Ecological Studies of the Sand-Dwelling Community of an East Texas Stream[1]

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Abstract. Between February 1976 and January 1977, an ecological study was made of sandy riffle areas of Mill Creek, Newton County, Texas. The psammonic community in the main channel of Mill Creek consisted of midges, oligochaetes, flatworms, micro-crustaceans, nematodes and tardigrades. The six dominant psammonic taxa with their annual mean densities and standard deviations (10^2X animals / m^2) were *Aeolosoma* spp. (1455 ± 3448), *Catenula* sp. (188 ± 605), *Parakiefferiella* spp. (307 ± 1169), Nematoda (43 ± 105), *Robackia demeijerei* (20 ± 30), and *Polypedium* spp. (20 ± 148). The following taxa were also present in descending order of abundance: *Eucyclops agilis, Macrobiotus* sp., *Hexagenia limbata,* Tanytarsini and *Parastenocaris* sp. Psammon densities were lowest in summer and highest in winter. Densities were highest in mid-riffle stations of upper and lower Mill Creek, and between mid-riffle and margin. Densities were lowest at the riffle's margin, pool and the Copperas Creek stations. Highest densities may be associated with intermediate water velocities which are slow enough to permit adequate deposition of detritus, but fast enough to prevent silt clogging and deoxygenation of sand interstices. *Parastenocaris* sp., *Rhynchataloma falcata,* Tanytarsini, and Nematoda did not differ significantly in vertical distribution (α=0.05). *Aeolosoma* spp., *Robackia demeijerei, Parakiefferiella* spp., *Polypedilum* spp., *Catenula* sp., *Eucyclops agilis* and *Hexagenia limbata* populations decreased with sand depth, while *Macrobiotus* sp. density increased with sand depth.

Organisms living in stream sands are ecologically limited by the abiotic constraints of their habitat. Often substrates are quite uniform with few microhabitats and a restricted number of available niches. Submerged surface sands are under constant flux, migrating between ephemeral ripples, dunes, bars and pools in a generally downstream direction. During spates, sands are especially unstable and are readily scoured and carried downstream in the current. Organisms living on submerged sand grains or in interstitial spaces of stream sands (stream hydropsammon vs. eu- and hygropsammon of moist and wetted beaches; Angelier 1953) must deal with the abrasion caused by shifting sands and recurrent habitat destruction from increased discharge. In addition, many sandy streams, because of their instability, have a notable lack of autochthonous primary production. This, coupled with a lack of organic matter in the sediment, results in the organisms being confronted with an unusually restricted range of available food sources compared to other biotopes (Angelier 1953; Hynes 1970).

An ecosystem which contains a restricted number of highly specialized species limited by such overt environmental stresses may be easier to describe ecologically than other more complex stream ecosystems. Quantitative horizontal and vertical sampling of this community are readily obtained since the sand substrate is relatively uniform and is penetrated easily with coring devices. The narrow size range and high density of the sands makes the separation of organisms from the substrate more complete than separation

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from finer textured sediments. Macro- and meiofauna can be recovered efficiently from sands by elutriation (Whitman et al. 1983), a much less time consuming procedure than the conventional sieving and picking techniques often employed in benthos sampling. Also, data on the interstitial chemical and physical parameters associated with this community are relatively easy to obtain.

In spite of the opportunities and advantages offered by this biotope, little is known about the ecology of stream psammon. This is understandable, since these shifting stream sands often have been considered biologically impoverished (Angelier 1953; Behning 1928; Berner 1951; Sterba & Holzer 1977; Wiszniewski 1934) or limited to only a select group of highly specialized microorganisms (Hynes 1970; Neiswestnova-Shadina 1935; Williams & Hynes 1974; Zhadin & Gerd 1961). In contrast, the pioneering work on exposed lake beach psammon by Pennak (1940) and Neel (1948) in North America, and Wiszniewski (1934) and Angelier (1953) in Europe revealed abundant and sometimes diverse sandy beach communities largely consisting of such meiofauna as rotifers, tardigrades and copepods. One of the earliest and biologically richest psammonic assemblage was described from the banks and wetted margins of the Oka River (Neiswestnova-Shadina 1935; Sassuchin, Kabanov & Neiswestnova-Shadina 1927). Various investigations later revealed little to contradict the belief that open sandy riffles were 'biological deserts' (see reviews by Angelier 1953; Husmann 1971; Jansson 1971; Motas 1963; Wiszniewski 1947). Consequently, most studies have emphasized the psammolittoral assemblages along the sandy banks of major river systems rather than the submerged sand community (e.g., Chappuis 1942; Greze 1953; Picard 1962; Ruttner-Kolisko 1961; Tilzer 1965; Wiszniewski 1934, 1947).

Aside from the early works on the Russian River Oka by Neiswestnova-Shadina (1935), Sassuchin et al. (1927), and the Volga River by Behning (1928) and more recently by Greze (1953) on the Angara River, Russia and Russev (1974) on the Danube River, little has been done that significantly increases our ecological knowledge of Eurasian stream hydropsammon.

In North America, stream hydropsammon communities have been described only recently. Urban (1971) studied the distribution of psammon of exposed and submerged sand bars and beaches of the Mississippi and Wildrice Rivers in Minnesota. Barton (1979) and Barton and Lock (1979) compared summer hydropsammon from several locations of the Athabasca River, Canada. Studies by Ingis, Clark, Irby and Moering (1976), Clark, Whitman and Lukins (1977), Whitman (1979) and Whitman and Clark (1982) on Mill Creek in east Texas probably represent the most extensive investigations of North American creek hydropsammon to date. To our knowledge, the Mill Creek investigations represent the only study of open riffle hydropsammon in a small stream system and, except for Barton (1979) and Barton and Lock (1979), it is the only North American ecological study which describes assemblages which differ substantially from communities normally reported in exposed lake and stream sands.

Our paper describes the spatial-temporal distribution of highly specialized psammonic meiofauna which often occurred in high densities in sandy riffle areas of a small east Texas stream from February 1976 to January 1977. The relationship of the horizontal and vertical distributions of this psammorheophilic community to stream velocity, dissolved oxygen and other physico-chemical characteristics of surface and interstitial waters is also discussed.

Description of Area

The Mill Creek drainage area (Lat. 31°09'N Long. 93°40'W) is located in the northeast corner of Newton County, Texas (Fig. 1), about 150 km north of the Gulf of Mexico and

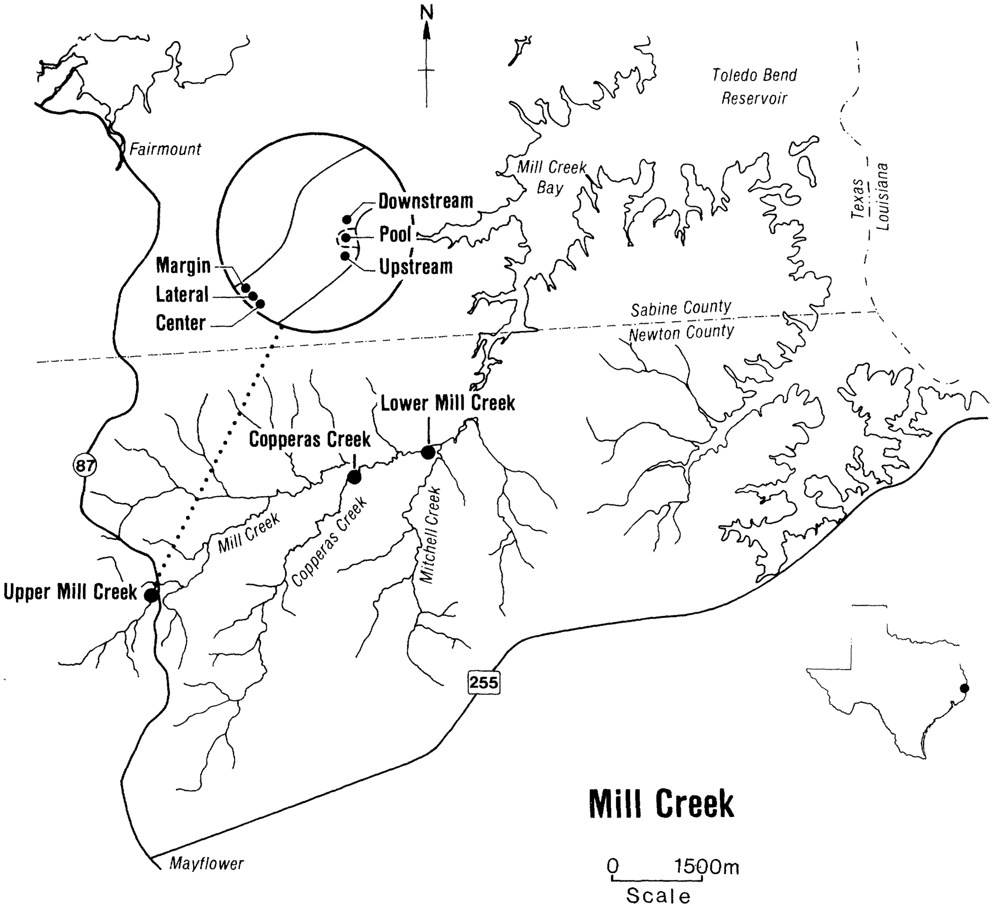

Fig. 1. Map of Mill Creek water shed and sampling sites.

within the western Gulf Coast plains area. The creeks comprising the drainage area are part of the Sabine River watershed and occur on the Kisatchie escarpment. The Mill Creek watershed is mostly forested, with upland mixtures of longleaf-slash pine and riparian beech-magnolia hardwoods. The climate is subtropical marine with warm summers and mild winters.

The Mill Creek drainage area encompasses 4916 ha with 106 km of stream bed and is a 4th order stream as it enters Toledo Bend Reservoir. Mill Creek, like its two major tributaries, Mitchell and Copperas Creeks, flows throughout the year and is maintained by groundwater originating from seeps and springs. The stream consists of sandy riffle runs separated by ephemeral pools created by channel meanders and obstructions such as fallen trees and shore vegetation. Cutbanks at stream margins and around obstructions are common. Sand depths ranged from 30-40 cm at center of most riffles to 5-10 cm near margins, and usually overlaid consolidated clay. Open riffle sands appeared 'cleaner' and more homogeneous, while pools and margins tended to have higher organic content and usually covered by a thin layer of silt (Whitman 1979).

Materials and Methods

A monitoring program was established in order to observe changes in psammon community composition, structure and density. Six sampling locations were selected at the upper Mill Creek site (Fig. 1). The locations of these sampling points were: 1) in the center of the riffle ('center' station); 2) midway between the riffle's 'center' and shoreline ('lateral'); 3) at the wetted margin of the riffle ('margin'); 4) approximately one meter above and 5) below the first pool encountered downstream of the sampled riffle ('upstream' and 'downstream', respectively); and 6) within that pool ('pool' station). A single 'center' station was used at the lower Mill and Copperas Creek sites.

Psammon were collected using coring devices consisting of 90 cm lengths of clear acrylic tube (3.85 cm i.d.) graduated by centimeters. Samples were taken by simultaneously pushing and rotating the cores by hand into the sediments to a 5 cm depth at the margin station and a 30 cm depth at the remaining stations. A rubber stopper was then placed in the top of the core. Disturbance and loss of the contents were minimized by placing a hand under the bottom end of the core sampler before slowly removing the corer from the substrate. When information concerning the vertical distribution was desired, the sand was let out in discrete units (30-20, 20-10, 10-5, and 5-0 cm). All samples were perserved in 5% formalin with 1% rose bengal dye added to facilitate sorting. Vertical distribution of the psammon was studied at the center station of the upper and lower Mill and Copperas Creek sites. The vertical sampling program began in July 1976 and continued through January 1977. All other locations consisted of integrated cores taken to a sand depth of 30 cm. Center stations also were sampled in this manner before adequate vertical sampling techniques were developed. Integrated core sampling began in February 1976 and continued through January 1977. All samples were taken in triplicate.

Separation of psammon from sediment samples was accomplished by a 'cone elutriator'. Details on the construction, efficiency, and operation of the 'cone elutriator' may be found in Whitman et al. (1983). Elutriates were retained by a No. 120 mesh sieve (0.124 mm openings) and transferred to a Petri dish for sorting and enumeration. Preliminary elutriation efficiency testing on replicates of psammon seeded sand indicated that elutriation recovery averaged 98% (S.D.=8%) for interstitial fauna typical of Mill Creek sands.

Psammon were enumerated and sorted by first systematically counting at 18× the entire contents of an 85 mm Petri dish with cm^2 grids. A second count of 108 subgrids (0.33 cm^2/subgrid) was performed at 50×. The purpose of this count was to enumerate small meiofauna species such as tardigrades, copepods and early instar midges that were difficult to recognize at 18×. In this latter count, or in cases where high detritus or organismal content forced sample dilution, enumeration proceeded (when feasible) until at least 50 organisms of the most dominant species were counted.

An interstitial water sampler (Whitman 1979) was used to retrieve pore water from sandy substrates. Water samples were transported on ice to the laboratory within 1.5 h of collecting. These samples were analyzed for specific conductance, bicarbonate alkalinity and pH. Dissolved oxygen and pH were immediately analyzed in the field. Fifty milliliters of water were collected from sand depths of 5, 10, 20, 30 cm. Direct surface water samples were also collected at the site of interstitial sampling. Water quality testing followed APHA's Standard Methods (American Public Health Association 1976). Sediment grain size distribution was determined on replicate sets of 3.85 cm cores taken at the upper Mill Creek center station. Samples were separated into 0-5, 5-10, 10-20 and 20-30 cm strata and passed through a sieve series of 1.0, 0.5, 0.25, 0.125, and 0.063 mm mesh openings. Statistical significance is set at α=0.05, unless otherwise noted.

Results and Discussion

Abiotic Components

Surface waters were high in dissolved oxygen (at or near saturation), slightly acid, low in specific conductance, chlorides, nitrates, alkalinity, total hardness, and phosphate (Clark, Whitman and Lukins 1977). Mean annual values for surface and interstitial dissolved oxygen, pH, bicarbonate alkalinity, specific conductance, and sediment ash-free dry mass are presented in Table 1. Mean base flow discharge at the upper and lower Mill Creek stations was 0.033 and 0.120 m^3/sec, respectively. Upper Mill's base flow in June and July (0.22 and 0.25 m^3/sec, respectively) was notably higher than the rest of the year which ranged from 0.08 to 0.14 m^3/sec (Fig. 2). On August 16, a storm hydrograph was constructed for the upper Mill Creek station from a 2 h, 1.91 cm rainfall. Discharge rose from pre-storm base flow of 0.036 m^3/sec to a peak discharge of 0.230 m^3/sec, some 2.5 h after the rain had ceased. Basin lag, the time of peak rainfall to discharge maximum, was 3.1 h and pre-storm base flow returned after 3.5 days.

Sediment Characteristics. - Nearly 50% of the Mill Creek's sediment consisted of particles between 0.5 and 0.25 mm and over 80% were between 1.0 and 0.125 mm. The homogeneity in sediment size distribution over the various depths sampled in Mill Creek sands is clearly demonstrated by Figure 3.

Interstices act as physical constraints on living and locomotive space for most Metazoa. Physical adaptations to interstitial existence may include a small, flexible and cylindrical body as seen in such psammorheophilic species as *Aeolosoma, Catenula, Parastenocaris, Macrobiotus,* nematodes, *Robackia, Parakiefferiella* and *Palpomyia.* Pore size may still impose physical limits on even the best adapted psammon. Porosity also plays an important role in the free exchange between the well oxygenated surface water and poorly oxygenated pore water. Ruttner-Kolisko (1961) postulated that grain size distribution must consist largely of medium grain sands (250-400 μm) for psammonic assemblages to develop. The present study, other unpublished observations by the senior author, and works by Tilzer (1968), Enckell (1968) and Urban (1971) appear to support Ruttner-Kolisko's premise.

Temperature. - Air, water and interstitial temperatures at 0-20 and 20-40 cm were monitored from March 3 to December 14, 1976, by a continuous multiprobe distance thermograph. The overall mean air temperature during this period was 19.9°C. Mean temperatures for surface water, and upper (0-20 cm) and lower (20-40 cm) sediments were 19.6, 17.5, and 16.1°C, respectively. Diel temperature variation decreased with increasing depth so that daily cycles became barely discernible at the 20-40 cm level; thus, all but longer-term temperature trends were filtered out. Temperature changes in shallow sediments usually lagged slightly behind ambient temperatures, but values usually approached that of surface waters when averaged over a day's period (Whitman & Clark 1982). Deeper sediments tended to be slightly cooler than overlying water in the summer, but during cooler seasons deeper interstitial waters tended to be warmer. Vertical

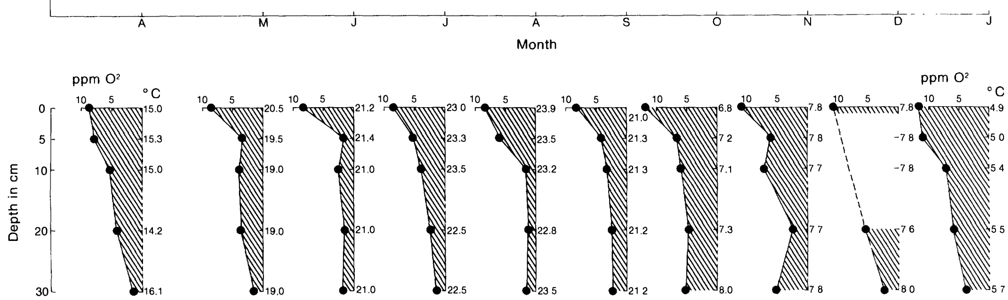

Fig. 2. Mean discharge by month (upper) and vertical distribution of dissolved oxygen and temperature (lower).

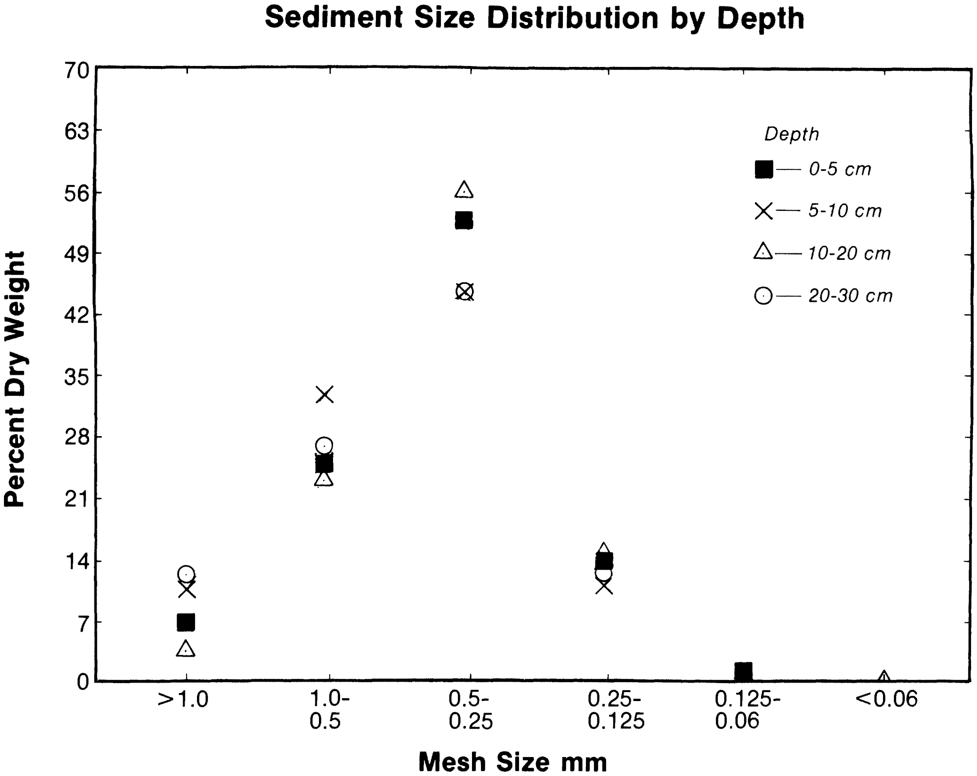

Fig. 3. Sediment size distribution at 0-5, 5-10, 10-20, and 20-30 cm depths.

temperature measurement of lake beach sands have been made by Angelier (1953), Pennak (1940), Ruttner-Kolisko (1957) and Wiszniewski (1934), but only Ruttner-Koliski (1961), Tilzer (1965) and Urban (1971) have inspected the temperature variations of submerged stream sands. Although most of these studies report non-continuous daytime temperatures, it appears that the major factors influencing vertical substrate temperature gradients include local climatic conditions, surface water depth, exposure, surface and ground water conditions, sediment porosity and, of course, recent meteorological history.

Angelier (1953) suggested that temperature ranks as the principal population regulator of psammon. One conspicuous problem with this view is the predominance of some cosmopolitan eurythermic stream psammon. For instance, *Robackia demeijerei* (Kruseman) ranked second numerically among Mill Creek psammonic midges and has been reported from a wide range of localities in the United States and Canada (Beck & Beck 1969; Roback 1953; Saether 1977; Soponis 1980) as well as western Russia (Zhadin & Gerd 1961). Its adaptations to this particularly harsh environment may account for its stenoecious, yet cosmopolitan distribution. Mill Creek's numerically dominant chironomid, an undescribed species of *Parakiefferiella,* may be the same undescribed species reported by Barton (1979) in Canada. We agree with Barton, who suggested that the absence of *Parakiefferiella* from other stream studies may be due to its restricted habitat preference, its small size relative to the coarse sands it normally occupies, its opaque body, and the relatively large mesh sieves usually employed in benthos studies.

Specific Conductance and Ash-free Dry Mass. - Specific conductance tended to increase with sand depth, although statistical analysis by ANOVA indicated that these means were not significantly different. Variations in specific conductance were, however, significantly correlated with bicarbonate alkalinity, pH, and dissolved oxygen. The relationship of these parameters may be from their association in community metabolism and/or the infusion of ground water.

Sediment organics at 0-5, 5-10, 10-20, and 20-30 cm depths were estimated by loss on ignition (550° C) on dried unsieved aliquots of Mill Creek open riffle sands. Although mean sediment organics varied between 0.21 and 0.32%, this component, like sediment grain size, was relatively homogeneous over the depth sampled (Table 1).

Dissolved Oxygen. - Although interstitial dissolved oxygen usually decreased markedly with depths down to 10 cm, it stabilized thereafter, and only once fell below 1 mg/liter at any of the depths sampled (Fig. 2). This latter occasion occurred 36 h after the August spate discussed above. Increased oxygen demand from organic particulates introduced by the storm's runoff may account for these lower values. In general, interstitial dissolved oxygen was higher in cooler months with the 5 cm stratum approaching that of the surface dissolved oxygen from November to December. Mill Creek sands lacked a distinct 'black layer' (which often characterizes the boundary of anaerobic and aerobic layers of sands) as described by Bruce (1928), Neel (1948), Pennak (1940, 1951), Brafield (1964), and Fenchel et al. (1967) in beach sands from freshwater and marine beaches.

The presence of oxygen in the deeper sediments of Mill Creek is consistent with the studies of Ruttner-Kolisko (1961) and Pechard (1962) in stream sands, and Schwoerbel (1961), Husmann (1971), and Poole and Stewart (1976) at similar depths of lotic gravel. Urban (1971) found Mississippi River sands devoid of oxygen below 6-9 cm, while William and Hynes (1974) rarely detected oxygen below 30 cm. Pennak (1940), Fenchel and Jansson (1966) and Fenchel (1971) found positive correlations between oxygen concentrations and animal distribution. It is interesting that most lake studies report no oxygen below 10 cm (Pennak 1940, 1951; Neel 1948), yet lotic studies often show the presence of oxygen at relatively greater depths.

An adequate supply of dissolved oxygen is critical to interstitial animal existence. Of

TABLE I

Mean surface and interstitial water quality and sediment ash-free dry weight by depth at upper Mill Creek's center station from February 1976 to January 1977. Means which are connected by underlining do not significantly differ at $\alpha = 0.05$ using Duncan's Multiple Range test.

Dissolved Oxygen (mg/liter)					
Depth	surface	5 cm	10 cm	20 cm	30 cm
Mean	8.89	6.49	4.16	2.95	2.49
Specific Conductance (µmhos/cm)					
Depth	surface	5 cm	10 cm	20 cm	30 cm
Mean	40.5	40.9	43.1	44.6	45.5
pH					
Depth	surface	5 cm	10 cm	20 cm	30 cm
Mean	5.96	5.75	5.51	5.63	5.63
Total Alkalinity (as mg/liter $CaCO_3$)					
Depth	surface	5 cm	10 cm	20 cm	30 cm
Mean	6.01	5.79	4.62	5.61	6.99
Sediment Percent Ash-free Dry Weight					
Depth	5 cm	10 cm	20 cm	30 cm	
Mean	0.21	0.22	0.32	0.31	

the chemical features investigated only this parameter was significantly correlated with the numerical density of dominant psammon such as *Aeolosoma, Parakieferiella, Macrobiotus, Robackia,* and *Catenula* (α=0.05, 0.018,0.0001, 0.008 and 0.0219, respectively). It is often assumed that pore water quickly becomes anaerobic given any appreciable oxygen demand within the sediments. Mill Creek may be characterized as an oligosaprobic soft water stream with strikingly clean sands and minimal autochthonous primary production. The only persistent autotroph found in open sandy areas of Mill Creek was *Tabellaria fenestrata* and its occurrence was sporadic. This diatom forms flat colonial chains and apparently persists by remaining in the boundary layer between the sand and surface water. Low organic content, shallow water depth with mean surface velocities of about 30 cm/sec and limited primary production may account for the near saturated dissolved oxygen found in surface waters (sometimes slightly supersaturated at dawn) and the persistence of dissolved oxygen in deeper sands. Populations may be low in summer because of higher temperatures which are associated with increased community respiration and reduced oxygen capacity. William and Hynes (1974) suggested that the occurrence of oxygen deep within stream gravel is related to surface velocity, in that increased flow directs oxygenated surface waters down into the substrate. While this is likely true of coarser grained stream beds, Figure 2 suggests that in sand, discharge and subsurface dissolved oxygen are often independent. Higher interstitial dissolved oxygen in Mill Creek, however, often occurred when instantaneous sediment temperatures equaled or exceeded that of surface water. This phenomenon, along with other evidence presented by Whitman and Clark (1982), suggests that thermal convective forces aid in the mixing of oxygenated surface and deoxygenated subsurface waters.

Bicarbonate Alkalinity and pH. - The pH tended to decrease from mean of 6.0 for surface water to 5.5 at the 10 cm sand depth. Below this depth, pH either tended to remain stable or actually increase slightly. The absolute difference in pH (0.5) of surface and 10 cm interstitial water is surprisingly close to values reported by Schwoerbel (1961), Husmann (1971), and Williams and Hynes (1974). These researchers found that pH dropped from 6.5 to 6.0, 7.5 to 6.5 and 8.0 to 7.5 over the same depth, respectively. Bicarbonate alkalinity was also generally lower at the 10 cm sediment depth, although overall trends are obscured by high experimental error encountered in the titration of these exceptionally low alkalinities. Neel (1948), Ruttner-Kolisko (1961) and Urban (1971) all show slight increases in bicarbonate alkalinity with sand depth.

Biotic Components

Of the 83 taxa reported for Mill Creek, 59 were recovered from open sandy areas (Table 2). Sixteen of the 59 occurred often enough to be classified either as psammophiles (non-obligate or opportunistic psammon) or psammobiotes (obligate psammon). Although the assemblage lacks variety, successful species often occur in large numbers. Six psammobiotes are presently under consideration for new species status (i.e., *Parastenocaris, Corynoneura, Cladotanytarsus, Tanytarsus* spp. and two species of *Parakiefferiella*). The other taxa listed are likely accidentals (psammoxenes) originating from backwater areas, submerged timber and occasional sandstone outcroppings. Gravel bottoms, sandstone outcroppings and associated assemblages rarely occur in Mill Creek.

One of the most numerous late summer species, *Hexagenia limbata* (Serville), may be psammoxenic and unable to complete its life cycle in Mill Creek. Clark, Whitman and Lukins (1977) showed that although *H. limbata* prefers pools, it was not consistently found in all pools. *Hexagenia limbata* is a burrowing mayfly living in tunnels that it excavates in the clay or silt substrates of slow moving rivers or lakes. This species occurs in relatively large numbers in early fall, but populations drop dramatically during late fall and winter. In contrast, the organism remains high in densities in the receiving waters of Toledo Bend Reservoir (Clark, Whitman & Lukins 1977). We suggest that early stages

TABLE II

List of organisms occurring in at least 2% of samples taken during 1976-1977 sampling period in open sandy riffles of Mill Creek (organisms occurring in at least 5, 10, or 25% of the samples examined are denoted by 1, 2, or 3 asterisks (*), respectively).

	Insecta continued
Chlorophyta	*Stenonema* sp.
Closterium sp.	*Beatis* sp.
Mougeotia sp.	Odonata
Sirogonium sp.	*Dromogomphus* sp.
Spirogyra sp	*Progomphus* sp.*
Bacillariophyta	Plecoptera
*Tabellaria fenestrata***	*Neoperla* sp.*
Protozoa	Coleoptera
Vorticella sp.	Elmidae
Coelenterata	Diptera
Hydra sp.	*Hexatoma* sp.
Platyhelminthes	*Limnophila* sp.
Catenula sp.***	*Crysops* sp.
Nematoda	*Tabanus* sp.*
Mesodorylaimus sp.	*Palpomyia* sp.*
Prismatolaimus sp.**	*Simulium* sp.
Priochulus sp.	*Cladotanytarsus* sp.
Rotifera	*Clinotanypus* sp.
Bdelloidea	*Coelotanypus* sp.
Tardigrada	*Corynoneura* sp.
Macrobiotus sp.	*Cricotopus* sp.*
Annelida	*Cryptochironomus* spp.*
*Aeolosoma tenebrarum****	*Endochironmus* sp.
Aeolosoma hemprichi	*Eukiefferiella* spp.
Pristina sp.	*Glyptotendipes* sp.
Chaetogaster sp.	*Microspectra* sp.
Mollusca	*Microtendipes* sp.
Pisidium sp.	*Orthocladius* sp.
Crustacea	*Parakiefferiella* spp.***
Moinodaphnia sp.	*Paralauterborniella* sp.
Alona setulosa	*Paratendipes* sp.
Eucyclops agilis	*Pentaneura* sp.
Parastenocaris sp.	*Polypedilum* spp.*
Insecta	*Robackia demeijerei***
Ephemeroptera	*Stempellina* sp.
Caenis sp.	*Tanytarsus* sp.*
*Hexagenia limbata**	*Zaverella* sp.

can tolerate the low silt content of Mill Creek, but that the substrate will not support larger burrows for later instars.

Overall mean psammon density and standard deviations for the 12 month sampling period was 193,000 ± 378,000 organisms/m^2. Individual samples ranged from 0 to 3919 organisms per core or 3,366,000 organisms/m^2. This maxium occurred in April at the upper Mill Creek center station. The other two replicate samples collected at that time contained 891,000 and 845,000 organisms/m^2. Although these latter two replicates are substantially less than the triplicate maximum, they still exceed that reported by most other sandy stream studies. Sassuchin et al. (1927) reported up to 95,000 organisms/m^2, consisting mostly of specialized protists of riverine beach sands. Behning (1928) reported a maximum of 9,500 metazoans/m^2; Greze (1953) 12,000/m^2; Zhadin (1956) 9,500/m^2; Barton (1979) 8,100/m^2; Barton and Lock (1979) 40,000/m^2; and Clark, Whitman and Lukins (1977) 98,000/m^2. Only Urban (1971) reported metazoan densities greater than that experienced in Mill Creek. He noted, for example, Diptera, Oligochaeta and Nematoda maxima of 56,76, and 216 organisms/cm^3 compared to our maxima of 5.2, 10.6, and 0.3 organisms/cm^3 for the same taxa, respectively.

Factors responsible for the high numerical density of the Mill Creek meiopsammon might include: 1) the greater core depth sampled versus the relatively shallower bite of the conventional grab samplers used in several of the above referenced studies, 2) the small mesh sieve (No. 120) used in the recovery of these organisms, 3) a long, mild growing season and absence of dramatic spring discharges resulting from snow melt, 4) the penetration of psammon and dissolved oxygen into deeper sands, and 5) the paucity of sandy stream studies in North America, especially in warm temperate regions. Many sand dwelling organisms living in this seemingly difficult abiotic environment can be classified as either highly specialized psammobiotes with narrow niche requirements or as opportunistic psammophiles with preadaptations to life in stream sands. Although clean shifting lotic sands afford few niches and low biological diversity, successful organisms occupy a relatively competition free environment. Small size, tolerance to low oxygen tension, interstitial locomotive behavior, and avoidance of surface sands are among the more salient adaptations for exploitation of interstitial microhabitats.

While this study supports Blum (1956), who states that 'Sand bottoms are unfavorable for algal attachment and sandy streams tend to be poor in benthic algae', it does not support the once popular belief which Hynes (1970) reviewed in his text on the ecology of running water, '...'clean' and therefore shifting sand is a relatively empty zone which is inhabited primaily by the microfauna... and by rather few large animals.' Larger organisms do appear endemic to several Eurasian streams associated with relic lakes (e.g., Lake Baikal, Black Sea, Caspian Sea, etc.), but appear absent from the psammorheophilic communities of not only glaciated North America (Barton 1979), but the southern United States as well.

In summary, *Aeolosoma* dominated the open sands of Mill Creek, followed by *Catenula, Parakiefferiella* and *Robackia*. In order of abundance, nematodes, *Polypedilum, Eucyclops, Hexagenia,* Tanytarsini, *Palpomyia,* gomphids, lumbriculids, stoneflies and several typically lentic species of midges dominated sandy pool areas. Of the literature reviewed, only Neiswestnova-Shadina (1935) found *Aeolosoma* as the most dominant member of the psammon. Barton (1979) found an undescribed species of *Parakiefferiella* as the most dominant animal in the Athabasca River sands.

Season Distribution. - ANOVA and Duncan's analysis of our 12 months of data (Table 3, Fig. 4) indicate that the greatest total densities generally occurred between December and April with a maximum density in February, although March was relatively lower than the other months in this period. Lower total densities were found from June to October. These generalities vary with species. First and second instars of *Parakiefferiella* dominated the population in early December 1976, and by the end of January 1977, the majority of *Parakiefferiella* were in instar III (the highest biomass in our 12 month sampling period, 154.8 mg/m^3). *Robackia* density remained relatively constant throughout the year. Populations of *Robackia* in December were made up almost exclusively by instars I and II, whereas pupae were recovered in early spring and fall. Biomass of *Robackia* tended to be higher in April and October (43.2 and 49.2 μm/m^3, respectively). Only *Hexagenia limbata* and *Eucyclops agilis* (Koch) were significantly more numerous in the fall, although *Parastenocaris* and Tanytarsini also ranked high during this period. Barton (1979) sampled psammon populations between June and October, and found that numerical densities consistently remained between 1,100 to 8,100 organisms/m^2, compared to the present study mean of 87,553 organisms/m^2 for the same period and 269,993 organisms/m^2 for the remaining months. Wiszniewski (1934) reported highest densities of European psammon in late spring and fall, although total numerical densities were not given and samples were not taken during the winter.

TABLE III

Significant difference in monthly mean density ($10^2 \times$animals/m^3) by taxon from February 1976 to January 1977, using Duncan's Multiple Range Test. Means which are connected by underlining do not significantly differ using Duncan's Multiple Range Test (α=0.05).

Month	7	9	8	6	5	3	11	10	12	4	1	2
Total	152	642	713	778	858	1459	1463	2093	2468	3440	4316	6927
Month	7	9	8	5	6	3	11	10	12	1	4	2
Aeolosoma	54	251	362	462	591	722	1206	1481	1940	2718	2921	5044
Month	7	2	5	3	6	4	11	9	12	8	10	1
Catenula	1.4	3.0	4.5	19	23	29	81	161	235	240	322	1128
Month	2	7	12	3	6	1	5	8	9	4	11	10
Eucyclops	0.00	0.00	0.75	1.3	4.9	5.6	5.6	5.9	10	22	27	39
Month	12	1	6	4	2	7	5	3	10	8	11	9
Hexagenia	0.00	0.37	0.72	1.1	1.3	1.4	3.0	3.9	4.9	8.2	9.0	35
Month	2	9	6	5	7	3	8	11	4	10	1	12
Macrobiotus	0.00	0.36	0.72	1.1	1.4	2.2	2.3	2.5	9.7	10	27	39
Month	8	7	6	3	11	9	2	10	5	4	1	12
Nematoda	3.6	10	15	20	32	32	34	42	43	56	64	150
Month	7	8	12	11	6	9	10	1	5	4	3	2
Parakiefferiella	51	56	61	71	103	104	112	204	323	374	655	1823

TABLE III continued.

Month	2	4	6	7	8	9	12	11	1	3	5	10
Parastenocaris	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.75	0.86	1.1	6.7
Month	7	2	5	4	3	6	11	12	9	8	10	1
Polypedilum	0.00	0.43	0.75	1.4	6.0	6.5	13	14	15	20	29	132
Month	8	5	1	11	7	2	6	12	4	10	9	3
Robackia	11	12	16	17	18	21	22	23	23	25	25	27
Month	2	7	8	6	1	3	12	11	5	4	10	9
Tanytarsus	0.00	0.00	0.00	0.36	0.37	0.86	1.1	1.4	1.5	2.5	6.0	6.8

Seasonal comparison with Urban (1971) is also not possible since he sampled essentially only summer months.

The interaction of several factors may be responsible for high winter populations. Fall recruitment from egg hatching gives rise to large numbers of early instars at a time when abiotic factors are favorable in warm temperate sandy streams. Sand stability is increased due to lowered winter base discharge and less frequent spates. Lower temperatures increase oxygen tension in surface and shallow interstitial waters, while retarding interstitial oxygen demand. Whitman and Clark (1982) have pointed out that deeper interstitial waters of Mill Creek in winter are usually warmer than overlying water and that well oxygenated surface water could displace pore water by simple thermal convective currents. Mill Creek's watershed has an annual snowfall of less than 2 cm with no significant stream surface or subsurface ice. Leaf detritus (an important food source) that is buried during fall, persists and increases in nutrient value during the winter and may be exported from the system by spring spates (Herbst 1980). Rapid density increases in winter by multivoltine species of *Parakiefferiella, Catenula,* and *Aeolosoma* (Whitman 1979) may reflect the ability of these species to respond to renewed food supply. The relatively stable annual densities of *Robackia,* which emerges primarily in September and April (Whitman 1979), suggest that this species may be less food limited and perhaps is well adapted to the abiotic stresses of interstitial existence.

Horizontal Distribution. - Eight locations in the Mill Creek watershed were monitored from February 1976 to January 1977 as described in the method section. Table 4 data show a clear difference between psammophiles and psammobiotes in horizontal locational preference. Psammophilic species such as *Eucyclops, Polypedilum,* Nematoda,Tanytarsini and *Hexagenia* were more prevalent in pools and along the water's edge, while most psammobiotes selected open sandy areas. The numerical density of *Parastenocaris* ranked highest at the stream's margin. Pool and stream margin species show even greater densities in silts and clay bottom of the contiguous waters of Toledo Bend Reservoir and the Sabine River (Clark, Whitman & Lukins 1977; Inglis et al. 1976).

Psammobiotes, such as *Catenula, Robackia,* and *Parakiefferiella, Macrobiotus* tended to concentrate in open sandy areas, rather than silt laden pools or margins. ANOVA and Duncan's mean separation indicate that significantly higher overall total abundance occurred at the lower and upper Mill center stations, and at the lateral station. Lower total densities occurred at the upper Mill Creek margin and pool station, and at Copperas Creek. *Parakiefferiella* ranked higher in density at both center stations of Mill Creek and just above and below pools while, *Macrobiotus* and *Catenula* ranked higher in density at the lateral station. Whitman (1979) using multivariate contrast analysis demonstrated that the five numerically dominant chironomid species of Mill Creek also followed horizontal density patterns similar to that of *Parakiefferiella.*

A number of factors may be responsible for the high numerical densities of psammon found in the open riffle areas of Mill Creek. Surface velocity, although quite possibly not affecting interstitial flow, may affect animal horizontal distribution by controlling the relative stability of sands and the distribution of allochthonous food material. Organismal horizontal distribution thus is controlled by an optimal flow regime and secondarily by available food and oxygen. Stream flow may act directly on psammon by scouring and creating instability of the sand habitat. In addition, increased velocity prevents suitable food items from settling and being incorporated in the sand. The increased densities of some psammobiotes in areas just above and below the pool or at the lateral station might possibly represent a compromise in surface flow regimes. These intermediate surface velocities might allow for food material to settle without increasing oxygen demand to critical levels or shifting the biocoenosis towards a pool community. Thus, siltation and organic loading in these sediments may be responsible for the

TABLE IV

Significant differences in density ($10^2 \times$animals/m^3) between stations by taxon. Means which are connected by underlining do not significantly differ using Duncan's Multiple Range Test (α=0.05). Stations are denoted as follows: 1 = Lower Mill Creek, 2 = Copperas Creek, 3 = 1 m upstream of pool, 4 = pool, 5 = 1 m downstream of pool, 6 = riffle's center, 7 = midway between riffle's center and stream margin, and 8 = the stream margin.

Station	8	2	4	3	5	6	1	7
Total Density	750	768	1094	1364	1950	2907	3743	3836
Station	8	3	4	2	5	6	7	1
Aeolosoma	194	499	535	555	908	2347	2965	3560
Station	8	1	2	5	3	4	6	7
Catenula	28	55	116	128	130	223	245	570
Station	5	1	3	7	2	6	4	8
Eucyclops	0.48	1.0	2.5	3.8	4.8	5.3	23	45
Station	1	5	4	6	2	3	8	7
Macrobiotus	0.00	0.48	1.1	1.7	2.3	4.4	9.7	46
Station	3	2	1	5	6	4	7	8
Nematoda	8.9	12	18	23	33	62	74	119
Station	2	1	7	4	8	6	3	5
Parakiefferiella	42	70	152	154	209	229	692	853
Station	1	5	6	3	2	7	4	8
Parastenocaris	0.00	0.24	0.24	0.25	0.26	0.51	0.56	4.8
Station	2	5	7	1	6	3	4	8
Polypedilum	0.25	0.48	0.76	0.78	1.2	2.0	75	91
Station	8	4	3	7	2	6	5	1
Robackia	8.9	9.2	13	14	17	31	31	34

observed shift in community composition from a strictly psammonic community to one more typical of those reported for slower moving streams. At pool and margin stations, for instance, the detritivore, *Parakiefferiella,* was replaced by *Polypedilum* and Tanytarsini, while *Robackia* was replaced by another morphologically similar predator, *Palpomyia* (Ceratopogonidae). Tipulids, tabanids, ephemerids, gomphids, nematodes, plecopterans (on exposed wood), sphaerids and lumbriculids were common in pools, but infrequently occurred in the relatively 'cleaner' sands of adjacent open riffles. Interstitial water quality examination in areas of high silt content was not possible because of silt and detritus clogging of the interstitial sampling apparatus.

Multivariate analysis of the five most dominant psammon indicated that the center stations of upper and lower Mill Creek had significantly higher densities than all other stations examined (α=0.05). This finding is in general agreement with Urban (1971) who found greatest psammon densities in 'stable clean' submerged sands and lowest densities at the waterline. Multivariate analysis of the 12 most dominant psammon indicated the Copperas Creek station had the lowest densities of the open riffle locations inspected.

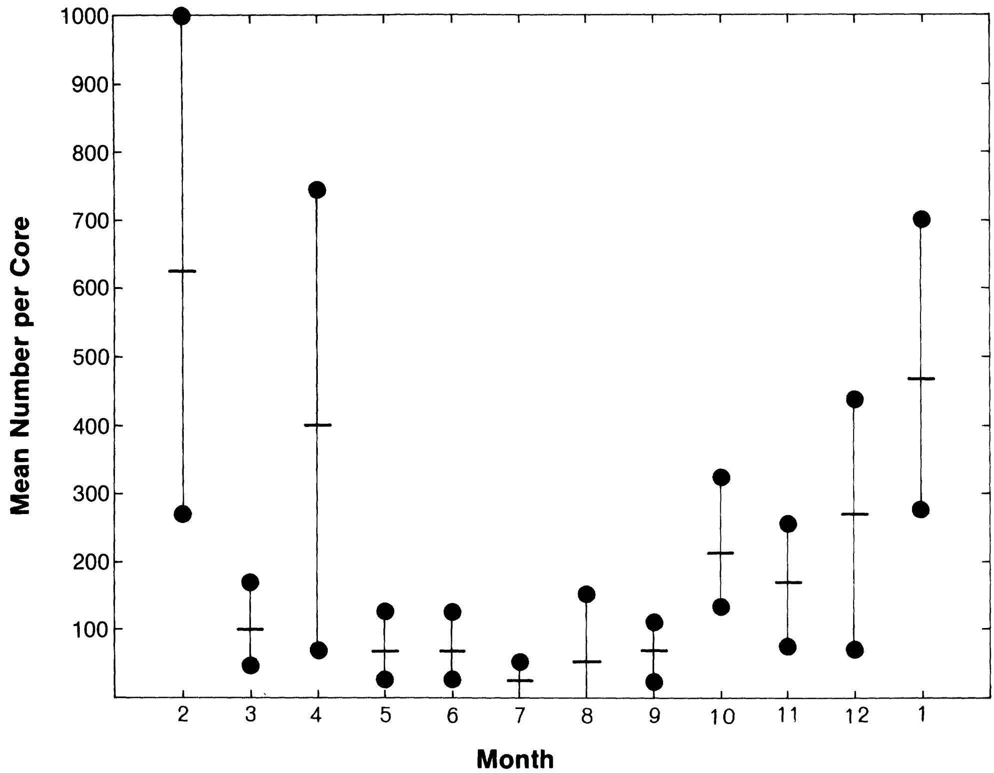

Fig. 4. Mean number of organisms per core (347 cm^3). Horizontal lines indicate means and vertical bars indicate 95% confidence intervals.

Clark, Whitman and Lukins (1977) reported that although specific conductance, bicarbonate alkalinity, total hardness and total phosphate differences between the two creeks were biologically insignificant, Mill Creek nitrate levels were much higher than Copperas Creek (0.44 vs. 0.09 mg/liter, respectively). Perhaps nitrate concentrations are limiting to the heterotrophic microflora of Copperas Creek on which at least some meiopsammon are presumably directly or indirectly dependent.

Vertical Distribution. - Figure 5 shows the depth distribution averaged over the sampling period for the nine most dominant Mill Creek psammon, while Figure 6 illustrates mean monthly vertical distribution for five selected animals. Vertical sample means (0-5, 5-10, 10-20, 20-30 cm) from collections between June, 1976 to January and April, 1977 indicate that *Parakiefferiella, Polypedilum, Catenula, Eucyclops,* Tanytarsini and *Hexagenia* usually decreased with increasing depth, although these trends varied seasonally. *Aeolosoma* and *Robackia* were significantly more dense at the 5-10 cm strata, while *Macrobiotus* concentrated at 20-30 cm levels. Mill Creek psammon differ from those of other psammonic studies in that organisms penetrated to greater depths. Ruttner-Kolisko (1961) and Urban (1971) rarely found organisms below 6 cm, Pennak (1940) 8 cm, Sassuchin et al. (1927) 10 cm, and Neel (1948) 5 cm. We postulate that the greater penetration of psammon in Mill Creek is due to the greater dissolved oxygen in the deeper sands. This, in turn, is due to a combination of factors including exceptionally good water quality, relative sparsity of organic particulates, the coarseness of the sand and increased thermal convective exchange due to greater diurnal temperature variations during cooler months in subtropical areas such as eastern Texas.

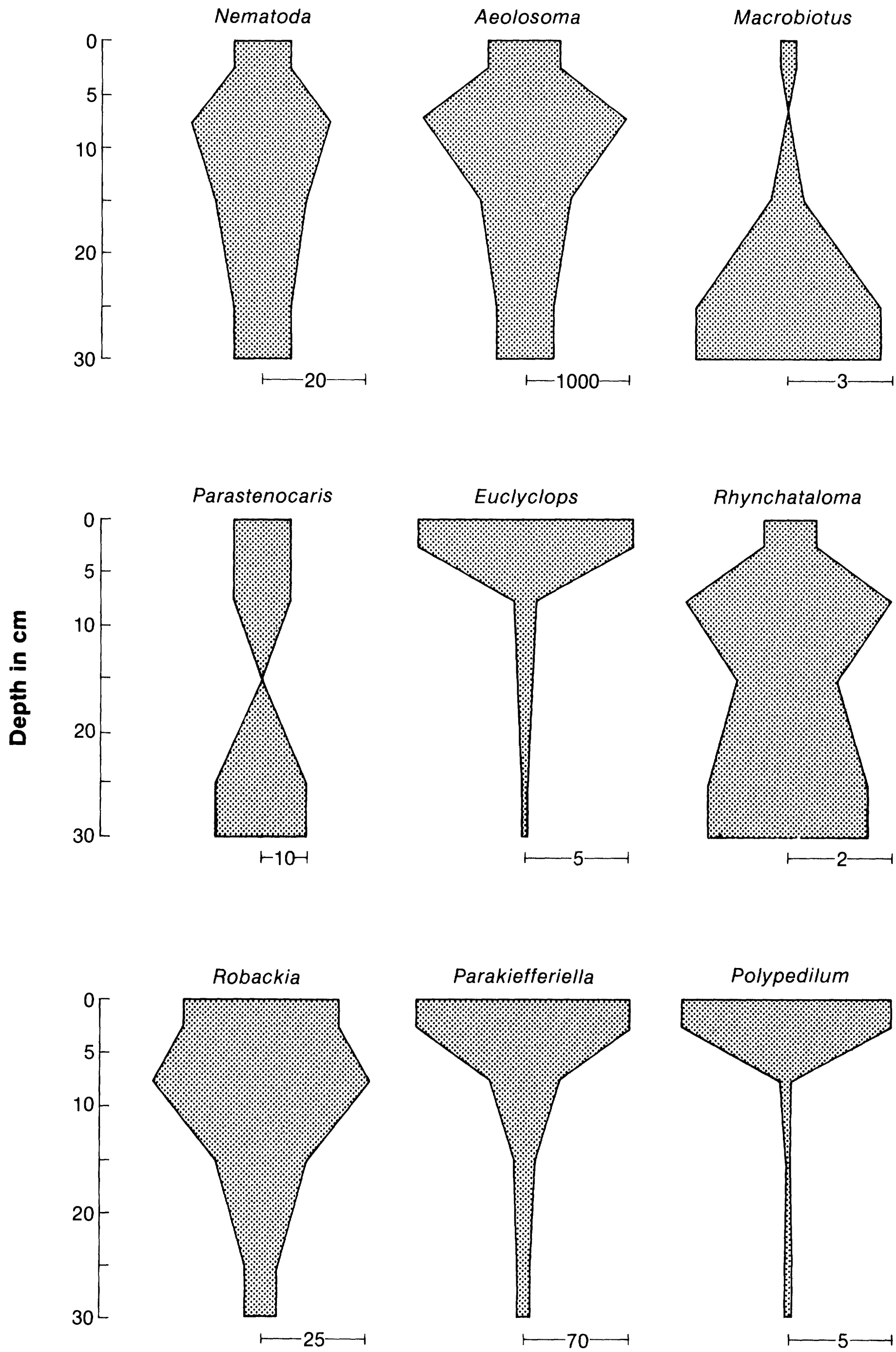

Fig. 5. Depth distribution for selected organisms. Scale units differ for each organism and are in units of mean number per dm^3 of sand.

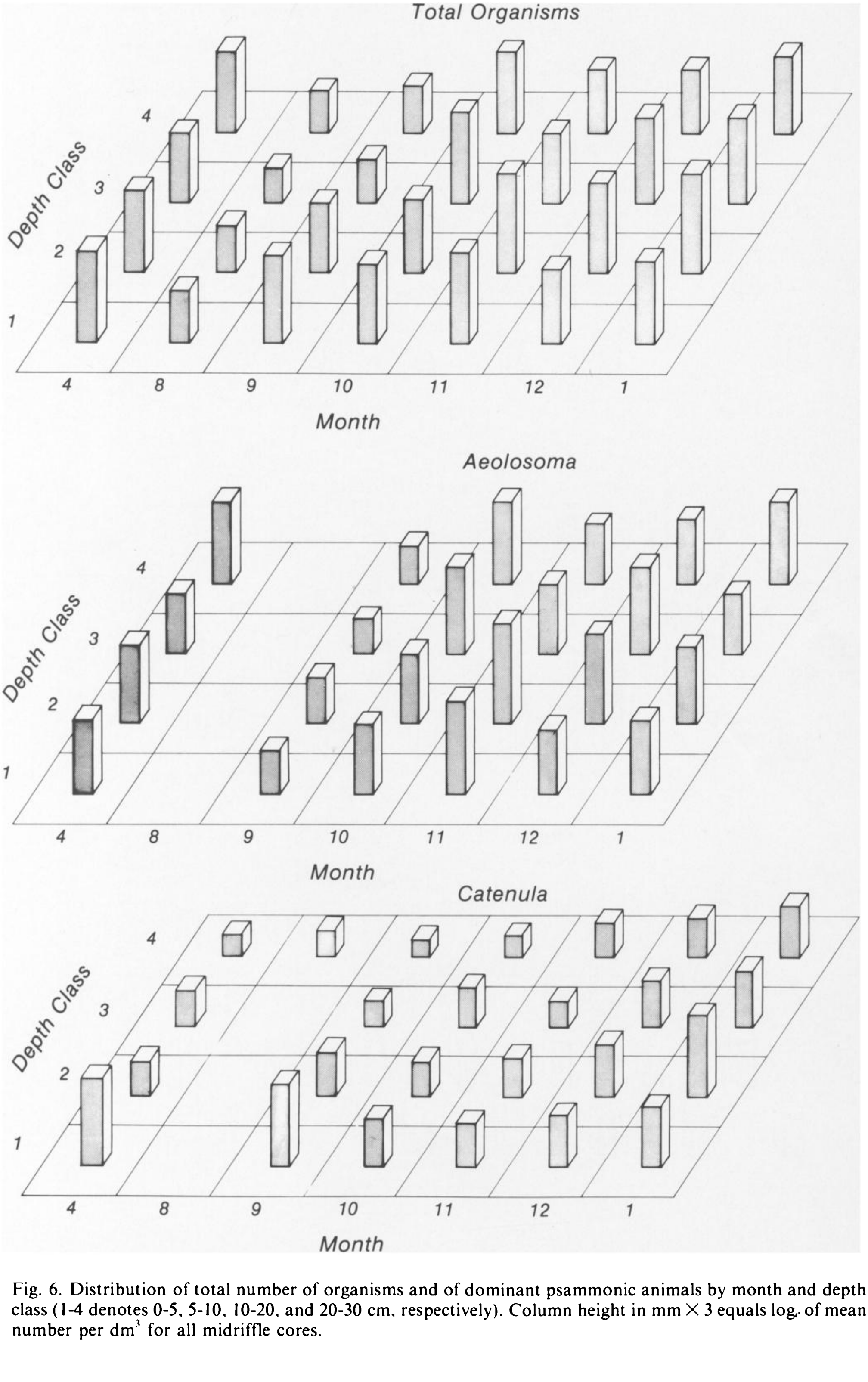

Fig. 6. Distribution of total number of organisms and of dominant psammonic animals by month and depth class (1-4 denotes 0-5, 5-10, 10-20, and 20-30 cm, respectively). Column height in mm $\times$ 3 equals $\log_e$ of mean number per dm^3 for all midriffle cores.

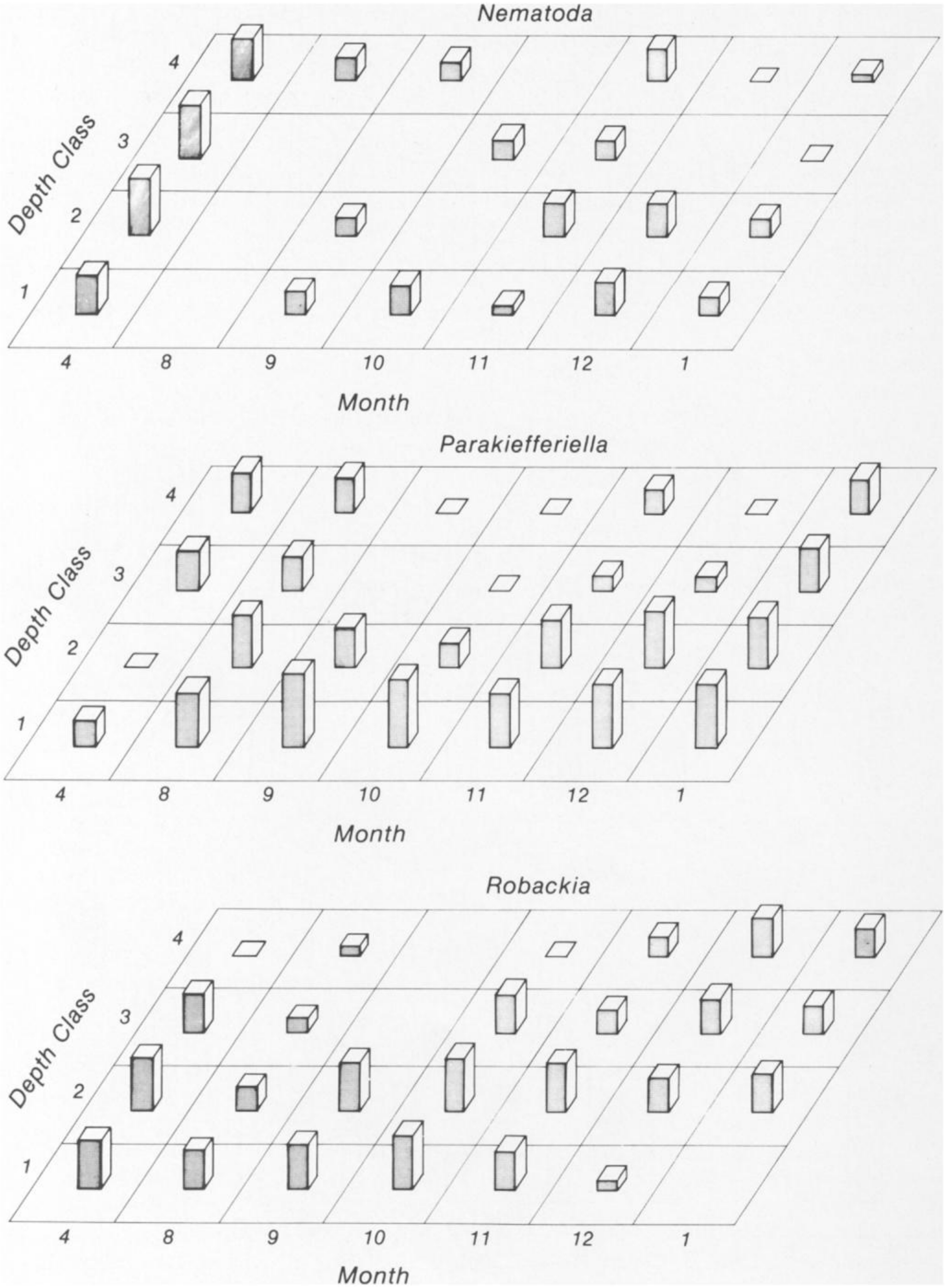

Figure 6 continued.

Organisms which occur in the pools and margins of Mill Creek were concentrated in the top few centimeters of sand, in contrast to species of open sands which were more evenly distributed over depth. This phenomenon agrees with most investigations dealing with the psammon of stream banks, large slow moving river psammon and emergent and submergent sand of lakes (Neel 1948; Pennak 1940; Ruttner-Kolisko 1961; Sassuchin et al. 1927; Urban 1971). These biotopes possibly have a greater tendency for interstitial spaces to become filled with particulates and silt, limiting oxygen at deeper depths.

Williams and Hynes (1974) have suggested that interstitial fauna migrate downward into warmer sediments during winter in order to optimize larval development. Midge larvae rearing experiments and instar analyses of field samples from Mill Creek indicated that most hatching occurs in late winter when populations usually are distributed evenly in the top 10 cm for *Parakiefferiella* and below 5 cm for *Robackia*. By April, most *Parakiefferiella* were found below 20 cm, while *Robackia* remained evenly distributed in the top 20 cm of sand. Clifford (1966) has suggested that stream benthos migrate downward into deeper sediments to find refuge during increased discharge. The vertical distribution of *Robackia*, for instance, shows little relationship to increased seasonal discharge, although some downward migration is indicated for this larger, more active predator (hence higher metabolic needs) during winter when deeper interstices contained greater quantities of dissolved oxygen. Another group of organisms (i.e., *Catenula*, Tanytarsini, and nematodes) show little vertical preference or response to surface conditions. During the August 16 rain, previously described, we obtained triplicate vertical samples at 4 h intervals from pre- to poststorm. Replicability within and between sample sets was relatively high and consistent, but there was little suggestion that vertical distribution of open riffle psammon changed with surface flow conditions or time of day (Whitman 1979).

In the constantly shifting sands of open riffle areas, it is not surprising that some organisms select intermediate depths; a possible compromise between increased stability of the deeper sands versus the decreased availability of dissolved oxygen. *Macrobiotus*, well known for its tolerance to low oxygen tension (Pennak 1940), takes advantage of the lowest depths available and it, along with *Parastenocaris*, is often found exclusively there.

Rotifera and Hydracarina are apparently common in North American exposed lake sands (Neel 1948; Pennak 1940) and Eurasian submergent and emergent stream sands (Angelier 1953; Behning 1928; Tilzer 1965; Wiszniewski 1934; Zhadin & Gerd 1961), but were notably lacking in the sands of Mill Creek. Both Urban (1971), working on upper Mississippi, and Barton (1979), on the Athabasca River, have also noted the sparseness of these taxa. However, it would be premature to conclude that this is characteristic of North American sandy streams, since so few have been inspected to date. Behning (1928) and Neiswestnova-Shadina (1935) in their classical works on the banks of Russian sandy rivers, reported a large variety of specialized protists equipped with adhesive organs for attachment to sand grains, but found submerged lotic sands biologically impoverished. Comparable attached protozoan assemblages were absent from both submerged and exposed sands of Mill Creek. Our study also differs in that the exposed wetted and moist shore sand communities (hygro- and eupsammon) were relatively low in density and diversity. This latter finding is consistent with observations by Urban (1971) on the Mississippi River. The sparseness of this component of the sandy stream community is in contrast to the rich bank fauna of lakes in areas more temperate than Texas. Warmer sediment temperatures, variable water levels, deposition of organic laden silts (hence higher oxygen demand), or the shallowness and finer texture of the bank sands could be important factors in excluding many psammon from exposed sands.

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