# The Culture and Ecology of Predatory Nematode Populations, especially of *Prionchulus punctatus*.

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## ABSTRACT

A simple culture technique using soil-extract agar allowed considerable numbers of Prionchulus punctatus to be produced on a laboratory scale. Experiments showed that the optimum culture regime was to maintain the cultures at 20-25°C and to sub-culture every four weeks; such factors as temperature, type of agar and method of sub-culturing influenced the population dynamics of the predators in these cultures. Mononchus aquaticus and Labronema sp. were cultured using the same technique.

The predators produced by the culture technique were used in pot experiments to give empirical data on the ability of predators to control some phytoparasitic nematode species. The degree of control depended on the species of plant-parasite and ranged from little effect on Helicotylenchus dihystera populations to significant reductions in the numbers of Meloidogyne incognita in soil and in the roots of the host plant.

The spatial distribution of predators and prey under natural conditions was studied on a scale related to the size of soil nematodes. Aggregated distributions were frequent in the upper soil layers, random distribution at lower depths, and occasionally regular distribution at the lowest depth investigated.

The results of the study are discussed with reference to the possible use of predatory nematodes as biological control agents of plant-parasitic nematodes.

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# I. INTRODUCTION

## Preamble and Mononchid Taxonomy.

Free-living nematodes are amongst the most widespread organisms known, ranking with the free-living insects in the number of habitats that they have colonised. Large numbers are found in soil, freshwater and marine habitats, where they inhabit the interstices of the substrate (Nicholas, 1975); the nature of these environments, combined with the small size of these animals, contributed to their late discovery compared with parasitic nematodes (Crofton, 1966). Even now detailed knowledge of free-living species is lacking and nematologists concentrate on the economically-important parasites of animals and plants.

Accounts of nematode ecology recognise several trophic groups amongst the free-living nematodes: fungivores, bacteriovores, omnivores, carnivores and usually "food unknown" (Overgaard-Neilsen, 1949; Banage, 1963; Yeates, 1968, 1971 and 1973). These trophic classifications do not follow the taxonomic classification so that predators, for example, are recognised in at least five orders: Tylenchida, Dorylaimida, Rhabditida, Enoplida and Mononchida. The present study is primarily concerned with members of the Mononchida; a comprehensive review of mononchid biology is lacking and the following survey outlines the existing literature on all aspects of mononchid biology. Although some aspects have not been investigated experimentally in this study they will be discussed in the concluding discussion.

The mononchids were amongst the first free-living nematodes to be described, starting with Dujardin's (1845) description of Oncholaimus muscorum, which was later placed in the genus Mononchus (Bastian, 1865). By 1977 this genus was only one of over twenty genera arranged into one of the superfamilies of the order Mononchida Jairajpuri 1969. Major developments in mononchid taxonomy are summarised in Table 1.

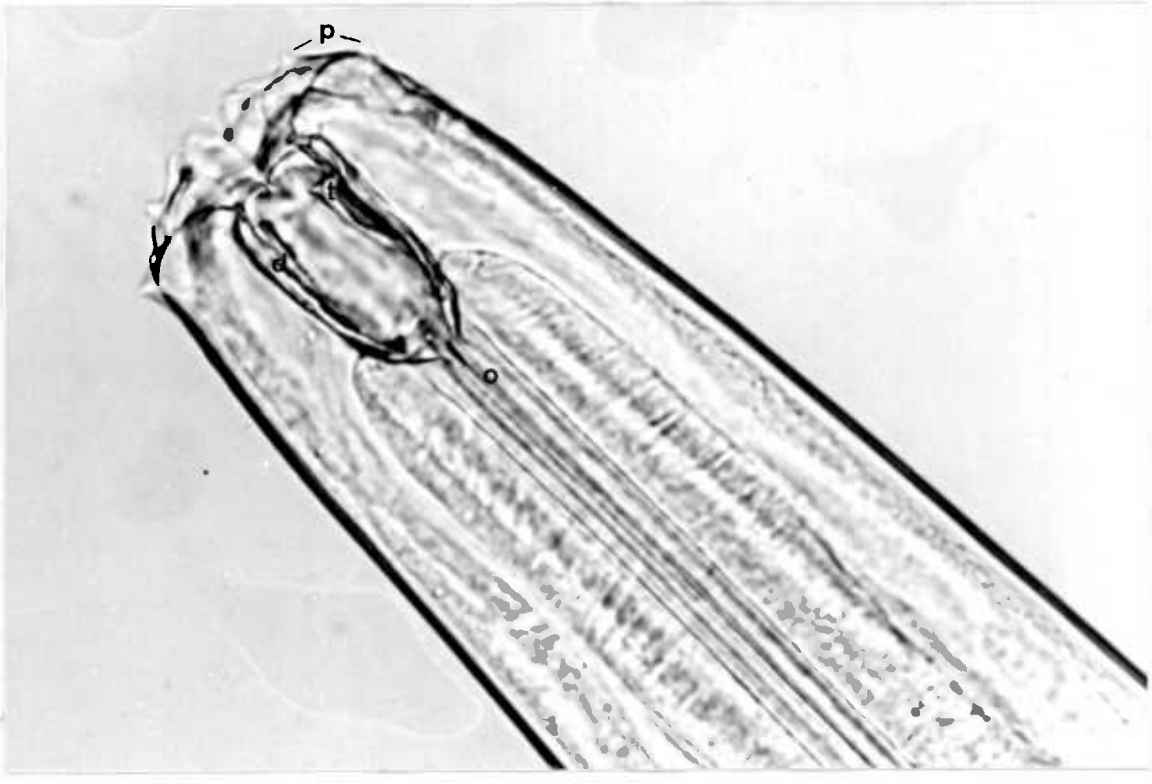
The rate at which new species were described quickened between 1880 and

and 1915 from authors such as Daday, de Man, Ditlevsen and Micoletzky. During the same period Cobb described much of the American fauna, culminating in his papers of 1916 and 1917 which firmly established the mononchids as a distinct group. Full descriptions of 57 species (32 that were new) and their arrangement into six subgenera (Table 1) were his major contributions, together with notes on the life-history and habits. Micoletzky (1922) synonymised many of Cobb's species but retained the six subgenera and the criteria for their recognition i.e. the position of the dorsal tooth and the number and arrangement of subventral denticles, which have remained the basis for generic differentiation of mononchids. In the following years new species and known species from new locations were described although the subgenera were rarely mentioned in these reports. The description of the American fauna was continued with accounts of the Utah representatives (Thorne, 1924) and the life-history of these species (Thorne 1927, 1928).

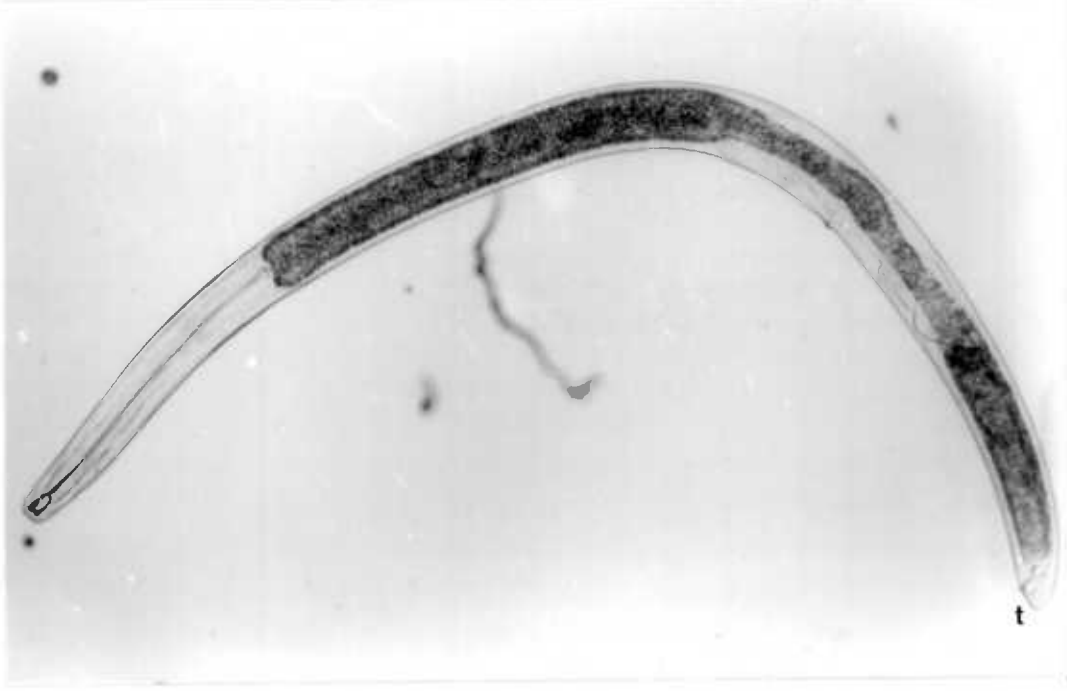
In time, Cobb's subgenera were all raised to full generic rank but the literature is confused. Wu and Hoeppli (1929) informally ranked Prionchulus as a genus but Clark (1960) quotes Chitwood and Chitwood (1937), in fact referring to Chitwood (1937), as the authority. De Coninck (1939) raised Anatonchus to generic rank and Altherr (1950, 1953) raised Iotonchus and Mylonchulus respectively. Mulvey (1963a) however, quotes Pennak (1953) as the authority for Iotonchus whilst noting that Andrassy (1958) was the first to use Iotonchus in combination with the specific epithet of the type species, I.gymnolaimus (Cobb 1893), Altherr 1950. It is apparent that Pennak (1953) treated all Cobb's subgenera as genera and should be credited with the raising of Sporonchulus to generic rank.

The systematics of the mononchids were clarified considerably by Andrassy (1958), although his work has provoked adverse comments from both Clark (1961a) and from Mulvey (1961a). Clark considered that Andrassy was too concerned with "tidying-up" and so had placed some probably valid species

Fig. 1. Photomicrographs of Prionchulus punctatus adults




a) Lateral view of anterior showing lips with labial papillae (P), buccal capsule with denticulate ridge (d) and dorsal tooth (t) and anterior oesophagus (o) (x 655).




b) Entire female with abnormal tail (t): normal tail-shape conoid-arcuate. (x65).

Table 1. Summary of the major developments in mononchid taxonomy

| Author | Date | Development |
|---|---|---|
| Dujardin | 1845 | Description of *Oncholaimus muscorum* |
| Bastian | 1865 | Erection of genus *Mononchus* (includes *O.muscorum*) |
| Cobb | 1917 | Suggests six subgenera: *Mononchus*, *Prionchulus*, *Sporonchulus*, *Mylonchulus*, *Anatonchus*, *Iotonchus*. |
| Micoletzky | 1922 | Revision of taxonomy; retains Cobb's subgenera. |
| Wu & Hoeppli | 1929 | *Prionchulus* raised to generic rank. |
| Chitwood | 1937 | Erection of family Mononchidae (within superfamily Tripyloidea) |
| de Coninck | 1939 | *Anatonchus* raised to generic rank. |
| Altherr | 1950 | *Iotonchus* raised to generic rank. |
| " | 1953 | *Mylonchulus* raised to generic rank. |
| Pennak | 1953 | *Sporonchulus* raised to generic rank. |
| Andrassy | 1958 | Revision of mononchid taxonomy; erection of genera *Miconchus*, *Brachonchulus*, *Cobbonchus*, *Granonchulus*, and *Judonchulus*. |
| Clark | 1960a | Description of tuberculate and non-tuberculate oesophago-intestinal junctions; *Anatonchus*, *Iotonchus*, *Miconchus* tuberculate group, *Mononchus*, *Prionchulus*, *Mylonchulus*, *Cobbonchus* non-tuberculate group. |
| " | 1961a | *Sporonchulus*, *Judonchulus*, *Granonchulus*, *Brachonchulus* added to non-tuberculate group. |
| " | 1961c | Erection of superfamily Mononchoidea. |
| Mulvey | 1961a | Review of *Mylonchulus* |
| " | 1961b | Review of *Anatonchus* |
| " | 1962 | Review of *Miconchus* |
| " | 1963b | Review of *Iotonchus* |
| " | 1963c | Review of *Sporonchulus*, *Granonchulus* and description of genus *Prionchuloides*. |
| " | 1967a | Review of *Mononchus* |
| " | 1967b | Review of *Prionchulus* |

Table 1 (cont).

| Author | Date | Development |
|---|---|---|
| Mulvey & Jensen | 1967 | Description of genera Crassibucca, Hadronchus, Polyonchulus, Prionchulellus. |
| Kirjanova & Krall | 1969 | Description of genus Tigronchus* |
| Jairajpuri | 1969 | Erection of order Mononchida with five families: Mononchidae, Mylonchulidae, Cobbonchidae, Anatonchidae, Iotonchidae. |
| " | 1970a | Division of genus Mononchus into Clarkus and Mononchus. |
| Ivanova & Dzhuraeva | 1971 | Description of genus Tigronchoides |
| Andrassy | 1972 | Description of genus Margaronchulus** |
| " | 1976 | Description of genus Oligonchulus; erection of subfamilies Prionchulinae and Miconchinae within family Mononchidae. |
| Baqri & Jairajpuri | 1973 | Description of genera Actus and Paracrassibucca |
| Tsalolichin | 1974 | Description of genus Tectonchus |
| Jairajpuri | 1977 | Division of genus Clarkus into Coomansus and Clarkus |

*Probably synonymous with Anatonchus according to Andrassy (1976).

**Description based on a single female.

in synonymy; Mulvey disliked Andrassy's concentration on genera at the expense of a detailed analysis of the species. Andrassy (1.c.) accepted Chitwood's (1937) creation of the family Mononchidae and recognised the additional genera Miconchus, Brachonchulus, Cobbonchus, Granonchulus, and Judonchulus. He repeated the elevation of Cobb's sub-genera to generic rank to give a total of eleven genera in the family. Andrassy's (1.c.) revision of Micoletzky's (1922) monograph was generally accepted and formed the basis for the large number of taxonomic publications that followed in the next decade.

Clark (1960a, b, c, d, e; 1961, a, b, c; 1962; 1963), in describing the New Zealand fauna, discussed aspects of mononchid taxonomy and evolution. He described two types of oesophago-intestinal junction within the Mononchidae and suggested that these were the expression of two major evolutionary trends that diverged early in Mononchid evolution (Clark, 1960a). The genera assigned to the two groups are recorded in Table 1. Clark further suggested that progressive reduction and eventual loss of the subventral teeth and denticles represented an evolutionary trend in both tuberculate and non-tuberculate groups (Clark, 1962).

Revising the order Enoplida, Clark (1961c) removed the Mononchidae from the superfamily Tripyloidea and established the superfamily Mononchoidea with two families, Mononchidae and Bathyodontidae. Clark (1960d, e; 1961b; 1963) dealt with the New Zealand fauna and described eleven new species (Table 2).

Mulvey (1961a, b; 1962; 1963a, b; 1967a, b) provided valuable reviews of the literature on nine genera, including a new genus Prionchuloides (Mulvey, 1963b). His papers provided the further descriptive information on species lacking in Andrassy's 1958 revision. Mulvey and Jensen (1967) described four new genera from Nigeria: Crassibucca, Hadronchus, Polyonchulus and Prionchulellus. Jensen and Mulvey (1968) reviewed the mononchid fauna of Oregon, and Mulvey (1973) that of Sable Island, Canada.

Table 2. Summary of recent (1931-1975) literature to illustrate the cosmopolitan distribution of the Mononchida, and the increase in described species.*

| Author** | Date | Location | Mononchids described or reported |
|---|---|---|---|
| Cassidy | 1931 | Hawaii | Mononchus cobbi, M.(Mylonchulus)hawaiiensis. 4 Mylonchulus spp., 2 Mononchus spp., and 1 sp. each of Clarkus, Iotonchus, Prionchulus reported. |
| Carvalho | 1951 | South America | Mononchus (Sporonchulus) ibitiensis |
| | 1955 | | M.(Iotonchus) risoceiae |
| | 1956a | | M.(Miconchus) soutoi |
| | 1956b | | M.(Sporonchulus) coronatus |
| | 1957 | | M. (Iotonchus) jairi |
| | 1960a | | M. (Cobbonchus) incultus |
| | 1960b | | M. (Iotonchus) piracicaboides |
| Williams | 1958 | Mauritius | Mononchus (Cobbonchus) mauritianus, 6 Mylonchulus spp., 2 Iotonchus spp., and 1 sp. of each of Clarkus, Miconchus, Mononchus, Prionchulus, Sporonchulus reported. |
| Altherr | 1958 | Germany | Mononchus (Clarkus) kastrolli, 1 sp each of Sporonchulus and Mylonchulus reported. |
| | 1960 | Cameroon | Mononchus (Cobbonchus) abrupticaudatus, 1 sp. of Iotonchus reported. |
| | 1963 | Argentina | Iotonchus arenicola, Cobbonchus regulus, 2 spp Mononchus and 1 sp Cobbonchus reported. |
| | 1968 | Germany | Mononchus sveltus, Anatonchus mamillatus, A.mulweyi, 2 spp. Mononchus, 2 spp Mylonchulus and 1 sp Anatonchus reported. |
| | 1971 | Rumania | Anatonchus filicaudatus, 2 spp Mononchus, 1 sp Mylonchulus and 1 sp Anatonchus reported. |
| | 1972 | Sweden | Mylonchulus longus, 1 sp. Mononchus, 1 sp. Iotonchus reported. |
| | 1974 | Germany | Anatonchus acultus, 1 sp. each of Anatonchus, Mylonchulus, Mononchus. |

*Where the specific name is given in full it represented a newly described species; where only the generic name is given it refers to previously-described species.

** Represents the authority for all new species

Table 2 (cont).

| Author | Date | Location | Mononchids described or reported |
|---|---|---|---|
| Altherr and Debouttéville | 1972 | U.S.A. | *Mononchus truncatus* reported; *Mononchus clarki*,* *Granonchulus auberti*, *Mylonchulus vulvapapillatus* and *My.boveyi* described. |
| Ameen | 1960 | Bangladesh | New (unnamed) genus and 1 sp. each of *Mylonchulus*, *Iotonchus*, *Mononchus* reported. |
| Clark | 1960c | New Zealand | *Mononchus (Clarkus) composticola*, *M. (Clarkus) mesadenus*, *M.(Clarkus) propapillatus*, 1 sp. *Prionchulus* reported. |
| | 1960d | | *Iotonchus basidontus*, *I.maragnus*, *I.ophiocercus*, *I.percivali*, 1 sp. *Iotonchus* reported. |
| | 1960e | | *Cobbonchus chauliodus*, *C.pounamua*. |
| | 1961b | | *Mylonchulus arenicolus*, *M.ubis*. |
| | 1963 | | *Anatonchus killicki*, *Cobbonchus australis*, 4 spp. *Mononchus*, 3 spp. *Mylonchulus*, 1 sp. *Prionchulus*, 1 sp. *Cobbonchus*, 4 spp *Iotonchus* reported. |
| Loof | 1964 | Venezuela | *Mononchus (Clarkus) venezolanus*, 2 spp. *Clarkus*, 1 sp. *Miconchus* and 1 sp. *Mylonchulus* reported. |
| | 1973 | Surinam | *Mononchus tunbridgensis* reported. |
| Coomans and Lima | 1965 | Italy | *Anatonchus amiciae*. |
| Buangsuwon and Jensen | 1966 | Thailand | *Iotonchus ainostomos*, *I.bangkokensis*, *I.chantaburensis*, *I.rayongensis*, *I.thailandensis*, *Miconchus triodontus*, 4 spp. *Mylonchulus* and 1 sp. *Iotonchus* reported. |
| Yeates | 1967 | New Zealand | *Miconchus kirikiri*, *M.reflexus*, *Mylonchulus psammophilus*, 1 sp. of *Iotonchus* and 1 sp. of *Mylonchulus* reported. |

*Synonymised with *M.truncatus* (Small and Grootaert, in press).

Table 2 (cont)

| Author | Date | Location | Mononchids described or reported |
|---|---|---|---|
| Heynes and Lagerwey | 1965 | S.Africa | Iotonchus pauli, I.geminus, I.transkeiensis. |
| Coetzee | 1965 | S.Africa | Cobbonchus eurystoma, C.heynsi, C.dianae, C.ockerti, 1 sp. Cobbonchus reported. |
| | 1966a | | Granonchulus subdecurrens, Cobbonchus charlesi, C.megalus, 1 sp. Granonchulus and 1 sp. Cobbonchus reported. |
| | 1966b | | Mylonchulus cereris, M.agriculturae, 3 spp. Mylonchulus reported. |
| | 1967 | | Iotonchus antedontoides, I.litoralis, I.rinae, I.spinicaudatus, 1 sp. Iotonchus reported. |
| | 1968a | | Mononchus (Clarkus) parvulus, M.(Clarkus) pretorensis, Mononchus (Clarkus) jugalis, M.aquaticus, 2 spp. Mononchus, 1 sp. Prionchulus reported. |
| | 1968b | | Cobbonchus artemisiae, C.thesigeri, C.rotundicaudatus, 3 spp. Cobbonchus, 4 spp. Mylonchulus, 2 spp Mononchus and 1 sp Granonchulus reported. |
| Mulvey and Jensen | 1967 | Nigeria | Crassibucca penicula, C.macrocauda, C.microdonta, Hadronchus bisexualis, H.monohystera, Iotonchus acuticaudatus, I.clarki, I.nigeriensis, I.parabasidontus, I.tarjani, Miconchus parrapax, M.thornei, Mylonchulus curvicaudus, Polyonchulus cobbi, P.medadontus, Prionchulellus cavenessi, 7 spp Mylonchulus, 4 spp. Iotonchus, 2 spp. Mononchus and 1 sp each of Granonchulus, Sporonchulus and Miconchus reported. |
| Jensen and Mulvey | 1968 | Oregon State, U.S.A. | Mylonchulus excacutus, M.bulbiferous, M.orbitus, Miconchus oregensis, Iotonchus ovatus, 8 spp Mylonchulus, 4 spp. Mononchus and 2 spp each of Prionchulus, Anatonchus and Miconchus reported. |
| Jairajpuri | 1969 | India | Hadronchus andamanicus, H.shakili, Iotonchus baqrii, I.indicus, Miconchus dalhousiensis, 1 sp of Iotonchus and 1 sp of Miconchus reported. |

Table-2 (cont)

| Author | Date | Location | Mononchids described or reported. |
|---|---|---|---|
| Jairajpuri | 1970a<br>1970b<br><br>1971 | India | 2 spp Clarkus and 1 sp each of Mononchus, Iotonchus and Prionchulus reported.<br>Mylonchulus mulveyi , M.dentatus , M.nainitalensis , M.muradi , M.contractus , 5 spp Mylonchulus reported.<br>Sporonchulus vagabondus . |
| Kirjanova and Krall | 1969 | Ukraine, U.S.S.R. | Tigronchus tauricus. |
| Ali, Farooqui and Tejal | 1970 | Kashmir | Prionchulus muscorum reported. |
| Lordello | 1970 | Brazil | Sporonchulus paucidentatus , 5 Iotonchus spp, 4 Mylonchulus spp, 3 Mononchus spp, 3 Sporonchulus spp and 1 sp each of Cobbonchus, Miconchus and Prionchulus reported. |
| Thong | 1970 | Singapore | Hadronchus yuenae , Iotonchus microdontus, 2 Iotonchus spp and 1 Mylonchulus sp reported. |
| Mulvey and Dickerson | 1970 | Kansas State, U.S.A. | Miconchus kansasensis. |
| Yokoo | 1970 | Japan | Branchonchulus sp. and Mylonchulus sp. reported. |
| Razzhivin | 1971 | Dzhungarian Alatau | Mylonchulus silvaticus , M.caespitosus , Iotonchus laticupulatus. |
| Andrassy | 1972 | Congo Republic | Margaronchulus mulveyi. |

Table 2 (cont).

| Author | Date | Location | Mononchids described or reported |
|---|---|---|---|
| Eroshenko | 1972 | Primorsk Territory U.S.S.R. | Clarkus arvensis, C.obliquoris, Mononchus fusiformis, M.scutarius. |
| | 1975 | | Clarkus silvius, C.scopulosus, Iotonchus acuticaudatus, I.cobbi, I.monticola, I.mucronatus, I.paraamphigonicus, Miconchus eurinus, Prionchulus medius, P.vescus. |
| Baqri and Jairajpuri | 1973 | El Salvador | Actus salvadoricus, Paracrassibucca jenseni, 6 spp Mylonchulus, 3 spp Miconchus, and 2 spp Iotonchus reported. |
| Mulvey | 1973 | Sable Island, Canada | 1 sp. Anatonchus, 3 spp Mononchus, 3 spp Mylonchulus, 2 spp Prionchulus reported. |
| Spaull | 1973 | Antartic | 1 sp Clarkus reported. |
| Zullini | 1973 | Nepal | 1 sp of Mononchus, Clarkus and Prionchulus reported. |
| Tsalolichin | 1974 | Lake Baikal, U.S.S.R. | Tectonchus absconditus. |

The mononchid fauna of Southern Africa formed the subject of several papers between 1965 and 1968. Heyns and Lagerwey (1965) described the representatives of the genus Iotonchus, including three new species. Six mononchid genera were discussed by Coetzee (1965; 1966a, b; 1967; 1968a, b) which included twenty-nine new species (Table 2).

Other papers published in the period 1960-1976 continued to reveal the cosmopolitan distribution of mononchids (Table 2). Some species (e.g. Prionchulus muscorum (Dujardin 1845) Wu and Hoeppli, 1929 are themselves widely distributed, but often new localities revealed new species of mononchids, suggesting that the group has undergone considerable speciation in the course of its evolution. Table 2 presents these species in some detail, partly because existing lists are out-dated and partly because the selection of particular species from particular localities may have consequences for future biological-control studies; these consequences will be discussed later (Section V).

The first descriptions of the Indian mononchid fauna were by Kannan (1960; 1961a, b, c) but the quality of the papers does not inspire confidence in the descriptions and both Mulvey (1967a) and Jairajpuri (1969) considered these descriptions inadequate, particularly those pertaining to "races" of known species. Jairajpuri (1969; 1970a, b; 1971) has done much to rectify this position and one of the most important contributions was the erection of the order Mononchida Jairajpuri 1969, which reflected the considerable increase and species described over the previous ten years. Baqri and Jairajpuri (1972) confirmed the validity of Mononchus aquaticus Coetzee 1968 and later the same authors described two new genera from El Salvador, Actus and Paracrassibucca (Baqri and Jairajpuri, 1973). Jairajpuri (1970a) proposed the division of the genus Mononchus (sensu lato) into two genera, Clarkus and Mononchus (sensu stricto) and later proposed the genus Coomansus to accommodate a further subdivision of the genus Clarkus (Jairajpuri, 1977).

Currently the order Mononchida is divided into the superfamilies Bathyodontoidea and Mononchoidea; the latter is arranged into five families: Mononchidae, Mylonchulidae, Cobbonchidae, Anatonchidae and Iotonchidae (Jairajpuri, 1969). Approximately 180 species in twenty-five genera have been described.

Mononchid Morphology and Physiology.

Most of the details of mononchid morphology are contained in the taxonomic publications which have been reviewed but some papers have dealt specifically with aspects of mononchid morphology. Embryonic and juvenile development of mononchids in culture has attracted some attention but very little information on the physiology of these nematodes is available.

Grootaert (1976b) described the ultrastructure of the head and buccal capsule of Mononchus aquaticus as having six lips bearing sixteen papillae which are associated with ciliary receptors. The stoma can be considered in three parts of which the anterior (bearing the dorsal tooth) and posterior parts consist of three jointed plates; in the mid-part the plates are fused. Grootaert (1976b) also noted that the cuticle followed the typical dorylaimid pattern which reflects the description by Mahadevan (1974) on Prionchulus muscorum. Matthews and Croll (1974) figured a scanning-electronmicrograph of the head of Prionchulus punctatus (Cobb 1917) Wu and Hoeppli 1929, which has a slit-like amphidial opening (see also Figs 2, 3).

Chitwood and Chitwood (1937) described the histology of the oesophagus of P.muscorum and Clark (1960a) distinguished two oesophago-intestinal junctions in mononchids, characterised by the presence or absence of tubercules at the junction. Chitwood and Chitwood (1950) and Clark (1960a) described other details of the mononchid oesophagous. Goodey (1942) described the anatomy of Mononchus (Anatonchus) tridentatus (de Man, 1876) de Coninck 1939, M. (Mylonchulus) brachyuris (Buetschli 1873) Altherr 1953 and other mononchid

Fig. 2 Scanning electron micrographs of the head region of Prionchulus punctatus adults.




a) Lateral view showing amphidial opening (a), labial papillae (p) and buccal plates (b) (x2500).




b) Dorso-lateral view of P.punctatus ingesting tail region of Panagrellus redivivus (P.r.) (x2640)

Fig.3 Scanning electron micrographs of Prionchulus punctatus fixed whilst feeding of Panagrellus redivivus.




a) Ingestion of body contents (b) showing collapse of body wall of P.redivivus (c) opposite site of attack (x1595)




b) Release of prey showing extruded body contents of P.redivivus (e) (x1370)

species, and is particularly useful for the details of the female reproductive tracts. Coomans and Lima (1965) described the male reproductive tract of Anatonchus amiciae Coomans and Lima 1965 in detail. Cassidy (1933) and Mulvey (1963c) both recorded bivulvular specimens of Prionchulus muscorum.

Jairajpuri and Khan (1975) described the excretory system of Prionchulus muscorum as consisting of a pair of renette cells leading into a pair of ducts that fuse to form an ampulla. The ampulla empties via the excretory pore. Jairajpuri, Azmi and Bajaj (1974) investigated the tolerance of Mylonchulus minor to pH and salt-concentration in vitro and found that it had a narrow pH optimum (5.6-6.4). The survival time of M.minor in various salt solutions was generally less than for the plant-parasitic species tested.

Grootaert and Maertens (1976) considered that the excretory system was involved in the moulting process of mononchids: at the moment of ecdysis in M.aquaticus the excretory pore became prominent and a fluid was released to form a transparent vesicle between the old and new cuticles. The vesicle acted as a point of flexure during the movements of the juvenile that finally caused the old cuticle to split at the level of the vesicle. The juvenile emerged from the old cuticle through this split.

Grootaert and Maertens (1976) also described the embryology of M. aquaticus which was similar, although slightly faster, to that of P.punctatus (Maertens, 1975). In P.punctatus the first division of the ovum occurred after seven hours and was followed by a rapid series of divisions until the blastula stage was reached 23 hours after oviposition. The tadpole stage was reached 16 hours later, followed by a period of growth until the first stage juvenile hatched 7 days after oviposition. Similar observations have been made on Clarkus sp. (Yokoo, Yasunaga and Yokoo, 1973). Jones (1977) used data from Grootaert and Maertens (1976) to calculate the temperature-rate curve and accumulated temperature necessary for the completion of the various life-stages of M.aquaticus.

Some details of the post-embryonic development of mononchids were recorded in the three studies that dealt with embryology; in addition, Coomans and Lima (1965) described the juvenile development of Anatonchus amiciae including the changes in dentition which occurred with successive moults; these differed from those described for Anatonchus tridentatus (Mulvey, 1961b). In A.tridentatus the teeth were directed anteriorly in first stage juvenile but became retrorse during the first moult; subsequent stages had retrorse teeth which assumed the adult position during the last moult. A.amiciae first and second stage juveniles had a single, functional, anteriorly-directed tooth that became retrorse during the second moult; the position of the teeth in fourth stage juveniles was variable.

Overgaard-Nielsen (1949), Klekowski et al (1972) and Yeates (1973) have estimated the oxygen consumption of mononchid nematodes; Clarkus papillatus (Bastian 1865) Jairajpuri 1970 is the only species common to all three publications and comparison is hampered by the differences in mean individual weights used by the authors, presumably resulting from the different methods used to estimate these weights. Overgaard-Nielsen (1949) used a mean weight of 5µg to calculate an oxygen consumption for C.papillatus of 850 ml $O_2$/kg/hr at 16°C but later considered that he had over-estimated the weight of the nematodes (Overgaard-Nielsen, 1967). The oxygen consumption of C.papillatus more than doubled over the temperature range 15°-25°C (Overgaard-Nielsen, 1949). Klekowski et al (l.c.) calculated a respiratory rate of 4.30µl $O_2 \cdot 10^{-3}$/individual hr but recorded a weight of 5.22µg for C.papillatus whereas Yeates (1973) used a weight of only 0.822µg. Individual oxygen consumption was not calculated but the annual oxygen consumption of a C.papillatus population in a Danish beech forest was 109 ml $O_2/m^2$ (Yeates, 1973).

Overgaard-Nielsen (1949) also calculated oxygen consumption rates of 1010 ml/kg/hr and 850 ml/kg/hr for Mononchus macrostoma Bastian 1865 and Mylonchulus brachyuris (Buetschli 1873) Altherr 1953 respectively (16°C; 5µg for both species). Yeates (1973) calculated an annual oxygen consumption

of 131 ml $O_2/m^2$ for a Prionchulus muscorum population (5.441 µg mean individual weight). All the authors agreed that mononchid respiration per unit biomass was greater than for most nematodes and Klekowski et al (l.c.) suggested that the greater respiratory rate was linked to the greater activity of predators when searching for prey.

The ability of predators to detoxify pesticides may be crucial to their use in integrated or biological control programmes. Nelmes and McCulloch (1975) found that mononchid numbers decreased in oxamyl-treated soils, juveniles being particularly susceptible. Phorate treatments did not significantly reduce the mononchid population but the nature (physiological, behavioural, etc) of this apparent resistance to phorate is not understood. Martin and Yeates (1975) found that the insecticides Fensulfothion, D.D.T., Carbofuran and Fenitrothion reduced the total nematode population by 50% but Tylenchus spp. and mononchids by a greater proportion. Recovery from the insecticide treatments was also slower in these two groups, with the effect of Fensulfothion still apparent after 56 weeks.

## Ecology of Mononchids.

Few studies have dealt specifically with the ecology of predatory nematodes. Much of the literature deals with general nematode ecology and often attempts to relate numbers, biomass or species composition with soil types of plant communities. Mononchids are frequently summarily dismissed as too few for consideration; their low numbers may make detailed analysis difficult but their large biomass and activity may produce an effect disproportionate to their numbers. Distribution of predatory nematodes may be influenced by two main factors: i) food and ii) physico-chemical properties of the environment.

i) Feeding relationships. Table 3 represents the positive results recorded by Szczygiel (1971) in a study of the gut contents of fifteen

mononchid species recovered from agricultural soils in Poland. The other species had no recognisable nematode remains in the gut, and the results for M.truncatus Bastian 1865 were based on a single specimen that contained two members of the Tylenchoidea. Szczygiel did not record the relative abundance of the prey groups in the soils so that prey selection can only be judged comparatively; P.muscorum and Anatonchus sp. would appear to have fed more on the phytoparasitic groups than the other mononchids. Cuany (reported in Ritter and Laumond, 1975) found that Anatonchus spp. selectively prey on Oxydirus spp. and Alaimus spp. under natural conditions.

Table 3. Percentage prey groups in the gut of some mononchid species (Szczygiel, 1971).

| | Percentage prey groups in gut | | | | |
|---|---|---|---|---|---|
| Mononchid species | Tylenchoidea | Dorylaimoidea | Rhabditoidea | Mononchida | Aphelenchoidea |
| Anatonchus tridentatus | - | - | 38 | - | 62 |
| A.ginglymodontus | 7 | - | 61 | 32 | - |
| Anatonchus sp. | 65 | - | 15 | 10 | 10 |
| Prionchulus muscorum | 55 | 10 | 10 | - | 25 |
| Mononchus truncatus | 100 | - | - | - | - |

In studies on the nematode fauna of dune sands Yeates (1967, 1968) recovered eight predatory species of which Nygolaimus directus Heyns 1968, Mylonchulus striatus (Thorne, 1924) Altherr 1953, M.psammophilus Yeates 1967 and Miconchus reflexus Yeates 1967 correlated most significantly with the distribution of their enchytraeid prey. In contrast, Synonchium pacificum Yeates 1967 and Enoploides sp., also predators of enchytraieds, correlated more closely with moisture, temperature, pH, salinity and organic residue. Nelmes and McCulloch (1975) could not detect a relationship between the numbers of predators and the number of potential prey

nematodes in soil under pasture.

Overgaard-Nielsen (1948) recorded juvenile Mononchus (Clarkus) papillatus apparently feeding on the alga Coccomyxa sp. and also maintained C.papillatus on the bacterium Micrococcus sp. for 29 days in the laboratory, but no eggs were deposited during this period. It was not stated that the nematodes were observed ingesting the bacteria and, as adult mononchids are able to withstand periods of starvation exceeding six weeks (Nelmes, 1974), the value of Overgaard-Nielsen's observation seems doubtful.

Boag (1974), studying nematodes in woodland sites, found significantly larger numbers of predators and species of Rotylenchus, Paratylenchus, Pratylenchus, Helicotylenchus and Tylenchorhynchus in sites with undergrowth. These genera may be suitable prey and so support a larger population of predators than elsewhere, although the hoplolaims appear resistant to predation (Esser, 1963; Nelmes, 1974; Cohn and Mordechai, 1974).

Yuen (1966) found greater numbers of predators in woodland than in grassland (21/100 g soil and 13/100 g soil respectively) and considered that vegetation was the major influence on the nematode fauna. Presumably the vegetation has an indirect effect on the predators through their prey; the species composition was similar in the two sites but the relative abundance of the principal trophic groups varied markedly. Calculations based on Yuen's data indicated that in grassland phytoparasites constituted 57% of the nematodes and bacterial feeders 18%, compared to 35% and 47% respectively in the woodland. This suggests (assuming that food is the major determinant of mononchid abundance in two sites chosen for their similar physico-chemical properties) that bacterial feeders can support a larger predator population than plant-parasites. It is not possible to determine whether this is due to a) prey selection by the predators or b) provision of a more suitable diet by bacterial feeders or c) greater turnover of bacterial feeders.

Total numbers of nematodes does not seem important as fewer were found in woodland (2376/100 g soil compared to 3311/100 g soil). Plant-parasites may be less satisfactory as prey because endoparasitic species are protected from attack once in the roots and ectoparasitic species may possess defensive mechanisms such as thick cuticles (Criconematidae) or possibly chemical repellents (e.g. Helicotylenchus; Esser, 1963; Nelmes, 1974; Cohn and Mordechai, 1974).

Twinn (1966) suggested that mononchids supplement their diet with small animals other than nematodes because he found that the mononchids had a biomass of 212µg/90 g soil and the other trophic groups a total biomass of 330µg/90 g soil. These figures represent standing-crops and Twinn appeared not to take account of the relative production of the two groups, which would enable more predators to be supported.

ii) Abiotic factors. Thorne (1927) recorded numbers ranging from "a few" to $3 \times 10^8$ mononchids per acre in sugar-beet fields in Utah and Idaho. He concluded that temperature was the most important ecological factor governing the populations because Mononchus (Mylonchulus)parabrachyuris (Thorne 1924) Altherr 1953 females were not gravid at temperatures below 10°C whereas My.sigmaturus (Cobb 1917) Altherr 1953 were gravid at 2.5°C but not when the soil was frozen. High summer temperatures also prevented reproduction. Thorne believed that vertical migration occurred in response to changes in temperature, and to a lesser extent soil-moisture, which only became critical when it decreased to 7-8% by weight. The topmost two inches of soil were always avoided by mononchids.

Arpin (1969, 1975a) however, demonstrated that mononchids are particularly susceptible to desiccation. A reduction in soil water from 75% to 18% resulted in 100% mortality of the predators, compared to 90-85% of the bacterial feeders and 7-0% of the plant-parasitic nematodes. Arpin (1975b) found that Clarkus papillatus and Prionchulus muscorum were

restricted to the topmost 2.5cm of soil at a site in the Sênart Forest; at Brunoy Park these species occurred at depths upto 10cm as did Mylonchulus brevicaudatus (Cobb, 1917) Altherr 1953, Anatonchus tridentatus and Miconchus studeri (Steiner 1914) Andrassy 1958. Arpin considered that this reflected the fertile basic soil with greater microbial activity and more diverse nematode fauna at the Brunoy Park site compared with the acidic (pH3) soil with less microbial activity and restricted nematode fauna in the Sênart Forest.

Szczygiel (1971) recovered a total of fifteen mononchid species from fruit tree nurseries, strawberry plantations and carrot fields in Poland. Where sufficient numbers occurred they were related to several abiotic factors. Soil texture appeared important for Mylonchulus spp (associated with lighter soils) and Anatonchus spp (associated with mixed soils) but not for Clarkus papillatus, Prionchulus muscorum or Miconchus studeri. Only P.muscorum and Anatonchus sp. were associated with wetter soils; all species were more common in soils of pH 7 approx., although C.papillatus occurred in soils with a pH as low as 4.5-5.5. All species except Mylonchulus incurvus (Cobb 1917) Altherr 1953 showed a positive correlation between their numbers and percentage organic matter. P.muscorum was associated with older strawberry plantations and M.incurvus with younger strawberry plantations.

In a study of the nematode fauna of moorland soils (Banage 1962, 1963) recorded five mononchid genera but numerically predators never represented more than 1% of the nematode fauna. The greatest number of predators were found in mineral soils under grassland and most genera were associated with particular pH ranges: Prionchulus 4.8-5.8, Anatonchus 4.9-5.8, Miconchus and Iotonchus 4.8-5.0. Only Mononchus occurred over the full pH range (3.4-5.8).

Twinn (1966) compared mull and moder woodland over two years; the former had a greater diversity of predatory species (C.papillatus,

Anatonchus, Nygolaimus, Aporcelaimus, Seinura and Tripyla) than the latter (P.punctatus and Seinura). The number of predators was greatest in mineral soil, with fewer in old leaf litter and none in new leaf litter. In the mull soil predators (combined with miscellaneous feeders) reached a numerical maximum in July (220 per 10g. dry soil) when they formed about 50% of the total nematode population. The other trophic groups had peaks in spring and autumn so that the three month interval may represent the delay (caused by the length of the life cycle of the predators under those conditions) in the response of predator numbers to increased prey density. Predator biomass never fell below 60µg per 10g dry soil and in July reached 200µg per 10g dry soil; the combined biomass of the remaining nematodes never exceeded 65µg per 10g dry soil, which may again reflect the respective production of prey and predator. Predators at the moder site occurred "sporadically" and were recovered only in spring. The maximum biomass of predators was 20µg per g. dry litter (March in dry ash litter and November in dry oak litter) representing 21% of the total nematode biomass. P.punctatus constituted 99.8% of the predators' biomass.

Boag (1974) found mononchids in 46% of all woodland sites sampled; they occurred more frequently in deciduous woods (42-81% of samples) than coniferous woods (23-40% of samples). This preference was also reflected in the numbers of individuals: 16-49 per 200g soil (≡ 6% of the total nematode population) in deciduous woods and 7-23 per 200g soil (≡ 3% of the total nematode population) in coniferous woods. Mononchid numbers and distribution did not correlate with soil type, moisture or altitude but showed a significant correlation with pH, the greatest numbers and incidence occurring at pH 5-5.4 in a pH range of 3.0-7.5. The preference for sites with undergrowth has been discussed above.

McCulloch (1973) compared the mononchid fauna of a grass ley and an adjacent ploughed plot. Five species were recovered but mononchids usually

represented less than 1% of the total nematode population. Nelmes and McCulloch (1975) added data from plots planted to barley. The study extended over several months and included details of the life-stages; peak numbers of juveniles occurred in the summer months for C.papillatus (particularly in June), A.tridentatus and M.sigmaturus. The percentage of gravid females did not vary greatly in the period April-November.

Probably the most comprehensive study of nematode ecology is that of Overgaard-Nielsen (1949) who compared the fauna of many soil types and plant communities over several years. Mononchids occurred in about 50% of the sites but were more often recovered from pastures than from moorlands. Numerically predators represented a mean of 4.6% of the fauna at those sites in which they were present, but 12.6% of the nematode biomass and 11% of the nematode respiration. Predators were particularly common in a moss-covered beach where they constituted 25% by numbers, 54% by biomass and 50% of the nematode respiration. A previous publication (Overgaard-Nielsen 1948) had also demonstrated that mononchids were particularly abundant in moss-cushions. The two species C.papillatus and Mylonchulus brachyuris comprised upto 17% of the fauna; surprisingly Overgaard-Nielsen dismissed Rahm's (1924) similar figure of 20% mononchids in the moss-cushion nematode fauna as being based on too small a sample.

Yeates (1972, 1973) recovered three mononchid species from a Danish beech forest, although P.muscorum and Iotonchus sp. were generally less than 1% of the total nematode population. C.papillatus represented 2.56% of mean total numbers but 7.58% of the biomass and 7.59% of nematode respiration; corresponding figures for P.muscorum are 0.47%, 9.26% and 9.12% respectively, again illustrating that the small numbers of mononchids have a disproportionate biomass. C.papillatus numbers showed maxima in April and July/August; the population of this species approached 40,000 per $m^2$ at these times but between the peaks declined to 5,000 per $m^2$, the minimum for the whole year.

Oteifa and Elgendi (1967) studied predatory nematodes in organically

manured soils. The mononchids (Iotonchus, Miconchus, Mononchus and Mylonchulus) were rare in soil treated with farm-yard manure and absent from poudrette and sewage treated soils; only Mononchus occurred in soils treated with stable manure. The occurrence of mononchids in untreated soils was not recorded. The fourteen dorylaimid genera also present in these soils were more variable in their distribution but most were present in at least two of the four treatments (Oteifa and Elgendi, 1967). Dorylaimids were most common in farm-yard manured soils (38.6% on the authors' General Frequency Index) followed by stable-manure treated soils (25.7%), poudrette treated (21.4%) and sewage treated (14.3%).

Detailed knowledge of mononchid ecology is lacking and often their contribution to total nematode populations in terms of biomass is underestimated. Mononchids occur in most soils and can be amongst the dominant species of some specialised habitats such as moss. The preference for moss as a habitat is surprising in view of Arpin's (1975a) results on mortality in dry soils, but may indicate that only some species have adapted to the extreme conditions of the moss environment. More generally mononchids rarely exceed 5% of nematode numbers but represent about 10% of nematode biomass and respiration.

Few studies have shown whether the variation in numbers with time is regular over several years, and the dates of recorded maxima and minima vary markedly between sites. Soil type and pH appear to influence distribution but many of the studies have involved only acid soils. Only Szczygiel (1971) studied agricultural soils of approximate pH 7 and he concluded that mononchids were more frequent in these soils; all the studies indicated that mononchids were most frequent in soils near the upper end of the pH ranges studied.

The prevalence of mononchids suggests that they are able to live and reproduce in many soils. The extent to which they feed upon nematodes, and especially plant parasitic nematodes is not known but the development

of culturing techniques will enable laboratory studies to elucidate the relationships between predators and their prey.

## Culture of Predatory Nematodes

The culture of free-living nematodes, particularly rhabditids has been reviewed by Dougherty and Calhoun (1948), Dougherty (1960) and Nicholas (1975). The paucity of successful methods for the culture of predatory nematodes (except possibly the diplogasterids) prevented their inclusion in these reviews.

Most laboratory studies on predators concerned embryonic and juvenile development (Table 40) with some observations on feeding habits, but even so knowledge of these processes is incomplete and restricted to a few species. Population development has been largely ignored, probably due to the lack of long-term culture techniques. Predator culture media have steadily increased in complexity but, unlike those for rhabditids, remain xenic and oligidic; modification of present techniques has only recently been attempted. The present study sought improvements in mononchid culture, and it is hoped that comparative studies will indicate those predators that can be cultured in large numbers so that, if their use in the biological control of plant parasitic nematodes becomes feasible, lack of predators will not further delay trials.

Steiner and Heinly (1922) were the first to attempt culture of predatory nematodes; Clarkus papillatus were placed in i) water droplets, ii) water droplets with added soil, iii) sterilised soil and iv) agar containing germinating seeds to act as a food source for the phytoparasitic nematodes used as prey. Suitable prey species included Heterodera spp, Rhabditis spp and Turbatrix aceti (Müller 1783) Peters 1927. Predators completed their life cycle only in soil and the best artificial medium contained some soil. The authors emphasise that soil is essential to the

predators, especially the first stage juveniles which were observed to ingest soil particles; in the absence of soil juveniles died within a few days of hatching. Reproduction was reduced in media containing only small amounts of soil, and no eggs were laid in water without soil. The life cycle (egg to egg) required 6-7 weeks in water plus soil but only 4-5 weeks in soil; a standard temperature was maintained but not specified. Moulting was not regularly recorded.

Cassidy (1931) attempted culture of Mylonchulus sigmaturus and Mononchus (Iotonchus) brachylaimus (Cobb 1917) Altherr 1950 using the techniques of Steiner and Heinly (1922). No success was forthcoming with My. sigmaturus: in sterile water a few prey Tylenchus (Rădopholus) similis (Cobb 1893) Thorne 1949 and Heterodera radicicola (Meloidogyne sp.) were eaten but all predators died within four days. In tap-water or sterile water plus soil the predators died within 24 hours following rapid growth of the bacterial population. Some I.brachylaimus survived for twelve weeks under similar conditions but Cassidy believed their behaviour to be abnormal, resulting from the unsuitable media. Feeding soon decreased and eggs were deposited only during the first three days of culture. In one culture the predators became "inert and listless" after four weeks but remained alive for a further seven weeks.

Esser (1963) placed populations of soil nematodes on water agar plates and found that survival time varied considerably between groups: mononchids entered the agar rapidly but many became quiescent within 5-10 minutes and remained in the same coiled position until dead. The remainder fed but did not reproduce, surviving for only 4-6 days, the shortest period for any nematode group. Predacious dorylaims adapted best to the agar cultures and reproduced well. Predacious aphelenchs deposited eggs which developed normally and hatched, but all died within a week.

Ferris (1968) used a similar technique to establish cultures of

Labronema spp; nematodes were allowed to migrate from the natural substrate placed in the centre of a petri dish into the surrounding 1% water agar. These were supplemented with nematodes extracted from larger quantities of the soil. Both Labronema spp. fed on all the saprophagous nematodes placed in the cultures and completed their life cycles in 3-4 months (L.ferox Thorne 1939) or 5-6 months (L.thornei Ferris 1968). New cultures were established by transferring the larger juveniles to new agar and adding prey, but a fungus weft appeared necessary for the females to deposit eggs (Ferris, 1968).

Mankau (1975) concentrated the nematodes from 10g of soil onto a 2.4cm filter paper which was then placed in the centre of a cornmeal agar plate. Populations of bacterial-and fungal-feeding nematodes developed rapidly whereas populations of predatory nematodes developed more slowly over several weeks. Mankau (pers.comm.) suggested the use of water agar and larger soil samples would be better suited to the culture of predacious nematodes by this method.

Before reviewing the culture methods available for mononchids similar to those used in the present study it is useful to survey methods of culture of predatory nematodes from other taxonomic groups. Hechler (1963) cultured Seinura tenuicaudata (de Man 1895) Goodey 1960 by transferring a few females to a culture of Aphelenchus avenae Bastian 1865 feeding on the fungus Pyrenochaeta terristris. Hechler and Taylor (1965; 1966a, b) used the same technique to culture several Seinura spp., some of which have a much contracted life-cycle since there are more within-egg moults (Table 40). The shortened generation time which results may have favourable implications for the use of these species as biological control agents.

Several diplogasterids have been cultured but as many are facultative predators the cultures are often first established on bacteria or bacteria/amoebae cultures. Pillai and Taylor (1968a) cultured Butlerius micans Pillai and Taylor 1968 on either Aerobactor aerogenes/Naegleria gruberi

cultures or by supplying the predators with Aphelenchus avenae, Panagrolaimus spp. or Rhabditis spp. Pillai and Taylor (1968b) cultured Mononchoides spp., Fictor anchicoprophaga (Paramonov 1952) Goodey 1963 and Butlerius sp. using the same two food sources but, in contrast, Labronema ferox and Mononchus sp. could only be cultured in the presence of other nematodes. Butlerius monhystera Taylor 1964 fed on nematodes but failed to become established in culture on A.avenae (Taylor, 1964).

Yeates (1969) maintained the facultative predator Mononchoides (Diplenteron) potohikus (Yeates, 1969) Yeates 1969 on Bacillus cereus var. mycoides cultured on asparagine-mannitol agar, but the nematode reproduced only when provided with a diet including nematodes. Eleven species of nematode were suitable as prey and mixed populations of these did not induce selective predation by the predators. Predation was also independent of the presence of old tracks of the prey, presence of a bacterial film and predator satiation, but it was dependent on prey-density. Contaminants such as water, agar from the stock-culture or patches of bacterial growth therefore caused significant changes in predation by inducing localised differences in prey-density. Male D.potohikus had greater predation rates than females, probably because they exhibited greater motility (related to mate finding) and so encountered more prey. Facultative predators may have an advantage as biological control agents in situations where plant-parasitic nematodes are periodically scarce or absent.

Nelmes (1974) cultured Prionchulus punctatus (Fig.1) on a soil-extract agar which Springett (1964) had used to culture Enchytraeidae. Nelmes did not investigate culture methods per se,but maintained the predators in culture to observe feeding behaviour. When Aphelenchus avenae were offered as prey there were few encounters and even fewer successful attacks by the predators. Unlike D.potohikus, successful attack was independent of prey density and predator satiation. Rapid ingestion of entire small juvenile prey contrasted with the slow, incomplete ingestion of larger juveniles and adults; Nelmes concluded that juvenile prey were

a better food source in terms of energy ingested per unit feeding time. Estimates suggested that P.punctatus adults ingested upto six times their own volume in prey per day.

Maertens (1975) studied the biology and life-cycle of P.punctatus at a range of temperatures using cultures supplied by Nelmes (pers.comm) (Table 40). The culture technique was successfully applied to Mononchus aquaticus and similar studies of this species have been completed (Grootaert and Maertens, 1976). The humus-extract used by Maertens (1975) for the P.punctatus culture medium was unnecessary for M.aquaticus (Grootaert and Maertens, 1976). Other predatory nematodes which have been cultured by the same basic method are Butlerius sp., Labronema sp., Aporcel aimellus sp. and Neoactinolaimus duplicidentatus (Andrassy 1968) Andrassy 1970 (Grootaert, pers.comm).

Maertens (1975) used five species as prey: Caenorhabditis briggsae (Dougherty and Nigon 1949) Dougherty 1953, Panagrellus redivivus (Linnaeus 1767) Goodey 1945, Turbatrix aceti, Eucephalobus striatus (Bastian 1865) Thorne 1937 and Mesodiplogaster lheritieri (Maupas 1919) Goodey 1963. The generation time of P.punctatus ranged from 200 days at 10°C (used by Maertens for holding stock-cultures) to 37 days at 22°C (used for mass cultures) but lengthened again to 47 days at 25°C (Maertens, 1975). The first moult occurred 4-5 days after hatching but subsequent moults were not recorded. Similar prey were used for the culture of M.aquaticus (Grootaert and Maertens, 1976); the generation time was considerably shorter than for P.punctatus (90 days at 10°C and 14-15 days at 28°C); embryonic development was similar.

Cultures of P.punctatus were sent to J.C.Cayrol who used Rhabditella axei (Cobbold 1884) Chitwood 1933 as prey; this nematode multiplied so rapidly that the predators were overwhelmed and further attempts to maintain cultures have been unsuccessful due to bacterial contamination (Cayrol, pers.comm.).

Thus early attempts at culturing predatory nematodes were failures, at best only maintaining a few nematodes for short periods. Later methods involving agar plates have met with more success but many problems remain unsolved; mononchids in particular appear sensitive to bacterial and fungal metabolites. No one has yet developed a continuous culture system, in which prey also actively reproduce, for mononchids. Such a system would be one approach to the commercial production of predators should this prove desirable in the future.

## Predatory Nematodes as Biological Control Agents

Since Cobb (1916) first found some mononchids to be predators of plant parasitic nematodes and therefore beneficial to man, the idea of using mononchids as biological control agents has attracted the imagination of the majority of authors who have written about these predators, but has led to remarkably little published experimentation.

In 1920 Cobb formulated proposals for the "transference of nematodes (mononchids) from place to place for economic purposes". The only attempts at such transfers are by Thorne, (1924, 1932b) who transferred colonies of Iotonchus amphigonicus (Thorne 1924) Altherr 1950 to sugar beet fields to attempt control of H.schachtii Schmidt 1871; two years later the predator was still present in low densities (Thorne, 1924). Thorne (1932b) described the transference of Clarkus papillatus, Prionchulus muscorum and I.amphigonicus from Utah to California to learn if the predators would control Caconema radicicola (Meloidogyne sp) in a date garden. The predator population was successfully established but no indication of the predator's effect on the pest nematode was recorded.

Steiner and Heinly (1922) studied Clarkus papillatus with the intention of assessing its potential for controlling plant parasitic nematodes. A variety of prey were used including Heterodera radicicola

(Meloidogyne sp). The authors showed that C.papillatus, chosen because Menzel (1920) had observed this species feeding on several nematode species, could thrive on a diet of infective second stage juveniles. The numbers of prey killed depended on the age of the predator: the first attacks were made 3-4 days after hatching and the number increased steadily to a maximum during the period of oviposition. During the "senile" period (in which no further eggs were deposited) the number of prey eaten decreased. A maximum of 83 Meloidogyne sp. juveniles were killed in one day by a single C.papillatus adult and in a twelve week life span another specimen killed 1332 juvenile Meloidogyne sp. The latter figure is often quoted but may not be as impressive as it first appears: assuming a mean of 450 eggs per Meloidogyne egg-mass, the single predator destroyed the progeny of approximately three females. Under field conditions, with egg hatch extending over a maximum of four weeks and with alternative food sources available, it seems unlikely that an individual C.papillatus would destroy the juveniles from a single egg mass.

Steiner and Heinly's observations on feeding revealed two other points that are relevant to potential biological control agents: i) physical contact with the prey is necessary before it is recognised and ii) many prey were attacked and damaged (so that they died) but few were ingested totally. The first observation would appear disadvantageous whereas the second would be advantageous to effective biological control. Steiner and Heinly's (l.c.) pot experiments failed and were not recorded in detail but their observations on predators in the laboratory led them to propose that under favourable conditions, Clarkus papillatus could partially, if not completely, control populations of plant parasitic nematodes. They noted that Meloidogyne spp would not be the best nematodes for trials as after penetration they are protected within the roots of the host plant. Despite references to the ongoing research and the optimism generated by their initial results, no further work on mononchids was published by these authors.

Thorne (1927) estimated the economic importance of mononchids by

sampling sugar-beet fields infested with Heterodera schachtii. He attempted to relate the numbers of mononchids recovered with temperature, moisture, food supply and the natural enemies of the predators. Conditions in the fields allowed predator reproduction between March and May, with only one generation per year. During the winter low temperatures and in the summer high temperatures and/or low soil moisture levels reduced or prevented reproduction, although this varied between years and between the four mononchid species. At soil moisture levels below 7-8% (by weight) the mononchids became inactive. Of the four species, only C.papillatus was regularly seen attacking nematodes. The remaining species, Mylonchulus sigmaturus, My.parabrachyuris and Mononchus macrostoma appeared to prey mainly upon rotifers and other micro-organisms and only occasionally were nematodes ingested.

The populations studied by Thorne were extremely unstable, at least partly due to sporozoan parasites that infected many of the mononchids, causing sterility and death. The combination of slow reproductive rate occurring too early in the season to interact with the H.schachtii population, the instability of the predator populations and the apparent food preferences of the predators led Thorne to conclude that the mononchids were unlikely to be economically important. This conclusion appears to have been widely accepted as few further attempts to assess the biological control potential of mononchids were made in the next few years, except for Cassidy (1931) who suggested that Iotonchus brachylaimus might be a suitable species for future study. Her reasons were: i) ease of identification and handling due to large size (3-4mm); ii) resistance to bacterial contamination of cultures; iii) exceptional strength of oesophageal muscles enabling successful attacks on many nematodes and large numbers of prey to be eaten in a short time; iv) voracity, as suggested by the many specimens found to contain remains of ingested phytophagous nematodes; v) cuticular properties, allowing the nematodes to float and so possibly

enabling distribution through irrigation channels.

Thorne (1932a) found the remains of Trichodorus obtusus Cobb 1913, Tylenchus (Rotylenchus) robustus (de Man 1876) Filipjev 1936 and the surprisingly large prey Xiphinema americanum Cobb 1913 in the gut of Mononchus (Iotonchus)acutus (Cobb 1917) Altherr 1950. Esser (1963) concluded that many ectoparasitic nematodes were resistant to predation by dorylaims and mononchids whereas the soil-stages of endoparasitic species were susceptible to predation. Defence mechanisms of the ectoparasites included thick cuticles with or without ornamentation (Hoplolaimidae, Criconematidae) and possibly chemical repellents (Helicotylenchus); some free-living nematodes avoided the predators with rapid escape responses on being touched (Esser, 1963; Croll and Smith, 1970).

The taxonomic work of the late 1950s and 1960s stimulated new investigations of the predatory habits of mononchids. Cohn and Mordechai (1973, 1974) recorded the predation rate of Mylonchulus sigmaturus on four plant parasitic species. Single predators in small volumes of water with excess prey devoured 66% of the juvenile Tylenchulus semipenetrans Cobb 1913 offered and 28% of the Meloidogyne javanica (Treub 1885) Chitwood 1949 juveniles but did not feed on Helicotylenchus multicinctus (Cobb 1893) Golden 1956 or Longidorus africanus Merny 1966. In a mixed population of T.semipenetrans and M.javanica equal numbers of each were eaten, suggesting that no prey selection operated. The predator remained extremely active and fed and functioned well in water (Cohn, pers.comm.) although P.punctatus often becomes quiescent in water; Steiner and Heinly's (1922) and Cassidy's (1931) results also suggest that deep water is not normally a suitable medium for mononchids. Cohn and Mordechai's pot trials, with T.semipenetrans as prey, indicated that large populations of the predator were associated with small populations of the prey. The predation was not sufficient however, to reduce the damage caused by T.semipenetrans (as assessed by plant weight) to the

host plant (sour-orange seedlings).

Patel (1972) used the approach later developed by Nelmes (1974) for observations on the feeding behaviour of P.punctatus in culture. In addition Patel used this predator in pot trials with two inoculum levels of Heterodera (Globodera) rostochiensis Wollenweber 1923 ( Mulvey and Stone 1976; 10, 40 and 75 predators inoculated into 50gms of soil gave a reduction in total prey population of 64%, 91% and 94% respectively after eight weeks. The hatch of G.rostochiensis in soil was only 0.14% of that expected from laboratory hatching trials, resulting in only 14 and 140 juvenile G.rostochiensis per pot at the two inoculum levels. A contaminant population of Rhabditis sp. was also controlled after two weeks by the two larger predator inocula.

Nelmes (1974) showed that Aphelenchus avenae were readily accepted as prey by P.punctatus, Anguina tritici (Steinbuch 1799) Chitwood 1935, less so, and no Helicotylenchus dihystera (Cobb 1893) Sher 1961 were eaten. Attacks on prey appeared independent of predator-satiation but food-deprivation for upto three weeks increased the time spent feeding when the predator was re-introduced to prey. Deprivation for longer periods resulted in loss of "appetitive behaviour" (Nelmes, 1974). The ability of predators to utilise the prey nematodes was dependent on the size of the prey, adult prey requiring a longer feeding time. Cuany (reported in Ritter and Laumond, 1975) established that Anatonchus spp., unlike P.punctatus, fed after every encounter with prey so that upto ten nematodes per hour were ingested.

Esser and Sobers (1964), reviewing natural enemies of nematodes, reported earlier publications but did not assess the feasibility of using predatory nematodes as biological control agents. Webster (1972) and Christie (1960) reviewed the biological control potential of predatory nematodes and concluded that effective control was unlikely. Jones (1974) considered that work on predatory nematodes was not justified because of the large numbers needed for a control programme, and because non-selective

predators do not exert more than partial control. Despite these generally accepted views the optimum conditions for even partial control need to be defined and the best predators and most susceptible prey selected, as the previous work that these reviews are based upon has not thoroughly tested the use of predatory nematodes as biological control agents.

The taxonomy and distribution of the mononchids is now soundly based (Andrassy 1958; Mulvey 1961a, b, 1962, 1963a, b, 1967a, b; Jairajpuri 1969, 1970a, b, 1971) although some proposals (e.g. the erection of the order Mononchida Jairajpuri 1969) will continue to be debated for some time. Previous work on the other aspects of predatory nematodes however, has progressed little over the past forty years and has done little more than indicate the scope for future detailed investigations. Three main areas of predator biology were chosen in this study i) culture ii) micro-distribution and iii) biological control, as revealed by pot experiments.

After many unsuccessful attempts at culture (Steiner and Heinly 1922, Cassidy 1931, Esser 1963) the method of Nelmes enabled his own observations on feeding behaviour (Nelmes, 1974), and the analysis of egg production, life cycle and embryology of mononchids (Maertens 1975, Grootaert and Maertens, 1976). Apart from any intrinsic value of culturing nematodes, the possibility of manipulative biological control using predatory nematodes rests on the ability to culture large numbers (Jones, 1974). Comparison among predators is now possible as culture techniques are available for most taxonomic groups (Hechler 1963, Yeates 1969, Ferris 1968). The comparatively large size of mononchids and dorylaims makes them suitable for physiological, biochemical and ultrastructural studies (Overgaard-Nielsen 1949; Klekowski et al. 1972; Yeates, 1973; Grootaert 1976b). Even taxonomy would benefit

if some specimens were cultured whenever sufficient material was available e.g. field populations of P.punctatus and P.muscorum can be distinguished by recording the presence or absence of echimulate ridges on eggs laid in culture; culture can also be used to increase the number of individuals available for taxonomic study (Hechler 1963; Ferris, 1968; Grootaert pers. comm.). In this study the population development of P.punctatus has been investigated (Section III) and improvements in culture technique sought so that relatively large populations can be reared without undue time or labour.

Mononchids are more numerous in some soils than in others and this has been associated with environmental factors such as pH, temperature, moisture, soil type and vegetation (Thorne, 1927; Yeates 1967, 1968, 1973; Szczygiel 1971; Boag 1974). Such variation in nematode numbers can be observed on several scales: worldwide (cosmopolitan and non-cosmopolitan species) national (Alphey and Boag, 1976; Boag and Orton-Williams, 1976; Taylor and Brown, 1976), local (Overgaard-Nielsen, 1949), field (Anscombe, 1950; Widdowson, 1962) and in small plots (Smith and Wallace 1976; Andrassy, 1962). These distributions are likely to reflect association with one or more of the environmental factors mentioned rather than resulting from the intrinsic behaviour of the nematodes. To study the latter requires samples approximating to the volume of soil in which a nematode could complete its life cycle. The micro-distribution of nematodes was therefore investigated (Section II); the predators were selected for emphasis in order to record any predator-prey associations that might indicate how the predators behaved under natural conditions e.g. whether food preferences led to association with either free-living or plant-parasitic nematodes. Aggregation in the region of root-tips would enhance the predators' value as biological control agents as some plant-parasitic species are known to aggregate at root-tips (Pitcher, 1967).

Finally an attempt was made to assess predatory nematodes as biological control agents of plant-parasitic nematodes in pot experiments (Section IV).

It is recognised that the debate on their potential will only be ended when field trials have been completed but without some preliminary indications of suitable predator-prey combinations such field trials are not justified (Jones, 1974). The recorded pot experiments (Cohn and Mordechai, 1974; Patel, 1972) gave encouraging results for two species of plant parasites and two species of predators. This study investigated four species of plant-parasitic nematodes (including the G.rostochiensis used by Patel) and, in one experiment, three species of predator. The plant parasitic nematodes used for the experiments were selected to provide a range of life histories etc. so that some indication of the most promising groups for further study were obtained.

# II. THE MICRO-DISTRIBUTION OF PREDATORY NEMATODES IN SOIL UNDER PASTURE.

## PREAMBLE

This study was designed as a preliminary investigation of the dispersion of nematodes in small volumes of soil under pasture. Aggregation of predators around dense prey groups had been observed on agar plates and if such aggregations occurred, and could be detected, in soil it might be possible to relate predator aggregations to features of the micro-environment of the soil, such as roots or decomposing organic matter, and their associated nematode fauna. Thus a knowledge of predator dispersion in soil provides a basis for studying predator feeding behaviour and ecology *in vitro*.

Previous studies on the ecology of soil-inhabiting nematodes have attempted to relate nematode numbers, biomass or species composition to various soil-types and plant-communities (Overgaard-Nielsen, 1949; Banage, 1963; Twinn, 1966; Yuen, 1966; Boag 1974). Overgaard-Nielsen (1949) and others remarked on the fact that the populations studied were rarely distributed uniformly, but showed a tendency to aggregate. Recognition of the importance of aggregated distributions in *Heterodera* (*Globodera*) *rostochiensis* led to detailed studies for use in advisory work (Anscombe, 1950; Widdowson, 1962). The sampling programmes of some ecological studies concerning nematodes have also been based on the statistical analysis of preliminary results (e.g. Arpin 1975b). All such studies have been concerned with the distribution over relatively large areas ($>1m^2$) but little is yet known of the small scale spatial dispersion of soil-inhabiting nematodes. Pitcher (1967) recorded aggregations of *Trichodorus viruliferus* Hooper 1963 on the tips of apple roots and aggregations of males around female nematodes are known (Green, 1971). In addition Arlt (1973) recorded small-scale aggregations of marine nematodes over an area of 40cm x 40cm.

Studies on the dispersion of insects and plants have provided many indices of dispersion including Taylor's Power Law which has been applied

to widely differing populations (Taylor, 1961). Amongst soil-invertebrates, earthworms and symphilids showed aggregated distributions whereas wireworms and cockchafer larvae were randomly distributed (Taylor, 1961). In this study the power law was applied to populations of nematodes in soil under pasture.

Although Taylor's power law had the advantage of covering a wide range of distributions, it had the disadvantage of requiring several sample means and variances. Other indices of dispersion, of which the simplest is the variance-mean ratio, could be based on a single set of samples, such as a single depth in soil-nematode studies.

Several frequency distributions have been shown to describe some biological data (Anscombe, 1949; Bliss and Fisher, 1953; Cassie, 1962; Neyman, 1939). For aggregated invertebrate populations the Negative Binomial often describes the frequency distribution although others also occur e.g. Neyman Type A (Neyman, 1939). Random dispersions are represented by the Poisson distribution and regular dispersions by the Binomial distribution.

Although conceived as a study of the micro-distribution, much data of a more general ecological nature was obtained. This extra data has been recorded because specific information on mononchid ecology is generally lacking, although Nelmes and McCulloch (1975) have studied the mononchid population of the area of grassland used in this study.

## MATERIALS AND METHODS

### Terminology.

The populations investigated were (within the limits of the extraction technique) the entire nematode population of blocks of soil with sides of either 25cm or 5cm. The blocks were subdivided into 125 cubes with sides of 5 x 5 x 5cm ($125cm^3$) or 1 x 1 x 1cm ($1cm^3$). Horizontal plane refers to soil layers such as 0-1cm depth or 10-15cm depth; vertical plane refers to sections down the soil profile.

The nematodes were recorded in groups: total others represented all non-mononchid nematodes in December 1974 and February 1975; in April 1976 total others referred to all non-predatory nematodes. Total others was therefore approximately representative of the potential prey of the predators. In April 1976 total others was further subdivided into nematodes with spears or stylets (spear-bearers) and nematodes without spears or stylets (non spear-bearers); spear-bearers was therefore approximately equivalent to the plant parasitic nematodes but probably included a few fungivorous species, whereas non spear-bearers represented the majority of the microbivorous nematodes. In April 1976 predatory dorylaims were recorded as a separate group; these nematodes were presumed to feed at least occasionally on other nematodes but some species were probably omnivores. Total predators represented the sum of predatory dorylaims and total mononchids.

Nelmes and McCulloch (1975) reported five mononchid species from this site: Clarkus papillatus, Anatonchus tridentatus, Prionchulus muscorum (possibly P.punctatus), Mylonchulus brachyuris and M.sigmaturus. In this study M.brachyuris was absent from the specimens examined; the other species agreed with those reported by Nelmes and McCulloch and therefore the genera can be considered as individual species, but are referred to by the generic epithet. Subdivisions of the genera are self-explanatory e.g. Clarkus total juveniles; Mylonchulus males; Anatonchus gravid females.

## Field techniques

In December 1974 the foliage covering an area of approximately 0.25m$^2$ was cleared. In the centre of this area a square of side 0.25m was marked on the soil surface using pegs; the soil around this square was dug out to leave intact a soil block with sides of 0.25m in the centre of a depression. The block was evenly divided into 125 cubes (each of 125cm$^3$) using a ruler and a large scalpel. Each cube was placed in a plastic bag labelled to indicate the exact position that the cube had occupied in the soil block.

In February 1975 a smaller block (5cm sides) was exposed as before and again evenly divided into 125 cubes (each of 1cm$^3$). The block was within 0.5m of the original site. In April 1976 a second set of 1cm$^3$ cubes were taken within 0.5m of the previous sites. The same techniques were used as in February 1975 but an extra depth (5-6cm) was included.

## Laboratory techniques

125cm$^3$ cubes. The cubes were stored (for a maximum of six weeks) at 10°C before the nematode population was extracted by the Whitehead tray method (Whitehead and Hemming, 1965) over 24 hours. The nematodes extracted were concentrated by passing the suspension twice through a 53µm aperture sieve, and were counted in a Doncaster counting dish (Doncaster, 1962). All mononchids were picked out and counted; the number of other nematodes was estimated by counting individuals in two rings (equivalent to 27% of the base area) of the dish.

The mononchids were identified to species and the numbers of males, non-gravid and gravid females, and juveniles for each species were recorded. Second and third stage juveniles of P.punctatus and C.papillatus could not be distinguished, so all juveniles without subventral teeth or denticles were classified as C.papillatus, as in Nelmes and McCulloch (1975).

Of the 125 cubes, sixty were treated as described; the nematodes from remainder were extracted and concentrated as above, but were then fixed in

hot T.A.F. (Courtney, Polley and Miller, 1955). Twenty-five cubes treated in this way were counted; the remainder were considered unlikely to significantly increase the statistical accuracy of the results and were therefore not included in the analysis. Fixation did not affect the ease of identification and was considered preferable to possible nematode mortality resulting from further storage.

1 $cm^3$ cubes. All 1$cm^3$ cubes were stored at 10°C (for a maximum of two weeks) before extraction using a miniature Whitehead tray technique in which the depth of the soil was similar to that used for the 125$cm^3$ cubes to give similar extraction efficiencies. All mononchids and other nematodes were counted in a modified de Grisse counting dish (de Grisse, 1963). The mononchids were identified to species and the numbers of males, gravid and non-gravid females and juveniles recorded; in April 1976 the four juvenile stages were recorded. Nematodes from all 125 cubes were counted for both dates and were included in the results.

## Analysis of Data

### i) Taylor's Power Law.

Taylor's power law is described by

$$s^2 = a\bar{x}^b$$

where $s^2$ is the variance, $\bar{x}$ is the mean, $a$ is a constant dependent on quadrat size and $b$ is a constant, the index of dispersion. With values of $a$ near to unity, values of $b$ approaching zero indicate that the population under study has a regular distribution; values of $b$ approximating to unity indicate a random distribution and values of $b$ approaching infinity indicate increasing contagion (Taylor, 1961). In practice, a value of $b$ exceeding 2 indicates a high degree of contagion with increasing density (Taylor, 1961). The value of $b$ is equal to the value of the gradient of the regression line of log. variance on log. mean. In this study the several sets of data

needed were obtained by treating each depth as a separate set. The value of b was therefore representative of the whole block.

The value of b from Taylor's power law can be used to determine the transformation of the data necessary before statistical techniques based on the normal distribution are employed (Taylor, 1961). The transformation is achieved by raising the data to the power p where $p=1-b/2$ (Elliott, 1971). This method was used to determine the transformation necessary for regression analysis but as many cubes contained no individuals of some groups $(x+1)^p$ was used, rather than $x^p$.

ii) Other dispersion indices.

In order to investigate differences in distribution at each depth an alternative to Taylor's power law was required, and where the data were suitable they were analysed by the TOPFIT computer-programme (Robles, 1969). The programme gave values for the following indices of dispersion: Variance-mean ratio; Lexis disturbance index (Beall, 1935); David and Moore 1954 index (David and Moore, 1954); Green 1966 index (Green, 1966); Imperial College 1968 index (Robles, 1969); Cancela da Fonseca 1966 indices (E and IA; Cancela da Fonseca, 1966); Cole 1946 index (Cole, 1946); Morisita 1959 index (Morisita, 1959); Charlier coefficient (Beall, 1935); Bliss and Fisher k-1 index (Bliss and Fisher, 1953).

The value of the variance-mean ratio was compared to that expected from a Poisson series by means of a chi-squared ($\chi^2$) goodness-of-fit test. An estimate of $\chi^2$ was obtained from

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

and compared to the values given in standard statistical tables for the 95% probability limits (Elliott, 1971).

iii) Frequency-distributions

The TOPFIT programme also compared the data with nine frequency-distributions and indicated those distributions that best described the data. The distributions tested were: Binomial, Poisson, Double Poisson, Neyman Type A, Negative Binomial, Truncated Poisson, Truncated Neyman Type A, Truncated Negative Binomial, and Logarithmic.

Many groups could not be analysed for one of three reasons: i) too many nematodes e.g. total mononchids in $125cm^3$ cubes, total others in all cube sizes; ii) too few nematodes e.g. Anatonchus males in $1cm^3$ cubes, Mylonchulus gravid females in $1cm^3$ cubes; iii) too few frequency classes e.g. Clarkus total at 4-5cm depth in February 1975, Anatonchus males at 5-10cm, 10-15cm and 15-20cm depths in December 1974.

iv) Pooling of data

To investigate whether cubes larger than $1cm^3$ may have been more suitable for analysis, the data from the $1cm^3$ cubes in the horizontal plane were combined to give sixteen "2cm x 2cm x 1cm samples" ("$4cm^3$") and nine "3cm x 3cm x 1cm samples" ("$9cm^3$"). The data so obtained was analysed using the TOPFIT programme. Similarly the data for the $125cm^3$ cubes was combined to give "10cm x 10cm x 5cm samples" and "15cm x 15cm x 5cm samples" and re-analysed so that sample sizes approaching those used by other authors were investigated. It was considered unnecessary to treat the data from the vertical plane in this way because the depth distribution of nematodes causes a bias towards aggregative distributions.

# RESULTS

## General

### i) Number of nematodes recorded.

The number of nematodes (per $dm^3$) recovered in December 1974 was lower than from either set of $1cm^3$ cubes, particularly for total other nematodes (Table 4). Most of the other groups showed some similarity between the 0-5cm level of the December 1974 estimate and the $1cm^3$ estimates, but Clarkus (and hence total mononchids) were less frequent in December 1974 (Table 4). On all counting dates the numbers of the mononchid genera decreased in the order Clarkus>Mylonchulus>Anatonchus>Prionchulus; this last genus was absent from the cubes in February 1975 and was rare in December 1974 (Table 4).

Predatory dorylaims formed 65% of the total predators (≡1.6% of the total nematodes) recovered in April 1976, the only occasion on which they were separately recorded. Mononchids represented 1.7%, 0.8% and 0.6% of the total nematodes recovered in December 1974, February 1975 and April 1976 respectively. Spear-bearing nematodes represented 29% of total other nematodes in April 1976.

### ii) Depth distributions

Most groups recorded in December 1974 followed the usual nematode depth distribution i.e. a steady decrease in numbers with increasing depth (Fig.4). Anatonchus deviated from this pattern (Fig. 4iii) and the rapid decrease in numbers of Clarkus was remarkable (Fig. 4i). The two P.punctatus individuals recovered in December 1974 both occurred at 0-5 cm depth.

The most noticeable difference between the two sets of $1cm^3$ cubes was in the greater density at intermediate levels in April 1976, with a corresponding decrease at 0-1cm depth (Fig. 5). This downward movement of the nematode population was exhibited by all the mononchid groups recorded. Single individuals of Anatonchus were found at 1-2cm and 2-3cm depths in

Table 4. Summary of numbers of each group of nematodes recovered on three sampling dates, including estimates of numbers per $dm^3$.

| Nematode Group | DECEMBER 1974 | | | | FEBRUARY 1975 | | | APRIL 1976 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean no per $125cm^3$ cube | Total | No./$dm^3$ | No./$dm^3$ 0-5cm only | Mean no per $1cm^3$ cube | Total | No./$dm^3$ | Mean no per $1cm^3$ cube | Total | No./$dm^3$ |
| Anatonchus | 4.24 | 360 | 34 | 81 | 0.02 | 2 | 16 | 0.07 | 11 | 73 |
| Mylonchulus | 20.56 | 1748 | 164 | 253 | 0.42 | 52 | 416 | 0.27 | 41 | 273 |
| Clarkus | 11.65 | 990 | 93 | 369 | 1.22 | 152 | 1216 | 1.00 | 150 | 1000 |
| Prionchulus | 0.02 | 2 | 0.2 | 1.00 | 0 | 0 | 0 | 0.02 | 3 | 20 |
| Total Mononchids | 36.47 | 3100 | 292 | 704 | 1.65 | 206 | 1648 | 1.37 | 205 | 1367 |
| Predatory Dorylaims | - | - | - | - | - | - | - | 2.53 | 380 | 2533 |
| Total Predators | - | - | - | - | - | - | - | 3.90 | 585 | 3900 |
| Spear-bearing nematodes | - | - | - | - | - | - | - | 70.64 | 10596 | 70640 |
| Non spear bearing nematodes | - | - | - | - | - | - | - | 187.72 | 28158 | 187720 |
| Total others | 2,081.18 | 176,900 | 16,642 | 24,950 | 204.22 | 25,528 | 204,224 | 241.69 | 36,254 | 241,693 |

February 1975; in April 1976 4 Anatonchus individuals were found at 0-1cm, 2 at 2-3cm, 1 at 3-4cm and 4 at 4-5cm so that the depth distribution resembled that in December 1974.

The four non-mononchid groups recorded also showed a greater density at 1-2cm depth than at 0-1cm depth (Fig.6). The number of non-spear bearing nematodes was approximately twice that of the spear-bearing nematodes at most depths (Fig. 6i). Predatory dorylaims represented 55-60% of total predators over 0-4cm depths but increased to 75%-80% at 4-6cm depth.

iii) Occurrence of juvenile stages.

Juveniles generally formed over half the individual mononchid genera populations, the exact proportion depending on depth and species (Figs.7-9). The proportion of juveniles in the total mononchid population was far more constant with depth however; 77% of the mononchids were juveniles in December 1974 (Fig. 7iv). The percentage of juveniles varied considerably for all groups in February 1975 and April 1976 (Figs. 8,9). The proportion over all depths on these dates were similar and approximately 10-20% greater than in December 1974. The two Anatonchus individuals recovered in February 1975 were both juveniles, as were two of the Prionchulus recovered in April 1976 (fourth-stage at 0-1cm depth and third stage at 5-6cm depth).

In April 1976 the ratios of fourth:third:second:first stage juveniles of Clarkus, Mylonchulus and total mononchids were 3 : 12 : 34 : 44, 15 : 27 : 27 : 7 and 34 : 32 : 18 : 7 respectively. Pooling the data for each genus to provide figures for total mononchids again reduced the between-depth variation of these ratios (Fig. 9).

iv) Occurrence of males and gravid females.

Males of Clarkus and Prionchulus were not found in the blocks. 7% of Anatonchus, 11% of Mylonchulus and 7% of total mononchids were male in December 1974. The percentage of males varied with depth but the variation

FIG. 4.

DEPTH DISTRIBUTIONS OF (i) CLARKUS (ii) MYLONCHULUS (iii) ANATONCHUS (iv) TOTAL MONONCHIDS (v) TOTAL OTHER NEMATODES

DECEMBER 1974

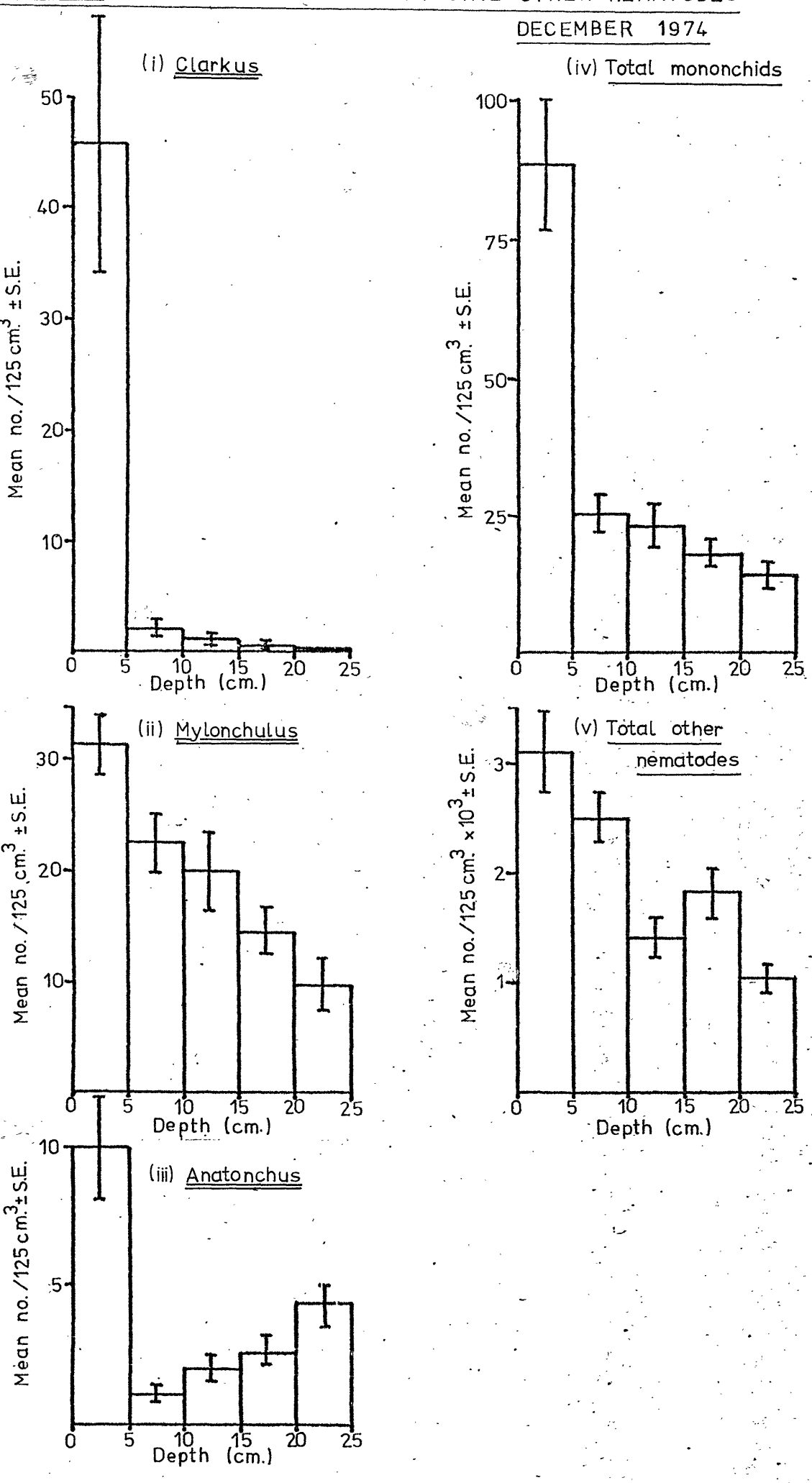


FIG. 5. DEPTH DISTRIBUTIONS OF (i) TOTAL MONONCHIDS (ii) MYLONCHULUS (iii) CLARKUS (iv) TOTAL OTHER NEMATODES

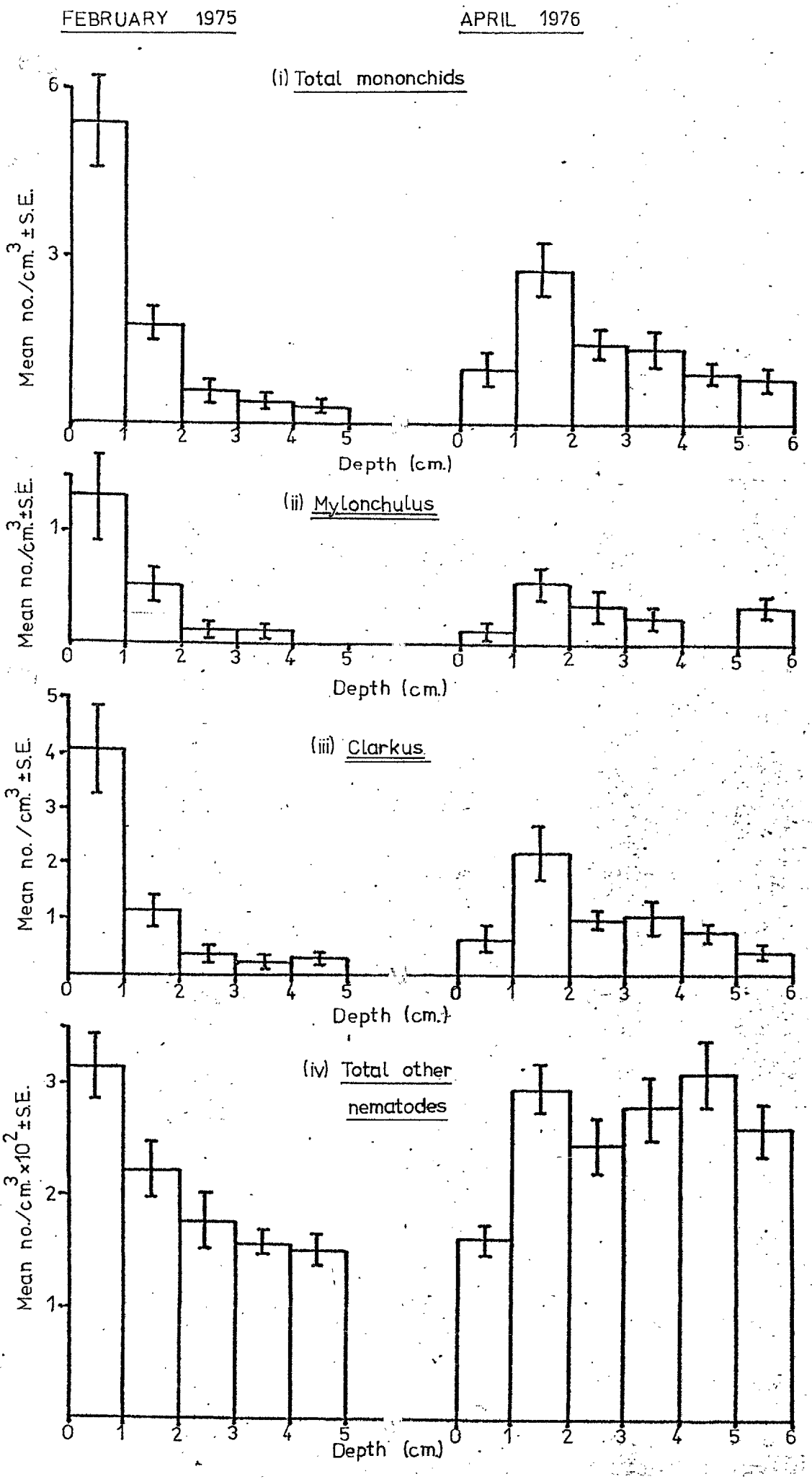
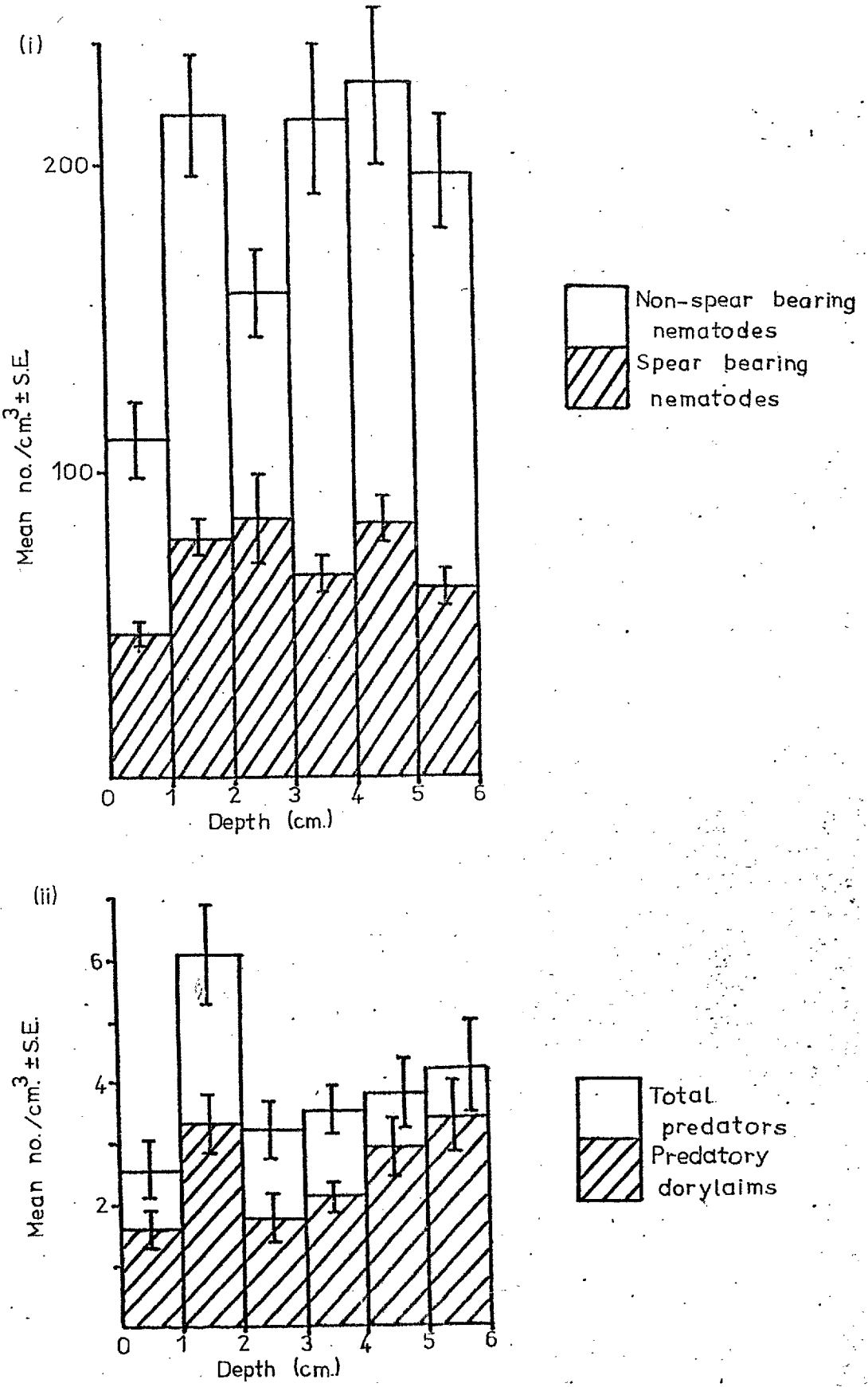


FIG. 6. DEPTH DISTRIBUTIONS OF (i) SPEAR BEARING AND NON-SPEAR BEARING NEMATODES (ii) PREDATORY DORYLAIMS AND TOTAL PREDATORS APRIL 1976



was less for total mononchids than for each genus considered separately (Fig. 7). The proportion of males was generally less in February 1975 and April 1976 than in December 1974 (Figs. 8-9).

Less than half of the mononchid females (5% of the total mononchid population) were gravid in December 1974 when approx. 10% of the mononchid population were non-gravid females (Fig. 7). The percentage of gravid and non-gravid females varied with depth, particularly for Clarkus (0-22% and 0-20% respectively). Two gravid Prionchulus females were recovered from the 0-5cm depth in December 1974. In February 1975 gravid females occurred infrequently but non-gravid females constituted upto a third of the Mylonchulus population at some depths (Fig. 8). Both gravid and non-gravid females were a little more frequent in April 1976 but represented a total of less than 10% of the total mononchid population. A single gravid Prionchulus female was found at 3-4cm depth.

The sex-ratio of Mylonchulus was approximately 1.6♀ : 1♂, 6♀ : 1♂ and 1♀ : 3♂ in December 1974, February 1975 and April 1976 respectively and approximately 1♀ : 1♂ for Anatonchus in December 1974.

v) Predator-prey correlations.

The values of p used to transform the data are recorded in Tables 8-13 with other results from the Taylor's power law analysis. Of the mononchid groups recorded in December 1974 three of the four Anatonchus subdivisions failed to correlate with total others i.e. the potential prey (Table 5). All the remaining groups correlated well ( p generally $<0.001$). Few groups were analysed in February 1975 but all showed highly significant correlations ($p<0.001$) with total other nematodes (Table 6). The subdivisions recorded in April 1976 allowed more detailed analysis of the relationships between the numbers of predators and potential prey (Table 7). Four groups correlated well with spear-bearers and only Mylonchulus total juveniles failed to correlate; similar correlations were recorded for non

FIG. 7. PROPORTION OF JUVENILES, SEXES, GRAVID AND NON-GRAVID FEMALES OF (i) ANATONCHUS (ii) MYLONCHULUS (iii) CLARKUS (iv) TOTAL MONONCHIDS

DECEMBER 1974

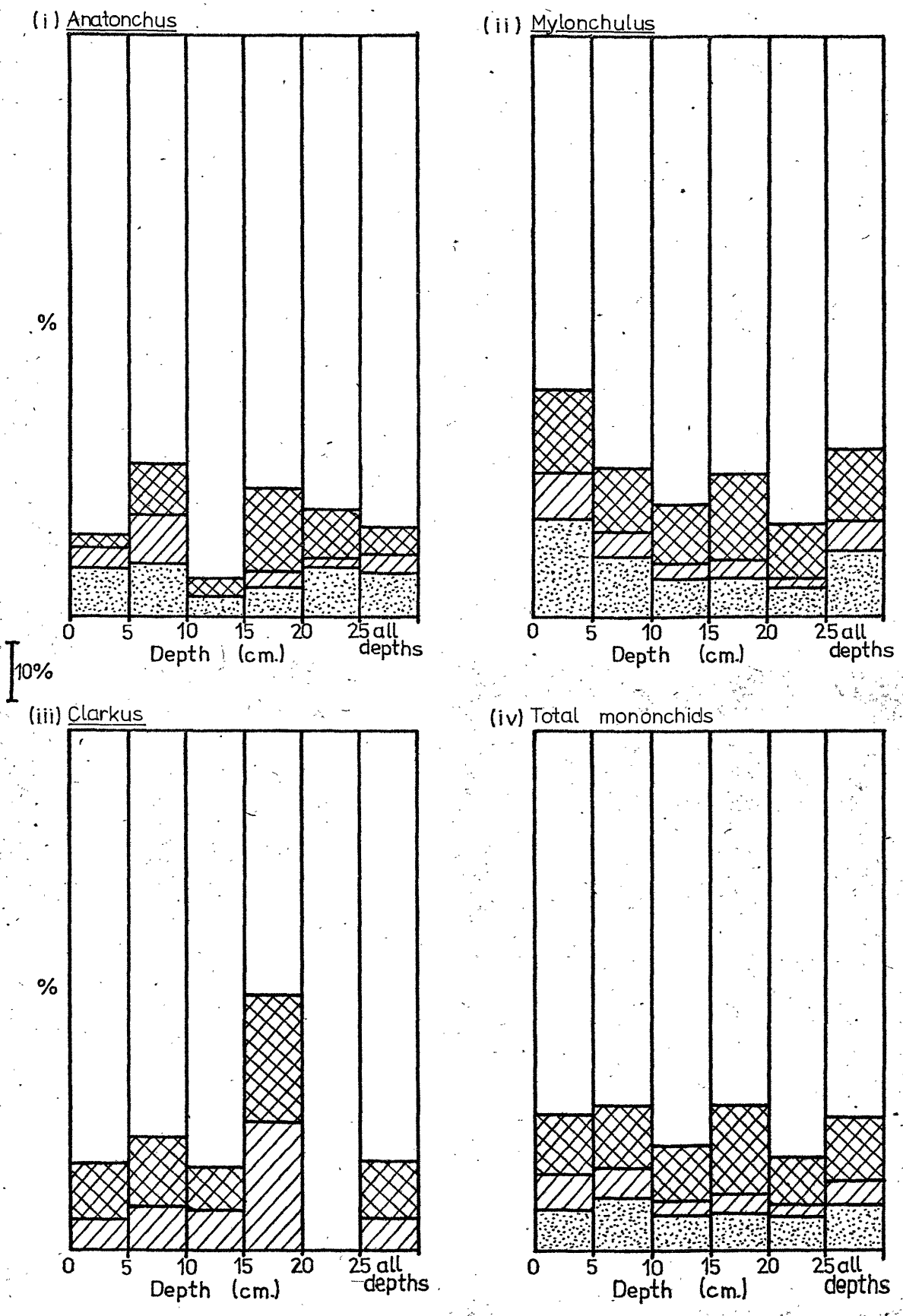


FIG. 8. PROPORTION OF JUVENILES, SEXES, GRAVID AND NON-GRAVID FEMALES OF (i) MYLONCHULUS (ii) CLARKUS

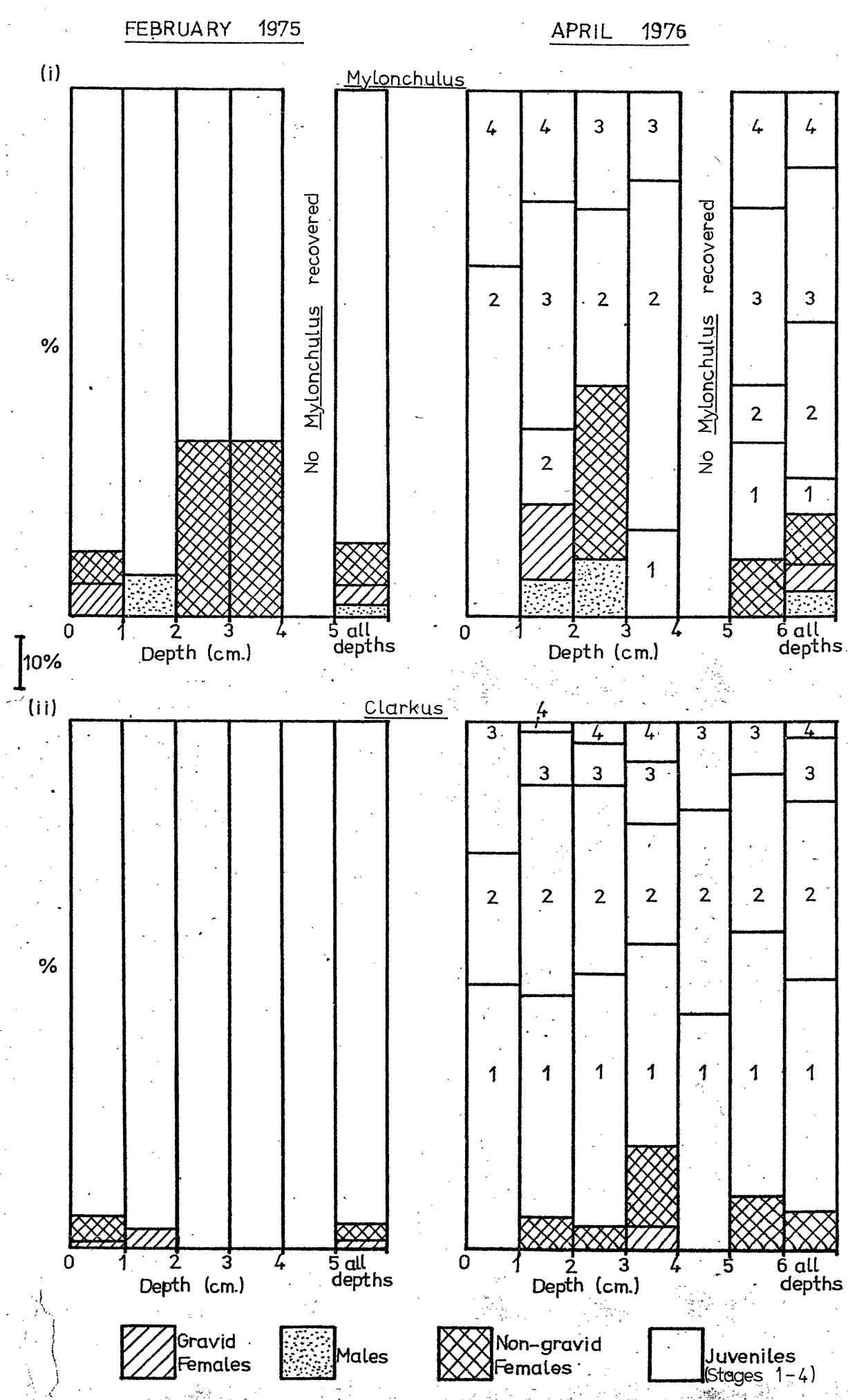
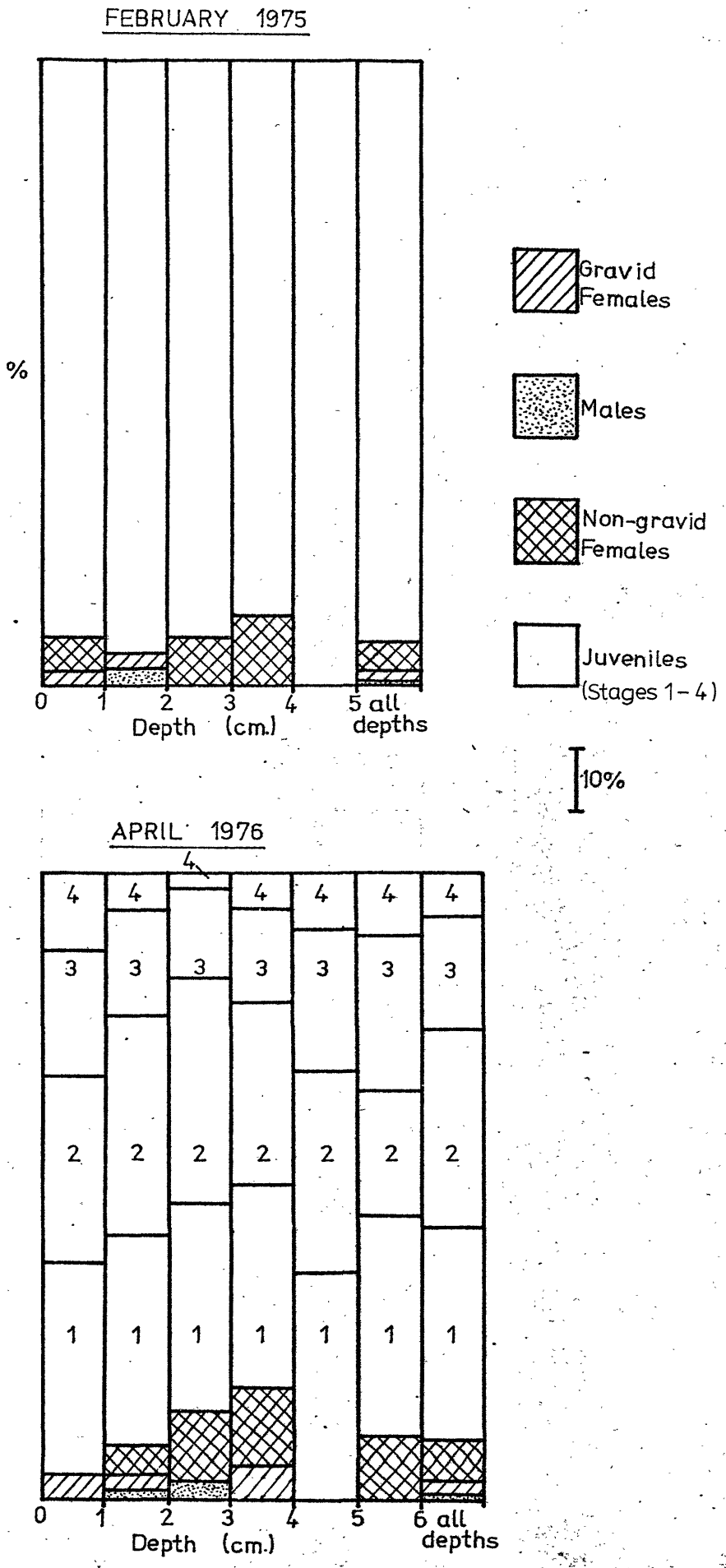


FIG. 9: PROPORTION OF JUVENILES, SEXES, GRAVID AND NON-GRAVID FEMALES OF TOTAL MONONCHIDS



spear-bearers, with the addition of total mononchids to the highly significant group. Clarkus first and second-stage juveniles correlated better with total others than with non-spear bearers, but Clarkus total juveniles and Clarkus total correlated less well. The negative values of the regression and correlation coefficients reflected the use of a negative power in the transformation of the data for both spear-bearers and total others; the untransformed data was always positively correlated, i.e. large numbers of mononchids were associated with large numbers of potential prey.

vi) Other associations

Regression analysis of the April 1976 data indicated a positive correlation between numbers of predatory dorylaims and numbers of total mononchids ($r=0.29$; $p=0.01$-$0.001$; $b=0.80$) and a positive correlation between numbers of spear-bearers and numbers of non spear-bearers ($r=0.67$; $p<0.001$; $b=-1.11$; negative coefficients caused by transformation of spear-bearing nematode data).

Positive correlations of mononchid juveniles and females were recorded in the December 1974 data. Mylonchulus juveniles and females correlated particularly well ($r=0.62$; $p<0.001$; $b=0.16$); the correlation for Anatonchus was not so marked ($r=0.19$, $p=0.1$-$0.05$, $b=0.68$). Clarkus was not analysed because of the few females at any depth except 0-5cm.

Micro-distribution analysis.

As a pictorial example Fig.10 represents an exploded view of the soil profile in February 1975 and April 1976. The figured Clarkus population featured many of the results that were recorded. The density of nematodes was greatest at 0-1cm depth in February 1975 and at 1-2cm depth in April 1976 (maximum number of Clarkus per $1cm^3$ was 18). The distribution in the upper levels was patchy but became more uniform with increasing depth;

Table 5. Correlation coefficients (r) and their significance (p), and the regression coefficients (b) for predators and potential prey (transformed data) December 1974

| Abscissa | TOTAL OTHERS | | |
|---|---|---|---|
| Ordinate | r | p | b |
| Anatonchus Total Females | 0.06 | N.S. | - |
| Anatonchus Adults | -0.02 | N.S. | - |
| Anatonchus Juveniles | -0.21 | 0.1-0.05 | -0.63 |
| Total Anatonchus | 0.06 | N.S. | - |
| Clarkus Juveniles | 0.46 | <0.001 | 0.47 |
| Total Clarkus | 0.51 | <0.001 | 0.53 |
| Mylonchulus Non-gravid females | 0.36 | <0.001 | 0.15 |
| Mylonchulus Gravid females | 0.32 | 0.01-0.001 | 0.19 |
| Mylonchulus Total females | 0.41 | <0.001 | 0.14 |
| Mylonchulus Males | 0.55 | <0.001 | 0.32 |
| Mylonchulus Adults | 0.46 | <0.001 | 0.16 |
| Mylonchulus Juveniles | 0.86 | <0.001 | 0.08 |
| Total Mylonchulus | 0.54 | <0.001 | 0.05 |
| Total Mononchids | 0.54 | <0.001 | 0.39 |

N.S.: Not significant

Table 6. Correlation coefficients (r) and their significance (p), and the regression coefficients (b) for predators and potential prey (transformed data).

February 1975

| Abscissa | TOTAL OTHERS | | |
|---|---|---|---|
| Ordinate | r | p | b |
| *Clarkus* Juveniles | 0.49 | <0.001 | 0.44 |
| Total *Clarkus* | 0.45 | <0.001 | 0.35 |
| Total *Mylonchulus* | 0.35 | <0.001 | 0.33 |
| Total Mononchids | 0.89 | <0.001 | 0.66 |

N.S.: Not significant

Table 7. Correlation coefficients (r) and their significance (p), and the regression coefficients for predators and potential prey (transformed data).

| Abscissa | Spear-Bearers | | | Non Spear-Bearers | | | Total Others | | |
|---|---|---|---|---|---|---|---|---|---|
| Ordinate | r* | p | b* | r | p | b | r* | p | b* |
| Clarkus 1st st.juveniles | -0.15 | 0.1-0.05 | -0.02 | 0.17 | 0.1-0.05 | 0.03 | -0.48 | <0.001 | -0.03 |
| Clarkus 2nd st.juveniles | -0.33 | <0.001 | -0.06 | 0.19 | 0.1-0.05 | 0.05 | -0.43 | <0.001 | -0.04 |
| Clarkus total juveniles | -0.23 | 0.02-0.01 | -0.04 | 0.41 | <0.001 | 0.11 | -0.19 | 0.05-0.02 | -0.02 |
| Total Clarkus | -0.40 | <0.001 | -0.07 | 0.38 | <0.001 | 0.11 | -0.18 | 0.1-0.05 | -0.02 |
| Mylonchulus total juveniles | -0.09 | N.S. | - | -0.02 | N.S. | - | -0.13 | N.S. | - |
| Total Mylonchulus | -0.14 | 0.1-0.05 | -0.03 | 0.16 | 0.1-0.05 | 0.08 | -0.04 | N.S. | - |
| Total Mononchids | -0.22 | 0.05-0.02 | -0.02 | 0.45 | <0.001 | 0.08 | -0.31 | <0.001 | -0.02 |
| Predatory Dorylaims | -0.41 | <0.001 | -0.13 | 0.50 | <0.001 | 0.25 | -0.39 | <0.001 | -0.07 |
| Total Predators | -0.38 | <0.001 | -0.06 | 0.31 | <0.001 | 0.07 | -0.44 | <0.001 | -0.04 |

N.S.: Not significant

*The data transformations for spear bearers and total others involves negative powers resulting in negative correlations of the transformed data. The untransformed data would be positively correlated.

although more cubes at 4-5cm in February 1975 contained Clarkus than at 3-4cm the density was less: no cubes contained >1 Clarkus so that the distribution at 4-5cm was more regular than at 3-4cm. The Clarkus population did not indicate as well as some other groups the with-depth continuity of areas of greater density; the depth distribution (Fig.5iii) indicated the abrupt change in density between 0-1cm and 1-2cm depths.

i) Taylor's Power Law

In general the analysis indicated that not all the groups studied were distributed in the same manner; values of b ranged from 0.58-4.00 indicating that almost the entire range of distributions from regular to aggregated were represented. Some of the groups were not analysed due to the small numbers recovered and some of the groups which were analysed using the power law were not used for the preceding regression analyses, as the large numbers of cubes without representatives of these groups would have obscured any relationships. Nonetheless the value of p was recorded for these groups (Tables 8-13).

Horizontal Levels. Values of b ranged from 0.63-1.97 in December 1974 (Table 8). All Mylonchulus groups, Anatonchus total females and Anatonchus adults had values of b that suggested a random distribution, but Anatonchus juveniles appeared to be aggregated (Table 8); the numerical dominance of the juveniles led to a b value suggesting aggregation of Anatonchus total. Clarkus juveniles and Clarkus total had b values indicative of aggregation, as did total mononchids and total others (Table 8).

In February 1975 values of b ranged from 1.14-1.86; again Mylonchulus was randomly distributed but all other groups appear to have been aggregated to some degree. Only total others was strongly aggregated (Table 9).

In April 1976 b values were generally less (0.58-3.00) but predatory dorylaims, total predators and the prey groups (particularly spear-bearing

EXPLODED VIEW OF THE SOIL PROFILE

FIG. 10. UNDER GRASSLAND SHOWING THE NUMERICAL DISTRIBUTION OF THE CLARKUS POPULATION IN 5 × 5 × 5 CM. BLOCKS OF SOIL

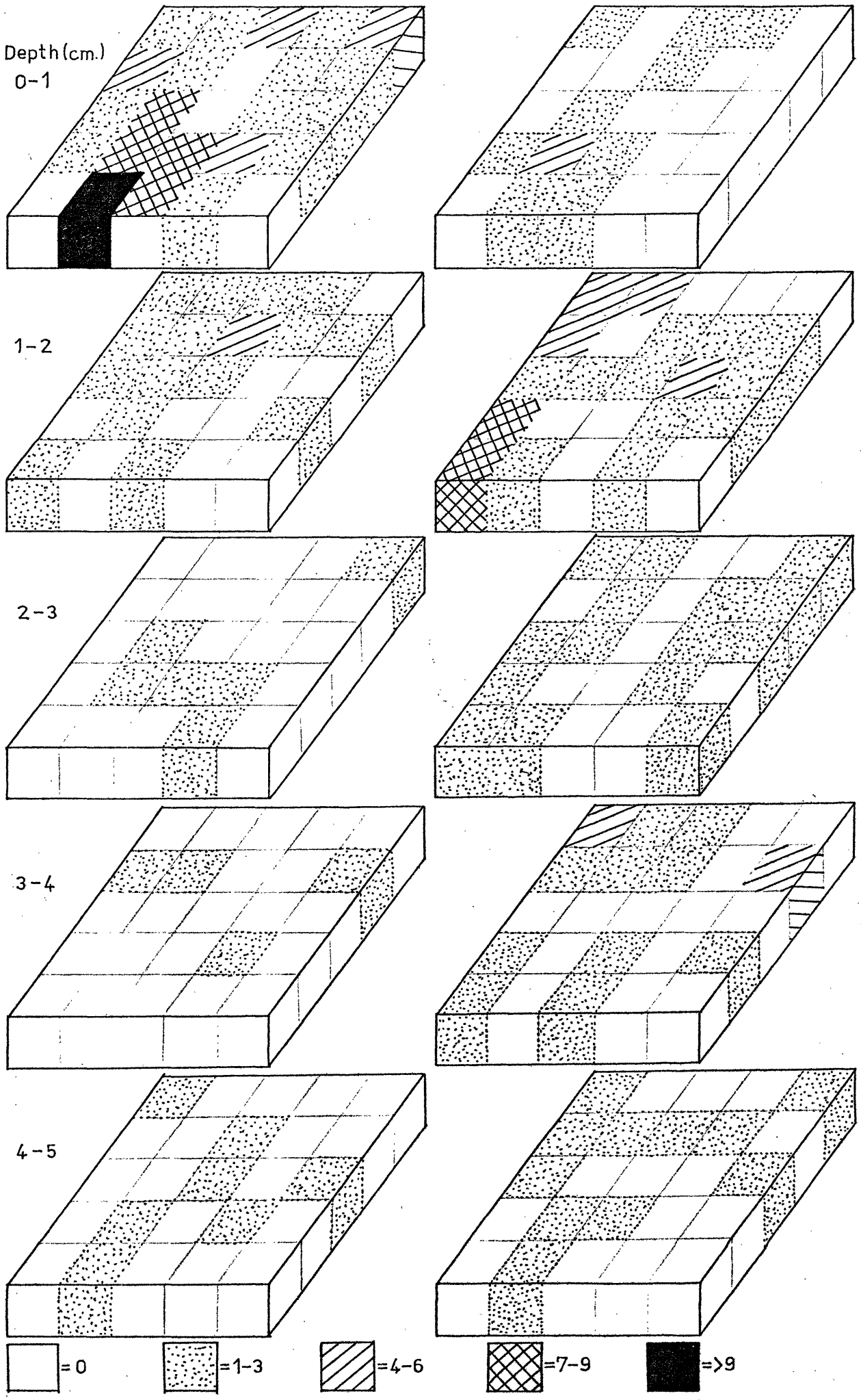


Table 8. Results of Taylor's Power Law analysis of December 1974 data; horizontal levels.

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| Mylonchulus Non-Gravid Females | 0.93-4.60 | 1,50-6.36 | 0.29 | 0.92 | 0.1>p>0.05 | 0.54 | $\sqrt{x+1}$ |
| Mylonchulus Gravid Females | 0.13-2.55 | 0.12-3.00 | 0.08 | 1.02 | 0.05>p>0.02 | 0.49 | $\sqrt{x+\frac{1}{4}}$ |
| Mylonchulus Total Females | 1.07-7.15 | 2.07-11.92 | 0.39 | 0.91 | N.S. | 0.54 | $\sqrt{x+1}$ |
| Mylonchulus Males | 0.47-5.20 | 0.70-16.27 | 0.24 | 1.38 | 0.01>p>0.001 | 0.31 | $(x+1)^{0.31}$ |
| Mylonchulus Adults | 1.53-12.35 | 2.84-29.71 | 0.38 | 1.14 | 0.1>p>0.05 | 0.43 | $(x+1)^{0.43}$ |
| Mylonchulus Juveniles | 8.20-19.30 | 50.07-131.3 | 1.13 | 0.63 | N.S. | 0.69 | $(x+1)^{0.69}$ |
| Mylonchulus Total | 9.73-31.65 | 72.95-197.1 | 1.15 | 0.73 | 0.1>p>0.05 | 0.64 | $(x+1)^{0.64}$ |
| Anatonchus Total Females | 0.07-0.55 | 0.07-0.55 | -0.12 | 0.69 | N.S. | 0.65 | $(x+1)^{0.65}$ |
| Anatonchus Adults | 0.13-1.35 | 0.12-2.03 | 0.04 | 1.08 | 0.02>p>0.01 | 0.46 | $\sqrt{x+1}$ |
| Anatonchus Juveniles | 1.87-8.75 | 1.08-58.51 | 0.01 | 1.82 | 0.01>p>0.001 | 0.09 | $(x+1)^{0.09}$ |
| Anatonchus Total | 1.15-10.10 | 1.71-73.67 | -0.01 | 1.78 | p<0.001 | 0.11 | $(x+1)^{0.11}$ |
| Clarkus Juveniles | 0.27-39.20 | 0.35-2258 | 0.64 | 1.72 | p<0.001 | 0.14 | $(x+1)^{0.14}$ |
| Clarkus Total | 0.27-46.10 | 0.35-2765 | 0.56 | 1.74 | p<0.001 | 0.13 | $(x+1)^{0.13}$ |
| Total Mononchids | 14.27-87.95 | 87.35-2761 | -0.38 | 1.97 | p<0.001 | 0.015 | log(x+1) |
| Total Others | 1041-3119 | 248,845-2,820,756 | -0.43 | 1.93 | 0.01>p>0.001 | 0.035 | log(x+1) |

N.S.: Not significant

Table 9. Results of Taylor's Power Law analysis of February 1975 data; Horizontal levels.

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| Mylonchulus Total | 0.12-1.32 | 0.11-3.56 | 0.20 | 1.14 | 0.01>p>0.001 | 0.43 | $(x+1)^{0.43}$ |
| Clarkus Juveniles | 0.24-3.80 | 0.21-13.17 | 0.25 | 1.38 | 0.01>p>0.001 | 0.31 | $(x+1)^{0.31}$ |
| Clarkus Total | 0.24-4.04 | 0.21-15.54 | 0.28 | 1.43 | p<0.001 | 0.285 | $(x+1)^{0.285}$ |
| Total Mononchids | 0.28-5.36 | 0.21-18.41 | 0.23 | 1.39 | p<0.001 | 0.305 | $(x+1)^{0.305}$ |
| Total others | 152.3-315.4 | 3456-22609 | -0.25 | 1.86 | N.S. | 0.07 | log(x+1) |

N.S.: Not significant

Table 10. Results of Taylor's Power Law analysis of April 1976 data; Horizontal levels.

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| Mylonchulus 2nd stage Juveniles | 0-0.16 | 0-0.14 | -0.19 | 0.58 | 0.01>p>0.001 | 0.71 | $(x+1)^{0.71}$ |
| Mylonchulus Total Juveniles | 0-0.44 | 0-0.51 | 0.02 | 0.97 | 0.027>p>0.01 | 0.51 | $\sqrt{x+1}$ |
| Mylonchulus Total | 0-0.56 | 0-0.59 | 0.11 | 1.16 | p<0.001 | 0.42 | $(x+1)^{0.42}$ |
| Clarkus 1st stage Juveniles | 0.20-0.92 | 0.31-2.24 | 0.32 | 1.25 | 0.05 >p>0.02 | 0.37 | $(x+1)^{0.37}$ |
| Clarkus 2nd stage Juveniles | 0.12-0.88 | 0.11-0.86 | 0.04 | 1.06 | p<0.001 | 0.47 | $\sqrt{x+1}$ |
| Clarkus 3rd stage Juveniles | 0.04-0.24 | 0.04-0.22 | 0.10 | 0.86 | 0.02>p>0.01 | 0.57 | $\sqrt{x+1}$ |
| Clarkus Total Juveniles | 0.36-2.08 | 0.49-5.99 | -0.02 | 1.39 | 0.01>p>0.001 | 0.31 | $(x+1)^{0.31}$ |
| Clarkus Total | 0.40-2.20 | 0.50-6.75 | 0.28 | 1.50 | 0.05>p>0.02 | 0.25 | $(x+1)^{0.25}$ |
| Anatonchus Total | 0-0.16 | 0-0.22 | 0.20 | 1.24 | 0.01>p>0.001 | 0.38 | $(x+1)^{0.38}$ |
| Total Mononchids | 0.80-2.76 | 1.19-6.69 | 0.21 | 1.25 | 0.01>p>0.001 | 0.375 | $(x+1)^{0.375}$ |
| Predatory Dorylaims | 1.60-3.40 | 1.72-10.67 | -0.01 | 1.70 | 0.02>p>0.01 | 0.15 | $(x+1)^{0.15}$ |
| Total Predators | 2.56-6.12 | 5.09-17.36 | 0.06 | 1.50 | 0.02>p>0.01 | 0.25 | $(x+1)^{0.25}$ |
| Spear-bearers | 47.44-85.52 | 399.6-5,716 | -2.42 | 3.00 | 0.05>p>0.02 | -0.50 | $\frac{1}{\sqrt{x+1}}$ |
| Non spear-bearers | 111.6-226.7 | 3,956-16,777 | -0.26 | 1.86 | 0.02>p>0.01 | 0.07 | $(x+1)^{0.07}$ |
| Total others | 159.0-310.4 | 4,764-24,528 | -1.00 | 2.14 | 0.01>p>0.001 | -0.07 | $\frac{1}{(x+1)^{0.07}}$ |

Table 11. Results of Taylor's Power Law analysis of December 1974 data; Vertical slices

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| Anatonchus Total | 3.12-6.40 | 4.91-99.15 | -0.76 | 3.40 | $p<0.001$ | -0.70 | $\frac{1}{(x+1)^{0.7}}$ |
| Clarkus Total | 0.80.32.67 | 1.01-4281 | 0.28 | 2.24 | $p<0.001$ | -0.12 | $\frac{1}{(x+1)^{0.12}}$ |
| Mylonchulus Total | 17.82-22.60 | 125.7-271.4 | 0.97 | 1.00 | N.S. | 0.50 | $\sqrt{x+1}$ |
| Total Mononchids | 24.45-58.40 | 155.6- 5535 | -3.20 | 4.00 | $p<0.001$ | -1.00 | $\frac{1}{(x+1)}$ |
| Total Others | 1700-2609 | 467888-4586002 | -3.77 | 3.00 | $0.05>p>0.01$ | -0.50 | $\frac{1}{\sqrt{x+1}}$ |

N.S.: Not significant

Table 12. Results of Taylor's Power Law analysis of February 1975 data; Vertical slices

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| *Clarkus* Total | 0.84-2.16 | 1.58-16.97 | 0.45 | 2.05 | $0.01>p>0.001$ | -0.025 | $\frac{1}{\log(x+1)}$ |
| *Mylonchulus* Total | 0.12-0.96 | 0.27-2.76 | 0.08 | 0.83 | N.S. | 0.59 | $(x+1)^{0.59}$ |
| Total Mononchids | 1.00-2.52 | 2.25-18.93 | 0.40 | 2.17 | $0.01>p>0.001$ | -0.09 | $\frac{1}{(x+1)^{0.09}}$ |
| Total Others | 171.9-229.4 | 7246-28980 | -0.44 | 2.00 | N.S. | 0 | $\log(x+1)$ |

N.S.: Not significant

Table 13. Results of Taylor's Power Law analysis of April 1976 data; Vertical slices.

| Nematode Group | Range of Mean | Range of Variance | 'a' Taylor's Power Law | 'b' Taylor's Power Law | Significance of correlation coefficient | 'p' Taylor's Power Law | Transformation |
|---|---|---|---|---|---|---|---|
| *Anatonchus* Total | 0-0.17 | 0-0.21 | 0.34 | 1.24 | $p<0.001$ | 0.38 | $(x+1)^{0.38}$ |
| *Clarkus* Total | 0.47-2.03 | 0.40-5.55 | -0.21 | 1.52 | $p<0.001$ | 0.24 | $(x+1)^{0.24}$ |
| *Mylonchulus* Total | 0.17-0.47 | 0.17-1.79 | 0.46 | 1.69 | $p<0.001$ | 0.155 | $(x+1)^{0.155}$ |
| Total Mononchids | 0.83-2.53 | 1.04-5.98 | 0.26 | 1.29 | $p<0.001$ | 0.355 | $(x+1)^{0.355}$ |
| Total Others | 202.6-310.1 | 7265-20951 | 0.60 | 1.50 | N.S. | 0.25 | $(x+1)^{0.25}$ |

N.S.: Not significant

nematodes) were aggregated (Table 10). Mylonchulus second stage juveniles and the juvenile stages of Clarkus were probably randomly distributed (with the possible exception of the first stage juveniles which may have been very weakly aggregated). Clarkus total juveniles had a b value suggesting weak aggregation and the inclusion of data for adult Clarkus increased the value of b to indicate stronger aggregation. The b values for Anatonchus total and for total mononchids may have indicated either weak aggregation or a random distribution (Table 10).

Vertical slices. As expected, the greatest b values for the vertical plane data were greater than for the horizontal plane, (Tables 11-13) ranging from 1.00-4.00 in December 1974 when aggregation of some groups was particularly marked (Table 11). Only Mylonchulus appeared to be non-aggregated. Strong aggregation of all groups except Mylonchulus was also recorded in February 1975 (Table 12); Mylonchulus was probably randomly distributed. All groups in April 1976 were probably aggregated although the greatest b values were less than for the previous dates; the b value for Anatonchus total and total mononchids may have represented a random distribution.

ii) Other Indices of Dispersion

The variance-mean ratio generally indicated that aggregated distributions were most frequent in the upper and intermediate levels with random distributions at lower levels (Tables 14-16). The values of all the dispersion indices are presented in Appendix 1 and Tables 14-16 represent a summary based on the 95% probability limits that the variance-mean ratio agreed with that expected from a Poisson series. The other dispersion indices agreed with the variance-mean ratio in the allocation of the groups to random, regular or aggregative distributions. Where two differing distribution types

represented the data at two depths within a level both are included in the summaries; the distribution type on the right of the pair represents the deeper depth e.g. in Table 14, Anatonchus juveniles in the upper levels were aggregated at 0-5cm and randomly distributed at 5-10cm.

In December 1974 values of the variance-mean ratio ranged from 0.20-9.86 for the unpooled data. Most Anatonchus groups were randomly distributed (Table 14) but juvenile Anatonchus showed aggregation at the 0-5cm and 20-25cm depths as did total Anatonchus at 0-5cm. All Mylonchulus groups were aggregated in the intermediate level (10-15cm depth) and Mylonchulus juveniles and Mylonchulus total were aggregated at all depths. The other subdivisions of Mylonchulus showed either random or aggregated distributions depending on depth. Clarkus gravid females were randomly distributed in the upper level; other Clarkus groups showed aggregation in the upper and intermediate levels and random distributions at lower depths.

Random distributions were more frequent in February 1975 (Table 15) with aggregation confined to the 0-1cm depth for all groups except total mononchids which were aggregated over 0-3cm depth. Values of the variance-mean ratio varied from 0.18-3.77 and were similar in April 1976 (0.14-3.54) when all Anatonchus and Mylonchulus subdivisions and most Clarkus subdivisions were randomly distributed; only Clarkus first stage and total juveniles and Clarkus total showed aggregation at some depths. Total mononchids, predatory dorylaims and total predaters were all aggregated in the upper levels but the distribution at other levels was variable (Table 16).

iii) Frequency distributions.

The full results of the frequency distribution analysis are presented in Appendix 2 (which includes the three best-fitting distributions) and are summarised in Tables 17-19. The Poisson distribution (random in Tables 17-19) fitted the data for those groups in which individuals were infrequently

Table 14. Summary of Indices of Dispersion*. December 1974 Samples.

| Nematode Group | Sample size 5x5x5cm | | | Sample size 10x10x5cm | | | Sample size 15x15x5cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels |
| Anatonchus Males | Ra | - | Ra | Ra | - | - | Ra | - | - |
| Anatonchus Gravid Females | - | - | - | Ra | - | - | Ra | - | - |
| Anatonchus Non-Gravid Females | - | - | - | - | - | Ra | - | - | - |
| Anatonchus Total Females | Ra | - | Ra | Re-Ra | - | Ra | Ra | - | Ra |
| Anatonchus Juveniles | A-Ra | Ra | Ra-A | A-Ra | Ra | Ra | A-Ra | Ra | Ra |
| Anatonchus Total | A-Ra | Ra | Ra | A | Ra | Ra | A | Ra | Ra |
| Mylonchulus Males | A | A | Ra | A | Ra | Re-Ra | Ra | Ra | - |
| Mylonchulus Gravid Females | Ra | A | Ra | Ra | A | Ra | Ra | Ra | - |
| Mylonchulus Non-Gravid Females | Ra-A | A | Ra | Ra-A | A | Ra | Ra | - | Ra |
| Mylonchulus Total Females | Ra-A | A | Ra-A | Ra-A | A | Ra | Ra | A | Ra |
| Mylonchulus Juveniles | A | A | A | A | A | A-Ra | A-Ra | A | Ra |
| Mylonchulus Total | A | A | A | A | A | A-Ra | A-Ra | A | Ra |
| Clarkus Gravid Females | Ra | - | - | Ra | - | - | - | - | - |
| Clarkus Non-Gravid Females | A | - | - | A-Ra | - | - | A-Ra | - | - |
| Clarkus Total Females | A | - | - | Ra | - | Ra | A-Ra | - | - |
| Clarkus Juveniles | A | A | A-Ra | A | A | Ra | A | A | - |
| Clarkus Total | A | A | Ra | A | A | Ra | A | A | Ra |

A: Aggregative Distribution; Ra: Random Distribution; Re: Regular Distribution.

Upper Levels: 0-5, 5-10cm depth; Intermediate Level : 10-15cm depth; Lower Levels: 15-20, 20-25cm depth.

*Based on the 95% probability limits of the variance-mean ratio agreeing with that expected from a Poisson series.

Table 15. Summary of Indices of Dispersion*. February 1975 Samples.

| Nematode Group | Sample size 1x1x1cm | | | Sample size 2x2x1cm | | | Sample size 3x3x1cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels |
| Mylonchulus Juveniles | A-Ra | - | - | A-Ra | - | - | A-Re | - | - |
| Mylonchulus Total | A-Ra | Ra | - | A-Ra | Ra | Ra | A-Ra | Ra | Ra |
| Clarkus Non-Gravid Females | Ra | - | - | Ra | - | - | Ra | - | - |
| Clarkus Total Females | Ra | - | - | A | - | - | Ra | - | - |
| Clarkus Juveniles | A-Ra | Ra | Ra | A | Ra | Ra-Re | A | Ra | Ra-Re |
| Clarkus Total | A-Ra | Ra | Ra | A | Ra | Ra-Re | A | Ra | Ra-Re |
| Total Mononchids | A | A | Ra | A | Ra | Ra-Re | A-Ra | Ra | Ra-Re |

A: Aggregative Distribution; Ra: Random Distribution; Re: Regular Distribution.

Upper Levels: 0-1cm, 1-2cm depth; Intermediate Level : 2-3cm depth; Lower Levels: 3-4, 4-5cm depth.

*Based on the 95% probability limits of the variance-mean ratio agreeing with that expected from a Poisson series.

Table 16. Summary of Indices of Dispersion*. April 1976 Samples

| Nematode Group | Sample Size 1x1x1cm | | | Sample size 2x2x1cm | | | Sample size 3x3x1cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Levels | Lower Levels | Upper Levels | Intermed. Levels | Lower Levels | Upper Levels | Intermed. Levels | Lower Levels |
| Anatonchus 4th st.Juveniles | - | - | - | - | - | - | - | - | Ra |
| Anatonchus Total Juveniles | - | - | Ra | Ra | - | Ra | Re | - | Ra |
| Anatonchus Total | Ra | - | Ra | Ra | - | Ra | Ra | - | Ra |
| Mylonchulus Non-Gravid Females | - | Ra | - | - | Ra | - | - | Ra | - |
| Mylonchulus Total Females | - | Ra | - | - | Ra | - | - | Ra | - |
| Mylonchulus 1st st.Juveniles | - | - | - | - | - | - | - | - | Ra |
| Mylonchulus 2nd st.Juveniles | - | - | - | - | - | - | - | Ra | - |
| Mylonchulus 3rd st.Juveniles | - | - | - | Ra | - | Ra | - | - | Ra |
| Mylonchulus 4th st.Juveniles | - | - | - | Ra | - | - | Ra | - | - |
| Mylonchulus Total Juveniles | Ra | Ra | Ra | Ra | Ra | Ra | Re | Ra | Ra |
| Mylonchulus Total | Ra | Ra | Ra | Ra | Ra | Ra | Ra | Ra | Ra |
| Clarkus Non-Gravid Females | - | Ra | - | Ra | Ra | - | Ra | Re | - |
| Clarkus Total Females | - | A | - | Ra | Ra | - | Ra | Ra | - |
| Clarkus 1st st.Juveniles | Ra-A | Ra-A | Ra-A | Ra-A | Ra-A | Ra | Ra | Ra | Ra |
| Clarkus 2nd st.Juveniles | Ra | Ra | Ra | Ra | Ra | Ra | Ra | Ra | Ra |
| Clarkus 3rd st.Juveniles | Ra | Ra | - | A-Ra | Ra | Ra | Ra | Ra | Ra |
| Clarkus 4th st.Juveniles | - | - | - | - | Ra | - | - | Ra | - |
| Clarkus Total Juveniles | A | Ra-A | Ra | A | Ra-A | Ra | A-Ra | - | - |
| Clarkus Total | A | Ra-A | Ra | A | Ra-A | Ra-A | A-Ra | Re-Ra | Ra |
| Total Mononchids | A | Ra-A | Ra-A | A | Ra | Ra-A | A-Ra | Re-Ra | Ra |
| Predatory Dorylaims | A | A-Ra | A | Ra-A | Ra | A | Ra-A | Ra | A |
| Total Predators | A | A-Ra | A | A | Ra | A | A | Re-Ra | A |

A: Aggregative Distribution; Ra: Random Distribution; Re: Regular Distribution.

Upper Levels: 0-1, 1-2cm depth; Intermediate Levels: 2-3, 3-4cm depth; Lower Levels: 4-5, 5-6cm depth

*Based on the 95% probability limits of the variance-mean ratio agreeing with that expected from a Poisson series.

recovered and was therefore more common at the lower levels where nematode density decreased; aggregated distributions (most frequently Neyman Type A or Negative Binomial in this study) were common in the upper levels. The Binomial distribution (regular) was rare but did describe the distribution of Mylonchulus gravid females at three depths in December 1974 and Mylonchulus total and Clarkus total at the lowest depths in April 1976. The frequency distribution results were very similar to the results of the indices of dispersion in the allocation of the groups to a distribution type.

In December 1974 less dense groups described by the Poisson distribution included Anatonchus females (Appendix 2, Table 1) but most groups were only described by this distribution at the lower depths e.g. Anatonchus males at 20-25cm (Appendix 2, Table 1) and Mylonchulus males and all Clarkus groups at depths below 15cm (Appendix 2, Tables 3, 6, 7). Mylonchulus non gravid and total females were exceptional in that the Poisson described their distributions at 10-15cm depth, but above and below this the Negative Binomial and Neyman Type A distributions provided the best fit of the data (Appendix 2, Table 4). The groups with greater density at most depths, and therefore described by aggregative distributions, were Anatonchus juveniles and total and Mylonchulus juveniles and total (Appendix 2, Tables, 2,5). Mylonchulus males and all Clarkus groups were described by aggregative distributions at depths down to 15cm and Anatonchus males only at 0-5cm depth (Appendix 2, Tables 1,3,6,7).

Similar results were obtained in February 1975 but the decreased density led to results for the upper levels only; total mononchids were described by the aggregative distributions at depths between 0 and 3cm. Four other groups were also aggregated (Table 18). The Poisson distribution occurred at 1-2cm depth for four groups and at 0-1cm depth for Clarkus non gravid females (Appendix 2, Tables 21,22).

Table 17. Summary of Computer Analysis of Frequency Distributions December 1974.

| Nematode Group | Sample size 5x5x5cm | | | Sample size 10x10x5cm | | | Sample size 15x15x5cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels |
| Anatonchus Males | A | - | Ra | Ra | - | - | Ra | - | - |
| Anatonchus Gravid Females | - | - | - | - | - | - | Re | - | - |
| Anatonchus Total Females | Ra | - | Ra | Re | - | Ra | Re | - | Re |
| Anatonchus Juveniles | A-Ra | Ra | A | A-Ra | Ra | Ra | Ra | Ra | Ra |
| Anatonchus Total | A | A | A | A | Ra | Ra | Ra | Ra | Ra |
| Mylonchulus Males | A | A | Ra | A-Ra | Re | Ra-A | Ra | Ra | - |
| Mylonchulus Gravid Females | Ra-Re | Ra | Re | Ra | Re | Ra-Re | Re | Ra | - |
| Mylonchulus Non-Gravid Females | A | Ra | A | Ra | Ra | Re | Ra | - | Ra |
| Mylonchulus Total Females | A | Ra | A | Ra-A | Ra | Re | Ra | Ra | Ra |
| Mylonchulus Juveniles | A | A | A | A | A | A-Ra | - | - | - |
| Mylonchulus Total | A | A | A | A | A | A-Ra | A | - | - |
| Clarkus Gravid Females | A | - | - | Re | - | - | - | - | - |
| Clarkus Non-Gravid Females | A | - | - | Ra | Re | - | Ra | - | - |
| Clarkus Total Females | A | - | - | A-Re | - | Ra | Ra-Re | - | - |
| Clarkus Juveniles | A | A | Ra | A | A | Ra | Ra | - | - |
| Clarkus Total | A | A | Ra | A | A | Ra | Ra | - | Ra |

A: Aggregative Distribution (most frequently Negative Binomial or Neyman Type A; Ra: Random distribution (Poisson); Re: Regular distribution (Binomial).

Upper Levels: 0-5, 5-10cm depth; Intermediate Level: 10-15cm depth; Lower Levels: 15-20, 20-25cm depth.

Table 18. Summary of Computer Analysis of Frequency Distributions. February 1975 Samples

| Nematede Group | Sample size 1x1x1cm | | | Sample size 2x2x1cm | | | Sample size 3x3x1cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Level |
| Mylonchulus Juveniles | A-Ra | - | - | A-Re | - | - | A-Re | - | - |
| Mylonchulus Total | A | - | - | A-Ra | Ra | Ra | A-Ra | Ra | Re |
| Clarkus Non-Gravid Females | Ra | - | - | Ra | - | - | - | - | - |
| Clarkus Total Females | - | - | - | Ra | - | - | - | - | - |
| Clarkus Juveniles | A-Ra | - | - | A | Ra | Ra-Re | A | Ra | Ra-Re |
| Clarkus Total | A-Ra | - | - | A | Ra | Ra-Re | A | Ra | Re |
| Total Mononchids | A | A | - | A | Ra | Re | A-Ra | Ra | Ra-Re |

A: Aggregative Distribution (most commonly Negative Binomial or Neyman Type A); Ra: Random Distribution (Poisson); Re: Regular Distribution (Binomial).

Upper Levels: 0-1, 1-2cm depth; Intermediate Level : 2-3cm depth; Lower Levels: 3-4, 4-5cm depth.

Table 19. Summary of Computer Analysis of Frequency Distributions. April 1976 Samples

| Nematode Group | Sample size 1x1x1cm | | | Sample size 2x2x1cm | | | Sample size 3x3x1cm | | |
|---|---|---|---|---|---|---|---|---|---|
| | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels | Upper Levels | Intermed. Level | Lower Levels |
| Anatonchus 4th st.Juveniles | - | - | - | - | - | - | - | - | Ra |
| Anatonchus Total Juveniles | - | - | Ra | Ra | - | Ra | Re | - | Ra |
| Anatonchus Total | Ra | - | Ra | A | - | Ra | Re | - | Ra |
| Mylonchulus Non-Gravid Females | - | Ra | - | - | - | - | - | Re | - |
| Mylonchulus Total Females | - | Ra | - | - | - | - | - | Re | - |
| Mylonchulus 1st st.Juveniles | - | - | - | - | - | - | - | - | Ra |
| Mylonchulus 2nd st.Juveniles | - | - | - | - | - | - | - | Ra | - |
| Mylonchulus 3rd st.Juveniles | - | - | - | Re | - | Ra | - | - | Ra |
| Mylonchulus 4th st.Juveniles | - | - | - | Re | - | - | Re | - | - |
| Mylonchulus Total Juveniles | Ra | Ra | Ra | Re | Ra-Re | A | Re | Ra-Re | Ra |
| Mylonchulus Total | Ra | A-Ra | Re | Re | Ra-A | Re-A | Re-Ra | Ra-Re | A |
| Clarkus Non-Gravid Females | - | Ra | - | Ra | Ra | - | Ra | Re | - |
| Clarkus Total Females | - | - | - | Ra | Ra | - | Ra | Re | - |
| Clarkus 1st st.Juveniles | Ra | Ra | Ra | A | Re-Ra | Ra-A | Ra | Ra-Re | Re-Ra |
| Clarkus 2nd st.Juveniles | Ra | Ra | Ra | Ra | Ra-Re | Ra | Re-Ra | Ra-Re | Ra |
| Clarkus 3rd st.Juveniles | Ra | Ra | - | Ra | Ra | Ra | Ra-Re | Ra | Ra |
| Clarkus 4th st.Juveniles | - | - | - | - | Ra | - | - | Ra | - |
| Clarkus Total Juveniles | A | Ra | Ra | A | Ra-A | Ra-A | A-Ra | Re-Ra | Ra |
| Clarkus Total | A | Ra-A | Ra-Re | A | Ra-A | Ra-A | A-Ra | Ra | Ra-A |
| Total Mononchids | Ra-A | A-Ra | Ra | A | Ra-A | Ra-A | A-Ra | Re-Ra | Ra |
| Predatory Darylaims | A | A-Ra | A | A | Ra-Re | Ra-A | Ra-A | Ra | A |
| Total Predators | A | A | A | A | Ra | Ra | A | Ra | A |

A: Aggregative Distribution (most commonly Negative Binomial or Neyman Type A); Ra: Random Distribution (Poisson); Re: Regular Distribution (Binomial).

Upper Levels: 0-1, 1-2cm depth; Intermediate Levels: 2-3, 3-4cm depth; Lower Levels: 4-5, 5-6cm depth.

In April 1976 the Poisson model was very frequent and described the distribution of all except the larger groups e.g. Clarkus total juveniles and total at 0-1 and 1-2cm depths. Predatory dorylaims and total mononchids were strongly aggregated with the Neyman Type A or Negative Binomial distributions occurring frequently (Appendix 2, Tables 31-38).

In the vertical slices (Appendix 2, Tables 23,24) the distributions of Mylonchulus and Clarkus varied markedly between slices; the Neyman Type A and Poisson occurred with equal frequency and often in adjoining slices. Only total mononchids appeared to be distinctly aggregated in all slices, but even so the particular distributions varied.

iv) Pooled Data

Pooling the original data tended to increase the value of the variance-mean ratio but the wider 95% probability limits caused more groups to be described as randomly or regularly distributed; nonetheless the pattern was not substantially altered (Tables 14-16). The variance-mean ratio varied from 0.17-18.96 (10x10x5cm) and from 0.17-21.50 (15x15x5cm) in December 1974 (Appendix 1, Tables 12-21 and 22-28 respectively. In February 1975 the range was 0.22-5.57 for the $4cm^3$ data and 0.14-5.09 for the $9cm^3$ data (Appendix 1, Tables 37-41 and 42-45 respectively). Similarly for April 1976 the range was 0.16-4.35 ($4cm^3$) and 0.20-3.52 ($9cm^3$) (Appendix 1, Tables 59-71 and 72-82 respectively).

Pooling the original data had a similar effect on the frequency distributions, with a decrease in aggregative distributions and consequent increase in Poisson and Binomial distributions (Tables 17-19; Appendix 2, Tables 8-52). This effect was apparent on all counting dates.

## DISCUSSION

The size of the soil cubes in this study were chosen to have some relevance to the size of the mononchids, which though large by soil nematode standards (mean lengths 1mm to 2.5mm) are nevertheless extremely small in relation to the commonly used sample sizes. The 125cm$^3$ cubes contained too many nematodes to be analysed by some of the techniques except when the smallest subdivisions (males, gravid females etc) were used; increasing the "size" of these cubes by pooling the data did not improve the analysis, but enabled comparison with the results of other authors. 1cm$^3$ cubes proved more appropriate, although data analysis as if from a cube with 2cm sides enabled the dispersion to be demonstrated even more clearly.

A second advantage of the small soil cubes was that complete counts including every nematode (within the limits of the extraction technique) could be analysed rather than the usual population estimates based on sampling. Concomitant with small samples however, were small means which restricted data analysis; it is believed that the advantages of relating sample size to the size of the nematodes, and to the smallest aggregations they are likely to form (e.g. aggregation around a feod source, or offspring around a parent) outweighed the disadvantages.

The study of animals in soil presents particular difficulties; extraction techniques introduce an error that is difficult to estimate and it has to be assumed that the error is similar for all samples of a particular size, provided the conditions of extraction are constant. A second problem is that soil sampling is destructive and it is therefore not possible to monitor changes in distribution with time at a particular site. The only alternative is to sample as close as possible to the original site.

In this study the micro-distribution results, and particularly the general ecology, refer only to the populations within the soil blocks on the counting dates; the techniques used were not designed to represent the

entire population of the grassland and represented a dynamic situation at one particular time. Nevertheless it is hoped that further studies will prove that the general conclusions drawn are correct and applicable to other populations.

The numbers of nematodes varied considerably between the counting dates and the effects of temporal fluctuations and cube size were difficult to separate. That the differences did represent density changes was suggested by four things: first, the differences between February 1975 and April 1976 when cube size was equal; second, differences in apparent density due to cube size should effect all groups in a similar manner, whereas the numbers/$dm^3$ of Anatonchus decreased and all other groups increased; third, the results of Nelmes and McCulloch (1975) showed that large fluctuations in mononchid density could occur over monthly intervals on this site and fourth (although this might also be influenced by cube size), the proportion of juveniles was 20-30% higher in the $1cm^3$ cubes, suggesting that the adults were actively reproducing.

Andrassy (1962) concluded that $1cm^2$ samples would produce similar estimates of the number of nematode species and individuals as samples upto $15cm^2$. Andrassy made no mention of extraction and probably made a similar assumption to that made in this study, that all sample sizes were extracted with similar efficiency. On a larger scale, Smith and Wallace (1976) concluded that sampling with an area of 4mx4m gave a better estimation of a Helicotylenchus dihystera population than larger areas, unless the number of samples was increased disproportionately.

Most of the general ecology recorded in this study needs little specific comment. The percentage of mononchids in the total nematode population was similar to that recorded by Nelmes and McCulloch (0.23-0.69%), especially for the only month common to both studies (April : 0.6% in this study; 0.69% in Nelmes and McCulloch, 1975). Low percentage mononchids were

also recorded by Yuen, 1966 (0.88% in woodland and 0.39% in grassland), Boag, 1974 (1.6-5.9% in deciduous forests and 1.2-3.33% in coniferous forests), and Banage, 1963 (0.2-1.0% in moorlands).

The sex ratios recorded are probably only accurate estimates in the $125cm^3$ cubes when they were similar to those in Nelmes and McCulloch (1975); the other cube sizes were too small for accurate estimates to be made. The proportion of gravid females was also similar to that recorded by Nelmes and McCulloch (l.c.) but whether a female was classified as gravid or non-gravid could change in a few moments if a single egg was deposited, and storage at 10°C could have changed the proportion radically.

The depth distribution for most of the groups recorded were not unusual but indicate that the density was greatest at the surface. Thorne (1927) observed that the topmost two inches of soil was avoided by mononchids, presumably because the climate in Utah and Idaho can lead to large fluctuations in temperature and soil moisture at this depth. In the more temperate climate of the Sénart Forest, Arpin (1975b) recorded that most mononchids were restricted to top 2.5cm of soil which agrees with the results of this study. In Brunoy Park mononchids were rarely found below 10cm (Arpin 1975b) whereas in this study mononchids were found in fairly large numbers at depths down to 25cm.

The depth distributions in February 1975 and April 1976 suggested a downward shift on the latter date; this was reflected in the micro-distribution results with aggregative distributions occurring at 1-2cm and 2-3cm depths and the Binomial at 5-6cm depth. It is conjectured that this trend represented the response of the nematodes to macro-climatic factors which can be illustrated by meteorological data recorded within 0.5km of the site: over the six weeks preceding 4-ii-75 115.4mm of rain fell and the mean daily temperature at 5cm depth was 6.3°C; comparative figures for 13-iv-76 were 17.5mm of rain and 5.9°C. The dry spring of 1976 was therefore unsuited to the usual spring increase in nematode numbers and any

consequent changes in distribution; nematode density was similar on both sampling dates (Table 4) but the dry weather in 1976 appeared to have caused the nematodes to migrate to the presumably more moist conditions at lower levels.

Application of the power law indicated that within the whole block, most of the soil nematode groups investigated were increasingly aggregated as the nematode density increased, this contagion being particularly noticeable in the vertical plane. The values of b obtained were generally within the range recorded in Taylor (1961) but the vertical plane data for total Anatonchus and total mononchids in December 1974 exceeded the maximum value of b (3.08 for symphilids) calculated by Taylor (1961).

The general aggregation of nematodes in the upper levels reflected the greater density of nematodes near the surface and conversely the subdivisions (males, females etc) tended to show random distributions more frequently than larger groupings. The aggregative tendency becomes disproportionately greater as density increases and hence when density has an environmental gradient, as with depth in this study, the density and depth effects are confounded.

Arpin (1975b) calculated variance-mean ratios for five species of soil nematodes in samples taken on a 1mx1m grid system. He concluded that all the species followed a Negative Binomial distribution; the variance-mean ratio decreased with depth and only at the greatest depth (7.5-10cm) approached the values recorded in this study. This difference can be related to the difference in sample size (300-400g in Arpin's study) and to the greater density of the species Arpin investigated. Smith and Wallace (1976) used the Poisson index of dispersion $\Sigma(x-\bar{x})^2 / \bar{x}$ to show that a soil population of Helicotylenchus dihystera was consistently patchy. The areas of high density changed markedly with time and did not seem correlated with environmental factors. Arlt (1973) mapped the distribution of marine nematodes over an area of 1600cm$^2$ and found a large variation in the number of nematodes

per $1cm^3$ sample.

Apart from the response to environmental factors in April 1976, the distribution of the nematodes in this study appeared reasonably constant, but the change in density with depth prevented any single distribution from adequately describing the distribution of a particular group. Total Clarkus and total mononchids were best described by the Negative Binomial or Neyman Type A distributions in the upper soil layers and the Poisson and its derivatives at greater depths. Total Mylonchulus followed a similar pattern in February 1975 and in April 1976 but was best described by the Negative Binomial or Neyman Type A distributions at all depths in December 1974. The Binomial distribution described the distribution of some groups at the lowest depths. As expected, the less dense subdivisions appeared to be described frequently by the Poisson distribution whilst the larger subdivisions such as total juveniles often had similar distributions to their respective generic totals. Predatory dorylaims appeared aggregated (Negative Binomial or Neyman Type A models) at most depths. The $125cm^3$ cubes did not deviate from these patterns, indicating that there were probably several overlying distributions on differing scales.

In considering how the observed distributions arose, it seems probable that they were related to food sources. Microbivorous nematodes are likely to aggregate in areas of high microbial activity, and some phytoparasitic nematodes are known to aggregate at the tips of plant roots (Pitcher, 1967). Predators observed in laboratory cultures congregated on the perimeter of dense prey aggregations and fed on those nematodes that migrated into the surrounding medium. The correlations between potential prey and predators recorded in this study (Tables 5-7) may have reflected a true predator-prey interaction, or may merely have indicated that the best micro-environmental conditions for the prey were also the most suitable for predators. Yeates (1968) demonstrated a correlation between numbers of predatory nematodes in sand dunes and numbers of their enchytraeid prey but Nelmes

and McCulloch (1975) found no correlation between the numbers of mononchids and various phytoparasitic nematode genera. Clarkus and Anatonchus are known predators of nematodes, but the food of Mylonchulus is less certain (Thorne, 1927; Szczygiel, 1971; Cohn and Mordechai, 1974; Nelmes and McCulloch, 1975) and the distribution of Mylonchulus may have reflected a food source other than nematodes, even though highly significant correlations with potential prey numbers were recorded in December 1974 and February 1975.

Nelmes and McCulloch (1975) reported that Prionchulus punctatus was very susceptible to bacterial metabolites; if this applies to other mononchid species it seems likely that predator aggregations would occur around the aggregations of microbivorous nematodes, rather than superimposed upon them. The results of the regression analyses of the April 1976 data did not indicate clear preferences for either spear-bearing or non spear-bearing nematodes by any predator. The positive correlation between spear-bearers and non spear-bearers suggested that these groups were associated (either by preference for particular micro-environmental factors, including space, or because microbial activity is often relatively great in the vicinity of plant roots), which may have explained the apparent lack of preference for either group on the part of the predators. The positive correlation between predatory-dorylaims and total mononchids indicated that a degree of competition may have existed. The variation with depth in the percentage of the various life stages of the mononchid genera tended to decrease when total mononchids were considered and may have indicated that competition between the mononchid species also existed; thus if all juvenile mononchids were competing for the same limited food source their numbers would be limited and it would be likely that they would represent a constant percentage of the populations, especially if the adults were similarly limited. The associations and the constant proportion of life stages suggested that the soil nematodes form a heterogeneous assemblage of trophic groups, possibly

confined to a relatively small space along plant roots.

Some evidence that the aggregations of mononchids include familial groups was recorded. Numbers of Mylonchulus and Anatonchus juveniles correlated with numbers of the respective adult females. Juveniles did not always correlate well with prey groups and where correlations did exist it is not possible to distinguish the components of the relationship, which may have included association with adults which were themselves correlated with prey numbers or similar micro-environmental preferences, as well as the direct predator-prey relationship. In culture, feeding groups are often formed when up to ten juveniles (and other adults) feed on a prey nematode immobilised by an adult mononchid. There would be survival value and hence a selective advantage in juveniles remaining in the vicinity of adults.

Wallace (1958) suggested that nematodes are limited in their ability to disperse by their inability to displace soil particles, which might also lead to concentrations of juveniles around reproducing females. The Neyman Type A model was generated to express the distribution of insect larvae dispersing from an egg batch; this situation may be simulated by a female mononchid limited to a small space and therefore depositing all her eggs in that space. Juveniles hatching from the eggs would be able to disperse further due to their smaller size. This capability for dispersion by juveniles does not seem to be reflected in the data for April 1976 when the juveniles had not migrated to lower levels to the same extent as the adults. Possibly adults can migrate more rapidly or the juveniles may have hatched after the moisture content of the soil became unsuitable for nematode movement (Wallace, 1958). The juveniles of many nematode species are more resistant to adverse conditions than the adults (Evans & Perry, 1976) but observations on mononchid juveniles suggested that this was not the case with these nematodes.

Elliott (1971, pp 51-52) gives four ways in which contagious distri-

butions can arise. The first is true contagion i.e. the presence of one individual or event increases the chance that another will occur in the same area. The discussions of feeding relationships and familial groups concern examples of true contagion. It does not appear that individual mononchids are actually attractive to one another (except possibly females attracting males) or true contagion would be expected to operate at all depths. The second possibility is the existence of constant death-birth-immigration rates. In soil under permanent pasture the conditions may be suitable for such rates to be constant, as the soil provides a buffered environment; mononchid nematodes in general appear to be slowly reproducing species maintaining fairly constant numbers and this would tend to promote constant birth, death and immigration rates.

The remaining two alternatives suggested by Elliott (1971) are more difficult to consider in the present context. The first requires the clumps of individuals to be dispersed at random whilst the number of individuals within the clump are logarithmically distributed. The second is the presence of compound Poisson distributions; the Double Poisson model provided good fits of the data for some groups and the combination of Poisson distributions exhibited by the smaller subdivisions may have led to the contagious distributions of some larger groups.

Random and regular distributions are more difficult to discuss without further evidence; the observed randomness may mean only that non-randomness has not been detected. Regular distributions rarely describe the dispersion of a population over a large area but sometimes apply on a small scale (Elliott, 1971) such as the one discussed here. Regular distributions are often associated with communication between the animals (e.g. territorial behaviour) but this is difficult to envisage for soil-nematodes.

The results lead to the conclusion that soil nematodes were aggregated on a scale related to the size of the animals, and that this aggregation was particularly marked in the upper soil layers. The importance of

quadrat size was re-emphasised for although marked contagion was demonstrated in both 125cm$^3$ and 1cm$^3$ cubes, the degree of aggregation was not uniform and was better illustrated by studying data from quadrats 2cm square. It is possible that the 125cm$^3$ cubes revealed the overlying aggregative distribution detected by other authors, or they may have observed an even larger-scale distribution pattern.

The aggregative distributions were frequently described by the Negative Binomial or Neyman Type A models. At lower depths the Poisson model represented the best fit of the data and the Binomial distribution occasionally occurred at the lowest depths. The distributions of the nematode groups were superimposed so that the various trophic groups were intimately associated. The influences leading to the observed distributions seemed likely to include food sources although other explanations were probably also involved.

The study illustrated the problems of applying techniques developed by insect-ecologists to the three-dimensional situation in soil, especially as direct, continuous observation is not possible. A major limitation to an appreciation of the factors governing mononchid distribution and abundance in soil was the lack of detailed knowledge of their population dynamics. This information is best gained under controlled conditions and experiments made to this end are reported in the next section. As a result of these difficulties this study of the micro-distribution of nematodes is considered a preliminary to more detailed investigations that will elucidate the relationships on the micro-scale. Smith and Wallace (1976) also considered that micro-environmental factors were responsible for the fluctuations in mean density of Helicotylenchus dihystera under kikuyu turf; the present study re-inforced their suggestion that "explanations may need to be sought at the level of the individual nematode".

# III CULTURE OF PREDATORY NEMATODES.

## PREAMBLE

The early attempts at culture of mononchid nematodes e.g. by Steiner and Heinly (1922) and Cassidy (1931) were either unsuccessful or required techniques unsuited to the easy maintenance of large numbers of nematodes. The observations of Esser (1963) and Mankau (1975) suggested that mononchids did not complete their life-cycles in agar culture, but the method of Nelmes (1974) has proved effective for several (but not yet all) mononchid species and also nematodes of several other taxonomic groups (Small, unpublished; Grootaert, pers.comm.). The population of Prionchulus punctatus originally cultured by Nelmes was the source of the nematodes used both in this study and by Maertens (1975).

Nelmes adapted the method devised by Springett (1964)to culture enchytraeid worms in which 2% soil-extract agar was poured into petri-dishes and allowed to set before a thin layer of soil was added to the surface. Nelmes used 1% soil-extract agar and did not add soil. Seventy adult P.punctatus, obtained from the soil of an experimental barley-plot at Ashurst Lodge, Imperial College Field Station (and possibly some from the Grassland Research Institute, Hurley, Berkshire) were placed on each of three dishes and Panagrellus redivivus and Aphelenchus avenae added as prey (Nelmes, pers.comm.). The descendants of these females have been continuously cultured for more than four years (approximately equivalent to 40 generations).

P.punctatus was maintained in xenic, oligidic culture on a diet apparently consisting entirely of nematodes but it was possible that the predators, particularly the juveniles, fed on other organisms. Reproduction was parthenogenetic and the juveniles underwent four moults after hatching from the eggs. The embryonic and some post-embryonic development was described by Maertens (1975) and closely resembled that of the other mononchids which have been studied (e.g. M.aquaticus, Grootaert and Maertens, 1976). The length of the life-cycle was temperature dependent

but was long compared to that of many soil-nematodes (approximately 5-7 weeks at 20°-25°C in agar culture). The present study mainly concerned P.punctatus but included some observations on M.aquaticus and Labronema sp. which were cultured by similar techniques.

The method described below for the routine culture of P.punctatus evolved through the combination of accumulated experience, experimentation, data in the available literature and personal communications. Details of the experiments are presented after the description of the routine method; the experiments concerned culture conditions (temperature, medium), population development from single females and critical stages in the life-cycle. These experiments were preceded by investigation of the efficacy of several micro-culture techniques.

## 1. Routine Culture of Prionchulus punctatus.

### i) Soil-extract agar

The soil-extract was prepared by thoroughly mixing soil obtained from the garden at Ashurst Lodge, Imperial College Field Station with an equal volume of de-ionised water (Springett, 1964). The resulting suspension was allowed to settle overnight before the supernatant was filtered through a 0.5cm approx. layer of asbestos wool (Hopkins and Williams Ltd., Chadwell Heath, Essex) covered by a 0.5cm approx. layer of Celite Hyflo-Super-Cel filter aid (Koch-Light Laboratories Ltd., Colnbrook, Bucks) (Nelmes, pers.comm.). The resulting extract was free from soil particles (although varying in colour from pale yellow to colourless) and was approximately pH 7.

The extract was used to make 1% agar with Davis Standard Agar (Davis Gelatine Ltd., Leamington Spa, Warwicks) and was autoclaved for 15 minutes at 1 bar in covered flasks. The agar could be stored at room temperature with no obvious deterioration and without the growth of micro-organisms for at least several months. When needed the agar was gently liquified

over a bunsen flame and poured into 9cm diameter plastic petri-dishes. A quantity of agar was not reheated more than twice.

ii) Renewal of P.punctatus cultures.

Under normal conditions the cultures of P.punctatus lasted for four weeks approximately (at 25°C) before the population began to decline; to prevent this decline the cultures were renewed at four-week intervals. In the last year of this study complete degradation of the agar to a liquid state occurred after 2-3 weeks, necessitating more frequent reculturing.

The nematodes were transferred together with some of the agar from the old culture. Depending on an estimate of the number of predators in the old culture, 3 or 4 new cultures were usually started from each old culture but the range was 1-6. Assessment of old cultures indicated that a "good" culture (suitable for starting 5 new cultures) contained approximately 4000 predators of which 1000 were adult (Fig. 12); comparative figures for average (3-4 new cultures) and poor (less than 3 new cultures) were 2000 (640 adults) and 360 (60 adults) respectively. Experience indicated that reculturing into at least three new cultures was preferable to either leaving an old, poor culture intact or to reculturing into one or two new cultures. Alternatively the predators were extracted using the Whitehead tray technique (Whitehead and Hemming, 1965) and recultured on a single plate.

The molten agar was poured into the plates within a laminar flow cabinet to reduce contamination; when the agar was cool but not set the portion of the old culture was added. This gave good contact between the old and new agar and the nematodes could migrate into either with ease and often aggregated at the interface. Old agar transferred to the surface of set agar often trapped a layer of water that inhibited nematode movement between the old and new agar. In addition water from the old agar

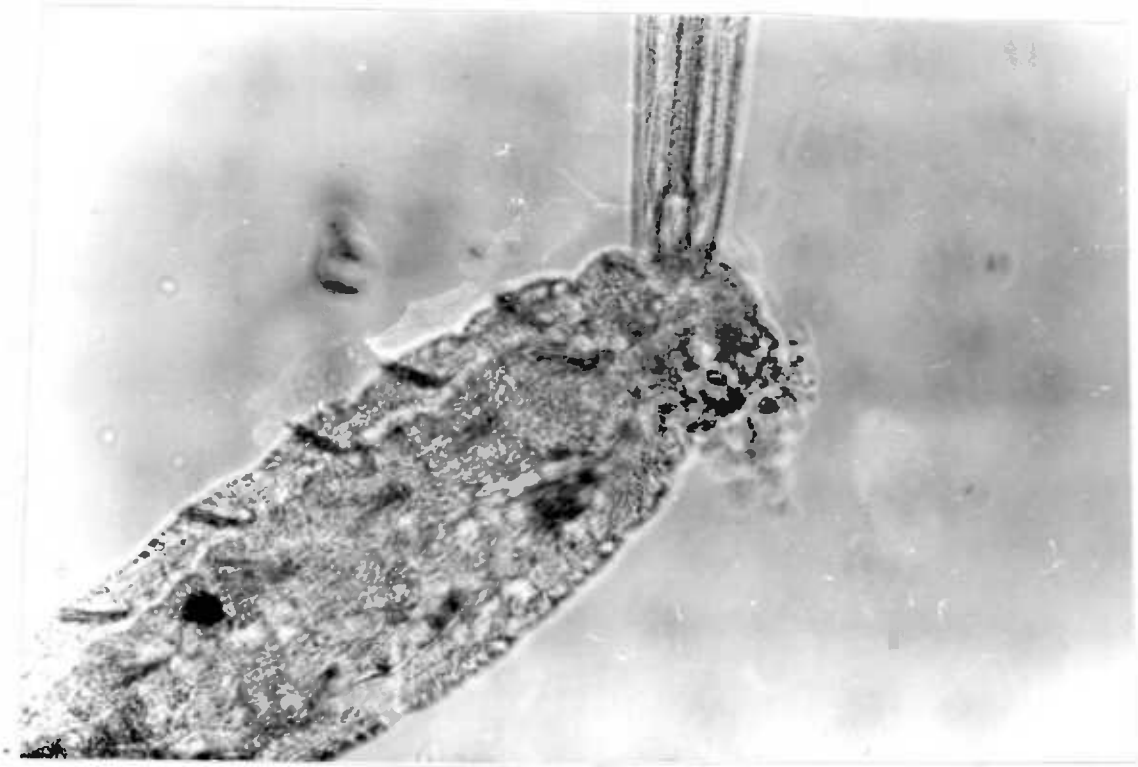


Fig. 11. Prionchulus punctatus apparently feeding upon an artificially wounded enchytraeid. (x260).

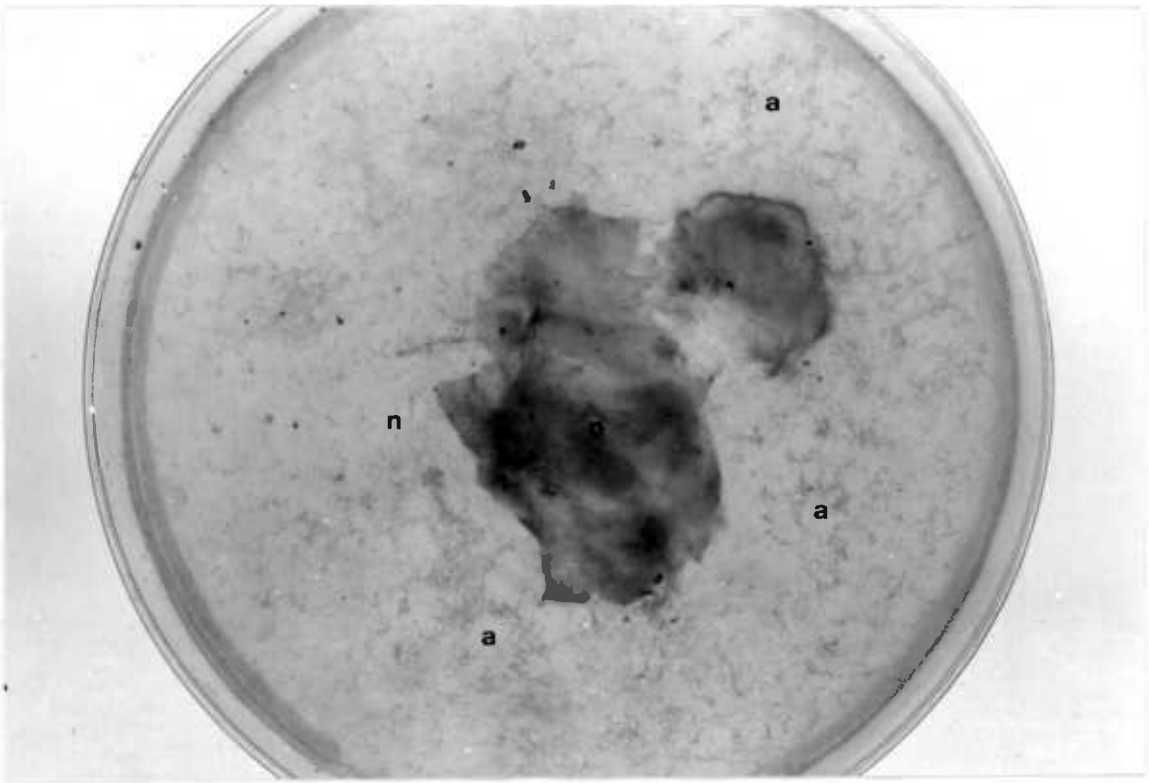



Fig.12. Example of a "good" culture containing approximately 4500 Prionchulus punctatus. Individual nematodes on or near the agar surface and aggregations (a) are visible o = "old agar" transferred from previous culture; n = "new agar"; p = 9cm. diam.petri dish. (xl.40)

accumulated on the surface of the new agar and again delayed predator colonisation. Long exposure in the laminar flow cabinet was needed to evaporate such water.

Prey nematodes were added to the newly-established culture which was left for 15-30 minutes in the laminar flow cabinet for any liquid on the agar surface to be reduced to a thin film.

iii) Maintenance of *P.punctatus* cultures

The cultures were incubated at 20°C or 25°C in the dark. Prey (*Panagrellus redivivus* or *Aphelenchus avenae*) were added at weekly intervals, although this was occasionally increased to accelerate predator population development or if the cultures contained many predators; conversely population growth could be retarded by less frequent prey additions. Prey were added by pipetting a few drops of a dense prey suspension in tapwater into the predator culture; when agar degradation became prevalent in the last year of the study, the suspension was filtered onto a 3.5cm diameter filter paper using a Büchner funnel. Pieces of the resulting mass of concentrated nematodes were placed on the agar surface of the predator cultures with a needle. After the addition of prey the cultures were left in the laminar flow cabinet for 15-30 minutes to reduce surface water and to aerate the cultures. *P.redivivus* did not survive or reproduce (other than females with fully developed eggs *in utero*) under the conditions of predators culture so that regular addition was necessary.

Population development in the cultures was not normally monitored (except for the assessment of predator numbers prior to reculture). A maximum of 150, (> 150,000 predators) but more commonly 50-60, cultures were maintained, requiring approximately twelve man-hours per week.

## 2. Culture of Prey Nematodes

### i) Panagrellus redivivus

Cultures of P.redivivus were maintained at room temperature on a thick paste of wholemeal flour (Allinsons Ltd., Castleford, Yorks) and tapwater (Ellenby and Smith, 1966). The paste was spread onto the bottom of 12.5cm diameter crystallizing dishes to form a 1cm thick layer. In the first year of the study the dishes containing newly constituted medium were autoclaved (15 minutes at 1 bar) prior to inoculation with P.redivivus. At the end of this period an unidentified, red coloured micro-organism always developed on the surface of the medium, and would spread to cover the entire surface within 72 hours. This organism appeared to suppress other micro-organisms and was not eaten by P.redivivus which died within a few days of inoculation. The micro-organism did not develop on non-autoclaved medium which was therefore used for the greater part of this study.

New cultures were started by rinsing the P.redivivus from the surface of old cultures and adding these nematodes to freshly constituted medium as a dense suspension. The nematodes from the old cultures were sufficient to inoculate an equivalent number of new cultures. These cultures were renewed every three weeks but were only harvested during the second week when the nematodes would move up the sides of the dishes in large numbers. The rate of population development could be increased by incubation at greater temperatures (25°C-28°C) but the medium was exhausted more rapidly.

Nematodes to be used as prey were scraped from the sides of the dish and suspended in tap-water. The small amount of medium adhering to the nematodes was removed either by repeated suspension, settling and decantation in tapwater, or by pouring the original suspension into a 53µm aperture sieve and rinsing the nematodes with a gentle stream of tapwater; the latter method was considerably quicker but resulting in the loss of the smaller juveniles. Finally the nematodes were concentrated in small

quantities of tapwater.

Caenorhabditis briggsae was also maintained by this method for a short period and was suitable as prey for P.punctatus.

ii) Aphelenchus avenae

Cultures of A.avenae were maintained on oat grain-fungus cultures by the method described by Evans (1970). This nematode was suitable as prey and was preferable to P.redivivus in micro-cultures where its smaller size and slower movement caused less disturbance to the medium.

iii) Plant-parasitic nematodes

No other nematodes were cultured in the laboratory but occasionally observations were made on the predation of P.punctatus on plant-parasitic nematodes. These nematodes were extracted from soil and concentrated by sieving. Individuals of Globodera rostochiensis and Meloidogyne incognita (Kofoid and White 1919) Chitwood 1949 were eaten by P.punctatus but these nematodes were not used for the general maintenance of the predator populations; Helicotylenchus dihystera was not eaten by P.punctatus.

3. Culture of Other Predatory Nematodes.

Many attempts to culture other predatory nematodes were made. Clarkus papillatus, Anatonchus tridentatus and Mylonchulus sigmaturus were extracted from soil taken from the orchard at Ashurst Lodge, Imperial College Field Station where they occurred in comparatively large, small and moderate numbers respectively (Nelmes and McCulloch, 1975; Small and Evans, in press).

Labronema sp. and Mononchus aquaticus were recovered from a greenhouse at Ashurst Lodge, Imperial College Field Station where both species were common contaminants of pot experiments and nematode stock-population pots.

Mesodiplogaster lheritieri was recovered from the fermentation layer (F-layer) of an area of bracken (Pteridium aquilinum)on Imperial College Field Station as were some Prionchulus punctatus used in attempts to establish new populations in culture. P.punctatus were also recovered from orchard soil but in small numbers (<20/dm$^3$) compared to the bracken F-layer (30-400/dm$^3$ approx.).

Soil-extract agar was used most commonly for the attempts at culture of these additional species and populations, but the soil-tube method (Steiner and Heinly, 1922) was also tried. Panagrellus redivivus was used as prey and, for C.papillatus, Aphelenchus avenae was also offered. The methods and results of the less successful trials are summarised in Table 20, and further details are given below, but quantitative data was not normally recorded.

i) Clarkus papillatus

C.papillatus appeared similar to P.punctatus in many aspects of its biology (e.g. normally parthenogenetic reproduction; predatory habit with the contents of the prey sucked out and ingested) and had been cultured by Steiner and Heinly (1922). Although therefore appearing suitable for culture by the same method as P.punctatus, cultures could not be established.

In soil-extract agar (with or without the soil said to be essential by Steiner and Heinly, 1922) C.papillatus penetrated the medium and fed on both P.redivivus and A.avenae; eggs, deposited in considerable numbers, developed normally and hatched but few juveniles survived longer than the second moult, and the populations died out after approximately three months. A population in a soil-tube declined over four months and the few remaining predators died within a further two months when transferred to a soil-extract plate.

Table 20. Summary of attempts to culture soil-nematodes other than P.punctatus.

| Nematode | Method: Culture Medium | Method: Inoculum | Method: Replicates | Results: Feeding | Results: Oviposition | Results: Juvenile Development | Results: Maximum Duration of Population |
|---|---|---|---|---|---|---|---|
| Clarkus papillatus | S.E.A. | ~30 | 1 | + | + | To 2nd moult | 3 months |
| | S.E.A. | ~25 | 1 | + | + | " " " | 3 " |
| | S.E.A. + Soil | ~25 | 1 | + | + | " " " | 3 " |
| | Soil | 31 | 5 | ? | ? | ? | 4 " |
| Anatonchus tridentatus | S.E.A. | 8 | 1 | + | ± | ? | 1 " |
| | S.E.A. | 22 | 1 | + | ± | ? | 1 " |
| | Soil | 15 | 1 | ? | ? | ? | 4 " |
| | Soil | 35 | 1 | ? | ? | ? | 4 " |
| | Soil | 81 | 1 | ? | ? | ? | 4 " |
| Mylonchulus sigmaturus | S.E.A. | 26 | 1 | - | - | - | 3 weeks |
| | S.E.A. | 64 | 1 | - | - | - | 3 " |
| | Algal culture* | 25 | 1 | + | - | - | 6 months |
| | S.E.A. + Algae | 5 | 1 | - | - | - | 2 weeks |
| Mesodiplogaster lheritieri | S.E.A. | >50 | 1 | + | + | + | 5 months |
| Mononchus aquaticus | S.E.A. | ~300 | 6 | + | + | + | > 5 months |
| | S.E.A. | ~50 | 1 | + | + | + | 7 weeks |
| Mononchus aquaticus + Labronema sp. | S.E.A. | ~300 | 1 | + | + | + | > 18 months |
| | | ~150 | | + | + | + | |
| Labronema sp. | S.E.A. | ~150 | 6 | + | + | + | > 18 months |
| | S.E.A. | >200 | 3 | + | + | + | > 16 months |

S.E.A.: Soil-extract agar

*See text for further explanation

+: feeding etc observed

-: feeding etc not observed

±: only those eggs already present in the oviducts at the time of inoculation were deposited.

ii) Anatonchus tridentatus

Attempts to culture A.tridentatus in both soil-extract agar and soil-tubes were not successful. A.tridentatus is a known predator but differs from P.punctatus in that the prey is frequently swallowed whole (Mulvey, 1961a; Szczygiel, 1971). Reproduction also differs as A.tridentatus appears to be obligately dioecious.

In soil-extract agar the predators were observed to feed and the few eggs present in the oviducts of the females were deposited; mating was not observed and no further eggs were produced. The deposited eggs hatched but the fate of the juveniles was not observed and within one month of inoculation no predators remained. In tubes of soil A.tridentatus did not survive for four months.

iii) Mylonchulus sigmaturus

The food preferences of M.sigmaturus have not been confirmed but probably include algae (Nelmes and McCulloch, 1975), "micro-organisms other than nematodes" (Thorne, 1927; Szczygiel, 1971) and nematodes (Cohn and Mordechai, 1974). Reproduction appears to be dioecious.

M.sigmaturus could not be cultured on soil-extract agar using nematodes as prey and the predators all died within three weeks. Dishes used to culture algal-feeding snails (Higby, pers.comm.) were also tried; the dish contained a 1cm deep layer of water agar and soil with a mixed culture of soil algae covering the agar surface. The algal layer also contained a mixed fauna of unidentified bdelloid rotifers and ciliates. Twenty-five M.sigmaturus were placed on the algal layer and left in daylight at room-temperature (~20°C) for two months before approximately one-fifth of the medium was searched for M.sigmaturus. Five nematodes were recovered but the absence of first stage juveniles and gravid females suggested that reproduction had not occurred. The gut contents of the adults included rotifer mastices and spherical bodies that could

have been either algal cells or ciliates; the gut contents of juveniles also included the spherical bodies.

The nematodes recovered were transferred to previously prepared soil-extract agar containing a small quantity of the soil used in the algal cultures; algae added to the agar surface did not increase either under ultra-violet light prior to nematode inoculation or in daylight after nematode inoculation. The nematodes all died within two weeks and no observations on feeding were made. The original culture was left for a further four months before half the remainder was searched for M.sigmaturus; the remaining portion was also searched two months later. No M.sigmaturus were recovered on either occasion.

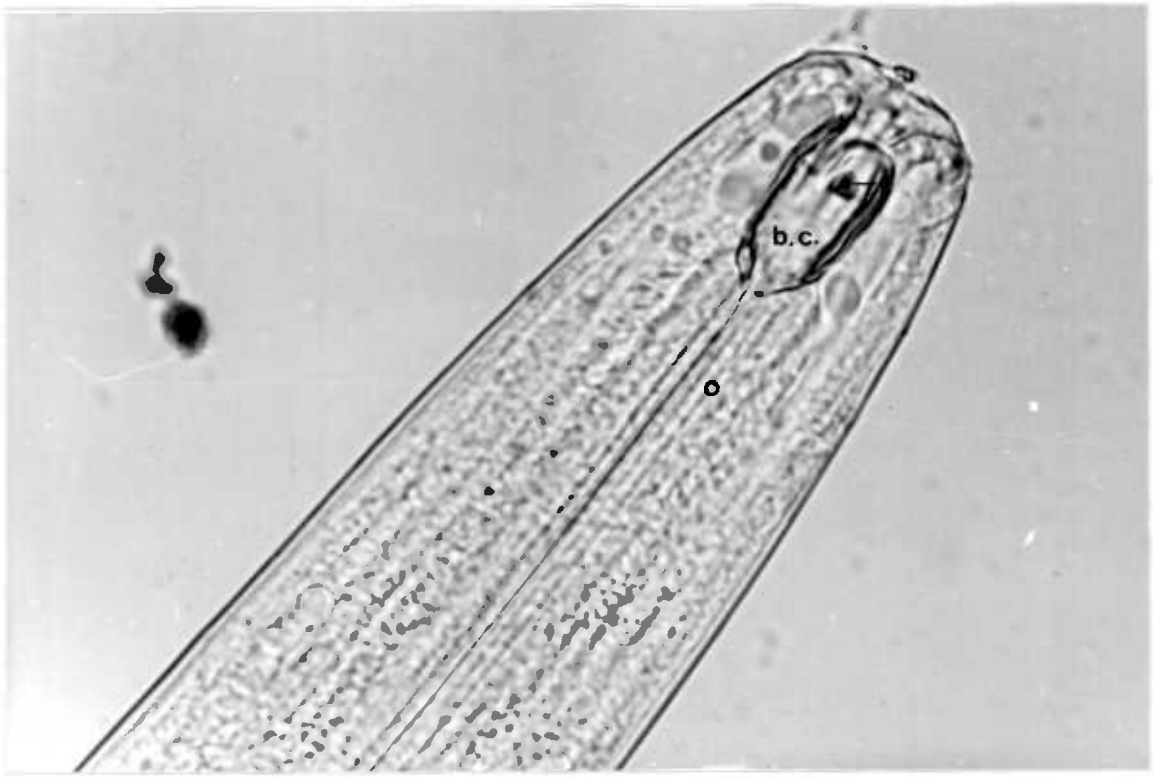
iv) Mesodiplogaster lheritieri

Large numbers of M.lheritieri developed in culture with P.punctatus from the bracken F-layer; M.lheritieri generally aggregated in the region of intense microbialactivity near detritus introduced from the F-layer material. Many eggs were deposited and the generation time at 25°C was approximately five days (twice as long as that recorded by Grootaert (1976a) probably because the soil-extract medium was less rich than that used by Grootaert). As successive recultures reduced the quantity of detritus per culture the numbers of M.lheritieri declined but some were still present five months after inoculation. These nematodes often fed on P.redivivus previously killed by P.punctatus but did not attack live nematodes. The rapid oesophageal pumping of both adults and juveniles suggested that they were primarily microbivorous. P.punctatus was not observed to attack M.lheritieri.

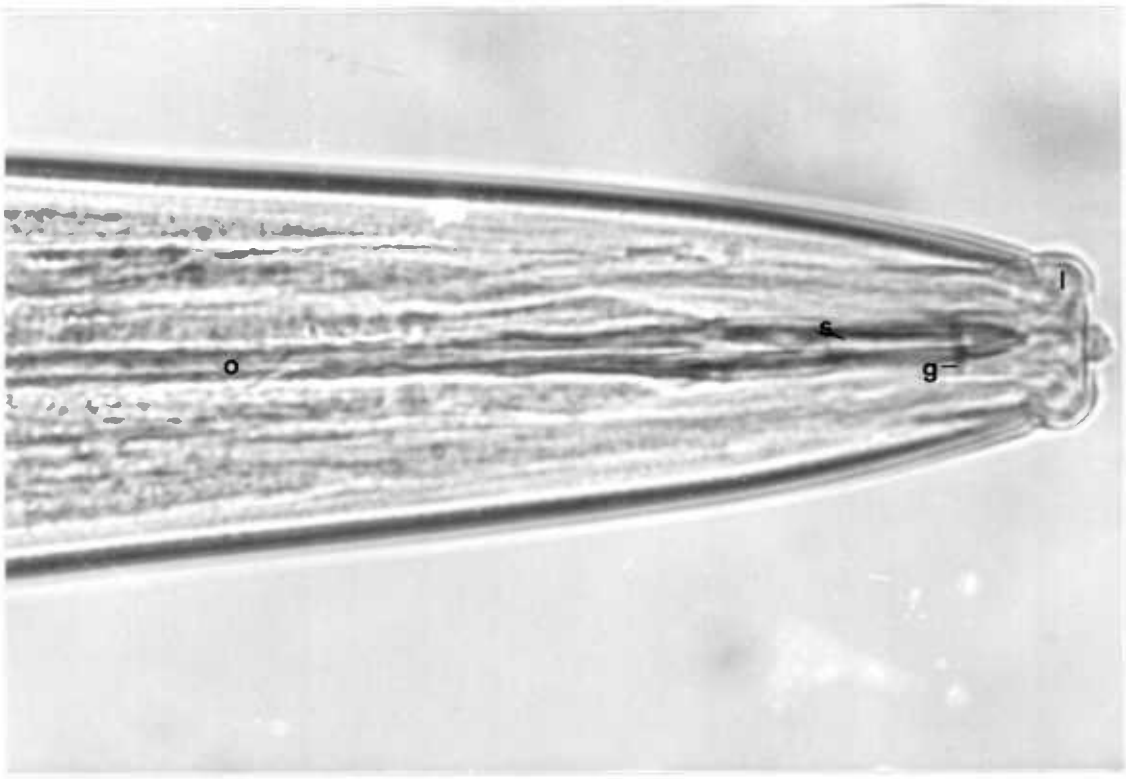
v) Mononchus aquaticus.

Specimens of M.aquaticus (Fig.13a) were originally noted in an

Fig.13. Anterior regions of Mononchus aquaticus and Labronema sp.

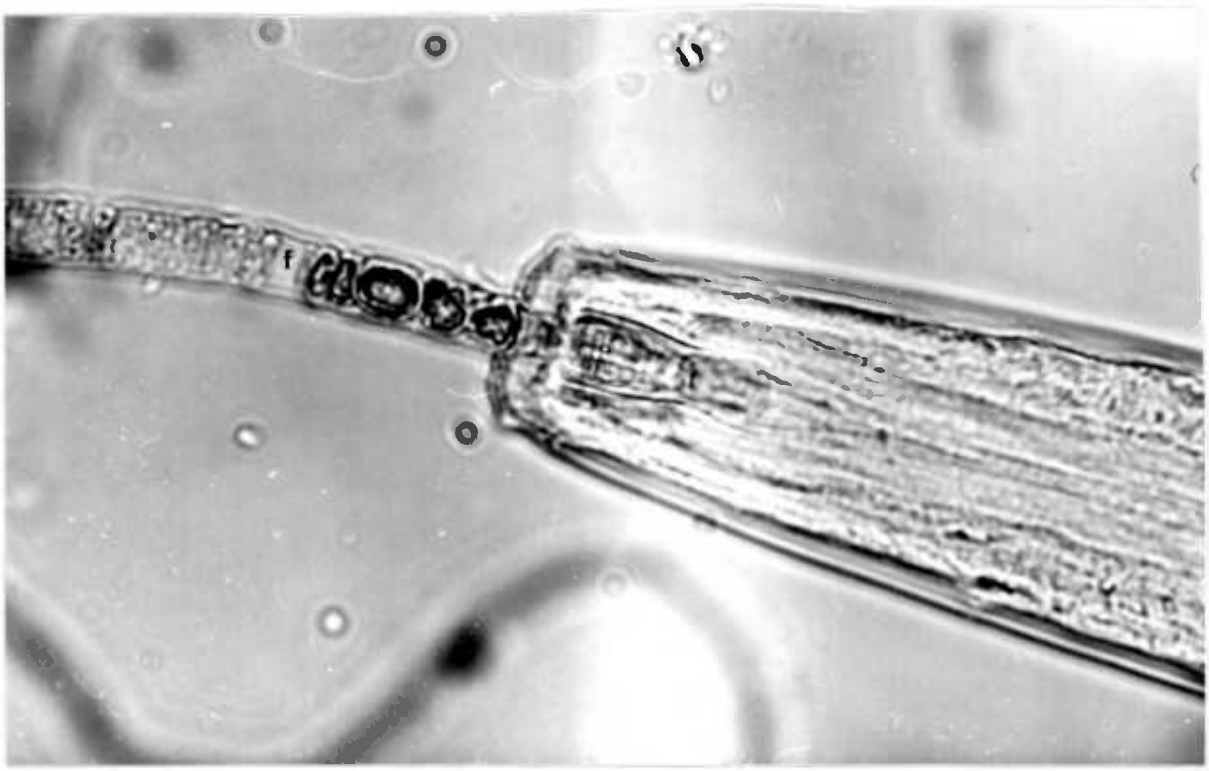



a) Ventral view M.aquaticus: note less pronounced lips and labial papillae and smaller buccal capsule than in P.punctatus. b.c = buccal capsule; t = dorsal tooth; o = anterior oesophag us. (x670).

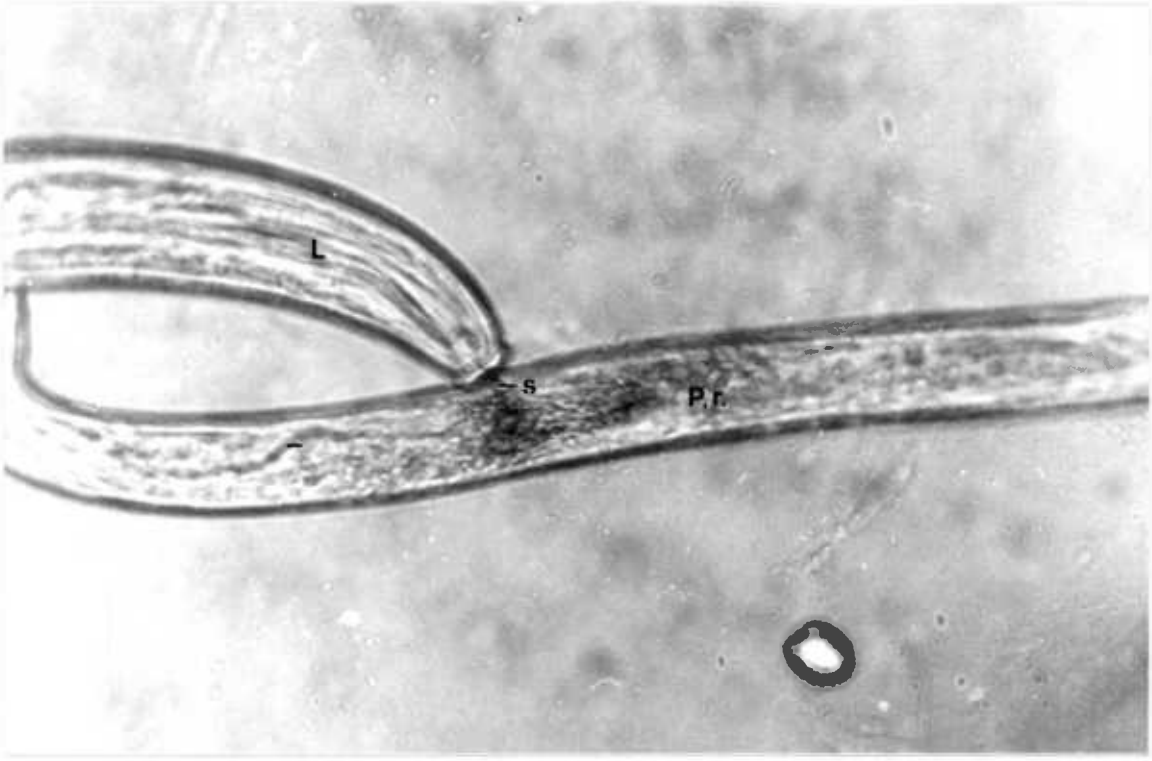



b) Lateral view Labronema sp: note pronounced lips (l), guiding ring (g), spear (s), and anterior oesophag us (o) (x670).

Fig. 14. Methods of feeding in Mononchida and Dorylaimida.




a) P.punctatus juvenile apparently ingesting an algal filament (f), showing the method of swallowing whole prey in Mononchida. (x515).




b) Adult Labronema sp. (L) feeding on an adult Panagrellus redivivus (P.r.); s = spear. (x415).

extract from a Helicotylenchus dihystera stock population pot; they were inoculated with the H.dihystera into a pot experiment where they increased in number to provide the nematodes used in attempts to establish cultures. The habits of M.aquaticus were then unknown but it has since been shown that nematodes provide an adequate diet and that reproduction is usually parthenogenetic (Grootaert and Maertens, 1976; Small, unpublished).

When inoculated onto soil-extract agar the first population of M. aquaticus reproduced rapidly for six weeks before the start of a slow decline in numbers that was not stopped by reculturing at four week intervals. Five months after the original culture was started so few M.aquaticus remained that they were added to subsequent cultures.

Some of the M.aquaticus from a second extraction of the pot experiment reproduced for seven weeks (1 reculture) when introduced into soil-extract agar. The population then declined until ten adults remained which were added to new populations in culture. The other nematodes from the second extraction of the pot experiment were placed on a separate plate and a mixed M.aquaticus/Labronema sp. population developed that has been maintained in culture for more than eighteen months. A single species culture of M. aquaticus has been maintained for more than a year. P.redivivus and A. avenae were suitable prey and similar routine culture methods to those used for P.punctatus were used with good results. The generation time at 25°C was a little over two weeks (Small, unpublished; Grootaert and Maertens, 1976).

vi) Labronema sp.

Labronema sp. (Fig.13b) were originally noted in the extract from H.dihystera stock population pots and were inoculated with the plant parasitic nematodes into a pot experiment, where their numbers increased. Labronema spp. were cultured by Ferris (1968) using rhabditid nematodes

as prey; unlike the mononchids Labronema spp. pierce their prey with a spear and ingest the disrupted body contents (Fig. 14a, b). Reproduction was dioecious.

Labronema sp. was seen to feed, mate and deposit eggs in soil-extract agar but the long generation time of 5-6 weeks at 25°C (Ferris, 1968; Small, unpublished) prevented a rapid increase in numbers. After three months the population began to noticeably increase; at the same time the populations of M.aquaticus in the same cultures were declining. For several months a population of Labronema sp. was maintained but eventually it was merged with other populations in culture.

Large numbers of Labronema sp. were obtained from a Hirschmanniella oryzae (van Breda de Haan 1902) Luc and Goodey 1964 stock population pot where they outnumbered the plant-parasites (Bababatola, pers.comm.). When introduced into soil-extract agar with P.redivivus as prey the Labronema sp. reproduced well and have been kept in continuous culture for more than 16 months. Ferris (1968) suggested that a fungal weft was necessary for the deposition of eggs but this was not found in this study. The original population was cultured with M.aquaticus but single-species cultures were easily established by transferring adults to fresh plates and adding P.redivivus. The culture technique was essentially the same as for P.punctatus but there were some indications that a 6-8 week period between recultures was beneficial to population development; this could not be confirmed as rapid degradation of the agar in the latter part of this study necessitated more frequent reculturing.

vii) New populations of P.punctatus.

Several attempts to repeat the establishment of P.punctatus in culture were made but few were successful. Small numbers of P.punctatus were introduced into soil-extract agar on three occasions; the predators penetrated the agar, fed on P.redivivus and deposited many eggs. Many juveniles

hatched but few passed the second moult and most died within two months.

P.punctatus extracted from bracken F-layer material were placed on soil-extract agar to which agar (without nematodes) from an old P.punctatus culture was added. The adult predators fed on P.redivivus and approximately 2 eggs/adult/day were deposited over the first eight days. The eggs hatched and the juveniles developed normally to give a large population within two months. The agar then started to degrade within two weeks of each reculture and the excess liquid and frequent reculturing appeared to adversely affect the predator population which never recovered the original density achieved. The population finally died out ten months after its establishment in culture.

A series of large samples ($2dm^3$ each) were taken over two months from the bracken F-layer; the P.punctatus density was low ($30/dm^3$ approx.) but each sample provided sufficient nematodes for a new culture. The nematodes were maintained for six months as a separate population to that established in culture by Nelmes. After six months the populations were merged.

4. Organisms Contaminating Predator Cultures.

The cultures of P.punctatus were never free from a wide range of contaminant organisms of which there were two groups: a) those that were continuously present, were difficult to remove and which completed their life cycles in the cultures (numbers i-v in Table 21) and b) those that were introduced with soil-extracts (numbers vi-x). Some organisms in the latter group would reproduce if not removed but most could be allowed to decline in numbers of their own accord. Few attempts were made to clear the cultures of group a) organisms as chemical treatments often failed (or were toxic to the predators) and hand removal, where possible, was too time consuming. Aspects of these contaminant organisms are summarised in Table 22 and some are discussed further below.

Table 21. Summary of observations on organisms contaminating P.punctatus cultures.

| No. | Taxonomic Group | Number and Identification of Species | Occurrence | Reproduction in culture | Duration of Population | Control of Contaminants | Interactions with P.punctatus | References for interactions with nematodes |
|---|---|---|---|---|---|---|---|---|
| i | Bacteria | Many spp.: Unidentified | Continuous | + | >3yrs | See text | See text | See text |
| ii | Fungi | Arthrobotrys sp.<br>Harposporium sp.<br>Many spp.Unidentified | Continuous | + | >3yrs | See text | See text | See text |
| iii | Ciliata | Many spp.Unidentified | Continuous | + | >3yrs | None | Occasionally ingested | See text |
| | Protozoa<br>Amoebae | 1? | Rare | + | 2months | None | Occasionally ingested | |
| iv | Acarina | 1-3 Unidentified | Continuous | + | >3yrs | See text | None observed | See text |
| v | Copepoda | 1: Phyllognathopus vigueri | Once | + | >1yr | None | See text | - |
| vi | Enchytraeidae | 1 Unidentified | Occasional | + | >1yr | Hand removal | None observed | - |
| vii | Rotifera:Bdelloidea (Fig.15) | 1 Unidentified | Occasional | -* | >3months | None | Occasionally ingested | - |
| viii | Tardigrada (Fig.16) | 1 Macrobiotus sp. (probably M.macronyx) | Occasional | -** | >2months | None | Occasionally attacked | Hutchinson & Streu,1960<br>Doncaster & Hooper 1961 |

*Reproduction occurred on one occasion.

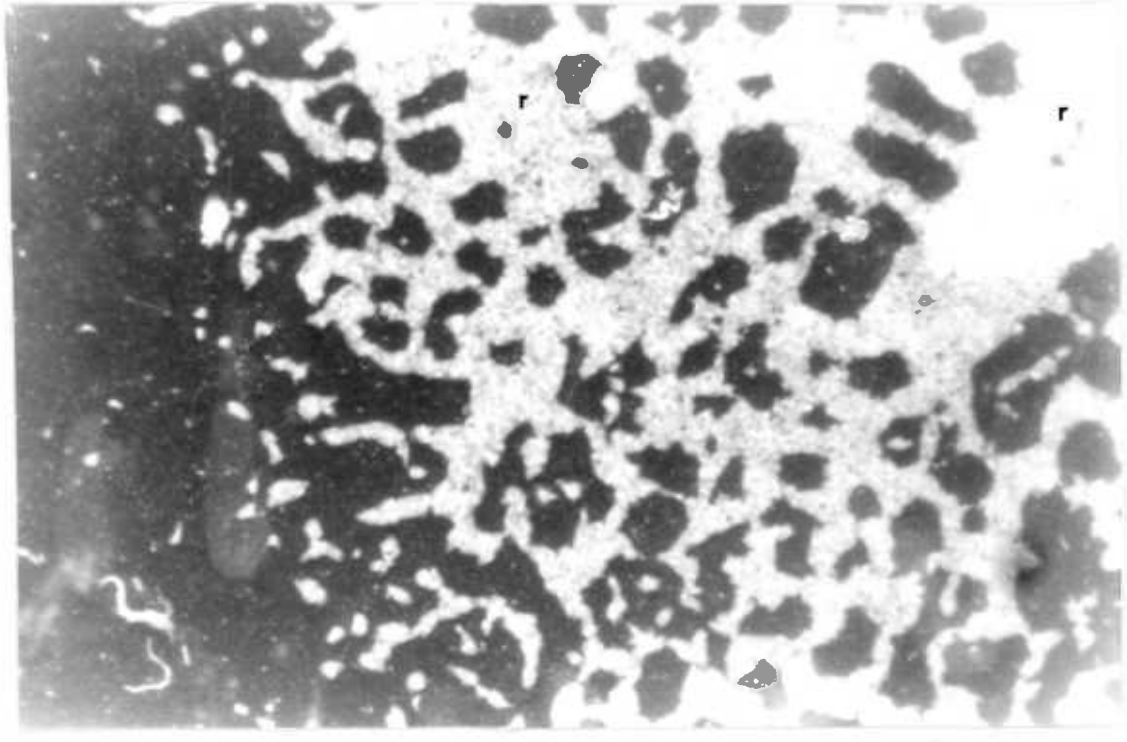
**Unsculptured eggs deposited in cast cuticles on one occasion.

Cont....

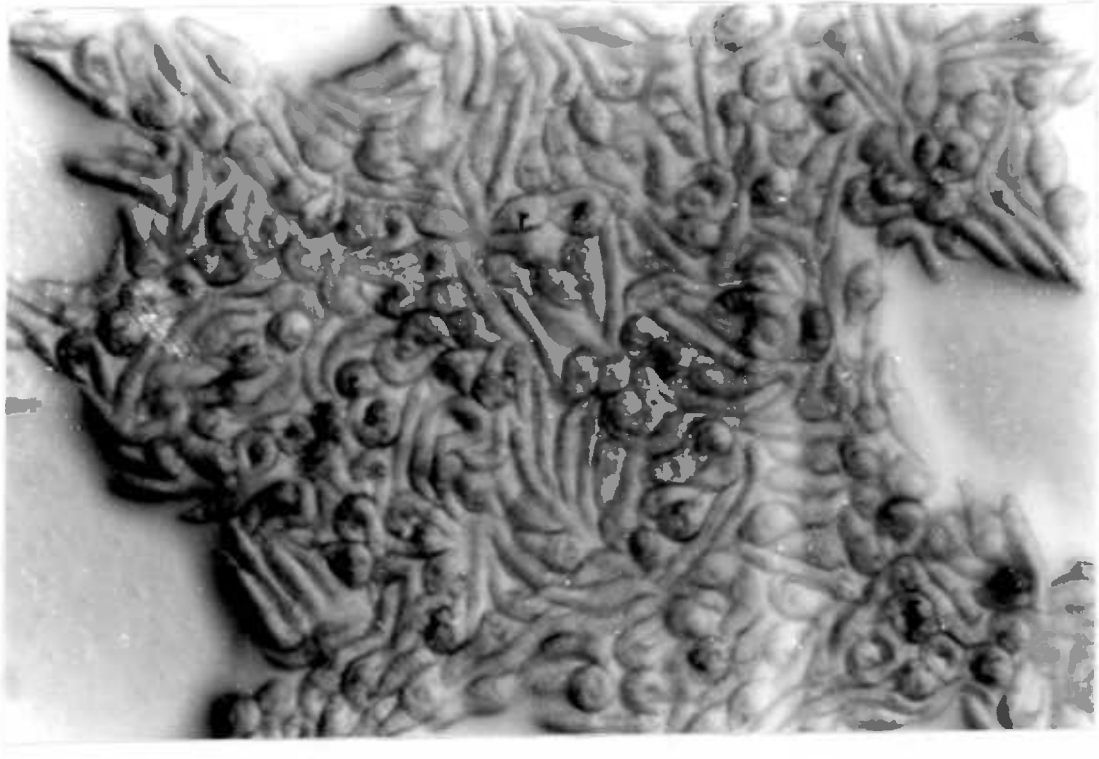
Table 21 Cont.

| No. | Taxonomic Group | Number and Identification of Species | Occurrence | Reproduction in culture | Duration of Population | Control of Contaminants | Interactions with P.punctatus | References for interactions with nematodes |
|---|---|---|---|---|---|---|---|---|
| ix | Dipteran larvae Insecta | ? Unidentified | Rare | - | 3wks | Hand removal | None observed | Rodriquez, Wade & Wells, 1962 |
| | Coleopteran larvae | ? Unidentified | Rare | - | 3wks | Hand removal | None observed | - |
| x | Turbellaria | 1 Unidentified | Rare | - | 2wks | None | None observed | Sayre & Powers 1966 |

Fig.15 Photomicrographs of a contaminant population of a bdelloid rotifer in a culture of P.punctatus.

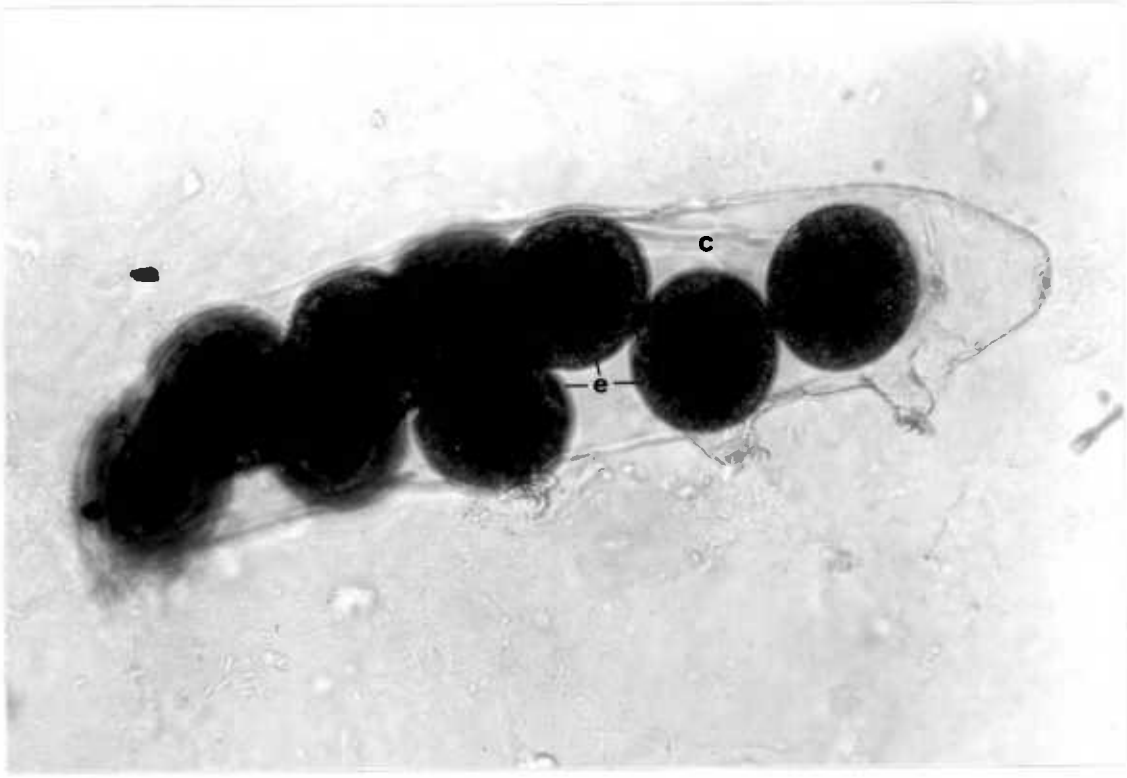



a) Rotifers migrating from old agar a few hours after reculturing; r = mass of rotifers; (x75)




b) Detail of a): individual rotifers within the mass are visible (r). (x1290).

Fig. 16. Photomicrographs of cast cuticles of Macrobiotus sp.(probably M.macronyx) containing eggs.




a) Whole cuticle (c) with nine eggs (e) (x260).




b) Anterior end of a cuticle that contained eight eggs; embryogenesis has started in the two most anterior eggs (e) (x515).

i) Bacteria

Old predator cultures contained many bacteria; these organisms were not identified but a search for the organism causing rapid agar degradation was made without success. Many different colonies of micro-organisms developed on nutrient agar plates even after $10^6$ dilution of the fluid from degraded cultures, but no indication of an agar-degrading bacterium, such as that investigated by Hofsten and Malmqvist (1975), was found.

Normal bacterial levels in cultures did not seem to affect P.punctatus but the steady increase in bacterial metabolites was believed to cause the eventual decline of predator populations if not recultured regularly. Nelmes and McCulloch (1975) reported that bacterial metabolites were very toxic to P.punctatus and this was confirmed in this study as P.punctatus placed in bacterial colonies would show violent activity for upto ten minutes. The movements were abnormal and distinctive, consisting of twisting the body about both the longitudinal and transverse axes, with acute turns that often caused the nematode's body to describe a completed figure-of-eight. Most of the movements were made whilst the nematode reversed and it appeared that normal forward motion was inhibited. The violent activity decreased after 5-10 minutes until the nematode assumed the relaxed posture; nematodes left in this position for a few minutes rarely recovered when transferred to sterile water or fresh agar.

Large numbers of dead predators contained dense colonies of bacteria but it was not possible to determine whether these were pathogenic and had caused the nematode's death, or whether they had colonised the tissues after death. Many dead predators had a distinctive brick-red colour and when placed on nutrient agar gave rise to cream-coloured colonies that became brick-red after 1-2 days. The appearance of the colonies conformed to the description of Serratia marsescens, a known insect pathogen (Burges and Hussey, 1971) and it seemed probable that this, or a closely related

organism, was responsible for the death of the nematodes. Whole cultures of P.punctatus were occasionally destroyed.

When rapid agar degradation became a serious problem attempts to establish relatively sterile cultures were made. Eleven treatments were tried over several months during the reculture of predators extracted from degraded agar (Table 22). Controls were included in each trial in which the predators were rinsed in sterile de-ionised water; this treatment delayed the onset of agar degradation by two weeks compared to routine reculturing by agar transference. Only the Penicillin/Streptomycin/ Nystatin treatment effectively delayed agar degradation and could be used regularly in reculturing with no detrimental effects to the predators.

Observations made during routine culturing suggested that bacteria transferred with the prey did not affect the predators. Prey were rinsed free of their culture medium but sterilisation was unnecessary.

ii) Fungi

Fungi, including nematode-trapping species, were very common on the cultures throughout the study but rarely caused serious losses of predators. The most common forms produced adhesive hyphal networks and included Athrobotrys sp. (Fig. 17a, b); occasionally constricting-ring fungi were observed in the cultures (Fig. 17c, d, e). Other parasitic species infecting the nematodes by adhesive or ingested conidia included Harposporium sp. Many dead nematodes were filled with fungal mycelia but infection may have occurred before or after death.

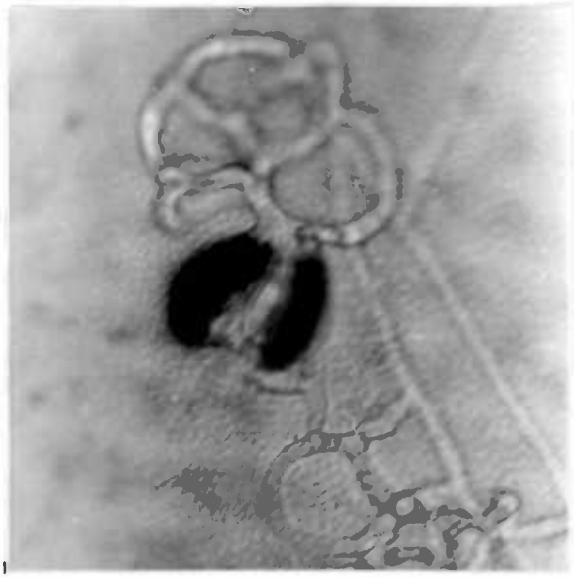
Adult and larger juvenile predators were not trapped, apparently because they were too large to enter the mycelial loops; first and second stage juveniles were frequently trapped and occasionally the losses were sufficient for the predator population to decline. The many trapped prey were more of a problem as once colonised by the mycelium, they were no longer available to the predators although attacks were frequent.

Table 22. Treatments used to counter rapid agar degradation.

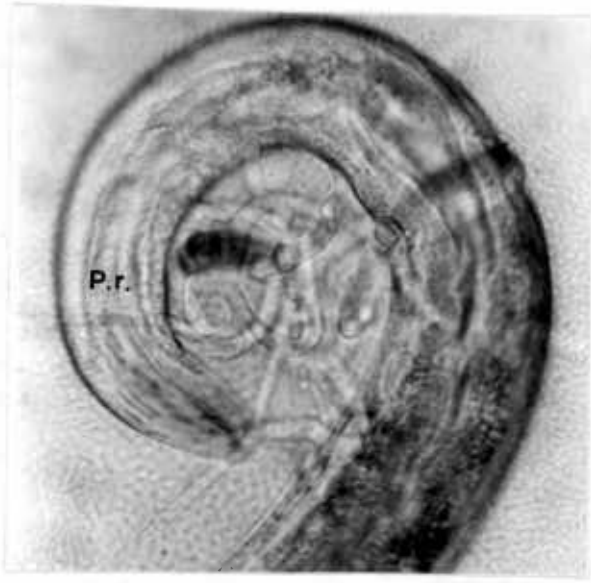
| Treatment No. | Sterilisant | Concentration (Aqueous solution) | Length of predator rinsing (min) | Additions to $25cm^3$ agar used for reculturing | Results |
|---|---|---|---|---|---|
| 1. | - | - | - | 100ppm $S.SO_4$ | Degradation delayed by 2 wks |
| 2. | - | - | - | 10ppm Benzylpen. | " " |
| 3. | $S.SO_4$ | 250ppm | 3 x 15 | - | " " |
| 4. | $S.SO_4$ | 1000ppm | 30 | - | " " |
| 5. | Benzylpen. | 10ppm | 10 | - | " " |
| 6. | Benzylpen. | 100ppm | 2 x 30 | - | " " |
| 7. | Hibitane | 0.25% | 5 | $1cm^3$ 0.25% Hibitane | Nematodes killed |
| 8. | Hibitane + $S.SO_4$ | 0.25% + 1000ppm | 5 | - | " " |
| 9. | Mercury II chloride | 100ppm | 5 | - | " " |
| 10. | Mercury II chloride | 100ppm | 5 | 100ppm Mercury II chloride | " " |
| 11. | Deionised water | - | 5 | 500 units Pen./Strept.+ 1000 units Nystatin | Degradation delayed by 2 months |
| Control | Deionised water | - | Variable | - | Degradation delayed by 2 wks |

$S.SO_4$: Streptomycin sulphate; Benzylpen.: Benzylpenicillin; Pen: Penicillin; Strept: Streptomycin.

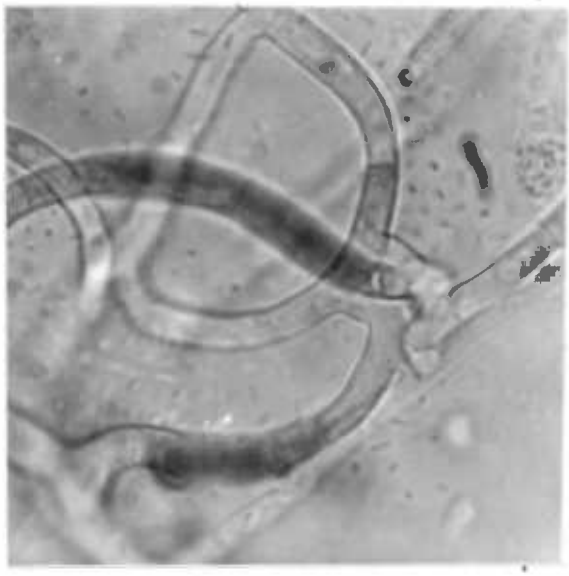
Fig.17 Photomicrographs of nematode-trapping fungi contaminating stock cultures of predatory nematodes



a) Ring traps of Arthrobotrys sp. (x465)




b) P.redivivus (P.r) trapped by Arthrobotrys sp. (x400)



c) Three-celled traps of an unidentified constricting-ring fungus (x845)




d) P.redivivus (P.r) trapped by a constricting-ring fungus (x470)



e) Detail of d) showing expanded cells of the trap (t) (x820)

Recently trapped prey were eaten by the predators which were not afterwards infected.

The only attempts to clear the cultures of fungi were those treatments which included fungicides as recorded in Table 22, but these failed.

iii) Protozoa

Large populations of various ciliate species lived in the agar; they had no apparent adverse effect on the predators; Nelmes (1974) reported that P.punctatus fed on ciliates and concluded that too few were ingested to maintain the predator without additional prey. Observations made in this study confirmed Nelmes' report as encounters between predators and ciliates were infrequent even in dense ciliate populations as the ciliates were often swept aside in the slipstream caused by the movement of the predator. Even when encounters did occur ingestion was rare.

Soil amoebae were sometimes included in soil extracts and on one culture reproduced rapidly to form an almost continuous layer on the agar surface. More usually they would not survive in the cultures; they were occasionally ingested by P.punctatus. Sporozoan parasites of mononchids reported by Thorne (1927) and others were not observed in this study.

iv) Acarina

Mites reproduced well in the cultures and often reached large populations. They fed on the detritus in the agar (and possible the agar itself) including dead nematodes but were not seen to attack live nematodes (Rockett and Woodring, 1966). They were the major vectors of bacteria and particularly fungi; the trapping fungi produced spores on short aerial branches of the mycelium and upto 100 were noted adhering to the setae of the mites. For this reason two attempts to clear the cultures of mites were made; in the first weeks of the study the few cultures of P.punctatus

were searched daily and the mites removed with a bristle. After three weeks the cultures were free of mites but this technique could not be used when the number of cultures increased.

Briefly flooding the plates with 100ppm Chlorfenvinphos solution killed both mites and predators; 10ppm Chlorfenvinphos was less toxic to the predators yet killed the mites and could possibly be used for regular treatments (or 1ppm Chlorfenvinphos could be incorporated into the agar).

v) Copepoda

A soil-dwelling harpacticoid copepod, Phyllognathopus vigueri was introduced with the nematodes extracted from the H.dihystera pot experiment although it also occurs in some locations on Imperial College Field Station. The copepod reproduced rapidly to attain large populations and has been kept in culture with M.aquaticus and Labronema sp.for more than 18 months. The only interaction with the nematodes occurred in a culture given to I.Van de Velde who observed both Labronema sp. and M.aquaticus attacking dead copepods and apparently ingesting the contents; predators were not seen attacking live copepods. This culture had not been supplied with nematode prey for two months and the attacks were probably abnormal behaviour.

vi) Enchytraeidae

An unidentified enchytraeid from soil on Imperial College Field Station reproduced (by depositing cocoons) and attained large numbers as would be expected in soil-extract agar (Springett, 1964). Agar and detritus was ingested but the enchytraeids were not seen to eat live nematodes and P.punctatus did not attack the enchytraeids unless they were artificially wounded (Fig. 11). Enchytraeids were removed with a

bristle as they disrupted the agar gel.

5. Alternative Culture Media.

Culture media more nearly approaching the conditions in soil, whilst retaining the good visibility of agar were sought.

i) Glass-wool

A thin layer of glass-wool was pressed against the sides of McCartney bottles and 3cm$^3$ of soil-extract solution added. After 24 hours (to allow the level of the water to equilibrate) nematodes were added either to the soil-extract or to the glass-wool but the nematodes did not survive for more than two days. The problem encountered in all trials was the maintenance of a water layer suitable for nematode activity.

ii) Glass beads

Glass beads with various diameters were used in a combination of depths and vessels ranging from small tubes made from one half of a Pasteur pipette to 9cm diameter plastic petri-dishes with a 0.5cm deep layer of glass beads. Again the water content was difficult to adjust and the ideal was not found; neither predators nor prey survived for more than three days.

iii) Soil

The use of small tubes containing soil (Steiner and Heinly, 1922) was discussed in relation to the culture of predators other than P.punctatus. The latter fared no better than the other predators when introduced into soil in small tubes; predators could be maintained for two months but reproduction was much reduced compared to soil-extract agar cultures. The tubes had to be inspected daily to prevent dehydration and the impossibility of observing predators led to the abandonment of soil as an alternative culture medium.

Constant moisture tensions could have been maintained in glass beads or soil using the technique described by De Guiran (1975) or the apparatus described by Wallace (1958). These techniques do not allow direct microscopic observation of the nematodes and were therefore not employed in this study but could be used when only the details of the final population are required.

6. Micro-cultures for Experimental Purposes

Mass cultures of predators were maintained on 9cm diameter plastic petri-dishes; other sizes (e.g. 5cm and 3.5cm diameter) were equally effective and were used for experiments requiring upto several hundred predators. Several alternatives were tried in a search for a culture vessel that would allow observation of single predators or small populations.

i) Embryo-dishes

Solid glass embryo-dishes were used for short-term observation of single predators e.g. the response of the predators to various prey nematodes. Three to four drops of soil-extract agar were placed in the bottom of the dish and the nematodes added when the agar had cooled. Dehydration of the agar occurred after 3-4 hours in uncovered dishes, 24 hours in covered (but not sealed) dishes and 5 days in covered dishes sealed with Vaseline. Visibility was reduced in sealed dishes by condensation on the cover; observation from below was impossible due to the thickness of the base.

$3cm^3$ of soil-extract agar placed in embryo-dishes was found to be unsuitable for observation of population development from single females because a film of water, in which the nematodes became trapped, formed between the agar and the glass in covered dishes. Uncovered dishes would dehydrate but such cultures could be used for recording egg production if the nematodes were transferred to new medium every 1-2 days.

ii) Leucocyte migration chambers

Leucocyte migration chambers consist of a plastic base with a number of moulded plastic rings (1.2cm diameter, 2mm depth). They have been used in contact nematicide tests by introducing the nematodes into a disc of agar cut from a shallow layer in a petri-dish and placed in the centre of the rings (Keetch, 1974). The rings can be sealed with a sheet of adhesive tape but when this method was tried the predators often migrated from the agar and became stuck to the tape. Lack of oxygen became a problem after 24 hours even if the nematodes remained in the agar. Coverslips sealed with Vaseline were similar to adhesive tape.

Leucocyte migration chambers were used with limited success in one pilot experiment: soil-extract agar discs were placed in the rings and a single predator added. P.redivivus were added at intervals. The rings were covered by glass-slides supported by plasticine at the corners so that they were close to, but not in contact with the rings. This arrangement allowed the diffusion of gases whilst reducing the rate of agar dehydration. The cultures were stored at 25°C in a covered plastic box with wet tissue to provide a humid atmosphere. The adult predators fed and deposited eggs (approx. 12 eggs/female/week) which hatched in approximately 7 days. The juveniles reached the second stage before the agar dehydrated necessitating the transference of nematodes to fresh medium. The life cycle was completed provided the cultures were checked every two days and transferences made as necessary but this culture technique better suited studies on egg production, embryology and the early stages of juvenile development than population studies.

iii) Perspex blocks

Small culture chambers (maximum depth 6mm; maximum diameter 6mm; approx volume $0.2cm^3$) were made by heating 2.5cm square pieces of 1.5cm thick perspex to 165°C; the squares were pressed against a metal former

in a vice to give four small chambers per square. Care was needed to avoid distortion of the perspex that reduced visibility through the base. Pilot experiments indicated that the predators could complete their life-cycle in the chambers before desiccation of the agar provided the squares were stored in a humid atmosphere. Longer periods required the addition of agar at regular intervals; observation was possible from above and below. The vessels were used for the experiments on population development from single females.

## Experiments on the Culture of Prionchulus punctatus.

Two experiments were made to determine the optimum temperature for culture of P.punctatus. The effect of reculturing and the best method for establishing new cultures from old cultures were investigated. These experiments, and observations made in routine culture, led to the investigation of critical stages in the life cycle and was combined with an investigation of different agar media in a series of experiments.

Nematodes were taken from stock cultures maintained on soil-extract agar (with P.redivivus as prey) at 25°C unless otherwise stated. Allocation of cultures to particular treatments was based on a table of random numbers (Fisher and Yates, 1963); similarly selection of cultures for extraction or reculturing during the experiment was based on the table of random numbers.

Petri-dish cultures were inoculated with predators by cutting 1.2cm diameter agar discs from existing stock cultures using a cork-borer; the discs were placed at the centre of the petri-dishes when a 0.4cm deep layer of fresh agar was cool but still molten. The number of nematodes in each disc was recorded. Single P.punctatus females were placed on the agar of perspex block cultures with a bristle.

All cultures were fed at the start of the experiments and at weekly intervals thereafter unless otherwise stated; P.redivivus was used as prey for the petri-dish cultures and A.avenae for perspex block cultures.

The nematodes were extracted from the agar of petri-dish cultures using a miniature Whitehead tray technique (Whitehead and Hemming, 1965). "Extraction" of nematodes from perspex-block cultures involved the gentle maceration of the agar in approximately $3cm^3$ of water in a counting dish until all nematodes and eggs were visible.

Further details of the experiments are summarised in Table 23.

Table 23. Summary of methods used in experiments on the culture of *P.punctatus*.

| Experiment No. | Aim | Culture vessel | Culture medium | Temperature °C | Prey species | Inoculum of *P.punctatus* per culture |
|---|---|---|---|---|---|---|
| i) | Optimum culture temperature | 3.5cm diameter plastic petri-dish | 1% soil-extract agar | 10 15 20 25 30 35 | *Panagrellus redivivus* | 14.97±0.91 adults * 55.24±3.36 juveniles |
| ii) | Optimum culture temperature | 3.5cm diameter plastic petri-dish | 1% soil-extract agar | 20 22 25 | *Panagrellus redivivus* | 9.83±0.35 adults * 24.71±1.31 juveniles |
| iii) | Effect of reculturing | 3.5cm diameter plastic petri-dish | 1% soil-extract agar | 15 20 25 | *Panagrellus redivivus* | 32.37±1.80 adults * 122.02±8.28 juveniles |
| iv) | Comparison of reculturing methods | 3.5cm diameter plastic petri-dish | 1% soil-extract agar | 25 | *Panagrellus redivivus* | 20 adults, 68 juveniles |
| v) | Comparison of reculturing methods | 3.5cm diameter plastic petri-dish | 1% soil-extract agar | 25 | *Panagrellus redivivus* | 20 adults, 68 juveniles |
| vi) | Population development | Perspex blocks | Variable | 20 | *Aphelenchus avenae* | 1 adult |
| vii) | Population development | Perspex blocks | Variable | 20 | *Aphelenchus avenae* | 1 adult extracted from Bracken F-layer material. |
| viii) | Population development | Perspex blocks | Variable | 20 | *Aphelenchus avenae* | 1 adult |

*Cultures inoculated by transferring a disc of agar containing nematodes from a stock culture; the numbers quoted are the mean ± S.E.

i) Determination of optimum culture temperature of P.punctatus.

Soil-extract agar was poured into 81 petri dishes and each was inoculated with P.punctatus. Fifteen cultures were maintained at each of 10°C, 15°C, 20°C, 25°C and 30°C; three cultures were maintained at both 5°C and 35°C. At two weekly intervals the nematodes were extracted from 5 replicates at each temperature (1 replicate at 5°C and 35°C). The number of adult and juvenile P.punctatus in each replicate was recorded.

Analysis of variance of the initial inocula indicated that despite the attempted randomisation, there was a significant difference in the number of adults in each treatment (Table 24). The number of juveniles and the total inocula did not differ significantly between treatments.

Results:

There was a marked response to culture temperature; at 30°C and 35°C all the predators were dead within 72 and 48 hours respectively. At 5°C no adults survived to four weeks when 3 juveniles were recovered; two weeks later a single juvenile was recovered. At the other temperatures some nematodes remained after six weeks (Fig. 18a-d) but at 10°C the population had declined steadily except for a temporary increase in number of juveniles after two weeks. At 15°, 20° and 25°C the population increased for four weeks but decreased in the last two weeks of the experiment. The population increase was significantly greater at 25°C and decreased in the order 25°C> 20°C>15°C>10°C, often with significant differences between the temperatures (Table 24).

Discussion:

Temperatures greater than 30°C and less than 10°C were unsuitable for the culture of P.punctatus. 15°C, 20°C and 25°C were all suitable for increasing the number of P.punctatus and the maximum increase was at 25°C,

FIG.18

RESPONSE OF P.PUNCTATUS POPULATIONS TO CULTURE TEMPERATURE I

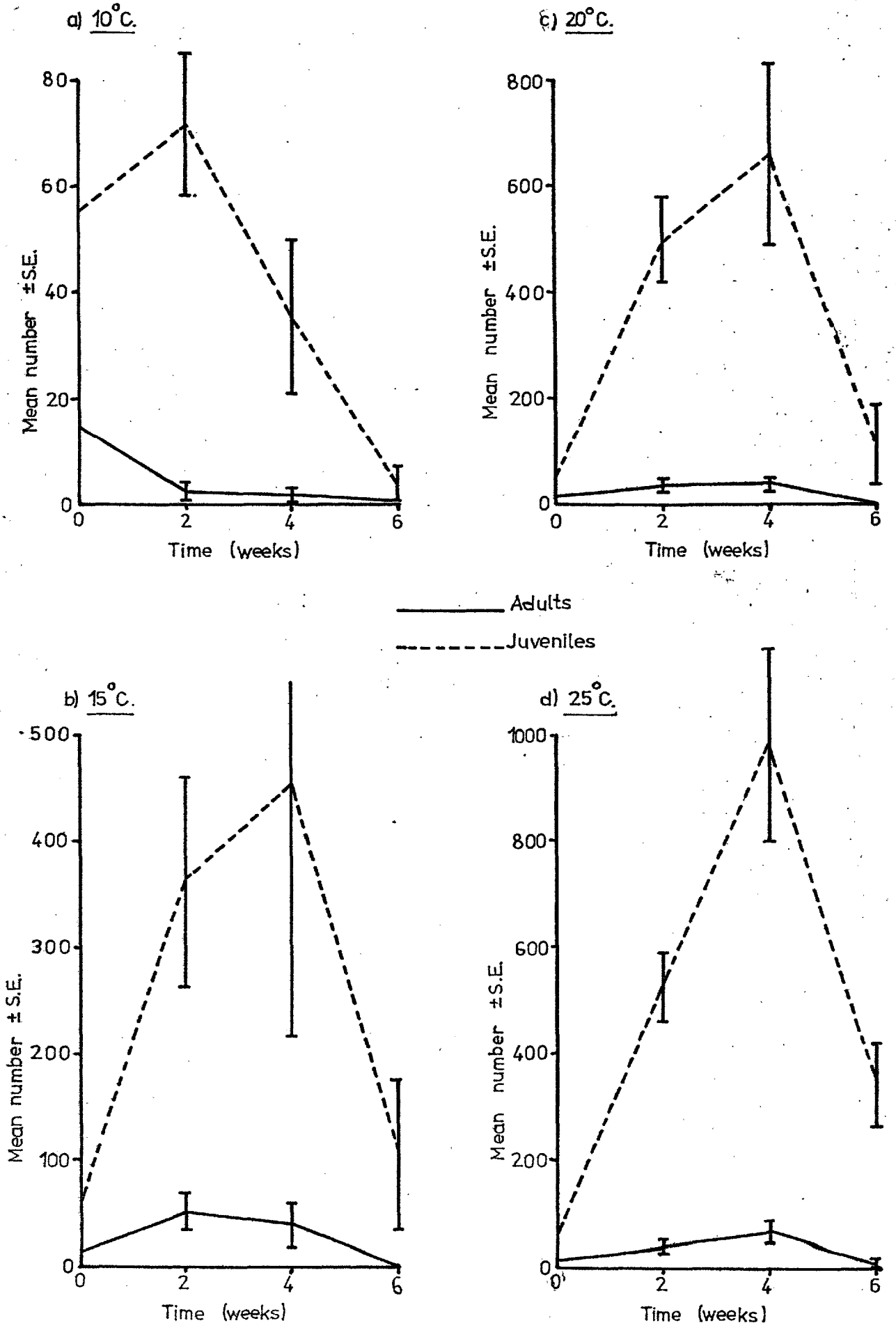


Table 24. Determination of optimum culture temperature for *P. punctatus*. Results of Analyses of Variance.

| Time (weeks) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| 0 | Adults | 3.87 | 0.05-0.01 | 25°>15°**** 25°>10°** 25°>20°* 20°>15°* |
| | Juveniles | 1.01 | N.S. | - |
| | Total | 1.41 | N.S. | - |
| 2 | Adults | 4.94 | 0.01-0.001 | 15°>10°**** 25°>10°** 20°>10°* |
| | Juveniles | 8.65 | 0.01-0.001 | 25°>10°***** 20°>10°***** 15°>10°*** |
| | Total | 10.59 | <0.001 | 25°>10°***** 20°>10°***** 15°>10°**** |
| 4 | Adults | 3.34 | 0.05-0.01 | 25°>10°**** 15°>10°* 20°>10°* |
| | Juveniles | 4.55 | 0.05-0.01 | 25°>10°**** 20°>10°** 25°>15°* |
| | Total | 4.53 | 0.05-0.01 | 25°>10°**** 25°>15°* 20°>10°** |
| 6 | Adults | 3.94 | 0.05-0.01 | 25°>10°** 25°>20°* |
| | Juveniles | 4.85 | 0.05-0.01 | 25°>10°**** 25°>15°, 20°** |
| | Total | 4.86 | 0.05-0.01 | 25°>10°**** 25°>15°, 20°** |

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01;

****: p=0.01-0.001; *****: p<0.001; N.S.: Not significant.

which was used throughout the study for stock cultures when large numbers of nematodes were needed. Grootaert and Maertens (1976) also used 25°C for mass cultures and obtained similar results at the other temperatures. In this study 10°C appeared unsuitable for culture but Grootaert and Maertens (1976) used this temperature to maintain populations of P.punctatus adults. At this temperature reproduction was greatly reduced (4.2 eggs/♀/wk) and development time very long (200 days) compared with higher temperatures but adults could be maintained for several months with minimal attention; when returned to 25°C reproduction and development was normal for P.punctatus at that temperature.

The increase in P.punctatus at the intermediate temperatures ceased after approximately four weeks. This temperature-independent response suggested that toxic substances (e.g. nematode or bacterial metabolites) were accumulating in the cultures and that these caused the population to decline when a critical concentration was reached.

ii) Optimum temperature for mass culture of P.punctatus.

The temperatures investigated were 20°C, 22°C and 25°C, and 24 replicates at each temperature were used; eight replicates from each treatment were extracted at two weekly intervals. Analysis of variance indicated no significant differences in initial inocula between the treatments (Table 25).

Results: Significant differences in nematode members between the three temperatures were recorded (Table 25); the population at 22°C was consistently greater than that at 20°C and 25°C. The population increases (at the same temperatures) were greater than those recorded in experiment i). All the populations decreased from week 4 onwards (Fig.19a, b).

Discussion: Of the temperatures tested 22°C appeared to be the optimum

FIG.19. RESPONSE OF P.PUNCTATUS POPULATIONS TO CULTURE TEMPERATURE II

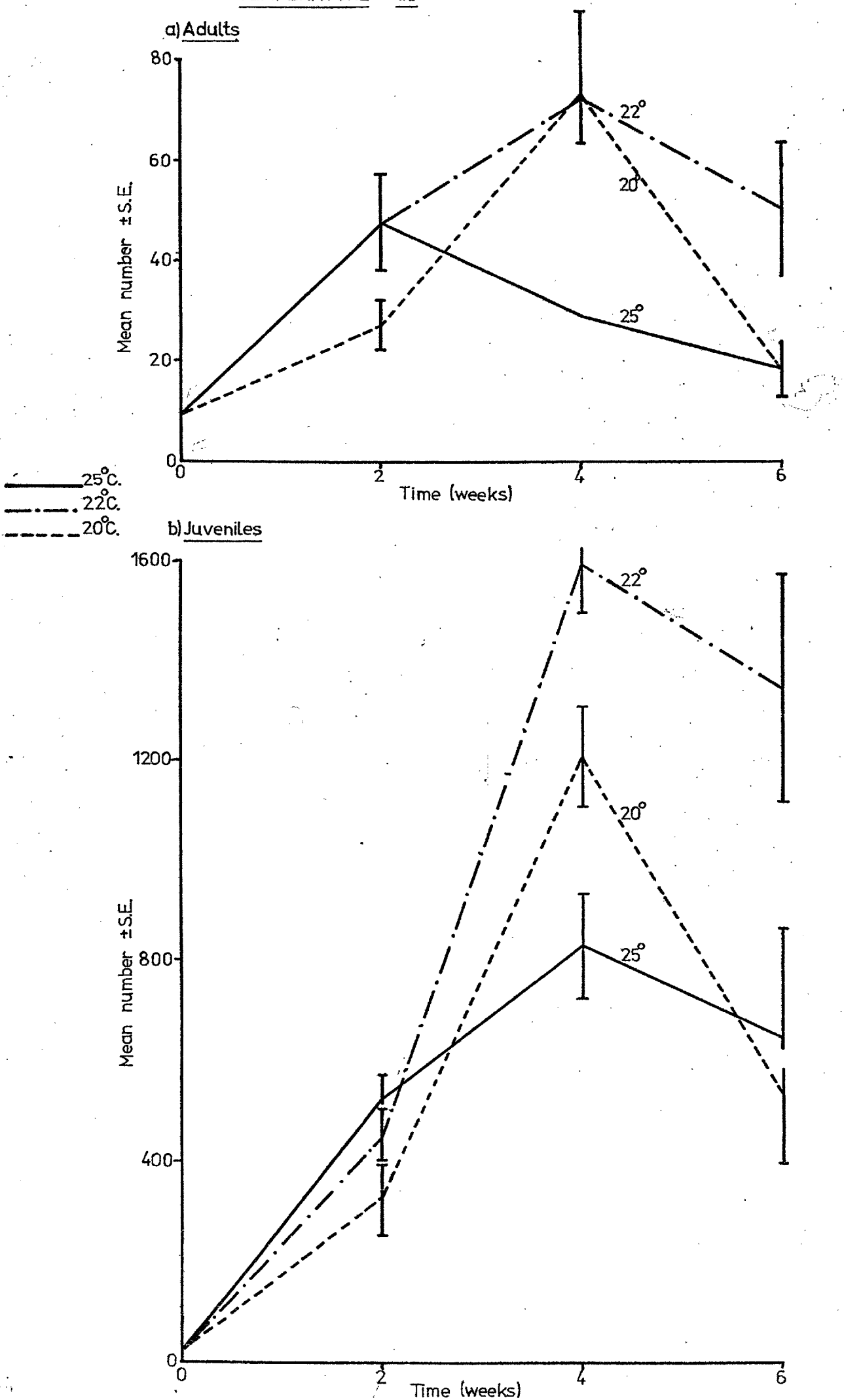


Table 25. Determination of optimum culture temperature for mass culture of P.punctatus. Results of analyses of Variance.

| Time (weeks) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| | Adults | 0.84 | N.S. | - |
| 0 | Juveniles | 1.07 | N.S. | - |
| | Total | 0.86 | N.S. | - |
| | Adults | 2.82 | 0.2-0.05 | 22°>20°*<br>25°>20°* |
| 2 | Juveniles | 2.30 | 0.2-0.05 | 25°>20°** |
| | Total | 2.88 | 0.2-0.05 | 25°>20°** |
| | Adults | 4.77 | 0.05-0.02 | 20°>25°***<br>22°>25°*** |
| 4 | Juveniles | 7.92 | 0.01-0.001 | 22°>25°*****<br>22°>20°* 20°>25°* |
| | Total | 8.61 | 0.01-0.001 | 22°>25°*****<br>22°>20°* 20°>25°** |
| | Adults | 3.89 | 0.05-0.01 | 22°>25°**<br>22°>20°** |
| 6 | Juveniles | 4.74 | 0.05-0.01 | 22°>20°****<br>22°>25°** |
| | Total | 4.76 | 0.05-0.01 | 22°>20°****<br>22°>25°** |

*: p=0.2-0.05; **: p=0.05-0.02; ***: p=0.02-0.01

****: p=0.01-0.001; *****: p<0.001; N.S.: Not significant.

temperature for mass culture of P.punctatus, which agreed with results of Maertens (1975) who found development time to be shortest and egg production rate to be greatest at this temperature. P.punctatus was similar in its temperature range to many other free-living nematodes although the optimum temperature was less than that for many saprophagous species (~28°C: Dougherty, 1960; Nicholas, 1975).

The relative increases at 20°C and 25°C were reversed from those of experiment i); from observation of the cultures the difference appeared to result from greater mortality at 25°C rather than from greater reproduction at 20°C, which was reflected in the decrease of adults from week 2 onwards at the higher temperature. Maertens (1975) recorded greater incidence of bacterial and fungal infections in P.punctatus at 25°C than at 22°C.

iii) Effect of reculturing on P.punctatus populations

P.punctatus were inoculated into 45 petri-dishes containing soil-extract agar. Fifteen cultures were placed at each of 15°C, 20°C and 25°C. After four weeks the nematodes from five cultures from each temperature were extracted and counted. A further five cultures from each temperature were recultured by dividing the agar into three equal portions; each portion was placed in a petri-dish of soil-extract agar. These new cultures were returned to the temperature at which the "parent" culture had been maintained.

Six weeks after the start of the experiment the nematodes from the five remaining original cultures at each temperature were extracted and counted. The development of trapping fungi on many of the recultured cultures had prevented normal P.punctatus population growth and the nematodes from only 4 cultures at each of 15°C and 25°C were extracted and counted; no cultures at 20°C were free of fungus. Eight weeks after the start of the experiment the nematodes from 3 fungus-free recultured cultures at 25°C were extracted

FIG. 20. THE EFFECT OF RECULTURING FOUR-WEEK OLD P. PUNCTATUS CULTURES ON THE SUBSEQUENT POPULATION DEVELOPMENT

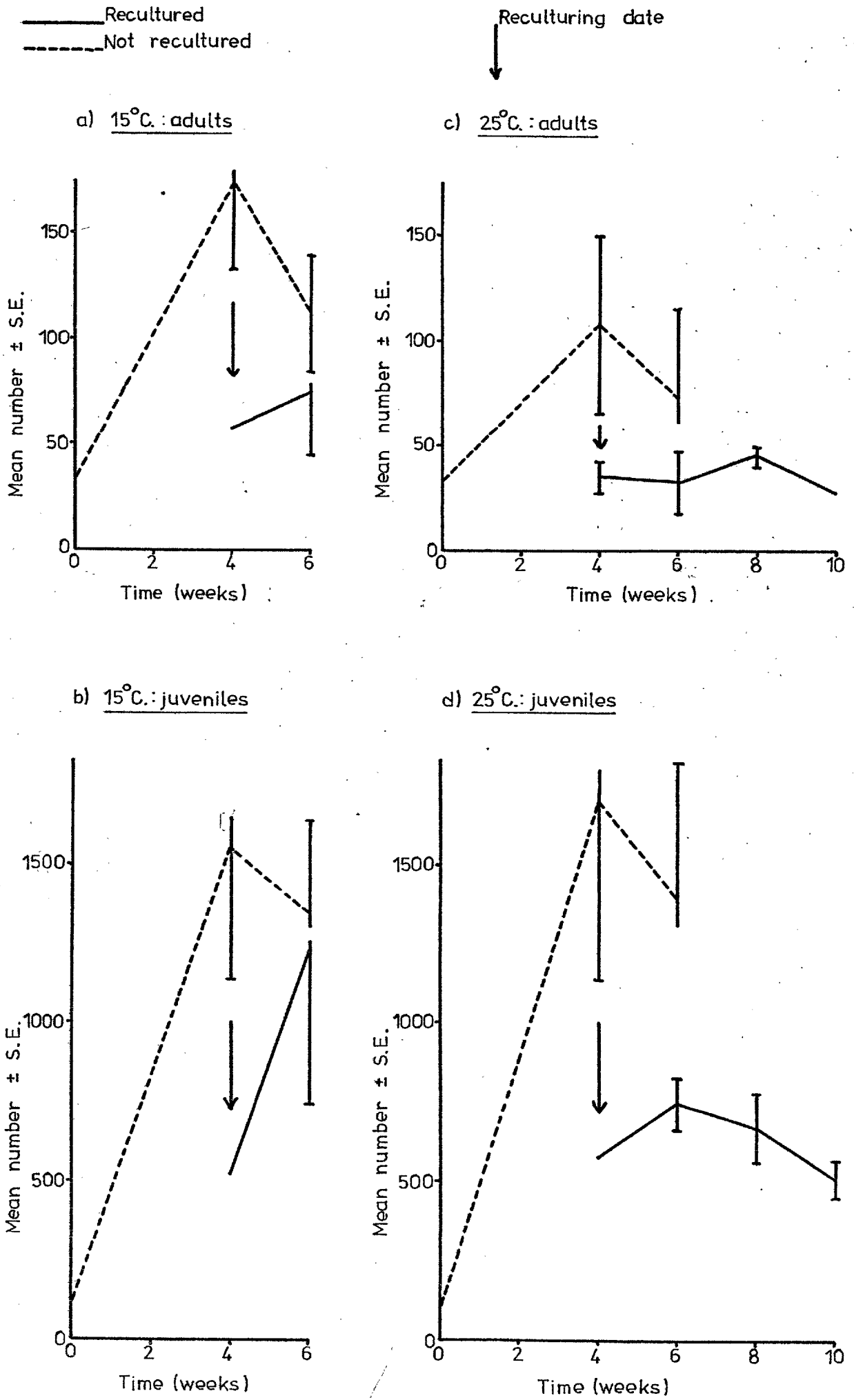


Table 26. Effect of reculturing on populations of *P.punctatus*: results of analyses of Variance.

a) Effect of temperature on number of *P.punctatus*.

| Time (weeks) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| 0 | Adults | 18.26 | <0.001 | 20°>25°, 15°*****<br>15°>25°***** |
| | Juveniles | 9.42 | <0.001 | 20°>25°*****<br>20°>15°**** |
| | Total | 9.02 | <0.001 | 20°>25°*****<br>20°>15°**** |
| 4 | Adults | 1.48 | N.S. | - |
| | Juveniles | 0.10 | N.S. | - |
| | Total | 0.01 | N.S. | - |
| 6 (Not Recultured) | Adults | 0.27 | N.S. | - |
| | Juveniles | 0.02 | N.S. | - |
| | Total | 0.01 | N.S. | - |

b) Effect of reculturing on numbers of *P.punctatus*

| Time (weeks) | Subject | Value of 'F' | Significance |
|---|---|---|---|
| 6 | Adults | 0.74 | N.S. |
| | Juveniles | 0.43 | N.S. |
| | Total | 0.41 | N.S. |

****: p=0.01-0.001; *****: p<0.001.

and counted, and similarly a further 4 after 10 weeks.

Analyses of variance indicated that there were significant differences in initial inocula between the treatments despite the precautions taken to avoid such differences (Table 26a).

Results: Analyses of variance indicated that after four and six weeks no significant differences between the non-recultured populations at the three temperatures existed (Table 26a). There was no significant difference between the recultured cultures at 15°C and 25°C (t=1.37, 0.94 and 0.98 for adults, juveniles and total respectively).

The initial inoculum of the recultured cultures was considered to be one-third of the mean population (as the original cultures were divided into three new cultures) at week 4 which was 107.20 $\pm$ 42.25 adults and 1696.60 $\pm$ 562.04 juveniles (1803.80 $\pm$ 602.13 total). At both 15°C and 25°C the number of juveniles increased after reculturing whilst the population in the non-recultured cultures was decreasing (Fig. 15b, d). Adults also increased in the recultured cultures at 15°C but at 25° there was a slight decrease which was less than that in non-recultured cultures (Fig. 15a, c). Analyses of variance of all treatments showed that there was no significant difference in the number of predators in the recultured and non-recultured cultures at six weeks (Table 26b). Data for further comparisons were not available due to the growth of trapping fungi on cultures maintained at 20°C and on cultures maintained at 15°C from week 6 onwards.

Discussion: The difference in initial inocula was considered unimportant as the smaller populations at the higher temperatures had reproduced more so that there was no significant difference after four weeks. Reculturing allowed the populations of P.punctatus to continue increasing during the post-four week period when non recultured cultures were declining. Two weeks after reculturing there were no significant differences between the

recultured and non-recultured populations, despite the reduction of the population in the former by 2/3 during reculturing. It therefore appeared that reculturing at four week intervals would allow continued increase in the population of P.punctatus; the four week interval was also indicated by the decrease in predators in recultured cultures four weeks after reculturing.

iv) Comparison of methods of reculturing P.punctatus I.

1% soil-extract agar was poured into 30 petri-dishes to a depth of 0.3cm approx. Twenty adult and sixty-eight juvenile P.punctatus (chosen to be proportional to the mean number of nematodes routinely transferred to 9cm diameter stock plates) were taken from a stock culture with a bristle, rinsed in sterile, deionised water and placed on each of 10 of the plates. Twenty 1.2cm diameter discs were cut from the stock culture using a cork borer; one disc was placed on each of the remaining 20 plates. The number of predators in each of ten discs was adjusted to give 20 adults and 68 juveniles per disc. All the predators were removed from the remaining discs and rinsed in sterile, deionised water before 20 adults and 68 juveniles were replaced in the agar disc. The number of adult and juvenile P.punctatus were counted by direct observation of the cultures at weekly intervals for nine weeks and finally at week 12.

Results: The three methods of reculturing P.punctatus caused large differences in the population development in subsequent weeks. Both adults and juveniles declined steadily in cultures without transferred agar (Figs.21, 22). The population curves of the two treatments in which agar from the old culture was transferred showed many similarities in general form but removing, washing and replacing the nematodes in the old agar resulted in a consistently smaller population for eight weeks (Figs. 21, 22). From week 8 onwards there was little difference between the two populations.

FIG.21. EFFECT OF METHOD OF RECULTURING ON POPULATIONS OF P.PUNCTATUS I : ADULTS

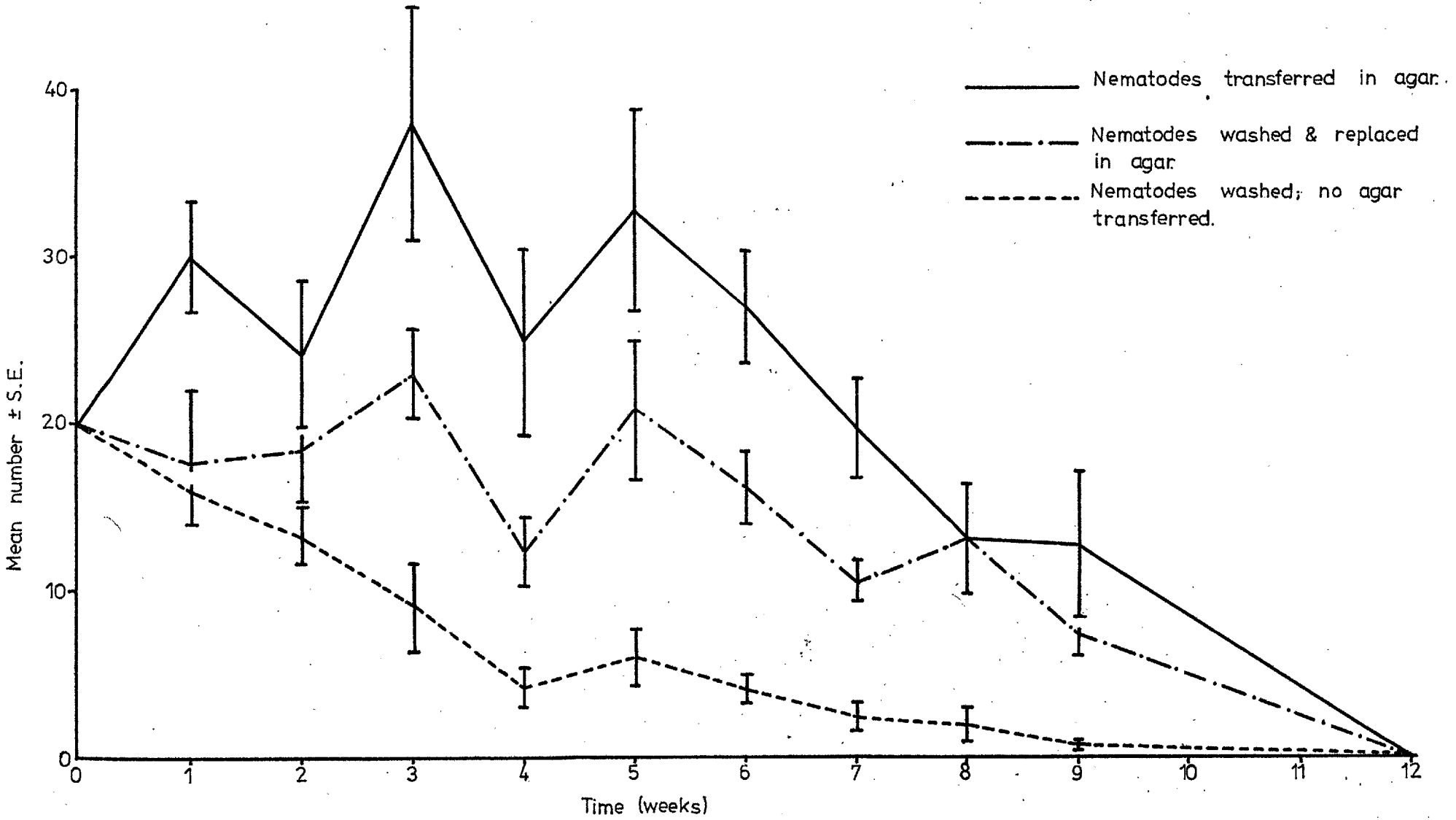


FIG. 22. EFFECT OF METHOD OF RECULTURING ON POPULATIONS OF P. PUNCTATUS I: JUVENILES

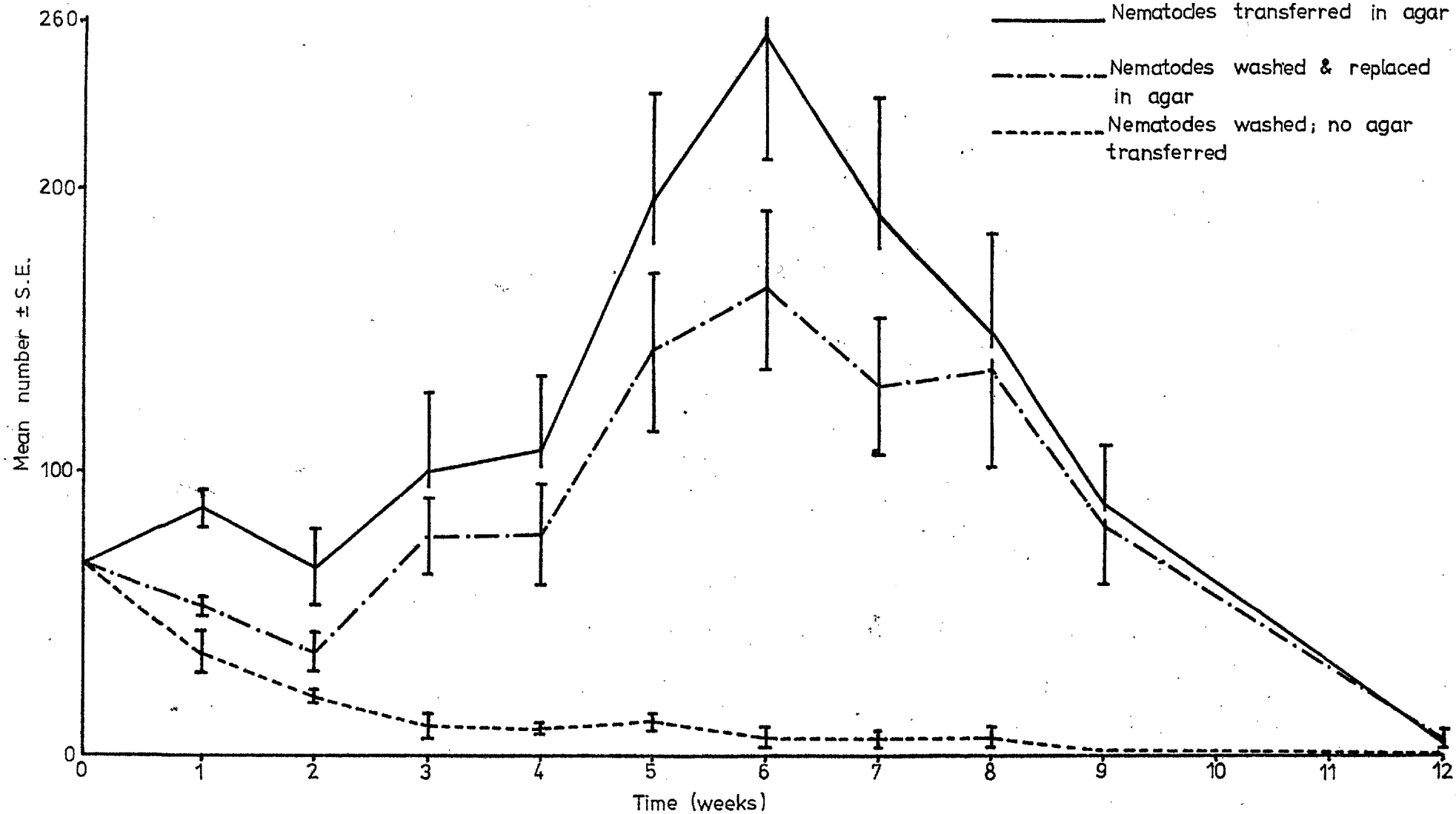


Table 27. Comparison of methods of reculturing P.punctatus I: results of analyses of variance (weeks 1-5).

| Time (weeks) | Subject | Value of 'F' | Significance | Significant Differences |
|---|---|---|---|---|
| | Adults | 10.98 | <0.001 | A>B, C***** |
| 1 | Juveniles | 34.87 | <0.001 | A>B, C*****<br>B>C*** |
| | Total | 31.33 | <0.001 | A>B,C*****<br>B>C** |
| | Adults | 2.96 | 0.1 -0.05 | A>C** |
| 2 | Juveniles | 7.27 | 0.01-0.001 | A>C*****<br>A>B*** |
| | Total | 6.56 | 0.01-0.001 | A>C****<br>A>B** |
| | Adults | 6.77 | 0.01-0.001 | A>C****<br>A>B* B>C* |
| 3 | Juveniles | 8.08 | 0.01-0.001 | A>C****<br>B>C**** |
| | Total | 6.84 | 0.01-0.001 | A>C****<br>B>C** |
| | Adults | 10.12 | <0.001 | A>C*****<br>A>B*** B>C* |
| 4 | Juveniles | 8.65 | 0.01-0.001 | A>C*****<br>B>C**** |
| | Total | 9.28 | 0.01-0.001 | A>C*****<br>B>C**** |
| | Adults | 11.80 | <0.001 | A>C*****<br>A>B** B>C**** |
| 5 | Juveniles | 17.19 | <0.001 | A>C*****<br>B>C***** |
| | Total | 18.01 | <0.001 | A>C*****<br>B>C***** |

A: Nematodes transferred in agar
B: Nematodes washed and returned to agar
C: Nematodes washed; no agar transferred

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001.

Table 27 (cont): Comparison of methods of reculturing P.punctatus
a) results of analyses of variance (weeks 6-9).

| Time (weeks) | Subject | Value of 'F' | Significance | Significant Differences | |
|---|---|---|---|---|---|
| | Adults | 27.52 | <0.001 | A>C***** | |
| | | | | A>B**** | B>C***** |
| 6 | Juveniles | 21.45 | <0.001 | A>C***** | |
| | | | | A>B** | B>C***** |
| | Total | 33.40 | <0.001 | A>C***** | |
| | | | | A>B*** | B>C***** |
| | Adults | 21.87 | <0.001 | A>C***** | |
| | | | | A>B**** | B>C**** |
| 7 | Juveniles | 15.78 | <0.001 | A>C***** | |
| | | | | A>B** | B>C***** |
| | Total | 17.43 | <0.001 | A>C***** | |
| | | | | A>B* | B>C***** |
| | Adults | 9.35 | 0.01-0.001 | A>C**** | |
| | | | | B>C**** | |
| 8 | Juveniles | 6.98 | 0.01-0.001 | A>C**** | |
| | | | | B>C**** | |
| | Total | 10.48 | <0.001 | A>C**** | |
| | | | | B>C***** | |
| | Adults | 8.45 | 0.01-0.001 | A>C***** | |
| | | | | A>B* | B>C*** |
| 9 | Juveniles | 8.76 | 0.01-0.001 | A>C**** | |
| | | | | B>C**** | |
| | Total | 9.36 | 0.01-0.001 | A>C**** | |
| | | | | B>C**** | |

A: Nematodes transferred in agar
B: Nematodes washed and returned to agar
C: Nematodes washed: no agar transferred

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001.

Throughout the experiment the difference between the populations in cultures with and without transferred agar were highly significant (Table 27). Significant differences between the two treatments with transferred agar were recorded in weeks 1, 2 and 6-9, but the significance levels were generally lower (Table 27). Often when significant differences in numbers of adults were recorded the number of juveniles (and hence the total population) also differed significantly between treatments. A 't' test on the number of juveniles remaining at week 12 indicated no significant difference between the two treatments with transferred agar ($t=0.19$, $d.f=11$).

During the course of the experiment the number of replicates decreased for various reasons e.g. trapping fungi. At the end of the experiment the number of replicates was 5 in treatment A, 8 in treatment B, and 9 in treatment C. The loss of replicates was considered not to have greatly altered the results except by increasing the standard error.

These results are discussed in conjunction with the results of the repeat experiment.

v) Comparison of methods of reculturing P.punctatus: II.

All experimental details were similar to the first experiment on methods of reculturing, except that the experiment was terminated after 6 weeks.

Results: The population curves of the treatments (Fig. 23)are similar to those recorded in the same period of the first experiment but maximum numbers in the treatments with transferred agar were reached earlier (3-5 weeks compared to 5-7 weeks in the first experiment). The population in the culture without transferred agar decreased more rapidly and no nematodes were observed from week 5 onwards. Highly significant differences in the number of nematodes in each treatment were recorded from week 1 onwards

FIG. 23. EFFECT OF METHOD OF RECULTURING ON POPULATIONS OF P. PUNCTATUS II

———— Nematodes transferred within old agar
– – – – – – – – Nematodes removed from old agar, washed & replaced in old agar
—·—·—·— Nematodes removed & washed; no old agar transferred

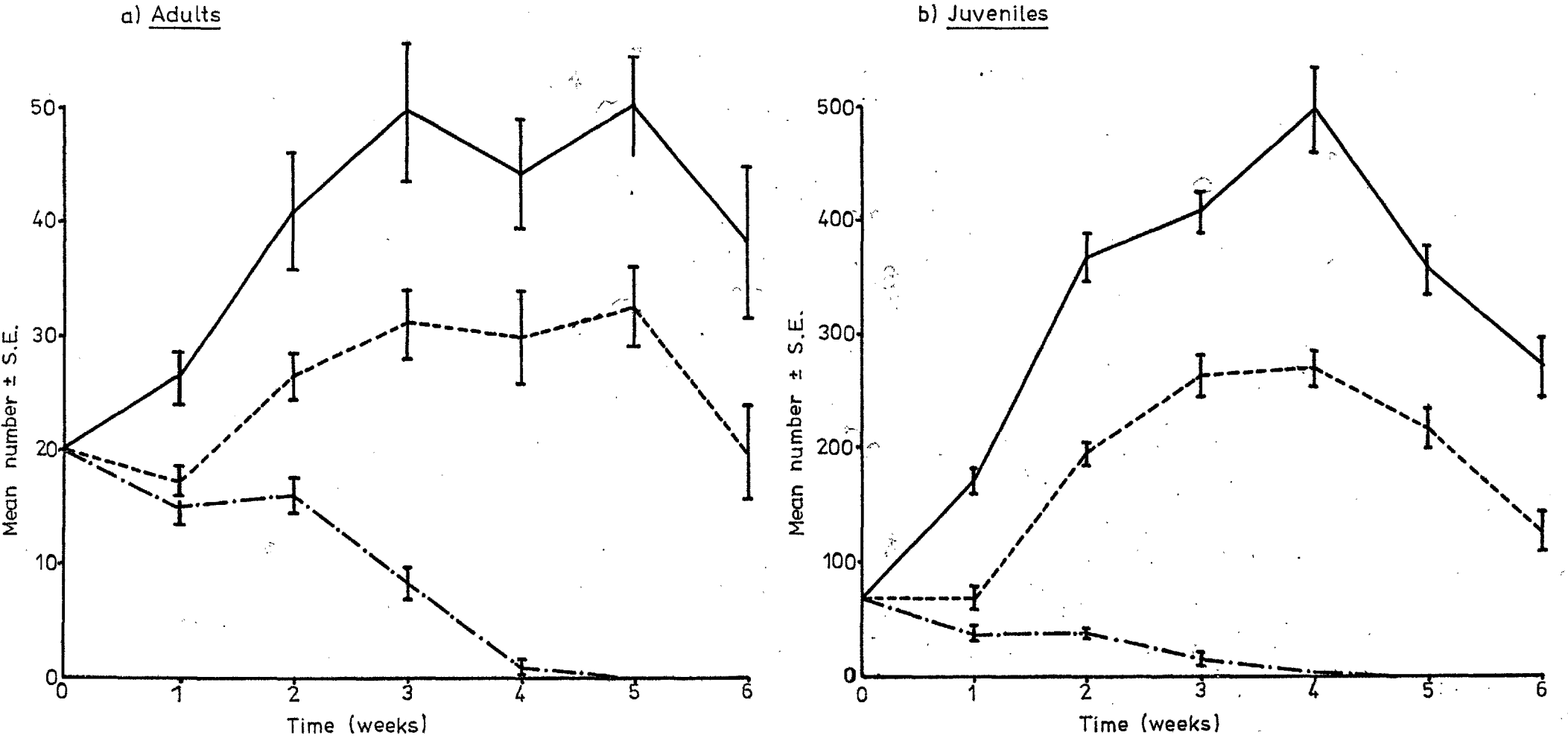


Table 28. Comparison of methods of reculturing P.punctatus II: results of analyses of variance.

| Time (weeks) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| | Adults | 6.09 | 0.01-0.001 | A>C****<br>A>B*** |
| 1 | Juveniles | 82.39 | <0.001 | A>B,C*****<br>B>C**** |
| | Total | 3.42 | 0.05-0.01 | A>C***<br>A>B** |
| | Adults | 13.91 | <0.001 | A>C*****<br>A>B**** B>C** |
| 2 | Juveniles | 185.62 | <0.001 | A>B,C*****<br>B>C***** |
| | Total | 162.37 | <0.001 | A>C*****<br>A>B***** B>C***** |
| | Adults | 28.85 | <0.001 | A>C*****<br>A>B**** B>C***** |
| 3 | Juveniles | 192.74 | <0.001 | A>C*****<br>A>B***** B>C***** |
| | Total | 190.29 | <0.001 | A>C*****<br>A>B***** B>C***** |
| | Adults | 42.68 | <0.001 | A>C*****<br>A>B**** B>C***** |
| 4 | Juveniles | 87.69 | <0.001 | A>C*****<br>A>B***** B>C***** |
| | Total | 115.93 | <0.001 | A>C*****<br>A>B***** B>C***** |

A: Nematodes transferred in agar
B: Nematodes washed and returned to agar
C: Nematodes washed: no agar transferred

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001.

Table 29. Comparison of methods of reculturing P.punctatus II: results of 't' tests.

| Time (weeks) | Subject | Value of 't' | Significance | Details |
|---|---|---|---|---|
| | Adults | 0.86 | N.S. | - |
| 5 | Juveniles | 5.13 | <0.001 | A>B |
| | Total | 5.13 | <0.001 | A>B |
| | Adults | 2.39 | 0.05-0.02 | A>B |
| 6 | Juveniles | 4.76 | <0.001 | A>B |
| | Total | 4.43 | <0.001 | A>B |

and continued throughout the experiment (Tables 28, 29).

Discussion: The results of the two experiments indicated that the method used to reculture P.punctatus had a significant effect on subsequent population development. The similarity between the population curves of the two experiments indicate that this effect was consistent and allows the two experiments to be discussed together.

The precise cause of the differences in population development between the three treatments was not established. During the process of picking nematodes out of the agar and transferring them to fresh medium some nematodes may have been damaged and all were subject to disturbance. Passage through water placed the nematodes under osmotic stress and these factors may have been sufficient to cause a temporary decrease in numbers in the first few days after reculturing, such as that recorded in the treatment in which the nematodes were first removed and then replaced in transferred old agar (Figs. 21-23). The transference of nematodes without agar from the old culture resulted in a steady decline which confirmed earlier observations of stock cultures established in this way. The difference between the two treatments in which the nematodes were removed, rinsed and then replaced suggested that the agar itself had a significant influence on subsequent population development, i.e. that a factor (or factors) beneficial to predator population development was present in the old agar. Unquantified observations suggested that second stage juveniles were most susceptible to the absence of old agar as most of those transferred died within two days and the few eggs that were deposited hatched but the juveniles rarely passed the second moult. No indication of the nature of the possible factor in old agar was obtained but it seemed probable that either the predators or one of the contaminant organisms altered the medium in some way and subsequent experiments were designed to test this hypothesis.

The best method for reculturing P.punctatus was therefore the transference of nematodes within the old agar. A disadvantage of this method was the transference of contaminant organisms present in the old culture. Nevertheless this method was adopted for routine reculturing of stock cultures and transference of nematodes without agar was employed only if the contaminant organisms in the old culture were particularly numerous. Such cultures rarely gave rise to large populations but sometimes maintained sufficient nematodes to allow reculturing by agar transference after four weeks and the population eventually increased. Grootaert (pers.comm.) regularly recultured stock cultures by transferring 50 mononchid females without agar from the old cultures and consistently obtained large populations. The reason for this discrepancy is not known.

In the first experiment the populations in cultures with transferred agar declined from week 5 (adults) or week 6 (juveniles) rather than the more usual week 4. This was believed to be related to the age of the culture used for the experiments: a ten-day old stock culture was used in the first experiment in place of the four-week old stock cultures used in the second and previous experiments. The concentration of nematode and microorganism metabolites in the old agar of the first experiment was therefore lower and may have allowed the population development to continue for the extra week.

vi) Population development from single P.punctatus females: I.

An aqueous extract of 15cm$^3$ agar taken from a "good" (i.e. > 3,500 P.punctatus) 4 week-old stock culture was prepared by shaking the agar with 56cm$^3$ of sterile de-ionised water and allowing the mixture to stand for 75 minutes at room-temperature (~ 27°C). The mixture was centrifuged at R.C.F. 738 and the 51cm$^3$ of supernatant recovered was mixed with 51cm$^3$ fresh, molten (but cool) 2% soil-extract agar to give a 1% agar (S.E.A.+extract). The remaining agar from the "good" culture was gently heated until molten and allowed to stand until the debris (including dead nematodes) had settled;

excess water on the agar surface was removed (Old S.E.A.). 1% water agar and 1% soil-extract agar (Fresh S.E.A.) were prepared by the usual methods.

Three to four drops of each agar were placed in each of 24 perspex-block culture chambers to give a total of 96 cultures. Single gravid female P.punctatus were placed in each culture together with approximately 150 Aphelenchus avenae. Groups of four prespex blocks were placed in depressions cut in a layer of water agar in 9cm diameter plastic petri-dishes; the water agar provided a humid atmosphere that reduced the rate of dehydration of the agar in the culture chambers. All the petri-dishes were placed in a plastic bag and incubated at 20°C inside a closed plastic container.

Counts of the life-stages of P.punctatus were made every 2-3 days (except for a ten-day interval at 72-82 days); first-stage juveniles that had fed (indicated by pigment in the intestinal walls) were grouped with second stage juveniles.* A.avenae were supplied whenever prey were few in the cultures and the agar was renewed whenever necessary by adding a few drops of the appropriate agar to the surface of the existing agar. Every two weeks the nematodes from a batch of six replicates from each treatment were extracted and counted (again grouping fed first-stage juveniles with second-stage juveniles). The extraction routine is summarised in Table 30 in which each batch (denoted by A,B,C or D) initially consisted of 6 cultures from each treatment. The nematodes extracted on week 2 were not returned to the experiment but thereafter the nematodes were replaced in a fresh quantity of the appropriate agar and were retained in the experiment. The experiment was terminated after 16 weeks when the nematodes from all the remaining cultures were extracted and counted.

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*This was partly because of the difficulty of distinguishing fed first-stage juveniles from second-stage juveniles and partly because previous observations had suggested that feeding was critical; the great majority of first stage juveniles moulted within 24 hours of feeding but would die within a few days in the absence of suitable food.

Table 30. Summary of the reculturing routine in population development from single female P.punctatus I.

| Weeks | 2 | 4 | 6 | 8 | 10 | 12 | 14 | 16 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Extraction Batch | A | B | C | D | B | C | D | B | C | D |
| Reculture interval (weeks) | 2 | 4 | 6 | 8 | 6 | 6 | 6 | 6 | 4 | 2 |

In addition to analyses of variance of the numbers of each life-stage present on each of the extraction dates, the percentage of eggs surviving to attain each juvenile stage and to adulthood was calculated. The percentages were based on the maximum of each stage recorded; the percentage data was arranged in 2x2 contigency tables after arcsin transformation to allow the differences between treatments to be assessed statistically. The percentage of each juvenile stage surviving to attain the next life-stage was investigated in a similar manner.

Results: The culture medium had a significant influence on the populations of P.punctatus originating from single females (Figs. 24, 25, 26; Tables 31, 32). The general form of the population curves, based on the counts at 2-3 day intervals, are presented in Figs. 24-26 which show the total population from the 25 females inoculated into each treatment; the means $\pm$ S.E. per culture are presented in Appendix III Tables 1-12 together with the number of replicates remaining in each treatment. The analyses of variance (Tables 31, 32) were based on the extraction data (Appendix III, Tables 13, 14) which were the more accurate population estimates (generally indicating a slightly greater population than that recorded by direct observation).

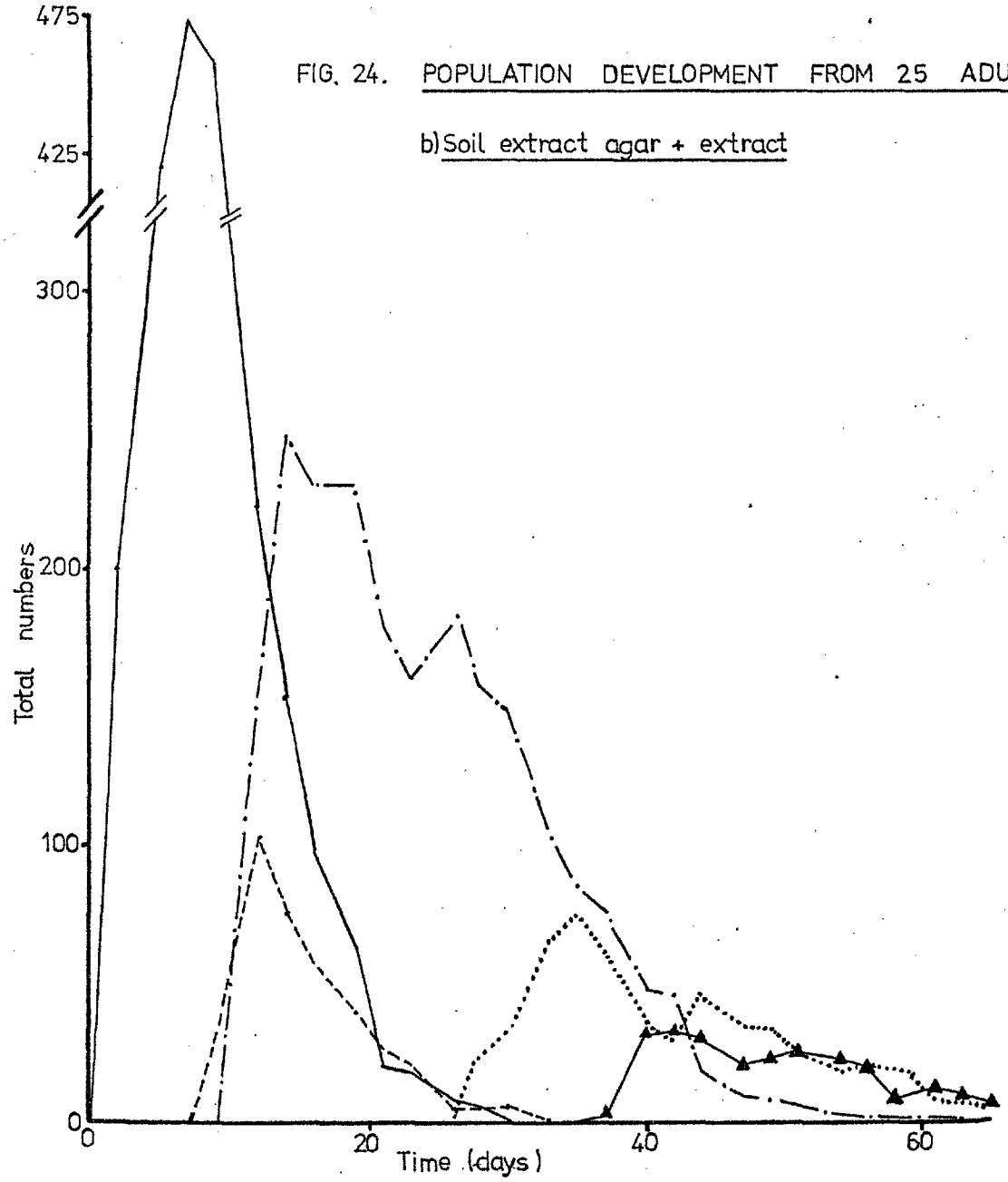
No nematodes survived for more than 54 days in old S.E.A.; the life-cycle was not completed and few juveniles reached the fourth stage (Fig. 24a). The number of eggs and juveniles produced was significantly lower except on the first extraction date when the number of unfed first stage juveniles was

greatest in old S.E.A. (Table 31). In S.E.A. + extract the egg production was as great as in fresh S.E.A. (Figs. 24b and 25 respectively) with an egg production of 2.70 eggs/female/day over the first week. The number of juveniles hatching and developing was consistently less in S.E.A. + extract than in fresh S.E.A. and after day 65 the population slowly declined until only one third stage and two fourth stage juveniles remained at the end of the experiment, although four nematodes had matured during the experiment (Appendix III, Tables 7-12; this period was not included in Fig. 24b as no major population fluctuations occurred).

In fresh S.E.A. 45 nematodes matured and the $F_1$ females deposited eggs, but at a much slower rate compared to the females inoculated; a maximum of approximately 135 eggs was recorded but this preceded the maximum number of $F_1$ adults (Fig. 25). In water agar, population development was intermediate between soil-extract agar and the other treatments: the number of eggs surviving to attain the second stage was lower but survival of third and fourth stage juveniles was similar to fresh soil-extract agar. Fewer nematodes matured during the experiment and egg production was correspondingly less (Fig. 26).

The rate of development was not affected by culture medium. Eggs hatched 7 days after deposition and the first-stage juveniles moulted 4-5 days later, provided they had fed during this period. The second moult occurred approximately 17 days after the first and the third after a further 9 days. The final moult occurred nearly seven weeks after the eggs were deposited and the first $F_2$ eggs were deposited two days later so that the total generation time (egg to egg) was approximately seven weeks. The rate of maturation of fourth-stage juveniles was initially greater in water agar than in fresh S.E.A. and the egg production rate was consequently greater, but from day 85 onwards the number of $F_1$ adults and $F_2$ eggs was greatest in fresh S.E.A. The differences between the four treatments were generally highly significant (Tables 31, 32) and arranging the treatments in order of

FIG. 24. POPULATION DEVELOPMENT FROM 25 ADULT FEMALE P. PUNCTATUS CULTURED INDIVIDUALLY AT 20°C. I.



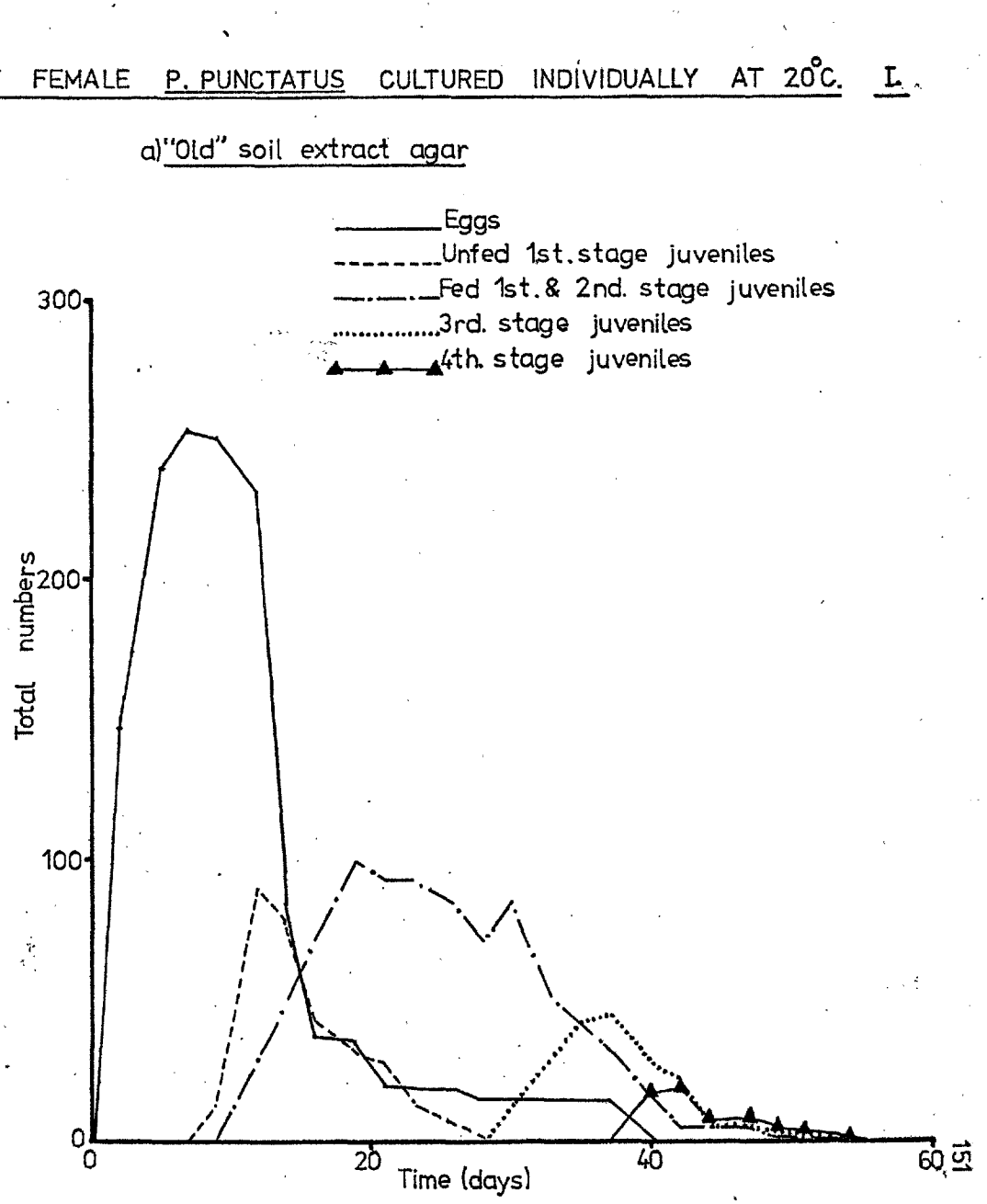



FIG. 25. POPULATION DEVELOPMENT FROM 25 ADULT FEMALE P.PUNCTATUS CULTURED INDIVIDUALLY AT 20°C. I.

Fresh soil extract agar

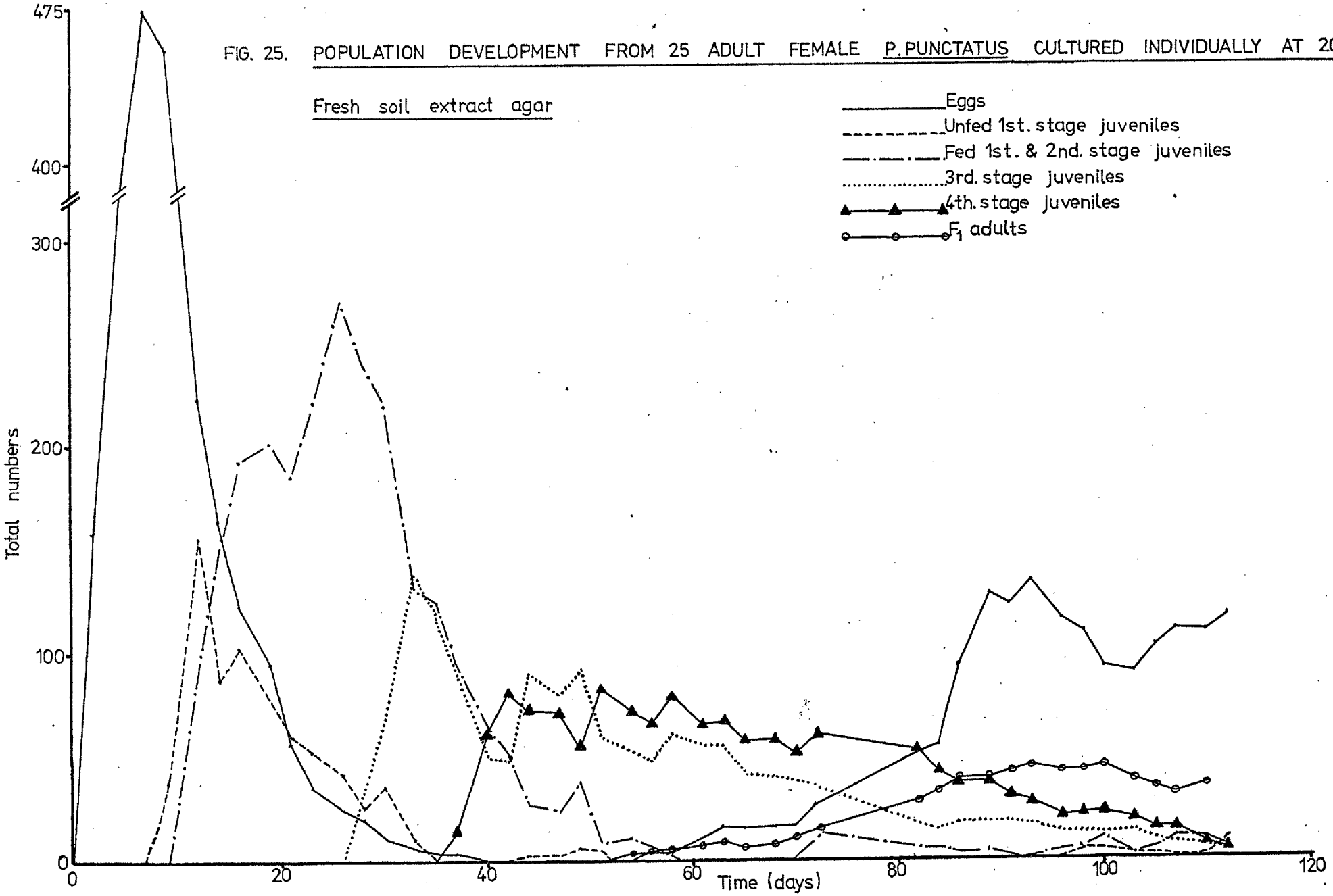


FIG. 26. POPULATION DEVELOPMENT FROM 25 ADULT FEMALE P. PUNCTATUS CULTURED INDIVIDUALLY AT 20°C. I.

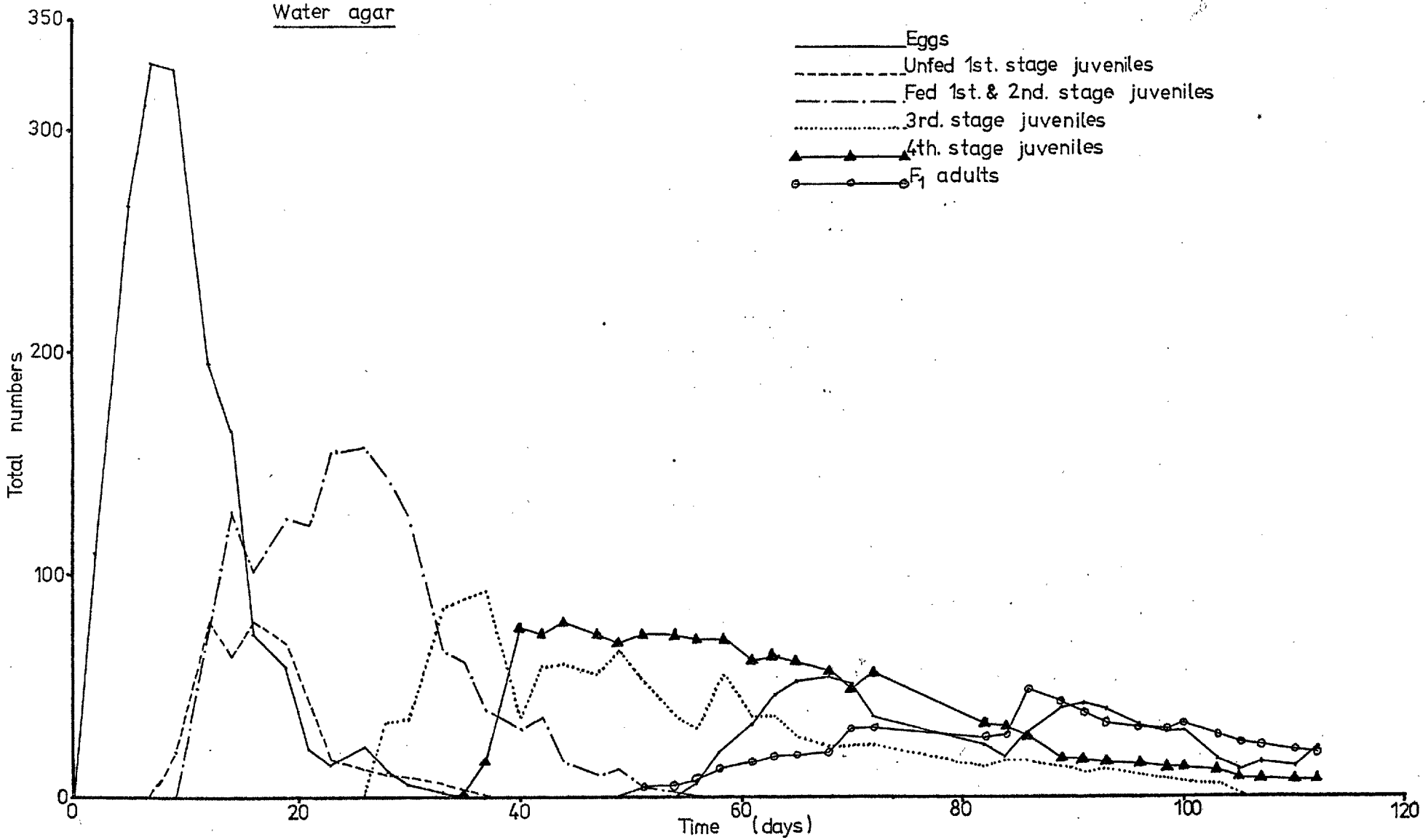


Table 31. Population development from P.punctatus females I; results of analyses of variance (14, 28 days).

| Time (days) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| 14 | Eggs | 0.81 | N.S. | - |
| | Unfed 1st stage juveniles | 3.22 | 0.05-0.01 | A>B*** A>D*** A>C* |
| | Fed 1st and 2nd stage juveniles | 1.86 | 0.2-0.05 | B>C** B>D* |
| | Total offspring | 0.59 | N.S. | - |
| | Adults | 0.51 | N.S. | - |
| 28 | Eggs | 2.13 | 0.2-0.05 | C>A** C>B** |
| | Unfed 1st stage juveniles | 2.03 | 0.2-0.05 | C>D** C>B* C>A* |
| | Fed 1st and 2nd stage juveniles | 3.95 | 0.05-0.01 | C>A**** C>D*** C>B** |
| | 3rd stage juveniles | 0.16 | N.S. | - |
| | Total offspring | 4.29 | 0.05-0.01 | C>A**** C>D**** C>B*** |
| | Adults | 0.89 | N.S. | - |

A: "Old" agar; B: Soil extract agar + extract; C: Fresh soil extract agar; D: Water agar.

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001.

Table 31 (cont) Population development from P.punctatus females I. results of analyses of variance (42, 56, 70 days)

| Time (days) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| 42 | Fed 1st and 2nd stage juveniles | 1.13 | N.S. | - |
| | 3rd stage juveniles | 0.86 | N.S. | - |
| | 4th stage juveniles | 0.64 | N.S. | - |
| | Total offspring | 2.87 | 0.2-0.05 | D>A**** B>A* C>A* |
| 56 | 3rd stage juveniles | 2.51 | 0.2-0.05 | C>A*** C>D* |
| | 4th stage juveniles | 1.63 | N.S. | - |
| | Total offspring | 2.35 | 0.2-0.05 | C>A*** C>B* |
| 70 | Eggs | 9.27 | 0.01-0.001 | D>C**** D>B**** |
| | 3rd stage juveniles | 6.64 | 0.05-0.01 | C>B**** C>D** |
| | 4th stage juveniles | 4.75 | 0.05-0.01 | C>B**** |
| | Adults | 18.25 | <0.001 | D>B***** D>C**** |
| | Total offspring | 6.27 | 0.05-0.01 | C>B**** D>B*** |

A: "Old" agar; B: Soil extract agar and extract; C: Fresh soil extract agar; D: Water agar.

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001.

Table 32. Population development from P.punctatus females I; results of "t" tests (84, 98 and 112 days).

| Time (days) | Subject | Value of 't' | Significance | Significant differences |
|---|---|---|---|---|
| 84 | Eggs | 0.03 | N.S. | - |
| | Third stage juveniles | 0.53 | N.S. | - |
| | Fourth stage juveniles | 0.64 | N.S. | - |
| | Total offspring | 0.43 | N.S. | - |
| | Adults | 1.31 | N.S. | - |
| 98 | Eggs | 1.62 | N.S. | - |
| | Fourth stage juveniles | 0.08 | N.S. | - |
| | Total offspring | 3.67 | 0.02-0.01 | C>D |
| | Adults | 0.69 | N.S. | - |
| 112 | Eggs | 1.95 | 0.1-0.05 | C>D |
| | Unfed First stage juveniles | 2.42 | 0.05-0.02 | C>D |
| | Fed 1st stage and second stage juveniles | 1.33 | N.S. | - |
| | Third stage juveniles | 0.98 | N.S. | - |
| | Fourth stage juveniles | 0.85 | N.S. | - |
| | Total offspring | 2.15 | 0.05-0.02 | C>D |
| | Adults | 1.59 | N.S. | - |

increasing population size most frequently indicated the series of old agar < S.E.A. + extract < water agar < fresh S.E.A.

Table 33. Population development from single P.punctatus females I: Percentage* of deposited eggs surviving to attain four subsequent life-stages and the percentage* of juveniles surviving to attain the next life-stage.

| Treatment | Percentage of eggs attaining | | | | Percentage surviving to next stage | | |
|---|---|---|---|---|---|---|---|
| | Second stage | Third stage | Fourth stage | Adult | Second to third st. | Third to Fourth stage | Fourth stage to Adult |
| A | 39 | 18 | 8 | 0 | 45 | 44 | 0 |
| B | 51 | 16 | 8 | 1 | 30 | 51 | 11 |
| C | 57 | 28 | 17 | 9 | 50 | 62 | 54 |
| D | 48 | 28 | 24 | 15 | 58 | 86 | 62 |

*Corrected to nearest 1%

A: Old S.E.A.; B: S.E.A.+ extract; C: Fresh S.E.A.; D: Water Agar.

The percentage of eggs deposited during the first week that survived to attain subsequent life-stages was greater in fresh S.E.A. and water agar than in old agar and S.E.A. + extract (Table 33); these differences were rarely significant except for the number of eggs surviving to adulthood. In passing from one juvenile stage to the next approximately 50% mortality frequently occurred (Table 33). Mortality in fresh S.E.A. and water agar was considerably less for the later juvenile stages but even so only 9% and 15% respectively of the potential population (i.e. the number of eggs deposited) reached maturity. Again the most significant differences between treatments were in the fourth stage to adult ratio with survival being significantly greater in fresh S.E.A. and water agar (Table 34).

Table 34. Population development from single P.punctatus females I: Results of $\chi^2$-test (2x2 contingency table) for percentage of various life-stages surviving to attain subsequent life-stages

| Developmental stages | | AvB | AvC | AvD | BvC | BvD | CvD |
|---|---|---|---|---|---|---|---|
| Eggs to second stage | $\chi^2$ | 0.27 | 13.52 | 0.61 | 0.26 | 0.07 | 0.60 |
| | Details | N.S. | C>A**** | N.S. | N.S. | N.S. | N.S. |
| Eggs to third stage | $\chi^2$ | 0.21 | 1.22 | 1.22 | 1.84 | 1.84 | 0 |
| | Details | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. |
| Eggs to fourth stage | $\chi^2$ | 0 | 2.03 | 4.88 | 2.03 | 4.88 | 0.64 |
| | Details | N.S. | N.S. | D>A* | N.S. | D>B* | N.S. |
| Eggs to adult | $\chi^2$ | 5.89 | 19.38 | 26.04 | 6.89 | 12.19 | 0.90 |
| | Details | B>A** | C>A**** | D>A**** | C>B*** | D>B**** | N.S. |
| Second stage to third stage | $\chi^2$ | 1.81 | 0.19 | 1.25 | 3.15 | 6.02 | 0.47 |
| | Details | N.S. | N.S. | N.S. | N.S. | D>B** | N.S. |
| Third stage to fourth stage | $\chi^2$ | 0.37 | 2.41 | 16.37 | 0.89 | 11.97 | 6.46 |
| | Details | N.S. | N.S. | D>A**** | N.S. | D>B**** | D>C** |
| Fourth stage to adult | $\chi^2$ | 22.20 | 64.13 | 73.14 | 18.54 | 24.67 | 0.50 |
| | Details | B>A**** | C>A**** | D>A**** | C>B**** | D>B**** | N.S. |

*: p=0.05-0.02; **: p=0.02-0.01; ***: p=0.01-0.001; ****: p<0.001.

A: Old S.E.A.; B: S.E.A. + extract; C: Fresh S.E.A.; D: Water Agar.

Discussion: The results suggested that the agar medium influenced the physiology and/or the behaviour of P.punctatus. The medium appeared to particularly affect three-stages in the life-cycle. The adult females appeared to be affected because the number of deposited eggs was significantly less in old S.E.A. than in the other treatments. The large number of eggs deposited in the first week of the experiment was probably in part a response to the abundance of food compared to that of the stock cultures. The comparatively large numbers of prey in a small volume of agar with no competition from other predators enabled the females to rapidly achieve their reproductive potential. The 19 eggs/♀/week in fresh S.E.A. and in S.E.A. + extract (20°C) was similar to the 16.6 eggs/♀/week (22°C) recorded by Maertens (1975) for P.punctatus reared under similar conditions, and probably represents the near maximum egg production rate of P.punctatus. The rate in old agar was only 10eggs/♀/week and as these females also experienced no competition for prey the difference between the two rates suggested that another factor was involved. The most likely explanation was the concentration of one or more metabolic wastes from the organisms in the stock culture. Water-soluble molecules or inorganic ions (e.g. ammonia, mineral salts) did not seem to be involved as it would be expected that the S.E.A. + extract would be similar to old S.E.A. in its culture properties, unless the 50% dilution with fresh soil-extract agar was sufficient to reduce the concentration to below a critical level.

The use of a soil-extract in the agar appeared beneficial to P.punctatus population development in culture as the number of eggs deposited (and the number of developing juveniles) was greater than in water agar. Maertens (1975) recorded an improved P.punctatus population growth in an agar medium including 1% humus-extract compared to that in the medium without the extract, but Grootaert and Maertens (1976) found that M.aquaticus cultures did not benefit from the same extract.

The first-stage juveniles were sensitive to adverse conditions in

this experiment and in stock cultures. The most important factor for continued development was food but this did not vary between the treatments of this experiment, suggesting that differences in medium were also important. Mortality was greatest in old agar and can be ascribed to toxic metabolites from the stock culture. As the first stage juveniles were so sensitive to environmental influences it would not be biologically advantageous for the females to deposit eggs in adverse environmental conditions; the decreased egg production in old agar may reflect this, rather than representing a direct effect on the physiology of the females. At best, only 57% of the deposited eggs survived to become second stage juveniles, the main cause being the large mortality of first stage juveniles. Less than 1% of eggs from all treatments failed to hatch, although Maertens (1975) records that 15% of P.punctatus eggs failed to hatch at 22°C.

The second stage was the longest juvenile stage (17 days) and appeared to be a period of accretion before rapid development through to the fourth stage. Second stage juveniles were robust compared to first stage juveniles and were very active. They fed frequently, most commonly on prey previously wounded by the adults, but also successfully attacked young juveniles of A.avenae. There was a considerable increase in size and intestinal pigmentation increased to the near-black colour of the older juveniles and adults. The rate of development and survival was not greatly affected by the medium and approximately 50% reached the third stage, which was comparatively short and uneventful.

The final moult was the third developmental process to be affected by the medium. In fresh S.E.A. and water agar 50-60% of the fourth stage juveniles moulted but survival was reduced to 11% in S.E.A. + extract and no nematodes matured in old S.E.A. If the non water-soluble metabolites that possibly affected egg production and first stage juvenile development were important, it would be expected that the extract of the old culture

would not affect the fourth stage juveniles. Three alternatives remained: first, that the fourth stage juveniles were tolerant of all metabolites; second, that water soluble molecules affected the fourth stage juveniles and third, that encounters with adults and/or active secretions (possibly pheromonal) of the adults inhibited development of the fourth stage juveniles. The evidence of non-maturation in old S.E.A. excluded the possibility of encounters with adults as none were present, whereas their products may have persisted from the stock culture. Most known pheromones are persistent under natural conditions and their half-life may have been extended under culture conditions (e.g. by absorption onto the agar). In the S.E.A. + extract one third and two fourth stage juveniles survived for a long period towards the end of the experiment which suggested that they may have needed conditions to change before being able to moult.

The total life-cycle of seven weeks was longer than the 41 days at 19°C recorded by Maertens (1975), probably because his cultures were supplied with prey every day. The rate of egg-production by $F_1$ adults was less than that of the inoculated adults probably because of the competition for prey. In fresh S.E.A. the maximum number of eggs deposited by $F_1$ adults preceded the maximum number of $F_1$ adults and the graph suggested that a new peak may have been reached if the experiment had continued (Fig. 25). Survival of $F_2$ first-stage juveniles was much reduced either by the metabolites of the older juveniles and adults or possibly by cannibalism.

The best medium for mass culture of P.punctatus was therefore fresh soil-extract agar in which the largest populations developed. Water agar was less good as fewer eggs were deposited, although the percentage survival was greater; the reverse applied to soil-extract agar with added extract of an old culture. Old soil-extract agar was the worst medium for population development, which confirmed earlier observations of stock cultures that were not recultured. The nature of the medium's influence appeared

complex and suggested the following experiments.

vii) Population development from single P.punctatus females recently extracted from the bracken F-layer.

This comparative experiment used P.punctatus females recently extracted from the bracken F-layer material by the Whitehead tray method (Whitehead and Hemming, 1965). The method was similar to that used for experiment vi) but included an extra treatment, an agar made using an extract of the bracken F-layer material (F.L.E.A.). This extract was prepared by the same method as the soil-extract and had a pH of 6.1. There were 11 replicates of each treatment. The nematodes from all replicates were extracted, counted and recultured on days 17 and 35; the experiment was terminated on day 70 when the nematodes were again extracted and counted. Statistical analysis was similar to that in experiment vi) but the percentage of eggs and fourth stage juveniles surviving to the adult stage was not investigated as the probable maximum number of adults had not been reached by day 70.

Results: Culture medium again had a significant effect on the development of P.punctatus populations; although tending to confirm the results of experiment vi), the mechanism of this effect was not elucidated. The population curves (Figs. 27, 28, 29) were based on the counts at 2-3 day intervals and the analyses of variance (Table 35) on the extraction counts (Appendix III, Tables 15-19). The error incurred by not replacing eggs after each extraction was reflected in the greater areas under the curves for the juvenile stages than for the eggs; the maxima for second stage juveniles also exceeded the maxima for eggs in water agar, F.L.E.A. and S.E.A. + extract. In the 2x2 contingency tables these were treated as 100% survival (Tables 36, 37).

The rate of egg production, and the total number deposited, was greatest

FIG. 27. POPULATION DEVELOPMENT FROM ADULT FEMALE P. PUNCTATUS EXTRACTED FROM BRACKEN FERMENTATION - LAYER MATERIAL AND CULTURED INDIVIDUALLY AT 20°C.

a) "Old" soil extract agar

b) Soil extract agar & extract

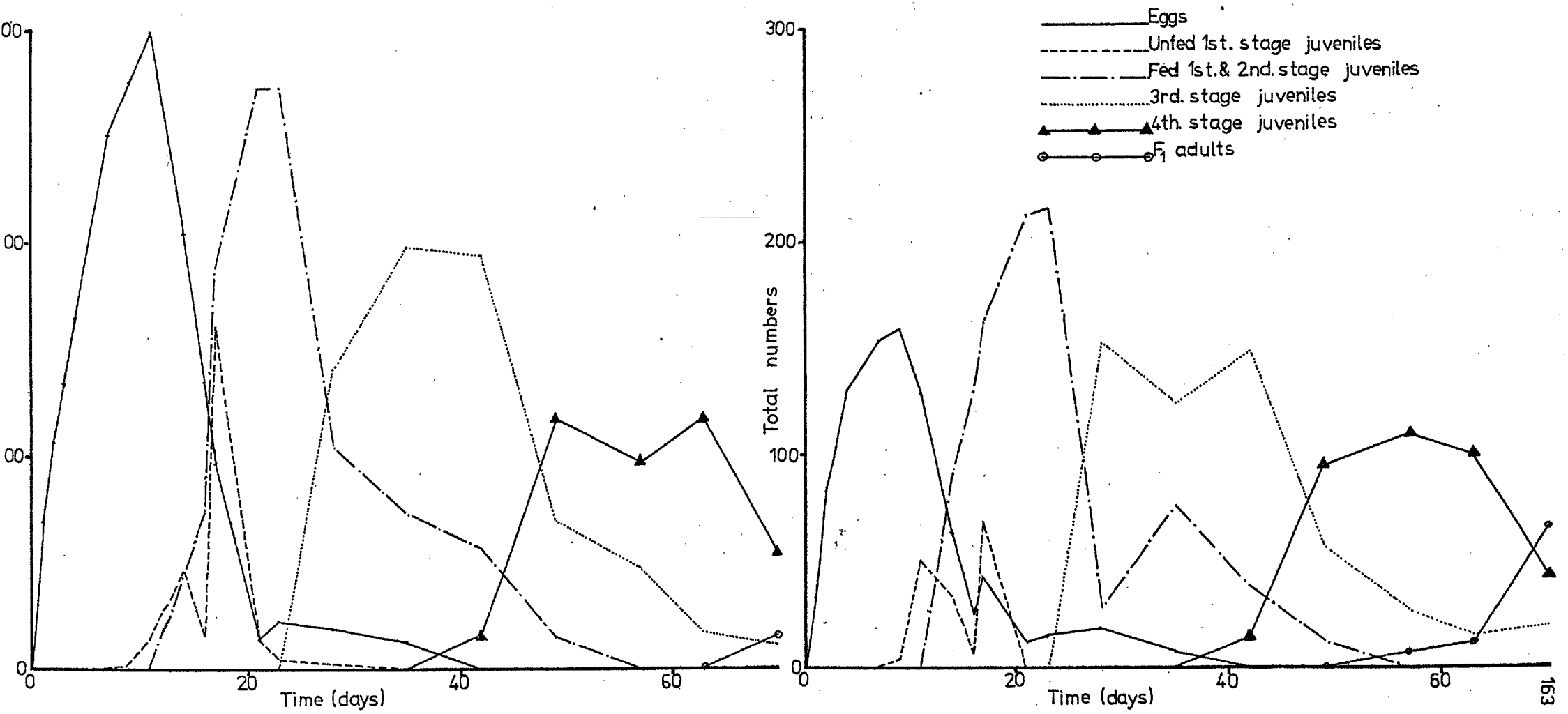


FIG. 28. POPULATION DEVELOPMENT FROM ADULT FEMALE P. PUNCTATUS EXTRACTED FROM BRACKEN FERMENTATION - LAYER MATERIAL AND CULTURED INDIVIDUALLY AT 20°C.

a) Fresh soil extract agar

b) Water agar

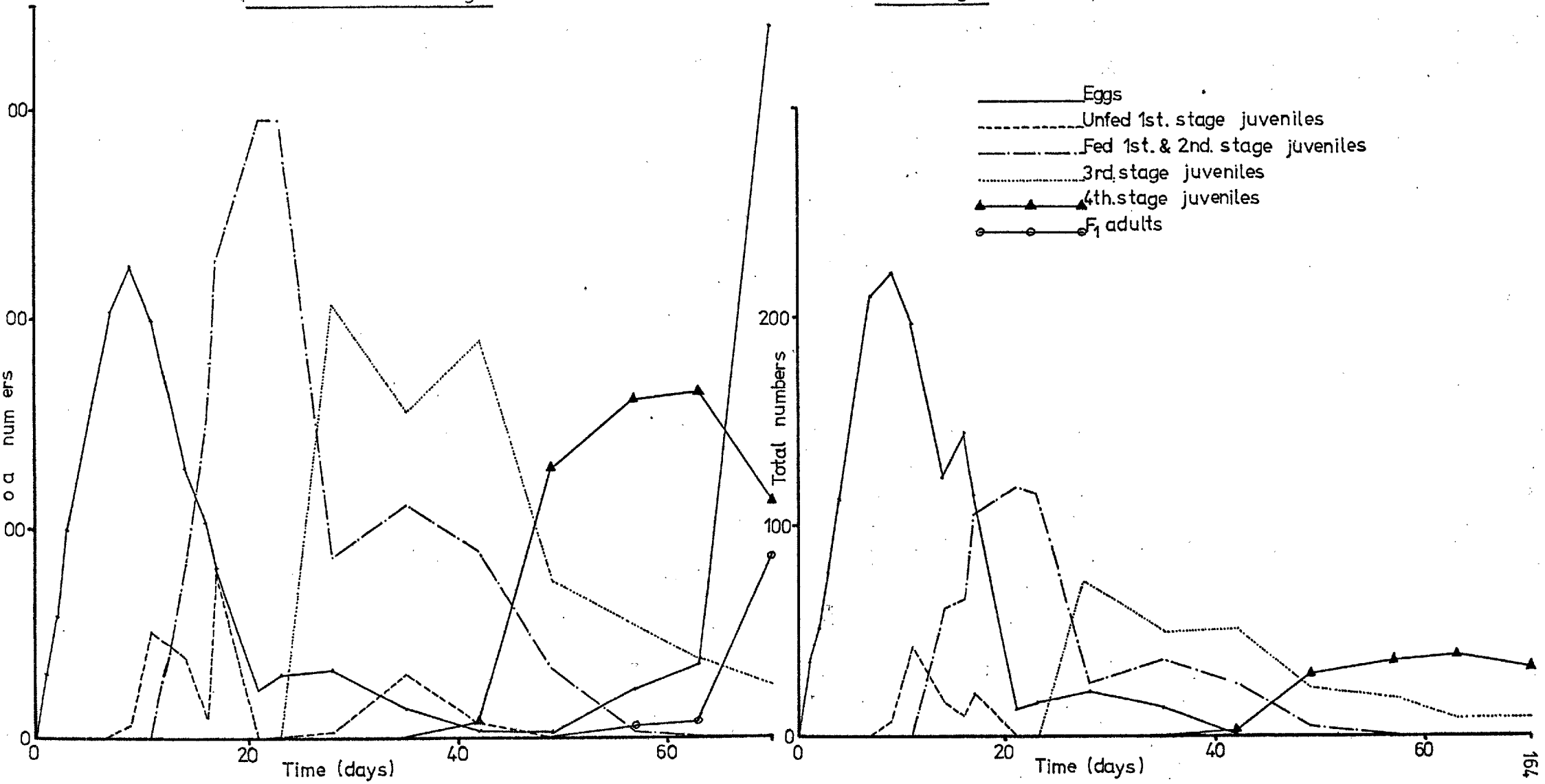


FIG. 29. POPULATION DEVELOPMENT FROM ADULT FEMALE P. PUNCTATUS EXTRACTED FROM BRACKEN FERMENTATION LAYER MATERIAL AND CULTURED INDIVIDUALLY AT 20°C.

F-Layer extract agar

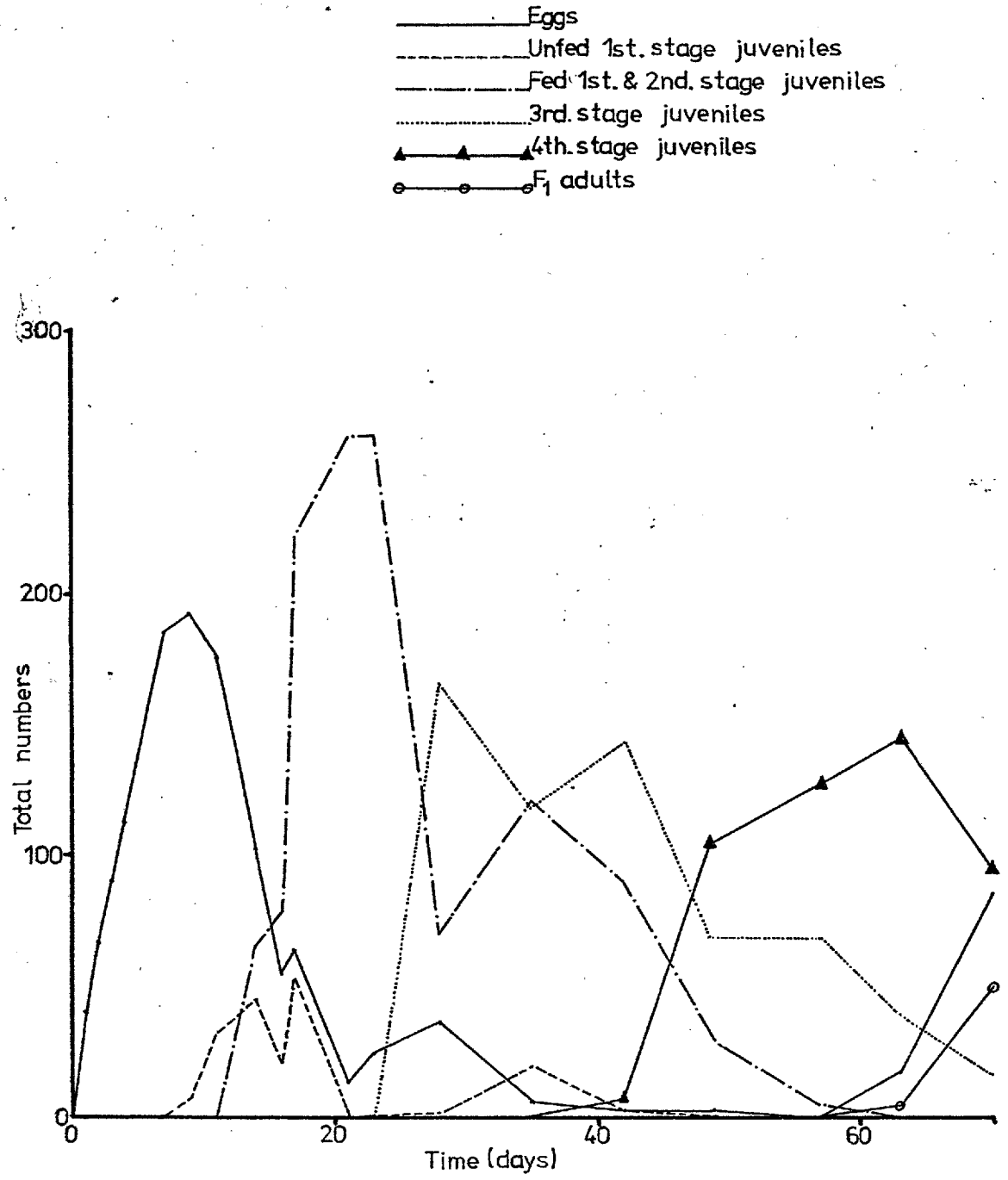


Table 35. Population development from P.punctatus females extracted from Bracken F-layer material and cultured individually at 20°C: results of analyses of variance.

| Time (days) | Subject | Value of 'F' | Significance | Significant differences |
|---|---|---|---|---|
| 17 | Adults | 0.16 | N.S. | - |
| | Eggs | 2.61 | 0.05-0.01 | D>B**** D>E*** D>C** D>A* |
| | Unfed 1st stage juveniles | 6.54 | <0,001 | A>D,E***** A>C,B*** B>D* C>D* |
| | Fed 1st stage and 2nd stage juveniles | 0.70 | N.S. | - |
| | Total offspring | 0.45 | N.S. | - |
| 35 | Adults | 0.36 | N.S. | - |
| | Eggs | 0.42 | N.S. | - |
| | Unfed 1st stage juveniles | 2.58 | 0.2-0,05 | C>A**** C>B** D>A* E>A* |
| | Fed 1st stage and 2nd stage juveniles | 2.55 | 0.2-0.05 | E>D**** E>A** C>D** |
| | 3rd stage juveniles | 2.37 | 0.2-0.05 | A>D**** B>D* C>D* |
| | Total offspring | 2.39 | 0.2-0.05 | C>D**** E>D*** A>D** B>D* |
| 70 | Adults | 10.06 | <0.001 | E>A*** C>D,A***** C>E* B>D,A***** E>D**** |
| | Eggs | 10.83 | <0.001 | C>A,E***** C>B* B>A***** B>E* |
| | Unfed 1st stage juveniles | 3.21 | 0.05-0.01 | B>E**** B>C** |
| | Fed 1st stage and 2nd stage juveniles | 0.57 | N.S. | - |
| | 3rd stage juveniles | 2.04 | 0.2-0.05 | C>D,A** B>D,A* |
| | 4th stage juveniles | 4.33 | 0.01-0.001 | C>D,B,A**** E>D,B,A** |
| | Total offspring | 15.68 | <0.001 | C>A,D,E***** C>B* E>D,A** B>D,A,***** B>E** |

A: "Old" soil-extract agar; B: Soil-extract agar + extract; C: Fresh soil-extract agar; D: Water agar; E: Bracken F-layer extract agar.
*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001.

Table 36. Population development from single P.punctatus females extracted from bracken F-layer material: Percentage* of deposited eggs surviving to attain three subsequent life-stages and the percentage* of juveniles surviving to attain the next juvenile stage.

| Treatment | Percentage of eggs attaining | | | Percentage surviving to next stage | |
|---|---|---|---|---|---|
| | Second stage | Third stage | Fourth stage | Second to Third stage | Third to Fourth stage |
| A | 92 | 66 | 40 | 73 | 60 |
| B | 100 | 97 | 70 | 71 | 72 |
| C | 100 | 70 | 57 | 70 | 82 |
| D | 53 | 33 | 17 | 61 | 53 |
| E | 100 | 86 | 75 | 64 | 87 |

*Corrected to nearest 1%

A: Old S.E.A.; B: S.E.A. + extract; C: Fresh S.E.A.; D: Water agar; E: F-layer extract agar.

Table 37. Population development from single P.punctatus females extracted from bracken F-layer material: results of $\chi^2$-test (2x2 contingency table) for percentage of various life-stages surviving to attain subsequent life-stages.

| Developmental Stages | | AvB | AvC | AvD | AvE | BvC | BvD | BvE | CvD | CvE | DvE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Eggs to second stage | $\chi^2$ | 18.04 | 18.04 | 18.14 | 18.04 | 0 | 57.02 | 0 | 57.02 | 0 | 57.02 |
| | Details | B>A**** | C>A**** | A>D**** | E>A**** | N.S. | B>D**** | N.S. | C>D**** | N.S. | E>D**** |
| Eggs to third stage | $\chi^2$ | 19.37 | 0.15 | 12.19 | 4.79 | 16.39 | 48.58 | 5.47 | 10.47 | 3.28 | 24.57 |
| | Details | B>A**** | N.S. | A>D**** | E>A* | B>C**** | B>D**** | B>E** | C>D*** | N.S. | E>D**** |
| Eggs to fourth stage | $\chi^2$ | 6.91 | 2.14 | 5.33 | 9.72 | 1.39 | 23.55 | 0.25 | 13.92 | 2.81 | 28.27 |
| | Details | B>A*** | N.S. | A>D* | E>A*** | N.S. | B>D**** | N.S. | C>D**** | N.S. | E>D**** |
| Second stage to third stage | $\chi^2$ | 0.04 | 0.09 | 1.28 | 0.74 | 0.01 | 0.86 | 0.43 | 0.70 | 0.32 | 0.74 |
| | Details | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. |
| Third stage to fourth stage | $\chi^2$ | 1.20 | 4.81 | 0.38 | 8.17 | 1.22 | 2.92 | 3.17 | 7.81 | 0.47 | 11.92 |
| | Details | N.S. | C>A* | N.S. | E>A*** | N.S. | N.S. | N.S. | C>D*** | N.S. | E>D**** |

*: p=0.05-0.02; **: p=0.02-0.01; ***: p=0.01-0.001; ****: p<0.001

A: Old S.E.A.; B: S.E.A. + extract; C: Fresh S.E.A.; D: Water agar; E: F-layer extract agar.

in old S.E.A. (approx. 22.7 eggs/♀/wk) and lowest in S.E.A. + extract (approx. 14.0 eggs/♀/wk); water agar, fresh S.E.A. and F.L.E.A. were all similar (19.09, 20.0, and 18.5 eggs/♀/wk respectively; all egg production rates refer to the first week of the experiment and are corrected for the loss of some females that migrated from the cultures and dehydrated). The extraction counts (Appendix III, Tables 15-19) indicated that subsequent population development was not as good in old agar. Significantly fewer eggs survived to the second and successive stages than in the other treatments, except for water agar which was consistently the worst medium by all methods of assessment.

Approximately 1.3% of the eggs failed to hatch (60% of these in old agar) and survival to the second stage was greater than in experiment vi); again the large percentage hatch indicates that first stage mortality was considerable in both old agar and particularly water agar where it approached 50%. Survival to subsequent stages was also good (Table 36). The total number of $F_1$ adults was not recorded but observation of the cultures indicated that the fourth stage juveniles were active and healthy in appearance, and it seemed probable that most would have matured. The exception was water agar in which survival was consistently lower than in the other treatments and only 17% of the eggs reached the fourth stage.

In fresh S.E.A. $F_1$ adults were noted on day 49 together with their deposited eggs; a pronounced increase in the number of $F_1$ adults in fresh S.E.A. on day 63 resulted in a large number of deposited eggs but the rate of egg production per female was lower than that of the inoculated adults (Fig. 28c). A less pronounced increase occurred in F.L.E.A. (Fig. 29) but eggs deposited by $F_1$ adults were absent from water agar, S.E.A. + extract and old S.E.A.

Development times were similar in all treatments except that the fourth-stage to adult period varied; in all treatments the eggs hatched

after 7 days and moults occurred 4, 16 and 28 days after hatching. The fourth to adult period was similar in fresh S.E.A. and S.E.A. + extract (14 and 13 days respectively) but was 18 days in old agar, 22 days in F.L.E.A. and 28 days in water agar. In general, fresh S.E.A. and F.L.E.A. gave the best population growth of P.punctatus (Figs. 28a, 29; Table 35). Water agar and old agar were generally the worst media and S.E.A. + extract was between these two extremes.

Discussion: The population curves were generally similar to those recorded in experiment vi); the overall conclusions regarding the efficacy of the various media for culture of P.punctatus were confirmed and need little further discussion. Those details that did differ from experiment vi) will be considered more fully.

The survival of the nematodes was much greater than for the offspring of females taken from stock cultures. The number of organisms infecting the nematodes in stock cultures was fairly large and although all the agars were heated before use, and the nematodes washed in sterile deionised water before inoculation, it was likely that some infective organisms were transferred to the experimental cultures, especially those that adhere to the nematodes' cuticle. Obvious contaminants, such as trapping fungi, were not recorded in either experiment but the tissues of dead nematodes in experiment vi) were often infected with bacteria either before or after death. The density of pathogens may be lower in humus, especially as predator density was considerably less than in stock cultures, and the fewer pathogens transferred to the experimental cultures may have allowed greater survival. Alternatively the nematodes from the bracken F-layer material were probably subject to greater selection pressure and would therefore be generally more resistant to adverse conditions than laboratory reared predators.

Soil extract and bracken F-layer extract had a beneficial effect on population growth, confirming the results of experiment vi) and Maertens

(1975). There was little difference between the two media until the end of the experiment when significantly more $F_1$ adults and eggs were recorded in soil extract agar. Old agar was again a poor medium but there was a very small population growth in water agar compared to experiment vi). Possibly the history of the experimental animals was again the important factor. In experiment vi) the nematodes from stock cultures reproduced well in water agar which did not differ greatly from fresh S.E.A., the best medium, indicating that media with dilute organic and mineral constituents were better than those with greater concentrations. The predators in F-layer material must have been adapted to comparatively large concentrations of organic acids etc. and water agar was least like their natural habitat. In old agar and S.E.A. + extract the disadvantages of metabolic products etc. may not have outweighed the advantages of high organic chemical concentrations; indeed, this may have caused the large egg production in old S.E.A. compared to other treatments, the adverse effects only becoming critical to the juveniles with their apparently greater sensitivity to adverse environmental conditions. The similarity of egg production rates in water agar, fresh S.E.A. and F.L.E.A. lends support to this hypothesis, and the lower egg production rate in S.E.A. + extract would result from the extraction of the detrimental water soluble molecules without the extraction of the beneficial organic molecules.

The development rates of both eggs and juveniles were remarkably constant in the five treatments, but the second stage was shorter by 5 days and the third stage longer by 3 days than in experiment vi). This was most probably the result of differences in the quantity of prey supplied in the two experiments. The between-treatment differences in the time taken for the fourth stage juveniles to moult was all the more marked by the constancy of the other developmental stages, and was difficult to understand. The long period in water agar was probably a feature of that medium's general unsuitability for culture of the F-layer nematodes and conversely

a short period might be expected in fresh S.E.A. The hypothesis that the fourth stage juveniles were sensitive to the metabolites or secretions of the adults could possibly explain the other results if the humus extract contained similar organic molecules. The lack of such molecules in S.E.A. + extract should have given it similar properties to fresh S.E.A. and the results indicated a similar fourth stage to adult period. Old agar containing the waste products of adults from the stock culture delayed maturation but not to the same extent as F.L.E.A. and yet it seemed unlikely that the concentration of metabolites was greater in F.L.E.A. The stock culture used for this experiment contained 2,750 predators (fewer than for experment vi) which represented a far greater density than in the bracken F-layer.

The general considerations of the life-cycle of P.punctatus were confirmed by this experiment. The adults, under suitable conditions, deposit a large number of eggs at a rate of approximately 20 eggs/female/wk; the eggs hatch in 7 days at 20°C. The first juvenile stage was very short but most of the mortality occurs in those four days; those nematodes passing the first moult enter a two week period of growth and accumulate reserves before passing through the twelve day third stage. The fourth stage varied in length; the egg production rate of the $F_1$ adults was lower than for the inoculated adults and again this probably reflected the greater competition for food. Such differences as did occur were probably the result of the different sources of the experimental animals and the natural variation between two distinct populations.

Of the hypotheses concerning the three sensitive stages in the life cycle of P.punctatus the response of adults to metabolites in four-week old cultures was not confirmed but neither could it be rejected totally. The general sensitivity and large mortality of the first stage juveniles was confirmed but survival was generally better, especially in old agar. Finally the fourth stage juveniles were sensitive to the medium but the nature of the sensitivity was not elucidated. In an attempt to clarify

the results of experiment vi) a final experiment, which concentrated on egg laying and first stage juvenile development, was made.

viii) Population development from single P.punctatus females II.

The four treatments (old agar, fresh S.E.A., S.E.A. + extract and water agar) were prepared in the same manner as in experiment vi). Three further agar treatments were investigated: Old agar from a two-week old stock culture of P.punctatus was used without any treatment except the removal of nematodes (i.e. not heated: untreated old S.E.A.). A length of dialysis membrane was ligated at one end, filled with the remaining agar from the stock culture and placed in 15cm$^3$ sterile deionised water for three hours. The dialysate obtained was mixed with 15cm$^3$ cool but molten, fresh 2% soil-extract agar and used for a second treatment (S.E.A. + dialysate). The dialysis membrane containing the dialysed agar was suspended under a running tap so that the water continually flowed over the surface of the membrane; it was left in this position for 22 hours. Finally it was placed in three changes of 30cm$^3$ sterile, deionised water for 1 hour each. The 25cm$^3$ dialysed agar obtained was mixed with 25cm$^3$ of 2% soil-extract agar and used for a third treatment (S.E.A. + dialysed agar). Fifty replicates of each treatment were used; assessment of population growth was based on the number of nematodes and eggs extracted after fourteen days.

Results: The stock population used for the experiment contained approximately 2000 nematodes of which 800 were adult; the density of eggs was low (approx. 5/cm$^3$) but the results presented in Table 38 have been corrected to allow for the eggs included in the untreated old S.E.A. and the S.E.A. + dialysed agar. Although as many females as possible were removed, many of the cultures in these two treatments contained more than one nematode on subsequent observation. This was exacerbated by migration between the cultures of the perspex blocks which were moist for a short time; in previous

Table 38. Population development from single P.punctatus females II; Mean number (± S.E.) of the various life stages of P.punctatus extracted on day 14.

| Treatment | No. of Replicates | Number of Adults | Number of Eggs | Number of First stage juveniles | Number of second stage juveniles | Total number of offspring |
|---|---|---|---|---|---|---|
| Old S.E.A. | 50 | 0.98± 0.06 | 16.18± 0.99 | 15.12± 1.02 | 32.26± 1.29 | 63.56± 2.34 |
| S.E.A. + extract | 50 | 0.84± 0.10 | 11.82± 1.07 | 13.60± 1.30 | 21.72± 1.73 | 47.14± 2.84 |
| Fresh S.E.A. | 50 | 0.88± 0.11 | 14.34± 1.42 | 13.02± 1.16 | 28.94± 2.33 | 56.30± 4.26 |
| Water agar | 50 | 0.68± 0.10 | 12.32± 1.62 | 7.38± 0.96 | 20.98± 2.07 | 40.68± 3.90 |
| Untreated old S.E.A.* | 15 | 1.00± 0 | 35.73± 11.21 | 9.47± 1.75 | 14.13± 2.57 | 59.33± 9.42 |
| S.E.A. + dialysate | 50 | 0.96± 0.10 | 16.44± 2.01 | 11.74± 1.46 | 8.82± 1.35 | 37.00± 4.11 |
| S.E.A. + dialysed agar* | 20 | 1.00± 0 | 28.60± 3.56 | 11.78± 1.77 | 15.55± 1.56 | 52.95± 5.44 |

*Using only cultures containing 1 female in treatments E and G.

Table 39. Population development from single P.punctatus females II: Results of the analyses of variance.[1]

| Subject | Value of 'F' | Significance | Significant Differences |
|---|---|---|---|
| Eggs | 10.08 | <0.001 | E>A, B,C,D,F,G***** G>B, D**** G>C*** G>A** G>F* |
| Unfed First-stage juveniles | 4.95 | <0.001 | A>D,F***** A>G** B>D,F***** B>E** C>D,F***** C>E** G>F**** |
| Fed First-stage juveniles and second-stage juveniles | 22.12 | <0.001 | A>E,F,G***** C>E,F,G***** C>B,D**** B>E***** B>G*** D>E*** D>G** G>F** |
| Total offspring | 6.68 | <0.001 | A>D,F***** A>B**** A>G* C>F***** C>D**** E>D,F***** E>B**** E>G*** E>C** B>F* G>F* |

A: Old S.E.A.; B: S.E.A. + extract; C: Fresh S.E.A.;

D: Water agar; E: Untreated old S.E.A.; F: S.E.A. + dialysate;

G: S.E.A. + dialysed agar.

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001;

*****: p<0.001.

1. Using only the cultures containing 1 female in treatments E and G.

experiments migration was minimal and approximately equal in all treatments and was considered not to affect the results substantially, but in this experiment 't' tests (not presented) indicated that population development in cultures with more than one female differed significantly from the population development in cultures with a single female. To allow comparison with the other treatments (and previous experiments) the results presented for untreated old S.E.A. and S.E.A. + dialysed agar refer to those cultures with one female only (Table 38); this reduced the number of replicates to 15 and 20 respectively. The analyses of variance (Table 39) are also based on data for the cultures with single females; analyses of the percentage survival were not included as in a two week period the maxima may not have been reached.

Grouping the treatments on the basis of the mean number of each life stage recorded did not show any pattern but the culture medium had a significant effect on the population development. Heating old agar had a significant effect on the culture of the nematodes as the mean number of eggs was greatest in untreated old S.E.A. and the mean number of unfed first stage and fed first stage plus second stage was greatest in old S.E.A. (Table 38). Egg production per female was much lower than in previous experiments (<1egg/♀/week in most treatments using the total number of offspring and assuming that most of the eggs were deposited in the first week).

The populations in fresh S.E.A. and in S.E.A. + dialysed agar were similar as were the populations in S.E.A. + extract and in water agar. The smallest population was recorded in S.E.A. + dialysate. On the basis of the total offspring the culture media can be arranged in the following order of increasing population and therefore suitability for P.punctatus culture: S.E.A. + dialysate < water agar < S.E.A. + extract < S.E.A. + dialysed agar < fresh S.E.A. < untreated old S.E.A. < old S.E.A. (Table 38).

Discussion: The reason for the lower number of eggs and juveniles per female in all treatments compared to previous experiments was not clear. Although the quantity of food probably varied between the experiments the variation was not enough to have caused such a large difference. A more likely explanation was that the females in the two-week old culture had been depositing eggs more frequently than those from four-week old stock cultures and did not have the accumulated reserves to rapidly increase their egg production rate.

That the predators responded to the different media was clearly demonstrated and led to highly significant differences between the treatments. Old agar from a two-week old stock culture appeared particularly beneficial to population growth and heating the agar did not greatly alter the total numbers recorded. It is possible that the females were physiologically adapted to conditions in the two week old culture and did not need a period of adjustment in the two old S.E.A. treatments. The difference in rate of development may have resulted from the loss of the volatile metabolites from the heated old agar, or the destruction of pathogenic organisms, but as most of the offpsring in the untreated old S.E.A. were unhatched eggs this would imply an effect on the embryology. It was possible that the eggs in the untreated old agar had ceased development and should not have been included in the results. The number of unfed first stage juveniles was not significantly different in heated and untreated old S.E.A. whereas the number of fed first-stage and second stage juveniles was significantly different and the extra detritus caused by heating the agar and killing the organisms present may have been a food source for the juveniles, allowing more rapid development.

The similarity between fresh S.E.A. and S.E.A. + dialysed agar suggested that dialysis had reduced the concentration of the compounds responsible for lowering egg production rates and retarding juvenile development. This was supported by the poor population growth in S.E.A. + dialysate and suggested that small molecules were responsible for the poor population

development. Similarly S.E.A. + extract was not a particularly good medium and fresh S.E.A. was a better medium for population development of P. punctatus.

This experiment suggested that the concentration of toxic chemicals in stock cultures increased with time and that the critical level had not been reached after two weeks. Indeed the concentration of such molecules at two weeks may have enhanced population development. The results of dialysing the agar tended to confirm that the toxic substances were small molecules and could therefore include known excretory products of nematodes such as ammonia and urea (Wright and Newall, 1976). Heating stock culture agar significantly increased the total offspring which might also suggest the loss of volatile excretory products (ammonia, carbon dioxide) but could also include the decomposition of larger molecules. Although not the best medium over a two week period, fresh S.E.A. was better than many of the media tested and was confirmed as a good medium for stock cultures.

## DISCUSSION

The major aim of the work described in this section was achieved: the development of a method suitable for the mass culture of Prionchulus punctatus. The optimum culture conditions for this species were defined and manipulation of these conditions should enable other predatory nematodes, both mononchids and representatives of other taxonomic groups, to be established in permanent culture. The method has already been applied to several other species (Grootaert, pers. comm.; Small, unpubl.) but the conditions necessary for culture of some species have not been elucidated. During the development of the culture method much has been learnt concerning the biology of P.punctatus, although it was recognised that this does not necessarily represent the biology under natural conditions. In particular the possible adaptation of the nematodes to the conditions of culture over four years cannot be ignored.

The culture method in its final form was capable of increasing the number of nematodes rapidly, allowing for the relatively long generation time of P.punctatus. Under ideal conditions the increase in the number of cultures, and therefore the total predator population, was exponential as each new culture could be divided into perhaps four new cultures every four weeks. Under such conditions a single good culture (3,000 P.punctatus) could give rise to 64 cultures, representing 192,000 P.punctatus, in four months; in practice this was not achieved but the maximum of 150 cultures (approx. ≡ 250,000 P.punctatus) maintained in this study required less than a year to accumulate. The method would therefore lend itself to an even larger scale but the necessity for reculturing would eventually prove limiting, even in large culture vessels.

Population growth in petri-dish cultures did not continue indefinitely and reculturing was shown to be necessary; in non-recultured cultures the population declined after four weeks. Most other nematodes that have been cultured were directly or indirectly dependent on nutrients in the medium (e.g. saprophagous nematodes, Dougherty, 1960; Seinura spp. Hechler and Taylor, 1966a) but this was not apparent in this study and alternative causes of population decline must be sought. The increase in metabolites from the organisms present in the cultures has been suggested as a possible contributory factor but the virtually constant period of four weeks also suggests that it may be linked to the life-cycle duration of the predator. In most four week old cultures the majority of juveniles were in the third or fourth stage (at 25°C) and it has been suggested that these stages were sensitive to population density and particularly that of the adults: in the presence of many adults maturation was delayed. Reculturing had three effects - reduction of predator density, reduction in micro-organism density and provision of a comparatively large volume of uncolonised medium free from metabolites of other organisms. The reduction in the concentrations of these factors may have allowed the rapid maturation of fourth stage

juveniles and would be enhanced by the reduced competition for food (although newly recultured cultures were supplied with less prey than four-week old cultures). In this way a new generation would begin whereas in the absence of reculturing, the fourth stage juveniles would not moult and the population would decline. The preferred minimum of three new cultures from one old culture, even if predator density was low, may be explained in terms of reducing these components sufficiently to allow the fourth stage juveniles to mature. Supporting evidence may also include the observation that Labronema sp. apparently benefited from a longer (6-8 wk) reculturing period as the life-cycle of these nematodes was longer (Ferris, 1968; Small, unpubl.) and 6-8 wks corresponds with the time required by Labronema juveniles to reach the 3rd-4th stage (Ferris, 1968). For this to support the hypothesis a similar method of population-limitation by non-maturation of fourth stage juveniles must be proposed for Labronema sp.

The method of reculture was also found to be important and for the greater part of this study the agar-transference method has been used to establish new cultures. The disadvantage of transfer of contaminated organisms was generally outweighed by the advantages which included minimal disturbance and the transference of any beneficial substances, which will be discussed further below. That the transference of nematodes alone can be a suitable method of establishing new cultures has been demonstrated by the success of Grootaert (pers. comm.) using this method. The other difference between his method and the one described here was that he used non-autoclaved humus-extract agar (Grootaert, pers.comm.) and possibly this was a better culture medium than that used in this study.

Optimum conditions for population development included the use of soil-(or humus-) extract agar which was shown to be beneficial to the growth of P.punctatus populations (Small, unpubl.; Maertens, 1975). M.aquaticus did not benefit from a humus-extract (Grootaert and Maertens, 1976) but neither was it detrimental (Small, unpubl.). The failure of Esser (1963) and Mankau (1975) to establish mononchids in culture may be related to the

use of water and corn-meal agars respectively; in particular corn-meal agar encouraged the growth of micro-organisms known to produce toxic metabolites (Nelmes and McCulloch, 1975; Small, unpubl.). The failure to establish permanent cultures of Clarkus papillatus and Anatonchus tridentatus may indicate that soil-extract agar was not a good medium for all mononchids; the lack of success in culturing Mylonchulus sigmaturus was more likely to relate to the prey supplied and more success may have been achieved using rotifers and ciliates as prey. Nonetheless the medium may be important as Cohn and Mordechai (1974) observed the predation of M.sigmaturus on nematodes; recently this species has deposited eggs, which have hatched, in humus-extract agar and readily fed on P.redivivus (Small, unpubl). Grootaert (pers. comm.) failed to establish C.papillatus and A.tridentatus in humus extract culture.

Although the culture method described was good for the large number of nematodes required in this study, some improvements were possible when fewer nematodes were needed. The conditions for maximum population growth included the maintenance of cultures at 20°-25°C, optimally 22°C, (Maertens, 1975; Small, unpubl) but as Maertens demonstrated that the egg production rate was greatest, and embryonic development time shortest, at 25°C whereas the total generation time was shortest at 22°C, it may be possible to increase the production of nematodes by transferring two-week old cultures (when most of the egg-deposition has occurred) from 25° to 22°C for the remainder of the life-cycle. Maertens (1975) and Grootaert and Maertens (1976) maintained stock-cultures of P.punctatus and M.aquaticus respectively at 10°C so that feeding was necessary only at two month intervals, and the period between reculturing was greatly extended because the population did not increase; these authors used 20-25°C for mass-cultures. The results of the first temperature experiment in this study suggested that predator populations declined rapidly at 10°C but the principle of reducing labour by maintaining cultures at a lower temperature remains. The reason for the

difference between minimum temperatures for maintenance of P.punctatus populations was not established. A second improvement to the technique was to prepare a large quantity of 10% soil (or humus-) extract which can be stored frozen until required; when needed it was thawed and added to water agar to form a 1% humus-extract agar (Maertens, 1975). These methods reduced the time and labour involved in maintaining predator cultures but did not increase the yield of nematodes. A culture method involving simultaneous culture of mononchids and their prey such as that used for Seinura spp. (Hechler, 1963) has not been developed. Recently it has been shown that the adults and larger juveniles of Rhabditis oxycerca de Man 1895 and Rhabditis insectivora Korner in Osche 1952 are not susceptible to the attacks of P.punctatus and M.aquaticus, whereas the young juveniles are susceptible; these Rhabditis spp. can be cultured on humus-extract agar by the addition of few particles of rolled oats that do not give very high densities of bacteria (Small, unpublished). It may be possible to use these species for a mixed predator-prey culture.

The wide variety of contaminant organisms present in the cultures suggested that it could be adapted to their study and to interactions between soil-organisms. Mites and trapping-fungi would need little modification of the medium but most of the organisms recorded (e.g. copepods, rotifers, protozoa, tardigrades) would probably benefit from a much softer medium (<0.5% agar). Examples of interactions have been recorded but a few may be particularly noted: mononchids were not often trapped by the fungi except as first stage juveniles and the possible use of trapping fungi as biological control agents may not seriously reduce the predation on plant-parasitic nematodes by predatory nematodes. Adult Labronema sp. were often observed after breaking the mycelia of these fungi, but always retaining the mycelial loop behind the lip region and these nematodes were parasitized by the fungus within a few days. The other fungi parasitizing P.punctatus may also be parasitic on plant-parasitic nematodes and may be

potential biological control agents. Few pathogenic bacteria have been recorded in nematodes and the organism believed to be Serratia marsescens (or a closely related organism) may also have potential as a biological control agent of plant parasitic nematodes.

Similarly some interactions between predators were recorded: the decrease in M.aquaticus while Labronema sp. populations were increasing in the early mixed cultures of these species may be linked as Labronema sp. readily feeds on the eggs of M.aquaticus. Eggs of Labronema sp. were also cannibalised in starved cultures, particularly by juveniles, but this behaviour must be distinguished from that described by Esser (1963) in which a female dorylaim "moved her lips over the (just deposited) egg" and showed a "strong affinity" for the egg. P.punctatus females often exhibited a similar behaviour pattern following oviposition; the lips and neck region were rubbed against the egg repeatedly, often displacing the egg several millimetres through the agar. This behaviour lasted for more than 5 minutes with short interruptions when the female appeared to "misplace" the egg. An attraction mechanism may have operated as the female unfailingly finds the egg after a short (<30 secs.) search and ignored other eggs in the vicinity. The reason for this behaviour was not elucidated and no secretions were observed; the behaviour may relate to intra-specific recognition or may be the selection of optimal micro-environmental conditions for the egg. The echinulate nature of the egg-shell was difficult to observe in utero and the oviposition behaviour may have helped the spines to become erect. Such affinity for the egg may be widespread amongst dorylaims and mononchids but it was not observed in M.aquaticus. All the predators were able to distinguish their own species and cannibalism was only noted in cultures in which prey had been scarce or absent for more than a week. That this differentiation of prey was specific was apparent in mixed P.punctatus and M.aquaticus cultures where the small juveniles of the other species were frequently ingested; attacks by either species on adults and larger juveniles

were not usually successful, and this also applied to intra-specific attacks.

The continuous presence of protozoa and bacteria may be important to the culture of P.punctatus either by altering the environment or by providing a food source for the juveniles. Springett (1964) suggested that a full soil fauna and flora were necessary for culture of enchytraeids and Steiner and Heinly's (1922) observation of juvenile C.papillatus in soil and water cultures ingesting soil particles is generally considered to indicate the need for bacteria or detritus. With respect to this observation two things may be important: first, the egg-shell figured by Steiner and Heinly was shown as bearing "protuberances" which were not present on the eggs of nematodes identified as Clarkus papillatus in this study, and second, mononchids in water frequently grip any nearby object, including other nematodes, with the lips without ingesting material and on this basis I am not convinced that ingestion of soil, detritus or bacteria is necessary for continued development of C.papillatus juveniles. The presence of soil in soil-extract agar did not improve its culture properties for this nematode.

The life-cycle of P.punctatus was shown to be relatively long and to include four moults all occurring after hatching; similar observations were made on Labronema sp. and M.aquaticus. Table 40 compares the life-histories of various predatory nematodes in culture. The dorylaimids and mononchids generally showed a correlation between larger size and longer life-cycle although the nematode described as C.papillatus in Steiner and Heinly (1922) was comparatively long for the size of C.papillatus, which may support the hypothesis that these workers were not using C.papillatus. M.aquaticus had the shortest recorded life-cycle for a mononchid whereas Labronema spp. had a longer development than mononchids (Ferris, 1968; Small, unpubl.). Both mononchids and Labronema spp. may be considered relatively K-selected species on this basis (Pianka, 1970).

Table 40. Summary of the life-histories of predatory nematodes in culture.

| Nematode | Culture Method | Temp °C | Egg development time[1]. | Duration of juvenile stages 1st | 2nd | 3rd | 4th | Gravid Period | Generation time Egg to Egg | Total life Cycle | Additional Information | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Clarkus papillatus* | Water and soil on slide | ?[2] | 6-7d | 6-7 weeks | | | | 20d | 7wks* | Up to 18 wks | Senile period (=post egg depositing stage) 10 wks | Steiner and Heinly (1922) |
| | Soil in tubes | ?[2] | 6-7d | 4-5 weeks minimum | | | | | 5wks* | >18wks | | |
| *Seinura tenuicaudata* | Potato-Dextrose Agar + *Pyrenochaeta tetrestris* (fungus) + *Aphelenchus avenae* | 28 | 26-30hr | Pre-hatch 5hr | 18hr | 46hr | | >7d | 5.5-6d | - | 2nd st.juvenile hatches Bisexual | Hechler (1963) |
| | | | | Post-hatch 11hr | | | | | | | | |
| *Seinura celeris* | | 28 | 9hr | 6hr | 12hr | 12hr | | - | 2.25-2.5d | - | Only 3 moults recorded. Hermaphrodite | Hechler and Taylor (1966a, b) |
| *Seinura oliveirae* | | 28 | 12hr | 7hr | 16hr | 24hr | | - | 2.5-3d | - | Only 3 moults recorded. Hermaphrodite | |
| *Seinura oxura* | | 28 | 11hr | 14hr* | 8hr | 16hr | 24hr | 57hr* | 3-3.5d | - | 3rd st.juvenile hatches Hermaphrodite | |
| *Seinura steineri* | | 28 | 35hr | 4hr | 28hr | 24hr | 27hr | - | 6-6.5d | - | 2nd st.juvenile hatches Bisexual | |
| *Labronema ferox* | Water agar | ? | 7d | 10-12d | 2-3wk | 1month | 1month | - | 3-4month | - | *L.thornei* generation time 5-6month | Ferris (1968) |
| *Prionchulus punctatus* | Humus-extract agar | 10 | 34d | 180d | | | | - | 200d | - | Minimum egg development time 6.1d at 25°C Min. gen.time 37d at 22°C | Maertens (1975) |
| | | 19 | 7d | 4-5d | 30d | | | | 41d | - | | |

Cont....

Table 40 (Cont.)

| Nematode | Culture Method | Temp °C | Egg development time[1] | Duration of juvenile stages 1st | 2nd | 3rd | 4th | Gravid Period | Generation time Egg to Egg | Total Life Cycle | Additional Information | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mononchus aquaticus | Bacto-agar | 15<br>28 | 12d<br>3.5d | 6d<br>3d | 6d<br>2d | 10.5d<br>2d | 7.5d<br>2d | - | 45d<br>14-15d | - | Egg production greatest at 22°C | Grootaert and Maertens (1976) |
| Prionchulus punctatus | Soil-extract agar | 20 | 7d | 4-5d | 17d | 9d | 9d | >2wk | 49d | >10wk | Development depends on temperature and medium | Present Study |
| Mononchus aquaticus | Soil-extract agar | 20 | 6d | Approx. 2 weeks | | | | >2wk | ~20d | >8wk | Stock culture data | |
| Labronema sp | Soil-extract agar | 25 | 9d | Approx.3 months | | | | - | 3-4 months | >5month | Stock culture data | |

1. Until movement of juvenile within egg begins with regard to Seinura spp.

2. Equal temperatures but value not stated.

*Present author's estimate based on data in original source.

In contrast Seinura spp. were relatively r-selected and some Seinura species have contracted the life-cycle by increasing the number of intra-egg moults (Hechler and Taylor, 1966a). One such moult was not observed in some species but it probably occurs in a rapid and perhaps modified form. Jones (1977) calculated the day-degrees required for the completion of the life-cycle of M.aquaticus and at a basal temperature for development of 5°C approximately 7 generations of this nematode could occur for every generation of Globodera rostochiensis (Jones, 1975); this assumes that the generation time of M.aquaticus was similar in culture to that under natural conditions. In reality the generation time of M.aquaticus would probably be extended by lower prey densities in soil, but the implication for biological control remains. P.punctatus was unlikely to complete 2 generations in soil during the generation time of G.rostochiensis.

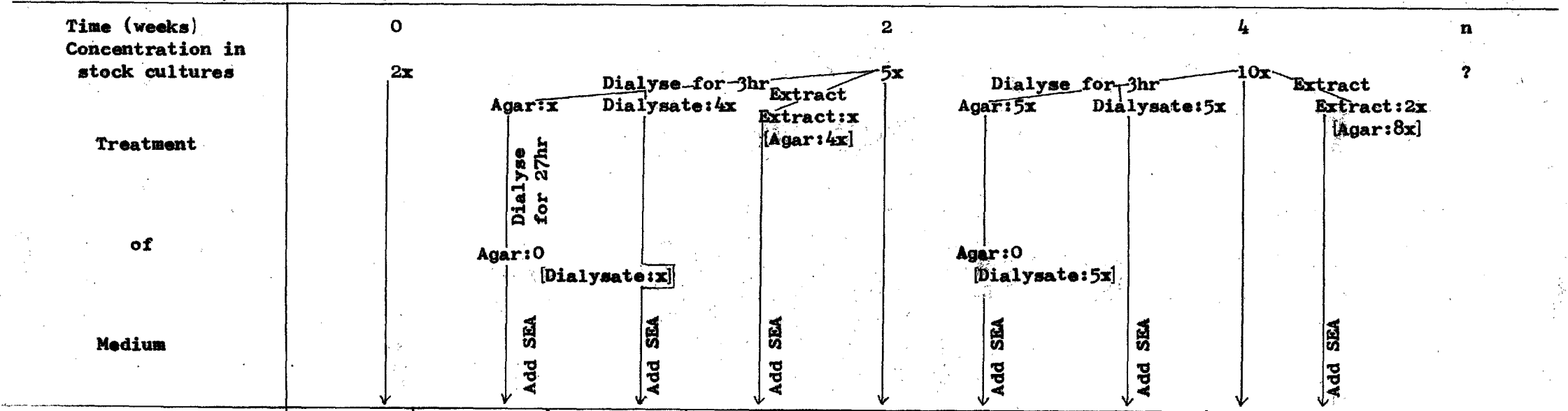
The development times of the four juvenile stages are included in Table 40. The first stage of P.punctatus was comparatively short and may be the expression of the general trend in nematodes to reduce the life cycle; often the first moult occurs within the egg (e.g. Seinura spp., Rotylenchus spp.). In contrast the second stage juvenile of P.punctatus was long-lived and the growth and reserves accumulation during this stage appeared to be a preparation for further development if conditions were suitable, or possibly as a survival stage in adverse conditions (Evans and Perry, 1976). Maturation of fourth stage juveniles also appeared to be delayed in adverse conditions, which was suggested as a means of regulating the density of adults and hence the total population - another K-selected feature. The substances involved in the regulation of developmental processes could include the metabolites of the nematodes or contaminant organisms (ammonia, urea, carbon dioxide; Wright and Newall, 1976) which would accumulate in the cultures until the concentration was too great for the nematodes to continue normal activities; in stock cultures this appeared to occur in four-week old cultures. Some nematodes are attracted to low concentrations of compounds that are toxic in greater concentrations e.g. carbon dioxide

(Green, 1971). Attractions to low concentrations of these compounds would benefit the predators by attracting them to aggregations of prey nematodes, and possibly by stimulating their reproduction and development. The separation of this latter response from the effects of increased prey density would be extremely difficult under field conditions.

Several models were tried to account for all the observations on the effect of culture medium on P.punctatus, and two possible models are presented in Figs. 30 and 31. The inherent problems of such models are clear in that the model is based on the data that it attempts to explain, and the unquantified factors such as the effect of extraction or dialysis, can be adjusted to suit the required result. Necessarily these models are speculative and serve only as hypotheses for further research.

The first model (Fig. 30 ) presupposed that only one factor was involved; this factor was produced continuously by the predators so that the concentration in agar cultures increased with time. In addition a low concentration of the factor, or an analogue, was present in soil-(or humus-)extract which promoted better population growth than water agar. At intermediate concentrations (2x-3x in Fig. 30) the factor stimulated P.punctatus population growth (more eggs, greater survival, more rapid juvenile development) and concentrations just above or below this concentration had a variable effect, perhaps depending on the number of predators already present and/or interacting with variables such as prey density and temperature. At yet greater concentrations (>6x) the factor inhibited further population growth and may even have been toxic, so reducing the predator population. The experimental concentrations depended on the age of the agar (0, 2 or 4 weeks), the treatment (extraction, dialysis) and the addition of fresh soil-extract agar. Of the ten media suggested in Fig. 30 results were available for eight and six fit the model; the remaining two results (S.E.A. + dialysate of 2 week-old agar and 2 week-old agar) may also fit the model but as these media were used only once it was not possible to determine the "variable

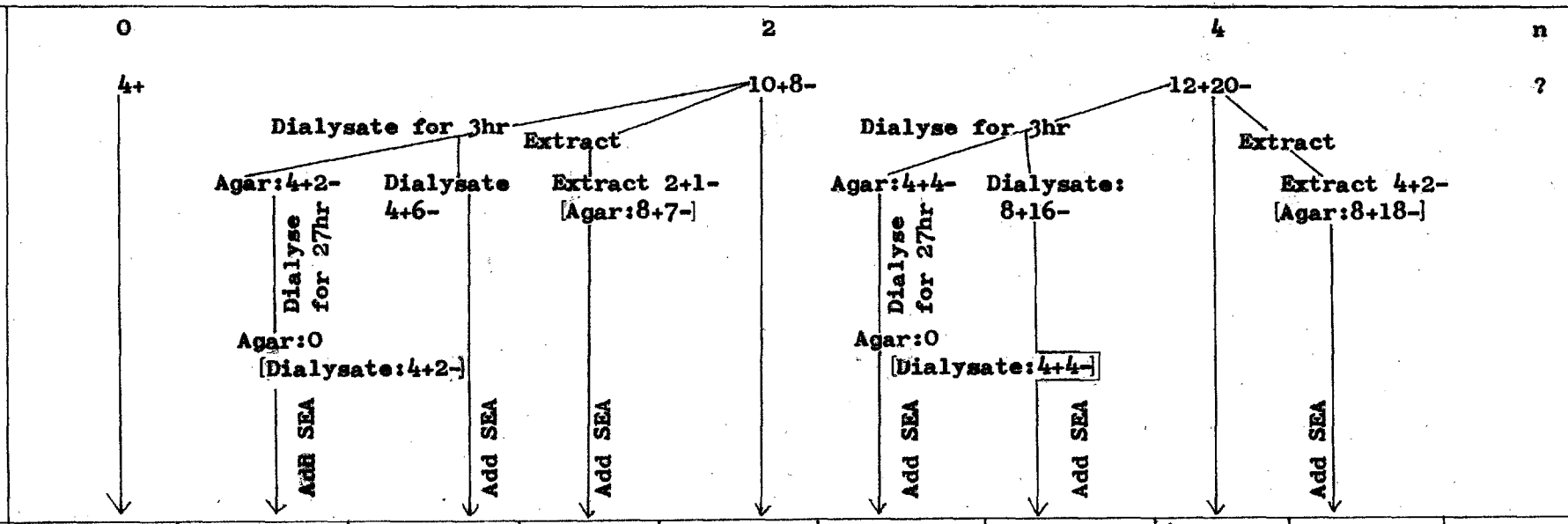
Fig. 30. One-factor model to describe the effect of medium on the population growth of P.punctatus in culture
Assumptions: One factor produced by predators; fresh SEA contains 2x. 0-x variable; 2x-3x stimulation; 4x-6x variable; >6x inhibition.




| Experimental Treatment | Fresh SEA | SEA+ dialysed 2wk | SEA+ dialysate 2wk | SEA+ extract 2wk | 2wk old agar | SEA+ dialysed 4wk | SEA+ dialsate 4wk | 4wk old agar | SEA + extract 4wk | Water Agar |
|---|---|---|---|---|---|---|---|---|---|---|
| Experimental Concentration | 2x | 2x | 6x | 3x | 5x | 2x | 7x | 10x | 4x | 0 |
| Sources | SEA | SEA | 2xSEA 4x dialysate | 2xSEA x extract | 2xSEA 3x Predators | 2xSEA | 2xSEA 5x dialysate | 2xSEA 8x Predators | 2xSEA 2x extract | - |
| Predicted effect on population growth | Stimulation | Stimulation | Variable | Stimulation | Variable | Stimulation | Inhibition | Inhibition | Variable | Variable |
| Observed effect on population growth | Stimulation | Stimulation | Inhibition | Stimulation | Stimulation | - | - | Inhibition | Variable | Variable |

[ ] Indicates loss of bracketed material from the experiments.

Fig. 31. Two-factor model to describe the effect of medium on the population growth of P.punctatus in culture. Assumptions: Two factors: stimulant (+) and inhibitor (-) produced by predators; fresh SEA contains 4+. <0= Inhibition 0-2+ = Variable >2+ = Stimulation.




| Experimental Treatment | Fresh SEA | SEA+ dialysed 2wk | SEA+ dialysate 2wk | SEA+ extract 2wk | 2wk old agar | SEA+ dialysed 4wk | SEA+ dialysate 4wk | 4wk old agar | SEA+ extract 4wk | Water Agar |
|---|---|---|---|---|---|---|---|---|---|---|
| Experimental Concentration | 4+ | 4+ | 4+<br>4+6- | 4+<br>2+1- | 10+8- | 4+ | 4+<br>8+16- | 12+20- | 4+<br>4+2- | 0 |
| Sources | SEA | SEA | 4+SEA<br>4+6- Dialysate | 4+SEA<br>2+1- extract | 4+SEA<br>6+8- predators | 4+SEA | 4+SEA<br>8+16- dialysate | 4+SEA<br>8+20- predators | 4+SEA<br>4+2- extract | - |
| Total | 4+ | 4+ | 2+ | 5+ | 2+ | 4+ | 4- | 8- | 2+ | 0 |
| Predicted effect on population growth | Stimulation | Stimulation | Variable | Stimulation | Variable | Stimulation | Inhibition | Inhibition | Variable | Variable |
| Observed effect on population growth | Stimulation | Stimulation | Inhibition | Stimulation | Stimulation | - | - | Inhibition | Variable | Variable |

[ ] Indicates loss of bracketed material from the experiments.

effect" predicted by the model.

Fig.31 represents a two-factor model in which one factor stimulated and the other inhibited P.punctatus population growth; both factors were produced continuously by the predators but fresh soil-extract agar contained only the stimulatory factor. An excess of the inhibitory factor resulted in inhibition but the concentration of stimulatory factor had to exceed the concentration of inhibitory factor by 2 units in order to consistently stimulate predator population growth; at intermediate concentrations (0-2+) the effect on population development was variable. Again the effect of treatment produced a range of concentrations which had similar properties to those predicted in the one-factor model; the number of fits and possible fits is therefore the same.

Comparison of S.E.A. + dialysed four-week old agar and S.E.A. + dialysate from four-week old agar with the other agar treatments would test the predictions of the model as well as confirming the recorded effects of the various media on P.punctatus population development. The nature of the factors involved also needs further investigation: it has been suggested that the metabolic products of the nematodes (carbon dioxide, urea, ammonia) are likely factors influencing population development. These could be incorporated into agar in a range of concentrations and the efficacy of the various media for population development tested. Those substances whose concentration varies with time may be indicated by analysis of predator culture media of varying age; alternatively investigation of predator excretory and secretory products may be useful. This would seem preferable to the many experiments required to eliminate all known nematode excretory products.

A standard method of culturing P.punctatus has been developed and comparatively large numbers of these nematodes can be obtained on a laboratory scale. The life-cycle of the predator in culture was recorded

and the investigation of culture conditions indicated certain sensitive stages but further research is needed to elucidate the nature of this sensitivity. The methods described have potential for research in other aspects of nematology including taxonomy, ecology and ethology. Although the results should reflect some of the biology of the nematodes under natural conditions, the following section was designed to investigate the behaviour of P.punctatus populations in soil (whilst retaining control of the major environmental conditions) and in particular their interaction with plant parasitic nematodes.

# IV. INTERACTIONS BETWEEN *PRIONCHULUS PUNCTATUS* AND PHYTOPARASITIC OR FREE-LIVING NEMATODE POPULATIONS IN SOIL POTS.

## PREAMBLE

The ability of predatory nematodes to control plant-parasitic nematodes has excited much speculation in the past (Cobb, 1917; Steiner and Heinly, 1922; Thorne, 1927) but little published information is available. It is generally considered that this ability can be tested in pots to determine i) whether the predators feed on the target nematode and ii) whether the level of predation is sufficient to cause a decrease in the number of plant-parasitic nematodes invading the roots of the host plant, which will often reflect the potential decrease in economic loss that can be obtained. The first can be partially answered by means of laboratory experiments (Steiner and Heinly, 1922; Cohn and Mordechai, 1974; Nelmes, 1974) but the question whether the results would apply under natural conditions remains. Field experiments may be designed to test this but the extremely large number of predators required would be difficult to obtain in practice. If conditions in pots approximate to the natural conditions of the soil environment and also permit flexible designs (replicates, treatments, temperature etc) as well as requiring fewer predators, then the biological control potential of different nematodes may be validly tested. The three biological components of such experiments (host plant, phytoparasite and predator) should be comparatively easy to establish and maintain in pots.

The second can be accurately assessed only in the field but there the effects of predators and phytoparasite will be confounded with the other environmental influences. The pot experiment simplifies this system by allowing a degree of control of the environment which should enable the main components of the system to be assessed in isolation. Whilst the results may not be directly related to the field situation, the most promising combinations of host-plant, pest and predator can be selected for further study.

Amongst the considerable discussion of predatory nematodes as biological control agents, the lack of published details of pot experiments suggests that these experiments have not been successful; those which have

been published were more fully discussed in the introduction, but to summarise Patel (1972) found that a population of Globodera rostochiensis was effectively reduced by P.punctatus within eight weeks but the low egg hatch of the plant-parasite throws some doubt on the validity of the results. A contaminant population of Rhabditis sp. was reduced after two weeks in that experiment. Cohn and Mordechai (1974) confirmed that Mylonchulus sigmaturus fed on Tylenchulus semipenetrans juveniles in vitro before using this predator-prey combination in pot trials; large populations of M.sigmaturus were associated with low populations of T.semipenetrans but the level of predation was insufficient to allow a significant increase in plant weight. In such experiments the choice of predator and prey may be crucial and in this study a variety of plant-parasites were used; P.punctatus was used in all experiments and compared with other predatory nematodes in one experiment.

P.punctatus was chosen principally because it could be cultured in sufficient numbers; the locally available alternatives were Clarkus papillatus, Mylonchulus sigmaturus and, in small numbers, Anatonchus tridentatus (Nelmes and McCulloch, 1975). P.punctatus and C.papillatus have been reared on a diet of nematodes (Nelmes, 1974 and Steiner and Heinly, 1922 respectively) and A.tridentatus is known to feed on nematodes (Mulvey 1961a; Szczygiel, 1971). The feeding habits of M.sigmaturus are less certain (Thorne, 1927; Nelmes and McCulloch, 1975; this study, Section III) but this nematode was used for pot experiments by Cohn and Mordechai (1974). P.punctatus therefore had the combined advantages of local availability, ease of culture and predatory habit. Sufficient numbers of Mononchus aquaticus and Labronema sp. had been cultured to enable their use in comparative treatments with P.punctatus in one pot experiment; various combinations of these predators were also used.

The prey species (Helicotylenchus dihystera, Hemicycliophora sp.,

Globodera rostochiensis and Meloidogyne incognita) were chosen, on the basis of their life-histories, to provide a variety of stages potentially susceptible to attack by predatory nematodes. Esser (1963) suggested that some ectoparasitic species have developed thick cuticles (e.g. Hoplolaimus spp., Criconemoides spp., Hemicycliophora spp) or chemical defence mechanism (Helicotylenchus spp.) as protection against predation. Nelmes (1974) and Cohn and Mordechai (1974) also reported that mononchids did not successfully attack Helicotylenchus spp. under laboratory conditions. A pot experiment involving Helicotylenchus dihystera and Hemicycliophora sp. was designed to test whether these results applied in the soil.

H.dihystera has a widespread distribution and is an ecto or semi-endo-parasite of a wide variety of host plants (Siddiqi, 1972). In Britain it is most important as a parasite of cereals but can occur in large numbers in soil under pasture (Jones, 1976). Both adults and juveniles are root-feeders and therefore should be exposed to attack whilst feeding. The population of H.dihystera was obtained from pots with perennial rye grass (Lolium perenne) as host.

Hemicycliophora is also a cosmopolitan genus although particular species are locally distributed (Jensen, 1972); these nematodes are ectoparasites and are more usually associated with woody plants than with herbaceous plants (Jenkins and Taylor, 1967). The species used in this experiment was not identified but may have been H.typica de Man 1921, a European species typical of light, sandy soils (Southey, 1965), and was obtained from the same pots as H.dihystera. Hemicycliophora spp. have a cuticular sheath which may be sufficient to protect them from attack by predatory nematodes.

Endoparasitic nematodes may have less need of defensive mechanisms as they are protected within the roots (Esser, 1963) but the infective stage, males and perhaps the adult females of cyst and root-knot nematodes are exposed to attack. The second pot experiment used Globodera rostochiensis which is an endoparasite of potatoes and can cause considerable economic loss wherever potatoes are grown (Winslow and Willis, 1972). The adult

females rupture the root-cortex as they mature but the thickened cuticle of the cyst-wall is probably an effective barrier to predatory nematodes. Males can be attacked by predatory nematodes as they migrate through the soil towards the females (Green, 1971) but they are only active for ten days (Stone, 1973); the second stage juvenile (=infective stage) is most susceptible to attack once it has left the protection of the cyst.

The third pot experiment used Meloidogyne incognita in which the second stage juvenile is again the infective stage and hence the most likely to be attacked by predatory nematodes. Female root-knot nematodes do not produce a cyst although they often protrude through the root-cortex and may therefore be attacked; reproduction is always parthenogenetic although males exist (Orton-Williams, 1973). The eggs are deposited into a gelatinous matrix which probably reduces water loss from the eggs; this matrix might be penetrated by predatory nematodes and the eggs eaten. M.incognita is an endoparasite of many host plants throughout the warmer parts of the world and causes considerable histological changes in the host plant (Orton-Williams, 1973). In the pot experiment tomato was chosen as M.incognita reproduces well on this host and the resulting galls are easily visible (Orton-Williams, 1973).

The plant parasitic nematodes used in the experiments therefore represented a range of habits, hosts, distributions and susceptibilities to attack by predatory nematodes, and in this way the most promising nematode groups for further research might be selected. Two other experiments were made: the first was designed to investigate the adaptation of agar-cultured P.punctatus to the likely conditions in pots. The second experiment was designed to establish a predator-prey interaction in pots of sand which would enable "screening" of various predators in a manner similar to that used for nematicides (Peacock, pers.comm.).

## MATERIALS AND METHODS

### General

All predators were extracted from soil-extract agar cultures (maintained at 20°C; Section III) by the Whitehead tray method (Whitehead and Hemming, 1965) for the 24 hours prior to inoculation. All active nematodes (i.e. excluding the eggs of *Globodera rostochiensis*) were inoculated in small quantities of water into a shallow groove around the host plant at a distance of approximately 5cm. In those experiments in which predators were inoculated on the same day as the plant parasitic nematodes separate grooves were used; the grooves were at least 2cm apart and the predators were inoculated into the groove nearest the plant. Control pots received an equal volume of water without the appropriate nematodes. After all inoculations the soil in all pots (including controls) was gently watered. Plants were usually watered at weekly intervals but more frequently if necessary. Every 2 weeks the plants were watered with a solution of "Phostrogen" (Phostrogen Ltd., Corwen, Clwyd, Wales) plant nutrient (1 teaspoon per $9dm^3$ of water).

Active nematodes were extracted from the soil or sand by the Whitehead tray technique (Whitehead and Hemming, 1965) over 24 hours (48 hours for experiments involving *Aphelenchus avenae* and *Meloidogyne incognita*). The extracted nematodes were concentrated by passing the suspension through two 53µm aperture sieves, and the nematodes were counted in de Grisse counting dish (de Grisse, 1963). Nematodes within, or attached to, roots were counted after fixation and staining in boiling methyl blue-lactophenol solution followed by clearing in lactophenol (Franklin and Goodey, 1949) except *M.incognita* which were counted in the fresh roots. The roots were compressed between glass plates for observation.

Fresh weight of the haulms and roots of the plants was recorded in the experiments involving phytoparasitic nematodes and other methods of assessing

Table 41. Interactions between P.punctatus and phytoparasitic or free-living nematode populations in soil pots: Summary of experimental details.

| "Prey" Nematodes | Predators | Host Plant | Number of Replicates per Treatment | Pot 1. Diameter or Dimensions (cm) | Medium | Volume of medium $(cm)^3$ | Environment | Temperature °C | Plant growth assessment |
|---|---|---|---|---|---|---|---|---|---|
| P.redivivus | P.punctatus | Lolium perenne* | 24 | 5x5x5 | Sterilised Sand | 100 | Glasshouse | 20±2 | - |
| A.avenae | P.punctatus | Fungi* | 5 | 5 | Sterilised Sand | ~68gm | Incubator | 20 | - |
| H.dihystera Helicotylenchus sp. | P.punctatus | Lolium perenne | 10* | 5x5x5 | Sterilised Sand | 60 | Glasshouse | 20±2 | Roots:F.W. Haulms:F.W. |
| G.rostochiensis | P.punctatus | Solanum tuberosum var.Majestic | 9 | 14 | Soil | 450 | Glasshouse | 20±2 | Roots:F.W. Haulms:F.W. Old Tuber:F.W. New Tubers:No.FW* |
| M.incognita | P.punctatus M.aquaticus Labronema sp. | Lycopersicon esculentum var.Moneymaker | 6 | 9 | LSP | 300 | Glasshouse | 20±2 | Root:L,F.W.,D.W. Haulm:L,F.W.,D.W. Leaves: No. Internodes:No. |

F.W.: Fresh Weight; D.W.: Dry Weight; L: Length; No.: Number

L.S.P.: Loam, sand and peat mixture (3:3:1 respectively).

1. All pots made of plastic.

*See text for further explanation.

plant production were adopted in the various experiments. These are summarised in Table 41. together with other experimental details, which will not be mentioned in the text unless further explanation is necessary.

Selection of pots for the various treatments and for nematode-extraction was based on a table of random numbers (Fisher and Yates, 1963).

For all experiments (except P.punctatus/A.avenae) the means $\pm$S.E. of the measures of plant growth, and of the counts of nematodes, were calculated. Analyses of variance were used to distinguish between treatments involving plant parasitic nematodes and in these experiments regression and correlation analyses were used to test for associations between the plant yield and the numbers of nematodes, and for association between the various nematode groups. In the M.incognita experiment the analysis was extended if the analyses of variance of the original data proved significant. The regression coefficient (b) of the regression of log.variance on log.mean was calculated for each treatment and was used to calculate the value of p where $p=1-b/2$ (Taylor, 1961). The data was transformed by raising each count or measure of plant yield to the power p i.e. $x^p$ where x is a count or measure of plant yield. The analysis of variance was repeated on the transformed data. These additional procedures were not considered necessary for the non-significant analyses of the original data or for the regression analyses as they were unlikely to substantially alter the conclusions of such analyses.

i) Changes in numbers of P.punctatus in pots of sand with P.redivivus as prey.

The sand used as the medium was watered before a ten-week old seedling of perennial rye grass (Lolium perenne) was planted to represent a typical host plant as used in the other pot experiments. Twenty-four pots were inoculated with 35 adult and 80 juvenile P.punctatus each and a further 24 pots with 180 adult and 400 juvenile P.punctatus (all obtained from

31±9 day old agar cultures; proportion of first and second stage juveniles to third and fourth stage = 15:85). Approximately 500 Panagrellus redivivus were added to all 48 pots at the start of the experiment; this number was designed to represent the inoculation of plant parasitic nematodes or a flush of juveniles hatching in response to root exudates under field conditions. At intervals of two weeks the nematodes from six pots from each treatment (=predator inocula) were extracted and the numbers of adults, first and second, and third and fourth stage juveniles counted.

Results: The population of P.punctatus decreased over eight weeks in pots, regardless of the initial predator inoculum; the rate of decline was most rapid in the first two weeks (Fig. 32a, b). The decrease in the pots with larger inocula was continuous whereas in the pots with smaller inocula both adults and juveniles showed a transitory increase in numbers. After two weeks there was no significant difference between the treatments and this continued throughout the experiment (Table 42). The final numbers (week 8) were very similar in the two treatments: mean ± S.E.=0.33±0.21 and 0.33±0.33 adults, 9.50±6.29 and 15.33±9.49 juveniles from large and small inocula respectively. The maximum number of juveniles in the pots with small predator inocula was extremely variable (mean ± S.E.=224.83±117.9; range 12-659).

Table 42. Changes in numbers of P.punctatus in pots of sand with P.redivivus as prey: Values of t

| Time (weeks) | 2 | | 4 | | 6 | | 8 | |
|---|---|---|---|---|---|---|---|---|
| Life Stage | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles |
| Values of t* | 0.53 | 1.30 | 0.10 | 1.37 | 0.84 | 0.81 | 0 | 0.51 |

*All values indicate no significant differences between the treatments.

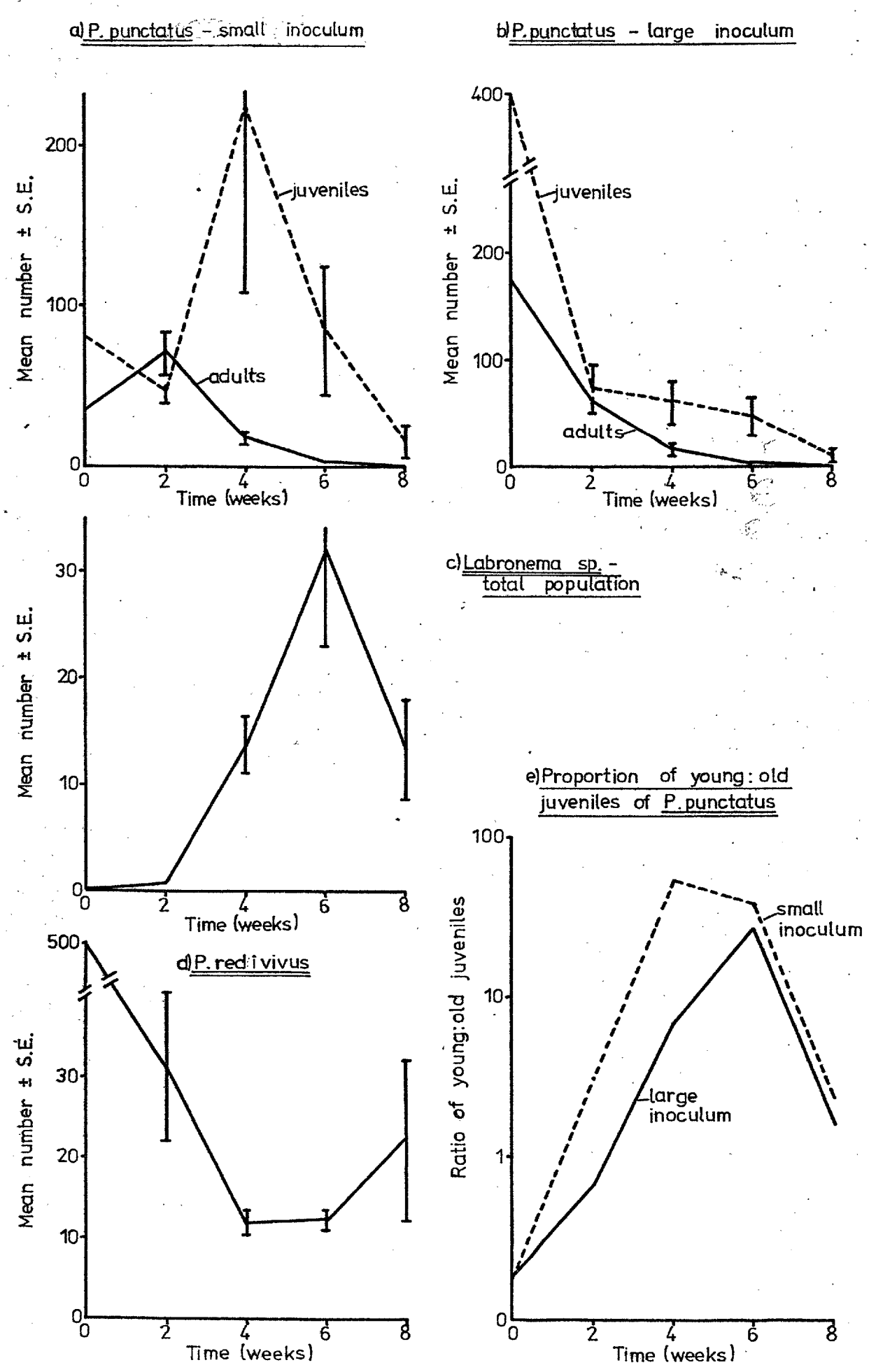
The proportions of the numbers of first and second stage juveniles to third and fourth stage juveniles varied considerably during the experiment (Fig. 32e). Older juveniles were in the majority at the start of the experiment but this was reversed by week 2 (small inoculum) or week 4 (large inoculum). Peaks were reached at weeks 4 and 6 for small and large inocula respectively. Both treatments showed a steep decrease in the value of this ratio from week 6 onwards (Fig. 32e) to reach approximately 2.5 young:1 older juvenile and 1.6 younger:1 older in the small inoculum pots and the large inoculum pots respectively at week 8.

The population of P.redivivus declined over the first four weeks but was recovering towards the end of the experiment (Fig. 32d). In contrast, a contaminant population of Labronema sp. reached a maximum ($32.08 \pm 9.07$ per pot) at week 6 but by week 8 had decreased to the same level as at week 4 (Fig. 32c). The changes in number of P.redivivus and Labronema sp. were very similar in the pots with both large and small P.punctatus inocula.

Discussion: The results suggested that the size of the initial inoculum of P.punctatus made little difference to the population remaining after two weeks; that the populations were approaching the same level was shown by the lack of significant difference between the treatment means after only two weeks. It seemed probable that the two populations would have stabilised at approximately the same level and that the few predators remaining would have been sufficient for the population to continue. It was noticeable that the final density of P.punctatus was only slightly greater than that recorded from field soil (Section II, Table 4).

Two probable causes of the decline in numbers of P.punctatus were a lack of prey or a previous adaptation to the environment of soil-extract agar cultures. The greater decrease in predator numbers in the large inoculum pots reflected the greater competition for the limited prey; in the small inoculum pots the temporary increase suggested that reproduction and development was continuing at the existing prey density. In both

FIG. 32. CHANGES IN NUMBERS OF P. PUNCTATUS IN POTS OF SAND WITH P. REDIVIVUS AS PREY : VARIATION IN NEMATODE POPULATIONS AND THE PROPORTION OF YOUNG TO OLD P. PUNCTATUS JUVENILES WITH TIME



treatments the increase in the ratio of young to old juveniles suggested that the populations were reproducing, even if not expanding. That agar adaptation was not the primary cause was suggested by the difference between the two treatments when agar-adaptation should have had equal consequences in both treatments. Sand and agar media differ in the amount of free water, inorganic salts and organic matter present; it may be that washed, sterile sand, rather than being a more natural habitat than agar, was too biologically pure for the nematodes to continue normal behaviour. Clark (1961a) was unable to culture Clarkus papillatus or Prionchulus muscorum in sterile silver sand. The various contaminant organisms would initially have a much lower density than in the stock cultures and possibly the stabilisation of the P.punctatus was related to the development of the fauna and flora.

Whilst the populations of P.punctatus were declining the contaminant population of Labronema sp. increased; if the food supply for P.punctatus was limiting it might be expected that it would be limiting for Labronema sp. also. The alternatives were i) Labronema sp. was exploiting a different food source, perhaps including eggs and juveniles of P.punctatus; although this has not been observed it is known that Labronema sp. feeds on M. aquaticus eggs. ii) Labronema sp. was a more efficient predator than P. punctatus, but since it moves more slowly, encounters prey less often and achieves fewer successful attacks per encounter than P.punctatus, at least in agar (Small, unpubl.) this seemed unlikely; iii) the increase of Labronema sp. represented continued migration into the pots from the source of the contamination. The presence of juvenile Labronema sp. suggested that reproduction was occurring in the pots.

The numbers of P.redivivus decreased during the period of predator increase; over the last two weeks P.redivivus numbers recovered to some extent, possibly as a result of an increase in food or because the predator populations were declining. More observations over a longer time period

would be needed to demonstrate a stable predator-prey relationship. A second experiment using an A.avenae-fungus system was intended to enable such observations.

ii) The predation of P.punctatus on Aphelenchus avenae under pot conditions.

Wholemeal flour (Allinson Ltd., Castleford, Yorks) was added to five 165gm portions of dry, sterilised sand in the following quantities: 0.66gm, 1.32gm, 1.98gm, 3.30gm and 6.60gm. The sand and flour were thoroughly mixed before the addition of $45cm^3$ of sterile, deionised water to each portion (to give flour concentrations of approximately 0.5%, 1%, 1.5%, 2.5% and 5% respectively, by weight). The resulting mixtures were autoclaved for 30 minutes at 1 bar.

Under sterile conditions each portion when cool was divided equally between three sterile pots (to give 15 pots in total). Five pots (one of each flour concentration) were inoculated with a disc of agar containing the fungus Botrytris cinerea (controls without nematodes); the remaining ten pots were similarly inoculated with a culture of Aphelenchus avenae on the fungus Corticium praticola. Five of these pots (one from each flour concentration) were also inoculated with 45 juveniles and 55 adult P.punctatus per pot. The predators had been rinsed five times in sterile, deionised water. All the pots were covered with aluminium foil, placed in a sterile container and incubated at 20°C.

After 26 days the extent of the fungal mycelium and the number of nematodes was assessed; watering had not been necessary during this period. The nematodes were extracted and the numbers of A.avenae and adult and juvenile P.punctatus recorded.

Results: Despite precautions the pots were colonised by mites which appeared to have introduced a mixed flora of bacteria and fungi. The bacteria especially flourished, causing the rapid decay of the flour and anaerobic conditions (indicated by the black-colouration and the smell

of hydrogen sulphide) at depths below 1cm from the sand surface. These conditions were lethal to both the nematodes and the inoculated fungi.

In the pots inoculated with Botrytris cinerea the fungus formed a dense mycelial mat on the sand surface but did not penetrate the sand for more than 0.5cm depth. In the pots without predators a total of 336 A.avenae were recovered; the mycelium of Corticium praticola also occupied most of the surface but had not developed at depths greater than 1cm. In the pots with predators a total of 36 A.avenae and a single P.punctatus were recovered. Contamination with bacteria was most noticeable in these pots and restricted the development of C.praticola to surface patches which extended approximately 2cm into the sand.

Discussion: It was not justified to ascribe the fewer A.avenae recovered from the pots with predators to predation by P.punctatus. The failure of this pilot experiment could be avoided in laboratories designed for sterile techniques and the A.avenae/fungus system could be of use for comparison of predators as well as enabling studies on the predator-prey relationship over considerable periods of time. A.avenae is a suitable subject for such screening procedures as it is closely related to plant-parasitic species yet can be reared in large numbers on fungi (Evans, 1970).

iii) The ability of P.punctatus to reproduce in pots of sand in the presence of Helicotylenchus dihystera and Hemicycliophora sp.

Forty-eight pots containing sterilised sand were stood in a shallow layer of "Phostrogen" plant nutrient solution and the water level allowed to equilibrate over 48 hours. A two-week old seedling of Lolium perenne, previously grown in sterilised sand, was transplanted into each of the pots. L.perenne was chosen as host because the plant parasitic nematode populations appeared stable in stock population pots using this host, although the food preferences of Helicotylenchus spp. have been shown to vary (Jones, 1976; Wallace, 1971). The plants were left for four days to become

established.

A population of Helicotylenchus dihystera and some other plant parasitic and free-living nematodes was inoculated into 36 of the pots (Table 43). The inoculations were extended over eight days because of the difficulty of obtaining the large numbers of plant parasitic nematodes required for 36 pots from the stock population pots.

Table 43. Numbers of H.dihystera, Hemicycliophora sp. and associated nematodes inoculated per pot.

| Inoculated Nematodes | H.dihystera | Hemicycliophora sp. | Criconemoides sp. | Pratylenchus thornei | Aphelenchoides sp. | Rhabditids | Labronema sp. | Mylonchulus sigmaturus | Mononchus aquaticus |
|---|---|---|---|---|---|---|---|---|---|
| Approx.total inoculated/ pot | 2400 | 620 | 20 | 40 | 40 | 40 | 60 | 20 | 20 |

The pots were left for 28 days in an unheated glasshouse before the nematodes from 6 of the pots previously inoculated with plant parasitic nematodes and 4 of the pots without inoculated nematodes were extracted and counted. The fresh weight of the stems and leaves, and roots of the plants taken from these pots were recorded.

The inocula of predators were based on the mean number of nematodes in the pots previously inoculated with plant parasitic nematodes and represented 5% and 15% of this mean* i.e. 3 adult and 20 juvenile P.punctatus (5%) and 10 adult and 60 juvenile P.punctatus (15%) respectively.

*The 5% inoculum was designed to represent the normal field population of predators and the 15% inoculum, an artificially increased predator population.

Table 44 summarises the treatments.

Table 44. Summary of experimental treatments.

| | Experimental Treatment | Number of Replicates | Time to extraction (days) |
|---|---|---|---|
| a | No nematodes | 4 | 28 |
| b | Plant-parasitic nematodes | 6 | 28 |
| A | Plant-parasitic nematodes only | 5 | 54 and 90 |
| B | Plant-parasitic nematodes + 5% *P.punctatus* | 5 | 54 and 90 |
| C | Plant-parasitic nematodes + 15% *P.punctatus* | 5 | 54 and 90 |
| D | *P.punctatus* only (≡15%) | 4 | 54 and 90 |

The pots were left in an unheated glasshouse for 22 days but the wide daily fluctuation in temperature towards the end of this period led to the transference of the pots to a glasshouse maintained at 20±2°C. Fifty-four days after predator inoculation, the nematodes in half the pots from each treatment were extracted and counted. The plants were weighed and the roots examined for attached ectoparasitic nematodes. The remaining pots were allowed to continue for a further 90 days before similar counts and weights were recorded.

Results: Twenty-eight days after their inoculation the number of plant parasitic nematodes had considerably decreased and the number of rhabditids had increased (Table 45); contaminant populations of rhabditids had developed in the control pots and 3 individuals of *Pratylenchus thornei* Sher and Allen 1953 were recovered from one control pot (Table 45). Comparison of the mean weights of stems and leaves, roots and total plant in control (a) and experimental pots (b) indicated that there was no significant difference between the two treatments ($t$ = 0.05, 0.84 and 0.58 respectively; 8d.f.). This showed that the plant-parasitic nematodes had not

significantly affected the plants prior to inoculation of the predators.

Table 45. Mean numbers (± S.E.) of H.dihystera, Hemicycliophora sp. and associated nematodes four weeks after their inoculation.

| | Nematodes | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | H.dihystera | Hemicycliophora sp. | Criconemoides sp | Pratylenchus thornei | Aphelenchoides sp. | Rhabditids | Labronema sp | Mylonchulus sigmaturus | Mononchus aquaticus | Total |
| Mean no.± S.E. in experimental pots | 156.80 ±10.21 | 18.00± 5.60 | 0.17± 0.17 | 7.67± 1.67 | 4.33± 2.14 | 272.33± 112.00 | 5.83± 2.01 | 0 | 0.33± 0.21 | 464.50± 120.90 |
| Mean no.± S.E. in control pots | 0 | 0 | 0 | 0.75± 0.75 | 0 | 54.50± 48.51 | 0 | 0 | 0 | 55.25± 49.26 |

a) 54 days after predator inoculation

Fifty-four days after the inoculation of the predators the number of plant parasitic nematodes had decreased in all experimental treatments, but contaminant populations of some species had developed in the controls (Table 46). No Criconemoides sp., Aphelenchoides sp. or M.sigmaturus were recovered from any treatment. The total numbers of plant parasitic nematodes was generally least (except for the plant-parasite free controls) in the 15% P.punctatus treatment (Table 46) but these differences were generally not significant (Table 48). The numbers of H.dihystera were significantly less in the 15% P. punctatus treatment than in either the 5% P.punctatus treatment or the no-predator control; "prey" nematodes (rhabditids plus plant parasitic nematodes) were significantly less in the 15% P.punctatus treatment than in the no predator control (Table 48). The number of P.punctatus and Labronema sp. were significantly greater in the "P.punctatus only" controls than in the

Table 46. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp.: Mean numbers (± S.E.) of nematodes per pot recovered 54 days after inoculation of P.punctatus.

| Treatments / Nematodes | Plant-parasitic nematodes only | Plant-parasitic nematodes + 5% P.punctatus | Plant-parasitic nematodes + 15% P.punctatus | P.punctatus only |
|---|---|---|---|---|
| Helicotylenchus dihystera | 45.40±5.53 | 47.20±5.30 | 27.20±11.58 | 6.25±2.02 |
| Hemicycliophora sp. | 0 | 5.20±3.18 | 2.00±0.32 | 2.25±0.75 |
| Criconemoides sp. | 0 | 0 | 0 | 0 |
| Pratylenchus thornei | 0 | 0.40±0.40 | 0.80±0.60 | 0.75±0.75 |
| Aphelenchoides sp. | 0 | 0 | 0 | 0 |
| Rhabditids | 101.20±24.58 | 60.60±18.19 | 50.60±21.55 | 41.75±17.17 |
| Labronema sp. | 5.00±2.00 | 6.00±2.61 | 3.00±2.02 | 16.00±4.02 |
| Mylonchulus sigmaturus | 0 | 0 | 0 | 0 |
| Mononchus aquaticus | 131.00±25.06 | 173.00±44.32 | 145.60±31.11 | 126.75±17.01 |
| Prionchulus punctatus | 0.60±0.40 | 0.40±0.40 | 0.60±0.40 | 4.00±2.42 |

other treatments (Table 48).

Differences in plant yields were not significant (Table 48) but mean total-plant weight tended to be greater in the predator only controls and in the 15% P.punctatus treatment (Table 47). Mean stem and leaf weight was greatest in the treatment with 15% predators but mean root weight was greatest in the plant parasitic nematodes only control. Plant yields were consistently least in the treatment with 5% P.punctatus (Table 47).

Few significant correlations between the numbers of the various nematode groups were recorded and plant yields did not correlate with any nematode group, except stem and leaf weight with Labronema sp. (Table 49). The number of rhabditids and the number of total others (i.e. all nematodes except M.aquaticus) were negatively correlated with M.aquaticus (Table 49).

b) 144 days after predator inoculation

The number of H.dihystera had increased considerably in the 90-day interval between sampling dates but no Hemicycliophora sp. were recovered from any treatment (Table 50). Criconemoides sp. and M.sigmaturus were again absent but small numbers of Aphelenchoides sp. were recovered from the 5% and 15% P.punctatus treatments. Although differences between treatments were not significant (Table 52), greater numbers of H.dihystera were recovered from the treatment with 15% P.punctatus than from the other treatments and the number of H.dihystera was also slightly greater in the 5% P.punctatus treatment than in the no-predator control. The few P.punctatus recovered prevented the use of correlation analysis for the investigation of causal relationships between the numbers of these nematodes. The mean number of rhabditids and Labronema sp. were also greatest in the 15% P.punctatus treatment, but fewest M.aquaticus occurred in this treatment (Table 50).

Analyses of variance indicated no significant differences in numbers of nematodes between any of the treatments, but significant differences in

Table 47. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp.: Mean weights (± S.E.) of the grass plants (Lolium perenne) 54 days after inoculation of P.punctatus (weights expressed in gms).

| Treatment / Part of Plant | Plant-parasitic nematodes only | Plant-parasitic nematodes + 5% P.punctatus | Plant-parasitic nematodes + 15% P.punctatus | P.punctatus only |
|---|---|---|---|---|
| Stem and leaf | 16.85±1.64 | 16.74±1.98 | 18.39±2.42 | 18.15±2.72 |
| Root | 15.30±2.95 | 10.05±0.82 | 14.65±2.80 | 15.00±2.92 |
| Total | 32.15±4.22 | 26.79±2.57 | 32.64±4.97 | 33.14±5.61 |

Table 48. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp.: Results of analyses of variance (54 days after inoculation of P.punctatus).

| Subject of Analysis | Value of 'F' ratio | Significance | Significant differences |
|---|---|---|---|
| Stem and leaf weights | 0.16 | N.S. | - |
| Root weights | 1.01 | N.S. | - |
| Total plant weights | 0.45 | N.S. | - |
| No.of H.dihystera | 6.15 | 0.01-0.001 | A>D****; B>D**** C>D* A>C* ; B>C* |
| No.of plant-parasitic nematodes | 5.27 | 0.05-0.01 | A>D**** B>D**** |
| No.of Rhabditids | 1.56 | N.S. | - |
| No.of prey nematodes[1] | 3.10 | 0.2-0.05 | A>D***; A>C*; B>D* |
| Total others[2] | 2.50 | 0.2-0.05 | B>D* |
| No.of M.aquaticus | 0.42 | N.S. | - |
| No.of Labronema sp. | 4.36 | 0.05-0.01 | D>C*****; D>A***; D>B*** |
| No.of P.punctatus | 2.48 | 0.2-0.05 | D>A**; D>B**; D>C** |

1. Prey nematodes = Rhabditids + plant parasitic nematodes.

2. Total others = Total nematodes less P.punctatus.

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001; N.S.: Not significant.

A = Plant parasitic nematodes only; B = Plant parasitic nematodes + 5% P.punctatus; C = Plant parasitic nematodes + 15% P.punctatus; D = P.punctatus only.

Table 49. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp: Results of correlation analyses (54 days after inoculation of P.punctatus).

| Abscissa / Ordinate | Prionchulus punctatus | Mononchus aquaticus | Labronema sp. | Helicotylenchus dihystera | Plant parasitic nematodes |
|---|---|---|---|---|---|
| H.dihystera | r=-0.26 N.S. | r=0.18 N.S. | r=-0.11 N.S. | - | - |
| Plant parasitic nematodes | r=-0.14 N.S. | r=0.11 N.S. | r=-0.22 N.S. | - | - |
| Rhabditids | r=-0.16 N.S. | r=-0.52** b=-0.37 | r=0.03 N.S. | - | - |
| Total others[1] | r=-0.26 N.S. | r=-0.40* b=-0.35 | r=-0.21 N.S. | - | - |
| P.punctatus | - | r=-0.11 N.S. | r=0.28 | - | - |
| Labronema sp. | - | r=-0.23 N.S. | - | - | - |
| Stem and leaf weight | r=0.13 N.S. | r=-0.14 N.S. | r=0.42* b=0.26 | r=0.23 N.S. | r=-0.05 N.S. |
| Root weight | r=0.23 N.S. | r=-0.03 N.S. | r=0.22 N.S. | r=-0.07 N.S. | r=-0.01 N.S. |
| Total plant weight | r=0.03 N.S. | r=-0.01 N.S. | r=0.06 N.S. | r=0.01 N.S. | r=-0.01 N.S. |

1. Total others = Total nematodes less the group indicated as the abscissa.

*: p=0.1-0.05; **: p=0.05-0.02; N.S.: Not significant.

mean plant yields were recorded (Table 52). Stem and leaf, root and total plant weights were significantly greater in the predator-only control than in the 15% P.punctatus treatment; further details are given in Table 52. M.aquaticus was negatively correlated with H.dihystera and hence with plant-parasitic nematodes, and also with stem and leaf, and total plant weights (Table 53). No other significant correlations were recorded.

Discussion: The initial decrease in the number of plant parasitic nematodes even in the absence of predatory nematodes probably arose from the disturbance caused by extraction and inoculation. Jones (1976) found that only 18% of an initial inoculum of H.dihystera remained one week after their inoculation; the population then remained constant for three weeks before increasing from week 8. In the present experiment the number of plant parasitic nematodes remaining at predator inoculation was estimated, but it was not possible to ascertain if the decline would have continued in the absence of predation. The results of Jones (1976) suggest that a stable population of H.dihystera should have been reached at the time of predator inoculation.

The disappearance from all treatments of all the plant-parasitic nematodes except H.dihystera precludes discussion of the influence of predation by P.punctatus on their numbers. After 54 days the significant decrease in numbers of H.dihystera in the 15% P.punctatus treatment suggests that the predators had some effect at this inoculum level. If predation was occurring it would contradict the observations of Nelmes (1974) and Cohn and Mordechai (1973) that mononchids did not feed on Helicotylenchus spp. It may be that the juveniles were successfully attacked but not the adults; the evidence is not sufficient to consider the contradiction proved. After 54 days the numbers of P.punctatus were much lower than the numbers of M. aquaticus but this latter species could not have been responsible for the reduction in the H.dihystera population, because the numbers of M.aquaticus did not differ significantly between treatments. The negative correlation

Table 50. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp.: Mean numbers (±S.E.) of nematodes per pot recovered 144 days after inoculation of P.punctatus.

| Treatments / Nematodes | Plant-parasitic nematodes only | Plant-parasitic nematodes + 5% P.punctatus | Plant-parasitic nematodes + 15% P.punctatus | P.punctatus only |
|---|---|---|---|---|
| Helicotylenchus dihystera | 216.40±127.12 | 235.20±83.90 | 340.80±189.75 | 5.75±2.53 |
| Hemicycliophora sp. | 0 | 0 | 0 | 0 |
| Criconemoides sp. | 0 | 0 | 0 | 0 |
| Pratylenchus thornei | 0.40±0.40 | 0.40±0.40 | 0.20±0.20 | 0 |
| Aphelenchoides sp. | 0 | 0.40±0.40 | 1.00±1.00 | 0 |
| Rhabditids | 321.60±89.72 | 238.20±71.13 | 585.20±443.07 | 304.50±145.37 |
| Labronema sp. | 46.80±10.46 | 34.60±3.49 | 58.80±18.54 | 34.25±11.25 |
| Mylonchulus sigmaturus | 0 | 0 | 0 | 0 |
| Mononchus aquaticus | 19.80±13.39 | 18.80±11.33 | 6.60±3.93 | 12.75±7.27 |
| Prionchulus punctatus | 0.20±0.20 | 0 | 0 | 0.25±0.25 |

Table 51. The ability of *P.punctatus* to reproduce in pots of sand in the presence of *H.dihystera* and *Hemicycliophora* sp.: Mean weights (± S.E.) of the grass plants (*L.perenne*) 144 days after inoculation of *P.punctatus*. (Weights expressed in gms).

| Treatment / Part of plant | Plant-parasitic nematodes only | Plant-parasitic nematodes + 5% *P.punctatus* | Plant-parasitic nematodes + 15% *P.punctatus* | *P.punctatus* only |
|---|---|---|---|---|
| Stem and leaf | 12.56±3.03 | 20.30±2.12 | 14.17±1.87 | 21.89±5.01 |
| Root | 15.90±3.72 | 17.21±2.23 | 11.62±2.01 | 23.99±4.93 |
| Total | 28.46±6.59 | 37.51±3.75 | 25.79±3.51 | 45.88±9.12 |

Table 52. The ability of *P.punctatus* to reproduce in pots of sand in the presence of *H.dihystera* and *Hemicycliophora* sp.: Results of analyses of variance (144 days after predator inoculation).

| Subject of Analysis | Value of 'F' ratio | Significance | Significant differences |
|---|---|---|---|
| Stem and leaf weights | 2.24 | 0.2-0.05 | D>A*; B>A* D>C* |
| Root weights | 2.31 | 0.2-0.05 | D>C*** |
| Total plant weights | 2.33 | 0.2-0.05 | D>C**; D>A* |
| No.of *H.dihystera* | 1.08 | N.S. | - |
| No.of plant-parasitic nematodes | 1.08 | N.S. | - |
| No.of rhabditids | 0.40 | N.S. | - |
| No.of prey nematodes[1] | 1.15 | N.S. | - |
| Total others[2] | 1.32 | N.S. | - |
| No.of *M.aquaticus* | 0.39 | N.S. | - |
| No.of *Labronema* sp. | 0.90 | N.S. | - |

1. Prey nematodes = Rhabditids + plant-parasitic nematodes.

2. Total others = Total nematodes less *P.punctatus*.

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; N.S.: Not significant

A: Plant parasitic nematodes only

B: Plant parasitic nematodes + 5% *P.punctatus*

C: Plant parasitic nematodes + 15% *P.punctatus*

D: *P.punctatus* only.

Table 53. The ability of P.punctatus to reproduce in pots of sand in the presence of H.dihystera and Hemicycliophora sp.: Results of correlation analyses (144 days after predator inoculation).

| Abscissa / Ordinate | Mononchus aquaticus | Labronema sp. | Helicotylenchus dihystera | Plant-parasitic nematodes |
|---|---|---|---|---|
| H.dihystera | r=-0.43* b=-5.92 | r=0.15 N.S. | - | - |
| Plant-parasitic nematodes | r=-0.44** b=-6.02 | r=0.25 N.S. | - | - |
| Rhabditids | r=-0.03 N.S. | r=-0.12 N.S. | - | - |
| Total others[1] | r=-0.27 N.S. | r=0.01 N.S. | - | - |
| Labronema sp. | r=-0.10 N.S. | - | - | - |
| Stem and leaf weight | r=-0.54*** b=-1.56 | r=0.03 N.S. | r=0.03 N.S. | r=-0.03 N.S. |
| Root weight | r=0.33 N.S. | r=-0.08 N.S. | r=-0.17 N.S. | r=-0.17 N.S. |
| Total plant weight | r=-0.47** b=-0.69 | r=-0.03 N.S. | r=-0.11 N.S. | r=-0.11 N.S. |

1. Total others = Total nematodes less the group indicated as the abscissa.

*: p= 0.1-0.05; **: p=0.05-0.02; ***: p= 0.02-0.01; N.S.: Not significant

between rhabditids and M.aquaticus implied that M.aquaticus was feeding on rhabditids. The significant correlation between Labronema sp. and stem and leaf weight can be ascribed to chance.

The increase in the number of H.dihystera from day 54 to day 144 indicated that control was not effected by any of the predators. They may have reduced the initial invasion of H.dihystera but their numbers (except for Labronema sp.) were later too small to reduce the subsequent generations. The possibility exists that competition by Labronema sp. led to the decline in mononchid numbers. Predation was insufficient to prevent a large increase in the rhabditid populations and these may have formed the major prey species for Labronema sp. as alternative prey was limited in the predator only controls.

The negative correlation between numbers of M.aquaticus and numbers of H.dihystera (and hence plant-parasitic nematodes) tended to support the possibility that M.aquaticus predated on H.dihystera and was responsible for the reduction in its numbers after 54 days. The negative correlation between stem and leaf, and total-plant weight with M.aquaticus may be the expression of a reduced plant-parasitism that allowed the plant some compensatory growth.

In the hope of improving reproduction of P.punctatus in pots some methods were modified in the experiments with Globodera rostochiensis and Meloidogyne incognita. Washed sand had been used in the H.dihystera experiment as the larger particles were considered an aid to predator dispersal but sand had two disadvantages: first, it contained very few plant nutrients and second, constant moisture relations were difficult to maintain. The first problem was overcome by regular watering with a plant fertiliser although the requirements of healthy plants were difficult to estimate. Stress induced by lack of water or nutrients is known to increase plant susceptibility to nematode attack and the regular supply of these require-

ments may have reduced the between-treatment differences in plant yield. A major aim of the following experiments was to quantify the reduction in root invasion by the plant parasitic nematodes, and the experiments were not continued for sufficient time for the plants to mature and crop yield to be assessed.

Watering even with a dilute salts solution may have subjected the nematodes to an osmotic shock. Jairajpuri, Azmi and Bajaj (1974) showed that Mylonchulus minor (Cobb 1893) Altherr 1953 survived for no more than 30 seconds in 0.4M solutions of five salts but up to 26½ hours in a 0.025M solution of potassium I chloride. Helicotylenchus indicus Siddiqi 1963 was more tolerant of all salts (except mercury II iodide) and survived for up to 17 min. in 0.4M solutions and more than 2 days in 0.025M solutions.

The second problem, the rapid draining of the sand, necessitated frequent watering which occasionally led to the sand being too wet. This was suggested by the colonisation of the pots by M.aquaticus which was described from a freshwater habitat (Coetzee, 1968a) and which survived longer in degraded agar than P.punctatus (Section III). In subsequent experiments the problems of using sand alone were avoided by using natural soil or a mixture of sand, loam and peat. The advantage of better moisture relations probably exceeded the disadvantage of reduced pore space, and soil corresponded more nearly to field conditions.

iv) The effect of predation by P.punctatus on populations of Globodera rostochiensis maintained in pots of soil.

The population density of Globodera rostochiensis in an experimental plot at Ashurst Lodge was estimated by extracting the cysts from four 50cm$^3$ soil samples using the Fenwick can technique (Fenwick, 1940). Cysts separated from the air-dried float were counted and an estimate of their contents obtained by breaking open ten cysts in 25cm$^3$ water; the juveniles

and eggs in four $3cm^3$ aliquots of the suspension were counted. The active nematodes in a further four $50cm^3$ soil samples were extracted and counted (Table 54).

Soil taken from the plot was mixed with an equal volume of sterilised soil by sieving and hand-mixing. The number of cysts, their contents and the number of active nematodes was estimated by the same procedures used for the plot soil (Table 54). $225cm^3$ of the mixed soil was placed in each of 36 pots. Potato tubers (Solanum tuberosum var.Majestic), previously stored in darkness at 5°C, were cut into pieces ($19.86\pm0.22gm$)* and one piece placed on the surface of the soil in each pot. The pieces were covered with a further $225cm^3$ of mixed soil and the pots watered.

P.punctatus were inoculated in $20cm^3$ water at the following densities: 0(Control), 500, 1000, and 5000 predators per pot, 9 replicates of each treatment. The pots were kept in a glasshouse maintained at $20\pm2$°C.

The experiment was continued long enough for the generation time of G. rostochiensis to be completed; 42 days after the inoculation of the predators the plants were removed from the pots, gently washed and dried; in addition to the fresh weight of the haulms and roots (which included newly-formed tubers judged to weigh less than 0.1gm), the numbers and the fresh weight of the newly formed tubers (>0.1gm) and the fresh weight of the tuber remnants were recorded. The soil from each pot was thoroughly mixed and divided into two, $200cm^3$ portions; the active nematodes were extracted from one portion and fixed in hot T.A.F. (Courtney, Polley, and Miller, 1955) before the population was estimated by counting the nematodes in five $4cm^3$ samples taken from $250cm^3$ of nematode suspension (i.e. approximately 4% of the population in each pot was counted). The P.punctatus recovered were counted as adults, first and second stage, and third and fourth stage juveniles.

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*The weight of the pieces was adjusted to reduce the substrate available to saprophagous nematodes (potential prey for P.punctatus) and to reduce the amount of rotting material in the pots; the weights included a variable number of shoots.

The cysts from the other portion of the soil were extracted, counted and cyst contents estimated as described above. Prior to examination soil samples were stored at 10°C.

Estimates of the mortality of G.rostochiensis were obtained from these counts i.e. mortality = number inoculated - (number in soil + number in roots + number remaining in the cysts at the end of the experiment); from this an estimate of the mortality due to predation by P.punctatus was obtained by subtracting the mean mortality of the control (≡ estimate of the mortality due to factors other than P.punctatus) from the total mortality in the other treatments i.e. mortality due to P.punctatus = Total mortality - mean mortality of the control.

Results: The number of G.rostochiensis in the roots was not significantly different between treatments; the number of G. rostochiensis in the soil (i.e. the males and second-stage juveniles) differed significantly between treatments with the control having significantly greater numbers than the treatments with 5000 and 1000 predators per pot. As the number of G.rostochiensis recovered from the soil greatly outnumbered those in the roots, total G.rostochiensis numbers reflected the differences between treatments shown by the numbers in the soil (Table 59). The numbers of G.rostochiensis in the roots were generally least in the treatment with 1000 predators per pot and greatest in that with 500 predators per pot, but the total in the latter was very similar to, and less variable than the control (Table 55). Most cysts were recovered from the pots with 500 predators which therefore had the largest estimate of eggs and juveniles remaining unhatched despite the small estimate of cyst contents (Table 56).

Mortality of G.rostochiensis was significantly affected by treatment, with greater mortality in the treatment with 5000 predators per pot than in that with 500 predators per pot (Table 59). The subtraction of the mean mortality of the control was equivalent to the subtraction of a constant

Table 54. The effect of predation by P.punctatus on populations of Globodera rostochiensis maintained in pots of soil: Estimation of the inocula of G.rostochiensis and associated nematodes.

| | Plot Soil | | | | | Sieved and mixed Soil | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Counts | | | | | Counts | | | | | |
| | 1 | 2 | 3 | 4 | Mean ±S.E. | 1 | 2 | 3 | 4 | Mean ±S.E. | Approx. number per pot. |
| Number of cysts/50cm$^3$[1.] | 47 | 59 | 63 | 48 | 54.25± 2.00 | 36 | 24 | 26 | 21 | 26.75± 1.63 | 120 |
| Cyst contents[2] | 147 | 122 | 117 | 114 | 125.00± 3.76 | 132 | 127 | 105 | 126 | 122.50± 2.99 | 12,360 |
| Active nematodes/50cm$^3$[3] | 133 | 218 | 166 | 38 | 138.75± 18.99 | 146 | 276 | 133 | 47 | 150.50± 23.63 | 680 |

1. 50cm$^3$ soil samples; Fenwick can technique

2. Eggs and juveniles in 3cm$^3$ aliquots from 25cm$^3$ suspension containing the contents of 10 cysts

3. Whitehead-tray extraction of 50cm$^3$ soil for 24 hours

Table 55. The effect of predation by *P.punctatus* on populations of *G.rostochiensis* maintained in pots of soil: Mean number (±S.E.) of *G.rostochiensis* associated with the roots of the potato plants*.

| Sex and life-stage | Control No predators inoculated | 500 predators per pot inoculated | 1000 predators per pot inoculated | 5000 predators per pot inoculated |
|---|---|---|---|---|
| Juveniles (excluding 4th st.♀♀) | 4.67± 3.03 | 3.17± 1.30 | 0.50± 0.34 | 0.33± 0.33 |
| 4th stage juvenile females | 4.83± 2.46 | 5.83± 2.06 | 1.00± 0.52 | 3.50± 1.57 |
| Adult females | 6.83± 4.28 | 14.67± 6.80 | 5.50± 1.77 | 9.17± 4.39 |
| Ensheathed males | 9.67± 5.51 | 3.83± 1.08 | 3.17± 1.56 | 5.50± 2.78 |
| Exsheathed males | 3.00± 1.86 | 2.50± 1.71 | 0.83± 0.54 | 1.17± 0.98 |
| Total | 29.00± 12.86 | 30.00± 10.49 | 11.00± 4.51 | 19.67± 8.01 |

*Includes nematodes within and attached to the roots, and also those floating free in the methyl blue-lactophenol used to fix and stain the roots.

Table 56. The effect of predation by *P.punctatus* on populations of *G.rostochiensis* maintained in pots of soil: Mean (±S.E.) of number of cysts per pot, cyst contents and number of viable juveniles per pot remaining in the cysts at the end of the experiment.

| | Control No predators inoculated | 500 predators per pot inoculated | 1000 predators per pot inoculated | 5000 predators per pot inoculated |
|---|---|---|---|---|
| No. of cysts[1] per pot | 178.12± 22.15 | 233.37± 18.84 | 194.11± 19.17 | 214.95± 21.23 |
| Cyst contents[2] (Eggs + Juveniles) | 7.41± 0.91 | 5.81± 1.37 | 6.84± 1.66 | 5.67± 1.34 |
| Viable juveniles in cysts (per pot) | 1254.67± 180.31 | 1417.33± 404.67 | 1308.33± 309.93 | 1279.83± 308.05 |

1. Based on the number recovered from 200cm$^3$ of soil using the Fenwick can technique.
2. Mean of four 3cm$^3$ aliquots from 25cm$^3$ suspension containing the contents of ten cysts.

Table 57. The effect of predation by *P.punctatus* on populations of *G.rostochiensis* maintained in pots of soil: Mean number (±S.E.) of active nematodes per pot recovered from the soil*.

| Nematode | Control No predators inoculated | 500 predators inoculated per pot | 1000 predators inoculated per pot | 5000 predators inoculated per pot |
|---|---|---|---|---|
| *G.rostochiensis* 2nd stage juveniles | 1188.17± 90.63 | 664.00± 81.72 | 533.17± 47.22 | 223.17± 54.90 |
| *G.rostochiensis* adult males | 216.17± 34.84 | 228.67± 40.96 | 145.33± 101.83 | 138.17± 23.13 |
| Rhabditids | 35,315.83± 2502.63 | 18370.50± 1225.00 | 19,217.17± 1622.31 | 12,742.67± 756.82 |
| *Labronema* sp. | 23.17± 9.80 | 5.33± 3.60 | 0 | 0 |
| *P.punctatus* 1st + 2nd stage juveniles | 26.67± 13.20 | 125.40± 35.04 | 166.50± 29.87 | 600.33± 80.29 |
| *P.punctatus* 3rd + 4th stage juveniles | 5.50± 4.90 | 24.83± 6.60 | 37.17± 18.51 | 308.17± 65.59 |
| *P.punctatus* adults | 7.17± 3.60 | 72.67± 18.71 | 109.83± 30.74 | 347.17± 65.80 |

*Based on the means ± S.E. of five $1cm^3$ aliquots from $25cm^3$ suspension containing the nematodes extracted from 200 $cm^3$ of soil per pot. These means and standard errors were multiplied by 25 (= number extracted from $200cm^3$ soil) and 2.125 (= total population in the $450cm^3$ soil in the pots). The figure presented is the mean of these means and standard errors.

Table 58. The effect of predation by P.punctatus on populations of G.rostochiensis maintained in pots of soil: Potato plant yields (mean ± S.E.; weights expressed in gms).

| Measure of plant growth | Control No predators inoculated | 500 predators inoculated per pot | 1000 predators inoculated per pot | 5000 predators inoculated per pot |
|---|---|---|---|---|
| Weight of haulm | 3.36± 1.36 | 4.38± 1.02 | 3.20± 0.80 | 3.61± 1.44 |
| Weight of roots (with new tubers weighing <0.1gm) | 0.95± 0.32 | 1.89± 0.53 | 0.04± 0.21 | 1.50± 0.64 |
| Weight of new tubers (>0.1gm) | 3.49± 2.13 | 5.20± 1.64 | 3.32± 1.42 | 2.81± 1.74 |
| Total plant weight | 7.87± 3.40 | 11.30± 2.97 | 9.13± 2.56 | 7.98± 3.07 |
| Number of new tubers (>0.1gm) | 5.67± 2.54 | 6.83± 1.20 | 4.33± 0.84 | 3.17± 1.01 |
| Total number of new tubers (>0.1gm + <0.1gm) | 8.17± 2.91 | 10.00± 1.71 | 6.17± 1.14 | 5.33± 1.65 |
| Weight of old tuber remaining | 0.97± 0.48 | 2.14± 0.85 | 1.58± 0.27 | 2.01± 0.92 |

Table 59. The effect of predation by *P.punctatus* on populations of *G.rostochiensis* maintained in pots of soil: Results of analyses of variance.

| Subject of Analyses | Value of 'F' ratio | Significance | Significant differences |
|---|---|---|---|
| No.of *G.rostochiensis* in soil | 4.61 | 0.05-0.01 | A>D***; A>C** |
| No.of *G.rostochiensis* in roots | 0.86 | N.S. | - |
| Total No. of *G.rostochiensis* | 4.93 | 0.05-0.01 | A>D***; A>C** |
| Mortality of *G. rostochiensis*[1] | 2.47 | 0.2-0.05 | D>B* |
| Mortality of *G. rostochiensis* caused by *P.punctatus*[1] | 2.47 | 0.2-0.05 | D>B* |
| No.of rhabditids | 2.02 | 0.2-0.05 | A>D* |
| Weight of haulm | 0.20 | N.S. | - |
| Weight of roots (including new tubers <0.1gm) | 0.92 | N.S. | - |
| Total plant weight | 0.28 | N.S. | - |
| No.of new tubers (>0.1gm) | 1.11 | N.S. | - |
| Total no.of new tubers (>0.1gm + <0.1gm) | 1.14 | N.S. | - |
| Weight of new tubers (>0.1gm) | 0.41 | N.S. | - |

*: p=0.05-0.02; **: p=0.02-0.01; ***: p=0.01-0.001; N.S.: Not significant

1. See text for further explanation

A: Control, no predators inoculated

B: 500 predators inoculated per pot

C: 1000 predators inoculated per pot

D: 5000 predators inoculated per pot

Table 60. The effect of predation by *P.punctatus* on populations of *G.rostochiensis* maintained in pots of soil: Results of correlation analyses.

| Abscissa / Ordinate | Total *P.punctatus* | Adult *P.punctatus* | *Globodera rostochiensis* in roots | *Globodera rostochiensis* in soil | *Globodera rostochiensis* in soil and roots | *Globodera rostochiensis* mortality[1] |
|---|---|---|---|---|---|---|
| *G.rostochiensis* in roots | r=0.09 N.S. | r=-0.05 N.S. | - | - | - | - |
| *G.rostochiensis* in soil | r=-0.46** b=0.51 | r=-0.42** b=-1.65 | - | - | - | - |
| *G.rostochiensis* in soil & roots | r=-0.49*** b=-0.55 | r=-0.50*** b=-1.98 | - | - | - | - |
| *G.rostochiensis*[1] mortality | r=0.39* b=0.79 | r=0.31 N.S. | - | - | - | - |
| Rhabditids | r=-0.34* b=-11.08 | r=-0.41** b=-4.62 | - | - | - | - |
| Haulm weight | r<0.01 N.S. | r=0.10 N.S. | r=0.54**** b=0.07 | r=-0.09 N.S. | r=-0.07 N.S. | r=-0.10 N.S. |
| Root weight | r=0.10 N.S. | r=0.20 N.S. | r=0.17 N.S. | r=-0.22 N.S. | r=-0.20 N.S. | r= 0.08 N.S. |
| Total plant weight | r<0.01 N.S. | r=0.06 N.S. | r=0.57**** b=0.18 | r=-0.25 N.S. | r=-0.22 N.S. | r=0.04 N.S. |
| No.of new tubers (>0.1gm) | r=-0.30 N.S. | r=-0.26 N.S. | r=0.66***** b=0.12 | r=-0.14 N.S. | r=-0.14 N.S. | r=-0.14 N.S. |
| Total no.of new tubers (>0.1gm +<0.1gm) | r=-0.28 N.S. | r=-0.26 N.S. | r=0.66***** b=0.14 | r=-0.22 N.S. | r=-0.20 N.S. | r=-0.14 N.S. |
| Weight of new tubers (>0.1gm) | r=-0.01 N.S. | r=-0.05 N.S. | r=0.46*** b=0.08 | r=-0.30 N.S. | r=-0.28 N.S. | r=0.10 N.S. |

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001; *****: p<0.001; N.S.: Not significant

1. See text for further explanation.

that therefore did not affect the analysis of variance and so the estimated mortality due to predation by P.punctatus was significant (p=0.2-0.05). Mortality was therefore significantly affected by the number of P.punctatus inoculated. The mean number of rhabditids per pot decreased in the sequence control > 500 predators per pot > 1000 predators per pot > 5000 predators per pot, but the only significant difference was between the control and the 5000 predators per pot treatment. Labronema sp. was recovered from two treatments (control and 500 predators per pot) and P.punctatus was recovered in low numbers from the controls, but in all other treatments the number of predators had greatly decreased from the inoculated number.

None of the parameters used to assess plant growth differed significantly between treatments (Table 58); the treatment with 500 predators per pot produced the greatest plant growth by all measures (Table 58). All the measures of plant growth except root weight were positively correlated with the number of G.rostochiensis in the roots and some of these correlations were very highly significant (Table 60). The numbers of G.rostochiensis in soil and total numbers were negatively correlated with both total and adult P.punctatus numbers (Table 60). Numbers of rhabditids were similarly negatively correlated with total numbers of P.punctatus and more significantly with adult P.punctatus numbers. No other correlations were significant.

Discussion: This experiment was easier to interpret than the H.dihystera/Hemicycliophora sp. experiment and the effects more obviously those of predation by P.punctatus. The number of G.rostochiensis in the soil (and hence total number) was significantly reduced by the two larger predator inocula and, although not significant, this was reflected in the number in the roots. Whether the reduction in number of G.rostochiensis would have been sufficient to prevent economic damage under field conditions is not known; that there was no significant difference in plant yields between the G.rostochiensis-

free controls and the other treatments was encouraging but would not necessarily represent the situation at the end of the growing season, especially as a small secondary invasion is likely, even in Britain (Evans, 1969). If predatory nematodes are to be used as biological control agents they must be capable of maintaining their numbers between the primary and subsequent invasions of the roots by plant parasitic nematodes. The evidence of this experiment was that the predators used did not maintain their numbers. The numbers of plant parasitic nematodes reaching the roots may be sufficient to ensure further generations and result in an overall increase in pest numbers during the growing season. The only advantage of using predatory nematodes would then become the reduction of the initial attack on the particularly susceptible young plants. Once the plants are established they can normally support fairly large populations of parasitic nematodes without great losses in final yield, unless stressed by adverse conditions.

In the other pot experiments of this study mortality of the plant parasitic nematodes can be considered as the excess of inoculum over those surviving to maturity. Separate analysis of estimated mortality was therefore not necessary as the estimate was inversely proportional to the numbers remaining at the end of the experiment. In this experiment some juveniles remained in the cyst and estimates of mortality had to allow for these unhatched eggs. The estimated mortality included the effects of inoculation and handling as well as natural causes in the soil; these causes of mortality should be approximately equal in all treatments and the mortality caused by predation by P.punctatus was the only variable factor. The mortality caused by handling was probably less than in other experiments because the juveniles were protected within the cyst. The predator-free treatment allowed estimation of mortality due to causes other than predation by P.punctatus and the latter could therefore be estimated. The actual numbers estimated were probably of little value because they were dependent on four estimates (number of cysts inoculated and the number remaining; cyst con-

tents before and after the experiment), but the mean differences between treatments may have had more value after suitable statistical analysis. Thus the "mortality due to P.punctatus" was significantly greater in the treatment with 5000 P.punctatus per pot than in the treatment with 500 P.punctatus per pot, but no other significant differences were recorded. This posed the problem of the optimum inoculum of predators: that 5000 per pot was better for control than 500 per pot was established but not that 5000 was better than 1000. Neither was 1000 per pot better than 500. Further study using a greater range of inocula is necessary but it seemed probable that if the experiment had continued to plant maturity, the larger inocula would have proved better as more predators should remain to counter subsequent generations of the plant parasites. It should be noted that the estimated mortality due to P.punctatus in the treatment with 500 predators per pot was less than the estimated mortality resulting from other factors.

The males of G.rostochiensis were exposed to attack by P.punctatus but as one surviving male was capable of fertilising several females (Green, Greet and Jones, 1970), reproduction was unlikely to be reduced greatly. The sex of individual G.rostochiensis is influenced by their nutrition as juveniles, with more males resulting from heavy infestations and inadequate food (Trudgill, 1967; Jones, 1974). Thus the proportion of females (and the number of eggs per female) may increase when predators reduce the number of juveniles invading the roots and the final population (= number of females x eggs per female) may therefore be greater. Jones (1974) related pre-planting and post-harvest numbers of G.rostochiensis. Predation effectively reduced the pre-planting population, so reducing intra-specific competition for root space and nutrients. At the population levels studied in this experiment the reduction in intra-specific competition may not greatly effect the final population, as the number of eggs would increase in those populations with fewer females. In larger populations the number of eggs per female and the proportion of females would increase if the predators reduced the number of

G.rostochiensis invading the roots, so that the $F_1$ population could be larger than without the predators. Unfortunately egg production was not complete at the end of this experiment so preventing comparison of "pre-planting" and "post-harvest" populations.

Predation by P.punctatus on the rhabditid populations was noticeable in the experiment: although the only significant difference was between the treatment with 5000 predators per pot and the no-predator control (the latter had approximately three times the rhabditid population of the former), the two other experimental treatments had only half the rhabditid population of the no-predator control. Predation on rhabditids was also suggested by the significant negative correlation between number of rhabditids and total number of P.punctatus. The regression between rhabditids and adult P.punctatus was more pronounced which suggested that adults in particular fed upon rhabditids. In contrast, the regression of number of G.rostochiensis on number of adult P.punctatus was less significant than that on total P.punctatus which suggested that juvenile P.punctatus were capable of predating on G. rostochiensis in soil as well as in agar. The decaying parent tuber, which provided a source of micro-organisms appeared not to have influenced the number of rhabditids.

Although P.punctatus populations had generally decreased, the many first and second stage juveniles ($\sim$ 50%) suggested that reproduction was continuing. If most of these juveniles had survived to maturity the population may have been sufficient to significantly reduce the second invasion of the roots by G.rostochiensis but the evidence of the other pot experiments, and particularly the experiments on nematodes in culture, suggested that few were likely to survive.

The highly significant positive correlations between the measures of plant growth (except root weight) and the number of G.rostochiensis in the roots again suggested compensatory mechanisms in plants with moderate nematode infestations. These would tend to increase the weight of the haulm

but it was surprising that the number (and hence weight) of new tubers should also increase. Videgard (1967) recorded that moderate G.rostochiensis infestations had little effect on potato haulm growth or tuber number but reduced tuber size; this reduction may have become apparent in this experiment if the plants had been grown to maturity.

v) The effects of predation by three species of predatory nematodes on populations of Meloidogyne incognita maintained in pots of soil.

The pots containing the loam, sand and peat mixture were left in a heated glasshouse (20±2°C) for 3 days to allow the soil temperature to equilibrate with the ambient before a single tomato seed (Lycopersicon esculentum var. Moneymaker) was planted in each of 48 pots and the soil watered; two further pots were planted with 8 seeds each.

Six days after the seeds were planted the soil was inoculated with the combinations of predators recorded in Table 61. After a further week incomplete germination necessitated the transplanting of some seedlings from the pots with eight seedlings. One pot in 3 treatments and 2 pots in the other 5 treatments received a transplanted seedling. To equalise the effects of the disturbance of the plants, those treatments not requiring two transplanted seedlings each had one seedling moved from the edge of a pot to the centre. In this way every treatment had two disturbed plants. The pots were left for seven days before inoculation with Meloidogyne incognita.

The roots of a tomato plant infected with M.incognita (obtained from I.C.I.Ltd., Jealott's Hill) were freed of the substrate by gentle agitation in a beaker of water. M.incognita egg masses were removed from the roots and placed on 2cm diameter sieves (aperture 250µm) resting in contact with distilled water in watchglasses. The second stage juveniles hatching over the next four days were collected and inoculated into 42 pots to give approximately 785 juveniles per pot; 6 pots were left as controls.

Seven weeks after inoculation of the M.incognita the tomato plants

Table 61. The effect of predation by three species of predatory nematodes on populations of Meloidogyne incognita maintained in pots of soil: numbers of predators, associated nematodes and M.incognita inoculated per pot.

| | Treatments | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Nematodes* | A | B | C | D | E | F | G | H |
| P.punctatus Adults | 41 | 83 | 207 | 13 | 55 | - | - | - |
| P.punctatus Juveniles | 230 | 562 | 1152 | 33 | 269 | - | - | - |
| M.aquaticus Adults | - | - | - | 319 | 138 | 158 | - | - |
| M.aquaticus Juveniles | - | - | - | 582 | - | 78 | - | - |
| Labronema sp. Adults | - | - | - | - | - | 7 | - | - |
| Labronema sp. Juveniles | - | - | - | - | - | 40 | - | - |
| Approx. Total Predators | 270 | 645 | 1360 | 950 | 460 | 285 | 0 | 0 |
| P.redivivus (from predator cultures) | 185 | 370 | 925 | 1530 | 950 | - | - | - |
| Meloidogyne incognita | 785 | 785 | 785 | 785 | 785 | 785 | 785 | 0 |

*Counts of three $1cm^3$ samples taken from approximately $65cm^3$ suspension, except for M.incognita for which five counts of $1cm^3$ samples taken from $420cm^3$ suspension were made.

were removed from the pots and the soil adhering to the roots gently removed as described above. The nematodes in the soil were extracted and all nematodes were counted. Plant growth was assessed using the measures recorded in Table 41 and the number of galls and adult females of M.incognita in the roots were also noted. The plants were dried to constant weight at 80°C.

Results: In all treatments fewer predators were recovered than were inoculated; no M.incognita were recovered from the soil and the numbers in the tomato roots showed significant differences depending on the treatment. No male M.incognita were recovered. Analyses of variance indicated that the number of M.incognita females, and hence the number of galls, differed to a highly significant degree between treatments (Tables 64, 65; Fig. 33); the number of rhabditids was also significantly different even with the exclusion from the analysis of Treatment E (from which no rhabditids were recovered). The details of the between-treatment differences showed that all experimental treatments had fewer M.incognita females than the no-predator control (Treatment G). The number of galls showed similar differences but there was no significant difference between the no-predator control and Treatment A (~ 270 P.punctatus per pot) which had significantly more M.incognita females and galls than Treatment C (~ 1360 P.punctatus per pot; Table 62). The difference in number of rhabditids was less significant but both predator-free controls had significantly more rhabditids than Treatments B, C and F (~645 P.punctatus, ~1360 P.punctatus and ~240 M.aquaticus + ~ 50 Labronema sp. respectively).

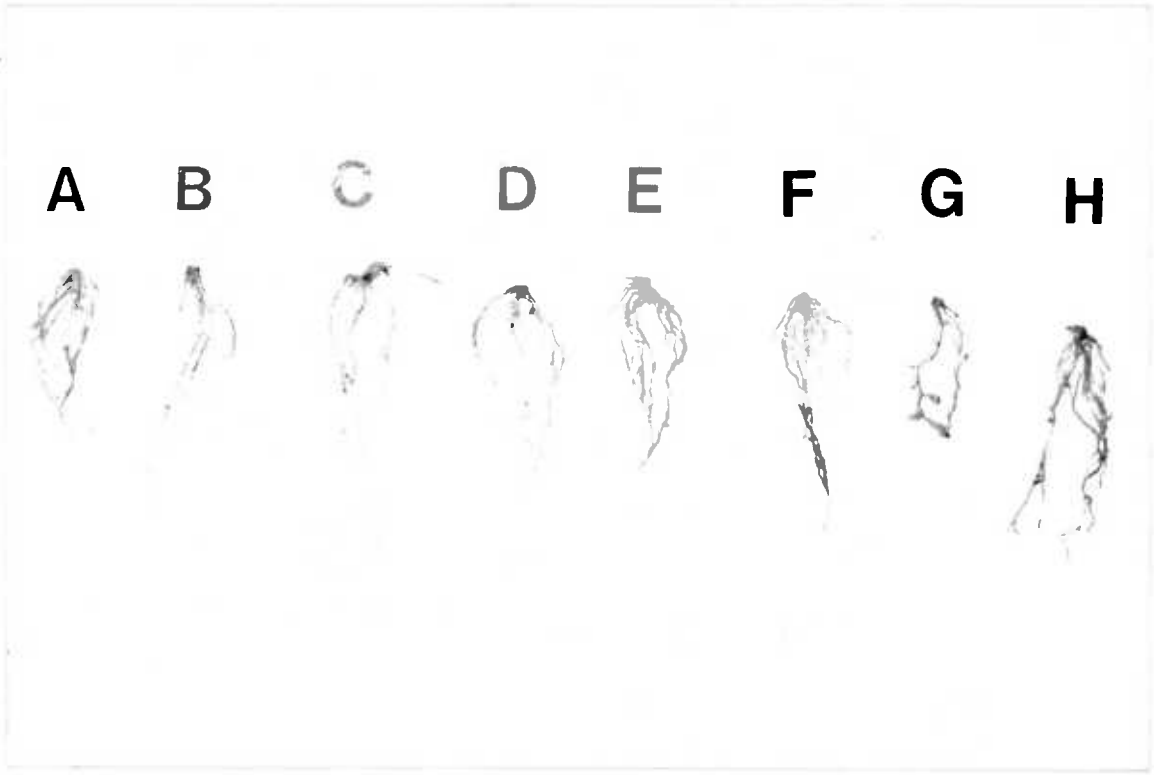
Of the measures of plant growth, only the fresh weight of the roots and the dry weight of the whole plants differed significantly between treatments (in Table 63 the two measures of plant growth had negative values of the index p which caused the greatest untransformed mean to become the least mean after transformation and vice-versa; the table refers to the transformed data i.e. Treatment C with the smallest untransformed mean is shown as having a

a significantly greater mean than the other treatments). No other effects of treatment were significant (Table 64) but in general plant growth appeared greater (as a result of galling) when the number of predators inoculated was <500 per pot approximately. The no inoculated nematode control often had the greatest mean plant weight or mean plant length and these measures in the M.incognita-only control were intermediate between the larger and smaller predator inocula treatments.

The numbers of M.incognita females in the tomato roots did not correlate with the numbers of predators except for a negative correlation with adult M.aquaticus (Table 66; the regressions were based only on the treatments that included the particular predator plus the no predator control Treatment G). The number of rhabditids showed a significant negative correlation with total P.punctatus. Many of the measures of plant growth were negatively correlated with the number of predatory nematodes, particularly P.punctatus for which significant regressions were more frequent and had greater significance than for M.aquaticus. Plant yields were also negatively correlated with total predators and occasionally these correlations had greater significance than with either P.punctatus or M.aquaticus (Table 66). Only the fresh weight of the roots was correlated with the number of M.incognita females in the roots; this correlation was positive and highly significant.

Discussion: In contrast to the G.rostochiensis experiment, only root weight correlated with the number of M.incognita in the roots, which was to be expected from the increase in galling with increasing number of M.incognita. Dry weights were more likely to indicate differences between treatments but this was not the case in the M.incognita experiment. The number of internodes and the number of leaves were unlikely to differ greatly in ten-week old plants; that the weight of young plants may not relate to eventual crop yield was discussed in relation to the potato plants in the

Fig. 33. The effects of predation by three species of predatory nematodes on populations of Meloidogyne incognita maintained in pots of soil: photograph of tomato plant root systems from each treatment.




(x0.33 approx).

A: 270 P.punctatus

B: 645 P.punctatus

C: 1360 P.punctatus

D: 45 P.punctatus + 900 M.aquaticus

E: 325 P.punctatus + 140 M.aquaticus

F: 235 M.aquaticus + 50 Labronema sp.

G: Meloidogyne incognita only

H: No nematodes inoculated.

Note severe galling of no-predator control (G) compared to all other treatments and dense root systems of treatments E and F which approaches that of the no-nematode control (H).

Table 62. The effect of predation by three species of predatory nematodes on populations of *Meloidogyne incognita* maintained in pots of soil: nematodes recovered at the end of the experiment (mean±S.E. per pot).

| Treatment (approx no.of predators inoculated per pot) | Number of *M.incognita* ♀♀ in roots | Number of Galls | Number of Rhabditids | No.of *P.punctatus* | | No.of *M.aquaticus* | | No.of *Labronema* sp. | | Total no. of Predators |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Adults | Juveniles | Adults | Juveniles | Adults | Juveniles | |
| A<br>270 *P.punctatus* | 27.00±<br>5.89 | 24.17±<br>5.16 | 11.17±<br>2.99 | 12.00±<br>5.58 | 49.67±<br>20.01 | 0.50±<br>0.02 | 1.83±<br>2.45 | 0 | 0 | 64.00±<br>26.03 |
| B<br>645 *P.punctatus* | 16.17±<br>2.86 | 12.50±<br>2.14 | 14.17±<br>11.84 | 19.00±<br>3.99 | 30.33±<br>13.21 | 0 | 0 | 0 | 0 | 49.33±<br>15.98 |
| C<br>1360 *P.punctatus* | 5.17±<br>1.78 | 4.33±<br>3.04 | 4.33±<br>3.04 | 34.50±<br>13.93 | 42.33±<br>17.64 | 0 | 0 | 0 | 0 | 76.83±<br>29.59 |
| D<br>50 *P.punctatus*+<br>900 *M.aquaticus* | 20.17±<br>11.35 | 15.83±<br>7.94 | 100.33±<br>86.71 | 1.50±<br>0.96 | 3.00±<br>1.51 | 30.33±<br>12.10 | 15.17±<br>8.43 | 0.17±<br>0.17 | 0 | 50.17±<br>21.63 |
| E<br>325 *P.punctatus*+<br>140 *M.aquaticus* | 12.83±<br>6.91 | 11.00±<br>5.85 | 0 | 9.17±<br>2.18 | 23.83±<br>8.44 | 32.33±<br>12.41 | 22.17±<br>9.73 | 0.17±<br>0.17 | 0 | 87.67±<br>30.44 |
| F<br>240 *M.aquaticus*+<br>50 *Labronema* sp. | 16.50±<br>6.07 | 14.67±<br>5.12 | 22.67±<br>16.43 | 1.67±<br>0.62 | 2.33±<br>1.18 | 55.67±<br>16.73 | 20.17±<br>9.94 | 8.50±<br>2.95 | 12.83±<br>5.36 | 90.40±<br>22.79 |
| G<br>*M.incognita* only | 58.83±<br>8.66 | 42.17±<br>6.57 | 160.17±<br>77.69 | 0.83±<br>0.65 | 1.83±<br>1.64 | 0.50±<br>0.22 | 0.17±<br>0.17 | 0 | 0 | 3.33±<br>2.14 |
| H<br>No nematodes inoculated | 0 | 0 | 255.83±<br>85.08 | 0.33±<br>0.21 | 0 | 0 | 0.33±<br>0.33 | 0 | 0 | 0.67±<br>0.49 |

Table 63. The effect of predation by three species of predatory nematodes on populations of *Meloidogyne incognita* maintained in pots of soil: assessment of tomato-plant growth (means ± S.E.).

| Treatment (approx no.of predators inoculated per pot). | Number of Leaves | Number of Internodes | Length (cm) | | | Fresh Weight (gm) | | | Dry Weight (gm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Haulm | Root | Total | Haulm | Root | Total | Haulm | Root | Total |
| A | 6.50± | 4.67± | 10.95± | 11.30± | 22.25± | 3.73± | 0.28± | 4.02± | 0.33± | 0.04± | 0.37± |
| 270 *P.punctatus* | 0.43 | 0.33 | 1.14 | 1.10 | 1.70 | 0.79 | 0.02 | 0.81 | 0.07 | 0.01 | 0.07 |
| B | 6.17± | 4.50± | 10.12± | 11.40± | 21.52± | 3.11± | 0.26± | 3.37± | 0.23± | 0.03± | 0.26± |
| 645 *P.punctatus* | 0.48 | 0.43 | 0.85 | 0.93 | 1.33 | 0.46 | 0.03 | 0.49 | 0.03 | 0.01 | 0.03 |
| C | 6.00± | 4.00± | 8.27± | 9.32± | 17.58± | 2.60± | 0.21± | 2.81± | 0.23± | 0.02± | 0.25± |
| 1360 *P.punctatus* | 0.68 | 0.51 | 1.16 | 1.49 | 2.39 | 0.69 | 0.08 | 0.75 | 0.05 | 0.004 | 0.05 |
| D | | | | | | | | | | | |
| 50 *P.punctatus* + | 5.50± | 3.67± | 9.55± | 11.33± | 20.88± | 2.91± | 0.19± | 3.10± | 0.22± | 0.03± | 0.25± |
| 900 *M.aquaticus* | 0.43 | 0.42 | 0.91 | 2.01 | 2.64 | 0.39 | 0.03 | 0.41 | 0.02 | 0.01 | 0.02 |
| E | | | | | | | | | | | |
| 325 *P.punctatus* + | 6.33± | 4.67± | 10.88± | 10.65± | 21.53± | 3.83± | 0.30± | 4.13± | 0.40± | 0.04± | 0.44± |
| 140 *M.aquaticus* | 0.33 | 0.33 | 0.86 | 1.56 | 1.90 | 0.49 | 0.04 | 0.51 | 0.10 | 0.01 | 0.10 |
| F | | | | | | | | | | | |
| 240 *M.aquaticus* + | 6.17± | 4.33± | 11.02± | 8.78± | 19.80± | 3.38± | 0.24± | 3.62± | 0.26± | 0.04± | 0.30± |
| 50 *Labronema* sp. | 0.60 | 0.42 | 1.16 | 0.52 | 1.54 | 0.77 | 0.05 | 0.80 | 0.05 | 0.01 | 0.05 |
| G | | | | | | | | | | | |
| *M.incognita* only | 6.83± | 4.33± | 10.45± | 9.98± | 20.43± | 3.35± | 0.37± | 3.72± | 0.27± | 0.04± | 0.31± |
| | 0.31 | 0.42 | 0.65 | 0.75 | 1.21 | 0.37 | 0.02 | 0.36 | 0.02 | 0.01 | 0.02 |
| H | | | | | | | | | | | |
| No nematodes inoculated | 6.67± | 4.67± | 11.22± | 11.07± | 22.28± | 4.30± | 0.42± | 4.72± | 0.34± | 0.05± | 0.39± |
| | 0.21 | 0.33 | 1.10 | 0.67 | 1.39 | 0.76 | 0.05 | 0.82 | 0.05 | 0.01 | 0.05 |

Table 64. The effect of predation by three species of predatory nematodes on populations of *Meloidogyne incognita* maintained in pots of soil: Results of analyses of variance (untransformed data).

| Subject of Analysis | Value of 'F' ratio | Significance |
|---|---|---|
| *M.incognita* ♀♀ in roots | 6.34 | <0.001 |
| Number of galls on roots | 5.28 | <0.001 |
| Number of Rhabditids* | 3.07 | 0.05-0.01 |
| Number of Leaves | 0.84 | N.S. |
| Number of Internodes | 0.79 | N.S. |
| Stem Length | 0.99 | N.S. |
| Root Length | 0.68 | N.S. |
| Total plant length | 0.72 | N.S. |
| Fresh weight of haulm | 0.79 | N.S. |
| Fresh weight of root | 3.29 | 0.01-0.001 |
| Total fresh weight of plant | 0.90 | N.S. |
| Dry weight of haulm | 1.46 | N.S. |
| Dry weight of root | 1.33 | N.S. |
| Total dry weight of plant | 1.55 | 0.2-0.05 |

*Analysis does not include treatment E from which no rhabditids were recovered.

Table 65. The effect of predation by three species of predatory nematodes on populations of Meloidogyne incognita maintained in pots of soil: Further analysis of those parameters which had significant 'F' ratios in the analyses of variance of the original data.

| Subject of Analysis | Transformation | | Analysis of Variance (transformed data) | | |
|---|---|---|---|---|---|
| | Value of b[1] | Value of p[1] | Value of 'F' ratio | Significance | Significant Differences |
| M.incognita ♀♀ in roots | 1.2467 | 0.3766 | 5.46 | <0.001 | G>C,E**** G>A* G>B, D, F*** A>C** |
| Number of galls on roots | 1.3892 | 0.3054 | 4.45 | 0.01-0.001 | G>C**** G>F** G>B,D,E*** A>C* |
| Number of rhabditids | 1.9095 | 0.0452 | 2.39 | 0.2-0.05 | H>C** G>B,C,F* H>B,F* |
| Fresh weight of root | 2.3497 | -0.1749 | 3.41 | 0.01-0.001 | C>H**** C>A** C>E,G*** D>G,H*** F>H*[2] |
| Total dry weight of plant | 3.2363 | -0.6182 | 1.38 | N.S. | C>E** C>A,H*[2] |

1. b and p refer to the statistics in Taylors Power Law (Taylor, 1961).
2. The negative index of the transformation reverses the greatest and smallest means; thus in the original data for fresh root weight H>C**** etc.

*: p=0.05-0.02; **: p=0.02-0.01; ***: p=0.01-0.001; ****: p<0.001; N.S.: Not significant

A: 270 P.punctatus; B: 645 P.punctatus; C: 1360 P.punctatus; D: 50 P.punctatus + 900 M.aquaticus; E: 325 P.punctatus + 140 M.aquaticus; F: 240 M.aquaticus + 50 Labronema sp.; G: M.incognita only; H: No nematodes inoculated.

Table 66. The effect of predation by three species of predatory nematodes on populations of Meloidogyne incognita maintained in pots of soil: Results of correlation analyses.

| Abscissa / Ordinate | P.punctatus[1] Adults | P.punctatus[1] Total | M.aquaticus[2] Adults | M.aquaticus[2] Total | Total[3] Predators | Meloidogyne incognita ♀♀ in roots |
|---|---|---|---|---|---|---|
| No.of M.incognita ♀♀ in roots | r=-0.24 N.S. | r=-0.17 N.S. | r=-0.36* b=-0.29 | r=-0.33 N.S. | r=0.20 N.S. | - |
| No.of galls on roots | r=-0.24 N.S. | r=-0.12 N.S. | r=-0.30 N.S. | r=-0.28 N.S. | r=-0.14 N.S. | - |
| No.of Rhabditids | r=-0.25 N.S. | r=-0.27* b=-0.69 | r=-0.27 N.S. | r=-0.24 N.S. | r=-0.24 N.S. | - |
| Fresh weight Haulm | r=-0.56***** b=-0.04 | r=-0.61***** b=-0.02 | r=-0.36* b=-0.01 | r=-0.41** b=-0.01 | r=-0.50***** b=-0.01 | r=0.07 N.S. |
| Fresh weight Root | r=-0.47**** b=-0.003 | r=-0.39*** b=-0.001 | r=-0.38* b=-0.001 | r=-0.34 N.S. | r=-0.38*** b=-0.0006 | r=0.43**** b=0.002 |
| Fresh weight Plant | r=-0.58**** b=-0.04 | r=-0.61**** b=-0.02 | r=-0.37* b=-0.01 | r=-0.42** b=-0.01 | r=-0.53***** b=-0.01 | r=-0.17 N.S. |
| Dry weight Haulm | r=-0.31* b=-0.002 | r=-0.41*** b=-0.001 | r=-0.33 N.S. | r=-0.35* b=-0.001 | r=-0.43**** b=-0.001 | r=-0.19 N.S. |
| Dry weight Root | r=-0.41*** b=-0.0004 | r=-0.37** b=-0.0001 | r=-0.07 N.S. | r=0.17 N.S. | r=-0.22 N.S. | r=0.14 N.S. |
| Dry weight Plant | r=-0.34** b=-0.003 | r=-0.47**** b=-0.001 | r=-0.33 N.S. | r=-0.36* b=-0.001 | r=-0.44**** b=-0.001 | r=-0.17 N.S. |
| Length of stem | r=-0.58***** b=-0.07 | r=-0.57***** b=-0.03 | r=-0.26 N.S. | r=-0.36 N.S. | r=-0.47**** b=-0.02 | r=-0.07 N.S. |
| Length of root | r=-0.30* b=-0.05 | r=-0.29* b=-0.02 | r=-0.35* b=-0.03 | r=-0.35* b=-0.02 | r=-0.40**** b=-0.20 | r=-0.02 N.S. |
| Length of plant | r=-0.50**** b=-0.01 | r=-0.37** b=-0.04 | r=-0.39* b=-0.05 | r=-0.42** b=-0.04 | r=-0.51***** b=-0.04 | r=0.09 N.S. |

1. 34 degrees of freedom (Treatments A-E, G)

2. 22 degrees of freedom (Treatments D-G)

3. 40 degrees of freedom (Treatments A-G).

*: p=0.1-0.05; **: p=0.05-0.02; ***: p=0.02-0.01; ****: p=0.01-0.001;

*****: p<0.001; N.S.: Not significant

G.rostochiensis experiment.

Counts of animals rarely follow a normal distribution and analysis should be made of transformed data. The increase in information obtained in this experiment was not sufficient to warrant this approach in the previous experiments. The large number of highly significant negative correlations between plant yields and the numbers of predators in the M. incognita experiment again suggested compensation by the plant after nematode attack. The low values of the regression coefficient indicated that the decrease in plant weight with increase in predator numbers remaining was negligible. The fewer correlations with M.aquaticus and their lower significance suggest that P.punctatus was a more effective predator than M.aquaticus. Nonetheless the significant difference between the no-predator control and the treatments with M.aquaticus indicated that this nematode did feed on M.incognita to a considerable extent. The low inocula and the very small recovery of Labronema sp. precluded discussion of this predator's ability to feed upon M.incognita. The number of rhabditids was again dependent on the treatment but was only correlated with the numbers of P.punctatus. A comparison of predators with different feeding mechanism to clarify predator-prey relationships is needed. It is known that mononchids feed on Meloidogyne naasi Franklin 1965 juveniles in vitro, but that Butlerius sp. (Diplogasteridae) rarely attacked this nematode and the attacks never penetrated the cuticle of M.naasi (Grootaert, Jaques and Small, in press).

The evidence of predation and at least partial control of M.incognita was striking. The number of females and galls in the roots were significantly reduced in all six experimental treatments and there was evidence that the larger predator inocula were more successful in controlling M. incognita than the smaller predator inocula. Particularly important was the considerable reduction in galling (Fig. 33) when the plants were young and most susceptible to attack by M.incognita; whether this would have been reflected in a significant increase in crop yield can be determined only from further study.

## DISCUSSION

The primary aim of these pot experiments was to elucidate the population changes of agar-cultured predatory nematodes when returned to a more natural environment. By using various prey nematodes, including some of economic importance, it was also possible to obtain information on the predation abilities of the predatory nematodes, which has implications for their potential use as biological control agents. That predation was not equally effective on all prey species was established and progressively more factors correlated significantly with predator numbers in successive experiments. The increase in significant correlations may have been related to the environment in the pots or to the prey species or, most probably, to a combination of these two factors.

The environment in relation to the medium used was discussed for the H.dihystera experiment; the better results in terms of plant parasitic nematode control in later experiments may have reflected the change from sand to natural or artificial soils. The greater motility of predators and prey consequent on better water conditions in soil would probably increase the frequency of predator-prey encounters and therefore the rate of predation. It was originally thought that the larger pore spaces in sand would allow greater predator motility but it may also have had the disadvantage that a much greater volume was available to both predators and prey. P.punctatus has been shown to effectively search very small areas (Nelmes, 1974) and the restriction of prey to smaller volumes in soil may also have increased the rate of encounters with predators. This would conflict with the frequently expressed opinion that prey nematodes could avoid predators by passing through pore spaces too small to allow predators to follow. Another possible reason for the improvement of predation rates in soil as opposed to sand, may be the relative quantities of organic matter: the results of the experiments on culture suggested that organic matter may be beneficial to predatory nematodes.

The densities of predators and prey exceeded those of natural soils

where predators rarely constitute more than 5% of the fauna and plant parasitic nematodes may be 30% (Overgaard-Nielsen, 1949; Banage, 1963; Nelmes and McCulloch, 1975). The plant parasitic nematodes probably had less distance to travel before reaching the roots in the pots than in agricultural soils. This may have been enhanced by the single centrally-placed host plant which allowed an even root diffusate gradient as opposed to the field situation where root diffusates may be diffusing from all directions.

It is necessary to consider the relevance of the pot environment to the field. The environmental preferences of soil-dwelling nematodes are poorly understood. Plant-parasitic nematodes will generally have adapted to the conditions under which their host grows. Of the nematodes used only P. punctatus had been reared in an artificial medium, so the use of predators from agar cultures may have affected their behaviour or physiology when transferred to soil.

The medium used in the later experiments approached natural soils and the temperature of 20°C used could be reached in summer in temperate regions and throughout the year in the tropics; most nematodes thrive at this temperature and plant growth is good. The environmental conditions used were therefore optimal, which is probably rare (especially for extended periods) under natural conditions and involved no diurnal or seasonal variation (except for light). The use of these conditions allowed near maximum plant growth, predation and invasion of the roots by the plant parasitic nematodes. The increased rate of these processes did not diminish their relevance to the field.

The pot environment used for these experiments proved suitable for achieving the aims suggested in the preamble: i) whether the predators feed on the target nematode and ii) whether the level of predation was sufficient to cause a decrease in the number of plant parasitic nematodes invading the roots. The three predators, P.punctatus, M.aquaticus and Labronema sp. differed in their abilities to feed on the prey nematodes, which included the contaminant rhabditid populations. The results sug-

gested that the predators fed upon G.rostochiensis, M.incognita and possibly the smaller juvenile stages of H.dihystera. The part played by each predator was difficult to assess because of the combined effects of relative predator density and predation ability. Observations in culture suggested that P.punctatus was a more efficient predator since it can ingest small prey more rapidly and can successfully attack larger prey more frequently. In the M.incognita experiment large numbers of M.aquaticus reduced the number of plant parasitic nematodes to a lesser extent than moderate numbers of P.punctatus, but small numbers of M.aquaticus (plus a few Labronema sp. ) reduced the number of M.incognita in the roots more than small numbers of P.punctatus. Whether this latter observation was due to the presence of Labronema sp. cannot be determined, but in general mixtures of predators appeared more effective than P.punctatus alone, possibly because predator size differences allowed greater volumes of soil to be searched. The predation abilities of Labronema sp. were difficult to assess owing to small numbers, but observations in culture suggested that these slow-moving nematodes would not be so effective as the faster moving mononchids especially with small, slow-moving prey.

In most experiments predation on rhabditids was apparent; this is often suggested as a contra-indication to the use of predatory nematodes as biological control agents. The rate of predation by P.punctatus was not greatly influenced by satiation (Nelmes, 1974) so that a predator that has just fed on a rhabditid may immediately afterwards attack a plant-parasitic nematode. Observations in culture also indicated that many potential prey were attacked and wounded by well-fed predators without ingestion; wounded prey are immobilised and this is adequate for biological control purposes. Predation on free-living nematodes may be advantageous in that larger predator populations can be supported so increasing the probability of encounters between plant-parasitic nematodes and predators and maintaining

predator populations when plant parasitic nematodes are scarce.

The results suggested that the rate of predation was sufficient to reduce all the prey populations except H.dihystera. The variable success achieved in reducing the plant parasitic nematode populations may reflect their relative susceptibility to attack. That some ectoparasitic species e.g. Helicotylenchus spp.are relatively resistant to attack by predatory nematodes has been discussed. The results of recent experiments have suggested that P.punctatus cannot puncture the cuticle of Rotylenchus robustus,another hoplolaim, but that second stage juveniles can be ingested whole (Small, unpubl.). The defence mechanism of Helicotylenchus spp. suggested by Esser (1963) appeared to be physical rather than chemical in R.robustus since Labronema sp. partially penetrates the cuticle but always withdraws before penetration is completed and often the spear was blocked by an extrusion from the prey cuticle (Small, unpubl.). It therefore seems that control of hoplolaims and possibly many other ectoparasitic species using predatory nematodes is unlikely.

The endoparasitic species appeared more susceptible to predation. G.rostochiensis numbers in soil, and to a lesser extent the numbers in the roots, were reduced by P.punctatus. Control of the important tropical pest M.incognita using predatory nematodes seemed the most likely to succeed if tested in the field. Further work is needed to establish the economically tolerable losses caused by M.incognita.

In selecting a biological control agent, predatory nematode species other than those tested may have advantages in terms of reproductive rate or predation success. Those aphelenchs which have been studied have a much shorter generation time (maximum $6\frac{1}{2}$ days) than mononchids (Hechler, 1963; Hechler and Taylor, 1966a, b), and are efficient predators of P.redivivus at least (Small, unpubl.). However it seems unlikely that these small predators could kill the larger ectoparasitic nematodes, but they may be capable of destroying the infective stages of some endoparasitic species.

Diplogasterids are less likely to have value as biological control agents: they are often associated with decaying organic matter as many are facultative saprophages. Diplenteron potohikus (Yeates, 1969) and Butlerius sp. (Grootaert, Jaques and Small, in press) successfully attacked a wide range of prey. The most promising nematodes for biological control are dorylaimids and mononchids which are capable of wounding the larger plant parasitic nematodes and killing large numbers of the smaller plant parasitic nematodes. Dorylaimid predators could be effective against criconematids, whereas mononchids cannot obtain a purchase on the annulated cuticle.

Dorylaims have been observed feeding on the eggs of H.schachtii (Thorne, 1928) and M.aquaticus (Section III); egg predation appears less frequent im mononchids although Thorne (1927) figured Mylonchulus sigmaturus feeding on eggs of H.schachtii. Predatory nematodes may be able to penetrate the gelatinous matrix of Meloidogyne spp. egg masses. Egg predation could be a very effective means of control particularly of cyst and root-knot nematodes where eggs are deposited in large groups; a single predator encountering such an egg batch could destroy many eggs.

# V. CONCLUDING DISCUSSION

By studying aspects of the life cycle, behaviour and ecology of Prionchulus punctatus, it has been possible to draw some conclusions regarding the biology of predatory nematodes.

P.punctatus underwent four moults after a period of embryonic development within the egg. The first juvenile stage was of relatively short duration which was probably the expression of the evolutionary trend in many nematode groups that leads to a reduction in the duration of the life-cycle. The first juvenile stage of many nematodes is passed entirely with the egg (e.g. Meloidogyne spp., Rotylenchus spp.) and in some Seinura spp. the first stage is of such short duration that it is indistinguishable from the second stage (Hechler and Taylor, 1966b). Postponing consideration of the second stage, the third juvenile stage of P.punctatus was also comparatively short and did not seem greatly affected by any experimental treatment. It therefore seems that evolutionary reduction of the life-cycle has particularly affected the first and third juvenile stages of P.punctatus.

The second and fourth juvenile stages were similar as both were of relatively long duration, involved considerable increase in biomass and were sensitive to environmental conditions. This last similarity had differing expressions in the two stages: in unfavourable conditions the second stage juveniles died within a critical period which depended upon the nature and intensity of the adverse factors. In contrast, the fourth stage was indefinitely prolonged in adverse conditions and moulting rapidly followed an environmental improvement. It is suggested that the second stage juvenile is adapted for resource-accumulation, allowing rapid development to the fourth stage in good conditions. The death of this stage in unfavourable conditions limits the population as well as selecting for the most environmentally fit individuals. Similar, but perhaps more advanced strategies (as they do not result in death), can be found in the second stage development of other nematodes e.g. the dauer larvae of Caenorhabditis elegans (Maupas 1899) Dougherty 1953. The second stage juveniles of many plant-parasitic nematodes (e.g. Meloidogyne spp., Heterodera spp.) are the

infective stage and whilst enclosed within the egg, many are resistant to adverse conditions and represent the stage adapted for awaiting favourable conditions, particularly the growth of the host plant. In general, second stage juveniles have exhibited a particular plasticity in the course of evolution and have come to represent a critical stage in the life-cycles of many nematodes. Nematode fourth-stage juveniles are the other stage that are often adapted to withstand adverse conditions e.g. Ditylenchus dipsaci (Kuhn 1857) Filipjev 1936 (as "eelworm-wool") and Aphelenchoides ritzemabosi (Schwartz 1911) Steiner and Buhrer 1932 (Evans and Perry, 1976), the ability to delay maturation prevents over-exploitation of existing resources but enables rapid exploitation of newly-available resources. Again P.punctatus seems to represent an early stage in the development of fourth-stage specialisation; the delay in maturation represents another population-limiting mechanism and may be very important to soil-populations by preventing over-exploitation of the food-resources available to the predators. It should be stressed that the "resistance" of fourth stage juvenile P.punctatus is relative to the other stages of the life-cycle, as no stage can be considered resistant when compared to the survival abilities of some nematode species. Indeed, mononchids appear very susceptible to many adverse factors such as desiccation (Arpin, 1969), pesticides (Martin and Yeates, 1975; Nelmes and McCulloch, 1975), antibiotics (Maertens, 1975) and bacterial metabolites (Nelmes and McCulloch, 1975).

The rate of egg production was also affected by environmental conditions; this is not considered a specialisation of the adults but rather the direct effect of the adverse conditions i.e. an organism cannot maintain maximum productivity in unfavourable circumstances. Nematode egg-deposition rates can be depressed by many non-optimal environmental factors including temperature, moisture, oxygen concentration etc. Like other nematodes P.punctatus females appear to have a particular reproductive potential and in unfavourable conditions the life of the females is prolonged until favourable conditions

allow rapid completion of egg-laying, usually followed shortly by the death of the nematode.

For this means of population regulation to occur it must have survival value to the predators in the soil; one of the most consistent features of published ecological surveys of nematodes is the relatively constant and small proportion of predators in the total nematode population (Thorne, 1927; Overgaard-Nielsen, 1949; Banage, 1963; Nelmes and McCulloch, 1975). This is not unexpected as it is characteristic of predators to occupy the upper strata of the pyramid of numbers; the numbers of predators recorded probably represent the carrying-capacity of the soils studied. Another feature of the P.punctatus populations recorded in this study was the similar age structure of populations that had reached stability (e.g. in four-week old agar cultures, at the end of pot experiments, and in a field soil). The percentages for the total mononchid population in April 1976 in the micro-distribution study (34% first stage juveniles, 32% second-stage, 18% third stage and 7% fourth stage; Section II) are representative figures. This constancy is evidence for the relevance of the pot and agar-culture experiments to soil populations. Population stability suggests a feed-back mechanism, either related to extra-specific factors such as prey density (as suggested for second stage juvenile development and egg-deposition rates) or an intra-specific stimulus (as suggested for fourth stage juvenile development).

Although the percentage of predators was low, a much more dense predator population was found in the F-layer of a patch of bracken (Section III); this combination of small percentage but large population suggests that the populations in most soils are limited by prey-availability whereas in the comparatively productive medium of humus, where the number of microbivorous nematodes is usually greater, more predators could be supported. Although this direct predator-prey relationship is probably the primary

factor determining predator population size, other chemical and physical factors may be involved as they are in agar-culture. Szczygiel (1971) recorded that Prionchulus muscorum was associated with soils of pH 6.5-6.9; which is similar to the pH of the extract of the bracken F-layer material. The pH of such an extract is unlikely to be greatly affected by heating (Poole, pers.comm.) yet Grootaert (pers.comm.) found that the population growth-stimulating properties of a humus extract were lost after heating the extract 3-4 times. This observation suggests the presence of a heat-labile or volatile chemical; in a humus-extract some organic molecules may be destroyed by heating and carbon-dioxide and ammonia driven-off. The improvement in P.punctatus population growth achieved by including a soil- or humus-extract in the agar medium further indicates the sensitivity of this nematode to its chemical environment.

Pianka (1970) suggested constant population size as one of the correlates of K-selected animals (Dobzhansky, 1950; MacArthur and Wilson, 1967) and many of the other correlates describe features of the biology of P. punctatus, especially in comparison to other soil-dwelling nematodes. The slow development, delayed reproduction, large body size, long life and apparently density-dependent mortality recorded in this study are all features of a K-selected organism and it is probable that other correlates would also apply to P.punctatus if information was available. Most other predators (with the exception of Seinura spp.) appear similar to P.punctatus. It is advantageous for predators to be K-selected because the "extinction" of the prey resulting from over-exploitation would be rapidly followed by the extinction of the predator.

Aggregation of the nematodes was demonstrated in soil and can be observed in agar (Sections II, III): P.redivivus, initially distributed at random, will form one or more aggregations within six hours (Small, unpubl.). Predators also form mono-specific aggregations in the absence of prey but tend to congregate around prey aggregations if these are present; similar

observations were made by Maertens (1975). Esser (1963) recorded mono-specific aggregations (= "swarming") of Helicotylenchus nannus Steiner 1945, Tylenchorhynchus claytoni Steiner 1937, and Criconemoides sp., and Nelmes (1974) terminated his experiments on predation by P.punctatus after several hours because of the aggregations formed by the prey, Aphelenchus avenae. These observations, and those discussed more fully in the micro-distribution section suggest that the ability to form mono-specific aggregations may be common to many nematode species and implies a means, probably chemical, of recognition. The survival value of such behaviour includes increased resistance to environmental extremes (e.g. A.avenae (Townshend, 1964), Rotylenchus robustus (Rossner, 1971), and Tylenchorhynchus martini Fielding 1956 (Hollis, 1962)) and dispersal (e.g. some rhabditid species in mushroom compost (Staniland, 1957)), as well as leading to concentration at a food source. I believe this last to be the dominant factor leading to aggregation of predators but the inter-specific response by which predators encountering prey tend to remain in the vicinity of the encounter is also involved. Once prey are encountered the area is searched by the "shunting" behaviour described by Nelmes (1974) for P.punctatus but which is common to many other predators. A feature of aggregation is the effect on prey and predator densities: Nelmes (1974) suggested that predator "displacement" only decreased at "abnormally high nematode densities not usual in soil" (i.e. above 2,500 prey/$cm^3$). The results of this study suggest that, depending on the size of the aggregations, such nematode densities may be reached in soil. The displacement of a predator may also be affected by the absence of specific stimuli relating to predator aggregations i.e. the single predators used by Nelmes may have been "searching" for other predators as well as prey.

Another consequence of predator aggregation in soil is the increase in inter-and intra-specific competition and it is interesting to note that keen competition is another correlate of K-selection (Pianka, 1970). It is usual for soils to contain several mononchid species and competition might

be expected; that only one species can occupy any particular niche in a given habitat (Gause, 1934) is widely accepted and suggests that the competitive exclusion principle i.e. two species co-existing in nature are not in direct competition (Hardin, 1960), must apply to the predatory nematode community. In the micro-distribution study the predatory species were found to aggregate in the same place and therefore space was not a niche-separation factor. Food preferences are probably involved as M.sigmaturus was suggested to be omnivorous while the other species appear to prey almost entirely upon nematodes. The concept of the resource-continuum may be used to explain the co-existence of these predators i.e. that niche-separation is a function of qualitative differences in the prey of each predator, such as preferred prey-size; Anatonchus spp. appear to ingest most of their prey whole and are able to predate on larger nematodes (dorylaimids, mononchids) unavailable to P.punctatus or C.papillatus. The retrorse teeth of Anatonchus spp. may represent an adaptation to swallowing whole prey, as in some snakes and fishes that swallow their live prey whole. A similar optimum prey-size may also separate C.papillatus and P.punctatus but for some communities the concept of the "multi-dimensional niche" with an infinite number of dimensions (MacArthur, 1968) may need to be invoked.

If two populations are utilising the same resource-continuum with some overlap, yet the preferred portions of the resource (e.g. preference for particular prey sizes) are separate and genetically-determined, then the two populations will diverge further because of the increased reproduction of those individuals not in competition (Ricklefs, 1973). It seems likely that this mechanism has contributed to mononchid speciation and the number of species suggests that some predator species may have adapted to particular prey or at least prey-size. It is also advantageous to the predators to increase the number of predation-strategies as the adaptations of the prey to avoid predation can only effectively cope with a relatively few types of predation i.e. as the number of predation-strategies increases, prey

adaptations become more compromised and less effective (Ricklefs, 1973). Increased knowledge of the specialisations against predation displayed by plant parasitic nematodes and the predation strategies of each predatory nematode species, would increase the probability of selecting the most effective predator for use in controlling a particular pest nematode.

The stability of predator populations may be related to the several species of predators normally found in soils as Watt (1964, 1965) found that the stability of the members of a trophic layer "(1) increases with the number of competitor species at that level, (2) decreases with the number of competing species that feed upon it, and (3) decreases with the proportion of the environment containing useful food". Possibly the fluctuations in free-living nematode populations, which appear to be more susceptible to predation than the more stable plant parasitic nematodes (Small, unpubl.) are also related to the mixed predator population. The third of Watt's maxims suggests that predator populations would be unstable if much of their environment were potential food. Since it has been suggested that predators congregate around aggregations of prey but that their populations remain stable, it seems likely that they feed only on some prey species.

I have suggested that an intra-specific stimulus limits the predator population. I wish now to consider the evidence, obtained mainly from culturing experiments, for how this mechanism, and that leading to aggregation, may operate. The results of the culturing experiments were discussed in terms of the relative concentrations of specific factors that stimulated and/or inhibited P.punctatus population growth. The chemical nature of the proposed "factors" was not investigated but as the evidence suggested that the predators themselves were the source, the known secretions and excretions of nematodes may be considered possible candidates. Ammonia, urea and carbon dioxide are all consistent with the known physical characteristics of the proposed factor e.g. water soluble and dialysable. Carbon dioxide is attractive to some plant parasitic nematodes (Green, 1971) but the

ammonium ion does not attract Caenorhabditis elegans (Ward, 1973) and inhibited hatching of Heterodera glycines Ichinohe 1952 eggs (Lehman, 1969). In the absence of detailed information on nematode (particularly predator) excretory products it is not possible to discuss the proteins, peptides and free amino acids that some nematodes excrete (Wright and Newall, 1976) but Joshi et al. (1974) recorded that four amino acids and three vitamins produced by a Vibrio sp. were attractive to Pelodera chitwoodi (Bassen, 1940) Dougherty 1955, although other unidentified chemicals were also involved. I suggest that carbon dioxide and/or ammonia should be tested as the most likely metabolites to affect P.punctatus population growth and lead to general nematode aggregation.

The simple excretory products discussed above probably represent the inhibitory factor; the chemical nature of the stimulatory factor is more difficult to consider but is more likely to be a predator-specific excretion (protein, peptide, free amino-acid) or secretion, rather than a widespread end-product of animal metabolism such as ammonia or carbon-dioxide. That specific substances can be detected by the predators is witnessed by the infrequency of cannibalism whilst attacks on closely related species (e.g. M.aquaticus and P.punctatus) are frequent. Many organic and inorganic molecules are known to be attractive to soil-dwelling nematodes, or to stimulate hatching or moulting (reviewed by Green, 1971 and Shepherd and Clarke, 1971 respectively) and any of these, and probably many others, may influence P.punctatus populations. Evidence of conditioning of agar media by nematodes has been recorded e.g. Caenorhabditis briggsae offspring developed faster than their parents (Dougherty et al., 1959), Rhabditis belari Nigon 1949 males were less frequent in old cultures (Nigon, 1952) whereas more dauer larvae, males and amphimictic reproduction occurred in crowded cultures of Caenorhabditis briggsae (Yarwood and Hansen, 1969). Similar effects were observed in cultures of M.aquaticus when males were found in old, crowded and poorly-fed cultures (Small and Grootaert, in press).

The range of possible stimulants and depressants may be extended by considering the chemicals in soil- and humus-extracts. The latter especially is likely to contain ammonia, carbon-dioxide and organic acids as well as proteins and amino-acids. It seems that the presence of one or more of these substances improves the culture properties of fresh agar. That the extract itself is the important component was suggested by the lack of a stimulatory effect of water agar; the variable results obtained with water agar may relate to the density of predators i.e. whether sufficient were present to produce a low concentration of stimulant before the effects of its absence were manifest.

It is also possible that the predators and/or prey modified the medium physically rather than chemically; the softness of the agar increased in older cultures and nematode movement became easier. The pH of old cultures was not substantially different from the fresh medium but the slightly more acid conditions may have been beneficial. These factors do not explain the differences between fresh soil-extract agar and fresh water agar however, as both had the same agar concentration and a similar pH.

In the discussion of possible factors I have deliberately selected the more simple mechanisms but it is possible that the mechanism is far more complex, either because the number of factors is greater or because specific secretions of the predators, are involved. The complexity will also be increased by the soil-environment; in agar excretory products can accumulate until toxic levels are reached whereas in soil, diffusion and the breakdown of the molecules by micro-organisms will cause a rapid decrease in the effect of even a large nematode aggregation. The concentration gradient of a chemical diffusing from a point source in soil is three-dimensional and is unlikely to extend more than 2-10cm which is the distance at which most plant parasitic nematodes can detect and orientate to the roots of the host-plant (Green, 1971). Within this distance several aggregations of predators and prey probably occur, and the gradients of each will merge. Nonetheless

aggregations of predators and prey were recorded and once an aggregation is formed, external or self-produced population stimulants or depressants could operate.

Finally the implications of the proposals discussed above for the potential use of predatory nematodes as biological control agents will be considered. In most soils several predatory nematode species co-exist. As plant-parasitic nematodes are successfully attacked a degree of natural control occurs, but is mitigated by predation on free-living nematodes and the various predation-avoidance adaptations found in both prey groups. The generally K-selected characteristics exhibited by most predators suggest that they would not respond by rapid increase in numbers to sudden increases in available prey e.g. the hatch of some plant-parasitic nematode eggs in response to host-plant root diffusates. Other features of predator biology can be compared to the attributes of some already proven biological control agents: predatory nematode fecundity is low and developmental period long compared to many plant-parasitic nematodes. The reproductive cycle does not appear to be linked to that of the plant-parasitic nematodes, although detailed information is lacking. Consideration of the predation characteristics of predatory nematodes is no more encouraging: without a distance-chemical sense the ability to locate prey is probably poor, especially when the "prey" consists only of the pest, although the ability to survive in the absence of the target organism will be increased by non pest-specific predation. The final attribute of a good biological control agent is that it should occupy all the micro-habitats occupied by the pest; whilst both predators and some stages of the pests are soil-dwelling the predators do not enter the roots in search of prey (with the possible exception of entering lesions when the "control" achieved will be too late). Some of the attributes, particularly those related to reproduction, are possessed by Seinura spp. (Hechler and Taylor, 1966a) but the small size of these

nematodes may reduce the number of phytoparasitic species that they can attack successfully. In general therefore, predatory nematodes do not possess many of the attributes normally associated with successful biological control agents, but as biological control of soil nematodes has not been attempted these attributes may be less important than in other biological control situations. More information is needed on the size and regulation of predator populations and their micro-distribution in the soil; if aggregations occur in the vicinity of roots the ability to search out prey is less important and the potential value of predators is considerably greater than if the population was distributed at random or aggregated away from roots. Information is also needed on prey preferences and the susceptibility of potential prey to attack. The pot experiments suggested that a large measure of control was possible under optimal conditions; the use of predatory nematodes in the controlled environment of glasshouses (where potential targets include Meloidogyne spp., Pratylenchus spp., and Ditylenchus spp. (Hague, 1972)) or mushroom houses (Aphelenchoides spp., Ditylenchus spp. (Hesling, 1972)), is therefore more feasible than their use in field situations.

Natural control can be increased by either adding more individuals of a predatory species already present in the soil, or by introducing a new predatory species. If such programmes were attempted, what effect would it have on predator populations? The pot experiments suggested that the effect of adding large numbers of predators would be short-lived and within a few months predator numbers would have returned to their previous level; this method seems unlikely to give adequate control unless timed to precisely coincide with the emergence of the pest. Even if control was achieved, annual additions would be necessary and many of the economic advantages of biological control compared to chemical control would be lost. As the decrease in inoculated numbers occurs rapidly, the natural population of predators

is unlikely to be greatly affected, although species in direct competition are likely to be temporarily suppressed.

The second method may have more durable effects: greater competition and specialisation to narrower portions of the resource-continuum are likely to result and the overall advantage for biological control is slight. With time the greater specialisation may allow the original populations to recover their former numbers even with the new species, and the advantage of more predator-strategies may result in greater natural control e.g. the addition of a large predator that ingests prey whole may increase predation on species resistant to attacks by smaller predators.

It is also interesting to speculate upon the effect of the arrival of a new prey species to a community; the range of many introduced nematode pests is still increasing, either by natural migration or by chance introductions. Two contradictory factors were involved in a cost-benefit analysis of the addition of a new prey species to the diet of a predator (MacArthur and Pianka, 1966): i) an increase in the number of individual prey potentially available and ii) a decrease in the average ease-of-capture and food value of the prey (because it was assumed that the best prey would be taken first). Thus the diet of a predator is broadened until the increase in capture-effort caused by the addition of a new prey species to the diet more than offsets the advantage of decreased search time. This analysis is not strictly applicable when a new prey species appears in a community for the first time, as it may represent a better prey in terms of capture-effort required and food value to the predator. It would be disadvantageous for a predator to decrease the number of prey species that it can attack and a new introduction may result in the broadening of the diet and possibly larger predator populations.

If the new species is well adapted to the host plant it may suffer little competition, especially if the host is also new to the habitat. The competition pressure on the existing plant parasitic nematode species

will probably be intensified; how great the competition becomes depends on the feeding habits of these original species. A new plant parasitic nematode and host will not greatly affect free-living nematodes, but competition with most unspecialised root-feeding nematodes, and particularly with host-specific endoparasites, will increase. This last group is likely to be displaced unless its host is grown within the nematode's survival-period. In effect the resource-continuum of the specialised endoparasites will be replaced by a new resource-continuum that they are unable to exploit.

The preceding discussion is necessarily based on the biology of the few predators that have been studied in any detail and may not apply to many cursorily- or un-studied predators. In most examples of successful biological control the agent was obtained from within the original geographical range of the pest where predators, parasites and pathogens associated with the pest are most likely to have evolved (DeBach, 1964; Huffaker, 1971). In the same way it may be possible to find predatory nematodes adapted to specific plant parasitic nematodes; further study would at least indicate the most voracious and most fecund predators which might be better suited as biological control agents than the predators studied to date. Combinations of two or more predatory species may also be more effective than a single predatory species as appeared to be the case in the M.incognita experiment.

I have attempted to describe the picture of predatory nematodes in soil suggested by the results of this study; a few concluding generalisations can be made. Most predatory nematodes are aggregated and it seems likely that the aggregations are related to the distribution of prey. The prey are also aggregated, probably around the roots or decomposing organic matter that represent their food sources. Although these aggregations consist of mixed populations, the ability to detect another nematode of the same species appears widespread and may represent one or more adaptations to survival, not least the avoidance of cannibalism amongst the predators. The populations

of predators are generally small in comparison with other nematode trophic groups but represent the carrying-capacity of the habitat for the predators; to prevent the predator population exceeding this capacity, which would lead to their local extinction, the predators have evolved several population-limiting strategies including delayed maturation and a disposable excess of second-stage juveniles under unfavourable conditions. The stability of the predator populations is increased by the several species in that trophic level and reflects the K-selected characteristics shown by most predators. These features, and the results of the pot experiments, suggest that at best, biological control of plant parasitic nematodes using predatory nematodes will be restricted to the controlled environments of glasshouses or mushroom-houses.

Methods of rearing predatory nematode populations sufficient for most laboratory or pot experiments have been developed and the groups of plant parasitic nematodes that should be selected for further study have been indicated. This study has also inaugurated the study of the micro-distribution of soil-dwelling nematodes and its relevance to their behaviour and biology.

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# APPENDIX 1. VALUES OF THE DISPERSION INDICES.

Appendix 1 - Values of the dispersion indices.

| | | | |
|---|---|---|---|
| Tables 1-11: | Samples taken 16-12-74; | Sample size 5x5x5cm | |
| Tables 12-21: | Samples taken 16-12-74; | Sample size 10x10x5cm | |
| Tables 22-28: | Samples taken 16-12-74; | Sample size 15x15x5cm | |
| Tables 29-33: | Samples taken 4-2-75; | Sample size 1x1x1cm | |
| Tables 34-36: | Samples taken 4-2-75; | Sample size 1x1x1cm; | Vertical Slices |
| Tables 37-41: | Samples taken 4-2-75; | Sample size 2x2x1cm | |
| Tables 42-45: | Samples taken 4-2-75; | Sample size 3x3x1cm | |
| Tables 46-58: | Samples taken 13-4-76; | Sample size 1x1x1cm | |
| Tables 59-71: | Samples taken 13-4-76; | Sample size 2x2x1cm | |
| Tables 72-82: | Samples taken 13-4-76; | Sample size 3x3x1cm | |

Abbreviations used in the tables:

| Abbreviation | Meaning |
|---|---|
| V.M.R. | Variance-mean Ratio |
| L.D.I. | Lexis Disturbance Index |
| D.M.I. | David and Moore (1954) Index |
| G.I. | Green (1966) Index |
| I.C.I. | Imperial College (1968) Index |
| C.D.F.E. | Cancela da Fonseca (1966) E Index |
| C.D.F.1A. | Cancela da Fonseca (1966) 1A Index |
| C.I. | Cole (1946) Index |
| M.I. | Morisita (1959) Index |
| C.C. | Charlier Coefficient |
| B.F.I. | Bliss and Fisher k-1 Index |
| D. | Distribution |
| T. | Zero-frequency class truncated |
| Ra | Random |
| Re | Regular |
| A | Aggregated |
| * | p=0.05-0.01 |
| ** | p=0.01-0.001 |

Values of the indices of dispersion at maximum regularity, randomness, and maximum contagion.

n = number of sampling units; $\bar{x}$ = sample mean; $S^2$ = sample variance; Ex = total number.

| Index | Formula | Max. Reg. | Random | Max. Cont. | Reference |
|---|---|---|---|---|---|
| Variance-Mean Ratio | $\frac{S^2}{\bar{x}}$ | 0 | 1 | Ex | |
| Lexis Disturbance Index | $\sqrt{\frac{S}{\bar{x}}}$ | 0 | 1 | $\sqrt{Ex}$ | Beall, 1935 |
| David and Moore Index | $\frac{S^2}{\bar{x}}-1$ | -1 | 0 | Ex-1 | David and Moore, 1954 |
| Green Index | $\frac{(S^2/\bar{x})-1}{Ex-1}$ | $-\frac{1}{Ex-1}$ | 0 | 1 | Green, 1966 |
| Imperial College Index | $1+\frac{1}{\bar{x}}$ | $\frac{(\bar{x}-1)}{\bar{x}}$ | 1 | $n+\frac{(\bar{x}-1)}{x}$ | Robles 1969 |
| Cancela da Fonseca E | $\bar{x}-\sqrt{\frac{S^2}{n}}$ | $\bar{x}$ | $\bar{x}-\sqrt{\frac{\bar{x}}{n}}$ | 0 | Cancela da Fonseca 1966 |
| Cancela da Fonseca 1A | $\sqrt{\frac{S^2/n}{\bar{x}}}$ | 0 | $\frac{1}{\sqrt{Ex}}$ | 1 | Cancela da Fonseca 1966 |
| Cole Index | $\frac{Ex^2}{(Ex)^2}$ | $\frac{1}{n}$ | $\frac{1}{n}+\frac{n-1}{n}(\frac{1}{Ex})$ | 1 | Cole 1946 b |
| Morisita Index | $n\frac{Ex^2-Ex}{(Ex)^2-Ex}$ | $1-\frac{n-1}{Ex-1}$ | 1 | n | Morisita 1959 |
| Charlier Coefficient | $100\sqrt{\frac{S^2-\bar{x}}{\bar{x}}}$ | Imaginary | 0 | $100n(1-\frac{1}{Ex})$ | Beall, 1935 |
| Bliss & Fisher Index | k-1 negative binomial | $-(\bar{x}-1)$ | $\pm\infty$ | $\frac{1}{n}(1+\frac{1}{Ex-1})$ | Bliss and Fisher, 1953 |

Each group has been assigned to a particular distribution (random, regular, aggregated) on the basis of the agreement of the variance-mean ratio with that expected from a Poisson series. This was tested by means of a $\underline{\chi}^2$ test in which an estimate of $\underline{\chi}^2$ is obtained from

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

which was compared to the percentage points of $\underline{\chi}^2$ in Table 8 of Pearsen and Hartley 1954 (Vol 1), with n-1 degrees of freedom. The probability level chosen were the 95% limits of $s^2/x$ agreeing with the expected value from a Poisson series. The probability levels of non-Poisson distributions have been included in the tables.

TABLE 1. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS MALES | | 0-5 | 1.26 | 1.12 | 0.26 | 0.02 | 1.33 | 0.58 | 0.28 | 0.13 | 1.33 | 57.35 | 3.04 | Ra |
| " " | T | 0-5 | 0.44 | 0.66 | -0.56 | -0.04 | 0.65 | 1.33 | 0.17 | 0.13 | 0.67 | I.V. | -2.88 | Ra |
| " " | | 20-25 | 1.14 | 1.07 | 0.14 | 0.04 | 1.43 | 0.17 | 0.48 | 0.28 | 1.50 | 65.47 | 2.33 | Ra |
| " " | T | 20-25 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS FEMALES | | 0-5 | 0.86 | 0.93 | -0.14 | -0.01 | 0.74 | 0.40 | 0.28 | 0.12 | 0.73 | I.V. | -3.83 | Ra |
| " " | | 5-10 | 1.37 | 1.17 | 0.37 | 0.12 | 2.84 | 0.08 | 0.58 | 0.38 | 3.33 | 135.72 | 0.54 | Ra |
| " " | T | 5-10 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Re ** |
| " " | | 15-20 | 1.18 | 1.09 | 0.18 | 0.03 | 1.39 | 0.27 | 0.41 | 0.22 | 1.43 | 62.74 | 2.54 | Ra |
| " " | T | 15-20 | 0.21 | 0.46 | -0.79 | -0.13 | 0.44 | 1.16 | 0.17 | 0.22 | 0.48 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |

TABLE 1. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATOLE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS JUVENILES | | 0-5 | 6.69 | 2.59 | 5.69 | 0.03 | 1.65 | 7.04 | 0.20 | 0.09 | 1.62 | 80.62 | 1.54 | A** |
| " " | T | 0-5 | 6.22 | 2.49 | 5.22 | 0.03 | 1.57 | 7.47 | 0.19 | 0.09 | 1.54 | 75.28 | 1.76 | A** |
| " " | | 5-10 | 1.27 | 1.13 | 0.27 | 0.02 | 1.32 | 0.62 | 0.27 | 0.12 | 1.32 | 56.61 | 3.12 | Ra |
| " " | T | 5-10 | 0.40 | 0.63 | -0.60 | -0.04 | 0.65 | 1.44 | 0.15 | 0.12 | 0.66 | I.V. | -2.83 | Ra |
| " " | | 10-15 | 1.21 | 1.10 | 0.21 | 0.008 | 1.11 | 1.48 | 0.21 | 0.11 | 1.11 | 33.88 | 8.71 | Ra |
| " " | T | 10-15 | 0.73 | 0.85 | -0.27 | -0.01 | 0.88 | 1.96 | 0.16 | 0.11 | 0.89 | I.V. | -8.56 | Ra |
| " " | | 15-20 | 1.46 | 1.21 | 0.46 | 0.01 | 1.22 | 1.68 | 0.21 | 0.11 | 1.21 | 46.65 | 4.59 | Ra |
| " " | T | 15-20 | 0.91 | 0.95 | -0.09 | -0.003 | 0.97 | 2.22 | 0.17 | 1.09 | 0.97 | I.V. | -29.33 | Ra |
| " " | | 20-25 | 3.11 | 1.76 | 2.11 | 0.04 | 1.28 | 2.68 | 0.24 | 0.12 | 1.57 | 77.24 | 1.68 | A** |
| " " | T | 20-25 | 2.55 | 1.60 | 1.55 | 0.03 | 1.38 | 3.18 | 0.22 | 0.12 | 1.36 | 61.73 | 2.62 | A** |
| | | | | | | | | | | | | | | |

TABLE 3. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS TOTAL | | 0-5 | 7.29 | 2.70 | 6.29 | 0.03 | 1.62 | 8.18 | 0.19 | 0.08 | 1.59 | 78.94 | 1.60 | A** |
| " " | | 5-10 | 1.49 | 1.22 | 0.49 | 0.02 | 1.43 | 0.86 | 0.25 | 0.11 | 1.42 | 65.26 | 2.35 | Ra |
| " " | T | 5-10 | 0.71 | 0.84 | -0.29 | -0.01 | 0.85 | 1.58 | 0.18 | 0.11 | 0.85 | I.V, | -6.55 | Ra |
| " " | | 10-15 | 1.57 | 1.25 | 0.57 | 0.02 | 1.29 | 1.54 | 0.23 | 0.12 | 1.28 | 53.45 | 3.50 | Ra |
| " " | T | 10-15 | 1.05 | 1.03 | 0.05 | 0.002 | 1.02 | 2.03 | 0.19 | 0.12 | 1.02 | 14.77 | 45.83 | Ra |
| " " | | 15-20 | 1.59 | 1.26 | 0.59 | 0.01 | 1.22 | 2.19 | 0.20 | 0.10 | 1.21 | 46.55 | 4.61 | Ra |
| " " | T | 15-20 | 0.88 | 0.94 | -0.12 | -0.003 | 0.96 | 2.92 | 0.15 | 0.10 | 0.97 | 19.06 | -27.52 | Ra |
| " " | | 20-25 | 1.49 | 1.22 | 0.49 | 0.009 | 1.14 | 2.94 | 0.17 | 0.09 | 1.13 | 37.26 | 7.29 | Ra |
| " " | T | 20-25 | 1.23 | 1.11 | 0.23 | 0.004 | 1.06 | 3.21 | 0.15 | 0.09 | 1.06 | 24.46 | 16.72 | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 4. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS MALES | | 0-5 | 3.13 | 1.77 | 2.13 | 0.02 | 1.41 | 4.30 | 0.17 | 0.08 | 1.39 | 63.99 | 2.44 | A** |
| " " | T | 0-5 | 2.85 | 1.69 | 1.85 | 0.02 | 1.34 | 4.57 | 0.17 | 0.08 | 1.32 | 58.13 | 2.96 | A** |
| " " | | 5-10 | 2.66 | 1.63 | 1.66 | 0.04 | 1.74 | 1.70 | 0.24 | 0.11 | 1.72 | 85.92 | 1.35 | A** |
| " " | T | 5-10 | 1.68 | 1.30 | 0.68 | 0.02 | 1.21 | 2.59 | 0.19 | 0.11 | 1.20 | 46.12 | 4.70 | Ra |
| " " | | 10-15 | 2.20 | 1.48 | 1.20 | 0.07 | 1.94 | 0.84 | 0.34 | 0.17 | 1.93 | 97.15 | 1.06 | A** |
| " " | T | 10-15 | 1.36 | 1.16 | 0.36 | 0.02 | 1.17 | 1.55 | 0.27 | 0.17 | 1.16 | 41.02 | 5.94 | Ra |
| " " | | 15-20 | 1.14 | 1.07 | 0.14 | 0.01 | 1.15 | 0.67 | 0.29 | 0.14 | 1.15 | 39.12 | 6.53 | Ra |
| " " | T | 15-20 | 0.50 | 0.71 | -0.50 | -0.04 | 0.68 | 1.26 | 0.19 | 0.14 | 0.69 | I.V. | -3.11 | Ra |
| " " | | 20-25 | 1.49 | 1.22 | 0.49 | 0.08 | 2.05 | 0.25 | 0.46 | 0.27 | 2.14 | 102.45 | 0.95 | Ra |
| " " | T | 20-25 | 0.57 | 0.76 | -0.43 | -0.07 | 0.69 | 1.00 | 0.29 | 0.27 | 0.71 | I.V. | -3.27 | Ra |
| | | | | | | | | | | | | | | |

TABLE 5. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS GRAVID FEMALES | | 0-5 | 1.18 | 1.08 | 0.18 | 0.004 | 1.07 | 2.16 | 0.15 | 0.07 | 1.07 | 26.23 | 14.54 | Ra |
| " " | T | 0-5 | 1.04 | 1.02 | 0.04 | 0.0007 | 1.01 | 2.30 | 0.14 | 0.07 | 1.01 | 11.75 | 72.47 | Ra |
| " " | | 5-10 | 0.83 | 0.91 | -0.17 | -0.01 | 0.82 | 0.75 | 0.21 | 0.09 | 0.82 | I.V. | -5.53 | Ra |
| " " | | 10-15 | 3.18 | 1.78 | 2.18 | 0.31 | 5.08 | 0.20 | 0.63 | 0.44 | 5.36 | 202.11 | 0.24 | A** |
| " " | T | 10-15 | 2.00 | 1.41 | 1.00 | 0.14 | 1.50 | 1.00 | 0.50 | 0.44 | 1.43 | 70.71 | 2.00 | Ra |
| " " | | 15-20 | 0.88 | 0.94 | -0.12 | -0.02 | 0.74 | 0.30 | 0.35 | 0.18 | 0.71 | I.V. | -3.81 | Ra |
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TABLE 6. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS NON-GRAVID FEMALES | | 0-5 | 1.38 | 1.18 | 0.38 | 0.004 | 1.08 | 4.04 | 0.12 | 0.06 | 1.08 | 28.82 | 12.04 | Ra |
| " " | T | 0-5 | 1.13 | 1.06 | 0.13 | 0.001 | 1.03 | 4.31 | 0.11 | 0.06 | 1.03 | 16.41 | 37.12 | Ra |
| " " | | 5-10 | 2.46 | 1.57 | 1.46 | 0.03 | 1.57 | 1.99 | 0,22 | 0.10 | 1.55 | 75.54 | 1.75 | A** |
| " " | T | 5-10 | 1.81 | 1.34 | 0.81 | 0.02 | 1.25 | 2.59 | 0.19 | 0.10 | 1.24 | 50.34 | 3.95 | Ra |
| " " | | 10-15 | 2.43 | 1.56 | 1.43 | 0.05 | 1.71 | 1.43 | 0.28 | 0.14 | 1.69 | 84.52 | 1.40 | A** |
| " " | T | 10-15 | 1.93 | 1.39 | 0.93 | 0.03 | 1.37 | 1.87 | 0.25 | 0.14 | 1.35 | 60.90 | 2.70 | Ra |
| " " | | 15-20 | 1.51 | 1.23 | 0.51 | 0.02 | 1.23 | 1.73 | 0.21 | 0.11 | 1.22 | 47.98 | 4.34 | Ra |
| " " | T | 15-20 | 0.93 | 0.97 | -0.07 | -0.002 | 0.98 | 2.29 | 0.17 | 0.11 | 0.98 | I.V. | -41.59 | Ra |
| " " | | 20-25 | 1.60 | 1.27 | 0.60 | 0.05 | 1.65 | 0.62 | 0.34 | 0.17 | 1.65 | 80.31 | 1.55 | Ra |
| " " | T | 20-25 | 0.78 | 0.88 | -0.22 | -0.02 | 0.87 | 1.34 | 0.24 | 0.17 | 0.88 | I.V. | -7.80 | Ra |
| | | | | | | | | | | | | | | |

TABLE 7. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL FEMALES | | 0-5 | 1.67 | 1.29 | 0.67 | 0.005 | 1.09 | 6.38 | 0.11 | 0.06 | 1.09 | 30.56 | 10.71 | Ra |
| " " | | 5-10 | 2.48 | 1.58 | 1.48 | 0.02 | 1.42 | 2.84 | 0.19 | 0.08 | 1.41 | 65.05 | 2.36 | A** |
| " " | T | 5-10 | 2.29 | 1.51 | 1.29 | 0.02 | 1.35 | 3.02 | 0.18 | 0.08 | 1.34 | 59.26 | 2.85 | A** |
| " " | | 10-15 | 4.67 | 2.16 | 3.67 | 0.1 | 2.45 | 1.64 | 0.35 | 0.18 | 2.39 | 120.41 | 0.69 | A** |
| " " | T | 10-15 | 4.07 | 2.02 | 3.07 | 0.08 | 1.97 | 2.13 | 0.33 | 0.18 | 1.91 | 98.41 | 1.03 | A** |
| " " | | 15-20 | 1.48 | 1.22 | 0.48 | 0.01 | 1.18 | 2.15 | 0.19 | 0.10 | 1.17 | 42.52 | 5.53 | Ra |
| " " | T | 15-20 | 1.28 | 1.13 | 0.28 | 0.007 | 1.10 | 2.35 | 0.18 | 0.10 | 1.09 | 31.56 | 10.04 | Ra |
| " " | | 20-25 | 1.94 | 1.39 | 0.94 | 0.06 | 1.88 | 0.70 | 0.35 | 0.18 | 1.88 | 93.75 | 1.14 | A* |
| " " | T | 20-25 | 1.00 | 1.00 | 0 | 0 | 1.00 | 1.50 | 0.25 | 0.18 | 1.00 | 0 | $\rightarrow \infty$ | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 8. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS JUVENILES | | 0-5 | 3.85 | 1.96 | 2.85 | 0.007 | 1.15 | 17.37 | 0.10 | 0.06 | 1.14 | 38.40 | 6.78 | A** |
| " " | | 5-10 | 4.22 | 2.06 | 3.22 | 0.01 | 1.19 | 14.82 | 0.11 | 0.06 | 1.18 | 43.94 | 5.18 | A** |
| " " | | 10-15 | 8.11 | 2.85 | 7.11 | 0.03 | 1.44 | 13.24 | 0.18 | 0.10 | 1.41 | 66.23 | 2.28 | A** |
| " " | | 15-20 | 4.52 | 2.13 | 3.52 | 0.02 | 1.32 | 9.24 | 0.17 | 0.09 | 1.30 | 56.43 | 3.14 | A** |
| " " | | 20-25 | 6.45 | 2.54 | 5.45 | 0.04 | 1.66 | 6.32 | 0.23 | 0.12 | 1.63 | 81.52 | 1.50 | A** |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-5 | 4.68 | 2.16 | 3.68 | 0.006 | 1.12 | 28.93 | 0.09 | 0.06 | 1.11 | 34.12 | 8.59 | A** |
| " " | | 5-10 | 6.61 | 2.57 | 5.61 | 0.01 | 1.25 | 19.73 | 0.12 | 0.06 | 1.24 | 49.98 | 4.00 | A** |
| " " | | 10-15 | 9.86 | 3.14 | 8.86 | 0.03 | 1.44 | 16.37 | 0.18 | 0.10 | 1.41 | 66.55 | 2.26 | A** |
| " " | | 15-20 | 4.97 | 2.23 | 3.97 | 0.02 | 1.27 | 12.46 | 0.15 | 0.09 | 1.25 | 52.05 | 3.69 | A** |
| " " | | 20-25 | 7.73 | 2.78 | 6.73 | 0.05 | 1.69 | 7.49 | 0.23 | 0.12 | 1.65 | 83.13 | 1.45 | A** |

TABLE 9. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS GRAVID FEMALES | | 0-5 | 1.33 | 1.15 | 0.33 | 0.007 | 1.13 | 2.09 | 0.16 | 0.08 | 1.13 | 36.13 | 7.66 | Ra |
| " " | T | 0-5 | 1.04 | 1.02 | 0.04 | 0.0008 | 1.01 | 2.38 | 0.14 | 0.08 | 1.01 | 12.00 | 6.94 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS NON-GRAVID FEMALES | | 0-5 | 7.38 | 2.72 | 6.38 | 0.07 | 2.45 | 3.13 | 0.29 | 0.13 | 2.39 | 120.40 | 0.69 | A** |
| " " | T | 0-5 | 5.03 | 2.24 | 4.03 | 0.05 | 1.59 | 5.15 | 0.24 | 0.13 | 1.56 | 77.12 | 1.68 | A** |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 0-5 | 5.78 | 2.40 | 4.78 | 0.03 | 1.69 | 5.49 | 0.20 | 0.09 | 1.66 | 83.23 | 1.44 | A** |
| " " | T | 0-5 | 5.00 | 2.24 | 4.00 | 0.03 | 1.52 | 6.21 | 0.19 | 0.09 | 1.50 | 72.25 | 1.92 | A** |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 10. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS JUVENILES | | 0-5 | 57.60 | 7.59 | 56.60 | 0.07 | 2.44 | 28.57 | 0.27 | 0.12 | 2.37 | 120.16 | 0.69 | A** |
| " " | | 5-10 | 5.31 | 2.30 | 4.31 | 0.13 | 3.61 | 0.99 | 0.40 | 0.20 | 3.56 | 161.67 | 0.38 | A** |
| " " | T | 5-10 | 3.77 | 1.94 | 2.77 | 0.09 | 1.84 | 2.18 | 0.34 | 0.20 | 1.78 | 91.69 | 1.19 | A** |
| " " | | 10-15 | 5.39 | 2.32 | 4.39 | 0.40 | 6.49 | 0.26 | 0.67 | 0.49 | 6.59 | 234.33 | 0.18 | A** |
| " " | T | 10-15 | 3.78 | 1.94 | 2.70 | 0.25 | 1.93 | 1.32 | 0.56 | 0.49 | 1.76 | 96.22 | 1.08 | A* |
| " " | | 15-20 | 2.00 | 1.41 | 1.00 | 0.25 | 4.00 | 0.12 | 0.63 | 0.44 | 4.50 | 173.21 | 0.33 | A* |
| " " | T | 15-20 | 0.80 | 0.89 | -0.20 | -0.05 | 0.88 | 1.00 | 0.40 | 0.44 | 0.90 | I.V. | -8.33 | Ra |
| " " | | 20-25 | 1.32 | 1.15 | 0.32 | 0.11 | 2.21 | 0.11 | 0.57 | 0.38 | 2.50 | 109.79 | 0.83 | Ra |
| " " | T | 20-25 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 11. DATE 16-12-74. SAMPLE SIZE 5x5x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-5 | 58.76 | 7.67 | 57.76 | 0.06 | 2.24 | 34.86 | 0.25 | 0.11 | 2.18 | 111.39 | 0.81 | A** |
| " " | | 5-10 | 6.13 | 2.48 | 5.13 | 0.13 | 3.50 | 1.26 | 0.39 | 0.19 | 3.44 | 158.26 | 0.40 | A** |
| " " | T | 5-10 | 5.12 | 2.26 | 4.12 | 0.10 | 2.31 | 2.04 | 0.35 | 0.19 | 2.24 | 114.27 | 0.77 | A** |
| " " | | 10-15 | 5.73 | 2.39 | 4.73 | 0.36 | 6.07 | 0.34 | 0.64 | 0.45 | 6.10 | 225.23 | 0.20 | A** |
| " " | T | 10-15 | 4.36 | 2.09 | 3.36 | 0.26 | 2.20 | 1.24 | 0.56 | 0.45 | 2.03 | 109.50 | 0.83 | A** |
| " " | | 15-20 | 1.62 | 1.27 | 0.62 | 0.08 | 2.03 | 0.35 | 0.42 | 0.23 | 2.08 | 101.57 | 0.97 | Ra |
| " " | T | 15-20 | 0.39 | 0.62 | -0.61 | -0.08 | 0.66 | 1.43 | 0.21 | 0.23 | 0.69 | I.V. | -2.95 | Ra |
| " " | | 20-25 | 1.32 | 1.15 | 0.32 | 0.11 | 2.21 | 0.11 | 0.57 | 0.38 | 2.50 | 109.79 | 0.83 | Ra |
| " " | T | 20-25 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 12. DATE 16-12-74. SAMPLE SIZE 10x10x5. CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS MALES | | 0-5 | 1.35 | 1.16 | 0.35 | 0.01 | 1.08 | 3.29 | 0.20 | 0.16 | 1.08 | 28.98 | 11.91 | Ra |
| " " | | 5-10 | 0.91 | 0.95 | -0.09 | -0.02 | 0.82 | 0.31 | 0.39 | 0.22 | 0.80 | I.V. | -5.50 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS GRAVID FEMALES | | 0-5 | 0.29 | 0.53 | -0.71 | -0.05 | 0.64 | 1.73 | 0.13 | 0.14 | 0.67 | I.V. | -2.80 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS NON-GRAVID FEMALES | | 15-20 | 0.48 | 0.69 | -0.52 | -0.03 | 0.77 | 1.88 | 0.16 | 0.15 | 0.78 | I.V. | -4.30 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL FEMALES | | 0-5 | 0.23 | 0.48 | -0.77 | -0.04 | 0.69 | 2.23 | 0.11 | 0.14 | 0.72 | I.V. | -3.24 | Re* |
| " " | | 5-10 | 1.64 | 1.28 | 0.64 | 0.13 | 2.27 | 0.24 | 0.52 | 0.33 | 2.40 | 112.82 | 0.79 | Ra |
| " " | T | 5-10 | 0.67 | 0.82 | -0.33 | -0.07 | 0.78 | 1.00 | 0.33 | 0.33 | 0.80 | I.V. | -4.50 | Ra |
| " " | | 15-20 | 0.59 | 0.77 | -0.41 | -0.02 | 0.83 | 1.96 | 0.18 | 0.15 | 0.84 | I.V. | -5.85 | Ra |

TABLE 13. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS JUVENILES | | 0-5 | 6.89 | 2.62 | 5.89 | 0.02 | 1.16 | 30.89 | 0.15 | 0.15 | 1.14 | 40.17 | 6.20 | A** |
| " " | | 5-10 | 1.85 | 1.36 | 0.85 | 0.02 | 1.23 | 2.99 | 0.20 | 0.12 | 1.21 | 47.57 | 4.42 | Ra |
| " " | T | 5-10 | 1.49 | 1.22 | 0.49 | 0.01 | 1.12 | 3.35 | 0.18 | 0.12 | 1.11 | 34.57 | 8.37 | Ra |
| " " | | 10-15 | 1.20 | 1.10 | 0.20 | 0.004 | 1.03 | 5.63 | 0.15 | 0.14 | 1.03 | 17.58 | 32.34 | Ra |
| " " | | 15-20 | 0.63 | 0.80 | -0.37 | -0.005 | 0.96 | 8.15 | 0.09 | 0.13 | 0.96 | I.V. | -24.65 | Ra |
| " " | | 20-25 | 1.62 | 1.27 | 0.62 | 0.01 | 1.04 | 11.62 | 0.17 | 0.27 | 1.03 | 21.03 | 22.62 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 14. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS TOTAL | | 0-5 | 7.50 | 2.74 | 6.50 | 0.02 | 1.15 | 36.77 | 0.15 | 0.14 | 1.13 | 38.81 | 6.64 | A** |
| " " | | 5-10 | 2.39 | 1.55 | 1.39 | 0.03 | 1.30 | 3.70 | 0.21 | 0.12 | 1.28 | 54.57 | 3.36 | A* |
| " " | T | 5-10 | 1.94 | 1.39 | 0.94 | 0.02 | 1.19 | 4.14 | 0.19 | 0.12 | 1.17 | 43.04 | 5.40 | Ra |
| " " | | 10-15 | 1.51 | 1.23 | 0.51 | 0.009 | 1.07 | 5.85 | 0.16 | 0.15 | 1.06 | 27.00 | 13.72 | Ra |
| " " | | 15-20 | 0.40 | 0.64 | -0.60 | -0.006 | 0.95 | 11.22 | 0.06 | 0.13 | 0.96 | I.V. | -20.16 | Ra |
| " " | | 20-25 | 0.35 | 0.59 | -0.65 | -0.01 | 0.96 | 15.78 | 0.07 | 0.25 | 0.97 | I.V. | -26.27 | Ra |
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TABLE 15. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS MALES | | 0-5 | 4.07 | 2.02 | 3.07 | 0.02 | 1.15 | 17.50 | 0.16 | 0.15 | 1.13 | 38.48 | 6.75 | A** |
| " " | | 5-10 | 2.54 | 1.59 | 1.54 | 0.01 | 1.14 | 9.78 | 0.14 | 0.10 | 1.13 | 36.86 | 7.36 | A** |
| " " | | 10-15 | 0.90 | 0.95 | -0.10 | -0.004 | 0.97 | 2.87 | 0.18 | 0.15 | 0.97 | I.V. | -34.30 | Ra |
| " " | | 15-20 | 0.17 | 0.41 | -0.83 | -0.02 | 0.82 | 4.44 | 0.07 | 0.13 | 0.84 | I.V. | -5.69 | Re* |
| " " | | 20-25 | 2.27 | 1.51 | 1.27 | 0.14 | 1.51 | 1.31 | 0.48 | 0.42 | 1.42 | 71.18 | 1.97 | Ra |
| " " | T | 20-25 | 1.30 | 1.14 | 0.30 | 0.03 | 1.09 | 2.13 | 0.36 | 0.42 | 1.07 | 30.00 | 11.11 | Ra |
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TABLE 16. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS GRAVID FEMALES | | 0-5 | 0.30 | 0.54 | -0.70 | -0.01 | 0.92 | 8.06 | 0.07 | 0.13 | 0.93 | I.V. | -12.25 | Ra |
| " " | | 5-10 | 0.81 | 0.90 | -0.19 | -0.004 | 0.96 | 3.79 | 0.12 | 0.10 | 0.96 | I.V. | -22.95 | Ra |
| " " | | 10-15 | 2.69 | 1.64 | 1.69 | 0.17 | 2.23 | 0.70 | 0.49 | 0.34 | 2.18 | 110.81 | 0.81 | A* |
| " " | T | 10-15 | 2.27 | 1.51 | 1.27 | 0.13 | 1.69 | 1.00 | 0.45 | 0.34 | 1.64 | 83.32 | 1.44 | Ra |
| " " | | 15-20 | 0.43 | 0.65 | -0.57 | -0.04 | 0.71 | 1.67 | 0.16 | 0.15 | 0.73 | I.V. | -3.50 | Ra |
| " " | | 20-25 | 0.67 | 0.82 | -0.33 | -0.11 | 0.67 | 0.59 | 0.41 | 0.38 | 0.67 | I.V. | -3.00 | Ra |
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TABLE 17. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS NON-GRAVID FEMALES | | 0-5 | 1.46 | 1.21 | 0.46 | 0.004 | 1.03 | 14.29 | 0.11 | 0.14 | 1.03 | 17.03 | 34.46 | Ra |
| " " | | 5-10 | 2.35 | 1.53 | 1.35 | 0.009 | 1.11 | 10.94 | 0.13 | 0.10 | 1.10 | 32.85 | 9.27 | A* |
| " " | | 10-15 | 2.41 | 1.55 | 1.41 | 0.03 | 1.23 | 4.88 | 0.22 | 0.17 | 1.20 | 47.52 | 4.43 | A* |
| " " | | 15-20 | 0.47 | 0.69 | -0.53 | -0.007 | 0.95 | 8.87 | 0.08 | 0.13 | 0.95 | I.V. | -18.27 | Ra |
| " " | | 20-25 | 0.67 | 0.82 | -0.33 | -0.006 | 0.98 | 16.31 | 0.11 | 0.34 | 0.99 | I.V. | -56.02 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL FEMALES | | 0-5 | 1.39 | 1.18 | 0.39 | 0.002 | 1.02 | 22.56 | 0.08 | 0.13 | 1.01 | 12.61 | 62.88 | Ra |
| " " | | 5-10 | 2.40 | 1.55 | 1.40 | 0.007 | 1.08 | 15.00 | 0.11 | 0.09 | 1.08 | 28.80 | 12.06 | A* |
| " " | | 10-15 | 4.19 | 2.05 | 3.19 | 0.05 | 1.42 | 5.63 | 0.26 | 0.19 | 1.37 | 64.73 | 2.39 | A** |
| " " | | 15-20 | 0.51 | 0.72 | -0.49 | -0.005 | 0.96 | 10.76 | 0.07 | 0.13 | 0.96 | I.V. | -23.95 | Ra |
| | | | | | | | | | | | | | | |

TABLE 18. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS JUVENILES | | 0-5 | 14.06 | 3.75 | 13.06 | 0.02 | 1.18 | 61.33 | 0.16 | 0.15 | 1.16 | 42.40 | 5.56 | A** |
| " " | | 5-10 | 3.52 | 1.88 | 2.52 | 0.003 | 1.04 | 66.76 | 0.06 | 0.09 | 1.03 | 18.81 | 28.27 | A** |
| " " | | 10-15 | 11.29 | 3.36 | 10.29 | 0.02 | 1.17 | 49.99 | 0.15 | 0.15 | 1.15 | 41.71 | 5.75 | A** |
| " " | | 15-20 | 5.21 | 2.28 | 4.21 | 0.01 | 1.09 | 42.64 | 0.12 | 0.14 | 1.08 | 29.54 | 11.46 | A** |
| " " | | 20-25 | 0.77 | 0.88 | -0.23 | -0.001 | 0.99 | 38.91 | 0.07 | 0.25 | 1.00 | I.V. | -183.48 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-5 | 18.96 | 4.35 | 17.96 | 0.02 | 1.15 | 102.21 | 0.14 | 0.14 | 1.13 | 38.84 | 6.63 | A** |
| " " | | 5-10 | 5.72 | 2.39 | 4.72 | 0.004 | 1.05 | 90.84 | 0.07 | 0.09 | 1.04 | 21.99 | 20.69 | A** |
| " " | | 10-15 | 13.84 | 3.72 | 12.84 | 0.02 | 1.18 | 59.23 | 0.16 | 0.15 | 1.16 | 42.74 | 5.47 | A** |
| " " | | 15-20 | 5.26 | 2.29 | 4.26 | 0.008 | 1.07 | 58.11 | 0.10 | 0.13 | 1.06 | 25.68 | 15.17 | A** |
| " " | | 20-25 | 0.88 | 0.94 | -0.12 | -0.0006 | 1.00 | 47.66 | 0.07 | 0.25 | 1.00 | I.V. | -410.68 | Ra |

TABLE 19. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS GRAVID FEMALES | | 0-5 | 0.63 | 0.79 | -0.37 | -0.005 | 0.96 | 8.63 | 0.09 | 0.13 | 0.97 | I.V. | -25.79 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS NON-GRAVID FEMALES | | 0-5 | 2.71 | 1.64 | 1.71 | 0.02 | 1.13 | 10.67 | 0.16 | 0.15 | 1.12 | 36.58 | 7.47 | A* |
| " " | | 5-10 | 1.73 | 1.31 | 0.73 | 0.09 | 1.97 | 0.42 | 0.44 | 0.26 | 2.00 | 98.47 | 1.03 | Ra |
| " " | T | 5-10 | 1.00 | 1.00 | 0 | 0 | 1.00 | 1.00 | 0.33 | 0.26 | 1.00 | 0 | $\rightarrow \infty$ | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 0-5 | 1.83 | 1.35 | 0.83 | 0.005 | 1.04 | 19.76 | 0.10 | 0.13 | 1.03 | 19.44 | 26.47 | Ra |
| " " | | 5-10 | 1.41 | 1.19 | 0.41 | 0.03 | 1.31 | 0.94 | 0.30 | 0.16 | 1.30 | 55.39 | 3.26 | Ra |
| " " | T | 5-10 | 0.95 | 0.98 | -0.05 | -0.003 | 0.97 | 1.34 | 0.24 | 0.16 | 0.98 | I.V. | -37.93 | Ra |
| " " | | 15-20 | 1.33 | 1.15 | 0.33 | 0.03 | 1.22 | 1.00 | 0.33 | 0.22 | 1.21 | 47.14 | 4.50 | Ra |
| " " | T | 15-20 | 0.80 | 0.89 | -0.20 | -0.02 | 0.90 | 1.48 | 0.26 | 0.22 | 0.91 | I.V. | -10.00 | Ra |

TABLE 20. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS JUVENILES | | 0-5 | 9.52 | 3.09 | 8.52 | 0.01 | 1.08 | 89.68 | 0.11 | 0.14 | 1.07 | 29.10 | 11.81 | A** |
| " " | | 5-10 | 2.79 | 1.67 | 1.79 | 0.03 | 1.31 | 4.59 | 0.20 | 0.12 | 1.29 | 55.74 | 3.22 | A** |
| " " | | 10-15 | 6.92 | 2.63 | 5.92 | 0.37 | 3.78 | 0.77 | 0.64 | 0.48 | 3.59 | 166.85 | 0.36 | A** |
| " " | T | 10-15 | 5.24 | 2.29 | 4.24 | 0.26 | 2.00 | 1.89 | 0.55 | 0.48 | 1.79 | 99.83 | 1.00 | A** |
| " " | | 15-20 | 0.95 | 0.98 | -0.05 | -0.004 | 0.97 | 1.08 | 0.28 | 0.19 | 0.97 | I.V. | -31.50 | Ra |
| " " | | 20-25 | 1.11 | 1.05 | 0.11 | 0.02 | 1.07 | 0.85 | 0.43 | 0.39 | 1.07 | 27.22 | 13.50 | Ra |
| " " | T | 20-25 | 0.50 | 0.71 | -0.50 | -0.10 | 0.75 | 1.42 | 0.29 | 0.39 | 0.80 | I.V. | -4.00 | Ra |
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TABLE 21. DATE 16-12-74. SAMPLE SIZE 10x10x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-5 | 9.52 | 3.08 | 8.52 | 0.009 | 1.07 | 112.93 | 0.10 | 0.13 | 1.06 | 26.09 | 14.69 | A** |
| " " | | 5-10 | 3.58 | 1.89 | 2.58 | 0.03 | 1.36 | 5.63 | 0.21 | 0.12 | 1.34 | 60.35 | 2.75 | A** |
| " " | | 10-15 | 6.63 | 2.57 | 5.63 | 0.30 | 3.25 | 1.06 | 0.58 | 0.42 | 3.07 | 150.04 | 0.44 | A** |
| " " | T | 10-15 | 5.38 | 2.32 | 4.38 | 0.23 | 2.09 | 1.93 | 0.52 | 0.42 | 1.92 | 104.58 | 0.91 | A** |
| " " | | 15-20 | 1.62 | 1.27 | 0.62 | 0.03 | 1.21 | 2.22 | 0.26 | 0.18 | 1.19 | 45.43 | 4.85 | Ra |
| " " | T | 15-20 | 0.50 | 0.71 | -0.50 | -0.02 | 0.88 | 3.42 | 0.14 | 0.18 | 0.89 | I.V. | -8.00 | Ra |
| " " | | 20-25 | 1.11 | 1.05 | 0.11 | 0.02 | 1.07 | 0.85 | 0.43 | 0.39 | 1.07 | 27.22 | 13.50 | Ra |
| " " | T | 20-25 | 0.50 | 0.71 | -0.50 | -0.10 | 0.75 | 1.42 | 0.29 | 0.39 | 0.80 | I.V. | -4.00 | Ra |
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DATE 16-12-74. TABLE 22. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS MALES | | 0-5 | 1.48 | 1.22 | 0.48 | 0.02 | 1.06 | 6.31 | 0.24 | 0.37 | 1.04 | 24.00 | 17.36 | Ra |
| " " | | 5-10 | 0.80 | 0.89 | -0.20 | -0.04 | 0.80 | 0.63 | 0.37 | 0.28 | 0.80 | I.V. | -5.00 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS GRAVID FEMALES | | 0-5 | 0.54 | 0.73 | -0.46 | -0.04 | 0.89 | 3.45 | 0.20 | 0.36 | 0.92 | I.V. | -9.39 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL FEMALES | | 0-5 | 0.17 | 0.41 | -0.83 | -0.05 | 0.86 | 5.42 | 0.10 | 0.34 | 0.90 | I.V. | -7.20 | Ra |
| " " | | 5-10 | 1.20 | 1.10 | 0.20 | 0.04 | 1.20 | 0.55 | 0.45 | 0.33 | 1.20 | 44.72 | 5.00 | Ra |
| " " | | 10-15 | 0.25 | 0.50 | -0.75 | -0.07 | 0.81 | 3.42 | 0.14 | 0.35 | 0.86 | I.V. | -5.33 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 23. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS JUVENILES | | 0-5 | 7.75 | 2.78 | 6.75 | 0.03 | 1.08 | 68.36 | 0.18 | 0.35 | 1.05 | 28.51 | 12.30 | A** |
| " " | | 5-10 | 0.92 | 0.96 | -0.08 | -0.002 | 0.99 | 6.58 | 0.14 | 0.18 | 0.99 | I.V. | -97.96 | Ra |
| " " | | 10-15 | 0.70 | 0.84 | -0.30 | -0.006 | 0.98 | 15.64 | 0.11 | 0.34 | 0.99 | I.V. | -58.52 | Ra |
| " " | | 15-20 | 1.05 | 1.02 | 0.05 | 0.0007 | 1.00 | 18.60 | 0.13 | 0.34 | 1.00 | 4.69 | 455.11 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL | | 0-5 | 8.59 | 2.93 | 7.59 | 0.03 | 1.08 | 80.64 | 0.17 | 0.35 | 1.05 | 27.93 | 12.82 | A** |
| " " | | 5-10 | 1.23 | 1.11 | 0.23 | 0.004 | 1.32 | 8.26 | 0.45 | 0.18 | 1.02 | 15.34 | 42.47 | Ra |
| " " | | 10-15 | 0.84 | 0.92 | -0.16 | -0.003 | 0.99 | 16.69 | 0.12 | 0.34 | 0.99 | I.V. | -120.33 | Ra |
| " " | | 15-20 | 0.39 | 0.62 | -0.61 | -0.008 | 0.98 | 24.81 | 0.07 | 0.34 | 0.98 | I,V. | -43.54 | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 24. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS MALES | | 0-5 | 2.78 | 1.67 | 1.78 | 0.01 | 1.04 | 42.57 | 0.14 | 0.35 | 1.02 | 19.02 | 27.66 | Ra |
| " " | | 5-10 | 1.09 | 1.04 | 0.09 | 0.0006 | 1.00 | 24.47 | 0.08 | 0.17 | 1.00 | 5.81 | 296.30 | Ra |
| " " | | 10-15 | 1.00 | 1.00 | 0 | 0 | 1.00 | 7.27 | 0.19 | 0.36 | 1.00 | 0 | $\rightarrow \infty$ | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS GRAVID FEMALES | | 5-10 | 0.25 | 0.50 | -0.75 | -0.01 | 0.93 | 9.51 | 0.06 | 0.17 | 0.94 | I.V. | -13.60 | Ra |
| " " | | 10-15 | 1.75 | 1.32 | 0.75 | 0.07 | 1.19 | 2.47 | 0.38 | 0.43 | 1.14 | 43.30 | 5.33 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS NON-GRAVID FEMALES | | 0-5 | 1.84 | 1.36 | 0.84 | 0.007 | 1.02 | 37.87 | 0.12 | 0.34 | 1.01 | 13.95 | 51.36 | Ra |
| " " | | 5-10 | 1.20 | 1.09 | 0.20 | 0.001 | 1.01 | 24.36 | 0.09 | 0.17 | 1.01 | 8.55 | 136.75 | Ra |
| " " | | 15-20 | 0.67 | 0.82 | -0.33 | -0.006 | 0.98 | 16.31 | 0.11 | 0.34 | 0.99 | I.V. | -56.02 | Ra |
| | | | | | | | | | | | | | | |

TABLE 25. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL FEMALES | | 0-5 | 2.20 | 1.48 | 1.20 | 0.006 | 1.02 | 55.57 | 0.11 | 0.34 | 1.01 | 13.89 | 51.81 | Ra |
| " " | | 5-10 | 0.83 | 0.91 | -0.17 | -0.0007 | 1.00 | 35.87 | 0.06 | 0.17 | 1.00 | I,V. | -227.61 | Ra |
| " " | | 10-15 | 4.08 | 2.02 | 3.08 | 0.05 | 1.16 | 14.49 | 0.26 | 0.38 | 1.11 | 39.60 | 6.38 | A* |
| " " | | 15-20 | 0.57 | 0.75 | -0.43 | -0.006 | 0.98 | 20.92 | 0.09 | 0.34 | 0.99 | I.V. | -52.90 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS JUVENILES | | 0-5 | 17.65 | 4.20 | 16.65 | 0.03 | 1.10 | 129.02 | 0.19 | 0.36 | 1.07 | 32.29 | 9.59 | A** |
| " " | | 5-10 | 0.93 | 0.96 | -0.07 | -0.0001 | 1.00 | 151.41 | 0.03 | 0.17 | 1.00 | I.V. | 2249.09 | Ra |
| " " | | 10-15 | 10.97 | 3.31 | 9.97 | 0.03 | 1.08 | 108.50 | 0.17 | 0.35 | 1.05 | 27.66 | 13.07 | A** |
| " " | | 15-20 | 2.94 | 1.71 | 1.94 | 0.007 | 1.02 | 89.15 | 0.10 | 0.34 | 1.01 | 14.00 | 51.05 | Ra |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | |

TABLE 26. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL | | 0-5 | 21.50 | 4.64 | 20.50 | 0.03 | 1.08 | 226.93 | 0.16 | 0.35 | 1.05 | 27.51 | 13.22 | A** |
| " " | | 5-10 | 1.44 | 1.20 | 0.44 | 0.0003 | 1.00 | 211.91 | 0.03 | 0.17 | 1.00 | 4.48 | 497.25 | Ra |
| " " | | 10-15 | 15.33 | 3.91 | 14.33 | 0.03 | 1.09 | 130.50 | 0.18 | 0.35 | 1.06 | 30.02 | 11.10 | A** |
| " " | | 15-20 | 2.93 | 1.71 | 1.93 | 0.005 | 1.01 | 119.04 | 0.09 | 0.34 | 1.01 | 12.18 | 67.41 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 27. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS NON-GRAVID FEMALES | | 0-5 | 7.74 | 2.78 | 6.74 | 0.09 | 1.25 | 18.37 | 0.31 | 0.40 | 1.17 | 50.26 | 3.96 | A** |
| " " | | 5-10 | 1.27 | 1.13 | 0.27 | 0.03 | 1.18 | 0.94 | 0.38 | 0.28 | 1.17 | 42.16 | 5.63 | Ra |
| " " | T | 5-10 | 0.94 | 0.97 | -0.06 | -0.007 | 0.97 | 1.22 | 0.32 | 0.28 | 0.97 | I.V. | -32.40 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 0-5 | 4.29 | 2.07 | 3.29 | 0.02 | 1.06 | 42.46 | 0.17 | 0.35 | 1.04 | 25.41 | 15.48 | A* |
| " " | | 5-10 | 0.80 | 0.89 | -0.20 | -0.01 | 0.93 | 2.37 | 0.21 | 0.20 | 0.94 | I.V. | -15.00 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS JUVENILES | | 0-5 | 7.88 | 2.81 | 6.88 | 0.009 | 1.03 | 222.80 | 0.10 | 0.34 | 1.02 | 16.64 | 36.11 | A** |
| " " | | 5-10 | 2.80 | 1.67 | 1.80 | 0.02 | 1.14 | 10.24 | 0.19 | 0.20 | 1.12 | 37.70 | 7.04 | A* |
| " " | | 10-15 | 10.23 | 3.20 | 9.23 | 0.77 | 3.13 | 0.49 | 0.89 | 0.86 | 2.54 | 145.95 | 0.47 | A** |
| " " | T | 10-15 | 9.31 | 3.05 | 8.31 | 0.69 | 2.28 | 1.00 | 0.85 | 0.86 | 1.69 | 113.05 | 0.78 | A** |

TABLE 28. DATE 16-12-74. SAMPLE SIZE 15x15x5 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-5 | 14.08 | 3.75 | 13.08 | 0.01 | 1.04 | 259.04 | 0.13 | 0.34 | 1.03 | 21.01 | 22.66 | A** |
| " " | | 5-10 | 3.46 | 1.86 | 2.46 | 0.03 | 1.16 | 12.66 | 0.19 | 0.20 | 1.13 | 39.66 | 6.36 | A** |
| " " | | 10-15 | 9.24 | 3.04 | 8.24 | 0.51 | 2.45 | 1.49 | 0.74 | 0.70 | 2.03 | 120.87 | 0.69 | A** |
| " " | | 15-20 | 1.50 | 1.22 | 0.50 | 0.03 | 1.08 | 4.27 | 0.29 | 0.39 | 1.06 | 28.87 | 12.00 | Ra |
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TABLE 29. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS JUVENILES | | 0-1 | 3.06 | 1.75 | 2.07 | 0.07 | 2.78 | 0.78 | 0.33 | 0.14 | 2.77 | 133.46 | 0.56 | A** |
| " " | T | 0-1 | 1.84 | 1.36 | 0.84 | 0.03 | 1.35 | 1.81 | 0.25 | 0.14 | 1.33 | 58.96 | 2.88 | Ra |
| " " | | 1-2 | 1.06 | 1.03 | 0.06 | 0.006 | 1.13 | 0.34 | 0.30 | 0.13 | 1.14 | 36.08 | 7.68 | Ra |
| " " | T | 1-2 | 0.18 | 0.43 | -0.81 | -0.07 | 0.39 | 1.17 | 0.13 | 0.13 | 0.41 | I.V. | -1.64 | Re* |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-1 | 2.70 | 1.64 | 1.70 | 0.05 | 2.29 | 0.94 | 0.29 | 0.12 | 2.27 | 113.38 | 0.78 | A** |
| " " | T | 0-1 | 1.48 | 1.22 | 0.48 | 0.02 | 1.19 | 2.00 | 0.21 | 0.12 | 1.18 | 43.70 | 5.24 | Ra |
| " " | | 1-2 | 1.30 | 1.14 | 0.30 | 0.03 | 1.58 | 0.36 | 0.32 | 0.14 | 1.60 | 76.12 | 1.73 | Ra |
| " " | T | 1-2 | 0.37 | 0.60 | -0.63 | -0.05 | 0.56 | 1.20 | 0.17 | 0.14 | 0.58 | I.V. | -2.28 | Ra |
| " " | | 2-3 | 1,61 | 1.27 | 0.61 | 0.31 | 6.09 | 0.03 | 0.73 | 0.56 | 8.33 | 225.67 | 0.20 | Ra |
| " " | T | 2-3 | 0.33 | 0.58 | -0.67 | -0.33 | 0.56 | 1.00 | 0.33 | 0.56 | 0.67 | I.V. | -2.25 | Ra |

TABLE 30. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **CLARKUS NON-GRAVID FEMALES** | | 0-1 | 1.25 | 1.12 | 0.25 | 0.06 | 2.25 | 0.10 | 0.50 | 0.28 | 2.50 | 111.80 | 0.80 | **Ra** |
| " " | T | 0-1 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V, | -1.56 | **Ra** |
| | | | | | | | | | | | | | | |
| **CLARKUS TOTAL FEMALES** | | 0-1 | 1.49 | 1.22 | 0.49 | 0.10 | 3.03 | 0.12 | 0.50 | 0.28 | 3.33 | 142.32 | 0.49 | **Ra** |
| " " | T | 0-1 | 0.22 | 0.47 | -0.78 | -0.16 | 0.48 | 1.21 | 0.19 | 0.28 | 0.53 | I.V. | -1.93 | **Ra** |
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TABLE 31. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS JUVENILES | | 0-1 | 3.46 | 1.86 | 2.46 | 0.03 | 1.65 | 3.07 | 0.19 | 0.08 | 1.63 | 80.54 | 1.54 | A** |
| " " | T | 0-1 | 2.73 | 1.65 | 1.73 | 0.02 | 1.38 | 3.76 | 0.17 | 0.08 | 1.37 | 61.89 | 2.61 | A** |
| " " | | 1-2 | 1.36 | 1.17 | 0.36 | 0.01 | 1.32 | 0.87 | 0.22 | 0.09 | 1.32 | 56.94 | 3.08 | Ra |
| " " | | 2-3 | 1.36 | 1.17 | 0.36 | 0.05 | 2.00 | 0.22 | 0.39 | 0.19 | 2.08 | 100.15 | 1.00 | Ra |
| " " | T | 2-3 | 0.20 | 0.45 | -0.80 | -0.10 | 0.47 | 1.28 | 0.15 | 0.19 | 0.50 | I.V. | -1.88 | Ra |
| " " | | 3-4 | 1.49 | 1.22 | 0.49 | 0.10 | 3.03 | 0.12 | 0.50 | 0.28 | 3.33 | 142.32 | 0.49 | Ra |
| " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.16 | 0.48 | 1.21 | 0.19 | 0.28 | 0.53 | I.V. | -1.93 | Ra |
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TABLE 32. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 3.77 | 1.94 | 2.77 | 0.03 | 1.69 | 3.22 | 0.19 | 0.08 | 1.67 | 83.23 | 1.44 | A** |
| " " | T | 0-1 | 3.00 | 1.73 | 2.00 | 0.02 | 1.42 | 3.94 | 0.17 | 0.08 | 1.40 | 64.82 | 2.38 | A** |
| " " | | 1-2 | 1.63 | 1.28 | 0.63 | 0.02 | 1.54 | 0.89 | 0.24 | 0.09 | 1.54 | 73.66 | 1.84 | Ra |
| " " | T | 1-2 | 0.97 | 0.99 | -0.03 | -0.001 | 0.98 | 1.48 | 0.18 | 0.09 | 0.99 | I.V. | -65.70 | Ra |
| " " | | 2-3 | 1.36 | 1.17 | 0.36 | 0.05 | 2.00 | 0.22 | 0.39 | 0.19 | 2.08 | 100.15 | 1.00 | Ra |
| " " | T | 2-3 | 0.20 | 0.45 | -0.80 | -0.10 | 0.47 | 1.28 | 0.15 | 0.19 | 0.50 | I.V. | -1.88 | Ra |
| " " | | 3-4 | 1.49 | 1.22 | 0.49 | 0.10 | 3.03 | 0.12 | 0.50 | 0.28 | 3.33 | 142.32 | 0.49 | Ra |
| " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.16 | 0.48 | 1.21 | 0.19 | 0.28 | 0.53 | I.V. | -1.93 | Ra |
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TABLE 33. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MONONCHIDS TOTAL | | 0-1 | 3.43 | 1.85 | 2.43 | 0.02 | 1.45 | 4.50 | 0.16 | 0.06 | 1.44 | 67.39 | 2.20 | A** |
| " " | T | 0-1 | 2.39 | 1.55 | 1.39 | 0.01 | 1.22 | 5.53 | 0.13 | 0.06 | 1.21 | 46.67 | 4.59 | A** |
| " " | | 1-2 | 1.67 | 1.29 | 0.67 | 0.02 | 1.39 | 1.38 | 0.20 | 0.08 | 1.38 | 62.53 | 2.56 | A* |
| " " | T | 1-2 | 1.12 | 1.06 | 0.12 | 0.003 | 1.05 | 1.90 | 0.16 | 0.08 | 1.05 | 23.17 | 18.63 | Ra |
| " " | | 2-3 | 1.78 | 1.33 | 0.78 | 0.07 | 2.50 | 0.33 | 0.37 | 0.17 | 2.56 | 122.64 | 0.66 | A* |
| " " | T | 2-3 | 0.44 | 0.66 | -0.56 | -0.05 | 0.70 | 1.52 | 0.18 | 0.17 | 0.72 | I.V. | -3.29 | Ra |
| " " | | 3-4 | 1.36 | 1.17 | 0.36 | 0.05 | 2.00 | 0.22 | 0.39 | 0.19 | 2.08 | 100.15 | 1.00 | Ra |
| " " | T | 3-4 | 0.20 | 0.45 | -0.80 | -0.10 | 0.47 | 1.28 | 0.15 | 0.19 | 0.50 | I.V. | -1.88 | Ra |
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TABLE 34. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | SLICE | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL | | B | 1.13 | 1.06 | 0.13 | 0.02 | 1.36 | 0.23 | 0.35 | 0.16 | 1.39 | 60.07 | 2.78 | Ra |
| " " | T | B | 0.98 | 0.43 | -0.81 | -0.10 | 0.37 | 1.10 | 0.14 | 0.16 | 0.39 | I.V. | -1.58 | Re* |
| " " | | C | 1.49 | 1.22 | 0.49 | 0.1 | 3.03 | 0.12 | 0.50 | 0.28 | 3.33 | 142.32 | 0.49 | Ra |
| " " | T | C | 0.22 | 0.47 | -0.78 | -0.16 | 0.48 | 1.21 | 0.19 | 0.28 | 0.53 | I.V. | -1.93 | Ra |
| " " | | D | 1.46 | 1.21 | 0.46 | 0.05 | 2.15 | 0.25 | 0.38 | 0.18 | 2.22 | 107.04 | 0.87 | Ra |
| " " | T | D | 0.16 | 0.40 | -0.84 | -0.09 | 0.50 | 1.46 | 0.13 | 0.18 | 0.53 | I.V. | -1.98 | Re* |
| " " | | E | 4.03 | 2.01 | 3.03 | 0.13 | 4.16 | 0.57 | 0.41 | 0.20 | 4.16 | 177.80 | 0.32 | A** |
| " " | T | E | 1.64 | 1.28 | 0.64 | 0.03 | 1.19 | 2.53 | 0.26 | 0.20 | 1.17 | 43.17 | 5.37 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 35. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | SLICE | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | A | 2.49 | 1.58 | 1.49 | 0.07 | 2.70 | 0.58 | 0.34 | 0.15 | 2.71 | 130.23 | 0.59 | A** |
| " " | T | A | 1.19 | 1.09 | 0.19 | 0.009 | 1.09 | 1.69 | 0.23 | 0.15 | 1.08 | 29.54 | 11.46 | A** |
| " " | | B | 7.86 | 2.80 | 6.86 | 0.13 | 4.18 | 1.34 | 0.38 | 0.18 | 4.11 | 178.19 | 0.31 | A** |
| " " | T | B | 6.30 | 2.51 | 5.30 | 0.10 | 2.37 | 2.54 | 0.34 | 0.18 | 2.30 | 117.18 | 0.73 | A** |
| " " | | C | 4.40 | 2.10 | 3.40 | 0.11 | 3.65 | 0.81 | 0.37 | 0.17 | 3.63 | 162.88 | 0.38 | A** |
| " " | T | C | 2,56 | 1.60 | 1.56 | 0.05 | 1.49 | 2.30 | 0.28 | 0.17 | 1.45 | 69.72 | 2.06 | A* |
| " " | | D | 1.71 | 1.31 | 0.71 | 0.03 | 1.78 | 0.67 | 0.27 | 0.11 | 1.78 | 88.08 | 1.29 | A* |
| " " | T | D | 0.52 | 0.72 | -0.48 | -0.02 | 0.77 | 1.78 | 0.15 | 0.11 | 0.78 | I.V. | -4.37 | Ra |
| " " | | E | 2.15 | 1.47 | 1.15 | 0.06 | 2.37 | 0.57 | 0.32 | 0.14 | 2.38 | 117.05 | 0.73 | A** |
| " " | T | E | 0.64 | 0.80 | -0.36 | -0.02 | 0.85 | 1.93 | 0.17 | 0.14 | 0.85 | I.V. | -6.53 | Ra |
| | | | | | | | | | | | | | | |

TABLE 36. DATE 4-2-75. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | SLICE | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MONONCHIDS TOTAL | | A | 2.25 | 1.50 | 1.25 | 0.05 | 2.25 | 0.70 | 0.30 | 0.13 | 2.25 | 111.80 | 0.80 | A** |
| " " | T | A | 0.98 | 0.99 | -0.02 | -0.001 | 0.99 | 1.82 | 0.20 | 0.13 | 0.99 | I.V. | -94.70 | Ra |
| " " | | B | 7.51 | 2.74 | 6.51 | 0.11 | 3.58 | 1.65 | 0.35 | 0.15 | 3.52 | 160.73 | 0.39 | A** |
| " " | T | B | 6.18 | 2.49 | 5.18 | 0.08 | 2.32 | 2.70 | 0.31 | 0.15 | 2.25 | 114.68 | 0.76 | A** |
| " " | | C | 5.05 | 2.25 | 4.05 | 0.11 | 3.66 | 0.97 | 0.36 | 0.17 | 3.63 | 163.24 | 0.38 | A** |
| " " | T | C | 2.85 | 1.69 | 1.85 | 0.05 | 1.49 | 2.76 | 0.27 | 0.17 | 1.45 | 69.85 | 2.05 | A** |
| " " | | D | 2.44 | 1.56 | 1.44 | 0.04 | 2.06 | 1.00 | 0.27 | 0.11 | 2.05 | 103.03 | 0.94 | A** |
| " " | T | D | 0.95 | 0.98 | -0.05 | -0.001 | 0.98 | 2.36 | 0.17 | 0.11 | 0.98 | I.V. | -58.87 | Ra |
| " " | | E | 4.74 | 2.18 | 3.74 | 0.08 | 3.03 | 1.25 | 0.32 | 0.14 | 3.00 | 142.59 | 0.49 | A** |
| " " | T | E | 2,43 | 1.56 | 1.43 | 0.03 | 1.34 | 3.22 | 0.23 | 0.14 | 1.32 | 58.49 | 2.92 | A* |
| | | | | | | | | | | | | | | |

TABLE 37. DATE 4-2-75. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS JUVENILES | | 0-1 | 4.44 | 2.11 | 3.44 | 0.05 | 1.81 | 3.16 | 0.26 | 0.12 | 1.77 | 89.96 | 1.24 | A** |
| " " | T | 0-1 | 4.16 | 2.04 | 3.16 | 0.05 | 1.70 | 3.41 | 0.25 | 0.12 | 1.66 | 83.43 | 1.44 | A** |
| " " | | 1-2 | 0.65 | 0.80 | -0.35 | -0.01 | 0.78 | 1.37 | 0.16 | 0.09 | 0.79 | I.V, | -4.59 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-1 | 3.14 | 1.77 | 2.14 | 0.03 | 1.42 | 4.12 | 0.20 | 0.10 | 1.40 | 64.69 | 2.39 | A** |
| " " | | 1-2 | 0.88 | 0.94 | -0.12 | -0.005 | 0.93 | 1.44 | 0.18 | 0.09 | 0.93 | I.V. | -14.13 | Ra |
| " " | | 2-3 | 0.98 | 0.98 | -0.02 | -0.002 | 0.97 | 0.54 | 0.29 | 0.14 | 0.97 | I.V. | -33.75 | Ra |
| " " | | 3-4 | 0.90 | 0.95 | -0.10 | -0.02 | 0.78 | 0.28 | 0.36 | 0.18 | 0.76 | I.V. | -4.59 | Ra |
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TABLE 38. DATE 4-2-75. SAMPLE SIZE 2x2x1. CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS NON-GRAVID FEMALES | | 0-1 | 1.53 | 1.24 | 0.53 | 0.03 | 1.47 | 0.80 | 0.29 | 0.14 | 1.46 | 68.37 | 2.14 | Ra |
| " " | T | 0-1 | 0.35 | 0.59 | -0.65 | -0.04 | 0.71 | 1.94 | 0.14 | 0.14 | 0.73 | I.V. | -3.46 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 0-1 | 1.93 | 1.39 | 0.93 | 0.04 | 1.67 | 0.97 | 0.30 | 0.14 | 1.66 | 82.12 | 1.48 | A* |
| " " | T | 0-1 | 0.49 | 0.70 | -0.50 | -0.02 | 0.82 | 2.34 | 0.15 | 0.14 | 0.83 | I.V. | -5.43 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 39. DATE 4-2-75. SAMPLE SIZE 2x2x1. CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS JUVENILES | | 0-1 | 4.88 | 2.21 | 3.88 | 0.02 | 1.25 | 13.33 | 0.14 | 0.08 | 1.24 | 50.02 | 4.00 | A** |
| " " | | 1-2 | 2.61 | 1.62 | 1.61 | 0.02 | 1.33 | 3.93 | 0.18 | 0.09 | 1.32 | 57.85 | 2.99 | A** |
| " " | | 2-3 | 1.18 | 1.09 | 0.18 | 0.007 | 1.10 | 1.39 | 0.21 | 0.10 | 1.10 | 32.16 | 9.67 | Ra |
| " " | T | 2-3 | 0.34 | 0.59 | -0.70 | -0.02 | 0.74 | 2.26 | 0.11 | 0.10 | 0.76 | I.V. | -3.87 | Ra |
| " " | | 3-4 | 1.01 | 1.01 | 0.01 | 0.0007 | 1.01 | 0.97 | 0.23 | 0.11 | 1.01 | 10.33 | 93.75 | Ra |
| " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.04 | 0.61 | 1.79 | 0.11 | 0.11 | 0.63 | I.V. | -2.57 | Re* |
| " " | | 4-5 | 0.38 | 0.61 | -0.62 | -0.03 | 0.53 | 1.14 | 0.13 | 0.08 | 0.53 | I.V. | -2.11 | Re* |
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TABLE 40. DATE 4-2-75. SAMPLE SIZE 2x2x1. C.M.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 5.57 | 2.36 | 4.57 | 0.02 | 1.27 | 14.45 | 0.14 | 0.08 | 1.25 | 52.04 | 3.69 | A** |
| " " | | 1-2 | 2.96 | 1.72 | 1.96 | 0.02 | 1.39 | 4.09 | 0.19 | 0.10 | 1.37 | 62.26 | 2.58 | A** |
| " " | | 2-3 | 1.18 | 1.09 | 0.18 | 0.007 | 1.10 | 1.39 | 0.21 | 0.10 | 1.10 | 32.16 | 9.67 | Ra |
| " " | T | 2-3 | 0.34 | 0.59 | -0.66 | -0.02 | 0.74 | 2.26 | 0.11 | 0.10 | 0.76 | I.V. | -3.87 | Ra |
| " " | | 3-4 | 1.01 | 1.01 | 0.01 | 0.0007 | 1.01 | 0.97 | 0.23 | 0.11 | 1.01 | 10.32 | 93.75 | Ra |
| " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.04 | 0.61 | 1.79 | 0.11 | 0.11 | 0.63 | I.V. | -2.57 | Re* |
| " " | | 4-5 | 0.37 | 0.61 | -0.62 | -0.03 | 0.53 | 1.14 | 0.13 | 0.08 | 0.53 | I.V. | -2.11 | Re* |
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TABLE 41. DATE 4-2-75. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MONONCHIDS TOTAL | | 0-1 | 4.08 | 2.02 | 3.08 | 0.009 | 1.14 | 19.60 | 0.11 | 0.07 | 1.13 | 37.44 | 7.13 | A** |
| " " | | 1-2 | 2.16 | 1.47 | 1.16 | 0.01 | 1.17 | 5.97 | 0.14 | 0.08 | 1.16 | 40.82 | 5.97 | A* |
| " " | | 2-3 | 1.38 | 1.18 | 0.38 | 0.009 | 1.14 | 2.26 | 0.18 | 0.09 | 1.13 | 37.26 | 7.20 | Ra |
| " " | T | 2-3 | 0.72 | 0.85 | -0.28 | -0.007 | 0.92 | 2.95 | 0.13 | 0.09 | 0.92 | I.V. | -11.91 | Ra |
| " " | | 3-4 | 1.30 | 1.14 | 0.30 | 0.01 | 1.21 | 1.10 | 0.24 | 0.12 | 1.20 | 45.35 | 4.86 | Ra |
| " " | T | 3-4 | 0.39 | 0.63 | -0.61 | -0.03 | 0.74 | 2.00 | 0.13 | 0.12 | 0.75 | I.V. | -3.78 | Ra |
| " " | | 4-5 | 0.38 | 0.61 | -0.62 | -0.03 | 0.53 | 1.14 | 0.13 | 0.08 | 0.53 | I.V. | -2.11 | Re* |
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TABLE 42. DATE 4-2-75. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS JUVENILES | | 0-1 | 4.97 | 2.23 | 3.97 | 0.05 | 1.46 | 6.38 | 0.25 | 0.17 | 1.42 | 68.13 | 2.15 | A** |
| " " | | 1-2 | 0.23 | 0.48 | -0.77 | -0.03 | 0.77 | 3.15 | 0.08 | 0.12 | 0.79 | I.V. | -4.45 | Re* |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-1 | 3.59 | 1.89 | 2.59 | 0.03 | 1.25 | 8.20 | 0.20 | 0.15 | 1.23 | 50.33 | 3.95 | A** |
| " " | | 1-2 | 0.34 | 0.58 | -0.66 | -0.02 | 0.82 | 3.29 | 0.10 | 0.12 | 0.84 | I.V. | -5.56 | Ra |
| " " | | 2-3 | 0.38 | 0.61 | -0.62 | -0.04 | 0.69 | 1.71 | 0.14 | 0.13 | 0.71 | I.V. | -3.20 | Ra |
| " " | | 3-4 | 0.50 | 0.71 | -0.50 | -0.06 | 0.50 | 0.76 | 0.24 | 0.16 | 0.50 | I.V. | -2.00 | Ra |
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TABLE 43. DATE 4-2-75. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS NON-GRAVID FEMALES | | 0-1 | 1.55 | 1.24 | 0.55 | 0.03 | 1.25 | 1.60 | 0.28 | 0.18 | 1.23 | 49.75 | 4.04 | Ra |
| " " | T | 0-1 | 0.32 | 0.57 | -0.68 | -0.04 | 0.80 | 2.91 | 0.12 | 0.18 | 0.82 | I.V. | -4.90 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 0-1 | 1.86 | 1.36 | 0.86 | 0.03 | 1.30 | 2.12 | 0.27 | 0.17 | 1.27 | 54.43 | 3.38 | Ra |
| " " | T | 0-1 | 0.25 | 0.50 | -0.75 | -0.03 | 0.83 | 3.91 | 0.10 | 0.17 | 0.85 | I.V. | -5.75 | Ra |
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TABLE 44. DATE 4-2-75. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS JUVENILES | | 0-1 | 4.28 | 2.07 | 3.28 | 0.01 | 1.10 | 29.25 | 0.12 | 0.12 | 1.09 | 31.42 | 10.13 | A** |
| " " | | 1-2 | 2.55 | 1.60 | 1.55 | 0.02 | 1.14 | 9.03 | 0.16 | 0.13 | 1.13 | 37.88 | 6.97 | A* |
| " " | | 2-3 | 0.85 | 0.92 | -0.15 | -0.005 | 0.96 | 3.18 | 0.16 | 0.13 | 0.96 | I.V. | -24.47 | Ra |
| " " | | 3-4 | 1.01 | 1.01 | 0.13 | 0.0007 | 1.01 | 0.97 | 0.23 | 0.11 | 1.01 | 10.33 | 93.75 | Ra |
| " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.04 | 0.61 | 1.79 | 0.11 | 0.11 | 0.63 | I.V. | -2.57 | Ra |
| " " | | 4-5 | 0.14 | 0.37 | -0.86 | -0.03 | 0.73 | 3.00 | 0.07 | 0.12 | 0.75 | I.V. | -3.74 | Re** |
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TABLE 45. DATE 4-2-75. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 5.09 | 2.26 | 4.09 | 0.01 | 1.11 | 31.59 | 0.13 | 0.13 | 1.10 | 33.66 | 8.83 | A** |
| " " | | 1-2 | 2.82 | 1.68 | 1.82 | 0.02 | 1.16 | 9.55 | 0.17 | 0.14 | 1.14 | 39.88 | 6.29 | A** |
| " " | | 2-3 | 0.85 | 0.92 | -0.15 | -0.005 | 0.96 | 3.18 | 0.16 | 0.13 | 0.96 | I.V. | -24.47 | Ra |
| " " | | 3-4 | 0.65 | 0.81 | -0.35 | -0.02 | 0.84 | 1.82 | 0.18 | 0.14 | 0.85 | I.V. | -6.35 | Ra |
| " " | | 4-5 | 0.14 | 0.37 | -0.86 | -0.03 | 0.73 | 3.00 | 0.07 | 0.12 | 0.75 | I.V. | -3.74 | Re** |
| | | | | | | | | | | | | | | |
| MONONCHIDS TOTAL | | 0-1 | 3.17 | 1.78 | 2.17 | 0.005 | 1.05 | 42.29 | 0.09 | 0.12 | 1.04 | 21.65 | 21.33 | A** |
| " " | | 1-2 | 1.81 | 1.34 | 0.81 | 0.006 | 1.05 | 13.06 | 0.12 | 0.12 | 1.05 | 23.36 | 18.32 | Ra |
| " " | | 2-3 | 1.16 | 1.08 | 0.16 | 0.003 | 1.03 | 5.33 | 0.14 | 0.13 | 1.02 | 15.85 | 39.82 | Ra |
| " " | | 3-4 | 0.70 | 0.83 | -0.30 | -0.01 | 0.88 | 2.11 | 0.17 | 0.14 | 0.89 | I.V. | -8.40 | Ra |
| " " | | 4-5 | 0.14 | 0.37 | -0.86 | -0.03 | 0.73 | 3.00 | 0.07 | 0.12 | 0.75 | I.V. | -3.74 | Re** |

TABLE 46. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS TOTAL JUVENILES | | 4-5 | 1.40 | 1.18 | 0.40 | 0.13 | 3.47 | 0.07 | 0.59 | 0.38 | 4.17 | 157.29 | 0.40 | Ra |
| " " | T | 4-5 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V, | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL | | 0-1 | 1.40 | 1.18 | 0.40 | 0.13 | 3.47 | 0.07 | 0.59 | 0.38 | 4.17 | 157.29 | 0.40 | Ra |
| " " | T | 0-1 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| " " | | 4-5 | 1.40 | 1.18 | 0.40 | 0.13 | 3.47 | 0.07 | 0.59 | 0.38 | 4.17 | 157.29 | 0.40 | Ra |
| " " | T | 4-5 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
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TABLE 47. DATE 13-4-76- SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS NON-GRAVID FEMALES | | 2-3 | 1.61 | 1.27 | 0.61 | 0.31 | 6.09 | 0.03 | 0.73 | 0.56 | 8.33 | 225.67 | 0.20 | Ra |
| " " | T | 2-3 | 0.33 | 0.58 | -0.67 | -0.33 | 0.56 | 1.00 | 0.33 | 0.56 | 0.67 | I.V. | -2.25 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL FEMALES | | 2-3 | 1.61 | 1.27 | 0.61 | 0.31 | 6.09 | 0.03 | 0.73 | 0.56 | 8.33 | 225.67 | 0.20 | Ra |
| " " | T | 2-3 | 0.33 | 0.58 | -0.67 | -0.33 | 0.56 | 1.00 | 0.33 | 0.56 | 0.67 | I.V. | -2.25 | Ra |
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TABLE 48. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **MYLONCHULUS TOTAL JUVENILES** | | 1-2 | 1.15 | 1.07 | 0.15 | 0.02 | 1.34 | 0.30 | 0.32 | 0.14 | 1.36 | 58.68 | 2.90 | Ra |
| " " | T | 1-2 | 0.19 | 0.44 | -0.81 | -0.08 | 0.41 | 1.19 | 0.13 | 0.14 | 0.44 | I.V. | -1.71 | Re* |
| " " | | 2-3 | 1.25 | 1.12 | 0.25 | 0.06 | 2.25 | 0.10 | 0.50 | 0.28 | 2.50 | 111.80 | 0.80 | Ra |
| " " | T | 2-3 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| " " | | 3-4 | 1.14 | 1.07 | 0.14 | 0.03 | 1.58 | 0.14 | 0.44 | 0.22 | 1.67 | 76.07 | 1.73 | Ra |
| " " | T | 3-4 | 0.17 | 0.41 | -0.83 | -0.17 | 0.31 | 1.00 | 0.17 | 0.22 | 0.33 | I.V. | -1.44 | Ra |
| " " | | 5-6 | 0.97 | 0.98 | -0.03 | -0.004 | 0.90 | 0.21 | 0.35 | 0.16 | 0.89 | I.V. | -10.24 | Ra |
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TABLE 49. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATOLE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **MYLONCHULUS TOTAL** | | 1-2 | 1.05 | 1.03 | 0.05 | 0.004 | 1.10 | 0.41 | 0.27 | 0.11 | 1.10 | 30.93 | 10.45 | Ra |
| " " | T | 1-2 | 0.19 | 0.44 | -0.81 | -0.06 | 0.42 | 1.24 | 0.12 | 0.11 | 0.44 | I.V. | -1.73 | Re** |
| " " | | 2-3 | 1.59 | 1.26 | 0.59 | 0.07 | 2.65 | 0.21 | 0.42 | 0.21 | 2.78 | 128.30 | 0.61 | Ra |
| " " | T | 2-3 | 0.47 | 0.68 | -0.53 | -0.07 | 0.64 | 1.16 | 0.23 | 0.21 | 0.67 | I.V. | -2.81 | Ra |
| " " | | 3-4 | 1.14 | 1.07 | 0.14 | 0.93 | 1.58 | 0.14 | 0.44 | 0.22 | 1.67 | 76.07 | 1.73 | Ra |
| " " | T | 3-4 | 0.17 | 0.41 | -0.83 | -0.17 | 0.31 | 1.00 | 0.17 | 0.22 | 0.33 | I.V. | -1.44 | Ra |
| " " | | 5-6 | 0.90 | 0.95 | -0.10 | -0.01 | 0.72 | 0.25 | 0.32 | 0.14 | 0.69 | I.V. | -3.53 | Ra |
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TABLE 50. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **CLARKUS NON-GRAVID FEMALES** | | 3-4 | 1.40 | 1.18 | 0.40 | 0.13 | 3.47 | 0.07 | 0.59 | 0.38 | 4.17 | 157.29 | 0.40 | Ra |
| " " | T | 3-4 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| **CLARKUS TOTAL FEMALES** | | 3-4 | 1.67 | 1.29 | 0.67 | 0.17 | 4.33 | 0.08 | 0.58 | 0.36 | 5.00 | 182.57 | 0.30 | A* |
| " " | T | 3-4 | 0.20 | 0.45 | -0.80 | -0.20 | 0.52 | 1.33 | 0.20 | 0.36 | 0.60 | I.V. | -2.08 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 51. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 1ST ST. JUVS. | | 0-1 | 1.23 | 1.11 | 0.23 | 0.03 | 1.72 | 0.19 | 0.39 | 0.19 | 1.79 | 84.63 | 1.40 | Ra |
| " " " " | T | 0-1 | 0.20 | 0.45 | -0.80 | -0.11 | 0.40 | 1.12 | 0.16 | 0.19 | 0.43 | I.V. | -1.67 | Ra |
| " " " " | | 1-2 | 2.44 | 1.56 | 1.44 | 0.07 | 2.56 | 0.62 | 0.33 | 0.14 | 2.57 | 125.04 | 0.64 | A ** |
| " " " " | T | 1-2 | 0.79 | 0.89 | -0.21 | -0.009 | 0.92 | 2.08 | 0.19 | 0.14 | 0.92 | I.V. | -12.37 | Ra |
| " " " " | | 2-3 | 1.24 | 1.11 | 0.24 | 0.02 | 1.49 | 0.33 | 0.32 | 0.14 | 1.52 | 70.14 | 2.03 | Ra |
| " " " " | T | 2-3 | 0.38 | 0.61 | -0.62 | -0.06 | 0.53 | 1.10 | 0.18 | 0.14 | 0.55 | I.V. | -2.13 | Ra |
| " " " " | | 3-4 | 2.71 | 1.65 | 1.71 | 0.19 | 5.27 | 0.19 | 0.52 | 0.30 | 5.56 | 206.66 | 0.23 | A ** |
| " " " " | T | 3-4 | 0.67 | 0.82 | -0.33 | -0.04 | 0.87 | 1.85 | 0.26 | 0.30 | 0.89 | I.V. | -7.50 | Ra |
| " " " " | | 4-5 | 0.97 | 0.98 | -0.03 | -0.004 | 0.90 | 0.21 | 0.35 | 0.16 | 0.89 | I.V. | -10.24 | Ra |
| " " " " | | 5-6 | 2.08 | 1.44 | 1.08 | 0.27 | 6.42 | 0.07 | 0.65 | 0.44 | 7.50 | 232.74 | 0.18 | A ** |
| " " " " | T | 5-6 | 0.80 | 0.89 | -0.20 | -0.05 | 0.88 | 1.00 | 0.40 | 0.44 | 0.90 | I.V. | -8.33 | Ra |

TABLE 52. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 2ND ST. JUVS. | | 1-2 | 0.98 | 0.99 | -0.02 | -0.001 | 0.97 | 0.69 | 0.21 | 0.08 | 0.97 | I.V. | -38.72 | Ra |
| " " " " | | 2-3 | 1.13 | 1.06 | 0.13 | 0.02 | 1.36 | 0.23 | 0.35 | 0.16 | 1.39 | 60.01 | 2.78 | Ra |
| " " " " | T | 2-3 | 0.19 | 0.43 | -0.81 | -0.10 | 0.37 | 1.10 | 0.14 | 0.16 | 0.39 | I.V. | -1.58 | Re * |
| " " " " | | 3-4 | 1.14 | 1.07 | 0.14 | 0.03 | 1.58 | 0.14 | 0.44 | 0.22 | 1.67 | 76.07 | 1.73 | Ra |
| " " " " | T | 3-4 | 0.17 | 0.41 | -0.83 | -0.17 | 0.31 | 1.00 | 0.17 | 0.22 | 0.33 | I.V. | -1.44 | Ra |
| " " " " | | 4-5 | 1.05 | 1.02 | 0.05 | 0.008 | 1.17 | 0.17 | 0.39 | 0.18 | 1.19 | 41.24 | 5.88 | Ra |
| " " " " | T | 4-5 | 0.14 | 0.38 | -0.86 | -0.14 | 0.27 | 1.00 | 0.14 | 0.18 | 0.29 | I.V. | -1.36 | Re * |
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TABLE 53. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 3RD ST. JUVS. | | 0-1 | 1.40 | 1.18 | 0.40 | 0.13 | 3.47 | 0.07 | 0.59 | 0.38 | 4.17 | 157.29 | 0.40 | Ra |
| " " " " | T | 0-1 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| " " " " | | 3-4 | 1.61 | 1.27 | 0.61 | 0.31 | 6.09 | 0.03 | 0.73 | 0.56 | 8.33 | 225.67 | 0.20 | Ra |
| " " " " | T | 3-4 | 0.33 | 0.58 | -0.67 | -0.33 | 0.56 | 1.00 | 0.33 | 0.56 | 0.67 | I.V. | -2.25 | Ra |
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TABLE 54. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL JUVS. | | 0-1 | 1.68 | 1.30 | 0.68 | 0.05 | 2.06 | 0.43 | 0.32 | 0.14 | 2.08 | 102.86 | 0.95 | A * |
| " " " | T | 0-1 | 0.72 | 1.85 | -0.28 | -0.02 | 0.83 | 1.26 | 0.21 | 0.14 | 0.83 | I.V. | -5.76 | Ra |
| " " " | | 1-2 | 2.88 | 1.70 | 1.88 | 0.04 | 1.90 | 1.59 | 0.24 | 0.09 | 1.89 | 95.11 | 1.11 | A ** |
| " " " | T | 1-2 | 1.90 | 1.38 | 0.90 | 0.02 | 1.29 | 2.47 | 0.19 | 0.09 | 1.28 | 54.21 | 3.40 | A * |
| " " " | | 2-3 | 1.17 | 1.08 | 0.17 | 0.007 | 1.18 | 0.75 | 0.22 | 0.09 | 1.18 | 42.10 | 5.64 | Ra |
| " " " | T | 2-3 | 0.40 | 0.63 | -0.60 | -0.03 | 0.65 | 1.49 | 0.13 | 0.09 | 0.66 | I.V. | -2.84 | Ra |
| " " " | | 3-4 | 1.75 | 1.32 | 0.75 | 0.04 | 1.90 | 0.60 | 0.29 | 0.12 | 1.90 | 94.74 | 1.11 | A * |
| " " " | T | 3-4 | 0.68 | 0.82 | -0.32 | -0.02 | 0.83 | 1.57 | 0.18 | 0.12 | 0.84 | I.V. | -5.90 | Ra |
| " " " | | 4-5 | 1.22 | 1.10 | 0.22 | 0.01 | 1.30 | 0.53 | 0.26 | 0.10 | 1.31 | 54.97 | 3.31 | Ra |
| " " " | T | 4-5 | 0.28 | 0.53 | -0.72 | -0.04 | 0.56 | 1.43 | 0.12 | 0.10 | 0.58 | I.V. | -2.27 | Re * |
| " " " | | 5-6 | 1.36 | 1.17 | 0.36 | 0.05 | 2.00 | 0.22 | 0.39 | 0.19 | 2.08 | 100.15 | 1.00 | Ra |
| " " " | T | 5-6 | 0.44 | 0.67 | -0.56 | -0.07 | 0.57 | 1.00 | 0.22 | 0.19 | 0.58 | I.V. | -2.31 | Ra |

TABLE 55. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 1.68 | 1.30 | 0.68 | 0.05 | 2.06 | 0.43 | 0.32 | 0.14 | 2.08 | 102.86 | 0.95 | A * |
| " " | T | 0-1 | 0.72 | 0.85 | -0.28 | -0.02 | 0.83 | 1.26 | 0.21 | 0.14 | 0.83 | I.V. | -5.76 | Ra |
| " " | | 1-2 | 3.07 | 1.75 | 2.07 | 0.04 | 1.94 | 1.68 | 0.24 | 0.09 | 1.92 | 96.96 | 1.06 | A ** |
| " " | T | 1-2 | 2.03 | 1.42 | 1.03 | 0.02 | 1.32 | 2.61 | 0.19 | 0.09 | 1.31 | 56.41 | 3.14 | A * |
| " " | | 2-3 | 1.08 | 1.04 | 0.08 | 0.003 | 1.08 | 0.79 | 0.21 | 0.08 | 1.08 | 28.87 | 12.00 | Ra |
| " " | T | 2-3 | 0.40 | 0.63 | -0.60 | -0.03 | 0.64 | 1.46 | 0.13 | 0.08 | 0.65 | I.V. | -2.78 | Re * |
| " " | | 3-4 | 2.04 | 1.43 | 1.04 | 0.04 | 2.00 | 0.75 | 0.28 | 0.12 | 2.00 | 100.08 | 1.00 | A ** |
| " " | T | 3-4 | 1.08 | 1.04 | 0.08 | 0.003 | 1.04 | 1.59 | 0.20 | 0.12 | 1.04 | 20.41 | 24.00 | Ra |
| " " | | 4-5 | 1.22 | 1.10 | 0.22 | 0.01 | 1.30 | 0.53 | 0.26 | 0.10 | 1.31 | 54.97 | 3.31 | Ra |
| " " | T | 4-5 | 0.28 | 0.53 | -0.72 | -0.04 | 0.56 | 1.43 | 0.12 | 0.10 | 0.58 | I.V. | -2.27 | Re * |
| " " | | 5-6 | 1.25 | 1.12 | 0.25 | 0.03 | 1.63 | 0.26 | 0.35 | 0.16 | 1.67 | 79.06 | 1.60 | Ra |
| " " | T | 5-6 | 0.40 | 0.63 | -0.60 | -0.07 | 0.52 | 1.00 | 0.20 | 0.16 | 0.53 | I.V. | -2.08 | Ra |

TABLE 56. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL MONONCHIDS | | 0-1 | 2.04 | 1.43 | 1.04 | 0.05 | 2.08 | 0.68 | 0.29 | 0.12 | 2.08 | 103.99 | 0.92 | A ** |
| " " | T | 0-1 | 1.16 | 1.08 | 0.16 | 0.007 | 1.09 | 1.44 | 0.22 | 0.12 | 1.08 | 29.41 | 11.56 | Ra |
| " " | | 1-2 | 2.42 | 1.56 | 1.42 | 0.02 | 1.52 | 2.24 | 0.19 | 0.07 | 1.50 | 71.83 | 1.94 | A ** |
| " " | T | 1-2 | 1.89 | 1.38 | 0.89 | 0.01 | 1.27 | 2.74 | 0.17 | 0.07 | 1.26 | 52.08 | 3.69 | A * |
| " " | | 2-3 | 1.22 | 1.10 | 0.22 | 0.006 | 1.15 | 1.17 | 0.18 | 0.07 | 1.15 | 39.08 | 6.55 | Ra |
| " " | T | 2-3 | 0.65 | 0.80 | -0.35 | -0.01 | 0.82 | 1.73 | 0.13 | 0.07 | 0.83 | I.V. | -5.67 | Ra |
| " " | | 3-4 | 1.77 | 1.33 | 0.77 | 0.02 | 1.57 | 1.05 | 0.23 | 0.09 | 1.56 | 75.23 | 1.77 | A * |
| " " | T | 3-4 | 0.85 | 0.92 | -0.15 | -0.005 | 0.93 | 1.91 | 0.16 | 0.09 | 0.94 | I.V. | -14.99 | Ra |
| " " | | 4-5 | 1.36 | 1.16 | 0.36 | 0.02 | 1.40 | 0.66 | 0.25 | 0.10 | 1.41 | 63.61 | 2.47 | Ra |
| " " | T | 4-5 | 0.53 | 0.73 | -0.47 | -0.02 | 0.72 | 1.43 | 0.16 | 0.10 | 0.73 | I.V. | -3.60 | Ra |
| " " | | 5-6 | 1.67 | 1.29 | 0.67 | 0.04 | 1.83 | 0.57 | 0.29 | 0.12 | 1.84 | 91.29 | 1.20 | A * |
| " " | T | 5-6 | 0.80 | 0.89 | -0.20 | -0.01 | 0.88 | 1.33 | 0.20 | 0.12 | 0.88 | I.V. | -8.33 | Ra |

TABLE 57. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PREDATORY DORYLAIMS | | 0-1 | 1.93 | 1.39 | 0.93 | 0.02 | 1.58 | 1.25 | 0.22 | 0.09 | 1.57 | 76.12 | 1.73 | A ** |
| " " | T | 0-1 | 1.30 | 1.14 | 0.30 | 0.008 | 1.14 | 1.82 | 0.18 | 0.09 | 1.13 | 36.74 | 7.41 | Ra |
| " " | | 1-2 | 2.03 | 1.43 | 1.03 | 0.01 | 1.31 | 2.84 | 0.16 | 0.06 | 1.30 | 55.39 | 3.26 | A ** |
| " " | T | 1-2 | 1.56 | 1.25 | 0.56 | 0.007 | 1.15 | 3.30 | 0.14 | 0.06 | 1.14 | 38.38 | 6.79 | Ra |
| " " | | 2-3 | 1.81 | 1.35 | 0.81 | 0.02 | 1.46 | 1.40 | 0.20 | 0.08 | 1.45 | 67.94 | 2.17 | A * |
| " " | T | 2-3 | 1.12 | 1.06 | 0.12 | 0.003 | 1.05 | 2.05 | 0.16 | 0.08 | 1.05 | 21.94 | 20.78 | Ra |
| " " | | 3-4 | 0.80 | 0.89 | -0.20 | -0.004 | 0.91 | 1.90 | 0.12 | 0.05 | 0.91 | I.V. | -10.68 | Ra |
| " " | | 4-5 | 2.17 | 1.47 | 1.17 | 0.02 | 1.40 | 2.42 | 0.17 | 0.07 | 1.39 | 63.21 | 2.50 | A ** |
| " " | T | 4-5 | 1.60 | 1.26 | 0.60 | 0.008 | 1.17 | 2.96 | 0.15 | 0.07 | 1.17 | 41.55 | 5.79 | Ra |
| " " | | 5-6 | 3.14 | 1.77 | 2.14 | 0.03 | 1.63 | 2.75 | 0.19 | 0.08 | 1.61 | 79.28 | 1.59 | A ** |
| " " | T | 5-6 | 2.48 | 1.58 | 1.48 | 0.02 | 1.37 | 3.36 | 0.17 | 0.08 | 1.35 | 60.52 | 2.73 | A ** |

TABLE 58. DATE 13-4-76. SAMPLE SIZE 1x1x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA- | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL PREDATORS | | 0-1 | 2.18 | 1.48 | 1.18 | 0.02 | 1.46 | 2.09 | 0.18 | 0.07 | 1.45 | 68.00 | 2.16 | A ** |
| " " | T | 0-1 | 1.83 | 1.35 | 0.83 | 0.01 | 1.29 | 2.42 | 0.17 | 0.07 | 1.28 | 53.43 | 3.50 | A * |
| " " | | 1-2 | 2.84 | 1.68 | 1.84 | 0.01 | 1.30 | 5.29 | 0.14 | 0.06 | 1.29 | 54.78 | 3.33 | A ** |
| " " | T | 1-2 | 2.58 | 1.60 | 1.58 | 0.01 | 1.25 | 5.55 | 0.13 | 0.06 | 1.24 | 49.71 | 4.05 | A ** |
| " " | | 2-3 | 1.85 | 1.36 | 0.85 | 0.01 | 1.27 | 2.71 | 0.15 | 0.06 | 1.26 | 51.51 | 3.77 | A * |
| " " | T | 2-3 | 1.40 | 1.18 | 0.40 | 0.005 | 1.11 | 3.15 | 0.13 | 0.06 | 1.11 | 33.26 | 9.04 | Ra |
| " " | | 3-4 | 1.45 | 1.20 | 0.45 | 0.005 | 1.13 | 3.07 | 0.13 | 0.06 | 1.12 | 35.63 | 7.88 | Ra |
| " " | | 4-5 | 2.19 | 1.48 | 1.19 | 0.01 | 1.31 | 3.22 | 0.15 | 0.06 | 1.30 | 56.03 | 3.19 | A ** |
| " " | T | 4-5 | 1.66 | 1.29 | 0.66 | 0.007 | 1.15 | 3.75 | 0.13 | 0.06 | 1.15 | 39.17 | 6.52 | Ra |
| " " | | 5-6 | 3.54 | 1.88 | 2.54 | 0.03 | 1.63 | 3.27 | 0.19 | 0.08 | 1.61 | 79.26 | 1.59 | A ** |
| " " | T | 5-6 | 3.17 | 1.78 | 2.17 | 0.02 | 1.49 | 3.61 | 0.18 | 0.08 | 1.47 | 70.12 | 2.03 | A ** |

TABLE 59. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS TOTAL JUVS. | | 0-1 | 0.90 | 0.95 | -0.10 | -0.02 | 0.78 | 0.28 | 0.36 | 0.18 | 0.76 | I.V. | -4.59 | Ra |
| " " " | | 4-5 | 1.16 | 1.08 | 0.16 | 0.04 | 1.51 | 0.16 | 0.48 | 0.28 | 1.60 | 71.55 | 1.95 | Ra |
| " " " | T | 4-5 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL | | 0-1 | 1.41 | 1.19 | 0.41 | 0.05 | 1.74 | 0.34 | 0.40 | 0.21 | 1.78 | 85.87 | 1.36 | Ra |
| " " | T | 0-1 | 0.47 | 0.68 | -0.53 | -0.07 | 0.64 | 1.16 | 0.23 | 0.21 | 0.67 | I.V. | -2.81 | Ra |
| " " | | 4-5 | 1.16 | 1.08 | 0.16 | 0.04 | 1.51 | 0.16 | 0.48 | 0.28 | 1.60 | 71.55 | 1.95 | Ra |
| " " | T | 4-5 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
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TABLE 60. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS NON-GRAVID FEMALES | | 2-3 | 1.25 | 1.12 | 0.25 | 0.03 | 1.41 | 0.40 | 0.35 | 0.18 | 1.42 | 63.67 | 2.47 | Ra |
| MYLONCHULUS NON-GRAVID FEMALES | T | 2-3 | 0.16 | 0.40 | -0.84 | -0.09 | 0.50 | 1.46 | 0.13 | 0.18 | 0.53 | I.V. | -1.98 | Re * |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL FEMALES | | 2-3 | 1.25 | 1.12 | 0.25 | 0.03 | 1.41 | 0.40 | 0.35 | 0.18 | 1.42 | 63.67 | 2.47 | Ra |
| MYLONCHULUS TOTAL FEMALES | T | 2-3 | 0.16 | 0.40 | -0.84 | -0.09 | 0.50 | 1.46 | 0.13 | 0.18 | 0.53 | I.V. | -1.98 | Re * |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 3RD ST. JUVS. | | 1-2 | 0.46 | 0.68 | -0.54 | -0.03 | 0.52 | 0.95 | 0.16 | 0.09 | 0.52 | I.V. | -2.08 | Ra |
| MYLONCHULUS 3RD ST. JUVS. | | 5-6 | 1.16 | 1.08 | 0.16 | 0.04 | 1.51 | 0.16 | 0.48 | 0.28 | 1.60 | 71.55 | 1.95 | Ra |
| MYLONCHULUS 3RD ST. JUVS. | T | 5-6 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 4TH ST. JUVS. | | 1-2 | 0.61 | 0.78 | -0.39 | -0.04 | 0.38 | 0.47 | 0.25 | 0.12 | 0.36 | I.V. | -1.62 | Ra |

TABLE 61. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL JUVS. | | 1-2 | 0.60 | 0.77 | -0.40 | -0.01 | 0.80 | 1.73 | 0.14 | 0.08 | 0.81 | I.V. | -5.00 | ■ |
| MYLONCHULUS TOTAL JUVS. | | 2-3 | 0.83 | 0.91 | -0.17 | -0.02 | 0.72 | 0.45 | 0.29 | 0.14 | 0.71 | I.V. | -3.61 | Ra |
| MYLONCHULUS TOTAL JUVS. | | 3-4 | 0.69 | 0.83 | -0.31 | -0.02 | 0.70 | 0.85 | 0.20 | 0.10 | 0.71 | I.V. | -3.39 | Ra |
| MYLONCHULUS TOTAL JUVS. | | 5-6 | 1.47 | 1.21 | 0.47 | 0.03 | 1.47 | 0.70 | 0.30 | 0.15 | 1.47 | 68.31 | 2.14 | Ra |
| MYLONCHULUS TOTAL JUVS. | T | 5-6 | 0.67 | 0.82 | -0.33 | -0.02 | 0.82 | 1.41 | 0.20 | 0.15 | 0.83 | I.V. | -5.42 | Ra |
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TABLE 62. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL | | 0-1 | 0.80 | 0.89 | -0.20 | -0.03 | 0.60 | 0.34 | 0.32 | 0.16 | 0.57 | I.V. | -2.50 | Ra |
| " " | | 1-2 | 0.78 | 0.88 | -0.22 | -0.006 | 0.91 | 2.03 | 0.14 | 0.08 | 0.91 | I.V. | -10.74 | Ra |
| " " | | 2-3 | 1.15 | 1.07 | 0.15 | 0.007 | 1.11 | 1.06 | 0.23 | 0.11 | 1.11 | 33.20 | 9.08 | Ra |
| " " | | 2-3 | 0.83 | 0.91 | -0.17 | -0.008 | 0.90 | 1.36 | 0.19 | 0.11 | 0.90 | I.V. | -9.71 | Ra |
| " " | | 3-4 | 0.69 | 0.83 | -0.31 | -0.02 | 0.70 | 0.85 | 0.20 | 0.10 | 0.71 | I.V. | -3.39 | Ra |
| " " | | 5-6 | 1.44 | 1.20 | 0.44 | 0.03 | 1.41 | 0.75 | 0.29 | 0.14 | 1.41 | 64.29 | 2.42 | Ra |
| " " | T | 5-6 | 0.59 | 0.77 | -0.41 | -0.03 | 0.78 | 1.54 | 0.19 | 0.14 | 0.79 | I.V. | -4.59 | Ra |
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TABLE 63. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS NON-GRAVID FEMALES | | 1-2 | 1.16 | 1.08 | 0.16 | 0.04 | 1.51 | 0.16 | 0.48 | 0.28 | 1.60 | 71.55 | 1.95 | Ra |
| CLARKUS NON-GRAVID FEMALES | T | 1-2 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| CLARKUS NON-GRAVID FEMALES | | 3-4 | 0.90 | 0.95 | -0.10 | -0.02 | 0.78 | 0.28 | 0.36 | 0.18 | 0.76 | I.V. | -4.59 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 1-2 | 1.16 | 1.08 | 0.16 | 0.04 | 1.51 | 0.16 | 0.48 | 0.28 | 1.60 | 71.55 | 1.95 | Ra |
| CLARKUS TOTAL FEMALES | T | 1-2 | 0.20 | 0.45 | -0.80 | -0.20 | 0.36 | 1.00 | 0.20 | 0.28 | 0.40 | I.V. | -1.56 | Ra |
| CLARKUS TOTAL FEMALES | | 3-4 | 1.07 | 1.03 | 0.07 | 0.01 | 1.13 | 0.32 | 0.37 | 0.19 | 1.14 | 36.51 | 7.50 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 64. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 1ST ST. JUVS. | | 0-1 | 1.60 | 1.26 | 0.60 | 0.03 | 1.40 | 1.11 | 0.26 | 0.13 | 1.39 | 63.25 | 2.50 | Ra |
| " " " " | T | 0-1 | 0.90 | 0.95 | -0.10 | -0.004 | 0.95 | 1.76 | 0.19 | 0.13 | 0.96 | I.V. | -21.82 | Ra |
| " " " " | | 1-2 | 2.44 | 1.56 | 1.44 | 0.03 | 1.48 | 2.32 | 0.23 | 0.11 | 1.46 | 69.39 | 2.08 | A ** |
| " " " " | T | 1-2 | 1.73 | 1.32 | 0.73 | 0.02 | 1.20 | 2.99 | 0.19 | 0.11 | 1.19 | 44.54 | 5.04 | Ra |
| " " " " | | 2-3 | 0.72 | 0.85 | -0.28 | -0.009 | 0.86 | 1.64 | 0.15 | 0.08 | 0.86 | I.V. | -6.93 | Ra |
| " " " " | | 3-4 | 2.29 | 1.51 | 1.29 | 0.07 | 2.03 | 0.83 | 0.34 | 0.17 | 2.02 | 101.72 | 0.97 | A ** |
| " " " " | T | 3-4 | 1.03 | 1.01 | 0.03 | 0.002 | 1.01 | 1.93 | 0.23 | 0.17 | 1.01 | 10.69 | 87.50 | Ra |
| " " " " | | 4-5 | 0.74 | 0.86 | -0.26 | -0.01 | 0.82 | 1.18 | 0.18 | 0.09 | 0.82 | I.V. | -5.51 | Ra |
| " " " " | | 5-6 | 1.69 | 1.30 | 0.69 | 0.07 | 2.00 | 0.42 | 0.39 | 0.21 | 2.04 | 100.25 | 1.00 | Ra |
| " " " " | T | 5-6 | 0.53 | 0.73 | -0.47 | -0.05 | 0.74 | 1.43 | 0.22 | 0.21 | 0.76 | I.V. | -3.88 | Ra |
| | | | | | | | | | | | | | | |

TABLE 65. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 2ND ST. JUVS. | | 0-1 | 0.83 | 0.91 | -0.17 | -0.02 | 0.72 | 0.45 | 0.29 | 0.14 | 0.71 | I.V. | -3.61 | Ra |
| " " " " | | 1-2 | 1.08 | 1.04 | 0.08 | 0.001 | 1.02 | 2.84 | 0.14 | 0.08 | 1.02 | 15.09 | 43.89 | Ra |
| " " " " | | 2-3 | 1.19 | 1.09 | 0.19 | 0.01 | 1.15 | 1.00 | 0.24 | 0.12 | 1.14 | 38.10 | 6.89 | Ra |
| " " " " | T | 2-3 | 0.57 | 0.76 | -0.43 | -0.02 | 0.78 | 1.59 | 0.16 | 0.12 | 0.79 | I.V. | -4.45 | Ra |
| " " " " | | 3-4 | 0.44 | 0.67 | -0.56 | -0.05 | 0.26 | 0.61 | 0.19 | 0.10 | 0.24 | I.V. | -1.35 | Ra |
| " " " " | | 4-5 | 1.15 | 1.07 | 0.15 | 0.008 | 1.12 | 0.90 | 0.25 | 0.12 | 1.12 | 35.23 | 8.06 | Ra |
| " " " " | T | 4-5 | 0.59 | 0.77 | -0.41 | -0.02 | 0.76 | 1.42 | 0.18 | 0.12 | 0.77 | I.V. | -4.21 | Ra |
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TABLE 66. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 3RD ST. JUVS. | | 0-1 | 1.88 | 1.37 | 0.88 | 0.09 | 2.29 | 0.40 | 0.41 | 0.22 | 2.33 | 113.45 | 0.78 | A * |
| " " " " | T | 0-1 | 0.32 | 0.56 | -0.68 | -0.07 | 0.69 | 1.83 | 0.17 | 0.22 | 0.73 | I.V. | -3.23 | Ra |
| " " " " | | 1-2 | 1.06 | 1.03 | 0.06 | 0.004 | 1.07 | 0.69 | 0.27 | 0.13 | 1.07 | 25.76 | 15.07 | Ra |
| " " " " | T | 1-2 | 0.30 | 0.55 | -0.70 | -0.05 | 0.58 | 1.43 | 0.14 | 0.13 | 0.60 | I.V. | -2.38 | Ra |
| " " " " | | 3-4 | 1.38 | 1.17 | 0.38 | 0.08 | 2.01 | 0.20 | 0.48 | 0.28 | 2.13 | 100.37 | 0.99 | Ra |
| " " " " | T | 3-4 | 0.22 | 0.47 | -0.78 | -0.16 | 0.48 | 1.21 | 0.19 | 0.28 | 0.53 | I.V. | -1.93 | Ra |
| " " " " | | 4-5 | 1.33 | 1.15 | 0.33 | 0.11 | 2.33 | 0.11 | 0.58 | 0.38 | 2.67 | 115.47 | 0.75 | Ra |
| " " " " | T | 4-5 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS 4TH ST. JUVS. | | 3-4 | 1.33 | 1.15 | 0.33 | 0.11 | 2.33 | 0.11 | 0.58 | 0.38 | 2.67 | 115.47 | 0.75 | Ra |
| " " " " | T | 3-4 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |

TABLE 67. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL JUVS. | | 0-1 | 3.33 | 1.82 | 2.33 | 0.05 | 1.83 | 2.05 | 0.27 | 0.13 | 1.79 | 91.00 | 12.08 | A ** |
| " " " | T | 0-1 | 2.68 | 1.64 | 1.68 | 0.04 | 1.48 | 2.62 | 0.24 | 0.13 | 1.46 | 69.62 | 2.06 | A ** |
| " " " | | 1-2 | 3.13 | 1.77 | 2.13 | 0.02 | 1.29 | 6.17 | 0.16 | 0.09 | 1.27 | 53.68 | 3.47 | A ** |
| " " " | | 2-3 | 0.93 | 0.97 | -0.07 | -0.001 | 0.98 | 3.11 | 0.13 | 0.08 | 0.98 | I.V. | -54.39 | Ra |
| " " " | | 3-4 | 2.18 | 1.48 | 1.18 | 0.03 | 1.45 | 2.03 | 0.23 | 0.11 | 1.43 | 66.98 | 2.23 | A * |
| " " " | T | 3-4 | 1.79 | 1.34 | 0.79 | 0.02 | 1.26 | 2.38 | 0.21 | 0.11 | 1.25 | 51.47 | 3.77 | Ra |
| " " " | | 4-5 | 0.97 | 0.98 | -0.03 | -0.0007 | 0.99 | 2.46 | 0.15 | 0.08 | 0.99 | I.V. | -90.17 | Ra |
| " " " | | 5-6 | 1.76 | 1.33 | 0.76 | 0.04 | 1.68 | 0.77 | 0.31 | 0.15 | 1.67 | 82.35 | 1.47 | Ra |
| " " " | T | 5-6 | 0.88 | 0.94 | -0.12 | -0.007 | 0.94 | 1.56 | 0.22 | 0.15 | 0.94 | I.V. | -16.00 | Ra |
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TABLE 68. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA- | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 3.33 | 1.82 | 2.33 | 0.05 | 1.83 | 2.05 | 0.27 | 0.13 | 1.79 | 91.00 | 1.21 | A ** |
| " " | T | 0-1 | 2.68 | 1.64 | 1.68 | 0.04 | 1.48 | 2.62 | 0.24 | 0.13 | 1.46 | 69.62 | 2.06 | A ** |
| " " | | 1-2 | 3.46 | 1.86 | 2.46 | 0.02 | 1.32 | 6.40 | 0.17 | 0.09 | 1.30 | 56.61 | 3.12 | A ** |
| " " | | 2-3 | 0.86 | 0.93 | -0.14 | -0.002 | 0.96 | 3.24 | 0.12 | 0.08 | 0.96 | I.V. | -25.90 | Ra |
| " " | | 3-4 | 2.30 | 1.52 | 1.30 | 0.03 | 1.42 | 2.45 | 0.21 | 0.11 | 1.40 | 64.46 | 2.41 | A ** |
| " " | | 4-5 | 0.97 | 0.98 | -0.03 | -0.0007 | 0.99 | 2.46 | 0.15 | 0.08 | 0.99 | I.V. | -90.17 | Ra |
| " " | | 5-6 | 2.05 | 1.43 | 1.05 | 0.06 | 1.88 | 0.80 | 0.33 | 0.16 | 1.87 | 93.84 | 1.14 | A * |
| " " | T | 5-6 | 1.12 | 1.06 | 0.12 | 0.007 | 1.06 | 1.60 | 0.24 | 0.16 | 1.05 | 23.68 | 17.83 | Ra |
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TABLE 69. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL MONONCHIDS | | 0-1 | 4.35 | 2.09 | 3.35 | 0.05 | 1.85 | 2.90 | 0.26 | 0.13 | 1.81 | 92.24 | 1.18 | A ** |
| " " | T | 0-1 | 3.43 | 1.85 | 2.43 | 0.04 | 1.50 | 3.71 | 0.23 | 0.13 | 1.47 | 70.87 | 1.99 | A ** |
| " " | | 1-2 | 2.58 | 1.61 | 1.58 | 0.01 | 1.16 | 8.79 | 0.13 | 0.08 | 1.15 | 39.59 | 6.38 | A ** |
| " " | | 2-3 | 1.38 | 1.18 | 0.38 | 0.005 | 1.07 | 4.58 | 0.13 | 0.08 | 1.07 | 27.05 | 13.67 | Ra |
| " " | | 3-4 | 1.67 | 1.29 | 0.67 | 0.009 | 1.14 | 3.99 | 0.15 | 0.08 | 1.14 | 37.81 | 6.99 | Ra |
| " " | | 4-5 | 1.01 | 1.01 | 0.01 | 0.0003 | 1.00 | 2.74 | 0.14 | 0.08 | 1.00 | 64.04 | 243.84 | Ra |
| " " | | 5-6 | 2.58 | 1.60 | 1.58 | 0.04 | 1.66 | 1.76 | 0.26 | 0.13 | 1.64 | 81.45 | 1.51 | A ** |
| " " | T | 5-6 | 2.23 | 1.49 | 1.23 | 0.02 | 1.45 | 2.06 | 0.24 | 0.13 | 1.43 | 67.45 | 2.20 | A * |
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TABLE 70. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PREDATORY DORYLAIMS | | 0-1 | 1.83 | 1.35 | 0.83 | 0.008 | 1.12 | 5.87 | 0.13 | 0.08 | 1.12 | 35.01 | 8.16 | Ra |
| " " | | 1-2 | 3.00 | 1.73 | 2.00 | 0.009 | 1.14 | 13.03 | 0.11 | 0.07 | 1.13 | 36.92 | 7.34 | A ** |
| " " | | 2-3 | 1.22 | 1.10 | 0.22 | 0.002 | 1.03 | 7.10 | 0.10 | 0.07 | 1.03 | 16.60 | 36.30 | Ra |
| " " | | 3-4 | 0.56 | 0.75 | -0.44 | -0.003 | 0.95 | 8.20 | 0.06 | 0.07 | 0.95 | I.V. | -19.72 | Ra |
| " " | | 4-5 | 4.19 | 2.05 | 3.19 | 0.02 | 1.24 | 11.44 | 0.14 | 0.08 | 1.23 | 48.98 | 4.17 | A ** |
| " " | | 5-6 | 3.38 | 1.84 | 2.38 | 0.01 | 1.21 | 9.71 | 0.14 | 0.08 | 1.20 | 46.03 | 4.72 | A ** |
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TABLE 71. DATE 13-4-76. SAMPLE SIZE 2x2x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL PREDATORS | | 0-1 | 3.75 | 1.94 | 2.75 | 0.02 | 1.26 | 9.10 | 0.15 | 0.08 | 1.24 | 50.74 | 3.88 | A ** |
| " " | | 1-2 | 3.90 | 1.97 | 2.90 | 0.007 | 1.12 | 22.29 | 0.10 | 0.07 | 1.11 | 34.22 | 8.54 | A ** |
| " " | | 2-3 | 1.56 | 1.25 | 0.56 | 0.003 | 1.04 | 11.99 | 0.09 | 0.07 | 1.04 | 20.71 | 2.33 | Ra |
| " " | | 3-4 | 1.12 | 1.06 | 0.12 | 0.0006 | 1.01 | 12.47 | 0.07 | 0.07 | 1.01 | 94.87 | 111.11 | Ra |
| " " | | 4-5 | 4.09 | 2.02 | 3.09 | 0.01 | 1.19 | 14.45 | 0.12 | 0.08 | 1.18 | 43.27 | 5.34 | A ** |
| " " | | 5-6 | 4.22 | 2.05 | 3.22 | 0.01 | 1.24 | 11.73 | 0.14 | 0.08 | 1.22 | 48.59 | 4.24 | A ** |
| | | | | | | | | | | | | | | |
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TABLE 72. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANATONCHUS 4TH ST.JUVS. | | 4-5 | 1.19 | 1.09 | 0.19 | 0.06 | 1.42 | 0.20 | 0.54 | 0.38 | 1.50 | 64.95 | 2.37 | Ra |
| " " " " | T | 4-5 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL JUVS. | | 0-1 | 0.25 | 0.50 | -0.75 | -0.09 | 0.25 | 0.83 | 0.17 | 0.14 | 0.25 | I.V. | -1.33 | Re * |
| " " " | | 4-5 | 1.50 | 1.22 | 0.50 | 0.10 | 1.75 | 0.33 | 0.50 | 0.33 | 1.80 | 86.60 | 1.33 | Ra |
| " " " | T | 4-5 | 0.67 | 0.82 | -0.33 | -0.07 | 0.78 | 1.00 | 0.33 | 0.33 | 0.80 | I.V. | -4.50 | Ra |
| | | | | | | | | | | | | | | |
| ANATONCHUS TOTAL | | 0-1 | 0.57 | 0.75 | -0.43 | -0.04 | 0.65 | 0.94 | 0.23 | 0.16 | 0.65 | I.V. | -2.83 | Ra |
| " " | | 4-5 | 1.50 | 1.22 | 0.50 | 0.10 | 1.75 | 0.33 | 0.50 | 0.33 | 1.80 | 86.60 | 1.33 | Ra |
| " " | T | 4-5 | 0.67 | 0.82 | -0.33 | -0.07 | 0.78 | 1.00 | 0.33 | 0.33 | 0.80 | I.V. | -4.50 | Ra |
| | | | | | | | | | | | | | | |

TABLE 73. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS NON-GRAVID FEMALES | | 2-3 | 0.34 | 0.58 | -0.66 | -0.05 | 0.58 | 1.31 | 0.16 | 0.13 | 0.59 | I.V. | -2.35 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL FEMALES | | 2-3 | 0.34 | 0.58 | -0.66 | -0.05 | 0.58 | 1.31 | 0.16 | 0.13 | 0.59 | I.V. | -2.35 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 1ST ST.JUVS | | 5-6 | 1.19 | 1.09 | 0.19 | 0.06 | 1.42 | 0.20 | 0.54 | 0.38 | 1.50 | 64.95 | 2.37 | Ra |
| " " " " | T | 5-6 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 2ND ST.JUVS. | | 2-3 | 0.89 | 0.94 | -0.11 | -0.02 | 0.86 | 0.50 | 0.36 | 0.22 | 0.86 | I.V. | -7.26 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 3RD ST.JUVS. | | 5-6 | 0.95 | 0.97 | -0.05 | -0.01 | 0.91 | 0.31 | 0.44 | 0.28 | 0.90 | I.V. | -11.11 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS 4TH ST.JUVS. | | 1-2 | 0.30 | 0.55 | -0.70 | -0.05 | 0.58 | 1.43 | 0.14 | 0.13 | 0.60 | I.V. | -2.38 | Ra |

TABLE 74. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYLONCHULUS TOTAL JUVS. | | 1-2 | 0.09 | 0.29 | -0.91 | -0.02 | 0.82 | 5.00 | 0.04 | 0.11 | 0.84 | I.V. | -5.71 | Re ** |
| " " " | | 2-3 | 0.77 | 0.88 | -0.23 | -0.02 | 0.81 | 0.90 | 0.27 | 0.17 | 0.82 | I.V. | -5.38 | Ra |
| " " " | | 3-4 | 0.28 | 0.53 | -0.72 | -0.03 | 0.73 | 2.38 | 0.11 | 0.12 | 0.75 | I.V. | -3.71 | Ra |
| " " " | | 5-6 | 1.51 | 1.23 | 0.51 | 0.03 | 1.27 | 1.33 | 0.30 | 0.19 | 1.26 | 52.20 | 3.67 | Ra |
| " " " | T | 5-6 | 0.94 | 0.97 | -0.06 | -0.004 | 0.98 | 1.86 | 0.24 | 0.19 | 0.98 | I.V. | -41.29 | Ra |
| | | | | | | | | | | | | | | |
| MYLONCHULUS TOTAL | | 0-1 | 0.69 | 0.83 | -0.31 | -0.04 | 0.65 | 0.63 | 0.29 | 0.19 | 0.64 | I.V. | -2.84 | Ra |
| " " | | 1-2 | 0.46 | 0.68 | -0.54 | -0.01 | 0.91 | 5.45 | 0.09 | 0.12 | 0.92 | I.V. | -11.08 | Ra |
| " " | | 2-3 | 0.83 | 0.91 | -0.17 | -0.006 | 0.94 | 2.47 | 0.18 | 0.14 | 0.95 | I.V. | -18.00 | Ra |
| " " | | 3-4 | 0.28 | 0.53 | -0.72 | -0.03 | 0.73 | 2.38 | 0.11 | 0.12 | 0.75 | I.V. | -3.71 | Ra |
| " " | | 5-6 | 1.50 | 1.22 | 0.50 | 0.03 | 1.25 | 1.42 | 0.29 | 0.19 | 1.24 | 50.00 | 4.00 | Ra |
| " " | T | 5-6 | 0.89 | 0.94 | -0.11 | -0.007 | 0.96 | 2.00 | 0.22 | 0.19 | 0.96 | I.V. | -23.14 | Ra |

TABLE 75. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS NON-GRAVID FEMALES | | 1-2 | 0.95 | 0.97 | -0.05 | -0.01 | 0.91 | 0.31 | 0.44 | 0.28 | 0.90 | I.V. | -11.11 | Ra |
| CLARKUS NON-GRAVID FEMALES | | 3-4 | 0.25 | 0.50 | -0.75 | -0.09 | 0.25 | 0.83 | 0.17 | 0.14 | 0.25 | I.V. | -1.33 | Re * |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL FEMALES | | 1-2 | 0.95 | 0.97 | -0.05 | -0.01 | 0.91 | 0.31 | 0.44 | 0.28 | 0.90 | I.V. | -11.11 | Ra |
| CLARKUS TOTAL FEMALES | | 3-4 | 0.33 | 0.57 | -0.67 | -0.08 | 0.39 | 0.91 | 0.18 | 0.14 | 0.40 | I.V. | -1.65 | Ra |
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TABLE 76. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS IST ST. JUVS. | | 0-1 | 1.15 | 1.07 | 0.15 | 0.005 | 1.05 | 2.58 | 0.20 | 0.15 | 1.04 | 21.33 | 21.99 | Ra |
| " " " " | | 1-2 | 0.80 | 0.90 | -0.20 | -0.003 | 0.97 | 6.00 | 0.11 | 0.12 | 0.97 | I.V. | -34.45 | Ra |
| " " " " | | 2-3 | 0.51 | 0.72 | -0.49 | -0.01 | 0.87 | 3.31 | 0.12 | 0.12 | 0.88 | I.V. | -7.78 | Ra |
| " " " " | | 3-4 | 1.07 | 1.04 | 0.07 | 0.0004 | 1.03 | 1.81 | 0.23 | 0.16 | 1.03 | 17.50 | 32.67 | Ra |
| " " " " | | 4-5 | 0.38 | 0.62 | -0.62 | -0.02 | 0.79 | 2.54 | 0.12 | 0.12 | 0.80 | I.V. | -4.69 | Ra |
| " " " " | | 5-6 | 1.18 | 1.09 | 0.18 | 0.02 | 1.15 | 0.82 | 0.33 | 0.21 | 1.15 | 38.57 | 6.72 | Ra |
| " " " " | T | 5-6 | 0.53 | 0.73 | -0.47 | -0.05 | 0.74 | 1.43 | 0.22 | 0.21 | 0.76 | I.V. | -3.88 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 77. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATOLE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 2ND ST. JUVS. | | 0-1 | 0.34 | 0.58 | -0.66 | -0.05 | 0.58 | 1.31 | 0.16 | 0.13 | 0.59 | I.V. | -2.35 | Ra |
| " " " " | | 1-2 | 0.70 | 0.84 | -0.30 | -0.004 | 0.96 | 6.79 | 0.10 | 0.12 | 0.96 | I.V. | -25.06 | Ra |
| " " " " | | 2-3 | 0.61 | 0.78 | -0.39 | -0.02 | 0.86 | 2.34 | 0.16 | 0.13 | 0.87 | I.V. | -7.12 | Ra |
| " " " " | | 3-4 | 0.50 | 0.71 | -0.50 | -0.04 | 0.68 | 1.26 | 0.19 | 0.14 | 0.69 | I.V. | -3.11 | Ra |
| " " " " | | 4-5 | 1.03 | 1.02 | 0.03 | 0.002 | 1.01 | 1.91 | 0.22 | 0.15 | 1.01 | 11.81 | 71.70 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS 3RD ST. JUVS. | | 0-1 | 1.39 | 1.18 | 0.39 | 0.04 | 1.32 | 0.79 | 0.36 | 0.22 | 1.31 | 56.22 | 3.16 | Ra |
| " " " " | T | 0-1 | 0.32 | 0.56 | -0.68 | -0.07 | 0.69 | 1.83 | 0.17 | 0.22 | 0.73 | I.V. | -3.23 | Ra |
| " " " " | | 1-2 | 0.29 | 0.54 | -0.71 | -0.04 | 0.66 | 1.85 | 0.12 | 0.12 | 0.68 | I.V. | -2.97 | Ra |
| " " " " | | 3-4 | 1.13 | 1.06 | 0.13 | 0.03 | 1.19 | 0.38 | 0.43 | 0.28 | 1.20 | 43.30 | 5.33 | Ra |
| " " " " | | 4-5 | 1.19 | 1.09 | 0.19 | 0.06 | 1.42 | 0.20 | 0.54 | 0.38 | 1.50 | 64.95 | 2.37 | Ra |
| " " " " | T | 4-5 | 0.25 | 0.50 | -0.75 | -0.25 | 0.44 | 1.00 | 0.25 | 0.38 | 0.50 | I.V. | -1.78 | Ra |

TABLE 78. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS 4TH ST. JUVS. | | 3-4 | 1.40 | 1.18 | 0.40 | 0.10 | 1.72 | 0.26 | 0.53 | 0.36 | 1.80 | 84.85 | 1.39 | Ra |
| " " " " | T | 3-4 | 0.20 | 0.45 | -0.80 | -0.20 | 0.52 | 1.33 | 0.20 | 0.36 | 0.60 | I.V. | -2.08 | Ra |
| | | | | | | | | | | | | | | |
| CLARKUS TOTAL JUVS. | | 0-1 | 2.25 | 1.50 | 1.25 | 0.02 | 1.21 | 4.78 | 0.20 | 0.15 | 1.19 | 45.64 | 4.80 | A * |
| " " " | | 1-2 | 1.23 | 1.11 | 0.23 | 0.002 | 1.01 | 15.16 | 0.09 | 0.12 | 1.01 | 11.75 | 72.46 | Ra |
| " " " | | 2-3 | 0.20 | 0.45 | -0.80 | -0.01 | 0.89 | 6.82 | 0.06 | 0.11 | 0.90 | I.V. | -9.03 | Re * |
| " " " | | 3-4 | 1.68 | 1.30 | 0.68 | 0.02 | 1.13 | 4.13 | 0.19 | 0.14 | 1.12 | 36.60 | 7.46 | Ra |
| " " " | | 4-5 | 0.60 | 0.77 | -0.40 | -0.008 | 0.93 | 5.16 | 0.11 | 0.12 | 0.94 | I.V. | -14.31 | Ra |
| " " " | | 5-6 | 1.24 | 1.11 | 0.24 | 0.01 | 1.11 | 1.57 | 0.26 | 0.17 | 1.11 | 33.49 | 8.91 | Ra |
| " " " | T | 5-6 | 0.95 | 0.98 | -0.05 | -0.003 | 0.98 | 1.84 | 0.22 | 0.17 | 0.98 | I.V. | -52.65 | Ra |
| | | | | | | | | | | | | | | |

TABLE 79. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA- | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLARKUS TOTAL | | 0-1 | 2.25 | 1.50 | 1.25 | 0.02 | 1.21 | 4.78 | 0.20 | 0.15 | 1.19 | 45.64 | 4.80 | A * |
| " " | | 1-2 | 1.51 | 1.23 | 0.51 | 0.003 | 1.03 | 15.52 | 0.10 | 0.12 | 1.03 | 17.15 | 34.01 | Ra |
| " " | | 2-3 | 0.17 | 0.41 | -0.83 | -0.01 | 0.89 | 7.07 | 0.05 | 0.11 | 0.90 | I.V. | -8.99 | Re * |
| " " | | 3-4 | 1.68 | 1.30 | 0.68 | 0.01 | 1.11 | 5.14 | 0.17 | 0.14 | 1.10 | 33.02 | 9.17 | Ra |
| " " | | 4-5 | 0.60 | 0.77 | -0.40 | -0.008 | 0.93 | 5.16 | 0.11 | 0.12 | 0.94 | I.V. | -14.31 | Ra |
| " " | | 5-6 | 1.55 | 1.24 | 0.55 | 0.03 | 1.25 | 1.60 | 0.28 | 0.18 | 1.23 | 49.75 | 4.04 | Ra |
| " " | T | 5-6 | 1.26 | 1.12 | 0.26 | 0.01 | 1.10 | 1.87 | 0.25 | 0.18 | 1.09 | 32.07 | 9.72 | Ra |
| | | | | | | | | | | | | | | |
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TABLE 80. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL MONONCHIDS | | 0-1 | 3.00 | 1.73 | 2.00 | 0.03 | 1.24 | 6.57 | 0.20 | 0.15 | 1.22 | 49.36 | 4.10 | A ** |
| " " | | 1-2 | 1.67 | 1.29 | 0.67 | 0.003 | 1.03 | 21.15 | 0.09 | 0.12 | 1.03 | 16.94 | 34.85 | Ra |
| " " | | 2-3 | 0.27 | 0.52 | -0.73 | -0.008 | 0.93 | 10.21 | 0.05 | 0.11 | 0.94 | I.V. | -14.83 | Re * |
| " " | | 3-4 | 1.49 | 1.22 | 0.49 | 0.005 | 1.05 | 8.92 | 0.13 | 0.13 | 1.04 | 21.81 | 21.02 | Ra |
| " " | | 4-5 | 0.63 | 0.79 | -0.37 | -0.007 | 0.94 | 5.78 | 0.10 | 0.12 | 0.95 | I.V. | -17.19 | Ra |
| " " | | 5-6 | 2.09 | 1.44 | 1.09 | 0.03 | 1.24 | 3.43 | 0.23 | 0.16 | 1.22 | 49.47 | 4.09 | Ra |
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TABLE 81. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATOLE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F. E | C.D.F. IA- | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PREDATORY DORYLAIMS | | 0-1 | 1.43 | 1.20 | 0.43 | 0.003 | 1.03 | 12.82 | 0.11 | 0.12 | 1.03 | 17.33 | 33.32 | Ra |
| " " | | 1-2 | 2.54 | 1.59 | 1.54 | 0.005 | 1.05 | 30.27 | 0.09 | 0.12 | 1.04 | 21.46 | 21.72 | A * |
| " " | | 2-3 | 0.41 | 0.64 | -0.59 | -0.004 | 0.97 | 17.31 | 0.05 | 0.11 | 0.97 | I.V. | -30.81 | Ra |
| " " | | 3-4 | 0.58 | 0.76 | -0.42 | -0.002 | 0.98 | 18.22 | 0.06 | 0.11 | 0.98 | I.V. | -46.24 | Ra |
| " " | | 4-5 | 3.23 | 1.80 | 2.23 | 0.008 | 1.07 | 28.30 | 0.11 | 0.12 | 1.06 | 26.53 | 14.21 | A ** |
| " " | | 5-6 | 2.92 | 1.71 | 1.92 | 0.009 | 1.08 | 20.90 | 0.12 | 0.12 | 1.07 | 28.45 | 12.36 | A ** |
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TABLE 82. DATE 13-4-76. SAMPLE SIZE 3x3x1 CM.

| NEMATODE GROUP | | DEPTH (cms.) | V.M.R. | L.D.I. | D.M.I. | G.I. | I.C.I. | C.D.F.E | C.D.F.IA | C.I. | M.I. | C.C. | B.F.I. | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TOTAL PREDATORS | | 0-1 | 3.16 | 1.78 | 2.16 | 0.01 | 1.10 | 19.74 | 0.12 | 0.12 | 1.09 | 30.95 | 10.44 | A ** |
| " " | | 1-2 | 3.52 | 1.88 | 2.52 | 0.005 | 1.04 | 51.85 | 0.08 | 0.12 | 1.04 | 21.12 | 22.41 | A ** |
| " " | | 2-3 | 0.15 | 0.38 | -0.85 | -0.003 | 0.97 | 28.31 | 0.02 | 0.11 | 0.97 | I.V. | -33.98 | Re ** |
| " " | | 3-4 | 1.29 | 1.13 | 0.29 | 0.001 | 1.01 | 27.50 | 0.07 | 0.12 | 1.01 | 9.85 | 103.11 | Ra |
| " " | | 4-5 | 3.44 | 1.85 | 2.44 | 0.007 | 1.06 | 34.29 | 0.10 | 0.12 | 1.06 | 25.30 | 15.62 | A ** |
| " " | | 5-6 | 2.99 | 1.73 | 1.99 | 0.008 | 1.07 | 25.05 | 0.11 | 0.12 | 1.06 | 26.62 | 14.11 | A ** |
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# APPENDIX 2. RESULTS OF THE COMPUTER ANALYSIS OF FREQUENCY DISTRIBUTIONS

**Appendix 2. Results of the computer analysis of frequency distributions.**

| | | |
|---|---|---|
| Tables 1-7: | Samples taken 16-12-74; | Sample size 5x5x5cm |
| Tables 8-14: | Samples taken 16-12-74; | Sample size 10x10x5cm |
| Tables 15,16: | Samples taken 4-2-75; | Sample size 1x1x1cm |
| Tables 17-19: | Samples taken 4-2-75; | Sample size 2x2x1cm |
| Tables 20-22: | Samples taken 4-2-75; | Sample size 3x3x1cm |
| Tables 23-30: | Samples taken 13-4-76; | Sample size 1x1x1cm |
| Tables 31-37: | Samples taken 13-4-76; | Sample size 2x2x1cm |
| Tables 38-44: | Samples taken 13-4-76; | Sample size 3x3x1cm |

Distributions tested and abbreviation used in the tables.

1. Binomial. (B.)
2. Poisson. (P.)
3. Double Poisson. (D.P.)
4. Neyman Type A. (N.T.A.)
5. Negative Binomial. (N.B.)
6. Truncated Poisson. (T.P.)
7. Truncated Neyman Type A. (T.N.T.A.)
8. Truncated Negative Binomial. (T.N.B.)
9. Logarithmic. (Log.)

N.B. The normal distribution was not included as the data is not continuous.

In most cases the number of frequency classes was too low for a standard chi-squared ($\underline{\chi^2}$) goodness-of-fit to be calculated and all results presented are obtained from the alternative $\underline{X}^2$ goodness-of-fit described by Fisher (1950).

Where the probabilities of two or more distributions are the same they have been placed in order using the calculated value of $\underline{X}^2$.

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm; TABLE 1

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Males | 0-5 | 0.80 | 6 | N.T.A. p = 0.5-0.3 | D.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Anatonchus Males | 20-25 | 0.33 | 2 | P p = 0.7-0.5 | B p = 0.5-0.3 | - |
| | | | | | | |
| Anatonchus Total Females | 0-5 | 0.55 | 2 | P p = 0.8-0.7 | B p = 0.7-0.5 | - |
| Anatonchus Total Females | 5-10 | 0.08 | 2 | P p = 0.3-0.2 | B p = 0.2-0.1 | - |
| Anatonchus Total Females | 15-20 | 0.47 | 2 | P p = 0.5-0.3 | B p = 0.2-0.1 | - |
| | | | | | | |
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SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm.

TABLE 2

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Juveniles | 0-5 | 8.75 | 5 | T.N.B. p = 0.98-0.95 | N.B. p = 0.98-0.95 | N.T.A. p = 0.98-0.95 |
| Anatonchus Juveniles | 5-10 | 0.85 | 5 | T.P. p = 0.8 - 0.7 | D.P. p = 0.7-0.5 | N.B. p = 0.7-0.5 |
| Anatonchus Juveniles | 10-15 | 1.87 | 8 | D.P. p = 0.95-0.90 | T.P. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 |
| Anatonchus Juveniles | 15-20 | 2.13 | 7 | N.T.A. p = 0.9-0.8 | D.P. p = 0.8-0.7 | N.B. p = 0.8-0.7 |
| Anatonchus Juveniles | 20-25 | 3.53 | 7 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 |
| Anatonchus Total | 0-5 | 10.1 | 4 | T.N.B. p = 0.98-0.95 | N.B. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 |
| Anatonchus Total | 5-10 | 1.15 | 7 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Anatonchus Total | 10-15 | 2.00 | 8 | N.B. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 | D.P. p = 0.8-0.7 |
| Anatonchus Total | 15-20 | 2.73 | - | NO | SIGNIFICANT | FITS |
| Anatonchus Total | 20-25 | 4.27 | 3 | D.P. p = 0.1-0.05 | N.T.A. p = 0.1-0.05 | N.B. p = 0.1-0.05 |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm.

TABLE 3

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Males | 0-5 | 5.20 | 4 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 |
| Mylonchulus Males | 5-10 | 2.25 | 6 | T.P. p = 0.5-0.3 | D.P. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Mylonchulus Males | 10-15 | 1.27 | 8 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | P. p = 0.5-0.3 |
| Mylonchulus Males | 15-20 | 0.93 | 6 | P. p = 0.5-0.3 | D.P. p = 0.2-0.1 | N.T.A. p = 0.2-0.1 |
| Mylonchulus Males | 20-25 | 0.47 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| Mylonchulus Gravid Females | 0-5 | 2.55 | 7 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Mylonchulus Gravid Females | 5-10 | 0.95 | 2 | B. p = 0.9-0.8 | P. p = 0.9-0.8 | - |
| Mylonchulus Gravid Females | 10-15 | 0.53 | 2 | P. p = 0.3-0.2 | B. p = 0.2-0.1 | - |
| Mylonchulus Gravid Females | 15-20 | 0.47 | 2 | B. p = 0.8-0.7 | P. p = 0.8-0.7 | - |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm.

TABLE 4

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Non-Gravid Females | 0-5 | 4.60 | 5 | D.P. p = 0.2-0.1 | N.B. p = 0.2-0.1 | T.P. p = 0.2-0.1 |
| Mylonchulus Non-Gravid Females | 5-10 | 2.55 | 7 | N.B. p = 0.98-0.95 | N.T.A. p = 0.95-0.90 | T.N.B. p = 0.95-0.90 |
| Mylonchulus Non-Gravid Females | 10-15 | 2.00 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | - |
| Mylonchulus Non-Gravid Females | 15-20 | 2.20 | 7 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.B. p = 0.7-0.5 |
| Mylonchulus Non-Gravid Females | 20-25 | 0.93 | 7 | N.B. p = 0.7-0.5 | Log p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Mylonchulus Total Females | 0-5 | 7.15 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total Females | 5-10 | 3.50 | 7 | T.N.B. p = 0.98-0.95 | N.B. p = 0.9-0.8 | Log. p = 0.8-0.7 |
| Mylonchulus Total Females | 10-15 | 2.53 | 7 | P. p = 0.5-0.3 | N.T.A. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Mylonchulus Total Females | 15-20 | 2.67 | 7 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | P. p = 0.5-0.3 |
| Mylonchulus Total Females | 20-25 | 1.06 | 8 | T.N.B. $p > 0.99$ | N.B. p = 0.99-0.98 | N.T.A. p = 0.98-0.95 |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm.

TABLE 5

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Juveniles | 0-5 | 19.30 | 4 | N.T.A. p = 0.9-0.8 | D.P. p = 0.9-0.8 | N.B. p = 0.8-0.7 |
| Mylonchulus Juveniles | 5-10 | 16.70 | 4 | D.P. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 | T.N.B. p = 0.8-0.7 |
| Mylonchulus Juveniles | 10-15 | 16.20 | 4 | N.T.A. p = 0.3-0.2 | D.P. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Mylonchulus Juveniles | 15-20 | 11.07 | 4 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Mylonchulus Juveniles | 20-25 | 8.20 | 5 | T.N.B. p = 0.9-0.8 | N.B. p = 0.9-0.8 | N.T.A. p = 0.7-0.5 |
| Mylonchulus Total | 0-5 | 31.70 | 5 | N.T.A. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Mylonchulus Total | 5-10 | 22.45 | 4 | D.P. p = 0.95-0.90 | N.T.A. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Mylonchulus Total | 10-15 | 20.07 | 4 | T.N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Mylonchulus Total | 15-20 | 14.67 | 4 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 |
| Mylonchulus Total | 20-25 | 9.73 | 5 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | N.T.A. p = 0.2-0.1 |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm

TABLE 6

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Gravid Females | 0-5 | 2.50 | 7 | D.P. p = 0.8-0.7 | N.B. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 |
| Clarkus Non-Gravid Females | 0-5 | 4.40 | 4 | T.N.B. p = 0.95-0.90 | N.B. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Clarkus Total Females | 0-5 | 6.90 | 3 | N.B. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Clarkus Juveniles | 0-5 | 39.20 | 3 | T.N.B. p = 0.8-0.7 | N.B. p = 0.8-0.7 | N.T.A. p = 0.1-0.05 |
| Clarkus Juveniles | 5-10 | 1.65 | - | NO | SIGNIFICANT | FITS |
| Clarkus Juveniles | 10-15 | 0.80 | 4 | N.B. p = 0.7-0.5 | N.T.A. p = 0.3-0.2 | T.P. p = 0.2-0.1 |
| Clarkus Juveniles | 15-20 | 0.33 | 2 | P. p = 0.3-0.2 | B. p = 0.2-0.1 | - |
| Clarkus Juveniles | 20-25 | 0.27 | 2 | P. p = 0.3-0.2 | B. p = 0.2-0.1 | - |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 5x5x5 cm.

TABLE 7

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Total | 0-5 | 46.10 | 4 | T.N.B. p = 0.9-0.8 | N.B. p = 0.9-0.8 | N.T.A. p = 0.3-0.2 |
| Clarkus Total | 5-10 | 2.05 | 3 | Log. p = 0.3-0.2 | N.B. p = 0.2-0.1 | N.T.A. p = 0.2-0.1 |
| Clarkus Total | 10-15 | 0.93 | 5 | N.B. p = 0.5-0.3 | N.T.A. p = 0.2-0.1 | P. p = 0.1-0.05 |
| Clarkus Total | 15-20 | 0.60 | 4 | T.P. p = 0.7 -0.5 | D.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Clarkus Total | 20-25 | 0.27 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| | | | | | | |
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SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm.

TABLE 8

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Males | 0-5 | 4.13 | 8 | T.P. p = 0.8-0.7 | P. p = 0.8-0.7 | T.N.B. p = 0.7-0.5 |
| Anatonchus Males | 5-10 | 0.50 | 2 | P. p = 0.9-0.8 | B. p = 0.8-0.7 | - |
| Anatonchus Gravid Females | 0-5 | 2.00 | 2 | B. p = 0.7-0.5 | P. p = 0.2-0.1 | - |
| Anatonchus Non-Gravid Females | 15-20 | 2.25 | 2 | B. p = 0.95-0.90 | P. p = 0.7-0.5 | - |
| Anatonchus Total Females | 0-5 | 2.50 | 2 | B. p = 0.5-0.3 | P. p = 0.3-0.2 | - |
| Anatonchus Total Females | 5-10 | 0.60 | 2 | B. p = 0.5-0.3 | P. p = 0.2-0.1 | - |
| Anatonchus Total Females | 15-20 | 2.38 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| | | | | | | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm. TABLE 9

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Juveniles | 0-5 | 36.50 | 5 | T.N.B. p = 0.3-0.2 | N.T.A. p = 0.3-0.2 | T.N.T.A. p = 0.3-0.2 |
| Anatonchus Juveniles | 5-10 | 3.75 | 7 | D.P. p = 0.7-0.5 | N.B. p = 0.7-0.5 | T.N.B. p = 0.5-0.3 |
| Anatonchus Juveniles | 10-15 | 5.88 | 8 | P. p = 0.95-0.90 | T.P. p = 0.95-0.90 | D.P. p = 0.95-0.90 |
| Anatonchus Juveniles | 15-20 | 7.88 | 2 | P. p = 0.8-0.7 | B. p = 0.2-0.1 | - |
| Anatonchus Juveniles | 20-25 | 14.00 | 7 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Anatonchus Total | 0-5 | 43.13 | 7 | T.N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Anatonchus Total | 5-10 | 4.67 | 3 | N.B. p = 0.3-0.2 | N.T.A. p = 0.2-0.1 | D.P. p = 0.2-0.1 |
| Anatonchus Total | 10-15 | 7.00 | 8 | D.P. p = 0.95-0.90 | N.B. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Anatonchus Total | 15-20 | 12.00 | 2 | P. p = 0.99-0.98 | B. p = 0.1-0.05 | - |
| Anatonchus Total | 20-25 | 17.00 | 2 | P. p = 0.7-0.5 | B. p = 0.1-0.05 | - |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm.

TABLE 10

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Males | 0-5 | 20.75 | 5 | N.B. p = 0.8-0.7 | D.P. p = 0.8-0.7 | T.N.T.A. p = 0.7-0.5 |
| Mylonchulus Males | 5-10 | 11.33 | 6 | D.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Mylonchulus Males | 10-15 | 3.50 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| Mylonchulus Males | 15-20 | 4.75 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Mylonchulus Males | 20-25 | 2.50 | 5 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Mylonchulus Gravid Females | 0-5 | 8.63 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Mylonchulus Gravid Females | 5-10 | 4.33 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Mylonchulus Gravid Females | 10-15 | 1.38 | 2 | B. p = 0.1-0.05 | P. p = 0.1-0.05 | - |
| Mylonchulus Gravid Females | 15-20 | 2.00 | 2 | P. p = 0.8-0.7 | B. p = 0.3-0.2 | - |
| Mylonchulus Gravid Females | 20-25 | 1.00 | 2 | B. p > 0.99 | P. p = 0.7-0.5 | - |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm. TABLE 11

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Non-Gravid Females | 0-5 | 14.75 | 7 | D.P. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Mylonchulus Non-Gravid Females | 5-10 | 12.50 | 7 | D.P. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 | T.N.T.A. p = 0.8-0.7 |
| Mylonchulus Non-Gravid Females | 10-15 | 6.25 | 7 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Mylonchulus Non-Gravid Females | 15-20 | 9.63 | 2 | B. p = 0.9-0.8 | P. p = 0.5-0.3 | - |
| Mylonchulus Total Females | 0-5 | 24.63 | 6 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Mylonchulus Total Females | 5-10 | 16.83 | 7 | N.B. p = 0.9-0.8 | D.P. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Mylonchulus Total Females | 10-15 | 7.63 | 7 | T.P. p = 0.8-0.7 | P. p = 0.8-0.7 | B. p = 0.7-0.5 |
| Mylonchulus Total Females | 15-20 | 11.63 | 2 | B. p = 0.5-0.3 | P. p = 0.1-0.05 | - |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm.

TABLE 12

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Juveniles | 0-5 | 7.263 | 5 | N.B. p = 0.2-0.1 | D.P. p = 0.2-0.1 | N.T.A. p = 0.2-0.1 |
| Mylonchulus Juveniles | 5-10 | 71.33 | 4 | N.T.A. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Mylonchulus Juveniles | 10-15 | 59.13 | 5 | N.B. p = 0.3-0.2 | T.N.B. p = 0.3-0.2 | D.P. p = 0.3-0.2 |
| Mylonchulus Juveniles | 15-20 | 48.25 | 5 | N.B. p = 0.7-0.5 | D.P. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Mylonchulus Juveniles | 20-25 | 41.75 | 1 | P. p = 0.7-0.5 | - | - |
| Mylonchulus Total | 0-5 | 119.00 | 4 | N.T.A. p = 0.5-0.3 | N.B. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Mylonchulus Total | 5-10 | 97.67 | 4 | N.B. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Mylonchulus Total | 10-15 | 70.25 | 5 | N.B. p = 0.3-0.2 | T.N.B. p = 0.3-0.2 | D.P. p = 0.2-0.1 |
| Mylonchulus Total | 15-20 | 64.63 | 5 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Mylonchulus Total | 20-25 | 51.00 | 1 | P. p = 0.5-0.3 | - | - |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm. TABLE 13

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Gravid Females | 0-5 | 9.50 | 1 | B. $p = 0.3-0.2$ | - | - |
| Clarkus Non-Gravid Females | 0-5 | 12.75 | 2 | D.P. $p = 0.1-0.05$ | N.T.A. $p = 0.1-0.05$ | - |
| Clarkus Non-Gravid Females | 5-10 | 0.75 | 2 | B. $p = 0.5-0.3$ | P. $p = 0.5-0.3$ | - |
| Clarkus Total Females | 0-5 | 22.25 | 6 | N.B. $p = 0.7-0.5$ | T.N.T.A. $p = 0.5-0.3$ | N.T.A. $p = 0.5-0.3$ |
| Clarkus Total Females | 5-10 | 1.33 | 6 | B. $p = 0.9-0.8$ | P. $p = 0.8-0.7$ | T.P. $p = 0.7-0.5$ |
| Clarkus Total Females | 15-20 | 1.50 | 8 | P. $p = 0.8-0.7$ | D.P. $p = 0.8-0.7$ | N.T.A. $p = 0.8-0.7$ |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 10x10x5 cm.

TABLE 14

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Juveniles | 0-5 | 100.63 | 5 | N.B. p = 0.2-0.1 | D.P. p = 0.2-0.1 | T.N.T.A. p = 0.2-0.1 |
| Clarkus Juveniles | 5-10 | 5.75 | 7 | N.T.A. p = 0.5-0.3 | D.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Clarkus Juveniles | 10-15 | 2.13 | 2 | N.B. p = 0.5-0.3 | N.T.A. p = 0.1-0.05 | - |
| Clarkus Juveniles | 15-20 | 1.50 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |
| Clarkus Juveniles | 20-25 | 1.50 | 5 | P. p = 0.95-0.90 | T.P. p = 0.8-0.7 | D.P. p = 0.8-0.7 |
| Clarkus Total | 0-5 | 125.13 | 5 | N.B. p = 0.2-0.1 | D.P. p = 0.2-0.1 | T.N.T.A. p = 0.2-0.1 |
| Clarkus Total | 5-10 | 7.08 | 7 | N.T.A. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 | P. p = 0.5-0.3 |
| Clarkus Total | 10-15 | 2.50 | 6 | N.B. p = 0.8-0.7 | Log. p = 0.8-0.7 | T.N.B. p = 0.8-0.7 |
| Clarkus Total | 15-20 | 3.00 | 4 | T.P. p = 0.9-0.8 | D.P. p = 0.5-0.3 | N.B. p = 0.3-0.2 |
| Clarkus Total | 20-25 | 1.50 | 5 | P. p = 0.95-0.90 | T.P. p = 0.8-0.7 | D.P. p = 0.8-0.7 |

SAMPLES TAKEN DECEMBER 1974: SAMPLE SIZE 15x15x5 cm. TABLE 15

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Males | 0-5 | 8.33 | 3 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | B. p = 0.2-0.1 |
| Anatonchus Males | 5-10 | 1.00 | 2 | P. p = 0.8-0.7 | B. p = 0.5-0.3 | - |
| | | | | | | |
| Anatonchus Gravid Females | 0-5 | 4.33 | 2 | B. p = 0.7-0.5 | P. p = 0.7-0.5 | - |
| | | | | | | |
| Anatonchus Total Females | 0-5 | 6.00 | 2 | B, p = 0.8-0.7 | P. p = 0.5-0.3 | - |
| Anatonchus Total Females | 5-10 | 1.00 | 2 | B. p = 0.7-0.5 | P. p = 0.5-0.3 | - |
| Anatonchus Total Females | 15-20 | 4.00 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 15x15x5 cm.

TABLE 16

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Juveniles | 0-5 | 83.00 | - | NO | SIGNIFICANT | FITS |
| Anatonchus Juveniles | 5-10 | 7.67 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |
| Anatonchus Juveniles | 10-15 | 17.67 | 2 | P. p = 0.7-0.5 | B, p = 0.1-0.5 | - |
| Anatonchus Juveniles | 15-20 | 21.33 | 2 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | - |
| | | | | | | |
| Anatonchus Total | 0-5 | 97.33 | - | NO | SIGNIFICANT | FITS |
| Anatonchus Total | 5-10 | 9.67 | 7 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Anatonchus Total | 10-15 | 19.00 | 2 | P. p = 0.7-0.5 | B. p = 0.1-0.5 | - |
| Anatonchus Total | 15-20 | 26.67 | 1 | P. p = 0.9-0.8 | - | - |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 15x15x5 cm. TABLE 17

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Males | 0-5 | 49.33 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Males | 5-10 | 26.67 | 4 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Mylonchulus Males | 10-15 | 9.00 | 2 | P. p = 0.7-0.5 | B. p = 0.2-0.1 | - |
| | | | | | | |
| Mylonchulus Gravid Females | 5-10 | 10.17 | 2 | B. p = 0.9-0.8 | P. p = 0.5-0.3 | - |
| Mylonchulus Gravid Females | 10-15 | 4.00 | 3 | T.P. p = 0.5-0.3 | P. p = 0.5-0.3 | B. p = 0.3-0.2 |
| | | | | | | |
| Mylonchulus Non-Gravid Females | 0-5 | 43.00 | 2 | P. p = 0.2-0.1 | T.P. p = 0.2-0.1 | - |
| Mylonchulus Non-Gravid Females | 5-10 | 26.67 | 4 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Mylonchulus Non-Gravid Females | 15-20 | 18.33 | 2 | P. p = 0.7-0.5 | B. p = 0.2-0.1 | - |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 15x15x5 cm.

TABLE 18

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Total Females | 0-5 | 62.33 | 2 | P. p = 0.1-0.5 | T.P. p = 0.1-0.5 | - |
| Mylonchulus Total Females | 5-10 | 38.17 | 1 | P. p = 0.95-0.90 | - | - |
| Mylonchulus Total Females | 10-15 | 19.67 | 2 | P. p = 0.1-0.05 | T.P. p = 0.1-0.05 | - |
| Mylonchulus Total Females | 15-20 | 23.00 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| | | | | | | |
| Mylonchulus Juveniles | 0-5 | 159.67 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Juveniles | 5-10 | 156.33 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Juveniles | 10-15 | 130.33 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Juveniles | 15-20 | 99.00 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 15x15x5 cm. TABLE 19

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Total | 0-5 | 271.00 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total | 5-10 | 219.17 | 4 | N.B. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 |
| Mylonchulus Total | 10-15 | 159.00 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total | 15-20 | 130.33 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |
| Clarkus Non-Gravid Females | 0-5 | 26.67 | - | NO | SIGNIFICANT | FITS |
| Clarkus Non-Gravid Females | 5-10 | 1.50 | 6 | P. p = 0.7-0.5 | B. p = 0.7-0.5 | T.P. p = 0.7-0.5 |
| | | | | | | |
| Clarkus Total Females | 0-5 | 51.00 | 2 | P. p = 0.1-0.05 | T.P. p = 0.1-0.05 | - |
| Clarkus Total Females | 5-10 | 3.00 | 2 | B. p = 0.5-0.3 | P. p = 0.3-0.2 | - |

SAMPLES TAKEN: DECEMBER 1974. SAMPLE SIZE 15x15x5 cm.

TABLE 20

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Juveniles | 0-5 | 248.33 | - | NO | SIGNIFICANT | FITS |
| Clarkus Juveniles | 5-10 | 12.67 | 8 | P. p = 0.8-0.7 | T.P. p = 0.8-0.7 | T.N.B. p = 0.7-0.5 |
| Clarkus Juveniles | 10-15 | 4.33 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |
| Clarkus Total | 0-5 | 296.33 | - | NO | SIGNIFICANT | FITS |
| Clarkus Total | 5-10 | 15.67 | 8 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | T.N.B. p = 0.2-0.1 |
| Clarkus Total | 10-15 | 5.67 | - | NO | SIGNIFICANT | FITS |
| Clarkus Total | 15-20 | 6.00 | 2 | P. p = 0.5-0.3 | B. p = 0.1-0.05 | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE lxlxl cm.

TABLE 21

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Juveniles | 0-1 | 1.16 | 6 | N.B. p = 0.9-0.8 | N.T.A. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 |
| Mylonchulus Juveniles | 1-2 | 0.32 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Mylonchulus Total | 0-1 | 1.32 | 5 | N.T.A. p = 0.2-0.1 | D.P. p = 0.2-0.1 | T.P. p = 0.2-0.1 |
| Mylonchulus Total | 1-2 | 0.52 | 6 | N.T.A. p = 0.2-0.1 | D.P. p = 0.9-0.8 | N.B. p = 0.8-0.7 |
| Mylonchulus Total | 2-3 | 0.12 | - | NO | SIGNIFICANT | FITS |
| Clarkus Non-Gravid Females | 0-1 | 0.16 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Clarkus Total Females | 0-1 | 0.20 | - | NO | SIGNIFICANT | FITS |
| Clarkus Juveniles | 0-1 | 3.80 | 5 | N.T.A. p = 0.5-0.3 | T.P. p = 0.3-0.2 | T.N.B. p = 0.3-0.2 |
| Clarkus Juveniles | 1-2 | 1.12 | 7 | P. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 | T.P. p = 0.9-0.8 |
| Clarkus Juveniles | 2-3 | 0.36 | - | NO | SIGNIFICANT | FITS |
| Clarkus Juveniles | 3-4 | 0.24 | - | NO | SIGNIFICANT | FITS |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 1x1x1 cm. TABLE 22

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Total | 0-1 | 4.00 | 5 | N.T.A. p = 0.5-0.3 | T.N.B. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Clarkus Total | 1-2 | 1.16 | 8 | P. p = 0.95-0.90 | N.T.A. p = 0.9-0.8 | T.P. p = 0.8-0.7 |
| Clarkus Total | 2-3 | 0.36 | - | NO | SIGNIFICANT | FITS |
| Clarkus Total | 3-4 | 0.24 | - | NO | SIGNIFICANT | FITS |
| Total Mononchids | 0-1 | 5.36 | 5 | T.N.B. p = 0.98-0.95 | N.T.A. p = 0.95-0.90 | D.P. p = 0.95-0.90 |
| Total Mononchids | 1-2 | 1.72 | 7 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Total Mononchids | 2-3 | 0.52 | 4 | N.T.A. p = 0.8-0.7 | T.P. p = 0.7-0.5 | D.P. p = 0.5-0.3 |
| Total Mononchids | 3-4 | 0.36 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 1x1x1 cm.

TABLE 23

| NEMATODE GROUP | VERTICAL SLICE | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Total | B | 0.36 | 1 | P. p = 0.5-0.3 | - | - |
| Mylonchulus Total | C | 0.24 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total | D | 0.40 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total | E | 0.92 | 6 | N.T.A. p = 0.8-0.7 | T.P. p = 0.8-0.7 | D.P. p = 0.7-0.5 |
| | | | | | | |
| Clarkus Total | A | 0.88 | 6 | N.T.A. p = 0.5-0.3 | N.B. p = 0.3-0.2 | T.P. p = 0.2-0.1 |
| Clarkus Total | B | 2.16 | 2 | Log. p = 0.5-0.3 | N.B. p = 0.3-0.2 | - |
| Clarkus Total | C | 1.28 | - | NO | SIGNIFICANT | FITS |
| Clarkus Total | D | 0.92 | 3 | T.P. p = 0.8-0.7 | D.P. p = 0.5-0.3 | Log. p = 0.1-0.05 |
| Clarkus Total | E | 0.84 | 4 | T.P. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 1x1x1 cm.

TABLE 24

| NEMATODE GROUP | VERTICAL SLICE | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Mononchids | A | 1.00 | 5 | T.P. p = 0.8-0.7 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Total Mononchids | B | 2.52 | 2 | Log. p = 0.5-0.3 | N.B. p = 0.3-0.2 | - |
| Total Mononchids | C | 1.52 | 3 | N.B. p = 0.3-0.2 | Log. p = 0.2-0.1 | T.N.B. p = 0.2-0.1 |
| Total Mononchids | D | 1.36 | 6 | N.T.A. p > 0.99 | D.P. p = 0.98-0.95 | T.P. p = 0.98-0.95 |
| Total Mononchids | E | 1.84 | 6 | N.B. p = 0.9-0.8 | T.N.B. p = 0.9-0.8 | Log. p = 0.7-0.5 |
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SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 2x2x1 cm. TABLE 25

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Juveniles | 0-1 | 4.13 | 4 | T.N.B. p = 0.7-0.5 | Log. p = 0.7-0.5 | N.B. p = 0.5-0.3 |
| Mylonchulus Juveniles | 1-2 | 1.63 | 2 | B. p = 0.3-0.2 | P. p = 0.3-0.2 | - |
| Mylonchulus Total | 0-1 | 5.13 | 5 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | D.P. p = 0.3-0.2 |
| Mylonchulus Total | 1-2 | 1.75 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Mylonchulus Total | 2-3 | 0.75 | 2 | P. p = 0.5-0.3 | B. p = 0.1-0.05 | - |
| Mylonchulus Total | 3-4 | 0.44 | 2 | P. p = 0.8-0.7 | B. p = 0.8-0.7 | - |
| Clarkus Non-Gravid Females | 0-1 | 1.13 | 3 | T.P. p = 0.5-0.3 | D.P. p = 0.1-0.05 | N.B. p = 0.1-0.05 |
| Clarkus Total Females | 0-1 | 1.38 | 3 | T.P. p = 0.9-0.8 | D.P. p = 0.5-0.3 | N.B. p = 0.2-0.1 |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 2x2x1 cm.

TABLE 26

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Juveniles | 0-1 | 14.88 | 4 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Clarkus Juveniles | 1-2 | 4.81 | 5 | T.N.B. p = 0.3-0.2 | N.B. p = 0.2-0.1 | D.P. p = 0.2-0.1 |
| Clarkus Juveniles | 2-3 | 1.75 | 4 | T.P. p = 0.3-0.2 | P. p = 0.1-0.05 | D.P. p = 0.1-0.05 |
| Clarkus Juveniles | 3-4 | 1.25 | 2 | P. p = 0.1-0.05 | T.P. p = 0.1-0.05 | - |
| Clarkus Juveniles | 4-5 | 1.31 | 2 | B. p = 0.95-0.90 | P. p = 0.2-0.1 | - |
| Clarkus Total | 0-1 | 16.88 | 5 | T.N.T.A. p = 0.5-0.3 | T.N.B. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Clarkus Total | 1-2 | 5.06 | 5 | T.N.B. p = 0.7-0.5 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Clarkus Total | 2-3 | 1.75 | 4 | T.P. p = 0.3-0.2 | P. p = 0.1-0.05 | D.P. p = 0.1-0.05 |
| Clarkus Total | 3-4 | 1.25 | 2 | P. p = 0.1-0.05 | T.P. p = 0.1-0.05 | - |
| Clarkus Total | 4-5 | 1.31 | 2 | B. p = 0.95-0.90 | P. p = 0.2-0.1 | - |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 2x2x1 cm.

TABLE 27

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Mononchids | 0-1 | 22.00 | 5 | N.T.A. p = 0.98-0.95 | T.N.T.A. p = 0.98-0.95 | D.P. p = 0.98-0.95 |
| Total Mononchids | 1-2 | 6.94 | 6 | D.P. p = 0.8-0.7 | N.B. p = 0.8-0.7 | N.T.A. p = 0.7-0.5 |
| Total Mononchids | 2-3 | 2.75 | 4 | T.P. p = 0.7-0.5 | D.P. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Total Mononchids | 3-4 | 1.44 | - | NO | SIGNIFICANT | FITS |
| Total Mononchids | 4-5 | 1.31 | 2 | B. p = 0.95-0.90 | P. p = 0.3-0.2 | - |
| | | | | | | |
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SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 3x3x1 cm.

TABLE 28

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Juveniles | 0-1 | 8.56 | 5 | T.N.B. p = 0.8-0.7 | N.B. p = 0.8-0.7 | D.P. p = 0.7-0.5 |
| Mylonchulus Juveniles | 1-2 | 3.44 | 2 | B. p = 0.7-0.5 | P. p = 0.1-0.05 | - |
| Mylonchulus Total | 0-1 | 10.22 | 4 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Mylonchulus Total | 1-2 | 3.67 | 2 | P. p = 0.2-0.1 | B. p = 0.2-0.1 | - |
| Mylonchulus Total | 2-3 | 2.00 | 1 | P. p = 0.7-0.5 | - | - |
| Mylonchulus Total | 3-4 | 1.00 | 2 | B. p = 0.8-0.7 | P. p = 0.3-0.2 | - |
| Clarkus Non-Gravid Females | 0-1 | 2.22 | - | NO | SIGNIFICANT | FITS |
| Clarkus Total Females | 0-1 | 2.99 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 3x3x1 cm.

TABLE 29

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Juveniles | 0-1 | 33.22 | 5 | N.B. p = 0.2-0.1 | T.N.B. p = 0.2-0.1 | T.N.T.A. p = 0.2-0.1 |
| Clarkus Juveniles | 1-2 | 13.00 | 6 | N.B. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 |
| Clarkus Juveniles | 2-3 | 3.78 | 2 | P. p = 0.7-0.5 | B. p = 0.2-0.1 | - |
| Clarkus Juveniles | 3-4 | 1.22 | 2 | P. p = 0.1-0.05 | T.P. p = 0.1-0.05 | - |
| Clarkus Juveniles | 4-5 | 3.22 | 1 | B. p = 0.5-0.3 | - | - |
| Clarkus Total | 0-1 | 36.11 | 5 | N.B. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Clarkus Total | 1-2 | 11.44 | 4 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Clarkus Total | 2-3 | 3.78 | 2 | P. p = 0.7-0.5 | B. p = 0.2-0.1 | - |
| Clarkus Total | 3-4 | 2.22 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| Clarkus Total | 4-5 | 3.22 | 1 | B. p = 0.5-0.3 | - | - |

SAMPLES TAKEN: FEBRUARY 1975. SAMPLE SIZE 3x3x1 cm. TABLE 30

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Mononchids | 0-1 | 46.33 | 6 | T.N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Total Mononchids | 1-2 | 14.78 | 7 | D.P. p = 0.8-0.7 | N.B. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 |
| Total Mononchids | 2-3 | 6.22 | 7 | P. p = 0.8-0.7 | T.P. p = 0.8-0.7 | T.N.B. p = 0.7-0.5 |
| Total Mononchids | 3-4 | 2.56 | 2 | P. p = 0.7-0.5 | B. p = 0.1-0.05 | - |
| Total Mononchids | 4-5 | 3.22 | 1 | B. p = 0.5-0.3 | - | - |
| | | | | | | |
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| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm.

TABLE 31

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Total Juveniles | 4-5 | 0.16 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | - |
| Anatonchus Total | 0-1 | 0.12 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | - |
| Anatonchus Total | 4-5 | 0.16 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | - |
| Mylonchulus Non-Gravid Females | 2-3 | 0.12 | 1 | P. p = 0.1-0.05 | - | - |
| Mylonchulus Total Females | 2-3 | 0.12 | 1 | P. p = 0.1-0.05 | - | - |
| Mylonchulus Total Juveniles | 1-2 | 0.44 | 2 | P. p = 0.3-0.2 | B. p = 0.1-0.05 | - |
| Mylonchulus Total Juveniles | 2-3 | 0.20 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | |
| Mylonchulus Total Juveniles | 3-4 | 0.24 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Mylonchulus Total Juveniles | 5-6 | 0.32 | 2 | P. p = 0.95-0.90 | B. p = 0.7-0.5 | - |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm. TABLE 32

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Total | 1-2 | 0.56 | 1 | P. p = 0.3-0.2 | - | - |
| Mylonchulus Total | 2-3 | 0.36 | 5 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Mylonchulus Total | 3-4 | 0.24 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Mylonchulus Total | 5-6 | 0.36 | 2 | B. p = 0.9-0.8 | P. p = 0.7-0.5 | - |
| | | | | | | |
| Clarkus Non-Gravid Females | 3-4 | 0.16 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | |
| Clarkus Total Females | 3-4 | 0.20 | - | NO | SIGNIFICANT | FITS |
| | | | | | | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm. TABLE 33

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus 1st Stage Juveniles | 0-1 | 0.32 | 2 | P. p = 0.3-0.2 | B. p = 0.1-0.05 | - |
| Clarkus 1st Stage Juveniles | 1-2 | 0.92 | 6 | T.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | D.P. p = 0.5-0.3 |
| Clarkus 1st Stage Juveniles | 2-3 | 0.48 | 6 | P. p = 0.7-0.5 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| Clarkus 1st Stage Juveniles | 3-4 | 0.40 | 5 | T.P. p = 0.98-0.95 | N.T.A. p = 0.98-0.95 | D.P. p = 0.9-0.8 |
| Clarkus 1st Stage Juveniles | 4-5 | 0.32 | 2 | P. p = 0.95-0.90 | B. p = 0.7-0.5 | - |
| Clarkus 1st Stage Juveniles | 5-6 | 0.20 | 2 | P. p = 0.2-0.1 | B. p = 0.2-0.1 | - |
| Clarkus 2nd Stage Juveniles | 1-2 | 0.88 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| Clarkus 2nd Stage Juveniles | 2-3 | 0.36 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Clarkus 2nd Stage Juveniles | 3-4 | 0.24 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Clarkus 2nd Stage Juveniles | 4-5 | 0.28 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm.

TABLE 34

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus 3rd Stage Juveniles | 0-1 | 0.16 | 2 | P. p = 0.2-0.1 | B. p = 0.1-0.05 | - |
| Clarkus 3rd Stage Juveniles | 3-4 | 0.12 | 1 | P. p = 0.1-0.05 | - | - |
| Clarkus Total Juveniles | 0-1 | 0.64 | 6 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | Log. p = 0.5-0.3 |
| Clarkus Total Juveniles | 1-2 | 2.08 | 5 | N.B. p = 0.9-0.8 | T.N.B. p = 0.8-0.7 | Log. p = 0.8-0.7 |
| Clarkus Total Juveniles | 2-3 | 0.96 | 4 | T.P. p = 0.7-0.5 | P. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Clarkus Total Juveniles | 3-4 | 0.84 | 5 | T.P. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Clarkus Total Juveniles | 4-5 | 0.72 | 5 | T.P. p = 0.3-0.2 | P. p = 0.3-0.2 | D.P. p = 0.2-0.1 |
| Clarkus Total Juveniles | 5-6 | 0.36 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm. TABLE 35

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Total | 0-1 | 0.64 | 6 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | Log. p = 0.5-0.3 |
| Clarkus Total | 1-2 | 2.20 | 5 | N.B. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 | Log. p = 0.5-0.3 |
| Clarkus Total | 2-3 | 1.00 | 5 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Clarkus Total | 3-4 | 1.04 | 5 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 | D.P. p = 0.3-0.2 |
| Clarkus Total | 4-5 | 0.72 | 5 | T.P. p = 0.3-0.2 | P. p = 0.3-0.2 | D.P. p = 0.2-0.1 |
| Clarkus Total | 5-6 | 0.40 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| | | | | | | |
| | | | | | | |
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SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm.

TABLE 36

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Mononchids | 0-1 | 0.96 | 6 | P. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 | T.P. p = 0.3-0.2 |
| Total Mononchids | 1-2 | 1.76 | 3 | N.B. p = 0.1-0.05 | N.T.A. p = 0.1-0.05 | T.N.B. p = 0.1-0.05 |
| Total Mononchids | 2-3 | 1.44 | 7 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.B. p = 0.7-0.5 |
| Total Mononchids | 3-4 | 1.36 | 7 | T.P. p = 0.98-0.95 | D.P. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 |
| Total Mononchids | 4-5 | 0.88 | 7 | D.P. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Total Mononchids | 5-6 | 0.80 | 6 | P. p = 0.7-0.5 | T.P. p = 0.5-0.3 | B. p = 0.5-0.3 |
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SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm. TABLE 37

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Predatory Dorylaims | 0-1 | 1.60 | 7 | T.N.B. p = 0.9-0.8 | Log. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Predatory Dorylaims | 1-2 | 3.36 | 7 | N.T.A. p = 0.9-0.8 | D.P. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Predatory Dorylaims | 2-3 | 1.76 | 6 | N.T.A. p = 0.5-0.3 | D.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Predatory Dorylaims | 3-4 | 2.16 | 2 | P. p = 0.3-0.2 | B. p = 0.2-0.1 | - |
| Predatory Dorylaims | 4-5 | 2.92 | 7 | N.T.A. p = 0.9-0.8 | N.B. p = 0.9-0.8 | D.P. p = 0.9-0.8 |
| Predatory Dorylaims | 5-6 | 3.40 | 6 | N.T.A. p = 0.95-0.90 | N.B. p = 0.95-0.90 | T.N.B. p = 0.9-0.8 |
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SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 1x1x1 cm. TABLE 38

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Predators | 0-1 | 2.56 | 5 | Log. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 | N.B. p = 0.3-0.2 |
| Total Predators | 1-2 | 6.12 | 4 | N.B. p = 0.8-0.7 | D.P. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 |
| Total Predators | 2-3 | 3.20 | 6 | D.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | T.P. p = 0.7-0.5 |
| Total Predators | 3-4 | 3.52 | 6 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | D.P. p = 0.3-0.2 |
| Total Predators | 4-5 | 3.80 | 7 | N.T.A. p = 0.9-0.8 | N.B. p = 0.8-0.7 | D.P. p = 0.8-0.7 |
| Total Predators | 5-6 | 3.88 | 4 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
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SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 39

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus Total Juveniles | 0-1 | 0.44 | 2 | P. p = 0.8-0.7 | B. p = 0.8-0.7 | - |
| Anatonchus Total Juveniles | 4-5 | 0.31 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Anatonchus Total | 0-1 | 0.56 | 6 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Anatonchus Total | 4-5 | 0.31 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Mylonchulus Non-Gravid Females | 2-3 | 0.63 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus Total Females | 2-3 | 0.63 | - | NO | SIGNIFICANT | FITS |
| Mylonchulus 3rd St. Juveniles | 1-2 | 1.13 | 2 | B. p = 0.95-0.90 | P. p = 0.2-0.1 | - |
| Mylonchulus 3rd St. Juveniles | 5-6 | 0.31 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Mylonchulus 4th St. Juveniles | 1-2 | 0.63 | 2 | B. p = 0.7-0.5 | P. p = 0.2-0.1 | - |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 40

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus Total Juveniles | 1-2 | 2.00 | 2 | B. p = 0.7-0.5 | P. p = 0.3-0.2 | - |
| Mylonchulus Total Juveniles | 2-3 | 0.63 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| Mylonchulus Total Juveniles | 3-4 | 1.06 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| Mylonchulus Total Juveniles | 5-6 | 1.00 | 8 | N.B. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 | D.P. p = 0.9-0.8 |
| Mylonchulus Total | 0-1 | 0.50 | 2 | B. p > 0.99 | P. p = 0.5-0.3 | - |
| Mylonchulus Total | 1-2 | 2.38 | 2 | P. p = 0.5-0.3 | B. p = 0.5-0.3 | - |
| Mylonchulus Total | 2-3 | 1.38 | 8 | T.N.B. p = 0.9-0.8 | Log. p = 0.8-0.7 | T.P. p = 0.7-0.5 |
| Mylonchulus Total | 3-4 | 1.06 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| Mylonchulus Total | 5-6 | 1.06 | 8 | N.T.A. p = 0.95-0.90 | D.P. p = 0.9-0.8 | T.P. p = 0.9-0.8 |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 41

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Non-Gravid Females | 1-2 | 0.31 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Clarkus Non-Gravid Females | 3-4 | 0.44 | 2 | P. p = 0.8-0.7 | B. p = 0.8-0.7 | - |
| Clarkus Total Females | 1-2 | 0.31 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Clarkus Total Females | 3-4 | 0.50 | 2 | P. p = 0.7-0.5 | B. p = 0.3-0.2 | - |
| Clarkus lst. st. Juveniles | 0-1 | 1.50 | 8 | N.B. p = 0.95-0.90 | N.T.A. p = 0.9-0.8 | D.P. p = 0.9-0.8 |
| Clarkus lst st. Juveniles | 1-2 | 3.00 | 7 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | D.P. p = 0.5-0.3 |
| Clarkus lst st. Juveniles | 2-3 | 1.94 | 2 | B. p = 0.95-0.90 | P. p = 0.7-0.5 | - |
| Clarkus lst st. Juveniles | 3-4 | 1.25 | 7 | T.P. p = 0.8-0.7 | D.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Clarkus lst st. Juveniles | 4-5 | 1.44 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |
| Clarkus lst st. Juveniles | 5-6 | 0.69 | 5 | N.T.A. p = 0.5-0.3 | N.B. p = 0.5-0.3 | T.P. p = 0.5-0.3 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2xl cm.

TABLE 42

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus 2nd st. Juveniles | 0-1 | 0.63 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| Clarkus 2nd st. Juveniles | 1-2 | 3.31 | 8 | P. p = 0.9-0.8 | T.P. p = 0.9-0.8 | D.P. p = 0.9-0.8 |
| Clarkus 2nd st. Juveniles | 2-3 | 1.31 | 8 | D.P. p = 0.95-0.90 | T.P. p = 0.95-0.90 | N.T.A. p = 0.95-0.90 |
| Clarkus 2nd st. Juveniles | 3-4 | 0.75 | 1 | B. p = 0.2-0.1 | - | - |
| Clarkus 2nd st. Juveniles | 4-5 | 1.19 | 8 | P. p = 0.95-0.90 | D.P. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Clarkus 3rd St. Juveniles | 0-1 | 0.69 | 3 | T.P. p = 0.5-0.3 | D.P. p = 0.2-0.1 | N.B. p = 0.1-0.05 |
| Clarkus 3rd st. Juveniles | 1-2 | 0.94 | 5 | P. p = 0.7-0.5 | T.P. p = 0.5-0.3 | D.P. p = 0.3-0.2 |
| Clarkus 3rd st. Juveniles | 3-4 | 0.38 | 1 | P. p = 0.2-0.1 | - | - |
| Clarkus 3rd st. Juveniles | 4-5 | 0.25 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 43

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus 4th st. Juveniles | 3-4 | 0.25 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Clarkus Total Juveniles | 0-1 | 2.81 | 4 | T.N.B. p = 0.95-0.90 | Log. p = 0.95-0.90 | N.B. p = 0.9-0.8 |
| Clarkus Total Juveniles | 1-2 | 7.38 | 5 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 | D.P. p = 0.7-0.5 |
| Clarkus Total Juveniles | 2-3 | 3.56 | 2 | P. p = 0.9-0.8 | B. p = 0.1-0.05 | - |
| Clarkus Total Juveniles | 3-4 | 2.63 | 8 | N.B. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 |
| Clarkus Total Juveniles | 4-5 | 3.88 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |
| Clarkus Total Juveniles | 5-6 | 1.13 | 7 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 | N.T.A. p = 0.5-0.3 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 44

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P> 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Total | 0-1 | 2.81 | 5 | T.N.B. p = 0.95-0.90 | Log. p = 0.95-0.90 | T.P. p = 0.95-0.90 |
| Clarkus Total | 1-2 | 7.69 | 5 | D.P. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 |
| Clarkus Total | 2-3 | 3.69 | 1 | P. p = 0.7-0.5 | - | - |
| Clarkus Total | 3-4 | 3.13 | 8 | T.N.B. p = 0.95-0.90 | N.B. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Clarkus Total | 4-5 | 3.88 | 2 | P. p = 0.9-0.8 | B. p = 0.5-0.3 | - |
| Clarkus Total | 5-6 | 1.19 | 7 | N.B. p = 0.8-0.7 | Log. p = 0.7-0.5 | T.N.B. p = 0.7-0.5 |
| Total Mononchids | 0-1 | 3.94 | 6 | N.T.A. p = 0.8-0.7 | N.B. p = 0.8-0.7 | T.N.B. p = 0.8-0.7 |
| Total Mononchids | 1-2 | 10.06 | 6 | T.N.B. p = 0.99-0.98 | N.B. p = 0.98-0.95 | D.P. p = 0.98-0.95 |
| Total Mononchids | 2-3 | 5.25 | 7 | P. p = 0.8-0.7 | T.P. p = 0.8-0.7 | D.P. p = 0.7-0.5 |
| Total Mononchids | 3-4 | 4.69 | 7 | T.N.B. p = 0.99-0.98 | N.T.A. p = 0.98-0.95 | P. p = 0.98-0.95 |
| Total Mononchids | 4-5 | 3.19 | 6 | P. p = 0.7-0.5 | T.P. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Total Mononchids | 5-6 | 2.38 | 7 | T.N.B. p = 0.98-0.95 | Log. p = 0.98-0.95 | N.B. p = 0.7-0.5 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 2x2x1 cm.

TABLE 45

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Predatory Dorylaims | 0-1 | 6.75 | 4 | T.N.B. p = 0.3-0.2 | D.P. p = 0.3-0.2 | N.B. p = 0.3-0.2 |
| Predatory Dorylaims | 1-2 | 14.69 | 7 | T.N.B. p = 0.9-0.8 | N.B. p = 0.9-0.8 | T.N.T.A. p = 0.9-0.8 |
| Predatory Dorylaims | 2-3 | 7.88 | 6 | D.P. p = 0.95-0.90 | P. p = 0.95-0.90 | T.P. p = 0.95-0.90 |
| Predatory Dorylaims | 3-4 | 7.75 | 2 | B. p = 0.95-0.90 | P. p = 0.8-0.7 | - |
| Predatory Dorylaims | 4-5 | 13.31 | 4 | D.P. p = 0.5-0.3 | T.N.B. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Predatory Dorylaims | 5-6 | 11.25 | 4 | T.N.B. p = 0.7-0.5 | N.B. p = 0.7-0.5 | N.T.A. p = 0.5-0.3 |
| Total Predators | 0-1 | 10.69 | 4 | T.N.B. p = 0.8-0.7 | N.B. p = 0.8-0.7 | N.T.A. p = 0.8-0.7 |
| Total Predators | 1-2 | 24.75 | 5 | T.N.B. p = 0.9-0.8 | T.N.T.A. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Total Predators | 2-3 | 13.06 | 7 | D.P. p = 0.9-0.8 | N.B. p = 0.8-0.7 | T.N.T.A. p = 0.8-0.7 |
| Total Predators | 3-4 | 13.44 | 6 | P. p = 0.8-0.7 | T.P. p = 0.8-0.7 | D.P. p = 0.8-0.7 |
| Total Predators | 4-5 | 16.50 | 4 | D.P. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 | N.B. p = 0.9-0.8 |
| Total Predators | 5-6 | 13.63 | 7 | D.P. p = 0.8-0.7 | N.B. p = 0.8-0.7 | T.N.B. p = 0.8-0.7 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm.

TABLE 46

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Anatonchus 4th st. Juveniles | 4-5 | 0.44 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Anatonchus Total Juveniles | 0-1 | 1.00 | 1 | B. p = 0.1-0.05 | - | - |
| Anatonchus Total Juveniles | 4-5 | 0.67 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| Anatonchus Total | 0-1 | 1.22 | 2 | B. p = 0.3-0.2 | P. p = 0.2-0.1 | - |
| Anatonchus Total | 4-5 | 0.67 | 2 | P. p = 0.8-0.7 | B. p = 0.7-0.5 | - |
| Mylonchulus Non-Gravid Females | 2-3 | 1.56 | 2 | B. p = 0.5-0.3 | P. p = 0.3-0.2 | - |
| Mylonchulus Total Females | 2-3 | 1.56 | 2 | B. p = 0.5-0.3 | P. p = 0.3-0.2 | - |
| Mylonchulus 1st st. Juveniles | 5-6 | 0.44 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Mylonchulus 2nd st. Juveniles | 2-3 | 0.78 | 2 | P. p = 0.8-0.7 | B. p = 0.5-0.3 | - |
| Mylonchulus 3rd st. Juveniles | 5-6 | 0.56 | 2 | P. p = 0.95-0.90 | B. p = 0.7-0.5 | - |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm.

TABLE 47

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Mylonchulus 4th st. Juveniles | 1-2 | 1.67 | 2 | B. p = 0.7-0.5 | P. p = 0.2-0.1 | - |
| Mylonchulus Total Juveniles | 1-2 | 5.22 | 1 | B. p = 0.5-0.3 | - | - |
| Mylonchulus Total Juveniles | 2-3 | 1.22 | 2 | P. p = 0.9-0.8 | B. p = 0.9-0.8 | - |
| Mylonchulus Total Juveniles | 3-4 | 2.67 | 2 | B. p = 0.7-0.5 | P. p = 0.1-0.05 | - |
| Mylonchulus Total Juveniles | 5-6 | 1.89 | 8 | P. p = 0.7-0.5 | D.P. p = 0.7-0.5 | N.B. p = 0.7-0.5 |
| Mylonchulus Total | 0-1 | 0.89 | 2 | B. p = 0.8-0.7 | P. p = 0.7-0.5 | - |
| Mylonchulus Total | 1-2 | 6.00 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| Mylonchulus Total | 2-3 | 3.00 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| Mylonchulus Total | 3-4 | 2.67 | 2 | B. p = 0.7-0.5 | P. p = 0.1-0.05 | - |
| Mylonchulus Total | 5-6 | 2.00 | 8 | D.P. p = 0.98-0.95 | N.T.A. p = 0.98-0.95 | N.B. p = 0.98-0.95 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3xl cm.

TABLE 48

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Non-Gravid Females | 1-2 | 0.56 | 2 | P. p = 0.95-0.90 | B. p = 0.7-0.5 | - |
| Clarkus Non-Gravid Females | 3-4 | 1.00 | 1 | B. p = 0.1-0.05 | - | - |
| Clarkus Total Females | 1-2 | 0.56 | 2 | P. p = 0.95-0.90 | B. p = 0.7-0.5 | - |
| Clarkus Total Females | 3-4 | 1.11 | 2 | B. p = 0.3-0.2 | P. p = 0.1-0.05 | - |
| Clarkus 1st st. Juveniles | 0-1 | 3.22 | 8 | P. p = 0.9-0.8 | T.P. p = 0.8-0.7 | D.P. p = 0.8-0.7 |
| Clarkus 1st st. Juveniles | 1-2 | 6.78 | 2 | P. p = 0.95-0.90 | B. p = 0.3-0.2 | - |
| Clarkus 1st st. Juveniles | 2-3 | 3.78 | 2 | P. p = 0.9-0.8 | B. p = 0.9-0.8 | - |
| Clarkus 1st st. Juveniles | 3-4 | 2.33 | 2 | B. p = 0.8-0.7 | P. p = 0.8-0.7 | - |
| Clarkus 1st st. Juveniles | 4-5 | 2.89 | 2 | B. p = 0.7-0.5 | P. p = 0.5-0.3 | - |
| Clarkus 1st st. Juveniles | 5-6 | 1.22 | 5 | P. p = 0.7-0.5 | D.P. p = 0.5-0.3 | T.P. p = 0.5-0.3 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm. TABLE 49

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus 2nd st. Juveniles | 0-1 | 1.56 | 2 | B. p = 0.7-0.5 | P. p = 0.5-0.3 | - |
| Clarkus 2nd st. Juveniles | 1-2 | 7.56 | 2 | P. p = 0.98-0.95 | B. p = 0.3-0.2 | - |
| Clarkus 2nd st. Juveniles | 2-3 | 2.78 | 2 | P. p = 0.5-0.3 | B. p = 0.5-0.3 | - |
| Clarkus 2nd st. Juveniles | 3-4 | 1.56 | 2 | B. p = 0.95-0.90 | P. p = 0.5-0.3 | - |
| Clarkus 2nd st. Juveniles | 4-5 | 2.44 | 7 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | D.P. p = 0.3-0.2 |
| Clarkus 3rd st. Juveniles | 0-1 | 1.22 | 4 | T.P. p = 0.5-0.3 | P. p = 0.2-0.1 | D.P. p = 0.2-0.1 |
| Clarkus 3rd st. Juveniles | 1-2 | 2.11 | 2 | B. p = 0.95-0.90 | P. p = 0.3-0.2 | - |
| Clarkus 3rd st. Juveniles | 3-4 | 0.67 | 2 | P. p = 0.5-0.3 | B. p = 0.2-0.1 | - |
| Clarkus 3rd st. Juveniles | 4-5 | 0.44 | 2 | P. p = 0.7-0.5 | B. p = 0.5-0.3 | - |
| Clarkus 4th st. Juveniles | 3-4 | 0.56 | 1 | P. p = 0.2-0.1 | - | - |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm.

TABLE 50

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Clarkus Total Juveniles | 0-1 | 6.00 | 7 | T.N.B. p = 0.7-0.5 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Clarkus Total Juveniles | 1-2 | 16.67 | 7 | T.P. p = 0.2-0.1 | P. p = 0.2-0.1 | N.B. p = 0.1-0.05 |
| Clarkus Total Juveniles | 2-3 | 7.22 | 2 | B. p = 0.95-0.90 | P. p = 0.9-0.8 | - |
| Clarkus Total Juveniles | 3-4 | 5.11 | 7 | P. p = 0.2-0.1 | T.P. p = 0.2-0.1 | B. p = 0.1-0.05 |
| Clarkus Total Juveniles | 4-5 | 5.78 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| Clarkus Total Juveniles | 5-6 | 2.11 | 8 | P. p = 0.95-0.90 | D.P. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 |
| Clarkus Total | 0-1 | 6.00 | 7 | T.N.B. p = 0.7-0.5 | N.B. p = 0.5-0.3 | D.P. p = 0.5-0.3 |
| Clarkus Total | 1-2 | 17.22 | 7 | D.P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | P. p = 0.5-0.3 |
| Clarkus Total | 2-3 | 7.44 | 2 | P. p = 0.9-0.8 | B. p = 0.8-0.7 | - |
| Clarkus Total | 3-4 | 6.22 | 7 | P. p = 0.95-0.90 | T.P. p = 0.95-0.90 | N.T.A. p = 0.9-0.8 |
| Clarkus Total | 4-5 | 5.78 | 2 | P. p = 0.5-0.3 | B. p = 0.3-0.2 | - |
| Clarkus Total | 5-6 | 2.22 | 8 | T.N.B. p = 0.95-0.90 | P. p = 0.95-0.90 | N.T.A. p = 0.9-0.8 |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm.

TABLE 51

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO $P > 0.05$ | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Total Mononchids | 0-1 | 8.22 | 7 | D.P. p = 0.99-0.98 | N.B. p = 0.99-0.98 | T.N.B. p = 0.98-0.95 |
| Total Mononchids | 1-2 | 23.22 | 6 | P. p = 0.5-0.3 | T.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 |
| Total Mononchids | 2-3 | 10.78 | 2 | B. p = 0.5-0.3 | P. p = 0.3-0.2 | - |
| Total Mononchids | 3-4 | 10.22 | 6 | P. p = 0.2-0.1 | T.P. p = 0.2-0.1 | D.P. p = 0.1-0.05 |
| Total Mononchids | 4-5 | 6.44 | 2 | P. p = 0.7-0.5 | B. p = 0.7-0.5 | - |
| Total Mononchids | 5-6 | 4.44 | 6 | T.P. p = 0.2-0.1 | P. p = 0.2-0.1 | T.N.B. p = 0.2-0.1 |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |

SAMPLES TAKEN: APRIL 1976. SAMPLE SIZE 3x3x1 cm. TABLE 52

| NEMATODE GROUP | DEPTH (cms.) | MEAN NO. OF INDIVIDUALS | NUMBER OF DISTRIBUTIONS FITTING TO P > 0.05 | THREE BEST FITTING DISTRIBUTIONS | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| Predatory Dorylaims | 0-1 | 14.33 | 8 | D.P. p = 0.95-0.90 | N.B. p = 0.95-0.90 | T.N.T.A. p = 0.95-0.90 |
| Predatory Dorylaims | 1-2 | 33.33 | 6 | N.B. p = 0.7-0.5 | T.N.T.A. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Predatory Dorylaims | 2-3 | 18.22 | 1 | P. p = 0.8-0.7 | - | - |
| Predatory Dorylaims | 3-4 | 19.33 | 2 | P. p = 0.99-0.98 | B. p = 0.5-0.3 | - |
| Predatory Dorylaims | 4-5 | 31.67 | - | NO | SIGNIFICANT | FITS |
| Predatory Dorylaims | 5-6 | 23.67 | 5 | D.P. p = 0.5-0.3 | N.B. p = 0.5-0.3 | T.N.T.A. p = 0.5-0.3 |
| Total Predators | 0-1 | 22.56 | 5 | D.P. p = 0.7-0.5 | T.N.T.A. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Total Predators | 1-2 | 56.56 | 6 | T.N.B. p = 0.9-0.8 | N.T.A. p = 0.9-0.8 | T.N.T.A. p = 0.9-0.8 |
| Total Predators | 2-3 | 29.00 | 2 | P. p = 0.7-0.5 | B. p = 0.2-0.1 | - |
| Total Predators | 3-4 | 29.56 | 6 | P. p = 0.7-0.5 | T.P. p = 0.7-0.5 | N.T.A. p = 0.7-0.5 |
| Total Predators | 4-5 | 38.11 | 5 | D.P. p = 0.1-0.05 | T.N.T.A. p = 0.1-0.05 | N.T.A. p = 0.1-0.05 |
| Total Predators | 5-6 | 28.11 | 5 | N.B. p = 0.7-0.5 | D.P. p = 0.7-0.5 | T.N.T.A. p = 0.7-0.5 |

# APPENDIX III. RESULTS OF THE EXPERIMENTS ON POPULATION DEVELOPMENT FROM SINGLE FEMALES OF P.PUNCTATUS.

Tables 1-12: Results of 2-3 day counts of predators in population development from single P.punctatus females I.

Tables 13,14: Results of fortnightly extractions of predators in population development from single P.punctatus females I.

Tables 15-19: Results of 2-3 day counts of predators in population development from single female P.punctatus extracted from Bracken F-layer material.

All tables show the Mean (± S.E.) number of predators per culture remaining on the day of counting.

In all the tables the treatments are as follows:

A: Old soil-extract agar

B: Soil-extract agar plus an extract of old soil-extract agar.

C: Fresh soil-extract agar.

D: Water agar.

In tables 15-19 E: Bracken fermentation layer material-extract agar.

TABLE 1

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 2 | A | 24 | 0.92 ± 0.12 | 6.08 ± 0.81 | - | - | - | - | - |
| | B | 24 | 1.00 ± 0.09 | 8.33 ± 1.13 | - | - | - | - | - |
| | C | 24 | 0.88 ± 0.11 | 6.58 ± 1.33 | - | - | - | - | - |
| | D | 24 | 0.88 ± 0.11 | 4.54 ± 0.83 | - | - | - | - | - |
| 5 | A | 24 | 0.92 ± 0.10 | 9.96 ± 1.47 | - | - | - | - | - |
| | B | 24 | 1.00 ± 0.09 | 17.50 ± 2.07 | - | - | - | - | - |
| | C | 24 | 0.88 ± 0.11 | 16.46 ± 2.71 | - | - | - | - | - |
| | D | 24 | 0.88 ± 0.11 | 11.08 ± 1.72 | - | - | - | - | - |
| 7 | A | 24 | 0.92 ± 0.12 | 10.54 ± 1.50 | - | - | - | - | - |
| | B | 24 | 1.00 ± 0.09 | 19.71 ± 2.30 | - | - | - | - | - |
| | C | 24 | 0.92 ± 0.12 | 19.79 ± 3.23 | - | - | - | - | - |
| | D | 24 | 0.88 ± 0.12 | 13.75 ± 2.21 | - | - | - | - | - |
| 9 | A | 24 | 0.83 ± 0.18 | 10.42 ± 1.46 | 0.54 ± 0.15 | - | - | - | - |
| | B | 24 | 1.00 ± 0.09 | 19.08 ± 2.23 | 1.38 ± 0.33 | - | - | - | - |
| | C | 24 | 0.92 ± 0.12 | 19.00 ± 2.95 | 1.58 ± 0.44 | - | - | - | - |
| | D | 24 | 0.88 - 0.14 | 13.63 - 2.24 | 0.80 - 0.20 | - | - | - | - |

TABLE 2

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 12 | A | 24 | 0.83 ± 0.17 | 5.46 ± 0.97 | 3.75 ± 0.45 | 1.17 ± 0.28 | - | - | - |
| | B | 24 | 1.00 ± 0.10 | 9.25 ± 1.20 | 4.25 ± 0.61 | 6.63 ± 0.80 | - | - | - |
| | C | 24 | 0.88 ± 0.11 | 9.29 ± 1.72 | 6.50 ± 1.51 | 3.96 ± 0.86 | - | - | - |
| | D | 24 | 0.88 ± 0.16 | 8.08 ± 1.54 | 3.29 ± 0.78 | 3.17 ± 0.50 | - | - | - |
| 14 | A | 24 | 0.92 ± 0.17 | 3.50 ± 0.66 | 3.21 ± 0.67 | 3.88 ± 0.83 | - | - | - |
| | B | 24 | 1.00 ± 0.13 | 6.33 ± 0.98 | 3.13 ± 0.44 | 10.13 ± 1.08 | - | - | - |
| | C | 24 | 0.92 ± 0.10 | 6.83 ± 1.32 | 3.63 ± 1.29 | 6.04 ± 1.05 | - | - | - |
| | D | 24 | 0.88 ± 0.17 | 6.83 ± 1.21 | 2.63 ± 0.51 | 5.33 ± 0.81 | - | - | - |
| 16 | A | 18 | 0.72 ± 0.20 | 2.06 ± 0.64 | 2.39 ± 0.56 | 3.89 ± 0.77 | - | - | - |
| | B | 18 | 0.89 ± 0.18 | 5.39 ± 0.90 | 3.17 ± 0.58 | 12.78 ± 1.76 | - | - | - |
| | C | 18 | 0.89 ± 0.14 | 6.83 ± 1.67 | 5.72 ± 1.64 | 10.72 ± 2.12 | - | - | - |
| | D | 18 | 0.72 ± 0.18 | 4.00 ± 1.14 | 4.33 ± 0.98 | 5.61 ± 1.08 | - | - | - |
| 19 | A | 18 | 0.72 ± 0.20 | 1.94 ± 0.66 | 1.72 ± 0.44 | 5.50 ± 0.93 | - | - | - |
| | B | 18 | 0.72 ± 0.18 | 3.50 ± 0.77 | 2.17 ± 0.49 | 12.72 ± 1.43 | - | - | - |
| | C | 18 | 0.78 ± 0.13 | 5.22 ± 1.59 | 4.22 ± 0.84 | 11.17 ± 2.00 | - | - | - |
| | D | 18 | 0.67 ± 0.18 | 3.22 ± 0.87 | 3.83 ± 1.03 | 6.94 ± 1.20 | - | - | - |

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 21 | A | 18 | 0.44 ± 0.15 | 1.06 ± 0.42 | 1.50 ± 0.54 | 5.17 ± 0.71 | - | - | - |
| | B | 18 | 0.56 ± 0.16 | 1.11 ± 0.51 | 1.44 ± 0.49 | 9.94 ± 1.14 | - | - | - |
| | C | 18 | 0.78 ± 0.15 | 3.11 ± 1.18 | 3.28 ± 0.77 | 10.28 ± 1.83 | - | - | - |
| | D | 18 | 0.56 ± 0.15 | 1.17 ± 0.44 | 2.28 ± 0.66 | 6.78 ± 0.96 | - | - | - |
| 23 | A | 18 | 0.44 ± 0.15 | 1.00 ± 0.40 | 0.72 ± 0.28 | 5.11 ± 0.69 | - | - | - |
| | B | 18 | 0.44 ± 0.12 | 1.00 ± 0.39 | 0.94 ± 0.31 | 8.89 ± 1.22 | - | - | - |
| | C | 18 | 0.78 ± 0.17 | 1.94 ± 0.67 | 2.89 ± 0.98 | 12.00 ± 2.22 | - | - | - |
| | D | 18 | 0.56 ± 0.20 | 0.83 ± 0.36 | 0.89 ± 0.42 | 8.56 ± 1.22 | - | - | - |
| 26 | A | 18 | 0.44 ± 0.15 | 1.00 ± 0.40 | 0.28 ± 0.20 | 4.67 ± 0.75 | - | - | - |
| | B | 18 | 0.50 ± 0.15 | 0.44 ± 0.33 | 0.22 ± 0.13 | 10.17 ± 1.57 | - | - | - |
| | C | 18 | 0.72 ± 0.16 | 1.33 ± 0.54 | 2.28 ± 0.97 | 15.00 ± 2.65 | - | - | - |
| | D | 18 | 0.61 ± 0.16 | 1.22 ± 0.53 | 0.67 ± 0.30 | 8.72 ± 1.34 | - | - | - |
| 28 | A | 18 | 0.33 ± 0.12 | 0.78 ± 0.36 | 0 | 3.94 ± 0.49 | 0 | - | - |
| | B | 18 | 0.33 ± 0.14 | 0.33 ± 0.23 | 0.28 ± 0.16 | 8.78 ± 1.51 | 1.17 ± 0.36 | - | - |
| | C | 18 | 0.67 ± 0.16 | 1.06 ± 0.38 | 1.39 ± 0.69 | 13.39 ± 2.30 | 1.78 ± 0.66 | - | - |
| | D | 18 | 0.56 ± 0.15 | 0.61 ± 0.31 | 0.50 ± 0.25 | 8.00 ± 1.23 | 1.83 ± 1.00 | - | - |

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 30 | A | 18 | 0.39 ± 0.12 | 0.78 ± 0.36 | 0.11 ± 0.11 | 4.67 ± 0.89 | 0.67 ± 0.24 | - | - |
| | B | 18 | 0.39 ± 0.12 | 0 | 0.33 ± 0.20 | 8.22 ± 1.52 | 1.78 ± 0.55 | - | - |
| | C | 17 | 0.76 ± 0.16 | 0.59 ± 0.26 | 2.06 ± 1.13 | 13.00 ± 2.75 | 3.94 ± 1.06 | - | - |
| | D | 17 | 0.47 ± 0.15 | 0.35 ± 0.24 | 0.47 ± 0.26 | 7.41 ± 1.05 | 2.00 ± 0.51 | - | - |
| 33 | A | 18 | 0.39 - 0.12 | 0.78 - 0.36 | 0.11 - 0.11 | 2.83 - 0.51 | 1.72 - 0.32 | | |
| | B | 18 | 0.28 ± 0.11 | 0 | 0 | 5.89 ± 1.43 | 3.83 ± 0.94 | - | - |
| | C | 17 | 0,76 ± 0.16 | 0.35 ± 0.24 | 0.53 ± 0.23 | 7.71 ± 1.88 | 8.06 ± 1.85 | - | - |
| | D | 17 | 0.41 ± 0.15 | 0.06 ± 0.06 | 0.35 ± 0.26 | 3.88 ± 0.96 | 4.94 ± 0.78 | - | - |
| 35 | A | 18 | 0.39 ± 0.12 | 0.78 ± 0.36 | 0.11 ± 0.11 | 2.22 ± 0.43 | 2.28 ± 0.39 | 0 | - |
| | B | 18 | 0.28 ± 0.11 | 0 | 0 | 4.67 ± 1.30 | 4.11 ± 1.01 | 0 | - |
| | C | 17 | 0.59 ± 0.15 | 0.18 ± 0.18 | 0 | 7.29 ± 1.82 | 6.82 ± 1.54 | 0 | - |
| | D | 17 | 0.41 ± 0.15 | 0 | 0.12 ± 0.12 | 3.53 ± 0.92 | 5.18 ± 0.70 | 0.06 ± 0.06 | - |
| 37 | A | 18 | 0.39 ± 0.12 | 0.78 ± 0.36 | 0 | 1.78 ± 0.45 | 2.39 ± 0.31 | 0 | - |
| | B | 18 | 0.11 ± 0.08 | 0 | 0.06 ± 0.06 | 4.22 ± 1.22 | 3.39 ± 0.69 | 0.17 ± 0.12 | - |
| | C | 17 | 0.41 ± 0.15 | 0.18 ± 0.18 | 0 | 5.59 ± 1.79 | 5.35 ± 0.98 | 0.82 ± 0.32 | - |
| | D | 17 | 0.29 ± 0.14 | 0 | 0 | 2.24 ± 0.69 | 5.35 ± 0.70 | 0.94 ± 0.55 | - |

TABLE 5

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 40 | A | 18 | 0.39 ± 0.12 | 0 | 0 | 0.61 ± 0.18 | 1.56 ± 0.23 | 0.94 ± 0.22 | - |
| | B | 18 | 0.17 ± 0.09 | 0 | 0 | 2.67 ± 0.81 | 1.94 ± 0.35 | 1.83 ± 0.51 | - |
| | C | 17 | 0.47 ± 0.15 | 0 | 0 | 3.76 ± 1.42 | 2.88 ± 0.66 | 3.59 ± 0.86 | - |
| | D | 17 | 0.24 ± 0.14 | 0 | 0 | 1.76 ± 0.48 | 2.06 ± 0.45 | 4.41 ± 0.70 | |
| 42 | A | 18 | 0.28 ± 0.11 | 0 | 0 | 0.28 ± 0.13 | 1.28 ± 0.20 | 1.11 ± 0.27 | - |
| | B | 18 | 0.17 ± 0.09 | 0 | 0 | 2.56 ± 0.82 | 1.61 ± 0.35 | 1.83 ± 0.50 | - |
| | C | 17 | 0.41 ± 0.15 | 0 | 0 | 3.00 ± 1.23 | 2.76 ± 0.65 | 4.76 ± 1.15 | - |
| | D | 17 | 0.12 ± 0.08 | 0 | 0 | 2.12 ± 0.78 | 3.41 ± 0.82 | 4.24 ± 0.67 | - |
| 44 | A | 13 | 0.23 ± 0.12 | 0 | 0 | 0.38 ± 0.18 | 0.46 ± 0.14 | 0.62 ± 0.24 | - |
| | B | 18 | 0.17 ± 0.09 | 0 | 0 | 1.00 ± 0.36 | 2.50 ± 0.44 | 1.67 ± 0.43 | - |
| | C | 17 | 0.41 ± 0.15 | 0 | 0.06 ± 0.06 | 1.53 ± 0.69 | 5.24 ± 1.01 | 4.24 ± 0.88 | - |
| | D | 17 | 0.12 ± 0.08 | 0 | 0 | 0.88 ± 0.35 | 3.47 ± 0.85 | 4.59 ± 0.69 | - |
| 47 | A | 13 | 0 | 0 | 0 | 0.38 ± 0.18 | 0.38 ± 0.14 | 0.69 ± 0.26 | - |
| | B | 18 | 0.17 ± 0.09 | 0 | 0 | 0.50 ± 0.25 | 1.89 ± 0.30 | 1.17 ± 0.33 | - |
| | C | 17 | 0.35 ± 0.15 | 0 | 0.06 ± 0.06 | 1.35 ± 0.59 | 4.65 ± 0.81 | 4.18 ± 0.79 | - |
| | D | 17 | 0.12 ± 0.08 | 0 | 0 | 0.53 ± 0.29 | 3.24 ± 0.78 | 4.24 ± 0.60 | - |

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 49 | A | 13 | 0 | 0 | 0 | 0.08 ± 0.08 | 0.23 ± 0.12 | 0.38 ± 0.14 | 0 |
| | B | 18 | 0.06 ± 0.06 | 0 | 0 | 0.44 ± 0.16 | 1.83 ± 0.35 | 1.28 ± 0.33 | 0 |
| | C | 17 | 0.28 ± 0.14 | 0 | 0.29 ± 0.29 | 2.18 ± 0.63 | 5.35 ± 0.98 | 3.18 ± 0.68 | 0 |
| | D | 17 | 0.13 ± 0.08 | 0 | 0 | 0.71 ± 0.33 | 3.82 ± 0.99 | 3.94 ± 0.53 | 0.06 ± 0.06 |
| 51 | A | 13 | 0 | 0 | 0 | 0.08 ± 0.08 | 0.15 ± 0.11 | 0.23 ± 0.12 | 0 |
| | B | 18 | 0 | 0 | 0 | 0.33 ± 0.20 | 1.39 ± 0.43 | 1.39 ± 0.43 | 0 |
| | C | 17 | 0.35 ± 0.15 | 0 | 0.18 ± 0.18 | 0.47 ± 0.21 | 3.47 ± 0.70 | 4.88 ± 1.08 | 0 |
| | D | 17 | 0.13 ± 0.08 | 0 | 0 | 0.18 ± 0.09 | 3.06 ± 0.69 | 4.29 ± 0.81 | 0.13 ± 0.08 |
| 54 | A | 13 | 0 | 0 | 0 | 0 | 0.15 ± 0.15 | 0.15 ± 0.11 | 0 |
| | B | 18 | 0 | 0.11 ± 0.11 | 0 | 0.11 ± 0.08 | 1.00 ± 0.29 | 1.28 ± 0.36 | 0.06 ± 0.06 |
| | C | 17 | 0.29 ± 0.14 | 0 | 0 | 0.59 ± 0.33 | 3.06 ± 0.77 | 4.18 ± 1.04 | 0 |
| | D | 17 | 0.06 ± 0.06 | 0 | 0 | 0.06 ± 0.06 | 2.12 ± 0.64 | 4.24 ± 0.74 | 0.18 ± 0.10 |
| 56 | A | 13 | 0 | 0 | 0 | 0 | 0.08 ± 0.08 | 0.08 ± 0.08 | 0 |
| | B | 18 | 0 | 0.11 ± 0.11 | 0 | 0.06 ± 0.06 | 1.11 ± 0.31 | 1.11 ± 0.32 | 0.06 ± 0.06 |
| | C | 17 | 0.06 ± 0.06 | 0.12 ± 0.12 | 0 | 0.24 ± 0.24 | 2.76 ± 0.69 | 3.82 ± 0.89 | 0.12 ± 0.08 |
| | D | 17 | 0.06 ± 0.06 | 0.35 ± 0.21 | 0 | 0 | 1.76 ± 0.51 | 4.12 ± 0.70 | 0.35 ± 0.12 |

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 58 | A | 8 | 0 | 0 | 0 | 0 | 0.13 ± 0.13 | 0 | 0 |
| | B | 16 | 0 | 0.13 ± 0.13 | 0 | 0.06 ± 0.06 | 1.06 ± 0.30 | 0.56 ± 0.24 | 0.19 ± 0.19 |
| | C | 16 | 0.13 ± 0.13 | 0.19 ± 0.19 | 0 | 0 | 3.75 ± 0.94 | 4.94 ± 1.03 | 0.13 ± 0.09 |
| | D | 17 | 0.08 ± 0.08 | 1.12 ± 0.72 | 0 | 0 | 3.18 ± 0.72 | 4.24 ± 0.65 | 0.65 ± 0.26 |
| 61 | A | 8 | 0 | 0 | 0 | 0 | 0 | 0.13 ± 0.13 | 0 |
| | B | 16 | 0.06 ± 0.06 | 0.06 ± 0.06 | 0 | 0.06 ± 0.06 | 0.50 ± 0.22 | 0.75 ± 0.38 | 0.25 ± 0.19 |
| | C | 16 | 0.19 ± 0.14 | 0.63 ± | 0.06 ± 0.06 | 0 | 3.44 ± 0.98 | 4.13 ± 0.84 | 0.31 ± 0.12 |
| | D | 17 | 0.06 ± 0.06 | 1.88 ± 1.08 | 0 | 0 | 2.06 ± 0.55 | 3.59 ± 0.66 | 0.82 ± 0.27 |
| 63 | A | 1 | 0 | 0 | 0 | 0 | 0 | 1.00 ± 1.00 | 0 |
| | B | 16 | 0.06 ± 0.06 | 0.06 ± 0.06 | 0 | 0 | 0.44 ± 0.22 | 0.56 ± 0.38 | 0.19 ± 0.19 |
| | C | 16 | 0.19 ± 0.14 | 0.94 ± 0.51 | 0 | 0 | 3.38 ± 0.84 | 4.19 ± 0.87 | 0.38 ± 0.13 |
| | D | 17 | 0.06 ± 0.06 | 2.71 ± 1.09 | 0 | 0 | 1.82 ± 0.46 | 3.65 ± 0.70 | 0.94 ± 0.26 |
| 65 | A | 1 | 0 | 0 | 0 | 0 | 0 | 1.00 ± 1.00 | 0 |
| | B | 16 | 0.06 ± 0.06 | 0.13 ± 0.13 | 0 | 0 | 0.31 ± 0.15 | 0.44 ± 0.38 | 0.19 ± 0.18 |
| | C | 16 | 0.06 ± 0.06 | 0.88 ± 0.52 | 0 | 0 | 2.56 ± 0.70 | 3.56 ± 0.70 | 0.31 ± 0.12 |
| | D | 17 | 0.06 ± 0.06 | 3.00 ± 1.04 | 0 | 0 | 1.59 ± 0.45 | 3.53 ± 0.62 | 0.94 ± 0.26 |

TABLE 8

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 68 | A | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | B | 16 | 0 | 0.19 ± 0.19 | 0 | 0 | 0.44 ± 0.22 | 0.31 ± 0.25 | 0.25 ± 0.15 |
| | C | 16 | 0.06 ± 0.06 | 0.94 ± 0.54 | 0 | 0 | 2.44 ± 0.71 | 3.56 ± 0.79 | 0.38 ± 0.13 |
| | D | 17 | 0.06 ± 0.06 | 3.12 ± 0.96 | 0 | 0 | 1.24 ± 0.34 | 3.24 ± 0.65 | 1.00 ± 0.26 |
| 70 | A | | | | | | | | |
| | B | 16 | 0 | 0.13 ± 0.13 | 0 | 0 | 0.50 ± 0.22 | 0.25 ± 0.19 | 0.19 ± 0.10 |
| | C | 16 | 0.13 ± 0.13 | 1.00 ± 0.36 | 0 | 0 | 2.81 ± 0.79 | 3.19 ± 0.74 | 0.56 ± 0.16 |
| | D | 17 | 0 | 2.94 ± 0.90 | 0 | 0 | 1.35 ± 0.37 | 2.88 ± 0.59 | 1.76 ± 0.55 |
| 72 | A | | | | | | | | |
| | B | 8 | 0 | 0.38 ± 0.26 | 0 | 0.13 ± 0.13 | 0.63 ± 0.26 | 0.63 ± 0.33 | 0.38 ± 0.18 |
| | C | 15 | 0 | 1.73 ± 0.86 | 0 | 0.80 ± 0.73 | 2.33 ± 0.64 | 4.07 ± 1.08 | 1.00 ± 0.22 |
| | D | 16 | 0 | 2.19 ± 0.51 | 0 | 0 | 1.38 ± 0.47 | 3.38 ± 0.69 | 1.94 ± 0.30 |
| 82 | A | | | | | | | | |
| | B | 8 | 0 | 0 | 0 | 0 | 0.38 ± 0.38 | 0.63 ± 0.33 | 0.25 ± 0.16 |
| | C | 15 | 0 | 3.40 ± 0.82 | 0.13 ± 0.09 | 0.27 ± 0.27 | 1.07 ± 0.41 | 3.53 ± 1.27 | 1.87 ± 0.34 |
| | D | 16 | 0 | 1.13 ± 0.46 | 0 | 0.06 ± 0.06 | 0.81 ± 0.32 | 2.00 ± 0.53 | 1.63 ± 0.36 |

TABLE 9

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 84 | A | | | | | | | | |
| | B | 8 | 0 | 0 | 0 | 0 | 0.38 ± 0.26 | 0.63 ± 0.42 | 0.25 ± 0.16 |
| | C | 15 | 0 | 3.67 ± 1.08 | 0 | 0.33 ± 0.33 | 0.93 ± 0.40 | 2.80 ± 0.91 | 2.20 ± 0.46 |
| | D | 16 | 0 | 1.06 ± 0.42 | 0 | 0 | 0.88 ± 0.32 | 1.88 ± 0.48 | 1.69 ± 0.30 |
| 86 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 0.75 ± 0.48 | 1.25 ± 0.63 | 0.25 ± 0.25 |
| | C | 15 | 0 | 6.20 ± 1.99 | 0 | 0.13 ± 0.13 | 1.13 ± 0.38 | 2.47 ± 0.75 | 2.53 ± 0.46 |
| | D | 14 | 0 | 2.00 ± 0.51 | 0.29 ± 0.16 | 0 | 1.00 ± 0.36 | 1.93 ± 0.51 | 3.43 ± 0.60 |
| 89 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 1.00 ± 0.41 | 1.25 ± 0.63 | 0.25 ± 0.25 |
| | C | 15 | 0 | 8.47 ± 2.50 | 0 | 0.20 ± 0.14 | 1.13 ± 0.39 | 2.47 ± 0.72 | 2.53 ± 0.43 |
| | D | 14 | 0 | 2.86 ± 0.92 | 0 | 0 | 0.86 ± 0.33 | 1.14 ± 0.39 | 3.00 ± 0.63 |
| 91 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 1.25 ± 0.63 | 1.25 ± 0.63 | 0.25 ± 0.25 |
| | C | 15 | 0 | 8.20 ± 2.20 | 0 | 0 | 1.13 ± 0.42 | 2.07 ± 0.70 | 2.87 ± 0.52 |
| | D | 14 | 0 | 2.93 ± 0.87 | 0 | 0 | 0.71 ± 0.30 | 1.14 ± 0.39 | 2.64 ± 0.67 |

TABLE 10

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 93 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 0.75 ± 0.25 | 1.25 ± 0.63 | 0.50 ± 0.50 |
| | C | 15 | 0 | 8.93 ± 2.26 | 0 | 0 | 1.07 ± 0.41 | 1.80 ± 0.70 | 3.00 ± 0.53 |
| | D | 14 | 0 | 2.79 ± 0.88 | 0 | 0 | 0.79 ± 0.32 | 1.00 ± 0.39 | 2.36 ± 0.69 |
| 96 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 0.50 ± 0.29 | 1.25 ± 0.95 | 0.50 ± 0.50 |
| | C | 15 | 0 | 7.73 ± 1.86 | 0.27 ± 0.15 | 0.20 ± 0.14 | 0.80 ± 0.30 | 1.40 ± 0.56 | 2.80 ± 0.55 |
| | D | 14 | 0 | 2.29 ± 0.87 | 0 | 0 | 0.64 ± 0.27 | 1.00 ± 0.32 | 2.21 ± 0.54 |
| 98 | A | | | | | | | | |
| | B | 4 | 0 | 0 | 0 | 0 | 0.50 ± 0.29 | 0.50 ± 0.50 | 0.25 ± 0.25 |
| | C | 15 | 0 | 7.33 ± 1.66 | 0.27 ± 0.15 | 0.33 ± 0.19 | 0.80 ± 0.28 | 1.47 ± 0.54 | 2.87 ± 0.54 |
| | D | 14 | 0 | 2.07 ± 0.83 | 0 | 0.07 ± 0.07 | 0.50 ± 0.17 | 0.86 ± 0.29 | 2.14 ± 0.50 |
| 100 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0.67 ± 0.67 | 0.67 ± 0.33 | 0.67 ± 0.33 | 0 ± |
| | C | 15 | 0 | 6.20 ± 1.87 | 0.27 ± 0.18 | 0.67 ± 0.37 | 0.73 ± 0.32 | 1.53 ± 0.54 | 3.07 ± 0.66 |
| | D | 11 | 0 | 2.64 ± 0.86 | 0 | 0.18 ± 0.18 | 0.55 ± 0.21 | 1.27 ± 0.30 | 3.00 ± 0.47 |

TABLE 11

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 103 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0.33 ± 0.33 | 0.33 ± 0.33 | 0.33 ± 0.33 | 0 |
| | C | 15 | 0 | 6.00 ± 1.89 | 0.13 ± 0.13 | 0.13 ± 0.09 | 0.87 ± 0.32 | 1.33 ± 0.42 | 2.60 ± 0.58 |
| | D | 11 | 0 | 1.45 ± 0.75 | 0 | 0 | 0.55 ± 0.16 | 1.27 ± 0.27 | 2.45 ± 0.62 |
| 105 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0 | 0.67 ± 0.67 | 0.33 ± 0.33 | 0 |
| | C | 15 | 0 | 6.87 ± 2.03 | 0.13 ± 0.13 | 0.33 ± 0 | 0.60 ± 0.26 | 1.00 ± 0.31 | 2.60 ± 0.58 |
| | D | 11 | 0 | 1.09 ± 0.53 | 0 | 0 | 0 | 0.82 ± 0.30 | 2.18 ± 0.74 |
| 107 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0 | 0 | 0.33 ± 0.33 | 0 |
| | C | 15 | 0 | 7.33 ± 2.09 | 0 | 0.67 ± 0.33 | 0.53 ± 0.27 | 1.00 ± 0.31 | 2.33 ± 0.55 |
| | D | 11 | 0 | 1.45 ± 0.62 | 0 | 0.09 ± 0.09 | 0 | 0.73 ± 0.36 | 2.09 ± 0.73 |
| 110 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0 | 0.33 ± 0.33 | 0.33 ± 0.33 | 0 |
| | C | 15 | 0 | 7.27 ± 2.17 | 0.07 ± 0.07 | 0.60 ± 0.32 | 0.33 ± 0.08 | 0.53 ± 0.19 | 2.20 ± 0.51 |
| | D | 11 | 0 | 1.18 ± 0.52 | 0.09 ± 0.09 | 0 | 0 | 0.73 ± 0.30 | 1.91 ± 0.74 |

TABLE 12

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 112 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0 | 0.33 ± 0.33 | 0.67 ± 0.33 | 0 |
| | C | 15 | 0 | 7.80 ± 2.17 | 0.60 ± 0.34 | 0.40 ± 0.23 | 0.33 ± 0.16 | 0.47 ± 0.19 | 2.40 ± 0.58 |
| | D | 11 | 0 | 1.91 ± 0.85 | 0 | 0 | 0 | 0.64 ± 0.31 | 1.82 ± 0.74 |
| | A | | | | | | | | |
| | B | | | | | | | | |
| | C | | | | | | | | |
| | D | | | | | | | | |
| | A | | | | | | | | |
| | B | | | | | | | | |
| | C | | | | | | | | |
| | D | | | | | | | | |
| | A | | | | | | | | |
| | B | | | | | | | | |
| | C | | | | | | | | |
| | D | | | | | | | | |

TABLE 13

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 14 | A | 6 | 1.17 ± 0.3 | 6.50 ± 1.15 | 10.50 ± 1.67 | 10.67 ± 2.89 | - | - | - |
| | B | 6 | 1.33 ± 0.33 | 5.50 ± 2.38 | 4.67 ± 1.78 | 15.83 ± 3.99 | - | - | - |
| | C | 6 | 0.83 ± 0.17 | 7.33 ± 1.74 | 5.83 ± 1.82 | 6.33 ± 2.17 | - | - | - |
| | D | 6 | 1.00 ± 0.36 | 9.67 ± 1.36 | 4.33 ± 0.92 | 8.33 ± 2.68 | - | - | - |
| 28 | A | 6 | 0.50 ± 0.34 | 0.67 ± 0.49 | 1.00 ± 0.45 | 5.83 ± 2.54 | 0 | - | - |
| | B | 6 | 0.33 ± 0.21 | 0.50 ± 0.50 | 0.83 ± 0.54 | 9.67 ± 1.38 | 0.83 ± 0.48 | - | - |
| | C | 6 | 0.83 ± 0.31 | 3.67 ± 1.56 | 5.17 ± 3.05 | 21.17 ± 5.45 | 1.17 ± 0.98 | - | - |
| | D | 6 | 0.33 ± 0.21 | 1.50 ± 1.02 | 0.33 ± 0.33 | 8.50 ± 2.92 | 0.67 ± 0.21 | - | - |
| 42 | A | 6 | 0 | 0 | 0 | 0.17 ± 0.17 | 0 | 0 | - |
| | B | 6 | 0.17 ± 0.17 | 0 | 0.17 ± 0.17 | 3.33 ± 2.22 | 2.00 ± 0.63 | 2.00 ± 0.78 | - |
| | C | 6 | 0.67 ± 0.33 | 0 | 0 | 1.00 ± 0.63 | 4.50 ± 2.32 | 2.83 ± 1.38 | - |
| | D | 6 | 0 | 0 | 0 | 0.33 ± 0.21 | 2.67 ± 1.50 | 6.00 ± 2.91 | 3.83 ± 1.20 |
| 56 | A | 6 | 0 | 0 | 0 | 0 | 0.17 ± 0.17 | 0 | 0 |
| | B | 6 | 0 | 0 | 0 | 0.33 ± 0.33 | 2.17 ± 0.83 | 0.67 ± 0.49 | 0.50 ± 0.50 |
| | C | 6 | 0 | 0 | 0 | 0 | 4.50 ± 2.01 | 5.17 ± 2.91 | 0 |
| | D | 6 | 0 | 0 | 0 | 0 | 1.67 ± 0.62 | 3.33 ± 0.85 | 0 |

TABLE 14

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 70 | A | | | | | | | | |
| | B | 6 | 0 | 0.83 ± 0.83 | 0 | 0 | 0.33 ± 0.21 | 0.50 ± 0.20 | 0.17 ± 0.17 |
| | C | 5 | 0 | 0.60 ± 0.40 | 0 | 2.80 ± 2.56 | 5.40 ± 1.50 | 4.40 ± 1.29 | 1.00 ± 0.32 |
| | D | 5 | 0 | 7.00 ± 1.73 | 0 | 0 | 1.60 ± 0.87 | 2.40 ± 0.68 | 3.00 ± 0.45 |
| 84 | A | | | | | | | | |
| | B | 1 | 0 | 0 | 0 | 0 | 1.00 ± 1.00 | 0 | 0 |
| | C | 5 | 0 | 7.60 ± 2.99 | 0.20 ± 0.20 | 0 | 1.00 ± 1.00 | 1.80 ± 0.97 | 2.80 ± 0.49 |
| | D | 6 | 0 | 7.50 ± 2.13 | 0.67 ± 0.33 | 0 | 1.67 ± 0.76 | 2.67 ± 0.96 | 4.50 ± 1.20 |
| 98 | A | | | | | | | | |
| | B | 1 | 0 | 0 | 0 | 3.00 ± 3.00 | 2.00 ± 2.00 | 2.00 ± 2.00 | 0 |
| | C | 5 | 0 | 9.40 ± | 0 | 0.20 ± 0.20 | 0.20 ± 0.20 | 1.80 ± 1.32 | 2.40 ± 1.75 |
| | D | 3 | 0 | 0.67 ± 0.67 | 0 | 0 | 0.67 ± 0.67 | 1.67 ± 0.66 | 4.00 ± 1.52 |
| 112 | A | | | | | | | | |
| | B | 3 | 0 | 0 | 0 | 0 | 0.33 ± 0.33 | 0.67 ± 0.33 | 0 |
| | C | 15 | 0 | 10.20 ± 3.27 | 2.13 ± 0.84 | 0.47 ± 0.26 | 0.40 ± 0.18 | 0.33 ± 0.16 | 3.20 ± 0.82 |
| | D | 11 | 0 | 3.45 ± 1.13 | 0.09 ± 0.09 | 0.09 ± 0.09 | 0.18 ± 0.12 | 0.82 ± 0.55 | 1.55 ± 0.64 |

TABLE 15

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 1 | A | 11 | 1.00 ± 0.14 | 6.27 ± 0.84 | - | - | - | - | - |
| | B | 11 | 1.00 ± 0.23 | 3.00 ± 0.94 | - | - | - | - | - |
| | C | 11 | 1.00 ± 0 | 2.73 ± 0.63 | - | - | - | - | - |
| | D | 11 | 1.00 ± 0.30 | 3.27 ± 1.30 | - | - | - | - | - |
| | E | 11 | 1.00 ± 0.19 | 3.64 ± 1.02 | - | - | - | - | - |
| 2 | A | 11 | 1.00 ± 0.19 | 9.64 ± 1.32 | - | - | - | - | - |
| | B | 11 | 1.00 ± 0.23 | 7.55 ± 2.19 | - | - | - | - | - |
| | C | 10 | 1.00 ± 0 | 5.70 ± 1.15 | - | - | - | - | - |
| | D | 11 | 1.00 ± 0.30 | 4.64 ± 1.58 | - | - | - | - | - |
| | E | 11 | 1.00 ± 0.19 | 6.09 ± 1.69 | - | - | - | - | - |
| 3 | A | 11 | 1.00 ± 0.19 | 12.18 ± 1.50 | - | - | - | - | - |
| | B | 11 | 1.00 ± 0.23 | 9.45 ± 2.75 | - | - | - | - | - |
| | C | 10 | 1.00 ± 0 | 9.90 ± 1.80 | - | - | - | - | - |
| | D | 11 | 1.00 ± 0.30 | 7.09 ± 2.48 | - | - | - | - | - |
| | E | 11 | 1.00 ± 0.19 | 8.18 ± 1.97 | - | - | - | - | - |
| 4 | A | 11 | 1.00 ± 0.19 | 14.91 ± 1.97 | - | - | - | - | - |
| | B | 11 | 1.00 ± 0.27 | 11.82 ± 3.49 | - | - | - | - | - |
| | C | 10 | 1.00 ± 0 | 12.30 ± 2.14 | - | - | - | - | - |
| | D | 11 | 1.00 ± 0.30 | 10.27 ± 3.46 | - | - | - | - | - |
| | E | 11 | 1.00 ± 0.19 | 10.27 ± 2.48 | - | - | - | - | - |

TABLE 16

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 7 | A | 10 | 1.10 ± 0.18 | 25.10 ± 2.95 | - | - | - | - | - |
| | B | 8 | 1.38 ± 0.26 | 19.25 ± 4.41 | - | - | - | - | - |
| | C | 10 | 1.00 ± 0 | 20.10 ± 2.94 | - | - | - | - | - |
| | D | 7 | 1.57 ± 0.30 | 30.00 ± 6.52 | - | - | - | - | - |
| | E | 8 | 1.25 ± 0.16 | 20.56 ± 3.80 | - | - | - | - | - |
| 9 | A | 10 | 1.10 ± 0.28 | 27.50 ± 3.25 | 0.10 ± 0.10 | - | - | - | - |
| | B | 8 | 1.38 ± 0.26 | 19.88 ± 4.87 | 0.50 ± 0.19 | - | - | - | - |
| | C | 10 | 1.00 ± 0.15 | 22.40 ± 2.68 | 0.60 ± 0.34 | - | - | - | - |
| | D | 7 | 1.57 ± 0.65 | 31.57 ± 6.24 | 1.14 ± 0.63 | - | - | - | - |
| | E | 8 | 1.11 ± 0.12 | 21.44 ± 4.16 | 0.78 ± 0.29 | - | - | - | - |
| 11 | A | 10 | 1.10 ± 0.28 | 29.90 ± 3.67 | 1.30 ± 0.45 | - | - | - | - |
| | B | 8 | 1.38 ± 0.26 | 16.00 ± 3.82 | 6.25 ± 2.72 | - | - | - | - |
| | C | 10 | 1.00 ± 0.15 | 19.70 ± 1.90 | 5.00 ± 1.43 | - | - | - | - |
| | D | 7 | 1.43 ± 0.57 | 28.00 ± 4.98 | 6.00 ± 2.39 | - | - | - | - |
| | E | 9 | 1.11 ± 0.26 | 19.44 ± 3.78 | 3.44 ± 0.60 | - | - | - | - |
| 14 | A | 10 | 1.10 ± 0.28 | 20.40 ± 2.70 | 4.60 ± 0.92 | 4.30 ± 0.73 | - | - | - |
| | B | 8 | 1.25 ± 0.31 | 7.75 ± 2.91 | 4.13 ± 0.92 | 11.63 ± 2.59 | - | - | - |
| | C | 10 | 0.90 ± 0.10 | 12.80 ± 1.51 | 3.70 ± 0.73 | 8.10 ± 1.78 | - | - | - |
| | D | 7 | 1.43 ± 0.57 | 17.57 ± 4.09 | 2.29 ± 0.57 | 8.71 ± 2.54 | - | - | - |
| | E | 8 | 1.11 ± 0.28 | 11.33 ± 2.58 | 5.00 ± 1.18 | 7.22 ± 1.77 | - | - | - |

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 16 | A | 10 | 1.10 ± 0.28 | 13.40 ± 2.66 | 1.60 ± 0.70 | 7.20 ± 1.04 | - | - | - |
| | B | 8 | 1.13 ± | 3.13 ± | 0.75 ± | 16.38 ± | - | - | - |
| | C | 10 | 0.90 ± 0.10 | 10.20 ± 1.37 | 1.00 ± 0.33 | 14.90 ± 3.47 | - | - | - |
| | D | 7 | 1.14 ± 0.46 | 20.57 ± 5.02 | 1.29 ± 0.84 | 9.29 ± 4.01 | - | - | - |
| | E | 9 | 1.00 ± 0.24 | 6.11 ± 1.24 | 2.33 ± 0.93 | 8.67 ± 2.61 | - | - | - |
| 17 EXT-RAC-TION | A | 10 | 1.10 ± 0.28 | 9.60 ± 2.60 | 16.00 ± 2.31 | 18.50 ± 3.05 | - | - | - |
| | B | 8 | 1.25 ± 0.25 | 5.13 ± 1.16 | 8.50 ± 2.29 | 20.25 ± 4.95 | - | - | - |
| | C | 10 | 1.00 ± 0.15 | 8.10 ± 1.49 | 7.80 ± 1.44 | 22.70 ± 3.34 | - | - | - |
| | D | 7 | 1.29 ± 0.52 | 16.29 ± 4.61 | 2.86 ± 1.81 | 15.00 ± 5.51 | - | - | - |
| | E | 9 | 1.11 ± 0.26 | 7.11 ± 1.71 | 5.78 ± 1.58 | 24.56 ± 4.89 | - | - | - |
| 21 | A | 10 | 1.10 ± 0.28 | 1.40 ± 0.67 | 1.40 ± 0.71 | 27.20 ± 3.60 | - | - | - |
| | B | 8 | 1.13 ± 0.23 | 1.50 ± 1.05 | 0 | 26.50 ± 4.20 | - | - | - |
| | C | 10 | 1.00 ± 0.15 | 2.20 ± 0.47 | 0 | 29.30 ± 4.27 | - | - | - |
| | D | 7 | 1.00 ± 0.31 | 1.71 ± 0.64 | 0 | 16.71 ± 6.46 | - | - | - |
| | E | 9 | 1.11 ± 0.26 | 1.44 ± 0.71 | 0 | 28.78 ± 6.13 | - | - | - |
| 23 | A | 10 | 1.00 ± 0.26 | 2.20 ± 0.97 | 0.40 ± 0.40 | 27.20 ± 3.33 | - | - | - |
| | B | 8 | 1.00 ± 0.19 | 1.88 ± 1.26 | 0 | 26.88 ± 4.06 | - | - | - |
| | C | 10 | 1.00 ± 0.15 | 2.90 ± 0.64 | 0 | 29.20 ± 4.13 | - | - | - |
| | D | 7 | 1.29 ± 0.42 | 2.29 ± 0.78 | 0 | 16.29 ± 6.23 | - | - | - |
| | E | 9 | 1.11 ± 0.26 | 2.78 ± 1.31 | 0 | 28.78 ± 6.12 | - | - | - |

TABLE 18

| Day | Treatment | No. of cultures | Inoculated adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| 28 | A | 10 | 0.90 ± 0.31 | 1.90 ± 0.89 | 0.20 ± 0.20 | 10.40 ± 2.16 | 14.00 ± 1.46 | - | - |
| | B | 8 | 1.00 ± 0.27 | 2.38 ± 1.35 | 0 | 3.50 ± 0.42 | 19.00 ± 3.50 | - | - |
| | C | 10 | 0.90 ± 0.10 | 3.20 ± 0.81 | 0.20 ± 0.13 | 8.60 ± 2.10 | 20.40 ± 4.00 | - | - |
| | D | 7 | 1.14 ± 0.46 | 3.00 ± 1.70 | 0 | 3.57 ± 2.25 | 10.29 ± 4.46 | - | - |
| | E | 9 | 1.00 ± 0.17 | 4.00 ± 1.77 | 0.11 ± 0.11 | 7.78 ± 1.51 | 18.44 ± 2.60 | - | - |
| 35 EXT-RAC-TION | A | 10 | 0.50 ± 0.31 | 1.20 ± 0.63 | 0.60 ± 0.34 | 7.20 ± 1.99 | 19.80 ± 3.57 | - | - |
| | B | 8 | 0.63 ± 0.26 | 0.63 ± 0.63 | 0.75 ± 0.41 | 9.50 ± 2.23 | 15.50 ± 3.30 | - | - |
| | C | 10 | 0.80 ± 0.20 | 1.30 ± 0.67 | 3.00 ± 0.76 | 11.00 ± 1.63 | 15.40 ± 2.35 | - | - |
| | D | 7 | 0.71 ± 0.29 | 1.86 ± 1.42 | 2.29 ± 0.94 | 5.14 ± 1.95 | 7.00 ± 2.73 | - | - |
| | E | 9 | 0.44 ± 0.18 | 0.67 ± 0.33 | 2.22 ± 0.80 | 13.44 ± 2.04 | 13.22 ± 2.16 | - | - |
| 42 | A | 10 | 0.40 ± 0.31 | 0 | 0 | 5.60 ± 1.80 | 19.40 ± 2.95 | 1.60 ± 0.60 | - |
| | B | 8 | 0.38 ± 0.18 | 0.38 ± 0.26 | 0 | 4.75 ± 1.30 | 18.63 ± 3.02 | 1.75 ± 0.68 | - |
| | C | 10 | 0.70 ± 0.21 | 0.30 ± 0.15 | 0.70 ± 0.37 | 8.80 ± 2.04 | 18.80 ± 2.64 | 0.70 ± 0.42 | - |
| | D | 7 | 0.43 ± 0.30 | 0 | 0.57 ± 0.37 | 3.43 ± 1.85 | 7.29 ± 3.21 | 0.29 ± 0.29 | - |
| | E | 9 | 0.44 ± 0.24 | 0.22 ± 0.22 | 0.22 ± 0.22 | 10.00 ± 1.93 | 15.78 ± 1.61 | 0.89 ± 0.45 | - |
| 49 | A | 10 | 0.20 ± 0.20 | 0 | 0 | 1.50 ± 0.65 | 7.00 ± 1.32 | 11.80 ± 2.30 | - |
| | B | 8 | 0.25 ± 0.16 | 0.25 ± 0.25 | 0 | 1.63 ± 0.60 | 7.13 ± 1.14 | 11.88 ± 1.94 | - |
| | C | 10 | 0.40 ± 0.16 | 0.20 ± 0.20 | 0 | 3.20 ± 0.76 | 7.40 ± 0.84 | 12.80 ± 0.93 | - |
| | D | 7 | 0.29 ± 0.19 | 0 | 0 | 0.57 ± 0.37 | 3.29 ± 1.77 | 4.14 ± 2.26 | - |
| | E | 9 | 0.22 ± 0.15 | 0.33 ± 0.24 | 0 | 3.22 ± 0.76 | 7.67 ± 0.97 | 11.67 ± 1.36 | - |

TABLE 19

| Day | Treatment | No. of cultures | Inoculated Adults | Eggs | First stage juveniles | Second stage juveniles | Third stage juveniles | Fourth stage juveniles | $F_1$ adults |
|---|---|---|---|---|---|---|---|---|---|
| | A | 10 | 0 | 0 | 0 | 0 | 4.70 ± 1.13 | 9.90 ± 2.71 | 0 |
| 57 | B | 8 | 0 | 0.63 ± 0.26 | 0 | 0 | 3.50 ± 1.27 | 13.75 ± 1.75 | 0.88 ± 0.29 |
| | C | 10 | 0.40 ± 0.16 | 2.30 ± 1.26 | 0 | 0.20 ± 0.13 | 5.20 ± 1.18 | 16.10 ± 1.10 | 0.50 ± 0.27 |
| | D | 7 | 0 | 0 | 0 | 0 | 2.57 ± 1.57 | 5.14 ± 2.35 | 0 |
| | E | 9 | 0 | 0 | 0 | 0.56 ± 0.56 | 7.67 ± 1.39 | 14.11 ± 2.04 | 0 |
| 63 | A | 10 | 0 | 0 | 0 | 0 | 1.80 ± 0.51 | 11.80 ± 3.14 | 0 |
| | B | 8 | 0.13 ± 0.13 | 2.13 ± 0.64 | 0 | 0 | 1.88 ± 1.17 | 12.63 ± 1.93 | 1.38 ± 0.38 |
| | C | 10 | 0.30 ± 0.15 | 3.40 ± 1.75 | 0 | 0 | 3.70 ± 1.01 | 16.40 ± 1.34 | 0.80 ± 0.29 |
| | D | 7 | 0 | 0 | 0 | 0 | 1.14 ± 0.55 | 5.43 ± 2.58 | 0 |
| | E | 9 | 0.44 ± 0.29 | 1.89 ± 0.95 | 0 | 0 | 4.33 ± 1.01 | 16.22 ± 2.15 | 0.11 ± 0.11 |
| 70 EXTRACTION | A | 10 | 0 | 2.50 ± 0.64 | 0.10 ± 0.10 | 0 | 1.20 ± 0.49 | 5.50 ± 1.42 | 1.60 ± 0.40 |
| | B | 8 | 0 | 22.25 ± 6.75 | 7.00 ± 2.63 | 1.63 ± 1.22 | 2.50 ± 0.65 | 5.38 ± 1.10 | 8.25 ± 1.64 |
| | C | 10 | 0 | 33.80 ± 5.69 | 2.30 ± 1.48 | 0.90 ± 0.90 | 2.50 ± 0.31 | 11.60 ± 1.06 | 8.60 ± 1.06 |
| | D | 7 | 0 | 0 | 0 | 0.14 ± 0.14 | 1.14 ± 0.46 | 4.71 ± 2.49 | 0.43 ± 0.30 |
| | E | 9 | 0 | 9.56 ± 1.83 | 0.11 ± 0.11 | 0 | 1.89 ± 0.48 | 10.33 ± 1.74 | 5.56 ± 1.64 |
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