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THE BIOLOGY OF MARINE GASTROTRICHA AT HAMPTON HARBOR, NEW HAMPSHIRE

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THE BIOLOGY OF MARINE GASTROTRICHA AT HAMPTON HARBOR, NEW HAMPSHIRE

by

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B. A., Northeastern University, 1966
M. S., University of New Hampshire, 1967

A THESIS

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ABSTRACT

THE BIOLOGY OF MARINE GASTROTRICHA AT HAMPTON HARBOR, NEW HAMPSHIRE

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KENNETH R. MC GEARY

Scientific investigations of the microscopic organisms living in water films between marine sand grains span the last fifty years; yet the biology of the protistan and metazoan populations dwelling within this labyrinthine universe remains poorly known. The influence of environmental factors in controlling the distribution and abundance of specific interstitial populations is only vaguely comprehended, as are interstitial food webs and energy flow within marine sand ecosystems.

Toward the development of a thorough understanding of the marine interstitial environment, I chose to study the biology of a single meiofaunal group - the Gastrotricha - inhabiting intertidal and sublittoral sands at Hampton Harbor. My goal was to define important environmental conditions surrounding resident interstitial communities while focussing attention on this single constituent group. Results are reported in three separate but related parts.

In Part I, MARINE INTERSTITIAL GASTROTRICHA FROM HAMPTON HARBOR, NEW HAMPSHIRE, I described nine gastrotrich species, representing seven families and two orders, encountered

within the estuary over a three-year period. I compared specimens with original descriptions and subsequent published reports. Observations of anatomy and natural history supplemented incomplete species descriptions, aided in interpretation of the morphology or function of questionable structures, and broadened knowledge of intraspecific geographic variation.

In Part II, ASPECTS OF THE ECOLOGY OF MARINE INTERSTITIAL GASTROTRICHA AT HAMPTON HARBOR, NEW HAMPSHIRE, I related field distribution patterns of intertidal and sublittoral gastrotrich populations to key abiotic factors. I retrieved seven of the nine species mentioned above during surveys of a sublittoral bottom transect of increasing overlying water depth. This area constitutes a porous habitat where swift tidal currents rearrange superficial sands and oxygenate strata at least 17cm below the sediment surface. Peak concentrations for abundant species (e.g. Dactylopodalia baltica, Turbanella cornuta) occurred at 5-7cm sand depths while lower densities characterized the upper 2cm of sand where sediment instability and superficial dinoflagellate mats created biologically stressful conditions.

Intertidally, I related seasonal distributional changes in three abundant gastrotrich species (i.e. Tetranchyroderma papii, Turbanella cornuta and Turbanella cirrata) inhabiting a Seabrook Beach transect to concomitant fluctuations in temperature, salinity, dissolved O_2, sediment grade, homogeneity and water content. Each species exhibited broad tolerances regarding habitable ranges of grain size, interstitial water content and temperature. Data implied relatively broad tolerance to changes in dissolved O_2 and salinity as well. Seasonal distribution patterns indicated dispersal and abundance declines following onset of stressful summer and winter temperatures. Declines, particularly in winter, involved abandonment of backshore and shallow foreshore zones which were at least partially repopulated following termination of stress. Maximal abundance declines coincided with higher temperatures for *T. papii* but lower temperatures for *T. cornuta* and *T. cirrata*. Co-occurrence data for the two turbanellid populations suggested competition between them.

Part III, METHODOLOGY FOR THE STUDY OF MEIOFAUNA-MICROFLORA RELATIONSHIPS, includes a synopsis of literature describing distribution and abundance of detritus, microalgae, and bacteria in marine sand and an evaluation of techniques for their quantitative enumeration. The latter relies in part on comparative enumerations of psammophilic microflora in Hampton Harbor sands obtained by employing both microscopic and cultural enumeration methods. In related field studies simultaneous quantitative enumerations of gastrotrichs and microfloral elements proved too narrow in scope for clarification of potential nutritional relationships.

Finally I described an experiment indicating that Hampton Harbor sands containing large numbers of *T. cirrata* in the field possess no attractive property to which specimens would respond in simple laboratory preference tests.

Methodology is contrasted with that employed in previously published studies.

INTRODUCTION

Gastrotrichs are minute, vermiform, metazoans which frequently comprise a significant fraction of the interstitial fauna isolated from marine and fresh water sand beaches. The animals living in the water films between sand grains - collectively known as the interstitial fauna or psammon - have been a topic for biological research only since the beginning of the present century. Biologists knew little about the psammon until the third decade of this century (Zinn, 1967a). Earlier work consisted primarily of a few minor papers on marine microopisthobranchs (Kowalevsky, 1901a,b), gastrotrichs and archiannelids (Giard, 1904), and nematodes (Cobb, 1917).

In the early 1920's Adolf Remane and his Kiel University associates began detailed systematic and ecological investigations of the marine interstitial fauna inhabiting German coastal strands. Within ten years their efforts resulted in the description of over 300 new species and the erection of numerous families and orders (Remane, 1933). Remane's approach has continually stressed the relationship between animal morphology and the structure of the interstitial environment. A similar faunistic approach has been adopted in work along the French coasts and in the Western Mediterranean where Delamare-Deboutteville and his associates have been active since the early 1950's. Interest in meiofaunal research has spread from these two foci during the 1950's and

1960's, and now is nearly world-wide. Active research groups are currently working throughout Europe, Scandanavia, the British Isles, the United States, and India. For a more detailed treatment of the historical origins of interstitial research consult Pennak (1968) and Delamare-Deboutteville (1960).

Nearly 50 years have passed since Remane's first pioneering studies of Kiel Bay, yet meiobenthologists still readily admit that interstitial research is still in its initial stages. The systematics of most interstitial groups remains poorly known; knowledge of the ecological factors governing the distribution and abundance of the meiofauna is rudimentary. Our knowledge of the marine Gastrotricha typifies this state of affairs. Since Remane's (1936) detailed review of early observations on gastrotrich biology, only one moderately detailed review in English has appeared (Hyman, 1951).

In most ecological publications dealing with marine Gastrotricha, data are too general to allow for characterizing either the ecology or species diversity, thus hiding relationships which are best viewed at the species level (Hummon, 1969a). In addition to short notes on associated fauna and cursory habitat descriptions numerous transect studies of gastrotrichs have been published. These attempt to assess ecological relationships between meiofaunal populations and local gradient complexes running perpendicular to the shoreline in both tidal beaches (Wieser, 1959; Ganapati & Rao, 1962; Renaud-Debyser, 1963; Hummon, 1967; Zinn, 1967b; Rao & Ganapati, 1968; Hummon, 1969a; Schmidt & Teuchert, 1969) and atidal beaches (Fize, 1963; DeZio & Grimaldi, 1964a; Schrom, 1966a; Fenchel, <u>et al</u>., 1967; Jansson, 1968a). Of these, only Renaud-Debyser (1963), Hummon (1969a) and Schmidt & Teuchert (1969) evaluated both vertical and horizontal population shifts on a seasonal basis. McIntyre (1969) emphasized the need for meiofaunal studies establishing absolute numerical density of both intertidal and sublittoral populations in order to furnish a more comprehensive base for calculations of meiofaunal biomass, generation time, and life cycle turnover rate than the limited data available for Gerlach's (1971) current estimates.

I have conducted ecological field and laboratory studies on a single meiofaunal group - the Gastrotricha - during a three year period from intertidal and sublittoral transects at Hampton Harbor, New Hampshire. Part I of this dissertation is a systematic survey, including observations regarding anatomy and natural history of gastrotrichs. Part II considers intertidal and sublittoral distribution in relation to important abiotic factors. The intertidal phase of this work surveys the dynamics of three abundant gastrotrich species on a seasonal basis. Part III contains evaluation of techniques currently used in studies of meiofaunal species and suspected food sources; critique is based on laboratory and field experiments utilizing Hampton Harbor gastrotrich populations and associated microfloral elements. I plan to submit Parts I and II as separate papers for publication in appropriate journals. The most promising techniques developed in Part III will be applied in future studies.

PART I

MARINE INTERSTITIAL GASTROTRICHA FROM HAMPTON HARBOR, NEW HAMPSHIRE

The marine gastrotrich fauna is best known from the coasts of continental Europe and Great Britain. Although knowledge of gastrotrich distribution on a world-wide basis is still far from complete, numerous publications over the last five years have contributed significantly in forming our present knowledge of geographical distribution patterns. Additional evidence is needed to ascertain whether particular gastrotrich species are truly cosmopolitan as generally has been assumed for the interstitial fauna as a whole (see Swedmark, 1964).

Five works constitute the total published record of gastrotrich distribution in the Indian Ocean. New species have been described from the Maldive Islands (Gerlach, 1961) and Malaya (Renaud-Mornant, 1967). The gastrotrich fauna of the Waltair coast of India has been discussed in three papers (Ganapati & Rao, 1967; Rao & Ganapati, 1968; Rao, 1970).

Investigations of the western Pacific Ocean are limited to those of Saito (1937) in Japan and Renaud-Mornant (1969) in the Tuamoto Islands. The description of a new *Turbanella* species in Brazil (Dioni, 1960) is the sole reference to the South American fauna.

On the western coast of North America Hummon (1966, 1969b) and Wieser (1957) have examined the fauna at Puget Sound. A short abstract by Friauf (1968) is the sole report of gastrotrichs from the U.S. Gulf coast. Thane-Fenchel (1970) surveyed the fauna from several south Florida beaches. Remane (1953) described a new Turbanella species from El Salvadore. Renaud-Debyser (1963) included one specific gastrotrich identification in her studies of Bimini beaches.

Schopfer-Sterrer (1969) and Ruppert (1970) described several new species taken in dredge hauls off the North Carolina coast. Hummon (1967, 1968, 1969a) described extensively the gastrotrich fauna from several Woods Hole beaches. My work constitutes the first report on the gastrotrich fauna north of Cape Cod, Massachusetts, and consequently establishes a range extension for each species considered.

Following is a comparison of specimens from Hampton Harbor, New Hampshire (70° 49' 13" W, 42° 53' 43" N) with original descriptions and subsequently published reports. The data supplement incomplete species descriptions, aid interpretation of the morphology or function of questionable structures and broaden knowledge of intraspecific geographical variation.

Most observations were made on living animals at 430X or 930X (oil immersion) of a phase contrast microscope. Permanently mounted specimens were prepared by the method outlined by Hummon (1969a).

Order Macrodasyoidea

Family Turbanellidae

Turbanella cirrata Papi, 1957

Table I and Figure 1

DISTRIBUTION: Spiaggia di Nicola (Near Cuma), Italy (Papi, 1957); Woods Hole, Massachusetts (Hummon, 1967, 1969a).

DISCUSSION:

Body Dimensions

Lengths ranged 165μm (presumably recently hatched juveniles) - 705μm. Measurements of 35 specimens divided into five size classes appear in Table I. Measurements of specimens in Size Class III are consistent with those on type material by Papi (1957). Hummon (1969a) noted that Woods Hole specimens occasionally are 800μm long.

Adhesive Tubules

Papi (1957) described 8-9 anterior tubules/supportive lamina, each tubule 4.5μm long; his illustrations portray them all the same length. However, in local specimens, juveniles (Size Classes I-II) lacked the full adhesive tubule complement, tubule number was 5-7/lamina and in Size Classes III-V, tubule number was 7-9/lamina. In over 50% of the individuals in Size Classes III-V the second innermost tubule on each lamina was nearly twice the length of other tubules in the array (See Fig. 1A,B). The supportive lamina itself has oblique, inwardly directed muscles extending to the anterior tubule bases. These muscles are similar in arrangement to those illustrated in Remane's (1952) description of *Turbanella lutheri*. Neither the increased length of the second innermost tubule nor the oblique muscle bands have been described by previous workers.

The original description stated that the 15-17 ciliated lateral tubules are non-functional; the non-ciliated pair of tubules located just anterior to the caudal support piece are the only functional lateral tubules. Hummon (1969a) disagreed, suggesting the cilium-bearing tubules are functional, whereas the more posterior, unciliated pair are non-functional, rudimentary palps. My observations of adhesive behavior during routine mouth-pipetting operations corroborate Hummon's interpretation.

I noted considerable variation in the number of cilium-bearing tubules, yet the single pair of rudimentary palps was visible on nearly every individual examined. In Size Classes IV and V specimens routinely displayed 15 cilium-bearing lateral tubules/side. Their number ranged between 4 and 14/side in Size Classes I-III and was directly proportional to body length. I have deliberately refrained from using the term "pair" when referring to the cilium-bearing tubules arising on each side of the body; their position is neither strictly symmetrical nor are the distance between tubules lying behind one another regular.

Papi described 9 posterior tubules/caudal lobe. I noted 6-12 tubules/caudal lobe in Size Classes IV and V; 3-10/lobe in Size Classes I and III. Once again tubule number was directly proportional to body length.

Caudal Lobe Morphology

A cilium $7\mu m$ long (not previously described) inserts on a slight ridge protruding from the anterior edge of each caudal lobe (see Fig. 1A,C).

Head Morphology

The median head lobe is dorsally elevated above the lateral lobes as described by Hummon, (1969a).

The outer margins of the mouth orifice are smooth but the anterior edges of buccal cavity's cuticular lining are lobed (see Fig. 1B).

Epidermal Glands

Papi described spherical cephalic glands in each lateral head lobe, with smaller glandular masses present medial to them. I found the cephalic glands to be morphologically identical with the numerous, refringent masses located in the body wall dorsal to the pharynx and intestine as well as similar masses visible along the lateral body margins. Comparison of Figure 1D with Papi's illustrations indicates a greater number and dissimilar arrangement of these refringent masses in local specimens.

Lateral Body Margins

Papi illustrated them as being uneven with sharp constrictions occuring between the mounds bearing the lateral tubule bases. This undulatory pattern is far less pronounced in local specimens (see Fig. 1A,B).

Ventral Ciliation Pattern

Both the median and lateral ciliary rows are essentially as described by Hummon (1969a), however, the fusion of the median rows differs slightly from Hummon's description in that it takes place approximately 50µm anterior to the anus. I also noted a previously undescribed tuft of cilia on the median tail cone (see Fig. 1E).

Sexual Organs

In Size Classes IV and V paired testes occur lateral to the anterior intestine and occasionally a ripe egg was visible dorsal and medial to the testes (see Fig. 1A). A single specimen in Size Class III showed evidence of developing testes. No sexual organs were visible in Size Classes I and II.

Ventral Cirriform Tubule Length

Measurement of cirriform tubule length in local specimens of T. cirrata ranged from 16-27µm; the ratio of cirriform tubule length to body width ranged from 0.27-0.54. D'Hondt (1965) described Turbanella digitifera as a close relative of T. cirrata which could be distinguished from it by head width, tegment folding in the region of the caudal lobes and ventral cirriform tubule length. Neither of the first two characteristics were noted explicitly in Papi's original description and must be inferred from illustrations, hence they are taxonomically indecisive (Hummon, 1969a). D'Hondt noted that T. digitifera's ventral cirriform tubule length is variable, but the ratio of cirriform tubule length to body width ranges from 0.5-1.0. Thus my measurements of local specimens overlap slightly into the critical ratio specified by D'Hondt for T. digitifera.

After comparing Woods Hole populations of T. cirrata with specimens collected from the type locality for T. digitifera, Hummon (1969a) concluded they were identical and suggested that _T_. _digitifera_ be considered a junior synonym of _T_. _cirrata_.

I cannot separate Hampton Harbor specimens into two species based solely on the ratio of cirriform tubule length to body width. Lacking a more stable basis for distinguishing _T_. _digitifera_ from _T_. _cirrata_, I agree with Hummon's proposed synonymy.

Turbanella _cornuta_ Remane, 1925

Table II and Figure 2

DISTRIBUTION: Kiel Bay, Germany (Remane, 1925, 1926); Helgoland, Germany (Forneris, 1961); Cuxhaven, Germany (Riemann, 1966); Sylt Island, Germany (Schmidt & Teuchert, 1969); Föroyar Islands (Remane, 1932); Kristineberg, Sweden (Boaden, 1960); Laxvik and several beaches in Stockholm Archipelago, Sweden, and Tyärminne, Finland (Karling, 1954); Helsingør, Denmark (Fenchel, et. al., 1967; Fenchel, 1969); Northern Ireland (Boaden, 1966); North Wales (Boaden, 1963); Calvados, France (Kaplan, 1958); Gascogne Gulf, France (d'Hondt, 1968a); Wimereux, France (d'Hondt, 1968b); Marseille, France (Swedmark, 1956a) Roscoff, France (Levi, 1950; Swedmark, 1955, 1956b); Arcachon, France (Renaud-Debyser, 1963); Naples, Italy (Wilke, 1954); Venice, Italy (Schrom, 1966a, 1966b); Black Sea (Valkanov, 1957; Rudescu, 1966); Puget Sound, Washington (Wieser, 1957); San Juan Archipelago, Washington (Hummon, 1966); Woods Hole, Massachusetts (Hummon, 1967, 1968, 1969a).

DISCUSSION:

Body Dimensions

Length of local specimens ranged from 143μm (presumably recently hatched juveniles) - 588μm. Morphometric data were compiled by measuring 36 specimens arbitrarily divided into five size classes (Table II). Maximum size of local specimens exceeds that indicated by Schrom (1966b), is approximately equal to measurements by Remane (1926), Swedmark (1956a), Valkanov (1957) and Rudescu (1966), but is much smaller than indicated by Wieser (1957), Riemann (1966) and Hummon (1969a). It is unwise to attach significance to size variation between geographically isolated populations, since previous authors failed to designate the number of specimens measured.

Growth Patterns

Teuchert (1968) outlined the post-embryonic development of _T_. _cornuta_ from hatching to a length of 400µm. Although growth patterns inferred from Table II generally agree with his observations on Kiel Bay populations, several discrepancies deserve attention. Firstly the ratio of mean pharynx length to mean intestine length in Size Classes IV and V (greater than 400µm) is smaller than the 1:2 ratio he specified (Size Class IV = 1:2.38; Size Class V = 1:2.76).

In addition, adhesive tubule number varies more than predicted by interpolation of Teuchert's data into the format of Table II. Thus Size Class II individuals would be expected to have 2-3 anterior tubules/lamina, 4-7 lateral tubules/side and 2-3 posterior tubules/caudal lobe. Actually I observed 5-6, 5-8, and 2-5 tubules respectively. Likewise in Size Class III expected values for this same series were 3-4, 7-10, and 3-4; observed values were 4-6, 7-14 and 4-7.

Size Class V individuals had a maximum of 7 anterior tubules/lamina, 17 lateral tubules/side and 7 posterior tubules/caudal lobe, further illustrating the variability in adhesive tubule number in adults from different geographic areas.

Head Morphology

Lateral head cones were less pronounced than illustrated for the type. Head margins anterior to the cones bore slight protuberances rather than smooth contours (compare Fig. 2A,B with Remane, 1926, Fig. 2). Like Riemann (1966), I observed several adult specimens exhibiting typical head cone development on one side of the head, while the opposite cone was represented only by a slightly projecting corner. Dorsal head ciliation also differed slightly from the original description (Fig. 2B).

Adhesive Tubules

Frequently the anterior, lateral and posterior tubules were asymmetrical.

The sensory cilia on the distal tips of the lateral tubules were much shorter than originally described, their maximum length approximately twice that of the tubule (Fig. 2C).

Ventral cirriform tubules were as described by Hummon (1969a). Table III suggests that their size is only slightly altered during growth.

Caudal Lobes

Caudal lobes of local specimens are much narrower than the trunk (see Fig. 2D) and more closely resemble those illustrated by Remane (1926) than figures by Wieser (1957).

Sexual Organs

Sexual development was noted only in Size Classes IV and V. In the largest Size Class IV specimen a single ripe egg was visible; other members of this class exhibited testes only. Both ripe eggs and testes regularly were observed in Size Class V individuals.

Family Thaumastodermatidae

Tetranchyroderma *papii* Gerlach, 1953

Table III and Figure 3

DISTRIBUTION: San Rossore (near Piza), Italy (Gerlach, 1953); San Cataldo (near Lecce), Italy (DeZio & Grimaldi, 1964a); Canet Plage (near Perpignan), France (Delamare-Deboutteville, 1954); Golfe d'Aigues Mortes, France (Fize, 1957, 1963); Woods Hole, Massachusetts (Hummon, 1967, 1968, 1969a).

DISCUSSION:

Body Dimensions

Body length ranged from 154-352µm in local specimens. Dimensions of type specimens generally correspond to limits of Size Class II (see Table III). Maximum size is nearly identical in Woods Hole (Hummon, 1969a) and local specimens.

Head Morphology

I believe that the pair of short, club-shaped tentacles described by Gerlach as inserting close to a longer pair of dorsal tubules are actually knob-like protuberances from which a pair of 25µm long, vibratile cilia arise (see Figure 3A). The ventral mouth margin appears scalloped in local specimens; also the number and arrangement of buccal bristles is different than illustrated in the original description (compare Fig. 3C with Gerlach, 1953, Fig. 2D).

Adhesive Tubules

My observations of adhesive behavior support Gerlach's view that the transverse structures closely appressed behind the ventral mouth surface are anterior adhesive tubules rather than cuticular mouth supports as held by Hummon (1969a).

Two pairs of ventrolateral adhesive tubules arise anterior to the level of the juncture of the pharynx and intestine in local specimens (see Fig. 3A). The ventrolateral series illustrated by Gerlach begin at the level of this juncture.

Gerlach described the posterior pedicles as trifid. Local specimens have a fourth pair of short, dorsally directed posterior tubules, each member of which arises at the base of the outer tubules making up the main fork (Fig. 3A,B).

Sexual Organs

Sexual organs are not present in Size Classes I and II, yet Gerlach described both the single testis on the right side as well as mature eggs in San Rossore specimens 210μm long. The single testis and several mature eggs were observed regularly in Size Classes IV and V. A previously undescribed copulatory bursa, 40-55μm long and 20-25μm wide, was noted in the posterior trunk region. Its orifice could not be traced; it may be ventral and slightly anterior to the juncture of the posterior pedicles. The vas deferens also opens to the outside in this area (see Fig. 3B).

Family Dactylopodaliidae

Dactylopodalia baltica Remane, 1926

Table IV and Figure 4

DISTRIBUTION: Kiel Bay, Germany (Remane, 1926; Forneris, 1961); Helgoland, Germany (Remane, 1927); Sylt Island, Germany (Schmidt & Teuchert, 1969); Danzig Bay, Poland (Roszczak, 1939);

Calvados, France (Kaplan, 1958); Roscoff, France (Levi, 1950; Swedmark, 1950, 1954, 1955, 1956b; Jouin, 1966) North Wales (Boaden, 1963); Northern Ireland (Boaden, 1966); Key Biscayne, Florida (Thane-Fenchel, 1970).

DISCUSSION:

Body Dimensions

Maximum size (only 11 specimens measured - Table IV) is slightly smaller than indicated by Remane (1926) or Schmidt & Teuchert (1969), but greatly exceeding measurements by Thane-Fenchel (1970).

Discrepancies in measurements by Remane (1927) and Thane-Fenchel (1970) and those in Table IV may reflect real geographical differences, but judgement must be reserved until census of larger samples from each region is completed.

Adhesive Tubules

Juveniles (Size Class I) had two anterior tubules on each side of the head. In Size Classes II and III four anterior tubules are present in a transverse row on each side. The two innermost pairs are approximately half as long as the two outer pairs (see Fig. 4A). Remane (1926) described two and rarely three anterior tubules/side in adults. Thane-Fenchel (1970) illustrated four anterior tubules/side which appear to be of equal length and oriented in a longitudinal rather than a transverse series.

Lateral tubule length and distribution are as originally described, but the external trunk pseudosegmentation described in relation to lateral tubule arrangement is absent in local specimens.

Posterior tubule number ranges 3-6 tubules/caudal lobe and is directly proportional to body size (see Fig. 4A,B).

Sexual Organs

Traces of developing gonads are visible in larger Size Class II individuals; well developed sexual organs occur regularly in Size Class III. Specimens display the marked protandry mentioned by Remane (1936), i.e. well developed testes and mature eggs are not simultaneously present in a single specimen. Sperm-filled testes, the recurved portion of the vas deferens and the copulatory bursa are visible in the male phase (see Fig. 4A). Degenerating testes, eggs in various developmental stages and the copulatory bursa are characteristic of the female phase (see Fig. 4B).

Family Lepidodasyidae

Acanthodasys aculeatus Remane 1927

Table V and Figure 5

DISTRIBUTION: Helgoland, Germany (Remane, 1927); Sylt Island, Germany (Schmidt & Teuchert, 1969); Amrum Island, Germany (Forneris, 1961); Kristineberg, Sweden (Swedmark & Teissier, 1967); North Wales (Boaden, 1963); Arcachon, France (d'Hondt, 1965); Mardyck (near Calais), France (d'Hondt, 1968b); Calvados, France (Kaplan, 1958); Roscoff, France (Levi, 1950; Swedmark, 1950, 1956b); Naples, Italy (Wilke, 1954); Venice, Italy (Schrom, 1966b); Black Sea (Rudescu, 1966); Maldive Islands (Gerlach, 1961); Waltair coast, India (Ganapati & Rao, 1967; Rao & Ganapati, 1968); Key Biscayne, Florida (Thane-Fenchel, 1970).

DISCUSSION:

Body Dimensions

Maximum size (11 specimens measured) is similar to reports by Remane (1927), Levi (1950), and Forneris (1961) but exceeds that mentioned by Ganapati & Rao (1967) and Schrom (1966b) (see Table V).

Trunk width is 1/5 - 1/6 total body length, a much smaller ratio than indicated by Levi (1950), Forneris (1961) and Ganapati & Rao (1967).

Cuticular Structures

Dorsal and ventral surfaces are covered by both keelless scales and spined scales. The former are 3-5µm long on both surfaces. The latter are oriented in all directions and are more numerous than originally described. Dorsal spined scales are 10-11µm long; their ventral counterparts reach half this length. Levi (1950) and Forneris (1961) describe the spined scales as T-shaped with recurved bases. I too have seen this "T morphology" when viewing spined scales in a single focal plane; however closer examination with serial adjustment of the focal plane from the scale base to the spine tip reveals that the spine shaft is nearly square in transverse section and inserts on the scale base as originally described (see Fig. 5C).

Adhesive Tubules

Anterior tubules are arranged in a backward-opening arc just posterior to the ventral mouth margin. The exact tubule number is difficult to ascertain owing to slight head movements occuring during microscopic examination at 970X magnification; I found a maximum of eight tubules in Size Class IV specimens (Fig. 5B).

Lateral tubules are arranged in distinct dorsolateral and ventrolateral rows. Their number is directly proportional to body size; in the largest individuals examined, 25-29 tubules/side were counted (Fig. 5A).

Posterior pedicles are trifid in all size classes as described by Levi (1950) and Boaden (1963).

Sexual Organs

Gonads were visible only in Size Classes III and IV. Paired testes begin approximately 20µm behind the juncture of the pharynx and intestine and run posteriorly to the level of the copulatory bursa where they link up with paired vas deferens. These ducts bend medially and merge at the male gonopore. Neither the ventral portions of the vas deferens nor the male gonopore were visible in local specimens. The rounded, sperm filled, copulatory bursa measured 85µm wide and 35µm long. Several mature eggs lie just posterior to it in the posterior third of the body (see Fig. 5A). I was unable to see the seminal receptacle described by Wilke (1954).

Family Macrodasyidae

Macrodasys caudatus Remane 1927

Table VI and Figure 6

DISTRIBUTION: Gulf of Naples, Italy (Remane, 1927; Wilke, 1954); Porto Paone (at Nisida), Italy (Boaden, 1965); Venice, Italy (Schrom, 1966b); Marseille, France (Swedmark, 1956a); Roscoff, France (Swedmark, 1956b); Ambleteuse (near Boulogne), France (d'Hondt, 1968b); North Wales (Boaden, 1963); Northern

Ireland (Boaden, 1966); Helgoland, Germany (Forneris, 1961); Sylt Island, Germany (Forneris, 1961; Schmidt & Teuchert, 1969); Kristineberg, Sweden (Boaden, 1960); Waltair coast, India (Ganapati & Rao, 1967; Rao & Ganapati, 1968); Woods Hole, Massachusetts (Hummon, 1968, 1969a).

DISCUSSION:

Systematics

Despite several morphological discrepancies with prior taxonomic studies, I have elected to identify local *Macrodasys* specimens as *Macrodasys caudatus* because of the concurrence in structure of the sexual organs with the original description. This character appears to be the most reliable systematic criterion available. Use of anterior adhesive tubule number and placement or presence and shape of the tail as specific characters has already been questioned (Thane-Fenchel, 1970).

Body Dimensions

Maximum length (6 specimens measured) (777µm) exceeds the previous record of 700µm for Marseille specimens (Swedmark, 1956a); also relative width of the body to its length is greater than previously reported (see Table VI).

Mean tail dimensions (Table VI) were based on measurement of three individuals; the tail was absent in the other three specimens examined. But this is not unusual; Remane (1927) indicates that the tail may easily be lost during isolation of specimens. Mean tail dimensions agree with data of Forneris (1961).

Adhesive Tubules

From 14-16 anterior tubules form a backward-opening arc on the ventral head surface (see Fig. 6B). Lateral tubules are variable (11-20/side) and of equal length. The tail bears 12-18 posterior tubules. (see Fig. 6A).

Ciliation

Cilia and bristles are as previously described (Swedmark 1956a; Hummon, 1969a).

Digestive Tract

In contrast to previous reports from other areas, ventral mouth margins appear scalloped (see Fig. 6B). Mesenchymal lacunae found along the gut are colorless as described by Hummon (1969a) rather than reddish as noted in Remane's original description.

Tail Morphology

The tail is not distinct from the body as illustrated by Swedmark (1956a), Ax (1963), or Ganapati & Rao (1967); instead it forms a short gradually tapered blunt appendage (see Fig. 6A).

Sexual Organs

Paired testes arise slightly anterior to the juncture of the pharynx and intestine as illustrated by Forneris (1961). The penis tapers slightly to tip and measures 75-95µm long. The posterior penis region is slightly bulbous; sperm bundles are coiled there and extend as an elongate strand to the penis tip (see Fig. 6C). Several refractile bodies are visible in the bulbous portion as previously described by Wilke (1954). Cuticular ridges on the penis tip (see Fig. 6C) are as described by Schrom (1966b). One or several large eggs occupy the area just anterior to the penis tip. The ventral copulatory bursa occupies much of the posterior trunk region and was 140-180μm long. Internally the bursa is as illustrated by Remane (1936, Fig. 129C).

Order Chaetonotoidea

Family Chaetonotidae

Chaetonotus aculifer Gerlach, 1953

Table VII

DISTRIBUTION: San Rossore (near Piza), Italy (Gerlach, 1953); Naples, Italy (Wilke, 1954); San Cataldo (near Lecci) and Cozze (near Bari), Italy (De Zio & Grimaldi, 1964a,b); Venice, Italy (Schrom, 1966b); Canet Plage (near Perpignan), France (Delamare-Deboutteville, 1954); Gascogne Gulf, France (d'Hondt, 1966a); Arcachon, France (Renaud-Mornant & Jouin, 1965; d'Hondt, 1968a); Mardyck (near Calais), France (d'Hondt, 1968b); Calvados, France (Kaplan, 1958); Woods Hole, Massachusetts (Hummon, 1967, 1969a).

DISCUSSION:

Body Dimensions

Morphometric data were compiled for only two specimens of this locally scarce species (Table VII). Dimensions are as originally described. These individuals possessed lateral scale pattern and body proportions nearly identical to Venice specimens illustrated by Schrom. Hence despite their much larger size, I have not included a figure.

Cuticle Morphology

Dorsal scales show a thickened anterior margin as described by Schrom. There are 14 ventrolateral spined scales/side rather than 13 as originally described. The shape of the basal scale of the ventrolateral spined scales is as originally described, but the subdivision of spine types shows that the anterior series of 7 bears accessory spines connected by a lamella whereas the posterior 7 bear lamellae only. This condition coincides with Hummon's (1969a) description and Schrom's Figure 3.

Ventral Ciliation Pattern

Ventral ciliation of the posterior body is as originally described. The more strongly developed cilia anterior to the level of juncture of the pharynx and intestine, though still restricted to the narrow space between the ventral midfield and ventrolateral scales, are employed in rapid swimming.

Family Xenotrichulidae

Xenotrichula beauchampi Levi, 1950

Table VIII and Figure 7

DISTRIBUTION: Roscoff, France (Levi, 1950); Canet Plage (near Perpignan), France (Delamare-Deboutteville, 1954); Calvados, France (Kaplan, 1958); Pas De Calais, France (d'Hondt, 1968a); Gascogne Gulf, France (d'Hondt, 1968a); Arcachon, France (d'Hondt, 1966a,b); Northern Ireland (Boaden, 1966); San Rossore (near Piza), Italy (Gerlach, 1953); Venice, Italy (Schrom, 1966b); Black Sea (Valkanov, 1957; Rudescu, 1966); Waltair coast, India (Ganapati & Rao, 1967); Woods Hole, Massachusetts (Hummon, 1967, 1969a).

DISCUSSION:

Body Dimensions

Body length conforms to Gerlach's (1953) emended description (see Table VIII). Although total toe length (i.e. toe spike + furcal base) is smaller in local specimens, the ratio of spike length to total toe length remains as Gerlach described. The body is much narrower than illustrated by Levi (1950), Gerlach, or Ganapati & Rao (1967); its outline is similar to the illustration accompanying the description of Xenotrichula beauchampi var angusta by d'Hondt (1966a).

Cephalic Appendages

As noted by Hummon (1969a) and Gerlach the cephalic appendages are actually cirri (see Fig. 7A). Their composition is as described by Hummon and their positions are as illustrated by Schrom (1966b).

Tactile Bristles

One pair of dorsolateral tactile bristles stands on the neck margins at the level of the posterior pharyngeal region; a second pair is visible slightly anterior to the outer proximal edges of the furcal branches; (see Fig. 7A) a third pair described by Hummon as located above the posterior tuft of ventral cirri is absent in local specimens.

Scale Pattern

Only dots, corresponding to scale stalks, are visible on dorsal and ventral body surfaces. Gerlach noted that the true nature of the stalked scales (i.e. the presence of both scale stalks and their distal end plates) is apparent only on the lateral body margins. From 52-55 transverse rows of such dots extend from the head to the furcal bases on the dorsum. These dots are arranged in 9-13 longitudinal rows in the head and neck regions, whereas 15-17 longitudinal rows are present at the widest point on the trunk (see Fig. 7A). Ventral scalation conforms to Hummon's description.

Digestive Tract

The mouth is surrounded by a striated ring and lies below a slight protuberance as illustrated by Gerlach (see Fig. 7B). The pharyngeal corona described by Hummon was absent in local specimens.

Ventral Cirri

The anterior fields extend approx. 15µm beyond the juncture of the pharynx and intestine (see Fig. 7B). The transverse bars lying lateral to these anterior fields are as described by Schrom (1966b) and Gerlach. Several specimens displayed only four cirri in each of the posterior tufts rather than five as originally described by Levi.

<u>Heteroxenotrichula</u> <u>squamosa</u> Wilke, 1954

DISTRIBUTION: Gulf of Naples, Italy (Wilke, 1954); Marseille, France (Swedmark, 1956a); Woods Hole, Massachusetts (Hummon, 1969a).

DISCUSSION: Only three specimens were isolated during this study; of these, detailed measurements were made on only one. It was 199µm long including the 51µm long toes. Pharynx, intestine and toe spike were 47, 86, and 51µm long respectively. Head width (at the level of the cephalic tentacles) was 41µm. Appearance of the dorsum was precisely as illustrated by Wilke. Minor variations from the original description in ventral cirri pattern and tactile bristles are as described by Hummon (1969a).

TABLE I. Mean ± standard deviation of measurements (µm) of five size classes of _Turbanella cirrata_ Papi, 1957.

Character	I (250-349µm)		II (350-424µm)		III (425-499µm)		IV (500-574µm)		V (575-620µm)	
Length:										
Entire body	308.6	36.53	379.4	25.48	461.6	20.06	540.1	21.00	596.8	15.71
Pharynx	128.0	9.31	144.4	10.45	154.0	14.04	178.9	14.74	196.8	2.21
Intestine	133.4	24.68	192.4	22.66	247.2	25.72	311.4	12.40	344.3	9.18
Width, at level of:										
Head lobes	48.4	2.44	51.0	4.36	57.7	2.82	62.5	4.65	62.5	1.00
Pharyngeal pores	41.1	3.66	45.6	3.43	53.9	3.56	58.1	4.27	56.3	4.50
Base of tail	20.0	3.48	23.2	2.05	25.2	3.96	25.9	1.86	26.0	1.41
Tips of outermost post ad. tubules	33.7	8.20	37.3	4.57	42.4	4.96	43.1	4.09	44.8	3.50
Sample Size	7		5		5		14		4	

TABLE II. Mean ± standard deviation of measurements (µm) of five size classes of *Turbanella cornuta* Remane, 1925.

Character	I (143-199µm)		II (200-299µm)		III (300-399µm)		IV (400-499µm)		V (500-588µm)	
Length:										
Entire Body	156.0	18.38	246.7	36.14	360.6	22.50	433.8	23.72	527.6	29.15
Pharynx	71.0	8.48	88.0	19.70	113.2	4.08	113.9	7.87	128.4	6.93
Intestine	71.0	8.48	120.0	15.62	208.4	20.55	271.5	15.61	354.3	27.96
Cirriform tubule	10.0	0.00	9.8	2.25	11.5	0.57	11.7	0.48	11.7	0.52
Width, at level of:										
Head cones	39.0	5.66	43.3	6.81	53.8	3.56	54.5	3.62	60.7	3.43
Pharyngeal pores	32.5	4.95	35.3	4.93	45.2	3.96	47.2	2.23	50.9	4.63
Base of tail	13.5	0.71	14.0	2.64	16.8	2.17	18.3	1.78	19.0	2.16
Tips of outermost post ad. tubules	17.5	4.95	22.0	6.00	27.2	3.70	29.7	3.26	29.7	2.93
Sample Size	2		3		5		13		13	

TABLE III. Mean ± standard deviation of measurements (µm) of four size classes of *Tetranchyroderma papii* Gerlach, 1953.

Character	I (154-199µm)		II (200-249µm)		III (250-299µm)		IV (300-352µm)	
Length:								
Entire body	169.4	15.96	231.4	13.31	271.1	14.10	324.6	14.82
Pharynx	72.6	4.39	76.9	10.85	88.8	8.90	100.3	3.45
Intestine	65.8	12.54	95.5	10.88	108.2	12.24	129.3	18.20
Lateral head tentacle	21.0	1.00	21.3	1.50	21.7	1.34	23.8	2.91
Width, at level of:								
Head	38.2	2.17	42.8	3.49	45.1	2.26	47.4	2.37
Post. end of pharynx	38.2	4.60	50.4	2.99	52.3	4.99	54.1	2.85
Base of feet	24.0	2.55	23.8	2.86	24.5	1.73	26.4	1.13
Sample Size	5		7		16		7	

TABLE IV. Mean ± standard deviation of measurements (µm) of three size classes of *Dactylopodalia baltica* Remane, 1926.

Character	I (200µm)	II (200-299µm)		III (300-360µm)	
Length:					
Entire body	190.0	243.6	25.82	322.2	23.46
Head (pharynx)	54.0	63.2	1.09	73.0	2.24
Intestine	102.0	136.8	17.07	185.6	27.23
Width, at level of:					
Head	47.0	56.6	3.29	62.6	3.51
Neck	27.0	34.2	2.17	39.2	6.26
Trunk	37.0	52.8	4.44	58.2	9.63
Base of tail lobes	23.0	27.7	2.36	27.6	2.07
Sample Size	1	5		5	

TABLE V. Mean ± standard deviation of measurements (µm) of four size classes of *Acanthodasys aculeatus* Remane, 1927.

Character	I (260-360µm)		II (410-421µm)		III (620-680µm)		IV (750-780µm)	
Length:								
Entire body	325.5	45.05	415.3	5.51	650.0	39.60	766.5	14.85
Pharynx	157.5	20.63	161.3	22.90	251.0	7.07	282.0	42.43
Intestine	129.0	8.91	180.7	17.10	328.0	14.14	428.5	112.43
Width, at level of:								
Head	39.3	4.19	46.3	0.58	69.0	11.31	91.5	2.12
Trunk	50.0	4.24	68.3	17.21	122.0	8.48	123.9	0.00
Base of feet	22.0	1.41	22.3	4.04	26.0	0.00	ND	ND
Sample Size	4		3		2		2	

TABLE VI. Measurements (µm) of Macrodasys caudatus Remane, 1927 (6 individuals, size range 666-777µm) Mean ± standard deviation.

Character	Mean	S.D.
Length:		
Entire Body	724.3	50.77
Pharynx	304.0	44.95
Intestine	373.8	60.62
Tail	37.0	14.42
Width, at level of:		
Head	92.4	13.81
Trunk	132.4	30.08
Tail	16.5	4.94

TABLE VII. Measurements (µm) of Chaetonotus aculifer Gerlach, 1953 (2 individuals, size range 167-177µm) Mean ± standard deviation.

Character	Mean	S.D.
Length:		
Body & toes	172.0	7.07
Pharynx	43.5	3.53
Intestine	85.5	6.36
Toe (including spike)	28.8	4.52
Width, at level of:		
Head	37.5	3.53
Neck	28.0	1.41
Trunk	48.2	0.35
Toe (between spike tips)	45.5	7.78

TABLE VIII. Measurements (μm) of _Xenotrichula beauchampi_ Levi, 1950 (6 individuals, size range 172-212μm) Mean ± standard deviation.

Character	Mean	S.D.
Length:		
Body & toes	201.8	17.30
Pharynx	49.4	2.79
Intestine	101.4	14.31
Toe (including spike)	30.6	15.20
Toe spike	16.3	1.30
Width, at level of:		
Head	36.4	4.04
Neck	29.4	2.07
Trunk	52.4	8.79

FIGURE 1. _Turbanella_ _cirrata_ Papi, 1957. A. Entire animal, ventral view B. Anterior end, ventral view C. Posterior end, ventral view D. Pattern of epidermal gland distribution E. Ventral ciliation pattern.
Scale unit at left of each drawing: A, D and E = 100µm; B and C = 50µm.

Abbreviations: at, anterior adhesive tubules; cm, cuticular margins of buccal cavity; csp, caudal support piece; eg, epidermal glands; i, intestine; l, supportive lamina; lt, lateral adhesive tubule; om, oblique muscles; p, pharyngeal pore; pt, posterior adhesive tubules; r, ridge bearing cilium; rp, rudimentary palp; t, testis; tc, median tail cone; vct, ventral cirriform tubule.

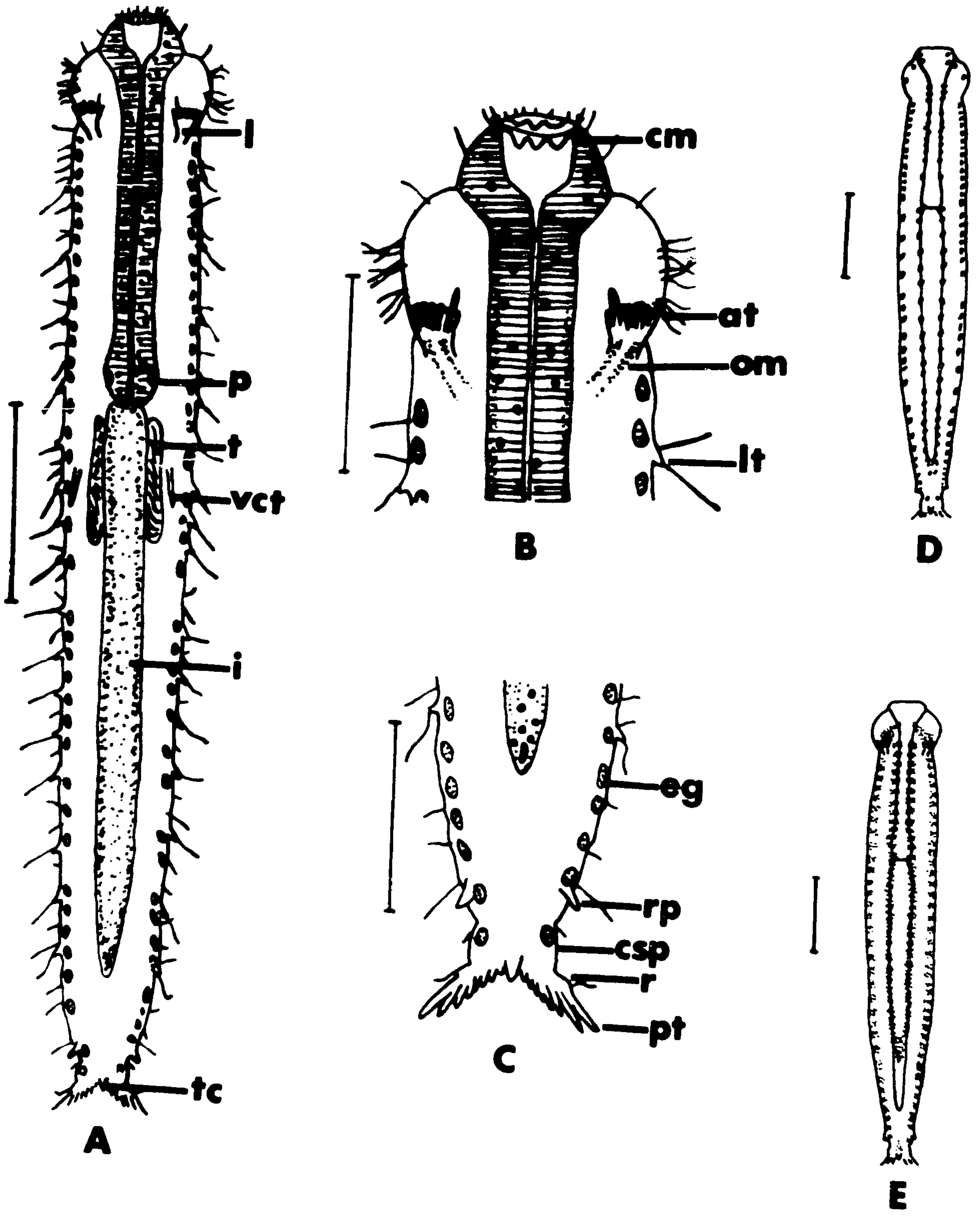

FIG. 1

FIGURE 2. Turbanella cornuta Remane, 1925. A. Entire animal, ventral view B. Head with two ciliary bands (dorsal view) C. Lateral body margin at level of anterior portion of intestine D. Posterior end, ventral view.
Scale unit at left of each drawing: A = 100µm; B, C and D = 25µm.

Abbreviations: at, anterior adhesive tubules; cl, caudal lobe; eg, epidermal gland; i, intestine; l, supportive lamina; lc, lateral head cone; lt, lateral adhesive tubule; p, pharynx; pt, posterior adhesive tubules; t, testis; tc, median tail cone; vct, ventral cirriform tubule.

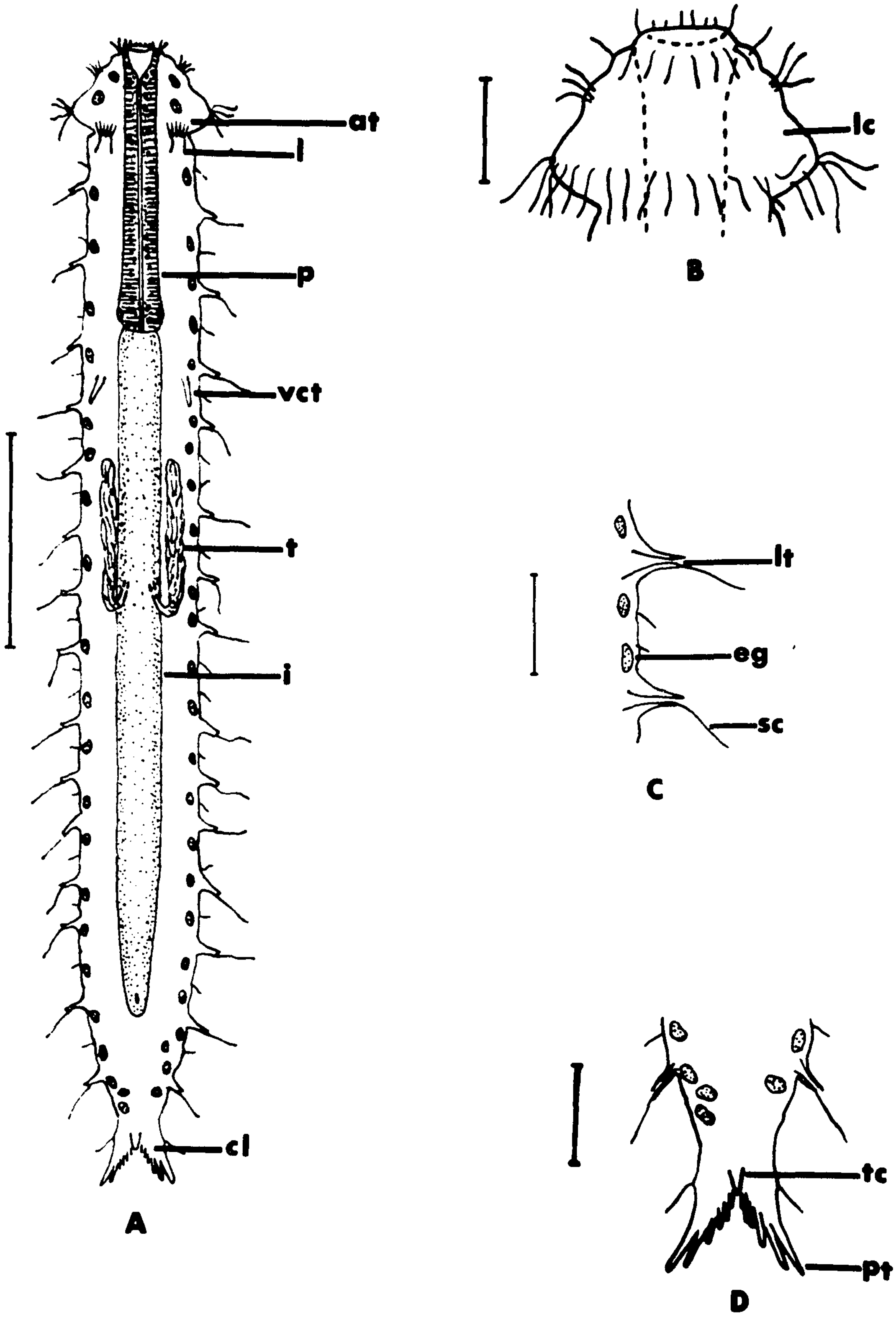

FIG. 2

FIGURE 3. Tetranchyroderma papii Gerlach, 1953. A. Entire animal, dorsal view B. Internal structures viewed from ventral surface C. Anterior end, ventral view D. Cluster of pentancres from dorsum.
Scale unit at left of each drawing: A, B = 100µm; C = 25µm; D = 5µm.

Abbreviations: at, anterior adhesive tubules; b, buccal bristles; c, vibratile cilium extending from knob-like protuberance; cb, copulatory bursa; dt, dorsal tubule on head; e, mature egg; eg, epidermal gland; ht, lateral head tentacle; i, intestine; p, pharynx; pn, pentancres; pt, posterior adhesive tubules; t, testis; vd, vas deferens; vlt, ventrolateral adhesive tubule.

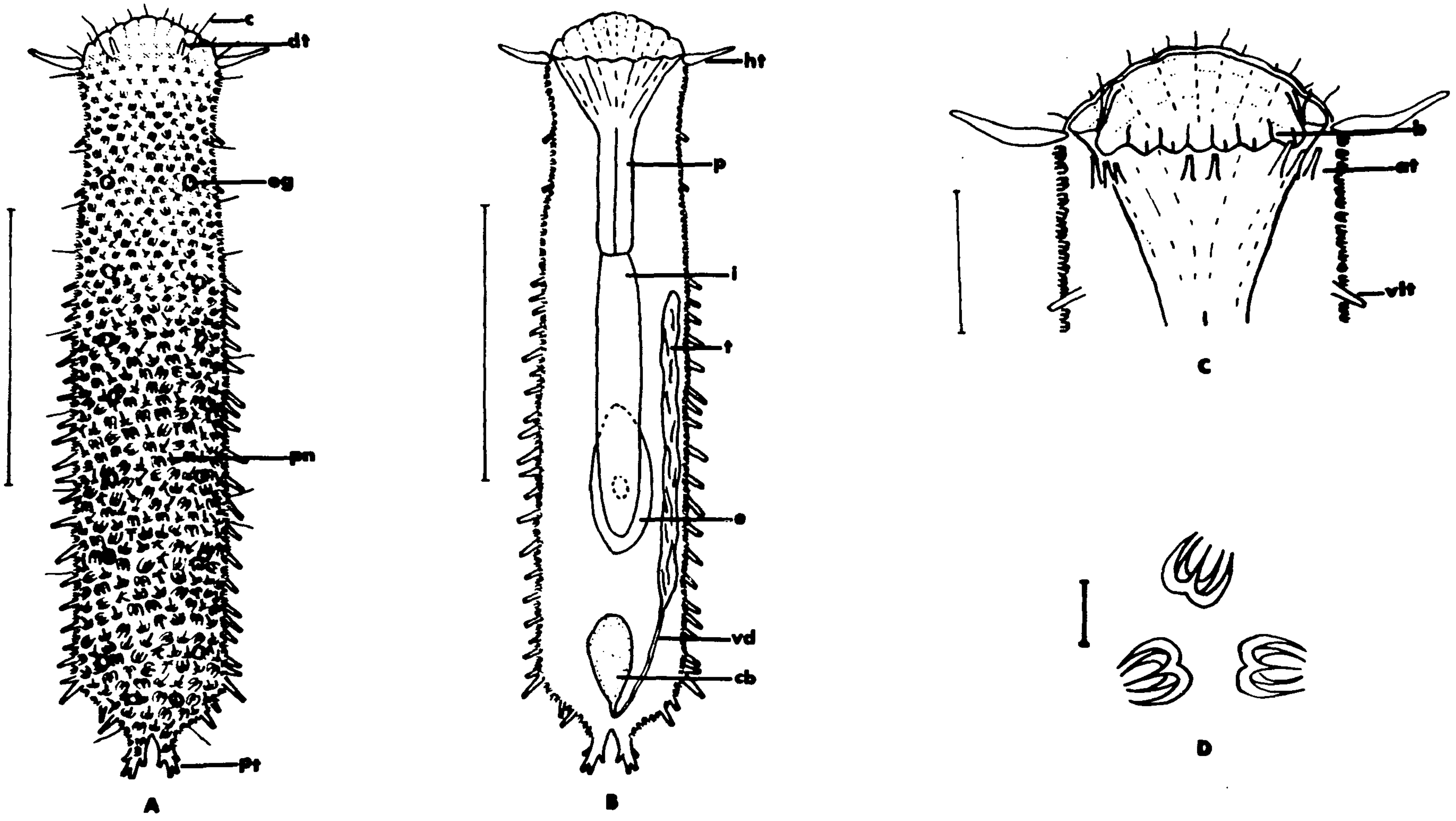

FIG. 3

FIGURE 4. Dactylopodalia baltica Remane, 1926. A. Entire animal, male phase, ventral view B. Entire animal, female phase, dorsal view.

Scale unit at left of each drawing: A, B = 100µm.

Abbreviations: at, anterior adhesive tubules; cb, copulatory bursa; dt, degenerating testes; e, eye; i, intestine; ie, immature egg; lt, lateral adhesive tubule; me, mature egg; p, pharynx; pt, posterior adhesive tubules; t, testes; vd, recurved portion of vas deferens.

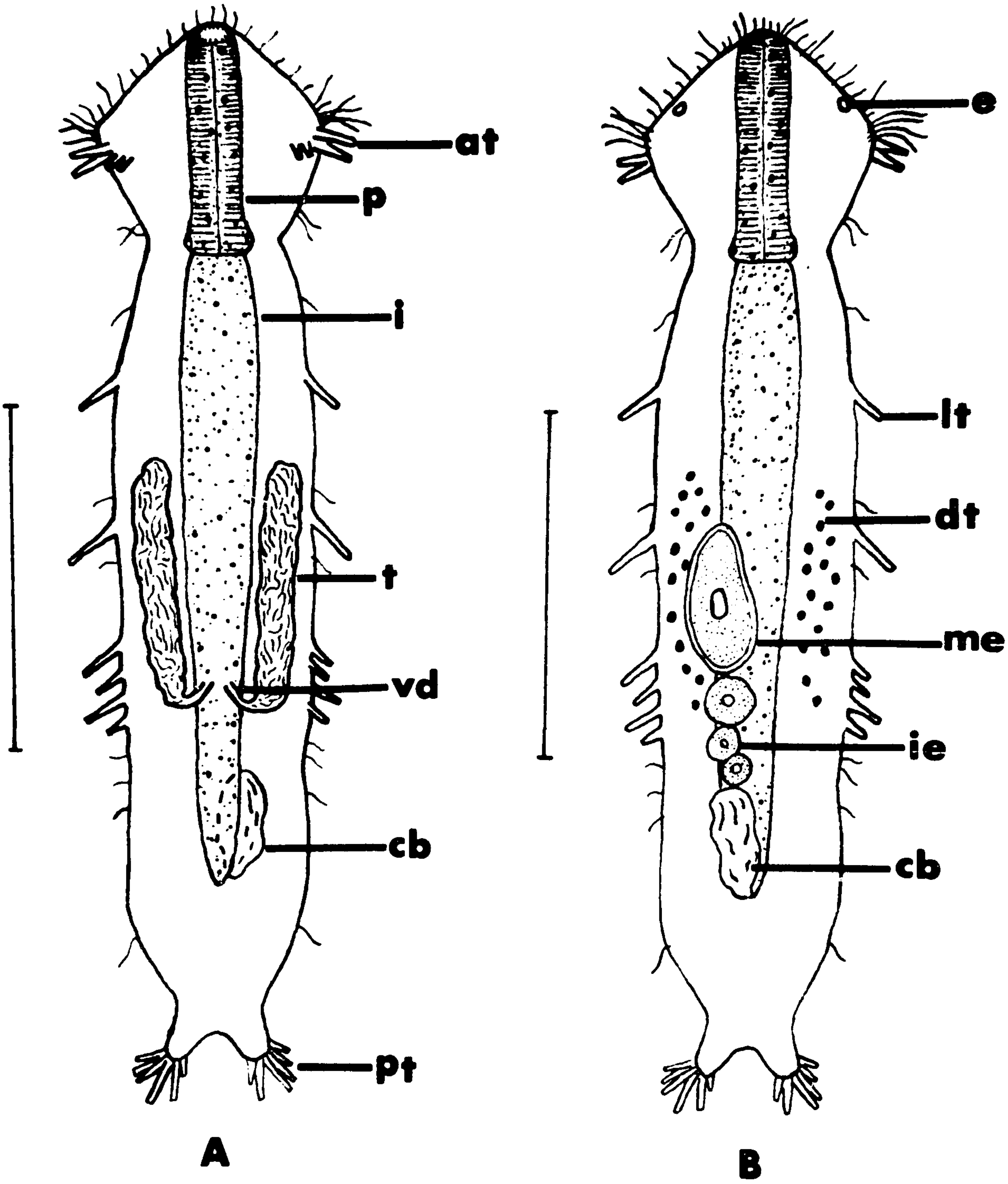

FIG. 4

FIGURE 5. Acanthodasys aculeatus Remane, 1927. A. Internal morphology viewed from dorsum B. Anterior end, ventral view C. Cuticular morphology viewed dorsally at level of anterior intestine.
Scale unit at left of each drawing: A = 100µm; B = 25µm; C = 10µm.

Abbreviations: at, anterior adhesive tubule; c, lateral cilia on head; cb, copulatory bursa; e, egg; es, elliptical, spineless scale; i, intestine; lt, lateral adhesive tubule; m, mouth; p, pharynx; pt, posterior adhesive tubules; ss, spined scale; t, testis; vd, vas deferens.

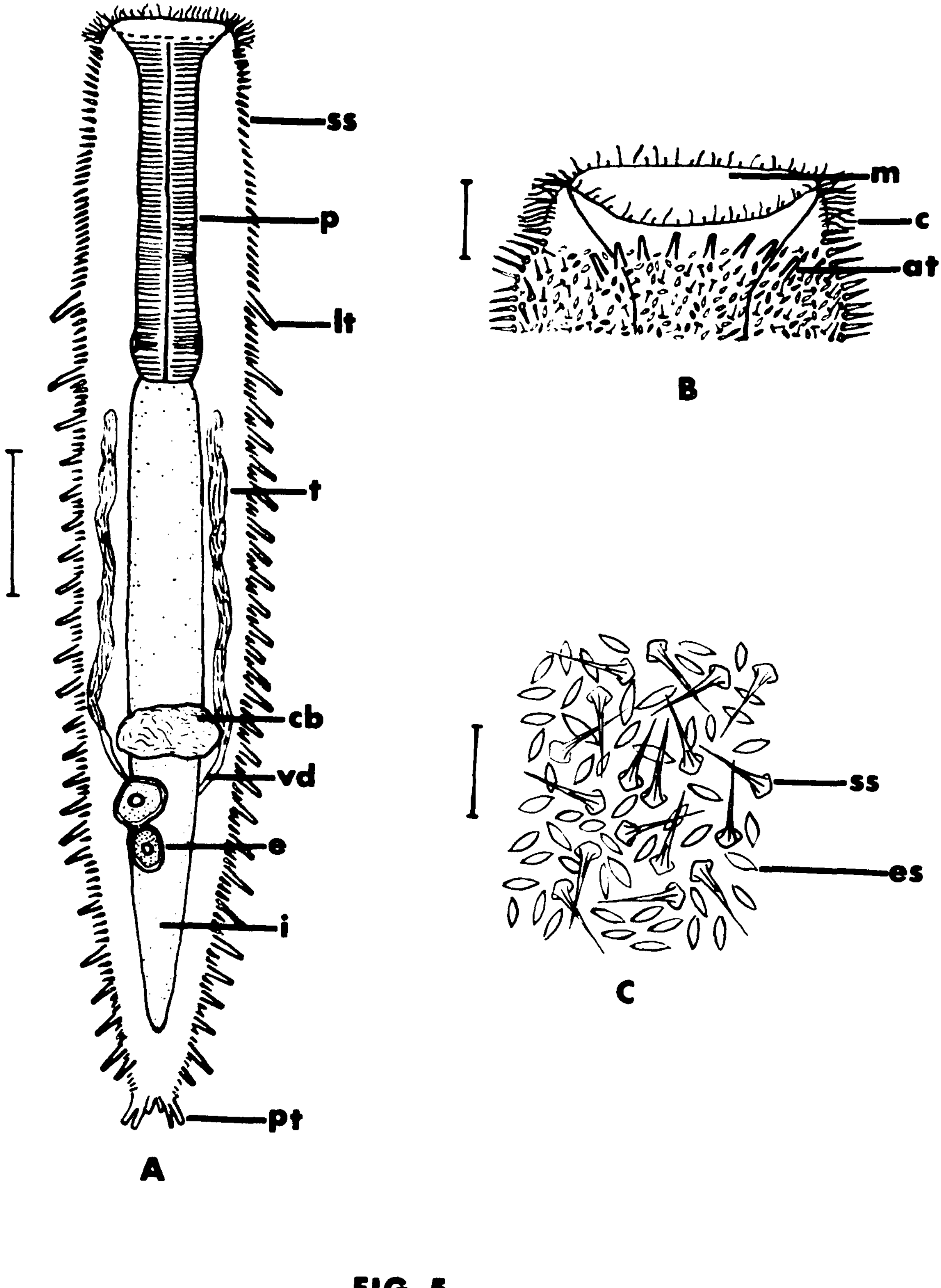

FIG. 5

FIGURE 6. Macrodasys caudatus Remane, 1927. A. Internal morphology, ventral view B. Anterior end, ventral view C. Penis morphology.
Scale unit at left of each drawing: A = 100µm; B, C = 25µm.

Abbreviations: at, anterior adhesive tubule; cb, copulatory bursa; cr, cuticular ridges; e, egg; i, intestine; lt, lateral adhesive tubule; m, ventral mouth margin; p, pharynx; pe, penis; pt, posterior adhesive tubule; rb, refractile body; sb, sperm bundle; t, testis; tb, tactile bristles; vd, vas deferens.

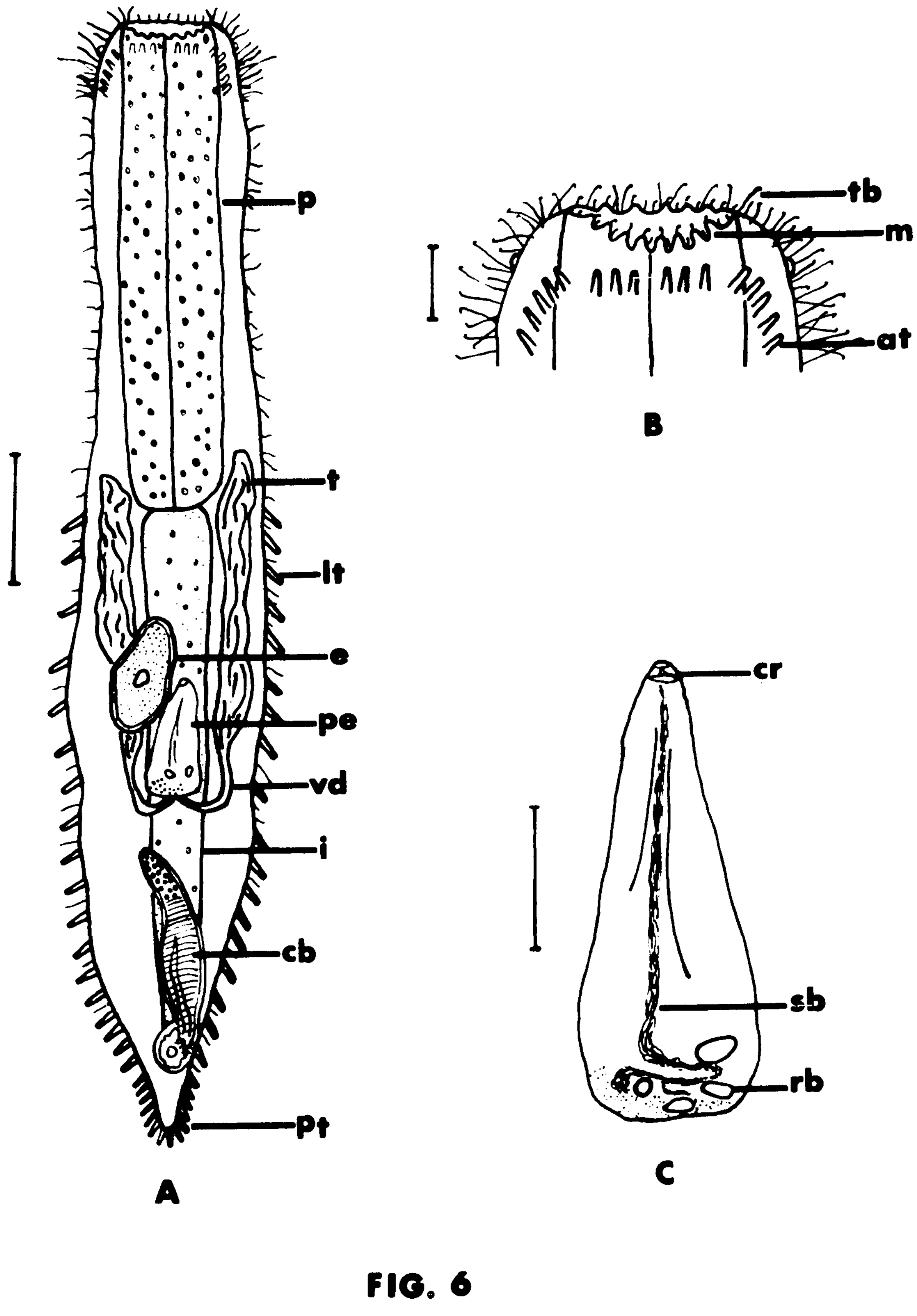

FIG. 6

FIGURE 7. Xenotrichula beauchampi Levi, 1950. A. Entire animal, dorsal view, showing scalation pattern B. Entire animal, ventral view, showing arrangement of ventral cirri and internal morphology.

Scale unit at left of each drawing = 25µm.

Abbreviations: ag, adhesive gland bulb; avc, anterior field of ventral cirri; db, dorsolateral tactile bristle; e, egg; fb, furcal base; i, intestine; lac, lateroanterior cephalic cirrus; lpc, lateroposterior cephalic cirri; mr, striated mouth ring; p, pharynx; pr, protonephridium; pvc, posterior tuft of ventral cirri; ss, stalked scales of lateral body margin; t, testis; ts, toe spike.

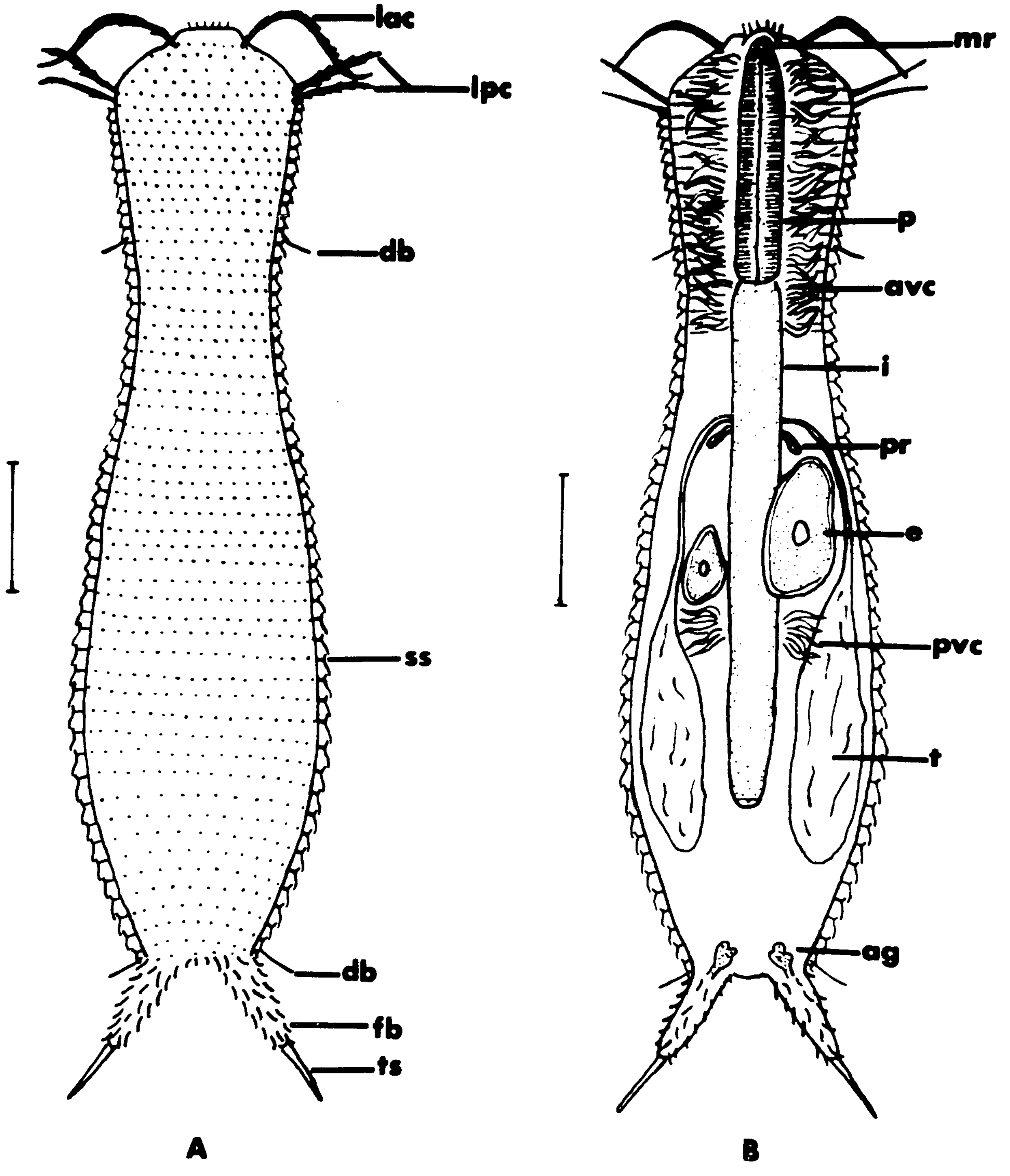

FIG. 7

PART II

ASPECTS OF THE ECOLOGY OF MARINE INTERSTITIAL GASTROTRICHA AT HAMPTON HARBOR, NEW HAMPSHIRE

Quantitative information on meiofauna is difficult to obtain; therefore, literature in this field is limited (Pollock, 1971). Past meiofaunal investigations have generally been semi-quantitative (i.e. they have not yielded estimates of absolute numerical density). As Gray & Rieger (1971) pointed out, truly quantitative valuation requires assessment of sampling, extraction, and counting efficiencies; yet few meiofaunal surveys have included estimates of any of these critical efficiencies. Most intertidal transect studies have been of too short a duration to perceive seasonal meiofaunal population oscillations. With few exceptions, these sampling schemes were insufficiently detailed for both vertical and horizontal meiofaunal population shifts to be followed. In my intertidal studies, I traced seasonal distributional changes in gastrotrich populations in a single beach and have related these changes to certain key abiotic factors. Numerical data have been qualified by inclusion of both extraction and observational efficiency estimates. Hopefully other meiobenthologists will adopt a methodology similar to that of Hummon (1969a) or Gray & Rieger (1971) in attempting to achieve estimates of absolute numerical density.

Only in this way will the disturbingly small pool of detailed seasonal data be expanded.

Quantitative sublittoral investigations of continental shelf meiofaunal have been primarily confined to shallow regions having non-porous sediments (mud or sand with clay-silt fractions over 5%) or sands in sheltered areas of reduced water circulation where anaerobic conditions develop within a few centimeters of the sediment surface. Rarely have samples been taken deeper than 10cm below the sediment surface. Most investigators have treated broad meiofaunal groups as units and have based their meiofaunal density estimates on a small number of samples. Semi-quantitative samples have been obtained by subsampling from conventional grab samplers; quantitative samples of superficial strata have been taken utilizing specially designed corers (Willemoes, 1964) or grabs (Muus, 1964). For a detailed summary of sublittoral meiofaunal research consult Wieser (1960) and McIntyre (1969).

It is not surprising that few sublittoral meiofaunal distribution studies include data on gastrotrichs, since one would not expect to find such aerobic forms in the non-porous, anaerobic sediments which have received the greatest attention; however, the "conservative macrodasyoids" mentioned by Fenchel & Riedl (1970) as residing in the "sulfide system" may prove to be exceptions.

Aside from Wieser's (1960) mention of gastrotrichs in the upper 7cm of Phleger cores from Buzzards Bay, publications by Fenchel & Jansson (1966) and Fenchel (1969) are the sole reports yielding data on vertical gastrotrich zonation in sublittoral sediments. My investigation is the most detailed treatment of gastrotrich distribution in sublittoral sediments to date. Distribution patterns were recorded from both isolated sampling localities and points arranged in a transect of increasing water depth. Possible relationship to several aspects of habitat dynamics are discussed.

Following a qualitative meiofaunal survey of numerous beaches along the southern Maine and New Hampshire shoreline, I selected the Hampton Harbor estuary (70° 49' 13" W, 42° 53' 43" N) for detailed study of its diverse gastrotrich fauna (Fig. 1A,B). I established an intertidal transect on the westernmost tip of that portion of Seabrook Beach extending inside the bascule bridge (this tip lies approximately 320m southwest of the bridge). The transect extended perpendicularly from the water's edge to the mean high water level and vertically from the sand surface to the level of the interstitial space saturation at low water (= water table). This transect is 30m long and nearly 1m deep in the high tidal region. It was bordered by muddy sand at its lower extremity and by a supralittoral Ammophila growth beginning 4.7m shoreward of the uppermost station.

Sublittoral sampling centered around points adjacent to and between the arms of the crescent-shaped sand bar 420m west of the bridge. A sublittoral transect, running north to south, was established on the southern arm of the sand bar approximately 30m west of the arm's eastward facing tip (See Fig. 1B). It measured 22.5m long and extended from 0.25m below the mean low water level at the arm's southern edge to a depth of approximately 3m in the Blackwater River side of the harbor.

Sands west of the bridge are not directly exposed to the ocean surf but are indirectly exposed to ocean swells which are reduced in size by the jetties and shoal areas on the seaward side of the bridge. Strong westerly winds often cause a sizable "chop" in the harbor. As Gilmore (1966) noted, ebbing and flooding tides are funnelled through the relatively narrow opening under the bridge. During the incoming tide, the tidal streams splits into two branches near the northern arm of the sand bar. The northerly stream floods the Hampton River side of the harbor. The southerly tidal stream flows nearly parallel to the east side of the sand bar and floods the Blackwater River side of the harbor. During the outgoing tides, the tidal flow from the Blackwater River side of the harbor flows over the surface of the sand bar. The more northerly tidal flow joins it at the north side of the sand bar. The velocity of the peak tidal current reaches 4-5 knots at the narrowest outlet of the harbor near the bridge. Such currents along with wind-driven waves provide adequate water circulation to maintain oxygenated sediments with low detritus levels in the areas of the littoral and sublittoral transects. Only in the more sheltered sublittoral sediments enclosed within the crescent-shaped arms of the sand bar is a distinct sulfide zone developed close to the sediment surface during summer months.

MATERIALS AND METHODS

INTERTIDAL PHASE

Six stations (A-F) were established at 6m intervals from the water's edge landward. Their approximate elevation was determined by several sightings with a surveyor's hand level and range pole. Datum was predicted mean low tide level (Fig. 2).

At each station samples were collected from the sand surface to as close to the low tide water table as practicable at depth intervals of 1, 4, 8, 12, 16, 20, 24, 28, 32, 36, 40, 50, 60, 70, 80, and 90cm. Maximum depths sampled ranged from 12cm at Station A to 90cm at Station F. Each depth from each station constituted a sampling site. Approximately $50cm^3$ of sand was taken from each sampling site with a hand trowel and transferred to a plastic bag for subsequent laboratory analysis. Sampling dates included March 30, July 5, September 20, November 23, 1970 and January 6, February 15, March 21, April 22, and June 11, 1971. On each date sampling began at the time of predicted low water and stations were sampled in order from A-F, allowing for the progressive lag in beach drainage first described by Emery and Foster (1948).

Air temperature, surface water temperature at the low tide level, and sand temperature at each sampling site were measured to the nearest 0.5^oC with a Thermistep Telethermometer (Yellow Springs Instrument Co.). I collected a $3cm^3$ water sample from the surface water at low tide level and from the ground water table at each station. Their chlorosity was determined by $AgNO_3$ titration of $1cm^3$ subsamples as outlined by Welsh, et al. (1968). Chlorosity values were converted to salinity values (accurate to the nearest 0.5°/oo) using appropriate tables (Strickland & Parsons, 1968). I measured dissolved O_2 content to the nearest 0.5ppm in $10cm^3$ water samples from these same areas by slight modification of Burke's (1962) method (i.e. thyodene was substituted for starch indicator and 0.025 N phenylarsine oxide for sodium thiosulfate).

Sand samples of $20cm^3$ were taken from each sampling site included in the July 5, 1970 collection (n = 62); they were subjected to granulometric analysis after their fauna had been extracted and tallied. Following a distilled water rinse for removal of salt, the samples were dried for 24 hours at 60°C and then sieved through -2, -1, -0.22, 1, 1.75, 2.25, and 3 phi screens representing 4000, 2000, 1186, 500, 297, 210, and 125µm mesh openings respectively. A Ro-Tap sieve shaker was used for sieving following procedures outlined by Folk (1965). Calculation of mean phi and sorting phi followed Inman (1952). Sand particles larger than 4000µm (less than -2phi) were excluded from the analyses, since such larger (heavier) particles tend to exaggerate available interstitial space (a point first raised by Boaden, 1966). Pollock (1969) noted that a distinction of 2mm is arbitrary, yet functional "living space" for epizoic meiobenthos generally consists of sand and spaces lying between these larger particles.

A series of $50cm^3$ sand samples was collected from surface, middle and ground water depths at Stations B, D and F and oven dried as described above. Triplicate analyses of

$5cm^3$ subsamples from each of the $50cm^3$ samples was carried out according to Hummon's (1969a) volume displacement technique for determining substratum pore space. Results established a minimum displacement value for measuring water content (expressed as per cent saturation) by Hummon's (1969a) field method. This method calls for the addition of $5cm^3$ of sand to $5cm^3$ of distilled water in a $10cm^3$ graduated cylinder. Agitation of the sand while it is being added simulates natural packing. The volume of air within the $5cm^3$ sample of naturally packed sand is indicated by the difference between the level of displaced water and the $10cm^3$ line. The technique is claimed accurate to the nearest 2% saturation. I applied it at each sampling site included in the September 20, 1970 and June 11, 1971 collection dates.

I employed a variation of Uhlig's seawater-ice technique (Uhlig, 1964; 1968) to extract gastrotrichs from field samples. After thoroughly mixing the sand in the plastic collection bag with a spatula, a $10cm^3$ subsample was transferred to a lucite tube (length = 12.7cm, inside diameter = 2.5cm) with 130µm Nitex gauze secured over one end. Next a thin cotton layer was placed over the sand and the remaining tube space was loosely packed with crushed seawater-ice (about 34^o/oo salinity). The entire apparatus was suspended with the Nitex-covered end touching the surface of $20cm^3$ filtered seawater in a phage counting plage (dimensions l = 9.5cm, w = 9.5cm, h = 1.0cm). While periodically adjusting the apparatus height to maintain only surface contact between the filter gauze and seawater, I allowed one hour for extraction. Culture dishes were systematically examined with a dissecting microscope at 14-25X magnification. Gastrotrichs were removed as identified and tallied to avoid duplicate counting. Duplicate $10cm^3$ subsamples were processed from each sampling site and a mean density value calculated for each species present. The usual number of subsamples/collection date was 134, requiring four to five days for analysis. Animals were found to remain viable and healthy for at least one week when stored at 12-14°C.

I checked the seawater-ice technique's extraction efficiency for each abundant gastrotrich species by subjecting ice-extracted subsamples to a rigorous series of elutriations. I transferred these subsamples to $100cm^3$ graduates and added $50cm^3$ of filtered seawater. The graduates were vigorously shaken for 30 seconds and the supernatant seawater was decanted through a 46μm pore diameter Nitex screen. This elutriation was repeated twice; the screen was then inverted over a gridded culture dish and the sand and animals retained were washed off with a jet of seawater. I then stirred $30cm^3$ of $MgCl_2$ solution (isotonic to 34^o/oo seawater) into the sand remaining in each graduate. After allowing ten minutes for anesthetization, six additional seawater rinses were made to insure complete faunal removal. Repeated tally with removal of gastrotrichs from the culture dishes yielded extraction efficiency estimates free of observational error. Estimation of this latter error incurred during routine collection analyses was carried out by randomly setting aside dishes for repeated recounts terminating only when three successive counts of the same dish failed to uncover any additional specimens.

SUBLITTORAL PHASE

Establishment of the sublittoral transect followed a preliminary survey of ten localities in Hampton Harbor. At three sites within a meter of one another at each locality I collected a "superficial" (sand surface - 5cm depth) and a "deep" (6-10cm depth) $50cm^3$ sand sample in screw-top jars which were capped underwater when filled. Laboratory analysis consisted of extraction and tally of gastrotrichs contained in duplicate $10cm^3$ subsamples from each jar (methodology as described for the intertidal phase).

The 22.5m long sublittoral transect selected for more detailed study consisted of ten stations spaced at 2.5m intervals (henceforth referred to as Stations I-X, progressing in the direction of increasing water depth, i.e. north to south). Station I (approximately 0.25m below the mean low water level) may have been exposed briefly during spring tides. Water depth increased to 2m at Station V and reached 3m at Station X. This circumstance necessitated the use of SCUBA for sampling Stations II-X. All sublittoral collecting was restricted to the one hour "slack water" intervals accompanying low tides; the harbor's swift tidal currents prevented safe diving operations at other times. Such currents only permitted sampling of Stations I-VI during the October 5, 1970 transect collection; however, in a later attempt on May 21, 1971, I was successful in sampling the entire sublittoral transect.

I obtained sand cores with a longitudinally bisected polyvinyl chloride tube (length = 34cm, inside diameter = 5.4cm) whose halves were rejoined with waterproof adhesive tape strips and hose clamps. I pushed this corer 10cm into the sand by hand, then rapidly drove it 15cm deeper with several blows from a sledge hammer. A rubber stopper was inserted into the tubes' exposed end, another into the buried end, following removal of surrounding sand with a hand trowel. I immediately surfaced and passed the corer to an assistant who removed the upper stopper and carefully drained off water overlying the sand. The clamps, tape, and one half of the corer body were then carefully removed. The sand core, 25cm long, was next cut into transverse sections; the 0-2, 5-7, 10-12, 15-17, and 20-22cm sections were transferred to plastic bags. Each of these segments will henceforth be considered as a sublittoral sampling site. Examination of sand cores indicated that insertion of the rubber stopper into the buried tube end may have significantly disturbed sand in the 22-25cm core sections; hence these lower strata were not included as sampling sites.

Gastrotrichs contained in duplicate 10cm^3 subsamples from each sublittoral sampling site were later extracted, tallied and their numbers averaged. Sand samples of 20cm^3 from each sampling site at Stations II, IV, VI, VIII and X in the May 21, 1971 collection (n = 25) were subjected to granulometric analyses. Low densities of all but one sublittoral species (Dactylopodalia baltica) precluded meaningful evaluation of extraction and observational efficiencies associated with their enumeration. Procedures for extraction and tally, granulometric analyses, and evaluation of extraction and observational efficiencies were as described for the intertidal phase.

RESULTS

INTERTIDAL PHASE

Physical environment. The region of the intertidal transect had an average slope of 5^o. Slope distances between each station were constant (i.e. 6m); yet some variation in station position occurred with respect to vertical elevation above and horizontal distance from the mean low water level. Such variations were caused by seasonal modification of beach profile. Strong winds, waves and tidal currents accompanying winter storms resulted in overall sand losses from the beach; apparently a slower sediment deposition over the spring and summer compensates for such losses.

Temperature. Temperatures were most variable near the surface of upper intertidal stations and more stable at lower beach stations and deep in the sand. Measurements taken when low water occurred either during late morning or early afternoon periods indicate four general beach temperature patterns. The typical summer pattern is similar to that depicted for 20 September 1970 (Fig. 3A). The temperature gradient from the sand surface to the low tide water table increased in a landward direction (i.e. in the direction of lengthened exposure to the atmosphere). The greatest vertical temperature drop occurred in the uppermost 20cm of the sand column; temperatures below this level were elevated only a few degrees above that of the low tide water table.

The second temperature pattern extended over late fall and early winter when air temperature dropped below that of the adjacent seawater. During this period a slight temperature inversion developed in which the sand surface was 2-3°C cooler than the low tide water table. Sand surface temperatures decreased slightly in a landward direction while, here again, the vertical temperature gradient was most pronounced in the uppermost 20cm of sand. The data depicted for 23 November 1970 typify this second pattern (Fig. 3B).

Extreme winter temperatures were exemplified by the stressful conditions present on the 15 February 1971 collection date (Fig. 3C). During the preceding two-three weeks air temperatures remained below freezing and approached -20°C on several occasions. While sampling I observed ice crystals within the uppermost 1-5cm at lower stations (Stations A-C). Solidly frozen sand extended through the upper 20cm of sand at Stations D and E and well below 90cm at Station F. The warmer water table accounted for slight temperature elevation of the 8-20cm sand strata at Station B and the 24-60cm strata at Stations C-E.

A fourth temperature configuration persisted from late March through the end of April. During this interval air temperature once again exceeded that of the adjacent seawater. This period, like the fall, is characterized by sand surface temperatures differing from ground water values by 1-3°C. Once again vertical temperature gradients are largely confined to the uppermost 20cm of sand. Data for 22 April 1971 typify this pattern (Fig. 3D).

Temperature extremes for four gastrotrichs encountered intertidally are presented in Table I. Since Heteroxenotrichula squamosa was retrieved from the intertidal transect only three times, it is difficult to speculate on its temperature tolerances; if, however, it is assumed that H. squamosa is a permanent intertidal resident, then it must successfully endure the minimum annual temperature range (-2 to 12°C) occurring within the most insulated sectors of the transect.

Salinity. Results of all groundwater salinity measurements showed a mean of 30.6°/oo (S.D. = 2.5, n = 46). Hampton Harbor surface water salinities on the same dates gave a mean of 30.8°/oo (S.D. = 3.1, n = 8). On no sampling date could a distinct pattern of salinity reduction in a shoreward direction be noted by inspection of groundwater values from Stations A-F. Since this survey was restricted to sand above the low tidal water table, the depth and chemistry of any continental groundwater was not within its scope. Its influence on conditions within the transect appears insignificant since little dilution of water at the low tidal water table occurred. Yet one significant dilution of both low tidal groundwater and adjacent surface water did take place during the investigation. A reduction in salinities was noted on the 21 March 1971 sampling date (surface water = 24.8°/oo mean salinity value for transect groundwater = 25.1°/oo, S.D. = 1.4, n = 6) and can be attributed to widespread melting of accumulated ice and snow on salt marshes east of Hampton Harbor over several days preceding and including this sampling date.

Oxygen Abundance. Results of all groundwater dissolved O_2 measurements gave a mean of 4.9 ppm (S.D. = 2.5, n = 46). Hampton Harbor surface water values for the same sampling dates showed a mean of 5.2 ppm (S.D. = 1.9, n = 8). No recurrent patterns of dissolved O_2 fluctuation in a landward direction were noted; however, seasonal concomitant extremes of grounwater and adjacent seawater dissolved O_2 values were observed. Highest values were recorded during the January 6, 1971 collection (surface water = 10.8 ppm, mean value for transect groundwater = 7.8 ppm, S.D. = 2.6, n = 6), despite the fact that air and water temperatures were considerably lower during the February 6, 1971 collection. This apparent inconsistency can be accounted for by noting that, in February, solidly frozen sand layers, increasing in thickness shoreward, tended to retard air and water circulation in underlying sand strata. Lowest values were recorded during the 5 July 1970 collection (surface water = 4.0 ppm; mean value for transect groundwater = 2.2 ppm, S.D. = 0.7, n = 6). The minimal observed dissolved O_2 value for the entire investigation occurred at the ground water table at Station E on this date (1.5 ppm). At no time during the investigation was a H_2S smell or black layer, indicating anaerobic conditions, located within the intertidal transect.

Substratum. Granulometric analyses yielded mean grain size values in either medium (250-500µm) or coarse

(501-1000µm) Wentworth size classes for all sampling sites processed following the 5 July 1970 collection. Intertidal transect sands were far from homogeneous; distinct sand layering was evident throughout the investigation. Generally the coarsest layers occupied the upper 4-12cm at each sampling station; mean grain size tended to decrease with increasing sand depth; yet this trend never persisted from the surface layers to the water table without the intrusion of at least one band of coarser sediment between two finer layers.

Assuming that Inman's (1952) Sorting Phi measure is roughly equivalent to Folk's (1965) Inclusive Graphic Standard Deviation, most sampling sites analyzed could be classified in Folk's scheme as either "moderately well sorted" (sorting phi values = 0.51-0.70 phi units) or "moderately sorted" (sorting phi values = 0.71-0.99 phi units); less than 7% of the sampling sites were "poorly sorted" (sorting phi values = 1.00-1.99 phi units). The maximum phi measure observed (maximum mean-plus-sorting phi combination at a single intertidal sampling site) was 2.57 phi (1.83 mean phi plus 0.74 sorting phi), which represents 168µm (approximately 16% of the sand was smaller than 168µm). The minimum phi measure observed (minimum mean-minus-sorting phi combination at a single site) was -0.62 phi (0.62 mean phi minus 1.24 sorting phi) which represents 1537µm (approximately 16% of the sand exceeded 1537µm).

Table II shows averaged values for mean grain size and sorting phi obtained by lumping the vertical sampling sites at each station. Overall mean grain size was smallest at Station D and increased slightly in both directions. Sand homogeneity, as reflected in averaged sorting phi values, was greatest at Station A and least at Station E. Such differences in station homogeneity and overall mean gain size may be somewhat exaggerated because of the unequal number of sampling sites analyzed from each station.

Gastrotrich distribution data for the July 5, 1970 collection were compared with the results of the granulometric analyses to locate sampling sites exhibiting maximum and minimum phi values for each species. These values are taken as approximate indices of habitable grain size range for each species (see Table I).

Substratum pore space and water content. Analyses of 27 subsamples of Seabrook Beach sand by Hummon's volume displacement technique gave an approximate grain to space ratio of 60:40% (i.e. a given volume of sand contains 60% sediment particles; the remaining volume consists of air, or water, or both). This ratio compares favorably with Graton and Fraser's (1935) general pore volume estimates for beach sand.

Field measurement of pore water content occurred on two sampling dates. Averaging the results gave a generalized picture of transect water depletion occurring at low tide. I compensated for the progressive lag in the occurrence of low tide in the water table from the low water line toward the landward stations by always sampling stations in order, from A to F. Generalized transect drainage is illustrated in Figure 4, where isobars of equal saturation percentages are arranged relative to approximate elevations above mean low water. Most sampling sites at stations C-F lose more than 50% of their saturation water content during ebb tide, while only the uppermost 4 to 8cm of sand at Stations D-F drain and evaporate below 10% of their full water saturation. Surface sand layers at Stations A and B apparently lose less than 40% of their saturation water content.

Obviously a survey of pore water content on two sampling dates is insufficient to adequately reflect drainage variations resulting from alternations of spring and neap tidal cycles. Since all saturation measurements were made during low tidal periods, no valuation of the rate of water loss or the duration of exposure to low saturation conditions was possible; consideration of such factors was beyond the scope of this investigation.

Comparison of gastrotrich distribution patterns with per cent saturation data for these same sampling dates yielded the observed range of water saturation encountered by each abundant species. Values are recorded in Table I.

Extraction and observation efficiencies. Both extraction and observation processes affect the overall efficiency of specimen retrieval. Oftentimes a failure to consider observational errors can lead to a significant overestimation of extraction efficiency. Hummon (1969a) noted that observation efficiencies play a large role in determining extraction efficiencies, since raw data from both routine and check extractions must be corrected for observational error. Table III lists retrieval rates for five gastrotrich species using seawater ice extractions checked against subsequent seawater and $MgCl_2$ elutriations. Per cent net efficiency, or retrieval efficiency, is obtained by multiplying the per cent extraction efficiency by the per cent observation efficiency. Note that all population numbers and densities referred to subsequently are based on observed and therefore minimal values.

Distribution and dynamics. In three years of intertidal sampling at Seabrook Beach, I encountered five species of marine gastrotrichs (*Turbanella cirrata*, *Turbanella cornuta*, *Tetranchyroderma papii*, *Xenotrichula beauchampi*, and *Heteroxenotrichula squamosa*); I discussed their morphology in Part I. Too few individuals of *X. beauchampi* and *H. squamosa* were collected from the intertidal transect to permit detailed analysis of their seasonal distribution patterns; therefore, only the more abundant species, *T. cirrata*, *T. cornuta* and *T. papii*, were selected for detailed study. Brief reference to the *X. beauchampi* population is included, though its abundance was never great enough to permit meaningful examination of seasonal patterns. The three abundant gastrotrich species inhabited nearly all of the transect. While distributions were at times widespread, areas of maximum density were present in a consistent pattern for each population.

Figure 5 depicts patterns of annual change in population abundance for each of four species. Each number plotted was obtained by adding the mean densities for sites sampled on a particular date. Variation in low tidal heights precluded census of all 67 sampling sites on every collection date;

i.e. occasionally several of the deeper sites were missed due to a temporary height increase of the low tide groundwater table. Data plotted in Figure 5 included only sites sampled on all collection dates. I believe that my exclusion of data from sites not always sampled does not significantly distort examination of population abundance, since these sites, located close to the groundwater table, routinely displayed only trace specimen densities. Tables IV-VI trace serial changes in the number of sampling sites occupied, the location of the sampling site exhibiting the maximum mean density, and the mean density values for the three abundant gastrotrich species. The sampling site exhibiting the maximum mean density (henceforth shortened to "site of maximal density") is coded by a letter-number combination; the former refers to the station, the latter indicates the sand depth in centimeters. In Figures 6 and 7, seasonal distribution shifts are depicted by enclosing sites containing trace specimen density within cross-hatching or stippling, thusly illustrating those transect portions occupied by each of the three abundant gastrotrich species on selected collection dates.

Tetranchyroderma papii was the most abundant species on all but two collection dates; *Turbanella cirrata* supplanted it as numerical dominant during September and November 1970 (compare Fig. 5A and B). Seasonal abundance peaks for *T. papii* occurred during spring and early winter collections. The most drastic population reduction coincided with summer temperature extremes; a second, less pronounced reduction accompanied the severe cold wave separating January and February 1971 collections (see Fig. 5A and Table IV). T. papii occupied an expansive portion of the transect on 30 March 1970. Trace densities were observed at 21 samplings sites extending from superficial strata at Station A to the 20-40cm depths at Station F (Fig. 6). The 5 July 1970 collection indicated a sharp reduction in population dispersal as well as a landward displacement of the site of maximal density (Fig. 6 and Table IV).

Several trends developed during fall and early winter collection dates: mean beach temperature progressively decreased; population dispersal (as indicated by the number of sampling sites occupied) progressively increased, while the site of maximal density shifted seaward and downward (see Fig. 6 and Table IV). During this period recolonization of Station F by T. papii was first observed on 6 January 1971. By 15 February 1971 the mean beach temperature had dropped to -3.5°C, the site of maximal density was displaced shoreward and downward, and population dispersal was markedly reduced (see Fig. 6 and Table IV). March and April 1971 samplings suggest a reexpansion resulting in a distribution pattern closely resembling that of the previous spring. By the 22 April 1971 collection the site of maximal density had moved vertically upward, the mean beach temperature had climbed considerably, and the number of sampling sites occupied by T. papii increased to 26 (Table IV). A late spring warming trend was underway by the 11 June 1971 collection; it was accompanied by a shoreward migration of the site of maximal density and a reduction in population dispersal. This reduction primarily involved an abandonment of deeper sampling sites at Stations D and E. This distribution pattern appears transitional between those of 22 April 1971 and 5 July 1970. Had a July 1971 collection been made, I suspect that it might have revealed a further shoreward migration of the site of maximal density along with a depopulation of sampling sites deeper than 24cm at all occupied beach stations.

The Turbanella cirrata population displayed peak abundance on 23 November 1970; following the peak, abundance decreased through the 15 February 1971 collection. Collateral reduction in population dispersal and a downward displacement of the site of maximum density were also observed (see Figs. 5B, 7, and Table V). March and April 1971 collections showed increased abundance coupled with a recolonization of the more superficial sand strata at Stations B-E which had been progressively vacated during stressful winter conditions. A continuous upward movement in the site of maximal density also occurred during this interval (see Figs. 5B, 7, and Table V). Note that trace densities extended to sampling site F-60 on the 22 April collection. The only other occupation of Station F by T. cirrata occurred on 30 March 1970 (trace densities also noted at F-60). Data from 11 June 1971 and 5 July 1970 suggest decreased abundance during late spring and early summer. While mean beach temperatures rose, the data indicate a reduction in population dispersal with a concomitant upward and seaward shift in the site of maximal density (see Figs. 5B, 7 and Table V). Data from 20 September 1970 suggest that by late summer the upswing in abundance and population dispersal leading to the late fall peak had already begun; yet the site of maximal abundance had not yet shifted shoreward and downward (see Fig. 5B and Table V).

The Turbanella cornuta population exhibited maximum abundance on the 11 June 1971 collection date. Data from summer sampling dates (5 July 1970 and 20 September 1970) indicate an abundance decrease correlated with increased mean of the beach temperatures. These data further suggest a downward migration of the site of maximal density with a concurrent expansion in the area of the transect occupied (see Fig. 5D, 7, and Table VI). Abundance remained low during fall and early winter collections; it reached its nadir with the onset of the most severe winter conditions. The site of maximal density moved continuously downward during the fall and early winter. All Station F sampling sites were solidly frozen on 15 February 1971; this circumstance prompted a seaward displacement of the site of maximal density. The number of sampling sites occupied on this date was markedly reduced when contrasted with the three preceding collection dates (see Figs. 5C, 7, and Table VI). March and April 1971 data suggest increased abundance as mean beach temperature increased. During this period the site of maximal density shifted upward and shoreward as T. cornuta recolonized Station F. Trace T. cornuta densities extended seaward to Station D only during February, March and April collections. At other times this species was retrieved exclusively from Stations E and F (see Figs. 5C, 7, and Table VI).

Xenotrichula beauchampi was sparsely distributed in the upper 24cm of Seabrook Beach at low tide. The population level was generally too low to yield significant data regarding seasonal changes in distribution. Dense concentrations of X. beauchampi were observed only on 20 September 1970 (Fig. 5D) when mean densities exceeding 10 specimens/10cm^3 sand were noted at sampling sites B-1 and C-4.

A general analysis of co-occurrences for the three abundant gastrotrich species can be derived by recording the percentage of the total of each population found co-occurring in subsamples with another gastrotrich species on each collection date. Animals occurring at less than five specimens/10cm^3 of sand were considered present in insufficient numbers to warrant inclusion. Pollock (1969) suggested that in such low densities, small meiofaunal animals occupying the comparatively spacious labyrinth of interstitial spaces are unlikely to encroach directly upon one another.

Widely ranging individuals of one species were often noted in subsamples containing larger numbers of a second species. More numerically extensive co-occurrences between T. papii and T. cirrata were frequently found throughout the investigation. Inspection of Tables IV and V reveals that on three occasions their sites of maximal density coincided; on two others, they were separated by less than 15cm vertically. During periods of peak co-occurrence more than 92% of the T. cirrata population overlapped the distribution of T. papii, while such co-occurrences never involved more than 73% of the T. papii population.

Only on 5 July 1970 did T. papii co-occur with T. cornuta at the minimal densities specified above. Though T. papii exhibited its lowest numerical abundance on this date (Fig. 5A), its site of maximal density was located further landward than noted at any other time (Table IV). Furthermore, stresses associated with summer temperature extremes may have forced T. cornuta to move vertically downward from the more superficial sand strata at Stations E and F which it occupied during cooler spring sampling dates thereby causing a merging of larger numbers of the two species than was observed at any other time during the investigation.

Co-occurrences between T. cirrata and T. cornuta invariably involved only trace densities of one or both species (i.e. the two were never observed together in the minimal densities described above). Such trace co-occurrences nearly always consisted of a single juvenile of one species with adults of the second species. No overlap in the distributional ranges of these two species was observed on January, February, or March collections. At other times traces co-occurrences were normally restricted to the uppermost 40cm of sand at Station E; their number was greatest on 22 April 1971 when both species were recolonizing shoreward transect zones abandoned during stressful winter conditions (see Fig. 7).

SUBLITTORAL PHASE

Preliminary survey. This survey, extending through May and June 1970, included ten localities adjacent to and between the arms of the crescent-shaped sand bar. Sampling with SCUBA apparatus permitted close observation of bottom contours. Generally speaking the sampling localities displayed one of two bottom morphology patterns. The first and more commonly encountered pattern consisted of a series of parallel sand waves (wavelength = 1-2m) running east to west; i.e. these waves were positioned at right angles to prevailing tidal currents. The sand wave crests were gently rounded; often the intervening troughs were partially filled with decaying macroalgae and terrestrial debris dropping from suspension as tidal currents waned. This material either resuspended as slack water ended or was partially buried by sand grains rolling into the troughs as current speed increased. The second pattern, presumedly arising when reduced tidal currents prevailed, extensively substituted a rhythmic pattern of similarly oriented, asymmetrical ripples for the larger sand waves. A third bottom morphology type was noted in areas further removed from the sand bar (e.g. the sublittoral areas just inside the bascule bridge and immediately adjacent to the intertidal transect). Portions of these areas consisted of mixtures of fine sand, mud and pebbles partially overgrown with Mytilus edulis clumps and Ulva lactuca. No gastrotrichs were collected in the latter zones where anaerobic conditions developed in the uppermost centimeter of sediment.

Sand surfaces adjacent to and between the arms of the crescent-shaped bar exhibited a patchy brown-black surface discoloration that may play some role in sublittoral gastrotrich distribution (see Transect distribution patterns - Dactylopodalia baltica). Microscopic examination revealed that the discoloration was caused by a single species of naked dinoflagellate (morphology of furrows, epicone and hypocone suggested probable membership in the Genus Amphidinium). Individual dinoflagellates were enclosed in a viscous, transparent matrix and often formed 1mm thick mats on the surface of the sand. The adhesive nature of the matrix led me to suspect that this species may be exclusively benthic. This hypothesis was supported by experiments in which I cultured these dinoflagellates in 250ml flasks containing 125ml of Gates & Wilson's (1960) artificial seawater medium (constant illumination, temp = 10-12°C). Cells multiplied, but could never be brought into suspension by shaking (i.e. they remained firmly attached to the bottom of culture flasks).

If such dinoflagellates are strictly benthic, the question arises as to how they sustain superficial mats on bottom localities where surface sand layers are periodically shifted by tidal currents. In further experiments I mixed the uppermost centimeter of sand and its overlying Amphidinium mat, and then set the mixture aside in Petri dishes for 24 hours (temperature and illumination as described above). Subsequent examination of the dishes showed a partial re-establishment of the mat on the sand surface suggesting that these dinoflagellates may undergo cyclic vertical migrations and in this way avoid being swept from shifting surface sands.

Seven gastrotrich species were found in sand samples from sublittoral localities adjacent to and between the arms of the sand bar. Of these, four were strictly sublittoral in distribution (Acanthodasys aculeatus, Chaetonotus aculifer, Dactylopodalia baltica and Macrodasys caudatus), while the remaining three (Tetranchyroderma papii, Turbanella cornuta and Xenotrichula beauchampi) had both intertidal and sublittoral populations within the Hampton Harbor estuary.

Maximal sublittoral densities were considerably lower than corresponding littoral densities (e.g. the greatest number of specimens for any gastrotrich species in a single $10cm^3$ sublittoral sand sample was 59, the corresponding littoral value was 273). Furthermore, specimen densities in excess of five individuals/$10cm^3$ of sand for any species were far less common in sublittoral sands than in littoral sands. I established the sublittoral transect on the sand bar's southern arm because this region showed slightly higher gastrotrich densities than the other nine localities included in the preliminary survey.

Transect distribution patterns. Distribution trends for the three most abundant species were similar on both collection dates. Since the 21 May 1970 collection included all ten stations (with a total of 50 individual sampling sites) I shall refer specifically to these data when describing salient distributional features for these species.

Dactylopodalia baltica was the most abundant species (i.e. the total obtained by adding the mean density values for all 50 individual sampling sites = 72.0) and was found at the greatest number of sampling sites (i.e. it exhibited at least trace densities at 17 sites). Mean density values listed in Table VII show that D. baltica occupied sampling sites in the upper 12cm of sand at eight of the ten stations. Highest specimen concentrations were localized in the 5-7cm sand strata at Stations VII and VIII.

Interactions between D. baltica and the unidentified Amphidinium population deserve brief mention. In sand cores where a superficial dinoflagellate mat was present, seawater-ice extraction of the uppermost 2cm of sand yielded 7200-10,000 living *Amphidinium* cells/10cm^3 of sand but only trace densities (i.e. less than five specimens/10cm^3 of sand) of *D. baltica*. While enumerating gastrotrichs in the phage counting plates, I frequently observed dead or dying *D. baltica* specimens entrapped in the adherent *Amphidinium* matrix.

A different situation existed at the 5-7cm sampling sites in such cores. Here 300-500 dead *Amphidinium* cells or cell fragments were extracted/10cm^3 of sand. The *Amphidinium* matrix was less extensive and *D. baltica* specimens moved freely. These gastrotrichs displayed gut contents identical in color to *Amphidinium* cells; yet I never actually observed them ingesting either living or fragmented dinoflagellate cells.

Turbanella cornuta was next in abundance (the sum of its mean density values for the 50 samplings sites = 62.5); it displayed at least trace densities at 15 sampling sites extending over nine stations at sand depths from 0-17cm. Peak densities occurred at the 5-7cm sampling sites of Stations VII and IX (see Table VIII).

Tetranchyroderma papii was less abundant (the sum of its mean density values for the 50 sampling sites = 19.5). It occupied 12 sampling sites extending over eight of the ten stations at sand depths from 0-17cm. Highest densities were noted at Station I, depth 15-17cm and Station VII, depth 5-7cm (see Table IX).

The remaining four gastrotrich species occurring within the sublittoral transect showed maximal mean densities of 0.5 specimens/10cm^3 of sand. Sampling sites where single specimens of these species were noted on either collection date are listed in Table X.

To generalize, only three gastrotrich species occupied more than 20% of the sampling sites; the remaining four were encountered far less frequently and at extremely low densities. Of the three abundant species, two (D. baltica and T. cornuta) exhibited their greatest densities at stations where overlying water depth exceeded 2m (i.e. Stations VI-X). No gastrotrich species displayed maximal density in the uppermost 2cm of sand where the likelyhood of sediment movement by currents was greatest. Finally, only a single gastrotrich species (A. aculeatus) was recovered 20-22cm below the surface of the sand.

Extraction and observation efficiencies. These efficiencies are listed in Table III for D. baltica, T. cornuta and T. papii. Although the efficiency estimates for the latter two species are based on tests using intertidal sand samples, I suspect they hold as reasonable approximations for sublittoral sands as well.

Substratum. All sampling sites had mean grain sizes in the medium (250-500µm) or coarse (501-1000µm) grain size ranges. No clear relationship between mean grain size and sand depth was evident at any of the five stations considered. All samples were either "moderately sorted" or "moderately well sorted" (see Results-Intertidal Phase). The maximum phi measures observed (maximum mean-plus-sorting phi combination) at a single sublittoral sampling site was 2.30 phi (1.77 phi, plus 0.53 sorting phi) representing 293μm. The minimum phi measures observed (minimum mean minus sorting phi combination at a single site) was -0.15 phi (0.78 phi, minus 0.93 sorting phi) representing 1109μm.

Table XI lists averaged values for mean grain size and sorting phi obtained by lumping the vertical sampling sites at each station. The data suggest a decrease in mean grain size with an increase in sand homogeneity proceeding in the direction of increasing overlying water depth.

Gastrotrich distribution data for the 21 May 1970 collection were compared with the results of granulometric analyses to locate sampling sites exhibiting the maximum and minimum phi values for each of four gastrotrich species occurring sublittorally. These values are taken as rough indices of habitable grain size ranges available in the area for each species (see Table XII).

DISCUSSION AND CONCLUSIONS

INTERTIDAL PHASE

In sandy beaches, the labyrinthine capillary network of water films in spaces between sand grains physically defines living space for the interstitial fauna. The dimensions of these spaces in turn depend on the size, shape, sorting and packing of the individual grains as well as the quantity of shell debris and detritus trapped between them (Fraser, 1935; Ruttner-Kolisko, 1956; Callame, 1963; Pollock, 1969). In marine beaches, tidal amplitude, beach slope, and interstitial space dimensions interact to determine the extent to which tidal water may circulate (Callame, 1963). Beach types range from flat, fine grained habitats where water circulates only in superficial sand strata to steeper, more porous, larger grained habitats (mean grain size exceeding 250µm) where water may circulate to sand depths greater than 1 meter in upper intertidal zones (Renaud-Debyser, 1963; Pollock, 1969). Although ecological meiofauna studies on flat, fine grained beaches are numerous (for a review see McIntyre, 1969), contrasting data from steeper, more porous habitats such as Seabrook Beach remain scarce.

When discussing the significance of specific environmental parameters for Seabrook Beach, contrasting conditions noted in reports from nonporous, atidal or freshwater beaches have been included where pertinent. Although the different parameters of the interstitial animals' "Umwelt" (=functional environment) are discussed separately, obviously they do not interact with each other or upon the animals singly but in aggregate; frequently situations arise where several parameters simultaneously dominate or act synergistically (Jansson, 1971).

Temperature. Intertidal sand temperature is controlled by general factors including seasonal and climatic weather conditions as well as time of day. Their effects are frequently modified by additional local factors including beach slope, sediment moisture content and insulation, as well as seawater and air temperatures (Pollock, 1971). At Seabrook Beach, temperatures of the low tide water table, adjacent seawater and deeper portions of the beach were similar to, and caused by seasonal thermal changes in the atmosphere. Vertical gradients of declining temperatures developed intertidally and were most pronounced at landward stations. Marked variation in their seasonal severity, as well as a sharp, winter reversal in gradient were indicated (see Fig. 3). Similar gradients have been described elsewhere (e.g. Bruce, 1928a; Jansson, 1967a); differences in their severity relate to geographic location. Aside from seasonal gradient reversals, sand temperature inversions may also occur at flood tide (Pollock, 1971) and at night (Jansson, 1967a). Sizable temperature gradients are experienced within the surface sands at higher beach elevations only during daytime portions of low tides. Seabrook Beach temperature profiles support the generalization that sediment temperatures are stable below a depth of about 20cm (Bruce 1928a, Jansson 1967a).

Salinity. Seawater, fresh continental groundwater, evaporation from superficial sand layers, and precipitation influence interstitial salinity (Jansson, 1968b). Tidal beaches with a negligible influx of subterranean groundwater display interstitial salinities close to those of the adjacent seawater (Bruce, 1928a; Jansson 1967a, 1968b; Pennak, 1951); yet horizontal gradients of increasing salinity extend seaward when terrestrial sources of fresh water exert a greater influence (Jansson, 1967a; Pollock, 1971). In either situation, interstitial salinities at lower beach levels may fluctuate less than in the adjacent seawater (Johnson, 1967).

In general, the greatest salinity fluctuations are confined to superficial sand strata at high beach stations where evaporation and precipitation occurring during the low tidal periods exert their greatest influence. Temperature and wind significantly influence the evaporation rate (Jansson, 1967a); salinity of the uppermost 3mm of sand may be 15 times that occurring at 10mm sand depth, yet such sharp gradients have only a slight further vertical extension (Gerlach, 1954). Rain apparently has little influence on interstitial salinities in temperate beaches (Linke, 1939), but may be of some importance in tropical beaches when unusually concentrated precipitation penetrates superficial sand strata having low saturation percentages (Ganapati & Rao, 1962). Both vertical and horizontal salinity gradients are steeper and more variable on atidal beaches (Jansson 1967a) than on tidal beaches where flooding and draining seawater reduces dilution from freshwater (Pollock, 1969).

On Seabrook Beach, groundwater salinities varied little from those of the adjacent seawater; the absence of a horizontally decreasing salinity gradient landward suggests that interstitial salinities are not diluted by continental groundwater. The maximal freshwater influence on salinity coincided with a widespread seasonal melt of ice and snow; the resultant decline in salinity was not confined to the low tide water table, but involved open seawater adjacent to the study area as well.

Salinity of the groundwater table reflects conditions in more insulated, deeper strata, hence is inadequate for evaluation of vertical gradients that might develop in superficial strata high on the beach. Low sand saturation in these strata usually permit the collection of only a few drops of interstitial water; such small volumes are probably best analyzed with a Goldberg refractometer (see Hulings & Gray, 1971). Only when this tool is employed routinely by meiobenthologists will our scant knowledge of salinity microstratification be supplemented. Even then, results will have to be viewed cautiously, since the ionic content of interstitial water may differ markedly from that of well buffered seawater (Jansson, 1962).

Dissolved O_2. Differences in O_2 abundance and distribution exist among tidal, atidal and freshwater beaches. Flat, fine-grain, tidal beaches may show prolonged periods of anaerobiasis at sand depths exceeding 10cm (Gordon, 1960; Fenchel & Jansson, 1966) while steeper, coarser-grain strands are rarely anaerobic, though their dissolved O_2 values may be considerably lower than in the adjacent seawater. (Renaud-Debyser, 1963). Freshwater beaches, generally have lower dissolved O_2 values than marine beaches, owing to the greater amounts of particulate organic matter and reduced water circulation within the former (Jansson, 1967b). Decreasing O_2 abundance landward is often observed on freshwater and atidal beaches (Pennak, 1940; Ruttner-Kolisko, 1956) but is less typical in tidal beaches (Jansson, 1967b). Generally, O_2 abundance decreases downward in beaches (Pennak, 1951; Jansson, 1967b; Pollock, 1971), yet uneven distribution of grain size and water content obliterate simple gradients and give rise to more complex patterns of O_2 abundance (Jansson, 1967b).

Renewal of dissolved O_2 depends largely upon water circulation during tidal flood (Gordon, 1960; Brafield, 1964), on groundwater outflow (Jansson, 1966) and wave action (Gordon, 1960; Jansson, 1967b) but may be influenced greatly by physical and chemical properties of the sand (Jansson, 1967b). Large quantities of detritus buried in sand often produce anaerobic conditions (Pennak, 1940; Renaud-Debyser, 1963). Solidly frozen sand surfaces may lead to reduced O_2 abundance (Jansson, 1967b) or total anaerobiasis (Straaup, 1970) in underlying sand strata, while rain may increase O_2 abundance in surface sand strata (Ganapati & Rao, 1962).

Dissolved O_2 values for the low tide water table and adjacent seawater at Seabrook Beach were generally similar and followed seasonal thermal fluctuations within the habitat. Reduced water and air circulation caused by extensive sand freezing may possibly explain why maximal dissolved O_2 values did not coincide with minimal beach temperatures. No horizontally decreasing landward gradient of dissolved O_2 content was observed; in fact, groundwater O_2 values at Stations A-F consistently displayed a markedly irregular distribution. This irregularity undoubtedly reflects spacial and temporal changes in the physical and chemical properties of the sand. The relatively large water samples requisite for dissolved O_2 analyses precluded survey of all but fully saturated sand strata; this circumstance prohibited estimation of O_2 microstratification in less saturated sand strata. Oxygen levels within the beach are probably maximal when decreased water content during low tide allows air to penetrate deep into interstitial spaces and again during flood tide as O_2-rich tidal water drips downward. However, the longer interstitial spaces are fully saturated with stagnant water, the lower is the expected O_2 level (Gordon, 1960; Jansson, 1967b; Pollock, 1969).

Mechanical properties of the sediment. Beach contour and grade are determined by wind, waves, currents, and tides (Bruce, 1928a) which continually rearrange particles in surface sand layers (Swedmark, 1964). Sediment characteristics fix the extent and dimensions of interstitial spaces which in turn govern the range and speed of water circulation (Pollock, 1969, 1971). Pennak (1951) suggested that, in freshwater beaches, breaking waves cause a selective landward transport of finer particles while coarser grains accumulate close to the water's edge; yet Bruce (1928a) pointed out that, in marine beaches, wave action and longshore drift are responsible for a landward transport of coarser sand grades. Investigations of grain size microdistribution often reveal marked heterogeneity, even within small sample volumes; distinct layers of coarse sand may often penetrate homogeneous fine sand (Jansson, 1968b). Yet studies of the tidal beach at Arcachon (Renaud-Debyser, 1963) and the atidal Canet Plage in the Mediterranean (Delamare-Deboutteville, 1960) indicate the relatively homogeneous nature of sediments on these strands. Contrasting work elsewhere (Pollock & Hummon, 1971; Strahler, 1966) suggests that the passage of a tide up or down the beach may result in variable but significant change in mean grain size and sorting. Such widely divergent patterns can be explained by noting that grain size distribution of a given beach is a function of the size range of locally available sediment particles and the amount of energy imparted to the sediment by local currents and turbulence (Folk, 1965).

Particle size composition by weight analyses yielding estimates of mean grain size and sorting are regularly included in ecological surveys; this circumstance has lead to an overemphasis of the importance of grain size as an ecological factor (Jansson, 1971). Although the exact geological significance of both measures remains unclear, they undoubtedly depend upon deposition type, current characteristics, and the size range of available particles. Folk (1965) suggested that currents of intermediate yet constant strength produce the best sorting. He further noted that, in general, sand is better sorted than either gravel or silt, and fine sand (mean grain size = 2-3 phi units) has better sorting than other sand grades.

The "marble cake" type blend of medium and coarse, moderately sorted sand at Seabrook Beach is partially related to the wide range of particle sizes available within the harbor. Furthermore, seasonal and tidal variations in current strength and direction suggest the possibility of periodic "dumping" of a given sand grade intertidally, followed by rapid burial by additional sediment differing in size, sorting, or both.

Porosity, or sediment pore space, is a function of grain size, shape, sorting, and geometrical packing (Fenchel, 1969). It increases as grain size decreases or sand homogeneity (sorting) improves (Fraser, 1935; Ruttner-Kolisko, 1961). Hummon (1969a) demonstrated that sorting may exert a greater influence on porosity than grain size. Changes in the geometry of sand grain lattices, epipsammic bacterial films, and the activities of burrowing animals influence sand consolidation and hence porosity (Webb, 1969). Beach sands seldom have interstitial volumes less than 36% or more than 43% (Pennak, 1951); various Seabrook Beach sampling sites exhibited a nearly uniform 40% interstitial volume.

A sediment's permeability is influenced to a greater extent by absolute grain size than porosity (Fenchel, 1969). The addition of particles smaller than 200µm to a sediment strongly decreases its permeability (Webb, 1969). A mean grain size of 250µm has been suggested as a border area for interstitial water circulation (Ruttner-Kolisko, 1961); this agrees well with the close correlation between high percentages of fine grain sizes and low oxygen abundance noted by numerous investigators (e.g. Brafield, 1964; Jansson, 1967b; Fenchel, 1969).

Speculation concerning permeability or water circulation at Seabrook Beach is difficult. To accurately gauge the extent of interstitial blockage by fine sediment one must know the size of individual interstitia; this cannot be inferred from sieving analyses alone, since grain shape and compaction must be taken into account (Fenchel, 1969). However, particles smaller than 210µm were not present in the high percentages characteristic of flat, fine grain beaches (maximum percentage by weight = 27.9%); furthermore, grains smaller than 125µm (particularly effective in reducing permeability) occurred only in trace amounts (maximum percentage of weight = 0.65%). Such granulometric data and the extensive drainage of interstitial pore water observed during low tide intervals are both incongruous with conditions of widespread interstitial blockage and reduced water circulation; hence extensive stagnation and poor water circulation seem unlikely at Seabrook Beach.

Like permeability, capillarity is mainly an inverse function of grain size, but may be greatly influenced by grain shape and packing. Molecular attractions between sand grain surfaces and their surrounding water films may cause water to rise 6-10cm higher than the local water table (Pennak, 1951). When such forces completely span interstitial pores (e.g. when silt, clay or detritus particles accumulate between larger sand particles), water is held tightly and permeability becomes low (Longwell, et. al., 1969).

Pore water content of intertidal sediments is determined by interaction of nearly all physical parameters discussed thus far (i.e. beach slope, tidal and wave activity of seawater, freshwater influx from precipitation and subterranean sources, evaporation, sediment grain size, sorting, porosity, permeability, and capillarity). In tidal beaches, daily flooding renews capillary water within the entire intertidal zone, while in atidal and freshwater beaches, moistening of drier backshore sediments occurs only during periods of vigorous wave action or precipitation (Pennak, 1951). Interstitial water distribution within tidal beaches depends primarily upon downward percolation of seawater and an upward capillary rise induced by **surface** evaporation (Pennak, 1940; Ruttner-Kolisko, 1956). Such a downward gradient of increasing pore water may be interrupted when an interposed layer of fine sand displays greater porosity and capillarity than a coarser layer lying directly beneath it (Jansson 1966b, 1967c,d). Detritus concentrations which locally increase sediment capillarity may cause other irregularities in pore water distribution (Jansson, 1967d).

At Seabrook Beach there were several instances of overlying sand strata with slightly higher saturation percentages than layers directly beneath them. I suspect that such irregularities were caused by layering of sands having different mechanical properties rather than localized detritus concentrations, since routine faunal extractions indicated only rare instances of abundant interstitial detritus. Similarly, the irregularity of the 30, 50, 90, and 100% saturation isobars depicted in Figure 4 probably reflect uneven drainage patterns caused by sand layering.

With the diurnal ebb and flow of tidal water to counter the pervasive atmospheric influence at Seabrook Beach, the latter factor was of major importance in deeper sand layers only in the upper beach during winter. Evaporation undoubtedly draws some interstitial water regularly from upper beach sediments and more broadly over the superficial few centimeters of sand during midsummer. Seabrook Beach experiences little runoff from rain water other than that falling directly onto the beach during low tide.

Responses to environmental factors by gastrotrichs. Many researchers have attempted to correlate field distributions of specific interstitial meiofauna with environmental parameters (see Jansson, 1968b; Pollock, 1971 for recent reviews). In particular, gastrotrich distribution patterns may follow changes in salinity (Fenchel, et. al. 1967), seasonal temperatures (Renaud-Debyser, 1963; Hummon, 1969a; Harris, 1972), O_2 abundance (Schmidt & Teuchert, 1969), grain size and porosity (Wieser, 1959; Schrom, 1966a), pore water content (Ganapati & Rao, 1962; Renaud-Debyser, 1963; Hummon, 1969a) or tidal elevation (Schmidt & Teuchert, 1969). Yet in the dense web of fluctuating parameters, it is nearly impossible to establish the effect of the separate factors on the animals without supplemental, controlled, laboratory tests of parameter tolerance and preference. Unfortunately such testing must await refinements in laboratory techniques for the handling and culture of marine interstitial gastrotrichs. Despite these drawbacks a generalized picture of gastrotrich response to particular environmental factors is emerging slowly.

The occurrence of gastrotrichs in marine, brackish and freshwater interstitial biotapes denotes their euryhalinity as a group, yet the broadness of salinity tolerance and preference for individual marine species remains largely untested. Nevertheless, recent salinity tolerance tests by Hummon (1969a) suggest that many marine species survive 24 hours at $10^{o}/oo$, but succumb to salinities of $2^{o}/oo$ within 10 minutes or $1^{o}/oo$ within one minute. His field data showed reduced densities or shifts in location down the beach for several gastrotrich species following periods of concentrated rainfall (e.g. over 14cm within 24 hours). Such downpours caused groundwater salinities at 5cm sand depths high on Crane's Beach to drop $3^{o}/oo$ below Buzzard's Bay surface waters. Such concentrated precipitation did not occur during the present investigation. The previously mentioned seasonal melt of ice and snow and the concomitant salinity minima at Seabrook Beach did not reduce population densities, in fact, the three abundant gastrotrich populations appeared to be increasing in numbers during this period (Fig. 5A-C).

Correlations between the geographic distribution of marine gastrotrichs and salinity characteristics of North, Baltic and Mediterranean waters prompted Remane (1936) to place known species within an arbitrary salinity tolerance ranking. More recently, field data suggest that Turbanella cornuta's distribution was limited to the foreshore in an atidal Øresund beach because fresh groundwater reduced backshore salinities to $2^{o}/oo$ (Fenchel, et. al., 1967).

Seasonal oscillations in gastrotrich abundance correlate closely with extremes in habitat temperature; data from various sources (e.g. Ganapati & Rao, 1962; Renaud-Debyser, 1963; Hummon, 1969a; Schmidt & Teuchert, 1969; and Harris, 1972) reveal declines in gastrotrich abundance accompanying summer and winter temperature extremes. In several cases (Renaud-Debyser, 1963; Hummon, 1969a) populations migrated to deeper sand strata during winter in response to extremes in temperature and salinity developing in superficial sands.

Observed temperature tolerances for species inhabiting Seabrook Beach are broad (Table I), but narrower than Hummon's (1969a) ranges for Woods Hole beaches (T. papii = -2.0-31.0; T. cirrata = -2.0-28.0; T. cornuta = -2.0-26.0; X. beauchampi = -3.0-33.0; H. squamosa = -2.0-26.0°C). Though Jansson (1968a) has retrieved live T. cornuta specimens from frozen sand, neither Hummon nor I have repeated this.

Interstitial gastrotrichs comprise a portion of the aerobic sand fauna and are usually absent from strata where lack of water circulation leads to severe O_2 depletion. Several investigators (e.g. Renaud-Debyser, 1963; Hummon, 1969a) have demonstrated markedly decreased specimen numbers close to the groundwater table. With several exceptions (see e.g. Table IV - data for 15 February 1971) my observations affirm such trends. Schmidt & Teuchert (1969) suggest that severe O_2 depletion in this region may account for a total absence of gastrotrichs. Only the highly aberrant, "conservative macrodasyoids" are presently believed capable of penetration into totally anaerobic zones underlying the groundwater table (Fenchel & Riedl, 1970).

Grain size may be extremely important ecologically when it forms an interstitial network either too large or too small for habitation by interstitial animals such as gastrotrichs (McIntyre, 1969). However, recent reviews of the relationship between grain size parameters and meiofaunal distribution patterns conclude that grain sizes act primarily by effecting other parameters such as drainage, water content, and O_2 abundance (see e.g. Pollock, 1971; Jansson, 1971).

While numerous marine gastrotrichs are usually associated with particular grades of sand, many others are distributed throughout wide ranges of sand texture (see Schmidt & Teuchert, 1969, for a comprehensive listing). By burying experimental tubules filled with graded fauna-denuded sand in a North Wales beach, Boaden (1962) found that the gastrotrich Tetranchyroderma polyacanthus Remane, 1927 only colonized grades exceeding 500μm in size; this suggests a real "preference" on the part of T. polyacanthus. Wieser's conclusions from investigation of Puget Sound beaches (1959) were that commonly occurring gastrotrichs consistently were restricted to particular sand grades and a median grain size of 100μm is a "critical grain size" below which habitation by ciliary gliders such as gastrotrichs is impossible. Hummon (1969a) recalculated Wieser's sieving data, and then pointed out that it supported neither of his claims. Renaud-Mornant & Serene's (1967) report of two species of gastrotrichs in sand samples having mean diameters of 102 and 82µm respectively, also contradict Wieser's assertions. Both Hummon (1969a) and Jansson (1971) pointed out the lack of adequate controls in the above-mentioned works by Boaden and Wieser.

Experiments by Jansson (1967d) suggest that animals which move by "creeping by a ventral ciliated surface" (e.g. gastrotrichs and some turbellarians) or "burrowing with peristaltic movements of the whole body" (e.g. certain tubificids) show no preference for sands of different porosity while forms moving by "nematode-like sliding" (e.g. certain oligochaetes and harpacticoids) exhibit definite sand grade preferences. Webb (1969) demonstrated that certain lancelets and interstitial harpacticoids have distributions unrelated to sand texture, but actually correlate well with subtle changes in porosity and preferential interstitial water flow. Such changes were caused by variations in sand compaction and were undetectable by sieving analyses. Similar studies on gastrotrich species inhabiting various sand grades may prove helpful.

At Seabrook Beach the ranges of grain size occupied by _T. papii_, _T. cirrata_ and _T. cornuta_ were broad, while that of _X. beauchampi_ was somewhat narrower (Table I). Hummon's (1969a) Woods Hole data show a similar pattern (i.e. a broad range for commonly occurring species with narrower ranges for species occurring less abundantly). The extreme ranges of grain size for the three Seabrook Beach sampling sites displaying the highest field densities of _T. papii_, _T. cirrata_ and _T. cornuta_ are still relatively broad (168-870µm for

T. papii and T. cirrata, 207-790µm for T. cornuta). Such field data suggest a wide grain size tolerance with no strong preference for sand of a particular grade on the part of these three species.

The narrower range for X. beauchampi could reflect narrower preferences or merely insufficient sampling. Once again, a look at Hummon's Woods Hole data proves instructive. His granulometric analyses encompassed five beaches and included 508 sampling sites which yielded an extreme range of grain sizes for all beaches of 175-3730µm. Within this more comprehensive framework X. beauchampi occurred at 38 sampling sites and showed an extreme range of grain sizes occupied of 205-3730µm. In fact, extreme ranges for T. papii, T. cirrata, and T. cornuta were also broader at Woods Hole (205-3730, 205-2300 and 190-2640µm respectively).

Since interstitial gastrotrichs are dependent upon water films surrounding sand grains for their activities one might expect pore water content to be extremely important ecologically. Intertidally the upper size limit of their interstitial habitat is determined by the dimensions of the interstitial spaces, while its lower limit is set by the quantity of water held within these spaces at low tide (Pollock & Hummon, 1971). Yet the extreme ranges of saturation withstood by gastrotrichs on Seabrook Beach are in close accord with data from Woods Hole beaches (Hummon, 1969a); both studies indicate broad tolerances to pore water content for these species (see Table I). Assuming that the generalized pattern of transect drainage undergoes no dramatic seasonal alterations excepting those associated with extensive freezing at Station F, it seems unlikely that seasonal, distributional changes for any gastrotrich species would permit a consistent correlation between a particular saturation level and maximum density (compare Figs. 6 and 7 with Fig. 4). In other words, field data do not suggest consistent preferences for specific saturation levels for any of the abundant gastrotrich species.

Gastrotrich distribution and dynamics. The preceding discussion summarized variations in physical and chemical parameters and their probable ecological significance for interstitial gastrotrich populations at Seabrook Beach. Extremes in these factors generally define habitable areas within the beach as a whole. Specifically, lack of interstitial water in zones of totally dry sand landward of Station F limited backshore gastrotrich distribution. Foreshore distribution was limited by an area of muddy sand seaward of Station A where a lack of interstitial space and O_2 precluded gastrotrich colonization. Since gastrotrichs are confined to areas where sufficient water circulation exists for oxygenation of interstitial water, their penetration into sand strata below the level of the low tide water table was unlikely. The regular occurrence of gastrotrichs in surface sands, particularly in the upper beach, must be restricted to species capable of withstanding extremes in temperature, salinity and pore water content characteristic of this zone where abrupt atmospheric changes may create biologically stressful conditions. Lower beach stations and deeper sand strata at higher elevations provide a more insulated milieu which is protected by low evaporation rates and the high density and specific heat of interstitial water.

Within the broad limits of these habitable zones, specific distributions differences are far more difficult to explain. Factors such as nutritional requirements, competition and predation are all likely to be important. Subsequent determinations of preference ranges within tolerable extremes of physical and chemical parameters also may aid interpretation of microdistribution patterns.

As the single, drastically changing parameter on a seasonal basis, temperature, either acting directly or through its effect on other physical and chemical parameters, must have exerted an important influence on gastrotrich distribution shifts. Species living totally or in part within superficial sand layers of low environmental stability may be especially subject to abrupt changes in abundance. For example, X. beauchampi exhibited maximal densities in the uppermost 4cm of sand during warm summer months but dropped to trace density levels as beach temperatures fell in late fall (Fig. 5D). The population level remained too low for effective sampling throughout the remainder of the study period; in fact, X. beauchampi may have been lost from the beach for a brief period during April 1971. Alternatively, its absence in April could be explained by a shift in its habitat and survival at extremely low densities. Hummon (1969a) reported sporadic occurrence of this species on Crane's Beach. Here too the population increased during late summer and early fall, but was set back severely by the onset of the first November frosts.

Maximum densities were greater at Crane's Beach than on Seabrook Beach (maximum specimen numbers/single 10cm^3 sand sample were 221 and 57 respectively).

At Seabrook Beach, seasonal distribution patterns for *T. papii*, *T. cirrata* and *T. cornuta* indicate declines in abundance and dispersal following onset of stressful summer and winter temperatures. The decreased dispersal, particularly in winter, involved reductions in the number of sampling sites occupied in zones of low environmental stability (i.e. backshore and shallower foreshore sampling sites), suggesting that differential mortality in these more stressful beach zones may be partially responsible for the declines in abundance. At least, partial recolonization of areas vacated during extreme conditions followed termination of stress in all cases. The major period of decline in abundance coincided with higher temperatures for *T. papii* but lower temperatures for *T. cirrata* and *T. cornuta*.

The distributions of *T. papii* and *T. cirrata* on Crane's Beach (Hummon, 1969a) were similar to Seabrook Beach patterns but that of *T. cornuta* differed in that it was split into two subpopulations; one beneath the upper beach, and a second in shallow, lower beach sands corresponding in tidal elevation to the muddy sand zone seaward of Station A on Seabrook Beach (compare Figs. 7 and 8 - Hummon 1969a with Fig. 7). The sporadic occurrence of *T. cornuta* on Crane's Beach makes seasonal comparisons impossible; however, investigations at Arcachon, France (Renaud-Debyser, 1963) and on Sylt Island, Germany (Schmidt & Teuchert, 1969) both indicated declines in abundance during the warmest summer months. Seasonal data for T. papii and T. cirrata on Crane's Beach indicated summer and winter declines in abundance as in the present investigation, though Hummon found that both the T. papii and T. cirrata populations were reduced more by summer than winter temperature extremes.

There is little quantitative data with which to compare the maximum specimen densities for the three abundant gastrotrichs occurring at Seabrook Beach. Maximum concentrations of T. papii and T. cirrata (expressed as maximum number of specimens/single $10cm^3$ sand sample) were both greater on Woods Hole beaches (Hummon, 1969a) vs. Seabrook Beach (1485 and 165 vs. 273 and $86/10cm^3$ respectively). Maximal T. cornuta specimen concentrations at Seabrook Beach ($55/10cm^3$) exceeded values for Arcachon ($3.3/10cm^3$) noted by Renaud-Debyser (1963) and in the Øresund ($18/10cm^3$) reported by Fenchel, et. al., (1967) but fell short of those indicated by Hummon (1969a) for Woods Hole beaches ($132/10cm^3$) and Schmidt & Teuchert (1969) on Sylt Island, Germany ($176/10cm^3$). Such interspecific comparisons of maximum specimen densities may reflect climatic differences, patterns of food distribution, or reproductive behavior. I have little doubt that the three abundant gastrotrich species on Seabrook Beach reproduce throughout the year, since juveniles were retrieved on all collection dates. Unfortunately, nothing has been published on natality and mortality rates for interstitial gastrotrichs; furthermore, the length of their life cycles from hatching to reproductive maturity and death remains unknown.

Biotic relationships. Little is known about the role of biotic factors in determining gastrotrich distribution patterns, though it is likely that nutritional requirements, competition, and predation are all influential. Data on gastrotrich food preferences are largely based on observations of gut contents. Such methodology may bias results in favor of easily recognizable food items (e.g. diatoms) or organisms having indigestible parts (e.g. trophi of rotifers) while ignoring easily digestible items which may be more important quantitatively (Straaup, 1970). Remane (1936) proposed small organisms such as ciliates, forams, and diatoms as the major food items for macrodasyoids; for the chaetonotoids he suggested organic detritus as the most likely choice, though several species regularly had diatoms as part of their gut contents.

With the exception of *T. cornuta*, nothing has been published regarding specific food preferences for the gastrotrich species occurring at Seabrook Beach. Several authors (e.g. Remane, 1926; Fenchel, 1969) have suggested diatoms as the preferred food for *T. cornuta* because dense concentrations often occur in diatom-rich sands. I too have noted diatoms as part of *T. cornuta's* gut contents along with what appeared to be bacterial cells and occasionally a dinoflagellate. Aside from a dark brown suspension of unknown composition found almost uniformly in the intestines of *T. papii* specimens, I have seen nothing but tiny spherical and rodlike bodies, presumedly bacteria, as gut contents on the remaining species collected on Seabrook Beach.

T. papii, T. cirrata and T. cornuta often made oral contact with pennate diatoms and ciliates (primarily holotrichs and hypotrichs) while swimming, yet always recoiled upon impact without swallowing them. Moreover, these macrodasyoids often hesitated while swimming over sand grains, then appeared to orally palpate grain crevices and angular surfaces while wriggling their pharynx with a "pump-sucking" gesture. Regrettably these observations were made at magnifications too low to ascertain whether microflora attached to the grains were ingested.

Further evidence emphasizing the importance of microfloral sand films comes from laboratory experiments by Gray & Johnson (1970) which demonstrated selective preference for three bacterial forms by Turbanella hyalina. Their subsequent field studies showed close correlation between the distribution and abundance of T. hyalina and that of the preferred bacteria (see Part III for a description of my efforts in this area).

In 15 months of sampling at Seabrook Beach I encountered only one macrofaunal specimen (i.e. an animal over 2mm long), the amphipod Haustorius canadensis. Feeding on gastrotrichs must be limited primarily to meiofaunal predators, since nearly all gastrotrich populations remained too deep in the sediment to be exposed to surface feeding macrofauna. Most likely candidates in this poorly studied feeding category include larger Turbellaria and Nematoda; yet during the entire investigation not one instance of a gastrotrich being eaten by another animal was recorded.

The numerically extensive co-occurrences of both *Turbanella* species with *Tetranchyroderma papii* have been described. The latter's wide funnel-like mouth is dissimilar to the narrower buccal capsules of the turbanellids, suggesting that it feeds in a manner different from theirs. On the other hand, likeness in buccal capsule morphology for the two turbanellids may signify similarities in their feeding methods. The infrequent co-occurrences of the two turbanellids were restricted to individuals which appeared to be of different age. Collectively these facts favor the possibility of intrageneric rather than intergeneric competition, thus helping to explain seasonal distribution patterns of *T. cirrata* and *T. cornuta*.

Hummon (1969a) believes that the niche of *T. cirrata* (known only from oceanic habitats) is included within that of *T. cornuta* (known from habitats ranging from oceanic to dilute estuarine) and that the former outcompetes the latter in mid-beach zones. Obviously my co-occurrence and seasonal distribution data are in accord with Hummon's notion (see Fig. 7). Reports of *T. cornuta* occupying mid-beach levels in the absence of *T. cirrata* (e.g. Renaud-Debyser, 1963) may indirectly support Hummon's hypothesis. Also, the partitioning of a Sylt Island beach (Schmidt & Teuchert, 1969) in which *Turbanella ambronensis* (possibly synonymous with *T. cirrata*) occupied mid-beach levels while *Turbanella subterranea* was confined to backshore sites, may represent a similar competitive situation.

In short, my ecological data indicate that gastrotrich species occurring in abundance within the intertidal transect have broad tolerances regarding habitable ranges of grain size, interstitial water content and temperature. Their occurrence in superficial sands and in strata adjacent to the groundwater table imply relatively broad tolerances to fluctuations in salinity and dissolved O_2 as well. Each abundant population experiences seasonal changes in numerical density and dispersal; declines following the onset of stressful summer and winter temperatures involve population reductions in zones of low environmental stability. Partial recolonization of these zones occurs subsequent to stress termination. Finally, co-occurrence data and seasonal distribution patterns for two resident turbanellid populations support Hummon's (1969a) hypothesis concerning their competitive interaction.

SUBLITTORAL PHASE

Publications on the vertical distribution of aerobic meiofauna in shallow sheltered sublittoral sands reveal only infrequent penetration below the uppermost 5cm of sand (e.g. Fenchel & Jansson, 1966; Fenchel, 1969). However this pattern does not hold for extensive coastal areas having porous sublittoral sediments and more vigorous water circulation. Aside from unpublished data referred to by McIntyre (1971), the present survey is the first attempt to characterize meiofaunal distribution in less sheltered sublittoral sands. McIntyre's examination of 23cm long cores collected by divers at up to 8m depth along the Scottish west coast revealed the presence of harpacticoids, turbellarians, nematodes, and gastrotrichs throughout their lengths, though densities were markedly reduced below 16cm; such data is in close accord with my own. Both sets of results undermine Gordon's (1960) claim that meiofauna at such sublittoral sand depths must experience continuous anaerobic conditions. McIntyre (1969) suggests that aerobic meiofauna may extend even deeper into sublittoral sediments; testing of this hypothesis must await the development of suitable sampling techniques.

Porous sublittoral sands are, by definition, always fully saturated; variations in their interstitial salinity and temperature are less pronounced than in the intertidal zone. This does not imply, however, that all physical and chemical parameters are more stable sublittorally. To the contrary, in the Hampton Harbor estuary, I have often observed that a single tide may alter sublittoral bottom morphology greatly while only slightly changing beach profile in adjacent littoral zones. Gomoiu (1971) has pointed out that shallow water zones, particularly in estuarine habitats, are constantly subjected to variations in topographical, geological, climatological, hydrological, and even anthropological factors of ecological significance.

Gastrotrich distribution and abundance. The present study includes the first sublittoral record of Tetranchyroderma papii; the remaining six species encountered sublittorally here, have been previously collected both subtidally and at various intertidal elevations (consult previous literature citations for each, in Part I). Species occurring only in trace densities are listed in Table X; maximum sublittoral specimen concentrations were 59,59, and 9/10cm^3 for *D. baltica*, *T. cornuta*, and *T. papii*, respectively.

No sublittoral, and only scarce littoral, quantitative data are available for comparison: Schmidt & Teuchert (1969) found greater maximum concentrations of *A. aculeatus* (19.8/10cm^3) but only trace concentrations of *D. baltica* (1/10cm^3) at Sylt; Hummon (1969a) noted only trace concentrations of *M. caudatus* (1/10cm^3) but much higher maximal concentrations of *C. aculifer* (54/10cm^3) at Woods Hole (for quantitative data on *T. papii*, *T. cornuta*, and *X. beauchampi* see Discussion-Intertidal Phase). Obviously more quantitative ecological study is required before any meaningful statements regarding the significance of comparative species abundance can be made. Differences in intertidal and sublittoral distribution and abundance of *T. papii*, *T. cornuta* and *X. beauchampi* obviously reflect habitat dissimilarities in both biotic and abiotic factors, which require further detailed investigation.

The extreme grain size range inhabited sublittorally by *T. papii* is close to its intertidal values, while that of *T. cornuta* is more restricted (compare Tables I and XII). I suggest that this more limited range reflects both insufficient sampling and the narrower range of grain sizes available sublittorally. The narrow range for *A. aculeatus* has a similar explanation; prior reports indicated its presence not only in fine sand (Levi, 1950; Forneris, 1961), but also in medium (Gerlach, 1961; Rao & Ganapati, 1968) and coarse sands (Boaden, 1963). Although the granulometric data suggest a clear restriction of *D. baltica* to finer grades, it has been collected elsewhere in medium (Forneris, 1961) and coarse sands (Roszcak, 1939; Thane-Fenchel, 1970).

Reports of D. baltica at lower beach levels (Schmidt & Teuchert, 1969) and sublittorally (Thane-Fenchel, 1970) indicated distributions similar to that in the sublittoral transect (i.e. individuals restricted to the uppermost 10-12cm of sand). Swedmark (see Schrom, 1966b) suggested that D. baltica's distribution may closely correspond to concentrations of diatoms in superficial sand strata. I suspect that within Hampton Harbor, D. baltica feeds on dead Amphidinium cells; furthermore this food organism may exhibit tidal migratory rhythms in the uppermost sand strata. Such rhythms have been previously reported for dinoflagellates associated with intertidal sands (Rao & Ganapati, 1968).

Gut contents for T. papii and X. beauchampi were as described for the intertidal phase. Aside from occasionally noting a diatom within the gut of M. caudatus or A. aculeatus, no additional observations on food preferences which might affect sublittoral distributions were made.

The uppermost several centimeters of sand may be stressful zones for habitation by sublittoral meiofauna. Visual observations of sand movement following termination of slack water intervals suggest that the interstitial fauna dwelling in this layer are likely to be displaced from the substratum, moved into sediments differing markedly in granulometric properties, or destroyed. The patchy, superficial dinoflagellate mats may have a negative influence on meiofauna dwelling directly beneath them. Microscopic observations of

D. baltica indicated its entrapment in the viscous matrix emanating from such mats. If this adherent matrix produces extensive clogging of interstitial pores, then it is certain to pose a hazard for interstitial animals attempting to swim through it.

I further speculate that a sand depth of 20-22cm may, at least during certain times of the year, form a lower limit for habitations by the aerobic meiofauna within the transect. In several cores I noted a change in sand color from yellow to gray and a faint sulfide odor in this segment. Fenchel & Riedl (1970) showed that such "gray zones" are transitional between oxidized and totally reduced sediments and tend to contain both oxygen and hydrogen sulfide in small amounts.

Explanation of meiofaunal concentrations at intermediate sand depths (e.g. the clumping of *T. papii*, *D. baltica* and *T. cornuta* at Station VII, sand depth 5-7cm, on 21 May 1971) is more difficult. Both biotic factors (e.g. distribution of preferred food organisms, predation, and competition) and abiotic factors (e.g. differential water flow through interstitial spaces) may interact to produce such patterns.

Finally, I believe that future investigations of shallow, lotic sublittoral habitats, such as that described within Hampton Harbor, will alter the already sterotyped conception of the sublittoral zone as an area where the aerobic meiofauna is confined within the uppermost few centimeters of sand. I disagree with Steele, Monroe, & Giese's (1970) hypothesis that sublittorally, pumping by wave induced pressure changes is the dominant method of introducing water into the interstitial ecosystem. I suspect that in shallow estuarine situations, laminar and turbulent water flow associated with tidal currents causes frequent large scale transport of bottom sand and permits oxygenation of interstitial pore water 15, 20 or more centimeters below the surface of the bottom.

TABLE I. Extreme range of intertidal beach temperature, grain size and per cent saturation observed for four gastrotrich species.

Species	Temperature range (°C)	Habitable Grain Size range (μm)	Per cent Saturation (% full saturation)
Tetranchyroderma papii	-2.0-22.5	168-1197	5-100
Turbanella cirrata	-2.0-22.5	168-1173	5-100
Turbanella cornuta	-2.0-21.5	168-1214	15-40*
Xenotrichula beauchampi	-2.0-24.0	210-599	5-50*

*If sublittoral occurrences were included here, maximal observed saturation values reach 100% for these species as well.

TABLE II. Some granulometric comparisons among sands from the six sampling stations along the intertidal transect at Seabrook Beach.

Parameter	A	B	C	D	E	F
1) Mean of mean grain sizes from station sampling sites (µm)	433.6	423.0	415.7	390.0	496.9	463.9
2) Standard deviation of 1) (µm)	69.5	66.3	73.9	89.9	97.5	121.2
3) Mean of sorting phi values (phi units) from station sampling sites	0.52	0.73	0.75	0.64	0.81	0.76
4) Standard deviation of 3) (phi units)	0.14	0.06	0.11	0.18	0.18	0.19
5) Number of sampling sites analyzed	3	5	12	13	13	16

TABLE III. Efficiencies associated with extraction and observation of five gastrotrich species, based on sea water ice extraction method.

Species	No. subsamples observed	No. specimens observed	Per cent extraction efficiency		Per cent observation efficiency		Per cent net efficiency
Dactylopodalia baltica	1	9	67.0	X	84.5	=	56.6
Tetranchyroderma papii	5	68	89.7	X	80.6	=	72.3
Turbanella cirrata	5	78	91.0	X	81.6	=	74.3
Turbanella cornuta	5	70	100.0	X	79.3	=	79.3
Xenotrichula beauchampi	3	4	50.0	X	44.4	=	22.2

TABLE IV. Seasonal changes in maximum densities of Tetranchyroderma papii within the Seabrook Beach intertidal transect.

Date & (mean beach temp^{o}C)	No. sampling sites occupied	Site with maximum mean density	Maximum mean density (#/10cm^3 sand)
3/30/70 (11.4)	21	D-12	234.0
7/5/70 (19.5)	13	E-16	27.0
9/20/70 (19.1)	17	D-16	33.0
11/23/70 (7.1)	25	C-12	73.5
1/6/71 (2.7)	27	C-36	36.0
2/15/71 (-3.5)	20	C-50	85.5
3/21/71 (4.3)	19	C-16	102.0
4/22/71 (6.4)	26	C-16	149.5
6/11/71 (14.7)	17	D-16	70.5

TABLE V. Seasonal changes in maximum densities of *Turbanella cirrata* within the Seabrook Beach intertidal transect.

Date & (mean beach temp°C)	No. sampling sites occupied	Site with maximum mean density	Maximum mean density (#/10cm^3 sand)
3/30/70 (11.4)	23	C-12	18.0
7/5/70 (19.5)	20	B-4	22.0
9/20/70 (19.1)	27	B-4	32.5
11/23/70 (7.1)	26	C-12	84.5
1/6/71 (2.7)	15	C-36	31.5
2/15/71 (-3.5)	13	C-36	25.5
3/21/71 (4.3)	20	C-20	22.5
4/22/71 (6.4)	29	C-16	62.5
6/11/71 (14.7)	26	C-12	15.0

TABLE VI. Seasonal changes in maximum densities of *Turbanella cornuta* within the Seabrook Beach intertidal transect.

Date & (mean beach temp°C)	No. sampling sites occupied	Site with maximum mean density	Maximum mean density (#/10cm^3 sand)
3/30/70 (11.4)	9	F-20	7.5
7/5/70 (19.5)	10	F-20	15.0
9/20/70 (19.1)	15	F-24	5.5
11/23/70 (7.1)	12	F-32	4.5
1/6/71 (2.7)	13	F-90	5.5
2/15/71 (-3.5)	6	E-28	1.5
3/21/71 (4.3)	15	F-24	15.0
4/22/71 (6.4)	18	F-20	19.5
6/11/71 (14.7)	8	F-12	47.5

TABLE VII. Distribution of *Dactylopalia baltica* along the sublittoral transect on 21 May 1971. Values expressed as mean specimen densities/10cm^3 of sand.

Station	Sand depth in cm				
	0-2	5-7	10-12	15-17	20-22
I	0.5	0.5	0.0	0.0	0.0
II	0.0	0.0	0.0	0.0	0.0
III	2.5	0.0	0.0	0.0	0.0
IV	2.0	4.0	0.0	0.0	0.0
V	0.5	0.5	0.0	0.0	0.0
VI	0.0	0.0	0.0	0.0	0.0
VII	2.5	14.0	0.0	0.0	0.0
VIII	1.5	24.0	5.0	0.0	0.0
IX	2.0	3.5	0.0	0.0	0.0
X	1.0	3.0	5.0	0.0	0.0

TABLE VIII. Distribution of Turbanella cornuta along the sublittoral transect on 21 May 1971. Values expressed as mean specimen density/10cm^3 of sand.

Station	Sand depth in cm				
	0-2	5-7	10-12	15-17	20-22
I	0.0	0.0	1.0	3.5	0.0
II	0.5	0.0	0.0	0.0	0.0
III	1.0	0.0	0.0	0.0	0.0
IV	0.0	0.0	0.5	0.5	0.0
V	0.0	0.5	0.0	0.0	0.0
VI	0.0	0.0	0.0	0.0	0.0
VII	1.5	36.0	0.5	0.0	0.0
VIII	0.5	0.0	0.5	4.0	0.0
IX	0.0	11.5	0.0	0.0	0.0
X	0.0	0.0	0.5	0.0	0.0

TABLE IX. Distribution of *Tetranchyroderma papii* along the sublittoral transect on 21 May 1971. Values expressed as mean specimen densities/10cm^3 of sand.

Station	Sand depth in cm				
	0-2	5-7	10-12	15-17	20-22
I	0.0	0.0	0.0	5.5	0.0
II	0.0	0.5	0.0	1.0	0.0
III	2.0	1.0	0.0	0.0	0.0
IV	0.0	0.0	0.5	0.0	0.0
V	0.0	0.0	0.0	0.0	0.0
VI	0.0	0.5	0.0	0.0	0.0
VII	0.0	4.0	1.5	0.0	0.0
VIII	0.0	0.0	0.0	0.5	0.0
IX	0.0	0.0	0.0	0.0	0.0
X	0.5	0.0	1.5	0.5	0.0

TABLE X. Sublittoral sampling sites exhibiting trace specimen densities for four gastrotrich species.*

	Date	
Species	5 October 1970	21 May 1971
Acanthodasys aculeatus	VI 5-7	VIII 20-22
Chaetonotus aculifer	I 5-7, I 10-12, III 15-17, VI 10-12	V 5-7
Macrodasys caudatus	VI 10-12	
Xenotrichula beauchampi		VII 5-7

*Each sampling site is indicated by a Roman numeral and two Arabic numbers separated by a dash. The former refers to the station, the latter to the sand depth in centimeters.

TABLE XI. Some granulometric comparisons among sands from five sampling stations along the sublittoral transect.

Parameter	Stations II	IV	VI	VIII	X
1) Mean of mean grain sizes from station sampling sites (µm)	481.0	410.2	340.6	371.2	341.2
2) Standard deviation of 1) (µm)	66.8	33.9	5.4	32.8	29.2
3) Mean of sorting phi values (phi units) from station sampling sites	0.73	0.69	0.58	0.55	0.53
4) Standard deviation of 3) (phi units)	0.15	0.23	0.02	0.03	0.02
5) Number of sampling sites analyzed	5	5	5	5	5

TABLE XII. "Habitable" range of grain size for four gastrotrich species within the sublittoral transect.

Species	Habitable grain size range (in µm)	Number of sand samples analyzed
Acanthodasys aculeatus	250-507	1
Dactylopodalia baltica	221-595	8
Tetranchyroderma papii	227-1109	8
Turbanella cornuta	221-883	7

Figure 1. The region surrounding Hampton Harbor, New Hampshire. Area enclosed within diagonal parallel lines in A is shown in greater detail in B. Numbers 1 and 2 indicate approximate locations of the intertidal and sublittoral transects, respectively.

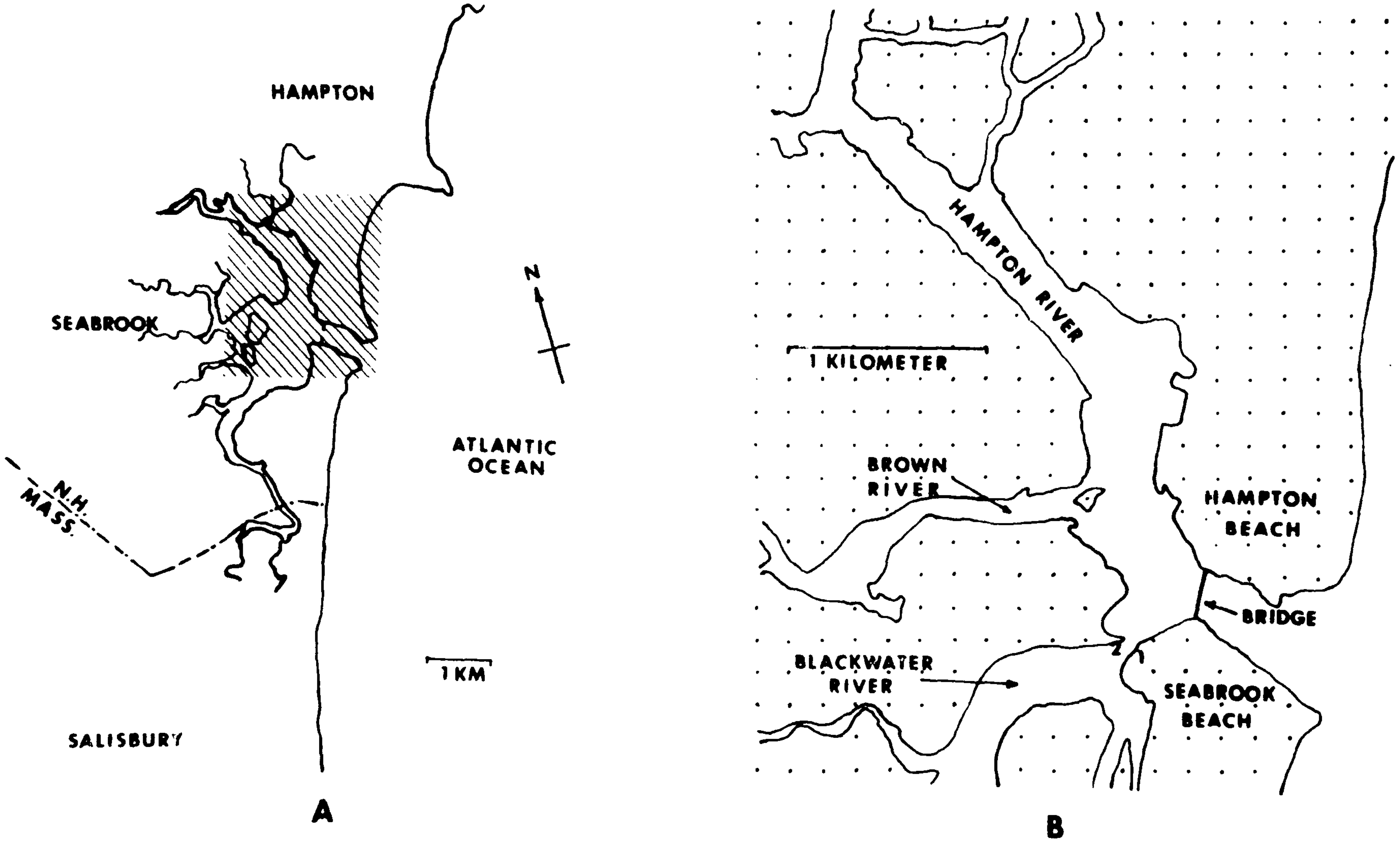
HAMPTON
SEABROOK
SALISBURY
N.H.
MASS.
N
ATLANTIC OCEAN
1 KM
A
HAMPTON RIVER
1 KILOMETER
BROWN RIVER
BLACKWATER RIVER
HAMPTON BEACH
BRIDGE
SEABROOK BEACH
B

FIG. 1

Figure 2. The Seabrook Beach profile showing the intertidal study transect, including Stations A-F.

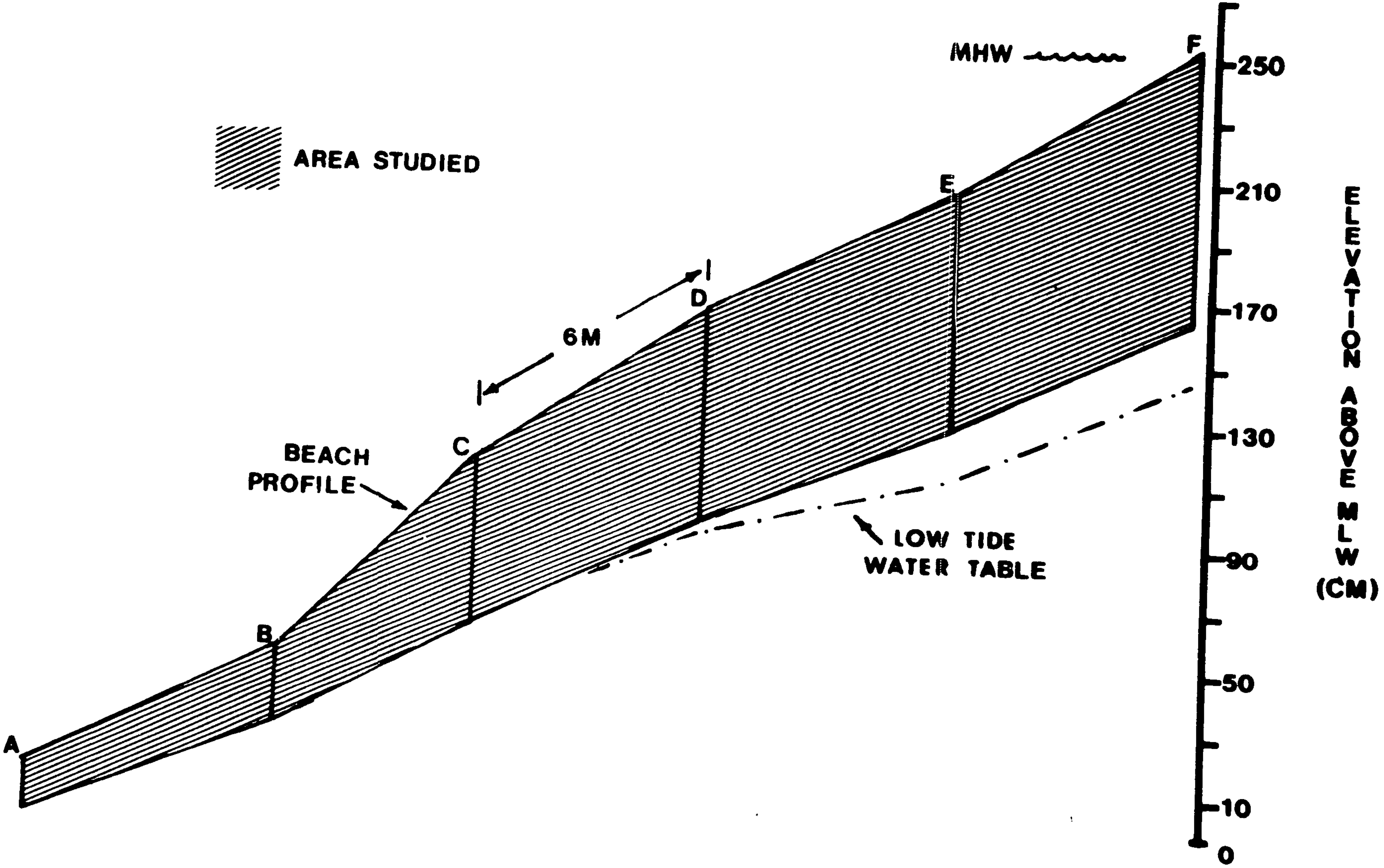
▨ AREA STUDIED
MHW
A
B
C
D
E
F
6 M
BEACH PROFILE
LOW TIDE WATER TABLE
250
210
170
130
90
50
10
0
ELEVATION ABOVE MLW (CM)

FIG. 2

Figure 3. Seasonal temperature patterns at lower (B), middle (D) and upper (F) beach stations along the intertidal transect.

A. 20 September 1970 (summer pattern)

B. 23 November 1970 (late fall - early winter pattern)

C. 15 February 1971 (extreme winter pattern)

D. 22 April 1971 (spring pattern)

Symbols: - - - - - - - - = Station B
— — — — — = Station D
———————— = Station F

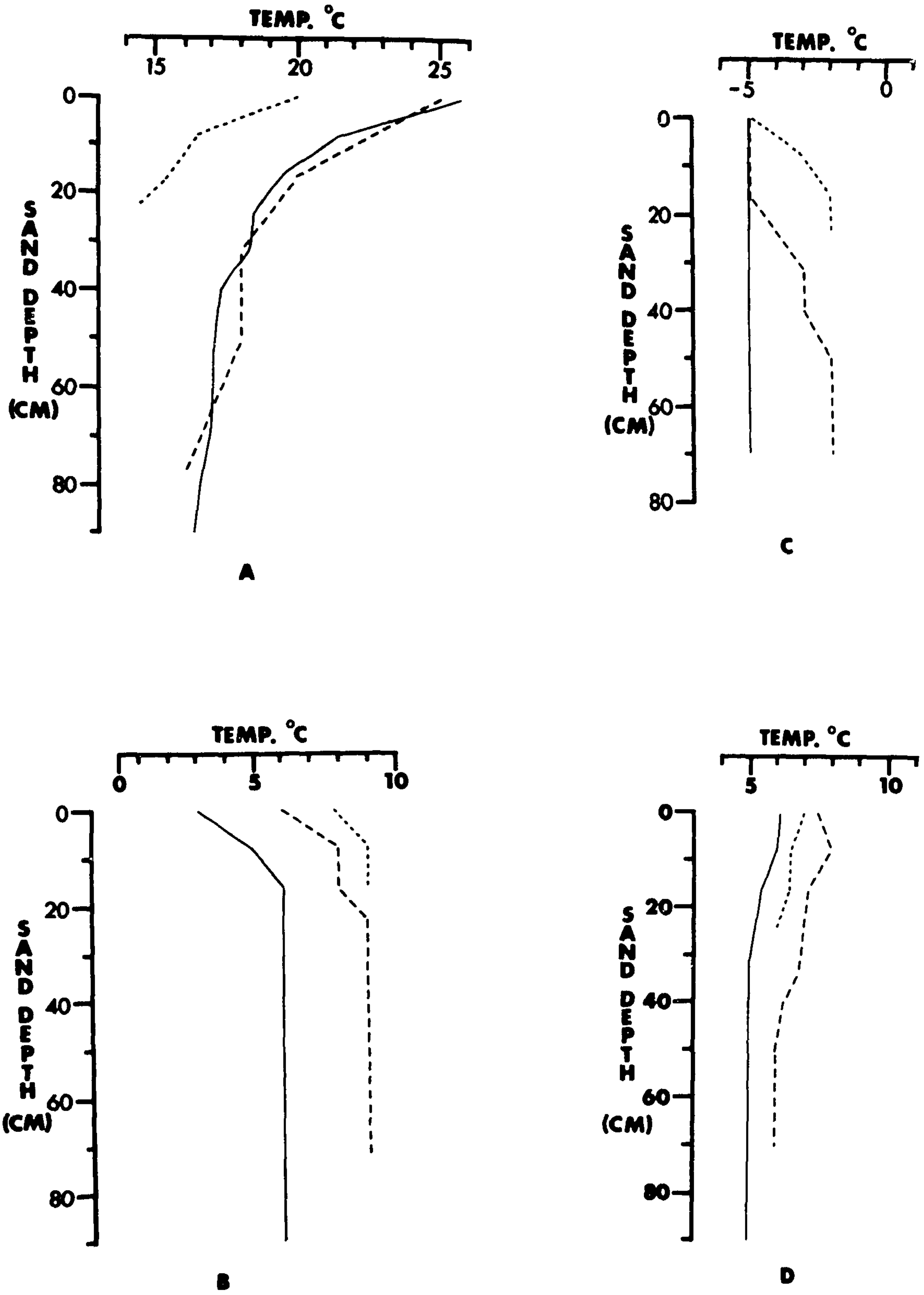
TEMP. °C
15
20
25
0
20
40
60
80
SAND DEPTH (CM)
A
TEMP. °C
-5
0
0
20
40
60
80
SAND DEPTH (CM)
C
TEMP. °C
0
5
10
0
20
40
60
80
SAND DEPTH (CM)
B
TEMP. °C
5
10
0
20
40
60
80
SAND DEPTH (CM)
D

FIG. 3

Figure 4. The Seabrook Beach profile showing isobars of equal saturation percentages along the study transect.

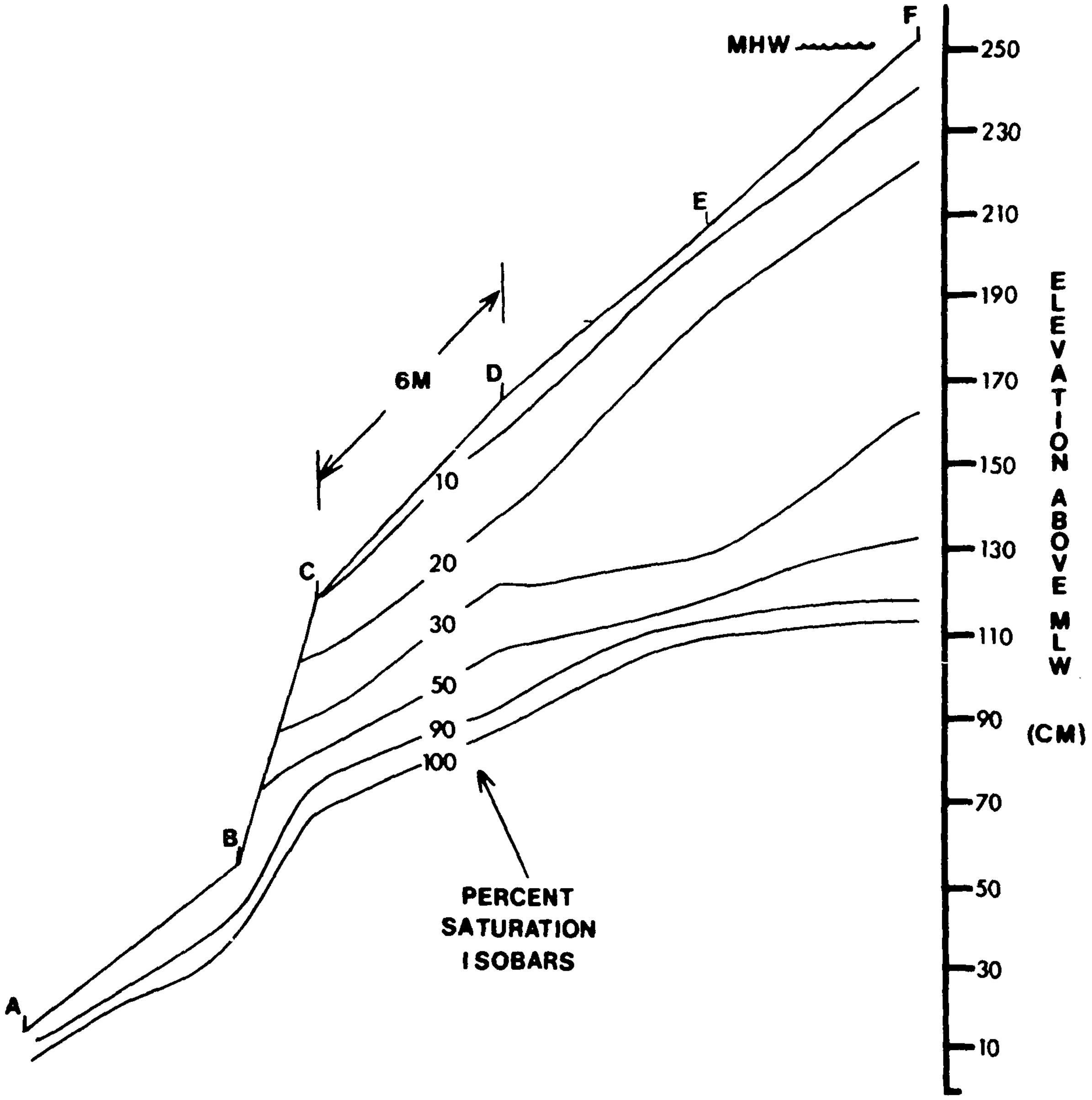
F
MHW
E
D
6M
C
B
A
10
20
30
50
90
100
PERCENT SATURATION ISOBARS
250
230
210
190
170
150
130
110
90
70
50
30
10
ELEVATION ABOVE MLW (CM)

FIG. 4

Figure 5. Patterns of annual change in gastrotrich population abundance, Seabrook Beach, 1970-1971.

A. Tetranchyroderma papii

B. Turbanella cirrata

C. Turbanella cornuta

D. Xenotrichula beauchampi

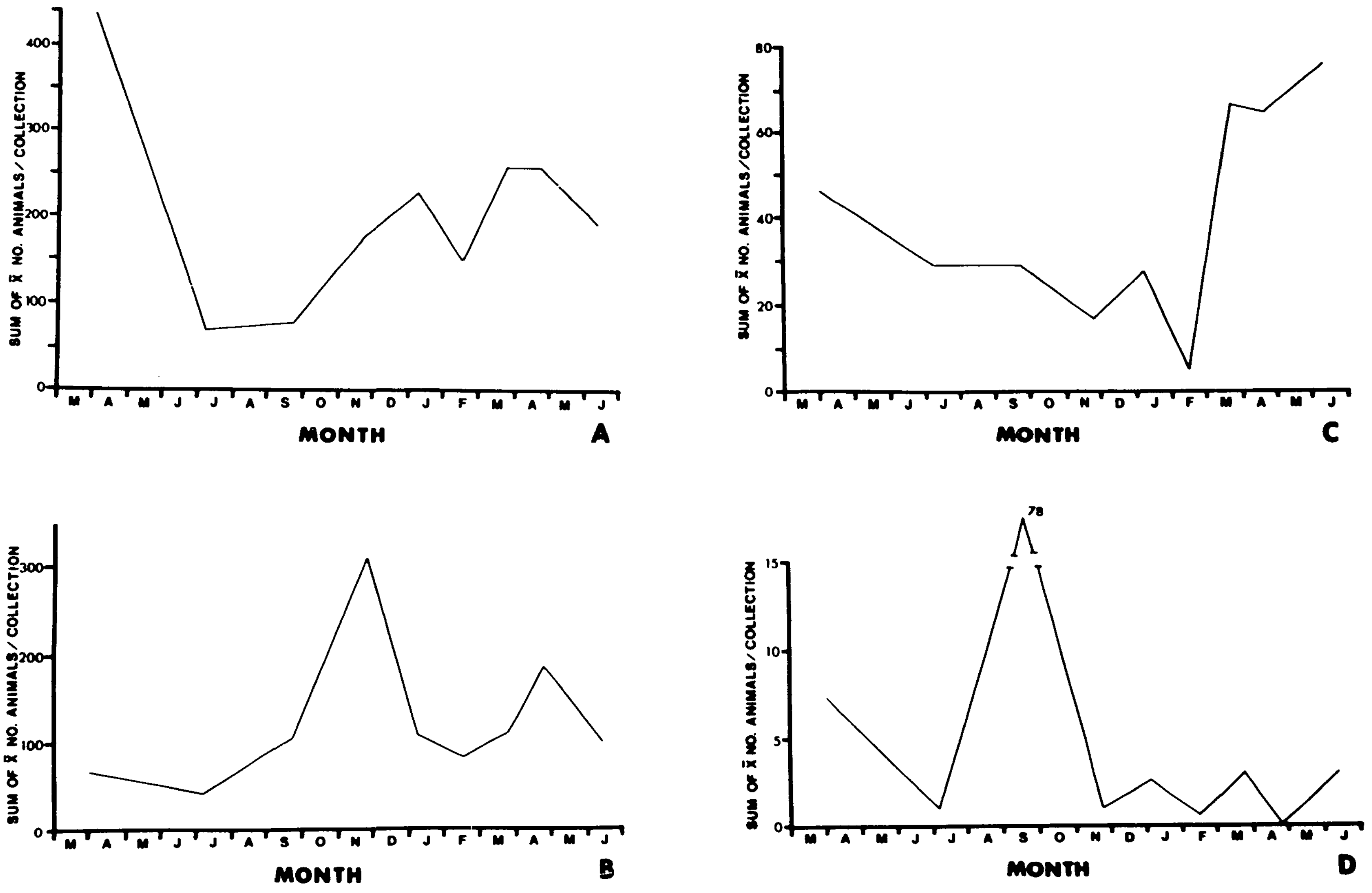
SUM OF $\bar{x}$ NO. ANIMALS / COLLECTION
0
100
200
300
400
M A M J J A S O N D J F M A M J
MONTH
A
SUM OF $\bar{x}$ NO. ANIMALS / COLLECTION
0
20
40
60
80
M A M J J A S O N D J F M A M J
MONTH
C
SUM OF $\bar{x}$ NO. ANIMALS / COLLECTION
0
100
200
300
M A M J J A S O N D J F M A M J
MONTH
B
SUM OF $\bar{x}$ NO. ANIMALS / COLLECTION
0
5
10
15
78
M A M J J A S O N D J F M A M J
MONTH
D

FIG. 5

Figure 6. Seasonal density and distribution changes for *Tetranchyroderma papii* on Seabrook Beach. Site of maximum density for each collection date is labelled and its location indicated by an "X".

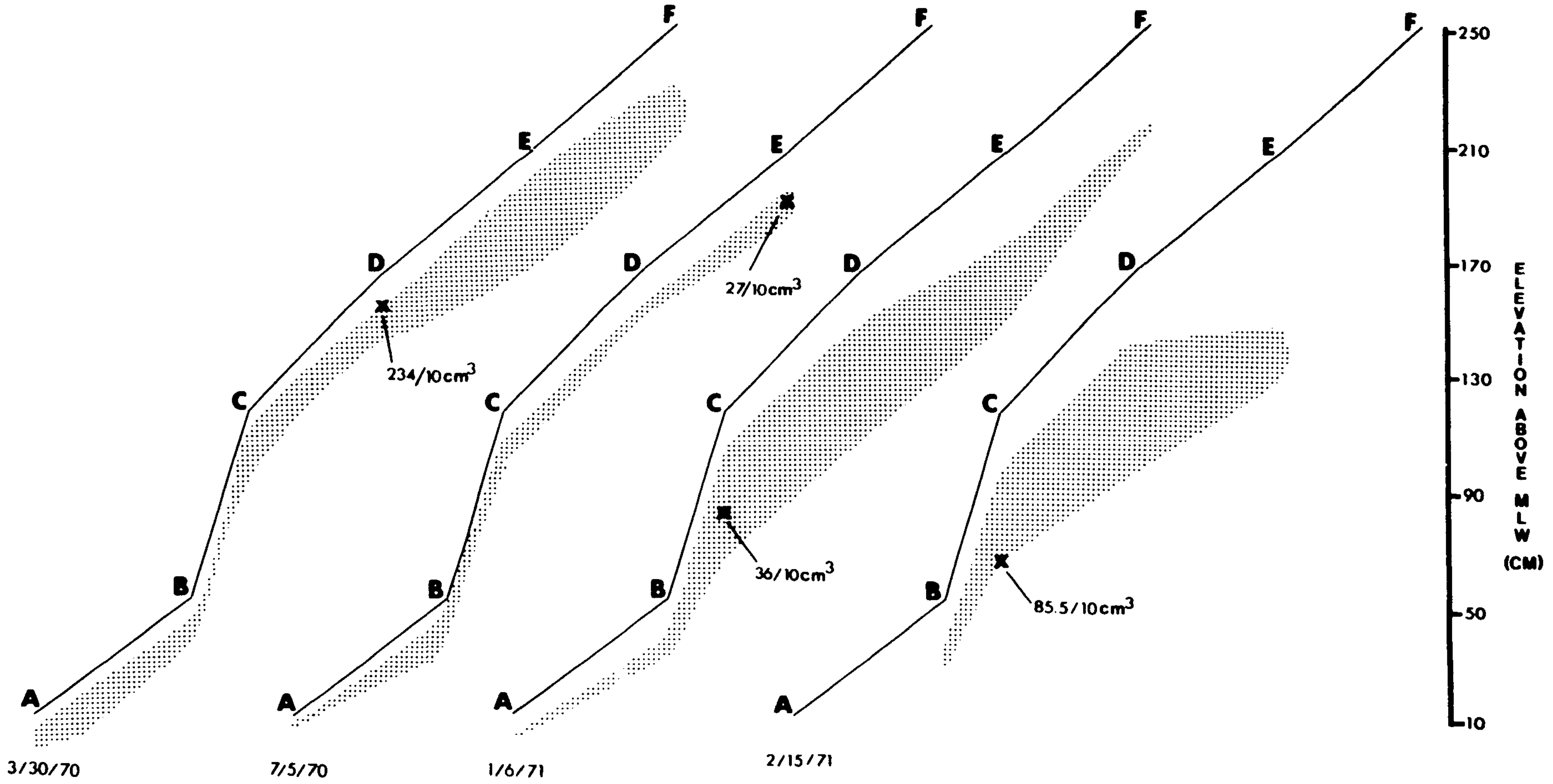
F
E
D
C
B
A
3/30/70
234/10cm^3
F
E
D
C
B
A
7/5/70
27/10cm^3
F
E
D
C
B
A
1/6/71
36/10cm^3
F
E
D
C
B
A
2/15/71
85.5/10cm^3
250
210
170
130
90
50
10
ELEVATION ABOVE MLW (CM)

FIG. 6

Figure 7. Seasonal density and distribution changes for *Turbanella cirrata* (stippling) and *Turbanella cornuta* (cross hatching) on Seabrook Beach. Sites of maximal density for each collection are labelled and their locations indicated by an "X".

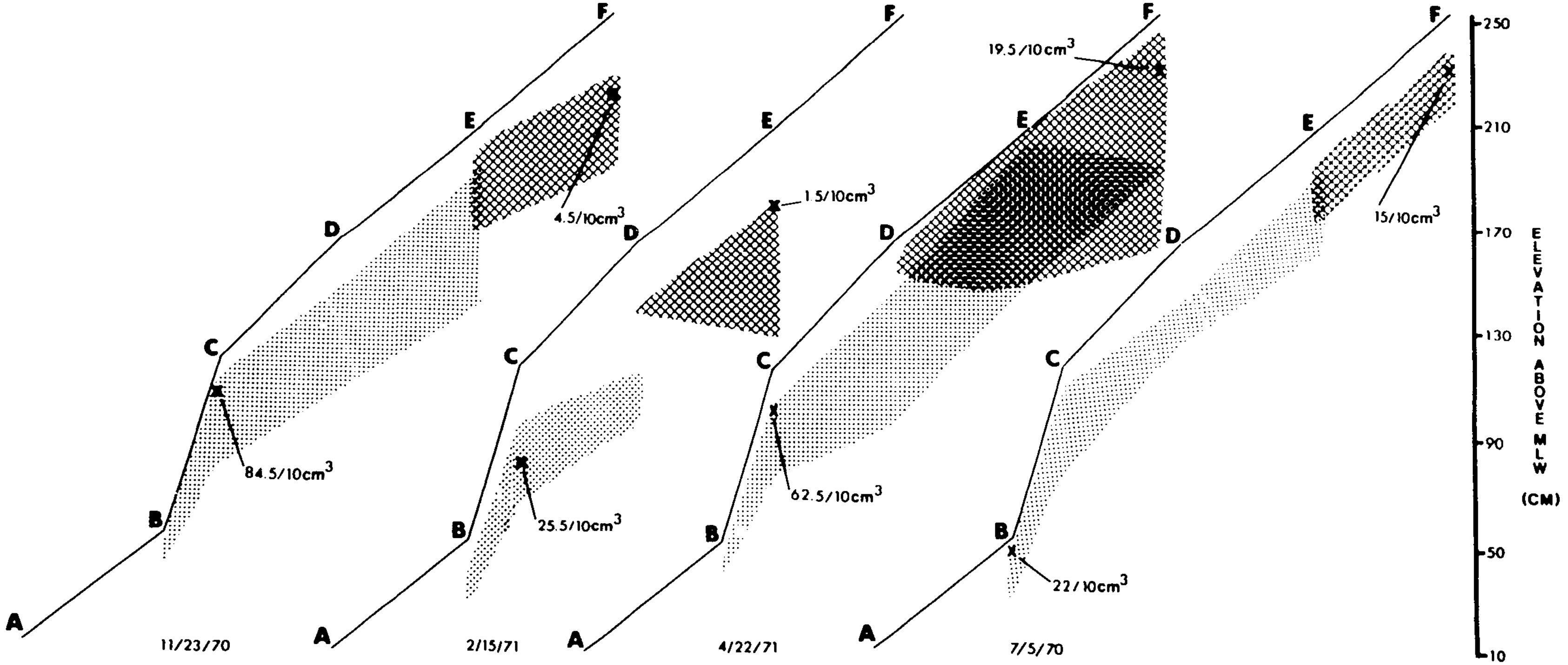
A
B
C
D
E
F
84.5/10cm³
4.5/10cm³
11/23/70
25.5/10cm³
1.5/10cm³
2/15/71
62.5/10cm³
19.5/10cm³
4/22/71
22/10cm³
15/10cm³
7/5/70
250
210
170
130
90
50
10
ELEVATION ABOVE MLW
(CM)

FIG. 7

PART III

METHODOLOGY FOR THE STUDY OF MEIOFAUNA-MICROFLORA RELATIONSHIPS

Field studies of various interstitial animals (e.g. Ganapati & Rao, 1962; Renaud-Debyser, 1963; Hummon, 1969a; Pollock, 1969) indicate that abiotic factors alone (e.g. temperature, salinity, sediment texture, etc.) fail to fully explain meiofaunal distribution patterns. Yet very little is known about the influence of biotic factors (e.g. competition, predation, and food preferences) on meiofaunal distribution patterns. Consider meiofaunal food preferences. Apart from several known predators (e.g. certain Hydrozoa, Nematoda, and Turbellaria) the bulk of the interstitial fauna is suspected to feed on microalgae, detritus, or bacteria (McIntyre, 1969). Unfortunately, with few exceptions (e.g. Perkins, 1958), knowledge of the food preferences of non-predatory meiofaunal species is based solely on gut content analyses and thus may be of questionable reliability (see Discussion - Part II).

Following is a brief review of what is known concerning the distribution and abundance of detritus, microalgae and bacteria in marine sand; each of these microfloral types is treated separately. Remarks center on evaluation of methods employed for quantitative enumeration of microflora as well as techniques utilized in attempts to link these suspected food sources with non-predatory members of the marine interstitial fauna. Such evaluation relies, in part, on the results of field and laboratory experiments utilizing Hampton Harbor gastrotrich populations and the associated microflora.

Detritus

Jansson (1968a) noted that detritus, in the broadest sense of the word, is composed of both a living fraction (i.e. bacteria) and a non-living fraction (i.e. decaying plant and animal materials); the former may exceed the latter in mass (Perkins, 1958) as well as in importance as a meiofaunal food source (Jansson, 1968b). Several authors (e.g. Remane, 1952; Perkins, 1958; Renaud-Debyser & Salvat, 1963) have suggested that interstitial members of several groups may feed primarily on detritus; careful determinations by Fenchel (1968) and Thane-Fenchel (1968) have indicated that certain detritus feeders may be highly selective in terms of the portions of the detritus they consume. Therefore it is probable that detritus includes a number of meiofaunal food niches.

On atidal beaches the narrow strip of sand above the water line forms a filtering site where detrital particles concentrate; on tidal beaches such a filtering zone is broader and the pattern of detrital buildup within the sand may be more complex (Jansson, 1966a). An approximation of detrital content can be made by examining sand microscopically. An abundant interstitial fauna has been associated with sands having intermediate detrital levels (Pennak, 1942; Renaud-Debyser & Salvat, 1963) or sands lacking any visible detritus (Renaud-Debyser, 1963; Jansson, 1966a, 1968a).

As an alternative to measuring detritus content visually, one may determine a sand sample's organic carbon content, although the potential ecological significance of the latter measure largely depends on how it is obtained. For example, treatment of an unaltered sand sample will yield an organic carbon value representing detritus in water films, organic matter adsorbed on sand grains and meiofauna within the sand. Only Tietjen (1969) has published measurements including correction factors for the weight of contained meiofauna. In another approach, Steele & Baird (1968) separated "particulate" and "attached" organic matter in sand by elutriating sand samples prior to determining their organic carbon content. Their results suggest that most organic material in sand is attached to the grains and the detritus constitutes less than 5% of the total organic carbon present.

I propose that the "particulate" fraction they spoke of is partially composed of the less thigmotactic members of the meiofauna present in their original sand samples. Since the meiofaunal mass is likely to change significantly within a relatively small sampling area, large changes in the organic carbon content of the "particulate" fraction may reflect differences in the abundance of the meiofauna rather than detritus. I suggest, then, that elutriating a sand sample so as to yield a measure of "attached" and "particulate" organic carbon present is of little value to the ecologist bent on clarifying the relationship between detritus and meiofauna.

A sediment's organic carbon content may be measured by dichromate wet oxidation or the simpler method involving loss of weight on ignition. Though the latter has been employed by meiobenthologists (e.g. Ganapati & Rao, 1962;

Gray, 1968), its use should be discontinued because the technique yields high, unreliable values(i.e. carbonates in shell fragments are driven off as CO_2 when the sand is heated). Several modifications of the wet oxidation technique (e.g. Gordon, 1966; Strickland & Parsons, 1968) yield organic carbon values free from interference by carbonate or chlorides.

I measured organic carbon levels within the intertidal transect described in Part II with the Walkley-Black Wet Oxidation Method as modified by Gordon (1966). Analysis of eight 2.1g sand samples, drawn from different tidal elevations and sand depths, yielded uniformly low values (range = 0.025-0.050% organic carbon by weight). Elsewhere similar levels were noted on intertidal sand beaches subject to moderate washing by waves (see e.g. Gordon, 1966; Pearse, et. al., 1942).

Whether what was measured is relevant to the meiofauna remains unknown. Hulings & Gray (1971) have pointed out that most organic matter in the deep sea may be refractory and unavailable to the meiofauna and perhaps even to the bacteria. Additional research is needed to determine what proportion of the detritus concentrated intertidally is composed of cellulose, lignin, chitin, and other complex organic molecules usually designated as unfit food sources for meiofauna.

At Hampton Harbor, I often extracted a rich meiofauna from sands displaying low or intermediate detrital levels, but routinely encountered a sparse meiofauna in detritus-clogged sands. Although I sporadically encountered detritus-laden sampling sites within the intertidal transect described in Part II, the beach lacked a readily discernible filtering zone where suspended organic matter routinely accumulated.

I question the importance of detritus for marine interstitial gastrotrichs. If it constituted a major food source, one might expect to observe gastrotrichs regularly browzing within detrital clumps, or find a positive correlation between the abundance of detritus and gastrotrichs in the field. Neither occurred during the present investigation.

Microalgae

Photosynthetic members of the marine sand microflora may include diatoms, dinoflagellates, blue green algae, early stages of brown algae, germinating spores of muticellular green algae and occasionally euglenoids (Pearse, et. al. 1942; Meadows & Anderson, 1968). Knowledge of microfloral distribution patterns in marine sands is at an elementary level. In the Øresund, Fenchel (1969) found dinoflagellates in all soft bottom substrata sampled; species of Amphidinium often dominated in cleaner sands where significant numbers penetrated to sand depths up to 10cm. At Etterick Bay, Scotland, blue green algae, of four genera attached to sand grains in the uppermost half centimeter of sand at lower littoral and sublittoral sampling sites; the same blue greens were absent in deeper strata (Meadows & Anderson, 1968).

More is known about the distribution and abundance of psammophilic diatoms. Generally they are most abundant in lower littoral and sublittoral zones (Jansson, 1968a; Meadows & Anderson, 1968) but their numbers are markedly reduced on atidal (Jansson, 1968b), and exposed (Steele & Baird, 1968) beaches. On temperate beaches they exhibit seasonal maxima during the spring and summer (Fenchel, 1969). Several workers (e.g. Ganapati & Rao, 1962; Jansson, 1968a) have suggested that diatoms only occur abundantly at or close to the sediment surface, yet increasing evidence (e.g. Steele & Baird, 1968; Meadows & Anderson, 1968; Fenchel, 1969) indicates that significant numbers of live diatoms often penetrate deeper. Such extended vertical distributions may be related to sand mixing caused by wave action (Steele & Baird, 1968) or to vertical diatom migrations (Round & Palmer, 1966). How marine littoral diatoms survive extended burial in aphotic sand strata remains unclear. Culture experiments (e.g. Lewin & Lewin, 1960) suggest that certain species survive heterotrophically, while other laboratory studies (Munro & Brock, 1968) indicate that other psammophilic species lack such heterotrophic capabilities. Steele & Baird (1968) hypothesized that certain psammophilic diatoms may be specially adapted for spending long periods in the dark at low metabolic rates with a negligible degradation of their photosynthetic pigments.

It may prove difficult to ascertain the roles played by particular diatom species within meiofaunal food chains. Identification of species inhabiting a particular coast may be a formidable task if Gomiou's (1971) estimate of over 210 microbenthic diatom species within the Romanian littoral proves typical for other areas. If, as Lewin & Lewin (1960) suggest, the identification of many small diatoms requires electron microscope studies of their acid-cleaned frustules, then progress in psammophilic diatom systematics and ecology may indeed be painstaking.

Several authors (e.g. Jansson, 1968a; Gomiou, 1971) have emphasized the importance of psammophilic microalgae as possible meiofaunal food sources. Microscopic observations of behavior indicate that certain ciliates feed on blue green algae (Fenchel, 1969) while some ostracods (Perkins, 1958) and ciliates (Fenchel, 1969) principally ingest diatoms. Laboratory preference experiments by Gray (1966) showed that the addition of diatoms to autoclaved sand partially restored its attractiveness to the archiannelid, Protodrilus symbioticus. The author did not, however, state that P. symbioticus definitely feeds on diatoms.

One may assess distribution patterns of microalgae by direct microscopic examination of untreated (Fenchel, 1969), or stained (Meadows & Anderson, 1968) sand grains. Alternatively, one may microscopically examine seawater samples which have been vigorously shaken with known volumes of beach sand (Fenchel, 1969), or inoculate aliquots from such water samples into agar-based media (Pearse et. al.; 1942).

Each method has inherent disadvantages. Microscopic examination of individual sand grains is always laborious, but appropriate staining prior to their inspection simplifies the process. Checking grain facets for hidden microalgae, particularly at 970X magnification, can cause lens damage, coverslip breakage, or both, unless extreme care is exercised. Microscopic examination of the seawater samples described above yields low estimates of microalgal density owing to the tenacity with which certain species adhere to sand grains. Plate culture of such water samples produces even lower estimates due to the inability of many algal species to survive in culture.

To shed light on possible microalgal-meiofaunal interactions occuring at Hampton Harbor I performed two series of experiments. First, I compared the diversity and abundance of intertidal and sublittoral psammophilic microalgae using several enumeration techniques. Then I contrasted gastrotrich and microalgal abundance patterns at selected littoral and sublittoral sampling sites.

Experiment M-1 (Microscopic Enumeration for Microalgae)

Materials and Methods. To compare Hampton Harbor microfloral diversity, distribution, and abundance with that reported from marine sands near Millport, Scotland by Meadows & Anderson (1968), I collected sand at the time of predicted low water on 4 December 1968, from five equally-spaced stations along a 66.7m long transect approximately 20m southwest of the intertidal transect described in Part II. The stations corresponded to the low tide mark, one quarter, one half, three quarter and high tide levels and will henceforth be referred to as Stations I-V respectively. At each I collected 10cm^3 sand samples from the upper 1-2mm as well as 1 and 4cm sand depths. The samples were fixed within seconds of collection in 2% osmic acid then transported to the laboratory where they were further treated with Bouin's fixative, rinsed in deionized water, then stained in Ziehl's carbol fuchsin as described by Meadows & Anderson (1968). After staining, the samples were stored in 10% unbuffered formalin until microscopic examinations could be made. The latter consisted of a 430 and 970X inspection of 25 grains chosen randomly from each sand depth sampled.

Since three depths were sampled at each of five stations, the results are therefore based on the examination of a total of 325 sand grains. The amount of staining material, type and number of blue green algae, diatoms, bacteria and unidentifiable forms adhering to the sand grains were recorded. Whenever possible, a photographic record was kept of the various microbial types encountered.

Results. Discussion now will be restricted to data pertaining to microalgae and staining material; bacterial distribution and abundance will be taken up in a subsequent division of Part III.

Low power microscopic examinations indicated that large areas of the sand grains may remain bare. Unworn, sharp-angled grains often had staining material restricted to surface depressions and crevices, while well worn, rounded, more opaque grains routinely had staining material spread over a greater proportion of their surfaces. No internal structure was seen on heavily stained surfaces, but microbial aggregates were often visible on less densely stained surfaces. Whether within or external to stained areas, microbes were always present as aggregates or true colonies. The nature of the staining material is unknown. Meadows & Anderson (1968) suggested that it may be an organic substance possibly absorbed from seawater or deposited as an extracellular secretion of bacteria, microalgae, or both.

Identification of microalgal types was perplexing; separating colonies of large bacteria from small blue green algae proved particularly troublesome.

Yet despite such difficulties I differentiated four microalgal types attached to marine sand grains. Aggregates of 5-10 pennate diatoms, 5-20μm long, occurred frequently within stained depressions and crevices (Fig. 1A). Larger diatoms, 25-40μm long, regularly attached to flat, unstained surfaces (Fig. 1B).

An unbranched trichrome lacking both heterocysts and hairs, tentatively identified as in the genus Oscillatoria (Family Oscillatoriaceae), grew typically as a long filament capable of wrapping completely around a sand grain several times (Fig. 1C). A second alga closely resembling in shape Merismopedia sp. (represented in Plate III, Fig. 22 of Meadows & Anderson, 1968) displays coccoid cells separated from one another by a gelatinous sheath (characteristics typical of the family Chroococcaceae), and was less frequently encountered.

Figure 1D depicts an unclassified microorganism, presumedly a blue green alga, henceforth referred to as Unknown A. It appeared as a cluster of four ovate cells lacking a gelatinous sheath. Each cell displayed a lighter band encircling its middle.

Quantitative results are presented in Table I and II; the former treats each station as a unit (i.e. microalgal counts from all three sand depths sampled at a given station are summed and reported as a single value), thus emphasizing horizontal distribution variations irrespective of vertical differences. In the latter the same data are presented but emphasis has been reversed by treating each sand depth sampled as a unit (i.e. microalgal counts for each of the five stations at a given sand depth are summed and reported as a single value).

Several horizontal distribution trends are apparent in Table I. Obviously diatoms were by far the most abundant microalgae adhering to sand grains; the total distribution fluctuations largely reflect changes in diatom numbers. Diatom numbers showed a steady dominution proceeding from Station I to V; in fact, they were 20 times more abundant at Station I than at Station V. The blue green Oscillatoria sp, though present at all stations, exhibited only trace densities at Stations I and V. Merismopedia sp. was only encountered at trace densities at Stations II-V. Unknown A was encountered at least once at every station and exhibited slightly higher densities at Stations II and III. Lower magnification (i.e. 430X) examination of sand grains indicated a gradual decrease in the amount of staining material present on grains from upper beach stations.

Vertical tabulation of the data (Table II) again emphasizes the numerical importance of diatoms. They were most abundant in the upper 1-2mm, and decreased steadily with sand depth. Numbers of Oscillatoria sp. increased steadily with sand depth. Merismopedia sp. was absent in the upper 2mm and was rarely encountered at greater sand depths. Unknown A occurred in low densities at all three levels sampled; it was least abundant at a depth of 4cm. Low magnification examination of sand grains indicated no readily visible variation in the amount of staining material with sand depth.

In short, several trends are apparent in the data. First, diatom abundance decreased with increasing sand depth and distance from the low water line. Moreover fewer microalgae of all types were noted above the half-tide line than below it.

Discussion. The present work provides an interesting contrast to European studies. A survey by Westheide (1968) reported the presence of yeasts as part of attached microflora of a North Sea beach, while I found none. My results are in accord with the findings of Meadows & Anderson (1968) on several points. Both investigations noted the presence of staining material in sand grain depressions and that the quantity of stain present decreased in a landward direction. Both recorded the presence of the blue-green algal genus *Merismopedia*. I also noted *Oscillatoria* sp. while the Scottish work instead recorded representatives of *Anabaena*, *Microcystis*, and possibly *Lyngbya*. Both studies found diatoms present on flat grain surfaces and stained hollows. Both works suggest that diatoms are more abundant in the lower littoral than in the upper intertidal zones.

There were several differences in vertical distribution patterns of microalgae between the study of Meadows & Anderson (1968) and my work. The former noted that in lower littoral samples the number of diatoms increased at depths of 2 and 6cm. The present study indicated a steady decrease in diatom abundance with depth. The former showed that blue greens did not extend below a depth of 4.5mm while my work indicated that all blue greens encountered extended to sand depths of 4cm.

Such microfloral distribution differences may have several possible explanations; samples may have been taken at different stages of the lunar tidal cycle or during different seasons (Meadows & Anderson omit stating when their samples were collected); there may have been differences in the physical parameters governing sand mixing in the two beaches; or the microalgae inhabiting the two beaches may have been made up of different species having divergent tolerances or preferences regarding the amounts of sand which cover them.

Experiment M-2

(Distribution of Microalgae and Gastrotrichs)

In this experimental series I compared the distribution and abundance of microalgae and gastrotrichs contained in littoral and sublittoral sands. In contrast to Experiment M-1, I employed a cultural method for microalgal enumeration rather than a microscopic technique.

Materials and Methods. On 3 May 1971 I collected 40cm^3 sand samples from sampling sites C-0, C-12, C-16 and C-20 within the intertidal transect described in Part II (letter-number coding as described in Part II). Likewise on 30 May 1971 I collected four 40cm^3 sand samples from a portion of the sublittoral transect described in Part II (specifically Station VII; sampling sites 0-1, 5-6, 11-12 and 20-21cm sand depths).

Sampling was initiated at the time of predicted low water on both dates.

Immediately upon return to the laboratory, each sample was processed as follows: First a subsample of approximately 1g was removed then added to 10cm^3 of sterile seawater (salinity = 32.5^o/oo) in a sterile test tube. The tube was next plugged with sterile cotton then agitated for two minutes on a Vortex Jr. Mixer to dislodge microflora attached to the sand grains. Next 1cm^3 of seawater containing suspended microflora was transferred from the first to a second test tube containing 9cm^3 of sterile seawater. This second tube was next plugged with sterile cotton then agitated for 30 seconds on the mixer. Finally triplicate 0.1cm^3 inocula from each of the two tubes were smeared onto Petri dishes containing a cooled, sterile agar medium. This "spread" plating was conducted as described by Buck & Cleverdon (1960). Inocula from the first and second tubes correspond to microfloral dilutions of 0.01 and 0.001 respectively.

The culture medium was Gates & Wilson's (1960) artificial seawater medium modified by the addition of 10g agar/l to induce solidification. Plates were incubated for 30 days, at 10^{o}C, under constant illumination, in an area humid enough to prevent appreciable drying of the agar. Colonies developing on the plates were identified by transferring cells to slides for microscopic examination. Microalgal density was estimated by counting and then averaging the number of colonies present in the triplicate platings. Such estimation is based on the assumption that each colony arose through the division of a single microalgal cell. The sand subsamples originally placed in the tubes were oven dried then weighed. The dry weights were used as a correction factor so that results could be expressed as the mean number of each microalgal type present/g dried sand.

Gastrotrich density was estimated by extraction and tally of specimens contained in triplicate 10cm^3 subsamples from each sampling site. Methodology was as described in Part II and results are expressed as mean number of gastrotrichs/10cm^3 sand.

Results. Only brown and rust colored pennate diatom colonies developed on the agar plates. The colonies were 1-25mm in diameter and often irregular in contour; individual cells comprising them were 10-30µm long. More specific diatom classification was not attempted. Yellow or white bacterial colonies composed of bacilli frequently contaminated the plates.

Living diatoms were isolated from all intertidal sampling sites (Table III). Their abundance decreased steadily with increasing sand depth. Diatom density within the uppermost centimeter of sand was nearly 39 times that observed at a sand depth of 36cm. Peak abundance for both gastrotrich species isolated from Station C occurred at sampling site C-12 where diatom density was about one third that encountered in the uppermost centimeter of sand. Sublittorally, no marked reduction in diatom abundance occurred with increasing sand depth; all sampling sites displayed diatom densities at least twice the maximal value observed intertidally. At Station VII gastrotrichs were isolated only from the 5cm sand depth where diatom densities were lowest.

Coefficients of correlation suggest no clear correspondence between the intertidal distribution of psammophilic pennate diatoms and that of gastrotrichs ($r = -0.19$ and -0.11 for diatoms vs. T. cirrata and T. papii respectively). The sparse sublittoral data indicate an inverse relationship between the distribution of diatoms and that of D. baltica ($r = -0.98$).

Discussion. The numerical data above are of questionable statistical and ecological significance for several reasons. First, a more comprehensive sampling scheme would be required to uncover any real correlations between the distribution of diatoms and that of gastrotrichs inhabiting the same intertidal and sublittoral sands. Moreover, even if such an exhaustive investigation revealed a high degree of positive correlation, this would only suggest the possibility of some causal relationship between the two variables. In the absence of additional evidence (e.g. laboratory studies confirming the ingestion of diatoms by gastrotrichs) such a correlation might well be accidental.

Microalgal diversity described by Pearse et. al. (1942) in studies of beaches at Beaufort, N.C. exceeded that of the present work although methodology and culture media employed were similar in both. The former investigation noted the presence of non-colonial blue green and green algae on agar plates. Although my cultural enumerations failed to detect these microalgal types, Experiment M-1 indicated that blue green algae do inhabit Seabrook Beach sand. Both investigations suggest that, in general, small species of psammophilic diatoms are more amenable to culture on solid media than larger species.

A comparison of the results from experiments M1 and M2 confirms that cultural enumeration yields lower estimates of microalgal diversity and abundance than direct microscopic counts. Such differences are partially explained by the selectivity of any culture medium. Beyond this, I suggest that complete removal of attached microflora by shaking sand in sterile seawater may be impossible. In spot checks of extraction efficiency, I found that agitation on the Vortex Jr. Mixer for 2 minutes removed approximately 50% of the attached microalgae from sand. I suggest the possibility that many highly thigmotactic types of microalgae may be ignored in distributional studies employing only cultural enumeration techniques.

My initial efforts to establish links between psammophilic microalgae and suspected meiofaunal herbivores have convinced me that more comprehensive field studies will demand the combined efforts of several researchers. It is impossible for a single individual to simultaneously enumerate meiofauna and microalgae contained within a large number of sampling sites. Despite the narrow scope of my efforts, the results of my microalgal enumerations are significant for several reasons. First, I have confirmed that significant numbers of psammophilic diatoms can be isolated from aphotic sand strata both intertidally and sublittorally. Moreover my studies constitute the first experimental confirmation of the general patterns for the spacial distributionof microalgae and staining material on sand grain surfaces described by Meadows & Anderson (1968).

Bacteria

Little has been published concerning the quantitative abundance of bacteria on marine sand beaches. Transect studies suggest that horizontal distribution maxima may occur in supralittoral sands (Westheide, 1968), at the high water mark (Pearse, et. al.; 1942) or at points between the mid and low tidal levels (Meadows & Anderson, 1968; Westheide, 1968). Vertically bacterial abundance declines with increasing sand depth (Meadows & Anderson, 1968; Westheide, 1968).

Valuation of the bacterial abundance in sand may be accomplished either directly by microscopic examination of fixed and stained sand grains, or indirectly by cultural enumeration techniques. But neither of these methods yields truly accurate estimates. Direct observation permits study of the spacial configuration of bacteria on the grains but overestimates their abundance because tiny detrital particles are easily confused with bacteria during microscopic examinations. Cultural enumeration involves procedures identical to those outlined for Experiment M-2. Such enumeration is superior to direct microscopic methods in that it permits specific identification of bacteria developing in mixed culture to be made through subsequent axenic study of their growth characteristics in selective media. Cultural methods do, however, underestimate bacterial abundance.

Fenchel (1969) pointed out that media commonly employed for quantitative work are totally unsuitable for detection of any anaerobic or chemoautotrophic bacteria possibly present in sand samples. Pearse, et. al. (1942) noted that an initial vigorous shaking of a sand sample in sterile seawater may fail to remove 10-30% of the adherent bacteria; subsequent shakings may kill significant numbers of bacteria still adhering to the grains.

Theoretically then, the most accurate enumerations of marine psammophilic bacteria will be obtained when both direct and cultural methods of enumeration are employed within the same experimental framework to supplement one another. Pearse et. al. (1942) cautioned that even if accurate enumeration at one time was possible, it would be of limited value because fluctuations in bacterial abundance probably occur quite rapidly in nature (e.g. populations may double within several hours under favorable conditions; conversely negative factors such as a rising tide or a hard rain may cut densities in half within the same short period.

The importance of bacteria in meiofaunal food chains has been recently underscored by evidence accumulating from several divergent lines of research. In long term laboratory experiments, McIntyre et. al. (1970) permitted natural, unfiltered, seawater to flow at a constant rate through two serially connected sand columns. Effluent passing through the second column primarily contained only "soluble" organic molecules (i.e. those smaller than 1μm); larger particulate material was almost entirely filtered out during passage of seawater through the first column. Yet interstitial copepods, turbellarians and nematodes were distributed throughout the length of both columns and some species successfully reproduced during the course of the investigation. Apparently then the animals do not nutritionally depend on particulate carbon. Lacking indications that the fauna consumed diatoms, the authors suggested the main energy source for the interstitial fauna would seem to be bacteria, which are, in turn, maintained by "soluble" organic materials in seawater. The authors postulated that all organic matter entering meiofaunal food chains must be passed through bacteria prior to utilization by the interstitial fauna. I view their speculation as somewhat premature because no research on the ability of the meiofauna to absorb soluble organic nutrients directly has, as yet, been undertaken.

Irrefutable nutritional links between meiofauna and bacteria have been established through laboratory culture experiments or careful microscopic examination of feeding behavior. Certain ciliated protozoa (Fenchel, 1968) as well as harpacticoid copepods and nematodes (Perkins, 1958) have been positively identified as bacteriovores.

Yet another approach for determining interactions between members of several meiofaunal groups and psammophilic bacteria was adopted in a series of laboratory "preference" studies by Gray (e.g. 1966, 1967, 1968) and Gray & Johnson (1970). I shall critically review this work and my attempts to employ similar methods in a subsequent division of Part III.

But first I shall outline the total breadth of my research efforts at Hampton Harbor.

To clarify possible interactions between psammophilic bacteria and gastrotrichs inhabiting Hampton Harbor sands, I conducted three experiments. First, I compared the diversity and abundance of intertidal and sublittoral psammophilic bacteria using several enumeration techniques. Secondly, I contrasted the distribution patterns of bacteria and gastrotrichs within selected littoral and sublittoral sampling sites. Finally, I performed laboratory preference experiments to determine whether Hampton Harbor sand possessed an attractive property to which resident gastrotrich species would respond.

Experiment B-1 (Microscopic Enumeration for Bacteria)

As mentioned earlier, bacterial enumeration was adjunct to the work described as Experiment M-1. Refer to this preceding section for a description of methods and materials employed.

Results. Since identification of microbes was based solely on microscopic observations of fixed and stained sand grains, bacteria could not be classified to genus, and were separated solely on morphological criteria. Two distinct bacterial types were encountered during routine microscopic examinations of sand grain surfaces. The first, henceforth called bacterium A, was a colonial form composed of cocci embedded in a well developed matrix. It was hump-shaped and most frequently occurred on unstained grain surfaces (Fig. 2A). The second, henceforth called bacterium B, was a staphylococcus-like aggregate of darkly staining cocci lacking a surrounding matrix. It was encountered on both stained and unstained grain surfaces (Fig. 2B).

As in Experiment M-1, quantitative transect data are summarized in two tables. Table IV treats each station as a unit and therefore emphasizes horizontal distribution variations irrespective of vertical differences. Table V treats each depth as a unit and therefore emphasizes vertical rather than horizontal distribution variations. Table IV shows that bacterium A was restricted to lower intertidal stations; bacterium B occurred at all stations but its density was markedly higher at Station III than elsewhere. Table V suggests that bacterium A did not extend below 1cm sand depth while bacterium B occupied all sand depths sampled and exhibited peak densities at the deepest level sampled.

Discussion. My results differ from those of Westheide (1968). His survey of a North Sea beach indicated that bacterial density was maximal at the sediment surface and diminished with increasing sand depth; he noted two horizontal distribution maxima, one in the lower littoral, a second in the supralittoral zone. My data suggest no decrease in the total number of colonies encountered at deeper sand strata (Table V) and no tendency for the total number of colonies present to increase in a landward direction, although I did not sample within the supralittoral zone itself (Table IV).

Both my work and that of Meadows & Anderson (1968) distinguish two types of bacterial aggregates adhering to sand grains: a matrix-enclosed, hump-shaped type, and a matrix-free type, both comprised of cocci. The latter study indicated that both types do not occur at sand depths exceeding 4.5mm while my work suggests that both extend to 1cm sand depth and the bacterium B penetrates to a 4cm sand depth. Such geographic variations may reflect differences in physical parameters, season, or bacterial species composition (see Experiment M-1).

Experiment B-2

(Distribution of Bacteria and Gastrotrichs)

Materials and Methods. As an adjunct to the work described as Experiment M-2 bacterial enumeration was conducted by removing a second series of $0.1cm^3$ inocula from the dilution tubes. These inocula were spread plated, in triplicate onto Petri dishes containing Medium 2216 of ZoBell (1941). Plates were incubated for 3 weeks at 12^oC in the dark. The number of bacteria present originally in each subsample of sand was estimated by counting, and then averaging the number of colonies arising in the triplicate platings. As before, the dry weights of the sand subsamples were used to derive a correction factor and final results were expressed as the mean number of bacteria present/g of dried sand.

Results. Examination of the agar plates following incubation revealed that pigmented colonies regularly constituted 4-17% of all colonies developing on Medium 2216. Most pigmented forms were yellow, though pink or orange hues were occasionally encountered.

Quantitative results are presented in Table VI. Intertidally, bacterial abundance decreased steadily with increasing sand depth. Bacterial density at the sediment surface was approximately five times that of the deepest level sampled. Sublittorally no uninterrupted decrease in abundance with increasing sand depth was observed. Bacterial density at the deepest sublittoral sampling site was about half that encountered in the uppermost centimeter of sand. Coefficients of correlation suggest no clear correspondence between the intertidal distribution of psammophilic bacteria and that of gastrotrichs ($r = +0.09$ and $+0.18$ for bacteria vs. *T. cirrata* and *T. papii* respectively). The sparse sublittoral data indicate an inverse relationship of a moderate degree between the distribution of bacteria and that of *D. baltica* ($r = -0.66$).

Discussion. I believe that the statistical and ecological significance of the numerical data above may be questioned on the same grounds as described for the quantitative data presented for Experiment M-2.

Comparison indicates that my estimates of bacterial abundance fall short of values obtained elsewhere. Pearse, *et. al.*; (1942) found an average of 1.10×10^5 bacteria/g of sand at intertidal sampling sites of approximately the same tidal elevation as my Station C. Westheide (1968) noted between 1×10^6 and 1.4×10^7 bacteria/cm^3 of sediment in his survey of a North Sea Sandy wadden. Lacking geographic or seasonal norms for the abundance of marine psammophilic bacteria, the ecological significance of such numerical differences remains unclear.

Experiment B-3 (Preference Experiment Methodology)

Introduction. Techniques utilized in this final experiment are based on a series of laboratory "preference" studies involving the archiannelids *Protodrilus symbioticus* (Gray, 1966) and *Protodrilus rubropharyngeus* (Gray, 1967), the copepod *Leptastacus constrictus* (Gray, 1968), and the gastrotrich *Turbanella hyalina* (Gray & Johnson, 1970). Therefore a careful review of this work is in order.

The experimental techniques employed were similar in each of these investigations. Large numbers of the meiofaunal animals to be tested were extracted from beach sand, usually by elutriation, then transferred to a petri dish containing seawater. Samples of the same sand, after the animals had been removed (termed natural sand in these studies) were treated in a variety of ways, then washed in fresh and seawater prior to being used in simple or multiple choice preference experiments. Piles of treated sand and untreated natural sand were added to the Petri dish containing the animals and seawater. After allowing the animals three hours to "choose" amongst the various piles, each sand pile was transferred by pipette to a separate dish and the animals contained within it were counted. The ratio of the number of animals in treated sand compared to the number in untreated sand yielded an index of the "attractiveness" of the sand after treatment. Control experiments consisting of four piles of natural sand always yielded ratios close to 1:1.

Parallels in methodology and results amongst Gray's investigations of *P. symbioticus*, *P. rubropharyngeus* and *L. constrictus* are such that the three works may be discussed together logically. First, observations on the behavior of each of these meiofaunal test subjects showed that the avoidance of, or attraction to any sand pile occurred only after direct contact with it. Moreover, sterilizing sand, by autoclaving or soaking it in concentrated nitric or sulfuric acid, invariably rendered it highly unattractive to each subject. Soaking this unattractive sand in seawater for several weeks usually resulted in complete restoration of its attractiveness, while soakings in distilled water or sterile seawater produced a much less pronounced, if any, reconstitution of attractiveness (Only P. symbioticus was exceptional in this regard. Soaking acid cleaned sand in sterile seawater more effectively restored its attractiveness to this species than soaking in untreated seawater).

Inoculation of a mixed culture of bacteria isolated from natural sand into sterilized sand completely restored its attractiveness to P. symbioticus and L. constrictus. Yet nearly complete restoration of the attractiveness of sterilized sand to P. rubropharyngeus was possible only when both natural sand bacteria and adult P. rubropharyngeus specimens were added to it. Gray suggested that both bacteria and a chemical produced by the animal itself play roles in the attractiveness of sand for this gregarious archiannelid species.

In preference tests dealing with the reconstitution of attractiveness to sterilized sand, mixed cultures of bacteria isolated from natural sand were inoculated into sterile sand which was then tested for attractiveness against natural sand in daily preference experiments. Simultaneously, cultural methods of bacterial enumeration were employed to determine the number of bacteria present on the grains each day. Results showed that increases in bacterial abundance on the initially sterile grains correlated positively with increases in the attractiveness of the sand to each of the three meiofaunal species tested.

In preference experiments designed to determine the role of bacterial specificity in attractiveness, sterile sand piles were inoculated either with one of several known species of marine bacteria or with a mixed culture of bacteria isolated from natural sand. The piles were incubated for 3-4 days then tested against one another in multiple choice preference experiments employing sterile sand as a control. Here again bacterial abundance was measured simultaneously with preferences. Results indicated significant qualitative differences in the ability of various species of bacteria to restore attractiveness. Yet bacterial abundance (irrespective of bacterial species) failed to correlate significantly with attractiveness of sand to *P. symbioticus* or *L. constrictus*, although a slight positive correlation between bacterial abundance and attractiveness of sand to *P. rubropharyngeus* was noted.

Therefore, the trails dealing with reconstitution of attractiveness suggested a correlation between bacterial abundance and attractiveness while tests of bacterial specificity implied that attractiveness depended more on the kind rather than the number of bacteria present in sand (except, possibly, in the case of *P. rubropharyngeus*). Gray resolved such inconsistencies by postulating that sterilizing sand destroys organic films laid down on the grains by bacteria. Initial reestablishment of such films correlates with increases in bacterial abundance. Once the films are established, however, fewer bacteria are required to maintain them and therefore the correlation between the number of bacteria and attractiveness disappears. Once organic films are completed, differences in attractiveness depend more on the types of bacteria present on the grains rather than their numbers. Unfortunately Gray failed to include examinations of stained sand grains in his investigations. Such examinations might have effectively tested his hypothesis concerning the establishment and maintenance of organic films on marine sand grains.

Several additional facets of Gray's investigations of P. symbioticus and P. rubropharyngeus deserve brief consideration. To determine whether removal of bacteria had any effect on the attractiveness of sand to these species, he vigorously shook a sample of natural beach sand in sterile seawater for 10 minutes. His data indicated that this treatment removed 90% of the adherent bacteria. Comparison of the shaken sand against untreated natural sand in a simple preference experiment showed that the treatment failed to reduce the sand's attractiveness to either meiofaunal subject. Furthermore, as mentioned earlier, soaking acid-cleaned sand in sterile seawater led to a partial restoration of the sand's attractiveness to P. symbioticus, yet by definition, sterile seawater contains no living microorganisms. These facts, taken together, prompted Gray to state, at least for P. symbioticus that "the presence of microorganisms, however, important in conferring attractiveness, are themselves neither essential nor perhaps very important in the attractive property itself."

Gray & Johnson's (1970) investigation of the contribution of bacteria in the attractiveness of sand to the gastrotrich Turbanella hyalina differed from Gray's earlier works in that it focused attention on the species composition of bacteria in marine sand. Initially they found that sand containing the highest numbers of T. hyalina in the field possessed an attractive factor to which the animal responded in laboratory preference experiments. The attractiveness could be destroyed by autoclaving, but was reconstituted by prolonged soaking of the autoclaved sand in seawater. Because soaking in distilled water or autoclaved seawater failed to restore attractiveness, the authors suggested that the attractive factor is likely derived from a microorganism present in natural seawater but absent in sterile seawater.

Further multiple-choice preference experiments indicated that 16 strains of bacteria isolated either from seawater or natural beach sand could be fitted into separate categories differing from one another with regard to their ability to restore attractiveness to autoclaved sand. Physiological characterization revealed that all strains in the most attractive category were non-pigmented cocci, resistant to penecillin but sensitive to treatment with lysozyme and EDTA.

The authors suspected that the attractive property produced by the favorable strains might be perceived by T.

hyalina as an excretory or secretory product of the bacteria. To investigate this possiblity a highly attractive strain was cultured in a nutrient broth for various time periods at 22 or 32°C. The cells were then removed by centrifugation and the supernatant passed through a 0.1µm filter to yield a final sterile "product" which was then added to autoclaved sand. If bacterial products constitute the attractive factor, cells cultured at 32°C might be expected to have more than cells grown at 22°C for the same period. Preference experiments employing preparations of autoclaved sand plus "product" failed to significantly improve the attractiveness of autoclaved sand. The authors concluded that bacterial excretions and secretions apparently do not confer attractiveness. I question whether such "products" forming in nutrient broth cultures are comparable to the organic films deemed of primary importance in Gray's earlier investigations of attractiveness.

The authors next lysed cells of a highly attractive bacterial strain by treating them with EDTA and lysozyme, then tested these lysed cells for attractiveness to T. hyalina. Their preference experiments showed that lysis does not alter the attractiveness of the cells thusly suggesting that the attractive property of the bacterium resides in its cell wall.

Finally the authors collected ten cores of beach sand, counted the number of T. hyalina contained in each, then estimated the number of bacteria/g of dried sand in each by a cultural method of bacterial enumeration. Specifically the technique involved removal of the bacteria by shaking sand in sterile seawater. Aliquots of the bacterial suspension were then plated on a 15% NaCl-0.04% fuchsin medium which selected for bacterial strains attractive to _T_. _hyalina_. Utilizing the same 10 sand cores an additional experiment was performed to determine if the attractive property in the field could be reproduced in a multiple-choice, laboratory test of preference. Results showed that the number of attractive bacteria is correlated with the number of animals in the field samples. Furthermore, the attractiveness of the sand (assessed by the number of animals entering each sand in the preference experiment) also correlated with the number of bacteria growing on the NaCl-fuchsin medium.

Thus, for _T_. _hyalina_, Gray & Johnson (1970) concluded that both the number and kind of bacteria present on sand grains are important in conferring attractiveness. They further suggested that when _T_. _hyalina_ makes contact with the substratum, it responds to the bacterial cell wall rather than to cell products deposited on the grains as postulated for the archiannelid _P_. _symbioticus_. If this is so, then the attractiveness of natural sand to _T_. _hyalina_ should be markedly reduced by shaking it in sterile seawater to remove adherent bacteria, then presenting it to the animal in a preference experiment against unshaken natural sand. Regrettably Gray & Johnson failed to include such a conclusive test as part of their experimental framework.

Materials and methods. To determine whether Gray & Johnson's conclusions regarding _T_. _hyalina_ were applicable to other macrodasyoids, I attempted to repeat their work substituting a gastrotrich common in Hampton Harbor sands for

T. hyalina. I considered *Tetranchyroderma papii* and *Turbanella cirrata* as likely test subjects because both could easily be collected in large numbers intertidally. I settled on *T. cirrata* for several reasons. First its buccal morphology more closely resembles that of *T. hyalina* than the broad, funnel-like mouth of *T. papii* (see Part I). Moreover, *T. cirrata* is less glutinous than *T. papii* and thus can be pipetted from one vessel to another with greater ease.

Obviously the first preference experiment required is a control series in which the subjects are presented with four piles of untreated natural sand. Further studies could logically be conducted only if such a control consistently indicated an attractiveness ratio close to 1:1.

On 7 November 1970 I collected a 200cm^3 sand sample from sampling site B-8 within the intertidal transect described in Part II. The sample was returned to the laboratory where a series of 10cm^3 subsamples were removed from it. Meiofauna was extracted from each subsample employing the seawater-ice technique described in Part II. Large numbers of *T. cirrata* were separated from other extracted meiofauna by pipetting them into a separate Petri dish containing sterile seawater. Sand remaining in one of the extraction tubes was removed then split into two 5cm^3 piles which were then transferred into separate fingerbowls containing sterile seawater. These two piles will henceforth be called natural sands A and B.

Preference tests were carried out in sterile phage counting plates (9.5cm long, 9.5cm wide, 1.0cm high) containing

$40cm^3$ of sterile seawater. Four sand piles, two each of the natural sands A and B, were arranged at equal distances from the center of the plate. Each pile was square (1.3cm by 1.3cm) and contained $0.25cm^3$ of sand. While checking effective transfer under a dissecting microscope, 100 T. cirrata specimens were pipetted into the center of the test chamber containing the four sand piles and sterile seawater. The chamber was then kept in the dark for 3 hours at a temperature of 12±1°C, after which the sand and animals contained in each pile were transferred by pipette to separate Petri dishes.

In preliminary transfer attempts I found it impossible to pipet out all sand in a given pile without sucking in a large volume of seawater from remote regions of the test chamber. I eliminated this problem by constructing four plastic tubes, open at both ends, measuring 2.1cm high with an inside diameter of 2.2cm. The lower end of each tube was lightly coated with a film of silicon stopcock grease, then one tube was pressed into a position encircling each sand pile (Fig. 3). A watertight chamber was thusly formed around each sand pile making it possible to transfer sand containing T. cirrata specimens while only draining seawater from the area immediately surrounding each pile.

After transfer to separate Petri dishes, the animals contained in each pile were counted under a dissecting microscope. Seawater remaining in the test chamber was also microscopically examined at the experiment's conclusion to determine whether any specimens remained within it. The experiment was run in triplicate; A and B sands were arranged in different configurations for each trial.

Results. Data are presented in Table VII. The "index of attractiveness" (fifth column) is the ratio of the number of animals isolated from the A sand piles as compared to the number isolated from B sand piles. The last column, designated "stragglers", lists the number of specimens remaining either in the seawater or on the bottom of the test chamber at the termination of the trials.

Discussion. Had no tally of the exact number of specimens initially introduced into the chamber and the number of stragglers remaining in the chamber at the trial's termination been made, the mean index of the attractiveness for the three trials might be viewed as suggesting that A and B sands are equal in terms of their possession of an attractive factor to which *T. cirrata* responds. However, I interpret the totals listed in the third, fourth and sixth columns of Table VII as suggesting that natural sand piles are no more attractive to *T. cirrata* than the water column and plate surfaces surrounding them. The locomotory abilities of *T. cirrata* are such that, during the course of each trial, the animals had ample time to sample, enter and remain in the sand piles, if indeed these piles were endowed with some attractive property. Lacking firm evidence that sands which contained large number of *T. cirrata* in the field could be demonstrated as attracting the animals in laboratory preference tests, I refrained from further investigations along these lines.

Obviously my results disagree with those of Gray (1966, 1967, 1968) and Gray & Johnson (1970). Several aspects of their methodology remain puzzling to me. First I am not convinced that, in all cases, the exact number of specimens initially introduced into their experimental chambers was known. Furthermore, I question whether their chambers were examined at the end of the trial; no mention of stragglers is to be found in any of their publications. Finally, I wonder exactly how sand piles can be efficiently transferred from experimental chambers to separate Petri dishes using only a pipette? My experience indicates that such pipetting is likely to suck up seawater (as well as any animals swimming within it) from remote areas of the test chamber in addition to the sand piles and animals contained within them.

I shall be interested to learn whether future researchers encountered the problems I have discussed in attempts to apply Gray's techniques for meiofaunal preference tests. Controversy now may be beneficial if it stimulates refinements in methodology such that readily repeatable results can be achieved by competent researchers closely following clearly outlined, well tested, experimental techniques.

My brief laboratory preference experiments failed to clarify nutritional interrelationships between marine gastrotrichs and elements of the psammophilic microflora; instead my work has raised questions concerning the accuracy of currently employed experimental techniques. My simultaneous samplings of bacteria, microalgae and gastrotrichs were too narrow in scope to determine what, if any, influence the field distribution patterns of microflora may exert on that of gastrotrichs. Despite these shortcomings, I believe that my experimental approach was valid and hopefully it may serve as a crude model for more sophisticated research.

Much remains to be learned concerning seasonal and geographic variations in the taxonomic composition, distribution and abundance of microflora and meiofauna in marine sand. Only by compilation of such data will a reasonably complete knowledge of energy flow and food webs existing in marine sediments be possible. I believe rapid advances are possible if marine zoologists, botanists and bacteriologists collaborate in the design and execution of laboratory and field studies of marine sediments. Such a pooling of expertise will allow meiobenthologists to effectively deal with ecological questions of far greater complexity than is currently possible through the efforts of specialists working alone.

TABLE I. Horizontal distribution of intertidal microalgae at Seabrook Beach as determined on 4 December, 1968. Data expressed in numbers of organisms/75 sand grains examined.

Sampling Site	Diatoms	*Oscillatoria* sp.	*Merismopedia* sp.	Unknown A	Total
Station I (Low water)	422	1	0	1	424
Station II (1/4 tide)	181	21	1	5	208
Station III (1/2 tide)	56	21	2	5	84
Station IV (3/4 tide)	35	8	1	3	47
Station V (high water)	19	2	1	1	23

TABLE II. Vertical distribution of intertidal microalgae at Seabrook Beach as determined on 4 December, 1968. Data expressed in numbers of organisms/125 sand grains examined.

Sand Depth	Diatoms	*Oscillatoria* sp.	*Merismopedia* sp.	Unknown A	Total
0-2mm	364	9	0	5	378
1cm	229	16	2	8	255
4cm	120	28	3	2	153

TABLE III. Distribution of diatoms and gastrotrichs in selected littoral and sublittoral sampling sites at Hampton Harbor.

Sampling site	Mean no. diatoms/g dried sand	Mean No. gastrotrichs/10cm^3 sand
a) littoral (3 May 1971)		
C-0	1240	0.00
C-12	380	25.00 *Tetranchyroderma papii* 33.33 *Turbanella cirrata*
C-16	210	0.33 *Tetranchyroderma papii* 6.00 *Turbanella cirrata*
C-36	32	1.00 *Turbanella cirrata*
b) sublittoral (30 May 1971)		
VII-0	3760	0.00
VII-5	2680	5.00 *Dactylopodalia baltica*
VII-11	3820	0.00
VII-20	3570	0.00

TABLE IV. Horizontal distribution of intertidal bacteria at Seabrook Beach as determined on 4 December 1968. Data expressed in numbers of colonies/75 sand grains examined.

Sampling Site	Bacterium A	Bacterium B	Total
Station I (low water)	20	11	31
Station II (1/4 tide)	19	7	26
Station III (1/2 tide)	1	25	26
Station IV (3/4 tide)	0	6	6
Station V (high water)	0	6	6

TABLE V. Vertical distribution of intertidal bacteria at Seabrook Beach on 4 December 1968. Data expressed in numbers of colonies/125 sand grains examined.

Sand Depth	Bacterium A	Bacterium B	Total
0-2mm	20	12	32
1cm	20	11	31
4cm	0	32	32

TABLE VI. Distribution of bacteria and gastrotrichs in selected littoral and sublittoral sampling sites at Hampton Harbor.

Sampling site	Mean no. diatoms/g dried sand	Mean No. gastrotrichs/10cm^3 sand
a) littoral (3 May 1971)		
C-0	7.88×10^4	0.00
C-12	4.94×10^4	25.00 _Tetranchyroderma papii_ 33.33 _Turbanella cirrata_
C-16	2.14×10^4	0.33 _Tetranchyroderma papii_ 6.00 _Turbanella cirrata_
C-36	1.57×10^4	1.00 _Turbanella cirrata_
b) sublittoral (30 May 1971)		
VII-0	8.29×10^4	0.00
VII-5	5.37×10^4	5.00 _Dactylopodalia baltica_
VII-11	6.59×10^4	0.00
VII-20	4.28×10^4	0.00

TABLE VII. Attractiveness of natural sand to the gastrotrich *Turbanella cirrata*.

Trail no.	No. of animals used	No. of animals in "A" sand piles	No. of animals in "B" sand piles	Index of Attractiveness	No. of "Stragglers"
1	100	38	43	0.88	19
2	100	30	24	1.25	46
3	100	31	29	1.07	40
	Total = 300	Total = 99	Total = 96	Mean = 1.03	Total = 105

Figure 1. Several microalgal types drawn from projected photographs. Stained sand grain surfaces indicated by stippling.

A. Cluster of small pennate diatoms within a sand grain depression (970X magnification).

B. Larger pennate diatoms on flat unstained sand grain surfaces (430X magnification).

C. Portion of Oscillatoria sp. trichrome partially obscurred by densely stained area on grain (970X magnification).

D. Unknown A in a sand grain depression surrounded by densely stained areas (970X magnification).

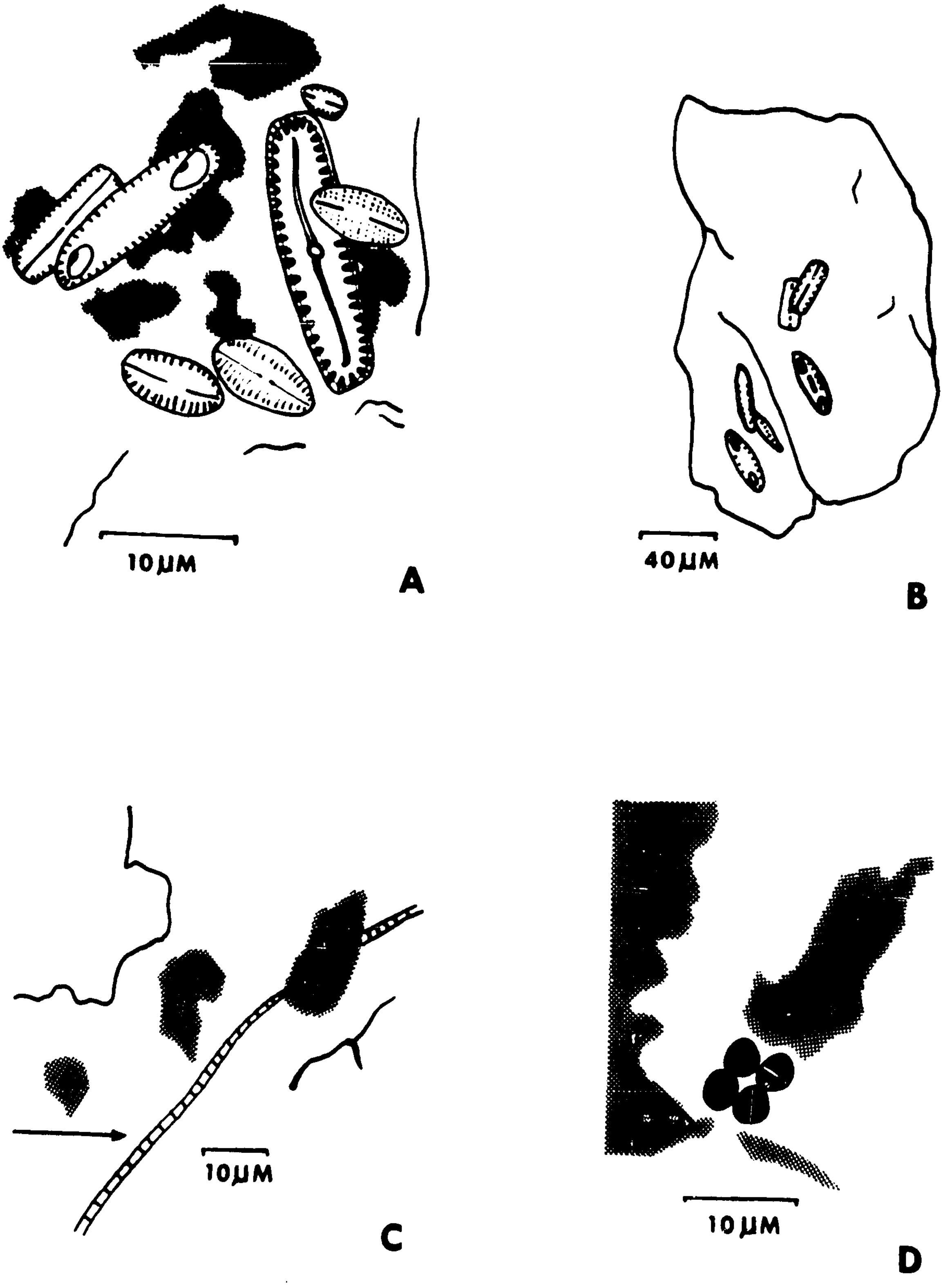

FIG. 1

Figure 2. Bacterial types adhering to marine sand grains.

A. Colony of bacterium A protruding from unstained sand grain surface (970X magnification).

B. Aggregate of bacterium B surrounded by deeply stained sand grain areas indicated by fine stippling. Both types drawn from projected photomicrographs.

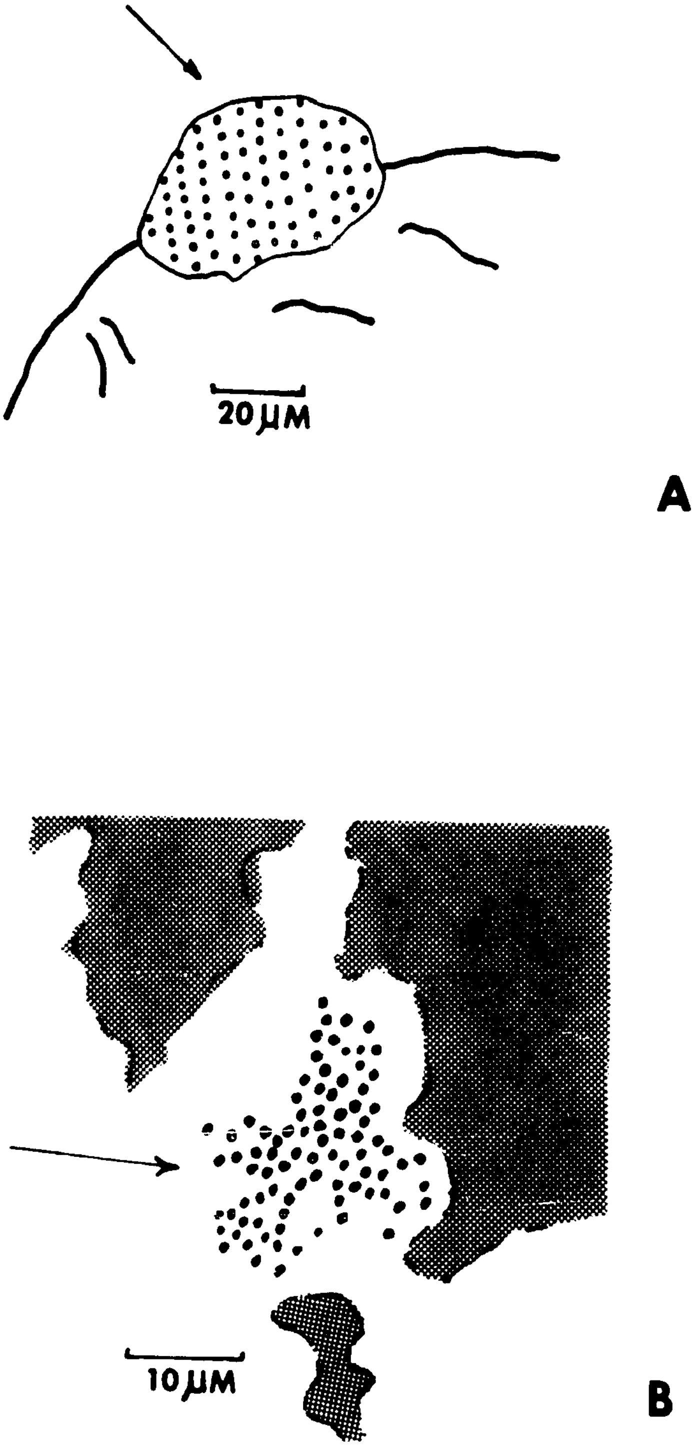

FIG. 2

Figure 3. Meiofaunal preference test chamber. Photograph illustrates position of sand piles and plastic tubes constructed to facilitate sand transfer.

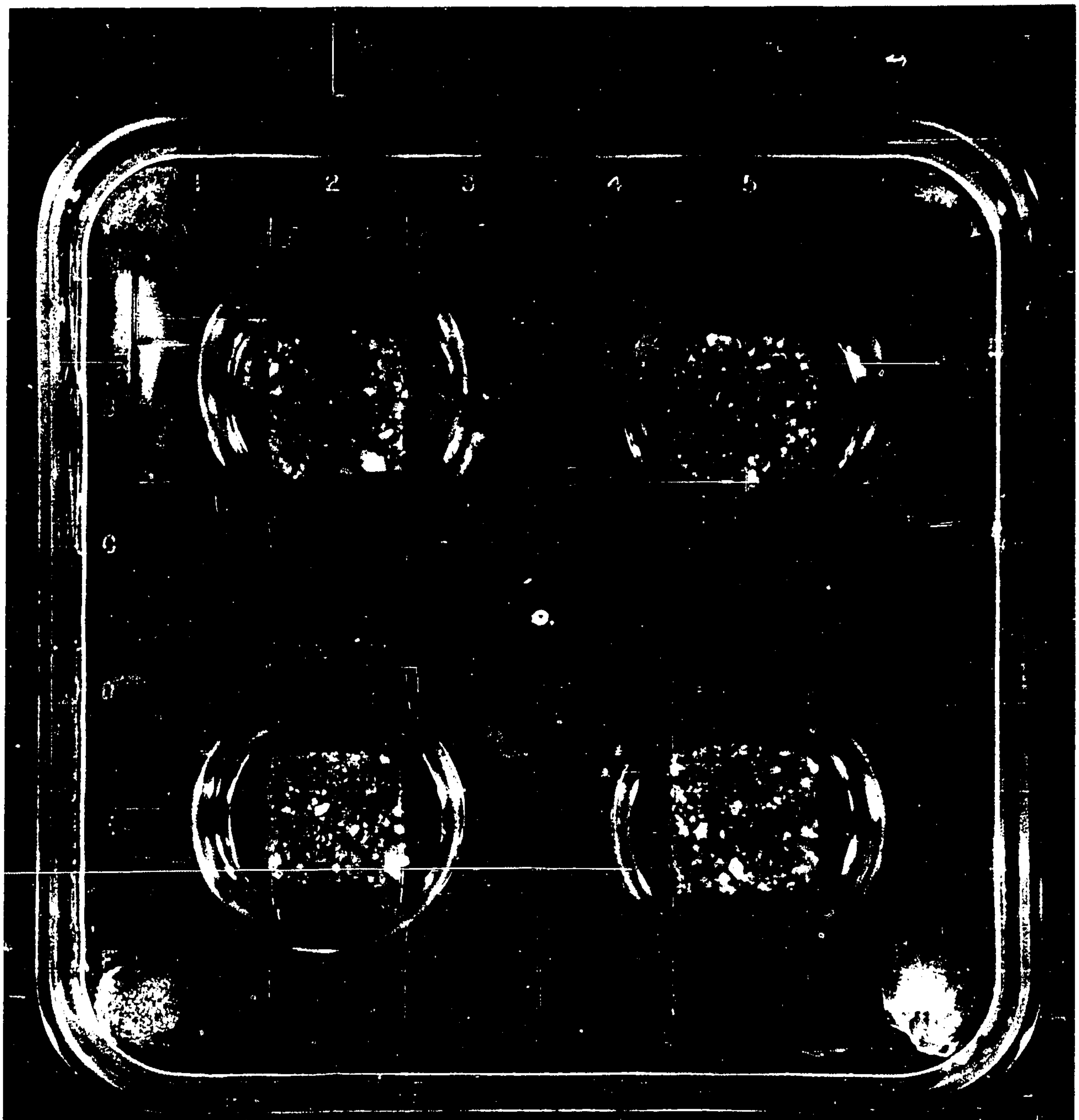

FIG. 3

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