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Ecology of the infauna of Spurn Bight mudflats : an area proposed for reclamation.

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by

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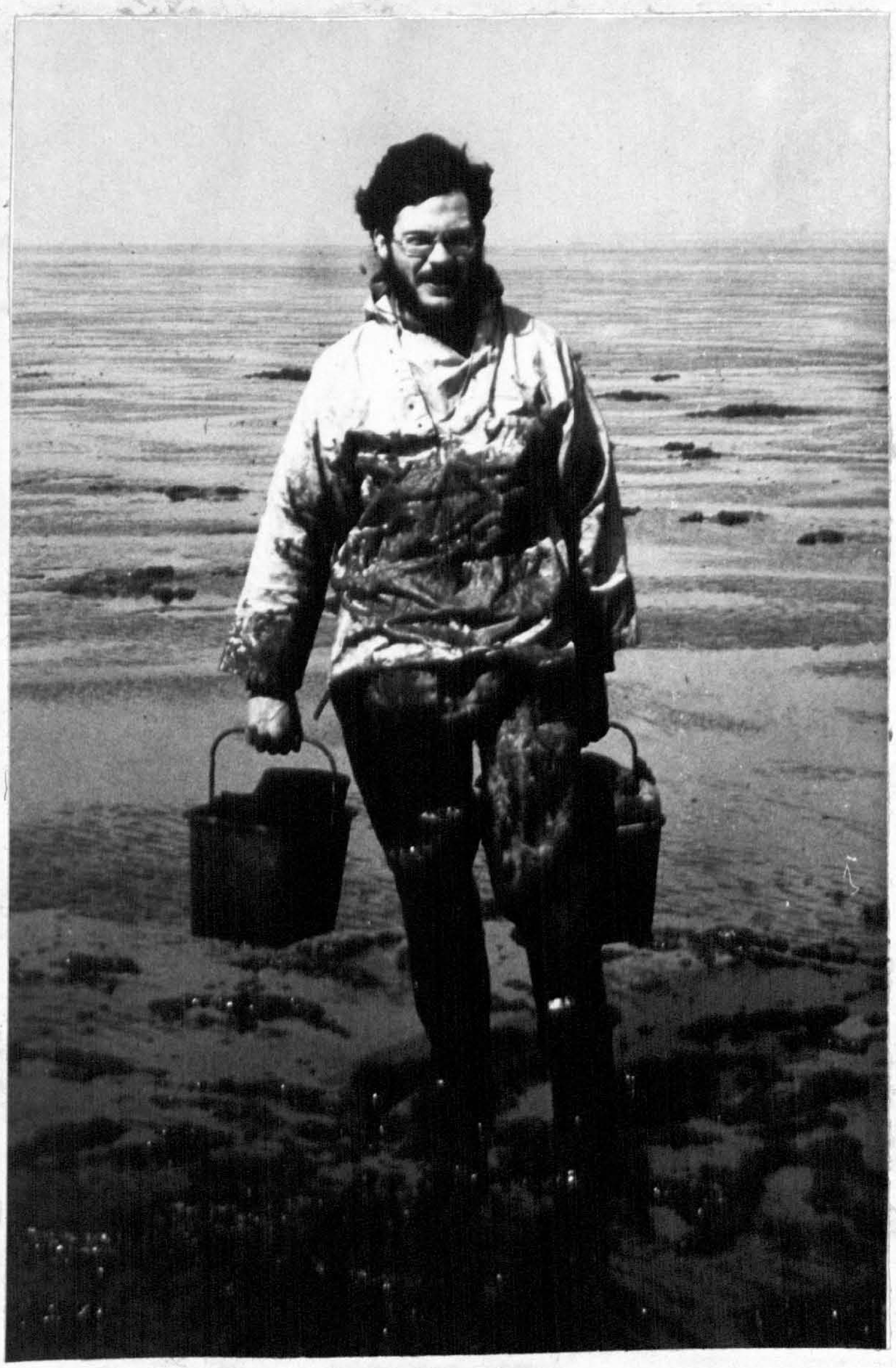

"The author looks back with nostalgic regret.".

(R.C. McLean 'Practical Field Ecology' 1946)

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ABSTRACT

The invertebrate infauna of Spurn Bight, an extensive area of mudflats in the outer Humber Estuary, internationally important for wildfowl and subject to land reclamation proposals, was studied in the form of a short term extensive survey of the wole area followed by a year long intensive study of the dynamics of the major species.

Two-way cluster analysis of species and sample stations revealed three subcommunities within a 'classic' boreal shallow mud '*Macoma*' community distributed in relation mainly to sediment type and position on the shore. Ordination showed these to be continuous rather than discrete but the clusters were used as convenient units for extrapolation of single species' dynamics determined from the longer term study.

Five major species:- *Nephtys hombergi*, *Hediste diversicolor*, *Cerastoderma edule*, *Macoma balthica* and *Retusa obtusa* were studied in detail and information on all other species was collated as an annotated list. For the major species, data on density, biomass, growth rate, mortality, production, elimination and productivity were analysed from the period March 1978 - March 1979. Mortality of certain species was found to be related to the very harsh winter and evidence was found of translocation of sediments and infauna within the Bight.

Certain species, notably *M. balthica*, *N. hombergi*, *R. obtusa* and *Eteone longa* were found to 'perform' exceptionally well in the Bight and the total community biomass was found to be exceptionally high for a temperate silt ecosystem.

The total invertebrate resource of the whole mudflat was estimated in conjunction with studies carried out on the avifauna over the same period and it is tentatively suggested that the mudflats may be able to support larger numbers of waders than at present. This is discussed in relation to the proposal for land reclamation and it is concluded that even partial schemes, designed to conserve part of the resource, would lead to the destruction of the most productive areas of mudflat in the middle and upper shore.

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CHAPTER ONE

CHAPTER 1

INTRODUCTION AND ORIGIN OF STUDY

Spurn Bight mudflats (lat 53°37' N, long 0°4' E), lie in the lee of Spurn Peninsula, a famous 5km long shingle spit topped with sand dunes derived from longshore drift of material eroded from the coast of Holderness. Proposals to derive 20,000+ acres of agricultural land from these flats date back to 1860 when J. Oldham, who had already been instrumental in the reclamation of extensive intertidal flats in the Humber at Sunk Island, suggested a sea wall from Hawkin's Point in the west to Spurn Point (ref. Fig 2i). High capital costs prevented his scheme from being implemented.

In 1969 the Central Unit for Environmental Planning produced a document:- "Humberside: a feasibility study" which included the proposal to infill the flats using colliery waste from the South Yorkshire Coalfield which then produced some 12 million tonnes of waste, mainly of carboniferous shales, per year. The Department of the Environment's Working Party on Solid Waste elaborated on the proposal in a document 'Solid Waste Disposal in Yorkshire & Humberside' (D. o. E. ; 1974). Infill would probably be by the construction of a 16km concrete or stone bund from Hawkin's Point to Spurn - later proposals suggested that consolidated waste might be considered as a cheaper option. The total project would have a capacity of 234 million cubic metres of waste and could take as long as 40 years to complete. Another similar proposal was to reclaim the Pyewipes area of Burcom Shoal, immediately west of Grimsby Docks (Fig 2i), on the South Bank of the estuary, where 440 ha of mudflats could form a repository for 20 million cubic metres of coal waste possibly including domestic rubbish from S. Humberside.

The South Yorkshire County Council produced an assesment of likely sites for waste disposal and methods of transport (Thomas; 1976) which identified Spurn Bight as one of several favourable areas for the disposal of colliery waste as well as pulverised fly ash from the South Yorkshire and Drax power stations. They suggested that transport might be by hydraulic or pneumatic pipeline at a cost of between £30 - 40 million.

In early considerations the reclaimed land was intended for agriculture but later proposals favoured capital intensive industrial development - refineries and petrochemicals - to provide a better return on the capital expenditure.

Ecological considerations were mentioned in the various proposal documents and an unpublished internal report of a Humberside County Council Planning Committee (18.10.74.) acknowledged that the unique ecological character of Spurn Bight and the peninsula would be unlikely to survive total reclamation, although a partial scheme may preserve some important elements.

In the late 1970's the Spurn Bight scheme was effectively shelved and the Humberside Structure Plan (1976) section on Industrial Development and the Humber Estuary stated that a Regional Working Party had investigated the possibilities and concluded that "there is now little prospect of tipping at Spurn Bight within the period of the Structure Plan". However in an internal report in 1979 the County Council stated that there was no firm policy over the scheme and it was not ruled out as an option for future development in view of the potential for growth in the Humber - "considering the importance of industry and employment, the County Council cannot be fully committed to the conservationists' view".

In 1981, Holderness Borough Council's Director of Development published "The reclamation of Spurn Bight - Threat or Opportunity" (Langton; 1981) outlining the history of development proposals and the current position, pointing out the potential advantages and pitfalls of the scheme.

Expressions of deep concern over, and objections to the Spurn Bight Scheme were received by Humberside County Council from numerous public and private bodies and individuals representing conservation, recreational, farming and local economic interests. The conservation case was detailed by Boatman (1974 & 1977) and a series of studies was initiated, mainly by the Department of Zoology at the University of Hull, to form an information baseline on the ecology of the Humber for any future impact assesment studies. The present study was set up jointly by the Natural Environment Research Council and the Department of Planning of Humberside County Council as a C.A.S.E. research studentship to investigate the ecology of the invertebrate resource of the area covered by the reclamation proposals.

Intertidal flats cover some 210,000 ha (500,000 acres) around the shoreline of the U.K. (Ranwell; 1979). The reclamation of 3077 ha in Spurn Bight might therefore seem relatively insignificant on a national scale (although no other extensive flats exist in Yorkshire). However, estuarine areas the length of the U.K. are either presently undergoing reclamation (The Tees Estuary - Evans et al.; 1979, Southampton Water - Glue; 1971), or have been subject to impact assesment studies over proposals either for freshwater impoundment (The Wash - Central Water Planning Unit; 1976, Morecombe Bay - Anderson; 1972, and the Dee Estuary - Buxton et al.; 1977), tidal power generation on the Severn (Shaw; 1975), or airport construction at Cublin/Foulness (Boorman & Ranwell; 1977). Other reclamation schemes are already under way on the eastern shores of the North Sea, especially in the Netherlands. The current economic climate is presently against the implementation of all the U.K. capital intensive schemes, including those in the Humber, but should any or all of these schemes come about in the future, considerable displacement of overwintering wildfowl can be expected. The ultimate distribution following displacement is impossible to predict but the very extensive resource offered by the Spurn mudflats may be of increasing importance to shorebirds in the future.

The shorebird capacity of an intertidal area is not easily determined and is governed by factors additional to the size of the food resource (Goss Custard & Charman; 1976), including roost site availability and inter- and intraspecific social interaction and aggression between birds, which were not taken into account in trophic equations put forward by Wolff et al. (1975).

Spurn Bight was already known to be of great importance to overwintering waders and wildfowl from the R.S.P.B./B.T.O./I.W.C. 'Birds of Estuaries Enquiry' (Prater; 1973 et seq.), and reports of the Humber Wildfowl Refuge (Chapman; 1971 et seq.). The study of Tasker & Milsom (1979) has shown four species of wader present in Spurn Bight in internationally significant numbers (at the 1% level), and a further six species of wader and duck in nationally significant numbers.

Recent studies on the invertebrates which form the food resource of the mudflats have been done by the Yorkshire River Authority (1971-73), and by Ratcliffe (1979), who found that certain species of invertebrates were exceptionally productive in Spurn Bight. The intention of the present work was threefold:- firstly, to form an inventory of those organisms inhabiting the flats from an extensive survey of the whole area so that future changes can be measured - this approach has been recommended by Ranwell (1979), but caution in interpreting such baseline studies in the absence of long term studies has been advised by Boesch et al. (1976) and Whitlach (1977). Second, the distribution of major invertebrate assemblages was to be identified, quantified and delimited so that estimates of species' dynamics, carried out as the third approach, could be extrapolated to give gross estimates of the total resource available in the various parts of the flats and to identify those parts of the flats which represent the most significant part of that resource and, therefore, most vulnerable to developments such as infilling.

Since the initiation of this project the major threat to the future of the flats has shifted away from human interference in the form of land reclamation to the likely effects of the imminent breach of Spurn Peninsula. Prior to 1960, the Ministry of Defence spent over £150,000 on sea defences along the seaward beach, including groynes and concrete and steel sea wall. Since 1973, the Yorkshire Naturalists' Trust, the present owners, have added coastal defences using old war-time blockhouses and concrete tank-traps. In 1982 the Trust used 700,000 tonnes of clay from the British Gas terminal at Easington to construct a flood bank against spring high tides but in February 1983, exceptionally high tides washed away much of the protective materials. The Trust has now conceded that without large-scale government assistance there is little the organisation can do to postpone an inevitable breach. This and previous studies may thus ultimately serve as a baseline to follow the effects of an entirely different phenomenon than the one for which it was originally intended.

CHAPTER TWO

CHAPTER 2

MATERIALS AND METHODS

2i The study area

2ia The Humber Estuary

Summaries of the geological history, current knowledge of the physical chemical and biological character of the estuary as a whole and the human uses of the Humber are given by Jones (1974) and the Natural Environment Research Council (1979) from which the following is summarised.*

The Humber, 62 km in length from the confluence of the Trent and Ouse to Spurn Point, drains approximately 20% of the land area of England - approx 26,000 km^2 (inset to Fig 2i), has a tidal volume of 1 - 1.7 x 10^9 m^3 and freshwater flow of 246 - 1550 cumecs depending on season. Water column suspended solid levels are exceptionally high - 0.2 - 3.0 grammes per litre, derived both from the freshwater discharge of its tributaries and from import of silts from the boulder clay cliffs of Holderness on the flood tide. The estuary is well mixed with little stratification in salinity.

Intertidal flats amount to some 93 km^2 around the whole estuary, of which 60% are made up of the extensive sand and mudflats of the outer reaches, downstream of Hawkin's Point on the North bank and Grimsby on the South.

Fisheries operating within the estuary are relatively unimportant, consisting mainly of long lining for cod, eel trapping and the collection of cockles from the outer southern sandflats. A shrimp fishery in the middle reaches has recently declined (Brennan; 1974 Rees; 1982a). Hull and Grimsby are declining fishing ports which were at one time operating large fleets of inshore and deep water trawlers. The estuary does not appear to be of particular importance for the breeding and nursery grounds of North Sea fish stocks (Riley; 1974). Angling is a popular and increasing recreational pursuit on the Humber, mainly for cod and flatfish.

The estuary is used as a major shipping channel for the Trent ports of Gunness, Keadby and Burton Stather, the Ouse port of Goole and the Humber ports of Hull, Saltend, Barton, Immingham and Grimsby. Considerable industry has built up on its banks, including heavy metal smelting at North Ferriby,

* Gameson (1982) is a similar, more recent work.

Titanium Dioxide manufacture at Killinghome and petrochemical and refinery industries at Saltend, between Immingham and Grimsby and on a smaller scale at Barton-upon-Humber. Industrial discharges amount to some 15 cumecs of flow, 80% derived from the tributary rivers which drain approximately 25% of Britain's industry. Major settlements along the estuary are Hull (population 267,000) on the North shore and Barton-upon-Humber (8,500), Immingham, North and South Killinghome (13,000), and Grimsby with Cleethorpes (160,000), on the South (Gill; 1983). Total domestic sewage flow amounts to 16.5 cumecs, 85% derived from the tributary rivers and the total human population of the drainage basin is almost 10 million, (Urquhart; 1979).

Investigations of the fauna along its length (Yorkshire and Lincolnshire River Authorities; 1971-1974,Rees et al.; 1982), indicate that the Humber is not grossly polluted and water quality studies have concentrated on dissolved oxygen (Urquhart;1979, Gameson; 1982), and heavy metals and hydrocarbons (Jones; 1979, Smith; 1982, Gardiner; 1982, Fernandez; 1983).

Recreational use of the Humber is relatively slight (Patmore; 1979), when compared to other U.K. estuaries.

Interest of conservationists in the Humber has mainly concentrated on its birdlife with many nationally important and, for some species, internationally important populations of waders and wildfowl (Cutts; 1979, Tasker & Milsom; 1979, Shepherd et al.; 1982). The conservation significance of the Humber is discussed by Boatman (1974).

The whole of the Humber flats and Marshes are designated as a Site of Special Scientific Interest, grade 1* in Ratcliffe (1977). Protected areas along the Humber are Blacktoft Sands Reserve (Royal Society for the Protection of Birds), The Humber Wildfowl Refuge (Wildfowling Association of Great Britain and Ireland), Barton Reedbeds and Donna Nook Reserves (Lincolnshire and South Humberside Trust for Nature Conservation), and Spurn Peninsula (Yorkshire Naturalists' Trust).

2ib <u>Spurn Bight Mudflats</u>

Spurn Bight (Figs 2i - 2iii), consist of ca. 30.8 km^2 of silt, sand and shingle flats overlying pleistocene boulder clay deposits in the lee of Spurn

Peninsula, which forms the northern outer limit of the estuary. The western limit of the flats is at Hawkin's Point at the southern end of the reclaimed Sunk Island Sands. The Bight is owned by the Crown and leased to the Associated British Ports for a 999 year period.

The history of the peninsula has been described by de Boer (1964) as having an approximately 250 year cycle with reconstruction of a new peninsula from longshore drift material following breaching of the previous peninsula at its base as a result of continual erosion along the Holderness coast. Remains of the most recent of the previous peninsulae - Ravenspurn, which was destroyed in 1608, are visible as a shingle bank, the Stony Binks, to the east of the present Spurn Head.

The existing peninsula was breached at the narrows in 1849 after which concern over the potential effects on the deep water channel of the estuary led to considerable protection measures including chalk bank defences and an extensive system of groynes, now partially derelict. As a result of that 1849 breach the Old Den was built up, comprising ca. 21 ha of shingle deposited in the lee of the peninsula through, the breach, (Plates 4 & 10). Sea defences have been added to constantly since then but the peninsula is again vulnerable to breaching during high tides with strong N.W. winds.

The sediments of Spurn Bight were investigated as part of a general survey of the Humber estuary by McQuillin et al. (1969) who produced a map indicating alternating sediment bands of sand and silt parallel to the shore. Drainage of the Bight is not indicated on the map and is only superficially represented on the Ordnance Survey coverage of the area.

After an initial foot survey in 1976 it became obvious that the above map was a considerable oversimplification and that it was necessary to know the position of major drainage creeks which posed barriers to access. Aerial photographs, taken by Huntings Surveys Ltd. of Borehamwood for Cambridge University were available at the York office of the Nature Conservancy Council. These, taken at low water on 23rd June 1976, showed all major drainage and surface features and these were traced to produce the drainage map in Fig 2ii and the outline used to produce all further maps of the Bight.

Although surface textures were visible from photographs, differentiation of sediment types was not obvious and further aerial photographs using infra-red film were taken on 3rd June 1977 by the University Air Squadron. Areas of fine sediment have been shown to be easily differentiated from sands by infra-red photography, owing to the higher levels of surface diatom cover with higher I.R. reflectivity (Steffensen & McGregor; 1976).

A series of oblique shots covering the whole Bight showed that areas known from the foot survey to be of sand or silt were divisible by colour on the infra-red film. Silty areas showed red-brown while hard sands appeared brown-green. Prints taken from the original colour I.R. transparancies are included as Plates 1 - 4, although rapid deterioration of the original transparancies following processing unfortunately has led to poor quality in the colour prints. The aerial photography also showed the extent of the region of Zostera noltii eelgrass along almost the full length of the peninsula. This was visible as a distinct red band 50 - 200 m from the shore.

Information on sediment distribution was transferred onto the map traced from aerial photographs to produce the sediment diagram in Fig 2iii.

Parallel but discontinuous sediment bands are apparent. Above an upper shore Spartina anglica marsh (Plate 5), was found a discontinuous narrow 'beach' of coarse sand, covered only at high water spring tides with an accumulation of much strandline débris. The Spartina marsh, resulting from several deliberate plantings, varies in width from a few metres to several hundred as at Welwick Saltmarsh and at Kilnsea (Plates 3 & 6).

Immediately downshore of the Spartina is usually found a 'band' of very silty, flat sediment, continuous from Hawkin's Point almost to the Old Den, gradually giving way to flat silty sand deposits. These become dendritically drained in the midshore region (Fig 2iii, Plate 7), and divided into a series of gullies varying in depth between 10 and 150 cm (Plate 8).

Drainage of the mudflats was found to be mainly towards the east, probably a result of the direction of the flood tide from around the head of the peninsula. Tides in this part of the estuary are almost exactly sinusoidal with a period of ebb and flow of 6¼ hours (Denman; 1974).

Freshwater flow onto the flats originates mainly from three sources. Winestead Drain, draining the parishes of Sunk Island and Patrington, flows into Patrington Channel, a 4 m wide dyke dredged by mechanical excavator close to the bank but rapidly becoming shallower further downshore. Water flow is very variable depending on rainfall and the activity of the Y.W.A. Patrington pumping station.

Skeffling Clough is a manually dredged channel taking water pumped by the Y.W.A. through the flood bank from the 6m wide land drain parallel to the bank along the middle section of the Bight between Welwick Marsh and Easington Clough. Skeffling Clough is protected by a groyne to the east and, beyond the end of the dredged section which is marked by a large post 500m from the shore, eventually flows out onto the mud surface to collect into the gulley system.

The only other significant freshwater flow is from Easington Clough, at the eastern end of the land drain, which flows through a pipe under the sea wall onto the mudflats and eventually drains into the North Channel.

Downshore sediments are of hard, ripple marked sand (Plate 9), widening towards the east and divided into segments by regions of gullied mud around major drainage channels. Sand bars are visible from the air along the west bank of North Channel and Trinity Runs and the surface of Trinity Sands is seen to have an unusual sand wave structure with numerous almost circular pools of standing water at low tide. It was not possible to approach these for closer examination.

The estuarine beach at Spurn Head is of fairly clean, coarse sand having a low amplitude ridge and runnel formation with sand waves obliquely angled to the shore reflecting the direction of flow of the Greedy Gut which is the drainage channel between the Old Den and the shore. West of the Old Den is an area of extremely fluid silt, possible suspended and redeposited with each tide.

The Old Den itself (Plate 10), is composed of shingle intermixed with sandy silt with cobbles up to 20cm. There is considerable macro-algal cover in places with small mussel beds and numerous small rock pools and drainage creeks. The fauna of the Den has been systematically investigated by Morgan (1969).

Total area in ha. of the different sediment types was deduced planimetrically from the sediment diagram in Fig 2iii. These are included in Table 2a together with the area of the remaining flats of the Humber estuary similarly determined from the Ordnance Survey 1:50,000 map.

Human use of the Bight itself is limited. Long lines for cod and flatfish are anchored to stakes far out on the flats and left for the duration of a single tidal cycle by a small number of individuals from the villages of Weeton, Easington and Kilnsea on a semi-commercial basis. Large numbers of anglers also use the Bight, fishing both from the peninsula and on the mudflats themselves (Forsberg; 1977). The mudflats are also the only local source of lugworm for bait and are dug at numerous locations in the Bight, especially from Kilnsea, Spurn narrows, Easington and Patrington Outstray, sometimes causing considerable disturbance to feeding wildfowl (Tasker & Milsom 1979).

The Bight is also popular with wildfowlers, mainly members of the Hull and East Riding, and Holderness and Humber Wildfowling Associations.

The estuarine beach at Spurn Head is also popular for recreation, mainly during the summer and particularly during times of easterly winds when the marine beach tends to be exposed. Patmore (1979), quoting figures supplied by Miss S. Glyptis found 148 people using the estuarine beach on an August afternoon in 1975, together with 466 on the seaward beach and 129 on the peninsula itself. Usher et al. (1974) documented the visitors' activities at Spurn Point Reserve and found that 38% of visitors engaged in some type of nature study, mainly birdwatching.

Other recreational activities around the Bight are mainly walking and horseriding along the flood banks mainly between Skeffling Clough and Kilnsea. The mudflats and saltmarshes are of particular interest to birdwatchers.

The educational and research potential of Spurn Bight is mainly used by the Institute of Estuarine and Coastal Studies and the Departments of Zoology, Plant Biology and Geography at the University of Hull and by the School of Science at Hull College of Higher Education. School use of the area is considerable but mainly restricted to studies on the peninsula itself.

Agricultural land around the Bight is mainly grade 2 with small areas of grades 1 and 3 and used for crops of cereals, oilseed rape, sugar beet, mangolds, potatoes and, occasionally, strawberries. A number of fields along the edge of the Bight, particularly between Weeton and Easington, are kept as pasture for dairy herds and riding ponies. The economy of eastern Holderness is almost exclusively agricultural, the main settlement being Patrington (population 1,850). Other settlements do not exceed a population of 600 and are mostly much smaller. They include the villages of Sunk Island, Winestead, Welwick, Weeton, Skeffling, Easington and Kilnsea. Spurn peninsula has a small settlement concerned with the operation of the pilot, coastguard and lifeboat stations.

There has been considerable land reclamation around the Bight, notably that of Sunk Island Sand, started in 1666 with the creation of Sunk Island from a sand bank, eventually connected to the mainland at the start of the 19th Century (de Boer; 1970). The most recent reclamation has been of an extensive area of Welwick Saltmarsh to the west of Patrington Channel, enclosed by a flood bank in the 1970's and the level raised by warping.

2ii Format of study

In order to gain a knowledge of the distribution of species and communities throughout the Bight, and also more specific information on certain aspects of the ecology of the major species, the project was split into two main parts.

After a period of familiarization with the study area, field methods and the taxonomy of the animal species within it, a single, large scale survey of the whole of Spurn Bight was carried out within the period of one month (May/June 1977). This is hereafter referred to as the extensive survey. Time and manpower available to complete the survey dictated that it would be somewhat superficial.

The extensive survey was followed by a year long intensive survey of a smaller number of sites chosen on criteria of

(i) ease of access

(ii) representativeness

That survey was designed to cover a single growth period and a single period of quiesence of the infauna.

2iii Transport and safety in the field

The mudflats pose considerable problems of access and safety to the estuarine ecologist. The sediments are extremely soft and extensively dissected by wide and deep drainge channels. Access by wheeled vehicles as, for example, used on the Dee and on Morecambe Bay, is consequently impossible. The large area and great width of the flats also restricts accessibility on foot and usually only a single transect of stations is possible during the course of a tide.

Samples were transported on a man-hauled, mud sledge, built of Dexion with wide plastic runners. Weight of the accumulated mud samples restricted the number of stations possible along a single transect to five, after which the sledge became too heavy to pull.

The dangerous, exhausting conditions on the mudflats necessitated strict safety precautions. All sampling was carried out during a falling tide, always in conditions of favourable visibility and with at least one other person present. One rocket and one coloured smoke flare were always carried in case of emergency, the whole of Spurn Bight being easily visible from Spurn coastguard station.

Sampling information was dictated onto a portable recorder wrapped in plastic for safety. The use of notebook and pencil was precluded by the muddy conditions.

An attempt was made to sample, by boat, the very outer lowest tidal sandflats of Trinity Sands, made inaccessible from the land by wide drainage channels and the distances involved. I am indebted to my brother for the attempt, minimally successful, which resulted in an uncomfortable night stranded on one of the Bight's sandbanks on a falling tide. Only one station was sampled at the site of the mishap. I can understand his reluctance to repeat the venture and the remainder of the outer sandflats had to remain unsampled!

2iv Location of sampling stations and site nomenolature

Location of transects on the large scale survey was, of neccesity, determined by points of access. The survey was initially planned using the sediment distribution map in McQuillin et al. (1969) but this proved unreliable for Spurn Bight. The great length of certain transects, up to 3½ km, made it impractical to space stations at regular intervals and eventually each was situated within one of the discontinuous bands of differing sediment types, usually parallel to the shore. Sample locations in Spurn Bight are depicted in Figure 2iv.

Discontinuities in sediment composition were noted on the outward 'trek' of a sampling trip and stations established and sampled on the return walk. Stations were marked using 5' garden bamboo canes, inserted into the sediment to a depth of 3'. To make these more conspicuous from the many other canes and stakes present on the mudflats, the canes were conspicuously marked with brightly coloured bands of 'Lasso' ¾" P.V.C. adhesive tape. This tape proved sufficiently resistant to withstand three years of exposure to the weather and tides without significant loss of colour or adhesion.

Sampling stations were located by triangulometric sighting of prominent distant landmarks using a hand bearing magnetic compass, later plotted on an Ordnance Survey map of the area after subtracting magnetic deviance from grid north. As many lines of sight as possible were plotted for greater accuracy, the main landmarks visible from the mudflats being:- Spurn lighthouse (TA 403113), Bull Sand Fort (TA 370093), Grimsby Hydraulic Tower (TA 280114), Patrington Church Steeple (TA 315225), and the starting point of the transect marked by the vehicle parked on the riverbank In this way it was possible to determine a 6 figure grid reference for each site. Sites very close to the sea wall were additionally located by pacing, an average pace being measured at 60cm whilst pulling the mud sledge.

Sites outside Spurn Bight were chosen to give representative coverage of the main intertidal features of the outer Humber. These include the very extensive sandflats on the south shore, east of Grimsby, and the areas of soft mud upriver from Spurn, polluted with heavy metals and hydrocarbons on the south bank. As these areas fall outside the main field of study, the number of sampling stations on each transect was kept to a minimum, in some cases one only.

Transect locations were lettered alphabetically from A to P (excluding I and O), from west to east on each bank of the estuary. Transects A,M,N, and P were located outside Spurn Bight. Along the transect the stations were labelled with Roman numerals I - V dependant on location down the shore. Thus:-

I within or at the very edge of the *Spartina* marsh

II within 100m of highwater usually in the soft silt at the top of the shore

III)
) middle shore stations
IV)

V stations positioned as near to MLWOT as practicality allowed.

Finally the Arabic numerals 1 - 6 were added to each station title to facilitate interpretation of computer readouts of community analysis. These were ascribed depending on sediment type thus:-

1 very soft silt/clay

2 soft silt

3 gullied sandy silt

4 gullied silty sand

5 flat silty sand

6 hard clean sand.

These were labelled subjectively from field observations while sampling. Subsequent sediment changes during intensive studies led to certain station names becoming inappropate (notably at GIII4), but the original names were retained for continuity between the two surveys.

Descriptions of each transect, including access, grid reference and location of sampling stations is given in the appendix to this chapter.

From the extensive survey the Skeffling and Easington transects were chosen for more intensive study over the following year, the former for continuity with the study of Ratcliffe (1979), and the latter to include stations where *Cerastoderma edule*, *Retusa obtusa* and *Nephtys hombergi* had been more abundant. Not all stations on each transect were sampled and the final intensive study stations became:-

Skeffling FI2 - among the advancing edge of the *Spartina* marsh
FII2 - topshore silt ca. 100m from the marsh
FIV4 - gullied sandy mud, representitive of the bulk of the mudflats
Easington GIII4 - flat sandy mud
GIV3 - gullied sandy mud

No stations of the downshore sandflats were sampled regularly because of the distances involved to reach them and their low biomass of infauna observed in the extensive survey. Tasker & Milsom (1979) showed that overwintering birds do not use the outer sandflats for feeding to any great extent.

An additional site CI2, at Patrington Outstray Cutoff was sampled seasonally to monitor a small population of *Scrobicularia plana*, not recorded elsewhere in numbers on the Bight during the extensive studies but formerly numerous all over the upper shore (Petch; 1907), and apparently recovering slowly from the winter of 1962 - 63.

2v Sampling methods

2va Core size

Two standard corers were used -(a) galvanised steel box corer 10cm x 10cm x 20cm deep, polyurethane varnished for easy removal of the core, and (b) perspex tubular corer of internal diameter 4cm, 30cm long, marked at 10cm and 20cm intervals and fitted with a rubber bung plunger to extrude the core. The 10 x 10cm cores were used to sample larger macrofauna and the 4cm cores for spat and meiofauna to reduce sieving and sorting time spent on more numerous organisms.

2vb Sample replication

Five cores of each size were taken at each site on each sampling occasion. Five additional 10 x 10cm cores were taken at the three downshore sites for estimation of less abundant larger organims. In addition a total of fifty 10 x 10 x 10cm deep cores were coarse sieved in the field using a 1/8" mesh cockle sieve in pooled groups of five at station GIV3 during the intensive survey for estimation of numbers of <u>Cerastoderma edule</u>. Cores and sievings were returned to the laboratory in individually prelabelled polythene bags. Sampling procedure is summarised in Table 2b.

2vc Confidence limits

For the sake of clarity of presentation, confidence limits are not presented with estimates of mean density and biomass throughout the study.

During early field trials fifty samples of each core size were taken at Skeffling Clough and the animals sorted and counted to test the consistency of the sampling technique. The mean and its 95% confidence limits were determined for random sets of five samples. The proportional size of the limits in relation to the mean was plotted against the mean density of organisms (Figure 2v). As expected, this demonstrated an increasing proportional size of limits with decreasing sample mean for both corers. It also indicated that the 4cm corer was inappropriate for organisms at lower densities than about 250 m^{-2} and that great caution is required when interpretting density figures lower than about 100 m^{-2} with the 10 x 10cm corer.

2vd Sampling interval

Sites were visited once only during the extensive survey. A sampling interval of one month was chosen for intensive studies. A two week interval, such as that used by Ratcliffe (1979), would have produced too great a burden of samples for analysis and trends between monthly samples produced little evidence that population changes on a smaller time scale were being missed. During the winter prohibitive weather conditions (fog in December, blizzards in February) prevented two sampling visits. Again trends between actual dates indicated little significant loss of information. Dynamics for those months were implied by interpolation between values from sampling occasions before and after. The total sampling period for the intensive survey was from March 1978 to March 1979.

2ve Sampling area

An individual station was regarded as covering a circular area of some 10m radius centred on the marker cane. Replicates were taken at random within this area by the system "two steps forward and place the corer while looking the other way" as by Ratcliffe (1979). A larger 100m square area was used for the estimation of cockles at GIV3 to minimise disturbance of the sediment by the larger number of samples needed and the field sieving method. It was possible to estimate the density of Arenicola and Mya during the extensive survey, present in too few numbers to be sampled directly, by counting the evident traces of their presence on the mud surface. The combined casts and feeding depressions of Arenicola and the large circular feeding depressions around the siphons of Mya were counted in five one metre squares, measured approximately by pacing.

2vf Nekton trapping

Seasonal samples of the nekton using the Bight at high water only were taken by placing a specially constructed net (Plate 13) with opening 50cm wide, 20cm high and net length of one metre, across one of the narrower creeks draining the Bight near to station CIV3. The method was not intended to be quantitative, but served to demonstrate the presence of such a fauna. On four separate occasions the net was placed within the drainage channel with the mouth pointing towards the shore. It was then left over two tidal cycles on the assumption that animals collected during the first of the two tides would be washed out by the flood of the second so that the bulk of the catch resulted from the ebb of the second tide.

2vg Sediment cores

Five samples for analysis of particle size facies, organic carbon, interstitial water content and salinity were taken at the same time as the fauna samples using the 4cm circular corer. Surface water collected with the sample was very carefully poured off, with minimal disturbance of flocculant surface sediments, to avoid contamination of the interstitial water. On return to the laboratory these were deep frozen and stored at -15°C so that analysis of all samples could be carried out simultaneously. Barnett (1980) pointed out that such freezing facilitates breakdown of flocculant aggregates prior to analysis.

2vh Erosion/deposition

Originally the method of Eddleston (1976) was used to try and determine net erosion and deposition between sampling dates by the undermining and subsequent reburial of a light aluminium washer placed around a fine brass rod pushed into the sediment to a fixed mark. This has been proved effective on firm sands but direct observation on the Humber showed the washer to sink into the sediment under its own weight. Net changes in sediment height were therefore measured by ruler against a marked brass rod pushed sufficiently deeply into the sediment to be anchored firmly in the more compacted deeper deposits. The rods were repositioned with the mark once more level with the mud surface on each sampling occasion. Erosional effects caused by the water turbulance around the rod were observed to be insignificant owing to its narrowness.

2vj Tidal position

The impracticality of measuring directly the tidal cover of all sites of the extensive survey was overcome by the expedient of plotting the position of each station by triangulation on the admiralty chart and then measuring the proportional distance downshore of each site as a percentage of the distance between MHWOT and MLWOT marked on the chart. This assumes i) even gradient of the beach and ii) flood and ebb in the direction measured ie. that of shortest distance between high and low water marks. Although not producing an absolute tidal height in relation to O.D. this was sufficient for comparative purposes between stations.

Tidal cover of the intensively sampled sites was determined by measuring the period of emersion on spring and neap tides on 22nd and 29th July 1978 using a telescope from the sea wall. The outer station at Easington was indistinguishable from other stakes and markers on the mudflats and the tidal cover was estimated for that site. The timing of the measurement corresponded to the summer minimum in the spring/neap amplitude cycle (ref Fig 3i).

2vk Temperature

Spot readings of sediment temperature taken on sampling trips would have been an inadequate measure of seasonal variation, particularly during the winter when mild days were deliberately chosen for sampling. Ratcliffe (1979) had experienced repeated loss of maximum-minimum thermometers but had shown a direct relationship between internal sediment temperature and overlying air temperature. It was therefore considered necessary only to include measurements of air temperature during the sampling period. The University weather recording station at Withernwick broke down during the intensive survey and daily temperature records made by the coastguard station at Spurn Point were obtained from the meteorological office at Bracknell. The mean of daily maxima and minima from a max/min thermometer in a standard Stephenson Screen was calculated for each week of the study period and the range of maxima and minima also recorded.

Continuous data for preceding years as a comparative measure was not available but data on sunshine, snow and frost days supplied by Barton-on-Humber C.o.E. school over the period 1975 - 1979 were used as a comparative measure of winter severity and summer sunshine between years.

2vi Laboratory methods - fauna

2via Sieving and extraction

Endecott's analytical sieves were used to extract organisms from samples.

For meiofauna during the extensive survey a mesh size of 76μ was used, slightly larger than that recommended by de Bovée et al. (1974) who showed that a 64μ mesh was 100% efficient in retaining all taxa except nematodes, of which 25% of the population was able to pass through. Estimates of nematodes are therefore likely to be considerable underestimates. A finer screen of 40μ was tried, but retained such large quantities of fine sand as to make sorting impracticable.

For macrofauna, the 10cm cores were sieved to 275μ for the quantitative estimation of all animals other than spat. 4cm diameter cores were sieved to 76μ. Samples for *Cerastoderma* at station GIV3 were field sieved using a 1/8" cockle sieve.

Most commonly in macrobenthic studies, a mesh size of 1mm has been used to quantify all individuals, including spat (eg. Anderson; 1972, Beukema; 1974, Kay & Knights; 1975, etc. - total fauna, Smith; 1967a - Retusa, Stephen; 1931, Kreger; 1940, Høpner-Petersen; 1958 - Cerastoderma). Other authors have used mesh sizes considerably greater than this (eg. Hughes; 1970a - 5mm for Scrobicularia, Seed & Brown; 1975 2mm for Cerastoderma). For the majority of species, however, juveniles as small as 0.2mm measured length were noted, easily capable of passing through much smaller mesh sizes. Problems resulting from interpretation of studies using too large mesh sizes are discussed in the relevant chapters.

10cm x 10cm cores were sieved by force-hosing them with running tapwater over the relevant sized sieve. It was also possible to sieve the sandier 4cm cores in this way but those containing higher proportions of silt proved too cohesive for hosing without damaging the more delicate organisms, particularly juvenile Hediste, tubificids and spionids. Soaking the cores in deflocculant solution ('Calgon' water softener - Sodium hexametaphosphate), overnight was effective, but proved lethal to the organisms and appeared to accelerate decay.

A method of reducing cohesive sediments to a sievable slurry was developed based on a commercially available gem tumble-polishing apparatus produced by Gemtek Ltd. of Hull. This consisted of a 15cm diameter sealable barrel normally filled with pebbles and abrasive suspension and rotated horizontally to produce a polishing effect.

Cores of mud placed in the barrel in deflocculant solution were rapidly broken down into spheres but these were eroded down very slowly as the dispersed mud lubricated the walls of the barrel. This effect was satisfactorily overcome by sealing in place 2½cm rubber bungs on the smooth inside of the barrel in alternating rows of three and four bungs (Plates 11 & 12). These acted as baffles to aid mechanical breakdown of the sample which was generally reduced to a sievable slurry in 5 - 30 minutes depending on cohesiveness. Samples were then able to be sieved with running tapwater with the minimum of applied pressure.

To test the effect of the apparatus on delicate organisms, cores of very cohesive, clay-rich samples from the Pyewipes region were rotated for periods up to one hour with known numbers of small Hediste and Macoma. Although all specimens were found to be dead after the longest periods of tumbling, the bodies were not disrupted and 100% recovery of individuals of all size groups was achieved.

An enlarged version of the apparatus (Plates 11 & 12), was made as soon as the method was found to be effective. This used a larger motor with variable speed controlled by rheostat and was able to rotate five such barrels and thus deal with all samples from one location simultaneously.

Sieving to 76µ retained large quantities of sand particles and these were removed using a modification of the method of Barnet (1968). A galvanised steel shute, open at one end approximately one metre in length, 7cm wide with 2½cm walls was roughened to retain sand by painting with ordinary gloss paint to which had been added coarse sand. Sievings from mud cores were washed into the closed end and gently hosed along the shute and into a second sieve where animals and detritus collected, free of the sand.

The efficiency of the method was tested using artificial samples of clean sand to which had been added known numbers of various meiofaunal groups and juvenile macrofauna. It proved 100% efficient for all groups other than ostracods of which an average of only 87% of specimens were collected during the course of five trials. Presumably the shapes and densities of these animals makes their behaviour on the shute similar to that of the sand grains and ostracods were therefore probably underestimated in the extensive survey.

2vib Preservation

All samples were decanted directly from the sieve into alcohol-formaldehyde solution except those animals intended for weighing These were deep frozen for storage as the preservative is known to alter considerably the animals' weight by dissolution of body lipids and calcium carbonate. (However, see Moreira; 1979 and below).

2vic Sorting

Various methods of differentiating the animal specimens from the considerably greater volume of plant detritus were tried including those of Hamilton (1969), using fluorescent dye and long-wave ultra-violet light and the flotation methods of Birkett (1957), Anderson (1959), and Teal (1960). The former was very efficient but inconvenient, necessitating darkening of the laboratory and exposure of the author to potentially hazardous radiation for long periods. Flotation methods proved ineffective in separating animals from plant materials of similar specific gravity.

The method of Williams & Williams (1974) was eventually used for all 4cm core sievings. Rhodamine β (200mg 1^{-1} of distilled water), was added directly to the sample upon preservation, staining all organic material bright pink. Prior to sorting the preservative was filtered from the sample and an aqueous solution of Chlorazol E black added. After 30 seconds the sample was re-sieved and rinsed. Plant detritus is counterstained black but animal tissues remain bright pink and therefore conspicuous.

The residue from 10 x 10cm cores, sieved to a coarser grade, contained a lower proportion of detritus and did not need to be stained.

Samples were sorted in a 10cm petri dish with a lattice of 5mm squares scratched onto the surface to facilitate systematic coverage of the whole sample. The x10 magnification of a Watson binocular microscope was used and data were recorded on standard sheets and the animal specimens preserved in alcohol/formaldehyde for further reference as necessary.

2vid Taxonomy

A list of identification literature used to determine both the fauna and flora of Spurn Bight is given below. As far as possible the most modern names available have been used, but well established names, superceded by recent taxonomic revisions, have been included for clarity. The layout of invertebrate higher taxa is as in Clark and Panchen (1971), except for the Insecta which is as in Borror et al. (1976). Vertebrate taxa are as in Jones (1967) and Bertin (1967). English names for invertebrates are those used by Barrett & Yonge (1958).

General identification

Barrett & Yonge (1958)

Eales (1967)

Invertebrates

Smidt (1951)	Hydrobia spp.
Lemche (1948)	Opsthobranchia
Thompson (1976)	
Tebble (1966)	bivalves
Pohlo (1963)	Cerastoderma sp
Høpner-Petersen & Russel (1973)	
Brock (1978)	
Fauvel (1923 & 1927)	Polychaeta
Clark (1960)	
Day (1967)	
Fauchald (1974)	Sphaerodoridae
Brinkhurst (1963)	Oligochaeta
Makings (1977)	Mysidacea
Lang (1948)	Harpactacoidea (nomenclature only)
Jones (1976)	Cumacea
Naylor (1972)	Isopoda
Sars (1895)	Amphipoda
Chevreux & Fage (1925)	
Reid (1944)	Gammaridae
Watkin (1938)	Bathyporeia spp.
Crawford (1937)	Corophium spp.
Smaldon (1979)	Decapoda
Joy (1932)	Coleoptera
Lindroth (1974)	Carabidae

Vertebrates

Barron (1976)	Gobiidae

Flora

Newton (1931)	Algae
Hubbard (1968)	Spartina spp.

2vie Measuring the macrofauna

Larger individuals of Macoma and Cerastoderma (>10mm) were measured to the nearest 0.5mm using Vernier Callipers. All other measurements were made using a microscope eyepiece graticule to the nearest 0.2mm. Parameters used to measure each species were as follows:-

Macoma balthica and Cerastoderma edule - maximum anterio-posterior shell length.

Hydrobia ulvae and Retusa obtusa - shell height from apex of spire to lowest point of shell aperture.

Hediste diversicolor - width of peristomal segment (referred to as 'headwidth'). This varied as to whether or not the pharynx had been everted as was quite common when the animal was killed. Separate regressions of peristomial width with and without everted pharynges to total body length were made and back calculation produced a conversion factor of x 0.7 for specimens with everted pharynges which was applied to all measurements of such animals. Often jaw length (Chambers & Milne; 1975a), or total body length (Smidt; 1951), have been used, although the former is very time consuming and the latter inaccurate owing to shrinkage during preservation. Heip and Herman (1979), used the width of the 10th segment, but this measure is also prone to distortion by pharyngeal extrusion.

Nephtys hombergi and *N. caeca* - body width of 10th segment. Unlike *Hediste* worms of this genus do not possess an expanded peristomium. The method is again subject to distortion by pharyngeal extrusion which was, however, found to be less common than in *Hediste*. Similar length/width regressions of everted and non-everted individuals produced a conversion of 0.95 x for specimens without everted pharynges. This was regarded as insignificant and not used when routinely measuring individuals. The only other parameter used for this genus in other works has been total length (Smidt; 1951, Kirkegaard; 1970), again subject to contraction on preservation.

2vif Ageing of macrofauna

Macoma balthica

Ratcliffe (1979) discussed the problems involved in ageing of the Humber populations of this species where few animals seem to possess winter growth interruption rings. Similar problems were encountered and obvious growth rings were found on <10% of individuals. Staining with Methylene Blue occasionally showed rings in the conchostracum, otherwise invisible, on a slightly higher proportion of individuals but insufficient data were available to ascribe accurately non banded specimens to particular age groups. The large number of modal classes, possibly greater than 10, prevented the use of the probability paper method of Harding (1949). Younger (1 - 3 years) age cohorts were separated by ascribing successive peaks on the size/frequency graphs to successive age classes but low density and overlap in size distribution of larger individuals made it impossible to differentiate older cohorts even when data from field sieving totals of fifty 10 x 10cm cores

~~was~~ were examined. Individuals with apparently complete sets of rings were used to help interpret size/frequency histograms, but it was not possible to separate classes older than three years which were subsequently treated as a single cohort leading to considerable underestimation of dynamics.

Cerastoderma edule

Rings were visible on almost all specimens. By plotting size of each ring against ring number for all specimens it was possible to isolate certain individuals not conforming to the average size/ring number relationship for the majority of individuals with similar numbers of growth rings. Close examination of these variants usually revealed either the presence of additional more faint disturbance rings, commonly caused by temporary cessation of growth after erosion from the sediment and subsequent reburial (Cole; 1956, Richardson et al.;1980), or absence of particular rings, presumably caused by continual slow growth throughout the winter. By ascribing those individuals to other age cohorts it was always possible to produce a good match with the average growth patterns within the cohort.

This was further complicated by uneven commencement of growth at the start of the growing season. During the months of April and May not all individuals of the same cohort started rapid growth simultaneously and, for example, the 3 year old cohort may temporarily have been represented by individuals with 2 or 3 growth rings. This was noted in *Cerastoderma glauca* by Persson (1976). It was always possible, however, to ascribe individuals to the correct year group.

Hediste diversicolor

It was usually possible to distinguish separate cohorts 'by eye' from size/frequency data.

Nephtys hombergi

Fairly clear division into distinct cohorts from size/frequency data was confirmed by examination of jaw growth rings of representitive individuals after the method of Kirkegaard (1970) and Olive (1977). Cohorts overlapping in size were occasionally found and these were separated by jaw ring determination.

Retusa obtusa

Size frequency data could be used to separate age cohorts except during the late summer when progeny from autumn and spring spawning reach the same size. '0' class and one year old individuals could be further differentiated by colour, the younger individuals being white and translucent, the older ones yellow and opaque.

2vig Weight measurement

Animals of all species were kept in 25‰ seawater for 24 hours to allow discharge of gut contents prior to weighing. They were then removed and animals of similar size deep frozen en masse so that all weighing operations could be carried out together at the end of the study. Moreira (1979) showed that significant weight losses can result from freezing and defrosting of mollusc tissue from the disruption of cell membranes and leakage of contents. This was not appreciated at the time of study and may have resulted in significant underestimation in biomass calculations in this and many previous works.

Groups of animals of similar size were weighed together in glass crystalising dishes on a toploading balance. Very small individuals (mollusc spat, juvenile polychaetes, meiofauna), were weighed in aluminium foil using a torsion balance. Pooling of numbers of individuals precluded limits to be set to the regression and so disguised the variability between individuals but allowed considerable saving in time spent on individual weighings. High correlation coefficients obtained from the regression - not less than 0.91 - justified the method used.

Pooled lots of animals were then desiccated to constant weight in an oven at 70°C for 48 hours. After reweighing the total weight of the dried animals was calculated by subtraction of the container weight. For entirely soft bodied organisms, mainly annelids, the balance reading was used as a direct measure of dry weight.

To calculate the biomass of shelled animals a new method was devised to avoid the significant loss of weight accompanying acid digestion of the calcium carbonate shell. This has been found to be up to 30% of total body weight by Ratcliffe (1979).

After drying and weighing the pooled organisms were lightly crushed and added to a 20% solution of potassium hydroxide in a boiling tube and incubated at 90°C. After one hour the tubes were vigorously mixed with a 'Whirlimix' to utilize shell fragments in a homogenising action on the remaining organic material. After 3 hours incubation the resulting, almost clear amber fluid was vaccuum filtered and rinsed on weighed 10cm filter papers. These were then dried at 70°C to constant weight and the weight of the calcium carbonate shell fragments found by subtraction.

This method has the advantage of including all organic tissue in the weighing, including conchostraca and ligaments whilst excluding any remaining sediments in the gut. All biomass values referred to are for dry weight of the organic material in the organism.

Size/weight power regression was performed on a Casio fx-180P programmable calculator. From the regression equations a series of idealised weights for particular size increments were back calculated and used in all subsequent biomass calculations.

2vii Laboratory measurements - sediment

2viia Water content and interstitial salinity

During intensive studies water content was determined incidentally while drying sediment for particle size analysis. Sediments were dried to constant weight and water content calculated as percentage of total weight. Interstitial salinity was recorded by removing water from the samples using the thixotropic nature of the mud. A single 4cm diameter core was placed in a plastic 500cm^3 container and vibrated against a 'Whirlimix' test-tube mixer. The mud puddled to an even consistency and subsequent resettlement over 24 hours (with lid on to prevent concentration by evaporation), usually produced 25 - 50 cm^3 of supernatant interstitial water. An 'Electronic Switchgear' salinometer was used to measure salinity. A measured volume of interstial water was made up to 250cm^3 with distilled water to accommodate the large salinometer probe in a 500cm^3 measuring cylinder. The original salinity was measured by back calculation.

2viib Particle size analysis

It was not possible to follow Ratcliffe (1979) in the use of the electronic 'Coulter' particle size counter as the high proportion of sand in most of the samples could not be accommodated by the available apparatus. The sedimentation technique of Bouyoucos (1936), using the interpretive tables in Cox (1967), was modified for use with estuarine sediments. Three cores, pooled to give an average reading as recommended by Anderson (1972), were oven dried for 48 hours at 90°C and then lightly broken up in a mortar and pestle while avoiding direct grinding of the sediment particles. A 50g sample was then soaked in $125cm^3$ of $40gm\ l^{-1}$ solution of sodium hexametaphosphate (Calgon) deflocculant for 24 hours for the accurate estimation of the clay fraction without aggregation. This was then sonicated to disaggregate further the finer particles and then made up to one litre with distilled water in a graduated measuring cylinder. This was then mixed thoroughly by repeated inversion of the stoppered cylinder to ensure complete suspension.

Bouyoucos hydrometer (calibrated in grammes of SiO_2 per litre) readings were taken after periods of 40 seconds, 2,5,10,15,30 minutes and 1,2,4,6, and 12 hours. Simultaneous recordings of temperature were also taken to compensate for differences in sedimentation rate at different temperatures and a correction for variation in specific gravity made from tables in Cox (1967). A mean specific gravity of 2.58 ± 0.06 (s.d.) $gm\ cm^{-3}$ was found between diverse sediments from the extensive survey, using a 25 cm^3 pycnometer in the method of Krumbein & Pettijohn (1938).

A further correction, to allow for the buoyant effect of the deflocculant and dissolved salts and organic material from the sediment, was made by centrifuging all particulate material from the supernatant after 12 hours sedimentation and testing this liquid with the hydrometer. Eight replicates produced a correction of 4.75 ± 0.05 (s.d.) gm SiO_2 per litre equivalent which was subtracted from all readings prior to further calculation.

Corrected readings were converted to particle diameter in millimetres and percentage in suspension from the tables and equations in Cox (1967).

After sedimentation, further analysis of the sand fraction was carried out by wet fractionation through a nest of Endecott's test sieves. Cumulative results were combined with those from sedimentation.

Particle sizes were then converted to the logarithmic Wentworth scale of ϕ ($-\log_n$ particle size in mm).

Cumulative percentage size/frequency curves were then plotted for each sample and cumulative percentiles noted for the calculation of median particle diameter (ϕM), the degree of sorting (ϕSo), skewness (ϕSk), and kurtosis (ϕKu) as measures of particle size distribution.

Formulae for ϕM, ϕSo, ϕSk, and ϕKu were taken from Inman (1962), being:-

$$\phi M = 50\%\text{-ile}$$

$$\phi So = \frac{84\%\text{-ile} - 16\%\text{-ile}}{2}$$

$$\phi Sk = \frac{25\%\text{-ile} + 75\%\text{-ile} - 2(50\%\text{-ile})}{2}$$

$$\phi Ku = \frac{75\%\text{-ile} - 25\%\text{-ile}}{2(90\%\text{-ile} - 10\%\text{-ile})}$$

Proportional composition of sand, silt and clay were calculated using definitions given in Shepard (1954), where sand $= < \phi 3$, silt $= \phi 3 - \phi 5.5$, clay $= > \phi 5.5$. Proportional composition was then ordinated as a standard ternary sediment diagram and Sheperd's nomenclature used to describe the sediments.

Cluster analysis using the method described below was carried out on extensive survey data and plotted as dendrograms to compare sedimentary characters with faunistic composition.

2viic Organic matter content

The presence of the dichromate equivalent of 3% carbon as ferrous and sulphide ions was recorded from sediments even after 48 hours drying at 90°C. This precluded the wet oxidation method of organic determination of Wakeel & Riley (1956) and its subsequent modifications. After experimentation with these methods and with gravimetric digestion with hydrogen peroxide, a 'Leco' (Laboratory Equipment Co. Inc. - manufacturers) WR12 total carbon gas determinator method was modified from Folger (1972). Standard, one gramme samples of dried sediment are fused electrically in a refractory crucible in a stream of oxygen and the resulting carbon dioxide from the sample determined by thermistor measurement of the thermal conductivity of the spent carrier gas. This method has been tested against other methods of soil analysis by Gaudette et al. (1974) and found to give very accurate results.

Ansell (1974) recommended acid treatment of samples to remove carbon in the form of carbonates in shell and limestone fragments. Dilute hydrochloric acid was added dropwise to the sample within the crucible until effervescence ceased. The resulting acidic liquid was neutralised using ammonium phosphate solution, added dropwise until yellow ferric chloride produced from iron in the sample was replaced with white ferric phosphate. This was necessary as the deliquescent nature of the ferric chloride would risk moisture condensation and subsequent cracking of the glassware within the analyser. After neutralisation samples were oven dried at 90°C for 48 hours before analysis, during which the ammonium chloride produced above sublimed off. Analysis was carried out at the British Steel Corporation Central Laboratories at Scunthorpe.

Initial tests on the reproducibility of the method gave agreement to within 1.7% of the total carbon between aliquots from the same sample. All subsequent results were based on single readings. A blank of incinerated sand treated with calcium carbonate, ferrous sulphide, hydrochloric acid and ammonium phosphate gave a reading of 0.009% by weight of carbon, an acceptable source of error.

A conversion factor for organic carbon to total organic material was made by analysing acid washed sand to which had been added 5% by weight organic detritus from estuarine sediment, collected by vigorous aeration of a suspension of estuarine mud in water. Aerophilic organic particles accumulate as a scum on the surface and can be skimmed off, rinsed and the process repeated until detritus free of mineral particles is collected. Five such standards produced a mean carbon content of 2.04% ± 0.09% (S.D.), giving a conversion factor of x 2.45 to total organic material.

Similar 5% organic detritus standards were used to estimate loss of carbon during acid treatment to remove carbonate. A loss of carbon content of 0.07% ± 0.011% (S.D.) of the total carbon on five replicates was regarded as negligible.

Coal present in the sample (visible as particles of size range 50μ - $>$1mm) from industrial activity and also found naturally from the drainage basin of the estuary is also included in the estimate of total carbon. Difficulties arising in analysis of organic carbon in the presence of coal have yet to be successfully resolved (Gaudette et al.; 1974), although colorimetric Kjeldahl estimation of protein as a measure of organic material, suggested by Buchanan & Longbottom (1970), significantly reduces but does not eliminate the problem. It was chosen to regard the presence of coal as representing an unavoidable, relatively constant source of minor error in the estimates of carbon.

2viid Iron content

The iron content of the sediment was measured during the extensive survey and was intended to give an indication of anaerobic conditions where ferrous sulphide accumulates. Analysis was carried out using an A.R.L. N940 Nondispersive X-ray fluorescence analyser at the British Steel Laboratories, Scunthorpe. Iron content was found to be so closely related to organic carbon content that analysis was not repeated during intensive studies.

2viie Detritus composition

While sorting sieved samples for fauna the composition of macrodetritus was noted to give an idea of its source. Few detrital particles were decomposed beyond recognition and types of particle were categorised subjectively as abundant, frequent and uncommon and the source of material divided into autochthonous and allochthonous in origin. The latter was subdivided into marine, freshwater, terrestrial/saltmarsh and anthropogenic fractions.

2viii Mathematical analysis

To extrapolate intensive study data to that from extensive studies it was necessary to identify recurrent species associations and their environmental relationships so that the distribution of each association within Spurn Bight could be inferred from knowledge of the environmental conditions gained from field sampling and remote sensing.

Analysis was carried out on the Hull University ICL 1900 computer using the 'SPSS' and 'CLUSTAN 1C' mulivariate packages (Nie et al.; 1975, Wishart;

1978).

2viiia Correlation analysis

Correlation analysis, recommended by Cassie (1961), was carried out to investigate the interrelationships between all variables, both faunistic and abiotic, using the 'NONPAR CORR' subroutine of 'SPSS'. Kendall's non parametric rank order correlation coefficient 'τ' was chosen as the data could not be assumed to be normally distributed. The significance of the correlation, tested using Student's 't', is also given by the subroutine.

The resulting matrix of correlation coefficients and their significances was then rearranged into trellis form so that intercorrelated assemblages could be identified for further analysis. Negative correlations were also included in the trellis diagram in order to demonstrate the degree of 'exclusiveness' of each assemblage.

The results of correlation analysis (see Chapter 4), indicated some degree of differentiation into associations and prompted further multivariate analysis of the whole data matrix.

2viiib Similarity analysis

Similarity analysis has the advantage of being able to produce a meaningful inverse analysis of stations as well as species and the matrix of coefficients provides the raw material for classification and ordination analysis.

Various indices of similarity were available on CLUSTAN 1C the relative merits of which are discussed by Day et al. (1971). That most widely used in previous benthic studies has been that of Czekanowski (1913) - Cz - which was adopted for comparability.

The equation is:-

$$Cz = \frac{\sum_1^n wi\ (xy)}{\sum_1^n (xi + yi)} \times 100$$

where:- wi (xy) is the lesser abundance value for species i from sites x and y

xi, yi are the abundance values of species i at sites x and y

n is the total number of species in the matrix.

Data ~~was~~ were log-transformed to reduce, but not eliminate, density dependence of the statistic which is known to be sensitive to numerical dominance by small numbers of abundant species. Only taxa identified to specific level were used in the analysis to prevent obscuring of subsequent analysis by mixed groups of species with differing ecological requirements.

For the ordination analysis, the similarity matrix was recomputed using data double standardised in the method of Bray & Curtis (1957) where each data point is represented by a relative importance value calculated by converting it to its proportional value of the maximum for the particular species, summing those values for each site and converting the singly standardised points to the proportional value of the total for the site. Double standardised data have the advantage of reducing overweighting of ubiquitous species in the coefficient.

2viiic Classification

The matrix of similarity coefficients formed the input to a sorting procedure in which pairs and groups of stations were produced to generate a hierarchy and so produce a dendrogram.

Group average clustering strategy was used, in which groups are classified on average similarity values. Field & McFarlane (1968) regard this method as logically the most justifiable method of linkage and the mathematical basis of the strategy is described in depth by Pielou (1969).

Cluster analysis was originally carried out on all species from the extensive survey, excluding those found at a single station only where the coefficient is incalculable. The resulting classification identified certain species as dissimilar outliers with no affinities for the major groups and these invariably turned out to be species occurring at very low density at scattered locations with no obvious relationships with sediment type. For further analysis of both species and stations, outliers were removed from the data as recommended by Stephenson et al. (1972).

Dendrograms were constructed for inter-station and inter-species classifications and a separate classification was also performed on untransformed environmental data from the extensive survey (particle size parameters organic and iron content), for comparison with faunistic analysis of stations. Mixed unit data were used, however, in this analysis, leading to invalidation of the resulting classification.

In order to define means and limits of biological and environmental variables within each of the clusters produced by CLUSTAN 1C, data from all cores were subjected to the descriptive statistics of subroutine 'CONDESCRIPTIVE' of SPSS (Nie et al.; 1975). This gave the mean, standard deviation and overall range of all variables within each cluster. Subroutine 'T-TEST' was used to test the significance between the means of each variable in the clusters using the standard Student's 't'. This was followed by an 'F' test of the difference between variances and, where this proved significant ($P = < 0.05$), a non parametric equivalent to 't'. Significance of the test was also computed and the results expressed in table form.

2viiid Ordination

Classifications can have the disadvantage of imposing mutually exclusive dichotomies on relatively homogeneous data and thus disguise continuity between apparent communities. By ordinating sampling stations in multi-dimensional space the relationship of all sites to each other was demonstrated and axes corresponding to environmental gradients subjectively applied to the ordination to interpret differentiation into site groups. Wisconsin Comparative polar ordination (Bray & Curtis; 1957) was chosen for its conceptual simplicity.

For each ordination axis two sites were chosen subjectively in having very low similarity with each other but high levels of similarity with some other sites. A single dimensional ordination of all sites in relation to these two was then produced using the geometrical method described by Cox (1967).

A further two sites, apparently close on the single dimensional ordination but with low similarity between them were then chosen as end points of a second one dimesional axis and the process repeated, generating a second one dimensional ordination which was combined with the first to give a scatter of sites in 2 dimensional space. Additional dimensions can be produced but an upper limit of three is usually imposed by the difficulty in visualising the results in higher dimensions.

Three 2-dimensional and a single 3-dimensional plot were prepared and axes of variation subjectively compared with the initial data for response to environmental gradients.

CLUSTAN groups were also superimposed as clouds of elements onto the three dimensional ordination to determine the degree of proximity or overlap of these clusters. In this way it was possible to see whether or not the clusters represented genuine dichotomies or artificial polarization of the ends of a continuum. Groups from CLUSTAN analysis of environmental variables were similarly superimposed on the ordination for comparison with the faunistic classifications and CLUSTAN faunistic station clusters were also added to the standard ternary sediment diagram in the method of McNulty et al. (1962), to observe the degree of overlap in sediment relationships.

2viiie Species diversity, richness and evenness

Species diversity of the macrofauna, using the H-statistic of Shannon & Weaver (1963), was calculated for all extensive survey stations using the formula:-

$$H = \frac{Ni}{N} \log_n \frac{Ni}{N} \quad ,$$

where:- N = total number of individuals in 0.05 m^{-2} (5 10x10cm cores)

Ni = total number of species 'i' in 0.05 m^{-2} (5 10x10cm cores)

This index is the one most commonly used in benthic diversity studies. Species richness - R and evenness - J were also calculated using the formulae given by Pielou (1966):-

$$R = \frac{S - 1}{\log_n N} \qquad J = \frac{H}{S}$$

where:- S = number of species in 0.05 m^{-2}

Although the concept of species diversity has been called into question by Hurlbert (1971), because of its insensitivity to richness and evenness, it was considered valid to calculate diversity when presented alongside those measurements. Sanders (1968), pointed out that 'H' is the index least heavily influenced by the numbers of individuals in the sample and therefore best for use with different values of 'N' as in the extensive survey.

H, R and J were calculated using a programmable calculator.

2ix Analysis of dynamics

2ixa Growth

Growth rates were determined by increments in mean individual size of recruitment cohorts and were therefore not genuinely indicative of growth rates of individuals. Only for Cerastoderma edule was it possible to determine the growth rate of individuals by using growth rings (see Chapter 8). These were used to construct standard Ford/Walford growth plots (Walford; 1946), where size at age 't' is plotted against size at age 't + 1' to give an indication of longevity and maximum attainable size.

2ixb Production, elimination and productivity

The removal-summation method of Crisp (1971), was used to estimate production and elimination by Nephtys hombergi, Hediste diversicolor, Eteone longa, Cerastoderma edule, Macoma balthica, Scrobicularia plana and Retusa obtusa. Other organisms were insufficiently numerous or too variable in occurence to produce values from which production could be calculated. For some of these P:B ratios calculated by other authors were applied to mean biomass estimates (as for older cohorts of Macoma and Hediste), to give a likely indication of production.

Production between two sampling dates was calculated from:-

$$P = n_2\ (\bar{w}2 - wi) + (ni - n2)\left(\frac{\bar{w}2 - \bar{w}i}{2}\right)$$

for each individual cohort where:-

ni = abundance of organisms on the first sampling occasion

n2 = " " " " " second " "

$\bar{w}i$ = mean individual weight on the first sampling occasion

$\bar{w}2$ = " " " " " second " "

and elimination from:-

$$E = (ni - n2)\left(\frac{\bar{w}i + \bar{w}2}{2}\right)$$

This assumes that:-

i) there is no migration into or out of the population

ii) mortality rate is constant between sampling dates

iii) growth and mortality rates are not size related

iv) recruitment is instantaneous at the time of sampling.

During recruitment no estimation of actual production of the 'O' group was in fact made. Production was assumed to be the increase in standing crop biomass of the 'O' group between sampling dates while recruitment was seen to be occurring as recommended by Chambers & Milne (1975a). Production and subsequent elimination by the 'O' group is therefore not taken into account.

Also, production of material lost to the organisms (gametes, partial predation and subsequent regeneration of (eg.) siphons etc.) is not included by the method.

Of necessity, abundance estimates used in the method have to be smoothed over time into a 'mortality' curve to eliminate effects of sampling error and population variability. Effects of apparent migration were likewise smoothed 'by eye' from the mortality curve to allow use of the removal-summation model.

Size-dependant mortality effects were apparent in most species (especially <u>Hediste</u> - Chapter 7), leading to periods of apparent negative production or to periods of apparent production in the winter.

Productivity ($\Sigma P:\bar{B}$ ratio), and elimination ratio ($\Sigma E:\bar{B}$ ratio), were calculated from mean monthly biomass over the twelve month sampling period and total production/elimination over that period for each cohort and for the whole population.

All calculations were performed using a programmable calculator.

2ixc Extrapolation

Estimates of production by the whole of each subcommunity were made by applying mean P:B* and E:B* ratios determined from intensive studies to whole community statistics determined from SPSS delimitation of variables within each cluster of CLUSTAN 1C analysis. This gave a very rough estimate of mean and range of production within each cluster.

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* B in this case is biomass recorded in the month of May in the intensive survey as the extensive survey was carried out in May/early June.

Total production and elimination of the whole area of mudflats was further extrapolated by muliplying total area of each community by production determined from application of P:B and E:B ratios to whole community biomass estimates. This assumes that:-

i) community TOPSILT occurs in all _Spartina_ marsh and all upshore soft silts

ii) community MIDMUD occurs in all flat and gullied silt/sand

iii) community SAND occurs in all hard sandflats

iv) productivity of _N. hombergi_ = that of _N. caeca_ at SAND stations.

From the number and scale of these assumptions it can be seen that such extrapolation is very tentative indeed and indicative only of the order of magnitude of productivity of the mudflats as a whole.

CHAPTER THREE

CHAPTER 3

ABIOTIC VARIABLES

Introduction

During the course of extensive and intensive surveys a number of environmental variables were recorded both to allow comparison with works of a similar nature in other areas and to investigate the relationships of the fauna with their abiotic environment. Tidal position and period of immersion, weather conditions, interstitial water content and salinity, sediment particle size and related variables, organic matter, and iron content were recorded. Linear, non parametric analysis (Kendall's Coefficient) between all these variables was carried out and the results presented together in Table 3a.

3i Tidal position and period of immersion

Table 3b documents actual downshore distance from M.H.W.O.T. and the relative tidal position as a percentage of total downshore distance of all sites of the extensive survey of May/June 1977. It was not possible to measure the period of immersion for these sites but this variable was recorded for the intensive survey sites for single spring and neap tidal cycles in July 1978, close to the summer minimum amplitude in the annual spring/neap cycle (see Fig 3i). Both days were relatively wind-free and it was not considered that wind effects altered the tidal period in any way as was observed during strong on-shore and off-shore winds. Tidal cover is recorded in Table 3c.

Particularly noteworthy is the absence of cover of site FI2 during neap tides, during which the surface of the mud dried and cracked during dry weather.

The spring/neap variations in cover also influences the interstitial water content and salinity. Sites receiving longer cover during each cycle will more nearly reflect the salinity régime of the overlying water-column and those exposed for longer periods will be more prone to the effects of precipitation and evaporation.

The spring/neap cycle of high and low tides for 1978-79 for Immingham, 10 km upriver of Hawkin's Point and on the south bank of the Humber is illustrated using data from Admiralty tide tables in Figure 3i. From this it can be seen that, fortuitously, all sampling dates of the intensive survey excepting March 1978, corresponded approximately to monthly spring low water and therefore variation in other variables, particularly water content and salinity, cannot be attributed to the position of the sampling dates in the spring/neap cycle.

3ii Air temperature and weather conditions

Mean weekly maxima and minima, together with the range of extremes from the Meteorological Office data for the period March 1978 to March 1979 are given in Table 3d and expressed graphically in Figure 3ii. Comparative data on sunshine, snow and frost days from the Barton School data for the period January 1975 to March 1979 is given in Table 3e and illustrated in Figure 3iii.

Absolute minimum air temperature recorded during the intensive study period was -4.6°C on a total of three occasions. These recorded minima appear surprisingly mild when the conditions of the 1978-79 winter are remembered and Meteorological Office staff pointed out that proximity of the recording position to the sea may have given a poor indication of more severe conditions experienced only slightly further inland. During early January and mid February remaining surface estuarine water froze over large areas of the Bight and large quantities of frozen mud, sea ice and snow were washed from the mudflats by the tide and deposited on the Spartina in a band of frozen material which reached one metre deep after strong onshore winds. This is the first record of such conditions since the extremely severe winter of 1962-63. Temperatures as low as -14°C were recorded at Hull. Beukema (1979), found the mean winter temperature in the Dutch Wadden Sea in 1978-79 to be 3°C lower than the longterm average. Ratcliffe (1979), found that the minimum temperatures in sediment did not fall below the air temperatures recorded by the University weather station at Withernwick, but in this study it must be concluded that the maritime influence prevented the local air temperature at Spurn Head from falling very low whilst temperatures on the mudflats became sufficiently low to freeze the estuarine water which was not found to fall below 18‰ salinity.

A maximum air temperature of 22.6^{o}C was recorded on 27th and 28th of July 1978 and the highest mean weekly maximum was of 19.1^{o}C for w/e 14th September 1978. This figure is again likely to be strongly influenced by the maritime position of the weather station and air temperatures over the mud surface are likely to have exceeded these figures. Dark areas of the mud not covered with water were felt to be significantly warmer than air temperature whilst sampling in July and August.

From the 1975-1979 data it is immediately obvious that the sampling period was distinctly cooler than the preceeding three years, with fewer sunshine days in the summer and considerably more snow and frost days. The winter of 1978-1989 terminated a period of exceptionally mild winters going back as far as 1971 (Beukema et al,; 1978, Beukema; 1979). Moreover the whole preceding period was further atypical in that, in addition to exceptionally mild winters, the summers of 1975 and 1976 were exceptionally sunny and dry, whilst that of 1978 was exceptionally wet. The sampling period must therefore be regarded as a particularly cool year during a period of variable climate.

The winter of 1978-79 also saw periods of extremely severe onshore gales, notably the nights of 31st January and 14th February 1979. Very severe winds were also noted on 11th and 15th September 1978.

3iii Interstitial water content and salinity

Sediment water content was not calculated for the extensive survey but data for the intensive survey sites are summarised in Table 3f and expressed graphically in Figures 3iv to 3viii. This showed little consistent variation with time and at four of the five study sites remained fairly stable over the whole study period. Only at FIV4 was there any appreciable variation with two maxima in the summer and a range of variation between 23.5 and 37.3% of total sediment weight. Water content showed significant correlation with particle size, sorting and organic matter ($P = 0.001$, 0.05 & 0.001 respectively), with higher levels in more poorly sorted finer sediments with higher sediment surface area for retention of water.

Interstitial sediment salinity of all stations of the extensive survey are recorded in Table 3g. The maximum range was between 23.0 and 32.5‰ in Spurn Bight and a minimum of 21.8‰ was found at Cherry Cob Sand, 9 km upstream from Hawkin's Point. No pattern was discernible in the Spurn Bight data and no downshore gradient in salinity was obvious. More easterly stations were not significantly different in salinity from those further west and no relationship was found between salinity and any other variable. It must be concluded that the salinity régime of Spurn Bight is relatively homogeneous within the above range, which is described as polyhaline in the Venice System and that those areas chosen for comparison with the Bight also fall within that range.

Variation in interstitial water salinity with time at the stations of the intensive survey are given in Table 3h and illustrated graphically in Figures 3iv to 3viii. Data from the Skeffling transect are included on a 3-dimensional graph in Figure 3ix to show variation in time and along the shore. A maximum salinity range of 18.5 - 35‰ was found, with a distinct cyclical change visible at Skeffling, with much higher interstitial salinities in summer than in winter, particularly at the upshore stations FI2 and FII2. This probably resulted from the effects of increased precipitation and freshwater flow in the Humber during the winter and increased evaporation in the summer months which would tend to be more extreme at the upper shore stations where tidal cover was shorter. A similar pattern was not visible with the Easington transect data and it may be that the pattern at Skeffling was significantly influenced by the increased rate of pumping of fresh land drain water onto the mudflats by the Yorkshire Water Authority pumps at Skeffling Clough during the winter.

3iv Sediment particle analysis

3iva Extensive survey

The distribution of particle sizes in terms of median particle diameter, degree of sorting, skewness and kurtosis and proportions of sand, silt and clay is described in Table 3j where stations are arranged into groups as per the results of cluster analysis (below). Sites were plotted on a triangular sediment diagram in Figure 3x, the sediment nomenclature following that recommended by Shepard (1954). Notable from this is the low proportion of clay in the samples - a maximum of 13% clay at FI2 from the Spartina zone within Spurn Bight and of 20% clay at MIII1 in the polluted mud at Pyewipes on the South Bank of the Humber.

Relationships between sediment characteristics were tested with Kendall's non-parametric correlation analysis and the results are included in Table 3a. Skewness and Kurtosis were found to be unrelated to any other variable and their analysis was discontinued in the intensive survey. Sorting was significantly related to median particle diameter ($p = 0.001$), with coarser sediments more well sorted. The relationship between these variables is illustrated in Figure 3xi. As might be expected, proportions of sand, silt and clay were significantly ($p = 0.001$) related both to median particle diameter and degree of sorting (Table 3a).

The proportions of sand, silt and clay were also significantly related to the tidal position, measured as percentage of total downshore distance ($p = 0.004$, 0.01, 0.002), although no significant relationship was found between median particle diameter and tidal position. Downshore sites contained much higher proportions of sand and upshore sites higher proportions of clay.

Cluster analysis was carried out on the sediment data using median particle diameter, degree of sorting, skewness and kurtosis. The resulting dendrogram is given in Figure 3xii and the descriptions of the sedimentary characters in Table 3j are grouped according to the cluster analysis. It is immediately apparent that the data evenly dichotomised at high levels of similarity, indicating imposition of a classification onto a homogeneous cline in sediment parameters.

Mean values of all variables used in the analysis were computed for each group or subgroup and corresponding exclusive pairs were compared with the non-parametric approximation to the Student's 't' test (Nie et al,; 1975), after application of an 'F' test to the variance of each showed the variance on most variables to be significantly different. The results are presented in hierarchical fashion in Table 3k.

The major division is into sandy and silty sediments - groups 1 and 2, those with a ømedian of 4.0 and above (mean 4.73) classified together and those below 3.8 forming a similar, if less homogeneous cluster with a mean ø median of 2.88. These are significantly different (p = 0.001) as are the coefficients of sorting.

This variation in sediment characteristics is, however, unlikely to be discontinuous and the exercise of cluster analysis was carried out mainly for comparison with similar treatment of faunistic data. It was repeated with the inclusion of particulate organic matter and iron content data and the results discussed below. (3vii).

3ivb Intensive survey

Variation in median particle size and degree of sorting and the proportions of sand, silt and clay of sediments are given in Table 3l and 3m and illustrated graphically in Figures 3xiii to 3xvii.

The Spartina band sediments of FI2 showed least variation with time with maximum variation between ømedian 6.05 and 6.7. This probably results from the protection from erosion of the sediment by established Spartina sward. Station FII2 showed a cyclical variation in ømedian with a steady decrease in median particle diameter over the summer and autumn reaching a minimum in November. This was apparent from direct observations as the upshore sediments at Skeffling (and Easington), became progressively more difficult to walk over. Median particle size and the proportion of sand increased rapidly from November onwards as more severe winter weather selectively eroded away finer sediments deposited over the summer. At both upshore stations at Skeffling there was no significant correlation between median particle diameter and degree of sorting.

At the three remaining sandier stations there was a tendency towards the higher proportions of silt as summer and autumn progressed with corresponding decrease in median particle diameter. At GIII4, however, there was a considerable increase in sandiness until July which cannot be explained in terms of unusual weather conditions. After November particle size increased considerably during the winter months as silts were re-eroded from the sediments.

The degree of sorting was significantly (p = 0.001), correlated with particle size at the three sandier stations, with coarser sediment being more well sorted.

The triangular sediment diagrams show the stability of particle distribution at each station and the finer upshore sediments of FI2 and FII2 were found to be the least variable with the greatest stability within the Spartina. Both can be described mainly as silts with clay. Of the sandier stations GIV3 showed most stability, mainly a silty sand, whilst FIV4 and GIII4 fluctuated considerably in proportions of sand, silt and clay. FIV4 can be described as a sandy silt/silty sand station whilst GIII4 varied considerably between silty sand, sand with silt and sand.

3v Sediment level

Changes in sediment level are given in Table 3n and shown graphically in Figures 3iv to 3viii. It was not possible to measure such changes at FI2 owing to continual loss of the marker between sampling occasions.

At FII2, FIV5 and GIV3 there was a gradual increase in sediment height over the summer with a maximum increase in sediment depth of 14cm at FII2 by November. During the winter months there was a considerable reduction in sediment level at all sites between November and January. At FIV4, however, sediment height increased by 3cm between January and March whilst decreasing considerably at all other stations. This indicates a redistribution of sediment about the Bight, probably by the gales of 14th February which was also illustrated by increases of the fauna at FIV4 whilst decreasing elsewhere (refer relevant chapters). Redistribution of sediment by high winds, possibly from east to west along the ebb/flood drainage of the Bight may be a common feature of these mudflats.

Only at GIII4 was the pattern mainly of erosion rather than deposition, even during the summer months, resulting in an overall decrease in sediment height of 10cm over the year. Overall changes at other sites varied from a net increase of 6cm at FIII4 to a net decrease of 10cm at GIII4 Ratcliffe (1979), found overall changes at Skeffling of between +6 and +10cm over the period January 1974 to January 1976.

3vi Detritus and organic matter content

During sorting of sieved samples records were made of the identification and subjective assessment of abundance of macrodetrital remains. These are listed in Table 3p, divided into autochthonous and allochthonous remains. It can be seen that the latter predominate and the source of detritus and thus nutrients for these mudflats is largely of terrestrial/saltmarsh origin and must be washed from the surrounding Spartina zones and brought downriver by the Humber. Odum (1961), and de la Cruz (1973), both concluded that allochthonous material is particularly significant in the nutrient budget of intertidal mudflats. Particularly interesting was the composition of the insect remains, including large numbers of elmid and helophorinid beetle elytra indicating a significant contribution to the detrital composition from the River Hull, the only likely source of such insects in the area.

Evidence of sewage contamination of the mudflats is given by the composition of the anthropogenic allochthonous detritus, although this is likely to add to the nutrient budget rather than have any adverse effect.

Proportion of organic material by weight in the sediments of the extensive survey is given in Table 3q, with a maximum of 8.4% at HI2 and minimum of 0.2% at LIV6. Sandy areas outside the Bight had low total carbon, even when observed to be contaminated with coal fragments and therefore this must be regarded as an insignificant source of error in the results. The polluted mud site at MIII1 had a very high total carbon content (3.5%), but this site was observed to be heavily polluted with hydrocarbons.

Total organic content was highly significantly correlated with sediment median particle size, (Figure 3xviii) degree of sorting and iron content (all at $p = 0.001$) and tidal height ($p = 0.009$). Highest organic matter levels were invariably in upper shore fine sediments and were predictably high within the Spartina zone and low in clean coarse sands.

Organic matter content of sediments in the intensive survey are given in Table 3r and expressed graphically in Figures 3iv to 3viii. Highest levels were again found in the fine upper shore sediments of FI2 and FII2 and these exhibited a cycle reaching a maximum in midwinter, probably corresponding to the die-back and breakdown of the Spartina, and then falling considerably between January and March resulting from erosion by winter gales. Organic content showed little consistent variation with time at the other stations. Organic levels at these stations were not significantly reduced during the winter, notwithstanding the erosion by the winter gales.

During the intensive survey, organic matter was related to median particle diameter ($p = 0.001$), water content ($p = 0.001$) and the degree of sorting ($p = 0.09$) indicating similar deposition characteristics of organic matter to those of silt and clay.

Dense microalgal blooms and cover by macroalgae, especially Enteromorpha sp., were noted during the summer months until November, at all three stations at Skeffling although not at Easington. The mud surface between the Spartina at FI2 also became covered with Cladophora sp., whilst dark green patches of microalgae became slightly raised (3-5mm) above the rest of the mudsurface and less smooth than surrounding mud at FII2 and FIV4, presumably by facilitation of deposition of finer particles. The contribution of autochthonous primary production to the nutrient cycle must therefore be regarded as likely to be of great significance but was not studied further in the present work.

3vii Iron content

The iron content of sediments as percentage by weight from the extensive survey is given in Table 3q and ranged from 7.2 - 13.4% in Spurn Bight sediments. An extreme figure of 16.4% iron was found at MIII1 but this area was subject to chronic pollution with hydrated ferric oxide from a titanium dioxide plant such that the mudsurface was blanketed with bright orange pollutant.

The iron content of unpolluted muds largely results from concentration by anaerobic bacteria and as such was found to be strongly correlated with the organic content of the mud ($p = 0.001$). Once deposited however, mainly as ferrous sulphide, the iron is easily re-oxidised when reworked by bioturbation, to more stable ferric compounds which remain in the sediment or are redistributed to other areas. Total iron cannot therefore be used as an indication of anaerobiosis and analysis for iron was not repeated for the intensive survey.

Cluster analysis of sedimentary parameters was repeated as described above with the inclusion of particulate organic carbon and iron data. The resulting dendrogram is illustrated in Figure 3xix. The clusters are almost identical with those produced from sediment data alone with the only significant changes being of transfer of stations CI2, DV6 and JIII6 to 'sandier' subgroups, all having lower than average carbon and iron content when compared with other members of their original subgroups. Carbon and iron content were found to be significantly different between all groups and subgroups (Table 3k). However, mixed unit data were used - see p38.

3viii Implications for the fauna

The salinity régime of Spurn Bight is likely to favour a euryhaline marine biota with little or no effect of variations in salinity over the area in question.

Tidal cover is obviously of importance to the infauna, particularly to obligate suspension feeders such as Cerastoderma and Mya, and long periods of exposure at the top of the shore help to explain the absence of such animals at these sites. During neap tides the absence of cover at the top of the shore, particularly amongst the Spartina, must be particularly limiting to the infauna which must at this time rely on interstitial water to prevent desiccation.

The effects of very severe winters, such as that of 1978-79 on the benthos is well documented, particularly for the exceptionally cold winter of 1962-63 (Jones; 1963 and Crisp; 1964a & b), and the sequence of severe winters in the early 1940's (Smidt; 1944). Beukema et al. (1978), studied macrofauna in the Dutch Wadden Sea in relation to a period of particularly mild winters between 1971 and 1977 and found that certain species known to be susceptible to low temperatures, notably Lanice conchilega, Nephtys hombergi and Tellina tenuis increased dramatically during that period whilst more cold tolerant species, especially Macoma balthica and Arenicola marina declined as warm winter temperatures inhibited the migratory habits of 'O' group individuals. The ice conditions of the 1978-79 winter terminated a long period of mild winters (Beukema; 1979), and are likely to have caused the observed extinction of Scrobicularia plana after its recent re-establishment in the Bight. The decline in numbers of other species, especially juveniles, is more likely attributable to erosion from the sediment by onshore gales.

The effects of sediment texture, in particular particle size distribution and degree of sorting, on the benthos have been well studied with many species restricted within a range of sediment parameters. Coupled with grain size is the availability of nutrients in the form of particulate organic matter and the deposition properties of organic material is similar to those of silts and clays, making the finer sediments considerably higher in nutrient availability than well sorted sands and consequently able to support a larger biomass. By offering a larger surface area, finer substrata also encourage higher production by microalgae and bacteria than do sands, again promoting higher secondary production in the finer sediments.

Temporal variations in particle size and sediment mobility are known to limit diversity (Sanders; 1968), by reducing the 'predictability' of the environment. Changes in particle size accompanied by erosion and deposition will obviously limit species with particular sediment preferences and such changeability is likely to cause repeated elimination of settlements of species with narrow sediment tolerances with resultant low productivity when compared with sediments of more stable particle composition.

The relations of individual species with abiotic variables is discussed more fully in the relevant chapters.

Summary of Chapter 3

Data on all abiotic environmental variables measured during both extensive and intensive surveys are presented in table and graphic form, including tidal position, air temperature, interstitial water content and salinity, sediment median particle size, degree of sorting, skewness and kurtosis, organic carbon and iron content and changes in sediment level. Correlation analysis showed several of these variables to be significantly related.

Cluster analysis was carried out using environmental variations for comparison with fauna analysis and produced groupings of stations for the extensive survey. Although representing part of a continuum rather than discontinuous groupings the clusters were found to be significantly different in terms of median particle size, degree of sorting, organic matter and iron content.

Variation in environmental parameters was recorded over time and highlighted in particular the severity of conditions during the winter. Translocation of sediment from east to west during gales is indicated. A net accretion of sediment is recorded from sampling stations at Skeffling and net erosion from stations at Easington.

Finally the implications of the described variables on the infauna of Spurn Bight is briefly considerded.

CHAPTER FOUR

CHAPTER 4

WHOLE COMMUNITY ANALYSIS

Data from the extensive survey were analysed in order to identify recurrent species associations, to determine the extent of those associations within the data, and to test the discontinuity of the data.

4i Abundance and biomass

Density and, where estimated, biomass of all taxa used in the analysis are presented in Table 4a and the occurrence of rarer species not used in the analysis but found in occasional samples is recorded in Table 4b. Species composition at each site, in terms of numbers and biomass of major macrofauna species is illustrated in 'pie' form on maps of Spurn Bight in Figs 4i and 4ii. Data on total numbers of individuals of all species and total community biomass are recorded in Table 4c and the relationship with abiotic variables included in Table 4d.

Abundance of individuals was found to be strongly correlated with tidal height, median particle diameter and the degree of sorting. Highest biomass figures were from midshore stations with higher densities of larger individuals of the main species than in upper shore sediments. Biomass was extremely low in lower shore sandy stations, probably reflecting the low level of available nutrients in the form of particulate organic matter and the instability of the substrate.

The relationship of total density and biomass with tidal position is illustrated in Fig 4iii.

4ii Species number, diversity, richness and evenness

The value of each of these parameters at all sites of the extensive survey is included in Table 4c and their relationship with abiotic variables given in Table 4d.

The maximum number of species recorded at any one station was thirteen in Spurn Bight and eighteen at Horseshoe Point. Within the Bight, the total number of species at a station was weakly negatively correlated with tidal height ($P = 0.06$), but unrelated to sediment parameters. Species richness, evenness and diversity were all more strongly correlated with tidal height and also negatively correlated with median particle diameter, the degree of sorting and the organic content. The relationship of diversity with tidal height, median particle diameter and the degree of sorting is illustrated in Figs 4iv and 4v.

Similar variation in diversity along particulate shores have been observed by previous authors. Johnson (1970), attributed an upshore decrease in diversity within a sediment type to a stress gradient brought about by increased exposure times. Such a relationship is obscured within Spurn Bight by the zonation of substrata with tidal position and clines in diversity functions observed probably resulted from a number of synergistic environmental variables.

It must be remembered that these dynamic functions vary considerably with time. These have been studied in detail in various benthic communities (e.g. Buchanan et al.; 1978, Watling; 1975), and have often been found to fluctuate cyclically with season. Numbers of juveniles are usually at a maximum during the summer leading to reduction in measured diversity and increase in evenness if differences in population structure are not taken into account.

It was not considered practical to continue to measure functions of diversity etc. during the intensive study as this would have necessitated the counting of all species. Diversity analysis of the extensive survey data, however, proved useful as a comparative measure between areas of different sediment facies.

Diversity and evenness were lowest on the upper shore silts, reflecting the numerical dominance of one or two species, notably Macoma balthica and Hydrobia ulvae at those stations. Rhoades (1974), postulated that few taxa have managed to adapt to the more difficult conditions of silt substrata and Gray (1974) pointed out that sandy sediments have a greater diversity of particle sizes and, therefore, offer a greater variety of niches leading to higher diversity.

The measured values of diversity are low when compared with fully marine biota and the low diversity of estuarine infauna communities has been well documented (Boesch; 1974).

4iii Correlation analysis

The 't' tested significance of Kendall's Rank Correlation Coefficient between all pairs of species is presented in trellis form in Fig 4vi.

Three apparent associations are revealed, with certain species intermediate between them. These proved either to be species present at very low density with accompanying high levels of sampling error, or more widespread species not restricted to any particular association.

The first of these associations, occurring to the bottom right of the trellis diagram, is of three species only and has stong positive correlation within the group and strong negative correlation with almost all other species. Members of the group were negatively correlated with median particle diameter, the degree of sorting and the organic content of the sediment and positively correlated with downshore distance.

The middle, largest, association is relatively homogenous and separated from the first by two species with only weak correlation with other species. Members of this group have little significant correlation with any environmental variable, although there is a slight trend towards weak positive correlation with median particle diameter. There is strong negative correlation with members of the first group but only a weak trend towards negative correlation with members of the third.

The remaining group is less homogenous than the two previous and members are positively correlated with median particle diameter, the degree of sorting and organic content and negatively correlated with downshore distance.

The correlation matrix is a relatively weak measure of species association, with analysis only of pairs of individual species. Its value lies in the identification of trends in the distribution of species in relation to environmental variables and these have been described in the relevant chapters. It is not easily possible with this method to investigate the extent of these associations within the data but the demonstration of three, fairly homogenous, associations indicated that multivariate treatment of the whole station and species data would be worthwhile.

4iv Cluster analysis of species

Early attempts at cluster analysis using the Czekanowski similarity coefficient and group average sorting strategy on the complete, untransformed data matrix revealed a very loose cluster structure with many outlying species with no particular affinities. Examination of the original data showed most of these to be relatively rare species, represented by very small numbers of individuals. These were eliminated from the data for further analysis.

Analysis using log-transformed data to reduce abundance weighting produced a dichotomy into sand and silt dwelling assemblages - Fig 4vii. Each assemblage was subdivided into more widespread species with less restricted sediment preferences and a less widespread group with more stenotypic sediment preferences.

Others have found similar animal/sediment relationships for this group of intertidal infaunal species, notably Anderson (1972), in Morecambe Bay, Boyden & Little (1973), in the Severn Estuary, Kay & Knights (1975), in South East English estuaries, and Withers (1977), along the South Wales coast. Ratcliffe (1979), used a similar technique to that used in this survey, on data from a single transect at Skeffling which did not extend into the Spartina marsh, nor into the downshore sandflats. The main difference between his analysis and the present work is his inclusion of Cerastoderma edule in the uppershore silt assemblage. He also included Protohydra leuckarti, Lumbricillus lineatus, Paranais littoralis and Cirriformia (=Audouinia) tentaculata in his analysis, none of which species were commonly found in this study.

4v Cluster analysis of stations

Similar treatment of data from individual stations, also using log-transformed data, [illegible] produced a dichotomy into sand and mud clusters (Fig 4viii), with the South Bank polluted mud station MIII1 as a very dissimilar outlier. The sand cluster, hereafter referred to by its S.P.S.S. subfile title, SAND, was less cohesive with relatively low similarity levels between individual stations and with Spurn Bight stations more similar to each other than to South Bank stations NII6 to PIV6. Such low similarity is likely to be caused by lower densities of a greater number of species at sandy stations, giving rise to a greater degree of sampling error.

With the exception of station KV2, which is discussed more fully below, the finer sediment stations were much more similar to one another, the cluster being complete at the 48% level. This was subdivided into upshore silty stations (S.P.S.S. subfile *TOPSILT*), and midshore sandy silt and silty sand stations (subfile *MIDMUD*). Stations FI2 and AIII2 are also differentiated from the rest of TOPSILT at the 48.5% level. Reference to the original data shows these to have in common extremely high densities of *Hediste diversicolor* and *Edukemius benedii*, very low densities of *Pygospio elegans* and complete absence of *Nephtys hombergi*.

The extent of each cluster in relation to sediment composition is shown on a ternary sediment diagram in the method of McNulty et al. (1962), in Fig 4ix This indicates a high degree of overlap between clusters in terms of proportional composition of the sediments in which they occurred.

Comparison of cluster analysis of the stations based on the fauna with that carried out on environmental variables (Chapter 3iv, Figs 3xii & 3xix), identifies considerable difference between the two. Stations of the faunal cluster MIDMUD were approximately evenly divided between silty and sandy sediment clusters. It appears that the cluster analysis of sediments imposed a very even series of dichotomies on a continuum in sediment nature and the response of the animal communities was not distributed evenly along the particle size gradient and is probably complicated by other variables including the tidal position.

The S.P.S.S. CONDESCRIPTIVE delimitation of each cluster is given in Table 4e, together with the 't' tested significance between the means of each variable between each pair of clusters. For this purpose no stations outside Spurn Bight were included so that the analysis was relevant only to the main area of interest. The outlying station KV2 was also omitted for reasons described below.

The mean of each variable from all cores from all stations of each cluster together with the overall range and standard deviation is expressed as a proportion of the maximum value reached by each variable in Spurn Bight, in diagramatic form in Fig 4x, so that areas of overlap between clusters can be identified.

Certain species were found to be restricted entirely to one or another of the clusters but the degree of overlap was considerable. 't' testing the difference between means of all variables between pairs of clusters indicated high levels of significance between most pairs of variables. Differences in population structure of individual species between clusters are discussed in the relevant chapters.

4vi Description of clusters

TOPSILT

Cluster TOPSILT occurred in fine, very poorly sorted organic rich silts and sandy silts towards the upper part of the shore. There was found to be moderately high biomass when compared with midshore stations, with very high numbers of individuals and low diversity, characterised by high densities of Hediste diversicolor, Eteone longa, Edukemius benedii, Hydrobia ulvae, unidentified turbellarians (PA1), and tabanid larvae with the occasional presence of Scrobicularia plana and Corophium volutator. Very high densities of Macoma balthica were mainly of the smallest individuals and this species consequently contributed less to the biomass than in other clusters where larger individuals were more predominant. Pygospio elegans, Streblospio shrubsoli, Nephtys hombergi, Arenicola marina, Retusa obtusa, Cerastoderma edule and Mya arenaria all occurred very sporadically at very low densities. No species characteristic of cluster SAND were found at any TOPSILT station. High densities of meiofauna were found with proportionally fewer ostracods, gastrotrichs and kinorhynchs than in other clusters.

MIDMUD

Cluster MIDMUD occurred in poorly sorted, medium organic content sandy silts and silty sands, mainly in the upper middle and middle of the shore. Very high biomass was found but lower numbers of individuals than TOPSILT stations and higher diversity. The biomass was dominated by high densities of larger sized Macoma balthica and also with high densities and biomass of Cerastoderma edule, Mya arenaria, Retusa obtusa, Nephtys hombergi, Arenicola marina and Pygospio elegans. There was sporadic occurrence of Hydrobia ulvae, Streblospio shrubsoli, Edukemius benedii, Eteone longa, Nephtys cæca and Bathyporeia pilosa. Very high densities of all meiofauna groups were found.

SAND

Cluster SAND was found in well sorted, low organic content fine to coarse sands, mainly towards the lower end of the shore and including the beach at Spurn Head. Very low densities of individuals and low biomass were found but with higher diversity than in TOPSILT and MIDMUD clusters. Characteristic species were Nephtys cæca, Bathyporeia pilosa and tanaidaceans with sporadic high densities of Mya arenaria and low densities of the largest individuals of Macoma balthica. Occasional specimens of Arenicola marina, Eteone longa, Nephtys hombergi, Pygospio elegans and Cerastoderma edule were found. There were much lower densities of meiofauna with relatively higher numbers of 'soft' meiofauna, particularly the Gastrotricha. Large numbers of species were present only as isolated individuals, indicating even higher diversity. These included Eteone lactea, Scoloplos armiger, Prionospio cirrifer, Travisia forbesi, Eurydice pulchra, Haustorius arenarius and Corophium arenarium. Similar in character were the South Bank sandy stations NII6 - PIV6 (S.P.S.S. SOUTHSAND), with higher biomass, particularly of M. balthica and even greater diversity including more very infrequent species.

Station MIII1 - Pyewipes

The sediment was of soft silt-with-clay, chronically polluted with sewage, olefines and ferric oxide giving very high carbon and iron levels. There was very reduced diversity but high biomass dominated by Edukemius benedii, Tubifex costatus, Pygospio elegans and Manayunkia aesturina, all species noted to be pollution tolerant, opportunist species characteristic of disturbed sediments (Gray; 1976). A high density of nematodes was the only meiofauna present.

Station KV2 - West of the Old Den

The sediment was of very fluid, sandy silt with a peculiar mixture of fauna including very small individuals of species characteristic of sands and muds as well as stranded pelagic organisms (Pseudocuma longicornis and Neomysis integer). Although composed of very fine sediments, this area is subject to very strong tidal currents and it may represent an area of continual deposition and resuspension, possibly by de- and re-flocculation. This is indicated by the very high water content of the sediment - over 50% by weight. It would appear that the fauna is derived largely from deposition of juveniles of species eroded from other areas.

It would appear that the fauna of clusters TOPSILT and MIDMUD correspond well with the 'classic' boreal shallow mud community described by Jones (1950), - the Macoma balthica community of Petersen (1913), and Thorson (1957). This is characterised by Macoma balthica, Arenicola marina, Mya arenaria, Cerastoderma edule, Corophium volutator and Hydrobia ulvae and may include Nephtys hombergi and Scrobicularia plana. Cluster SAND has elements of the boreal shallow mud and the boreal shallow sand communities (Jones op. cit.) and may represent a transition between the two. Typical species of the boreal shallow sand community, the Tellina tenuis/Tellina fabula community of Thorson, are Nephtys cæca, Bathyporeia sp. and Arenicola marina but other 'typical' species of that assemblage are either absent from SAND or replaced by the similar ecotype from the Macoma community.

The Old Den

While not sampled as part of the extensive survey, a list of the fauna and flora for this area was determined from several visits and from reference to prior work on the area (Morgan; 1969). It is unique within the Humber Estuary as the only area of intertidal shingle and has a very diverse fauna containing both rocky and soft shore elements.

Macoma balthica is still the dominant member of the infauna, with occasional Cerastoderma edule and numerous Mya truncata, a chacteristic shingle dwelling species. Littorina spp., Hydrobia ulvae and Retusa obtusa were found to be present in small numbers and the most abundant gastropod was Nucella lapillus, predating the abundant barnacle population on the stones as well as the smaller bivalve species. Feeding relations of Nucella on the Old Den are discussed by Morgan (1972). Polychaetes include Hediste diversicolor, mainly under stones, Nephtys hombergi, low numbers of Arenicola marina and a very dense population of Amphitrite johnstoni with its commensal Gattyana cirrosa. Barnacles, Cyathura carinata and Carcinus maenas were the only abundant crustaceans. The whole area supported a luxuriant epiflora and epifauna with green, brown and red algae, mussels, barnacles thecate hydrozoans and occasionally bryozoans. The fauna of the Old Den represents a continuation of the 'boreal shallow mud' association into the 'boreal shallow rock' association of Jones (1950), and illustrates the continual nature of community differentiation.

The Strandline

This was not included in the sampling programme but represents a fairly discrete community relying on imported nutrients in the form of dead seaweed, Spartina debris, driftwood and human jetsam at the upper limit of the tide extending to E.H.W.S. level. Primary consumers were observed to be podurid springtails, mites, woodlice, dipteran larvae mainly of the families Muscidae and Coelopidae, histerid, hydrophilid and tenebrionid beetles and crustaceans of the genera Orchestia, Talitrus and Ligia as well as decay fungi. Beetles of the family Carabidae and Staphylinidae were present as secondary consumers with six halophyllic species of the genus Bembidion and one species of Notiophilus, specialist predators on springtails and mites. The larger carabids (excluding Broscus cephalotes which is a specialist predator of talitrid amphipods), staphylinids and spiders are predatory on other insects, particularly the dipteran larvae. The carnivorous beetles were seen to venture into the Spartina marsh, presumably to prey on the population of the large springtail Anurida in this region. Additionally, two species of halophyllic wood-eating beetles were present - Nacerdes melanura and Pselactus spadix, utilizing the large accumulation of driftwood, both natural and anthropogenic, scattered around the Bight. Insects of certain groups appeared to be subject to considerable parasitoid predation by ichneumenoids and proctotrupoids present among the litter. Top predators of this community were observed to be turnstone, Arenaria interpres, and, along the peninsula, sanderling, Calidris alba, together with terrestrial passerine birds. The feeding distribution of the first two species, in Spurn Bight is described by Tasker & Milsom (1979).

The synecology of this type of community appears to have been studied neither by estuarine ecologists nor by entomologists and would repay further investigation as a mixture of terrestrial and marine species. The nutrient resource is very large at certain times of the year and the productivity of the invertebrates utilizing it may be very high. A speculative food web for the observed species is outlined in Fig 4xi.

4vii Ordination

In order to test the degree of discontinuity produced by CLUSTAN analysis, 2- and 3-dimensional ordination was performed after data had been double standardised, using similarity axes based on dissimilar pairs of stations (axis x; FI2 - DV6, axis y; FIV4 - PII6, axis z; KV2 - HI2). The results are illustrated in Figs 4xii - 4xv.

By this method, a three way division into TOPSILT, MIDMUD and SAND clusters is not obvious. Discrete clouds of elements are not apparent, although there is an aggregation within some of the sandy silt and silt stations corresponding to parts of TOPSILT and MIDMUD.

Superimposition of CLUSTAN analysis of stations based on environmental data (Fig 4xvi), indicated that a gradient of particle size existed through the ordination. Element clouds overlapped more than those based on fauna-based clusters (below), but a similar sequence across the ordination was apparent. A second axis of variation was identifiable among stations of finer sediment composition, that of downshore distance, although this was not apparent among sandy stations. No third axis of variation appeared to be present.

Superimposition of fauna-based clusters onto the 3-dimensional ordination (Fig 4xvii), shows that the three clusters are almost mutually exclusive with only slight overlap between MIDMUD and TOPSILT element clouds, involving a single station from each, and no overlap at all with cluster SAND. Aberrant stations MIII1 and KV2 do not fall within the dimensional space of any of the clusters.

The proximity of TOPSILT and MIDMUD indicates that these clusters represent ends of a continuum and that the dichotomy between them is an artifact of the clustering procedure and that there is no natural boundary between mutually exclusive communities. The degree of overlap in species composition and sediment relations (Figs 4ix & 4x), would support this.

Cluster SAND is more diffuse on the ordination, reflecting the lower degree of similarity between the more diverse station elements, but is discrete from TOPSILT and MIDMUD. The spatial separation of SAND and the other clusters is less than most of the inter-element divisions within SAND and this again indicates a continual gradient rather than exclusive dichotomy between communities.

The degree of specificity of those species occurring only in the more coarse sediments appears to be greater than that of species found mainly in silts (with the exception of tabanid fly larvae which need vegetation cover of the *Spartina* as sites for oviposition). These are the more stenotypic members of the 'classic' communities of Jones (1950) and Thorson (1957).

Anderson (1972), found very simlar continuous variation in a *Macoma* dominated mudflat in Morecambe Bay, from an upper shore *Hydrobia*/*Corophium*/*Macoma* assemblage (formerly including *Scrobicularia* before the winter of 1962-1963), with continuous gradation to downshore sandflats dominated by *Tellina tenuis*, although she found *Nephtys hombergi* to prefer the sandier end of the sediment gradient unlike the present findings in Spurn Bight.

Kay & Knights (1975), also found similar subdivisions within a classic *Macoma* community covering large areas of flats in South East England with silty areas dominated by *Hydrobia*, sandy mud by *Cerastoderma* and low biomass sands by *Nephtys cæca*.

The present study supports the continuum idea of community differentiation put forward by Sanders (1960) and Mills (1971), - individual species react separately to the whole range of environmental gradients within a region to produce continuous variation in community structure rather than reacting together as a discrete unit.

The almost non-overlapping nature of the CLUSTAN element clouds when superimposed on polar ordination, however, together with the high degree of significance of the difference of the means of most variables between them (Table 4e), justified continued separate treatment of the clusters as convenient units for extrapolation of individual species dynamics estimates to whole community data (Chapter 11).

Summary of Chapter 4

Data from an extensive survey of sites within and outside Spurn Bight during the early summer of 1977 are presented together with measures of species diversity, richness and evenness, which were found to be related both to tidal height and sediment facies.

The whole data matrix was analysed by correlation and similarity/cluster analysis of species and stations and indicated differentiation into upper shore silt (TOPSILT), middle shore silt/sand (MIDMUD), and lower shore sand (SAND), assemblages. The clusters of stations were statistically defined for future extrapolation of estimates of single species dynamics from more intensive studies and their association with their abiotic environment delimited for inference of likely community composition from environmental information. Community structure is described in comparison with results from similar studies.

Polar ordination of sites showed that although these assemblages were almost mutually exclusive in dimensional space, their proximity indicated that the clusters were artificial polarizations of an essentially continual cline in community composition from silty to sandy conditions.

The significant difference between clusters and their lack of overlap in the ordination was considered sufficient to continue their further use as convenient units for further analysis.

CHAPTER FIVE

CHAPTER 5

THE FAUNA AND FLORA OF SPURN BIGHT

Introduction

In addition to my own observations, I have drawn heavily on previously published works for the construction of this annotated list. Petch (1907), Morgan (1969), the Yorkshire River Authority biological survey reports of 1971 - 1973 and Ratcliffe (1979), list invertebrates. Fish are recorded by Riley (1973), Brennan (1973), and Forsberg (1977) and birds by Tasker & Milsom (1979). The flora is described by Crackles (1966) and Boatman (1974). Doubtful records are indicated by the use of brackets.

Invertebrates

5i Protozoans- Foraminifera

Calcareous forams were undoubtedly among the most abundant large microfaunal organisms in all sediment conditions from coarse sand to very fluid silt. It was possible to differentiate about a dozen forms subjectively, and it is unlikely that the actual number of species was very much higher although Lipps and Valentine (1970) point out that species diversity of forams is fairly low in muddy bottom shelf communities. No attempt was made to identify the species present, nor to work out abundance save on single cores from each station of the Skeffling transect in May 1977. Living specimens could generally only be differentiated from dead tests by the use of Rose Bengal stain.

Single 4cm cores from stations FI2, FII2, FIII4, and FIV4 produced 25, 347, 574 and 481 specimens respectively. This corresponds to densities of 19,800, 276,100, 456,700 and 382,700 individuals per square metre.

Literature on foram productivity is scarce - Boltovsky and Lena (1969), produced data from which a mean individual weight for an 'average foram' of 0.00443mg and a P:B ratio of 11.37 can be worked out for a Patagonian mud flat. Application of these figures to the Spurn Bight data give standing crop biomass figures of 0.087, 1.22, 2.02 and 1.70 gm m^{-2}. The productivity figure cannot be applied with any justification as the two populations are likely to be very different and the May biomass is unlikely to be representative of the mean annual biomass.

Foram densities are rarely quoted in general benthic surveys although a density of 2.5 x 10^6 m^{-2} is quoted by Phleger (1960), for an undisclosed locality. With such a high biomass they are likely to be important links in the food chain as primary consumers of diatoms and dissolved organic matter (Boltovsky and Lena; 1969). They are often important constituents of the diet of deposit feeding bivalves and gastropods (Morton; 1958), and are said to form the principal diet of the Retusiidae (Mollusca: Opisthobranchia), (Bacescu and Caraion; 1956, Morton; 1958, Moore; 1961, Burn & Bell; 1974).

5ii Coelenterates

5iia Hydrozoans

Protohydra leuckarti Greef

Ratcliffe (1979) recorded this species as occurring intermittently at Skeffling, on one occasion at a density of 10,000 m^{-2}. It was not encountered at all in this survey.

Laomedea flexuosa Hincks

Common on larger pebbles on the Old Den.

Obelia dichotoma (L.)

Recorded from wooden groynes at Spurn by Langston (1972).

Obelia geniculata (L.)

Recorded from the lifeboat station pier at Spurn by Langston (1972).

Petch (1907) recorded three further species of Campanulariidae from Spurn Bight, Campanularia angulata Hincks, Obelia gelatinosa Pallas, Gonothyraea loveni (Allman).

Dynamena (= Sertularia) pumila (L.) - sea oak, Kirchenpaueria (= Plumularia) pinnata (L.), Tubularia larynx Ellis & Sollander.

Recorded from the lifeboat station pier and on groynes at Spurn by Langston (1972).

5iib Scyphomedae: Jellyfish

Aurelia aurita (L.) common jellyfish.

Recorded in sweepings from Spurn Head by Levell (1971).

5iic Anthozoans: sea anemones

Petch (1907), Morgan (1969), and Squire (1973) recorded the following species from the Old Den, and Spurn Head. Searches were made but no anemones were found in 1977. Actinaria equina (L.) - beadlet anemone, Taelia crassicornis (Müller) - dahlia anemone, Anemonia sulcata (Pennant) - snakelocks anemone, Sagartia nivea Gosse.

5iii Platyhelminthes: flatworms

An unidentified flatworm was occasionally common in samples. A single species appeared to be present and it was included in the community analysis, coded 'PA1'. The maximum density recorded during the May/June survey was 380 m^{-2} at DI3 although it occurred more commonly at densities of between 80 - 160 m^{-2}. It was found only in muddy sand, (ϕ median, 3 - 4), but a very similar species, coded 'PA2' was found in coarse sands on the south bank (sites NV6, PII6, PIV6). Both species are illustrated by drawings - Figure 5i. During the longer term survey only occasional individuals were found in the samples throughout most of the year. Large numbers suddenly appeared at sites FIV4, GIII4 and GIV3 in September, reaching a maximum of 1300 m^{-2} at FIV4. This population declined gradually throughout the winter, falling to 540 m^{-2} in March at the end of the survey. Fluctuation in numbers are given in Table 5a and Figure 5ii.

5iv Nemerteans: ribbon worms

Lineus gesserensis (Müller) was recorded by Petch (1907) from under stones. Specimens of Lineus sp. were found under stones at Kilnsea in December 1976.

Amphiporus lactifloreus (Johnston)

This species was recorded from Spurn Bight by Petch (1907).

Nemertopsis flavida (McIntosh)

Recorded from upper and lower shore mud at Patrington Haven by Langston (1972), but not found there in this study.

5v Gastrotrichs and Kinorhynchs

Small numbers of both these pseudocoelomate phyla were present in the meiofauna of sands and silts during the May/June survey. Kinorhynchs proved far more abundant - maximum 3,980 m^{-2}, than gastrotrichs - maximum 1060 m^{-2} and both groups were more numerous, when compared with other meiofauna, in sands rather than mud. Ratcliffe (1979) recorded larger numbers of kinorhynchs than gastrotrichs in the mud at Skeffling, with a maximum of 600 m^{-2} for gastrotrichs and 20,000 m^{-2} for kinorhynchs in January. Abundance of the two groups in the survey is included in Table 4a.

Neither group has ever been recorded as being of great importance in a benthic ecosystem. Warwick et al. (1979) gave a figure of 0.05 gm organic carbon m^{-2} annual production ($\equiv$ 0.125gm dry weight), for a population with mean density 25,313 m^{-2} on mudflats of the R. Lynher.

5vi Nematodes: eelworms

The most abundant meiofaunal animals in all samples except the coarsest sand at LIV6. Densities range from 1740 m^{-2} at KIII6 to 864,000 m^{-2} at FIV4 for individuals retained by a 40μ sieve. A sample of 1,000 nematodes were dried and weighed, giving a dry weight per nematode of 0.00035mg as compared with 0.0028mg quoted by Wieser (1960). This gives a range of biomass of 0.61 to 302mg m^{-2}, but nematodes are known to have very high turnover rates and productivities (McIntyre; 1964, Gerlach; 1971, Warwick et al.; 1979), and therefore these figures may be indicative of considerable annual production. Nematode numbers were generally much higher than found by Ratcliffe (1979) who recorded a maximum of 170,000 m^{-2} and commented that nematode densities were much lower than recorded elsewhere. These figures are more in agreement with the figures of 0.8 - 1.9 x 10^6 m^{-2} of Wieser (1960) and McIntyre (1964). The numbers and estimated biomass are given in Table 4a.

Nematodes were most abundant in sandy silts/silty sands (ϕ median 3.4 - 4.6), and were markedly less numerous in downshore sands, fluid silts, and anaerobic Spartina marsh conditions. Outside the Bight they were abundant in coarse sands at Humberston and Horseshoe Point on inshore clean sand flats. Unlike the downshore sandflats at Spurn, these flats also have high densities of macrofauna. Nematodes were also very abundant (491,200 m^{-2}) in the very soft silt at Pyewipes (MIII1). Here there was no macrofauna other than small oligochaetes but very high densities of meiofauna, a similar condition to that observed in the Tees by Gray (1976), where the community diversity was reduced by pollution stress but the fauna maintained high productivity.

Bregnballe (1961) found nematodes to form an insignificant part of the diet of 'O' group flatfish and they are not reported in the diet of wild fowl, although they are likely to be included by the filter-feeding shelduck Tadorna tadorna. Warwick et al. (1979) reported them as constituting part of the food of Nephtys sp.. They are also likely to be included in the diet of non-selective deposit feeders.

5vii Annelids

5viia Polychaetes

Phyllodoce maculata (L.)

This species was recorded as common on the Old Den by Morgan (1969). A single specimen was found in coarse sand close to station LIV6 in November 1976, another at GIV3 on 20.7.78 and a density of of 120 m^{-2} was found at FIV4 for one month only on 16.1.79.

Eteone lactea (Claparède)

Small numbers were found at stations KIII6 and LIV6 in Spurn Bight as well as at Horseshoe Point (PII6 & PIV6) on the South bank, always in slightly silty sand.

Eteone longa (Fabricius)

Ratcliffe (1979) recorded a maximum density of 1200 m^{-2} at Skeffling in June 1975 and did not find that it had a particular sediment preference. The survey of May/June 1977 was not ideally timed to record this species which spawns in the early spring and larval settlement follows either a planktonic phase or a period of incubation by the female in the tubes of spionid worms (Rasmussen; 1956). Small numbers were found, at densities no greater than 40 m^{-2}, at sites CI2, DI3, EII4, GII4, GIII4, HI2, and JI3, invariably quite high on the shore in very silty sediments.

During the intensive survey, the population started at a very low level (20 - 160 m^{-2}) at four of the five regular sampling stations in March - it was never found at FI2 among the Spartina. Numbers dropped further between March and April, presumably as adults died after breeding. Settlement of juveniles was found to have started by May 24 and was at a peak in mid June with a maximum density of 2140 m^{-2} at FIV4 and GIV3. Numbers dropped steadily at the Easington stations for the rest of the summer, with an accelerated decline between November and March. At FIV4 numbers dropped sharply between August and September and then remained almost constant until the following March whilst at FII2 the population was constantly low, rising to a maximum in March 1979, possibly as a result of immigration of individuals displaced from downshore sediments by the winter storms. The populations at all sites were considerably higher in March 1979 than in March 1978. An almost exactly similar cycle of abundance was found by Ratcliffe (1979) for this species at Skeffling during 1974 - 1975, with a maximum density of juveniles of 1200 m^{-2} on 25th June.

The decline in numbers of this species at a particular site is not necessarily related directly to mortality. It is an active swimmer at high water and therefore redistribution of juveniles from areas of dense settlement is possible. Ratcliffe (1979) found a sharp increase in density at Skeffling between 31st October and 13th November 1973 which must be attributed to immigration.

Biomass was calculated indirectly as too few larger sized individuals were available for weighing. An estimate was made by comparison with similar sized specimens of <u>Hediste</u>. A maximum of 2.44 gm m^{-2} was estimated at GIV3 in November 1978 with a maximum mean annual biomass of 0.90 gm m^{-2} at GIV3. Biomass of <u>E. longa</u> represented between 1.9 - 2.2% of total measured community biomass at the three midshore stations.

Production figures must be interpreted with caution because of the possibilities of emigration/immigration by swimming, but was calculated to be 2.34 gm m^{-2} at FIV4, 2.14 gm m^{-2} at GIII4 and 2.77 gm m^{-2} at GIV3 giving production/biomass ratios of 3.7 : 1, 2.82 : 1 and 3.08 : 1 respectively. Abundance, biomass and production of <u>Eteone</u> is summarised in Table 5b and Figure 5iii. Cohorts were diffentiated purely subjectively and individual cohort data are not presented here.

Little appears to be known of the ecology of this species other than its reproduction development. Khlebovich (1959) reported <u>E. longa</u> feeding exclusively on <u>Spio filicornis</u> and Simon (1965) recorded <u>E. heteropoda</u>, a closely related species, feeding as a deposit feeder at high tide and a carnivore on small Nereis when the tide is out. E. longa in the Humber could thus be feeding on Pygospio elegans and possibly Hediste diversicolor as well as ingesting sediment.

Densities quoted elsewhere appear only to refer to mature individuals. The highest density recorded in the literature appears to be by Muus (1967), at 216 m^{-2} and therefore the densities recorded in this study for adult specimens, 200 - 640 m^{-2}, in March 1979 are considerably higher than recorded elsewhere. It appears that, in the Humber, the species is univoltine with only a single age cohort present at any one time.

Eteone has not been recorded in feeding studies of fish or wildfowl, but it would seem likely that both groups will take the species whenever it is encountered.

Lepidisthenia argus Hodgson

This species has been found on the Old Den by Dr. D. Lewis of Hull University (pers. comm.). It was not found during this study.

Harmathöe impar Johnston

A single specimen, found in sand at JIII6.

Gattyana cirrosa (Pallas)

This scale worm was found consistently as a commensal in the tubes of the terebellid polychaete Amphitrite johnstoni on the Old Den. Almost all burrows of Amphitrite housed a scale worm. The autecology of this species is outlined by Curtis (1977) in Greenland and by Wolff (1973) in the Netherlands Delta region.

Neanthes virens (Sars) - ragworm

A 10cm length from a very large nereid was found in a 10cm core of soft silt at Skeffling in November 1976. It was identified as N. virens on parapodial structure, although the species has not previously been recorded in the Humber. The species is more characteristic of silty sands (Kay & Brafield; 1973). Muus (1967) reported that this species is far less tolerant of salinity changes than H. diversicolor and therefore less abundant in estuarine conditions.

Hediste (=Nereis = Neanthes) diversicolor (O.F. Muller) - ragworm

Treated separately in chapter 7

Nephtys hombergi (Savigny) - catworm

Treated separately in Chapter 6.

Nephtys cæca (Fabricius) - catworm

This species is characteristic of the boreal shallow sand community described by Jones (1951). Kay & Knights (1975) reported N. cæca replacing N. hombergi in cleaner sands. It was found mainly in the downshore sandy sediments of the Bight (see Table 4a). The distribution in relation to environmental variables is described with N. hombergi in Chapter 6.

A mixed population of juveniles of N. cæca and N. hombergi was found in very fluid silts of KV2, but it may be that the whole fauna at this site is derived from animals washed from other sediments. Other than at KV2, where a density of 460 m^{-2} was found, the highest density found in more typical sediments was 375 m^{-2} at CV6. Small numbers (60 - 80 m^{-2}), were also found on sands on the South Bank at NII6, NV6, PII6 and PIV6.

No specimens were recorded from the 1978 - 79 study and biomass figures for the 1977 survey were calculated using regressions derived for N. hombergi. No attempt was made to analyse the age structure of the populations.

Wolff (1971) recorded all species of the Nephtyidae to be predatory, but Warwick et al. (1979) include substrate and phytobenthos feeding as well as predation on the meiofauna for N. hombergi.

It is likely that N. cæca forms the greatest proportion of the macrofauna biomass of the outer sand flats of the Bight. Kay & Knights (1975) similarly found low biomass sands dominated by N. cæca. Together with Bathyporeia it provides the only resource for wildfowl and fish in these areas.

(Nephtys longosetosa (Oersted))

Petch (1907) recorded this species from sandy mud at Stone Creek and Skeffling etc. Wolff (1971), describing the distribution of four species of Nephtys along the Dutch coast, recorded N. longosetosa as occurring in clean sands, and it seems likely that Petch was referring either to N. hombergi or N. cæca, neither of which he mentioned.

Sphaerodoropsis minuta (Webster & Benedict)

Specimens of this minute, papillate polychaete were found at JIII6 and KV2 in May 1977 with a maximum density of 120 m^{-2} at KV2. The species has been found at much higher densities (1000 m^{-2}) at South Killingholme by Smith (1982). Little seems to be known of its ecology although the biology of the Sphaerodoridae is outlined by Fauchauld (1974).

Scoloplos armiger (Müller)

Four specimens of this species were found among cores taken at KIII6 in May 1977. Muus (1967) recorded it as rare in shallow mesohaline localities and that its distribution is related to a sandy bottom.

Spio seticornis (Fabricius)

Petch (1907) recorded this species from Skeffling "amongst clusters of mussels in the Zostera beds". This habitat appears now to be non existent and this species was not observed in this study.

Spio filicornis (Müller)

Odd specimens were found at AIII2 (outside the Bight), and at FIV4 and KV2.

Prionospio cirrifer Wiren

A single specimen was found at DV6 in hard sand.

Pygospio elegans Claparède

By far the most numerous polychaete on the Bight. This species proved difficult to count because of the persistence of the tubes in which it lives, constructed with sand grains and often impregnated with iron oxides. These tubes have to be carefully broken apart to identify the presence of a living spionid within.

This species was also one of very few which were successful in colonising the sides of the draining channels of the Bight. Extensive 'reefs' of spionid tubes, up to 50cm in diameter, were exposed along the edges of these creeks as well as on the mudflat surface and investigation showed them to contain living Pygospio.

Pygospio was found in all types of sediment within the Bight, including the coarsest sand at LIV6. The highest densities, however, were found in silts and sandy muds rather than hard clean sand, with a maximum density of 7120 m^{-2}

at EII4 (Table 4a). It was also extremely abundant in the anaerobic polluted silt at Pyewipes, with a density of 9020 m^{-2}. These densities are very low when compared with the figures of Ratcliffe (1979) for Skeffling, where he found a maximum of 15,000 m^{-2} in February 1975. During the period 1978 - 1979 the highest density recorded was 15,200 m^{-2} in July 1978 at GIII4, but the densities recorded show no pattern with time (Table 5c). This is likely to be a result of the patchy nature of the distribution of this species. Two 10 cm cores from the same site could produce numbers as wide apart as 381 and 15 specimens per core (FIV4, October 1978). Standard deviations from the mean from five cores usually exceeded the mean by 200%, indicating the species tendency towards dense aggregations resulting from asexual reproduction (Muus; 1967).

Densities of Pygospio are recorded in most estuarine studies, but figures for biomass are less common. Warwick et al. (1979) give a biomass of 0.174 gm organic carbon m^{-2} ($\equiv$ 0.435 gm m^{-2} dry weight) for a mixed population of Pygospio and Streblospio at a density of 11,789 m^{-2}. This gives a mean individual weight of 0.0369 mg and application of this value to the density for Spurn Bight gave a maximum annual mean biomass of 0.299 gm m^{-2} at GIV3, 0.5% of the total measured community biomass. Warwick et al. used a P:B ratio of 5.5 : 1 and this would mean annual production of 1.62 gm m^{-2} in the Bight, although confidence limits would be very large.

As this species is very widespread on Spurn Bight it must therefore contribute significantly to the food budget of the mudflats. Spionids are included in the food of invertebrate predators such as Eteone (Simon; 1965), and Nephtys (Warwick et al.; 1979), and are likely to feature heavily in the diet of shore crabs, Carcinus, and the various species of shrimp and prawn which use the mudflats at high water. They are regarded as important in the food of 'O' group flatfish, particularly plaice, Pleuronectes platessa, and flounder, Platichthys flesus (Smidt; 1951, Bregnballe; 1961, Edwards & Steele; 1968, Wolff et al.; 1981). No direct reference could be found to the inclusion of spionids in the diet of wildfowl, although Goss-Custard et al. (1977) stated that they are likely to be important in the diet of dunlin, Calidris alpina, but that their rapid digestion prevents their detection stomach content analysis. By their feeding method, the dabbling shelduck, Tadorna tadorna, are also likely to include large numbers of spionids in their diet.

Together with Streblospio shrubsolii, Pygospio is likely to be highly important in the sediment accretion/erosion cycle of the Bight, serving both to bind the sediment and thus resist erosion and also facilitate deposition by interfering with water flow at the mud/water interface. Spionid 'reefs' were commonly ½ - 2cm higher than the surrounding mud surface.

Nerine cirratulus (Delle Chiajé)

Five specimens of this species were found in hard sand at Spurn Head on the estuarine beach in November 1976. The species was also found in 10cm cores at Humberston (NV6) in May 1977. Langston (1972) recorded Nerine sp. at a density of 112 m^{-2} in midshore sand at Spurn Point.

Nerine coniocephalus Johnston

Petch (1907) recorded this species from under stones at the Old Den. It was not seen in this study.

Streblospio shrubsolii (Buchanan)

Although less numerous than Pygospio, most of what has been said about that species can be applied to Streblospio. Its distribution,however, was more even and little tendency towards reef formation was observed. No sediment preference was observed in May/June 1977, the animals being found amongst the Spartina, in soft silt and fairly coarse sand (Table 4a), with a maximum density of only 280 m^{-2} at FII2 in May 1977. The 1978 - 1979 survey showed that the species is at its lowest density at that time of year, and therefore it may have been missed at sites where it is abundant later in the year. Density reached a maximum of 4240 m^{-2} in October 1978 at FII2, although Ratcliffe (1979) found 7500 m^{-2} at his downshore site at Skeffling. Data is summarised in Table 5d and Figure 5iv.

It would appear that this species spawned during the mid-summer months of 1978 with recruitment throughout August to October followed by a heavy mortality in the winter months. Ratcliffe (1979) did not find a similar pattern of distribution with time over the period October 1973 to February

1975, but did find minima during the spring months. He found a maximum of 7500 m^{-2}. The cycle described here may therefore not be typical of other years.

As with Pygospio, mean annual biomass figures and production were calculated using a mean individual weight of 0.0420 mg and a P:B ratio of 5.5 : 1 calculated from Warwick et al. (1979), who found Streblospio producing 0.726 gm organic carbon m^{-2} (≡ 1.815 gm dry weight), per year. This gave a maximum mean annual biomass of 46.9 mg m^{-2} at station FII2, 0.4% of the measured community biomass and production of 258.0 mg m^{-2} at FII2.

Gray (1976) found this to be an opportunist species and common in polluted sands and muds in the Tees estuary. Streblospio is likely to be included in the diet of any organism which also takes Pygospio.

Cirriformia tentaculata (Montagu)

Ratcliffe (1979) recorded Audouinia (= Cirriformia) tentaculata occurring rarely and in association with Cerastoderma edule on the upper shore at Skeffling. A single specimen was found at Skeffling (close to FIII4) in November 1976.

Sabellaria alveolata (L.) - honeycomb worm

Petch (1907) recorded this species dredged from Trinity Sand on the outer sandflats of the Bight. It was not found during this study.

Capitella capitata (Fabricius)

This species is characteristic of disturbed and oxygen deficient muds and sands and is commonly associated with the effect of pollution (Gray; 1976, Warren; 1977). Odd specimens were found during the intensive survey at FI2 and FII2, and at FII6 and PIV6 at Horseshoe Point in the extensive survey, but never in large numbers. Smith (1982) recorded high densities on the polluted mudflats around industrial complexes on the South Bank of the Humber.

Arenicola marina (L). - lugworm

Petch (1907) recorded this species from Stone Creek eastwards, but Spurn Bight now remains the only site at which the lugworm still occurs on the North Bank of the Humber.

The maximum density found in Spurn Bight, estimated by counting casts at low tide - a method which may lead to overestimation as worms can produce several casts (Anderson; 1972), was 25 m^{-2} at EIII6. This, however, was exceptional - more commonly densities ranged from 1 - 6 m^{-2} (Table 4a). On the sandflats of the South Shore of the outer Humber, at Horseshoe Point and Humberston, the species was much more abundant, with densities of 35 and 25 m^{-2} respectively at PIV6 and NV6.

Densities as high as 70 m^{-2} (Raymont; 1955, Longbottom; 1970) have been recorded elsewhere, and Muus (1967) found adults at 100 m^{-2} at Ajstrup Bay in Denmark. 30 - 50 m^{-2} seems to be an average density in suitable sediments. Longbottom (1970) summarised densities recorded prior to 1970.

The size reached by the Spurn Bight population was likewise small in comparison to the South Bank. No animals larger than 10cm in length were found while digging for the species, whereas specimens collected by bait diggers at Cleethorpes and Humberston are commonly double that size (own observation).

Arenicola was only found on flat, muddy sand and was absent from the proximity of drainage channels and the cleaner sands at Spurn Head. Longbottom (1970) and Anderson (1972) recorded similar sediment preferences on the North Kent coast and in Morecambe Bay. It was not quantified further in this study, although it must represent a large standing crop biomass owing to its large size. Beukema (1976) found Arenicola contributing as much as 33% of the total biomass in the Dutch Wadden Sea, but the Humber populations would not reach this percentage.

No settlement of juveniles was recorded, only one specimen of length 4cm being found in a sample core. Smidt (1951) indicated that recruitment was low and adults long-lived in the Danish Wadden Sea.

Arenicola is an important item in the diet of the larger wading birds, especially curlew and whimbrel, Numenius sp. (Green; 1968, McLusky; 1971) and godwits, Limosa sp. (Smith & Evans; 1973), and part of the diet of various larger flatfish (Braber and de Groot; 1973, de Vlas; 1979, Wolff et al.; 1981), and cod (Forsberg; 1977). It is unlikely that such low density population of undersized individuals is of major importance as a food resource of the area.

The Spurn Bight population is, however, an important one for Yorkshire's anglers. Lugworms are not found abundantly anywhere along the Yorkshire and Holderness coast, being dug for only at Scarborough South Bay and Bridlington. Nowhere is it ever as abundant as it is at Spurn, which therefore represents the main source of this angling bait. Lugworms on sale in Hull and Bridlington are not locally caught but come from the extensive flats around Lindisfarne in Northumbria. The intensity of disturbance of wildfowl by diggers, shown by Tasker & Milsom (1979) reflects well the distribution of the lugworm in the Bight.

The autecology of *A. marina* is dealt with exhaustively in Volume 13 parts 3 & 4 (1979) of the Netherlands Journal of Sea Research which is devoted entirely to papers on the species.

Travisia forbesii Johnston

Odd specimens of this species were found in very coarse sand at LIV6 and at NV6 at Humberston in May 1977. It is a non selective deposit feeder, characteristic of clean sands, usually subtidally (Wolff; 1973).

Amphitrite johnstoni Malmgren

This large polychaete was found to be abundant under stones on the Old Den, making tubes of mud held together with mucus. Tubes are usually shared with the commensal polynoid *Gattyana cirrosa* (q.v.). This species is likely to be included only in the diet of curlew, *Numenius arquata*, and turnstone, *Arenaria interpres*, in the Humber, which Tasker & Milsom (1979) recorded as constantly feeding on the Old Den. These worms are collected for bait by sea anglers.

Lanice conchilega (Pallas) - mason worm

A small colony of this worm, which makes tubes of coarse sand grains protruding up to 3cm above the surface of the sand, was found close to one of the groynes in hard sand at Spurn Point. Petch (1907) recorded it from the Old Den, but it was not found there by Morgan (1969). It is a short lived species, rarely surviving more than two winters, and characteristically having a clustered distribution (Beukema et al.; 1978).

Pectinaria belgica (Pallas)

Petch (1907) recorded this species from Trinity Sands, and large numbers of empty Pectinaria tubes were found in the region of GV6 and beyond in May 1977. Occasionally the delicate tubes are washed up in the sand around the Bight.

Ampharete acutifrons Grubé

A single specimen was found in mud at JIV3 in May 1977. Its production ecology is described by Warwick and Price (1975) and Price and Warwick (1980).

Laeospia (= Spirorbis) borealis (Daudin)

Petch (1907) recorded this species on macroalgae from the Old Den. It was found to be common on Fucus in the same area.

Manayunkia aestuarina (Bourne)

Ratcliffe (1979) recorded this species as occurring irregularly among samples from Skeffling. It was not encountered there in this study, but was found in small numbers in slime tubes attached to the surface of stones on the Old Den. It was also found to be abundant in anaerobic mud at Pyewipes on the South Bank, at a density of 1160 m^{-2}, and Gray (1976) reported it from a similar polluted environment community from the Tees estuary.

5viib Oligochaetes

Paranais littoralis (Müller)

Ratcliffe (1979) recorded low densities of this species from Skeffling, averaging 2000 m^{-2}, and becoming scarce after January 1975. It was not found during this study. Its ecology is outlined by Muus (1967).

Edukemius (= Peloscolex = Tubificoides) benedii (= benedini) d'Udekem

This species was found to be abundant only in the finer sediments of the upper shore, in agreement with Ratcliffe (1979), who found much higher densities at Skeffling on the upper shore than on the lower. The maximum density found in May/June was 2780 m^{-2} at BI2. Much higher densities were found outside Spurn Bight, with 20,260 m^{-2} at Cherry Cob (AIII2) and 161,240 m^{-2} at Pyewipes (MIII1), both in extremely soft sediments, the latter highly polluted. This figure for MIII1 is extremely high when compared with other authors.

Hunter & Arthur (1978) record a maximum of 142,000 m^{-2} in the Thames, while other populations are usually at a density less than half this figure. McLusky et al. (1977), who found 60,000 m^{-2} in the polluted Forth Estuary, suggest that high densities of this species are indicative of organic pollution. Densities for May/June (1977) are given in Table 4a.

During 1978 - 79, high densities were found only on the two upper shore stations at FI2 and FII2, the maximum downshore density being at GIII4 in May 1978 (350 m^{-2}), (Table 5e and Figure 5v). Numbers increased sharply after June 1978, although the 'new' animals were equally as large as those found previously, indicating either immigration of adults into the area or very rapid growth of young worms. An indication of the growth rate of Edukemius is given by Hunter & Arthur (1978).

Mean dry weight per individual was calculated by direct weighing of 300 individuals and found to be 0.045 mg. This figure has been used to calculate the biomass figure in the Table 5e. Maximum biomass was 1.29 gm m^{-2} at FI2 in October 1978 and a mean value of 0.59 gm m^{-2} over the year. This represented 5.0% of the total community measured at that station.

The predators of benthic oligochaetes are discussed Gière (1975). Among the invertebrates, nematodes, turbellarians and nereids are important predators mainly on tubificids. They have been recorded as important in the diet of flatfish and gobies (Bregnballe; 1961, Muus; 1967, Summers; 1980), and very important in the diet pf certain wildfowl, particularly shelduck, Tadorna tadorna, redshank, Tringa totanus, and dünlin, Calidris alpina, (Evans et al,; 1979). All three of these species were found to concentrate their winter feeding activities on the upper shore sediments and Spartina belt by Tasker & Milsom (1979), and it is likely that Edukemius may provide a proportion of the diet of these birds.

(Tubifex costatus Claparède)

One tubificid oligochaete, possibly of this species was found in the extremely fluid sediment at KV2 in May 1977. It is abundant outside the Bight - a density of 12,200 m^{-2} was found in a mixed population with Edukemius benedii in very soft polluted sediement at MIII1

Lumbricillus lineatus (Müller)

Recorded by Ratcliffe (1979) from occasional specimens from Skeffling and as single specimens at AIII2 and CII4 in this study.

5viii Molluscs

5viiia Amphineura - chitons

Lepidochitona cinerea (L.)

This species was recorded by Petch (1907) and by Morgan (1969) from the Old Den. Petch found it "common - Well Creek to Spurn". It was not observed during the present study.

5viiib Gastropods

Patella vulgata (L.) - common limpet

Recorded by Petch (1907) and Morgan (1969) on the Old Den but not found in this study.

Littorina littorea (L.) - edible winkle

This species was common wherever there was a suitable substrate in Spurn Bight, in particular on the stone sea wall at Kilnsea, the concrete blocks at Easington, groynes at Kilnsea and Spurn, and it was especially numerous on the Old Den. Occasional specimens were observed in the Spartina zone, particularly at Welwick Saltmarsh, but none were encountered in samples.

Littorina littoralis (L.) - flat winkle

Small numbers of this species were found among algae on the Old Den.

Littorina neritoides (L.) - small winkle

Recorded by Langston (1972) from scrapings on the upper pier of the lifeboat station at Spurn Point at a density of 736 m^{-2}.

Littorina saxatilis (Olivi) - rough winkle

Common at around M.H.W.O.T. along rocky areas of the sea wall, notably on piles of slag at Skeffling and along the sea wall at Kilnsea.

Hydrobia ulvae (Pennant) - mud snail

H. ulvae was found to be abundant at TOPSILT, MIDMUD and occasionally SAND stations of the extensive survey (Table 4a, Fig 5ix), reaching a maximum density of 19,780 m^{-2} at station FI2 among the Spartina, although averages were much lower than this figure. High biomass values were recorded and the mud snail is known to feature heavily in the diet of certain shorebirds. For that reason it was decided to concentrate studies on H. ulvae, along with the other major species.

During intensive studies, however, H. ulvae turned out to be less abundant than encountered in the extensive survey and extremely variable in its occurrence (Table 5f, Figures 5vii - 5x), with a population structure that was impossible to interpret (Figure 5x). It proved impossible to investigate population dynamics in terms of recruitment, mortality and production and instead, mean biomass values were determined and the P:B ratios calculated by other authors used to give some idea of the species' dynamics.

Although occurring along almost the full length of the shore (Figure 5vi) H. ulvae was more abundant at the top end, particularly among the Spartina march and, at Welwick and Horseshoe Point, in the saltmarsh, particularly under, and climbing on Halimione.

There was little definite relationship with sediment character and specimens were found in clean sand at Humberston and Horseshoe Point, but not on the estuarine beach at Spurn where the tidal scour is greater. No relationship at all was noted with the degree of sediment sorting.

Fenchel et al. (1975) noted that H. ulvae selectively grazes surface diatoms and ingests relatively large particulate matter - up to 200μ. Barnes and Greenwood (1978) found that in N. Norfolk, H. ulvae showed little sediment preference in the field although in the laboratory, snails were found to prefer finer substrates. Barnes (1979), however, found that between 10 and 15% of a population of H. ulvae selected sandier substrata.

It was obvious from intensive studies (Figure 5x), that very large snails (>6.5mm) were found only at upshore stations FI2 and FII2. This is in keeping with the findings of Chatfield (1972), who found that populations of H. ulvae from saltmarshes lived longer and grew to a larger size than those from sandflats. This was also noted in snail populations in the Dyfi estuary by Fish & Fish (1974), who considered the greater size in muddy substrata to be a result of increased growth rate.

Extreme variablity in density in Spurn Bight would strongly suggest a great deal of mobility of the snails - possibly the result of floating behaviour noted by Smidt (1951), Newell (1962) and Anderson (1971), although the significance of the floating mechanism for dispersal of H. ulvae has been questioned by Little & Nix (1976) and Barnes (1981). Floating behaviour was not looked for in the Spurn Bight population. It is unlikely that populations from different levels of the shore remain isolated on these mudflats and it is more probable that the larger specimens select the upper part of the shore.

Variations in density of the whole population with time are shown in Figure 5vii. It was not possible to differentiate separate cohorts although occasionally the population structure appeared regularly bimodal, possibly resulting from chance. Peaks in abundance were not synchronised between stations and only at FII2 in the upshore silts was the species consistently more abundant in summer than in the winter. There was some evidence of a negative relationship in density between sites FI2 and FII2, possibly indicating that H. ulvae moved out of the Spartina onto silts at the top of the shore in high summer. In common with other species H. ulvae was apparently eliminated from station GIII4 during the harsh winter period November 1978 - January 1979.

From the population structure (Figures 5.ix & 5 x), no period of recruitment was obvious and very small individuals (shell length <0.5mm), were found at varying densities from March through to September, but not afterwards. Breeding has been noted as occurring mainly in late spring in N. Kent (Chatfield; 1972) and the Dyfi estuary (Fish & Fish; 1974), although the latter authors found a second breeding period in the late summer. Snails bearing egg capsules, as many as twelve per shell, were observed in all months from April to October in this study.

A single length/weight regression was carried out on animals collected in May 1977. This gave an equation:-

$$\text{flesh dry weight (mg)} = 0.081 \times \text{shell height}^{2.31}$$

$$(r = 0.94)$$

This was used to calculate all biomass figures.

Variations in monthly biomass are in Table 5f and illustrated in

Figure 5viii.

Maximum biomass recorded was of 15.5gm m^{-2} at FI2 in May 1977, but of only 2.3gm m^{-2} at the same site throughout 1978 - 79. Mean biomass at that site over the year was found to be 1.1gm m^{-2} equivalent to 9.4% of total measured biomass at that site, the highest proportion reached. At midshore sites, mean biomass was between 0.9 - 1.6% of the total. The mean biomass among the saltmarsh at Welwick may well be much higher but investigation of the population there was outside the scope of this study. McLusky et al. (1977) and Elliot (1979) found mean annual biomass of 3.6 - 4.7gm m^{-2} in the Firth of Forth.

Production by H. ulvae has been studied by McLusky et al. and Elliot (op cit) and Wolff and de Wolf (1977), and a mean P:B ratio of 1.51 was derived from their results, which had a range of 1.24 - 1.78. This value was used to give a tentative estimate of production and elimination (assuming $P \doteq E$), Table 5g. On this basis, maximum production would be of 1.69gm m^{-2} at station FI2, rather low, in comparison with studies elsewhere, contributing 1.8 - 5.9% of total production by the infaunal community (ref. Chapter 11).

Summers (1980) found H. ulvae the second most important food resource for flounder Platichthys flesus in the Ythan Estuary, after Corophium volutator which is not found in great numbers in Spurn Bight. Wolff et al. (1981) similarly found it to be very significant both to flounder and plaice Pleuronectes platessa in the Oosterschelde estuary.

Mudsnails have been shown to be important in the diet of shelduck, Tadorna tadorna (Olney; 1965, Bryant & Leng; 1975) and also very important to dunlin, Calidris alpina and sometimes to knot, Calidris canutus, and redshank, Tringa totanus, (Goss-Custard, Jones & Newberry; 1977). As all of these species have been found to be present in internationally significant numbers in Spurn Bight during the winter (Tasker & Milsom; 1979), H. ulvae represents a potentially very significant bird food resource and this very variable population would repay further investigation.

(Hydrobia ventrosa (Montagu)) - mud snail

This species is recorded as occurring in "brackish ditches and pools outside the bank"at Easington by Petch (1907). This is surprising as H. ventrosa is usually recorded as preferring lower salinities (6 - 20‰) than H. ulvae (Muus; 1963), and is very common on tipped boulder sea wall and among Spartina at South Ferriby Sluice (SE975212), 43km upstream from Easington (own observation). A representative fraction of all Hydrobia from the May/June survey were dissected and the structure of the penis compared with illustrations in Muus (1967). All were found to be H. ulvae.

Thais (= Nucella) lapillus (L.) - dog whelk

Very common on the Old Den. Morgan (1968 & 1972) discussed the interrelationship of these species with its main foods Balanus balanoides and Cerastoderma edule. This species is more typical of rocky conditions than muddy estuaries.

(Ocinabra erinacea (L.)) - sting winkle

Several empty shells were found on the Old Den but no live specimens were seen. The species was not mentioned either by Petch (1907) or by Morgan (1969). Specimens of Macoma with circular drill holes in the umbo region were occasionally found on the mudflats, both in cores and on the mud surface. Such drilling is typical of both this species and the previous one.

Buccinium undatum (L.) - common whelk

Empty shells are occasionally washed up on the riverside beach at Spurn although these may have been washed round the peninsula from the Holderness coast. Morgan (1969) recorded the species from the Old Den, and Squire (1973) found it at Spurn Head.

Retusa obtusa (Montagu) - pearl bubble shell

Treated separately in Chapter 10.

Philine minuta (Brown)

Four specimens of an unknown shelled opisthobranch were found in a single core at FII2 and were kindly identified as this species by Dr. V. Fretter of the University of Reading.

Limapontia depressa Alder & Hancock

Small numbers were found among green alga collected from the Spartina at Welwick Saltmarsh at Easington in October 1976. den Hartog & Swennen (1952) stated that this can be important in the utilisation of filamentous and thalloid green algae. The species was not encountered on the mudflats themselves.

(Physa fontinalis (L.))

One specimen, either alive or very recently dead, was found in the DI3 sample in May 1977. This is a freshwater species and must have been very recently discharged onto the mudflat from the Holderness land drains.

5viiic Bivalves

Mytilus edulis (L.) - common mussel

Very small numbers were to be found on the Old Den attached to the largest pebbles, and groynes along the peninsula from Kilnsea to Spurn Head also supported small populations. Mytilus plantigrades were occasionally found in cores, although never at densities higher than 60 m^{-2}.

Petch (1907) recorded Spio seticornis occurring among the clusters of mussels in the Zostera beds at Skeffling. This would indicate that, at this time, beds of Mytilus used to occur on the surface of the mudflats, presumably on the sandy areas. These have not been recorded in the Bight since that time, although some small mussel beds do exist between Humberston and Cleethorpes on the South Bank. Hinton-Clifton (1963) noted that commercial fisheries used to exist for mussels in the Humber in the last century but their collection ceased with the increase of sewage pollution.

Modiolus modiolus (L.) - horse mussel

Large empty shells are occasionally found on the shore of the river side of the peninsula, probably washed around the peninsula from the Holderness Coast. Squire (1973), however, recorded it from the pilings of the lifeboat station at Spurn.

(Ostrea edulis L.) - oyster

Empty shells are regularly found on the beach at Spurn and subfossil remains occur in the boulder clay under the sea beach. No live specimens were found although small numbers of oysters are occasionally found live at Cleethorpes on the South Bank.

Cerastoderma edule (L.) - common cockle

Treated separately in Chapter 8.

(Cardium echinatum L.) - prickly cockle

Several empty shells were found on the riverside beach at Spurn. These are unlikely to have originated from the Bight as this is mainly a sublittoral species.

(Cyprina islandica (L.))

One valve of this deep-water species was found on the beach at Greedy Gut.

Scrobicularia plana (da Costa) - peppery furrow shell

Petch (1907) found this species abundant from Skeffling to Spurn and shells eroded from the banks of the deepest creeks in the Bight support this. Similar remains are equally common in the Pyewipes area near Grimsby. Hinton-Clifton (1964), Morgan (1969), the various Yorkshire River Authority reports (1971 - 1974), and Ratcliffe (1979), failed to find the species and the survey of May/June 1977 found no adult specimens. Spat and one year old specimens, however, were found intermittently throughout the Bight (stations CI2, CII4, EII4, FII2, GIV3, KV2 and also in hard mid-tidal sand at Horseshoe Point PIV6). The only large specimen recently recorded from the estuary was one specimen found at Kilnsea by Dr. N. V. Jones (pers. comm.) in Autumn 1978.

The maximum density recorded in 1977 was 620 m^{-2} at CI2 and 380 m^{-2} at PIV6, only odd specimens being recorded elsewhere. This does, however, indicate that an adult population must exist somewhere in the Bight, possibly at very low density. Similar population structures were found by Spooner & Moore (1940), and Warwick & Price (1975), in different parts of the Tamar Estuary, Cornwall, with very low densities (2 - 4 m^{-2}) of adults in spite of appreciable spatfalls.

During the course of 1977 - 1979, station CI2 was visited on six occasions at approximately 4 monthly intervals to monitor this low density population. All fauna was counted (Table 5h), and the size/frequency distribution of Scrobicularia recorded (Figure 5xi). Insufficient animals were available for length/weight analysis and therefore an average of the eleven monthly relationships given in Hughes (1970b), and calculated by Warwick & Price (1975), to be:-

$$\log_{10} (\text{dry flesh weight-gm}) = 3.0 \times \log_{10} (\text{shell length}) - 5.12$$

was used to calculate biomass. The results are given in Table 5j.

The actual period of spatfall was not recorded but was found to have occurred by November 1977 and again between July and November 1978, reaching a maximum density of 1240 m^{-2} in 1978. Hughes (1970a) recorded gamete release in August and September on the Aber foreshore in North Wales, but Warwick & Price (1975) found spat settlement in April in the Lynher Estuary in Cornwall. Evidence of two separate settlements during the summer of 1977 was given by the bimodal size/frequency distribution histogram for the 1977 cohort which persisted through the winter. A similar phenomenon is visible in the data of Raymont (1955), from Loch Sween, in Scotland.

Cohorts were easily separable by prominant winter rings which became obvious after the start of new growth in the spring. No individuals older than two winters were ever found, although deep (20cm) cores were used to sample for this species. Hughes (1970b) found no animals deeper than 18cm in the sediment.

Mortality was found to be very high in this population and reached 100% for the 1976 settlement cohort by November 1978. The population was found to be extinct at CI2 in March 1979, presumably as a result of the very severe ice conditions in January and March 1979.

Scrobicularia is well known for its susceptibility to low temperatures. Crisp (1964a) and Anderson (1972) found 100% mortality in South East England and Morecambe Bay during the severe winter of 1962 - 1963. Beukema (1979), however, commented on the relatively light mortality during ice conditions on the Dutch Wadden Sea during the winter of 1978 - '79. This was in complete contrast with that found in Spurn Bight.

Since 1963 the species appears to have been more successful in recolonising the southern portion of its range. Smidt (1944), who observed very high mortalities in the Danish Wadden Sea in the winters of 1928, 1929, 1939, 1940, 1941 and 1942, pointed out that the species has a southern origin of distribution and is consequently the most sensitive species of northern bivalve to the cold. Muus (1967) and Anderson (1972) reported populations at very low levels when compared with pre - 1963 studies in Danish estuaries and Morecambe Bay, and Anderson suggested that competition with the more cold tolerant Macoma balthica may inhibit re-establishment.

Growth of the Spurn Bight population appeared at first to be slow when compared with rates found by Green (1957) in the Gwendraeth Estuary in South Wales and on the Aber foreshore by Hughes (1970a). They record that spat grew 5 - 6mm before their first winter. These authors, however, used mesh sizes in excess of 5mm to extract their animals and admit that spat smaller than this were not recorded. Hughes considered spat to include all animals under 10mm in length. It would seem from this study that Scrobicularia, in common with Macoma, settles in the summer of gamete release and grows to no more than 2mm before cessation of growth at the onset of the first winter. Animals settled in 1976 were found to have reached a mean size of 4.4mm at the end of their second growing season in November 1977, and the 1977 recruitment reached a mean shell length of 6.3mm by November 1978. These figures are in accordance with the first season's growth recorded previously, and it would seem that the use of too large a mesh size has caused misinterpretation of the recruitment of this species. Raymont (1955) and Warwick & Price (1975), using 1mm and 0.5mm mesh sieves, found the size distribution of the smaller individuals from Loch Sween and the Lynher to be similar to those from this study. However, they both interpret the 2 - 5mm animals found in spring and early summer as having settled that year. In this study animals with shell-lengths as small as 0.5mm were found in the autumn and it is likely that these were able to pass through the meshes used by the above authors. Restarting of growth in the spring would rapidly bring these animals up to a size at which they would be retained by these sieves, and this may have been misinterpreted as a spring spat settlement.

Production figures are given in Table 5j but are likely to be underestimates owing to the long sampling interval.

It must be concluded that conditions in the Humber remain unfavourable at the moment for the re-establishment of this species, possibly because of competition with Macoma balthica, and also that the winter of 1978 - 79 proved disastrous for recent spatfalls.

(Tellina tenuis da Costa) - thin tellin

Petch (1907) found this species to be "common, R. Humber" but was not more specific. The species occurs, though is not common on the sandflats at Cleethorpes and Humberston, but was surprisingly not found in the sandflats on the outer regions of the Bight, nor on the estuarine sandy beach at Spurn Head, in spite of an otherwise typical 'boreal shallow sand' community. Jones (1950), Holme (1949), Perkins (1956), and Anderson (1972) all found that Tellina replaced Macoma in downshore estuarine sands in the Exe, Dee and Morecambe Bay, but Beukema et al. (1978) noted that this species is very susceptible to cold winters, with almost 100% mortality in the German Bight in the 1962 -63 winter. No evidence of old shells of Tellina were found in the sandy sediments, but as the sands are more mobile than the upshore silts, this cannot be taken as indicating that a population has not previously existed in the Bight.

Macoma balthica (L.) - baltic tellin

Treated separately in Chapter 9.

Mya arenaria L. - soft shell clam, sand gaper

This is a North American species introduced during the last century (Wolff; 1972), and now is widespread on sandy muds on the coasts of N.W. Europe. Petch (1907) recorded it from "Skeffling to Spurn".

Large specimens of Mya were found on sandy mud areas of the middle and lower shore all over Spurn Bight in May/June 1977 (Table 4a). They could not, however, be counted by coring as most specimens were buried much deeper than the 20cm core depth used in that survey. The largest specimens, between 10 and 15cm in length, were found as much as 50cm deep in the sediment. Evidence of the larger specimens was given by the very characteristic feeding holes on the surface of the mud, and digging under one of these holes invariably produced a specimen. This was used to estimate numbers m^{-2} but undoubtedly resulted in an underestimate as the feeding marks of the smaller individuals are usually obscure and easily missed.

'O' group individuals and animals as large as 30mm shell length were very occasionally found in cores, during both the extensive and intensive surveys, but never in sufficient numbers to merit further study. The maximum density of larger animals was 5 m^{-2} at GV6 on 4.5.77 and of juveniles (0 - 5mm) to be 60 m^{-2} in May 1978 at GIV3.

It would appear that this species did not produce a successful spatfall during the period of study. Warwick & Price (1975) speculated that surface deposit feeding by Scrobicularia may destroy newly settled Mya spat and that a large single cohort of older animals represents the 1963 settlement, immediately after the destruction of the Scrobicularia population by the preceding severe winter. Macoma uses a similar feeding method to Scrobicularia and may therefore similarly prevent successful spatfall in the Humber.

A population with a similar age structure to that in the Humber was recorded from the Dutch Wadden Sea by Beukema et al. (1978) where a declining population was found, dominated almost entirely by large individuals of the 1964 settlement. He observed spatfalls to fail consistently between 1971 and 1977 and recruitment into larger size categories was consequently very low. A density of 3.75 specimens larger than 6cm in length per square metre gave a biomass of 15gm m^{-2} in 1971, 50% of the total macrofauna biomass. Similar densities of even larger animals were found in the Humber and this species may represent one of the largest standing crops of biomass per unit area. It was not possible to age the Humber specimens using growth rings.

Productivity of such mature individuals is likely to be low in absence of successful recruitment. Three estimates of productivity of this species were available - Munch-Peterson (1973), Burke & Mann (1974), and Warwick & Price (1975), gave P:B ratios of 0.6:1 in Roskilde Fjord, Denmark, 2.54:1 in Petpeswick Inlet, Nova Scotia and 0.5:1 in the Lynher Estuary, Cornwall. These estimates however include production by newly settled individuals and the productivity of the Humber population would be much less than this.

Mya arenaria is a commercial species on the continent and in North America (Coe; 1956), but no fishery exists for it in Britain. Muus (1967) found young Mya to be the prey of shore crabs, and that eels and flounders eat the siphons of older animals. De Vlas (1979 & 1981) found that grazing by plaice and flounder accounted for 0.3gm m^{-2} of the elimination of Mya in the Dutch Wadden Sea. It is likely that mollusc-feeding waders will take smaller Mya when available. Owing to the age distribution of the population, this species is unlikely to represent an important food resource of the mudflats.

Mya truncata L. - blunt gaper

Petch (1907) recorded 'distorted specimens' of Mya arenaria 'among stones on the Old Den'. These would appear to be the same population of M. truncata found by Morgan (1969), and still to be found in small numbers among the shingle.

Barnea candida L. - white piddock

Fresh shell valves, usually with the hinge ligament intact, were quite common in the bottom of the Greedy Gut creek draining the Old Den. No live specimens were found but it seems likely that the species occurs somewhere on the Old Den. Petch (1907) found the species on Kilnsea Skerries off the Holderness coast. The species is usually restricted to subfossil peats and boulder clay exposures (Wolff; 1973).

5ix Chelicerates

5ixa Arachnids - Acari - mites

Bright green halacarinid mites were found to be abundant among Enteromorpha growing on rocks on the shore at Kilnsea in November 1976. They were reported to be carnivorous on other meiofauna by Green (1968).

5ixb Pycnogonids - sea spiders

Pycnogonum littorale (Ström)

Recorded from scrapings from the lifeboat pier at Spurn Point by Langston (1972).

5x Crustaceans

5xa Ostracods

Ostracods were common in almost all meiofauna samples taken during 1977, being absent only from coarse sands at CV6 and LIV6, the softest silts at KV2 and the Pyewipes site MIII1. They were, however, most abundant in sand/silt mixtures, being less abundant both in sands and silts, although occurring in small numbers even among the Spartina. The maximum density recorded was

15,000 m^{-2} at JIV3, the numbers and biomass are recorded in Table 4a. These figures are likely to be slightly underestimated as the shute used to remove sand (see materials and methods), did not recover 100% of ostracods.

Mean individual organic weight was found to be 0.0027mg by digestion in KOH solution of 700 individuals and this was used to calculate biomass. This gave a maximum of 0.041gm m^{-2} at JIV3. Warwick et al. (1979) found a mean biomass of 0.08gm m^{-2} organic carbon (≡ 0.2gm m^{-2} dry weight), and a P:B ratio of 11.13:1. Application of this figure to the samples from a single month is not justifiable as temporal variations in abundance have not been taken into account.

5xb Harpacticoid copepods

After nematodes, harpacticoid copepods were the most abundant of the meiofauna, being absent only from the heavily polluted anaerobic mud at MIII1, and reaching a maximum density of 68,240 m^{-2} at FIII4 in May 1977 (Table 4a). They were notably less abundant in the clean outer sands at CV6, KIII6 and LIV6 in Spurn Bight, but abundant (8,480 - 21,480) in the hard sands at Humberston and Horseshoe Point. Except for the fluid silt at KV2, they were also abundant, unlike ostracods, in the more silty upshore sediments and in the *Spartina* zone.

Biomass figures were worked out using a mean individual flesh weight of 0.0011mg calculated from the digestion of 720 individuals. A maximum of 0.075gm m^{-2} was found at FIII4. This is considerably less than the figure given by Warwick et al. (1979), who found a mean annual biomass of 0.317gm organic carbon m^{-2} (≡ 0.793gm dry weight m^{-2}), and a P:B ratio of 17.97:1.

The study of Ratcliffe (1979) indicated an abundance maximum during the winter months and therefore the biomass figures calculated for May 1977 are unlikely to be representative of mean monthly biomass.

Both ostracods and copepods are known to feature in the diet of *Nephtys* (Warwick et al.; 1979) and *Neomysis* (Mauchline; 1971a) and are especially important to gobiids and 'O' group flatfish (Bregnballe; 1961, Muus; 1967, Edwards & Steele; 1968, Braber & de Groot; 1973). They are only likely to feature in the diet of the filter feeding shelduck - *Tadorna tadorna* among the wildfowl.

A survey of the harpacticoid species occurring at Skeffling was made by Dr. J. Lance of Hull University in 1963 (unpublished), and a list of species is included in appendix to Chapter 5.

5xc Cirripedia - barnacles

Balanus balanoides (L.). - common barnacle

Common on any exposed hard surface anywhere within Spurn Bight and extending as far up-river as Paull. Especially large concentrations on groynes on the peninsula, on concrete blocks at Easington and also as an epizoite on exposed shells of Mya and on stakes on the mudflats. Petch (1907) did not record this species which is surprising as it now appears to be the most abundant species of barnacle in the estuary.

Balanus crenatus Bruguière

Recorded by Morgan (1969) at low water on the Old Den and by Langston (1972) and Squire (1973) from pilings at Spurn. Not observed in this study.

(Balanus improvisus Darwin)

Recorded by Petch (1907) "at Well Creek (near Paull), etc.". Not observed in this study.

Elminius modestus Darwin

This Australasian species has been imported into European waters as recently as 1953 (McLusky; 1971), and an unsuccessful settlement was recorded by Morgan (1969) on the Old Den. It was found to be slightly less common than Balanus balanoides on pebbles on the Old Den, but very abundant as an epizoite on Fucus, especially on the stipe and holdfast. It was considerably less common than B. balanoides on stakes out on the mudflats.

Chthamalus stellatus (Poli)

Recorded by Petch (1907), from Skeffling, but no chthamalids were recorded in this study from Spurn Bight.

5xd Mysidacea - opossum shrimps

Neomysis integer (Leach)

Occasional stranded specimens were found in mud cores in areas where standing water remained after the tide had receded and large numbers were observed swarming along the drainage channels in the central areas of the mudflats. A net positioned in a drainage channel near to CIV5 repeatedly caught very large numbers of this species over the course of two tidal cycles (ref. appendix to this Chapter). This catch, however, was not quantitative as many, probably most, of the mysids were seen actively to avoid the net. The catch of 218gm dry weight of Neomysis in July was calculated to contain 16,150 individuals on the basis of a dry weight of 13.5mg from direct weighing, inclusive of the calcareous fraction. From the aerial photographs, an estimated 7,400 similar sized creeks drain the Bight. If the 218gm were representative for all of these, this would represent 1.6 tonnes of mysids with 119 x 10^6 individuals over the whole Bight. Much larger numbers evade the net and probably leave the Bight at low water along the mud surface rather than in the drainage channels, therefore, the total biomass entering and leaving the Bight with each tide must be very much greater than this figure. Collections made in other months produced much smaller numbers of mysids, especially during the winter.

The ecology of N. integer in Loch Etive is described by Mauchline (1971a & b) and was found to have three generations per year feeding on organic detritus from the mud surface, unicellular and filamentous algae, diatoms and also preying on the meiofauna, especially the micro-crustacea. Such a large migrating population probably represents the largest single export of the products of the Bight during the summer months, transferring nutrients and organic material from the mudflat into the main body of the estuary. Mysids are known to form very high proportions of the diet of estuarine fish, especially the flatfish (Hartley; 1940, Braber & de Groot; 1973), and it is likely that they are also taken by other estuarine species, such as cod and eels.

(Neomysis vulgaris Thompson)

Recorded by Petch (1907) from "Skeffling to Spurn" and in freshwater at Easington. No species of Neomysis other than N. integer is known to occur in Britain (Makings; 1977), and it is assumed that N. vulgaris is a superceded synonym of N. integer, although no reference as such could be found.

Leptomysis sp.

Recorded from Spurn Head and Patrington Haven by Levell (1971), Gelder (1972), and Langston (1972).

5xe Cumaceans

Pseudocuma longicornis (Bate)

A single specimen was found in very fluid mud at KV2 in May, 1977. Vader and Wolff (1973) state that this species is characteristic of clean sands, although Fage (1951) also records it from mud. It is likely that this specimen was stranded by the receding tide.

5xf Tanaidaceans

Unidentified tanaidaceans were found in almost all of the clean sandy areas of Spurn Bight (CV6, DV6, GV6, KIII6, LIV6), and also on the South Bank (NII6, NV6). Maximum density was 160 m^{-2} at DV6 in the Bight and 1780 m^{-2} at Humberston. Very little information could be found on the ecology of these animals.

5xg Isopods

Cyathura carinata (Krøyer)

Abundant among gravelly mud on the Old Den, particularly in the small drainage channels that occur in the area. Naylor (1972) stated that this species is particularly common where seawater is diluted slightly and Spooner & Moore (1940) found it to be the dominant species in the middle reaches of the Tamar Estuary. It is also found in polluted muds on the industrial South Bank of the estuary (Smith; 1982) although Wolff (1973) found it to be eliminated from polluted muds in the Dutch Deltaic regions.

Eurydice pulchra Leach

This species was found to be abundant, with Bathyporeia sp., swimming at the edge of the advancing tide at Spurn Head in November 1976. A single specimen was found in a core sample at KIV6 in May 1977. Langston (1972) recorded a density of 21 m^{-2} in midshore sand at Spurn, corresponding to station LIII6.

Wolff (1973) described its sediment requirement in the Deltaic region mainly between ømedian 1.46 - 2.9. Its swimming periodicity is well known

(Jones; 1970), and, together with Bathyporeia sp. forms the main food of sanderling, Calidris alba.

Spaeroma rugicauda Leach

Recorded by Petch (1907) from Patrington Haven in an old dock but not seen in this survey. Abundant at South Ferriby in August, 1978.

Idotea viridis Slabber.

A single specimen was found swimming in a pool at the edge of a Spartina clump at JI3 in May 1977.

(Idotea marina (L.))

Recorded by Petch (1907), in Zostera pools, Skeffling to Spurn. It would seem likely that this is a misidentification as I. marina is not recorded as a British species (Naylor; 1972).

Jaera nordmani (Rathke)

Recorded from the Old Den by Petch (1907), and Jaera sp. was found at Spurn Head by Squire (1973).

(Asellus aquaticus (L.)) - hog louse

A single specimen, found at FIV4 in May 1978, is assumed to have been pumped onto the mudflats from the drainage channels near Skeffling.

Ligea oceanica (L.) - sea slater

Specimens were found under stones at the base of pilings at Kilnsea in November 1976 and October 1978. Petch (1907) recorded it from all the chalk banks in the Humber.

5xh Amphipods

Bathyporeia pilosa Lindström

This species, typical of the boreal shallow sand community of Jones (1950), occurred in almost all sandy substrata during May/June 1977, with a maximum density of 320 m^{-2} at GV6 in the Bight and 660 m^{-2} at NV6 at Humberston (Table 4a). Specimens were also seen swimming at the edge of the advancing tide in company with Eurydice at Spurn Point in November 1976. A mixed population of B. pilosa and B. pelagica (Bate) was found at the downshore sand site NV6 at Humberston, but B. pelagica was not found in Spurn Bight.

The ecology of the Haustoriidae was described from the Netherlands by Vader (1965), and from the Isle of Man by Fincham (1971). Vader found B. pilosa to be the dominant species in the littoral sands. Withers (1977), recorded B. pilosa at densities up to 2200 m^{-2}, occurring only in fine sands ($>70\% < 210 \mu m$), and replaced by B. pelagica at similar densities in coarser sediments and by B. sarsi Watkin and B. guilliamsoniana (Bate), in silty sediments in South Wales. A single specimen of Bathyporeia was found in silt at FIII4 in June 1978, but was too badly damaged for identification.

Anderson (1972) records B. pilosa being found mainly on the upper shore in Morecambe Bay, in contrast to the findings from the Humber. These amphipods form the second largest resource, after Nephtys cæca, of the low biomass downshore sandflats of the Bight.

Bathyporeia sp. and Eurydice sp. are known to be important in the diet of sanderling, Calidris alba, and dunlin, Calidris alpina, (Bengtson & Svensson; 1968, Wolff; 1969) and in the diet of various flatfish species (Bregnballe; 1961, Edwards & Steele; 1968). Sanderling in particular were found to be confined in their feeding during autumn passage to the sandy beaches at Spurn Head by Tasker & Milsom (1979), and it is likely that they are feeding almost exclusively on these crustaceans.

Urothöe sp.

Single specimens of an unidentified species of Urothöe were found at Spurn Head and NII6 at Humberston.

Haustorius arenarius (Slabber)

Single specimens were found in coarse sand at LIV6 at Spurn Head and NV6 at Humberston.

Gammarellus homari (Fabricius)

Three specimens were found among mysids in the nekton trap at CIV3 in April 1978.

Gammarus zaddachi Sexton

Common everywhere where freshwater flowed into the estuary and where cover was provided by large algae and stones, such as at Kilnsea, Easington and Skeffling Cloughs and Patrington Haven. Its estuarine distribution and that of other species of Gammarus is described by Spooner (1947).

Gammarus duebeni Liljeborg

A single specimen was found among the mysids in the nekton trap at CIV3 in April 1978.

Marinogammarus marinus Leach

Common under stones, seaweed and strandline debris everywhere on Spurn Bight, especially the Old Den and the chalk banks.

Talitrus saltator (Montagu)

Common in sand on the upper shore at Spurn in November 1976, but not found in the sample cores in May 1977. It is also abundant in the coarse sand above the Spartina zones at Skeffling and Easington. Petch (1907) recorded it (as Talitrus locusta (L.)) at Kilnsea and Easington.

Orchestia gammarella (Pallas)

Very abundant along the strandline all around the Bight up to E.H.W.S. Petch (1907) recorded it as Orchestia littorea (Montagu).

Hyale sp.

Recorded from both intertidal sand and among algae on pilings at Spurn Head by Levell (1971), Gelder (1972), and Langston (1972).

Gammarids and talitrids are reported to be the main food items in the diet of turnstone, Arenaria interpres, by Davidson (1971), Prater (1972a), and Jones (1975). The work of Tasker & Milsom (1979) shows that the turnstones feed mainly on the gravel and shingle of the Old Den and along the strandline among and above the Spartina, all areas where these groups of amphipods occur.

Corophium volutator (Pallas)

As in the study of Ratcliffe (1979), this species was found only sporadically at very low densities in Spurn Bight. He found C. volutator to be far more abundant in the silts at Paull, reaching a maximum density of 10,500 m^{-2} in September 1976. Isolated specimens were found in the finer upshore sediments at sites BI2, CII4, FI2 and GII4 in May 1978 (Table 4a) and sporadically during the 1978 - 79 survey at FI2 and FII2.

This species is of high importance in the diet of wildfowl elsewhere, especially redshank, Tringa totanus, (Goss-Custard; 1969, 1977 etc.), as no doubt it is at Paull. It is unlikely to be of any significance in Spurn Bight. Its ecology is described by Gee (1961), Meadows (1964 a, b & c), McLusky (1968), and Birkland (1977).

This species is recorded by Petch (1907), as C. longicorne (Fabricius).

Corophium arenarium Crawford

In coarse sediments in estuaries, C. volutator is replaced by C. arenarium (Gee; 1961, Meadows; 1964 a & c). A single specimen was found in Spurn Bight at KV6, but the species was found to be more abundant in sandflats of the South Bank, reaching a density of 3580 m^{-2} at PIV6 in May 1977, where it undoubtedly forms a significant food resource for birds.

5xj Decapoda - shrimps, prawns and crabs

Palaemonetes varians Leach

Very abundant in shoals in the creeks draining the saltmarsh at Welwick but not seen on the mudflats themselves. Recorded by Petch (1907) in pools at Easington, and in brackish ditches at Easington, Cherry Cob and Sunk Island.

(Palaemon elegans Rathke)

Recorded (as Leander squilla Kemp), from Patrington Channel by Langston (1972). This species is easily confused with Palaemonetes varians, which was found to be common at Patrington, and it is likely that this record is a result of misidentification.

Pandalus annulicornis Leach - aesop prawn

Recorded as dredged off Trinity Sand by Petch (1907).

Crangon crangon (L.) - common shrimp

Specimens were very occasionally included in sample cores, presumably individuals stranded by the receding tide. Several individuals were found with Palaemonetes varians in the creeks at Welwick, and the nekton trap produced a maximum of 23 specimens in July 1978. It was seen to be most abundant, however, in the Greedy Gut stream separating the Old Den from the peninsula in May 1977.

Shrimps migrate up and down shore with the tide and emigrate from estuaries into marine conditions at the start of winter (Lloyd & Yonge; 1947), and thus represent a mode of export of the products of the mudflats into the estuary and the sea. They are omnivorous, taking algae and detritus and are also predators of benthic animals, particularly meiofaunal crustacea, bivalve spat and small polychaetes (Green; 1968). In turn they are important in the diet of predators and were described as featuring heavily in the diet of cod in the Humber by Forsberg (1977), and by Brennan (1973), who also described the decline of the fishery for shrimps in the Humber. This does not seem to be linked with the disappearance of the shrimps, but rather a long term migrational or behavioural change.

Pagurus bernhardus (L.) - hermit crab

Reported as dredged off Trinity Sand by Petch (1907) and found on the Old Den by Morgan (1969), but not seen in this study.

Carcinus maenas (L.), - shore crab

The shore crab is common up the length of the estuary, at least as far upstream as Winteringham Haven (own observation), and very abundant around the edges and on the mudflats of Spurn Bight. Juveniles up to 2cm. carapace width occurred reasonably commonly, although sporadically, in the sample cores from all stations during 1978 - 79 and were found in occasional samples of the May/June 1977 survey from among the Spartina, in soft silt and sandy mud, but were never found in clean sand. Larger individuals, up to 8cm across the carapace formed numerous burrows up to 1m in horizontal length, in the side of the drainage channels and were also occasionally found half buried in soft sediments on the mudflats. Crabs are also abundant in the creeks of Welwick Saltmarsh and under stones on the Old Den.

Carcinus is a generalised predator eating anything it can catch (Green; 1968), and is migratory over the surface of the mudflats with peaks of activity at high tide and at night (Naylor; 1958). It is, therefore, likely to be a major secondary/tertiary consumer on these mudflats and responsible for the translocation of energy and nutrients. No estimates could, however, be made of its population dynamics owing to its mobility.

Carcinus is a major food item in the diet of curlew, Numenius arquatus (Wolff; 1969, Goss-Custard et al.; 1977). From the small number of crop contents examined in this study contributed by members of the Holderness

Wildfowling Association, it would appear equally so in the Humber. Five guts were examined, two of which contained Carcinus remains. One bird shot on December 18th 1977 at Skeffling contained one 5cm crab and 32 2cm crabs, and another, shot at East Bank on September 15th 1977, contained a single 6cm crab. Forsberg (1977) described large shore crabs in the guts of cod caught in Spurn Bight.

Pinnotheres pisum (Pennant) - pea crab

Morgan (1969) reported this species, commensal in the shells of Mytilus, as common on the Old Den. It was not looked for in this study.

5xi Collembola - springtails

Hydropodura aquatica L.

Small (c.a. 1.5mm), grey waxy springtails, almost certainly of this species, were occasionally abundant on the mudsurface and on the surface of pools of standing water during the summer. On one occasion they were sufficiently numerous to colour the surface of the mud grey, and an estimate of 150,000 m^{-2} taken from the surface of five 10cm cores at GV6 on 4th May 1977, must be regarded as a considerable underestimate, as large numbers were able to escape during sample collection and extraction.

Collembolans do not appear to have been counted previously from mudflat surfaces, although they are recorded in swarms on saltings and the surface of creek waters at Scolt Head Island by Ellis (1960), and from intertidal mud in the Severn by Boyden et al. (1977). They may play a small role in the redistribution of nutrients by being transported passively on the surface of each advancing and receding tide.

Anurida maritima Guèrin

Larger, brownish springtails, probably of this species were found on the mud surface among Spartina during the summer but never occurred in the sediment cores. Ellis (1960) recorded this species from this habitat at Scolt Head Island.

Borror et al. (1976) reported springtails to have a herbivorous and detritivorous diet and therefore those on the mudflats must either be primary consumers or scavangers. Large numbers of springtails, probably of terrestrial species, are abundant among the strandline detritus. They are important as the food of smaller carabid and staphylinid beetles of the strandline community.

5xii Insects

5xiia Diptera - flies

Limonia sp.

Tipulid larvae are reported from among algal scrapings from the lifeboat station pier at Spurn by Langston (1972). This is the typical habitat for Limonia sp. (Colyer & Hammond; 1968), and it is assumed that these larvae were of that genus.

Chrysops sp. - horse flies

Tabanid fly larvae were found occasionally in cores, reaching a maximum density at FII2 of 240 m^{-2} in October 1978. Two genera of tabanids are known to have halophyllic larvae, Tabanus and Chrysops (Edwards et al.; 1939). Larvae did not reach sufficient size to produce Tabanus nigrifacies Gobert, commonly 13 - 16mm and the only British halophyllic Tabanus, and therefore it must be concluded that the larvae are of the genus Chrysops.

Larvae were rarely found far from the edge of the Spartina, although a density of 100 m^{-2} was found at CII4 in May 1977. Other stations at which they were found in May/June 1977 were BI2, CI2, CII4, DI3 and JI3 (Table 4a). During the 1978 - 79 study these larvae were found only at FI2, in the Spartina and at FII2. The cycle of abundance throughout the year is given in Table 5k and Figure 5xii from which it becomes apparent that pupation, emergence and egg laying occurs between May and August, with a single generation produced during the year.

Mortality was low between August and January and a reduced population survived at both sites through to March, indicating that the species was not catastrophically affected by the large build up of ice on the Spartina belt during January 1979.

The life cycle of Spartina-dwelling species of tabanid was described by Axtell (1976). Eggs are deposited on the Spartina plants themselves in cohesive batches. Larvae drop onto the mudsurface and burrow into the sediment, feeding on detritus, algae and bacteria, as well as predating small invertebrates (Wall; 1973). Specimens found downshore must presumably be transported by the tide. Pupation is reported to occur 'in situ', close to the mud surface, but no pupae were found during the study.

The adults were not encountered during the flying period of June to August during 1978, although the author was bitten by a Chrysops on the sea wall at Weeton in May 1977. Adult female tabanids are notorius blood-feeders, although the males feed entirely on nectar (Roberts; 1967). They are reported to feed on avian as well as the more usual mammalian blood (Bennet; 1960), and it is likely that bird blood forms the main diet of these flies as the area around the mudflats is mainly arable.

The role of these larvae in the mudflat ecosystem is poorly understood (Teal; 1962) and they are rarely recorded in benthic studies. Boyden et al. (1977) record fly maggots as common in mudflats in the Severn at densities up to 80 m^{-2} just below the saltmarsh, and it is likely that this is a reference to tabanid or dolichopodid larvae.

Thinophilus flavipalpis Zetterstedt

Dolichopodid fly larvae were occasionally found in mud cores, usually in the TOPSILT community. This habitat description fits that of T. flavipalpis given in Colyer & Hammond (1968).

5xiib Coleoptera - beetles

Thirty six species of beetle were found on the foreshore of the Bight, particularly along the peninsula, mainly under stones and strandline debris, and on sandy beaches behind the Spartina subjected to flooding only at spring tides. A list is included in the appendix to this chapter.

All carabidae and staphylinidae are carnivores, mostly specialising in springtails or dipteran larvae. Broscus cephalotes (L.) specialises in feeding on the sandhoppers Orchestia and Talitrus.

With the exception of Nacerdes melanura and Pselactus spadix both of which feed specifically on the bark of salt-water soaked timber, all other species are general scavengers, feeding on decaying seaweed etc., and facultatively on dipteran larvae (Joy; 1932).

5xiii Ectoprocta - bryozoans

Membranipora monostachys Busk

Reported by Petch (1907) on stones near high water at Skeffling and on shells of *Mytilus*. Bryozoans were found on *Mytilus* on the Old Den but not identified to species.

Membranipora membranacea L.

Recorded among scrapings from jetty pilings at Spurn Head by Levell (1971), and Gelder (1972).

Flustra foliacea (L.) - hornwrack

The dead skeletons of this seaweed-like bryozoans were common in the strandline all around the Bight. No living colonies have been observed, and it is possible that the skeletons came from colonies on the bed of the estuary or the Holderness coast.

5xiv Echinoderms - sea urchins etc.

(*Echinocardium cordatum* (Pennant)) - sea potato

Fragments of test were occasionally found on the shore at Spurn Head, although living specimens were not observed. They are infrequent on the southern sandflats east of Humberston but common on the Lincolnshire coast (Hinton-Clifton; 1964 and own observations).

The Vertebrates

5xv Fish

The following list results from observations gleaned from the long-line fishermen and anglers who use the Bight and also a few of my own. The full list for the estuary is likely to be quite long - Perkins (1973) records 131 species of fish from the Solway Firth and there is no reason why the total for the Humber should not approach this number. (addendum; Rees (1982b) records 60 species from the Humber) It is difficult, however, to determine which species actually use Spurn Bight either as a feeding ground for adults or nursery ground for young fish. Direct observations are recorded below.

Lampetra fluviatilis (L.) - river lamprey

Recorded by the long line fisherman at Easington.

Sprattus sprattus (L.) - sprat

A single sprat was found in the nekton trap at CIV3 on 12th April 1978.

Anguilla anguilla (L.) - common eel

Trapped semi-commercially in the Humber and taken frequently on Spurn Bight. Langston (1972) recorded specimens netted in Patrington Channel.

Sygnathus acus (L.) - great pipe fish

A single specimen was found by eel trappers in 1978.

Gadus morhua (L.) - cod/codling

A small commercial fishery exists by long lining mainly for cod on the Bight, and it is most popular with sea anglers at Hawkin's Point, Spurn Point and also at the more accessible edges of the Bight mudflats at low water. Forsberg (1977) described the unique cod-angling offered by the Bight and the diet of the cod using it.

Merlangius merlangus (L.) - whiting

Commonly caught with cod by long liners and sea anglers.

Pomatoschistus minutus (Pallas) - sand goby

Common in the Greedy Gut draining the Old Den. Also recorded as common in the main body of the estuary by Riley (1973).

Pomatoschistus microps (Krøyer) - common goby

Very common in the creeks on Spurn Bight and at Welwick Saltmarsh, where it is popular with small boys with nets and jam-jars!

Callionymus lyra L. - dragonet

A single specimen was caught by the author in the Greedy Gut.

Ammodytes sp. - sand eels

Very common in pools around groynes at Spurn Head and in the Greedy Gut.

Liparis liparis (L.) - sea snail

A fresh dead specimen was found among the strand line refuse at Spurn Point in November 1976.

Gasterosteus aculeatus (L.) - three spined stickleback

A specimen was found in the nekton trap at CIV3 on 12th April 1978. It is very common in the creeks on the Bight and at Welwick Marsh where it is fished for by local children.

Scophthalmus maximus (L.) - turbot

Recorded from Patrington Channel by Levell (1971) and Gelder 1972 but not found by long liners or sea anglers using the Bight.

Limanda limanda (L.) - dab

Commonly caught by long liners and anglers from the Bight. Taken in Patrington Channel by Levell (1971) and Gelder 1972.

Pleuronectes platessa L. - plaice

Commonly caught by long liners and anglers in the Bight. Found in large numbers in the Greedy Gut in May 1977.

Platichthys flesus (L.) - flounder

Juveniles ($<$ 10cm in length) are commonly found stranded on the mudflats in the summer months. Two juveniles were caught in the nekton trap at CIV3 on 12th April 1978. This species is very commonly caught by long liners on the Bight and by the sea anglers at Spurn Point and Hawkin's Point.

Solea solea (L.) - sole

Frequently taken by fishermen on the Bight, though not as commonly as the previous three species.

5xvi Aves - birds

No attempt was made to include the birds in this study, which are regularly monitored from the Spurn observatory and also by members of the Hull Natural History Society on the monthly R.S.P.B./B.T.O. estuarine counts (Prater 1973 et seq). A monographic study of the birds of the estuary, under contract from the N.C.C. was prepared by Tasker & Milsom (1979), from which the appendix list is taken.

5xvii Mammals

Common seals Phoca vitulina L. are regularly seen on the beach at Spurn, occasionally on the estuarine side. Common porpoises Phocaena phocaena (L.) are regularly seen off Spurn Head and Hawkin's Point. Strandings of both species were observed on the estuarine beach at Spurn during the study period.

5xviii Flora

No attempt was made to study the flora of the area in any detail. Micro-algae etc. were ignored completely and a simple list of macroalgae and angiosperms compiled. Only plants of the mudflats proper are included and the vegetation of Welwick Saltmarsh is described by Crackles (1966) and Boatman (1974). I am indebted to Dr.D.J.Boatman of Hull University for the checking and correction of my algal identification and to Mr. B. Pashby for information on Zostera sp.

5xviiia Algae

Cladophora sp., Chaetomorpha sp. and Bryopsis sp.

On groynes along the peninsula, on rocks on the Old Den and forming a 'mat' between Spartina plants.

Ulva sp. - sea lettuce

On rocks of the Old Den.

Enteromorpha sp.

Particularly abundant wherever freshwater enters the Bight, also on the sea wall at Kilnsea, on stones on the Old Den, on posts on the mudflats and occasionally forming mats with Cladophora on sandy mud in summer over large areas of the Bight, especially among Zostera and among the Spartina roots.

Fucus vesiculosus L. - bladder wrack

Common on any hard surface all over the estuary especially on groynes, sea walls, stakes and posts on the mudflats and on stones on the Old Den. The most important constituent of the strandline.

Red algae:- all species were found attached to stones on the Old Den.

Porphyra umbilicalis (L.) Lyngb, Chondrus crispus (L.) (Stackh.) - carragheen, Dumontia incrassata (Müll) Lamour, Corallina officinalis L. - coral weed, Ceramium rubrum (Huds) Ag.

5xviiib Angiosperms

Salicornia sp. - samphire

Common as a primary coloniser of bare mud only at Welwick Saltmarsh, where shoot densities of 20 plants m^{-2} occur, often intermixed with advancing Spartina but always colonising in advance of it. Relatively uncommon east of Weeton Track End, occasional plants are found among Spartina. It was not found west of the Patrington Channel.

Although occurring abundantly at Welwick, this tasty species is not collected for human consumption as it is on the sandflats of the South Bank, particularly at Horseshoe Point. Semi-commercial samphire beds exist near Somercoates on the Lincolnshire coast. The Welwick population represents the only source of samphire in Yorkshire and the plants are equally delicious as those of South Humberside (own observation)!

(Zostera marina L. - grass wrack)

Pashby (1977), quoting Robinson (1902), gave an old record for this species in 1888. There appears to be no subsequent record.

Zostera angustifolia (Horenem.) Reichb

Pashby (1977) recorded isolated patches 55m from the shore of the 'narrow neck' area of Spurn in 1976.

Zostera noltii (Hornem)

This plant was found as an approximately 100m wide band 150m from the shore at Spurn on the 'J' transect in May 1977. Subsequent aerial photography revealed an extensive Z. noltii zone stretching from the Old Den almost to Kilnsea (Plate 3). The history of Z. noltii at Spurn is discussed by Pashby (1977).

Spartina anglica C. E. Hubbard

Spartina forms an almost continuous strip along the inner edge of Spurn Bight, from Hawkin's Point to the Old Den, being broken only at Kilnsea where there is a piled sea wall (Figure 2ii). It varies from a dense sward as at Welwick Marsh and at the base of the peninsula to separate circular patches which appear to be declining as at Hawkin's Point. Boatman (1974), quoting Good & Waugh (1934), gives the history of the species (as S. x townsendii, from which S. anglica is derived by amphidiplody) in Spurn Bight. It was first planted at Welwick in 1926 and has been subsequently planted to stabilise and reclaim the mudflats.

Summary of Chapter 5

Autecological notes are given on all species of invertebrates found to occur in Spurn Bight, excluding those described in greater detail in other chapters.

An annotated species list of vertebrates and plants of the mudflats and a full list of all taxa are included as an appendix.

170 identified species of invertebrates are recorded from 148 genera, 93 families, 38 orders, 24 classes and 14 phyla. 65 species of vertebrates are recorded from 48 genera, 28 families, 18 orders and 4 classes. 11 identified species of plants are recorded from 14 genera, 11 families from 4 divisions.

CHAPTER SIX

CHAPTER 6

NEPHTYS HOMBERGI (SAVIGNY)

Introduction

The 'catworm' Nephtys hombergi (Savigny) is collected as a low quality bait by Spurn's sea anglers along with the lugworm, Arenicola marina, over most of the sandier parts of the Bight. The two worms are commonly found together and, although Nephtys occurs at far higher densities than Arenicola, large sized animals are relatively uncommon and the species does not advertise its presence with casts as does the lugworm. Consequently it is not sought specifically but larger individuals, together with Nephtys cæca Fabricius, from cleaner sands, are taken when found.

Warwick & Price (1975) found the species to be a major producer in the Lynher estuary and it was found to be present at exceptionally high densities in Spurn Bight. The major part of the study of Ratcliffe (1979) concentrated on sites where Nephtys was less frequent and his data included only density values. Efforts were therefore concentrated on the species to ascertain its relative importance within the infauna as a potential source of food for larger predators using the Bight.

6i Taxonomy and identification

Petch (1907) records Nephtys longisetosa Oersted "in sandy mud, Stone Creek, Skeffling etc." Wolff (1971) gives the ecological preference of N. longisetosa as clean sands and it is therefore likely that Petch was referring to N. hombergi.

The Lincolnshire River Authority Surveys (1971 - 1974), variously record N. cæca (Fabricius), N. hombergi and N. cirrosa Ehlers, mainly from Humberston but also from South Killingholme and Grimsby and there is probably taxonomic confusion between the surveys.

From an examination of the distribution of Nephtys sp. it was clear that two species were present in the Bight - N. hombergi and N. cæca. Identification was straightforward using Fauvel (1923), and no evidence of N. cirrosa or N. longisetosa was found during the extensive survey on either bank of the estuary, although the survey by Wolff (1971) in the Rhine/Meuse/Scheldte estuarine system led us to expect to find both species. Curiously, he found N. cæca absent from the intertidal zone, but it was found to be dominant in intertidal clean sand on both the North and South banks of the Humber.

Small specimens of N. hombergi and N. cæca were found to be very similar in appearance and misidentification is likely when superficially examining large numbers of specimens. During the extensive survey all specimens of the genus were checked and sympatric populations were only observed at three very sandy sites as well as in peculiar conditions at station KV2 in fluid mud immediately west of the Old Den (discussed in Chapter 4). N. cæca was absent from all sediments with high silt content and it was decided safe to assume all specimens of Nephtys present in extensive studies to be N. hombergi.

6ii Distribution in and around the Humber

N. hombergi is recorded as far upstream as Stone Creek by Petch (1907) (as N. longosetosa, see above) and Levell (1971). Ratcliffe (1979) did not find it at Paull or Hessle. It was not encountered at Cherry Cob Sand in 1977 and sediments there at that time were probably unsuitable for the species.

On the South bank N. hombergi is referred to specifically by Gelder (1971) who differentiates N. cæca and N. hombergi at Humberston, and by Beard (1974), also at Humberston. Other Lincolnshire River Authority Surveys refer to N. cirrosa (above). N. cæca, but not N. hombergi, was found at Humberston and Horseshoe Point in Spring 1977 in this study.

Suitable sediments for N. hombergi are not found along the Holderness coast, where N. cæca is present in Bridlington Bay and further north at Filey (own observation). Along the Lincolnshire coast N. cæca is dominant in sands except in small estuarine areas such as at Saltfleetby where N. hombergi occurs.

6iii Ecological relationships

6iiia Salinity

All areas investigated were well within the known salinity tolerance limits outlined by Wolff (1971) who gives a salinity as low as 17‰ as the species' lower limit. Boyden & Little (1973) note that the species is most commonly encountered in estuarine areas but conclude that particle size preferences and not reduced salinity conditions are responsible for this. Anderson (1972) noted that *N. hombergi* was negatively correlated with truly estuarine species in Morecambe Bay.

6iiib *Tidal position*

The effects of the related variables, tidal height and sediment composition, are difficult to differentiate in Spurn Bight. The distribution of both *Nephtys* species with tidal distance during the extensive survey are illustrated in Figure 6i and there is a good indication that *N. cæca* replaces *N. hombergi* down the shore. Highest densities of *N. hombergi* occurred in mid shore sediments and biomass values followed an exactly similar relationship.

Smidt (1951) concluded that "duration of water covering is of decisive influence" and Raymont (1955) regarded the species as being "fairly restricted to low tidal levels". Wolff (1973) recorded all species except *N. cæca* as common intertidally and quotes Thamdrup (1935); that *N. hombergi* is absent in places where immersion times are less than 30% of the tidal cycle and makes a similar observation, also recording the species subtidally to 33m.

6iiic *Particle size distribution*

Density and biomass of both species of *Nephtys* in relation to particle size and sorting at extensive survey sites are given in Figures 6ii and 6iii. There is very little overlap in distribution between the two, particularly with regard to sorting and *N. cæca* is restricted to coarser, better sorted sands (ϕm 3.5, ϕSo 0.65). *N. hombergi* is much more common in poorly sorted muddy sands (ϕm 3.0 - 5.0, ϕSo 0.4 - 1.7), but not in fine organic silts with ϕm in excess of 5.0. Similar sediment preferences are recorded for the two species by Clark and Haderlie (1960) in South Wales, Wolff (1971 and 1973) in the Netherlands deltaic region and by Kay & Knights (1975) in S.W. England. Wolff (1971), however, found no difference in sediment sorting preferences between the two species.

Boyden et al. (1977) found *N. hombergi* present in liquid mud at low water at three sites in the Severn Estuary (cf. the area west of the Old Den?) as well as in mud polluted with sewage at Magor. It is therefore unlikely that high organic levels and anoxic levels of the upper shore are limiting to the species - indeed Rosenberg (1977) found N. hombergi the most anoxia tolerant species in a benthic fauna in an oxygen deficient Swedish estuary.

6iiid Temperature and extremes of weather

Reductions in density over the 1978 - 79 winter were less than those recorded for shallow burrowing molluscs.

There is less evidence of the adverse effects of extremes of temperature on the species of Nephtys than for estuarine mollusc species although Beukema (1979) has shown a definite relationship with severity of winter temperatures and mortality of N. hombergi and Smidt (1944), found considerable reduction of the species in the Waddensea in the very severe winters of the early 1940s. Beukema et al. (1978) also found a consistent increase in biomass of N. hombergi over a decade of mild winters in the Dutch Waddensea, but this was terminated by massive mortality in the winter of 1978 - 79 (Beukema; 1979).

The worms are relatively deep burrowing and are probably able to escape all but the most extreme deep freezing of the mud as well as erosion by storms.

6iiie Depth distribution

Sediment cores were taken to 20cm specifically to sample the more deeply burrowing polychaetes but no attempt was made to measure their depth distribution. Very occasionally burrows were seen penetrating below this depth after the core had been extracted and this is likely to have led to some degree of underestimation of the dynamics of larger individuals. Interpretation of the decline in numbers of older cohorts with age must be made with the increased facility for deeper burrowing in mind. Such deep burrows were very infrequent, however, and the decline in density of larger animals must certainly reflect a genuine mortality or emigration rather than simply retreat to greater depth in the sediment.

The deep burrowing of the worms must also be considered when assessing the species as a food resource for fish and wildfowl. Only curlew are likely to be able to take deeper burrowed specimens although shorter beaked birds and fish may be able to take advantage of the species when present nearer the surface.

6iv Density

The density of N. hombergi and N. cæca found during the extensive survey of 1977 is recorded in Table 4a and during intensive studies of 1978 - 1979 in Table 6a and illustrated in Figures 6iv - vi.

The maximum density of N. hombergi recorded in 1977 was 900 m^{-2} at FIV4, mainly for one year old specimens, contrasting with a maximum for N. cæca of 375 m^{-2} at CV6 (excluding 460 m^{-2} in unusual conditions at KV2). N. hombergi was never found at the upper shore intensive survey stations FI2 and FII2, and reached a maximum density of 1640 m^{-2} at site CIV4 in September 1978 at the height of recruitment of juveniles.

Ratcliffe (1979) observed a maximum density of "nearly 3000 m^{-2}" in September 1974 at Skeffling and, although he did not record population structure, stated that the large numbers were made up almost entirely of very small individuals less than 6mm in length. Throughout the rest of his study numbers fluctuated between 200 and 700 m^{-2}.

Density values for N. hombergi, as with Retusa obtusa, appear to be higher in the Humber than have been recorded elsewhere. Ratcliffe's figure is the highest that could be found for the species in the literature, the highest outside the Humber being that of Warwick & Price (1975) in the Lynher estuary - maximum value 1104 m^{-2}. Smidt (1951) gave densities of juveniles of 1000 m^{-2} in the Danish Waddensea but this refers to much smaller individuals. Densities of 'adults' elsewhere is usually recorded at around 100 m^{-2} (refer Table 6b), and this is consistent with values in Spurn Bight for cohorts older than one year.

6v Population structure

Size/frequency histograms of the population structure of N. hombergi are given for extensive and intensive survey data for sites FIV4, GIII4 and GIV3 in Figures 6vii to 6ix. The maximum number of cohorts present at any one time was four, with animals dating from 1975 present at low density at the start of the year becoming extinct in the autumn at all sites. Animals spawned in 1976 likewise became extinct at the end of 1978 and the most likely explanation for this is post spawning mortality of both older cohorts (below).

The population structure in May 1977 was similar at all sites to that one year later although with smaller mean individual size of each cohort.

Studies on the population structure of populations of N. hombergi have been carried out by Kirkegaard (1970), Warwick & Price (1975), Olive (1977) and Price & Warwick (1980). Size/frequency data found by the first two authors is very similar to that of the present study and the age interpretation of individual cohorts is supported by tooth growth ring studies by Kirkegaard. Study of tooth rings by Olive, however, of a population of N. hombergi in the Tyne, produced a very different interpretation with five strongly overlapping cohorts with little size/frequency differentiation. The results of the present study are more in keeping with those of the first two authors. Monthly histograms are very similar to those of Warwick & Price, both in terms of density and growth rate. Recruitment in the Humber in 1978 appeared to start considerably earlier than in the Lynher in 1972 or 1973.

6vi Spawning and recruitment

'O' group individuals with a 'head' width of 0.2mm started to appear in small numbers at the three sandier intensive study sites in July 1978, with a maximum density of 100 individuals m^{-2} at GIII4. There followed a rapid increase over August to reach a peak in September at all sites, maximum 1190 m^{-2} at GIV4, followed by an abrupt decline before October, continuing throughout the winter.

Smidt (1951) recorded spawning in May/June in the Dutch Waddensea with highest recruitment in June of 1000 m^{-2}. Olive (1977) described the early larval life of N. hombergi and N. cæca and found young larvae of only nine setigers as early as June. These are considerably smaller than the smallest individuals encountered in the Humber (15 or more setigers) and the vigorous sieving method possibly destroyed the youngest larvae, even with the gentle CALGON/roller treatment.

Warwick & Price (1975) and Price & Warwick (1980) found possible evidence of spawning in July from an inflection in the head width/weight relationship followed by recruitment of 6mm individuals (32 setigers), starting in September and peaking in October. They quote P.E. Gibbs (unpublished), that settlement of smaller juveniles occurred in the subtidal zone.

The actual date of spawning in the Humber was probably earlier than July. The failure to detect very small individuals is therefore a source of underestimation in calculations of dynamics of the 'O' group.

6vii Mortality, migration and predation.

At all three sites mortality of the oldest, 1975 settled animals, reached 100% by early autumn and that cohort was not seen after November 1978. This fits the life history model of Warwick & Price (1975), comparable with Neanthes virens, where there is a heavy, post spawning mortality at the end of the second year with a very few animals surviving into a third year to grow very large and die after a second spawning. The population structure observed in May 1977 also supports this model.

Apart from minor fluctuations, attributable either to sampling error or minor migration, changes in density at sites FIV4 and GIV3 were fairly smooth and continuous for cohorts younger than the 1975 settlement. At GIII4 there were wild fluctuations in density of all cohorts and it was not possible even to smooth the mortality curves. Similar fluctuations were observed at this site for other species (q.v.), and it was not possible to analyse the dynamics of N. hombergi further there.

Decline in density of the 'O' group appeared to be highest immediately after the peak of recruitment in September , amounting to 57% of the total at FIV4 between September and October, although mortality/migration during the period of recruitment was impossible to measure. Smidt (1951) concluded that predation 'by enemies' was the most significant cause of mortality of the 'O' group but it is possible that inhalation into bivalve siphons may be significant although this has only been reported for bivalve spat which are less motile than young polychaetes. Total mortality/ emigration for this cohort between the peak and March 1979 varied between 92% at station GIII4 and 71% at GIV3.

There was also evidence of size specific mortality in the younger cohorts during the winter. The mean size of the 1977 cohort fell steadily between November and March at FIV4 by a total of 32% over the four month period, clearly evidence of selection against, or emigration of, larger individuals, probably a result of predation by wading birds.

In contrast, the mean size of the 'O' group at all sites increased between November and March, unlikely to be the result of growth and probably indicative of selection against smaller individuals and, therefore, more likely to result from erosion and temperature effects on the smaller, less deeply buried individuals. The species, therefore, seems to be subject to selection against the smallest and largest individuals by different agents.

Migration of adults of this species has not been reported but it is able to swim well when disinterred from the sediment and active or passive migration following erosion may be significant in its density changes. Specimens of neither species of *Nephtys* were obtained in the nekton traps in drainage creeks and, as it was not possible to allow for migration in dynamics calculations, all reductions in density have been assumed to be the result of mortality.

At the observed density and biomass, *N. hombergi* is a large potential food resource for higher predators. Smidt (1951) recorded *Crangon* as regularly feeding on *Nephtys* and it is likely that the large numbers of *Carcinus* in the Bight also include all available polychaetes in their diet.

Smidt (op. cit.) records *Nephtys* 'of importance' in the diet of larger 'O' group and older plaice, *Pleuronectes platessa*, and *Nephtys* sp were found in the gut of 'O' group plaice but not dab, *Limanda limanda*, by Edwards & Steele (1968). Wolff et al. (1981) found *N. hombergi* to be significant both to plaice and flounder, *Platichthys flesus*. *Nephtys* sp. has been recorded in the diet of numerous species of wading birds, notably dunlin, *Calidris alpina*, in which *Nephtys* can form a significant proportion of the food intake (Goss-Custard, Jones & Newbury; 1977), and also redshank, *Tringa totanus* (summary of feeding studies in Goss-Custard; 1977b), bartailed godwit, *Limosa lapponica*, curlew, *Numenius arquatus*, and grey plover, *Pluvialus squatarola* (Goss-Custard et al. 1977).

The study of all these species of wader in Spurn Bight by Tasker & Milsom (1979) shows their preferred feeding grounds to coincide with the midshore sandy silt where *N. hombergi* abound. This polychaete is, therefore, likely to form a significant proportion of the diet of certain waders which are present at nationally and occasionally internationally significant levels.

6viii Biomass

All biomass figures were calculated using a 'head' width/flesh dry weight relationship calculated from 842 animals collected in May 1977 at station GIV3 and using pooled numbers of animals of similar head widths. The overall equation was found to be:-

$$\text{dry flesh weight} = 2.08 \times \text{head width}^{3.20} \qquad r = 0.94$$

Seasonal variation in the relationship was therefore not taken into account. Using similar regressions carried out monthly by Warwick & Price (1975), a 60% difference in weight of a standard sized individual can be calculated between a summer maximum value and a winter minimum. Their value for May is 8% higher than the mean for the year and this must be regarded as a source of error in the dynamics calculations in the present study.

Values for dry weight biomass at all sites in Spurn Bight during the extensive survey are given in Table 4a and total population and individual cohort biomass figures at the three sites of intensive study are given in Table 6c, and monthly biomass statistics are expressed graphically in Figures 6x - 6xii. Peaks in biomass were not found to be synchronous between stations, rising to maxima in September 1978 at GIV3, October at GIII4 and November at FIV4. The maximum value recorded was 10.05 gm m^{-2} at FIV4 in November. Mean monthly biomass was also highest at FIV4 - 5.45 gm m^{-2} and lowest at GIII4 - 3.16 gm m^{-2}. Biomass of N. hombergi was found to contribute between 5.5 - 18.5% of total measured mean monthly community biomass in midshore sandy mud stations (ref. Chapter 11).

Variation in total biomass followed a roughly similar cycle over the year at each station, rising to a maximum in the late summer/autumn and falling continuously over the winter to a minimum value the following March. At all three sites biomass in March 1979 was considerably less than in March 1978, as the 1976 cohort did not appear to survive the winter as had the 1975 one.

Breakdown of biomass into values for individual cohorts shows the variation in proportional composition of the population over the year. In spring 1978, the 1976 cohort contributed the bulk of the biomass. Older, 1975, animals comprised 25 - 30% of the total in March and this proportion was maintained until the cohort was eliminated by post spawning mortality in the late summer.

The dominance by two year old animals continued until the autumn when a combination of mortality and the rapid growth of the younger animals resulted in dominance of the biomass by the 1977 cohort. The 1978 '0' group at no time contributed more than 5% of the total biomass.

The value of 5.45 gm m^{-2} for mean biomass over the year is high when comared with previous records. Ratcliffe (1979) estimated a mean value of 3.25 gm m^{-2} at his regular Skeffling site (corresponding to station FIII4). Warwick & Price (1975) and Price & Warwick (1980) found a mean biomass ranging from 3.21 - 4.76 gm m^{-2} in the Lynher Estuary in Cornwall between 1972 and 1977 where N. hombergi contributed 30% of the total community biomass. Smidt (1975) found a maximum of 3.0 gm m^{-2} in Danish midshore sandy Waddensea and Beukema et al. (1978) found mean values ranging from 0.16 to 0.84 gm m^{-2} over the period 1969 - 77 in the Dutch Waddensea.

It would appear that conditions in Spurn Bight were particularly favourable for this species during the study period.

6ix Growth

Changes in mean individual weight of each cohort are given in Table 6d and illustrated in Figures 6xiii to 6xv. The curves more correctly illustrate growth in body width as weight is calculated directly from a single relationship and seasonal variation is not taken into account (see above). The curves cannot, therefore, indicate changes in body weight resulting from gamete release etc.

There were found to be considerable differences in rate of change in individual weight between sites. The oldest animals - the 1975 cohort - were present in insufficient numbers for sampling error not to disguise the overall changes in mean size as a result of growth. At station FIV4, these animals appeared to undergo exponential growth from March to August 1978 after which they probably died after spawning.

Remaining cohorts at station FIV4 similarly underwent exponential growth up to November when the 1976 cohort became extinct and factors other than growth became significant for other cohorts (see below).

At the two Easington stations there was much slower growth of the 1976 animals in a less obviously exponential pattern. At both sites mean size became smaller in the late summer, probably because post spawning mortality was size-related with larger animals maturing and thus dying earlier.

The growth rate of this species has been studied in the Lynher Estuary, Cornwall by Warwick & Price (1975) and Price & Warwick (1980) and the results from the Humber are very similar to their study with periods of approximately exponential growth interrupted by winter periods of zero growth. Considerable variation in growth rates between succesive years was found in Lynher populations.

The population investigated by Olive (1977) was sufficiently different in structure and longevity from this study and that of Warwick & Price to make comparison difficult.

6x Production, elimination and productivity

Owing to very large fluctuations in density of all cohorts it was impossible to investigate productivity of N. hombergi at station GIII4. It was similarly impossible to assess accurately the contribution of the three year old 1975 cohort at the other station because of the large sampling error of the low densities of large animals. Production by this group was estimated by subtracting biomass at the start of the study period from the maximum value reached. Increments by animals subsequently lost through mortality are, therefore, not included and may lead to underestimation.

Elimination was more simply derived as the cohort was found to be extinct by the autumn. Elimination was assumed to be equal to the highest biomass value reached by the cohort before extinction. This leads to considerable underestimation.

Values of production and elimination for this species each month for each cohort are given in Table 6e with a summary of yearly dynamics in Table 6g. Total and monthly cohort values are expressed graphically in Figures 6xvi – 6xix.

Elimination was found to exceed production at both study sites, mainly because the oldest, 1975, cohort was not succeeded in the following March by the 1976 cohort which became extinct in the late summer.

Annual production totalled 13.96 gm m^{-2} at FIV4 and 7.38 gm m^{-2} at GIV3 with elimination values of 16.16 and 9.91 gm m^{-2}. This represented 16.3 - 35.0% of total estimated community production and 13.5 - 32.3% of total community elimination (Chapter 11).

Peaks in monthly production were not found to coincide in timing at the two sites with a maximum at FIV4 between October and November and between July and August at GIV3. At both sites the one and two year old cohorts (1977 and 1976), contributed approximately 90% of the total population production in almost equal proportions and the oldest and youngest animals contributed only between 3 and 8% each.

Peaks in elimination similarly did not coincide exactly although there was an overall maximum at both sites over the late summer and autumn corresponding to the period of post spawning mortality and a separate sub-maximum in the late winter. There was also considerable elimination by the two year old cohort at station GIV3 between April and May resulting from high mortality (or migration?) which was not repeated at FIV4.

Apparent negative production was calculated for the oldest animals during the winter months and continuing production of the '0' group also seemed apparent. Both of these observations are probably artifacts resulting from size-dependant mortality of larger individuals of the older cohorts and of smaller individuals of the '0' group as all biomass values were based on a single size/weight relationship and therefore insensitive to changes in body weight through negative production. Size dependant mortality is discussed in section 6vii.

$\Sigma P:\bar{B}$ and $\Sigma E:\bar{B}$ ratios, for each month and over the whole year for each cohort and for the whole population are given in Table 6f. Unlike the results from the mollusc populations, mean monthly ratios do not differ greatly between cohorts. Ratios were found to be consistently higher for data from station FIV4 than for GIV3.

Ratcliffe (1979) estimated a total production of 6.2 gm m^{-2} for this species at Skeffling using the $\Sigma P:\bar{B}$ ratio given by Warwick & Price (1975) calculated for the population of *N. hombergi* in the Lynher Estuary. They found the species to be the largest producer in a *Macoma/Cerastoderma/Mya/ Scrobicularia/Ampharete* assemblage with a total production of 7.335 gm m^{-2} and $\Sigma P:\bar{B}$ ratio of 1.9:1, very similar to results calculated from site GIV3. They found productivity to decline considerably over the period 1973 - 1977, falling to 2.84 gm m^{-2} (Price & Warwick; 1980). Mean biomass and yearly production at site FIV4 were found to be double the Lynher value.

Production for *N. hombergi* has also been estimated using the $\Sigma P:\bar{B}$ ratio of Warwick & Price (op.cit), at 0.935 gm m^{-2} for a subtidal population in a *Venus* community in the Bristol Channel by Warwick et al. (1978). Otherwise the productivity of this species has been little studied.

Sanders (1956) calculated productivity of a population of *N. incisa* in Long Island Sound and found a $\Sigma P:\bar{B}$ ratio of 2.16. Later (Sanders; 1960), he concluded that it was inconceivable that such a dominant species in terms of biomass could be a predator and concluded that it must be a non-selective deposit feeder. Clay (1967) summarised previous literature on *N. hombergi* and concluded it to be carnivorous and Warwick & Price (1975) suggested that it may be a predator of the meiofauna. Warwick et al. (1979) found however, that it may feed exclusively on algal cells and that it is probably a broad spectrum omnivore taking about 10% animal food.

N. hombergi was found to be the second largest producer in the midshore sandy sediments after *Macoma balthica*. The majority of this production was found to be eliminated from the population during the autumn and it was unclear whether the lost biomass would be available to predators. Most elimination during that period followed spawning and, unlike *Hediste*, *Nephtys* was not seen to be abundant on the mud surface in an exhausted condition following gamete release. The long time between spawning and mortality of the adults implies that they survived for a considerable period. It may be that the spent adults eventually die below the mudsurface and are not easily available to predators. Their remains would then enter the detritivore cycle.

A second peak in elimination during the winter months is more likely to be the result of direct predation, amounting to 3.38 gm m^{-2} between December and March at station FIV4.

The substratum in which N. hombergi abounds is the most widespread in the Bight and whether or not autumn elimination is available to predators the species must be regarded as one of the most significant potential food resources in the Bight. The concentration of those wading birds known to feed on Nephtys on the midshore sediments (Tasker & Milsom; 1979) indicates that the resource is being exploited.

Summary of Chapter 6

Nephtys hombergi has been found by Ratcliffe (1979) at higher densities in Spurn Bight than had hitherto been described elsewhere. The present study was intended to ascertain the relative importance of the species as a potential food for wading birds.

Two species of *Nephtys*, *N. hombergi* (Savigny) and *N. cæca* (Fabricius) were found in the Bight with different distributions. The distribution of the two species in and around the Humber is described along with their ecological preferences in terms of tidal height, sediment and temperature relations. *N. hombergi* was found to be most abundant in midshore sandy silts and *N. cæca* in clean sands.

Variation in density over the period March 1978 to March 1979 is described together with the population structure. A maximum density of 1640 m^{-2} was found to be mainly composed of 'O' group individuals. Some animals are able to survive to three years of age but the majority die after spawning in their second year. All two year old animals were found to have died out after spawning in 1978.

Recruitment was observed to start in July 1978, implying that spawning was probably one month earlier. Mortality was highest of juveniles immediately after recruitment and adults some time after spawning and there was evidence of size dependent mortality of the largest and smallest animals. Migration is possible but could not be detected.

The predators of *Nephtys* spp. are described from the literature.

Head width/dry weight relationship and growth rate as increase in mean individual weight are described. Growth was found to be rapid at all ages, almost exponential during the summer.

Biomass, production, elimination and productivity statistics for the whole population are presented from two study sites. Highest biomass and productivity were found to occur in late summer and autumn with highest elimination in autumn and winter.

A mean monthly biomass of 5.45 gm m^{-2}, production of 13.96 gm $m^{-2}y^{-1}$ elimination of 16.16 gm m^{-2} and $\Sigma P:\bar{B}$ and $\Sigma E:\bar{B}$ ratios of 2.617 and 3.029 are higher than previously recorded for the species.

N. hombergi was found to be the second largest producer in midshore sandy sediments and a significant proportion of the elimination was found to be during the winter when the biomass would be available to feeding birds. There is some evidence that this biomass was being exploited.

CHAPTER SEVEN

CHAPTER 7

HEDISTE DIVERSICOLOR (O.F. MÜLLER)

Introduction

The common ragworm, Hediste (= Nereis) diversicolor (O.F. Müller) (Polychaeta; Nereidae), was not recorded as abundant by Ratcliffe (1979) during his study of Spurn Bight. Further upriver, however, at Paull, he found H. diversicolor to be the most dominant organism in terms of biomass at 14 gm m^{-2}.

In the present study in Spurn Bight, H. diversicolor was observed in large numbers only in the Spartina region not sampled by Ratcliffe, and in soft silts immediately below this zone. The species was observed to be particularly abundant at the colonising edge of Welwick Saltmarsh, among the Salicornia and Spartina.

Except immediately after spawning, H. diversicolor was found at lower shore sites as isolated individuals only and the 'O' group disappeared from these stations very rapidly. Study was therefore concentrated on this species at the Skeffling stations FI2 and FII2, and its presence elsewhere simply noted.

7i Taxonomy and identification

The only other nereid encountered in the mudflats was a single specimen of Neanthes virens (Sars), represented by a 10cm mid-body section collected by the corer and identified on parapodial structure. During initial field trials of sampling technique large numbers of nereids were checked for identity. All were found to be H. diversicolor.

7ii Distribution in and around the Humber

From the extensive survey (Table 4a), H. diversicolor was found to be present at very low density at almost all stations in upshore silt and midshore sandy silt locations. It was found to be totally absent from all stations of CLUSTAN community SAND and to be much more abundant in TOPSILT stations.

H. diversicolor was often found to congregate under stones, pieces of wood, jetsam etc. which remained on the mudflat surface, especially within the Spartina zone and care was taken to avoid sampling in the vicinity of surface objects to avoid this effect. It was also abundant under stones of the Old Den.

H. diversicolor was not found at any of the sample stations on the South Bank of the estuary but was very abundant at AIII2 on Cherry Cob Sands.

Other studies in the Humber have noted *H. diversicolor* from the full length of the estuary downstream of the Trent/Ouse confluence, with maximum density and biomass in the region of Hull Docks on the North Bank and between South Ferriby and North Beck on the South Bank (Hinton-Clifton; 1963, and Yorkshire River Authority and Lincolnshire River Authority reports 1971 - 1973). Jones (1979) studied the effects of heavy metal pollutants on *H. diversicolor* and found it to be the only organism present along the full length of the estuary.

Outside the Humber, it appears to be absent from the Holderness coast south of Bridlington harbour as suitable sediments are not found. It is present in suitable estuarine conditions (eg. at Saltfleetby), along the Lincolnshire coast and in the Wash.

7iii Ecological relationships

7iiia Salinity and downshore distribution

The distribution of *H. diversicolor* in the Humber is typical of its distribution with salinity in other estuaries. The salinity tolerance of *H. diversicolor* has been extensively investigated by Smith (1955 et seq.) and the species has been found to be tolerant down to a salinity of 1‰. Seaward, *H. diversicolor* has often been found to be replaced by *Nepthys hombergi* Savigny (eg Warwick & Price; 1975), probably by substrate selectivity or competitive exclusion. *H. diversicolor* is capable of living in full strength seawater.

The relationship with tidal level in Spurn Bight is illustrated in Figure 7i and the increase in density upshore is very marked. The relationship of biomass with tidal height is less clear. As with *Macoma balthica*, 'O' group individuals were numerically dominant only in upshore silts but small numbers of very large individuals were found in midshore locations, giving biomass values similar to upper shore stations.

Similar variation in density with tidal height have been observed in other estuaries, notably by Boyden & Little (1973), Wharfe (1977b), and especially Anderson (1972). Ratcliffe (1979) found similar variation at

Skeffling but did not extend his transect into the *Spartina* and missed the highest densities of *H. diversicolor*. At Paull he observed no such variation in vertical distribution and the sediments at Paull are more uniform in composition along the shore. The relationship with tidal height in this and most other studies may be related to sediment preferences rather than actual tidal position.

7iiib Particle size distribution and organic matter

The relationship of density and biomass of *H. diversicolor* to median particle size and the degree of sorting in May/June 1977 is illustrated in Figures 7ii and 7iii.

Both density and biomass were found to be highly significantly inversely correlated with median particle diameter ($P = 0.0009$ and 0.00012). Density and biomass were very low below ØM 3.5 and maxima were noted in the very finest sediments - ØM 5.5.

Wolff (1973) noted that, in the Dutch deltaic system, *H. diversicolor* had a preference for fine and muddy sands with a median particle size between 3.0 and 4.0 and was absent subtidally when ØM exceeded 4.0. He did, however, note that it was present in stiff clays of smaller particle size and also in submerged peat. Anderson (1972) also noted a preference of *H. diversicolor* for finer sediments and concluded that Morecambe Bay was on the whole too sandy to support high densities of this polychaete.

Muus (1967) noted that *H. diversicolor* was absent from black anaerobic muds, in contrast to the present study where highest densities were found in the blackest of muds beneath the *Spartina*, presumably obtaining oxygen by ventilation of the burrows.

Biomass was relatively higher than density in slightly coarser sediments owing to the variation in population structure in relation to tidal level and hence sediment grade.

Density and biomass were likewise related to sediment sorting with maximum values in the poorest sorted sediments and the species was absent from well sorted sands. Wolff (1973), however, noted that "the degree of sorting of the sediments does not seem important". Median particle diameter and sediment sorting are, however, strongly related and it is here impossible to differentiate the effects of related variables.

The distribution in relation to organic matter was very similar to that with particle size with very strong positive correlation of both density and biomass with percentage organic matter ($P = 0.0002$ and 0.00006). Maximum densities were found over an organic matter content of 5% by weight and density and biomass were very low below 1.4%. This relationship is again very likely compounded by distribution in relation to the above variables which have been shown in Chapter 3 to have a direct effect on organic carbon content.

Muus (1967) summarised the various feeding methods of H. diversicolor and concluded that it can act as a deposit feeder, suspension feeder using a mucous net, a predator on the meiofauna, and an algal grazer. The organic matter content of the sediment is therefore unlikely directly to effect such an opportunistic feeder.

7iiic Temperature and weather

There is little evidence in the data of increased mortality during the ice conditions of the 1978 - 79 winter. There was what appeared to be an upshore migration into the Spartina zone and this was likely to have been a result of the loss of suitable silts at the top of the shore through erosion followed by passive transport of the worms.

Mass mortality of H. diversicolor due to severe winters have been described from the Dutch Waddensea in the 1941/42 winter (Smidt; 1944) and in the 1962/63 winter (Muus; 1967) and in the Dutch Deltaic region in 1962/63 (Wolff; 1973), but conditions in these winters were more severe and protracted than those of 1978 - 79. Beukema (1979) found mortality of H. diversicolor in the Dutch Waddensea to be insignificantly greater in the 1978/79 winter than during the previous milder winters. Wolff also noted that erosion by storms may be one of the factors preventing H. diversicolor from establishing in more sandy conditions.

7iiid Depth distribution

Cores were taken to a depth of 20cm and only occasionally at the midshore, more sandy stations, - FIV4, GIV4 and GIV3, were burrows detected penetrating deeper than this. In early sampling trials these were followed downwards and all these deep burrows were ascribed to Nephtys hombergi (Savigny).

Depth distribution studies were not attempted but Ratcliffe (1979) studied this aspect of the worm's ecology at Paull in February 1976. He found a clear relationship between size and burrowing depth with 55% of the 'O' group in the 2-4cm level and almost all 1 and 2 year old animals between 4 and 12cm. No specimens were found below 12cm in depth.

Studies in sandier areas (eg. Muus; 1967) have found H. diversicolor to penetrate as deep as 55cm.

Depth distribution measurements of this kind are not an indication of availability as a food resource as the sampling method is thought to cause all worms to retreat to the very bottom of their burrows. Whether the feeding activities of waders cause similar disturbance appears to be unknown.

7iv Density

Variation in density of H. diversicolor at all sites studied in the extensive survey of spring 1977 are recorded in Table 4a.

Densities throughout Spurn Bight appeared to be very low in comparison to those noted in later intensive studies but recruitment of younger animals had not begun during the earlier survey which only found small numbers of older animals. These corresponded to similar densities found one month earlier in intensive studies.

A maximum density within the Bight of 600 m^{-2} was observed at FI2 with slightly higher numbers - 800 m^{-2} only being found elsewhere at AIII2 on Cherry Cob Sand. Densities outside the Spartina zone were much lower - a maximum of 320 m^{-2} at BI2 and a mean density was found among TOPSILT stations of 275 m^{-2} and among MIDMUD stations of 37 m^{-2}. These figures are quite in keeping with those of Ratcliffe (1979), who found average winter and spring densities of less than 200 m^{-2} at his regular sampling station at Skeffling (= FIII4), but he did not extend studies into the Spartina.

Monthly fluctuations in density of individual cohorts are given in Table 7a and illustrated graphically in Figures 7iv - 7viii.

After May the population at all sites was numerically dominated by the

'O' group, with a maximum total population density of 11,760 m^{-2} at FII2 in September 1978, composed almost entirely of that year's settlement cohort. Comparable densities were found at FI2 but considerably lower maxima were observed at all other sites with an overall number of 1840 m^{-2} in June 1978 at FIV4 and only 340 m^{-2} at GIII4 in July.

With the exception of densities at sites FI2 and FII2, the figures are again comparable with those of Ratcliffe (1979), and other authors working in sandier environments than those optimal for the species. At Paull, however, Ratcliffe found a maximum density of 12500 m^{-2} similar to observations in the present study at the top of the shore at Skeffling. He pointed out that the only comparative density figures from the literature are those of Wharfe (1977b), from equally fine, organic rich sediments in the Medway Estuary, Kent.

7v Population structure

On almost all occasions it was possible to identify cohorts from the size/frequency distribution of individuals and for the few samples where there was continuity or overlap of cohorts they were fitted 'by eye' onto the histograms.

Insufficient numbers of animals were available from extensive studies to determine differerences in population structure between individual stations and data from all TOPSILT and all MIDMUD atations were pooled to show an 'average' population structure within each cluster. The results expressed in mean numbers m^{-2} are presented in Figure 7ix.

A few larger individuals were noted from MIDMUD stations where the population appeared possibly to be trimodal, indicating that recruitment of the 1978 'O' group had only just begun at the time of sampling.

Differentiation of cohorts from the TOPSILT composite histogram was not possible although the population appeared to be bimodal with the smallest modal class not corresponding to any of those within the MIDMUD cluster. True population structure within the TOPSILT cluster was probably obscured by the method of coalescing data from individual sites with slightly different size frequency distribution.

Variation in population structure at intensive study sites FI2 and FII2 are presented in Figures 7x and 7xi. Insufficient animals were available from sites further down the shore to compose meaningful histograms and the division into cohorts for density and biomass estimates was inferred from the size frequency distribution at the two more upshore stations. Variations in size/frequency distributions with shore level was therefore not detected and, if present, not taken into account in division into cohorts. All further studies were concentrated at the two sites where the species was more abundant.

Population structure was essentially the same at these two stations. At the start of the intensive study two cohorts were differentiable, the 1977 '0' group and a much larger sized 1976 cohort at much lower density.

Subsequent tracing of the fate of the older cohort, and that of 1977, indicated that no animals older than those of the 1976 settlement were present among the older animals.

A maximum of three cohorts were present simultaneously during the summer months following recruitment of the 1978 '0' group and a bimodal size distribution was resumed after the extinction of the 1976 cohort probably resulting from spawning. The latest date on which 1976 animals were encountered was in September 1978 at FI2.

There was evidence of considerable redistribution, particularly of smaller individuals, discussed below under 'mortality and migration (7viii). Redistribution probably brought in a size-dependant factor as the mean size of each cohort at station FII2 decreased during the period of rapid decrease in density while exactly the opposite was found to have occurred at station FI2. This, together with the necessity to smooth out fluctuations in density into more or less continuous mortality curves, introduced an unquantifiable source of error into subsequent productivity calculations.

The observed population structure is in accordance with that observed for the species in other estuaries as well as that at Paull by Ratcliffe (1979). No study has detected a greater number than three cohorts extant together (Muus; 1967, Chambers & Milne; 1975, Mettam; 1979). Muus, together with Heip & Herman (1979), however, found that smaller individuals were present throughout the year, an observation not made in other studies including the present. Mettam (1979), in contrast to the other authors, found very considerable overlap in cohort size frequency but was able to distinguish older cohorts by the presence of mature oocytes.

The present study, therefore, supports all previous studies on the species in finding that individuals live to no longer than two years, undergoing somatic growth but no reproduction in their first year and die as a result of spawning at the end of their second.

7vi Spawning and recruitment

Ripe green H. diversicolor were noted within core samples and on the mud surface during the whole duration of the extensive survey of spring 1977 and were first noted in April 1978 and on all subsequent sampling occasions until September. Ratcliffe (1979) noted similar ripe Hediste from all months other than February, March and October in 1974 and 1975.

Oocyte maturation and release were not investigated in this study but, subjectively, it appeared that the maximum numbers of spent dying green worms on the mud surface were found in the warmest summer months between May and August. Large dead specimens appeared to be more common in downshore parts of the beach than in upshore silts when collecting samples, but data from cores failed to substantiate this observation.

Gamete release in this species results from rupture of the coelomic wall and although a proportion of females may survive to release further gametes from a second oocyte maturation later in the year (Mettam; 1979), the process is generally fatal to males and ultimately so to females (Dales; 1951).

Onset of spawning has been recorded from February (Wharfe; 1976) to July (Smidt; 1951), and in this study probably started in March or April and continued through at least until September.

Smidt (1951) observed the youngest H. diversicolor with three chaetigerous segments and headwidth of approximately 0.1mm. The extraction method used in this study apparently missed animals as small as this. Specimens with a headwidth approximately 0.2mm and 8-10 segments started to appear in cores from May onwards in 1978, with peak numbers occurring in July at station FI2 and August at FII2 but with evidence of continuing recruitment (ie the presence of the smallest sized individuals), continuing until November at FI2. Recruitment lagged at FI2 initially but ultimately maximum densities of 'O' group individuals - 11,500 m^{-2} were noted at that station in August. Smidt (1951) found the densites of the current season's 'O' group as high as 23,000 m^{-2} in the Danish Waddensea.

At the lower shore stations, FIV4 and GIV3, peaks of abundance, albeit much smaller than those upshore, were noted earlier in June, possibly indicating either earlier spawning and recruitment or more vigorous transportation away of juveniles later in the year. Chambers & Milne (1975) noted earlier spawning lower on the shore in the Ythan Estuary.

7vii Growth

Changes in mean peristomial - 'head'-width, body length and mean somatic weight of each cohort are presented in Tables 7b and 7c and Figures 7xii - 7xvii. Size dependent effects preclude these from being true growth curves and selective predation of larger individuals at FII2 may have resulted in the decline in mean size at that site over the winter months. Differential mortality of smaller individuals among those eroded from downshore sediments passively or actively migrating upshore into the *Spartina* may similarly have led to successful settlement mainly of larger individuals at FI2 showing as a steady increase in mean size over the winter. Alternatively, but perhaps less likely, this increase in size may have been the result of active growth but it was impossible to differentiate either effect.

A regression was carried out between head width and body length in 148 worms and found to be:-

$$\text{length} = 34.5 \times \text{head width}^{1.226} \qquad r = 0.91$$

and all head width measurements were converted to lengths using this regression for comparability.

Maximum growth rates were found to be during the summer months - May to September, but growth appeared to continue at FI2 throughout the winter - probably the result of size dependent effects discussed above. The gradient of the curve was steeper for the 1977 'I' group and possibly in the 1976 'II' group (overall number of individuals too low to produce a reliable curve), than for the 1978 'O' group and in this instance *H. diversicolor* did not, therefore, conform to the model of decreasing growth rate with increasing age noted by Heip & Herman (1979), but is in keeping with Chambers & Milne (1975), Mettam (1979) and Ratcliffe (1979).

Growth rates of individuals of the 1978 'O' group were probably considerably greater than revealed by the curve for the cohort overall, as continual recruitment during the summer would tend to reduce the mean size for the cohort and mask rapid growth of the individuals.

The 1978 'O' group grew to a mean head width of slightly less than 0.8mm (≡ 16mm length) at the end of the first season's growth, while the survivors of the 1977 'O' group in March 1978 appeared to have overwintered at about 0.9mm head width (≡ 19.5mm in length). These figures are in excess of those found by Ratcliffe at Paull, who found that each of the 1973, 1974 and 1975 year classes overwintered after their first season's growth with a head width of approximately 0.35mm (≡ 7mm length), and are more in keeping with those of Dales (1951) in the Thames estuary. Such variation may be a function of different growth rates during different years or differences between study sites along the length of the Humber.

Mean individual size at the end of the second season's growth was between 1.9 - 2.1 mm head width (= 45 - 50 mm length), again in excess of sizes reached at Paull during the similar period in 1974 and 1975 and equivalent to the maximum size reached by this species in the Ythan by Chambers & Milne (1975).

By the time of extinction of the cohort resulting from spawning in August/ September 1978, a mean individual head width of 2.4 - 2.5 mm (≡ 60mm length), had been reached, again larger than the maximum size reached at Paull during 1974 -75. Occasional worms in excess of this size were noted among those spent individuals seen on the mud surface during sampling excursions, sometimes as large as 12cm in length, but none of these turned up in core samples, indicating either very low densities or burrow depths greater than the 20cm deep cores used.

7viii Mortality migration and predation

There was considerable evidence of redistribution of H. diversicolor in this study and negative changes in density could not reliably be regarded as resulting from mortality. Various observations indicate redistribution:-

1) Decline of the 1977 cohort at FI2 during July to November among the Spartina with a corresponding peak in abundance at FII2 in the topshore silt during the same period. This may indicate active migration of deeper burrowing larger worms to avoid the extreme anaerobic conditions below the Enteromorpha cover between the Spartina in the summer.
2) Reappearance of the 1977 cohort in the Spartina station during the winter corresponding to an equivalent decline within the rapidly eroding sites.
3) Earlier peaks in abundance of the 1978 'O' group at downshore sites followed by a rapid decline during the period when recruitment at upshore sites was greatest. This may indicate that much of the early recruitment occurred in the middle shore followed by migration upshore and subsequent resettlement. The large area of midtidal flats in relation to the narrow band of topshore silts would account for the enormous disparity in density of juveniles.

Mortality following spawning of the 1976 cohort was seen to occur with large numbers of spent individuals on the mud surface. Many of these were, however, still alive and swimming in surface water and those which survived to mature a second batch of oocytes would almost certainly be redistributed around the shore by the tide.

The decline of the 1978 cohort subsequent to the peak in abundance during July - September is, however, almost certainly attributed to actual mortality. No large scale immigration of juveniles was reported at any site on the shore, although the apparent increase in the size of that cohort together with that of 1977 at FI2 over the winter was probably a result of differential survival of the larger individuals, possibly during upshore migration. Other size-selected phenomena are discussed above.

There was an overall reduction in density of 94% between July 1978 and

March 1979 at FI2 and of 98% between September and March at FII2 with the largest single decline (89% of total), between November and January.

Migration, mainly of 'O' group *H. diversicolor*, has been noted by a number of authors. Smidt (1951) noted upshore migration in the Danish Waddensea of the entire 'O' group from an initially very high recruitment (69,000 m^{-2}) on the lowest part of the shore to the highest part of the shore between May and July 1947. Muus (1967) noted sudden reappearance of animals, possibly from below tidal level, in the summer of 1963 following almost complete annihilation of the species during the winter of 1962 - 63 and Evans et al. (1979) noted the sudden appearance of small worms on Seal Sands in the Tees and attributed this to immigration. Mettam (1979) noted upshore migration of the 'O' group in the Severn following failure of recruitment at upshore sites during the very dry summer of 1976. It would, therefore, seem that active or passive migration of *H. diversicolor* is the norm rather than exception and that estimates of mortality and elimination should be interpreted with this in mind.

H. diversicolor is known to form a very significant component of the diet of many species of wading bird, in particular of dunlin - *Calidris alpina* (Bengston & Svensson; 1968, Wolff; 1967, Davidson; 1971, Goss-Custard, Jones & Newberry; 1977 and Evans et al.;1979), and all observers are in agreement that the smaller worms (<3cm in length) are important to the birds. This is most likely to be a result of the short bill length of dunlin in relation to the burying depth of larger worms. Larger worms are known to be more significant to curlew, *Numenius arquatus*, bar tailed godwit, *Limosa lapponica* and redshank, *Tringa totanus*, (Goss-Custard; 1969, 1977b, Davidson; 1971, Smith & Evans; 1973, Goss-Custard, Jones & Newberry; 1977, Bryant; 1979, Evans et al.; 1979). *Hediste* is known to be relatively unimportant to knot, *Calidris canutus* (Bengston & Svensson; 1968, Prater; 1972b), although Wolff (1969) found them to form a significant part of knot diet in the Dutch delta area.

Other waders known to feed heavily on *Hediste* are grey plover, *Pluvialis squaterola* (Evans et al; 1979) and avocet, *Recurvirostra avosetta* (Madon; 1935).

In the study of Tasker & Milson (1979) of feeding distribution of estuarine waterfowl in the Humber, curlew were found to concentrate their feeding efforts on areas found in this study to have the highest biomass of *H. diversicolor*, during the winter and spring only. Whimbrel, *Numenius phaeopus*, was found by them to feed almost exclusively in the *Spartina* zone but little seems to be known of the birds' feeding habits. Feeding areas of redshank were found to extend to the very top of the shore but those of the smaller waders, knot and dunlin, seemed particularly to avoid highest areas of the shore where *Hediste* was most frequent. Considering the near dependence of dunlin on *H. diversicolor* elsewhere, this was unexpected and possibly the birds avoided the *Spartina* owing to the cover afforded to potential predators. Tasker (op. cit.) found dunlin to concentrate feeding activities at Paull where *Hediste* contributes the most significant part of the biomass.

Of the estuarine fish, Muus (1967) found that the adult sand gobies, *Potamoschistus microps* (very abundant in Spurn Bight), and *P. minutus* predominantly fed on juvenile *Hediste*, and Braber & de Groot (1973) found the worm to be most important in the diet of sole, *Solea solea* and dab, *Limanda limanda*, but not so much in plaice, *Pleuronectes platessa*. Summers (1980) found *H. diversicolor* more significant in the diet of flounder, *Platichthys flesus*, in the autumn and winter months and Wolff et al. (1980) found *H. diversicolor* to be significant in the diet of both plaice and flounder.

The proportion of the biomass of the *H. diversicolor* population available to predators has not been calculated directly but Kay & Brafield (1973) considered that less than 10% of the production of *Neanthes virens* is ever taken by predators. This is a much larger, more deeply burrowing worm than *H. diversicolor* and the proportion is likely to be higher for the latter species. Figures for elimination are not, however, a good indication of levels of predation as the population in Spurn Bight turned out to be very mobile and also mortality of the largest worms occurred after spawning and the corpses probably passed directly into the decomposer cycle.

7ix *Biomass*

All biomass figures were calculated from a single head width/tissue dry weight regression made for animals collected in May 1977. Seasonal variations in condition factor have not been so well studied as for M. balthica but differences as great as five-fold have been found for the smallest individuals using a jaw length/dry weight regression on animals in the Ythan by Chambers & Milne (1979), although for larger animals the greatest difference was found to be two-fold.

Chambers & Milne.(1979) found that the highest condition factor was found in June and July, just before the peak of gamete release which was noted to be approximately one month earlier in the Humber from observations on recruitment of the 'O' group. The regression used in the present study was therefore probably carried out on animals at the peak of condition and this may have led to overestimation in further calculations of energetics.

Single regressions on body width and weight have been used by Heip & Herman (1979) and by Ratcliffe (1979) who found a maximum difference of 30% for larger animals only, between the relationship during spring and an addition regression carried out in the autumn with the higher values found in the autumn. He,too,only used the spring relationship and the findings of this study should therefore be in line with those of the earlier work.

The relationship for 148 worms was found to be:-

tissue dry weight (mg) = 3.027 x head width $(\text{mm})^{2.387}$

$r = 0.97$

Biomass values for all stations sampled during spring 1977 are recorded in Table 4a and the maximum value recorded in Spurn Bight was found to be 6.2 gm m^{-2} at FI2, although 14.3 gm m^{-2} was noted at AIII2 on Cherry Cob Sand. A mean value of 3.02 gm m^{-2} was found among TOPSILT stations and a mean of 1.14 gm m^{-2} among MIDMUD stations, with considerable overlap between ranges.

Data on total and cohort biomass of H. diversicolor at each station for intensive studies are presented in Table 7d and graphically in Figures 7xviii to 7xxii.

The mean annual biomass was almost the same at the two upshore stations at approximately 9.5 gm m^{-2} but this concealed a difference in distribution of biomass with time. 87% of the total mean biomass was contributed by the 1978 'O' group at FII2 and 71% at FI2 while at all three lower shore stations the proportion was 15 - 16%. Mean biomass of H. diversicolor at the middle shore stations was between 6 - 16% of that on the upper shore.

H. diversicolor was found to contribute 80 - 82.6% of total measured mean monthly community biomass at the two upshore sites at Skeffling, but only between 1.6 - 5.2% at the three midshore sandy mud stations (ref. Chapter 11).

The overall pattern in variation of biomass with time was similar at each site with a major peak during the summer months June - September, although the composition of that peak was different at the two upper shore stations from that at the three stations on the lower shore, which was almost entirely of growth of the 1977 and 1976 cohorts. At FI2 and FII2 the peak was mainly composed of recruitment and explosive growth of the 1978 'O' group.

Maximum recorded biomass was of 29.4 gm m^{-2} in October 1978 at FII2, following a very rapid rise between July and August. This fell to only 0.7 gm m^{-2} by March 1979, 2.3% of the peak value.

Maximum biomass was noted in August at FI2, reaching 13.9 gm m^{-2} and falling much less rapidly over the autumn and winter to 4.4 gm m^{-2} by March 1978, 31.7% of the maximum value.

Biomass levels at all stations were fairly similar in March 1978 and March 1979, the exception being at GIII4 where, in common with most other species, there was a drastic decline of H. diversicolor over the autumn resulting in total extinction by January.

Significant levels of biomass of H. diversicolor remained only among the Spartina at FI2 following the harsh weather between January and March 1979.

Values for biomass of H. diversicolor elsewhere vary depending on location. Gray (1976) found 0.7 gm m^{-2} in the Tees and Beukema (1976) found 1.4 gm m^{-2} on the Dutch Waddensea, similar to values found at lower shore stations in Spurn Bight. At the other end of the scale Muus (1967) found a mean biomass of 13.75 gm m^{-2} (max 18 gm m^{-2}) in Niva Bay in Denmark and Heip & Herman (1979) found a mean of 26.3 gm m^{-2} in a brackish pool by the Zwin saltmarsh in Belgium, reaching a maximum of 38.5 gm m^{-2}, the highest ever recorded for the species.

The values found in Spurn Bight in this study are therefore average for the species and very similar to those found upstream at Paull by Ratcliffe (1979) who found means of 9.3 and 9.7 gm m^{-2} in 1974 and 1975. The composition of the biomass in that population was, however, completely different with only between 1 and 5% contributed by the '0' group in its first year.

7x Production, elimination and productivity

Values for production and elimination are given in Table 7e and whole population data are summarised in Table 7f. Monthly values are only given for site FI2 - Figures 7xxiii and 7xxiv and the 1978 '0' group at station FII2. Low and rapidly fluctuating densities made it impossible to determine monthly values at other sites and for older cohorts at FII2 and all annual values are extrapolated from mean annual biomass figures by multiplication by P:B and E:B ratios worked out for site FI2. The atypicality of this site (among the Spartina) made it unlikely, however, that the relationship was fully representitive of other stations. Even at site FI2, fluctuation in density through migration over the winter months and size-dependent mortality and secondary recruitment (refer above) probably led to considerable error in productivity calculation. Immigration and apparent production through size-dependent effects were subjectively eliminated from the total production estimates.

The majority of production at the two upshore sites appear to have been contributed by the 1978 '0' group but a large part of this is likely to result from considerable immigration of individuals from lower on the shore.

Production of the 1976 cohort is also likely to be considerably underestimated as, during the equivalent period, Chambers & Milne (1975) estimated that a total of 40% of production (and hence a significant proportion of elimination) was accounted for by gamete production and release.

Bearing the above in mind, there were two apparent peaks in production at FI2, the first between June and July 1978, totalling 8.49 gm m^{-2}, which probably included a significant proportion of immigration of '0' group individuals from downshore and a second peak of 3.07 gm m^{-2} between October and November, again probably a combination of actual growth, immigration and size-dependent effects. The apparent minor peak in production between January and February 1979 was almost certainly attributable entirely to size-dependent mortality of smaller individuals.

Annual production thus estimated was found to be of 25.3 gm m^{-2} at station FI2, with an overall $\Sigma P:\bar{B}$ ratio of 2.15, and of 31.5 gm m^{-2} at FII2 with a P:B ratio of 3.32. Much lower values were calculated from lower shore stations. Annual production of H. diversicolor was found to contribute a maximum of 87.5% of measured total community production and 89.3% of elimination at site FI2. At midshore sites production formed 1.1 - 2.8% of the community total (Chapter 11).

Elimination was calculated to be highest from August to November at FI2, the major part being contributed by the 1978 'O' group. A later peak between January and March was again seen to result mainly from decline of the 'O' group. Total elimination at all sites other than FII2 was found to exceed production, probably indicating the considerable effects of migration. Maximum annual elimination was calculated to be 29.9 gm m^{-2} at FI2.

The productivity figures so derived are rather higher than those recorded elsewhere for the species. Chambers & Milne (1975) found a $\Sigma P:\bar{B}$ ratio (excluding gamete production at 40%) of 1.8 in the Ythan (although Heip & Herman; 1979, pointed out that production of the large part of the 'O' group was missed by using too large a mesh size) and Ratcliffe (1979) found the total population $\Sigma P:\bar{B}$ ratio to be 1.3 and 1.6 at Paull in 1974 and 1975. Heip & Herman (1979) found a higher value of 2.44 for a non tidal brackish water population of H. diversicolor, probably much higher than ever found in open estuarine conditions owing to higher temperatures.

The values recorded here are likely to be considerable overestimates resulting from a number of factors including immigration, size-dependent effects on mortality and probably the use of only a single head width/weight regression. It is clear that the removal/summation method of calculation of production and elimination, which assumes no such effects, is unable to cope with the variability of the Spurn Bight population of H. diversicolor.

Summary of Chapter 7

Hediste diversicolor was noted at higher densities at the top of the shore in Spurn Bight than had been noted in previous studies in the area.

The distribution of H. diversicolor in and around the Humber is described and its distribution in Spurn Bight related to the tidal position and to sediment characteristics. It was found to be much more abundant among the Spartina at the top of the shore and in the finest silts immediately below that zone.

Variation in density with time over the period spring 1978 - spring 1979 is recorded with a maximum of 11,760 m^{-2} in upshore silts in September, composed mainly of the 1978 recruitment.

Variation in population structure with time is recorded at two stations and inferred at three others. A maximum of three cohorts was found to be present at any one time and it was concluded that the worm lives for a maximum of two years after which it dies on spawning.

Spawning was not investigated directly but the presence of ripe adults was noted and recruitment, starting in May and continuing until September, recorded. Settlement reached a maximum at downshore sites one month earlier than among the Spartina, possibly indicating redistribution and secondary settlement.

Growth is recorded in terms of head width of each cohort and converted into mean body length and somatic weight by regression. Most rapid growth appeared to be during the second summer but rates were obscured by size-dependent effects and continual recruitment throughout the summer. Mean size during overwintering was found to be considerably larger than recorded by an earlier work at an upstream location in the Humber.

It proved impossible to differentiate mortality from the effects of redistribution and active and passive migration between regions of the shore were recorded throughout the year. Known predators of H. diversicolor are described from the literature.

Biomass values were calculated from a single size/weight regression, possibly leading to overestimation in subsequent calculations. Significant differences in biomass between upshore silts and midshore sandy mud sub-communities were noted and variation in biomass with time recorded at the five intensive survey stations. A mean annual biomass of 9.5 gm m^{-2} was noted at the two upshore sites and considerably less at mid tidal levels. A maximum biomass of 29.4 gm m^{-2} was found in October 1978 in the upper shore silt at FI2.

Production, elimination and productivity were calculated at a single location in the *Spartina* only and P:B and E:B ratios from there were used to convert mean biomass values to production and elimination elsewhere.

Production and productivity estimates are given with maximum production of 31.5 gm m^{-2} and {$P:\bar{B}$ ratio of 3.32 in silts below the *Spartina*. These estimates are discussed in relation to the known sources of error and concluded to be overestimates.

CHAPTER EIGHT

CHAPTER 8

CERASTODERMA EDULE (LINNAEUS)

Introduction

Commercial fisheries for cockles exist on the South Bank of the estuary mouth between Cleethorpes and Donna Nook where individual workers are able to harvest as much as ten x 1cwt sacks (approx 500Kg) per day (Brennan; 1973). These beds are on midshore extensive sandflats such as are not found on the North Bank of the estuary where the cockle population, although present, was found to consist of small individuals. The difficulty of access to the Spurn Bight cockle beds - over the soft inshore sediments, has prevented the formation of a similar industry on the North Bank.

The Bight's cockles, however, may provide a considerable food resource for overwintering wildfowl but the species was not studied in detail by Ratcliffe (1979) and special attention was therefore paid to it in this study.

Low densities of larger animals made this a difficult species to sample and the extra work involved (see materials and methods, Chapter 2) made it practicable to study the species at a single station only. Densities in the Bight were found to be very low when compared with other studies and density dependent effects on growth dynamics were therefore not expected to be significant. The station which was found to have the highest densities of C. edule during the extensive survey of 1977 was chosen for intensive study to minimise sampling effort needed to obtain large numbers of animals for measurement. This may have introduced a bias into study of productivity as factors causing maximum density may similarly influence other aspects of the species' dynamics leading to over - or under - estimation of extrapolations to other sites. Cockle spat were recorded at all stations.

8i Taxonomy and identification

The inner parts of Spurn Bight appeared suitable to support a population of C. glaucum (Bruguière), which is described as occurring in 'sheltered parts of estuaries' (Russel; 1971), and sympatric populations of the C. glaucum and C. edule have been described from the Crouch estuary by Boyden (1971) and in Southampton Water by Barnes (1973).

All specimens from the extensive survey were checked against descriptions in Pohlo (1963), Høpner-Petersen & Russel (1973) and Brock (1978) for C. glaucum and other N. European brackish-water species of the genus, C. exiguum (Gmelin) and C. hauniense (Høpner-Petersen & Russel; 1973). All specimens were found to be C. edule (L.) and specific determination was not repeated during the intensive survey.

8ii Distribution in and around the Humber

C. edule is abundant in muddy sands along the whole Lincolnshire coast from Skegness to Cleethorpes (own observation), and semi-commercial beds exist close to the tourist resorts. Strongest populations within the Humber, in terms of size of individuals, occur between Humberston and Donna Nook and cockles are dominant members of the fauna as far west as the entrance to Grimsby Harbour. Apart from occasional spatfalls at Pyewipes, immediately west of Grimsby (P. Smith, pers. comm.), Cerastoderma species are absent upriver of Grimsby on the South, and Hawkin's Point on the North Bank of the estuary. Subfossil evidence exists of a flourishing cockle population, along with whelks and oysters, in sands beneath the polluted silts of Pyewipes. Absence of suitable substrata has probably prevented colonisation of the upper estuary by more brackish water tolerant members of the genus.

Within Spurn Bight cockles were found sporadically along most transects as isolated individuals except in midshore sandy muds where a low density population of undersized individuals was consistently found. They were absent from the Spartina zone and from densely packed sands of the lower shore and along the peninsula although it was found to be present in the gravels of the Old Den.

Cockles appear to be absent from the South Holderness coast where the tidal scour is too great. Small numbers are found in Bridlington Bay.

8iii Ecological requirements

8iiia Salinity

The salinity tolerances of Cerastoderma species are well documented. Rygg (1970) found that laboratory populations of C. edule could withstand salinities between 10-45‰ indefinitely and between 3-60‰ for several days.

Field observations by numerous authors, including Cole (1956), Kristensen (1957), Høpner-Petersen (1958), Muus (1967) and Rygg (op.cit.), have shown that the natural lower salinity limit for the species is 18‰ but that growth, longevity and maximum attainable size are non-optimal below 27‰ and that the species grows well in full seawater. The susceptibility of spat to low salinities is known to be greater than that of larger individuals. Kristensen (op.cit.) found that heavy summer rain onto flat cockle beds at low tide produced very high mortality of young spat.

The salinity regime of Spurn Bight, which was found to vary with time between 18.5 and 35‰ and averaged in the low 20's, is below the optimal level and likely to have a negative influence on the dynamics of the species. The regions of the outer estuary with commercial beds have average salinities in excess of 30‰ (Denman; 1973).

8iiib Tidal position

Both density and biomass of C. edule were found to be highest in the upper middle shore region (Table 4a, Figure 8i), with very low values at the extremes of the tidal range.

C. edule is mainly a suspension feeder (Smidt; 1951) and the period of emersion is known to limit directly the upshore distribution of the species. Although populations have been found to extend even into the silts in the Spartina zone (Green; 1940), there is general agreement that the species is most abundant in midshore intertidal sediments (Stephen; 1931, Smidt; 1944 & 1951, Wolff; 1973, Seed & Brown; 1975 etc.). Stephen (1931) and Kreger (1940) have shown differential growth rates at different shore levels with slower growth and smaller maximum size towards high water level. Kristensen (1957), however, found that mortality was unrelated to shore level. Wolff (op.cit.) stated that cockles are very rare (and small) where tidal cover is less than 3-4 hours per tide, a view supported by Cole (1956).

8iiic Sediment

C. edule was found to be far more abundant in poorly sorted muddy sands (ØM 3-4.5) than either highly organic silts or clean sands although the relationship is closely tied to tidal position (q.v.). Cockles were also abundant among the gravels of the Old Den and the commercial beds of the South Bank occur in fine sands with a low silt content. The relationship of density and biomass with median particle diameter and degree of sorting is illustrated in Figures 8ii and 8iii.

Eisma (1966), reviewing all previous works on the sediment relations of C. edule, noted that the species had been recorded as preferring clean sand, muddy sand, fine sand and mud and concludes that it has very catholic tastes in grain size. Similar conclusions were reached by Walton (1919), Kreger (1940), Cole (1956), Baggerman (1951), and Smidt (1951). Kristensen (1957) found, however, evidence of a relationship between mortality and grain size with highest rates in finer sediments. He also found that high suspended solid levels in the overlying water led to low growth rates - presumably either by increasing energy expenditure during feeding or by direct clogging of the feeding apparatus.

Wolff (1973) concluded that hyrodynamics are much more important than grain size - current strength can be limiting either by eroding the animals from the sediment or burying them in it.

8iiid Temperature

High mortality of adult and juvenile cockles was recorded in Spurn Bight during the severe winter of 1978-79.

Mortality of cockles during severe winters followed by dominance for several years by a single settlement cohort is well known (Stephen; 1931, Thamdrup; 1935, Kreger; 1940, Smidt; 1944, Kristensen; 1957, Crisp; 1964a & b, Franklin & Pickett; 1968, Anderson; 1972, Boyden; 1972, Wolff; 1973, Hibbert; 1975, Seed & Brown; 1975 and Beukema; 1979). Smidt inferred that the success of the subsequent settlement was partly the result of low levels of trematode infection of the juveniles after elimination of most of the infected parent stock.

Dominance of the Spurn Bight population by the 1976 settlement was probably a result of high survivorship of juveniles following elimination of the adults during extremely high temperatures of the summer of 1976.

Very hot summer temperatures were found by Seed & Brown (1975) to produce very high mortality in cockles in Strangford Lough in Northern Ireland and Orton (1934) noted similar very high summer mortality on the Dee in 1933. Kristensen (1957), however, found no significant effect of high temperatures on cockle mortality in the Dutch Waddensea. The discrepancy may be salinity or sediment related as Rygg (1970) found the upper tolerance to be affected by particle size, mainly because cockles were found to bury less deeply in finer sediments such as those found in the Humber.

Low summer temperatures were found to have no apparent effect on growth rate in a Hebridean cockle population by Cole (1956), and it is therefore possible that the cool, damp summer of 1978 may not have led to atypically low dynamics.

8iiie Depth distribution

No attempt was made to determine depth distribution of cockles in this study. C. edule is essentially a shallow burrowing species, being restricted by the very short siphon lenth and the whole population is restricted to the top few centimetres of sediment and therefore more exposed to erosion, predation and extremes of temperature than deeper burrowing bivalves.

Walton (1919) and Figuèras (1966) noted that cockles buried by sand blown over an area were subject to mass mortality. A similar effect was observed at sites along the Kilnsea and Spurn ('H' & 'J') transects after the storms of January 1978 covered most of Kilnsea clays with a 2-7cm deep layer of sand.

8iv Density

The only previous density estimate for C. edule in Spurn Bight, that of Ratcliffe (1979), gives a maximum of 250 m^{-2} at a midshore station at Skeffling. The maximum recorded in May 1977 was 800 m^{-2} at Easington (GIV3). Densities at all sites during that survey are recorded in Table 4a.

Intensive study at GIV3 showed a lower density of 470 m^{-2}, a year later in May 1978, rising to a maximum of 920 m^{-2} at the height of spatfall. Changes in total population and individual cohort density at this site are given in Table 8a and illustrated in Figure 8iv.

These densities are very low when compared with studies on commercial beds where several thousands of large animals per m^2 have been recorded by various authors (eg Wright; 1926 - 8000 m^{-2}, Kreger; 1940 - 2160 m^{-2}, Cole; 1956 - 4350 m^{-2}, Hancock & Urquart; 1965 - 6070 m^{-2}). Low densities similar to those found in the Humber were found in parts of the Dutch Waddensea by Kristensen (1957), in Morecambe Bay by Anderson (1972), and in S. Wales by Withers (1977), all in very silty conditions.

8v Population structure

The size/frequency histogram for the cockle population at GIV3 during May 1977 is given in Figure 8v. A further histogram for the population at site PIV6 at Horseshoe Point is given in Figure 8vi for comparison of size structure. Monthly histograms from site GIV3 during extensive studies are given in Figure 8vii.

Cohort differentiation using growth rings on all individuals was straightforward in spite of occasional disturbance rings, missing rings and asynchronous resumption of growth after the winter. Cohorts for 1975, 1976, 1977 and 1978 spatfalls were distinguishable and overlapped little in size range. Individuals dating back as far as the 1971 settlement were identifiable at very low densities and data for older animals is included together in Table 8a.

At all sites in May 1977 the population was found to be dominated in abundance and biomass by 1976 settled animals. This domination was seen to continue until the end of intensive studies in spring 1979. The population at Horseshoe Point in May 1977 (Figure 8vi) was similarly dominated by a single cohort of similar aged individuals of a larger size, indicative of more favourable growth conditions on the South Bank beds.

The drought summer of 1976 was extremely hot and sunny and the dominance of animals settled in that summer may have been the result either of lack of competition following elimination of a high proportion of older individuals through their inability to withstand high temperatures, as has been observed in a cockle population in Northern Ireland by Seed & Brown (1975), or of optimum growing conditions for the spat provided by high levels of insolation leading to an abundance of phytoplankton food, or a combination of both factors.

The population of C. edule in the Dutch Waddensea during the study period of the present work was found by Beukema (1979) to be dominated by the 1975 settlement in contrast to the finding from Spurn Bight.

Similar population structures dominated by single settlements have most commonly in the past been attributable to mass mortality of adults during severe winter weather (refer citation list under 8iid) followed by very high recruitment in the absence of competition. This was not the case in the study population as the period coincided with the end of a period of exceptionally mild winters (Beukema et al.; 1978).

8vi Spawning and recruitment

From indirect evidence of mortality, production and changes in mean individual weight (below), it would seem that all age groups spawned initially between April and May giving rise to high post spawning mortality in the 1975 and older cohorts. Subsequent spawning by 1976 animals in July/August and 1975 animals again in August/September is inferred from productivity and flesh weight figures (q.v.) and continued recruitment through to September.

Double spawning periods have been noted in the past in certain cockle populations studied by Høpner-Petersen (1958) and by Hancock & Franklin (1972).

Density changes of 'O' group individuals at all sites are recorded in Table 8b and Figure 8viii.

An extended period of recruitment was observed, commencing at all stations in June 1978 but producing maxima of 'O' group animals in June at FIV4, in August at GIV3 and in September at GIII4. Kreger (1940) and Boyden (1971) give the planktonic lifespan of the veliger as between two and five weeks and therefore gamete release must have commenced during May. Recruitment of 0.3mm individuals continued until September.

Spatfall has been observed lasting three months by Baggerman (1953) in the Dutch Waddensea and double spatfalls in early and late summer by Kreger (op.cit) and Hancock & Franklin (1972). Although indirect evidence of double spawning periods was found (above), separate size frequency peaks in the 'O' group were not observed.

Newly settled animals were found to possess shell diameters no greater than 0.35mm and this calls into question a high proportion of previous studies on cockle recruitment which used mesh sizes of 0.5 - 5mm.

The maximum spat density in 1978 was found to be 1120 m^{-2} at GIV4 and only 530 m^{-2} at GIV3. Spatfall during 1976 must have been considerably higher as a density of 560 m^{-2} of one year old animals was found in May 1977 at GIV3. Density of 'O' groups was very low compared with some previous works. Orton (1934) records 100,000 m^{-2} at Clarke Sands and over 30,000 m^{-2} was observed by Wohlenberg (1937) in the German Bight.

Kristensen (1957) observed mass mortality of veligers and young spat following inhalation into the siphons of adult C. edule, and the high densities of Macoma balthica may have exerted a similar effect in this case. Thamdrup (1935) and Boyden (1972) noted an inverse relationship between success of larval settlement and density of adult cockles and this may hold true for mixed species populations.

High densities of Pygospio elegans and Retusa obtusa, known predators of bivalve spat (Høpner-Petersen; 1958 and own studies) may have contributed to low spat density and high turbidity levels and poor summer weather with consequent low phytoplankton production may have led to lack of success of the 1978 settlement.

8vii Mortality, migration and predation

Regular transport of newly settled cockle spat is known to be commonplace until a shell size of 2mm is reached (Baggerman; 1953). Numbers of 'O' group individuals began to decline in September 1978, drastically so at site FIV4, but it was impossible to determine whether this was due to mortality or migration. By November at FIV4 the 'O' group were no longer present.

Evidence of translocation of these animals during the winter storms is given by their reappearence at FIV4 at a density of 420 m^{-2} in January 1979, coinciding with the highest decline in numbers at the Easington stations further east. A similar effect was observed with Retusa obtusa (q.v.), one month later with an apparent translocation westwards.

Between January and March 1979 there was complete elimination of the 'O' group at Easington and an 18% reduction at the Skeffling site, probably resulting from the severe cold weather and gales.

Mortality of 1977 animals was very high between March and May 1978 which cannot be explained either by erosion or as a result of spawning. After May mortality continued at a steady rate and the year group was finally eliminated at GIV3 between January and March 1979. Low density of this age group, coupled with their low growth rate (below) and high mortality, indicates that both this cohort and the 1978 settlement were unable to compete with the dominating 1976 cohort. A similar fate may have befallen the 1974 cohort which was found to be present at unusually low density and its growth ring pattern revealed a similarly low growth rate.

Mortality of the 1976 year group amounted to 37% between May 1977 and March 1978. It remained low until August after which there appeared to be post spawning mortality of 27%. Mortality over the whole year amounted to 57% of the total.

The 1975 animals showed definite evidence of post spawning mortality between April and May. Orton (1933) also found that such mortality was highest among older individuals. There was little further reduction of this year group over the winter and mortality over the year was 51%.

Earlier year groups, observed during May 1977 all over the Bight, were present at such low density during intensive study a year later that data for all months had to be pooled for analysis of growth etc. Seed & Brown (1978) found that few cockles survived their third year and this is supported by the present study.

During the winter sampling trips large numbers of live and dead cockles of all sizes were observed on the surface of the mudflats and in the strand-line at the seaward edge of the <u>Spartina</u>. Significant increases of 1976 and 1975 cockles at GIV3 were noted between November 1978 and January 1979 (Figure 8iv, Table 8b), probably as a result of passive immigration from elsewhere. Live cockles were also found in the nekton traps laid in the western creek in the summer, indicating that erosion and redistribution was also happening then.

Beukema (1979) found massive mortality of as much as 88% of the total biomass of the C. edule population on the Danish Waddensea in the winter of 1978-1979 and has shown a significant correlation of winter mortality with cold temperature over the period 1972 - 1979.

Kristensen (1957) noted that the lower lethal temperature for cockles kept without sediment was 6.3°C higher than for normally burrowed animals and exposure such as observed in the Bight is likely to contribute significantly to winter mortality. Kristensen found that up to 26% of older animals were so redistributed in the Waddensea, but Kreger (1940) regarded such emigration from a study site as insignificant when compared with true mortality. Increases observed in winter 1979 in the Bight indicates that at least some of the redistributed older cockles were able to survive and rebury.

The relationship between cockles and the oystercatcher, Haematopus ostralegus, has been studied in detail by Drinnan (1957), Drinnan & Cole (1957), Hancock & Urquart (1965), Davidson (1967) and O'Connor & Brown (1977), and it is apparent that this bird is the main predator of large cockles during the winter months. Davidson reports than an oystercatcher feeding exclusively on cockles in the Burry Inlet beds consumed 303gm of cockle meat in a 24 hour period.

Tasker & Milsom (1979) reported a nationally important overwintering population of oystercatcher confined to Spurn Bight on the North Bank of the estuary, peaking at over 2,600 birds in February 1979. Their map of feeding distribution indicates that the birds concentrate on areas of highest cockle density (community MIDMUD), and evidence of feeding on cockles was found in numerous characteristically opened shells on the mudflat surface observed during winter sampling.

Bryant (1979) found that the feeding distribution of knot, Calidris canutus, was positively correlated with the density of smaller cockles. Tasker & Milsom (1979) found that the feeding distribution of knot was concentrated on mid-tidal sandy muds where cockles were found to be most abundant in the present study.

Cockle density and biomass in the Bight were so low when compared with

Macoma that it is extremely unlikely that either oystercatcher or knot are especially dependent on them as a food source. The feeding distribution of these waders on the South Bank cockle beds has not been investigated but those beds are likely to provide a significant resource for the birds.

Predation of cockles by migratory flatfish has been investigated by Hancock & Urquart (1965) and Wolff et al.(1981) and found to be significant only in the summer. Small animals, up to 12mm in shell length, are taken and the small sized individuals of the Bight population may provide a significant resource for the fish.

de Vlas (1979 & 1981) found that plaice, Pleuronectes platessa, and flounder, Platichthys flesus, also grazed heavily on cockle siphons and tips of the foot, reaching a maximum of 1.4 gm m^{-2} in the Dutch Waddensea, an average of 4% of the total elimination resulting from mortality. Heaviest grazing was found to be in August and September. Elimination of such regenerable parts is not taken into account in the removal/summation method used to calculate production.

Crabs are also known to take cockles up to 15mm (Hancock & Franklin; op. cit.) and the abundant Carcinus population in the Bight is likely to exert an effect on cockle mortality. The predation by Retusa on cockle spat is discussed elsewhere in Chapter 10.

8viii Growth in shell length

As well as observing changes in mean shell length of each cohort during the intensive survey (Table 8c, Figure 8ix), it was possible to determine growth rates of individual animals by counting growth rings (noting the presence of disturbance rings and occasional missing rings - see Materials and Methods, Chapter 2), and so determine the mean individual size of the survivors of each cohort at the time of the winter growth stop. Size-specific mortality, resulting from differential predation or erosion, may induce a degree of error. Growth ring data are summarised in Tables 8d, 8e and 8f as actual and percentage increments per growth season of individual cohorts as well as means for each year of growth from settlement. Growth curves for each settlement cohort are given in Figure 8x, mean values plotted in 8xi and percentage increment and its normal log plotted against time in Figures 8xii to 8xiv.

The average shell length reached after the first season's growth for all settlement years 1971 - 1978 was 4.6mm (range of annual means 1.8mm(1977) to 7.5mm (1976)). This is very low compared with most other studies of cockle growth but a degree of caution must be observed when interpreting studies using mesh sizes 0.5-5mm to detect young cockles. Additional confusion may arise in interpretation of the first growth ring which is sometimes very faint. The studies of Orton (1926), Wohlenberg (1937), Kreger (1940), Baggerman (1951), Cole (1956), Kristensen (1956), Hancock & Urquart (1965), Boyden (1971 & 1972) and Hancock & Franklin (1972) indicate that the usual size attained after the first season's growth is between 10 and 28mm shell length. Baggerman plotted the growth month by month of juveniles settled in May in the Dutch Waddensea and found growth from 0.8mm to 11mm in just 72 days.

Other studies of cockles in less favourable areas - ie. of reduced salinity and/or of very fine particulate substrate, notably those of Stephen (1931), Høpner-Petersen (1958), Barnes (1973), Seed & Brown (1958) and Hibbert (1976) show reduced rates of growth comparable to those found in Spurn Bight.

That conditions are not very favourable in the Bight is inferred by comparison of the size structure of the pooled data from Spurn Bight with that from Horseshoe Point in May 1977, (Figures 8v and 8vi). The dominating 1976 cohort at PIV6 has a mean individual shell length of 14.2mm in contrast to a mean of 6.6mm in the Bight. Seed & Brown (1978) suggest that very rapid growth to sexual maturity in a single year is a survival strategy to compensate for continuing very high mortality of older individuals.

Monthly observations of growth increments (Figure 8ix) showed a period of maximum growth between March and July with growth continuing through to November. Growth rates were seen to be higher in younger year groups, a phenomenon well known in most groups of animals, including the cockle (Richardson et al.; 1980).

Plots of percentage growth increment and its natural log (Figures 8xii to 8xiv) showed a ± inverse exponential decline in growth rate with age but which did not translate into a linear function when log transformed. Logarithmic plots of individual cohort data all show a point of inflexion during the summer of 1975 and 1976 with greater growth rate than predicted from an exponential model, again pointing to very favourable growth conditions in those summers. Log-normal plot of pooled data of all cohorts gives a very smooth curve - Figure 8xiv.

Ford-Walford equations of growth were calculated from data from the 1971, 1972 and 1973 cohorts - Table 8g. Later cohorts had insufficient data points to produce meaningful plots. A plot was made of data from all cohorts together (Figure 8xv), and gave a maximum attainable size of 31.2mm corresponding to an age of 8-9years. A similar maximum size was observed in Danish brackish-waters by Høpner-Petersen (1958), but a Ford-Walford plot of brackish-water cockles by Hibbert (1976) gave maximum sizes ranging from 38.1-43.5mm. Cole (1956) described commercial cockle beds producing animals in excess of 50mm in length in the Outer Hebrides.

It seems that unfavourable conditions of reduced salinity, non optimal sediment composition and overly turbid column water has led to low growth rates and small maximum size of cockles in Spurn Bight although without apparently affecting longevity which is comparable with elsewhere.

8ix Mean individual weight and biomass

Only for C. edule were separate monthly length/weight regression calculations made and the resultant equations are given in Table 8h. Variations in mean individual weight with time are included in Table 8c and biomass statistics for the whole population and individual cohorts in Table 8j and illustrated in Figures 8xvi to 8xviii.

The maximum biomass recorded for the whole population was 13.05 gm m^{-2} in July 1978 and a mean monthly biomass of 9.67 gm m^{-2}. This represents 15.9% of the measured mean monthly total community biomass at that site. This is very low in comparison with studies on commercial beds where biomass is measured in hundreds rather than tens of grammes per m^2 (eg. Kay & Knights; 1975). Low biomass populations similar to those in the Bight have been noted by Warwick & Price (1975) in the Lynher, Beukema (1976) in the Dutch

Waddensea, Hibbert (1976) in Southampton Water, Wolff and de Wolf (1977) in the Grevelingen and by McLusky et al. (1977) in the Clyde, all in areas of either reduced salinity or fine substrata.

Mean individual weight reached a minimum in the two dominating cohorts in May 1978, probably owing to the onset of gamete release. Weight loss from later gamete release was in part obscured by somatic growth, noted by Hancock & Franklin (1972).

Mean weight of the 1975 animals peaked in August and afterwards fell sharply to a value that was maintained until the following March. A peak of newly settled spat recruitment was recorded at GIII4 in September and the sharp decline in flesh weight is indicative of gamete release at that time.

The pattern of weight change was slightly different for the 1976 cohort which showed a pause in somatic weight increase between July and August which did not correspond to a pause in shell growth. A peak was reached in September with only slight decrease in mean weight over the following months. The most probable interpretation is that this cohort spawned earlier than the preceeding one and the cockles were able to increase further in weight prior to the winter growth stop. In retrospect, this inferred asynchrony in gamete release and, therefore, in length-weight relationship, would have made it more correct to have calculated separate length weight relationships for each cohort to produce more correctly interpreted results.

Changes in weight of the 1977 animals were less easy to observe as the decrease in numbers between March and May was so great that sampling produced too few animals for reliable weighing and sampling uncertainty probably induced error in the size/frequency relationship. The peak in flesh weight appeared to occur somewhere in the September - November period.

The 1978 and 1977 cohorts showed a steady increase in weight until November, peaking considerably later than other year groups, followed by a decrease to January after which the populations became extinct.

Chambers & Milne (1979) found contrasting patterns of variation in flesh weight in cockles from the Ythan in 1973-74 with a peak in flesh weight in May. Gamete release was not, however, noted until July/August.

There was surprisingly little decrease in individual weight over the winter. 1975 animals remained almost at constant weight and those of the 1978 settlement decreased in weight by only 13%. The decline in shellfish meat weight during the winter is well studied. Hancock & Franklin (1972) and Beukema (1974) noted between 35 - 41% decrease in weight of large cockles over the winter. Hancock & Franklin noted that the reduction in flesh weight of cockles in a mild winter may be ⅓ as great as that in a severe one, but the winters which they and Beukema (1974) investigated were notably mild (Beukema et al; 1978) and that of the study period relatively severe. Size-specific mortality is unlikely to be involved in the Bight population as mean individual shell length remained almost constant in each cohort over the winter.

8x Production, elimination and productivity

Owing to apparently large fluctuations in numbers, probably resulting from the very low density, it was not possible to calculate directly the contribution of the older, pre-1975 cohorts, and the decreasing series of P:B and E:B ratios determined from younger animals was extrapolated backwards to give ratios for a single older cohort. These ratios were applied to the mean monthly biomass of all older cohorts together to give the production figures presented here.

Monthly statistics of production, elimination, $\Sigma P/\bar{B}$ and $\Sigma E/\bar{B}$ are given for individual cohorts in Table 8k; monthly figures are illustrated in Figures 8xix and 8xx.

Total production over the year by the whole population amounted to 5.38 gm m^{-2} and elimination to 8.27 gm m^{-2}; 11.9 and 11.3% of the total community production and elimination at this site (Chapter 11). Negative production was recorded at the begining of the year for the two dominant cohorts and their productivity fell again during the late summer. This probably corresponded to periods of gamete release as indicated by data on mean individual weight and 'O' group recruitment. True production at this time would have been positive with the inclusion of gamete production. Regeneration of siphon tips predated by flatfish is similarly not taken into account and is discussed above in 8viii.

Elimination was found to be highest during periods of post spawning mortality, particularly between June and July for 1975 animals and between August and September for the 1976 cohort.

As expected $\Sigma P:\bar{B}$ ratio over the year was found to be highest for the youngest (1977) cohort, with progressively lower values for the older age groups. Monthly values showed a maximum in productivity between May and June for 1977 animals and between June and July for older animals which would have been spawning earlier. An overall $\Sigma P:\bar{B}$ ratio of the whole population was found to be 0.56:1 with an $\Sigma E:\bar{B}$ ratio of 0.86:1.

Production studies of C. edule elsewhere (Warwick & Price; 1975, Hibbert; 1976, McLusky et al; 1977, Wolff & de Wolf; 1977) have largely been in similar environments to those in Spurn Bight rather than in commercial populations. Warwick & Price found a $\Sigma P:\bar{B}$ ratio as low as 0.2:1 in the Lynher while Wolff & de Wolf recorded a maximum ratio of 8.92:1 for a submerged population in the Grevelingen estuary. It is interesting to note that they recorded P:B ratios at a number of sites in the estuary and found considerable variation with tidal position. Mid shore sites showed ratios between 0.69:1 and 2.56:1, more in keeping with the present study.

The value of 0.56:1 found in the Bight is relatively low when compared with most of the results of the above authors, probably explained by the low density and high mortality of the younger age groups and domination by the older, less productive 1976 cohort.

Summary of Chapter 8.

Although semi-commercial cockle beds are found on the southern part of the outer estuary, the Bight's population was composed of undersized individuals at lower densities than occur in commercial beds.

The distribution in the outer Humber and the Holderness and Lincolnshire coasts is described. In the Bight, cockles are most abundant in midshore sandy mud sediments with isolated individuals found elsewhere.

The ecological requirements of the species are discussed and the conditions of salinity, tidal position, sediment and temperature found in the Humber compared with those of cockle populations studied elsewhere. Low salinity, fine particle size and high water column turbidity are the likely causes of reduced growth in Spurn Bight. Very high temperatures of the 1976 summer are the likely cause of domination of the population by the settlement cohort of that year and the severe weather conditions of the 1978-79 winters led to very high mortality, particularly of smaller individuals.

A maximum density of 920 m^{-2}, including spat, was recorded - very low when compared with elsewhere. The population structure is recorded using growth ring data revealing dominance by the 1976 cohort and subsequent failure of the 1977 and 1978 spatfalls.

Two periods of spawning were noted in 1978 - April/May and August/September with continual recruitment of spat from June to September. Very high mortality of spat was observed and the year group was found to be extinct by the following March.

Mortality is described and is concluded to derive from post spawning effects on older animals and competition between the dominating 1976 and younger cohorts. Erosion was found to make a significant contribution to mortality and there was also evidence of redistribution of cockles by the tide. Predation is discussed and the species is likely to be a small but significant resource for predators mainly in the summer.

Growth is described from growth ring data and found to be much slower than for commercially exploited populations. Peculiarities in the growth curves of the 1974 and 1977 cohorts are noted. A Ford-Walford growth plot indicated a small maximum attainable size but longevity of 8-9 years comparable with elsewhere.

Biomass was calculated from monthly length/weight regressions, with a maximum recorded value of 13.05 gm m^{-2} and a mean of 9.67 gm m^{-2}. Fluctuations in mean individual weight are recorded giving a minimum level in May and maximum in August with indications of inflection from gamete release. There was found to be surprisingly little reduction in mean flesh weight during the winter months.

The total annual production of 5.38 gm dry flesh weight per m^2 was found to be exceded by elimination which was of 8.27 gm m^{-2} indicating a poor performance by the species during the study period. Monthly productivity values showed a maximum between June and July. Production was low when compared with elsewhere.

CHAPTER NINE

CHAPTER 9

MACOMA BALTHICA (LINNAEUS)

Introduction

The Baltic tellin *Macoma balthica* L. is the 'type' species of the boreal shallow mud association of Jones (1950), and is probably the most well documented estuarine invertebrate. Ratcliffe (1979) studied the species at Skeffling and found higher densities, biomass and production than has previously been recorded for the species and consequently concentrated study on it. At such high biomass it represents the single largest food resource for fish and wildfowl present in the Bight.

Comparable densities were observed over most of the Bight during the extensive survey of 1977 and distinct variation in population structure was noted between areas of the shore. *M. balthica* was, therefore, studied at all sites of the intensive survey.

9i Taxonomy and identification

No other species of tellinid bivalve were found during the survey and no trouble with identification was encountered. Juvenile *Scrobicularia* were superficially similar to *Macoma* of eqivalent size but were easily separated on shell shape, opacity and the occurrence of distinct growth rings in all *Scrobicularia*.

9ii Distribution in and around the Humber

Within Spurn Bight, *M. balthica* was found to be absent only from very coarse sands on the estuarine beach at Spurn Head (ref. Table 4a). Considerable variation in density was noted, related to particle size and tidal position (q.v.). It was also abundant on the Old Den.

Elsewhere on the North Bank of the estuary it was found to be abundant at Cherry Cob Sands, the population including much larger individuals than were found in Spurn Bight. Ratcliffe (1979) observed it as isolated individuals at Paull, and the Yorkshire Water Authority surveys of Levell (1971) and Gelder (1972) recorded it as far upstream as Alexandra Dock at Hull at very low biomass. On the South Bank it has been recorded as far upstream as New Holland in the Lincolnshire River Authority reports (1971-1974), and spatfalls were recorded at Pyewipes by P. Smith of Hull University (pers.comm.). It was not found there in 1977, probably owing to chronic pollution.

At Humberston and Horseshoe Point it was found to be present in hard sand flats and it is abundant along most of the Lincolnshire coast and into the Wash (own observation).

North of the Humber it is absent from the beaches of Holderness which support populations of Tellina and Spisula. It is found in Bridlington Harbour (D. Lewis, pers. comm) and in Scarborough South Bay (own observation).

9iii Ecological relationships

9iiia Salinity

The distribution of M. balthica in the Humber is typical of its distribution in other estuaries. Spooner & Moore (1940) noted that M. balthica has a preference for those parts of estuaries where salinity is highest.

Its upstream limits would not seem to be limited directly by its salinity tolerance, however, as it is a dominant component of the Baltic macrofauna at salinities as low as 4‰ (Muus; 1967), and 3‰ in the Dutch deltaic area (Wolff; 1973). Wolff suggested that very low salinity during periods of extreme freshwater flow probably prevent successful survival of spat at upriver sites.

M. balthica is able to thrive in full strength seawater and the salinity regime of Spurn Bight is not likely to limit the species in any way.

9iiib Tidal position

The distribution of M. balthica in May/June 1977 in relation to tidal height is illustrated in Figure 9i. It is immediately clear that biomass and density were not equally related to tidal position. Highest densities were found in upshore positions but the highest biomass values were recorded from midshore stations.

Reference to the population structure (Figures 9ix - 9xi), shows the reason for this discrepancy. Upshore sites were dominated by '0' group individuals of the previous year, with very small numbers of older animals, while midshore sediments had at the same time lower densities of '0' group and higher densities of older and, therefore, heavier individuals.

Spatfall is known to be more successful on more sheltered, silty upshore parts of tidal flats (Beukema; 1973) leading to higher densities of younger animals. Similar size distribution has been observed in many other estuaries (Anderson; 1972, de Wilde; 1975, Little & Boyden; 1976, Myren & Pella; 1977, Reading; 1979).

Migration and 'secondary spatfall' of year old individuals has been shown to lead to a dominance of the population in midshore sediments by older animals (Beukema; 1973).

Little & Boyden (1976) also found M. balthica to extend its distribution upshore during the winter months, although this was not observed in this study in Spurn Bight. de Wilde (1975) concluded that lower availability of food from lower primary productivity resulted in reduced densities at the bottom end of the shore while shorter tidal cover limits the time available for suspension feeding and thus its extreme upshore distribution.

9iiic Particle size composition and organic content

Distribution of numbers and biomass of M. balthica in relation to median particle size and degree of sorting in 1977 is illustrated in Figures 9ii and 9iii.

Density was found to increase consistently with median particle size with the highest densities in the finest sediments (ø median 4.0-5.5). Two stations with finer sediments had lower densities of Macoma, appearing to contradict the relationship, but these were both situated within the Spartina sward and, therefore, probably limited by tidal emersion.

M. balthica was also found to be abundant in mud pockets among gravel/ shingle of the Old Den.

Biomass was distributed differently with highest values in slightly coarser sediments - median particle size ø 2.9-4.7 and biomass was found to be much lower in the finest sediments. This reflects the different population structure in the upshore, silty stations from the midshore sandy stations (Figures 9ix-9xi) and is discussed more fully below.

Distribution of numbers and biomass in relation to sediment sorting similarly differed because of the different population structure in different sediments. Highest numbers were in the poorest sorted sediments while biomass peaked in poorly, but not the poorest, sorted media.

Ratcliffe (1979) did not find a similar relationship of M. balthica with sediment composition along his transect at Skeffling, probably because sandy extremes were not included. Similar relationships with sediment composition have been noted by Newell (1965), Anderson (1972), Wharfe (1977b) and Reading (1979).

Newell (1965) considered feeding requirements to cause the relationship with particle size. Wernsteadt (1942) found that benthic diatoms are important in the diet of M. balthica and Newell showed that benthic bacteria are important to the species when deposit feeding. He found bacteria to be less frequent in coarser deposits and, therefore, concluded that food availability in terms of organic carbon and nitrogen was the overriding factor involved in the relationship with sediment size.

The relationship of density and biomass to sediment organic matter showed no consistent variation other than that sediments with very low levels of organic carbon - the downshore sands, had low density and biomass of M. balthica. Above 3% organic matter there was no trend. It would, therefore, seem that factors other than food availability in sandy silts and silts cause the relationship of distribution with sediment composition.

Reading (1979) found significantly different relationships between the different size categories of M. balthica and median particle size, with smaller animals being more strongly correlated with finer particles. From analysis of sediment in the animals' guts he concluded that larger animals selectively inhaled larger particles from the sediment and smaller individuals select smaller particles. Together with vertical redistribution of spat (Beukema; 1973), this would explain the variation in population structure with tidal height and sediment size as observed in this study.

9iiid Temperature and extremes of weather

With its boreal distribution M. balthica might be expected to be far less susceptible to extremes of cold than more southerly distributed species.

Observations of several authors following severe winters (Smidt; 1944, Crisp; 1964, Beukema; 1979) showed that M. balthica indeed was affected far less by freezing of the sediment than, say, Cerastoderma edule or Scrobicularia plana.

Mortality in this survey (q.v.) during the ice conditions of the 1978-79 winter was far less than for more cold susceptible species.

de Wilde (1975) investigatedvarious aspects of the metabolism of M. balthica in relation to temperature and found that growth was faster and mortality lower in temperatures less than 15°C.

Mass mortality of M. balthica in periods of high summer temperatures (eg 1975-76) does not appear to have been noted.

Beukema et al. (1978) found a significant decline in M. balthica in relation to other species during a period with mild winters and it may be that Macoma is only able to compete with certain other species through its tolerance of extreme winters.

9iiie Depth distribution

No attempt was made to investigate the depth distribution of M. balthica in this study. Ratcliffe (1979) found a clear relationship between burying depth and size, with larger specimens with their larger siphons, burrowing more deeply. The relationship held true at all times of the year but he observed increased stratification to greater depths during the autumn and winter months. Increased anoxia of deeper sediments in the summer probably accounted for shallower burrowing at that time.

Reading & McGrorty (1978) looked at the availability of Macoma as bird food in relation to burying depth and concluded that only 4% of total biomass would be available to knot, Calidris cornutus, during the winter months.

The depth distribution of this species is, therefore, extremely important in the significance of the species as a resource for overwintering wildfowl.

9iv Density

Variations in density of M. balthica throughout Spurn Bight and comparative sites in the outer Humber noted in the 1977 extensive study is included in Table 4a. A maximum density of 18,700 individuals m^{-2} was observed at HI2, mainly composed of the 1976 'O' group. Variation in density largely reflected the distribution of the 1977 cohort in relation to tidal position and sediment nature (q.v.).

This range of density values is rather higher than average in comparison with ranges recorded in other estuarine studies (refer list in Ratcliffe; 1979). He found densities at Skeffling in excess of 40,000 m^{-2} subsequent to the summer spatfall, higher than had previously been recorded in the literature and the timing of the present extensive survey did not allow the detection of peak densities.

During intensive studies - Table 9a - a maximum post spatfall density fo 37,860 m^{-2} was recorded at FII2 in July 1978. This again is high when compared with most studies elsewhere although some higher values have been noted (eg. Anderson; 1972 in Morecambe Bay- 56,000 m^{-2}) and the spatfall of 1978 was not as great as that observed at Skeffling in 1973 by Ratcliffe.

Temporal variation in density of the total population and of individual cohorts is illustrated in Figures 9iv - 9viii.

9v Population structure

Similar difficulty in ageing M. balthica from Spurn Bight was encountered as had Ratcliffe (1979), who found that less than 5% of animals showed growth rings. This he attributed to continual slow growth through mild winters.

From the size/frequency histograms (Figures 9ix to 9xv) it became possible to recognize 'O', I and II group cohorts. In addition, individuals were often differentiable into cohorts on opacity of the shell and, occasionally, the presence of growth rings.

Objective methods, using probability paper etc. (eg Harding; 1949), were not used. These assume a normally distributed size/frequency relationship within each modal class, whereas size dependent mortality through erosion and predation is likely to occur. Cohorts were, therefore, ascribed subjectively 'by eye' and with the aid of the few reliably aged individuals with rings.

The age structure was found to vary considerably from site to site during the extensive survey of 1977 (Figures 9ix - 9xi), with consistent differences between upshore, midshore and downshore silts, muds and sands. The results are here presented in three blocks from CLUSTAN analysis of sites on faunal composition and the mean size/frequency relationship from all samples from all sites within the cluster given as an additional histogram.

It is immediately obvious that sites of cluster TOPSILT (Figure 9ix), were dominated numerically by the 1976 'O' group and members of older cohorts are relatively far less common than at sites in other clusters. Size/frequency peaks for older cohorts are barely distinguishable.

Although still dominated, but to a lesser extent, by the 1976 cohort, older animals were more frequent and were more easily differentiated into I, II and II+ cohorts in sites of cluster MIDMUD.

The population structure of the stations in the cluster SAND was found to be dominated by the oldest, II+, individuals with comparatively few smaller individuals and an overall very low density.

Variation in population structure of M. balthica with tidal height and sediment composition have been observed elsewhere (Myren & Pella; 1977, Wolff & de Wolf; 1977, Beukema et al.; 1978, Reading; 1979). They are attributable to differential passive movement of spat along the shore after initial settlement at the highest shore levels (Beukema; 1973, Wolff & de Wolf; 1977, Ratcliffe et al; 1981), differential preference for larger particle sizes by larger individuals (Reading; 1979) and differential growth rates at different shore levels (Green; 1973).

Beukema et al. (1978) also noted that in the Dutch Wadden Sea, during the period of mild winters preceding the present study, redistribution of spat was much less prevalent, leading to dominance of upshore sediment by small individuals and very poor recruitment at downshore locations which remain dominated by very old animals dating from the previous harsh winter. This may be the case in Spurn Bight but it was not possible to investigate the effects of the severe 1978/79 winter on the extreme downshore populations.

Segerstråle (1962 et seq.) has also postulated that predation or competitive exclusion of smaller Macoma by amphipods lead to changes in population structure with depth in the Baltic, supported by intertidal observations in San Francisco Bay by Vassalo (1969) on *M. inconspicua* now synonymised with *M. balthica* (Coan; 1971). This is unlikely to be the case in SAND communities in Spurn Bight as densities of potential predators are so low and are composed of relatively small individuals.

Evidence from changes in population structure with time (below), indicate that this variation with shore level results entirely from passive downshore movement of the majority of the 'O' group. Low densities, especially of smaller individuals, in SAND stations is likely to be a result of repeated erosion from more mobile sediments and the unsuitability of the coarser sediment for the feeding or burrowing mechanism of smaller individuals.

An apparently unusual population structure was found at station AIII2 on Cherry Cob Sands, upstream of Spurn Bight, a site clustering with TOPSILT. This had a clearly identifiable 1977 'O' group but the site was sampled last, on 14th June, and recruitment was then under way.

Population changes with time during intensive studies are illustrated in Figures 9xii to 9xv. Site FI2 is excluded as, in effect, only the 1978 cohort was present in any numbers and the density graph, Figure 9iv, adequately illustrates the population structure.

The population at FII2 was composed almost entirely of 'O' and I group cohorts of the 1977 and 1978 recruitment, while at downshore stations a discrete 1976 cohort was visible. On certain sampling dates at certain stations a separate size/frequency peak for the 1975 cohort was also visible (eg. Figure 9xiv - 24.4.78, Figure 9xv - 16.3.78), but overall the sampling error was too large to treat cohorts older than 1976 separately.

The 1976 cohort was, like that of *Cerastoderma edule* (q.v.), seen to dominate the population numerically, although not to the extreme degree as observed with *Cerastoderma*. The density of the 1977 cohort was either the same or lower than that of the 1976 settlement indicating a poor survival, possibly through competition with a very heavy spatfall of 1976. Pre-1976 animals were relatively frequent and there did not appear to have been mass mortality resulting from the extreme summer conditions.

9vi Spawning and recruitment

Reproduction of M. balthica was not investigated in this study but spawning has been recorded in the past from March onwards (Caddy; 1967) and may continue well into the summer months.

Recruitment commenced in June 1978 at all stations but maxima in density of the 'O' group were noted earlier at the four more upshore sites, in July at FI2 and in August at FII2, FIV4 and GIII4 and at the lower shore site GIV3 in September. This is probably attributable to post settlement redistribution, discussed elsewhere.

Recruitment was highest at the topshore silt site FII2, reaching a maximum of 37,460 m^{-2} of individuals with mean shell length of 0.42mm. Far fewer young animals settled within the Spartina and subsequent migration or mortality reduced the density to 0.6% of the maximum value by November.

Maximum recruitment downshore, possibly of a secondary nature was of 21,710 m^{-2} animals of mean shell length 0.71mm.

These values are again relatively high when compared with literature although not as high as recorded by Ratcliffe in 1973.

9vii Growth and longevity

The mean shell length of each distinguishable cohort each month at each site is given in Table 9b and expressed graphically in Figures 9xvi - 9xx.

These are probably not true growth curves as size dependent effects on mortality and passive migration were apparent, especially during the winter. Continual recruitment throughout the summer also disguised actual growth of individuals which had settled as early as June.

As rings could not be detected it was not possible to measure the growth rates of older individuals and so to compare growth in the 1978 cool wet summer with previous season's growth.

Maximum growth was observed for all cohorts between June and September although increments in length attributable to growth continued until November at most sites.

Continued growth through the winter was apparent at station GIII4 but this was likely to be a size dependent effect of the extremes of erosion that occurred at this site removing the smaller, more easily transported individuals. A similar effect was noted at station FII2 during the winter where again erosion was at a maximum.

At other sites there was a slight decrease in mean size over the winter, possibly attributable to size-dependent predation.

Mean shell length of each cohort was greater at site FIV4 than at either of the Easington stations, smallest individuals occurring at station GIV3. This may result from a density, or, more likely, biomass dependent effect on growth rate as highest densities were recorded at GIV3 with lower densities at the Skeffling site. The 1978 cohort grew to its largest size at site FII2, where biomass-dependent effects would be even less. It would seem that growth rate is related either to tidal height, sediment composition or biomass of M. balthica but it is impossible in this study to distinguish between the effects of related variables.

Maximum size reached by the 'O' group at the end of the first summer's growth was 1.72mm, a figure comparable to that found at Skeffling by Ratcliffe (1979). He discussed his result in comparison with growth of spat recorded elsewhere which have been observed growing to as much as 5.9mm at the end of the first year (Lammens; 1967). He concluded that sieve sizes used by other authors allowed the entire 'O' group to pass through and that what was actually being measured was the growth of the previous year's cohort. The results of this study are in keeping with that conclusion.

Growth of the 1976 and 1977 settled animals was again similar to that observed by Ratcliffe. 1977 animals grew from between 1.1 - 2.4mm to between 5.1 - 6.8mm and the 1976 cohort grew from between 4.8 - 6.1 to 8.8 - 10.0mm.

Growth was continuous over the summer rather than primarily in the spring as observed in the Waddensea by Lammens (1967). It would seem that the growth pattern of M. balthica in Spurn Bight is consistently different to that observed in the Waddensea.

It was not possible to carry out Ford-Walford growth analysis on M. balthica for the Humber but, on those individuals with growth rings, a maximum of 8 were observed on several individuals of lengths 17 - 18mm from

Spurn Bight.

From samples taken at Cherry Cob Sands (AIII2) in June 1977 a number of individuals of 21mm in shell length were found but lacking in growth rings. Only four individuals larger than 18mm were found in Spurn Bight during both surveys, none larger than 20mm. McErlean (1964) observed increased size of M. balthica upriver of the mouth of the Middle Patuxent estuary and attributed this to salinity effects. It would repay further study to discover if the larger size at Cherry Cob Sand was a result of increased growth rate or greater longevity.

9viii Mortality, migration and predation

Evidence of redistribution of M. balthica of all ages is apparent from various observations:-

(i) later peak in "recruitment" at downshore sites of larger individuals.

(ii) size-dependent effects at sites most prone to erosion pressure.

(iii) reappearence of significant densities of all age groups at upshore sites in the winter.

(iv) rapid increase in density of year-old animals between March and May at station GIII4 compared with a decline elsewhere.

Reduction in density cannot therefore be regarded as evidence of mortality and 'elimination' must be understood to include passive emigration of still living individuals that resettle elsewhere. Similarly, sudden large increases have had to be 'smoothed' out of density figures to give values upon which production analysis was carried out.

Highest overall reduction in density was found of the 1978 'O' group at the two upshore sites. This was absent by January 1979 at the Spartina zone site at Skeffling - FI2 but subsequently reappeared in March. Much of this density reduction may be true mortality at this site. Interference with water flow by Spartina sward would probably rule out much passive transport and continual exposure and drying out of the mud surface during neap tides would lead to very high mortality of obligate filter/deposit feeding juveniles restricted to the top centimetre of mud by a short siphon length.

Downshore migration from an initial upshore settlement is well documented

(Beukema; 1973, Wolff & de Wolf; 1977, Beukema et al; 1978, Reading; 1979). Little & Boyden (1976) also found M. balthica to extend its range upshore during the winter and may be comparable to the observed reappearence of M. balthica at FI2 and FII2 between January and March 1979.

Ratcliffe et al. (1981) demonstrated the susceptiblity of juvenile M. balthica (>1.5mm) to erosion from sediments, particularly where higher densities of larger individuals result in constant bioturbation of the upper levels of the sediment, and added that colder temperatures reduced the activity of the bivalves and rendered them more susceptible to erosion.

The more or less steady decline of all older cohorts at all sites (Figures 9iv - 9viii) is probably a result of actual mortality. No periods of particularly high mortality were observed which might have followed spawning. Unlike C.edule, M. balthica is not known to be subject to high post spawning mortality.

Decline in numbers was also not significantly greater in winter than in summer, despite harsh weather and the presence of large numbers of overwintering waders. Very large numbers of older individuals were, however, noted in the strandline during the winter months, indicating mortality through erosion as being significant.

M. balthica is known to form a very significant part of the diet of many species of wading birds, notably dunlin, Calidris alpina, knot, Calidris canutus, redshank Tringa totanus, turnstone, Arenaria interpres, oystercatcher, Haematopus ostralegus and bar tailed godwit, Limosa lapponica (Davidson; 1971, Goss-Custard; 1969 & 1977b, Milne & Dunnet; 1972, Prater; 1972b, Goss-Custard, Jones & Newbury; 1977). It is also important to certain sea duck, particularly goldeneye, Bucephala clengula, tufted duck, Aythya juligula and scaup, Aythya marila (Pehrsson; 1976).

The relationship between burying depth and availability as prey is well known and as little as 4% of the total biomass may be available to shorter billed birds during the winter months (Reading & McGrorty; 1978).

The study of Tasker & Milsom (1979) showed that oystercatcher, bar tailed godwit and knot in particular concentrate their feeding efforts on midshore sandy mud sediments - those dominated in terms of biomass by M. balthica. In addition, dunlin were noted to switch from more upshore feeding grounds to midshore sandy muds during the coldest part of the winter of 1978-79.

Of the sea-duck, only scaup were found by them to be present in significant numbers in this part of the estuary. Other species seemed to concentrate their feeding efforts on freshwater habitats around the Bight.

M. balthica are known to be important in the diet of flatfish, notably plaice, Pleuronectes platessa, and dab, Limanda limanda (Braber & de Groot; 1973). They noted that large plaice (>30cm) fed mainly on whole bivalves while other flatfish were unable to 'crunch' whole bivalves. Wolff et al. (1981) found M. balthica to be very significant in the diet of plaice and flounder, Platichthys flesus in the Oosterscheldte estuary. Braber & de Groot also noted that siphons of M. balthica formed a very significant part of the diet of 'O' group plaice and dab. The mollusc is capable of regenerating lost siphons and continual grazing of siphons may lead to considerable underestimation of total production. de Vlas (1979, 1981) found that as much as 279 mg m^{-2} or 10% of total elimination resulting from mortality, was taken as siphon tips from a population of M. balthica in the Dutch Wadden Sea.

Macoma spat as food for Retusa obtusa are discussed in the chapter on that species.

9ix Biomass and individual weight

All biomass figures were calculated from a single shell-length/tissue dry weight calculation made for animals collected during May 1977. The seasonal variation in condition factor for this species has been well studied (Chambers & Milne; 1975b, Beukema & de Bruin; 1977) and a peak in condition factor found to occur immediately prior to spawning. As much as a two-fold difference between maximum and minimum value in condition factor has been observed.

In each of the above studies it was possible to calculate that the May figure approximated to the annual mean and it was considered expedient to use a single regression equation to save time.

The relationship was found to be:-

flesh dry wt (mg) = 0.0206 x shell length (mm)$^{2.727}$

$n = 1419$ $\qquad\qquad\qquad$ $r = 0.98$

A further source of underestimation in biomass calculations may have originated in the freeze-storing of specimens prior to weighing (discussed in Moreira; 1979 and in Materials and Methods).

Biomass values for all stations of the extensive survey are recorded in Table 4a and a maximum of 23.36 gm m^{-2} was found at station GIV3. Statistically significant differences were found between the mean biomass of TOPSILT, MIDMUD and SAND stations although there was considerable overlap between the first two.

Data on total and cohort biomass from intensive surveys are given in Table 9c and illustrated graphically in Figures 9xxi - 9xxviii.

The pattern of variation was different at each station. At the Spartina and upshore silt sites at Skeffling - FI2 and FII2, changes in total biomass reflected migration of older individuals and the biomass of the 'resident' 1977 cohort at FII2 remained almost constant throughout the year after an initial rise in spring.

Maximum biomass at station FIV4 was recorded in September and November 1978 at 26 gm m^{-2}, following a steady rise starting in May. Biomass fell steadily through the winter to reach a minimum in March 1979 at 54% of the maximum value.

A similar pattern was noted at station GIII4. Total biomass fell to a minimum in May 1978, mainly as a result of an apparently size dependent effect on mortality of the <1976 animals. Maximum biomass at 37.6 gm m^{-2} was recorded in September 1978, corresponding to the maximum value of the 1976 cohort. Biomass then fell steadily over the winter to a minimum in March 1979 at 63% of the total value.

At station GIV3 the pattern was different - a maximum value of 62.5 gm m^{-2} was recorded in March 1978 and the value declined steadily throughout the year, peaking again in August 1978 at 57.8 gm m^{-2} and then declining very steadily through the winter to a minimum of 31.2 gm m^{-2} in March 1979.

Mean annual biomass figures are also included in Table 9c - a maximum value of 44.6 gm m^{-2} recorded at GIV3 of which 76% was contributed by older animals than the 1976 cohort and a further 22% comprised the 1976 animals.

Contribution by M. balthica to the measured mean monthly total community biomass varied from 4.8% at station FI2 in the Spartina and 10.0% at FII2 in upshore silts, to 75.1 - 85.1% of the total in midshore sandy muds (ref. Chapter 11).

This is a very high value compared with those recorded elsewhere. Ratcliffe (1979) found a maximum mean annual biomass of 37.1 gm m^{-2}, a previously record high figure. It would seem that conditions in Spurn Bight during the 1970's were exceptionally favourable for this species, leading to very high biomass.

Variation in mean individual weight of each cohort is given in Table 9d. These are a direct function of shell length as they result from a single length/weight relationship only and discussions used above referring to shell length increments are equally relevant to mean individual weight as presented here.

9x Production, elimination and productivity

It was not possible to differentiate cohorts older than the 1976 settlement and it was therefore impossible to measure directly their productivity and elimination. A mean annual $P:\bar{B}$ ratio of 0.257 for cohorts older than two years was calculated from values in Ratcliffe (1979), and this figure was applied to mean bimass figures to give an approximate figure for production. Elimination rates were not, however, described by Ratcliffe and a normal calculation was performed on mixed cohort data to give at least some estimate of elimination of these older animals.

Monthly values for production, elimination, productivity and $E/\bar{B}$ ratio for each cohort of M. balthica at each intensive survey station are given in Tables 9e and 9f and expressed graphically in Figures 9xxix - 9xli. Total population values are summarised in Table 9g.

Negative production/productivity was recorded during certain months. This did not represent true negative production as all biomass values were taken from a single length/weight regression. Rather, negative values represent periods of size-dependent mortality, a source of error not accounted for in the removal - summation method used to calculate production.

Highest production was found to be of the 1976-settled animals at all sites other than the topshore silt and Spartina where older animals formed an insignificant part of the population. This contrasts with Ratcliffe who found that 45% of total production at his regular site at Skeffling (= FIV4) was contributed by animals in their first year of growth and only 22% by second year animals corresponding to the 1976 cohort in this study.

Peaks in production of different cohorts were asynchronous with that of animals one year younger. Production was insignificant before May and after October 1978 and at a maximum between June and August. No consistent dip in somatic production was noted corresponding to gametogenesis and it is likely that all cohorts studied intensively (1976 et seq.) were sexually immature at the start of the year. Lower apparent autumn production of the 1976 cohort may however be a result of spawning although this was not checked by gonad analysis.

Maximum production was observed at the Easington downshore sites, 22.9 gm m^{-2} at GIII4 and 22.7 gm m^{-2} at GIV3. The proportion of the measured total community production contributed by M. balthica varied between 0.3% at site FI2 to 62.4% at GIII4 and 0.3 - 63.1% of total community elimination (Chapter 11).

Elimination was highest by animals older than the 1976 cohort. Overall rates were highest in the autumn rather than in midwinter but there was little correlation between rates of elimination between study sites and, taken in total, there was high elimination throughout the year with varying contribution from different cohorts.

Maximum elimination was of 44 gm m^{-2} at station GIV3. It was impossible to ascertain what proportion of that elimination would be available to predators.

Total elimination exceeded production at all downshore sites where animals of older cohorts formed the significant part of the population biomass. The method used to estimate the dynamics of the older cohorts may, however, have been sufficiently inaccurate for the above observation to be an artifact of that method. For all younger cohorts production exceeded elimination.

Annual productivity was found to be highest for the youngest cohorts with progressively lower values for older cohorts.

There was little consistency between sites in the pattern of variation in productivity with time although at all sites it started low in March, rose to a maximum somewhere between May and July and declined almost to zero by the end of autumn. E:$\bar{B}$ ratios similarly showed little consistency between sites on the whole remaining low during the summer, rising in the autumn and falling again in the winter. There were, however, unexplainable peaks observed during the summer and the E:$\bar{B}$ ratio of the 1977 cohort at station FII2 was higher in the summer than in the winter.

Total population productivity over the year varied between 0.51 gm dry weight per m^2 at GIV3 where the proportion of older animals was highest, to 2.08 gm m^{-2} at FII2 where it was lowest.

In common with the previous study of *M. balthica* at Skeffling by Ratcliffe (1979), values for production were higher than have been recorded elsewhere in cold temperate mudflats (Table 9g). Nichols (1977), however, found a population of *M. balthica* in San Francisco Bay (warm temperate) to produce 46.6 gm m^{-2} with a{P:$\bar{B}$ ratio of 4.5:1. The results of this study were not, however, as high as those of Ratcliffe.

Productivity was not found to be exceptionally high and the very high production values are purely a function of the very high biomass, probably encouraged by the very high turbidity levels of the Humber water with its associated organic material.

Summary of Chapter 9

Macoma balthica has already been observed to occur at higher densities and biomass in Spurn Bight than previously found elsewhere. It represents, therefore, the single largest food resource of these mudflats.

The distribution of *M. balthica* in and around the Humber is described and its distribution in Spurn Bight related to salinity, tidal position, sediment particle size and sorting and temperature. Density was found to be inversely related to median particle diameter and the population structure was found to change downshore in relation to sediment composition. Higher densities of older animals, and therefore higher biomass, was recorded from midshore sandy silts.

A maximum density of 37,860 individuals m^{-2} was recorded at FII2 in July 1978 at the height of spatfall and the variations in densities of each cohort were was described. A dominance of the 1976 cohort over that of 1977 was observed.

Recruitment at mean shell size 0.42 mm was noted from June onwards and there was evidence of redistribution downshore. Maximum growth was observed between June and September.

Mortality and emigration are discussed together and little difference in rate was found between summer and winter despite apparently massive erosion during the winter gales.

Biomass was calculated from a single length/weight regression on frozen animals, two probable sources of error. Variation in biomass throughout the year is recorded.

A maximum mean annual biomass of 44.6 gm m^{-2}, peaking at 62.5 gm m^{-2} in March 1978, was recorded at GIV3, the highest ever recorded for this species.

Production, at a maximum of 22.9 gm m^{-2} was similarly high, resulting from high biomass. Around 50% of this was contributed by two year old animals of the 1976 cohort. Productivity fell in the middle of the known range for *M. balthica*.

Maximum elimination of 44 gm m^{-2} was recorded although it was impossible to ascertain what proportion of this would be available to predators.

CHAPTER TEN

CHAPTER 10

RETUSA OBTUSA (MONTAGU)

Introduction

Retusa obtusa (Montagu) was found to be abundant in sandy muds all over Spurn Bight and was also found at Horseshoe Point on the South Bank although not at Humberston. Dr. P. Smith of Hull University (pers. comm.) did not find it at any of his sample sites to the west of Grimsby but this absence probably results from the effects of pollution and lack of suitable sediment types. The species had only previously been recorded from the Humber by Ratcliffe (1979), and is not mentioned in the studies of Petch (1907), Hinton-Clifton (1964), nor in any of the water authority reports (1971 - 1974). It seems unlikely, however, that the Spurn Bight population is so recently established as direct development from the egg, as occurs in R. obtusa, would make extension of range extremely slow.

Little has been previously published on the ecology of R. obtusa compared with equally abundant estuarine organisms. The only monographs are by Smith (1967a & b) who described the feeding habits, breeding cycle and embryology of specimens from Barry Harbour in South Wales, whilst Elliot (1979) described its productivity in relation to Hydrobia ulvae in Torry Bay in the Firth of Forth. A short resumé of previous knowledge was given by Thompson (1976) and Lemche (1941) described the distribution of the species in Northern Europe.

10i Taxonomy and identification

Specimens occurring in the Humber conformed to the description of R. obtusa var. pertenuis (Mighels) given in Thompson (1976) which has previously been known as a separate species, Retusa pertenuis. This variety has a truncate spire and a much smaller maximum size (4mm) than the typical form which can reach 10mm. Lemche (1941) described var pertenuis as "a degenerate form occurring in such localities where physical conditions are not optimal for the species" and recorded it from subtidal sands off East Greenland from depths between 6 and 30m. Thompson (1976) recorded the typical form from sandier sediments whilst var. pertenuis occurs in "finer substrates where it seldom reaches 3mm in length". Smith (1967a), Rasmussen (1973) and

Elliot (1979) refer to var. *pertenuis* whereas other studies have not specified the variety.

Occasional specimens with an extended spire were found in the Humber and this, together with the slightly larger maximum size, suggests that the population is of intermediate form, closer to *pertenuis* than to *obtusa* (sensu stricta) Elliot (1979) found a mixed population of *pertenuis* and the typical form in Torry Bay. Lemche (1948) observed that forms transitional between the southern form *obtusa* and the northern form *pertenuis* are found in Greenland, Norway and Denmark and especially around the British coast. He also pointed out that the form *pertenuis* is dominant in brackish waters and it is likely that the form is purely ecotypic.

10ii Distribution in and around the Humber

With the exception of the work of Ratcliffe (1979), the species has not been observed in the past in the Humber, or on the Holderness or Lincolnshire coast.

10iii Ecological relationships

10iiia Salinity

Although Smith (1967a) found *R. obtusa* to be tolerant of short periods of immersion in fresh water, the species appears to have been recorded only from the lower reaches of estuaries and in truely marine conditions. In the Humber its furthest upriver station was at Hawkin's Point - BI2 - with an interstitial salinity of 26.8‰. Salinity tolerances were not studied but previous works indicate its preferred range seems to be between 24‰ and full seawater. Wolff (1973) found it to occur in Dutch estuaries down to 12‰ chlorinity (= 19.7‰ salinity).

10iiib Tidal position

Distribution in relation to tidal position is illustrated in Figure 10i and highest densities are apparent at upper/middle shore stations.

Jeffreys (1867), Lemche (1929), and Pruvôt-Fôl (1954) describe *R. obtusa* as a deep water species while Thompson (1976) records it to 300m. In the majority of estuarine studies, however, it has been recorded intertidally. Wolff & de Wolff (1977) found *R. obtusa* in 15.8% of all intertidal samples and only 0.5% of subtidal ones in the Grevelingen estuary. Macmillan (1968) described the species as commonest intertidally in muddy estuaries and shallow waters. Elliot (1979) suggested that R. obtusa is an almost exclusively intertidal and very shallow subtidal species, and that earlier studies of sublittoral populations refer in fact to Retusa retusa (Maton & Racket), a similar species. Wolff (1973) suggested that it is also unable to withstand long periods of emersion on the higher parts of the shore. Little & Boyden (1976) and Ratcliffe (1979) are in agreement with the present study in finding the highest densities in midshore sediments in sandy mud.

10iiic Particle size

With the exception of the study of Smith (1967a), who records R. obtusa from "fine sloppy, almost liquid mud" it has been found in the past mainly in sandy muds rather than silts, in common with this study. Thompson (1976) stated that the form pertenuis is characteristic of finer substrata. No R. obtusa were found in sediments of a greater median particle size than ∅2.8 or less than ∅5.5 and by far the highest densities were between ∅median 3.25 and 4.65 (Figure 10ii). Wolff (1973) found R. obtusa in sediments with median particle size between ∅1.25 and ∅3.02, with largest numbers between ∅2.59 and ∅3.02.

10iiid Temperature and extremes of weather

A sharp reduction in population density was found to have occurred at two of the main study sites between January and February 1979 but numbers increased at the third sampling station and it is likely that the reduction resulted from passive movement of individuals by the gales which accompanied the very cold weather.

Crisp (1964a & b) Smith (1967a) found the species to be almost unaffected by the extremely low temperatures of the 1962-63 winter. This is reflected by its distribution which extends north from the Mediterranean to Greenland, Iceland, Arctic Canada and Alaska (Lemche; 1941), - the species is obviously able to withstand cold condition.

Smidt (1944) found R. obtusa to appear suddenly in areas from which it had not previously been found after the icy winter of 1942-43 in the Danish

Waddensea. This implies removal of competition or some limiting influence, perhaps bioturbation by bivalves, rather than a temperature effect.

10iiie Depth distribution

No attempt was made to study the sediment depth distribution of R. obtusa in the Humber. Smith (1967a), found the entire population to occur in the top 3-3.5cm of very soft mud.

10iv Interspecific relationships

In intertidal studies R. obtusa is commonly described from boreal shallow mud communities, as described by Jones (1950), together with Macoma balthica, Cerastoderma edule, Hydrobia ulvae, Hediste diversicolor, Nephtys hombergi and Corophium volutator. The form pertenuis has also, however, been recorded from the boreal deep mud Macoma calcarea community by Lemche (1941). It does not appear to have been recorded from shallow sand Tellina communities, where it is replaced by Retusa truncatula Bruguière (Rasmussen; 1973).

The apex of the spire of R. obtusa in Spurn Bight was invariably covered with brown, stalked chitinous epizoites, often as many as twenty per shell. Thompson (1976) illustrated a R. obtusa shell with similar epizoites but did not refer to them, while Elliot (1979) found stalked thecate ciliate protozoa on R. obtusa shells in Torry Bay. It is assumed that those on animals in the Humber were of a similar nature.

Egg capsules of Hydrobia ulvae were occasionally found attached to the shell of adult Retusa although never in large numbers. Anderson (1971) recorded similar oviposition sites by H. ulvae in the Ythan estuary. Rasmussen (1973) also recorded egg cocoons of turbellarians occurring commonly on Retusa sp. in the Danish Waddensea, but these were not observed in the Humber population.

Feeding relations are discussed in 10xii below.

10v Density

A maximum density of 1880 m^{-2} was found at station GIII4 in the extensive survey of May/June 1977, and of 7740 m^{-2} at GIV3 in October 1978 during the intensive study. Ratcliffe (1979) found a maximum of 2000 m^{-2} at Skeffling, approximately at FIII4, in April 1975. The density at all stations during the spring 1977 survey is given in Table 4a. Changes in total population and individual cohort density at the regular sampling sites during 1978-79 is given in Table 10b and illustrated in Figures 10iii - 10vi.

Outside the Humber R. obtusa has only been occasionally mentioned in estuarine surveys - a summary of previous records is given in Table 10a. The highest density recorded elsewhere has been 1280 m^{-2} by Elliot (1979) at Torry Bay in the Firth of Forth in July 1975, although the figure of 300 per 5 litres of mud given by Smith (1967a) may refer to a higher density but the sample area is not given. The Spurn Bight population, therefore, seems to represent the highest density recorded for an infrequently studied species and for this reason it was decided to concentrate on its autecology.

10vi Population structure

Cohort differentiation was straightforward and it was not necessary to resort to probability paper analysis as did Smith (1967a). Older animals were always larger, darker and more opaque yellow than the thin shelled younger generation. The only problem was with the overlapping in size of the rapidly growing spring cohort with that of the previous autumn, although separate size/frequency peaks remained identifiable until September. After this the groups were treated as a single cohort and the distribution of mortality between the two cohorts during the autumn spawning period was not distinguishable.

Population structure as size/frequency histograms for all sites where R. obtusa occurred is illustrated in Figure 10vii and monthly variation at midshore sandy mud intensive survey sites in Figures 10viii to 10x. The population structure at site FIV4 on 19th January 1977 calculated during preliminary investigations is illustrated in Figure 10xi for comparison with that one year later. Growth rates for shell length and flesh dry weight is presented in Table 10c and illustrated in Figures 10xii - xiv and 10xvi - xviii.

The maximum number of cohorts present at any one time was three, although these were subsequently not found to be year cohorts (see below). The population was bimodal at the start of the survey in March 1978 and the older animals were extinct at all sites by July. This slightly preceded the recruitment of a new cohort and mortality of the older animals was assumed to be a result of spawning. Smith (1967a) noted that animals in the laboratory died almost immediately after oviposition, usually within 24 hours, and this was observed in the laboratory in this investigation.

10vii Reproduction and development

Smith (1967a) showed R. obtusa to be a protandrous hermaphrodite and that ripe autosperm are present in the ovotestis by the autumn after spring recruitment and that allosperm are collected into the receptaculum seminis at the same time. It is, therefore, probable that copulation both amongst and between both cohorts occurs at this time, after which animals recruited in the previous autumn spawn and die while those of the spring cohort store the allosperm until oocytes ripen in the gonad to produce the subsequent spring generation. A single copulation period in the autumn is, therefore, all that is necessary to ensure fertilisation of both spring and autumn cohorts. Smith (1967a) showed, however, that the male half of the ovitestis was still functional in the spring and that a second fertilization period is possible to compensate for any failure of the autumn copulation. Gene flow is, therefore, possible between spring and autumn cohorts which would otherwise be reproductively isolated.

R. obtusa is unique among the Retusidae in undergoing direct development with no planktotrophic stage (Smith; 1967a, Thompson; 1976), producing small numbers of large lecithitrophic eggs in masses which are sometimes attached to the shells of other Retusa (Thorson; 1946). Smith (1967a) interprets this as an adaptation to a boreal distribution by a small species which would otherwise waste a large proportion of its energies in producing sufficient planktonic larvae to ensure survival in rigorous conditions.

The development of R. obtusa is described in full by Smith (1967a & b), and no serious attempt was made to investigate this aspect of its biology. During April 1978, however, animals from the regular samples were observed ovipositing soon after sieving from the sediment. The egg masses were retained (those adhering to the adult shell were removed), and incubated at 10 - 13^{o}C in 25‰ seawater and the development observed. 100% mortality of the parents was found to have occurred within 24 hours of oviposition, usually with advanced autolysis of the body tissues. It must be assumed that the animals had previously spawned in the wild as Smith (1967a) noted that adults regularly laid up to four egg masses totalling 50+ eggs and died immediately after the last one. Of the twenty egg capsules thus observed, a mean of 18.5 eggs per capsule (range 8 - 27, standard deviation 4.8) was noted. Juveniles hatched after a mean of 21.5 days incubation (range 20-24, s.d. 0.8, n = 352), immediately before which the young animal could be seen rotating vigorously inside the transparent egg capsule. Smith (1967b), incubating egg masses from Barry Harbour at 12°C in full strength seawater, found hatching to occur 28 days after oviposition, slightly longer than those from the Humber. Newly hatched juveniles had a mean shell length of 0.19mm (range 0.17-0.22mm, s.d. 0.04mm, n = 352) and were quantitatively retained by a 76μ mesh sieve.

10viii Recruitment and growth

The young animals were recruited at a mean shell length of between 0.12 and 0.15mm and grew very rapidly during the following four months. The mean individual shell length quickly approached that of the younger of the two overwintering cohorts which was much more slow growing. By the start of the second period of recruitment in September, they had reached a mean size of 2.68 - 3.19mm and the two cohorts were separable only by a slight bimodality in the size/frequency distribution, being indistinguishable in appearance.

Recruitment to the autumn spawned cohort was higher than to the spring one at the two downshore stations (FIV4 and GIV3) and slightly lower at the midshore site, GIII4. A maximum density of newly hatched juveniles of 7360 m^{-2} was reached at GIV3, at an initial size of 0.12-0.16mm. These animals inreased rapidly in size until cessation of growth in November, when a mean size of between 0.35 and 1.13 had been reached, and the total population size distribution resembled that of March 1978. This would indicate that the younger animals at that time represented the autumn 1977 recruitment, and that the older animals were spawned in spring 1977. A similar population structure was found at FIV4 in January 1977 (Figure 10 xi), during sampling trials, indicating spring and autumn cohorts from 1976.

Ratcliffe (1979) found a seven-fold inrease in numbers at Skeffling between November and December 1973 and attributed this to gale-induced movements. Unfortunately, he did not describe the population structure of these animals but it would seem possible that the increase could also have been a result of an autumn recruitment. He also found recruitment between April and May 1974 after a heavy post gamete-release mortality. In autumn 1974 he found a very small inrease in numbers but this was followed by heavy mortality between July and August which was likely to have been a result of gamete release.

Smith (1967a) also found a small autumn recruitment in 1964 in the population of R. obtusa at Barry Harbour in South Wales. His growth data are presented in Figure 10xv. An autumn 1963 cohort is not, however, identifiable from the population structure described for spring 1964. The use of too large a mesh size (250µ) to collect newly hatched juveniles prevented the detection of the actual recruitment, but animals slightly over one millimetre in length were present by mid December. He recorded very high mortality of this autumn cohort during the winter and stated that they bred the following spring when only an average 1.7mm in length. In the Humber the corresponding animals did not breed in the spring but survived to the autumn to produce another autumn cohort.

The Barry Harbour population also differed from that in Spurn Bight in earlier spring recruitment - March/April in 1964 and 1965 as opposed to June in 1978 in the Humber. Presumably this was a result of milder spring conditions in this westerly facing locality. Smith also found growth of the spring cohort to be very rapid between actual recruitment and attainment of mesh retension size (0.15 to 1mm in two weeks), after which growth was very slow and continuous until the following spring when the breeding size of 3mm was reached. In the Humber, growth was much more rapid in the summer, attaining 3mm in four months and overwintering at breeding size.

Elliot (1979) also missed the actual period of autumn recruitment at Torry Bay by using too large a mesh size (500µ), but found that animals became recoverable from December onwards and, probably incorrectly, attributed this to continual winter recruitment. Evidence of autumn recruitment is visible in his data for 1975 and 1976 and these animals did not breed until late the following year when they reached full adult size.

From these studies, and the present one, it would seem likely that faculatative autumn breeding is quite common for R. obtusa and not purely a response to exceptionally favourable conditions as suggested by Smith (1967a), who considered it feasible that breeding is triggered by the presence of large densities of the prey species of R. obtusa, especially H. ulvae.

10ix Mortality and migration

Post spawning mortality was very high among the older animals between March and July 1978 by which time the spring 1977 cohort was extinct at all three sites. The autumn 1977 cohort declined at all three sites between March and April 1978 and continued to do so at FIV4 until June. At GIII4, however, there was a 136% increase between April and May which must have been a result of immigration of animals displaced from elsewhere in the Bight. The decrease in density at the other two stations must therefore not be considered entirely a result of mortality. Density of the autumn 1977 animals increased between June and July 1978 by 10% at FIV4 and by 25% at GIV3 whilst decreasing at GIII4 by 28%, again indicating migration between areas of the Bight.

Initial mortality/emigration of the spring 1978 cohort was very high during the month after recruitment, reaching 91% between June and July 1978 at GIV3. During later months reductions in density were much smaller.

Mortality was again very high amongst the autumn 1977/spring 1978 group between September and November 1978 during the autumn spawning period, reaching 84% between October and November 1978 at FIV4. It is assumed that this mortality was mainly of the autumn animals.

Post recruitment mortality/emigration of the autumn 1978 cohort varied between 23% and 92% between October and November 1978 and the numbers of these animals continued to fall throughout the following winter.

A massive decline in the population of all age groups occurred at both the Easington stations, between January and March 1979, particularly at GIII4 where there was a reduction in density of 96% of the autumn, and 86% of the spring 1978 cohorts. At FIV4, however, there was a 251% increase in numbers of the smaller animals and it is apparent that animals displaced from the midshore areas of the more easterly part of the Bight by the severe February gales were redeposited further west. This reflects the drainage pattern of this part of the Bight which floods from an easterly direction.

Other periods of migration between areas of the Bight of large numbers of *Retusa*, namely the increases in the autumn 1977 cohort between April and May 1978 at GIII4 and between June and July at FIV4 and GIII4, cannot be attributed to extremes of wind and tide and it would seem that passive migration of *R. obtusa* is commonplace in the Humber. Ratcliffe (1979) found a 600% increase in density at his Skeffling site following severe gales in early December 1973.

Population redistribution during the winter has been recorded from the Severn estuary by Little & Boyden (1976) who found *R. obtusa* to extend its range upshore in the winter. Upshore migration was not observed in this study and the species was not found to have extended to FI2 and FII2 after the gales. Smidt (1944) also found changes in the distribution of *R. obtusa* following the 1941/42 winter in the Danish Waddensea. Elliot (1979) recorded small *Retusa* transported by wave movements in Torry Bay although he did not observe significant population changes as a result of migration.

There are few reports of predation on *R. obtusa* by higher predators. Smidt (1951) and Wolff et al. (1981) found the species in the gut of plaice, *Pleuronectes platessa*, in the Dutch Waddensea and Oosterscheldte estuary. Smidt stated that *R. obtusa*, where present, is a favourite food. Summers (1980) found it forming a minor part of the diet of flounder, *Platichthys flesus*, as did Wolff et al. (op. cit.).

Rooth (1964) included *R. obtusa* among the important food items of waders in the Dutch Waddensea and Elliot (1979) indicated *R. obtusa* in the diet of dunlin, *Calidris alpina*, in Torry Bay in the Firth of Forth. No quantification of the predation on *R. obtusa* has been carried out to date. It is, therefore, highly likely that R. obtusa provides a small resource both for the waders and demersal fish using the Spurn Bight mudflats mainly during the summer months when biomass, production and elimination are at their highest. Size specific mortality of larger Retusa in the winter indicates that they are also being taken at that time but elimination is so low that they cannot be a significant food resource.

10x Biomass

All biomass figures were calculated from a single shell height/flesh weight regression (Figure 10xix), produced by weighing animals from a large bucketfull of surface mud collected from GIV3 in May 1977. Any seasonal variation in shell height/flesh weight relationship was consequently not taken into account in the year long survey. Elliot (1979) found no significant change in shell weight:flesh ratio with time over a whole year.

A regression equation was found to be:-

dry flesh weight = 0.228 x shell height$^{3.399}$ $r = 0.97$ $n = 1125$

Observed and idealized mean individual weights of each size category are given in Table 10d and these were used in all biomass calculations.

Monthly variation in the total population biomass and distribution of biomass between cohorts at each of the three sites is given in Table 10e and illustrated in Figures 10xx to 10xxv.

A sharp maximum in biomass was found at all three sites - during September at GIV3 and in October at the other two. A maximum of 1147 mg m^{-2} was recorded at GIV3 in September 1978 against a previously recorded maximum of 382 mg m^{-2} by Elliot (1979) in Torry Bay. Mean monthly biomass values varied between 0.23 - 0.54 gm m^{-2}, representing a maximum of 1.1% of the mean monthly total community biomass at site FIV4 (ref. Chapter 11). At each site the biomass maximum was a result mainly of pre-spawning growth of the autumn 1977 cohort and the rapid decline in total biomass between October and November a result of post-breeding mortality of these animals.

The pattern of variation in biomass contrasted sharply between station GIII4 and the other two. Total biomass at FIV4 and GIV3 increased at an approximately constant rate between March and September/October 1978, accelerating during periods of immigration, whereas at GIII4, emigration (and possibly mortality), between June and August produced a fall in biomass until August whereafter growth of the remaining animals again produced an increase up to the maximum in October.

Mean annual biomass figures are included in Table 10e with a maximum value of 543 mg m^{-2} at GIV3 and average between the three stations of 361 mg m^{-2}.

10xi Production, elimination and productivity

Mean monthly and annual production and elimination values are given in Table 10f and productivity values ($\Sigma P:\bar{B}$ ratio and $\Sigma E:\bar{B}$ ratio), in Table 10g. Variation in production, elimination and productivity are illustrated in Figures 10xxvi to 10xxxvii.

Total production was highest at all three sites between September and October 1978, mainly resulting from pre-spawning growth of the combined autumn 1977/spring 1978 group. Before this, total production at FIV4 and GIII4 rose steadily from March 1978 onwards, but fell between May and August at GIII4 as a result of emigration. Production of the autumn 1978 cohort reached its maximum between October and November 1978, slightly later than the old combined autumn 1977/spring 1978 group which suffered heavy post-spawning mortality in October.

Similarly, elimination peaked during the late summer/early autumn, coinciding with post-spawning mortality of these animals giving rise to the autumn cohort. Elimination at all other times was relatively negligible and very little organic material would be available to predators from this species during the winter.

Productivity of the autumn 1977 cohort was highest in the early spring, between March and April 1978 and remained stable throughout the summer, increasing just prior to spawning in September and declining through mortality, very rapidly afterwards. The sharp decline in productivity at GIII4 during the summer was again a result of emigration.

Productivity of the newly recruited spring and autumn cohorts of 1978 began very high, reaching a maximum $\Sigma P:\bar{B}$ ratio of 2.4 at GIV3 between June and

July, but declined rapidly in both cohorts at all three sites. At GIV3 the production of the spring 1978 cohort re-accelerated after an initial steep decline to reach a second peak ({P:$\bar{B}$ of 1.6) between August and September. This resulted from a much lower mortality between these months than between July and August, rather than an increase in growth rate.

Production and productivity became negative between certain monthly samples at all three sites during the 1978-79 winter. As all biomass figures were calculated from a single regression equation, negative figures must therefore represent size dependent mortality of larger individuals or sampling error of the population at low densities. Size-selected mortality of larger individuals is more likely to result from predation than erosion from the sediment, which would more than likely remove the smaller, more easily transported, individuals.

Total annual production and productivity was highest at GIV3 producing 2681 mg m^{-2} dry flesh weight with a {P:$\bar{B}$ ratio of 4.97. A mean total production of 1726 mg m^{-2} and {P:$\bar{B}$ ratio of 4.75 was found between the three stations.

Total elimination was similarly highest at station GIV3, a total of 2741 mg m^{-2} organic material lost from the population. {E:$\bar{B}$ ratio was highest at station GIII4 at 5.31, however, reflecting the higher mortality rate at that station as noted with other species. Mean total elimination of 1764 mg m^{-2} and {E:$\bar{B}$ ratio of 4.89 was found between the three stations. *R. obtusa* was found to contribute between 3.0 - 5.9% of total measured community production and 2.6 - 3.4% of total community elimination (Chapter 11).

Production and productivity of *R. obtusa* has only previously been investigated by Elliot (1979), who found a maximum production of 774 mg ash free dry weight m^{-2} (average 158 mg a.f.d.w. m^{-2}) and a {P:$\bar{B}$ ratio of 3.45. The {P:$\bar{B}$ ratio of 4.747 recorded here is quite high but within the range of 0.2 - 5.8 tabulated from other molluscan studies by Greze (1978). This high value is likely to result from the short life cycle of the species. Zaika (1973) found a negative correlation between productivity and life-span for all groups of invertebrates, explained by the fact that the growth rate of younger, smaller animals is invariably higher than older, larger animals.

10xii *Food relations*

R. obtusa was first described as a predator of the prosobranch *Hydrobia ulvae* by Jeffreys (1867) and subsequently by Smidt (1951), Smith (1967a), Muus (1967), Rasmussen (1973) and Elliot (1979). Muus suggested that large populations of *R. obtusa* considerably influence the mortality of *Hydrobia* although Elliot considered the opisthobranch to be a minor predator of *H. ulvae* in Torry Bay when compared with vertebrate predators. Although Smith (1967a) found that in the laboratory, *R. obtusa* was unable to capture uninjured *Hydrobia*, wild caught specimens were found to contain small snails in the crop. Elliot (1979) recorded 4.5mm *Retusa* with 2.5mm *Hydrobia* in the crop, such that the predator was unable to withdraw into its shell. Both authors were in agreement, however, that smaller *Retusa* are unable to take *Hydrobia*.

Predation of foraminifera by *Retusa* has been recorded by a number of authors (Pruvôt-Fol; 1954, Bacescu & Caraion; 1956, Morton; 1958, Moore; 1961, Hurst; 1965, Marcus & Marcus; 1969, Rudman; 1971, Burn & Bell; 1974) and Elliot (1979) suggested that these protozoans are likely to form the food of smaller *Retusa*.

Other organisms found in the diet of *R. obtusa* include copepods, bivalve spat, rissoid snails, juvenile *Retusa* (Hurst; 1965) and the egg cocoons of turbellaria (Rasmussen; 1973). Other species of *Retusa* are known to be predatory on prosobranchs and/or foraminifera (Burn & Bell; 1974). Ratcliffe (1979) noted the dissimilar distributions of *H. ulvae* and *R. obtusa* at Skeffling, a feature that was also noted in this study (Table 4a), and suggested that sedentary polychaetes such as *Pygospio* may be important in the diet.

No specimens of *R. obtusa* were found in this study to contain *Hydrobia* laboratory feeding trials were set up to ascertain the likely feeding relations in the Humber. Adult and juvenile *Retusa* and suitable prey species were collected from surface mud near to station GIII4 in April 1979. Pots containing ten adults (>3.5mm in shell length) or ten juveniles (<1.5mm) and 20 potential prey items in 25l seawater over a silt substratum (filtered to

40μ to remove meiofauna) were kept between 10 and 13°C for one week and the survival of the prey species recorded. Identical control pots containing prey items only were kept simulataneously to record survivorship in the absence of R. obtusa. Results are recorded in Table 10h.

From the results it is obvious that, at least under laboratory conditions, H. ulvae is not a favourite food item of the Humber Retusa and that the prey items taken most frequently by adults are juvenile Macoma up to 1.5mm in shell length, juvenile Retusa and foraminifera, although failure to recover all foram specimens from the control throws doubt on that particular result. Juvenile Retusa possibly took small numbers of forams and the disappearence of small numbers of nematodes, Hediste and Pygospio cannot be attributed to predation as these soft bodied animals decay rapidly after death and would thereafter not be recoverable in the event of mortality not resulting from predation.

The experiment was repeated using smaller forams to try and confirm the feeding of younger Retusa on these animals, but recovery of the controls was insufficently reliable to make conclusions regarding the disappearence of forams in pots containing Retusa.

Ratcliffe et al. (1981) repeated this experiment with M. balthica spat and found that two adult R. obtusa consumed an average of 3.6 spat during a 96 hour period.

It would seem from these results that larger Retusa are able to prey on any suitable sized sedentary or slow moving calcareous shelled organisms, including smaller Retusa and they will not take soft bodied or active organisms. Mobile prosobranchs seem to be too active for Retusa to overpower under these conditions, although feeding on such snails is known to occur in nature (see above), No author has recorded observing the actual act of ingesting a snail and it may be that only incapacitated snails are taken.

At such high densities as are found on the Spurn Bight mudflats R. obtusa must be an important predator, particularly of benthic forams and Macoma spat. Assuming an ecological efficiency of between 5:1 and 10:1 (Slobodkin; 1960), the production of 2.68 grammes dry flesh weight of R. obtusa per m^2 at

GIV3 must represent a consumption of between 13.4 and 26.8 grammes of food organisms per m^{-2} and this species is therefore an important link in the food web of the sand/silt regions of the Bight.

Summary of Chapter 10

A summary of previous literature referring to *Retusa obtusa* (Montagu) is given and the ecological pre-requisites of the species are discussed. The distribution in relation to environmental variables of the species is described over the whole of Spurn Bight and it was found to be most numerous in midshore sandy muds.

The numerical abundance, recruitment, growth rate, mortality, biomass, production, elimination and productivity are described from two sites at Easington and one site at Skeffling.

A maximum density of 7740 individuals m^{-2} was found which is considerably higher than previously recorded for the species.

The population structure of the species is described and shown to consist of separate, but reproductively interconnected, spring and autumn recruited cohorts. A speculative model of the reproductive cycle of the species is proposed which is compatible with the population structure observed in previous studies. Observations on egg number and development in the laboratory are recorded.

Migration of individuals both into and out of the study area are recorded and therefore caution is advised on interpretation of mortality and production statistics.

A maximum mean monthly biomass of 543 mg m^{-2} is recorded with a maximum production of 2681 mg m^{-2} and $\Sigma P:\bar{B}$ ratio of 4.94 and $\Sigma E:\bar{B}$ ratio of 5.31.

Finally the food relations of *R. obtusa* in the Humber are discussed in light of evidence from feeding experiments. The species is likely to be a significant predator on benthic forams and *Macoma* spat but an insignificant resource for the waders and demersal fish using the Bight, mainly in the summer.

CHAPTER ELEVEN

CHAPTER 11

SYNTHESIS, DISCUSSION AND CONCLUSION

11i Total biomass, production and elimination - intensive studies

From the preceding chapters, a picture of the total biomass and productivity of the macrobenthos at the five intensive survey sites can be put together from studies on individual species (Tables 11a - 11f, Figs 11i - 11v), and the contribution of each species determined as a proportion of the whole. It must be noted that estimates have not been made of the biomass and productivity of Cerastoderma edule at any site other than GIV3 and no estimates were made for Arenicola marina and Mya arenaria, nor for the meiofauna. The inclusion of these would probably increase greatly the total values and at the same time reduce the proportional contribution by the individual species as described below.

Maximum estimates were : biomass - 60.9 gm dry flesh weight per m^2, production - 45.4 gm m^{-2}, elimination - 73.3 gm m^{-2}, all at station GIV3. By far the largest proportion was of Macoma balthica at midshore stations, where between 45 and 85% of the total was attributable to this species, although Nephtys hombergi was found to contribute 35% of total production at station FIV4. The biomass and productivity at the two upper shore stations was dominated by Hediste diversicolor, with a maximum of 87.5% of total production at station FI2.

11ii Extrapolation to communities and the whole area

There are obvious disadvantages in combining the results of a single, year-long survey with the results of a single extensive survey carried out in a preceding year in order to make generalizations about the fauna of such an extensive area as Spurn Bight. Long term population variability (c.f Boesch et al.; 1976, Whitlach; 1977, Beukema et al.; 1978, Price & Warwick; 1980 etc) is not taken into account, nor are the differences between successive years resulting from changes in population structure, climate etc. Boesch et al. and Whitlach (op. cit.) both specifically argue against the application of short term studies as useful indicators of likely impact assessments.

Climatically, the study period was found to be atypical of the preceding decade (Beukema et al.; 1978, Beukema; 1979) and mass mortality of the less cold-tolerant species led to excessive elimination of certain species when compared with their productivity. Furthermore, the variability of conditions within Spurn Bight, leading to considerable differences in productivity between sites, are not adequately compensated for by only five intensive study sites divided between three different biomes. For example, the great differences between stations GIII4 and FIV4, with initially similar environmental conditions probably resulted from considerable differences in erosion and deposition regimes at the two sites, indicating net sediment transport, along with some the infauna, from east to west during extreme weather conditions.

Nevertheless, such a combination of data was carried out to give a very gross approximation of the invertebrate dynamics of the whole of the area in question. This should be interpretted with the above reservations in mind.

Mean total production : May biomass ratios were applied to S.P.S.S. derived community parameters (ref. chapter 2, section 2ixc and chapter 4) to give estimates of production based on the extensive survey data. The results are presented in Table 11g and give some indication of the macroinvertebrate resource offerd by these mudflats to potential predators - i.e. migratory crustaceans, fish and birds.

Mean May biomass of the various subcommunities of the flats were found to vary from 6.0 gm m^{-2} in downshore SAND communities, to 33.6 gm m^{-2} in MIDMUD sandy silts. Production and elimination (Table 11j) were found to be highest in TOPSILT and Spartina zone communities, at 57.5 gm m^{-2} production in TOPSILT and 57.6 gm m-2 elimination in the Spartina, owing to the apparently very high productivity of the population of H. diversicolor (however refer chapter 7, section 7x). Production and elimination were estimated to be lowest in SAND communities at 4.1 and 7.3 gm m^{-2}.respectively.

These total values are very high when compared with similar Macoma communities that have been studied elsewhere, especially noting that the contribution by certain species is not included in the estimates (above). Comparable studies are few in number (Table 11g) and support the observation by Ratcliffe (1979), that the mean biomass and production of the benthos of Spurn Bight mudflats are considerably in excess of findings for similar communities elsewhere. Higher values have been found in communities dominated by *Mytilus* by Wolff et al. (1975) in the Grevelingen estuary in the Netherlands ($\bar{B}^{max}$ = 173 gm m^{-2}, P^{max} = 253 gm m^{-2}) and by *Cerastoderma* and *Mercenaria* by Hibbert (1976) on Hamble Spit in Southampton Water ($\bar{B}^{max}$ = 190 gm m^{-2}, P^{max} = 220 gm m^{-2}).

Extrapolating further to the whole area of the flats assumed to be represented by each community type (Chapter 2, section 2ixc, Table 2a), the whole resource offered by those species for which dynamics were estimated was calculated to be 749 tonnes dry flesh weight of standing crop biomass, a production of 927 tonnes and elimination of 1093 tonnes, mainly of *M. balthica* and with significant contributions by *C. edule*, *N. hombergi* and *H. diversicolor* (Tables 11h and 11j).

It is possible thus to identify those areas of the mudflats of Spurn Bight which support the highest standing crop biomass and give rise to the highest production and, therefore, offer the greatest potential resource to the consumers. Upper and middle shore sediments in total represent 93.7% of the total standing crop biomass of the flats and 96.5% of their estimated secondary production, while downshore sands, although extensive in area, contribute only 6.2% and 3.5% of the total biomass and production respectively.

11iii Utilization of the resource by the avifauna

Using data from Tasker & Milsom (1979), and the trophic equations of Wolff et al. (1976) and Evans et al. (1979), an assessment of the total predation pressure of all birds using the North Bank of the outer estuary is possible (Table 11k). This gives a total consumption of 32.65 tonnes of food over the study period mid-March 1978 - mid-March 1979. Making the rather tentative assumption that feeding activities are spread proportionally by area between Spurn Bight, Cherry Cob Sand and Paull Foreshore, the areas investigated by Tasker & Milsom, a total consumption in Spurn Bight of 23.24 tonnes or 0.76 gm m^{-2} over the whole area can be calculated.

Condensing the feeding area maps of Tasker & Milsom into one map (Fig 11vi, reproduced from Jones & Key;/ in press), however, shows that the feeding pressure is likely to be considerably greater in near and midshore sediments and on the Old Den than on the outer sandflats - i.e. the birds were concentrating on areas of highest prey availability.

It would seem, therefore, from the above calculations (despite the liberal scatter of assumptions and estimations) that only a small fraction of the total production of the invertebrate resourceis being utilised by the overwintering birds. Goss-Custard (1976) has, however, pointed out that measures of food abundance over a certain density is inappropriate as an estimate of the bird carrying capacity of an estuarine area as spatial and seasonal variations in the invertebrate prey and social interactions between birds play an important role in determining the feeding patterns of the birds. It may, therefore, not be the case that the invertebrate resource of the mudflats is being under-utilised by the birds as might seem to be the natural conclusion from measurement of the gross size of the resource. The estimate made of total elimination by the invertebrates is, moreover, not easily broken down into fractions available to the avifauna, migratory fish and crustaceans as well as that entering the decomposer cycle, or that lost to the mudflats through erosion and transport into the main body of the estuary or onto the strandline.

If the variables described by Goss-Custard (above) are not, however, limiting the feeding distribution of the birds in Spurn Bight, it would seem that the mudflats would be able to support larger numbers of birds displaced from other estuarine systems should any of the proposals outlined in the introduction to this thesis come about.

11iv Impact assessment

The above has considerable implications for assessment of the likely impact of the proposed infill of the mudflats. Obviously, total reclamation would cause loss of the whole resource. Partial infill schemes have, however, been considered (see introduction), and it would be most logical that these would reclaim the upper and middle shore areas of the Bight, those areas found to offer the greatest resource and found to be most used by the overwintering birds. It is unknown whether a similar upper and middle shore productive community would develop outside an infill barrier, or whether they would remain as low biomass hard sands as at present. The sediment regime would change as a result of reclamation but the liklihood of conditions favourable to the building up of extensive silt deposits is low (Anderson; 1972) and the area of such deposits would necessarily be low. Such considerations might usefully be considered an integral part of any engineering proposals for the area.

Implications are similar for the likely effects of a breach of the Spurn Peninsula by the sea at the Narrows. Flooding from the north, a proportion of the incoming tide would be expected to enter the Humber through the breach, leading to considerable erosion of sediment in the Bight as has been recorded in previous breaches of earlier peninsulae (de Boer; 1964). The sediments most likely to be affected are those of the upper and middle shore of the eastern half of the Bight because (a) they are composed of very fine materials and therefore liable to erosion, and (b) they are likely to be directly in the path of such a flood tide.

11v In conclusion.

This study, together with that of Ratcliffe (1979), has identified the invertebrate fauna of Spurn Bight mudflats as the most productive example of this type of community so far investigated in northern temperate waters. Several species :- M. balthica, N. hombergi, R. obtusa and E. longa have been found at higher densities and biomass than ever recorded elsewhere and the study has also identified certain areas where further research is necessary for a more complete understanding of the dynamics of the whole region. Certain species, notably H. ulvae, M. arenaria and A. marina proved too variable in occurrance or were present at too low densities of very large individuals to give a reasonable estimate of biomass and productivity with the methods used and would be worthy of further investigation, as would the synecology of the Old Den and the autecology of those species found to 'perform' exceptionally well in this area.

Spurn Bight cannot with justification be considered in isolation of the rest of the outer Humber flats and the study area for future work might sensibly be extended to encompass the potentially very large invertebrate resource of the South Bank sandflats and the mudflats of the Cherry Cob Sand region.

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THE UNIVERSITY OF HULL

Ecology of the infauna of Spurn Bight mudflats : an area proposed for reclamation.

Volume II

being a Thesis for the Degree of

Doctor of Philosophy

in the University of Hull

by

Roger Stephen Key B.Sc. (Hons Zoology) Nottingham University

September 1983

PLATES

Plates 1 - 4 False colour I.R. photographs of Spurn Bight Mudflats, taken by University Air Squadron, Finningly, on 3rd June 1977.

Plate 1 Sunk Island Sands and Hawkin's Point from the east (red lines are scratches on film).

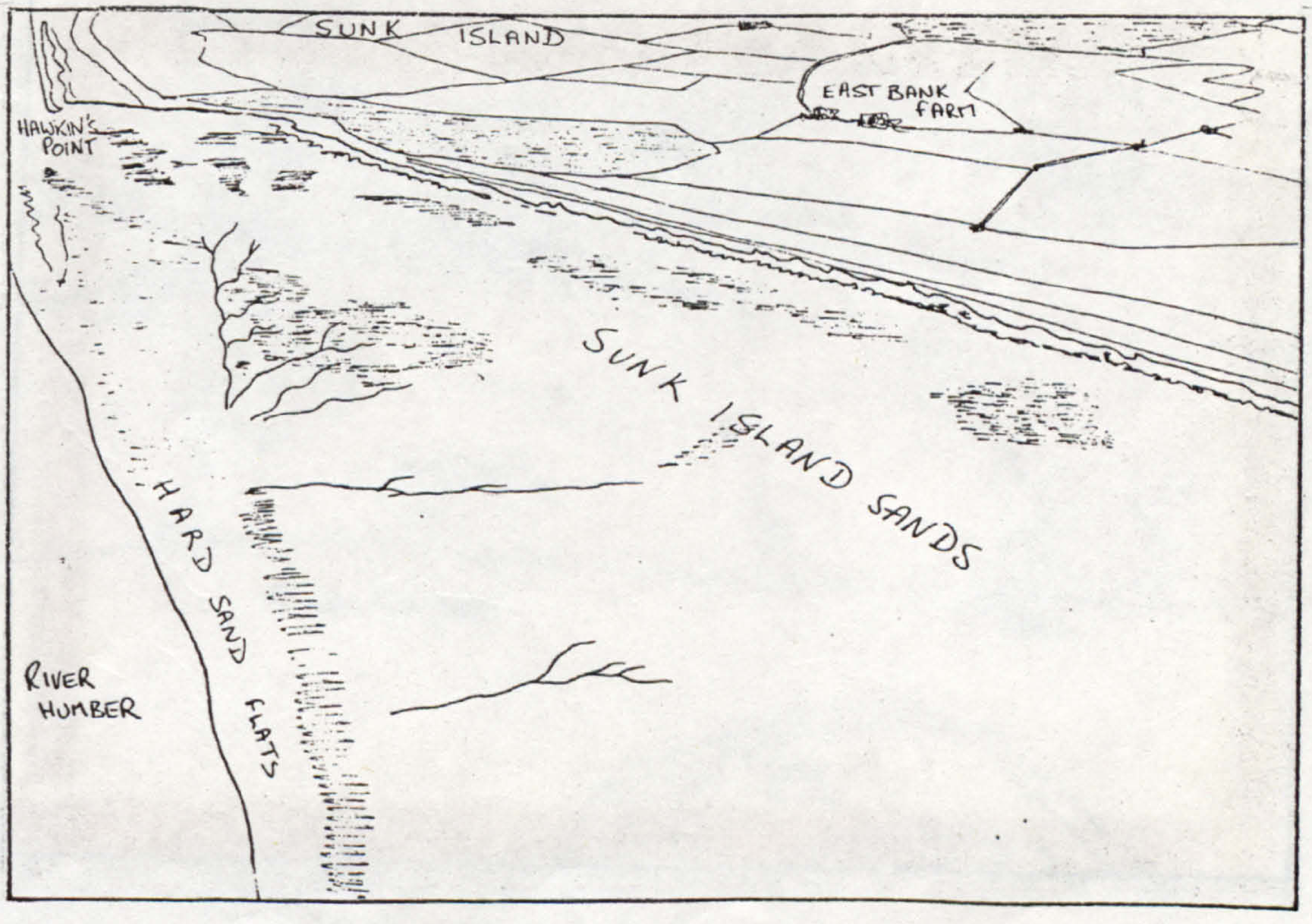


Plate 2 Spurn Bight from due south of Weeton showing whole length of Patrington Channel.

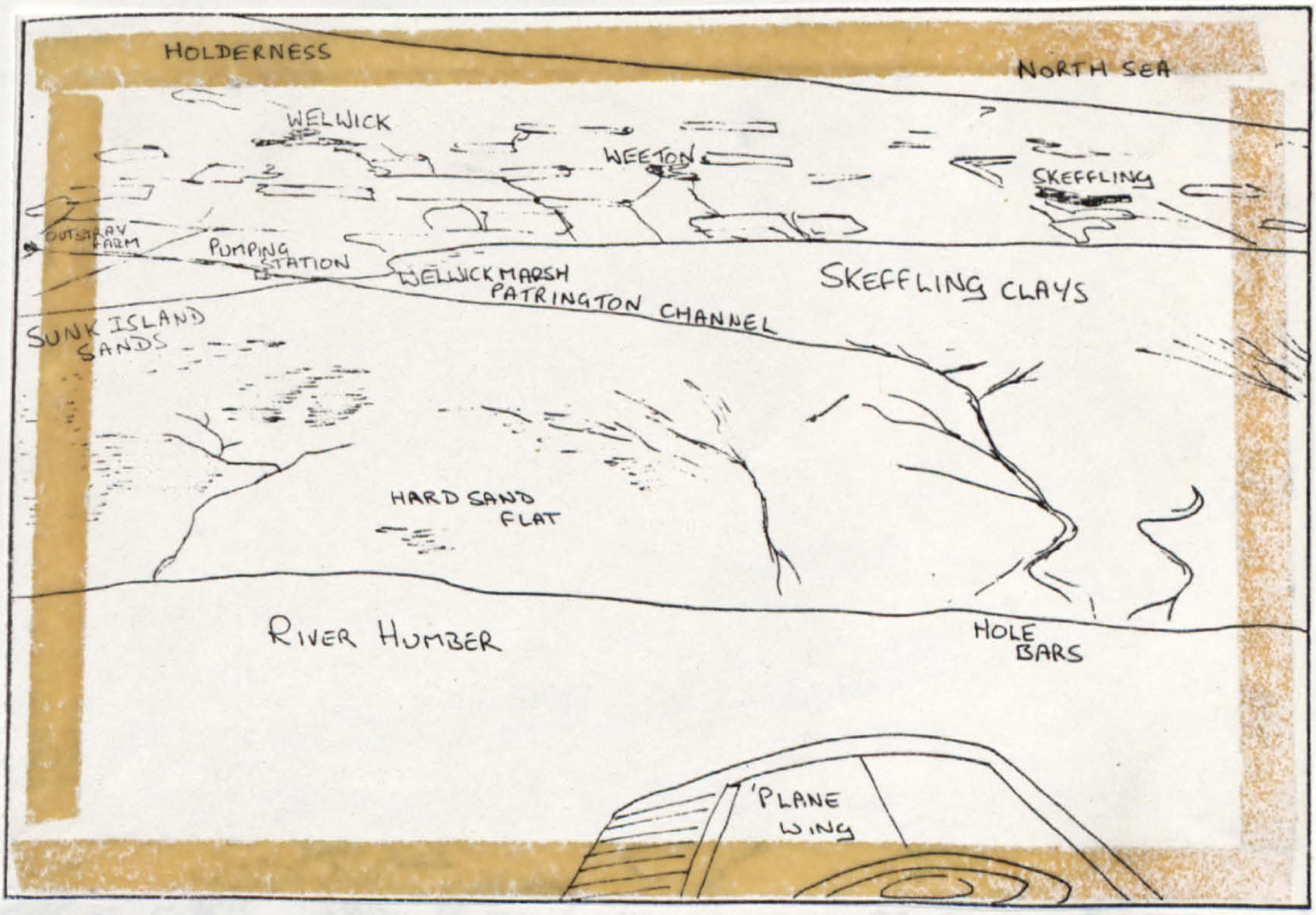


Plate 3 Kilnsea Clays and Spurn Peninsula taken from south east. Note Zostera noltii and Spartina marsh parallel to peninsula.

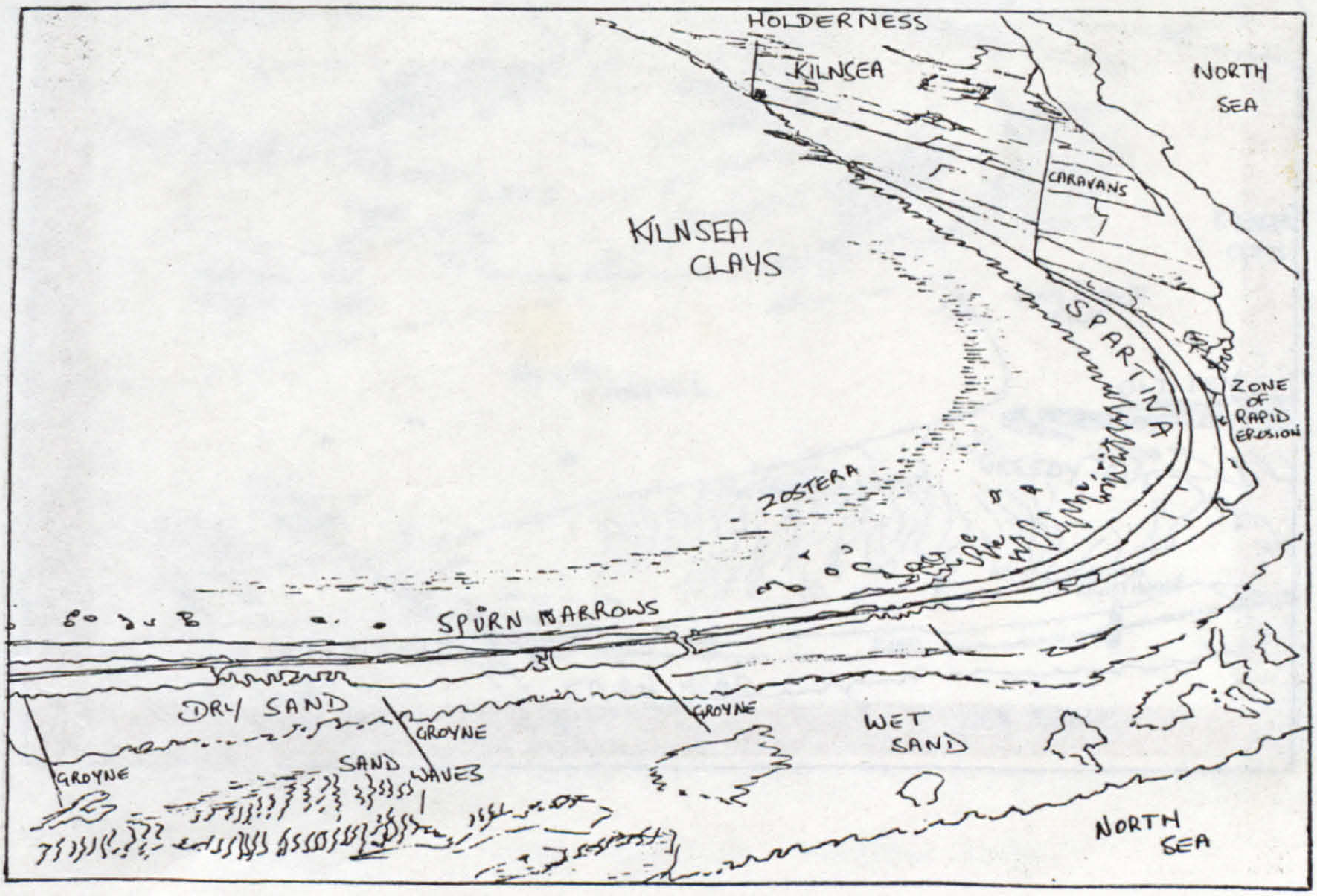


Plate 4 Spurn Point and Spurn Bight from east south east.

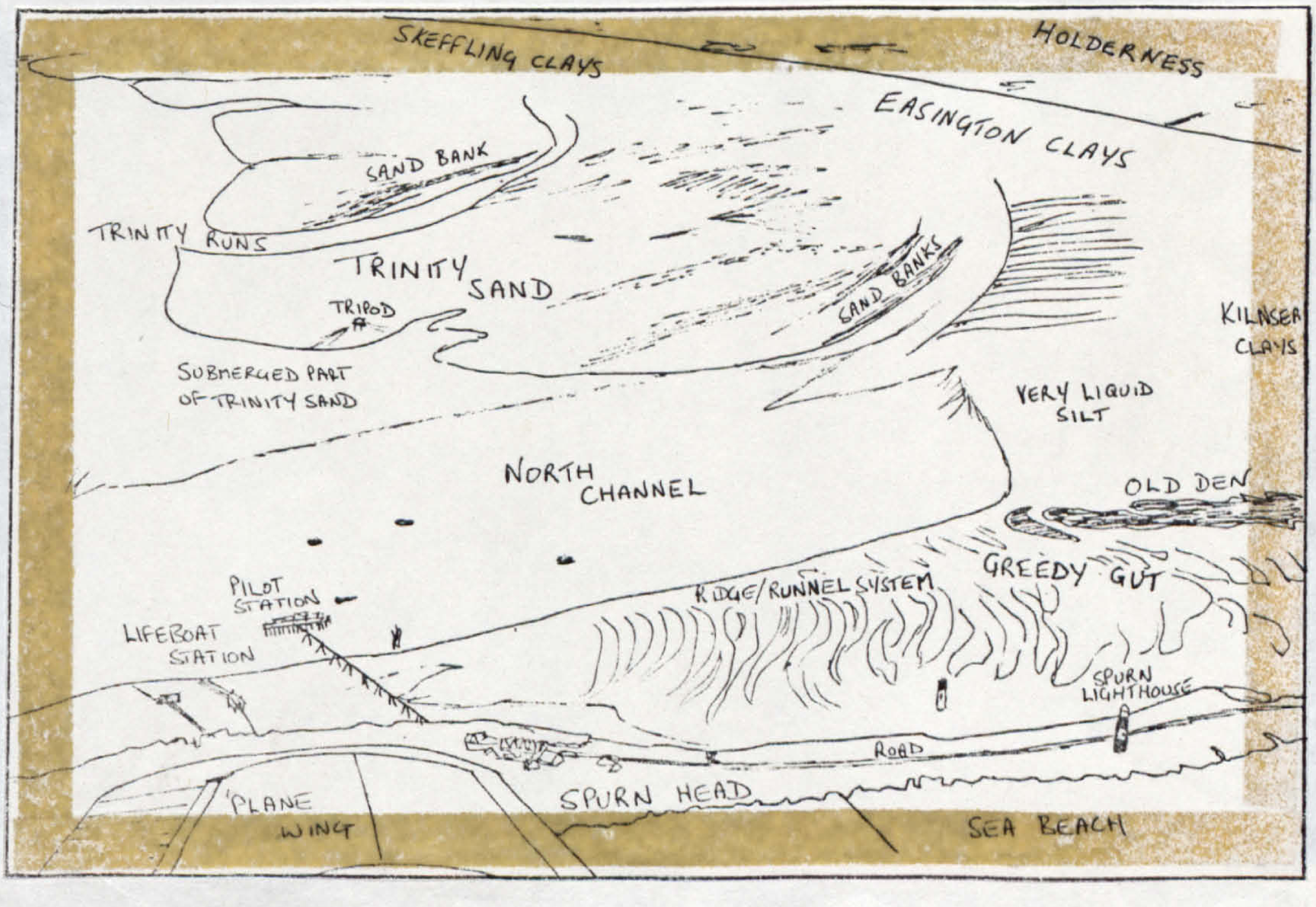


Plate 5 Upper shore of Spurn Bight at Easington. Note coarse sand 'beach' with strandline and extensive Spartina. November 1976.

Plate 6 Advancing Spartina at Welwick Saltmarsh. November 1976.

Plate 7 Dendritic drainage channels in midshore sediments. Close to station CIII5. May 1977.

Plate 8 Gullied mud in midshore sediments. Station CIV3 May 1977. On skyline are Grimsby hydraulic tower (to left) and chimney of British Titan works (right).

Plate 9 Hard, downshore sandflats. Easington station GV6. May 1977.

Plate 10 Shingle of the Old Den. May 1977.

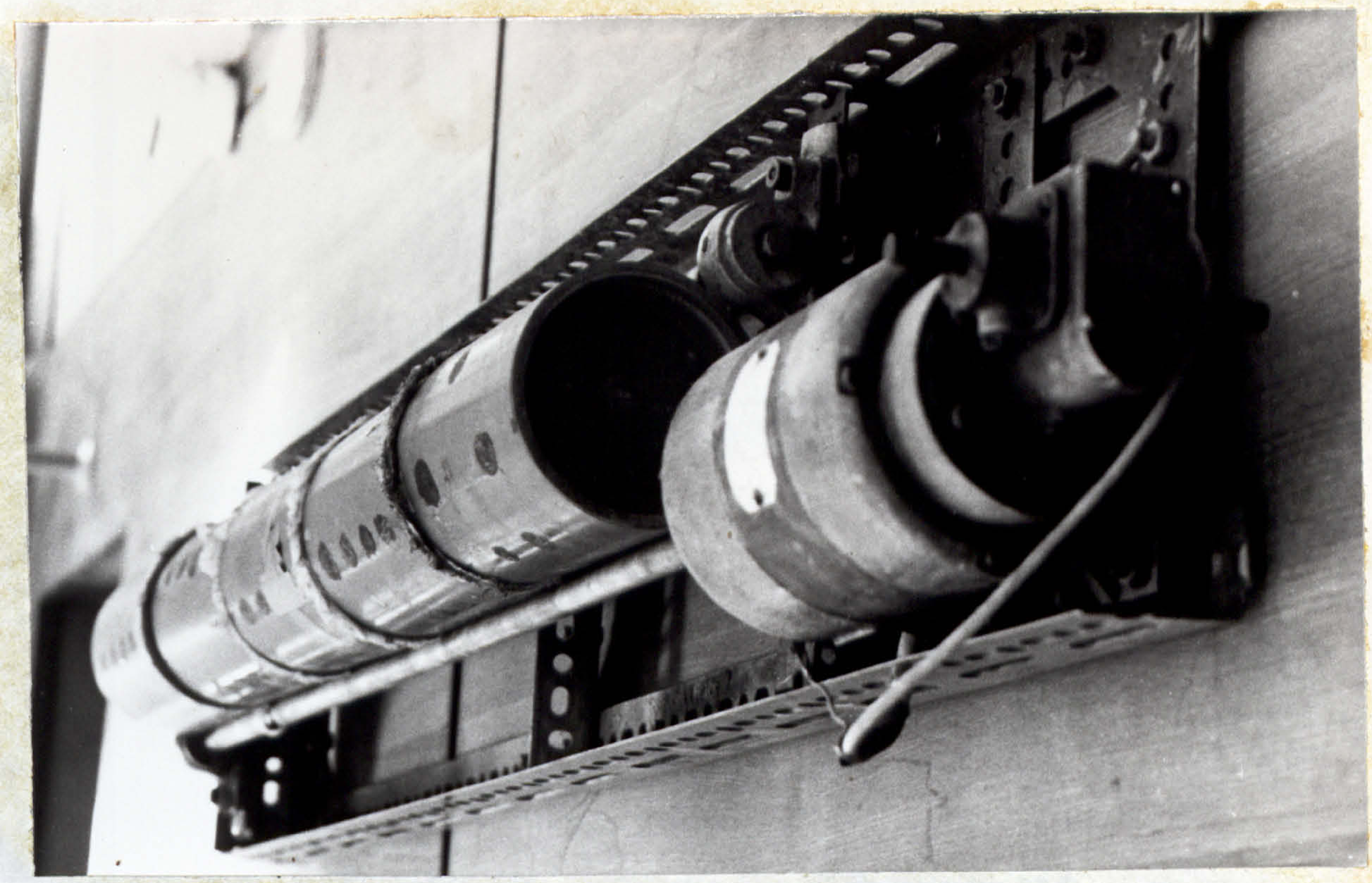


Plate 11 Mud dispersing apparatus based on 'Gemtek' tumble polisher.

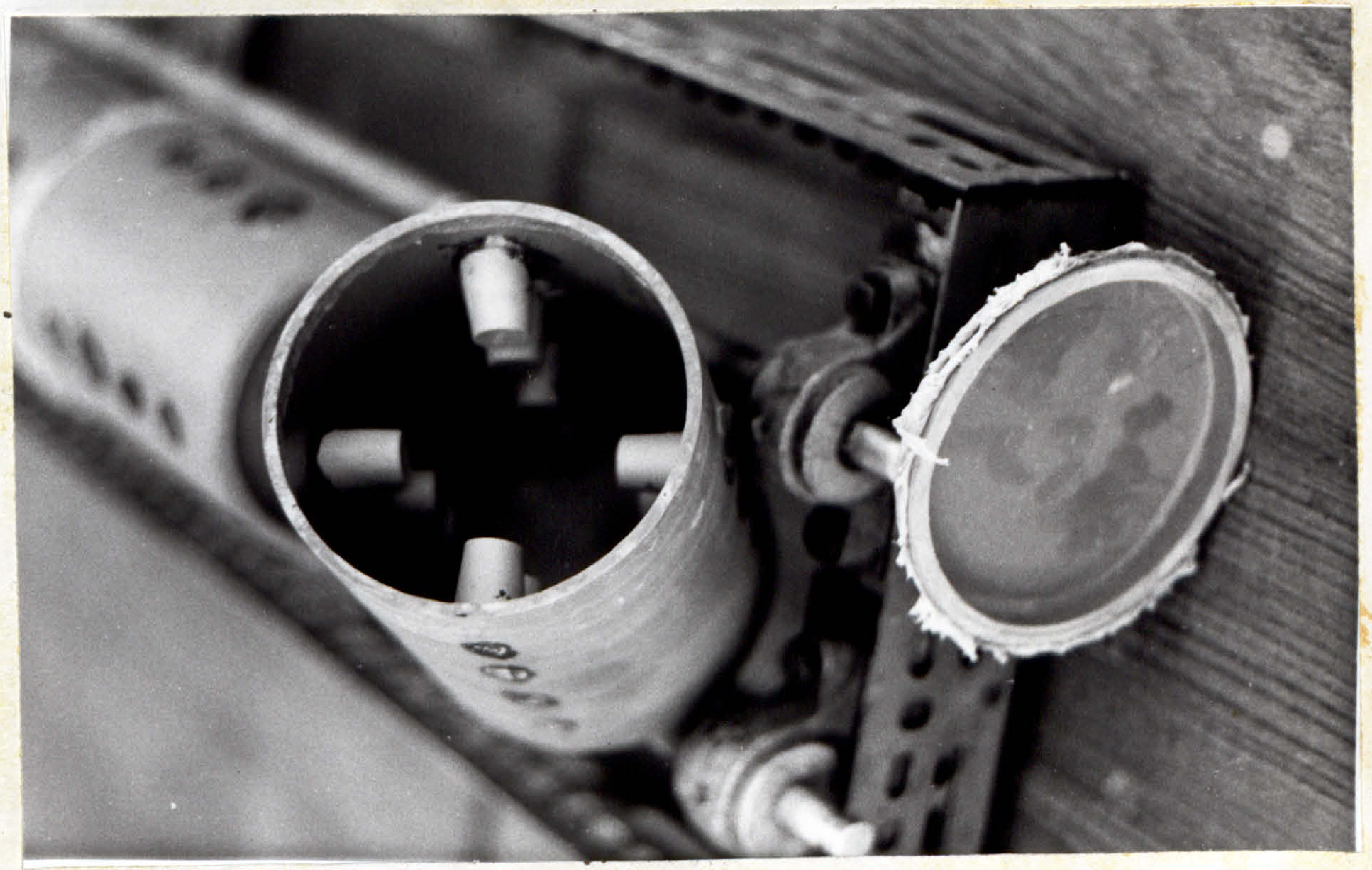


Plate 12 Interior of 'Gemtek' barrel showing arrangement of baffle bungs.

Plate 13 Nekton sampler trap in drainage gully.

TABLES

Table 2a Total area of different sediment types in Spurn Bight[1] and the rest of the Humber tidal flats[2].

Sediment/region	Area (Ha)
SPURN BIGHT	
Spartina marsh	91
saltmarsh (Welwick & Outstray Marsh)	37
flat silt at top of shore (TOPSILT)	332
flat sandy silt (MIDMUD)	558
runnelled sandy silt (MIDMUD)	1189
fluid silt west of Old Den	63
shingle (Old Den)	21
downshore sand (SAND)	721
beach sand at Spurn (SAND)	65
TOTAL SPURN BIGHT	3077
sand flats Donna Nook - Grimsby	2332
remaining intertidal flats S. bank[3]	1833
remaining intertidal flats N. bank	1847
TOTAL HUMBER	9089

[1] calculated planimetrically from figure 2iii

[2] calculated planimetrically from 1:50,000 O.S. map

[3] including Whitton Middle, Pudding Pie and Redcliffe Middle shoals.

Table 2b Sampling Procedure.

Core size	10 x 10 x 20cm deep		4cm diameter x 10cm deep	
number	50 (10cm deep) (10 pooled lots of 5)	5 - 10	5	5
sites	GIII4	all	all	all
sieved to	1/8"	275µ	76µ	
purpose	enumeration large *Cerastoderma*	all macrofauna	spat and meiofauna (extensive only)	sediment analysis

Table 3a Correlation matrices of abiotic environmental variables. Upper figures:- Kendall's non parametric correlation coefficient, lower figures, probability. N.S. = not significant.

	∅Median	∅Sorting	∅Skewness	∅Kurtosis	% Sand	% Silt	% Clay	% Org. Matter	% Iron	% Water	Salinity	Tidal Position
∅ Median		0.80 0.001	0.21 N.S.	0.30 N.S.	0.97 0.001	0.94 0.001	0.91 0.001	0.87 0.001	0.81 0.001	-	0.14 N.S.	0.28 N.S.
∅ Sorting	0.82 0.05		0.31 N.S.	0.04 N.S.	0.95 0.001	0.89 0.001	0.81 0.001	0.93 0.001	0.87 0.001	-	0.21 N.S.	0.31 N.S.
∅Skewness	0.15 N.S.	0.03 N.S.		0.13 N.S.	0.17 N.S.	0.20 N.S.	0.04 N.S.	0.04 N.S.	0.01 N.S.	-	0.02 N.S.	0.13 N.S.
∅ Kurtosis	0.21 N.S.	0.20 N.S.	0.03 N.S.		0.02 N.S.	0.05 N.S.	0.01 N.S.	0.07 N.S.	0.05 N.S.	-	0.003 N.S.	0.04 N.S.
% Sand	0.98 0.001	0.97 0.001	0.02 N.S.	0.04 N.S.		0.81 0.001	0.79 0.001	0.80 0.001	0.79 0.001	-	0.14 N.S.	0.69 0.004
% Silt	0.95 0.001	0.95 0.001	0.10 N.S.	0.11 N.S.	0.77 0.001		0.92 0.001	0.97 0.001	0.84 0.001	-	0.21 N.S.	0.37 0.01
% Clay	0.67 0.05	0.63 0.05	0.09 N.S.	0.10 N.S.	0.80 0.001	0.77 0.001		0.96 0.001	0.93 0.001	-	0.03 N.S.	0.71 0.002
% Organic matter	0.98 0.001	0.71 0.09	0.11 N.S.	0.09 N.S.	0.81 0.001	0.97 0.001	0.98 0.001		0.96 0.001	-	0.14 N.S.	0.41 0.009
% Iron	-	-	-	-	-	-	-	-		-	0.03 N.S.	0.66 0.004
% Water	0.94 0.001	0.86 0.001	0.21 N.S.	0.14 N.S.	0.91 0.001	0.83 0.001	0.97 0.001	0.91 0.001	-		-	-
Salinity	0.08 N.S.	0.13 N.S.	0.23 N.S.	0.03 N.S.	0.04 N.S.	0.10 N.S.	0.14 N.S.	0.04 N.S.	-	0.12 N.S.		0.03 N.S.

Extensive survey May/June 1977

Intensive survey March 1978 - March 1979

Table 3b Downshore distance and relative tidal height (as percentage of total downshore distance) of sampling sites of extensive survey.

Station Number	Distance (m)	Percentage Total	Station Number	Distance (m)	Percentage Total
AIII2	70	50	GIII4	500	16
BI2	190	50	GIV3	800	35
CI2	150	14	GV6	1600	66
CII4	460	26	HI2	160	5
CIII5	760	40	HIII5	530	28
CIV3	1220	60	HIV4	1060	52
CV6	1820	94	JI3	15	5
DI3	190	8	JIII6	570	26
DIII4	530	20	JIV3	1300	56
DV6	2400	96	KIII6	190	28
EII4	270	7	KV2	570	96
EIII6	760	31	LIV6	190	84
FI2	120	4	MIII1	240	42
FII2	230	10	NII6	170	21
FIII4	610	19	NV6	1020	98
FIV4	1480	45	PII6	640	12
GII4	150	6	PIV6	1820	34

Table 3c Period of immersion of intensive survey sites during one spring and one neap tide.

	Spring	Neap
Date	22.7.78	29.7.78
Amplitude*	0.3-7.3m	2.3-5.8m
FI2	3hrs 20mins	0
FII2	4hrs 15mins	3hrs 5mins
FIV4	5hrs 20mins	8hrs 30mins
GIII4	4hrs 50mins	4hrs 10mins
GIV3**	6¼hrs	9¼hrs

* taken from Admiralty tide tables.

** approximate figure - station GIV3 indistinguishable from shore.

Table 3d Mean weekly maximum and minimum temperatures and extreme range. Spurn Point Coastguard Met. Office data

16th March 1978 - 28th March 1979.

Week	Mean Minimum	Mean Maximum	Range	Week	Mean Minimum	Mean Maximum	Range
16 III - 23 III	2.7	7.1	1.3 - 8.6	22 IX - 28 IX	11.9	16.7	9.5 - 20.6
24 III - 30 III	5.3	11.2	3.9 - 11.7	29 IX - 5 X	9.4	14.0	6.6 - 16.8
31 III - 6 IV	5.1	7.9	4.1 - 8.6	6 X - 12 X	11.6	16.9	8.6 - 18.4
7 IV - 13 IV	2.8	6.8	-0.9 - 9.8	13 X - 19 X	9.4	12.1	6.8 - 13.8
14 IV - 20 IV	3.3	9.5	3.0 - 10.9	20 X - 26 X	9.9	13.6	7.5 - 16.8
21 IV - 27 IV	4.7	8.4	3.7 - 9.6	27 X - 2 XI	10.8	14.0	9.3 - 15.0
28 IV - 4 V	5.7	8.4	4.7 - 9.4	3 XI - 9 XI	9.2	13.2	7.0 - 14.8
5 V - 11 V	7.2	10.9	6.4 - 11.5	10 XI - 16 XI	7.4	12.0	5.6 - 14.0
11 V - 18 V	7.0	11.2	6.2 - 11.7	17 XI - 23 XI	9.2	12.7	5.6 - 15.1
19 V - 25 V	7.6	12.4	6.4 - 15.9	24 XI - 30 XI	2.6	5.8	1.4 - 11.0
26 V - 1 VI	9.2	14.9	7.0 - 17.7	1 XII - 7 XII	3.5	6.0	0.3 - 6.7
2 VI - 8 VI	12.7	17.7	12.0 - 18.9	8 XII - 14 XII	5.7	9.2	3.1 - 10.6
9 VI - 15 VI	9.8	14.5	8.4 - 19.2	15 XII - 21 XII	2.6	6.0	-0.5 - 7.3
16 VI - 22 VI	10.3	15.8	8.9 - 18.9	22 XII - 28 XII	3.6	7.3	-0.3 - 12.0
23 VI - 29 VI	10.8	14.9	9.5 - 15.9	29 XII - 4 I	-1.5	1.7	-4.5 - 3.7
30 VI - 6VII	10.7	14.2	9.6 - 16.6	5 I - 11 I	1.0	4.4	-1.9 - 7.5
7 VII - 13 VII	10.2	14.9	9.0 - 17.6	12 I - 18 I	0.9	3.5	-1.0 - 4.7
14 VII - 20 VII	12.0	15.9	11.0 - 17.8	19 I - 25 I	0.0	2.6	-2.3 - 3.2
21 VII - 27 VII	12.7	19.0	11.1 - 22.6	26 I - 1 II	-0.9	2.6	-4.6 - 3.7
28 VII - 3 VIII	14.3	17.3	13.6 - 22.6	2 II - 8 II	0.4	4.2	-2.7 - 5.7
4 VIII - 10 VIII	13.2	16.3	12.0 - 18.0	9 II - 15 II	1.6	3.2	0.3 - 3.6
11 VIII - 17 VIII	12.8	18.6	10.2 - 20.5	16 II - 22 II	-1.2	1.1	-4.4 - 3.8
18 VIII - 24 VIII	13.3	18.5	12.5 - 21.4	23 II - 1 III	0.4	5.4	-1.8 - 6.4
25 VIII - 31 VIII	11.9	15.4	10.4 - 18.0	2 III - 8 III	3.2	8.3	2.0 - 10.9
1 IX - 7 IX	11.8	15.6	10.6 - 18.0	9 III - 15 III	2.9	7.3	1.4 - 12.0
8 IX - 14 IX	13.6	19.1	11.1 - 22.3	16 III - 22 III	1.3	4.1	0.6 - 5.8
15 IX - 21 IX	11.5	17.6	9.2 - 20.6	23 III - 28 III	2.5	7.5	0.7 - 11.5

Table 3e Number of days with direct sunshine (SN), snow (SW), and subzero temperatures (FR), per month.

Barton School data. January 1975 - March 1979.

	1975			1976			1977			1978			1979		
Month	SN	SW	FR	SN	SW	FR	SN	SW	FR	SN	SW	FR	SN	SW	FR
I	6	0	0	6	5	6	8	4	10	2	5	6	1	14	19
II	7	0	1	14	0	1	11	0	0	7	8	12	9	9	9
III	6	5	6	10	1	5	14	1	1	13	1	0	8	3	5
IV	17	4	2	17	0	1	11	3	3	14	3	6			
V	19	0	0	12	0	0	17	0	0	19	0	0			
VI	22	1	0	26	0	0	17	0	0	12	0	0			
VII	26	0	0	31	0	0	16	0	0	17	0	0			
VIII	19	0	0	31	0	0	19	0	0	17	0	0			
IX	10	0	0	14	0	0	9	0	0	13	0	0			
X	14	0	0	10	0	0	14	0	0	17	0	0			
XI	15	0	1	12	0	0	6	0	4	16	1	5			
XII	10	1	2	8	4	9	4	0	1	9	4	5			

Table 3f Variation in sediment water content (percentage by weight), with time. Intensive survey.

March 1978 - March 1979. All stations.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Mean
Year	78	78	78	78	78	78	78	78	78	78	79	79	79	
station														
FI2	43.0	43.0	43.8	42.0	43.5	41.4	45.7	45.9	45.6	-	45.2	-	44.6	44.0
FII2	44.1	41.9	43.0	44.8	39.5	43.2	38.8	41.8	40.1	-	41.7	-	38.2	41.6
FIV4	27.8	31.3	34.8	31.0	31.0	37.3	34.6	33.1	31.5	-	25.5	-	23.5	31.0
GIII4	29.0	25.0	31.3	28.5	25.3	38.5	27.0	26.9	26.8	-	26.4	-	24.3	27.2
GIV3	29.0	28.3	29.4	28.0	26.3	28.2	26.0	26.8	27.7	-	26.4	-	26.4	27.5

Table 3g Interstitial sediment salinity. All stations.
May/June extensive survey 1977.

Site	Salinity ‰	Site	Salinity ‰
AIII2	21.8	GIII4	24.0
BI2	25.3	GIV3	23.5
CI2	26.8	GV6	23.0
CII4	27.5	HI2	24.5
CIII5	29.5	HIII5	23.8
CIV3	29.0	HIV4	25.0
CV6	29.5	JI3	24.5
DI3	28.5	JIII6	23.0
DIII4	26.25	JIV3	24.7
DV6	28.5	KIII6	26.5
EII4	32.5	KV2	26.5
EIII6	30.1	LIV6	-*
FI2	23.5	MIII1	25.0
FII2	29.0	NII6	25.0
FIII4	28.0	NV6	27.0
FIV4	28.3	PII6	-*
GII4	23.0	PIV6	29.7

* insufficient water in sediment for reading.

Table 3h Variation in interstitial salinity (‰) with time. Intensive survey.

March 1978 - March 1979. All stations.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Mean
FI2	22.5	26.0	32.0	32.0	30.0	32.0	32.0	28.5	26.0	-	18.5	-	20.0	27.2
FII2	24.5	26.0	24.0	30.0	28.5	32.0	30.0	30.5	27.0	-	22.0	-	22.0	26.95
FIV4	25.0	28.0	30.0	28.0	32.0	26.0	28.0	29.5	28.0	-	21.5	-	23.0	27.2
GIII4	30.5	27.4	29.5	30.5	27.0	35.0	30.0	22.0	28.5	-	26.0	-	28.0	28.6
GIV3	32.0	30.0	28.0	32.5	30.5	32.5	25.0	31.0	30.0	-	27.0	-	27.0	29.6

Table 3j Median particle size (øM), sorting (øS), skewness (øSK), kurtosis (øKu), percentage organic material (% Org), percentage iron content (% Fe), and proportions of sand (Sa), silt (Si), and clay (Cl), as percentages by weight. Extensive survey May/June 1977. All sites, divided into groups as per CLUSTAN analysis of sedimentary data alone.

Station	øM	øS	øSK	øKu	% Org	% Fe	Sa	Si	Cl
AIII2	5.1	1.9	0.22	1.5	6.2	12.3	24	66	10
CI2	4.9	1.5	0.26	1.3	4.8	10.1	27	70	3
BI2	4.8	1.1	0.33	1.5	6.2	11.3	24	74	2
FI2	5.5	1.9	0.42	1.2	8.1	12.3	15	72	13
KV2	5.6	2.0	0.37	1.0	6.9	13.4	16	73	11
HI2	5.4	1.9	0.35	1.0	8.4	12.1	22	69	9
MIII1	6.3	2.4	0.38	1.2	(9.0	(16.4)	4	76	20
CIV3	4.6	1.5	0.48	1.3	3.8	10.0	37	59	4
DI3	4.6	1.5	0.35	1.3	3.8	10.2	42	51	7
JIV3	4.6	1.7	0.31	1.1	6.2	11.1	43	53	4
FII2	4.7	0.9	0.23	1.5	3.5	10.7	35	62	3
EII4	4.0	1.3	0.37	1.2	3.4	9.9	60	36	4
FIII4	4.0	1.4	0.46	1.5	5.1	9.7	61	33	6
GII4	4.3	1.2	0.24	1.2	5.6	9.5	50	46	4
GIV3	4.2	1.8	0.49	1.1	4.4	10.0	48	47	5
HIV4	4.1	1.6	0.53	1.0	4.0	10.0	55	42	3
JI3	4.2	2.2	0.57	1.0	5.7	10.3	47	46	7
FIV4	4.2	1.4	0.32	1.2	3.7	11.5	54	45	1

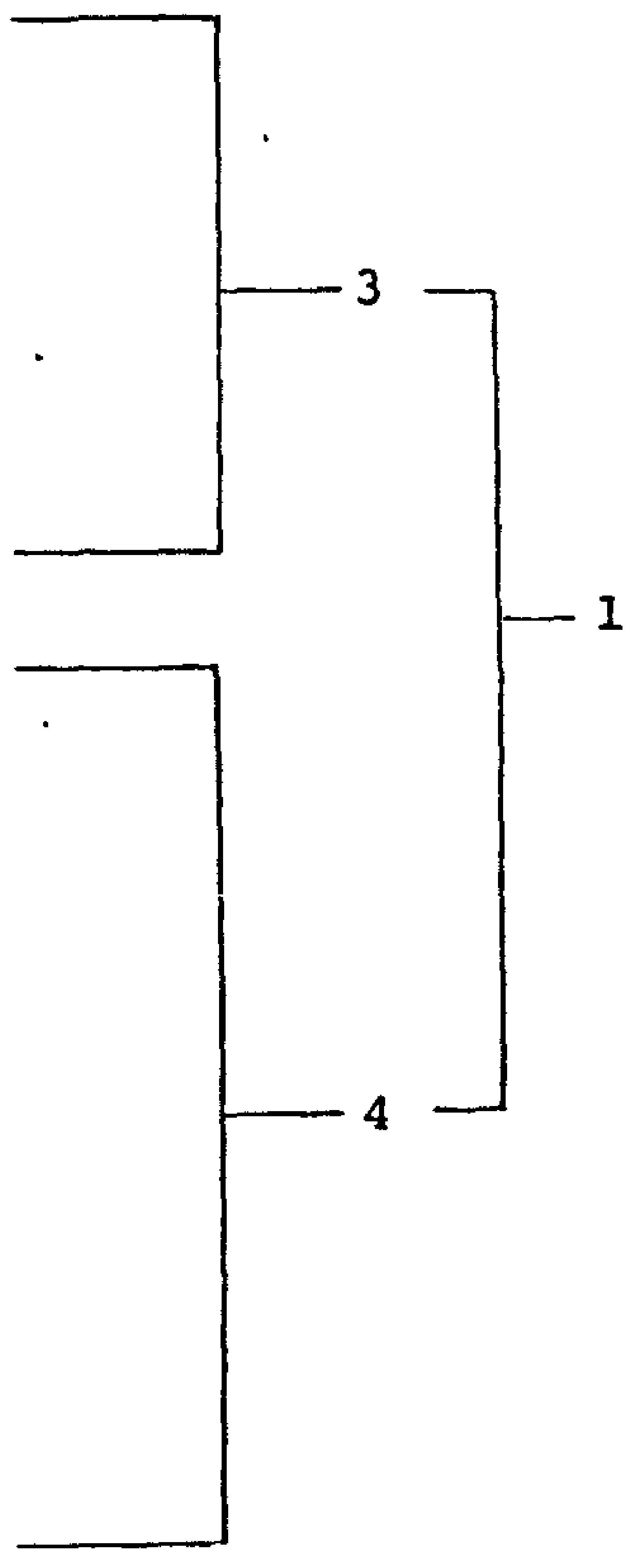


Table 3j continued.

Station	∅M	∅S	∅SK	∅Ku	% Org	% Fe	Sa	Si	Cl
CII4	3.8	1.1	0.42	1.2	2.5	8.5	67	30	3
DIII4	3.7	1.0	0.40	1.0	2.2	8.9	63	36	1
GIII4	3.7	0.9	0.53	1.2	5.1	9.7	74	21	5
CIII5	3.3	0.8	0.70	1.5	1.4	7.9	82	15	3
HIII5	3.3	0.9	0.44	1.2	1.6	8.9	81	18	1
JIII6	3.4	0.5	0.25	1.3	0.9	8.4	88	11	1
CV6	3.1	0.5	0.45	2.2	0.6	7.5	91	6	3
PII6	3.0	6.6	0.04	1.6	0.6	7.5	92	6	2
DV6	2.8	0.5	0.11	1.1	0.4	7.4	96	3	1
EIII6	2.8	0.7	0.40	1.1	0.8	8.0	94	5	1
GV6	2.9	0.6	0.69	1.3	1.0	8.8	90	9	1
KIII6	1.5	0.5	0.16	1.3	0.4	7.2	96	3	1
LIV6	1.5	0.5	0.10	1.1	0.2	8.2	98	1	1
NII6	2.4	0.4	0.15	1.3	0.4	7.1	95	2	3
NV6	2.4	0.4	0.10	1.0	0.3	7.0	98	1	1
PIV6	2.4	0.4	0.07	1.1	0.5	7.1	97	2	1

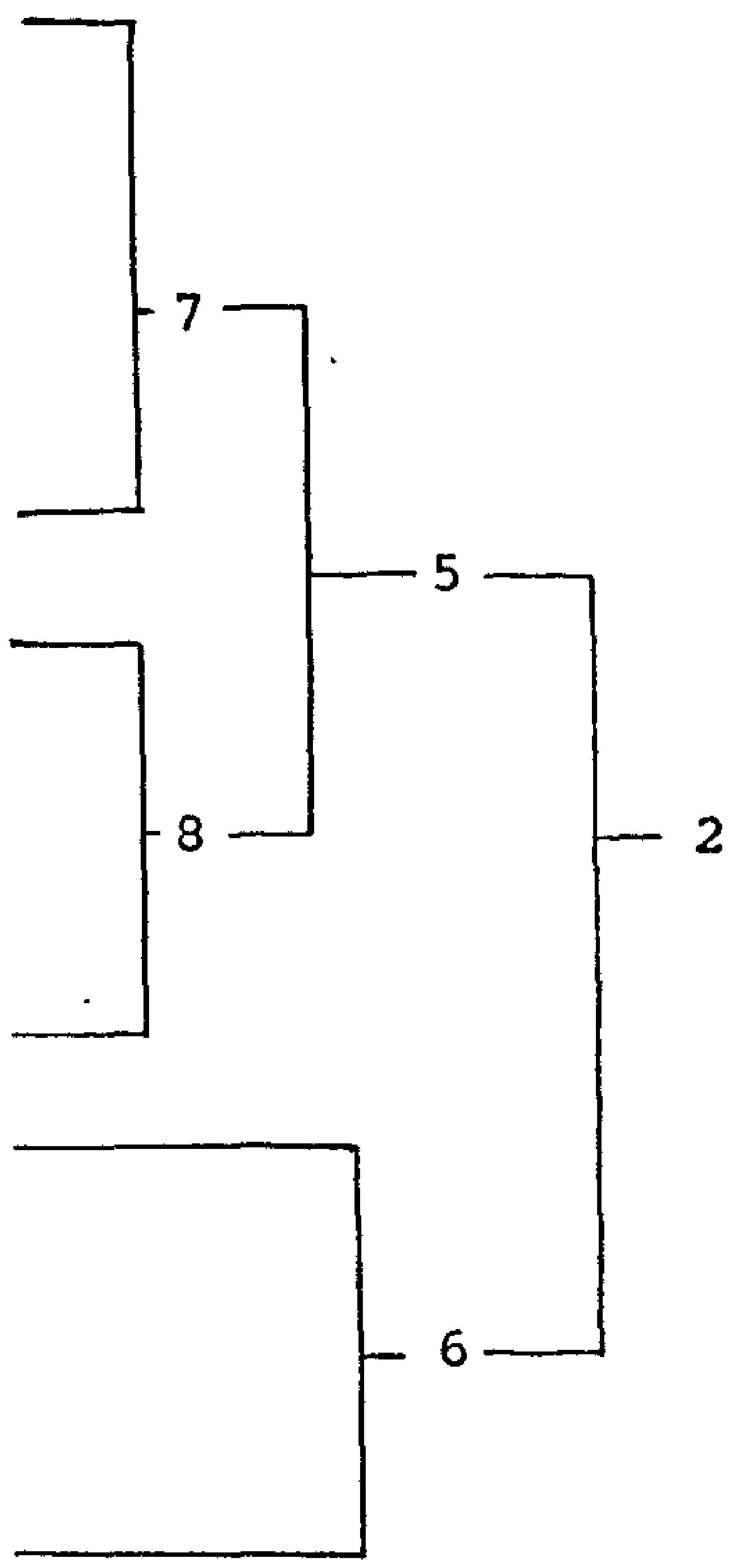


Table 3k Means of:- median particle size (øM), sorting coefficient (øSo), skewness (øSK), kurtosis (øKu), percentage organic matter and percentage iron content of clusters of sites from extensive survey May/June 1977. Values of 't' (upper figure) and probability (lower figure) for difference between means.*

Group 1	t/p	Group 2	Variable
4.73	8.0 0.001	2.88	ø M
1.62	8.9 0.001	0.66	ø So
0.37	0.96 N.S.	0.31	øSK
1.2	0.60 N.S.	1.3	øKu
5.5	8.3 0.001	1.2	% Org
10.65	3.5 0.01	8.0	% Fe

Group 3	t/p	Group 4	Group 5	t/p	Group 6	
5.4	5.1 0.001	4.3	3.3	4.9 0.001	2.07	øM
1.80	1.7 N.S.	1.50	0.74	4.3 0.001	0.44	øSo
0.33	1.4 N.S.	0.40	0.40	4.4 0.001	0.12	øSK
1.3	0.3 N.S.	1.2	1.3	1.49 N.S.	1.2	øKu
7.4	5.3 0.001	4.5	1.67	2.99 0.01	0.36	% Org
13.0	3.6 0.01	10.3	8.4	3.76 0.01	7.3	% Fe

Group 7	t/p	Group 8	
3.5	5.6 0.001	2.9	øM
0.90	3.1 0.02	0.60	øSo
0.46	0.88 N.S.	0.34	øSK
1.2	0.87 N.S.	1.4	ø Ku
2.56	2.65 0.05	0.78	% Org
8.78	1.90 0.1	8.04	% Fe

*using mixed unit data (ref. p38).

Table 31 Variation in median particle size (ϕM), and sorting coefficient (ϕS), with time. Intensive survey. March 1978 - March 1979. All stations. Pearson correlation coefficient (r) and probability (p).

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Mean	r/p
Year		78	78	78	78	78	78	78	78	78	78	79	79	79		
FI2	ϕM	6.5	6.7	6.35	6.4	6.5	6.35	6.35	6.05	6.5	-	6.4	-	6.1	6.37	0.05
	ϕS	1.27	1.31	1.30	1.33	1.33	1.28	1.36	1.29	1.33	-	1.32	-	1.32	1.31	N.S.
FII2	ϕM	5.85	6.4	6.0	5.9	5.9	6.25	6.35	6.4	6.7	-	6.05	-	5.25	6.10	0.04
	ϕS	1.31	1.26	1.24	1.25	1.3	1.26	1.28	1.29	1.29	-	1.30	-	1.28	1.28	N.S.
FIV4	ϕM	3.55	3.85	4.65	4.2	4.35	4.5	4.4	4.7	4.25	-	3.45	-	4.2	4.19	0.75
	ϕS	1.28	1.24	1.34	1.26	1.28	1.33	1.27	1.37	1.24	-	1.20	-	1.25	1.28	0.01
GIII4	ϕM	4.0	4.2	4.15	3.95	3.4	3.45	3.6	3.75	3.85	-	3.75	-	3.1	3.75	0.95
	ϕS	1.23	1.19	1.26	1.31	1.16	1.23	1.23	1.23	1.29	-	1.22	-	1.19	1.23	0.01
GIV3	ϕM	3.9	3.75	3.75	3.55	4.0	3.45	3.65	3.9	4.05	-	3.5	-	3.15	3.70	0.93
	ϕS	1.35	1.25	1.25	1.24	1.26	1.22	1.26	1.22	1.29	-	1.20	-	1.20	1.25	0.01

Table 3m Variation in proportions of sand, silt and clay (percentage by weight), with time.

Intensive survey. All stations.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Mean
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
FI2	Sa	10	8	11	12	12	7	10	8	9	-	13	-	8	9.8
	Si	65	65	67	62	63	69	65	72	66	-	64	-	72	66.4
	Cl	25	27	22	26	25	24	25	20	25	-	23	-	20	23.8
FII2	Sa	13	6	7	7	5	7	8	5	7	-	9	-	12	7.5
	Si	69	72	74.5	77	79	74	73	72	66	-	71	-	71	72.8
	Cl	18	22	18.5	16	16	19	19	23	27	-	20	-	17	19.7
FIV4	Sa	64	62	43	53	49	46	48	40	51	-	67	-	67	53.6
	Si	27	30	45	39	40	42	42	45	36	-	25	-	26	36.1
	Cl	9	8	12	8	11	12	10	15	13	-	8	-	7	10.3
FIII4	Sa	60	63	60	57	78	70	69	67	60	-	63	-	73	65.5
	Si	32	32	28	33.5	17	20.5	24	27.5	33	-	30	-	21.5	27.2
	Cl	8	5	12	9.5	5	9.5	7	5.5	7	-	7	-	5.5	7.3
GIV3	Sa	65	63	63	61	60	67	65	62	57	-	69	-	69	63.7
	Si	31	28	30	32	35	28	28	20.5	22.5	-	26	-	22	29.5
	Cl	4	9	7	7	5	5	7	7.5	9.5	-	5	-	9	6.8

Table 3n Changes in sediment level (in cm), with time. Intensive survey. All stations.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Net Change
Year	78	78	78	78	78	78	78	78	78	78	79	79	79	
FI2				No information available										
FII2	-	+2	+1	+1	+1	+1	0	+4	+4		-6		-6	+2
FIII4	-	0	+4	+1	+1	+3	+1	+2	-4		-5		+3	+6
GIII4	-	-4	+1	+1	-2	+2	-1	+1	+3		-4		-6	-10
GIV3	-	+2	+2	0	+1	0	0	-1	0		0		-8	-4

Table 3p Composition of Macrodetrital remains. Subjective abundance.

Autochthonous	Allochthonous Marine	Allochthonous Freshwater	Allochthonous Terrestrial/saltmarsh	Allochthonous Anthropogenic
Algal filament cells	Hydroid perisarc** (various species)	Duckweed pseudothalli	Grass leaf cells**	Paper fragments**
Enteromorpha fragments**		Planorbid shells	Grass stem nodes**	Rubber fragments**
Spionid tubes	Bryozoan fragments*	*Limnaea* shells	Grass Seeds*	Human hair
Hediste jaws	Sponge spicules	*Physa* shells	Dicot leaf veinlets**	Textile fragments
Hydrobia operculae*	Fish vertebrae	helophorinid & elmid beetle fragments*	Plant vascular strands**	Paint flakes
Hydrobia jaws	Fish scales		Rootlets**	Nylon filaments
conchostracum fragments**		*Asellus* remains	Bud scales*	Polystyrene spherules**
Hinge ligaments**			Wood chips**	Wood chips**
Mollusc shell fragments**			Bark fragments	
Crustacean segments			Rose thorns	
Dipteran puparia			Legume pod scleroderm*	
(Fish vertebrae)			Legume seeds	
(Fish scales)			Moss sporophytes**	
Feather fragments*			Insect fragments**	
Foram tests**			Dipteran puparia	

* frequent ** abundant

Table 3q Percentage by weight organic material (≡ total carbon x 2.45) and iron. All stations. May/June extensive survey 1977.

Site	% Organic	%Iron	Site	% Organic	% Iron
AIII2	6.2	12.3	GIII4	1.6	10.1
BI2	6.2	11.3	GIV3	4.4	10.0
CI2	4.8	10.1	GV6	1.0	8.8
CII4	2.5	8.5	HI2	8.4	12.1
CIII5	1.4	7.9	HIII5	1.6	8.9
CIV3	3.8	10.0	HIV4	4.0	10.0
CV6	0.6	7.5	JI3	5.7	10.3
DI3	3.8	10.2	JIII6	0.9	8.4
DIII4	2.2	8.9	JIV3	6.2	11.1
DV6	0.4	7.4	KIII6	0.4	7.2
EII4	3.4	9.9	KV2	6.9	13.4
EIII6	0.8	8.0	LIV6	0.2	8.2
FI2	8.1	12.3	MIII1	*	16.4
FII2	3.5	10.7	NII6	0.4	7.1
FII4	5.1	9.7	NV6	0.3	7.0
FIV4	3.7	11.5	PII6	0.6	7.5
GII4	5.6	9.5	PIV6	0.5	7.1

* a total carbon content of 3.5% (≡ 9.0% organic matter), was recorded at station MIII1 but this area was subject to chronic hydrocarbon pollution and therefore total carbon cannot be used as an indication of organic matter content.

Table 3r Variation in sediment organic matter content (percentage by weight organic carbon x 2.451), with time. Intensive survey. All stations.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Mean
FI2	9.01	9.39	9.12	9.81	10.12	9.39	9.42	9.20	10.02	-	11.05	-	9.20	9.61
FII2	7.23	7.43	8.26	7.89	8.06	8.36	7.40	8.50	8.65	-	7.87	-	5.25	7.72
FIV4	2.99	5.00	4.85	3.75	4.49	5.54	5.34	5.61	3.00	-	2.40	-	3.03	4.18
GIII4	3.75	2.70	3.92	4.24	3.17	2.77	3.21	2.45	3.92	-	2.97	-	2.04	3.19
GIV3	3.01	4.68	3.95	4.40	4.60	3.24	3.29	3.33	4.35	-	3.64	-	3.77	3.84

Table 4a Numerical abundance (n, No. m^{-2}) and biomass (where recorded)(b, mg m^{-2}) for all taxa at all stations.

Extensive survey May/June 1977.

		AIII2	BI2	CI2	CII4	CII5	CIV3	CV6	DI3	DIII4	DV6	EII4	EIII6
Turbellarian PA1	n	20	80	20	-	40	-	-	380	-	-	80	-
Gastrotricha	n	-	160	-	160	800	1110	160	800	950	950	800	480
Kinorhyncha	n	950	800	160	950	2390	3980	480	1750	3180	1590	1270	1270
Nematoda	n	104400	161540	84350	126530	79570	564200	2380	624520	840810	18620	375120	14640
Nematoda	b	36.4	56.6	29.5	42.3	28.1	197.7	0.86	218.6	294.3	6.5	131.5	5.1
ANNELIDA													
Hediste diversicolor	n	800	320	180	240	40	-	-	160	20	-	160	20
Hediste diversicolor	b	14300	4900	3650	3550	2087	-	-	2820	480	-	1280	8
Nephtys hombergi	n	-	60	620	40	740	420	-	80	290	-	400	480
Nephtys hombergi	b	-	166	476	532	1984	1046	-	150	1540	-	1740	1340
Nephtys cæca	n	-	-	-	-	-	-	375	-	-	40	-	20
Nephtys cæca	b	-	-	-	-	-	-	410	-	-	300	-	152
Eteone longa	n	-	-	20	-	-	-	-	40	-	-	20	-
Eteone longa	b	-	-	14	-	-	-	-	28	-	-	14	-
Arenicola marina	n	-	-	-	3	6	2	0	2	-	1	1	25
Pygospio elegans	n	20	180	220	640	600	2200	325	580	1040	40	7120	900
Steblospio shrubsolii	n	-	-	-	-	-	-	-	40	60	-	-	20
Edukemius benedii	n	20260	2780	1540	120	20	40	-	1640	-	-	120	-

Table 4a continued.

		FI2	FII2	FIII4	FIV4	GII4	GIII4	GIV3	GV6	HI2	HIII5	HIV4
Turbellarian PA1	n	60	-	-	-	80	-	-	-	100	40	-
Gastrotrichs	n	-	-	1110	1110	160	954	1110	800	480	800	640
Kinorhyncha	n	-	640	3340	2860	1750	2700	3980	1910	1750	2860	1910
Nematoda	n	167320	471580	621660	864850	401230	647760	810260	11140	312740	24670	417680
Nematoda	n	65.6	165.0	217.6	302.7	140.5	226.7	283.6	3.9	109.4	8.7	146.2
ANNELIDA												
Hediste diversicolor	n	600	180	80	20	60	60	-	-	160	20	20
Hediste diversicolor	b	6280	1050	2200	12	1820	4190	-	-	3800	480	3300
Nephtys hombergi	n	-	-	220	900	200	340	680	320	80	400	580
Nephtys hombergi	b	-	-	410	3549	444	2032	1850	1080	520	2960	2240
Nephtys cæca	n	-	-	-	-	-	-	-	40	-	-	-
Nephtys cæca	b	-	-	-	-	-	-	-	190	-	-	-
Eteone longa	n	-	-	-	-	40	20	-	-	40	-	-
Eteone longa	b	-	-	-	-	28	14	-	-	28	-	-
Arenicola marina	n	-	-	2	-	-	2	2	4	-	-	-
Pygospio elegans	n	20	640	460	660	720	1440	1180	460	-	1620	440
Streblospio shrubsolii	n	-	280	40	20	-	180	80	-	-	100	-
Edukemius benedii	n	4580	980	20	20	600	60	-	-	500	-	20

Table 4a continued.

		JI3	JIII6	JIV3	KIII6	KV6	LIV6	MIII1	NII6	NV6	PII6	PIV6
Turbellarian PA1	n	100	-	20	-	-	-	-	-	-	20	40
Gastrotricha	n	-	480	800	800	-	-	-	800	2390	800	1110
Kinorhyncha	n	-	1430	1910	2230	-	640	-	3980	3020	1910	3020
Nematoda	n	184780	417640	481620	8280	1750	-	491200	84200	127400	181460	478320
Nematoda	b	64.3	146.2	168.6	2.9	0.61	-	171.9	29.5	44.6	63.5	167.4
ANNELIDA												
Hediste diversicolor	n	80	-	40	-	-	-	-	-	-	-	20
Hediste diversicolor	b	960	-	810	-	-	-	-	-	-	-	900
Nephtys hombergi	n	40	100	600	-	400	-	-	-	-	-	-
Nephtys hombergi	b	300	1200	2930	-	460	-	-	-	-	-	-
Nephtys cæca	n	-	80	-	100	460	20	-	60	80	-	60
Nephtys cæca	b	-	910	-	1140	2200	230	-	697	910	-	680
Eteone longa	n	40	-	-	-	-	-	-	-	-	-	-
Eteone longa	b	28	-	-	-	-	-	-	-	-	-	-
Arenicola marina	n	-	2	-	2	-	-	-	2	25	2	35
Pygospio elegans	n	60	840	280	-	240	20	9020	20	20	-	-
Streblospio shrubsolii	n	-	160	20	-	-	-	-	20	20	40	20
Edukemius benedii	n	560	-	-	-	-	-	161240	-	-	-	40

Table 4a continued.

		AIII2	BI2	CI2	CII4	CIII5	CIV3	CV6	DI3	DIII4	DV6	EII4	EIII6
MOLLUSCA													
Macoma balthica	n	3140	7600	6100	1640	3400	2920	500	13320	4280	140	6800	2180
Macoma balthica	b	12460	16600	5590	4760	16996	11960	2570	11300	15620	85	14390	12170
Scrobicularia plana	n	-	-	620	-	-	-	-	-	-	-	20	-
Scrobicularia plana	b	-	-	476	-	-	-	-	-	-	-	5	-
Cerastoderma edule	n	-	20	-	-	60	40	-	-	-	-	80	140
Cerastoderma edule	b	-	47	-	-	122	1124	-	-	-	-	3950	1830
Mya arenaria	n	-	-	-	2	2	2	-	2	2	-	-	-
Hydrobia ulvae	n	140	1500	2240	120	1340	1500	150	1640	940	40	700	500
Hydrobia ulvae	b	142	780	1490	100	1150	590	130	2330	1120	27	1180	240
Retusa obtusa	n	-	380	-	340	620	40	-	400	100	-	800	120
Retusa obtusa	b	-	74	-	30	82	10	-	66	10	-	140	8
CRUSTACEA													
Harpacticoida	n	4770	40740	36290	46150	6200	48540	320	35010	47430	8440	27060	8910
Harpacticoida	b	5	45	40	51	7	54	1	38	52	9	30	10
Ostracoda	n	800	6370	4770	3340	160	13200	-	9390	14640	640	6840	800
Ostracoda	b	2	17	13	9	1	35	-	25	39	2	18	2
Corophium volutator	n	40	20	-	40	-	-	-	-	-	-	-	-
Bathyporeia pilosa	n	-	-	-	-	-	-	25	-	-	140	-	-
Bathyporeia pilosa	b	-	-	-	-	-	-	17	-	-	390	-	-
Tanaidacean	n	-	-	-	-	-	-	40	-	-	160	-	-
Tanaidacean	b	-	-	-	-	-	-	40	-	-	80	-	-
INSECTA													
Tabanid larvae	n	-	40	20	100	-	-	-	20	-	-	-	-

Table 4a continued.

		FI2	FII2	FIII4	FIV4	GII4	GIII4	GIV3	GV6	HI2	HIII5	HIV4
MOLLUSCA												
Macoma balthica	n	2220	15380	10300	6880	21460	8700	3980	1020	18700	3740	2380
Macoma balthica	b	1640	24480	21800	20540	9089	19360	23360	17120	5200	25440	14140
Scrobicularia plana	n	-	80	-	-	-	-	20	-	-	-	-
Scrobicularia plana	b	-	34	-	-	-	-	1	-	-	-	-
Cerastoderma edule	n	-	-	140	80	-	40	800	60	-	440	180
Cerastoderma edule	b	-	-	26940	8620	-	2310	6860	1930	-	8880	2970
Mya arenaria	n	-	-	3	2	-	2	2	5	-	-	-
Hydrobia ulvae	n	19780	560	360	80	640	1160	220	-	260	440	1200
Hydrobia ulvae	b	15520	660	340	85	807	1610	369	-	190	650	1670
Retusa obtusa	n	40	620	660	680	900	1880	940	-	100	1380	960
Retusa obtusa	b	1	81	410	93	65	276	275	-	5	256	330
CRUSTACEA												
Harpacticoida	n	11140	18300	68270	47240	13280	17830	56740	800	28880	42780	29460
Harpacticoida	b	12	20	75	52	15	53	62	1	32	53	32
Ostracoda	n	800	1270	15120	11780	4770	11140	12410	160	4620	9390	8280
Ostracoda	b	2	3	41	31	13	63	30	1	12	25	22
Corophium volutator	n	40	-	-	-	40	-	-	-	-	-	-
Bathyporeia pilosa	n	-	-	-	-	-	-	-	120	-	20	-
Bathyporeia pilosa	b	-	-	-	-	-	-	-	89	-	55	-
Tanaidacean	n	-	-	-	-	-	-	-	20	-	-	-
Tanaidacean	b	-	-	-	-	-	-	-	10	-	-	-
INSECTA												
Tabanid larvae	n	20	40	-	-	-	-	-	-	-	-	-

Table 4a continued.

		JI3	JIII6	JIV3	KIII6	KV6	LIV6	MIII1	NII6	NV6	PII6	PIV6
MOLLUSCA												
Macoma balthica	n	8320	3120	2320	160	60	-	-	400	80	-	1040
Macoma balthica	b	3460	4360	12090	760	71	-	-	6170	1220	-	8210
Scrobicularia plana	n	-	-	-	-	20	-	-	-	-	-	380
Scrobicularia plana	b	-	-	-	-	1	-	-	-	-	-	120
Cerastoderma edule	n	-	80	260	-	-	-	-	40	-	-	300
Cerastoderma edule	b	-	1450	12790	-	-	-	-	690	-	-	11040
Mya arenaria	n	-	-	-	-	-	-	-	-	-	-	-
Hydrobia ulvae	n	8480	3460	1760	-	20	-	-	600	20	1420	5740
Hydrobia ulvae	b	13650	1960	2190	-	8	-	-	534	24	1420	6070
Retusa obtusa	n	100	400	580	-	20	-	-	-	-	-	100
Retusa obtusa	b	2	30	170	-	1	-	-	-	-	-	6
CRUSTACEA												
Harpactacoida	n	8440	21420	39840	800	160	160	-	17160	8440	10340	21480
Harpactacoida	b	9	22	44	1	1	1	-	29	9	11	24
Ostracoda	n	1110	7160	7160	640	-	-	-	1590	2070	4770	7320
Ostracoda	b	3	19	19	2	-	-	-	4	5	13	20
Corophium volutator	n	-	-	-	-	-	-	-	-	-	-	-
Bathyporeia pilosa	n	-	20	-	20	-	40	-	60	660	20	140
Bathyporeia pilosa	b	-	55	-	55	-	11	-	165	18	20	55
Tanaidacean	n	-	-	-	20	-	100	-	60	1780	-	-
Tanaidacean	b	-	-	-	10	-	50	-	30	890	-	-
INSECTA												
Tabanid larvae	n	40	-	-	-	-	-	-	-	-	60	-

Table 4b Species encountered during the extensive survey in insufficient numbers for inclusion in mathematical analysis - numbers of individuals from five cores at stations at which they were found.

POLYCHAETA	
Eteone lactea	FII6 (2), LIV6 (2), PII6 (1), PIV6 (1)
Unidentified Nereid	NII6 (29), PIV6 (1)
Sphaerodoridium minutum	JIII6 (2), KV2 (6)
Scoloplos armiger	KIII6 (4)
Spio filicornis	AIII2 (3), FIV4 (3), KV2 (2)
Prionospio cirrifera	DV6 (1)
Nerine cirratulus	NII6 (1)
Unidentified Spionids	4 spp - 1 individual each
Capitella capitata	PII6 (2), PIV6 (20)
Travisia forbesii	LIV6 (1), NV6 (1)
Lanice conchilega	PII6 (1)
Ampharete acutifrons	JIV3 (1)
Manayunkia aestuarina	KV2 (1), MIII1 (58)
Unidentified polychaeta	2 spp. - 1 individual each
OLIGOCHAETA	
Tubifex costatus	KV2 (1-?), MIII1 (613)
Lumbricillus lineatus	AIII2 (1), CII4 (1)
MOLLUSCA	
Mytilus edulis spat	FIII4 (1), GII4 (1), GIII4 (1), JIII6 (3), NII6 (1)
Spisula sp.	PIV6 (1)
CRUSTACEA	
Neomysis integer	KV2 (1)
Pseudocuma longicornis	KV2 (1)
Eurydice pulchra	KIV6 (1)
Asellus aquaticus	FIV4 (1)
Corophium arenarium	KIV6 (1), NV6 (1), PII6 (179), PIV6 (32)
Haustorius arenarius	LIV6 (1), NII6 (1)
Urothoe sp.	NV6 (1)
Crangon vulgaris	HIII5 (1)
Carcinus maenas	CIII5 (1), FI2 (1), GIII4 (1), HI2 (1)
INSECTA	
Hydropodura aquatica	CIV3 (1), GV6 (7500 approx)
Anurida maritima	FI2 (1)

Table 4c Total number of individuals(all species) - Ni, biomass - B (gm m^{-2}), number of species per 0.05 m^{-2} - Ns, Shannon-Weiner diversity index - H, species richness - SR and evenness - J, extensive survey May/June 1977. Spurn Bight data only.

	Ni	B	Ns	H	SR	J
AIII2	24480	47.4	8	0.60	0.69	0.28
Bi2	13480	25.5	11	1.31	2.1	0.54
CI2	11580	13.0	10	1.41	1.9	0.61
CII4	3285	9.8	11	1.55	2.9	0.64
CIII5	6868	23.0	11	1.46	2.4	0.61
CIV3	7102	17.0	9	1.31	1.9	0.59
CV6	1415	3.5	6	1.47	1.9	0.82
DI3	18604	18.9	13	1.07	2.3	0.42
DIII4	6732	19.8	8	1.11	1.7	0.53
DV6	580	0.9	7	1.71	3.4	0.88
EII4	16301	29.9	12	1.25	2.2	0.50
EIII6	4405	15.3	10	1.45	2.4	0.63
FI2	27280	28.2	8	0.86	1.2	0.41
FII2	18720	28.2	8	0.78	1.3	0.38
FIII4	12233	52.7	10	0.72	1.9	0.31
FIV4	9382	33.6	10	0.97	2.0	0.42
GII4	24740	13.7	10	0.62	1.6	0.27
GIII4	13884	32.5	12	1.13	2.2	0.65
GIV3	7904	34.5	10	1.49	2.1	0.65
GV6	2249	21.7	9	1.47	2.6	0.67

Table 4c continued.

	Ni	B	Ns	H	SR	J
HI2	19440	10.2	8	0.34	1.3	0.16
HIII5	8220	40.4	11	1.56	2.3	0.65
HIV4	5780	35.2	8	2.56	1.7	0.75
JI3	17820	19.0	10	0.96	1.7	0.42
JIII6	8302	10.9	11	1.74	2.3	0.72
JIV3	6000	31.3	11	1.02	2.4	0.43
KIII6	406	2.0	7	1.51	4.3	0.78
KV2	1460	3.0	11	1.81	1.4	0.75
LIV6	260	0.4	8	1.64	7.3	0.79
MIII1	183680	170.0	5	0.47	0.33	0.29
NII6	2502	10.0	14	1.21	4.0	0.46
NV6	3005	3.3	15	2.10	4.1	0.78
PII6	15262	11.4	11	0.93	2.0	0.39
PIV6	9735	29.2	18	1.59	3.7	0.55

Table 4d Correlation (Kendall) and probability of relationship of whole community faunistic variables with abiotic variables.

	Tidal height	φ Median	φ Sorting	Organic content
No. individuals	-0.65	0.61	0.41	0.53
	0.00	0.001	0.002	0.001
Total biomass	0.41	0.33	0.31	0.28
	0.002	0.008	0.01	0.02
No. species	-0.2	0.01	0.12	0.14
	0.06	N.S.	N.S.	N.S.
Diversity	0.50	-0.40	-0.35	-0.51
	0.001	0.002	0.004	0.001
Species richness	-0.40	-0.51	-0.36	-0.60
	0.002	0.001	0.004	0.001
Evenness	0.28	-0.29	-0.40	-0.52
	0.02	0.02	0.002	0.001

Table 4e Description of clusters TOPSILT, MIDMUD, SAND and TOPSILT/MIDMUD. Mean ($\bar{x}$), standard error (S.E.) and range of all samples from stations in each cluster, with t value (t), and significance (p) of difference between means.

n = density - numbers m^{-2} b = biomass - mg m^{-2}

** Number of samples analysed * non-parametric equivalent of 't' used.

		TOPSILT (45)**			TOPSILT vs MIDMUD		MIDMUD (65)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Macoma	n	10500	2350	1640-21400	2.4*	0.04	4690	728	2180-10300
Macoma	b	9120	2450	1640-24500	2.6	0.018	16400	1610	4360-25400
Scrobicularia	n	69	69	0-620	0.9*	N.S.	3.1	2	0-20
Cerastoderma	n	2	2	0-20	2.9*	0.01	180	61	0-800
Cerastoderma	b	5	5	0-47	2.4*	0.03	5990	2060	0-26900
Mya	n	0.4	0.3	0-2	2.9*	0.01	1.2	0.3	0-3
Hydrobia	n	3910	2160	120-19800	1.3*	N.S.	1050	247	80-3460
Hydrobia	b	3950	2030	100-15500	1.7*	N.S.	1090	220	85-2610
Retusa	n	320	99	0-900	2.0	0.04	707	144	40-1880
Retusa	b	36	12	0-80	3.0*	0.01	156	39	1-410
Turbellarian PA1	n	91	38	0-380	2.0*	0.08	12	7	0-80
Hediste	n	275	86	60-820	2.8*	0.03	37	12	0-160
Hediste	b	3020	660	180-6280	2.6*	0.02	1140	390	0-4190
N. hombergi	n	124	65	0-620	3.8	0.001	473	62	100-900
N. hombergi	b	230	74	0-530	6.7*	0.0001	1910	240	410-3550

Table 4e continued.

		TOPSILT (45)**			TOPSILT vs MIDMUD		MIDMUD (65)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
N. cæca	n	0	0	-	1.0	N.S.	7.7	6.2	0-80
N. cæca	b	0	0	-	0.16	N.S.	81	70	0-900
Eteone	n	20	6	0-40	2.4*	0.04	3	2	0-20
Arenicola	n	0.5	0.4	0-3	1.4*	N.S.	3.2	1.9	0-25
Pygospio	n	340	100	0-720	2.2*	0.05	1450	495	280-7120
Streblospio	n	31	31	0-280	0.4	N.S.	46	17	0-180
Edukemius	n	1480	471	120-4580	3.1*	0.015	23	10	0-120
Tabanid larvae	n	24	11	0-100	2.7	0.01	0	0	-
Corophium	n	16	6.5	0-40	2.4	0.009	0	0	-
Bathyporeia	n	0	0	-	1.2	N.S.	3.1	2.1	0-20
Tanaidacean									
Copepods	n	26500	4670	8420-46200	1.6	N.S.	38200	5100	6240-68200
Ostracods	n	4070	944	820-9400	1.6	0.02	7680	945	160-14600
Nematodes	n	284000	60600	84400-625000	2.3	0.03	520000	73300	147000-865000
Gastrotrichs	n	226	89	0-800	6.5	0.001	872	55	160-1060
Kinorhynchs	n	889	254	0-1820	4.3	0.001	2540	266	1200-3980
Total biomass		18500	2500	9800-28200	2.2	0.04	28200	3100	10900-52700
Number individuals		17200	2380	3280-27300	3.3*	0.007	8710	956	4400-16300

Table 4e conintued.

	TOPSILT (45)**			TOPSILT vs MIDMUD		MIDMUD (65)**		
	$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Number species	9.9	0.56	8-13	0.5	N.S.	10.2	0.36	8-12
Diversity H.	1.81	0.13	0.34-1.55	2.4	0.03	1.34	0.08	0.72-1.74
Species richness $\frac{s-1}{InN}$	1.81	0.18	1.3-2.9	1.6*	N.S.	2.12	0.07	1.7-2.4
Evenness J	-0.43	0.05	0.16-0.64	2.1*	0.05	0.56	0.04	0.31-0.75
∅ Median	4.70	0.19	3.8-5.5	3.7	0.002	3.83	0.45	2.8-4.6
∅ Sorting	1.47	0.15	0.92-2.22	1.6	N.S.	1.18	0.12	0.48-1.70
% Sand	36.5	5.5	15-67	3.7	0.001	64.6	4.9	37-94
% Silt	58.1	5.0	33-74	3.7	0.002	32.4	4.7	5-59
% Clay	8.4	3.0	2-30	1.8	N.S.	3.0	0.5	1-6
% Organic matter	5.2	0.7	2.5-8.4	2.7	0.014	3.0	0.5	0.8-6.2
% Iron	10.6	0.4	8.5-12.3	2.0	0.06	9.6	0.3	7.9-11.5
Tidal height	14.2	5.0	4-50	2.8	0.01	33.4	4.5	7-60

Table 4e continued.

		MIDMUD (65)**			MIDMUD vs SAND		SAND (25)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Macoma	n	4690	728	2180-10300	5.7	0.0001	364	183	0-1020
Macoma	b	16400	1610	4360-25400	3.8	0.002	4110	3290	0-17100
Scrobicularia	n	3.1	2.0	0-20	0.9	N.S.	0	0	-
Cerastoderma	n	180	61	0-800	2.7*	0.02	12	12	0-60
Cerastoderma	b	5990	2060	0-26900	2.7*	0.02	390	390	0-1930
Mya	n	1.2	0.3	0-3	0.15	N.S.	1	1	0-5
Hydrobia	n	1050	247	80-3460	4.1*	0.002	38	29	0-150
Hydrobia	b	1090	220	85-2610	4.7	0.001	30	30	0-130
Retusa	n	707	144	40-1880	3.0	0.009	0	0	-
Retusa	b	156	39	1-410	2.4	0.03	0	0	-
Turbellarian PA1	n	12	7	0-80	1.1	N.S.	0	0	-
Hediste	n	37	12	0-160	1.9	N.S.	0	0	-
Hediste	b	1140	390	0-4190	1.8	N.S.	0	0	-
N. hombergi	n	473	62	100-900	3.8	0.002	64	64	0-320
N. hombergi	b	1910	240	410-3550	4.1	0.001	130	210	0-1030

Table 4e continued.

		MIDMUD (65)**			MIDMUD vs SAND		SAND (25)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
N. cæca	n	7.7	6.2	0–80	2.7*	0.02	115	66	20–375
N. cæca	b	81	70	0–900	2.6	0.02	510	150	190–1140
Eteone	n	3	2	0–20	0.22	N.S.	4	4	0–20
Arenicola	n	3.2	1.9	0–25	0.9	N.S.	1.4	0.7	0–4
Pygospio	n	1450	495	280–7120	2.5	0.03	169	94	0–460
Streblospio	n	46	17	0–180	1.6	N.S.	0	0	–
Edukemius	n	23	10	0–120	2.4	0.03	0	0	–
Tabanid larvae	n	0	0	–	–	–	0	0	–
Corophium	n	0	0	–	–	–	0	0	–
Bathyporeia	n	3.1	2.1	0–20	3.1*	0.006	109	57	20–320
Tanaidacean	n	0	0	–	4.2	0.001	68	27	20–160
Copepods	n	38200	5100	6240–68200	6.8*	0.0001	2124	3529	160–8420
Ostracods	n	7680	945	160–14600	7.9*	0.0001	316	148	0–640
Nematodes	n	520000	73300	147000–865000	6.7*	0.0001	21300	15000	0–84600
Gastrotrichs	n	872	55	160–1060	2.3	N.S.	568	185	0–950
Kinorhynchs	n	2540	266	1200–3980	3.4	0.004	1330	337	480–2140
Total biomass		28200	3100	10900–52700	4.0	0.001	5700	4000	400–21700
Number individuals		8710	956	4400–16300	7.5*	0.0001	981	375	260–2250

Table 4e continued.

				MIDMUD vs				
	MIDMUD(65)**			SAND		SAND (25)**		
	$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Number species	10.2	0.36	8-12	4.3	0.001	7.4	0.51	6-9
Diversity H.	1.34	0.08	0.72-1.74	2.4*	0.03	1.56	0.05	1.47-1.71
Species richness $\frac{s-1}{\ln N}$	2.12	0.07	1.7-2.4	1.9*	N.S.	3.9	0.94	1.9-7.3
Evenness J	0.56	0.04	0.31-0.75	4.5*	0.001	0.79	0.04	0.67-0.88
∅ Median	3.83	0.45	2.8-4.6	4.6	0.001	2.36	0.35	1.5-3.1
∅ Sorting	1.18	0.12	0.48-1.70	5.6*	0.001	0.51	0.03	0.45-0.61
% Sand	64.6	4.9	37-94	0.5	N.S.	94.2	1.6	90-98
% Silt	32.4	4.7	5-59	5.7*	0.0001	4.4	1.4	1-9
% Clay	3.0	0.5	1-6	2.0	0.005	1.4	0.4	1-3
% Organic matter	3.0	0.5	0.8-6.2	5.0*	0.0001	0.52	0.14	0.19-1.03
% Iron	9.6	0.3	7.9-11.5	1.9*	N.S.	7.8	0.29	7.2-8.8
Tidal height	33.4	4.5	7-60	3.8	0.002	73.6	12.5	28-96

Table 4e continued.

		TOPSILT & MIDMUD (110)*			SAND vs TOPSILT/MIDMUD		SAND (25)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Macoma	n	7080	1200	1640-21460	5.5*	0.0001	364	183	0-1020
Macoma	b	13400	1550	1640-25400	2.6	0.02	4110	3290	0-17100
Scrobicularia	n	30	28	0-620	0.5	N.S.	0	0	-
Cerastoderma	n	107	40	0-800	2.3*	0.03	12	12	0-60
Cerastoderma	b	3540	1350	0-26900	2.2*	0.04	390	390	0-1930
Mya	n	0.9	0.2	0-3	0.1*	N.S.	1	1	0-5
Hydrobia	n	2220	917	80-19800	2.4*	0.03	38	29	0-150
Hydrobia	b	2260	870	85-15500	2.6*	0.02	30	30	0-130
Retusa	n	549	101	0-1880	2.5	0.02	0	0	-
Retusa	b	107	26	0-410	4.1*	0.001	0	0	-
Turbellarian PA1	n	45	18	0-380	2.5*	0.02	0	0	-
Hediste	n	134	43	0-820	3.1*	0.005	0	0	-
Hediste	b	1910	400	0-6280	4.8*	0.0001	0	0	-
N. hombergi	n	330	58	0-900	2.1	0.05	64	64	0-320
N. hombergi	b	1220	230	0-3550	3.3*	0.002	130	210	0-1030

Table 4e continued.

		TOPSILT & MIDMUD (110)*			SAND vs TOPSILT/MIDMUD		SAND (25)**		
		$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
N. cæca	n	4.5	3.7	0–80	3.6*	0.001	115	66	20–375
N. cæca	b	48	41	0–910	3.4*	0.002	510	150	190–1140
Eteone	n	10	3.4	0–40	0.8	N.S.	4	4	0–20
Arenicola	n	2.1	1.1	0–25	0.5*	N.S.	1.4	0.7	0–4
Pygospio	n	993	314	0–7120	2.5*	0.02	169	94	0–460
Streblospio	n	40	16	0–280	2.5*	0.02	0	0	–
Edukemius	n	618	242	0–4580	2.5*	0.02	0	0	–
Tabanid larvae	n	10	5	0–100	2.0*	0.06	0	0	–
Corophium	n	6.3	3	0–40	2.1*	0.05	0	0	–
Bathyporeia	n	1.8	1.3	0–20	4.2	0.001	109	57	20–320
Tanaidacean	n	0	0	–	5.6	0.0001	68	27	20–100
Copepods	n	33400	3710	6240–68200	7.8*	0.0001	2124	3529	160–8420
Ostracods	n	6210	768	100–14600	7.5*	0.0001	316	148	0–640
Nematodes	n	423000	55000	14700–845000	7.0*	0.0001	21300	16000	0–84600
Gastrotrichs	n	608	84	0–1060	0.2	N.S.	568	185	0–950
Kinorhynchs	n	1862	255	0–3980	0.9	N.S.	1330	337	480–2140
Total biomass		24200	2300	9800–52700	3.5	0.002	5700	4000	400–21700
Number individuals		12200	1420	3290–27300	7.6*	0.0001	981	375	260–2250

Table 4e continued.

	TOPSILT & MIDMUD (110)*			SAND vs TOPSILT/MIDMUD		SAND (25)**		
	$\bar{x}$	S.E.	range	t	p	$\bar{x}$	S.E.	range
Number species	10.1	0.31	8-13	3,9	0.001	7.4	0.51	6-9
Diversity H.	1.19	0.08	0.34-1.74	4.0*	0.001	1.56	0.05	1.47-1.71
Species richness $\frac{s-1}{\ln N}$	1.99	0.09	1.3-2.9	2.0*	0.06	3.9	0.94	1.9-7.3
Evenness J	0.50	0.03	0.18-0.75	5.0*	0.0001	0.79	0.04	0.67-0.88
ϕ median	4.19	0.14	2.8-5.5	5.3	0.0001	2.36	0.35	1.5-3.1
ϕ sorting	1.29	0.09	0.48-2.2	7.9*	0.0001	0.51	0.03	0.45-0.61
% Sand	53.1	4.7	15-94	8.3*	0.0001	94.2	1.6	90-98
% Silt	42.9	4.3	5-74	8.4*	0.0001	4.4	1.4	1-9
% Clay	5.2	1.3	1-30	2.7*	0.01	1.4	0.4	1-3
% Organic matter	3.88	0.45	0.79-8.4	7.1*	0.0001	0.52	0.14	0.19-1.03
% Iron	9.8	0.3	0.8-12.3	3.8	0.001	7.8	0.29	7.2-8.8
Tidal height	25.5	7.9	4-60	4.8	0.0001	73.6	12.5	28-96

Table 5a Abundance of unidentified turbellarian 'PA1' at Skeffling and Easington. March 1978 – March 1979.

Density in numbers m^{-2}.

	Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III
	Year	78	78	78	78	78	78	78	78	78	78	79	79	79
Site	Station													
Skeffling	FI2	0	0	0	0	0	0	0	0	0	-	0	-	0
	FII2	0	0	0	0	0	0	40	0	20	-	0	-	20
	FIV4	20	0	0	0	0	0	1300	700	680	-	300	-	540
Easington	GIII4	20	0	0	0	0	0	100	280	0	-	0	-	0
	GIV3	0	0	0	0	0	0	900	840	0	-	40	-	80

Table 5b Estimates of abundance (n, No. m^{-2}), biomass* (b, mg m^{-2}) and production and elimination (p,e, mg m^{-2}) of Eteone longa at Skeffling and Easington. March 1978 - March 1979. (No specimens at FI2).

	Month		III		IV		V		VI		VII		VIII		IX		X		XI		XII*
	Year		78		78		78		78		78		78		78		78		78		78
Site	Station																				
Skeffling	FII2	n	20		0		40		120		140		100		120		40		100		90
		b	40		0		3		10		30		60		140		7		180		165
		p		0		3		7		20		47		80		60		170		0	
		e		-		-		-		-		-		-		120		-		19	
	FIV4	n	160		40		340		2140		1860		1550		680		650		660		700
		b	300		70		30		190		410		950		780		1200		1220		1295
		p		0		30		160		260		660		590		470		20		150	
		e		220		0		0		43		129		761		45		-		-	
Easington	GIII4	n	140		20		220		1600		1140		1050		1080		1100		1000		910
		b	260		40		20		140		250		640		1230		2030		1850		1685
		p		0		20		120		180		430		590		800		0		0	
		e		222		0		0		71		37		0		0		185		107	
	GIV3	n	160		40		800		2140		1840		1460		1240		1320		1240		940
		b	300		70		70		190		400		890		1410		2440		2290		1735
		p		0		70		120		260		640		720		1030		0		0	
		e		222		0		0		47		158		193		0		148		555	
Mean individual weight mg			1.85		1.85		0.09		0.09		0.22		0.61		1.14		1.85		1.85		-

Table 5b continued.

	Month		XII*		I		II*		III		Mean		Total		P/E:B
	Year		78		79		79		79						
Site	Station														
Skeffling	FII2	n	90		80		40		0		-		-		-
		b	165		150		75		0		60		-		-
		p		0		0		0		-		(387)		(6.5)	
		e		19		75		75		-		(308)		-	
	FIV4	n	700		740		690		640		-		-		-
		b	1295		1370		1275		1180		620		-		-
		p		0		0		0		-		2340		3.77	
		e		-		93		93		-		1384		2.23	
Easington	GIII4	n	910		820		510		200		-		-		-
		b	1685		1520		945		370		760		-		-
		p		0		0		0		-		2140		2.82	
		e		167		573		573		-		1996		2.62	
	GIV3	n	940		640		510		380		-		-		-
		b	1735		1180		940		700		900		-		-
		p		0		0		0		-		2770		3.08	
Mean individual weight mg			-		1.85		-		1.85		-		-		-

* by interpolation

** Calculated for Hediste of similar dimensions.

Table 5c Numerical distribution (No. m^{-2}), biomass* (mg m^{-2}) and production* (mg m^{-2}) of *Pygospio elegans* at Skeffling and Easington. March 1978 - March 1979.

	Month	V	III	IV	V	VI	VII	VIII	IX	X	XI	XII
	Year	77	78	78	78	78	78	78	78	78	78	78
Site	Station											
Skeffling	FI2	20	180	180	0	20	40	100	120	0	180	-
	FII2	640	320	120	520	640	860	740	80	680	1400	-
	FIV4	660	1040	1540	750	1200	780	11240	680	1780	5200	-
Easington	GIII4	1440	3580	960	1060	3280	13200	4740	3940	3800	12600	-
	GIV3	1180	5680	4140	5570	10620	8400	7900	11120	12480	11780	-

Table 5c continued.

	Month	I	II	III	Mean	Biomass*	Production*
	Year	79	79	79	Density		
Site	Station						
Skeffling	FI2	180	-	40	88	3.2	17.3
	FII2	340	-	220	589	21.7	117.2
	FIV4	6800	-	2940	2880	106.2	573.5
Easington	GIII4	3480	-	120	4350	160.5	866.7
	GIV3	9740	-	8760	8114	299.4	1616.8

*Biomass and productivity calculated for figures in Warwick et al. (1979).

Table 5d Numerical distribution (No. m^{-2}), biomass* (mg m^{-2}) and production* (mg m^{-2}) of *Streblospio shrubsolii* at Skeffling and Easington. March 1978 - March 1979.

	Month Year	V 77	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78
Site	Station											
Skeffling	FI2	0	0	0	20	0	20	0	0	40	0	-
	FII2	280	120	40	140	120	180	780	3120	4240	3180	-
	FIV4	0	60	100	20	0	0	480	1460	3760	2460	-
Easington	GIII4	180	100	60	40	60	20	380	2860	2600	3180	-
	GIV3	80	160	180	225	240	180	480	1200	3880	3400	-

Table 5d continued.

Site	Month Year	I 79	II 79	III 79	Mean Density	Biomass*	Production*
	Station						
Skeffling	FI2	0	-	0	7	0.3	1.6
	FII2	1200	-	0	1117	46.9	258.0
	FIV4	620	-	200	763	33.0	176.0
Easington	GIII4	1020	-	0	875	36.8	202.4
	GIV3	640	-	180	904	38.0	209.0

* Biomass and Productivity figures calculated from figures in Warwick et al. (1979) (in mg m^{-2}).

Table 5e Abundance (n, No. m^{-2}) and biomass (b, mg m^{-2}) of <u>Edukemius benedii</u> at Skeffling and Easington.

March 1978 - March 1979.

	Month		V	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Mean
	Year		77	78	78	78	78	78	78	78	78	78	78	79	79	79	
Site	Station																
Skeffling	FI2	n	4580	6020	5240	4740	6200	10400	9020	17680	28740	17780	-	21290	-	14700	-
		b	203	271	236	213	279	468	442	796	1293	800	-	958	-	662	594
	FII2	n	980	340	320	220	480	1180	1120	1200	1840	1525	-	1880	-	2040	-
		b	46	15	14	10	22	53	50	54	83	69	-	85	-	92	54
	FIV4	n	20	0	40	30	80	20	50	0	40	100	-	120	-	0	-
		b	1	0	2	1	4	1	2	0	2	5	-	5	-	0	2
Easington	GIII4	n	60	20	40	40	60	180	75	40	100	120	-	0	-	0	-
		b	3	1	2	2	2	8	4	2	4	5	-	0	-	0	3
	GIV3	n	0	80	240	350	120	220	40	100	120	0	-	20	-	20	-
		b	0	4	11	16	5	9	2	5	5	0	-	1	-	1	5

Table 5f Abundance (n, No. m^{-2}) and biomass (b, mg m^{-2}) of *Hydrobia ulvae*. All sites, intensive survey.

March 1978 - March 1979.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Mean
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
FI2	n	560	1140	620	500	800	160	340	0	520	-	160	-	320	436
	b	950	1171	1765	1552	2268	629	947	0	1722	-	624	-	777	1128
FII2	n	200	240	20	120	660	580	580	140	200	-	50	-	100	262
	b	564	640	52	247	1307	2693	1757	436	218	-	167	-	284	723
FIV4	n	310	710	200	480	40	115	215	250	220	-	240	-	200	271
	b	427	970	388	808	60	282	260	388	376	-	459	-	402	438
GIII4	n	280	260	20	160	210	450	420	320	200	-	0	-	0	214
	b	590	731	52	216	602	977	1197	738	668	-	0	-	0	524
GIV4	n	470	420	225	300	160	440	380	160	60	-	160	-	125	264
	b	928	923	472	573	347	600	766	296	161	-	351	-	405	529

Table 5g Production (or Elimination assuming E≑P), in mg m^{-2} of *Hydrobia ulvae* assuming a P:B ratio of 1.5 derived from McLusky et al.; 1977, Wolff & de Wolf; 1977, and Elliot; 1979.

Station	Production
FI2	1692
FII2	1085
FIV4	657
GIII4	786
GIV3	794

Table 5h All species present at CI2 (No. m^{-2}) and median particle size.

Date	16.5.77	24.11.77	24.4.78	21.7.78	16.11.78	27.3.79
S. plana	620	1350	500	360	1440	0
M. balthica	6100	4875	3680	9340	11200	5240
H. ulvae	2240	1600	500	8220	240	0
R. obtusa	0	40	80	180	0	0
H. diversicolor	180	400	60	4800	8920	1240
N. hombergi	0	60	0	140	0	0
E. longa	20	140	80	480	160	0
P. elegans	220	880	720	420	1200	820
E. benedii	1540	4100	1880	8240	4980	600
Tabanid larvae	20	140	20	0	480	0
ϕ median	4.95	4.8	3.9	4.9	4.75	3.8

Table 5j Abundance (n, No. m^{-2}), biomass* (b, mg m^{-2}), mean individual weight ($\bar{w}$, mg) and production (p, mg m^{-2}) for <u>Scrobicularia plana</u> at CI2. May 1977 - March 1979.

Month Year		May 1977	November 1977	April 1978	July 1978	November 1978	March 1979
1976	n	600	450	60	20	0	0
Cohort	b	148	313	12	52	0	0
	$\bar{w}$	0.246	0.696	0.205	2.602	0	0
	p		236.25	-125.21	95.88	0	0
1977	n	0	900	440	340	200	0
Cohort	b	0	37	10	85	403	0
	$\bar{w}$	0	0.0412	0.0221	0.251	2.0142	0
	p		37.1	-12.797	89.291	476.064	0
1978	n					1240	0
Cohort	b					59	0
	$\bar{w}$					0.0473	0
	p					0.0473	0

Σ	Nov	Nov		
1977 cohort	1977	1978	$P = 552.538$	$\bar{B} = 534.8$
1976 cohort	1977	1978	$P = 206.92$	$\bar{B} = 377.3$
1978 cohort	1977	1978	$P = 0.0473$	

* Calculated from the length/weight regression equation given in Hughes (1970b).

Table 5k Abundance of tabanid larvae at Skeffling 1978 - 1979. No. m^{-2}.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III
Year	78	78	78	78	78	78	78	78	78	78	79	79	79
FI2	140	180	120	0	0	180	220	180	200	-	220	-	100
FII2	40	60	40	0	0	160	160	240	180	-	220	-	60

Table 6a Density (No. m^{-2}) of <u>Nephtys hombergi</u>. Intensive survey March 1978 - March 1979.

Stations FIV4, GIII4 and GIV3.

o - observed value
s - value from smoothed mortality curve.

Month Year		III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	Site
1975	o	20	10	10	20	20	14	0	0	0	-	0	-	0	FIV4
	o	0	0	20	20	0	80	20	40	0	-	0	-	0	GIII4
	o	20	40	0	20	0	0	20	0	0	-	0.	-	0	GIV3
1976	o	190	240	210	140	100	130	110	70	40	-	0	-	0	FIV4
	s	217	202	185	165	147	130	110	70	40	0	0	0	0	
	o	300	180	240	40	120	40	80	40	0	-	0	-	0	GIII4
	s	-	-	-	-	-	-	-	-	-	-	-	-	-	
	o	260	240	140	140	120	80	100	40	20	-	0	-	0	GIV3
	s	260	240	140	140	120	100	70	40	20	0	0	0	0	
1977	o	550	520	330	440	500	470	340	270	260	-	260	-	80	FIV4
	s	550	520	480	445	410	375	340	270	260	260	260	167	80	
	o	140	40	120	240	220	115	180	160	100	-	120	-	0	GIII4
	s	-	-	-	-	-	-	-	-	-	-	-	-	-	
	o	580	520	375	340	260	280	260	240	200	-	200	-	120	GIV3
	s	580	520	375	340	280	270	260	240	220	210	200	155	120	

Table 6a continued.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
1978	o	-	-	-	-	80	770	1190	750	700	-	500	-	240	FIV4
	s	-	-	-	-	80	770	1190	750	700	600	500	370	240	
	o	-	-	-	-	100	120	260	260	200	-	160	-	20	GIII4
	s	-	-	-	-	-	-	-	-	-	-	-	-	-	
	o	-	-	-	-	20	510	700	580	480	-	400	-	200	GIV3
	s	-	-	-	-	20	510	700	580	480	440	400	300	200	
Total	o	760	770	550	600	700	1385	1640	1090	1000	-	760	-	320	FIV4
	s	787	732	675	630	657	1288	1640	1090	1000	880	760	537	320	
	o	440	220	380	300	440	355	540	500	300	-	280	-	20	GIII4
	s	-	-	-	-	-	-	-	-	-	-	-	-	-	
	o	860	800	515	500	400	870	1080	860	720	-	600	-	320	GIV3
	s	860	800	515	500	420	880	1050	860	720	660	600	455	320	

* by interpolation.

Table 6b Maximum densities of Nephtys hombergi recorded in the literature. (Numbers per m^{-2}).

Thamdrup (1935)	90	Skalling Wadden, Denmark.
Spooner & Moore (1940)	300	R. Tamar, Cornwall.
Brady (1943)	60	Northumberland coast.
Holme (1949)	100	R. Exe.
Smidt (1951)	100	Danish Waddensea.
Smidt (1951)	1000 - juveniles	Danish Waddensea.
Raymont (1955)	210	Loch Sween, Argyll.
Anderson (1973)	100	Morecambe Bay.
Warwick & Price (1975)	1104	R. Lynher, Cornwall.
Beukema (1976)	17	Dutch Waddensea.
Little & Boyden (1976)	28	Severn Estuary.
Olive (1977)	19 (excl 'O' group)	R. Tyre.
Rosenberg (1977)	98	W. Sweden.
Warwick & Davies (1977)	160	Bristol Channel.
Withers (1977)	140	S. Wales.
Warwick et al. (1978)	49	Bristol Channel.
Ratcliffe (1979)	almost 3000 (incl 'O' group)	Skeffling (Humber).
Key - present study	1640 (incl 'O' group)	Skeffling (Humber).

Table 6c Biomass (mg m^{-2}) of Nephtys hombergi. Intensive survey March 1978 - March 1979.

Stations FIV4, GIII4 and GIV3.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	$\bar{B}$	Site
1975	996	498	626	1252	1550	1599	0	0	0	0	0	0	0	(1087)	FIV4
	0	0	1550	996	0	3766	1250	3100	0	0	0	0	0	(1333)	GIII4
	996	1374	0	1250	0	0	1550	0	0	0	0	0	0	(739)	GIV3
1976	2462	2034	2522	3252	3228	3086	3815	3722	3442	0	0	0	0	(3063)	FIV4
	3222	1962	2784	673	2022	1224	2448	1192	0	0	0	0	0	(1941)	GIII4
	2584	3389	2115	2147	2117	2908	2363	1774	778	0	0	0	0	(2242)	GIV3
1977	225	245	465	748	1300	2248	3052	4322	6094	5454	4817	2874	1271	2547	FIV4
	32	9	79	484	1252	805	2176	2299	2014	-	2244	-	0	1132	GIII4
	274	313	474	454	910	1301	2209	2130	2413	2220	2034	1571	1212	1347	GIV3
1978	-	-	-	-	3	59	123	160	511	435	358	283	208	(238)	FIV4
	-	-	-	-	4	9	29	34	47	-	47	-	13	(26)	GIII4
	-	-	-	-	1	32	144	152	153	151	149	117	86	(109)	GIV3
Total	3683	2777	3613	5252	6081	6992	6990	8204	10047	5889	5175	3157	1479	5334	FIV4
	3252	1971	4413	2153	3278	5804	5904	6555	2061	2176	2291	1152	13	3156	GIII4
	3854	5076	2589	3851	3028	4241	62266	4056	3284	2371	2183	1688	1298	3368	GIV3

* by interpolation.

Table 6d Mean individual weight (mg) of Nephtys hombergi. Intensive survey March 1978 - March 1979.

Stations FIV4, GIII4 and GIV3.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Site
Year	78	78	78	78	78	78	78	78	78	78	79	79	79	
1975	49.8	49.8	62.6	62.6	77.5	114.2	-	-	-	-	-	-	-	FIV4
	-	-	79.5	49.8	-	47.1	62.5	77.5	-	-	-	-	-	GIII4
	49.8	34.4	-	62.5	-	-	77.5	-	-	-	-	-	-	GIV3
1976	11.4	10.1	13.6	19.7	22.0	23.9	33.5	53.2	86.1	-	-	-	-	FIV4
	10.7	10.9	11.6	16.8	16.9	30.6	30.6	29.8	-	-	-	-	-	GIII4
	9.9	14.1	15.1	15.3	17.6	29.1	33.8	44.4	38.9	-	-	-	-	GIV3
1977	0.4	0.5	1.0	1.7	3.2	6.0	9.0	16.0	23.4	21.0	18.5	17.2	15.9	FIV4
	0.2	0.2	0.7	2.0	5.7	7.0	12.1	13.9	20.1	-	18.7	-	-	GIII4
	0.5	0.6	1.3	1.3	3.3	4.8	8.5	8.9	11.0	10.6	10.2	10.1	10.1	GIV3
1978	-	-	-	-	0.04	0.08	0.10	0.21	0.73	0.72	0.72	0.79	0.86	FIV4
	-	-	-	-	0.04	0.07	0.11	0.13	0.24	0.27	0.29	0.48	0.67	GIII4
	-	-	-	-	0.04	0.06	0.21	0.26	0.32	0.35	0.37	0.40	0.43	GIV3

* by interpolation.

Table 6e Production (p) and elimination (e) of Nephtys hombergi. Intensive survey March 1978 - March 1979.

Stations FIV4 and GIV3.

Month year		III -IV 78	IV -V 78	V -VI 78	VI -VII 78	VII -VIII 78	VIII -IX 78	IX -X 78	X -XI 78	XI -XII 78	XII -I 79	I -II 79	II -III 79	Total	Site
1975	p	-	-	-	-	-	-	-	-	-	-	-	-	603	FIV4
	e	-	-	-	-	-	-	-	-	-	-	-	-	1599	
	p	-	-	-	-	-	-	-	-	-	-	-	-	554	GIV3
	e	-	-	-	-	-	-	-	-	-	-	-	-	991	
1976	p	-267	689	1064	351	270	1159	1813	1808	-	-	-	-	6887	FIV4
	e	161	201	333	375	413	430	1907	2088	3442	-	-	-	9350	
	p	1045	188	31	300	1258	398	582	-164	-	-	-	-	3638	GIV3
	e	241	1462	0	330	467	943	1172	832	778	-	-	-	6225	
1977	p	34	248	329	637	1108	1074	2144	1957	-637	-637	-281	-163	5813	FIV4
	e	13	29	46	85	160	270	864	197	0	0	1662	1439	4965	
	p	72	296	25	594	431	972	97	481	-86	-82	-6	-5	2789	GIV3
	e	32	135	46	138	40	7	174	198	108	104	457	354	1853	
1978	p	-	-	-	3	56	67	107	375	-5	-4	33	23	655	FIV4
	e	-	-	-	-	-	-	69	24	73	72	98	108	444	
	p	-	-	-	1	31	113	36	30	12	11	11	8	253	GIV3
	e	-	-	-	-	-	-	28	29	13	14	39	42	165	
Total	p	-233	937	1393	991	1434	2300	4064	4140	-642	-642	-248	-140	13958	FIV4
	e	173	230	379	460	573	700	2840	2309	3515	72	1760	1547	16157	
	p	1117	484	56	895	1720	1483	715	347	74	-71	5	3	7376	GIV3
	e	273	1597	46	468	507	1010	1374	1059	899	118	496	396	9910	

Table 6f Monthly and yearly production/biomass ($P:\bar{B}$) and elimination/biomass ($E:\bar{B}$) ratios for *Nephtys hombergi*.

Intensive survey March 1978 - March 1979. Stations FIV4 and GIV3.

Month Year		III -IV 78	IV -V 78	V -VI 78	VI -VII 78	VII -VIII 78	VIII -IX 78	IX -X 78	X -XI 78	XI -XII 78	XII -I 79	I -II 79	II -III 79	Overall	Site
1976	$P:\bar{B}$	0.35	0.07	0.01	0.14	0.50	0.15	0.28	(0)	-	-	-	-	1.62	FIV4
	$E:\bar{B}$	0.08	0.53	0	0.15	0.19	0.36	0.12	(2)	-	-	-	-	2.78	
	$P:\bar{B}$	-0.12	0.30	0.37	0.11	0.09	0.34	0.48	0.51	(0)	-	-	-	2.25	GIV3
	$E:\bar{B}$	0.07	0.15	0.12	0.12	0.13	0.12	0.51	0.58	(2)	-	-	-	3.05	
1977	$P:\bar{B}$	0.25	0.75	0.05	0.87	0.39	0.55	0.04	0.21	-0.04	-0.04	-0.03	-0.04	2.07	FIV4
	$E:\bar{B}$	0.11	0.34	0.10	0.20	0.04	0.04	0.08	0.09	0.05	0.05	0.25	0.25	1.38	
	$P:\bar{B}$	0.14	0.70	0.54	0.62	0.62	0.41	0.58	0.38	-0.11	-0.12	-0.07	-0.08	2.28	GIV3
	$E:\bar{B}$	0.06	0.08	0.08	0.08	0.09	0.10	0.23	0.38	0	0	0.43	0.69	2.57	
1978	$P:\bar{B}$	-	-	-	-	-	-	0.24	0.2	0.08	0.07	0.08	0.08	2.30	FIV4
	$E:\bar{B}$	-	-	-	-	-	-	0.19	0.19	0.09	0.59	0.29	0.41	1.51	
	$P:\bar{B}$	-	-	-	-	-	-	0.76	1.12	-0.01	-0.01	0.10	0.09	2.76	GIV3
	$E:\bar{B}$	-	-	-	-	-	-	0.49	0.07	0.17	0.18	0.31	0.44	1.87	

Table 6g Total production dynamics for *Nepthys hombergi* for the year March 1978 to March 1979 at sites FIV4 and GIV3.

	FIV4	GIV3
Mean annual biomass	5.33	3.37
Total production	13.9	7.38
Total elimination	16.16	9.91
$\xi P:\bar{B}$ ratio	2.617	2.190
$\xi E:\bar{B}$ ratio	3.029	2.942

Table 7a Density in No. m^{-2} (O - observed, S - smoothed mortality curve data), of <u>Hediste diversicolor</u>.

Monthly March 1978 - March 1979. All stations.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
1976	O	140	140	220	120	120	40	20	0	-	-	-	-	-	FI2
	S	295	240	155	120	80	40	20	0	-	-	-	-	-	
	O	40	20	0	20	0	120	0	-	-	-	-	-	-	FII2
	O	20	20	20	40	20	60	80	0	-	-	-	-	-	FIV4
	O	40	20	40	0	20	60	0	-	-	-	-	-	-	GIII4
	O	20	60	0	20	20	60	20	0	-	-	-	-	-	GIV3
1977	O	840	460	480	520	490	325	140	120	120	-	420	-	380	FI2
	S	840	490	490	490	490	325	140	120	120	(120)	(120)	(120)	(120)	
	O	360	120	20	120	100	420	260	480	120	110	100	60	20	FII2
	O	160	180	140	160	60	120	100	40	20	40	60	60	0	FIV4
	O	0	40	60	0	60	20	40	0	20	10	0	0	0	GIII4
	O	80	80	100	40	60	0	60	80	20	20	20	30	40	GIV3
1978	O	0	0	3600	6740	10880	10760	9520	8080	4880	3970	3060	1850	640	FI2
	O	0	0	20	1400	2640	11180	11500	9820	7405	4115	825	503	180	FII2
	O	0	0	880	1640	1220	220	340	100	0	20	40	50	60	FIV4
	O	0	0	100	220	300	240	80	100	0	0	0	0	0	GIII4
	O	0	0	400	1220	1020	200	40	40	80	40	0	0	0	GIV3

Table 7b Mean head width (w) and length (l) (calculated directly from w by power regression, $l = 22.1 \times w^{1.076}$, $r = 0.99$, $n = 48$), in mm for each cohort of <u>Hediste diversicolor</u>. Monthly March 1978 - March 1979. Upshore silt stations only.

Month Year Cohort		III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Site
1976	w	2.09	1.91	2.24	2.10	2.23	2.60	2.60	-	-	-	-	-	-	FI2
	l	49	44	53	49	52	62	62	-	-	-	-	-	-	
	w	1.90	2.40	-	2.60	-	2.27	-	-	-	-	-	-	-	FII2
	l	44	57	-	62	-	53	-	-	-	-	-	-	-	
1977	w	0.93	0.88	1.08	1.25	1.42	1.64	1.91	1.90	2.00	-	2.16	-	2.19	FI2
	l	20	19	24	28	32	38	44	44	47	-	51	-	51	
	w	0.90	1.07	0.60	1.40	1.24	1.53	1.88	2.00	2.22	-	2.20	-	2.00	FII2
	l	19	24	13	32	28	35	44	47	52	-	52	-	47	
1978	w	-	-	0.26	0.32	0.50	0.53	0.58	0.64	0.74	-	0.77	-	0.89	FI2
	l	-	-	5	6	10	11	12	14	16	-	17	-	19	
	w	-	-	0.20	0.26	0.50	0.71	0.74	0.98	0.82	-	0.73	-	0.78	FII2
	l	-	-	4	5	10	15	16	22	18	-	16	-	17	

Table 7c Mean individual dry weight (mg) of each cohort of *Hediste diversicolor*. Monthly March 1978 - March 1979.

Upshore silt stations only.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
1976	O*	19.4	15.7	23.4	19.9	22.0	32.6	32.6	-	-	-	-	-	-	FI2
	S*	15.9	18.5	21.1	23.7	26.2	28.8	31.3	-	-	-	-	-	-	
		15.0	26.7	-	32.6	-	23.2	-	-	-	-	-	-	-	FII2
1977		3.1	2.8	4.0	5.6	7.6	11.1	15.3	15.1	17.2	19.0	20.8	21.3	21.7	FI2
		2.9	3.1	(0.9)	5.4	5.7	9.1	14.8	17.4	22.3	22.1	22.0	19.5	17.0	FII2
1978		-	-	0.13	0.25	0.83	1.00	1.17	1.50	1.94	2.03	2.12	2.18	2.84	FI2
		-	-	0.06	0.13	0.64	1.53	1.79	2.14	2.44	2.26	2.07	2.08	2.09	FII2

O* observed values
S* values deduced from linear growth curve.

Table 7d Biomass (mg m^{-2}) of *Hediste diversicolor*. Monthly March 1978 - March 1979. All stations.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Mean	Site
Year	78	78	78	78	78	78	78	78	78	78	79	79	79		
Cohort															
1976	3816	3607	3270	2844	2096	1152	626	0	-	-	-	-	-	(2487)	FI2
	600	534	0	652	0	2789	0	-	-	-	-	-	-	(653)	FII2
	388	315	468	796	439	1955	2607	0	-	-	-	-	-	(955)	FIV4
	775	330	937	0	430	1974	0	-	-	-	-	-	-	(717)	GIII4
	301	1602	0	651	570	1861	619	0	-	-	-	-	-	(800)	GIV3
1977	2635	1357	1965	2764	3709	3600	2140	1813	2061	(2280)	(2500)	(2550)	(2600)	2460	FI2
	1033	309	17	645	573	3736	3856	8318	2672	2437	2001	1270	339	2112	FII2
	502	499	561	902	454	1330	1529	604	343	760	1250	1275	0	770	FIV4
	0	111	241	0	473	222	611	0	299	151	0	-	-	162	GIII4
	253	221	401	226	435	0	917	1209	307	365	382	411	481	431	GIV3
1978	0	0	469	1694	8989	10730	11097	12120	9485	7986	6488	4153	1819	(6820)	FI2
	0	0	1	184	1699	17088	20615	21041	18046	9300	1705	1046	377	(8282)	FII2
	0	0	48	201	784	337	609	214	0	48	90	104	125	(233)	FIV4
	0	0	9	29	193	367	153	0	-	-	-	-	-	(89)	GIII4
	0	0	22	161	656	306	72	86	196	91	0	0	0	(145)	GIV3
Total	6451	4964	6184	7302	14794	15482	13863	13933	11546	10266	8988	6703	4419	9607	FI2
	1633	843	18	1481	2272	23613	24471	29409	20718	11737	3906	2316	716	9472	FII2
	890	814	1077	1899	1677	3622	4745	818	343	806	1340	1379	125	1502	FIV4
	775	445	1187	29	1096	2563	754	153	299	151	0	0	0	573	GIII4
	554	1823	423	1038	1661	2167	1608	1295	503	456	382	411	481	962	GIV3

* by interpolation.

Table 7e Production (P) and elimination (E) mg m^{-2} of Hediste diversicolor. Monthly March 1978 - March 1979.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Σ	Site
		IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III		
Year		78	78	78	78	78	78	78	78	78	79	79	79		
Cohort															
1976	P	566	455	358	250	156	75	-	-	-	-	-	-	1859	FI2
	E	744	792	784	998	1100	601	626	-	-	-	-	-	5701	
	P	-	-	-	-	-	-	-	-	-	-	-	-	570	FII2*
	E	-	-	-	-	-	-	-	-	-	-	-	-	1749	
	P	-	-	-	-	-	-	-	-	-	-	-	-	713	FIV4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	2182	
	P	-	-	-	-	-	-	-	-	-	-	-	-	536	GIII4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	1638	
	P	-	-	-	-	-	-	-	-	-	-	-	-	598	GIV3*
	E	-	-	-	-	-	-	-	-	-	-	-	-	1828	
1977	P	-246	608	799	946	1430	979	-23	247	220	220	50	50	4740	FI2
	E	1034	0	0	0	1538	2439	304	0	0	0	336	0	5651	
	P	-	-	-	-	-	-	-	-	-	-	-	-	4079	FII2*
	E	-	-	-	-	-	-	-	-	-	-	-	-	2938	
	P	-	-	-	-	-	-	-	-	-	-	-	-	1483	FIV4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	1663	
	P	-	-	-	-	-	-	-	-	-	-	-	-	312	GIII4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	350	
	P	-	-	-	-	-	-	-	-	-	-	-	-	830	GIV3*
	E	-	-	-	-	-	-	-	-	-	-	-	-	931	

Table 7e continued.

Month		III IV	IV V	V VI	VI VII	VII VIII	VIII IX	IX X	X XI	XI XII	XII I	I II	II III	Σ	Site
Year		78	78	78	78	78	78	78	78	78	79	79	79		
Cohort 1978	P	-	469	1225	7295	1807	1724	2930	2851	398	(316※)	(844※)	(448※)	18699	FI2
	E	-	-	-	-	110	1324	1920	5504	1806	1888	2783	3219	18572	
	P	-	1	183	1515	15389	3527	3731	-2584	-1037	-469	7	3	26930	FII2
	E	-	-	-	-	-	-	3301	5530	7732	7123	669	673	25028	
	P	-	-	-	-	-	-	-	-	-	-	-	-	639	FIV4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	634	
	P	-	-	-	-	-	-	-	-	-	-	-	-	244	GIII4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	242	
	P	-	-	-	-	-	-	-	-	-	-	-	-	397	GIV3*
	E	-	-	-	-	-	-	-	-	-	-	-	-	395	
Total	P	320	1532	3174	8491	3393	2778	2907	3071	618	220	50	50	25298	FI2
	E	1808	792	784	998	2748	4382	2850	5504	1806	1888	3119	3219	29924	
	P	-	-	-	-	-	-	-	-	-	-	-	-	31496	FII2
	E	-	-	-	-	-	-	-	-	-	-	-	-	29458	
	P	-	-	-	-	-	-	-	-	-	-	-	-	2835	FIV4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	4479	
	P	-	-	-	-	-	-	-	-	-	-	-	-	1092	GIII4*
	E	-	-	-	-	-	-	-	-	-	-	-	-	2230	
	P	-	-	-	-	-	-	-	-	-	-	-	-	1825	GIV3*
	E	-	-	-	-	-	-	-	-	-	-	-	-	3154	

* calculated from biomass figures and P:B and E:B ratio calculated at FI2

※ apparent production from size selected mortality not included in total.

Table 7f Total population mean biomass, production, elimination, $\Sigma P:\bar{B}$ and $\Sigma E:\bar{B}$ ratios of *Hediste diversicolor* during intensive study period.

		$\bar{B}$	ΣP	ΣE	$\Sigma P:\bar{B}$	$\Sigma E:\bar{B}$
FI2	1976 cohort	2487	1859	5701	0.748	2.295
FI2	1977 cohort	2460	4740	5651	1.927	2.161
FI2	1978 cohort	6821	18699	18572	2.741	2.723
FI2	Total	11768	25298	29924	2.149	2.543
FII2	Total	9479	31496	29458	(3.322)*	(3.108)*
FIV4	Total	1502	2835	4479	(1.887)*	(2.982)*
GIII4	Total	573	1092	2230	(1.906)*	(3.279)*
GIV3	Total	962	1825	3154	(1.897)*	(3.279)*

* values calculated from figures derived using $\Sigma P:\bar{B}$ and $\Sigma E:\bar{B}$ ratios from site FI2.

Table 8a Individual cohort total and density of Cerastoderma edule ($N\ m^{-2}$) observed and smoothed mortality curve (s) data. May 1977 and monthly between March 1978 and March 1979. Easington station GIV3.

Month	V	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III
Year	77	78	78	78	78	78	78	78	78	78	78	79	79	79
Cohort <1975	52	12	16	2	10	7	2	2	8	8	-	4	-	4
1975	127	90	94	116	68	52	44	64	42	26	-	46	-	44
s	-	96	94	80	68	51	49	48	48	47	47	46	45	44
1976	564	356	280	320	314	314	334	242	226	184	-	234	-	154
s	-	356	337	320	314	314	314	242	226	211	196	183	168	154
1977	-	168	140	32	28	16	14	6	10	8	-	4	-	0
s	-	168	140	32	28	16	14	12	10	8	6	4	-	-
1978	-	-	-	-	120	160	530	486	440	330	-	220	-	0
s	-	-	-	-	120	160	530	486	440	330	270	220	110	0
Total	743	626	530	470	540	549	924	800	726	556	-	508	-	202
s	-	632	587	434	540	548	909	790	732	604	519*	457	323*	202

* by interpolation.

Table 8b Density (No m^{-2}) of '0' group <u>Cerastoderma edule</u>. March 1978 - March 1979.

All stations Easington and Skeffling.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	I 79	III 79
Site											
FI2	0	0	0	0	0	0	0	0	0	0	0
FII2	0	0	0	0	40	20	0	0	0	0	0
FIV4	0	0	0	1120	740	530	100	40	0	420	80
GIII4	0	0	0	120	150	220	310	300	280	40	0
GIV3	0	0	0	120	160	530	490	440	330	110	110

Table 8c Mean individual shell length (mm) and flesh dry weight (mg) of _Cerastoderma edule_.

May 1977 and monthly between March 1978 and March 1979. Easington station GIV3.

Month		V	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III
Year		77	78	78	78	78	78	78	78	78	78	78	79	79	79
Cohort															
1975	L	14.8	18.5	20.0	19.6	19.8	20.6	20.7	20.8	20.8	21.0	-	20.8	-	21.1
	W	16.8	37.6	35.3	26.3	39.3	62.0	74.7	58.4	54.8	54.4	54.8	55.3	54.9	54.5
1976	L	6.7	14.5	14.5	14.1	14.7	15.8	16.0	16.4	16.9	17.1	-	17.0	-	16.8
	W	1.8	14.5	12.5	9.6	15.7	26.0	26.0	31.6	29.3	30.5	30.5	30.5	28.4	26.6
1977	L	-	1.8	2.1	3.7	5.2	5.4	5.6	6.7	6.4	7.8	-	8.0	-	-
	W	-	0.12	0.14	0.16	0.75	1.18	1.29	2.83	1.80	4.05	3.34	2.62	-	-
1978	L	-	-	-	-	0.3	0.6	1.0	1.2	1.8	1.9	-	2.0	-	-
	W	-	-	-	-	0.005	0.011	0.03	0.06	0.085	0.113	0.081	0.069	-	-

* by interpolation.

Table 8d Mean shell length of each growth ring of Cerastoderma edule per cohort 1971 - 1978 and mean for each growth ring and number of individuals checked. Data from all individuals from extensive survey.

	Ring number								
	I	II	III	IV	V	VI	VII	VIII	N
Cohort									
1978	2.0								164
1977	1.8	7.9							214
1976	7.5	14.7	16.9						1480
1975	3.8	15.6	19.4	21.1					363
1974	4.5	8.0	12.7	16.3	*				3
1973	4.9	12.1	17.5	22.6	24.6	25.3			16
1972	6.1	14.3	19.6	22.3	25.2	26.7	27.5		13
1971	5.4	13.0	20.6	24.5	26.6	28.3	30.0	30.8	6
Mean *(all data)*	4.6	12.4	17.7	21.5	24.3	26.9	28.9	30.8	

* the 1974 cohort became extinct before the Vth growth ring was laid down.

Table 8e Percentage increment (upper figure) and its natural log (lower figure) by shell length between growth rings. Per cohort 1971 - 1978.

	Year of growth							
Cohort	1971	1972	1973	1974	1975	1976	1977	1978
1977							-	339.0
							-	5.8
1976						-	96.0	15.0
						-	4.6	2.7
1975					-	310.5	24.4	7.7
					-	5.7	3.2	2.0
1974				-	77.8	58.8	28.3	*
				-	4.4	4.1	3.3	*
1973			-	147.0	44.6	29.1	8.8	2.8
			-	5.0	3.8	3.4	2.2	1.0
1972		-	134.4	37.1	13.8	13.0	6.0	3.0
		-	4.9	3.6	2.6	2.5	1.8	1.1
1971	-	141.0	59.5	18.9	8.6	6.4	6.0	2.5
	-	4.9	4.1	2.9	2.2	1.9	1.8	0.9

* the 1974 cohort became extinct before the Vth growth ring was laid down.

Table 8f Mean percentage increment (+ normal log) and number of specimens - n, of each years' growth for C. edule. Data for all cohorts pooled.

Year	0-1	1-2	2-3	3-4	4-5	5-6	6-7
% incr	178.0	39.7	19.6	10.1	5.1	4.5	2.5
Ln %	5.18	3.68	2.98	2.31	1.61	1.5	0.9
n	2095	1881	401	38	35	19	6

Table 8g Ford-Walford equations for growth of *Cerastoderma edule*. Individual cohorts and pooled data for all cohorts.

Cohort			
1971	$L^{n+1} = 10.19 + 0.689\ L^{n}$	Lmax = 32.8	$r = 0.99$
1972	$L^{n+1} = 9.18 + 0.646\ L^{n}$	Lmax = 29.1	$r = 0.99$
1973	$L^{n+1} = 9.18 + 0.687\ L^{n}$	Lmax = 29.3	$r = 0.99$
All data	$L^{n+1} = 8.50 + 0.728\ L^{n}$	Lmax = 31.2	$r = 0.97$

Table 8h Regression equation values of flesh dry weight with shell length for *Cerastoderma edule*.

dry weight (mg) = A x shell length (mm) ^{B}
r = regression coefficient
n = number of specimens weighed

Month/Year	A	B	r	n
V '77	0.30	2.65	0.95	222
III '78	0.0018	3.34	0.95	202
IV '78	0.00093	3.53	0.92	255
V '78	0.0014	3.53	0.90	282
VI '78	0.0044	3.04	0.94	279
VII '78	0.010	3.06	0.92	222
VIII '78	0.10	3.04	0.89	242
IX '78	0.010	2.74	0.91	174
X '78	0.0034	3.04	0.93	174
XI '78	0.020	2.66	0.91	137
I '79	0.0022	3.33	0.90	190
III '79	0.010	2.83	0.92	106

Table 8j Biomass (mg m^{-2}) of Cerastoderma edule. Whole population and cohort values and smoothed mortality curve data. May 1977 and March 1978 - March 1979. Easington station GIV3.

Month	V	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Mean
Year	77	78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort <1975	7350	3020	1500	560	1520	1710	500	0	996	612	369	126	1075	2020	1077
1975	2135	3610	3316	2104	2673	3162	3660	2798	2629	2556	2577	2543	2471	2399	2808
1976	999	5175	4213	3074	4929	8160	8160	7652	6622	6436	5978	5582	4771	4100	5760
1977	-	20	20	5	21	19	18	34	18	32	20	10	-	-	17
1978	-	-	-	-	1	2	16	29	37	37	22	16	-	-	20
Total	9540	11825	9049	5743	9144	13953	12354	19513	19302	9673	8966	8277	8328	8519	9672

* by interpolation.

Table 8k Production (P), elimination(E, mg m^{-2}) and productivity ($P:\bar{B}$ & $E:\bar{B}$ ratios) of *Cerastoderma edule*. May 1977 - March 1979. Easington station GIV3.

Month		V	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Total
		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	
Year		77/78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
<1975	P	-	-	-	-	-	-	-	-	-	-	-	-	-	215
	E	-	-	-	-	-	-	-	-	-	-	-	-	-	754
	$P:\bar{B}$	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
	$E:\bar{B}$	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7
1975	P	2319	-219	-783	962	1351	635	-795	-169	-18	-21	20	-17	-16	929
	E	843	73	431	394	861	137	67	0	55	0	55	55	55	2183
	$P:\bar{B}$	-	-0.06	-0.29	0.4	0.46	0.19	-0.25	-0.06	-0.01	-0.01	-0.01	-0.01	-0.01	0.331
	$E:\bar{B}$	-	0.02	0.16	0.16	0.3	0.04	0.02	0	0.02	0	0.02	0.02	0.04	0.777
1976	P	7498	-693	-953	1934	3234	0	1557	-438	262	0	0	-369	-290	4144
	E	3016	257	188	76	0	0	2074	487	449	458	397	442	385	5213
	$P:\bar{B}$	-	-0.15	-0.26	0.48	0.49	0	0.20	-0.08	0.04	0	0	-0.07	-0.07	0.719
	$E:\bar{B}$	-	0.05	0.05	0.02	0	0	0.26	0.07	0.07	0.07	0.07	0.09	0.09	0.905
1977	P	-	3.1	1.7	17.1	9.5	1.7	20.0	-11.3	20.3	-5.0	-3.6	x	-	54.1
	E	-	3.6	16.2	1.8	11.6	2.5	4.1	4.6	5.9	7.4	6.0	10.0	-	73.7
	$P:\bar{B}$	-	0.16	0.14	0.36	0.48	0.09	0.76	-0.43	0.81	-0.19	-0.24	x	-	3.24
	$E:\bar{B}$	-	0.18	1.30	0.13	0.58	0.13	0.16	0.18	0.23	0.28	0.40	x	-	4.41
1978	P	-	-	-	0.6	0.8	6.6	15.4	11.6	10.8	-9.6	-2.9	x	-	33.3
	E	-	-	-	-	-	-	2.0	3.3	10.9	5.8	3.8	16.2	-	42.0
	$P:\bar{B}$	-	-	-	-	(0.67)	(0.75)	0.68	0.34	0.29	-0.32	-0.15	x	-	(1.66)
	$E:\bar{B}$	-	-	-	-	-	-	0.09	0.09	0.29	0.20	0.20	x	-	(2.09)
Total	P	9817	-909	-1734	2914	4595	643	797	-691	-243	-36	13.5	-386	-306	5375
	E	3859	334	635	472	873	140	2147	495	521	471	462	507	440	8266
	$P:\bar{B}$	-	-	-	-	-	-	-	-	-	-	-	-	-	0.556
	$E:\bar{B}$	-	-	-	-	-	-	-	-	-	-	-	-	-	0.855

x cohort became extinct.

Table 9a Density No. m^{-2} (observed O and smoothed mortality curve data S) of <u>Macoma balthica</u>.

Monthly March 1978 - March 1979. All stations.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
<1976	O	520	410	360	400	340	300	350	340	340	-	150	-	140	FIV4
	S	520	410	400	400	350	345	340	340	340	250	150	145	140	
	O	1160	1200	1160	1000	740	840	1050	1000	840	-	700	-	640	GIII4
	S	1160	1125	1075	1035	1000	950	910	870	840	760	700	675	640	
	O	1880	1900	1400	1460	1360	1480	1300	1100	700	-	660	-	840	GIV3
	S	1880	1770	1050	1550	1470	1320	1220	1100	850	820	800	770	750	
1976	O	220	140	20	0	0	60	0	0	0	-	40	-	0	FII2
	O	1780	1930	1830	1700	1740	1240	1050	1190	1120	-	580	-	870	FIV4
	S	1950	1900	1850	1790	1740	1240	1150	1070	1000	920	850	760	690	
	O	2300	2910	1200	2480	1780	2220	1990	1630	1050	-	1340	-	1180	GIII4
	S	2750	2600	2430	2260	2100	1940	1770	1630	1050	875	660	660	660	
	O	3600	2620	3420	3140	2020	1840	1920	1900	1120	-	1340	-	1180	GIV3
	S	3600	3400	3050	2550	2020	1950	1870	1800	1250	1220	1210	1200	1180	
1977	O	0	60	20	0	40	0	0	0	80	-	20	-	660	FI2
	O	1140	1180	740	840	540	340	240	400	135	-	150	-	220	FII2
	S	1250	1070	900	740	540	340	310	280	255	245	215	200	175	
	O	2540	2320	1180	1520	1300	1230	875	640	620	-	540	-	510	FIV4
	S	2540	2320	1470	1390	1300	1230	875	640	620	580	540	525	510	
	O	1590	2210	3700	3320	2610	2100	1850	1760	1195	920	640	470	300	GIII4
	O	2220	2020	1530	1480	1360	860	820	700	520	-	560	-	380	GIV3
	S	2220	2020	1530	1480	1360	860	820	700	670	620	500	420	380	

Table 9a continued.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Cohort															
1978	O	-	-	-	1040	6790	2420	1160	720	40	-	0	-	440	FI2
	O	-	-	-	14740	36640	37460	11500	2080	1180	-	800	-	1460	FII2
	S	-	-	-	14740	36640	37460	11500	2080	1180	1180	1180	1180	1180	
	O	-	-	-	3180	5890	13340	8270	5190	5340	-	3900	-	4460	FIV4
	S	-	-	-	3180	5890	13340	8270	5190	4950	4720	4500	4250	4000	
	O	-	-	-	3400	5100	12690	4360	4520	1780	970	160	80	0	GIII4
	O	-	-	-	1270	4620	15600	21710	15760	12900	9400	5900	4155	2410	GIV3
Total	O	0	60	20	1040	6830	2420	1160	720	120	-	20	-	1100	FI2
	O	1360	1320	700	15580	37180	37860	11740	2480	1305	-	950	-	1680	FII2
	S	1470	1210	920	15480	37180	37860	11810	2360	1435	1425	1395	1380	1355	
	O	4840	4660	3370	6800	9270	16110	10545	7360	7420	-	5170	-	5980	FIV4
	S	5010	4630	3720	6760	9280	16155	10635	7240	6910	6470	6040	5680	5340	
	O	5050	6380	7160	10200	9280	17850	9250	8910	4865	-	2140	-	1620	GIII4
	S	5500	5935	7205	10015	9860	17680	8890	8780	4865	3525	2160	1885	1600	
	O	7700	6540	6350	7350	9360	10780	25750	19460	15240	-	8460	-	4810	GIV3
	S	7700	7190	6230	6850	9470	19730	25620	19360	15670	12060	8410	6545	4720	

* by interpolation.

Table 9b Mean shell length (mm) of 1976, 1977 and 1978 cohorts of <u>Macoma balthica</u>.

Monthly March 1978 - March 1979. All stations.

Month Year Cohort	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	Site
1976	6.1	6.2	6.6	6.8	7.7	9.1	9.6	9.8	10.0	10.0	9.9	9.8	9.8	FIV4
	4.8	4.9	4.9	5.5	6.6	7.7	8.3	8.4	9.0	9.0	9.0	9.2	9.3	GIII4
	5.6	5.5	6.0	6.6	7.6	8.0	8.3	8.6	8.8	8.8	8.9	8.8	8.7	GIV3
1977	2.4	2.7	3.3	3.6	4.2	5.2	5.1	5.5	5.1	5.4	5.8	5.8	5.8	FII2
	1.4	1.4	2.1	2.3	2.7	4.1	5.6	6.0	6.8	6.8	6.6	6.4	6.3	FIV4
	1.1	1.2	1.2	1.5	2.0	3.1	3.6	4.3	5.1	5.6	6.0	6.0	6.1	GIII4
	1.4	1.4	2.0	2.3	3.3	4.1	4.6	5.1	5.1	5.1	5.2	5.1	5.1	GIV3
1978	-	-	-	0.42	0.47	0.48	0.63	0.60	0.42	-	-	-	0.75	FI2
	-	-	-	0.42	0.49	0.59	0.74	0.91	1.51	1.62	1.72	1.68	1.62	FII2
	-	-	-	0.42	0.49	0.54	1.12	1.30	1.59	1.54	1.48	1.43	1.36	FIV4
	-	-	-	0.42	0.42	0.48	0.54	1.01	1.30	1.35	1.40	1.40	-	GIII4
	-	-	-	0.42	0.42	0.54	0.71	0.87	0.91	0.94	1.00	1.00	1.18	GIV3

* by interpolation.

Table 9c Biomass (mg m^{-2}) of Macoma balthica. Monthly March 1978 - March 1979. All stations

* by interpolation ** this cohort includes all animals <1977 *** this cohort includes all animals <1978

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Mean	Site
Year	78	78	78	78	78	78	78	78	78	78	79	79	79		
Cohort															
<1976	14970	11520	10200	11200	10500	12830	12650	11750	12190	9840	6430	5760	5160	5120	FIV4
	28420	25330	23110	24740	27100	25550	24480	21580	21730	19610	17990	17620	16900	22710	GIII4
	54330	38110	44220	38750	41750	45280	27170	27170	27460	25170	23200	22330	21750	34054	GIV3
1976	2730	2890	100	0	0	703	0	0	0	-	1330	-	0	(600)	FII2**
	5750	5760	6340	6880	9240	10640	11120	11130	11030	10070	9270	8090	7160	8680	FIV4
	4130	4160	3890	4970	7560	10280	11870	11250	8610	7260	5540	5810	6070	7030	GIII4
	8100	7310	8250	8920	10490	11630	12560	13190	9680	9550	9590	9170	8700	9780	GIV3
1977	0	800	25	0	870	0	0	0	1210	-	140	-	4210	(560)	FI2***
	290	320	490	500	570	620	540	600	440	510	520	490	430	480	FII2
	110	120	220	290	400	1220	2010	1700	2410	2180	1960	1760	1560	1230	FIV4
	45	70	130	210	340	980	1260	1890	2610	2060	1480	1170	860	1010	GIII4
	110	110	210	290	700	840	1090	1240	1170	1100	900	750	670	706	GIV3
1978	-	-	-	2	16	7	9	44	1	-	0	-	110	19	FI2
	-	-	-	25	125	190	100	30	80	90	110	100	90	94	FII2
	-	-	-	6	20	50	230	220	360	320	270	230	190	190	FIV4
	-	-	-	7	11	36	17	100	70	40	8	4	0	30	GIII4
	-	-	-	3	9	70	160	210	210	160	110	90	80	110	GIV3
Total	0	800	25	2	886	7	9	44	1211	-	140	-	4320	-	FI2
	3010	3210	590	525	695	1513	640	630	520	600	1960	590	520	1150	FII2
	20830	17400	16760	18370	20140	24750	26010	24800	26000	22410	17920	15830	14030	20435	FIV4
	32600	*30560*	*27130*	*29920*	*35010*	*36850*	37630	34820	33080	28970	25010	24600	23830	30770	GIII4
	62540	45530	52180	47060	52950	57820	46990	41810	38520	25980	33800	32340	31200	44620	GIV3

Table 9d Mean individual weight (mg) per cohort of _Macoma balthica_. March 1978 - March 1979. All stations.

Cohorts older than 1976 considered together.

Month Year Cohort	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Site
<1976	-	-	-	-	-	-	-	-	-	-	-	-	-	FI2
	-	20.6	-	-	-	-	-	-	-	-	33.2	-	-	FII2
	28.8	28.1	25.5	28.0	30.0	37.2	37.2	34.6	35.9	39.4	42.8	39.7	36.6	FIV4
	24.5	23.7	21.5	23.9	27.1	26.9	26.9	24.8	25.9	25.8	25.7	26.1	26.4	GIII4
	28.9	21.5	26.8	25.0	28.4	34.3	27.2	24.7	32.3	30.7	29.0	29.0	29.0	GIV3
1976	-	-	-	-	-	-	-	-	-	-	-	-	-	FI2
	-	-	5.0	-	-	-	-	-	-	-	-	-	-	FII2
	2.9	3.0	3.6	3.8	5.3	8.6	9.7	10.4	11.0	10.9	10.9	10.6	10.4	FIV4
	1.5	1.6	1.6	2.2	3.6	5.3	6.7	6.9	8.2	8.3	8.4	8.8	9.2	GIII4
	2.3	2.2	2.7	3.5	5.2	6.0	6.7	7.3	7.7	7.8	7.9	7.7	7.4	GIV3
1977	-	-	-	-	-	-	-	-	-	-	-	-	-	FI2
	0.23	0.30	0.54	0.07	1.05	1.83	1.75	2.14	1.73	2.08	2.42	2.45	2.48	FII2
	0.05	0.05	0.15	0.21	0.31	0.99	2.30	2.70	3.90	3.80	3.60	3.30	3.10	FIV4
	0.03	0.03	0.04	0.06	0.13	0.47	0.68	1.13	1.76	2.25	2.73	2.80	2.86	GIII4
	0.05	0.05	0.14	0.19	0.52	0.97	1.34	1.77	1.75	1.78	1.80	1.78	1.77	GIV3
1978	-	-	-	0.002	0.002	0.003	0.008	0.062	0.009	-	-	-	0.25	FI2
	-	-	-	0.002	0.003	0.005	0.009	0.016	0.064	0.077	0.090	0.084	0.077	FII2
	-	-	-	0.002	0.003	0.004	0.028	0.042	0.073	0.067	0.061	0.055	0.048	FIV4
	-	-	-	0.002	0.003	0.003	0.004	0.022	0.042	0.047	0.052	0.052	-	GIII4
	-	-	-	0.002	0.002	0.004	0.008	0.14	0.016	0.018	0.019	0.026	0.032	GIV3

Table 9e Monthly and total production (P) and elimination (E) for each cohort of <u>Macoma balthica</u>. All stations.

Intensive survey March 1978 - March 1979.

Month Year Cohort		III IV 78	IV V 78	V VI 78	VI VII 78	VII VIII 78	VIII IX 78	IX X 78	X XI 78	XI XII 78	XII I 79	I II 79	II III 79	Σ	Site
1976	P	-	-	-	-	-	-	-	-	-	-	-	-	2668	FIV4
	E	3130	268	0	1450	168	186	0	0	3389	4110	206	191	13077	
	P	-	-	-	-	-	-	-	-	-	-	-	-	5836	GIII4
	E	844	1130	908	893	1350	1076	1034	761	2068	1545	648	919	13174	
	P	-	-	-	-	-	-	-	-	-	-	-	-	8752	GIV3
	E	2772	2898	2590	2136	4702	3075	3114	7125	945	597	870	580	31404	
1976	P	193	1125	364	2648	4917	1315	777	621	-48	-44	-242	-145	11481	FIV4
	E	148	165	222	228	3475	823	804	749	878	765	968	735	9960	
	P	268	88	1325	3052	3434	2597	340	1740	96	77	-	-	13017	GIII4
	E	232	275	326	464	712	1020	952	4379	1444	1795	-	-	11599	
	P	-350	1613	2240	3885	1588	1337	1101	610	124	122	-301	-298	11671	GIV3
	E	440	858	1550	2306	392	508	490	4125	233	79	78	151	11210	
1977	P	81	236	107	740	499	-26	115	-109	88	81	4	6	1822	FII2
	E	48	71	97	281	288	54	58	48	19	68	37	62	1126	
	P	12	190	86	135	860	1380	303	756	-60	-112	-160	-104	3285	FIV4
	E	10	85	14	23	46	584	588	66	154	148	52	48	1818	
	P	(28)	(58)	91	203	809	415	812	931	518	374	39	23	3865	GIII4
	E	-	-	19	63	168	143	81	816	551	697	470	481	3491	

Table 9e continued.

Month Year Cohort		III IV 78	IV V 78	V VI 78	VI VII 78	VII VIII 78	VIII IX 78	IX X 78	X XI 78	XI XII 78	XI I 79	I II 79	II III 79	Σ	Site
1977	P	0	160	75	469	500	311	327	-14	19	11	-9	-4	1845	GIV3
	E	10	47	8	43	372	46	187	53	88	315	143	71	1283	
1978	P	-	-	2	14	18	9	50	-20	-	-	-	-	73	FI2
	E	-	-	-	-	11	7	15	24	0.4	-	-	-	57	
	P	-	-	25	100	63	98	48	78	15	15	-7	-8	427	FII2
	E	-	-	-	-	-	181	118	36	0	0	0	0	335	
	P	-	-	6	14	31	259	94	157	-29	-28	-26	-29	449	FIV4
	E	-	-	-	-	-	81	108	14	16	14	15	13	261	
	P	-	-	7	4	25	4	79	63	7	3	0	0	194	GIII4
	E	-	-	-	-	-	27	2	82	36	40	4	4	196	
	P	-	-	3	6	60	99	112	29	17	11	33	21	288	GIV3
	E	-	-	-	-	-	-	65	43	57	64	39	50	318	

Table 9f Monthly and yearly P:$\bar{B}$ and E:$\bar{B}$ ratios for each cohort of Macoma balthica. All sites intensive survey March 1978 - March 1979. Mean annual E:B ratios for <1976 cohorts:-

FIV4; 1.262, GIII4; 0.580, GIV3; 0.922.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Total	Site
		IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III		
Year		78	78	78	78	78	78	78	78	78	79	79	79		
Cohort															
1976	P:$\bar{B}$	0.03	0.18	0.05	0.33	0.49	0.12	0.07	0.06	-0.004	-0.005	-0.02	-0.02	1.322	FIV4
	E:$\bar{B}$	0.03	0.03	0.03	0.03	0.35	0.08	0.07	0.07	0.08	0.08	0.11	0.10	1.147	
	P:$\bar{B}$	0.06	0.02	0.30	0.49	0.38	0.23	0.03	0.18	0.01	0.01	0.04	0.04	1.851	GIII4
	E:$\bar{B}$	0.06	0.07	0.07	0.07	0.08	0.09	0.08	0.44	0.18	0.28	-	-	1.650	
	P:$\bar{B}$	-0.05	0.21	0.26	0.40	1.44	0.11	0.09	0.05	0.01	0.01	0.03	0.03	1.193	GIV3
	E:$\bar{B}$	0.06	0.11	0.18	0.24	0.04	0.04	0.04	0.36	0.02	0.01	0.01	0.01	1.146	
1977	P:$\bar{B}$	0.27	0.58	0.22	1.39	0.84	-0.04	0.20	-0.21	0.18	0.16	0.01	0.01	3.780	FII2
	E:$\bar{B}$	0.16	0.18	0.20	0.53	0.48	0.09	0.10	0.09	0.04	0.13	0.07	0.13	2.336	
	P:$\bar{B}$	0.10	1.14	0.34	0.39	1.06	0.85	0.16	0.37	-0.03	-0.05	-0.09	-0.06	2.679	FIV4
	E:$\bar{B}$	0.09	0.51	0.05	0.07	0.05	0.36	0.32	0.03	0.07	0.07	0.03	0.02	1.483	
	P:$\bar{B}$	(0.47)	(0.56)	0.54	0.75	1.23	0.37	0.52	0.41	0.22	0.21	0.03	0.02	3.828	GIII4
	E:$\bar{B}$	-	-	0.11	0.23	0.05	0.13	0.05	0.36	0.23	0.39	0.36	0.47	3.458	
	P:$\bar{B}$	0	0.97	0.30	0.95	0.65	0.32	0.28	-0.01	-0.02	0.01	-0.01	-0.01	2.512	GIV3
	E:$\bar{B}$	0.09	0.29	0.03	0.09	0.48	0.05	0.16	0.04	0.08	0.22	0.17	0.10	1.817	
1978	P:$\bar{B}$	-	-	-	(1.60)	(1.56)	1.13	1.89	-0.90	0	-	-	-	(3.904)	FI2
	E:$\bar{B}$	-	-	-	-	(0.96)	0.88	0.57	1.08	(2)	-	-	-	(3.648)	
	P:$\bar{B}$	-	-	-	(1.33)	(0.40)	0.67	0.70	1.43	0.18	0.5	-0.07	-0.08	(4.55)	FII2
	E:$\bar{B}$	-	-	-	-	-	1.24	1.72	0.66	0	0	0	0	(3.57)	
	P:$\bar{B}$	-	-	-	(1.08)	(0.87)	1.82	0.42	0.54	-0.09	-0.11	-0.12	0.14	(2.351)	FIV4
	E:$\bar{B}$	-	-	-	-	-	0.57	0.48	0.05	0.05	0.05	0.07	0.06	(1.366)	
	P:$\bar{B}$	-	-	-	(0.44)	(1.09)	0.35	1.37	0.73	0.12	0.12	0	0	(6.567)	GIII4
	E:$\bar{B}$	-	-	-	-	-	1.02	0.03	0.95	0.63	1.63	0.67	(2)	(6.635)	
	P:$\bar{B}$	-	-	-	(1.00)	(1.60)	0.86	0.52	0.14	0.09	0.08	0.32	0.25	(3.518)	GIV3
	E:$\bar{B}$	-	-	-	-	-	-	0.31	0.21	0.31	0.47	0.38	0.59	(2.883)	

Table 9g Total mean annual biomass ($\bar{B}$), total annual production and elimination (ΣP, ΣE, gm m^{-2}), productivity and $\Sigma E/\bar{B}$ ratio for <u>Macoma balthica</u>. All stations. Extensive survey March 1978 - March 1979 and other relevant works.

Site	$\bar{B}$	ΣP	ΣE	$\Sigma P/\bar{B}$	$\Sigma E/\bar{B}$	Author
FI2	0.25	0.13	0.06	0.528	0.428	Present study
FII2	1.15	2.40	2.00	2.080	1.739	" "
GIII4	30.77	22.91	28.46	0.745	0.925	" "
GIV3	44.62	22.66	44.22	0.508	0.991	" "
approx FIV4	37.10	29.60	-	0.80	-	Ratcliffe (1979)
Petpeswick Inlet	1.30	1.90	-	1.5	-	Burke & Mann(1974)
Ythan	4.90	10.10	-	2.1	-	Chambers & Milne (1975b)
Lynher	0.28	0.31	-	0.9	-	Warwick & Price (1975)
San Fransisco	10.35	46.60	-	4.5	-	Nichols (1977)
Grevelingen	2.90	3.40	-	1.9	-	Wolff & de Wolf (1977)

Table 10a Presence, density and biomass of *Retusa obtusa* recorded in the literature.

Country	Area	Density (Maximum)	Biomass (Maximum)	Author(s)
Denmark	Holbaek Fjord	-	-	Petersen (1891)
Ireland	Dublin Bay	'abundant'	-	Colgan (1914)
Faroe Islands	-	-	-	Lemche (1929)
Wales	Dyfi Estuary	7 ft^{-2}	-	Beanland (1940)
Greenland	East Coast	-	-	Lemche (1941)
Denmark	Skålling, Wadden	-	-	Smidt (1944)
Denmark	Wadden Sea	20-20 m^{-2}	300 mg m^{-2}	Smidt (1951)
England	Scolt Head Island	-	-	Serventy (1960)
Denmark	Øresund	-	-	Hurst (1965)
Wales	Barry Harbour	-	-	Hurst (1965)
Denmark	Ajstrup Bigt	50 m^{-2}	-	Muus (1967)
Wales	Barry Harbour	300/51 mud	-	Smith (1967a)
Scotland	Ythan Estuary	-	-	Anderson (1971)
England	Weston-super-Mare	56 m^{-2}	-	Boyden & Little (1973)
Netherlands	Delta region	-	-	Wolff (1973)

Table 10a continued.

Country	Area	Density (Maximum)	Biomass (Maximum)	Author(s)
Denmark	Isefjord	'not very common'	-	Rasmussen (1973)
Scotland	St. Andrew's Bay	'not uncommon'	-	Laverack & Blackler (1974)
Scotland	Solway Firth	-	-	Perkins (1973)
England	Lynher Estuary	2 m^{-2}	0.6 mg m^{-2}	Warwick & Price (1975)
England	Weston-super-Mare	<100 m^{-2}	-	Little & Boyden (1976)
England	Severn Estuary	-	-	Boyden et al. (1977)
Netherlands	Grevelingen Estuary	3-9 m^{-2}	6 mg m^{-2}	Wolff & de Wolf (1977)
Scotland	Firth of Forth	-	42 mg m^{-2}	McLusky et al. (1977)
Scotland	Torry Bay - Forth	1280 m^{-2}	381.6 mg m^{-2}	Elliot (1979)
England	Spurn Bight - Humber	2000 m^{-2}	-	Ratcliffe (1979)
Netherlands	Oosterscheldte	9 m^{-2}	-	Wolff et al. (1981)
England	Spurn Bight - Humber	7740 m^{-2}	1147 gm m^{-2}	present study

Table 10b Density (No. m^{-2}) of <u>Retusa obtusa</u> between March 1978 and March 1979. Per cohort and total population stations FIV4, GIII4 and GIV3. Observed (O) and smoothed mortality curve data (S).

Month Year		III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Site
Spring 1977	O	40	30	20	20	0	-	-	-	-	-	-	-	-	FIV4
	S	40	30	20	20	-	-	-	-	-	-	-	-	-	
	O	40	20	20	0	-	-	-	-	-	-	-	-	-	GIII4
	S	40	20	20	0	-	-	-	-	-	-	-	-	-	
	O	120	60	0	-	-	-	-	-	-	-	-	-	-	GIV3
	S	120	60	0	-	-	-	-	-	-	-	-	-	-	
Autumn 1977	O	1040	1000	720	600	660	384	-	-	cont. with spring '78 (below)					FIV4
	S	1040	1000	720	685	660	384	-	-						
	O	940	780	1840	1150	830	300	240	-	" " " " "					GIII4
	S	940	780	1840	1150	830	300	240	-						
	O	1700	1560	1425	1220	1530	1487	940	-	" " " " "					GIV3
	S	1700	1560	1520	1470	1420	1230	940	-						
Spring 1978	O	-	-	-	1600	240	228	-	-	cont. with autumn '77 (below)					FIV4
	S	-	-	-	1600	240	228	-	-						
	O	-	-	-	4200	430	150	140	-	" " " " "					GIII4
	S	-	-	-	4200	430	150	140	-						
	O	-	-	-	4840	445	472	350	-	" " " " "					GIV3
	S	-	-	-	4840	470	430	350	-						

Table 10b continued.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	Site
Year		78	78	78	78	78	78	78	78	78	78	79	79	79	
Autumn	O	-	-	-	-	-	612	605	650	50	-	100	-	160	FIV4
1977	S	-	-	-	-	-	631	631	631	100	100*	100	100	100	
+															
Spring	O	-	-	-	-	-	-	380	340	60	-	140	-	20	GIII4
1978	S	-	-	-	-	-	-	380	340	100	100*	100	60	20	
Autumn	o	-	-	-	-	-	-	1000	6930	2130	-	780	-	2740	FIV4
1978	s	-	-	-	-	-	-	1000	6930	2130	1455*	780	-	-	
	o	-	-	-	-	-	-	680	4300	2320	-	1880	-	80	GIII4
	s	-	-	-	-	-	-	680	4300	2320	2100*	1880	980*	80	
	o	-	-	-	-	-	-	1800	7360	5640	-	2370	-	260	GIV3
	s	-	-	-	-	-	-	1800	7360	5640	4005*	2370	1315*	260	
Total	O	1080	1030	740	2220	900	612	1505	7580	2180	-	880	-	2900	FIV4
	S	1080	1030	740	2305	900	631	1631	7561	2230	1555*	880	(880)*	(880)**	
population															
	O	980	800	1860	5350	1260	450	1060	4640	2380	-	2020	-	100	GIII4
	S	980	800	1860	5350	1260	450	1060	4640	2420	2200*	1980	1040*	100	
	O	1820	1620	1425	6060	1975	1960	3090	7740	5720	-	2450	-	420	GIV3
	S	1820	1620	1520	6310	1910	1660	3090	7740	5760	4125*	2490	1435*	380	

* by interpolation

** for the sake of production studies, immigration at FIV4 is ommitted from smoothed curve data.

Table 10c Mean individual shell length (mm) and flesh weight (mg) of <u>Retusa obtusa</u>. March 1978 - March 1979.

Per cohort. Stations FIV4, GIII4 and GIV3.

Month Year		III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	site
spring	l	2.75	2.80	2.80	3.00	-	-	-	-	-	-	-	-	-	FIV4
1977	w	0.72	0.76	0.75	0.96	-	-	-	-	-	-	-	-	-	
	l	2.80	2.40	2.80	-	-	-	-	-	-	-	-	-	-	GIII4
	w	0.78	0.45	0.75	-	-	-	-	-	-	-	-	-	-	
	l	3.37	3.40	-	-	-	-	-	-	-	-	-	-	-	GIV3
	w	1.43	1.47	-	-	-	-	-	-	-	-	-	-	-	
autumn	l	1.03	1.32	1.79	2.07	2.32	3.02	-	-	cont. with spring '79 (below)					FIV4
1977	w	0.04	0.11	0.18	0.29	0.42	0.93	-	-						
	l	0.92	1.34	1.55	2.00	2.04	2.55	2.92		" " " " "					GIII4
	w	0.03	0.08	0.13	0.24	0.29	0.32	0.88							
	l	1.04	1.41	1.68	1.94	2.29	2.55	3.23		" " " " "					GIV3
	w	0.04	0.10	0.16	0.24	0.41	0.56	1.02							
spring	l	-	-	-	0.12	1.05	2.48	-	-	cont. with autumn '77 (below)					FIV4
1978	w	-	-	-	0.006	0.03	0.38	-	-						
	l	-	-	-	0.12	0.93	1.50	2.29	-	" " " " "					GIII4
	w	-	-	-	0.006	0.03	0.11	0.32							
	l	-	-	-	0.15	0.98	1.33	2.53	-	" " " " "					GIV3
	w	-	-	-	0.006	0.04	0.07	0.52							

Table 10c continued.

month year		III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	site
Autumn 1977 + Spring 1978	1	-	-	-	-	-	2.89	3.19	3.83	3.56	3.63	3.70	3.41	3.13	FIV4
	w	-	-	-	-	-	0.73	1.13	1.66	1.76	1.71	1.67	1.39	1.11	
	1	-	-	-	-	-	-	2.68	3.13	3.53	3.45	3.37	3.39	3.40	GIII4
	w	-	-	-	-	-	-	0.68	1.35	1.69	1.56	1.44	1.49	1.53	
	1	-	-	-	-	-	-	3.04	3.49	3.85	3.60	3.35	3.47	3.58	GIV3
	w	-	-	-	-	-	-	0.88	1.81	2.24	1.85	1.45	1.62	1.80	
Autumn	1	-	-	-	-	-	-	0.12	0.15	0.85	0.90	0.95	0.79	0.63	FIV4
	w	-	-	-	-	-	-	0.006	0.006	0.029	0.032	0.033	0.026	0.018	
	1	-	-	-	-	-	-	0.12	0.21	0.89	0.96	1.03	1.19	1.35	GIII4
	w	-	-	-	-	-	-	0.005	0.008	0.043	0.046	0.049	0.065	0.081	
	1	-	-	-	-	-	-	0.16	0.24	1.13	1.09	1.05	0.97	0.88	GIV3
	w	-	-	-	-	-	-	0.006	0.009	0.042	0.037	0.032	0.030	0.028	

* by interpolation

Table 10d Observed and idealized dry flesh weights of *Retusa obtusa* for animals of a given length. Station GIV3, May 1977.

l = shell length (mm)
wt = observed weight (mg)
n = number of animals weighed
wt' = idealized weight from regression equation (mg).

l	wt	n	wt'
0.1	-	-	0.000009
0.3	-	-	0.00038
0.5	-	-	0.0022
0.7	0.0035	57	0.0068
0.9	0.025	128	0.016
1.1	0.048	120	0.032
1.3	0.047	154	0.056
1.5	0.079	185	0.091
1.7	0.14	188	0.139
1.9	0.21	112	0.202
2.1	0.27	12	0.284
2.3	0.39	16	0.382
2.5	0.55	24	0.514
2.7	0.63	41	0.669
2.9	0.80	62	0.852
3.1	1.00	13	1.069
3.3	1.20	13	1.322
3.5	-	-	1.614
3.7	-	-	1.950
3.9	-	-	2.332
4.1	3.0	1	2.764
4.3	-	-	3.250

Table 10e Cohort and total population biomass (mg m^{-2}) of <u>Retusa obtusa</u> March 1978 - March 1979.

Stations FIV4, GIII4 and GIV3.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII 78	I 79	II 79	III 79	Mean annual	Site
Spring 1977	29	23	15	19	0	-	-	-	-	-	-	-	-	-	FIV4
	31	9	15	0	-	-	-	-	-	-	-	-	-	-	GIII4
	171	88	0	-	-	-	-	-	-	-	-	-	-	-	GIV3
Autumn 1977	41	108	127	196	276	359	-	cont.	with	spring	1978	(below)		-	FIV4
	26	60	231	273	244	95	212	"	"	"	"	"		-	GIII4
	61	155	237	356	584	693	955	"	"	"	"	"		-	GIV3
Spring 1978	-	-	-	8	8	87	-	cont.	with	autumn	1977	(below)			FIV4
	-	-	-	23	13	16	45	"	"	"	"	"			GIII4
	-	-	-	30	19	33	181	"	"	"	"	"			GIV3
Autumn '77	-	-	-	-	-	460	711	1048	176	171	167	139	111	-	FIV4
+	-	-	-	-	-	-	257	459	169	156	144	89	31	-	GIII4
Spring '78	-	-	-	-	-	-	1136	688	269	222	174	195	216	-	GIV3
Autumn 1978	-	-	-	-	-	-	6	47	61	43	26	37	49	-	FIV4
	-	-	-	-	-	-	4	36	99	90	80	43	7	-	GIII4
	-	-	-	-	-	-	12	63	238	157	75	42	10	-	GIV3
Total Population	70	201	142	223	283	446	717	1095	237	215	193	177	160	313	FIV4
	57	69	246	296	256	111	261	495	268	246	224	131	37	227	GIII4
	232	244	237	385	604	723	1147	751	507	378	249	238	226	543	GIV3

Table 10f Production and elimination (mg m^{-2}) of *Retusa obtusa* per cohort and total population. Monthly and total annual (March 1978 - March 1979). Sites FIV4, GIII4 and GIV3.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Total	Site
		IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III		
Year		78	78	78	78	78	78	78	78	78	79	79	79		
Spring 1977	P	2	-1	4	0	-	-	-	-	-	-	-	-	5	FIV4
	E	7	8	0	19	-	-	-	-	-	-	-	-	34	
	P	-10	6	0	-	-	-	-	-	-	-	-	-	-4	GIII4
	E	12	6	15	-	-	-	-	-	-	-	-	-	27	
	P	4	0	-	-	-	-	-	-	-	-	-	-	4	GIV3
	E	87	88	-	-	-	-	-	-	-	-	-	-	175	
Autumn 1977	P	70	58	79	89	270	-	cont.	with	spring	1978	(below)		-	FIV4
	E	3	40	8	9	187	-	"	"	"	"	"		-	
	P	43	89*	167	56	14	152	"	"	"	"	"		-	GIII4
	E	8	0	125	85	162	36	"	"	"	"	"		-	
	P	104	87	129	244	202	491	"	"	"	"	"		-	GIV3
	E	10	87	10	16	93	229	"	"	"	"	"		-	
Spring 1978	P	-	-	8	24	82	-	cont.	with	autumn	1977	(below)		-	FIV4
	E	-	-	-	24	3	-	"	"	"	"	"		-	
	P	-	-	23	55	22	31	"	"	"	"	"		-	GIII4
	E	-	-	-	54	19	2	"	"	"	"	"		-	
	P	-	-	29	96	12	192	"	"	"	"	"		-	GIV3
	E	-	-	-	105	3	23	"	"	"	"	"		-	

Table 10f continued.

Month		III IV	IV V	V VI	VI VII	VII VIII	VIII IX	IX X	X XI	XI XII	XII I	I II	II III	Total	Site
Year		78	78	78	78	78	78	78	78	78	79	79	79		
Autumn	P	-	-	-	-	-	253	337	35	-5	-5	-28	-28	1240	FIV4
1977	E	-	-	-	-	-	0	0	909	0	0	0	0	1182	
+	P	-	-	-	-	-	-	243	74	-12	-12	3	2	950	GIII4
Spring	E	-	-	-	-	-	-	41	365	0	0	59	60	1015	
1978	P	-	-	-	-	-	-	785	108	-47	-47	20	20	2425	GIV3
	E	-	-	-	-	-	-	1225	527	0	0	0	0	2328	
Autumn	P	-	-	-	-	-	6	40	99	4	3	-	-*	152	FIV4
1978	E	-	-	-	-	-	-	-	86	20	22	-	-	128	
	P	-	-	-	-	-	4	30	116	-1	-1	1	0	148	GIII4
	E	-	-	-	-	-	-	-	50	9	9	39	56	164	
	P	-	-	-	-	-	12	51	219	-26	-17	6	7	252	GIV3
	E	-	-	-	-	-	-	-	43	65	56	35	39	238	
Total	P	72	57	91	113	352	259	377	134	-1	-2	-28	-28	1380	FIV4
	E	10	48	8	42	190	0	0	995	20	22	0	0	1544	
	P	33	95	190	111	36	183	273	190	-13	-13	4	2	1097	GIII4
	E	20	6	140	139	181	38	41	415	9	9	98	116	1207	
	P	108	87	158	340	214	683	836	327	-73	-64	26	27	2681	GIV3
	E	97	175	10	121	96	252	1225	570	65	56	35	39	2741	

* immigration not included in production figures.

Table 10g Productivity (P/$\bar{B}$ and E/$\bar{B}$ ratios) of <u>Retusa obtusa</u>. Monthly per cohort and annual value for whole population. March 1978 - March 1979. Sites FIV4, GIII4 and GIV3.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Site
		IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	
Year		78	78	78	78	78	78	78	78	78	79	79	79	
Spring	P/$\bar{B}$	0.04	0.01	0.17	(0)	-	-	-	-	-	-	-	-	FIV4
1977	E/$\bar{B}$	0.29	0.04	0	(2)	-	-	-	-	-	-	-	-	
	P/$\bar{B}$	-0.27	0.36	(0)	-	-	-	-	-	-	-	-	-	GIII4
	E/$\bar{B}$	0.61	0.50	(2)	-	-	-	-	-	-	-	-	-	
	P/$\bar{B}$	0.20	(0)	-	-	-	-	-	-	-	-	-	-	GIV3
	E/$\bar{B}$	0.67	(2)	-	-	-	-	-	-	-	-	-	-	
Autumn	P/$\bar{B}$	0.73	0.34	0.35	0.27	0.59	-	cont.	with	spring	1978	(below)		FIV4
1977	E/$\bar{B}$	0.04	0.34	0.05	0.04	0.59	-	"	"	"	"	"		
	P/$\bar{B}$	0.77	0.51	0.45	0.14	0.05	0.76	"	"	"	"	"		GIII4
	E/$\bar{B}$	0.19	0	0.49	0.32	0.95	0.23	"	"	"	"	"		
	P/$\bar{B}$	0.15	0.32	0.31	0.38	0.22	0.42	"	"	"	"	"		GIV3
	E/$\bar{B}$	0.09	0.44	0.03	0.03	0.14	0.28	"	"	"	"	"		
Spring	P/$\bar{B}$	-	-	(2)	1.90	0.90	-	cont.	with	autumn	1977	(below)		FIV4
1978	E/$\bar{B}$	-	-	-	3.10	0.05	-	"	"	"	"	"		
	P/$\bar{B}$	-	-	(2)	1.86	1.01	0.81	"	"	"	"	"		GIII4
	E/$\bar{B}$	-	-	-	3.04	1.32	0.07	"	"	"	"	"		
	P/$\bar{B}$	-	-	(2)	2.40	0.49	1.60	"	"	"	"	"		GIV3
	E/$\bar{B}$	-	-	-	4.18	0.13	0.22	"	"	"	"	"		

Table 10g coninued.

Month		III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	Site
		IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	
Year		78	78	78	78	78	78	78	78	78	79	79	79	
Autumn	P/$\bar{B}$	-	-	-	-	-	0.31	0.27	0.03	-0.02	-0.02	-0.12	-0.14	FIV4
1977	E/$\bar{B}$	-	-	-	-	-	0	0	1.49	0	0	0	0	
+	P/$\bar{B}$	-	-	-	-	-	-	0.50	0.14	-0.05	-0.05	-0.02	0.02	GIII4
Spring	E/$\bar{B}$	-	-	-	-	-	-	0.11	1.16	0	0	0.50	1.01	
1978	P/$\bar{B}$	-	-	-	-	-	-	0.53	0.13	-0.12	-0.15	0.08	0.07	GIV3
	E/$\bar{B}$	-	-	-	-	-	-	1.34	1.10	0	0	0	0	
Autumn	P/$\bar{B}$	-	-	-	-	-	(2)	1.36	1.28	0.05	0.05	-	-	FIV4
1978	E/$\bar{B}$	-	-	-	-	-	-	-	1.59	0.39	0.03	-	-	
	P/$\bar{B}$	-	-	-	-	-	(2)	1.39	1.36	-0.01	-0.01	0	0	GIII4
	E/$\bar{B}$	-	-	-	-	-	-	-	0.75	0.10	0.11	0.63	2.25	
	P/$\bar{B}$	-	-	-	-	-	(2)	1.20	1.20	-0.08	-0.09	0.06	0.15	GIV3
	E/$\bar{B}$	-	-	-	-	-	-	-	0.28	0.33	0.48	0.60	1.47	

Total population annual ΣP:$\bar{B}$ FIV4 - 4.47 GIII4 - 4.83 GIV3 - 4.94

ΣE:$\bar{B}$ FIV4 - 4.30 GIII4 - 5.31 GIV3 - 5.05

Table 10h Results of feeding trials on *Retusa obtusa*. Single pots containing 10 adult or juvenile *Retusa* plus 20 potential prey organisms. Results after one week. Prey size in mm.

s = survived
m = died but not eaten
d = disappeared

Adult *Retusa*	*Macoma* <0.5	*Macoma* 0.5-1.0	*Macoma* 1.0-1.5	*Macoma* 1.5-2.0	*Hydrobia* <0.5	*Hydrobia* 0.5-1.0	*Hydrobia* 1.0-2.0	*Retusa* 0.5	*Retusa* 0.5-1.5
s	2	1	8	19	20	20	20	8	7
m	0	0	2	1	0	0	0	0	2
d	18	19	10	0	0	0	0	12	9
Control									
s	19	15	20	20	20	20	20	15	19
m	1	5	0	0	0	0	0	5	1
d	0	0	0	0	0	0	0	0	0
Juvenile *Retusa*									
s	17	20	18	20	20	20	20	-	-
m	3	0	2	0	0	0	0	-	-
d	0	0	0	0	0	0	0	-	-

Table 10h continued.

Adult <u>Retusa</u>	Harpacticoids	Ostracods	Nematodes (large)	<u>Hediste</u> smallest	<u>Pygospio</u> (ex tube)	Foraminifera	Foraminifera (no silt)
s	16	20	23!	20	27!	0	0
m	0	0	0	0	0	0	0
d	4	0	0	0	0	20	20
Control							
s	18	19	14	19	14	0	1
m	0	1	0	0	0	15	13
d	2	0	6	1	6	5	6
Juvenile <u>Retusa</u>							
s	20	14	12	19	18	0	0
m	0	6	0	0	0	4	16
d	0	0	8	1	2	16	4

Table 11a Monthly biomass, mean monthly biomass and percentage contribution to total by main species of macrofauna.

Intensive survey. Station FI2 March 1978 - March 1979.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	Mean	% of total
E. benedii	0.27	0.24	0.21	0.28	0.47	0.44	0.80	1.29	0.80	0.88	0.96	0.81	0.66	0.59	5.0
H. diversicolor	6.45	4.96	6.18	7.30	14.79	15.48	13.86	13.93	11.55	10.27	8.99	6.70	4.42	9.61	80.8
H. ulvae	0.95	1.17	1.77	1.55	2.27	0.63	0.95	0	1.72	1.17	0.62	0.70	0.78	1.13	9.4
M. balthica	0	0.80	0.03	0.01	0.89	0.01	0.01	0.04	1.21	0.68	0.14	2.23	4.32	0.57	4.8
Total	7.67	7.14	8.19	9.14	18.42	16.56	15.62	15.26	15.28	13.00	10.71	10.44	10.18	11.90	100

* by interpolation.

Table 11b Monthly biomass, mean monthly biomass and percentage contribution to total by main species of macrofauna.

Intensive survey. Station FII2 March 1978 - March 1979.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Mean	% of total
Year	78	78	78	78	78	78	78	78	78	78	79	79	79		
E. benedii	0.02	0.01	0.01	0.02	0.05	0.05	0.05	0.08	0.06	0.08	0.09	0.09	0.09	0.05	0.4
H. diversicolor	1.63	0.84	0.02	1.48	2.27	23.61	24.47	29.41	20.72	11.74	3.91	2.32	0.72	9.47	82.6
P. elegans	0.01	0.01	0.02	0.02	0.03	0.03	0.01	0.03	0.05	0.03	0.01	0.01	0.01	0.02	0.2
S. shrubsolii	0.01	0.01	0.01	0.01	0.01	0.03	0.13	0.18	0.13	0.09	0.05	0.02	0	0.05	0.4
H. ulvae	0.56	0.64	0.05	0.25	1.31	2.69	1.76	0.44	0.22	0.19	0.17	0.23	0.28	0.72	6.4
M. balthica	3.01	3.21	0.59	0.53	0.70	1.51	0.64	0.63	0.52	0.60	1.96	0.59	0.52	1.15	10.0
Total	5.24	4.72	0.70	2.31	3.58	27.81	27.16	30.77	21.70	12.73	6.19	3.26	1.62	11.46	100

* by interpolation.

Table 11c Monthly biomass, mean monthly biomass and percentage contribution to total by main species of macrofauna.

Intensive survey. Station FIV4 March 1978 - March 1979.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	Mean	% of total
E. longa	0.30	0.07	0.03	0.19	0.41	0.95	0.78	1.20	1.22	1.30	1.37	1.28	1.18	0.62	2.2
N. hombergi	3.68	2.78	3.61	5.25	6.08	6.99	6.99	8.20	10.05	5.89	5.18	3.16	1.48	5.33	18.5
H. diversicolor	0.89	0.81	1.88	1.90	1.68	3.62	4.75	0.82	0.34	0.81	1.34	1.38	0.13	1.50	5.2
P. elegans	0.04	0.06	0.03	0.04	0.03	0.41	0.02	0.06	0.19	0.22	0.25	0.18	0.10	0.10	0.3
S. shrubsolii	0.01	0.01	0.01	0	0	0.02	0.06	0.16	0.10	0.06	0.03	0.02	0.01	0.03	0.1
H. ulvae	0.43	0.97	0.39	0.81	0.06	0.28	0.26	0.39	0.38	0.42	0.46	0.43	0.40	0.44	1.6
R. obtusa	0.07	0.20	0.14	0.22	0.28	0.45	0.71	1.10	0.24	0.22	0.19	0.18	0.16	0.31	1.1
M. balthica	20.83	17.40	16.76	18.37	20.14	24.75	26.01	24.80	26.00	22.41	17.92	15.83	14.03	20.44	71.10
Total	26.25	22.30	22.05	26.78	28.68	37.46	39.58	36.59	38.52	31.33	26.74	22.46	17.49	28.77	100

* *by interpolation.*

Table 11d Monthly biomass, mean monthly biomass and percentage contribution to total by main species of macrofauna.

Intensive survey. Station GIII4 March 1978 - March 1979.

Month	III	IV	V	VI	VII	VIII	IX	X	XI	XII*	I	II*	III	Mean	% of total
Year	78	78	78	78	78	78	78	78	78	78	79	79	79		
E. longa	0.26	0.04	0.02	0.14	0.25	0.64	1.23	2.03	1.85	1.69	1.52	0.95	0.37	0.76	2.10
N. hombergi	3.25	1.97	4.41	2.15	3.28	5.80	5.90	6.56	2.06	2.18	2.29	1.15	0.01	3.16	8.8
H. diversicolor	0.78	0.45	1.19	0.03	1.10	2.56	0.75	0.15	0.30	0.15	0	0	0	0.57	1.6
P. elegans	0.13	0.03	0.04	0.12	0.49	0.17	0.15	0.14	0.46	0.30	0.13	0.07	0.01	0.16	0.4
S. shrubsolii	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.12	0.11	0.13	0.08	0.04	0.04	0.04	0.1
H. ulvae	0.59	0.73	0.05	0.21	0.60	0.98	1.20	0.74	0.67	0.33	0	0	0	0.47	1.4
R. obtusa	0.06	0.07	0.25	0.30	0.26	0.11	0.26	0.50	0.27	0.25	0.22	0.13	0.04	0.23	0.6
M. balthica	32.60	30.56	27.13	29.92	35.01	36.85	37.63	34.82	33.08	28.97	25.01	24.60	23.83	30.77	85.1
Total	37.68	33.82	32.83	32.87	41.10	47.12	47.14	45.03	38.80	33.50	29.25	26.94	24.31	36.16	100

* by interpolation.

Table 11e Monthly biomass, mean monthly biomass and percentage contribution to total by main species of macrofauna.

Intensive survey. Station GIV3 March 1978 - March 1979.

Month Year	III 78	IV 78	V 78	VI 78	VII 78	VIII 78	IX 78	X 78	XI 78	XII* 78	I 79	II* 79	III 79	Mean	% of total
E. longa	0.30	0.07	0.07	0.19	0.40	0.89	1.41	2.44	2.29	1.73	1.18	0.94	0.70	0.90	1.5
N. hombergi	3.85	5.08	2.59	3.85	3.03	4.24	6.27	4.06	3.29	2.37	2.18	1.69	1.30	3.37	5.5
H. diversicolor	0.55	1.82	0.42	1.04	1.66	2.17	1.61	1.30	0.50	0.46	0.38	0.41	0.48	0.96	1.6
P. elegans	0.21	0.15	0.21	0.39	0.31	0.29	0.41	0.46	0.43	0.40	0.36	0.34	0.32	0.30	0.5
S. shrubsolii	0.01	0.01	0.01	0.01	0.01	0.02	0.05	0.16	0.14	0.09	0.03	0.01	0.01	0.04	0.06
H. ulvae	0.93	0.92	0.47	0.57	0.35	0.60	0.77	0.30	0.16	0.26	0.35	0.38	0.41	0.53	0.9
R. obtusa	0.23	0.24	0.24	0.39	0.60	0.72	1.15	0.75	0.51	0.38	0.25	0.24	0.23	0.54	0.9
C. edule	11.83	9.05	5.74	9.14	13.95	12.35	19.51	19.30	9.67	8.97	8.28	8.33	8.52	9.67	15.9
M. balthica	62.54	45.53	52.18	47.06	52.95	57.32	46.99	41.81	38.52	25.98	33.80	32.34	31.20	44.62	73.2
Total	80.45	62.87	61.93	62.64	73.26	78.60	78.17	70.58	55.51	40.64	46.81	44.68	43.17	60.93	100

* by interpolation.

Table 11f Total annual production (P), elimination (E, gm m^{-2}) and percentage of total (%) by main species of macrofauna at intensive survey sites. March 1978 – March 1979.

		FI2	FII2	FIV4	GIII4	GIV3
E. benedii	P	1.8[2]	0.2[2]	0	0	0
	%	6.2	0.6	-	-	-
	E	1.8[1]	0.2[1]	0	0	0
	%	5.4	0.6	-	-	-
N. hombergi	P	0	0	13.9	7.6	7.4
	%	-	-	35.0	20.7	16.3
	E	0	0	16.16	9.4	9.9
	%	-	-	32.3	20.8	13.5
H. diversicolor	P	25.3	21.5[3]	2.8[3]	1.1[3]	1.8[3]
	%	87.5	86.8	7.0	3.0	4.0
	E	29.9	29.5[3]	4.5[3]	2.2[3]	3.2[3]
	%	89.3	87.8	9.0	4.9	4.4
E. longa	P	0	0.7	2.3	2.1	2.8
	%	-	1.9	5.8	5.7	6.2
	E	0	0.4	1.4	2.0	2.4
	%	-	1.2	2.8	4.4	3.3
P. elegans) *S. shrubsolii*)	P	0	0.4	0.8	1.1	1.8
	%	-	1.1	2.1	3.0	4.0
	E	0	0.4[1]	0.8[1]	1.1[1]	1.8[1]
	%	-	1.2	1.6	2.4	2.5
H. ulvae	P	1.7[4]	1.1[4]	0.7[4]	0.8[4]	0.8[4]
	%	5.9	3.0	1.8	2.2	1.8
	E	1.7[1]	1.1[1]	0.7[1]	0.8[1]	0.8[1]
	%	5.1	3.3	1.4	1.8	1.1
R. obtusa	P	0	0	1.4	1.1	2.7
%	%	-	-	3.5	3.0	5.9
	E	0	0	1.3	1.2	2.7
	%	-	-	2.6	2.7	3.7
C. edule	P	0	?	?	?	5.4
	%	-				11.9
	E	0	?	?	?	8.3
	%	-				11.3
M. balthica	P	0.1	2.4	17.8	22.9	22.7
	%	0.3	6.6	44.8	62.4	50.0
	E	0.1	2.0	25.1	28.5	44.2
	%	0.3	5.9	50.2	63.1	60.3
Total	P	28.9	36.3	39.7	36.7	45.4
	E	33.5	33.6	50.0	45.2	73.3

1 assuming $E \,\hat{=}\, P$
2 assuming a P:B ratio of 3 (Sanders; 1956)
3 using P:B ratio calculated for other sites in Spurn Bight
4 assuming a P:B ratio of 1.51 (Elliot; 1979, Wolff & de Wolf; 1977)

Table 11g Values of total community biomass and production. Present study and studies elsewhere.

Area	Community type	Total biomass gm m^{-2}	Total production gm m^{-2}	Author
Buzzards Bay Massachusetts	Subtidal *Macoma*	12.2	-	Sanders (1960)
Petpeswick Inlet Nova Scotia	*Macoma* (molluscs only)	20.5	21.2	Burke & Mann (1974)
S.E. England estuaries	mainly *Macoma*	15.9 - 125.2	-	Kay & Knights (1971)
Lynher estuary Cornwall	*Macoma*/*Nephtys*	13.24	13.31	Warwick & Price (1975)
Grevelingen estuary	*Macoma*	mean 25.7	mean 50.0	Wolff & de Wolf (1971)
Dutch Wadden Sea	*Macoma*	17.5 - 46.0	-	Beukema (1976)
San Fransisco Bay	E.Pacific *Macoma*	13.24	53 - 100	Nicholls (1977)
Orwell estuary, Kent	varied *Macoma*/*Tellina*	52.9	-	Boorman & Ranwell (1977)
Stour estuary, Kent	" " "	32.1	-	
Blackwater estuary, Kent	" " "	11.2	-	
Skeffling, Humber	*Macoma*	20.4	23.3	Ratcliffe (1979)
Paull, Humber	*Hediste*/*Lumbricillus*	16.0	35.5	
Station FI2 1978-79	*Macoma*	11.9	28.9	Present study
FII2 "	"	11.5	36.3	
FIV4 "	"	28.8	39.7	
GIII4 "	"	36.2	36.7	
GIV3 "	"	60.9	45.4	
mean TOPSILT 1977		27.5	57.4	
mean MIDMUD 1977		33.6	37.6	
mean SAND 1977		6.0	4.1	

Table 11h Estimates of total standing crop biomass (tonnes) of species and areas of Spurn Bight mudflats from combination of mean values derived from S.P.S.S. delimitation of extensive survey communities to total area assumed to be covered by each community. May 1977.

	Spartina zone	TOPSILT community	MIDMUD community	SAND community	Total	% of total
E. benedii	1.3	4.7	0.4	-	6.4	0.85
E. longa[1]	-	-	13.2	-	13.2	1.8
H. diversicolor	8.7	12.7	25.3	-	46.7	6.2
N. hombergi	-	0.9	61.9	1.9	64.7	8.6
N. cæca	-	-	2.6	7.4	10.0	1.3
Spionids	-	0.2	3.9	-	4.1	0.54
M. balthica	0.2	59.6	321.1	32.0	412.9	55.1
C. edule	-	0.02	134.2	3.9	138.1	18.4
H.ulvae	14.1	13.1	19.0	0.2	46.4	6.2
R. obtusa	-	0.2	5.1	-	5.3	0.7
Tanaid	-	-	-	0.5	0.5	0.07
B. pilosa	-	-	-	0.9	0.9	0.12
Total area (ha)	91	332	1747	786	2956	-
Total biomass	24.3	91.5	586.7	46.8	749.2	-
% of total 3.2	3.2	12.2	78.3	6.2	-	-
gm m^{-2}	26.7	27.5	33.6	6.0	25.3	-

[1] calculated entirely from intensive survey data.

Table 11j Estimates of total production (P) and elimination (E, tonnes per year) of species and regions of Spurn Bight mudflats derived by extrapolation of P:B May and E:B May ratios to mean biomass values arrived from S.P.S.S. delimitation of extensive survey communities to total area assumed to be covered by each community.

		Spartina	TOPSILT	MIDMUD	SAND	Total	% Total
E. benedii[1]	P	3.9	0.7	-	-	4.6	0.50
	E	3.9	0.7	-	-	4.6	0.42
E. longa[2]	P	-	-	41.9	-	41.9	4.5
	E	-	-	33.4	-	17.5	1.6
H. diversicolor	P	22.2	42.0	83.4	-	147.6	15.9
	E	27.1	39.8	79.2	-	146.1	13.4
N. hombergi	P	-	2.2	141.0	4.3	147.5	15.7
	E	-	2.6	161.3	4.9	168.8	15.4
N. cæca	P	-	-	6.0	17.0	23.0	2.5
	E	-	-	6.8	19.4	26.2	2.4
Spionids[1]	P	-	1.3	21.5	-	22.8	2.5
	E	-	1.3	21.5	-	22.8	2.1
M. balthica	P	0.1	123.9	229.0	8.3[4]	361.3	39.0
	E	0.05	103.6	339.0	29.5[4]	472.2	43.2
C. edule	P	-	0.01	80.5	2.4	82.9	8.9
	E	-	0.02	116.8	3.4	120.2	11.0
H. ulvae[1]	P	21.3	19.8	28.7	0.3	70.1	7.6
	E	21.3	19.8	28.7	0.3	70.1	6.4
R. obtusa	P	-	1.0	24.0	-	25.0	2.7
	E	-	1.1	27.7	-	25.8	2.4
Total area		91	332	1747	786	2956	-
Total	P	47.5	190.9	656.0	32.3	926.7	-
	E	52.4	168.9	814.4	57.5	1093.2	-
% of total	P	5.1	20.6	70.8	3.5	-	-
	E	4.8	15.5	74.5	5.3	-	-
gm m^{-2} y^{-1}	P	52.2	57.5	37.6	4.1	31.3	-
	E	57.6	50.9	46.6	7.3	37.0	-

1 assuming P = E
2 derived entirely from intensive survey data
3 assuming P:B ratio = that of N. hombergi
4 assuming P:B/& E:B ratios equal to that of older cohorts elsewhere.

Table 11k Total numbers of bird feeding days per species in the northern outer Humber flats over the period mid March 1978 - mid March 1979, derived from data in Tasker & Milsom (1979), extrapolated to total energy consumption and total food intake (a.f.d.w.) using trophic equations of Wolff et al. (1975) and Evans et al. (1979).

	Total bird days	Kcal ($x10^6$)	tonnes organic material
Oystercatcher	372327	17.5	3.5
Ringed plover	20256	0.53	0.11
Grey plover	51492	1.34	0.27
Turnstone	75530	1.13	0.23
Curlew	327803	24.26	4.85
Whimbrel	4689	0.35	0.07
Bar tailed godwit	63403	1.84	0.37
Redshank	548470	9.87	1.97
Greenshank	1241	0.02	0.004
Knot	1470631	26.47	5.29
Dunlin	3383988	33.8	6.76
Sanderling	13818	0.14	0.03
Brent goose	7653	0.75	0.15
Shelduck	200631	18.26	3.65
Wigeon	43729	2.62	0.52
Teal	21815	0.94	0.19
Mallard	264248	21.93	4.39
Pintail	20968	1.49	0.30
		163.24	32.65

FIGURES

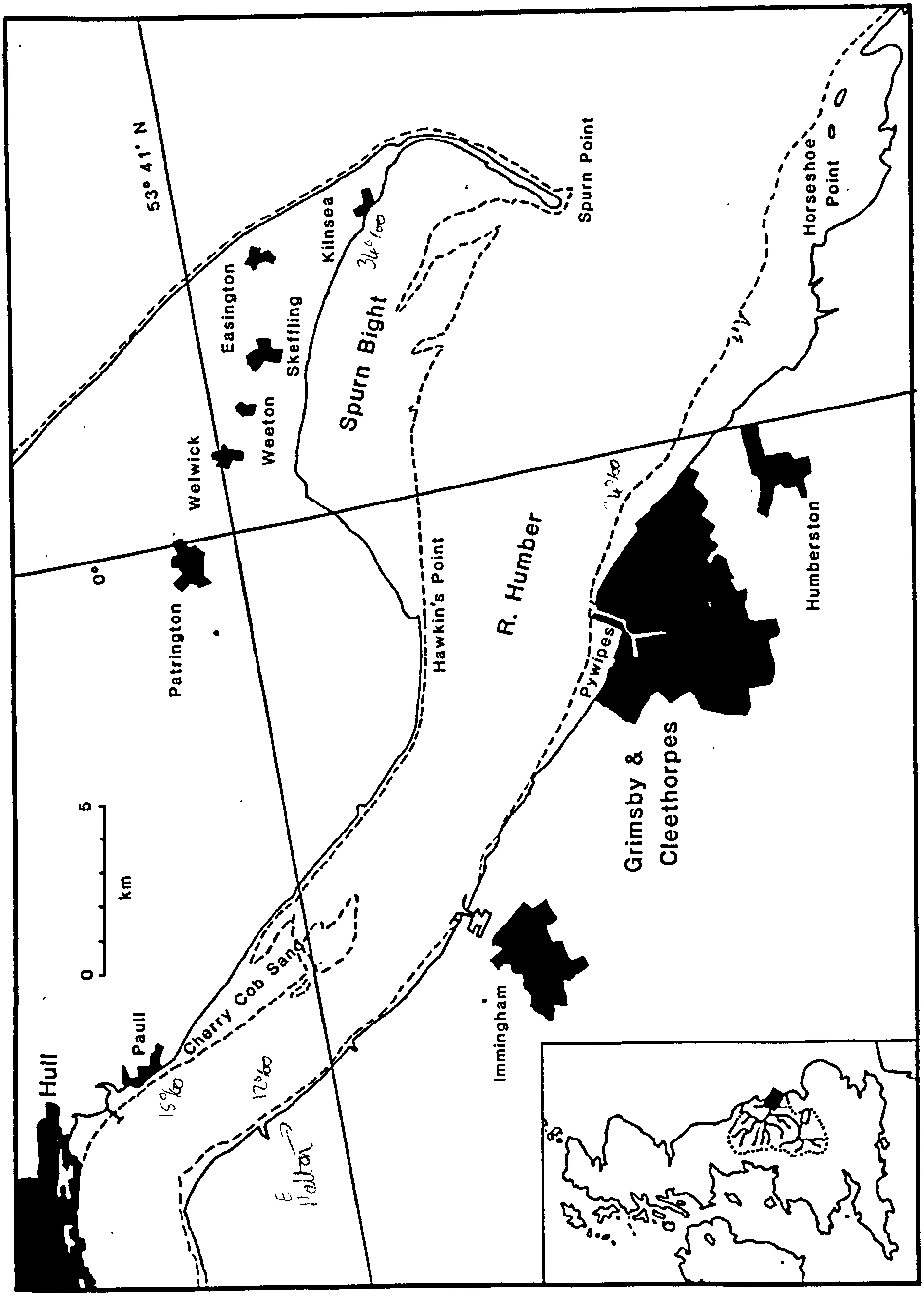


Figure 2i The outer Humber Estuary (inset location and drainage basin).

Figure 2ii Drainage and nomenclature of Spurn Bight Flats taken from aerial photographs 23 VI 76. Spartina in black

Figure 2iii Sediment types of Spurn Bight Flats taken from field visits and remote sensing.

Figure 2iv Location of extensive survey sampling stations in Spurn Bight.

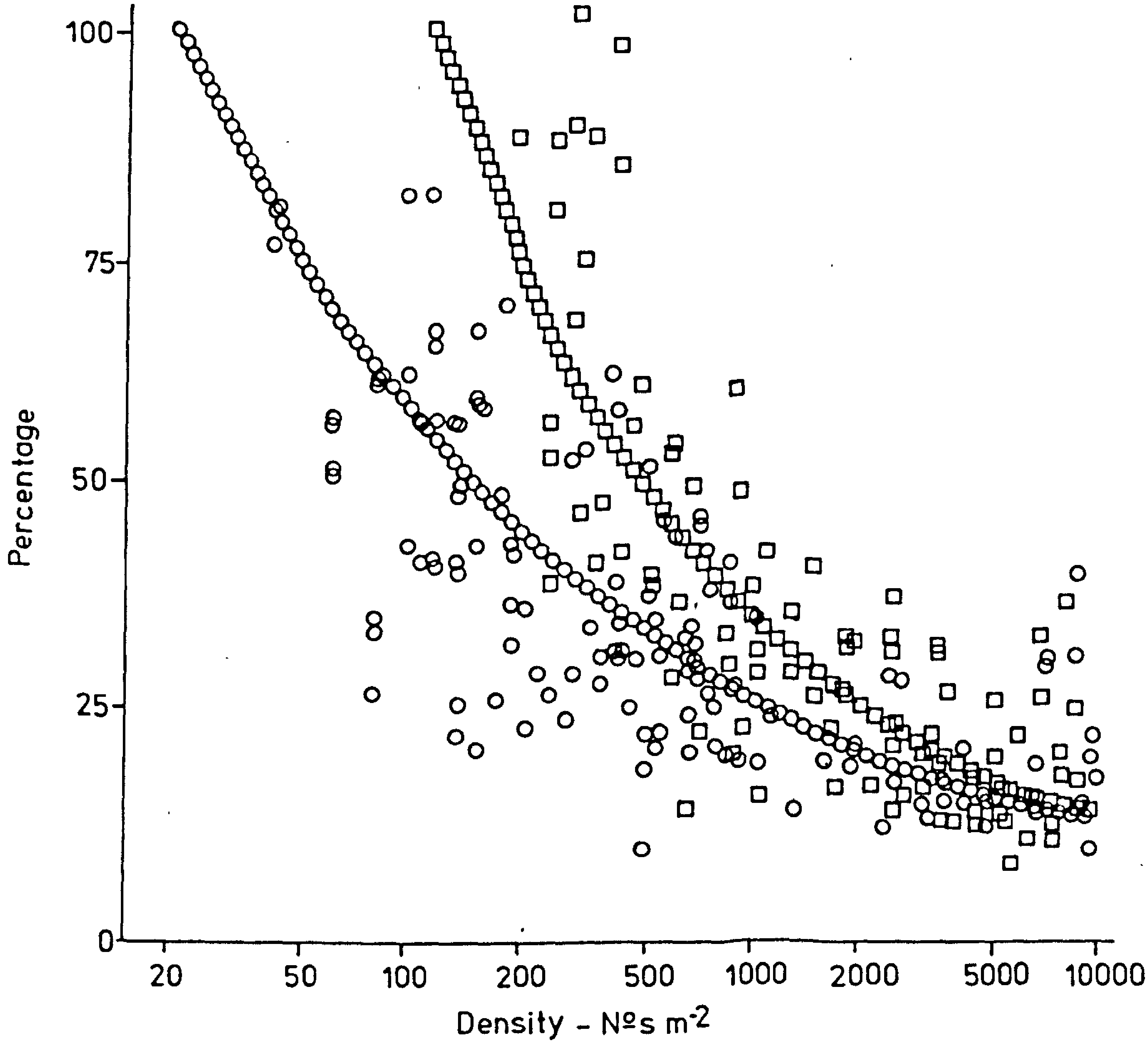


Figure 2v 95% confidence limits expressed as percentage of sample mean as a function of estimated population density from mean of 5 samples. Circles - results of 10x10x20 cm deep cores. Squares - results of 4cm diam x 10cm deep cores.

Regression equations:-

(10x10x20) $\frac{\text{95\% limit}}{\text{mean}} \times 100 = 292 \times \text{density}^{-0.35}$ $r = 0.56$

(4cm diam) $\frac{\text{95\% limit}}{\text{mean}} \times 100 = 998 \times \text{density}^{-0.48}$ $r = 0.46$

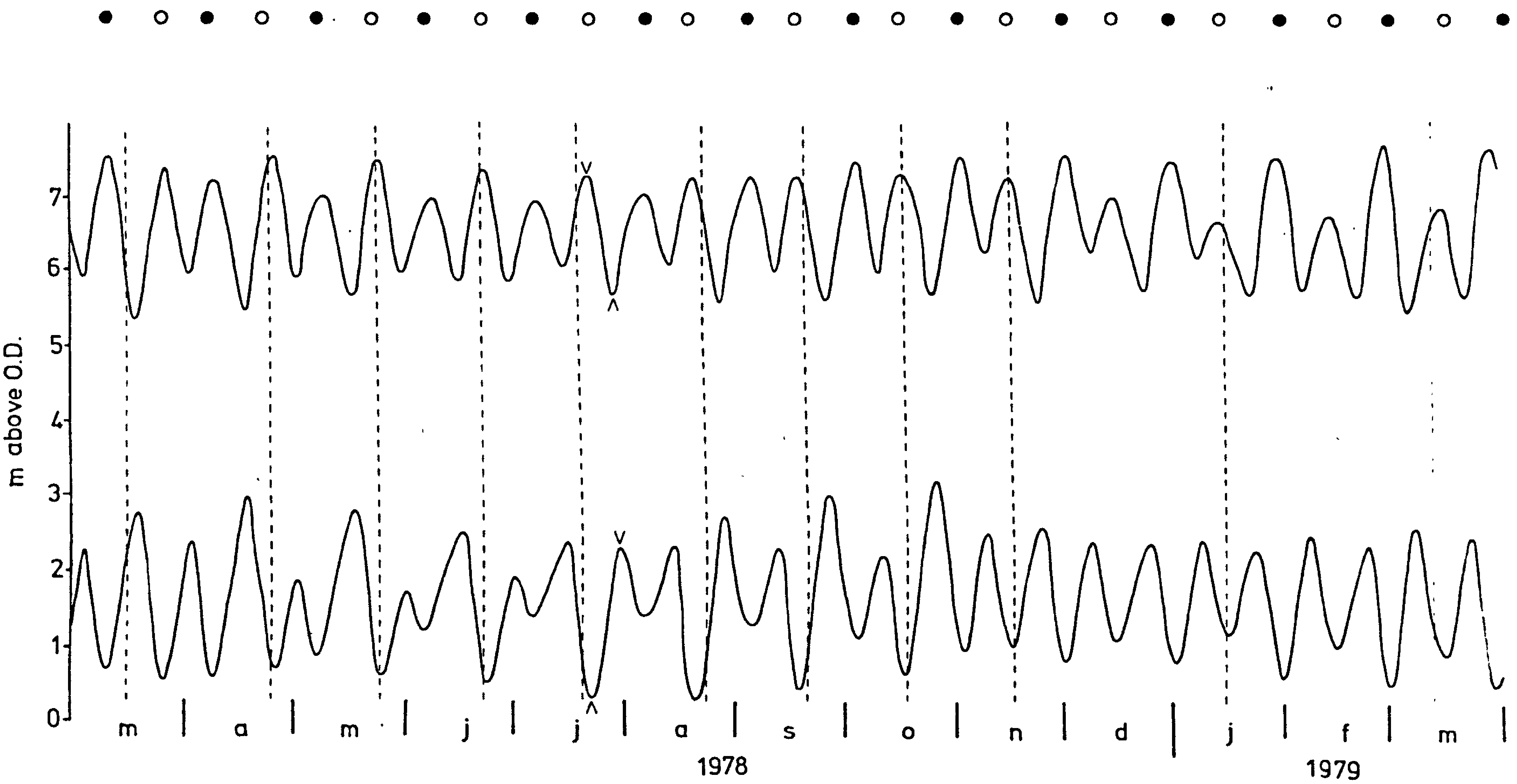


Figure 31 Tidal amplitude. High (upper curve), and low (lower curve), tides with spring/neap and lunar cycles for period March 1978 - March 79. Taken from Admiralty charts for Immingham. Date of measuring spring and neap tidal cover of intensive survey sites in July 1978 arrowed. Dotted lines denote monthly sampling dates.

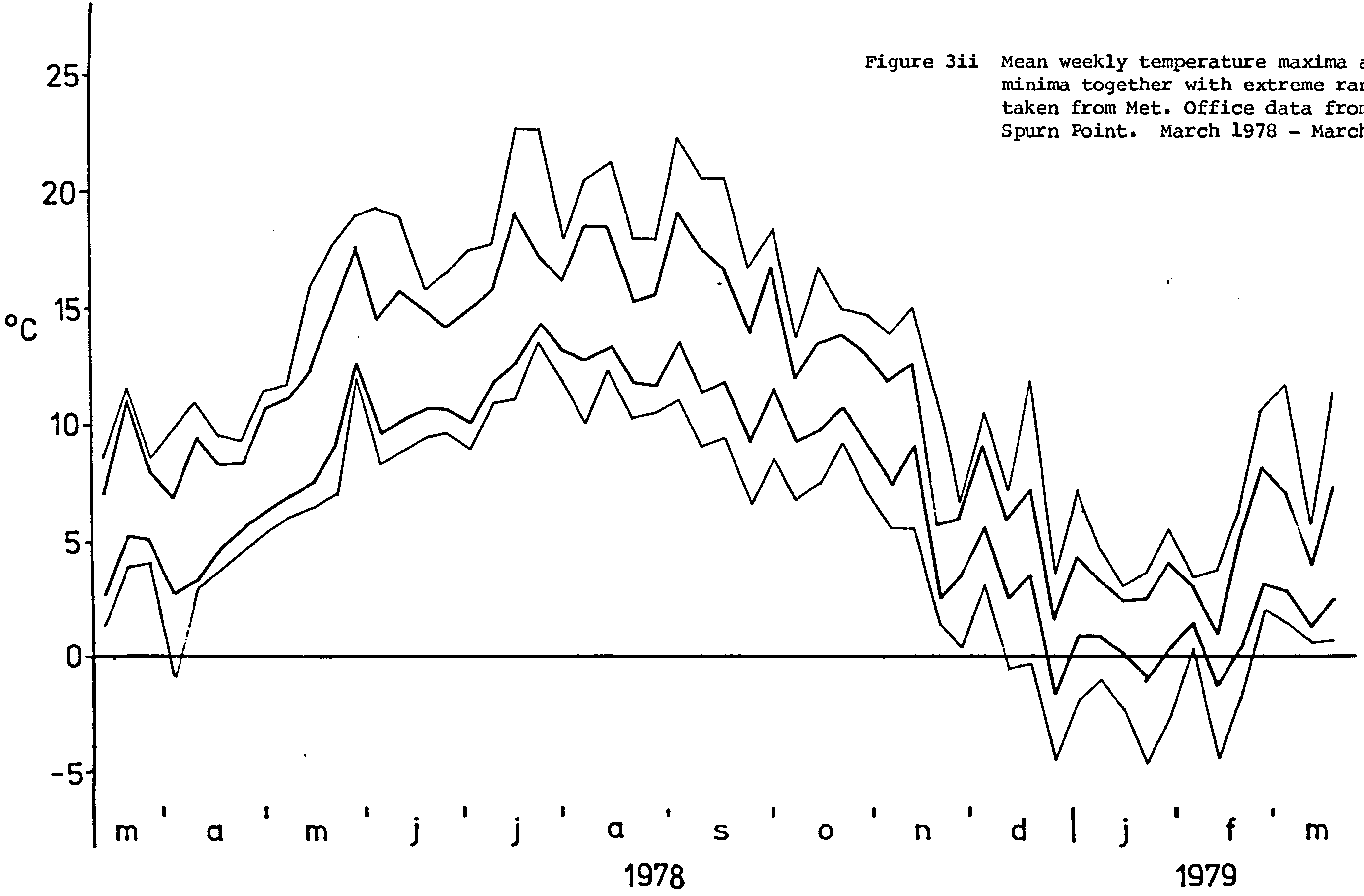


Figure 3ii Mean weekly temperature maxima and minima together with extreme range taken from Met. Office data from Spurn Point. March 1978 - March 79.

Figure 3iii Sunshine, snow and frost days per month at Barton upon Humber. 1975 -1979. Barton School data.

Figures 3iv - 3viii

a) Median particle diameter øM (x)
Sediment sorting coefficient øSO (+)

b) Sediment water content - percentage by weight

c) Sediment organic content - percentage by weight

d) Sediment level - cm above/below first reading

e) Interstitial water salinity - ‰

Monthly, March 1978 - March 79

Figure 3iv FI2

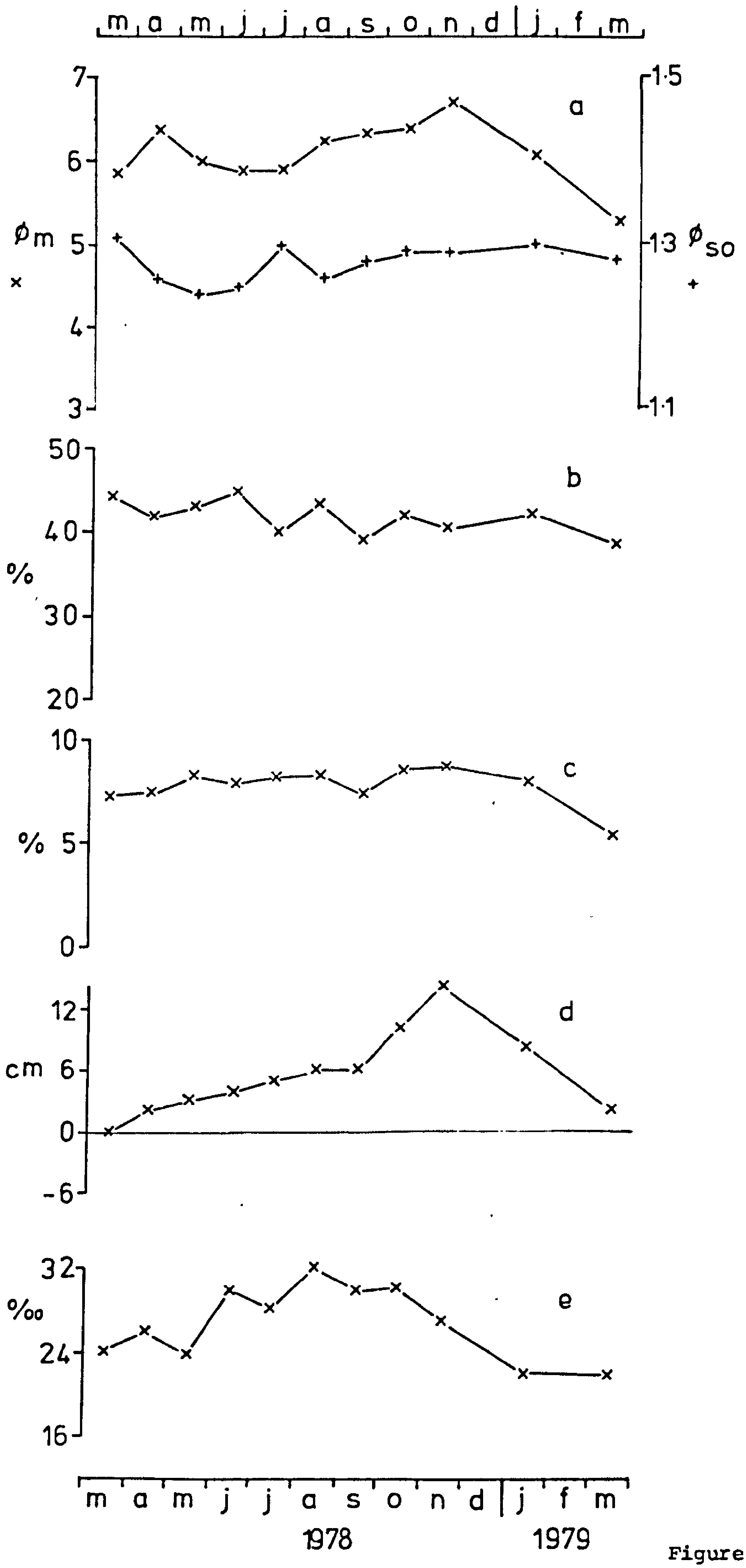


Figure 3v FII2

Figure 3vi FIV4

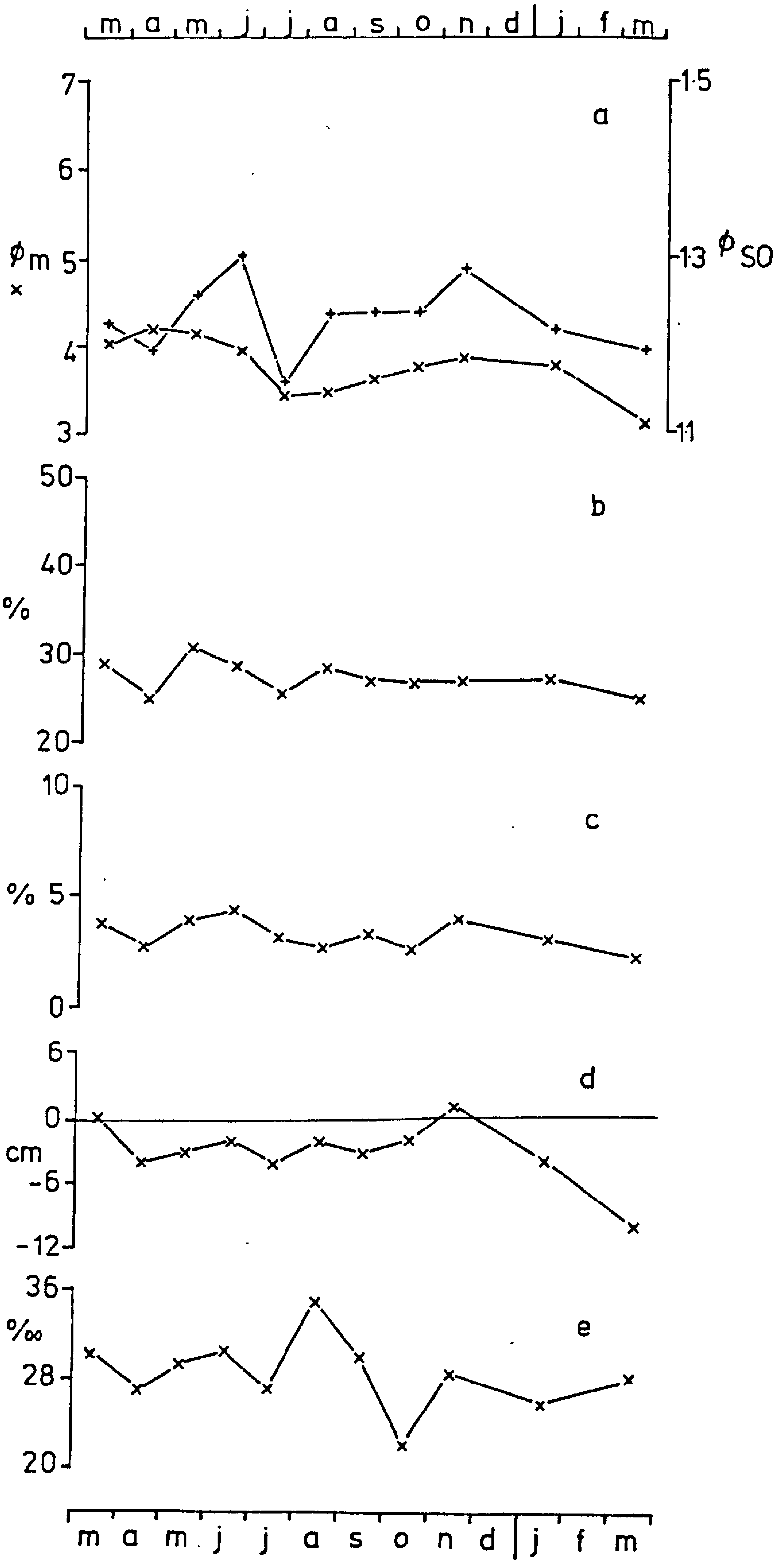


Figure 3vii GIII4

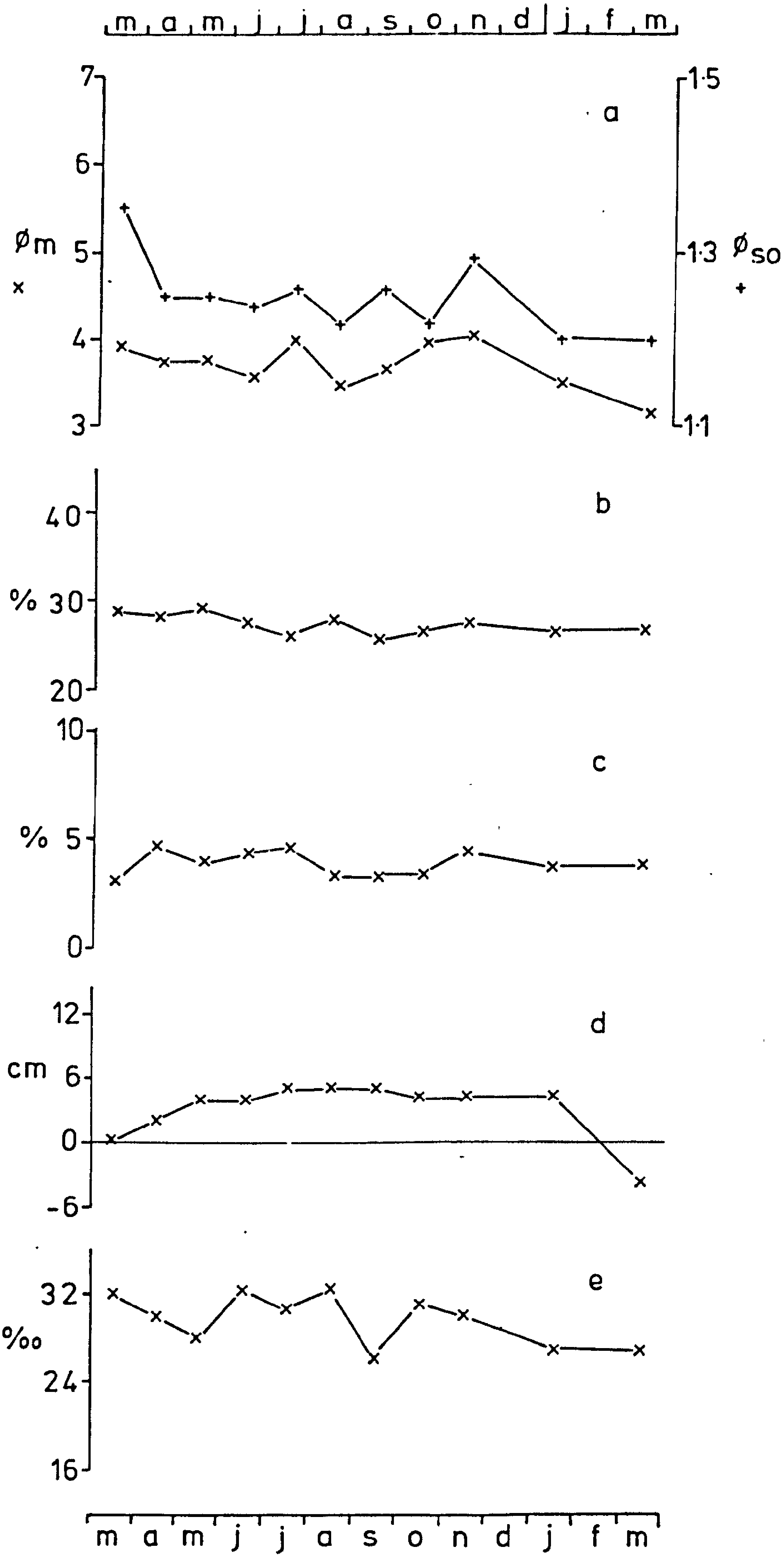


Figure 3viii GIV3

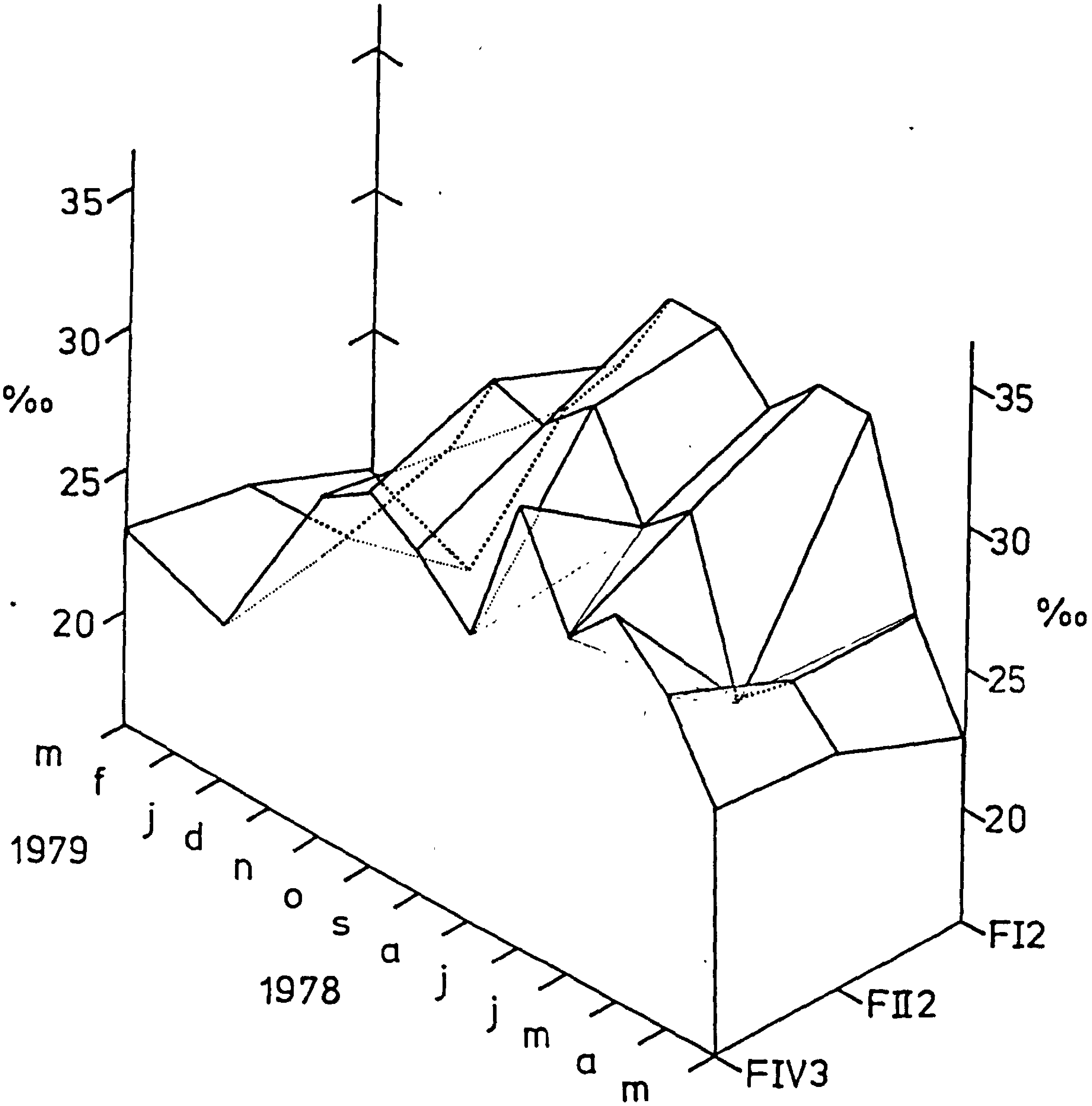


Figure 3ix Downshore variation in interstitial water salinity - ‰. Skeffling transect. March 1978 - March 79.

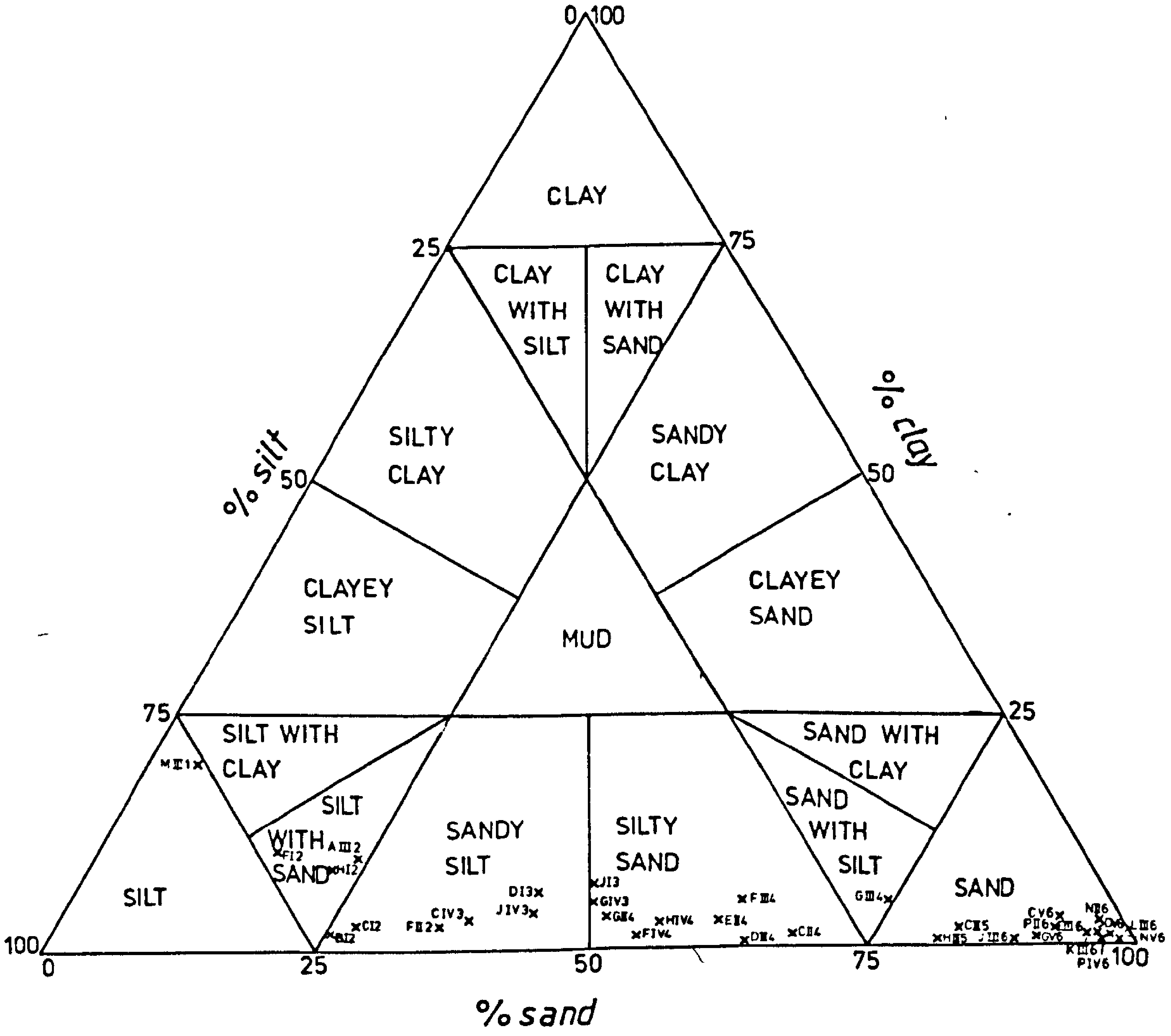


Figure 3x Ternary sediment diagram including all stations of extensive survey (May/June 1977).

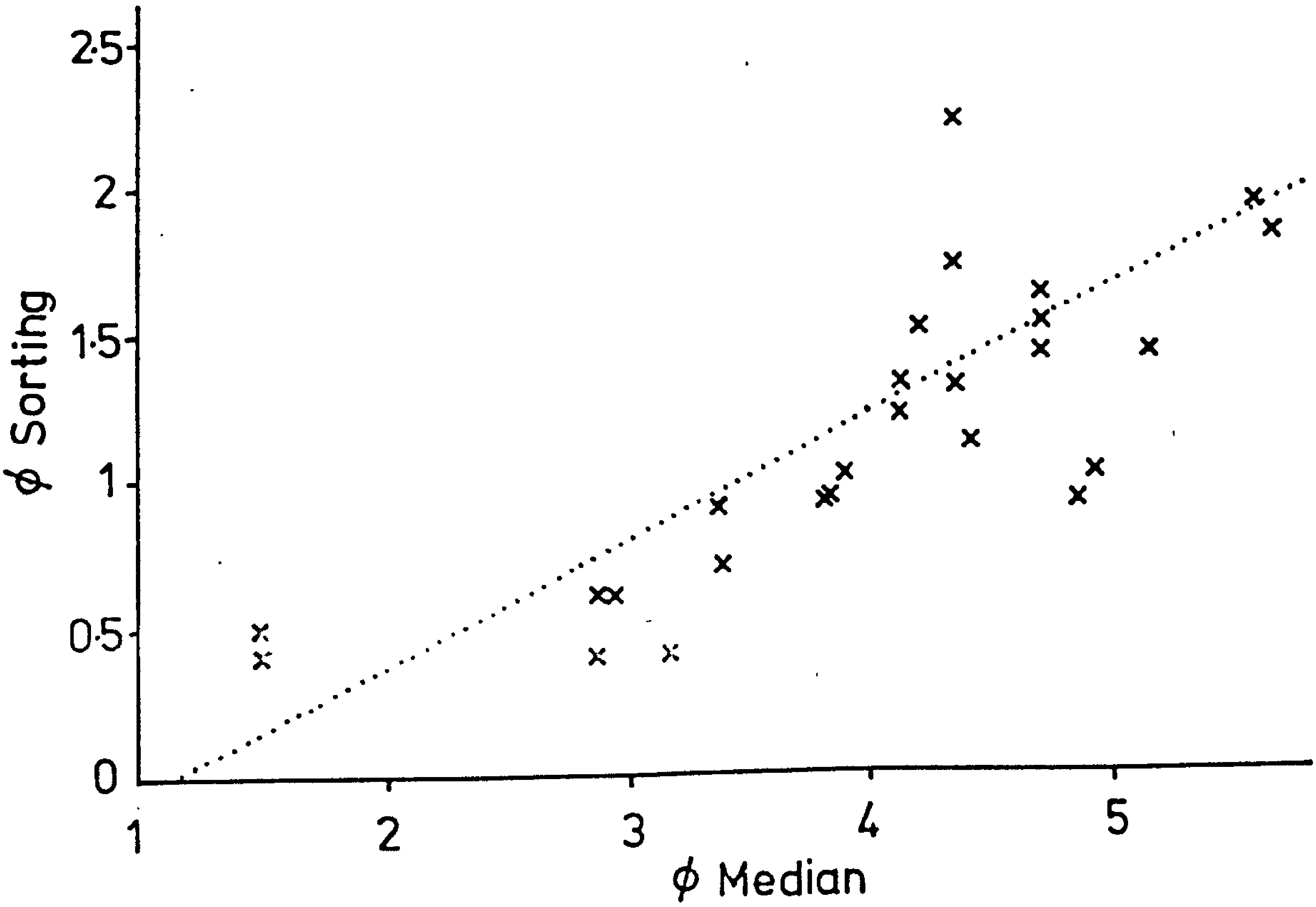


Figure 3xi Relationship between sediment sorting and median particle diameter. Extensive survey (May/June 1977). Spurn Bight stations only.

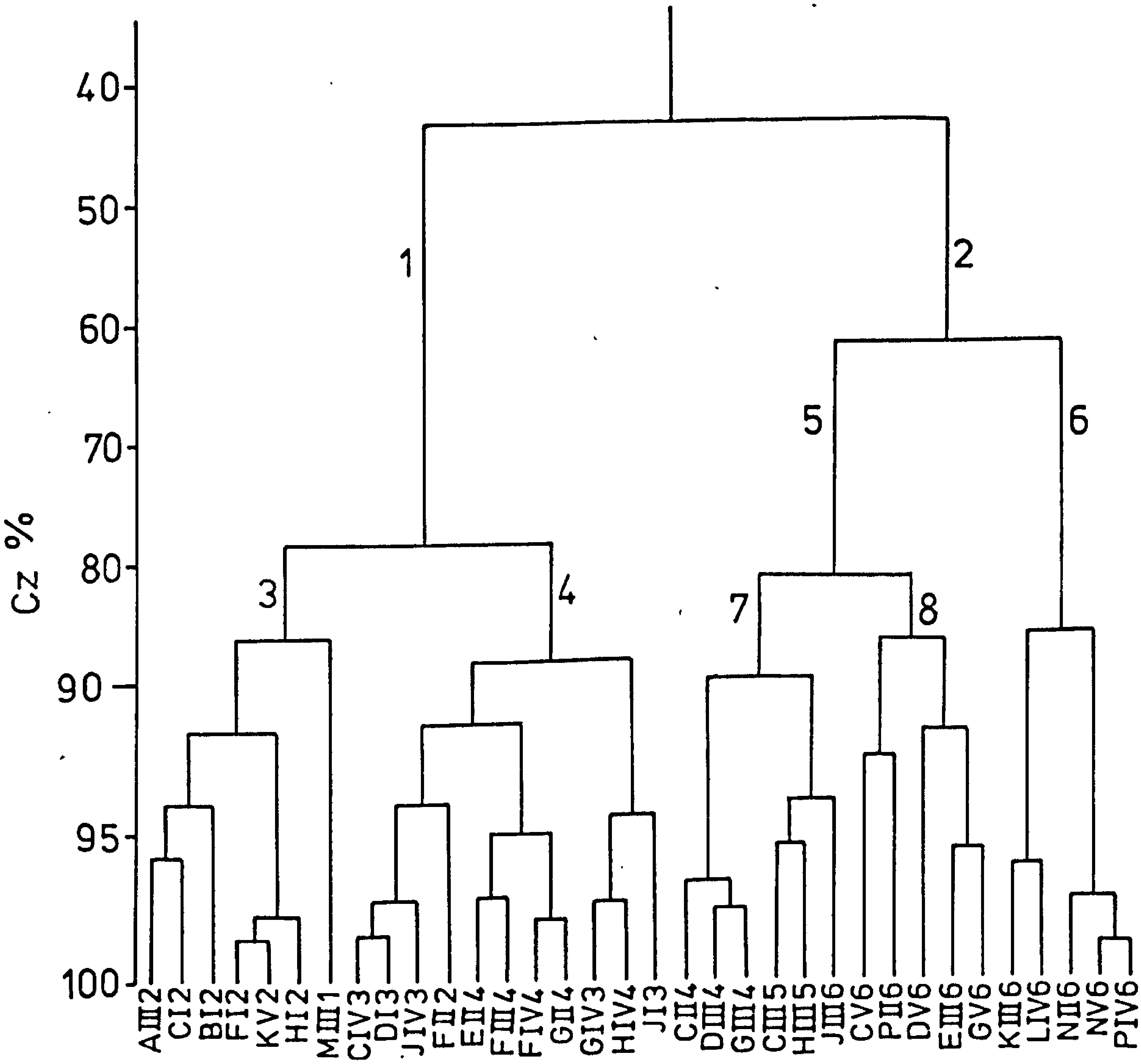


Figure 3xii Hierarchical classification of extensive survey (May/June 77) stations based on sediment parameters alone. Czekanowski similarity coefficient (Cz.), with group average sorting.

Figures 3xiii - 3xvii
Ternary sediment diagrams showing variation in sediment composition with time at each site of intensive survey. March 1978 - March 79.

Figure 3xiii

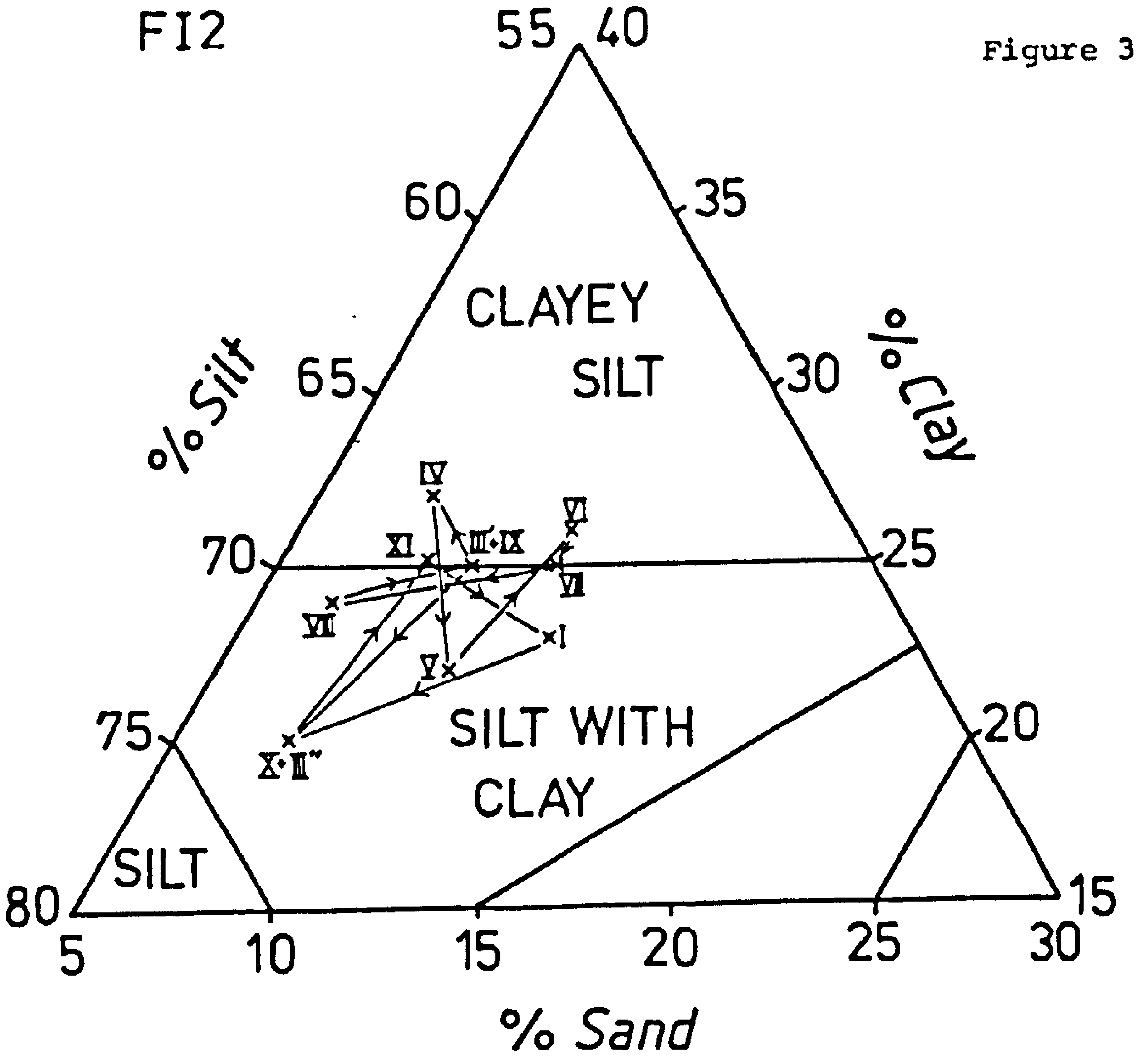
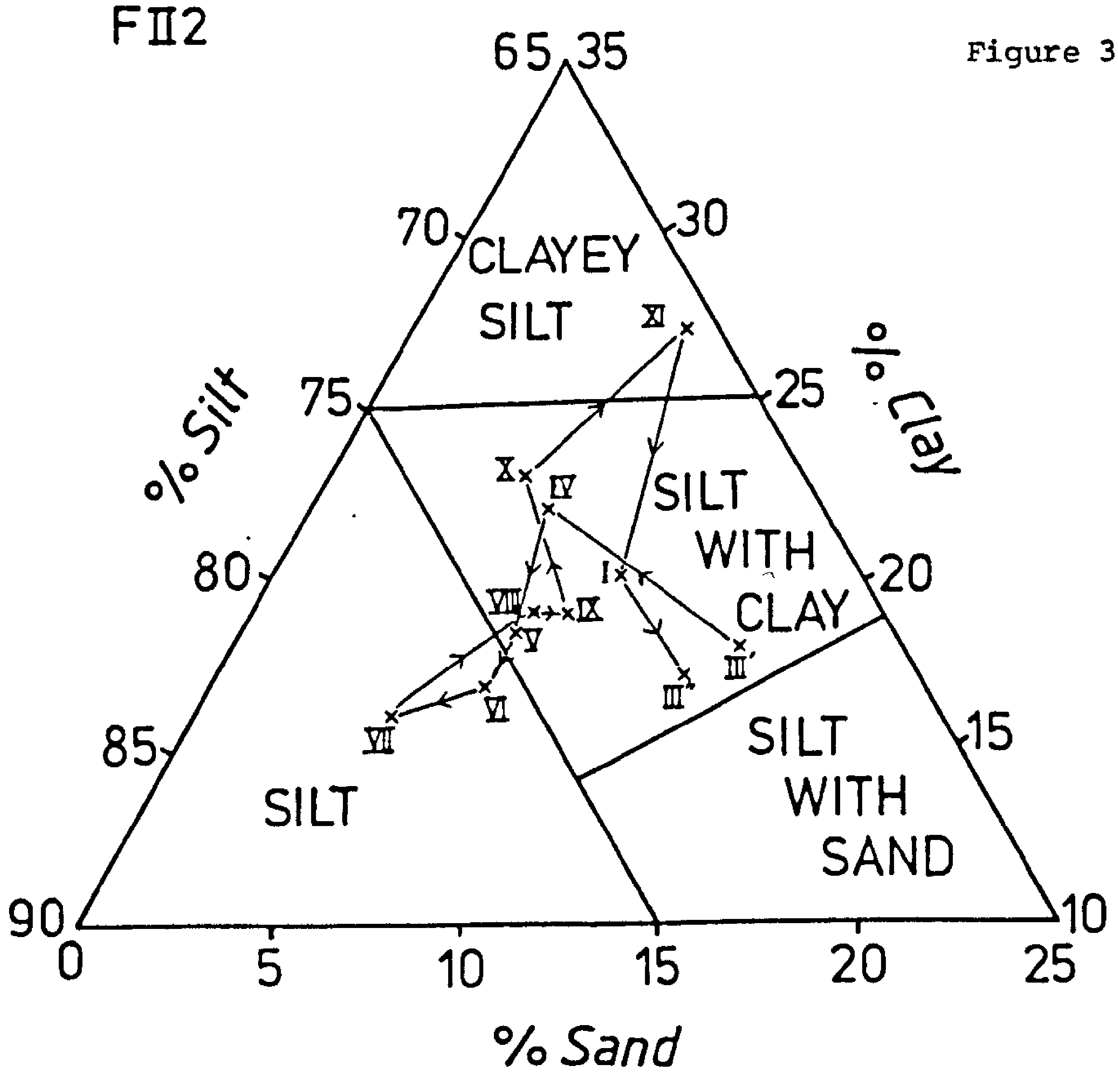


Figure 3xiv



FIV3

Figure 3xv

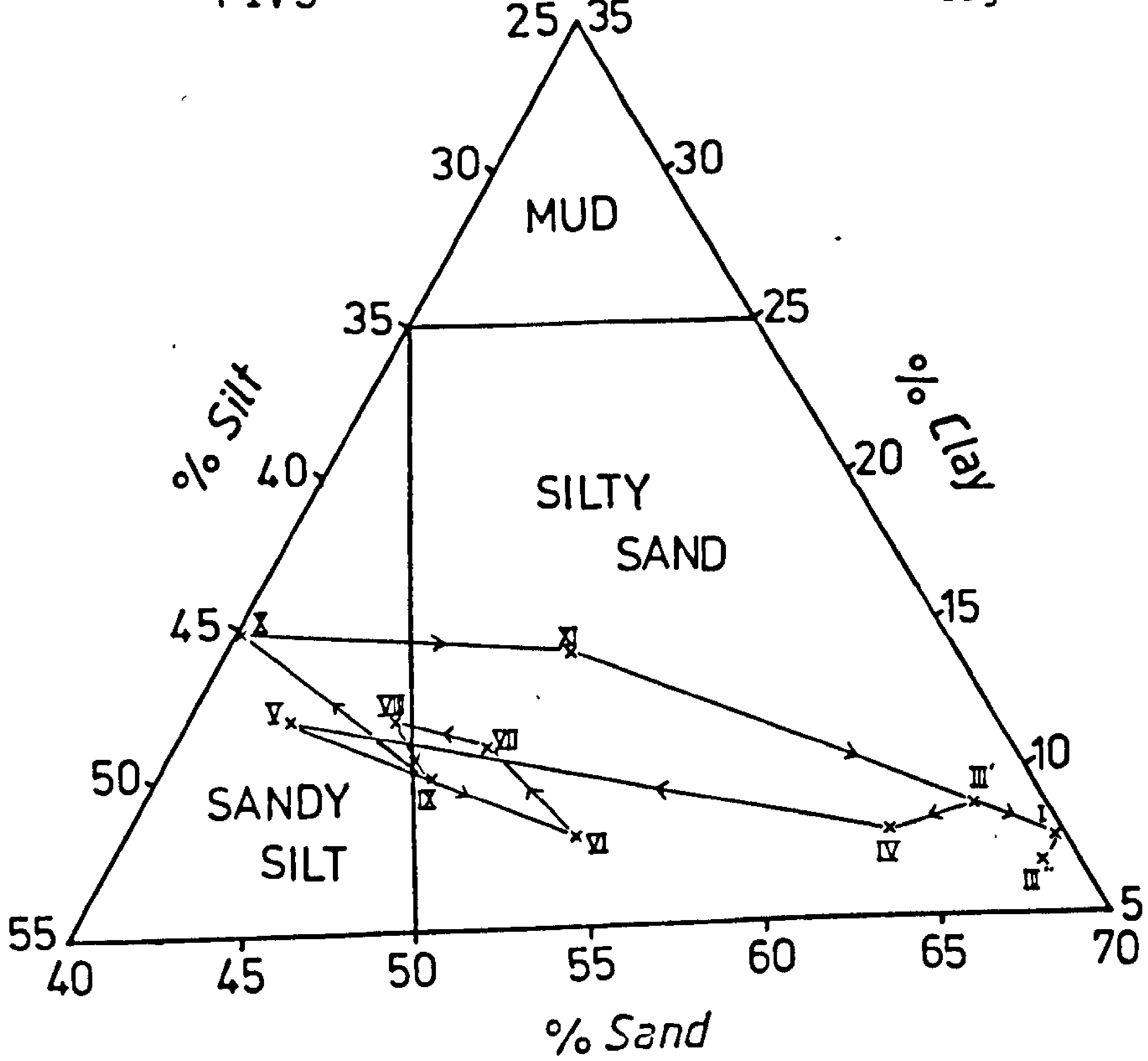


Figure 3xvi

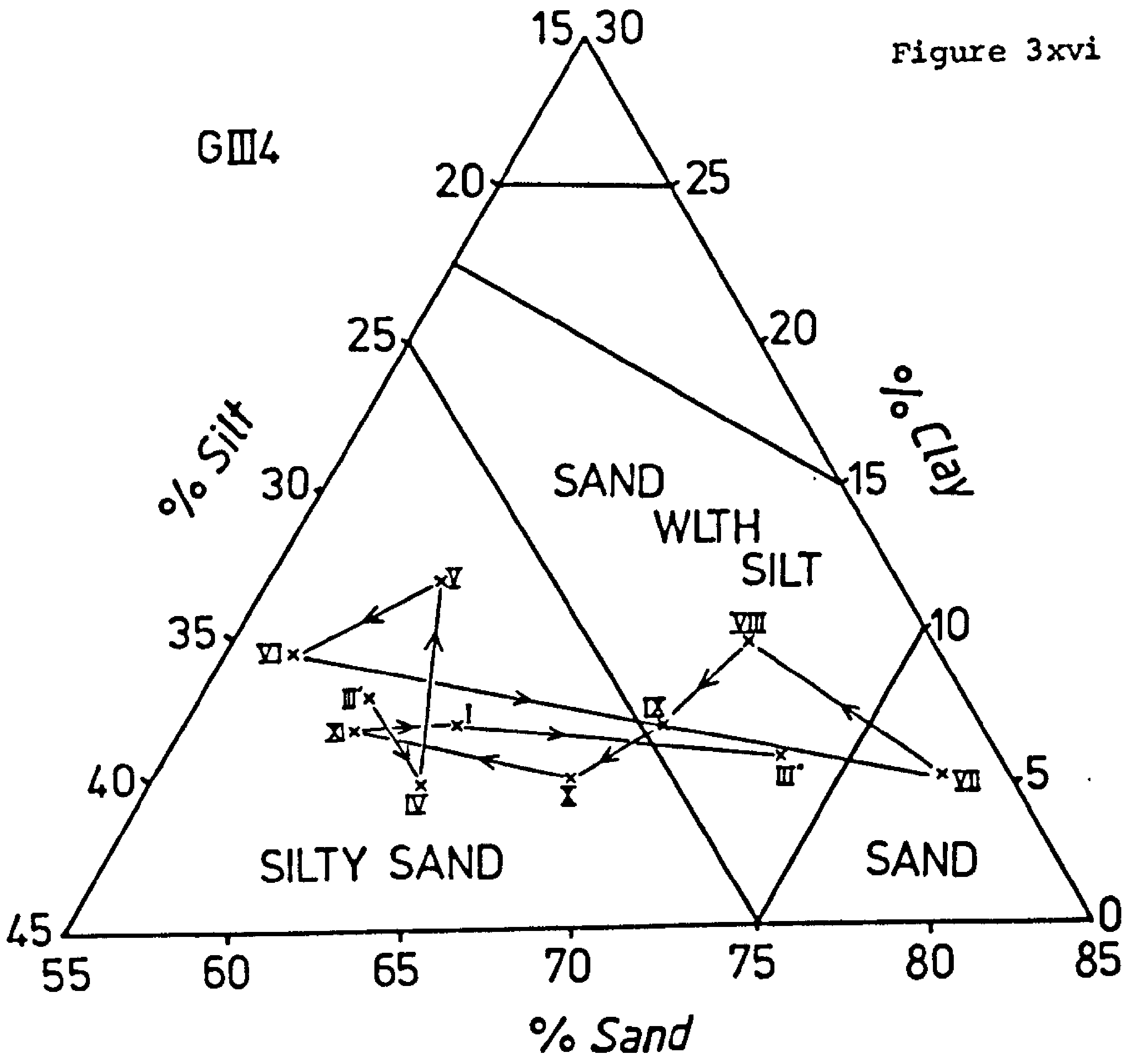
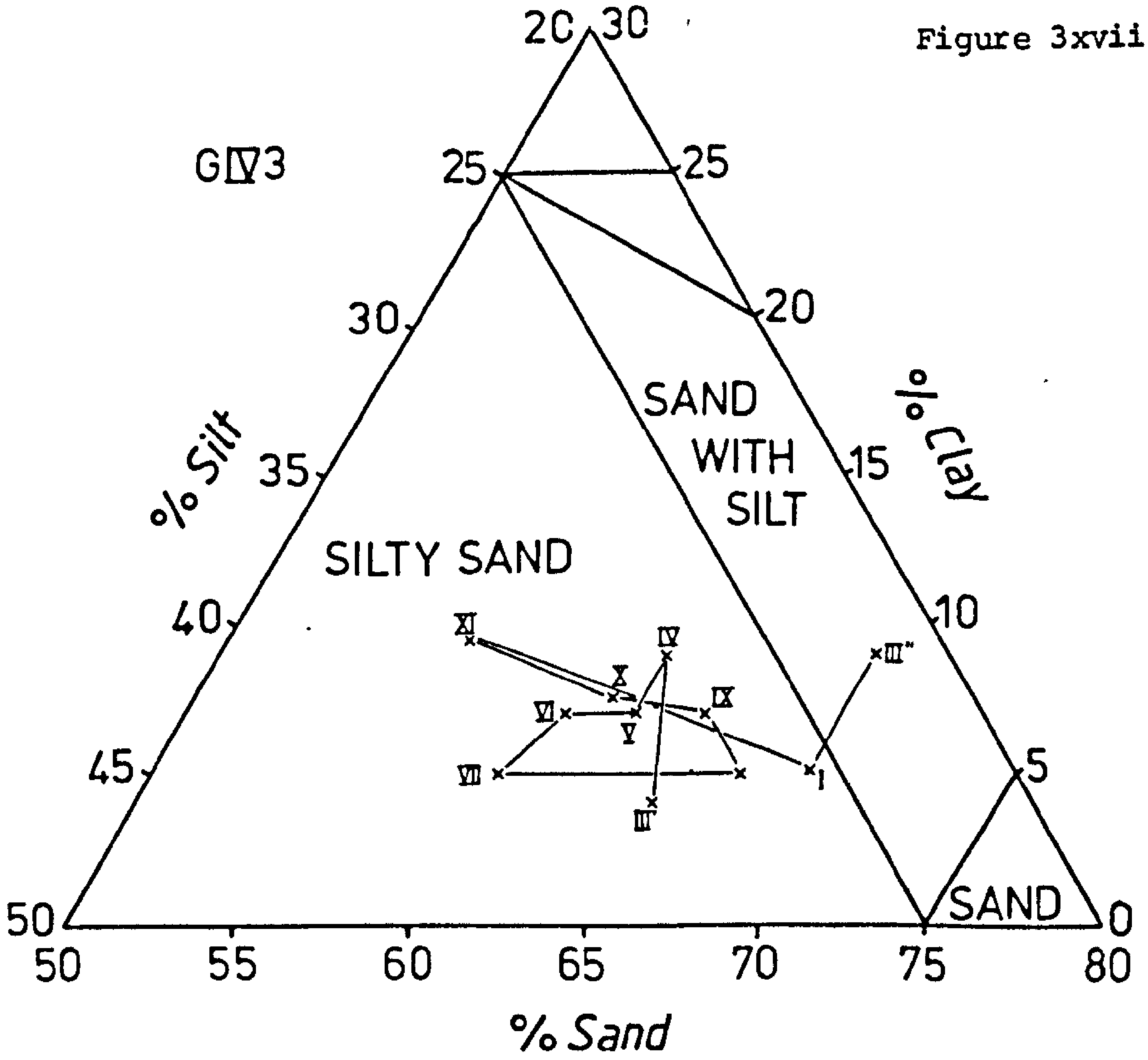


Figure 3xvii



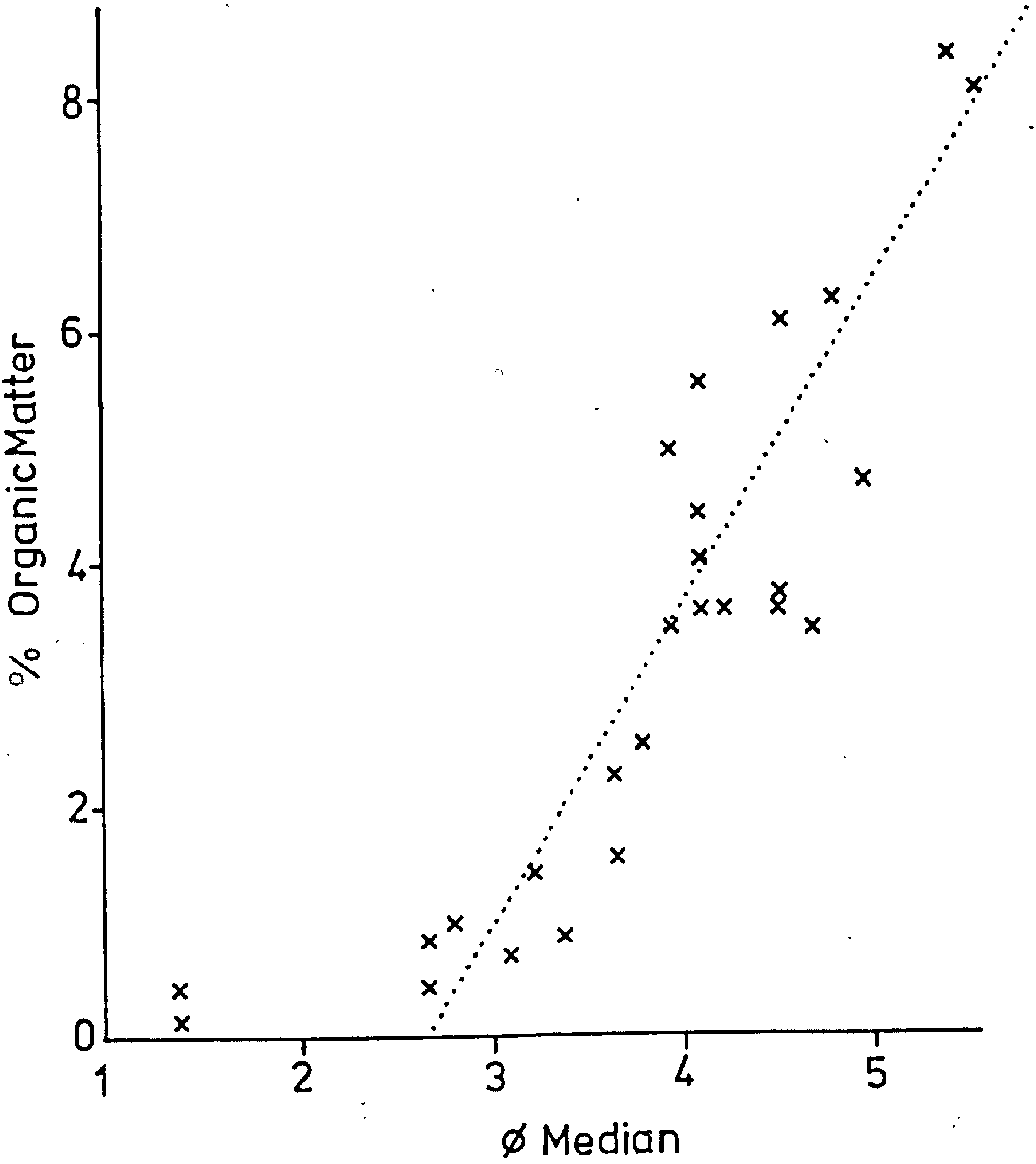


Figure 3xviii Relationship between sediment organic content and median particle diameter. Extensive survey (May/June 1977). Spurn Bight sites only.

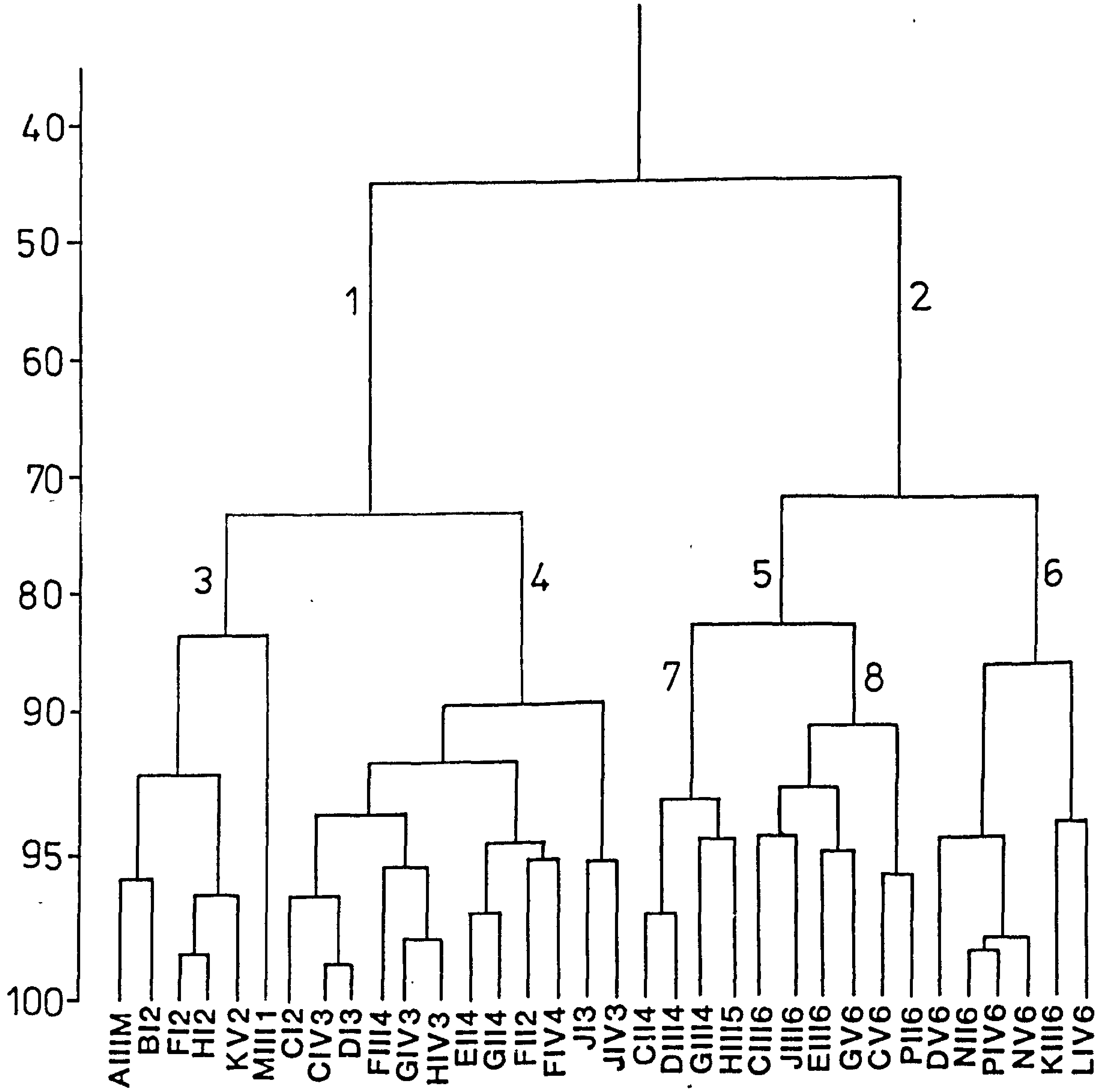


Figure 3xix Classification (cf. Fig 3xii), based on sediment data with the addition of organic matter and iron content data.

Mixed unit data used - see p38.

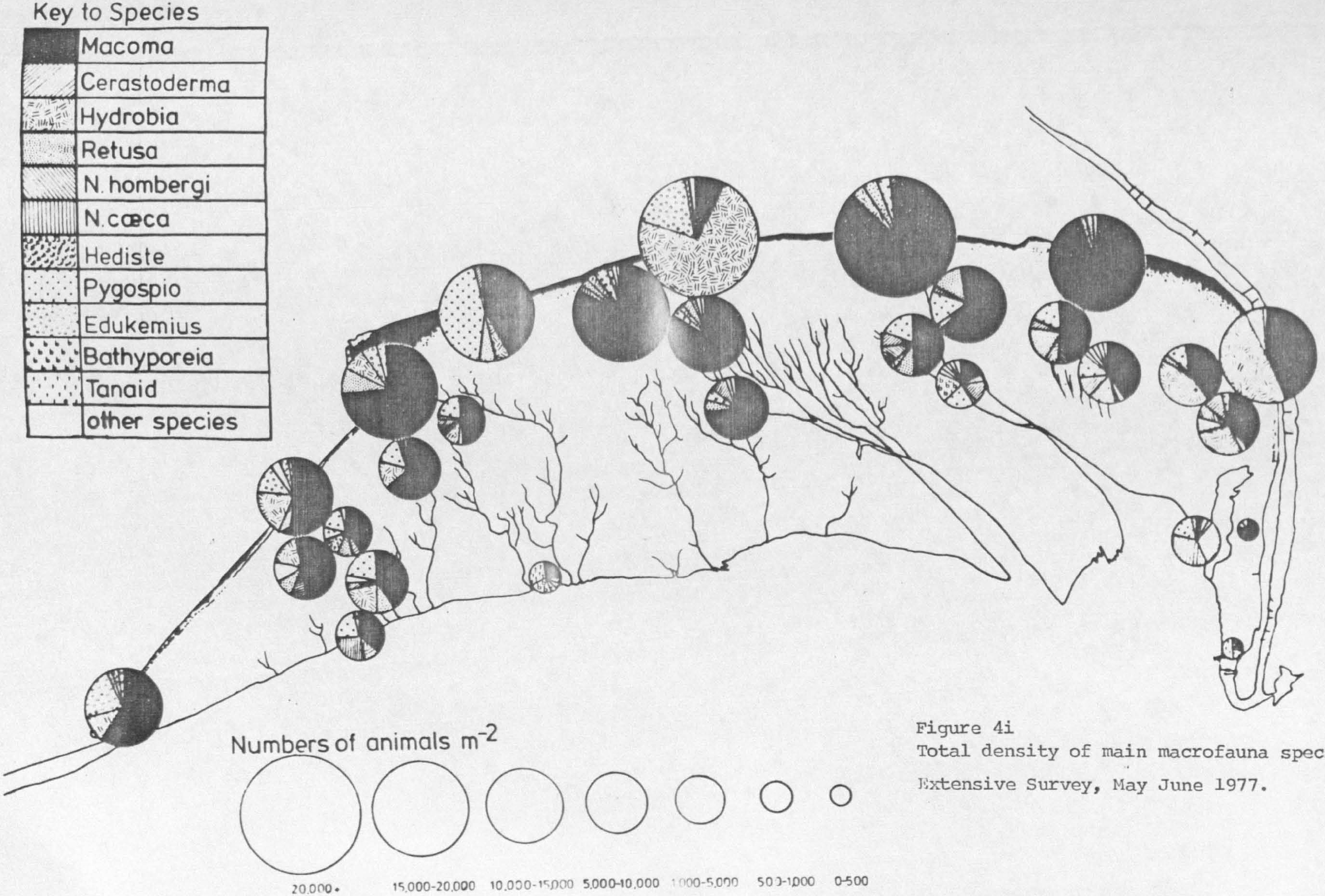


Figure 4i
Total density of main macrofauna species.
Extensive Survey, May June 1977.

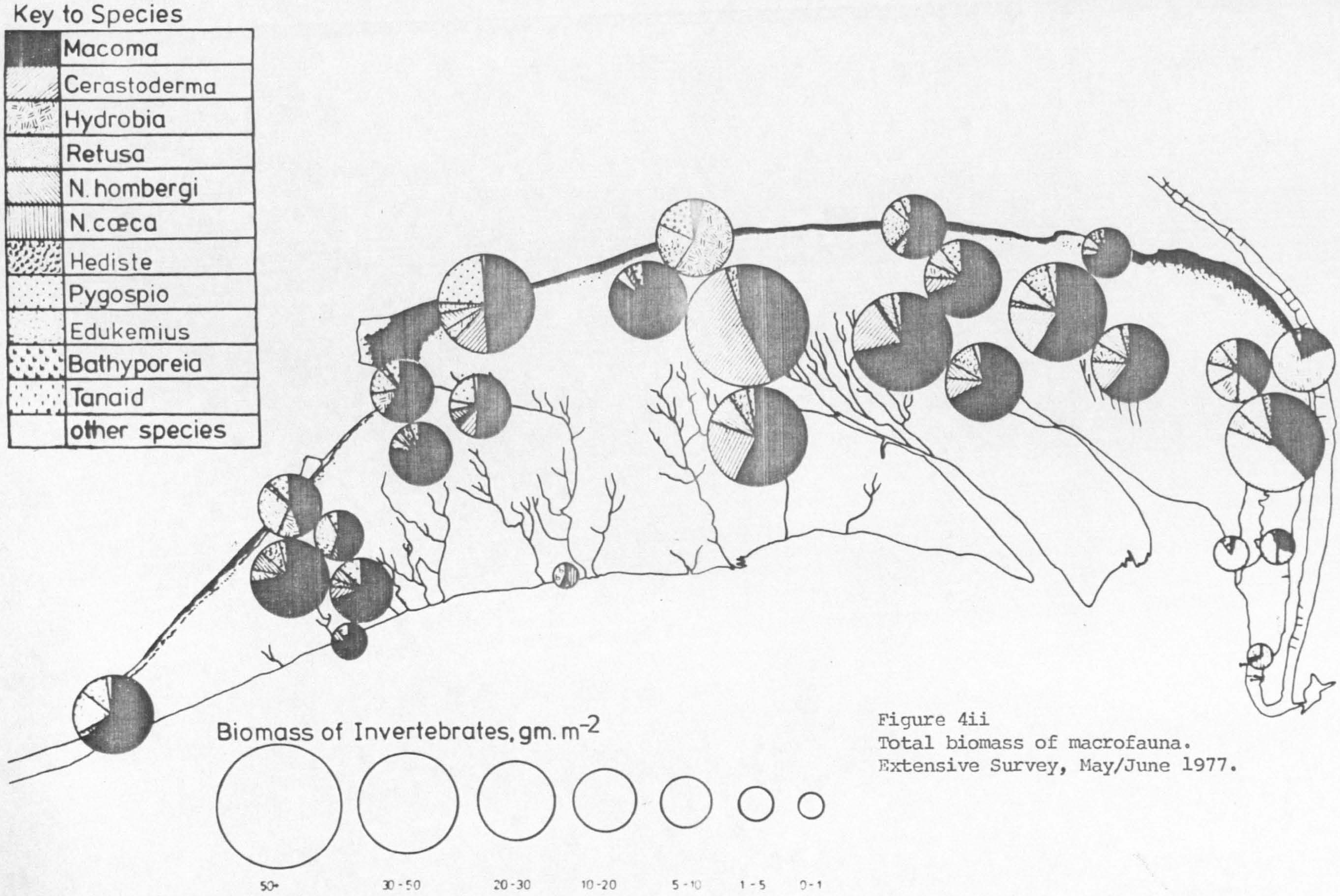


Figure 4ii
Total biomass of macrofauna.
Extensive Survey, May/June 1977.

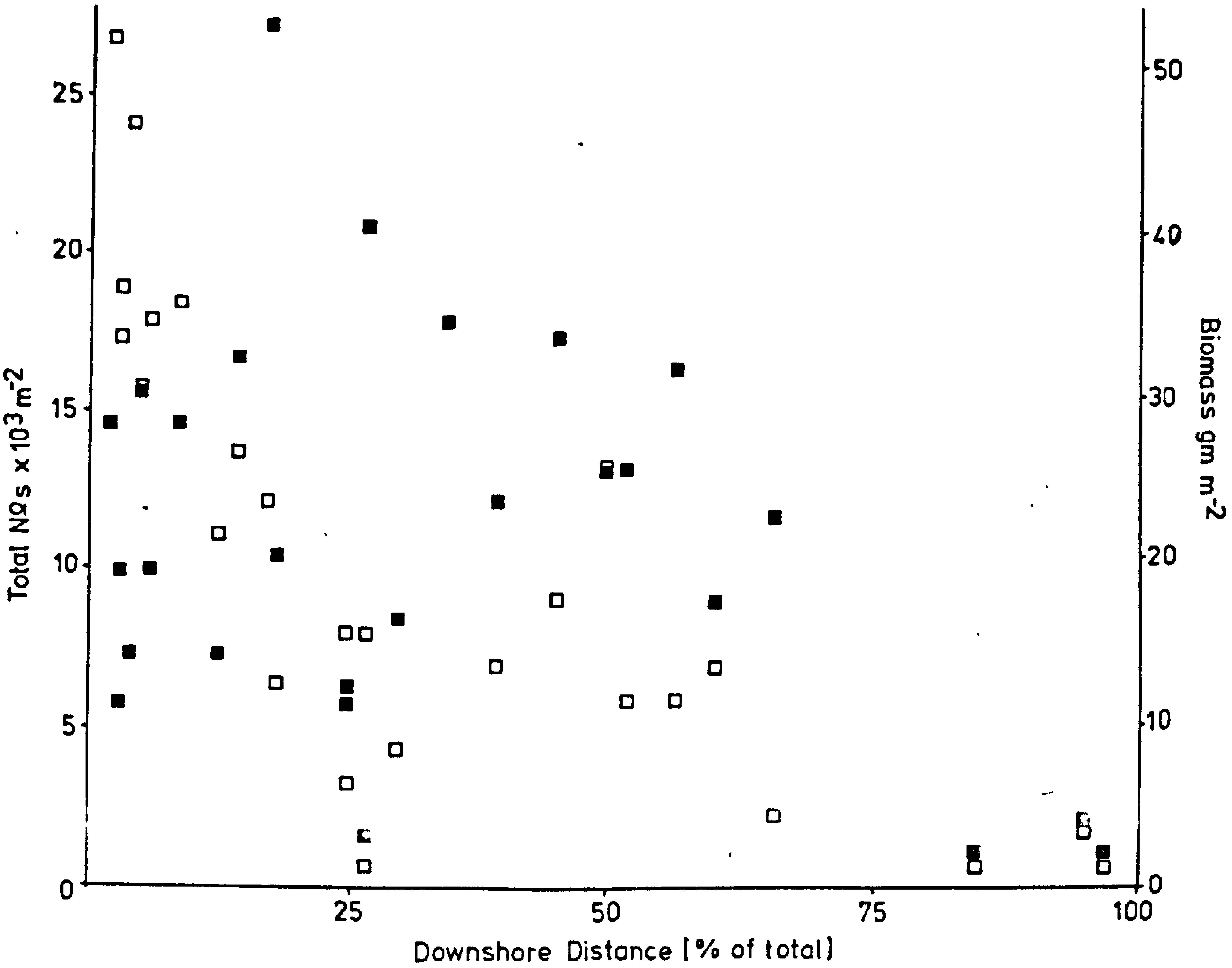


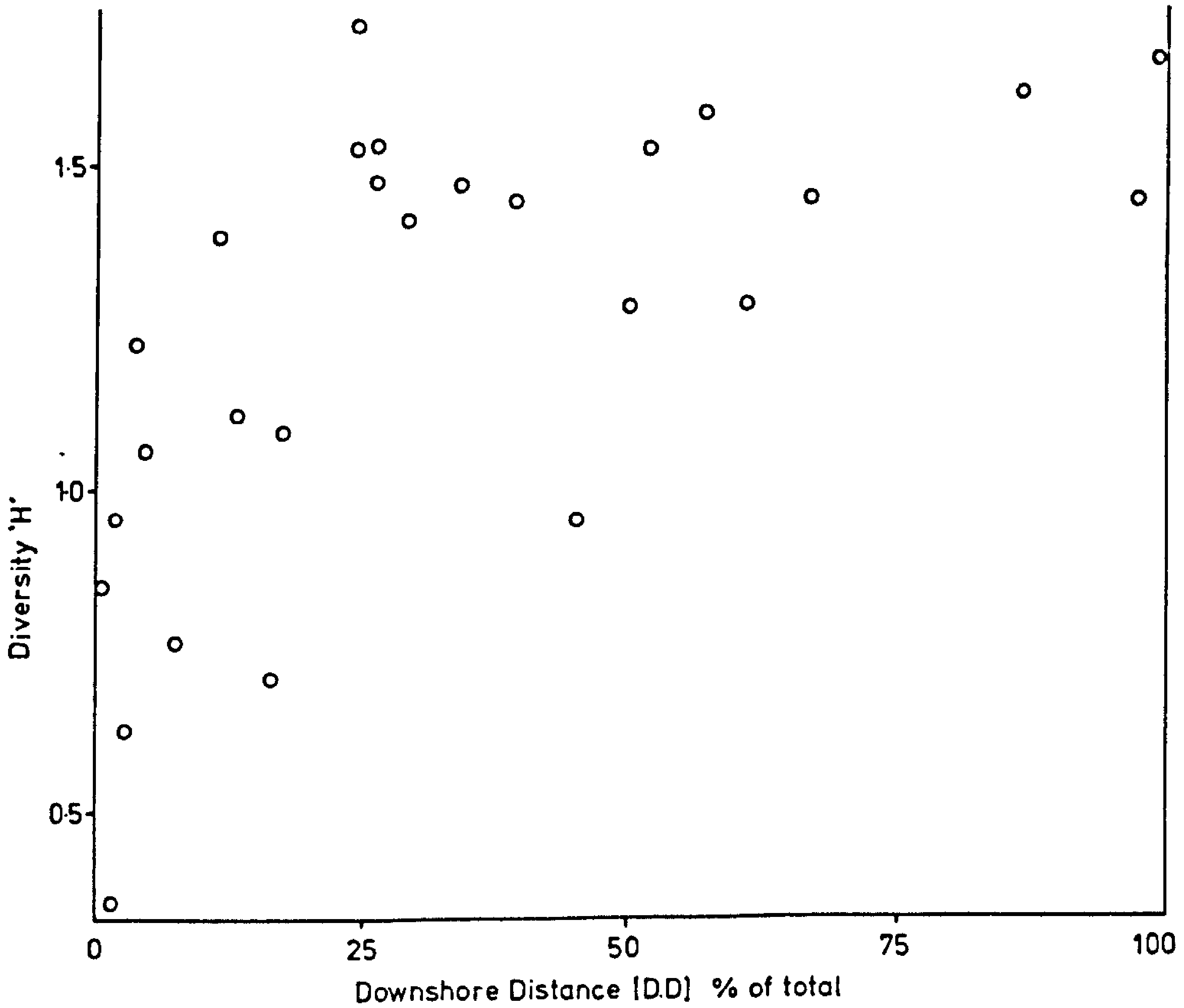
Figure 4iii Total macrofauna density and biomass in relation to tidal position (% age downshore distance). Extensive survey. May/June 1977.

Density - open squares, biomass - closed squares.

Figure 4iv Variation in macrofaunal diversity with tidal height (as percentage of total downshore distance). Extensive survey, May/June 1977. Spurn Bight Stations only.

Figure 4v Variation in macrofaunal diversity with median particle diameter (lower scale), and the degree of sorting (upper scale). Extensive survey, May/June 1977. Spurn Bight stations only.

solid symbols = ∅ sorting
open symbols = ∅ median


Diversity 'H'
1·5
1·0
0·5
0
25
50
75
100
Downshore Distance (D.D) % of total

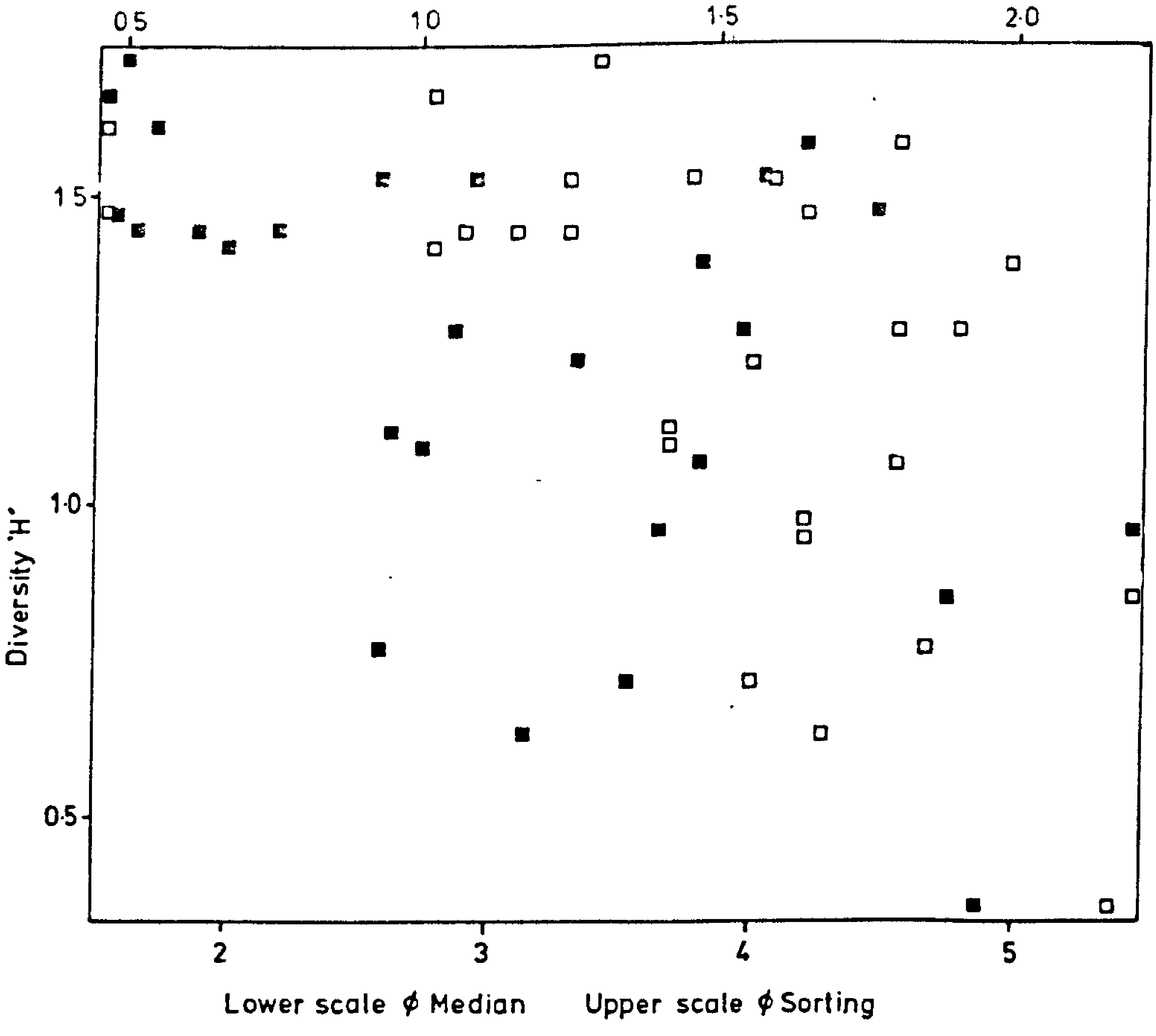
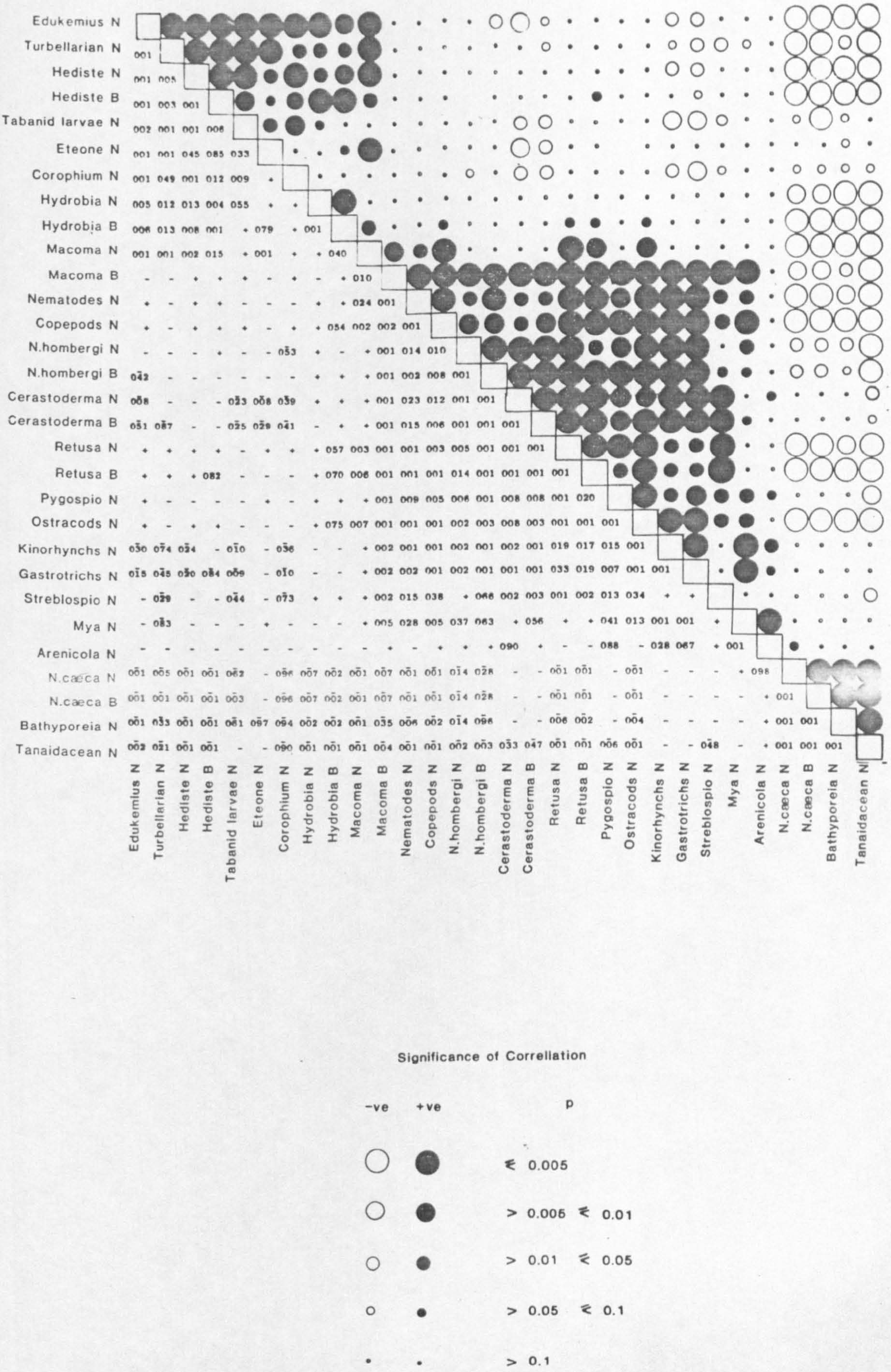

0·5
1·0
1·5
2·0
Diversity 'H'
1·5
1·0
0·5
2
3
4
5
Lower scale ϕ Median
Upper scale ϕ Sorting

Figure 4vi Correlation matrix ('t' tested significance of Kendall's rank correlation coefficient), of all fauna from extensive survey, May/June 1977 using Spurn Bight data only. Significant negative correlation barred. Decimal point excluded in all values. Non significant positive and negative correlations expressed by sign alone. Expressed in pi/trellis form on upper right of diagram. Positive correlation as filled circles, negative correlation as open circles.

N = density
B = biomass


Edukemius N
Turbellarian N 001
Hediste N 001 005
Hediste B 001 003 001
Tabanid larvae N 002 001 001 008
Eteone N 001 001 045 085 033
Corophium N 001 049 001 012 009 +
Hydrobia N 005 012 013 004 055 + +
Hydrobia B 008 013 008 001 + 079 + 001
Macoma N 001 001 002 015 + 001 + + 040
Macoma B - - + + + - + - + 010
Nematodes N + - + + - - - + + 024 001
Copepods N + - + + + - + + 054 002 002 001
N.hombergi N - - - + - - 05̄3 + - + 001 014 010
N.hombergi B 04̄2 - - - - - - + + + 001 002 008 001
Cerastoderma N 00̄8 - - - 02̄3 00̄8 03̄9 + + + 001 023 012 001 001
Cerastoderma B 05̄1 08̄7 - - 02̄5 02̄9 04̄1 - + + 001 015 006 001 001 001
Retusa N + + + + - + + + 057 003 001 001 003 005 001 001 001
Retusa B + + + 082 - - - + 070 006 001 001 001 014 001 001 001 001
Pygospio N + - - - - + - + + + 001 009 005 006 001 008 008 001 020
Ostracods N + - + + - - - + 075 007 001 001 001 002 003 008 003 001 001 001
Kinorhynchs N 03̄0 07̄4 02̄4 - 01̄0 - 03̄6 - - + 002 001 001 002 001 002 001 019 017 015 001
Gastrotrichs N 01̄5 04̄5 03̄0 08̄4 00̄9 - 01̄0 - - + 002 002 001 002 001 001 001 033 019 007 001 001
Streblospio N - 02̄9 - - 04̄4 - 07̄3 + + + 002 015 038 + 066 002 003 001 002 013 034 + +
Mya N - 08̄3 - - - + - - - + 005 028 005 037 063 + 056 + + 041 013 001 001 +
Arenicola N - - - - - - - - - - + - + + + 090 + - - 088 - 028 067 + 001
N.caeca N 00̄1 00̄5 00̄1 00̄1 06̄2 - 09̄6 00̄7 00̄2 00̄1 00̄7 00̄1 00̄1 01̄4 02̄8 - - 00̄1 00̄1 - 00̄1 - - - + 098
N.caeca B 00̄1 00̄1 00̄1 00̄1 00̄3 - 09̄6 00̄7 00̄2 00̄1 00̄7 00̄1 00̄1 01̄4 02̄8 - - 00̄1 00̄1 - 00̄1 - - - - + 001
Bathyporeia N 00̄1 03̄3 00̄1 00̄1 08̄1 09̄7 09̄4 00̄2 00̄2 00̄1 03̄5 00̄6 00̄2 01̄4 09̄8 - - 00̄6 00̄2 - 00̄4 - - - - + 001 001
Tanaidacean N 00̄2 02̄1 00̄1 00̄1 - - 09̄0 00̄1 00̄1 00̄1 00̄4 00̄1 00̄1 00̄2 00̄3 03̄3 04̄7 00̄1 00̄1 00̄6 00̄1 - - 04̄8 - + 001 001 001
Edukemius N
Turbellarian N
Hediste N
Hediste B
Tabanid larvae N
Eteone N
Corophium N
Hydrobia N
Hydrobia B
Macoma N
Macoma B
Nematodes N
Copepods N
N.hombergi N
N.hombergi B
Cerastoderma N
Cerastoderma B
Retusa N
Retusa B
Pygospio N
Ostracods N
Kinorhynchs N
Gastrotrichs N
Streblospio N
Mya N
Arenicola N
N.cæca N
N.cæca B
Bathyporeia N
Tanaidacean N
Significance of Correlation
-ve
+ve
p
≤ 0.005
> 0.005 ≤ 0.01
> 0.01 ≤ 0.05
> 0.05 ≤ 0.1
> 0.1

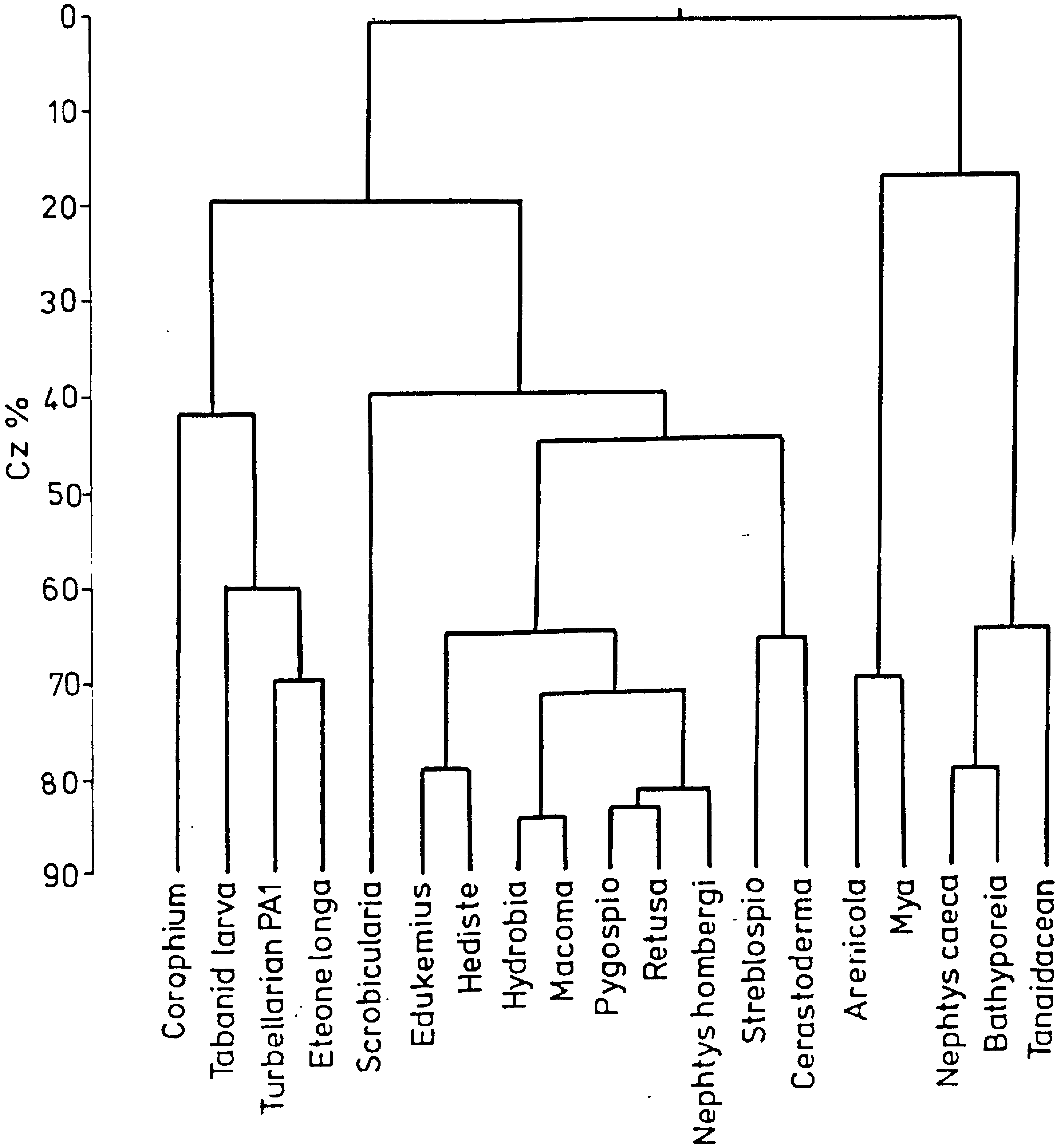


Figure 4vii. Hierarchical classification of main macrofaunal species. Extensive survey, May/June 1977. Czekanowski similarity coefficient and group average sorting.

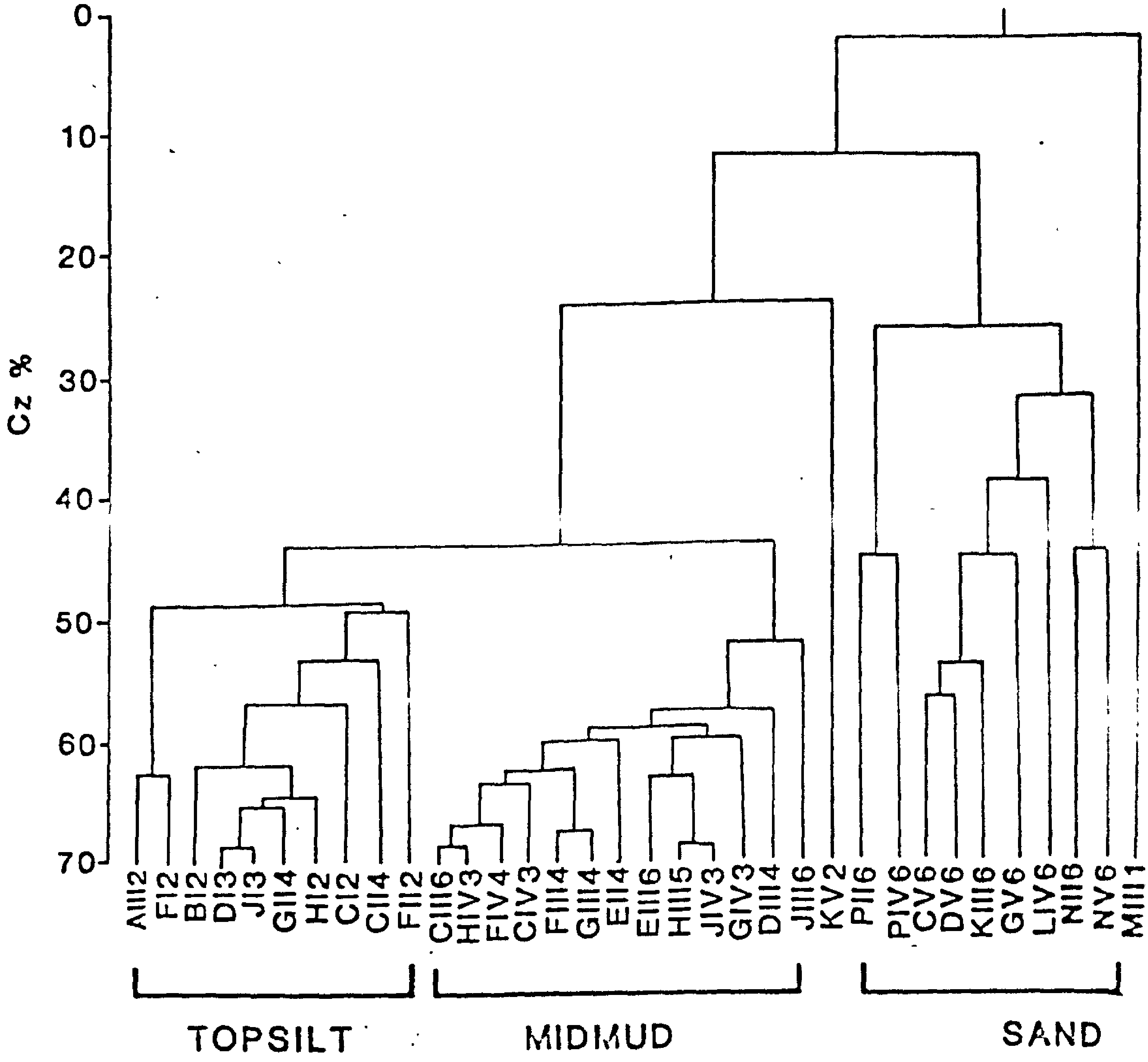


Figure 4viii Hierarchical classification of site groupings using macrofaunal data (log transformed). Extensive survey, May/June 1977. Czekanowski similarity coefficient and group average sorting.

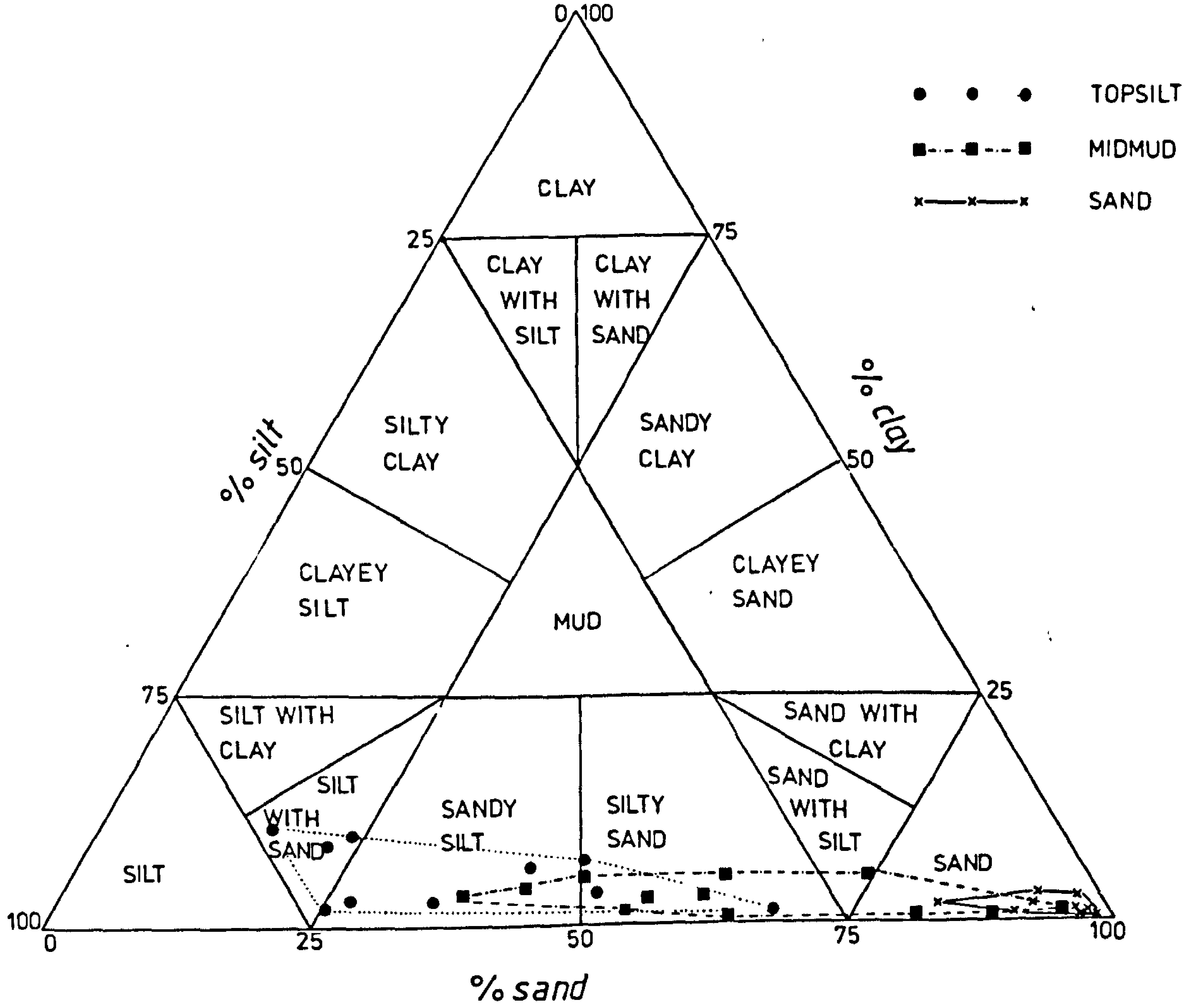
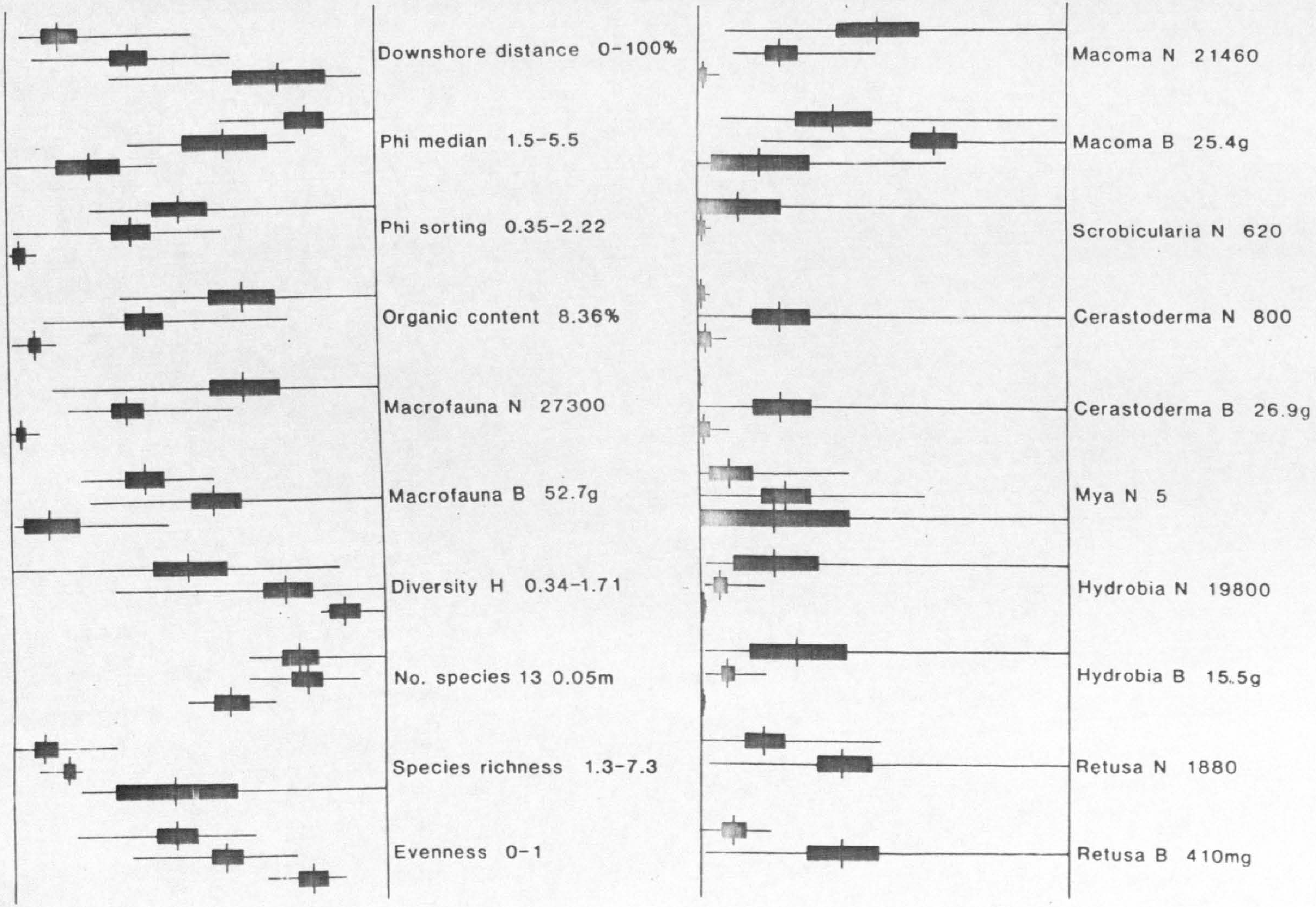
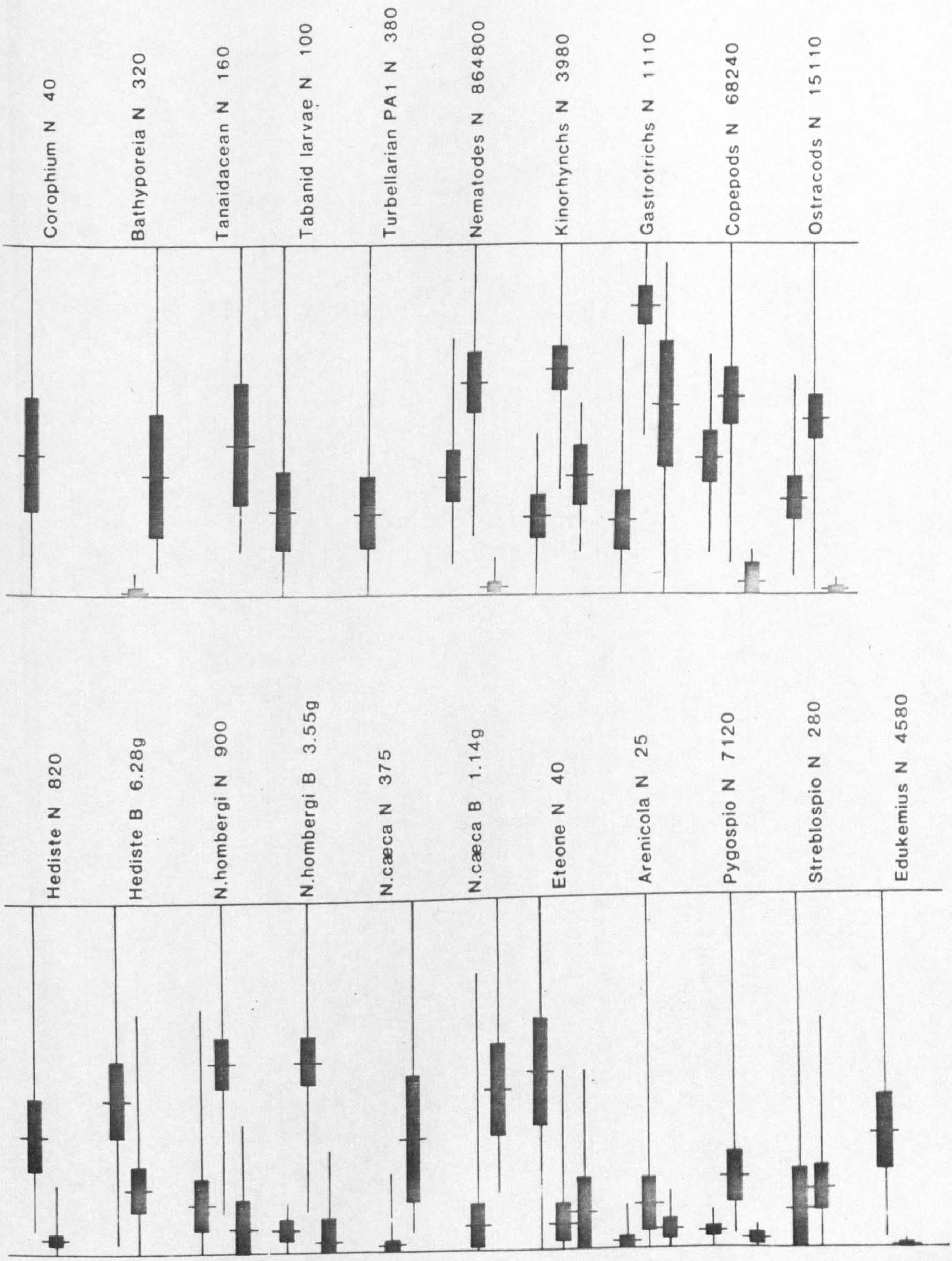


Figure 4ix Ternary sediment diagram with CLUSTAN clusters TOPSILT, MIDMUD and SAND superimposed.

Figure 4x (in two parts)

Mean, standard deviation and range of all variables in each of clusters TOPSILT (upper figure), MIDMUD (middle figure), and SAND (lower figure). Total width of scalagram represents the maximum value or range of the variable, expressed after variable label. Density and biomass in units per m^2, maximum to right of diagram. Extensive survey, May/June 1977. Spurn Bight data only.


Downshore distance 0-100%
Phi median 1.5-5.5
Phi sorting 0.35-2.22
Organic content 8.36%
Macrofauna N 27300
Macrofauna B 52.7g
Diversity H 0.34-1.71
No. species 13 0.05m
Species richness 1.3-7.3
Evenness 0-1
Macoma N 21460
Macoma B 25.4g
Scrobicularia N 620
Cerastoderma N 800
Cerastoderma B 26.9g
Mya N 5
Hydrobia N 19800
Hydrobia B 15.5g
Retusa N 1880
Retusa B 410mg


Corophium N 40
Bathyporeia N 320
Tanaidacean N 160
Tabanid larvae N 100
Turbellarian PA1 N 380
Nematodes N 864800
Kinorhynchs N 3980
Gastrotrichs N 1110
Copepods N 68240
Ostracods N 15110
Hediste N 820
Hediste B 6.28g
N.hombergi N 900
N.hombergi B 3.55g
N.cæca N 375
N.cæca B 1.14g
Eteone N 40
Arenicola N 25
Pygospio N 7120
Streblospio N 280
Edukemius N 4580

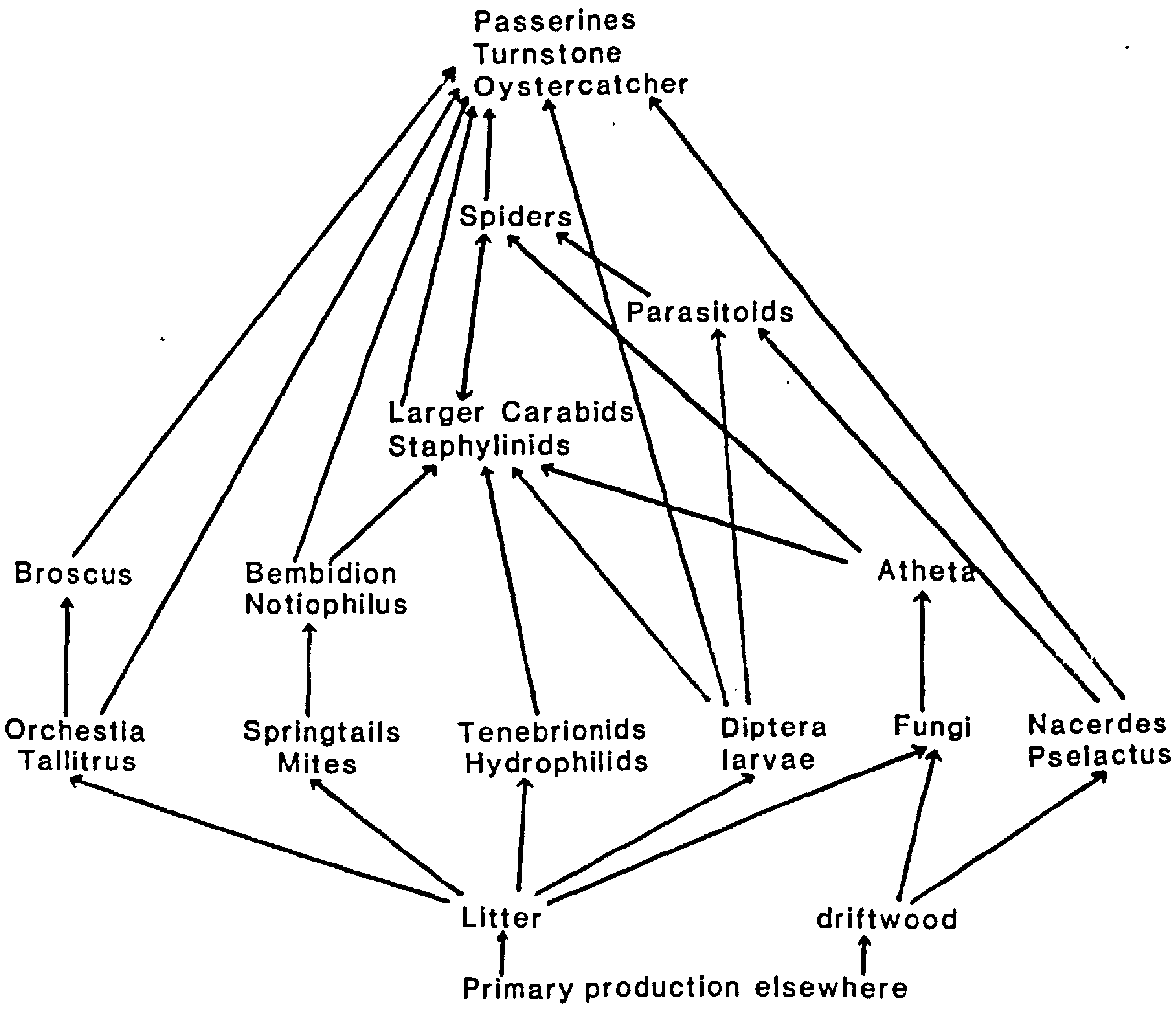


Figure 4xi Speculative food relations of components of strandline community, incorporating those species found in Spurn Bight.

Figures 4xii, 4xiii & 4xiv.

Two dimension polar ordinations of stations of extensive (May/June 1977) survey. Gradients of median particle size (ϕ), and tidal height (hw - lw), fitted by eye.

Figure 4xii

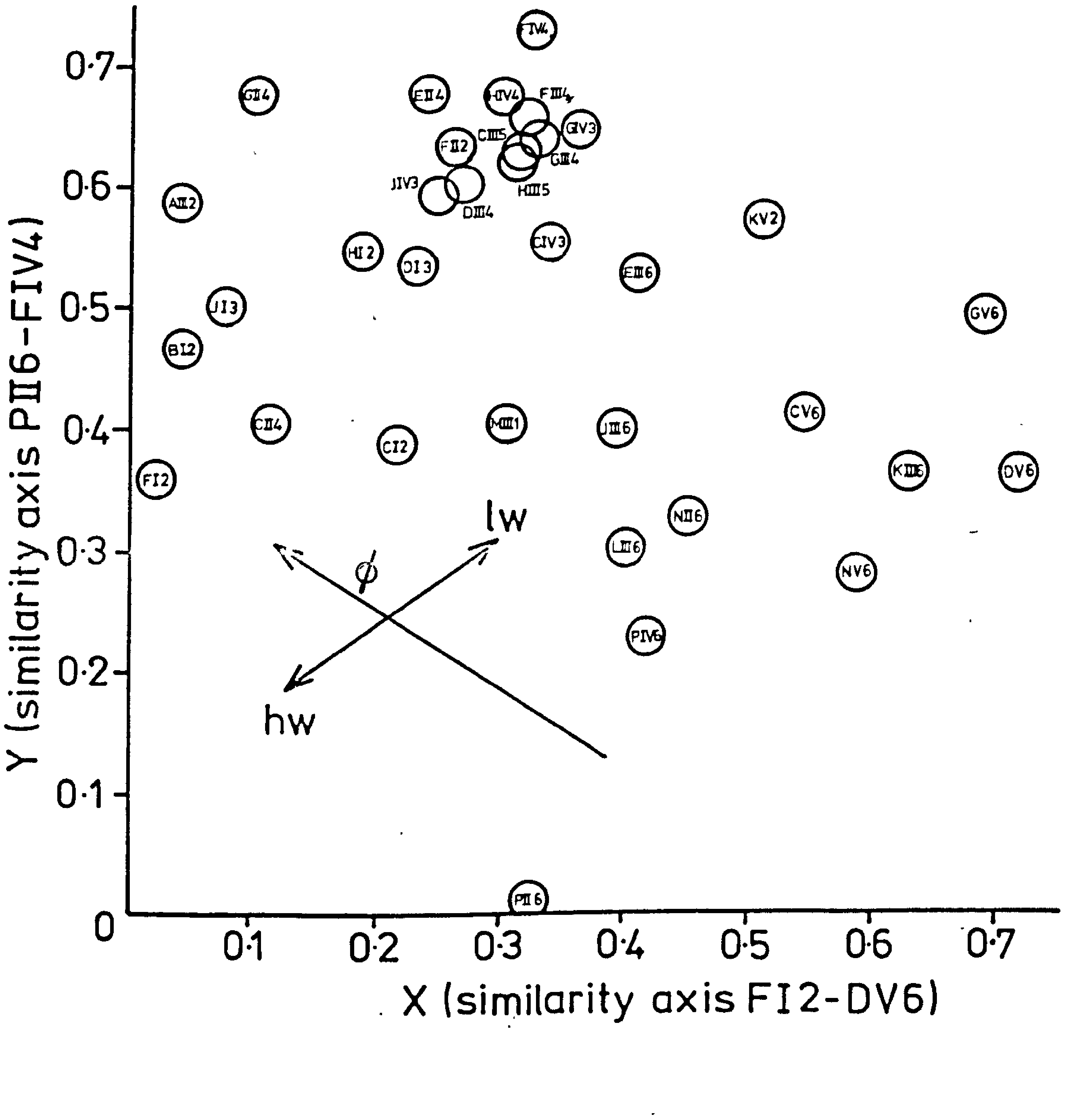

FIV4
GII4
EII4
HIV4
FIII4
GIV3
CIII5
FII2
GIII4
JIV3
HIII5
DIII4
AIII2
KV2
CIV3
HI2
DI3
EIII6
JI3
GV6
BI2
CV6
CII4
MIII1
JIII6
CI2
FI2
KIII6
DV6
lw
NII6
ϕ
LIII6
NV6
PIV6
hw
PII6
Y (similarity axis PII6–FIV4)
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
X (similarity axis FI2–DV6)

Figure 4xiii

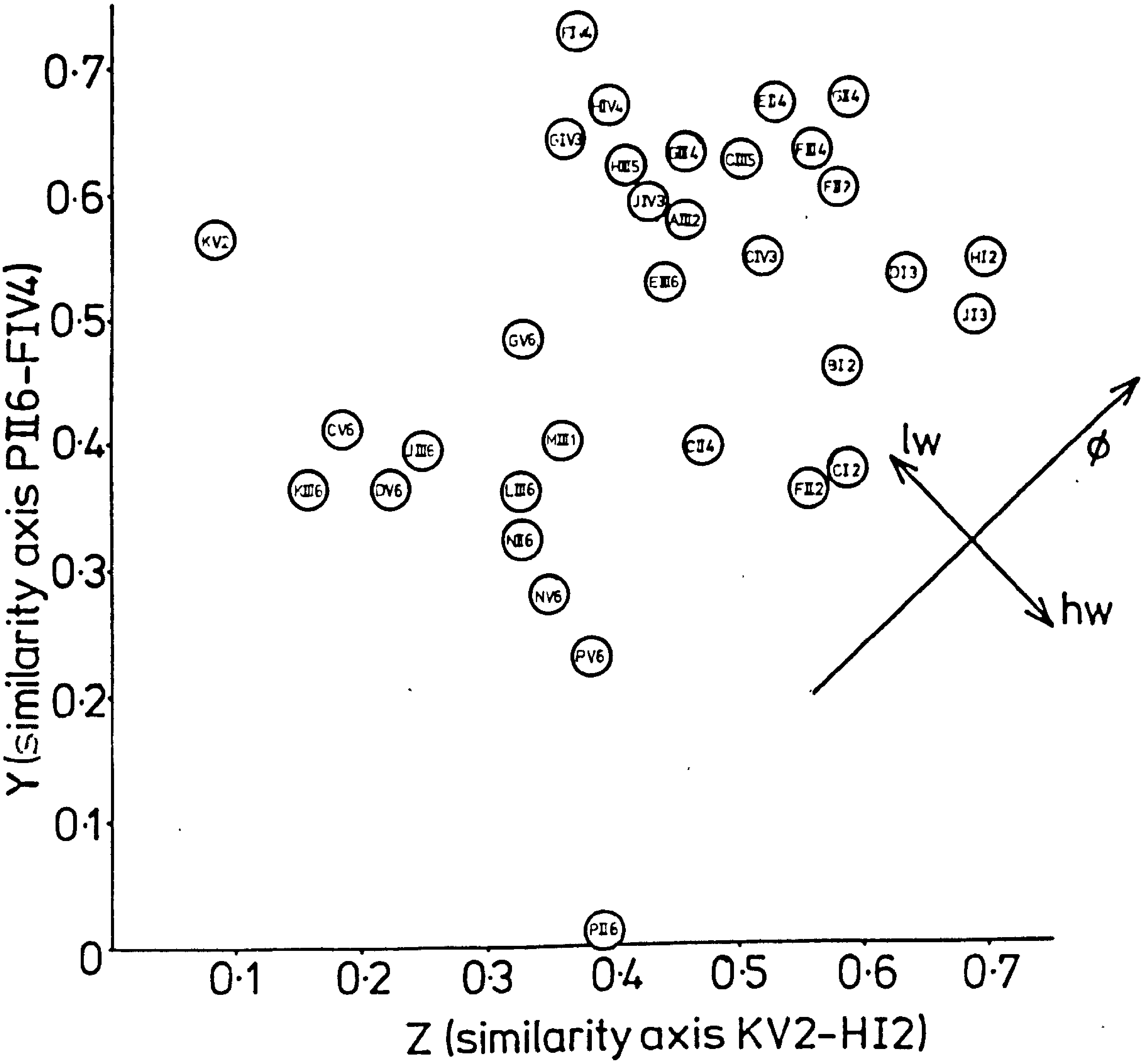
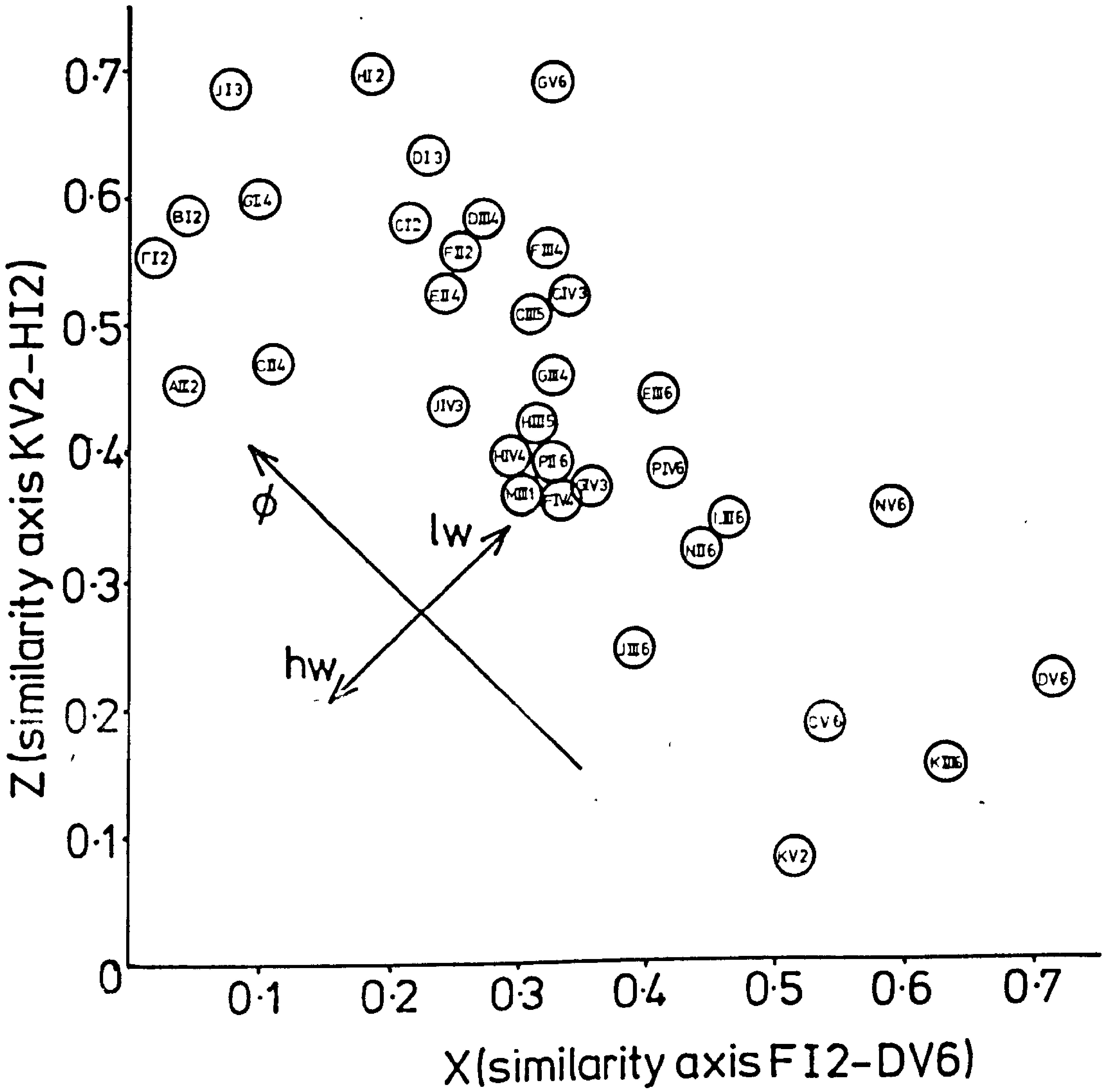


Figure 4:xiv


0·7
0·6
0·5
0·4
0·3
0·2
0·1
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
Z(similarity axis KV2–HI2)
X(similarity axis FI2–DV6)
JI3
HII2
GV6
DI3
GI4
BI2
FI2
CI2
DIII4
FII2
FIII4
EII4
CIV3
CIII5
CII4
AII2
GIII4
EIII6
JIV3
HIII5
HIV4
PII6
GIV3
MIII1
FIV4
PIV6
III6
NII6
NV6
JIII6
DV6
CV6
KIII6
KV2
ϕ
lw
hw

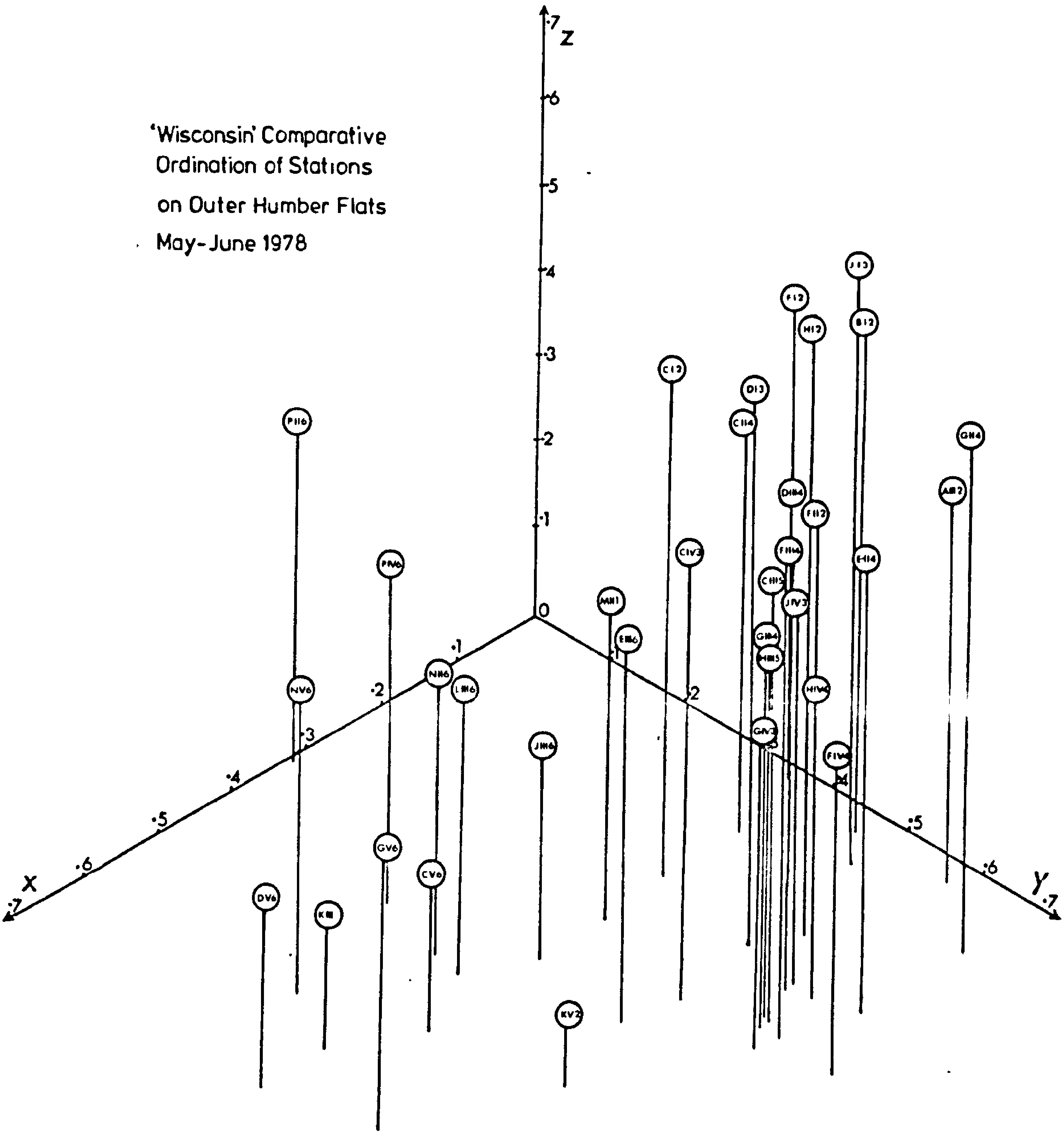


Figure 4xv Three dimensional polar ordination of stations of extensive (May/June 1977), survey.

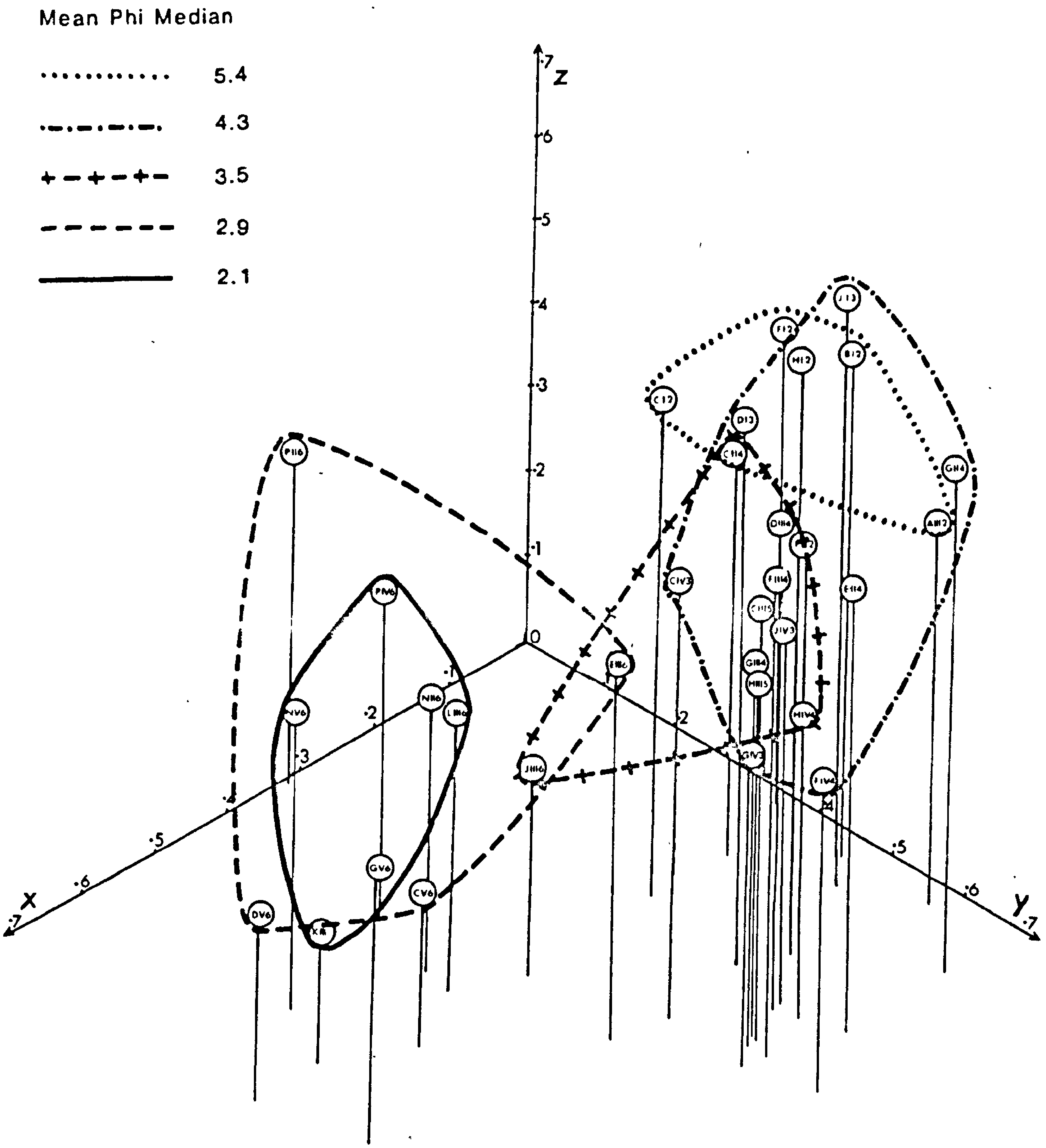


Figure 4xvi Three-dimensional polar ordination of stations of extensive (May/June 1977), survey with clusters of CLUSTAN analysis of sediment parameters (expressed as mean ϕ median).

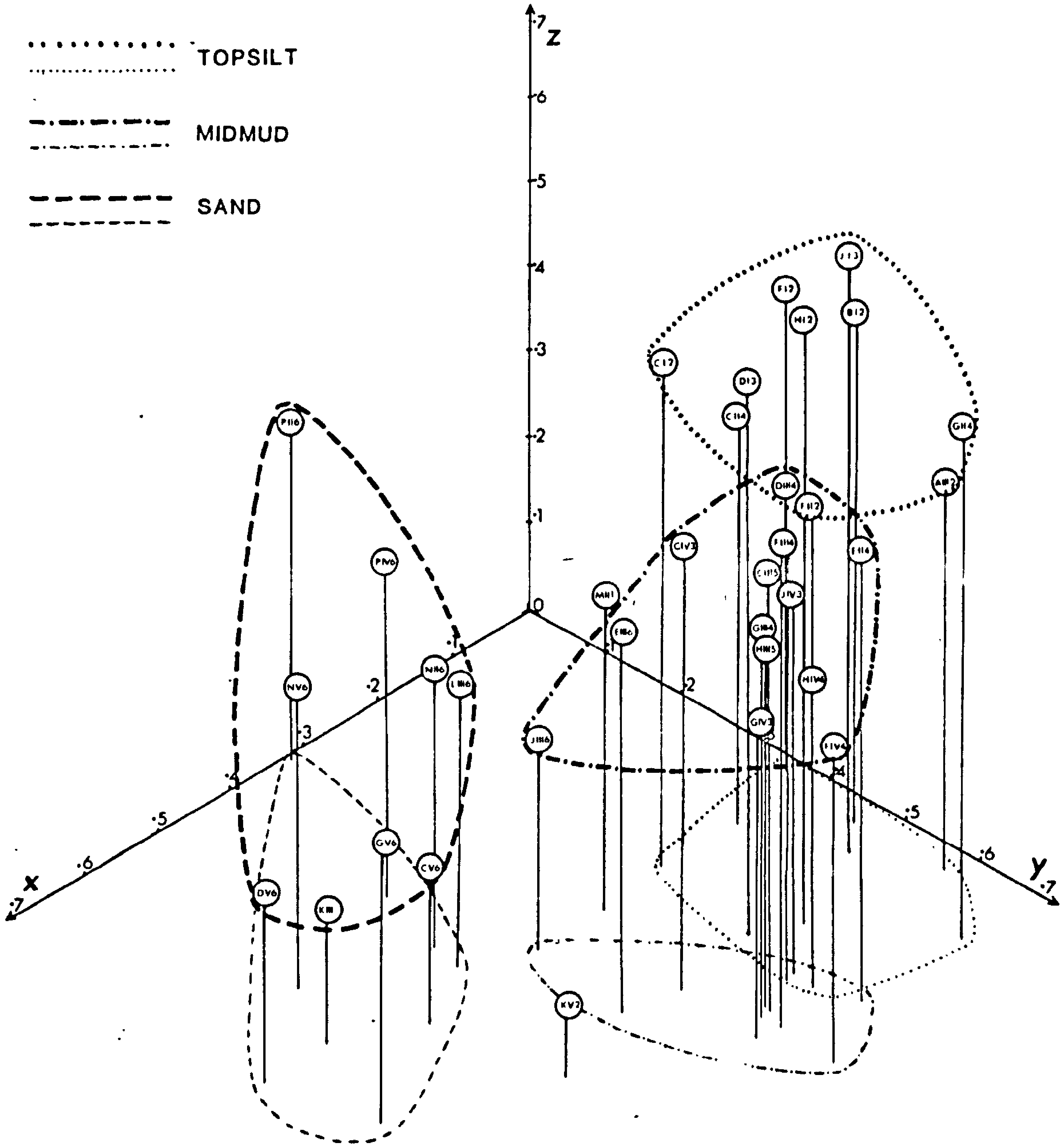


Figure 4xvii Three dimensional polar ordination of stations of extensive survey (May/June 1977), with clusters TOPSILT, MIDMUD and SAND from CLUSTAN analysis of macrofauna superimposed.

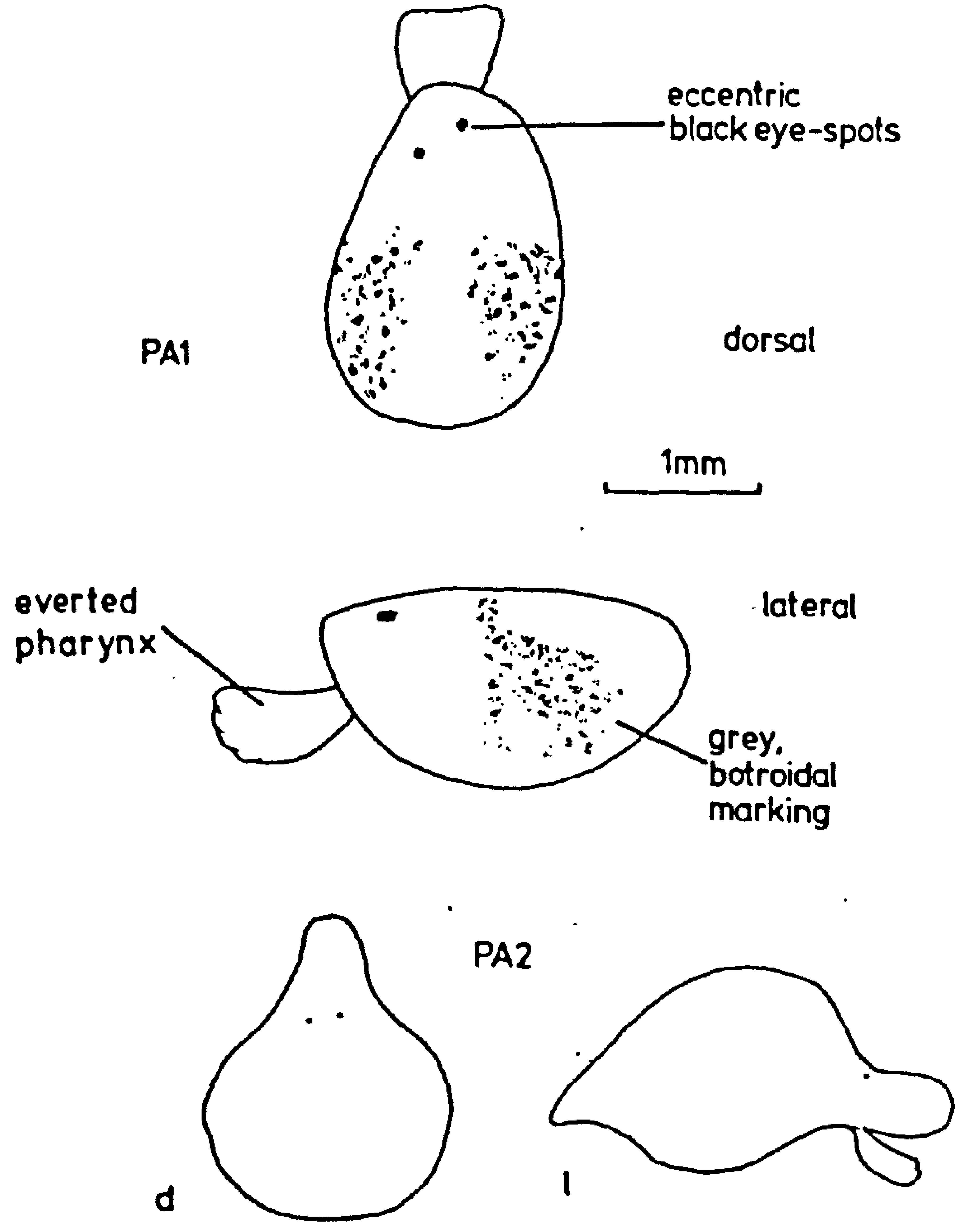


Figure 5i Appearence of Turbellarian 'PA1' and 'PA2' found at Spurn and Horseshoe Point.

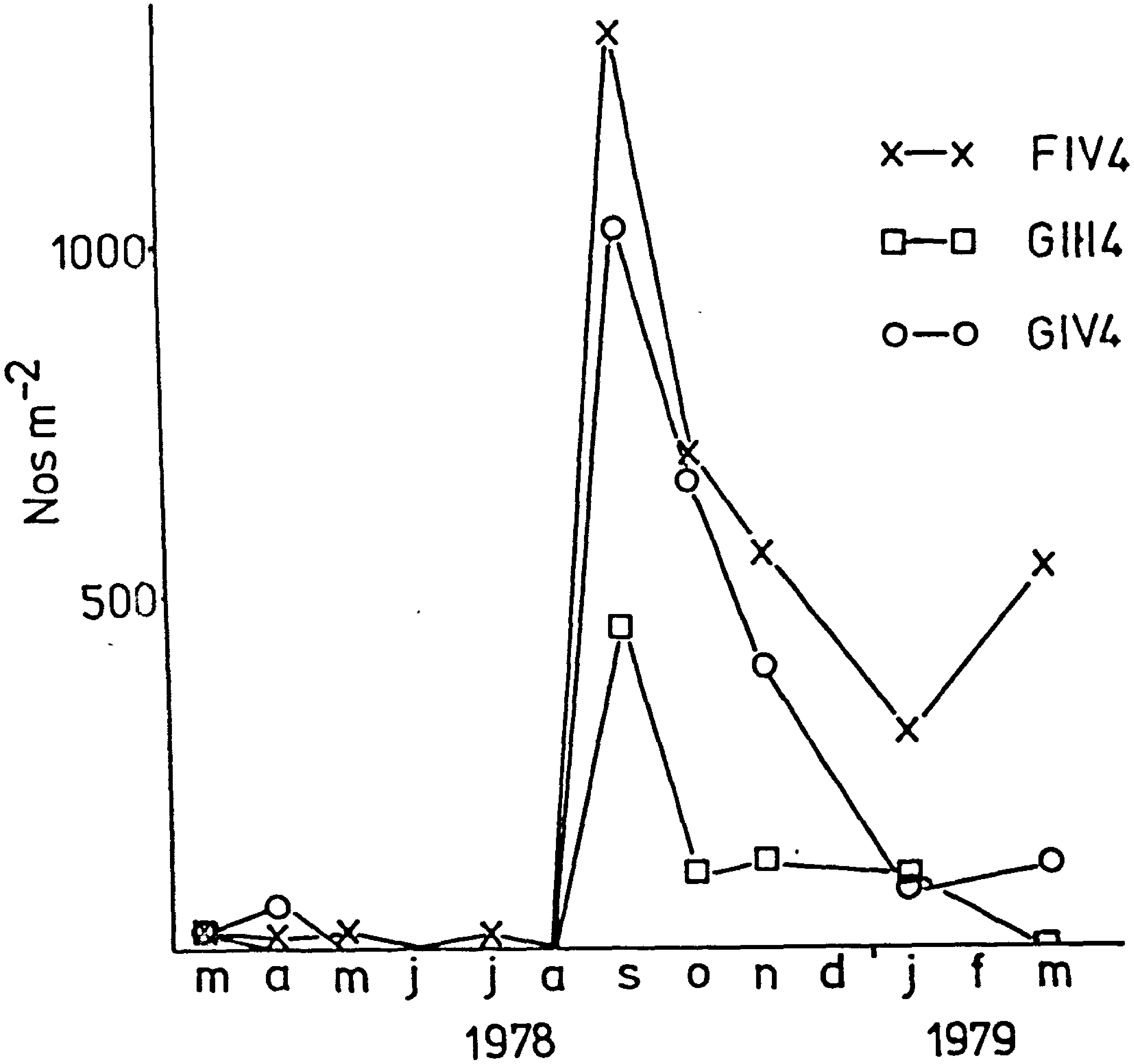


Figure 5ii Fluctuations in abundance of Turbellarian 'PA1' March 1978 - March 1979.

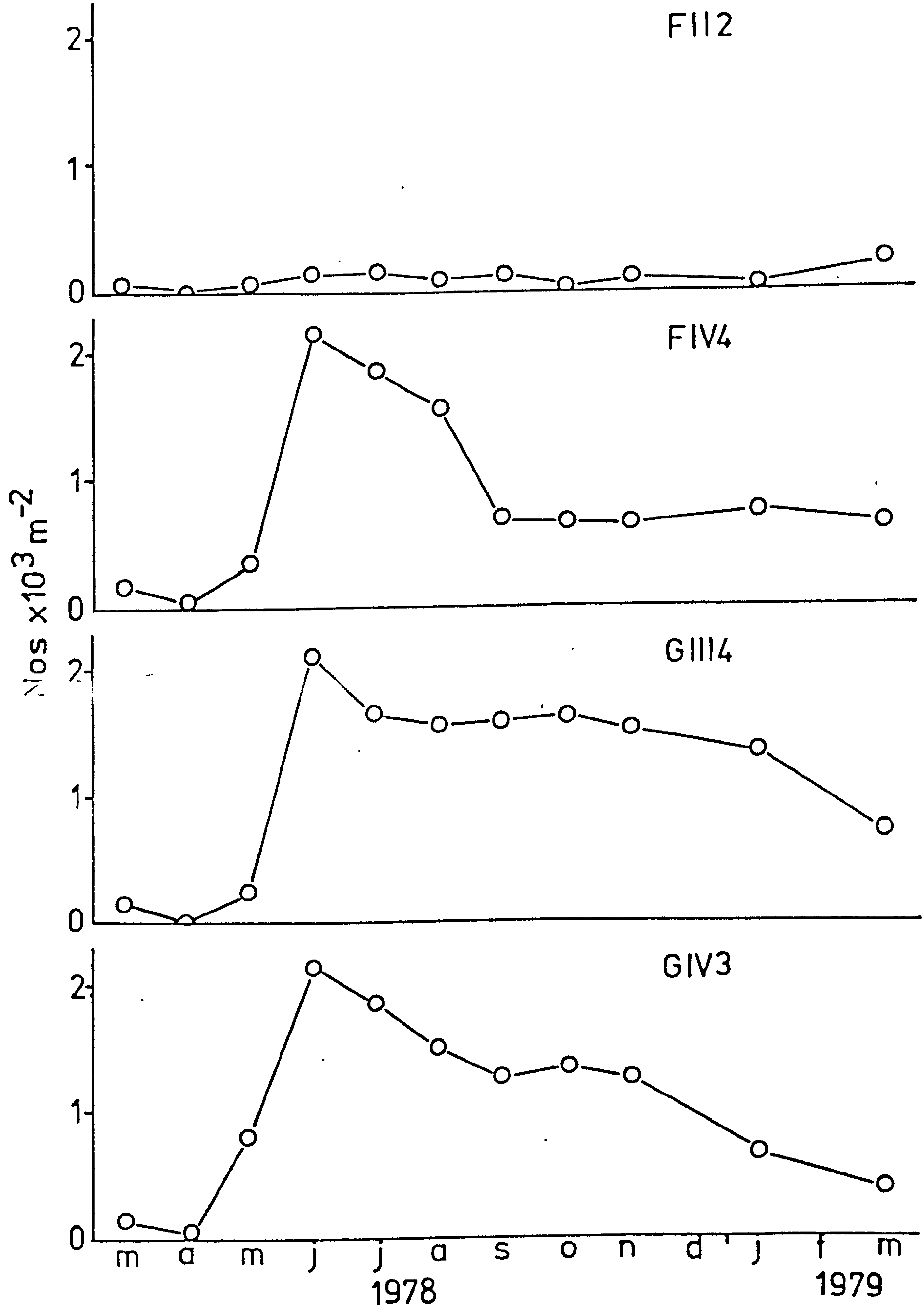
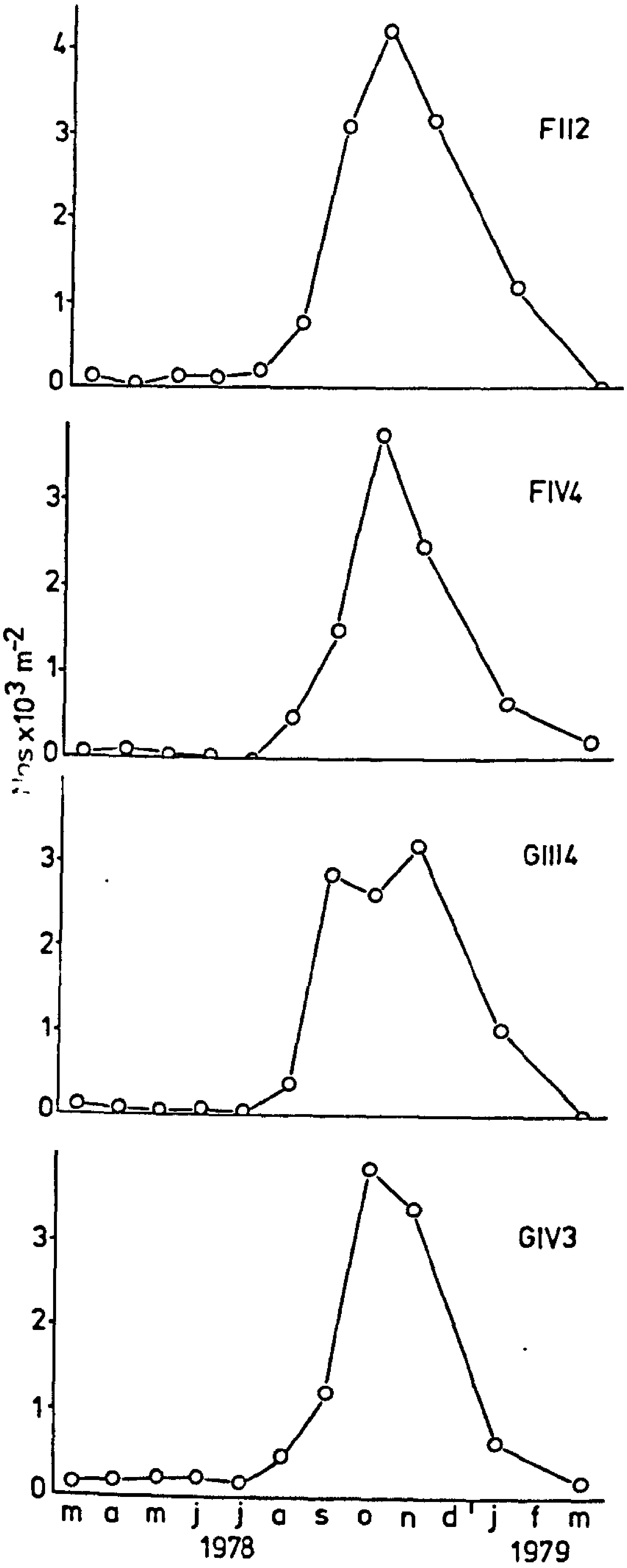


Figure 5iii Fluctuations in density of Eteone longa. March 1978 - March '7



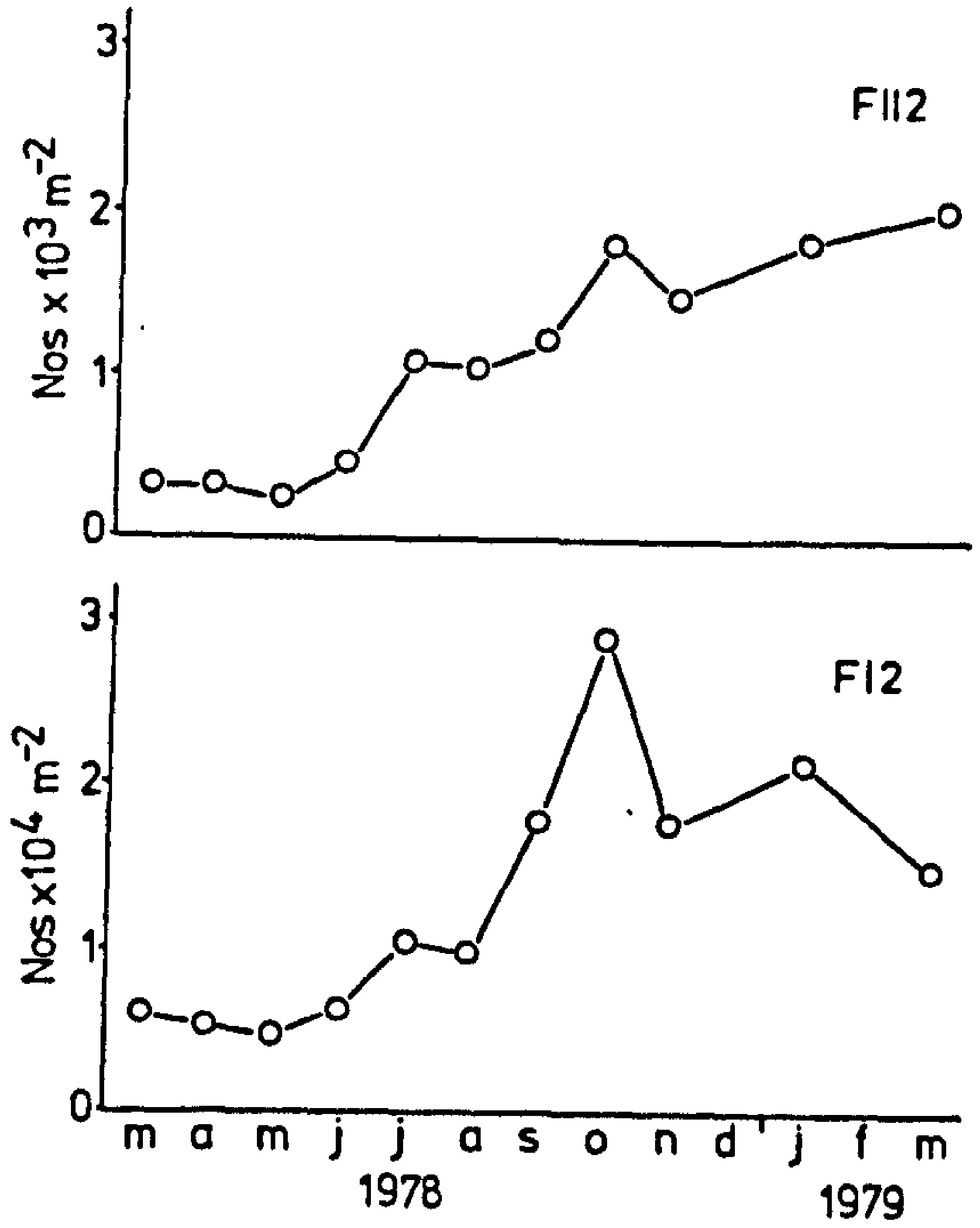


Figure 5iv (left). Fluctuations in abundance of <u>Streblospio shrubsolii</u>. March 1978 - March 1979.

Figure 5v (above). Fluctuations in abundance of <u>Edukemius benedii</u>. March 1978 - March 1979.

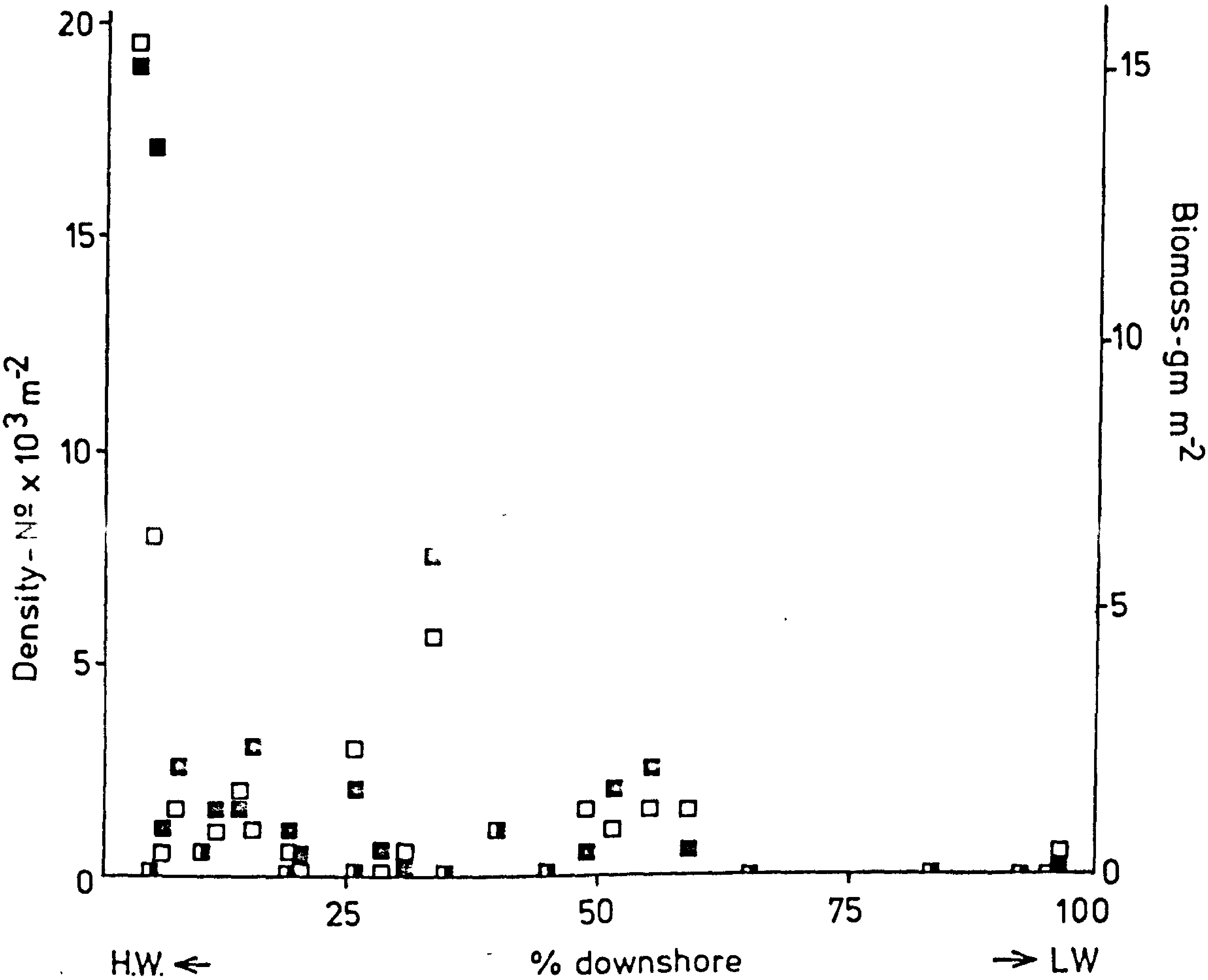
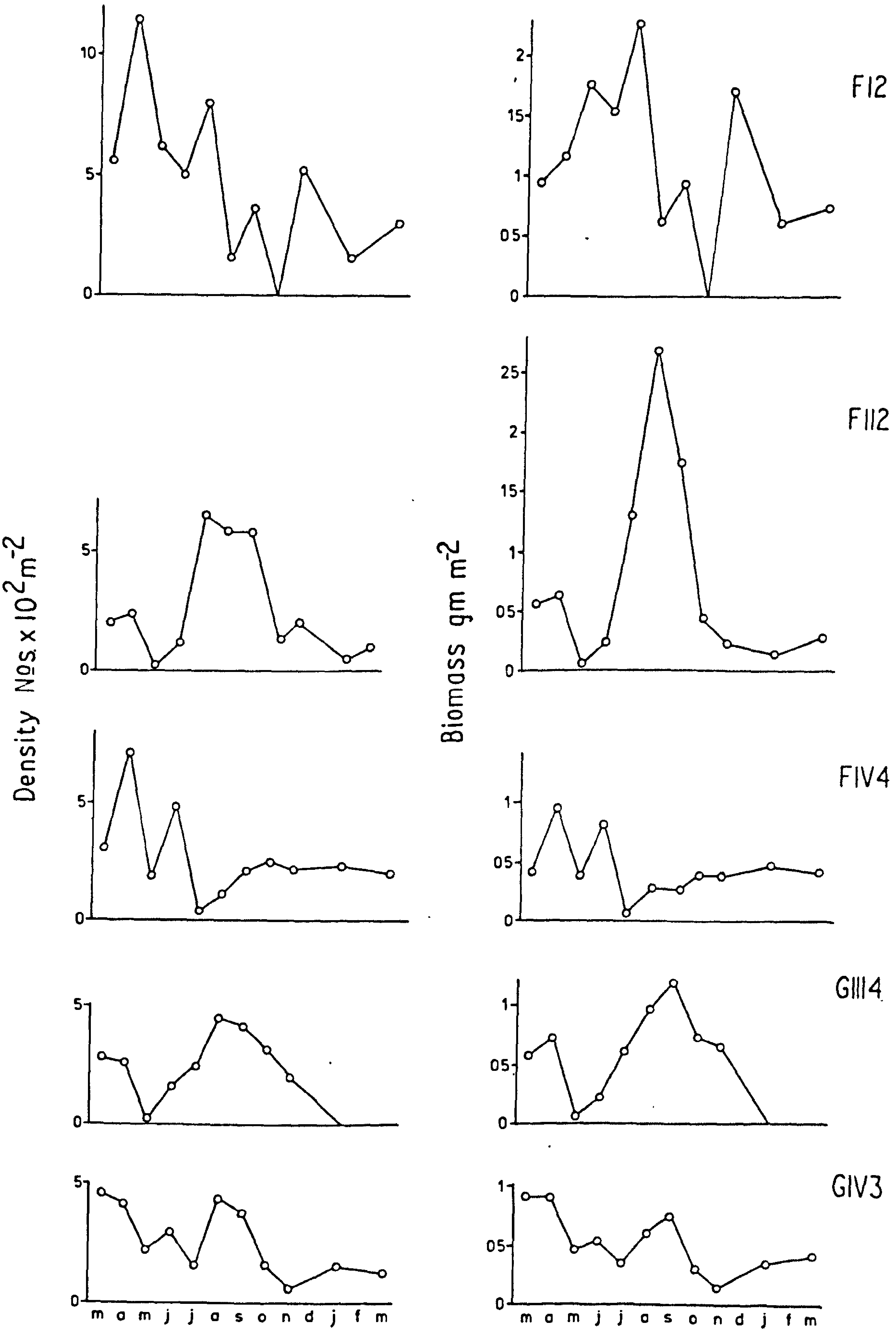


Figure 5vi Distibution of Hydrobia ulvae in relation to tidal height. (as percentage of downshore distance). Extensive survey, May/June 1977. Spurn Bight only.



Figures 5vii & 5viii. Density and biomass of Hydrobia ulvae.
All intensive survey stations. March 1978 - March 1979.

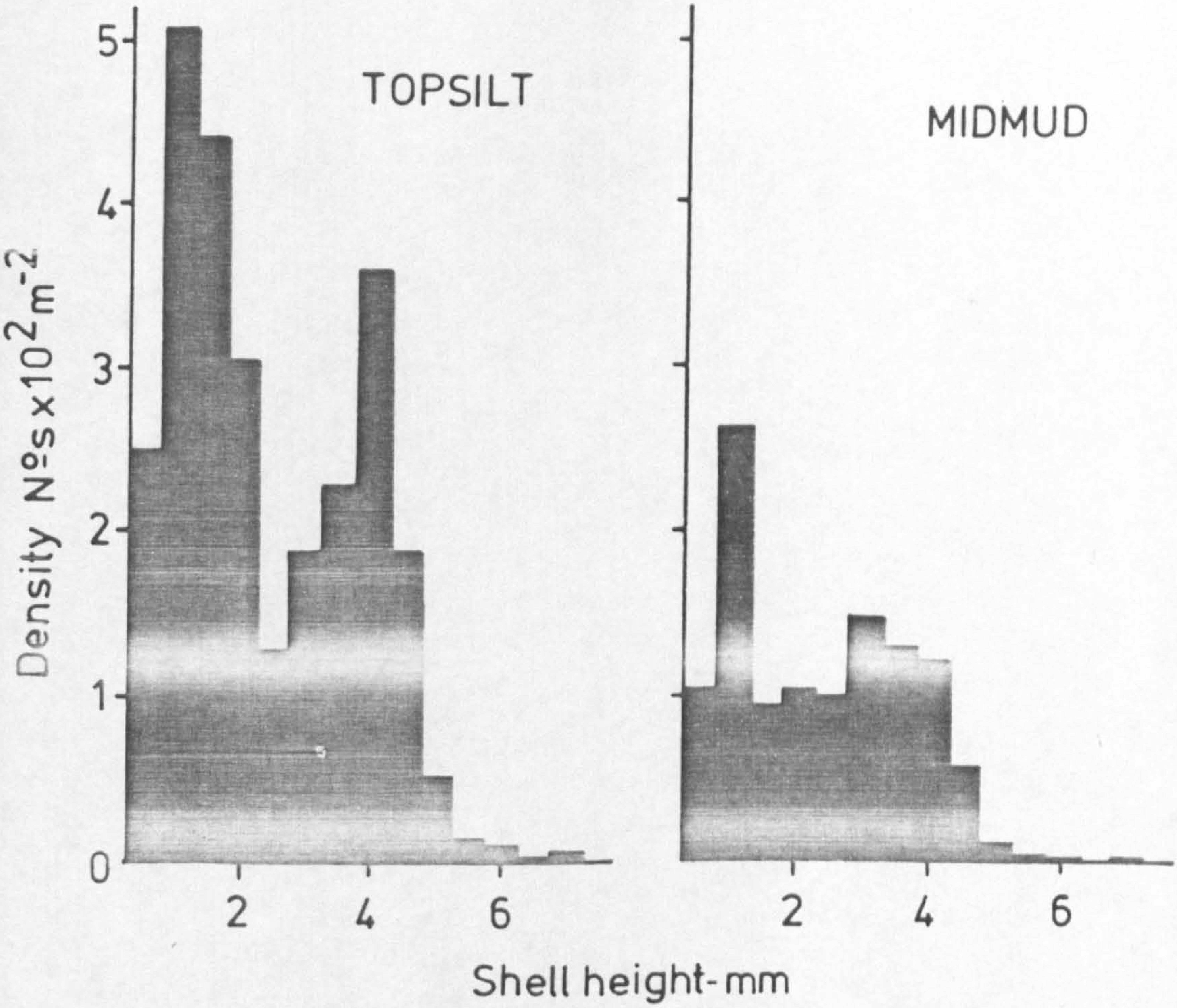


Figure 5ix. Mean population structure of Hydrobia ulvae - all stations of TOPSILT and MIDMUD communities. Extensive survey, May/June 1977.

Figure 5x Variation in population structure of Hydrobia ulvae at all intensive survey stations. March 1978 - March 1979.

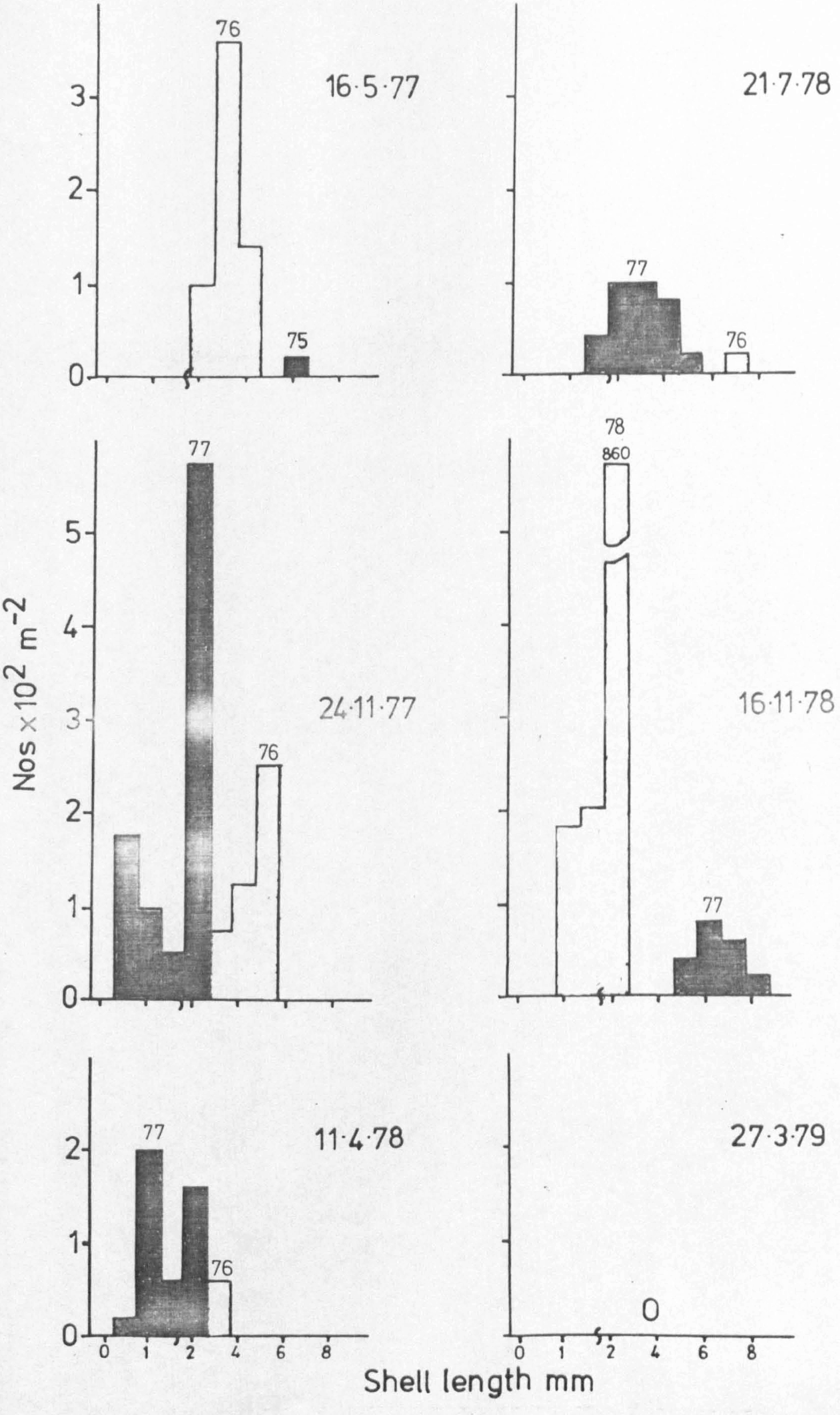


Figure 5xi Population structure of Scrobicularia plana at station CI2. May 1977 - March 1979.

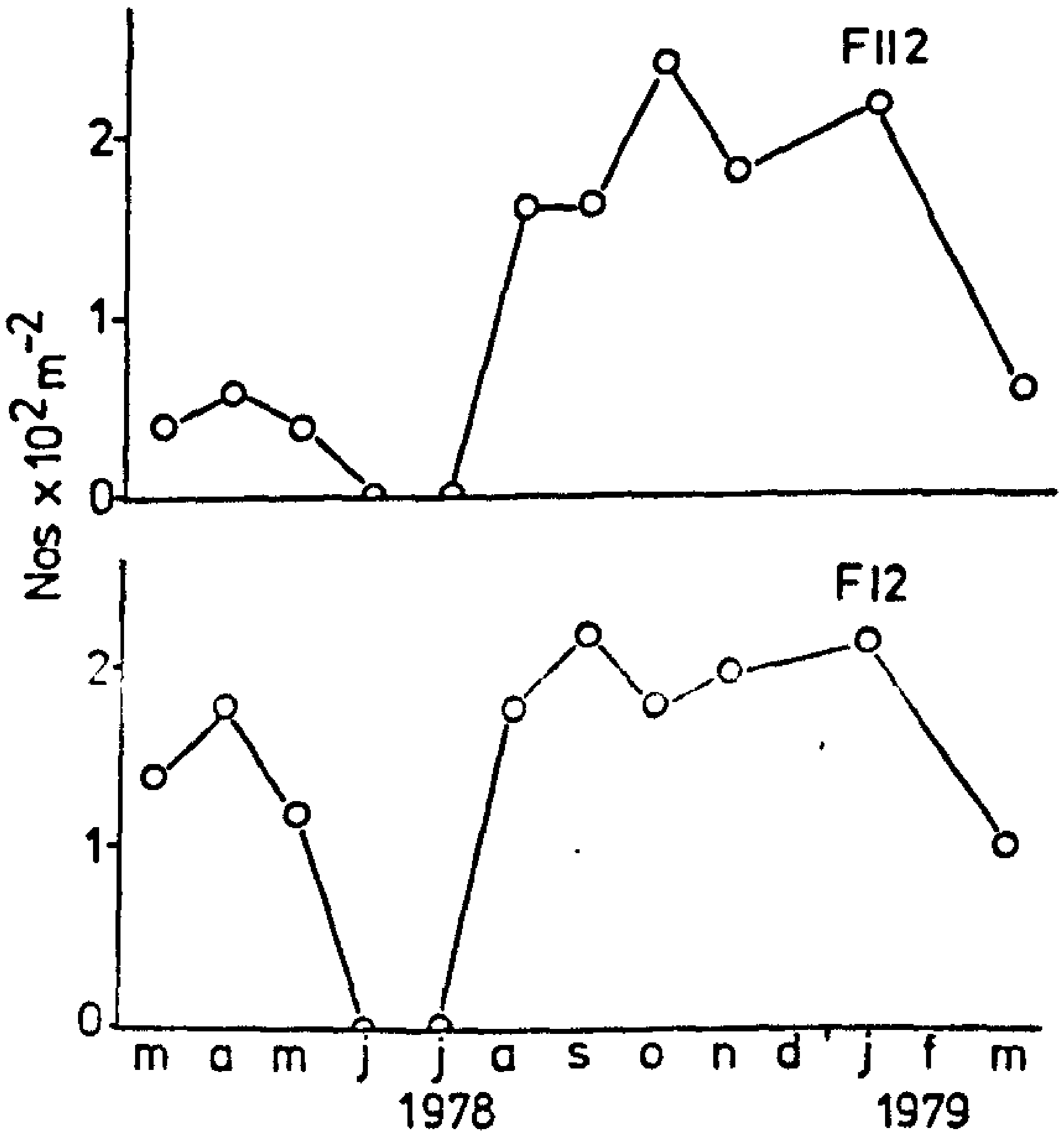


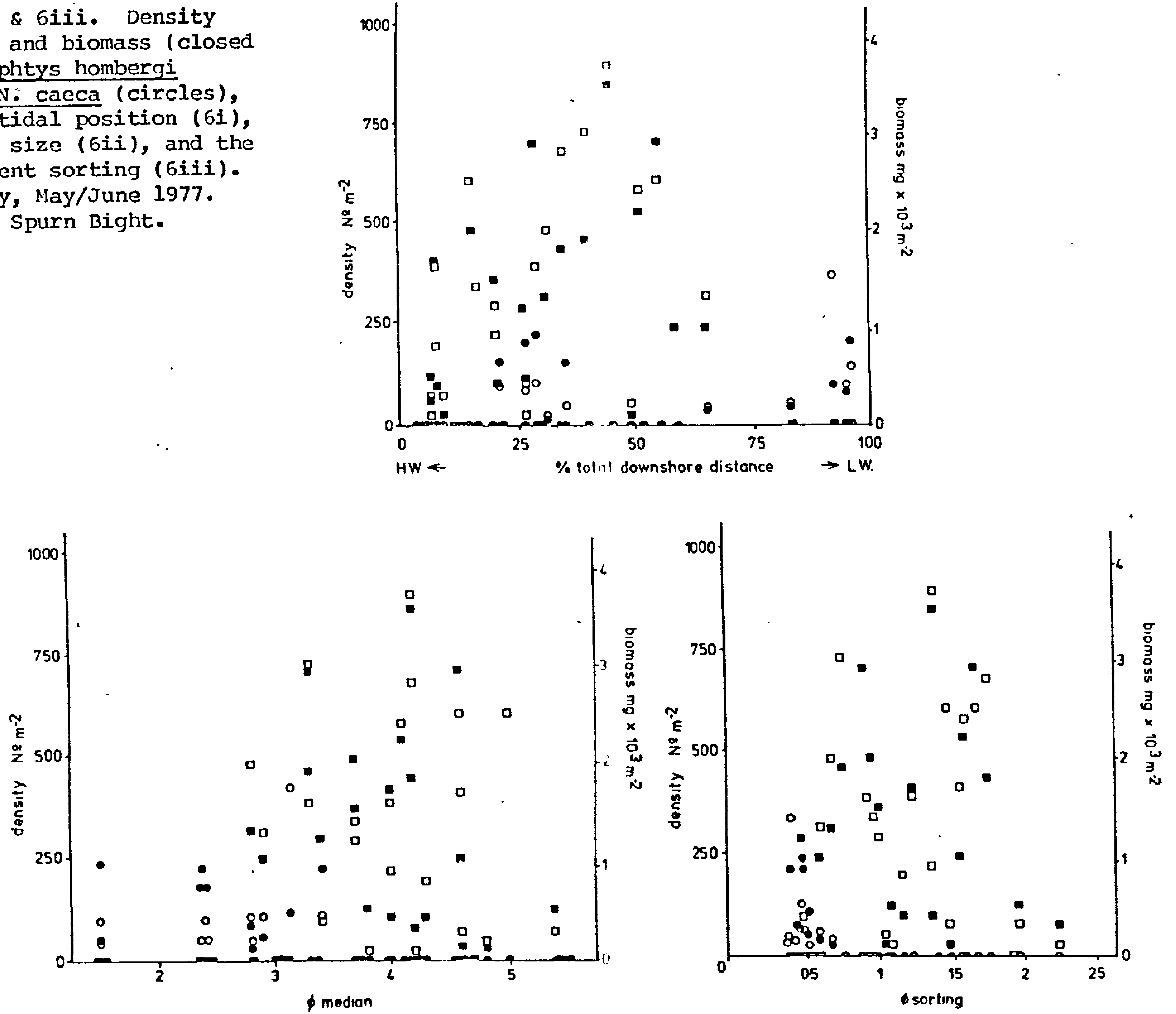
Figure 5xii Fluctuations in density of Tabanid larvae at Skeffling. March 1978 - March 1979.

Figures 6i, 6ii & 6iii. Density (open symbols), and biomass (closed symbols), of Nephtys hombergi (squares), and N. caeca (circles), in relation to tidal position (6i), median particle size (6ii), and the degree of sediment sorting (6iii). Extensive survey, May/June 1977. All stations in Spurn Bight.

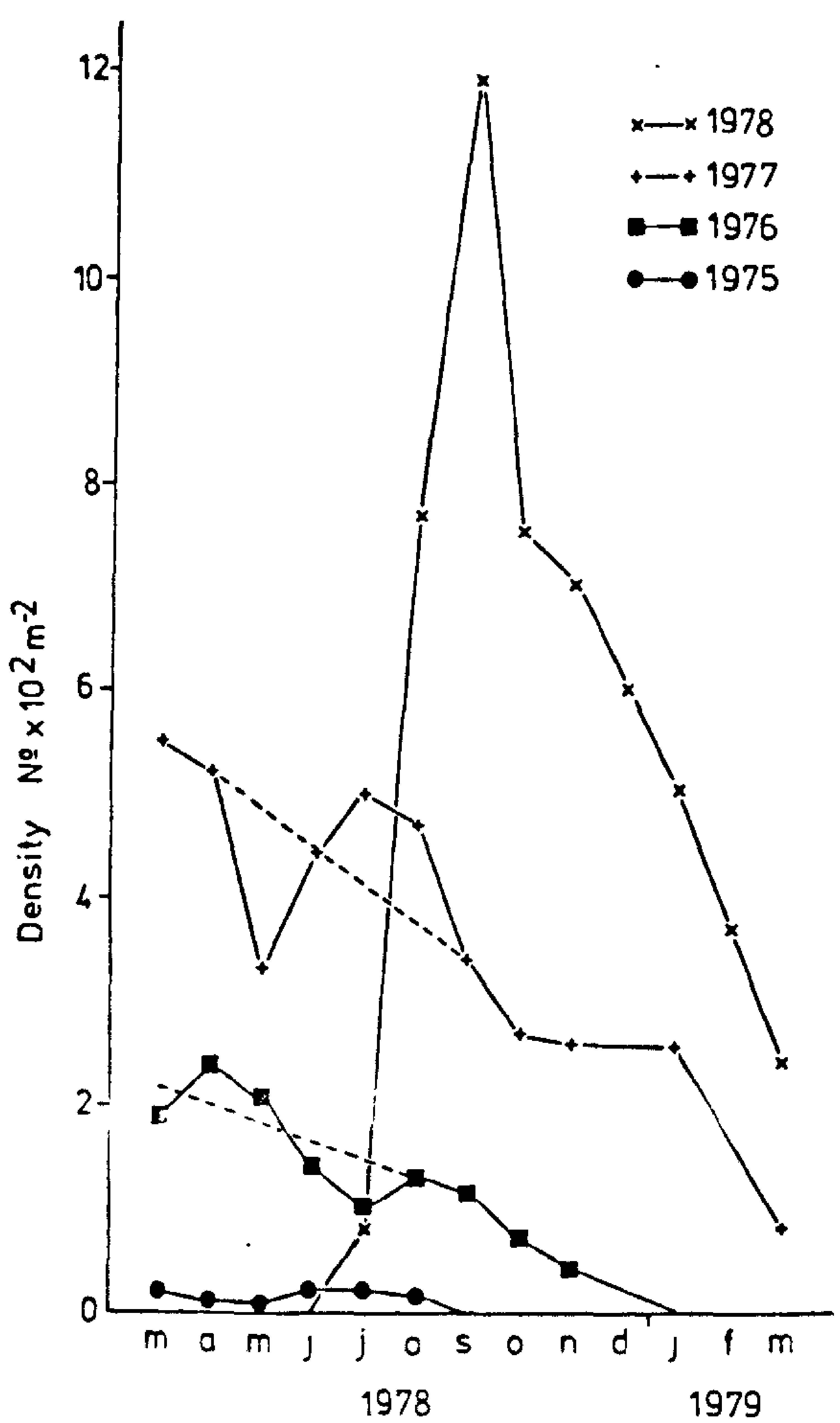
6i

6ii

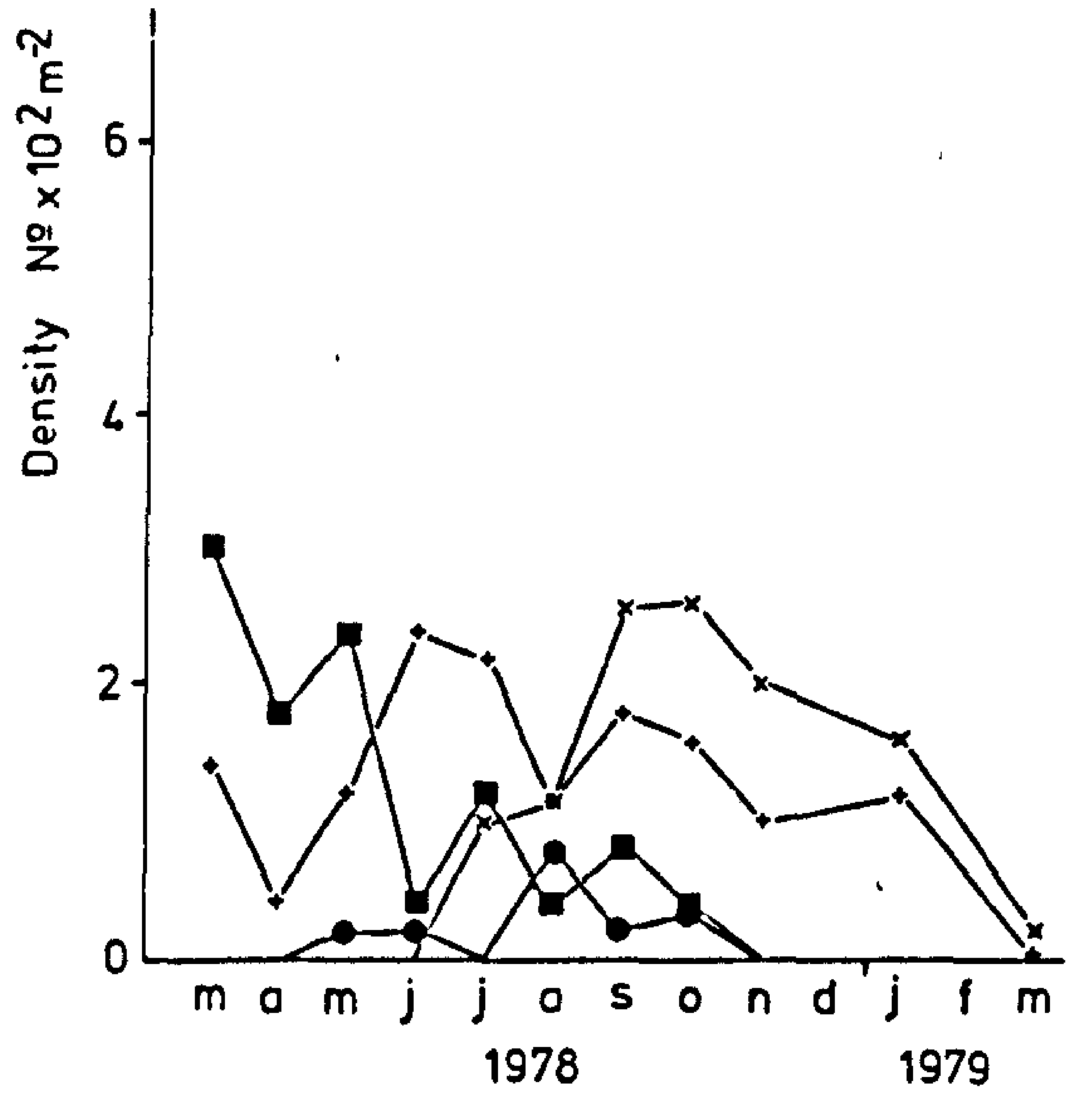
6iii



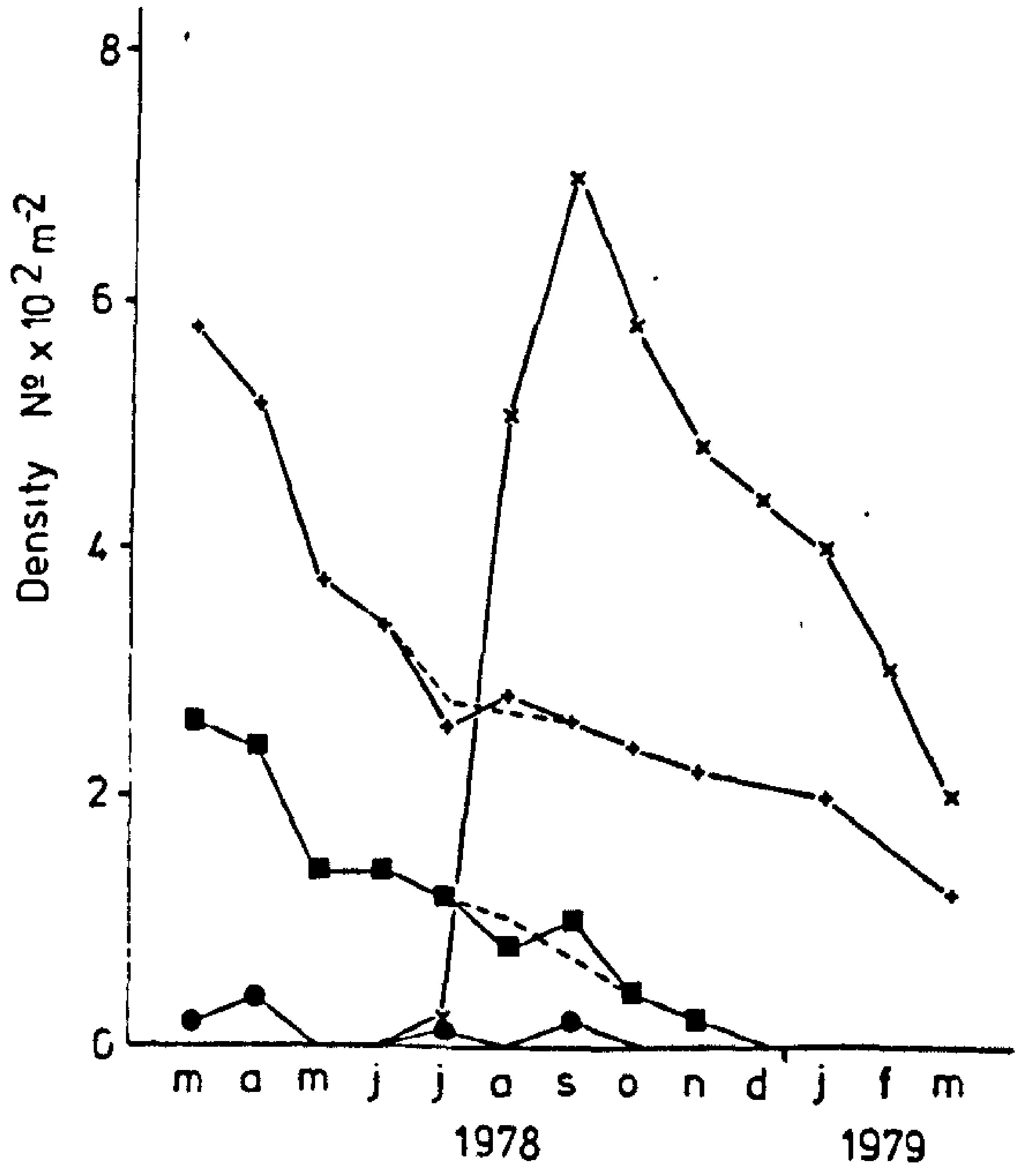
6iv FIV4



6v GIII4



6vi GIV3



Figures 6iv, 6iv & 6vi. Variation in density of each cohort of *Nephtys hombergi*. Intensive survey March 1978 - March 1979.

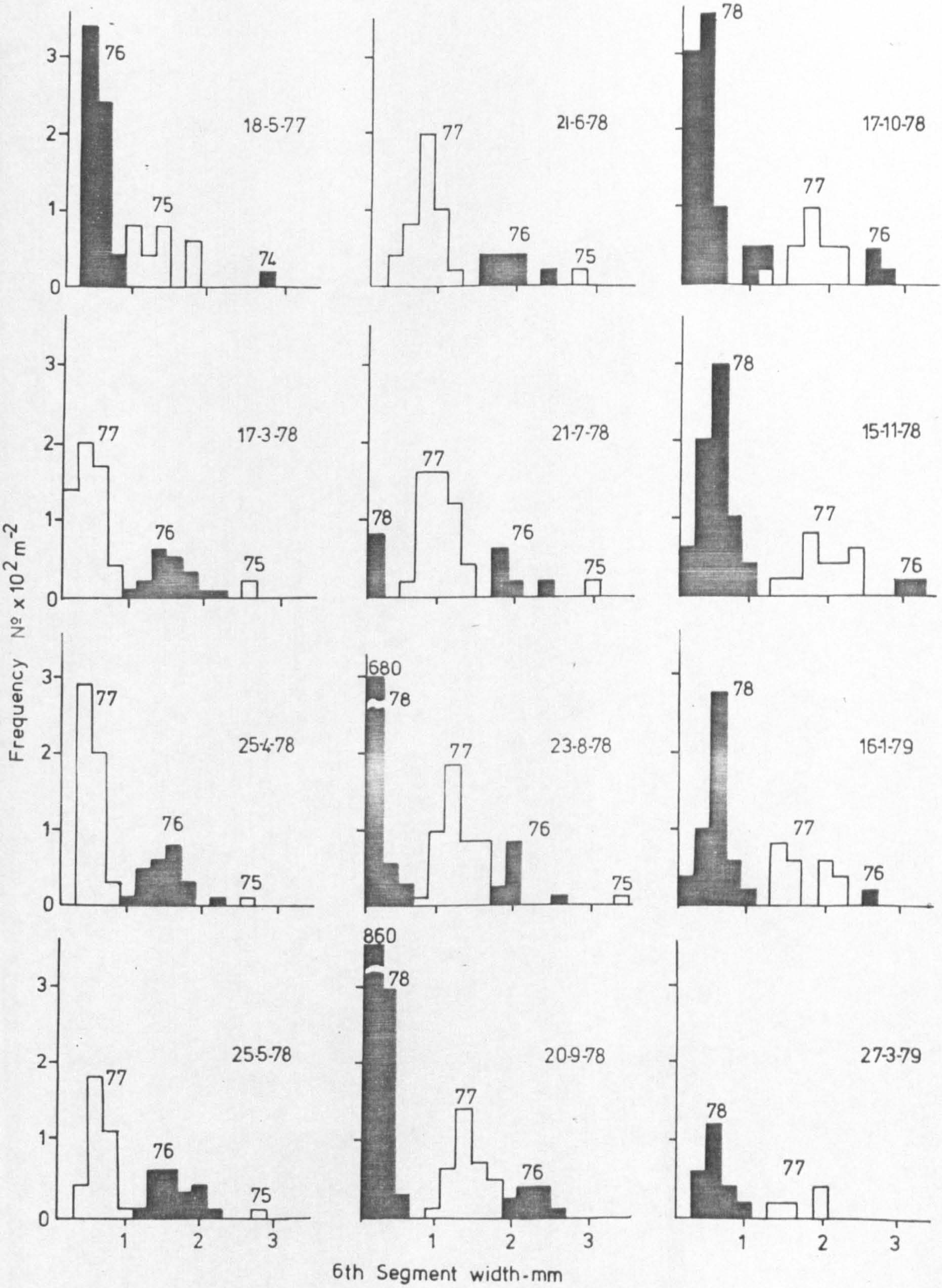


Figure 6vii. Population structure of Nephtys hombergi at Skeffling station FIV4. March 1978 - March 1979.

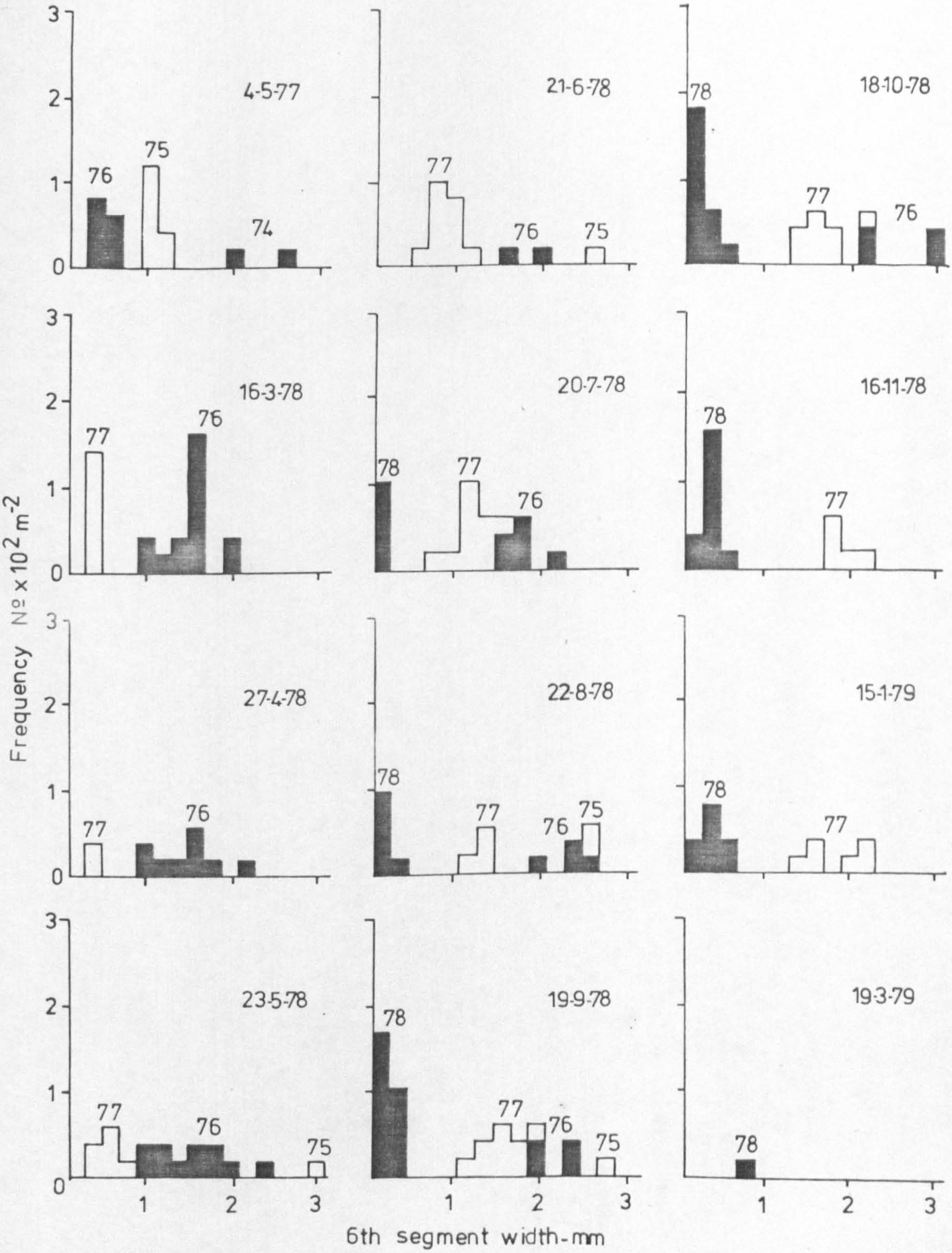


Figure 6viii. Population structure of Nephtys hombergi at Easington station GIII4. March 1978 - March 1979.

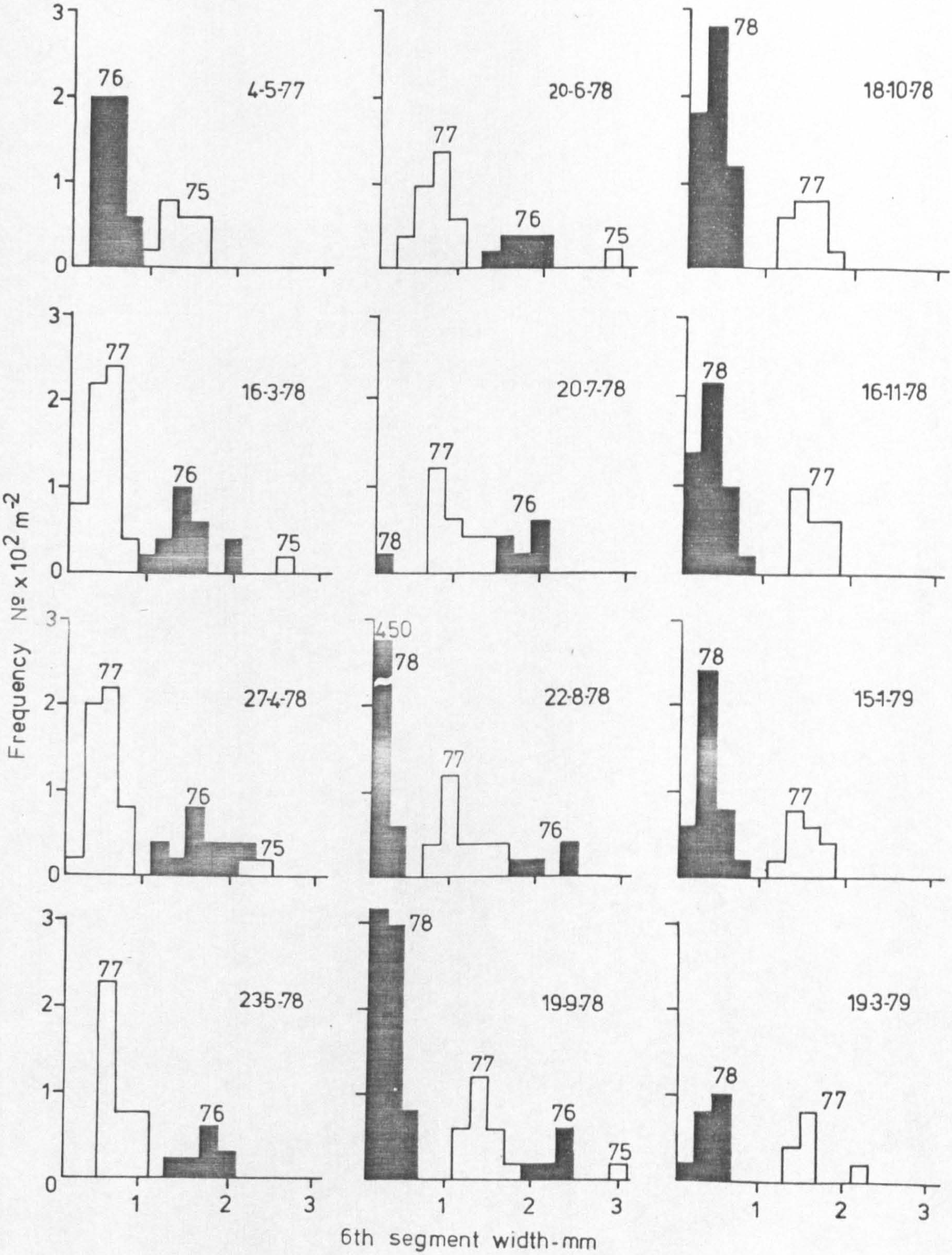
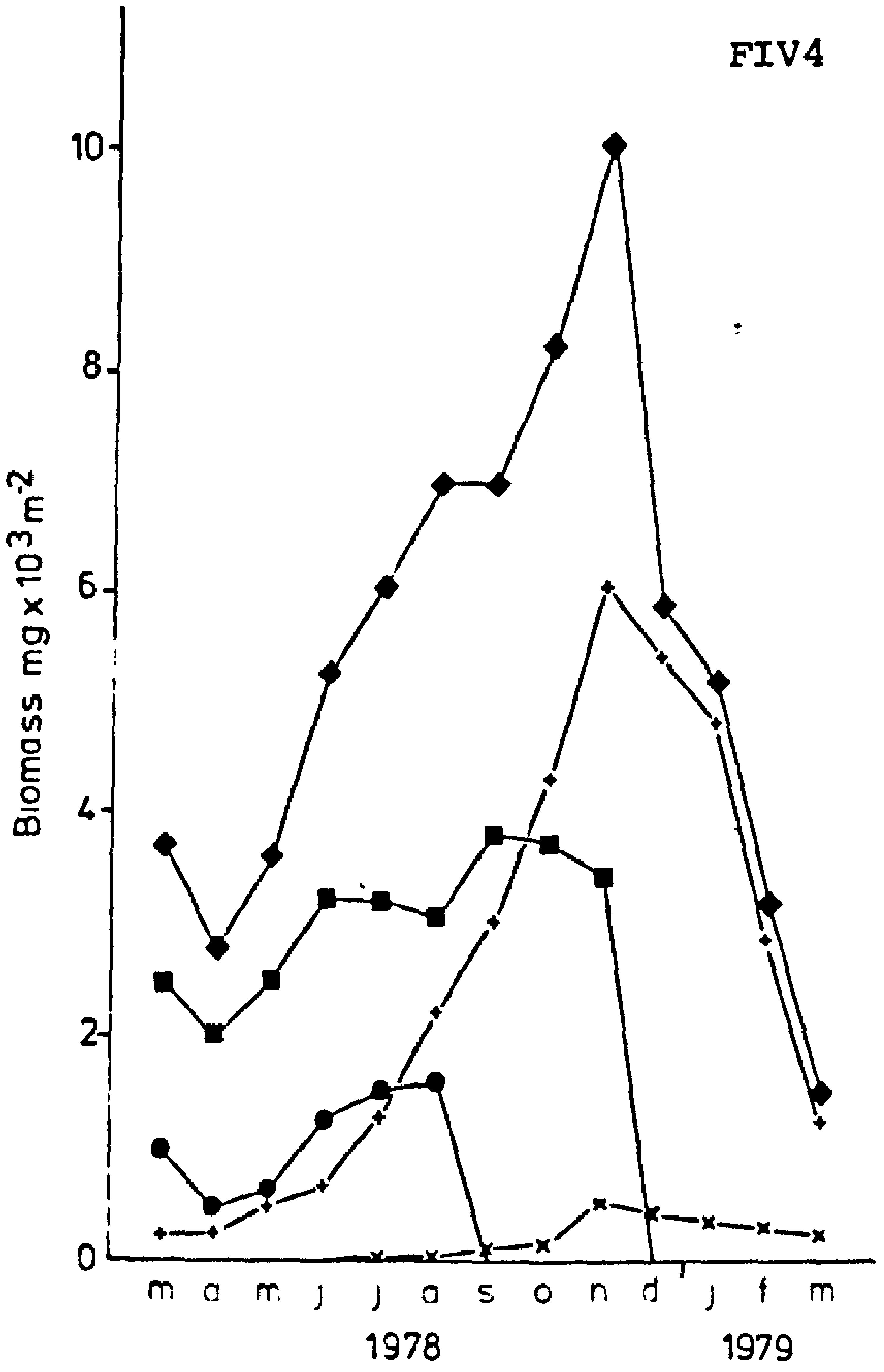
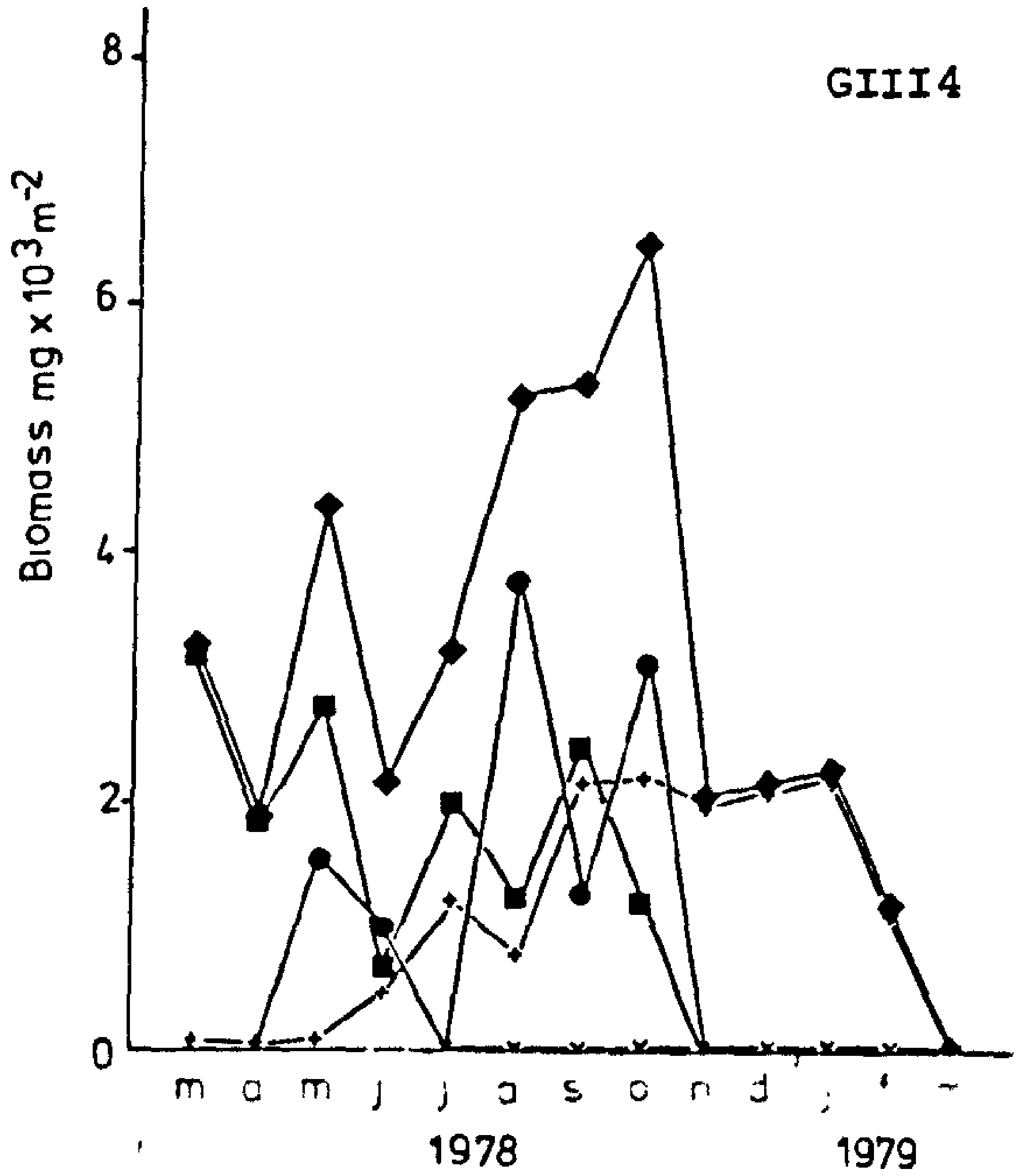


Figure 6ix. Population structure of <u>Nephtys hombergi</u> at Easington station GIV3. March 1978 - March 1979.

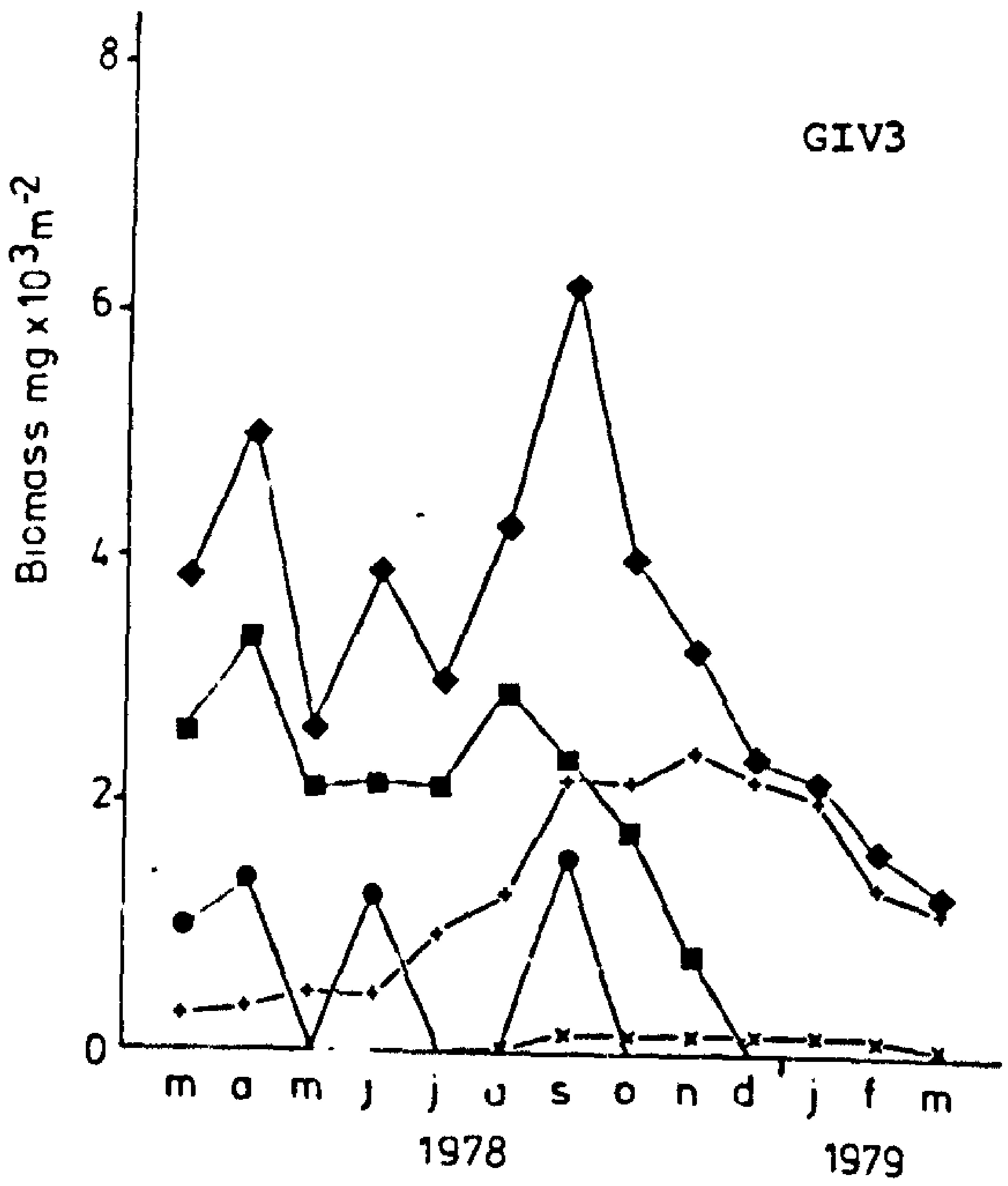
6x



6xi

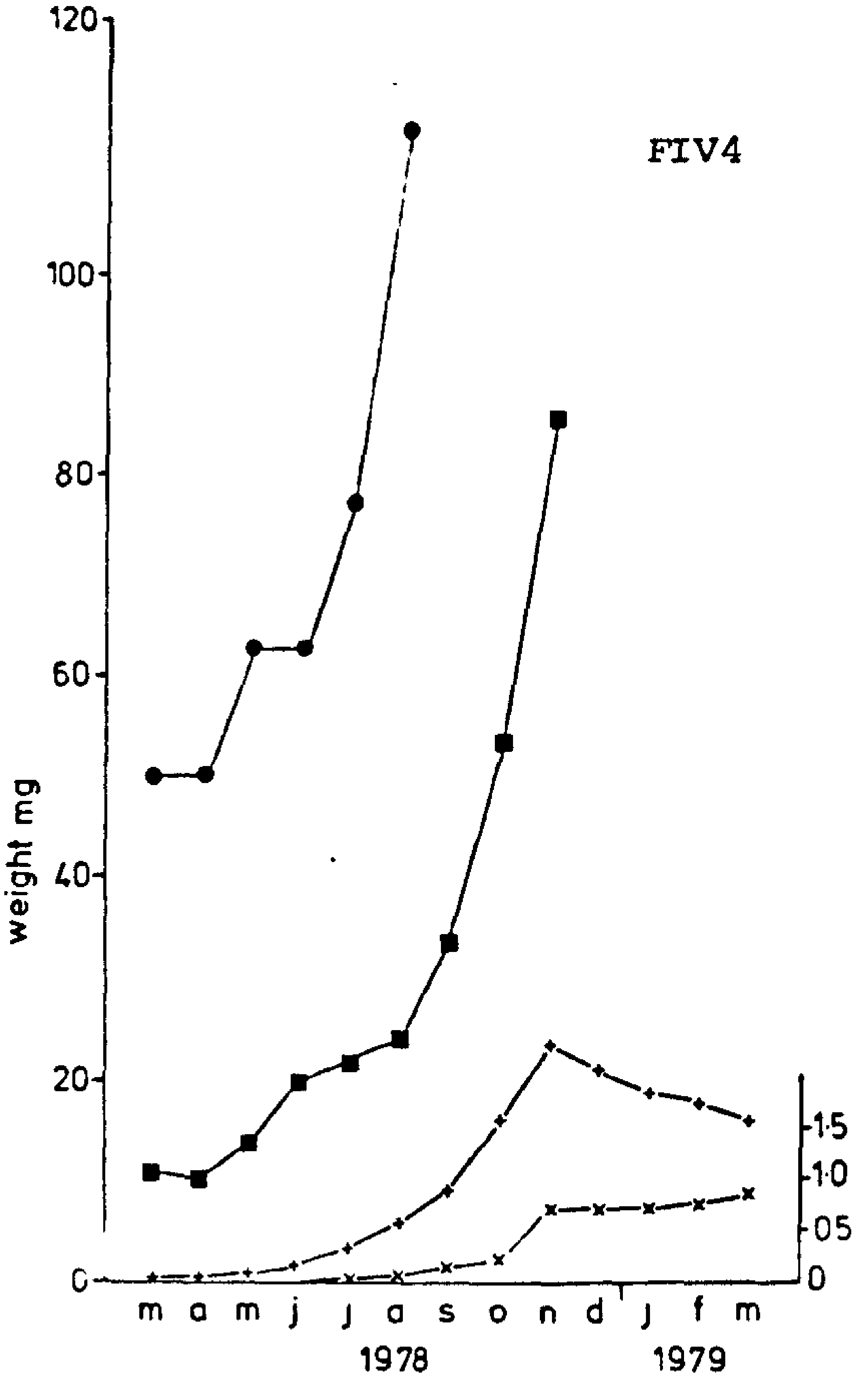


6xii

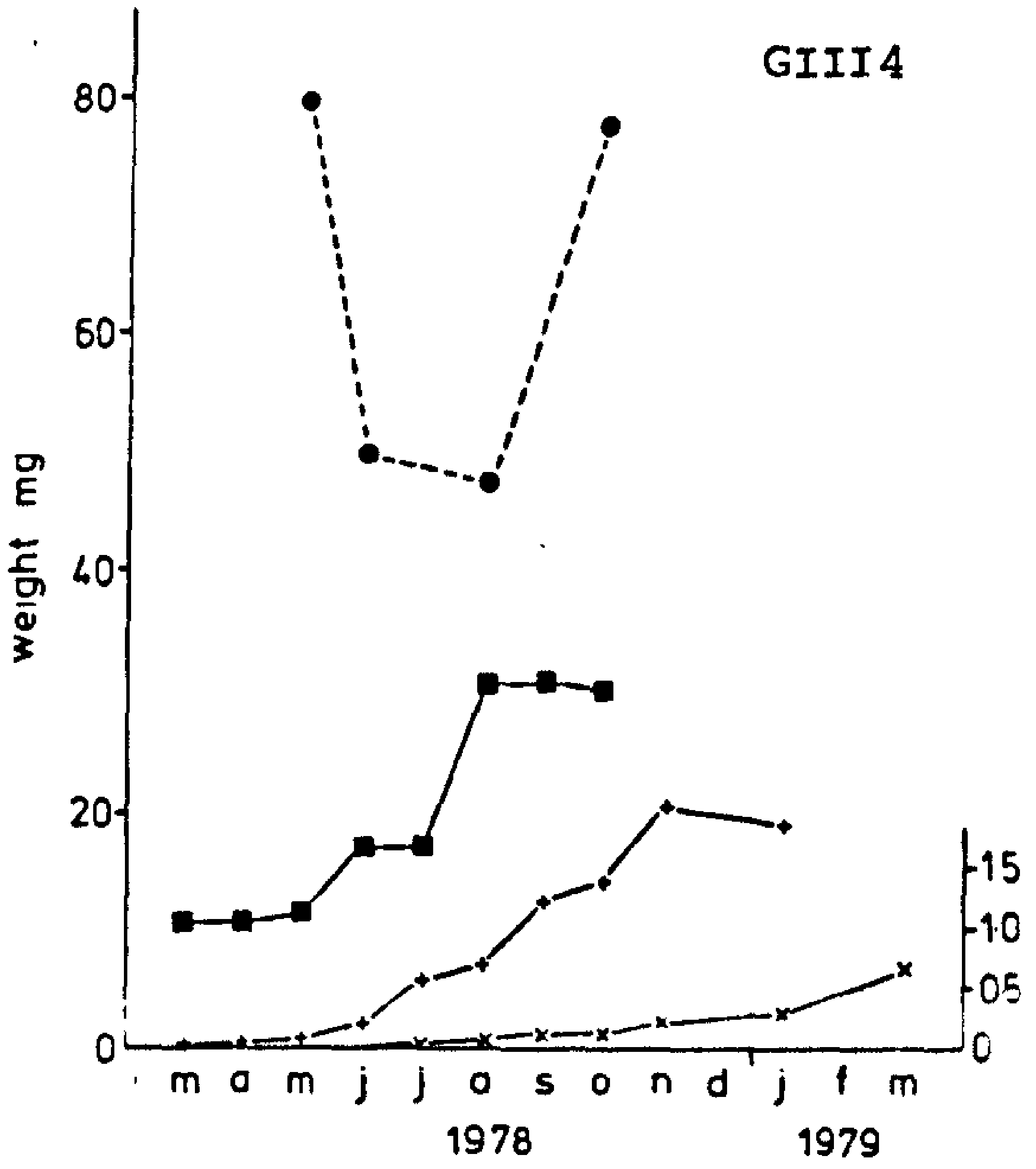


Figures 6x, 6xi & 6xii. Variation in biomass of each cohort of <u>Nephtys hombergi</u>. Intensive survey, March 1978 - March 1979. Symbols as Fig 6iv with the addition of total biomass - ◆—◆

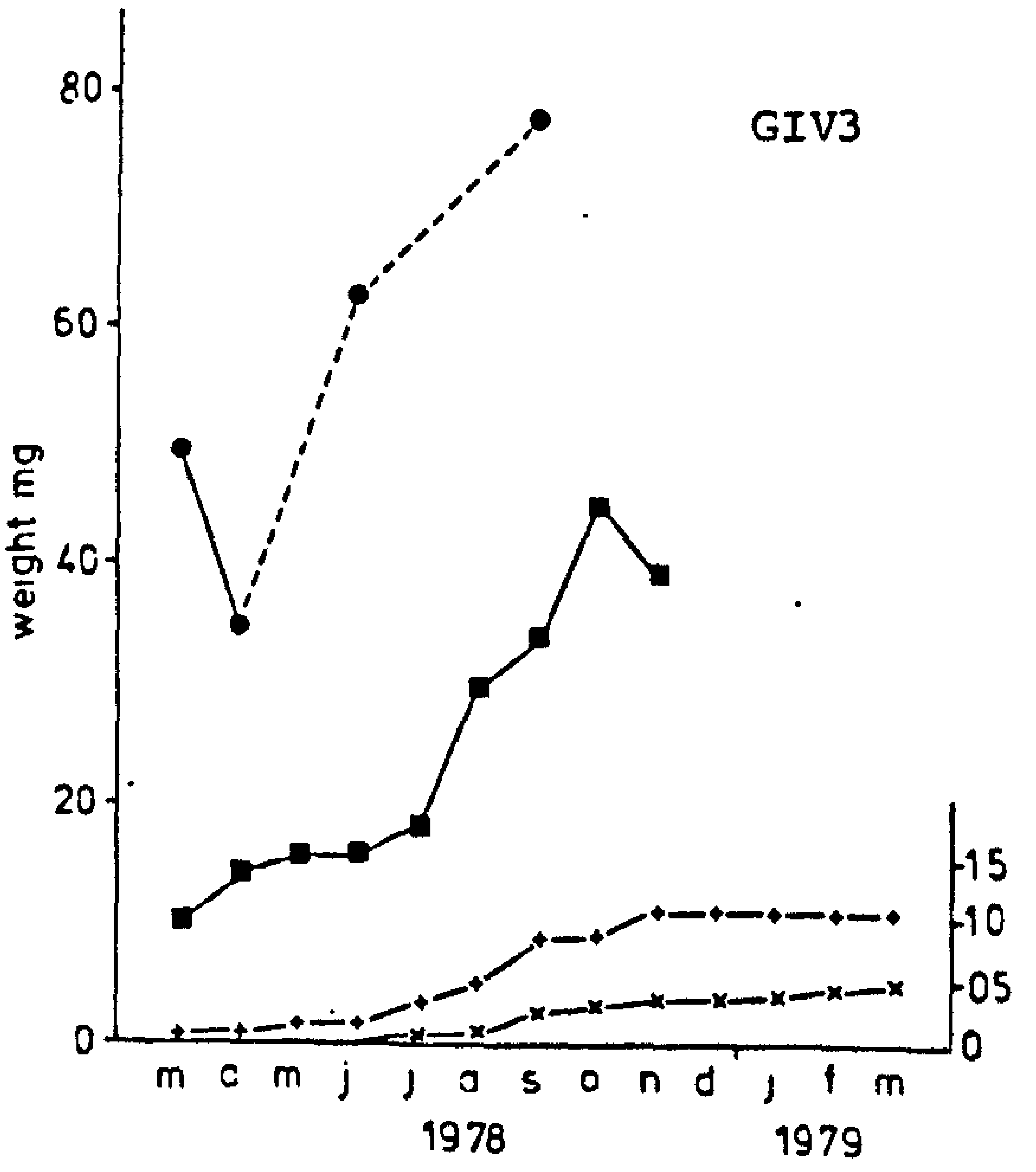
6xiii



6xiv

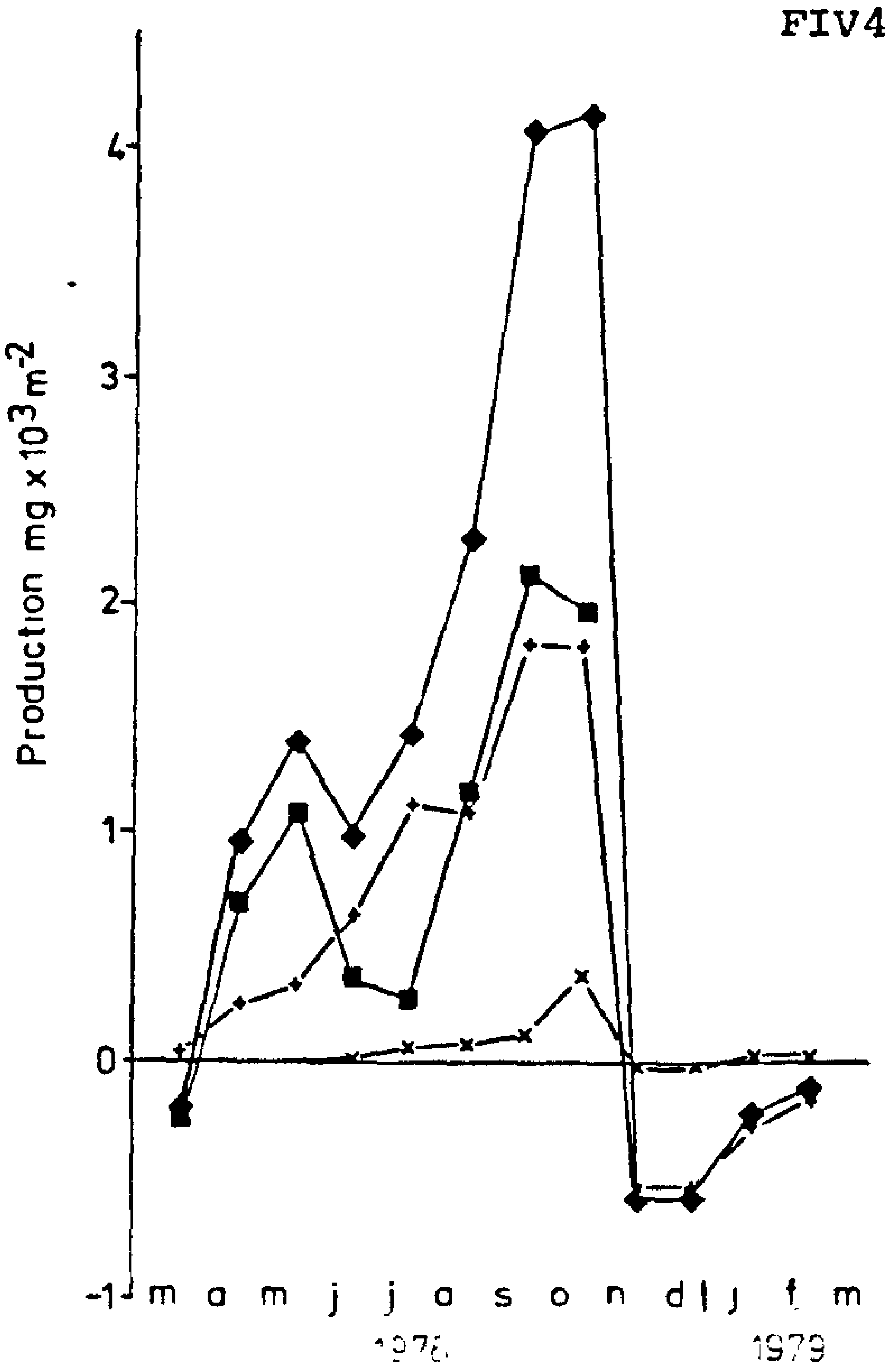


6xv

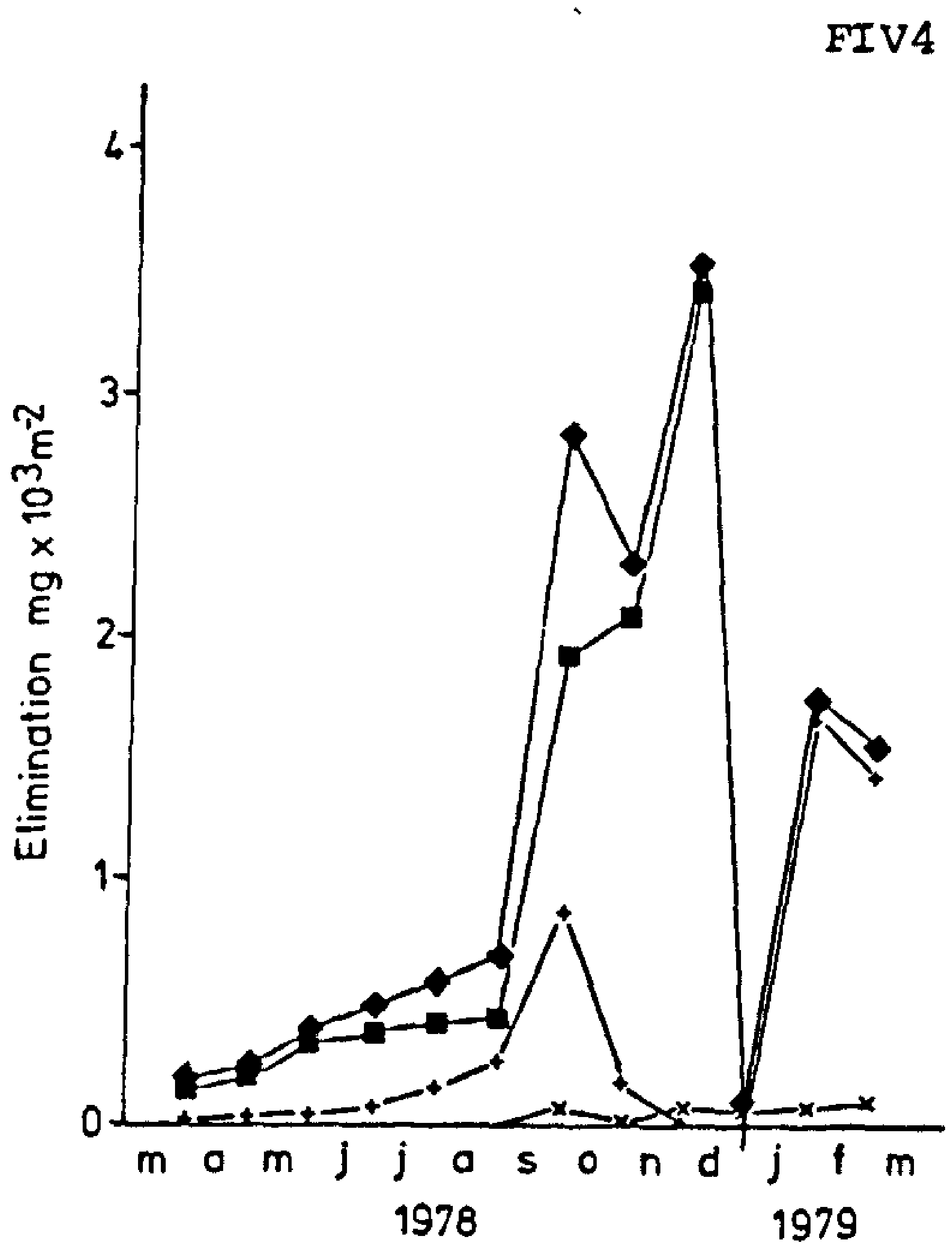


Figures 6xiii, 6xiv & 6xv. Variation in mean individual flesh dry weight of each cohort of Nephtys hombergi Intensive Survey, March 1978 - March 1979. Symbols as Fig. 6iv.

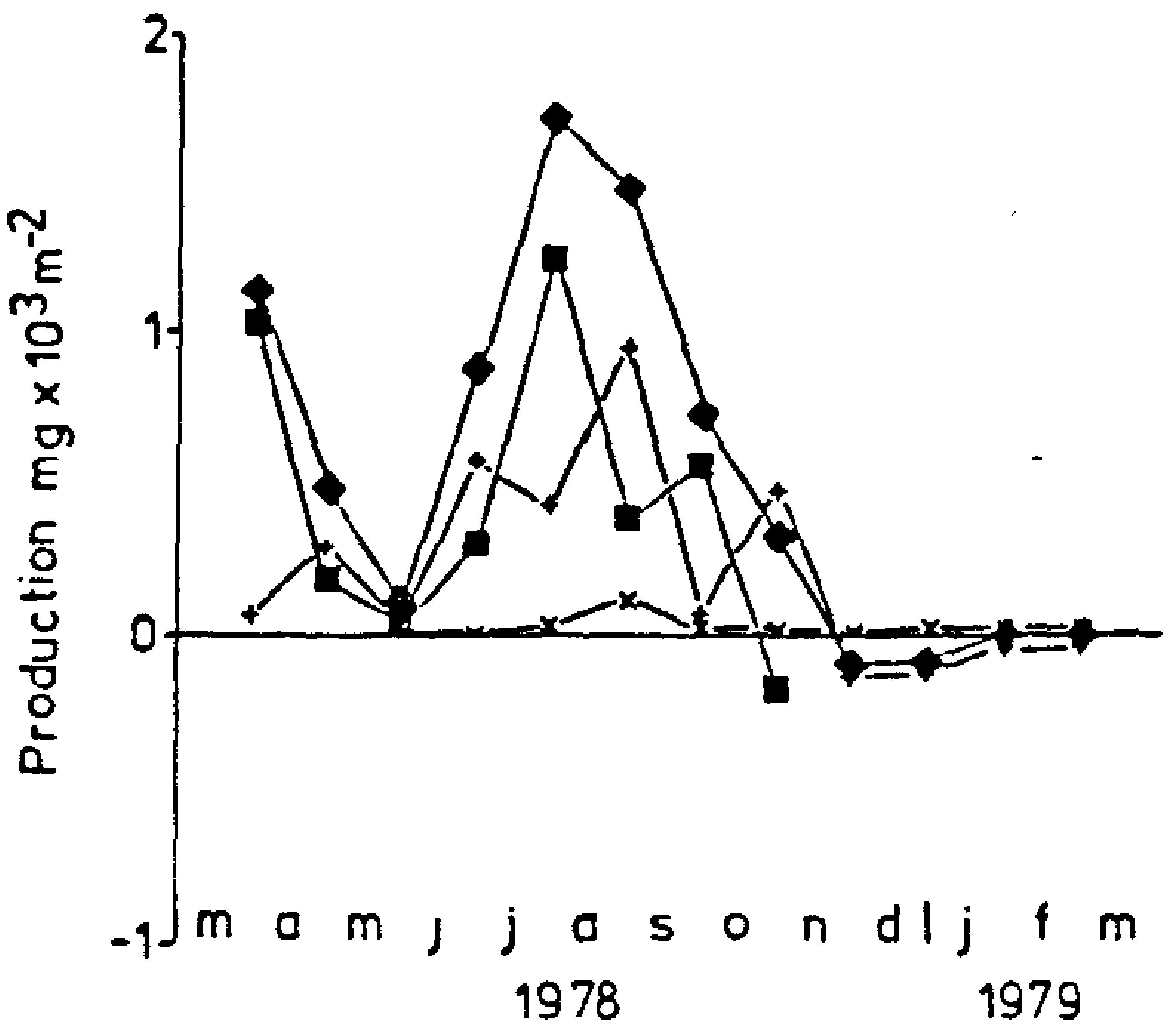
6xvi



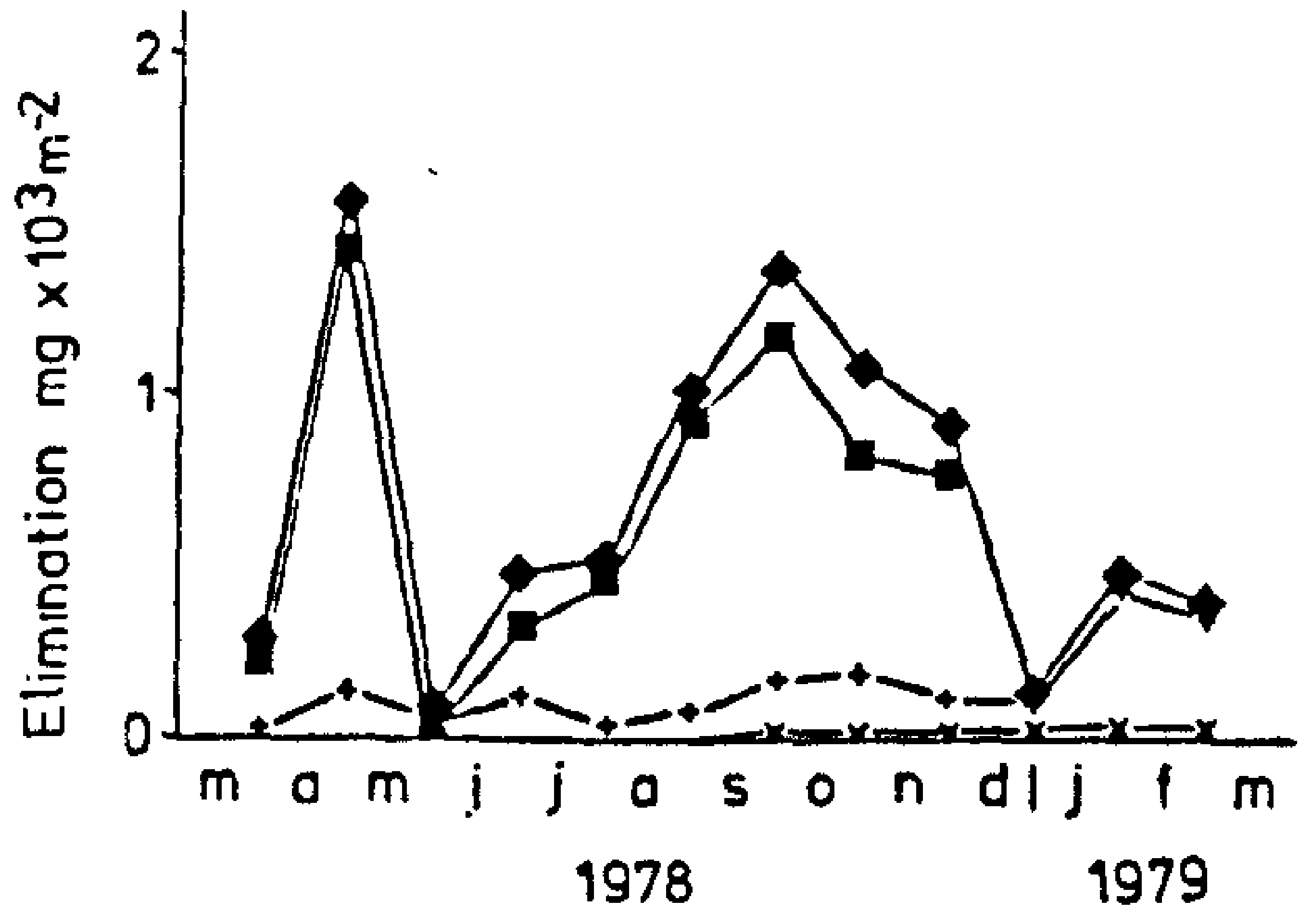
6xviii



6xvii



6xix



Figures 6xvi, 6xvii, 6xviii & 6xix. Production and elimination of Nephtys hombergi. Intensive survey, March 1978 - March 1979. Symbols as Fig. 6iv with the addition of total - ◆—◆

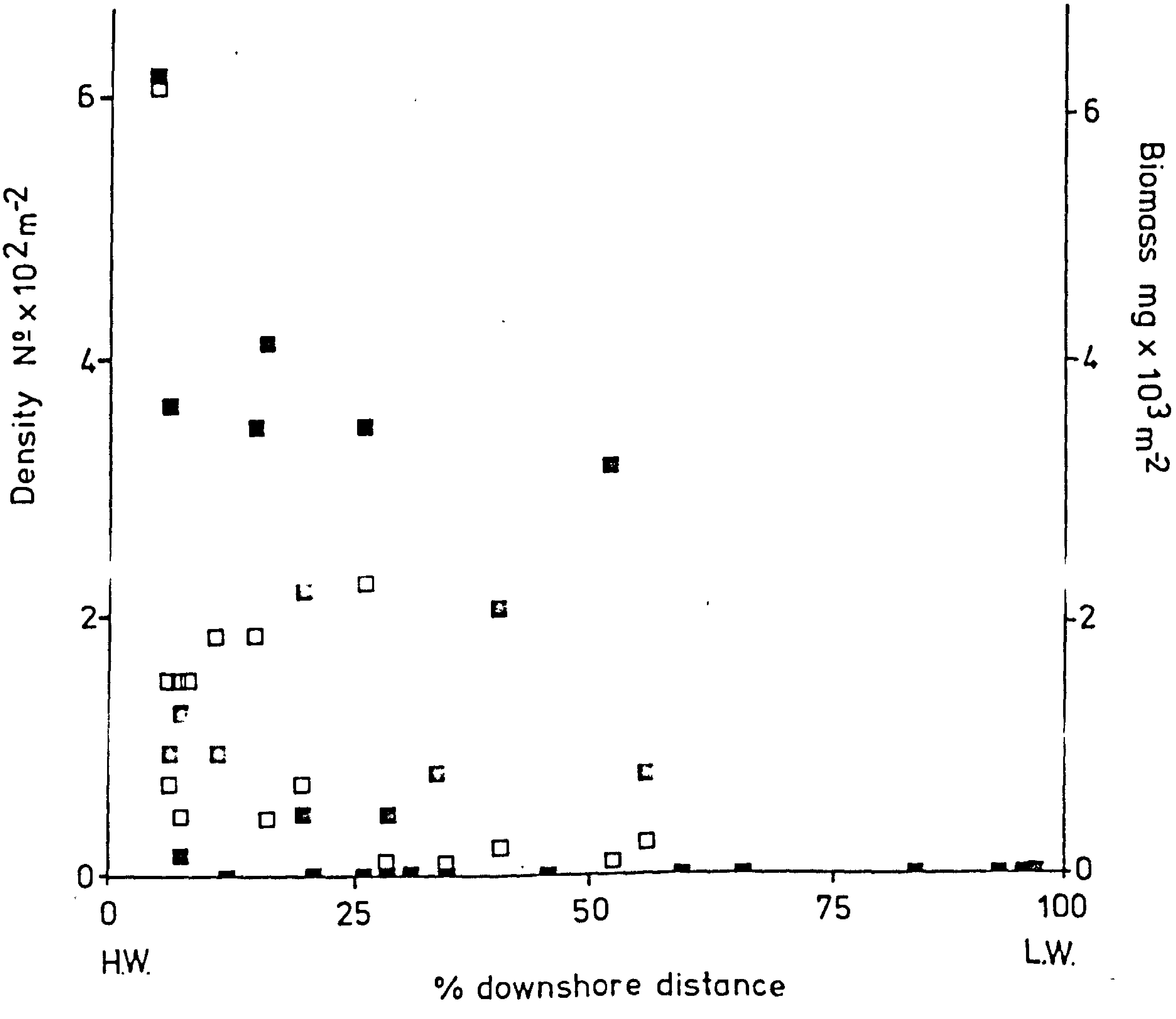


Figure 7i Density (open squares) and biomass (closed squares) of Hediste diversicolor in relation to tidal level. Extensive survey, 1977, Spurn Bight only.

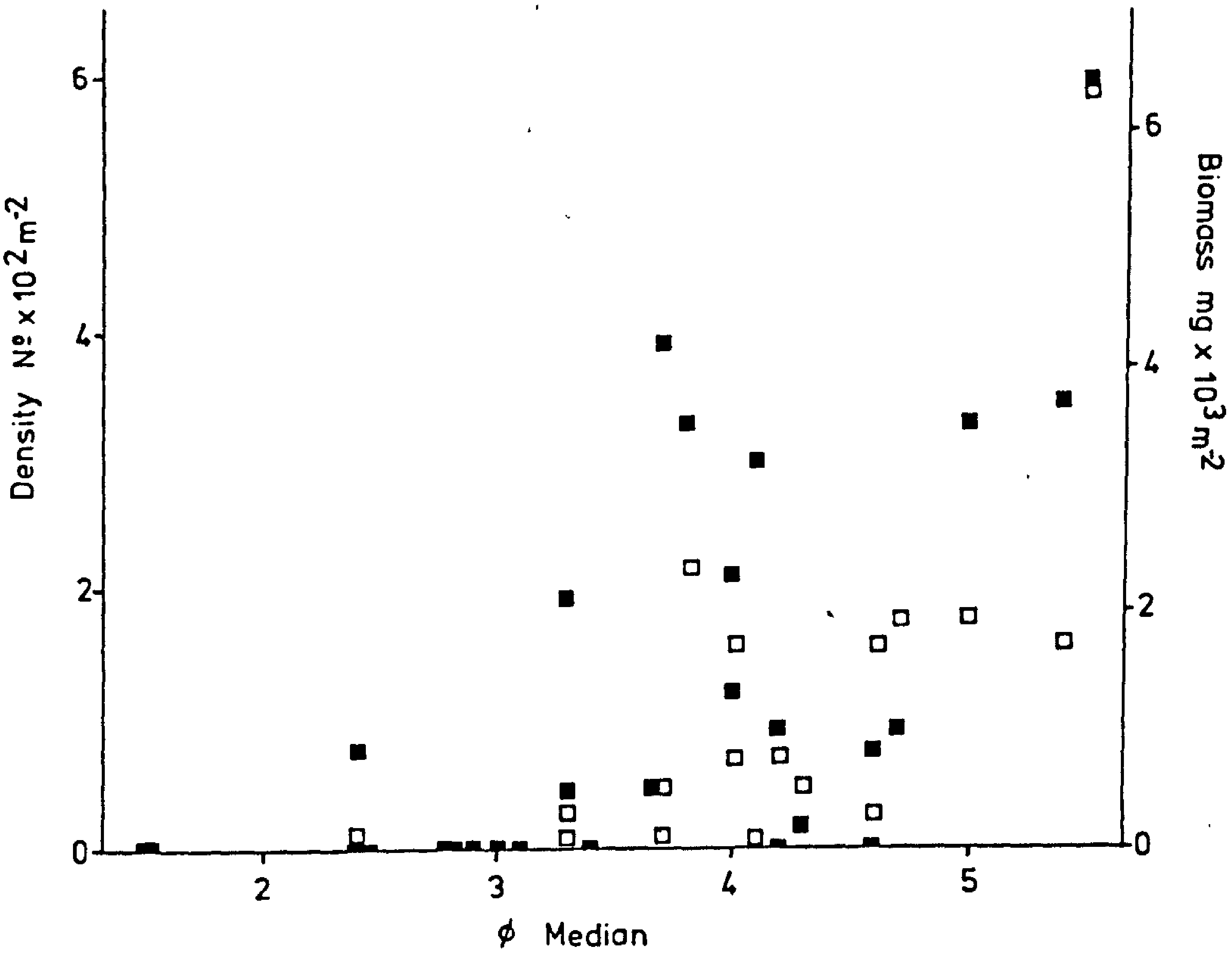


Figure 7ii Density (open squares) and biomass (closed squares) of <u>Hediste diversicolor</u> in relation to median particle size.

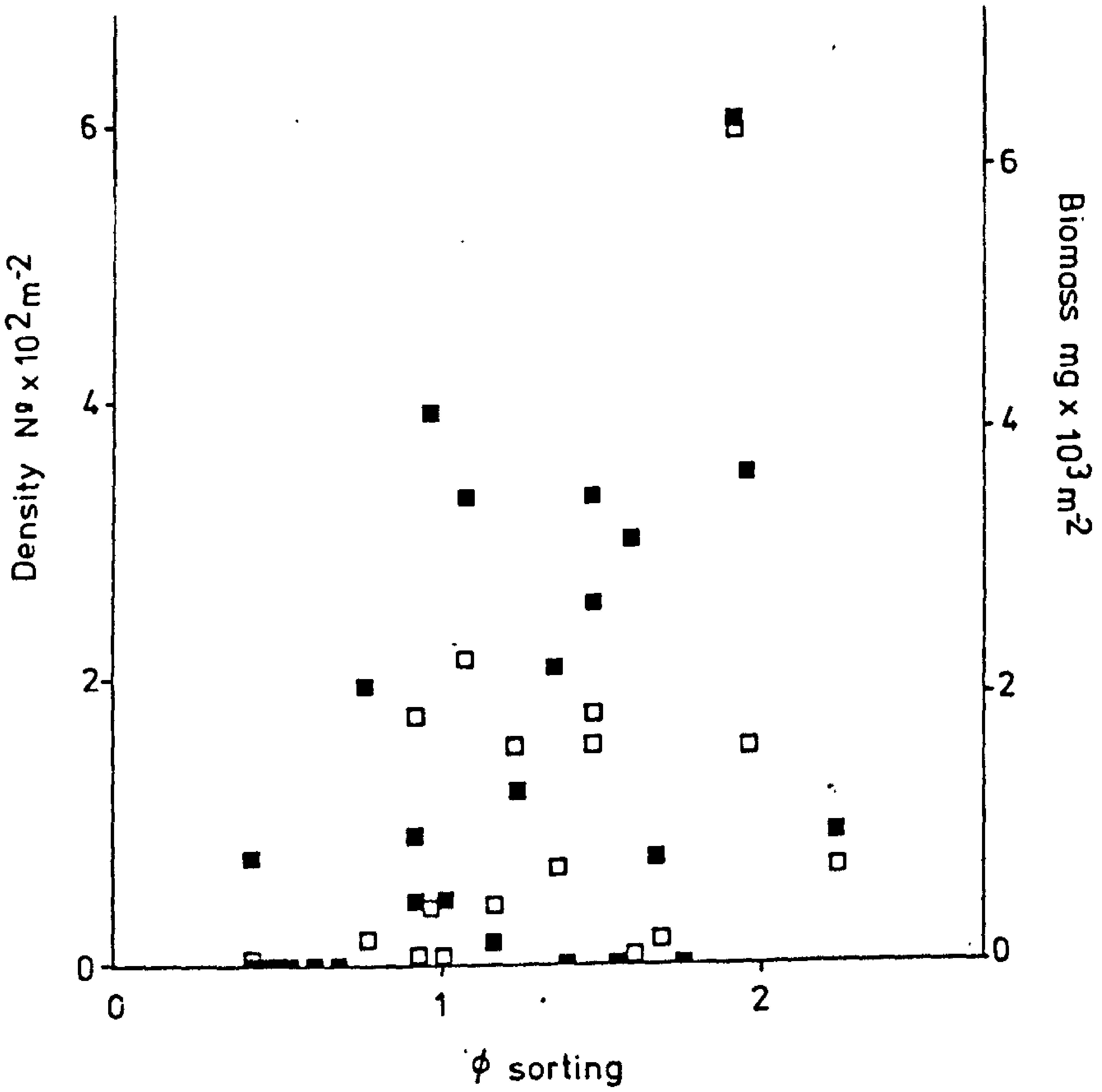
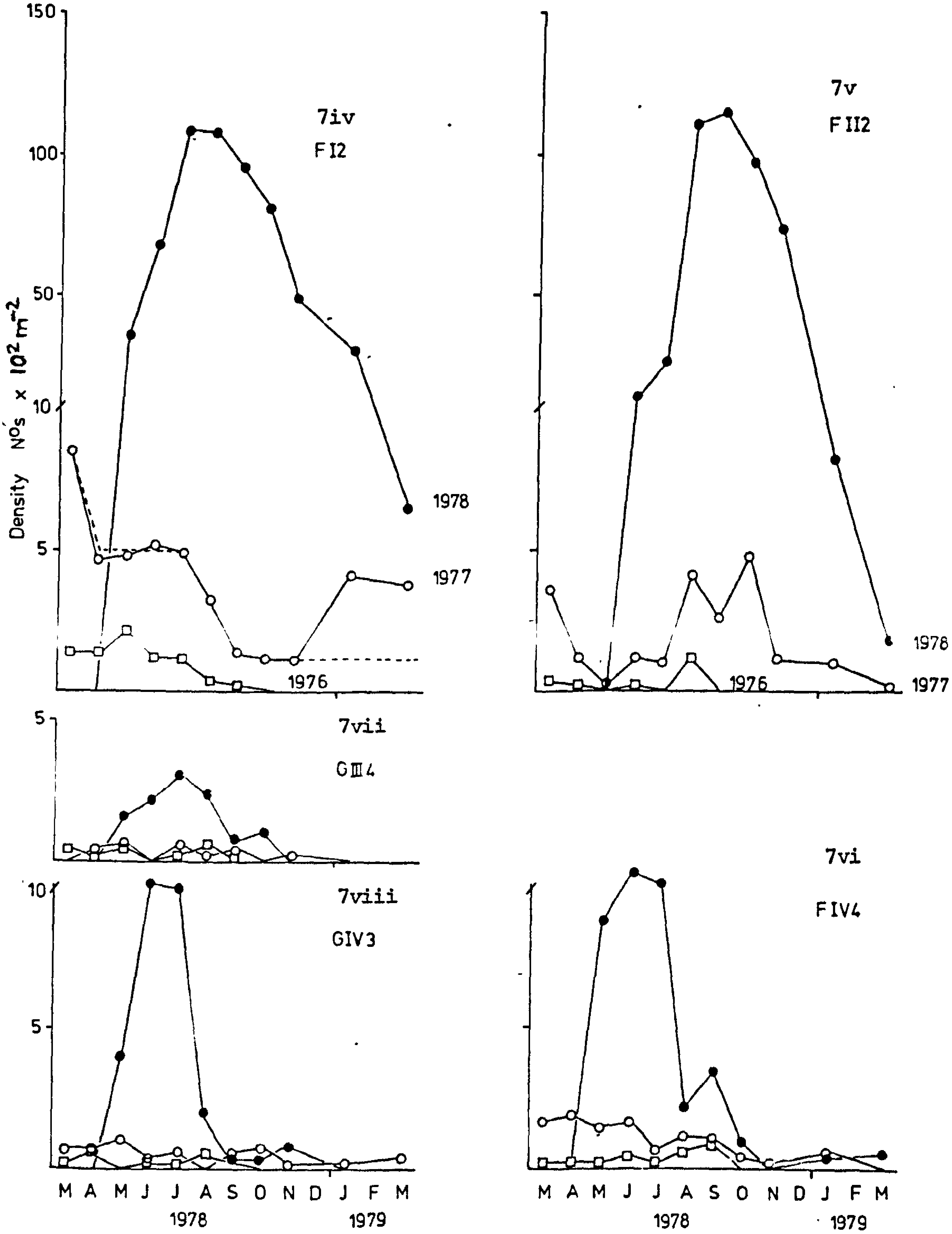


Figure 7iii Density (open squares) and biomass (closed squares) of <u>Hediste diversicolor</u> in relation to sediment sorting. Extensive survey.



Figures 7iv - 7viii Variation in cohort density of Hediste diversicolor with time. Intensive survey, all sites, March 1978 - March 1979.

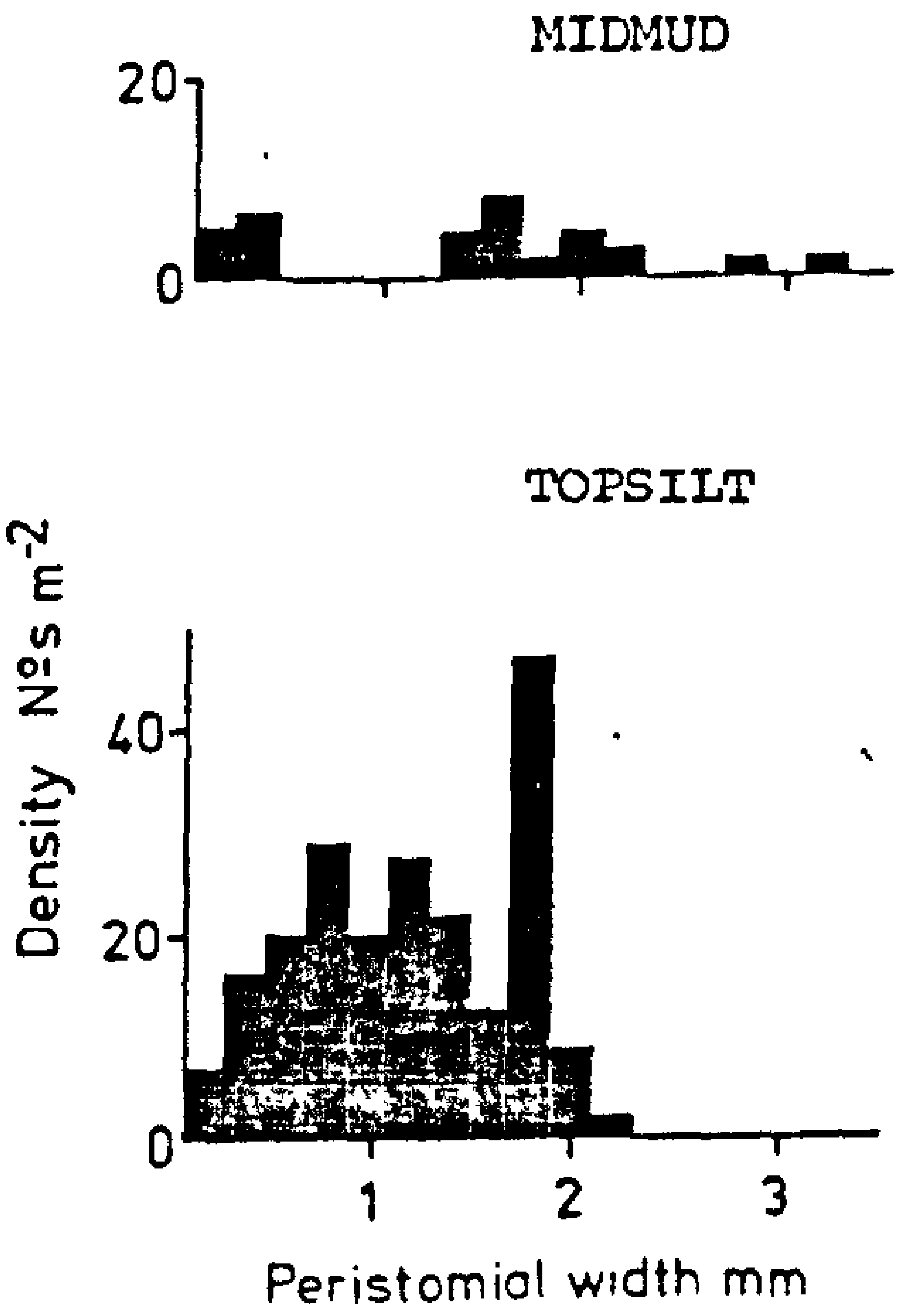


Figure 7ix Population structure of Hediste diversicolor. Mean derived from all TOPSILT and MIDMUD samples. Extensive survey, May/June 1977.

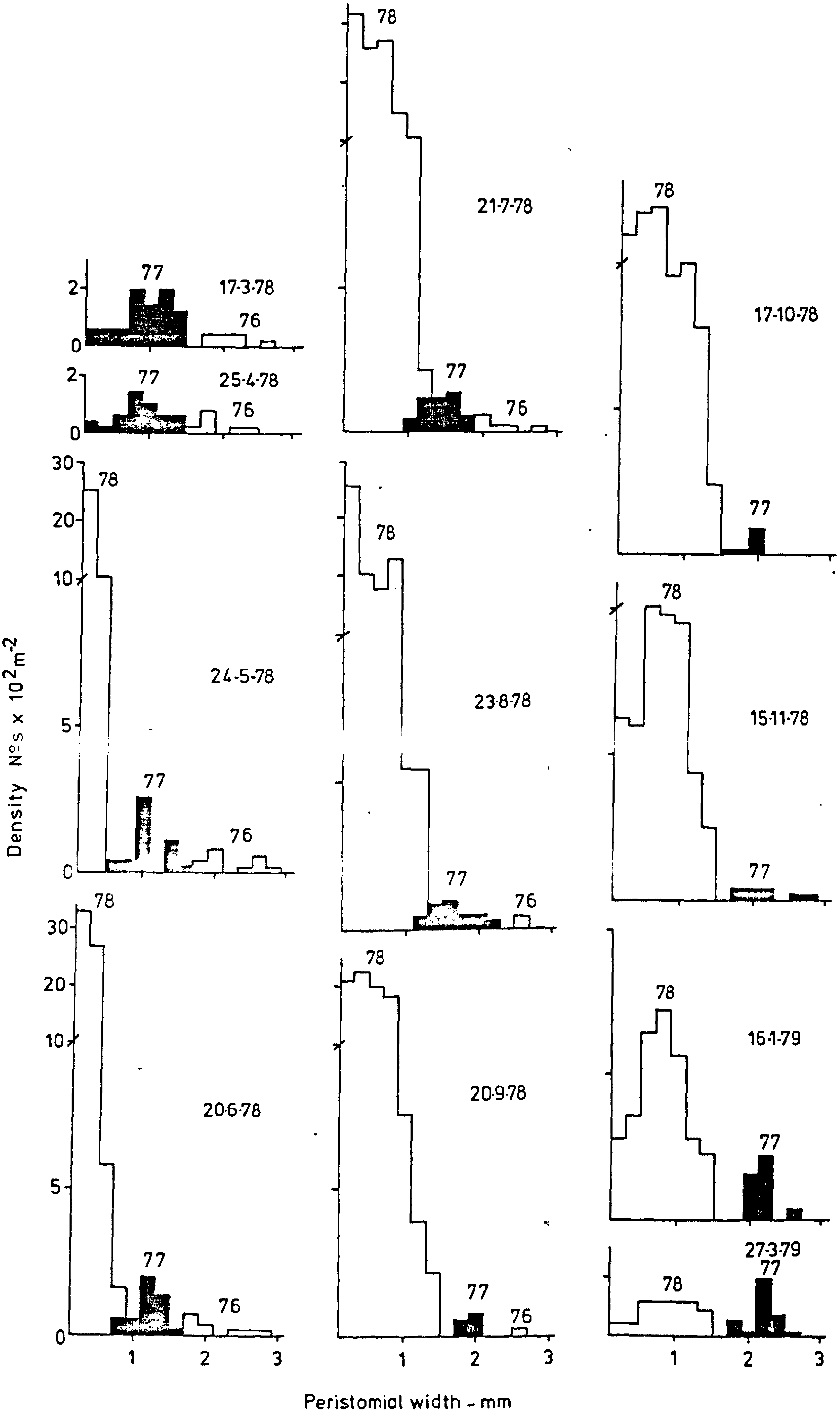


Figure 7x Monthly population structure of Hediste diversicolor. Station FI2 March 1978 - March 1979.

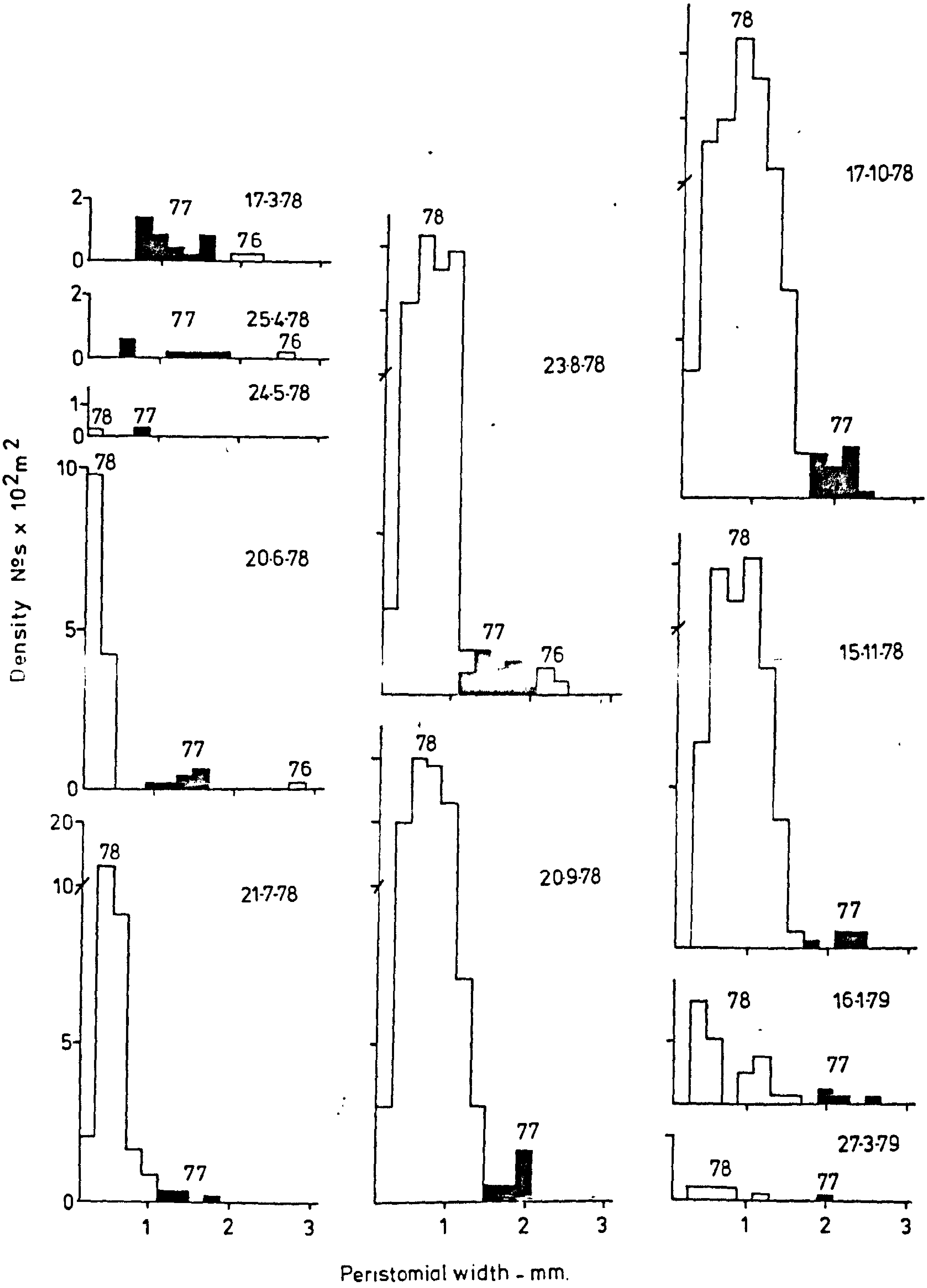
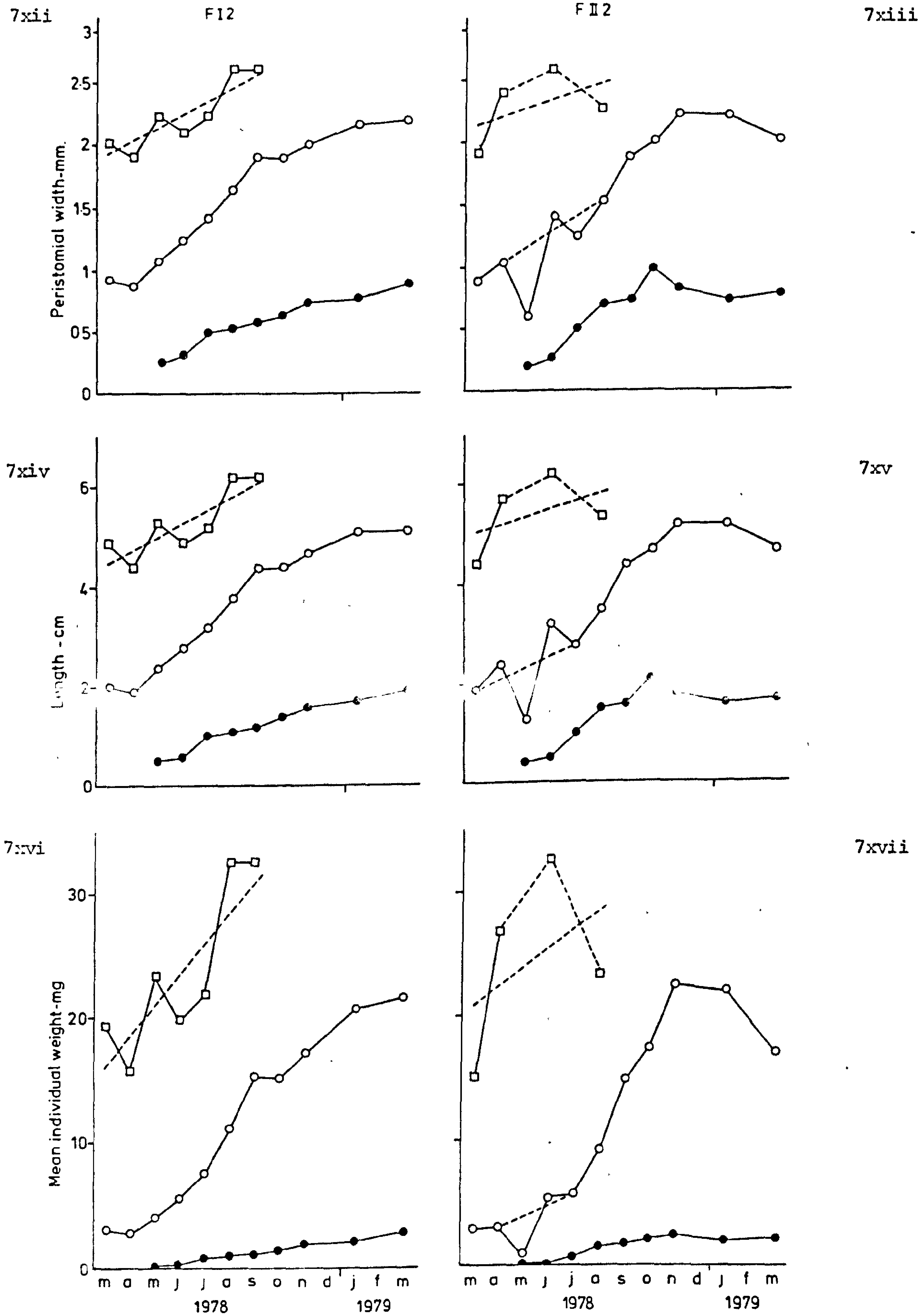
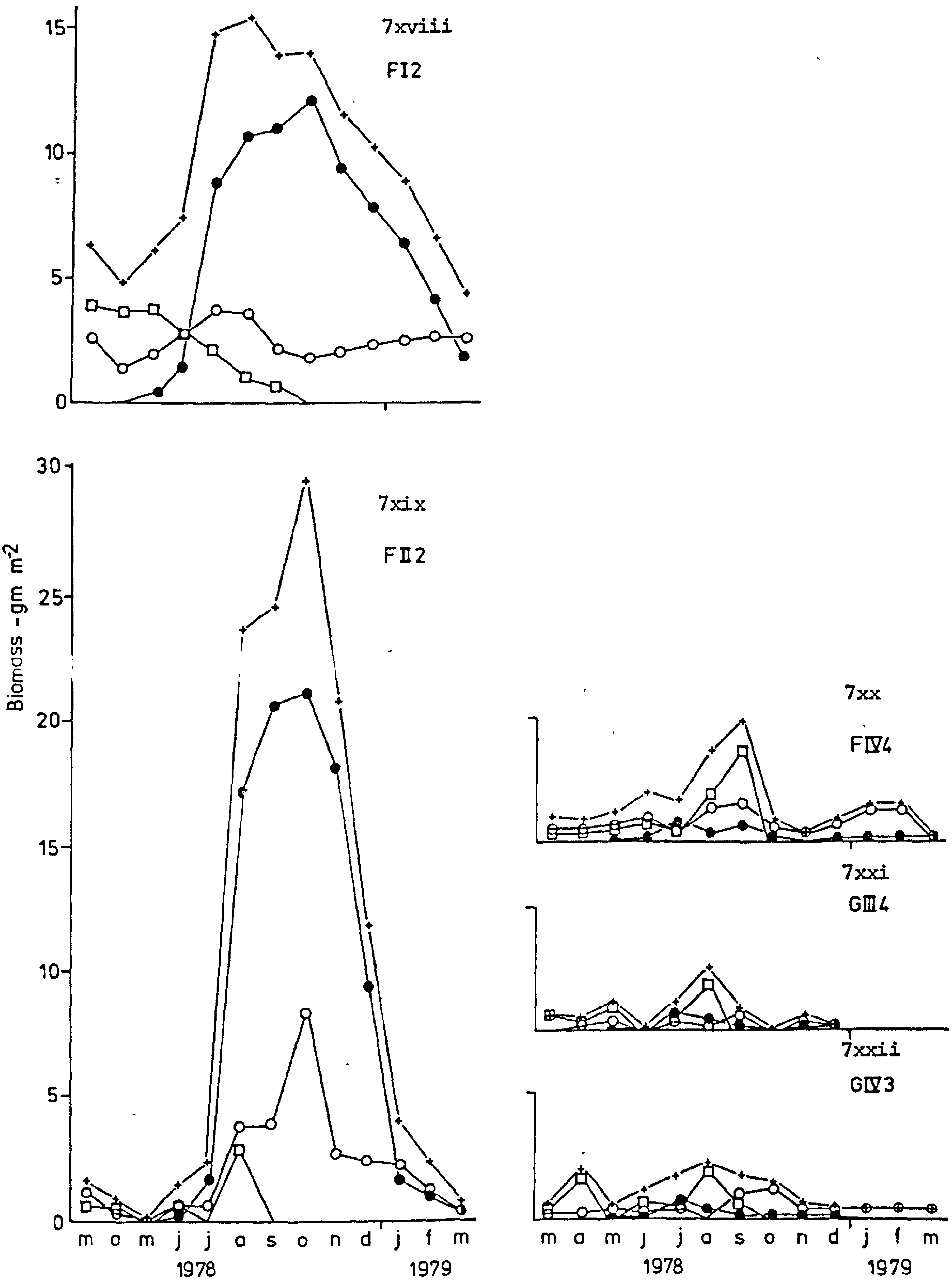


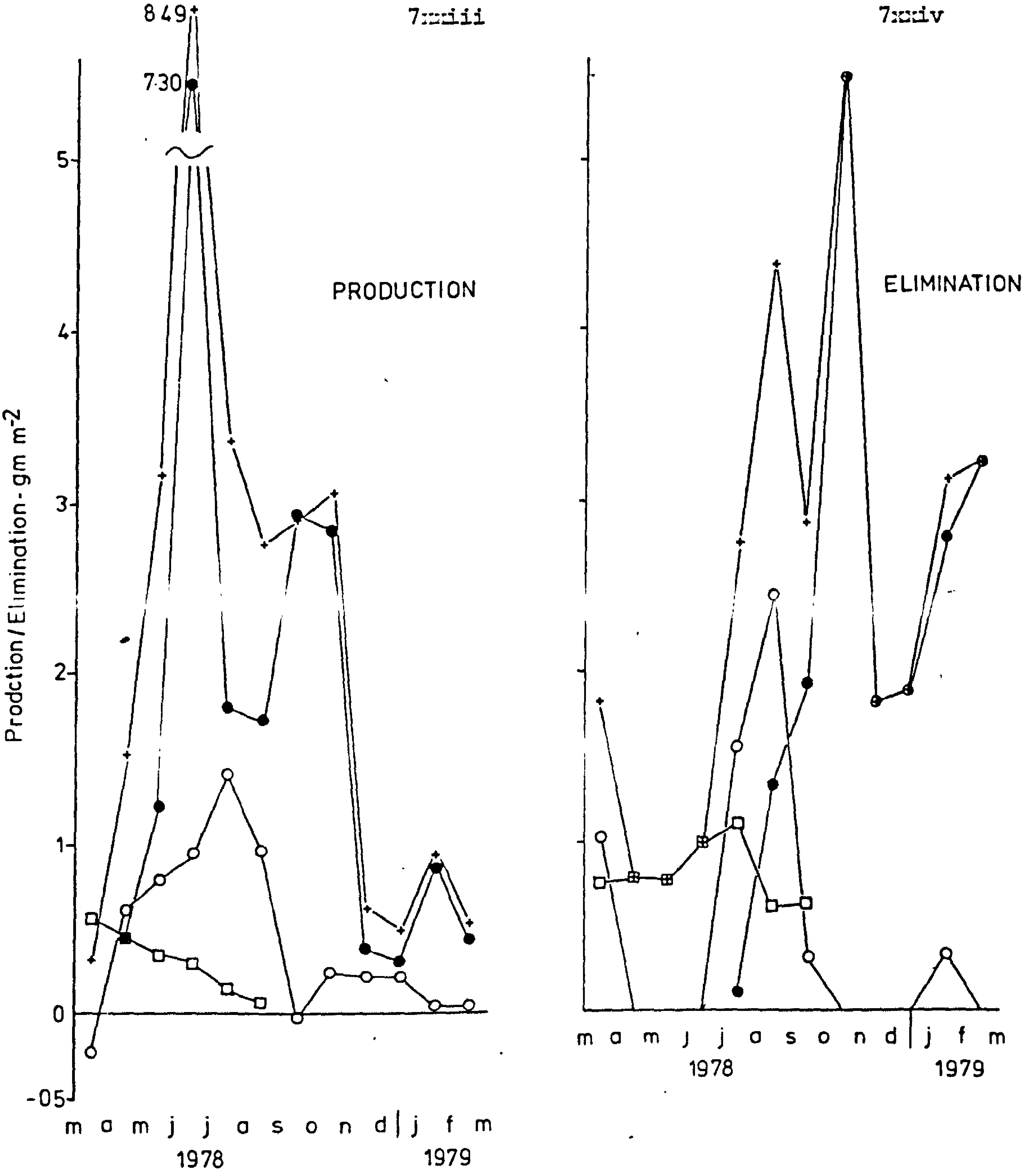
Figure 7xi Monthly population structure of Hediste diversicolor. Station FII2 March 1978 - March 1979.



Figures 7xii - 7xvii Variation in peristomial width, body length and mean individual dry weight of <u>Hediste diversicolor</u>. Sites FI2 and FII2. March 1978 - March 1979. Symbols as Figure 7iv.



Figures 7xviii - 7xxii Variation in total population and cohort biomass of Hediste diversicolor. All sites, March 1978 - March 1979. Symbols as Figure 7iv with the addition of crosses for total.



Figures 7xxiii and 7xxiv Total and cohort production of Hediste diversicolor. March 1978 - March 1979. Symbols as Fig 7iv with the addition of crosses for total.

Figure 8i

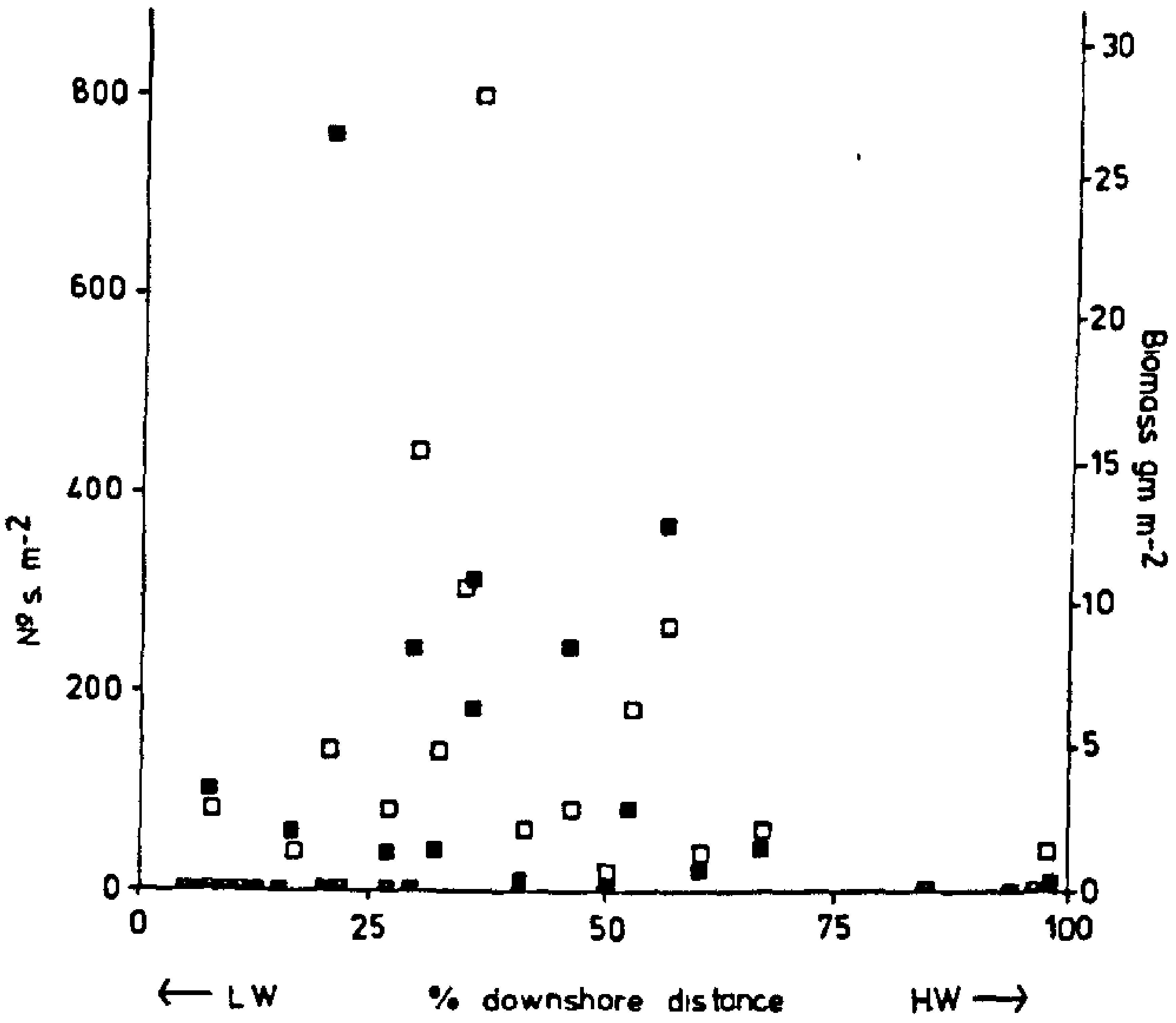


Figure 8ii

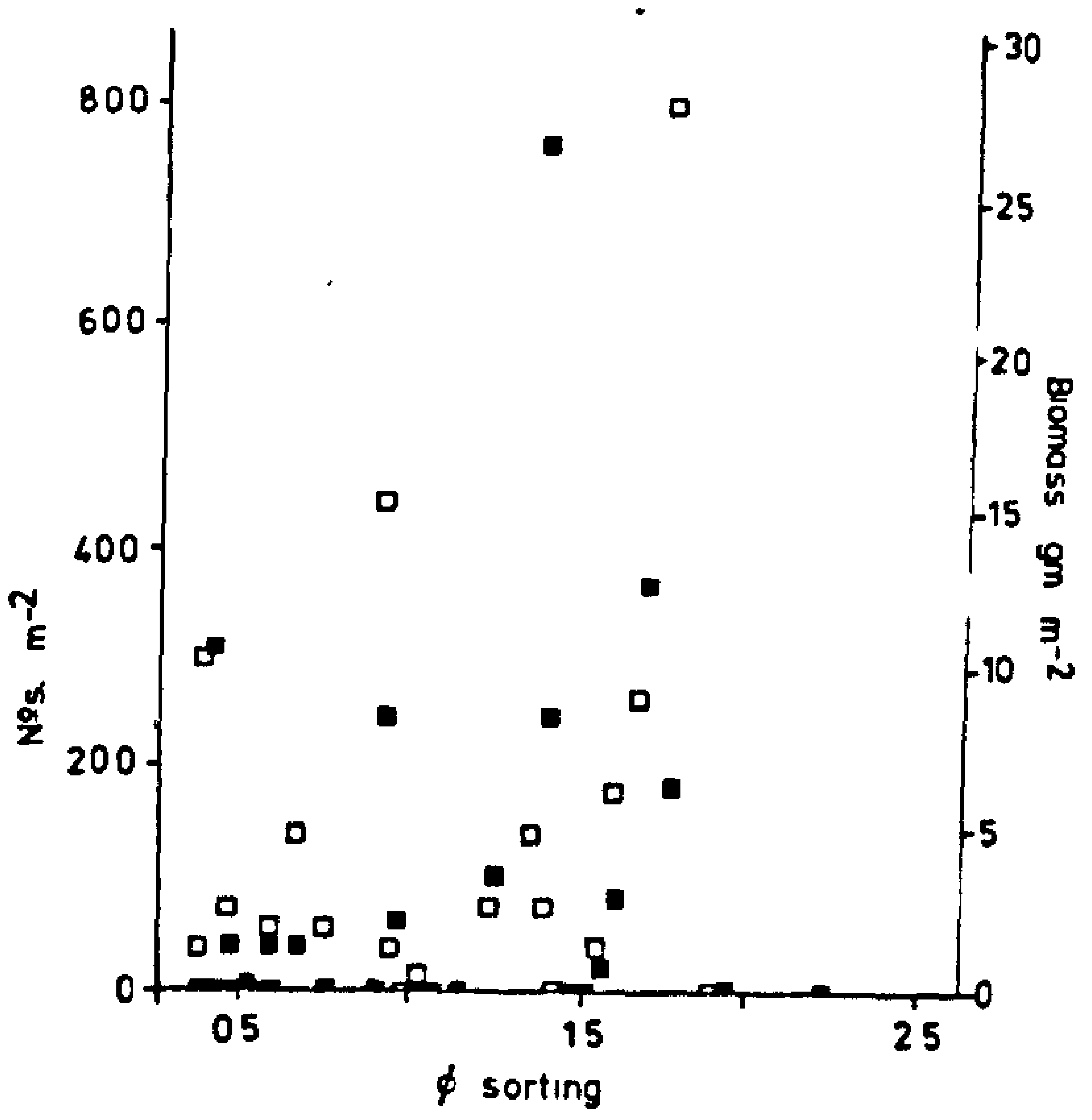
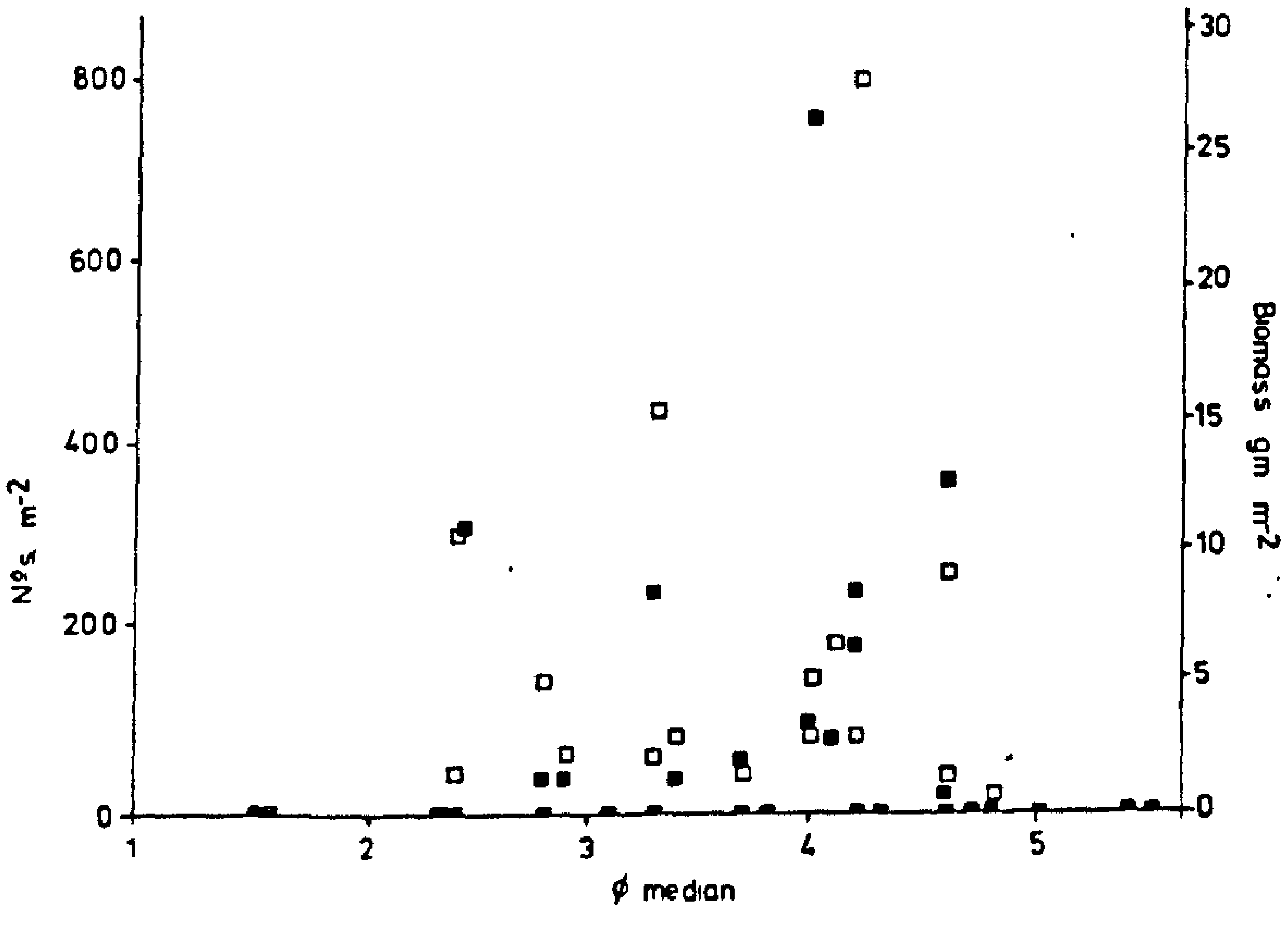


Figure 8iii



Figures 8i, 8ii and 8iii. Density (open squares), and biomass (closed squares), of Cerastoderma edule in relation to tidal position, median particle size and degree of sediment sorting. May/June 1977. Spurn Bight Stations.

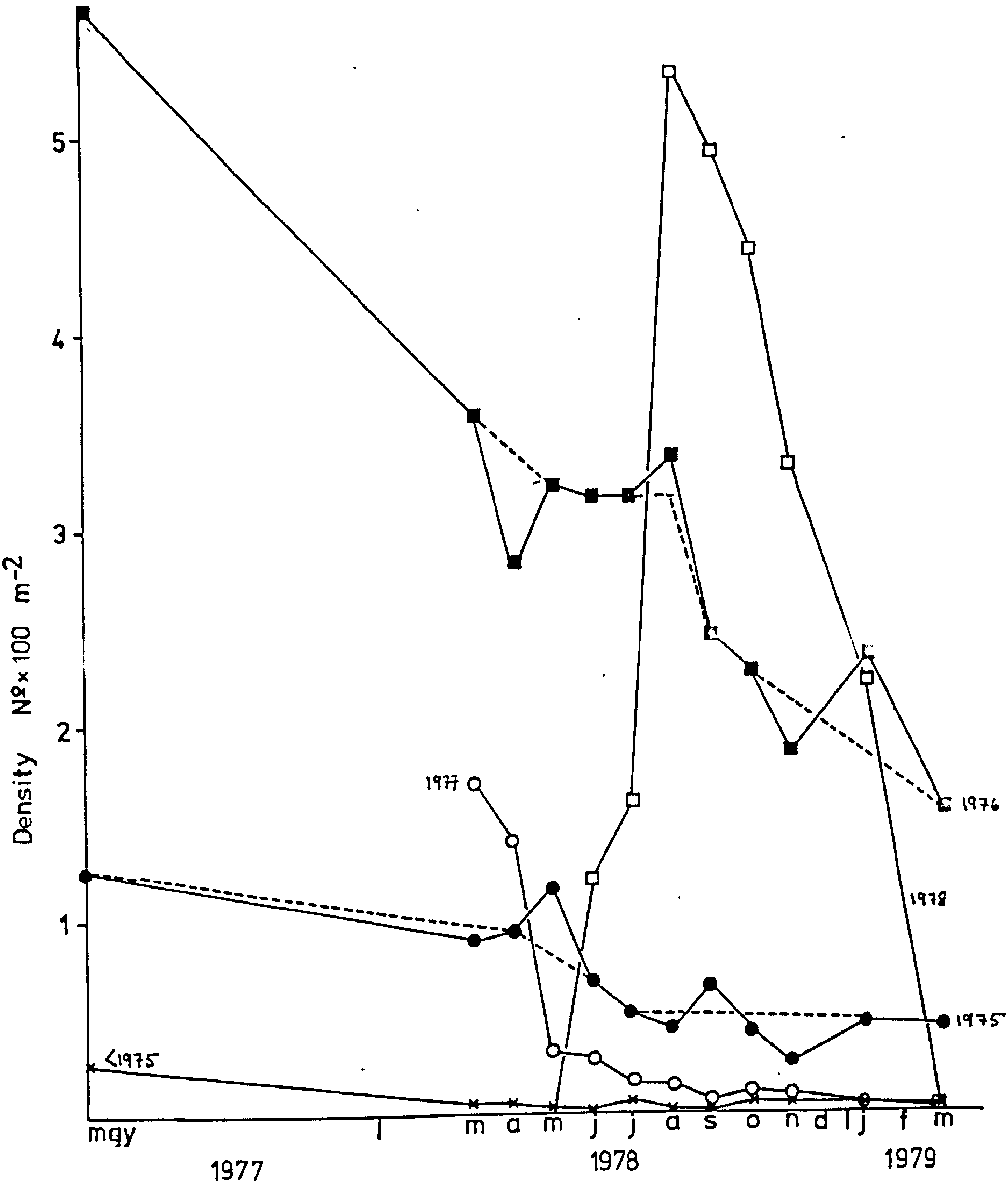


Figure 8iv Density of Cerastoderma edule per cohort. Station GIV3, May 1977 - March 1979.

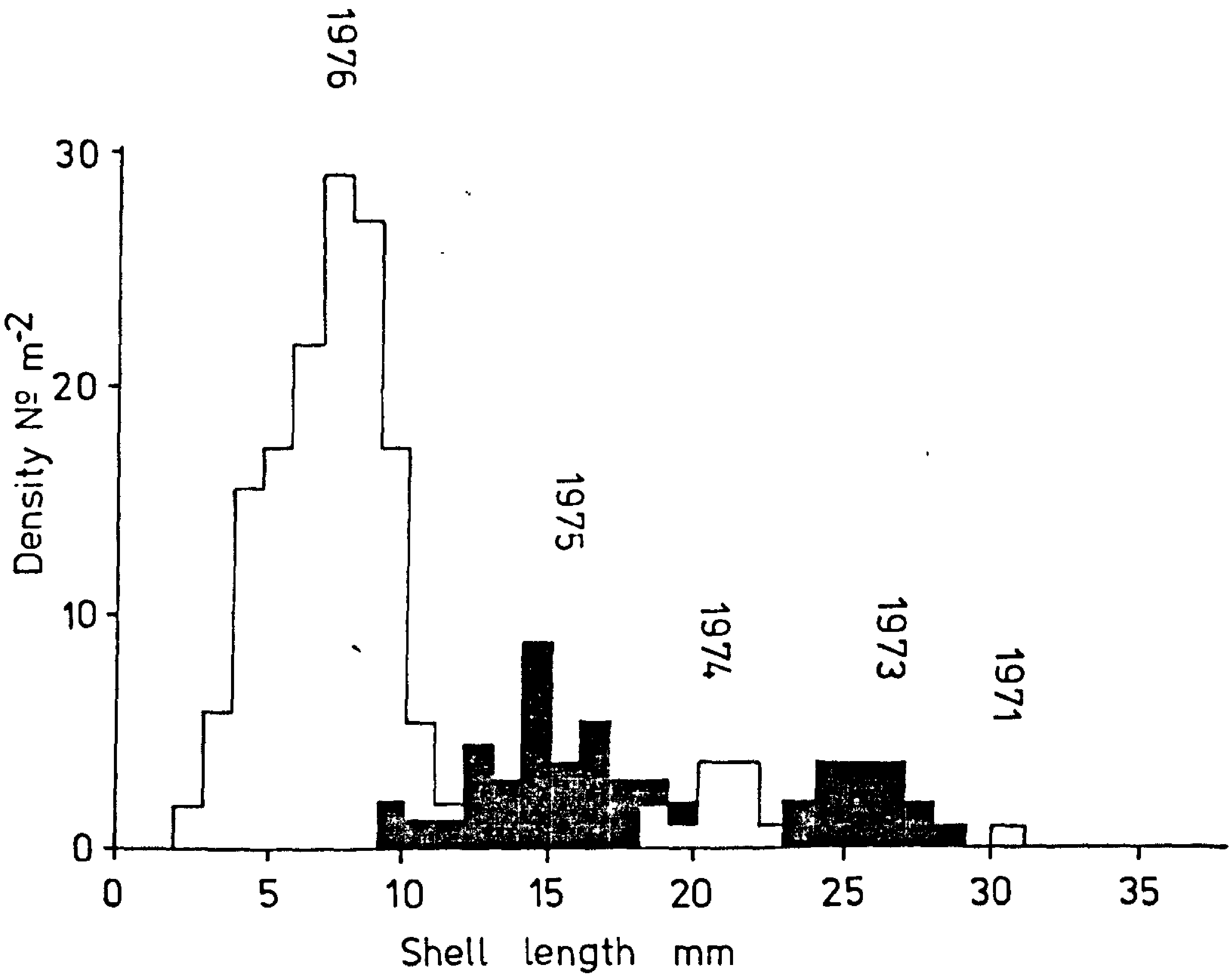


Figure 8v Population structure of Cerastoderma edule at station GIV3. May 1977.

Figure 8vi Population structure of C. edule at Horseshoe Point - station PIV6. May 1977.

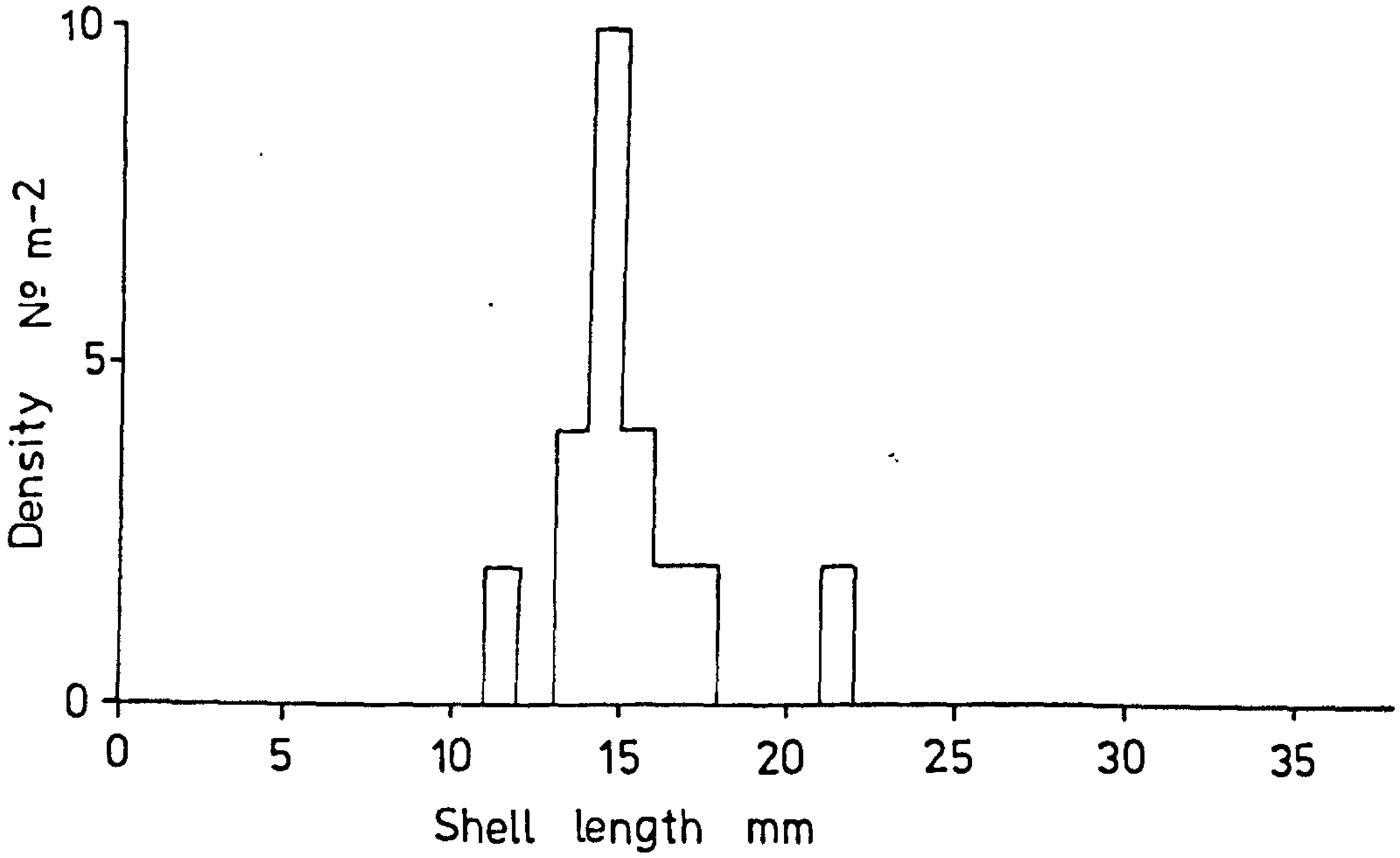
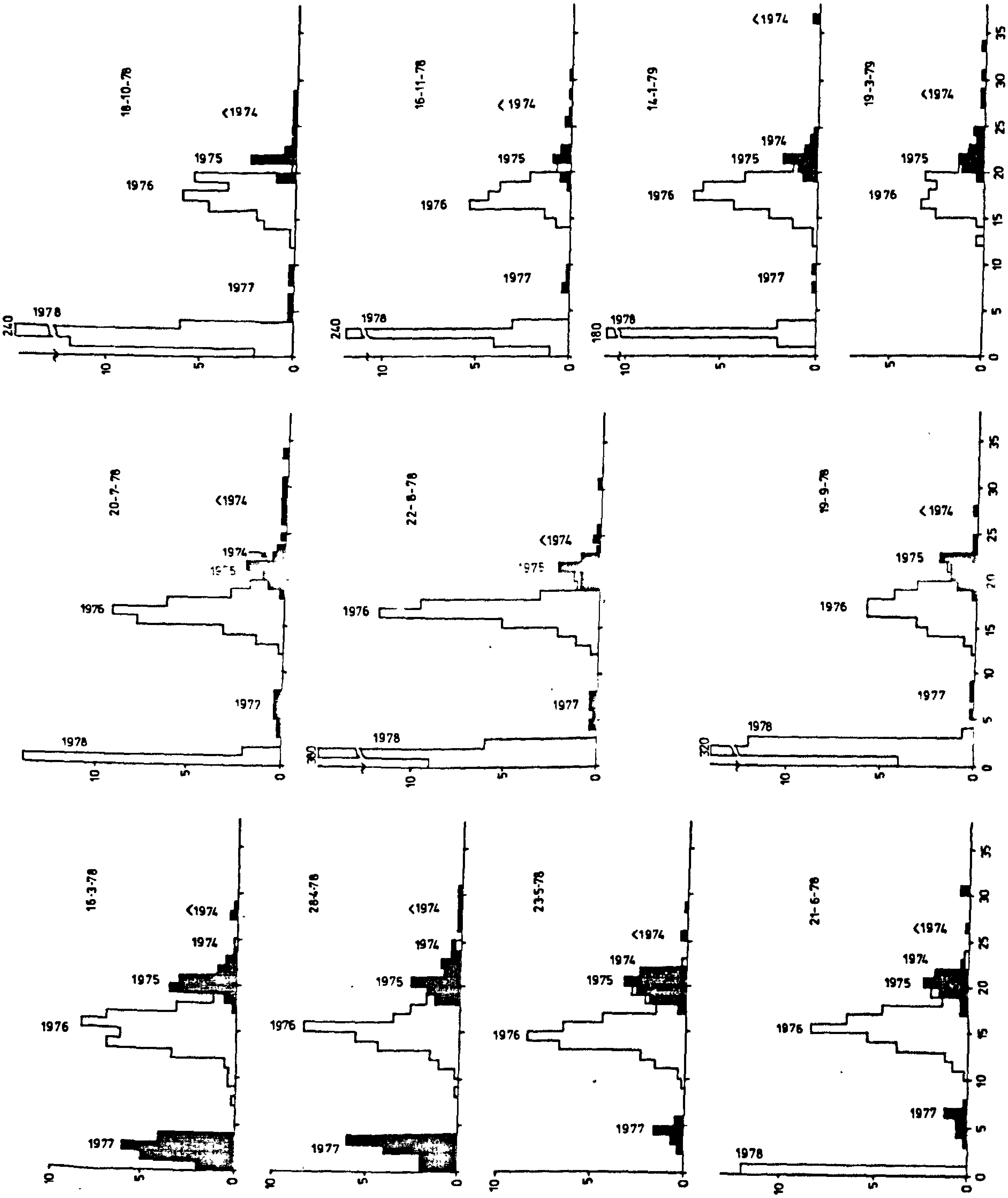


Figure 8vii Population structure of C. edule at station GIV3. Monthly, March 1978 - March 1979.



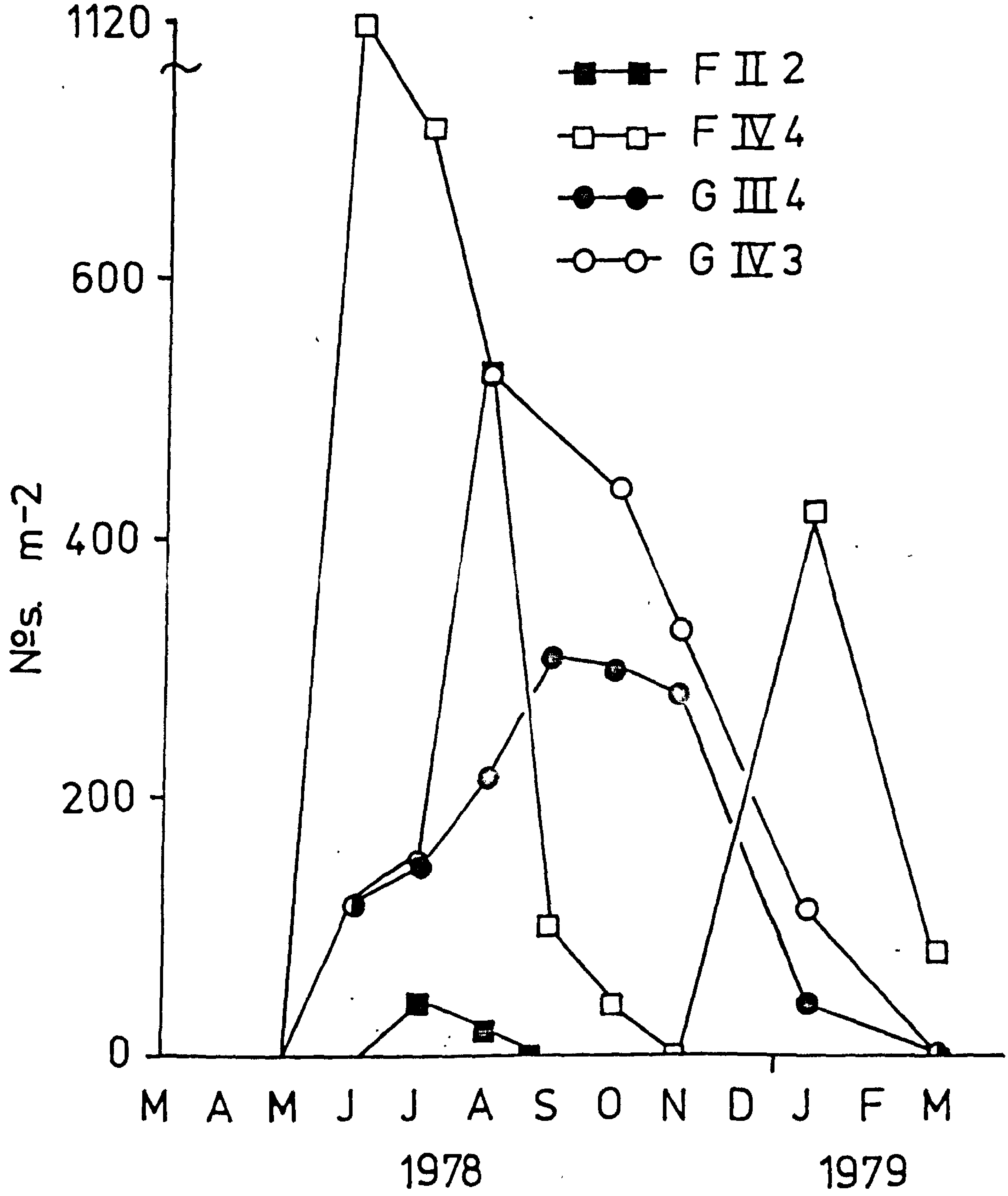


Figure 8viii Variation in density of the 1978 'O' group of *Cerastoderma edule* All stations, March 1978 - March 1979.

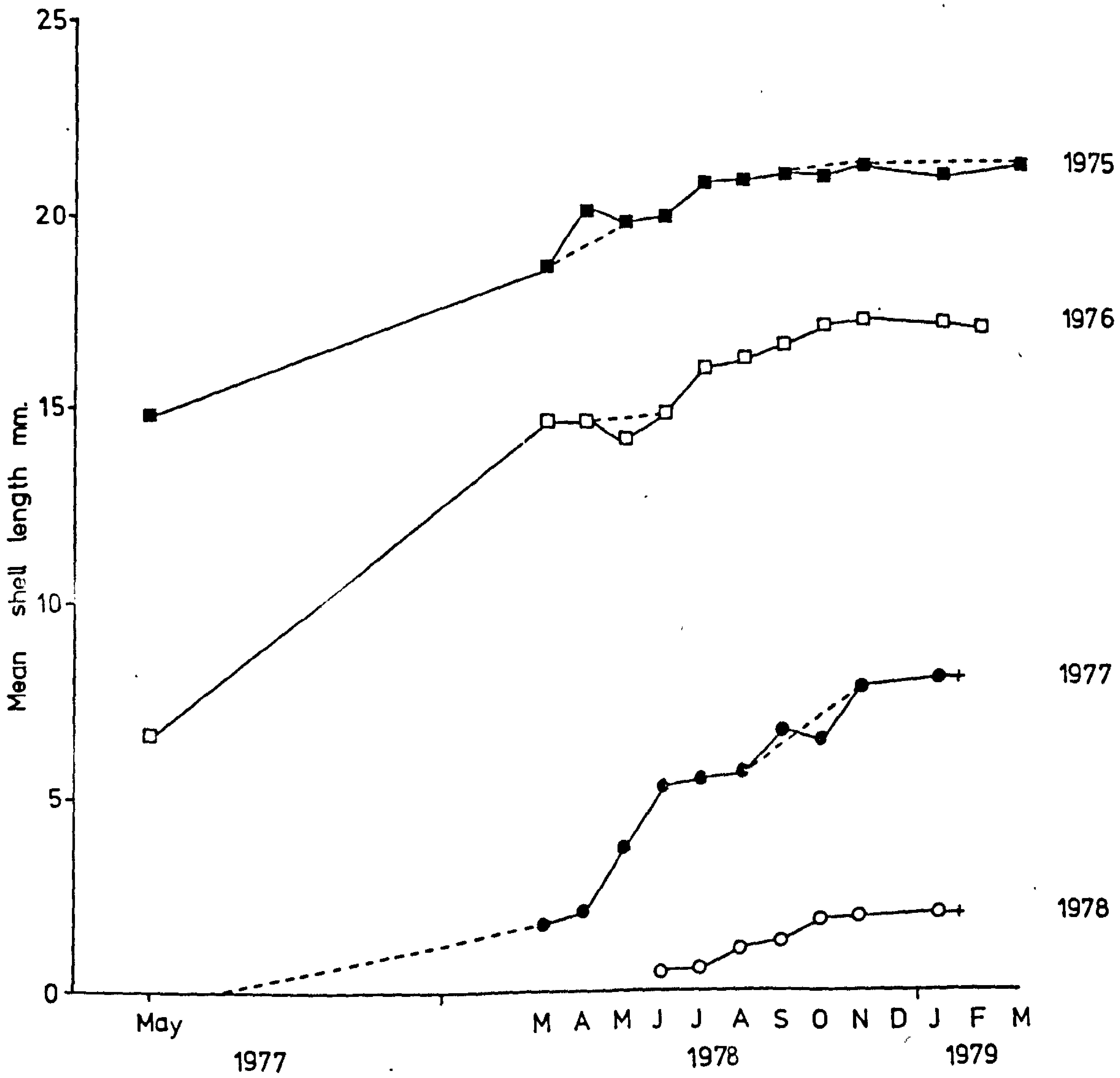
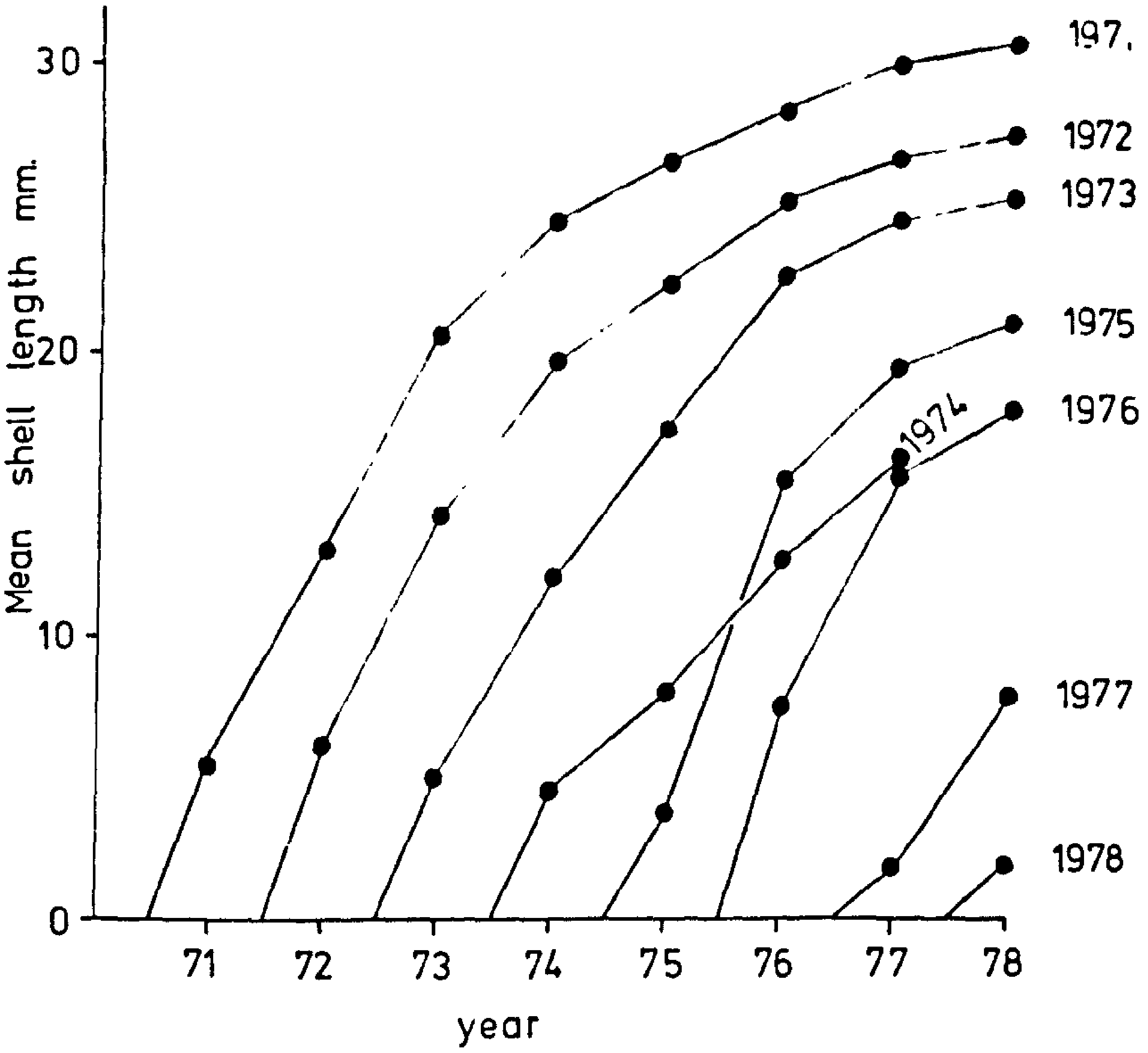


Figure 8ix Change in mean shell length of each cohort of *Cerastoderma edule* with time. Station GIV3, May 1977 - March 1979.

Figure 8x



Figures 8x and 8xi Growth curves of <u>Cerstoderma edule</u>. Station GIV3.

8x - individual cohorts.

8xi - mean for each year of growth.

Figure 8xi

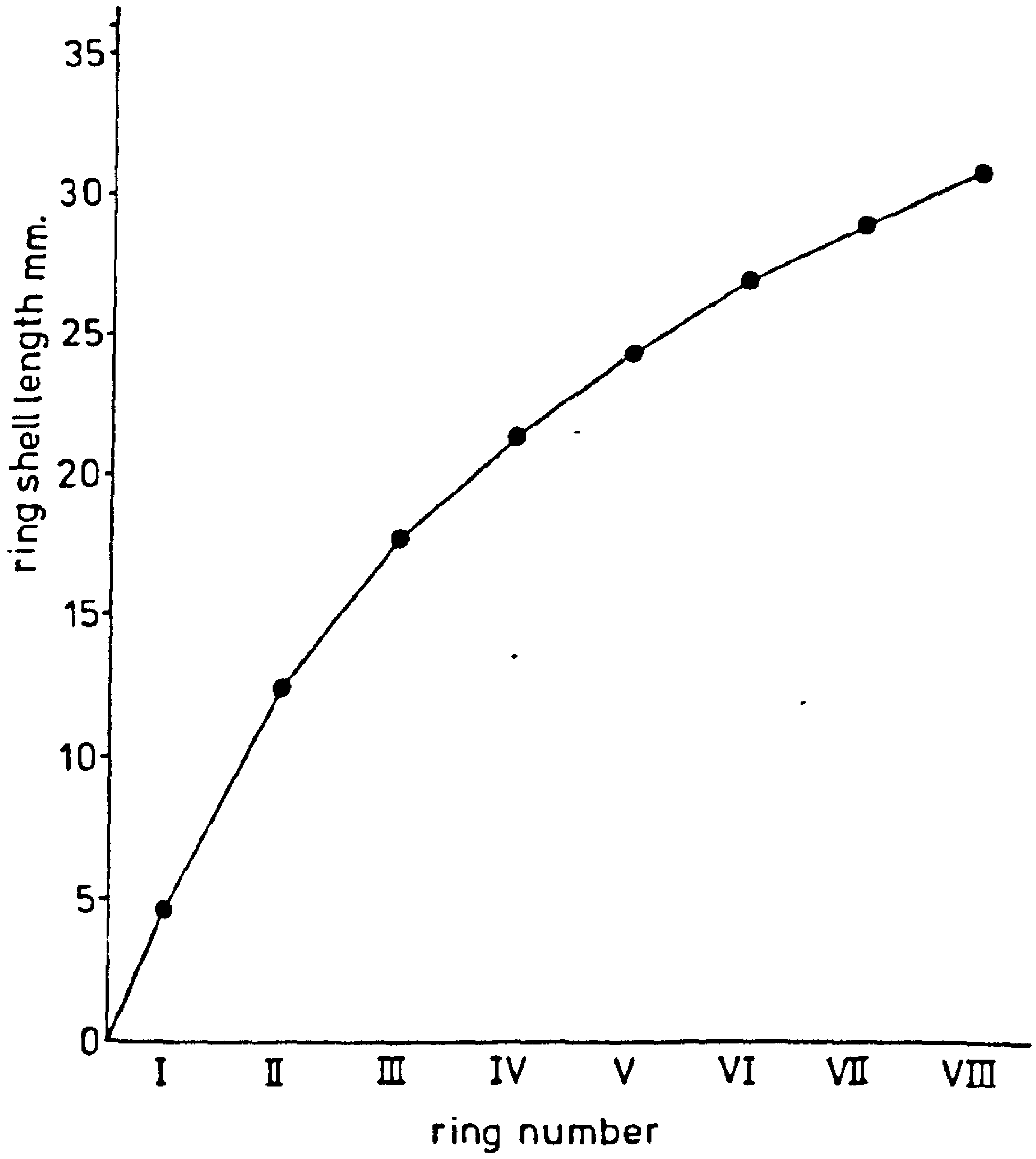


Figure 8xii

Percentage growth increment in shell length of <u>Cerastoderma edule</u> versus year of growth. Pooled data from all cohorts. Station GIV3.

Figure 8xiii

Log_n [illegible] percentage increment in shell length of <u>C. edule</u> for each settlement cohort versus year of growth. Station GIV3.

Figure 8xv

Ford-Walford growth plot for <u>C. edule</u>. Station GIV3.

Figure 8xiv

Log_n [illegible] percentage increment in shell length of <u>C. edule</u>. Data from all cohorts pooled. Station GIV3.

Figure 8xii

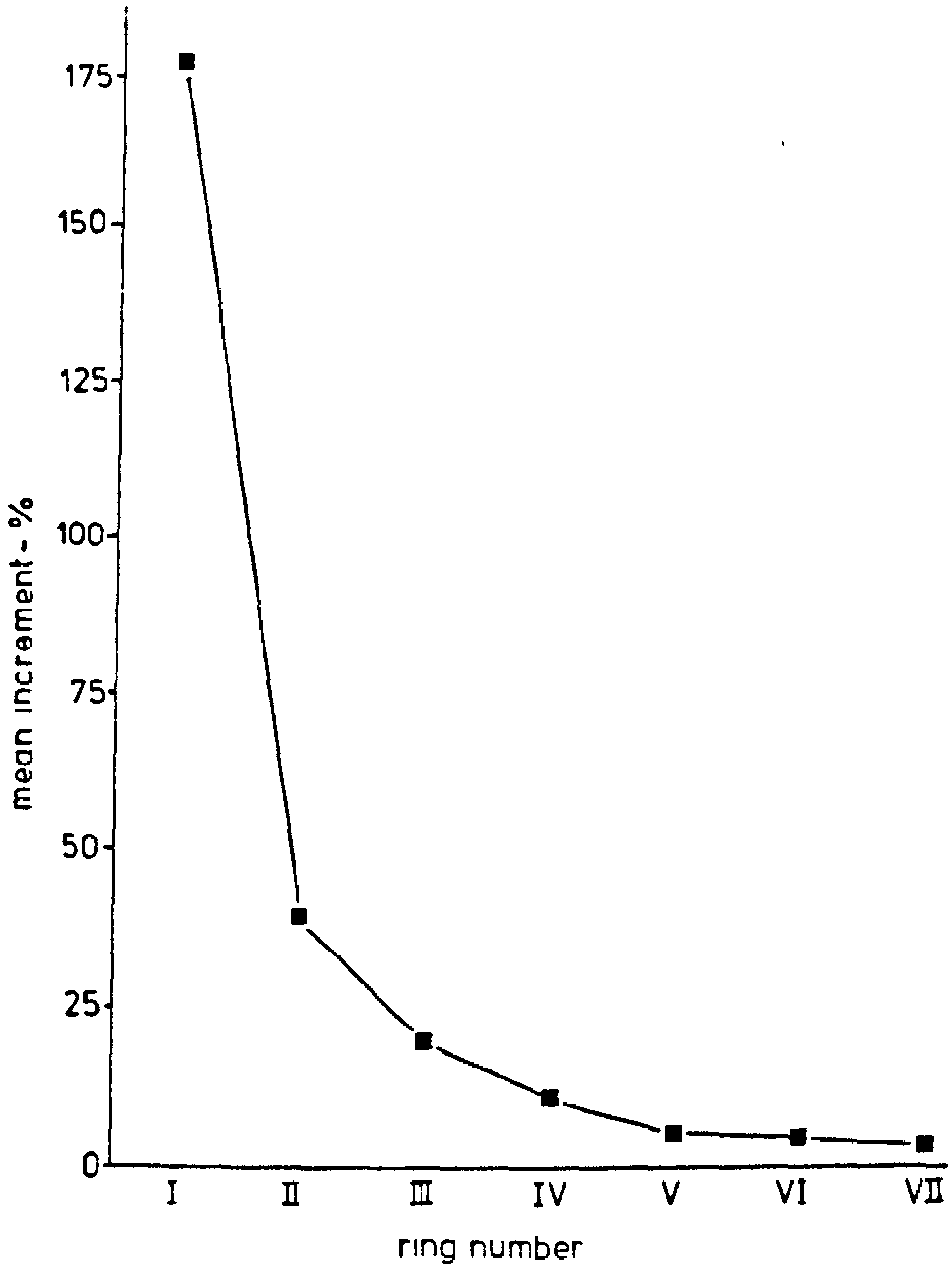
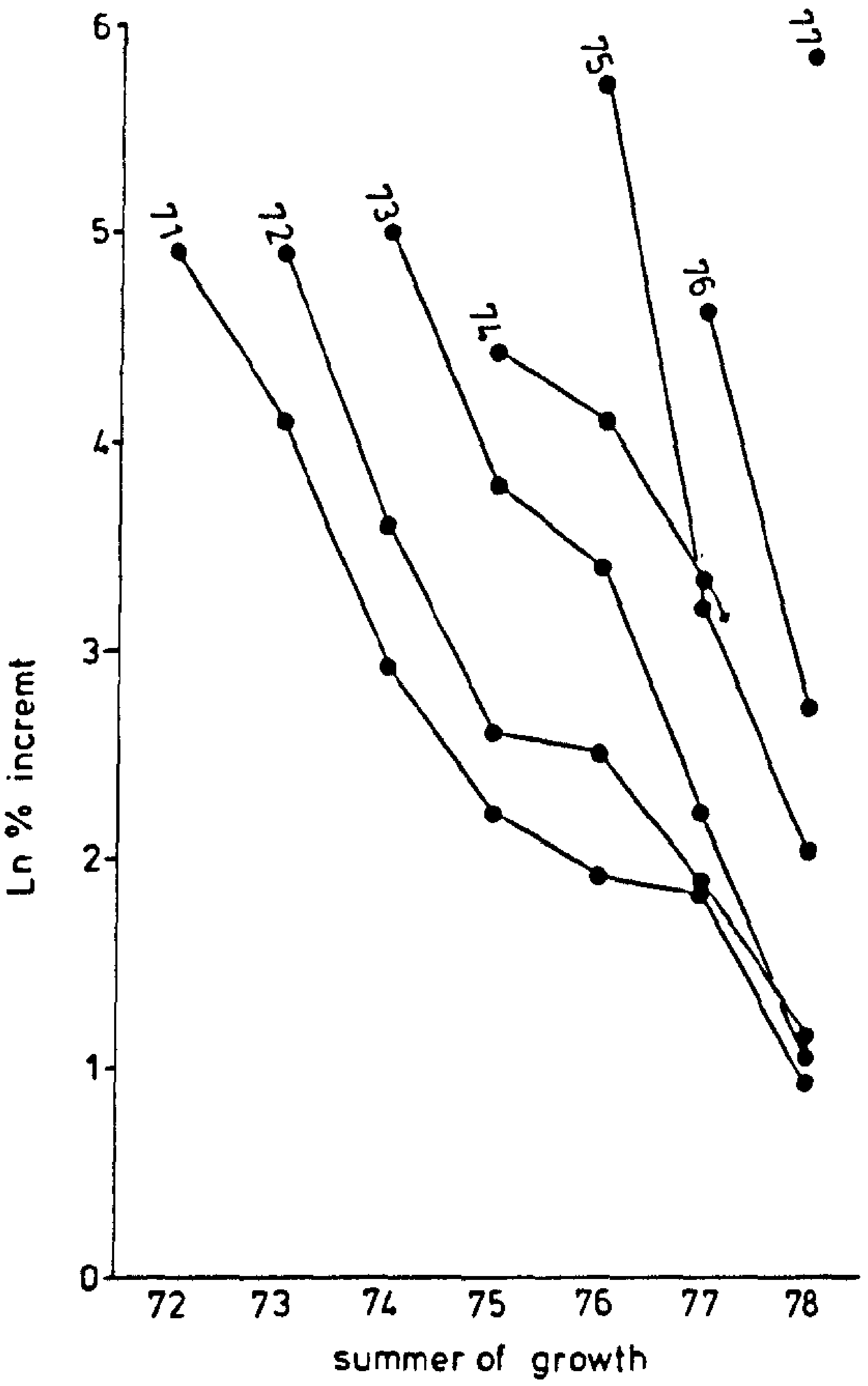


Figure 8xiii



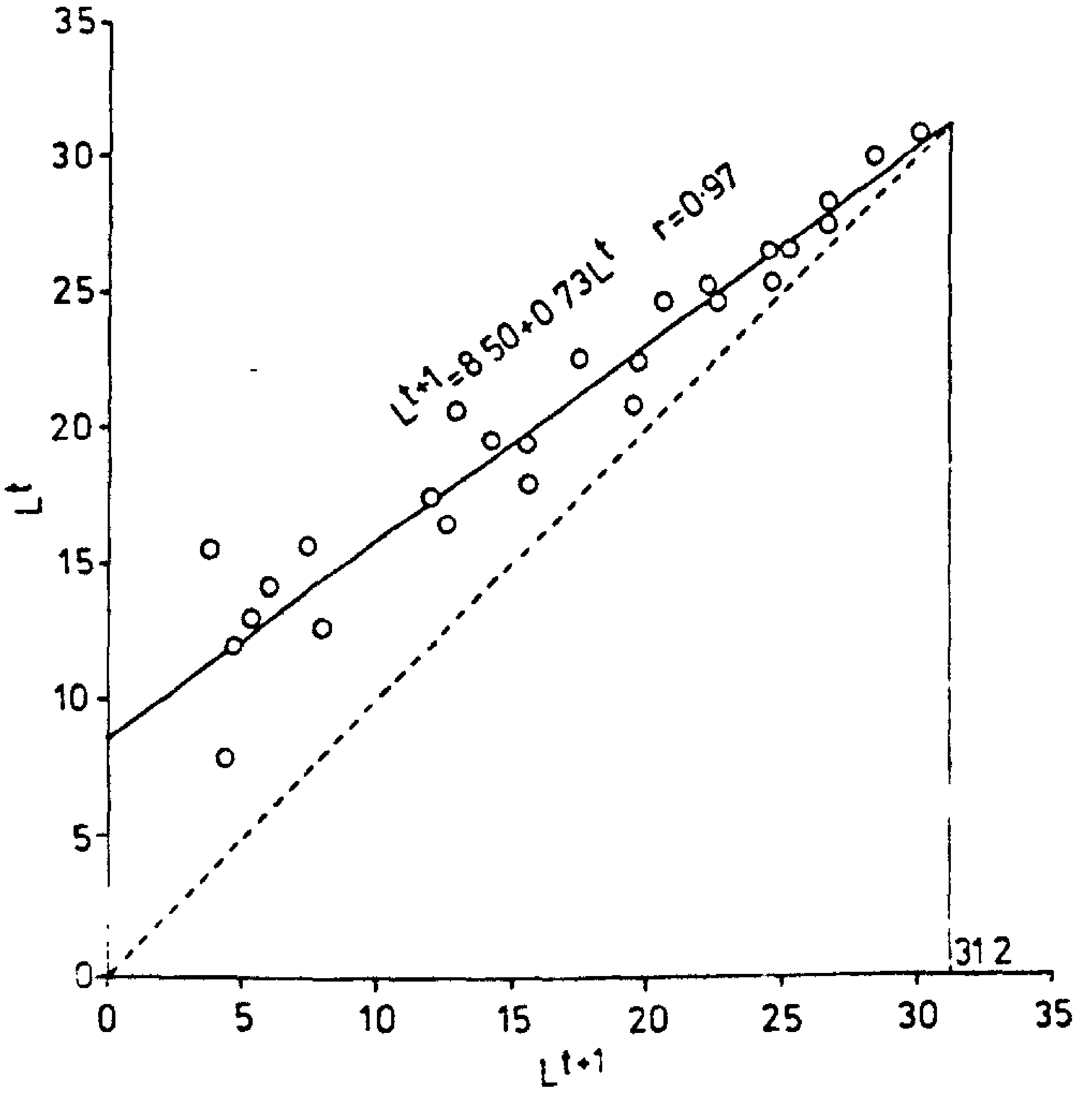


Figure 8xv

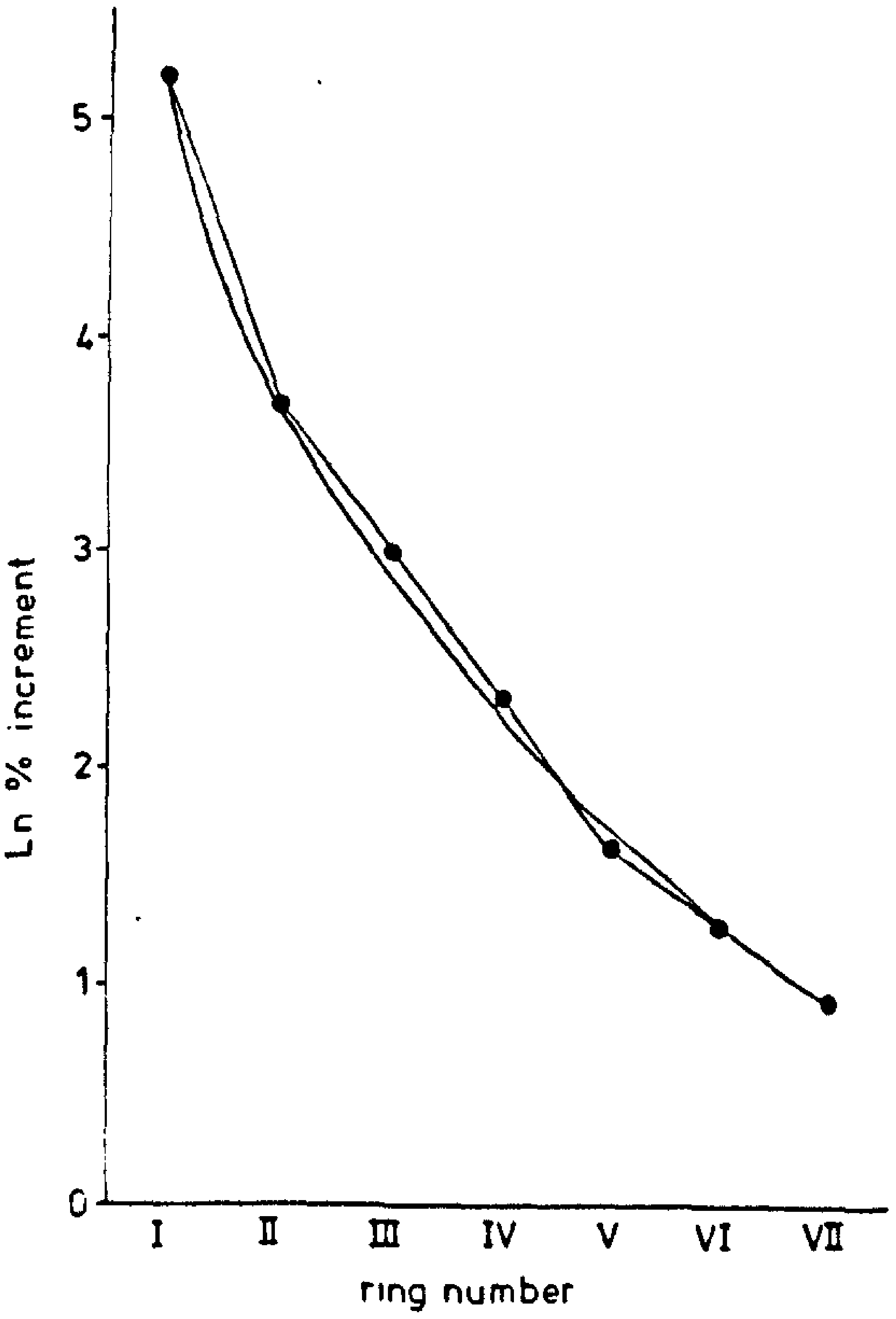


Figure 8xiv

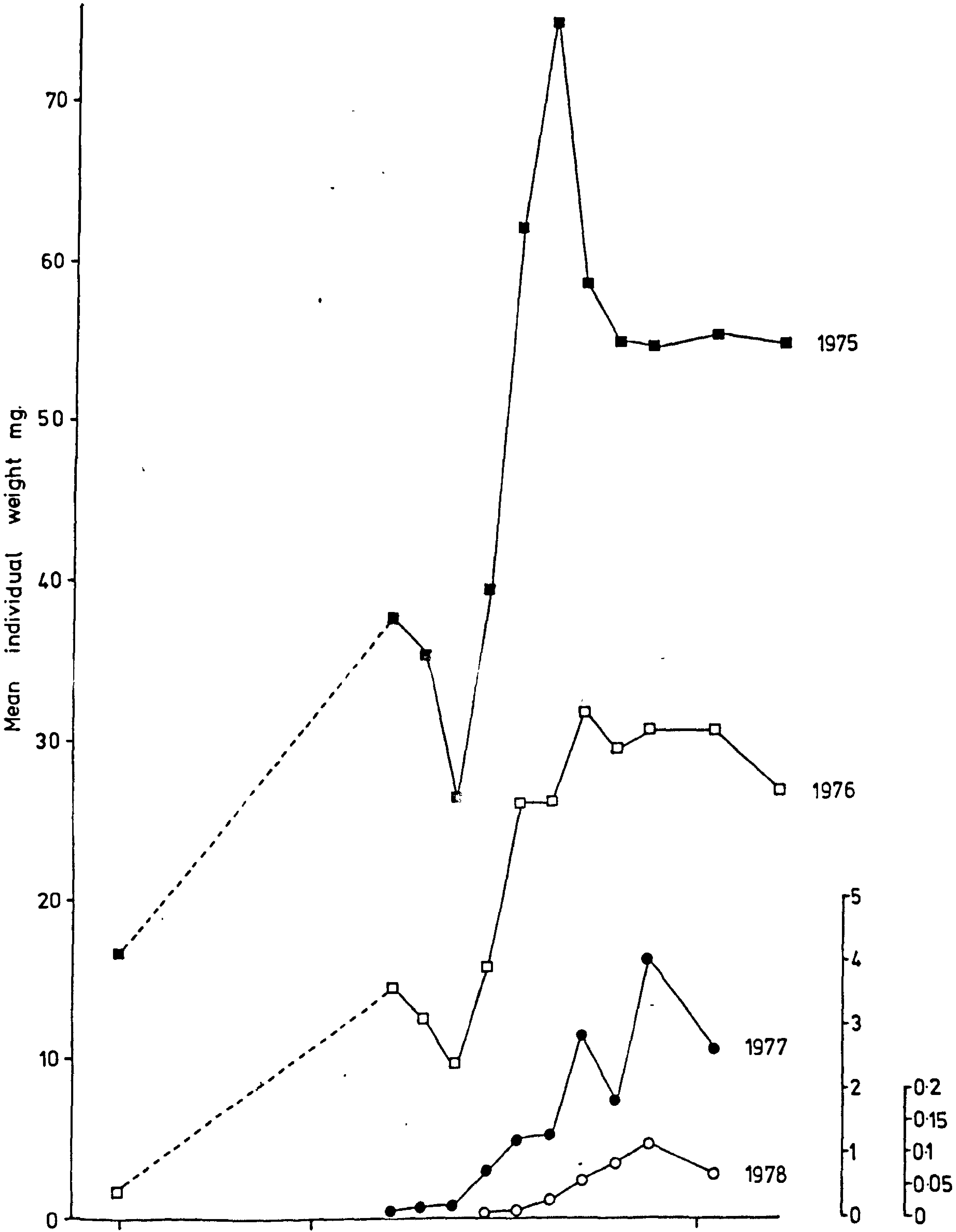


Figure 8xvi Mean individual flesh dry weight of each cohort of <u>Cerastoderma edule</u>. Station GIV3, May 1977 - March 1979. n.b. separate y axes for 1977 and 1978 cohorts.

Figure 8xvii

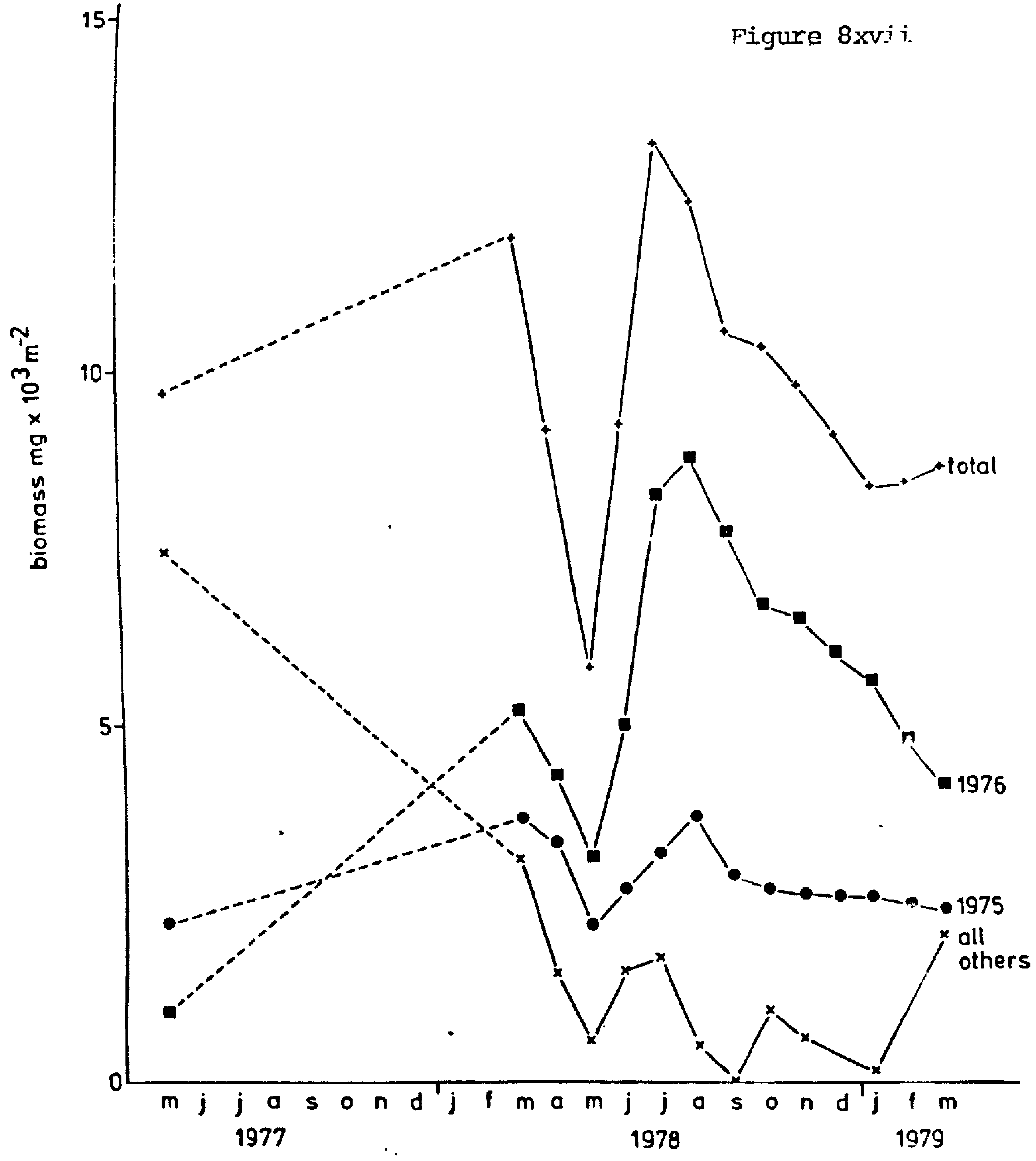
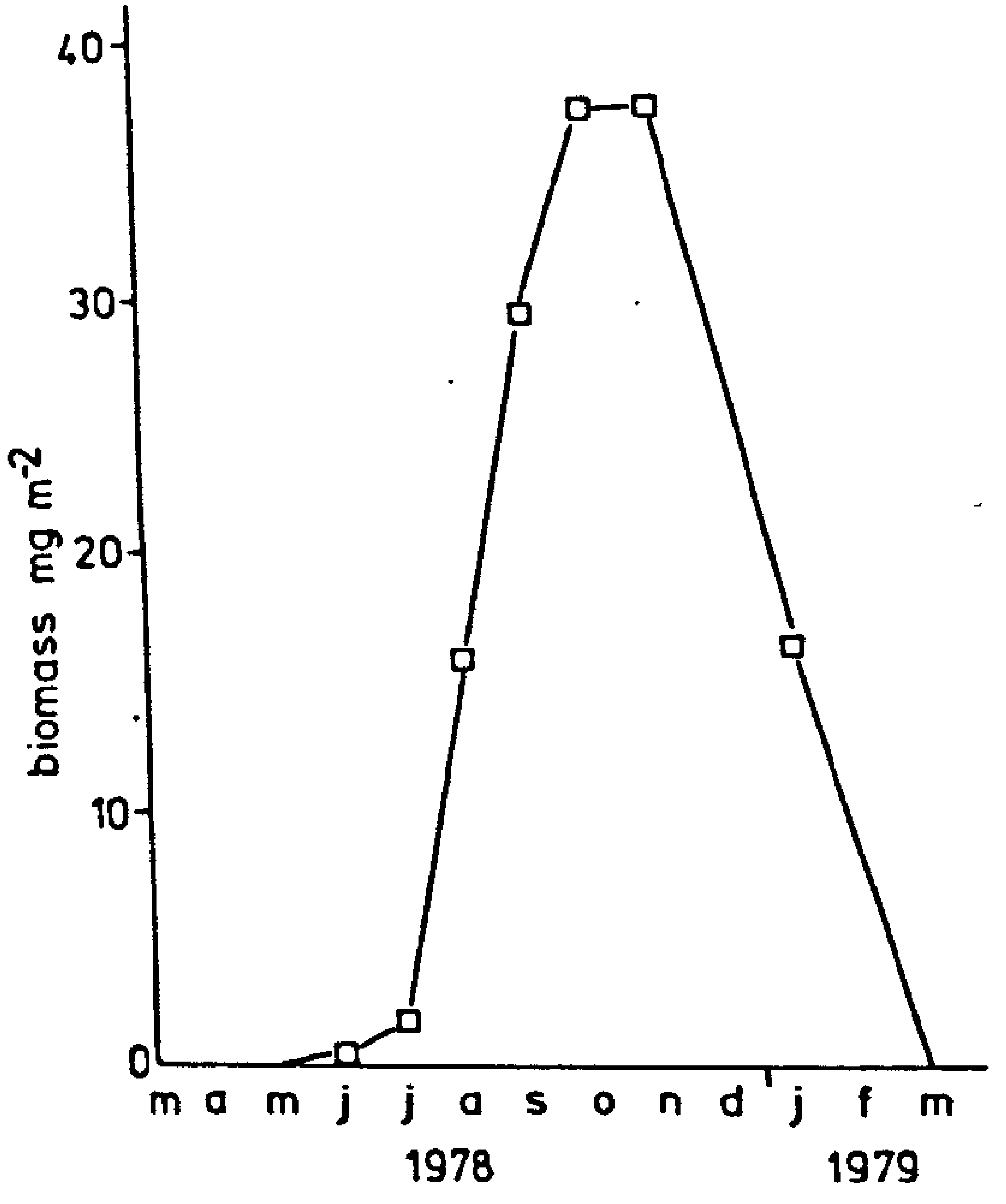


Figure 8xviii



Figures 8xvii and 8xviii Biomass of *Cerastoderma edule*. Station GIV3, May 1977 - March 1979.
8xvii Total and all cohorts older than 1978. 8xviii 1978 cohort.

Figure 8xix

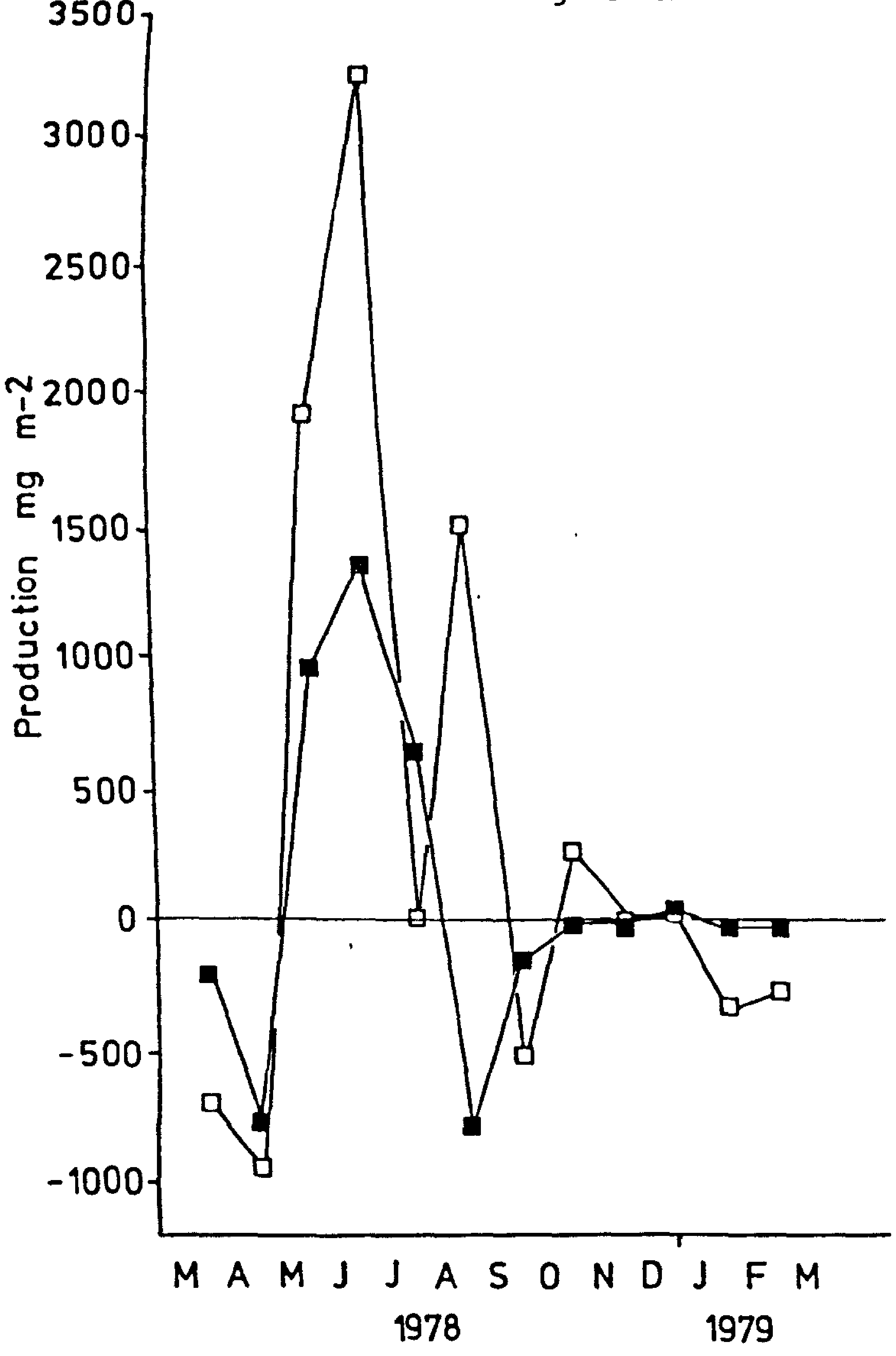
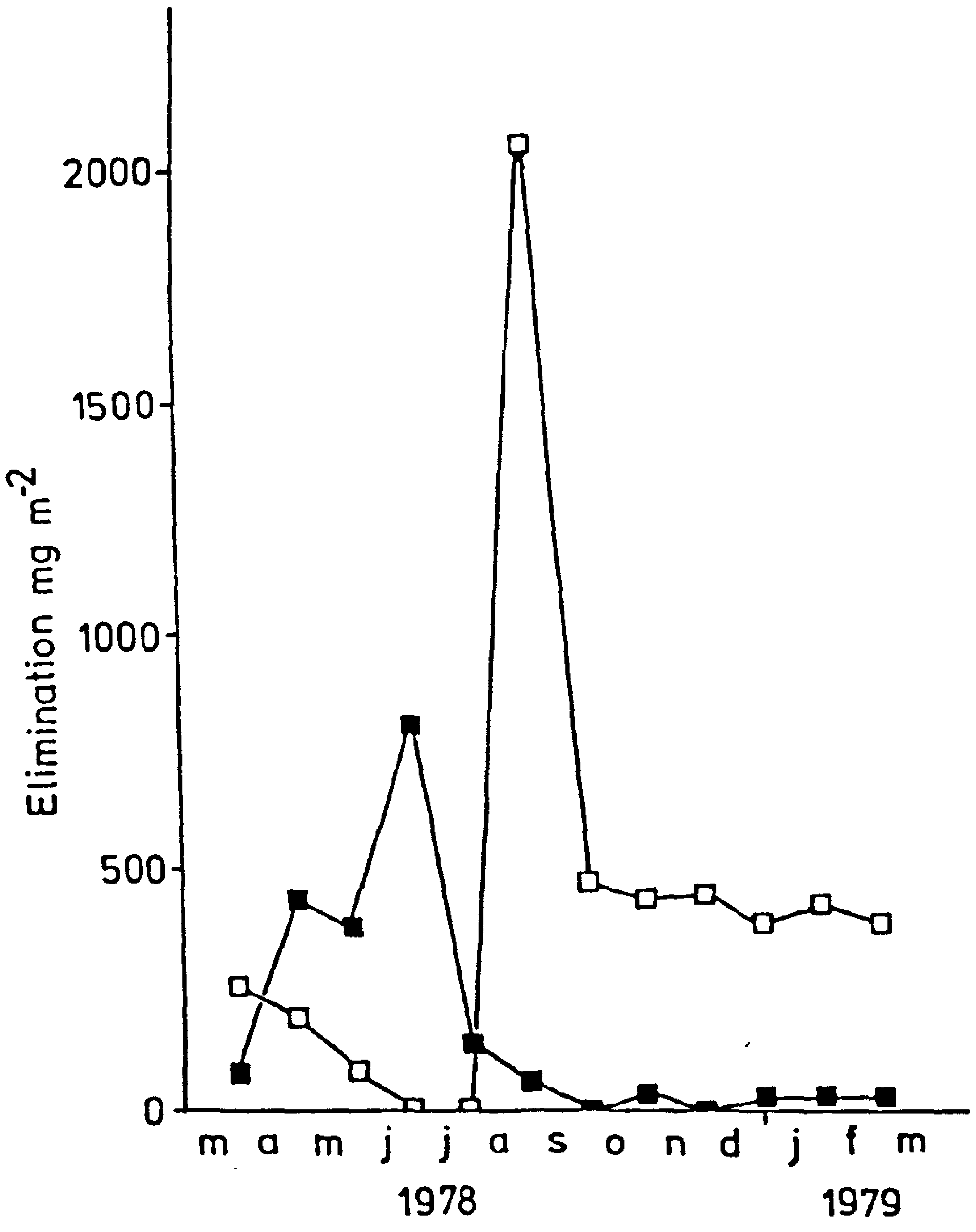
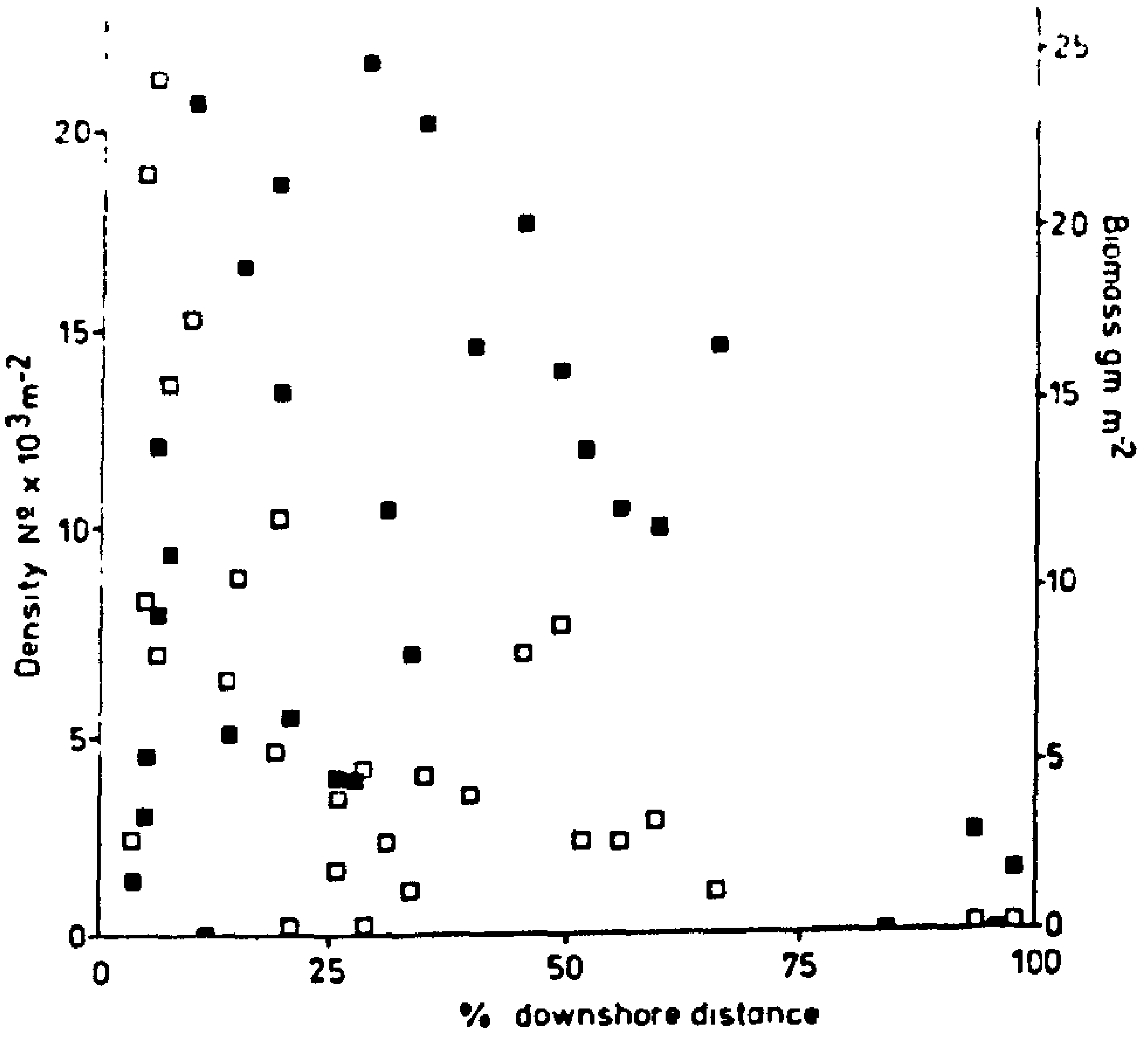


Figure 8xx

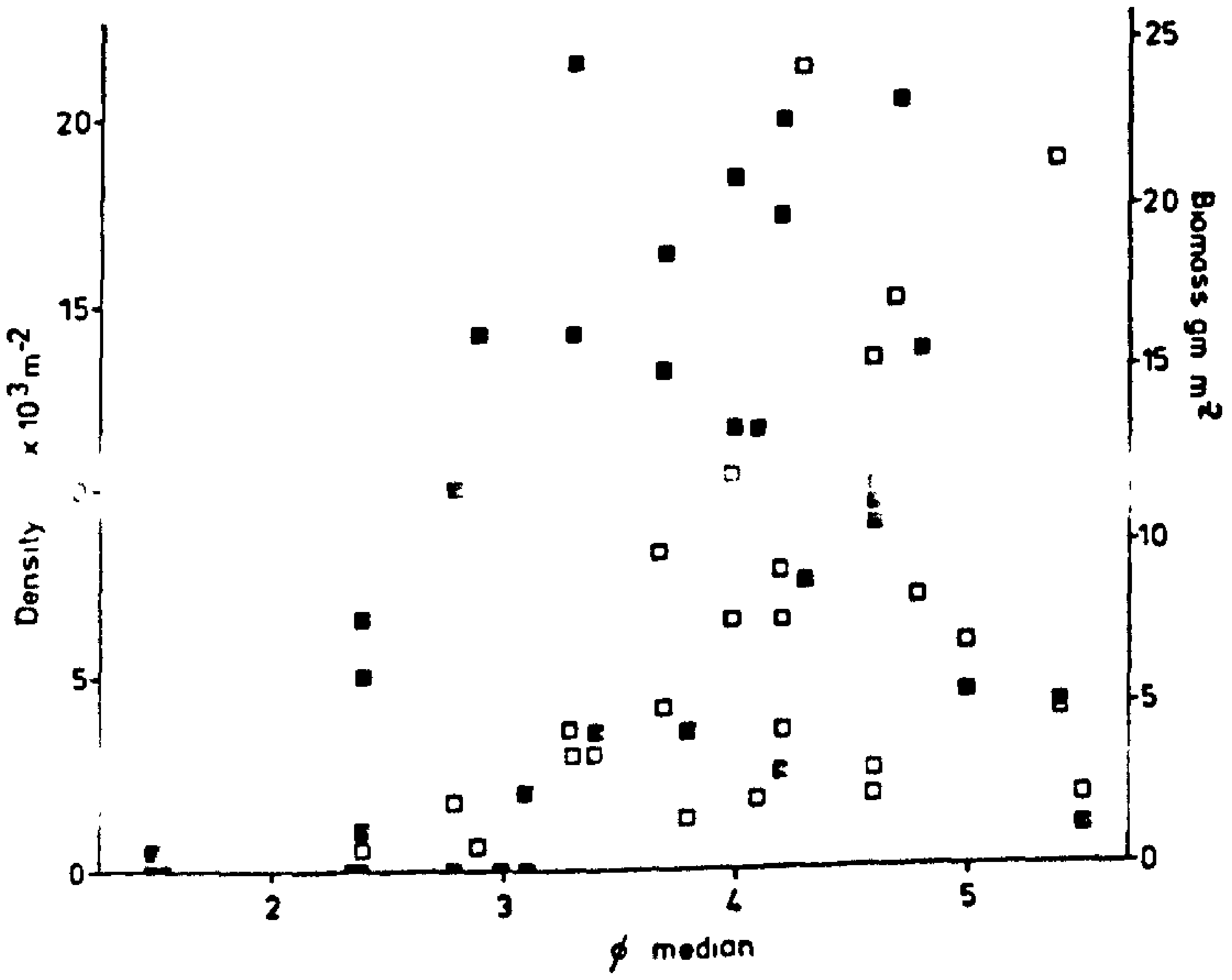


Figures 8xix and 8xx Monthly production and elimination of <u>Cerastoderma edule</u>, 1975 (closed squres) and 1976 (open squares) cohorts. Sation GIV3, March 1978 - March 1979.

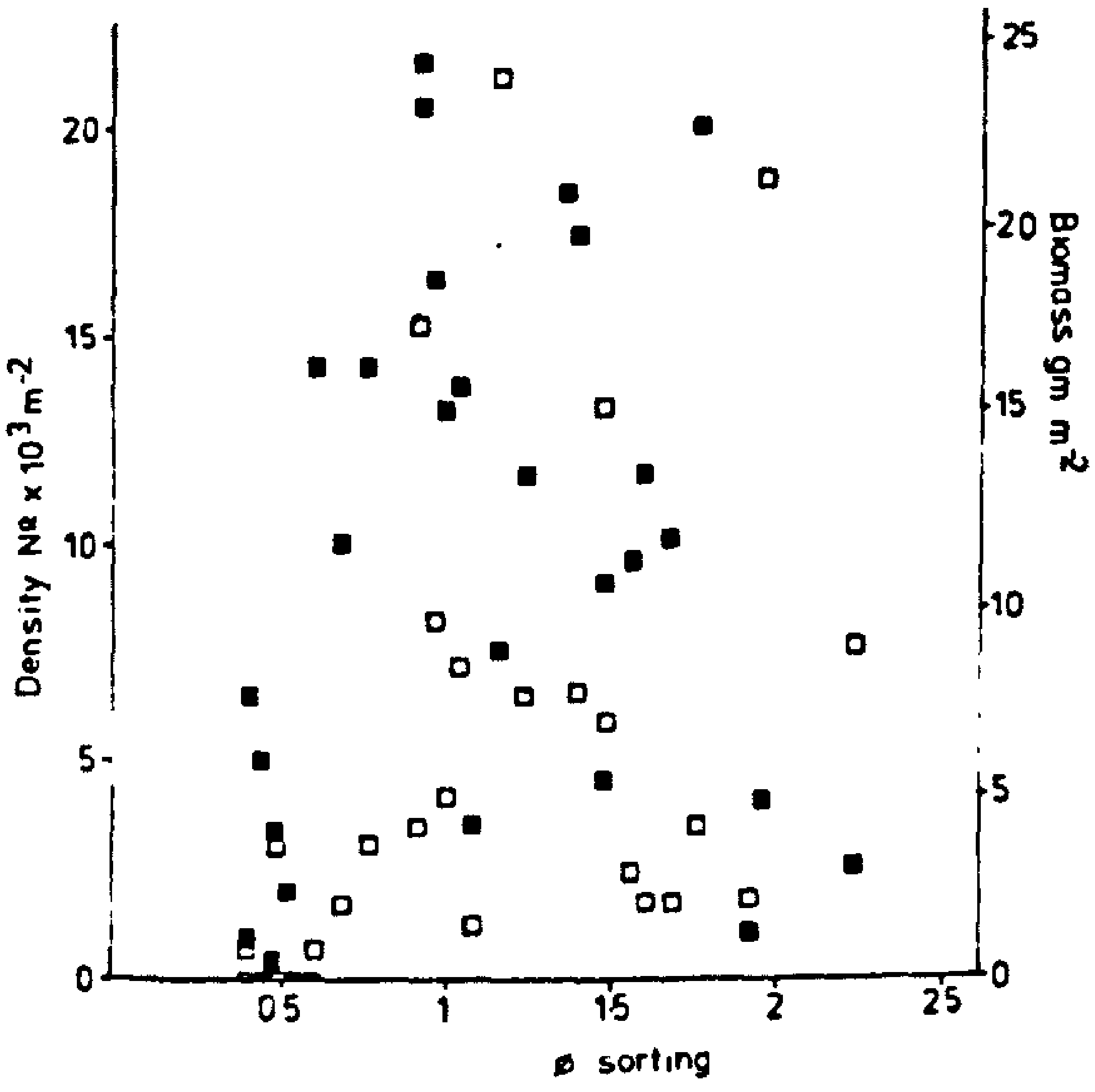
9i



9ii

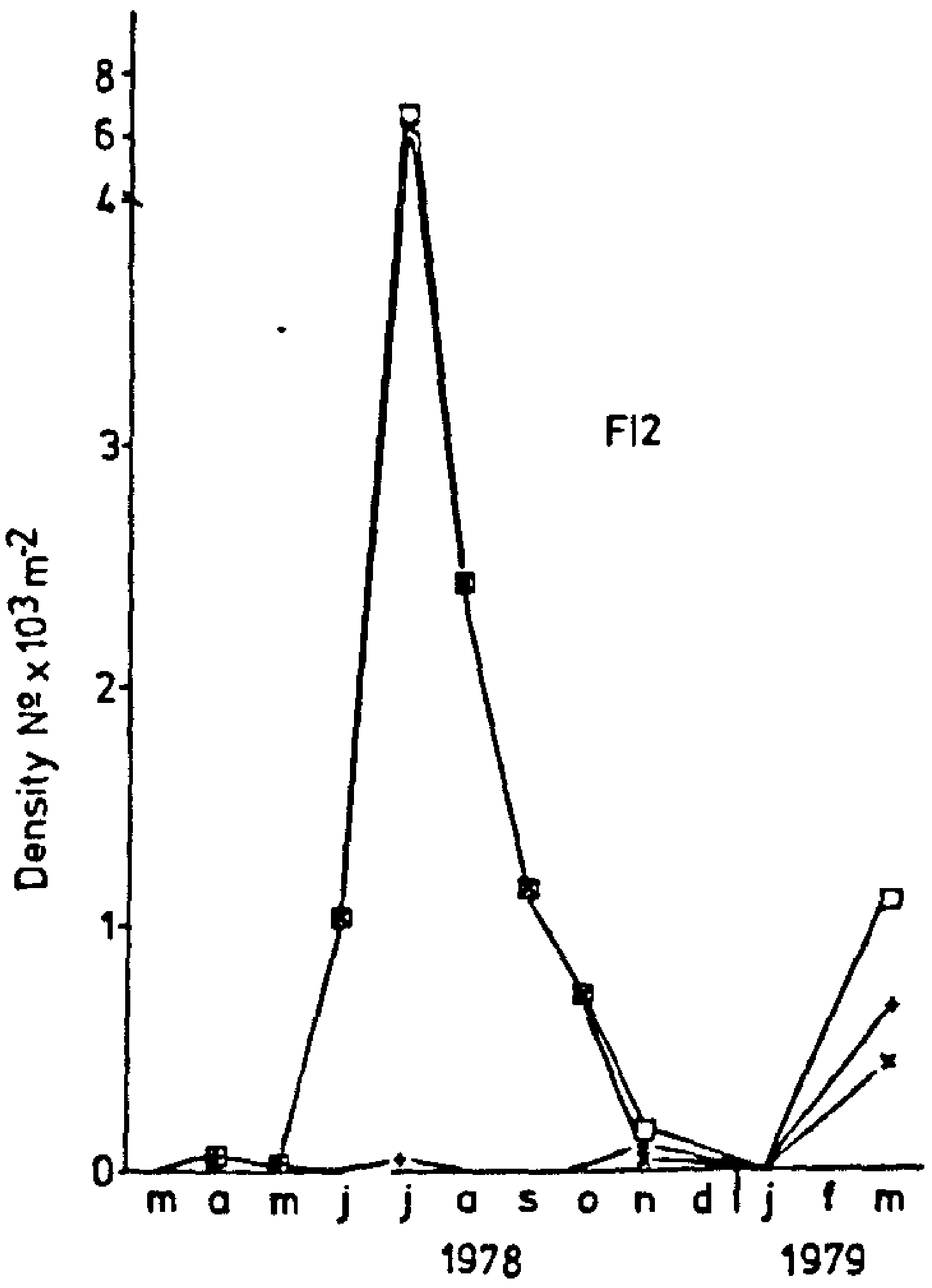


9iii

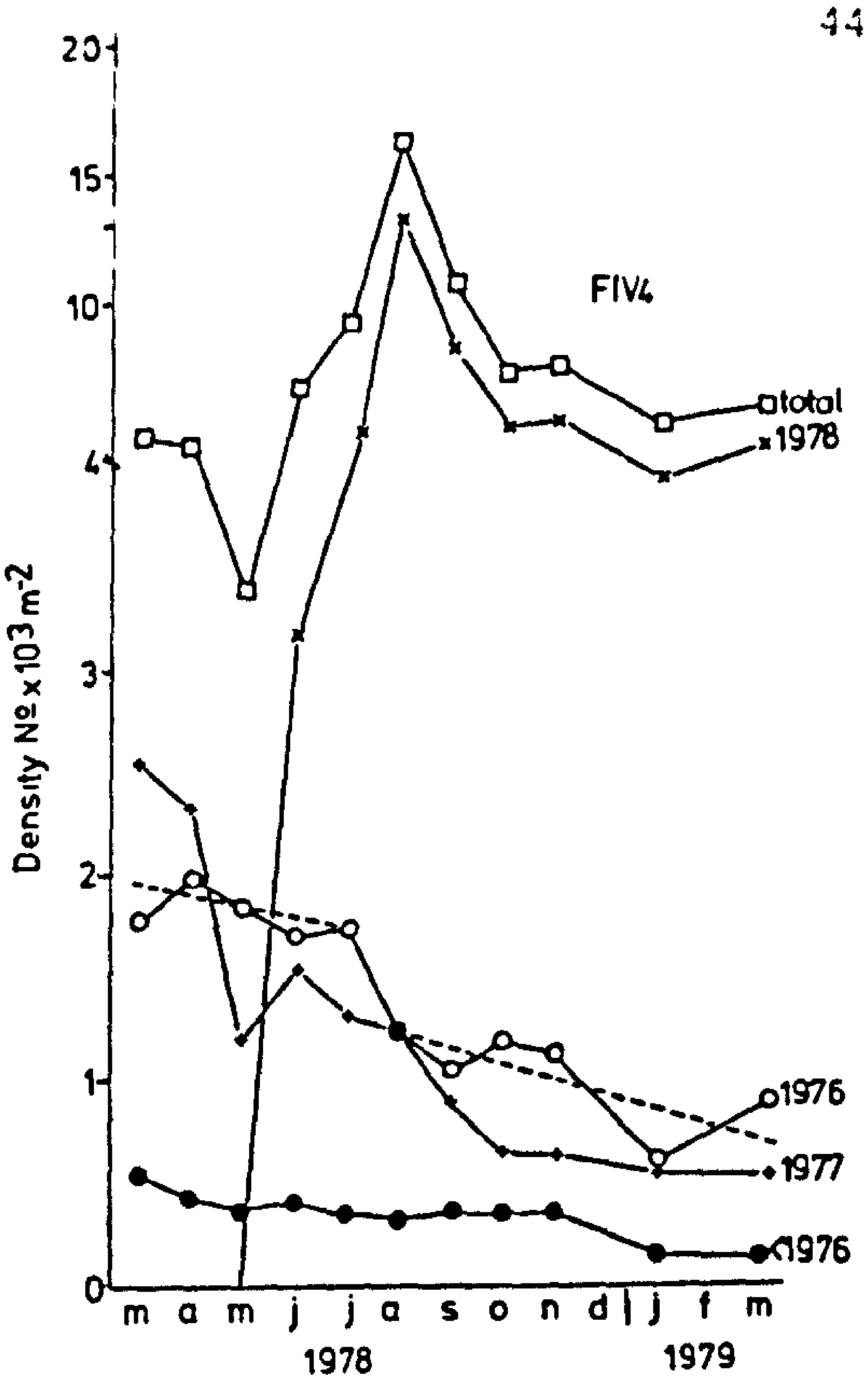


Figures 9i, 9ii and 9iii. Density (open squares) and biomass (closed squares) of <u>Macoma balthica</u> in relation to tidal height, sediment size and sorting. Extensive survey, May/June 1977. Spurn Bight stations only.

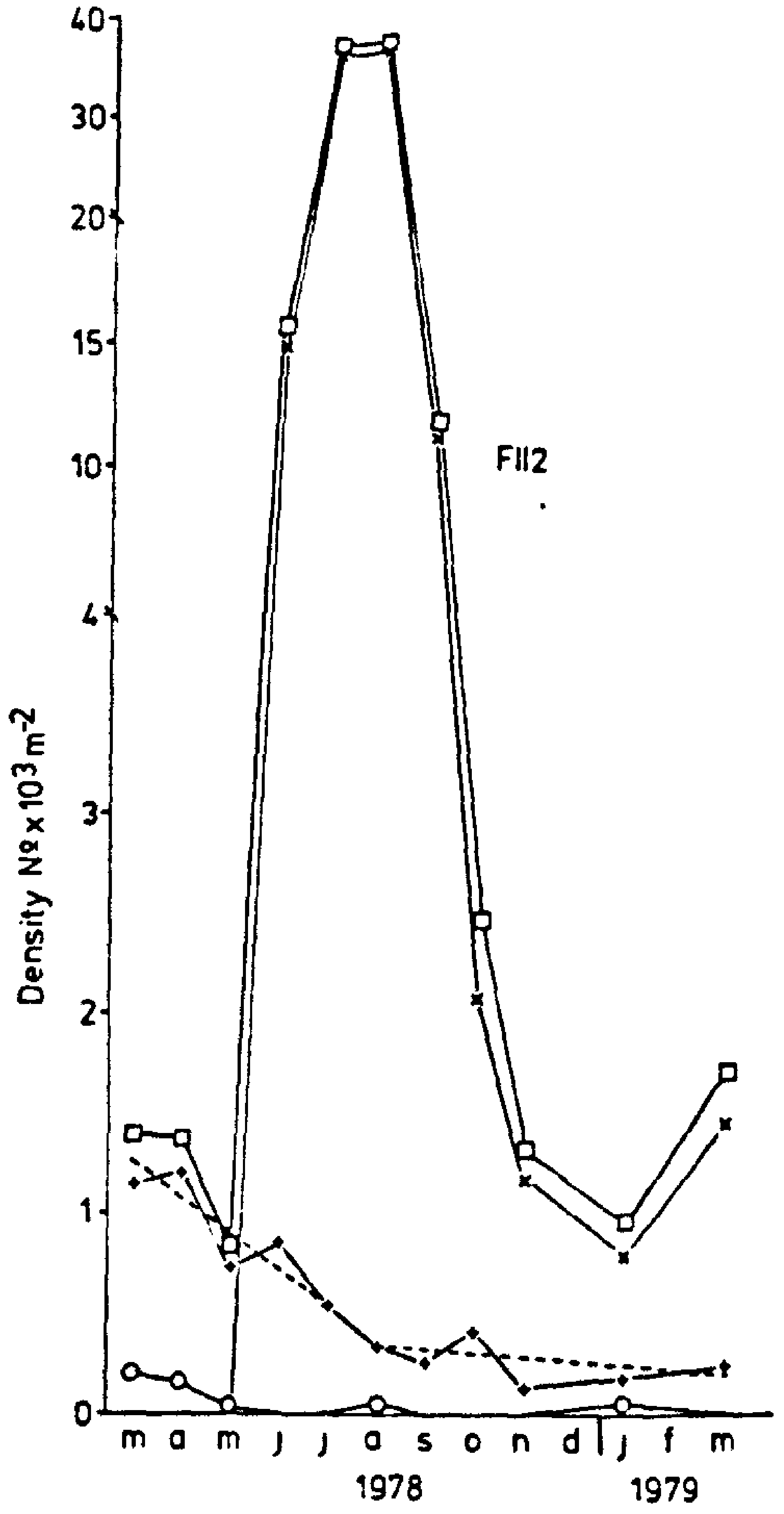
9iv



9vi

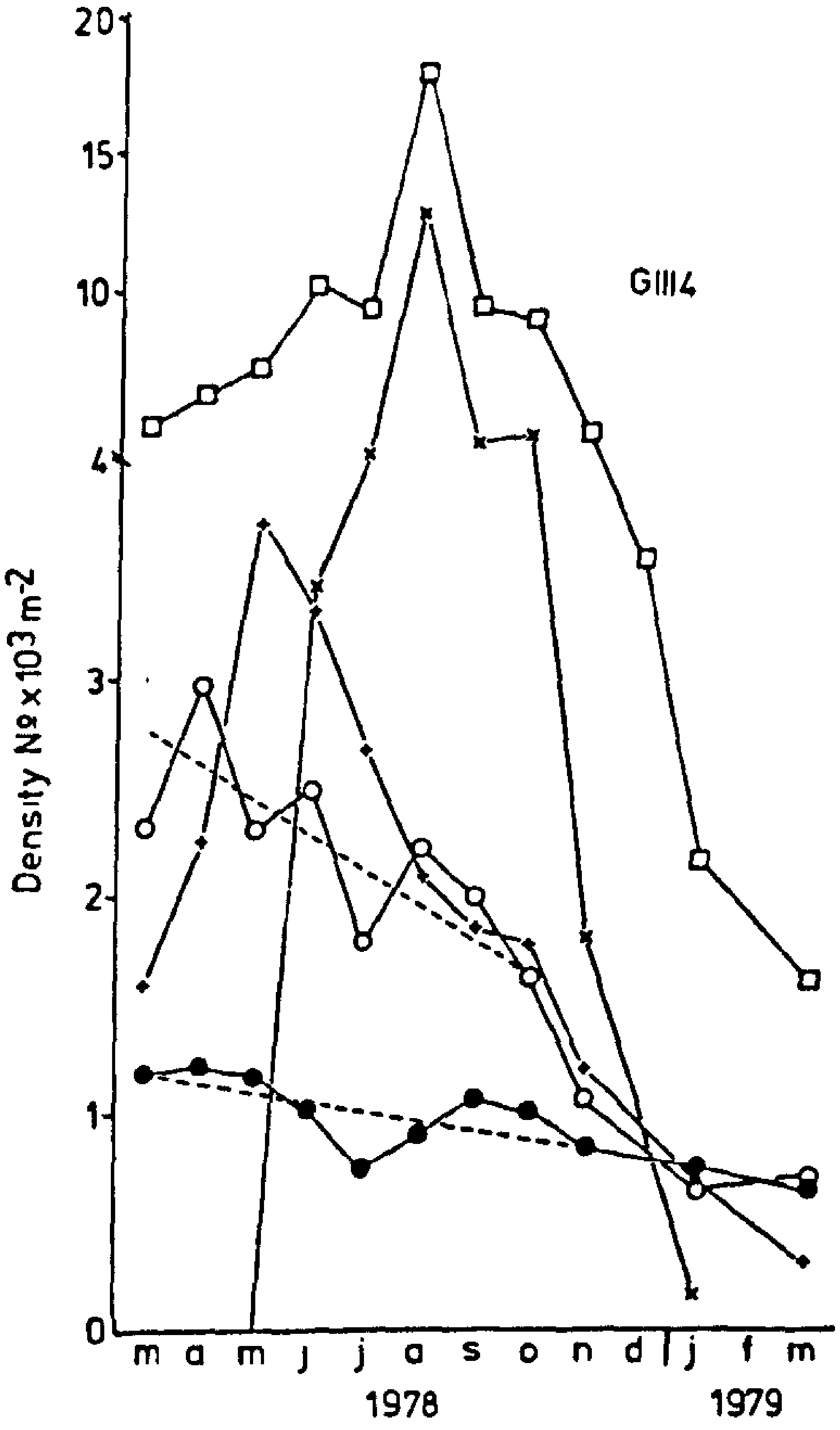


9v

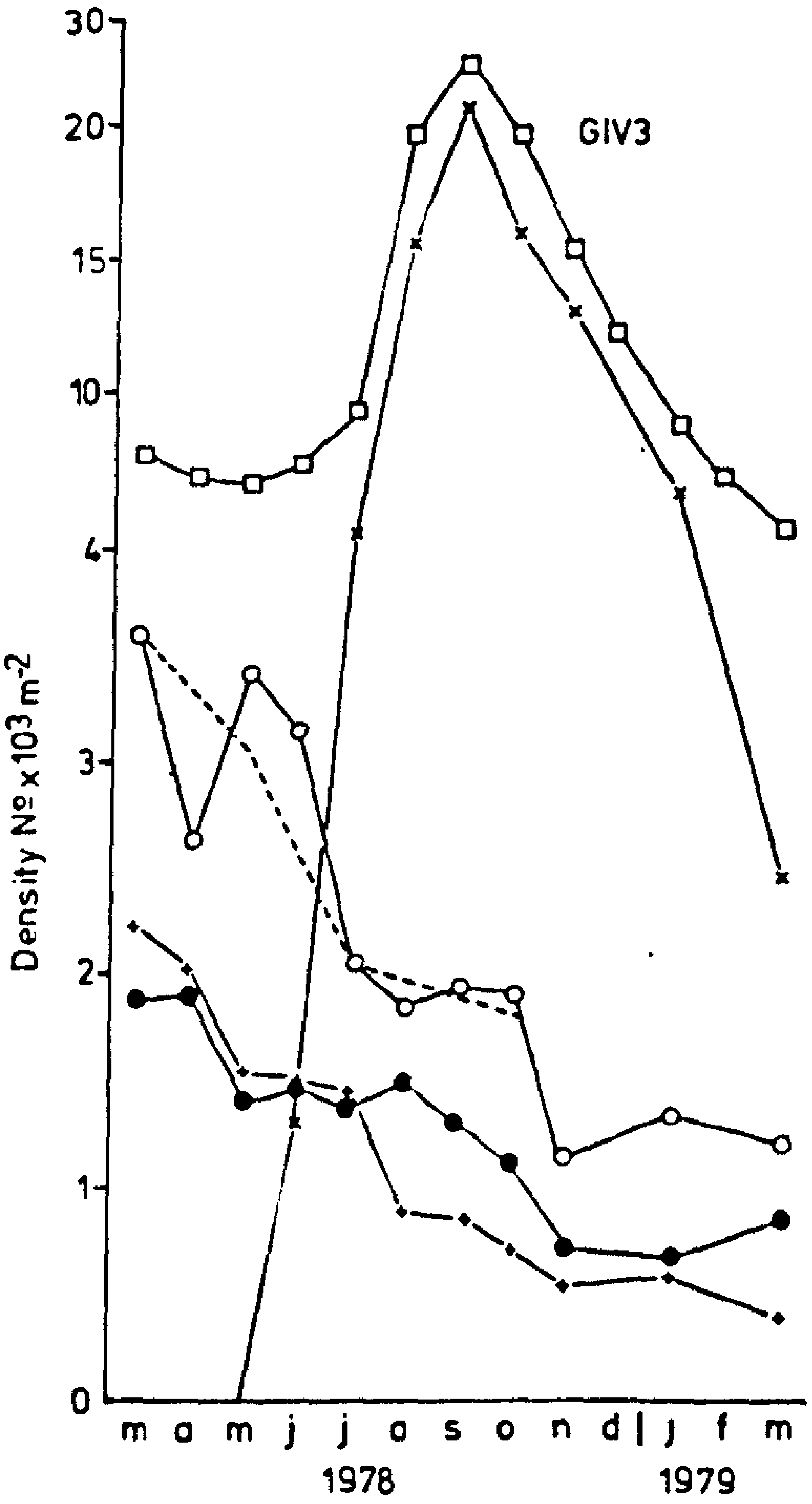


Figures 9iv - 9viii
Variation in total and cohort density of Macoma balthica with time. March 1978 - March 1979. Dotted line - smoothed 'mortality' curve.

9vii


GIII4
Density Nº x 10³ m⁻²
20
15
10
4
3
2
1
0
m a m j j a s o n d | j f m
1978
1979

9viii


GIV3
Density Nº x 10³ m⁻²
30
20
15
10
4
3
2
1
0
m a m j j a s o n d | j f m
1978
1979

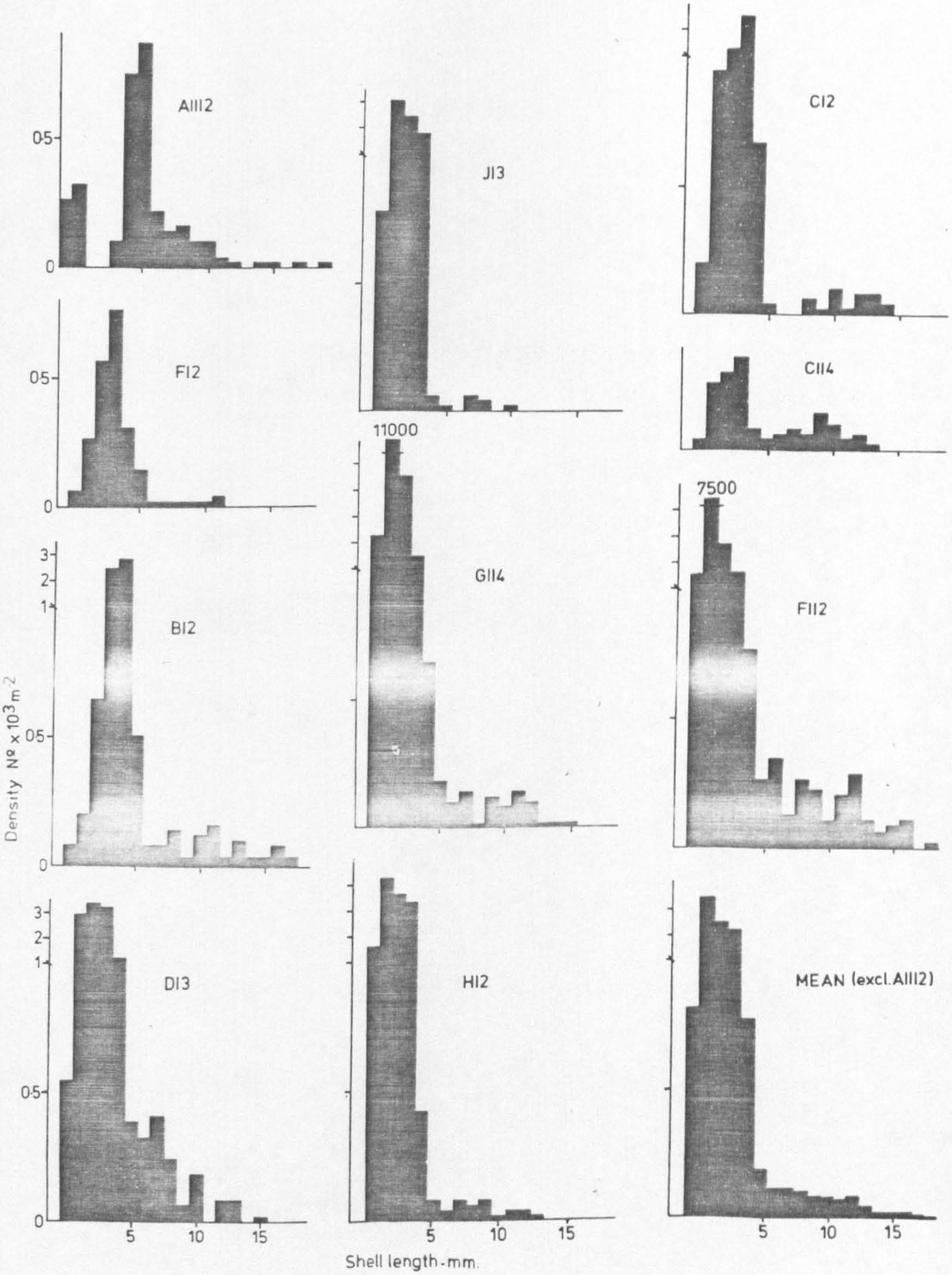


Figure 9ix Size/frequency distribution of Macoma balthica. Extensive survey, May/June 1977. TOPSILT stations, individually and mean of all stations of subcommunity.

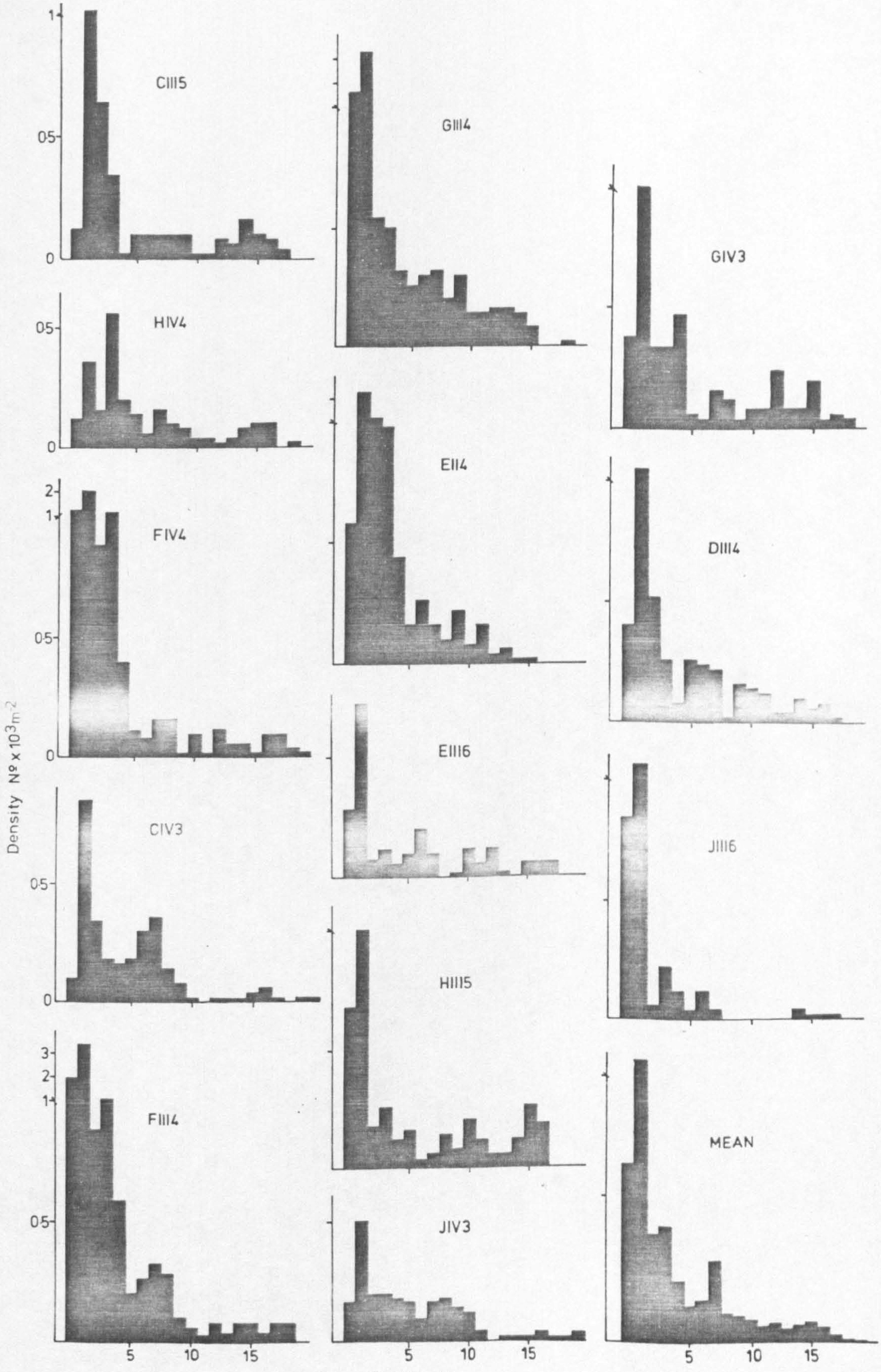


Figure 9x Size/frequency distribution of Macoma balthica. Extensive survey, May/June 1977. MIDMUD stations, individually and mean of all stations.

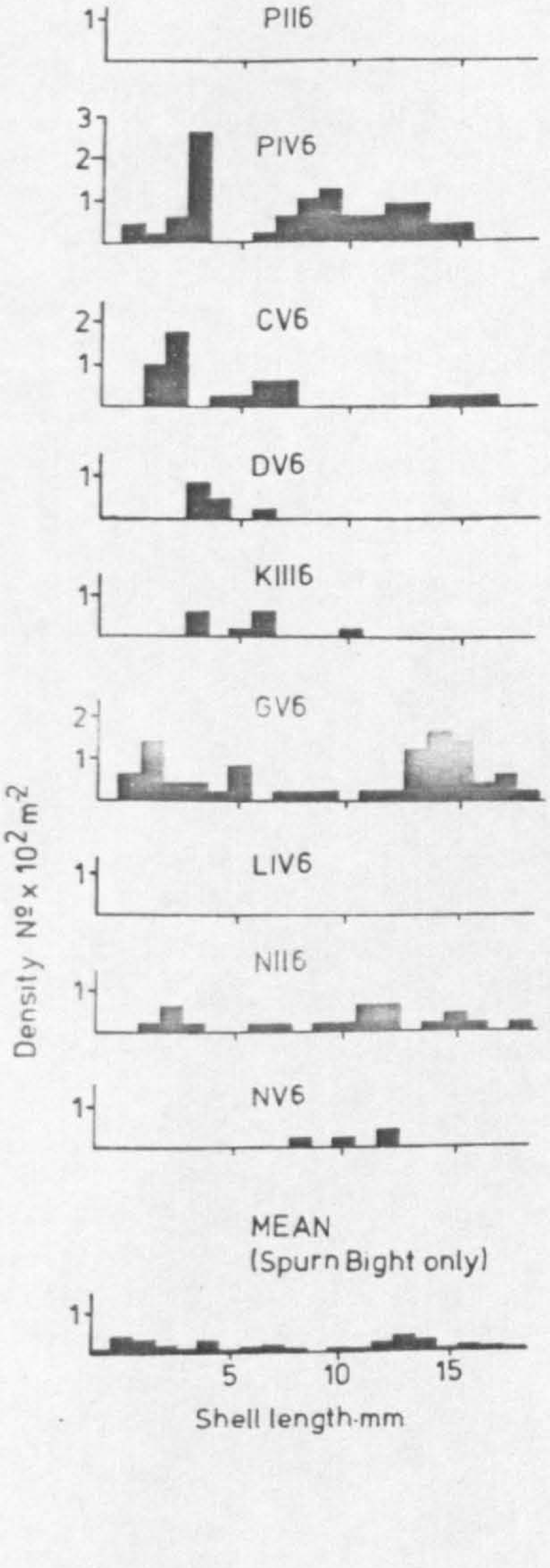


Figure 9xi Size/frequency distribution of Macoma balthica. Extensive survey, May/June 1977. SAND stations, individually and mean of all stations in Spurn Bight.

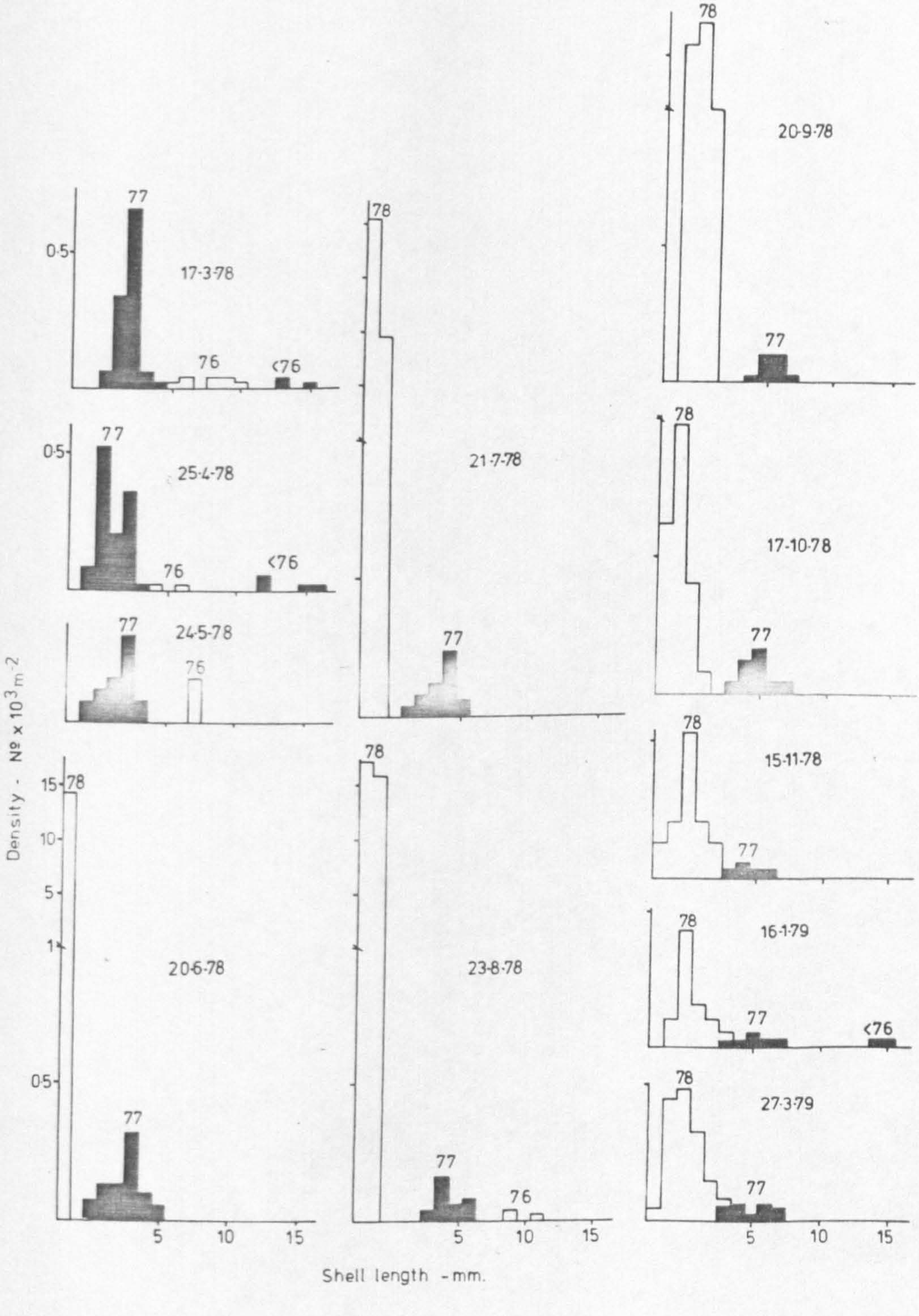


Figure 9xii Population structure of Macoma balthica, station FII2, March 1978 - March 1979. Cohorts older than 1976 considered together.

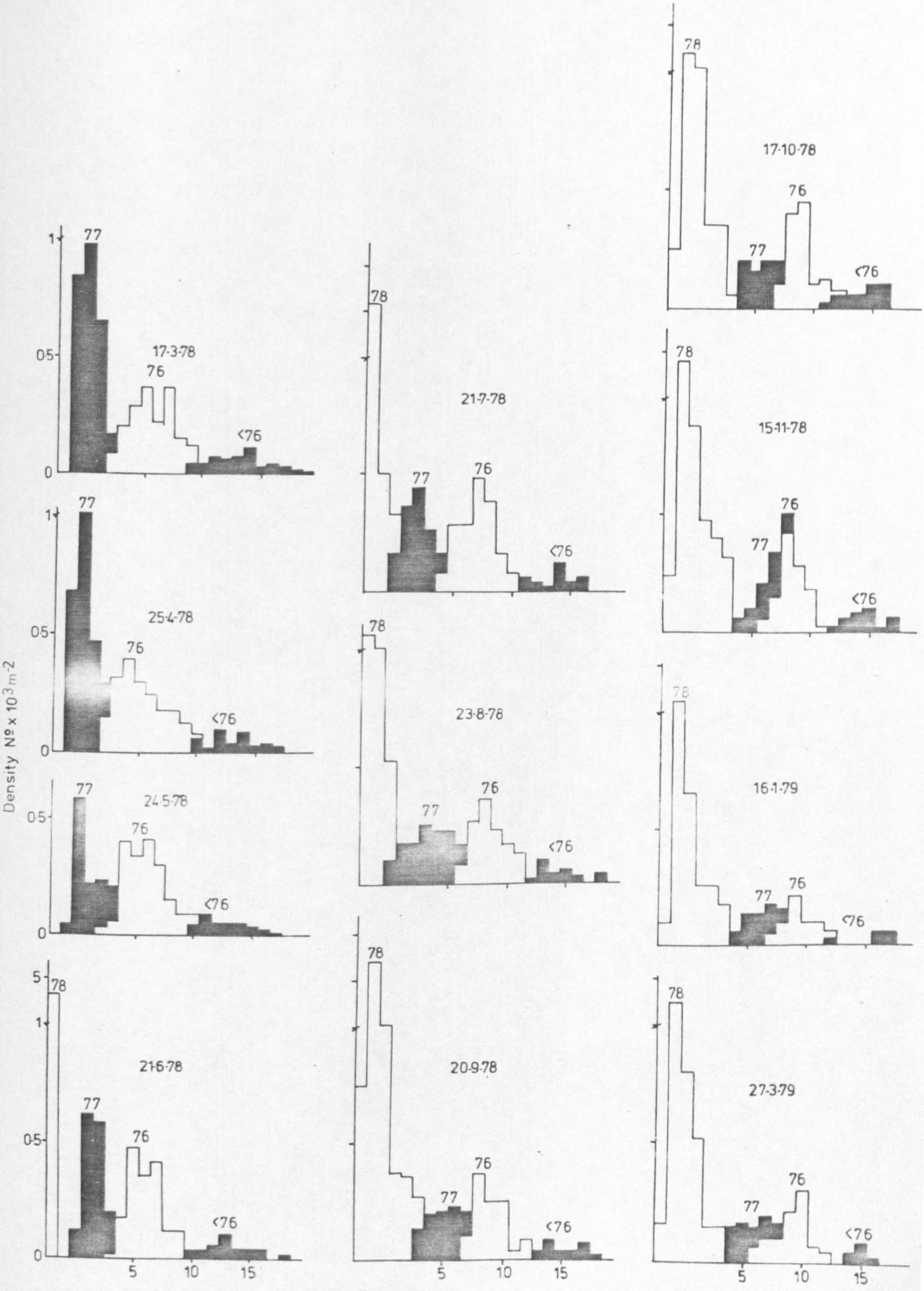


Figure 9xiii Population structure of Macoma balthica, station FIV4, March 1978 - March 1979. Cohorts older than 1976 considered together.

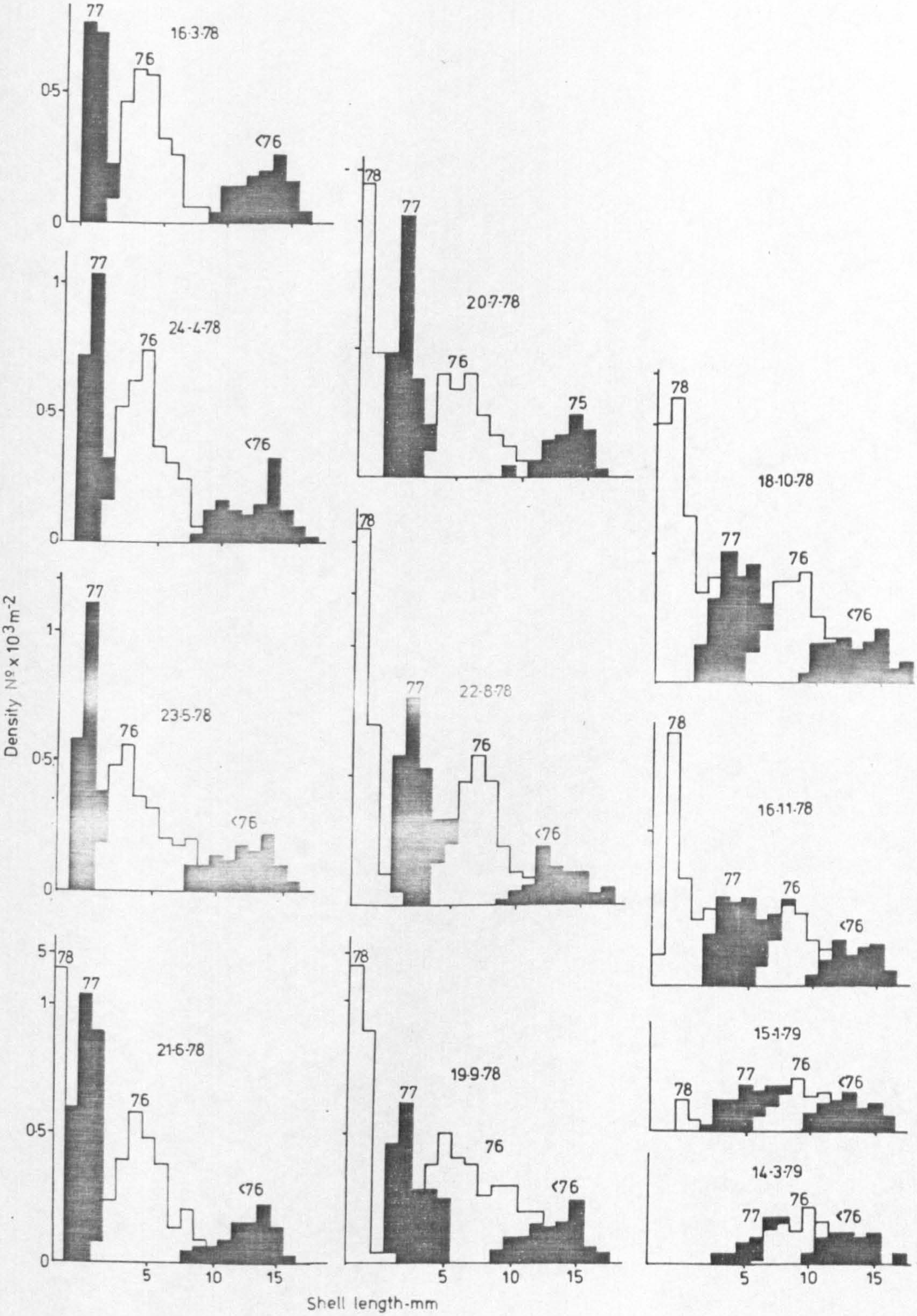


Figure 9xiv Population structure of Macoma balthica, station GIII4, March 1978 - March 1979. Cohorts older than 1976 considered together.

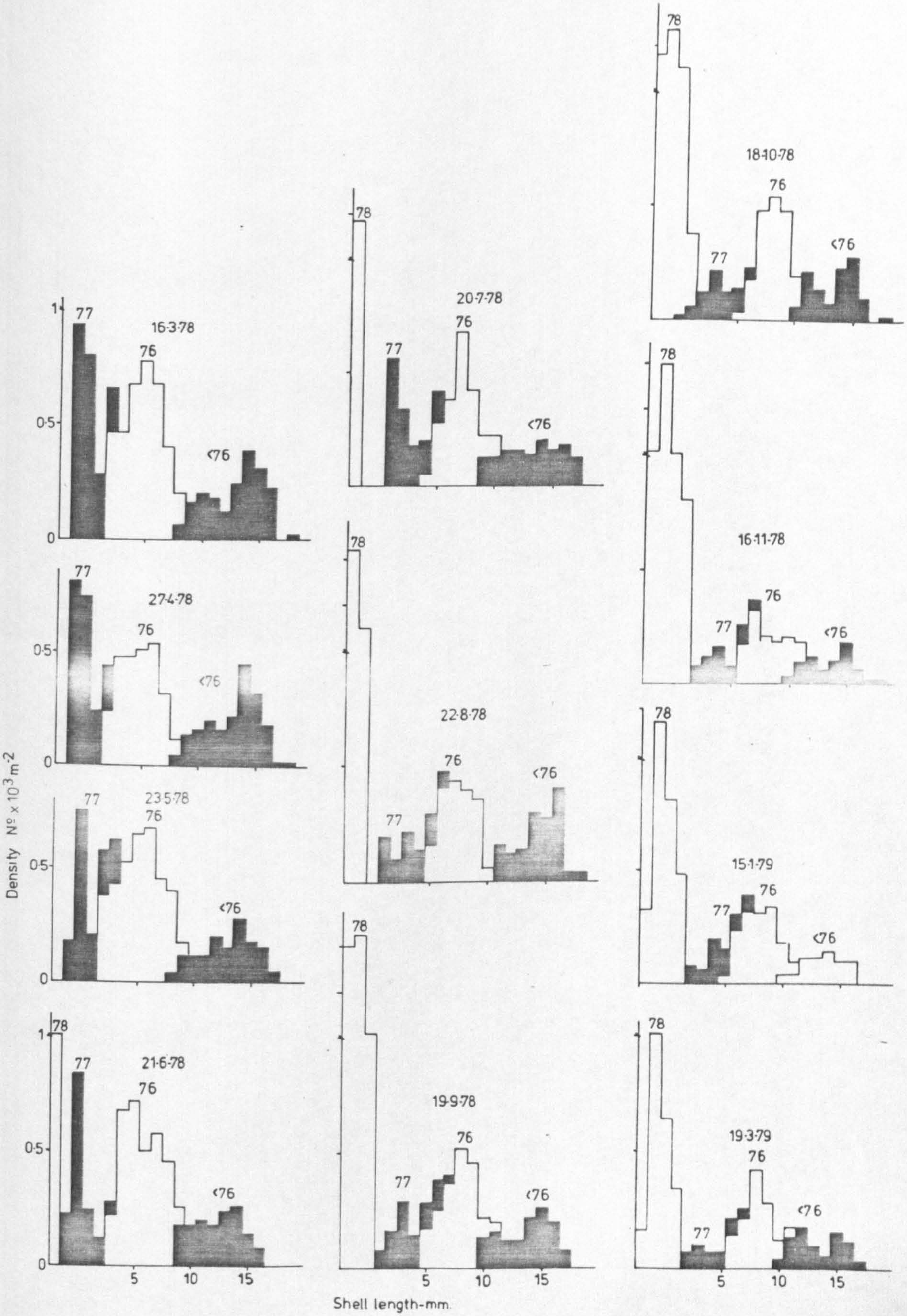
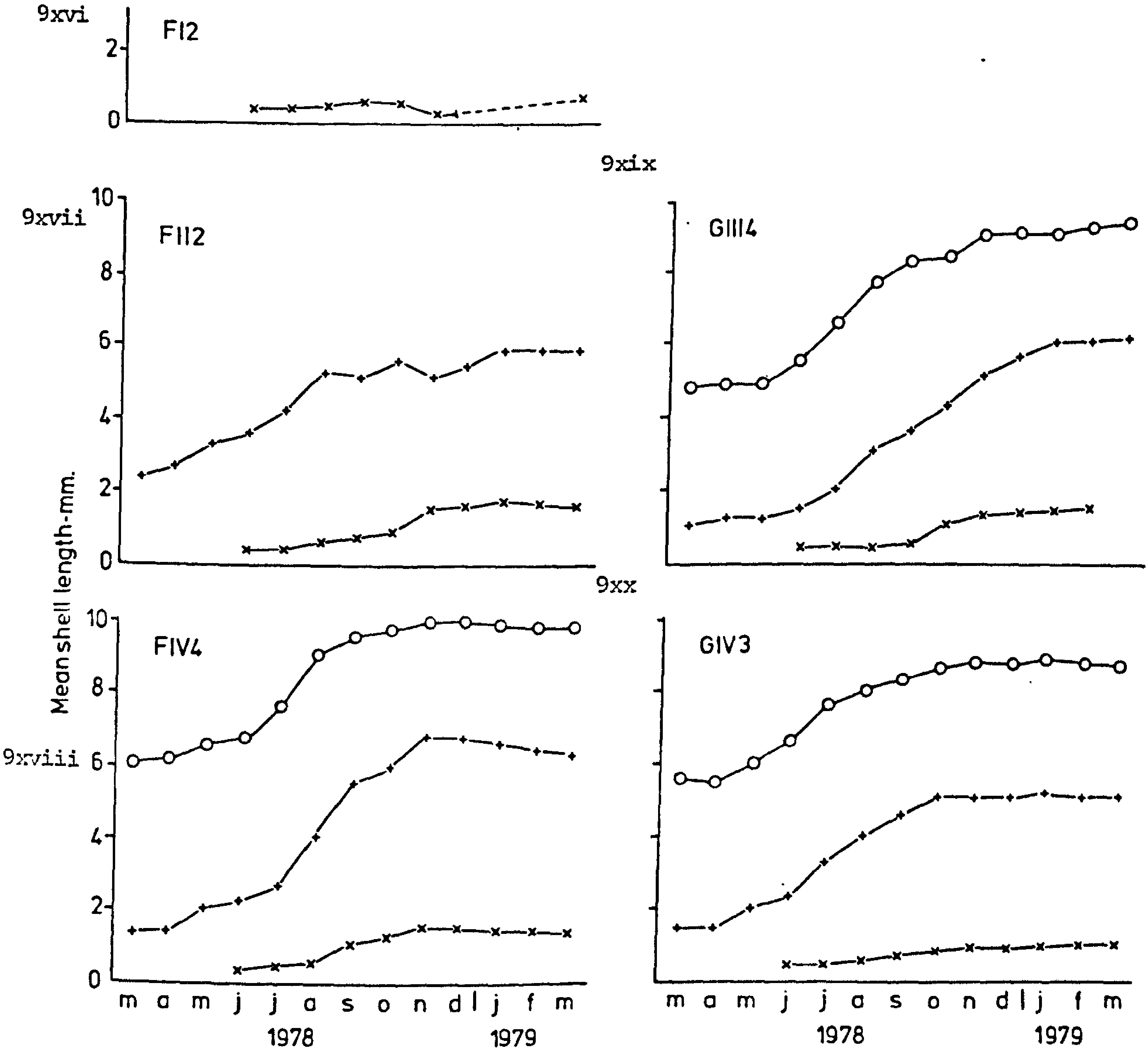
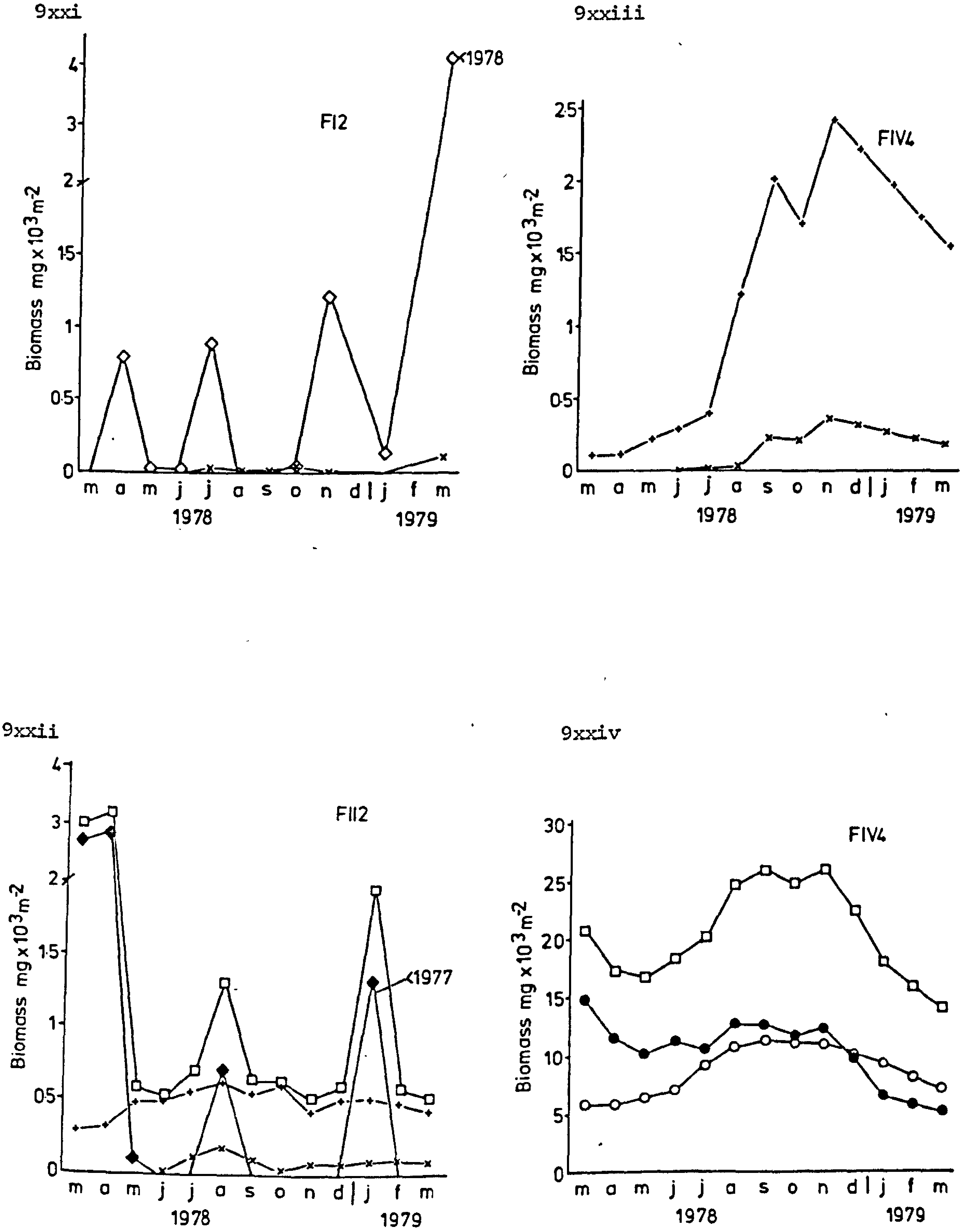


Figure xv Population structure of Macoma balthica, station GIV3, March 1978 - March 1979. Cohorts older than 1976 considered together.

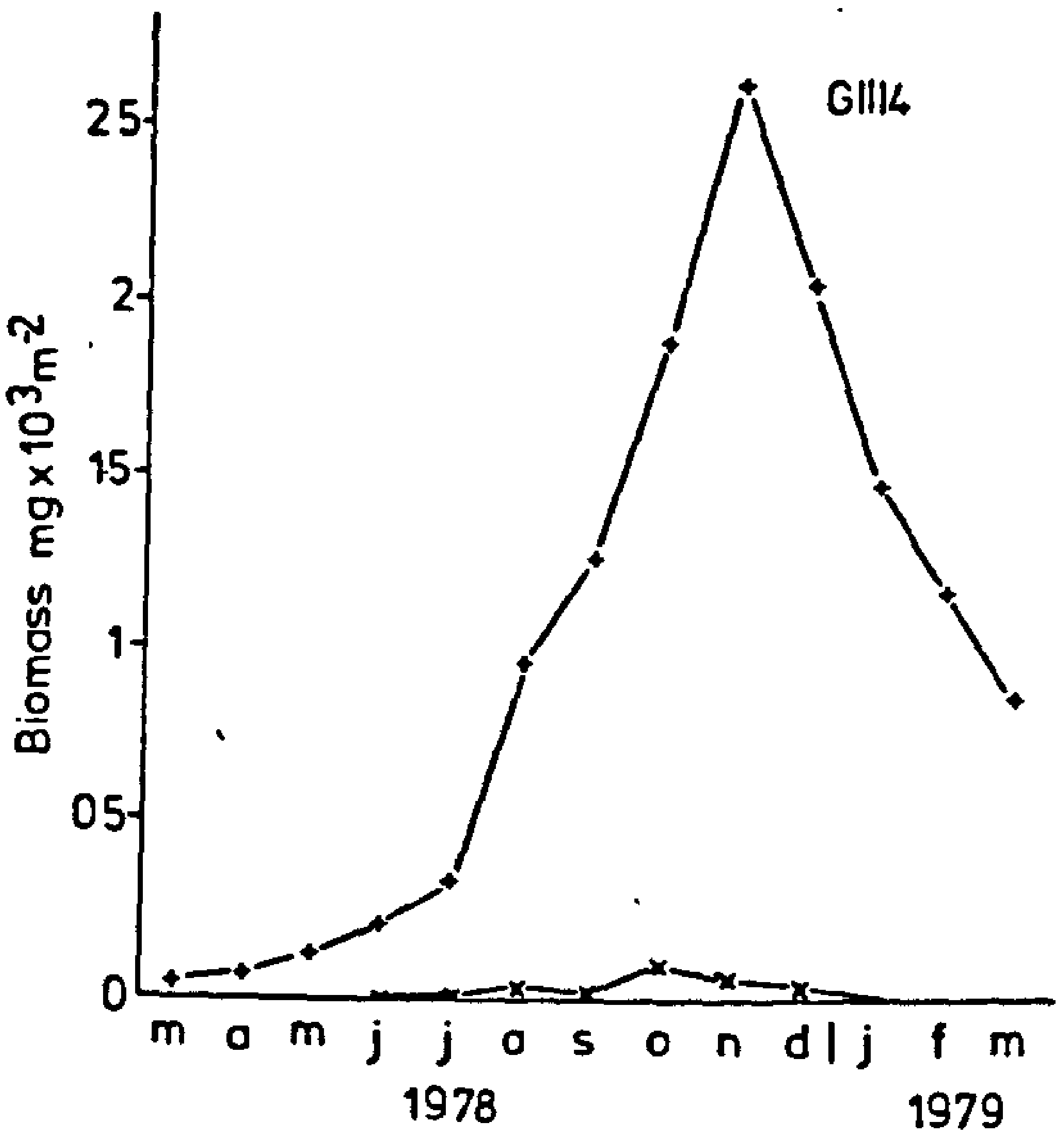


Figures 9xvi - 9xx Increase in mean shell length of individual cohorts of *Macoma balthica*. March 1978 - March 1979. Cohorts as Fig. 9vi.

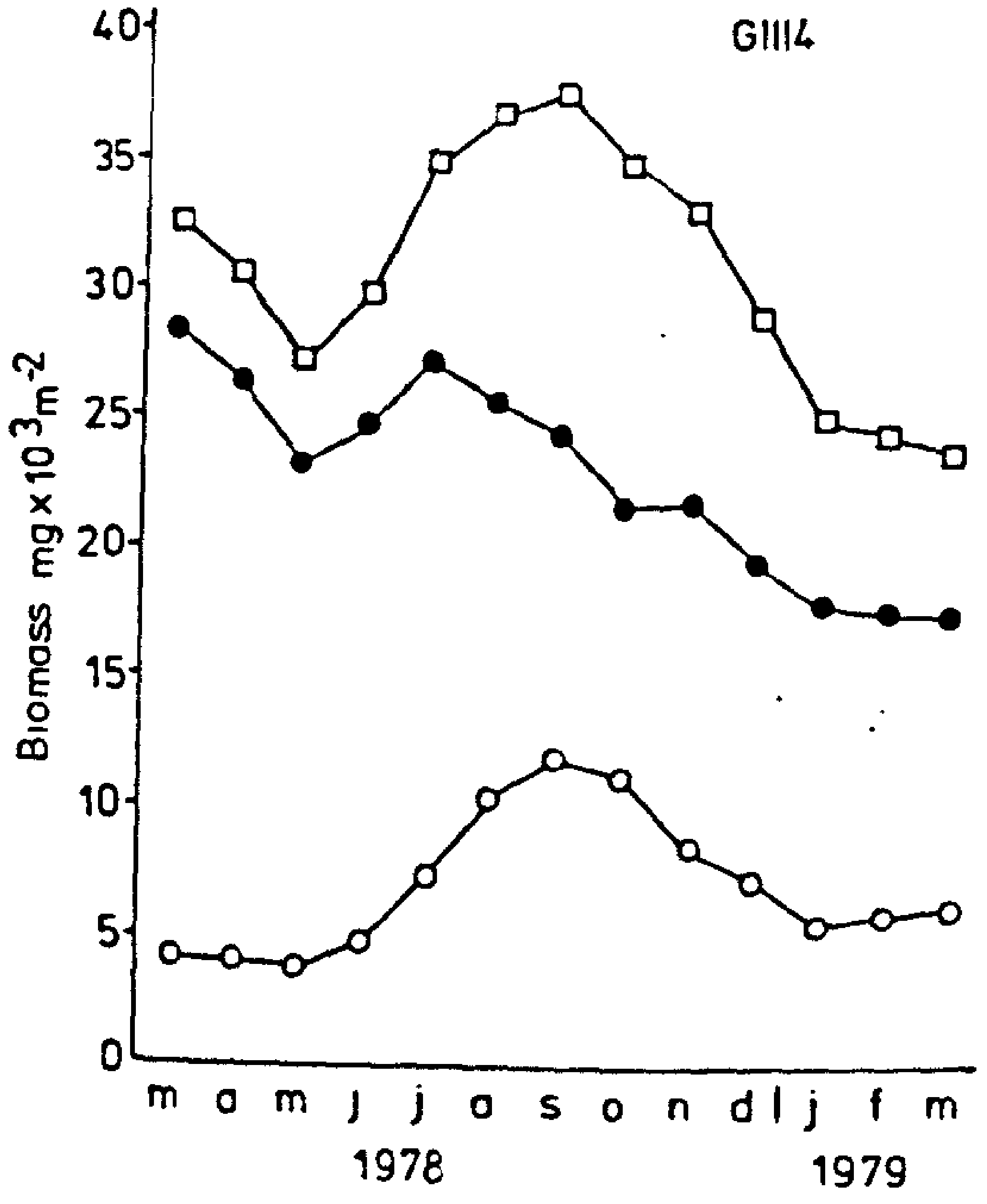


Figures 9xxi - 9xxiv Variation in total and cohort biomass of Macoma balthica. March 1978 - March 1979. Cohorts as Fig. 9vi. Youngest two cohorts on separate axes at station FIV4.

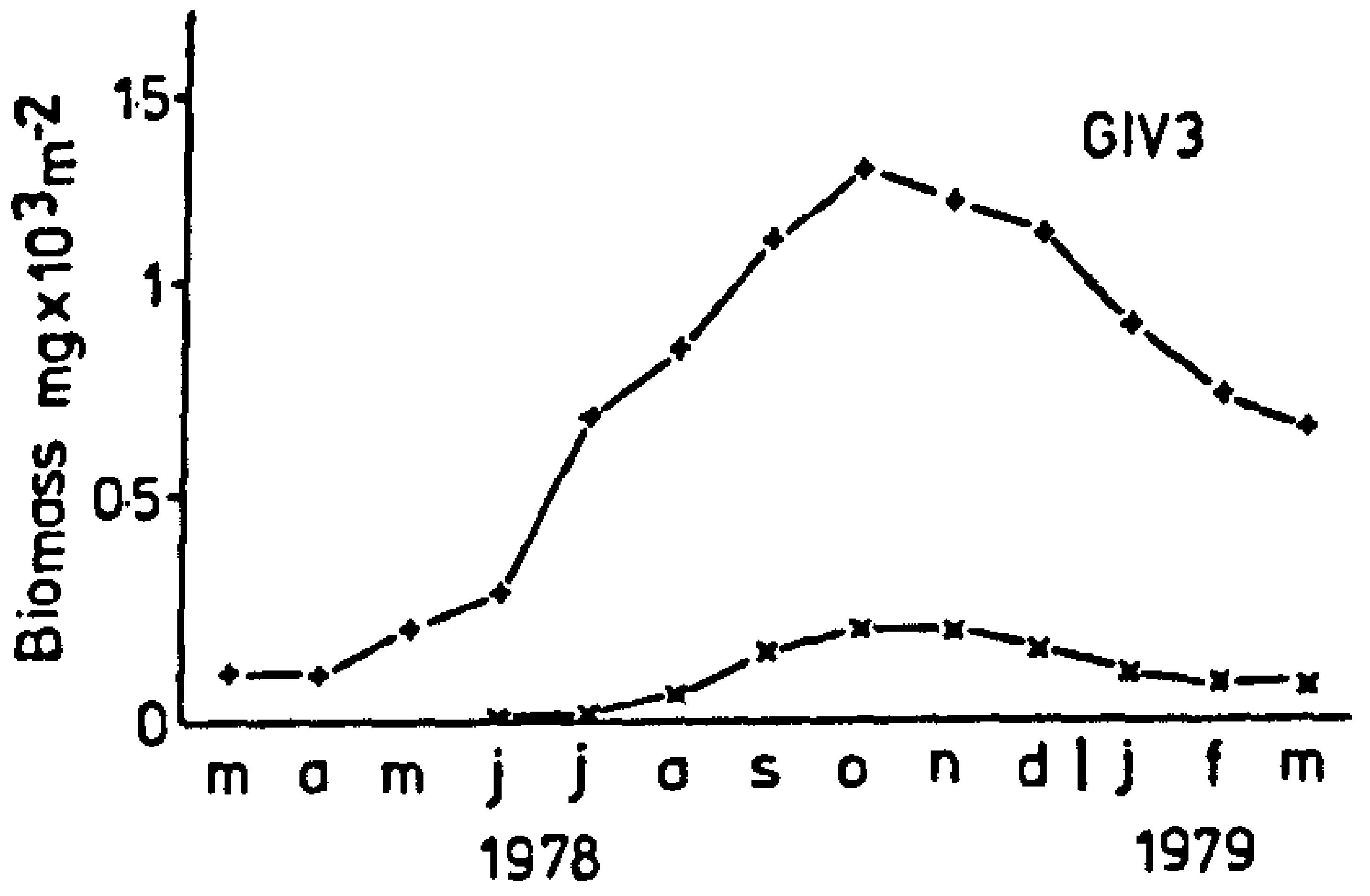
9xxv



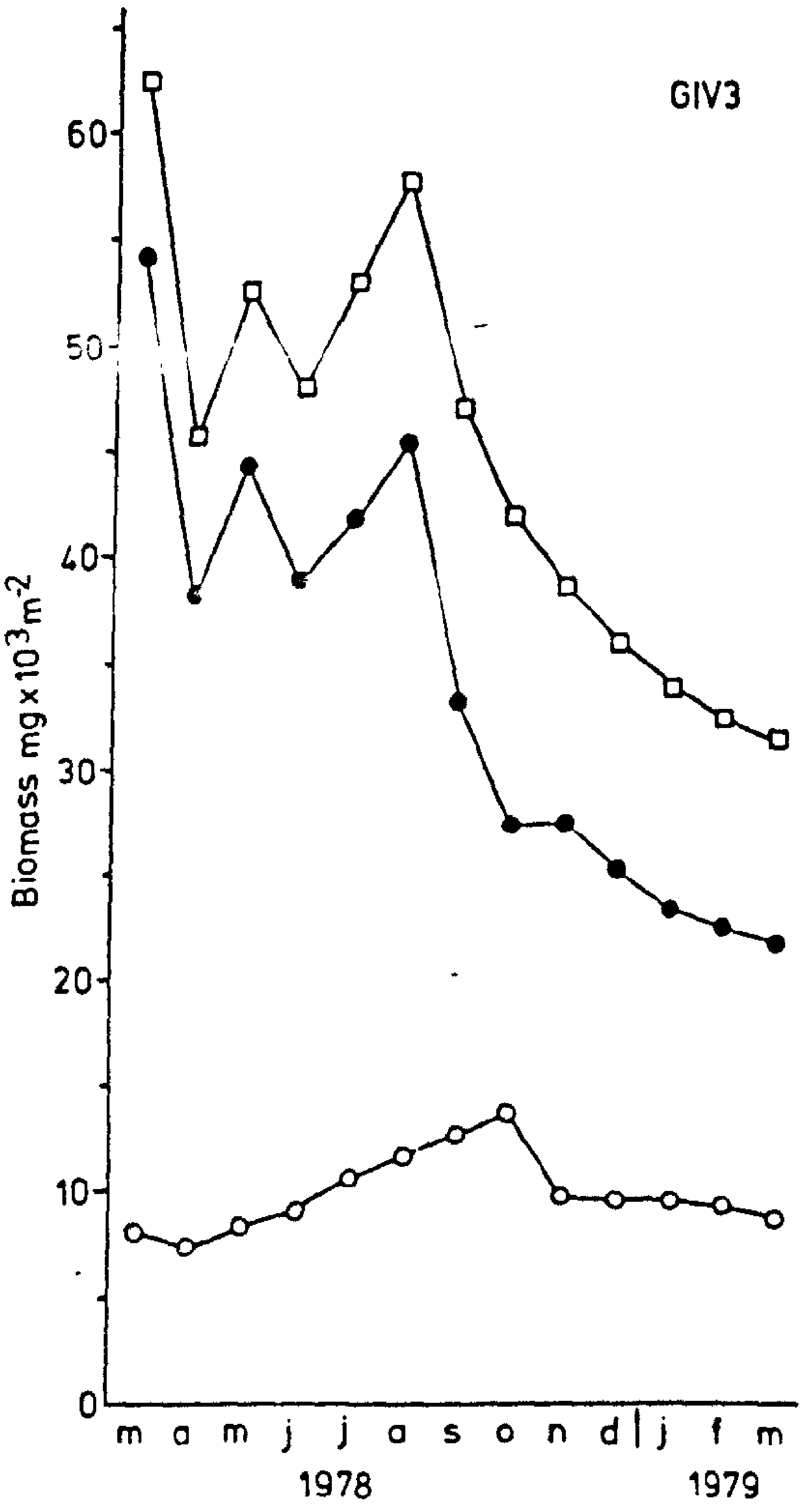
9xxvi



9xxvii



9xxviii

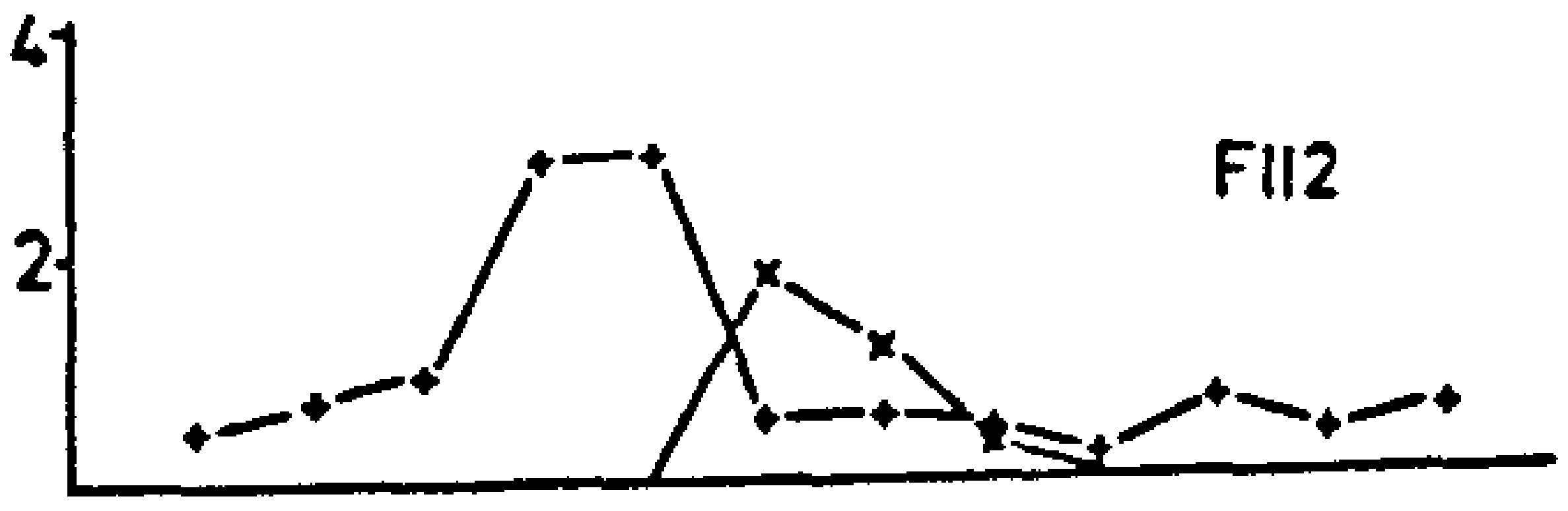


Figures 9xxv - 9xxviii Variation in totalaand cohort biomass of Macoma balthica. March 1978 - March 1979. Cohorts as Fig. 9vi. Youngest two cohorts on separate axes.

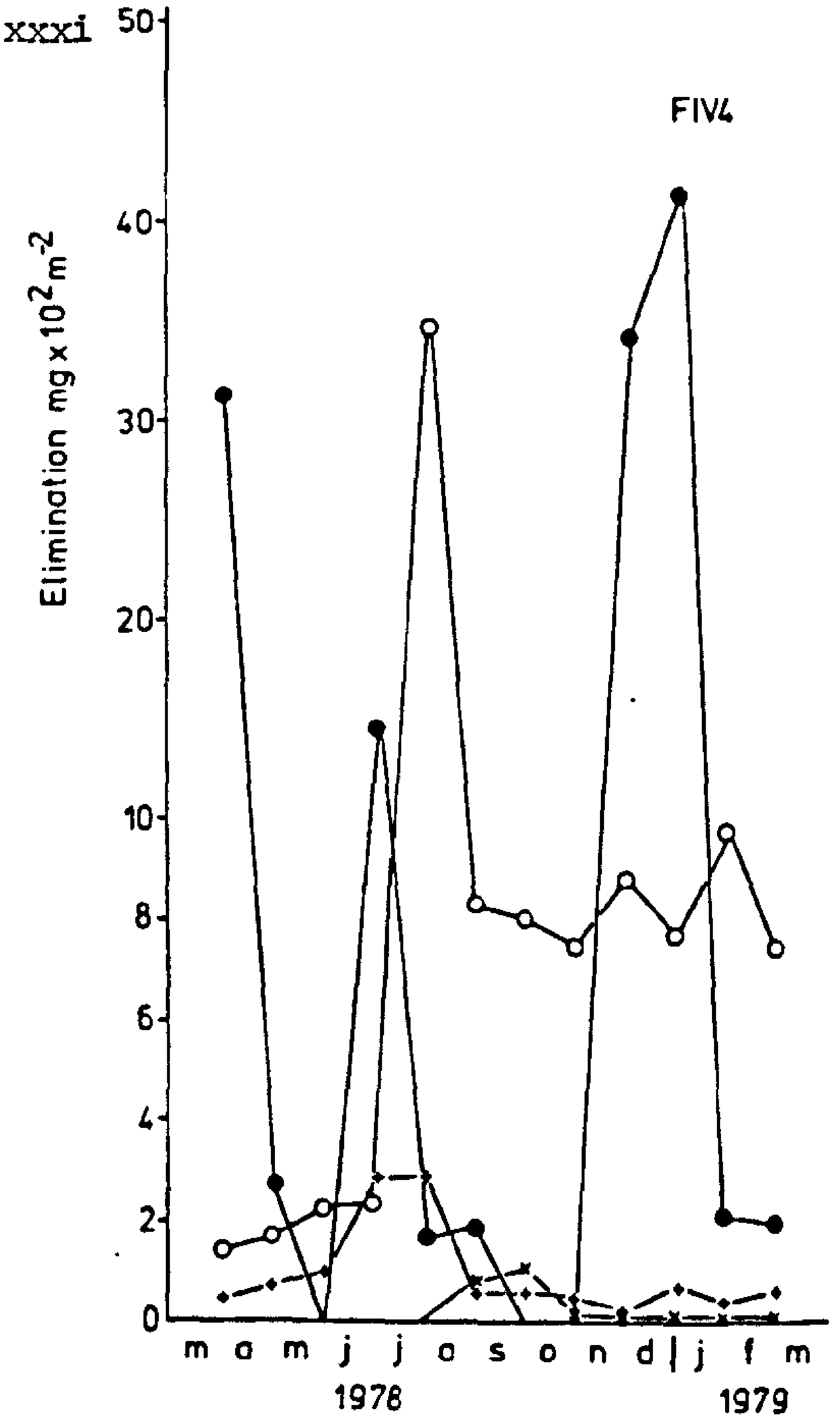
Figures 9xxix - 9xxxvii
Monthly cohort production and
elimination by *Macoma balthica*.
March 1978 - March 1979.
Cohorts as Fig. 9vi.

9xxix

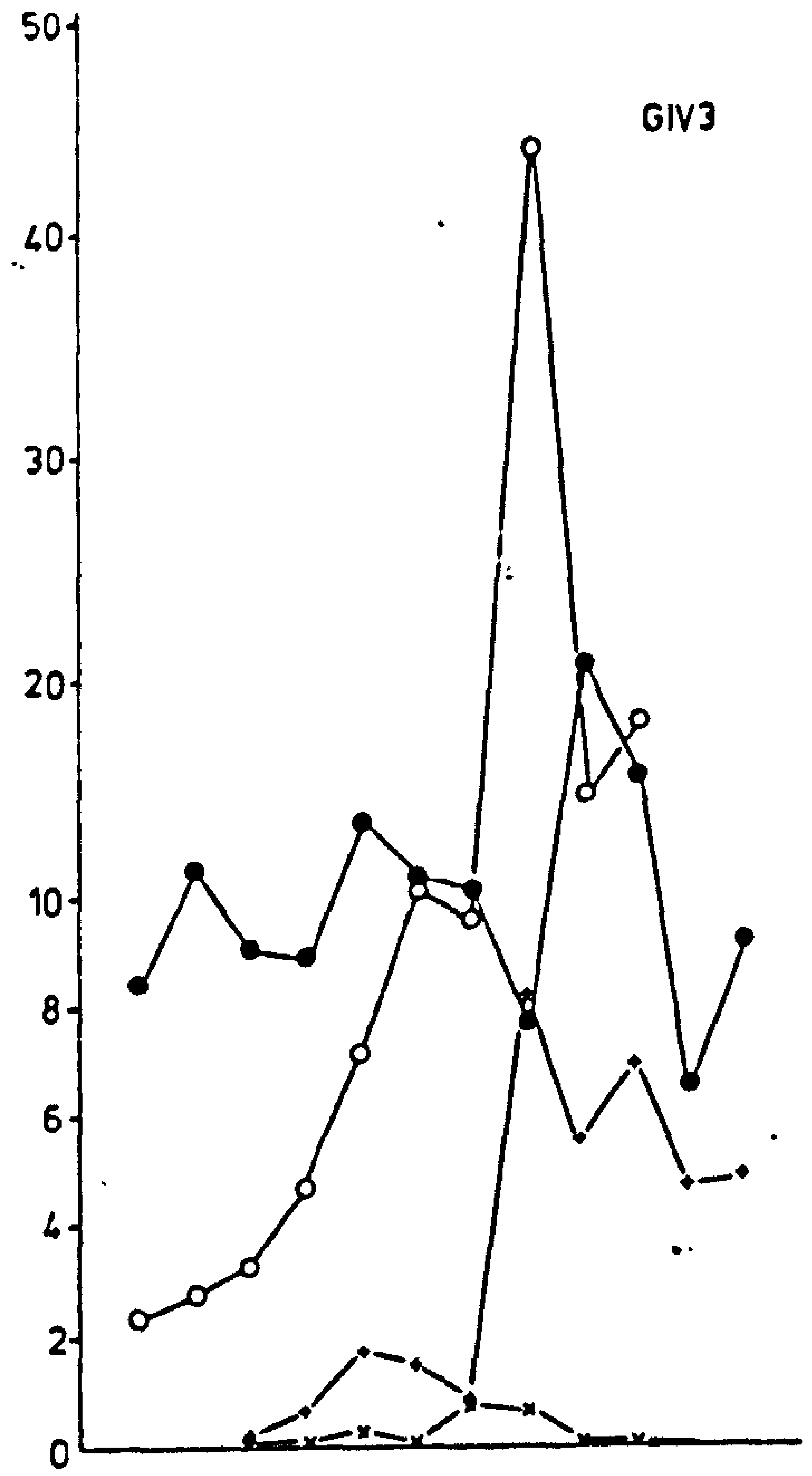
9xxx



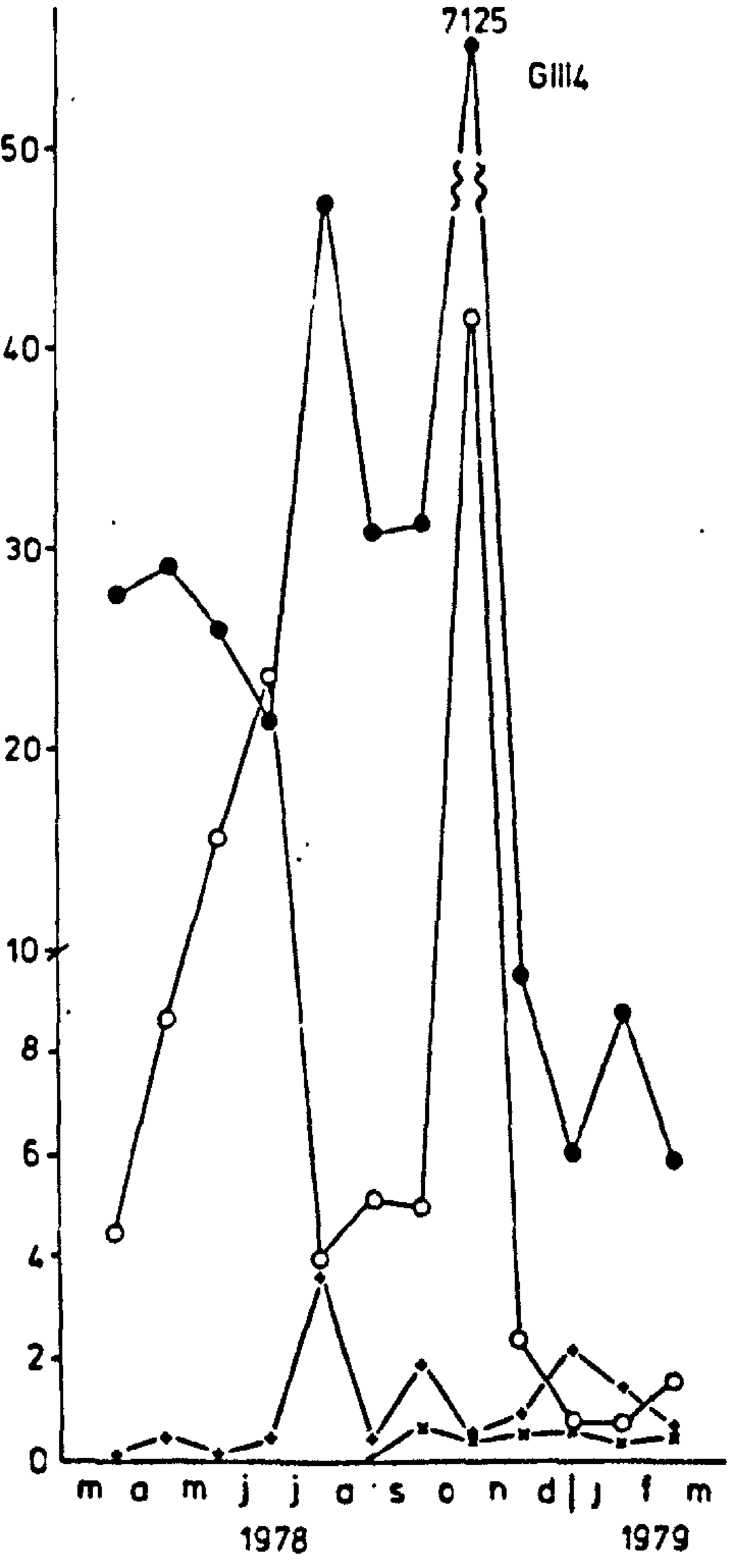
9xxxi



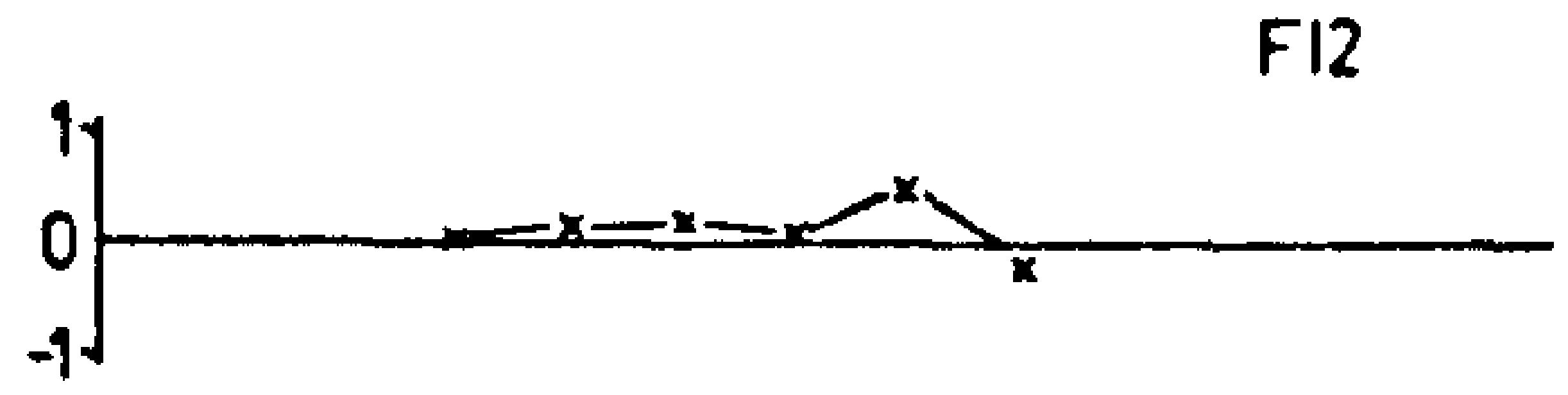
9xxxii



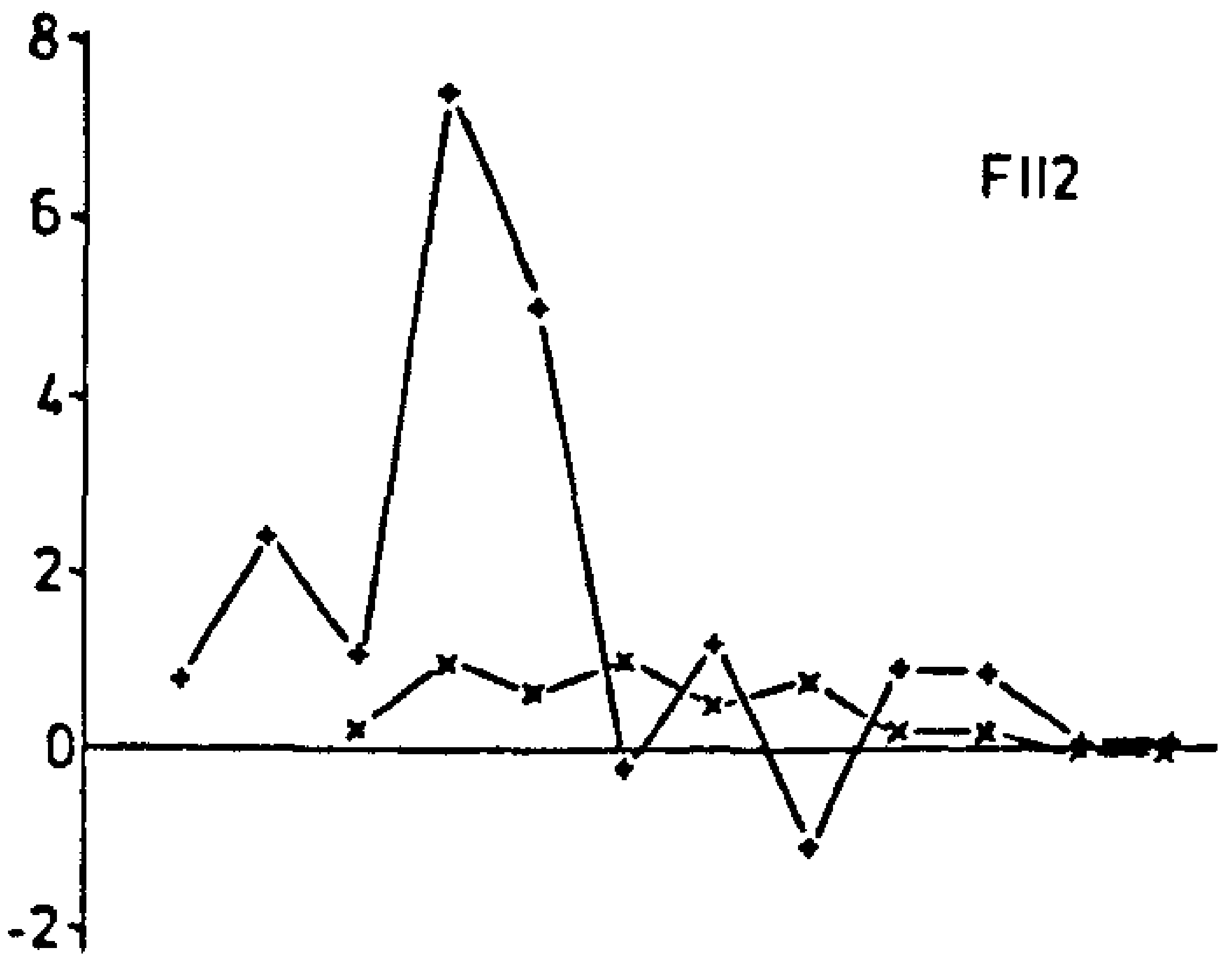
9xxxiii



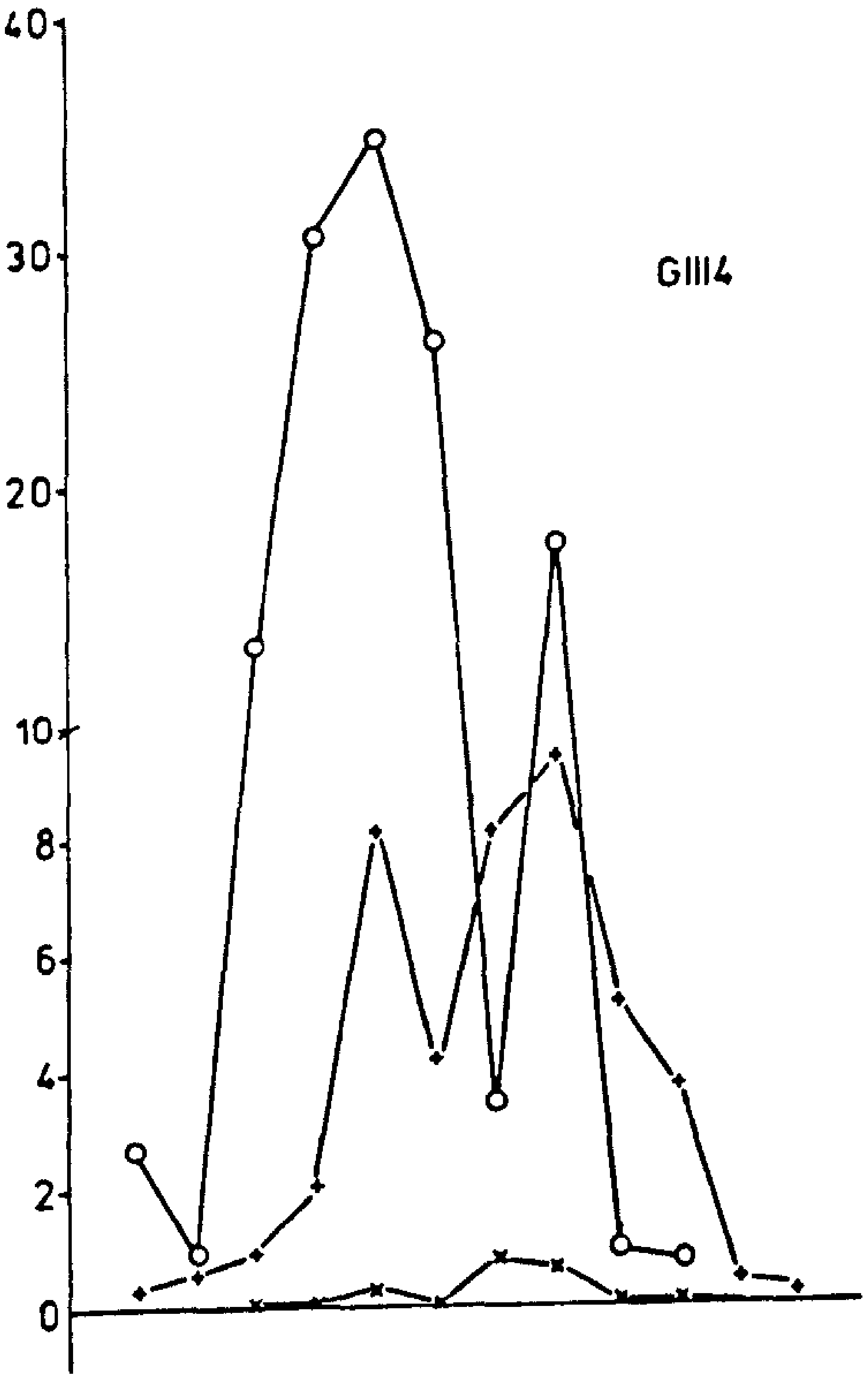
9xxxiv



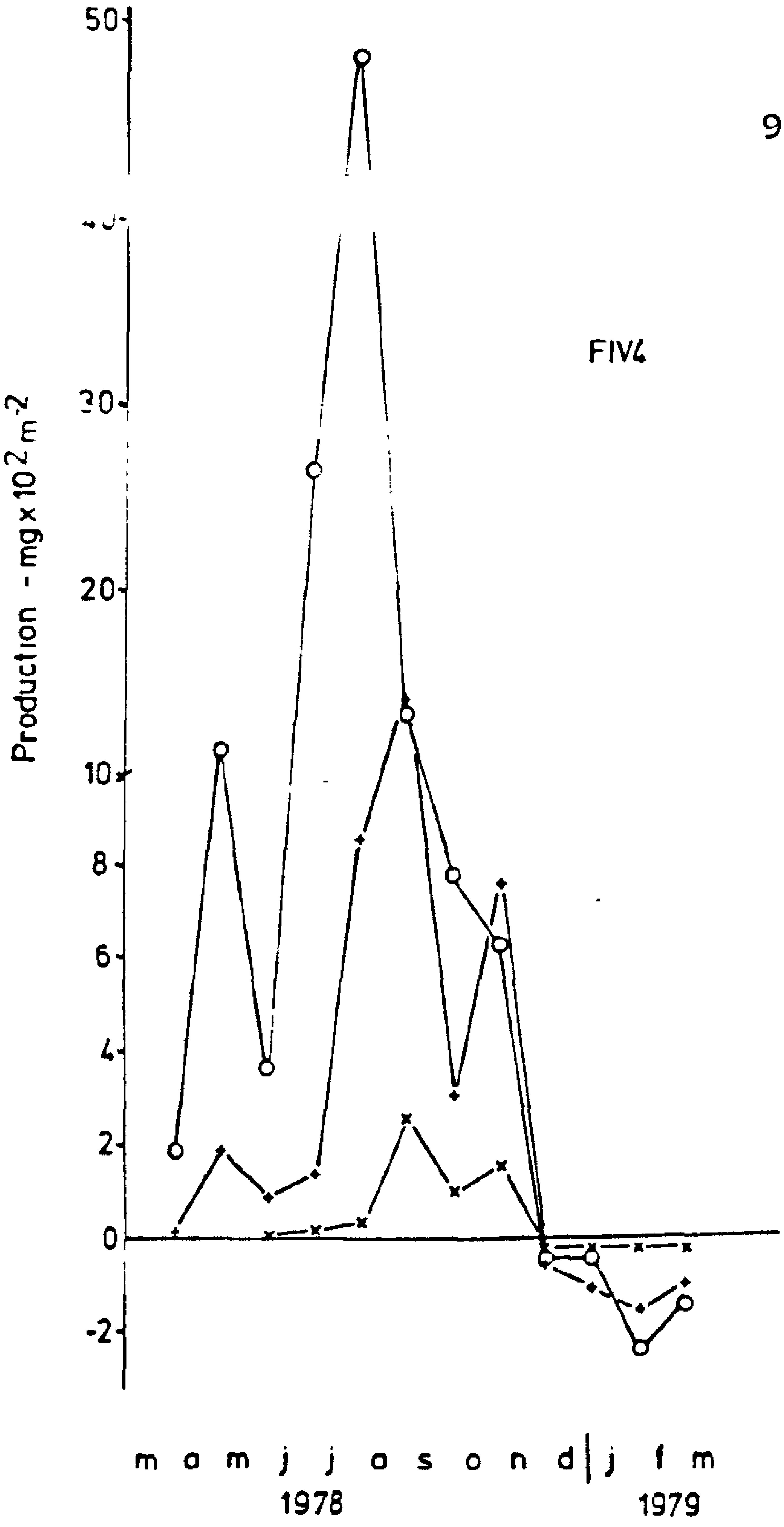
9xxxv



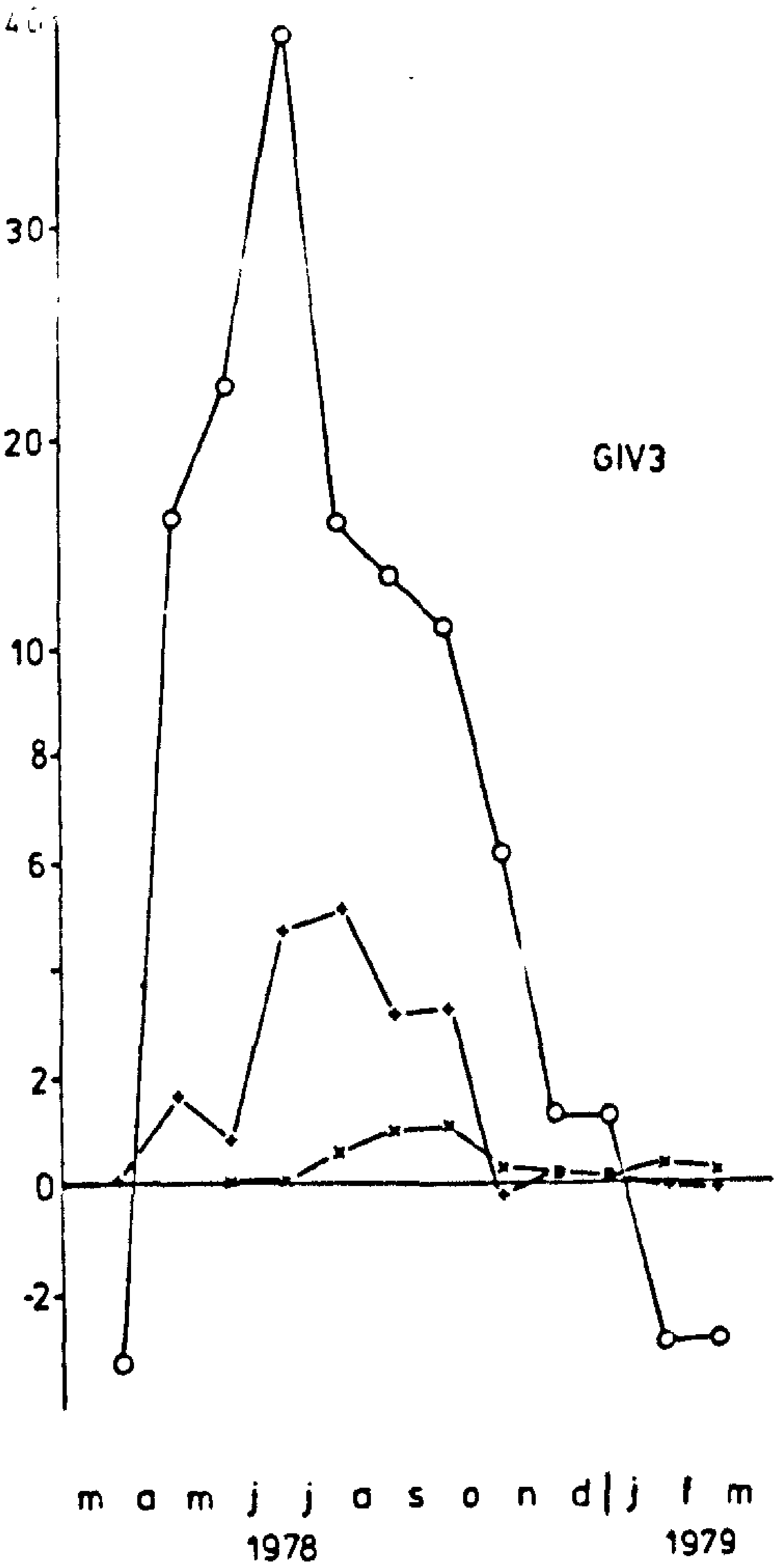
9xxxvi



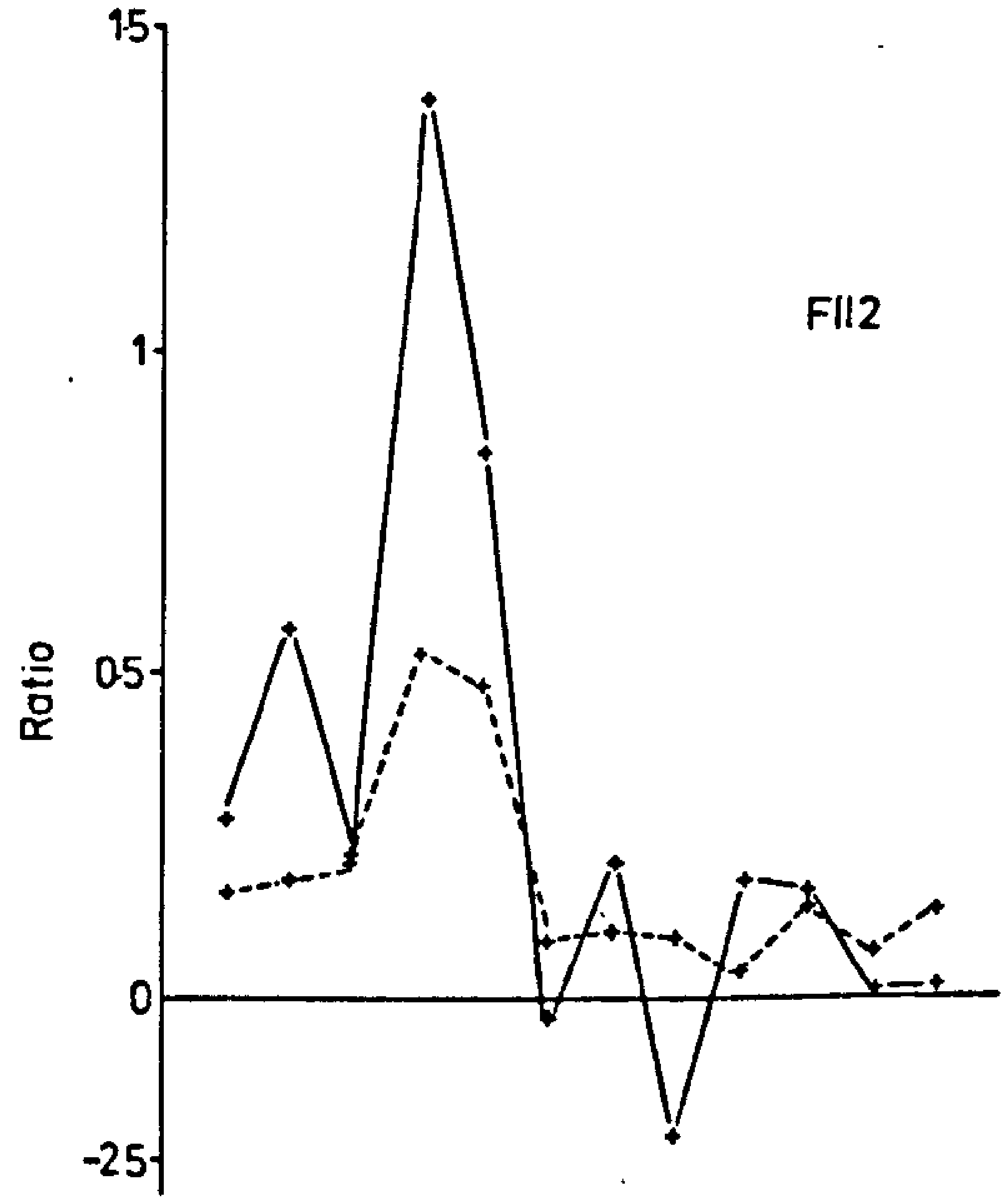
9xxxvi



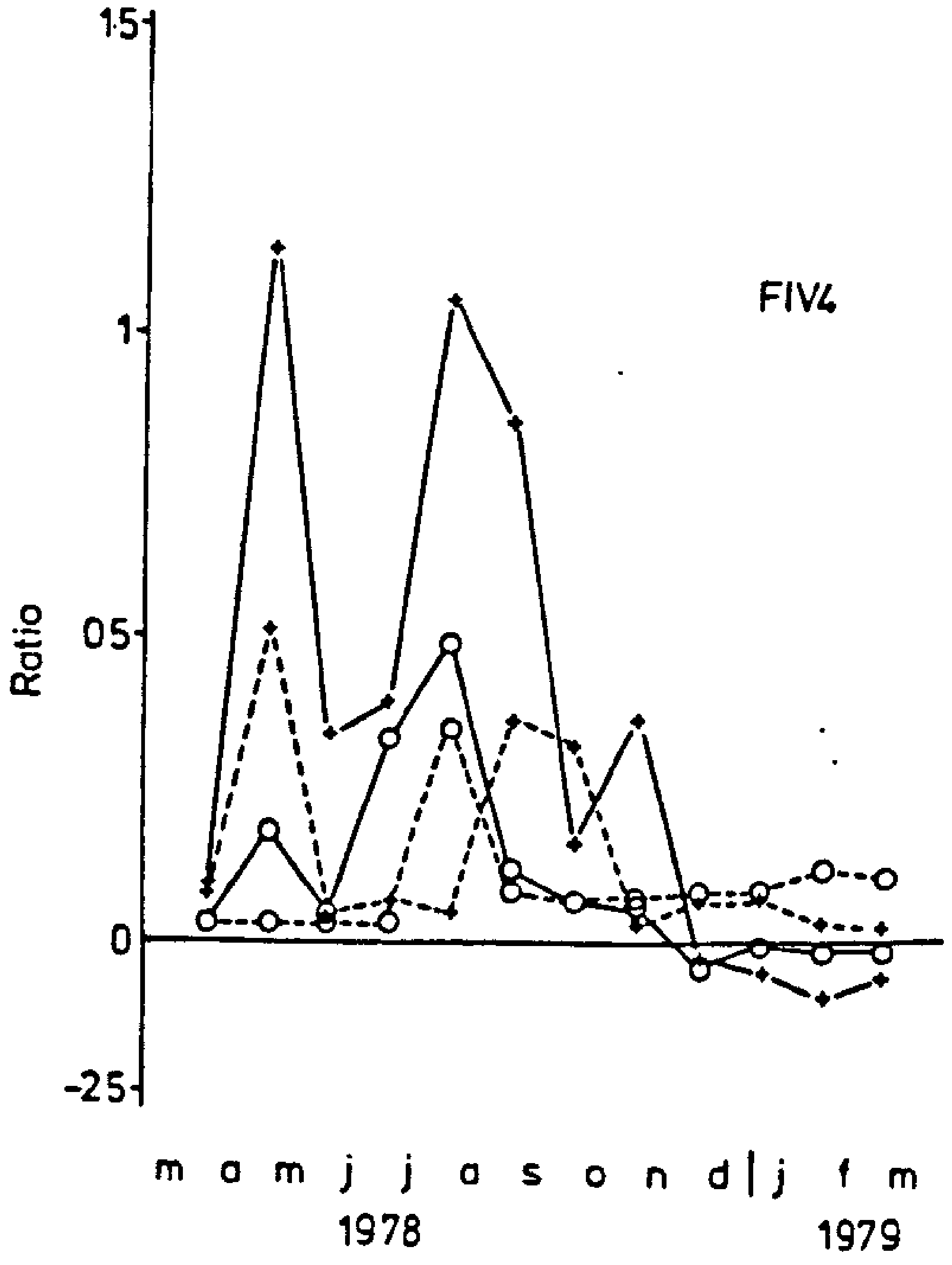
9xxxvii



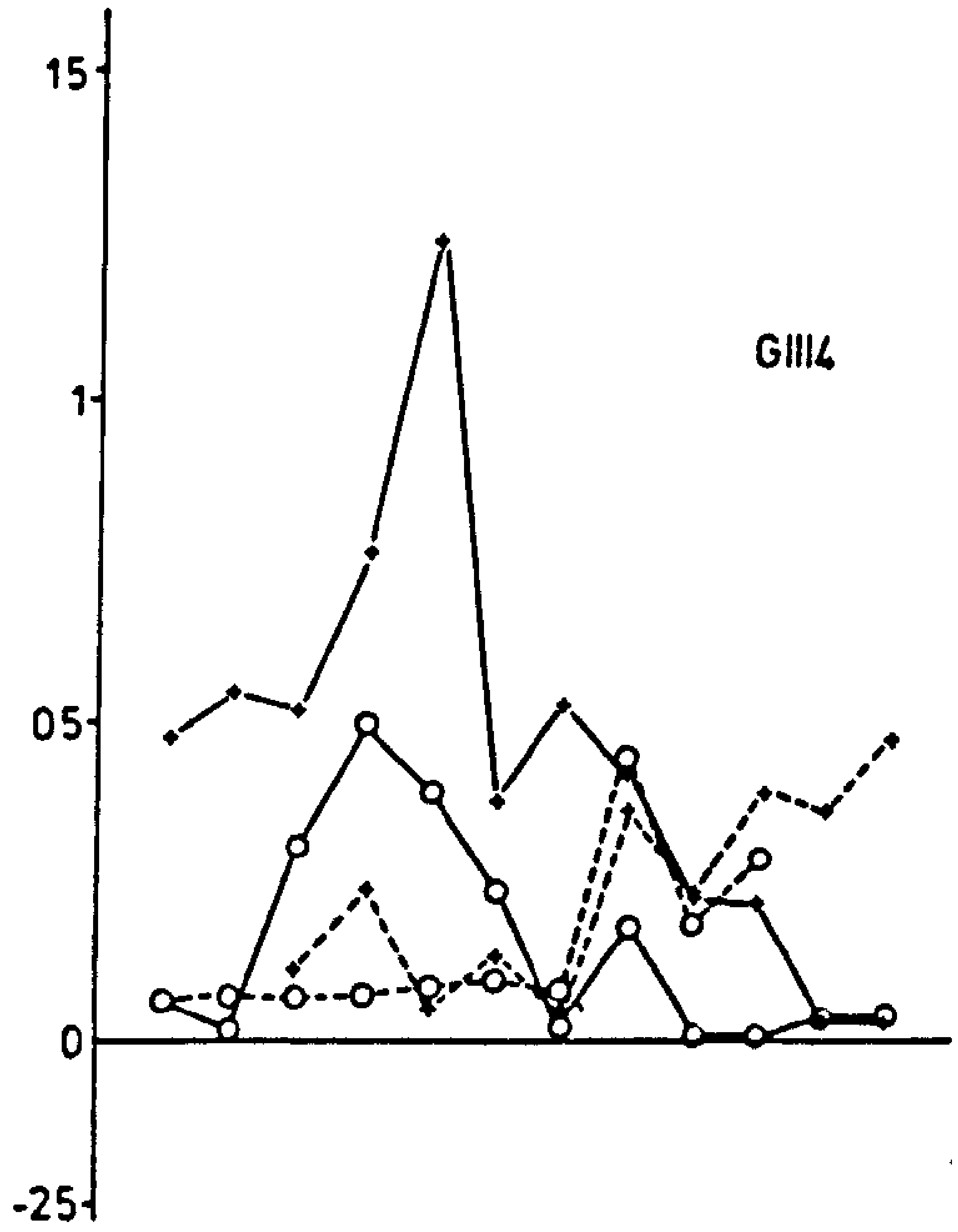
9xxxviii



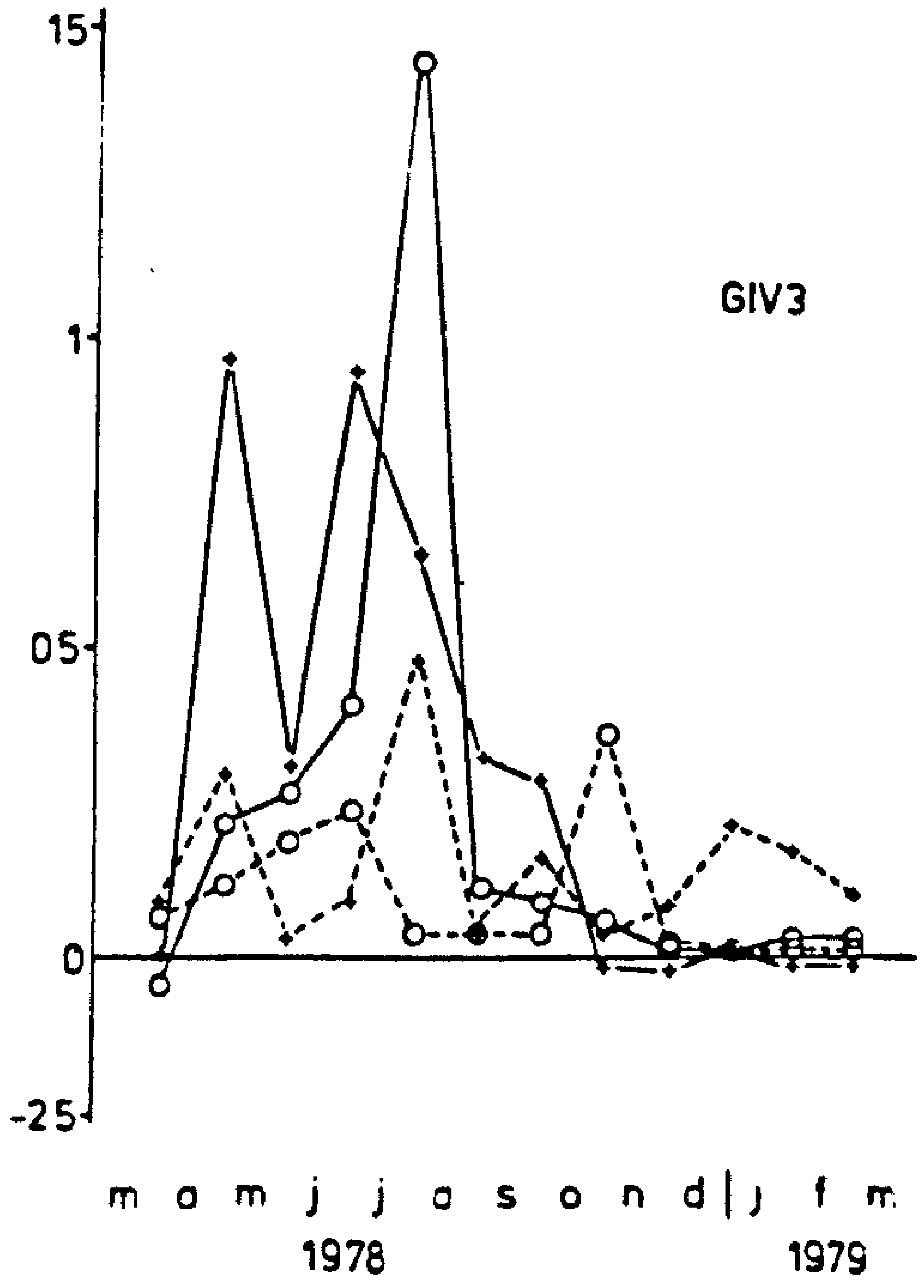
9xxxix



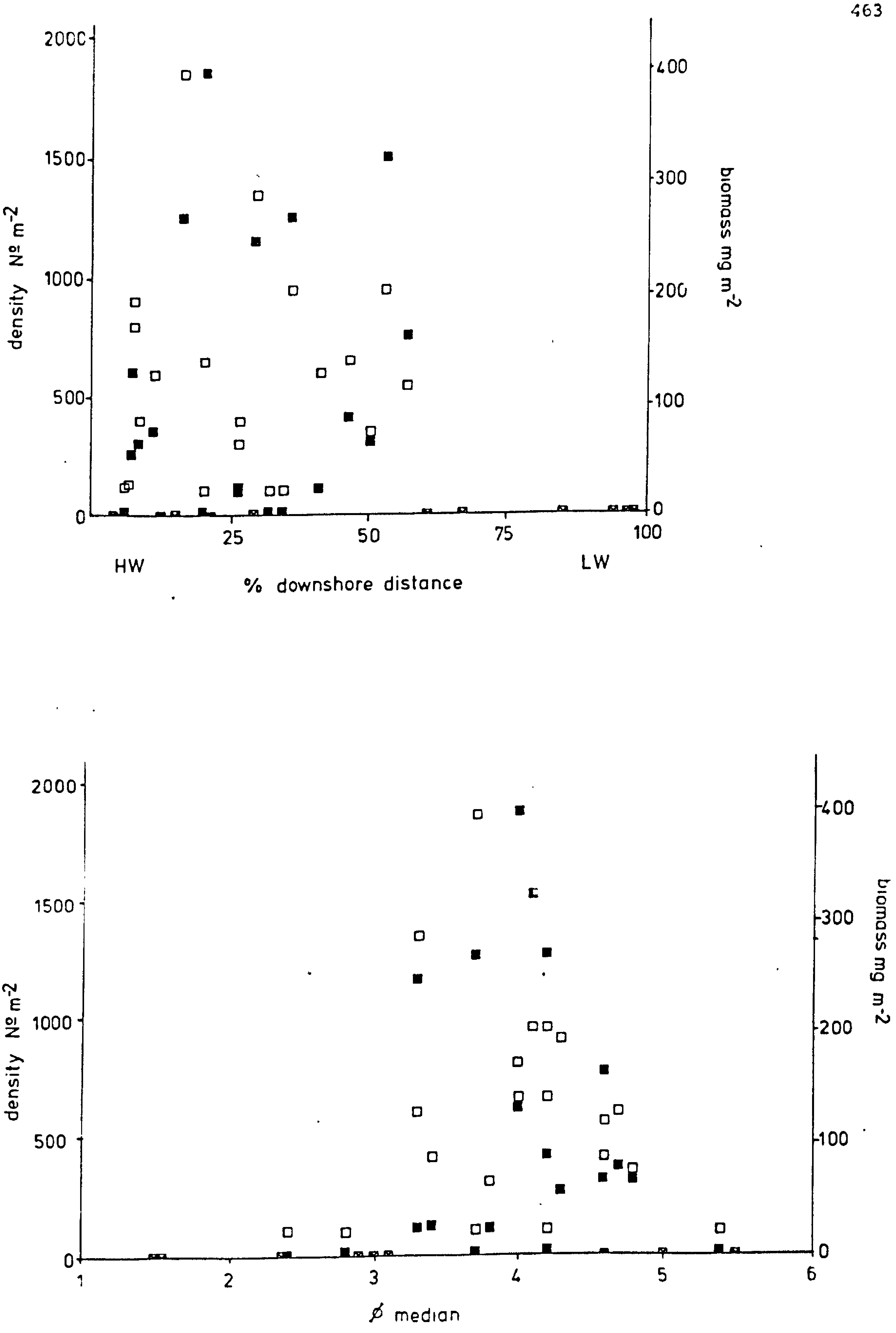
9xl



9xli



Figures 9xxxviii - 9xli Monthly P:B (solid lines) and E:B (dashed lines) ratios for Macoma balthica. March 1978 - March 1979. Cohorts as Figures 9vi



Figures 10i and 10ii Density (open squares) and biomass (closed squares) of <u>Retusa obtusa</u> in relation to tidal height and median particle diameter. Extensive survey, May/June 1977.

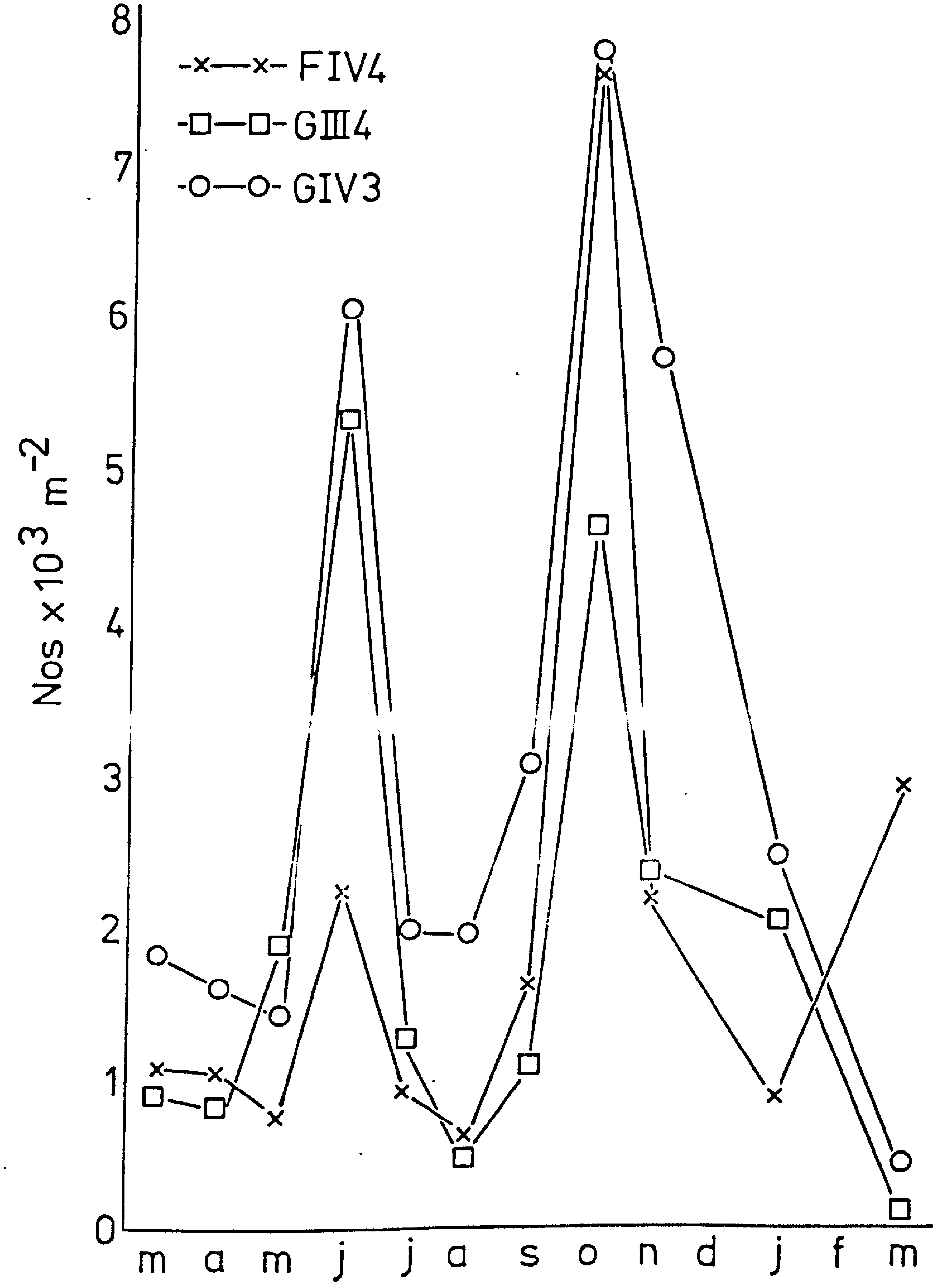


Figure 10iii Variation in density of <u>Retusa obtusa</u> - whole population. March 1978 - March 1979. All sites.

Figures 10iv, 10v and 10vi Cohort density of [illegible]usa obtus March 1978 - March 1979. Smoothed curve dotted.

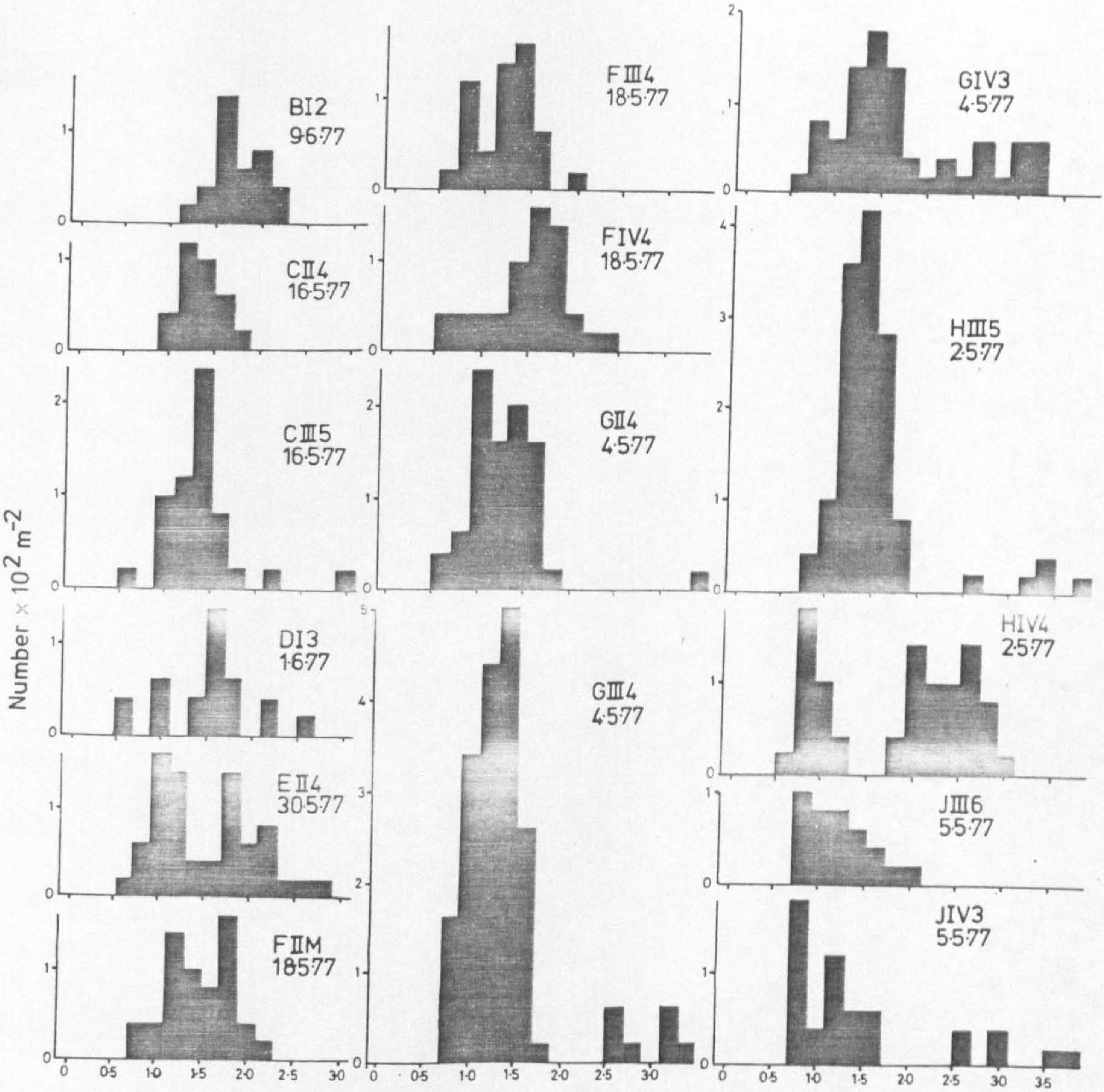


Figure 10vii Size/frequency distribution of *Retusa obtusa*. Extensive survey, May/June 1977. All sites.

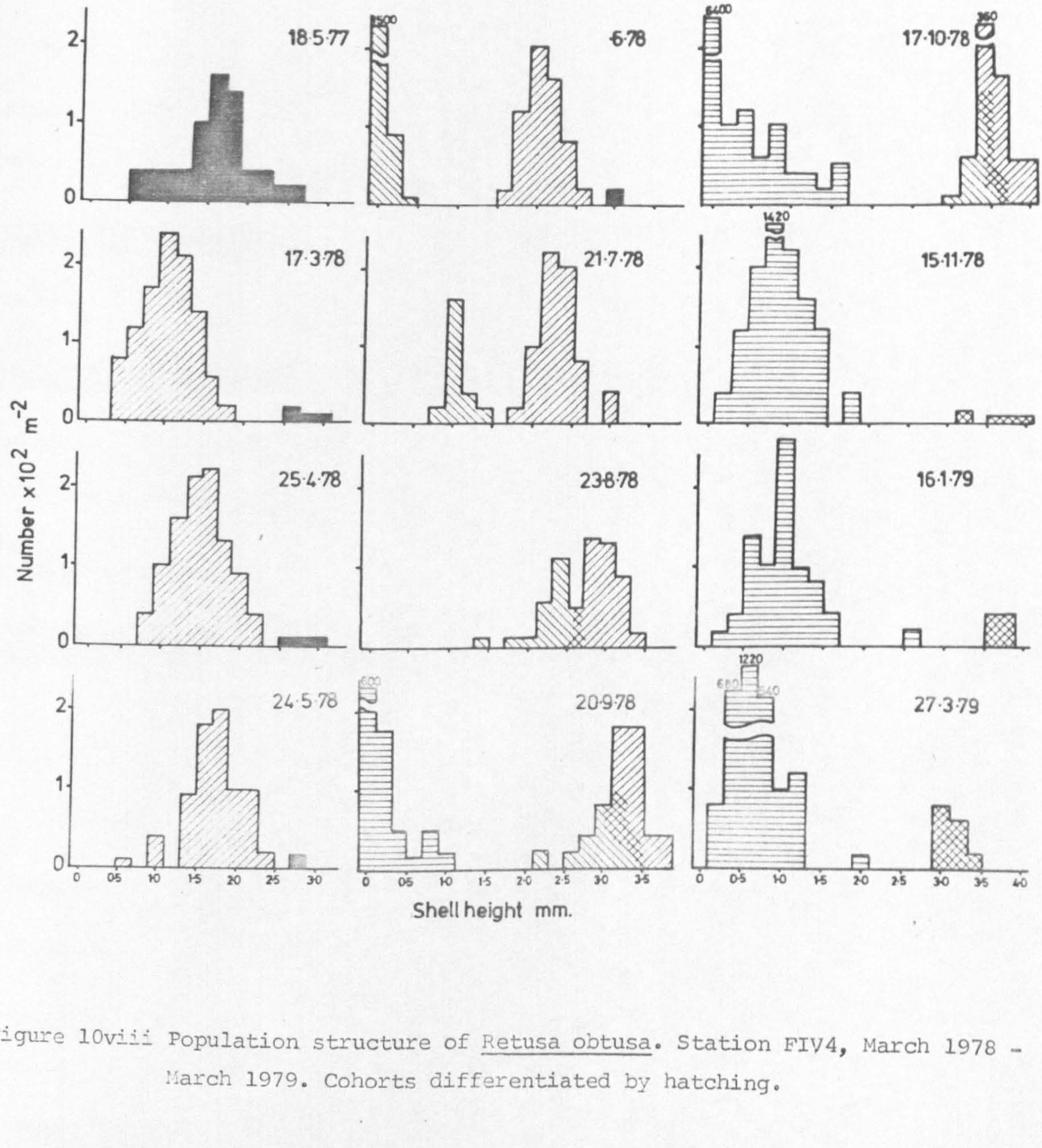


Figure 10viii Population structure of Retusa obtusa. Station FIV4, March 1978 - March 1979. Cohorts differentiated by hatching.

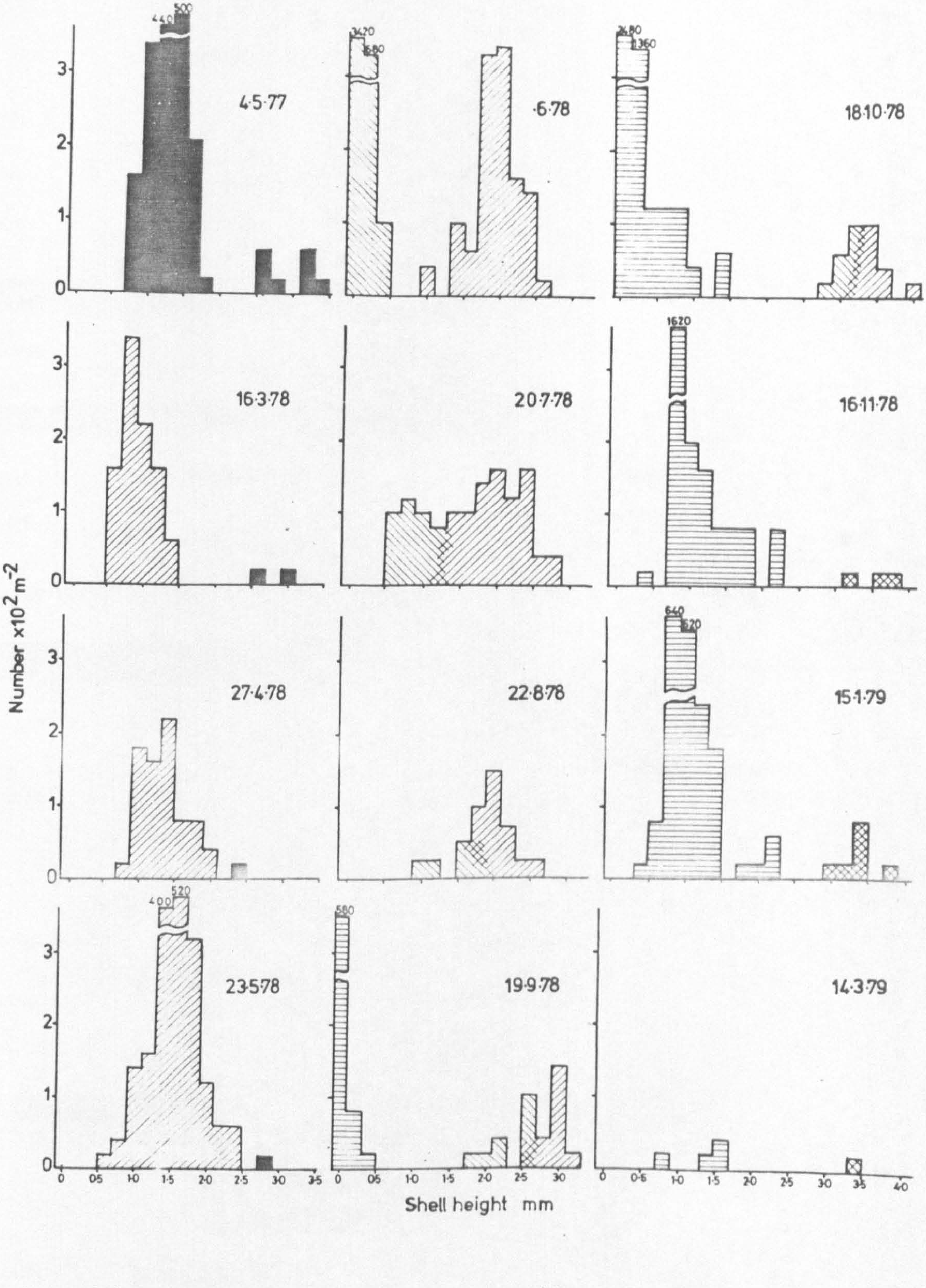


Figure 10ix Population structure of Retusa obtusa. Station GIII4 March 1978 – March 1979. Cohorts differentiated by hatching.

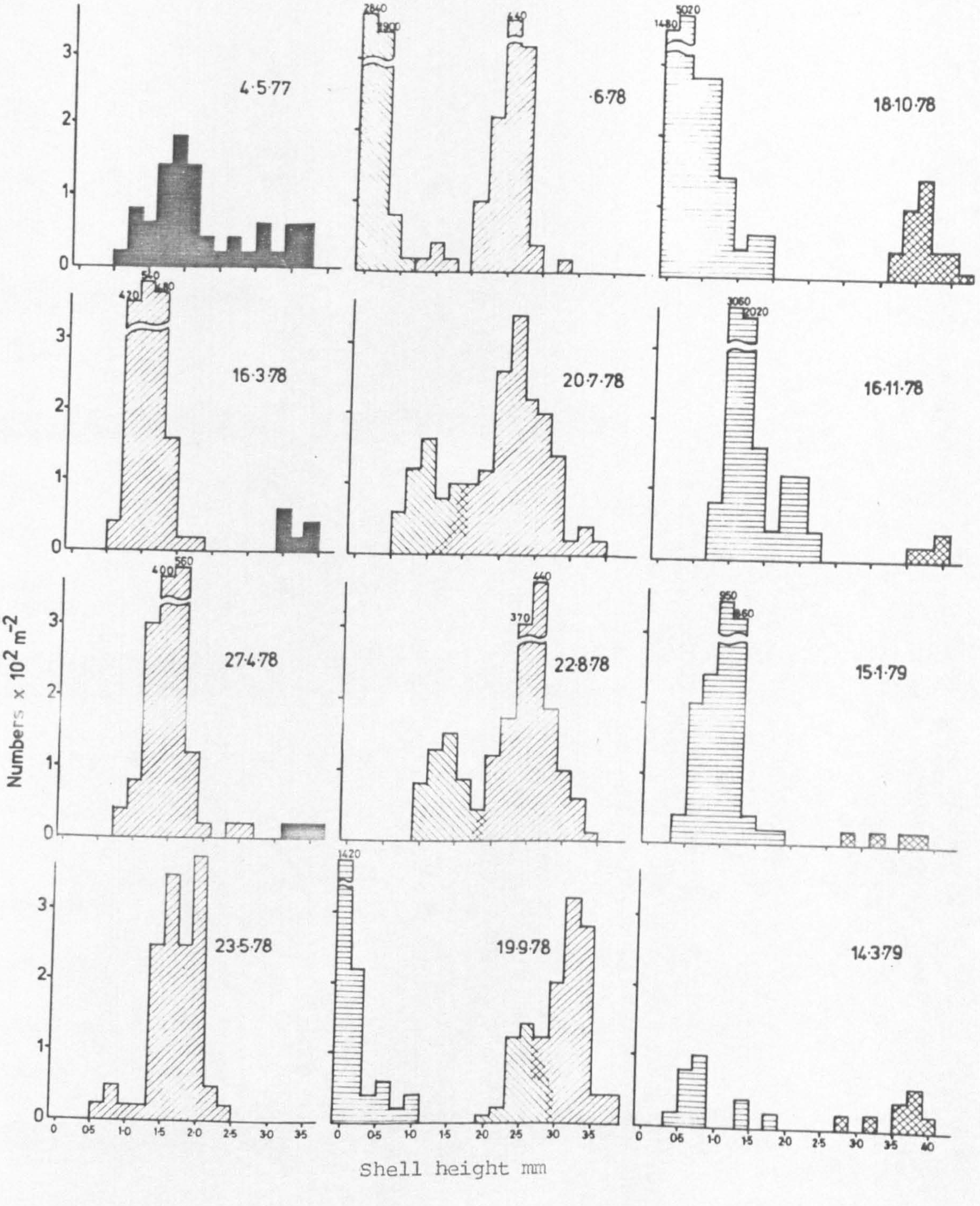


Figure 10x Population structure of Retusa obtusa. Station GIV3, March 1978 - March 1979. Cohorts differentiated by hatching.

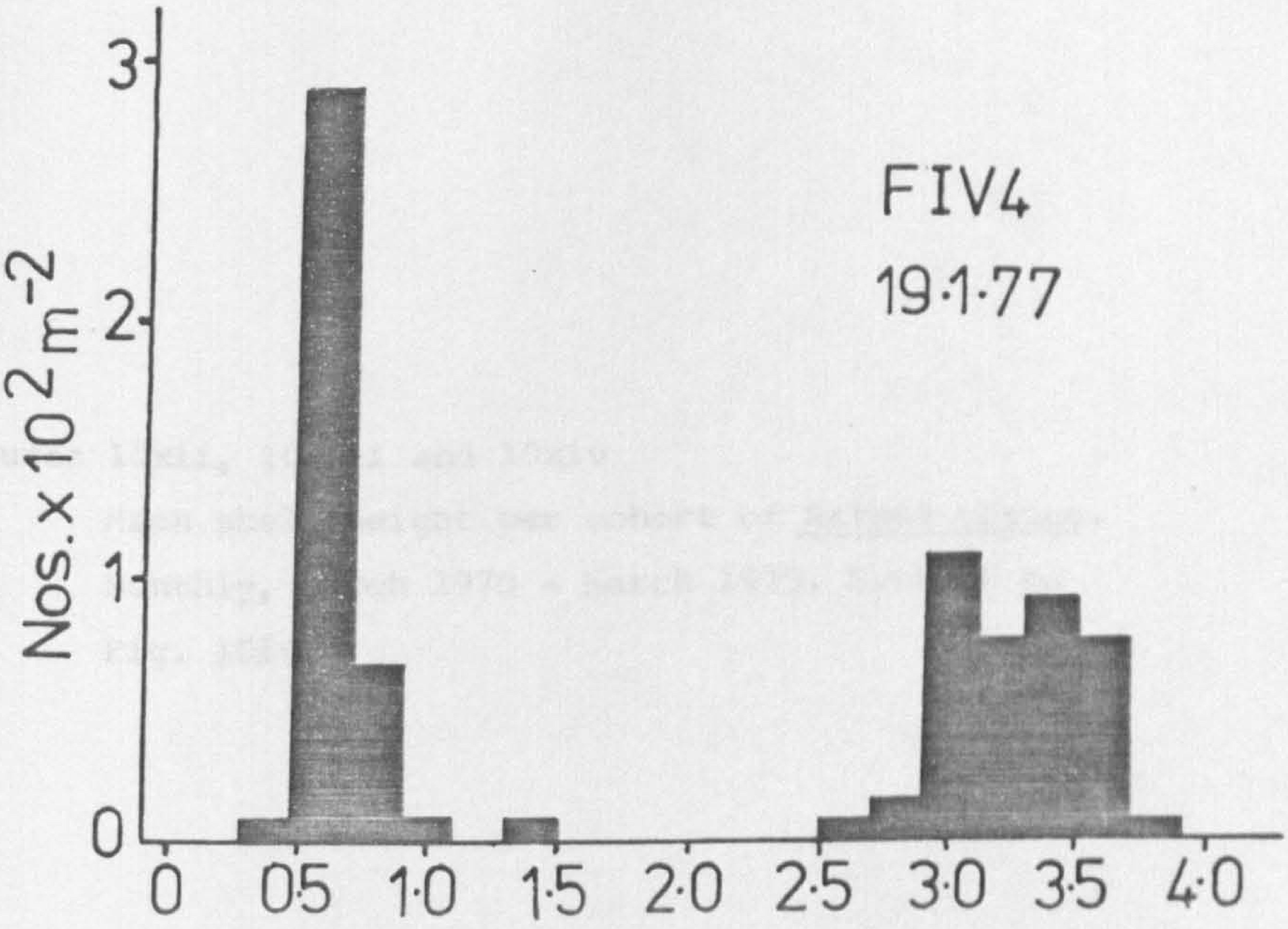


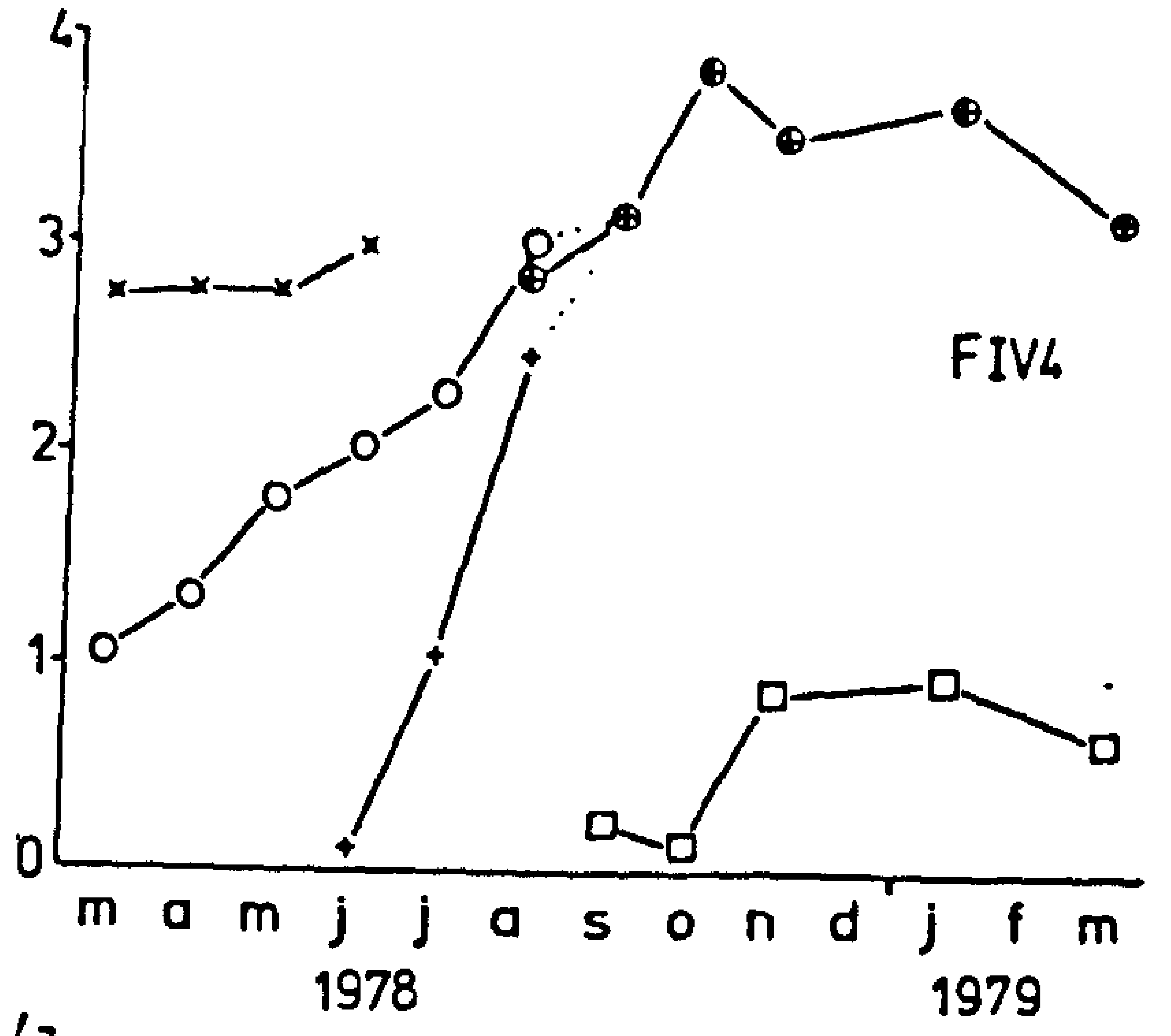
Figure 10xi Size/frequency distribution of <u>Retusa obtusa</u>. Station FIV4. January 1977.

Figures 10xii, 10xiii and 10xiv

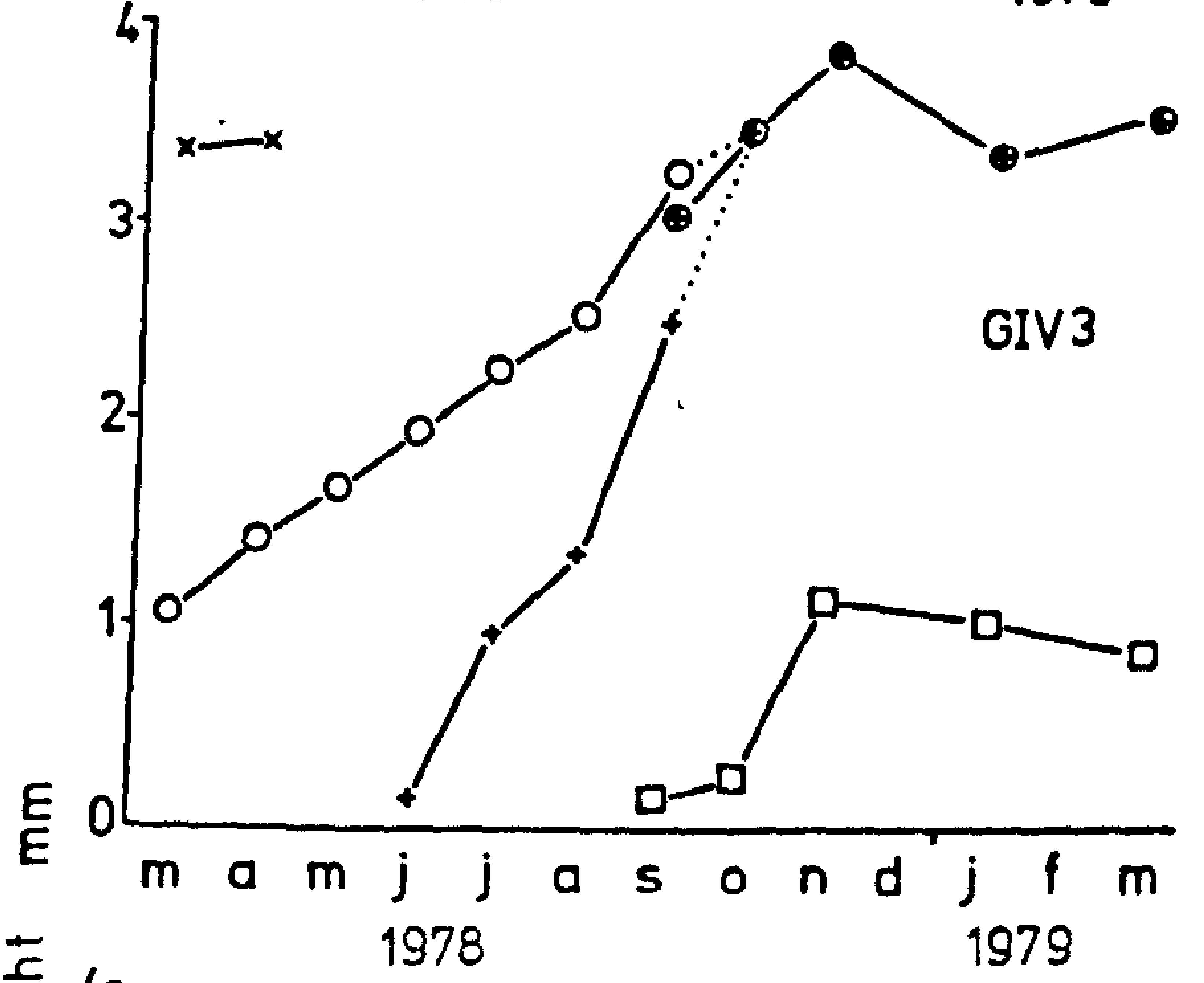
Mean shell height per cohort of Retusa obtusa. Monthly, March 1978 - March 1979. Symbols as Fig. 10iv.

Figure 10xv

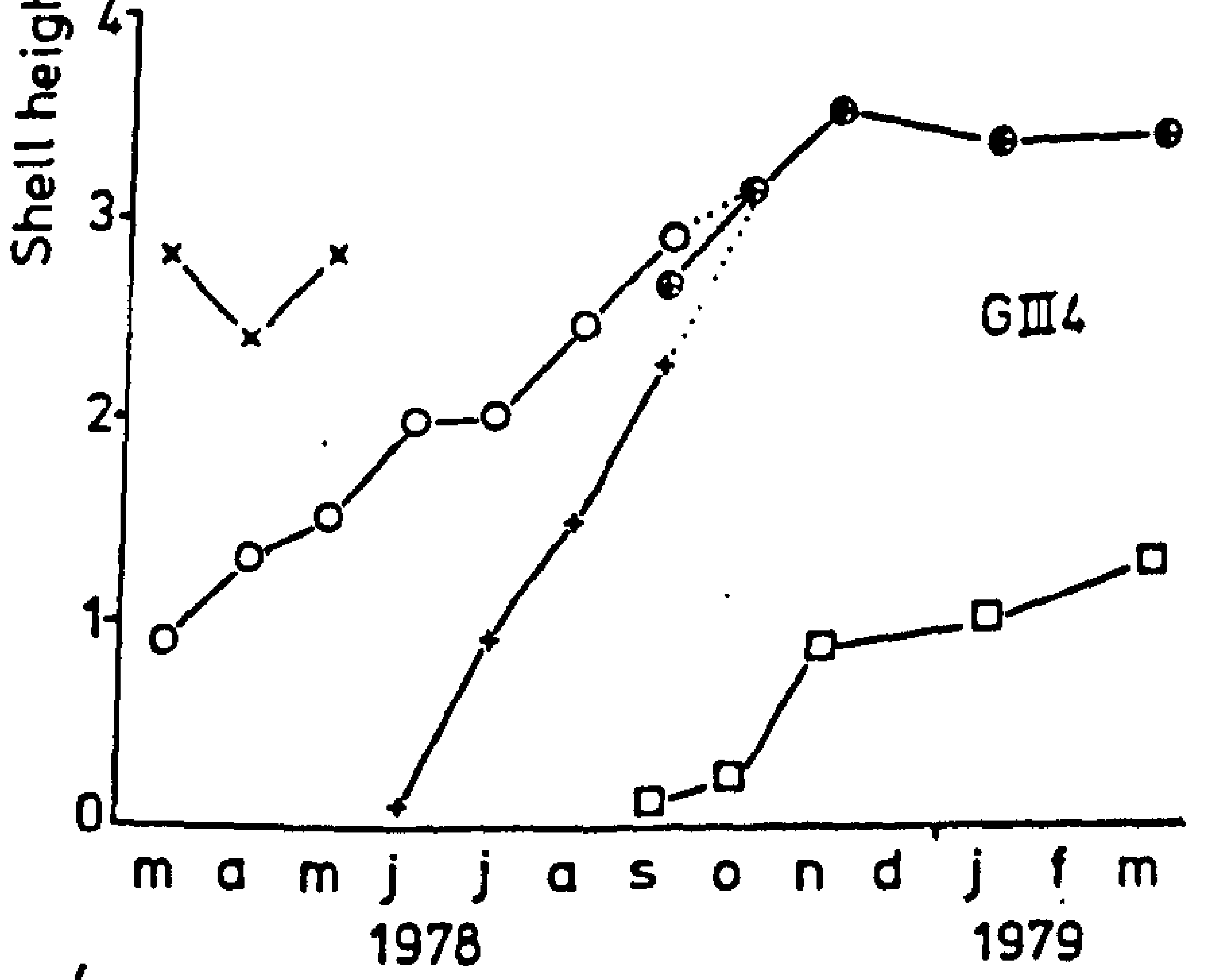
Mean shell height of Retusa obtusa. March 1964 - May 1965. Barry Harbour, South Wales. Data from Smith (1967a).



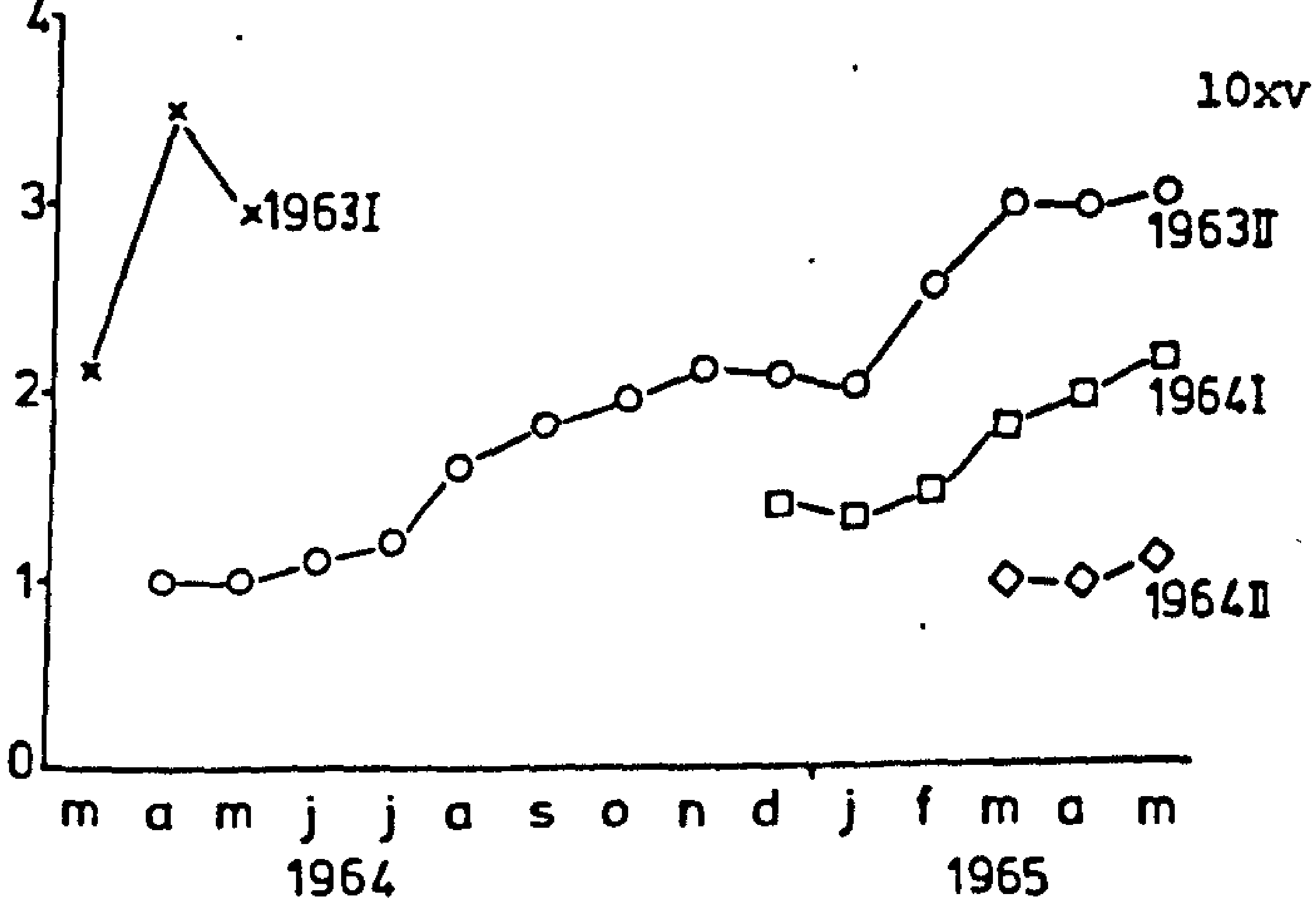
10xii



10xiii



10xiv



10xv

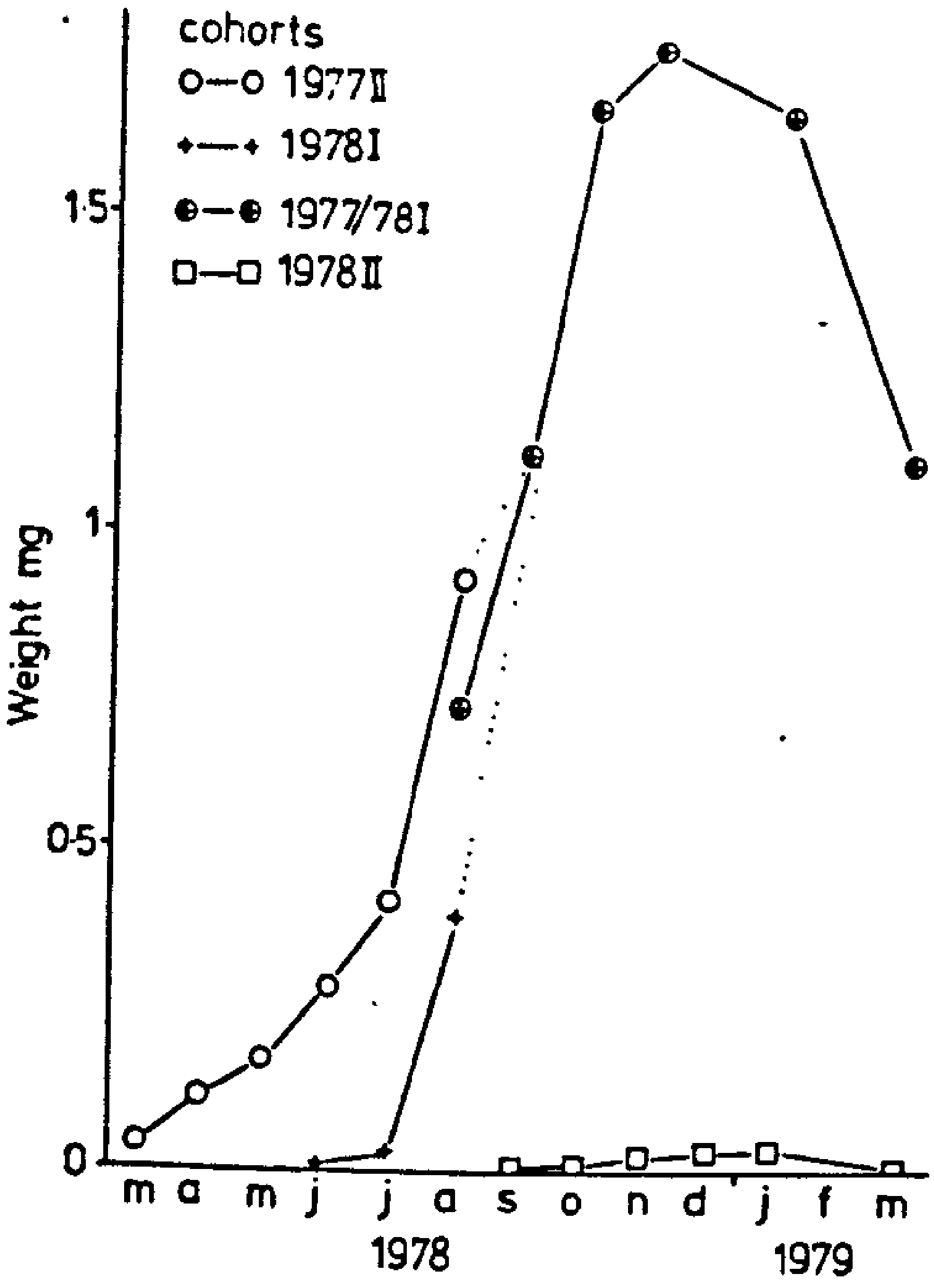
Figures 10xvi, 10xvii and 10xviii

Mean individual flesh dry weight per cohort of Retusa obtusa. Monthly, March 1978 - March 1979. Symbols as Fig 10iv.

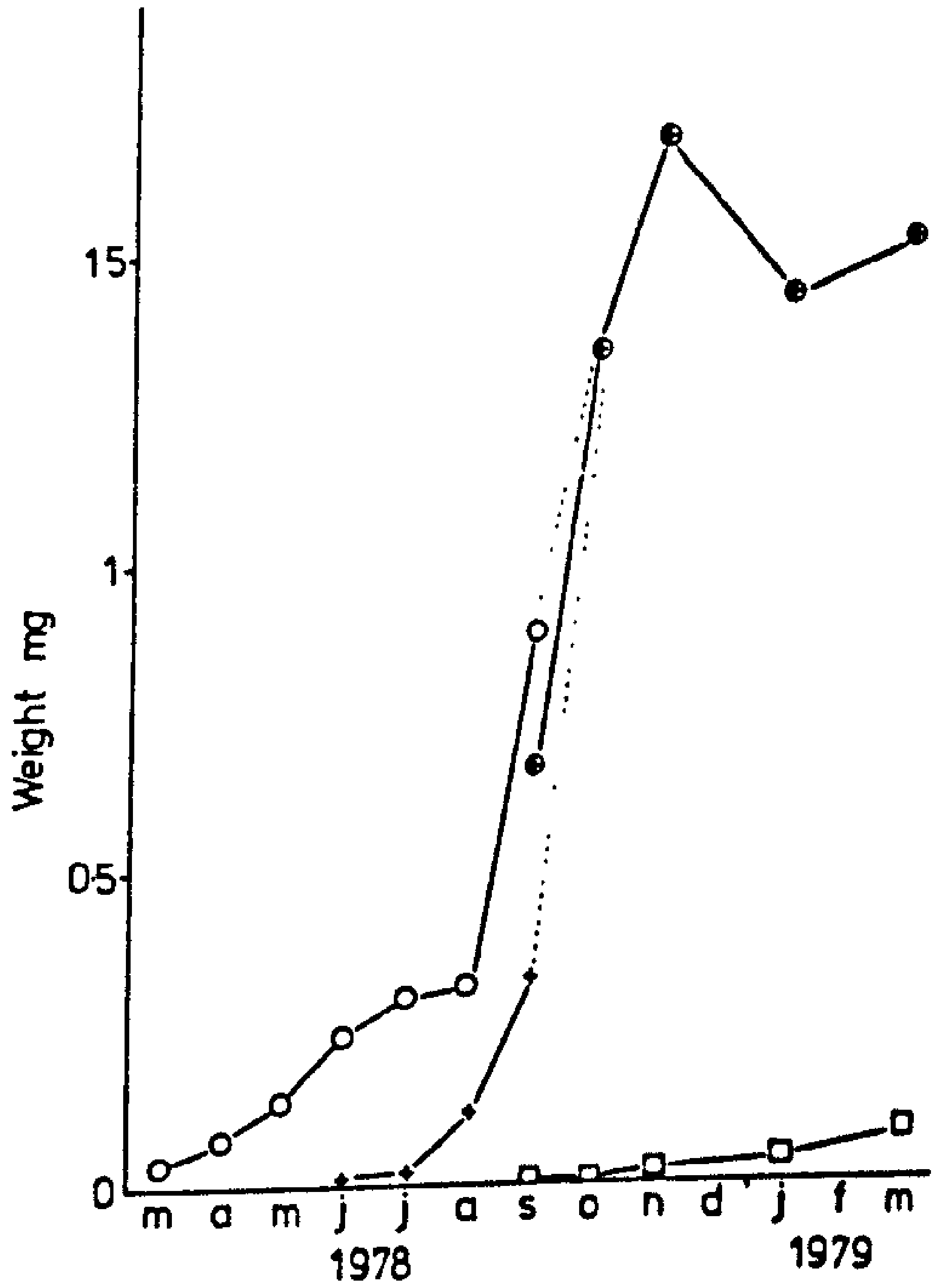
Figure 10xix

Relationship of flesh dry weight to shell height for Retusa obtusa. Station GIV3, May 1977. Data from 1125 animals, pooled into 0.2mm length categories.

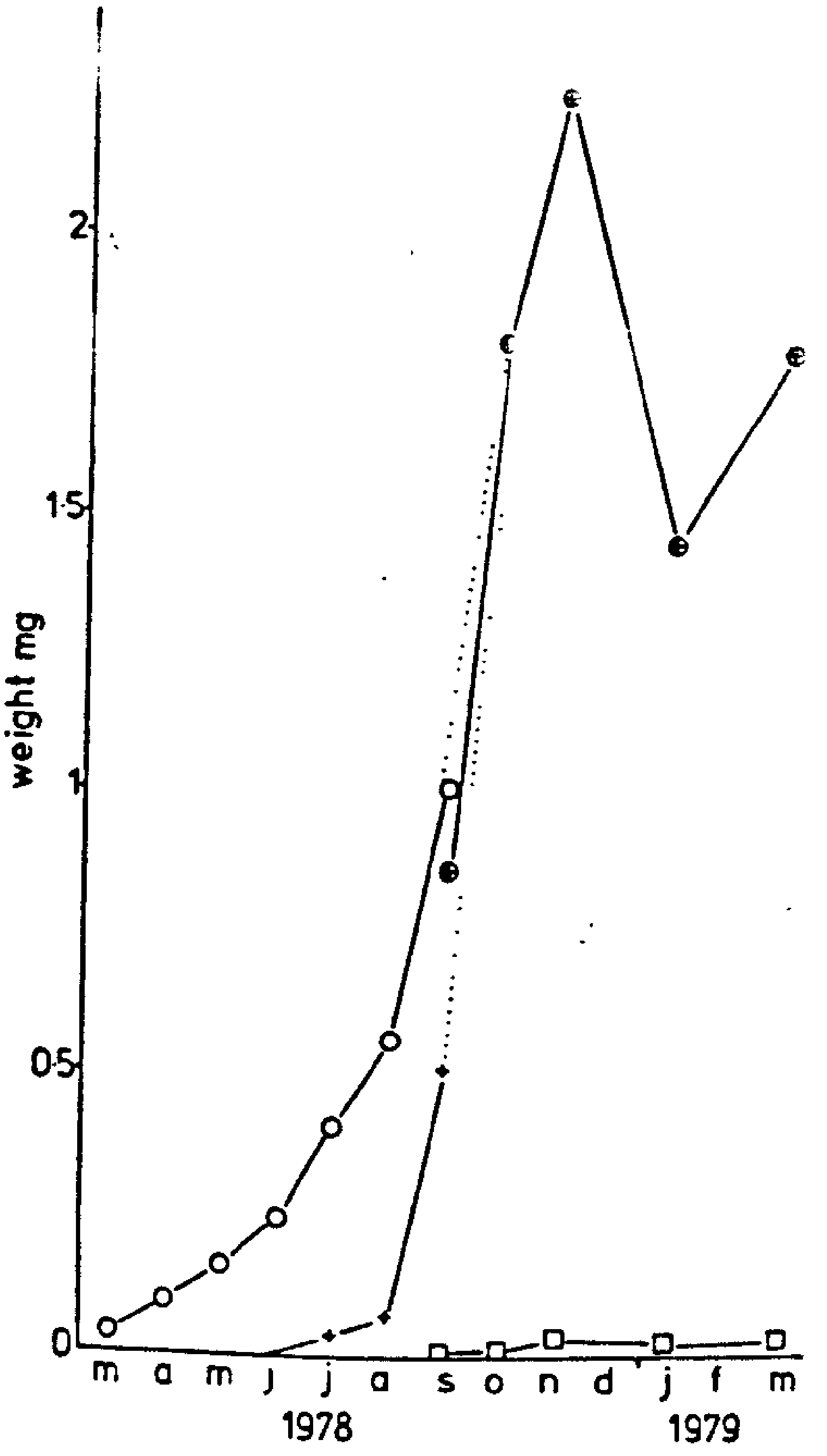
10xvi



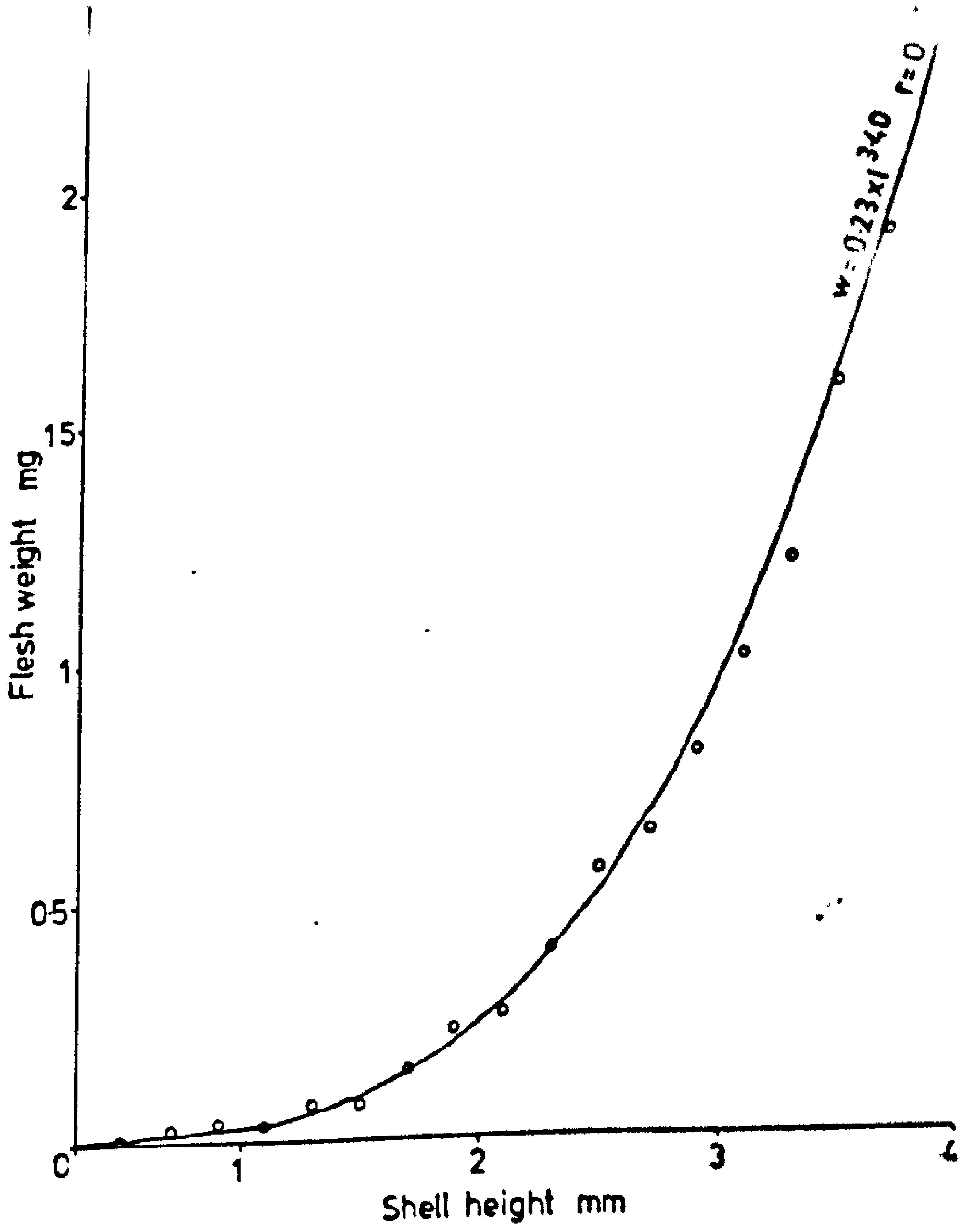
10xviii

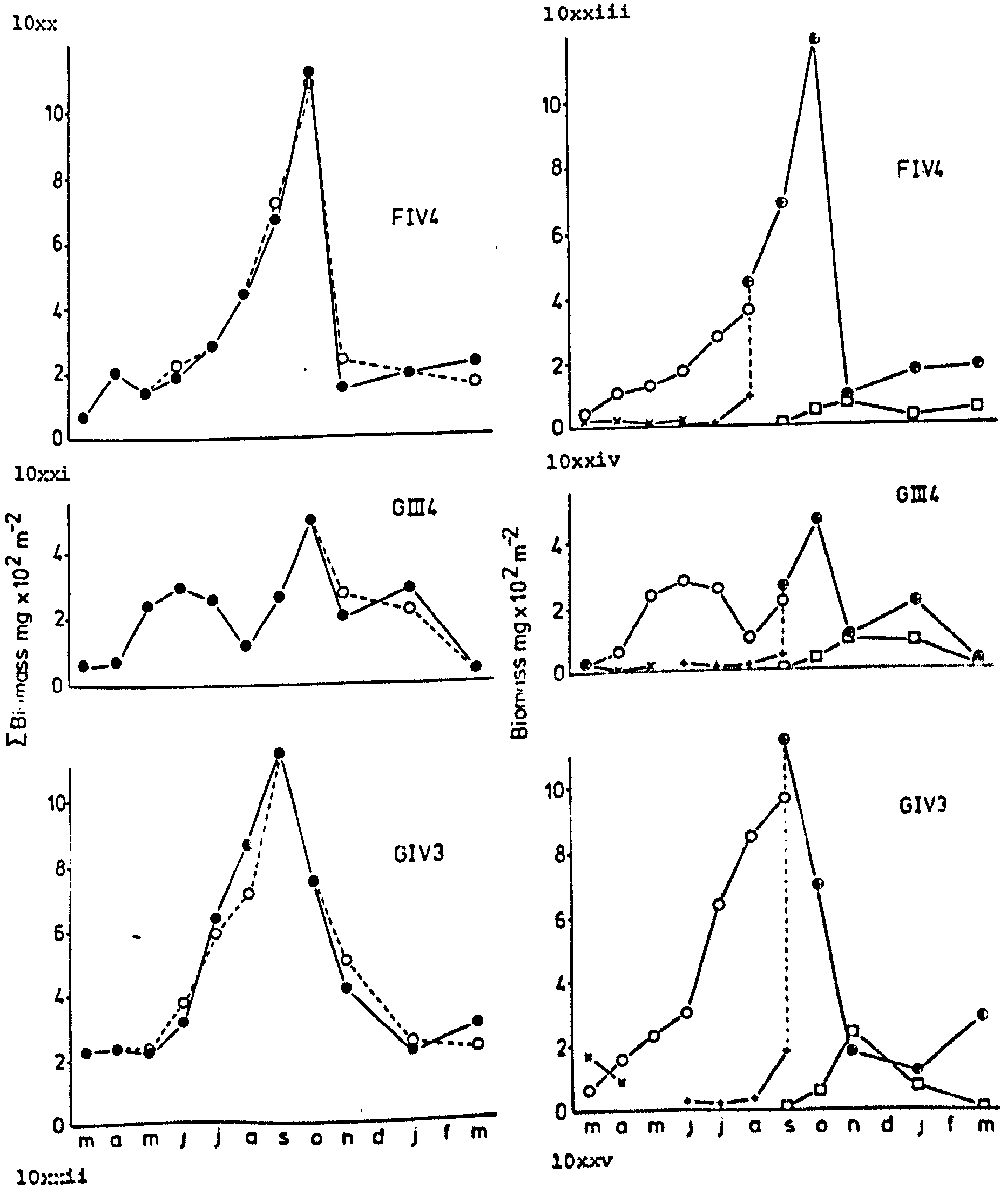


10xvii

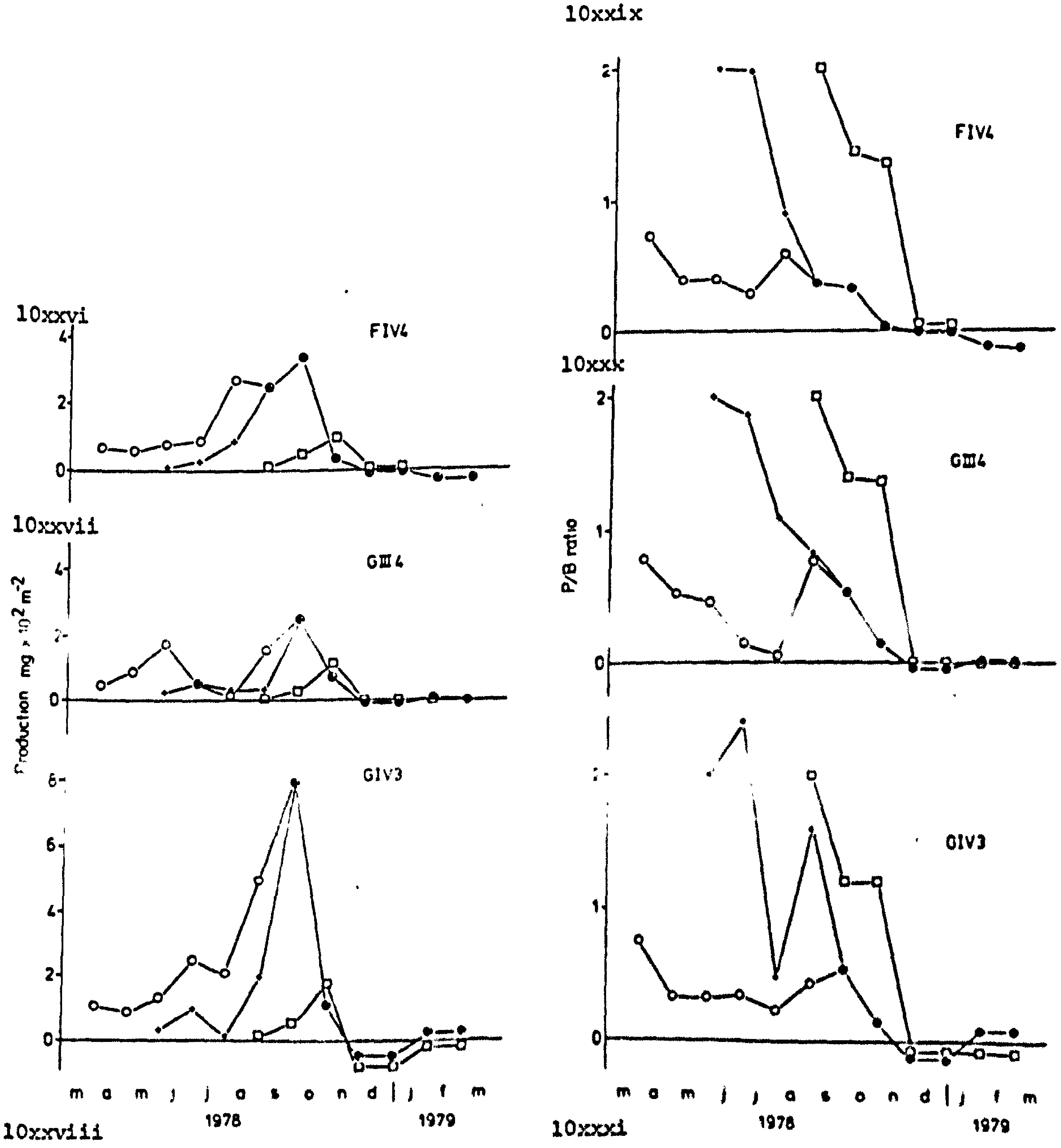


10xix





Figures 10xx - 10xxvi Variation in total biomass (10xx - 10xxiii) and cohort biomass (10xxiv - 10xxvi) of <u>Notusa obtusa</u>. March 1978 - March 1979. Symbols as Fig 10iv.



Figures 10xxvi - 10xxxi Production and productivity (P/B ratio) of *Retusa obtusa* March 1978 - March 1979. Symbols as Fig 10iv.

Figures 10xxxii - 10xxxvii Elimination and E:B ratio of Retusa obtusa.
March 1978 - March 1979. Symbols as Fig 10iv.

▥ others

▨ E.benedii

▥ N.hombergi

▤ H.diversicolor

░ E.longa

▒ H.ulvae

□ R.obtusa

✚ C.edule

⊞ M.balthica

Figures 11i - 11v
Total measured biomass of the infauna and breakdown into contribution by the major species. Intensive survey, all sites. Monthly : March 1978 - March 1979.

Figure 11i

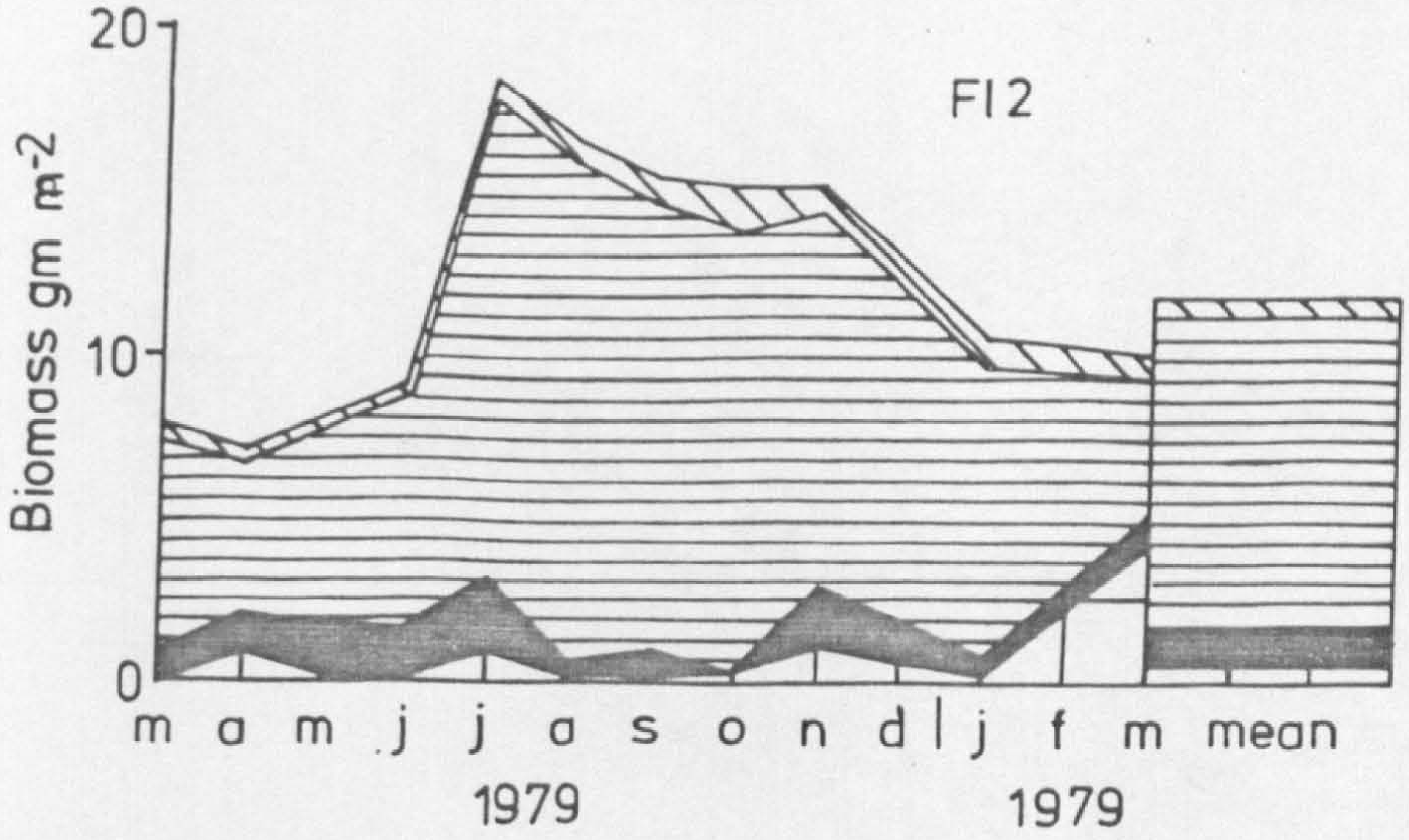


Figure 11ii

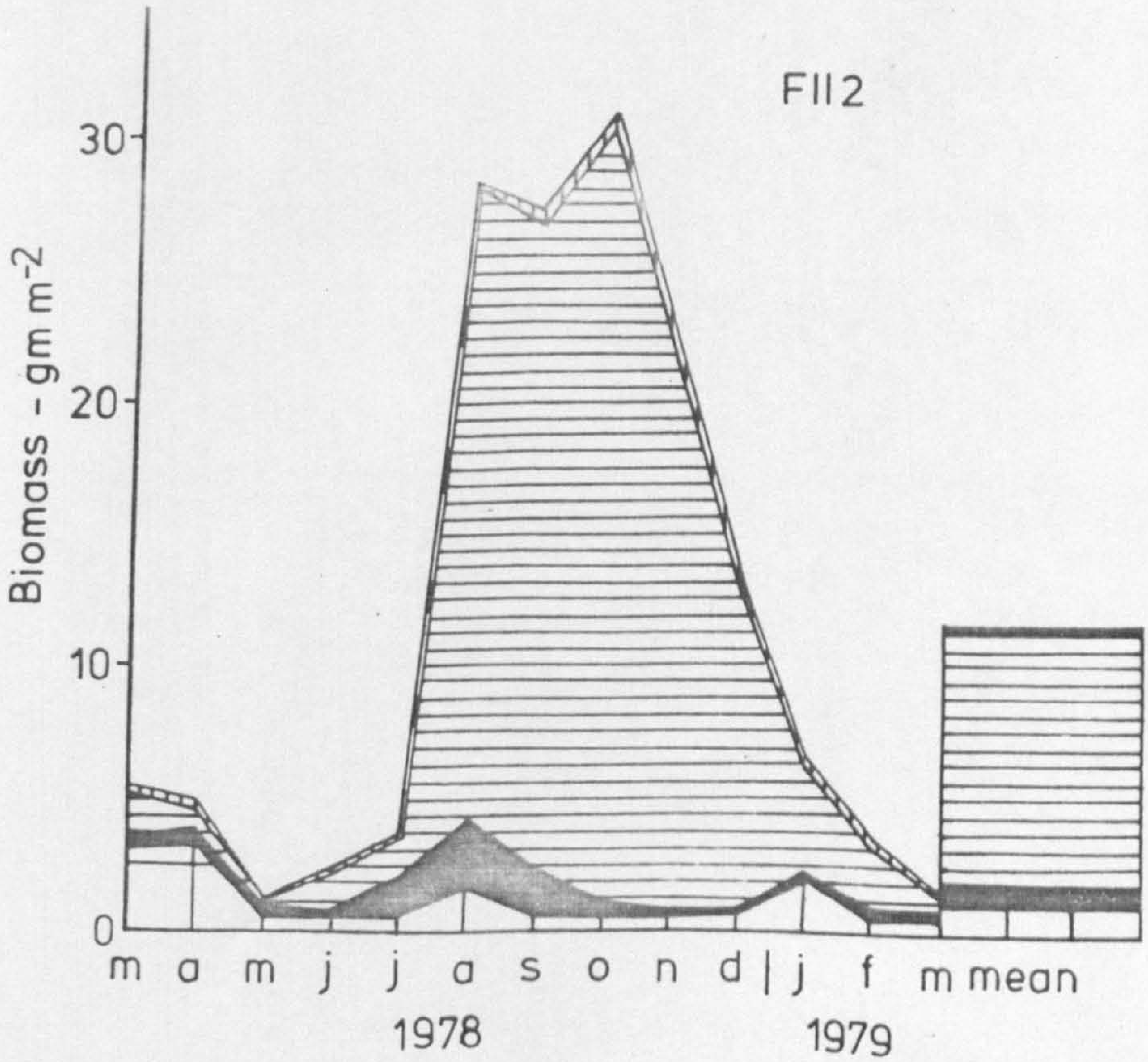


Figure lliii

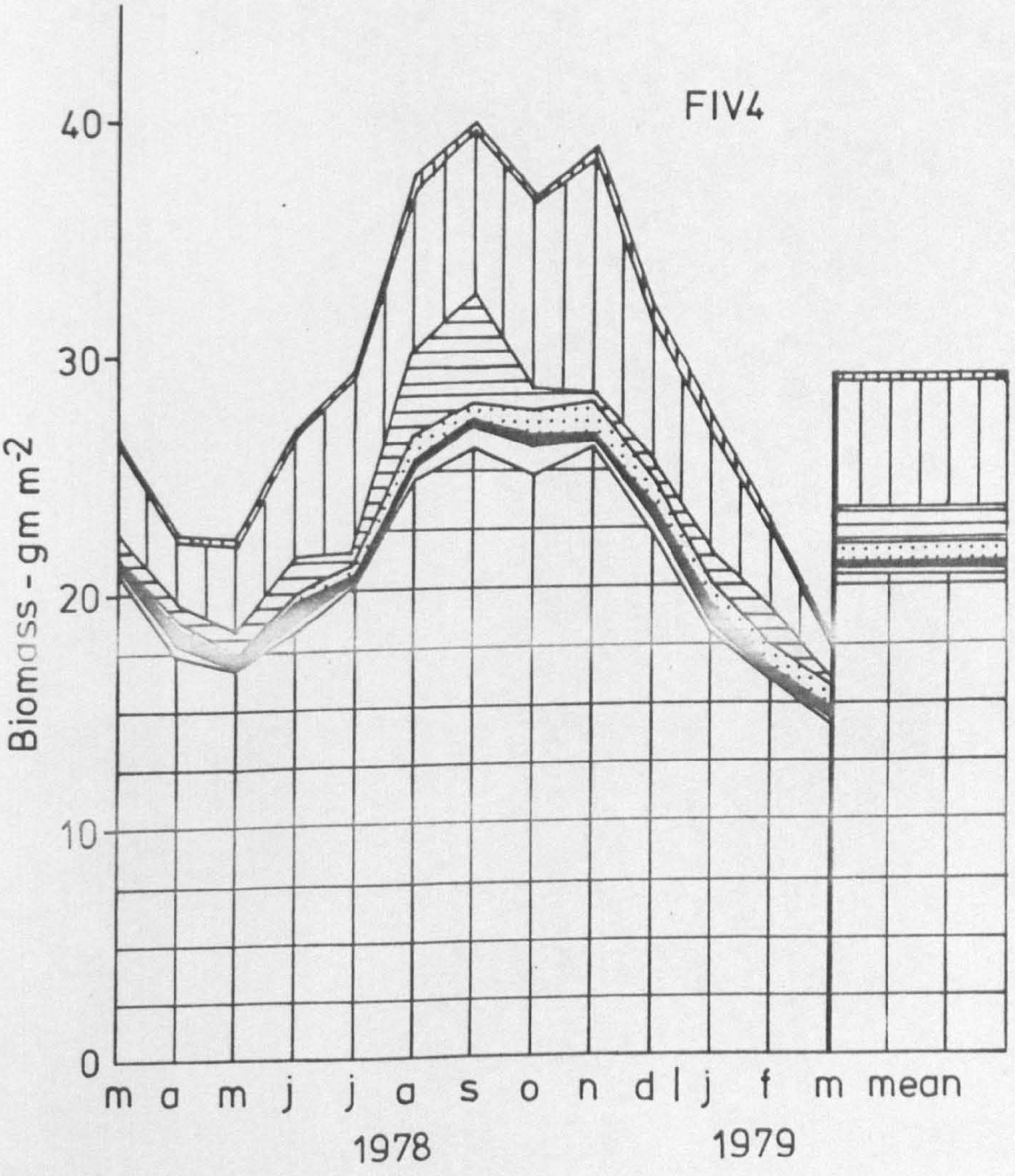


Figure 11iv

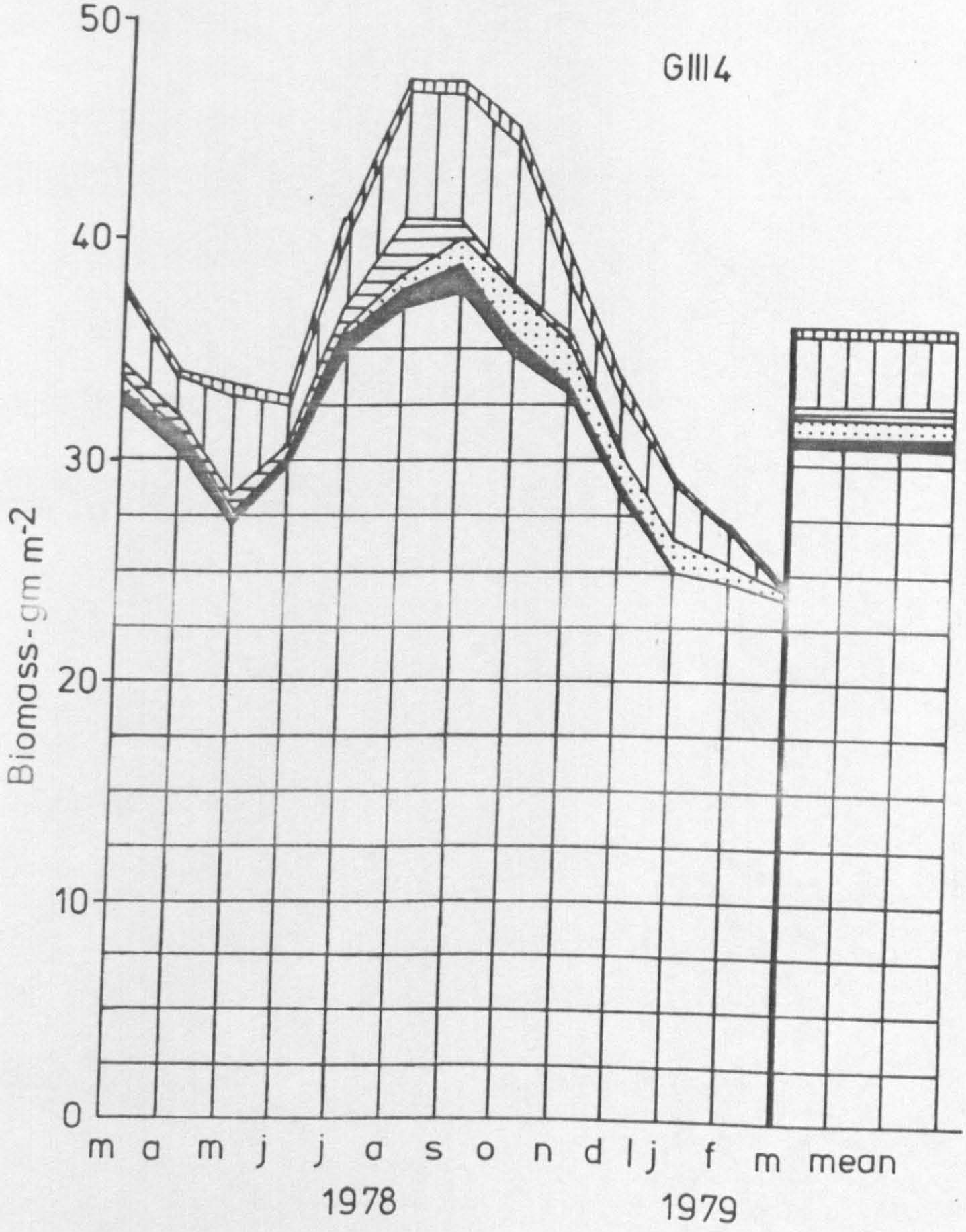

GIII4
Biomass-gm m-2
50
40
30
20
10
0
m
a
m
j
j
a
s
o
n
d
j
f
m
mean
1978
1979

Figure 11v


GIV3
Biomass -gm m^{-2}
0
10
20
30
40
50
60
70
80
m
a
m
j
j
a
s
o
n
d
j
f
m
mean
1978
1979

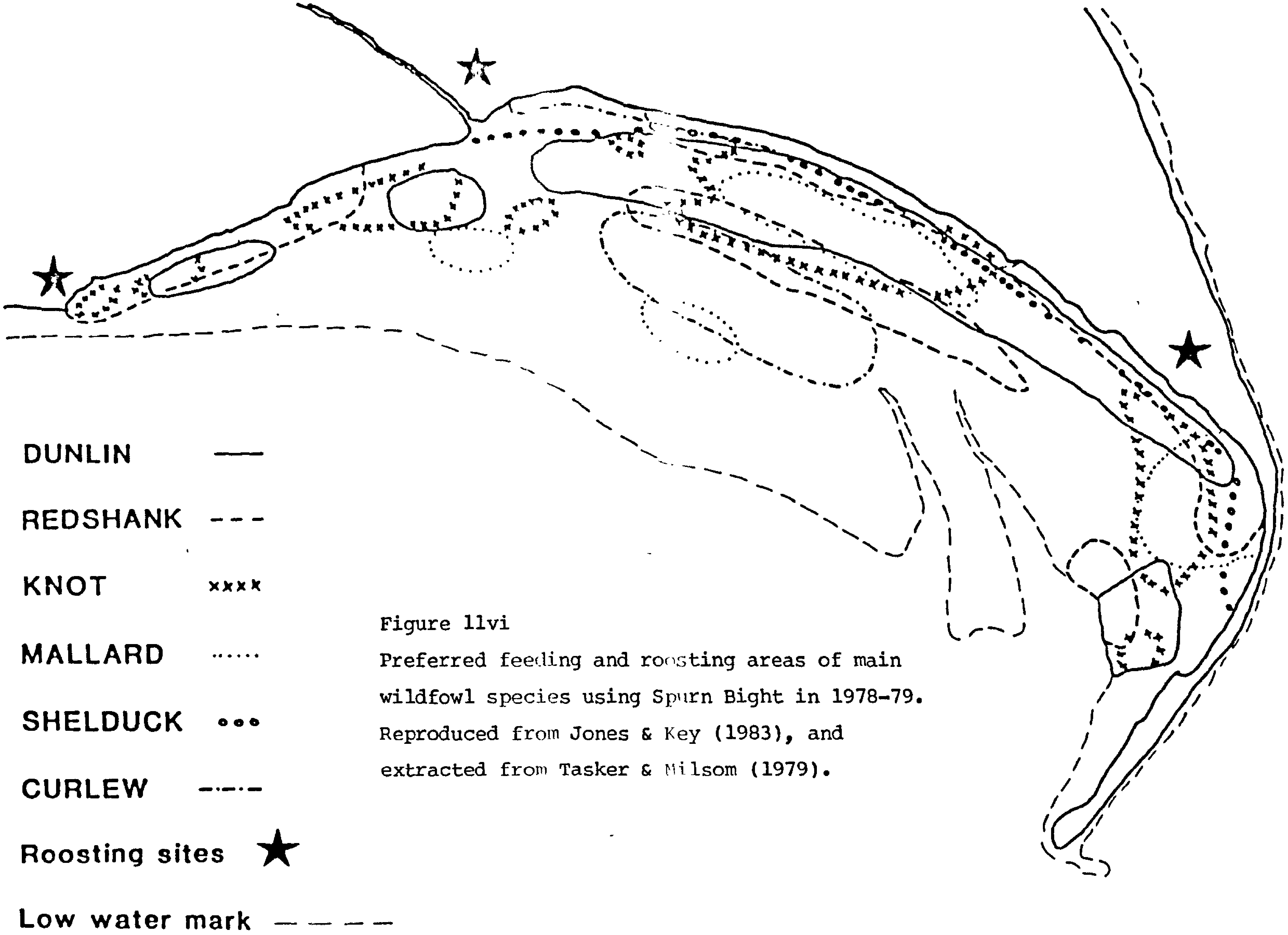


Figure 11vi
Preferred feeding and roosting areas of main wildfowl species using Spurn Bight in 1978-79. Reproduced from Jones & Key (1983), and extracted from Tasker & Milsom (1979).

APPENDICES

Appendix to Chapter 2

Sampling transects - Spurn Bight. Initial grid ref. is point of access.

B Hawkin's Point TA288165 Sample date 9.6.77

Access by permission from East Bank Farm, using rough track from the farm to the sea wall. Mud immediately south of the point is steeply shelving and completely fluid with a total length of ca. 120m to M.L.W. Post war Spartina plantings by the proprietor of Old Hall Farm have not been successful and the grass exists as small, unconnected patches. The sea wall is partially protected by two sets of groynes, one perpendicular and one parallel to the shore. Sampling station BI2 located at TA294167 in the lee of the Point where MHWOT - MLWOT approx 400m.

C Patrington Outstray Cutoff TA320180 Sample date 16.5.77

Access by permission from Outstray Farm by rough track along inside of sea wall. The 'Cutoff' is the junction between the newest and earlier sea walls where there is a small saltmarsh. Failing Spartina plantings grow right up to high water. Total shore width 1860m due south but the transect, angled on a bearing towards Grimsby tower totalled 2130m to low water. Each of five successive sediment bands were sampled.

From the Spartina:-

flat silt	100m wide	CI2	TA321179
flat silty sand	330m wide	CII4	TA319178
flat sand	400m wide	CIII5	TA318175
gullied sandy mud	730m wide	CIV3	TA315171
hard flat sand	400m wide	CV6	TA312155

D Patrington Haven TA334185 Sample date 1.6.77

Access by Y.W.A. gated road to Patrington Haven Pumping Station car park, sited on recently reclaimed part of Welwick Saltmarsh. Total shore width 2530m. Three sediment bands were sampled:-

very soft silt	400m wide	DI3	TA332182
gullied sandy mud	1700m wide	DIII4	TA330175

Gullies are extremely deep - up to 1½ metres, preventing further access with the mud sledge. Aerial photography revealed that this gullied mud changed abruptly to hard sand 500m wide extending to low water. This area was sampled by boat - station DV6 - TA338160.

E <u>Weeton</u> TA348189 Sample date 30.5.77

Access by Humber Side Road, an unsurfaced track from the village. This area is immediately east of Welwick Saltmarsh and the band of *Spartina* is very wide - almost 200m. The transect extended 1060m SSW. crossing Patrington Channel and was eventually obstructed by extremely deep gullies.

Two sampled sediment types:-

Flat sandy silt 880m wide EII4 TA342186 sharply delimited by Patrington Channel.

Flat silty sand EIII6 TA339179 again abruptly delimited by impassable gullies and continuing as gullied sandy mud 330m in width, abruptly changing to hard sand 1000m to MLWOT. Total width of shore 3300m.

F <u>Skeffling</u> TA369184 Sample date 18.5.77

Access by Short Lane from village to Y.W.A. car park and huts. Transect 200m W of Skeffling Clough. Four sucessive sediment types were sampled.

Spartina marsh	90m wide	FI2	TA369183
flat soft silt	200m wide	FII2	TA368181
flat sandy silt	660m wide	FIII4	TA366177
gullied sandy mud	2000m wide	FIV4	TA367165

This latter region was bisected by the main feed channel of Trinity Run, 6m wide, powerfully flowing of indeterminate depth and which prevented access further downshore. From aerial photographs the gullied mud could be seen to extend to within 900m of MLWOT, continuing thereafter as hard flat sand. The mudflats are at their widest point here - 3850m to low water.

G <u>Easington</u> TA393172 Sample date 4.5.77

Access by Humber Side Lane from the village to car park, Y.W.A. huts and triangulation pillar. The transect was sited 300m W of Easington Clough.

Sediment Types:-

dry coarse sand, devoid of fauna 20m wide - not sampled

Spartina marsh	60m wide	GI2	TA392171	sample lost
flat sandy silt	200m wide	GII4	TA391170	

flat silty sand	600m wide	GIII4	TA391166
gullied sandy mud	660m wide	GIV3	TA387163

This was sharply delimited to seaward by a 6m wide shallow sandy bottomed creek forming the main feed to North Channel.

Hard flat sand (Trinity) 930m GV6 TA381154

This reverted to gullied muddy sand, 600m in width, beyond the range of the mudsledge, delimited to seaward by Trinity Runs with an approximately 2m high sand bar on the seaward bank. Aerial photography showed hard flat sand to extend another 750m to MLWOT. Total width of shore - 3800m.

H Kilnsea TA409158 Sample date 2.5.77

Access from car park of Crown and Anchor public house on road to Spurn Head. There is no flood bank rather a boulder clay 'cliff' 1½m high topped by the road. Soft mud 'beach' reinforced with dumped chalk and slag boulders in band 10m in width. A large number of small pleasure boats are permanently moored to buoys 100m from the shore, connected by ropes directly to the bank. The movement of these ropes keep Spartina from colonising this part of the flats which are consequently very soft. Activities of bait diggers create small pockets of thixotropic 'quick' sediment, an unpleasant impediment to progress.

Sediment bands:-

very soft silt	60m wide	HI2	TA409157
silty sand	600m wide	HIII5	TA408155
gullied mud	1400m wide	HIV4	TA400149

This is delimited by the North Channel and the shore extended over Trinity Sands to reach a total length of 2130m in a S.E. direction.

J Spurn Narrows TA421137 Sample date 5.5.77

Access from the road along the peninsula. The shingle spit is here reinforced with a chalk bank with a narrow belt of developing saltmarsh on the estuarine side. Spartina forms the primary colonising band 100m in width - station JI3 TA420137. Additional bands:-

liquid silt	10m wide	not sampled	
silty sand	530m wide	JIII6	TA417138

gullied sandy mud 1660m wide JIV3 TA412142

This gradually became more and more fluid and gullies became shallower and more numerous until only a few centimetres deep and 30cm wide, <1m apart. The fluid nature of this sediment made it impossible to continue. Total width of shore 2130m due west.

K <u>Old Den</u> TA410123 Sample date 5.5.77

Access from peninsula road. A ridge and runnel beach system occupies the Greedy Gut Channel separating the Old Den from the peninsula, with sand waves in the direction of flow of the channel.

Hard sand - station KIII6, TA407122.

The Old Den itself is composed of an unsorted mixture of cobbles, pebbles, sand and silt, impossible to sample quantitatively and a collection of organisms made to establish a species list (appendix to Chapter 4). West of the Old Den the silt was completely fluid, 1m in depth by the edge of the shingle, overlaying hard sand, station KV2 TA404124.

I <u>Spurn Head</u> TA400110 Sample date 5.5.77

Access from tourist car park by old explosives magazine. The riverside bank is protected by concrete and steel piled sea defences with numerous groynes perpendicular to the shore. The whole beach is of hard sand with a continuation of the ridge and runnel system of the Greedy Gut. Total length of shore by lifeboat station 400m. Sampling station LIV6, approximately midshore - TA400110.

<u>Comparative stations in Outer Humber</u>

A <u>Cherry Cob Sand</u> TA211226 Sample date 14.6.77

Access by permission from New House Farm by track off Thorngumbald to Stone Creek road. Saltmarsh 1000m wide outside the flood bank. The sandy area of Foul Holme Spit is separated from 300m wide silty shore by Foul Holme Channel and hence inaccessible.

Single station AIII2 200m from shore at TA202217.

M <u>Pyewipes mudflats</u> TA249121 Sample date 16.6.77

Access from A.W.A. flood bank by Woad Farm (ruins) at side of British Titan factory. Exterior to flood bank is a beach of chalk rubble stained orange by iron oxide pollutant. The shore is extremely soft, 500m in length of black 'wobbly' silts (c.f. petroleum jelly) overlain by thin veneer of bright orange iron oxide. Very odorous. Single station at TA251123.

N Humberston Sand Flats TA333060 Sample date 15.5.77

Access from Humberston Fitties caravan park. Degenerating dunes are reinforced by a bank of slag blocks, 4m high enclosed in steel netting.

Flat slightly muddy sand to low water shore 1600m long. Two sample sites-

midshore	NIII6	TA336066
low water	NV6	TA338077

P Horseshoe Point TA381018 Sample date 15.5.77

Access by road from Northcoates. Hard sand to low water. Upper and lower-midshore samples

PII6	TA390022
PIV6	TA394028.

APPENDIX TO CHAPTER 5

List of the fauna and flora of Spurn Bight.

INVERTEBRATES

Phylum	Protozoa				
Class		Sarcodina			
Order			Foraminiferida		
					unidentified forams
Phylum	Cnidaria				
Class		Hydrozoa			
Order			Athecata		
Family				Hydridae	
					Protohydra leuckarti Greef
Order			Thecata		
Family				Campanularidae	
					Laomedea flexuosa Hincks
					Obelia dichotoma (L.)
					Obelia gelatinosa Pallas
					Obelia geniculata (L.)
					Campanularia angulata Hincks
					Gonothyraea loveni (Allman)
Family				Sertulariidae	
					Dynamena pumila (L.)
Family				Plumulariidae	
					Kirchenpaueria pinnata (L.)
Family				Tubulariidae	
					Tubularia larynx Ellis & Sollander
Class		Scyphomedusae			
Order			Semaeostomeae		
Family				Aureliidae	
					Aurelia aurita (L.)
Class		Anthozoa			
Order			Actiniaria		
Family				Actiniidae	
					Actinia equina (L.)
					Tealia crassicornis (Müller)
					Anemonia sulcata (Pennant)
Family				Sagartiidae	
					Sagartia nivea Gosse
Phylum	Platyhelminthes				
Class		Turbellaria			
					unidentified turbellarian 'PA1'
Phylum	Nemertini				
Class		Anopla			
Order			Palaeonemertini		
Family				Lineidae	
					Lineus gesserensis (Müller)
Class		Enopla			
Order			Hoplonemertini		
Family				Amphiporidae	
					Amphiporus lactifloreus (Johnston)
Family				Emplectonematidae	
					Nemertopsis flavida (McIntosh)
Phylum	Gastrotricha				
					unidentified gastrotrichs
Phylum	Kinorhyncha				
					unidentified kinorhynchs
Phylum	Nematoda				
					unidentified nematodes

Phylum	Mollusca				
Class		Amphineura			
Order			Chitonida		
Family				Lepidochitonidae	
					Lepidochitona cinerea (L.)
Class		Gastropoda			
Order			Archaeogastropoda		
Family				Patellidae	
					Patella vulgata L.
Order			Mesogastropoda		
Family				Littorinidae	
					Littorina littorea (L.)
					Littorina littoralis (L.)
					Littorina neritoides (L.)
					Littorina saxatilis (Olivi)
Family				Hydrobiidae	
					Hydrobia ulvae (Pennant)
					(Hydrobia ventrosa (Montagu))
Order			Stenoglossa		
Family				Muricidae	
					Thais lapillus (L.)
					Buccinium undatum L.
					(Ocinabra erinacea (L.))
Order			Bullomorpha		
Family				Retusiidae	
					Retusa obtusa (Montagu)
					form pertenuis (Mighels)
Family				Philinidae	
					Diaphana minuta (Brown)
Order			Sacoglossa		
Family				Limapontiidae	
					Limapontia depressa Alder & Hancock
Order			(Basommatophora)		
Family				(Physidae)	
					(Physa fontinalis (L.))
Class		Bivalvia			
Order			Anisomyaria		
Family				Mytilidae	
					Mytilus edulis (L.)
					Modiolus modiolus (L.)
Family				(Ostreidae)	
					(Ostrea edulis L.)
Order			Heterodonta		
Family				Cardiidae	
					Cerastoderma edule (L.)
					(Cardium echinatum L.)
Family				(Cyprinidae)	
					(Cyprinus islandica (L.))
Family				Scrobiculariidae	
					Scrobicularia plana (da Costa)
Family				Tellinidae	
					(Tellina tenuis da Costa)
					Macoma balthica (L.)
Order			Adepodonta		
Family				Myidae	
					Mya arenaria L.
					Mya truncatula L.
Family				Pholadidae	
					Barnea candida (L.)
Phylum	Annelida				
Class		Polychaeta			
Order			Phyllodocemorpha		

Family	Phyllodocidae
	Phyllodoce maculata (L.)
	Eteone lactea (Claparède)
	Eteone longa (Fabricius)
Family	Polynoidae
	Lepidisthenia argus Hodgson
	Harmathoe impar Johnston
	Gattyana cirrosa (Pallas)
Family	Nereidae
	Neanthes virens (Sars)
	Hediste diversicolor (Müller)
Family	Nephtyidae
	Nephtys cæca (Fabricius)
	(*Nephtys longosetosa* (Oersted))
	Nephtys hombergi (Savigny)
Family	Sphaerodoridae
	Sphaerodoropsis minuta (Webster & Benedict)
Order	Spiomorpha
Family	Orbiniidae
	Scoloplos armiger (Müller)
Family	Spionidae
	Spio filicornis (Müller)
	Spio seticornis (Fabricius)
	Prionospio cirrifer Wiren
	Pygospio elegans Claparede
	Nerine cirratulus (Delle Chiaje)
	Nerine coniocephalus Johnston
	unidentified spionids 4 spp.
Family	Cirratulidae
	Cirriformia tentaculata (Montagu)
	Streblospio shrubsolii (Buchanan)
Family	Sabellariidae
	Sabellaria alveolata (L.)
Order	Drillomorpha
Family	Capitellidae
	Capitella capitata (Fabricius)
Family	Arenicolidae
	Arenicola marina (L.)
Family	Opheliidae
	Travisia forbesii Johnston
Order	Terebellomorpha
Family	Terebellidae
	Amphitrite johnstoni Malmgren
	Lanice conchilega (Pallas)
Family	Pectinariidae
	Pectinaria belgica (Pallas)
Family	Ampharetidae
	Ampharete acutifrons Grubé
Order	Serpulimorpha
Family	Serpulidae
	Laeospia borealis Daudin
Family	Sabellidae
	Manayunkia aestuarina (Bourne)
Class	Oligochaeta
Order	Plesiothecata
Family	Naididae
	Paranais littoralis (Müller)
Family	Tubificidae
	Tubifex costatus (Clarapède)
	Edukemius benedii (d'Udekem)

Order Prosothecata
Family Enchytraeidae
Lumbricillus lineatus (Müller)

Phylum Chelicerata
Class Arachnida
Order Acari
Family Halacaridae
unidentified halacarid mites

Class Pycnogonida
Order Pycnogonomorpha
Family Pycnogonidae
Pycnogonum littorale (Ström)

Phylum Crustacea
Class Ostracoda
unidentified ostracods

Class Copepoda
Order Harpacticoidea
Family Canuellidae
Canuella perplexa T. & A. Scott
Family Ectinosomidae
Ectinosoma elongatum Sars
Pseudobradya fusca T. & A. Scott
Family Tachidiidae
Tachidius discipes Giesbrecht
Microarthridion littorale Popper
Family Peltidae
Alteutha interrupta Goodsir
Family Thalestridae
Parathalestris clausi Norman
Rhynchothalestris rufocincta Brady
Family Diosaccidae
Stenhelia palustris Brady
Bulbamphiascus imus (Brady)
Bulbamphiascus denticulatus (Thompson)
Amphiascella debilis (Giesbrecht)
Amphiascella limicola (Brady)
Family Cletodidae
Cletodes longicaudatus (Boeck)
Enhydrosoma bucholtzi (Boeck)
Enhydrosoma curticauda Boeck
Enhydrosoma garienis Gurney
Enhydrosoma longifurcatum Sars
Enhydrosoma sarsi (T. Scott)
Nannopus palustris Brady
Stylicletodes longicaudatus (Brady & Robertson)
Family Laophontidae
Paralaophonte congenera (Sars)
Asellopsis intermedia (T. Scott)
Platychelipus littoralis Brady
Cleta lamellifera Claus
Order Cyclopoidea
Family Cyclopidae
Halicyclops magniceps Liljeborg

Class Cirripedia
Order Thoracia
Family Balanidae
Balanus balanoides (L.)
Balanus crenatus Bruguière
(*Balanus improvisus* Darwin)
Elminius modestus Darwin
Family Chthamalidae
Chthamalus stellatus (Poli)

Class	Malacostraca
Order	Mysidacea
Family	Mysidae
	Neomysis integer (Leach)
	Leptomysis sp.
Order	Cumacea
Family	Pseudocumatidae
	Pseudocuma longicornis (Bate)
Order	Tanaidacea
	unidentified tanaids
Order	Isopoda
Family	Anthuridae
	Cyathura carinata (Krøyer)
Family	Cirolanidae
	Eurydice pulchra Leach
Family	Sphaeromatidae
	Sphaeroma rugicauda Leach
Family	Idoteidae
	Idotea viridis Slabber
	(*Idotea marina* (L.))
Family	Janiridae
	Jæra normandi (Raithke)
Family	(Asellidae)
	(*Asellus aquaticus* (L.))
Family	Ligiidae
	Ligia oceanica (L.)
Order	Amphipoda
Family	Haustoriidae
	Bathyporeia pilosa Lindström
	Urothöe sp.
	Haustorius arenarius [illegible]
Family	Gammaridae
	Gammarellus homari (Fabricius)
	Gammarus duebeni Liljeborg
	Gammarus zaddachi Sexton
	Marinogammarus marinus Leach
Family	Talitidae
	Talitrus saltator (Montagu)
	Orchestia gammarella (Pallas)
	Hyale sp.
Family	Corophiidae
	Corophium volutator (Pallas)
	Corophium arenarium Crawford
Order	Decapoda
Family	Palaemonidae
	(*Palaemon elegans* Rathke)
	Palaemonetes varians Leach
Family	Pandalidae
	Pandalus annulicornis Leach
Family	Crangonidae
	Crangon crangon (L.)
Family	Paguridae
	Pagurus bernhardus (L.)
Family	Portunidae
	Carcinus maenas (L.)
Family	Pinnotheridae
	Pinnotheres pisum (Pennant)
Phylum	Uniramia
Class	Collembola
Family	Hypogasturidae
	Anurida maritima Guèrin

Family	Poduridae
	Hydropodura aquatica (L.)
Class	Insecta
Order	Diptera
Family	Chironomidae
	unidentified chironomid larvae
Family	Tipulidae
	Limonia sp. (larvae)
Family	Tabanidae
	Chrysops sp. (larvae)
Family	Dolichopodidae
	Thinophilus flavipalpis Zetterstedt? (larvae)
Order	Coleoptera
Family	Carabidae
	Notiophilus biguttatus (Fabricius)
	Loricera pilicornis (Fabricius)
	Broscus cephalotes (L.)
	Trechus quadristriatus (Schrank)
	Bembidion aeneum Germar
	Bembidion lampros (Herbst)
	Bembidion lunatum (Duftschmidt)
	Bembidion maritimum Stephens
	Bembidion minimum (Fabricius)
	Bembidion varium (Olivier)
	Pterostichus strenuus (Panzer)
	Agonum albipes (Fabricius)
	Calathus mollis (Marsham)
	Amara convexiuscula (Marsham)
	Amara tibialis Paykull
	Harpalus tardus Panzer
	Dicheirotrichus gustavi Crotch
	Demetrias atricapillus (L.)
Family	Hydrophilidae
	Cercyon littoralis (Gyllenhal)
Family	Histeridae
	Carcinops pumillo (Erichson)
Family	Staphylinidae
	Micralymma marina (Ström)
	Anotylus rugosus (Fabricius)
	Quedius molochinus (Grevenhorst)
	Gyrohypnus angustatus Stephens
	Xantholinus linearis (Olivier)
	Xantholinus tricolor (Fabricius)
	Lathrobium fulvipenne (Gravenhorst)
	Mycetoporus splendidus (Gravenhorst)
	Tachinus signatus Gravenhorst
	Atheta sp.
Family	Anthicidae
	Notoxos monoceros (Fabricius)
Family	Oedemeridae
	Nacerdes melanura (L.)
Family	Tenebrionidae
	Opatrum sabulosum (L.)
	Phaleria cadaverina (Fabricius)
Family	Curculionidae
	Pselactus spadix (Herbst)
Phylum	Ectoprocta
Class	Gymnolaemata
Order	Cheilostomata
Family	Membraniporidae
	Membranipora monostachys Busk

	Membranipora membranacea L.
	(*Flustra foliacea* (L.))
Phylum	(Echinodermata)
Class	(Echinoidea)
Order	(Spatangoidea)
Family	(Echinocardiidae)
	(*Echinocardium cordatum* (Pennant))

VERTEBRATES

Phylum	Chordata
Class	Marsipobranchii
Order	Petromyzontiformes
Family	Lampetridae
	Lampetra fluviatilis (L.)
Class	Osteichthyes
Order	Isospondyli
Family	Clupeidae
	Sprattus sprattus (L.)
Order	Apoda
Family	Angullidae
	Anguilla anguilla (L.)
Order	Solenichthyes
Family	Sygnathidae
	Sygnathus acus (L.)
Order	Anacanthini
Family	Gadidae
	Gadus morhua (L.)
	Merlangius merlangus (L.)
Order	Percomorphi
Family	Gobiidae
	Pomatoschistus minutus (Pallas)
	Pomatoschistus microps (Krøyer)
Family	Callionymidae
	Callionymus lyra (L.)
Family	Ammodytidae
	Ammodytes sp.
Family	Cyclopteridae
	Liparis liparis (L.)
Order	Scleroparei
Family	Gasterosteidae
	Gasterosteus aculeatus (L.)
Order	Heterosomata
Family	Bothidae
	Scophthalmus maximus (L.)
Family	Hippoglossidae
	Limanda limanda (L.)
	Pleuronectes platessa L.
	Platichthy flesus (L.)
Family	Soleidae
	Solea solea (L.)
Class	Aves
Order	Gaviiformes
Family	Gaviidae
	Gavia immer Brunnich
Order	Pelecaniformes
Family	Phalacrocoridae
	Phalacrocorax carbo L.
Order	Ciconiiformes
Family	Ardeidae
	Ardea cinerea (L.)

Order	Anseriformes
Family	Anatidae
	Cygnus cygnus L.
	Anser brachyrhynchus Baillon
	Anser anser (L.)
	Branta bernicla (L.)
	Tadorna tadorna (L.)
	Anas penelope (L.)
	Anas crecca (L.)
	Anas platyrhynchus (L.)
	Anas clypeata (L.)
	Aythya ferina (L.)
	Aythya fuligula (L.)
	Aythya marila (L.)
	Somateria mollissima (L.)
	Melanitta nigra (L.)
	Melanitta fusca (L.)
	Bucephala clangula (L.)
	Mergus albellus (L.)
	Mergus serrator (L.)
	Mergus merganser (L.)
Order	Gruiformes
Family	Rallidae
	Fulica atra (L.)
Order	Charadriiformes
Family	Haematopodidae
	Haematopus ostralegus (L.)
Family	Charadriidae
	Charadrius dubius Scopoli
	Charadrius hiatacula (L.)
	Pluvialis squatarola (L.)
	Pluvialis apricaria (L.)
	Vanellus vanellus (L.)
Family	Scolopacidae
	Calidris canuta (L.)
	Calidris alba (L.)
	Calidris ferruginea (Pontoppidan)
	Calidris alpina (L.)
	Gallinago gallinago (L.)
	Limosa limosa (L.)
	Limosa lapponica (L.)
	Numenius phaeopus (L.)
	Numenius arquata (L.)
	Tringa erythropus (Pallas)
	Tringa totanus (L.)
	Tringa nebularia (Gunnerus)
	Actitis hypoleucos (L.)
	Arenaria interpres (L.)
Family	Phalaropidae
	Phalaropus lobatus (L.)
	Phalaropus lulicarius (L.)
Family	Laridae
	Larus ridibundus (L.)
	Larus canus (L.)
	Larus marinus (L.)
Order	Passeriformes
Family	Corvidae
	Corvus frugilegus (L.)
	Corvus corone (L.)
Class	Mammalia
Order	Odontoceti
Family	Phocaenidae

Phocaena phocaena (L.)

Order Carnivora
Family Phocidae
Phoca vitulina L.

FLORA

Division Chlorophyta
Family Cladophoraceae
Cladophora sp.
Chaetomorpha sp.
Bryopsis sp.
Family Ulvaceae
Ulva lactuca (L.)
Enteromorpha sp.

Division Phaeophyta
Family Fucaceae
Fucus vesiculosus L.

Division Rhodophyta
Family Bangiaceae
Porphyra umbilicalis (L.) Lyngb.
Family Gigartinaceae
Chondrus crispus (L.) (Stackh)
Family Dumontiaceae
Dumontia incrassata (Müll) Lamour
Family Corallinaceae
Corallina officinalis L.
Family Ceramiaceae
Ceramium rubrum (Huds.) Ag.

Division Angiospermae
Family Chenopodiaceae
Salicornia sp.
Family Zosteraceae
(*Zostera marina* L.)
Zostera angustifolia (Hornem) Reichb.
Zostera noltii (Hornem)
Family Graminae
Spartina anglica C.E. Hubbard

APPENDIX 5b

Composition of contents of nekton/drift net inserted into creek near to station CIV4 for the period of two tides. Weight of detritus are dry weights.

	12.4.78	20.7.78	18.10.78	15.1.79
Fish				
<u>Pleuronectes platessa</u>	2	2	2	-
<u>Sprattus sprattus</u>	1	-	-	-
<u>Gasterosteus aculeatus</u>	1	-	2	-
Crustaceans				
<u>Carcinus maenas</u>	4	3	5	3
<u>Crangon crangon</u>	-	23	14	-
<u>Neomysis integer</u>	92	ca.16,000	108	-
<u>Gammarellus homari</u>	3	-	-	-
Polychaetes				
<u>Hediste diversicolor</u> (ripe)	3	4	-	-
<u>Sphaerodoropsis minutus</u>	1	-	-	-
<u>Pygospio elegans</u>	1	-	-	12
Molluscs				
<u>Hydrobia ulvae</u>	3	1	-	1
<u>Macoma balthica</u>				
<10mm	3	-	-	4
>10mm	156	12	41	18
<u>Cerastoderma edule</u>				
<15mm	-	-	1	3
>15mm	1	7	1	1
Detritus				
Hydroid skeletons	ca.74g	ca.12g	ca.12g	ca.25g
<u>Enteromorpha</u> fragments	ca.2g	ca.4g	-	-
<u>Ulva</u> fragments	½g	-	-	-
<u>Puccinellia</u> (whole plants)	1	-	-	4
<u>Spartina</u> fragments	½g	-	-	ca.80g
Feathers	1	-	3	2
Man made materials	ca.12g	½g	-	½g