15

ASPECTS OF THE POPULATION DYNAMICS AND ECOLOGY OF THE BLOODWORM (*Arenicola loveni* Kinberg).

Thesis

Submitted for the Degree of

Master of Science.

University of Cape Town

by

CHRISTO MARIUS GAIGHER.

1979.

CONTENTS

CHAPTER 1 : INTRODUCTION AND GENERAL ACCOUNT

INTRODUCTION

Recreational salt-water angling in the Cape Province is increasing annually in importance, making it potentially a valuable industry with various, and far-reaching socio-economic benefits. With the growing interest in sport angling come various conservation and management problems. One of these is the protection of estuarine bait resources. Arenicola loveni Kinberg (known in South Africa as bloodworm, a colloquial term which is shared with such divergent forms as glycerid polychaetes and chironomid larvae) is an important estuarine (and marine) bait species which in many estuaries is subject to heavy exploitation. This research project was undertaken by the Department of Nature and Environmental Conservation to gather the essential data on which to base the management of the species, following reports that it was becoming rare or even extinct in a number of Cape Estuaries.

The Arenicolidae in general are used extensively as bait by salt-water anglers from Japan and Korea to the European Continent and British Isles, while in the United States a study was recently undertaken on a grant from the U.S. Department of Commerce into commercial production of A. cristata Stimpson, to supply the vast potential market (D'Asaro 1976). This Author records that in the U.S.A. 9,5 million recreational salt-water anglers spent 146 million dollars on bait in 1970, showing the importance of this facet of the recreation industry.

In South Africa there is doubtless a potential market for estuarine bait species, but only a very limited degree of commercial esploitation is allowed in the Cape Province, while the Natal Park's Board itself undertakes the exploitation and marketing of some estuarine bait species in that Province. In the Cape this form of management is not possible due to high costs and management requirements. The Department does however recognise its function in (a) preserving healthy stocks of bait species as an important component of the

estuarine ecology, and (b) at the same time encouraging the maximum, non-detrimental exploitation of estuarine bait species. At present the only restrictive measure is a blanket 'bag limit' of 5 worms per angler per day.

A. loveni has not previously been studied in any detail in South Africa, which is surprising because large populations are known from a number of estuaries and sheltered bays from Durban to Saldanha Bay (Wells 1962). It is however far from ideal study material as it is relatively cryptic and inaccessible, burrowing up to a meter deep in sand or sandy-mud banks, which are at best only exposed at certain phases of the tidal cycle.

In Britain and on the Continent A. marina has been the subject of much study and a favoured experimental animal over the last forty years, and the reproduction, mechanics of burrowing, pumping, blood chemistry, digestion and other aspects have been well studied. This species is however much smaller than A. loveni (maximum mass around 15 g compared to 150 g in A. loveni) and occurs in much higher densities and so shallowly that they are readily obtained by raking or forking. No detailed work on age structures or population dynamics of any Arenicola species has yet appeared in print, probably because for various reasons they are also difficult subjects for this kind of study. This knowledge is however vital to the management of the species and in this study attempts are made for the first time to quantify some of these aspects.

Because so many factors are of importance in guiding management, the scope of the present study is of necessity very wide, so that many aspects could not be investigated in great depth. This study is therefore of an applied nature rather than purely academic. Aspects studied were population dynamics (density fluctuations, growth rate, recruitment, etc.), the reproductive cycle and fecundity, some habitat features (salinities, temperature and pH fluctions), and substrate analyses as related to distribution.

TAXONOMY

In order to interpret the research results, it is useful to see A. loveni in context with others of the family which are better known. According to Wells (1964) such 'comparisons are valuable because the way of life and general appearance of the 24 named lugworm varieties are the same'. The affiliations of A. loveni with other members of the family are brought out clearly, especially from the taxonomic work of Wells.

The taxonomy of the Arenicolidae was revised by Wells (1959). He recognised three clearly defined genera. Previously Ashworth (1912 b in Wells 1959) had recognised only two: all species but one were included in the genus Arenicola Lamarck. The three genera of Wells are Arenicolides, Arenicola and Abarenicola. The genus Arenicola Lamarck 1801 is described as having an achaetous tail; small retractable prostomium; statocysts present; setigers divided into 5 annuli; branched gills, the first of which may be reduced or absent on setiger vii; neuropodia on the hinder branchial segments approaching close to the mid-ventral line; a pair of oesophageal caeca opening separately; septal pouches present and there are five to seven pairs of nephridia, which open on setiger iv or v.

Two subspecies of Arenicola loveni Kinberg 1866 were first recognised by Stach (1944). These are Arenicola loveni loveni (the South African form) and A. l. sudaustraliense (the Australian form). Wells (1962) also recognised the two subspecies, although he rejected Stach's main character, a large gonad on the anterior face of septum 3. There are however a number of other differences between the subspecies, for example: greater proliferation of caudal segments in A. l. loveni and larger septal pouches; transverse striation of notopodial chaetae in A. l. loveni; preventricular dilations of the dorsal blood-vessel in A. l. sudaustraliense (Wells 1962).

Arenicola loveni is one of the largest of the Arenicolidae but a large part of the length (and mass) consists of the caudal section.

Wells (1962) described the 'proliferation of the segments in the tail of the African specimens' as 'quite astonishing', while he regarded the species as 'rather apart' from the other species in the genus. In a paper on the zoogeography of the Arenicolidae (Wells 1964) the genus Arenicola is proposed as having radiated 'from an ancestral stock in the Northern cool-water zone'. Both forms of A. loveni, although geographically widely separated are found near the southern 20°C summer surface-water isotherm. He concluded from the distribution of the Arenicolidae that 'temperature, acting either directly or indirectly is a factor of outstanding importance in the control of lugworm distribution'. It is interesting in this regard that the furthest known distribution of A. loveni on the West Coast is Langebaan lagoon, which although in the cold Benguela current zone, is a large shallow and sheltered bay shown by Day (1959) to maintain far higher temperatures at least over summer than open water on this coast. This population might be a remnant of a historical wider distribution, when warm currents penetrated higher up the coast than present.

The other members of the family Arenicolidae which occur along the southern African coast are a subspecies of Abarenicola affinis, namely A. a. africana, which is known from the West Coast from Langebaan lagoon and Lüderitz Bay, and Abarenicola gilchristi from False Bay and Buffels Bay (on the Cape peninsula) (Wells 1963). The study area in the Breede River Estuary is more than 150 km from the most easterly known locality where either occur, and no specimen of either species has ever been identified in samples.

GENERAL ACCOUNT OF ARENICOLA LOVENI IN SOUTHERN CAPE ESTUARIES

There are no published data on even general behavioural aspects of the ecology of A. l. loveni. These however have considerable management implications. Before discussing in depth the study of the A. loveni population in the Breede River Estuary, it is necessary therefore to give a general account of the species, in the southern Cape.

Occurence

A. loveni occurs along the southern African coast from Saldanha Bay to Durban in estuaries, lagoons, marine bays and beaches both on intertidal banks and sublittorally. A feature of suitable localities is that they are protected from excessive wave action. Stach (1944) records for A. loveni in Australia that he only found the species in Moreton Bay on Reevesby Island, where there was protection from both northerly and southerly prevailing winds. Other bays without this protection were 'destitute of Arenicola'. A. l. loveni are well known from a number of southern Cape estuaries, but their marine distribution has received little attention. Beach populations are however known from Muizenberg, the Strand, Franskraal, Pearly Beach and Struis Bay.

The sublittoral distribution is even more obscure due to sampling problems, and because this aspect has previously received little attention. Few of the southern Cape estuaries are more than a few meters deep, but in almost all cases sublittoral populations extend from intertidal ones, and such populations are known from Knysna lagoon, Breede River, Heuningnes River, Uilenkraals River, etc. The sublittoral depth to which A. loveni may extend is unknown. Day and Morgans (1956) however have a record of the species dredged from the open water in Durban Bay, while the University of Cape Town has samples from 30 m in Saldanha Bay (Branch 1977).

Substrate

The substrate inhabited by A. loveni in southern Cape estuaries and on beaches ranges from coarse shelly sand through uniform clean beach sand (the habitat also described for Abarenicola gilchristi (Day 1955)), to silty or muddy sand. Distribution however does appear to be limited by the 'hardness' of the substrate, and worms are not found in firm claybound substrates. Very large individuals can apparently inhabit areas unsuitable for smaller specimens. At Knysna, for example, very large solitary specimens which could not be captured, but which were probably well in excess of 100 g, were found in soft

mud in Zostera beds. Areas colonised by exceptionally large worms also occur in the Breede River Estuary.

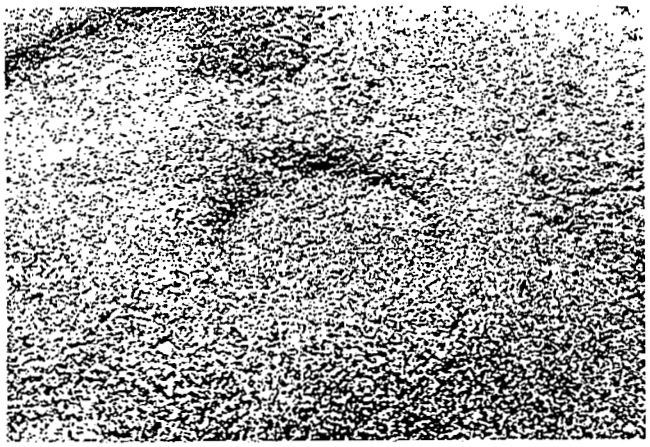
Other Arenicola species are described from a range of substrates:

A. marina	Sandy beach	Chapman (1949)
	dark, muddy sand	Jacobsen et al (1968)
	sandy mud	Duncan (1960)
A. cristata	wide range including white, calcareous sand	Wells (1962)
A. caroledna	sandy shore	Wells (1962)
A. glasseli	sheltered muddy beach	Wells (1962)
A. bombayensis	internal muddy flat	Wells (1962)
A. ecaudata and A. branchialis	under stones and in gravel	Eve and Southway (1958)

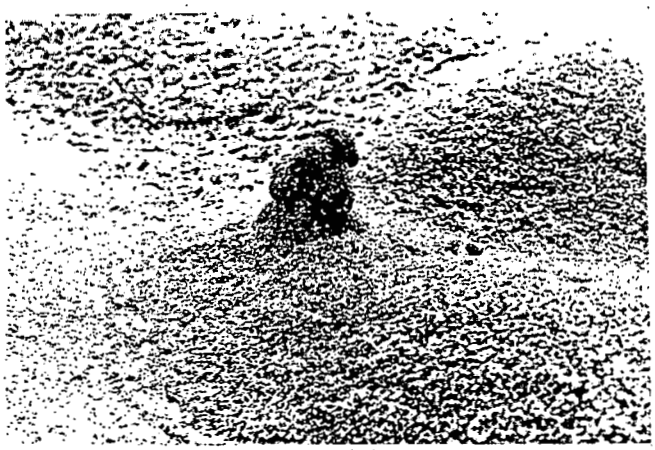
Some species do however exhibit a high degree of substrate selection, for example two proposed subspecies of Abarenicola claparedii were particularly associated with certain substrate types (Healy et al. 1959). A. c. pacifica and A. c. vagabunda were found in the same bay on San Juan Island. The former occurred mainly on the gravelly, stony margins of the bay, while A. c. vagabunda were abundant in deep, loose sand in the entrance and central part of the bay. There was no overlap in types and it was apparent that substrate and not tidal effects determined their distribution.

The depth of the substrate is recognised as one of the major factors influencing distribution. Chapman et al. (1949) determined that the irregular distribution of A. marina at Whitstable was caused by differences in the depth of muddy sand overlying clay. Stach (1944) discussed various densities of A. loveni, and concluded that at least 30 cm of sand overlying an impenetrable layer was a prerequisite for suitable habitat in the area studied. At Breede River distribution is certainly largely influenced by the depth of sand overlying extinct Upogebia beds in clay, and may be a factor influencing both growth rates and dispersion as will be shown later.

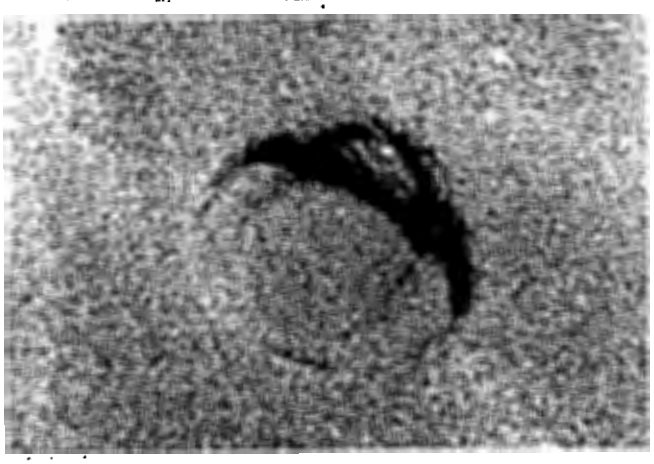
Plate 1 ; Surface signs



Developing funnel



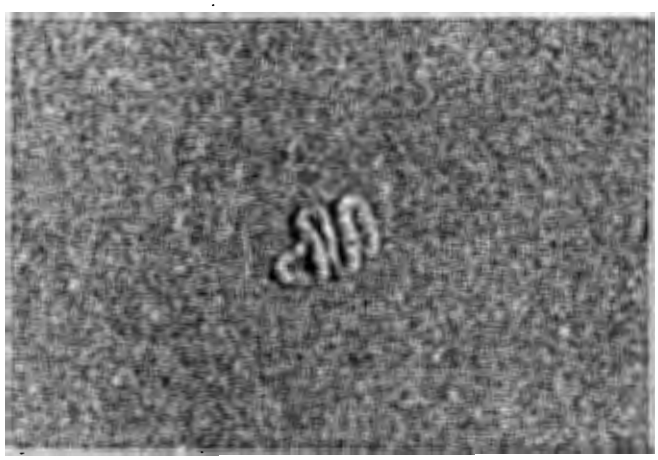
Cast (young worm)



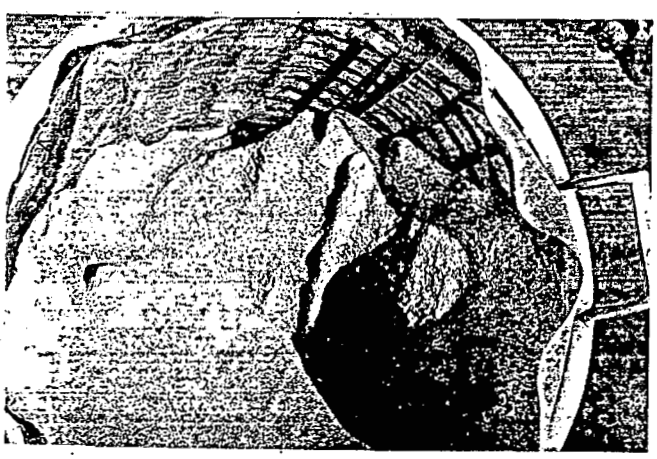
Developing funnel

Cast (adult)

Fully developed



'Sand-rope' cast, Muizenberg



Burrow exposed by washing

Another factor of uncertain importance in distribution is the organic content of the substrate. Longbottom (1968 in Newell 1970) found good correlation between total biomass of A. marina and the organic carbon and nitrogen of the deposit. A. loveni have however been found in substrates of very low natural organic content.

Burrowing and Surface signs

The presence of bloodworm in a specific substrate is marked by the presence of surface signs, which although highly variable, typically consist of a funnel shaped depression at the one end, and pile of faecal sand at the other. These mark the head-end and tail-end respectively of an approximately 'L' shaped, and mucus-lined burrow. In this, the worm lies with its head downward and its tail extending towards the surface. The burrow is completed by a zone of subsidence (marked by a funnel-shaped surface depression) caused by feeding at depth. Under certain conditions the funnel subsides further as a tubular opening, which makes the burrow appear continuous and which gave rise to the original concept of the burrow of the Arenicolidae being a double open-ended 'U', until the first 'L' shape was described for A. marina by Bohn in 1903 (Wells 1944). It is described as a vertical or gently curving shaft, turning to run horizontally for varying distances to a blind end which may be slightly raised toward the surface (Wells 1945). All A. loveni burrows examined in this study complied to this basic description, although depth and angle were often modified by hard layers under the surface. The depth of the head-shaft was often in excess of 75 cm and only the smallest worms had burrows less than 30 cm deep.

Day (1955) first described the funnel-shaped depression at the head-end of the funnel of A. loveni, but did not see castings. The surface signs of A. loveni, are also very variable, and are a function of the tidal phase, substrate, locality and size of worm. Stach (1944) described heaped coiled castings 6 to 10 cm high for the Australian subspecies, and in fact coiled castings are typical in most species and may be individual faecal cylinders or piles of coiled casts (Wells

1962). These in A. caroledna are so persistent that Okada (1941) used the diameter as an index of size and growth. Casts of A. loveni range from watery spurts on the sand surface to simple 'sand rope' coils to irregular high-piled mounds showing traces of layering. In sublittoral specimens featureless mounds of defaecated sand of up to 15 cm high are common. Signs are often typical for a given locality; at Leisure Island, Knysna for example, Arenicola casts mainly consist of only local discolouration of the surface, while the tail end of the burrow is marked by a small respiratory opening; On Muizenberg beach 'sand rope' casts which were almost immediately erased by wave action were recognised; at Langebaan although multiple subsidence funnels are common, faecal casts are rare; at Breede River casts were distinctive enough to allow an assessment of the population, and greatly exceeded the number of head-shaft depressions.

Casts of juvenile worms are usually clearly distinguishable from those of larger worms, by their size and nature. Casts of small worms were proportionately higher-piled with cylindrical coiling of small diameter and more apparent than in larger worms. Juveniles of 0,01 g could already be located by their casts.

The conical depression on the head-shaft is equally variable. It has frequently been described for A. marina (Wells 1945, Ziegelmeier 1964, Newell 1970) and other species such as A. cristata and A. caroledna (Wells 1962). Stach (1944) does not describe this feature for A. loveni sudaustraliense but they are described by Day (1955) for A. l. loveni. As with the casts, the form of the head-shaft depression is determined by a number of habitat characteristics. They range from barely discernable saucer-shaped depressions in the sand to 20 cm deep funnels or irregular hollows, and appear (except in extremes) to bear little correlation with the size of the worm. In Zostera beds head shafts can often not be seen, but are located by feeling for softer substrate.

The main part of the burrow of A. loveni is thickly lined with mucus. This impregnates the substrate around the burrow so that it can be

exposed intact by careful washing (in small enough worms) and this method was used to obtain unharmed, small worms for experimental work. Mucus-lined burrows are also described for other Arenicolidae, for example A. marina (Healy et al. 1959, Seymour 1971).

Behaviour

Evidence suggests that once a burrow has been established it may be functional for extended periods, and Seymour (1971) states that 'it would appear that burrowing takes place comparatively rarely in nature'. Captive specimens of A. loveni in gauze-lined plastic baskets showed infrequent changes in the position of surface signs. Due to the mucus lining of the burrow, a history of change in position between two-monthly examinations was left, and this rarely showed more than two or three slight modifications of the burrow, and this usually by slight changes in the position of the head-end. This is at variance with Stach's (1944) description of feeding behaviour of A. l. sudaustraliense which he records as burrowing after a buried layer of Prosidonia australis, 'the attrition and decay of which probably provides the bulk of the organic debris upon which the lugworm feeds'. A. loveni, although it was found in a large variety of substrates, inhabited some which were extremely poor in organic matter (for example Muizenberg beach, Heuningnes Estuary). Even in substrates where there was a black layer of decaying organic matter, there was no evidnece that extensive use was made of this and the head-shaft of 'clean sand' could be distinguished cutting through the black layer. Occasional discolouration of the faecal cast probably resulted from incidental inclusion rather than selective feeding on the deposit.

If A. loveni is more or less sedentary in substrates sometimes very poor in organic matter, the problem arises in understanding how the animal's nutritional requirements are met. This problem has received much attention in A. marina. Wells (1945) originally stated that a drag action was used by the worm to draw organic matter from the surface down the head-shaft, Kruger (1959 in Jacobsen 1967) proposed that the head-shaft acted as a filter for suspended organic material when

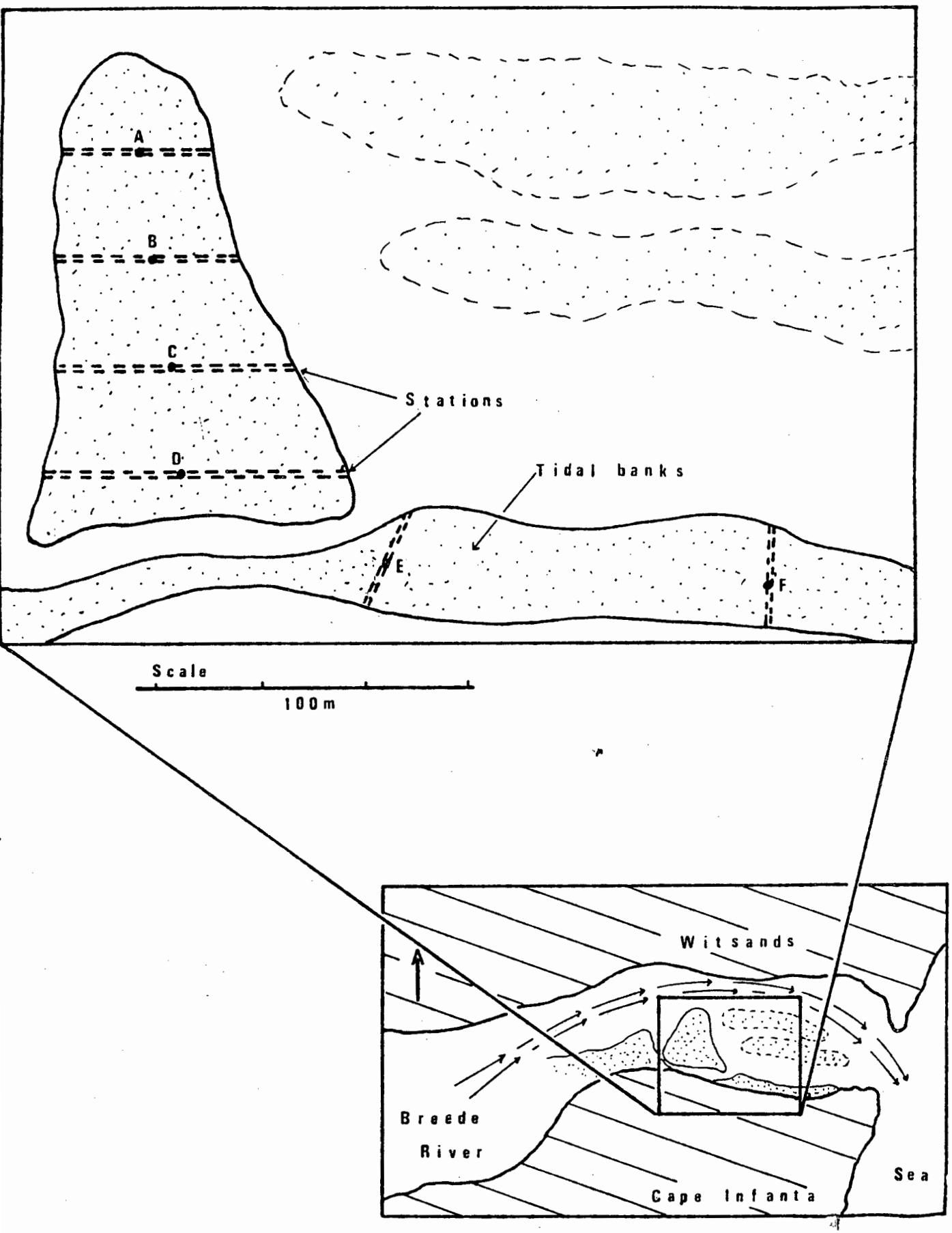
ventilation currents were drawn through the burrow, and that A. marina was actually a suspension-feeder. Jacobsen (1967) queried this because in many localities the period of submergence of the burrow, and volume of ventilation currents were too low to allow sufficient accumulation of material by filtration. Newell (1970) quotes as support to A. marina being a deposit-feeder the work of Longbottom which showed a correlation between the worm biomass and levels of organic carbon and nitrogen in deposits. A completely-new approach is that of Hylleberg (1975) who, working on the genus Abarenicola, proposed that lugworms actually 'garden'. He found that the organic matter in the faeces was consistently more concentrated than in the substrate upon which the worm was supposedly feeding. He also found that most of the detritus upon which the worm was supposedly feeding passed through the gut undigested, but that detritus and 'pocket sand' at the base of the head shaft was an ideal culture medium for micro-organisms, particularly due to irrigation of this area by the worm. These cultures were then ingested, and 'all ciliates and flagellates, most nematodes, motile bacteria and some motile diatoms' were digested from them. The rest passed through the gut alive.

Combining these several theories, a feeding mechanism for A. loveni can be proposed. Even in substrates with little buried organic deposit, local enrichment in the head shaft could be caused by filtration of organic matter from ventilating currents, the subsidence of organically richer surface sand and/or the incidental or active trapping of macro-organic particles in the funnel when the tide recedes. (Half buried Zostera or algal debris is commonly seen in the head shaft funnel). This organic material would provide the culture medium for micro-organisms, ingestion of which would supply the worm's nutritional needs. Newell (1970) says of A. marina that it is possible that the worm 'may use different mechanisms of food collection to utilise such food as may be locally available'. This is probably true too for A. loveni and explains how specimens are able to survive in Zostera beds or muddy substrates where subsidence of the surface is impeded, but organic material is plentiful. Differences

in feeding behaviour would also explain the variety of surface signs seen in different localities.

Whatever the organic level of the substrate, deoxygenation is a potential environmental hazard which has to be faced by burrowing organisms. Of the many factors involved, Bradfield (1964 in Newell 1970) concluded that drainage was of major importance in 'controlling oxygen levels of interstitial water'. Poorly drained substrates are commonly colonised by Arenicola and several behavioural adaptations must be employed in coping with such conditions. Circulation of well oxygenated water during periods of submergence supply the worm's oxygen requirements. (The mucus lining of the burrow might be of importance here in maintaining a gradient between oxygen levels in the burrow and interstitial water). During periods of tidal exposure van Dam (1938 in Dales 1958), Wells (1945 and 1949 a) and others have demonstrated aerial respiration by the worm trapping air bubbles in the burrow at the water/air interface, and by peristaltic contractions forcing the air over the gills. When respiration is not possible, for example when the burrow is covered in deoxygenated water the worm survives mainly by quiescence (Dales 1958), interrupted at intervals by testing movements (Wells 1949, Newell 1970). This has the advantage that potentially harmful water is not actively circulated through the burrow, and under conditions of fresh-water flooding must have considerable survival value. This would explain the virtual absence of surface signs of A. loveni during winter floods at Breede River, which was recorded in the following section.

FIGURE 1 STUDY AREA in Breede River Estuary



CHAPTER 2: DENSITY AND MIGRATION

THE STUDY AREA

For the purposes of this study, a large bloodworm population, not excessively modified by human interference was sought. The completely protected population at Heuningnes River Estuary (in a Forestry Reserve) where work by this Department had commenced, unfortunately became extinct following years of drought and closure of the mouth. The Breede River Estuary was therefore chosen. This had an extensive population of Arenicola loveni, which because of its distance from major cities is only exploited to a limited degree, and this is restricted to long weekends and holiday seasons.

The Breede River is one of the three major drainage systems of the South Western Cape, and has its catchment in the Winter Rainfall Area. Winter flooding and reduced summer flow are therefore characteristic. It has a permanently open estuary and is almost 1,5 km wide, so that bait areas about a kilometre from the sea are subject to a marine regime for most of the year. Flooding is of limited duration and effect.

As shown in the map (Figure 1), the main course sinuates from close inshore along the southern bank at the mouth, to close inshore along the northern bank past the old pier, Botel and Oyster Beds Hotel. Extensive shallows are hereby formed off the southern bank and include a transverse island and sandflats of the seaward side, which are exposed at low tides.

As in most estuaries, the size and shape of the sand-banks and channels are dynamic. For example, during the course of this study, the channel between the island and the southern bank decreased from more than a meter deep to a matter of centimeters. There is also the common seasonal build-up and degradation of the sediment on the banks according to the prevailing currents and winds. There is evidence that a large part of the sand deposit on the island and southern bank is of relatively recent origin and occurs over extinct Upogebia beds.

The firm dark layer of clay underlies most of the Arenicola beds at varying depths and effects their distribution.

Upstream of the island, the substrate becomes muddy and extensive Zostera capensis beds are found. Upogebia africana are locally abundant, but the most seaward populations are insecure due to sand deposition. On the southern bank seaward of the island, isolated patches of Zostera still occur and a few remnant Upogebia survive. Sand prawn (Callianassa kraussi) do not occur in the study area, nor have they been previously recorded from this estuary (Day, personal communication). They have, however been recently reported from the most seaward reaches of the Estuary by the public.

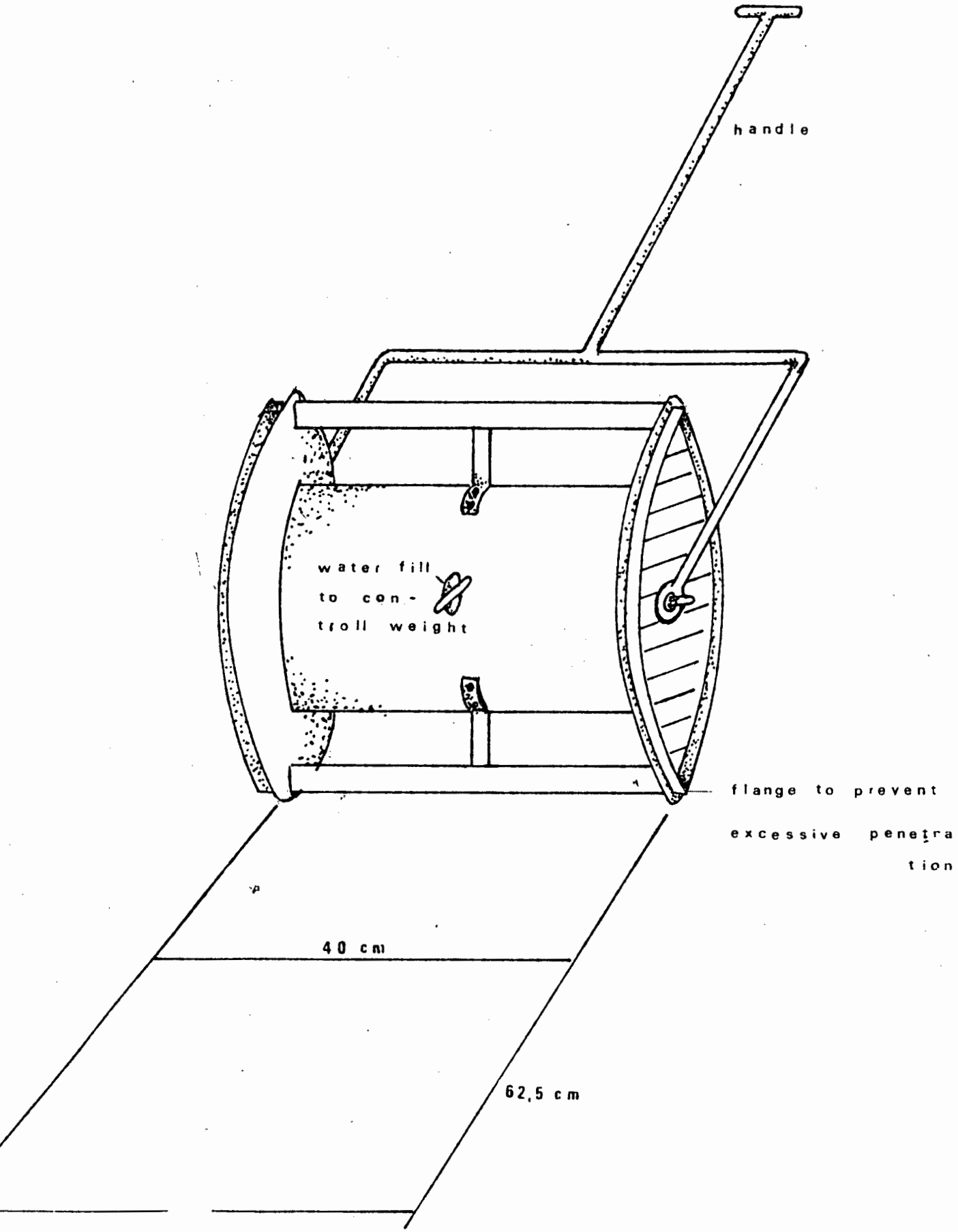
The Island and seaward sand flats are extensively colonised by blood-worm. Areas most consistently exposed at low tides were selected making regular survey work and sampling possible. These are also the areas where exploitation was most common.

Density and Migration

One of the most important aspects of this study was to devise for management purposes, a practical and as accurate as possible a means of assessing the density and extent of a population. The size of A. l. loveni and the depth to which it burrows makes standard sampling techniques impractical. The depth of the burrow of A. l. loveni is exceptional. Adult A. l. sudaustraliense are described by Stach (1944 a) as inhabiting burrows 30 cm deep, while in all localities examined, only the smallest specimens of A. l. loveni (up to an average mass of around 5 g) were found at his depth, the burrows of large mature specimens being up to a meter deep.

Previously density counts of the Arenicolidae have been made of actual specimens removed from a given sample area (Okada 1941, Newell 1947, Chapman et al. 1949, Holme 1949, Duncan 1960). These authors were working at depths of 20 or at most 30 cm, with species which reached densities as high as 50 or more adults per m^2, whereas at Breede River

FIGURE 2 QUADRAT MARKER



the average adult density in the richest areas is less than 5 worms/m^2.

At Breede River, surface signs are readily distinguished under normal conditions and appeared to offer a means of assessing density. To enable the largest possible number of quadrats to be counted in the brief period of exposure at low tides, a marker was designed. This consisted of a roller with sharp rims on broad flanges to regulate penetration, (Figure 2). Quadrats 64,5 cm by 40 cm (i.e. 0,25 m^2) are marked; a rectangular area rather than a square was chosen to facilitate scanning.

METHODS

Six sample stations, A to F were marked permanently by driving 1,25 m hickory rake handles with extensible barbs a meter into the sand. (The barbed stakes were impossible to extract manually and remained in place for the duration of sampling). Stations A, B, C and D lay in line and 100 meters apart on the Island, and were chosen due to a previously established apparent gradient in densities from A to D. Stations E and F were on the southern bank, E being just across the narrow channel which separates the Island from the southern bank, and F being some 600 meters further along the bank where surface signs appeared smaller and more numerous. (Stations are shown in Figure 1).

To establish whether surface signs gave a usable index of the population density, trial counts were done in an area near Station D, which was chosen for its apparent uniformity. 10 Parallel transects, 100 quadrats long and a meter apart were marked. Results are given below. (Only casts are included as the proportion of funnels to casts was as low as 0,09 : 1 in some transects).

Density estimates and standard deviations between transects on the following two days in the same area were 1,83 ($\pm$ 0,21) and 1, 68 ($\pm$ 0,20), the latter count being made under drizzly and windy conditions.

Table 1. Density estimates from parallel transects near Station D.

Transect No. (100 quadrats, i.e. 42,5 m)	Counts (No. of casts)	
1	48	
2	42	
3	50	
4	48	
5	48	Mean Count 47,06
6	49	Standard deviation
7	51	between counts 2,16
8	45	or Density 1,88 casts/m^2
9	44	($\pm$ 0,08) (one standard
10	45	deviation).

These trial density counts at Station D showed remarkably low standard deviation between parallel transects on a given day, and therefore that individual transects were a meaningful estimate of density. There was a greater variation between days. How much of the variation between transects on a given day was due to actual density discontinuity and how much was due to failings in the technique is not apparent.

This experimental work indicated that cast counts would provide at least a repeatable index of actual densities, and as standard procedure, two parallel transects a meter apart were marked through stations A to F; from water's edge to water's edge across the Island, and from beach to water's edge on the bank. Counts were made on three consecutive days if possible, as close as possible to the full moon spring tides, and repeated at two monthly intervals from January 1975 to January 1976.

With experience it was found possible to distinguish between juvenile worms up to about 1 year old and adults, by the size and nature of the cast. These were recorded separately. Counting commenced at the latter half of the tidal exposure to allow full time for the surface signs to develop, and only casts were used in computing results.

In computing results, counts were tabulated as numbers of casts per 20 quadrats (i.e. 5 m^2), counting in both directions from the Station marker. Where fair counts on a transect could not be made due to incomplete drainage, counts were supplemented by data from previous or following days. The density figure recorded for each station for the month was therefore the mean of a maximum of 6 determinations (paired transects on three consecutive days) and recorded separately for adult and juvenile worms (as distinguished by their casts).

As mentioned previously, density figures obtained from surface signs are not absolute values, but rather an index of density. To interpret these estimates and determine whether a single worm could be responsible for more than a single faecal pile during a tidal exposure, counts were made of surface signs of captive worms. Some of these data are included in the following table:

Table 2. Cast counts of captive worms, March 1975 to December 1975.

Date	Casts	Worms recovered	Date	Casts	Worms recovered
25/3/75	18		20/8/75	7	
27/3/75	17		21/8/75	12	14
29/3/75	18		19/8/75	7	
28/4/75	16		21/9/75	6	
29/4/75	15	15	21/10/75	7	
22/5/75	15		22/10/75	8	9
24/5/75	14		19/11/75	11	
26/5/75	16		20/11/75	12	
16/6/75	13		17/12/75	14	16
22/6/75	8	13			

This shows in many cases the close correlation between the faecal cast counts and the actual number of worms as determined at two monthly intervals. The most significant point however is that even where correlation was not good, the number of casts never exceeded the number of worms present. This can be expected from the semi-permanence of the burrow and the fact that signs are erased by the

FIGURE 3 **KNYSNA Density estimates**

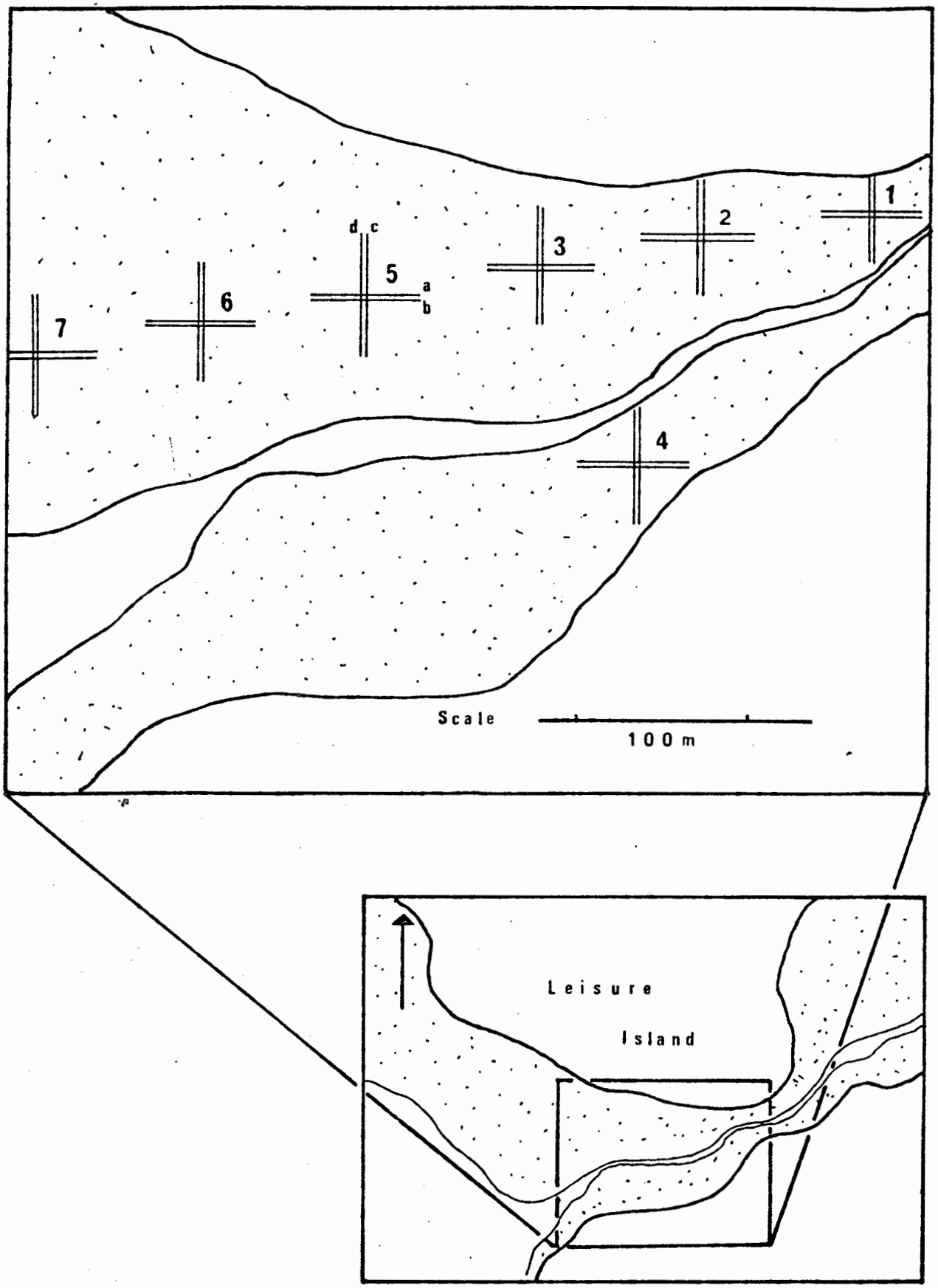
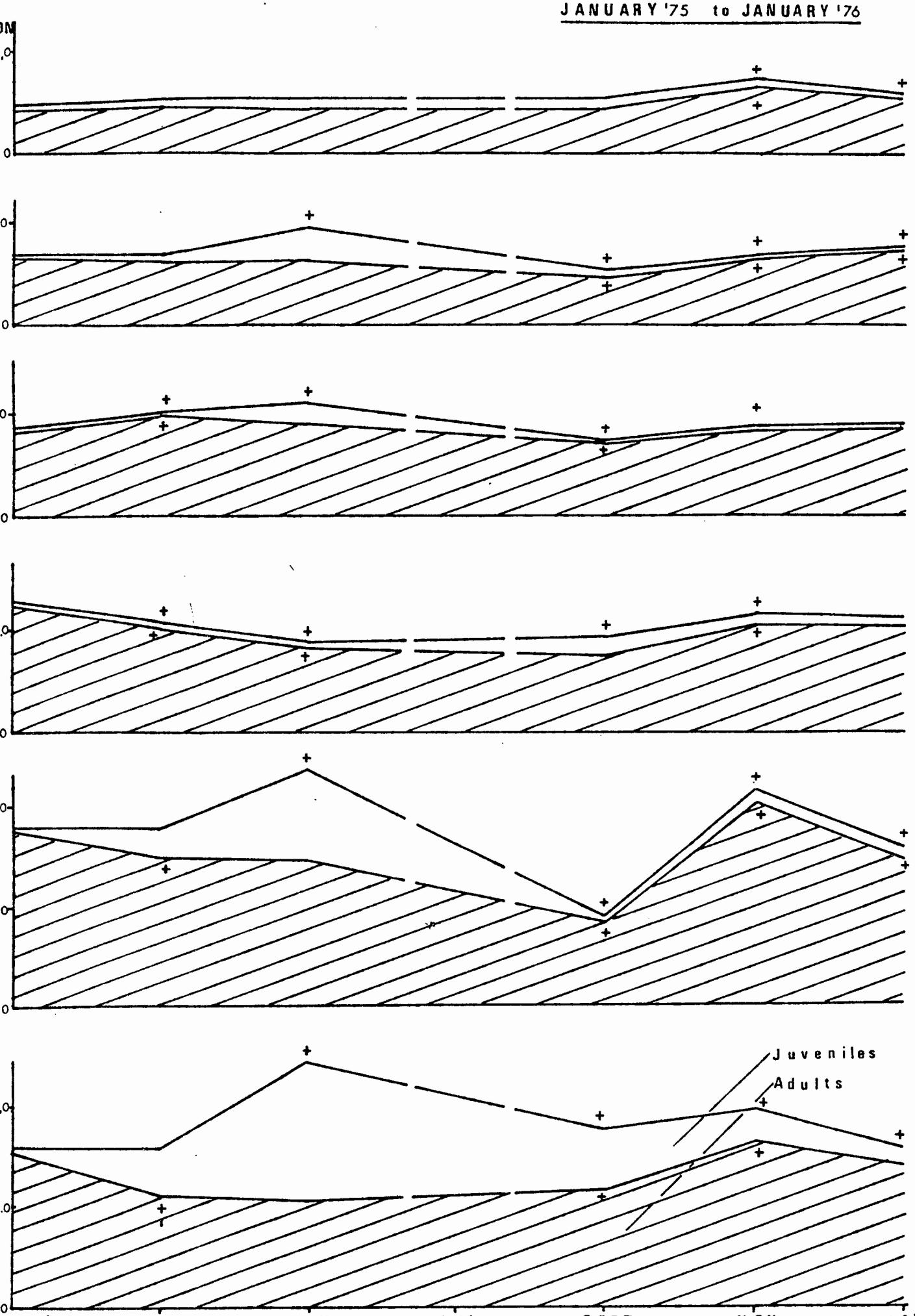


FIGURE 4 DENSITY FLUCTUATIONS ; STATIONS A to F

JANUARY '75 to JANUARY '76



changing tides. From this and other evidence it can be concluded that a count of the number of casts cannot give an over-estimate of the density.

Although not an absolute figure, cast counts offer a very valuable means of assessing Arenicola populations and are of particular use in monitoring change. This combined with the rapid transect laying using the Marker makes it possible to estimate the density and distribution of an Arenicola population very rapidly. As a trial, this was done on the seaward side of Leisure Island at Knysna using two pairs of bisecting transects a to d, each 40 quadrats long and marked as shown in Figure 3. The results are given in the following table.

Table 3. Density determinations at Leisure Island, Knysna. (Juvenile worms shown in brackets).

	Transect				Mean Density/m²	
Site	a	b	c	d	Adults	Juveniles
1	(2)	(1)	(2)	-	-	0,1
2	8	9(4)	12	11	1,0	0,1
3	12(3)	20(1)	15(2)	13(1)	1,5	0,2
4	20(1)	19	24(4)	17(1)	2,0	0,15
5	27(1)	28(2)	17(3)	27(1)	2,5	0,1
6	11	17	14	18	1,5	-
7	20	24	19	17	2,0	-

This shows again the close correlation between most of the transects, especially those parallel, and also the rapid and practical nature of the survey technique. (The whole process took two and a half hours).

RESULTS AND DISCUSSION

The results of the two-monthly density estimates at Stations A to F are represented by Figure 4. No counts could be made in July, when the river was in flood and adults on the Island were not actively feeding or ventilating their burrows, judging from the complete absence of surface signs.

Before being able to discuss the significance of fluctuations in the

density estimates at the various sample stations over the twelve months, it must be decided what significance can be attached to fluctuations in density, determined by surface signs, and how far they represent real fluctuations in density of the population. Newell (1947) regarded the 'tedious method' of manually digging out A. marina for density determinations as essential, because counting of surface casts was a most unreliable index of the number of worms, varying as it did, amongst others with the state of the tide. Holme (1949) found however that counts of the casts of A. marina per square meter 'agreed well' with actual densities found on digging, but under his conditions casts persisted for several days, and corrections had to be made for worms which had produced more than one cast. Chapman and Newell (1949) working on non-uniform distribution found that although the number of castings was not necessarily the same as the number of worms, it was 'fair to use the population of castings as an indication of the population of worms'. Due to the depth of the burrow, the problem of working in wet intertidal sand and the sparsity of A. l. loveni no practical alternative could be found to using surface signs and the accuracy of the method has to be gauged by comparing repeat transects in a given month.

During the routine two-monthly counts the standard error of the mean of the six estimates of density (three pairs of transects) for each station ranged from 4,3% to 8%. To what extent the standard error of the mean density estimate for a particular station reflects actual differences in repeatability of counts at different stations is uncertain. It is possible that the nature of the substrate surface, such as its texture and rippling effects the repeatability of counts. (It is more difficult to distinguish casts in coarse sand or strongly rippled substrate). There also appears to be a density factor, in that the standard error of the mean density tends to be greater at higher densities. Based on such sparse data the numerical value of the 95% confidence limits of the density estimate for the Station are probably mainly theoretical, but they do provide some standard whereby two-monthly fluctuation can be evaluated. 95% confidence limits, as percentages of the respective mean density for a station in a given month, are as follows:

Table 4. 95% Confidence limits of the two-monthly density estimate for Stations A to F.

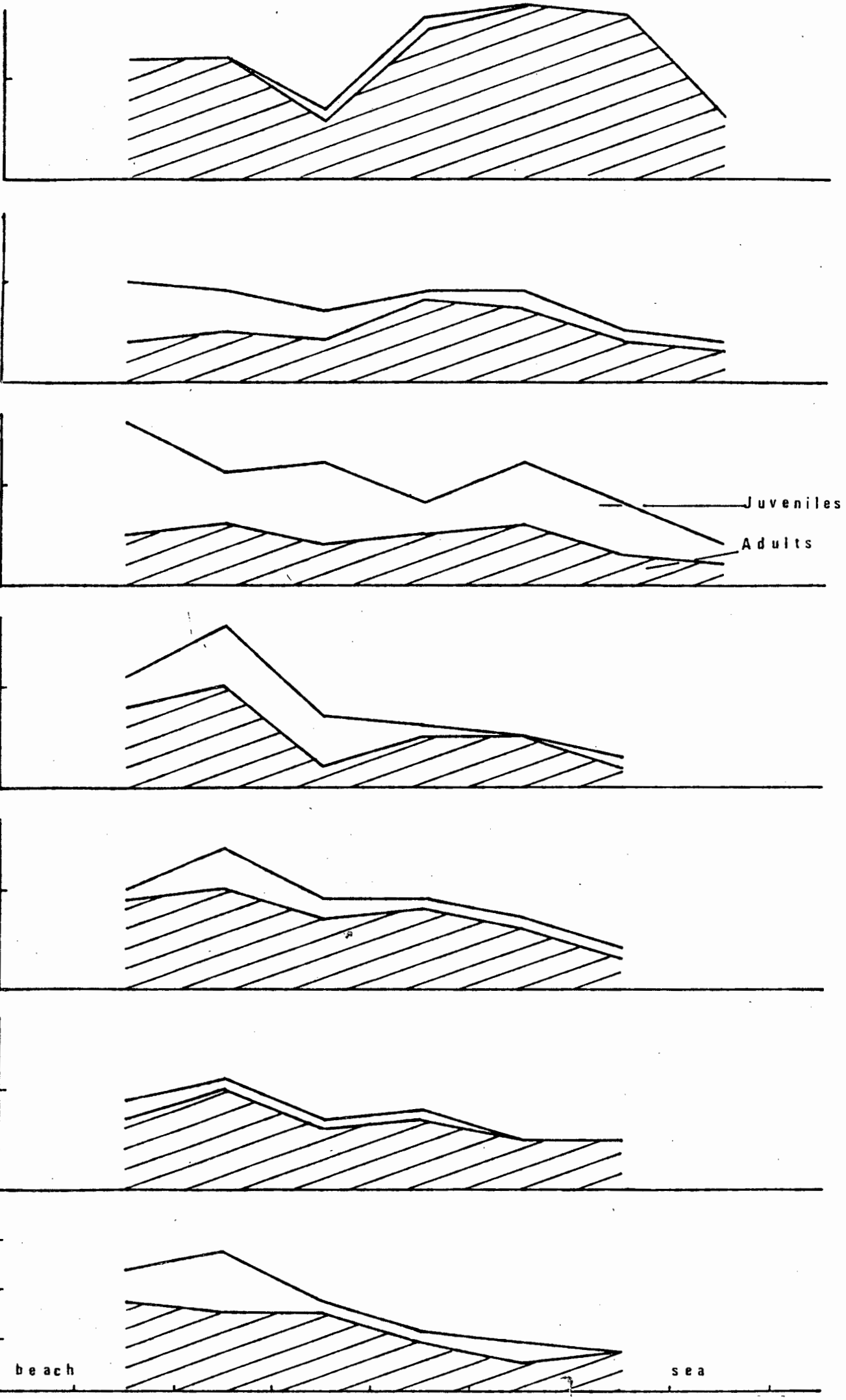
Station	95% Confidence limits
A	Mean Density for Station ± 8,4%
B	" " " " ± 12,1%
C	" " " " ± 8,6%
D	" " " " ± 14,3%
E	" " " " ± 12,0%
F	" " " " ± 15,7%.

Judged by the above criterion, consecutive density estimates which differ statistically significantly (at the 95% confidence level) can be identified. These are indicated in Figure 4. As can be seen, most of the density estimates, especially those which include a strong juvenile component, and those in the latter part of the year are statistically significant at this high level. Major trends observed during the year therefore appear real, although the actual numerical value of the index might have a fair range.

The most important fact to emerge from the density data in figure 4 is that the southern bank, as represented by Stations E and F acts as the nursery area of the population. This is most apparent at Station F, where casts of juveniles first appeared in large numbers in March, and reached a maximum in May. The sudden disappearance of the juvenile sector (and a large part of the adult population) at Station E in September was due to flood damage when a section of the bank was destroyed. This however was followed by rapid recolonisation by adult worms when conditions returned to normal.

Nursery areas are known from the literature on the Arenicolidae. Newell (1947 and 1949) found 'enormous numbers of minute castings' of A. marina along the shoreward edge of the Fucus zone, amongst pebbles and sand at H.W.N.H.T. from where they migrated when large enough. Holme (1949) also found large numbers of juveniles of this species

FIGURE 5. DENSITY PROFILES STATION F ; January '75 to March '76



(up to 100 per m^2) amongst Zostera below the pebble zone and suggested that larvae developed there, 'subsequently migrating to the regions where adults occur'. Similar data is given by Newell (1947) and Eve and Southway (1958).

From September to January emigration of small worms of the first-year class from the 'nursery' appears to have taken place, so that by January 1976 more or less original densities had been restored. From spawning data, this would have coincided with the deposition and development of the following generation. This seasonal cycle is illustrated more clearly by detailed transect results from Station F. (Figure 5) (Data for Station E cannot be used in the same way due to the anomaly caused by flood damage). The figure shows that the juvenile component first becomes apparent in density counts in March 1975 and is spread over the whole tidal flat, although in greatest numbers towards the beach. The greatest loss is between May and September although there is a steady decline thereafter, until the next generation appears in March 1976. Nursery areas have been identified in most other areas populated by A. loveni and visited during this study. They are normally in the most sheltered part of the habitat and comparatively high up in the tidal reach (probably also round H.W.M.N.T.). (Data for Leisure Island - table 3, figure 3, shows juvenile worms in the curve of the bay). These areas are normally more silty, and it is theorised that the same tidal current-flow patterns which are responsible for creating such areas, would also carry and deposit fertilised ova there from more exposed Arenicola beds. This is discussed more fully in later sections.

Figure 4 shows that a certain amount of juvenile development did occur on the Island. The largest part of this component did, however, not become established and in fact worms of the 1st year class are rare on the island. This could be due to the high degree of exposure of the island. Juvenile worms are at first only buried in the top 5 or 10 cm of substrate, and the surface must be very unstable judging by the gross rippling of the surface due to strong tidal surges and scouring. Another reason could be that juvenile worms are more

vulnerable to adverse conditions on the island during fresh-water flooding than in more protected areas. The role of physical substrate parameters is discussed in the relevant section.

Another point which emerges from Figure 4 is that Arenicola populations at Stations A to D on the island are relatively stable, ranging from sparse at Station A (average 0,6 per m^2) to more dense at Station D (average 1,1 per m^2). Adult populations are at their lowest just after winter, and reach their greatest density in late spring and early summer. There is no evidence of the 'rather sudden drop in numbers after spawning' recorded by Newell (1947) for A. marina. At this time he found large numbers of worms 'dead, spent and washed up on the beaches' after spawning.

The Arenicola population at Breede River also shows no response to the peak exploitation period over December indicating that at present bait-taking is having no significant effect on the Arenicola stock.

A further important conclusion from density data (figure 4) is that density is maintained in the island population by the recruitment during spring/early summer of adult worms, and not by the development of the following generation in loco, as discussed previously. (Most of the juvenile worms found in May are absent by the end of the year). Recruitment will be discussed more full in the following chapter.

MIGRATION

Transects have shown that an area on the southern bank of the Breede River Estuary acts as a nursery for successive generations of Arenicola. What becomes of the first year class when it disappears off the bank? An unknown factor in the consideration of migration, and one which could not be quantified in this study, is the role of the sublittoral Arenicola populations of the extensive shallow bay, as for practical reasons the only areas which were routinely sampled were marginal, tidally exposed edges of this large expanse. There is much evidence for A. l. loveni and other of the Arenicolidae that substrate subject to tidal exposure is not obligatory even if it

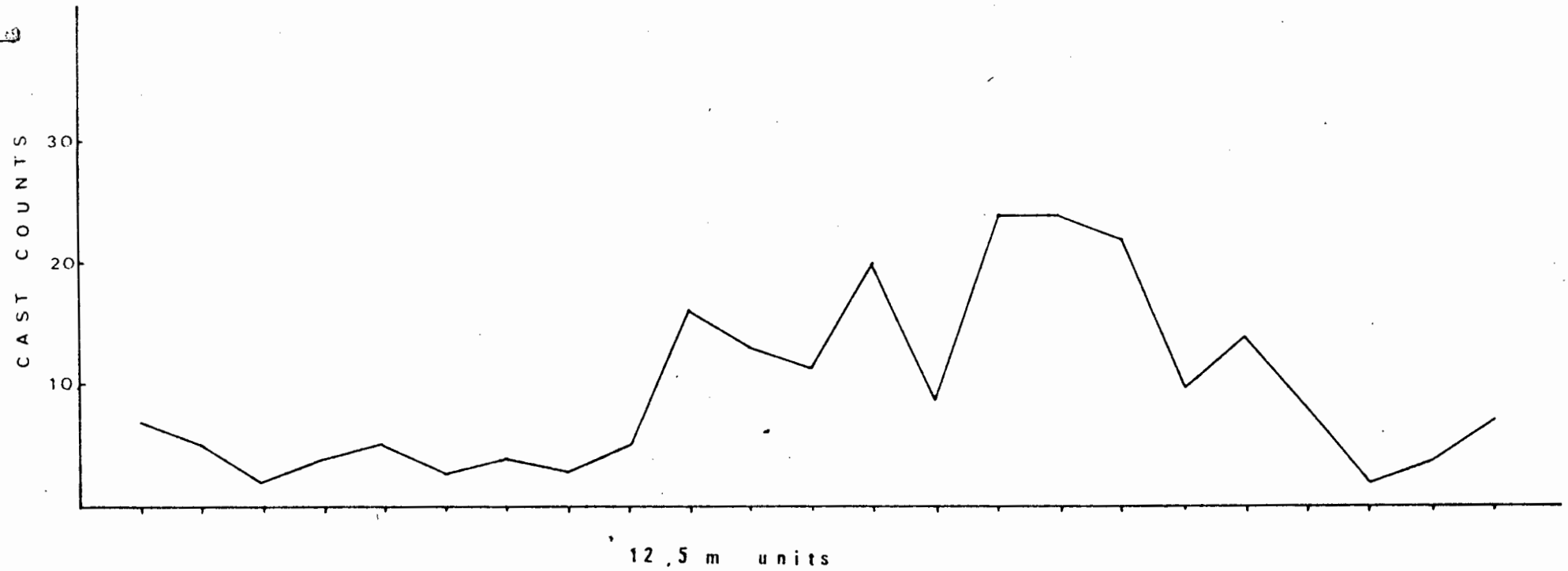


FIGURE 6 Transect of Mid-bay sand-bar

appears optimal (as mentioned in the general account). For example bloodworm at Muizenberg beach are commonly collected by wading waist deep into the surf and pumping blind. Populations must be extensive to allow sufficient bait to be taken.

At Breede River there is also evidence of large sublittoral populations. An exceptionally low spring tide allowed a density transect on an infrequently exposed sand bar in the middle of the Estuary. Results are shown in Figure 6. The highest adult densities were found here, and it is interesting that casts indicated that the worms were small, possibly in their 2nd or 3rd year (if they had grown normally).

There is no evidence that juvenile worms migrate along the bank towards the island in large numbers, or that such a migration arrives there. It is more likely that worms migrate off the bank into the shallow bay and from there maintain the relatively stable densities on the island. Whether this is by gradually changing the position of the burrow or by leaving the substrate and moving by water, could not be determined.

There has been much speculation on how the Arenicolidae migrate. There are many reports of A. marina swimming. (Newell 1947, Duncan 1959, Seymour 1971). Seymour (1972) describes the actual mechanism, which occurred spontaneously in tanks without sand. He concludes, however that extensive migration by swimming is unlikely due to its ineffectual nature and the slow speed (4 times the body length per minute).

No swimming movements have been recorded for A. loveni, although small worms in aquaria are capable of some progression by seemingly erratic jerking. These movements are extremely clumsy and unlikely to assist materially in migration. A more effective agent in dispersion would be the strong tidal currents to which the banks are subject. Possible evidence of this comes from the Heuningnes Estuary in which Arenicola had become extinct following prolonged closure.

The Estuary reopened in July 1976, and by January 1977 young worms ranging between 0,15 g and 3 g (estimated a year old) were found in the first sand bars alongside the main channel within the mouth.

Burrowing migration is known for other polychaetes. For example Klawe and Dickie (1957) suggest migration by burrowing for Glycera dibranchiata at a rate of almost a meter a day. (These authors also concluded that a large part of the stock was sublittoral).

In summary, the following main conclusions can be drawn from density fluctuations and migration:

(1) An area on the southern bank acts as a nursery for successive generations of bloodworm.

(2) The adult populations on the island are relatively stable and maintained by adult immigration.

(3) The extensive shallow bay plays an important role in the migration cycle.

CHAPTER 3: POPULATION STRUCTURE AND GROWTH

Population structures and growth rates of A. loveni, and also that those of most other of the family have not previously been studied. The limited data available are of limited relevance due to the exceptional sizes reached by this species, and in any case suggest only the first or at most second year's growth of the species concerned.

In managing the bloodworm stocks, the growth rate is of particular importance because in South Africa anglers give preference to the largest specimens available due to the limit of 5 worms per angler per day. This differs from usage elsewhere. D'Asaro (1976) for example, regards A. cristata of 12 cm as of good marketable size. He quotes Smidt (1951) that at least a year is required for A. marina to reach a marketable size of 6 cm. Worms of this size would meet with little favour in South Africa.

A basic problem with the Arenicolidae is how to express size of an animal whose considerable extensibility is not limited by skeletal material. A variety of parameters have been used. Okada (1941) used extended lengths for A. caroledna and describes maximum lengths of 30 cm. Newell (1947) and Wells (1962) used as their index of the size of worms, the length of the body excluding tail 'in moderate contraction' regarding this as a refinement due to the frequently damaged and shortened tail. Duncan (1960) admitted that this was a crude measure due to variable states of contraction, and refined this with volume measurement of the intact animal (with the inherent error caused by non-intact specimens). He rejected weight due to possible errors caused by sand in the gut.

The size measure used in this study is the formalinised mass. This was selected because of the unsatisfactory nature of many of the other units, and because of the exceptional caudal lengths of A. l. loveni, and the large potential error factor due to variable states of contraction even when anaesthetised. Worms were however first held in fresh sea water for several hours, and had mostly voided the

sand in their gut before being preserved. Large samples could thus be worked through more easily under laboratory conditions.

A basic problem in interpreting population dynamics results is deciding to what extent size is correlated with age in an animal subject to a large variation in food availability and substrate conditions. Under unfavourable conditions worms react by a loss in mass. A sample of 10 worms kept in the laboratory, lost an average of 43% of original mass in two months; and in three months the two survivors had lost a mean of 68%. There is also evidence of a wide range of growth rates under both natural and experimental conditions. It is within these limitations that size frequency data have to be evaluated.

METHODS

Sampling of juvenile and adult worms required different techniques. A manual, stainless steel suction pump, 75 cm long and with diameter of 4,5 cm, the implement used by anglers, was used to sample adult worms. Sampling was restricted to the vicinity of Station D to prevent possible disturbance in other areas. The pump was used on headshaft funnels selected randomly but with a success rate which varied with the season and phase of low tide, and was at times well below 10%. There was no size selectivity in sampling as the smallest depressions sometimes yielded the biggest worms. 100 Adult worms were sampled at monthly intervals from January 1975 to January 1976. In July and August only 9 and 32 worms respectively could be obtained due to freshwater flooding.

Juvenile worms were sampled on the southern bank in the vicinity of Station F. Worms were selected by marking a grid of quadrats and spading out intact all burrows contained therein. Specimens were obtained by gently washing out the intact, mucus-lined burrow and extricating the worm. This method was selective for worms between 0,01 and 3 g. A sample of 50 small worms a month was taken, including those months when a full adult sample could not be taken. (There were still sufficient surface signs to make this possible).

Worms were held in fresh seawater for 3 to 4 hours, to void sand, and then preserved in 10% neutral formalin in seawater. In the laboratory, worms were paper-towel dried and weighed intact. They were then degutted and reweighed, and the degutted branchial mass was also recorded by reweighing after excising the caudal section at its junction with the branchial section. These additional mass measurements were an attempt to refine the data. Correlation coefficients between various measurements are given in the following table:

Table 5. Correlation coefficients and regression formulae for various pairs of size parameters.

Parameters	Correlation coefficients	Regression formulae
Live volume (cc) and live mass (g)	$r = 0,98$	$y = 0,54 + 1,13\ x$
Live mass (g) and preserved intact mass (g)	$r = 0,98$	$y = -1,81 + 0,93\ x$
Preserved intact mass (g) and degutted branchial mass (g)	$r = 0,98$	$y = 0,49 + 0,63\ x$
Preserved intact mass (g) and degutted mass (g)	$r = 0,89$	$y = 0,16 + 0,43\ x$
Degutted mass (g) and ovendried degutted mass (g)	$r = 0,97$	$y = -0,12 + 0,22\ x$
Live mass (g) and anaesthetised length (cm)	* $r^2 = 0,80$	$y = x^{2,95}$
Live mass (g) and anaesthetised branchial length (cm)	* $r^2 = 0,91$	$y = x^{3,63}$

* Coefficient of determination

These correlation coefficients all show very close correlation between the respective pairs of parameters. Correlation between live mass and preserved mass for example was so good that there was no apparent loss in accuracy working with preserved specimens. So also did degutting and oven drying (for 48 hours at 60°C) not refine or improve the data.

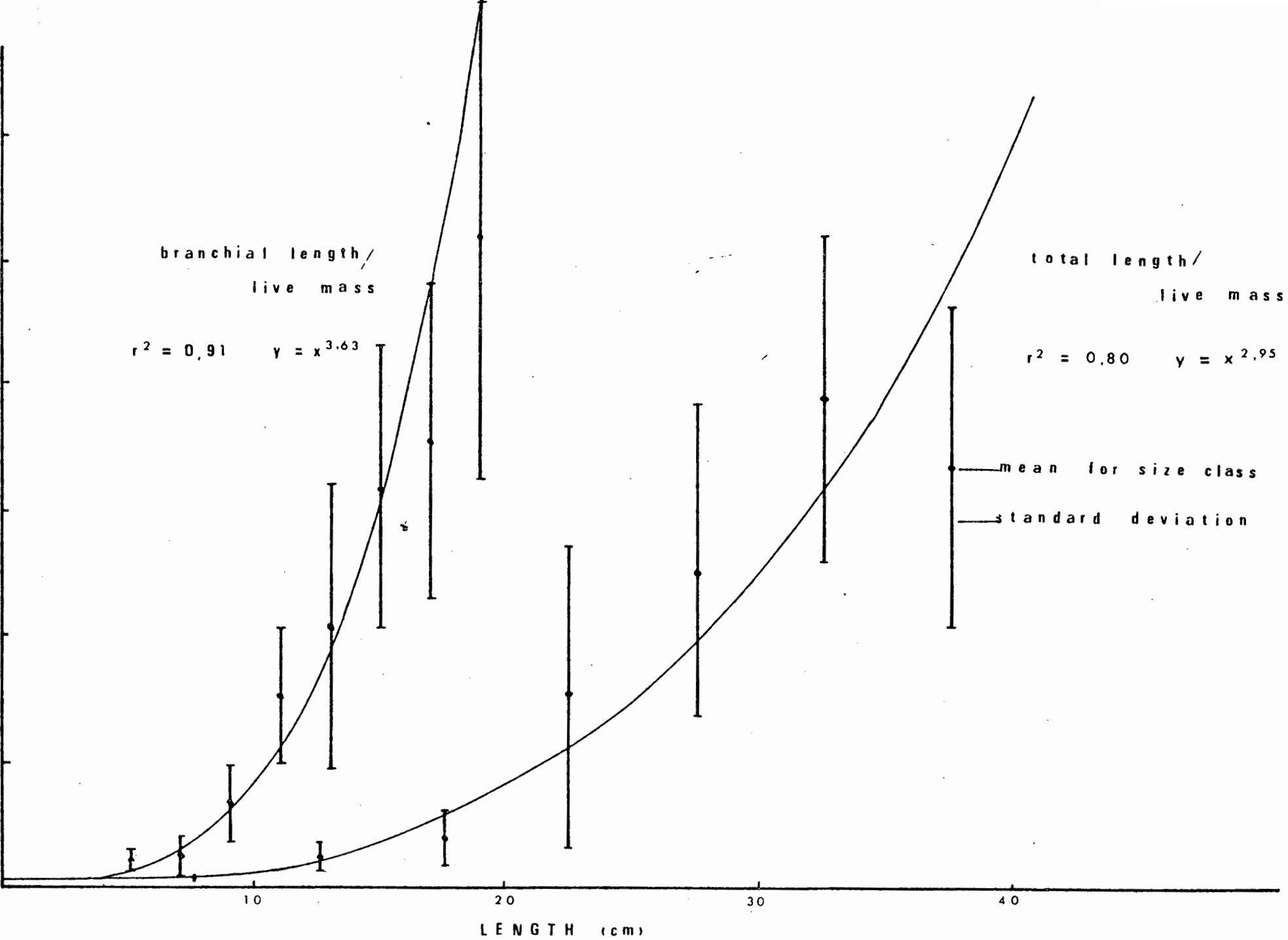


FIGURE 7 LENTH / MASS RELATIONSHIPS

Figure 8 Size Composition ; Adults, Station D (monthly)

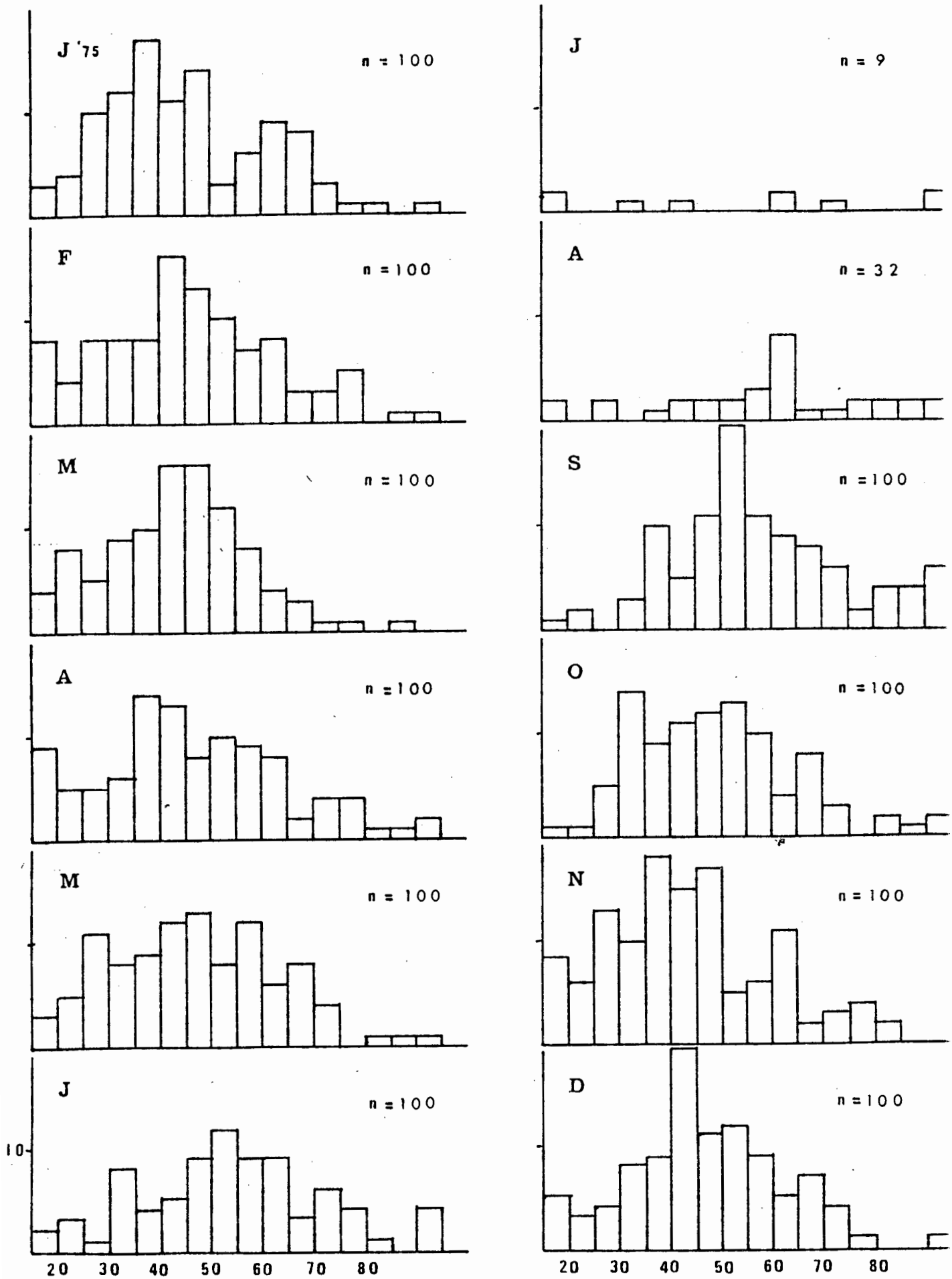
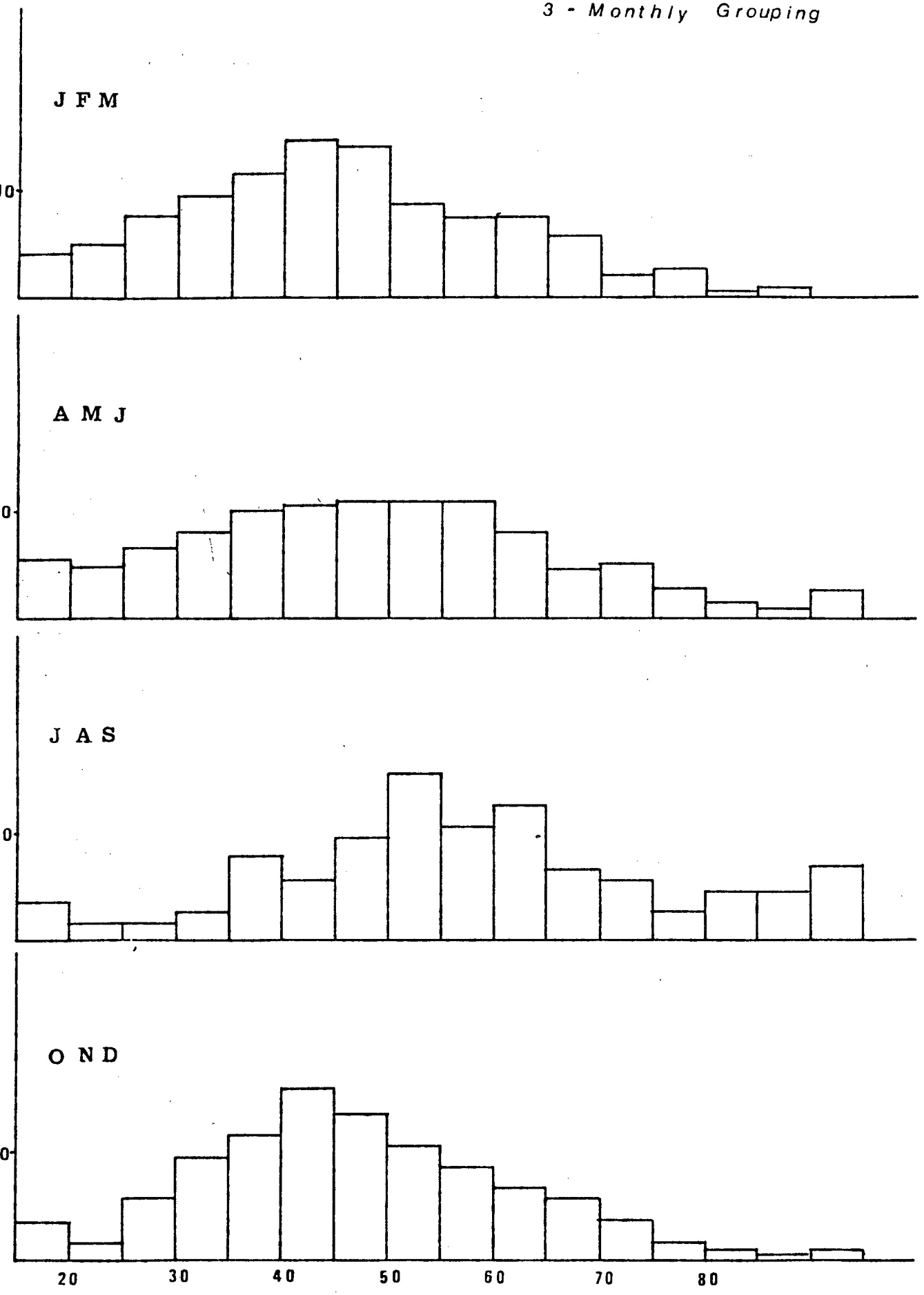


Figure 9 Size Composition, Adults, STATION D.

3 - Monthly Grouping



Correlation between intact and degutted mass was not as good as between intact and degutted branchial mass. This was because in a large proportion of the worms short portions of the extensive caudal section were lost (although obviously damaged worms had been discarded). In intact specimens this was negligible, but in degutted specimens, which had lost 57% of their mass in gut and coelomic fluid, these errors are magnified by a factor of about 2,3 and correlation is reduced.

The relationship between anaesthetised total length and live mass, and branchial length and live mass show the considerably greater correlation in the case of the latter. This indicates that although commonly used, length measurements which include the tail are poor indications of size. The computed curve, where length measurements are plotted against mass is given in Figure 7. This allows worms of a given mass to be visualised.

RESULTS AND DISCUSSION

Histograms of the monthly size composition of the adult worm sample (using intact preserved mass) are shown by Figure 8. From these it is not possible to recognise age classes or to follow their progression. The reason for this is the relatively small sample size (n = 100) which is spread over a large size range; but mainly because age-classes due to apparent divergent growth rates overlap.

To determine whether there are any trends in the size composition data, three-monthly data are pooled in Figure 9 (although hereby growth over this period is lost). The result of increasing the sample size is the creation of four superficially almost normal distributions, but with obviously differing means. This again shows the absence of strong recruitment classes or clearly defined age groups. To test for normality, a pre-requisite for the standard t-test for the significance of differences between populations, pooled data were analysed using the x^2 'Goodness of fit' test for normality (as described by Steel and Torrie 1960). It was found that the first two quarters did not differ signi-

ficantly from a random normal distribution at the 1% level; that the x^2 value for the third quarter was rather large (due to the small sample ?); and that the last quarter was not normally distributed but strongly skewed to the left as a result of a large sampling of worms in the 15 g to 30 g size class.

Because the data (at least for the first three quarters) are basically normal, the standard t-test for significance of differences between the means and standard deviations or pairs of data can be applied. Results are as follows:

Table 6. T-test for differences between size composition between quarters.

Quarter	Mean mass (g)	Standard deviation	t	p
Jan., Feb., Mar.	35,06	16,65	2,358	< 0,06
Apr., May, Jun.	38,40	18,11	4,986	< 0,001
Jul., Aug., Sept.	48,43	20,90	(5,868)	< 0,001
Oct., Nov., Dec.	38,06	15,04		

This indicates that quarterly populations do differ significantly. The progression of the mean for the first three quarters gives some idea of the mean growth of the adult component, and is around 13 g over the nine month period January to September. The reduced mean in the fourth quarter indicates that recruitment took place during this time. This is substantiated by the size frequency histograms, where a much higher sampling of worms of the 15 g to 35 g size classes at this time is obvious. (This is well correlated with trends apparent from density estimates over this period, where lowest densities occurred in September, and thereafter numbers steadily increased). That recruitment to the adult population on the island is not by development of a juvenile sector *in loco*, is also reaffirmed.

Mortality and recruitment

In order to quantify recruitment and mortality from size distribution

data, all specimens are normally samples from a known, measured area (Hughes 1970 for Scrobularia plana, Greenway 1969 for Amphidesma ventricosum, et c.). As mentioned previously this was not possible for A. loveni due to their burrow depth and dispersion, and the monthly sample consisted of the first 100 worms obtained from an unspecified area. The only density data available are the indices derived in the previous section. As described there, lowest values were obtained in September, and between September and January there was a mean increase for all stations of 39,1% in adult counts on the island. At Station D where population samples were taken, this increase was 36%.

According to size frequency data, there are 26,8% less worms in the above 40 g size classes between the third and fourth quarters. This is either associated with a sudden mortality of large worms, or a large immigration of smaller worms (decreasing the proportions of the larger worms). Density estimates indicate that the latter was the case.

According to Ricker's estimate of survival (Ricker 1975, p 30).

$$S = \frac{\geq N - No}{N}$$

where S = survival
and N = successive numbers of individuals in successive size classes, with reference to a specific number (No) of worms in a particular size class. This gives a mean survival rate, based on worms larger than 35 g of S = 76,6% (or mortality of 23,4%) according to data for the fourth quarter. (The same value for the First quarter is S = 76,8%).

Recruitment to maintain original densities according to size frequency data is therefore close to 23%. According to density estimates however, the density in January 1976 was 13,75% higher than in January 1975, so that the total recruitment over this period was something in the order of (23% + 14%), i.e. 37%. This is very close

to the 36% recruitment deduced entirely from differences in estimates of density.

Age composition

The size reached by large mature specimens of A. loveni indicates a considerable longevity. In the previous section it was apparent that the age structure of the island population could not be readily established from size distribution data. To assist in recognition of age classes, data in various groupings of months was subjected to polymodal frequency analysis using normal probability paper. (Harding 1949, Cassie 1950, 1954 and 1963). This method allows the recognition of the component parts (in this case year classes) of which the total population is composed, by establishing the modes of the components and correcting for overlap. Modes are determined visually from points of inflection on a plot of the cumulative percentage size classes on normal probability paper. The method is largely subjective depending on how well defined the subgroups are. Age groups in this case were so ill-defined that only with groupings of three monthly or more data could modes be fixed with any certainty. Even then no individual analysis was significant when Cassie's x^2 test for goodness of fit was applied. This same author however states: "Validity of the estimated parameters may often be better assessed by examining their consistency with one another, and their agreement with similar parameters obtained independently". (Cassie 1963).

Results of polymodal analysis of size frequency data are given in the Table 7.

Significance can be seen in the fact that four size classes were recognised in each of the series of completely independent attempts at establishing modal structure, but with varying modes as would be expected. This indicated that the adult population at Station D consisted mainly of worms of four age classes, with successive modes in the order of 13,8 g, 28,1 g, 42,4 g and 54,9 g.

Figure 10 Size Composition ; *Juveniles - Monthly*

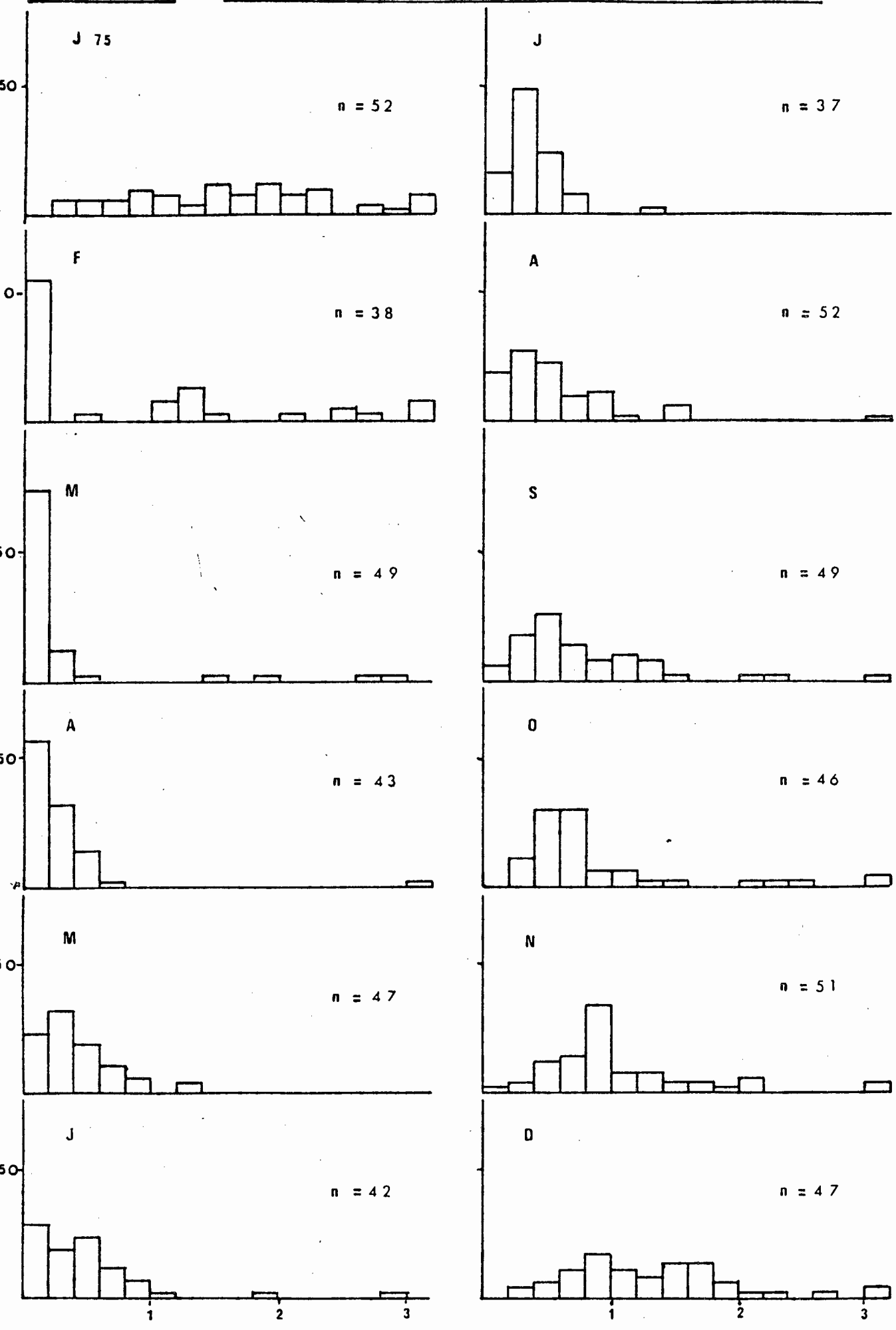


Table 7. Modes of age classes as determined by polymodal analysis.

Age class	3 Monthly JFM	AMJ	JAS	OND	JFMA	4 Monthly MJJA	SOND	6 Mnthly J-J	J-D	12 Mnthly J-D
x	12,5	15,0	7,5	12,8	17,0	17,5	15,8	14,0	15,4	10,8
							$\bar{X}$ = 13,8		s = 2,9	
x + 1	24,6	29,0	24,3	28,9	29,1	31,6	27,0	26,6	30,9	29,1
							$\bar{X}$ = 28,1		s = 2,3	
x + 2	38,1	43,3	43,9	40,7	42,5	45,0	42,0	40,8	45,3	42,2
							$\bar{X}$ = 42,4		s = 2,1	
x + 3	51,3	57,9	59,7	49,8	54,1	53,5	55,7	55,8	56,8	54,1
							$\bar{X}$ = 54,9		s = 2,8	

An indication of growth rate is given by these 10 sets of analysis. Means and standard deviations (in brackets) are:

x to x + 1 years old	14,14($\pm$2,3) g/year
x + 1 to x + 2 years old	13,38($\pm$1,6) g/year
x + 2 to x + 3 years old	12,87($\pm$2,3) g/year

(Compared with the general growth rate of the whole adult component, deduced in the previous section to be 13 g in nine months). Data indicate that growth is retarded with increasing age. This is similar to findings of Klawe and Dickie (1957) for Glycera dibranchiata whose growth decreased after the third year.

To determine the age (x) of the first year class well represented on the island, data for juvenile worms (from Station F) and growth of captive worms have to be considered. Figure 10 gives the monthly size composition histograms of the juvenile worms sample. The large range of juvenile size classes representing the previous season's spawning can be seen in January 1975. The first specimens of the following generation, small worms of around 0,01 g are first sampled in February and this component dominates until May. (This is well correlated by spawning data as will be shown). At first growth is fairly rapid until in the mid-winter months of July and August when

Figure 11 **Individual Growth of Captive Worms**

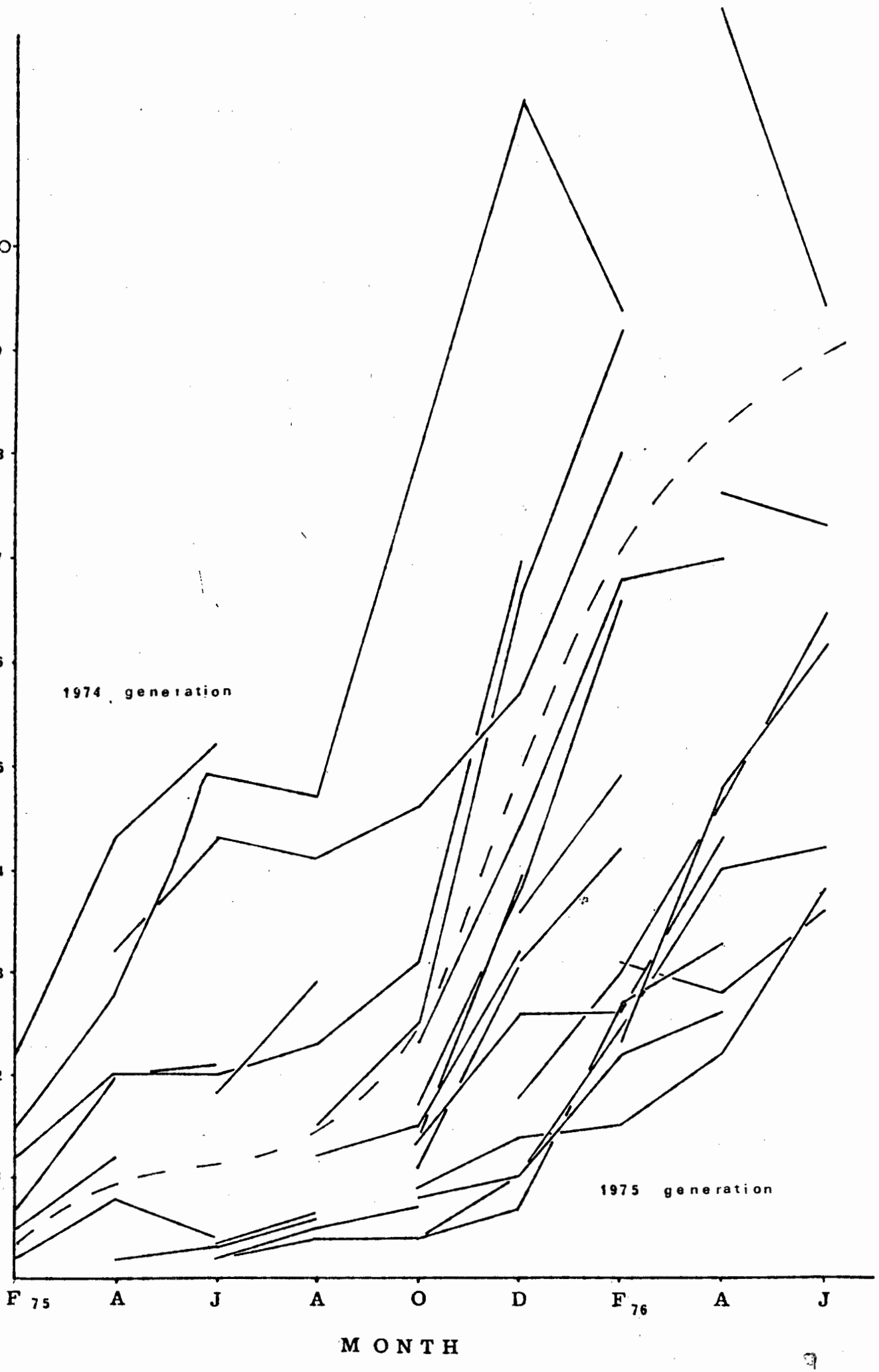
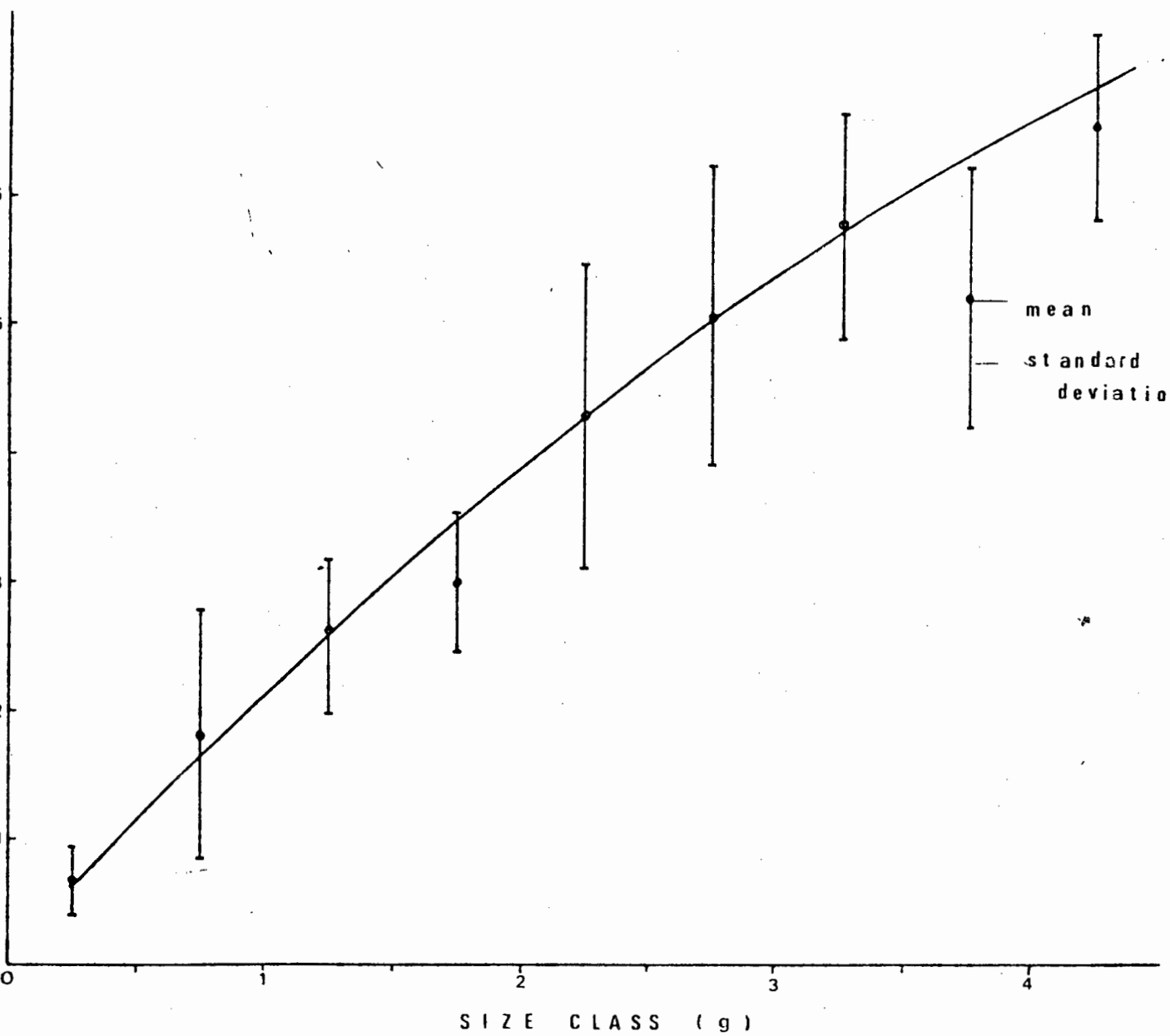


FIGURE 12 Growth of Captive Worms (2 month intervals)



there is even evidence of 'degrowth'. The same is suggested by Newell (1947) who first found A. marina larvae in summer, whereas adults appeared to have spawned in autumn. He suggests that larvae 'stagnated' through winter until growth was resumed in spring.

Surface signs at Breede River indicated on emigration of juvenile worms from the nursery area in the last quarter of the year (as discussed previously), so that by December only a remnant of the population was left, and ranged in size from 0,2 g to almost 3 g. This gives a maximum growth in the first year of about 3 g.

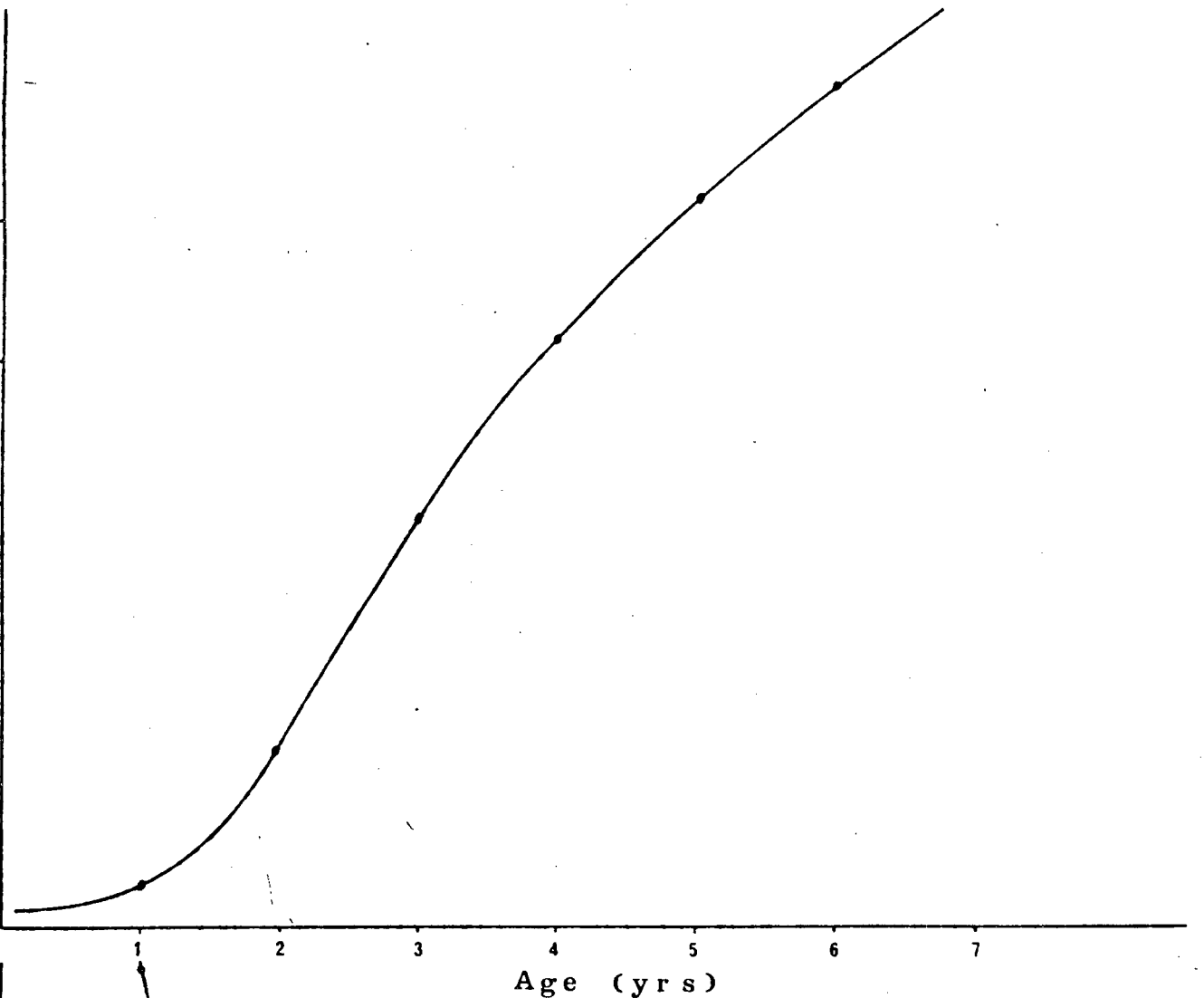
Captive worms

In order to determine potential growth in the second year, captive worm data have to be considered. These worms were held, two each, in ten plastic laundry baskets which were 50 cm in diameter and 40 cm in depth, and which were lined with P.V.C. coated fibre-glass gauze, filled with sieved nursery sand and planted in the Nursery. Baskets were raised at two-monthly intervals and specimens reweighed after voiding sand. Growth of individual worms during a 16 month period is shown in Figure 11.

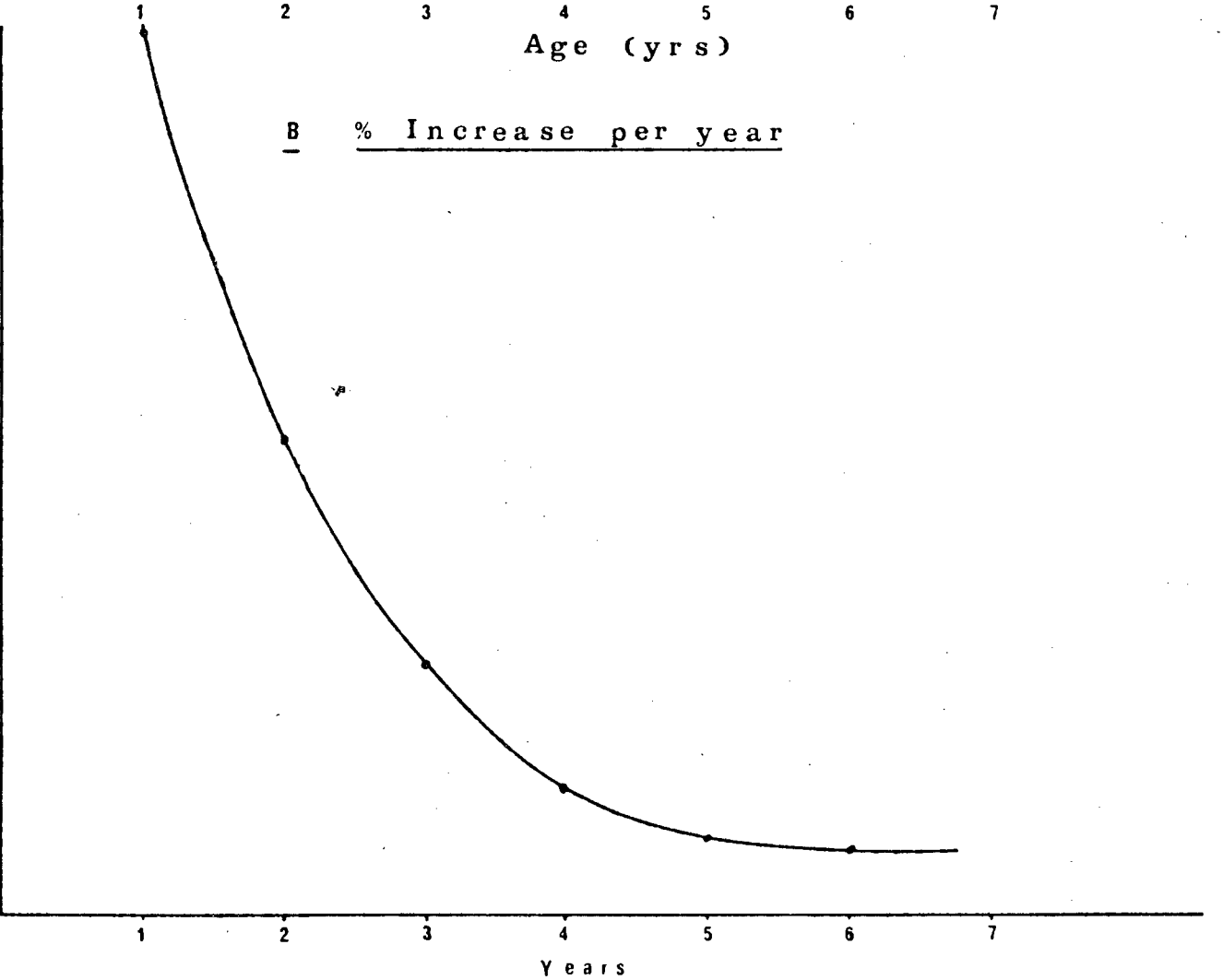
The stocking in February 1975 apparently consisted of worms of two generations (as indicated in the figure). Individuals showed highly divergent rates of growth, and even in cases negative growth under these experimental conditions. In almost all there was reduced growth over the cold winter months. In December 1975 one year old worms ranged from 0,6 g to 4,2 g, and two year old worms, 5,5 g to 11,2 g.

Mean growth of worms in various size classes, derived from captive worms data between two monthly weighings is represented in Figure 12. How representative this is of maximum growth rates of worms of a year class is uncertain because much of the data come from apparently stunted worms, but the decreasing growth rate with advancing age is apparent, although this again could have been influenced by the restricted volume and depth of the baskets.

Figure 13 A Theoretical Growth Curve



B % Increase per year



Combining all data from adult size composition analysis, 'nursery area' samples of small worms and captive worm growth, theoretical growth of A. l. loveni in the Breede River Estuary can now be proposed, and is represented in Figure 13A. This as percentage increases is represented in Figure 13B. These representations are largely theoretical as the range in practice is probably extremely wide. There are no comparable growth curves for other Arenicola species. Size of the very much smaller Arenicola marina is given as 6 cm at 1 year old (Smidt 1951 in D'Asaro 1976) or 2 to 3 cm 'chaetegerous length in their second year' (Duncan 1960). This is minimal growth compared to A. loveni. A more comparable species, A. cristata is given as reaching 9 cm in 140 days (D'Asaro 1976), which is similar to growth of A. loveni.

The basic population dynamics and recruitment cycle of A. loveni at Breede River can now be expounded: The major part of the larval development took place on a portion of the southern bank, and larvae were found from February. By the age of a year most juveniles (of around 3 g in mass) had left the 'nursery'. The adult population on the island, consisting mainly of worms older than two years (and up to 7 years old) had a mortality of around 23% per year. Original densities were maintained by immigration mainly in spring and early summer of worms in their third and fourth year to maintain approximately constant densities.

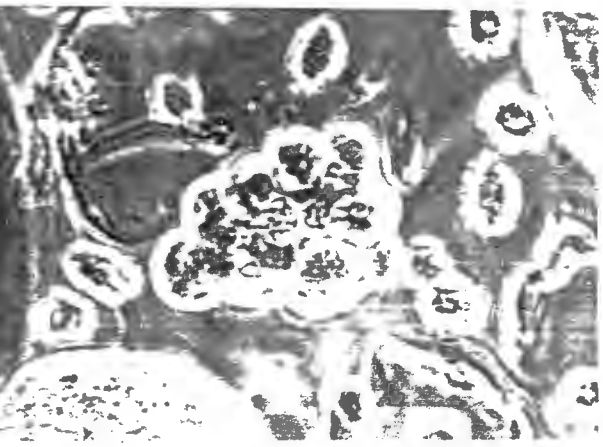
CHAPTER 4: REPRODUCTION

Reproduction is well documented for several of the Arenicolidae, but there are no published data for *A. l. loveni*, although Stach (1944 a and b) records some observations for *A. l. sudaustraliense*. This aspect was studied in some detail in the bloodworm population in the Breede River Estuary.

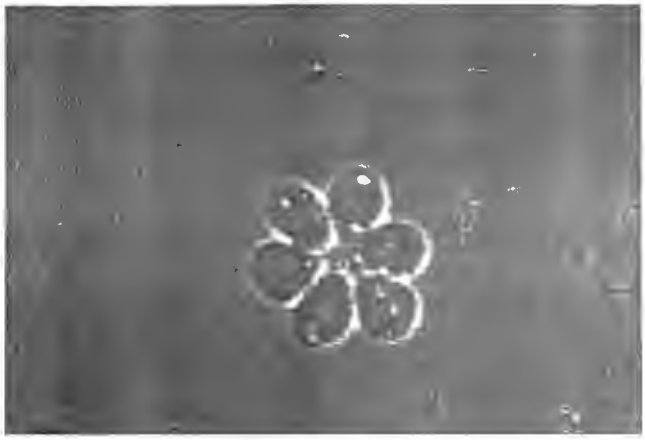
In the Arenicolidae gonads are poorly developed, and represented by areas of 'discrete germinal epithelium' (Clark et al. 1973). Generative products of the dioecious worms are thus released into the coelomic fluid at a very early stage of development, and it was found possible to sex worms from coelomic fluid examination as early as seven months before spawning. Sexually mature worms could often be sexed externally by appearance: Ripe males assumed a creamy pink colouration, while females were darker, redder and often distended.

In most of the Arenicolidae spawning occurs by the simple emission of genetal products in the burrow, from where they are expelled onto the surface of the sand (*A. marina* - Newell 1947, Howie, 1961, *A. branchialis* and *A. ecaudata* - Southward et al. 1958). Stach (1944 a and b) however describes 'numerous long slender, clavate, gelatinous masses studded with minute eggs (which) were seen issuing from burrows of the same diameter as those of *A. loveni*'. He concluded that these were 'almost certainly' egg masses of *A. l. sudaustraliense*. Although similar structures were seen in the Breede River Estuary in November 1975, anchored to the substrate by stalks, the highly active larvae were identified by University staff as veliger of a large marine gasteropod. In addition *A. l. loveni* has been observed in the laboratory and in the field to spawn by the simple emission of the genetal products through the mixonephria. Spawning behaviour of this subspecies therefore appears to differ from that of *A. l. sudaustraliense* (if Stach's deductions were valid). Differences in spawning behaviour between closely related types is known from work by Healy et al. (1959). The proposed subspecies *A. claparedii pacifica* spawned by the male ejecting spermatophores

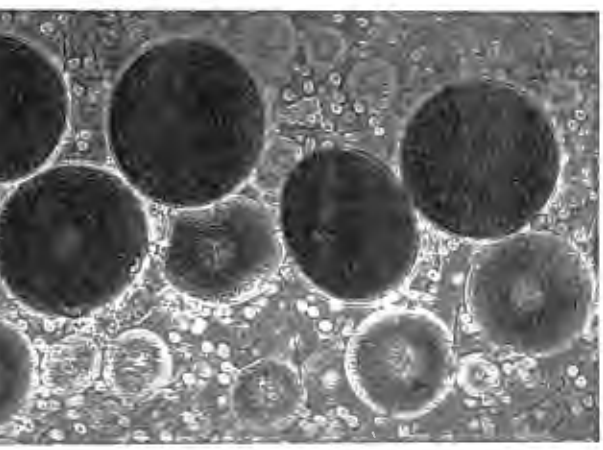
Plate 2 : Development of Gametes



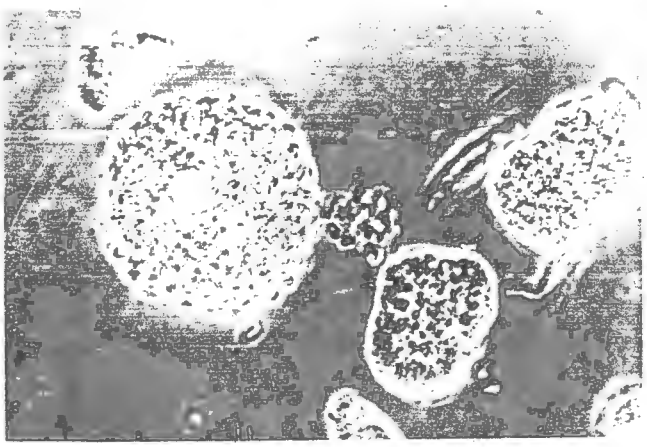
Aggregation of oocytes (x 900)



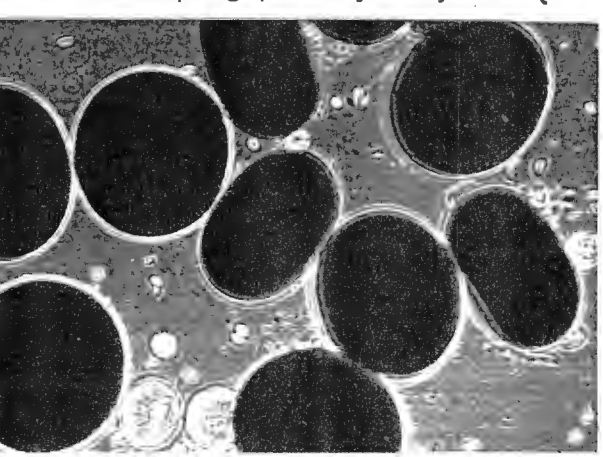
e : Spermatogonia (X 1000)



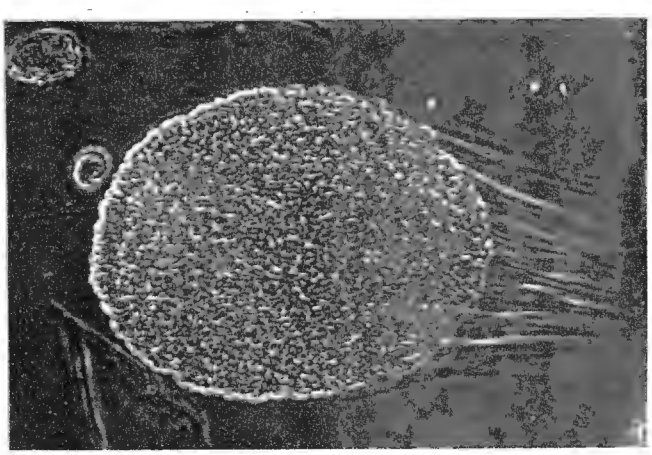
: Developing primary oocytes (X 120)



f : Developing morulae (X 500)

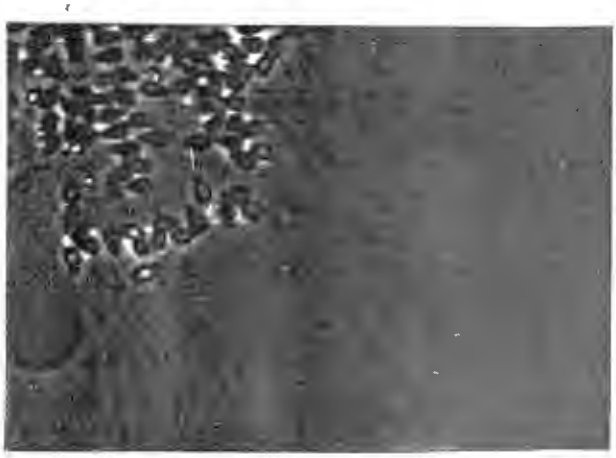


Mature ova (X 120)



g : Mature sperm-disc (X 525)

Released ovum (X 300)



h : Sperm plate disintegrating (X 1000)

and the female releasing ova in the burrow, while the proposed subspecies A. c. vagabunda crept out of the burrow onto the surface to spawn.

METHODS

The sample of 100 adult worms per month used for population size-structure analysis was also used for reproduction studies. Coelomic fluid samples were obtained by cutting the worm open from proboscis to anus over a glass funnel and collecting as complete a sample as possible of the coelomic fluid. A sample of the fluid was examined under a Wild phase-contrast microscope at 100 X and 400 X magnification.

Microphotographs of all samples of immature gametes were taken under the above magnifications. Mature ova (on a glass slide under coverslip) were photographed at 30 X enlargement, and negatives projected through a photographic enlarger, marked on paper, and maximum diameters measured. A sample of between 30 and 60 ova per specimen were measured depending on the size range in the sample; 30 was regarded as adequate for fully mature ova with a small size range.

Fecundity was determined by taking the mean of 10 counts of each sample in a Levy cell counting chamber under 30 X magnification. Samples were diluted until counts were within a manageable range. A further 50% dilution with glycerol increased the viscosity and decreased the deviation between determinations.

RESULTS AND DISCUSSION

Gamete development

The series of micro-photographs in plate 2 shows the development and maturation of oocytes and spermatocytes during the reproductive cycle. The first recognisable gametes amongst the litter of coelocytes

occurred in a few female specimens in April 1975. These were the very immature oocytes of less than 10 µm (compared to the mature size of 180 µm) which are illustrated in plate 2 a. The minute oocytes often occurred in large aggregations, the form in which they are presumably generated by the rudimentary ovary. These aggregations disintegrate and the oocytes increase in size to form the 'primary oocyte' (Okada 1941) and finally the mature ovum (plate 2 b and c). A diagnostic feature even from the earliest stage is the proportionally large and prominent nucleus. The mature primary oocyte is discoid but dorso-ventrally flattened, giving the appearance when seen edge-on of being ovoid. Plate 2 d shows the mature ovum awaiting fertilisation after expulsion through the mixonephrium. This is spherical and the size has increased to 240 µm. The large and distinctive perivitteline space is now apparent.

Plate 2 e to h shows the very interesting development of the male gametes. The precursors are the lobed, flower-like structures which were first observed in April. These spermatophores (of Okada 1941, who described them as being formed by several young spermatogonia coming together), are initially simple structures with a small number of lobes, which through cell division become multi-cellular morulae. These in turn subdivide into two, four or more entities which develop into complex, granular sperm discs. Shortly hereafter the first 'fuzz' of developing flagella becomes apparent. These are at first multidirectional, but as maturity approaches, flagella become well developed and aligned in one or several tufts. This has not been described in literature and its function is unknown, unless it assists in some kind of directional movement. Motility of 'live' sperm-discs has, however not been observed.

Plate 2 h shows the disintegration of the sperm-disc and the release of free spermatozoa following expulsion through the nephromixia. This was induced experimentally under conditions of stress by raising the temperature. The disintegration of sperm-discs outside the body is also described for A. caroledna by Okada (1941) but according to Howie (1961) in A. marina this occurs in the coelom, and only the free spermatozoa are accepted by the nephromixia.

Reproductive cycle

The reproductive cycle of 1975/76 for A. loveni in the Breede River Estuary was determined by inspection of coelomic fluid samples. Worms which could be sexed were placed in the following categories:

Developing: Containing predominantly immature gametes.

Mature : Containing predominantly mature gametes.

Spent/Inactive: Containing only extremely sparse mature gametes, or no gametes.

In addition an arbitrary classification of frequency of gametes was applied, with two categories: 'present' (X) - less than 20 in the sample under a standard square coverslip; and 'frequent' (XX) - more than 20.

Results are given in the following table:

Table 8. The development of gametes: 1975/76 Reproduction Cycle.

Months	Inactive/ Spent	MALES					FEMALES					♀
		Developing		Mature		Total worms	Developing		Mature		Total worms	
		#X	XX	X	XX		X	XX	X	XX		
Jan. '75	79	-	-	2	4	6	-	-	12	3	15	-
Feb.	94	-	-	-	-	0	-	-	6	-	6	-
Mar.	96	-	-	1	-	1	-	-	3	-	3	-
Apr.	88	3	-	-	-	3	8	-	-	1	9	-
May	35	29	8	1	-	37	7	11	3	-	20	8
June	15	6	37	1	1	45	3	36	4	13	36	4
Aug.	1	40	10	10	3	40	3	50	3	46	56	3
Sept.	1	1	60	7	45	60	1	36	1	36	38	1
Oct.	2	7	40	3	45	60	-	46	-	44	46	1
Nov.	-	24	28	4	48	52	26	22	2	46	48	-
Dec.	6	19	28	18	33	56	15	12	6	30	38	-
Jan. '76	34	4	3	26	16	45	1	1	14	8	21	-

#X =<20 in sample XX =>20 in sample

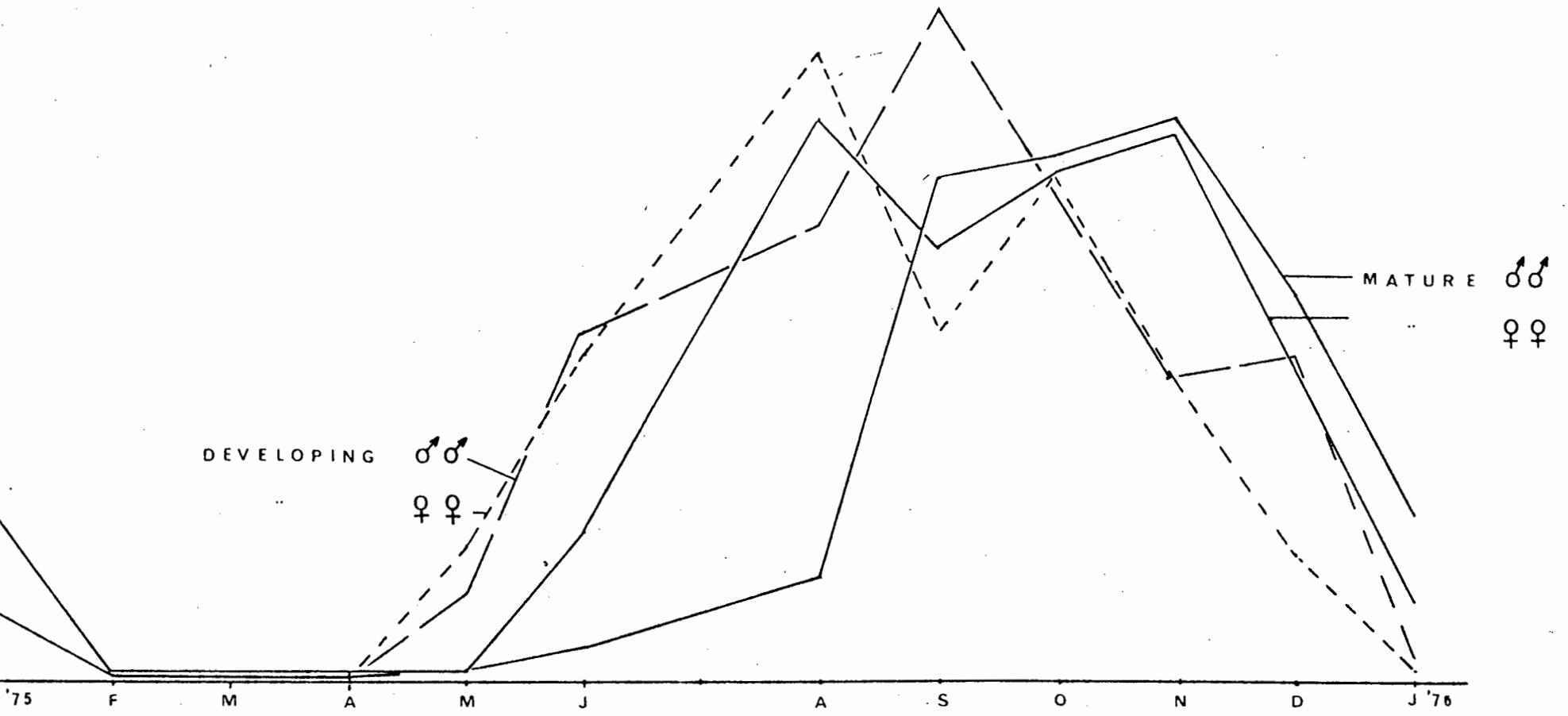


FIGURE 14 DEVELOPMENT OF GAMETES

These data are represented in figure 14. In January 1975 only 15% of the worms could be sexed by their remnant gametes. This declined further through February and March until the first, very immature gametes of the next generation could be identified in samples in April. The maturation of male and female gametes thereafter can be seen as changing proportions in 'developing' and mature categories. The slight lag in the development of males is apparent, and is also described for A. marina on the Isle of Man by Duncan (1960).

Maximum numbers of worms with mature ova and spermatozoa occurred in November and spawning must have commenced before the sampling in December, and have continued into January.

Large numbers of specimens with mature gametes occurred in the population as early as August, but spawning only occurred four months later, as a result of 'extrinsic signals ... upon the intrinsic control mechanism' (Clark et al. 1973). The intrinsic control mechanism is a 'maturation stimulating hormone' secreted by the supra-oesophageal ganglion, and only when gametocytes are mature are the 'environmental triggers' effective.

The nature of these triggers in the Arenicolidae are still conjecture, but it seems likely that temperature plays a major role. A. marina in the British Isles and Europe generally has single annual spawning in autumn, lasting up to three weeks (Newell 1949, Duncan 1953 and 1960, Howie 1959) and it was deduced that the first distinct drop in temperature was that stimulus. Howie (1959) however describes a population at Millport with a spring and autumn spawning and he concluded that a distinct change in temperature was sufficient. Periodicity of spawning for other species is as follows:

A. branchialis	4 - 6 months in winter (Eve and Southway 1958)
A. ecaudata	all year round; variable (Eve and Southway 1958)
" "	Spring and autumn (Newell 1947)

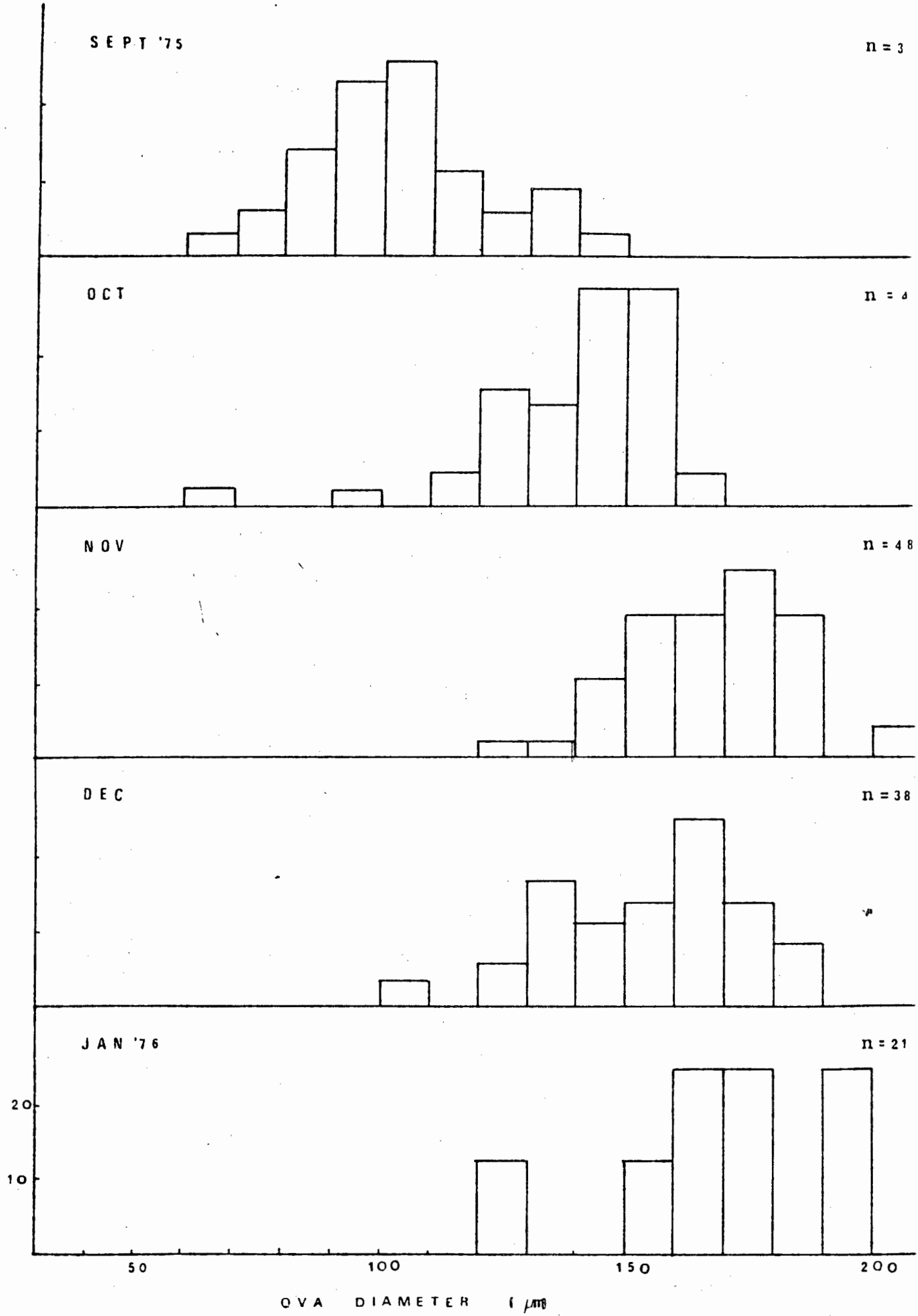
A. caroledna	Mid July to Mid September (Japan) (Okada 1941)
A. cristata	Extended period in summer (D'Asaro 1976)
A. l. sudaustraliense	December onwards (Stach 1944)

Spawning in different Arenicola species thus covers all seasons.

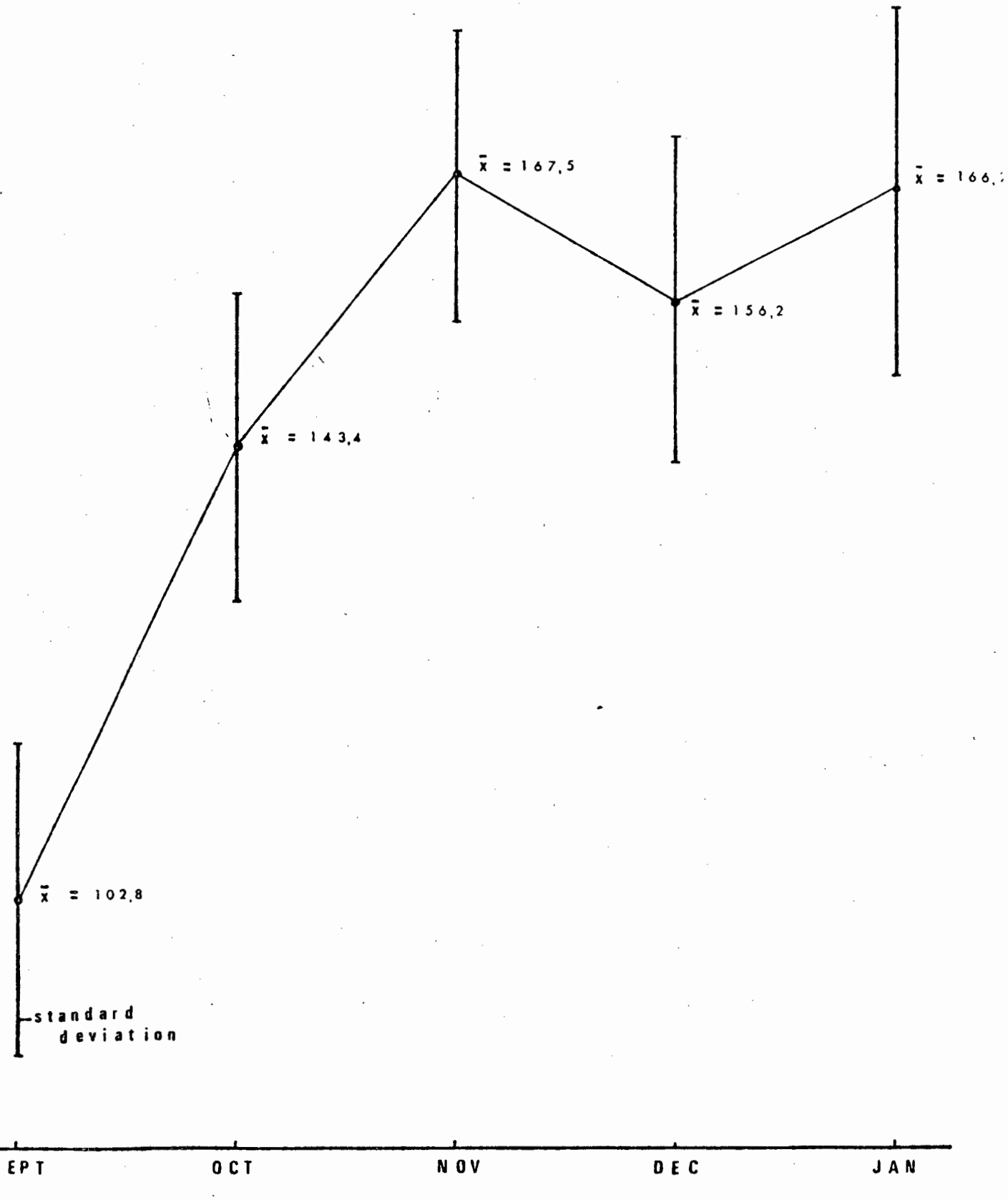
The two subspecies of A. loveni both spawn in mid-summer. This they share with A. cristata, another 'warm-water lugworm' (Wells 1962), and it appears that in these, rising rather than falling temperatures might be the trigger. In the following section it will be shown that spawning in the Breede River Estuary coincides with the first rise in temperature at 50 cm substrate depth to above 20°C. More significant are the experimental results of D'Asaro (1973) who could induce spawning almost at will by controlled increases in temperature.

Another point of significance which arises from table 8 (and figure 14) is that in January 1975 only 21% of the worms could be sexed, and of these only 7% had fair numbers of mature ova or sperm-discs. In contrast, in January 1976 66% of the worms still could be sexed, and of these 24% contained gametes in large numbers. This indicates that the 1975/76 breeding season was less discrete (or started later) than the 1974/75 one, and this is probably related to climatic or sea temperatures over this period. It can thus be concluded that spawning seasons are not rigid even at a given locality, and there is variation between seasons. This is known from literature for other species. Eve and Southway (1958) for example, describe a discrete spawning season for A. ecaudata in 1954/55, but a continuous spawning for most of the following year. It is also very likely that details of spawning cycles for A. loveni differ from locality to locality (as is known for other species) but this aspect will have to be investigated. For example, in April 1976 numerous ripe worms were found at Knysna, while in the Breede River Estuary worms only contained very immature gametes.

Figure 15 Maturation of Ova



GURE 16 MONTHLY MEAN OVA DIAMETERS



Two other points of interest arise from table 8: (a) The ratio of males to females from July to December (when most worms could be sexed) does not differ significantly from a 50 : 50 proportion. This agrees with A. caroledna (Okada 1941) but differs from A. marina for which Newell (1947) recorded a ratio of 3,7 females to 1 male. (b) A very interesting observation was the occurrence in several specimens of very immature gametocytes of both sexes in a single specimen. After maturity was reached in October, only one such individual was found. These temporarily bisexual worms covered all size classes and it is presumed that the maturation of the 'wrong' sex's gametes was suppressed by sex-specific maturation hormones.

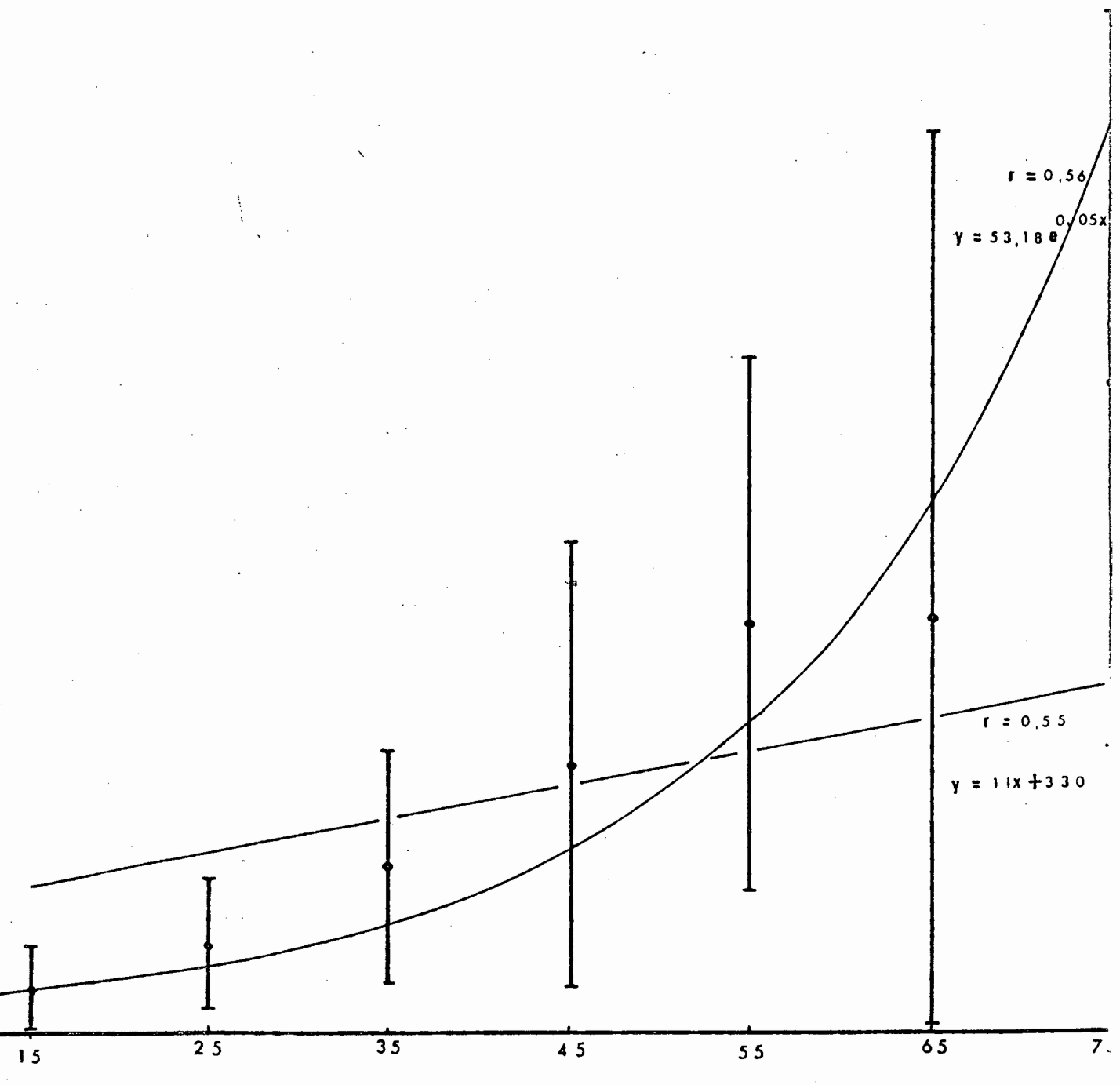
Ova maturation

Mean ova sizes clearly indicate the attainment of maturity of the female component. Results are given in figures 15 and 16, as means for individual females in the monthly sample, and means (and standard deviations) for the whole monthly component respectively. These clearly indicate that maturation was complete by November 1975, when ova diameters ranged between 170 µm and 200 µm. This agrees well with data for other Arenicolidae. Duncan (1959) found that at maturity, 90% of the 'healthy' ova of A. marina were around 170 µm and 5% between 180 µm and 190 µm. A. branchialis is described as having mature ova of 170 µm to 187 µm and A. ecaudata, about 170 µm (Eve and Southway 1958). The mature ova of A. caroledna were however smaller, at 150 µm (Okada 1941). The drop in mean size in December 1975 for A. loveni is similar to that described by Duncan (1960) for A. marina, and it is explained by the loss at the onset of spawning of accumulated large, ripe ova. In a previous paper (1959) the same author found no correlation between mean egg size and worm size. The same was found for A. loveni where the size of mature ova in a specimen of ,9 g had the same range as those of a female of 80 g.

Fecundity

The results of ova counts for females approaching maturity are given in figure 17, which illustrates fecundity as a function of worm mass.

GURE 17 RELATIONSHIP between FECUNDITY and Worm mass



Although there is a distinct correlation with size, the very large standard deviation of the mean for a given size class is apparent. The correlation coefficients (and significance of these) between worm mass and ova count is given in the following table:

Table 9. Correlation coefficients (r) between worm mass and fecundity.

September 1975	$r = 0,59$	$P < 0,001$
October	$r = 0,51$	$P < 0,001$
November	$r = 0,62$	$P < 0,001$
December	$r = 0,30$	$P > 0,05$

This shows that there is highly significant correlation between mass and fecundity for the three months preceding spawning, but that in December (when spawning is in progress) this relationship breaks down.

The correlation coefficient for the three months preceding spawning combined is $r = 0,58$, and the least squares estimate of the relationship between ova count and mass is a power curve with the formula

$$y = 13,34 \cdot x^{0,18}$$

where y = fecundity $\times 10^3$
x = worm mass (g).

A linear regression with formula $y = 11x + 330$ for the same measures, and with $r = 0,55$ (also highly significant) also describes the relationship between the variables, but gives a very low estimate of fecundity in larger sized worms. (These regression lines are also shown in Figure 17). Due to the very high individual variation these have very little predictive value, but in the first case illustrates the high potential fecundity of larger worms. This could be of importance in management.

The large range of ova counts for worms of a similar size prior to

spawning has several possible explanations: (a) Loss of ova from worms damaged in sampling (although healthy worms appeared to seal injuries immediately by constriction); (b) Premature spawning due to stress (particularly thermal), and water in which worms were held close to spawning often contained visible ova and sperm-discs; or (c) Divergent growth due to substrate or environmental variation so that worms of a certain size class might include older but stunted individuals, and this could effect fecundity.

Age at maturity

Another factor of prime importance in determining the reproductive potential of the population is the age at which worms become mature. Juvenile worms in the 'nursery area' were not included in reproductive studies due to the difficulty in obtaining a coelomic fluid sample, and because the first samples examined contained no recognisable gametes. In February and March 1975 however, several worms of juvenile size contained ova. Details are as follows:

Table 10. Ova counts of small worms.

Month	Intact mass (g)	Ova count
February 1975	1,21	6 400
	1,20	8 200
	1,17	10 000
	1,20	19 600
	0,90	22 500
	1,06	50 000
March 1975	1,48	30 000
	1,92	26 200
	2,90	74 300
	2,64	133 000

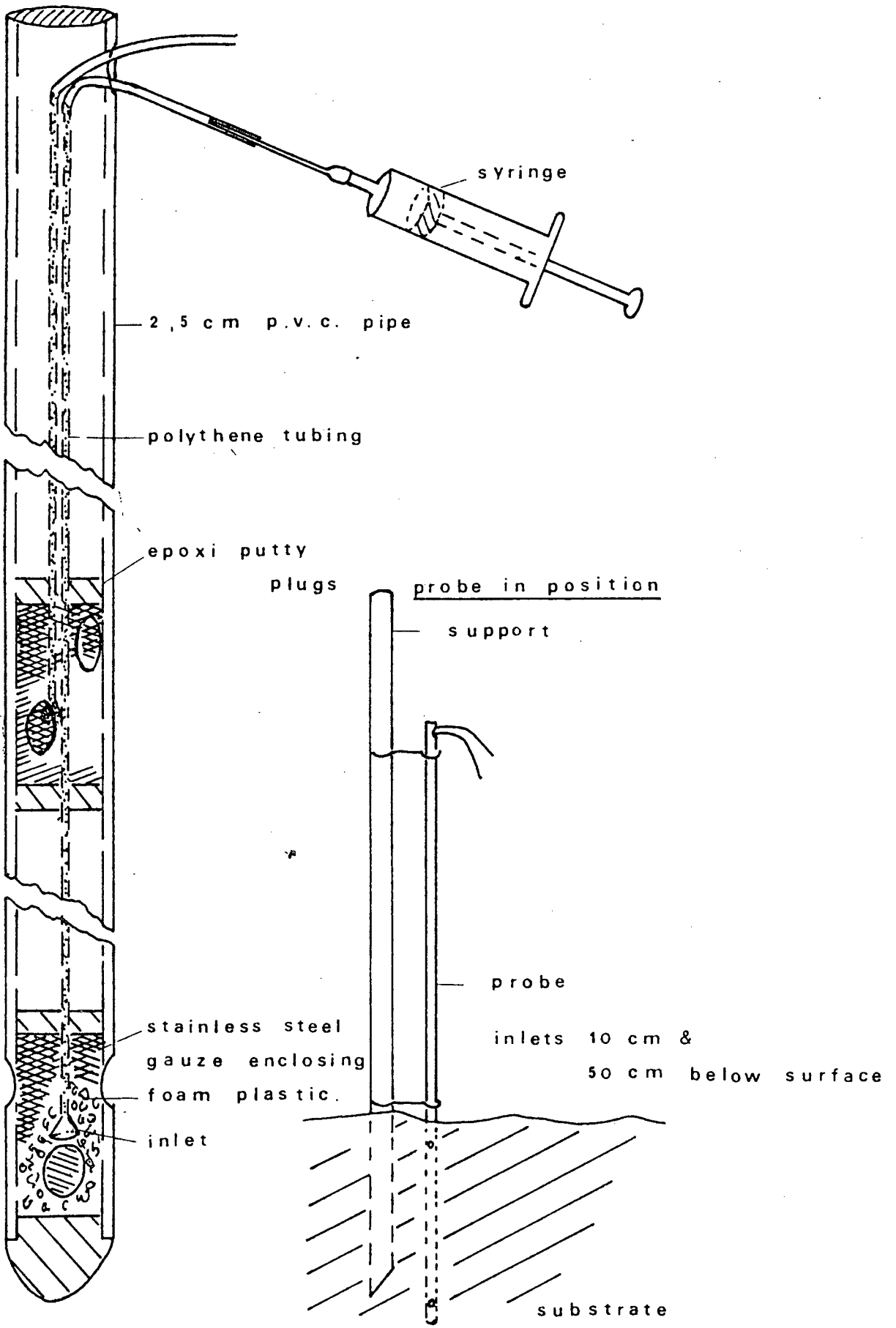
No males of this size range were identified, and the smallest specimen containing sperm morulae was 4,97 g.

A. marina become sexually mature in their second year at a volume of 0,5 cc (approximately 0,5 g) (Duncan 1960, Newell 1949). Ripe female A. loveni sampled in the Breede River Estuary in February and March 1975 were too large to have been progeny of the 1974/75 breeding season and must thus have been small specimens also in their second year. Their contribution to the annual spawning is uncertain as at this time no large adult worms were ripe, and if rising temperatures are responsible for inducing spawning it is unlikely that they would have spawned.

To determine whether there was any difference between the size composition of adult males and females, data for all worms which could be sexed were analysed. The means and standard deviations (in brackets) for females and males were 41,8 g (15,43) and 39,8 g (16,12) respectively. The t-test indicated that these did not differ significantly ($t = 1,53$ $p = 0,1$) and that there was therefore no difference between the size composition of the two sexes.

In summary, the spawning season in the Breede River Estuary for 1975/76 occurred over mid-summer, and lasted for several weeks. This is substantiated by ova maturation and fecundity studies. Worms become sexually mature at a very small size in their second year, females sooner than males.

Figure 18 CONSTRUCTION OF PROBE



CHAPTER 5: HABITAT FEATURES

In previous chapters the systematic differences in densities of *A. loveni* in the Breede River Estuary, and also the different size compositions of the island and southern bank populations are discussed. In an attempt to correlate these findings with actual habitat features, various physical, chemical and substrate parameters were determined. A further object was to determine general habitat requirements of bloodworm, with a view to possible restocking or introductions to suitable areas as a management measure. Because of the secondary nature of this study, only the most basic features were studied. These were in two categories: (a) Environmental features, which included pH, salinity and temperature (all of which were measured for two depths of interstitial water at low-tide, and also for the surface and bottom of the overlying water at high tide), and (b) Substrate features which included structure analysis and organic carbon determination by 'wet oxidation'.

a) ENVIRONMENTAL FEATURES

Methods

Probes, the construction of which is illustrated in figure 18 were planted and attached to firm supports at each of the six stations (illustrated in figure 1). This was necessary due to the severe currents and wave action to which the island in particular was subjected. Using a 10 mℓ syringe, interstitial water samples were taken from 10 cm and 50 cm depth by withdrawing water from the respective polythene tube (and rejecting the first few cc's as possibly contaminated). Operating from a dingy at high tide, surface and bottom water samples as well as interstitial water samples were taken. Sampling was done on three consecutive days around the full-moon spring tide, at two-monthly intervals for a year, and starting in January 1975. Samples were taken within an hour of the peak low and high tide indicated by tide-tables of the S.A. Naval Hydrographic Office.

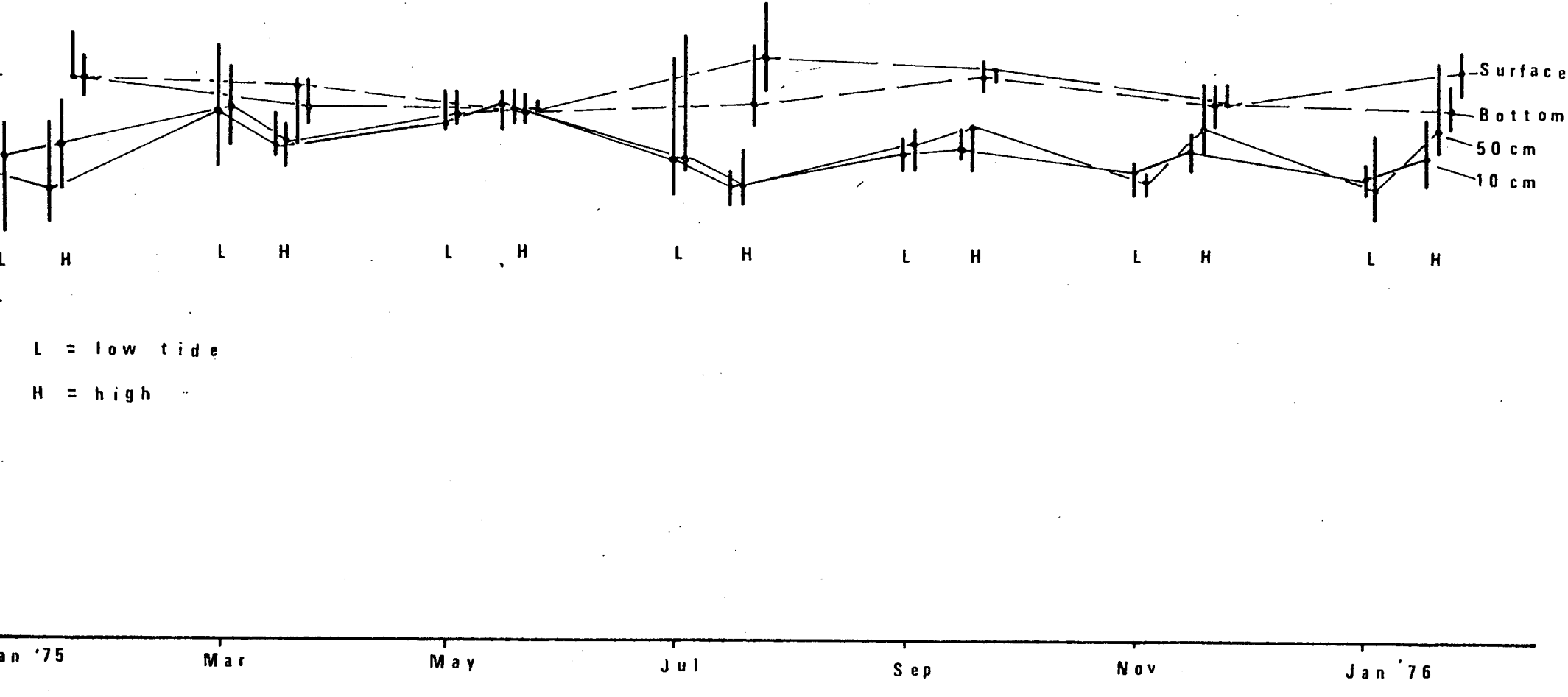


FIGURE 19 pH FLUCTUATIONS over SAMPLING PERIOD

(Medians and range for all stations)

pH Determinations were made *in loco* using a model 610 Corning-Eel pH meter. Salinities were determined by use of a model 10400 T.S. Refractometer, calibrated with standard sea-water.

Temperatures were determined using a Y.S.I. thermistor probe sealed in epoxi-resin in a 1,2 m stainless-steel tube with 15 mm external diameter, with only the temperature sensitive point protruding. Substrate temperatures were taken by forcing the probe gently to the required depth (with reference to the rigid support at high tide) and allowing a few minutes to equilibrate before taking a reading.

Results and Discussion

pH

Results of pH fluctuations over the sampling period are given as modes and range for all stations in figure 19. This shows that there was little systematic fluctuation between either stations or over the sampling period, but rather erratic local variation even between low and high tide determinations at the same station. These erratic fluctuations are common in interstitial water of marine sediments and differences of 1 pH unit within 1 cm depth have been measured in estuaries (Jansson 1968 in Perkins 1974). The pH at 50 cm tended however to be lower than at 10 cm depth of substrate. This is also a common feature of marine sediments in which pH 'generally falls with increasing depth' (Perkins 1974), due to bacterial decay of organic matter under the more anaerobic conditions. The pH of the sea water over the sand-banks also was consistently lower than at the bottom than at the surface. The range of pH's over the twelve months, and between stations was so small however (about 1 pH unit) that it is unlikely this in any way influenced the burrowing *Arenicola*. The mucoid lining of the burrow (which was described in the first section) would in any case assist in isolating the animal from unfavourable chemical conditions in

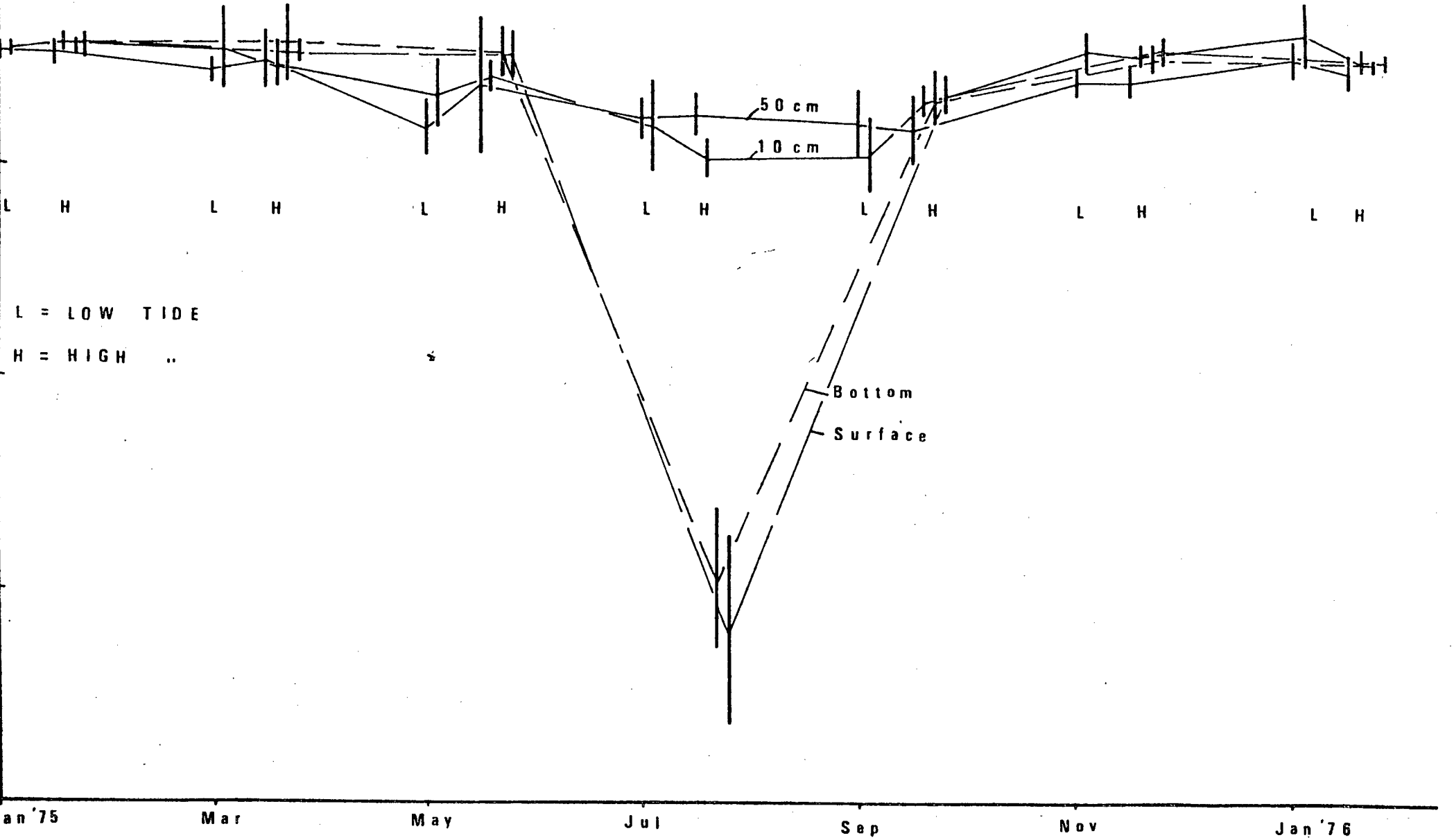


FIGURE 20 SALINITY FLUCTUATIONS over SAMPLING PERIOD

(Means and standard deviations for all stations)

the substrate, and the pH of water circulating through the burrow is likely to be of more importance.

Salinity

Figure 20 shows the remarkably constant salinity regime of the Arenicola beds in the Breede River Estuary for the greatest part of the year. The overlying water at high tide is basically marine due to the extensive estuary and for most part low volume of flow of the river. During most of the year the fresh-water of the river therefore has little effect on the interstitial water of the substrate.

Samples taken in July were in the midst of a flood following heavy rains in the catchment. This flood dramatically reduced the salinity of the overlying water but had little effect on the substrate as illustrated by the fluctuation in salinity in the interstitial water even at 10 cm depth of sand. There was however a delayed effect at some stations. This is shown by table 11 which records salinities at the six stations on consecutive days in July 1975.

Table 11. Salinities at Stations A to F (‰) at High tide on consecutive days.

		Salinity (‰)	
Station	Sample	23/7/75	24/7/75
A	Surface	9,47	27,4
	Bottom	11,0	28,4
	10 cm	30,5	22,9
	50 cm	31,6	32,6
B	Surface	13,2	30,5
	Bottom	13,2	29,5
	10 cm	28,4	22,6
	50 cm	33,1	32,6

Station	Sample	Salinity (‰) 23/7/75	24/7/75
C	Surface	12,6	30,5
	Bottom	13,7	30,5
	10 cm	16,8	29,5
	50 cm	32,1	32,1
D	Surface	5,3	30,5
	Bottom	11,6	31,0
	10 cm	30,0	28,4
	50 cm	31,0	33,1
E	Surface	2,6	17,4
	Bottom	6,8	31,0
	10 cm	31,6	31,6
	50 cm	32,1	31,6
F	Surface	4,7	16,8
	Bottom	5,8	32,6
	10 cm	30,5	30,5
	50 cm	33,7	32,6

Stations A, B and D (the stations closest to the main drainage channels) showed depressed salinities on the second day, although by then the overlying water was approaching normal. This table also illustrates the rapid recovery of salinities of the overlying water following floods, by the large scale dilution by sea-water.

The effects of low salinity water on A. loveni at this time are significant. As mentioned previously no density estimates could be made, or population samples taken in July due to the virtual absence of surface signs. The following month however, normal casts were once more apparent indicating that the population had not been adversely effected, but had merely suspended activity. Circulation of excessively hypotonic water through the burrow would have obvious disadvantages. The mechanism of the behaviour can be deduced from work on A. marina. Wells (1949 b) describes feeding of A. marina as consisting of characteristic cyclical patterns under the influence

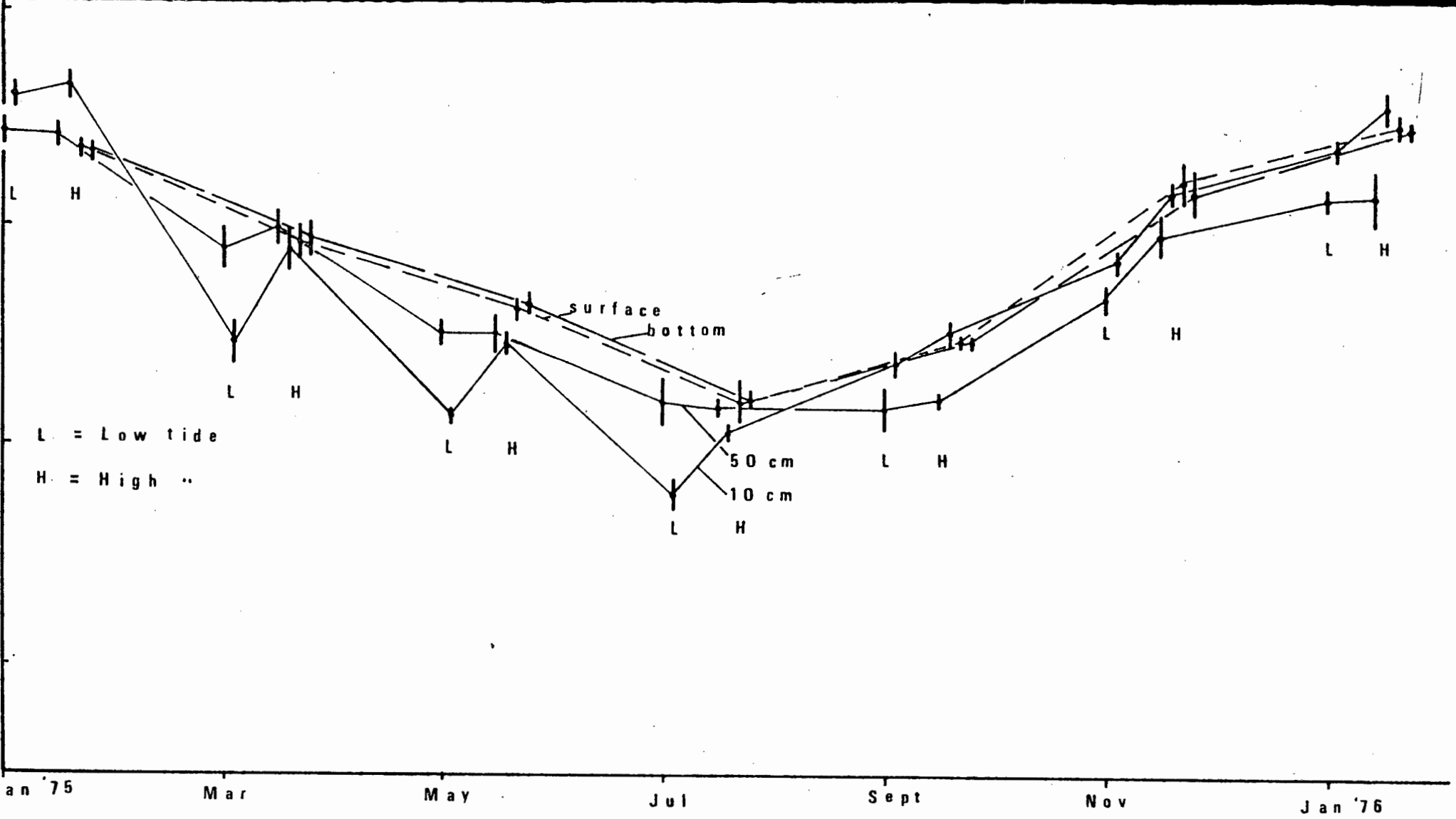


FIGURE 21 TEMPERATURE FLUCTUATIONS over SAMPLING PERIOD

Means and standard deviations for all stations

of an oesophageal pace-maker. In a previous paper (1949 a) he also describes cyclical respiratory movements which were not 'altered radically' by oxygen lack, but merely decreased in intensity and consisted rather of a 'periodic testing of conditions' by tailward creeping of the animal towards the surface. This would have obvious survival advantages if the overlying water was harmful to the inhabitant (as in freshwater flooding). Under flood conditions, then, A. loveni would react by a suspension of feeding and respiratory water circulation, and would only revert to normal behaviour when 'testing' revealed normal salinities. This kind of behaviour under unfavourable conditions is also described for A. marina by Shumway and Davenport (1977).

The fact that surface signs of juvenile worms on the southern bank persisted throughout this period is less easy to explain, unless this was due to differences in habitat characteristics or juvenile worm behaviour. To test whether there was any difference in tolerance to hyposalinity between juvenile and adult worms, 5 adults (20 g to 30 g) and 5 juveniles (1 g to 3 g) were placed in 0%, 25% and 50% sea-water. In 0% sea-water all 5 juveniles and one adult were dead within $2\frac{1}{2}$ hours. After 5 hours 3 adults were dead, while the last two survived for 10 hours. In 25% sea-water, all juveniles were dead within $3\frac{1}{2}$ hours whereas the first adult died after 22 hours, and all were dead after 27 hours.

In 50% sea-water the first juvenile only died after 29 hours and all were dead after 46 hours, when 3 adults still survived. Results therefore indicate that low salinities were more lethal to juveniles than to adult worms. The southern bank of the Estuary does however have different substrate characteristics which will be discussed.

Temperature

The distinct seasonal temperature cycle in the Breede River Estuary is shown in figure 21 as means and standard deviations for all stations. The temperature at 10 cm depth clearly fluctuates the most widely and

is obviously moderated by the temperature of the overlying sea-water at high tide. The temperature at 50 cm depth (which would most influence large breeding worms) shows a steady cycle of decrease in late summer and autumn and a slightly retarded increase in spring and early summer. Temperature within the actual burrow of Arenicola would, however probably be largely modified by the circulation through the burrow of sea-water at high tide.

Temperature appears to be of considerable importance to Arenicola and Wells (1964) states that 'temperature acting either directly or indirectly is a factor of outstanding importance in the control of lugworm distribution', but he could 'present no suggestion ... on the mechanism'. As mentioned previously the distribution of A. loveni along the South African coast shows the same correlation with temperature, although worms showed no signs of stress to reasonably low temperatures, and in fact worms in the laboratory survived best when held at below 15°C and were fully active in the field at 11°C.

As discussed under the section on reproduction, temperature (acting together with hormonal control) might, however be an important factor in initiating spawning. Spawning in the Breede River Estuary commenced shortly after the temperature of the sand at 50 cm depth exceeded 20°C. Temperatures at 10 cm depth at this time were several degrees higher, and the temperature of standing water on the flats at low tide reached for short periods at least, temperatures around 25°C, so that during low tides worms could raise the temperature in their burrows by circulating this water. Shumway and Davenport (1977) have also recently shown that interstitial water may be circulated by A. marina during low tides.

Some success was achieved in the laboratory in inducing spawning by increasing the water temperature to 27°C. D'Asaro (1973) states that A. cristata can be induced to spawn at will by raising the temperature; 'Several days before embryos are needed, the temperature is raised gradually to 17,8°C (64°F) and then rapidly to 27,8°C (82°F). When illumination and water level are properly regulated spawning occurs within 24 hours and egg masses occur on the sand in 48 hours'. As

mentioned in Chapter 5 however, data for other Arenicola spe are contradictory.

The general conclusions from the consideration of pH, salinity a temperature fluctuations are that in the Breede River Estuary the themselves are not limiting factors in the distribution of A. lover nor are there systematic differences between stations which would explain density or size compositions differences. The substrate must thus be considered.

b) SUBSTRATE ANALYSIS

Methods

I Structure

The substrate was sampled on three occasions, in May 1975 (before winter floods), in October (after winter floods) and in January 1976 (mid-summer). Samples were taken at 25 m intervals along the transects through stations A to D across the island and at 12,5 m intervals through stations E and F on the southern bank. These were obtained by taking a core with a standard prawn-pump of 4 cm diameter and separating two fractions: 0 - 25 cm and 25 - 50 cm substrate depth. (The pump proved highly practical for taking sand samples, as the sample could be lifted and expelled intact by maintaining vacuum with the plunger). Samples were immediately transferred to polystyrene containers and kept cool until they could be stored in a freezer until convenient to process.

Sample preparation and dry sieving was adapted from procedures described by Krumbein and Pettijohn (1938), Morgans (1956) and Carver (1971) as follows: Samples were thawed, placed in dialysis tubing of 31,8 mm diameter and hung in fresh flowing water for 48 hours to desalinate. Samples were then oven-dried at 105°C for 48 hours, sand grains gently separated in a porcelain mortar and a sample of 150 mℓ (about 200 g) sieved through a nest of Wentworth grade scale

sieves of 2 mm, 1 mm, 0,5 mm, 0,25 mm, 0,125 mm and 0,063 mm conforming to Phi notation -1, 0, 1, 2, 3 and 4 where Phi is defined as

$$\text{Phi} = - \log 2 \left\{ \frac{(x \text{ mm})}{(1{,}00 \text{ mm})} \right\}$$

Welch (1948).

Standard sieving was performed by an Endecott E.F.L. test-sieve shaker for a standard time of 10 minutes. Sieve grades were not oven-dried prior to weighing as described by Morgans (1956) but allowed to equilibrate with room humidity (Carver 1971). This author, quoting Falk (1968) regards the oven-drying of samples prior to weighing as less accurate due to the 'rapid absorbtion of moisture by the sample, between dessicator and balance'.

II Organic Characterisation

Organic carbon content of samples was determined by wet combustion using the so-called Walkley and Black method (Morgans 1956) as modified by this author. 1,2 g Aliquots were treated with 10 mℓ of N potassium dichromate and 20 mℓ of concentrated sulphuric acid in a 15 cm white porcelain dish as described. After 30 minutes 200 mℓ of distilled water, 10 mℓ of concentrated phosphoric acid and 1 mℓ diphenylamine indicator solution were added and this solution titrated with N ferrous sulphate (using a magnetic stirrer). The amount of carbon oxidised as a percentage of the sample was obtained by the expression -

$$\% \, C = (V_1 - V_2)/W \times 0{,}003 \times 100$$

where V_1 = volume of N $K_2Cr_2O_4$

V_2 = volume of N $FeSO_4$

W = weight of sample.

FIGURE 22 CUMULATIVE CURVES OF PARTICLE SIZE

STATIONS A TO F ; FRACTIONS a AND b

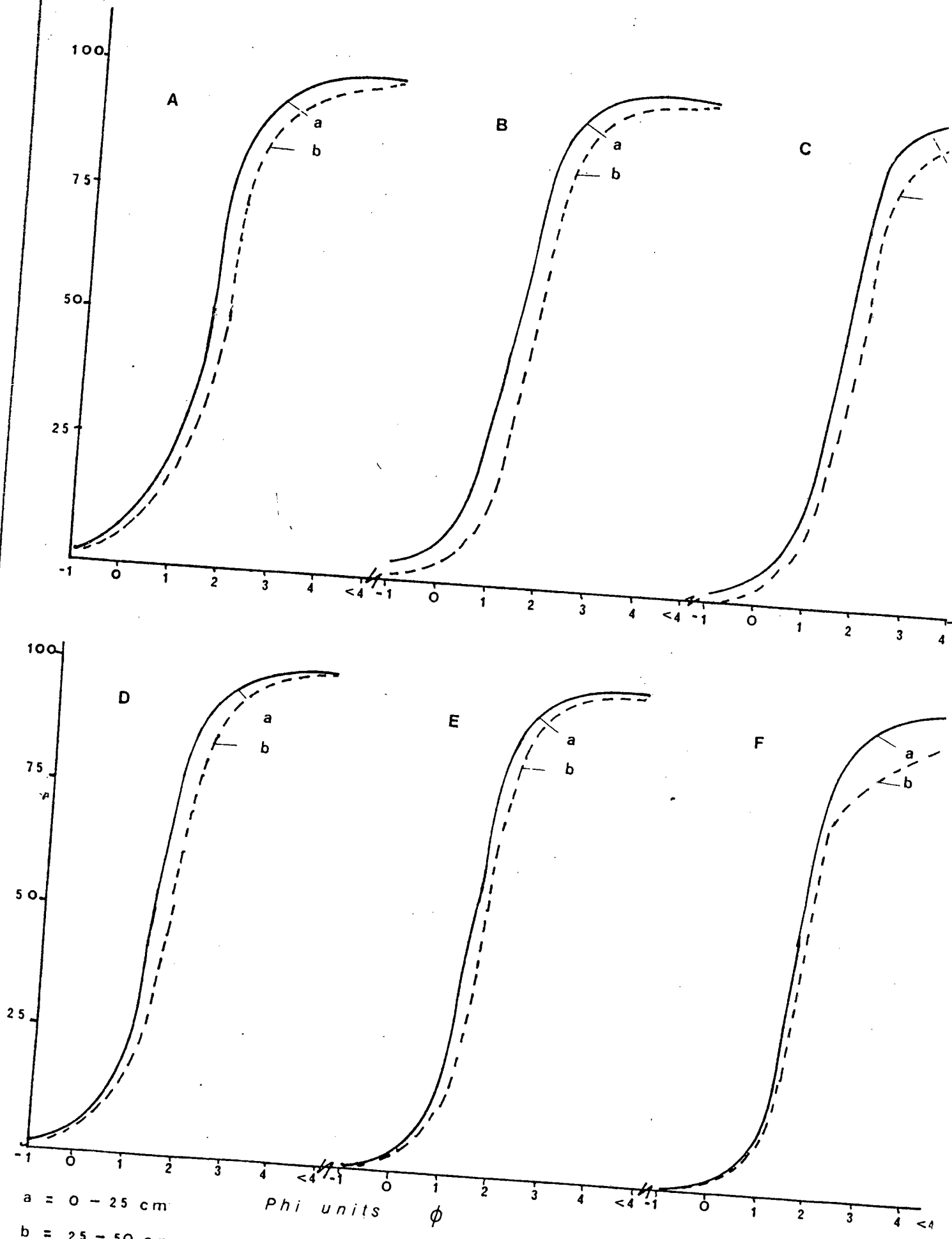


Figure 23 Mean Particle Size (Md ϕ) Mean for Stations

May '75, Oct '75, Jan '76

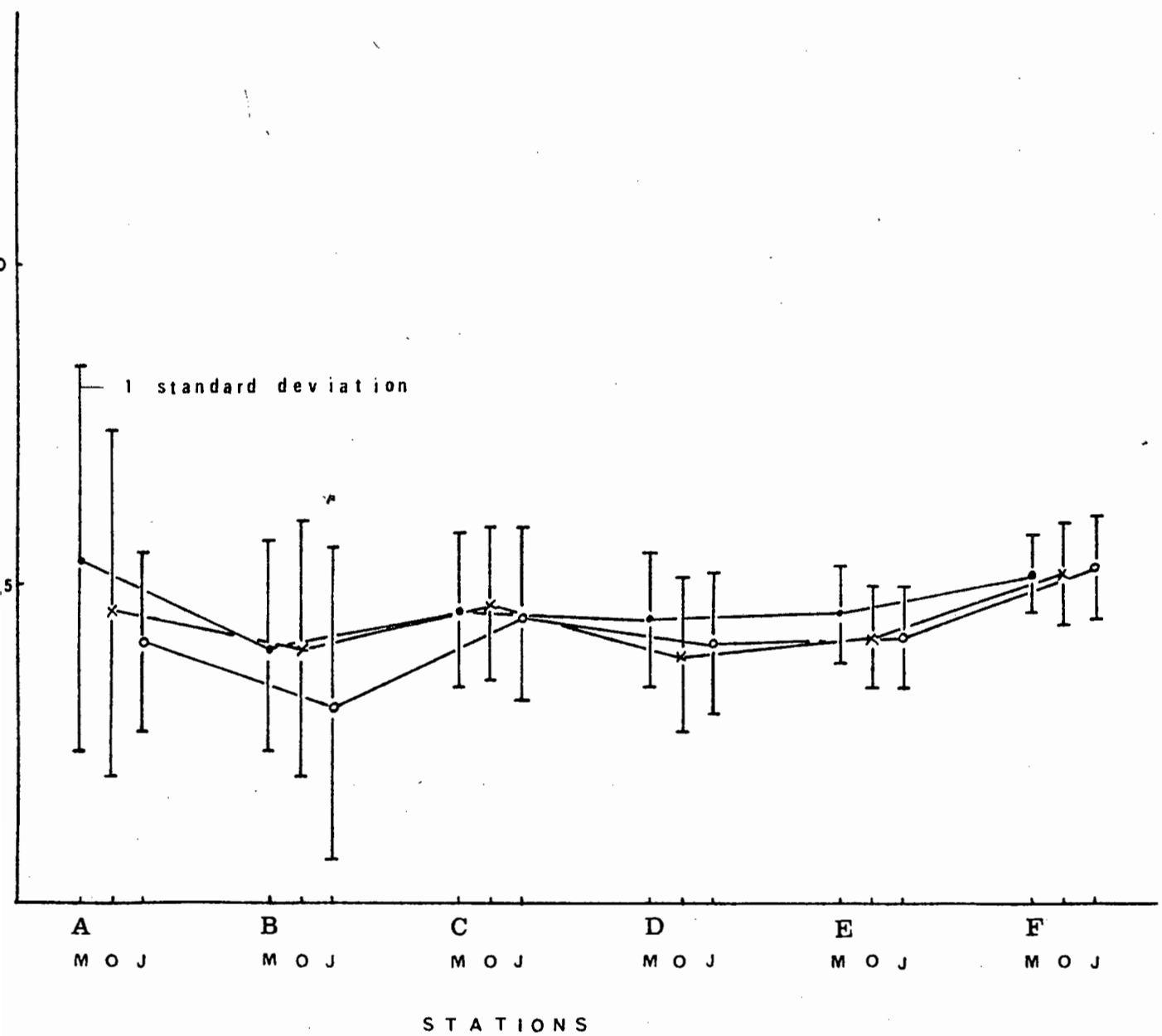
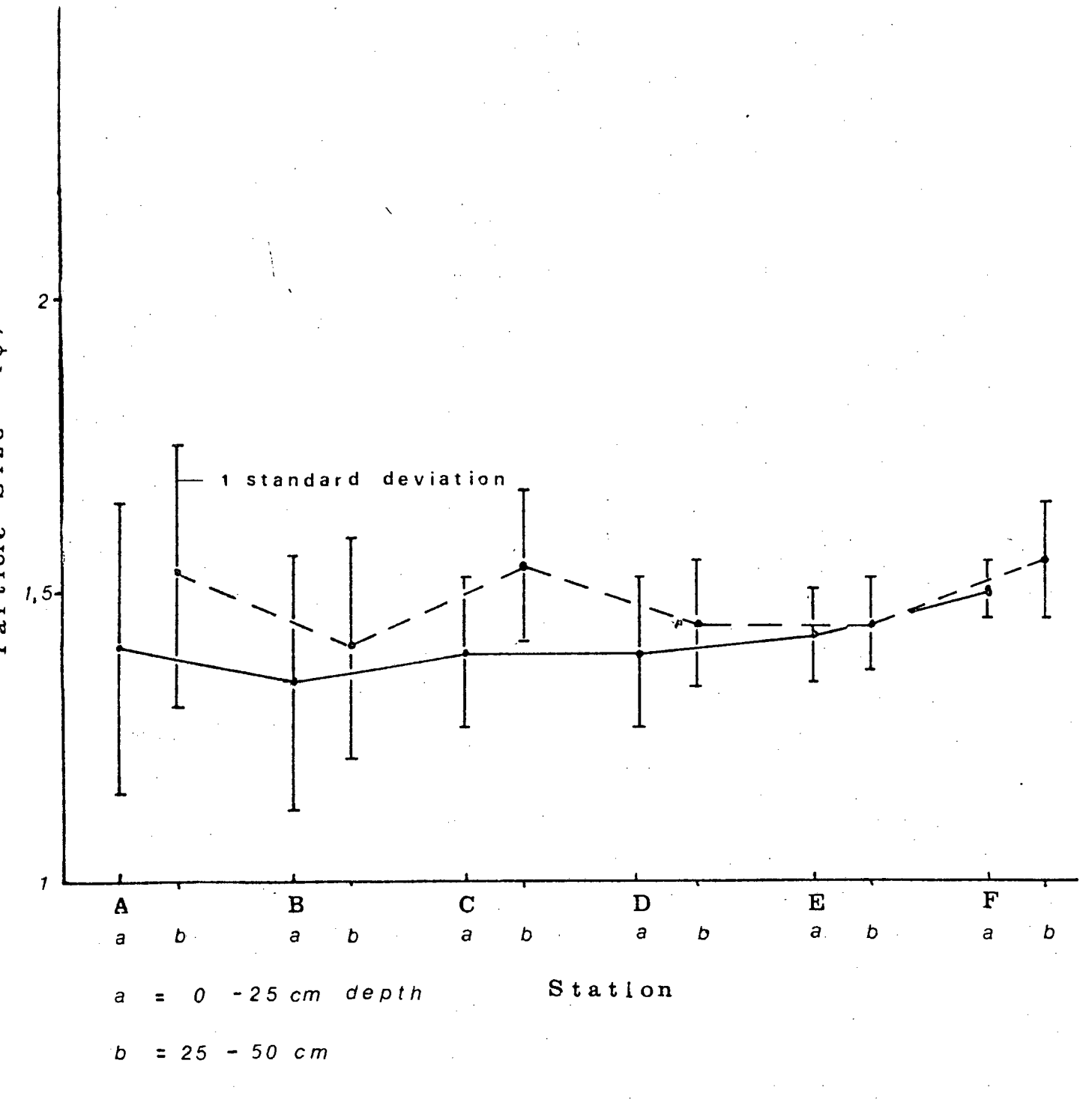


Figure 24 **Mean Particle Size (Mdϕ)** *Mean for sampling period*



No correction factors were applied, as the analysis was performed to characterise the substrate rather than determine finite values of the available organic carbon, and besides, results were very low (all less than 0,4% which Morgans (1956) regarded as negligible).

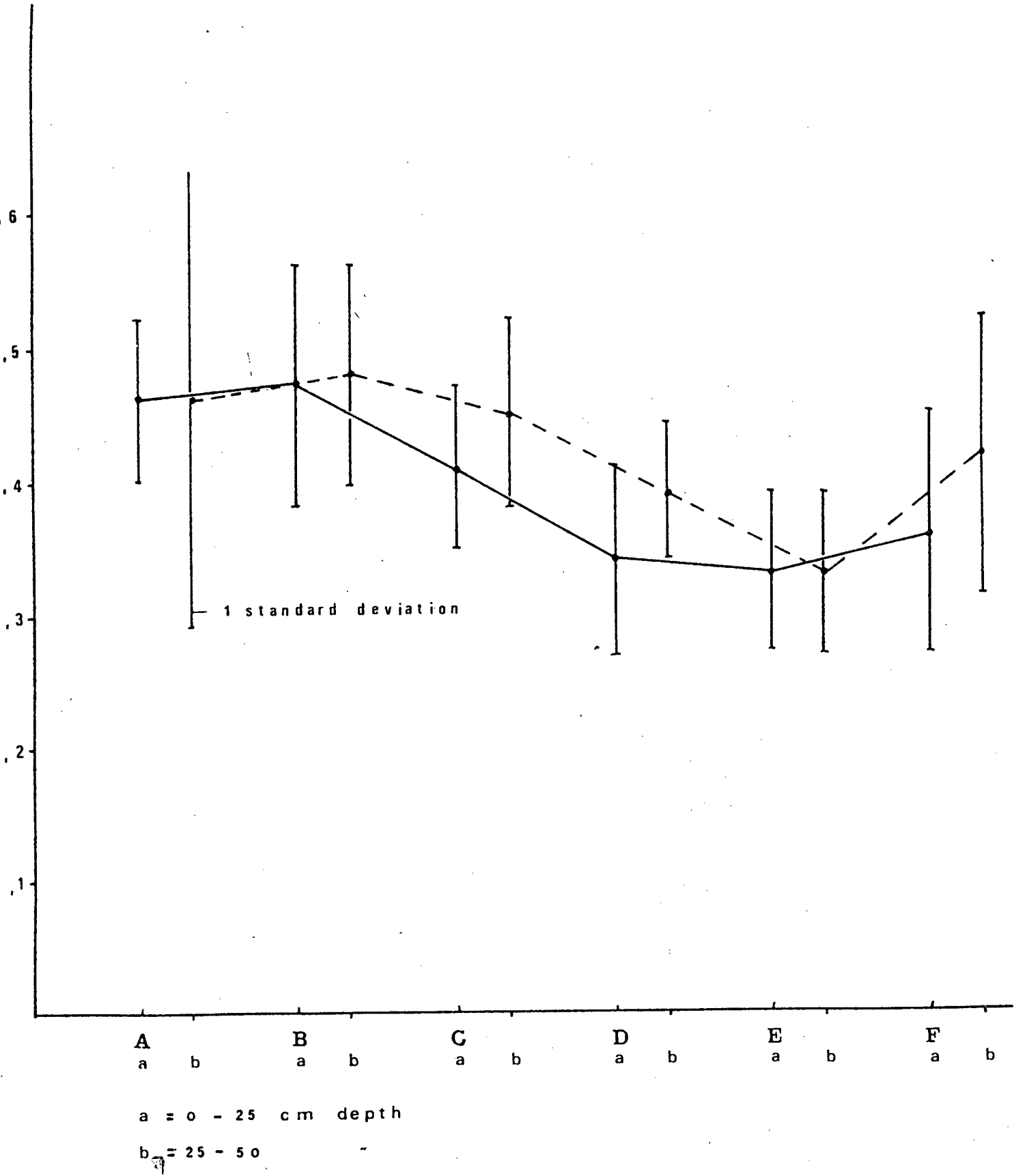
Results and Discussion

I Structure

Results of sieving are expressed as suggested by Morgans (1956) by constructing cumulative percentage curves based on the Phi (ϕ) scale notation. From these curves the median grain size (Mdϕ) and grain diameters of the first (Q1ϕ) and third quartile (Q3ϕ) were determined for each sample. Representative results are given in figure 22 which illustrates cumulative curves of particle size for station A to F for May 1975, for the two fractions a (0 - 25 cm) and b (25 - 50 cm substrate depth). These curves indicate that the substrate in general can be classed as 'medium sand' (grain diameter 0,5 to 0,25 mm) according to Wentworth's scale (Welch 1948). It is also apparent, and was found typically that the 'b' fraction was finer than the more superficial sand. This was in some cases due to the inclusion in the sample of a hard silt and clay substratum (previously inhabited by Upogebia) which underlies the sand in many places.

In figure 23 the median particle size (Mdϕ) and standard deviation for each station is shown separately for the three sampling times. This shows that the Mdϕ's cover a fairly narrow range and that there is little systematic variation between May 1975 and January 1976. The greater standard deviation range of samples taken from the two Stations closest to the main channel (A and B) is however apparent, as is the narrow range and stability of the stations on the southern bank (E and F). Figure 24 shows the means over the sampling period but for the two fractions a and b separately. This again shows that the median grain diameter is smaller in the b fraction, but also the tendency for the surface substrate to become finer from A to F.

Figure 25 Phi Quartile Deviation (Q.D ϕ) MAY '75

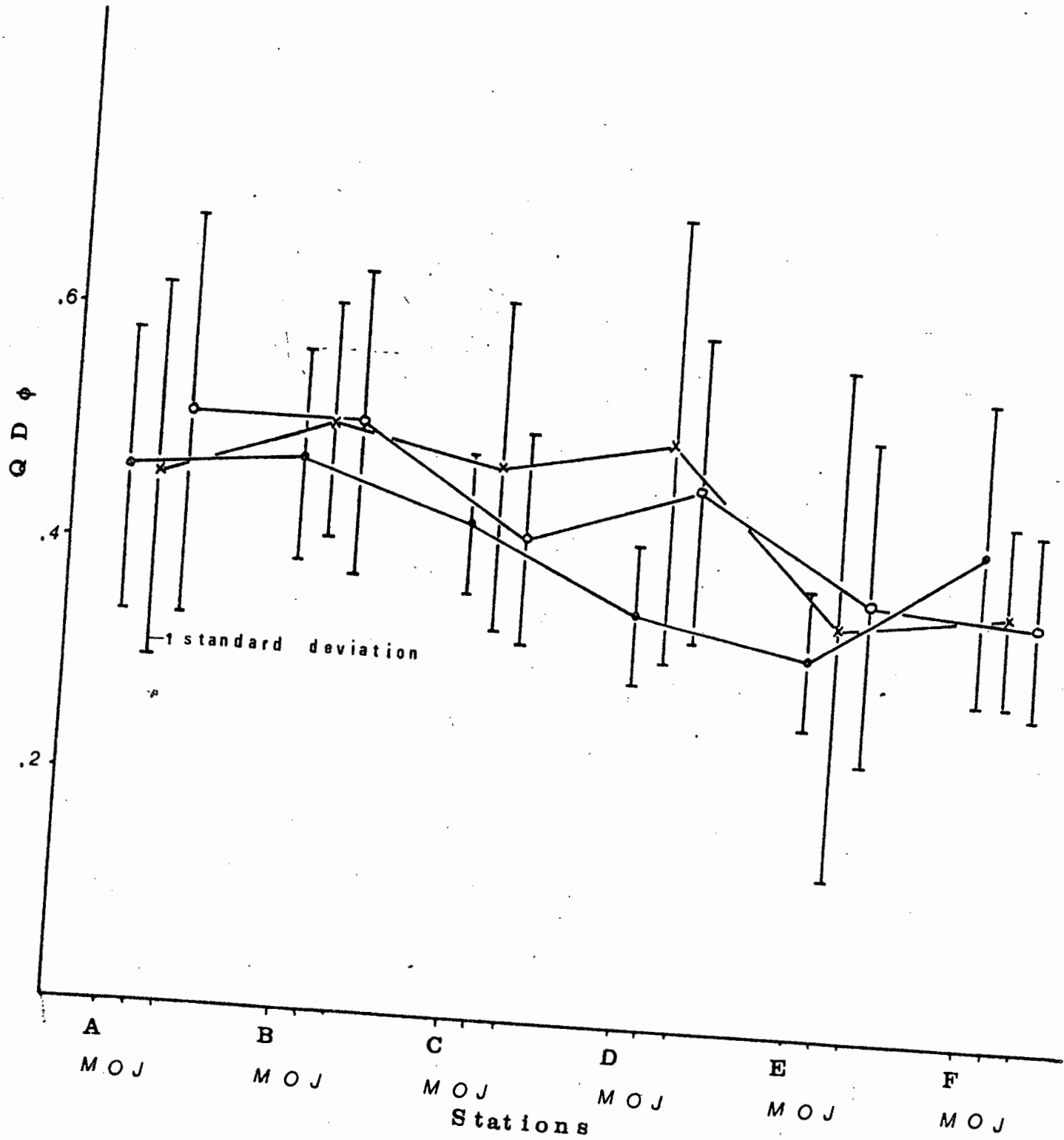


a = 0 - 25 cm depth

b = 25 - 50

Figure 26 **Phi Quartile Deviation (Q D ϕ)**

Mean for Stations A to F; May '75, Oct, Jan '76



Bascom (1951 in Newell 1970) found that particle size was related to the degree of turbulance to which the substrate is subjected, while Morgans (1956) states that fine sediments are deposited under more sheltered conditions, and tend to be more uniform. From this it is clear that stations A and B are most exposed, and station F most sheltered and stable. Conversely coarse deposits are considerably more mobile than fine deposits, where only the surface few centimeters are disturbed by wave action (Perkins 1974). This would have obvious implications for small worms in surface layers, and might explain the inability of young worms to establish themselves on the island.

The Phi quartile deviation (QDϕ), where

$$QD\phi = \frac{Q3\phi - Q1\phi}{2}$$

indicates the slope of the cumulative curve between the first and third quartiles, and hence the 'sorting efficiency of the sedimentary agencies' (Morgans 1956). By this definition the substrates samples are all fairly well sorted. Figure 25 illustrates the mean and standard deviation range of QDϕ's for May 1975 and shows that the a fraction is generally better sorted than the b fraction. The stations closest to the bank are better sorted than those close to the main channel (A, B and C). The poor sorting of the b fraction at station F is due to anomalies caused by inclusion of the clay substratum.

Phi quartile deviation plots for the three sampling periods separately, but for the a and b fractions combined (figure 26) shows an increase in the standard deviation of means for the station, but also the tendency for the substrate in May to be better sorted than in the other two sampling periods.

According to Newell (1970), the sorting of the substrate is very important to burrowing organisms and effects the physico-chemical properties of the substrate, namely the organic and oxygen content, salinity and temperature, but perhaps most important, the water

Figure 27 Phi Quartile Skewness, *Mean for Sampling Period*

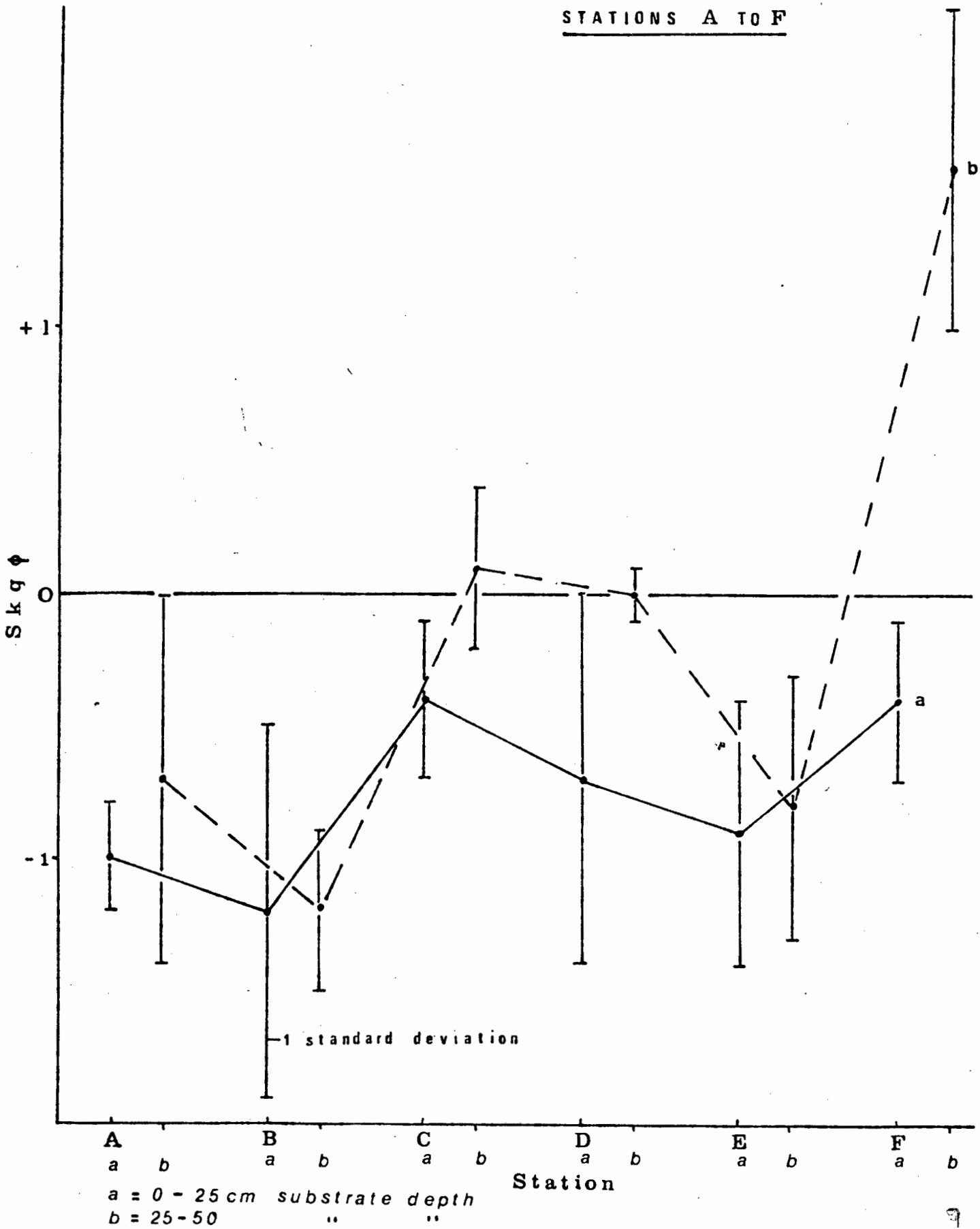
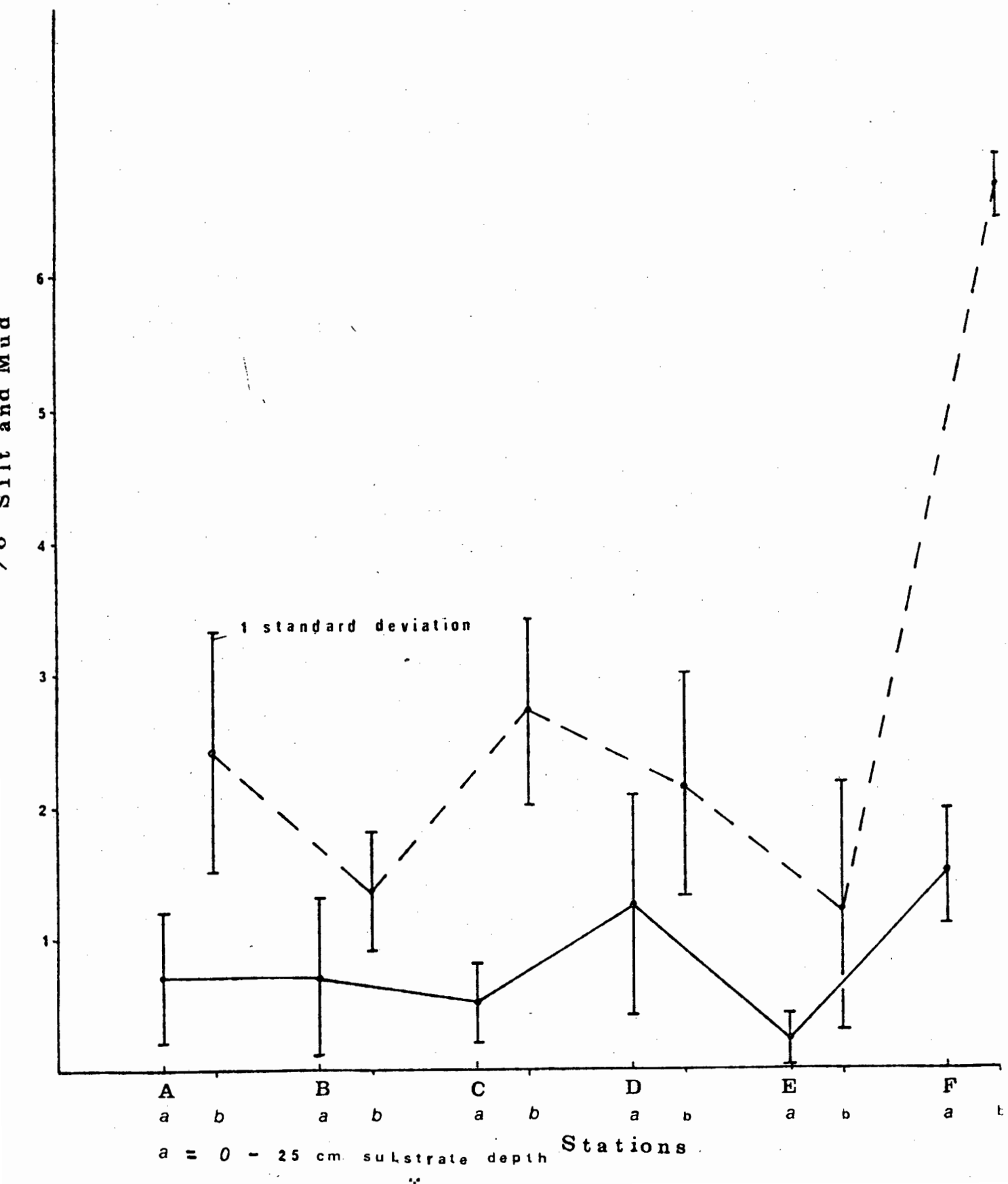


Figure 28 Mean Silt and Mud Content ; Stations A to F



content and drainage of the deposit. 'Ungraded, poorly sorted sands have much lower pore space (and) much reduced water retention'. The 'wetness' of the substrate effects the 'hardness', and hence the ability of the lugworm to burrow. Wells (1944 and 1945) found that drainage was important in the distribution of A. marina and only small and few specimens were found in rapidly draining substrates.

The Phi quartile skewness (Sk q ϕ) indicates whether smaller or larger particles in the substrate are better sorted and is defined as

$$SK\ q\ \phi = \frac{Q3\phi + Q1\phi - 2\ Md\phi}{2}$$

(Morgans 1956).

Figure 27 illustrates mean SK q ϕ's over the sampling period for stations A to F, and with the two depth fractions separate. From this it can be deduced that in almost all cases the smaller particles are better sorted than the larger particles (they have a negative value), with the notable exception of the b fraction at station F, where the smaller particles are badly sorted (again as a result of inclusion of the under-layer).

In the substrate samples from the Breede River Estuary, the silt and clay content (that is particles of diameter less than 0,0625 mm) was very low (generally less than 3%), so that this fraction is not represented within the third quartile. This fraction is however of great importance due to the high levels of organic matter, and hence bacterial activity of this fraction. Nichols (1972) found by rank correlation techniques when studying the relation between benthic polychaetes and the sediment, that the clay content was 'highly correlated with station similarity', while mean grain sizes and some other parameters were less important. Data for Breede River are represented in figure 28 which shows the mean silt and mud content over the sampling period for the stations A to F, and for the two fractions a and b separately. Here again the percentage silt and clay is consistently highest in the b fraction, while the highest

Figure 29 Silt and Mud Content ; Station F

0 - 25 cm depth

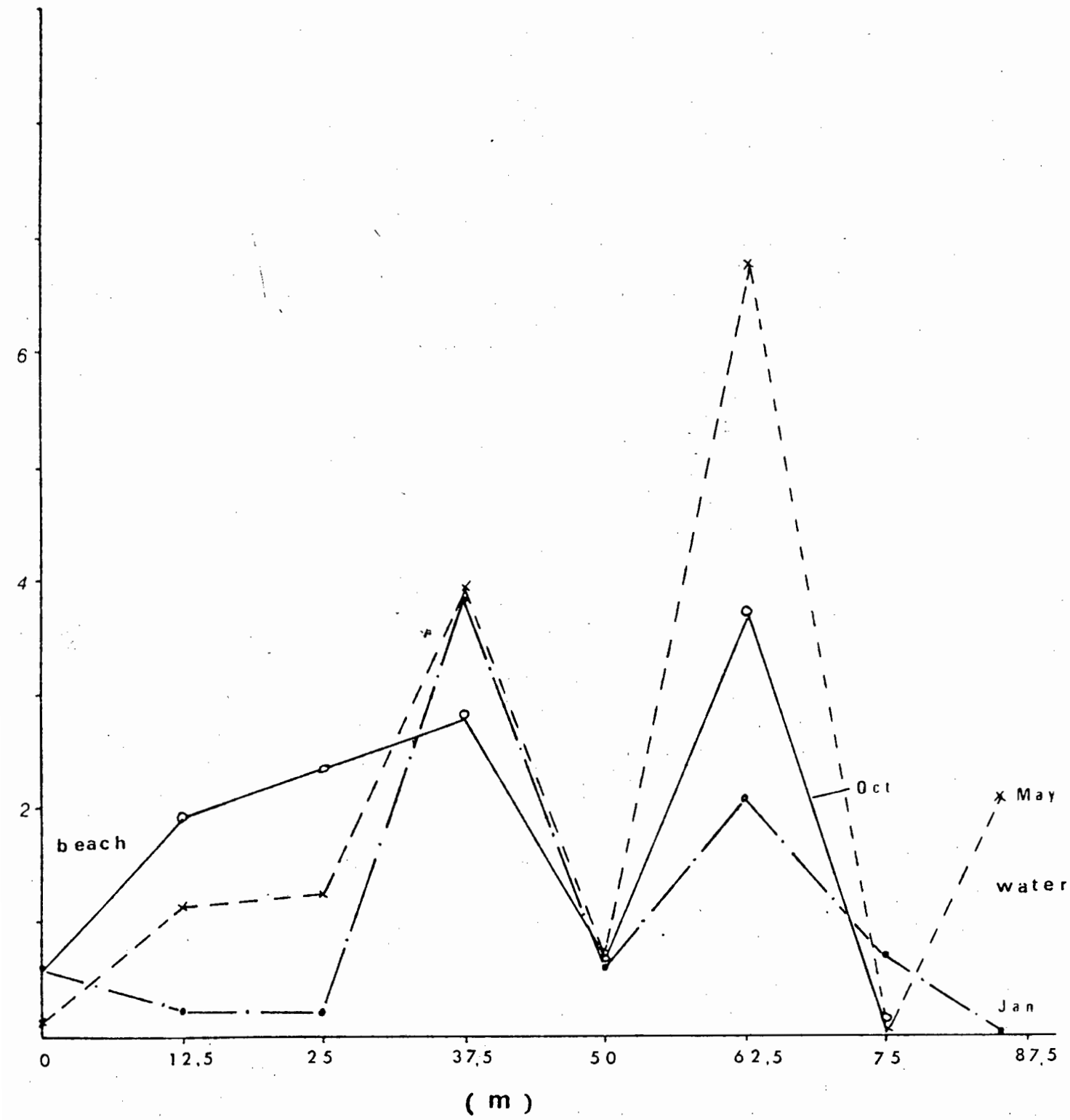
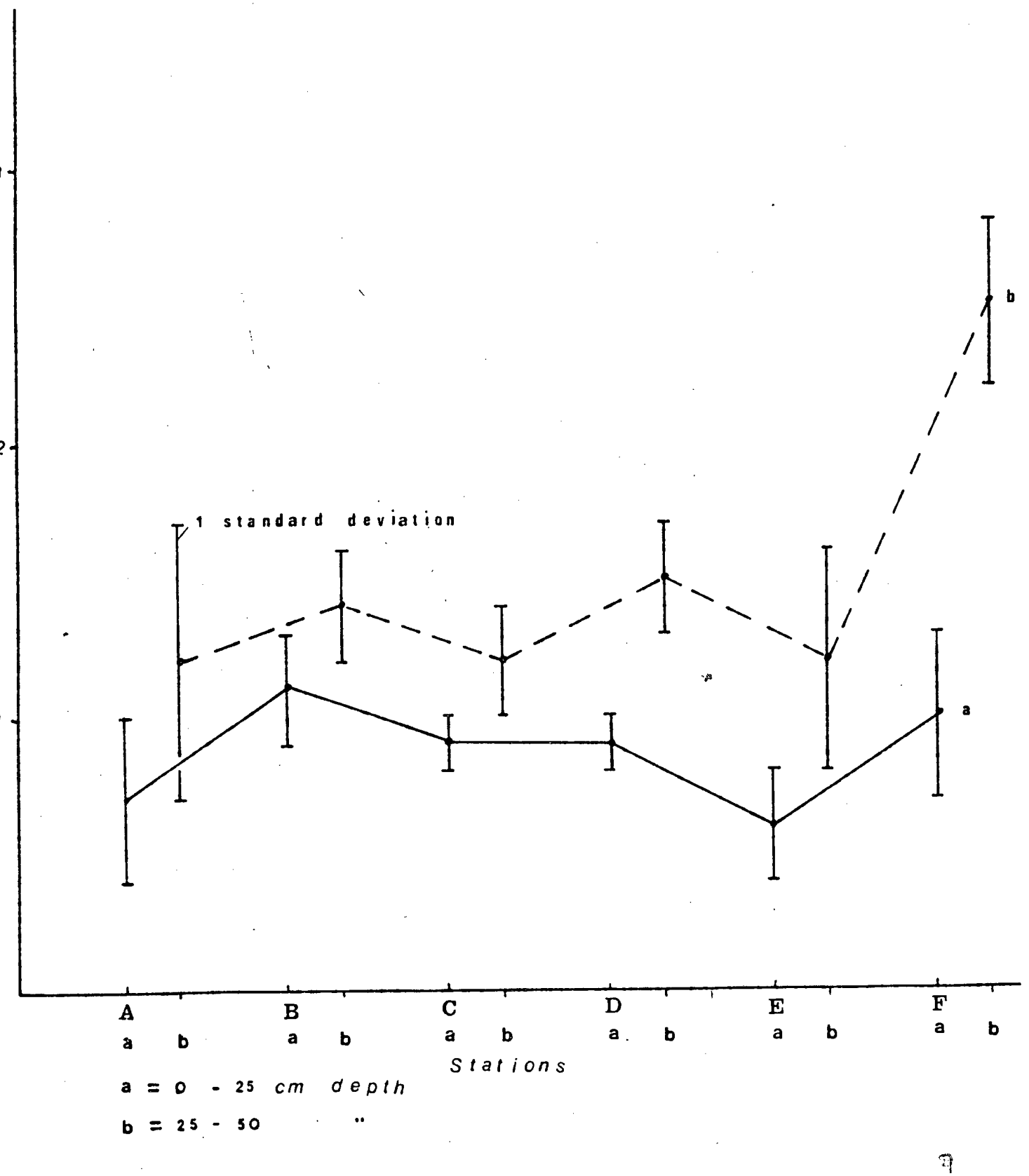


FIGURE 30 Mean Organic Carbon ; *Stations A to F*



percentages in the a fraction (0 - 25 cm) is found at station F.

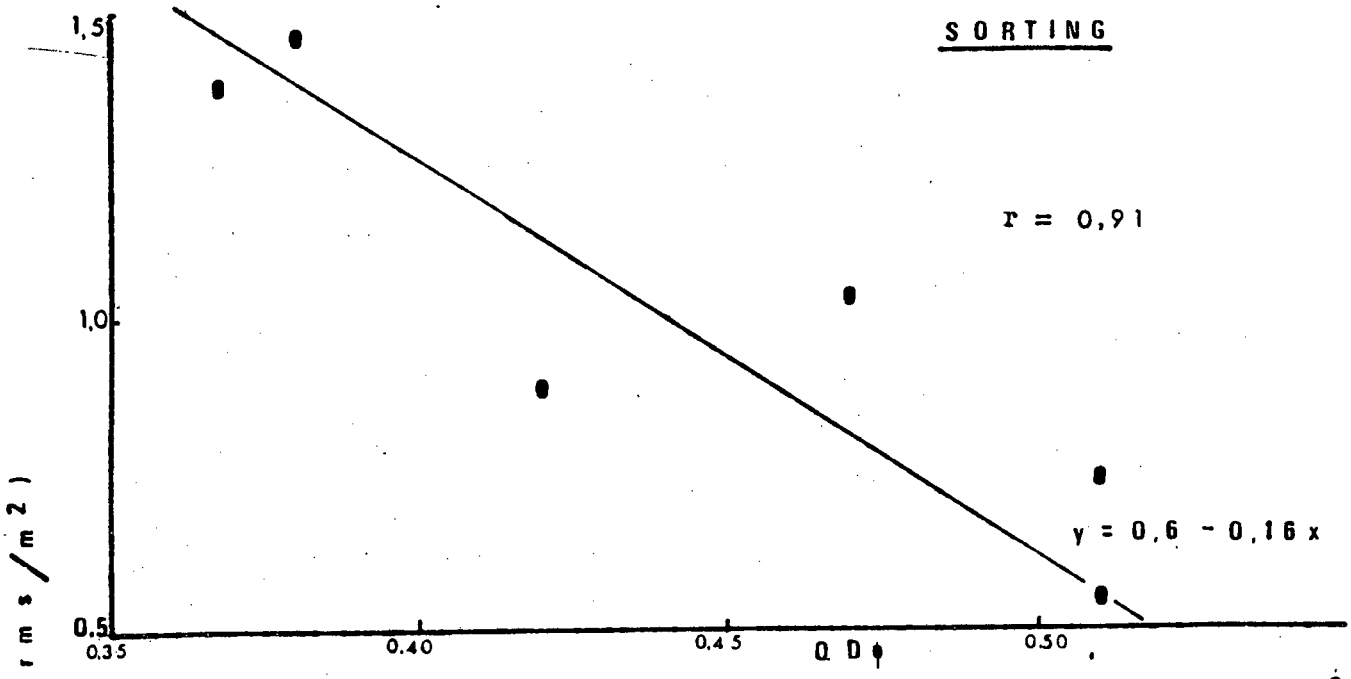
The origin of the silt and clay fraction in the superficial layers is significant, and in figure 29 detailed results for the transect through station F for the three sampling times are given. There is no evidence of large scale silt deposition by winter floods (at least during the period of sampling), in fact in several cases higher percentages occurred in May before winter floods. This probably resulted from early winter erosion of the marine sediments, so that the a fraction included more of the underlying clay. Conversely the low silt and clay content in most of the samples in January probably resulted from a larger proportion of sediment of marine origin in the sample at this time. The constant figure at 50 m is interesting. The sampling point occurred in a drainage channel off the bank, and was not subject to significant deposition or erosion.

II Organic Carbon

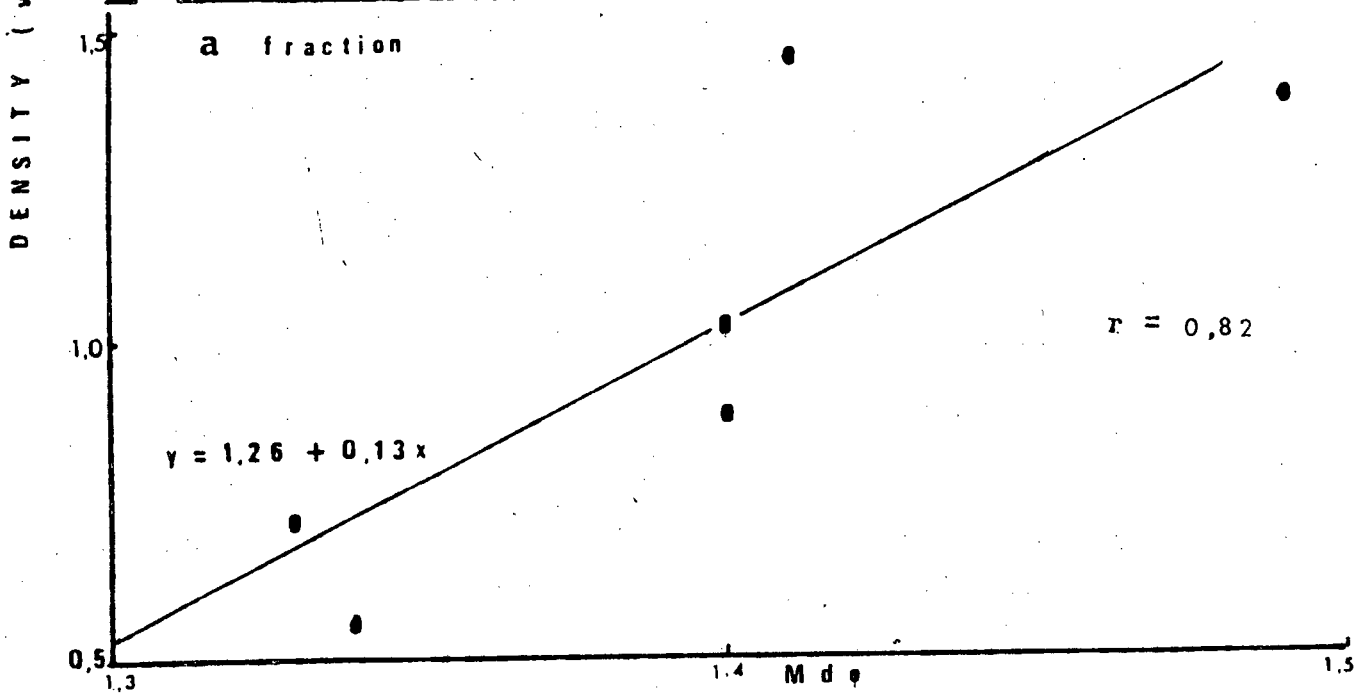
Mean percentages of organic carbon at station A to F and for the two depth fraction a and b are given in figure 30. As mentioned previously these figures are so low as to be discardable (Morgans 1956). Results are, however, well correlated with silt and clay content at station A to F. This is to be expected because 'clay particles tend to bind organic matter in greater quantities, owing to their high surface-to-volume ratio' (Sanders 1956 and 1958 in Nichols 1972). Again the values for the b fraction are higher than for the a fraction throughout.

Stach (1944 b) stated that the principle factor determining distribution of A. l. sudaustraliense was the large proportion of organic debris in the sand. In contrast even the highest organic carbon measurements from Breede River were too low to support an animal the size of Arenicola. Small differences between stations also indicate that organic content of the substrate was not a limiting factor in distribution but was associated with other environmental features which determined density.

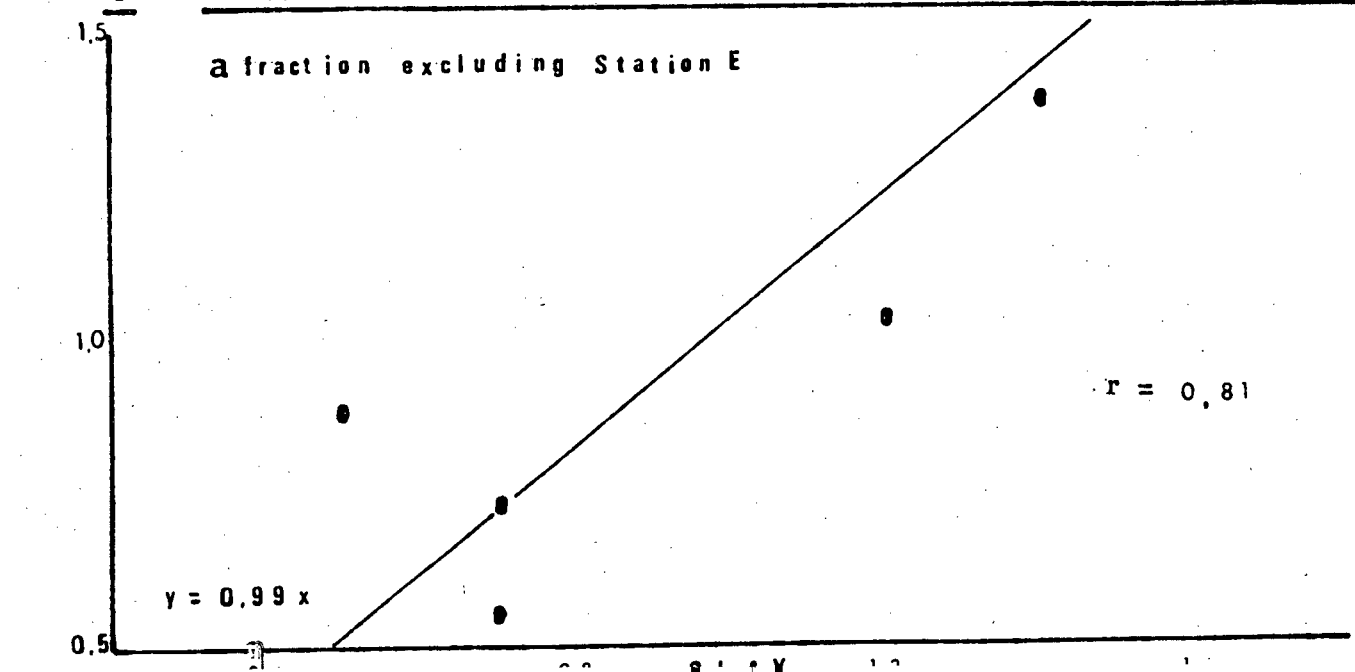
FIGURE 31 A CORRELATION between DENSITY and SORTING



B CORRELATION between DENSITY and MEAN PARTICLE SIZE



C CORRELATION between DENSITY and SILT and CLAY CONTENT



DENSITY (worms/m2)

Substrate analysis of the sediments inhabited by A. loveni in the Breede River Estuary can be summarised as follows. The substrate was shown to be fairly well sorted 'medium sand', but with a tendency to become better sorted, finer and have a higher silt and clay (and hence organic) content towards the southern bank, and especially at station F. This is related to reduced turbulence away from the main river channel.

The density of Arenicola is similarly graded, indicating a correlation with substrate features of the sustained density of worms. This is substantiated by plotting densities against substrate parameters. Figures 31A, 31B and 31C show the relationship between sorting (QDϕ), median particle diameter (Mdϕ) and silt and clay content with density. Although based on comparatively crude mean values correlation is good as shown by the correlation coefficients in the following table.

Table 12. Correlation coefficients of various substrate parameters with density, for January 1976.

Parameter	Correlation coefficient	
Sorting (QDϕ)	r = 0,91	P <0,05
Median particle diameter (Mdϕ) whole sample	r = 0,58	P >0,10
Median particle diameter 0 - 25 cm fraction	r = 0,82	P <0,05
% Clay and silt, 0 - 25 cm fraction	r = 0,65	P >0,10
% Clay and silt, 0 - 25 cm (excluding station E)	r = 0,81	P >0,05, <0,10
% Organic carbon, whole sample	r = 0,50	P >0,10
% Organic carbon (whole sample, excluding station E)	r = 0,82	P >0,05, <0,10

Significant correlation is shown between Density and sorting, density and median particle diameter of the a fraction at the 0,05 level and density and percentage clay and silt (excluding station E, where flood damage during winter could have caused the anomalous reading), at the 0,10 but not 0,05 level. There is also significant

correlation between Density and percentage organic carbon (excluding station E) but also only at the 0,10 level.

The full range of substrates is however successfully colonised, so that these characteristics in themselves are not narrowly limiting, but they do appear to determine the carrying capacity of the substrate and indicate optimal substrate conditions for A. loveni. A mechanism for this control can be derived from feeding specialisations discussed in Chapter 1. It was suggested that organic matter was actively concentrated by the worm, and used as a culture medium for micro-organisms which supplied the actual nutritional requirements. Substrate characteristics (such as grain size, sorting and natural organic deposit) could determine the productivity of such cultures and hence the suitability of the substrate for Arenicola.

Longbottom (1968 in Newell 1970) found good correlation between the biomass of A. marina and the organic content of the deposit. This could however also have been associated with other substrate features, rather than being in itself determinate. Other factors such as substrate depth must however also be important, and Chapman and Newell (1949) found that the main factor influencing distribution of A. marina at Whitstable was the depth of muddy sand overlying a hard clay stratum.

Station F as mentioned previously, functions as a nursery in the Breede River population. Substrate parameters here tend to reach optimal values, although the substrate depth is determined by the hard clay underneath. This is an ideal substrate for juvenile development, and it follows that the same tidal flow patterns which determine the sedimentary characteristics of the southern bank, deposit fertilised ova on this most suitable substrate. Substrate analyses thus show a very fine balance between Arenicola and the sediments it inhabits.

CHAPTER 6: CONSERVATION, EXPLOITATION AND MANAGEMENT

The two main considerations in the conservation of Arenicola loveni in Cape Estuaries, where 'conservation' is defined as 'the wise utilisation of', are (a) Protection of the resource as part of the ecological integrity of the estuarine system in which it occurs, and (b) Managing the resource due to its socio-economic importance to allow maximal, non-detrimental exploitation.

The more important findings of this study, and their management implications are discussed below:

1) Arenicola and the ecology of the estuary.

The assessment of the role of Arenicola loveni in the ecology of the estuarine system, rests on a variety of considerations. At first glance Arenicola would appear to be too sparse and deeply burrowing to be of importance even to predators, but the opposite is indicated. The fact that A. loveni is able to meet its nutritional requirements in substrates which are sometimes very poor, implies behavioural specialisations whereby the nutritional status of the substrate is actually increased rather than diminished by being colonised by these worms. The possible mechanisms of this process are discussed in earlier sections. The ventilation currents operated by Arenicola in themselves, must be beneficial. Although these currents are individually not very substantial (up to 200 mℓ per hour for worms of 10 to 15 g dried mass, according to Kruger 1964 for A. marina) they could result in around half a litre of oxygenated water per square meter of substrate, being forced through the substrate from an average depth of 50 cm in denser A. loveni areas, with resulting benefit to various strata of fauna, and especially bacterial activity in natural organic deposit.

Due to their specialised feeding Arenicola could have a marked

effect on the substrate itself. In almost all A. loveni burrows examined, a pocket of well washed coarse shell and grit particles occurred at the base of the head shaft. These are also described for A. marina (Wells 1945, Kruger 1971) and form the 'Hydrobia' layer of Van Straaten (1952 in Cadee 1976). The reworking of the substrate can also be considerable. Cadee (1976) estimated an annual sediment reworking by A. marina of 33 cm in one locality. Much of this is surface sand which is being recycled, but because of particle-size selectivity this can result in changes in the basic structure of the sediment and also the formation of coarse, organically rich buried layers.

Because of the depth of the burrow A. loveni would appear to be protected from external predators. Mehl's (1972) data from Heuningnes Estuary however show that up to 50% of the stomachs of Lithognathus included bloodworm at certain times of the year. These were presumably mainly young worms occurring shallowly in the substrate. In the relaxed state, or when defaecating, the tail lies at the surface, and Stach (1944 b) states that 'the oyster-catcher (Haematopus fulignosus) was often observed to peck off the tails of lugworm extruding their castings' which illustrates the 'usefulness of a long proliferating tail'. (Wells 1962). Steenbras are also known to bite off the tip of the tail of adult worms after 'blowing away the sand'. (Branch 1977). If migration by swimming occurs in A. loveni this must also be a time of heavy predation. In most estuaries however man is probably by far the greatest predator.

2) Competition with other burrowing species.

A bit shortfall in our understanding of the ecology of the estuarine bait species, is the lack of knowledge of the interaction of species in an estuary. Forbes (1973) discusses the mutual exclusion of Callianassa kraussi and Upogebia africana and states: 'the continual burrowing activities of C. kraussi would interfere with the more sedentary habits of U. africana'. He quotes Hill (1968) who showed that the latter was an 'energetic defender of its burrow'. In this

context A. loveni can be equated with Upogebia in being of a sedentary nature, but lacking the defence mechanisms of the latter. Although this was not specifically investigated, there was much evidence in this study that A. loveni seldom is found with large densities of Callianassa, and that in fact the latter might exclude or even displace Arenicola. This could however be related to substrate features. At Langebaan, where A. loveni did occur with large densities of Callianassa, the substrate was silty and organically rich, and Callianassa would probably not have to burrow extensively to meet nutritional requirements. In Uilenkraals River a badly designed road bridge resulted in extensive sandbank formation followed by a 'population explosion' of C. kraussi. Within three years A. loveni had disappeared although the substrate was apparently suitable but organically poor. The degree of disturbance by Callianassa, which might in turn depend on the nutrient status and structure of the sediment might be a deciding factor. It is also possible that if Arenicola created locally enriched substrate this would attract Calianassa, and the former would suffer harassment and even starvation.

The mechanisms of maintaining a balance under natural conditions are not clearly understood, but the effects of human interference can clearly be drastic, and habitat disruption could have far more detrimental and far reaching effects than direct physical exploitation.

3) Behavioural features which protect the worm.

One of the features which protects A. loveni from over exploitation is the depth to which it burrows in the substrate. The only legal method of obtaining bloodworm (other than by digging by hand) is the use of the prawn-pump. This is not highly efficient and can do a certain amount of unspecified damage. Large worms in some localities however burrow deeper than the reach of the pump. An example of this is the clean beach sand at Leisure Island, Knysna where after many years of exploitation, up to three casts per square meter can still be counted.

Another feature which protects the worm is the low proportion of head-shaft depressions to casts on the surface in most localities (although at Langebaan up to 8 worms shared a head-shaft (Branch 1977) and casts were rare). In the Breede River Estuary this proportion is as low as 9 : 100, so that in a given low tide only 10% of the population may be vulnerable, because pumping has to be done on the head-shaft for success. This combined with the low rate of success in pumping worms even on distinct head-shafts (sometimes also as low as 10%) means that when the effort in obtaining the present legal limit of 5 worms becomes too great for the average angler there might still be a population of reasonable size.

There is evidence from many estuaries that besides the above, a portion of the population is not vulnerable to human exploitation. These are worms occurring sublittorally. The importance of such population is as yet not clearly understood, but with present means of bait-taking, these populations are virtually unassailable. If all exposed stocks were destroyed therefore, they could at least act as a source of recruitment. In an estuary however, such populations may be particularly vulnerable to adverse conditions such as prolonged freshwater flooding or pollution.

4) Reproduction

One of the most important aspects of this study has been the identification of areas in the estuary which serve as the nursery for the population, where fertilised ova are deposited and develop, and from where the bulk of juvenile recruitment must come. These nursery areas are determined by the natural current flow patterns in the estuary. It is obvious what far reaching effects disturbance of the flow whether natural or by human agency could have on the population either resulting in deposition of fertilised ova on unsuitable substrate or carrying them out of the estuary. Even comparatively minor modifications in tidal flow patterns by, for example, bridge building in the sensitive tidal area of the river could thus be far more

detrimental to the bloodworm population than large scale direct exploitation.

Once larval development in nursery areas is completed juveniles of around a year old migrate to adult areas. Migration from the nursery area, if by swimming (as proposed for some other Arenicola species), must be a very vulnerable phase in the life-cycle and a time of very high predation.

On the credit side however is the high individual fecundity of bloodworm and the attainment of sexual maturity at a very small size. Under ideal conditions a relatively small number of worms thus have the potential of rapidly recolonising an area. In the Southern Cape, where temporary or prolonged closure of estuaries is common, this could be of importance to management, and where populations have become extinct due to temporarily unfavourable conditions, restocking whether natural or artificial, could be highly effective in re-establishing a population. Heuningnes River is an example of incipient natural recovery.

Artificial propagation although at present perhaps not justified might in the future be required to satisfy the bait demand and relieve exploitation pressure on natural stocks. Experimental work in this direction will continue.

5) Habitat and substrate

Although a large range of substrates can be successfully colonised by A. loveni and a naturally organically rich substrate is not a pre-requisite, density is broadly correlated with certain substrate parameters, and the carrying capacity of the substrate is determined by these. Optimal substrates are associated with habitats protected from excessive wave action and strong currents. The substrate allows the worm through behavioural specialisations to protect itself from temporarily unfavourable water conditions, the extent and duration of these must however also be limiting. For example, extended periods of exposure to harmfully hypo- or hyper-saline conditions when the

estuary is closed does have a drastic effect.

From their geographical distribution, one would assume that temperature was an important limiting factor in the distribution of Arenicola. A. loveni however appears capable of tolerating a wide range of temperatures. How this effects their distribution is uncertain unless it acts (following gamete maturation under hormonal influence) in triggering spawning.

EXPLOITATION

Exploitation at a sustainable level must be related to the natural density dependent mortality in a population. Ricker (1954) discusses the difficulty in defining mortality as density dependent, as it embraces two concepts; mortality which becomes more effective as density increases and that which becomes less so. It is however the former which controls the population size, and according to Nicholson (1933 in Ricker 1954) this mechanism of control must always involve competition in its broadest sense (that is, it includes all mortality factors whose effectivity increases with stock density). It is difficult in the case of Arenicola to visualise how competition in any form controls the sustained natural density, if feeding does not consist of physically seeing out and feeding on a limited food supply, and natural predation appears very limited. There is also little evidence of territoriality and at Langebaan several worms can operate one head-shaft. Only a certain level of disturbance might however be tolerable. In heavily exploited populations, human predation would probably be the major density dependent mortality factor.

No evidence was found in the Breede River Estuary that there was a sudden reduction in density following the peak exploitation period around December, the present exploitation level is too low to be having an effect. Klawe and Dickie (1957) concluded for the Glycera dibranchiata bait fishery that 'there was little risk of the fishery endangering the survival of an adequate spawning population'. In this fishery 50% of the stock was removed annually, but in this species worms only spawn once and then die. They also concluded that spawning sublittoral worms helped to maintain intertidal stocks.

Some idea of the Arenicola stock in the Breede River Estuary can be gained from density estimates. The island alone is some 125 000 m^2 in extent with average density estimated at 0,75 worms/m^2. This gives a standing crop of almost 100 000 worms on the island (large adult stocks on the southern bank and off-shore sand bars must at least double this figure). If even 20% were removed annually the

island alone would provide some 4 000 daily bait quotas annually (at the present bait limit of 5 worms per day). At present therefore, there appears to be no danger of overexploitation in the Breede River. The main flow in this argument is that an unknown number of worms are injured or killed in the process of taking bait, and bait collectors tend to discard fragmented worms. These aspects will have to receive attention.

MANAGEMENT

Few aspects of Arenicolan ecology lend themselves to management. It is, however, apparent that direct human exploitation for bait is a far lesser threat than more indirect results of human activity, such as changes in flow patterns as a result of bridge building, head-water abstraction which could result in prolonged closure of estuaries, pollution and so on. It is in fact doubtful that human exploitation could cause total extinction even of a small local population. Bloodworm, through its way of life, has inherent protection and when bait-taking becomes unrewarding, there could still be a strongly viable population. The problem is thus rather one of bait availability than extinction of populations by exploitation.

The bag limit of five worms per day serves to prevent wastage and should be maintained and strictly enforced. The policy of the Sea Fisheries Branch (of the Department of Industries) is to make bait commercially available. Bait taking is however to many an integral part of estuarine fishing enjoyment, and the effort involved acts in limiting exploitation. Bait in an estuary is a limited public resource managed by the Department and no commercial exploitation should be permitted.

Forbes (1973) recommended a rotating closed area system in the conservation of Callianassa, to ensure that there is always an undisturbed section of the breeding stock. In Arenicola maturity is achieved early and individuals are highly fecund. Juveniles develop outside the main adult stocks so that closed areas would appear to serve little purpose other than resulting in temporary increase in availability. If nursery areas are being excessively disturbed there might be a case for closing them, although at present there is little interest in worms of this size.

Surface signs (in most localities) provide a means of assessing the extent of a bloodworm population. Their absolute correlation with numerical density has yet to be determined and is likely to vary

between tides and localities. However if interpreted within these limitations, surface signs can be of great value in managing Arenicola stocks in individual estuaries, and of particular value in locating nursery areas and assessing potential recruitment.

The long time required for worms to reach a good size (4 + years) and divergent growth rates would appear to be a management disadvantage. Under artificial conditions however (particularly from D'Asaro's (1976) work) this could be accelerated. There also appears to be scope for artificially propagating A. loveni, although at present the extent of natural existing bait stocks would probably not justify this. Arenicola is however a much sought-after bait, and demand is likely to increase annually so that in the future, farming Arenicola as is now proposed in the U.S.A. could also here become a profitable undertaking. This would also serve a conservation function in relieving pressure on natural stocks.

CONSERVATION RECOMMENDATIONS.

The following are recommended:

(a) That human interference with normal estuarine flow patterns be recognised as a far greater threat to survival of bloodworm in estuaries than direct exploitation, and the Department remain informed of such developments.

(b) That 'nursery areas' ~~as~~ in estuaries be located and closed to bait-taking if they are restricted or vulnerable. (Juvenile worms are not at present taken, but large scale interference could be detrimental).

(c) That the bag limit of 5 worms per day be retained to prevent wastage of bait.

(d) That prawn-pumps (and hand digging) remain the only permitted form of exploitation, and the former be restricted to their present size.

(e) That the total effect of prawn-pump taking of bait be investigated.

(f) That estuaries requiring individual conservation action be managed individually.

(g) That no commercial taking of bait in any form be allowed in any estuary, but that if in the future controlled bait taking is regarded as essential, this be done by the Department.

(h) That artificial propagation with a view to filling bait requirements be reviewed in the future, and private enterprise in this connection be encouraged.

ACKNOWLEDGEMENTS

I would like to thank the following for making this study possible, helping in analyses of samples and preparation of the manuscript:

(1) The Department of Nature and Environmental Conservation, by whom I am employed, and who allowed me to submit this work study for an M.Sc. degree.

(2) Dr Fairall, then Assistant Director (Research) for encouragement and many stimulating discussions.

(3) My promotors Prof. Brown and Dr Branch for their interest and assistance.

(4) Dr Field for critically reading the manuscript.

(5) The various technical assistants at Jonkershoek Nature Conservation Station who helped at various times and during various phases of the research.

(6) The librarians at Jonkershoek and Cape Town for their efforts in tracing my literature requests.

(7) Everyone involved in the preparation of the manuscript.

REFERENCES

Borradaile, L.A. et al. 1958. The Invertebrata. University Press, Cambridge.

Branch, G. 1977. Pers. comm.

Cadee, G.C. 1976. Sediment reworking by Arenicola marina on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 10(4):440-460.

Carver, R.E. 1971. Procedures in Sedimentary Petrography. J. Wiley and Sons, N.Y., Lond.

Cassie, R.M. 1950. The analysis of Polymodal Frequency Distributions by the Probality Paper Method. N.Z. Sci. Rev. 8:89-91.

Cassie, R.M. 1954. Some uses of Probality Paper in the Analysis of Size Frequency Distributions. Aust. J. Mar. Freshw. Rev. 3: 513-22.

Cassie, R.M. 1963. Test of Significance for Probality Paper analysis. N.Z. J. Sci 6: 474-482.

Chapman, G. and Newell, G.E. 1949. The distribution of Lugworms (Arenicola marina L.) over the Flats at Whitstable J. mar. biol. Ass. U.K. 28: 1949, 627-634.

Clark, R.B. 1969. Endocrine influences in Annelids. Gen. camp. Endocr. Suppl. 2: 572-581.

Clark, R.B. and Olive, P.J.W. 1973. Recent advances in Polychaete endocrinology and Reproductive biology. Oceanogr. Mar. Biol. Ann. Rev. 11: 175-222.

Creaser, E.P. 1973. Reproduction of the bloodworm (Glycera dibranchiata) in the Sheepscot Estuary, Maine. J. Fish. Res. Bd. Can. 30: 161-166.

D'Asaro, C.N. 1973. Cultured Lugworms - A new source of bait for Marine sport fishermen. Amer. Fish Farmer Sept. 1973: 4-7.

D'Asaro, C.N. 1976. Lugworm Aquaculture. Florida Sea Grant Program. Rep. 16.

Day, J.H. 1955. The Polychaeta of South Africa. Part 3. Sedentary species of Cape Shores and estuaries. Linn. Soc. (Zool.) 42: 407.

Day, J.H. and J.F.C. Morgans, 1956. The ecology of South African Estuaries VII. The ecology of Durban Bay. Ann. Natal Mus. 13(3).

Day, J.H. 1959. The biology of Langebaan Lagoon. Trans. roy. Soc. S. Afr. 35: 475-547.

Day, J.H. 1976. Pers. comm.

Dales, R.P. 1958. Survival of anaerobic periods by two intertidal Polychaetes Arenicola marina (L) and Owenia fusiformis Della Chiaje. J. Mar. biol. Ass. U.K. 37: 521-529.

Duncan, A. 1953. Spawning of Arenicola marina (L). Brit. J. Anim. behav. 1: 85-86.

Duncan, A. 1959. Local races in Lugworms (Arenicola marina (L)). Nature 184 (4679): 71-72.

Duncan, A. 1960. The spawning of Arenicola marina (L) in the British Isles. Proc. Zool. Soc. London 134 (1): 137-156.

Eve, C. and A.J. Southway. 1958. The breeding of Arenicola ecaudata Johnston and A. branchialis Edw at Plymouth. J. mar. biol. Ass. U.K. 37: 267-287.

Forbes, A.T. 1973. A study of the burrowing sandprawn Callianassa krausii Stebbing Ph. D. Thesis, Rhodes University.

Greenway, J.P.C. 1969. Population surveys of Toheroa (Mollusca: Eulamellibranchiata) of Northland beaches. 1962 - 1967. N. Z. J. mar. Freshwat. Res. 3: 318-38.

Greenway, J.P.C. 1975. The effect of a limited open season for Toheroa on Dargaville Beach 1974. N.Z. Min. Agric. and Fish. Fish. Tech. Rep. 139: 1-6.

Harding, J.P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. mar. biol. Ass. U.K. 28: 141-153.

Healy, E.A. and G.P. Wells. 1959. Three new lugworms (Arenicolidae, Polychaeta) from the North Pacific area. Proc. Zool. Soc. London 133 (2): 315-335.

Holme, N.A. 1949. The fauna of sand and mud banks near the mouth of the Exe Estuary. J. mar. biol. Ass. U.K. 28: 139-235.

Howie, D.I.D. 1959. The spawning of Arenicola marina (L). I. The breeding season. J. mar. biol. Ass. U.K. 38: 395-406.

Howie, D.I.D. 1961. Spawning mechanisms in the male lugworm. Nature 192 (4807): 1100-1101.

Howie, D.I.D. 1961 a. The spawning of Arenicola marina (L). II. Spawning under experimental conditions. J. mar. biol. Ass. U.K. 41: 127-144.

Howie, D.I.D. 1961 b. The spawning of Arenicola marin. III. Maturation and shedding of ova. J. mar. bio. U.K. 41: 771-783.

Howie, D.I.D. and C.M. McClenaghan 1965. Evidence of a feed mechanism influencing spermatogonial division in the lugworms. Gen. Comp. Endocrin. 5(1): 40-44.

Hughes, R.N. 1970. Population dynamics of the bivalve Scrobularia plana (Da Costa) on an intertidal mud-flat in North Wales. J. Anim. Ecol. 39: 333-356.

Hylleberg, J. 1975. Selective feeding by Abarenicola pacifica, with notes on Abarenicola vagabunda and a concept of gardeni in lugworms. Ophelia 14 (1-2): 113-137.

Jacobsen, V.H. 1967. The feeding of the lugworm Arenicola marina (L.), Quantative studies. Ophelia 4, 91-109.

Klawe, W.L. and L.M. Dickie. 1957. Biology of the bloodworm Glycera dibranchiata. J. Fish. Res. Bd. Canada 115: 1-37.

Kruger, F. 1964. Messungen der Pumptätigkeit von Arenicola marina l. in watt. Helgolander Wiss. Meeresunters. 11: 70 - 91.

Kruger, F. 1971. Bau und Leben des Wattwormes Arenicola marina. Helgolander Wiss. Meeresunters. 22(2): 149-220.

Krumbein, W.C. and F.J. Pettijohn. 1938. Manual of Sedimentary Petrography. New York and Lond.

Levington, J. 1972. Stability and trophic structure in depositfeeding and suspension-feeding communities. Amer. Nat. 106 (950): 472-486.

Longbottom, M.R. 1970. Distribution of Arenicola marina with particular reference to the effects of particle size and organic matter of the sediments. J. mar. biol. Ecol. 5(2): 138-157.

Mehl, J. 1972. Unpublished data for Ph. D. Thesis for Univ. of Stellenbosch.

Moore, H.B. 1958. Marine Ecology. Wiley & Sons, New York. 493 pp.

Morgans, J.F.C. 1956. Notes on the analysis of shallow-water soft substrata. J. Anim. Ecol. 25: 367-387.

Newell, G.E. 1948. A contribution to our knowledge of the life history of Arenicola marina L. J. mar. biol. Ass. U.K. 27: 554-80.

Newell, G.E. 1949. The later larval life of Arenicola marina L. J. mar. biol. Ass. U.K. 28: 635-639.

Newell, R.C. 1970. Biology of intertidal animals. Logos Press Ltd. London.

Nichols, F.H. 1972. Benthic polychaete assemblages, and their relationship to the sediment in Port Madison, Washington in Readings in Aquatic Ecology, Ford & Hazen (Saunders).

Okada, K. 1941. Gametogenesis, breeding habits and early development of Arenicola cristata Stimpson, a tubiculous polychaete. Sci. Rep. Tohoku Univ. 16: 99-145.

Patel, S. and C.P. Spencer. 1963. Studies on the haemoglobin of Arenicola marina. Comp. Biochem. Physiol. 8(2): 65-82.

Perkins, E.J. 1974. The biology of estuaries and coastal waters. Acad. Press. London. 678 pp.

Ricker, W.E. 1954. Stock and Recruitment. J. Fish. Res. Bd. Canada 11(5): 559-623.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Dept. Env. Fish. Mar. Ser. Ottawa. Bul. 191.

Seymour, M.K. 1971. Burrowing behaviour in the European lugworm Arenicola marina L. J. Zool. (London) 164(1): 93-132.

Seymour, M.K. 1972. Swimming in Arenicola marina L. Comp. Biochem. Physiol. 41(2): 285-288.

Shumway, S.E. and J. Davenport. 1977. Some aspects of the physiology of Arenicola marina (Polychaeta) exposed to fluctuating salinities. J. mar. biol. Ass. U.K. 57: 907-924.

Stach, L.W. 1944 a. Arenicola from South-Eastern Australia. Rec. Austr. Mus. 21: 272-277.

Stach, L.W. 1944 b. Ecology of the sand flats of Moreton Bay. Trans. Roy Soc. S. Austr. 68(2): 177-181.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co. New York.

Trueman, E.R. 1966. Observations on the burrowing behaviour of Arenicola marina (1). J. expt. Biol. 44(1): 93-118.

Trueman, E.R. 1967. The mechanisms of burrowing in the polychaete worm Arenicola marina (1). Biol. Bull. 131(2): 369-377.

Welch, P.S. 1948. Limnological Methods. McGraw-Hill. New York.

Wells, G.P. 1945. The mode of life of Arenicola marina L. J. mar. biol. Ass. U.K. 26(2): 170-207.

Wells, G.P. 1949 a. Respiratory movements of Arenicola marina L. Intermittant irrigation of the tube and intermittant aerial respiration. J. mar. biol. Ass. U.K. 28: 447-464.

Wells, G.P. 1949 b. Behaviour of Arenicola marina L. in sand, and the role of spontaneous activity cycles. J. mar. biol. Ass. U.K. 28: 465-478.

Wells, G.P. 1953. Defecation in relation to the spontaneous activity cycles of Arenicola marina L. J. mar. biol. Ass. U.K. 32: 51-63.

Wells, G.P. 1958. The genera of Arenicolidae (Polychaeta). J. Zool. (London) 133 (2): 301-314.

Wells, G.P. 1962. The warm water lugworms of the World. J. Zool. (London) 128: 331-353.

Wells, G.P. 1963. The lugworms of the cold temperate zones. J. Zool. (London) 140(1): 121-159.

Wells, G.P. 1964. Temperature, taxonomic techniques and the zoogeography of lugworms (Arenicolidae, Polychaeta). Helgolander Wiss. Meeresunters. 10(14): 404-410.

Ziegelmeier, E. 1964. Uber die Wohnbau-Form von Arenicola marina L. Helgolander Wiss. Meeresunters. 7: 157-160.