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Ph.D. THESIS

The biology of *Capitella capitata* (Fabricius) and a review of the genus *Capitella* Blainville.

BEDFORD COLLEGE

UNIVERSITY OF LONDON

MARCH 1975

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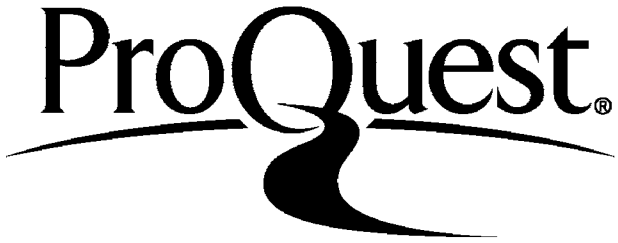

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ABSTRACT.

The thesis is concerned with the biology of Capitella capitata in British waters and the validity of the genus Capitella throughout the world.

Material from Europe, America and Australia has been examined and an extensive review of the literature on the taxonomy of Capitella has been made. As a result the generic description has been modified to include the genus Capitellides.

The description of C. capitata has been widened to account for variations between populations and the subspecies C. capitata ovincola and C. capitata tripartita have been elevated to specific level.

An ecological study of some British populations has been made and it is shown that while C. capitata will occur under a wide range of conditions, it is predominant where other polychaetes are less common.

The life history has been investigated and it has been shown to reproduce in Britain throughout the year. Two larval types have been found.

The effects of various ecological factors have been studied in the laboratory. Both adults and larvae were found to be resistant to conditions of low salinity and, especially, low oxygen tension. The species is, however, very sensitive to increases in temperature.

The feeding biology has been studied and an estimate of the available organic content in the substrate made.

The relationship of the species to polluted conditions is discussed.

In conclusion it is noted that C.capitata owes its worldwide distribution to its adaptability allowing it to penetrate a variety of habitats. This same lack of specialisation, however, makes it unsuccessful as a competitor with species more narrowly adapted to particular sets of environmental conditions.

ACKNOWLEDGEMENTS.

This work was carried out whilst in receipt of a research studentship awarded by the Natural Environment Research Council.

Material was kindly loaned for taxonomic purposes by Dr. P. Hutchings, Dr. D.J. Reish, Dr. G. Bellan, Dr. van der Land, Dr. W. Dohle, Dr. J.D. George and Dr. K. Fauchald. Miss S.V. Cowper gave invaluable assistance in the preparation of scanning electron micrographs.

I am grateful to Dr. J.D. George of the British Museum (Natural History) for allowing access to the collection of preserved material and for useful discussion on Chapter 2.

I am indebted to Mr. C.F. Tydeman for help in the field and to the Director and staff of the Marine Biological Association U.K. for the provision of laboratory facilities.

It is a pleasure to acknowledge the assistance given by Dr. R.M.G. Wells with respect to Chapter 4.

Mr. D. Field and the laboratory staff of the Zoology Dept., Bedford College, have been most helpful and I take this opportunity to thank them.

My thanks are due to Miss King and Miss S.E. Tydeman for the translation of Chinese and German papers, and to Dr. S. Kemplay who has very patiently assisted in the preparation of this thesis.

Finally I should like to thank Professor R.P. Dales, without whose encouragement and critical discussion this thesis would not have been possible.

INDEX.

1. INTRODUCTION.

Capitella capitata (Fabricius) is a cosmopolitan species occurring in cold temperate and warm waters throughout the world. Originally described by Fabricius (1780) in his survey of the fauna of Greenland, it has since been recorded in many localities in the Arctic, including the White Sea; Barents Sea and Kara Sea along the Russian coastline and in Alaska. Fig. 23 shows the location of these, and other, points of distribution more precisely.

Further south, it is known from the North Sea (e.g. the British Isles and Holland) and extends into the Baltic. It is widely distributed in the warm temperate waters of the Mediterranean, being found along the coasts of southern France, western Italy and Morocco. It has spread from the Mediterranean into the Black Sea and the Sea of Azov.

It has been reported from both sides of the North Atlantic Ocean. In the east it is found in the Hebrides and off the Irish coast. On the western seaboard of America it is known from Labrador and Nova Scotia, and along this coast the range extends much further south to the warmer waters of the Gulf of Mexico.

The species is also widely distributed in the Pacific Ocean. There are many records of its occurrence off the Californian coast and in the western Pacific it is known from China and Japan. Aiyar (1933) reported the presence of larval stages of the genus Capitella from the coast of Madras in the Indo-Pacific region.

Capitella capitata is well known from the southern hemisphere with records from South Africa, Australia, New Zealand and the tip of South America. In the colder antiboreal waters it has been found in South Georgia and the Falkland Islands.

C.capitata is often associated with conditions of reduced salinity. Thus Hartman (1947) described it as euryhaline and went on to say that it

"occupies beds of considerable extent, especially in estuarine and also brackish water".

This statement is upheld by many reports in the literature. Muus (1967) found it scattered throughout the shallow mesohaline waters of Danish estuaries and lagoons. Leppäkoski (1969) found it at 80m depth in the Bornholm basin showing that the species can penetrate a long way into the low salinity waters of the Baltic Sea. He explains the depth distribution as an example of "brackish water submergence". In New Zealand, Estcourt (1967) found it down to a salinity of 0.4 °/oo in the Heathcote estuary. Filice (1958) found C.capitata at the extremes of the salinity range of the estuarine portion of the San Francisco Bay, such that it occurred down to 8 - 10 °/oo with an average salinity of 24°/oo and again between 0.4 - 0.6 °/oo. Despite the range of salinities tolerated by the species it is doubtful if any given population is subjected to the complete range. Thus Stone and Reish (1965) found that rainfall of more than 0.5" reduced a population normally living at 33.7 °/oo, although the authors could not be sure that this was not due to the increased flow washing the polychaetes away.

Truly cosmopolitan species are relatively uncommon and several subspecies and varieties have been erected to account for the differences in populations of C.capitata from different regions (for example see Wu 1964). This is particularly true for the deep water specimens found off California. There is, however, a danger in splitting the species up too far so that each population could be set up as a separate variety. On of the main purposes of this study was to examine the genus Capitella in order to assess the validity of the subspecies.

C.capitata has recently gained the interest of ecologists with respect to its ability to withstand polluted conditions. There are many records of its occurrence in organically rich substrates where the oxygen levels are low and reducing conditions are indicated by the black coloration and the smell of hydrogen sulphide.

It is, for example, often encountered in harbours and other enclosed areas of water where organic pollution is high. Thus Blegvad (1932) found it in Copenhagen harbour and Cognetti (1972) describes it from the very polluted waters of the inner docks in the harbour at Livorno. Reish has made an extensive study of the relationship of C.capitata to pollution in the Los Angeles-Long Beach harbour system. He proposed zones of pollution and described the fauna associated with each (1955). C.capitata was the dominant organism in the most polluted zone still able to support life. Similar studies have been described in Marseilles harbour (Bellan 1967) and in the polluted waters of the inland sea of

Japan (Kitamori and Funae 1960). In each case C.capitata was abundant in the most polluted zones. The correlation between C.capitata and polluted conditions has led to the idea that it could be used as an indicator of organically polluted conditions. Wass (1967) reviews the literature on the subject. Since then Henriksson (1969) has shown a high correlation between the occurrence of C.capitata and numbers of bacteria in the Sound.

The picture is not, however, as clear-cut as it would first appear. The species is often found in areas where there is no pollution at all. Filice (1959) found it in normal, as well as polluted, areas in the San Francisco Bay estuary and Reish and Winters (1954) found a similar situation in the Alamitos Bay, California. Muus (1967) could not relate it to polluted conditions at all and Wolff (1973) concluded that the species is of doubtful use as an indicator.

Some experimental work has been carried out on the response of C.capitata to pollution (Bellan et al. 1972, Reish 1966,1970) but without any sound knowledge of the general biology of the species the results cannot be related to field conditions. Eisig (1887) made a detailed study of the biology of capitellids but paid little attention to the ecology. Since then very little has been added to our knowledge and it seemed worthwhile to investigate the ecology of this species in relatively unpolluted conditions prior to considering any relationship with pollution.

2. REVIEW OF THE GENUS CAPITELLA.

2.1 Introduction.

The family Capitellidae was first recognised as a taxonomic unit in 1863 when Grube described the three known genera, *Capitella*, *Notomastus* and *Dasybranchus* under the name Capitellacea. Since then twenty-seven other genera have been described. Hartman (1947) outlined the principal features of the family, and there is no disagreement on this point. The status of the genus *Capitella* is, however, open to some dispute, and it is with this genus and closely related ones that this review is concerned. The genera in question are *Capitella*, *Capitellides* and *Branchiocapitella*. These are all similar in that they all have a thorax of nine segments, all setigerous, and they all possess some form of copulatory apparatus on the last two thoracic segments. *Capitomastus* also has genital hooks but in this instance there are ten thoracic segments, the first being asetous. *Pulliella* has the same number of thoracic segments as *Capitella* but a copulatory apparatus is absent.

A review of the literature on *Capitella* and closely related genera is found in the following sections. In some cases it has been possible to examine type material. Hartman (1947) believed the structure of the hooded hooks to be one of the best taxonomic characters at specific level. Recent advances in the use of scanning electron microscopy have enabled a much more detailed examination of the structure of the hooded hooks, and this technique has

been used whenever possible.

In addition to the type material examined a more detailed study was made of several European populations. It is very difficult to assess the importance of a given morphological feature when one is studying a small sample of fixed material, especially when there is little other available information on the population. By taking larger samples from populations being studied ecologically it has been possible to evaluate the variation of some features statistically. Three British populations have been treated in this way. These are from Plymouth, Whitstable and Anglesey (see Figs. 24 - 26). The loan of a very large sample of material from the Dutch delta area has made possible a similar study on a North Sea population (see Fig. 12).

2.2 Materials and Methods.

2.2.1 The structure of the hooded hooks.

(The basic structure of the hooded hooks is given in Fig. 1).

Both British and, where available, foreign worms were used. In most cases one or two worms from each population were examined. Further details are given in Table 1.

It is important when comparing hooks from different specimens to ensure that the material is taken from the same region, as variation is known to occur in some species according to the segment (Pettibone 1953). Material was therefore always taken from the third abdominal segment. Similarly, mature worms of approximately the same age and sex were examined as it is possible that

TABLE 1. Localities of material used in stereoscan studies.

Sample	Locality	Origin of Material	Preservation
C. capitata	Plymouth	1971 - 1974 this study	Fixed 4% formalin stored in 70% alcohol
C. capitata	Whitstable	1973 this study	Fixed 4% formalin stored in 70% alcohol
C. capitata	Nova Scotia Canada	1963 George	Stored in 70% alcohol
Capitella sp.	Onkaparinga Estuary S. Australia	1973 Shepherd	Stored in 70% alcohol at the Australian Museum, Sydney Cat. no. W6069
C. capitata oculata	Southern California	1961 Hartman	Stored in 70% alcohol at the Allan Hancock Foundation Ref. no. poly 0445 - 6
C. capitata ovincola	Monterey Bay California	1947 Hartman	Stored in 70% alcohol at the Allan Hancock Foundation poly 0442. Transferred to British Museum (Nat. Hist.), Cat. no. ZB 1974.1339 - 1358.
C. hermaphrodita	Banyuls-sur-Mer France	1966 Boletzky and Dohle	Stored in 70% alcohol at Kiel University

the setal structure may vary with size, age and sexual condition (Reish 1954).

In addition to examining the variation between individuals, the importance of the position of the hooks was also investigated by examining their structure along the length of a worm. The effect of age was also studied by taking hooks from young worms and comparing these with some from adults.

For light microscopy a small section of body wall, together with the parapodial ridge, was removed from the third abdominal segment of the worm. In most cases the material had been fixed in 4 % formalin in seawater and transferred to 70 % alcohol after two or three days, but occasionally worms fixed in 70 % alcohol were used. In the case of the foreign material details of fixation were not known but the specimens had been stored in alcohol in every instance. The piece of body wall was mounted on a slide in polyvinyl-lactophenol stained with lignin pink. This mountant has the advantage of remaining pliable so that specimens can be moved after mounting by exerting light pressure on the coverslip. This is particularly useful in the study of hook structure since the hooks tend to lie on their sides and it is only by such manipulation that the hooks can be made to lie flat with the fang presenting itself in frontal view.

The material was examined under oil immersion with phase contrast.

For stereoscan microscope studies sections of body wall were

removed in the same way for larger worms and for small specimens, either the whole worm or the whole of abdominal segment three was used.

The material was then washed thoroughly in distilled water straight from 70 % alcohol. This is unlikely to cause any drastic damage to a hard structure such as the hooks and seemed more efficient at removing dirt and dust adhering to the specimens. Two further rinses in distilled water followed and the material was then mounted on to a stub using double-sided sellotape. After rapid air-drying the stubs were coated with a gold-palladium mixture using an Edwards coating apparatus, model 306 and examined on a Cambridge Scanning Electron Microscope (Stereoscan), model S4 /10.

2.2.2 The structure of the villi on Capitella 'villose'.

In addition to examination under the light microscope a small sample was prepared for scanning electron microscopy. Two segments from the end of a worm were transferred progressively from 70 % alcohol to 100 % acetone and the specimen was then dried in a Polaron critical point drier. The sample was then attached to a stub with silver dag and coated with gold /palladium, and examined as above.

2.3 Historical review of the genus Capitella.

The first reliable mention of the family Capitellidae was by Fabricius in 1780. He gave a description of Capitella capitata, as Lumbricus capitatus, from specimens collected in Greenland.

He mentioned an earlier work by Olafsen (1774) in which the species is reported from Iceland as Lumbricus littoralis minor. However, the description is very sketchy and it is difficult to be certain that Olafsen is referring to C.capitata.

The relationship of the genus to other annelid genera remained a problem for some time. In 1820 Savigny decided that it was most like the genus Clymene in the family Maldanidae.

Blainville erected the genus Capitella in 1828. He did not examine the worm himself, but based his description on that of Fabricius, altering the specific name to C.fabricii. Because of the brevity of Fabricius' description Blainville had difficulty in classifying his new genus but tentatively suggested that its lack of branchiae should place it near Clymene. The presence of a sandy tube, however, led him to include it in the same order as the sabellids and serpulids.

Oersted (1842) merely added to the confusion over the classification. He divided the oligochaetes into three groups: - Terricolae, Lumbricillae and Naides. C.capitata, described here as Lumbriconais marina, was contained in the Naides and was believed to form a transition between the latter and the Lumbricillae. Oersted thought that Lumbricus capitatus Fabricius was synonymous with his Glycera capitata.

Frey and Leuckart (1847) discovered C.capitata in Heligoland and were the first to recognise that the sexes were separate.

They realised that Fabricius and Oersted were both describing the same species and accordingly erected the name Lumbriconais capitata. Leuckart (1849) emphasised this fact further by stating that Fabricius' description does not apply to Glycera capitata Oersted but instead to Lumbriconais marina Oersted.

Shortly before this Nardo (1847) described Lombricus canalium (a mis-spelling of Lumbricus canalium) from the Adriatic. Grube (1863) examined the material and concluded that it was C. capitata.

In 1846 Grube discovered a second capitellid genus, Dasybranchus. The presence of feathery gills led him to place it in the family Telethusa along with Arenicola. Shortly after, Sars (1850) described a third genus, Notomastus, and recognised its similarity to Dasybranchus.

The relationship of Capitella to these genera was not obvious for some time. Thus in 1851 Grube placed it in the oligochaete Naidea, but left Dasybranchus in the Telethusa.

The main difficulty in classifying Capitella lay in the lack of sufficient information on its morphology. Superficially the genus bears a strong resemblance to the oligochaetes and a deeper knowledge of the anatomy was needed to dispel this notion. Beneden (1857) gave an account of the natural history of C.capitata noting, in particular, the lack of any vascular blood system; the presence of separate sexes and the larval development followed by

metamorphosis, all of which suggest a polychaete rather than oligochaete stock. He dismissed all the evidence, however, and concluded that Fabricius was correct in showing the affinity of Capitella to Lumbricus, although he accepted that it might represent a transition between the lumbricids proper and the polychaetes. Beneden was, in any event, the first author to use the combination Capitella capitata. He also erected another species, C.fimbriata, to the genus. D'Udekem (1859) placed both species in the " Annélides setigères abranches " of Cuvier, although he did subdivide the group so that Capitella was separated from the lumbricids, tubificids, enchytraeids and naiids.

Claparède (1861) examined specimens of C.capitata from the Hebrides. He found himself in close agreement with Beneden over morphological details but could not interpret his results in the same way. He was impressed by the nature of the setae and saw a resemblance to maldanids in the swellings around the hooks. He concluded that one could possibly erect a new family for capitellids under the name " Abranches polychètes ".

The family Capitellidae as now understood was proposed by Grube in 1863. He made a detailed study of the anatomy of C.capitata and was struck by the resemblance to Dasybranchus and Notomastus. He was convinced of their affinity with the polychaetes and placed them in the family Capitellacea, which he believed was closely related to the Arenicolae.

In the same year Carus and Gerstacker proposed an entirely

different classification which resulted in the three capitellid genera being placed in separate families, with Capitella in the Halelminthea, with the opheliid Polyophthalmus and some oligochaetes. Furthermore this family was in a separate class from the one containing Dasybranchus and Notomastus. Although the authors were probably unaware of Grube's work their separation of the capitellid genera makes the classification completely unacceptable. It is now only of historical interest.

In 1865 Johnston reclassified C.capitata, which he had previously described as Lumbricus littoralis (1827) and L.capitatus (1835) as Valla ciliata in the family Lumbricidae. He did not refer to the work of Claparède or Grube and it seems likely that his scheme was drawn up without any knowledge of the current literature.

In 1862 Keferstein described another species of Capitella, C.rubicunda. Claparède (1863) also described this species but believed it to be synonymous with Notomastus latericeus Sars, a view which is now generally accepted. Claparède (1864) further added to the genus with the description of C.filiformis and in 1868 described more capitellids from the Gulf of Naples. He noted that specimens from the Mediterranean differed in size, and in type and arrangement of setae on the thorax, from material he had examined in the Hebrides, but believed the differences were insufficient to warrant the erection of a new species. He did, however, describe two new species. The first, C.costana, is distinguished by the great elongation of the mid-body segments and by the poss-

ession of a different type of seta in addition to the capillaries and hooded hooks. The second species, C.major, was described from two fragments only and Claparède expressed doubt as to its correct placing in the genus Capitella.

Czerniavsky (1881) followed up the information given by Claparède on regional differences. He described the capitellid fauna of the Black Sea and proposed three new species: - C.prototypa, C.similis and C.intermedia. In addition he recognised a subspecies of C.capitata which he named C.capitata suchumica. He also reviewed the literature on C.capitata and decided that the species really included several varieties. Thus Lumbriconais marina Oersted became C.capitata danica and the material from Western Europe examined by Beneden was named C.capitata belgica. Referring to the variation found by Claparède, Czerniavsky decided that the different forms could be separated and named them C.capitata hebridarum and C.capitata neapolitana.

The wide distribution of C.capitata was indicated by Webster and Benedict (1884) who recorded it on the east coast of North America. Previously Verrill had described capitellids from the same area. In 1874 he mentioned C.capitata under the name Ancistria acuta but in 1880 he changed this to Notomastus acutus and described another possible Capitella species as N.gracilis.

The known distribution of the genus was extended even further by the discovery of a species from the Antarctic. This was originally described as Isomastus perarmatus Gravier (1911), but

Hartman (1959a), in her catalogue, referred to it as C.perarmata.

A species from the western United States was described by Johnson (1901) who erected the species C.dizonata for a single incomplete specimen found in the Puget Sound region. Another species, C.minima, which was distinguished by the presence of a copulatory apparatus in both sexes, was described from Madeira by Langerhans (1880).

More recently, Boletzky and Dohle (1967) have discovered a hermaphrodite species, C.hermaphrodita, from the south of France and Hartman and Fauchald (1971) have given the name C.aberranta to a specimen found in deep water in the North Atlantic.

Many more subspecies have been described. In 1930, Monro reported the presence of C.capitata antarctica in kelp holdfasts off South Georgia. Hartman has described several subspecies from American waters. Two of these, C.capitata ovincola Hartman (1947) and C.capitata floridana Hartman (1959b) are known only from squid egg masses. C.capitata tripartita Hartman (1961a) is described from deeper water off southern California, mainly in muddy sands, and C.capitata oculata Hartman (1961a), a subspecies parasitized by the copepod Monstrilla capitellicola, was found in the same area as C.capitata tripartita.

Since then Hartman (1961b) has described additional varieties of C.capitata, such as C.capitata 'punctate' and C.capitata 'villose' and in 1971 Hartman and Fauchald recorded the occurrence of Capit-

ella 'near capitata'.

A Japanese subspecies was described by Kitamori (1960) from specimens collected in polluted waters in the Inland Sea.

In 1964 Wu reviewed the literature on the distribution of C.capitata and erected a new subspecies for European populations, C.capitata europaea. He did not accept the validity of C.capitata japonica but concluded that it was synonymous with C.capitata capitata, a subspecies with a wide distribution in the North Pacific. He also described a possible subspecies from South Africa based on a description by Day (1961).

Hartman (1951 , 1959a, 1965) summarized the literature on capitellids. In the following section the present situation is outlined and some earlier descriptions are examined in the light of more recent information.

2.4 Systematic diagnoses.

Throughout this account C refers to capillary seta; H to hooded hook; G to genital hook and M to mixed. This indicates either bundles containing both capillaries and hooks or segments with capillary-containing bundles and ones made up of hooks only.

2.4.1 Capitella Blainville.

The description given by Hartman (1947) outlines the main features of this genus as it was then known.

Briefly, the genus is characterized by the presence of a thorax of nine setigerous segments of which the first seven have capillary setae. Hooded hooks are present on posterior thoracic segments, sometimes forming mixed bundles with capillaries. In the eighth and ninth notopodia of the male, genital hooks replace the hooded hooks. In the abdomen hooks like those of the thorax are found exclusively.

The prostomium is a conical lobe with or without eyes in the adult stage; nuchal slits are poorly developed. Lateral sense organs are absent. Nephridia are polymeric in some abdominal segments but the openings are not clearly visible. Genital apertures are restricted to the last two or three thoracic segments.

Branchiae are absent.

2.4.1.1 Capitella capitata (Fabricius,1780).

For synonyms see historical review (section 2.3).

The original description by Fabricius is not sufficiently detailed to define the species accurately, and the description given by Eisig (1887) is perhaps the most comprehensive. His description is, of course, based on European specimens and some differences have been recorded for more widely distributed populations. Nevertheless, Eisig's description provides a good basis for discussion and is summarized below.

The prostomium is a flattened conical lobe with eyes clearly visible in smaller individuals. Of the nine thoracic segments six bear only capillaries and the seventh usually has a mixture

of capillaries and hooks. Segments eight and nine bear hooded hooks only in the female but in the male these are replaced in the notopodia by genital hooks. The abdomen has hooded hooks only.

Genital openings in the female are found laterally between segments seven and eight and in mature individuals the epithelium around the openings is very swollen. In the males the genital opening is dorsal at the centre of the genital spines.

The maximum length is 70 mm with a width of 2 mm but lengths in the range of 20 to 40 mm are more usual.

Hartman (1947) gave a key to the known species of Capitella but she gave no detailed description of C.capitata. She did, however, give an account of the setal structure of worms from the western seaboard of North America. The precise location of the population is not given. No other information on this population is available although it may be assumed from the key that some, but not all, of the worms had mixed setae on segment seven.

Berkeley and Berkeley (1952) reported C.capitata from Vancouver. Their description gave a thoracic setal formula of 1 - 7C 8 - 9G /H with no mixing of setal types on segment seven.

Pettibone (1954) describes a population from Point Barrow, Alaska. This agrees with European populations of C.capitata in that the setal formula is 1 - 7C 8 - 9G /H or 1 - 6C 7M 8 - 9G /H

but genital hooks were present on all the specimens examined, male or female, suggesting the genus Capitellides. However, in view of the larger number of genital hooks present on these worms, Pettibone refers them to C.capitata.

This problem is discussed more fully below, in section 2.7, but it may be noted here that while the genus Capitella may apply to these worms the presence of genital hooks in both sexes must place them in a different species.

I have examined specimens of C.capitata from various sites in Nova Scotia, Canada. Larger specimens (thoracic length greater than 7 mm) all had capillaries only in the first seven segments but in two collections of smaller worms (thoracic length 1.9 - 2.6 mm) some worms had hooded hooks as well as capillaries on segment seven.

One specimen was of particular interest. This had been collected from the Halifax area of Nova Scotia and was labelled as identified as C.capitata by Pettibone. It was a very large specimen with a thoracic length of 15.5 mm. It was incomplete but the total length for forty-five segments was 67 mm. The thoracic setal formula was: -

1 - 7C 8 - 9G in the notopodium and

1 - 7C 8 - 9H in the neuropodium.

The genital hooks were very small and difficult to see. There were two pairs in each segment.

White swellings were present laterally on segments seven and

eight and the abdomen contained developing eggs.

This description suggests a change of sex from female to male and is reminiscent of the condition seen in a population from Whitstable (see section 2.5.2). The small size of the genital hooks indicates the development of male characteristics but the large size of the worm shows that it is not a young individual. Furthermore the white swellings are only found in female worms and the developing eggs confirm the female sex. It is, of course, possible that this worm is the same type as those described by Pettibone from Point Barrow. However, in this instance the genital hooks are very small, both in size and number, and obviously not fully formed. No developing sperm were found in the coelomic fluid of the worm. The worm is, therefore, in the process of acquiring male characteristics. Whether the development of the eggs would have continued is not known. Usually in this species males can be recognised at a smaller size, and thus an earlier age, than females. If this specimen is a contemporary hermaphrodite therefore, it is strange that the female features have developed first.

Dr. Hutchings (pers. comm.) has examined Australian populations of C.capitata and reports considerable variations especially in the Port Philip population. I have examined two specimens (a male and a female) from South Australia. These differ from European specimens in having capillary setae on segment eight with a thoracic setal formula of: -

1 - 7C 8 - 9G in the notopodia

1 - 6C 7 - 8M 9H in the neuropodia in the male and: -

1 - 7C 8M 9H in the notopodia

1 - 7C 8M 9H in the neuropodia in the female.

They thus agree with the description of C.perarmata, also from the southern hemisphere. It must be assumed that these specimens belong to the latter species.

Wu (1964) diagnoses the main features of C.capitata capitata, the most important of which is the presence of capillaries only on the first seven segments. Wu's definition is thus more restrictive than the ones above and, of these, applies only to the description of Berkeley and Berkeley.

Capitella capitata subspecies.

The location and literature of each of these is summarized in Table 2.

C.capitata ovincola Hartman, 1947.

This was originally described by Hartman (1947) as a new species but she subsequently referred it to the subspecific level.

It differs from C.capitata in being much larger (but see C.capitata oculata), 60 mm for a mature individual, and in having greatly elongated abdominal segments which are three times as long as wide and are also thicker than in C.capitata capitata. Hooded hooks extend further forward into the thorax and are present in the sixth and seventh segments and in some cases the fifth. There are four or five pairs of genital hooks in the eighth and three or four pairs on the ninth segment. These are slightly

TABLE 2. Capitella capitata subspecies.

Subspecies	Author	Date	Location	no. of samples	Habitat
C.capitata ovincola	Hartman	1947	Monterey Bay California	'many'	squid egg masses at 60 - 80 m
C.capitata floridana	Hartman	1959 b	St. Andrew's Bay Florida	'many'	squid egg cases
C.capitata oculata	Hartman	1961 a	Sthn California. Type loc:La Jolla Canyon	12 locs with from 3-14145	deep water up to 637 m
C.capitata tripartita	Hartman	1961 a	Sthn California. San Pedro & Mugu Canyons	100 + at 2 locs	46 - 119 m deep mud, sand, at base of Loligo egg masses
C.capitata antarctica	Monro	1930	Cumberland Bay S. Georgia	4	kelp holdfast
C.capitata japonica	Kitamori	1960	Inland Sea Japan	-	polluted coastal waters
C.capitata europaea	Wu	1964	Sea of Azov,Black Sea,North Sea, Mediterranean Sea,European coastal waters	-	-
C.capitata danica	Czerniavsky	1881	Denmark	-	-
C.capitata belgica	Czerniavsky	1881	W. Europe	-	delicate tubes in sand under stones
C.capitata hebridarum	Czerniavsky	1881	Isle of Skye	-	membranous tubes between rocks
C.capitata suchumica	Czerniavsky	1881	Black Sea	-	2 m deep in mud
C.capitata neapolitana	Czerniavsky	1881	Naples	-	-

different in structure in that they show fewer cross-striations than in C.capitata capitata. The structure of the hooded hooks is different, C.capitata capitata having three teeth above the fang and C.capitata ovincola having four or five. These are illustrated in Figs. 1 and 2.

This subspecies is also different in its habitat, being found only in squid egg masses.

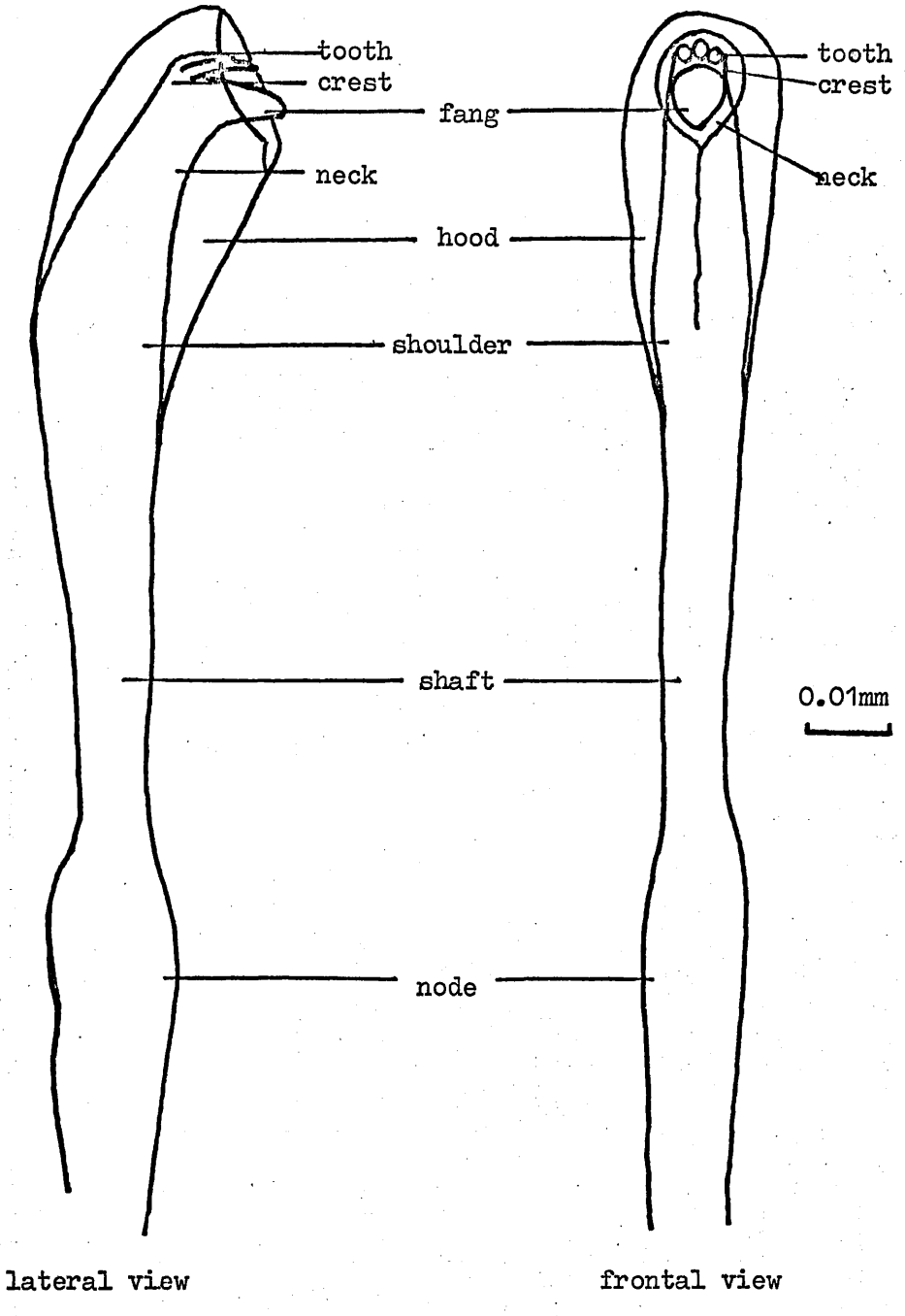
I have examined twenty paratypes of this subspecies. The range of setal arrangement on the thorax was quite large (see Table 3).

TABLE 3. Thoracic setal arrangement in C.capitata ovincola.

Setal arrangement	Numbers of worms
1 - 4C 5 - 7M 8 - 9G /H	7
1 - 5C 6 - 7M 8 - 9G /H	8
1 - 5C 6 - 7M 8 - 9H	1
1 - 3C 4 - 7M 8 - 9G /H	3
1 - 3C 4 - 7M 8 - 9H	1
numbers refer to numbers of segments.	

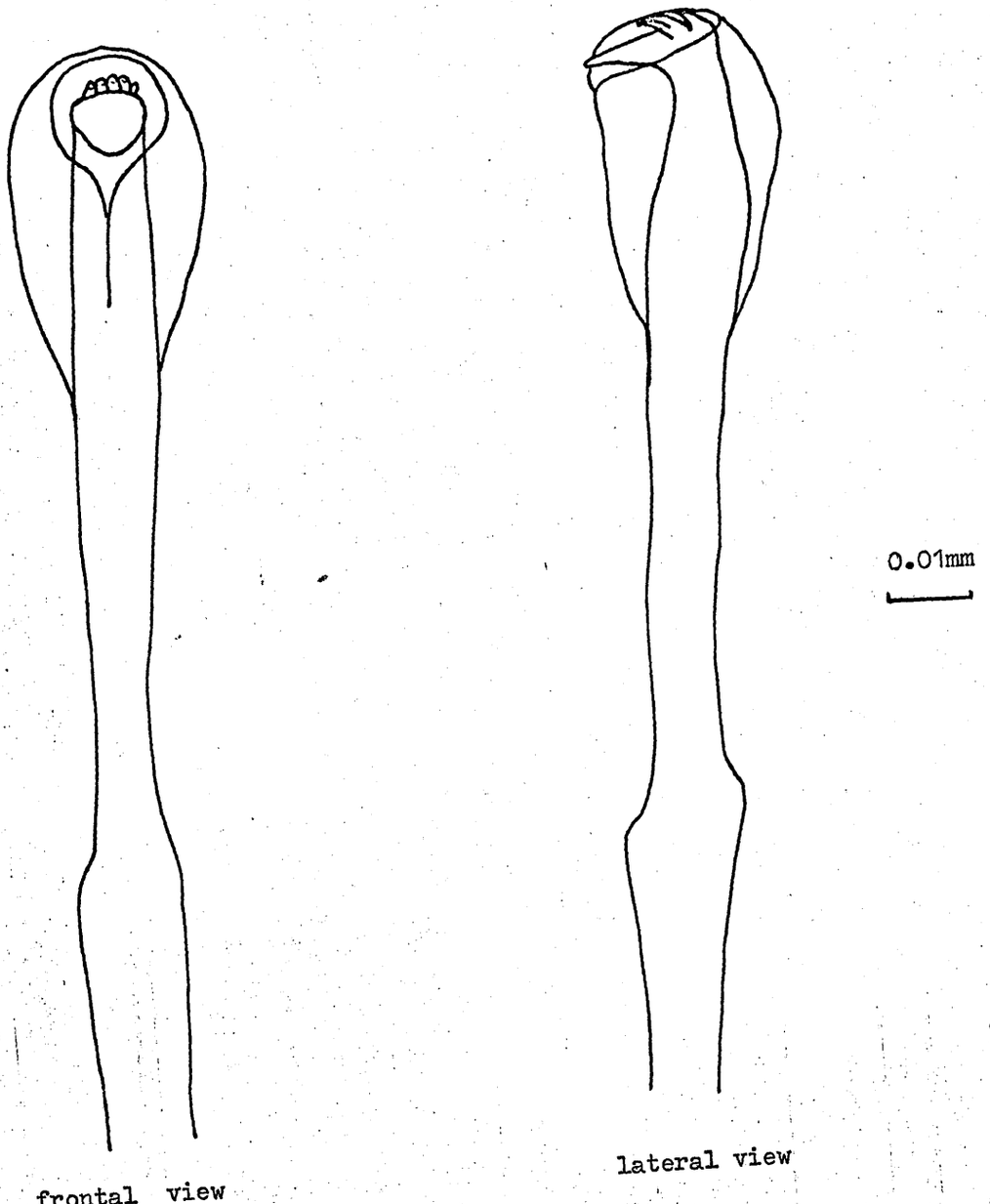
Segments with mixed setae usually showed a similar pattern with capillaries only in the notopodia and capillaries and hooks in the neuropodia although in some instances the notopodia of segment seven do contain both types of setae. Despite the variation shown in the setal arrangement the difference from the

FIG. 1. Capitella capitata. Structure of the hooded hook.



Redrawn from Hartman (1947).

FIG. 2. Capitella capitata ovincola. Structure of the hooded hook.



Redrawn from Hartman (1947).

stem form is quite consistent. Whether such a difference is sufficient grounds for erecting a new subspecies is less certain. Considerable variations in patterns of this type have been recorded for C.capitata from different areas (see Table 12) and from the same population (Table 8).

Differences relating to overall size and to the size and shape of abdominal segments are equally unsatisfactory as taxonomic criteria since they are subject to considerable change and variation in life. This is particularly true in this instance as Hartman partly based her decisions on the comparative lengths of worms. Thus Hartman (1947) said when describing C. capitata ovincola: - "C. ovincola differs from C.capitata grossly in being noticeably larger". C.capitata ovincola is about 60 mm long. Yet in her description of C.capitata oculata (1961a) she states that : - "The subspecies differs from the stem, C.capitata Fabricius, in being much smaller, usually less than 20, instead of (up) to 100 mm long".

The only remaining difference lies in the setae. The described number of genital hooks is not different from that found in European populations and the difference in their structure is minimal. Furthermore, in the specimens that I examined six of the eighteen males examined had only two or three genital spines in segment eight, which is also within the range shown in European populations.

The structure of the hooded hooks themselves, however, is

more conclusive. It is not known on which population Hartman based her study of C.capitata capitata hooks but in any event it is very difficult to be certain of the number of teeth using light microscopy. Stereoscan pictures of hooded hooks from C. capitata ovincola do however show consistent differences from any other Capitella specimens examined (Fig. 19). The difference does not lie in the arrangement of the teeth themselves but in the shape of the fang, and can in fact be seen in Hartman's figures (Figs. 1 and 2).

Such a difference, coupled with the morphological variations already mentioned, may be sufficient to warrant specific rank. However, the unusual habitat may have an effect on the development of the hooks which is purely phenotypic. Unfortunately it has not been possible to examine hooks from other subspecies living in squid egg masses for comparison. M^{c}Gowan (1954) also found worms of this type, which suggests that the population is well established, and in 1955 Hartman found several hundred in an egg mass of Loligo in the San Pedro Basin, off southern California.

C.capitata floridana Hartman, 1959 .

This differs from the stem form in its thoracic setal formula which is: -

1 - 4C 5 - 7H 8 - 9G in the notopodia of the male and

1 - 4C 5 - 9H in the male neuropodia and in the female.

Four, instead of three teeth, are present on the hooded hooks. Like C.capitata ovincola it occurs in squid egg masses but it is much smaller than this subspecies, only attaining a length of

6.2 mm for a ripe female. Its setal formula is evidently much less variable than that shown in C.capitata ovincola, but it continues the trend shown in this species of a gradual reduction in the number of capillaries.

I have examined the holotype of this material, which was a ripe female. It showed the same swelling around the genital opening as is found in the stem form. A lateral view of the hooks showed a pattern similar to that shown by Hartman (1959b) but it would be difficult to preclude the possibility of more teeth being present. Unfortunately it has not been possible to examine the fine structure of the teeth using the stereoscan, so no real conclusion can be based on this point.

It is very difficult to place this subspecies. The constancy of the setal arrangement and the different structure of the hooks suggest a real difference, but a comparison with C.capitata ovincola shows that this too has a similar modification in the setal arrangement which may be purely phenotypic. In the absence of any further information concerning the ecology of this subspecies and the effect of its habitat on the arrangement of hooks it seems preferable to place it at non-specific level. It is, of course, possible that C.capitata floridana represents the offspring of a single female, as Hartman gives no details of numbers; in which case the population becomes a rather special one which cannot be assessed by normal methods.

C.capitata oculata Hartman, 1961.

This differs from C.capitata capitata in being smaller, only 20 mm long. Hartman appears to be in some confusion as to the

size relations of these subspecies (see C.capitata ovincola). Eyes are present at all stages of growth. In addition, 1 % of the sample contained a parasitic copepod, Monstrilla capitellicola. The thoracic setal arrangement is identical to C.capitata capitata.

I have examined the holotype and fifteen paratypes of this subspecies and can find no significant difference between them and C.capitata capitata. Furthermore, a large sample of Capitella sp. from the same station showed the same features. The length was not that quoted by Hartman, the holotype being 50 mm long, but in any event, size alone cannot be acceptable taxonomically. It is true that eyes are seldom visible in adult worms but this is because they are occluded by pigment in the epithelium rather than by their absence. The fact that in this population the eyes are not covered is not sufficient to merit specific recognition. Possibly their presence is related to the depths at which this subspecies lives.

C.capitata tripartita Hartman (1961).

This subspecies is defined by the tripartite nature of the setal formula, in which the first three segments have capillaries only and the next four are mixed. Genital hooks are present in the notopodia of segments eight and nine of the male and hooks in the female. Eyes are occasionally present. The length is very variable with adults ranging from 9 to 90 mm. There is no information available on the structure of the hooded hooks.

I have only been able to examine the holotype of this subspecies. This was a ripe female of 17.5 mm. The setal formula follows the basic pattern above but the mixed segments are made up

of mixed bundles and bundles of different types of setae on the same segment: -

Left notopodium 1 - 5C 6M 7 - 9H

Right notopodium 1 - 4C 5 - 7M 8 - 9H

Left neuropodium 1 - 3C 4 - 6M 7 - 9H

Right neuropodium1 - 4C 5 - 7M 8 - 9H

which gives an overall arrangement of 1 - 3C 4 - 7M 8 - 9H.

It is very difficult to deduce anything from a single specimen but the fact that Hartman records this subspecies from two different localities suggests that her conclusions are valid. C.capitata tripartita was not found in the same area as C.capitata capitata.

C.capitata antarctica Monro, 1930 (as a variety).

This was separated from the stem by the highly developed copulatory apparatus which is made up of five to six pairs of genital hooks in the eighth notopodia and four pairs in the ninth. In addition the parapodial ridges in the abdomen are slightly more developed than in C.capitata capitata. Monro also draws parallels with C.perarmata (Gravier) which has a similarly highly developed copulatory apparatus.

In view of the wide range of genital hook numbers found in any given population (see, for example, Imajima and Hartman 1964) it seems unnecessary to erect a new subspecies for this variety.

C.capitata japonica Kitamori, 1960.

Kitamori regards this subspecies as being closely allied to C.capitata sensu Eisig (Beneden) from which it is distinguished

by the presence of a mud tube. It is similar also to C.capitata floridana but has more segments. The author distinguishes it from C.capitata (Fabricius) as described by Fauvel (1927), Hartman (1947) and Berkeley and Berkeley (1952), by its length, number of segments and shape of posterior end. Imajima and Hartman (1964) compare the subspecies with Japanese specimens of C.capitata and distinguish it by the number of genital hooks present. In C.capitata there are two pairs of hooks in segment nine, whereas in C.capitata japonica there are four or five pairs. The length of a preserved specimen was 45 mm. In their description they state that the first segment may lack setae giving a setal formula of: -

1- 2 - 7C 8 - 9G /H

However, Wu (1964) also noticed this feature and in personal communication with Dr. Kitamori discovered that the setae on the first segment were very difficult to see but were not absent. As this feature is the only one of real taxonomic importance one must agree with Wu in deciding that there are no grounds for maintaining this subspecies.

C.capitata europaea Wu, 1964.

Wu separates this subspecies from the type on the basis of its setal formulation, which is: -

1 - 6C 7M 8 - 9G /H in the notopodia

1 - 6C 7 - 9H in the neuropodia

for specimens from the Mediterranean Sea and European coasts where the salinity is high and: -

1 - 6C 7M 8 - 9G /H in the notopodia

1 - 6C 7M 8 - 9H in the neuropodia

for specimens from low salinity waters in the Black Sea and the Sea of Azóv.

The widespread presence of capillaries in segments eight and nine of the high salinity populations must be restricted to northern European waters. Its occurrence in the Mediterranean or in western Europe is unknown from the literature. Fauvel (1927) does not refer to this and I have seen it in only two individuals of the European populations that I have sampled. In this event Wu's subspecies needs redefining at the very least.

Czerniavsky's subspecies.

In 1881 Czerniavsky described five 'forms' or subspecies of C.capitata. Hartman (1959a) decided that these are not valid and a brief examination of the literature confirms this.

Firstly he named subspecies for the populations studied by Oersted, Beneden and Claparède.

Oersted's Lumbriconais marina from Denmark becomes C.capitata forma danica, and is distinguished by the presence of a variable number of capillary-bearing segments (4 - 6) followed by segments with hooks only. Eyes may or may not be present. This subspecies is hardly separate from C.capitata belgica (Beneden) which has six segments with capillaries and one with mixed bundles of setae.

He reflected the distinction shown by Wu (1964) in erecting a new subspecies for Claparède's European material. This is C.capitata hebridarum, which has seven capillary-bearing segments

and is thus different from the other subspecies. The difference is not, however, considered sufficient to warrant the naming of a new subspecies.

C.capitata neapolitana was erected for a population inhabiting Naples Bay, Italy. Czerniavsky referred to Claparède's work in this region but disagreed with the latter in his assessment of the status of the population. Claparède realised that one could not establish specific differences in this genus based on the size of the animal or on changes in the setal pattern.

He also described a new subspecies, C.capitata suchumica, described from the Black Sea. It has capillaries only in the first six segments and hooks only thereafter, with a large number of setae in each bundle. It is a small worm. There is apparently no difference between this subspecies and C.capitata danica.

2.4.1.2 Capitella intermedia Czerniavsky, 1881.

C.intermedia is the first species described by Czerniavsky. It was found in sand in the Black Sea. It is separated from C.capitata by its thoracic setal formula which resembles that of C.tripartita: -

1 - 3C 4 - 6M 7 - 9H

Eyes are present. It attains a length of 12 mm. Czerniavsky did not refer to genital hooks nor to the presence of genital products so that, in view of the small size of this specimen, it is almost certain that the description applies to a young specimen of C. capitata.

2.4.1.3 Capitella prototypa Czerniavsky, 1881.

This is represented by three specimens collected from the shore of the Black Sea. Like the above species these are probably young C.capitata since the setal formula of: -

1 - 3C 4 - 9H

is that of recently-metamorphosed C.capitata. The presence of eyes and the small size of the worms (5.5 - 10.5 mm) corroborates this.

2.4.1.4 Capitella similis Czerniavsky, 1881.

The description is based on one specimen found in mud in the Black Sea. The specimen has six segments with capillaries and reaches 21 mm in length. Eyes are not present. It is difficult to see why Czerniavsky placed this specimen in a new species since, as its name suggests, it is similar to C.capitata.

2.4.1.5 Capitella perarmata Gravier, 1911.

This was originally described by Gravier (1911) as Isomastus perarmatus, but was transferred to the genus Capitella by Hartman (1947). It differs from C.capitata only in the presence of capillary setae on segments eight and nine, together with hooded hooks. The copulatory apparatus of the male is well-developed but, as in the case of C.capitata antarctica, this is not thought to be of any great significance. The genital hooks of segment nine are described as overlapping those of eight. This is not the normal arrangement, as the setae in the ninth segment are

often buried deeply. However, the bundles are very flexible and occasionally worms showing this pattern are found. In specimens which I have examined* the copulatory apparatus appears typical of C.capitata.

Gravier does not describe the precise distribution of the capillaries on segments eight and nine. Presumably they are absent from the notopodia in the males. In specimens from Kerguelen they are restricted to the neuropodia of segment eight.

Augener (1932) described the setal formula in an adult male. He found that the neuropodia of segments seven to nine bore capillaries only. He did not consider that such a difference deserved generic recognition however and concluded that Isomastus was probably a subgenus of Capitella.

* British Museum (Natural History) 1941 .3.3. 101 - 118. (Kerguelen) and 1924 .6.15. 4 - 14. (Deception Island).

2.4.1.6 Capitella aberranta (Hartman and Fauchald, 1971).

This species differs from C.capitata in its possession of modified setae in the notopodia of segments six to nine. The full thoracic setal formula in an adult female is as follows:-

1 - 5C 6 - 9 modified hooks in the notopodia

1 - 5C 6 - 9H in the neuropodia.

The capillaries are very long compared with those found in C.capitata. Hartman and Fauchald described an asetous peristomium which would not fit in with the generic diagnosis. I have exam-

ined the holotype and disagree with this. Instead, the prostomium appears constricted so that its fusion with the peristomium becomes more clear as shown in Fig. 3. This is a condition that often occurs on fixation but is not visible in life. The modified setae are illustrated in Fig.4. Hartman and Fauchald figured these as capillaries with a swollen region just below the tip but the swelling has more the appearance of a tightly closed hood enclosing the seta.

Although only one incomplete specimen is known of this species, its rank seems justified, in so far as it is difficult to relate the new setae to the normal ones, so that their presence cannot be explained away as phenotypic variation. The restriction of capillaries to the first five segments is also different from C.capitata. The presence of nine thoracic segments is the main reason for placing this specimen in the genus Capitella, as in the absence of a male specimen it is not known whether or not a copulatory apparatus is present.

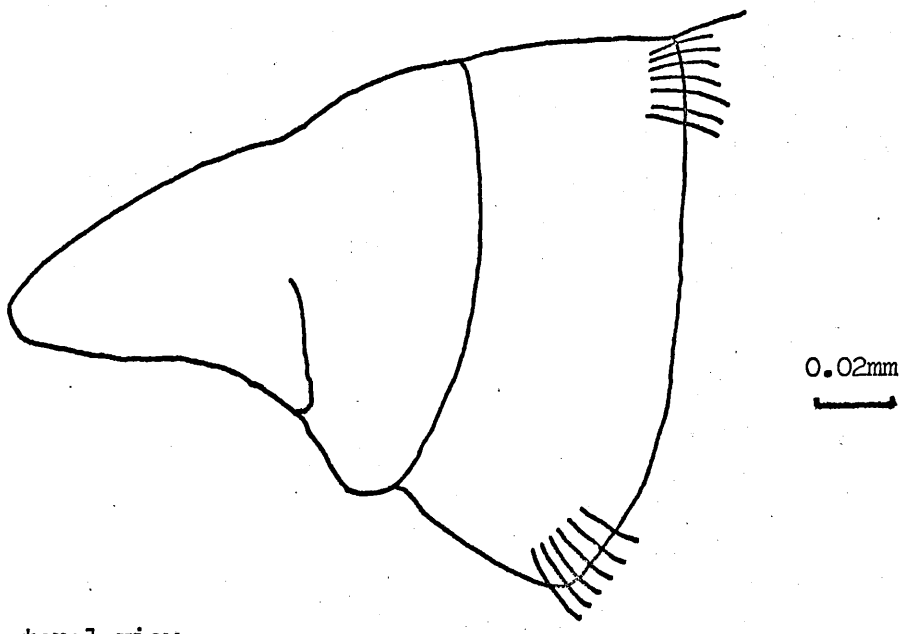
2.4.1.7 Capitella hermaphrodita Boletzky and Dohle, 1967.

A new species of Capitella was described from Loligo egg masses collected from Banyuls-sur-Mer, France. It is distinguished from other species by the thoracic setal formula and also by its reproductive biology.

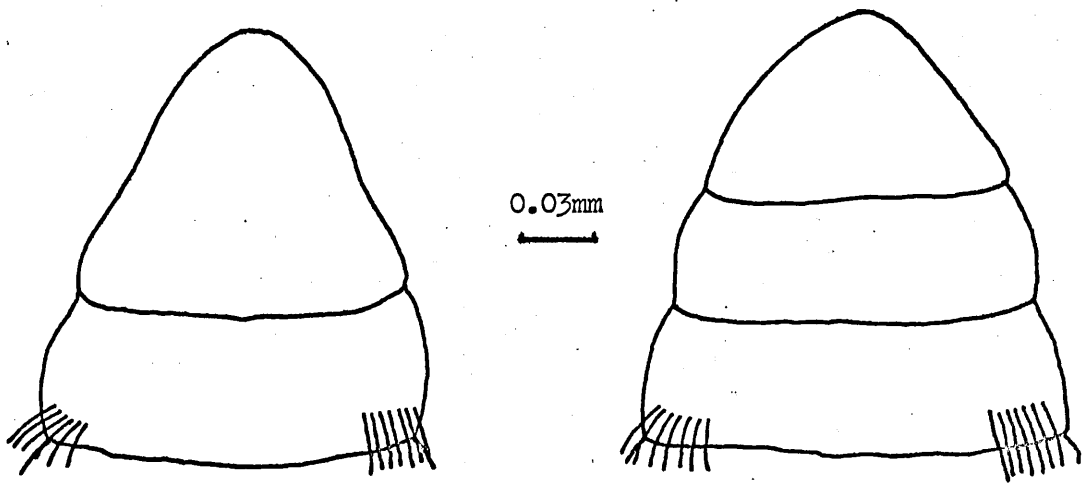
The thoracic setal formula is consistent for the first seven segments, being: -

1 - 4C 5 - 7H.

FIG. 3. Capitella aberranta. Prostomium and first setiger.



lateral view



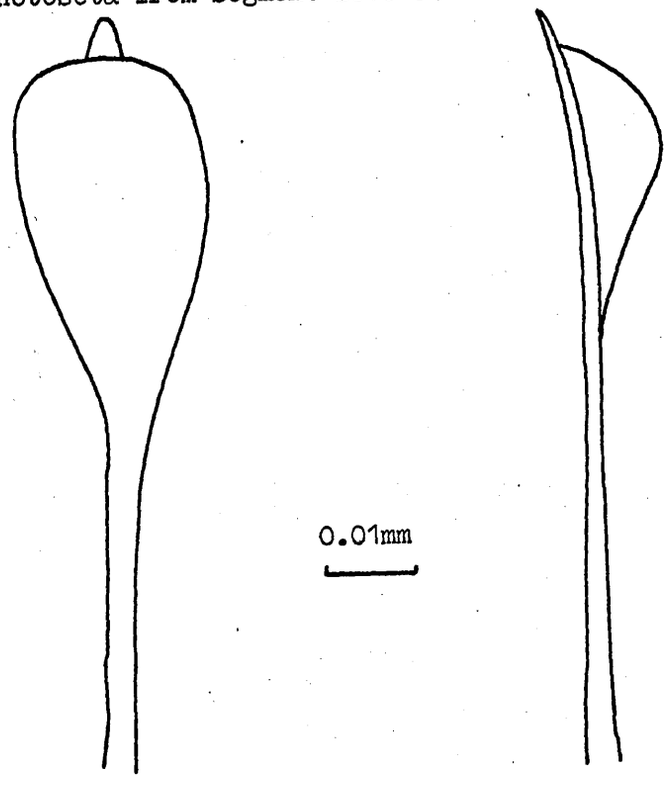
dorsal view

dorsal view

Redrawn from Hartman and Fauchald (1971).

FIG. 4. Capitella aberranta. Modified seta.

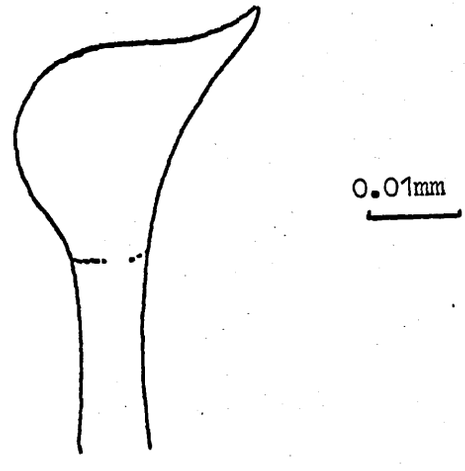
a. Modified notoseta from segment seven.



dorsal view

lateral view

b. Modified notoseta from segment eight.



lateral view

Redrawn from Hartman and Fauchald (1971).

Segments eight and nine have either normal hooks in the notopodia or alternatively genital hooks. Mixed arrangements with hooded hooks on segment eight and genital hooks on segment nine also occur. In one example hooded hooks and genital hooks were found in the same bundle. The setal arrangement can be correlated with the sexual condition. Worms with no trace of ovaries have genital hooks. Where distinct eggs are visible either hooded hooks or genital hooks or both may be found.

Ovigerous worms were found to contain early stages of sperm as well as mature sperm, thus demonstrating the hermaphroditic nature of the species.

Boletzky and Dohle attempted to raise larvae of this species. Early development appeared typical of Capitella, but the telotroch remained unchanged for over a month when kept in seawater at 12°C. The authors do not offer any explanation for this but it is likely that under normal circumstances the larvae do not undergo a planktonic period of development but remain with the parent until metamorphosis. In this case it is possible that development is halted due to the lack of a suitable substrate (Wilson 1937).

I have examined a sample of this material and found five worms with the female formula of: -

1 - 4C 5 - 9H.

Two of these had clearly distinct ovaries but the others could not be examined more closely. Two were labelled as hermaphrodites and the rest as females. Seven specimens had a copulatory apparatus

with a formula of: -

1 - 4C 5 - 7H 8 - 9G /H

Large ovaries were visible in three of these, of which two were labelled hermaphroditic and the other as a female with genital hooks. Sperm were present in one specimen, labelled as a male. The other three worms in this group were not categorised sexually. One worm with hooded hooks and genital hooks was found, with clearly visible eggs. According to the authors it was hermaphroditic. The last worm had very small hooded hooks in the notopodia of segments eight and nine indicating a developing male and yet it contained large eggs.

The interpretation of these results is discussed more fully in section 2.7 but it may be noted that a change in sex from female to male is indicated. The condition of the material prevented a closer examination of their nature, but Boletzky and Dohle have studied this in detail. Presumably those worms with only single sex characteristics had either undergone or were about to undergo a change of sex. A detailed study of the life history would be needed to confirm this, but the authors indicate that no pure males or females were present in this population.

2.4.1.8 Capitella dizonata Johnson, 1901.

This was erected for an incomplete specimen from the intertidal zone at Port Orchard, Washington, and is distinguished from C.capitata by the absence of any setae from the notopodia of segments eight and nine. A reference to capillaries occurring on the notopodia of segment ten is probably incorrect as hooks

are later described for this segment. The specimen has the typical female pores placed laterally between segments seven and eight.

In the light of present knowledge concerning sex changes in C.capitata it seems unwise to place this specimen in a separate category. It probably represents an immature male, but it may be a female which has lost its hooks prior to the acquisition of genital hooks. The specimen is, unfortunately, not available for examination.

2.4.1.9 Capitella sp.

In addition to the above species there are references in the literature to material rather uncertainly ascribed to the genus Capitella. For example, Hartman (1961b) gives a key to Capitella-like species from California, which is reproduced here in Table 4.

I have examined the material on which this key was based. This was separated into four groups labelled 'A' - 'D'.

'A' contained two specimens both with villi. The first segment was setigerous although in one of the specimens there was some evidence of a furrow across the prostomium which gave the impression of an asetous segment. Neither specimen had eyes nor any sign of spotting. The thoracic setal formulae were different:-

'a' 1 - 3C 4 - 6M 7 - 9H Thoracic length - 1.2 mm

'b' 1 - 5C 6M 7 - 9H Thoracic length - 1.5 mm

The first specimen 'a' was incomplete, but as indicated by

TABLE 4. Key to Capitella-like species.

from Hartman 1961b

1. First visible segment without parapodia.....2

1. First visible segment with parapodia and setae.....3

2. Prostomium followed by a smooth peristomium, and this by 3 or 4 segments with pointed setae, and 6 or 5 segments with long handled hooks.....*Capitomastus* sp.

2. Prostomium followed by a smooth peristomium and 6 setigers; in both male and female individuals the last 3 thoracic neuropodia with hooks, and notopodia with hooks in the 7th, and genital spines in the 8th and 9th segments.....*Capitellides* sp.

3. Body larger, finely speckled with punctate dark spots; prostomium followed by 7 segments with pointed setae and 2 segments with genital spines in the notopodia.....*Capitella* punctate

3. Body smaller, epithelium not punctate.....4

4. External surface of body villose; first 5 or 6 segments with setae in neuropodia and notopodia, followed by one segment with setae and hooks, and this with long handled hooks only.....*Capitella* villose

4. External surface of body smooth; in female individuals thorax consisting of 6 setigerous and 3 uncinigerous notopodia, and male individuals with 4 setigerous, 2 with setae and hooks mixed, and 3 with hooks (genital spines absent).....*Capitella* ?*capitata*

the length of its thorax, was smaller than specimen 'b' which was a ripe female. Possibly the different setal arrangements can be accounted for by the immaturity of the first specimen. These specimens presumably correspond to Capitella 'villose' but it is not clear why they were separated from 'D' which also contained worms with villi.

'B' contained seven specimens all with the following thoracic setal formula: -

1- 2 - 5C 6 - 8H 9 - 10G

Mature specimens of both sexes were represented. This pattern fits most closely with Capitomastus which is listed in Hartman's key. However, in her description of this genus, Hartman makes no mention of genital hooks. The correct thoracic setal formula for this genus, as given by Eisig (1887), is: -

1- 2 - 4C 5 - 8H 9 - 10G in females

1- 2 - 5C 6 - 8H 9 - 10G in males

The specimens thus agree with the diagnosis of male specimens of Capitomastus. As slight variations in setal arrangements are known to occur with age and condition in this family there seems to be no problem in placing this material in the genus Capitomastus.

It is of interest to note that two of these specimens had a few villi present on the thorax.

Tube 'C' had fourteen specimens and was labelled'Capitellides Station 5027'. The thoracic setal formula was:-

1 - 7C 8 - 9G /H

There was one exception to this. One of the worms had no genital hooks. However, this worm was different in other respects too (e.g. its lack of eyes) and probably was better placed with group 'D' with which it was similar in having villi.

It proved difficult to determine the sex of the specimens but at least two of them, with well-developed genital hooks, had eggs in the abdomen. This would suggest that these specimens belong to Capitellides. The prostomium is not quite as would be expected for this genus as there is no indication of an asetous peristomium being present. However, examination of a wide range of preserved material shows that this feature is often quite indistinct and it seems best to place these specimens in the genus Capitellides. The validity of this is discussed below (section 2.4.2). In its size and thoracic setal arrangement this material most closely resembles Capitellides giardi, although it differs in consistently having capillaries in segment seven.

Half of the specimens had dark red granular markings in the skin. These correspond to the Capitella 'punctate' of Hartman's key. These spots are found scattered all over the worm but are most abundant on the ventral surface of the abdomen, thinning out laterally. They vary considerably in size and shape and bear some resemblance to the eyespots found in Capitella. These have the same red coloration in the larvae but become duller as they are covered with more flesh. The markings are very superficial and are possibly an accumulation of excretory material. Their taxonomic importance is doubtful as they are found on worms together

with similar worms without any spots.

Two of the punctate specimens also had villi on the thorax and abdomen.

Tube 'D' contained ten specimens, of which eight had villi (Fig. 5). The arrangement of the setae was very variable in this group as can be seen from Table 5, but the overall pattern is: -

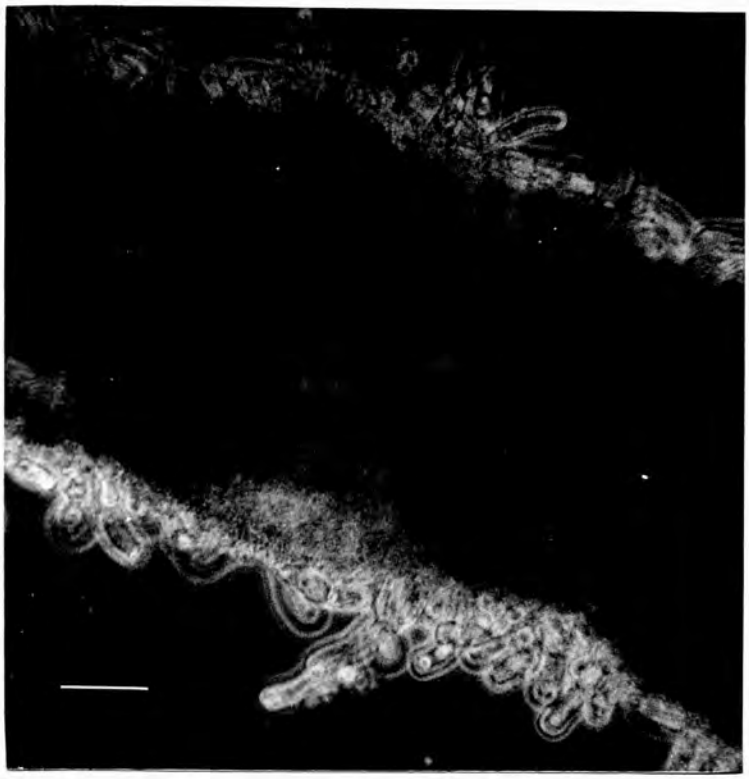
1 - 5C 6M 7 - 9H or 1 - 6C 7 - 9H

In two specimens the hooks in segments eight and nine were very small or absent, suggesting the possible appearance of genital hooks. The setal arrangements of 'A' fit in with this group. This description corresponds to that given for Capitella 'villose' by Hartman. For several reasons this grouping appears to be inaccurate. Firstly the specimens appear to be young individuals or immature females. The adult male is therefore unknown but the presence of genital hooks may be presumed. The immaturity of the worms would explain the variation in setal pattern shown and would invalidate its use as a taxonomic criterion for this sample.

The presence of villi has no significance taxonomically. This is shown by the occurrence of villi in all the specimens examined which covered three genera. Furthermore, Hartman and Fauchald (1971) reported the presence of long papillae in a dispersed arrangement over the surface of nine specimens dredged from abyssal depths in the North Atlantic. The thoracic setal formula of these (1 - 7C 8 - 9G /H) is indicative of C.capitata

FIG. 5. Capitella 'villose'. Photomicrograph of a specimen with an extensive covering of 'villi'. Scale represents 20 μm.

FIG. 6. Capitella 'villose'. Photomicrograph to show the fine structure of the villi. Scale represents 10 μm.



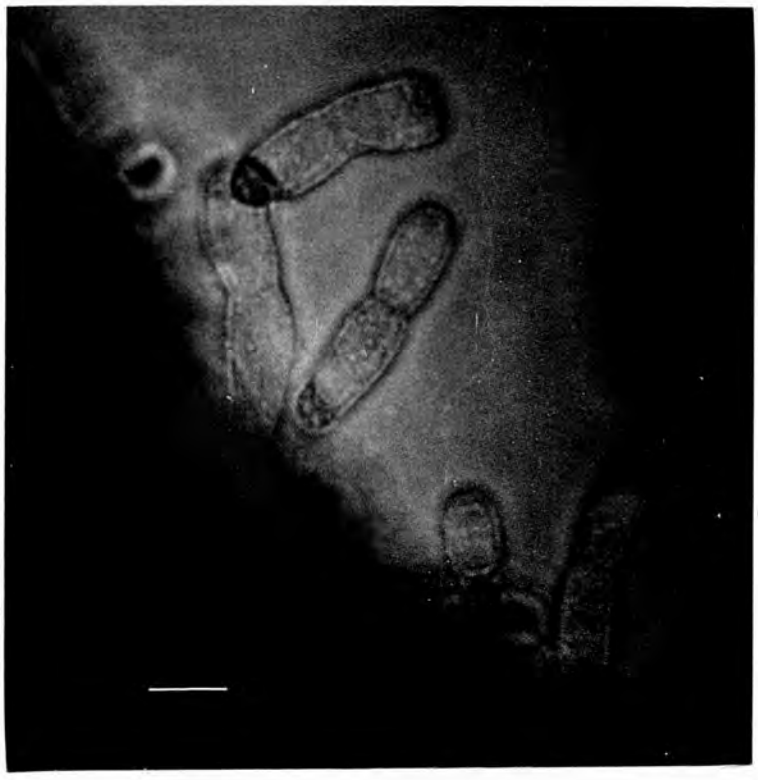


TABLE 5. Thoracic setal formulae in Capitella 'villose', tube D.

Length of thorax in mm	Setal formula	Villi
1.2	notopodial - 6C 7B 8 - 9H neuropodial - 6C 7B 8 - 9H	+++
2.1	notopodial - 4C 5 - 6M 7H 8 - 9- neuropodial - 3C 4 - 5M 6 - 9H	+
1.2	notopodial - 6C 7 - 9H neuropodial - 5C 6M 7 - 9H	+
1.8	notopodial - 6C 7 - 9H neuropodial - 4C 5 - 6M 7 - 9H	-
1.2	notopodial - 5C 6M 7 - 9H neuropodial - 4C 5M 6 - 9H	+++
approx. 1.5	notopodial - 6C) rest of worm neuropodial - 6C) in tube	++
1.8	notopodial - 6C7B 8 - 9H neuropodial - 6C 7 - 9H	++
1.6	notopodial - 7C 8 - 9H neuropodial - 6C 7 - 9H	+
1.4	notopodial - 6C 7 - 9H neuropodial - 6C 7 - 9H	++
1.2	notopodial - 6C 7 - 9H neuropodial - 5C 6M 7 - 9H	-

C = capillary seta M = mixed bundles or segments with capillaries and hooks
H = hooded hook
B = broken seta - = no seta

+ = few villi ++ = villi common +++ = villi all over worm

but in view of the papillae the authors described it as Capitella 'near capitata'.

It is also of interest to note that some of these specimens were speckled with black on the abdomen, a condition which suggests Capitella 'punctate'.

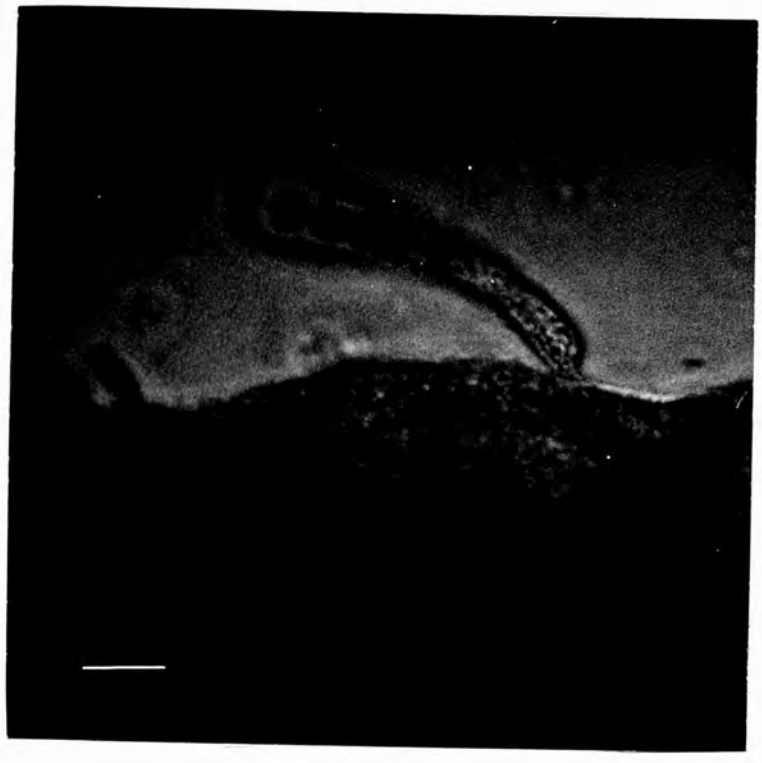
The fine structure of the villi has been examined (see Fig. 6) and it appears that they are not coelomic extensions as previously thought, but epizoic attachments of unknown nature. The point of attachment with the worm is very small (Fig. 7) and in specimens where the cuticle has lifted off, the villi have come away complete with this, and show no sign of a ruptured connection with the worm (Fig. 8). The number of villi on a worm varies from one or two, usually close together, to a complete covering all over the worm.

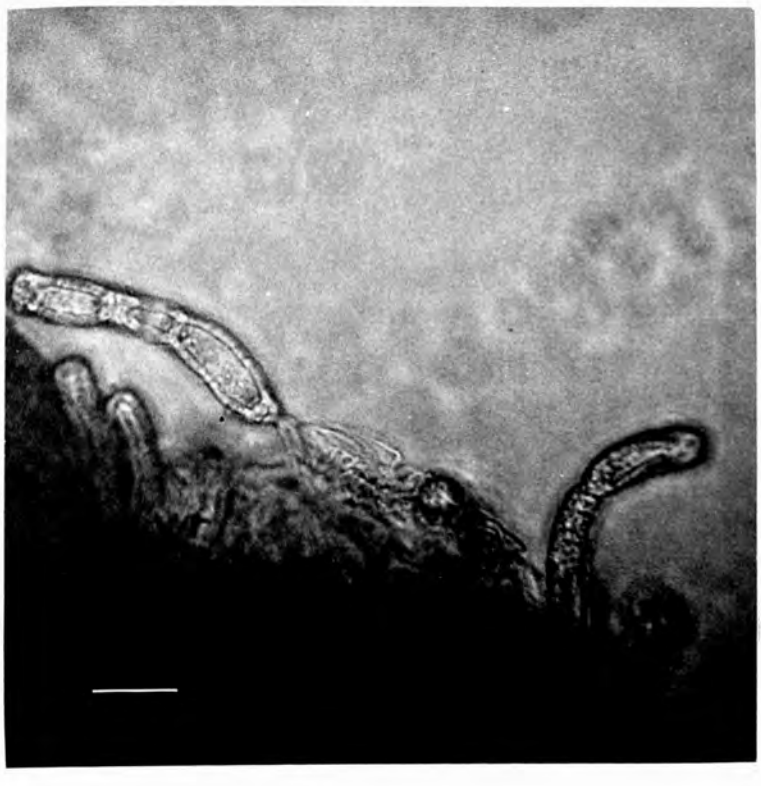
No specimens of Capitellides as described by Hartman have been found in this collection. This was presumably based on a collection from a different station.

Specimens described as Capitella ?capitata were not examined either. The description of the setal arrangement would be covered by 'D' but no adult males were present here. Eisig (1887) records the presence of sperm in immature females and believed this was due to copulation with ripe males. This is possibly the case here although Hartman's interpretation cannot be dismissed. With no further information it is not possible to take this matter further.

FIG. 7. Capitella 'villose'. Photomicrograph to show nature attachmant of 'villi' to worm. Scale represents 10 µm.

FIG. 8. Capitella 'villose'. Photomicrograph showing attachment of 'villus' to cuticle. Scale represents 10 µm.





Day (1961) also described a possible species of Capitella from the docks at Table Bay, South Africa. He examined 168 specimens, some of which were typical C.capitata ; others showed an odd setal formula on the thorax;-

1 - 7C 8 - 9H in the female notopodium

1 - 6C 7M 8 - 9H in the female neuropodium

1 - 4C 5 - 6M 7H 8 - 9G in the male notopodium

1 - 4C 5 - 6M 7 - 9H in the male neuropodium

Day was hesitant about erecting a new subspecies for this material as the sample was very small. It is possible that this setal arrangement represents young adults in the population and that with increasing age the thoracic hooks will be replaced with capillaries. However, without access to the whole range of material it is not possible to be certain, and one must refer these specimens to C.capitata.

In addition to these species there are some which are now only of historical value. In many cases even the generic name does not tie in with the description. Most of these discrepancies are due to lack of information by the respective authors and can be readily corrected in the light of present knowledge. Hartman (1959_a) has reviewed these species and her conclusions are given in tabular form in Table 6.

Capitella gracilis (Verrill) does however present some problems. Hartman (1959a) referred Notomastus gracilis Verrill to this giving the following information: - " N.gracilis Verrill 1880 (16, p. 180) Connecticut in 4 - 5 fms. See Capitella gracilis ".

TABLE 6. A revision of some species of Capitella according to Hartman 1959a.

Species	Author	Date	Revised name
C.fimbriata	Beneden	1857	Heteromastus filiformis ?
C.rubicunda	Keferstein	1862	Notomastus latericeus
C.filiformis	Claparède	1864	Heteromastus filiformis
C.costana	Claparède	1868	Heteromastus filiformis
C.major	Claparède	1868	Notomastus profundus ?
C.minima	Langerhans	1880	Capitomastus minimus

Under C.gracilis the date of Verrill's paper is given as 1879.

The 1879 and 1880 references are believed to relate to the same publication (Verrill 1880) in which the author gave a very brief description of N.gracilis, which is impossible to assess accurately. Six capillary-bearing segments are described, followed by segments with hooks only. No information concerning the number of thoracic segments was given. Verrill drew similarities between his new species and Notomastus filiformis which Hartman placed in the genus Heteromastus. However his original description of N.filiformis (1873) differs from that given in the 1880 paper. Hartman (1942) reviewed Verrill's type material but was unable to locate N.gracilis. She did find a jar labelled " N.filiformis " but this was found to contain a small capitellid, probably Capitellides, thus adding to the confusion. In 1947 Hartman discussed the relationship between N.gracilis and Heteromastus and believed that it may be a member of this genus, although the presence of six instead of seven segments with capillaries would preclude this.

2.4.2 Capitellides Mesnil, 1897 .

This genus was described by Mesnil in 1897 from material collected from laminarian holdfasts in the English Channel. The genus is distinguished from Capitella by the presence of a copulatory apparatus in the female as well as the male.

The type species is Capitellides giardi. This is only 10 mm long with 35 - 45 segments. There are nine thoracic segments with a setal formula of: -

1 - 6C 7H 8 - 9G /H

Occasionally the seventh segment contains capillaries, either exclusively , or in bundles also containing hooks. The copulatory apparatus is made up of four genital hooks with a smaller, presumably replacement hook, alongside the main one in each bundle.

A second species was described by Treadwell (1939) as Capitellides teres and is now of questionable status (Hartman 1959b). In 1959 Hartman described Capitellides jonesi from Florida. This species differs from Capitellides giardi in its thoracic setal formula:-

1 - 3C 4 - 7H 8 - 9G

Furthermore the genital armature is better developed with three to four pairs of hooks in each of segments eight and nine.

The first segment is of great interest in this genus. Mesnil referred to this and decided to discount it in his thoracic count as he believed it to be fused with the next, i.e the first setigerous segment, as in Capitella. He referred here to Eisig. Hartman (1959b) described the first segment as an incomplete asetous ring visible only from the dorsal side. This gives a thorax of ten segments. This arrangement is clearly visible in living specimens of Capitellides giardi. However, it is not so obvious in preserved material and is often only evident as a slight indentation in the prostomium, with which it is in reality fused (Fauvel 1927). This is the case for the material described earlier under Capitella sp. 'C'. Similarly Hartman (1947) makes no mention of an asetous peristomium in her diagram of the thoracic setal formula of Capitellides, and Fauvel(1927) gives only nine thoracic

segments in his key for Capitellides.

Day (1937) has studied the development of Capitellides giardi and finds it remarkably similar to that of Capitella capitata. The female broods the larvae in a mucous cocoon until metamorphosis. Total development time under the conditions of study was five days. In Capitella the larvae spend twelve days in the tube and are then usually released for a planktonic stage of nine days. However, Grassle and Grassle (1974) have found specimens of Capitella capitata in which the larvae do not leave the parental tube. The cilia pattern on the larvae is very similar to that of Capitella capitata. The development of eyes and nuchal organs is the same and the gut is formed in the same way, although it opens at different times in the two genera. In Capitella capitata it is open at the beginning of the planktonic stage whereas in Capitellides giardi it remains closed until after metamorphosis. In both genera the segments are formed prior to the opening of the gut. In Capitella capitata there is an asetous peristomium, three capillary-bearing segments and ten with hooks at metamorphosis. In Capitellides giardi there are thirteen hooked setigers present.

The close resemblance of the two genera in development and morphology and habit suggests that their division is false. Since the original description of Capitella as a genus with separate sexes with genital hooks in the male only, several variations in the theme have been encountered. A sex change is known to occur and there is a hermaphroditic species. Bearing these facts in mind, the occurrence of genital hooks in the female as well as the male

does not seem to be sufficient to warrant generic status. I would suggest, therefore, that Capitellides should be included in the genus Capitella.

2.5 Study of European populations.

2.5.1 Plymouth. Grid ref. SX 538 478 Warren Point.

This is a large population with up to 78,000 animals per square metre. Further details of the area under study can be found in the section on ecology (3.1).

Living and preserved material was examined over a period of two years. Over 2,000 individuals were examined, of which about 400 were adult. The following description of the population is based on a study of these adults.

The prostomium is a large well-developed cone sometimes showing an indication of fusion with the true first segment. This division appears and disappears according to the state of extension of the prostomium in living worms and is occasionally seen in fixed material. Eyes are present in young individuals but rarely remain visible in the adult. Nuchal slits are very indistinct.

The proboscis is eversible but is seldom seen in this state. This fact provides a useful field distinction from the related genus Notomastus in which the proboscis is continually being everted and withdrawn. The surface of the proboscis is shiny in appearance.

The thorax is made up of nine segments, all setigerous. In

living worms the surface of the thorax has a crazy paving appearance, being divided up into hexagonal segments especially in the first four or five segments. This pattern disappears in preserved materials. A mid-ventral furrow begins in segment five and runs backwards to the end of the body. Two lateral furrows are less well-marked. The thoracic segments are sometimes divided by incomplete annulae, especially in mid-segment along the line of the parapodia. The latter are very poorly developed and only recognisable by the presence of the setae.

The thoracic setal formula varies considerably. Statistical analyses show, that this is largely due to age, as represented by the length of the thorax. Taking one core sample (for details of collection see section 3.2.1) the length of the thorax was plotted against the setal formula. For this purpose the variations were ranked as shown below in Table 7.

TABLE 7. Ranking of thoracic setal formulae.

setal formula	rank
1 - 3C 4 - 9H	1
1 - 3C 4M 5 - 9H	2
1 - 4C 5 - 9H	3
1 - 4C 5M 6 - 9H	4
1 - 5C 6 - 9H	5
1 - 5C 6M 7 - 9H	6
1 - 6C 7 - 9H	7
1 - 6C 7M 8 - 9G /H or H	8
1 - 7C 8 - 9G /H or H	9

The regression equation of setal formula on thoracic length was calculated as shown in Fig. 9.

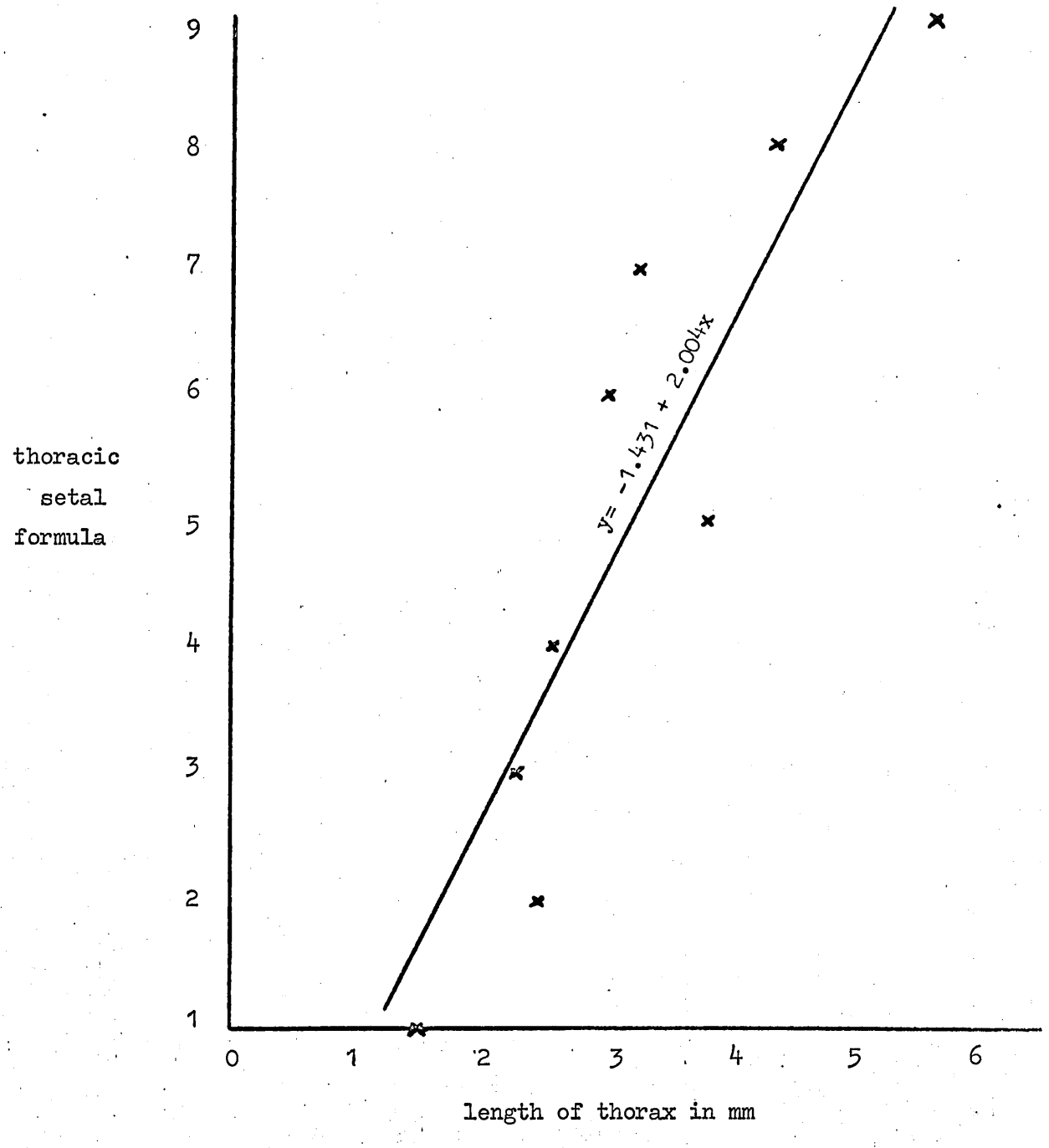
However, worms with both types of setae on segment seven have been found with developing gametes, as shown in Table 8. These worms are shorter than those with capillaries only on segment seven, although the difference is significant only for female worms (Table 9). It is possible that the smaller mean length is due to a proportion of immature, rather than unripe, worms in the sample. Nevertheless, there are indications here that the onset of sexual maturity in this population occurs, in some individuals at least, before the complete development of the setal pattern.

The abdomen is thinner and flatter than the thorax and terminates in a simple collar-like pygidium. The abdominal segments are from three-quarters to one and a half times as long as wide depending on the state of contraction and are generally slightly shorter than the thoracic segments. All abdominal segments bear hooded hooks on poorly defined parapodial ridges placed near the rear of the segment.

Mature females are recognised by the presence of white pads around the genital pores and the presence of eggs free in the coelom.

Adult males are equipped with genital hooks on segments eight and nine. These vary in number as shown in Fig. 10. Sometimes male genital hooks are present but these can only be detected by dissections. The scatter diagram of the number of genital hooks

FIG. 9. Relationship between mean length of thorax and thoracic setal formula in C.capitata from Plymouth.



't' = 6.015. The regression line is therefore significant at the 5 % level.

TABLE 8. Variations in the thoracic setal formula of adult C.capitata from Plymouth, Devon.

Formula	No. worms	No. examined for genital products	No. with developing genital products	Mean length of thorax in mm
1 - 7C 8 - 9G /H	109	32	27 (84 %)	6.437 ± 0.591
1 - 7C 8 - 9H	145	145	71 (49 %)	6.227 ± 0.193
1 - 6C 7M 8 - 9G /H	60	13	8 (61 %)	5.734 ± 0.825
1 - 6C 7M 8 - 9H	101	45	6 (13 %)	4.961 ± 0.125
1 - 6C 7M 8 - 9-	23	10	1 (10 %)	4.403 ± 0.154

TABLE 9. Comparison between mean thoracic lengths of worms from Plymouth, Devon.

Thoracic setal formulae	't' mm	significance at 5 % level
1 - 7C 8 - 9G /H 1 - 7C 8 - 9H	0.2627	-
1 - 6C 7M 8 - 9G /H 1 - 6C 7M 8 - 9H	0.9268	-
1 - 7C 8 - 9G /H 1 - 6C 7M 8 - 9G /H	0.6926	-
1 - 7C 8 - 9H 1 - 6C 7M 8 - 9H	4.9612	+

against thoracic length (Fig. 10b) suggests that there is no significant relationship between these parameters.

Mature worms have been found in all months of the year and two larval types, planktonic and benthonic, are known.

One individual showing signs of sex reversal has been found in a sample from this population.

Complete specimens of adults were rarely encountered so that it is difficult to give an accurate assessment of the number of segments, or total length.

This material should fit in with C.capitata europaea (Wu 1964) but the high proportion of worms with a setal formula of 1 - 7C suggests his C.capitata capitata. Furthermore capillaries have never been found on segments eight and nine as suggested by Wu (1964) for the European populations of C.capitata europaea.

The fine structure of the setae in this population has been studied using light and scanning electron microscopy. The results are shown in Figs. 13 - 17 and Fig.22.

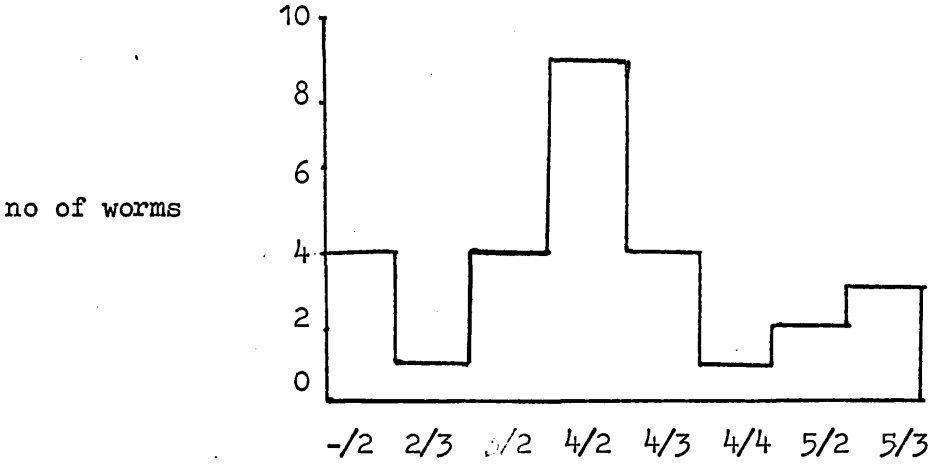
2.5.2 Whitstable population. Grid ref. TR 108 672.

This population was sampled several times over a three year period and the following description is based on living and preserved material.

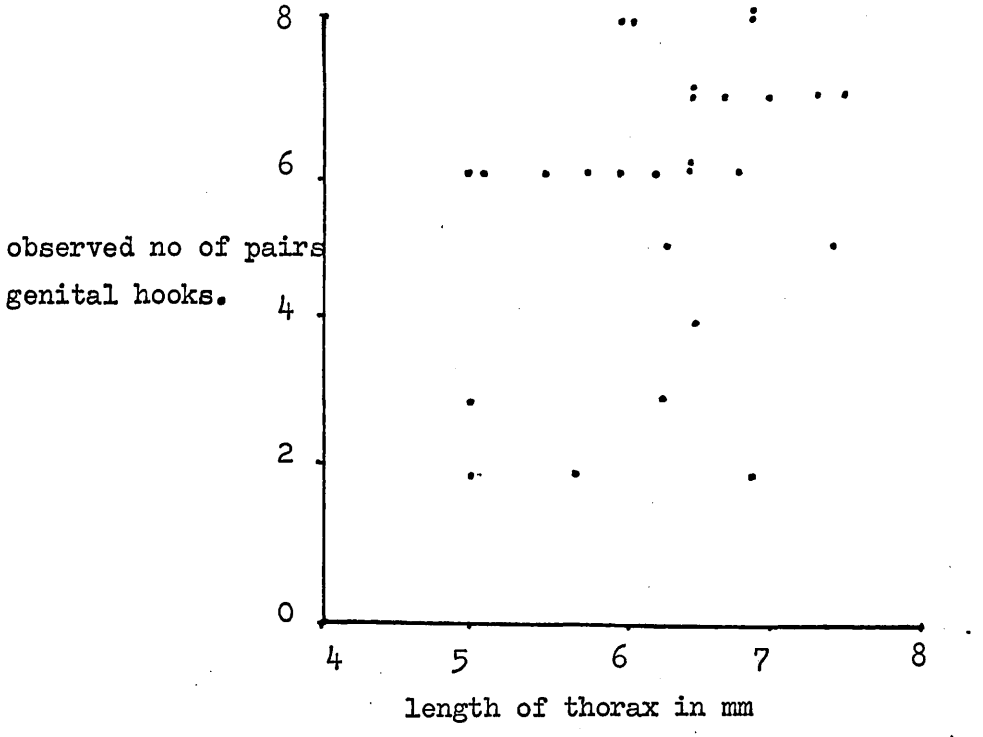
In general body form this population does not differ from the

FIG. 10. Genital hooks in C.capitata from Plymouth.

a. Variation in numbers of genital hooks.



b. Relationship between the number of genital hooks and the length of the thorax.



one from Warren Point, although Whitstable worms are significantly larger (Table 10). The thoracic setal formula shows a similar variation as shown in Table 11. One important difference from the Plymouth population lies in the presence of capillary setae in segments eight and nine. Two specimens collected in January 1973 had the following thoracic setal formula: -

1 - 7C 8 - 9G (notopodia)

1 - 7C 8 - 9H and M (neuropodia) and

1 - 7C 8 - 9G (notopodia)

1 - 7C 8M 9H and M (neuropodia).

This pattern is reminiscent of that found in C.perarmata and is also similar to that of the western coastal populations of C.capitata europaea as described by Wu (1964). However its restriction to only two specimens (2.7 % of the sample) prevents it playing an important part in the description of the population. Its significance with regard to the overall taxonomy of C.capitata is discussed below (section 2.7).

A small proportion of the worms examined had blackened capillaries instead of the more usual yellow coloration. The black setae are arranged in a definite way with the most dorsal setae in the notopodia and the most ventral in the neuropodia showing this pigmentation. Sometimes the blacking is restricted to the base of the capillaries and in some instances the whole structure is affected. In males the genital hooks are very occasionally black as well. This colouring is never found in the hooded hooks.

As can be seen from Table 11 it is often difficult to accur-

TABLE 10. Comparison of mean lengths of different populations of C.capitata from western Europe.

Population	Mean length with standard error	't' mm	significance at 5 % level
Plymouth	5.940 ± 0.316	Plymouth /Whitstable 4.797	+
Whitstable	8.360 ± 0.392	Whitstable /Rhosneigr .836	-
Rhosneigr	7.885 ± 0.410	Rhosneigr /Plymouth 3.752	+
Dutch	3.971 ± 0.131	Dutch /Plymouth 5.742	+

TABLE 11. Variations in thoracic setal formula of C.capitata from Whitstable, Kent.

Formula	No. of worms	Sex	No. examined for genital products	No. with developing gametes	No. with black setae	No. with spots	Mean length of thorax and S. E.
1 - 6C 7M 8 - 9H	3	young	3	0	0	0	8.750 ± 1.654
1 - 6C 7M 8 - 9G/H	4	male	1	1	0	0	4.933 ± 1.508
1 - 7C 8 - 9G/H	23	male	10	8 (80%)	6	5	8.072 ± 0.713
1 - 7C 8 - 9H	29	female	29	21 (75%)	9	2	8.535 ± 0.533
1 - 7C 8 - 9-	3	young male	3	1 (33%)	0	0	7.366 ± 0.119
1 - 7C 8 - 9 smallH	6	both	6	2male 2female	1	1	8.300 ± 0.695
1 - 6C 7M 8H 9-	2	young	2	0	1	0	5.950 ± 3.058
1 - 7C 8H 9-	4	changing	4	4female	1	2	8.605 ± 0.367

ately determine the sex of worms from this population. In most samples there is no problem and adult worms of both sexes can easily be recognised as for the Plymouth population (see Fig. 11), but in two samples (taken in January 1973 and February 1974) the picture was confused. Worms with the setal formula

1 - 7C 8 - 9-

are normally taken as young males in which the genital hooks have not yet developed. This is indicated by the flattened shape of segments eight and nine and appears to be the case in the three examples here, one of which contained sperm morulae. Worms in which setae are absent from the ninth notopodia only or where very small setae are present are more difficult to assess. Of six worms with minute hooks, two were ripe males and two contained developing ova, although in the latter category the shape was definitely that of a male. Four worms with the formula

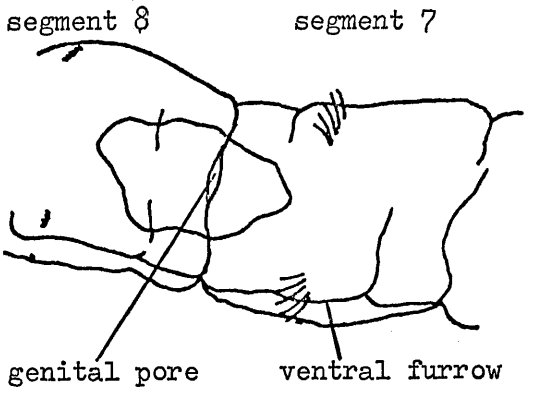
1 - 7C 8H 9-

were collected. All had the typical male shape and yet all contained developing ova. In three cases, the eggs were free in the coelom and almost fully developed. No signs of sperm development were seen in these worms at the time of collection. Fortunately it was possible to maintain some of these specimens in the laboratory and to observe any further changes. The results of this are outlined in Table 12. From this one must conclude that these worms are undergoing a change in sex from female to male (see also section 2.4.1.1).

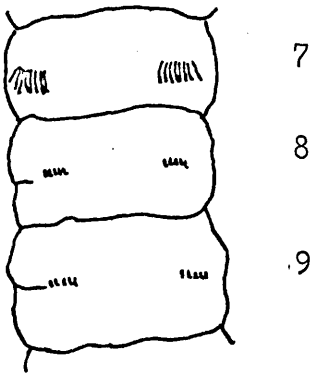
The population is very small, occupying only $2m^2$ in its full extent and it is quite possible that sex changes are related to

FIG. 11. External differences between the sexes in C.capitata..

a. Adult female lateral view.

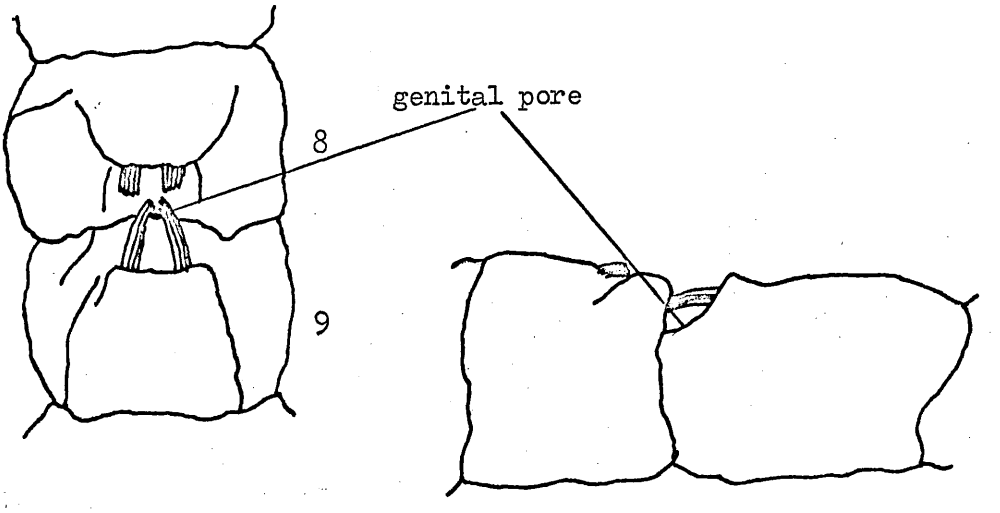


b. Adult female dorsal view.



c. Adult male dorsal view.

d. Adult male lateral view.



e. Transitional stage.

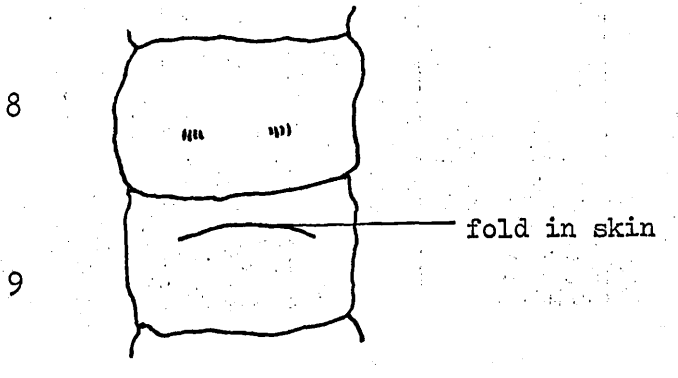


TABLE 12. Sex changes in C.capitata from Whitstable, Kent.

TIME IN DAYS	0	2	5	13	23	59
worm 1.	1 - 7♂ 8♀H 9- male shape eggs present	NO CHANGE			1 - 7♂ 8? 9♀G /H lot of free eggs	1 - 7♂ 8 - 9♀G /H
worm 2.	1 - 7♂ 8 - 9♀H female no sign of eggs through body wall	NO CHANGE		1 - 7♂ 8smallH 9? male shape	1 - 7♂ 8♀H 9♀G /H	1 - 7♂ 8 - 9♀G /H sperm morulae present
worm 3.	1 - 7♂ 8smallH 9- male shape	1 - 7♂ 8♀H 9♀G /H	1 - 7♂ 8 - 9♀G /H			

this. The reversal did not appear to occur at a particular size or stage in the female sex cycle and it is likely that it is a response to external conditions. The type of change is however unusual. Female C.capitata are known to store sperm so that a single mating with a male will enable the worm to produce larvae at several subsequent dates. It would therefore seem more 'useful' in terms of increasing the population if males changed into females. Possibly this sex change represents a reversal to the male state of worms which were originally male and changed to female for one season. There is, however, no evidence for this.

Grassle and Grassle (1974) have found indications of a change from male to female in populations from Massachusetts, U.S.A. and have confirmed this in the laboratory. They believe that the hermaphrodite individuals may be self-fertilising before the sex change is complete. This would be of obvious advantage in rapidly establishing a population where only a few individuals have settled.

A small number of the worms collected at Whitstable had a spotted appearance on the ventral surface of the thorax, especially around segments five and six. The markings are not restricted to one sex and the worms affected could not be distinguished in any other way. They were different from the spots found on Capitella 'punctate' and instead resembled small blisters. It is, of course, possible that they were, in fact, a response to some infection.

2.5.3 Rhosneigr population, Anglesey. Grid ref. SH 315 727.

One sample was taken from this population in October 1972.

The worms were found in sand, covered with rotting seaweed along the course of a drainage channel on the beach at Rhosneigr. The size of the population was not estimated but it stretched over a large area and the worms were in large numbers.

The thoracic setal formulae of these worms is illustrated in Table 13. Although basically similar to the patterns shown in the previous populations there are many more mature individuals with capillaries and hooks on segment seven. This is a significant difference from the Whitstable population and may indicate a genetic difference between these populations (Table 14). However, the relationship between setal formulae and size has already been mentioned. The worms from Rhosneigr are significantly larger than those from Plymouth (see Table 10) and may not achieve their final setal formula until reaching a larger size still. In this case a sample taken at a later date would no longer show a preponderance of individuals with mixed setae on segment seven.

Three of the worms from this sample had the spotted condition reported from the Whitstable worms.

2.5.4 Dutch populations. For localities see Fig. 12.

C.capitata has been collected by previous workers from many localities along the Dutch coast. Wolff (1973) has discussed the ecology of the worm in the estuarine conditions of the Dutch delta area. The following description is based on many samples taken over several years and deposited in the Rijks-Museum van Natuurlijke Historie, Leiden, the Netherlands.

FIG. 12. Map of the Dutch delta area to show localities of samples.

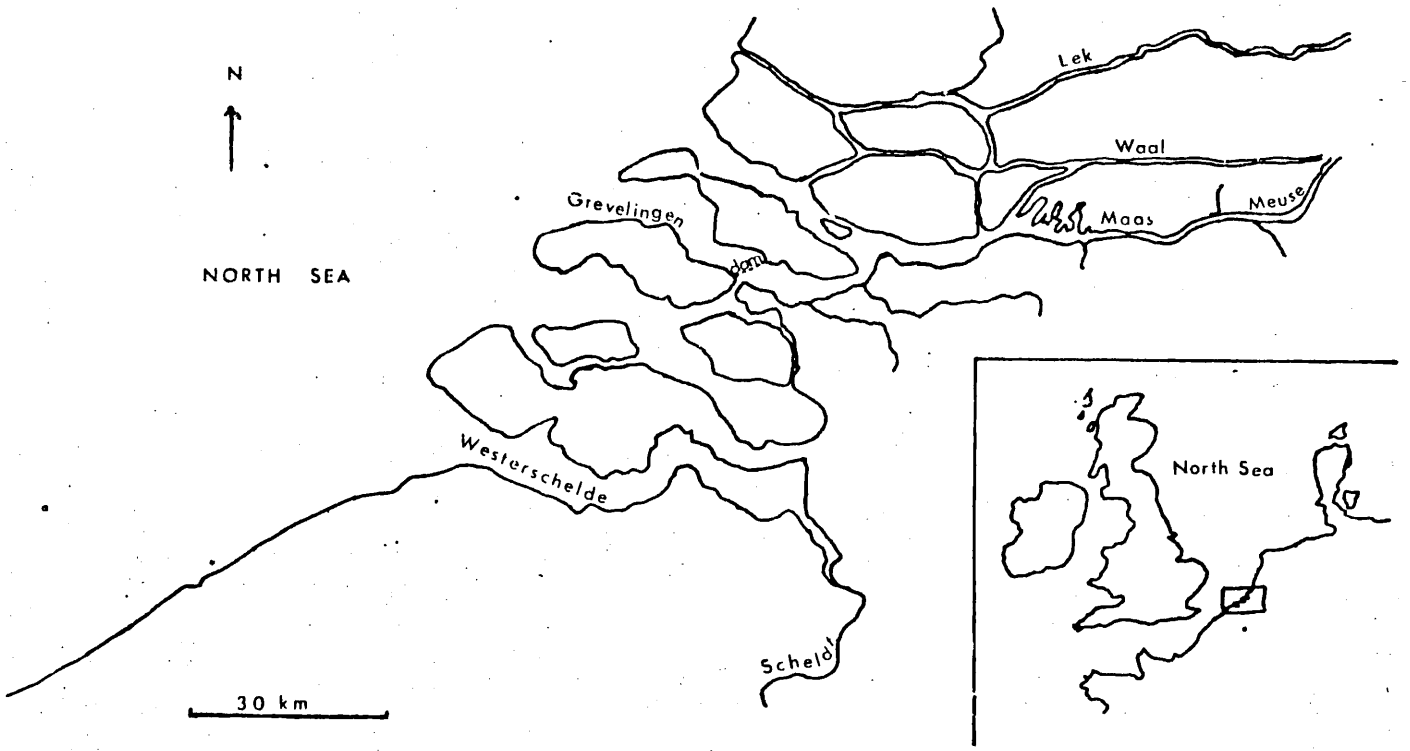


TABLE 13. Thoracic setal formula of C.capitata from Rhosneigr.

Formula	no worms	no worms with gametes	Mean length of thorax in mm
1 - 7C 8 - 9H	8	6	9.762 ± 0.200
1 - 7C 8 - 9G /H	1	1	9.0
1 - 6C 7M 8 - 9H	8	5	6.581 ± 0.336
1 - 6C 7M 8 - 9G /H	6	4	7.483 ± 0.991

TABLE 14. Distribution of thoracic setal formulae in British populations of C.capitata.

Population	Thoracic setal formula 1 - 7C	1 - 6C 7M	χ^2	significance at 5 % level
Plymouth	254	184	Plymouth /Whitstable 24.011	+
Whitstable	65	9	Whitstable /Rhosneigr 23.015	+
Rhosneigr	9	14	Rhosneigr /Plymouth 3.175	-

Because of the nature of these samples it has not been possible compare them directly with the British populations. Firstly, the poor preservation has precluded any examination for genital products in most instances. Secondly, the lack of detailed ecological information makes it impossible to relate the thoracic setal formulae to the onset of sexual maturity. Furthermore, it is often difficult to relate one sample to another as the precise interrelations of the different sampling areas are not known. In view of this, the study was concentrated on two main sampling areas, the Westerschelde and Grevelingen estuaries. As can be seen from Fig. 12 these are not directly connected to each other. In addition several coastal samples have been examined, and in view of the constancy of the material, grouped together. The data obtained are summarized in Table 15.

It is at once obvious that the worms from Westerschelde are different. A wide range of thoracic setal formulae was found, the principal ones being illustrated below in Table 16. The most striking feature is that in some worms hooks are retained in segment four after their replacement in following segments so that the development of capillaries appears to occur in reverse of normal order. The presence of a large number of individuals with a full complement of capillaries suggests that the odd thoracic setal formulae represent an unusual sequence of setal replacement rather than a different pattern as such. This is further evidence for the notion that the development of setal types in this species is very plastic and may be affected by environmental factors. It would be very interesting to examine this population more closely

TABLE 15. Thoracic setal formulae of Dutch populations of C.capitata.

Locality	no.of specimens	1 - 7C 8 - 9G/H or H	1 - 6C 7M 8 - 9G /H or H	other setal formulae
Westerschelde	50	33	2	15
Grevelingen	84	46	36	2
other localities	28	27	1	0

TABLE 16. Thoracic setal formulae of the Westerschelde population of C.capitata.

Thoracic setal formula	no. of worms
1 - 3C 4 - 7H 8 - 9G /H	1
1 - 3C 4 - 5H 6M 7H 8 - 9G /H	1
1 - 3C 4M 5 - 7H 8 - 9G /H	1
1 - 3C 4 - 5M 6 - 7H 8 - 9G /H	2
1 - 3C 4 - 6M 7H 8 - 9G /H	2
1 - 3C 4 - 7M 8 - 9G /H	1
1 - 3C 4M 5 - 6C 7H 8 - 9G /H	1
1 - 3C 4M 5 - 7C 8 - 9G /H	1
1 - 4C 5M 6 - 7H 8 - 9G /H	1
1 - 5C 6 - 7H 8 - 9G /H	2
1 - 5C 6M 7H 8 - 9G /H	1
1 - 5C 6 - 7M 8 - 9G /H	1
1 - 6C 7M 8 - 9G /H	2
1 - 7C 8 - 9G /H	33

and to follow the development through in the laboratory.

The population from Grevelingen more closely resembles British populations in that virtually all the worms examined had six segments with capillaries only. Segment seven was variable with 44 % of the specimens having hooks as well as capillaries. Due to insufficient data it has not been possible to relate the formula to thoracic length.

In all cases the size of the worms was very small. The range from one sample to another was very small and the mean length of them all has been calculated and found to be significantly shorter than that of Plymouth populations (see Table 10). It is very interesting to note that in these smaller worms the eyes are often visible in adult specimens.

2.6 The structure of the hooded hooks in Capitellidae.

Hartman (1947), referring to hooded hooks in Capitellidae stated that "These hooks are not only highly specific ....but so different extraspecifically as to be one of the finest means of speciation that has been discovered". However, as she also pointed out "The minuteness of these structures enhances the possibilities of aberration or misinterpretation". Using the highest magnifications available with light microscopy Hartman was able to determine the setal structure, as shown in Figs. 1 and 2, of C.capitata. Although she believed specific differences

occurred in many aspects of the hooks the number and arrangement of the teeth was considered to be most important. She investigated many capitellids and found that the teeth were most commonly found in a single, slightly arched row, with several rows occurring only rarely.

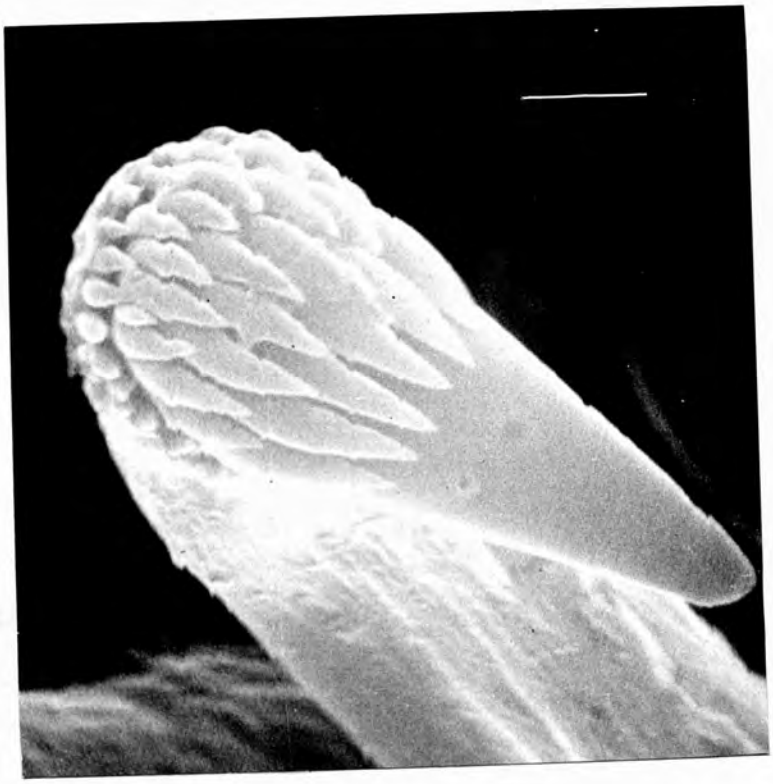
Fig. 13 illustrates the difficulties encountered by Hartman and her contemporaries. This shows a hooded hook from the third abdominal segment of C. capitata from Plymouth. As can be seen, it is extremely difficult to assess the number of teeth present. Even by adjusting the position of the hook it was not possible to distinguish more than four teeth with any certainty.

Fig. 14 is a scanning electron micrograph of a hooded hook taken from the same worm. It is immediately obvious that previous descriptions have been unsatisfactory as there are indeed several rows of teeth present here with at least five teeth in a row. This fact sheds much doubt on the usefulness of light microscopy for the description of setae but there is one major advantage in this method. In Fig. 14 the teeth are visible because the hood has been pulled back, or torn, but if the fang had been enclosed within the hood, as is the most usual case, the teeth would no longer be visible (see Fig. 22 c, d, e). When viewed under the light microscope the hood is transparent and a superficial idea of the underlying fang structure may be ascertained.

Fig. 14 is typical of the C. capitata hooks. The fang is long

FIG. 13. Capitella capitata, Plymouth. Photomicrograph of hooded hook. Phase contrast. Scale represents 20 µm.

FIG. 14. Capitella capitata, Plymouth. Scanning electron micrograph of a hooded hook to show the arrangement of teeth. Frontal view. Hood removed. Scale represents 1 µm.



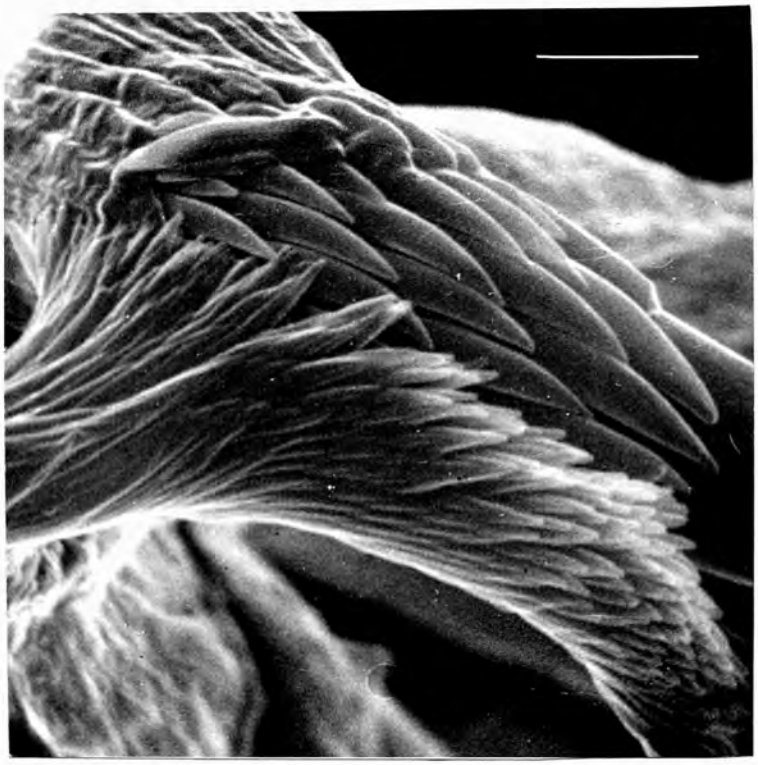
and pointed. There are four rows of teeth with the teeth in one row alternating with those in the next to give an interlocking pattern. The teeth get smaller towards the top of the hook. As viewed from this angle there are thirty-five teeth with six in the first row; eight in the second; then ten and finally a row of eleven smaller teeth. In many instances the central teeth of each row are slightly larger than the others, although this is not obvious from this micrograph. The hood is absent completely from this hook.

A very similar pattern was found in all the hooks of C.capitata from the Plymouth population. An estimate of the number of teeth present was made, although this was sometimes rather rough as the complete surface of the hook could not be examined. Nevertheless, the numbers were very similar with six or seven in the first row and eight or nine in the second. The third row was often difficult to see but at least seven teeth were present in all cases. In some specimens only three rows were present but in others the precise arrangement was disrupted and there were six or seven incomplete rows as shown in Fig. 15. This apparent inconsistency might be due to the curvature of the rows making it difficult to distinguish one row from another at certain angles.

In most cases the hood surrounded the fang so that one could not be certain that all the teeth were visible (see Fig. 16). However, in some instances the hood is drawn right back and the

FIG. 15. Capitella capitata, Plymouth. Scanning electron micrograph of a hooded hook with hood partially covering fang. Scale represents 1 µm.

FIG. 16. Capitella capitata, Plymouth. Scanning electron micrograph of a hooded hook with hood covering fang. Scale represents 1 µm.



origin of the teeth can be seen when the hook is examined from the side as in Fig. 17.

This basic pattern was found in all the worms examined from Plymouth regardless of position on the body or age or state of sexual maturity.

Examination of hooks from other populations of C.capitata showed no clear differences. Specimens from Whitstable showed four rows of teeth with an estimated six teeth in the first row and at least eight in the second. The smaller teeth of the other rows could not be counted.

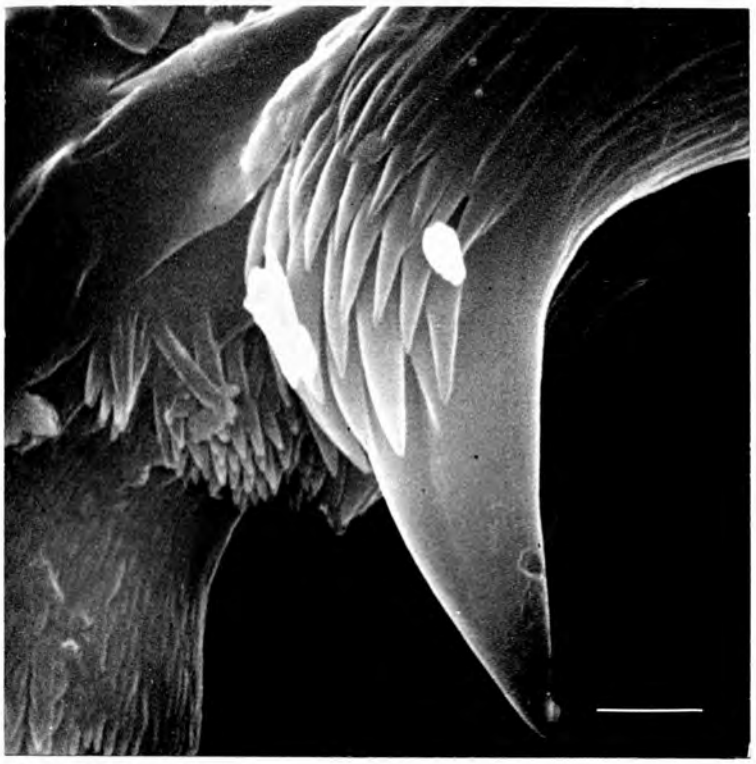
Material from Canada also showed several rows of teeth on the hook, many of which were unfortunately damaged. It was difficult to separate the rows in these specimens but at least four were present. The teeth themselves were very large and fairly widely spaced, but there were still five or six in the first row.

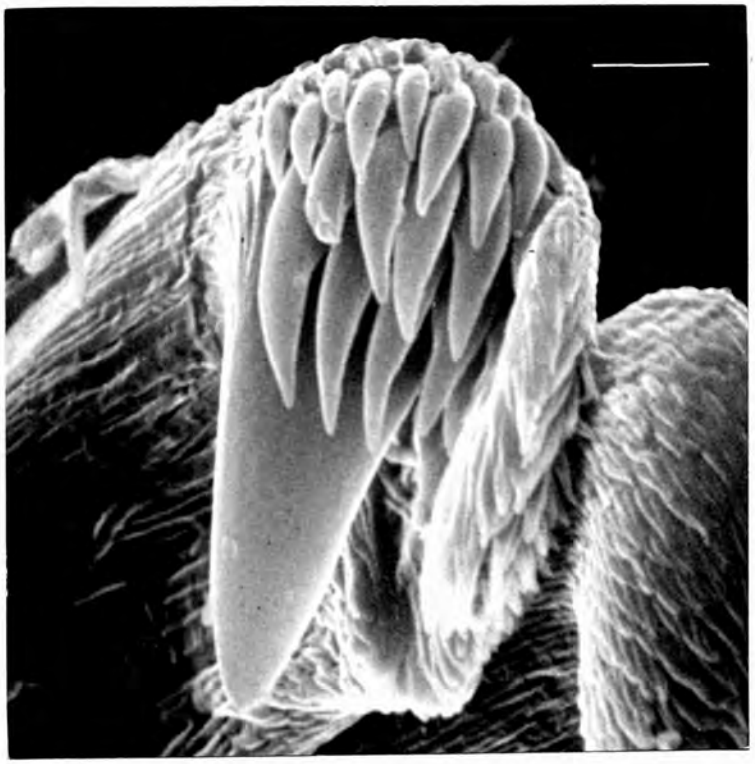
Capitella sp. from Australia showed four very clear rows of teeth and, in overall shape, was inseparable from the Plymouth specimens, as shown in Fig. 18. The hood structure in this worm was also like that of the Plymouth worms as shown in Fig. 22d.

Capitella capitata oculata also showed several rows of teeth but only three were distinct. A fourth, less marked row, representing the serrated edge of the outer layer of the fang, similar to that shown in Fig. 17, was also present.

FIG. 17. Capitella capitata, Plymouth. Scanning electron micrograph of a hooded hook with hood removed. Lateral view. Scale represents 1 µm.

FIG. 18. Capitella sp., Australia. Scanning electron micrograph of a hooded hook. Frontal view. Scale represents 1 µm.





C.capitata ovincola differed from the other samples in the shape of the fang. Although the shape does vary, and in some Plymouth specimens is very pointed, the condition in this sample is extreme (Fig. 19). Again several rows of teeth are present.

One specimen of C.hermaphrodita was examined and found to be identical to the Plymouth worms. Four rows of teeth were present with six in the first row, seven in the second, at least six in the third and at least seven in the fourth.

For comparison the hooded hooks of Notomastus latericeus were studied. These are basically similar to those of C.capitata but there are more rows (up to five being normal) and many more teeth as shown in Fig. 20. In addition the teeth of the first row are very large as shown in Fig. 21.

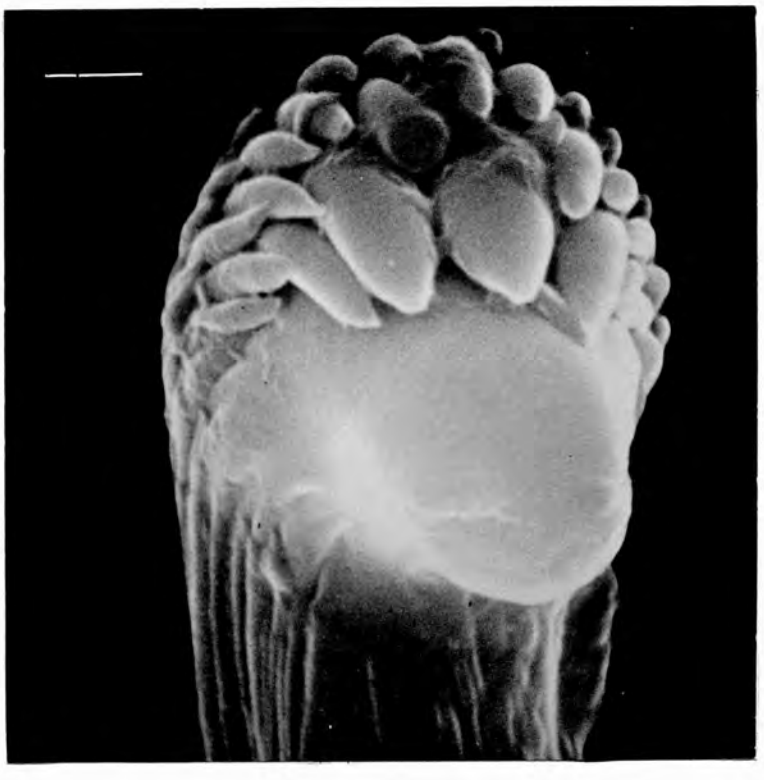
Furthermore, Thomassin and Picard's study of the hooks in Dasybranchus caducus (1972) shows a very similar arrangement of teeth with four rows. Six large teeth occur in the first row; eight in the second; five smaller ones in the third with the very small teeth of the fourth row forming a crescent around the other rows. This arrangement of the rows themselves is the principal difference from C.capitata hooks.

Thomassin and Picard believe that stereoscan techniques enable the taxonomist to separate geographical varieties of cosmopolitan species. Whilst recognising that many features of the hook may show variation they believe that only differences

FIG. 19. Capitella ovincola. Scanning electron micrograph of hooded hooks to show the shape of the fang. Scale represents 2 μm.

FIG. 20. Notomastus latericeus. Scanning electron micrograph of a hooded hook to show the rows of teeth. Scale represents 1 µm.

FIG. 21. Notomastus latericeus. Scanning electron micrograph of a hooded hook with hood removed. Frontal view. Scale represents 0.5 µm.



in the teeth arrangements can be used since these are sufficiently constant intraspecifically. However, their own results illustrate the difficulties in precisely describing this feature and some of the micrographs of Dasybranchus spp. are indistinguishable from Capitella. This is not to say that the arrangements of the teeth are not very specific but that it is virtually impossible to determine this arrangement accurately. However, these authors also noticed very marked differences in the structure of the hoods in Dasybranchus but were doubtful of their significance. This is a very easy feature to study and, although no great variation was shown in Capitella, it could prove a very useful taxonomic feature in other members of the family. However, the manner of preparation can alter this as shown in Fig. 22 c, d, e. In the latter critical point drying has been used and the hood takes on the serrated appearance described for Dasybranchus.

From these results one can conclude that the variation in setal structure between species is no greater than that occurring between individuals. Indeed the difference between genera is itself not great, and in view of the intraspecific variation it is not a very satisfactory taxonomic feature.

This study illustrates the importance of studying the hooks from the same angle wherever possible. Fig. 22 shows the effects of altering the angle of the hook on the general impression obtained. Thus in Fig. 22a the size of the teeth on the two

FIG. 22. The effect of different preparatory techniques on the interpretation of scanning electron micrographs.

FIG. 22a. Notomastus latericeus. Two hooded hooks showing the effect of the viewing angle on the apparent size of the teeth. Scale represents 1 µm.

FIG. 22b. Capitella hermaphrodita. View of hooded hooks from below. Scale represents 1 µm.

hooks cannot be accurately assessed. In Fig. 22b the hooks are examined from underneath showing details of the hood. The effect of changing the angle on the picture of the hood is illustrated in Figs. 22c and d.

In dealing with preserved material, much of it with little known history, it is difficult to be certain whether any observed setal variations are individual or specific differences. In this study very little variation was found according to the position on the body, save that there were fewer hooks towards the end of the body. Similarly there was no apparent difference which could be related to age or sex. Nevertheless it is reasonable to expect that changes due to the environment could occur during the life of a worm, and indeed there was much evidence of damage to hooks in the material studied. Replacement hooks, developed under different conditions to the original ones, could well be different in their form. Hillger and Reish (1970) demonstrated the plasticity of setal structure in polynoid polychaetes in noting the effects of temperature on the form of regenerated setae in Halosydna spp. However, Gaffney (1973) questioned their conclusions and recognised that there was extreme heterogeneity in natural populations of H.brevisetosa. He was unable to explain this variation, but it may be supposed that some environmental factor could account for some of it at least.

In any event, it seems certain that Hartman's statement on the specificity of setal structure is no longer acceptable.

FIG. 22c. Capitella capitata, Plymouth. View of hood from above. Scale represents 1 µm.

FIG. 22d. Capitella capitata, Plymouth. Frontal view of hood. Scale represents 1 µm.

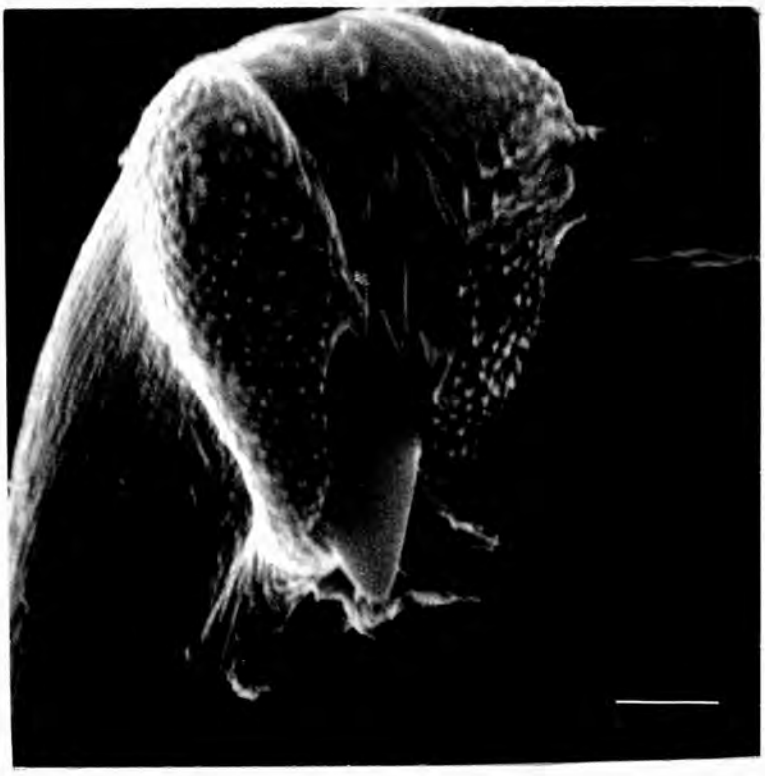


FIG. 22e. Capitella capitata, Plymouth. View of hood following critical point drying. Scale represents 1 μm.

Many factors, both genetic and environmental, may alter the form of the setae and in addition the subjective approach of investigators makes it necessary to exercise extreme caution when evaluating the importance of setal structure.

2.7 Discussion and conclusions.

From the above descriptions it is immediately clear that the existing criteria used in making taxonomic decisions in this family are unsatisfactory. Most obvious in this respect is the size factor. Hartman (1947) took the length of specimens as one reason for erecting a new subspecies, C.capitata ovincola, although the lengths measured were well within the range found for the type. In material that I have examined adult worms have been found with a thoracic length of only 1.9 mm (total length approx. 6 mm) from Holland ranging up to 15.5 mm for the thoracic length, with a total length of over 67 mm for a specimen from Canada. As early as 1868 Claparède recognised that the size of worms varied according to the locality and that this feature was of no use taxonomically. This is because size can be affected very greatly by environmental conditions. In the colder higher latitudes body size is often very great in polychaetes, and this is true for C.capitata. Claparède (1861) for example, found worms up to 140 mm long in the Hebrides. In warmer waters the relationship between size and maturity is changed and the worms are sexually precocious in their development. Similarly the amounts of food available must exert an effect on the size, but it is not usually possible to assess this factor when studying the taxonomy of a population.

The most important, indeed in some cases the only, diagnostic feature separating genera in the Capitellidae is the

number of segments in the thorax and the type of setae present on these. The number of segments is determined at a very early stage of development and is not therefore subject to environmental modification. In general it can be easily determined and is a very useful key feature. There are, however, two instances in which difficulties are encountered. In some capitellids the boundary between thorax and abdomen is not precise and one or more transitional segments occur. This happens in the genus Mediomastus Hartman where different species have a different number of thoracic segments. In such cases one must refer to other features and make detailed comparisons with similar genera. Fortunately this problem is not encountered in Capitella or closely related genera. The relationship between the prostomium and the first setiger can, however, cause difficulties. Capitella has nine thoracic segments all of which are setigerous. In all other genera, except for those closely associated with Capitella, there is an asetous peristomium. It is thought that this situation has arisen by the fusion of two segments. Eisig (1887) gave evidence for the fusion of the buccal segment with the prostomium and this view is upheld by Fauvel (1927) and Berkeley and Berkeley (1952). Mesnil (1897) believed that the peristomium was fused with the first setiger or second segment, but this notion was based on a misconception of Eisig's work. In any event the result of this fusion is usually clear cut in Capitella. However, as described above in section 2.4.1.6 the shape of the prostomium can lead to the assumption that an asetal peristomium is present. Hartman and

Fauchald (1971) also described Capitella near capitata which also has an asetous peristomium although they did not distinguish it from C.capitata by this feature.

The problem became even more confusing when considering Capitellides. Like Capitella it has nine setigerous segments in the thorax and the first anatomical segment is fused with the peristomium. However, as described in section 2.4.2, in this instance the fused segment is sometimes still distinct, especially when viewed from above. The degree to which this half-segment can be seen depends greatly on the state of preservation. Thus Hartman (1947) recognised nine setigerous segments but later in 1961 she described an asetous peristomium. These discrepancies emphasise the importance of realising the underlying anatomy when comparing samples. The fact that both Capitella and Capitellides have this fusion of segments demonstrates their similarity and attempts to separate them by the degree to which the join is visible are unfounded.

The setae present on the thorax and their arrangement (i.e. the thoracic setal formula) are also important in determining a genus and they form the basis of specific differentiation in Capitella. The extreme variability of this feature in this genus has been emphasised throughout. That differences occur has been known for many years. Thus Claparède (1868) states:

> "Si j'insiste si longuement sur ces détails, c'est qu'ils prouvent amplement qu'on ne saurait, chez les Capitelles, établir de différences spécifiques basées comme chez les

Serpulacés sur le numero des segments où le changement de soies à lieu."

In the populations studied in detail here segment seven has shown several setal patterns which are apparently not significant taxonomically. Nevertheless most of the species and subspecies are separated principally by their setal formula and despite variations within populations those between them can be much greater. Fig. 23 shows the locality of many populations of C.capitata and subspecies. The January and July air 0°C and 21°C isotherms are also given. It is of interest to note that in the colder regions of the high latitudes the number of capillary-bearing segments is large. Gravier's C.perarmata has capillaries on segments eight and nine and Wu (1964) refers to populations with this formula from northern Europe. Unfortunately it has been impossible to trace his references but these apparently refer to populations on the Russian coastline. This suggests that the colder temperatures may have an effect on the setal formula and that Wu's specimens are probably synonymous with C.perarmata. The most widely distributed formulae, with seven capillary-bearing segments or six and one mixed are found in the colder temperate regions, centreing on western Europe, Japan and South America. The worms with more unusual setal formulae are all found in warm temperate, almost tropical conditions, mainly around Central America. Thus C. capitata ovincola; C.capitata tripartita; and Capitella 'villose' are all found in the same general locality off California. C.capitata floridana is found in the warm Gulf

FIG. 23. Map to show the distribution of known species of Capitella.
Key to symbols used.

■ Capitella capitata capitata

△ C.capitata floridana

○ C.ovincola

▽ C.tripartita

□ C.perarmata

● C.hermaphrodita

▼ C.giardi

▲ C.jonesi

✚ C.aberranta

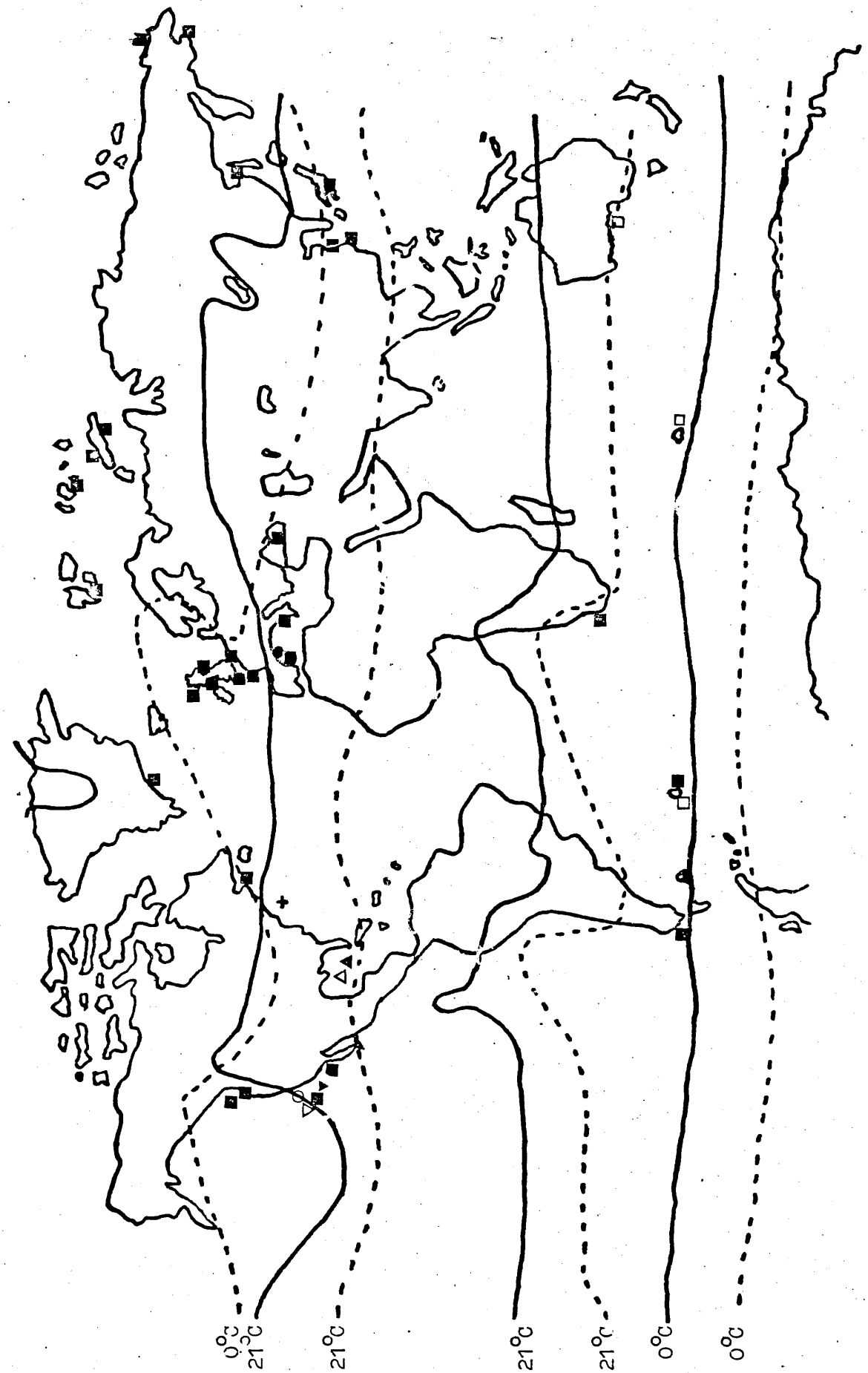


FIG. 23. Map to show the general distribution of some species of Capitella.

of Mexico. In Europe, C.hermaphrodita, with the same formula as C.capitata floridana, occurs in slightly cooler conditions than the latter species. In the southern hemisphere Day's population of C.capitata (1961) occurs in similar conditions to the Californian populations. The worms from the Westerschelde estuary are in cooler conditions where, according to this hypothesis, one would expect to find worms with the full complement of capillaries. However, as the majority of the worms in the sample did show this formula, with the variations occurring in only very small numbers, this presents no problem.

At the moment the theory that temperature may affect the distribution of setae cannot be substantiated but it should be possible to check this by raising worms from different known populations under controlled conditions of temperature. As discussed above, changes in setal structure are known to occur due to environmental change, so that a similar effect on their distribution is not unexpected.

Until recently it has been accepted that the genus Capitella is gonochoric with the males recognised by their copulatory apparatus. Worms without genital hooks are assumed to be female. Even where ovaries are clearly visible the presence of sperm-developing cells cannot be overruled. In most cases there is probably no problem as worms with genital hooks are not found with ovaries. However, this is by no means always the case. The occurrence of worms changing sex

from female to male has been recorded from Whitstable, England and from Nova Scotia, Canada and there is no reason why it may not also occur elsewhere. These changes take place only in a small proportion of individuals of populations which are otherwise normal. Grassle and Grassle (1974) found changes in the reverse direction in some worms from Massachusetts, U.S.A. It is not until C.hermaphrodita is studied that a completely hermaphroditic population is found. The variety in setal formula suggests that change from female to male may again be occurring. All the ovigerous worms have signs of sperm production and showed various setal types on segments eight and nine. On the other hand, where ovaries were absent there were always genital hooks on segments eight and nine indicating normal males. C.capitata floridana has the same thoracic setal formula as C.hermaphrodita but Hartman (1959b) gives no indication of anything unusual with regard to the sex of these specimens. Once it is realised that Capitella shows variations in its reproductive biology, Capitellides becomes much closer. In this genus the sexes are believed to be separate but both male and female have genital hooks. The number and arrangement of these is different from C.capitata but Pettibone's specimens from Alaska may be a link between the two.

Bacci (1965) has studied the determination of sex in great detail. The Whitstable population of C.capitata fits in his category of unbalanced hermaphroditism where several phenotypes may occur with extreme variability. This is similar to the

situation in Ophryotrocha puerilis but in this case the changes are protandric rather than protogynous. Some of the variation is known to be phenotypic being induced by environmental factors. Thus Müller (1962) showed that male O.puerilis will not alter into females if they do not have sufficient food. Similarly the stimulus of a female worm must also be provided. Bacci shows that the sex determination in this species is not entirely environmental though, and believes that the species is polygametic, so that many types of sex-determining gametes may be produced from the hermaphrodites.

Grassle and Grassle (1974) emphasised the genetical flexibility of Capitella and indicate why this is of such importance in an opportunistic species. The several variations found in different populations are just one aspect of this plasticity.

Discussion of each of the criteria used in the systematics of Capitella demonstrates the inherent variability shown in all features of this genus. Nevertheless by looking at several features together it is possible to draw certain conclusions about the interrelationships of the populations described above. These are summarised below.

Capitella capitata capitata (Fabricius 1780).

A cosmopolitan species showing equatorial submergence (Ekman 1953).

Habitat - sand or mud, often in conditions of low oxygen. Common in estuaries and other areas of low salinity.

Thoracic setal formula - 1 - 7C 8 - 9G /H or 1 - 6C 7M 8 - 9G /H

This species is based on the constancy of the thoracic setal formula with the mixed bundles on segment seven generally occurring on smaller worms. Sexes are usually separate, but with a proportion of hermaphroditic individuals in some populations.

Capitella ovincola (Hartman, 1947).

California, U.S.A.

Habitat - squid egg masses (Loligo opalescens).

Thoracic setal formula - very variable but with 2 - 4 mixed segments. The fang of the hooded hook is very long and pointed.

The species is justified on the above features. Its occurrence in several egg masses over a long period in time indicates that the population is not just the offspring of a single female (although it may have originated in this way). Hartman's view that it is merely a subspecies of C.capitata (1959a) may be correct but it would be necessary to culture the worms under laboratory conditions to test this.

Capitella capitata floridana (Hartman, 1959).

Florida.

Habitat - squid egg masses.

Thoracic setal formula - 1 - 4C 5 - 7H 8 - 9G

This population may not even constitute a subspecies. Whilst it is true that the thoracic setal formula is different and constant there are no other differences and the population is small and could well represent the offspring of a single female C.cap-

itata in which the phenotypic expression of setal types is modified by the environment. The exploitation of squid egg masses as a source of food and a site for reproduction is to be expected in an opportunistic species.

Capitella capitata oculata Hartman, 1961 = C.capitata capitata.

California, U.S.A.

Habitat:- sand and mud, possibly under conditions of reduced salinity.

Thoracic setal formula - 1 - 7C 8 - 9G /H.

This subspecies does not differ from the type in any significant feature except for the presence of eyes in a large number of the adults.

Capitella tripartita Hartman, 1961 as C.capitata tripartita.

California, U.S.A.

Habitat - sand and mud, possibly under conditions of reduced salinity.

Thoracic setal formula - 1 - 3C 4 - 7M 8 - 9G /H.

This species is based on its thoracic setal formula. This formula could be related to temperature, especially as the formula is not constant, but this species was found in the same general area as C.capitata oculata above, which showed no reduction in capillaries. Without laboratory examination of living material one cannot be completely certain of this conclusion however.

Capitella capitata antarctica (Monro, 1930) = C.capitata capitata.

South Georgia.

Habitat - in kelp holdfasts.

Thoracic setal formula - 1 - 7C 8 - 9G /H

This subspecies does not differ in any significant way from C.capitata capitata and the increased development of the copulatory apparatus is a difference in degree only.

Capitella capitata japonica (Kitamori, 1960) = C.capitata capitata.

Japan

Habitat - black mud.

Thoracic setal formula - 1 - 7C 8 - 9G /H.

Again there are no significant differences between this and the type. The original description is somewhat confusing but the thoracic setal formula is that of C.capitata capitata.

Capitella capitata europaea Wu, 1964. = C.capitata capitata.

Western Europe and the Mediterranean Sea.

Habitat not stated, but reduced salinity in some areas.

Thoracic setal formula - 1 - 6C 7M 8 - 9G /H or 1 - 6C 7M 8 - 9G /CH

These populations do not constitute a subspecies. The presence of mixed bundles of setae on segment seven has been shown to occur commonly in C.capitata capitata. The capillaries in the neuropodia of segments eight and nine in some specimens suggests C.perarmata. Unfortunately the author does not locate this population but he refers to several Russian authors so possibly these worms are found in the colder parts of northern Europe and may in fact correspond to C.perarmata.

Czerniavsky's species, as discussed above, cannot be con-

sidered as the samples are very small and appear to be descriptions of young worms. Similarly his subspecies all refer to populations of C.capitata capitata.

Capitella perarmata Gravier 1911 .

South Georgia and South Australia.

Habitat not stated.

Thoracic setal formula - 1 - 7C 8 - 9G /CH with capillaries in the neuropodia of eight and nine.

This species is recognised by the presence of capillaries in the eighth segment and sometimes the ninth. Samples from the Arctic were very large worms but the Australian ones were of more normal dimensions. As for the warm temperate species with reduced numbers of capillaries, the increase in numbers in this instance could be related to temperature. However, C.capitata capitata has also been found in the same locality with a thoracic setal formula of 1 - 7C 8 - 9G /H.

Capitella aberranta Hartman and Fauchald 1971 .

North Atlantic.

Habitat not stated, but from abyssal depths.

Thoracic setal formula - 1 - 5C 6 - 9 modified setae (notopodia) 1 - 5C 6 - 9H (neuropodia).

This species is maintained because of the presence of the modified setae on segments six to nine which are unique amongst capitellids.

Capitella hermaphrodita (Boletzky and Dohle 1967).

South of France.

Habitat - Loligo vulgaris egg masses.

Thoracic setal formula - 1 - 4C 5 - 7H 8 - 9G /H.

This species is distinguished by the constancy of its thoracic setal formula, which is like that of C.capitata floridana. However, in this instance the worm is hermaphroditic. Although only 25 specimens were obtained they were found in several egg masses. The lack of any single-sex individuals is possibly related to the small size of the population. If this increases and becomes established the balance of hermaphroditism may alter.

Capitella dizonata (Johnson 1901) = C.capitata capitata.

Puget Sound, U.S.A.

This species is not acceptable because of the lack of sufficient information to warrant a new species. The specimen described was probably an immature C.capitata.

Capitella 'villose' (Hartman 1961).

California, U.S.A.

Habitat not given.

Thoracic setal formula - 1 - 5C 6M 7 - 9H or 1 - 6C 7 - 9H.

The material in this sample shows a very interesting setal formula which might be indicative of a new species. However, as no adult males were found in this sample the formula may reflect the immaturity of the worms. Because of this, it is

not possible to place this sample with any accuracy and it must be assumed to be a population of C.capitata.

Capitellides Mesnil = Capitella Blainville.

Capitellides is considered to be congeneric with Capitella because the presence of a copulatory apparatus in the female is not considered sufficient to warrant generic recognition.

The original type species was C.giardi (Mesnil) which has a thoracic setal formula of 1 - 6C 7M 8 - 9G /H with capillaries occasionally present in segment seven. The copulatory apparatus is made up of four genital hooks only, with tiny replacement ones sometimes visible at the base of these. The habitat is commonly kelp holdfasts.

Capitella 'C' 'punctate' Hartman is a sample of C.giardi. The specimens were larger than usual and the seventh segment consistently had capillaries but this is not considered significant. The copulatory apparatus consisted of one or two with occasionally three pairs of genital hooks on segment eight and one pair on segment nine.

C.jonesi was described by Hartman (1959b) and is distinguished by its thoracic setal formula of 1 - 3C 4 - 7H 8 - 9G /H. In addition the copulatory apparatus is better developed with three to four pairs of genital hooks per segment.

C.teres (Treadwell 1939) is apparently C.giardi. This

species was erected for a single specimen which had a notopodial formula of 1 - 8C 9G. This probably represents an individual in which the genital hooks are not yet fully developed despite its sexual maturity, a condition also found in C.capitata. Mesnil (1897) himself observed several individuals with abnormal arrangements on these segments.

As discussed above the genetic flexibility of Capitella makes it very difficult to evaluate any given characteristic taxonomically, especially when decisions must be based on preserved material. Laboratory experiments may show that the species outlined above are not reproductively isolated and therefore not specifically separate. However, one must reach a compromise in this matter. It is impossible to check the reproductive potential of all the samples, yet it is not feasible to place all of them in the same specific category in the absence of this information. One must bear in mind that taxonomic classifications have a great practical use for ecologists and other biologists as well as forming an important part in our understanding of evolution. In view of this it seems better to separate the populations as above. Subspecific differentiation should be avoided where possible since every population will show its own idiosyncrasies and is potentially a subspecies.

The genus Capitella is closely related to Branchiocapitella Fauvel and Pulliella Fauvel with which it shares its fusion of the anatomical first segment with the prostomium. Branchiocap-

itella is known by one species, B.singularis Fauvel (1932) from India. It is distinguished from Capitella by the presence of branchiae. This may seem insufficient to merit generic consideration but it is in fact a major difference. Whilst many capitellid genera have branchiae to increase the surface area for respiratory purposes, such features are completely absent from Capitella which irrigates its tube to increase the flow of oxygen. In addition its haemoglobin is adapted for conditions of low oxygen and gills would be superfluous if not dangerous. B.abranchiata Hartmann-Schröder (1962) is almost certainly a species of Capitella as it lacks branchiae. It has not been possible to examine any specimens but the type description is close to that of C.capitata.

Pulliella, which is known from one species P.armata Fauvel (1929) from the Gulf of Manaar and New Caledonia, is different from Capitella in its absence of a copulatory apparatus. Whilst a considerable variation in this feature is shown in Capitella its complete absence would seem to prevent copulation so that the internal fertilisation so typical of Capitella cannot occur. At best a form of pseudocopulation like that of Notomastus may be possible.

Of the genera with an asetous peristomium Capitella is most closely related to Capitomastus. This has ten thoracic segments with genital hooks on the last two as in Capitella. Both sexes have these hooks. Hauenschild (1954) studied a hermaphroditic population from Rhodes and found that the worms

were self-fertilising. In some instances male characteristics developed first showing protandry. Hauenschild kept his worms individually and thus under very abnormal conditions, and it is possible that this affected the degree of expression of the hermaphroditism. Nevertheless, it is evident that the trends shown in Capitella are not restricted to this genus.

3. ECOLOGICAL STUDIES OF SOME BRITISH POPULATIONS OF CAPITELLA CAPITATA.

3.1 Introduction.

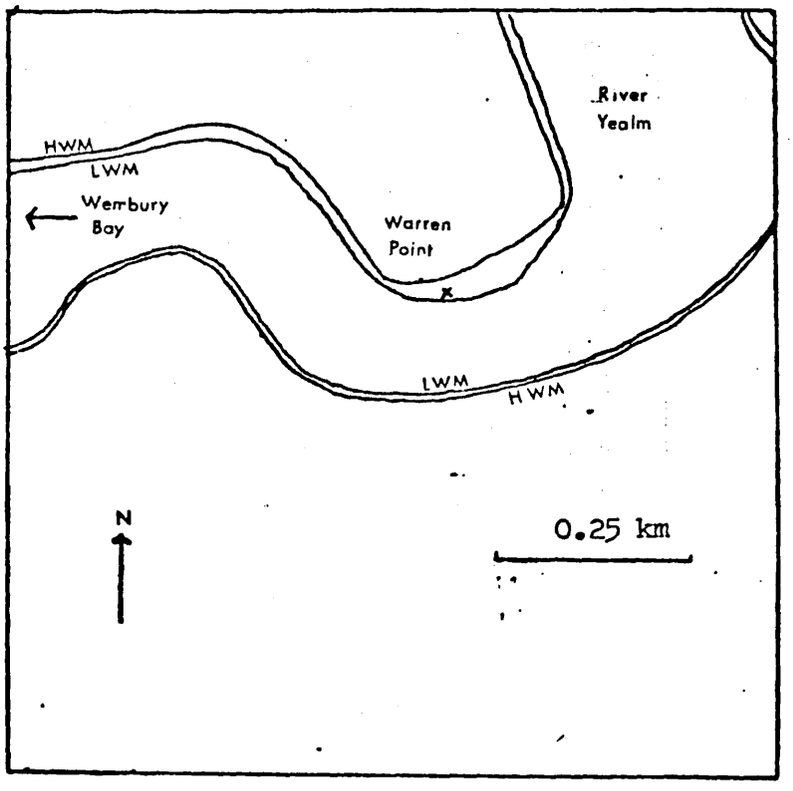
The principal site of study was Warren Point, near Plymouth, Devon, but comparative studies were made on populations at Whitstable, Kent and Rhosneigr, Anglesey. Details of the collecting sites are given in Figs. 24 - 26.

Warren Point is a small spit extending into the Yealm estuary. It is situated on the inside of the bend of the river course so that deposition occurs. The river drops a lot of sediment from its load but in addition large items of debris carried down the river from the nearby villages and waste material from the yachting concerns at Newton Ferrers are deposited. Warren Point is the last barrier against the sea and west of this the river flows on a fairly straight course. As a consequence large quantities of storm debris, mainly laminarians and other seaweeds, are thrown on to the point forming a ridge of rotting vegetation which provides shelter to the sand flats behind. The substrate at Warren Point is basically muddy sand (see section 3.3.1.1) but a considerable admixture of the deposited material also occurs giving the sediments a very heterogeneous nature.

The sampling site was selected as that offering the highest density of worms accessible each month at low tide. As described below (section 3.2.1) marking the precise sampling site presented problems.

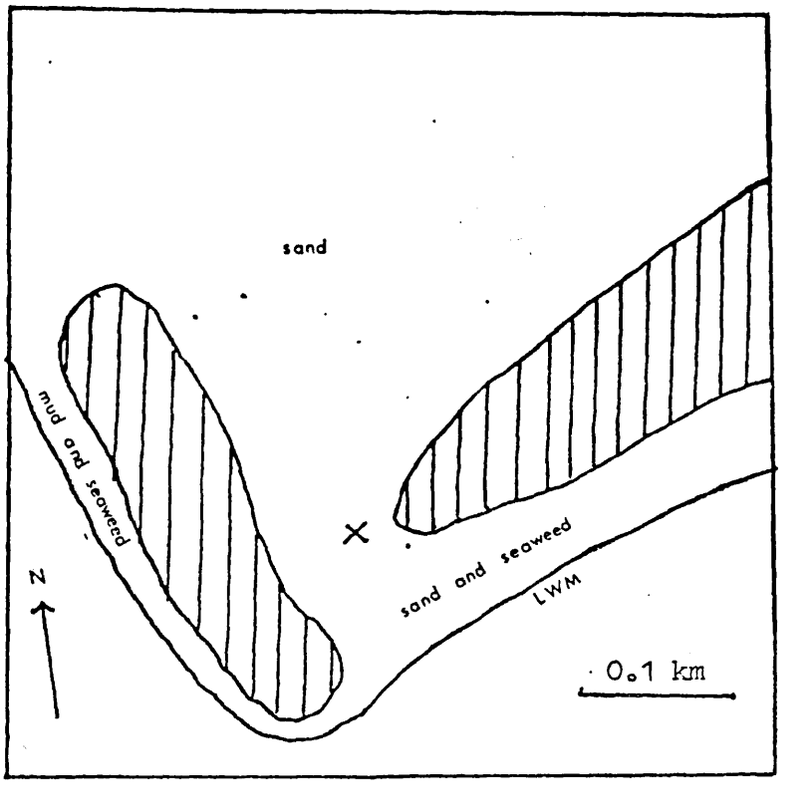
FIG. 24. Site of collection at Warren Point, near Plymouth, Devon.

a. General locality of collecting area.



× collecting site

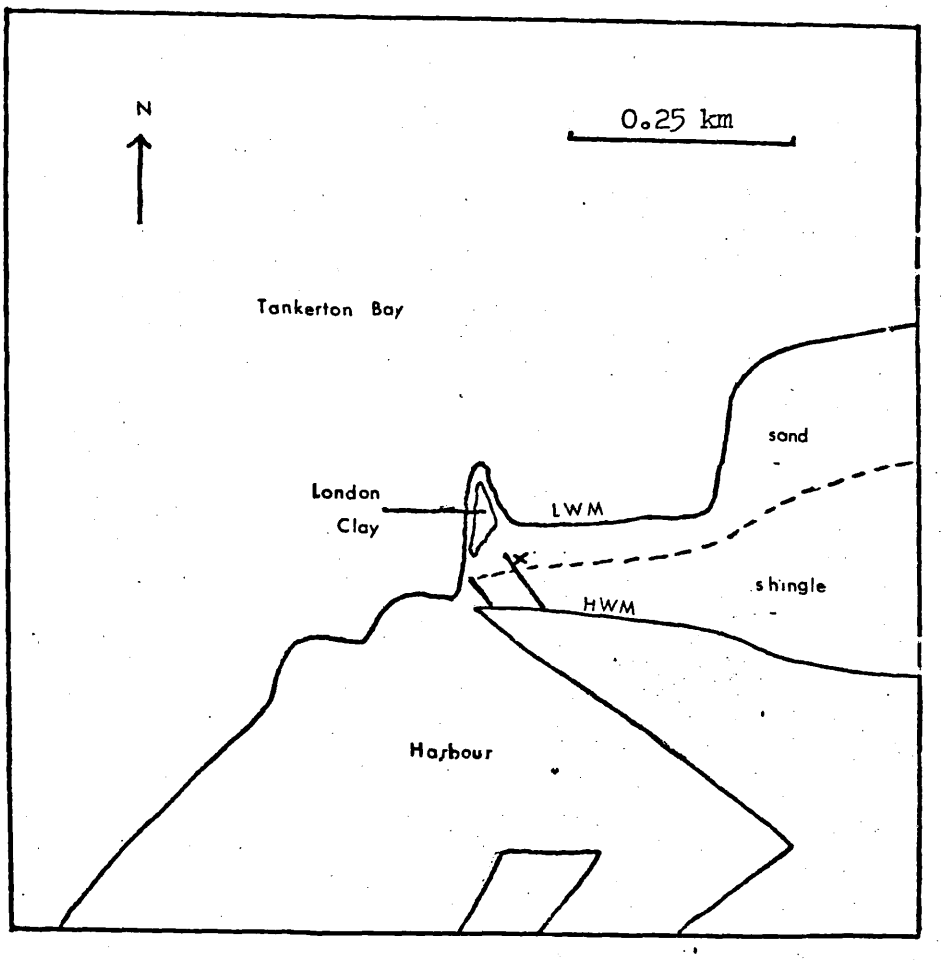
b. Detailed sketch map of Warren Point



× collecting site

▥ seaweed ridge

FIG. 25. Site of collection at Whitstable, Kent.



× collecting site

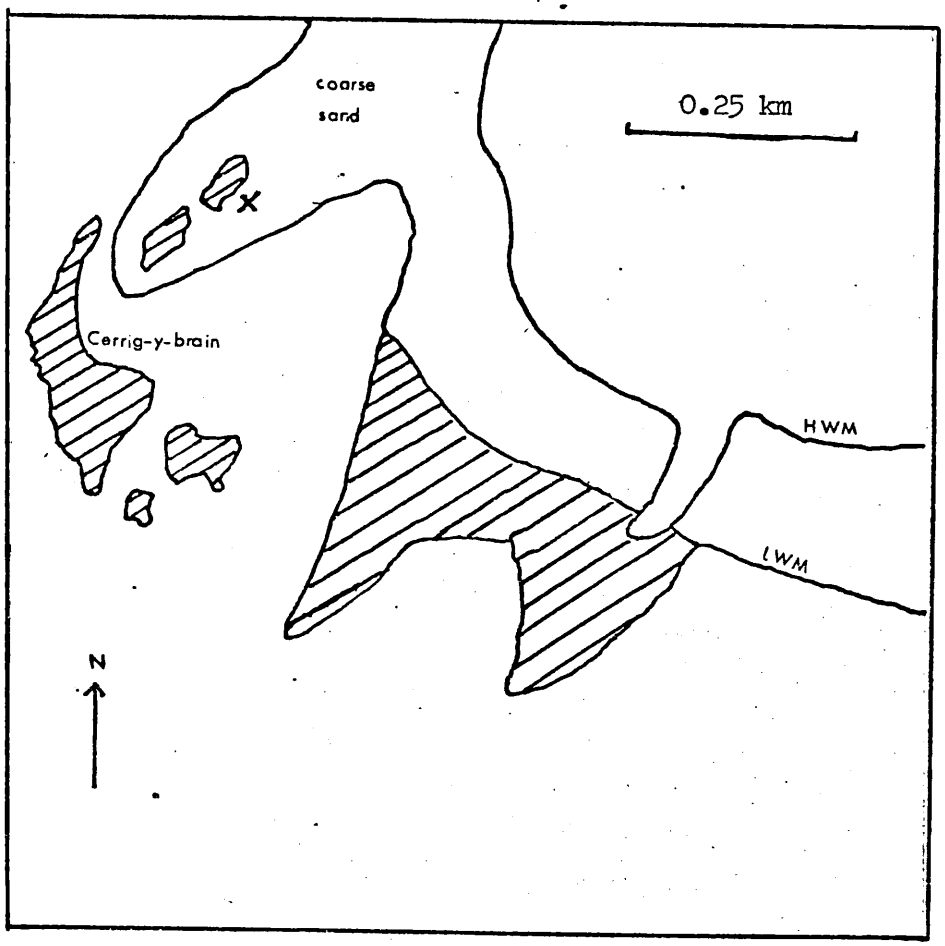
Conditions at Whitstable, Kent have been described in detail by Newell (1954). Capitella capitata was only found in a small area to the east of the harbour (Fig. 25). The sampling site was on the uppermost reaches of the flats against the side of a groyne, which presumably offers some protection against wind. As at Warren Point the sheltered site accumulated a large quantity of strand line debris, mainly seaweeds.

Rhosneigr (Fig. 26) is a sandy beach with considerable fresh water run-off. C.capitata was sampled from under stones and banks of seaweed along the edge of a drainage channel.

The sites were chosen because they presented a range of conditions. The population at Warren Point is large and well established whereas that at Whitstable is very small and unstable. The worms at Rhosneigr were in clean-looking sand compared with the highly organic appearance of the substrate at Warren Point.

There is no information available on the ecology of C.capitata and yet its relationship to polluted conditions has been discussed endlessly (e.g. Reish 1972). Recently there has been evidence to suggest that the correlation is not simple (Eagle and Rees 1973) and it seemed essential to gain an understanding of the ecology of the species in relatively unpolluted environments before drawing conclusions about its occurrence under polluted conditions.

FIG. 26. Site of collection at Rhosneigr, Anglesey.



X collecting site

rock outcrops

3.2 Materials and Methods.

3.2.1 Quantitative sampling of worms.

Quantitative sampling of the Warren Point population was carried out at monthly intervals for just over a year. The other populations were not sampled in this way.

On each visit two or three core samples were taken from the same general site. Conditions on the point altered greatly from month to month, especially during the winter, when whole banks of sand were swept up taking the worms with them. Because of this shifting it was not possible to locate precisely a sampling site and it was necessary to fix positions by using large items of rubbish, mainly from boats, as markers. The shore is covered with debris, largely due to the extensive yachting interests in the estuary, and large pieces of canvas etc. would act as barriers against the wind and waves to some extent. By noting the trends of shifting each month, and by observing the positions of these makeshift markers, it was possible to pinpoint the sampling area. This was very important as there was some evidence of separate populations occurring here. For example, the worms on the extreme tip of the point, which was exposed only at very low tides, were very much larger than those from the sampling area and seemed to be isolated from the main group. Obviously, with a planktonic larva, this separation will not be permanent, but sampling must be restricted to a particular group of animals in order to ensure a similar past history for each sample.

Core sampling was selected as the most accurate method of quantifying the worms. A circular cover of diameter 8.3 cm was used, taking an area of 54 cm^2 in each sample, this size being chosen as that containing the most suitable number of animals for study. The core sampler took sand down to a depth of 25 cm. After sampling each core was emptied into a jar of 5 % neutralised formalin within two hours of collecting. No attempt was made to keep the cores intact as the relationship of these worms to depth was shown to vary continually due to the shifting substrate (see section 3.3.2.1).

The nature of the substrate at this site had another important effect on this method of sampling. To use the word 'sand' to describe it is really a misnomer. In fact the basic muddy sand was mixed with an enormous quantity of debris both of natural (rotting vegetation, larger stones) and human origin (broken bottles and tins, old socks, canvas etc.). Thus some cores contained little sand and were nearly all seaweed and rotting terrestrial vegetation. By taking more than one core it was hoped to minimise the effect of the great heterogeneity on the estimate of the population.

The species has a very patchy distribution (see section 3.3.2.2), and it was essential to ensure that the samples were taken from a region of high density. Before taking cores, therefore, the substrate was examined for the presence of C.capitata. Nevertheless a core would sometimes yield very few worms, in which case the sample was discounted.

Core samples were also taken to investigate the microdistribution of the species. Vertical distribution was studied by keeping the cores intact and fixing them in ten sections each containing three cm of substrate. A larger number of cores were taken for horizontal microdistribution studies as explained in section 3.3.2.2.

3.2.2 Plankton samples.

Sampling for larval C.capitata was carried out at monthly intervals at Warren Point. Plankton sweeps were made off the end of the point at low tide, using a net of 7.5 cm diameter and a mesh size of 0.055 mm. In addition a large hole (approx. 0.25 m^2 x 20 cm deep) was dug in the immediate vicinity of the sampling area and sweeps made with the plankton net through the water collecting in the hole.

The samples collected in this way were examined for the presence of larvae under a low power binocular microscope within two hours of collection.

3.2.3 Laboratory treatment of samples.

The cores were sorted in the laboratory by sieving. A stack of sieves with pore sizes of 1.0 mm, 0.250 mm and 0.062 mm was set up and the substrate washed through the widest mesh sieve using tap water. Worms were easily separated from the remaining material in the top sieve, their pink coloration and large size making them clearly visible. This procedure could not be used for the finer meshes since the smaller, colourless

worms were hidden by sand and mud particles. At first all of the sand in the sieves was examined under a low power binocular microscope and the worms removed. This was very time-consuming however and it was necessary to devise a more satisfactory method. Flotation techniques involving the use of hypertonic solutions such as those proposed by Anderson (1959) and Lackney and May (1971) were not used because shrinkage can occur under these conditions and the size relationships of the animals are very important in this instance. Small quantities of the sievings were placed in a glass container and swirled around with tap water. By this method the lighter, organic material, including the worms, was floated out from the sediment. The worms were separated from the remaining material by systematic examination under the microscope. Originally, mud passing through the finest sieve and collecting in the tray was examined for the very young stages of the worm but it was soon discovered that these were all retained by the sieves and the procedure was discontinued.

After sorting the worms were examined individually under the microscope and the following data obtained : -

3.2.3.1 Size of worms.

Most of the worms were incomplete and it was necessary to devise a suitable method for estimating the size and thus the age of the worms. Weighing was not possible because of the fragmentation and length of worms was similarly affected.

Eventually it was decided to measure the thoracic length of the worm. This was done using millimetre graph paper attached to a petri dish on the stage of the microscope. The state of contraction of the worm at the time of fixation affected this length and where very tightly contracted worms were encountered gentle pressure was applied to stretch the thorax to more normal dimensions. Measurements of the width of the thorax were abandoned as differences between worms were very small.

3.2.3.2 The sexual condition of the worms.

All of the 'adult' worms were examined for their sexual condition. The recognition of an adult worm was based on a number of factors investigated in many samples. For example it was soon found that worms with a thoracic length of less than 4 mm did not usually show signs of gamete production and similarly worms with less than six capillary-bearing segments were immature. As a result all worms longer than 4 mm in the thorax or with six capillary-bearing segments were examined.

Female worms were cut open mid-ventrally in the abdomen and the gut wall examined for the presence of ovaries. Where present these were removed and examined under a high power microscope and an attempt made to measure the diameter of the oocytes using a micrometer eyepiece. This was often very difficult when the oocytes were small and closely associated but unfortunately Goodrich's solution, as used by Gibbs (1968) did not succeed in separating them. In larger gonads the oocytes could be pulled apart by teasing with an entomological pin. In some instances

eggs were free in the coelom. A sample of coelomic fluid was taken and the diameter of these eggs was measured separately from those still attached in the ovary. Twenty to fifty oocytes were measured for each worm and placed in size classes of 7 µm. Where the oocytes were not completely round, as was often the case, the width of the cell across the side that presented itself to the micrometer scale was measured. Oocytes smaller than 28 µm in diameter could not be recognised.

The number of oocytes per ovary, and hence per worm, was estimated in two ways. Intact gonads were removed and teased apart so that the numbers could be counted directly. For smaller gonads this method could not be used and the oocytes were counted in serial sections of the ovaries prepared in situ. Worms were removed from the core prior to the addition of formalin and kept in clean sea water for 24 hours to remove sand grains from the gut. They were then fixed in Bouin's fixative and embedded in paraffin wax. 7µm sections were cut and stained either with haematoxylin (Ehrlich's) and eosin or in Mallory's triple stain. The methods are described in Gurr (1956).

3.2.4 Measurement of external factors.

3.2.4.1 Estimation of particle size.

Despite the obvious advantages of devising a unified technique for grade analysis this has still not been achieved. This is partly because the method used must vary according to the nature of the investigation. The principal discrepancies lie in the pretreatment of the samples. The techniques as originally

described (see Krumbein and Pettijohn 1938) were designed for geological investigations of soils and require the sediment to be broken up into its constituent parts. The binding properties of organic and carbonaceous elements in the soil are therefore destroyed by various methods of pretreatment. For the marine ecologist however the crumb structure of the sediment is vitally important, since the fauna will be physically affected by this rather than by the constitution of the individual aggregates. Morgans (1956) discusses this in detail and emphasises the importance of maintaining the sample in its natural conditions. Unfortunately his proposals are still not completely followed. For example, Holme and M^{c}Intyre (1971) describe a method for sorting sediments using dried samples. The hard aggregates formed by this pretreatment must be broken up mechanically before sieving can commence. The fine structure of the sediment is thus lost. In addition, they suggest the removal of organic matter with hydrogen peroxide. Although the presence of organic material can be a complication, it is nevertheless part of the substrate inhabited by the fauna and cannot be discarded. The method used in this study is one based on that described by Morgans (1956).

Samples were taken from all three collecting sites and from adjacent areas where C.capitata was absent. The variations in particle size distribution with depth were investigated by taking a core sample and separating different sections according to depth.

A small core was used taking about 60g (100 cm^{3}) of sediment.

This was found to be the largest quantity that could be efficiently sorted. Upon arrival at the laboratory (usually within two hours of sampling) the sample was wet-sieved through a 0.062 mm sieve, using sea water to wash it through. This is necessary because some of the later stages of sorting can affect the coherence of particles so that conglomeration of the finer muds occurs, preventing them from passing through the sieves. Both subsamples were then thoroughly washed with distilled water to remove the salt. If this is not done considerable errors can occur during weighing. In addition to the salt itself its hygroscopic qualities add to the weight. It adheres to the grains of sediment during drying and in the fine substrates, which present a larger surface area, the additional weight can be considerable. The subsamples were then dried to a constant weight at 105°C. This took approximately 24 hours. The temperature is important since some of the organic matter is oxidised if the heat is too great. The subsamples were then allowed to cool in a desiccator and the subsieve sample then weighed. The other subsample was placed in the top of a stack of sieves of decreasing size in the Wentworth scale (2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.062 mm) (Wentworth 1922) and shaken for one hour using an Endecotts sieve shaker model no. EFL 2. The sediment remaining in each sieve was dried to constant weight at 105°C, cooled in a desiccator and weighed.

The results were expressed graphically by plotting the cumulative percentage weight against particle size in terms of

Phi (ϕ) units (Krumbein 1939, Morgans 1956). The median particle diameter was calculated and the efficiency of sorting in the sediment given in terms of Phi quartile deviations and the Phi quartile skewness. The relevance of these statistics is discussed below (section 3.3.1.1). Details of the calculations involved are given in Holme and M^{c}Intyre (1971). Inman (1952) criticises this method of mathematical analysis because it only deals with 50 % of the sample. However his procedure requires a more careful sorting of the samples especially in the subsieve region where errors can be very great.

Using this method of sieving, the statistics can only be calculated where the subsieve sample does not make up more than 25 % of the total weight of the sample. Where this is not the case separation of subsieve particles must be carried out using elutriation or a comparable method. Fortunately this was not necessary in the present investigation.

3.2.4.2 Organic content of substrate.

Analysis of substrate samples for organic content were carried out to determine the food available for C.capitata. Samples of about 100 g were taken. Immediately on arrival at the laboratory all large organisms were removed from the sample and it was wet-sieved through a 0.062 mm sieve to separate the finer particles. Both subsamples were then thoroughly washed with distilled water and dried at 105^{o}C. This process ensures that the micro-organisms present are killed and cannot therefore reproduce causing any increase in the organic content. Longbottom (1970) showed

that the organic content of the faeces of Arenicola marina increased significantly if kept in sea water for only twelve hours. After drying, the large sized sample was sorted into large, medium and fine particle classes, which were stored in a desiccator until required for analysis, when a subsample from each size class was taken.

Several methods of organic analysis are available. Loss of weight on ignition was commonly used in early work and has the advantage of being very simple. But, as Pirrie et al. (1932) and Beanland (1940) recognised, there are certain problems involved in this method, the most obvious being the effect of carbonates. However, even if these are removed, the colloidal water cannot be compensated for. Lynn and Yang (1960) were unable to achieve constant results using this method and in view of the extreme heterogeneity of the substrates, especially at Warren Point, this method was rejected. Instead an indirect method of determining organic content was used. Trask (1939) pointed out that the precise relationships between the main elements in organic matter enable one to estimate the organic content of a sample by measuring a single element such as nitrogen or carbon. Several methods are available. Trask (1939) describes a method for determining carbon as carbon dioxide but this is very lengthy. The nitrogen content has been used as a measure of organic content (Sverdrup et al. 1942, Longbottom 1970) and can be readily determined. But the presence of nitrogen in organic matter is fairly low and variable so the method is not accurate enough to be used on its own. Hughes (1969) describes a method

for determining the caloric value of marine sediments. This is particularly useful in studies of ecological energetics but a correction factor, derived from the Kjeldahl nitrogen content, must be applied to compensate for the incomplete oxidation of proteins. It was decided that the most suitable scheme for the present investigation was the wet oxidation method for estimating carbon content. Various routines have been described with one based on that of Walkley and Black (1934) as described by Holme and M^{c}Intyre (1971) being used here.

The accuracy of this method is affected by several factors. Maximum recovery is achieved by carefully balancing the concentration of acid used with the temperature. Schollenberger (1927) boiled the reagents under flux, but, as Walkley (1947) showed, this causes decomposition of the acid. Walkley recommended that a ratio of two parts sulphuric acid to one part aqueous solution be used with no additional heat beyond the heat of reaction. However, digestion is very slow at these temperatures and it seems better to sacrifice some efficiency for a saving of time.

Several substances interfere with the process and can give rise to misleading results unless taken into account. Chlorine must be removed since it is known to form chromyl chloride under the conditions of the titration (Wakeel and Riley 1957). Rinsing with distilled water helps by removing some of the salt and any remaining is precipitated as silver chloride by the addition of silver sulphate to the reaction vessel. Lynn and

Yang (1960) had difficulty dissolving the reagent and applied a correction factor for chlorine instead. No problem was encountered in this instance.

Reducing agents are more difficult to deal with, the most troublesome being the ferrous ion. Walkley (1947) and Wakeel and Riley (1957) concluded that the effects were minimal but Southward (1952) pointed out that in very blue mud the ferrous sulphide content may have a considerable effect. Slinn (1956) gives a method for quantifying ferrous ions but this was considered unnecessary in the present investigation. Manganese ions, which are important factors in soils, are believed to be of minimal effect in marine sediments (Walkley 1947). Carbonates are stabilised by the addition of phosphoric acid.

The major problem in this method lies in the presence of elemental carbon and carbon in the form of coal. There is no way of compensating for these in this analysis, and unrealistically high values of carbon content can occur. However, the method is imperfect in any event as there is no way of knowing what proportion of the organic carbon content is available as food. The presence of coal in the samples at Warren Point was therefore not a problem in itself. To estimate the amount of assimilable carbon present further tests were carried out.

Firstly the size of particles ingested by the worm was studied. C.capitata feeds by everting its proboscis into the

sediment and taking in particles engulfed by it. Examination of the gut contents of many specimens showed that particles larger than 0.1 mm in diameter were not taken in and it was assumed that the larger material is selectively rejected by the worm. Because of this only particles smaller than 0.125 mm (the nearest sieve size) were used for organic analysis.

Secondly it is clear that much of the organic material in the subsample will be locked up in a form which cannot be attacked by the worm. To determine the percentage of assimilable organic carbon in the substrate each sample was divided into two halves. The first of these was treated for total organic content as above and the second subdivided into three samples, two of which were incubated at 35°C for four days under sea water containing trypsin, α amylase, invertase and lipase. These enzymes had been shown to occur in the gut of C.capitata (see section 4.1.2.2). The third subsample was incubated in sea water only as a control (George 1964a).

Attempts to collect faeces and determine their content were not carried out because pellets would have to be collected over a long period of time, thus affecting the organic content (Longbottom 1970). The small size of the pellets made it impracticable to collect them individually. Furthermore the pellets are encased in mucus which would contribute a large proportion of the total amount of organic carbon.

The results are given as percentages of organic carbon, Walkley and Black value. As a complete recovery is not achieved by this method these results must be multiplied by a suitable factor (Morgans, 1956, suggests 1.3) to give a more accurate value. Conversion to percentage organic matter is given by multiplying by 1.8 as suggested by Trask (1939).

3.2.4.3 Salinity.

The salinity of the water at low tide at each of the collecting sites was determined using a Simac conductivity meter model no. 63 AT. The water overlying the collecting site at Warren Point at high tide was also measured. Samples of about 50 cm^3 of sea water were taken from the sea and from interstitial water and the chlorinity assessed more accurately by titrating against silver chloride. Chlorinity values were converted to salinity using the formula ;

$$\text{Salinity} = 0.03 + (1.805 \times \text{chlorinity})$$

as given by Knudsen (1902).

The interstitial water samples were taken by digging a hole and collecting some of the water filling it.

3.2.4.4 Oxygen content.

The oxygen tension of the interstitial water at Warren Point was measured in connection with experiments on the respiration of C.capitata (section 4.3). A Y.S.I. portable oxygen meter and oxygen probe model 54 were used. The substrate at this site is very loose and unstable and measurements were made by placing the

electrode at a depth of 8 - 10 cm below the surface in pools of water percolating into small holes in the substrate. Readings were taken after a few minutes to allow the sediment time to recover from distortion.

The method can be criticised in that it cannot be ensured that no interference occurs in actually taking the sample, but the results were reproducible and seemed satisfactory for the purpose of gaining an indication of the pO_2 gradient across the body wall of the worm. In any event the heterogeneity of the substrate at Warren Point undoubtedly affects the oxygen tension from place to place. The relationships between particle size and oxygen content as described by Brafield (1964) become very complex under these conditions and there seemed little point in taking more precise measurements.

3.3 Results and discussion.

3.3.1 External factors.

3.3.1.1 Analysis of particle size.

Three core samples were taken from the collecting site at Warren Point, two from regions of high density of C.capitata and the third from a site where the species was absent. The samples were taken at the depth at which C.capitata was found. This varied but was generally at about 12 cm. The relationship of particle size to depth was analysed for one sample taken from Warren Point. The results are given in Table 17. One sample was taken from Rhosneigr. Three cores were analysed from the small sampling site at Whitstable and a fourth was taken from the adjacent sand where there was no C.capitata.

Cumulative frequency graphs were constructed for each of these samples and the following statistics calculated for these:-

Md Ø This is the median particle size. 50 % of the sample has a diameter larger than this value and 50 % smaller. The Ø value is converted to millimetres by using Fig. 27.

QD Ø This is the Phi quartile deviation, a statistic describing the horizontal spread of the data. A low value indicates a well sorted sediment with the middle 50 % of the sample spreading over a small range of particle sizes.

SkqØ This is the skew quartile. It indicates whether the curve is straight or curved over the median 50 % of the range. A

TABLE 17. The relationship between particle size and depth at Warren Point.

Depth of sample (mm)	Md Ø (mm)	QD Ø	Skq Ø
0 - 5	0.245	1.46	-0.96
6 - 10	0.229	1.41	-0.965
11 - 15	0.220	0.75	-0.30
16 - 20	0.230	0.80	-0.30
21 - 25	0.212	0.53	-0.125

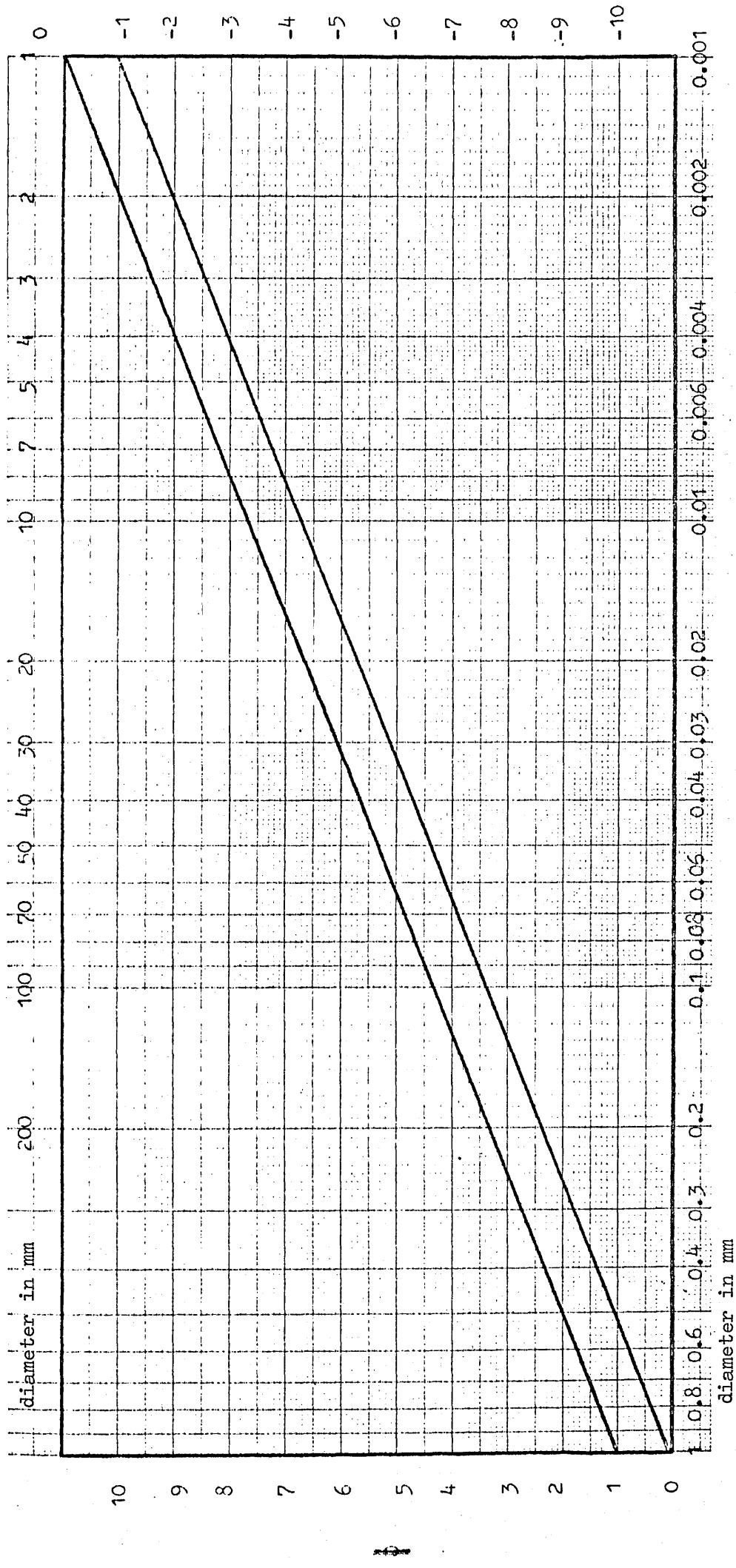


FIG. 27 Conversion graph, ϕ to diameter in mm.

negative value shows that the sorting in the sediment is less efficient towards the larger particle sizes.

These statistics are given for each of the samples in Table 18. Representative graphs from each of the sampling sites are given in Figs. 28 - 30. The raw data are presented in appendices 1 and 2.

From these results it can be seen that C.capitata is usually encountered in fine to medium sandy substrates at all these collecting sites. All the samples were fairly well sorted with the range between the first and third quartiles seldom exceeding two Whitworth categories. As might be expected sorting of the larger particles is generally less efficient.

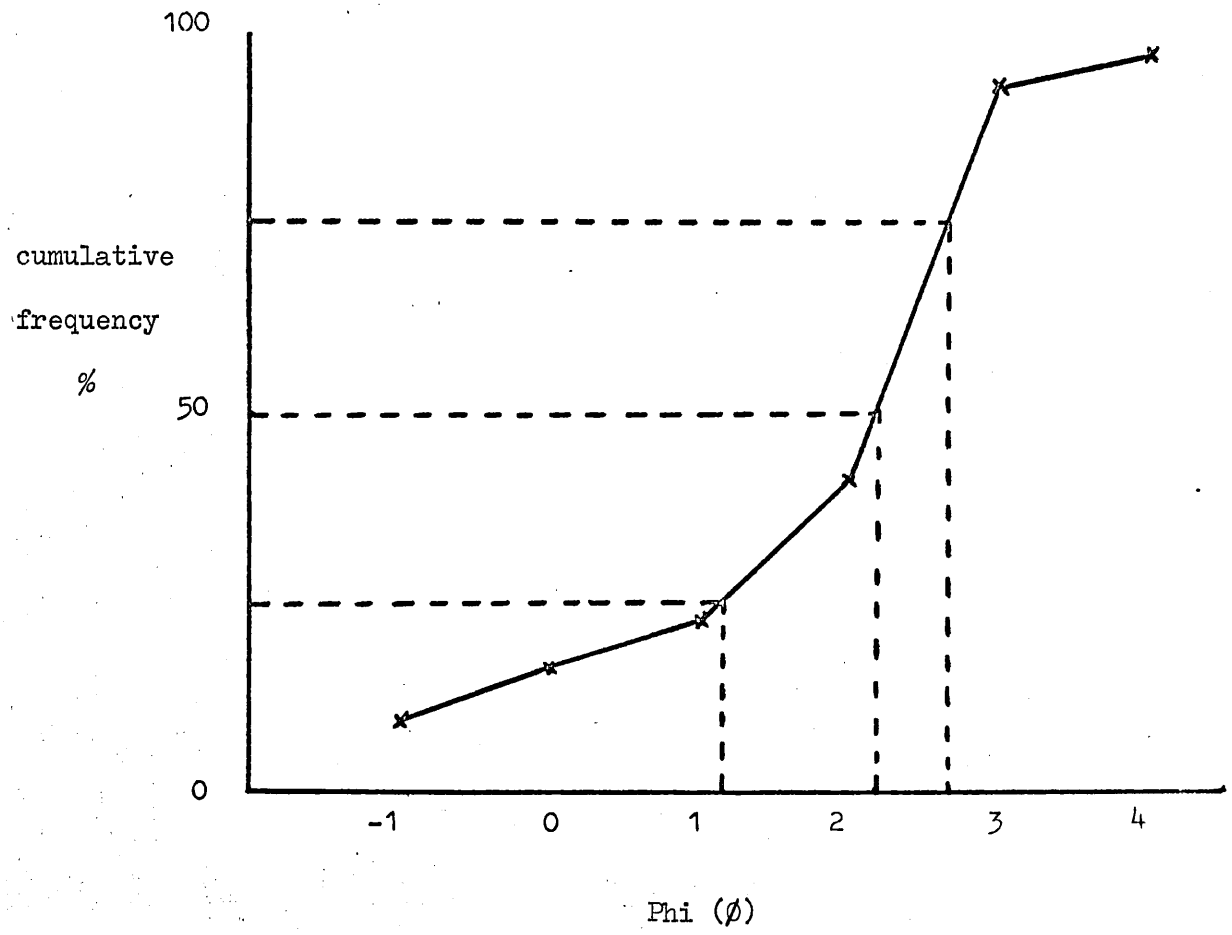
The samples from Whitstable are remarkably similar, indicating a well sorted, stable sediment. χ^2 analysis shows that the samples are not significantly different ($\chi^2 = 16.238$; P = 30 %) including that which contained no C.capitata.

The heterogeneity at Warren Point is expressed in the data from these samples. All three were taken from the same immediate vicinity but a χ^2 test indicates that they are significantly different ($\chi^2 = 53.407$; P < 0.1 %). Comparisons of pairs of samples show that a and b (the sample with no C.capitata) could be from the same mathematical population ($\chi^2 = 15.873$; P > 0.1 %) as could b and c ($\chi^2 = 17.574$; P > 0.1 %) but a and c are significantly different with $\chi^2 = 18.680$ and P << 0.1 %. Nevertheless the structure of the substrate is broadly similar to that at Whitstable with a similar Md ϕ and QD ϕ . The quartile skew-

TABLE 18. Analyses of particle sizes from British sites.

Sample	Md Ø (mm)	Md Ø (Whitworth class)	QD Ø	Skq Ø
Warren Point a	0.325	medium sand	0.52	0.07
Warren Point b	0.226	fine sand	0.64	-0.05
Warren Point c	0.174	fine sand	0.875	0.145
Rhosneigr	0.199	fine sand	0.33	0.05
Whitstable a	0.228	fine sand	0.75	-0.26
Whitstable b	0.280	medium sand	1.38	-0.71
Whitstable c	0.211	fine sand	0.755	-0.265
Whitstable d	0.205	fine sand	0.70	-0.23

FIG. 28 Analysis of particle sizes at Whitstable.



Md ø = 2.16 = 0.228 mm diameter (fine sand)

Q_1 ø = 1.15

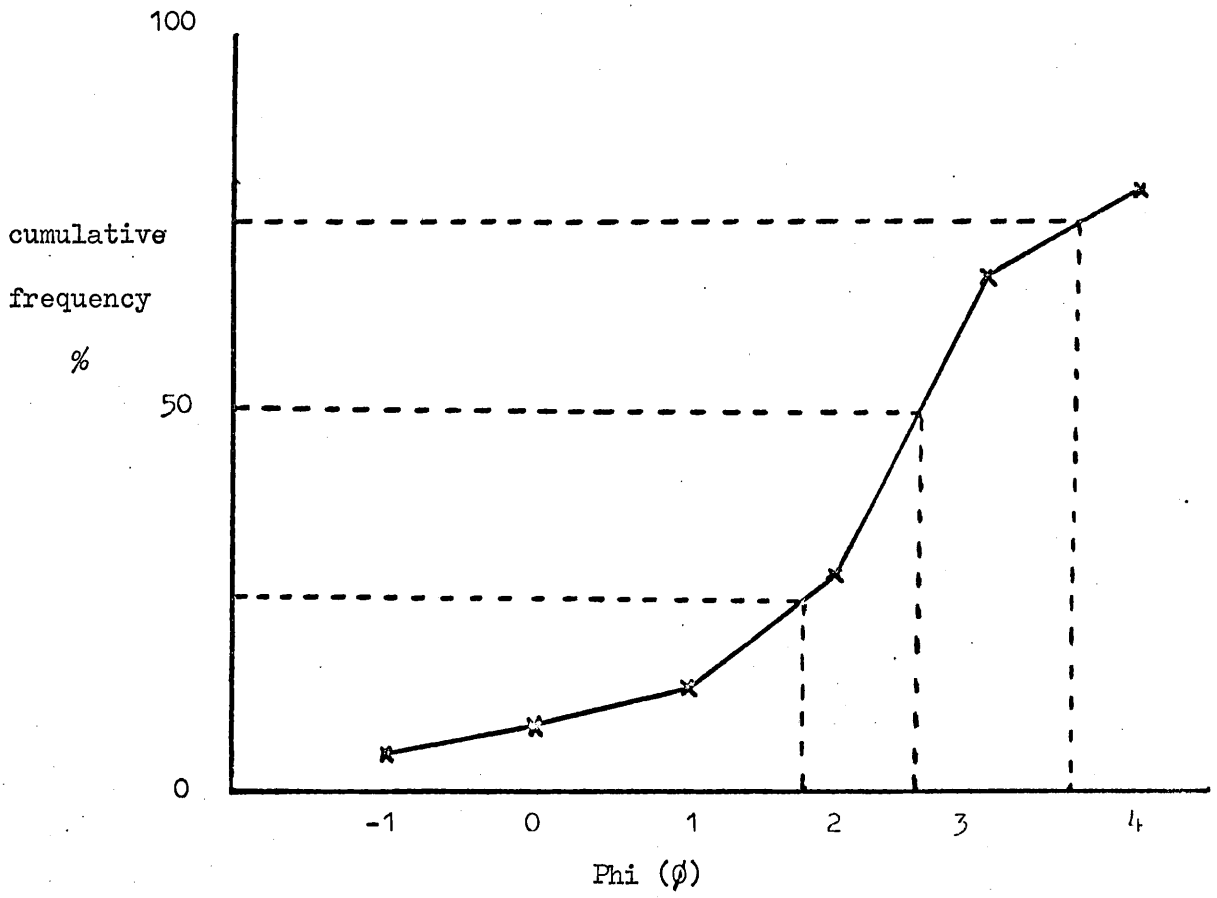
Q_3 ø = 2.65

Therefore QDø = 0.75 which is a range from 0.162 - 0.460 mm

This is a spread across two Whitworth classes (fine sand - medium sand)

Skq ø = -0.26

FIG. 29 Analysis of particle sizes at Warren Point.



Md ø = 2.54 = 0.174 mm diameter (fine sand)

Q_1 ø = 1.81

Q_3 ø = 3.56

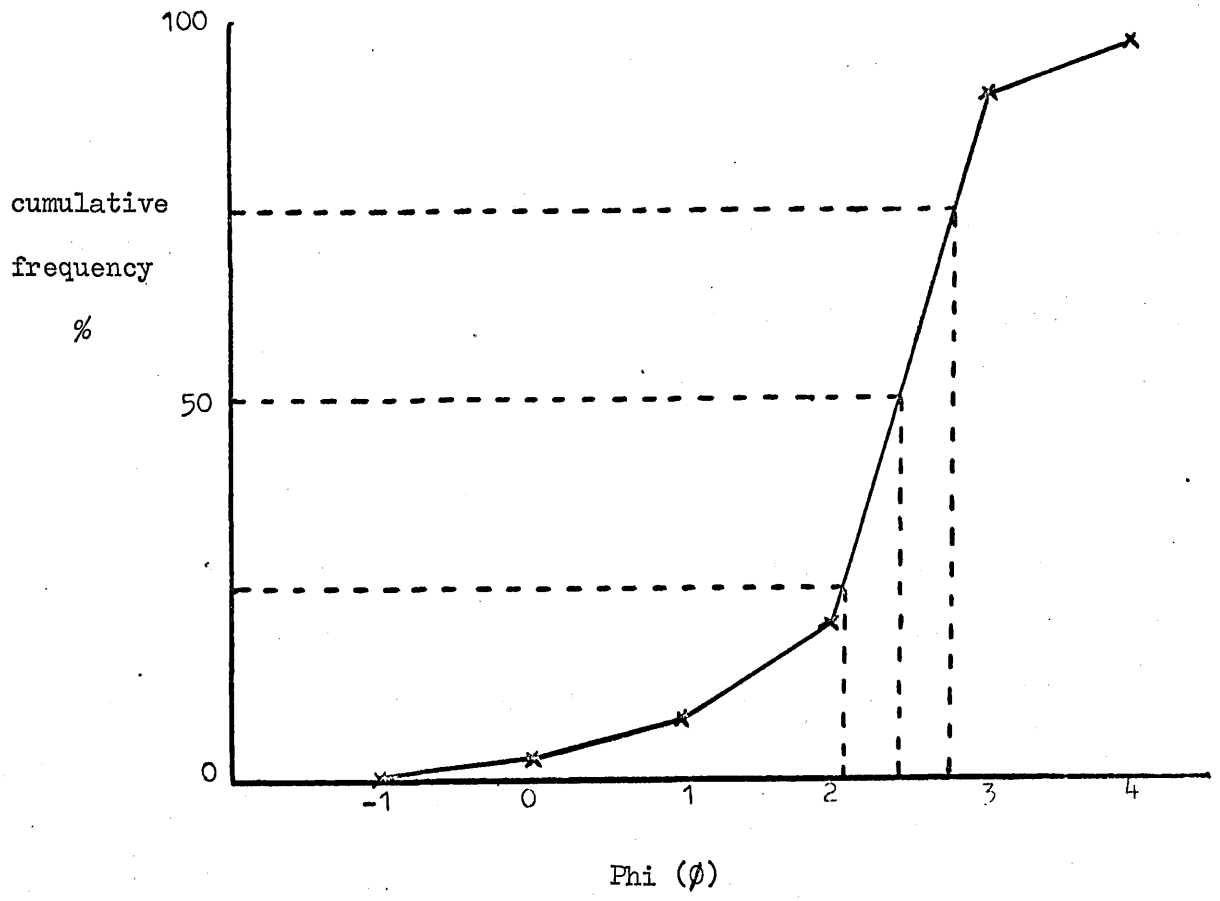
Therefore QD ø = 0.875 which is a quartile range from 0.086 - 0.289 mm

This is a spread across three Whitworth classes

(very fine sand - medium sand)

Skq ø = +0.145

FIG. 30 Analysis of particle sizes at Rhosneigr.



Md ø = 2.53 = 0.199 mm diameter (fine sand)

Q_1 ø = 2.07

Q_3 ø = 2.73

Therefore QD ø = 0.33 which is a quartile range from 0.152 - 0.244 mm

This is within one Whitworth class (fine sand)

Skq ø = +0.05

ness, however, is positive in two of the samples. This reflects the instability of the substrate at this site, although the Skq Ø values are very low.

The sample from Rhosneigr is again comparable with that from Whitstable in its Md Ø, but the low value for QD Ø suggests that this sediment is very well sorted.

The analysis of particle size with depth is summarised in Table 17. The median particle size increases with depth and the efficiency of sorting increases. Examination of the quartile skewness data shows that this is mainly due to improved sorting of the larger particles.

These results indicate that C.capitata may show a preference for fine sandy substrates. However, the absence of the species from samples showing similar characteristics in the particle size analyses shows that this is not the only factor involved in the distribution of the species.

In fact, the results of previous surveys suggest that particle size is not a factor in the distribution of C.capitata. Pirrie et al. (1932) discussed the significance of soil grades and related C.capitata to black or grey sand. In 1957 Southward surveyed deposits in the Irish Sea and found C.capitata in the largest size category, clean sand. On the other hand, Barnard and Reish (1959) found the species in black mud. Filice (1958) concluded that C.capitata showed no preference for any grade as

it occurred in sediments ranging from mud to sand in the estuarine part of San Francisco Bay. Eliason (1962) again found the species in muddy sediments in the Oresund and in the Heathcote estuary, New Zealand, it occurred in very fine sand and some muddier substrates (Estcourt 1967). Schulz (1969) found it in a variety of sediments but it was most common in muddy sand and sandy mud. Wolff's investigation of the Dutch delta area (1973) gives a similar pattern to that in the present study, with the species showing a slight leaning towards well sorted fine and muddy sands. Reish (1971) induced C.capitata to settle on wooden blocks in Los Angeles harbour.

Thus, although it is sometimes possible to correlate the distribution of isolated populations of C.capitata with particle size, the relationship breaks down on any larger scale. In any event, correlation with particle size may only reflect an underlying association with some factor itself correlated with particle size.

3.3.1.2 Organic content.

Three samples (01 - 03) were taken from the collecting site at Warren Point. A fourth sample, containing no C.capitata, was taken from nearby (04). Cores were taken from Whitstable and Rhosneigr for comparison. The results of these analyses are given in Table 19 ; with the raw data in appendix 3. The results show great variation in total organic matter, especially amongst the Warren Point samples. These cores contained a very large quantity of material which was retained by

TABLE 19. Organic analyses of substrate.

Sample	% organic carbon (whole sample) W & B value	% organic matter	% organic carbon(<0.125 mm) W & B value	% organic matter (<0.125 mm)
Warren Point				
01	0.850	2.041	3.110	7.464
02	3.948	9.476	3.700	8.880
03	5.512	13.229	3.975	9.540
04	2.231	5.356	3.602	8.644
Whitstable	1.431	3.434	2.427	5.824
Rhosneigr	1.723	4.135	2.951	7.082

W & B value = Walkley and Black value

the largest sieve (1 mm) including much rotting vegetation. At this stage it was thought possible that C.capitata might feed by rasping material from the decaying matter and it was included in the analysis. Any sediment adhering to the larger pieces of plant material was washed off prior to analysis. The figures for organic matter in the sediment with a particle diameter of less than 0.125 mm are more consistent with an average value of 8.6 % at Warren Point.

The results of the digestion experiments are given in Table 20. They show that there was about 1.5 % of digestible organic matter in the finer grades of sediment. This amounts to just under 20 % of the total organic content of this fraction. This estimate of assimilable organic matter is still high. The digestion experiments were carried out in ideal conditions with plenty of enzymes and virtually unlimited time. But food passes through the gut of C.capitata in two days at most and it is unlikely that such a high rate of assimilation would be achieved. George (1964a), working on the polychaete Cirriformia tentaculata, found 0.44 % digestible material in the mud by using enzyme digestion, but only 0.33 % by comparing the carbon content of mud and faeces.

It is very difficult to compare these results with those obtained in previous samples. Methods of analysis vary and, as indicated by these results, percentages obtained for the whole substrate can be misleading. Nevertheless it is clear that all three sampling sites are very organically rich. Allen et al.

TABLE 20. Digestion of substrate by selected enzymes.

Sample	Before digestion		After digestion		Digestible organic matter	% organic matter digested
	% organic C (<0.125 mm) W & B value	% organic matter (<0.125 mm)	% organic C (<0.125 mm) W & B value	% organic matter (<0.125 mm)		
a	3.216	7.718	2.588	6.212	1.506	19.52
b	3.109	7.461	2.528	6.069	1.392	18.65
c control	3.058	7.339	3.011	7.226	-	-

W & B = Walkley and Black

(1953) estimated that organic carbon made up 7.59 % of the dry weight of sediment from Tilbury, in the Thames estuary. Reish (1957a) found from 2.0 % to 4.8 % organic carbon in polluted parts of the Los Angeles harbour where C.capitata occurred, although values as high as 10.7 % were attained for abiotic zones near to the source of pollution. On the other hand, Longbottom (1970) calculated values of less than 1 % carbon for sand flats along the north Kent coast and related the amount of organic matter to median particle size. He concluded that most of the organic material was in the form of micro-organisms rather than detritus. This does not appear to be the case in this instance. All of the sediments contained much organic debris in the form of sea-weed and leaves. This is largely unavailable to C.capitata, which cannot digest cellulose (see section 4.1.2.2). The common occurrence of C.capitata on the vegetation itself, rather than in the sand, suggests that the worm is feeding on the micro-organisms breaking down the leaves. It is hoped that washing the plant material at the start of the analyses transferred this material to the appropriate fraction for analysis.

The high percentage of organic matter in the form of plant material explains the inefficiency of digestion by enzymes. In fact the true value for available organic matter for feeding is given by these experiments. All the other organic material is locked up in a form which is not available to the worm.

3.3.1.3 Salinity.

The collecting site at Warren Point is situated about two

kilometres from the sea and is thus subject to variations in salinity during the tidal cycle. The salinity at high tide was 32.9°/oo compared with values of 17°/oo and 19.2°/oo at low tide. The interstitial water, sampled at low tide, had a mean salinity of 27.8°/oo ± 0.10°/oo. These results are comparable with those of Alexander et al. (1932) who investigated changes in salinity under estuarine conditions. They found an interstitial value of 28.4°/oo when the estuarine low tide salinity was 12.6°/oo compared with 30.0°/oo at high tide. This is because, as first shown by Reid (1930), the interstitial water is not closely connected with the surface water. The influence of the surface water is dependent on depth, and in the first few inches the salinity may undergo considerable variation. This may account for the comparatively low value recorded for the interstitial water at Warren Point. However, the effect of surface water is almost certainly minimal at the depths at which C.capitata occurs (> 8 cm). George (1964b) found that salinity variations were not marked at this depth in a mud flat. In any event, the sampling area is only exposed for about three hours at low spring tides and surface water influences are likely to be small.

Although Whitstable is on the Thames estuary it is known that the salinity is fairly constant, ranging seasonally from 28.5 to 35.0°/oo (Gibbs 1968, Longbottom 1970). The measurements made here accord well with this, the surface water being 33.6°/oo. Readings of the interstitial water

were not made but it is reasonable to expect that the salinity will not differ greatly from that of the overlying water.

At Rhosneigr the offshore water had a salinity of 32.9°/oo. There was a considerable fresh water run-off over the shore which must exert an influence on the upper layers of sediment, but probably only affects the salinity around C.capitata during periods of long exposure, if then.

The results show that C.capitata tolerates lowered salinities but that it is not exclusively estuarine in its habitat. Varying salinities do not seem to be a factor. There are many references to C.capitata occurring at low salinities (see section 1) down to 0.4°/oo in the Heathcote estuary, New Zealand (Estcourt 1967). It occurs in the Baltic (Leppäkoski 1969) but may reflect a possible influence of the lowered salinity in its small size (Muus 1967).

One can conclude that salinity is not a prime factor influencing the distribution of this species although its tolerance of lowered salinity allows it to penetrate into a wider range of habitats.

3.3.1.4 Oxygen content.

Three samples were taken giving a mean value of 10 mm Hg = 0.40 ppm O_2 (range 8 - 12 mm Hg). The relationship of C.capitata to low oxygen tensions has been discussed in

great detail with respect to organic pollution. Reish (1955, 1957, 1959) found the species at 3.5 ppm O_2. In 1960 Reish and Barnard computed from field toxicity tests that oxygen tensions of 3.5 ppm or more were necessary for reproduction but that the species would continue to feed down to 2.9 ppm. Bagge (1969a) found C.capitata in conditions where the oxygen tension ranged from 0.3 to 13.5 ppm with the greatest densities occurring above 3 ppm.

The influence of lowered oxygen tensions on the distribution of this species is discussed in more detail below (section 5.).

3.3.2 Microdistribution of C.capitata.

3.3.2.1 Vertical distribution.

The relationship of C.capitata to the depth of the substrate at Warren Point was investigated to ascertain the optimum depth for sampling. Cores taking 30 cm of substrate were used and these were cut into sections in the laboratory prior to the quantitative sampling of worms. These were divided into immature and mature categories. The results of three such cores are shown in Table 21.

The results show that C.capitata is not restricted to a particular depth but that it does not penetrate below 24 cm. It is seldom found in the upper layers at Warren Point, presumably because these are so unstable and subject to varying conditions due to the effects of exposure at low tide. The

TABLE 21. Vertical distribution of C.capitata at Warren Point.

Depth (mm)	Core 1.no worms			Core 2.no worms			Core 3.no worms		
	Young	Adult	Total	Young	Adult	Total	Young	Adult	Total
0 - 3	0	1	1	0	0	0	0	0	0
3 - 6	1	1	2	0	0	0	0	0	0
6 - 9	4	2	6	2	1	3	0	0	0
9 - 12	18	3	21	5	3	8	16	1	17
12 - 15	26	5	31	7	1	8	35	6	41
15 - 18	24	3	27	5	1	6	50	3	53
18 - 21	6	3	9	11	2	19	5	2	7
21 - 24	0	0	0	0	2	2	0	1	1
24 - 27	0	0	0	0	0	0	0	0	0
27 - 30	0	0	0	0	0	0	0	0	0

largest number of worms was found at 12 to 15 cm in the first core, 18 to 21 cm in the second and 15 to 18 in the third. It is believed that this variation is due to the shifting of the substrate piling up extra layers of sand. A similar situation was found at Whitstable. Usually the worms occurred at about 20 cm but on one occasion they were beyond a spade's depth, at least 35 cm below the surface. The substrate at this depth was the blackened sand typical of this site. The surface deposits were completely different, however, consisting exclusively of granular particles (> 4 mm in diameter). The site is situated in front of a marine dredged aggregates and cement works and it is thought that unwanted material from this is dumped on the beach and almost certainly accounts for this deposit over the collecting site. On the next visit, several months later, the substrate was sandy and the worms were found at 20 cm again.

Referring again to the Warren Point samples it can be seen that the young worms occur at the same depths as the adults.

As a result of these investigations it was decided to take cores from 0 to 25 cm for quantitative estimates of C.capitata.

3.3.2.2 Horizontal microdistribution.

The horizontal distribution of C.capitata was investigated at Warren Point. Eleven core samples were taken from an area where the species was known to be common. The cores were taken from squares in a grid, the positions being determined using a

table of random numbers (Fisher and Yates 1963). The number of samples and the size of each core was the largest that could be efficiently sorted. The size of the core is very important since in an aggregated population too small a core will not sample the clumps accurately and a value indicating a regular dispersion will be obtained whereas too large a core will include several clumps so that their presence is missed.

The number of worms per core was counted and the coefficient of dispersion as proposed by Blackman (1942) was calculated. The expression $\frac{\sum(x - \bar{x})^2}{\bar{x}\,(n-1)}$ where n is the number of samples, approximates to unity when individuals are randomly dispersed. For aggregated populations the value of the coefficient is greater than 1 whereas a value below unity indicates a regular dispersion pattern. The significance of the calculated coefficient is given by the formula $\sqrt{\frac{2n}{(n-1)}}2$ which gives the amount by which the observed value of the coefficient must depart from zero to indicate a departure from randomness.

Other methods of describing distributions exist but the coefficient of dispersion is well known, easy to use and applicable to investigations into marine benthic organisms (Holme 1950, Clark and Milne 1955, Franz 1973).

Each of the analyses showed a significant aggregation (Table 22). A random population would be expected to have a coefficient of dispersion of 1 ± 0.469.

TABLE 22. Horizontal microdistribution of C.capitata at Warren Point.

	No young worms per core	No adult worms per core	Total no worms per core
	16	7	23 (01)
	26	8	34
	14	5	19
	8	4	12
	16	3	19 (02)
	1	3	4
	7	5	12
	0	1	1
	24	11	35
	0	3	3 (03)
	2	3	5
Coefficient of dispersion	6.591	1.697	9.259

These results have important consequences with regard to sampling techniques, as well as their ecological interest. Any estimates of population density will be less accurate than those based on randomly dispersed individuals unless the number of samples is increased beyond practical means. Studies on the structure of the population must also be based on either a large number of cores, or on those from previously selected areas of high density, as in the present case. Fortunately, both adult and juvenile worms show an aggregated pattern, although this is less marked in the mature animals. This means that these will be relatively under-sampled but sufficiently large samples were taken to make this unimportant.

The reasons for this aggregation are not explained by this analysis. While it could be a feature related to the reproductive biology of the species the influence of external factors cannot be overruled (Reys 1972). The only elements likely to vary over such a small area at Warren Point are particle size and organic content. The former is known to be of little influence on the distribution of the species, but it is certain that the amount of food present will. The organic content of the substrate from three of the cores was therefore calculated (01 - 03 section 3.3.1.2). The number of worms in each of these cores is indicated in Table 22. Thus, while the number of animals present was very variable the organic content was almost constant (average value of 8.628 ± 0.061). The clumped dispersion of C.capitata is most likely therefore a normal

feature of its biology. As it is a species undergoing copulation it is reasonable to expect an aggregation of individuals at least during breeding periods. The brooding of the larvae, in some cases up to metamorphosis, will also result in an aggregation of young worms.

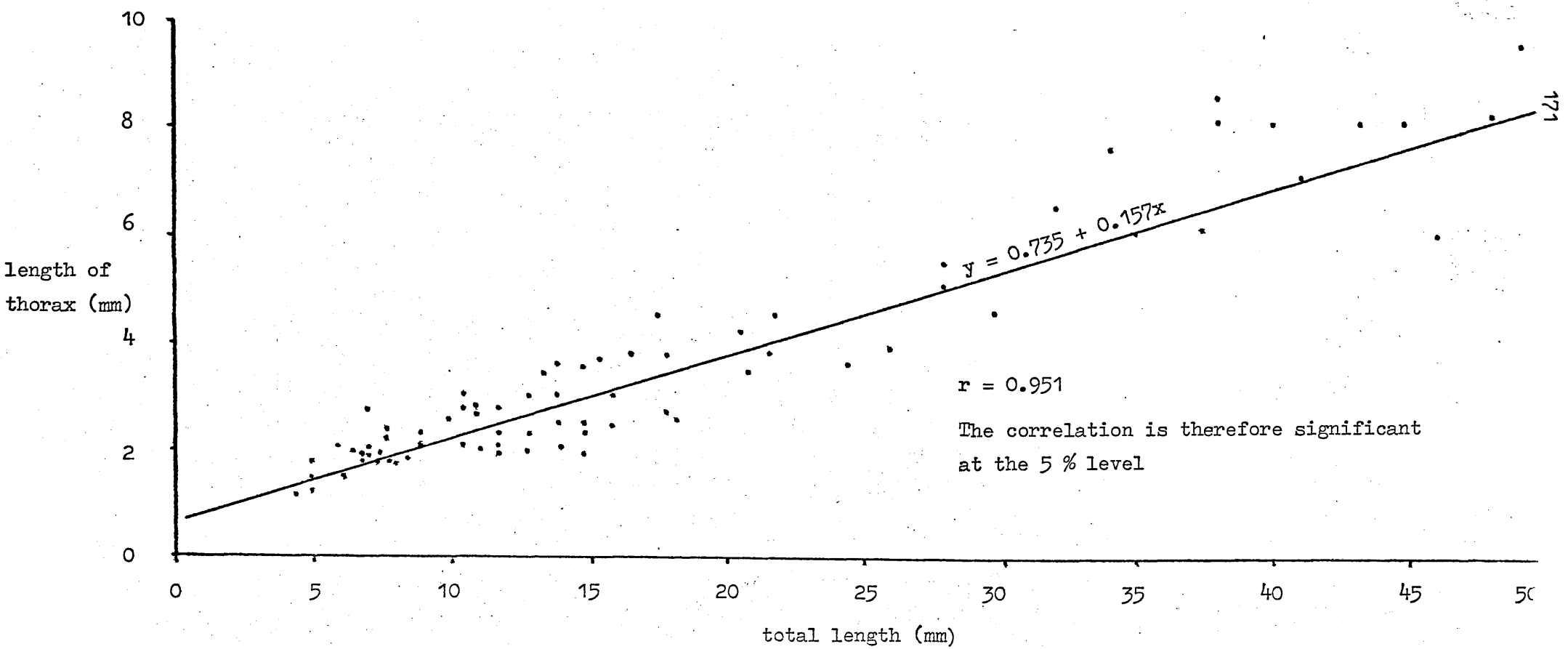
Rosenberg (1972) also found an aggregated population structure for C.capitata, but relates this to the increased abundance of the species in the fjord under study. Kosler (1968) appreciated that relative abundance and density can affect the microdistribution of a species and it is possible that similar factors are important at Warren Point.

3.3.3 Population Studies.

3.3.3.1 Size Relationships.

Due to the fragmentation of worms it was not possible to assess age by taking direct measurements of weight or length. Fig. 31 shows that the length of the thorax is positively correlated with the total length of the worm, especially for smaller worms, and it was decided to use this feature to estimate the relative age of individuals. The relationship is based on the fact that increase in total length results in an increase in segment size. In young stages growth also involves an increase in segment number. Above a certain size it is probable that no new segments are produced and all further growth occurs by increases in segment size ; both in length and width. Unfortunately few very large complete worms were found in the samples and some of these showed signs of regen-

FIG. 31 Relationship between length of thorax and total length in C.capitata from Warren Point.



eration. These factors explain why the correlation between the two parameters is not as close for the larger sized worms. Nevertheless, this method seemed acceptable for the smaller worms at least, and in conjunction with estimates of reproductive state, a reasonable picture of the population structure was obtained.

3.3.3.2 The structure of the population.

Monthly samples of the population were made from January 1973 to February 1974. In some instances only one core was used for estimates of the population, but where each sample contained a large number of worms both were used. Size frequency histograms were constructed for each month based on the data given in Appendix 4. These are shown in Fig. 32.

The histograms do not allow clear definition of age groups. It is possible to follow through some of the peaks, as discussed below, but, in the larger sizes especially, the patterns are indistinct. This is undoubtedly partly because of insufficient sampling of larger worms together with the breakdown of the length relationship used, but the results also suggest that the population is not neatly divided into year classes. This implies that reproduction occurs throughout the year and is not restricted to a limited breeding season. Olive (1970) found a similar structure in a population of Cirratulus cirratus from Northumberland, but in this case the monthly histograms were all very similar indicating a completely asynchronous pattern of reproduction resulting in a dynamically stable

FIG. 32. Monthly length frequency histograms of C.capitata from Warren Point.

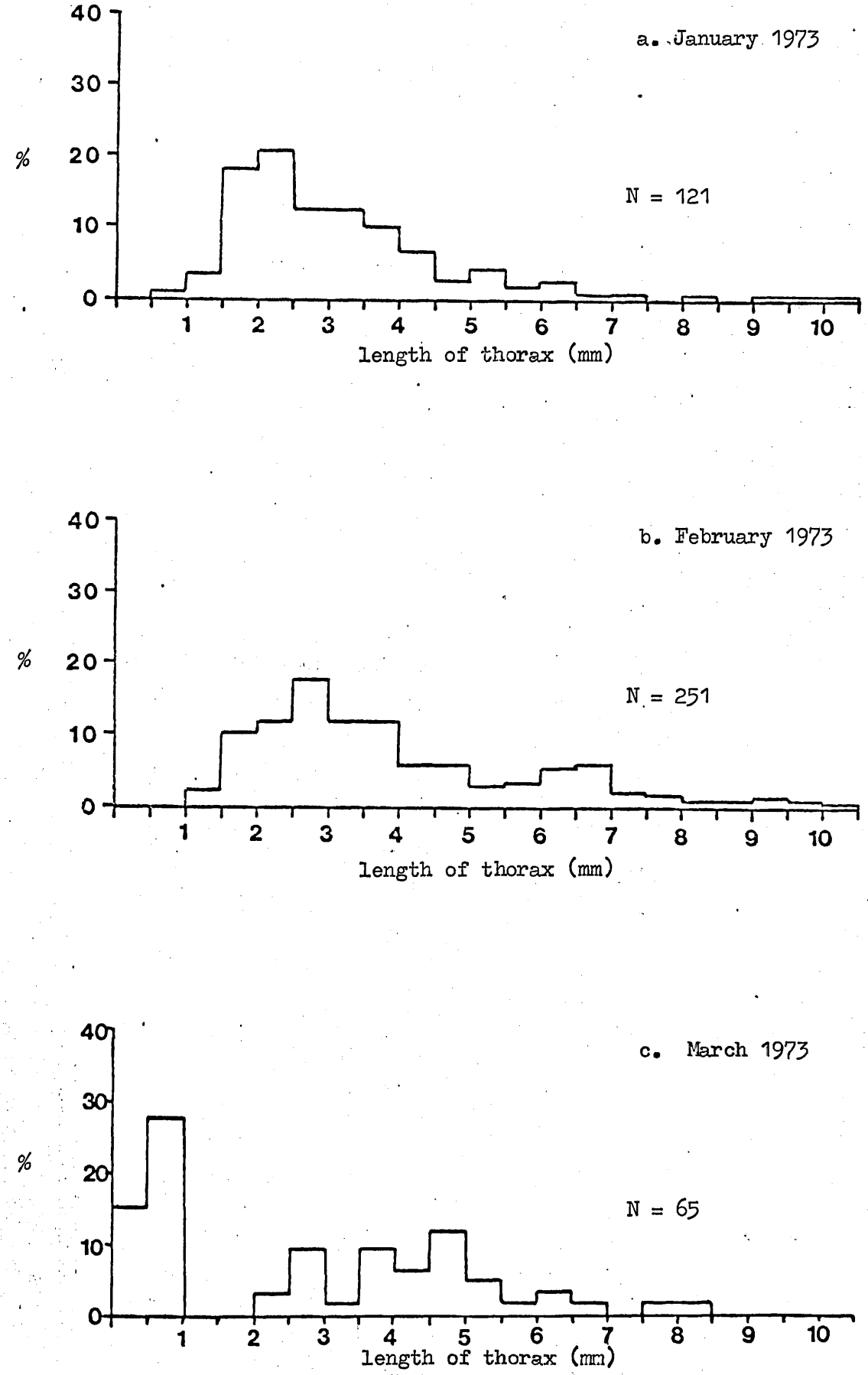
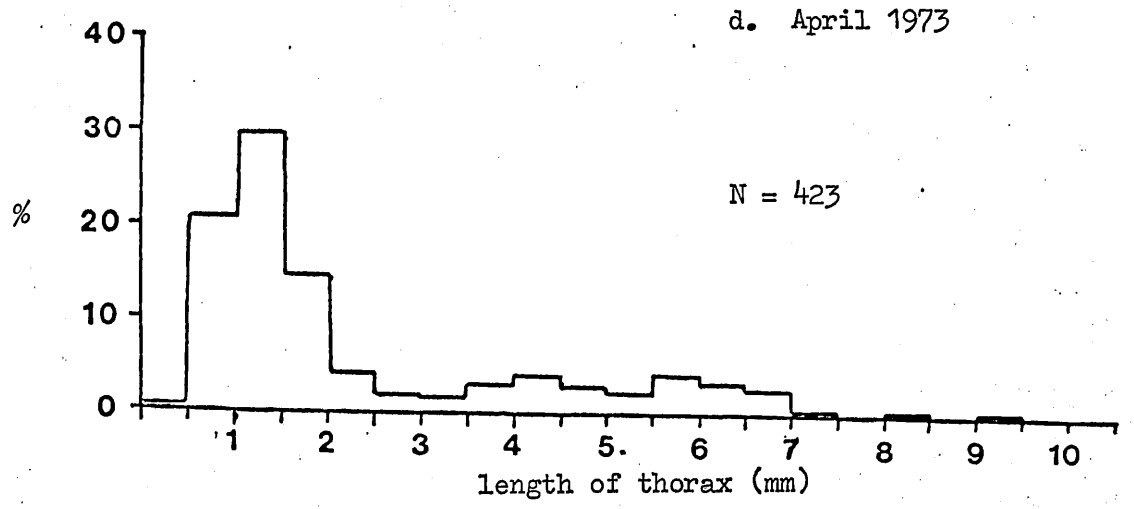
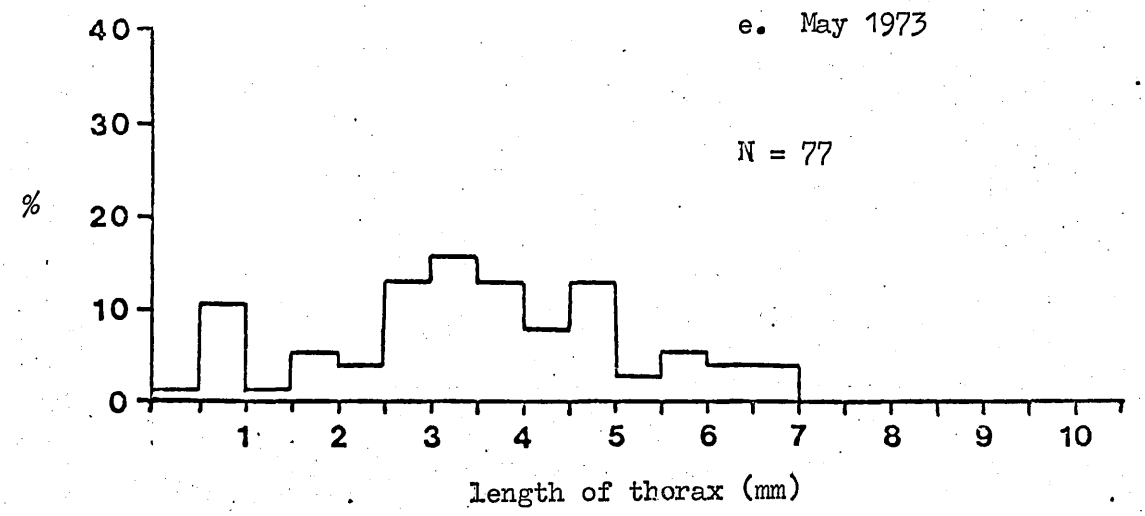


FIG. 32 (cont).


d. April 1973
N = 423
%
40
30
20
10
0
1
2
3
4
5.
6
7
8
9
10
length of thorax (mm)


e. May 1973
N = 77
%
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
length of thorax (mm)

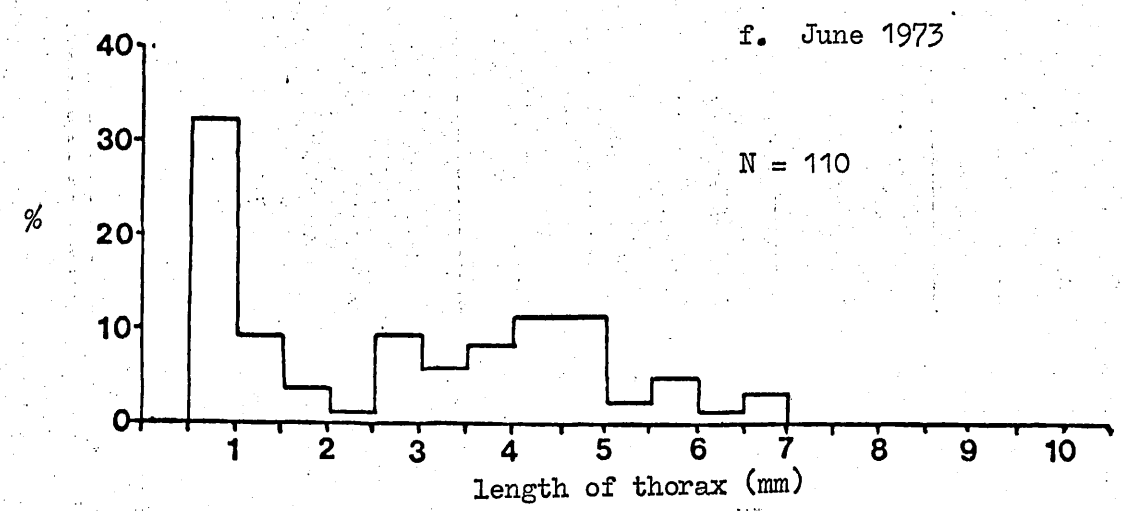
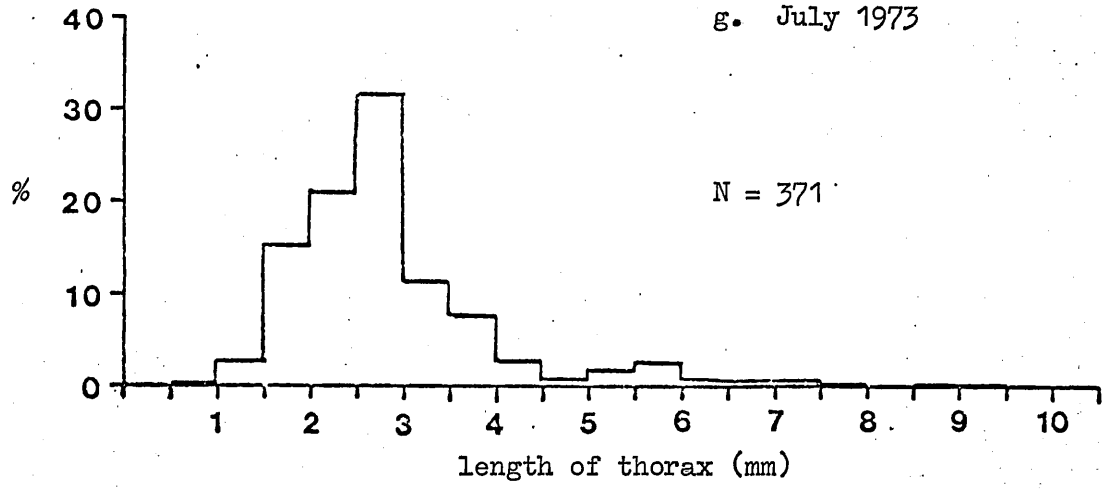
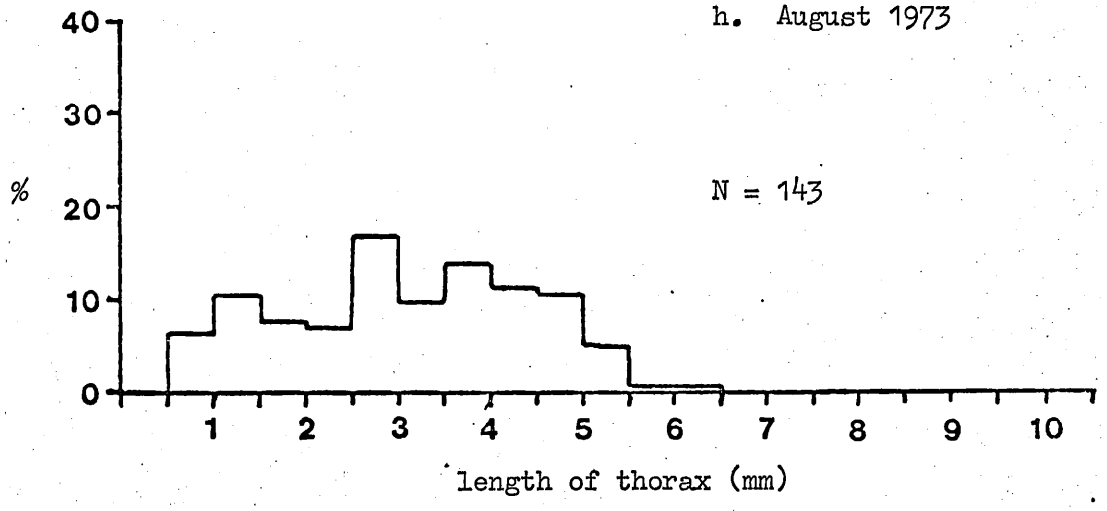

f. June 1973
N = 110
%
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
length of thorax (mm)

FIG. 32 (cont).


g. July 1973
N = 371
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)


h. August 1973
N = 143
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)

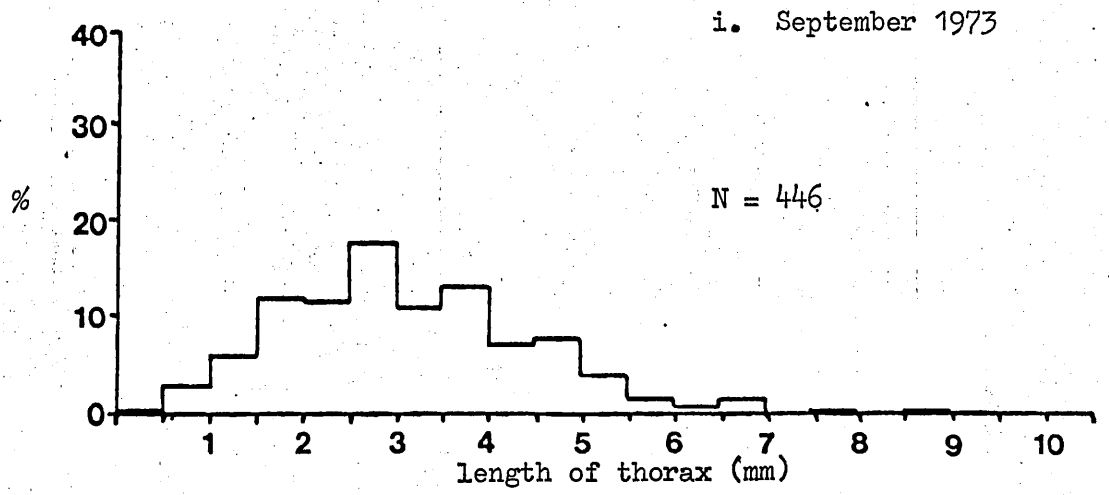
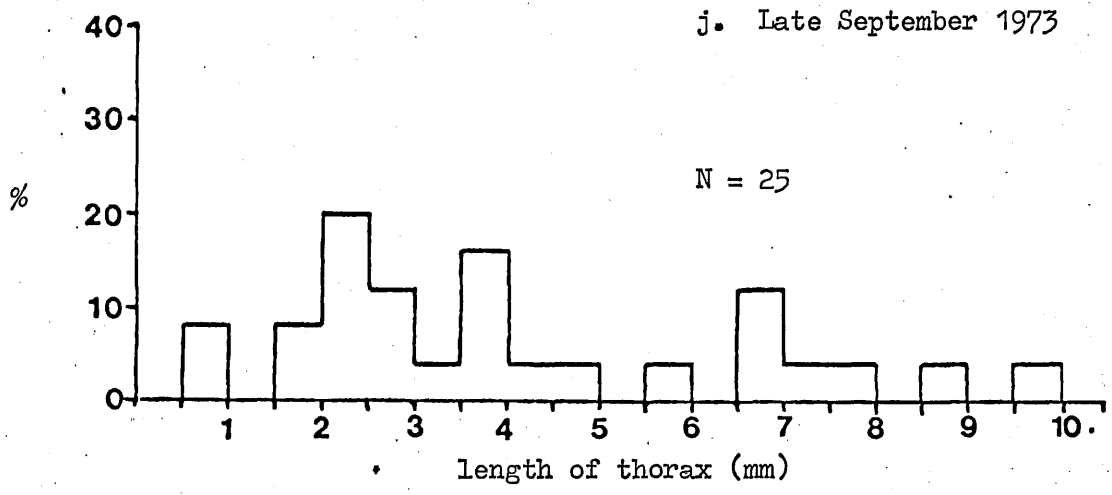
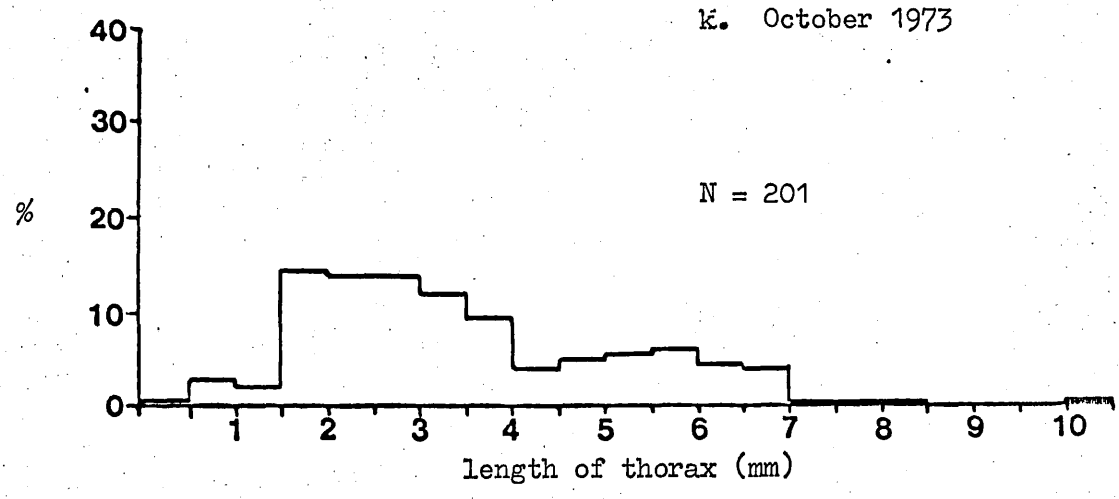

i. September 1973
N = 446
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)

FIG. 32 (cont).


j. Late September 1973
N = 25
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)


k. October 1973
N = 201
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)

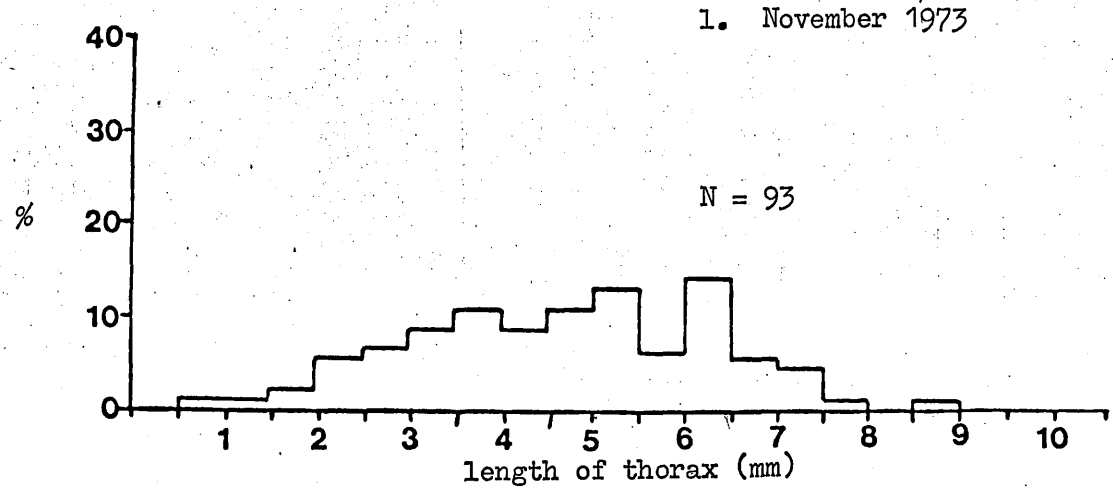
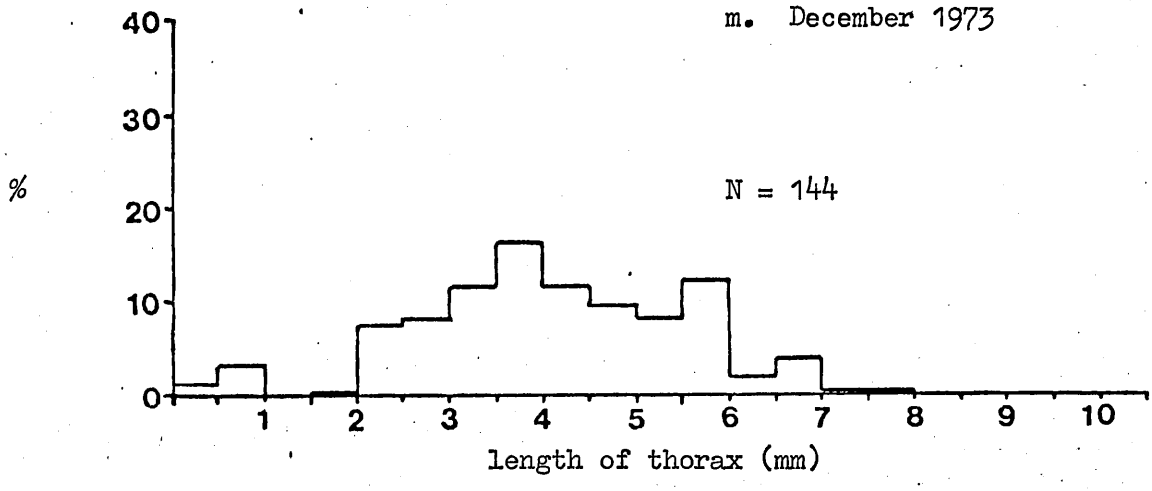
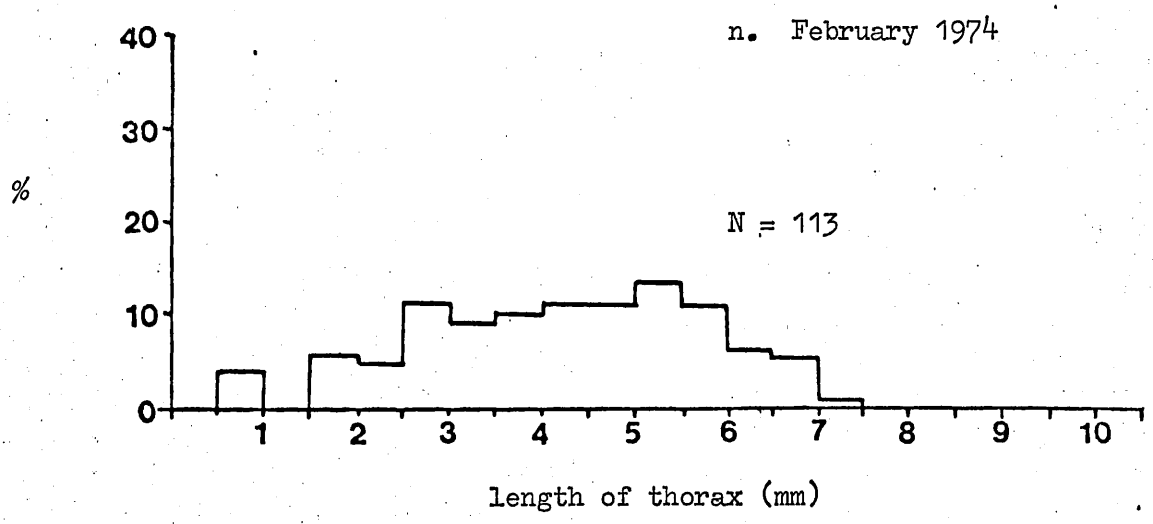

l. November 1973
N = 93
%
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10
length of thorax (mm)

FIG. 32 (cont).


m. December 1973
N = 144
%
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
length of thorax (mm)


n. February 1974
N = 113
%
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
length of thorax (mm)

structure. That there is some co-ordination of reproduction in the Warren Point population of C.capitata is evident by the presence of peaks which can be followed through from month to month. These become less distinct with increasing size because of different growth rates and the loss of a large part of the brood through mortality.

Because breeding can occur over an extended period, it is not possible to age the population by conventional methods. Instead one must relate information on the growth rate of worms with that on the time taken to develop ripe gonads.

3.3.3.2.1 Growth of worms.

By analysing the data graphically (Harding 1949, Cassie 1950), it is possible to break down the size distributions into separate statistical populations. This method enables one to separate different broods and follow their growth from month to month. Because of the effects of continuous breeding the peaks are not very clear in this study and it is sometimes difficult to distinguish different size groups with any reliability. Bearing this in mind, however, it is possible to calculate growth rates for worms of different sizes (see Table 23).

Three populations can be recognised from the January sample and these can all be followed through into February. The smallest size class shows an imcrease of 2.39 mm in total length which gives a growth rate of 28.7 mm per year. The growth rate could not be determined for the second group but the larger,

TABLE 23. Results of graphical analysis of monthly size frequency data.

Month	Mean thoracic length of populations with standard error (mm)				
January	2.4 ± 1.01	6.4 ± 1.9	8.6 ± 1.12		
February	2.79 ± 1.14	6.3 ± 0.9	9.02 ± 0.42		
March	0.51 ± 0.41	2.51 ± 0.18	4.2 ± 0.5	6.57 ± 1.43	
April	1.29 ± 0.43	4.25 ± 0.75	6.48 ± 0.72		
May	0.51 ± 0.11	1.58 ± 0.21	3.09 ± 0.51	4.44 ± 0.16	5.99 ± 0.67
June	0.62 ± 0.82	3.65 ± 0.77	5.38 ± 0.24	6.51 ± 0.18	
July	2.57 ± 0.78	5.4 ± 0.7	+ two larger size classes which cannot be analysed		
August	1.2 ± 0.66	3.41 ± 0.39	+ one larger size class which cannot be analysed		
September	1.68 ± 0.72	2.51 ± 0.4	4.0 ± 1.11	+ one larger size class which cannot be analysed	
late September	2.2 ± 0.39	3.71 ± 0.49	6.6 ± 0.7	+ one larger + one smaller size class which cannot be analysed	
October	1.13 ± 0.31	3.1 ± 0.92	6.2 ± 0.7	+ one larger sample which could not be analysed	
November	3.1 ± 1.06	4.79 ± 0.40	6.09 ± 0.75	+ one larger sample which could not be analysed	
December	0.56 ± 0.24	3.58 ± 1.02	5.7 ± 0.45	6.2 ± 1.12	
February 1974	approx. 0.7 (from histograms)	approx 1.7	2.6 ± 0.27	4.86 ± 1.09	

adult worms showed a growth rate of 19.2 mm per year. Very young worms first appear in March where four size classes are indicated. It is difficult to correlate these with the February peaks but the largest category probably corresponds with the middle one of January and February, indicating a growth rate of 20.4 mm per year. The large worms of the previous months were not present in sufficient quantities for analysis. The smallest worms in the April sample have a mean thoracic length of 1.29 mm. The group is probably made up of young worms spawned at different times over a period of more than one month including those represented in the smallest size group of March. Assuming only these latter worms are present one can calculate a growth rate of 39.6 mm per year for these very small worms. The statistics are rather doubtful however, and this figure is not very reliable. Young worms are still present in May. The smallest worms in the April sample are represented with a mean thoracic length of 1.58 mm. This gives a growth rate of 21.6 mm per year. This figure is probably underestimated due to the effect of continuous spawning on the position of the mean. The group of young adults in the April population (mean thoracic length = 4.25 mm) now has a mean length of 4.44 mm which gives a growth rate of 14.4 mm per year. In June young stages are still present suggesting a continuous spawning throughout the month. Graphical analysis is not possible because of this overlap. There are no young stages in the July sample, the smallest category representing the early stages of the distribution for April. The growth over the three months is 8.1 mm.

Similarly, the May and June young classes can be followed through into August and September showing an increase in total length of 4.0 mm and 6.3 mm respectively. The figures for late September are less clear. The increase in the mean size of the three populations is too great for these to represent the September broods, but the analyses are based on a very small sample number and may be inaccurate. The sample for October shows a brood of young worms with a mean thoracic length of 1.13 mm. Allowing for two weeks development prior to metamorphosis these worms are probably about two months old and represent a spawning in late August or early September. The November sample is difficult to analyse as there are no peaks but graphical analysis suggests three populations. These cannot be correlated with the previous month's sample. In December a few young worms are present indicating the onset of a further breeding period and small-sized worms also occur in the February 1974 sample although there are insufficient data for graphical analysis.

These results illustrate the complex nature of the population dynamics in this species. The presence of young worms in eight months of the year confirms the initial impression that breeding is not restricted to any season. The absence of young stages in the other months does not necessarily indicate that spawning has been interrupted. For example, the small mean thoracic length of worms in August would indicate that young worms should be present in July, but these are not revealed by graphical analysis. Sampling errors of this type

are to be expected with a species showing such a marked aggregation, especially as the larval development may be benthonic.

Despite the problems involved in this analysis it is possible to draw some conclusions. Spawning almost certainly occurs throughout the year and the worms grow from 14 mm to 40 mm per annum according to age. Thus the smallest worms show the fastest growth rate. This appears to level off with increasing age. However, no clear correlation between thoracic length and growth rate was obtained and it is possibly an apparent relationship only, brought about by the method of measuring age. Any growth an animal makes will be expressed in three dimensions but the measurements of length take account of only two. The resulting discrepancies will be greater with increasing size.

Taking a value of 30 mm per year for the growth rate and assuming a two to three week larval development, worms would take about seven months to reach adult size (see section 3.3.3.2.2). Allowing three to four months for development of ripe gametes (see section 3.3.3.2.3) this would enable worms to reproduce in their first year.

3.3.3.2.2 Sex ratio of worms.

Adult worms can be sexed by differences in their external morphology, males having a copulatory apparatus which is absent in the female. Females containing fairly well-developed oocytes can easily be recognised by the white swellings around

the coelomoducts. Because the worms cannot be placed into year categories it is difficult to define the thoracic length at which maturity is attained but the absence of developing gametes in any males smaller than 3.8 mm and any females smaller than 4.2 mm in thoracic length has led to all worms larger than these sizes being taken as adult. In any population there will be some individuals achieving sexual maturity at an earlier age and it is almost certain that many of the worms with a thoracic length of about 4 mm are in fact juveniles.

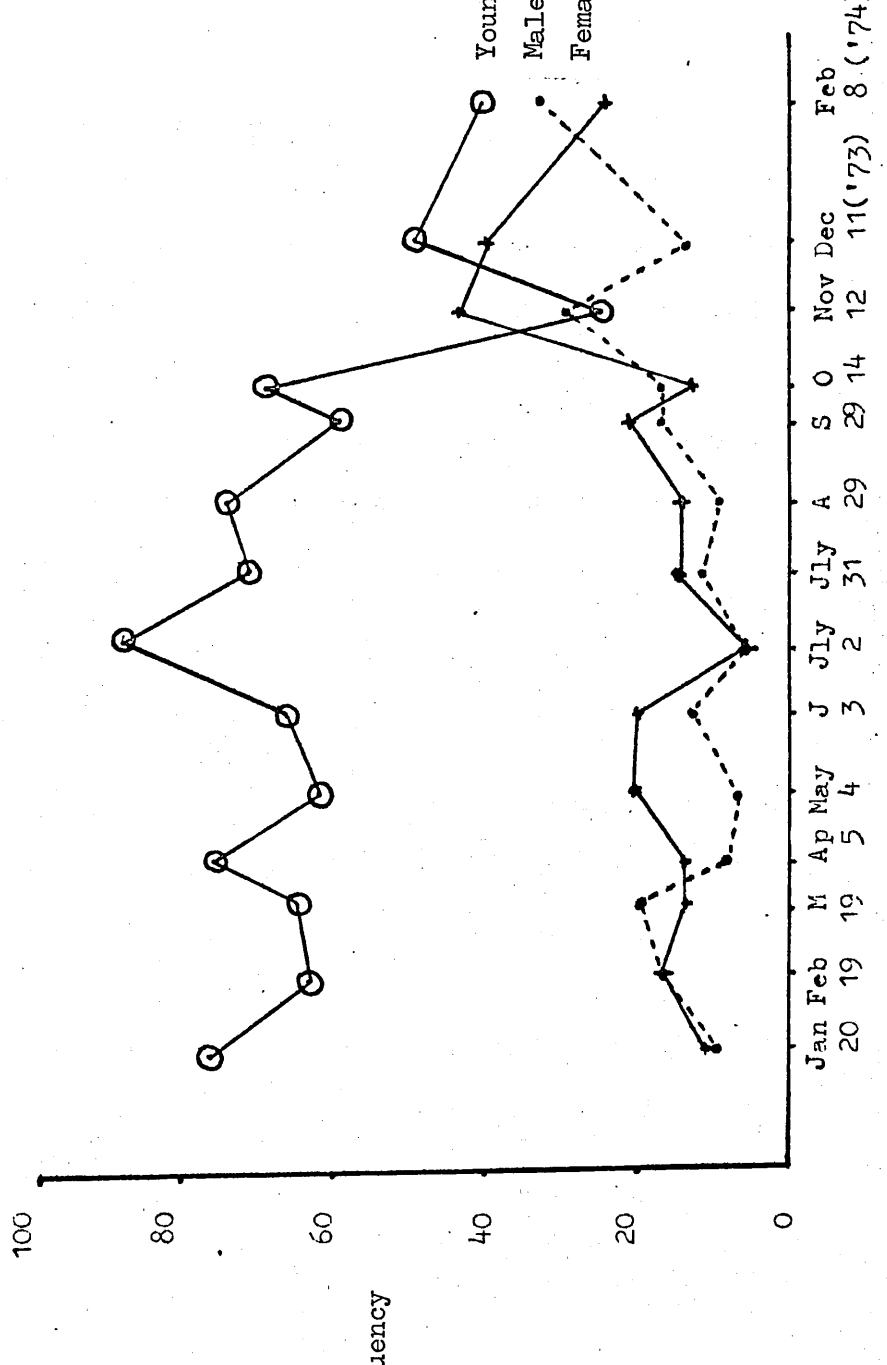
Nevertheless, taking 4 mm as the standard, the worms were divided according to their sex. The results are shown in Fig. 33. It can be seen that the sexes occur in roughly equal proportions except for the samples taken in the winter of 1973/1974 where females outnumber males. There are no obvious reasons for this, the overall sex ratio being 54.55 % females to 46.45 % males. This difference is not significant ($\chi^2 = 1.232$).

3.3.3.2.3 Seasonal variations in the sexual maturity of the population.

Males.

Coelomic samples were taken from suitable preserved worms each month and the fluid scanned for stages of spermatogenesis. Sperm rosettes were present in all the samples examined and the majority of worms also contained ripe sperm and sperm morulae. The more advanced stages of development

FIG. 33 Ratio between the sexes of C.capitata at Warren Point.



were sometimes absent from the smaller worms. The sperm type was that figured by Franzen (1956).

Thus ripe worms were found in samples throughout the year. The percentage of adult males containing ripe sperm in each month is given in Fig. 34a.

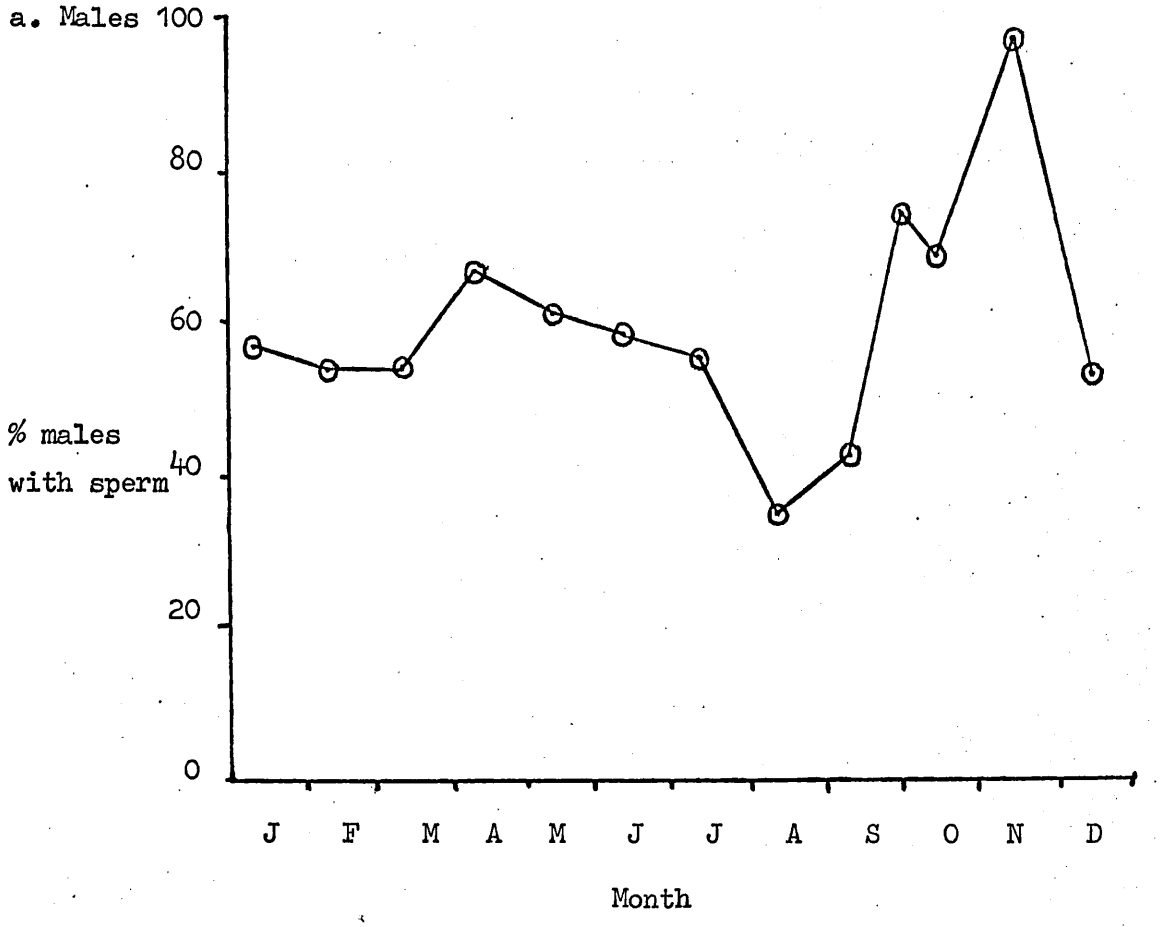
Females.

The oocytes of C.capitata are not released into the coelom until they are almost fully developed. Monthly measurements of oocyte diameters were made and the mean oocyte diameter calculated for each female and for all the females each month. In some females oocytes of very different sizes were encountered in which case the different size categories were treated separately. Similarly oocytes which were free in the coelom were sampled separately from those still attached to the gonad.

The results show that the mean oocyte diameter varies considerably amongst individuals (Fig. 35) but remains fairly constant from month to month (Fig. 36). This is a further aspect of the dynamic stability of this population.

The smallest oocytes which could be detected in the ovary had a diameter of 28 µm. At a diameter of 85 µm the oocytes begin to detach from the gonad and are found free in the coelom. The largest oocytes encountered were 105 µm in diam-

FIG. 34 Seasonal variations in sexually mature worms.



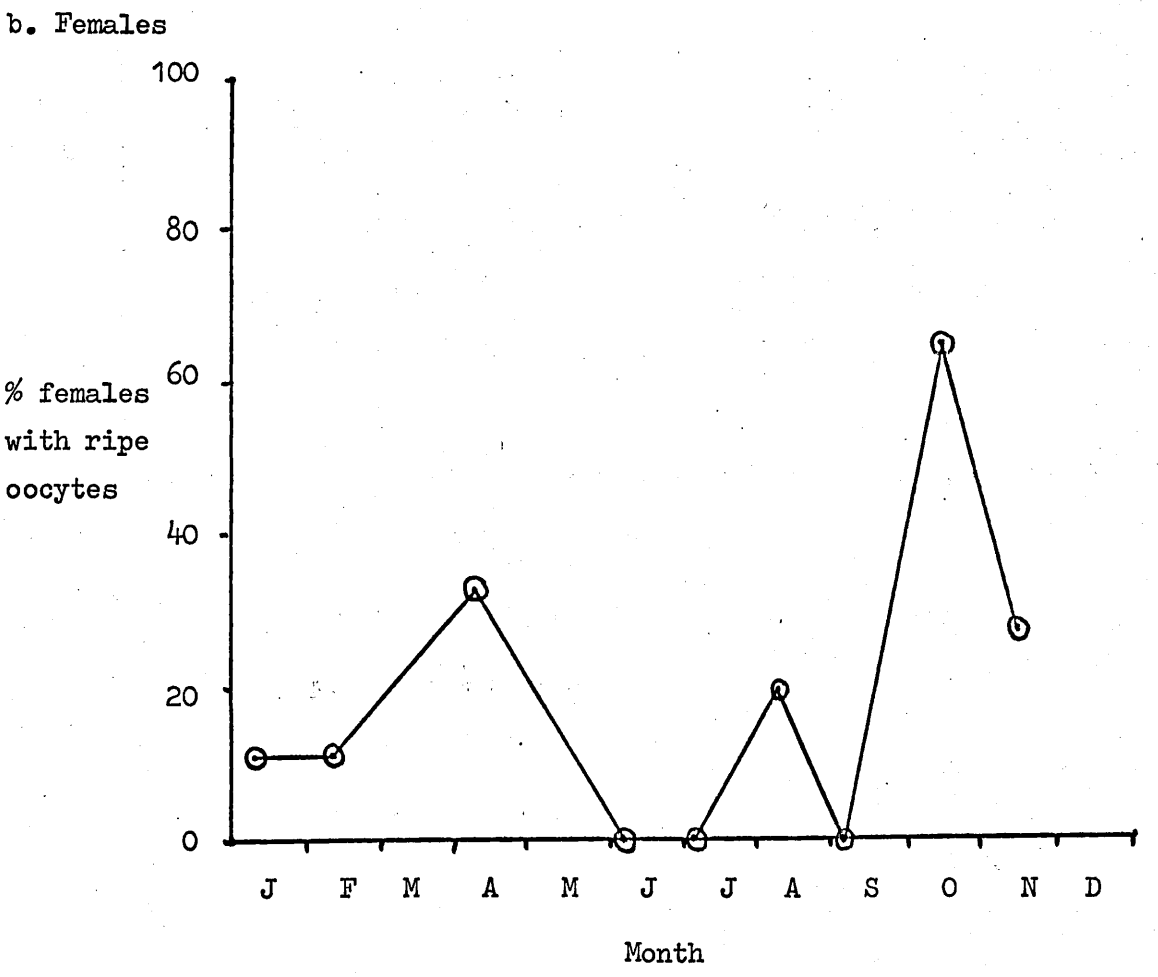


FIG. 35. Variations in mean oocyte diameter in individual females each month.

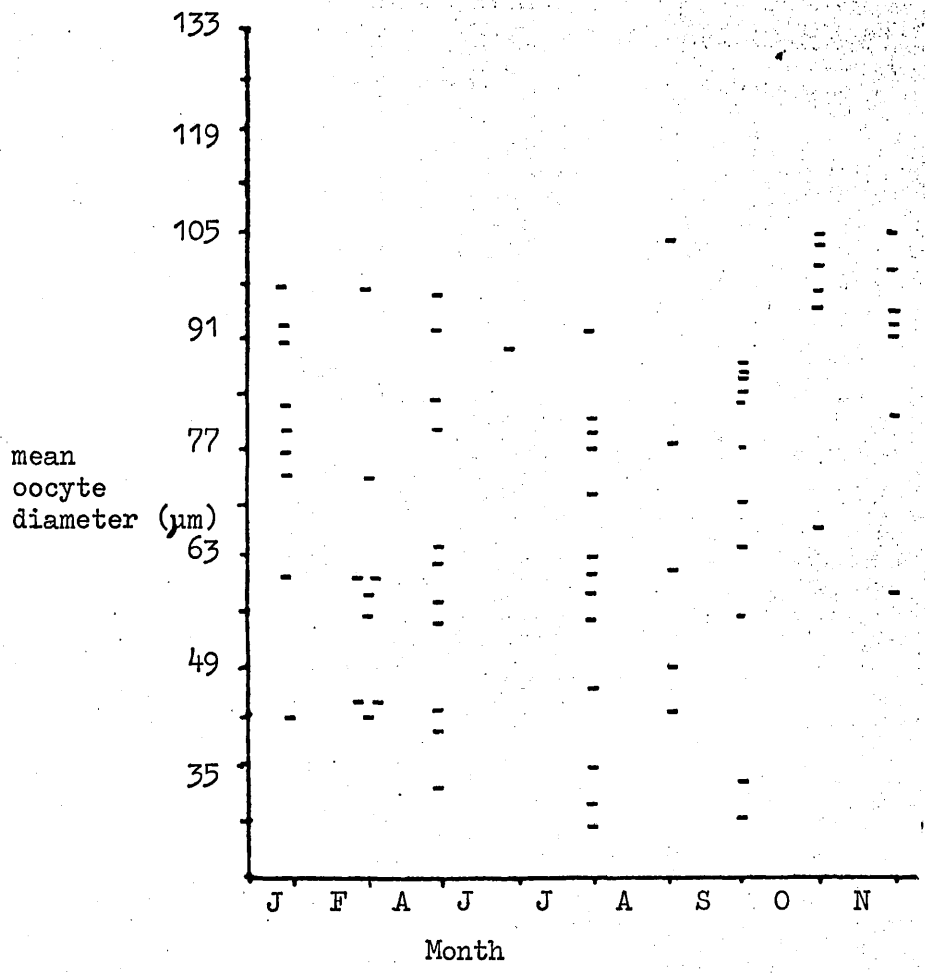
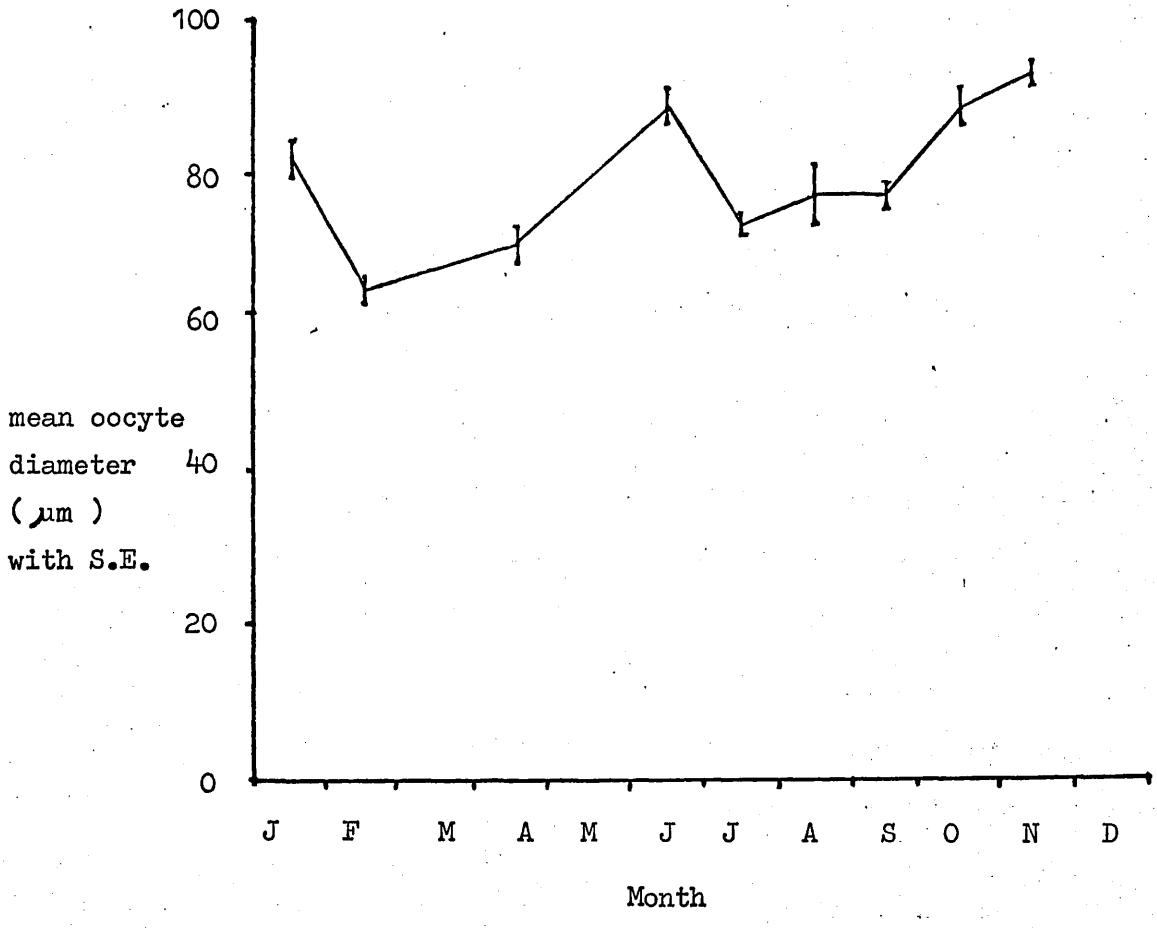


FIG. 36 Seasonal variations in mean oocyte diameter.



eter, but it is known from samples of fertilised eggs taken from the parental tube that some eggs are ripe at 95 µm in diameter. However, most of the fertilised eggs showed a diameter of over 100 µm.

The percentage of females containing ripe oocytes was very low (Fig. 34b) but such females were present throughout the year.

The mean oocyte diameter for each female was plotted against thoracic length in an attempt to deduce the age structure of the female population. The resulting scatter diagram is shown in Fig. 37. The worms were divided into three arbitrary categories according to oocyte diameter and the length frequency distribution of each group analysed graphically to separate populations. The smallest category, consisting of worms with a mean oocyte diameter of less than 45 µm, was not large enough to be analysed and the data were combined with the next class instead. The analysis yielded three statistical populations as shown in Table 24. This suggests that the population at Warren Point is made up of three breeding classes. The difference in absolute length of the worms in each group is about 10 mm. This represents about four months' growth, assuming a 30 mm per annum growth rate. This means that female worms can spawn every four months.

It is known that female worms begin to develop oocytes

FIG. 37 Relationship between the mean oocyte diameter and thoracic length.

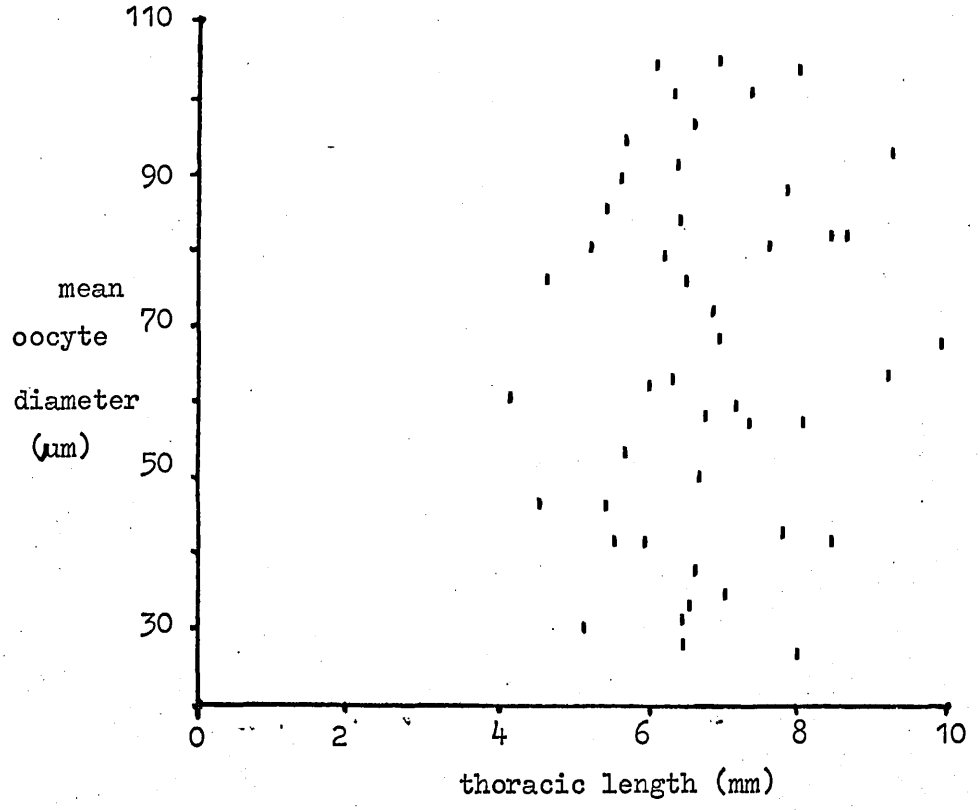


TABLE 24. Results of graphical analyses showing derived breeding classes.

Oocyte diameter (µm)	Mean length of thorax (mm)	Standard deviation	% of population
70	8.40	1.40	20
	6.08	0.61	54
	5.08	0.45	26
45 - 70	8.16	0.82	15
	6.72	0.58	40
	5.04	0.75	45
< 70	8.20	0.90	26
	6.51	0.48	24
	5.24	0.76	50

Mean length of thorax from all populations (mm)	Total length of each population (mm)	Difference (mm)
8.25	48.4	11.3
6.49	37.1	9.0
5.12	28.1	

at about 4 mm thoracic length ; i.e. after about seven or eight months. Assuming that some worms spawn at 6 mm thoracic length, worms are about a year old when they first spawn. This implies that, even if they survive to spawn a second and third time, very few worms survive a second year.

3.3.3.2.4 Female fecundity.

The number of eggs produced by a female is related to age. Ovaries begin in the first abdominal segment and continue nearly to the end of the body. Only the thinner, newly added segments near the pygidium show no sign of gamete production. The number of oocytes per ovary was fairly constant with no marked increase in older worms. Estimates of the total number of eggs produced range from 10,000 in young females to 14,400 in older worms and these figures compare well with the counts of fertilised eggs in the female's tube after spawning. Thus most of the eggs are released at a single spawning and any remaining are presumably resorbed. The presence of different size categories of eggs suggests that the production of a new series of oocytes is started prior to spawning, although the oocytes remain too small to be easily sorted for several weeks.

3.3.3.2.5 Occurrence of larvae.

Females with fertilised eggs in their tubes were found in all the samples except those taken in January and November. Examination of these showed that in most instances the larvae were several days old, so that it is unlikely that spawning

is induced by the collection itself. In a few cases the larvae in the tubes were very well-developed with no signs of ciliary rings. The growth rate of the larvae was studied under various conditions in the laboratory and this aspect is discussed more fully in section 4.2.2. However, the presence of larvae almost ready to metamorphose and yet still in the parental tube indicates that these worms may be undergoing a purely benthonic development.

Plankton sweeps yielded larval C.capitata on five occasions (February, May, September , October and February 1974) from samples of interstitial water, but the species was never collected in the offshore samples. This could possibly be due to insufficient sampling of the latter.

3.3.3.3 Population density.

Because of the heterogeneity of the substrate and the patchiness of the distribution in this species it is not possible to give an accurate estimate of the population density at Warren Point. Many samples would be needed for this and the labour involved did not seem worthwhile. However, a very rough estimate can be made from the monthly cores which show a mean density of 26,459 m^{-2} with a maximum possible value of 78,424 m^{-2}.

3.3.3.4 Discussion.

The results show that the Warren Point population of C.capitata is able to breed throughout the year and that there is very little synchronisation of reproduction between females. Previous workers have also found an extensive breeding season. Thus Eisig (1887) collected sexually mature worms from November to May in Naples. Bhaud (1967) found capitellid larvae in the plankton from January to March, June and July and October to December in the Mediterranean, and from February to April, June to August and October and November in the Oresund (Denmark) and classified the family as eurythermal with temperate affinities. Casanova (1953) found C.capitata larvae throughout the year in the Mediterranean, although Guerin (1973) discovered that they were virtually absent from the Marseilles region in the summer months. Rasmussen (1956) collected ripe females from the Isefjord (Denmark) in April and May, and October and November but his sample was very small and he considered it possible that reproduction occurred in the intervening summer months as well. Smidt (1951) found larval C.capitata in plankton samples from the Danish Waddensea in June, and from August to November.with the largest numbers occurring in early autumn. Thorson (1946) found the larvae throughout the year in the Oresund and concluded that the extensive breeding period was related to varying temperature maxima at different localities. Reish (1961) also found that C. capitata larvae settled throughout the year in Californian

waters.

It is unusual for polychaetes which spawn large numbers of gametes to have an extended breeding season although this occurs in some serpulids (Knight-Jones 1951, Rothlisberg 1974) which release only small numbers of eggs at a time. Olive (1970) found an almost completely asynchronous extended breeding season in Cirratulus cirratus, but here individual females spawned approximately yearly. Arenicola ecaudata also breeds throughout the year, although there are two peaks of spawning activity (Southward and Southward 1958).

When food is always available, as is undoubtedly the case at Warren Point, asynchronous reproduction allows the species to exploit the resources to the full, without placing too heavy a demand on food supplies at any one time.

For such behaviour to be successful, however, the species must be capable of reproducing at the extremes of temperature to which it is exposed. A continuous temperature record of the substrate at Warren Point was not made but monthly readings do not show a particularly wide range (5°C - 14°C). C.capitata is essentially a temperate and high latitude species and it is unlikely that a temperature of 5°C would adversely affect reproduction, although growth is presumably reduced according to van't Hoff's generalisation. It must be remembered, however, that the winters of 1972/3 and 1973/4 were very mild and the effects of a severe winter (such as that of 1962/3) might be detrimental. Temperature tolerance experiments

(section 4.2.1) show that the species can survive a temperature of 4°C for several days, but no test of reproductive ability under these conditions was made. However, Grassle and Grassle (1974) found that the species reproduced throughout the year at Buzzard's Bay, Massachusetts where the temperature ranged from -0.5°C to 27°C (Driscoll 1972). Temperature tolerance experiments involving higher temperatures showed that the species was fairly sensitive and this may explain the lack of reproductive individuals in the summer months at Naples. The lethal temperature of 31.5°C is well above the highest temperature experienced at Warren Point.

The number of eggs produced at each spawning is usually related to the consequent fate of the larvae. The development of C.capitata has been described in detail (Claparède and Mecznikow 1869, Eisig 1887,1889, Leschke 1903 and Hofker 1930) and it is known to produce a yolky egg undergoing ten to fourteen days development in the maternal tube and a further seven days as a lecithotrophic pelagic larva. The size of the eggs is related to the yolk content and as a general rule large eggs are smaller in number than those with less yolk, although there is considerable variation on this point. Unfortunately there is little detailed information available on this relationship in C.capitata. Eisig (1887) measured ripe oocytes at just under 300 µm in diameter compared with 100 µm in the present study. Rasmussen (1956) found that larval C.capitata were about 400 - 500 µm in length. There

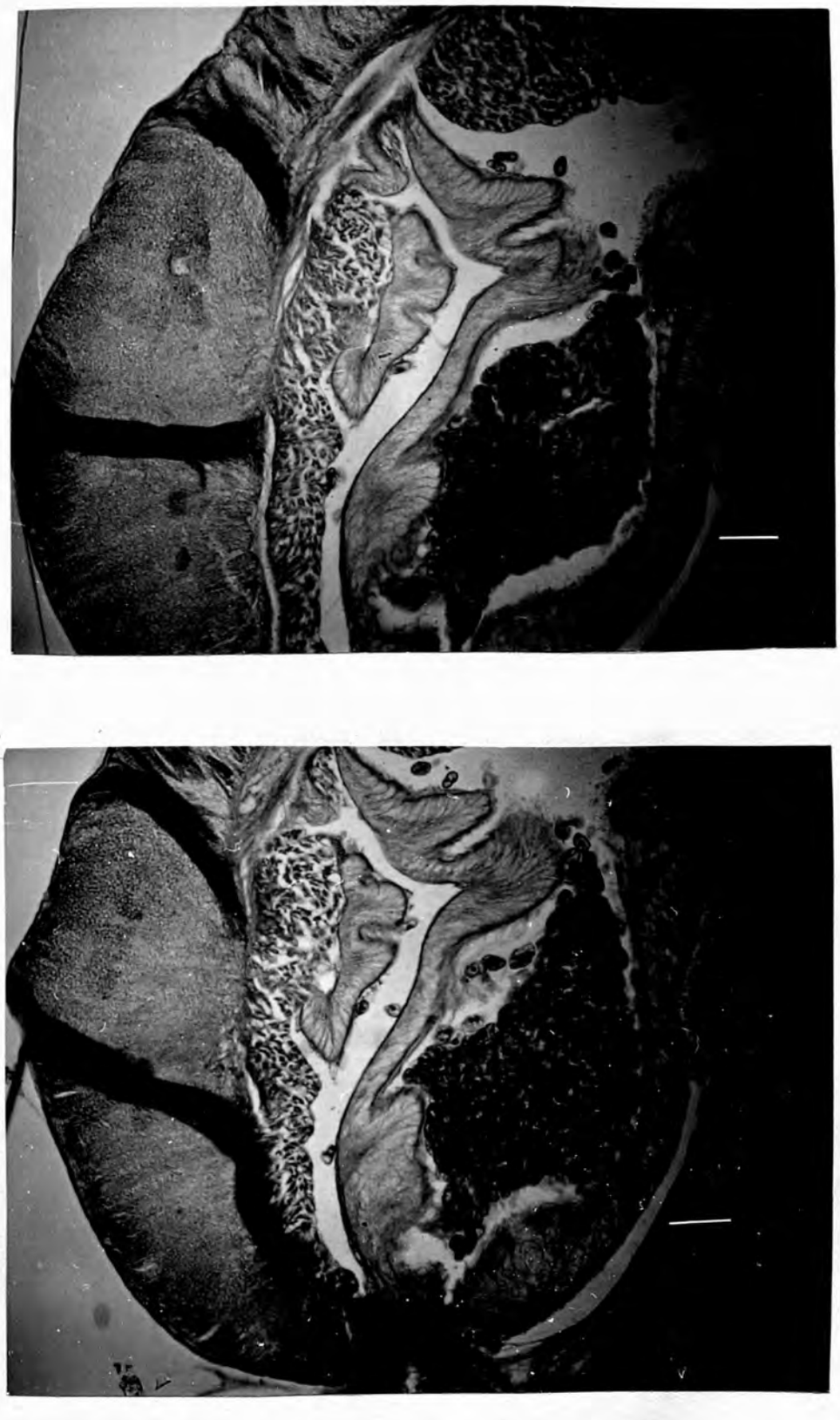
are some data available on the number of eggs produced. Reish (unpublished) computes that laboratory-cultured females of Californian stock lay 150 - 250 eggs and Bellan et al. (1972) calculated the mean number of eggs per female as 285 for a population from Banyuls-sur-Mer, France. Muus (1967) found about 130 eggs in each female tube. It is important to consider the size of the worms when interpreting these data. Reish's population and the one from the south of France were both very small in size, with adult worms of about 10 mm (personal communication with Drs. Reish and Bellan) and Muus (1967) reported that most of the animals in his study were less than 12 mm in length. Grassle and Grassle (1974) found from 40 - 500 eggs in females and showed a positive correlation between egg number and the length of the worm. The population in the present study seems to be at the extreme of the egg size/number relationship as it produces a large number of small eggs. A similar condition is indicated for C.hermaphrodita (Boletzky and Dohle 1967).

Larval protection in polychaetes may have several functions. In C.capitata the tube obviously affords protection from predators for the early stages of development and also maintains the larvae under optimum conditions. The protective advantages are to some extent nullified by the disadvantage of having all the larvae together. This may, however, have an effect on the dispersal of the larvae. By keeping them together for the first two weeks the larvae are to some extent kept in the favourable adult habitat. This effect would be

extended even further by cutting out the planktonic stage completely. Rasmussen (1956) first found evidence of this in females he collected from the Isefjord. He found that the larvae grew up to 1200 µm in the tube and when removed from it showed no planktonic attributes but crawled across the bottom of the collecting vessel. Muus (1967) also found larvae of over 1000 µm in their parental cases in Danish waters. Grassle and Grassle (1974) found a similar condition in Massachusetts and completely benthic larvae have been found in the present study. This means that the eggs must be provided with sufficient food material to complete development and one would expect to find a reduction in egg number, although this is not the case here.

Brood protection necessitates some modifications in the method of fertilisation. C.capitata is believed to have internal fertilisation but copulation has never been observed. However, the modified genital structures would suggest that copulation does occur and there is some evidence to suggest that fertilisation is internal. The spermatozoon has been described by Franzen (1956) and shows modifications in the middle piece which has many mitochondria. This is typical of those species in which the female stores sperm. Eisig (1887) found sperm in young females, and although this might indicate hermaphroditism, it is simpler to propose sperm storage. Sexually mature females develop pads around the coelomoducts (Fig. 38) at certain times and these are believed to play a part in copulation. The swollen cells

FIG. 38. Capitella capitata, Plymouth. Photomicrographs of female coelomoduct. Scale represents 100 µm.



regress as the oocytes increase in size. It seems likely, therefore, that copulation occurs before maturation of the oocytes. The site of sperm storage was not located but Eisig (1887) described spermatophores.

The time taken to complete the life cycle is also relatively short when compared to other polychaete species. Thus a Northumberland population of Melinna cristata first breeds when it is two years old and then at yearly intervals (Hutchings 1973) and Cirratulus cirratus breeds at intervals in excess of one year (Olive 1970). The time taken to develop ripe gametes in C.capitata is reckoned at four months in the present study but this is itself high when compared with times given by previous workers. For example Reish and Barnard (1960) estimate a 30 - 60 day life cycle and Grassle and Grassle (1974) suggest 30 - 40 days.

The reproductive biology of C.capitata reflects its opportunistic nature. Its extended breeding period allows it to exploit food resources throughout the year and by brooding the larvae dispersal is minimised. The population is further built up by its short reproductive cycle which enables a female to reproduce several times each year.

4. LABORATORY EXPERIMENTS.

4.1 Digestion of food.

A knowledge of the digestive processes in C.capitata was necessary for the recognition of assimilable organic matter in the substrate. The digestive region of the gut was recognised and analysed for enzymes as described below. Worms collected from Warren Point were used in every case.

4.1.1 Morphology and histology of the gut.

4.1.1.1 Methods.

The morphology of the gut was investigated by the dissection of fresh and preserved material. Worms were relaxed prior to dissection or fixation with a saturated solution of magnesium chloride diluted to 50 % with seawater.

The histology of the different regions of the gut was studied by taking serial sections. Four adult worms were kept in mud under laboratory conditions for two weeks before experimentation. They were then transferred to clean dishes of filtered seawater for 24 hours in order to remove sand particles from the gut. The worms were fixed in Bouin's fixative and after embedding in paraffin wax 7 µm serial sections were cut from three of the worms. The fourth specimen was sectioned longitudinally. Selected transverse sections were stained with Ehrlich's haemat-

oxylin and eosin, Mallory's triple stain, Heidenhain's iron haematoxylin or toluidine blue. The longitudinal sections were stained with Mallory's stain.

Worms which were heavily infected with the intestinal parasite Ancora sagittata (Cecconi 1905, Ganapati 1946) were not used in this study.

4.1.1.2 Results.

The gut was found to consist of four regions: - buccal cavity, eversible proboscis, oesophagus and intestine. The muscles of the proboscis apparatus hold the expanded pharynx firmly in place. This latter region apart, the oesophagus is about half as wide as the intestine, and it is confined to the thorax. The first abdominal segment marks the start of the intestine which continues straight to the anus. It can be divided into regions from histological evidence. Accompanying the intestine for most of its length is an intestinal siphon which joins at the junction of the thorax and abdomen and merges with the gut again towards the anus. This accessory canal is present in several, possibly all, capitellids, and is believed to function as a pump drawing water into the body for respiratory purposes (Eisig 1887).

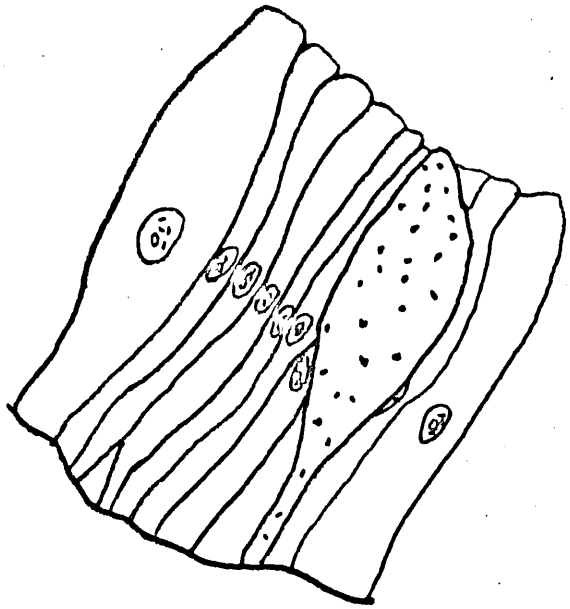
Histologically the buccal cavity appears to be similar to the oesophagus with many mucous cells in both regions. Cilia are present in the buccal cavity but are absent from the phar-

yngeal region which is very muscular, having the apparatus for the eversion of the proboscis. Glandular cells are common in both regions. Michel (1967) has studied the proboscis of Notomastus latericeus in detail and suggests that the glandular secretion, which is composed of complex acid mucopolysaccarides and lipids, may play a role in protecting the epithelial surface.

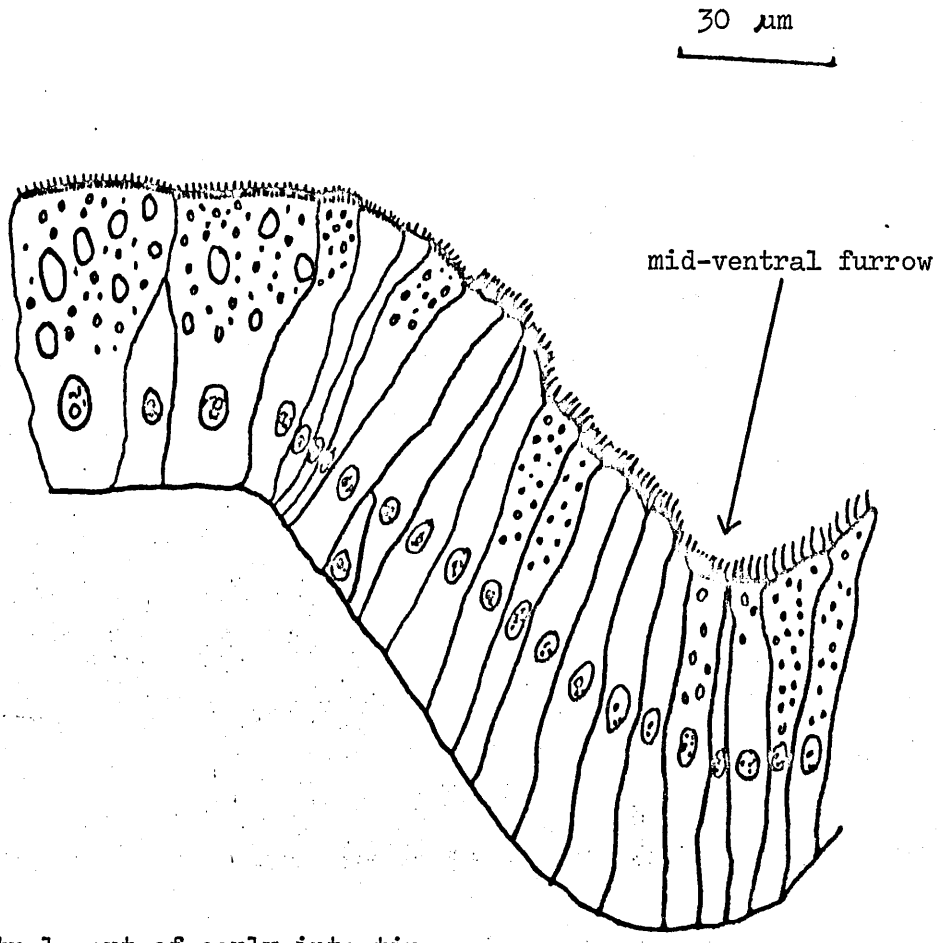
The intestine can be divided into several regions according to the cell types present. Fischer (1884) gave a brief account of the gut in C.capitata and in 1887 Eisig described the histology of the intestine, although Brasil (1904) questioned his results. The first part of the intestine is fairly muscular and there is no sign of a ventral gutter. The principal cell type is a tall columnar cell with a granular nucleus and clear cytoplasm which appears pale blue in Mallory's stain. The nucleus contains dark blue granules and an orange nucleolus. In iron haematoxylin the cells are dark and the granular nucleus has a black nucleolus. Globular shaped cells are also present in small numbers. These stain very faintly in Mallory's and have blue cytoplasmic granules. Staining with iron haematoxylin results in a darker cytoplasm. A nucleus cannot be detected. These cell types are illustrated in Fig. 39a.

A mid-ventral furrow first appears at the beginning of the intestine. Its cells are distinguished from others in the same region by the presence of very long cilia. Various states of

FIG. 39 The histology of the intestine in C.capitata.



a. TS Beginning of intestine



b. TS Ventral part of early intestine

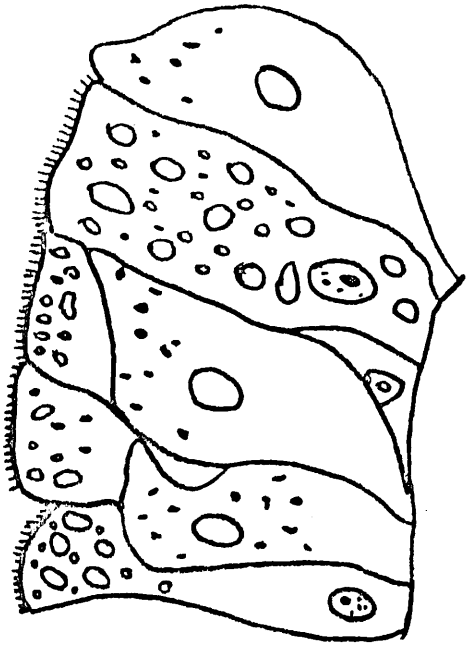
vacuolation occur (Fig. 39b). The columnar cells found in the first part of the intestine also occur in this region but here they contain vacuoles distally which stain orange in Mallory's stain. In addition the cells often have a swollen tip. In some sections this type is almost completely replaced by a similar one which differs only in degree in that it is packed with vacuoles and is very swollen. The nucleus is very granular with a large nucleolus.

A third cell type was encountered occasionally, usually in groups. In iron haematoxylin it shows a very heavily stained cytoplasm and dark granules are sometimes present distally. The nucleus does not take up the stain. (Fig. 39c).

The cell types found in this region would seem to indicate a high degree of secretion. This condition is also found in the next part of the intestine which is wider and rather folded. The extent of secretion varies from section to section but the basic columnar cell is still predominant with or without vacuoles. The very heavily vacuolated cells usually occur in groups. A new cell type is found in this region, being rounded or claviform in shape with clear cytoplasm and a strongly eosinophil nucleus. Cilia are absent (Fig. 39d).

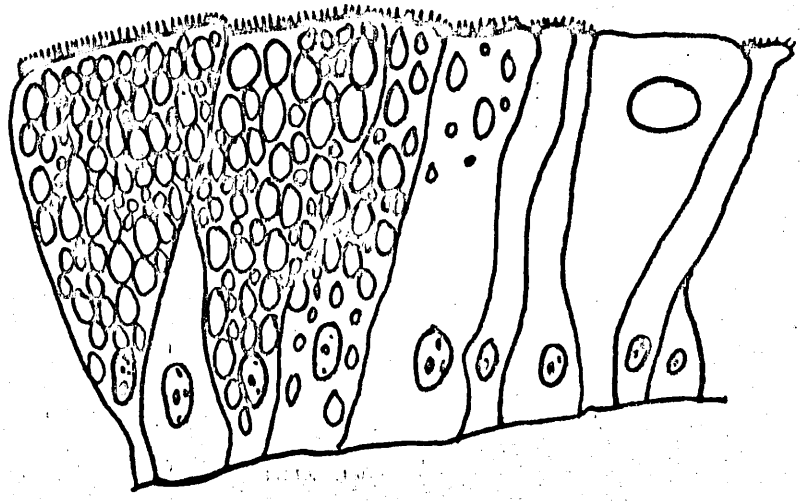
Towards the rear of the intestine vacuolated cells become less common and secretory granules are absent. The cells gradually become shorter towards the rectum which is characterised

FIG. 39 cont.



c. TS Fore intestine to show heavily staining granular cells

35 µm



d. TS Mid-intestine

by the presence of a cuticle. Glandular cells are common and the tract is ciliated.

The function of the various parts of the gut can be interpreted from this histological evidence. The presence of a large number of mucous cells in the oesophagus would suggest a transport function for this region. Digestion would seem to begin in the intestine as secretory cells occur in the largest numbers in the fore-intestine. The presence of a brush border in the latter portions of the intestine would indicate absorption.

The variations in level of secretion may be related to the timing of the last food intake and the passage of this material through the gut (Marsden 1963a). The ciliated ventral furrow almost certainly has a transport function. Dales (1955) postulates that in terebellids it serves to rapidly remove indigestible material from the region of absorption. The ventral furrow at the extreme end of the gut is believed to be related to the intestinal siphon and here the cilia control the flow of water rather than solid particles.

From this study it can be concluded that digestive enzymes are likely to be found in the fore-intestine and this information was used in analysing the enzymes as described in the following section.

4.1.2 The presence of digestive enzymes.

4.1.2.1 Methods.

Twenty five large specimens were used in these analyses. These had been kept in mud under circulation up to the time of experimentation to ensure a high level of digestive enzymes (Marsden 1963b). Each worm was anaesthetised by the dropwise addition of 70 % alcohol to the seawater and the intestine was removed by dissection. It was immediately transferred to chilled seawater and the approximate wet weight of all the intestines measured. The material was then ground in a tissue homogeniser with about 1 ml seawater (approximately 10 % w /v). Because of the small quantities involved the extract was not purified. A few drops of the extract were used in the following enzyme tests. Each test was repeated once and controls set up with boiled extract.

α amylase..

Five drops of extract were added to 1 ml of starch solution in a test tube and incubated at 25°C. A drop of the solution was tested for the presence of starch with iodine twice daily.

Invertase.

Five drops of extract were added to 1 ml of sucrose solution and incubated at 25°C. Five drops were removed twice daily and tested with Fehling's solution for the presence of reducing sugars.

Lipase.

One ml of olive oil was mixed thoroughly with five drops of sodium tauroglycocholate and an equal volume of distilled water added. Five drops of phenol red were added with enough 0.05N sodium carbonate to turn the solution pink. Five drops of extract were added to this solution and the tube incubated at 25°C. The colour of the solution was examined twice daily.

Protease.

Five drops of extract were placed in a watch glass and a few grains of stained fibrin added. The watch glass was covered and incubated at 25°C and inspected twice daily for signs of change.

Cellulase.

Two methods were used to test for the presence of this enzyme. Cellulase hydrolyses cellulose to glucose which is a reducing sugar. Five drops of extract were added to a solution of sodium carboxymethylcellulose and incubated at 25°C. A few drops were removed twice daily and tested with Fehling's solutions.

Bacteria do not hydrolyse cellulose to glucose but instead break it down to methane and hydrogen with several organic acids. The presence of symbiotically produced cellulases was tested for by incubating five drops of the extract with sodium carboxymethylcellulose to which phenol red and sodium carbonate had been added as for the lipase test. The solution was examined for signs of a colour change indicating increased activity twice daily.

The pH of the extract was measured using commercial pH papers.

4.1.2.2 Results.

Amylase, invertase, protease and lipase were all positively identified in the extract. The results of the tests are shown in Table 25. Cellulase activity was not detected in either of the tests and it is assumed that this enzyme is not available to C.capitata. The results of the control experiments were all negative.

The pH of the extract was 7.6. This is of questionable reliability however as the extract had not been purified.

4.2 The effect of external factors on the growth and survival of larval and adult C.capitata.

4.2.1 Temperature tolerance levels in C.capitata.

4.2.1.1 Methods.

Worms were collected from Warren Point and kept in artificial seawater (Instant Ocean) at 10°C for ten days before the experiments.

Ten adult worms were used in each experiment. The worms were placed in a beaker of artificial seawater and heated in a water bath at a rate of 1°C every five minutes. Above 28°C the beakers were removed at 1°C intervals and the water allowed to return to

TABLE 25. Digestive enzymes in C.capitata.

Enzyme	Results of test	Time taken for positive result
Amylase	Brown colour with iodine indicating absence of starch.	48 hours
Invertase	Red precipitate indicating presence of reducing sugars	42 hours
Lipase	Pink → yellow colour change indicating increased acidity	24 hours
Protease	Rounded edges to fibrin particles	18 hours
Cellulase	No precipitate with Fehling's No colour change with phenol red	-

room temperature (19°C). The activity of the worms was tested by prodding with a blunt seeker and the percentage alive after 24 hours was calculated. Each experiment was repeated once. A control experiment was maintained at 10°C.

Larval C.capitata were removed from the maternal tube and tested as above. The criterion for death was taken as the cessation of all ciliary movement in the larvae when observed under the microscope.

Tolerance of low temperature conditions was investigated in a similar manner. Worms were placed in beakers of seawater and placed in an incubator at 4°C. Worms were removed from the incubator when they had reached this temperature and the percentage survival value after 24 hours calculated as for the higher temperatures. The temperature of the incubator was then lowered at a rate of 1°C every ten minutes and worms removed at 1°C and -1°C.

4.2.1.2 Results.

The percentage mortality of adult and larval worms is shown in Table 26. All the worms showed increased activity with increasing temperature. At 31 - 32°C.the worms developed lesions along their length which sometimes resulted in the loss of a large quantity of coelomic fluid. Despite this most worms were still moving at 33°C although activity did decrease at 34°C. After 24 hours, however, these worms were all dead and the rupture of the body wall was taken to signify death as no worm survived this.

TABLE 26. The % mortality of adult and larval C.capitata subjected to high temperatures.

Temperature (°C)	% mortality of adults		% mortality of larvae	
	1st trial	2nd trial	1st trial	2nd trial
28	0	0	0	0
29	0	0	0	0
30	0	10	0	0
31	10	20	0	0
32	90	80	80	100
33	100	100	100	100
34	100	100	100	100
control (10)	0	0	10	0

TABLE 27. The % mortality of adult and larval C.capitata over a narrow range of high temperatures.

Temperature (°C)	% mortality of adults		% mortality of larvae	
	1st trial	2nd trial	1st trial	2nd trial
30.0	0	0	0	0
30.5	0	20	0	0
31.0	50	20	0	0
31.5	50	50	20	30
32.0	80	90	90	100
32.5	80	100	90	100
33.0	80	100	100	100
33.5	100	100	100	100
34.0	100	100	100	100

To analyse the lethal temperature more precisely the experiment was repeated over the 30 - 34°C range with 1°C increases every five minutes. The results are given in Table 27.

The upper lethal temperature was taken as that at which 50 % mortality occurred. For adult worms it is 31.5°C and for larval C.capitata something slightly above this. The larvae differ from the adults in the restricted range of lethal temperatures. This probably reflects the similarity between the animals, which were all from the same brood. The adults, on the other hand, were of different sexes and of different sizes. A closer interpretation of the results showed that females containing ripe oocytes succumbed at a lower temperature than other worms. Insufficient numbers prevented a closer examination of this feature.

Both adults and larvae were very tolerant of low temperatures, the results of the experiments being given in Table 28.

These experiments indicate that larval C.capitata are more tolerant of temperature extremes than the adults. Previous workers (e.g. George 1964b and Kinne 1970) have recorded similar results. The physiological basis of this increased resistance is not clearly understood but there are obvious advantages in producing an adaptable larval stage since the species is at its most vulnerable during the period of dispersal.

TABLE 28. The % mortality of adult and larval C.capitata subjected to extreme low temperatures.

Temperature (°C)	% mortality of adults		% mortality of larvae	
	1st trial	2nd trial	1st trial	2nd trial
4	0	0	0	0
1	20	30	10	20
-1	50	60	30	40

4.2.2 The effect of temperature on the growth of larval *C.capitata*.

4.2.2.1 Methods.

It was not possible to induce spawning in the laboratory. Various external stimuli are known to bring about the onset of spawning behaviour in certain polychaetes but these had no effect on *C.capitata*, possibly because internal fertilisation makes synchronised spawning unnecessary.

Because of this inability to induce spawning, and a similar failure to raise larvae from artificial fertilisations it was not possible to determine precisely the age of larvae used in these experiments, nor to follow the complete development through.

Instead, larval *C.capitata* were removed from the tube of a female worm collected from Warren Point which had recently spawned. About 200 larvae were used in each experiment. The larvae were pipetted into clean dishes containing aerated filtered seawater at 10°C. The dishes were kept in the dark at 10, 15 and 20°C and the length of ten randomly selected larvae measured using a calibrated eyepiece at regular intervals. The larvae were not returned to the experimental vessel after measuring. Each trial was repeated once.

4.2.2.2 Results.

The mean lengths of the larvae at different temperatures are shown in Fig. 40. The untreated data are presented in Appendix 5.

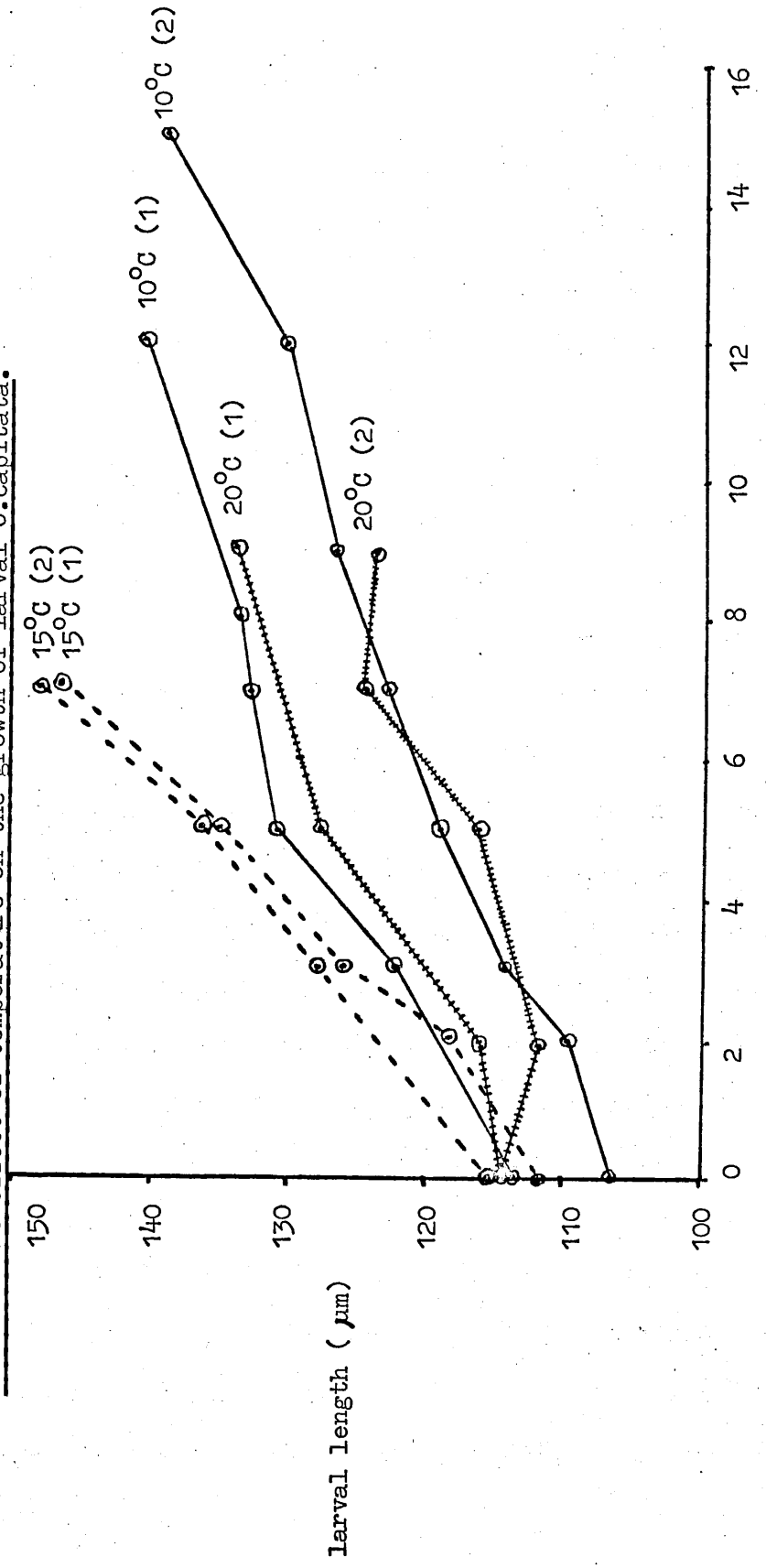


FIG. 40 The effect of temperature on the growth of larval C.capitata.

With the exception of the second trial at 10°C all the larvae were from the same worm. By extrapolation from Fig. 40 it is estimated that the larvae were between four and five days old at the start of the experiment, assuming that the eggs are about 95 µm in diameter when fertilised and that the growth rate is constant. The larvae used for the second 10°C trial were taken from a different female and their smaller size suggests that they were about one day younger than the other larvae.

The results show that the optimum temperature for growth is in the region of 15°C. Below this temperature growth was slower and at 20°C the rate of growth approximated that at 10°C. At this higher temperature, however, growth was more erratic and there was a higher mortality rate. After ten days no larvae were left alive. The larval survival is possibly related to the presence of ciliates in the experimental medium which reached very high numbers in the 20°C experiments, although Åkesson (1967) believes that a ciliate culture may have advantages in the rearing of polychaetes as the protozoans kill and digest subvital larvae, bacteria and waste products in the culture vessels. In any event larval C.capitata can certainly tolerate temperatures above 20°C and mortality cannot be due to this factor alone.

A complete temperature record of the substrate at Warren Point was not made but monthly readings coupled with data on the sea temperature in Plymouth Sound (Cooper 1958, Southward and Butler

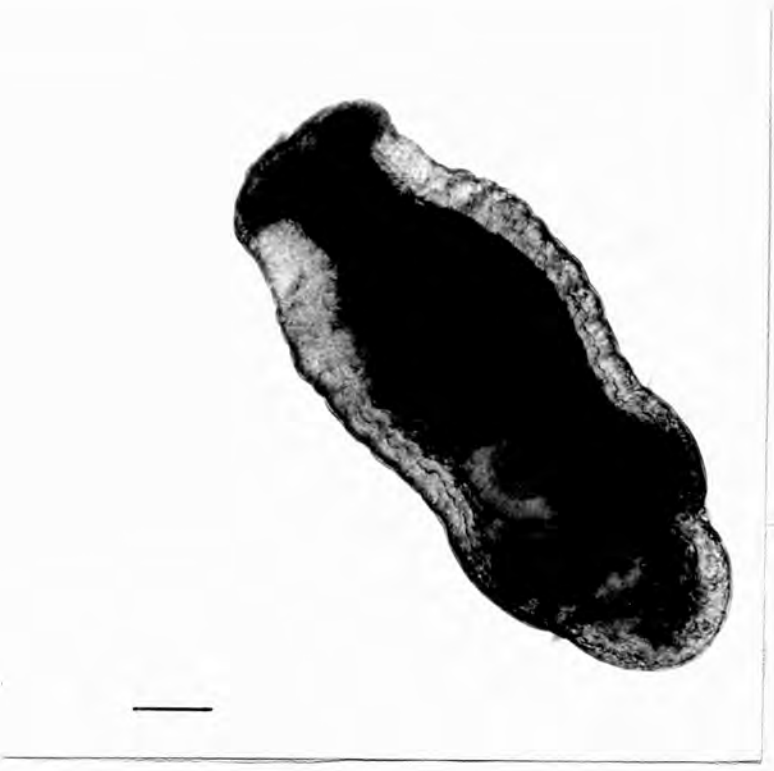
1972) indicate a range from about 4°C to 16°C. Larvae are produced throughout the year at Warren Point and it must be concluded that development proceeds at a somewhat slower rate in the winter months.

At the end of the experiment the larvae at 10, 15 and 20°C were about 20, 12 and 14 days old respectively. Unfortunately a breakdown in the 15°C temperature control unit prevented the continuation of this experiment. Tests at the other temperatures were terminated when the larval mortality became too high for sampling to be carried out.

C.capitata is known to spend ten to twelve days in the maternal tube and the early stages of this experiment cover this stage of development. A typical trochophore is shown in Fig. 41. As discussed previously (section 3.3.3.4) the length of planktonic existence is variable and trochophores removed from the parental tube will show swimming behaviour although only three or four days old. In these experiments, for example, the larvae were constantly moving about under ciliary action for several days. With increasing size, however, the larvae become more muscular, subject to violent contraction and are benthonic in their behaviour (see Fig. 42.). This stage was reached in the worms kept at 10°C after seventeen days. The cilia gradually regress and the young metamorphosed worms adopt a crawling method of locomotion utilising the setae (Fig. 43). Insufficient numbers prevented the measurement of the growth rate of these larger

FIG. 41. Capitella capitata, Plymouth. Photomicrograph of a trochophore larva. Scale represents 20 µm.

FIG. 42. Capitella capitata, Plymouth. Photomicrograph of a 14 day larva. Scale represents 50 µm.



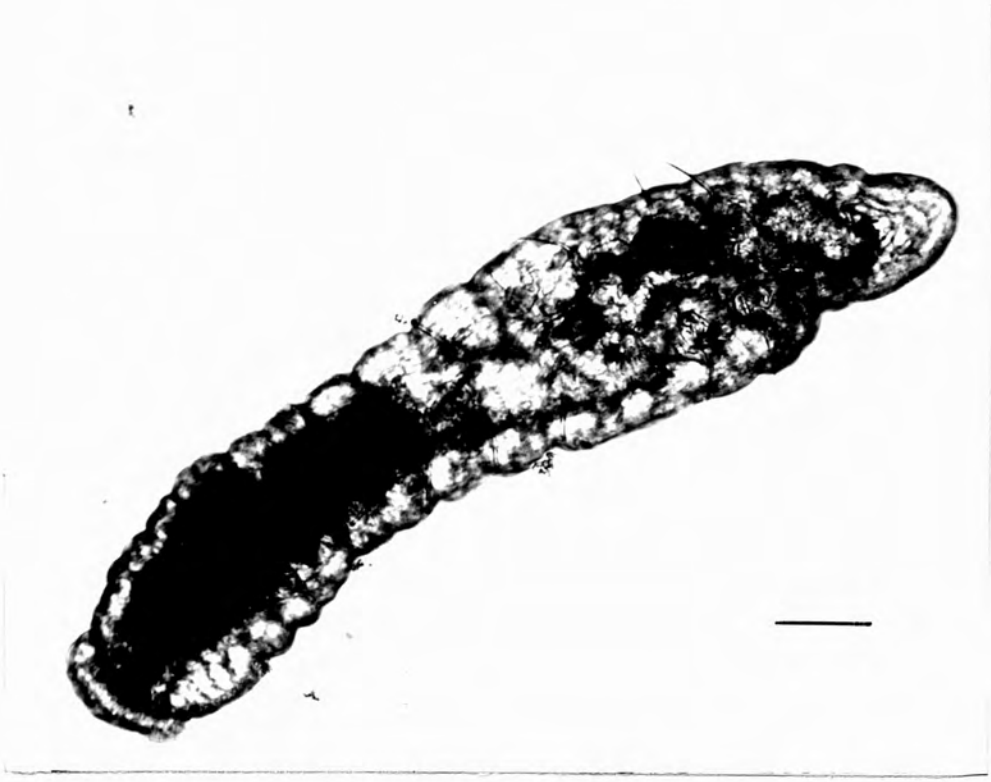


FIG. 43. Capitella capitata, Plymouth. Photomicrograph of a recently metamorphosed worm. Scale represents 142 µm.

larvae but after the termination of the 15°C experiment the test worms continued to grow and metamorphosed in 20 days at 15 ± 4°C. The ability of the larvae to metamorphose under the experimental conditions indicates that these were not too abnormal and a fair level of confidence can be placed in the results obtained. The young worms were fed either on dried Enteromorpha or Tetramin, a commercial fish food, whose use was suggested by Guerin (1970).

4.2.3 Salinity tolerance in C.capitata.

C.capitata is known to occur under a wide variety of salinities ranging from 0.4°/oo to 35°/oo (see sections 1 and 3.3.1.3). This does not imply that individual worms are euryhaline, however, and the effect of marked salinity changes on worms collected from Warren Point was investigated to discover the effect of this factor on the distribution of the species.

4.2.3.1 Methods.

Adult worms collected from Warren Point (salinity 27.8°/oo see section 3.3.1.3) were used in these experiments. Worms were selected at random, although incomplete or damaged specimens were rejected. Twenty worms, in four groups of five, were tested at each salinity. The larvae used in these tests were all taken from the same tube. They were approximately five days old at the start of the experiment.

Various dilutions of seawater were made up by adding dist-

illed water to filtered artificial seawater (33°/oo) to which the worms had been acclimated for one week. The salinities thus obtained were measured by titration against silver nitrate with potassium chromate as the indicator.

Five worms were placed in dishes containing 500 ml of seawater at the required dilution. The dishes were kept in the dark at 15°C and the seawater was aerated. It was changed daily. The worms were examined at regular intervals and their activity tested by prodding with a blunt seeker. Any worm not responding to touch was transferred to a dish of clean seawater at 33°/oo. Worms still not responding after 24 hours were assumed to be dead. The experiment was repeated three times at each salinity.

A similar set of dishes was set up to assess the effect of a short exposure to a lowered salinity. After given periods of time the worms were removed from the experimental vessel and returned to seawater at 33°/oo. The percentage mortality after 24 hours was calculated. This experiment was repeated.

Ten larvae were tested at each salinity. These were removed from the maternal tube with a syringe and placed in a solid watch glass, which was then filled with seawater at the concentration under test. The dishes were covered and kept in the dark at 15°C. The seawater was changed daily. The percentage mortality after given time intervals was calculated. Where all the larvae died suddenly and a bacterial infection was suspected the results were discarded and the test repeated. Two trials

were carried out at each salinity.

The effect of a short exposure to different salinities was investigated for a few selected salinities. The larvae were treated as above and after given periods of time the test solution was drawn out of the dish with a syringe and replaced with water at 33°/oo at the same temperature. The mortality after 24 hours was calculated as a percentage.

4.2.3.2 Results.

The results show that adult C.capitata are tolerant of reduced salinities down to about 20°/oo (Table 29). Below this value the worms are capable of surviving for a few days but death occurred after four days exposure to water at 17°/oo S. Although the salinity of the interstitial water at Warren Point was 27.8°/oo the worms were readily acclimated to seawater at 33°/oo.

Extensive tests on the larval C.capitata showed that they were more tolerant of reduced salinities than the adult worms, living for about a week at 15.5°/oo S. Below a salinity of 10°/oo death occurred within 24 hours (Table 30). Tests on the effect of short exposure to reduced salinities in a critical range of dilutions showed that below about 13.5°/oo S death occurred within an hour (Table 31). Adult worms were more tolerant of short periods of exposure (Table 32) a fact which may be related to their larger size. Nevertheless 30 minutes exposure to 1°/oo S resulted in 100% mortality.

TABLE 29. The percentage mortality of adult C.capitata under conditions of reduced salinity.

Salinity (°/oo)	Time (days)				
	0	1	2	3	4
1	0	100			
	0	100			
	0	100			
	0	100			
5.5	0	80	80	100	
	0	100			
	0	80	100		
	0	80	100		
17	0	0	0	60	100
	0	0	40	80	100
	0	0	40	100	
	0	0	60	100	
33	0	0	0	0	0
	0	0	0	0	0
	0	0	0	0	0
	0	20	20	20	20

TABLE 30. The percentage mortality of larval C.capitata under conditions of reduced salinity.

Salinity (°/oo)	Time (days)																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
2	0	100															
	0	100															
9	0	100															
	0	100															
13.5	0	40	50		60	70	80	80	80			90		0			
	0	20	20		20	20	20	20	40			40		50	50	70	80
15.5	0		0	0	0	0	0			0		50	70	80	90	100	
	0		0	0	0	0	10			10		40	60	80	80	90	100
18	0	0	0		0	0	0	0	10			40		40	40	90	90
	0	0	0		70	70	70	70	70			70		70	100		
26	0	0	0	0	0	0	0	0	10	0		100					
	0		0		0	0	0					20	30	30	30	100	
33	0	10	10		20	20	20	40	40			70		70	80	90	100
	0	0	0		0	0	0	0	0			0		0	0	0	0

TABLE 31. The % mortality of larval C.capitata subjected to short periods of exposure to reduced salinities.

Salinity (°/oo)	Exposure time (mins)						
	0	30	60	80	95	115	135
8.5	0	70	100				
11.0	0	40	100				
13.5	0	0	0	0	0	0	0
15.5	0	0	0	0	0	0	0

TABLE 32. The recovery of adult C.capitata after a limited exposure to conditions of reduced salinity.

Salinity (°/oo)	Length of exposure.											
	1 min		15 min		30 min		1 hour		3 hours		24 hours	
	% recovery (%)	time to recover (T)	%	T	%	T	%	T	%	T	%	T
1	60	1 min	60	2 min	0	-						
	60	1 min	40	2 min	20	6 min						
5.5	100	0 min	100	0 min	80	0 min	80	1 min	60	1 min	20	5 min
	100	1 min	80	1 min	80	0 min	60	2 min	60	1 min	20	1 min
17.	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min
	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min
33	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min
	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min	100	0 min

One can conclude from these results that the Warren Point population of C.capitata is capable of withstanding any reduction in salinity that it is likely to encounter under normal conditions but that it is intolerant of extreme reductions in salinity. The higher degree of tolerance shown by the larvae parallels the response shown to extremes of temperature and is probably an important factor in the survival of the species. Other authors have obtained similar results notably Lyster (1965) who worked on Notomastus sp. The effect of salinity in controlling the distribution of the species is discussed further in section 5.

4.2.4 The acute toxicity of inorganic mercury to adult C.capitata.

Because of the widespread acceptance of C.capitata as an indicator of polluted conditions the following tests were carried out to assess the effect of a heavy metal on the species. The experiment parallelled that of Brown and Ahsanullah (1971) on Ophryotrocha labronica and it was hoped to compare the response of the two polychaetes to similar concentrations of toxicant.

4.2.4.1 Methods.

Worms were collected from Warren Point and experiments carried out upon return to the laboratory in London.

A solution of mercuric chloride was made up in seawater to give a 0.1 M stock solution. Dilutions were made from this to give solutions of mercury in seawater of 50, 10, 5, and 1 ppm.

These were made up using freshly prepared stock, as mercuric chloride is known to be unstable in seawater (Corner and Rigler 1957). A solution of sodium chloride containing the same concentration of sodium as mercury in the test solution was made up as a control. All experiments were carried out at 10°C. The water was changed once for the lowest concentration.

Ten adult worms were used in each test, two of which were carried out at each concentration. The worms were examined at regular intervals and any changes recorded. Worms not responding to touch were transferred to clean seawater and their mortality after 24 hours noted. Cumulative curves of the percentage mortality against time were plotted and the time taken for 50 % mortality to occur (LD_{50}) was estimated.

4.2.4.2 Results.

The effect of exposure to various concentrations of mercury is given in Table 33.

From the graph of mortality against time (Fig. 44) it can be seen that the time taken till 50 % mortality increases with decreasing mercury concentration. The LD_{50}s are 1.08 - 1.20h for 50 ppm, 6.50 - 7.00h for 10 ppm, 8.20 - 8.40h for 5 ppm and 36 - 37h for 1 ppm.

Observations made during the experiment illustrate the extreme toxicity of 50 ppm mercury. The worms became immobile

TABLE 33. The percentage mortality of C.capitata exposed to various concentrations of inorganic mercury.

Concentration of mercury (ppm)	Time (hours) 0	0.25	0.5	1	2	3	4	5	7	9	18	42	66	90
50	0	0	20	20	100									
	0	0	10	20	100									
10	0	0	0	0	10	10	10	30	60	90	100			
	0	0	0	0	0	0	10	20	50	100	100			
5	0	0	0	0	0	0	30	30	60	70	90	100		
	0	0	0	0	0	0	30	40	60	70	100	100		
1	0	0	0	0	0	0	0	0	0	0	0	70	90	100
	0	0	0	0	0	0	0	0	0	0	0	60	100	100
control	0	0	0	0	0	0	0	0	0	0	0	10	10	10
	0	0	0	0	0	0	0	0	0	0	0	0	0	0

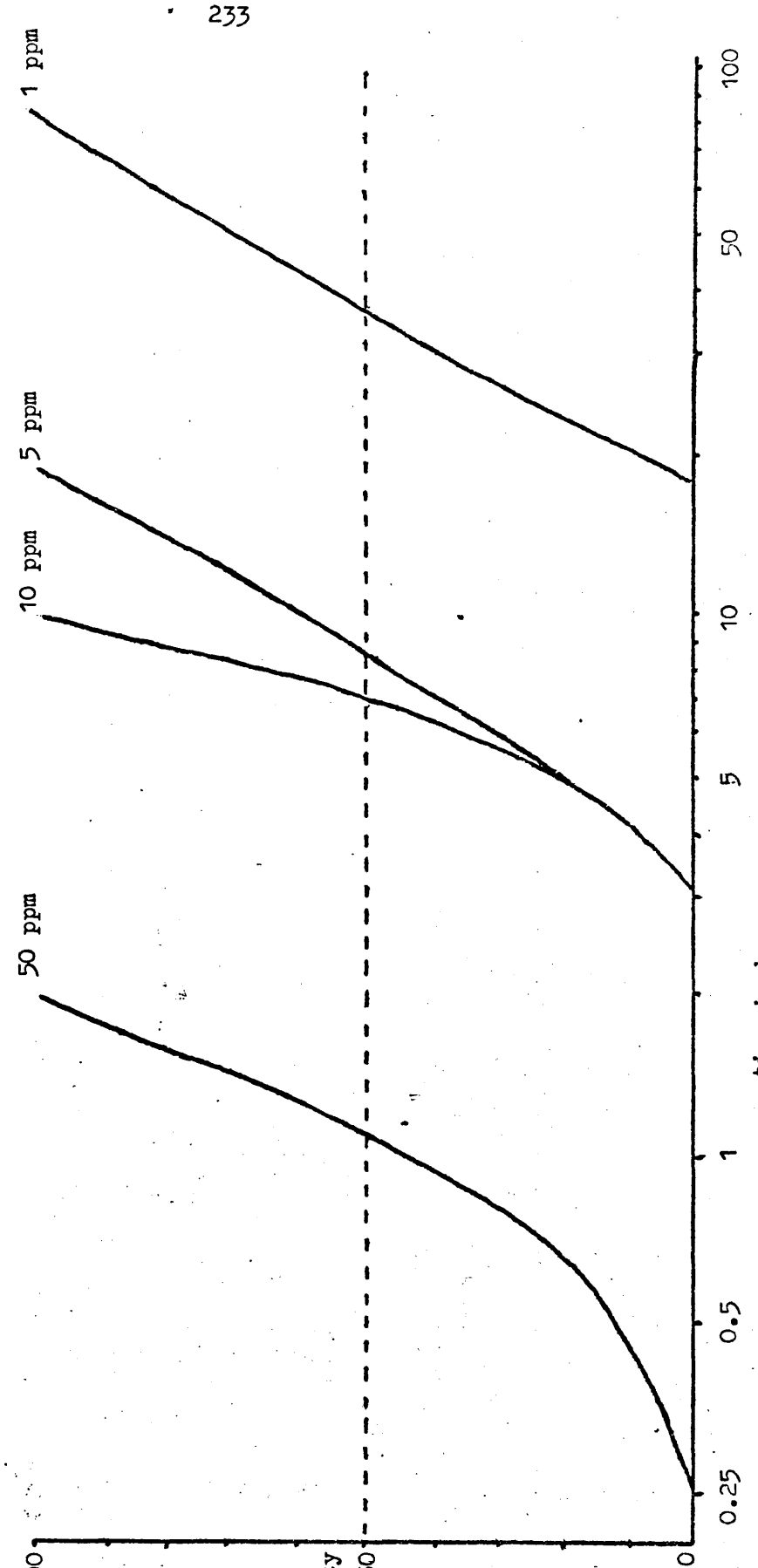


FIG. 44. The effect of mercury concentration on the mortality of C.capitata.

within minutes of contact with the solution and although no obvious damage could be detected worms failed to recover after about 1h exposure. Worms kept in 5 and 10 ppm mercury behaved similarly and although the LD_{50} is shorter at 10 ppm there was a wide range of response times in both concentrations. Worms in these solutions showed a definite pre-death state. This was characterised by the production of copious amounts of mucus followed by lesions along the body and a loss of coelomic fluid. This was particularly noticeable in gravid females which were apparently more vulnerable than other worms. A similar phenomenon was noted in response to temperature changes (section 4.2.1.2).

Worms kept at 1 pmm mercury showed no ill-effects after nearly two days of exposure. Mortalities occurred during a period when the intervals between readings were high and any pre-death characteristics could not be observed.

The relationship between the LD_{50}s and concentration is given in Fig. 45.

These results show that C.capitata is very much more resistant to inorganic mercury poisoning than O.labronica which showed an LD_{50} of 30 h in 0.01 ppm mercury. In 0.5 ppm mercury 50 % mortality was reached in 2h. However, O.labronica was particularly sensitive to mercury as opposed to other heavy metals and it is possible that special factors are involved here.

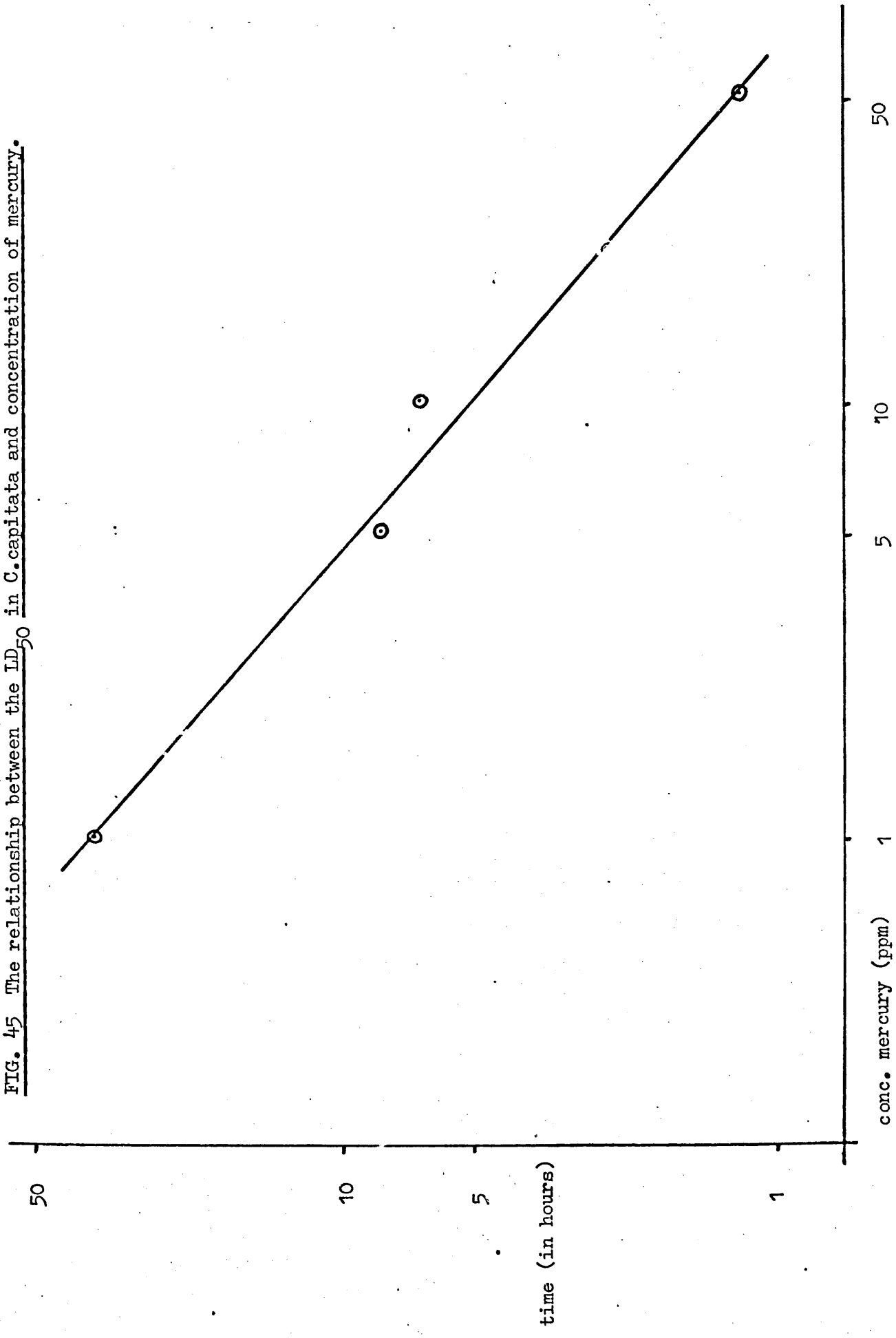


FIG. 45 The relationship between the LD_{50} in C.capitata and concentration of mercury.

The processes of mercury toxicity are very complex and Corner and Sparrow (1956) have shown that resistance to organic mercury is much less than to the inorganic form in the brine shrimp Artemia salina and it is possible that C.capitata may respond similarly.

Nevertheless, in spite of the difficulties in interpreting these results it seems that C.capitata may show a potential for tolerating pollution from heavy metals. A more detailed discussion of this problem is given below.

4.3 The relationship of C.capitata to conditions of low oxygen concentrations.

This study was partly carried out in conjunction with Dr. R.M.G. Wells who devised the method for analysis of oxygen in blood samples.

C.capitata is often found in environments where the oxygen level is very low (e.g. Cognetti 1972). It was the purpose of this study to gain an understanding of the oxygen equilibrium characteristics of its haemoglobin and to relate this to the mode of life.

4.3.1 Methods.

Worms were collected from Warren Point and the blood analysed on the day of collection.

C.capitata does not possess a blood vascular system, but the coelom contains large numbers of cells containing haemoglobin. These were sampled by rupturing the body wall of the worm and drawing up the coelomic fluid into a micropipette. It was noted that the haemoglobin rapidly denatured on contact with air so analyses were always made on fresh blood.

The blood was analysed for combined oxygen using a technique based on the principle that oxygen bound by haemoglobin is released into solution if a blood sample is diluted with a large volume of ferricyanide solution and modified for very small samples of 3 - 5 µm (Wells and Dales 1974). Oxygen equilibrium data were obtained from the oxygen contents of samples equilibrated with gas mixtures containing progressively more oxygen to avoid haemoglobin denaturation during the early stages of the experiment. Readings were taken using a Radiometer E5046 electrode. The results were analysed by logarithmic transformation according to Hill's approximation.

Laboratory experiments on the tolerance of C.capitata to low oxygen concentrations were carried out in conjunction with the physiological study.

Filtered artificial seawater (33°/oo S) to which a little streptomycin had been added was used for all the experiments. 250 ml of this seawater were placed in a 1 litre Erlenmayer

flask and nitrogen bubbled through for several hours to reduce the oxygen tension. Despite literature reports to the contrary (Reish and Richards 1966) it was found to be very difficult to obtain very low oxygen tensions by this method and instead a few crystals of sodium sulphite were added. It is unlikely that this chemical would have an adverse effect on the animals since, in the presence of oxygen, sulphate ions are formed and the buffering properties of seawater should minimise any effect on the pH. When the required oxygen tension was reached (as measured with a Radiometer E 5046 electrode) ten healthy worms were added to the flasks which were then sealed with Parafilm (Gallenkamp). The flasks were kept at 15°C and all but one were kept in the dark. The other flask was subjected to light for 12 hours each day. The flasks were examined at regular intervals and the number of dead worms noted. The experiment was repeated once. The oxygen tension in the vessels was measured again at the end of each experiment.

4.3.2 Results.

The oxygen equilibrium curve for C.capitata is hyperbolic and can be described by Hill's approximation : -

$$y = \frac{100p\ /p50}{1 + p\ /p50}$$

where y = % haemoglobin

p = partial pressure of O_2 (mm Hg)

p50 = value of p at which the proportion of oxyhaemoglobin and deoxyhaemoglobin are equal

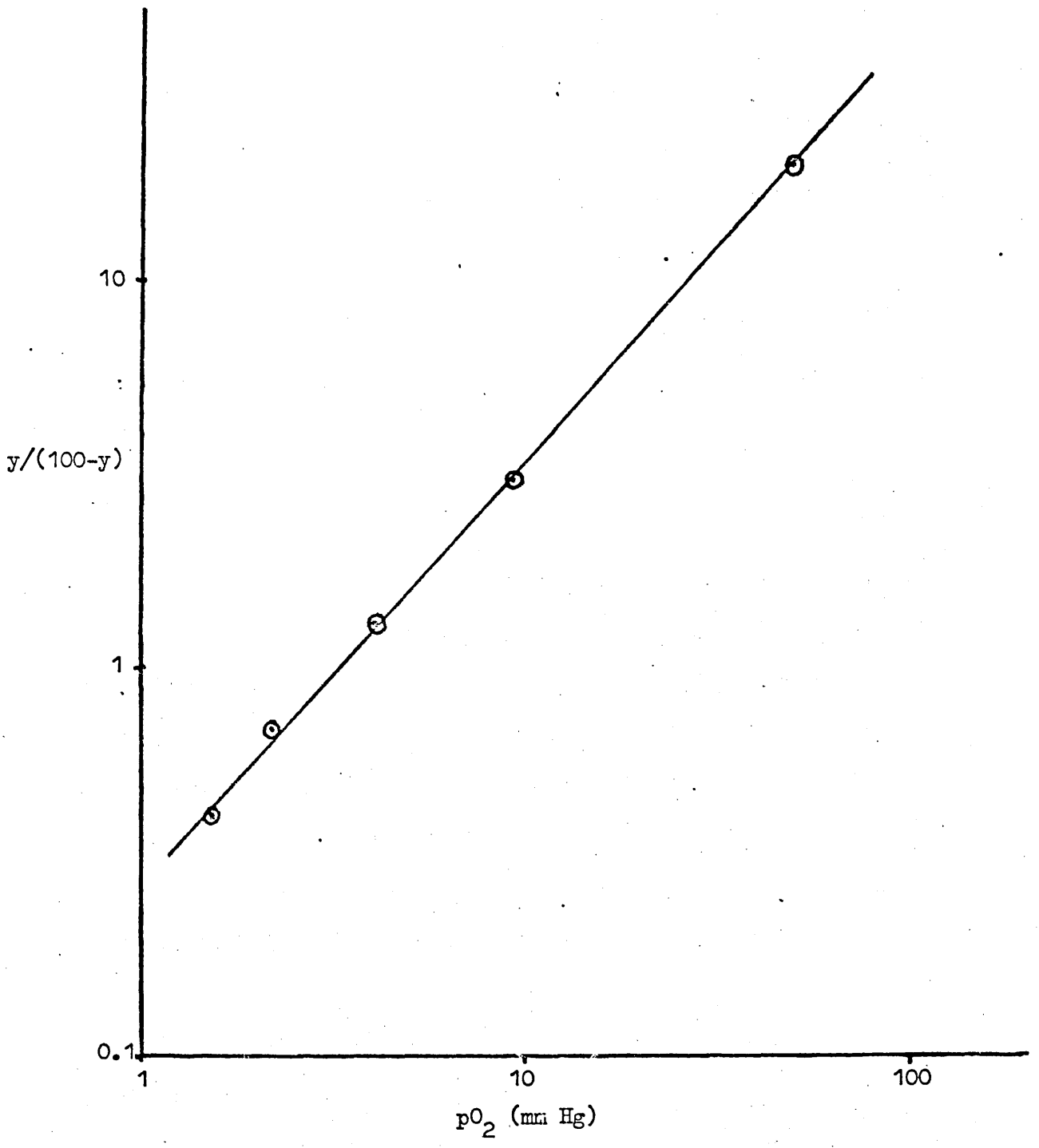
A linrear transformation of the data is given in Fig. 46, the slope of 1.0 indicating a lack of haem-haem interactions. The oxygen combining capacity of C.capitata blood was 3-4 vols % and there was a high affinity for oxygen, the p 50 being 3 mm Hg (0.4 kN m^{-2}).

The p O_2 of the interstitial water from the substrate inhabited by C.capitata at Warren Point was 8-12 mm Hg (1.1 -1.6 kN m^{-2}) as described in section 3.3.1.4. The loading tension of the haemoglobin is thus well matched to the availability of oxygen in the immediate environment. Allowing for a modest diffusion barrier across the body wall the p 50 at equilibrium appears to be closely adjusted to the unloading p O_2.

Peristaltic movement of the body wall affords some circulation of the respiratory pigment (Haffner 1930) and is evidence for the postulated function of haemoglobin in oxygen transport at low ambient pO_2s. However, in the presence of haemoglobin oxygen diffuses at a rate faster than would be predicted from the concentration difference, and this 'facilitated diffusion' (Kreuzer 1970) implies that the functions of storage and transport are oversimplifications. Since C.capitata lacks a specialised respiratory surface the term 'diffusive transport' used by Manwell (1960a) may be more acceptable.

The denaturing of the haemoglobin in C.capitata was not studied, but in Notomastus latericeus spectral analyses (using a DK2 spectrophotometer) of the denatured pigment suggested the formation of haematin and it is likely that a similar process occurs when C.capitata haemoglobin is exposed to air. This brown derivative was not observed in the field.

FIG. 46 Oxygen equilibrium of coelomic cell haemoglobin of C.capitata using the linear transformation log y /100 - y as a function of log pO_2.



The results of the oxygen toleration tests are given in Table 34. Although only one worm died in the air saturated vessels all the worms showed a change in the colour of the haemoglobin from red to brown. The extent of the change varied from worm to worm. This contrasts with the findings of Mangum and Winkle (1973) who found no ill-effects of exposure to high oxygen levels in this species. Manwell (1960b) proposed that haemoglobin might function by maintaining low internal pO_2s thus protecting the tissues from oxygen poisoning in species living in poorly oxygenated environments. The instability of the haemoglobin from C.capitata and N.latericeus under conditions of high oxygen levels suggests that this is not the case for capitellids.

The worms showed a high survival rate down to very low oxygen tensions. In anoxic conditions, however, mortality was fairly high. This is possibly due to the experimental procedure. Under natural conditions this population of C.capitata is subject to tidal changes and encounters periods of exposure when the pO_2 of the interstitial water is likely to fall. With the incoming tide, however, the oxygen tension will rise again. Only rarely is a substrate completely anoxic and in these cases there is usually no life at all (Reish 1955, Bellan 1967).

Reish (1966) carried out a similar series of experiments on the tolerance of low oxygen concentrations by C.capitata. His figures for the LD_{50} are however rather high (1.5mg /1).

Unfortunately his experiments were not carried out under conditions of constant temperature and the addition of food material to the experimental vessels might affect the results. Nevertheless his conclusions on the minimum oxygen concentrations necessary for survival, feeding and reproduction are useful.

Rosenberg (1972) investigated the survival of C.capitata in reduced oxygen conditions. He found that 80 % of the sample survived for 24 days at an oxygen concentration of 2.1 mg /l and 50 % survived for 13 days at 1.3 mg /l, at a temperature of 5 - 6°C. As salinity conditions were not given it is difficult to compare the results directly but it is interesting to note that C.capitata was more tolerant than Polyphysia crassa, a polychaete associated with slightly less polluted conditions.

TABLE 34. The percentage mortality of adult C.capitata subjected to low oxygen tensions.

Oxygen tension (mm Hg)	Time (days) 0	1	5	7	10	12	15	20	25	30	35
160 air sat.	0	0	0	0	0	0	10	10	10	10	10
(6 ppm) dark	0	0	0	10	10	10	10	10	20	20	20
160 air sat.	0	0	0	0	0	0	0	0	0	10	10
(6 ppm) light	0	10	10	10	10	10	10	10	10	10	10
2	0	10	10	10	10	20	20	20	30	30	30
(0.8 ppm)	0	0	0	0	0	0	20	20	20	20	30
<< 1mm	0	60	60	70	70	70	80	100			
(with Na_2SO_3)	0	0	20	30	50	80	90	90	90	100	

5. DISCUSSION.

The cosmopolitan distribution of C.capitata implies that it is highly adaptable to a wide range of environmental variables. This adaptability could be due to the tolerance of individual worms or to the flexible genetic constitution allowing the selection of appropriate genotypes according to the conditions. In order to assess the relative importance of these factors the effect of external conditions on the distribution of the species is discussed with reference to this investigation and to those of previous workers.

Particle size and associated parameters apparently exert no marked effect on the distribution of the species. In the populations under study C.capitata was found mainly in deposits of fine sand but, as discussed in section 3.3.1.1 other workers have located it in substrates ranging from mud (Barnard and Reish 1959, Hartman 1947) to sand (Southward 1957). Where particle size does influence the distribution of a species this can be due to several aspects. Firstly the porosity of the substrate will be related to the size of the particles. Webb (1958) discusses the mathematical relationships between particle size and porosity and his work has been followed up by Williams (1972). This is an important factor for interstitial fauna inhabiting the voids between sand grains but has little direct relevance for the macrofauna. However, the pore size

is directly related to other physical properties of the substrate, principally the permeability which affects the drainage of water through the deposit. This in turn will influence the stability of the substrate which may limit the distribution of certain species according to their ability to form burrows. C.capitata does not build a permanent burrow like that of Arenicola marina, for example (Wells 1945), but lives in temporary mucus-lined tubes which are not arranged at any definite angle. Only brooding females appear to live in permanent tubes and here the mucus is stiffened by the adhesion of sand particles to the outer surface of the tube. Hartman (1947) reported that the presence of C.capitata could be detected by cone-shaped mounds above the entrance of the burrows but I have never observed this. It is possibly related to the finer nature of the substrate. Mud will not give the support necessary to maintain a loosely-formed tube and under these conditions C.capitata may form more permanent habitations which are well supported by mucus.

The size of the particles is also closely related to the organic content. Newell (1965) and Longbottom (1970) showed a positive correlation between particle size and organic content which they concluded is due to the increased surface area allowing a greater growth of micro-organisms. Furthermore, detritus is more likely to settle out with the lighter, smaller mineral particles, which automatically make these potentially richer in food material.

The organic content is undoubtedly an important factor affecting the distribution of C.capitata. The sites examined in this study were all very rich in organic carbon in the grades of substrate available to the species and the estimates of assimilable organic matter are also very high (1.5 %). The only directly comparable figures are those of George (1964a) who found that 0.44 % of the substrate was digestible by Cirriformia tentaculata. Previous workers only give the total organic content of the substrate but in view of the heterogeneity of the deposits at Warren Point it is virtually impossible to compare their results.

One important feature of interest is the nature of the organic material. Longbottom (1970) concluded that micro-organisms were the main food source for Arenicola marina at Whitstable and George (1964a) proposes a similar idea for Cirriformia tentaculata. Both these species feed on the surface layer of the sand whereas C.capitata has no mechanisms for this behaviour, and is limivorous.

Pearson (1972) and Bagge (1969a) both associate the presence of the species with layers of rotting vegetation. The ability of C.capitata to utilise this material as a food source probably contributes to its extensive breeding period. However, its digestive physiology does not show any marked adaptation to a diet of detritus. Hylleberg (1972) investigated the carbohydrases of various invertebrates with a view to

relating these to the food. Although the overall role of the enzymes in metabolism remains unknown Hylleberg concluded that bulk degradation of structural polysaccharides, such as cellulose, does not occur. Several of the animals under investigation were found to contain a cellulase and Yokoe and Yasamasu (1964) believe them to be widespread amongst invertebrates. However these enzymes are thought to need several hours to attack their substrate and the passage of the food through the gut is almost certainly too rapid for much digestion to occur. Although rather superficial in nature the results of the present study show that C.capitata does not possess a cellulase and cannot therefore attack the dead plant material making up detritus. Because of this it must ingest vast quantities of the substrate in order to obtain sufficient food. The apparent preference for decaying vegetable matter is presumably related to the rich source of nutriment that it provides for the micro-organisms.

The influence of salinity on the distribution of C.capitata has been discussed in some detail in sections 3.3.1.3 and 4.2.3. The species is found under a wide range of salinities from almost fresh water to full strength seawater, although there is some evidence that reduced salinities are preferred. Thus Hartman (1961a) believed that its occurrence in large numbers to the exclusion of other polychaete species indicated conditions of reduced salinities in the deep canyons off California and there are many records of its occurrence in estuaries

(e.g. Macginitie 1935, Scott et al. 1952 and Estcourt 1967). Nevertheless its relative rarity in higher salinities may be due to its inability to compete with other species rather than an aversion to the salinity conditions themselves. For example it is very common in the polluted waters of Livorno harbour (35°/ooS) where other species are unable to colonise. (Cognetti 1972).

Individual worms do not show such a wide tolerance of salinity conditions (although they are readily acclimated to different concentrations of seawater) and the euryhaline nature of the species is probably due to its genetic flexibility.

Temperature may play an important part in limiting the spread of C.capitata. Tolerance experiments (section 4.2.1) showed that the Warren Point population succumbed at a fairly low temperature. With acclimation this could probably be raised but the world distribution of the species and its reproductive biology suggest that it is essentially a cold water species. It is very widely distributed along the coasts of northern Europe and North America and in the southern hemisphere it occurs in the cold Antarctic waters. Its extensive breeding season in the higher latitudes indicates that cold temperatures do not inhibit its reproductive potential. Nevertheless populations do occur in the warmer temperate waters, especially around the Americas, and it is of interest to note that many of the varieties described are from this region and it is poss-

ible that adaptation to higher temperatures accounts for the difference.

The relationship of C.capitata to low oxygen environments has been widely discussed and is the basis of its use as an indicator of polluted conditions. Laboratory experiments in the present study indicate a high tolerance of low oxygen conditions but this is parallelled by other species, not generally associated with poorly oxygenated habitats (Theede et al. 1969). Reish has made a very detailed study of the tolerance of the species to low oxygen concentrations (1966, 1970) and relates the results to field conditions (Reish 1959, 1960 and Reish and Barnard 1960). However, as Muus (1967) points out, his findings do not indicate a marked tolerance of low oxygen levels and indeed Neanthes arenaceodentata and Dorvillea articulata, species which Reish associates with his semi-polluted zone, show a higher tolerance than C.capitata which occurs in the most polluted zone. Also, Reish (1966) points out that field measurements indicate a lower tolerance level than the laboratory tests would suggest but reflects that this could be due to difficulties in sampling. Interpretation of the oxygen equilibrium curve is difficult because of the lack of information on diffusion barriers within the worm but its high oxygen affinity and its hyperbolic nature (a feature typical of cellular haemoglobins in polychaetes) suggest that it is well adapted to low oxygen tensions. However the characteristics of the curve are not markedly different from those of

Notomastus latericeus, a species seldom associated with polluted environments (Wells and Warren, in press).

In fact any direct relationship to pollution is rather doubtful, although numerous workers have recorded its presence in polluted conditions, notably Reish (1956, 1957), Gilet (1960), Clark and Dawson (1963), Henriksson (1968), Bagge (1969a), Crippen and Reish (1969), Rosenberg (1972) and Wade et al. (1972).

The pollution is usually of an organic nature resulting from domestic wastes, paper production etc., and its main effect is to lower the oxygen tension. C.capitata has often been associated with these conditions and is known to occur where the oxygen is reduced (e.g. Reish 1963, Cognetti 1972). However, as discussed above, its resistance to low oxygen levels is not remarkable and other factors must be involved. A tolerance of hydrogen sulphide may be important and several workers have reported its presence in areas rich in this compound (Jacobuva and Malm 1931 and Wohlenberg 1937). Theede (1973) has studied the effect of sulphide ions on the survival of certain polychaetes in anoxic conditions and has shown that those species tolerant of low oxygen levels tend to be more resistant to hydrogen sulphide. Work of a similar nature is being undertaken at the present time and it will be interesting to know the tolerance of C.capitata to the compound.

C.capitata is seldom associated with other pollutants

although it is used extensively as a test organism (Reish 1973). Thus Sanders et al. (1972) noted its sensitivity to oil and Bellan et al. (1972), investigating the influence of oil detergent on its life history, found a marked adverse effect. Reish et al. (1974) found similar sublethal effects from heavy metal poisoning. In the present study C.capitata withstood 1 ppm mercury for several days. Similar concentrations of this metal have been found off La Jolla where the sediment contained 0.02 - 1.0 ppm according to the distance from a sewage outfall (Klein and Goldberg 1970). The average concentration in the world oceans up to recent times is 0.00003 ppm (Krauskopf 1956).

The association between C.capitata and regions of pollution has led to its being used as an indicator of such conditions. The concept of indicator species for polluted conditions was first devised by Gaufin and Tarzwell (1952) for freshwater ecosystems. They gave the following criteria for the use of indicator species: -

1. A large number of individuals
2. A low species diversity
3. A scavenging mode of life
4. Either a toleration of low oxygen conditions or a suitable adaptation to such conditions

As early as 1916 Wilhelmi proposed a similar function for C.capitata in marine environments. By dividing a polluted area

into zones according to the degree of pollution it is possible to select certain species typical of each zone and use them to indicate possibly polluted waters elsewhere. This practice has become widespread in studies of marine pollution. In 1955 Reish divided the Los Angeles-Long Beach harbour system into five zones with C.capitata as the indicator of the polluted zone. He refers to the indicative use of the species again in 1960 and in 1967 Bellan proposed a similar zoning arrangement for the harbour at Marseilles. Again the presence of C.capitata indicated the polluted zone. Cognetti (1972) divided Livorno harbour into regions of pollution according to certain physico-chemical characteristics but was impressed by the uneven distribution of polychaete species in polluted conditions. C.capitata assumed the same role as in previous studies but he noted that certain other species not normally associated with polluted conditions were also present. One of these, Syllides edentula, has a modified life history and eliminated the pelagic larval stage. Cognetti speculates that penetration of polluted environments by any given species is dependent on the genotypes in the population concerned and where the necessary adaptability is not present colonisation cannot occur. Rowe et al (1972) show similar ideas in relating pollution indicators to 'r' and 'k' selected species, where 'r' selection refers to the effects of the physical environment and 'k' is a constant relating to overall individual fitness (MacArthur and Wilson 1967). C.capitata fits most closely in the 'r' selected group of species.

Grassle and Grassle (1974) have followed up this idea in great

detail . They believe that C.capitata is a typical opportunistic species as defined by Mozley (1960) and by Wilson and Bossert (1971) and is able to penetrate a wide variety of habitats because of its genetic flexibility. Thus the genotypes of C.capitata are sufficiently plastic for it to adapt to most environmental conditions. Its presence in polluted areas does not, therefore, mean that it favours such conditions, merely that it is able to adapt readily.

Its ability to withstand a wide variety of environmental conditions is undoubtedly important in determining its distribution and partly accounts for its presence in polluted areas. However, its reproductive biology is responsible for its apparent preference for such conditions. It is a species which can produce very many eggs, in some cases throughout the year, and this, coupled with its brood behaviour, enables it to rapidly colonise a new environment. The ability to produce benthonic larvae, possibly in response to adverse conditions (Henriksson 1969) and hermaphroditic reproduction where population numbers are low, is also important here. But this can only occur where competition from other species is at a minimum. Larval protection and the concentration of all the animals in one area makes the population highly susceptible to predation, and competition for food will also limit its potential. Nevertheless, C.capitata's slight advantage in tolerating adverse conditions enables it to take over whole areas very quickly.. Very large densities have been recorded ranging from 95,355 - 451,000 per square metre

(U.S. Department of the Interior 1967, Caspers 1964). However, repeated sampling of a polluted environment shows that this condition is not permanent. As other species appear, a succession can be detected in which C.capitata gradually disappears (Reish 1962 and Rosenberg 1973). This is normally taken to indicate an abatement of pollution but this is not necessarily the case. Bagge (1969b) studied the succession of fauna in polluted estuarine habitats and again discovered C.capitata as an early coloniser. However, as other species intruded the numbers of C.capitata were not diminished and the species played an important role in the climax communities forming a dominant association with either Scolelepis fuliginosa or Polydora ciliata. In a discussion of this paper Mileikovsky (Bagge 1969b) sheds doubt on the use of C.capitata as an indicator of polluted conditions since it also occurs in clean substrates and the importance of considering the whole community, rather than a few isolated species, is emphasised. Other workers have questioned the use of C.capitata as an indicator species (Muus 1967 and Wolff 1973) and Eagle and Rees (1967) show the need for caution in interpreting field observations. Wass (1967) discusses the overall role of indicator species and stresses the need to consider the community as a whole.

A picture of C.capitata as a species with a great potential for adaptation is emerging. This accounts for its distribution in a variety of habitats and explains the variation seen from

population to population. The difficulties encountered in taxonomic studies of C.capitata also reflect the extreme genetic variability. The mechanisms of its adaptability are at present poorly understood but the use of electrophoretic techniques by Grassle and Grassle (1974) has thrown some light on this problem. The potential for further research in this field is great and it is to be hoped that interest in the topic will be maintained.

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APPENDIX 1. Weights of sediments in particle size analysis.

	Sample							
Sieve size (mm)	W Pt a	W Pt b	W Pt c	Rh	Wh a	Wh b	Wh c	Wh d
2	5.3878	1.3271	4.2215	0.3616	9.7035	18.2832	8.4460	6.0417
1	2.5353	2.0938	4.0324	2.3350	7.3263	9.0974	6.8619	6.3684
0.5	6.9719	4.4651	4.8257	5.2046	5.8351	5.7929	6.6631	7.2111
0.25	54.1828	36.7003	15.1203	12.1301	18.7092	20.3504	15.9743	15.6252
0.125	28.0062	40.9689	39.8903	70.9100	51.7488	41.7936	49.8965	52.3608
0.062	1.5089	5.3312	11.8499	6.9310	4.0472	2.9391	6.0667	7.0770
< 0.062	1.4092	9.1238	20.0402	2.1412	2.6299	1.7475	6.0985	5.3246

W Pt = Warren Point Rh = Rhosneigr Wh = Whitstable

APPENDIX 2. Weights of sediments in particle size analysis according to depth.

Sieve size (mm)	Depth in mm 0.- 5	6 - 10	11 - 15	16 - 20	21 - 25
2	17.0051	19.9802	14.3103	16.1600	9.8222
1	12.3606	6.2097	4.9278	3.8409	4.3358
0.5	5.9752	3.2564	3.0171	3.5582	3.7883
0.25	12.0397	12.0400	16.5492	18.0698	21.8429
0.125	53.2201	53.2198	54.3304	52.7601	56.2344
0.062	2.7339	4.1156	4.3836	4.2848	3.4674
< 0.062	1.3293	1.1538	2.5033	1.4864	0.4733

APPENDIX 3. Data from organic carbon analyses.

Sample	Organic C (g) W & B value	Weight (g) subsample	Weight (g) sieve sample	Weight (g) Organic C in sieve
01 a	0.01047	1.4629	108.7416	0.7782
b	0.02088	0.5814	4.9113	0.1763
c + d	0.00879	0.2813	0.5465	0.0170
02 ai	0.02145	1.5454	29.9656	0.4159
ao	0.03031	0.2108	10.0906	1.4504
b	0.00675	0.6335	9.4454	0.1006
c	0.01098	0.3081	0.8623	0.0243
d	0.01826	0.4851	4.1020	0.1594
03 ai	0.19320	1.6685	13.3588	0.1546
ao	0.01565	0.0975	9.6024	1.5363
b	0.01239	1.1705	7.5114	0.0795
c	0.01176	0.3962	0.9233	0.0272
d	0.01603	0.3851	4.9708	0.2069
04 ai	0.00717	1.5833	55.7212	0.2523
ao	0.09144	0.0974	6.1063	1.2187
b	0.00588	0.6335	11.0318	0.1023
c	0.01104	0.3516	0.8666	0.0272
d	0.01592	0.4260	2.9868	0.1116
Wh ai	0.00782	1.7215	59.7309	0.2706
ao	0.03399	0.2416	5.1479	0.7242
b	0.00126	0.5387	6.8971	0.0161
c	0.00468	0.1594	0.2953	0.0086
d	0.01403	0.3622	0.4931	0.0191
Rh a	0.02339	1.3342	67.9905	1.1922
b	0.00547	0.4219	12.6057	0.1632
c	0.01129	0.3610	1.5109	0.0471
d	0.01518	0.5613	1.1523	0.0311

ai = mineral material retained by large sieve (> 0.5 mm)

ao = plant and shell material retained by large sieve

b = medium sieve (0.125 - 0.5) c = fine sieve (0.062 - 0.125)

d = subsieve sample (< 0.062)

APPENDIX 4. Thoracic length data from monthly samples.

Sample	Length categories (mm) 0 – 0.5	0.6 – 1.0	1.1 – 1.5	1.6 – 2.0	2.1 – 2.5	2.6 – 3.0	3.1 – 3.5	3.6 – 4.0	4.1 – 4.5	4.6 – 5.0	5.1 – 5.5	5.6 – 6.0	6.1 – 6.5	6.6 – 7.0	7.1 – 7.5	7.6 – 8.0	8.1 – 8.5	8.6 – 9.0	9.1 – 9.5	9.6 – 10.0	10.1 – 10.5
January 1973 Nos	0	1	4	22	25	15	15	12	8	3	5	2	3	1	1	0	1	0	1	1	1
February 1973 Nos	0	0	6	26	30	42	30	30	13	13	7	8	13	14	5	4	2	2	3	2	1
March 1973 Nos(1)	0	3	0	0	1	5	1	5	4	7	2	1	2	1	0	1	0	0			
(2)	10	15	0	0	1	1	0	1	0	2	1	0	0	0	0	0	1	0			
(1 + 2)	10	18	0	0	2	6	1	6	4	9	3	1	2	1	0	1	1	0			
April 1973 Nos	2	74	125	61	19	9	7	13	19	13	10	20	14	12	3	1	3	1	2		
May 1973 Nos	1	8	1	4	3	10	12	10	6	10	2	4	3	3							
June 1973 Nos(1)	0	7	4	3	0	1	2	2	4	4	1	4	0	3							
(2)	0	28	6	1	1	9	4	7	8	8	1	1	1	0							
(1 + 2)	0	35	10	4	1	10	6	9	12	12	2	5	1	3							
July 1973 Nos	0	1	8	57	78	117	42	28	10	3	6	9	3	3	3	1	0	1	1		
August 1973 Nos	0	9	15	11	10	24	14	20	16	15	7	1	1								

APPENDIX 4. Cont.

Sample	Length categories (mm)																			
	0 0.5	0.6 1.0	1.1 1.5	1.6 2.0	2.1 2.5	2.6 3.0	3.1 3.5	3.6 4.0	4.1 4.5	4.6 5.0	5.1 5.5	5.6 6.0	6.1 6.5	6.6 7.0	7.1 7.5	7.6 8.0	8.1 8.5	8.6 9.0	9.1 9.5	9.6 10.0	10.1 10.5
September 1973 Nos (1)	0	4	14	23	32	66	38	51	30	32	15	6	3	6						
(2)	1	11	13	31	21	14	12	9	3	3	3	1	2	1	0	1	2	1		
(1 + 2)	1	15	27	54	53	80	50	60	33	35	18	7	5	7	0	1	2	1		
Late September 1973 Nos	0	1	0	1	5	3	1	4	1	1	0	1	0	3	1	1	0	1	0	1
October 1973 Nos	1	6	4	29	28	28	24	19	8	10	11	12	9	8	1	1	1			
November 1973 Nos.	0	1	1	2	5	6	8	10	8	10	12	6	13	5	4	1	0	1		
December 1973 Nos	2	5	0	1	11	12	17	24	17	14	12	18	3	6	1	1				
February 1974. Nos (1)	0	3	0	3	1	6	3	4	4	7	8	5	2	1	1					
(2)	0	1	0	3	4	6	7	7	8	5	7	7	5	5						
(1 + 2)	0	4	0	6	5	12	10	11	12	12	15	12	7	6	1					

APPENDIX 5. Lengths of larval C.capitata kept at different temperatures.

Lengths are given in micrometer eyepiece divisions. One division is equal to 13.9 µm. The mean lengths are also given in µm.

a. 10°C First experiment.

Time (days)					
0	3	5	7	8	12
7.5	9.0	9.0	9.1	9.9	10.5
7.0	8.9	10.5	9.5	9.5	10.6
7.5	8.8	9.3	10.3	9.0	10.3
8.1	8.2	10.0	8.4	10.0	10.1
8.0	9.1	8.5	9.5	9.5	9.9
9.0	8.9	8.8	9.5	9.4	9.7
9.0	9.0	8.5	10.5	9.3	10.1
8.9	8.7	10.0	9.7	9.7	10.7
9.0	9.0	10.0	9.6	10.1	10.1
7.9	8.3	9.0	9.2	9.6	10.0
$\bar{x}$=8.19	8.79	9.46	9.53	9.60	10.10
=113.8µm	122.1µm	131.0µm	132.4µm	133.4µm	140.3µm

APPENDIX 5. Cont.

b. 10°C Second experiment.

Time (days)							
0	2	3	5	7	9	12	15
7.7	7.8	8.4	8.5	8.5	7.5	9.0	10.5
7.3	7.6	7.5	8.9	8.7	10.0	10.1	10.1
7.0	9.0	8.4	8.5	9.3	9.0	9.1	9.5
7.9	8.6	8.0	9.0	9.0	10.0	9.5	9.7
8.1	8.5	8.8	8.5	8.7	9.0	9.0	10.3
7.9	7.5	8.6	8.5	10.0	10.0	10.1	10.1
8.5	8.0	8.3	9.1	8.0	9.1	9.5	10.6
7.9	8.0	7.5	8.3	8.5	8.5	9.5	9.5
7.0	7.8	8.0	8.1	9.2	9.0	9.1	9.8
7.1	8.4	8.8	8.1	8.6	9.1	9.0	10.0
$\bar{x}$=7.65	7.80	8.23	8.55	8.85	9.12	9.39	10.01
=106.3µm	109.8µm	114.2µm	118.8µm	123.0µm	126.7µm	130.5µm	139.1µm

APPENDIX 5. Cont.

c. 15°C First experiment.

Time (days)				
0	2	3	5	7
8.1	8.3	9.0	10.5	9.9
7.6	8.3	8.5	10.5	10.5
8.3	7.9	9.5	8.4	10.3
8.2	8.7	9.9	9.0	11.8
8.6	8.6	8.4	9.8	10.5
8.2	8.4	9.1	10.0	11.5
8.1	8.8	9.8	10.0	10.5
8.0	8.8	8.5	9.8	12.0
8.0	9.0	9.0	9.7	9.9
7.5	8.2	8.8	9.6	9.5
$\bar{x}$=8.06	8.50	9.05	9.73	10.64
=112.9µm	118.1µm	125.8µm	135.1µm	147.8µm

APPENDIX 5. Cont.

d. 15°C Second experiment.

Time (days)			
0	3	5	7
8.6	8.0	9.0	9.9
8.1	7.9	9.9	10.3
8.0	10.5	10.0	10.5
7.9	9.9	10.7	11.5
8.5	9.9	10.2	10.5
8.7	9.2	10.0	11.0
8.3	8.9	10.5	11.7
8.1	10.0	9.1	10.5
8.1	9.0	9.5	10.5
8.8	9.0	9.3	10.7
$\bar{x}$=8.31	9.23	9.82	10.61
=115.4 µm	128.1 µm	136.4 µm	147.4 µm

APPENDIX 5. Cont.

e. 20°C First experiment.

Time (days)				
0	2	5	7	9
7.5	8.9	9.0	9.7	10.3
8.1	8.1	8.7	9.8	10.1
8.5	8.3	9.6	10.1	9.0
8.5	8.5	9.3	9.0	9.1
8.3	8.0	9.5	9.0	9.7
8.1	9.2	9.1	8.8	9.8
8.1	8.1	9.1	9.6	9.3
8.2	8.2	8.9	9.5	9.9
8.4	8.3	9.2	9.3	9.9
8.6	8.6	9.1	9.8	9.6
$\bar{x}$=8.23	8.42	9.15	9.46	9.67
=114.2 µm	116.9 µm	127.1 µm	131.4 µm	134.3 µm

APPENDIX 5. Cont.

f. 20°C Second experiment.

Time (days)				
0	2	5	7	9
8.2	9.0	8.5	9.8	9.2
7.9	8.2	8.7	8.6	9.5
7.6	7.5	8.2	8.7	8.6
8.5	8.0	8.3	9.2	8.7
8.5	8.1	8.5	8.8	8.9
8.3	8.0	8.5	8.0	8.8
8.1	8.0	8.1	9.4	8.9
8.2	8.0	8.2	9.3	9.2
8.2	7.7	8.4	9.0	9.1
8.2	8.0	8.4	9.0	8.6
$\bar{x}$=8.17	8.05	8.38	8.98	8.95
=113.3 µm	111.9 µm	116.3 µm	124.7 µm	124.3 µm