	9.000	0.8500	0.7800	0.7700	9.000	12.50	46.00
436.0	0.6330E 06	0.6376E 06	2.000	1.000	1.890	0.7700	10.00	15.00	46.00
1351.	0.6330E 06	0.5205E 06	4.000	0.8500	1.290	0.8100	10.00	15.00	34.00
1124.	0.7223E 06	0.6955E 06	3.000	1.000	1.470	0.8700	10.00	15.00	34.00
137.0	0.5339E 06	0.4742E 06	2.000	0.8700	6.300	0.8200	9.000	16.50	29.00
0.3958E 05	0.6357E 06	0.5414E 06	8.000	1.490	0.2800	0.8200	8.000	18.00	42.00
0.4418E 05	0.6357E 06	0.5414E 06	8.000	1.720	0.2800	0.8200	8.000	18.00	42.00
0.2697E 05	0.6546E 06	0.4966E 06	8.000	1.490	0.5300	1.000	8.000	18.00	42.00
0.2761E 05	0.6546E 06	0.4966E 06	8.000	1.720	0.5300	1.000	8.000	18.00	42.00
2067.	0.6393E 06	0.4195E 06	8.000	1.490	4.110	0.8700	8.000	19.00	42.00
3313.	0.6393E 06	0.4195E 06	8.000	1.720	4.110	0.8700	8.000	18.00	42.00
1624.	0.4933E 06	0.3647E 06	7.000	1.490	5.680	0.8700	8.000	18.00	42.00
1943.	0.4933E 06	0.3647E 06	7.000	1.720	5.680	0.8700	8.000	18.00	42.00
1506.	0.4739E 06	0.3962E 06	7.000	1.490	4.840	0.8600	8.000	18.00	42.00
1747.	0.4739E 06	0.3962E 06	7.000	1.720	4.840	0.8600	8.000	18.00	42.00
2424.	0.4277E 06	0.3506E 06	8.000	1.490	2.710	0.8100	8.000	18.00	42.00
2658.	0.4277E 06	0.3506E 06	7.000	1.720	2.710	0.8100	8.000	18.00	42.00
5321.	0.3326E 06	0.3200E 06	5.000	0.9200	0.2000	0.8700	8.000	18.00	48.00
790.0	0.2736E 06	0.2726E 06	5.000	0.9200	0.7100	0.9100	8.000	18.00	48.00
514.0	0.2615E 06	0.2578E 06	3.000	1.040	0.6400	0.9600	9.000	27.00	90.00
5174.	0.2615E 06	0.2579E 06	8.000	1.520	0.6400	0.8600	8.000	27.00	90.00
3939.	0.2615E 06	0.2578E 06	8.000	1.380	0.6400	0.8600	9.000	27.00	90.00
3241.	0.3375E 06	0.2915E 06	4.000	1.060	0.4300	0.6600	8.000	27.00	36.00
8555.	0.3374E 06	0.2915E 06	8.000	1.470	0.4300	0.6600	8.000	27.00	36.00
5243.	0.3374E 06	0.2915E 06	8.000	1.170	0.4300	0.6600	8.000	27.00	36.00
5106.	0.3379E 06	0.3597E 06	6.000	1.060	0.3900	0.6600	8.000	27.00	36.00
0.1261E 05	0.3379E 06	0.3597E 06	8.000	1.470	0.3900	0.6600	8.000	27.00	36.00
8292.	0.3379E 06	0.3597E 06	7.000	1.170	0.3900	0.6600	8.000	27.00	36.00
3900.	0.3359E 06	0.3285E 06	6.000	1.380	0.4800	0.8700	8.000	27.00	90.00
6946.	0.3359E 06	0.3285E 06	7.000	1.520	0.4800	0.8700	8.000	27.00	90.00
2743.	0.3114E 06	0.2870E 06	6.000	1.060	0.7600	0.8100	8.000	27.00	36.00
6482.	0.3114E 06	0.2870E 06	8.000	1.470	0.7600	0.8100	8.000	27.00	36.00
4364.	0.3114E 06	0.2870E 06	8.000	1.170	0.7600	0.8100	8.000	27.00	36.00
1699.	0.2418E 06	0.2590E 06	6.000	1.380	1.030	0.9300	8.000	27.00	90.00
2777.	0.2418E 06	0.2590E 06	7.000	1.520	1.030	0.9300	8.000	27.00	90.00
1300.	0.7015E 06	0.7715E 06	4.000	1.170	0.6100	0.6100	15.00	28.00	29.00

NAME	MEANS	STD.DEV.	CORRELATIONS										39. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	
D1	7258.95	10202.5	1.0000										
D2	484394.	194207.	0.3566	1.0000									
D3	409276.	138188.	0.2662	0.9137	1.0000								
D4	6.43589	1.90283	0.4455	-0.0644	-0.2855	1.0000							
D5	1.27614	0.374358	0.2969	-0.2723	-0.3271	0.5801	1.0000						
D6	1.56332	1.78802	-0.3490	0.1134	0.0101	-0.0777	0.2968	1.0000					
D7	0.814615	0.938599E-01	0.1283	-0.0273	-0.1523	0.1063	0.3382	0.2434	1.0000				
D8	8.46153	1.23216	-0.1713	0.4453	0.7087	-0.4585	-0.3471	-0.0687	-0.3625	1.0000			
D9	21.1153	5.54348	-0.1602	-0.8025	-0.6341	0.1286	0.2661	-0.3557	-0.2663	-0.1062	1.0000		
D10	49.9742	19.9822	-0.1253	-0.4534	-0.4291	0.0508	0.1595	-0.2249	0.4318	-0.2529	0.3630	1.0000	

5. *SIMREG*

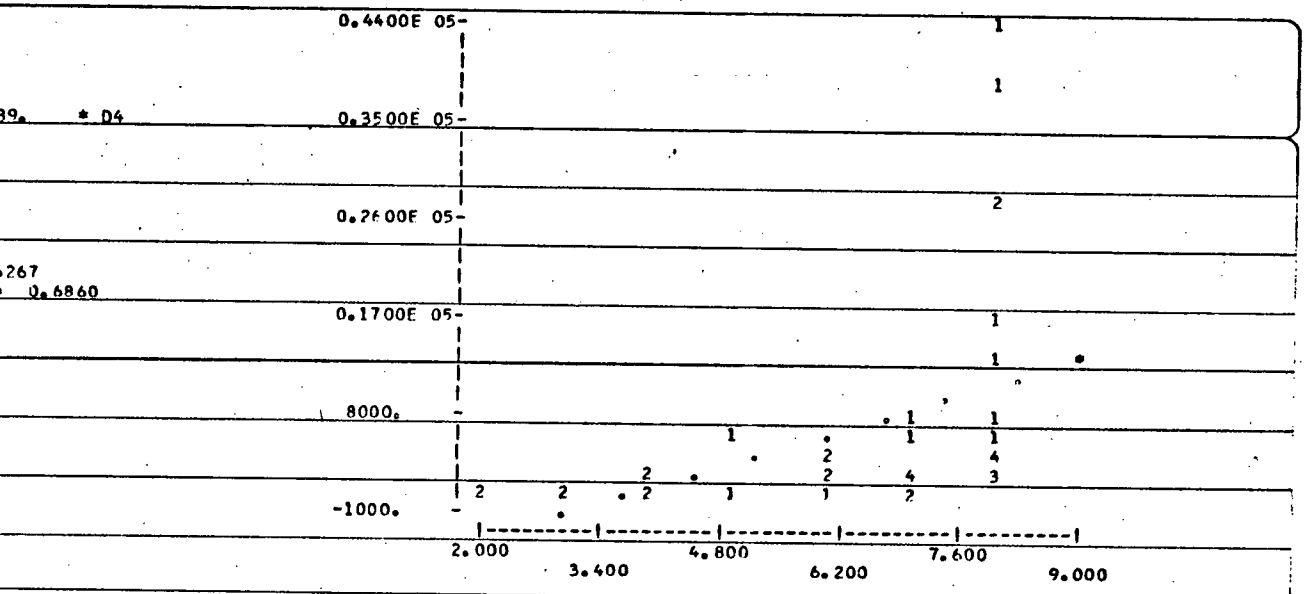

D1 = -1815. + 0.1873E-01* D2
FRATIO(COEFF.)= 5.390
FPROB(COEFF.)= 0.0246
STD.ERR.CONST.= 4203.
STD.ERR.COEFF.= 0.3069E-02
STD.ERR. D1 = 7560.
RSQ = 0.1271
DURBIN-WATSON STA.= 0.8675
AUTOCORRELATION COEFF.= 0.5250
0.4400E 05
0.3500E 05
0.2600E 05
0.1700E 05
8000.
-1000.
0.2300E 06
0.3500E 06
0.4700E 06
0.5900E 06
0.7100E 06
0.8300E 06


D1 = -786.3 + 0.1966E-01* D3
FRATIO(COEFF.)= 2.823
FPROB(COEFF.)= 0.0976
STD.ERR.CONST.= 5047.
STD.ERR.COEFF.= 0.1170E-01
STD.ERR. D1 = 5566.
RSQ = 0.0709
DURBIN-WATSON STA.= 0.9716
AUTOCORRELATION COEFF.= 0.5319
0.4400E 05
0.3500E 05
0.2600E 05
0.1700E 05
8000.
-1000.
0.2200E 06
0.3300E 06
0.4400E 06
0.5500E 06
0.5600E 06
0.7700E 06

Appendix 1. (Cont'd)

D1 = -8114. + 2389. * D4

FRATIO(COEFF.)= 9.161
FPROB(COEFF.)= 0.0045
STD.ERR.CONST.= 5291.
STD.ERR.COEFF.= 789.2
STD.ERR. D1 = 9257.
RSQ = 0.1995
DURBIN-WATSON STA.= 0.6267
AUTOCORRELATION COEFF.= 0.6860



D1 = -4658. + 9338. * D5

FRATIO(COEFF.)= 3.576
FPROB(COEFF.)= 0.0634
STD.ERR.CONST.= 6497.
STD.ERR.COEFF.= 4938.
STD.ERR. D1 = 9873.
RSQ = 0.0981
DURBIN-WATSON STA.= 0.7023
AUTOCORRELATION COEFF. = 0.6443

D1 = 0.1926E 05+ -1418. * D8

FRATIO(COEFF.)= 1.118
FPROB(COEFF.)= 0.2977
STD.ERR.CONST.= 0.1146E 05
STD.ERR.COEFF.= 1341.
STD.ERR. D1 = 0.1019E 05
RSQ = 0.0293
DURBIN-WATSON STA.= 0.8225
AUTOCORRELATION COEFF. = 0.5963

D1 = 0.1037E 05+ -1991. * D6

FRATIO(COEFF.)= 5.131
FPROB(COEFF.)= 0.2280
STD.ERR.CONST.= 2373.
STD.ERR.COEFF.= 879.1
STD.ERR. D1 = 9599.
RSQ = 0.1218
DURBIN-WATSON STA.= 0.6177
AUTOCORRELATION COEFF. = 0.6763

D1 = 0.1348E 05+ -294.9 * D9

FRATIO(COEFF.)= 0.9746
FPROB(COEFF.)= 0.3218
STD.ERR.CONST.= 6515.
STD.ERR.COEFF.= 298.7
STD.ERR. D1 = 0.1021E 05
RSQ = 0.0257
DURBIN-WATSON STA.= 0.8434
AUTOCORRELATION COEFF. = 0.5706

D1 = -4104. + 0.1395E 05* D7

FRATIO(COEFF.)= 0.6194
FPROB(COEFF.)= 0.4413
STD.ERR.CONST.= 0.1433E 05
STD.ERR.COEFF.= 0.1772E 05
STD.ERR. D1 = 0.1025E 05
RSQ = 0.0165
DURBIN-WATSON STA.= 0.8449
AUTOCORRELATION COEFF. = 0.5746

D1 = 0.1039E 05+ -63.69 * D10

FRATIO(COEFF.)= 0.5902
FPROB(COEFF.)= 0.4531
STD.ERR.CONST.= 4397.
STD.ERR.COEFF.= 83.29
STD.ERR. D1 = 0.1026E 05
RSQ = 0.0157
DURBIN-WATSON STA.= 0.8640
AUTOCORRELATION COEFF. = 0.5585

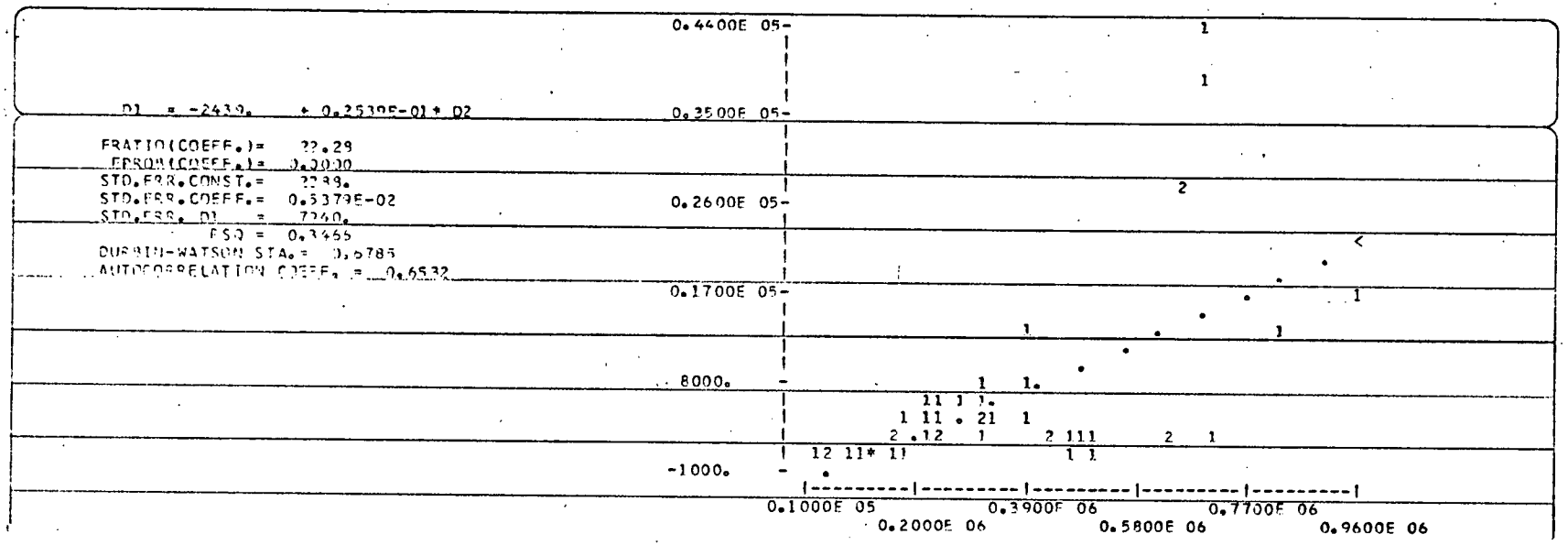
Appendix 2. Coulter Counter Data. *Tintinnopsis subacuta* on natural particles. E.S.O. method.

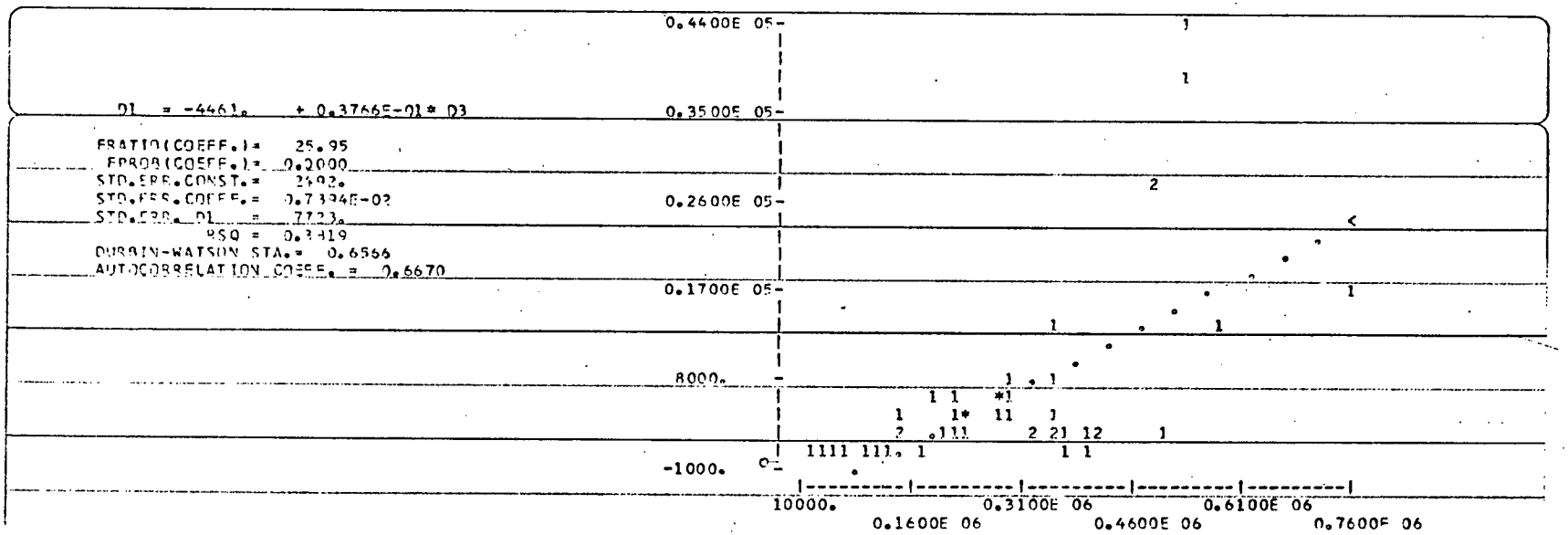
D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
3334.	0.47575E 06	0.3306E 06	4.000	0.5900	0.4800	0.7700	9.000	12.50	46.00
0.1440E 05	0.9625E 06	0.7576E 06	8.000	0.8500	0.4800	0.7700	9.000	12.50	46.00
3440.	0.7112E 06	0.5073E 06	6.000	0.6500	0.7800	0.7700	9.000	12.50	46.00
0.1270E 05	0.8816E 06	0.5965E 06	9.000	0.8500	0.7800	0.7700	9.000	12.50	46.00
1715.	0.1547E 06	0.1477E 06	2.000	1.350	1.890	0.7700	10.00	15.00	34.00
2594.	0.2286E 06	0.2047E 06	4.000	1.450	1.290	0.8100	10.00	15.00	34.00
550.0	0.3773E 05	0.2151E 05	1.000	1.210	0.9200	0.8800	10.00	15.00	34.00
3551.	0.3335E 06	0.2416E 06	3.000	1.010	1.470	0.8600	10.00	15.00	34.00
137.0	0.9329E 05	0.6892E 05	2.000	0.8300	6.300	0.8200	9.000	14.00	29.00
0.3959E 05	0.2757E 06	0.5414E 06	8.000	1.490	0.2800	0.8200	8.000	18.00	42.00
0.4418E 05	0.3137E 06	0.5414E 06	8.000	1.720	0.2800	0.8200	8.000	18.00	42.00
0.2697E 05	0.1956E 06	0.4966E 06	8.000	1.490	0.5300	1.000	8.000	18.00	42.00
0.2761E 05	0.1956E 06	0.4966E 06	8.000	1.720	0.5300	1.000	8.000	18.00	42.00
2047.	0.5833E 06	0.4185E 06	8.000	1.490	4.110	0.8700	8.000	18.00	42.00
3313.	0.5833E 06	0.4185E 06	9.000	1.720	4.110	0.8700	8.000	18.00	42.00
1624.	0.4583E 06	0.3647E 06	7.000	1.490	5.680	0.8700	8.000	18.00	42.00
1843.	0.4933E 06	0.3647E 06	7.000	1.720	5.680	0.8700	8.000	18.00	42.00
1506.	0.4733E 06	0.3962E 06	7.000	1.490	4.840	0.8600	8.000	18.00	42.00
1747.	0.4733E 06	0.3962E 06	7.000	1.720	4.840	0.8600	8.000	18.00	42.00
2424.	0.4277E 06	0.3506E 06	8.000	1.490	2.710	0.8100	8.000	18.00	42.00
2558.	0.4277E 06	0.3506E 06	7.000	1.720	2.710	0.8100	8.000	19.00	42.00
735.0	0.3333E 05	0.3626E 05	1.000	1.020	0.2700	0.8700	8.000	19.00	48.00
6414.	0.2213E 06	0.1977E 06	5.000	0.9100	0.2000	0.8700	9.000	18.00	48.00
1833.	0.1551E 06	0.1436E 06	5.000	0.9600	0.7100	0.9100	8.000	18.00	48.00
693.0	0.1037E 06	0.1073E 06	3.000	1.130	0.6400	0.8600	8.000	19.00	90.00
5328.	0.2222E 06	0.2264E 06	8.000	2.040	0.6400	0.8600	8.000	27.00	90.00
3039.	0.2222E 06	0.2264E 06	8.000	1.380	0.6400	0.8600	8.000	27.00	90.00
2519.	0.1729E 06	0.1497E 06	4.000	1.090	0.4300	0.6600	8.000	27.00	36.00
5555.	0.3376E 06	0.2915E 06	8.000	1.470	0.4300	0.6600	8.000	27.00	36.00
5243.	0.3376E 06	0.2915E 06	8.000	1.170	0.4300	0.6600	9.000	27.00	36.00
5106.	0.3379E 06	0.3517E 06	6.000	1.060	0.3900	0.6600	8.000	27.00	36.00
0.1261E 05	0.3379E 06	0.2587E 06	8.000	1.470	0.3900	0.6600	8.000	27.00	36.00
8092.	0.3379E 06	0.2587E 06	7.000	1.170	0.3900	0.6600	8.000	27.00	36.00
1217.	0.1238E 06	0.1217E 06	3.000	1.150	0.4800	0.8700	8.000	27.00	90.00
4416.	0.2249E 06	0.2295E 06	6.000	1.520	0.4800	0.8700	8.000	27.00	90.00
7081.	0.3741E 06	0.2974E 06	7.000	2.040	0.4800	0.8700	8.000	27.00	90.00
2987.	0.2406E 06	0.2271E 06	6.000	1.000	0.7600	0.8100	8.000	27.00	36.00
6492.	0.3114E 06	0.2470E 06	8.000	1.470	0.7600	0.8100	8.000	27.00	36.00
4254.	0.3114E 06	0.2970E 06	8.000	1.170	0.7600	0.8100	8.000	27.00	36.00
441.0	0.5333E 05	0.5253E 05	2.000	1.170	1.030	0.9300	8.000	27.00	90.00
1569.	0.1744E 06	0.1315E 06	6.000	1.000	1.030	0.9300	9.000	27.00	90.00
2977.	0.2163E 06	0.2333E 06	7.000	2.040	1.030	0.9300	8.000	27.00	90.00
2055.	0.3033E 05	0.3106E 06	4.000	1.270	0.6100	0.6100	15.00	28.00	29.00
1677.	0.1333E 06	0.1267E 06	1.000	0.9700	0.6700	0.5900	15.00	28.00	29.00

NAME	MEANS	STD.DEV.	CORRELATIONS D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	6765.53	9707.84	1.0000									
D2	362499.	225096.	0.5987	1.0000								
D3	298072.	153283.	0.6180	0.9777	1.0000							
D4	5.96636	2.38421	0.4472	0.6772	0.7467	1.0000						
D5	1.31181	0.360214	0.2237	0.0861	0.1517	0.4560	1.0000					
D6	1.46225	1.70757	-0.3106	0.1335	0.0541	0.0513	0.2214	1.0000				
D7	0.815908	0.973917E-01	0.1012	0.0104	-0.0530	0.0651	0.3074	0.2131	1.0000			
D8	8.61363	1.54342	-0.1603	-0.1313	-0.1345	-0.4736	-0.2480	-0.0932	-0.4780	1.0000		
D9	21.1115	5.32258	-0.1543	-0.4652	-0.3371	0.0902	0.2394	-0.3348	-0.2910	0.0216	1.0000	
D10	49.7498	21.2144	-0.1404	-0.2966	-0.2591	0.0082	0.2491	-0.2205	0.4713	-0.3212	0.3339	1.0000

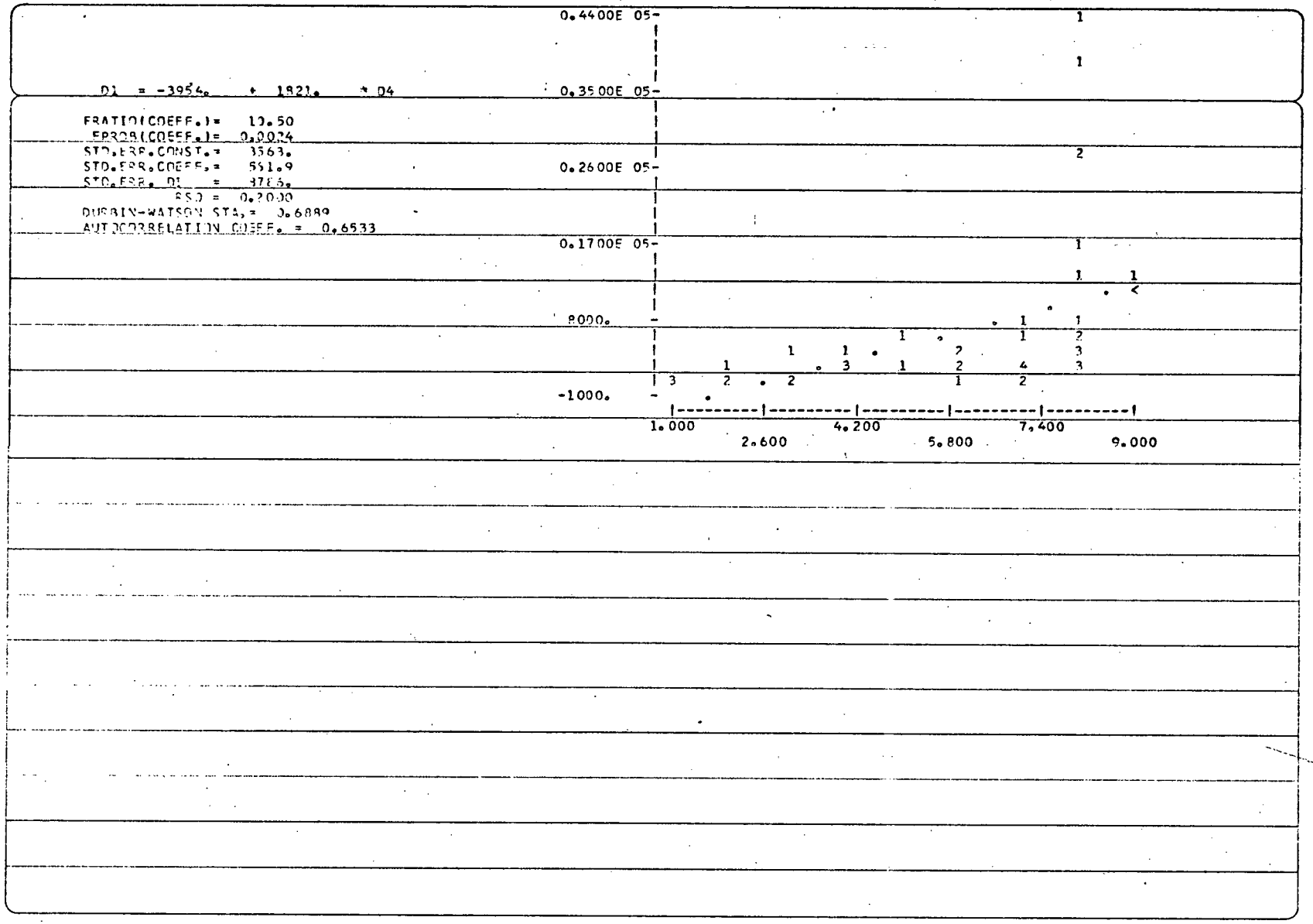
44. OBSERVATIONS

5. *SIMREG*


D1 = -2439. + 0.2539E-01* D2
FRATIO(COEFF.)= 22.29
PROB(COEFF.)= 0.0030
STD.ERR.CONST.= 2289.
STD.ERR.COEFF.= 0.5379E-02
STD.ERR. D1 = 7240.
RSQ = 0.3465
DURBIN-WATSON STA.= 0.5785
AUTOCORRELATION COEFF. = 0.6532
0.4400E 05
0.3500E 05
0.2600E 05
0.1700E 05
8000.
-1000.
0.1000E 05
0.2000E 06
0.3900E 06
0.5800E 06
0.7700E 06
0.9600E 06


D1 = -4461. + 0.3766E-01* D3
FRATIO(COEFF.)= 25.95
PROB(COEFF.)= 0.0000
STD.ERR.CONST.= 2492.
STD.ERR.COEFF.= 0.7394E-02
STD.ERR. D1 = 7723.
RSQ = 0.3819
DURBIN-WATSON STA.= 0.6566
AUTOCORRELATION COEFF. = 0.6670
0.4400E 05
0.3500E 05
0.2600E 05
0.1700E 05
8000.
-1000.
10000.
0.1600E 06
0.3100E 06
0.4600E 06
0.6100E 06
0.7600E 06

Appendix 2. (Cont'd)



Appendix 2. (Cont'd)

D1 = -1143. + 6028. * D5

FRATIO(COEFF.)= 2.212
FPROB(COEFF.)= 0.1405
STD.ERR.CONST.= 5509.
STD.ERR.COEFF.= 4053.
STD.ERR. D1 = 3574.
RSQ = 0.0500
DURBIN-WATSON STA.= 0.7275
AUTOCORRELATION COEFF. = 0.6350

D1 = 0.1545E 05+ -1008. * D8

FRATIO(COEFF.)= 1.108
FPROB(COEFF.)= 0.2991
STD.ERR.CONST.= 3380.
STD.ERR.COEFF.= 953.0
STD.ERR. D1 = 3696.
RSQ = 0.0257
DURBIN-WATSON STA.= 0.8217
AUTOCORRELATION COEFF. = 0.5878

D1 = 9347. + -1765. * D6

FRATIO(COEFF.)= 4.484
FPROB(COEFF.)= 0.3381
STD.ERR.CONST.= 1862.
STD.ERR.COEFF.= 833.9
STD.ERR. D1 = 3337.
RSQ = 0.0365
DURBIN-WATSON STA.= 0.6295
AUTOCORRELATION COEFF. = 0.6759

D1 = 0.1249E 05+ -271.3 * D9

FRATIO(COEFF.)= 1.025
FPROB(COEFF.)= 0.3185
STD.ERR.CONST.= 5844.
STD.ERR.COEFF.= 268.0
STD.ERR. D1 = 3735.
RSQ = 0.0238
DURBIN-WATSON STA.= 0.8467
AUTOCORRELATION COEFF. = 0.5711

D1 = -1467. + 0.1009E 05* D7

FRATIO(COEFF.)= 0.4348
FPROB(COEFF.)= 0.5203
STD.ERR.CONST.= 0.1257E 05
STD.ERR.COEFF.= 0.1530E 05
STD.ERR. D1 = 3772.
RSQ = 0.0102
DURBIN-WATSON STA.= 0.8364
AUTOCORRELATION COEFF. = 0.5797

D1 = 9963. + -64.26 * D10

FRATIO(COEFF.)= 0.8449
FPROB(COEFF.)= 0.3664
STD.ERR.CONST.= 3774.
STD.ERR.COEFF.= 69.91
STD.ERR. D1 = 3725.
RSQ = 0.0197
DURBIN-WATSON STA.= 0.8572
AUTOCORRELATION COEFF. = 0.5645

Appendix 3. Coulter Counter data. Tintinnopsis subacuta on laboratory food. N.T.C. method.

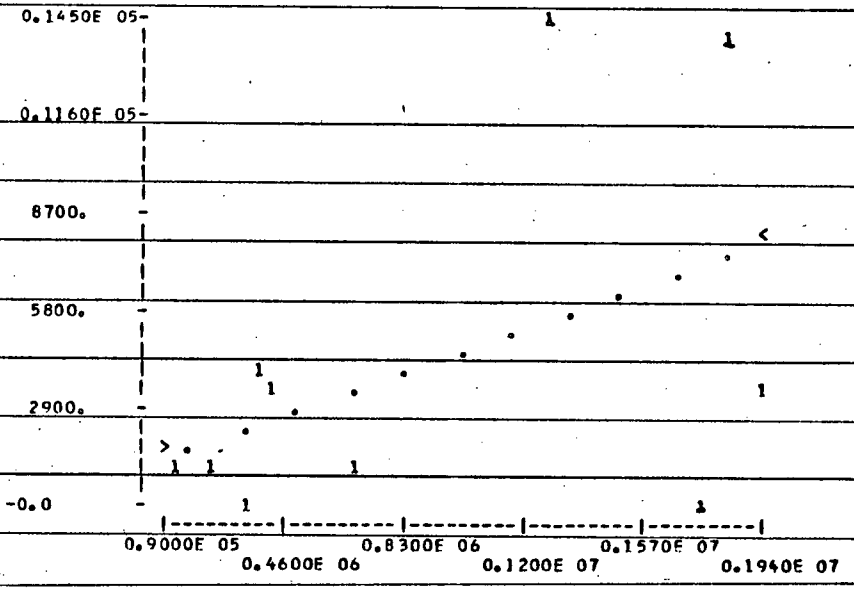
D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
0.1376E 05	0.1819E 07	0.1662E 07	4.000	0.9000	0.4200	0.8600	9.000	15.50	58.00
0.1449E 05	0.1219E 07	0.1146E 07	6.000	0.9100	0.6400	0.8800	10.00	15.00	24.00
4262.	0.3155E 06	0.2472E 06	4.000	0.5500	0.7900	0.8100	9.000	25.00	24.00
3458.	0.1939E 07	0.1919E 07	3.000	1.040	1.390	0.8000	10.00	25.50	30.00
17.00	0.1770E 07	0.1597E 07	2.000	0.8200	1.390	0.9600	10.00	25.50	30.00
970.0	0.1303E 06	0.1231E 06	6.000	2.830	2.580	0.6800	8.000	24.00	36.00
951.0	0.2337E 06	0.2361E 06	1.000	1.390	0.8200	0.7200	8.000	24.00	36.00
1298.	0.6341E 06	0.7340E 06	5.000	1.310	1.450	0.7200	8.000	24.00	36.00
11.00	0.3383E 06	0.2513E 06	3.000	0.5400	2.230	0.8000	8.000	25.00	24.00
3511.	0.4123E 06	0.4247E 06	6.000	0.8400	1.850	0.7500	8.000	25.00	24.00

NAME	MEANS	STD.DEV.	CORRELATIONS									10. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	4272.70	5402.62	1.0000									
D2	901075.	724635.	0.4633	1.0000								
D3	824520.	696477.	0.4274	0.9946	1.0000							
D4	4.00000	1.76383	0.3835	-0.1827	-0.1945	1.0000						
D5	1.11300	0.663425	-0.2266	-0.3278	-0.2756	0.2925	1.0000					
D6	1.35600	0.708178	-0.6680	-0.4555	-0.4345	0.2428	0.4699	1.0000				
D7	0.739000	0.852135E-01	0.3967	0.7330	0.6693	-0.2513	-0.6129	-0.4601	1.0000			
D8	8.80000	0.918935	0.4425	0.8327	0.8057	-0.1371	-0.3488	-0.4777	0.8031	1.0000		
D9	22.8500	4.04867	-0.9409	-0.3778	-0.3511	-0.3345	0.0695	0.5931	-0.3391	-0.3076	1.0000	
D10	31.6000	8.08443	0.2776	0.2950	0.3276	-0.1276	0.3418	-0.2899	-0.0834	-0.1198	-0.4096	1.0000

5. *SIMREG*

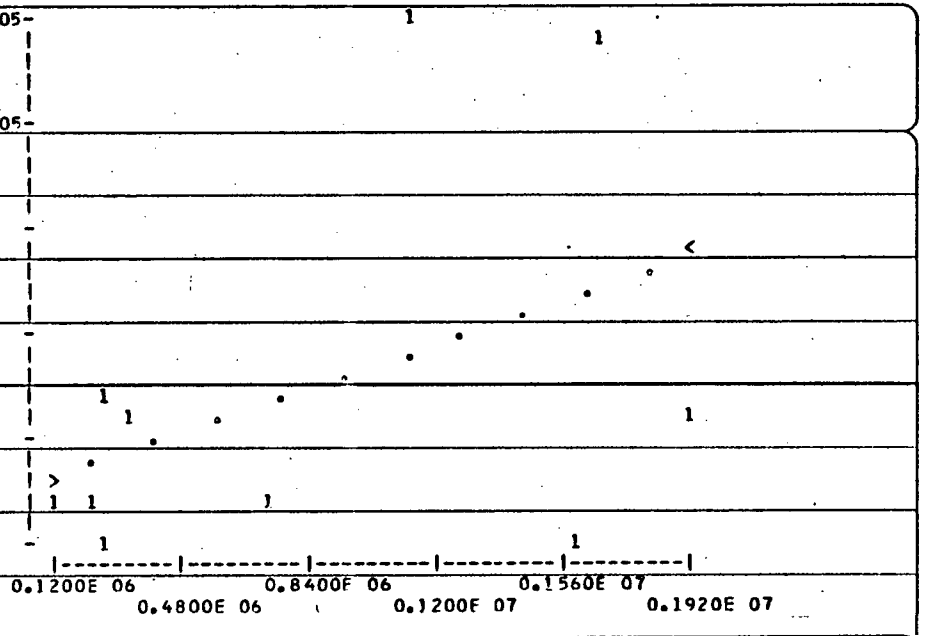
D1 = 1161. + 0.3454E-02* D2

FRATIO(COEFF.)= 2.186
FPROB(COEFF.)= 0.1754
STD.ERR.CONST.= 2647.
STD.ERR.COEFF.= 0.2336E-02
STD.ERR. D1 = 5178.
RSQ = 0.2146
DURBIN-WATSON STA.= 0.7702
AUTOCORRELATION COEFF. = 0.5165



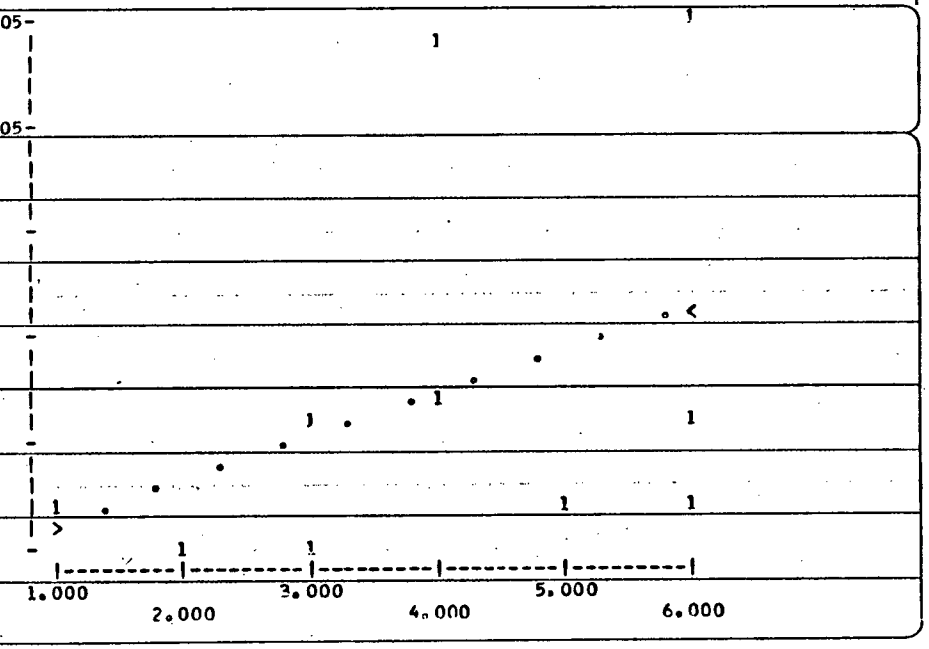
D1 = 1539. + 0.3315E-02* D3

FRATIO(COEFF.)= 1.788
EPROB(COEFF.)= 0.2165
STD.ERR.CONST.= 2620.
STD.ERR.COEFF.= 0.2479E-02
STD.ERR. D1 = 3191.
RSQ = 0.1827
DURBIN-WATSON STA.= 0.7043
AUTOCORRELATION COEFF. = 0.5418



D1 = -425.9 + 1175. * D4

FRATIO(COEFF.)= 1.379
EPROB(COEFF.)= 0.2739
STD.ERR.CONST.= 4336.
STD.ERR.COEFF.= 1000.
STD.ERR. D1 = 5292.
RSQ = 0.1471
DURBIN-WATSON STA.= 0.6175
AUTOCORRELATION COEFF. = 0.4690



D1 = 6326. + -1845. * D5

FRATIO(COEFF.)= 0.4330
FPROB(COEFF.)= 0.5345
STD.ERR.CONST.= 3586.
STD.ERR.COEFF.= 2804.
STD.ERR. D1 = 5591.
RSQ = 0.0513
DURBIN-WATSON STA.= 0.7495
AUTOCORRELATION COEFF. = 0.4552

D1 =-0.1862E 05+ 2602. * D9

FRATIO(COEFF.)= 1.949
FPROB(COEFF.)= 0.1995
STD.ERR.CONST.= 0.1648E 05
STD.ERR.COEFF.= 1864.
STD.ERR. D1 = 5139.
RSQ = 0.1958
DURBIN-WATSON STA.= 0.6487
AUTOCORRELATION COEFF. = 0.4814

D1 = 0.1118E 05+ -5096. * D6

FRATIO(COEFF.)= 6.447
FPROB(COEFF.)= 0.0338
STD.ERR.CONST.= 3037.
STD.ERR.COEFF.= 2007.
STD.ERR. D1 = 4264.
RSQ = 0.4463
DURBIN-WATSON STA.= 1.804
AUTOCORRELATION COEFF. = 0.1124E-01

D1 = 0.3296E 05+ -1256. * D8

FRATIO(COEFF.)= 51.77
FPROB(COEFF.)= 0.2001
STD.ERR.CONST.= 3702.
STD.ERR.COEFF.= 159.8
STD.ERR. D1 = 1240.
RSQ = 0.8853
DURBIN-WATSON STA.= 1.013
AUTOCORRELATION COEFF. = 0.4299

D1 =-0.1580E 05+ 0.2515E 05* D7

FRATIO(COEFF.)= 1.494
FPROB(COEFF.)= 0.2558
STD.ERR.CONST.= 0.1650E 05
STD.ERR.COEFF.= 0.2059E 05
STD.ERR. D1 = 5260.
RSQ = 0.1574
DURBIN-WATSON STA.= 1.023
AUTOCORRELATION COEFF. = 0.3462

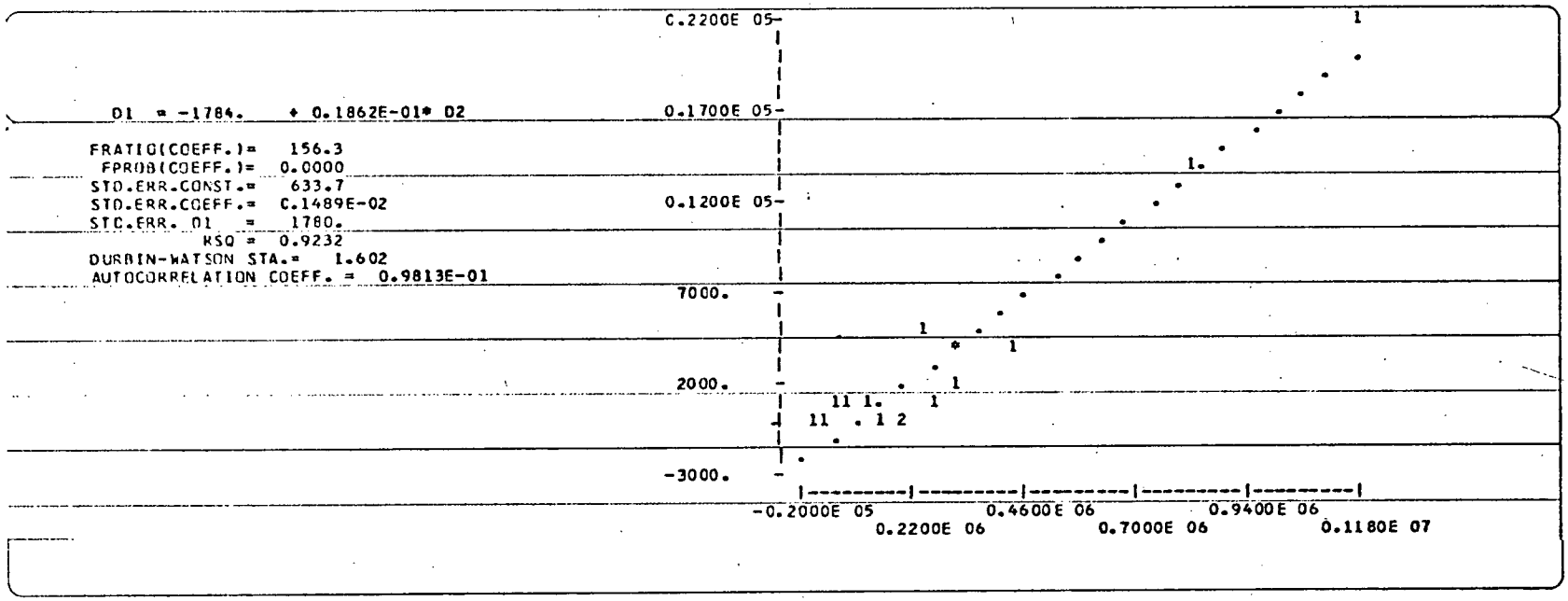
D1 = -1062. + 169.8 * D10

FRATIO(COEFF.)= 0.5680
FPROB(COEFF.)= 0.4419
STD.ERR.CONST.= 6755.
STD.ERR.COEFF.= 206.5
STD.ERR. D1 = 5505.
RSQ = 0.0771
DURBIN-WATSON STA.= 0.6706
AUTOCORRELATION COEFF. = 0.5899

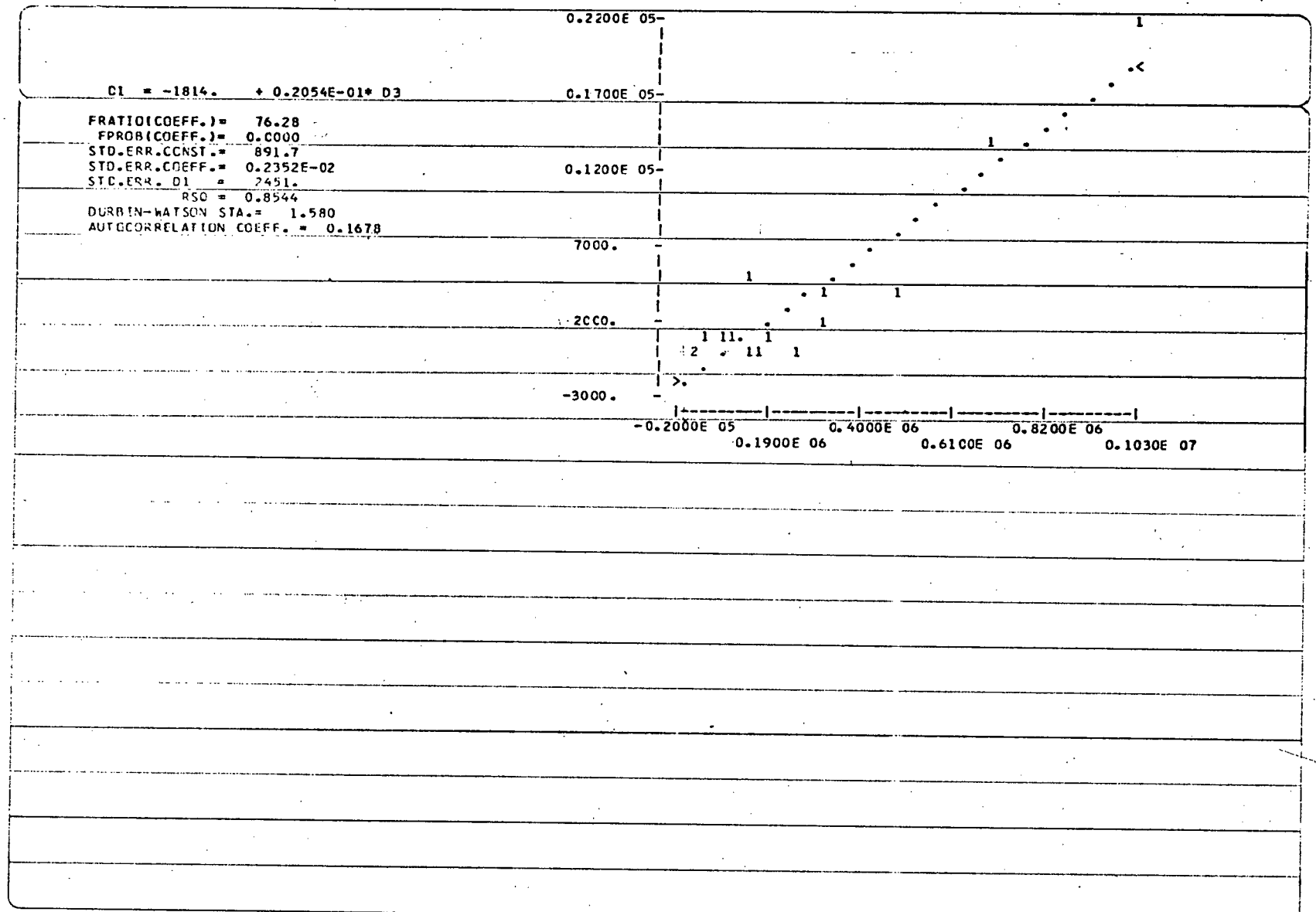
Appendix 4. Coulter Counter data. Tintinnopsis subacuta on laboratory food. E.S.O. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
0.2170E 05	0.1179E 07	0.1030E 07	4.000	0.9400	0.4200	0.8600	9.00	15.50	52.00
0.1449E 05	0.8295E 06	0.6874E 06	6.000	1.000	0.6400	0.8800	10.00	15.00	24.00
4882.	0.2418E 06	0.1410E 06	4.000	0.6100	0.7900	0.8100	9.000	25.00	24.00
3580.	0.3148E 06	0.4751E 06	3.000	2.880	1.390	0.8000	10.00	25.50	30.00
927.0	0.2625E 06	0.1798E 06	2.000	0.5400	1.390	0.9600	10.00	15.50	30.00
1020.	0.1246E 06	0.1164E 06	6.000	2.930	2.580	0.6800	8.000	24.00	36.00
167.0	0.1085E 05	0.1213E 05	1.000	3.110	1.600	0.6800	8.000	24.00	36.00
1106.	0.7528E 05	0.7934E 05	1.000	1.650	0.8200	0.7200	8.000	24.00	36.00
1625.	0.3261E 06	0.3140E 06	5.000	1.190	1.450	0.7200	15.00	28.00	37.00
252.0	0.1890E 06	0.2523E 06	3.000	2.230	5.390	0.6800	15.00	28.00	37.00
140.0	0.1424E 06	0.1524E 06	2.000	1.450	4.550	0.6800	9.000	15.50	52.00
420.0	0.1961E 06	0.1774E 06	2.000	0.8700	0.5500	0.7700	9.000	15.50	52.00
367.0	0.2315E 05	0.2566E 05	1.000	1.620	0.5200	0.7800	9.000	15.50	52.00
569.0	0.4767E 05	0.3774E 05	3.000	1.710	2.230	0.8000	8.000	25.00	24.00
3822.	0.4323E 06	0.3247E 06	6.000	0.8400	1.850	0.7500	8.000	25.00	24.00

NAME	MEANS	STD.DEV.	CORRELATIONS									15. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	3671.32	6190.55	1.0000									
D2	293013.	319468.	0.9606	1.0000								
D3	267055.	278599.	0.9243	0.9727	1.0000							
D4	3.26666	1.83095	0.4309	0.5179	0.4723	1.0000						
D5	1.57400	0.857535	-0.3334	-0.4144	-0.2674	-0.1709	1.0000					
D6	1.74466	1.46703	-0.3984	-0.3174	-0.2455	-0.0008	0.3424	1.0000				
D7	0.771333	0.834835E-01	0.5001	0.5127	0.4431	0.0863	-0.5902	-0.5473	1.0000			
D8	9.66666	2.28869	-0.0662	0.0856	0.1680	0.1591	-0.0393	0.3815	-0.1134	1.0000		
D9	21.3999	5.19684	-0.3670	-0.3490	-0.2761	0.2207	0.4404	0.3133	-0.5109	0.3363	1.0000	
D10	36.3999	10.9270	0.0313	0.0272	0.0684	-0.4484	0.0123	0.0455	-0.2528	0.0228	-0.5112	1.0000



Appendix 4. (Cont'd)



D1 = -1088. + 1457. * D4

FRATIO(COEFF.)= 2.965
FPROB(COEFF.)= 0.1057
STD.ERR.CONST.= 3143.
STD.ERR.COEFF.= 846.2
STD.ERR. D1 = 5797.
RSQ = 0.1857
DURBIN-WATSON STA.= 0.6110
AUTOCORRELATION COEFF. = 0.3485

D1 = 7460. + -2407. * D5

FRATIO(COEFF.)= 1.626
FPROB(COEFF.)= 0.2229
STD.ERR.CONST.= 3358.
STD.ERR.COEFF.= 1888.
STD.ERR. D1 = 6057.
RSQ = 0.1112
DURBIN-WATSON STA.= 0.6274
AUTOCORRELATION COEFF. = 0.3980

D1 = 6604. + -1681. * D6

FRATIO(COEFF.)= 2.452
FPROB(COEFF.)= 0.1383
STD.ERR.CONST.= 2413.
STD.ERR.COEFF.= 1073.
STD.ERR. D1 = 5893.
RSQ = 0.1587
DURBIN-WATSON STA.= 0.5371
AUTOCORRELATION COEFF. = 0.4547

D1 =-0.2493E 05+ 0.3708E 05* D7

FRATIO(COEFF.)= 4.335
FPROB(COEFF.)= 0.0554
STD.ERR.CONST.= 0.1381E 05
STD.ERR.COEFF.= 0.1781E 05
STD.ERR. D1 = 5563.
RSQ = 0.2501
DURBIN-WATSON STA.= 0.8300
AUTOCORRELATION COEFF. = 0.3139

D1 = 5403. + -179.1 * D8

FRATIO(COEFF.)= 0.5726E-01
FPROB(COEFF.)= 0.8000
STD.ERR.CONST.= 7423.
STD.ERR.COEFF.= 748.5
STD.ERR. D1 = 6410.
RSQ = 0.0044
DURBIN-WATSON STA.= 0.3226
AUTOCORRELATION COEFF. = 0.5385

D1 = 0.1303E 05+ -437.2 * D9

FRATIO(COEFF.)= 2.024
FPROB(COEFF.)= 0.1757
STD.ERR.CONST.= 6755.
STD.ERR.COEFF.= 307.3
STD.ERR. D1 = 5976.
RSQ = 0.1347
DURBIN-WATSON STA.= 0.4674
AUTOCORRELATION COEFF. = 0.5060

D1 = 3026. + 17.73 * D10

FRATIO(COEFF.)= 0.1275E-01
FPROB(COEFF.)= 0.8770
STD.ERR.CONST.= 5952.
STD.ERR.COEFF.= 157.1
STD.ERR. D1 = 6421.
RSQ = 0.0010
DURBIN-WATSON STA.= 0.3012
AUTOCORRELATION COEFF. = 0.5553

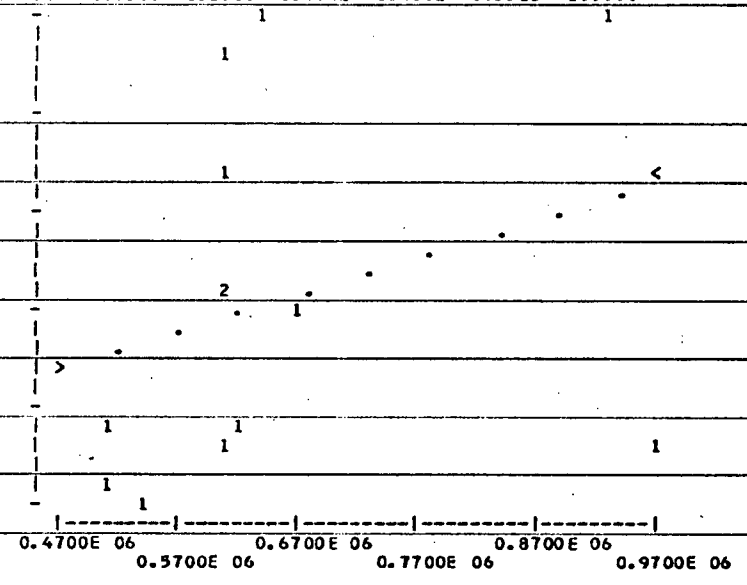
Appendix 5. Coulter Counter data. Stenosomella ventricosa on laboratory food. N.T.C. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
1255.	0.5121E 06	0.7030E 06	3.000	1.930	3.280	0.9600	8.000	25.00	39.00
628.0	0.5121E 06	0.7030E C6	4.000	1.860	3.280	0.9600	8.000	25.00	39.00
4114.	0.6078E 06	0.8023E 06	3.000	1.930	1.410	0.9400	8.000	25.00	39.00
2797.	0.6078E 06	0.8023E 06	3.000	1.860	1.410	0.9400	8.000	25.00	39.00
5378.	0.6121E 06	0.7562E 06	4.000	1.930	1.140	0.9400	8.000	25.00	39.00
1022.	0.6121E 06	0.7562E 06	5.000	1.470	1.140	0.9400	8.000	25.00	39.00
2829.	0.6121E 06	0.7562E 06	4.000	1.860	1.140	0.9400	8.000	25.00	39.00
5904.	0.9336E 06	C.9644E C6	6.000	1.190	1.130	0.8200	20.00	26.00	36.00
959.0	0.9673E 06	0.8088E 06	3.000	0.7500	1.940	0.7300	22.00	25.00	36.00
464.0	0.5405E 06	0.5505E C6	2.000	1.200	5.850	0.8900	13.00	30.00	22.00
1369.	0.6157E 06	0.6397E C6	7.000	1.300	2.940	0.8800	10.00	28.00	42.00
2563.	0.6698E 06	0.6213E 06	5.000	0.9400	0.6700	0.8300	17.00	26.00	35.00
5872.	0.6441E 06	0.6012E 06	3.000	0.9500	0.2200	0.5600	18.00	26.00	20.00

NAME	MEANS	STD.DEV.	CORRELATIONS				13. OBSERVATIONS					
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	2704.15	2011.26	1.0000									
D2	649792.	141593.	0.2937	1.0000								
D3	728092.	109496.	0.3693	0.5976	1.0000							
D4	4.00000	1.41421	C.1047	0.2398	C.2190	1.0000						
D5	1.47461	0.441654	0.0100	-0.6199	0.2188	-0.1508	1.0000					
D6	1.96538	1.51603	-C.6660	-0.3652	-0.4187	-0.2748	0.0716	1.0000				
D7	0.871538	0.115819	-C.3878	-0.5020	0.1829	0.0712	0.7910	0.3375	1.0000			
D8	12.0000	5.33853	0.2167	0.8114	0.0956	0.0552	-0.8956	-0.1866	-0.8060	1.0000		
D9	25.8461	1.51911	-C.2449	-0.1357	-0.5765	0.0388	-0.4025	0.6684	-0.1359	0.1850	1.0000	
D10	35.6923	6.77475	-0.1829	-0.0018	0.5214	0.4784	0.5369	-0.1800	0.6772	-0.4862	-0.5313	1.0000

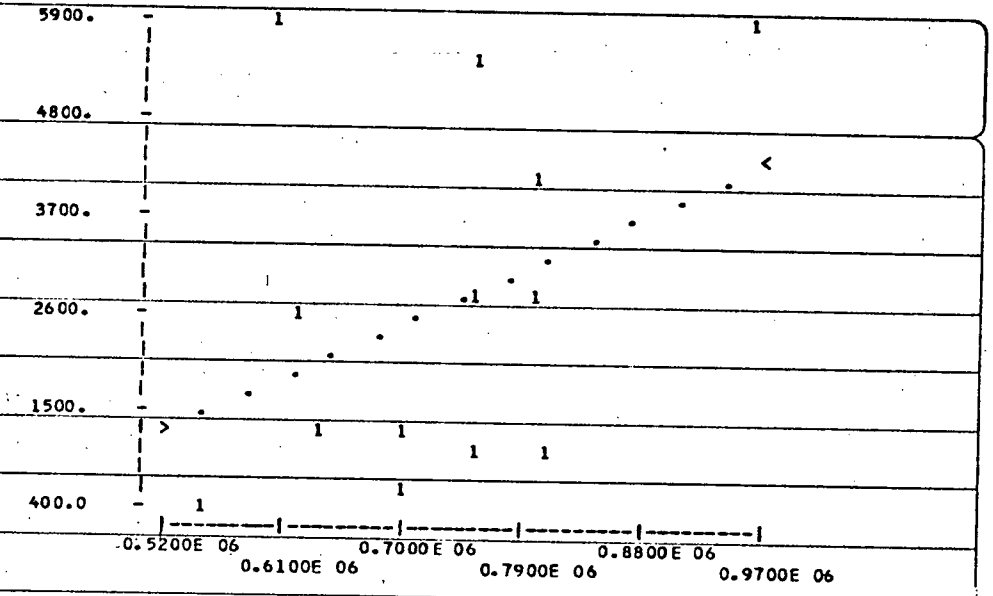
D1 = -6.506 + 0.4172E-02* D2

FRATIO(COEFF.)= 1.038
FPROB(COEFF.)= 0.3318
STD.ERR.CONST.= 2718.
STD.ERR.COEFF.= 0.4094E-02
STD.ERR. D1 = 2008.
RSQ = 0.0862
DURBIN-WATSON STA.= 1.892
AUTOCORRELATION COEFF. = -0.6970E-01



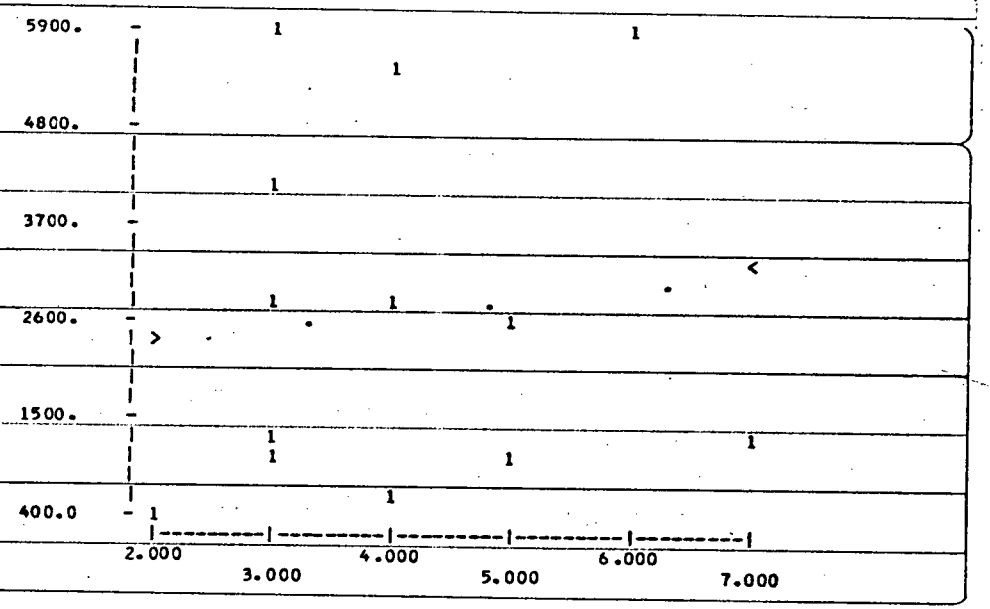
D1 = -2235. + 0.6784E-02* D3

FRATIO(COEFF.)= 1.737
FPROB(COEFF.)= 0.2125
STD.ERR.CONST.= 3786.
STD.ERR.COEFF.= 0.5147E-02
STD.ERR. D1 = 1552.
RSQ = 0.1364
DURBIN-WATSON STA.= 1.761
AUTOCORRELATION COEFF. = -0.9352E-01



D1 = 2108. + 149.0 * D4

FRATIO(COEFF.)= 0.1220
FPROB(COEFF.)= 0.7298
STD.ERR.CONST.= 1801.
STD.ERR.COEFF.= 426.4
STD.ERR. D1 = 2089.
RSQ = 0.0110
DURBIN-WATSON STA.= 1.852
AUTOCORRELATION COEFF. = -0.5815E-01



Appendix 5. (Cont'd)

D1 = 2637. + 45.71 * D5

FRATIO(COEFF.)= 0.1108E-02
FPROB(COEFF.)= 0.9242
STD.ERR.CONST.= 2107.
STD.ERR.COEFF.= 1373.
STD.ERR. D1 = 2101.
RSQ = 0.0001
DURBIN-WATSON STA.= 1.860
AUTOCORRELATION COEFF. = -0.5712E-01

D1 = 1634. + 89.19 * D8

FRATIO(COEFF.)= 0.6531
FPROB(COEFF.)= 0.4410
STD.ERR.CONST.= 1440.
STD.ERR.COEFF.= 110.4
STD.ERR. D1 = 2041.
RSQ = 0.0560
DURBIN-WATSON STA.= 1.868
AUTOCORRELATION COEFF. = -0.2283E-01

D1 = 4441. + -883.6 * D6

FRATIO(COEFF.)= 8.769
FPROB(COEFF.)= 0.0126
STD.ERR.CONST.= 729.9
STD.ERR.COEFF.= 298.4
STD.ERR. D1 = 1567.
RSQ = 0.4436
DURBIN-WATSON STA.= 3.005
AUTOCORRELATION COEFF. = -0.5532

D1 = 0.1109E 05+ -324.3 * D9

FRATIO(COEFF.)= 0.7019
FPROB(COEFF.)= 0.4244
STD.ERR.CONST.= 0.1002E 05
STD.ERR.COEFF.= 387.0
STD.ERR. D1 = 2037.
RSQ = 0.0600
DURBIN-WATSON STA.= 2.084
AUTOCORRELATION COEFF. = -0.1879

D1 = 8574. + -6735. * D7

FRATIO(COEFF.)= 1.948
FPROB(COEFF.)= 0.1881
STD.ERR.CONST.= 4240.
STD.ERR.COEFF.= 4826.
STD.ERR. D1 = 1936.
RSQ = 0.1504
DURBIN-WATSON STA.= 1.993
AUTOCORRELATION COEFF. = -0.1944E-01

D1 = 4643. + -54.31 * D10

FRATIO(COEFF.)= 0.3809
FPROB(COEFF.)= 0.5557
STD.ERR.CONST.= 3193.
STD.ERR.COEFF.= 88.00
STD.ERR. D1 = 2065.
RSQ = 0.0335
DURBIN-WATSON STA.= 1.887
AUTOCORRELATION COEFF. = -0.1788E-01

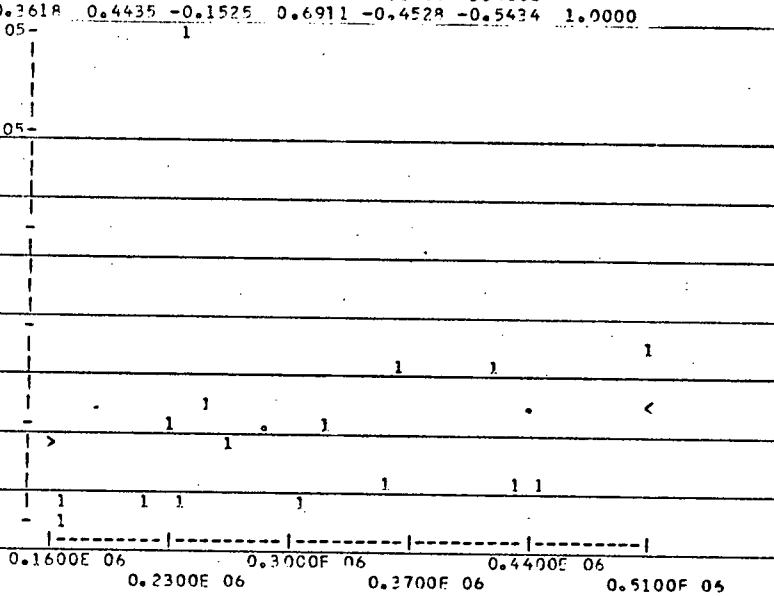
Appendix 6. Coulter Counter data. *Stenosomella ventricosa* on laboratory food. E.S.O. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
1717.	0.33305 06	0.42465 06	3.000	2.260	3.280	0.9600	8.000	25.00	39.00
967.0	0.21535 06	0.23595 06	3.000	2.220	3.280	0.9600	9.000	25.00	39.00
1239.	0.23465 06	0.33065 06	4.000	2.930	3.280	0.9600	8.000	25.00	39.00
5421.	0.41545 06	0.48025 06	3.000	2.260	1.410	0.9400	8.000	25.00	39.00
3114.	0.23015 06	0.30995 06	2.000	2.320	1.410	0.9400	8.000	25.00	39.00
2886.	0.23435 06	0.33405 06	3.000	2.120	1.410	0.9400	8.000	25.00	39.00
5279.	0.35355 06	0.39425 06	4.000	2.340	1.140	0.9400	8.000	25.00	39.00
1612.	0.43335 06	0.46845 06	5.000	1.410	1.140	0.9400	8.000	25.00	39.00
3586.	0.32345 06	0.32795 06	4.000	2.160	1.140	0.9400	8.000	25.00	39.00
5904.	0.50765 06	0.50315 06	6.000	1.750	1.130	0.9200	20.00	26.00	36.00
348.0	0.16735 06	0.14565 06	3.000	0.9500	1.360	0.8300	22.00	25.00	36.00
1273.	0.30345 06	0.27685 06	3.000	1.070	1.940	0.7400	22.00	25.00	36.00
527.0	0.16545 06	0.15435 06	2.000	1.270	5.850	0.8900	13.00	30.00	22.00
1798.	0.44435 06	0.44655 06	7.000	1.410	2.940	0.8800	10.00	28.00	42.00
2250.	0.29435 06	0.23875 06	5.000	0.9400	0.6700	0.8300	17.00	26.00	35.00
0.15425 05	0.23215 06	0.17265 06	3.000	1.220	0.2200	0.5600	18.00	26.00	20.00

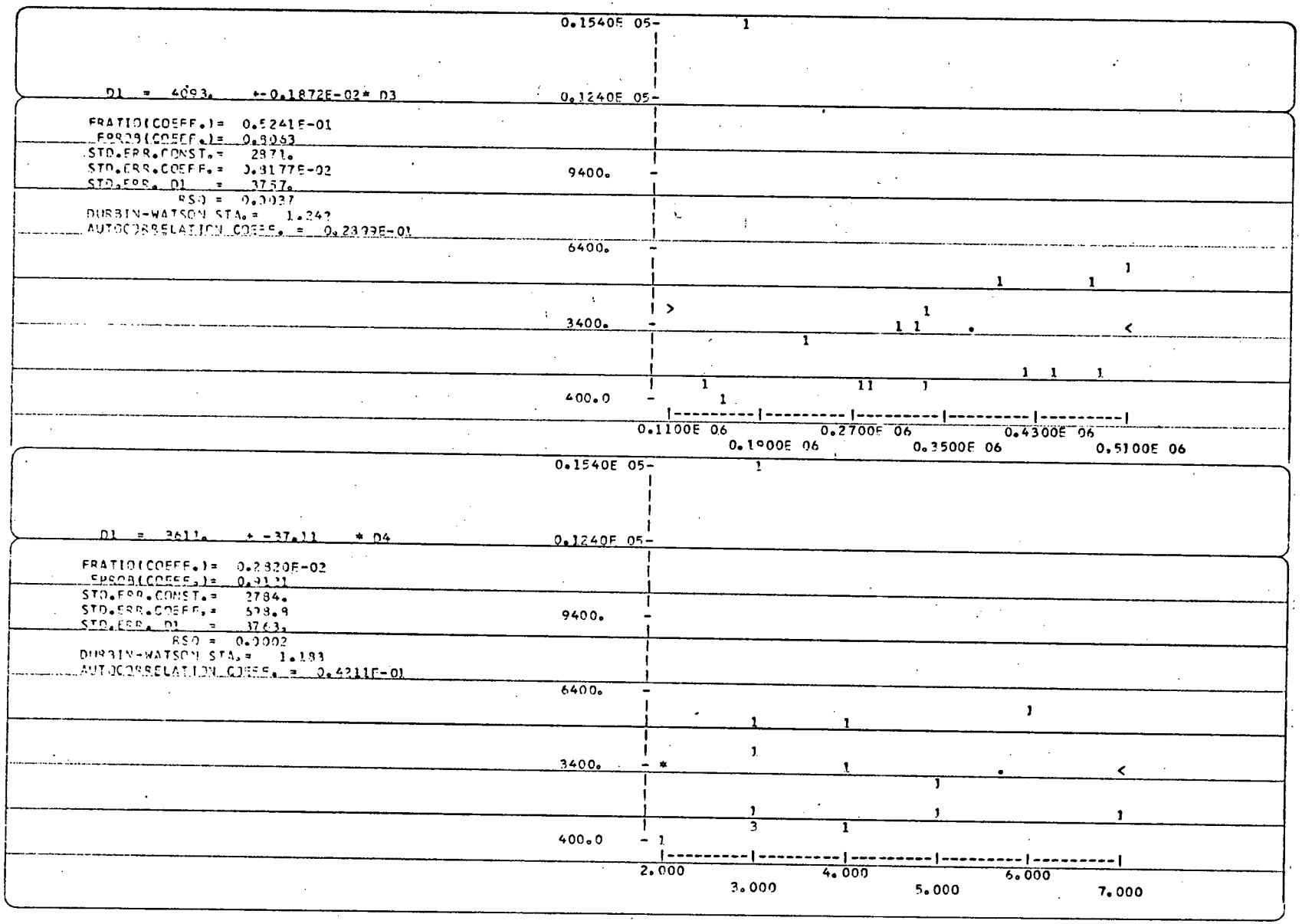
NAME	MEANS	STD.DEV.	CORRELATIONS D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
			16. OBSERVATIONS									
D1	3472.19	3536.13	1.0000									
D2	307180.	103960.	0.1136	1.0000								
D3	331782.	113621.	-0.0611	0.9034	1.0000							
D4	3.7500	1.39344	-0.0142	0.7130	0.5463	1.0000						
D5	1.85812	0.636993	-0.0590	0.0075	0.3725	-0.2071	1.0000					
D6	1.93750	1.41378	-0.5650	-0.3826	-0.1544	-0.2248	0.1080	1.0000				
D7	0.839375	0.106935	-0.6742	0.1072	0.4470	-0.0101	0.6371	0.3586	1.0000			
D8	12.1250	5.61990	0.1906	-0.1169	-0.4437	0.0640	-0.7429	-0.2285	-0.7699	1.0000		
D9	25.6875	1.40990	-0.0770	-0.0901	-0.2524	0.1283	-0.3775	0.6182	-0.1661	0.1408	1.0000	
D10	36.1250	6.16305	-0.5140	0.4278	0.6376	0.3618	0.4435	-0.1525	0.6911	-0.4528	-0.5434	1.0000

D1 = 2252. + 0.39725-02* D2

ERATIO(COEFF.)= 0.1829
ERROR(COEFF.)= 0.6771
STD.ERR.CONST.= 3002.
STD.ERR.COEFF.= 0.92875-02
STD.ERR. D1 = 3739.
RSQ = 0.0129
DURBIN-WATSON STA.= 1.106
AUTOCORRELATION COEFF. = 0.55365-01



Appendix 6. (Cont'd)



Appendix 6. (Cont'd)

D1 = 4052. + -312.1 * D5

FRATIO(COEFF.)= 0.4886E-01
FPROB(COEFF.)= 0.8113
STD.ERR.CONST.= 2787.
STD.ERR.COEFF.= 1412.
STD.ERR. D1 = 3757.
RSQ = 0.0035
DURBIN-WATSON STA.= 1.215
AUTOCORRELATION COEFF. = 0.3633E-01

D1 = 1977. + 123.3 * D8

FRATIO(COEFF.)= 0.5275
FPROB(COEFF.)= 0.4854
STD.ERR.CONST.= 2256.
STD.ERR.COEFF.= 169.9
STD.ERR. D1 = 3695.
RSQ = 0.0363
DURBIN-WATSON STA.= 1.198
AUTOCORRELATION COEFF. = 0.6631E-01

D1 = 6342. + -1453. * D6

FRATIO(COEFF.)= 6.563
FPROB(COEFF.)= 0.3217
STD.ERR.CONST.= 1363.
STD.ERR.COEFF.= 567.2
STD.ERR. D1 = 3106.
RSQ = 0.3192
DURBIN-WATSON STA.= 1.739
AUTOCORRELATION COEFF. = -0.1972

D1 = 8608. + -199.9 * D9

FRATIO(COEFF.)= 0.8357E-01
FPROB(COEFF.)= 0.7630
STD.ERR.CONST.= 0.1772E 05
STD.ERR.COEFF.= 691.6
STD.ERR. D1 = 3753.
RSQ = 0.0059
DURBIN-WATSON STA.= 1.196
AUTOCORRELATION COEFF. = 0.2694E-01

D1 = 0.2364E 05+-0.2293E 05* D7

FRATIO(COEFF.)= 11.67
FPROB(COEFF.)= 0.0042
STD.ERR.CONST.= 5943.
STD.ERR.COEFF.= 6712.
STD.ERR. D1 = 2780.
RSQ = 0.4546
DURBIN-WATSON STA.= 1.063
AUTOCORRELATION COEFF. = 0.3696

D1 = 0.1443E 05+ -303.3 * D10

FRATIO(COEFF.)= 5.023
FPROB(COEFF.)= 0.0393
STD.ERR.CONST.= 4032.
STD.ERR.COEFF.= 135.3
STD.ERR. D1 = 3223.
RSQ = 0.2642
DURBIN-WATSON STA.= 1.472
AUTOCORRELATION COEFF. = 0.9040E-01

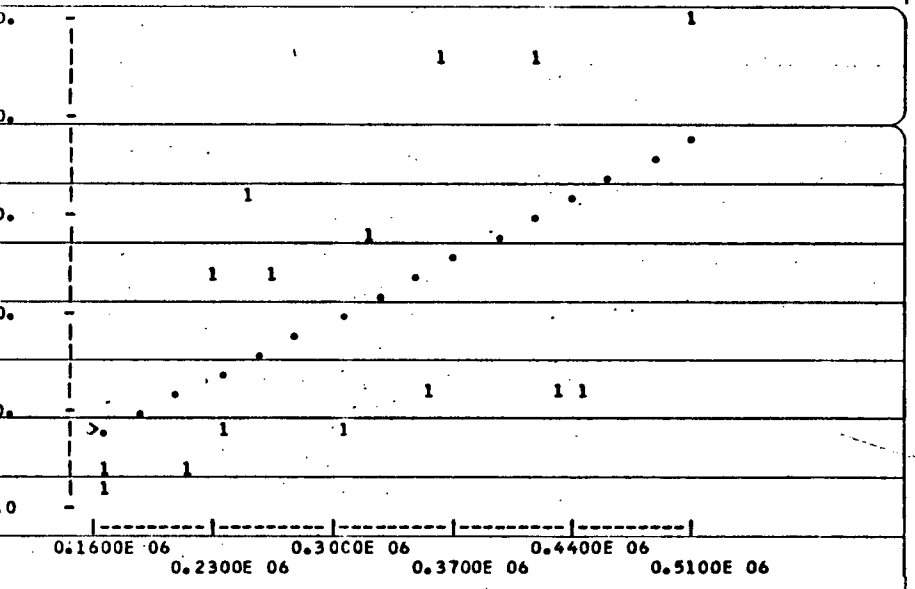
Appendix 7. Coulter Counter data. *Stenosomella ventricosa* on laboratory food. E.S.O. method. One value omitted.

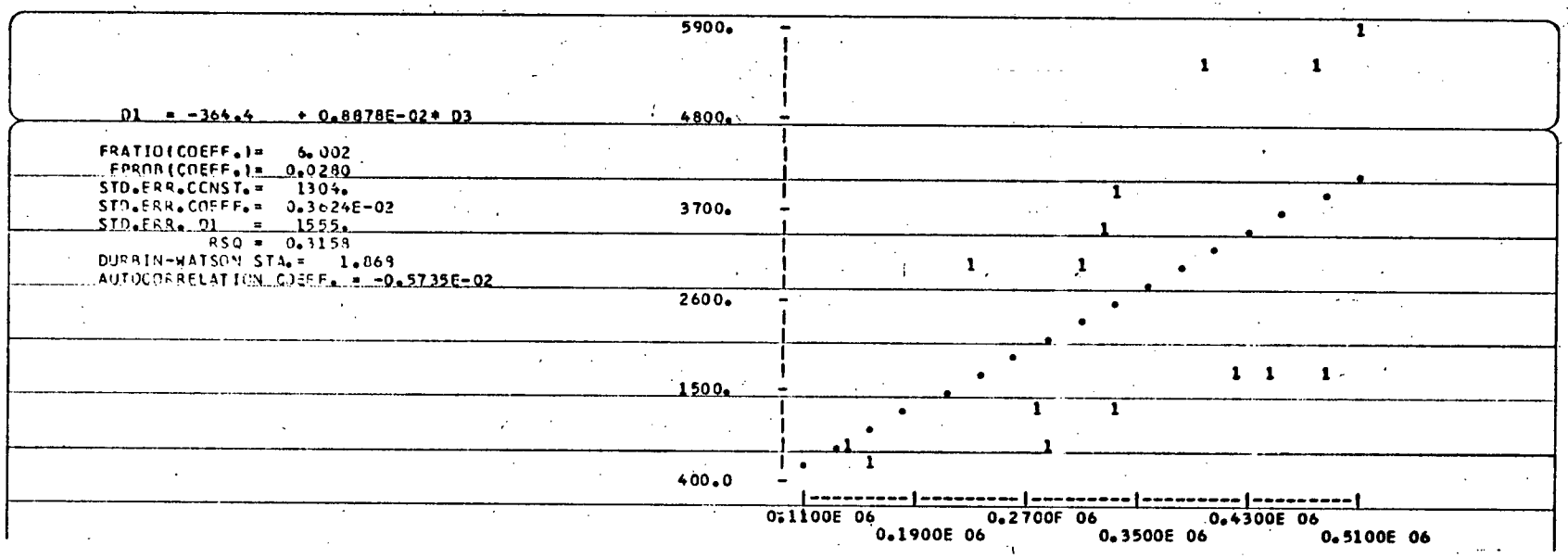
D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
1717.	0.3330E 06	0.4246E 06	3.000	2.260	3.280	0.9600	8.000	25.00	39.00
867.0	0.2159E 06	0.2859E 06	3.000	2.220	3.280	0.9600	8.000	25.00	39.00
1239.	0.2345E 06	0.3306E 06	4.000	2.930	3.280	0.9600	8.000	25.00	39.00
5421.	0.4154E 06	0.4802E 06	3.000	2.260	1.410	0.9400	8.000	25.00	39.00
3114.	0.2301E 06	0.3099E 06	2.000	2.320	1.410	0.9400	8.000	25.00	39.00
3896.	0.2483E 06	0.3340E 06	3.000	3.120	1.410	0.9400	8.000	25.00	39.00
5378.	0.3595E 06	0.3942E 06	4.000	2.340	1.140	0.9400	8.000	25.00	39.00
1612.	0.4333E 06	0.4884E 06	5.000	1.410	1.140	0.9400	8.000	25.00	39.00
3586.	0.3234E 06	0.3279E 06	4.000	2.160	1.140	0.9400	8.000	25.00	39.00
5904.	0.5076E 06	0.5081E 06	6.000	1.750	1.130	0.8200	20.00	26.00	36.00
848.0	0.1673E 06	0.1456E 06	3.000	0.9500	1.360	0.8300	22.00	25.00	36.00
1273.	0.3038E 06	0.2768E 06	3.000	1.070	1.940	0.7400	22.00	25.00	36.00
527.0	0.1654E 06	0.1543E 06	2.000	1.370	5.850	0.8900	13.00	30.00	22.00
1799.	0.4431E 06	0.4465E 06	7.000	1.410	2.940	0.8800	10.00	28.00	42.00
2950.	0.2543E 06	0.2287E 06	5.000	0.9400	0.6700	0.8300	17.00	26.00	35.00

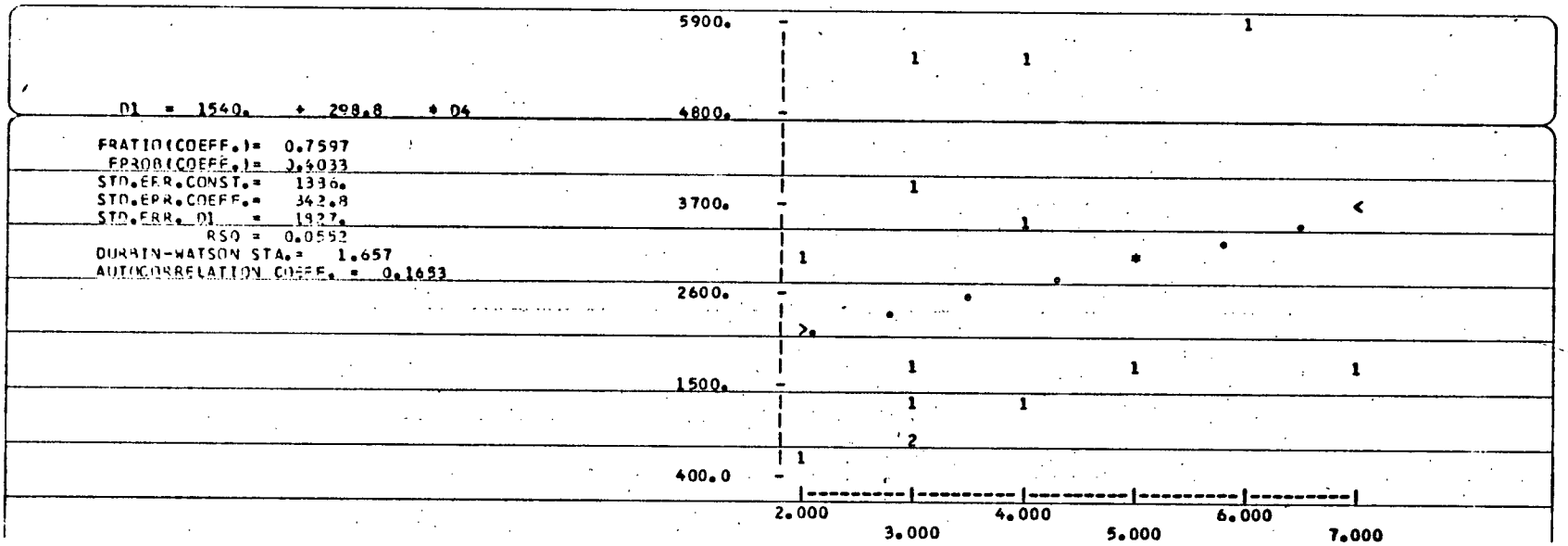
NAME	MEANS	STD.DEV.	CORRELATIONS									15. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	2675.33	1311.22	1.0000									
D2	311717.	105957.	0.5626	1.0000								
D3	342392.	114657.	0.5620	0.9146	1.0000							
D4	3.80000	1.42428	0.2350	0.7060	0.5355	1.0000						
D5	1.90066	0.688945	0.3392	-0.0374	0.3138	-0.2532	1.0000					
D6	2.09200	1.38090	-0.6051	-0.3664	-0.3096	-0.2918	0.0294	1.0000				
D7	0.900656	0.669184E-01	0.0824	-0.0535	0.2869	-0.2083	0.7508	0.1664	1.0000			
D8	11.7333	5.58654	-0.1164	-0.0722	-0.3836	0.1095	-0.7243	-0.1503	-0.9434	1.0000		
D9	25.6666	1.44750	-0.2689	-0.0811	-0.2479	0.1386	-0.3751	0.6772	-0.1966	0.1296	1.0000	
D10	37.2000	4.57008	0.2830	0.4338	0.5799	0.3687	0.3899	-0.5672	0.3125	-0.3755	-0.7018	1.0000

D1 = -322.5 + 0.9617E-02* D2

FRATIO(COEFF.)= 6.021
PROB(COEFF.)= 0.0278
STD.ERR.CONST.= 1296.
STD.ERR.COEFF.= 0.3919E-02
STD.ERR. D1 = 1554.
RSQ = 0.3165
DURBIN-WATSON STA.= 1.643
AUTOCORRELATION COEFF.= 0.1409




D1 = -364.4 + 0.8878E-02* D3
FRATIO(COEFF.)= 6.002
PROB(COEFF.)= 0.0280
STD.ERR.CONST.= 1304.
STD.ERR.COEFF.= 0.3624E-02
STD.ERR. D1 = 1555.
RSQ = 0.3158
DURBIN-WATSON STA.= 1.869
AUTOCORRELATION COEFF. = -0.5735E-02
5900.
4800.
3700.
2600.
1500.
400.0
0.1100E 06
0.1900E 06
0.2700F 06
0.3500E 06
0.4300E 06
0.5100E 06


D1 = 1540. + 298.8 * D4
FRATIO(COEFF.)= 0.7597
PROB(COEFF.)= 0.4033
STD.ERR.CONST.= 1336.
STD.ERR.COEFF.= 342.8
STD.ERR. D1 = 1927.
RSQ = 0.0552
DURBIN-WATSON STA.= 1.657
AUTOCORRELATION COEFF. = 0.1653
5900.
4800.
3700.
2600.
1500.
400.0
2.000
3.000
4.000
5.000
6.000
7.000

Appendix 7. (Cont'd)

D1 = 980.3 + 891.8 * D5

FRATIO(COEFF.)= 1.691
FPROB(COEFF.)= 0.2142
STD.ERR.CONST.= 1381.
STD.ERR.COEFF.= 685.9
STD.ERR. D1 = 1768.
RSQ = 0.1151
DURBIN-WATSON STA.= 1.855
AUTOCORRELATION COEFF. = 0.3649E-01

D1 = 4336. + -793.7 * D6

FRATIO(COEFF.)= 7.510
FPROB(COEFF.)= 0.0163
STD.ERR.CONST.= 718.6
STD.ERR.COEFF.= 289.6
STD.ERR. D1 = 1496.
RSQ = 0.3662
DURBIN-WATSON STA.= 2.428
AUTOCORRELATION COEFF. = -0.2266

D1 = 666.7 + 2230. * D7

FRATIO(COEFF.)= 0.8886E-01
FPROB(COEFF.)= 0.7624
STD.ERR.CONST.= 5755.
STD.ERR.COEFF.= 7481.
STD.ERR. D1 = 1673.
RSQ = 0.0068
DURBIN-WATSON STA.= 1.803
AUTOCORRELATION COEFF. = 0.8350E-01

D1 = 3118. + -37.75 * D8

FRATIO(COEFF.)= 0.1797
FPROB(COEFF.)= 0.6907
STD.ERR.CONST.= 1153.
STD.ERR.COEFF.= 89.31
STD.ERR. D1 = 1867.
RSQ = 0.0136
DURBIN-WATSON STA.= 1.804
AUTOCORRELATION COEFF. = 0.8157E-01

D1 = 0.1131E 05+ -336.5 * D9

FRATIO(COEFF.)= 1.013
FPROB(COEFF.)= 0.3343
STD.ERR.CONST.= 8592.
STD.ERR.COEFF.= 334.3
STD.ERR. D1 = 1810.
RSQ = 0.0723
DURBIN-WATSON STA.= 1.932
AUTOCORRELATION COEFF. = 0.1566E-01

D1 = -1497. + 112.2 * D10

FRATIO(COEFF.)= 1.132
FPROB(COEFF.)= 0.3077
STD.ERR.CONST.= 3749.
STD.ERR.COEFF.= 105.4
STD.ERR. D1 = 1803.
RSQ = 0.0801
DURBIN-WATSON STA.= 1.958
AUTOCORRELATION COEFF. = 0.1836E-02

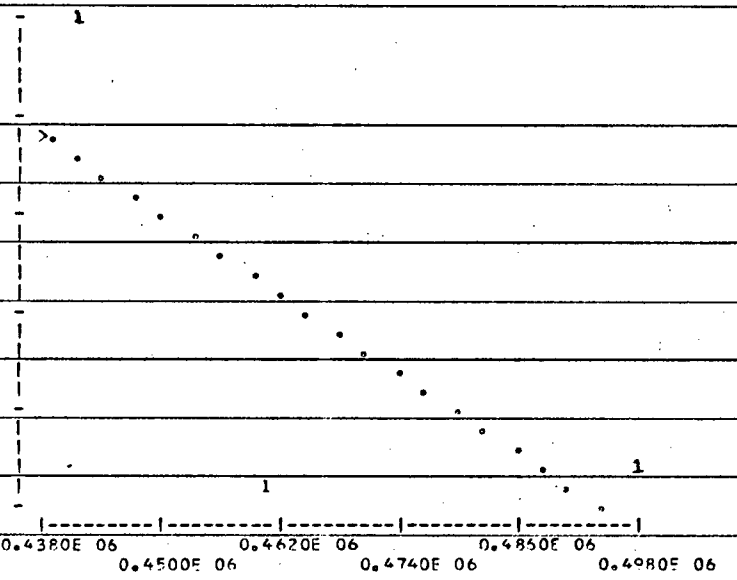
Appendix 8. Coulter Counter data. Barnacle and Copepod nauplii on laboratory food. N.T.C. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
633.0	0.4607E 06	0.4749E 06	4.000	1.200	2.970	0.9500	13.00	30.00	22.00
1042.	0.4978E 06	0.5510E 06	2.000	1.290	1.080	0.9600	16.00	28.00	42.00
8285.	0.4414E 06	0.3607E 06	6.000	0.8400	0.6400	0.9000	8.000	25.00	24.00

NAME	MEANS	STD.DEV.	CORRELATIONS									3. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	3320.00	4304.68	1.0000									
D2	466621.	28651.7	-0.7301	1.0000								
D3	462184.	95777.9	-0.8979	0.9564	1.0000							
D4	4.00000	2.00000	0.8413	-0.9836	-0.9934	1.0000						
D5	1.11000	0.238119	-0.9719	0.9704	0.9763	-0.9449	1.0000					
D6	1.56333	1.23791	-0.6815	-0.0025	0.2897	-0.1777	0.4900	1.0000				
D7	0.936667	0.331455E-01	-0.9793	0.4532	0.9684	-0.9333	0.9994	0.5193	1.0000			
D8	12.3333	4.04145	-0.9029	0.9478	0.9966	-0.9837	0.9820	0.3165	0.9750	1.0000		
D9	27.6667	2.51661	-0.0355	0.4416	0.6844	-0.5960	0.8260	0.8961	0.8447	0.7046	1.0000	
D10	29.3333	11.0151	-0.2757	0.0076	0.7454	-0.8171	0.5833	-0.4222	0.5554	0.7263	0.0240	1.0000

D1 = 0.5450E 05+-0.1097 * D2

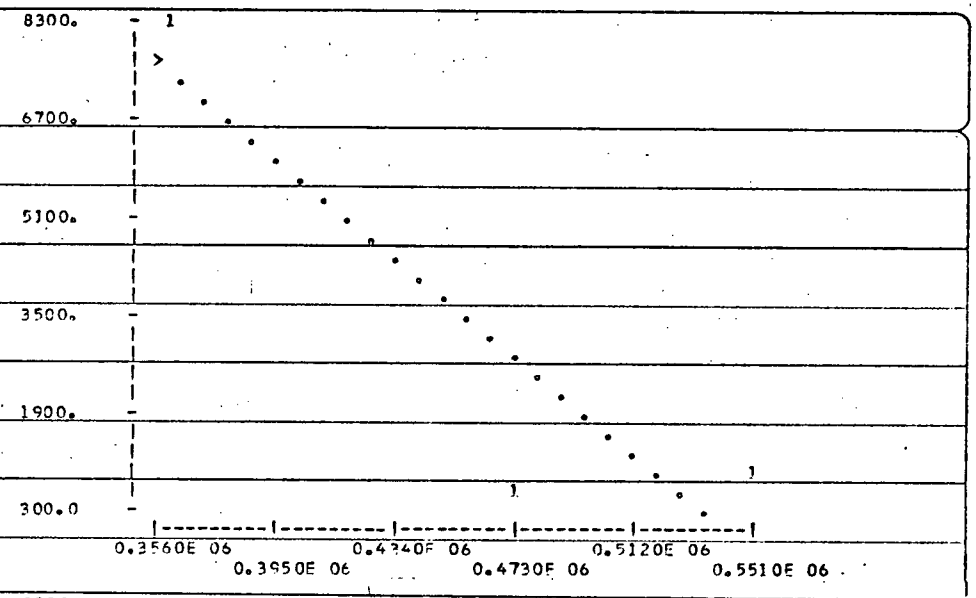
FRATIO(COEFF.)= 1.141
ERROR(COEFF.)= 0.4795
STD.ERR.CONST.= 0.4796E 05
STD.ERR.COEFF.= 0.1027
STD.ERR. D1 = 1160.
RSQ = 0.5330
DURBIN-WATSON STA.= 1.225
AUTOCORRELATION COEFF. = -0.7514E-01



Appendix 8. (Cont'd)

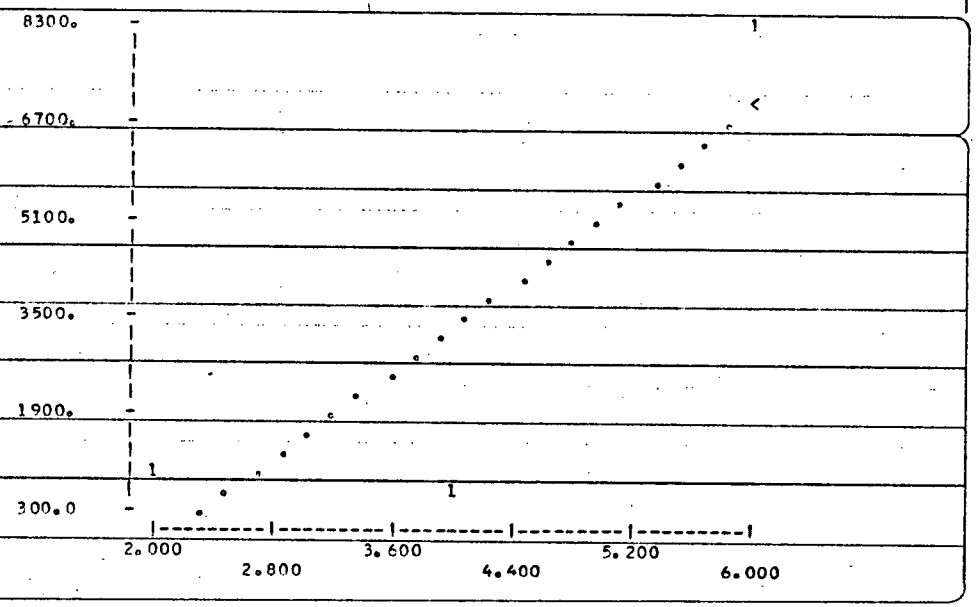
D1 = 0.2197E 05+-0.4035E-01 * D3

FRATIO(COEFF.)= 4.159
PROB(COEFF.)= 0.2381
STD.ERR.CONST.= 9276.
STD.ERR.COEFF.= 0.1979E-01
STD.ERR. D1 = 2630.
RSQ = 0.8061
DURBIN-WATSON STA.= 1.711
AUTOCORRELATION COEFF. = -0.2370



D1 = -3923. + 1811. * D4

FRATIO(COEFF.)= 2.422
PROB(COEFF.)= 0.1677
STD.ERR.CONST.= 5027.
STD.ERR.COEFF.= 1164.
STD.ERR. D1 = 3291.
RSQ = 0.7378
DURBIN-WATSON STA.= 1.500
AUTOCORRELATION COEFF. = -0.1667



Appendix 8. (Cont'd)

D1 = 0.2282E 05+-0.1757E 05* D5

FRATIO(COEFF.)= 17.04
FPROB(COEFF.)= 0.1735
STD.ERR.CONST.= 4796.
STD.ERR.COEFF.= 4256.
STD.ERR. D1 = 1433.
RSQ = 0.9446
DURBIN-WATSON STA.= 2.143
AUTOCORRELATION COEFF. = -0.3810

D1 = 0.1527E 05+ -969.2 * D8

FRATIO(COEFF.)= 4.811
FPROB(COEFF.)= 0.2814
STD.ERR.CONST.= 5541.
STD.ERR.COEFF.= 441.9
STD.ERR. D1 = 2523.
RSQ = 0.3279
DURBIN-WATSON STA.= 1.765
AUTOCORRELATION COEFF. = -0.2551

D1 = 7025. + -2370. * D5

FRATIO(COEFF.)= 0.3671
FPROB(COEFF.)= 0.5221
STD.ERR.CONST.= 4738.
STD.ERR.COEFF.= 3945.
STD.ERR. D1 = 4455.
RSQ = 0.4644
DURBIN-WATSON STA.= 2.771
AUTOCORRELATION COEFF. = -0.5904

D1 = 0.4759E 05+ -1600. * D7

FRATIO(COEFF.)= 7.011
FPROB(COEFF.)= 0.2625
STD.ERR.CONST.= 0.1677E 05
STD.ERR.COEFF.= 604.3
STD.ERR. D1 = 2151.
RSQ = 0.8752
DURBIN-WATSON STA.= 2.974
AUTOCORRELATION COEFF. = -0.6579

D1 = 0.1252E 06+-0.1311E 04* D7

FRATIO(COEFF.)= 23.44
FPROB(COEFF.)= 0.1555
STD.ERR.CONST.= 0.2538E 05
STD.ERR.COEFF.= 0.2709E 05
STD.ERR. D1 = 1232.
RSQ = 0.9591
DURBIN-WATSON STA.= 2.210
AUTOCORRELATION COEFF. = -0.4032

D1 = 7627. + -146.8 * D10

FRATIO(COEFF.)= 0.1644
FPROB(COEFF.)= 0.7435
STD.ERR.CONST.= 0.1111E 05
STD.ERR.COEFF.= 362.2
STD.ERR. D1 = 5642.
RSQ = 0.1412
DURBIN-WATSON STA.= 1.016
AUTOCORRELATION COEFF. = -0.5495E-02

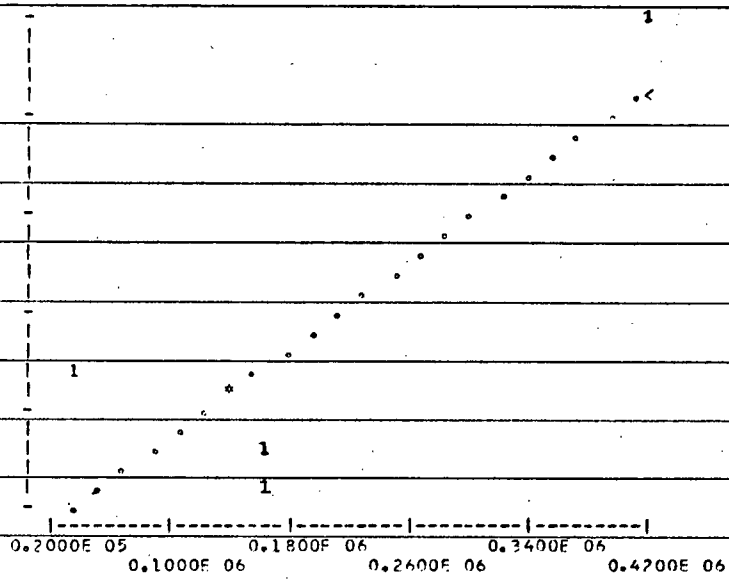
Appendix 9. Coulter Counter data. Barnacle and Copepod nauplii on laboratory food. E.S.O. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
623.0	0.1543E 06	0.1482E 06	4.000	1.110	2.970	0.9500	13.00	30.00	22.00
1515.	0.1341E 06	0.1766E 06	2.000	1.080	1.080	0.9600	16.00	28.00	42.00
2368.	0.1395E 06	0.1370E 06	2.000	0.1900	0.1900	0.8300	17.00	26.00	35.00
3153.	0.3327E 05	0.2871E 05	3.000	0.4100	0.4100	0.9100	8.000	25.00	24.00
9800.	0.4207E 06	0.3457E 06	6.000	0.6400	0.6400	0.9000	8.000	25.00	24.00

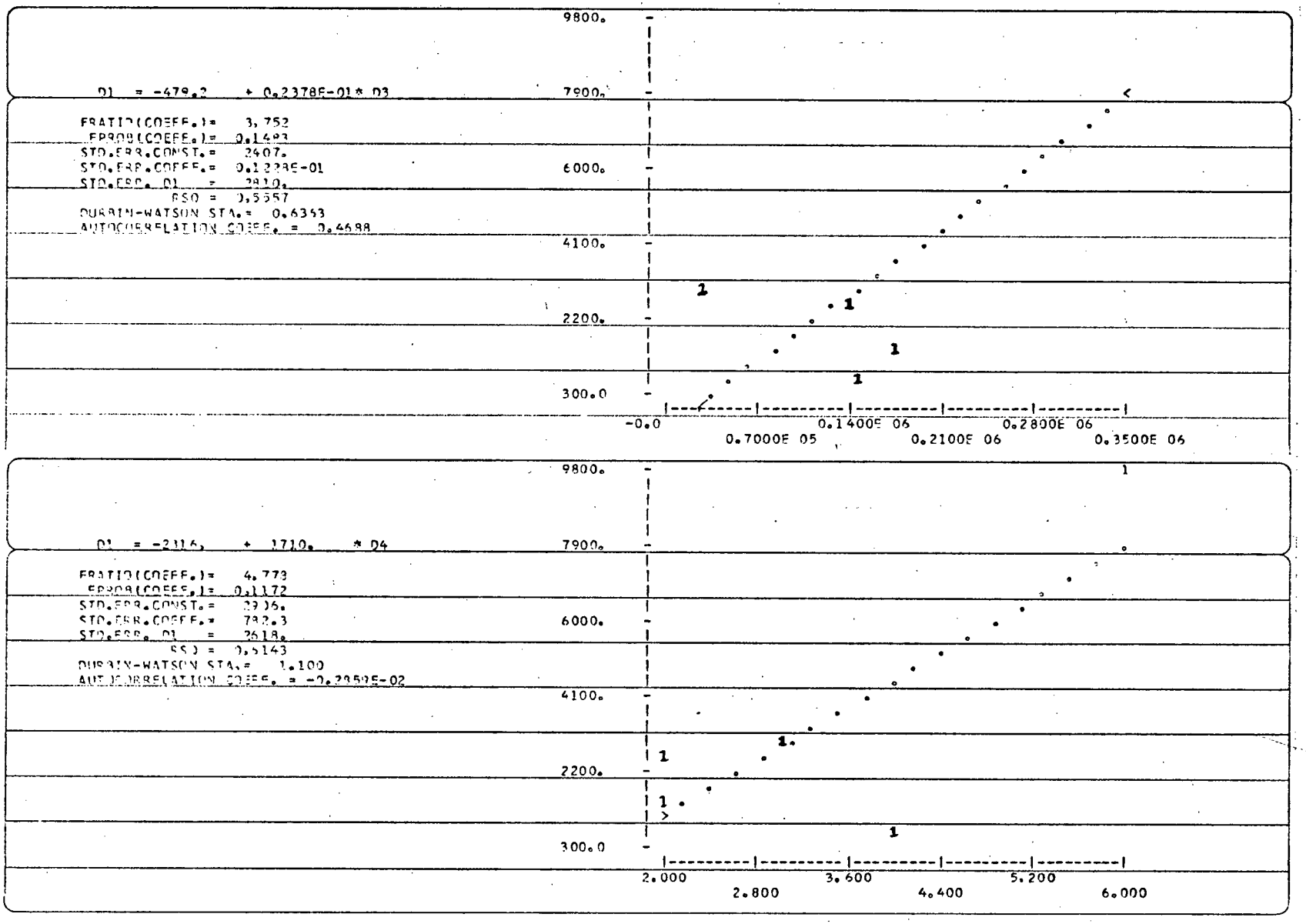
NAME	MEANS	STD.DEV.	CORRELATIONS									5. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	3497.60	3650.77	1.0000									
D2	1.85370.	141426.	0.8191	1.0000								
D3	1.67240.	114449.	0.7455	0.9878	1.0000							
D4	3.40000	1.67332	0.7878	0.7943	0.7011	1.0000						
D5	0.696000	0.405092	-0.2766	0.1533	0.2187	0.1428	1.0000					
D6	1.35800	1.11851	-0.4266	-0.0062	0.0101	0.2009	0.7971	1.0000				
D7	0.913000	0.5147815-01	-0.2512	-0.0203	0.0145	0.1161	0.9187	0.6565	1.0000			
D8	12.4000	4.27785	-0.6416	-0.2843	-0.1492	-0.7264	0.1153	0.1005	-0.1362	1.0000		
D9	26.8000	2.16795	-0.6750	-0.1753	-0.0581	-0.1792	0.7970	0.3029	0.6049	0.4960	1.0000	
D10	29.4000	8.70631	-0.3308	-0.1715	-0.0314	-0.7173	0.0557	-0.3331	-0.0235	0.7666	0.0848	1.0000

D1 = -422.0 + 0.21145-01* D2

FRATIO(COEFF.)= 5.116
ERROR(COEFF.)= 0.3299
STD.ERR.CONST.= 1319.
STD.ERR.COEFF.= 0.9550E-02
STD.ERR. D1 = 3419.
RSD = 0.5709
DURBIN-WATSON STA.= 0.7416
AUTOCORRELATION COEFF.= 0.4116



Appendix 9. (Cont'd)



Appendix 9. (Cont'd)

D1 = 5204. + -2497. * D5

FRATIO(COEFF.)= 0.2486
PROB(COEFF.)= 0.6517
STD.ERR.CONST.= 3872.
STD.ERR.COEFF.= 4989.
STD.ERR. D1 = 4051.
RSQ = 0.0765
DURBIN-WATSON STA.= 1.150
AUTOCORRELATION COEFF. = 0.1882E-02

D1 = 0.10295 05+ -547.5 * D9

FRATIO(COEFF.)= 2.099
PROB(COEFF.)= 0.2434
STD.ERR.CONST.= 4304.
STD.ERR.COEFF.= 377.9
STD.ERR. D1 = 3234.
RSQ = 0.4116
DURBIN-WATSON STA.= 2.250
AUTOCORRELATION COEFF. = -0.4702

D1 = 4971. + -1392. * D6

FRATIO(COEFF.)= 0.6675
PROB(COEFF.)= 0.4763
STD.ERR.CONST.= 2492.
STD.ERR.COEFF.= 1704.
STD.ERR. D1 = 3813.
RSQ = 0.1920
DURBIN-WATSON STA.= 1.220
AUTOCORRELATION COEFF. = 0.1298E-01

D1 = 0.3396E 05+ -1137. * D9

FRATIO(COEFF.)= 2.511
PROB(COEFF.)= 0.2112
STD.ERR.CONST.= 0.1927E 05
STD.ERR.COEFF.= 717.3
STD.ERR. D1 = 3110.
RSQ = 0.4557
DURBIN-WATSON STA.= 1.675
AUTOCORRELATION COEFF. = -0.1611

D1 = 0.1971E 05+-0.1782E 05* D7

FRATIO(COEFF.)= 0.2021
PROB(COEFF.)= 0.6812
STD.ERR.CONST.= 0.3611E 05
STD.ERR.COEFF.= 0.3963E 05
STD.ERR. D1 = 4090.
RSQ = 0.0631
DURBIN-WATSON STA.= 1.002
AUTOCORRELATION COEFF. = 0.7539E-01

D1 = 7575. + -138.7 * D10

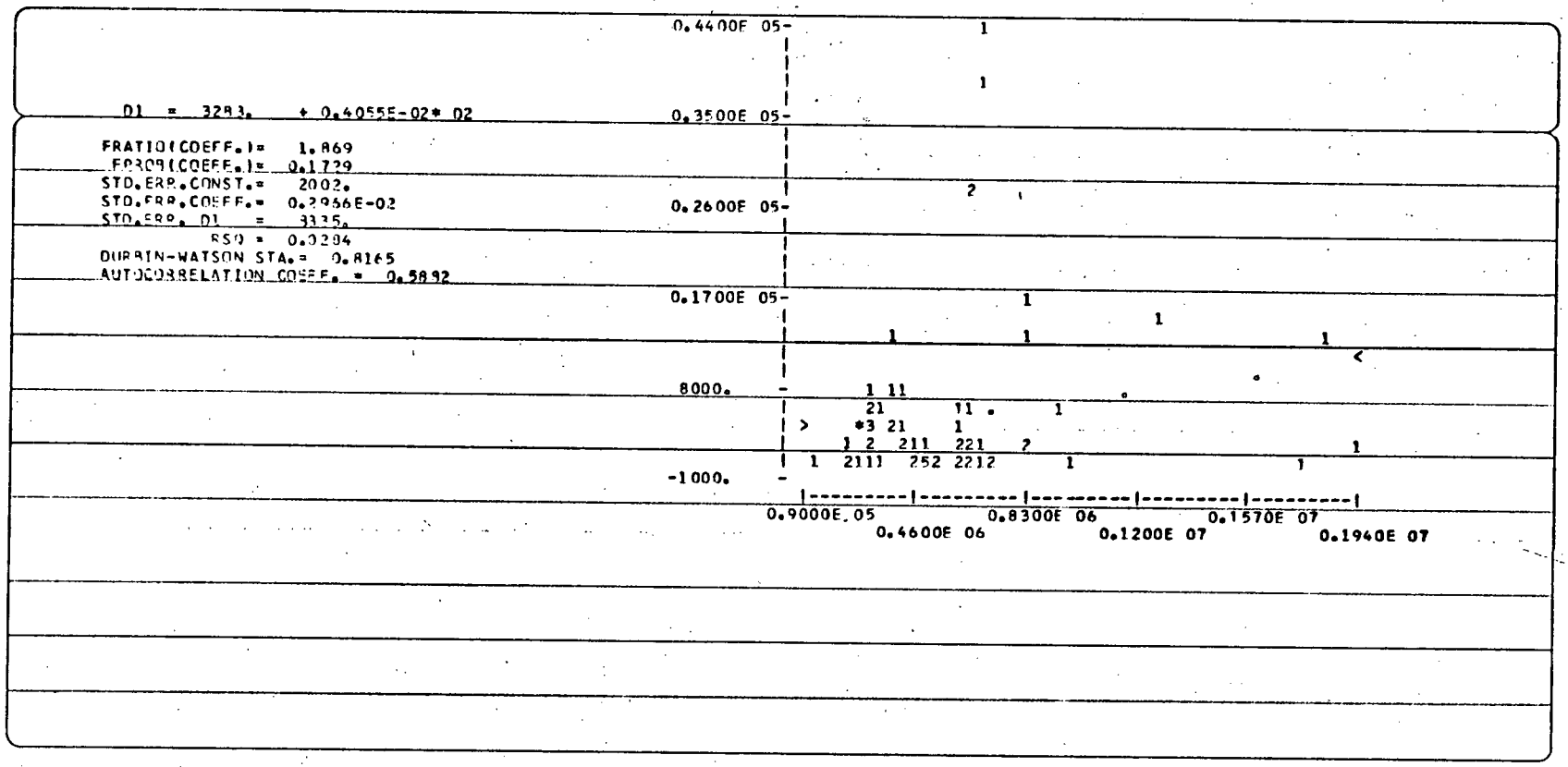
FRATIO(COEFF.)= 0.3685
PROB(COEFF.)= 0.5883
STD.ERR.CONST.= 4940.
STD.ERR.COEFF.= 228.5
STD.ERR. D1 = 3278.
RSQ = 0.1094
DURBIN-WATSON STA.= 1.234
AUTOCORRELATION COEFF. = -0.1020

Appendix 10. Coulter Counter data. All samples. N.T.C. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
3334.	0.8323E 06	0.5989E 06	4.000	0.6200	0.4800	0.7700	9.000	12.50	46.00
0.1640E 05	0.8323E 06	0.5989E 06	8.000	0.8500	0.4800	0.7700	9.000	12.50	46.00
3449.	0.8316E 06	0.5865E 06	6.000	0.6200	0.7800	0.7700	9.000	12.50	46.00
0.1270E 05	0.8316E 06	0.5965E 06	9.000	0.8500	0.7800	0.7700	9.000	12.50	46.00
436.0	0.6360E 06	0.6376E 06	2.000	1.000	1.890	0.7700	10.00	15.00	46.00
1351.	0.6380E 06	0.5205E 06	4.000	0.8500	1.290	0.8100	10.00	15.00	34.00
1124.	0.7229E 06	0.6555E 06	3.000	1.000	1.470	0.8700	10.00	15.00	34.00
137.0	0.5358E 06	0.4742E 06	2.000	0.8700	6.300	0.8200	9.000	16.50	29.00
0.3858E 05	0.5357E 05	0.5414E 06	8.000	1.490	0.2800	0.8200	8.000	18.00	42.00
0.4418E 05	0.6357E 06	0.5414E 06	9.000	1.720	0.2800	0.8200	8.000	18.00	42.00
0.2697E 05	0.6546E 06	0.4966E 06	8.000	1.490	0.5300	1.000	8.000	18.00	42.00
0.2761E 05	0.6546E 06	0.4966E 06	8.000	1.720	0.5300	1.000	8.000	18.00	42.00
2067.	0.6333E 06	0.4185E 06	8.000	1.490	4.110	0.8700	8.000	18.00	42.00
3313.	0.6393E 06	0.4185E 06	8.000	1.720	4.110	0.8700	8.000	18.00	42.00
1624.	0.4993E 06	0.3647E 06	7.000	1.490	5.680	0.8700	8.000	18.00	42.00
1843.	0.4993E 06	0.3647E 06	7.000	1.720	5.680	0.8700	8.000	18.00	42.00
1506.	0.4739E 06	0.3962E 06	7.000	1.490	4.840	0.8600	8.000	18.00	42.00
1747.	0.4739E 06	0.3962E 06	7.000	1.720	4.840	0.8600	8.000	18.00	42.00
2424.	0.4277E 06	0.3506E 06	8.000	1.490	2.710	0.8100	8.000	18.00	42.00
2658.	0.4277E 06	0.3506E 06	7.000	1.720	2.710	0.8100	8.000	18.00	42.00
5221.	0.3526E 06	0.3200E 06	5.000	0.9200	0.2000	0.8700	8.000	18.00	48.00
790.0	0.2356E 06	0.2726E 06	5.000	0.9200	0.7100	0.9100	8.000	18.00	48.00
514.0	0.2515E 06	0.2578E 06	3.000	1.040	0.6400	0.8600	8.000	27.00	90.00
5174.	0.2515E 06	0.2578E 06	8.000	1.520	0.6400	0.8600	8.000	27.00	90.00
3309.	0.2515E 06	0.2578E 06	8.000	1.380	0.6400	0.8600	8.000	27.00	90.00
3241.	0.3376E 06	0.2915E 06	4.000	1.060	0.4300	0.6600	8.000	27.00	36.00
8565.	0.3376E 06	0.2915E 06	8.000	1.470	0.4300	0.6600	8.000	27.00	36.00
5243.	0.3376E 06	0.2915E 06	8.000	1.170	0.4300	0.6600	8.000	27.00	36.00
5106.	0.3379E 06	0.3597E 06	6.000	1.060	0.3900	0.6600	8.000	27.00	36.00
0.1261E 05	0.3379E 06	0.3597E 06	8.000	1.470	0.3900	0.6600	8.000	27.00	36.00
8282.	0.3379E 06	0.3597E 06	7.000	1.170	0.3900	0.6600	8.000	27.00	36.00
3900.	0.3059E 06	0.3285E 06	6.000	1.380	0.4800	0.8700	8.000	27.00	90.00
6946.	0.3059E 06	0.3285E 06	7.000	1.520	0.4800	0.8700	8.000	27.00	90.00
2743.	0.3114E 06	0.2870E 06	6.000	1.060	0.7600	0.8100	8.000	27.00	36.00
6492.	0.3114E 06	0.2870E 06	8.000	1.470	0.7600	0.8100	8.000	27.00	36.00
4344.	0.3114E 06	0.2870E 06	8.000	1.170	0.7600	0.8100	8.000	27.00	36.00
1699.	0.2618E 06	0.2590E 06	6.000	1.380	1.030	0.9300	8.000	27.00	90.00
2777.	0.2618E 06	0.2590E 06	7.000	1.520	1.030	0.9300	8.000	27.00	90.00
1000.	0.7015E 06	0.7715E 06	4.000	1.170	0.6100	0.6100	15.00	28.00	29.00
0.1376E 05	0.1119E 07	0.1663E 07	4.000	0.9000	0.4200	0.8600	9.000	15.50	52.00
0.1449E 05	0.1239E 07	0.1146E 07	6.000	0.9100	0.6400	0.8800	10.00	15.00	24.00
4262.	0.3355E 06	0.2472E 06	4.000	0.5500	0.7900	0.8100	9.000	25.00	24.00
3458.	0.1239E 07	0.1919E 07	3.000	1.040	1.390	0.8000	10.00	25.50	30.00
17.00	0.1770E 07	0.1597E 07	2.000	0.8200	1.390	0.9600	10.00	25.50	30.00
970.0	0.1300E 06	0.1231E 06	6.000	2.830	2.580	0.6800	8.000	24.00	36.00
951.0	0.2237E 06	0.2361E 06	1.000	1.390	0.8200	0.7200	8.000	24.00	36.00
1298.	0.6341E 06	0.7340E 06	5.000	1.310	1.450	0.7200	8.000	24.00	36.00
11.00	0.3339E 06	0.2513E 06	3.000	0.5400	2.230	0.8000	8.000	25.00	24.00
3511.	0.4323E 06	0.3247E 06	6.000	0.8400	1.850	0.7500	8.000	25.00	24.00
1255.	0.5121E 06	0.7030E 06	3.000	1.930	3.280	0.9600	8.000	25.00	39.00
628.0	0.5121E 06	0.7030E 06	4.000	1.860	3.280	0.9600	8.000	25.00	39.00
4114.	0.6378E 06	0.8023E 06	3.000	1.930	1.410	0.9400	8.000	25.00	39.00
2797.	0.6378E 06	0.8023E 06	3.000	1.860	1.410	0.9400	8.000	25.00	39.00
5378.	0.6121E 06	0.7562E 06	4.000	1.930	1.140	0.9400	8.000	25.00	39.00
1022.	0.5121E 06	0.7562E 06	5.000	1.470	1.140	0.9400	8.000	25.00	39.00
2629.	0.6121E 06	0.7562E 06	4.000	1.860	1.140	0.9400	8.000	25.00	39.00
5904.	0.9336E 06	0.9644E 06	6.000	1.190	1.130	0.8200	20.00	26.00	36.00
959.0	0.3573E 06	0.3099E 06	3.000	0.7500	1.940	0.7300	22.00	25.00	36.00
464.0	0.5935E 06	0.5505E 06	2.000	1.200	5.850	0.8000	13.00	30.00	23.00
1369.	0.6137E 06	0.6397E 06	7.000	1.300	2.940	0.8800	10.00	28.00	42.00
2563.	0.5598E 06	0.6213E 06	5.000	0.9400	0.6700	0.8300	17.00	26.00	35.00

5872.	0.6441E 06	0.6012E 06	3.000	0.9500	0.2200	0.5600	18.00	26.00	20.00
633.0	0.4637E 06	0.4749E 06	4.000	1.200	2.970	0.9500	13.00	30.00	22.00
1042.	0.4078E 06	0.5510E 06	2.000	1.290	1.080	0.9600	16.00	28.00	42.00
8285.	0.4414E 06	0.3607E 06	6.000	0.8400	0.6400	0.9000	8.000	25.00	24.00
955.0	0.5120E 06	0.3766E 06	4.000	0.5900	1.740	0.8500	10.00	25.00	39.00

NAME	MEANS	STD.DEV.	CORRELATIONS									66. OBSERVATIONS
			D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
D1	5633.22	8390.22	1.0000									
D2	579723.	348534.	0.1684	1.0000								
D3	536900.	333589.	0.0603	0.9494	1.0000							
D4	5.43938	2.12343	0.4618	-0.2415	-0.3719	1.0000						
D5	1.27256	0.425065	0.1175	-0.2871	-0.1476	0.2559	1.0000					
D6	1.61377	1.56421	-0.3633	-0.0525	-0.0656	-0.0930	0.2466	1.0000				
D7	0.829333	0.591048E-01	0.0370	0.1004	0.1752	-0.0733	0.2454	0.2224	1.0000			
D8	9.40909	3.01778	-0.1439	0.2854	0.2953	-0.3459	-0.2977	-0.0280	-0.1873	1.0000		
D9	22.6666	5.35517	-0.2998	-0.3116	-0.1234	-0.1756	0.1534	-0.1517	-0.0685	0.2047	1.0000	
D10	42.6818	17.8162	0.0010	-0.2719	-0.2525	0.2738	0.1808	-0.2041	0.2492	-0.2611	0.0739	1.0000

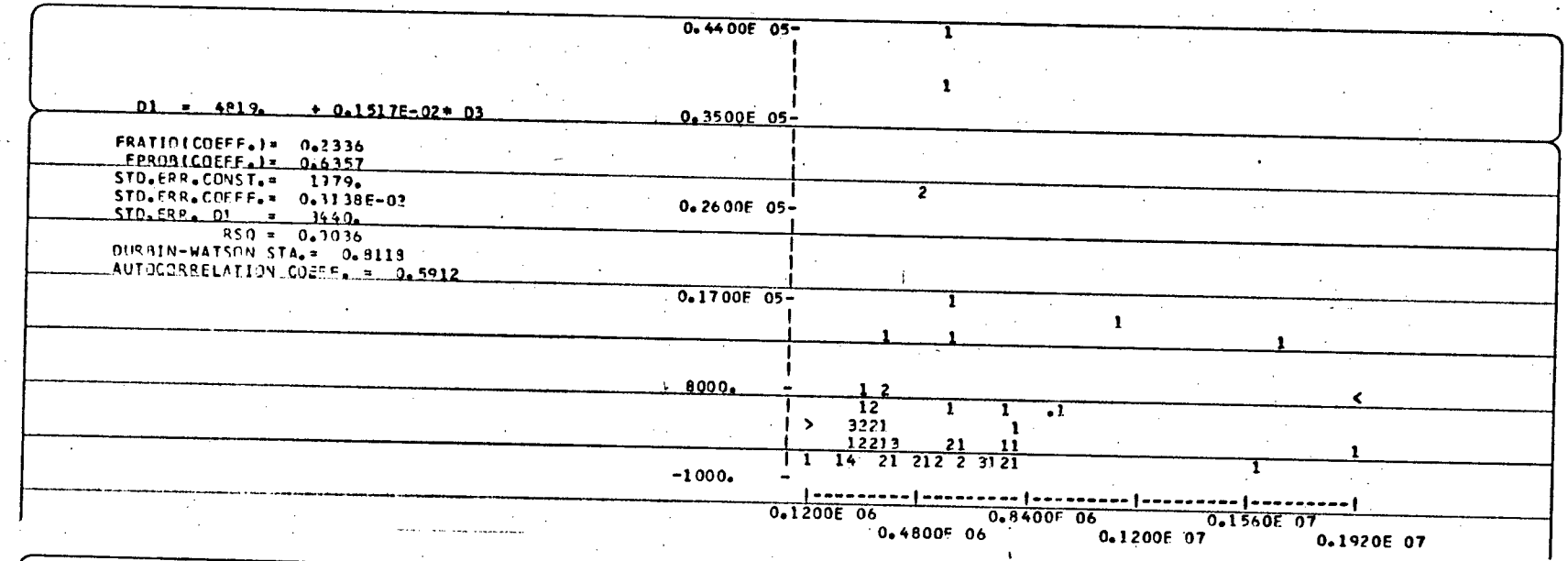


D1 = 3283. + 0.40555E-02* D2

FRATIO(COEFF.)= 1.869
PROB(COEFF.)= 0.1729
STD.ERR.CONST.= 2002.
STD.ERR.COEFF.= 0.2966E-02
STD.ERR. D1 = 3335.
RSQ = 0.0284
DURBIN-WATSON STA.= 0.8165
AUTOCORRELATION COEFF. = 0.5892

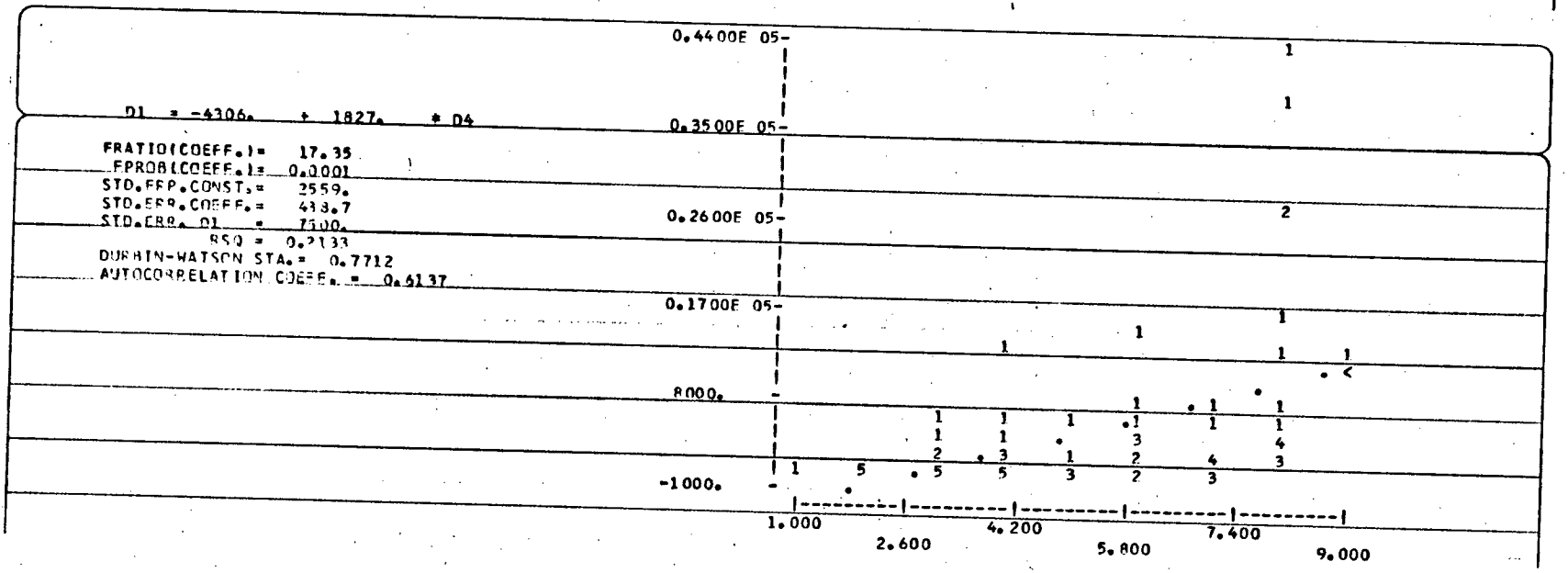
D1 = 4819. + 0.1517E-02* D3

FRATIO(COEFF.)= 0.2336
FPROB(COEFF.)= 0.6357
STD.ERR.CONST.= 1379.
STD.ERR.COEFF.= 0.3138E-02
STD.ERR. D1 = 3440.
RSQ = 0.0036
DURBIN-WATSON STA.= 0.8118
AUTOCORRELATION COEFF.= 0.5912



D1 = -4306. + 1827. * D4

FRATIO(COEFF.)= 17.35
FPROB(COEFF.)= 0.0001
STD.ERR.CONST.= 2559.
STD.ERR.COEFF.= 438.7
STD.ERR. D1 = 7500.
RSQ = 0.2133
DURBIN-WATSON STA.= 0.7712
AUTOCORRELATION COEFF.= 0.6137



Appendix 10. (Cont'd)

D1 = 2682. + 2319. * D5

FRATIO(COEFF.)= 0.8955
FPROB(COEFF.)= 0.3501
STD.ERR.CONST.= 3285.
STD.ERR.COEFF.= 2450.
STD.ERR. D1 = 8357.
RSQ = 0.0138
DURBIN-WATSON STA.= 0.7913
AUTOCORRELATION COEFF. = 0.6032

D1 = 9397. + -400.0 * D8

FRATIO(COEFF.)= 1.353
FPROB(COEFF.)= 0.2478
STD.ERR.CONST.= 3396.
STD.ERR.COEFF.= 343.9
STD.ERR. D1 = 8368.
RSQ = 0.0207
DURBIN-WATSON STA.= 0.8313
AUTOCORRELATION COEFF. = 0.5814

D1 = 8778. + -1948. * D6

FRATIO(COEFF.)= 9.729
FPROB(COEFF.)= 0.0028
STD.ERR.CONST.= 1399.
STD.ERR.COEFF.= 624.7
STD.ERR. D1 = 7878.
RSQ = 0.1320
DURBIN-WATSON STA.= 0.6744
AUTOCORRELATION COEFF. = 0.6577

D1 = 0.1691E 05+ -497.4 * D9

FRATIO(COEFF.)= 4.518
FPROB(COEFF.)= 0.0139
STD.ERR.CONST.= 4594.
STD.ERR.COEFF.= 197.9
STD.ERR. D1 = 3067.
RSQ = 0.0899
DURBIN-WATSON STA.= 0.8583
AUTOCORRELATION COEFF. = 0.5628

D1 = 3039. + 3129. * D7

FRATIO(COEFF.)= 0.8763E-01
FPROB(COEFF.)= 0.7611
STD.ERR.CONST.= 9925.
STD.ERR.COEFF.= 0.1057E 05
STD.ERR. D1 = 1450.
RSQ = 0.0014
DURBIN-WATSON STA.= 0.8249
AUTOCORRELATION COEFF. = 0.5845

D1 = 5613. + 0.4706 * D10

FRATIO(COEFF.)= 0.6391E-04
FPROB(COEFF.)= 0.9413
STD.ERR.CONST.= 2720.
STD.ERR.COEFF.= 59.87
STD.ERR. D1 = 3455.
RSQ = 0.0000
DURBIN-WATSON STA.= 0.8207
AUTOCORRELATION COEFF. = 0.5966

Appendix 11. Coulter Counter data. All samples. E.S.O. method.

D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
3334.	0.47575E 06	0.33306E 06	4.000	0.5900	0.4800	0.7700	9.000	12.50	46.00
0.16405E 05	0.95325E 06	0.75376E 06	8.000	0.8500	0.4800	0.7700	9.000	12.50	46.00
3449.	0.71125E 06	0.50735E 06	6.000	0.6500	0.7800	0.7700	9.000	12.50	46.00
0.12705E 05	0.83165E 06	0.58855E 06	9.000	0.8500	0.7800	0.7700	9.000	12.50	46.00
1715.	0.13475E 06	0.14775E 06	2.000	1.250	1.890	0.7700	10.00	15.00	34.00
2534.	0.22365E 06	0.20425E 06	4.000	1.450	1.290	0.8100	10.00	15.00	34.00
660.0	0.37735E 05	0.21515E 05	1.000	1.210	0.9200	0.6800	10.00	15.00	34.00
3651.	0.33355E 06	0.24165E 06	3.000	1.010	1.470	0.9600	10.00	15.00	34.00
1374.0	0.93035E 05	0.68305E 05	2.000	0.8300	6.300	0.8200	9.000	16.00	29.00
0.13595E 05	0.15375E 06	0.15415E 06	8.000	1.490	0.2800	0.8200	8.000	18.00	42.00
0.44185E 05	0.65375E 05	0.54145E 06	8.000	1.720	0.2800	0.8200	8.000	18.00	42.00
0.26975E 05	0.65465E 06	0.49665E 06	8.000	1.490	0.5300	1.000	8.000	18.00	42.00
0.27415E 05	0.65465E 06	0.49665E 06	8.000	1.720	0.5300	1.000	8.000	18.00	42.00
3367.	0.63335E 06	0.41955E 06	8.000	1.490	4.110	0.8700	8.000	18.00	42.00
3313.	0.63335E 06	0.41855E 06	8.000	1.720	4.110	0.8700	8.000	18.00	42.00
1624.	0.49335E 05	0.36475E 06	7.000	1.490	5.680	0.8700	8.000	18.00	42.00
1473.	0.47335E 06	0.36475E 06	7.000	1.720	5.680	0.8700	8.000	18.00	42.00
1506.	0.47335E 06	0.35625E 06	7.000	1.490	4.840	0.8600	8.000	18.00	42.00
1367.	0.47335E 06	0.33625E 06	7.000	1.720	4.840	0.8600	8.000	18.00	42.00
2424.	0.42775E 06	0.35065E 06	8.000	1.490	2.710	0.8100	8.000	18.00	42.00
2659.	0.42775E 06	0.35065E 06	7.000	1.720	2.710	0.8100	8.000	18.00	42.00
735.0	0.33315E 05	0.26265E 05	1.000	1.020	0.2700	0.8700	8.000	18.00	42.00
6414.	0.22115E 06	0.18775E 06	5.000	0.9100	0.2000	0.8700	8.000	18.00	42.00
1853.	0.16515E 06	0.14355E 06	5.000	0.9600	0.7100	0.9100	8.000	18.00	42.00
603.0	0.10975E 05	0.10735E 06	2.000	1.130	0.6400	0.8600	8.000	18.00	90.00
5339.	0.33335E 06	0.22645E 06	8.000	2.040	0.6400	0.8600	8.000	27.00	90.00
3939.	0.22335E 06	0.22645E 06	8.000	1.380	0.6400	0.8600	8.000	27.00	90.00
3610.	0.17335E 06	0.14975E 06	4.000	1.090	0.4300	0.6600	8.000	27.00	36.00
8555.	0.33735E 06	0.29155E 06	8.000	1.470	0.4300	0.6600	8.000	27.00	36.00
5243.	0.33745E 06	0.29155E 06	8.000	1.170	0.4300	0.6600	8.000	27.00	36.00
5106.	0.33735E 06	0.35975E 06	6.000	1.060	0.3900	0.6600	8.000	27.00	36.00
0.13615E 05	0.33735E 05	0.35975E 06	8.000	1.470	0.3900	0.6600	8.000	27.00	36.00
8332.	0.33735E 06	0.35975E 06	7.000	1.170	0.3900	0.6600	8.000	27.00	36.00
1207.	0.12335E 05	0.12175E 06	3.000	1.150	0.4800	0.8700	8.000	27.00	90.00
4416.	0.22745E 06	0.22955E 06	6.000	1.520	0.4800	0.8700	8.000	27.00	90.00
7991.	0.27415E 06	0.29745E 06	7.000	2.040	0.4800	0.8700	8.000	27.00	90.00
2887.	0.24365E 06	0.22715E 06	6.000	1.000	0.7600	0.9100	8.000	27.00	36.00
6482.	0.31145E 06	0.28705E 06	8.000	1.470	0.7600	0.9100	8.000	27.00	36.00
4364.	0.31145E 06	0.28705E 06	8.000	1.170	0.7600	0.8100	8.000	27.00	36.00
461.0	0.53335E 05	0.52535E 05	2.000	1.170	1.030	0.9300	8.000	27.00	90.00
1539.	0.17435E 06	0.19155E 06	6.000	1.000	1.030	0.9300	8.000	27.00	90.00
2377.	0.21535E 06	0.23335E 06	7.000	2.040	1.030	0.9300	8.000	27.00	90.00
2055.	0.23535E 06	0.21265E 06	4.000	1.270	0.6100	0.6100	15.00	28.00	90.00
1577.	0.13395E 06	0.12675E 06	1.000	0.9700	0.6700	0.5900	15.00	28.00	90.00
0.21705E 05	0.11795E 07	0.10305E 07	4.000	0.9400	0.4200	0.9800	9.000	15.50	52.00
0.14495E 05	0.92355E 05	0.63745E 06	6.000	1.000	0.6400	0.9800	10.00	15.00	34.00
4812.	0.24145E 06	0.14035E 06	4.000	0.6100	0.7900	0.6100	9.000	25.00	34.00
3580.	0.31645E 06	0.47515E 06	3.000	2.880	1.390	0.8000	10.00	25.50	30.00
927.0	0.29235E 06	0.17985E 06	2.000	0.5400	1.390	0.9600	10.00	15.50	30.00
1020.	0.12545E 06	0.11645E 06	6.000	2.930	2.580	0.6800	8.000	24.00	34.00
167.0	0.10995E 05	0.12135E 05	1.000	3.110	1.600	0.6800	8.000	24.00	36.00
1106.	0.75295E 05	0.79345E 05	1.000	1.690	0.8200	0.7200	8.000	24.00	36.00
1525.	0.33515E 06	0.31405E 06	5.000	1.190	1.450	0.7700	15.00	29.00	37.00
252.0	0.13305E 06	0.25235E 06	3.000	2.230	5.390	0.6800	15.00	28.00	37.00
140.0	0.14345E 06	0.15245E 06	2.000	1.450	4.550	0.6800	9.000	15.50	52.00
420.0	0.13315E 06	0.12745E 06	3.000	0.8700	0.5500	0.7700	9.000	15.50	52.00
367.0	0.23155E 05	0.25665E 05	1.000	1.620	0.5200	0.7800	9.000	15.50	52.00
549.0	0.47575E 05	0.37745E 05	3.000	1.730	2.230	0.8000	8.000	25.00	24.00
3922.	0.43235E 06	0.32475E 06	6.000	0.8400	1.850	0.7500	8.000	25.00	24.00
1717.	0.35335E 06	0.42465E 06	3.000	2.260	3.280	0.9600	8.000	25.00	30.00
857.0	0.21595E 06	0.22595E 06	3.000	2.220	3.280	0.9600	8.000	25.00	30.00

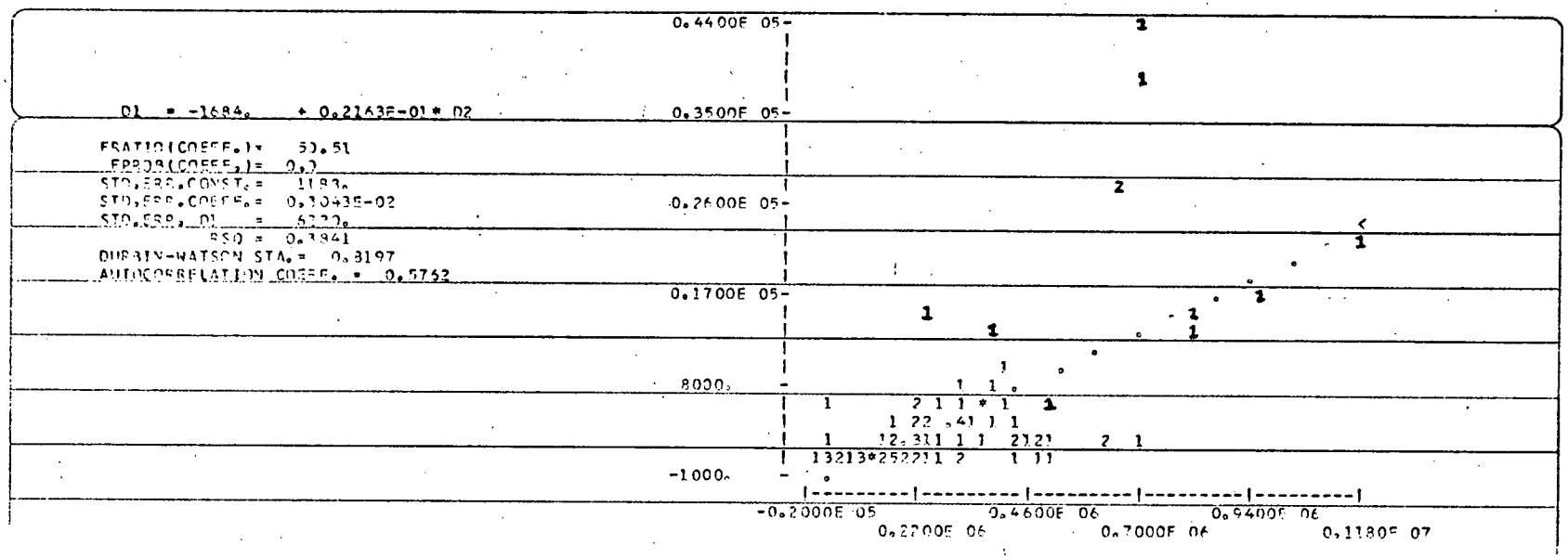
Appendix 11. (Cont'd)

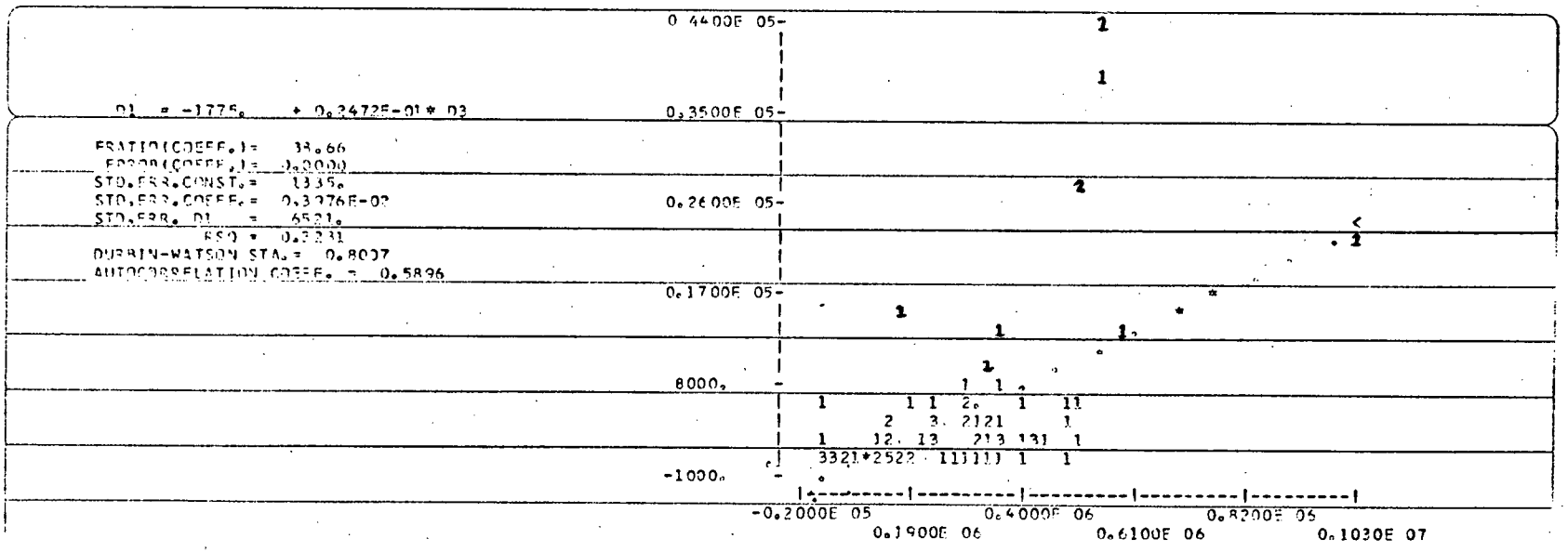
1239.	0.2345E 06	0.2306E 06	4.000	2.930	3.280	0.9600	8.000	25.00	39.00
5421.	0.4154E 06	0.4902E 06	3.000	2.260	1.410	0.9400	8.000	25.00	39.00
3114.	0.2311E 06	0.3009E 06	2.000	2.320	1.410	0.9400	8.000	25.00	39.00
3396.	0.2433E 05	0.3340E 06	3.000	3.120	1.410	0.9400	8.000	25.00	39.00
6378.	0.3395E 06	0.5942E 06	4.000	2.240	1.140	0.9400	8.000	25.00	39.00
1612.	0.4333E 06	0.4884E 06	5.000	1.410	1.140	0.9400	8.000	25.00	39.00
3586.	0.3214E 06	0.3279E 06	4.000	2.160	1.140	0.9400	8.000	25.00	39.00
5304.	0.5176E 06	0.5081E 06	6.000	1.750	1.130	0.8200	20.00	26.00	36.00
848.0	0.1573E 06	0.1456E 06	3.000	0.9500	1.360	0.8300	22.00	25.00	36.00
1173.	0.3398E 06	0.2764E 06	3.000	1.070	1.940	0.7400	22.00	25.00	36.00
527.0	0.1454E 06	0.1543E 06	2.000	1.370	5.850	0.9900	13.00	30.00	22.00
1708.	0.4431E 06	0.4456E 06	7.000	1.410	2.040	0.8500	10.00	28.00	42.00
2850.	0.3363E 06	0.2287E 06	5.000	0.9600	0.6700	0.8300	17.00	26.00	35.00
0.1542E 05	0.2311E 06	0.1726E 06	3.000	1.220	0.2200	0.5600	18.00	26.00	30.00
633.0	0.1343E 06	0.1432E 06	4.000	1.110	2.970	0.9500	13.00	30.00	22.00
1515.	0.1541E 06	0.1766E 06	2.000	1.080	1.080	0.9600	16.00	28.00	42.00
2398.	0.1399E 06	0.1370E 06	2.000	0.1900	0.1900	0.8300	17.00	26.00	35.00
3133.	0.3327E 05	0.2371E 05	3.000	0.4100	0.4100	0.9100	8.000	25.00	24.00
9409.	0.4207E 06	0.3457E 06	6.000	0.6400	0.6400	0.9000	8.000	25.00	24.00
620.0	0.9834E 05	0.6552E 05	1.000	0.5900	1.310	0.8700	9.000	16.50	22.00
855.0	0.2132E 06	0.1511E 06	1.000	0.6400	1.740	0.8500	10.00	25.00	39.00
9701.	0.3396E 05	0.2497E 06	4.000	1.650	0.8000E-01	0.7300	18.00	26.00	20.00

NAME	MEANS	STD.DEV.	CORRELATIONS										83. OBSERVATIONS
			01	02	03	04	05	06	07	08	09	010	
01	5238.53	7376.85	1.0000										
02	319622.	225706.	0.6197	1.0000									
03	283260.	191092.	0.5684	0.9514	1.0000								
04	4.71093	2.40693	0.4602	0.6162	0.56147	1.0000							
05	1.41409	0.620741	-0.0107	-0.0788	0.0932	0.0445	1.0000						
06	1.57263	1.55279	-0.3416	-0.0015	-0.0106	-0.0229	0.2568	1.0000					
07	0.826742	0.100573	0.0236	0.0912	0.1375	-0.0021	0.1096	0.1344	1.0000				
08	9.84335	3.44462	-0.1115	-0.1475	-0.1375	-0.2850	-0.1980	-0.0270	-0.2659	1.0000			
09	22.4398	6.12021	-0.2181	-0.4119	-0.2584	-0.0326	0.2292	-0.0998	-0.1049	0.2643	1.0000		
010	42.7467	18.1361	-0.0392	-0.0604	-0.0367	0.1863	0.0824	-0.1690	0.2523	-0.2956	0.0339	1.0000	

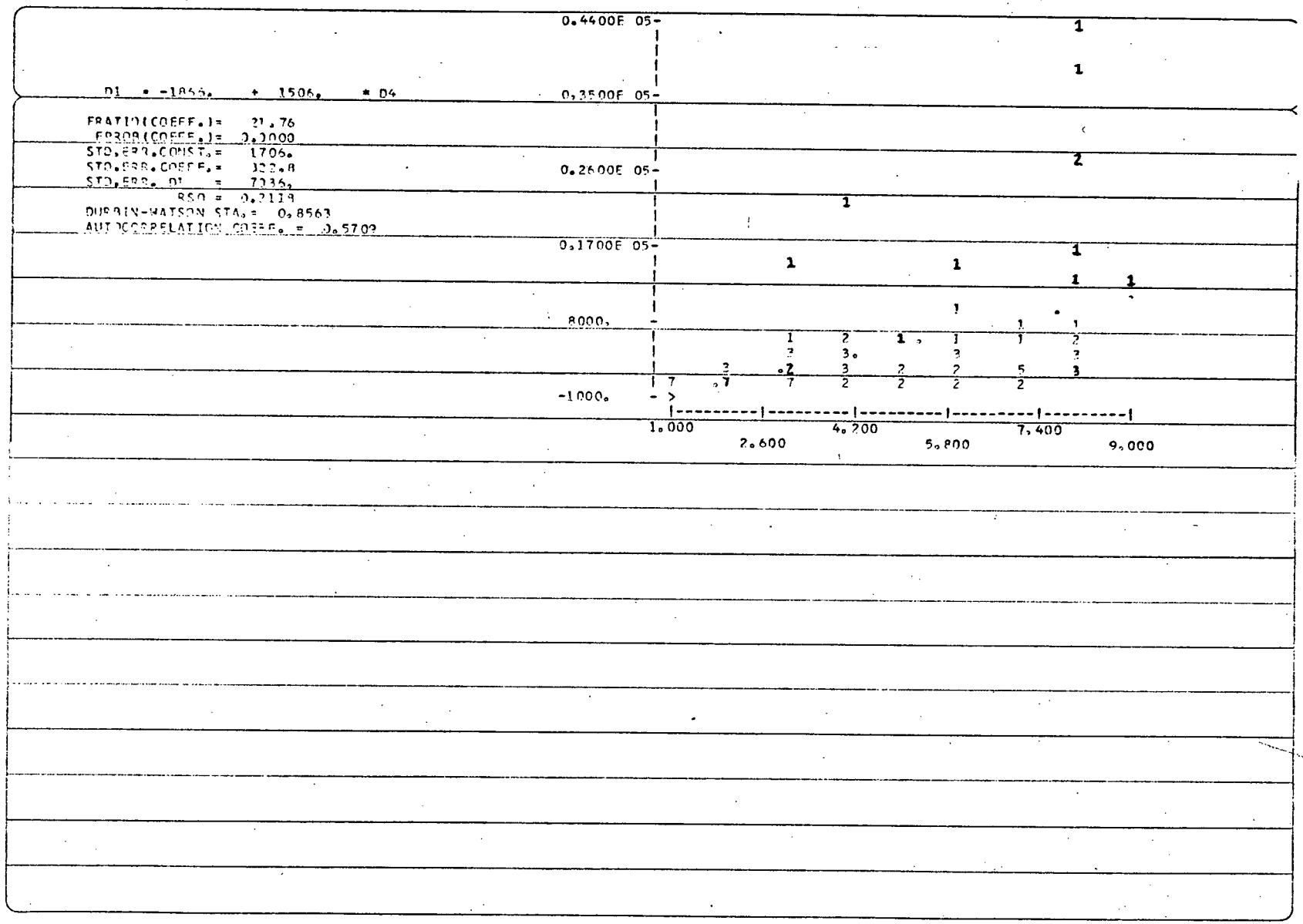
5, *SIM356*

Appendix 11. (Cont'd)





Appendix 11. (Cont'd)



Appendix 11. (Cont'd)

D1 = 5421. + -135.9 * D5

FRATIO(COEFF.)= 0.9295E-02
PROB(COEFF.)= 0.9359
STD.ERR.CONST.= 2175.
STD.ERR.COEFF.= 1410.
STD.ERR. D1 = 7225.
RSQ = 0.0001
DURBIN-WATSON STA.= 0.8864
AUTOCORRELATION COEFF.= 0.5562

D1 = 7739. + -255.1 * D8

FRATIO(COEFF.)= 1.020
PROB(COEFF.)= 0.3167
STD.ERR.CONST.= 2631.
STD.ERR.COEFF.= 252.5
STD.ERR. D1 = 7376.
RSQ = 0.0134
DURBIN-WATSON STA.= 0.8998
AUTOCORRELATION COEFF.= 0.5494

D1 = 7954. + -1733. * D6

FRATIO(COEFF.)= 10.70
PROB(COEFF.)= 0.2017
STD.ERR.CONST.= 1167.
STD.ERR.COEFF.= 529.7
STD.ERR. D1 = 7449.
RSQ = 0.1167
DURBIN-WATSON STA.= 0.7640
AUTOCORRELATION COEFF.= 0.6163

D1 = 0.12765 05+ -335.6 * D9

FRATIO(COEFF.)= 4.046
PROB(COEFF.)= 0.0451
STD.ERR.CONST.= 3838.
STD.ERR.COEFF.= 166.8
STD.ERR. D1 = 7734.
RSQ = 0.0476
DURBIN-WATSON STA.= 0.9210
AUTOCORRELATION COEFF.= 0.5369

D1 = 3704. + 1945. * D7

FRATIO(COEFF.)= 0.4501E-01
PROB(COEFF.)= 0.8151
STD.ERR.CONST.= 7237.
STD.ERR.COEFF.= 8700.
STD.ERR. D1 = 7223.
RSQ = 0.0005
DURBIN-WATSON STA.= 0.8880
AUTOCORRELATION COEFF.= 0.5554

D1 = 5956. + -17.02 * D10

FRATIO(COEFF.)= 0.1244
PROB(COEFF.)= 0.7232
STD.ERR.CONST.= 2237.
STD.ERR.COEFF.= 49.22
STD.ERR. D1 = 7319.
RSQ = 0.0015
DURBIN-WATSON STA.= 0.8884
AUTOCORRELATION COEFF.= 0.5554

BLACKBOURN

PUBLICATIONS:

T.R. PARSONS AND D. J. BLACKBOURN (1963)
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