COMMUNITY STRUCTURE AND PRODUCTION OF THE BENTHIC MACRO-INFAUNA OF SOUTHAMPTON WATER

by

Joseph Adegoke Oyenekan, M.Sc., M.I.Biol.

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Department of Oceanography,
University of Southampton,
SOUTHAMPTON, SO9 5NH.

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ABSTRACT

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By Joseph Adegoke Oyenekan

The study area covers some 600 hectares of the sublittoral zone of the industrialized region of Southampton Water. The sublittoral benthic macro-infauna was sampled in May 1978 and repeated in May 1979. Four selected stations were sampled bimonthly between July 1978 and March 1980. Physico-chemical and biological parameters affecting the community structure in the area were discussed. Seasonal changes in the parameters were followed to assess factors affecting the distribution and abundance of major faunal species.

Polychaetes were numerically dominant, *Caulleriella* being dominant on the eastern side and the mouth of the estuary and *Capitella* on the western side. Diversity and faunal indices measured showed the community to be unstable. The number of species at all selected stations declined throughout the study.

The life cycle of some dominant species were investigated. Many of the species bred throughout the year with peak recruitments in summer. Their life cycle and those of related species elsewhere are discussed.

Biomass and secondary production estimates were calculated for eighteen species. *Mercenaria* emerged as the most productive and biomass dominant species. Total macro-faunal production is compared with other studies.

The community of the study area compares well with a typical *Macoma* community with *Mercenaria* and *Crepidula* replacing *Macoma balthica*. The study area is a physically controlled community, with greater stress on the western side. The effects of pollutants such as hydrocarbon and sediment metals on the community are discussed.

ACKNOWLEDGEMENTS

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DEDICATION

To the evergreen memory of my sisters,

Mrs. Adedoyin Olukanni

and

Mrs. Aderonke Oyeniyi

who passed to the great beyond during the

the course of this study

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SECTION ONE

GENERAL INTRODUCTION

One of the most important principles in ecological thought and practice is the concept of community which emphasises that diverse organisms usually live together in an orderly manner. A biotic community was described by Odum (1971) as an assemblage of populations living in a prescribed area or physical habitat possessing some unique attributes. Communities are often named and classified according to major structural features such as dominant species (Petersen, 1913; Thorson, 1957); physical habitat (Jones, 1950); functional attributes, for example, type of community metabolism (Odum, 1971).

Investigations of the intertidal and sublittoral communities in both coastal and estuarine waters (Buchanan, 1963; Cassie and Michael, 1968; Gray, 1974; Warwick and Davies, 1977) have largely been confined to the distribution of the constituent species and their sediment relationships. Such an approach is of limited value since it lacks an understanding of the fundamental ecology of the species, a prerequisite towards establishing inter-relationships. Changes in the community structure, biomass and production not only provide adequate ecological information, but also permit comparisons between different ecosystems. Regular short interval sampling over a long period of time allows changes in community structure to be followed.

Most information on secondary production of benthic marine systems has accumulated since 1970 in spite of various attempts by several workers over two decades ago (Sanders, 1956; Knuenzler, 1961). Much of benthic secondary production studies have focused attention on single species populations (Golikov and Scarlatto, 1970; Chambers and Milne, 1975; Sheader, 1977). Few estimates of total macrofaunal secondary production have been made over short periods usually less than three years (Buchanan and Warwick, 1974; Warwick and Price, 1975; Rosenberg, 1977; Warwick et al, 1977, 1978); long term studies of Buchanan et al (1974) suggest a considerable variation in species composition with overall production remaining stable.

In Southampton Water, an estuary of multiple usage, several ecological studies have been made: harpacticoids, (Barnett, 1959; Wormald, 1972); polychaetes (George, 1962; 1964; Esser, 1972); lamellibranchs (Ansell, 1963a; Barnes, 1973; Mitchell, 1974; Hibbert, 1976); general macrofaunal species (Soulsby, 1978; Levell, 1979).

Apart from Hibbert's (1976) investigation of the bivalve populations of the intertidal Hamble Spit, production studies of the benthic macrofaunal species in Southampton Water have been neglected. This makes it impossible to assess changes within communities which might have taken place during the progressive industrialization of the area.

The effects of industrialization on ecological systems have long been of great concern to biologists. The level of environmental factors and their rates of change in coastal and estuarine waters are determined by natural and man imposed conditions. Estuaries have been of particular interest as a sink for disposal of domestic and industrial effluents. The biological activities of estuaries provide support for shell fisheries. Some deleterious effects, however, arise from the addition of certain substances to estuarine systems or redistribution of such substances within estuaries. Industrial and municipal wastes form the bulk of pollution in estuaries, although land run-off containing fertilizers and pesticide residues carried into estuaries by rivers and land drainage are a significant component.

Some of the effects of both organic and inorganic industrial pollutants on marine and estuarine organisms are well documented (Naylor, 1965; Baker, 1969). The mechanisms possessed by organisms allowing them to cope with natural fluctuations in the concentrations of toxic substances are particularly important in polluted regions. Species vary in their degree of tolerance with the result that under polluted conditions, the ecological balance may change in favour of the more tolerant organisms, some of which have become useful indicators of pollution. The pollution stress on an ecosystem is manifested clearly on responses affecting a variety of parameters, for example, diversity, stability, biomass and production. Production may, to a certain extent, be increased at the expense of diversity and biomass. Nevertheless, beyond a certain optimal point, production itself becomes adversely affected.

The most obvious effect of moderate levels of pollution on an ecosystem is the reduction in species diversity (Anger, 1975; Pearson, 1975; Pearson and Rosenberg, 1978; Gray, 1979). Those organisms incapable of tolerating the effects of the pollutants decline while those which can, proliferate and may then exclude further species over which they have a competitive advantage. In severe pollution circumstances, both diversity and biomass are reduced up to a critical point where the environment may become azoic. A great impoverishment of the environment has been reported in the immediate vicinity of the oil refinery outfall in Southampton Water (Baker, 1969) which is within the area of the present study. Garber (1960) found that there was little correlation between free floating marine plankton populations and the presence of pollution and suggested the use of benthic organisms as pollution parameters. An interesting study by Grassle and Grassle (1974) suggested the polychaetes Capitella capitata and Polydora (ligni) ciliata as indicators of organic pollution in soft sediments.

The few secondary production studies of the benthic macrofauna so far carried out have been largely restricted to either intertidal or marine subtidal communities (Lie, 1969; Peer, 1970; Buchanan and Warwick, 1974; Kirkegaard, 1978) with a handful of studies in the estuarine littoral environment (Warwick and Price, 1975; Rosenberg, 1977). The present study is perhaps the first investigation of secondary production of the benthic macro-infauna in an industrialized estuary. Williams (1976) showed that the primary productivity of the phytoplankton community in Southampton Water far exceeds that of benthic microalgae. He suggested that in view of the high sedimentation rate in the estuary and the high tendency for the benthic microalgae to be cut off from the light source, the low benthic primary productivity would have significant effects on the secondary production of the benthos at the higher trophic levels.

Many detailed studies on the community structure of the benthos at certain localities around the British Isles are documented (Buchanan, 1963; Gage, 1972; Buchanan et al, 1974; Gray, 1976; Warwick and Davies, 1977; Buchanan et al, 1978). Studies in Southampton Water have met limited success. The Southern Water Authority's annual summer samplings of the estuary and the Solent provided useful information on the community structure on which detailed further studies of the benthic macrofauna of the estuary could be based. Nevertheless, the annual samplings of the Authority (1975-1976) and of the Field Studies Councils, Oil Research Unit, Orielton (1977-78) gave no information regarding seasonal fluctuations in the benthic macrofauna of the estuary.

The main objectives of the present study were:

(i) To investigate spatial and temporal changes in the community structure of the benthic macrofauna of the central industrialized area of Southampton Water (see Fig. 2.1) over a 20 month period.

(ii) To study the seasonal cycles in abundance, species composition and relative abundance at four selected sites with a view to providing baseline data on the distribution and abundance of benthic macro-infauna within the estuary.

(iii) To examine the influence of industrial discharge around Fawley (in particular, hydrocarbon and trace metals) on the ecology of the macrofauna.

(iv) To study the life cycle of the dominant faunal species in the area with a view to establishing the reproductive strategies of the species in an industrialized estuary.

(v) To estimate the secondary production of the dominant benthic macrofaunal species and the total macrofaunal community in the study area in order that estuarine sublittoral production might be compared with that of intertidal and marine sublittoral communities.

Detailed study was made at four selected sites to allow temporal changes in species composition, diversity and biomass over a period of 20 months (July 1978 - March 1980) to be followed. This was aimed at providing insights into the probable influence of the industrial discharges on the benthic communities.

SECTION TWO

SURVEY OF THE BENTHIC MACRO-INFAUNA OF SOUTHAMPTON WATER

2.1. Introduction

Many faunistic surveys of British estuaries have so far been carried out, e.g. Exe, (Holme, 1949); Tamar and Lynher, (Spooner and Moore, 1940); the Cheshire Dee,(Stopford, 1951); the Severn,(Rees, 1940); Mersey, (Bassindale, 1938: Corlett, 1948); Southampton Water (George, 1962; Ansell, 1963; Barnes et al, 1973; Soulsby, 1978; Levell, 1979). Most investigations on the bottom fauna of Southampton Water have hitherto been largely confined to the littoral zone (Barnett, 1959; Baker,1971; Essex,1972; Hibbert,1976). Some of the studies have been directed towards the ecology of single species (Ansell,1968; Barnes,1973; George,1962) with only a little attention devoted to multiple species studies (Hibbert,1976; Lauriston,1977).

In the sublittoral, the investigations on the benthic estuarine organisms in Southampton Water have focused exclusively on surveys covering the entire estuary including in most cases the Solent. These include studies of the plankton (Raymont,1972); the lamellibranchs (Barnes et al,1973; Coughlan and Holmes,1971); the benthic diatoms (Hatton,1977); and total macrofauna (Barnes et al,1971; Soulsby,1978; Levell,1979). Previous studies of the benthic organisms of the estuary suggested that Southampton Water is an estuary where sediment is predominantly mud with varying degrees of intermixed sand with impoverished fauna (Baker,1971; Dyer,1973; Dicks,1976).

The distribution of benthic organisms may be influenced by a wide range of physical and environmental factors. An attempt to interpret benthic distribution with regard to all such environmental factors would be a major piece of work. It is generally considered that such studies deal with a complex interaction of factors, many of which are difficult to quantify and measure. Sediment types, salinity, temperature, light intensity, nutrient levels and wave action, all undoubtedly influence faunal distribution, the first three are often considered as being of fundamental importance.

Although the effects of discharge from the refinery at Fawley (see Figure 2.1) on the salt marshes of Southampton Water have been discussed (Baker,1971; Dicks,1976), the influence of the industrial

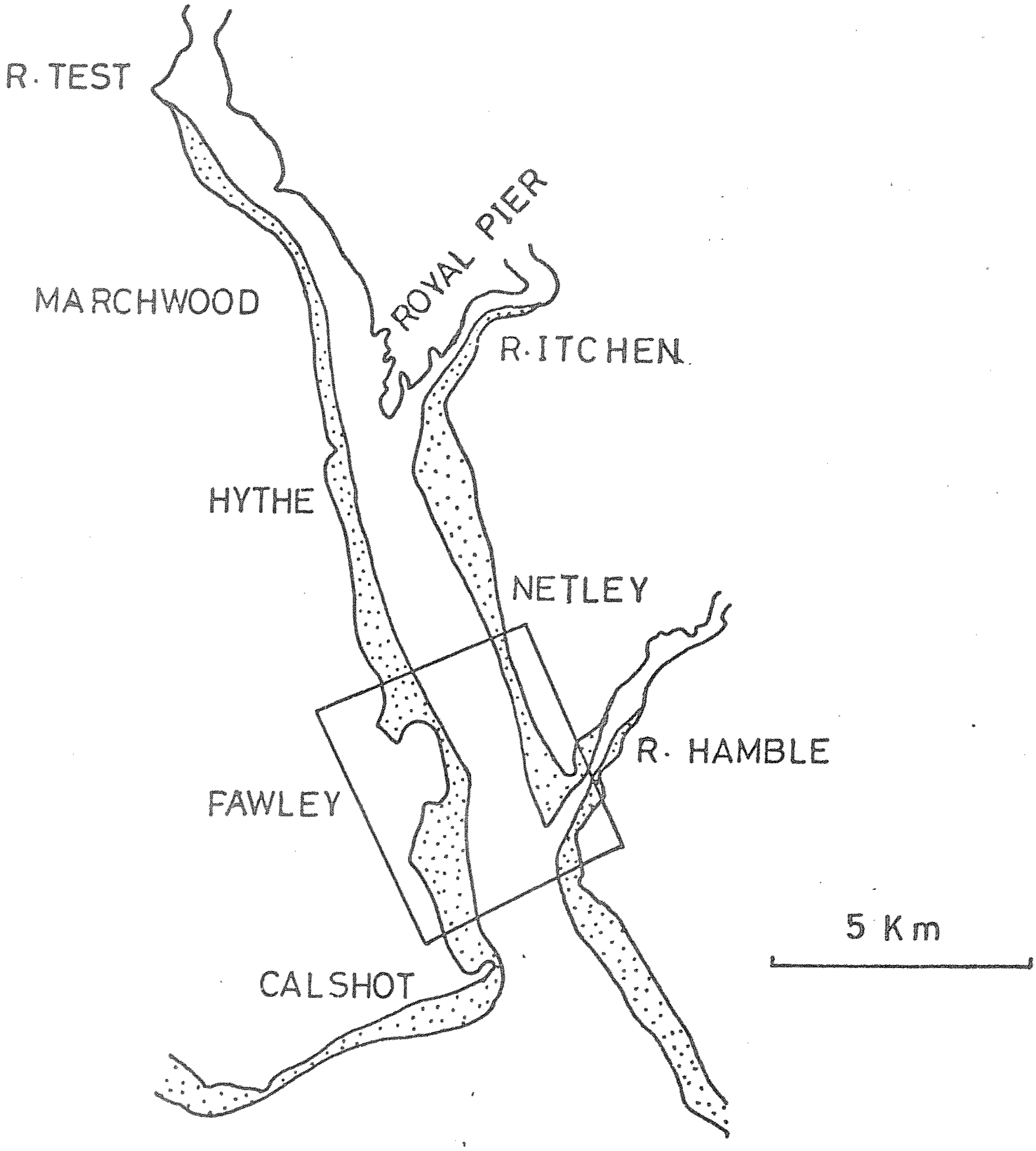


FIG. 2.1 MAP OF SOUTHAMPTON WATER SHOWING STUDY AREA INSERT.

discharge on the sublittoral ecology of the estuary has suffered considerable neglect. The present study area was chosen since it represents probably the area within the estuary subject to the greatest amount of industrial discharge. Refinery effluent, one of the major industrial discharges into Southampton Water, contains materials other than petroleum hydrocarbon, which may have deleterious effects on the estuarine organisms. Jenkins (1964) studied the toxic effects of phenols, ammonia and sulphides on fish and concluded that the increased pH of some refinery waste water led to higher mortalities as a consequence of the ammonia levels present. Reish (1964) studied the effects of oily discharges on marine organisms and concluded that toxic refinery wastes may be directly responsible for mortality of marine organisms. A secondary effect could result in oxygen depletion of the water as a consequence of biological oxidation of the organic part of the effluent.

Trace metals are often present in the refinery effluent, copper being the most notable. Copper chloride is used as a 'sweetening' agent and acts by converting mercaptans to disulphides (Knap,1978). Copper is very toxic at low concentrations (Bryan,1971).

In spite of the potential effects of industrial wastes on the estuarine fauna, particularly the benthos, the sublittoral community of Southampton Water have lacked any previous intensive studies. The annual summer samples of the Southern Water Authority, Central Electricity Generating Board and Orielton Oil Pollution Research Unit ignored seasonal changes in species composition between the sampling periods. Long term studies off the coast of Northumberland (Buchanan et al,1978) provide useful information on the factors affecting production. The present study in an industrialized estuary is assumed to elucidate the effects of industrial discharge on the community structure and production of Southampton Water.

The study area was limited to a sizable part of Southampton Water which could be easily covered in detail and the stations sampled evenly spaced so as to give a clear picture of spatial distribution of the benthic macro-infauna. The mesh size of the sieve used in the present study was o.5mm. Previous studies on the benthic macrofauna of Southampton Water have used 1 mm. sieves, which must have resulted in the loss of many small polychaetes, characteristic of silty soft bottom deposits. Buchanan et al (1974) estimated a loss of almost 75% of the total individuals of three important producers off the coast of Northumberland due to the use of sieves of mesh size greater than 0.5mm. The present study aimed at providing accurate production estimates by using a 0.5 mm sieve.

Twenty-four evenly selected stations (Fig. 2.2) were sampled in May 1978 and repeated in May 1979. Four stations were selected for monitoring and sampled regularly every two months with the aim of assessing changes in the benthic macrofaunal assemblages. The species distribution in relation to the physico-chemical parameters of the study area was investigated to establish the role of the constituent species in the ecosystem. The influence of human activities on the composition and distribution of the macroinfauna of the estuary was also studied.

2.2 General description of the study area

Southampton Water, a 16 kilometer long estuary runs in a north west-south-easterly direction and opens at its seaward end to the Solent. It is the drowned lower portions of the Test and Itchen rivers, forming a typical coastal plain estuary (Dyer,1973). Near the mouth of Southampton Water, the depth is of the order of 12 to 13 metres; the rest of the estuary has banks of soft mud with a deep channel dredged to a depth of more than 10 metres. Figure 2.2 is a map of the study area showing the location of the sampled stations in the surveys.

Owing to the interfacing properties of estuaries, there often arise conflicts of interest on how best the facilities provided by estuaries may serve the population. Southampton Water serves as a sea port, a centre of recreational sailing, a sink for the disposal of domestic and industrial wastes, as well as a site for shell fisheries. The study area, approximately 600 hectares in area, accommodates the outfalls of 'satellite' industries: Union Carbide, Monsanto Chemicals, International Synthetic Rubber and the Esso Petroleum refinery on the western side and Shell Mex jetty and the Hamble river mouth on the eastern side. The Esso refinery at Fawley is at present the largest petroleum refinery in the United Kingdom and one of the largest in Europe. The expansion of the refinery in 1971 makes it the sixth largest refinery in the world, with a total refinery capacity of about 20 million tonnes per year.

In spite of air fin cooling technology beginning to replace the need for copious quantities of cooling water, Esso refinery at Fawley in 1976 used about 450 million litres of sea water daily. This water

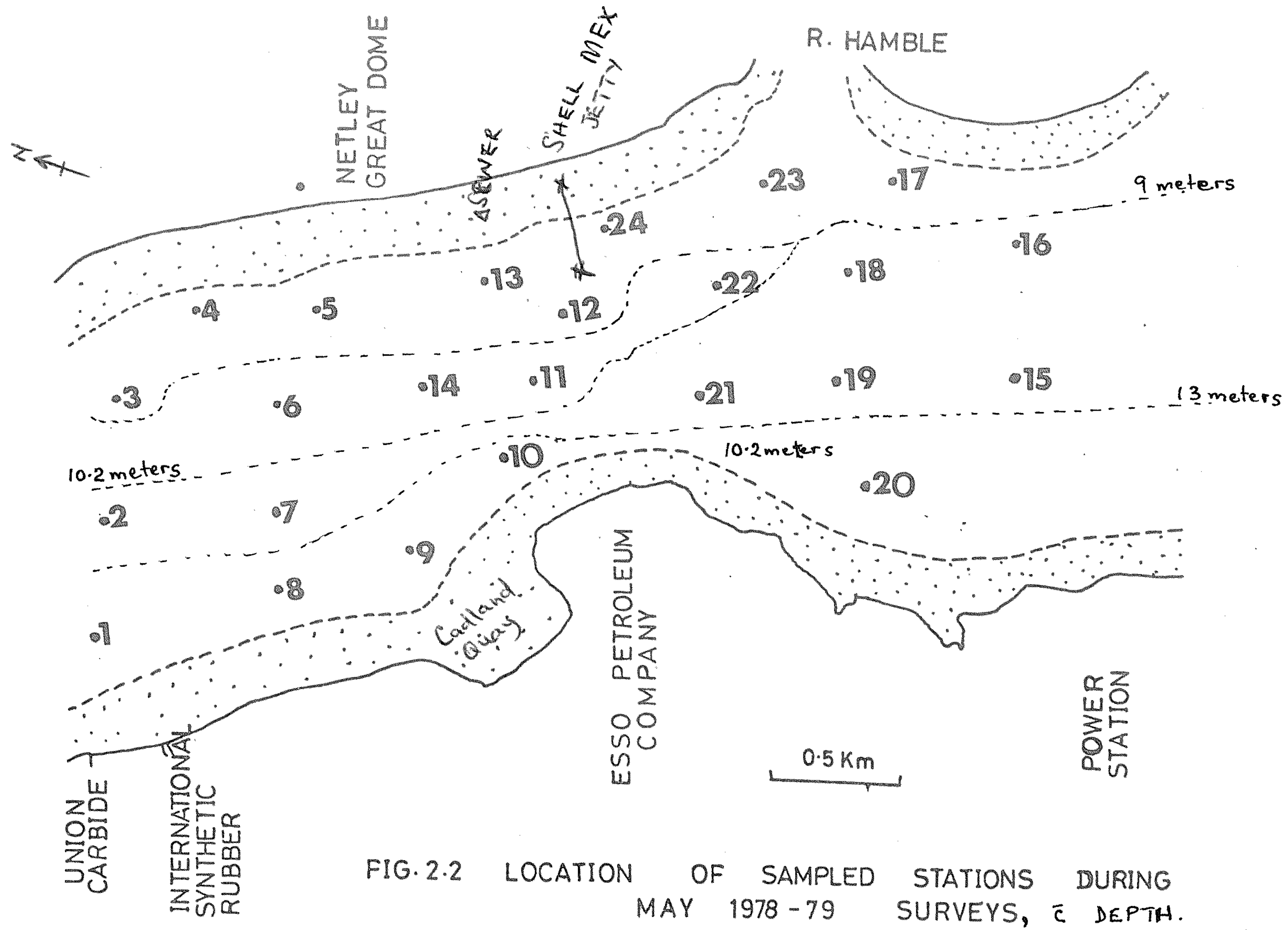


FIG. 2.2 LOCATION OF SAMPLED STATIONS DURING MAY 1978 - 79 SURVEYS, c̄ DEPTH.

contains organic effluent from the refinery processes (Knap,1978). The majority of heavy and floating oils are removed by the A.P.I. separators within the refinery complex. Nevertheless, some dissolved and particulate absorbed hydrocarbons are discharged into the estuary. Baker (1973) estimated the release of twenty tonnes of oil into Southampton from all sources daily. Williams (1976) estimated a total yearly input of 13,500 tones of organic carbon into the estuary in 1974, originating as effluents from the major industries within the area. Eighty per cent of the organic carbon came from the refinery alone. Knap (1978) estimated a daily input of about 10-15 tons of hydrocarbon into the estuary, a value which far exceeds the 0.4 tons per day discharged into a larger area of San Fransisco Bay (Disalvo, Guard and Hunter, 1975). Disalvo et al (1975) regarded the fauna of San Fransisco Bay as polluted by petroleum hydrocarbon. In that case, some concern should be given to the situation in Southampton Water.

The influence of freshwater flow from the Hamble river is slight with the water column in the study area remaining almost homogenous, though the inflow from the Test and Itchen rivers is marked in the upper reaches of Southampton Water. Dyer (1973) found that the salinity increased only gradually towards the mouth of the estuary. Although the area may be referred to as an estuary, Southampton Water is essentially marine in character. At high water, the mouth of Southampton Water shows salinities throughout the water column exceeding 34‰ and near the Royal Pier, the salinity never falls below 31‰ at low water. Raymont (1972,) Dyer (1973) described Southampton Water as moderately stratified.

2.3. Spatial distribution of the physico-chemical parameters.

2.3.1. Field studies

Twenty four evenly spaced stations about 300 metres apart (fig.2.2) were sampled in May 1978 and repeated in May 1979. Four $0.1m^2$ van Veen grab samples were taken with the boat anchored at each of the stations, which were located with the aid of a marine boat 'sestrel skipper' compass and land marks. Three grab samples were washed carefully through a 0.5mm sieve by gentle agitation to prevent damage to the infaunal species. Material retained on the sieve was preserved in labelled jars containing a 5% formalin-sea water solution and stained in Rose Bengol. The dye stained organic matter including the fauna red to ease further sorting in the laboratory. The top 10cm of the fourth grab sample at each station was placed in a labelled polythene bag and stored in a deep freeze prior to ovendrying for further analysis.

2.3.2 Laboratory investigations

(a) Sediment Analysis

(i) Method

The particle size analysis of the sediment was essentially the rapid analysis of sediment outlined and recommended by Buchanan and Kain (1971). An accurately weighed 25g sample of the oven-dried sediment from each station was pretreated with a solution containing a sequestering agent (sodium hexametaphosphate) overnight. The sample was initially wet sieved through a 63 µm sieve to separate the sediment into sand and above and silt/clay fractions. The retained material on the sieve was dried to constant weight at 80°C and placed on a mechanical shaker for 15 minutes. Any remaining silt/clay fraction passed through the sieve. The percentage fines (particles of silt and clay, diameter 63 µm) was calculated by subtraction of the oven dried weighed fraction retained on the sieve after shaking from the initial weight of the oven dried sediment sample.

(ii) Results

Though the sediment analysis is often presented in the form of a cumulative curve, the result is here presented in sand and silt/clay fractions owing to the muddy nature of the study area. Table 2.1. shows the percentage composition of sand and silt/clay fractions of the sediments at the stations during the two surveys. The study area was predominantly mud with varying degrees of intermixed sand. The western side possessed in general higher silt/clay but the proportion of sand increased eastwards and seawards. The distribution of the fines (particles with 63 µm diameter) in May 1978 survey is shown in figure 2.3.

The sediment of the western side around stations 2 and 9 contained less than 20% sand. The region was characterised by black oily mud with a distinct hydrogen sulphide odour and contained a few dead shells mainly of *Cerastoderma edule*, *Mercenaria mercenaria* and occasionally *Hydrobia spp.* The sediment became greyish towards the eastern side where the sand content was generally higher. The eastern side sediments were sandy mud and were more compact than the softer western sediment.

No. of Station	1978	1979
1	91.87	99.51
2	75.02	99.22
3	78.70	99.02
4	65.93	97.52
5	55.11	96.51
6	92.35	95.50
7	76.77	99.16
8	74.60	99.26
9	80.58	96.87
10	76.89	98.78
11	83.52	77.53
12	45.23	75.41
13	38.37	38.27
14	71.89	66.73
15	72.03	92.44
16	57.67	49.77
17	33.19	94.69
18	19.64	96.05
19	55.35	82.81
20	67.27	87.38
21	77.93	98.26
22	76.09	77.05
23	78.08	93.18
24	62.27	86.03

Table 2.1 The percentage of the silt-clay fraction at the sampling stations during the 1978 and 1979 surveys.

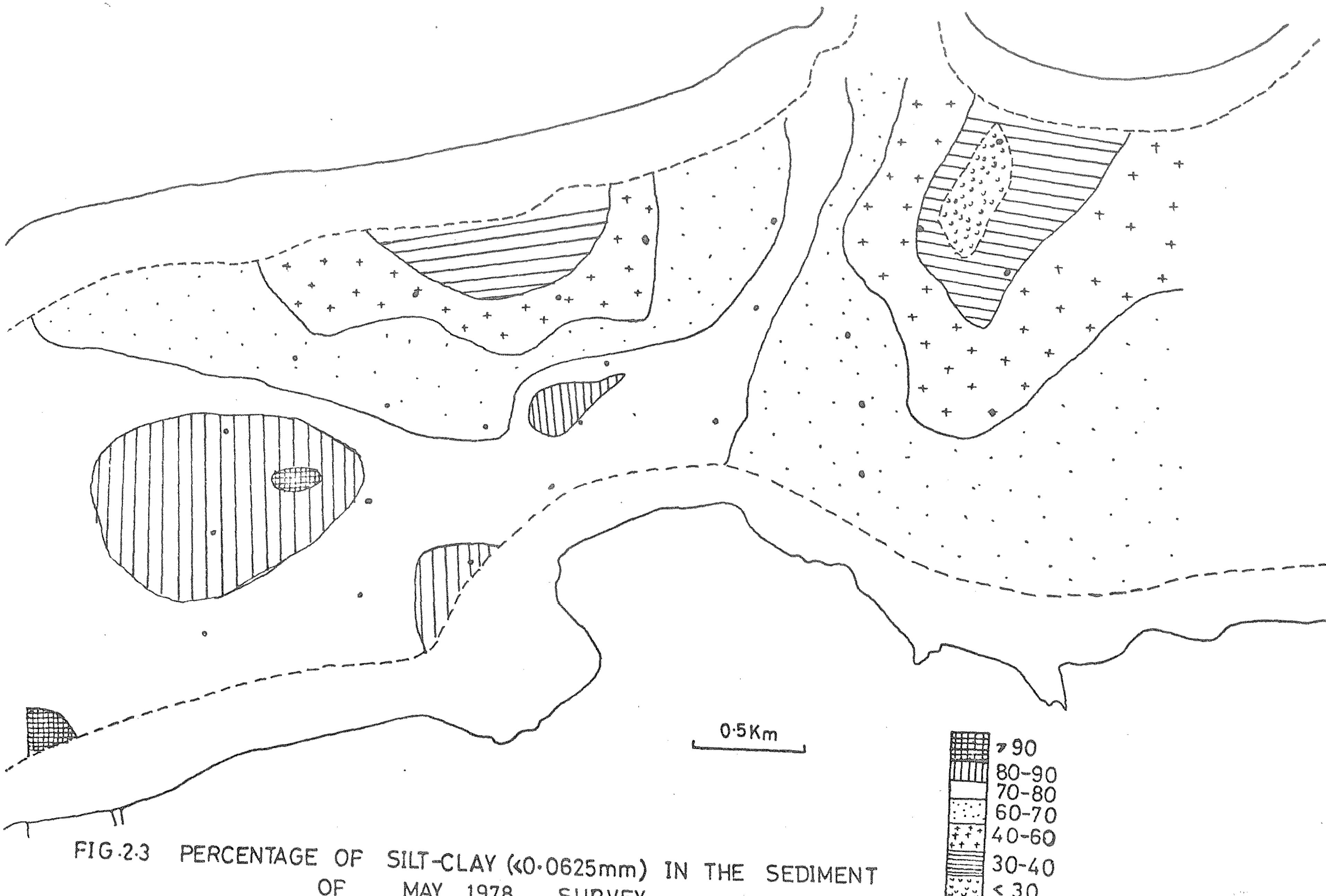


FIG. 2·3 PERCENTAGE OF SILT-CLAY (<0·0625mm) IN THE SEDIMENT OF MAY 1978 SURVEY.

There was a remarkable increase in the silt/clay content of the sediment of the study area between the 1978 and 1979 surveys. Curry et al (1968) working on the sedimentation rate at Fawley estimated a yearly sedimentation rate of 1mm. Knap (1978) estimated a rate of 8cm year^{-1} on the western side of Southampton Water. The sediment towards the entrance of the estuary contained high sand content (>30%) but the midchannel was mainly pebbles and gravels with varying proportions of fines. There were rapid changes in the sediment of the study area, within relatively short distances. The continuous dredging of the channel may be responsible for its high sand content.

(b) Total organic matter (T.O.M.)

(i) Method

Sediment which has been ovendried to constant weight at 80^{o}c was placed in a tared crucible and reweighed before ignition in a muffle furnace at 550^{o}c. After cooling, the crucible and content were reweighed. The loss in weight after removal from the furnace was calculated. The percentage combustible material in the sediment, the total organic matter (T.O.M.) was estimated as

$$\frac{\text{Loss in weight on ignition}}{\text{Initial weight before ignition}} \times 100\%$$

The dissociation of $CaCO_3$ content of the sediment at 550^{o}c was minimal.

This simple and rapid method provides a rough estimate of the total organic matter but does not necessarily measure the quantity of organic matter directly available to the macrofauna. Nevertheless, T.O.M. gives an indication of the amount of food available to benthic animals (Byers et al,1978).

(ii) Results

Table 2.2 shows the percentage total organic matter of the study area during the two surveys. The western side contained higher T.O.M. than the eastern side, with the highest levels around the industrial outfalls (figure 2.4). Generally total organic matter decreased eastwards except around Netley where sewage was discharged. There was a decline in the T.O.M. of the study area between May 1978 and May 1979. There was no significant correlation between T.O.M. and the silt/clay fractions in the investigated area.

No. of Station	1978	1979
1	12.55	10.53
2	12.36	9.91
3	9.36	10.82
4	9.98	7.52
5	7.25	16.12
6	9.58	6.16
7	6.22	5.02
8	12.96	5.32
9	11.92	3.25
10	11.21	10.33
11	10.48	9.19
12	8.75	8.81
13	6.34	3.97
14	14.41	7.65
15	8.19	6.12
16	8.66	2.83
17	4.90	1.70
18	3.62	8.52
19	8.34	10.60
20	7.53	7.05
21	8.27	6.51
22	7.09	3.40
23	17.34	1.45
24	2.61	0.79

Table 2.2. The percentage total organic matter at all stations in 1978 and 1979 surveys

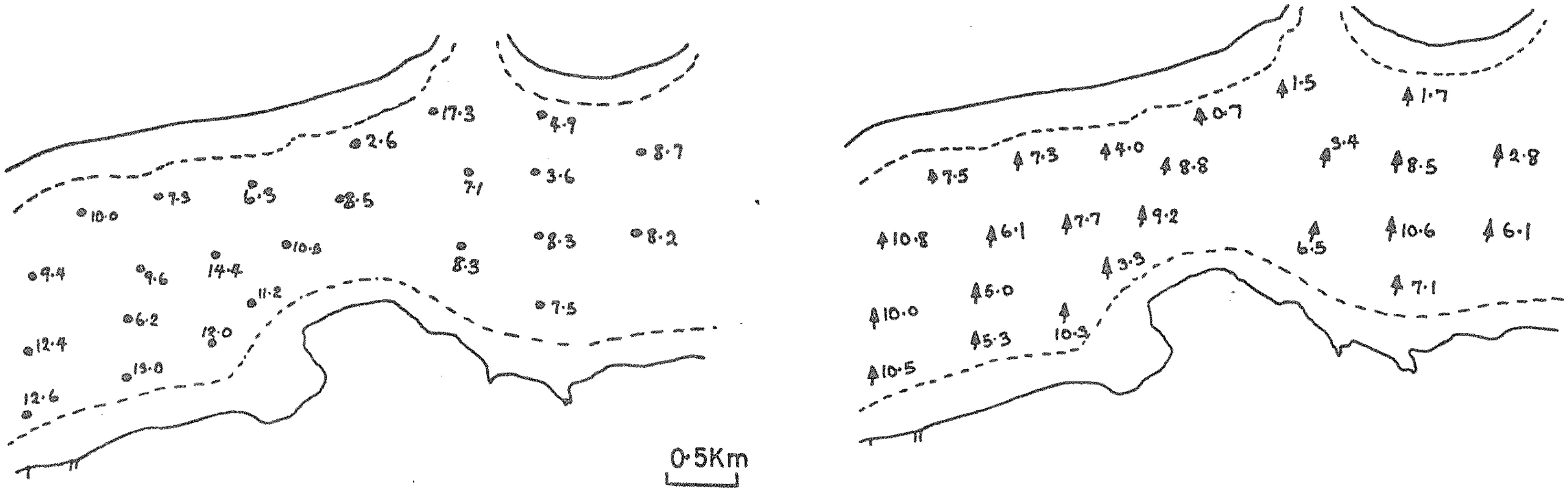


FIG. 2.4 DISTRIBUTION OF TOTAL ORGANIC MATTER (%) IN 1978(•) AND 1979(↟) SURVEYS

(c) Sediment Metals

The methods employed in the determination of the sediment metals vary with different disciplines. The simplest method used inthe present study aims at estimating the total metal level in the sediment and involves X-ray fluorescence spectrometry. This is a device involving excitation of characteristic X-rays by means of a primary X-ray beam. Though qualitative analysis permits samples to be placed in an X-ray spectrometer in virtually any form, quantitative analysis demands compact self-supporting samples prepared in a reproducible fashion. Powdered sediment samples were made into pellets using the procedure described by Norrish and Chappel (1977).

(i) Sample preparation

Ovendried sediment samples were finely ground into powder. Each sample was prepared as a pellet using the technique outlined by Norrish and Chappel (1977) by applying a 4 ton pressure to form a coherent sample. The identity of each sample was written with a marking pen on the boric acid back.

The pellets were then introduced into the X-ray spectrometer, an instrument for dispersing X-rays and for measuring their intensity as a means of making qualitative and quantitative analysis. The X-ray detectors in the spectrometer convert the energy of the individual X-ray photon hitting the sample into measurable impulses of electrical energy. Metals whose levels were measured in the sample depended on the particular programme of metals that the spectrometer was set to identify. Copper, Lead, Zinc and Arsenic were measured but of greatest interest was copper which is used in the refinery processes and therefore could possibly be linked in distribution with hydrocarbons.

(ii) Results

The levels (parts per million) of sediment metals (Cu, Zn, Pb and As) for the study area in May 1978 and 1979 are given in Table 2.3. The distribution of the sediment copper and zinc for the survey in May 1978 is shown in Figs. 2.5, 2.6. In general, the western side contained higher sediment copper and zinc than the eastern side with a high level of sediment copper at a single station (station 13) between Netley Dome and the entrance of River Hamble in 1978. Sediment copper increased at all western stations between May 1978 and May 1979 except those in the mid channel (7, 10, 11, 19). The high decrease at station 13 was

	May 1978				May 1979			
No. of Station	Cu	Zn	Pb	As	Cu	Zn	Pb	As
1	194	182	82	34	179	187	74	24
2	148	150	77	33	272	168	75	23
3	51	91	54	22	65	105	62	18
4	26	69	38	31	30	81	48	21
5	41	81	48	26	28	84	44	14
6	47	117	56	44	65	110	83	20
7	271	160	77	41	111	104	50	7
8	200	179	82	55	290	154	61	22
9	579	138	55	44	854	164	75	22
10	304	137	61	35	89	99	57	12
11	57	112	61	35	42	98	55	7
12	22	98	64	33	43	116	68	21
13	279	159	75	33	15	78	54	11
14	50	220	172	44	25	107	56	19
15	35	85	53	35	32	88	48	15
16	24	81	49	35	21	87	55	13
17	34	86	51	28	11	61	24	14
18	21	40	21	23	29	94	61	19
19	42	135	103	40	17	84	31	43
20	39	122	69	37	74	89	43	16
21	51	108	66	23	87	102	53	19
22	35	97	68	32	40	97	48	27
23	124	102	66	32	15	53	19	13
24	322	145	65	30	15	74	32	19

Table 2.3 Sediment metal levels (in parts per million) at all stations in 1978/79 surveys.

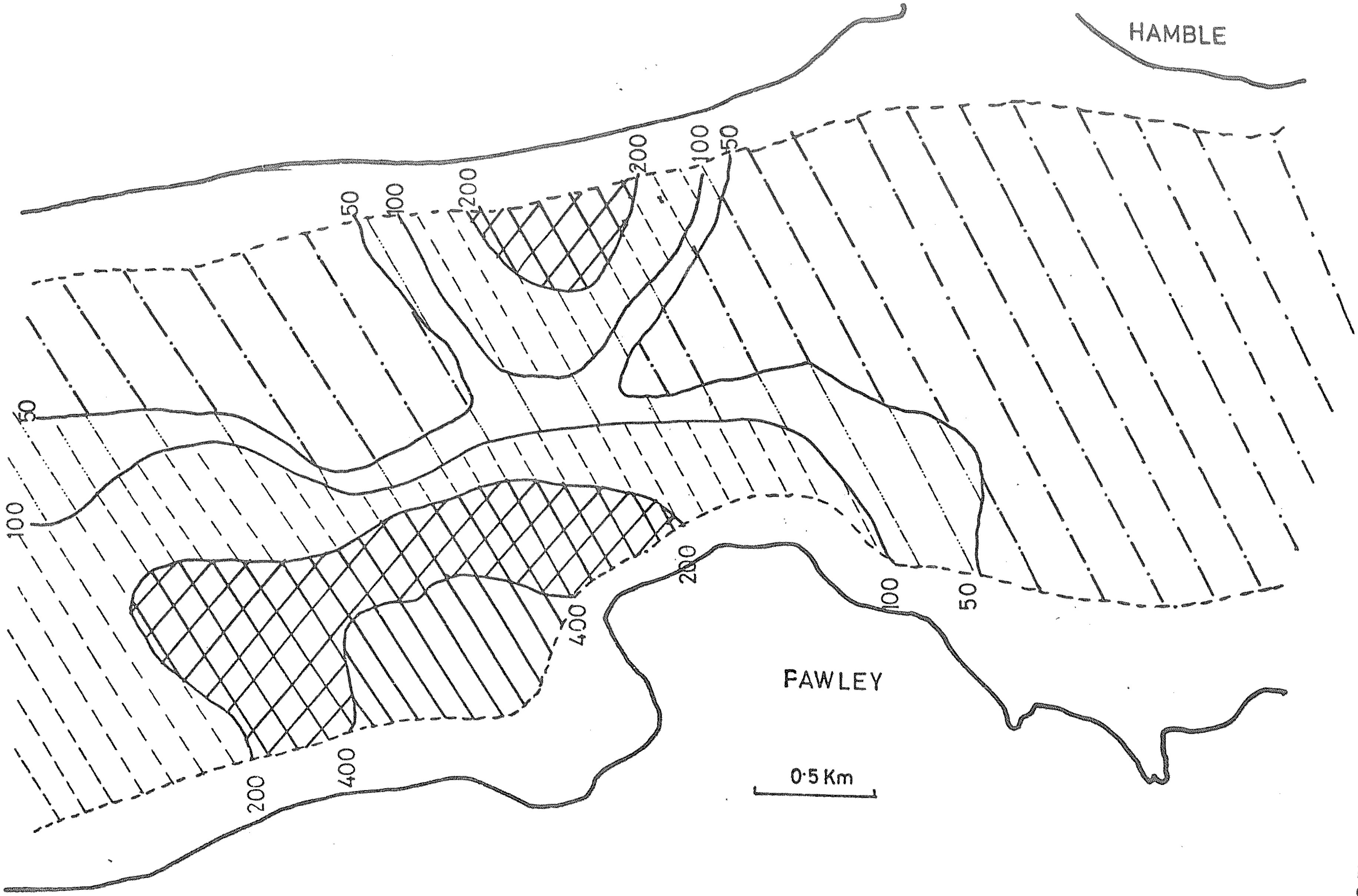


FIG. 2·5 DISTRIBUTION OF SEDIMENT COPPER (p.p.m) IN MAY 1978 SURVEY.

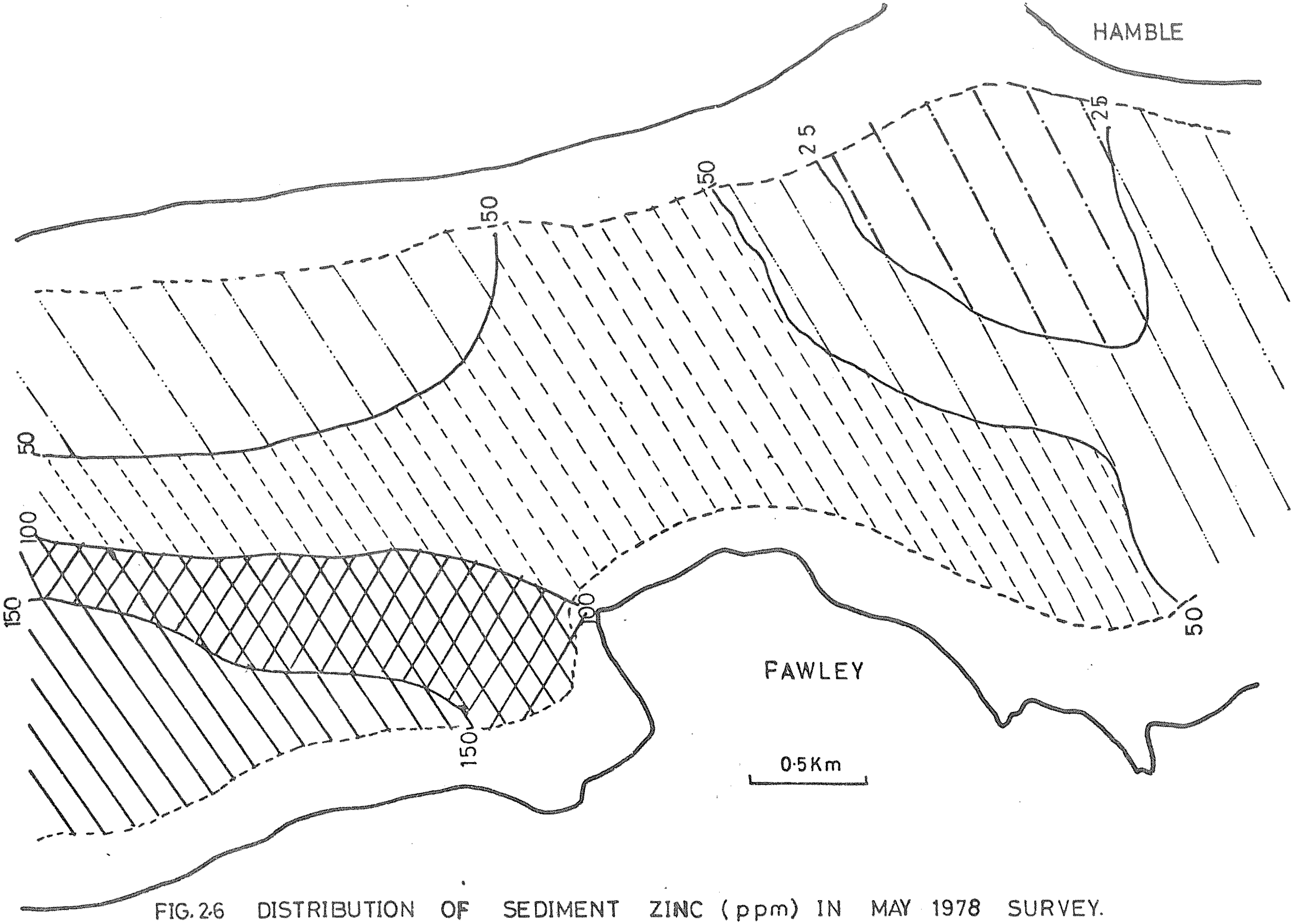


FIG. 2·6 DISTRIBUTION OF SEDIMENT ZINC (ppm) IN MAY 1978 SURVEY.

probably due to the closure of the sewage outfall in the area. The highest concentrations of sediment copper in the study area were in the Cadland quay area.

(d) Sediment hydrocarbons

(i) Method

May 1978 samples were analysed for hydrocarbon content by Cedeno (a post-graduate visitor in the department in 1978) using the method developed by Kiel laboratory and published by Ehrhardt (1972). Each sample was extracted thrice with 50ml aliquots of purified n-pectane, by shaking in a PTFE stopperedseparating funnel. The combined extracts were dried over anhydrous sodium sulphate. The extracts were evaporated to less than 0.5ml in a Bucchi Rotary evaporator and then applied to a 1.5 x 20cm column. The contents, consisting of a top 0.5cm layer of aluminium oxide (120 mesh) were deactivated with 5% water. The hydrocarbon fraction of the contents was eluted with 50ml of 20% benzene in pectane while the lipid fraction remained in the column.

The eluate from the column was evaporated to dryness and redissolved in 1ml of pectane. An aliquot (typically 200ml) was added as a 1 inch band to a silica gel plate. Prior to use, the plate was purified by prerunning in the solvent and then activated by heating at about 160°C. The plate was developed in purified octane.

The various fractions of the hydrocarbon were located by viewing under an ultraviolet source (maximum emission 254 nm) and were identified as follows:

Fraction		Colour
1	Aliphatics	Colourless
2	1-ring aromatics	Dark quenching
3	2 & 3-ring aromatics	Purple
4	4-ring aromatics	Light blue
5	5-ring and above aromatic	Blue

The flourescent binder support contained in the thin layer chromatographic plate was not eluted with benzene but the gross hydrocarbon content of the elutes was obtained by evaporating aliquots and combusting them in a carbon analyser.

(ii) Results

Table 2.4 shows the hydrocarbon content of the sediments taken during the May 1978 survey. The n-alkanes accounted for 7-30% of the thin layer chromatographic (T.L.C.) fraction 1. As judged from the ultra-violet spectrum, the fraction contained no aromatics. The remainder of the fraction was mainly cycloparaffins and branched saturated aliphatics (Knap, 1978). The aromatic fractions accounted for 16-25% of the total hydrocarbon fraction, the 2-3 ring usually being the major though not the dominant one.

The sediment of the study area contained mainly fraction 1, the aliphatics which from T.L.C. analysis was the major output from the oil refinery at Fawley (Knap, 1978). Sediment of Cadland Creek showed high levels of hydrocarbon which decreased eastwards and towards the mouth of Southampton Water (figure 2.7). There was a high significant statistical correlation between copper and hydrocarbon in the study area ($p = 0.001$). Based on the distribution of hydrocarbon, the area of study could be divided into three regions, viz: the Cadland quay as high hydrocarbon region, the deep channel and Esso jetty as region of medium hydrocarbon and the low hydrocarbon region comprising the eastern side and the mouth of the Southampton Water.

(c) Temperature

The average monthly maximum and minimum bottom water temperatures between January 1976 and March 1980 as supplied by the British Transport Docks Board are shown in Fig. 2.8. The temperature at the refinery outfall was about 10° higher than at the jetty southend. The spring water temperature at the jetty was lower in 1977 than in 1976 and continued to fall up to 1980.

2.4.1. Animal sorting

In the laboratory, subsequent treatment and sorting of the preserved material, reduced to manageable size by initial sieving (0.5mm) on deck, followed the procedure recommended by Birkett and McIntyre (1971). The stained material was washed free of formalin through a 0.5mm sieve using tap water. It was later placed in a white plastic tray from which every animal contained in the material was carefully picked. Each major animal taxon was placed in separate petri-dishes. Every individual animal was identified to species where possible and counted. Polychaetes were identified according to the nomenclature of Fauvel (1923; 1927) and

No. of Station	Hydrocarbon (Mg.g-1)
1	1.180
2	1.320
3	1.470
4	.196
5	.276
6	1.222
7	1.827
8	1.996
9	2.434
10	.369
11	.676
12	.764
13	.654
14	.380
15	.180
16	.099
17	.209
18	.327
19	.426
20	1.467
21	.829
22	.554
23	.293
24	.423

Table 2.4 Hydrocarbon measurements (Mg/g) at all stations in May 1978

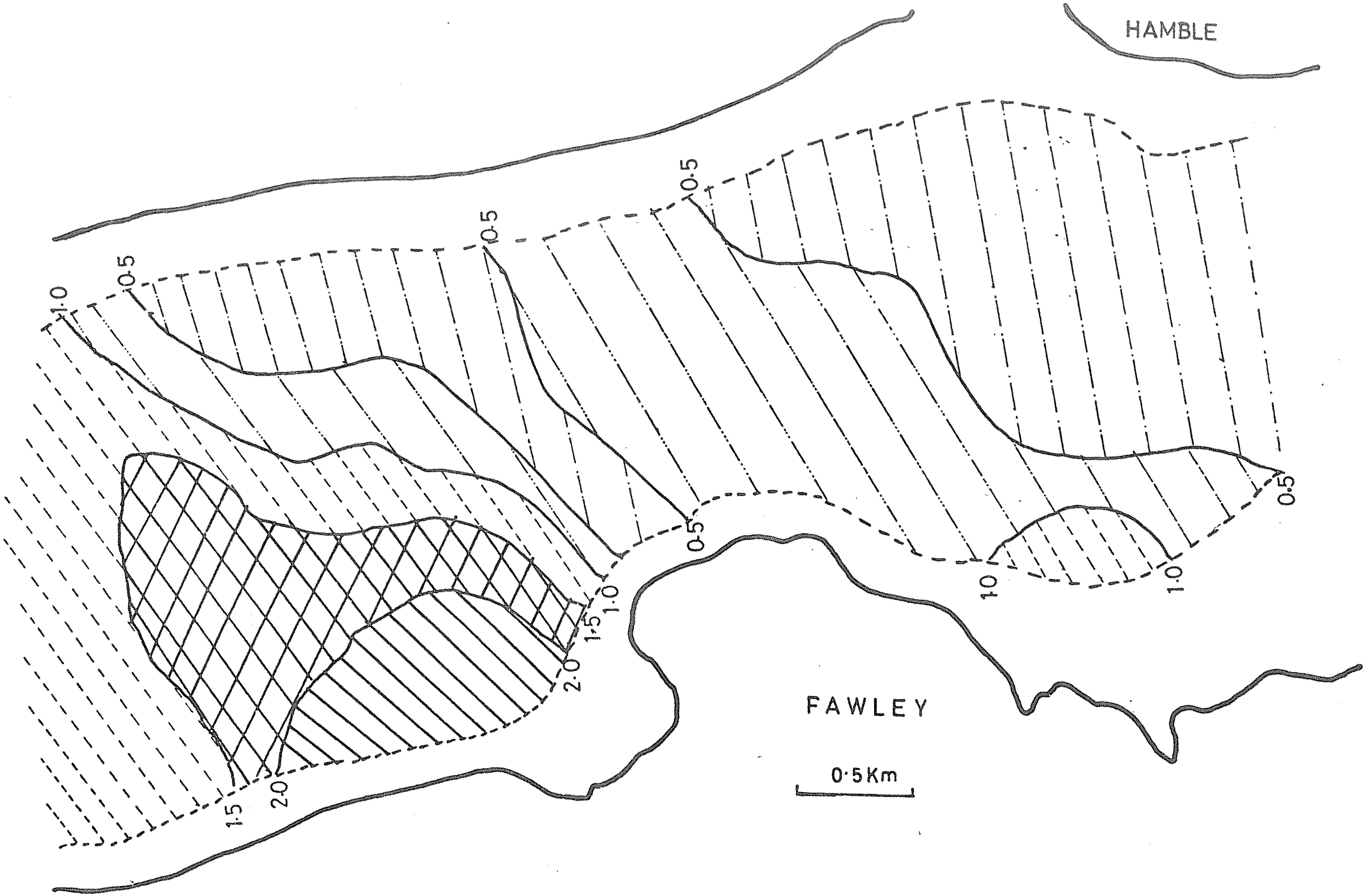


FIG.2.7 DISTRIBUTION OF SEDIMENT HYDROCARBON ($mg.G^{-1}$) IN MAY 1978 SURVEY.

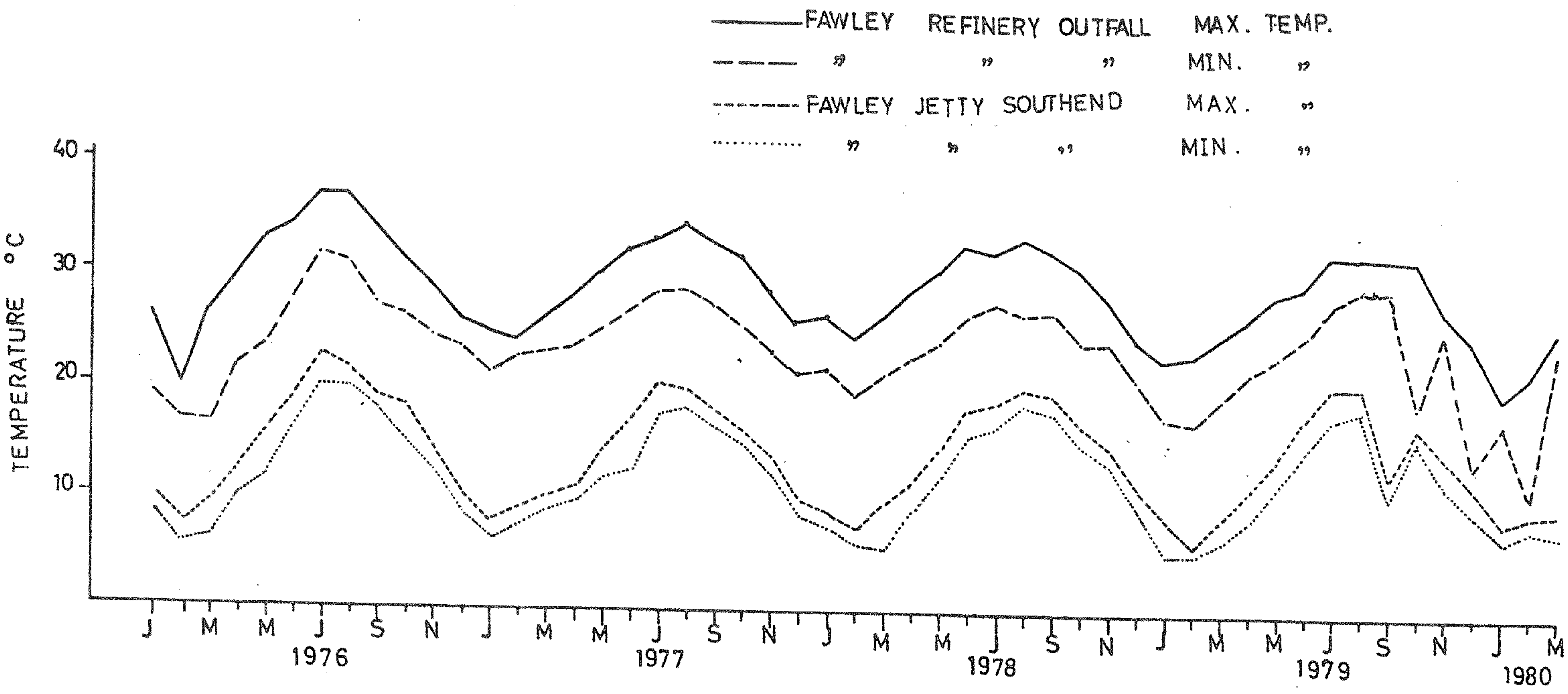


FIG. 2.8. MAXIMUM AND MINIMUM WATER TEMPERATURES (JAN.1976 - MAR.1980)

Pettibone (1954; 1956; 1963). Bivalves were identified according to Tebble (1966) and crustaceans according to Sars (1895-1928); Chevreux and Fage (1925); Naylor (1972) and Lincoln (1979). Echinoderms did not occur in the samples.

2.4.2. Spatial distribution of the biological parameters.

Benthic organisms have been classified mainly on either the nature of bottom deposits or the characteristic elements of the constituting faunal species (Hedgepeth, 1954). Each method of classification has its limitations but generally a relationship appears to exist between the type of community and the nature of bottom deposit. In the present study, classification was based on both the nature of bottom deposit and the characteristic elements of the fauna, with priority on the latter whenever conflict arose.

The numerical abundance of the species recovered in both surveys is given in Appendices I and II. The study area could be conveniently grouped into three regions on the basis of the species richness (number of species per unit area) as follows:

(a) Region of high species richness comprising the eastern side and the mouth of Southampton Water with 9-12 species/$0.3M^2$.

(b) Region of medium species richness comprising the mid-channel and south western side (north of Calshot) containing 6-9 species/$0.3M^2$.

(c) Region of low species richness comprising the Cadland Creek and Fawley Esso refinery jetty with about 3-6 species/$0.3M^2$.

A total of 41 species of benthic macro-infauna were recorded at each survey (a total of 57 species in both surveys) Table 2.5 shows the species richness and numerical abundance of major animal taxa for the two surveys. The polychaetes emerged as the dominant benthic faunal assemblage during the two surveys and accounted for greater than 93% of the total individuals though constituted less than 50% of the total number of species at each survey. The crustaceans represented by a larger number of species than the bivalves were less abundant numerically than the latter.

Number of species (S)

Figure 2.9 shows the distribution of the total macrofaunal species for the two surveys. The net gain or loss between 1978 and 1979 surveys

May 1978

	No. of Species	% of Total S	$^N/7.2M^2$	% of Total N
Polychaeta	20	48.78	12932	93.94
Crustacea	9	21.95	56	0.41
Bivalvia	5	12.20	717	5.21
Gastropoda	5	12.20	52	0.38
Pycnogonida	1	2.44	1	0.007
Tunicata	1	2.44	8	0.06

May 1979

	No. of Species	% of Total S	$^N/7.2M^2$	% of Total N
Polychaeta	17	41.46	57499	97.95
Crustacea	15	36.58	273	0.47
Bivalvia	4	9.76	874	1.49
Gastropoda	3	7.32	51	0.09
Pycnogonida	2	4.88	4	0.07

Table 2.5 The species richness and numerical abundance of major animal taxa from all samples in total area investigated during May 1978 and May 1979 surveys

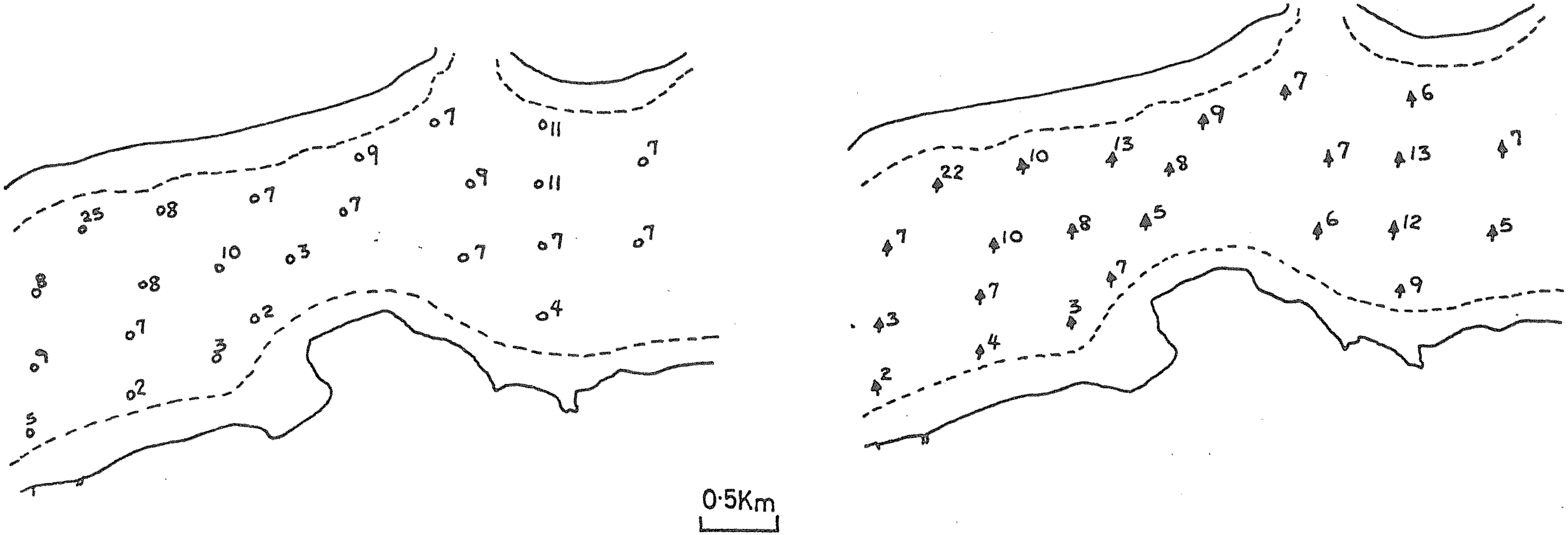


FIG. 2.9. DISTRIBUTION OF NUMBER OF MACROFAUNAL SPECIES /0·3M² IN 1978(○) AND 1979(♠) SURVEYS.

is shown in Fig. 2.10. Though the total number of species during each survey remained stable, there was some degree of change in the species composition at each station. The region of high species richness showed an increase in the number of species by 1979. Twenty five species were common to both surveys; 16 species were recorded only in the 1978 survey and 16 only in the 1979 survey. Of the 17 species of polychaetes recorded in the 1979 survey 13 species were common to both surveys. Five crustacean species were common to the two surveys, but 10 new species, not previously recorded in 1978, occurred in the 1979 survey. Six molluscan species were common to both.

Number of individuals

Figure 2.11 shows the distribution of the total number of individuals (numerical abundance) of the animals in the 1978 survey. The distribution of net gain or loss in the numerical abundance at the two surveys is given in Fig 2.12. The total number of individuals at all stations sampled increased about four fold by May 1979 except at the region of low species richness where the abundance fell drastically. Two species, Caulleriella caputesocis and Abra nitida ranked topmost and were similar in densities in the two surveys while other top ranking species changed in abundance as shown in Table 2.6.

Species distribution

The spatial distribution of the numerically dominant species are discussed below. The benthic macro-infauna occurring in less than 25% of the sampled stations and those with low densities were excluded from the discussion of the species distribution but included in the species and biomass lists in the appendix.

Caulleriella caputesocis

This is a widely distributed cirratulid worm in Southampton Water and occurred at high densities at 22 stations in each of the surveys. It was the numerically dominant species at most stations throughout the study and accounted for 86.2% ($11859/7.2M^2$) and 94.99% ($55758/7.2M^2$) of the total macrofaunal numerical abundance in the 1978 and 1979 surveys respectively. Figure 2.13 shows the numerical abundance distribution of C. caputesocis at both surveys. The worm occurred at high densities in the region of high species richness and by 1979 had increased four fold in abundance. Low densities of the worm were recorded on the western side where further decline occurred in the

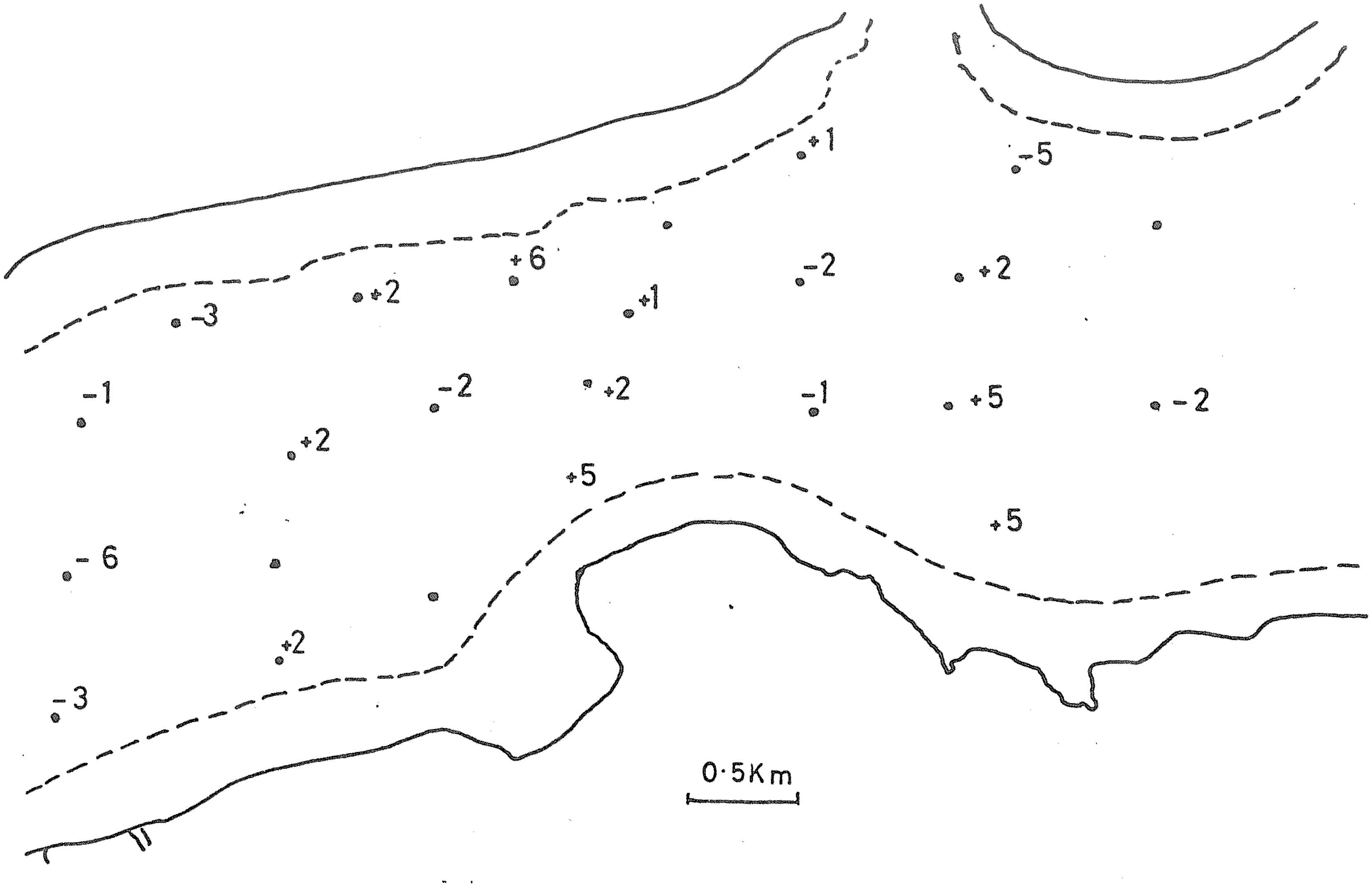


FIG. 2.10. NET GAIN OR LOSS IN NUMBER OF SPECIES /0.3m² BETWEEN 1978 & 1979

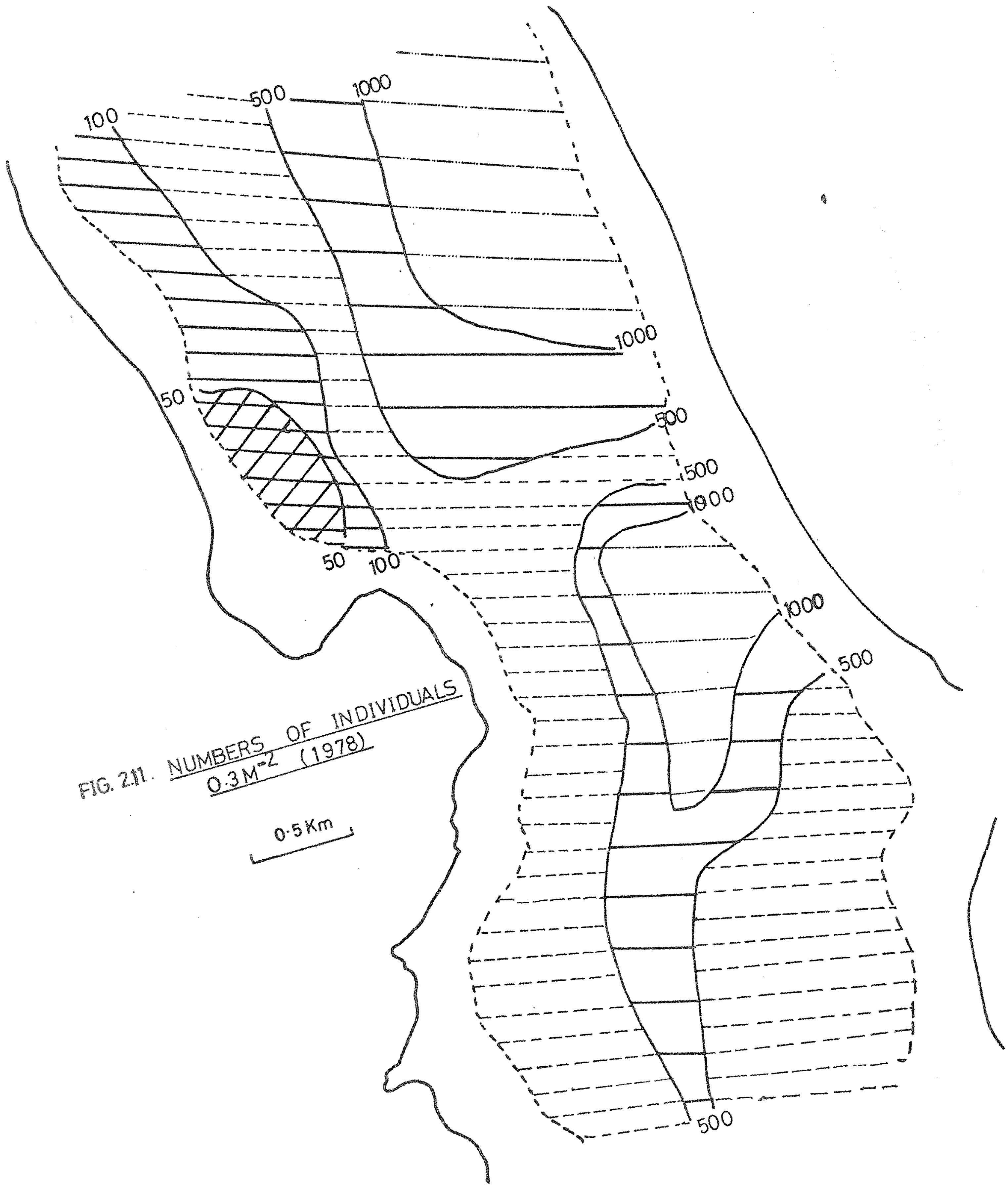


FIG. 2.11. NUMBERS OF INDIVIDUALS 0·3 M^{-2} (1978)

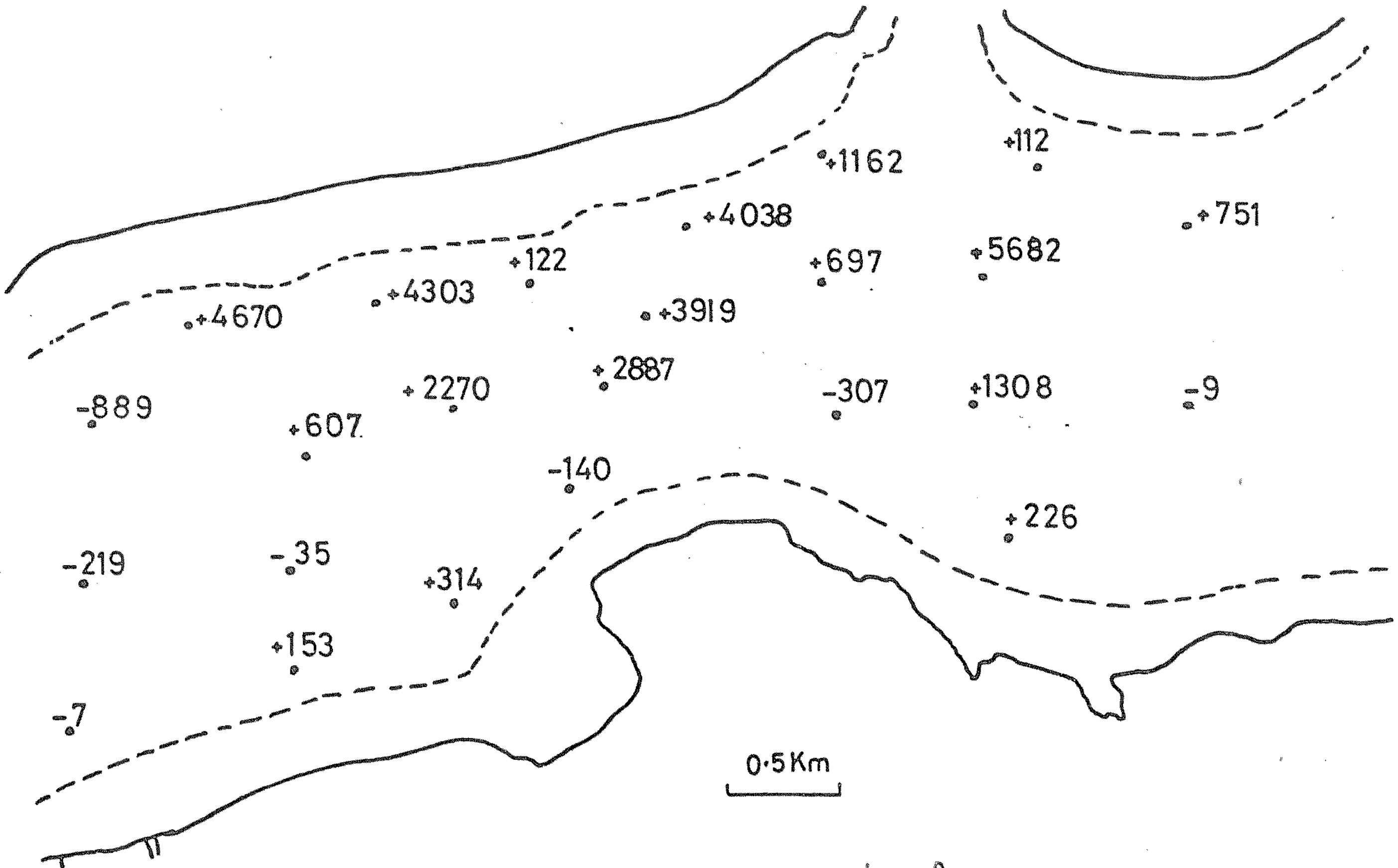


FIG. 2.12. NET GAIN OR LOSS IN NUMERICAL ABUNDANCE /03M^2 BETWEEN 1978 & 1979

Table 2.6

Table showing the species abundance ranking of the top ten species in May 1978 and May 1979

	May 1978			May 1979		
Species	Abund. ranking	No/7.2M^2	% of Total N	Abund. ranking	No/7.2M^2	% of Total N
Caulleriella caputesocis	1	11859	86.08	1	55758	94.99
Abra nitida	2	674	4.90	2	825	1.41
Nephtys hombergi	3	570	4.12	5	367	0.63
Eteone longa	4	173	1.26	4	384	0.65
Melinna palmata	5	111	0.81	9	55	0.09
Nereis diversicolor	6	85	0.62	3	583	1.00
Cirratulus cirratus	7	47	0.34	13	31	0.05
Eudorella truncatula	8	41	0.30	7	171	0.29
Crepidula fornicata	9	32	0.23	11	44	0.08
Mercenaria mercenaria	10	30	0.22	12	39	0.06
Capitella capitata	12	18	0.13	6	206	0.35
Sabella pavonina	-	-	-	8	63	0.11
Philomedes globosus	17	6	0.04	10	45	0.08

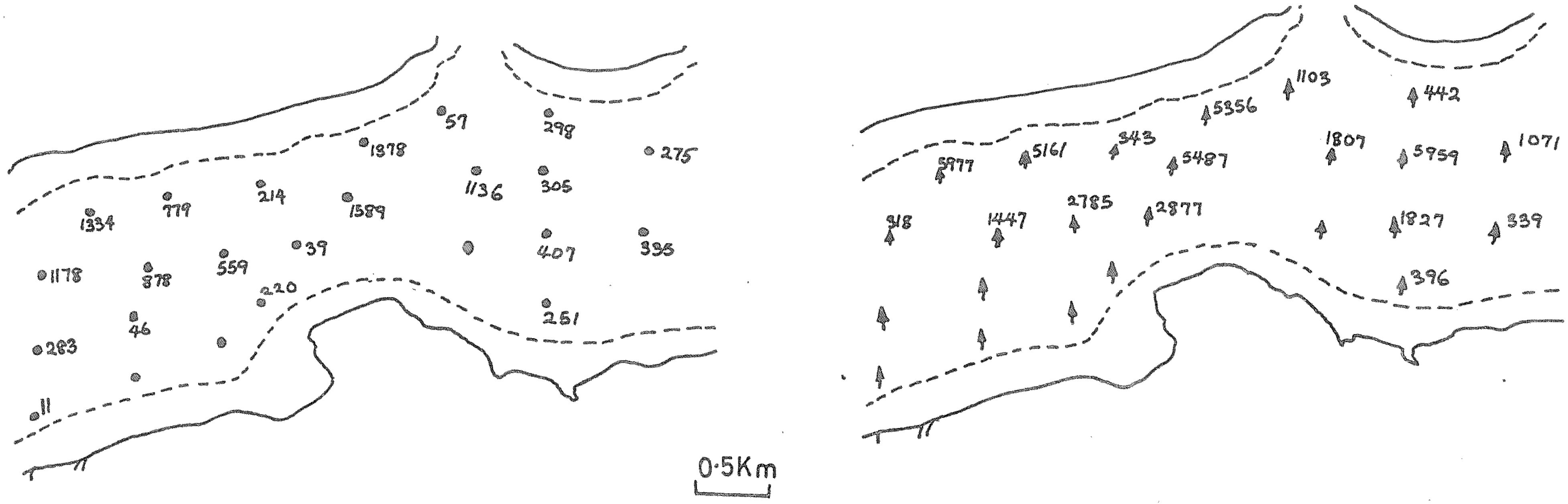


FIG 2.13. DISTRIBUTION OF <u>CAULLERIELLA CAPUTESOCIS</u> /0·3M² IN 1978(•) & 1979(↑) SURVEYS

1979 survey. Levell (1979) recorded reduced densities of Caulleriella north of Esso jetty compared with the rest of the estuary and further reduction in densities in 1976 compared with 1975.

Eteone longa

This phyllodocid worm showed restricted distribution in the study area with great concentration around Cadland creek. It showed a wide range of densities, between 2 and 108 per $0.3M^2$, greater densities occurring on the western side. E. longa was almost absent in the region of high species richness on the eastern side but in the 1979 survey showed an increase in its population density on the western side.

Nereis diversicolor

The distribution of N. diversicolor was similar to that of E. longa but covered a wider region, extending to the mid-channel where it occurred at low densities. Figure 2.14 shows the distribution of N. diversicolor in the 1978 and 1979 surveys. The population on the western side was higher in 1979 compared with 1978 but the eastern side population declined in abundance.

Nephtys hombergi

This wide ranging species was present at all stations except those around Cadland creek on the western side. Barnes et al (1973) described a N. hombergi/Abra nitida association on the south western shore of the estuary. N. hombergi was often found in the present study together with Crepidula fornicata (L.) on the eastern side but with A. nitida in the seaward region of the estuary.

Figure 2.15 shows the distribution of N. hombergi at both surveys. The worm occurred at high densities in the 1978 survey on the eastern side and at low densities in the relatively silty sediments on the western side. The population in the 1979 survey suffered heavy mortality and was absent from samples taken on the western side with reduced densities in the mid-channel and on the eastern side. Near Netley, the density fell from $105/0.3M^2$ in the 1978 survey to only $32/0.3M^2$ in 1979 at the same station.

Capitella capitata

This capitellid worm was restricted in distribution in the present study and occurred at low densities around Cadland creek (Fig. 2.16). The 1978 survey revealed low densities but by 1979 the population

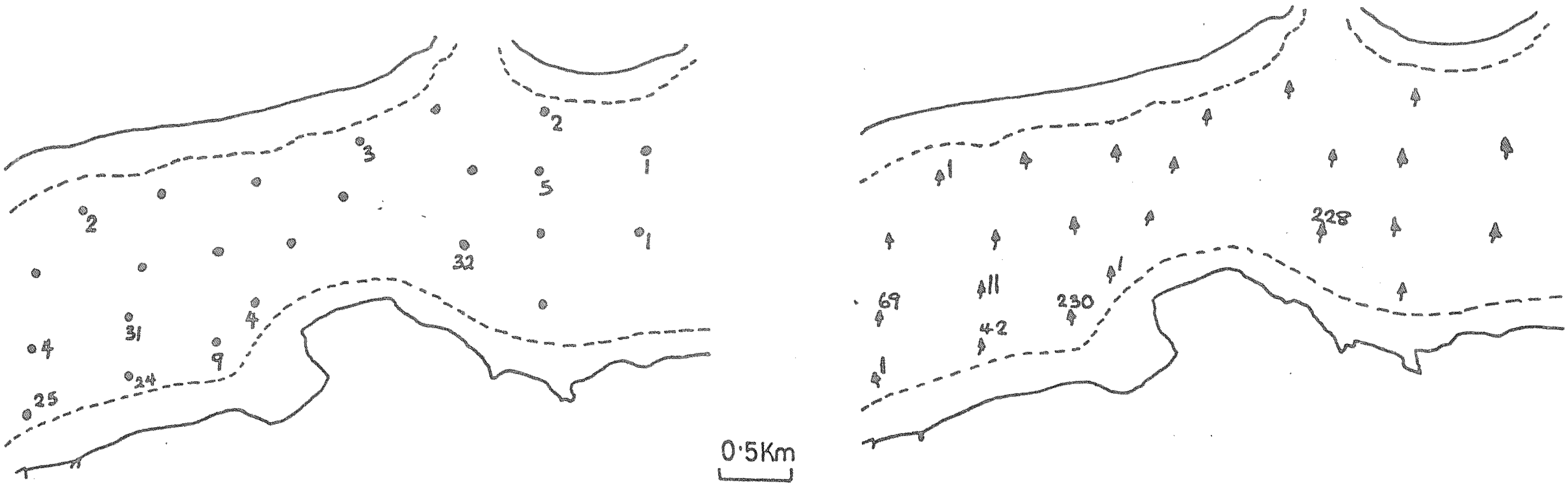


FIG. 2.14. DISTRIBUTION OF <u>N. diversicolor</u> /0·3M² IN 1978(•) & 1979(▲) SURVEYS

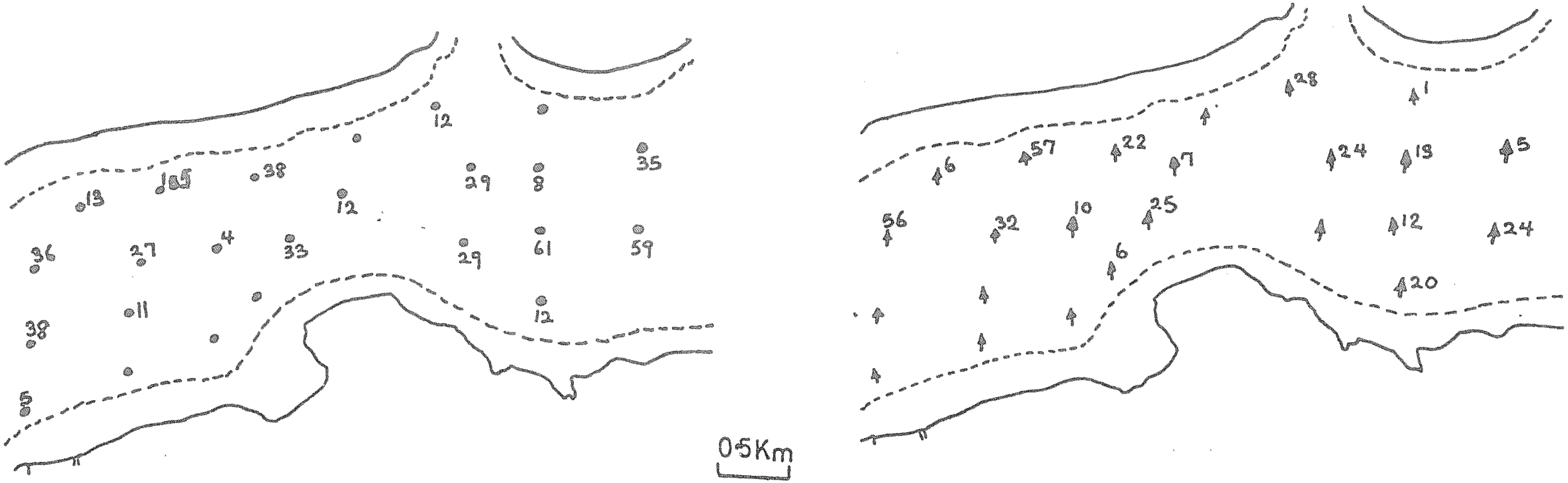


FIG. 2.15. DISTRIBUTION OF N. hombergi IN /0·3M^2 1978 (•) & 1979 (↑) SURVEYS

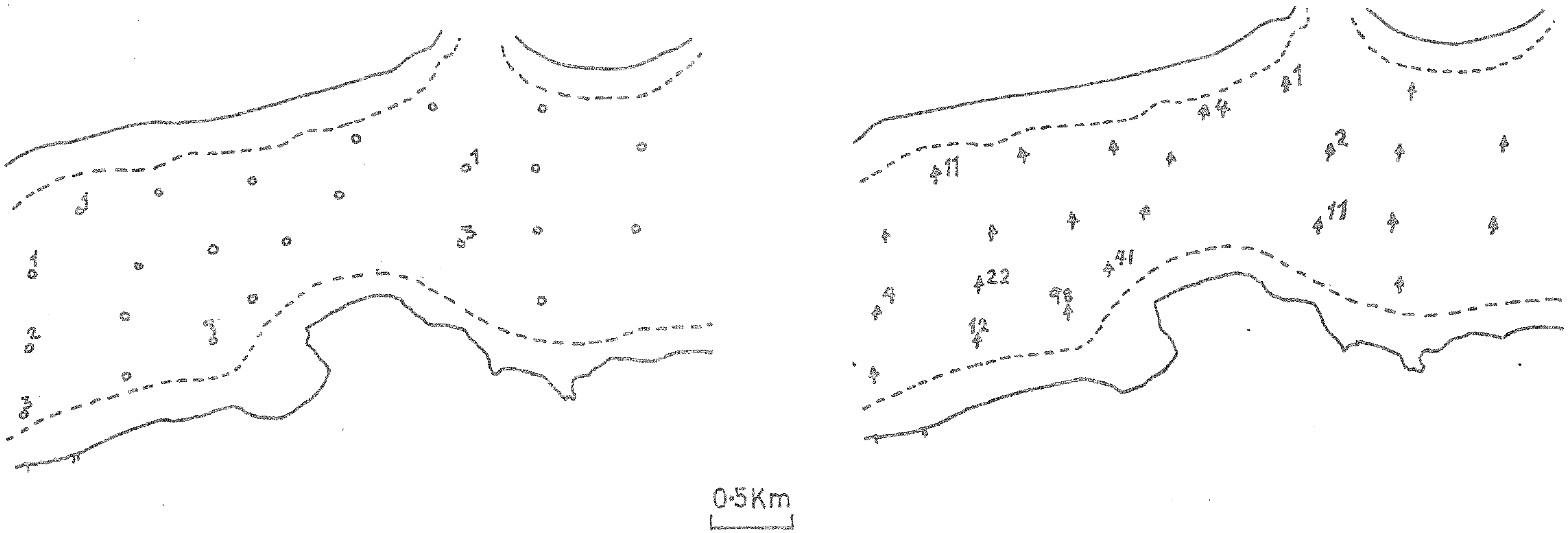


FIG.2.16. DISTRIBUTION OF CAPITELLA CAPITATA /0·3M² IN 1978(o) AND 1979(♦) SURVEYS.

density increased by ten fold. C. capitata was apparently absent in the region of high species richness, an indication of its poor competitive ability (Grassle and Grassle, 1974). In Southampton Water C. capitata often occurred in association with Polydora ciliata, E. longa and N. diversicolor.

Melinna palmata

This is a widespread species found at its highest densities on the eastern side particularly between Netley and the mouth of the River Hamble. Figure 2.17 shows the abundance distribution of M. palmata at both surveys. Towards the mid-channel, M. palmata often occurred in association with N. hombergi. Melinna was numerically dominant on the eastern side with a density of $30/0.3M^2$ and at low densities ($1/0.3M^2$) in the mid-channel. The population had suffered heavy mortality by May 1979, though the highest recorded density ($40/0.3M^2$) at one station in the 1979 survey was higher than the highest density at any one station in the 1978 survey.

Cirratulus cirratus

The distribution of C. cirratus in the present study showed a similar trend to that of M. palmata. The highest density ($28/0.3M^2$) was recorded in the mid-channel with no specimens recorded on the western side of the study area in either survey. There was a drastic decline in density by May 1979.

Other polychaete species

Some polychaetes occurred at low densities and were restricted to certain regions of the study area. Lepidonotus squamatus L, Aphrodita aculeata L, Anaitides maculata L, Ophiodromus flexuosus, Scalibregma inflatum, Eulalia pusilla and Pherusa plumosa, all of which occurred at low densities, were restricted to the regions of high species richness. Polydora ciliata occurred at low densities but showed a wide range of distribution, extending from the Cadland Quay to the mid-channel

Crustaceans

Fifteen species of crustacea were recorded in the study; three species which occurred in more than 3 stations are considered in detail below:

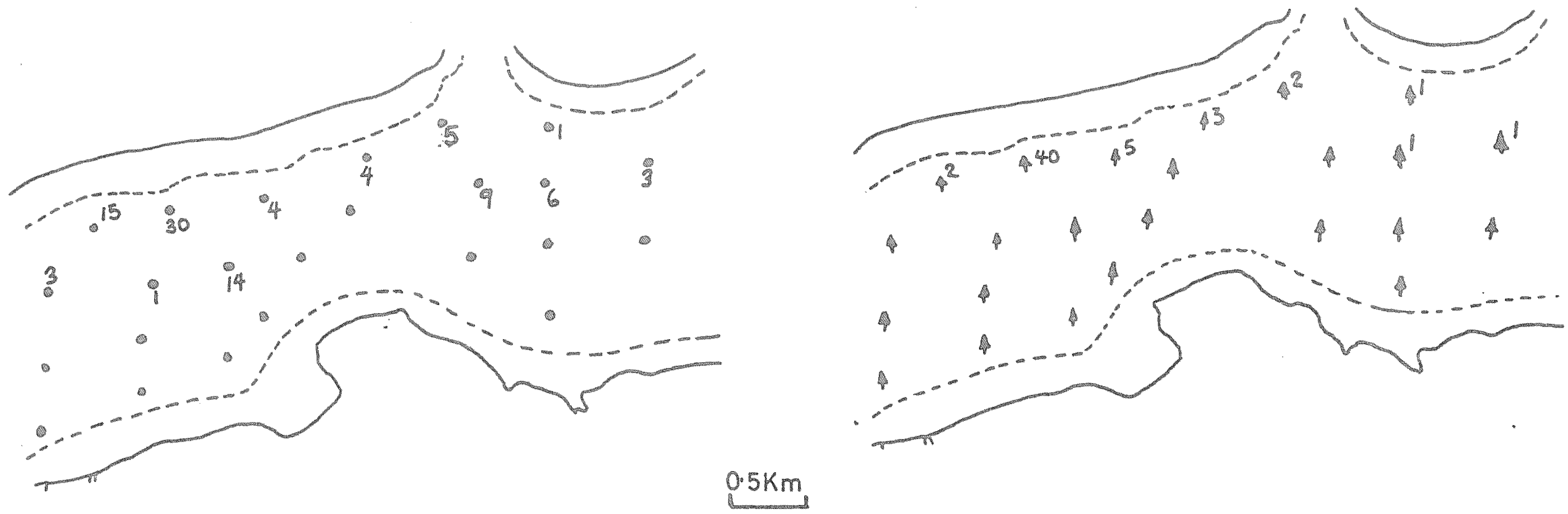


FIG. 2.17. DISTRIBUTION OF *M. palmata* / $0{\cdot}3M^2$ IN 1978 (•) & 1979 (♠) SURVEYS

Philomedes globosus

This ostracod had a wide distribution in Southampton Water, and occurred at low densities at most stations but was absent in the Cadland creek area. Highest densities were recorded on the eastern side, particularly near Netley with a density of $22/0.3M^2$ in the 1979 survey. A lower density of $3/0.3M^2$ was recorded at the same station in 1978. Generally, densities were higher in the 1979 survey.

Eudorella truncatula

This widely distributed cumacean species occurred at its highest density in the mid-channel and in the regions of high species diversity. Abundance increased by 1979.

Pariambus typicus

Again, this amphipod was restricted in distribution to the regions of high species richness where it occurred at low densities. P. typicus occurred at higher densities and over a wider area in the 1979 survey.

Other Crustacean species

Other crustacean species recorded at both surveys showed restricted distribution to the regions of high species richness where they occurred sporadically and at low densities. Such crustaceans were amphipods: Microdeutopus gryllotalpa, Corophium insidiosum, Corophium tuberculatum, C. volutator, C. sextoni, Mesopodopsis spp, Leucothoe spinicarpa, Jassa marmorata. Others were Perioculodes longimanus, Atylus vedlomensis, Chierocratus intermedius and Aora gracilis. The decapods which occurred mainly on the eastern side and in the mid-channel were Crangon vulgaris, Carcinus maenas and Gammarus locusta. The only isopod recorded was Idotea chelipes.

Molluscs

The molluscs showed a widespread distribution in the present study and were represented by both bivalves and gastropods in both surveys.

Abra nitida

This small bivalve was widespread but absent from Cadland creek. Its patchy distribution in Southampton Water in the present study was in agreement with Levell (1979). At most stations, A. nitida was the numerically dominant bivalve with greater density on the eastern side and the mouth of the estuary. In the 1978 survey, the highest density

($108/0.3M^2$) was recorded near Netley. There was a general increase in numbers by 1979 especially on the eastern side and at the mouth of Southampton Water. Barnes et al (1973) found an Abra/Nephtys association on the south western side, at the mouth of Southampton Water and intertidally on the reclaimed land at Millbrook.

Mercenaria mercenaria

The hard shell clam was fairly widespread in Southampton Water especially on the eastern side where it occurred in samples taken throughout the year at densities up to 66 m^{-2}. Figure 2.18 shows the abundance distribution of M. mercenaria in the two surveys. The clam showed a wider distribution in the 1979 survey, extending further west of the mid-channel. Table 2.7 shows the age distribution of the specimens collected in the 1979 survey. Unfortunately the 1978 survey samples of Mercenaria were removed from the deep freeze in the department by person or persons unknown and thus are absent from the results. Station 4 near Netley Great Dome had the highest densities of Mercenaria. There had been no successful settlement of Mercenaria in the last two years. The large animals were heavily fished for commercial purposes, but in spite of heavy fishing on the eastern side, the area still showed a good representation of the older age groups.

Cerastoderma edule

This bivalve was widespread in Southampton Water though it occurred at low densities. Barnes (1973) described the intertidal population density of C. edule to range between 20-35M^{-2} at the mouth of Southampton Water and 400M^{-2} near the head. In the present study, the density varied between 1 and $3/0.3M^2$. The intertidal population density might be higher than the sublittoral. There appeared to be little change in density between the two surveys.

Other bivalves

The other bivalves recorded in the two surveys appeared sporadically and at low densities. Abra alba occurred only once in the 1978 survey at station 2 and Venerupis pullastra once at station 4 in each of the surveys.

Gastropods

The gastropods occurred sporadically in the study area and were restricted to the eastern side between Netley Great Dome and the mouth of River Hamble.

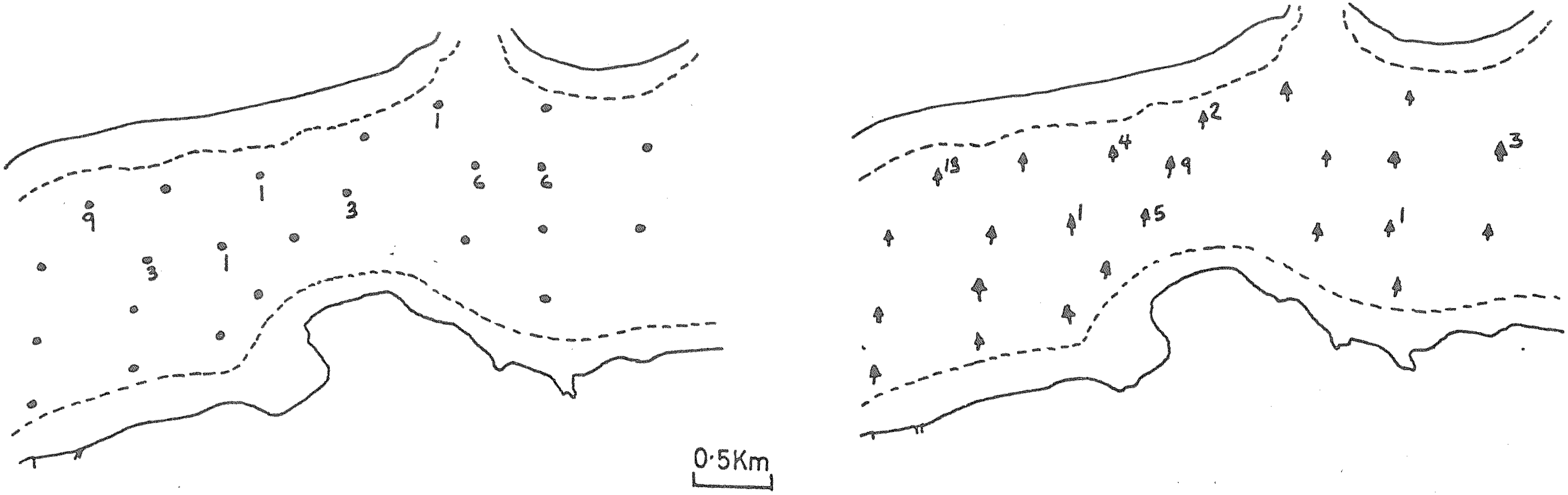


FIG 2.18 DISTRIBUTION OF <u>M. mercenaria</u>/0·3M² IN 1978(•) & 1979(↑) SURVEYS

Station No.	Year Class 1979	1978	1977	1976	1975	1974	1973	1972	1971	1970	1969
4	-	-	-	-	1	3	4	3	2	-	-
5	-	-	-	-	1	2	-	1	-	-	-
6	-	1	-	-	-	-	-	-	-	-	-
12	-	-	1	3	-	1	-	-	-	-	-
16	-	-	-	1	-	2	-	-	-	-	-
19	-	-	1	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	-	-	-	-	1
24	-	-	-	2	-	2	1	3	-	-	-
Total	0	1	2	6	2	10	5	7	2	0	1

Table 2.7

Mercenaria densities (N.03M^{-2}) of each year class recovered in the 1979 survey.

<u>Crepidula fornicata</u>

<u>Crepidula fornicata</u> occurred at low densities ($1-17/0.3M^2$) on the eastern side and the mid-channel of the study area. Barnes et al (1973) found that the Solent benthos was dominated by <u>C. fornicata</u>. The presence of <u>C. fornicata</u> often alters the nature of the sediment in that the animal produces faeces and pseudo-faeces in large quantities and its empty shells provide additional substratum for the attachment of epifauna such as hydrozoans and bryozoans.

<u>Nassarius reticulatus</u>

This gastropod occurred only on the eastern side near the mouth of the River Hamble in 1978 but extended to the Netley region by 1979 where it occurred at low densities ($1-4/0.3M^2$). The 1979 survey showed an increase in abundance over the preceding year.

<u>Other gastropods</u>

Other gastropods recorded in both surveys were restricted in their distribution to the region of high species richness, where they occurred at low densities. <u>Gibbula cineraria</u> and <u>Littorina littorea</u> occurred once each at station 18.

<u>Pycnogonids</u>

The sea spiders occurred at the mid-channel stations (11, 12, 24) in the surveys. The two specimens recorded, <u>Achelia echinata</u> (Hodge) and <u>Pycnogonum littorale</u> (Strom) occurred as single specimens.

<u>Tunicates</u>

Eight specimens of tunicates were found at station 4 in May 1978 but were damaged and therefore were not identified.

2.5 Diversity and faunal indices

An important feature of an animal community is its diversity, a measure of the number of species present and how evenly the individuals are distributed among the constituent species (Margalef, 1951; Lloyd and Ghelardi, 1964; Sanders, 1968). Diversity measurements are considered in detail in Section III. In general a community consisting of a large number of species represented by equal number of individuals would be considered to be highly diverse. A community with a small number of species and exhibiting high dominance is considered as less diverse.

Margalef's d value

This measure of diversity is obtained using the equation

$$d = \frac{S - 1}{\log_e N}$$

where d = Margalef's diversity index
S = number of species
N = number of individuals

This index of diversity is largely a measure of species richness. The results of Margalef's d values measured in the two surveys are presented in Table 2.8 and Figure 2.19.

Shannon-Wiener information function (Hs)

The idea that the 'information content' could be used as a measure of diversity was first introduced by Margalef (1957) and was first applied to plankton samples. High species dominance results in low equitability (the degree of evenness in the distribution of individuals among species) and produces a lower value of the Shannon-Wiener index.

The Shannon-Wiener index is calculated as

$$Hs = \quad pi\log_2 pi$$

$$\text{or} \quad Hs = 3.322 \left(\sum_{i=1}^{S} pi\log_{10} pi\right)$$

where Hs = Shannon-Wiener diversity index
S = total number of species
pi = the observed proportion of individuals that belong to the i^{th} species (1, 2, 3 --- etc.)

The values of Shannon-Wiener Index calculated for the two surveys are presented in Table 2.9(a) and Fig. 2.20.

Table 2.8

Margalef's d values for the two surveys

Station No.	1978	1979
1	1.02	0.26
2	1.37	0.42
3	0.97	0.96
4	3.29	2.41
5	1.15	1.05
6	1.21	1.22
7	1.51	1.43
8	0.24	0.56
9	0.55	0.34
10	0.19	1.35
11	0.46	0.63
12	0.81	0.81
13	1.06	1.99
14	1.41	0.88
15	0.97	0.65
16	1.03	0.86
17	1.71	0.82
18	1.70	1.38
19	0.95	1.46
20	0.53	1.29
21	0.93	0.86
22	1.11	0.79
23	1.15	0.84
24	1.10	0.93

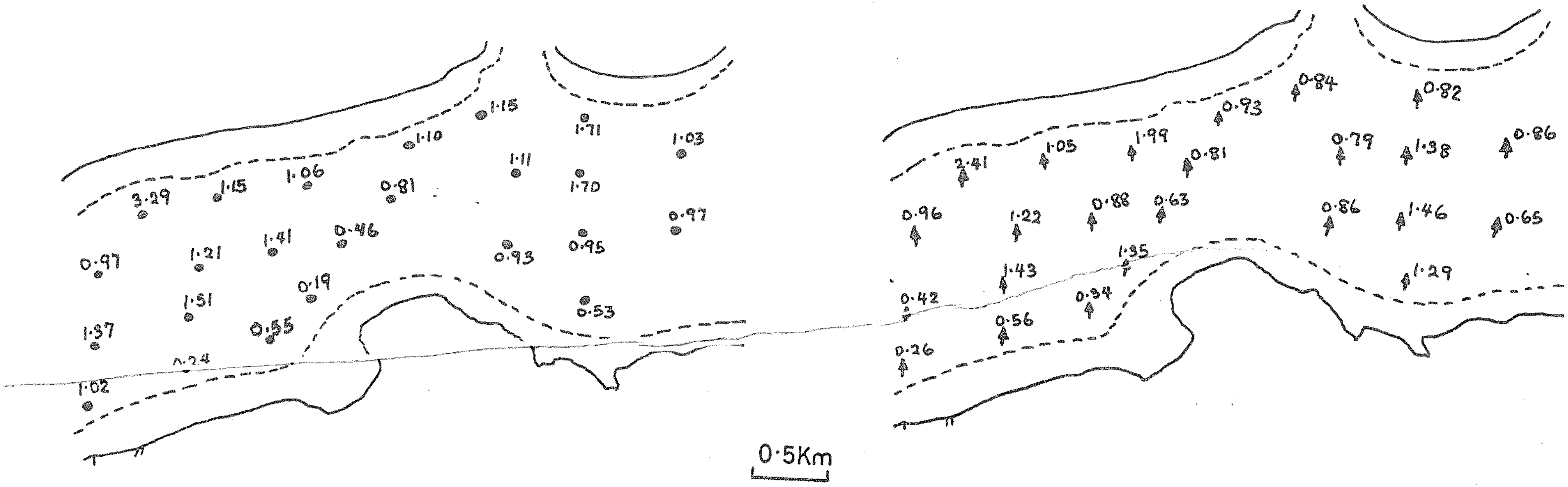


FIG.2.19. MARGALEF'S D VALUES /0·3M² IN 1978(•) AND 1979(↑) SURVEYS

Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1978	1.98	1.24	0.79	0.96	1.47	0.72	1.93	0.94	1.40	0.13	1.25	0.25	1.25	0.50	1.48	1.02	0.91	1.35	1.43	0.71	0.98	0.89	1.46	0.26
1979	0.16	1.16	1.39	0.30	0.29	0.51	2.34	0.18	0.78	0.92	0.23	0.11	0.99	0.22	1.14	0.16	0.29	0.09	0.18	1.08	1.18	0.51	0.68	0.17

Table 2.9(a) Shannon-Wiener information function (Hs) for 1978 and 1979 surveys

Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1978	0.85	0.37	0.22	0.21	0.46	0.24	0.69	0.94	0.88	0.13	0.79	0.08	0.45	0.14	0.49	0.36	0.25	0.39	0.44	0.31	0.35	0.26	0.49	0.08
1979	0.16	0.73	0.50	0.06	0.09	0.16	0.83	0.09	0.49	0.68	0.08	0.04	0.27	0.07	0.49	0.06	0.11	0.02	0.25	0.34	0.46	0.18	0.29	0.05

Table 2.9(b) Equitability values (j) for 1978 and 1979 surveys

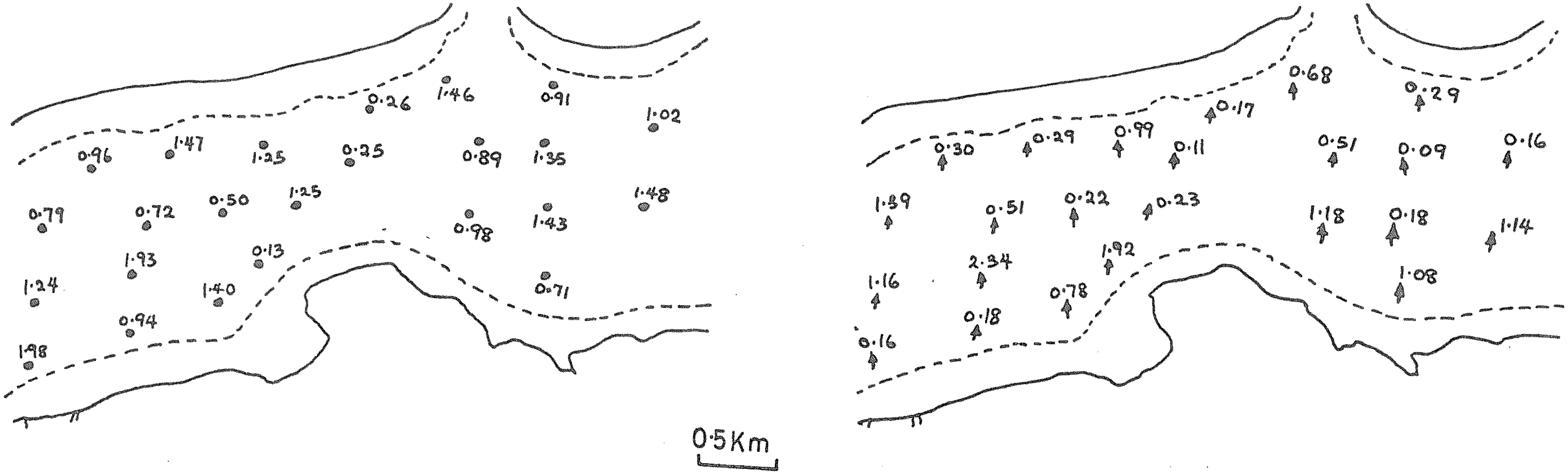


FIG. 2.20. SHANNON-WIENER (Hs) VALUES /0·3M² FOR 1978(•) AND 1979 (↟) SURVEYS

Equitability

Lloyd and Ghelardi (1964) put forward a measure of how evenly the species are distributed in a sample or community and used the term 'equitability' to express the measure.

The measure is calculated using the equation

$$j = \frac{Hs}{Hmax}$$

or

$$j = \frac{Hs}{\log_2 S}$$

where j = equitability measure
Hs = Shannon-Wiener information function
S = Number of species in a sample or community.

The values of equitability for the two surveys are presented in Table 2.9(b) and Fig. 2.21.

In the present study, higher values of Margalef's d occurred on the eastern side of the estuary and towards the mouth of Southampton Water corresponding to the regions of high species richness. Low values occurred around the Cadland creek, the region of low species richness. This was due to the fact that Margalef's d is largely influenced by the species richness. On the contrary, high values of Shannon-Wiener index occurred on the western side and lower values on the eastern side and towards the mouth of Southampton Water due to lower dominance diversity on the western side and higher dominance diversity on the latter at the time of sampling. The Shannon-Wiener index is sensitive to both species and dominance diversities. In general, there were lower values of Margalef's d, Shannon-Wiener and equitability measurements by 1979 compared with 1978.

2.6. Biomass

The biomass of each species at each station (excluding molluscan shells) expressed in terms of ash free dry weight per $0.3M^2$ is shown in Appendix III and Appendix IV for the 1978 and 1979 surveys respectively. The biomass for *Mercenaria* in the 1978 survey was assumed to have remained unchanged by 1979 and the biomass for the 1979 survey was used to calculate that of the 1978 samples in stations where the clam occurred in both surveys. In the two surveys *Crepidula fornicata* emerged as the biomass dominant for the whole area when *Mercenaria* biomass was not considered. When *Mercenaria* biomass was included, *Mercenaria* was biomass dominant

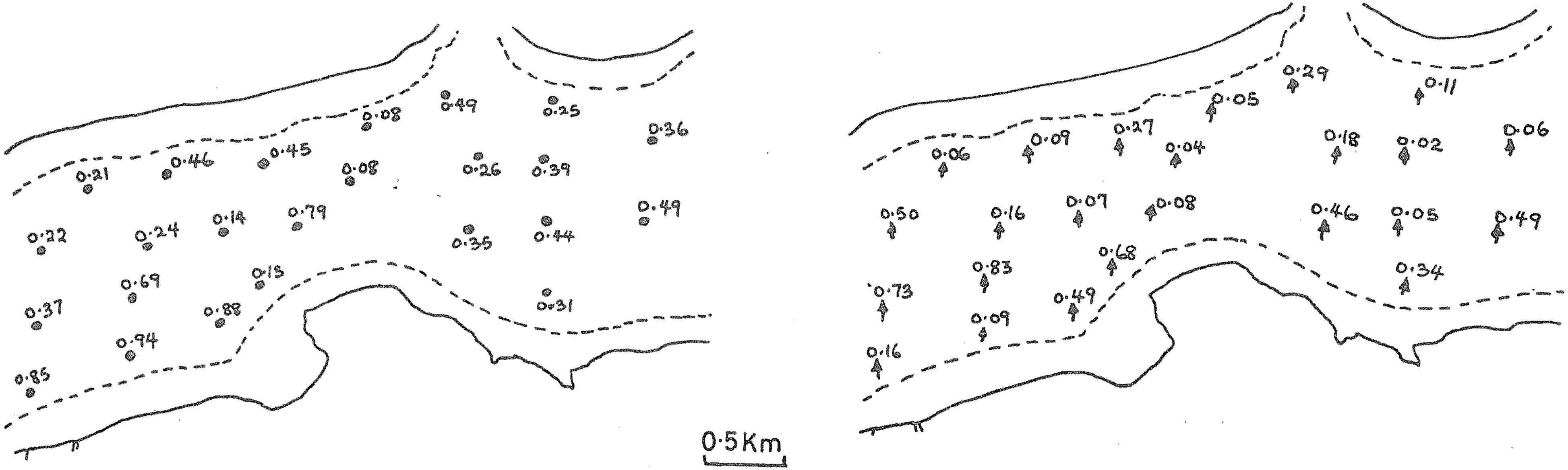


FIG. 2.21. EQUITABILITY (j) VALUES $/0.3M^2$ FOR 1978(•) AND 1979(↑) SURVEYS

and *C. fornicata* probably second.

The molluscs as a group were responsible for most of the macrofaunal biomass, amounting to 49.91% and 64.41% of the total macrofaunal biomass in the study area in the 1978 and 1979 surveys respectively. The polychaetes accounted for 49.81% in 1978 and 33.30% in May 1979 while the crustaceans accounted for only 0.27% and 2.28% of the total macrofaunal biomass in the 1978 and 1979 surveys respectively. The pycnogonids amounted to 0.1% and 0.2% of the total biomass in 1978 and 1979 respectively.

The biomass dominant polychaete was *C. caputesocis* and it accounted for 19.4% and 13.7% of the total macrofaunal biomass in the 1978 and 1979 surveys. Table 2.10 shows the total biomass and percentage biomass of the major animal taxa in the two surveys. The total macrofaunal biomass for the study area had more than doubled over a period of one year (May 1978 - May 1979). The biomass of the gastropods increased about four fold. The increase in the biomass of the gastropods was due mainly to *C. fornicata*.

The distribution of the total macrofaunal biomass (excluding *Mercenaria*) in the study area in the 1978 survey is presented in Fig. 2.22. By 1979, seven stations, 1 & 7 on the western side; 17 & 24 on the eastern side and 14, 15 & 21 in the mid-channel had reduced in the total macrofaunal biomass. Five polychaetes, *Lepidonotus squamatus*, *Scalibregma inflatum*, *Cirratulus cirratus*, *Melinna palmata* and *Eulalia pusilla* and the phoronid *Phoronis sp* declined in biomass by 1979 compared with 1978. Only two molluscs, *Abra nitida* and *Cerastoderma edule* fell in biomass by 1979 compared with 1978. The net gain or loss in the total macrofaunal biomass between 1978 and 1979 is given in Fig. 2.23.

2.7 Relationship between physico-chemical and biological parameters

When different pairs of parameters were correlated, the results of regression and logarithm regression equations together with the correlation coefficients, slopes and intercepts and the levels of significance best fit are shown in Table 2.11. There were good relationships between all pairs of parameters except silt/clay and number of species; silt/clay and total number of individuals, copper and biomass in the two surveys, and biomass and number of species in May 1979. Copper and hydrocarbon were significantly correlated in May 1978. The number of species and abundance in 1979 were positively correlated but in 1978 the logarithm of the number of species and that of numerical abundance showed positive significant correlation. The logarithm of numerical abundance and that

1978 Survey	Biomass ($g/7.2M^2$)	% of total Biomass
Polychaetes	10.2269	49.81
Bivalves	2.8447	13.86
Gastropods	7.4024	36.05
Crustaceans	0.0557	0.27
Pycnogonids	0.0012	0.01
Total	20.5309	
Crepidula fornicata	6.3254	30.8
Caulleriella caputesocis	3.9836	19.4

1979 Survey		
Polychaetes	14.6329	33.30
Bivalves	1.9337	4.40
Gastropods	26.3797	60.01
Crustaceans	1.0028	2.28
Pycnogonids	0.0108	0.02
Total	43.9599	
Crepidula fornicata	21.3348	48.5
Caulleriella caputesocis	6.0001	13.65

Table 2.10. Total macrofaunal and major animal taxa biomass for 1978 and 1979 surveys (*Mercenaria* biomass excluded).

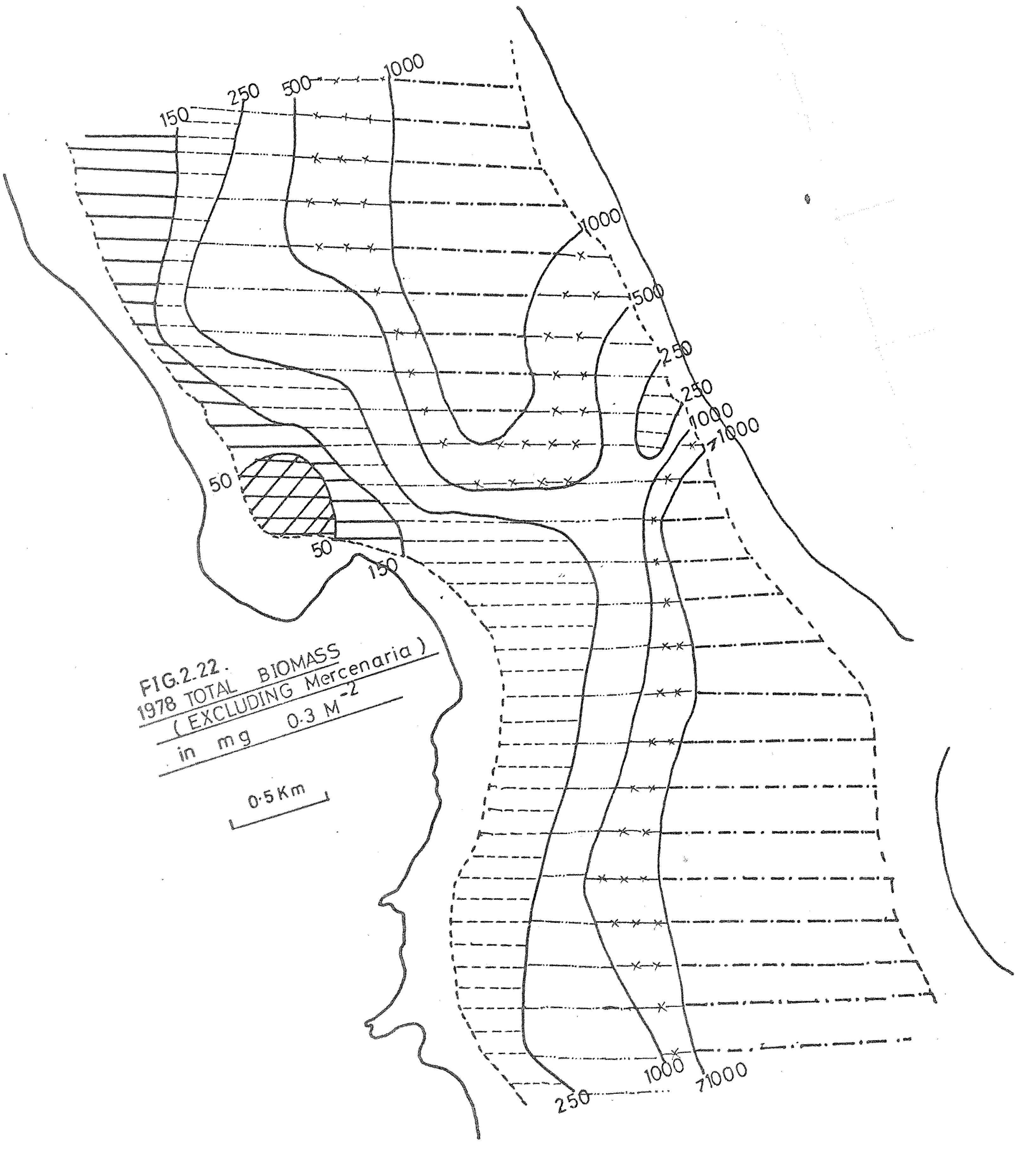


FIG. 2.22. BIOMASS
1978 TOTAL (EXCLUDING Mercenaria)
in mg 0·3 M^{-2}

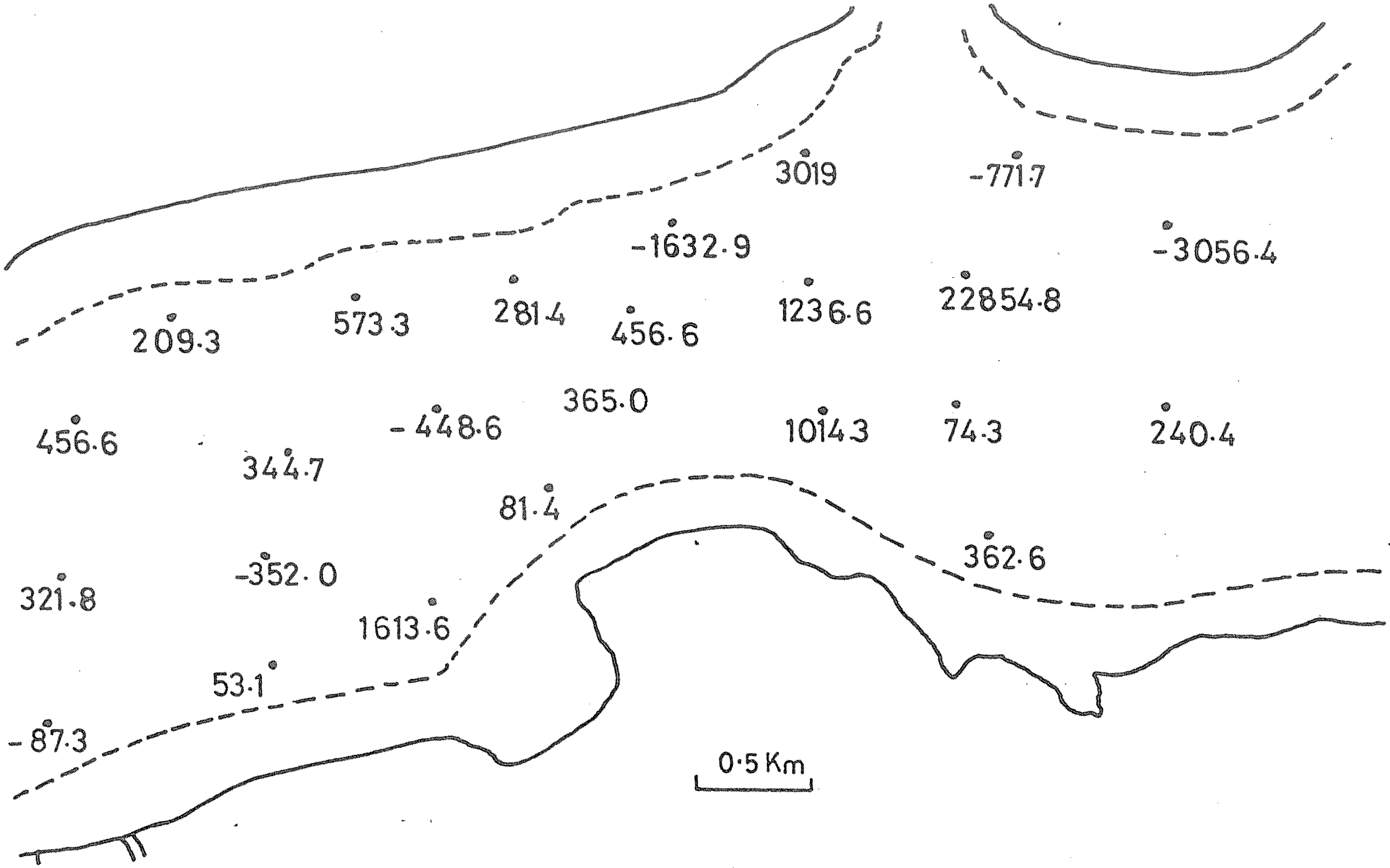


FIG. 2.23. NET GAIN OR LOSS IN TOTAL MACROFAUNAL BIOMASS BETWEEN 1978 & 1979
(mg/0.3M² EXCLUDING MERCENARIA)

	r	b	a	Level of Significance
Copper and Hydrocarbon (1978)	0.6460	3.1297	470.8676	***
Hydrocarbon and Biomass (1978)	-0.5397	0.8483	1526.4745	***
Hydrocarbon and Silt/clay (1978)	0.4466	0.0125	56.7418	*
Silt/clay and S (1978)	-0.2906	0.0720	12.4053	---
Silt/clay and S (1979)	-0.1541	0.0402	11.4133	---
Log_{10} H/c and S (1978)	0.4593	-5.776	24.077	*
H/c and S (1979)	-0.2746	-0.2230	772.8029	–
Cu and S (1978)	-0.4456	-0.0137	9.0814	*
Cu and S (1979)	-0.4338	-0.0103	8.9666	*
Cu and Biomass (1978)	-0.1682	-0.3141	1901.0725	---
Cu and Biomass (1979)	0.0733	-2.1205	2048.8684	---
Cu and N (1978)	-0.4882	-1.9356	804.1475	**
Cu and N (1979)	-0.3225	-3.9330	2307.7895	–
$log_{10}N$ and $log_{10}S$ - - - (1978)	0.6659	0.3238	0.0145	***
N and S - - - - - - - - - (1979)	0.6178	0.0012	5.6264	***
log_{10} Cu and log_{10} silt/clay - - - - (1978)	0.3533	0.1323	1.5640	*
log_{10} Cu and log_{10} silt/clay - - - - (1979)	0.3727	0.0871	1.7837	*
Silt/clay and N (1978)	-0.1142	-3.3121	812.5645	---
Silt/clay and N (1979)	0.01966	3.2122	2001.765	---
log_{10} N and log_{10} Biomass - - - (1978)	0.6095	0.6365	1.0120	***
log_{10} N and log_{10} Biomass - - - - (1979)	0.7195	0.6970	0.7541	***
Silt/clay and Biomass (1978)	-0.4894	-22.9938	2242.9279	*
Silt/clay and Biomass (1979)	0.1323	42.3713	-1855.7907	---
Log_{10} Biomass and log_{10} S - - - - (1978)	0.6837	0.3223	-0.0085	***
Log_{10} Biomass and log_{10} S - - - (1979)	0.5153	0.3789	-0.1356	**

Table 2.11. The correlation coefficient (r), slope (b), intercept (a) and the level of significance of physico-chemical and biological parameters in the 1978/79 surveys

*** p = 0.001
** p = 0.01
* p = 0.1

of biomass in 1979 showed positive significant correlation. Logarithmic numerical abundance and biomass in 1978, biomass and number of species in both surveys, hydrocarbon and silt/clay 1978, silt/clay and numerical abundance in 1979 showed positive correlations but at lower levels of significance. Copper and number of species in the two surveys, copper and numerical abundance in both surveys, silt/clay and biomass, 1978, and hydrocarbon and biomass in 1978, all showed negative correlation. The increase of one decreased the other.

Cluster analysis

Benthic survey data are often subjected to several numerical analyses in identifying species associations. Such methods employ statistical criteria to evaluate the frequency of occurrence and abundance of species in quantifying associations as groups through various types of similarity analyses. The main aim of such numerical analyses is to group stations as to faunal similarity in order to compile species list characteristic of each group.

In the present study, two similarity coefficients have been applied to characterise the site groups of heterogeneous types of benthic communities. Jaccard's coefficient is the number of species common to both samples expressed as a percentage of the total number of species in both samples:

$$JC = \frac{c}{a + b + c} \times 100$$

where a = number of species in sample A only
b = number of species in sample B only
c = number of species common to both samples

Bray & Curtis (1957) modified Czekanoskwi's coefficient as

$$C_N = 2jN\ (aN + bN)$$

where aN = total individuals sampled in habitat a
bN = " " " " " b
jN = sum of lesser values for the species common to both habitats.

In the present study, clustering analysis using both coefficients was performed on May 1979 samples since the abundance was almost four fold that of the 1978 samples but the number of species in the samples for the whole area was constant. Two main site groups emerged from the clustering and these are shown in the dendrograms in Figures 2.24 and 2.25. The first site group represents the low diversity region around the industrial outfall region of the study area and comprises stations 1, 2, 7, 8, 9, 10

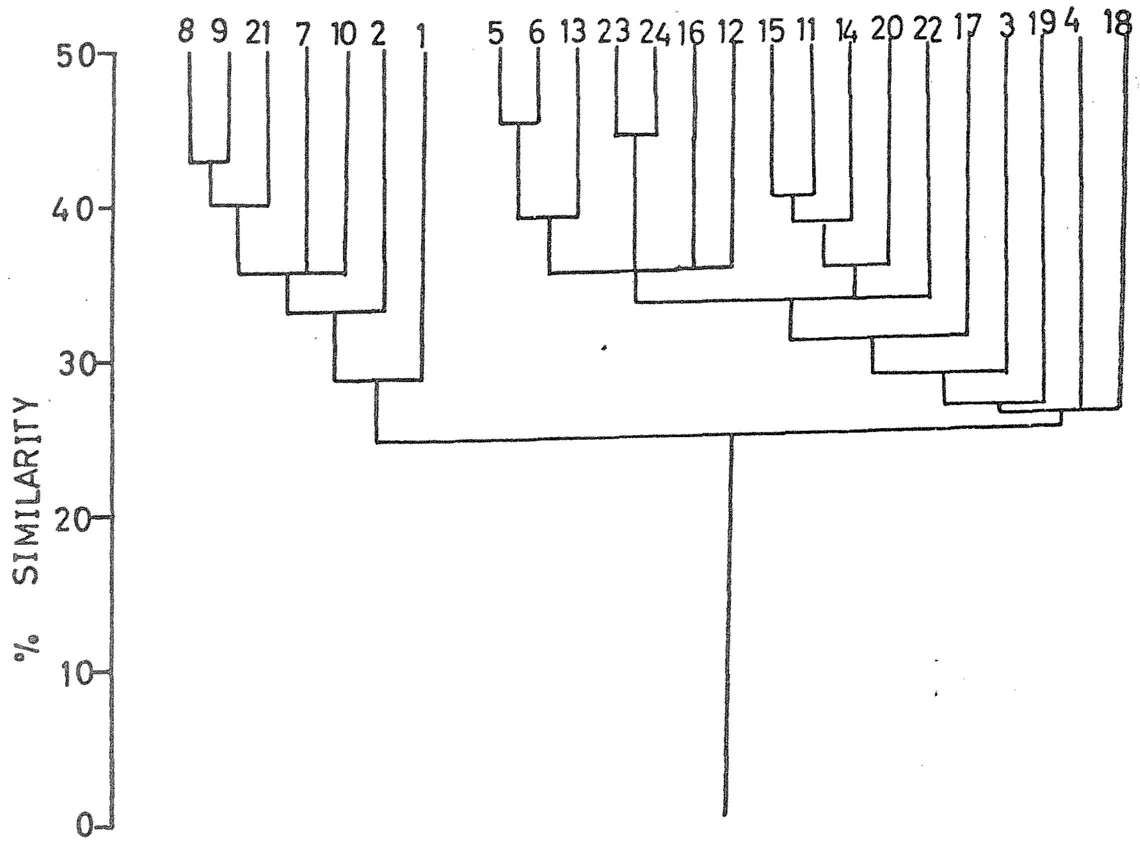


FIG.2.24. DENDROGRAM OF SITE GROUPS ANALYSIS OF MAY 1979 SAMPLES USING JACCARD'S COEFFICIENT.

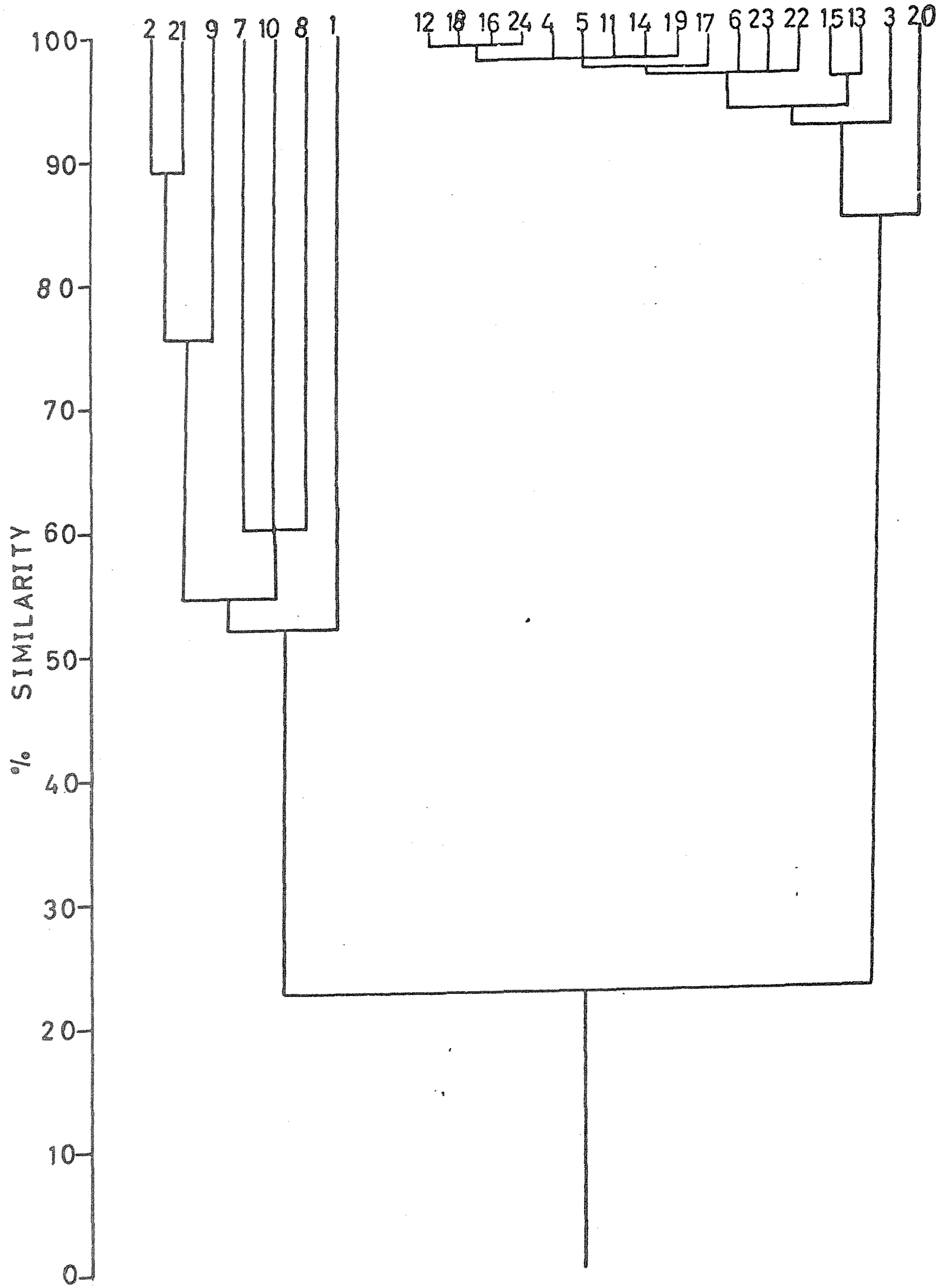


FIG. 2.25. DENDROGRAM OF SITE GROUPS ANALYSIS OF MAY 1979 SAMPLES USING CZEKANOWSKI'S COEFFICIENT.

and 21. Higher similarity occurred between stations when Czekanowski's coefficient was applied, greatest similarity occurring between stations 2 and 21. Using Jaccard's coefficient, stations 8 and 9 showed highest similarity.

The other site group represents the high diversity region of the study area and comprised seventeen stations. Four stations, 12, 16, 18 and 24, showed highest similarity of 98% (Czekanowski's coefficient) and only two, 5 and 6, showed the highest similarity of 43% when Jaccard's coefficient was considered.

2.8 DISCUSSION

Analysis of data from this type of survey is by no means an easy task since the relationship between the sampling sites and between years can be examined in a number of ways. A general view of the spatial distribution of the faunal assemblages of the study area shows a considerable change between 1978 and 1979 with accompanying changes in the sediment parameters. Pratt (1973) demonstrated that the composition of benthic communities on the Atlantic Continental Shelf was influenced by the hydrodynamically active sediments. Boesch and Rackley (1974) also reported reduced numbers of species and low diversities from an estuarine situation with sediment instability, resulting from the dissipation of wave energy on a shallow bar.

The faunal composition of bottom communities is to a large extent influenced by the bottom substrate (Longhurst, 1958; Ursin, 1960; Buchanan, 1963; Warwick and Davies, 1977). Nevertheless, a community may occupy a rather wide range of substrates, as for example, a West African <u>Amphioplus</u> community cited by Longhurst (1958) and the <u>Amphiura</u> community off the coast of Northumberland (Buchanan, 1963). In Southampton Water, differences in the distribution of benthic macrofauna between the eastern and western sides of the estuary can be explained by the type of substratum and pollution load. The particle size distribution was different at stations on both sides of the estuary in the 1978 survey, the western side being predominantly fine sediment (particles $< 63\ \mu m$ in diameter). The stations on the eastern side and towards the mouth of the estuary contained greater amounts of sand and gravel. The differences in the particle size distribution were less obvious in the 1979 survey with a general increase in the fines at all stations especially those on the eastern side and towards the mouth of the estuary. In spite of the relatively small differences in the particle size of the sediment at both sides of the estuary in 1979, the overall faunal distribution remained similar to that found in 1978.

The sediment at the stations located on the western side of the study area contained higher levels of copper and hydrocarbon than the eastern side. The tolerance to copper and hydrocarbon might have limited the occurrence and survival of some species on the western side. A significant positive correlation ($P = < 0.1\%$) was found between sediment copper and hydrocarbon suggesting a common source. The evidence suggests a high correlation of both in Cadland creek, and judging from the work of Knap (1978), the major source of copper and hydrocarbon is probably the Esso petroleum refinery at Fawley. The sediment copper and hydrocarbon decreased eastwards and the number of species and abundance of individuals increased. A negative correlation was found between sediment copper and abundance of individuals. Sediment copper and hydrocarbon were measured in the present study and the significant correlation between log. hydrocarbon and number of species and logarithm of copper and number of species suggests that both the sediment copper and hydrocarbon influenced the distribution of benthic macroinfauna in Southampton Water.

Other studies on the effects of pollutants on the macrofauna in Southampton Water tend to emphasise the level of occurrence of various trace metals and their tolerance by specific species (Knap,1972; Romeril, 1974, 1979). Results of the present study showed that the distribution of the macrofauna is related to the sediment trace metals.

The general fall in total organic matter in the 1979 survey compared with 1978 could tempt one to assume a reduction in the total number of individuals and a decrease in the faunal biomass in 1979. Though Byers et al (1978) suggested that total organic matter is indicative of the amount of food available to the deposit feeding benthic organisms, the abundance of individuals increased in the 1979 survey. This confirmed the correlation between total organic matter and abundance of individuals as insignificant in both surveys. Nevertheless, there was a significant correlation between total organic matter and biomass in conformity with the idea of Byers et al (1978).

Though the species richness remained relatively similar at the two surveys, there was, in general, greater dominance and a higher number of individuals in 1979 compared with the 1978 survey. The increase in abundance in 1979 may be attributed to higher recruitment and lower mortality of a few key species such as C. caputesocis, C. capitata, M. palmata, N. Hombergi and N. diversicolor. In 1978, C. caputesocis was present at high densities in many stations but at low densities in the 1979 survey on the western side.

Other polychaetes showed considerable fluctuations in numbers between the two surveys, increasing in some samples but decreasing or disappearing from others. Similar situation was reported by Soulsby (1978) for Tharyx marioni, a closely related species, which occurred in large numbers in 1975 but were absent in 1976. The reasons for such fluctuation are not clear and it is apparent that the fauna of Southampton Water lacks stability to a certain extent, with regard to the relative abundance of constituent species.

The occurrence of Capitella capitata at high densities on the western side and its sporadic occurrence or absence on the eastern side could be attributed to the degree of pollution and low species diversity (reducing competition) on the western side. A lot of argument has generated from the studies of the species. Reish (1960) regarded C. capitata as a universal indicator of organic pollution, generally occurring in large populations with very few, if any, other species present. C. capitata has also been recorded in large numbers in areas where there is no pollution (Muus,1967; Wolff,1973). Gray (1976) found that C. capitata was present in large numbers in the central region of Seal Sand, where pollution was least but absent where pollution was greatest. In Southampton Water, the greatest population was associated with regions of high sediment copper and hydrocarbon (around Cadland creek). Around the creek where C. capitata occurred in large numbers, only few species occurred as a result of environmental disturbance.

Grassle and Grassle (1974) suggested that C. capitata is 'opportunistic', occurring in low numbers normally, but with an environmental change, resulting in a decrease in species diversity, the worm rapidly exploits the vacant feeding niches. Since the species has a variety of larval genotypes, it can undergo intensive short-term selection. The authors also indicated that Polydora ciliata (ligni) is similarly adapted.

The benthic macro-infauna of the low diversity region of the study area could be grouped into 'pollution tolerant' species comprising C. capitata, P. ciliata, and Nereis diversicolor. These species occurred at relatively high densities on the western side but at low densities or were absent on the eastern side. The 'pollution intolerant' species, comprising Caulleriella caputesocis, Nephtys hombergi, Melinna palmata, Mercenaria mercenaria, Crepidula fornicata and Venerupis pullastra, occurred at high densities on the eastern side and only sporadically on the western side of Southampton Water.

In the Tees estuary, Gray (1976) found that Cerastoderma edule and Nephtys hombergi were absent in 1973, both of which were prominent in the estuary in 1935 when pollution was considerably lower. He stressed that the dominant macrofauna in the Tees estuary were being replaced by those with short-lived larvae (e.g. N. diversicolor) as the pollution load increased. Henriksson (1969) showed that in the polluted areas of the Oresund, C. capitata brooded its larvae in the parental tube and suggested that such a reproductive strategy was advantageous when living in polluted areas. In the present study, those species with long-lived planktotrophic larvae tend to be excluded from the western side, probably because of their 'non-opportunistic' reproductive strategies, as suggested by Henriksson.

Other factors affecting species distribution and composition include salinity and water movement. Muus (1967) found that in Danish waters, at salinities above 22‰, Nereis diversicolor was outcompeted by N. virens. Within the study area, at a salinity of around 32‰, N. diversicolor is by far the commoner of the two species. N. virens occurred at a maximum density of $4m^{-2}$. Faunal assemblages in estuaries are often unstable due to fluctuations in the salinity regime; but in situations where little change in salinity occurs (such as in the present study) one would expect stability in the faunal structure. On the contrary, large faunal fluctuations and low diversities occurred within the study area. Such fluctuations are probably due to other physical parameters imposing stress on the benthic community in the area.

Sanders (1968) suggested that in the environments where the physical conditions fluctuate widely, the animals are exposed to severe physiological stress and named such a community a 'physically controlled community' (PCC). Such a community is characterised by a small number of species. He explained that in some communities where physical conditions are rather constant and uniform for long periods of time, the biological stress (intense competition, prey-predation relationship) results in the evolution of biological accommodation. He named such community a 'biologically accommodated community' (BAC). BAC are characterised by a large number of species. The faunal assemblages of the present study can be described as physically controlled communities, though the degree of stress is variable within the area.

The top two dominant species as regard biomass in both surveys, Mercenaria mercenaria and Crepidula fornicata, occurred at relatively few stations. While C. fornicata was found attached to broken bottles and other hard substrates, Mercenaria burrowed the substrate. Caulleriella caputesocis emerged as polychaete biomass dominant in the two surveys. Esser (1972) found that the biomass of three dominant polychaetes, Cirriformia tentaculata, Nereis diversicolor and Arenicola marina, on the Hamble Spit amounted to 60-70g dry weight m^{-2}. Hibbert (1976) using a 1cm mesh sieve, estimated the total macrofaunal biomass (polychaetes and bivalves) as 200g dry weight m^{-2} for Hamble Spit. Assuming that the biomass of Mercenaria recorded in the two surveys remained stable, the total macrofaunal biomass for the present study was estimated as 10.2g and 13.4g ash free dry weight m^{-2} for 1978 and 1979 respectively.

Though comparisons of benthic biomass data elsewhere with the present study may be difficult because of the different units of measurements adopted by various workers, such comparisons are useful. Dry weight (Longbottom , 1970; McIntyre, 1970); ash free dry weight (Buchanan and Warwick, 1974) and calorific values (Hughes, 1970) have been used to express biomass. Comparisons of the benthic biomass data are given in Table 2.12. In general, higher values were reported in the intertidal zone than sublittoral.

The benthic macrofaunal community in the present study appears similar to the Macoma community described by Petersen (1913) with Mercenaria mercenaria replacing Macoma balthica. Barnes (1973) suggested that the benthic faunal associations found in Southampton Water conformed to the Macoma community of Thorson (1950) with Cerastoderma edule replacing Macoma balthica as the dominant bivalve. He suggested that the introduced species such as M. mercenaria and Crepidula fornicata were superimposed upon the classical Macoma community. In the present study, several faunal associations, for example, Melinna palmata/Abra nitida, Abra/Nephtys occurred in different regions of the study area. On the eastern side, M. palmata, N. hombergi, C. caputesocis and M. mercenaria dominated. On the western side, C. capitata and N. diversicolor were dominant though the two associations overlapped in mid-channel. Towards the mouth of Southampton Water, N. hombergi and A. nitida were dominant. The presence of such faunal associations results in the two main site groups in the dendrograms and confirms the tolerance of physical stress on the community components.

The presence and influence of the American slipper limpet, Crepidula fornicata, on the eastern side and at the mouth of Southampton Water inflict a major departure from the M. palmata/N. hombergi/M. mercenaria association characteristic of the eastern side of Southampton Water. Barnes et al (1973) described C. fornicata as the dominant species of the benthic fauna of the Solent and the north-eastern half of Southampton Water with increasing densities towards the estuary entrance. Levell (1979) suggested that the presence of the limpet in large numbers might determine the type of community. When large numbers of Crepidula become established, there is always a general increase in the epifaunal species. The faeces and pseudo-faeces of the limpet alter the nature of the sediment and empty shells provide suitable sites for attachment of epifauna.

In general, species of benthic macroinfauna found in the present study are essentially similar to Jones (1950) and Gray (1976). Nevertheless, none of the communities or faunal associations are exact descriptions of the benthic faunal communities of Southampton Water. The major departure arose from domination by Caulleriella caputesocis in Southampton Water. This is not unexpected as any particular region

INTERTIDAL COMMUNITIES

	Biomass	Authority
Scotland	0.3-22	McIntyre (1970)
Hamble Spit (bivalves)	27-129	Hibbert (1976)
Hamble Spit (polychaetes)	60-70	Esser (1976)

SUBLITTORAL COMMUNITIES

	Biomass	Authority
Northumberland	3-4	Buchanan et al (1974)
Washington U.S.A.	0.5-5.4	Buchanan & Warwick (1974)
		Lie (1974)
Southampton Water	10-13.4	Present study

Table 2.12 Comparisons of the biomass for several community studies expressed in g ash free dry weight m^{-2}.

will have its own unique physico-chemical and biotic parameters which may result in variations from the classical communities to a greater or smaller extent.

SECTION THREE

TEMPORAL VARIABILITY IN THE STRUCTURE OF SUBLITTORAL BENTHIC MACROFAUNAL COMMUNITIES OF SOUTHAMPTON WATER

3.1. Introduction

Ecologists have paid considerable attention to the concept of stability of communities but as Margalef (1958) pointed out, there are different definitions of stability which provide ample ground for confusion. The most common definition of stability of communities is constancy in numbers, that is, communities evolve in the direction of small numerical variability in habitats with constant external conditions. Durbar (1960) found small numerical variability as a characteristic feature of tropical communities in which species diversity is typically high. He suggested a relationship between species and community stability. Mac-Arthur (1955) stated that the higher the species diversity at each trophic level, the more stable would be the energy flow through the community.

Sanders (1968, 1969) postulated the Stability Time Hypothesis to explain observed patterns of diversity in the sea. Nevertheless, Slobodkin (1964) and Sanders (1969) affirmed that it was the degree of predictability of the environmental fluctuations rather than their absolute magnitude that was of importance for species diversity. Lie and Evans (1973) stated that constancy of species numbers in a community could be maintained if drastic changes in the relative importance of a species took place.

Few temporal investigations of benthic infauna comparable to the present study have been carried out. Petersen (1913, 1918) and Ziegelmeier (1963) made extensive investigations of general areas in Danish waters and the German Bight respectively rather than at exact locations as in the present study. Buchanan et al (1974) studied the long term population trends of the macrofauna in the Northumberland offshore mud over a period of four years. They found substantial stability in the number of species and the total estimated secondary production, but the number of individuals more than doubled over the period. The authors found temporal variation in the number of individuals to be reflected in a considerable fluctuation in diversity measurements, due almost entirely to the redistribution of the proportions of a number of high ranking species. In a later paper in 1978, the same authors assessed sources of variability in the benthic macrofauna off the Northumberland coast between 1971 and 1976. They observed that the distribution of faunal assemblages had remained essentially stable for more than a decade. The authors, therefore, suggested a community maximizing its performance throughout a broad range of environmental variability.

Southampton Water has been a site of many ecological studies. Nonetheless, temporal variability in the fauna of the estuary has been neglected. Studies of fauna carried out in and around Southampton Water have been restricted mainly to the summers of successive years (Soulsby, 1978; Levell, 1979) while short term temporal studies on the fauna of the intertidal zone have been carried out over a few summer months (George, 1962; Wormald, 1972; Lauriston, 1977). The interest in the temporal variability of the Southampton Water benthos derives from a lack of knowledge of the structure of the benthic communities around the central industrialized region of the estuary.

Intensive sampling was started at four selected stations, 2, 5, 9 and 20 (figure 3.1) for the purpose of assessing secondary production for a period of twenty months based on bimonthly samples between July 1978 and March 1980. The stations were chosen because the preliminary survey in May 1978 showed that stations 2 and 9 which differed in distance from the refinery outfall, both had sediments with similar silt-clay fractions. Station 5 on the eastern side had a different sediment type with high species diversity. Station 20 situated south of Fawley's Esso jetty, though on the western side, had a lower sediment silt-clay level than stations 2 and 9 and appeared to be fairly diverse.

Sediments act as a very important sink for trace metals and several studies have shown them to be good indicators of pollution. The release of metals into the estuarine environment other than by natural processes has been a consequent result of industrial development. Metals that are toxic at high concentrations may be essential to life at lower concentrations. Some metals are present to a greater extent in association with particulate matter than dissolved matter or vice versa. Deposit and filter feeders are efficient in concentrating some metals which they obtain from detrital materials. Cutshall (1972) stated that estuaries contain significant amounts of trace metals since they serve as funnels through which land run-off is transported to the coastal ocean. Attempts were made during the present investigation to study the influence of sediment metals and hydrocarbon on the benthic macrofaunal communities of the study area.

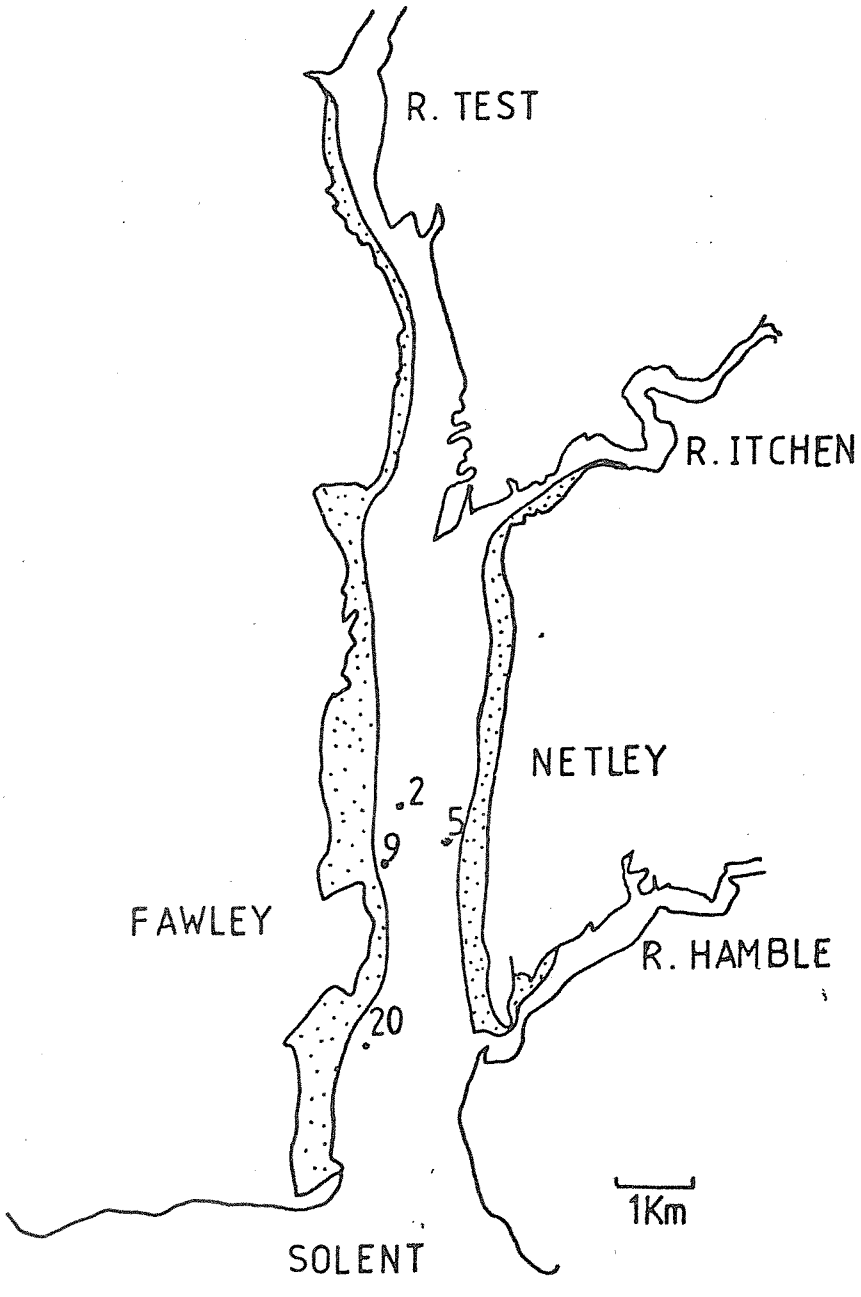


FIG. 3.1. MAP OF SOUTHAMPTON WATER SHOWING LOCATION OF THE SELECTED STATIONS.

3.2 Method

The sampling technique and the subsequent treatment of the samples are essentially identical to those described in Section II. Ten replicate $0.1M^2$ Van Veen grab samples were taken bimonthly at each of stations 2 and 9; and five replicate $0.1M^2$ grab samples at each of stations 5 and 20. The preliminary survey in 1978 showed convincingly that five grab samples at stations 5 and 20 were sufficient to provide data for estimating secondary production whereas ten grab samples were considered necessary at stations 2 and 9, owing to the low species diversity and abundance at the latter stations.

All benthic macro-infauna retained on a 0.5mm sieve were fixed in 4% formalin and stained in Rose B engale solution. These were later identified, counted and the ash free dry weight determined for individual species or cohorts by drying at 80°c in an oven and ashing at 550°c in a muffle furnace.

The sediment samples collected by the technique outlined in Section II were separated into sand and fines (particles less than 63μm in diameter) portions. The separation into sand and silt-clay fractions was considered of possible relevance to the distribution of the infauna.

The total organic matter of the sediment was estimated by loss of weight on ignition in the muffle furnace at 550°c. It is assumed that negligible amounts of inorganics, notably phosphorus and nitrogen, would be lost at this temperature. Details of estimation of other physical and chemical parameters such as temperature, metals, hydrocarbons, are given in the relevant sections.

3.3 Results

3.3.1. Physico-chemical parameters

(a) Sediment types

The sand and the silt-clay (fines) proportions expressed as percentage composition of the sediments for all selected stations are shown in Table 3.1. The temporal changes in the fines portions are expressed graphically in figure 3.2.

The sediment at station 2 is predominantly mud with the fines (diameter $\angle$ 63μm) always above 70% of the total composition. Between July and November 1978, the proportion of the fines in the sediment was almost stable but rose following the winter of 1978/79. The fines proportion decreased between March and May 1979 before a return to a high level

	Station 2		Station 5		Station 9		Station 20	
	Sand	Silt/Clay	Sand	Silt/Clay	Sand	Silt/Clay	Sand	Silt/Clay
1978 July	20.8	97.2	16.6	83.4	20.6	79.4	32.3	67.7
September	24.6	75.4	18.0	82.0	15.6	84.4	36.0	64.0
November	23.1	76.9	18.5	81.5	18.3	81.7	34.3	65.7
1979 January	13.9	86.1	18.2	81.8	14.0	86.0	38.0	62.0
March	2.6	97.4	3.2	96.8	1.7	98.3	23.7	76.3
May	11.5	88.5	11.5	88.5	2.4	97.6	15.5	84.5
July	0.8	99.2	10.8	89.2	1.0	99.0	31.5	68.5
September	0.7	99.3	11.8	88.2	1.7	98.3	21.8	78.2
November	0.5	99.5	3.0	97.0	1.7	98.3	7.8	92.2
1980 January	0.3	99.7	6.8	93.2	0.8	99.2	25.6	74.4
March	2.2	97.8	12.6	87.4	4.2	95.8	25.3	74.7

Table 3.1. Percentage of sand and silt-clay fractions in sediments of the selected stations

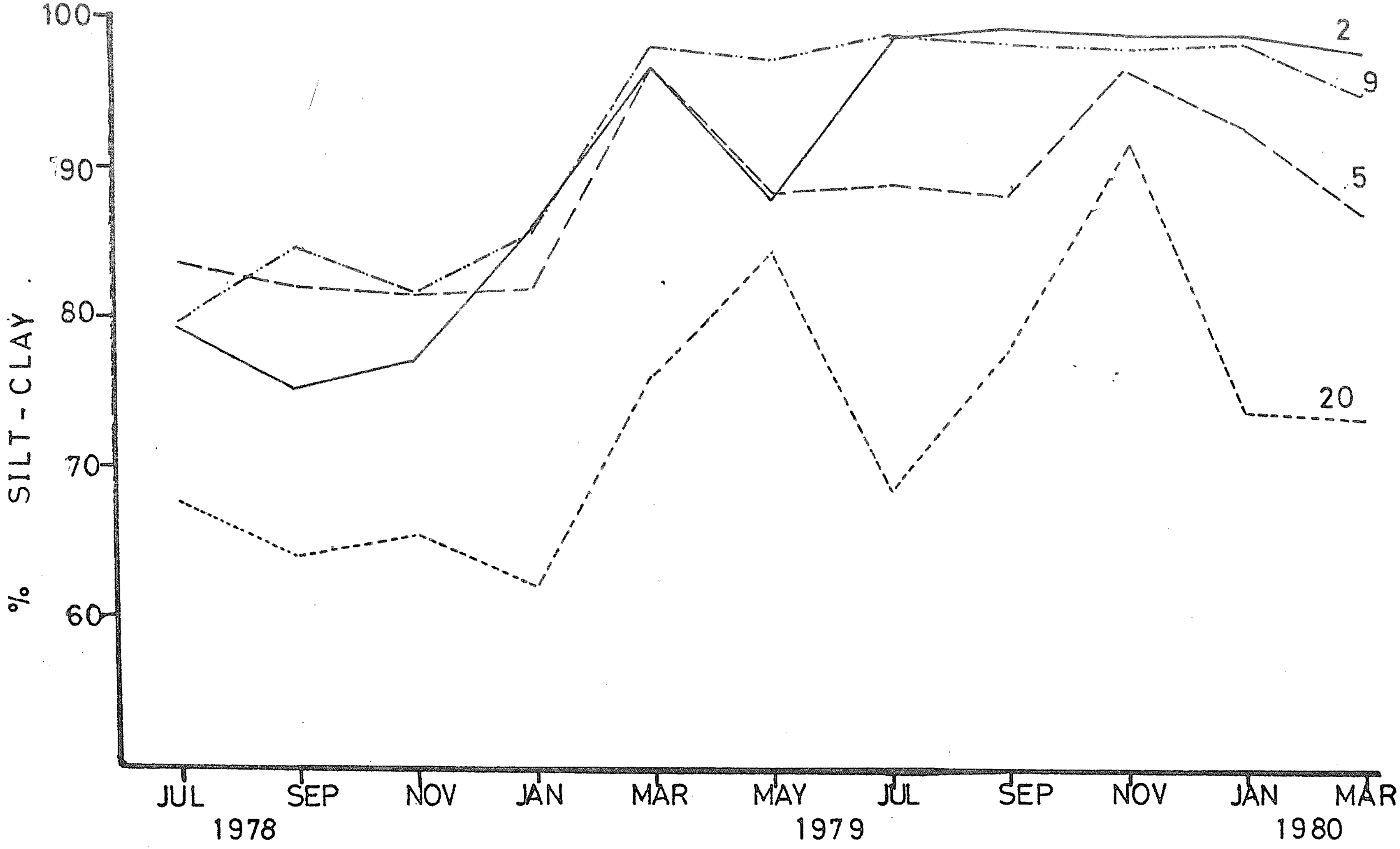


FIG.3.2. SEASONAL VARIATIONS IN SILT-CLAY AT SELECTED STATIONS

of fines which rose to remain stable from summer 1979 onwards.

Various factors may influence the settlement of material, among which the tidal currents may play a prominent role. Tidal currents at station 2 were weak, often less than 1 knot, which resulted in fine particles settling rapidly. Patchiness in the substratum might be responsible for some of the variation in the proportion of fines as sediments often varied significantly within short distances (Jones,1950).

Station 5 on the eastern side consisted of a greyish compact sediment often loaded with bivalve shells notably those of Mercenaria, Mya, Ostrea and Venerupis species. The sediment contained a high proportion of fines ($<63\mu m$ in diameter) intermixed with coarse sand and gravel. There was a fair stability in the silt-clay portion of the sediment at the station except for some odd peaks in March 1979 and the winter of 1979/80. Greater deposition of fines occurred in the winter months than in the summer months when the proportion of sand in the sediment was higher. Stronger tidal currents (2-2.5 knots) washed gravels from the beach on the eastern side down into the subtidal region where they later settled. (Dyer,1973).

The sediment at station 9 closely resembled that of station 2. The sediment at this station was soft black and oily with a higher proportion of fines than at station 2. There was a continuous increase in the deposition of fines at the station except in November 1978 when the sand proportion rose by 3% over the preceding sample. The proportion of fines at the station remained high and fairly constant from spring 1979.

Station 20, the seaward station, contained sediment containing fairly large proportion of sand and fine particles. The sand component varied between 15 and 32% with greater fluctuations in the proportion of fines. The high sand content at the station could be attributed to the influence of water flow from the River Hamble coupled with strong tidal currents within the area.

In general, all stations sampled showed an increase in the silt-clay percentage from a low level between July 1978 and January 1979 to a higher level between March 1979 and March 1980 as shown below. This indicates a higher net sedimentation in the area, in the second period.

Station	% Silt-clay July 1978-Jan. 1979	Standard Deviation	% Silt-clay March 1979-March 1980	Standard Deviation
2	79.4	± 4.7	97.3	± 4.0
5	82.9	± 2.9	98.1	± 1.1
9	82.2	± 0.8	91.5	± 4.1
20	64.9	± 2.4	78.4	± 7.7

(b) Total Organic Matter (T.O.M.)

The percentage total organic matter of the sediment samples measured as loss of weight on ignition are presented in Table 3.2 and figure 3.3. The four stations showed high values of the total organic matter with the highest values at stations 2 and 9, within the vicinity of the industrial outfalls on the western side of the estuary.

The average total organic matter with the standard deviation used as a measure of variability for the stations are:

Station	Average T.O.M. values	Standard Deviation
2	10.9	± 0.8
5	9.3	± 1.2
9	10.00	± 1.4
20	6.8	± 1.2

Station 20 had the lowest T.O.M. values and station 9 the greatest variability in the values.

By splitting the data into three groups, viz:

Summer/Autumn (July - September)
Autumn/Winter (November - January)
Winter/Spring (March - May)

based on the average values of T.O.M. for the period between July 1978 and March 1980, there was a clear seasonality at all stations with high total organic matter between July and September but generally falling to a minimum between March and May (Fig. 3.4). Stations 5 and 20 cycles were most marked, but the cycle was less marked at station 2 and less evident at station 9.

(c) Sediment metals

The values of sediment metals measured in parts per million using X-ray fluorescence at all selected stations are shown in Table 3.3. and

	Station 2	Station 5	Station 9	Station 20
1978 July	11.7	10.5	12.6	8.7
September	11.1	13.7	9.4	7.3
November	10.8	8.2	9.8	7.1
1979 January	10.7	10.5	7.6	6.6
March	10.9	8.9	9.7	6.9
May	10.5	6.8	8.5	4.7
July	11.4	10.2	11.6	8.6
September	12.3	10.5	9.6	6.3
November	9.4	8.4	9.8	6.5
1980 January	11.4	9.7	11.1	6.7
March	10.1	9.4	10.3	5.4
Mean.	10.9	9.3	10.0	6.8
S.D.	± 0.8	± 1.2	± 1.4	± 1.2

Table 3.2. Total Organic Matter (in percentage) for all selected stations

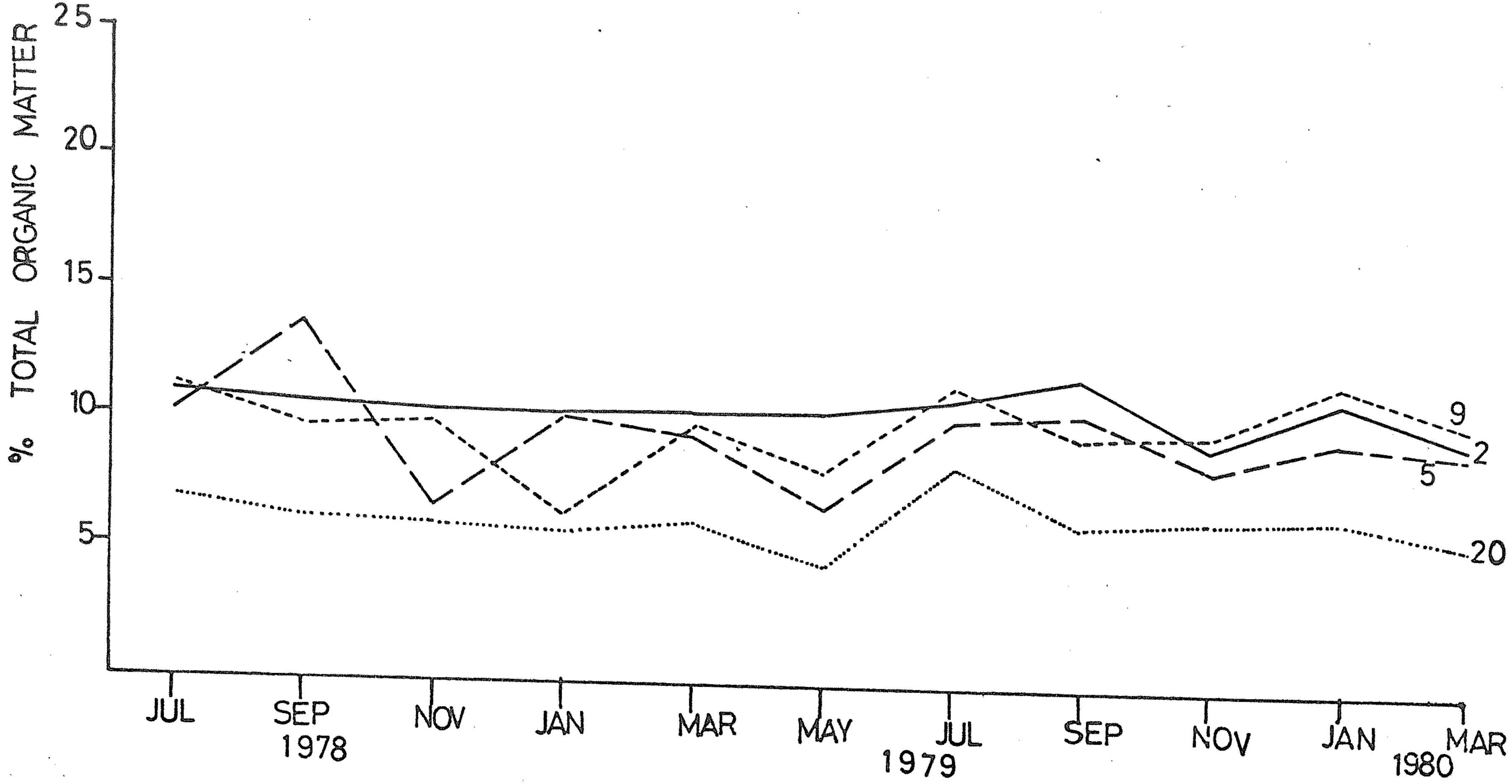


FIG. 3.3. SEASONAL VARIATION IN TOTAL ORGANIC MATTER IN SELECTED STATIONS

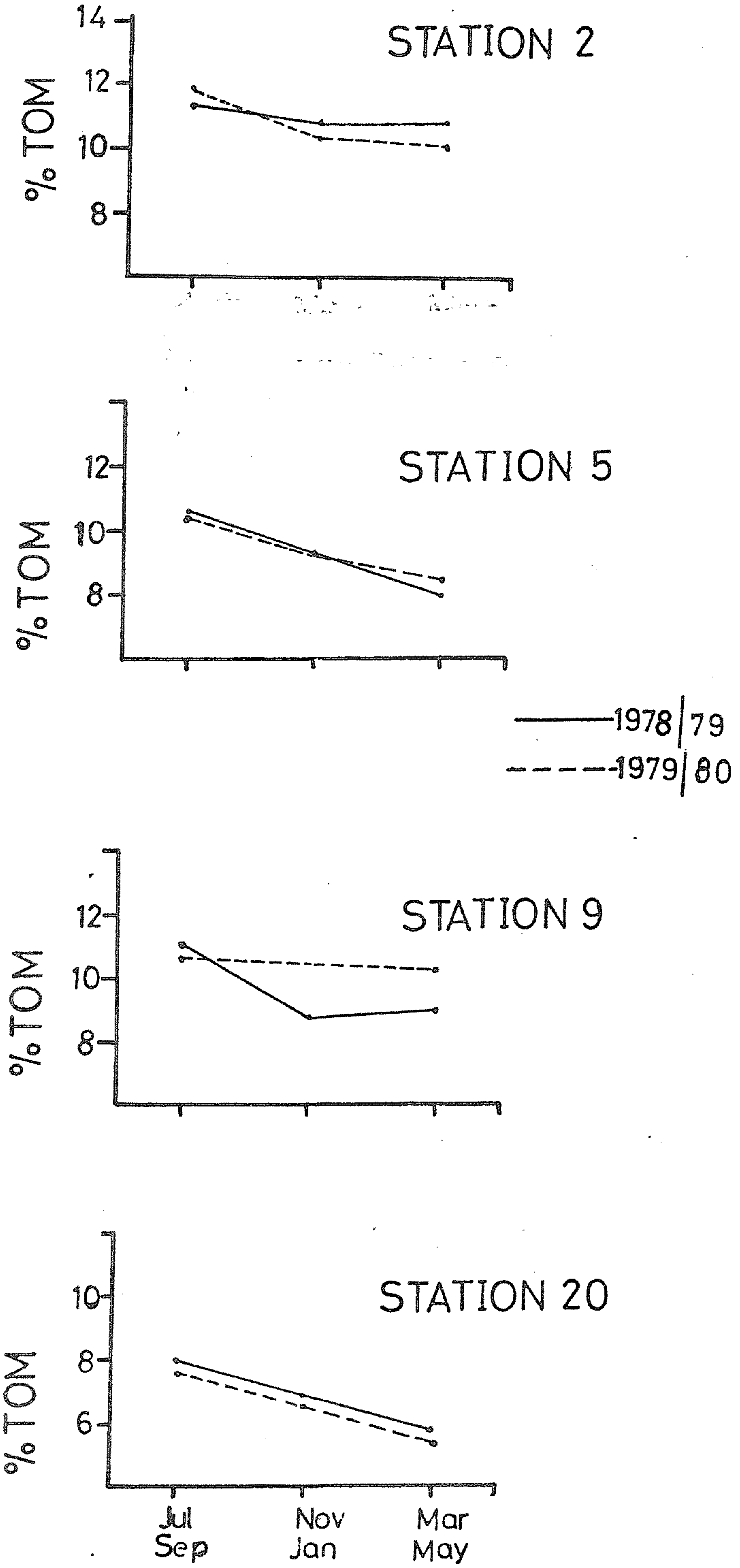


FIG.3.4. CHANGES IN AVERAGE VALUES OF TOTAL ORGANIC MATTER (JULY 1978 MARCH 1980)

	Station 2				Station 5				Station 9				Station 20			
	Lead	Arsenic	Zinc	Copper	Lead	Arsenic	Zinc	Copper	Lead	Arsenic	Zinc	Copper	Lead	Arsenic	Zinc	Copper
1978																
May	77.0	32.5	149.7	149.9	47.9	26.3	81.0	40.6	55.1	43.8	137.6	579.4	69.1	36.5	122.4	38.6
July	70.8	40.1	146.5	140.0	42.0	28.6	79.3	25.2	76.5	38.0	152.4	341.7	46.7	27.7	88.6	59.2
Sept	70.5	35.4	140.9	184.9	31.4	70.5	60.9	21.7	82.4	36.7	163.8	673.8	48.5	23.7	86.1	45.0
Nov	75.1	33.0	171.7	297.2	60.5	34.1	110.3	47.4	91.0	29.8	170.3	847.8	41.1	20.5	72.9	42.9
1979																
Jan	71.2	20.8	148.3	242.6	441.1	20.1	81.5	28.5	56.8	11.3	151.9	369.2	40.2	14.5	73.4	51.3
March	72.8	22.3	179.9	358.5	48.6	23.3	89.7	32.3	59.9	13.9	172.8	351.7	38.1	15.5	67.2	36.8
May	81.1	21.6	136.8	174.5	79.4	19.6	99.8	42.9	70.2	21.3	141.1	823.4	70.6	12.6	76.9	51.3
July	82.3	21.0	142.2	146.9	127.1	13.5	93.5	30.8	84.2	17.4	130.5	267.8	48.7	15.3	84.0	48.1
Sept	85.9	20.8	122.4	148.8	97.7	16.7	106.7	35.5	69.2	14.0	118.0	209.2	42.7	14.4	80.0	45.4
Nov.	101.2	18.2	139.2	413.1	44.4	17.3	76.7	19.5	57.5	17.5	119.0	157.8	47.4	13.7	86.0	57.8
1980																
Jan.	69.6	21.8	141.0	176.2	73.6	15.8	89.2	33.6	60.4	16.1	141.4	248.7	43.4	14.7	71.5	43.1
March	71.2	22.1	160.5	267.4	61.1	19.6	89.5	33.0	60.2	15.0	157.1	300.2	40.8	15.1	69.4	40.0
Average	77.4	25.8	148.3	225.0	63.2	25.5	88.2	32.6	68.6	22.9	146.3	430.9	48.1	18.7	81.5	46.6

Table 3.3 Trace metals in sediments measured in parts per million at the selected stations

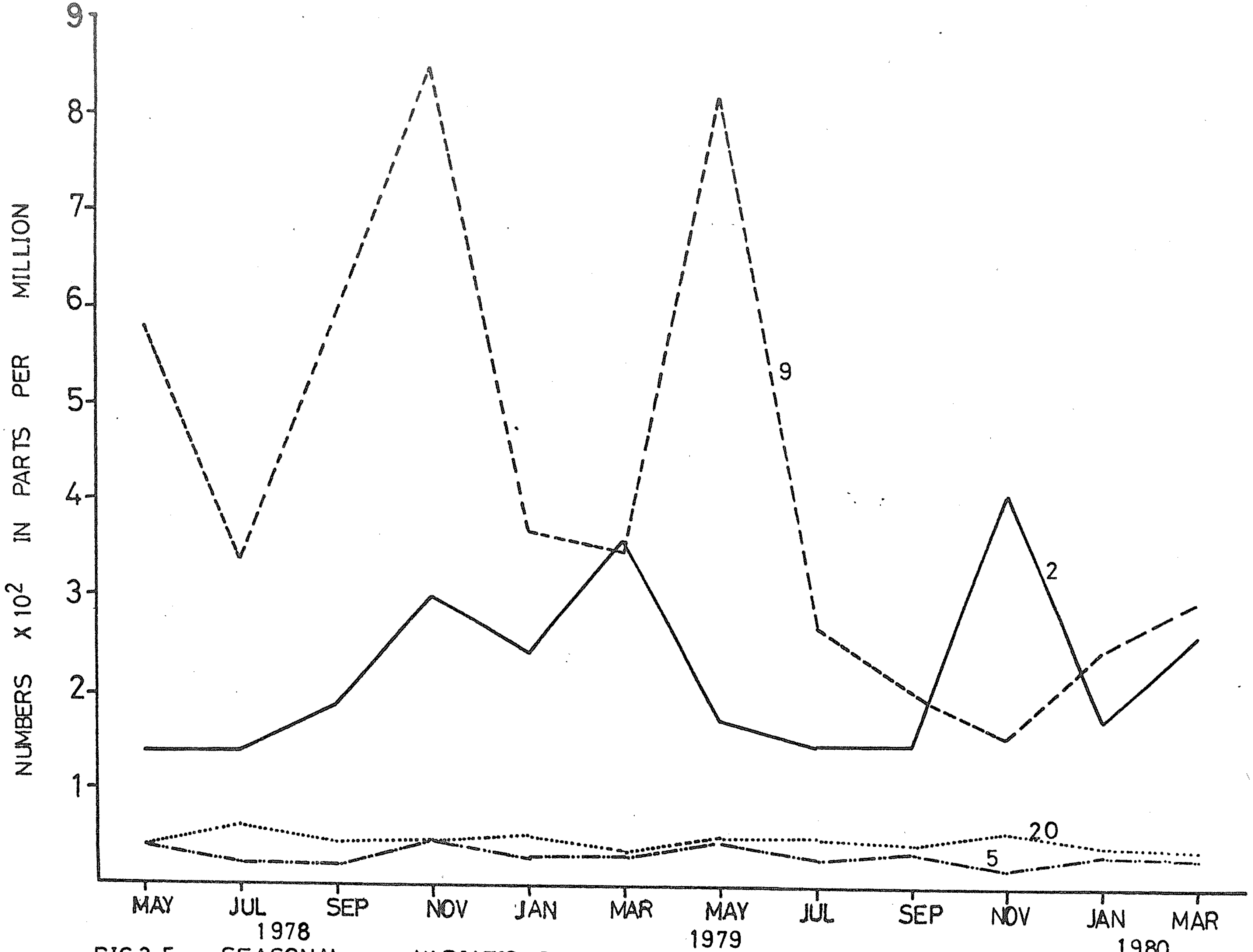


FIG.3. 5. SEASONAL VARIATIONS IN SEDIMENT COPPER

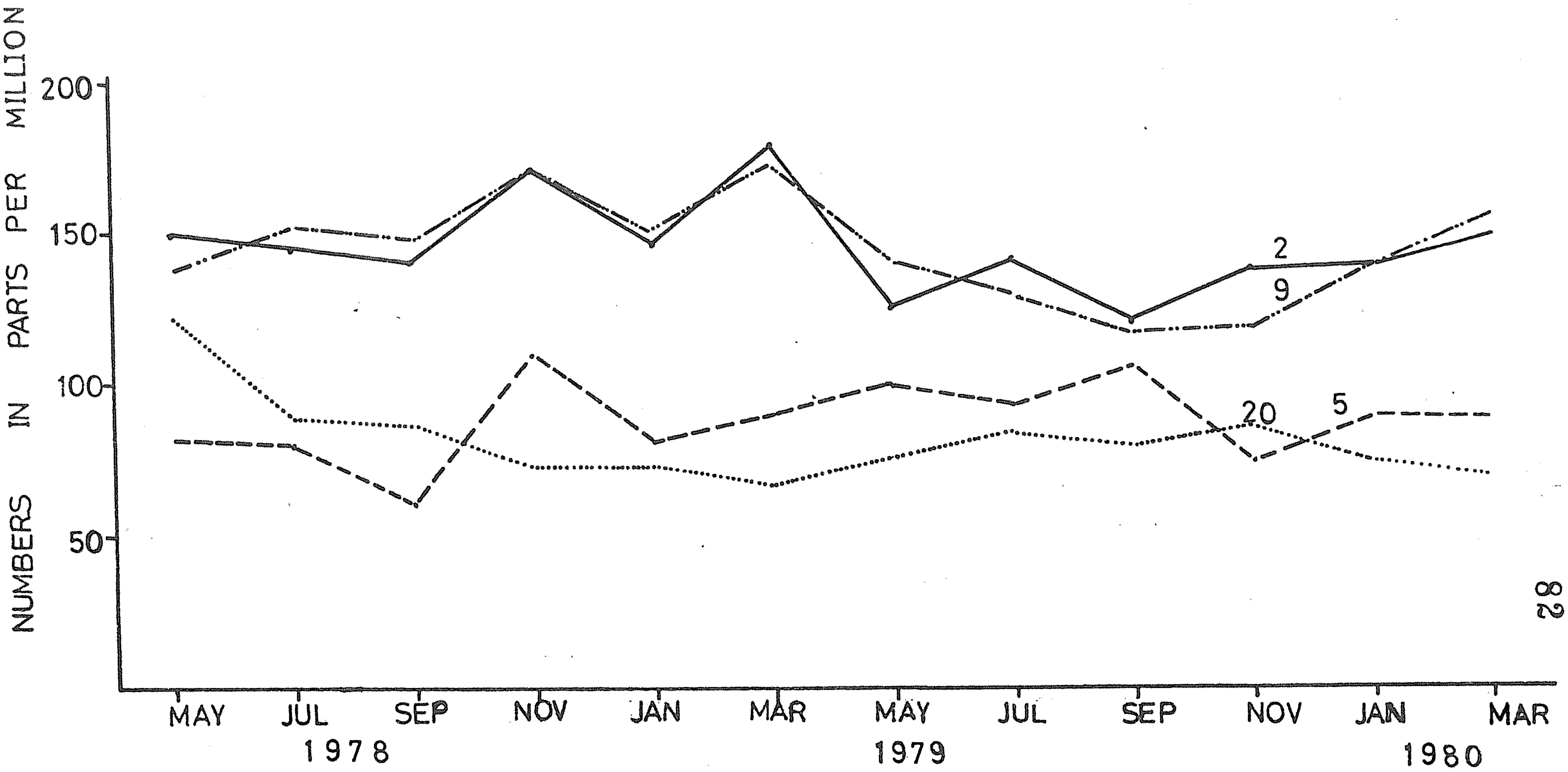


FIG. 3.6. SEASONAL VARIATION IN SEDIMENT ZINC

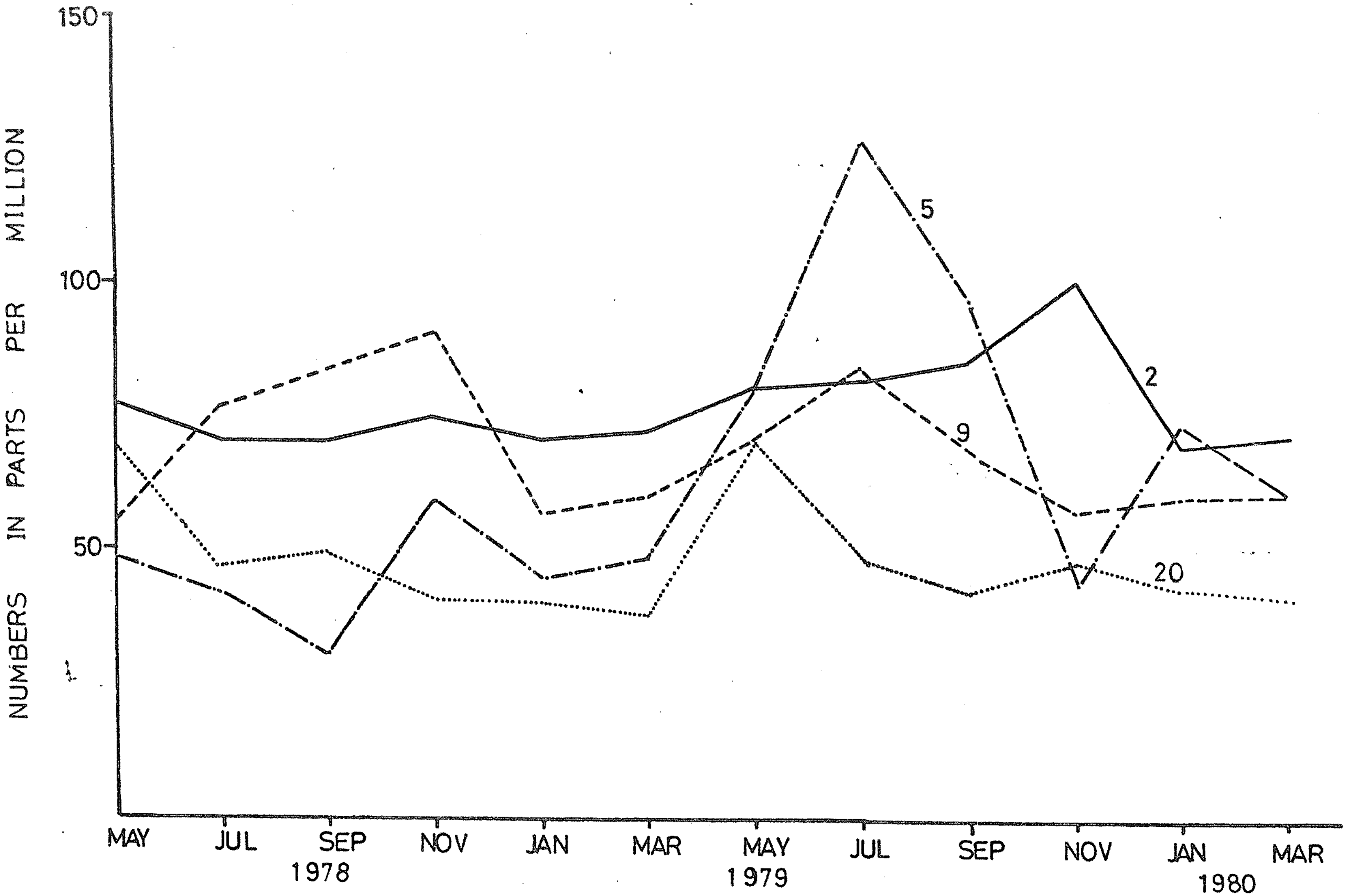


FIG.3.7 SEASONAL VARIATIONS IN SEDIMENT LEAD

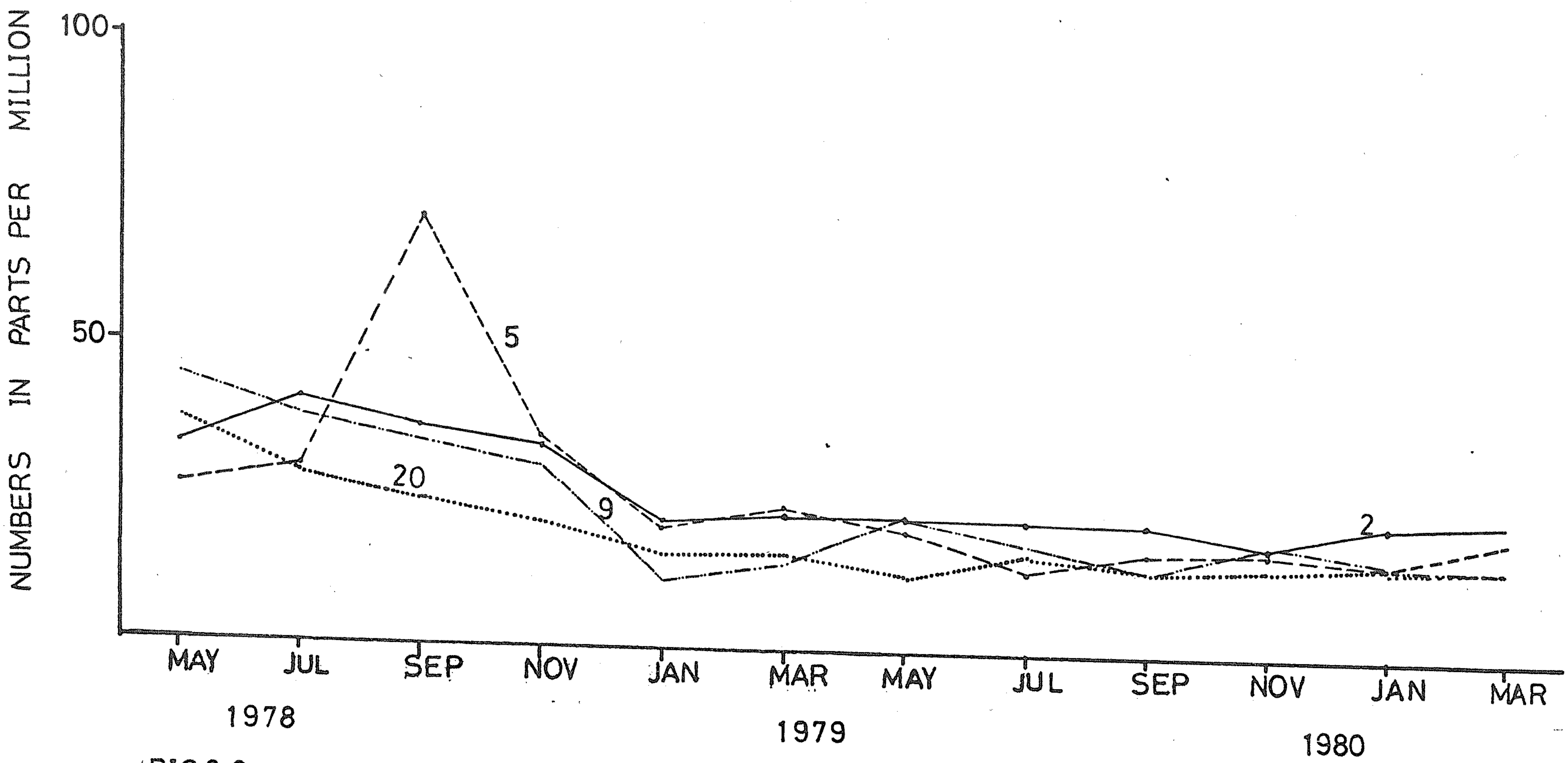


FIG.3.8. SEASONAL VARIATIONS IN SEDIMENT ARSENIC

Figures 3.5 (copper); 3.6 (Zinc); 3.7 (Lead) and 3.8 (Arsenic).

(i) Sediment copper

The sediment copper was high at stations 2 and 9 on the western side but low at stations 5 and 20 on the eastern side and towards the mouth of Southampton Water. Station 9 showed the highest sediment copper level, and ranged between 158 and 848 parts per million (p.p.m.) with peaks in November 1978 and May 1979. At station 2, there was an increase in the copper level between May and November 1978 and this was followed by a fall in the winter months. Another rise in the summer months was followed by a fall in winter. Copper which is used as a 'sweetening' agent in the refinery process (Knap 1978) probably accounts for the high levels of sediment copper on the western side. Stations 5 and 20 showed low levels (less than 60 ppm) of sediment copper.

The selected stations may conveniently be grouped according to the amount of sediment copper as 'high copper stations' (containing $>$ 200 ppm sediment copper) and 'low copper stations' (containing $<$ 100 ppm). On this basis, stations 2 and 9 would fit into the 'high copper stations' and stations 5 and 20 into the 'low copper stations'.

(ii) Sediment Zinc

All the selected stations showed low and constant levels in the sediment zinc throughout the study period. Higher levels of sediment zinc occurred at station 2 where it ranged between 122 ppm in September 1979 and 180 ppm in March 1979. Similar but lower values were obtained at station 9. The levels ranged between 120 ppm and 170 ppm. The high zinc level in the sediment at station 2 may be attributed to the proximity of the station to the outfalls of both Synthetic Rubber and Union Carbide industries. Station 20 showed the least level of sediment zinc, the low level possibly being due to the distance from the industrial outfalls.

(iii) Sediment Lead

High fluctuations in the sediment lead at all four stations were recorded during the study period. There was a gradual increase in the sediment lead at station 2 between May 1978 and November 1979 when a peak value of 101 ppm was obtained. The main source of lead in the estuary has been associated with the industry, but the river flows of the Test, Itchen and Hamble may play a major role (Burton, personal communication). All four stations showed a gradual increase in sediment lead between spring and summer 1979. This was probably due to increased river flows into the estuary in late spring.

(iv) Sediment Arsenic

There was a gradual decline in the sediment arsenic at all four stations (except at station 5 in September 1978). The level of sediment arsenic in the estuary was low with highest level occurring at station 2. At this station, the value of arsenic in the sediment ranged between 18 and 40 ppm with no seasonal trend. Arsenic enters Southampton Water mainly through domestic sewage and the decline throughout the study period may be due to a change in the sewage treatment.

(d) Bottom water temperature

The bottom water temperature for Fawley Esso south-end jetty and the refinery outfalls, as supplied by the British Transport Docks Board, are presented in Fig. 3.9. The refinery outfall water temperature was about 10^{o}c higher than the jetty's, but the effect of the difference in temperature on the bottom animals could be negligible as the volume of water from the refinery is little compared with the bulk of estuarine water. Highest water temperatures were between July and September and minimum temperatures recorded in January. There was no significant change in the bottom water temperature in 1978 and 1979.

3.3.2. BIOLOGICAL PARAMETERS

Conflicts often arise on how best benthic communities can be classified. The disagreement lies between a classification based primarily on the nature of bottom deposits (Jones, 1950) called a 'biotype' and that based upon the characteristic elements of the constituent species called biocenosis (Hedgepeth, 1954). Each method of classification has its own limitations. Nevertheless, a relationship has been found between the community and the nature of bottom deposit. A deposit based classification often suffers from problems of precise categorisation of the sediment types and the hydrodynamics of the sediment (Sanders, 1956). Two apparently identical silty sediments may vary in origin. In one, the silt may be in the process of transport through the system due to the dynamic processes operating in the area.

Such sediments, though similar in grain size, would contain different types of fauna. A faunal based classification leaves anomalies and grades between the communities. The method employed in the present study is based partly on the nature of the bottom deposits in which the benthic communities occur and on the characteristic elements of the

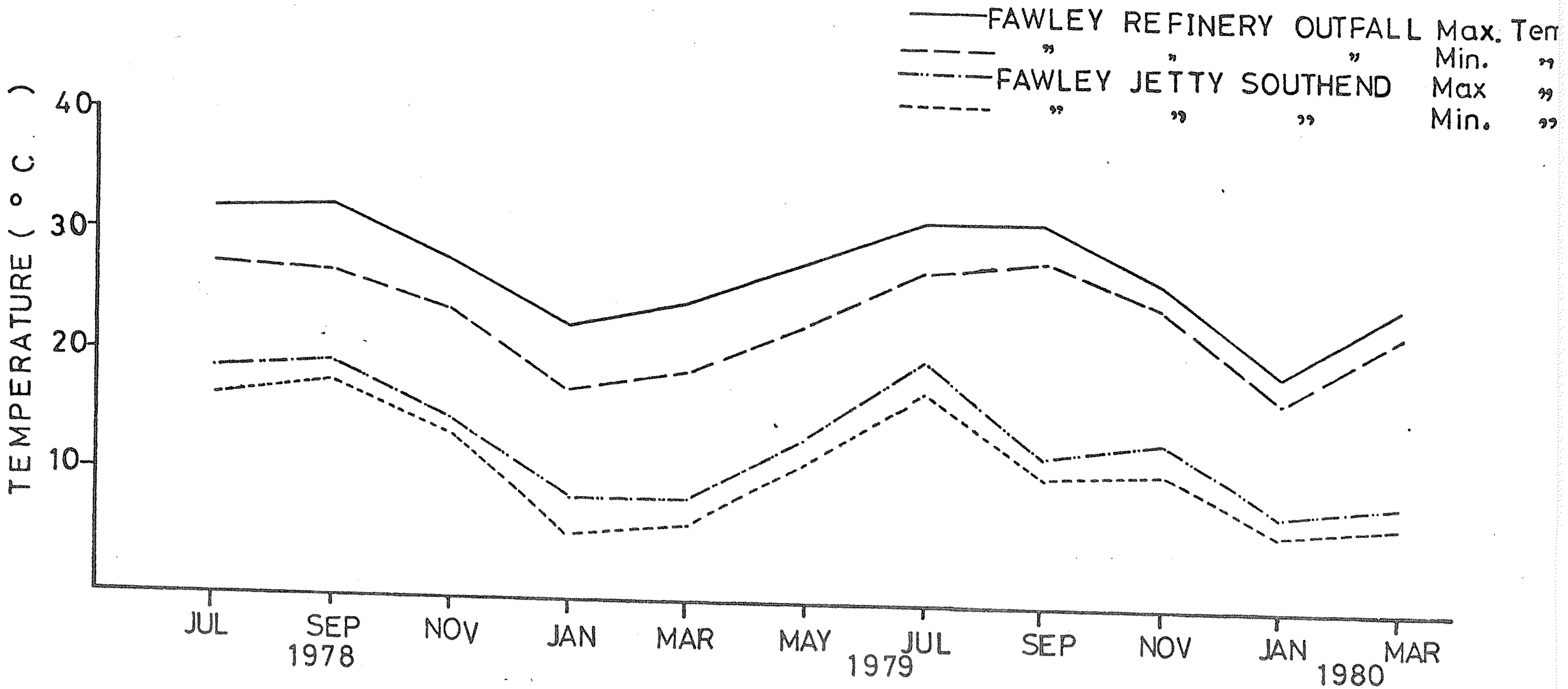


FIG.3.9. SEASONAL VARIATIONS IN BOTTOM WATER TEMPERATURES AT FAWLEY'S REFINERY OUTFALL AND JETTY (SOUTHEND)

fauna.

The short-term population trends of the benthic macrofauna of the study area were investigated and the population parameters including the number of species and individuals as well as diversity were studied. Each station is treated separately so as to give information on the temporal variability.

STATION 2

Located about 600 metres east of the Union Carbide outfall on the western side of Southampton Water, the station was characterised by a high silt-clay fraction (average 90% silt-clay) and supported a fairly rich benthic macrofauna. A total of 23 different species were recorded at the station in the bimonthly samples during the 20 month period. A species list with percentage numerical abundance at each bimonthly sample is presented in Table 3.4a,b. Polychaetes constitute 45.5% (10) of the total species, crustaceans 40.9% (9) and molluscs 13.6% (3). The numbers in parentheses are the actual numbers of the species. The polychaetes comprised both errentia and sedentarians and the crustaceans were represented by amphipods, isopods, ostracods and decapods.

The variation in the number of species and numerical abundance at station 2 is shown in Figure 3.10. The number of species declined throughout the study period except in September 1978. The maximum number of species of macrofauna recorded at the station was $17m^{-2}$ in September 1978. The number fell gradually until a minimum of $3m^{-2}$ was recorded from November 1979 onwards. The trend of the numerical abundance of the animals at the station was similar to the number of species until July 1979. Between July 1978 and May 1979 the number of species and individuals decreased by more than half.

Changes in the number of species lack information as to how relative abundance of major animal taxa are represented in the successive bimonthly samples. Only detailed analysis of the species composition of the animal taxa revealed such information. The percentage numerical abundance of the major animal taxa is given in Table 3.5.

Polychaetes dominated at the station throughout the study period and occurred at a percentage greater than 85%. The crustacean and molluscan elements of the fauna were relatively less important with regard to the number of species. They gradually declined and were lost during the course of study. This possibly suggests that the habitat at station 2 was undergoing a gradual change which became unfavourable to the crustaceans and molluscs and which resulted in their complete disappearance

Table 3.4a FAUNAL LIST AND NUMBERS M^{-2} AT STATION 2 BETWEEN JULY 1978 and MARCH 1980.

SPECIES	1978 July	1978 Sept	1978 Nov	1979 Jan	1979 Mar	1979 May	1979 July	1979 Sept	1979 Nov	1980 Jan	1980 March
Caulleriella caputesocis (St. Joseph)	3425	1220	251	324	2	1	--	4	--	--	1
Abra nitida Müller	585	1	--	--	--	--	--	--	--	--	--
Nephtys hombergi (Aud & M-Edw)	100	3	2	32	--	--	--	--	--	--	--
Cerastoderma edule L.	17	2	1	--	--	--	--	--	--	--	--
Philomedes globosus (Baird)	12	4	--	--	--	--	--	--	--	--	--
Polydora ciliata (Johnston)	9	1086	17	42	--	1	54	--	--	--	--
Mercenaria mercenaria L.	5	--	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	3	563	808	269	266	109	65	3	28	26	13
Cirratulus cirratus (Müller)	2	--	--	--	--	--	--	--	--	--	--
Crangon crangon L.	1	--	--	--	--	--	--	--	--	--	--
Sabella pavonina Sarvigny	--	1740	2733	57	--	--	--	--	--	--	--
Nereis diversicolor Müller	--	699	848	333	388	10	149	63	442	358	352
Capitella capitata (Fabricius)	--	608	76	2	372	21	282	169	120	205	25
Anaitides maculata St. Joseph	--	5	--	3	--	--	--	--	--	--	--
Idotea linearis L.	--	3	--	--	1	--	--	--	--	--	--
Carcinus maenas L.	--	1	1	--	--	--	--	--	--	--	--
Dexamine spinosa Montagu	--	1	--	--	--	--	--	--	--	--	--
Atylus vedlomensis (Bate & Westwood)	--	1	--	--	--	--	--	--	--	--	--
Ophiodromus flexuosus Delle Chiaje	--	1	--	--	--	--	--	--	--	--	--
Unidentified polychaete	--	2	--	--	--	--	--	--	--	--	--
Jassa marmorata Holmes	--	--	--	1	--	--	--	--	--	--	--
Unidentified mite	--	--	--	--	--	1	--	--	--	--	--
Praunus flexuosus (Müller)	--	--	--	--	--	--	1	--	--	--	--
Corophium insidiosum Crawford	--	--	--	--	--	--	1	--	--	--	--
Total number of individuals	4159	6162	4837	1063	1029	143	552	237	590	589	391

Table 3.4b - LIST OF MACROFAUNA WITH PERCENT NUMERICAL ABUNDANCE OF INDIVIDUALS AT STATION 2

SPECIES	1978 July	1978 Sept	1978 Nov	1979 Jan	1979 Mar	1979 May	1979 July	1979 Sept	1979 Nov	1980 Jan	1980 Mar
Caulleriella caputesocis (St. Joseph)	82.45	19.80	5.30	30.48	0.19	0.69	--	1.68	--	--	0.25
Abra nitida Müller	14.07	0.02	--	--	--	--	--	--	--	--	--
Nephtys hombergi (Aud & M-Edw.)	2.40	0.05	0.04	3.01	--	--	--	--	--	--	--
Cerastoderma edule L.	0.41	0.03	0.02	--	--	--	--	--	--	--	--
Philomedes globosus (Baird)	0.29	0.06	--	--	--	--	--	--	--	--	--
Polydora ciliata (Johnston)	0.22	11.68	0.36	3.95	--	0.69	9.78	--	--	--	--
Mercenaria mercenaria L.	0.12	--	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	0.07	9.14	17.01	25.31	25.88	77.20	11.77	1.27	4.75	4.42	3.33
Cirratulus cirratus (Müller)	0.05	--	--	--	--	--	--	--	--	--	--
Crangon crangon L.	0.02	--	--	--	--	--	--	--	--	--	--
Sabella pavonina Sarvigny	--	28.24	57.70	5.36	--	--	--	--	--	--	--
Nereis diversicolor Müller		11.34	17.90	31.33	37.74	6.99	26.99	26.58	74.92	60.78	90.03
Capitella capitata (Fabricius)	--	9.87	1.60	0.19	36.19	14.69	51.08	70.46	20.33	34.80	6.39
Anaitides maculata L.	--	0.08	--	0.28	--	--	--	--	--	--	--
Idotea linearis L.	--	0.05	--	--	0.09	--	--	--	--	--	--
Carcinus maenas L.	--	0.02	0.02	--	--	--	--	--	--	--	--
Dexamine spinosa Montagu	--	0.02	--	--	--	--	--	--	--	--	--
Atylus vedlomensis	--	0.02	--	--	--	--	--	--	--	--	--
Ophiodromus flexuosus Delle Chiaje	--	0.02	--	--	--	--	--	--	--	--	--
Jassa marmorata Holmes	--	--	--	0.09	--	--	--	--	--	--	--
Praunus flexuosus Müller	--	--	--	--	--	--	0.18	--	--	--	--
Corophium insidiosum Crawford	--	--	--	--	--	--	0.18	--	--	--	--
Unidentified mite	--	--	--	--	--	0.69	--	--	--	--	--
Total number of species	10	16	9	9	5	6	6	4	3	3	4

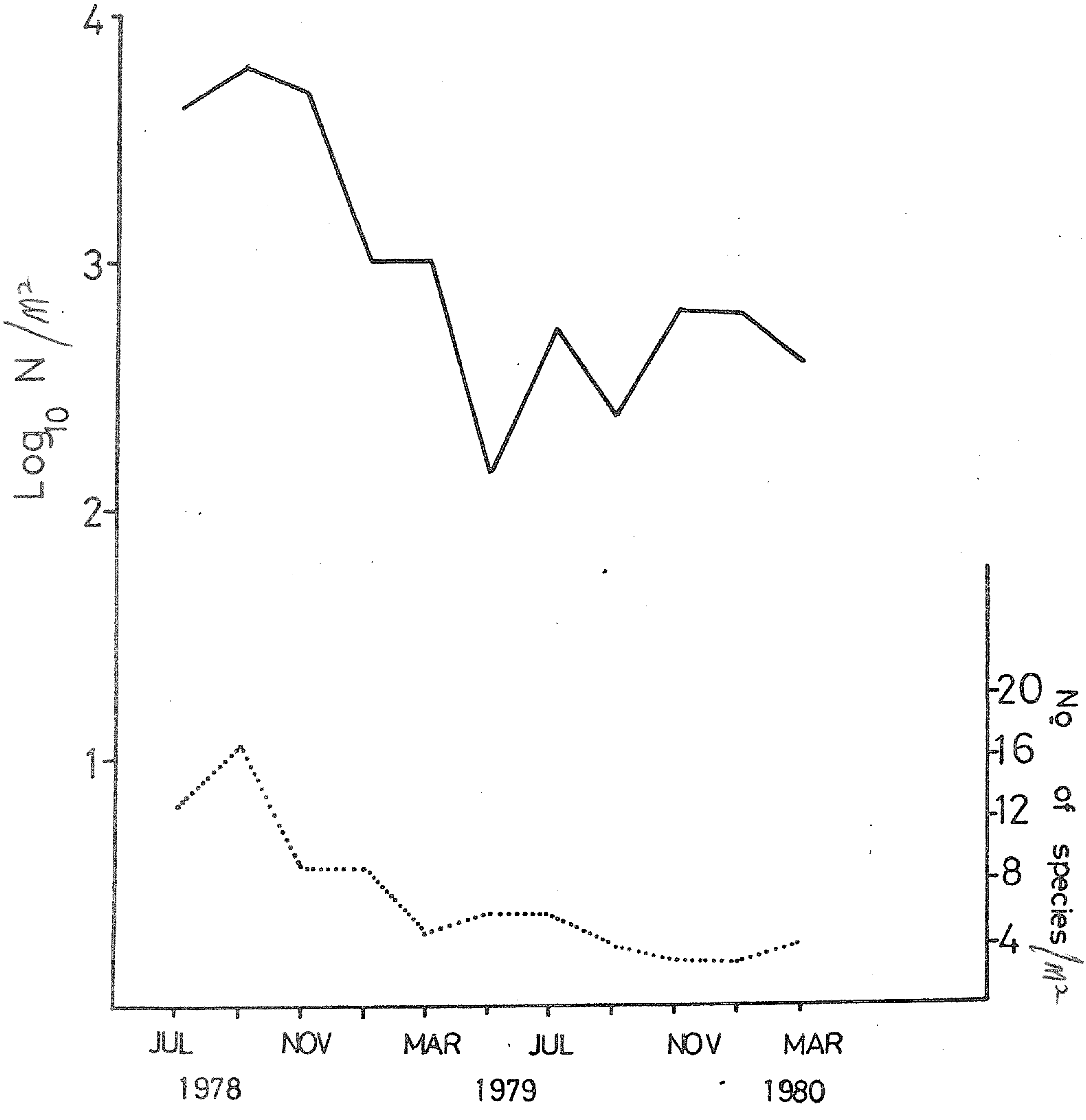


FIG.3.10. SEASONAL VARIATION IN NUMBER OF SPECIES AND TOTAL INDIVIDUALS AT STATION 2

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Polychaeta	85.10	99.76	99.95	99.91	99.90	99.31	100	100	100	100	100
Crustacea	0.31	0.15	0.02	0.09	0.10	--	--	--	--	--	--
Mollusca	14.60	0.05	0.02	--	--	--	--	--	--	--	--
Others	--	--	--	--	--	0.69	--	--	--	--	--

Table 3.5. Percentage numerical abundance of major animal taxa at Station 2

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Caulleriella caputesocis	1	2	4	2	4	5	-	3	-	-	4
Abra nitida	2	-	-	-	-	-	-	-	-	-	-
Nephtys hombergi	3	-	-	-	-	-	-	-	-	-	-
Cerastroderma edule	4	-	-	-	-	-	-	-	-	-	-
Philomedes globosus	5	-	-	-	-	-	-	-	-	-	-
Capitella capitata	-	5	5	-	2	2	1	1	2	2	2
Sabella pavonina	-	1	1	4	-	-	-	-	-	-	-
Polydora ciliata	-	3	-	5	-	4	4	-	-	-	-
Nereis diversicolor	-	4	2	1	1	3	2	2	1	1	1
Eteone longa	-	-	3	3	3	1	3	4	3	3	3
Idotea vulgaris	-	-	-	-	5	-	-	-	-	-	-
	-	-	-	-	-	-		-	-	-	-

Table 3.6. Abundance ranking of top five species at Station 2

from the samples.

A detailed analysis of the changes in population densities showed that only four polychaete species, Caulleriella caputesocis, Nereis diversicolor, Capitella capitata and Eteone longa emerged as the major constituents of the polychaete population at the station. These polychaetes accounted for more than 90% of the total fauna numerically.

Individual species

The abundance ranking of the top five species at station 2 is presented in Table 3.6. The instability in the ranking of the individual dominant species as evidenced by Spearman's concordance (w = 0.009) showing complete randomness in the allocation of the ranking, may be attributed to several environmental factors. At the start of the study in July 1978, C. caputesocis occurred at high densities ($3425m^{-2}$). Other polychaetes, for example, N. hombergi, P. ciliata and E. Longa, also occurred in reasonably high numbers. In the succeeding samples, the sabellid worm, Sabella pavonina which was absent in the July 1978 sample had a large settlement. The species ranked first in September and November 1978. The specimens collected were, however, juveniles, measuring less than 4mm long. The dominance of S. pavonina was short lived, and the species disappeared without reaching maturity in the following winter months. From January 1979, N. diversicolor and C. capitata became dominant, ranking as the top two species in the samples. Neither the filter-feeding bivalve Cerastoderma edule nor Abra nitida, which featured prominently in theJuly 1978 samples, occurred in such densities as to rank within the top five species in the succeeding samples.

The phyllodocid, Anaitides maculata and the hesionid Ophiodromus flexuosus, occurred at low densities prior to the winter of 1978/79. The filter-feeding bivalve, A. nitida, declined in density from $585m^{-2}$ in July 1978 to less than $20m^{-2}$ in the succeeding samples. Other bivalves showed sporadic occurrence possibly due to patchiness in distribution. Five specimens of Mercenaria mercenaria were recovered at one occasion and one or two specimens of the cockle, C. edule, were often present in the samples. Nevertheless, empty shells of many molluscs especially Hydrobia sp, C. edule, M. mercenaria and Crepidula fornicata, were recorded in fairly large numbers.

The time series of samples from the station showed that the fauna could be grouped into 'dominant' species defined here as those species each accounting for more than 3% of the total abundance, and as 'numerically unimportant' species comprising the remaining species. To understand the role of the individual 'dominant' species in the numerical abundance variations at the station, the recruitment and mortality pattern of each species was studied.

The seasonal recruitment and mortality of the dominant species at station 2 is shown in Fig. 3.11. There was great fluctuation in the recruitment and mortality patterns between species.

Caulleriella caputesocis

This species declined numerically between November 1978 and January 1979 with a rapid decrease between January and May 1979, after which it remained at a low level of abundance. The sudden and short-lived recruitment in September 1979 was probably due to an influx of newly settled summer juveniles or possibly to immigration from outside the sampling area.

Nephtys hombergi

This worm suffered heavy mortality between July and November 1978, followed by a heavy but short-lived winter recruitment. The species disappeared from samples from March 1979.

Sabella pavonina

This sabellid had a short but remarkable occurrence at the station, and appeared first in the September 1978 samples. It reached its maximum density in November 1978. The density fell sharply during the winter months of 1978/79 and it was absent from samples after January 1979.

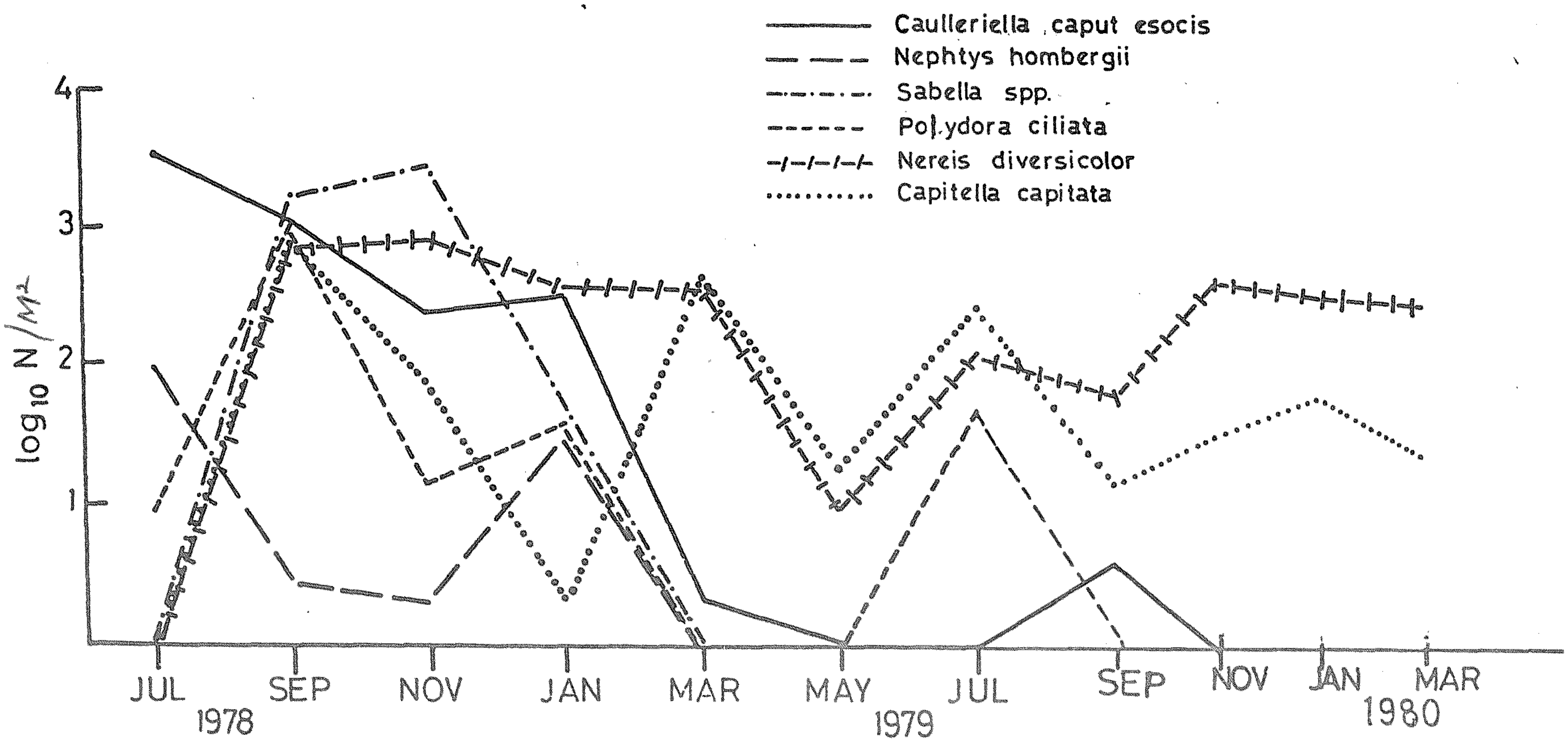
Polydora ciliata

This worm exhibited sporadic occurrence at the station. It reached its maximum density in September 1978 when it was first recorded at this station. It suffered heavy mortality by November 1978 and disappeared from samples by March 1979, only reappearing on a single occasion during the rest of the study.

Nereis diversicolor

The nereid was relatively stable in density at the station. Although it suffered heavy mortality in May 1979, its high recruitment in July 1979 returned the density to the previous high level.

FIG.3.11. SEASONAL RECRUITMENT & MORTALITY OF DOMINANT SPECIES IN ST. 2



Capitella capitata

This worm was first recorded at the station in September 1978 and showed high levels of recruitment in the summer months and heavy mortality in the winter months.

Table 3.7 shows the average species abundance ranking for the dominant species for the eleven bimonthly samples. Seven species, six being polychaetes, accounted for about 98% of the numerical abundance of benthic macrofauna at the station. The six polychaetes alone accounted for about 95% of the total macrofaunal numerical abundance. No crustaceans ranked among the top seven species. Two top ranked species, Caulleriella caputesocis and Sabella pavonina, occurred together only on three occasions, but the former occurred in more samples.

Major animal taxa

The seasonal variation in the number of species and abundance of the major animal taxa is shown in figure 3.12. The polychaetes dominated both in the number of species and abundance and reached peaks in September 1978. Thereafter, there was a steady decline in abundance which remained stable between November 1979 and March 1980. The numbers of individuals of the crustaceans reached a peak in July 1978 but the number of species in September 1978, with smaller peaks in July 1979 for both the number of species and individuals. After July 1979, the crustaceans were absent from the samples. The molluscs which originally comprised three species and were dominant numerically by A. nitida declined from the start of the study. A. nitida declined from September 1978 and disappeared from samples by November 1978.

The general dominant position of the polychaetes in the community at station 2 is further indicated in Table 3.8. It could be seen that the polychaetes dominated not only in terms of individuals but also in species.

STATION 5

This station, located about 600 metres south-west of Netley Great Dome, was the only selected station on the eastern side of Southampton Water. The sediment was greyish sandy mud with the sand component consisting of pebbles, gravels and coarse sand. Its greater particle size diversity presented a greater variety of ecological niches possibly explaining the observed higher species diversity (Gray,1974; Ward,1975).

Rank	Species	Average no. M^{-2}	%	Cumulative %
1	*Caulleriella caputesocis*	457.3	26.60	26.60
2	*Sabella pavonina*	411.8	23.05	49.65
3	*Nereis diversicolor*	331.1	18.53	68.18
4	*Eteone longa*	195.7	10.96	79.14
5	*Capitella capitata*	170.7	9.56	88.70
6	*Polydora ciliata*	109.9	6.15	94.85
7	*Abra nitida*	53.3	2.98	97.83

Table 3.7 Station 2 average species abundance ranking of dominant species (73% of total N) for the 20 month period.

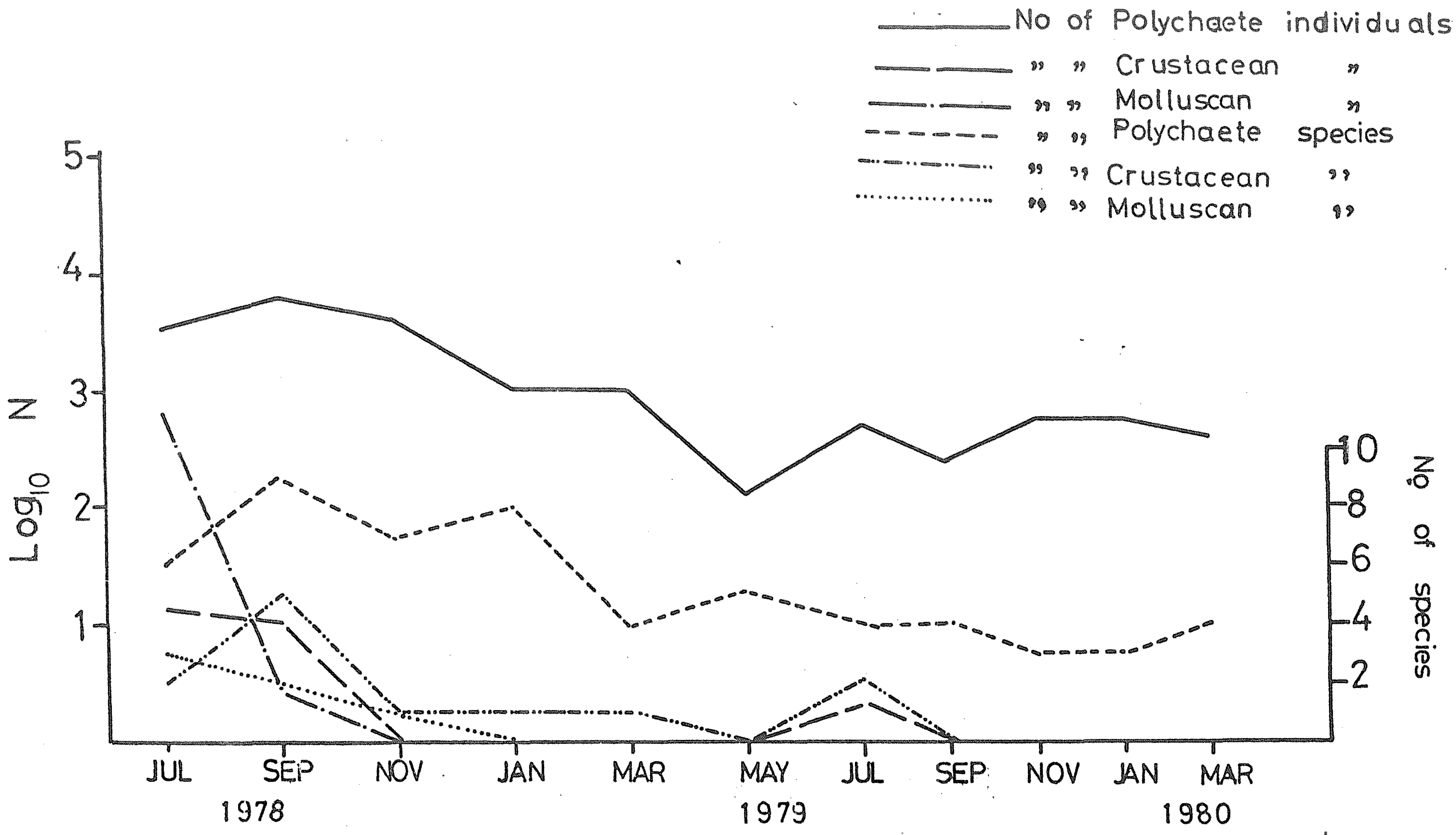


FIG. 3.12. SEASONAL VARIATION IN NUMBER OF SPECIES AND INDIVIDUALS/M² OF MAJOR ANIMAL TAXA AT STATION 2

Table 3.8

STATION 2

REPRESENTATION OF THE VARIOUS PHYLA IN NUMBERS AND SPECIES

Individuals per m^2 as % of total (figures in parenthesis represent actual numbers)

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	85.10 (3539)	0.31 (13)	14.60 (590)	- -
September	99.76 (6149)	0.51 (10)	0.05 (3)	- -
November	99.95 (4735)	0.02 (1)	0.02 (1)	- -
1979				
January	99.91 (1062)	0.09 (1)	- -	- -
March	99.90 (1028)	0.10 (1)	- -	- -
May	99.30 (142)	- -	- -	0.69 (1)
July	99.62 (550)	0.36 (2)	- -	-
September	99.99 (237)	- -	- -	0.01 (1)
November	100 (590)	- -	- -	- -
1980				
January	100 (589)	- -	- -	- -
March	100 (391)	- -	- -	- -

Species per m^2 as % of Total

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	54.55 (6)	18.18 (2)	27.27 (3)	- -
September	52.94 (9)	29.4 (5)	11.76 (2)	- -
November	77.8 (7)	12.3 (1)	12.3 (1)	- -
1979				
January	88.9 (8)	11.1 (1)	- -	- -
March	80.0 (4)	20.0 (1)	- -	- -
May	83.3 (5)	- -	- -	16.66 (1)
July	66.6 (4)	33.3 (2)	- -	- -
September	100 (4)	- -	- -	- -
November	100 (3)	- -	- -	- -
1980				
January	100 (3)	- -	- -	- -
March	100 (4)	- -	- -	- -

The fines (<63μm in diameter) at the station accounted for roughly 80-97% of the sediment by weight and the total organic matter ranged between 6.8 and 10.5%. Rhoads (1974) stressed that, in general, soft silty sediments present a difficult environment to which relatively few invertebrates have managed to adapt, and that these sediments typically show low species diversity in comparison with coarser sediments.

The bimonthly samplings at the station revealed a total of 59 species. The species and their numerical abundance in percentage during the 20 month period is presented in Tables 3.9 (a and b). The polychaetes comprised 42.4% (25); crustaceans, 38.9% (23); molluscs 13.6% (8); pycnogonids 3.4% (2) and fishes 1.7% (1) of the total number of species. The actual numbers of species are in parentheses.

Species richness and individuals abundance

The variation in the number of species and the total number of individuals at station 5 are shown in Fig. 3.13. At the start of the study, the number of species was high, between 66 and 70m^{-2}. Numbers of species fell rapidly between September 1978 and March 1979 and between May 1979 and end of study in March 1980, when the numbers of species reached 14m^{-2}. The number of species during the latter half of study was less than half the original number in July 1978. The abundance of individuals at the station showed a different trend from the number of species. Between July 1978 and May 1979, the fauna at the station declined in abundance in the winter months, the abundance of the individuals rose rapidly in the warmer months possibly due to high recruitment. The community then suffered a gradual and slight fall in abundance from July 1979.

An attempt was made to follow the contribution of each major animal taxon to the total abundance of individuals. The percentage abundance of the major animal taxa at the station is given in Table 3.10. The fauna at the station was once again dominated by the polychaetes which comprised more than 94% of the abundance of the individuals at each of the bimonthly samplings. There was no seasonal trend in the occurrence of the polychaetes at the station, but the number of polychaete species fell from the start to the end of the sampling period.

Looking at the ratio of the maximum number to the minimum number of species found in samples during the course of study, the result for the mollusc is 2.3, crustaceans 7, and polychaetes 3. It becomes evident that the crustaceans had the greatest variability in species numbers,

Table 3.9(a) FAUNAL LIST AND NUMBERS/0.5M^2 AT STATION 5 BETWEEN JULY 1978 and MARCH 1980

SPECIES	1978 July	1978 Sept	1978 Nov	1979 Jan	1979 Mar	1979 May	1979 July	1979 Sept	1979 Nov	1980 Jan	1980 March
Caulleriella caputesocis (St. Joseph)	5444	13060	12736	8385	2533	5735	10563	4288	2825	2568	4571
Cirratulus cirratus (O.F. Müller)	228	104	101	1	3	1	--	57	4	--	12
Pariambus typicus (Krøyer)	84	57	14	5	4	4	--	--	1	--	2
Microdeutopus gryllotalpa Coasta	70	60	2	1	--	--	1	--	--	--	--
Melinna palmata Malmgren	64	41	107	90	33	100	127	97	41	64	18
Aora gracilis Bate	57	28	21	1	--	--	--	--	--	--	9
Polydora ciliata (Johnston)	47	18	2	4	1	--	--	--	--	--	--
Mercenaria mercenaria L.	32	33	25	15	19	11	11	27	30	12	30
Nephtys hombergi (Audouin & M-Edw)	30	21	96	111	42	112	97	70	70	68	22
Anaitides maculata St. Joseph	24	14	5	8	2	3	3	--	--	--	--
Abra nitida (Müller)	23	13	14	39	4	89	55	8	15	4	4
Philomedes globosus Baird	15	80	11	15	7	3	16	7	11	1	1
Cerastoderma edule L.	12	6	1	1	2	3	77	6	1	--	--
Corophium insidiosum Crawford	9	3	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	8	1	1	6	3	2	6	1	--	--	1
Spio filicornis (O. F. Müller)	4	--	--	--	--	--	--	--	--	--	--
Melita palmata (Montagu)	4	--	--	--	--	--	--	--	--	1	--
Carcinus maenas L.	4	14	6	3	--	--	--	--	1	--	1
Euderella truncatula Bate	4	7	10	21	14	45	1	--	3	--	1
Capitella capitata (Fabricius)	3	--	--	--	--	--	--	--	--	--	--
Nereis diversicolor Müller	3	2	4	2	--	--	--	--	--	1	--
Sthen lais boa Johnston	3	4	--	--	--	--	--	--	--	--	--
Venerupis pullastra (Montagu)	3	2	--	1	--	--	--	1	--	--	--

Table 3.9(a) (cont.)	1978 July	Sept	Nov	1979 Jan	Mar	May	July	Sept	Nov	1980 Jan	March
Atylus vedlomensis (Bate & Westwood)	2	--	--	--	--	--	--	--	--	--	--
Pygospio elegans Claparede	2	1	--	--	--	--	--	--	--	--	--
Panoploea minuta Sars	1	--	--	--	--	--	--	--	--	--	--
Lepidonotus squamatus L.	1	--	1	--	--	--	--	--	1	--	1
Poutocrates arenarius Sars	1	--	--	--	--	--	--	--	--	--	--
Unidentified Amphilochidae	1	2	--	--	--	--	--	--	--	--	--
Leucothoe spinicarpa Abildgaard	1	20	7	1	--	--	--	--	--	--	1
Idotea chelipes (Pallas)	--	10	--	--	--	--	--	--	--	--	--
Crepidula fornicata L.	--	6	--	--	--	--	--	--	--	--	--
Nassarius reticulatus L.	--	6	2	1	--	3	--	1	4	1	2
Perioculodes longimanus (Bate & Westwood)	--	1	--	--	--	--	--	--	--	--	--
Atylus falcatus (Metzger)	--	1	--	--	--	--	--	--	--	--	--
Achelia echinata Hodge	--	1	1	--	--	--	--	--	--	--	--
Petricola pholadiformis (Strom)	--	1	--	--	--	--	--	--	--	--	--
Gasterosteus aculeatus L.	--	1	--	--	--	--	--	--	--	--	--
Bodotria scorpiodes (Montagu)	--	1	--	--	--	--	--	--	--	--	--
Lumbrineris latreilli (Aud. & M-Edw)	--	1	--	--	--	--	--	--	--	--	--
Crangon vulgaris L.	--	1	--	--	--	--	--	--	--	--	--
Apherusa ovalipes Norman & Scott	--	--	8	--	--	--	--	--	--	--	--
Hydroides norvegica (Gunnerus)	--	--	3	--	--	--	--	--	--	--	--
Eulalia pusilla Oersted	--	--	2	--	--	--	--	--	--	--	--
Unidentified shrimps	--	--	2	--	--	--	--	--	--	--	--
Polydora antennata Claparede	--	--	1	--	--	--	--	--	--	--	--
Amphrodite aculeata L.	--	--	1	--	--	--	--	--	--	--	--
Scalibregma inflatum Rathke	--	--	1	--	--	--	--	--	--	--	--

Table 3.9(a) (cont.)

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Eusyllis lamelligera	--	--	1	2	--	--	--	--	--	--	--
Syllis sp	--	--	--	2	--	--	--	--	1	--	--
Jassa marmorata Holmes	--	--	--	1	--	--	--	--	--	--	--
Nereis virens Sars	--	--	--	--	1	1	1	1	1	2	--
Sabella pavonina Savigny	--	--	--	--	--	--	--	--	--	--	--
Unidentified polychaete	--	--	--	--	1	--	--	--	--	--	--
Pycnogonum littorale Strom	--	--	--	--	1	--	--	--	--	--	--
Corophium volutator (Pallas)	--	--	--	--	--	2	--	--	--	--	--
Nucula turgida Leckenby & Marshall	--	--	--	--	--	--	--	--	--	1	--
Phtisica marina Slabber	--	--	--	--	--	--	--	--	1	--	--
Total number of individuals	6185	13638	13186	8716	2673	6114	10974	4504	3010	2723	4676

Table 3.9(b) LIST OF MACROFAUNA WITH PERCENT NUMERICAL ABUNDANCE OF INDIVIDUALS AT STATION 5

SPECIES	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Caulleriella caputesocis (St. Joseph)	88.02	95.76	96.59	96.20	94.77	93.80	96.25	93.95	93.85	94.30	97.75
Cirratulus cirratus (O. F. Müller)	3.69	0.76	0.77	0.01	0.11	0.02	--	1.25	0.13	--	0.26
Pariambus typicus (Krøyer)	1.36	0.42	0.11	0.06	0.15	0.07	--	--	0.07	--	0.04
Microdeutopus gryllotalpa Coasta	1.13	0.44	0.02	0.01	--	--	0.01	--	--	--	--
Melinna palmata Malmgren	1.04	0.30	0.81	1.03	1.23	1.64	1.16	2.13	1.36	2.35	0.39
Aora gracilis Bate	0.92	0.21	0.16	0.01	--	--	--	--	--	--	0.19
Polydora ciliata (Johnston)	0.76	0.13	0.02	0.05	0.04	--	--	--	--	--	--
Mercenaria mercenaria L.	0.52	0.24	0.19	0.17	0.71	0.18	0.10	0.60	0.99	0.44	0.64
Nephtys hombergi (Aud. & M-Edw)	0.49	0.15	0.73	1.27	1.58	1.83	0.88	1.53	2.33	2.50	0.47
Anaitides maculata St. Joseph	0.39	0.10	0.04	0.09	0.07	0.05	0.03	--	--	--	--
Abra nitida Müller	0.37	0.10	0.11	0.45	0.15	1.46	0.50	0.18	0.49	0.15	0.09
Philomedes globosus (Baird)	0.24	0.59	0.08	0.17	0.26	0.05	0.15	0.15	0.37	0.04	0.02
Cerastoderma edule L.	0.19	0.04	0.01	0.01	0.07	0.05	0.70	0.13	0.03	--	--
Corophium insidiosum Crawford	0.15	0.02	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	0.13	0.01	0.01	0.07	0.19	0.03	0.05	0.02	--	--	0.02
Spio filicornis (O.F. Müller)	0.06	--	--	--	--	--	--	--	--	--	--
Melita palmata (Montagu)	0.06	--	--	--	--	--	--	--	--	0.04	--
Carcinus maenas L.	0.06	0.10	0.05	0.03	--	--	--	--	0.03	--	0.02
Eudorella truncatula Bate	0.06	0.05	0.08	0.24	0.52	0.74	0.01	--	0.10	--	0.02
Capitella capitata (Fabricius)	0.05	--	--	--	--	--	--	--	--	--	--
Nereis diversicolor Müller	0.05	0.02	0.03	0.02	--	--	--	--	--	0.04	--
Sthen lais boa Johnston	0.05	0.03	--	--	--	--	--	--	--	--	--
Venerupis pullastra (Montagu)	0.05	0.02	--	0.01	--	--	--	0.02	--	--	--
Atylus vedlomensis (Bate & Westwood)	0.03	--	--	--	--	--	--	--	--	--	--

Table 3.9(b) (cont.)

	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Pygospio elegans Claparede	0.03	0.01	--	--	--	--	--	--	--	--	--
Panoploea minuta Sars	0.02	--	--	--	--	--	--	--	--	--	--
Lepidonotus squamatus L.	0.02	--	0.01	--	--	--	--	--	0.03	--	0.02
Pontocrates arenarius Sars	0.02	--	--	--	--	--	--	--	--	--	--
Unidentified amphilochidae	0.02	0.02	--	--	--	--	--	--	--	--	--
Leucothoe spinicarpa Abildgaard	--	0.15	0.05	0.01	--	--	--	--	--	--	0.02
Idotea chelipes (Pallas)	--	0.07	--	--	--	--	--	--	--	--	--
Crepidula fornicata L.	--	0.04	--	--	--	--	--	--	--	--	--
Nassarius reticulatus L.	--	0.04	0.02	0.01	0.05	--	0.02	0.13	0.04	0.02	0.04
Perioculodes longimanus (Bate & Westwood)	--	0.01	--	--	--	--	--	--	--	--	--
Atylus falcatus (Metzger)	0.02	0.01	--	--	--	--	--	--	--	--	--
Achelia echinata Hodge	--	0.01	0.01	--	--	--	--	--	--	--	--
Petricola pholadiformis (Strom)	--	0.01	--	--	--	--	--	--	--	--	--
Gasterosteus aculeatus L.	--	0.01	--	--	--	--	--	--	--	--	--
Bodotria scorpiodes (Montagu)	--	0.01	--	--	--	--	--	--	--	--	--
Lumbrineris latreilli (Audouin & M-Edwards)	--	0.01	--	--	--	--	--	--	--	--	--
Crangon crangon L.	--	0.01	--	--	--	--	--	--	--	--	--
Apherusa ovalipes Norman & Scott	--	--	0.06	--	--	--	--	--	--	--	--
Hydroides norvegica (Gunnerus)	--	--	0.02	--	--	--	--	--	--	--	--
Eulalia pusilla Oersted	--	--	0.02	--	--	--	--	--	--	--	--
Unidentified shrimps	--	--	0.02	--	--	--	--	--	--	--	--
Polydora antennata Claparede	--	--	0.01	--	--	--	--	--	--	--	--
Aphrodita aculeata (L)	--	--	0.01	--	--	--	--	--	--	--	--
Scalibregma inflatum Rathke	--	--	0.01	--	--	--	--	--	--	--	--
Eusyllis lamelligera	--	--	0.01	0.02	--	--	--	--	--	--	--

Table 3.9(b) (cont.)

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Syllis sp	--	--	--	0.02	--	--	--	0.03	--	--	--
Jassa marmorata Holmes	--	--	--	0.01	--	--	--	--	--	--	--
Nereis virens Sars	--	--	--	0.04	0.02	0.01	0.02	0.03	0.07	--	--
Sabella pavonina Savigny	--	--	--	0.04	--	--	--	--	--	--	--
Unidentified polychaete	--	--	--	0.04	--	--	--	--	--	--	--
Pycnogonum littorale (Strom)	--	--	--	--	0.03	--	--	--	--	--	--
Corophium volutator (Pallas)	--	--	--	--	--	--	0.02	--	--	--	--
Nucula turgida Leckenby & Marshall	--	--	--	--	--	--	--	--	0.04	--	--
Phtisica marina Slabber	--	--	--	--	--	--	--	0.03	--	--	--
Total number of species	31	34	29	23	16	15	12	13	16	11	15

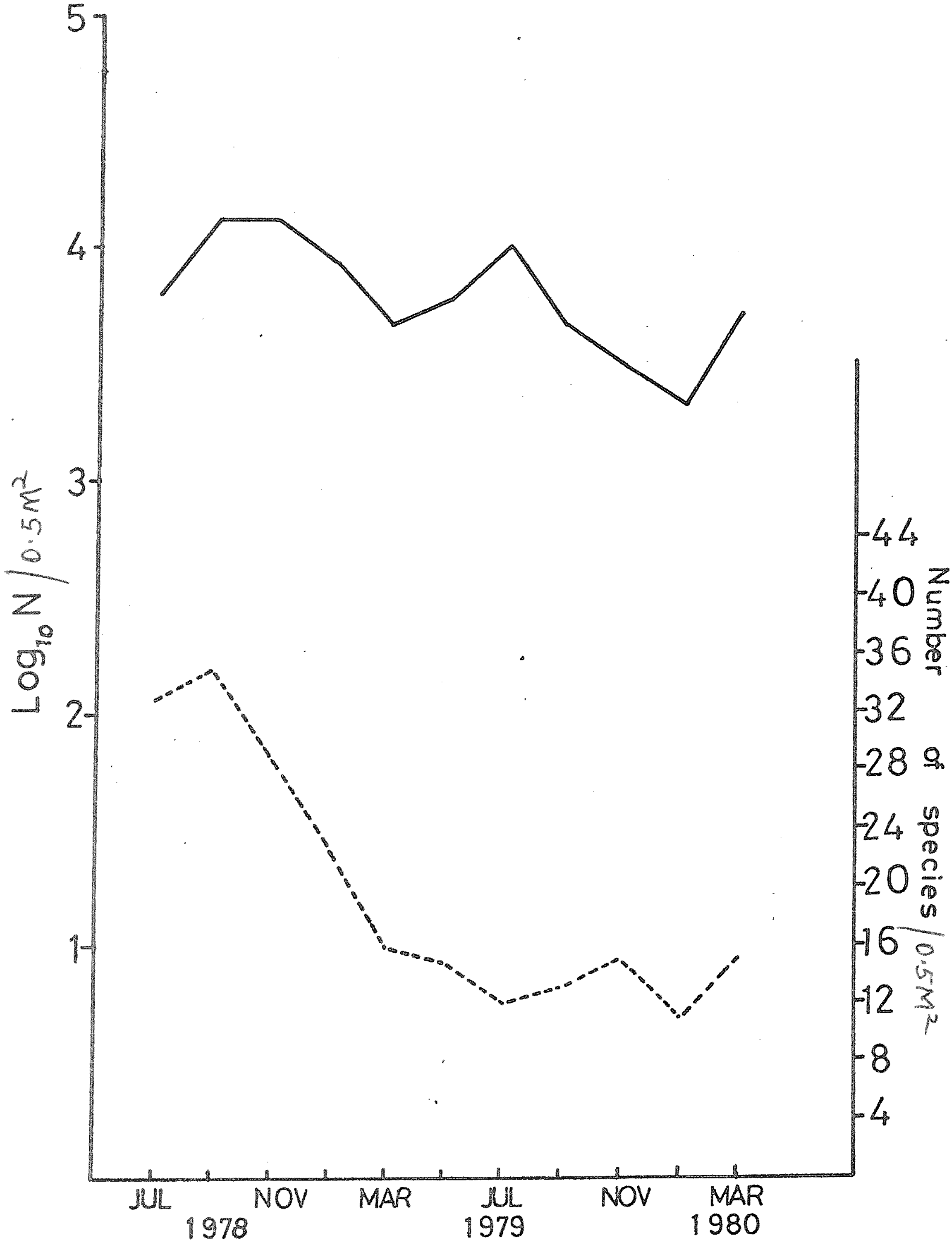


FIG.3.13. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS AT STATION 5

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Polychaetes	94.80	97.41	99.07	98.78	98.11	97.39	98.38	98.92	97.76	99.26	98.91
Crustacea	4.09	2.11	0.57	0.54	0.93	0.86	0.17	0.15	0.54	0.08	0.31
Bivalves	1.13	0.41	0.31	0.64	0.93	1.69	1.30	0.91	1.54	0.63	0.73
Gastropods	--	0.08	0.02	0.01	--	0.05	--	0.02	0.13	0.04	0.04
Pycnogonid	--	0.01	0.01	--	--	0.03	--	--	--	--	--
Vertebrata	--	0.01	--	--	--	--	--	--	--	--	--

Table 3.10. Percentage abundance of major animal taxa at Station 5

and the molluscs the lowest, resulting in the demonstrated fall in the number of species at station 5. Unlike the molluscs and polychaetes, the crustaceans showed a steady decline throughout the study period.

The variation in the number of species and abundance of individuals of the major animal taxa are shown in Figure 3.14. The number of species of the polychaetes declined throughout the study period. The peaks were obtained in November 1978 when 30 species per squared metre was recorded. The numbers fell steadily between November 1978 and March 1980, with a minimum of $12m^{-2}$. The number of crustacean species followed a similar trend with a gradual fall between September 1978 and September 1979, when only two species were recovered. There was a slight increase in the number of crustacean species after September 1979. The molluscs showed some stability in the number of species throughout the study period. The numbers varied between $14m^{-2}$ in September 1978 and $6m^{-2}$ in March 1980.

The abundance of individuals of polychaetes at the station remained more or less stable during the study period. There were slight falls in the winter months and increases in the summer months. The crustaceans showed a steady fall in abundance but the molluscs remained fairly stable throughout the period of study. The polychaete dominance at this station is further exhibited by the group being dominant in both the number of species and individuals' abundance as seen in Table 3.11.

Individual species

The numerical abundance of polychaete species at this station depended to a great extent on a single species, C. caputesocis, which dominated in all samples and comprised about 90% of the total individuals. The ranking of the top ten abundant species at the station during the study period is given in Table 3.12. C. caputesocis was the single dominant species throughout the study period but showed pronounced seasonality in abundance in spite of its numerical dominance. The Spearman's correlation coefficient (0.002) confirms randomness in the rank allocation at the station. The variation in the numerical abundance of the dominant species at the station is shown in Figure 3.15. C. caputesocis occurred in peak densities in the summer months and at lowest densities in the winter months.

Occurring at high densities with Caulleriella were N. hombergi and the sedentary ampharetid, Melinna palmata. These showed considerable variations in their abundance rankings. While M. palmata showed greater densities in the summer months, it only occurred sporadically during the

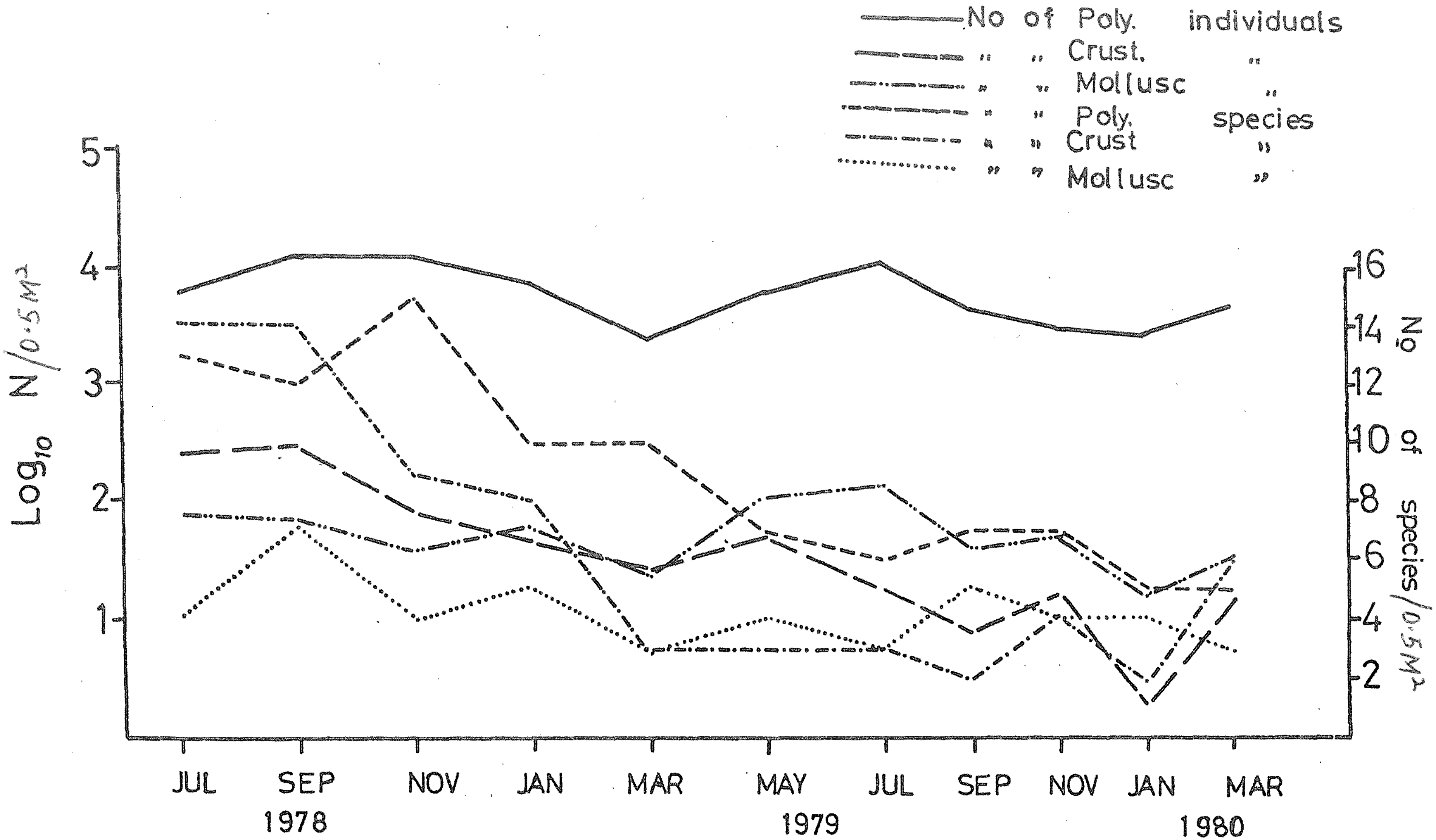


FIG. 3.14. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS OF MAJOR ANIMAL TAXA AT STATION 5

Table 3.11

STATION 5

REPRESENTATION OF VARIOUS PHYLA IN NUMBERS AND SPECIES

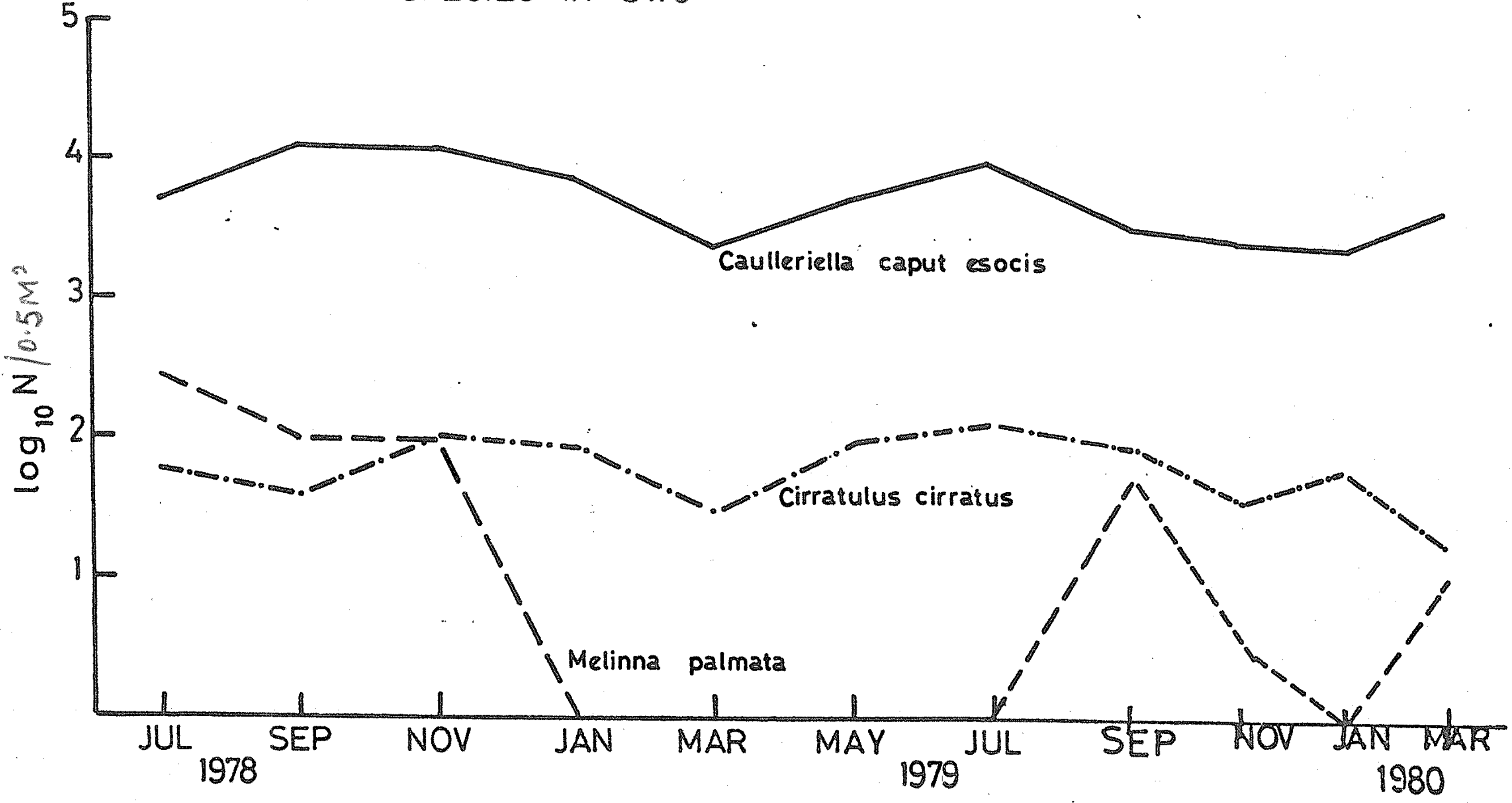
Individuals per $0.5m^2$ as % of total (figures in parentheses represent actual numbers)

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	94.70 (5857)	4.09 (253)	1.13 (70)	
Sept	97.4 (13,282)	2.09 (285)	0.44 (61)	0.07 (1)
Nov	99.09 (13,059)	0.57 (81)	0.33 (42)	0.01 (1)
1979				
Jan	98.8 (8611)	0.55 (48)	0.65 (57)	
March	98.11 (2622)	0.93 (25)	0.93 (25)	0.03 (2)
May	97.4 (5954)	0.86 (51)	1.68 (103)	
July	98.4 (10,796)	0.17 (18)	1.3 (143)	
Sept	98.9 (4514)	0.15 (8)	0.9 (43)	
Nov	97.8 (2943)	0.54 (17)	1.64 (50)	
1980				
Jan	99.3 (2703)	0.08 (2)	0.67 (18)	
March	98.91 (4625)	0.31 (15)	0.77 (36)	
		Species per $0.5m^2$ as % of total		
1978				
July	41.93 (13)	45.16 (14)	12.90 (4)	
Sept	34.3 (12)	40.0 (14)	20.0 (7)	5.71 (1)
Nov	51.7 (15)	31.0 (9)	13.8 (4)	3.5 (1)
1979				
Jan	43.48 (10)	34.8 (8)	21.74 (5)	
March	62.5 (10)	18.8 (3)	18.8 (3)	6.6 (1)
May	46.7 (7)	20.0 (3)	26.7 (4)	
July	50.0 (6)	25.0 (3)	25.0 (3)	
Sept	46.0 (6)	15.4 (2)	38.46 (5)	
Nov	46.7 (7)	26.7 (4)	26.7 (4)	
1980				
Jan	45.5 (5)	18.18 (2)	36.36 (4)	
March	40.0 (6)	40.0 (6)	20.0 (3)	

Species	1978 July	1978 Sept	1978 Nov	1979 Jan	1979 Mar	1979 May	1979 July	1979 Sept	1979 Nov	1980 Jan	1980 Mar
Caulleriella caputesocis	1	1	1	1	1	1	1	1	1	1	1
Cirratulus cirratus	2	2	3	-	10	-	-	4	7	-	5
Pariambus typicus	3	5	7	10	8	7	-	-	10	-	8
Microdeutopus gryllotalpa	4	4	-	-	-	-	10	-	-	-	-
Melinna palmata	5	6	2	3	3	3	2	2	3	3	4
Aora gracilis	6	8	6	-	-	-	-	-	-	-	6
Polydora ciliata	7	-	-	-	-	-	-	-	-	-	-
Mercenaria mercenaria	8	7	5	7	4	6	7	5	4	4	2
Nephtys hombergi	9	9	4	2	2	2	3	3	2	2	3
Anaitides maculata	10	-	-	8	-	-	9	-	-	-	-
Philomedes globosus	-	3	9	6	6	10	6	7	6	7	10
Leucothoe incisa	-	10	-	-	-	-	-	-	-	-	-
Abra nitida	-	-	8	4	9	4	5	6	5	5	7
Eudorella truncatula	-	-	10	5	5	5	-	-	9	-	10
Eteone longa	-	-	-	9	7	-	8	-	-	-	-
Cerastoderma edule	-	-	-	-	-	8	4	8	-	-	-
Nassarius reticulatus	-	-	-	-	-	9	-	-	7	7	8
Nereis virens	-	-	-	-	-	-	-	9	-	6	-
Venerupis pullastra	-	-	-	-	-	-	-	10	-	-	-
Nereis diversicolor	-	-	-	-	-	-	-	-	-	7	-
Melita palmata	-	-	-	-	-	-	-	-	-	7	-

Table 3.12. Abundance ranking of top ten species at Station 5

FIG.3·15. SEASONAL RECRUITMENT & MORTALITY OF DOMINANT SPECIES IN ST.5



cold winter months. N. hombergi occurred at higher densities as N. Palmata declined in abundance, possibly due to competition between the two species. Other polychaetes of sparse occurrence at the station included Anaitides maculata, Eteone longa, Cirratulus cirratus, Nereis diversicolor, N. virens and Polydora ciliata. Only one specimen of S. pavonina was recovered at the station during the study. Other polychaetes at the station only occurred sporadically.

At the present station, the crustaceans ranked second to the polychaetes in terms of the number of species. Twenty one species were recorded and comprised 15 amphipods, 2 decapods, 2 cumaceans, one each of isopod and ostracod. The dominant amphipods were Microdeutopus gryllotalpa, Atylus vedlomensis, Pariambus typicus, Aora gracilis, Corophium insidiosum and Atylus falcatus. Others occurring at lower densities were Melita palmata, Panoploea minuta, Pontocrates arenarius, Leucothoe spinicarpa, Perioculodes longimanus, Jassa marmorata and an unidentified Amphilochidae.

Two decapods, Carcinus maenas and Crangon vulgaris were often captured by the grab. The two cumaceans, Eudorella truncatula and Bodotria scorpiodes were often found in reasonable numbers with the former occurring at high densities so as to rank amongst the top ten species during the 1978/79 winter months. The ostracods, though represented by a single species, Philomedes globosus, occurred in large numbers, being present in all but July 1978 samples, and ranked within the top 10 species. The only isopod, Idotea chelipes, found at the station occurred sporadically.

Two gastropods, Nassarius reticulatus and Crepidula fornicata, were recorded at the station. The former occurred very frequently but the latter only once in September 1978.

The dominant bivalves at the station were Mercenaria mercenaria and Abra nitida. The former occurred at high densities ($66m^{-2}$) and ranked among the top 8 species in terms of abundance. Patchiness in the distribution of A. nitida often resulted in a considerable variation in the numbers captured within samples. Other bivalves occurred irregularly and at low densities. Such species included Cerastoderma edule, Venerupis pullastra and Petricola pholadiformis which was recorded only once.

The pycnogonids occurred sporadically and were represented by two species, Achelia echinata and Pycnogonum littorale. Only two specimens of the former and one of the latter were found at the station.

The 3-spined stickleback, Gasterosteus aculeatus, was found once in September 1978 and was the only vertebrate taken at the station.

The species abundance ranking averaged for the eleven bimonthly samples at station 5 is presented in Table 3.13. Four polychaetes accounted for about 98% of the individuals' abundance with Caulleriella alone contributing 95% of the total.

STATION 9

This station, situated about 400 metres east of Fawley's Esso petroleum refinery outfall, had silty sediment, the fines (< 63 µm in diameter) ranging between 88 and 99% all the year round with high organic matter. Since the amount of organic matter is often taken as an indication of the quality and quantity of food settling on to the sediment from the water column (Byers et al,1978), this present station would be expected to contain high amounts of available food for benthic animals. But as Rhoads (1974) indicated, low species richness and large population abundance might also result from a lack of ecological niches resulting from the low spatial heterogeneity of the substrate. Station 9 showed the lowest species richness amongst the four stations at any sampling time.

At the station, a total of 21 species of benthic macro-infauna were recovered during the present study. The species list with percentage numerical abundance at the station is shown in Tables 3.14 (a & b). The polychaetes comprised 42.9% (9); crustaceans 42.9% (9); molluscs 9.5% (2) and fish 4.7% (1) of the total species. The actual numbers of the species are in parentheses.

Species richness and abundance of individuals

The variation in the number of species and the abundance of individuals at the station is given in Figure 3.16. The maximum number of species ($14m^{-2}$) was recorded in July 1978 at the start of study. There was a gradual decrease in the number of species during the course of study with a rapid fall between September 1978 and January 1979. Thereafter, the species richness remained between 2 and $6m^{-2}$.

The abundance of individuals showed considerable fluctuations during the study. The peaks were reached in September 1978 and Sep-

Rank	Species	Average No/0.5m^2	%	Cumulative %
1	*Caulleriella caputesocis*	6609.8	95.17	95.17
2	*Melinna palmata*	71.1	1.02	96.19
3	*Nephtys hombergi*	67.2	0.97	97.16
4	*Cirratulus cirratus*	46.4	0.67	97.83
5	*Abra nitida*	24.4	0.35	98.18
6	*Mercenaria mercenaria*	22.3	0.32	98.50
7	*Pariambus typicus*	15.6	0.23	98.73
8	*Philomedes globosus*	15.2	0.22	98.95

Table 3.13 Station 5 average species abundance ranking for the 20 month period.

Table 14a FAUNAL LIST AND NUMBERS M^{-2} at STATION 9 BETWEEN JULY 1978 AND MARCH 1980

SPECIES	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Caulleriella caputesocis (St. Joseph)	422	58	--	--	--	--	--	--	--	--	
Nereis diversicolor O. F. Müller	162	169	153	62	7	200	7	6	56	16	1029
Polydora ciliata (Johnston)	50	51	1	--	--	--	1	--	--	--	--
Capitella capitata (Fabricius)	45	24823	13262	1582	2287	5837	944	7736	6841	724	814
Abra nitida Müller	14	--	--	--	--	--	--	--	--	--	--
Nephtys hombergi (Audouin & M-Edwards)	10	--	--	--	--	--	--	--	--	4	--
Cirratulus cirratus (O. F. Müller)	3	1	--	--	1	--	--	--	--	--	--
Crangon vulgaris L.	3	--	--	--	--	--	--	--	--	--	--
Tryphosites longipes	2	--	--	--	--	--	--	--	--	--	--
Chaetogammarus marinus (Leach)	1	--	--	--	--	--	--	--	--	--	--
Atylus fulcatus (Bate & Westwood)	1	--	--	--	--	--	--	--	--	--	--
Carcinus maenas L.	1	--	--	--	--	--	1	--	--	--	--
Mercenaria mercenaria L.	1	--	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	1	21	45	1	37	15	1	--	7	3	76
Sabella pavonina Savigny	--	111	28	1	--	--	--	--	--	--	--
Syllis sp	--	1	--	--	--	--	--	--	--	--	--
Idotea linearis L.	--	1	--	--	--	--	--	--	--	--	--
Philomedes globosus (Baird)	--	--	1	--	--	--	--	--	--	--	--
Unidentified mysid	--	--	--	--	--	2	--	--	--	--	--
Corophium insidiosum Crawford	--	--	--	--	--	1	--	--	--	--	--
Gasterosteus aculaetus L.	--	--	--	--	--	--	1	--	--	--	--
Total number of individuals	716	25236	13490	1646	2332	6055	955	7742	6904	747	1919

Table 3.14b LIST OF MACROFAUNA WITH PERCENT NUMERICAL ABUNDANCE OF INDIVIDUALS AT STATION 9

SPECIES	1978 July	1978 Sept	1978 Nov	1979 Jan	1979 Mar	1979 May	1979 July	1979 Sept	1979 Nov	1980 Jan	1980 Mar
Caulleriella caputesocis (St. Joseph)	58.94	0.23	--	--	--	--	--	--	--	--	--
Nereis diversicolor O. F. Müller	22.63	0.67	1.13	3.77	0.30	3.30	0.73	0.08	0.81	2.14	53.62
Polydora ciliata (Johnston)	7.00	0.20	0.01	--	--	--	0.10	--	--	--	--
Capitella capitata (Fabricius)	6.28	98.36	98.30	96.11	98.07	96.39	98.74	99.92	99.08	96.92	42.42
Abra nitida Müller	1.96	--	--	--	--	--	--	--	--	--	--
Nephtys hombergi (Aud & M-Edw.)	1.40	--	0.01	--	--	--	--	--	--	0.54	--
Cirratulus cirratus (O. F. Müller)	0.42	0.01	--	--	0.04	--	--	--	--	--	--
Crangon vulgaris L.	0.42	--	--	--	--	--	--	--	--	--	--
Tryphosites longipes	0.28	--	--	--	--	--	--	--	--	--	--
Chaetogammarus marinus (Leach)	0.14	--	--	--	--	--	--	--	--	--	--
Atylus fulcatus	0.14	--	--	--	--	--	--	--	--	--	--
Carcinus maenas L.	0.14	--	--	--	--	--	0.21	--	--	--	--
Mercenaria mercenaria L.	0.14	--	--	--	--	--	--	--	--	--	--
Eteone longa (Fabricius)	0.14	0.08	0.33	0.06	1.59	0.25	0.10	--	0.10	0.40	3.96
Sabella pavonina Savigny	--	0.44	0.21	0.06	--	--	--	--	--	--	--
Syllis sp	--	0.01	--	--	--	--	--	--	--	--	--
Idotea linearis (L)	--	0.01	--	--	--	--	--	--	--	--	--
Philomedes globosus (Baird)	--	--	0.01	--	--	--	--	--	--	--	--
Mysid (unidentified)	--	--	--	--	--	0.03	--	--	--	--	--
Corophium insidiosum Crawford	--	--	--	--	--	0.02	--	--	--	--	--
Gasterosteus aculeatus L.	--	--	--	--	--	--	0.01	--	--	--	--
Total number of species	14	9	7	4	4	5	6	2	3	4	3

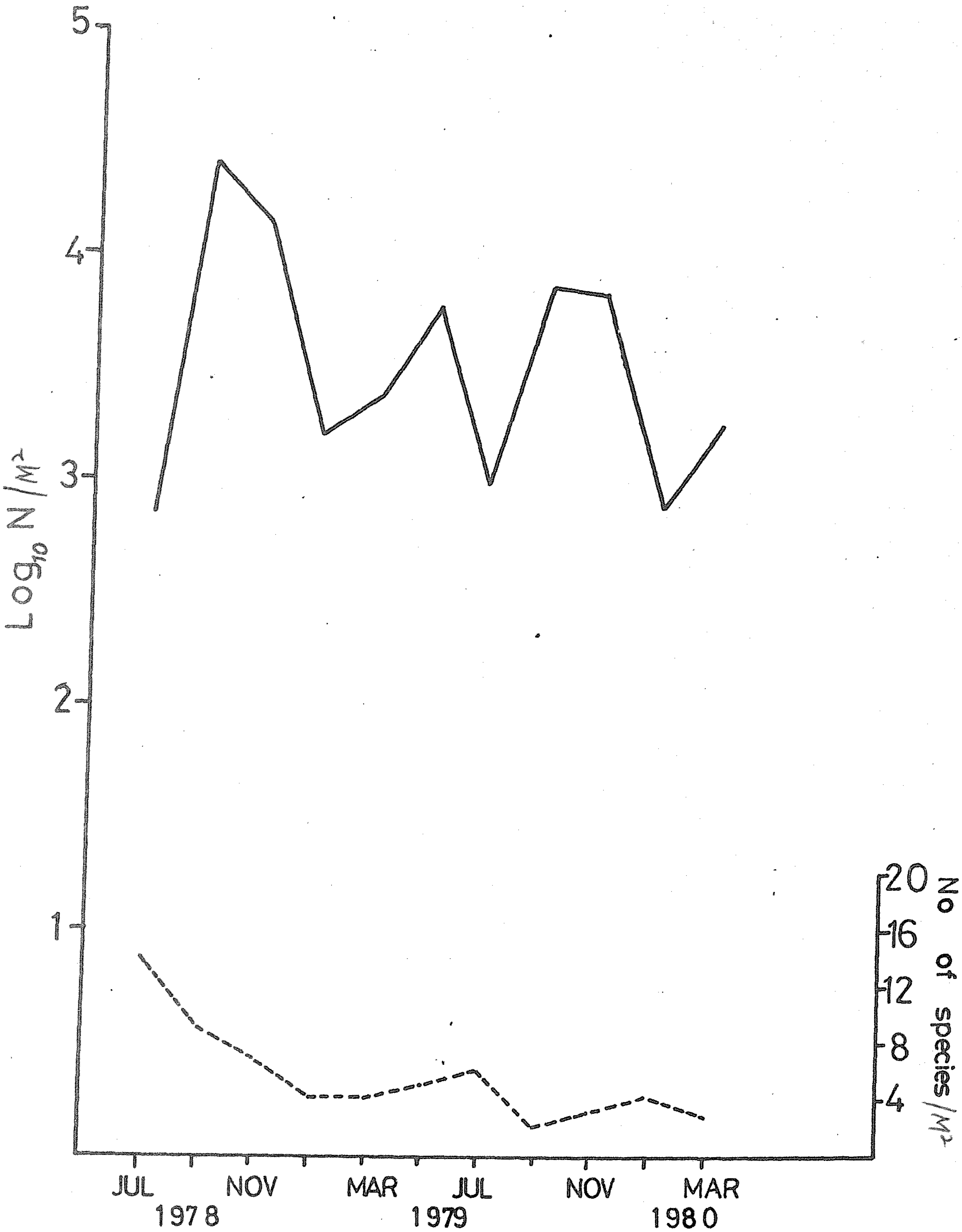


FIG.3.16. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS AT STATION 9

tember 1979 but fell sharply in the succeeding winter months. The decline in the total number of individuals coincided with a drop in the density of Capitella capitata and an increase in species richness at the station.

Major animal taxa

The polychaetes as a group emerged as the dominant animal taxon at the station. The variations in the number of species and abundance of individuals of major animal taxa are shown in Figure 3.17. The polychaetes showed peaks in the number of species in September 1978, July 1979 and January 1980. At other times, the number of species varied between 7 and $2m^{-2}$. The crustaceans exhibited seasonal trends in species richness with peaks in the summer months with the number ranging between 6 and $2m^{-2}$, but they were absent in the winter months. Only two species of molluscs were recovered on a single occasion in July 1978.

In terms of abundance of individuals, the polychaetes showed possible seasonality with peaks in the summer months. The crustaceans occurred in very low numbers during the study. Though the number of species of polychaetes and crustaceans were equal at the station, the former were numerically dominant. The percentage numerical abundance of individuals of the major animal taxa is shown in Table 3.15. The polychaetes accounted for greater than 96% of the total individuals throughout the time of investigation.

Individual species

The abundance ranking of the top four species at this station is shown in Table 3.16. The numerical dominance of C. caputesocis was short-lived and the species disappeared from samples by November 1978. Capitella capitata, though ranked fourth in July 1979, became and remained the numerically dominant species from September 1978 onwards. The species showed a high recruitment in the 1978 summer months and the density rose from $45m^{-2}$ in July to $24823m^{-2}$ in September 1978, but mortality was high in the succeeding winter months. C. capitata accounted for more than 96% of the total numbers at the station except in July 1978 and March 1980.

Nereis diversicolor remained fairly stable numerically at the station, retaining a fairly constant ranking position throughout the study. Other polychaetes, for example, Eteone longa, Polydora ciliata and Sabella pavonina occurred in reasonably large numbers. The occurrence of S. pavonina at this station was similar to station 2 with the

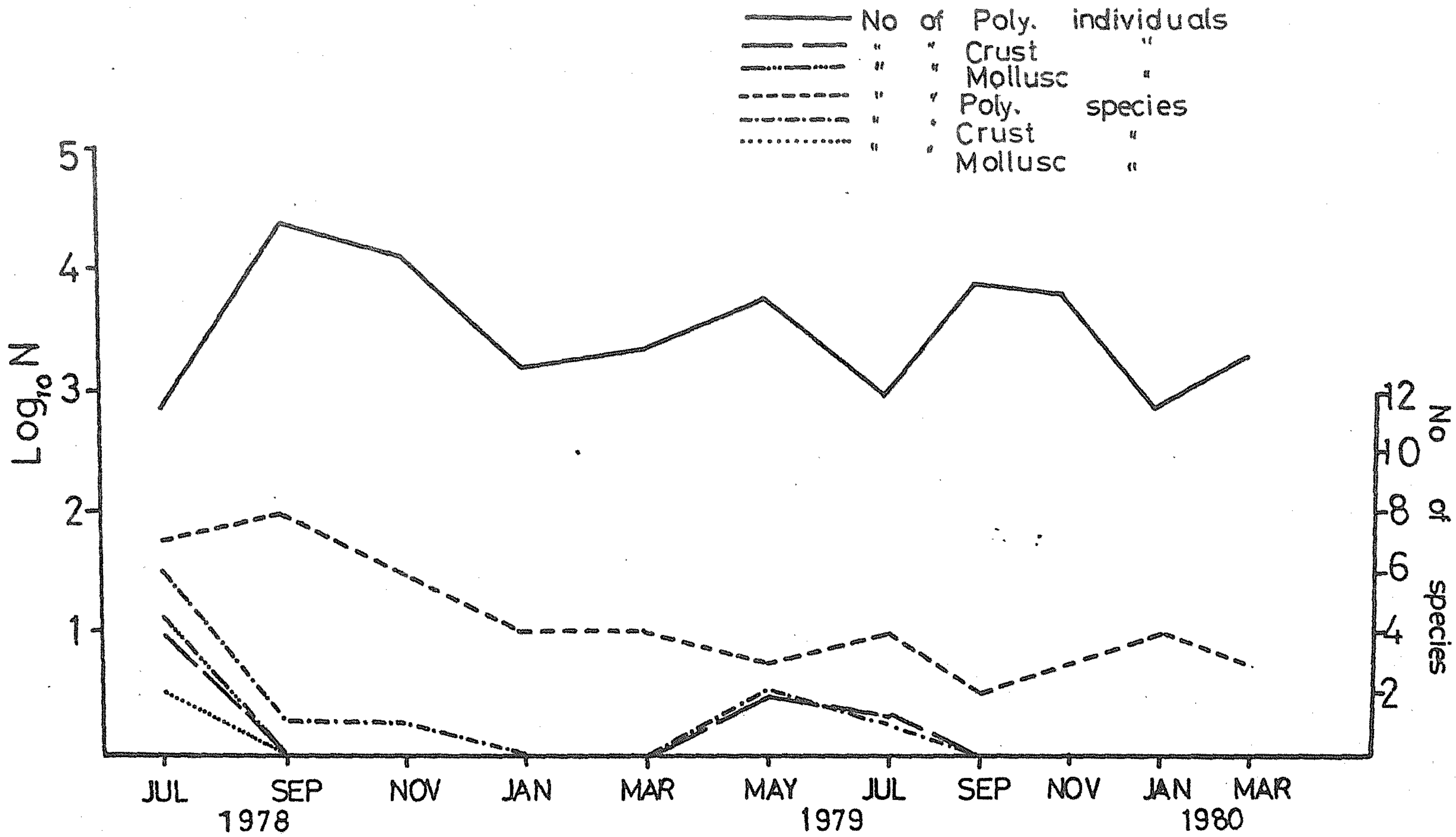


FIG.3.17. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS OF MAJOR ANIMAL TAXA AT STATION 9

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Polychaeta	96.81	100	99.99	100	100	99.95	99.67	100	100	100	100
Crustacea	2.1	0.01	0.01	--	--	0.05	0.21	--	--	--	--
Bivalvia	1.12	--	--	--	--	--	--	--	--	--	--
Gastropoda	--	--	--	--	--	--	--	--	--	--	--
Vertebrata	--	--	--	--	--	--	0.10	--	--	--	--

Table 3.15 Percentage abundance of major animal taxa at Station 9

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Caulleriella caputesocis	1	4	--	--	--	--	--	--	--	--	--
Nereis diversicolor	2	2	2	2	3	2	2	2	2	2	1
Polydora ciliata	3	--	--	--	--	--	--	--	--	--	--
Capitella capitata	4	1	1	1	1	1	1	1	1	1	2
Sabella pavonina	--	3	4	4	--	--	--	--	--	--	--
Eteone longa	--	--	3	3	2	3	4	--	3	4	3
Cirratulus cirratus	--	--	--	--	4	--	--	--	--	--	--
Nephtys hombergi	--	--	--	--	--	--	--	--	--	3	--

Table 3.16 Abundance ranking of top four species at Station 9

specimens disappearing from samples before reaching maturity.

The crustaceans at the station accounted for less than 3% of the total individuals. The amphipods were represented by Tryphosites longipes, Atylus falcatus, Corophium insidiosum and Chaetogammarus marinus. The decapods were represented by Crangon vulgaris and Carcinus maenas, both of which showed only sporadic occurrence. Only one specimen each of the isopod, Idotea linearis, and the ostracod, Philomedes globosus, were recovered. Only two species of bivalves, Abra nitida and Mercenaria mercenaria were obtained each on a single occasion in July 1978. Gasterosteus aculeatus was recovered only in July 1979.

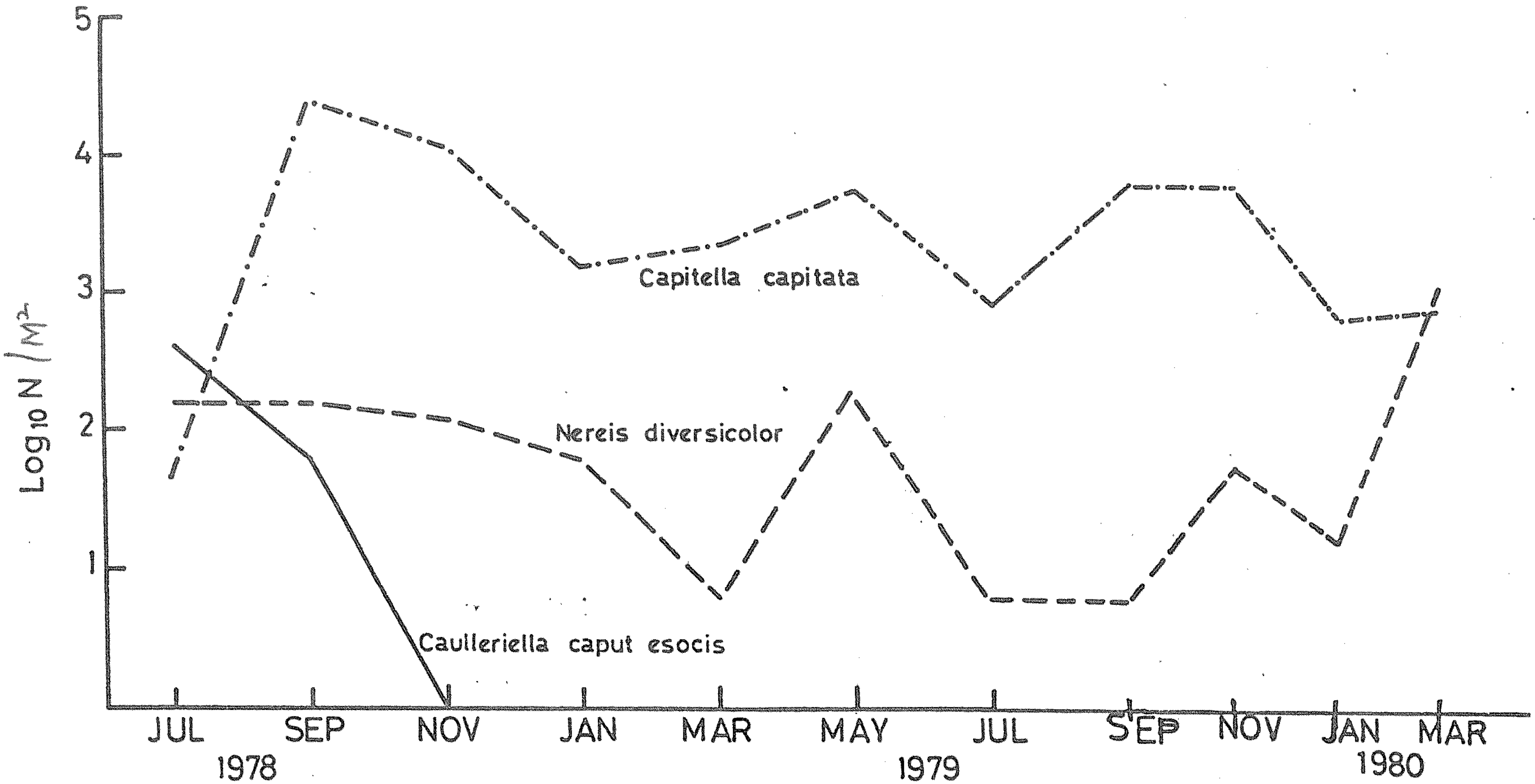
The recruitment and mortality pattern of the numerically dominant species at this station is shown in Fig. 3.18. C. capitata emerged as the most dominant and had peak abundance in September 1978, May, September and November 1979. This species showed increased density as the density of Caulleriella caputesocis declined. This, possibly, was the result of competition between these two small deposit feeding polychaetes. N. diversicolor was stable in density between July 1978 and January 1979 but declined in numbers by March 1979. High recruitment occurred in the summer months with peaks in May and November 1979. The mortality in January 1980 was followed by a high recruitment in March 1980 when the species was numerically dominant.

The species abundance ranking averaged for the eleven bimonthly samples is shown in Table 3.17. Two polychaetes, Capitella capitata and Nereis diversicolor, accounted for more than 98% of the total numerical abundance; C. capitata alone comprising about 95% of the total macrofaunal numerical abundance. The dominant position of the polychaetes is further evidenced in Table 3.18, both in respect of number of species and individuals.

STATION 20

The station, situated almost one kilometer southwest of Esso jetty at Fawley, contained sediment which was predominantly sandy mud; the sand component was made up of fine sand. The sediment at the station was low in total organic matter. A total of 21 species of benthic macro-infauna were recovered during the study and comprised polychaetes 52.4% (11); crustaceans 33.3% (7); and molluscs 14.3% (3) of the total species. The actual figures of the species are shown in parentheses. The species list with the percentage abundance at the station

FIG.3.18. SEASONAL RECRUITMENT & MORTALITY OF DOMINANT SPECIES IN ST.9



Rank	Species	Average No/m^2	%	Cumulative %
1	Capitella capitata	5899.6	95.79	95.79
2	Nereis diversicolor	169.7	2.76	98.55
3	Caulleriella caputesocis	43.6	0.71	99.26
4	Eteone longa	18.8	0.31	99.57
5	Sabella pavonina	12.7	0.21	99.78
6	Polydora ciliata	9.4	0.15	99.93

Table 3.17 Average species abundance ranking for the 20 month period (July 1978 - March 1980) at Station 9.

Table 3.18 STATION 9

REPRESENTATION OF VARIOUS PHYLA IN NUMBERS AND SPECIES

Individuals per m^2 as % of total
(figures in parentheses represent actual numbers)

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	96.65 (693)	1.26 (9)	2.09 (15)	--
Sept	99.99 (25235)	0.003 (1)	- -	--
Nov	99.99 (13489)	0.007 (1)	- -	--
1979				
Jan	100 (1646)	- -	- -	--
March	100 (2332)	- -	- -	--
May	99.95 (6052)	0.05 (3)	- -	--
July	99.67 (953)	0.20 (2)	-- -	--
Sept	100 (7742)	- -	- -	--
Nov	100 (6804)	- -	- -	--
1980				
Jan	100 (747)	- -	- -	--
March	100 (1919)	- -	- -	--

Species per m^2 as % of total

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	46.66 (7)	40.0 (6)	13.33 (2)	--
Sept	88.88 (8)	11.1 (1)	- -	--
Nov	85.70 (6)	14.3 (1)	- -	--
1979				
Jan	100 (4)	- -	- -	--
Mar	100 (4)	- -	- -	--
May	60 (3)	40.0 (2)	- -	--
July	66.66 (4)	16.7 (1)	- -	--
Sept	100 (2)	- -	- -	--
Nov	100 (3)	- -	- -	--
1980				
Jan	100 (4)	- -	- -	--
Mar	100 (3)	- -	- -	--

during the study is shown in Tables 3.19(a & b).

The seasonal variation in the number of species and abundance of individuals at the station is shown in Figure 3.19. Peaks in the number of species occurred in September 1978 and March 1979 but declined gradually throughout the study period with the number of species ranging between 14 and 26m^{-2}. There was no obvious seasonal trend, with the number of species reaching peaks in both summer and winter months.

The numerical abundance of individuals remained stable between July 1978 and July 1979 but decreased in the winter months. A heavy recruitment following a sharp drop in September 1979 kept the individual abundance almost stable from November 1979 onwards.

Major animal taxa

The polychaetes emerged as the numerically dominant animal taxon throughout the study period. The percentage numerical abundance of the major animal taxa for the period of study at station 20 is shown in Table 3.20. The polychaetes comprised more than 80% of the total individuals. The animal taxon showed no seasonal trend in the number of individuals and increased both in the summer and the winter months. The crustaceans and bivalve species occurred only in reasonable numbers, showing paucity in occurrence and patchiness in distribution at this station.

The variations in the number of species and numerical abundance of the major animal taxa are presented in Figure 3.20. The polychaetes as a group showed a marked variation in the numbers of species between 12 and 20m^{-2}, and peaks in November 1978 and March 1979. The crustaceans as a group ranged between 2 and 10m^{-2} in species richness and had peaks in September 1978 and January 1979. The molluscs, represented by only two species had the lowest species richness at the station.

The number of individuals of polychaetes remained stable between July 1978 and July 1979, after which great fluctuations with peaks in November 1979 and March 1980 were recorded. The crustacean abundance showed little stability, with a steady fall in abundance between September 1979 and January 1980. The 1979/80 winter recruitment, however, increased the abundance in March 1980. The molluscs suffered heavy decline in numbers except in May and July 1979 and in March 1980 when slight recruitment at the station boosted the abundance of the group.

Table 3.19(a) FAUNAL LIST AND NUMBERS/.5m^2 AT STATION 20 BETWEEN JULY 1978 AND MARCH 1980

SPECIES	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Caulleriella caputesocis (St.Joseph)	4755	3884	2816	3360	1842	1408	2782	586	1997	2612	2070
Abra nitida Müller	271	33	15	16	7	404	258	6	15	1	12
Nephtys hombergi (Aud.& M-Edw.)	92	85	110	80	93	85	88	63	45	45	56
Eteone longa (Fabricius)	53	94	25	33	29	11	25	--	7	25	28
Polydora ciliata (Johnston)	21	163	2	2	2	3	--	--	--	3	1
Cerastoderma edule L.	8	9	1	--	--	--	--	--	--	--	--
Eudorella truncatula Bate	7	22	--	9	15	15	--	--	1	--	3
Nereis diversicolor O. F. Müller	2	1	15	82	21	2	--	4	10	60	29
Philomedes globosus (Baird)	2	42	2	6	4	1	16	3	6	--	--
Paraphoxus oculatus Sars	1	1	--	--	--	--	--	--	--	--	2
Anaitides maculata St. Joseph	1	--	2	21	16	2	--	--	--	3	--
Melinna palmata Malmgren	1	--	--	--	1	--	--	--	--	--	--
Sabella pavonina Savigny	--	240	112	--	2	507	11	4	23	--	4
Pariambus typicus Krøyer	--	2	--	--	--	--		--	--	--	--
Carcinus maenas L.	--	1	--	1	--	--	1	--	--	--	--
Cirratulus cirratus (O. F. Müller)	--	--	18	--	1	--	--	--	--	--	--
Microdeutopus gryllotalpa Coasta	--	--	1	1	--	--	--	--	--	--	--
Nereis virens Sars	--	--	--	--	2	--	--	--	--	--	--
Abra alba (Wood)	--	--	--	--	--	--	28	--	--	--	--
Capitella capitata (Fabricius)	--	--	--	--	--	--	1	3	4	1	--
Corophium volutator (Pallas)	--	--	--	--	--	--	--	--	--	1	--
Total number of individuals	5214	4577	3119	3611	2035	2438	3210	669	2108	2751	2205

Table 3.19(b) LIST OF MACROFAUNA WITH PERCENTAGE NUMERICAL ABUNDANCE OF INDIVIDUALS AT STATION 20

SPECIES	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Caulleriella caputesocis (St.Joseph)	91.19	84.86	90.29	93.02	90.51	57.75	86.67	87.59	94.73	94.95	93.88
Abra nitida Müller	5.20	0.72	0.48	0.44	0.34	16.57	8.04	0.89	0.71	0.04	0.54
Nephtys hombergi (Aud. & M-Edw.)	1.77	1.86	3.53	2.22	4.57	3.49	2.74	9.42	2.13	1.64	2.54
Eteone longa (Fabricius)	1.02	2.05	0.80	0.91	1.43	0.45	0.78	--	0.33	0.91	1.27
Polydora ciliata (Johnston)	0.40	3.56	0.06	0.06	0.10	0.12	--	--	--	0.11	0.05
Cerastoderma edule L.	0.15	0.20	0.03	--	--	--	--	--	--	--	--
Eudorella truncatula Bate	0.13	0.48	--	0.25	0.74	0.62	--	--	0.05	--	0.14
Nereis diversicolor O. F. Müller	0.04	0.02	0.48	2.27	1.03	0.08	--	0.60	0.47	2.18	1.32
Philomedes globosus (Baird)	0.04	0.92	0.06	0.17	0.20	0.04	0.50	0.45	0.29	--	0.09
Paraphoxus oculatus Sars	0.02	0.02	--	--	--	--	--	--	--	--	--
Anaitides maculata St. Joseph	0.02	--	0.06	0.58	0.79	0.08	--	--	--	0.11	--
Melinna palmata Malmgren	0.02	--	--	--	0.05	--	--	--	--	--	--
Sabella pavonina Savigny	--	5.24	3.59	--	0.10	20.80	0.34	0.60	1.09	--	0.18
Pariambus typicus (Krøyer)	--	0.04	--	--	--	--	--	--	--	--	--
Carcinus maenas L.	--	0.02	--	0.03	--	--	0.03	--	--	--	--
Cirratulus cirratus (O. F. Müller)	--	--	0.58	--	0.05	--	--	--	--	--	--
Microdeutopus gryllotalpa Coasta	--	--	0.03	0.03	--	--	--	--	--	--	--
Nereis virens Sars	--	--	--	--	0.10	--	--	--	--	--	--
Abra alba (Wood)	--	--	--	--	--	--	0.87	--	--	--	--
Capitella capitata (Fabricius)	--	--	--	--	--	--	0.03	0.45	0.19	0.04	--
Corophium volutator (Pallas)	--	--	--	--	--	--	--	--	--	0.04	--
Total number of species	12	13	12	11	13	10	9	7	9	9	9

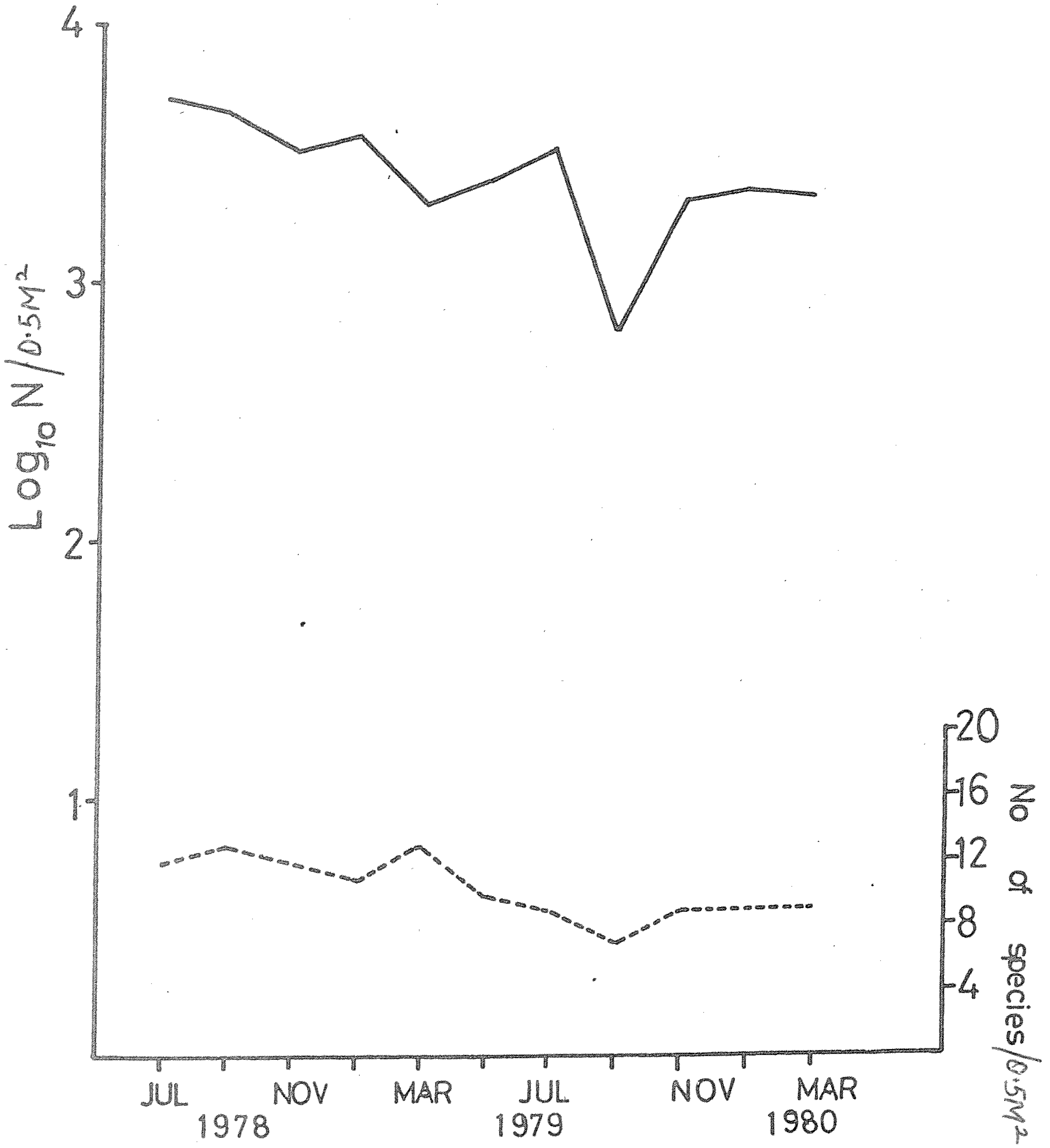


FIG.3.19. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS AT STATION 20

Table 3.20 Percentage abundance of major animal taxa at Station 20

	1978			1979						1980	
	July	Sept	Nov	Jan	March	May	July	Sept	Nov	Jan	March
Polychaetes	94.46	97.59	99.39	99.06	98.73	83.77	90.56	98.66	98.94	99.94	99.04
Crustaceans	0.19	1.48	0.09	0.48	0.94	0.66	8.91	0.45	0.34	0.04	0.23
Bivalves	5.35	0.92	0.51	0.44	0.34	16.57	0.53	0.89	0.71	0.04	0.54
Gastropods	--	--	--	--	--	--	--	--	--	--	--

Table 3.21 Abundance ranking of top five species in Station 20

	1978			1979						1980	
	July	Sept	Nov	Jan	March	May	July	Sept	Nov	Jan	March
Caulleriella caputesocis	1	1	1	1	1	1	1	1	1	1	1
Abra nitida	2	-	-	-	-	3	2	3	4	-	5
Nephtys hombergi	3	5	3	3	2	4	3	2	2	3	2
Eteone longa	4	4	4	4	3	-	5	-	-	4	4
Polydora ciliata	5	3	-	-	-	-	-	5	-	-	-
Sabella sp	-	2	2	-	-	2	-	-	3	-	-
Cirratulus cirratus	-	-	5	-	-	-	-	-	-	-	-
Nereis diversicolor	-	-	-	2	-	-	-	4	5	2	3
Anaitides maculata	-	-	-	5	4	-	-	-	-	5	-
Eudorella truncatula	-	-	-	-	5	5	-	-	-	-	-
Abra alba	-	-	-	-	-	-	4	-	-	-	-

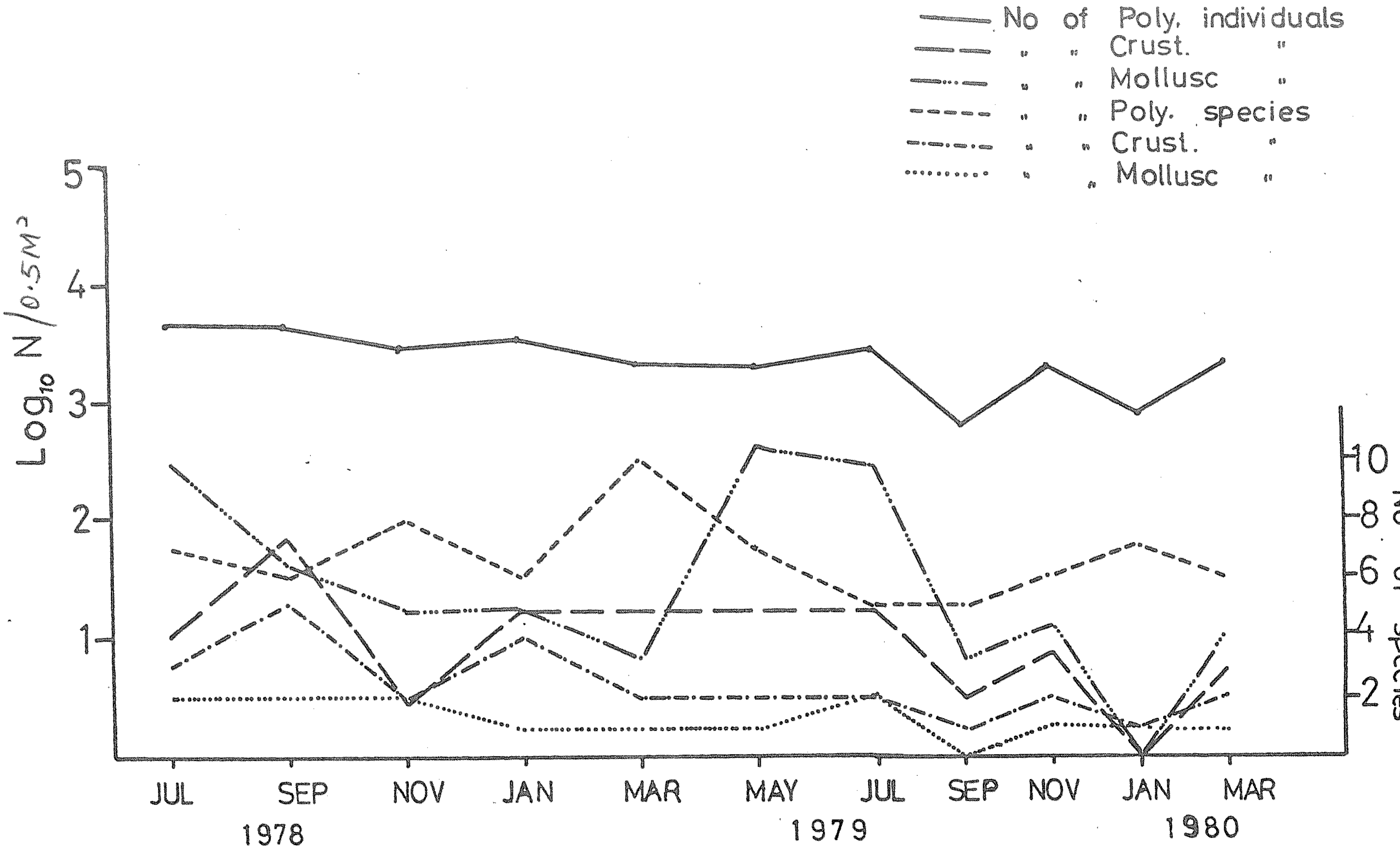


FIG. 3.20. SEASONAL VARIATIONS IN NUMBER OF SPECIES AND INDIVIDUALS OF MAJOR ANIMAL TAXA AT STATION 20

Individual species

Caulleriella caputesocis emerged as the numerically dominant species. The abundance ranking of the top five species at the station during the study is presented in Table 3.21. The cirratulid worm, C. caputesocis, accounted for more than 80% of the total individuals except in May 1979. With the exception of September 1979 and March 1980, the worm occurred at a high and fairly constant density (more than $5000m^{-2}$) throughout the study at the station.

Other species occurring in large numbers at different times at the station included N. hombergi. This polychaete occurred at high densities and featured prominently among the dominant species. The changes in the abundance of the dominant species at station 20 are presented in Figure 3.21. S. pavonina occurred only sporadically but at high densities between September and November 1978, and ranked among the top five species.

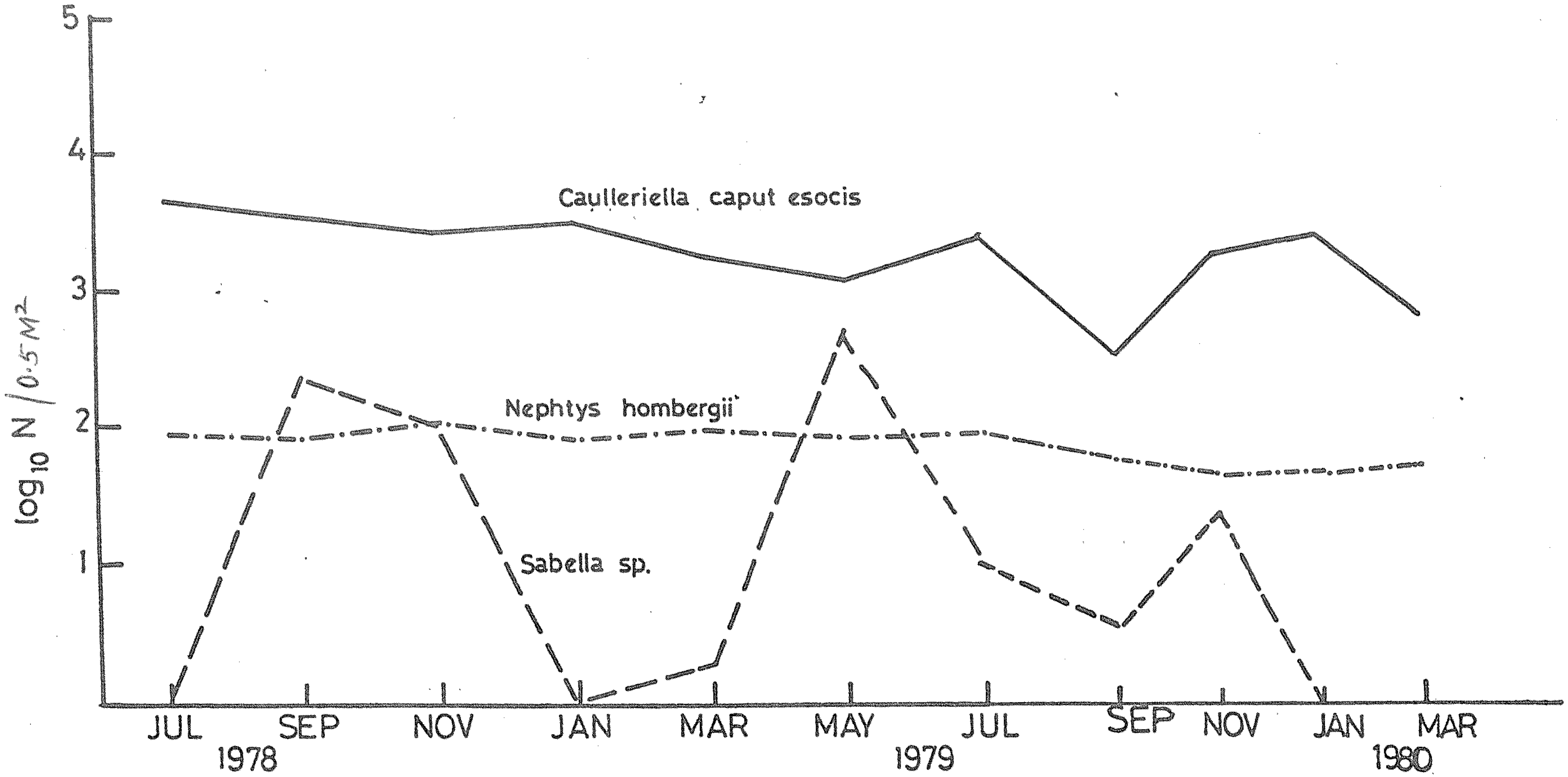
Some polychaetes, for example, A. maculata, P. ciliata, C. cirratus and E. longa, were often found during the study. E. longa remained fairly stable in abundance and in the ranking position but showed a seasonal trend in numbers. The species had high recruitments in the summer months but suffered heavy mortality in the winter months.

Only one species of crustacean, E. truncatula, occurred at a sufficiently high density to rank among the top five species. P. globosus, though commonly found in samples, occurred in low numbers. Other crustaceans of low densities include C. volutator, P. typicus, Paraphoxus oculatus, M. gryllotalpa and C. maenas.

Three species of bivalves, A. nitida, A. alba and C. edule, were recovered at the station. A. nitida occurred in large numbers in some samples so that it ranked among the top five species but the other bivalves occurred only sporadically. Owing to the patchiness in the distribution of A. nitida, the bivalve failed to appear among the top five species between September 1978 and March 1979.

The species abundance ranking averaged for the eleven bimonthly samples is shown in Table 3.22. Six species, five being polychaetes, accounted for more than 95% of the total individuals. The five polychaetes were responsible for nearly 93% of the total macrofaunal abundance. C. caputesocis and N. hombergi accounted for more than 90% of the total abundance. The dominance of polychaetes at the station is further shown in Table 3.23 where the group were dominant both in the number of species and individuals.

FIG. 3.21. SEASONAL RECRUITMENT & MORTALITY OF DOMINANT SPECIES IN ST. 20



Rank	Species	Average No/ $0.5m^2$	%	% Cumulative
1	Caulleriella caputesocis	2555.5	88.02	88.02
2	Nephtys hombergi	76.6	2.64	90.66
3	Abra nitida	73.5	2.53	93.19
4	Eteone longa	27.7	0.96	94.15
5	Nereis diversicolor	20.6	0.71	94.86
6	Polydora ciliata	17.9	0.62	95.48
7	Philomedes globosus	7.6	0.26	95.74
8	Eudorella truncatula	6.6	0.23	95.97

Table 3.22. Station 20 Average species abundance ranking for the 20 month period (July 1978 - March 1980).

Table 3.23

STATION 20

REPRESENTATION OF VARIOUS PHYLA IN NUMBERS AND SPECIES

Individuals per $0.5m^2$ as % of total (figures in parentheses represent actual numbers)

Month	Polychaeta	Crustacea	Mollusca	Others
1978				
July	94.46 (4923)	0.19 (10)	5.35 (279)	
Sept	97.59 (4467)	1.49 (68)	0.91 (42)	
Nov	99.4 (3101)	0.09 (3)	0.5 (16)	
1979				
Jan	99.1 (3578)	0.05 (17)	0.5 (17)	
March	98.77 (2007)	0.94 (19)	0.34 (7)	
May	83.77 (2018)	0.66 (16)	16.57 (404)	
July	90.77 (2907)	0.53 (17)	8.91 (286)	
Sept	98.77 (660)	0.45 (3)	0.9 (6)	
Nov	98.94 (2086)	0.34 (7)	0.71 (15)	
1980				
Jan	99.94 (2749)	0.04 (1)	0.04 (1)	
March	99.04 (2108)	0.23 (5)	0.54 (12)	

Species per $0.5/m^2$ as % of total

1978				
July	58.33 (7)	25.0 (3)	16.67 (2)	
Sept	46.15 (6)	38.4 (5)	15.38 (2)	
Nov	66.7 (8)	16.7 (2)	16.7 (2)	
1979				
Jan	50.0 (6)	33.3 (4)	16.7 (2)	
March	76.9 (10)	15.4 (2)	7.6 (1)	
May	70.0 (7)	20.0 (2)	10 (1)	
July	55.6 (5)	22.2 (2)	22.2 (2)	
Nov	66.7 (6)	14.3 (1)	14.3 (1)	
1980				
Jan	77.8 (7)	11.1 (1)	11.1 (1)	
March	66.7 (6)	22.2 (2)	11.1 (1)	

3.33 Diversity and faunal indices in benthic animals

An outstanding feature of animal communities is their diversity. Several attempts have been made to explain why certain environments support a more diverse fauna than others (Margalef, 1958; Gray, 1974; Sanders, 1968). A number of faunal indices which describe ways in which individuals are distributed between species in a community have been used.

In comparing different communities, it is essential to consider two major aspects of the community structure; the species composition and the total number of individuals. The concept of species diversity has been evolved to relate these two aspects, though definitions of diversity have often resulted in some degree of confusion. In one form, diversity is a measure of relative numerical composition of the various species present in a sample. The more the constituent species are represented by equal numbers of individuals, the more diverse is the fauna. The less numerically equal the species are, the less diverse the sample is, or the greater the dominance in the sample. The less the dominance in a sample, the greater the equitability.

The second component of diversity is measured by the number of species or species richness. Samples containing a large number of species per unit area have greater diversity. Such diversity can be designated 'species diversity'. The two components of diversity, the number of species present and the degree of dominance, are generally assumed to be highly correlated with one another. A large number of species per unit number of individuals exhibits low dominance and a small number of species often indicates high dominance. The extent of correlation seems to be sample size dependent. A strong correlation occurs in small samples but gets weaker as the sample size is increased. Among the largest samples, species diversity and dominance diversity are not significantly correlated (Fager, 1972).

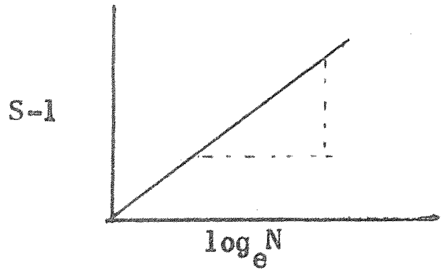
Some faunal indices are dependent on sample size or some sort of distribution of individuals between species. A diversity measurement which is independent of sample size is desirable.

Margalef's d value

Early studies of diversity express a value which depends almost wholly on the total number of individuals, thus the diversity index becomes unsatisfactory. Margalef (1951) recognised that in general, a relationship exists between the number of species in samples and the logarithm of the total number of individuals. He then proposed a diversity index which is dependent on a straight line relationship between the number of species (S) and the logarithm of the total number of individuals (N).

Since $S = k \log_{10} N$, where k is a constant, k should be independent of sample size.

Margelef then modified $d = \dfrac{S-1}{\log_e N}$ so that when $d = 0$, $S = 1$



d = Margalef's index of diversity

S = number of species

N = number of indivuals

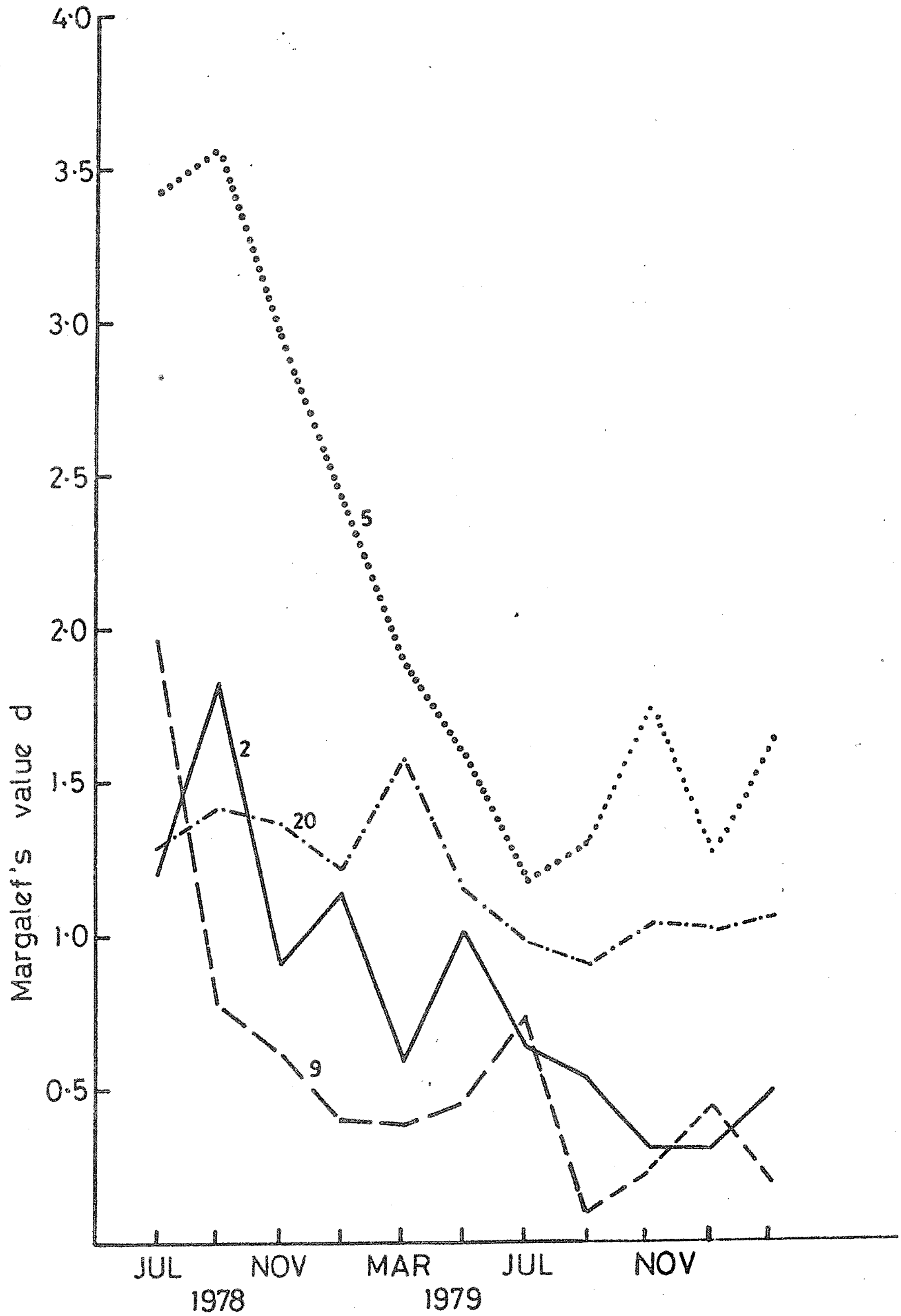
Relatively large changes in N are required to significantly change the index, whereas small changes in S greatly influence it. Therefore Margalef's d value is largely a measure of species richness.

Margalef's d values calculated for the four stations during the study are shown in Fig. 3.22. All the stations showed a decrease in species diversity during the study, with greatest decline at station 5 and smallest at station 20. At station 2, Margalef's d value reached a maximum in September 1978 and a minimum between November 1979 and January 1980. Peak value at Station 5 was obtained in September 1978 and a minimum value in July 1979. At Station 9 a maximum value of the index was obtained in July 1978 but a minimum value obtained in September 1979. At Station 20, maximum value was in March 1979 and a minimum value was obtained in September 1979. In general, there were two phases, a decline between July 1978 and September 1979 and a period of relatively low diversity afterwards.

Shannon-Wiener information function (Hs) and Equitability

The Shannon-Wiener information function (Hs) is a diversity index which provides a measure of how indivuals are apportioned among the constituent species and incorporates a measure of dominance diversity. The idea was originally introduced by Margalef (1957) as a measure of diversity of plankton samples. The index Hs can be equated as the degree of uncertainty involved in predicting the species identity of a randomly selected individual. This index Hs which has been widely used (Shannon and Weaver, 1963) in benthic studies is calculated using the equation

FIG. 3.22. Margalef's value d for stations 2, 5, 9, 20.



$$Hs = \sum_{i=1}^{s} pi \log_2 pi$$

or $$Hs = -3.3220 \left[\sum_{i=1}^{s} pi \log_{10} pi \right]$$

where S = total number of species

pi = the observed proportion of individuals that belong to the i^{th} species (1, 2, 3 --- etc.)

This index is influenced both by the number of species present and 'equitability' which determines how evenly or unevenly the individuals are distributed among the constituent species. The function, therefore, is sensitive to both species and dominance diversities.

Lloyd and Ghelardi (1964) proposed an index of equitability using H(s). In practice, it is rare to find a community in which two species show numerical equality since a community may not necessarily comprise species whose numerical abundance would be essentially equal. Equitability is calculated using the equation:

$$j = \frac{H(s)}{H(s)\ max.}$$

where j = index of equitability

H(s) = Shannon-Wiener information function

H(s) max = $\log_2$ of the total number of species in the sample.

Seasonal variations in the Shannon-Wiener information function and equitability measurements for the four stations are presented in Fig. 3.23. Station 2 showed a decline in the species diversity (Hs), species richness (d) and equitability appeared to influence diversity to a great extent, with species richness showing greater influence. At station 5, after an initial decline in the species diversity (Hs) between July and November 1978, there appeared to be some degree of stability in diversity at this station. Equitability remained fairly constant and did not appear to influence the diversity to a great extent. At this station, diversity seemed to be influenced by species richness. At station 9, both species diversity (Hs) and equitability (j) showed similar trend. Species diversity at this station was influenced to a large extent by equitability. Similar situation was found at station 20 where the diversity and equitability showed similar trends throughout the study and both remained more or less stable except for a peak in May 1979. In general, a decrease in equitability is due to the influx of juveniles which occurred in samples occasionally.

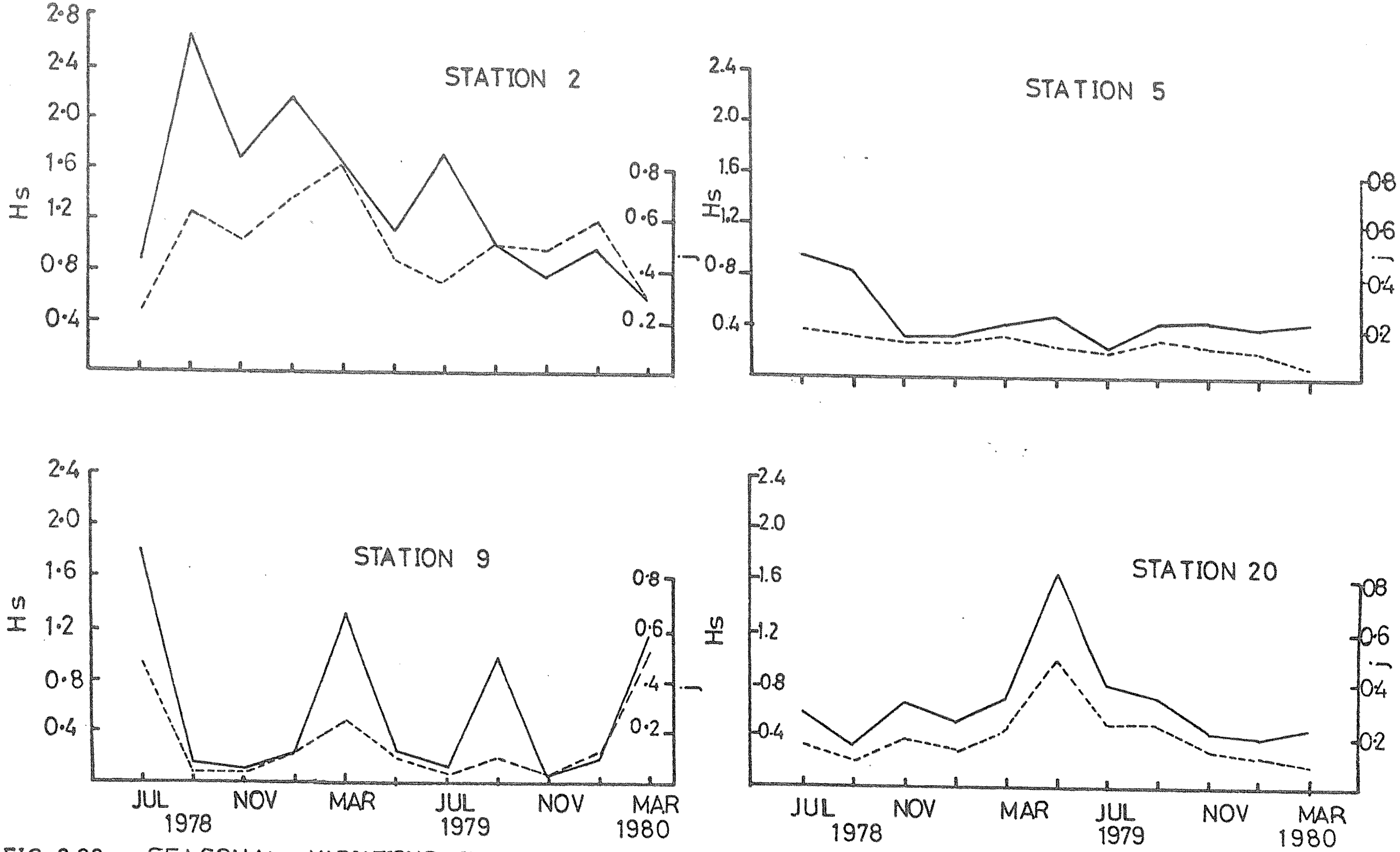


FIG. 3.23. SEASONAL VARIATIONS IN SHANNON WIENER INDEX (Hs) AND EQUITABILITY (j)

—— Hs ...... j

Sander's Rarefaction Method

Since most measurements of diversity are affected to some degree by sample size, this method which is independent of sample size allows direct comparisons between samples of different sizes to be made. The measure is dependent on the shape of the curve of species abundance rather than the absolute number of individuals present in the sample. The method was first used by Sanders (1968) for a polychaete-bivalve fraction of samples rather than the entire fauna from the soft oozes. The high abundance percentage of the two animal taxa in the present study justifies the application of the method to the samples of the study.

In producing the species abundance curve, the procedure is to keep the percentage composition of the component species constant but to reduce the sample size. This is to artificially create results that would have been obtained had smaller samples with the identical fauna composition been taken. The species are thus ranked by abundance and the percentage composition of each species and the cumulative percentage plotted. Table 3.24 shows the percentage composition and cumulative percentage of the species at station 2 in July 1978 as an example.

10 species had a numerical abundance of 4159 individuals. The number of species at the 100 individual level can be determined. The percentage composition of each species will be the same as in the original sample but the number of individuals is now reduced to 100. The 100 individuals in the reduced sample represent 100% of the individuals. Each individual, therefore, forms 1% of the sample. In the example (July 1978 sample at station 2) three species comprised 1% or more and totalled 98.82% of the sample numerically. Each of the three species will be present in the reduced sample, with a residue of 1.18% of the original sample as the remaining seven species.

Since none of the residual species form more than 1% of the original sample, such species comprising the group (residual) cannot be represented by more than one individual. However, one individual specimen constitutes 1% of the reduced sample, therefore $1.18/1\% \approx 1.18$ species

Hence $(3+1.18)$ species = 4.18 species are present per 100 individuals.

In a similar way, the number of species per 500 individuals can be determined. Each individual forms 0.2% of the sample and 6 species

Rank of Species by abundance		Total	% of Sample	Cumulative % of Sample
1	Caulleriella caputesocis	3425	82.35	82.35
2	Abra nitida	585	14.07	96.42
3	Nephtys hombergi	100	2.40	98.82
4	Cerastoderma edule	17	0.41	99.23
5	Philomedes globosus	12	0.29	99.52
6	Polydora ciliata	9	0.22	99.74
7	Mercenaria mercenaria	5	0.12	99.86
8	Eteone longa	3	0.07	99.93
9	Cirratulus cirratus	2	0.05	99.98
10	Crangon vulgaris	1	0.02	100.00

Table 3.24 Species list with percentage and cumulative percentage of individual species at Station 2 in July 1978

No. of Individuals	Each Individual represents X% of the sample X%	No. of Species in original sample comprising -X%	Residue %	Other species in reduced sample. Residue %÷X%	No. of species per n individuals
100	1.0	3	1.18	1.18	4.18
500	0.2	6	0.26	1.3	7.3
1000	0.1	8	0.14	0.7	8.7
2000	0.05	10	0.02	--	10

Table 3.25 The number of species at different individual levels for July 1978 sample at Station 2

(Table 3.25), each represent $\geqq 0.2\%$ of the sample, amounting to 99.74% of the original sample. The residue 0.26% then accounts for 0.26/0.2 = 1.3 species.

Hence (6+1.3) species = 7.3 species are present per 500 individuals

The arithmetic plots of the number of species at different population levels using Sander's rarefaction methodology for the four stations are shown in Figures 3.24 - 3.27. For clarity and easy understanding, plots for one year samples (July 1978 - July 1979) have been shown. The plots for the remaining period of study were essentially similar to the previous year.

The curvilinear trend of the lines is due to the constant rate at which the individuals are being added on the assumption that aggregation of the individuals is not important. The progressively rarer species were added at a continuously decreasing logarithmic rate. The actual numbers of species and individuals present in the samples are indicated by the point of termination of the lines. The theoretical number of species at different population levels can be easily interpolated from the curves.

Different environments showed characteristic rates of species increment. A low species diversity environment showed low numbers of species per unit number of individuals while a high species diversity environment exhibited high number of species per unit number of individuals. At station 2, the highest diversity was in September 1978 but gradually decreased thereafter. There was no remarkable increase in the number of species above 3000 individual level. Station 5 showed a large number of species and high species diversity with a peak in September 1978. Very little increase in the number of species above the 2000 individual level occurred. Station 9 showed the lowest species diversity with a peak in July 1978. Little increase in species diversity above the 2000 individual level occurred at the station. Station 20 showed peak species diversity in March 1979 but greater stability in the diversity throughout the study period. In general, the higher the curves are, the greater the species diversity, and the closer the curves are to the Y-axis, the greater the equitability of the sample.

Sander's rarefaction method of measuring faunal diversity, though allowing comparisons between different communities, is only valid when fauna is randomly or evenly distributed and not aggregated.

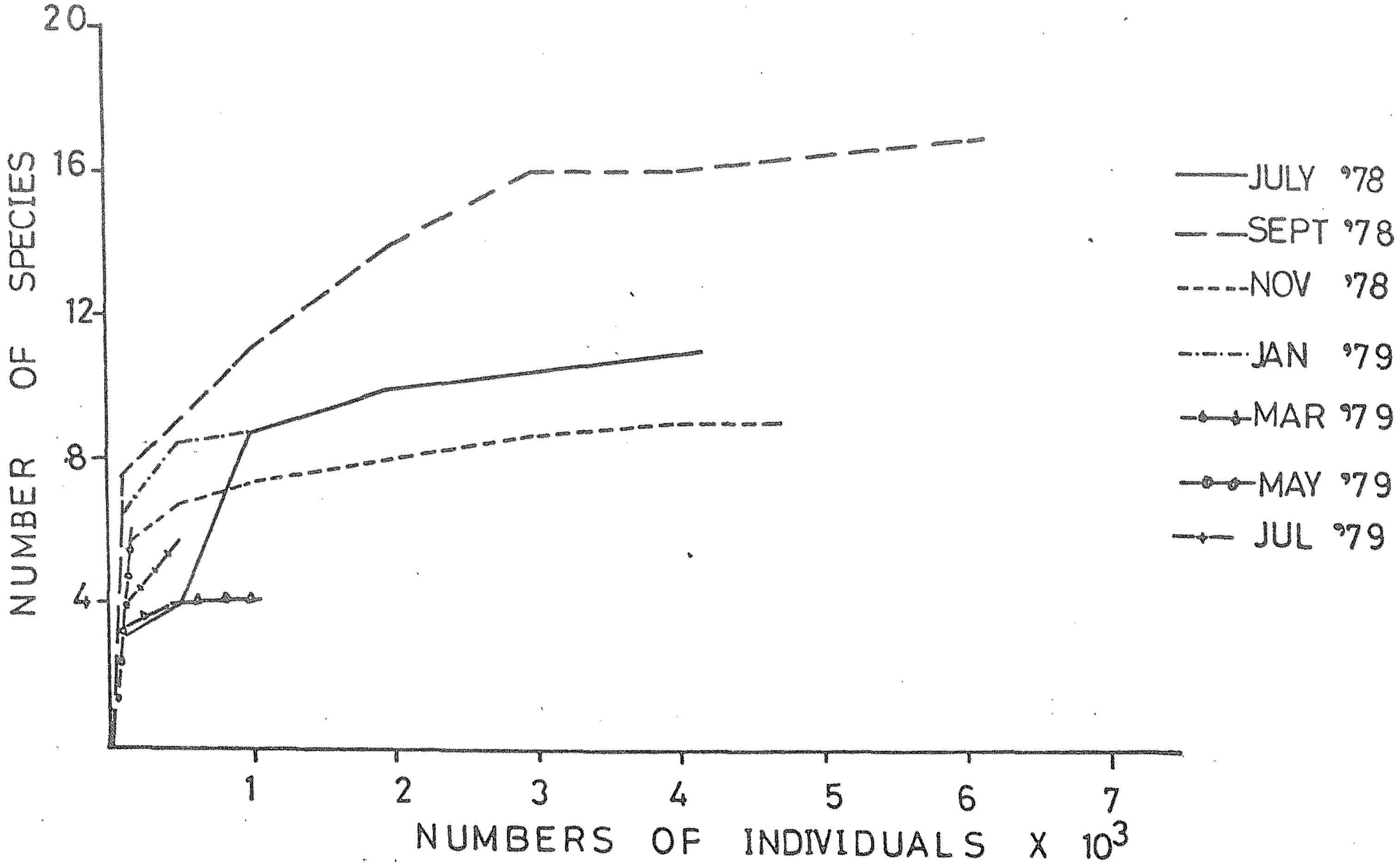


FIG. 3.24. SANDERS' RAREFACTION FOR STATION 2

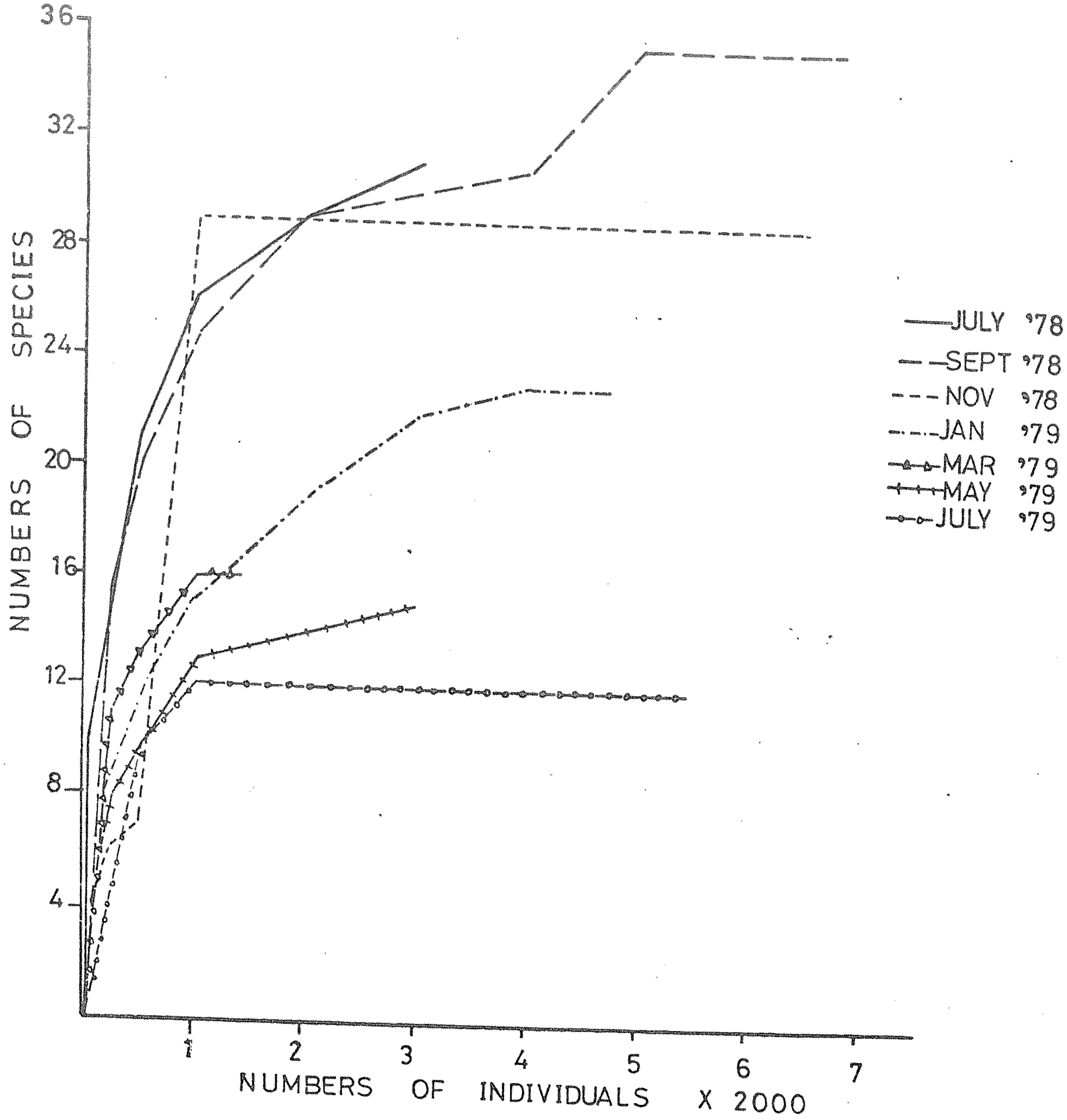


FIG. 3.25. SANDERS' RAREFACTION DIVERSITY FOR STATION 5

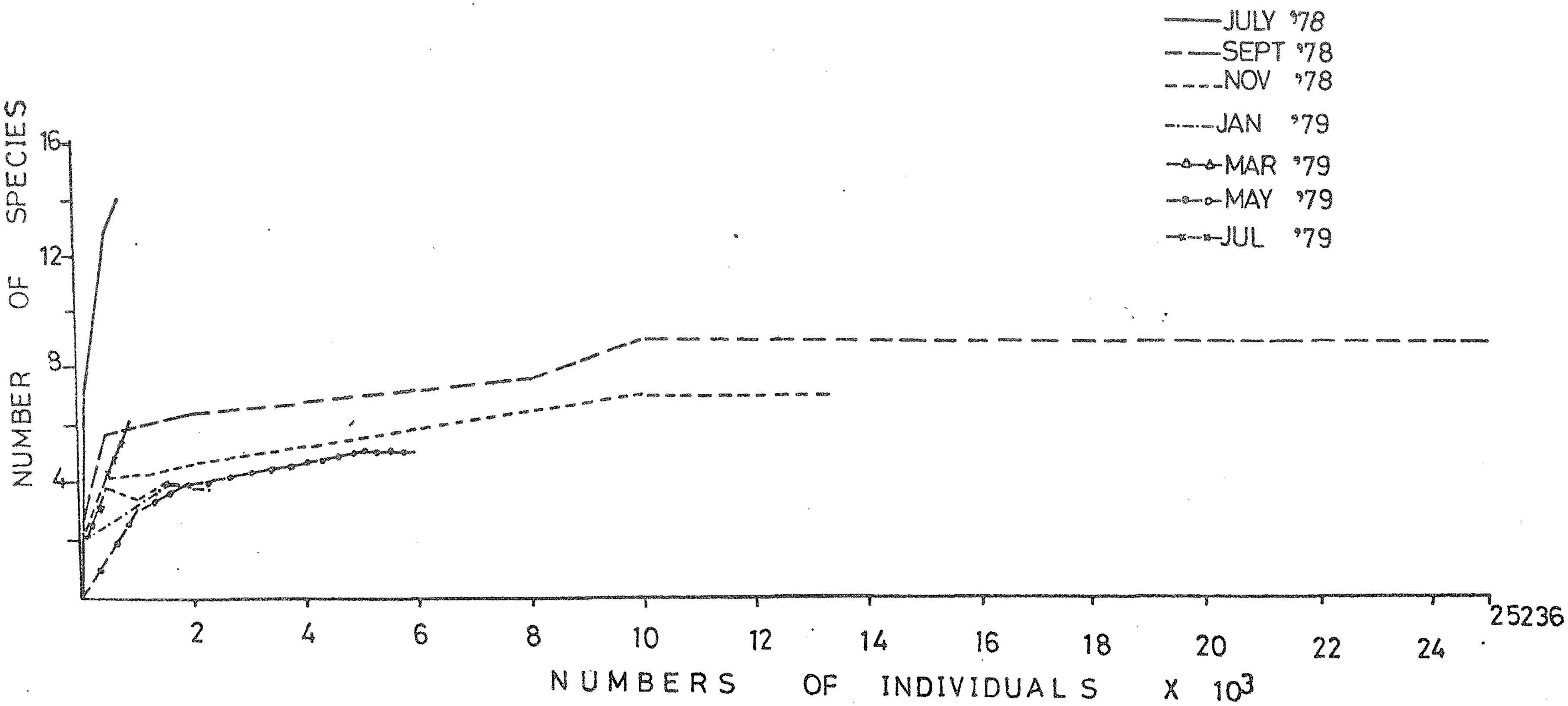


FIG. 3.26. SANDERS RAREFACTION DIVERSITY FOR STATION 9

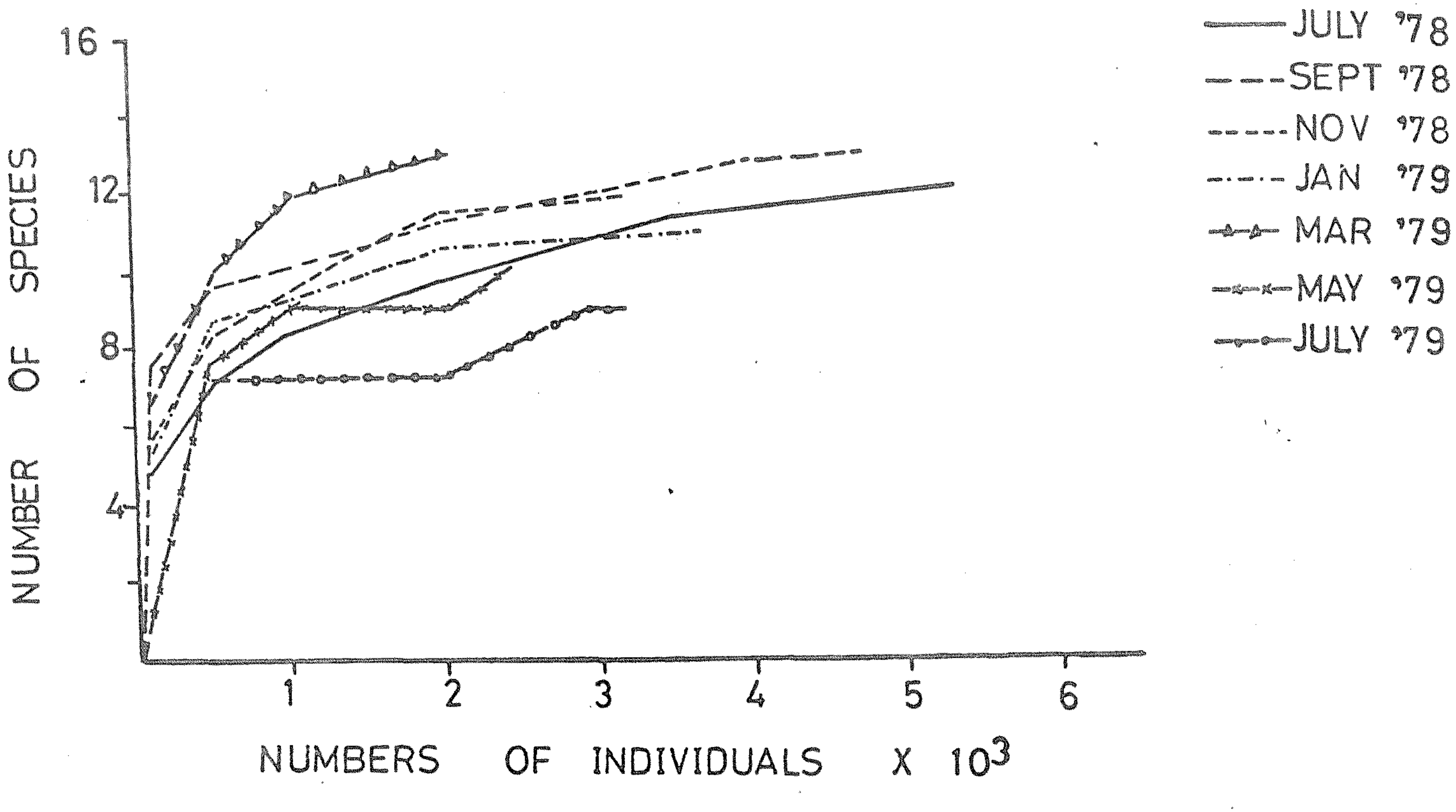


FIG. 3.27. SANDERS RAREFACTION DIVERSITY FOR STATION 20

3.4 Similarity between samples

Several numerical analyses have been applied to benthic survey data as an alternative approach to identifying species associations. Such methods use statistical criteria in evaluating the frequency of occurrence or the abundance of species and to quantify faunal associations. The numerical methods aim at grouping stations as to faunal similarity and to compile species list characteristic of each group.

Usually, two similarity coefficients are applied to characterise species groups when samples include heterogeneous types of benthic communities. The coefficient used in the present study is Jaccard's coefficient which expresses the number of species common to both samples as percentage of the total number of species in both samples. The other coefficient, Czekanowski's coefficient, is used to compare species composition and relative percentage abundance between samples. This was used by Buchanan et al (1978).

Jaccard's coefficient

Jaccard's coefficient considers the presence or absence of species in a set of samples and has been used to measure the relationship between different types of communities or samples in terms of species composition. This coefficient has been applied to samples taken at the same or different stations (Lauriston, 1977). The higher the coefficient, the higher the similarity between samples and vice versa. The values ranged between 0 and 100% indicating no species overlap between samples and exactly the same species in the samples respectively.

Jaccard's coefficient (JC) is calculated using the equation

$$JC = \frac{c}{a + b + c} \cdot 100$$

where c = number of species common to both
a = number of species in sample A only
b = number of species in sample B only

Variation in similarity between the four stations using Jaccard's coefficient is presented in Figure 3.28. Stations 2 and 9 showed the highest degree of similarity and ranged between 38 and 60% between July 1978 and September 1979. A complete species overlap between the stations occurred in November 1979. Stations 5 and 9 showed least similarity and the value was less than 20% throughout the study except in July 1978. Stations 5 and 20 showed a fair similarity and the per-

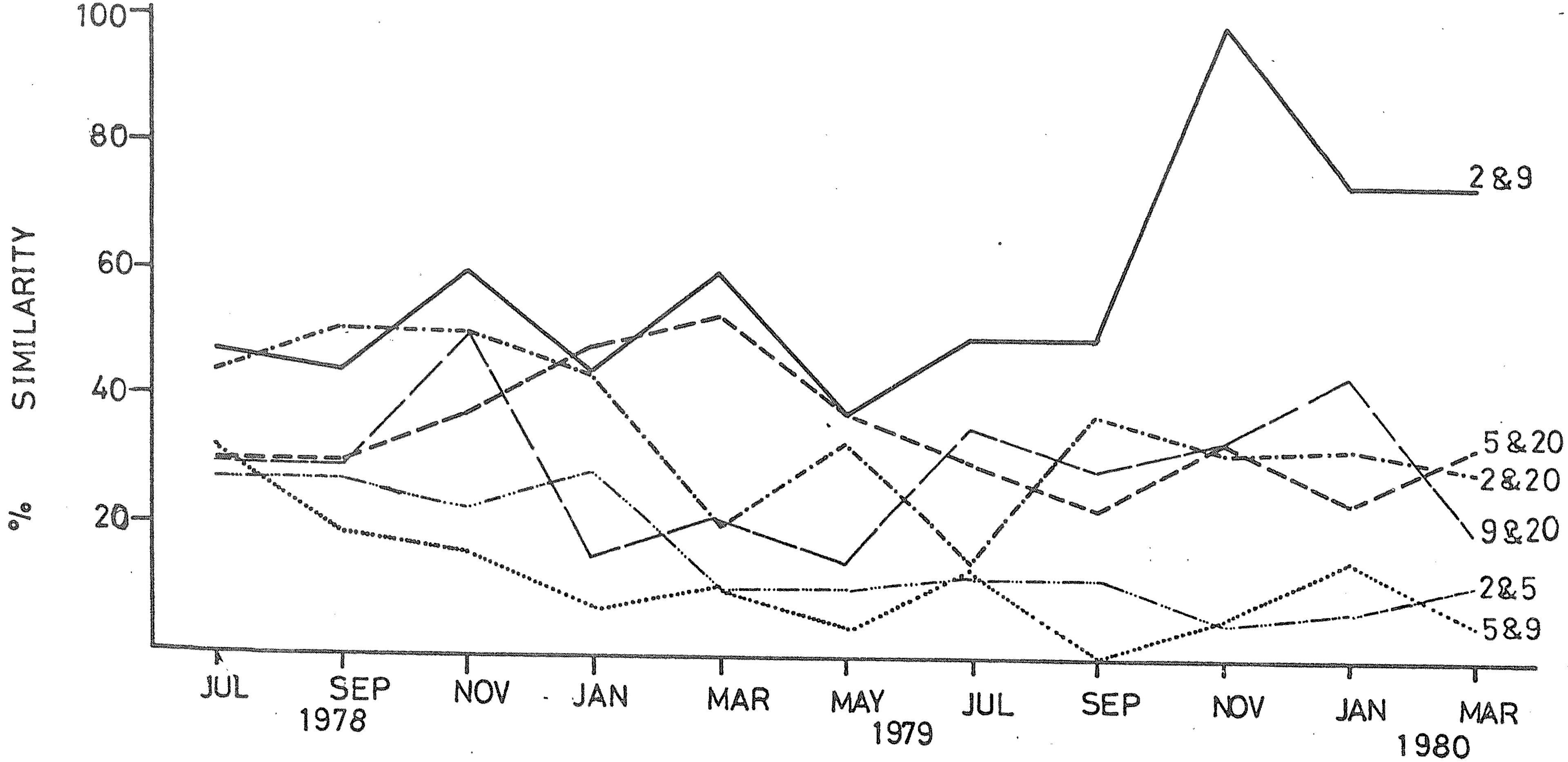


FIG.3.28. VARIATIONS IN % SIMILARITY OF STATIONS

centage similarity between the two stations ranged between 30 and 36% except for peaks in March 1979. Greater similarity between stations 2 and 9 may be attributed to similarity in the physico-chemical parameters notably particle size, sediment total organic matter and hydrocarbon levels. In general low degree of similarity occurred between stations between July 1978 and September 1979, but stations 2 and 9 became more similar at new low species diversity situation.

3.5. Lognormal distribution of species between individuals' geometric classes

The concept of the distribution of species between the geometric classes of individuals showing a lognormal distribution was first described by Preston (1948). Using populations of breeding birds and moths in light traps, he postulated that for naturally occurring biological populations, species show a lognormal distribution when arranged in geometric classes of the individuals. Patrick et al (1954) and Patrick and Strawbridge (1963) showed that Preston's postulate also applies to diatoms from soft and brackish water. Thorrington-Smith (1971) also applied it to phytoplankton samples from the Indian Ocean.

Edden (1971) studied the relationship between species diversity and the lognormal distribution of species between geometric classes of individuals using phytoplankton samples from the Indian Ocean. Since the use of certain distribution statistics permits separation of diversity into the 'species richness' and 'dominance' components, which can be quantitatively estimated, she was able to demonstrate considerable advantage in defining measures of diversity and equitability based on the lognormal species/individual curve. The method has only recently been applied to the marine sublittoral benthos: Saltkallefjord (Rosenberg, 1973); Kiel Bay (Anger, 1975); Lock Eil (Pearson, 1975); Northumberland coast (Buchanan et al, 1978). Gray (1979) applied the method to studies of pollution induced changes in populations.

Theoretically, the whole lognormal curve would be obtained if a complete population universe were sampled. In practice, the whole universe is never sampled and a truncated lognormal curve is obtained. The degree of truncation is determined by the proportion of the universe that has been sampled (Preston, 1948). Gray (1979) indicated that in an unstressed community, a lognormal curve results in a straight line when the cumulative percentage species is plotted on probability paper against the geometric classes of individuals. Since no record of the application of the method in an estuarine environment has hitherto been available, it was considered worth using with the Southampton Water communities.

Method

Each sample was divided into lognormal geometric classes using the method outlined by Preston (1948). If a lognormal relationship occurs, plots of cumulative percentage species on probability paper against geometric classes should give a straight line. According to Gray (1979), deviation from a straight line results from environmental disturbance which alters the equilibrium in the community structure.

Results

The plots for the cumulative percentage species against geometric classes at station 2 are presented in Figure 3.29. In July 1978, the plot approximated to a straight line with increase in geometric classes III and V. The increase shifted to geometric classes II and III in September 1978 while there was reduction in the classes III and VI in November 1978. Change in the community structure was gradual with an increase in geometric class II but reduction in classes III and IV in January 1979. By March 1979, there was reduction in geometric class V. The plot returned to an approximated straight line in May 1979 but in July 1979 there was reduction in geometric class IV. A rise in geometric class II in September 1979 was followed by a return to an approximate straight line from November 1979 to March 1980, possibly indicating stability in the community.

The plots at Station 5 are shown in Fig. 3.30. The plots approximated to straight lines between July 1978 and January 1979, possibly with no change in the community structure. Deviations from lognormal curves with reduction in geometric classes II and III in March 1979 but an increase in the classes and reduction in class V in May 1979. Slight reductions in geometric classes II - IV in July 1979 were repeated in September 1979 but only in classes III andIV in November 1979. Reduction in geometric class IV took place in January and March 1980.

At Station 9 (Fig. 3.31) the plots approximated to a straight line in July 1978 but showed reduction in geometric classes III in September and November 1978. In January 1979, reduction occurred in class IV but increased in classes II and III in March 1979, in class IV in May 1979 and in class III in July September and November 1979. By January 1980, the plots showed an increase in geometric classes II and IV and

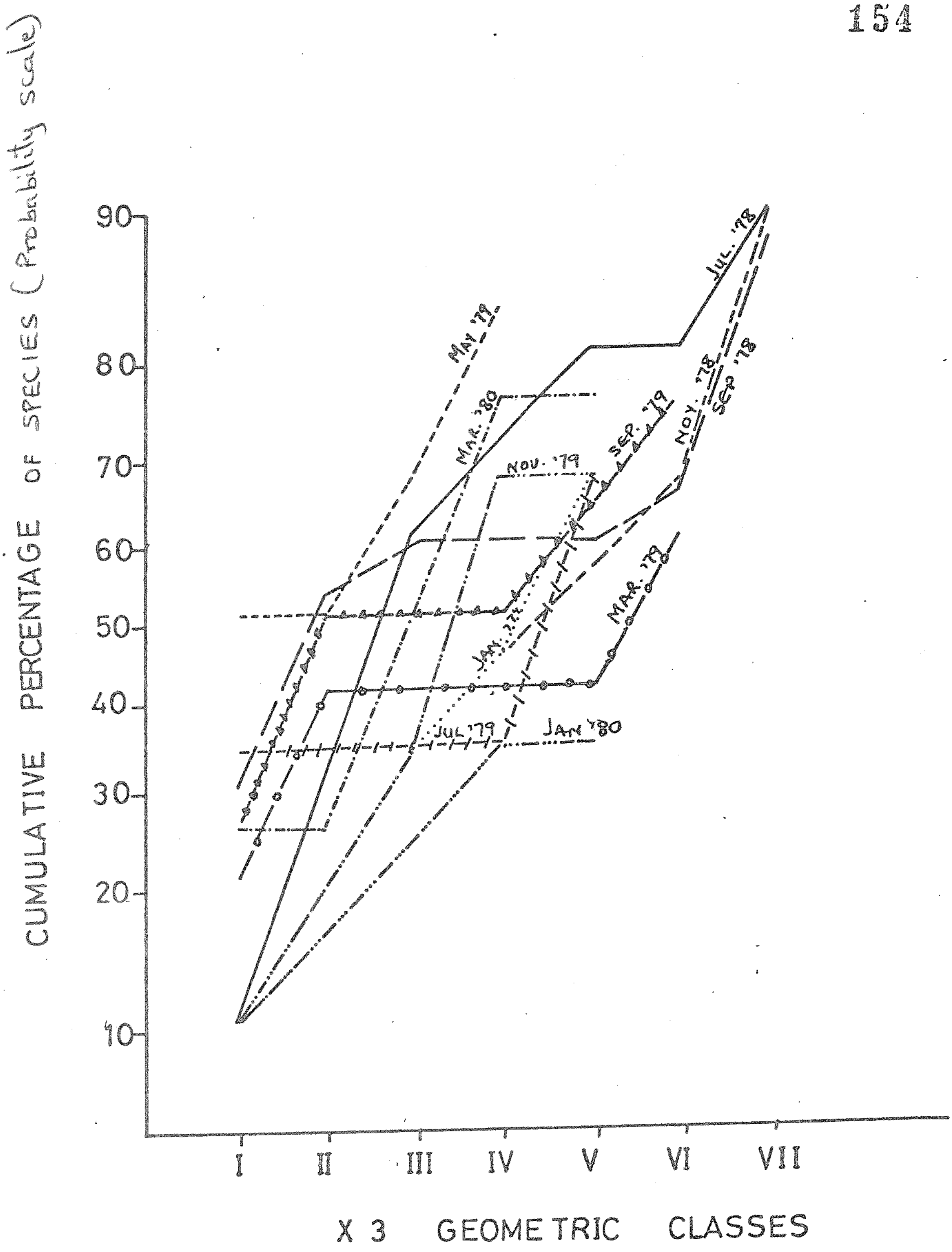


FIG.3.29. LOGNORMAL PLOTS OF INDIVIDUALS PER SPECIES AT STATION 2

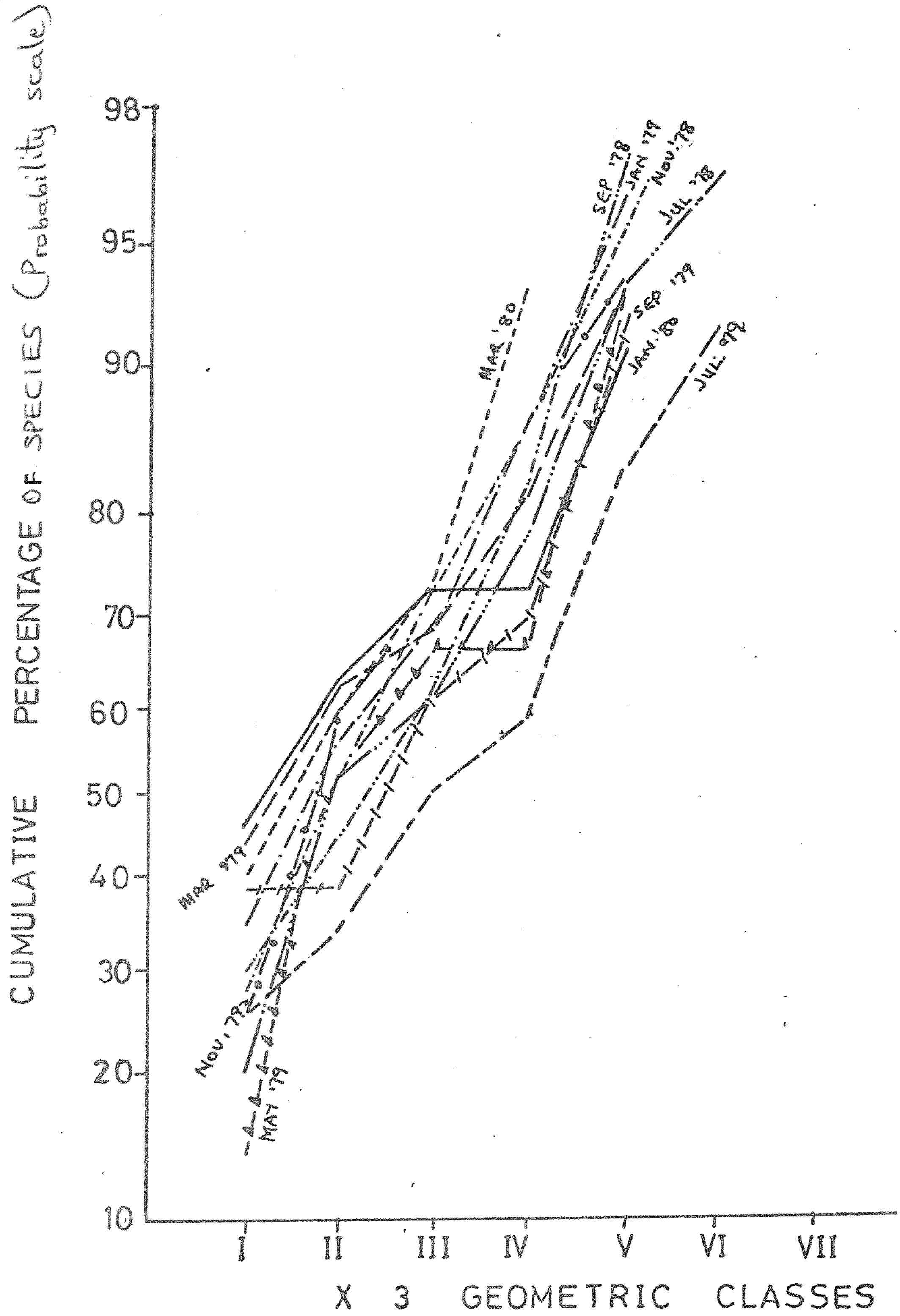


FIG. 3.30. LOGNORMAL PLOTS OF INDIVIDUALS PER SPECIES AT STATION ÷ 5

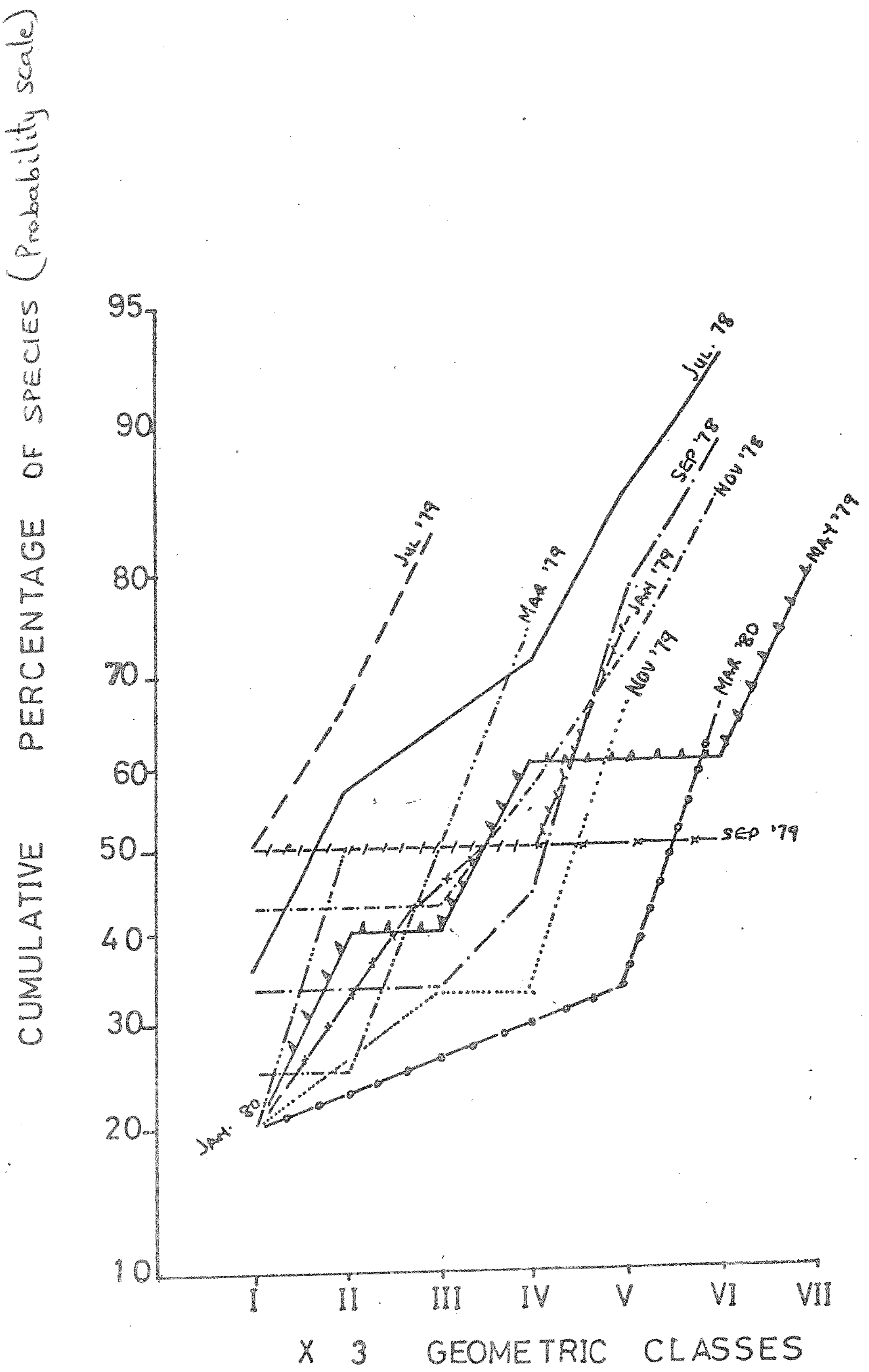


FIG. 3-31. LOGNORMAL PLOTS OF INDIVIDUALS PER SPECIES AT STATION 9

approximated to a straight line in March 1980.

The plots at station 20 are shown in Fig. 3.32. While the July 1978 plot approximated to a straight line, those of September 1978 showed reductions in geometric classes II - V. There was an increase in geometric class II but reduction in class III in November 1978. Slight reductions in classes II and III were obvious from January 1979 plots, but March 1978 showed a reduction in class III and an increase in class IV. By May 1979, there were increases in classes II - V but a reduction in geometric class VI. A reduction in classes II and III in July was followed by massive reduction in class I but an increase in classes II - IV in September 1979. Reduction was limited to class III in November 1979 but extended to class IV in January 1980 but only in geometric class II in March 1980.

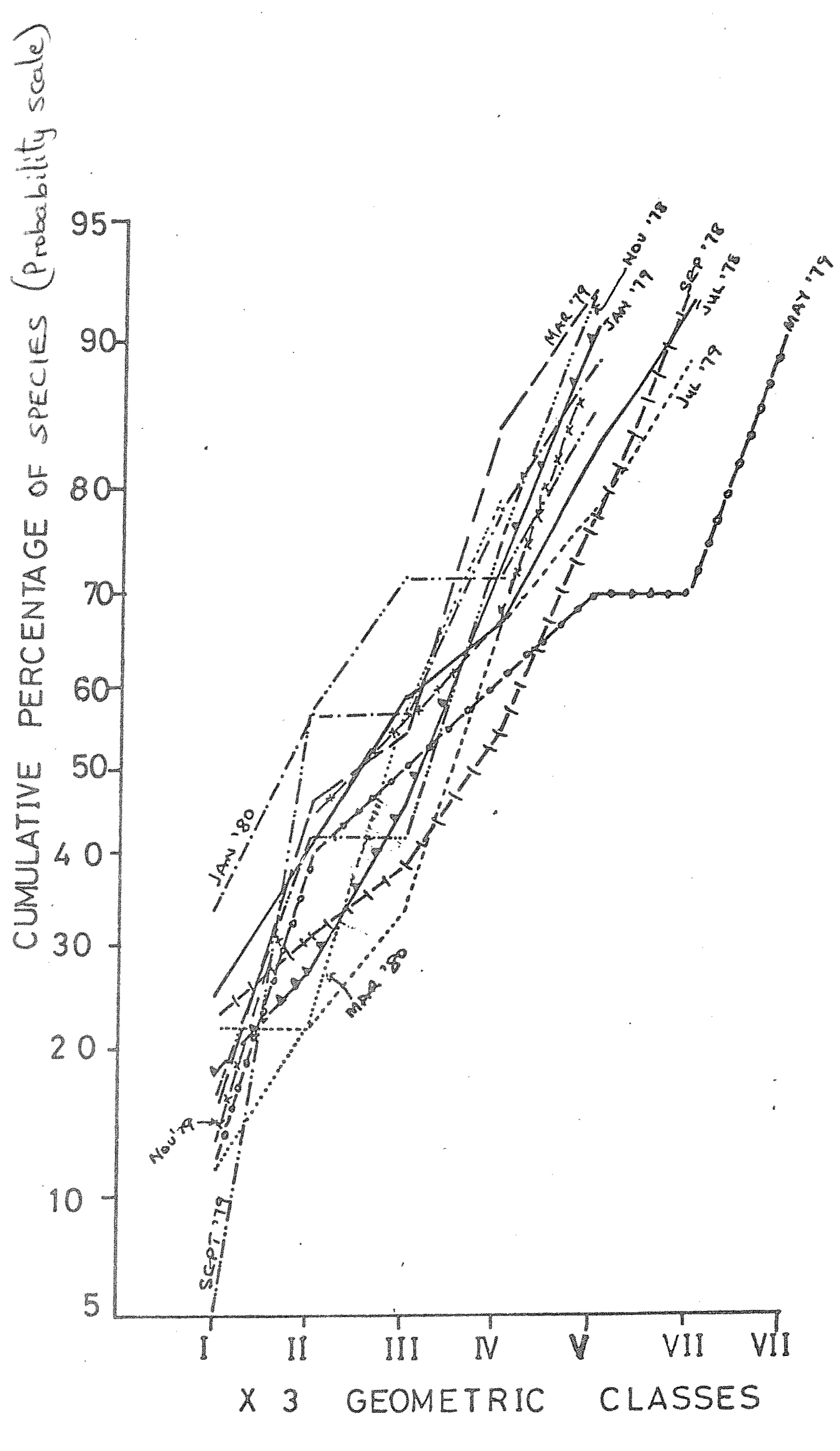


FIG 3.32. LOGNORMAL PLOTS OF INDIVIDUALS PER SPECIES AT STATION 20

3.6 DISCUSSION

The results of the present investigation indicate a high degree of variability in the physico-chemical and biological parameters of the study area. Given the sediment type, location and time of year, the macrobenthic fauna of Southampton Water may to a limited extent be predicted. Many species populations fluctuated in response to seasonal recruitment and mortality. Remarkable variations in abundance patterns within different habitats and seasons were apparent within the species associations.

The relatively high fractions of silt-clay in the sediment on the western side indicate a high sedimentation rate possibly in part due to the high hydrocarbon content which is thought to induce sedimentation (Knap, 1978). Sedimentation is high on the western side where water currents are appreciably lower (less than 1 knot). Stronger currents on the eastern side and towards the mouth of the estuary are continuously eroding and depositing sand which consequently allows little deposition of fines (particles less than 63 μm in diameter)(Dyer, 1973). The increase in the level of fines at all stations between January 1979 and March 1980 probably suggests higher sedimentation rate during the period.

The higher total organic matter in the sediment on the western side (Stations 2 and 9) was probably due in part to industrial effluents. Station 2 receives effluents from the Petrochemical and Synthetic Rubber industries and station 9 receives the effluents of the Esso Petroleum company. Williams (1976) estimated about eighty per cent of the yearly organic carbon input originate as effluents from the major industries in the area. Although station 5 on the eastern side was situated near a sewage outfall, the total organic matter at this station was low compared with the other stations. The total organic matter at the four stations showed distinct seasonality with maximum values occurring in July-September and minimum in March - May. This cycle was more marked at stations 5 and 20 but less at stations 2 and 9. Although Byers et al (1978) suggested that the total organic matter could be used as an index of the amount of food available to benthic animals, this does not necessarily hold in all situations. If it is the case, stations 2 and 9 with higher total organic matter would be expected to support a greater production and abundance of deposit feeders than stations 5 and 20. On the contrary, the abundance and production of the deposit feeders were greater in the latter stations except in September 1978 when the abundance of a single species, C. capitata, was at its peak. It can be argued that the total organic matter only serves as an index of quantity rather than quality of the refractile material available to benthic animals. In the same way, the accumulation of the organic matter in an area is a dynamic process which is subject to change with time, the total organic matter cannot be related to the amount of food available to benthic animals.

The sediment metals in the study area varied to a large extent with time and the particular metal in question. Some determinations of sediment trace metals in Southampton Water had previously been made (Leatherland and Burton,1974; Romeril,1974, 1976; Armansson,1978); none of the results are directly comparable with the present study. The methodology and location of sampled areas differed. Sediment copper in the present study was particularly high on the western side especially at station 9 (near Esso petroleum refinery outfall) but decreased eastwards. The high sediment copper at station 9 may be attributed to the copper released with the refinery effluents since copper, as copper chloride, is used as a 'sweetening agent' in the refinery process. In the present study, the lowest level of sediment copper was recorded at Station 5, but Romeril (1974) using atomic absorption spectrometry, estimated the sediment copper at Netley as 18.2 ± 0.64 ug/g, a lower estimate by Romeril (1974) may possibly be attributed to lower measures obtained from atomic absorption spectrometry since the atomic absorption only measures the absorbed quantity, but X-ray fluorescence spectrometry (employed in the present study) measures total metal in the sediment.

There was significant correlation between sediment copper and zinc at all stations investigated though there was none between lead, zinc and arsenic. Sediment zinc at all stations remained low and constant throughout the study but large fluctuations in sediment lead were noticed. Such fluctuations are attributable possibly to the amounts of riverflow into Southampton Water since input from the Test, Itchen and Hamble form the main sources of lead and arsenic in the estuary (Burton, personal communication).

Direct comparisons between values of sediment metals obtained by previous workers and in the present study may be difficult. Some useful inference, nevertheless, can be drawn. Romeril (1974) based his results on core samples taken around the mouth of the River Hamble. His estimate of sediment copper at Calshot was similar to that obtained at Station 20 in the present study, though the particle size of the sediments from the two sites differed. Armansson (1978) observed some significant differences in trace metals of sediments with different fine fractions. The heterogeneity of the sediment of the study area could be responsible for the variability in the levels of sediment metals. An absolute lack of seasonality in the levels of sediment metals in the study area weakens any suggestion that a single rather than multiple factors could be responsible for the variability.

Results of the biological parameters suggest a gradual and steady decrease in the number of species throughout the study. At station 2 between September 1978 when the number of species reached its peak and March 1979 when the minimum number of species was recorded, eleven species were lost. Nearly all the crustaceans recorded in September 1978 had been lost by March 1979, all the bivalves and five polychaete species were lost. During the same period, seven amphipods, one isopod, one cumacean and two decapod species and one pycnogonid were lost at Station 5. In the same station, two gastropods, two bivalves, one fish and three polychaete species, all of which are associated with the sediment surface, were lost. During the same period at Station 9, four polychaetes and one crustacean species and at Station 20, three crustacea and a bivalve species were lost. All the species lost between September 1978 and March 1979 were responsible for the general decline in the number of species at each of the four stations. The numerical abundance at the four stations, however, showed seasonal trends in recruitment and mortality of some specific species.

Within the species at each station, it is possible to recognise two groups (three at station 9), defined by the nature of their population changes between September 1978 and March 1979. The 'gaining' species (G) which exhibit net gains over the period and the 'losing' species which show significant losses during the period. At station 9, only Cirratulus cirratus shows no significant population change over the period and is designated a 'neutral' species. The gaining and losing species at each of the stations between September 1978 and March 1979 are shown in Table 3.26. Gains are low but similar in 'highly similar' stations. Stations 2 and 9 became more similar at the new low diversity situation.

Lie and Evans (1973) found that only small annual variability in the number of species occurred in Puget Sound, U.S.A., over a period of three years, but Buchanan et al (1974) recorded a substantial stability in the number of species off the coast of Northumberland over a period of four years, though the total number of individuals had doubled over the same period. In the present study, polychaetes dominated both in the number of species and numerical abundance. Changes in the number of species were affected to a large extent by

GAINING SPECIES		LOSING SPECIES		NEUTRAL SPECIES
Species	Gain m^{-2}	Species	Loss m^{-2}	
STATION 2		Sabella pavonina	1740	
		Caulleriella caputesocis	1218	
		Polydora ciliata	1086	
		Nereis diversicolor	311	
		Capitella capitata	236	
		Eteone longa	297	
		Anaitides maculata	5	
		Nephtys hombergi	3	
		Ophiodromus flexuosus	1	
		Philomedes globosus	4	
		Idotea linearis	2	
		Cerastoderma edule	2	
		Abra nitida	1	
		Carcinus maenas	1	
		Dexamine thea	1	
		Atylus falcatus	1	
STATION 9				
Eteone longa	16	Capitella capitata	22536	Cirratulus cirratus
		Nereis diversicolor	162	
		Sabella pavonina	111	
		Caulleriella caputesocis	58	
		Polydora ciliata	51	
		Syllis sp	1	
		Idotea chelipes	1	

Table 3.26 The gaining, losing and neutral species at selected stations (September 1978 – March 1979)

GAINING SPECIES Species	Gain m^{-2}	LOSING SPECIES Species	Loss m^{-2}	NEUTRAL SPECIES Species
STATION 5				
Nephtys hombergi	42	*Caulleriella caputesocis*	21054	
Eudorella truncatula	14	*Cirratulus cirratus*	202	
Eteone longa	6	*Philomedes globosus*	146	
Nereis virens	2	*Microdeutopus gryllotalpa*	120	
Sabella pavonina	2	*Pariambus typicus*	114	
		Melinna palmata	16	
		Mercenaria mercenaria	28	
		Aora gracilis	56	
		Leucothoe spinicarpa	40	
		Carcinus maenas	28	
		Anaitides maculata	24	
		Abra nitida	18	
		Idotea linearis	20	
		Crepidula fornicata	12	
		Cerastoderma edule	8	
		Nassarius reticulatus	12	
		Sthenelais boa	8	
		Corophium insidiosum	6	
		Amphilochidae	4	
		Nereis diversicolor	4	
		Perioculodes longimanus	2	
		Atylus falcatus	2	
		Achelia echinata	2	
		Petricola pholadiformis	2	
		Gasterosteus aculeatus	2	
		Bodotria scorpiodes	2	
		Pygospio elegans	2	
		Lumbrineris latreilli	2	
		Crangon vulgaris	2	

Table 3.26 (cont.)

GAINING SPECIES		LOSING SPECIES		NEUTRAL SPECIES	
Species	Gain m^{-2}	Species	Loss m^{-2}	Species	
STATION 20					
Nephtys hombergi	16	*Caulleriella caputesocis*	4084		
Nereis diversicolor	40	*Sabella pavonina*	476		
Anaitides maculata	32	*Polydora ciliata*	322		
Nereis virens	4	*Eteone longa*	130		
Melinna palmata	2	*Philomedes globosus*	76		
Cirratulus cirratus	2	*Eudorella truncatula*	14		
		Pariambus typicus	4		
		Carcinus maenas	2		
		Paraphoxus oculatus	2		
		Abra nitida	52		
		Cerastoderma edule	18		

Table 3.26 (cont.)

the sporadic occurrence of rare species that when present occurred at densities of one or two specimens per metre^2. In the regions of high species richness (Stations 5 and 20), the numerical abundance appeared to be controlled by a single dominant species, C. caputesocis, and in the region of low species richness (Stations 2 and 9) by C. capitata. Similar situations were found in the offshore mud of Northumberland coast (Buchanan et al,1974), where variations in the population density of Ammotrypane aulogaster and Abra nitida played a crucial role in the numerical abundance and production of the community as a whole. An interesting aspect of the present study concerns the relative abundance of C. caputesocis and C. capitata when both occurred in the same sample. C. caputesocis occurred in high numbers and C. capitata in low numbers in the region of high species diversity but C. capitata occurring in high numbers and C. caputesocis in low numbers in the region of low species diversity. This probably suggests that C. caputesocis can withstand competition while C. capitata cannot.

Though the feeding biology of the two species was not investigated in the present study, there is little evidence to suggest competition for food as responsible for the low numbers of either of the polychaetes when they occurred together. C. capitata has been suggested to be a poor competitor (Hartman,1961; Barnard,1970; Leppakoski,1969) achieving large population sizes when the population of other species are reduced. Other workers (Reish and Winter,1954; Wass,1967) ranked C. capitata first among other species as indicators of organic pollution, based on the abundance and presence in the most polluted stations of Alamitos Bay in Southern California. Rosenberg (1972) found that C. capitata was the pioneering species that settled in the formerly azoic areas following the closure of a pulp mill in a Swedish fjord. An interesting study by Grassle and Grassle (1974) suggested that the worm is opportunistic, withstanding low oxygen and a variety of conditions toxic to other spionids and capitellids. The degree of opportunism exhibited by C. caputesocis and C. capitata is demonstrated by their relative abundance at the stations on the western side with high pollution load. It is reasonable to assume that the presence or absence of important species such as C. caputesocis and C. capitata could influence the rest of the community.

In biologically accommodated community, increase in the number of individuals has been suggested as compensatory adjustments to the trophic energy released by the failure of one important producer and the abundance of multispecies population determined to some extent by interspecific interactions (Buchanan et al,1974). In the physically controlled community as in the present study, some macrofaunal species such as N. diversicolor, P. ciliata and C. capitata, together described by Grassle and Grassle (1974) as 'opportunistic', co-occurred. It is remarkable that these species occurred in high numbers only on the western side of the study area where high amounts of organic matter, sediment copper and hydrocarbons were present. N. diversicolor occurred in high densities ($1029m^{-2}$) on the western side. The high density may be attributed to the polychaete's tolerance to high levels of trace metals (Bryan and Hammerstone 1971, 1973) which at station 9 reached 848 ppm for copper and 173 ppm for zinc.

The densities of N. diversicolor in the present study conformed to those recorded in the Tees estuary (Gray,1976) but were higher than those in Chalkwell (Dales,1951) and lower than those in the Danish estuaries (Muus,1967); the Severn estuary (Boyden and Little,1973), the Medway (Wharfe,1977) and the Zwin saltmarsh (Govaere,1969). Herpin and Herman (1979) suggested that population dynamics of N. diversicolor showed local characteristics. The difference in the abundance of Nereis in various localities, for example, Chalkwell ($55m^{-2}$) and Southampton Water ($10 - 1029m^{-2}$) is probably attributable to food availability which consequently affects the reproductive capability of the species. A variety of methods employed in sampling and sorting of the animal could possibly affect the numbers recovered. For example, Dale's handpicking method could have resulted in the juveniles being lost. Such small animals were possibly retained by 0.5mm screen used in the present study.

Nereis populations in Southampton Water contained large numbers of juveniles throughout the year. It is not certain whether the presence of the juveniles in samples throughout the year is due to a constant low reproduction or to delayed development. The main variation in the density of the worm at all four stations was apparently due to the abundance of the juveniles since the adult individuals comprised a more stable population.

N. hombergi and M. palmata often occurred together in the present study with the density of the former decreasing as that of the latter increased. The co-occurrence of the two polychaetes may not necessarily be due to competition for food, as they differ in their feeding habits. Melinna is a sedentary deposit feeder and Nephtys a selective omnivore.

The crustaceans ranked next to polychaetes in the present study with regard to species numbers, showing a decline in species richness at all stations. There was a decrease in the number of species during the winter months with an increase in summer due to an increased recruitment with increase in water temperature. The greater number of species and increased abundance of the group in sandier sediments may be attributed to the higher sedimentation rate on the western side and possibly their low tolerance to industrial wastes. The sediment at Station 5 possibly provided a better spatial heterogeneity and higher currents that aid in their feeding. The amphipods dominated but no single crustacean species was numerically dominant throughout the study. Five amphipods, P. typicus, M. gryllotalpa A. gracilis, C. insidiosum and A. falcatus, occurred in high numbers. Also occurring in significant numbers were P. globosus, the only ostracod found during the study and the cumacean, E. truncatula.

The molluscan population was dominated by bivalves, M. mercenaria, V. pullastra and A. nitida. All were largely restricted to the eastern side and the mouth of the estuary except for occasional occurrence of the latter on the western side. Barnes et al (1973) designated the benthic community at the mouth of Southampton Water as A. nitida/N. hombergi association and that of River Meon at Titchfield Haven as A. Nitida/ C. fornicata association.

The nature of the substratum appeared to influence the distribution of gastropods during the study. N. reticulatus and C. fornicata were recorded in Stations 5 and 20 where gravel and sand were present. C. fornicata was absent in these stations where suitable substrates, such as broken bottles and pebbles, on which it lives, were absent.

The few pycnogonids so far recorded in Southampton Water (2 species in the present study) and six species recorded by Levell (1979) appeared to be restricted to the eastern side of Southampton Water.

Several methods of estimating benthic faunal diversity were employed in the present study, allowing comparisons between the four stations. The results obtained using Margalef's (1957) index are largely influenced by species richness and showed a similar trend to the number of species. Higher values were obtained at stations 5 and 20.

The Shannon-Wiener information function (Hs) used in the present study has the advantage of combining species richness and equitability. Higher species diversity occurred at Stations 5 and 20 which showed low equitability, thus indicating high dominance of a few species in these communities. Low species diversities but high equitability (low dominance) occurred at Stations 2 and 9 throughout the study except during peak recruitment period of C. capitata at Station 9.

Sander's rarefaction method was employed since it allows comparisons between different habitats or samples and predictions of species diversity at different individual levels. This technique, though valid when similar groups of organisms collected with the same gear and processed by the same method are compared, is applicable in the present study, since all samples were collected and treated in exactly the same way. The method is sample size independent and allows comparisons between communities of different environments.

The low degree of species similarity obtained at Stations 5 and 9 and the high values between Stations 2 and 9, using Jaccard's coefficient showed that high diversity on the eastern side of the estuary may be due to the heterogeneity of the sediment on the eastern side providing greater niches to many benthic species.

The communities of the study area appear to be physically controlled with greater stress at Stations 2 and 9 around Cadland creek. At these stations, the species diversity gradually diminishes towards a minimum but reach a higher level at Stations 5 and 20 where smaller stress was evident.

Recent work on benthic communities suggests that species from clean and deep marine benthic environments are distributed normally between geometric classes and give a straight line lognormal distribution when plotted on probability paper (Bliss,1966; May,1975; Gray,1979). Gray (1979) showed that changes in community structure were correlated with environmental disturbances notably pollution, which resulted in the increase in the 'middle order' species (i.e. those in geometric classes V - VII). The present study, as yet the only available data for a low diversity estuarine situation, showed better straight line relationships for communities at Stations 5 and 20, possibly with lower pollution loads. Stations 2 and 9, situated near the industrial outfalls, showed less well marked relationships. All the four stations showed a progressive fall in diversity between the start and end of study, implying a gradual change in the structure of the community in response to increased environmental disturbance or stress. If the straight line relationship between cumulative percentage species and the geometric classes as proposed by Gray (1979) is well defined, estuaries such as Southampton Water which contain physically controlled communities in a permanently stressed state might not be expected to give as good a straight line relationship as found in more biologically accommodated communities.

In biologically accommodated communities such as the Puget Sound (Lie and Evans, 1973) and off the coast of Northumberland (Buchanan et al, 1974), the faunal communities may show considerable stability. Comparisons of the communities of such areas with the present study could be invalid due to differences in the types of communities.

In conclusion, it is often difficult to assess the effects of human populations on the benthic communities of estuaries such as Southampton Water, which are heavily exploited for commercial, industrial, domestic and recreational purposes. Continuous dredging of Southampton Water, allowing easy passage of ships and ferries, alters the bottom topography and the sediments of the estuary. One is often limited to the consideration of only gross alteration when monitoring the effects of pollution on biotic populations. Nevertheless, analysis of the community structure provides a basis for a long-term study of natural changes in the community. In such situations, diversity indices may provide information on the perturbed systems. Though an account of man-induced alteration of the community structure may be documented, the implication of such alteration with respect to economies both of the ecosystem and of man remains less convincing.

SECTION FOUR

LIFE CYCLE OF BENTHIC MACROFAUNA

4.1 Introduction

Of paramount importance in the study of ecology and production of the benthic macrofauna of an aquatic environment is a knowledge of the timing of reproduction and larval settlement and subsequent growth. Previous studies on the reproductive biology of the macrofauna of Southampton Water have largely been directed towards single species populations: Cirriformia (Audouinia) tentaculata (George, 1962) and Mercenaria mercenaria (Mitchell, 1974). Few multispecies studies have hitherto been carried out. Esser (1972) investigated the polychaete distribution in Southampton Water and Hibbert (1976) studied the bivalve populations of the Hamble Spit. No study on the reproductive biology of the sublittoral macrofauna of Southampton Water has so far been made.

Though polychaetes occur in high numbers in Southampton Water, their reproductive biology has suffered considerable neglect. Any descriptive work on the biology of polychaetes is of particular interest because the group forms a substantial part of most bottom assemblages (Curtis, 1977). In Southampton Water, the polychaetes, crustaceans and molluscs dominate most benthic communities and they are likely to be utilized as food by fish and other demersal predators. It seems important, therefore, to examine the dynamic processes involved in the maintenance of their populations in the marine-estuarine ecosystems. In pursuance of this, attention should be focused on the sensitive stages within the life cycle of the animals, the period of breeding and larval development. As Thorson (1950) suggested, the conditions of breeding and larval development constitute a very essential point for all studies of reproduction and fundamental ecology of marine bottom invertebrates.

The life cycle of some common benthic polychaetes around the British Isles is well documented (Dales, 1950; 1951a; 1951b; Dorsett, 1961; Bradfield and Chapman, 1967; Olive, 1977; 1978; Hutchings, 1974). Those of Southampton Water have received little attention. George (1962) found that the littoral Cirriformia tentaculata population at Hamble Spit lacked a truly pelagic trocophore, whereas the same species at Plymouth (Wilson, 1936) produced typically pelagic larvae. Although most of the benthic macrofaunal species in Southampton Water have had their life-cycle studied elsewhere, benthic species vary considerably in their time of spawning and larval development from one locality to another, depending on ecological conditions. Thorson (1950) stated that polychaetes 'show an astonishing lability' in their mode of development, and cited Nereis zonata as having non-pelagic larvae in the inner fjords of East Greenland and pelagic development on the open coast. Other species of both pelagic and non-pelagic larval types include N. pelagica (Herpin, 1925); Arenicola claparedii (Guberlet, 1934), Pygiospio elegans (Thorson, 1946) and Capitella capitata (Grassle and Grassle, 1974).

The present study affords a comparison of life cycles of species occurring in this study to those already reported elsewhere by several workers.

Initially, an attempt was made to study the life cycle of all species present in the study area. The study was eventually restricted to those species that were numerically abundant, allowing information on the breeding seasons, reproductive modes and age at maturity to be assessed. No detailed histological study of the gonads of any particular species was made but ovaries of species were examined and where possible, the diameter of the oocytes measured. The time of appearance of juveniles in the 0.5mm sieve was noted for each species.

The study was based upon materials from the time series collections taken between July 1978 and March 1980 at the four selected stations, and treated as described in Section II.

The maximum width of either the collar, or the first or third segment behind the head, in case of polychaetes or the entire length of crustaceans and the anteroposterior length of molluscs in each sample was measured. The animals were separated into size groups and the size frequency histograms drawn for each sample. Each group was dissected and the diameter of oocytes when present measured to the nearest micrometre. Observations made on individual species are presented separately with a general discussion of life cycles at the end of the present section.

4.2. Polychaetes

Melinna palmata

Melinna palmata occurred mainly on the eastern side of the study area at a maximum density of $240m^{-2}$. The biology of the related species M. cristata has been studied (Nyholm, 1951; Hutchings, 1973; 1974) but little is known about M. palmata. Nyholm (1951) found that M. cristata population in Gulmar fjord spawned throughout the year with a peak in January, and suggested that spawning continued for some time after the main peak as mature gametocytes were found after January. Hutchings

(1974) observed a more well-defined spawning period in the population of M. cristata off the coast of Northumberland, with the population spawning between the end of December and the beginning of January, in a short period lasting only 2 to 3 weeks.

Synchronized spawning which ensures a high degree of successful fertilization in dioecious polychaetes has been reported as common in those species which shed their gametocytes into the water. Buchanan (1963) suggested mass spawning as effective if a population is highly aggregated as in sedentary species such as Arenicola marina and M. cristata.

In the present study, in July 1978, three distinct age groups were observed in the population of M. palmata at Station 5 (Fig. 41.) The individuals belonging to the largest sized group were the breeding stock in 1978. Members of the group contained mature oocytes which measured between 180 and 240 µm in diameter. The group was designated Cohort 'II', spawned and disappeared from samples by January 1979.

The medium size group in July 1978 was designated Cohort 'I' as members contained immature oocytes which measured between 60 and 80 µm in diameter between July 1978 and May 1979. Members of the cohort spawned in July 1979 and thereafter declined in abundance, disappearing from samples by September 1979.

The smallest sized individuals in July 1978 and designated '0' cohort lacked obvious gametocytes in their coelom until May 1979. The oocytes matured in late autumn and the cohort spawned in January 1980. The decline in the abundance of the cohort after spawning possibly resulted from post-spawning mortality. The sieve recruitment of juveniles which began in May 1979 was in progress when sampling ceased in March 1980.

The Southampton Water population of M. palmata appeared to have an extended breeding period with peaks in July and December and juvenile recruitment into the sieve occurring throughout the year. The population in Southampton Water seemed to breed only in their third year with post-spawning mortality. Growth occurred mainly in the first year and gonad development with gametocyte maturation in the second year. No resorption of unshed oocytes was observed suggesting that all gametocytes were released and that the population bred only once and died.

Nereis diversicolor

This common brackish water species is often of great importance in estuarine food webs. As a predator of benthic organisms and a scavenger

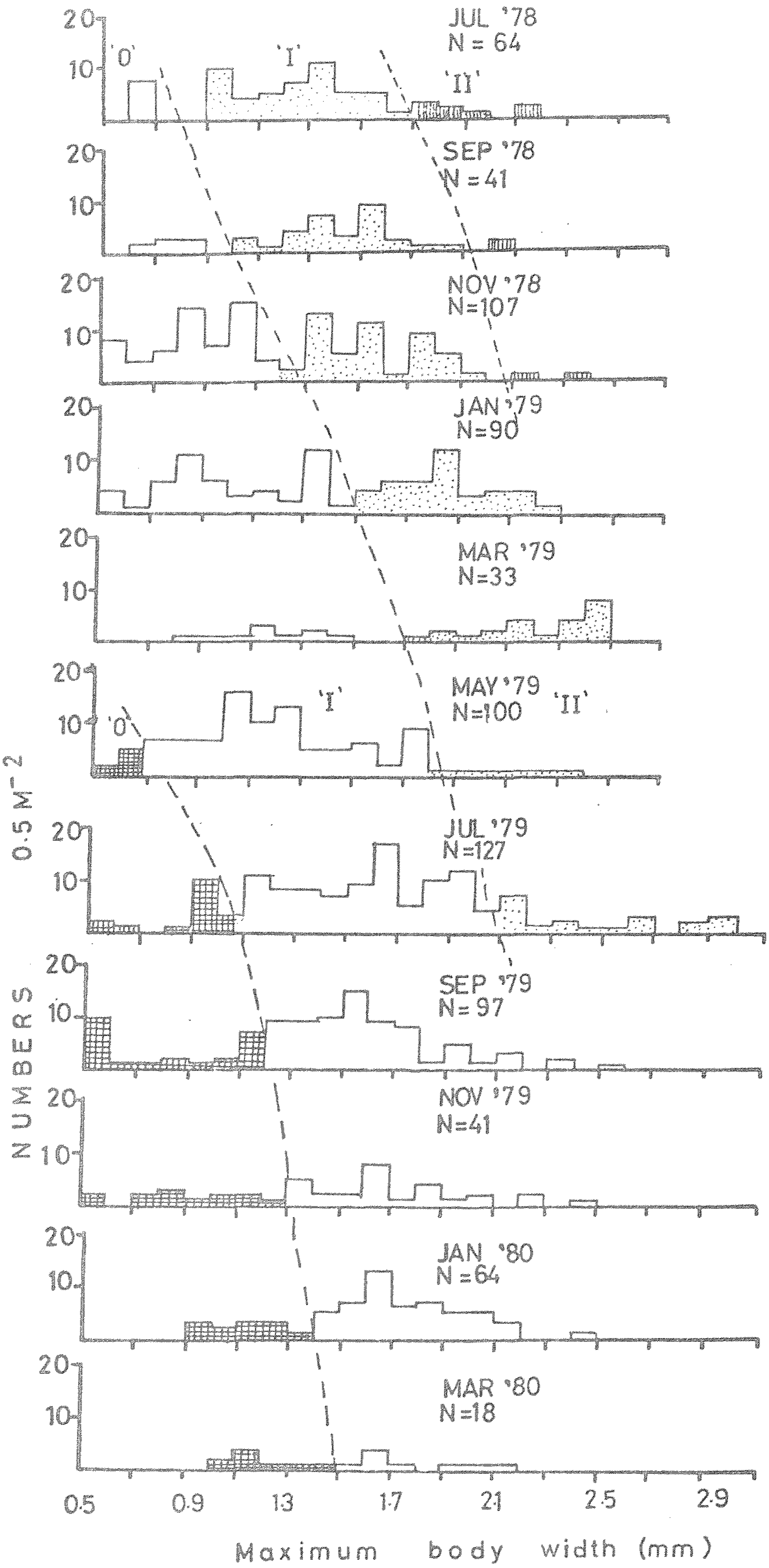


FIG.4.1. STATION 5 MELINNA PALMATA SIZE FREQUENCY HISTOGRAMS

as well as food to both fishes and birds, N. diversicolor has increased the interests of scientists in estuarine processes and the polychaete in particular. Substantial literature exists on the biology of this worm (Dales, 1950; 1951; Bryan and Hummerstone, 1971; 1973; Clark and Olive, 1973; Chambers and Milne, 1975; Heip and Herman, 1979).

Dales found that Essex populations of N. diversicolor spawned within a two week period towards the end of February, when there was a marked rise in temperature, the eggs being released by rupture of the body wall. The increase in temperature was suggested as a major factor influencing spawning. He found that the oocytes in the females which failed to spawn gradually disintegrated into a white milky mass in the coelom, two months after the main spawning period. Heip and Herman (1979) reported the presence of juveniles throughout the year in a Dievengart (Belgium) population of N. diversicolor and suggested that breeding occurred in the worm throughout the year. In the Ythan estuary Chambers and Milne (1975) found that N. diversicolor population of the estuary spawned between January and March and also in the summer months, and suggested that the growth rates of the polychaetes could vary from year to year. The results of the previous studies were used as a comparison to the present study.

N. diversicolor occurred in high numbers on the western side of the present study area, with a maximum density of $1,029 m^{-2}$ and at lower density (less than $100 m^{-2}$) on the eastern side. The size frequency histograms of the worm at the selected stations are shown in Figs. 4.2, 4.3, 4.4. Because N. diversicolor showed scant occurrence at Stations 5 and 20, the life cycle of the worm in the present study was based on the populations at Stations 2 and 9.

At station 2 in July 1978, no specimens of N. diversicolor were present, but three cohorts, differing in their degree of sexual maturity were present in September 1978, probably migrating into the area from nearby. The largest sized cohort designated cohort 'II' was comprised of a few spent individuals with large yolky oocytes that were gradually being resorbed. This cohort declined in abundance, disappearing from samples by winter (December - January). The medium sized group in September 1978 designated cohort 'I' comprised individuals with maturing oocytes which measured between 120 and 140 μm in diameter. The oocytes were fully mature by November 1978, measuring between 180 and 200 μm in diameter and spawning occurred in December 1978. The cohort suffered post-spawning mortality in January 1979 and disappeared from samples by March 1979. Juveniles were recruited into the sieve in September 1978

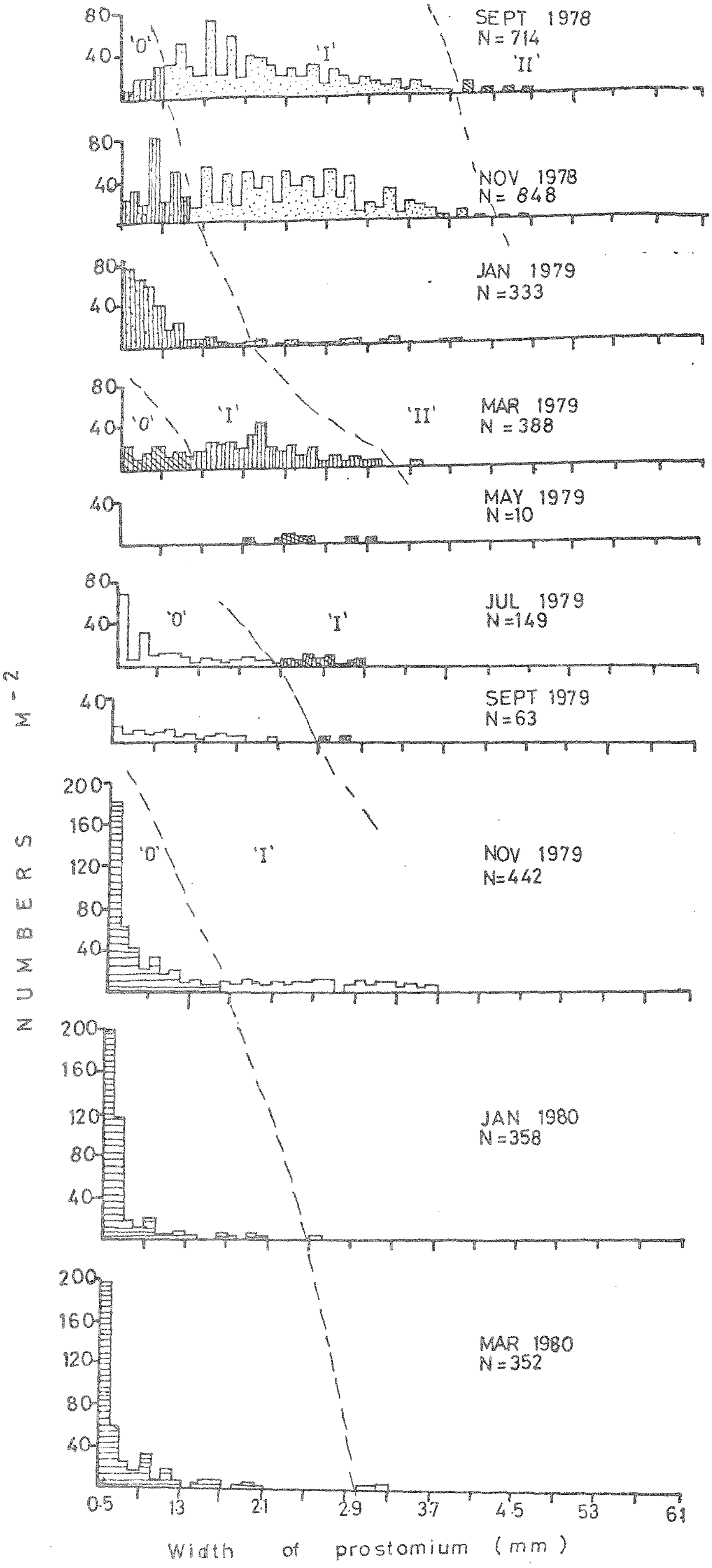


FIG.4.2. STATION 2 NEREIS DIVERSICOLOR SIZE FREQUENCY HISTOGRAMS

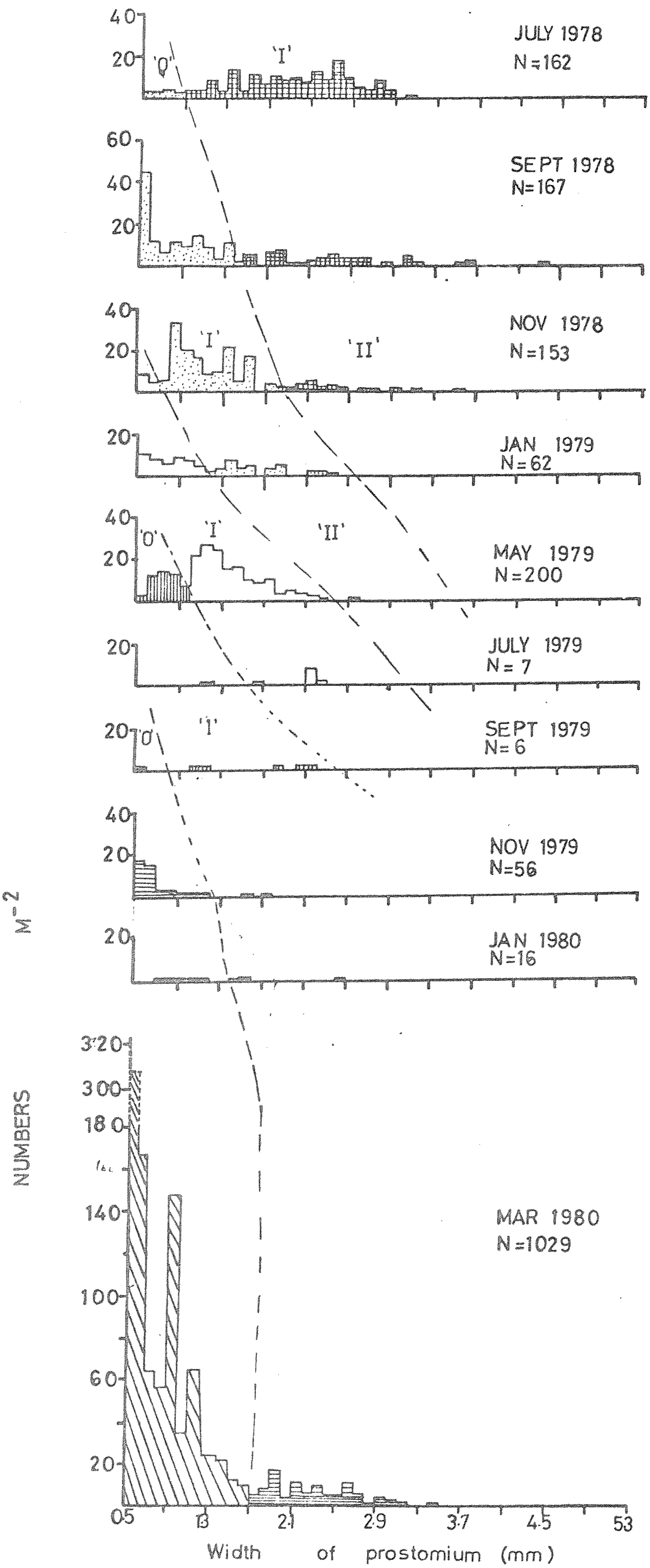


FIG.4.3. STATION 9 NEREIS DIVERSICOLOR SIZE FREQUENCY HISTOGRAMS

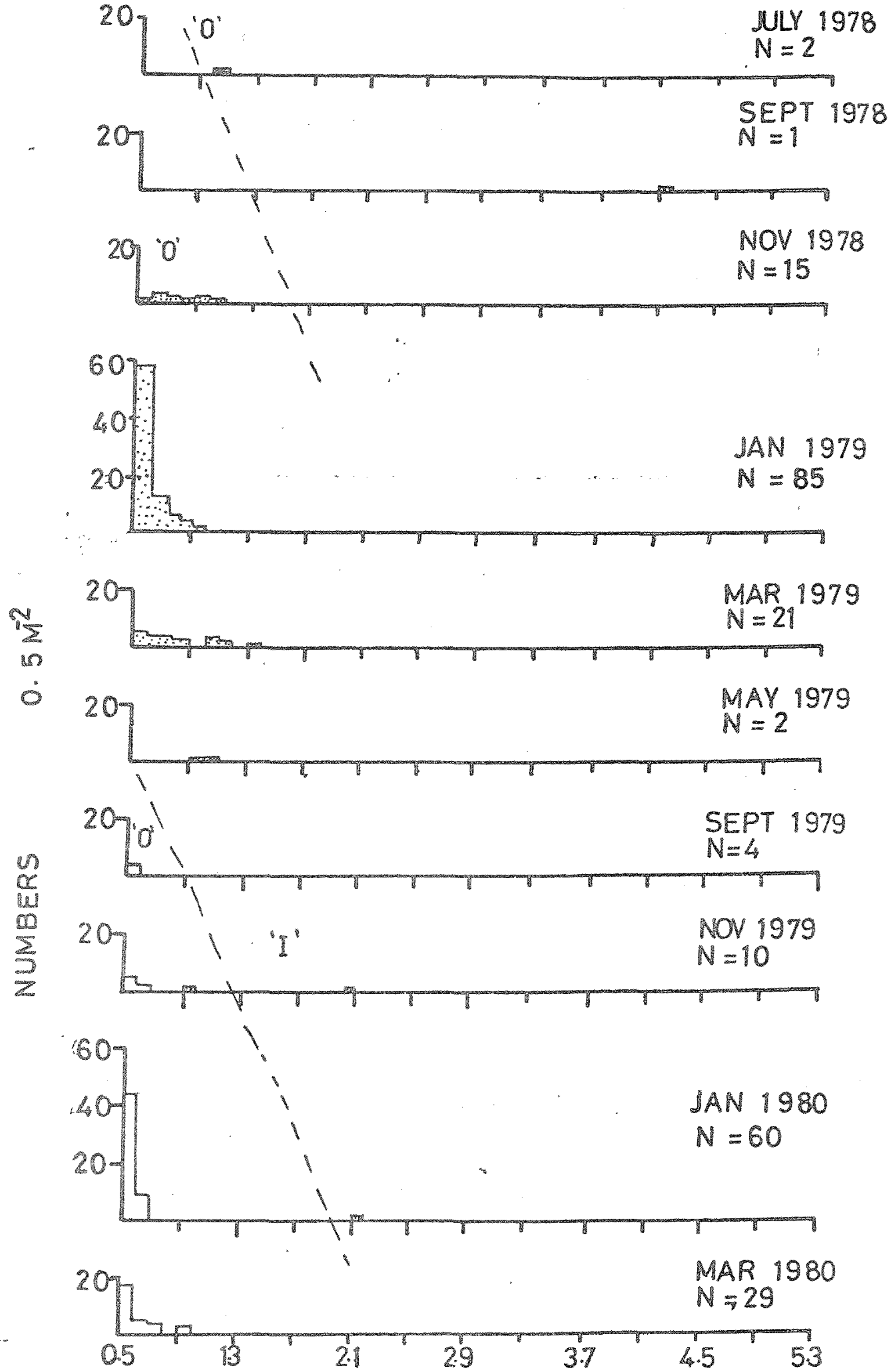


FIG. 4.4. STATION 20 NEREIS DIVERSICOLOR SIZE FREQUENCY HISTOGRAMS

and lacked distinct oocytes in their coelom until November 1978 when further recruitment took place.

The small sized individuals were designated cohort '0' and by January 1979, oocytes measuring between 40 and 80 μm in diameter appeared in their coelom. The cohort contained mature oocytes by March and spawned in April 1979. The cohort suffered post-spawning mortality with no specimens of the cohort present in May 1979.

Recruitment into the sieve commenced in March 1979 and growth of the newly recruited cohort was rapid between March and May1979, spawning at the end of July 1979. The cohort disappeared from samples by November 1979. Another recruitment into the sieve occurred in July 1979 and spawned in December 1979. A new recruitment in November 1979 grew slowly during winter and failed to reach sexual maturity when sampling ceased in March 1980.

At station 9, two cohorts were distinct in July 1978 samples. The bigger sized group designated cohort 'I', comprised individuals with immature oocytes which measured between 60 and 80 μm in diameter. The cohort spawned in October 1978 and declined in abundance afterwards and disappeared from samples by November 1979. The smaller sized group in July 1979, designated cohort '0', comprised juveniles which lacked obvious oocytes in their coelom between July and September 1978. Maturation of oocytes in the cohort occurred in autumn and spawning took place between late December 1978 and early January 1979. Only a few spent individuals resorbing their unspawned oocytes were present in the January 1979 sample. Recruitment ofjuveniles into the sieve occurred between November 1978 and January 1979 but no specimens of _N. diversicolor_ were present in March 1979. This absence may be due to the mass emigration of the population from the station due to predation and/or environmental disturbance.

Two cohorts 'I' and '0', based on sexual maturation, were massively recruited into the station in May 1979. Members of cohort 'I' had mature oocytes, measuring about 200 μm in diameter, and spawned in late June. A few specimens of the cohort, possibly resorbing their unshed oocytes, were present in the July 1979 samples and these disappeared from samples by September 1979. The '0' cohort in May 1979 declined in abundance without reaching sexual maturity before sampling ceased in March 1980.

A recruitment into the sieve in September 1979 comprised individuals containing only immature oocytes, around 60 μm in diameter when sampling ceased in March 1980. Massive recruitment of juveniles into the sieve occurred in March 1980.

The Southampton Water population of N. diversicolor showed low but constant breeding throughout the year. The individual specimens spawned when about a year old or less with the oocytes measuring around 200 µm in diameter. Most spent and unspent mature individuals suffered post-spawning mortality with the unspawned oocytes being gradually re-sorbed.

Nephtys hombergi

Several studies on the family Nephtyidae have shown the group to be potentially long lived species whose individuals can be aged with some degree of accuracy from the structure and annual growth lines on their teeth (jaws) (Kirkegaard,1978; Olive,1970; Buchanan and Warwick,1974; Retiere,1976; Warwick and Price,1980; Warwick and George,1980. Retiere (1976) stated that the family showed descrete iteroparous reproduction with members of a number of different year classes in a population of Nephtys hombergi having similar sized oocytes and the individuals becoming mature and breeding simultaneously. Olive (1978) described such animals as capable of producing a single large cohort of gametocytes which are usually released together all at once in a year.

In Southampton Water, populations of N. hombergi have been found in association with Abra nitida (Barnes,1973) but the lifecycle has been hitherto neglected. The results of the previous studies could serve as a comparison to the present study.

N. hombergi occurred in high numbers on the eastern side and towards the mouth of Southampton Water but in low numbers on the western side. The size frequency histograms of the species at the selected stations are presented in Figs. 4.5, 4.6, and 4.7. Since Stations 5 and 20 had higher densities of the worm, the populations at these stations were used in the life-cycle studies.

At Station 5 in July 1978, two cohorts, based on their sexual maturity were present. The larger sized group, comprising only 3% of the total numbers, was designated cohort 'I' and contained a few mature oocytes with a diameter of around 160 µm in their coelom. The group probably represented the spent individuals resorbing their unspawned oocytes. The cohort continued its appearance in samples until November 1979 when it was absent. The smaller sized group in July 1978, designated cohort 'O' contained few oocytes which measured between 40 and 60 µm in diameter. Maturation of the oocytes in this cohort was rapid in autumn and the

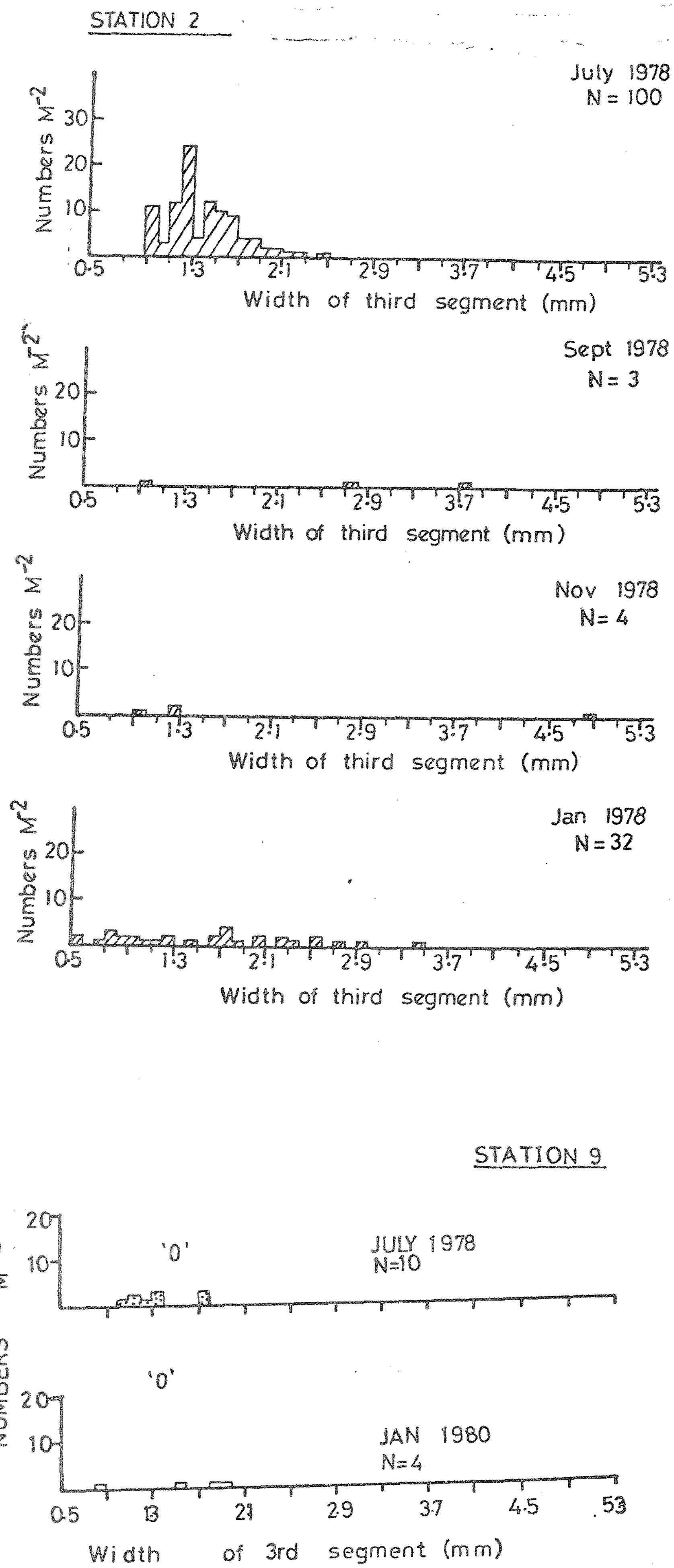


FIG.4.5. STATIONS 2& 9 NEPHTYS HOMBERGII
SIZE FREQUENCY HISTOGRAMS

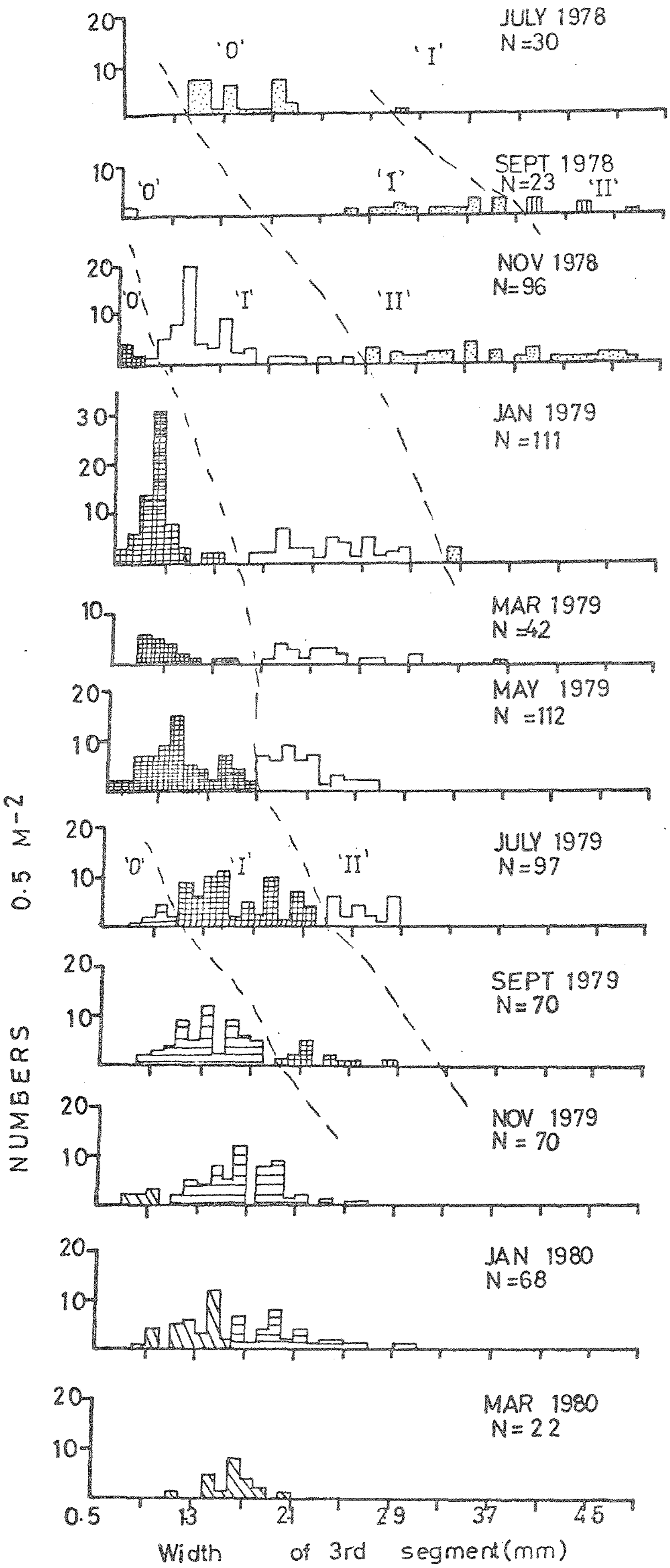


FIG.4.6. STATION 5 NEPHTYS HOMBERGII
SIZE FREQUENCY HISTOGRAMS

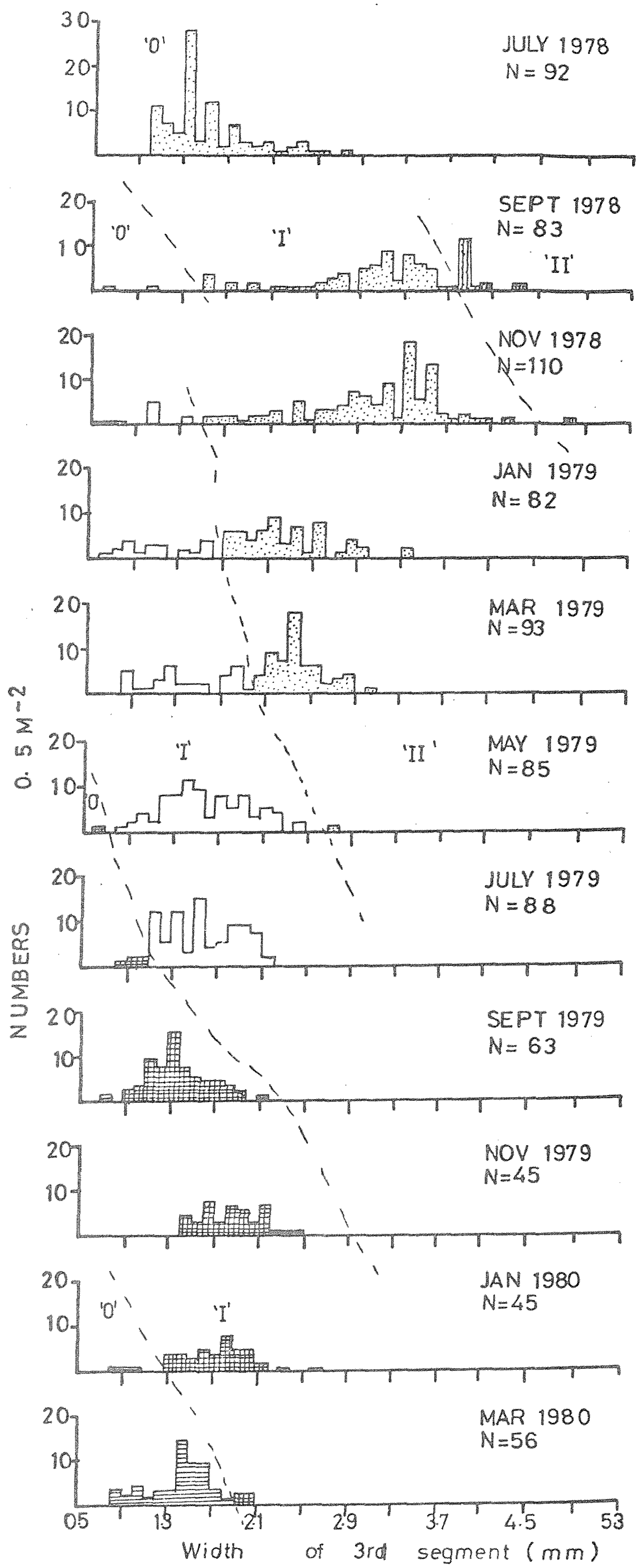


FIG .4.7. STATION 20 NEPHTYS HOMBERGII
SIZE FREQUENCY HISTOGRAMS

cohort spawned in November 1978, followed by a post-spawning mortality. The cohort disappeared from samples by May 1979.

The recruitment into the sieve in September 1978 which continued to November 1978 comprised individuals which lacked obvious oocytes between September and December 1978. Immature oocytes measuring 40-60 µm in diameter were distinct in the January 1979 samples and these matured in spring with the cohort spawning in July 1979. Following a post-spawning mortality, the cohort disappeared from samples by September 1979.

Another recruitment into the sieve in November 1978 comprised a cohort which suffered heavy mortality in 1978/79 winter but the successfully overwintered individuals developed immature oocytes (40-60 µm in diameter) in spring 1979. The cohort matured its oocytes in summer and spawned in August 1979 and disappeared from samples by November 1979. A new recruitment into the sieve between May and September 1979 matured in 1979/80 winter and spawned in January 1980 after which they suffered a post-spawning mortality. Those juveniles which recruited in November 1979 contained no obvious oocytes when sampling ceased in March 1980.

At station 20 in July 1978, a single cohort consisting of individuals with immature oocytes which measured 40-60 µm in their coelom was present. In September 1978, three cohorts distinguished by their degree of sexual maturity were present and these were designated cohorts 'O', 'I' and 'II'. The 'II' cohort in September 1978 consisted of large, mature and ready to spawn individuals containing oocytes measuring around 200 µm in diameter; spawning in this cohort took place in October 1978 followed by post-spawning mortality. The cohort disappeared from samples by January 1979. The cohort 'I' in September 1978 consisted of individuals which spawned in December 1978 and suffered heavy mortality in the 1978/79 winter. The successfully overwintered individuals of the cohort disappeared from samples by July 1979.

Juveniles recruited into the sieve between September 1978 and July 1979 with a maximum recruitment in May 1979 spawned in July 1979 when their oocytes measured greater than 200 µm in diameter. The cohort suffered a post-spawning mortality and disappeared from samples by September 1979. A newjuvenile recruitment between July 1979 and March 1980 with a peak in September 1979 spawned in January 1980. The recruitment of juveniles into the sieve which started in January 1980 was still in progress when sampling ceased in March 1980.

Capitella capitata

C. capitata has been reported present in a variety of habitats; clumps of detached algae (Muus,1967); basins following a period of oxygen depletion (Leppakoski,1969); estuaries of high mixing and heavy sedimentation (Wolff,1973); harbours and sewage outfalls (Reish,1956, 1959), and sediments contaminated by oil (Reish,1965; Sanders et al, 1972). The worm has been ranked as an indicator of organic pollution (Waas,1967) and unpredictable environments in shallow waters all over the world in both high and low latitudes (Schulz,1969; Wolff,1973).

Grassle and Grassle (1974) showed that the polychaete has the ability of producing both benthic and planktonic larvae which can either settle on the bottom immediately or delay metamorphosis, allowing widespread dispersal. The authors in a later paper in 1977 described *C. capitata* as a 'metaspecies' comprised of a short-lived subspecies with a life-span less than six weeks; 'intermediate' subspecies with a life-span between three and six months and an annual subspecies living up to a year. The complexity in the life cycle of *C. capitata* indicated that the species breeds throughout the year, requiring a relatively short period of maturation, dependent on the degree of stress in the environment. Blackstock et al (1979) described *C. capitata* as an 'opportunistic' polychaete occurring widely in low numbers in a variety of benthic infaunal habitats subject to periodic influxes of organic material. The authors stated that during such periods, the worm is capable of explosive population growth, often becoming predominant under high input levels, to the exclusion of nearly all other species.

In the present study, *C. Capitata* occurred at high densities (300-25236m^{-2}) on the western side but infrequently on the eastern side of the study area. Three juveniles of the worm were present in July 1978 at Station 5 and less than five specimens at Station 20. The life-cycle study of the polychaete was based on the populations at Stations 2 and 9. The size frequency histograms of *C. capitata* at these stations are shown in Figs. 4.8 and 4.9.

At Station 2 no specimens of *C. capitata* were present in the July 1978 samples, but one cohort was distinct at the station between September 1978 and January 1979. This cohort comprised individuals with mature oocytes which measured 140-180 μm in diameter and spawned in October 1978. The individuals in the November 1978 samples contained no oocytes indicating a complete spawning with all potential breeders spawning. Only two specimens of *C. capitata* were present in the January 1979 samples at the

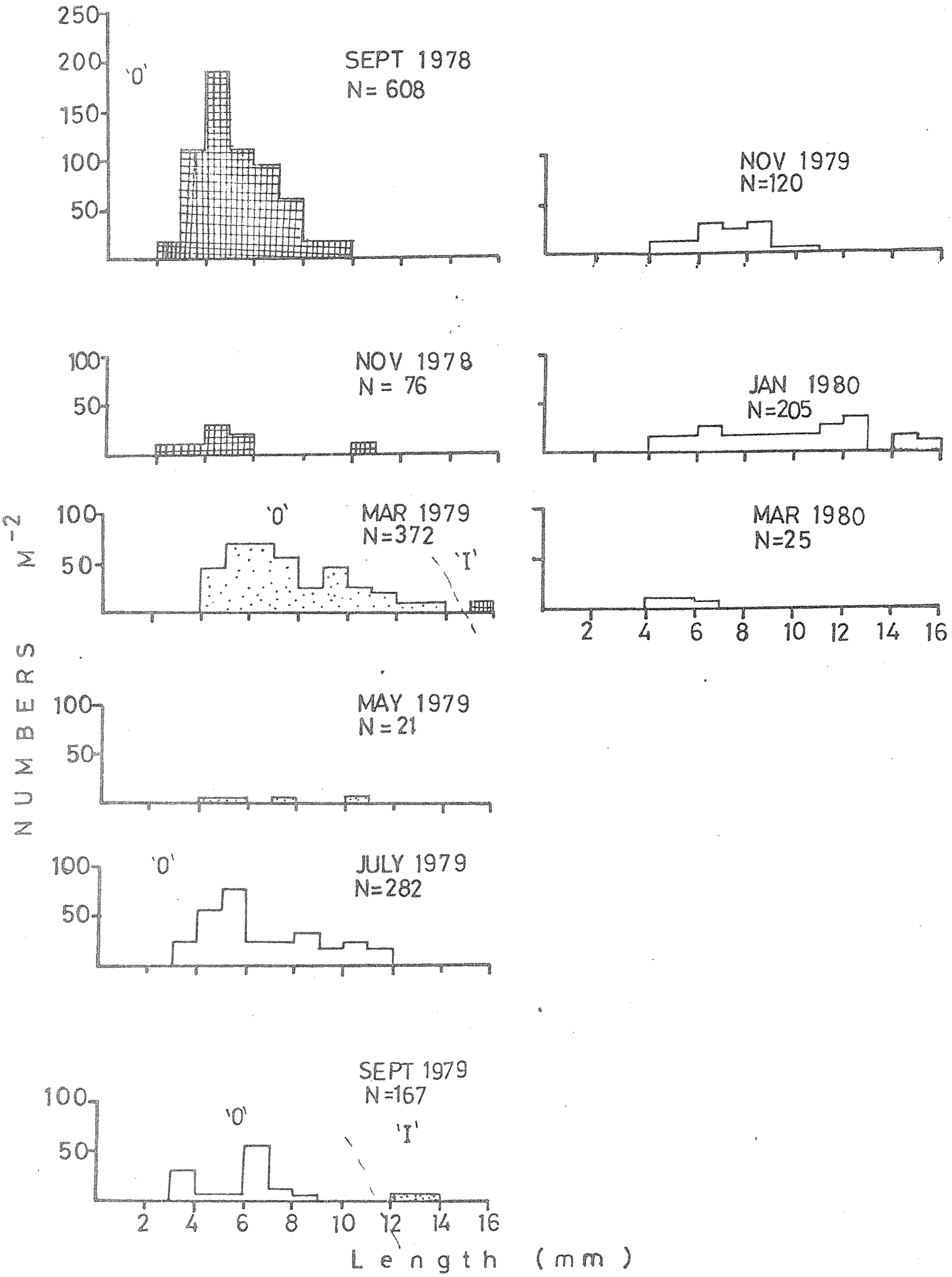


FIG.4.8. STATION 2 CAPITELLA CAPITATA SIZE FREQUENCY HISTOGRAMS

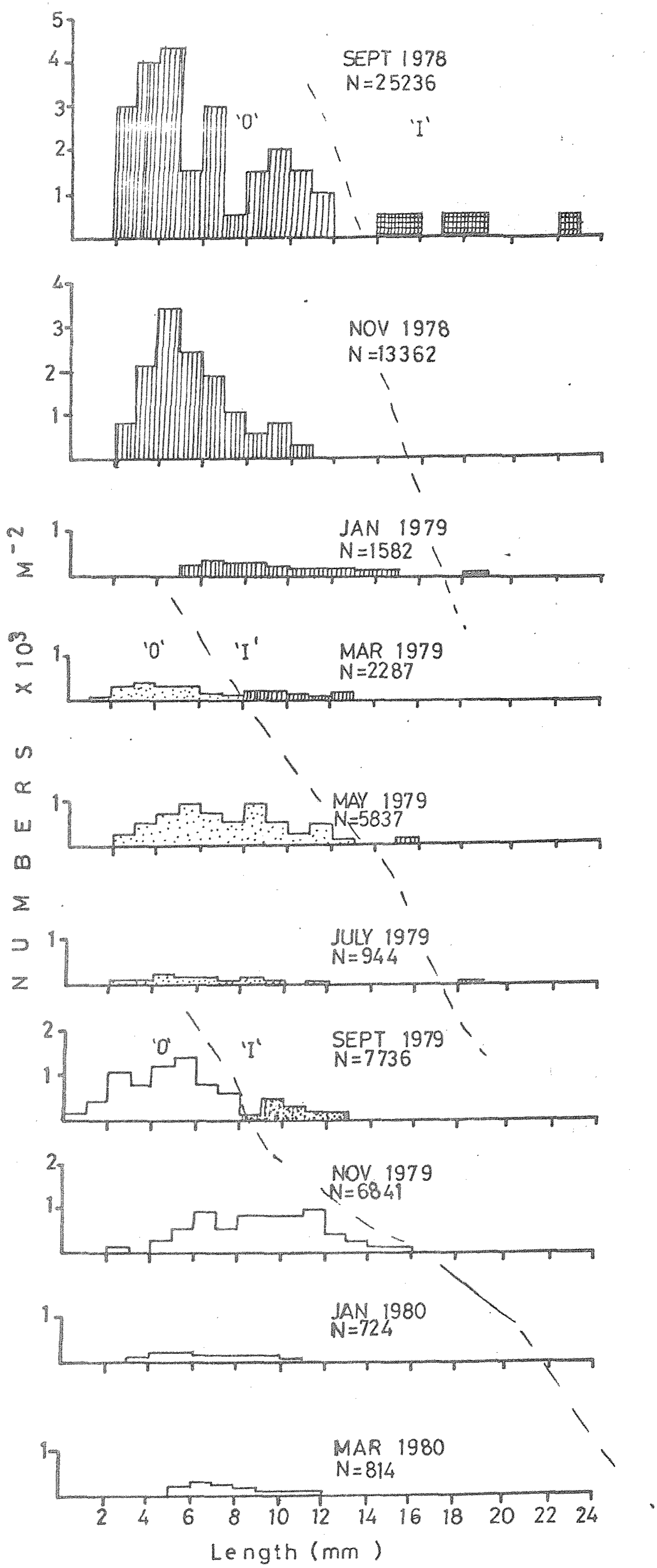


FIG.4.9. STATION 9 CAPITELLA CAPITATA SIZE FREQUENCY HISTOGRAMS

station.

Recruitment into the sieve occurred in March 1979 and the new cohort grew and matured its oocytes rapidly in spring with the oocytes attaining a size of 240 μm in diameter by May 1979. These oocytes were brooded in the tubes of adult specimens where they were shed in May 1979. Such large oocytes probably gave rise to benthic larvae, capable of direct and demersal development with rapid settlement. The cohort suffered heavy post-spawning mortality. The new recruitment appeared in the sieve by July 1979, and grew gradually with obvious oocytes appearing by November 1979. The oocytes at this stage were immature, measuring less than 60 μm in diameter. Maturation of the oocytes occurred in 1979/80 winter and the cohort spawned in February 1980. Only few individuals of the cohort, with no oocytes in their coelom were present in the March 1980 samples.

At station 9 there were few specimens of C. capitata present in July 1978, but in September 1978 two cohorts, distinguished by size and the level of sexual maturity, were present. The larger sized group, designated cohort 'I' lacked oocytes in their coelom. This cohort probably represents the spent individuals that spawned earlier and migrated to the area. The cohort did not appear in the November 1978 samples but reappeared at low abundance in January 1979 after which it disappeared from samples. The smaller size group in September 1978 and designated cohort '0' comprised individuals with mature oocytes (160-180 μm in diameter). The cohort spawned in winter of 1978/79, followed by a post-spawning mortality and disappeared from samples by September 1979.

Juveniles recruited into the sieve between March and July 1979 grew rapidly in summer and brooded their large oocytes, measuring more than 240 μm in diameter in their tubes in July 1979. The cohort suffered post-spawning mortality and disappeared from samples by November 1979.

A new recruitment of juveniles into the sieve in September 1979 spawned in the 1979/80 winter months. The overwintered specimens of the cohort lacked obvious oocytes in their coelom when sampling ceased in March 1980.

Caulleriella caputesocis

The biology of the family Cirratulidae, comprising truly sedentary polychaetes with a world wide distribution, has gained much attention. Around the British Isles the cirratulids frequent sandy mud, although some species e.g. *Dodecaceria* bore into limestone. (Dales,1950) studied the reproduction and early development of *Tharyx marioni* (St. Joseph) at Essex, and found that the population showed a sharply defined spawning period (16-18 April). George (1962) found that the population of *Cirriformia tentaculata* at Hamble Spit had a prolonged breeding season, extending throughout the summer months; though Wilson (1936) reported ripe individuals of the worm at Plymouth only between June and July. Olive (1970) found that the population of *Cirratulus cirratus* off the coast of Northumberland lacked a distinct breeding season. He found that each female bred several times at intervals probably in excess of one year with small numbers of ripe and spent females throughout the year.

Caulleriella caputesocis, first described by St. Joseph (1864) under the name *Heterocirrus* was first reported in Southampton Water by Soulsby (1978) and Levell (1979) suggested that the worm appeared as the dominant polychaete in the estuary.

In the present study, *C. caputesocis* had a wide occurrence, being present on both sides of the study area. It was present in higher numbers on the eastern side than on the western side. The size frequency histograms of *C. caputesocis* at the selected stations are shown in Figs. 4.10, 4.11, 4.12. At Station 9, the animal was found on only two occasions (July and September 1978) at densities of 58 and 422m^{-2}. The life cycle of *C. caputesocis* was determined using the populations at the other selected stations.

At Station 2, two cohorts, distinguished by size and degree of sexual maturity, were obtained in the July 1978 samples. The larger size group contained mature oocytes measuring 120-140 μm in diameter in their coelom. The group, designated cohort 'I', consisted of animals about to spawn which disappeared from samples after spawning. The small size group, designated cohort '0', grew rapidly between July and September 1978 and spawned between September and November 1978. After spawning the cohort disappeared from samples by March. Sieve recruitment of juveniles at this station occurred in September 1978. The cohort grew rapidly in autumn but slowly in winter, and suffered heavy mortality between January and March 1979. Only two specimens of the cohort were present in March 1979 and disappeared from samples by May 1979.

At station 5, three cohorts were distinct in the July 1978 samples. Cohort 'II', comprising the largest size individuals contained mature but unspawned oocytes (120-140 μm in diameter), gradually declined in abundance between July and November 1978 and finally disappeared from samples by

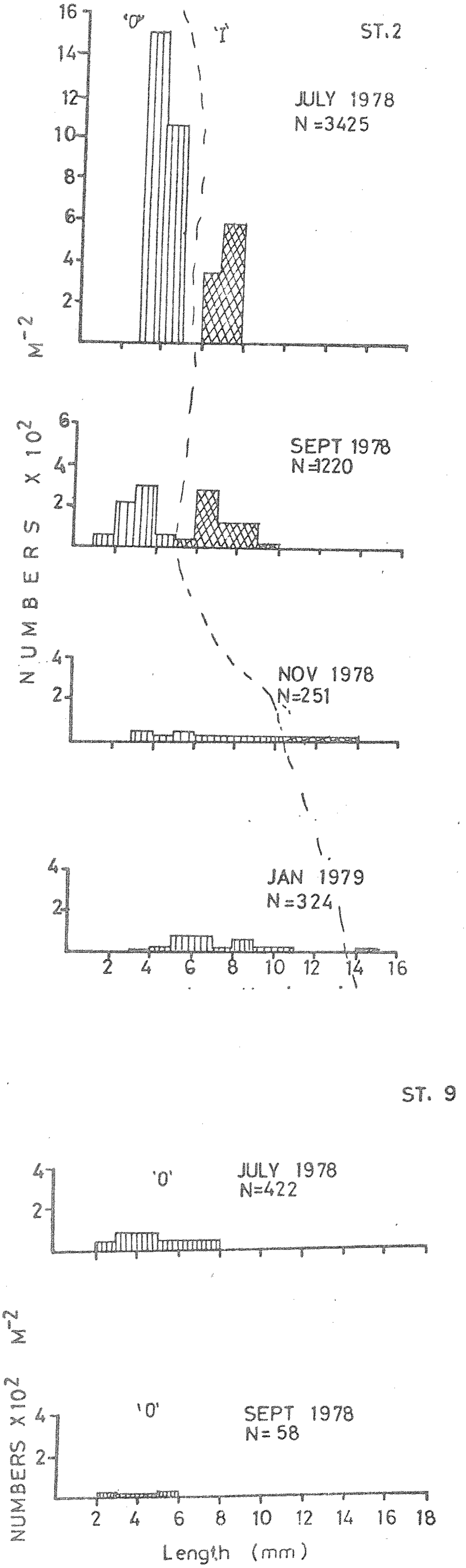


FIG.4.10. STATIONS 2&9 CAULLERIELLA CAPUTESOCIS

SIZE FREQUENCY HISTOGRAMS

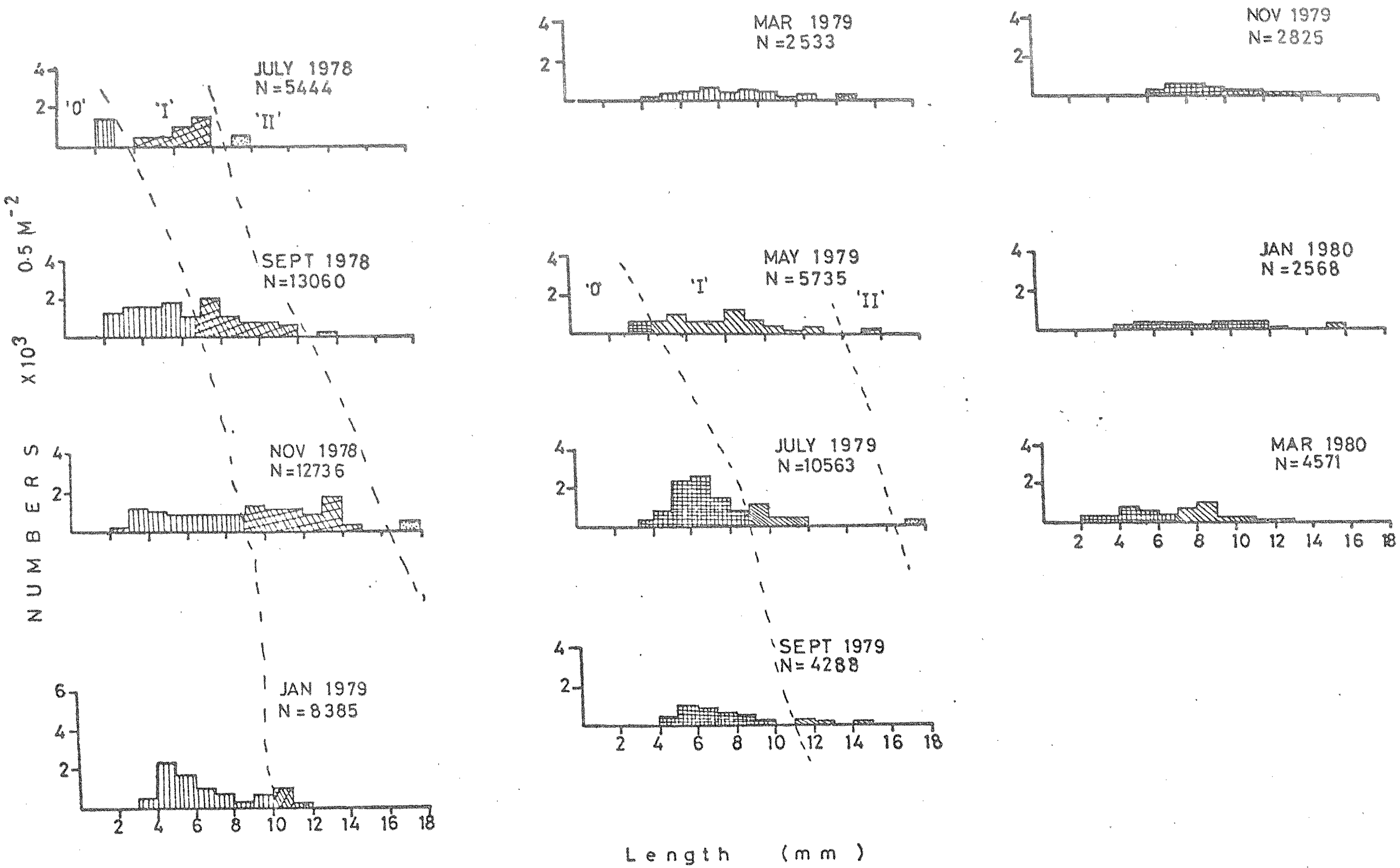


FIG.4.11. STATION 5 CAULLERIELLA CAPUTESOCIS SIZE FREQUENCY HISTOGRAMS

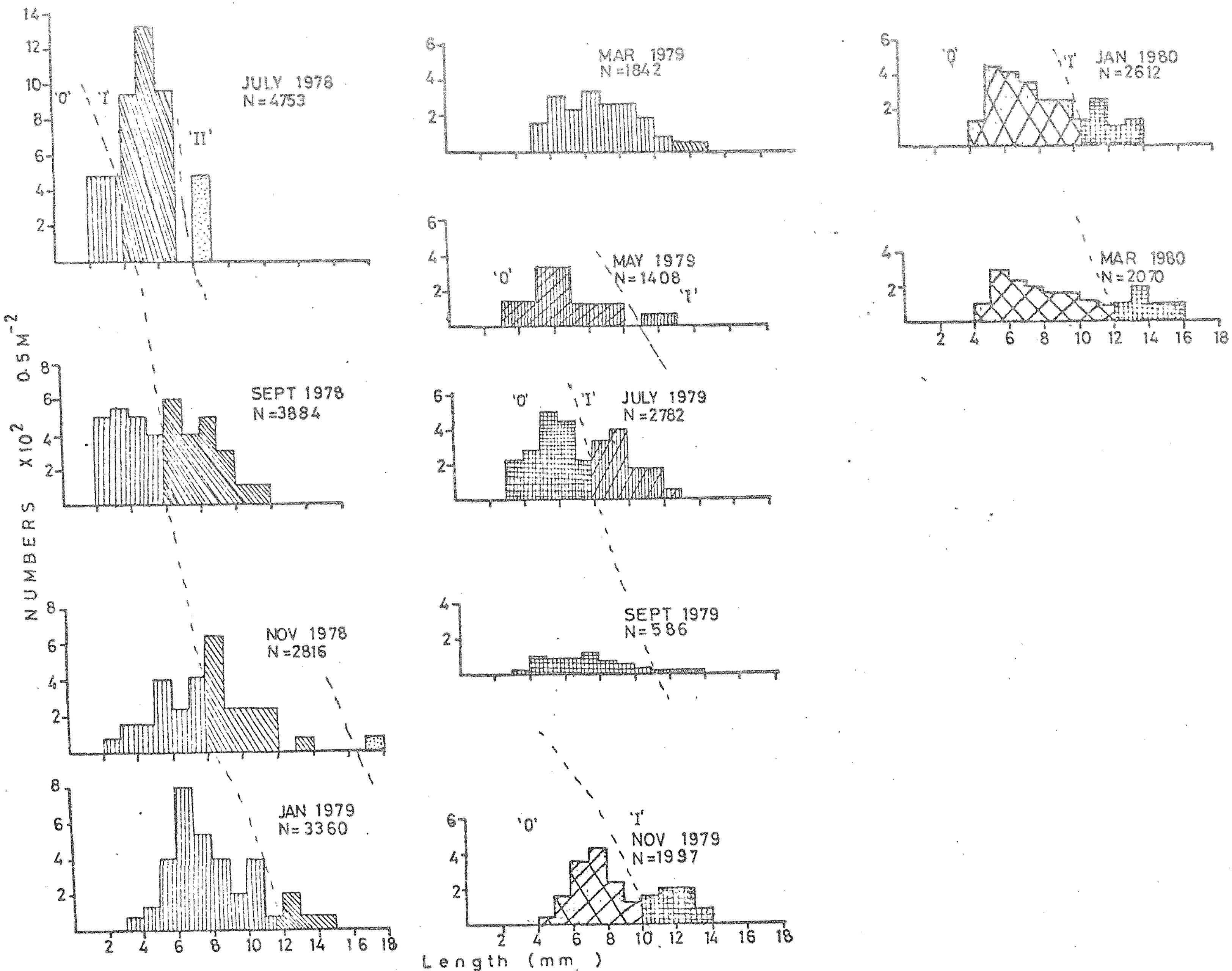


FIG.4.12. STATION 20 CAULLERIELLA CAPUTESOCIS SIZE FREQUENCY HISTOGRAMS

January 1979. Cohort 'I', consisting of 'medium' size individuals whose oocytes measured between 40-60 μm in diameter, spawned in 1978/79 winter (December 1978 - January 1979) after which it declined in abundance. The unspawned oocytes were resorbed. The '0' cohort in July 1978 comprising newly recruited juveniles lacked any obvious gametocytes. During 1978/79 winter, members of the cohort had developed oocytes which remained immature (less than 80 μm in diameter) during spring. The cohort spawned between June and August 1979 and disappeared from samples by March 1980.

Sieve recruitment of juveniles in May and July 1979 contained immature oocytes between September and November 1979. The oocytes matured in the winter months and spawning took place in March 1980. A new recruitment had just started when sampling ceased in March 1980.

At Station 20, three cohorts were distinguished in the July 1978 samples, and these were based on size and level of sexual maturity. Members of the cohort 'II' containing mature oocytes (140-160 μm in diameter) were probably the spent individuals resorbing their unspawned oocytes. The cohort gradually declined in abundance and disappeared from samples by January 1979. Cohort 'I' in July 1978, whose individuals contained immature oocytes at the start of study, matured rapidly in autumn and spawned in 1978/79 winter. The spent and overwintered individuals of the cohort gradually declined in abundance and disappeared from samples by May 1979. The cohort '0' consisting of the newly recruited juveniles in July 1978 grew rapidly between July and November 1978. Maturation of the oocytes of this cohort occurred in the 1978/79 winter months and the cohort spawned between April and May 1979. Gradual resorption of the unspawned oocytes occurred in the cohort between May and June. The cohort suffered post-spawning mortality and disappeared from samples by July 1979.

Juveniles recruited into the sieve in May 1979 grew rapidly during the summer months and spawned in July 1979. Few individuals of the cohort, resorbing unspawned oocytes, were present in samples in September 1979 but disappeared by November 1979. Another recruitment in July 1979 grew rapidly between July and November 1979 but did not reach sexual maturity until January-February 1980. These spawned in March 1980. A new recruitment of juveniles in November 1979 did not attain sexual maturity when sampling was terminated in March 1980.

SPECIES	Spawning Period	Oocyte Diameter (um)	Peak Sieve recruit-ment	App. Age at Spawning	Post-spawn mortality	Authority
Melinna palmata	June-July Dec.-Jan.	180-240 200-240	Throughout the year. Peaks in Sept and May	2 years	+	Present study
M. cristata	Late Dec. early Jan. (2 - 3 weeks)	360	Jan.-Feb.	2 years		Hutchings (1974)
Nereis diversicolor	Late Feb (12-27)	200-275	March-April		+	Dales (1950)
	June August	200 200	March-May	10 months		Chambers & Milne (1975)
	Throughout the year	200-250	Throughout the year			Herpin (1925)
	May-Dec. Peak in Aug.		August			Heip & Herman (1979)
	Throughout the year Peak in April and August	180-200	March, Nov.	9-12 months	+	Present study
Nephtys hombergi	May	100-150		2 years		Olive (1978)
	June-August January	180-200	Sept. March	1 year	+	Present study

Table 4.1. Comparison of life cycles of benthic polychaetes in several areas

SPECIES	Spawning Period	Oocyte Diameter (um)	Peak Sieve recruit-ment	App Age at Spawning	Post spawn mortality	Authority
Capitella capitata	Throughout the year		Throughout the year	Few months		Grassle & Grassle (1974)
	Throughout the year		Throughout the year	35-43 days		Blackstock et al (per comm)
	Throughout the year. Peaks in June-Aug.	140-180	Sept	3 months	+	Present study
	Nov-Jan		March	1 year		
Cirriformia tentaculata	May-Sept	100-110	June-Oct			George (1962)
Tharyx marioni	16-18 April		May			Dales (1951)
Caulleriella caputesocis	June-Nov Dec-Jan	120-160	October May	3-7 months	+	Present study

Table 4.1. (cont.)

4.3 Molluscs

Mercenaria mercenaria

M. mercenaria, the hard shell clam, a native of the eastern seaboard of North America has been the subject of many studies with regard to growth (Ansell, 1968); reproduction (Porter, 1967) and larval biology (Loosanoff and Davis, 1950; Davis and Calabrese, 1964). Heppel (1961) first noted its existence in Southampton Water and it has since been studied in some detail (Ansell, 1968; Mitchell, 1974; Hibbert, 1976). Ansell (1968) suggested that *Mercenaria* in Southampton Water behaved like a species near the northern most limit of its range and Mitchell (1974) concluded that recruitment of all local populations of *Mercenaria* probably relied on the species spawning in the upper reaches of the Test. Hibbert (1976) examined the organic production and growth rate of the population at Hamble Spit.

Previous studies on the population dynamics of *M. mercenaria* in Southampton Water (Ansell, 1963a; 1963b; 1964a; 1964b; 1967; Ansell and Lander, 1967; Ansell et al, 1964; Mitchell, 1974; Hibbert, 1976), showed that the clam is widely distributed within the estuary. The population stretched from the Admiralty Grounds above Marchwood to Hythe on the western side of Southampton Water and extended along the eastern shore as far as Stokes Bay Pier in the Solent. Barnes et al (1973) suggested that the sublittoral region of both Southampton Water and the Solent had reduced densities of *Mercenaria* compared to densities found in the littoral zone.

Mature specimens of *Mercenaria* containing ripe gametes in Southampton Water have been reported to spawn during the summer months when the animals were transferred from the estuary into the laboratory and the ambient temperature increased by 2^{o}c (16-18.6^{o}c). Ansell (1963a) found that in the laboratory the animals required a temperature between 17.8 and 26.9^{o}c to spawn. He then suggested that *Mercenaria* population in Southampton Water has lower spawning temperatures indicating that the species has become acclimatized to temperatures in Southampton Water which rarely exceed 22.0^{o}c.

In the present study, attempts were made to examine the growth rate of the sublittoral population of *M. mercenaria* in Southampton Water and compare the estimates with those of the intertidal Hamble Spit (Hibbert, 1976) with the aim of assessing the factors governing the growth rates. The estimates were based on the population at Station 5 where the clams occurred at high densities.

Growth in *Mercenaria* in the present study was estimated as the increase in length of the animal's shells within successive periods. Since a growth ring is formed during each winter when the shell growth is reduced, each clam was considered to be conveniently aged from the ring count. The growth data was estimated using the method developed independently by Ford (1933) and Walford (1946) from which a Ford-Walford plot, shown in Fig. 4.13 was obtained. The growth ring length at one winter (Lt-1) was plotted against the ring length of the succeeding winter (Lt). A straight line is then produced and the line is described by the equation

$$Lt = L\infty\,(t - e^{-kt}) + Lt - 1^{e-kt}$$

where t = time interval in years

k = coefficient of catabolism of van Bertalonffy, a constant describing the rate at which the theoretical maximum length ($L\infty$) is reached.

$L\infty$ (where Lt = Lt - 1) is obtained at the point where the plot of Lt against Lt - 1 intersects a line drawn at 45^{o} from the common origin of Lt and Lt - 1.

The lengths of growth rings of each year class of *Mercenaria* found in May 1979 survey are shown in Table 4.2. The plots of the ring length at one winter against the length at previous winter give a more useful comparison of rates of growth of the animal at different locations. There were no significant differences ($p > 0.05$) between the means of length of growth rings, indicating a similar rate of growth in *Mercenaria* present in this study irrespective of sediment type. The largest individual found in this study measured 87mm in length (antero-posterior), a measure higher than the theoretical maximum length of 80mm. The maximum length of the largest specimen recovered in the present study was, however, lower than those of Hamble Spit. Mitchell (1974) found the specimen of *Mercenaria* at Hamble Spit to measure 103mm ($L\infty$ = 90.4) and Hibbert (1976) recorded the length of the largest specimen in the same area to be 102.3mm ($L\infty$ = 82mm). It is not clear what could be responsible for the smaller size of *Mercenaria* in the sublittoral zone; a continuous shifting of the sediment and other physical stress on the animal may possibly play a major role.

Many predators, notably *Carcinus*, various fish species and wading birds have been associated with larval stages of the clam (Hibbert, 1976). Voracious members of the zooplankton e.g. *Pleurobrachia pileus* and *Aurelia aurita* have been suggested to account for a considerable

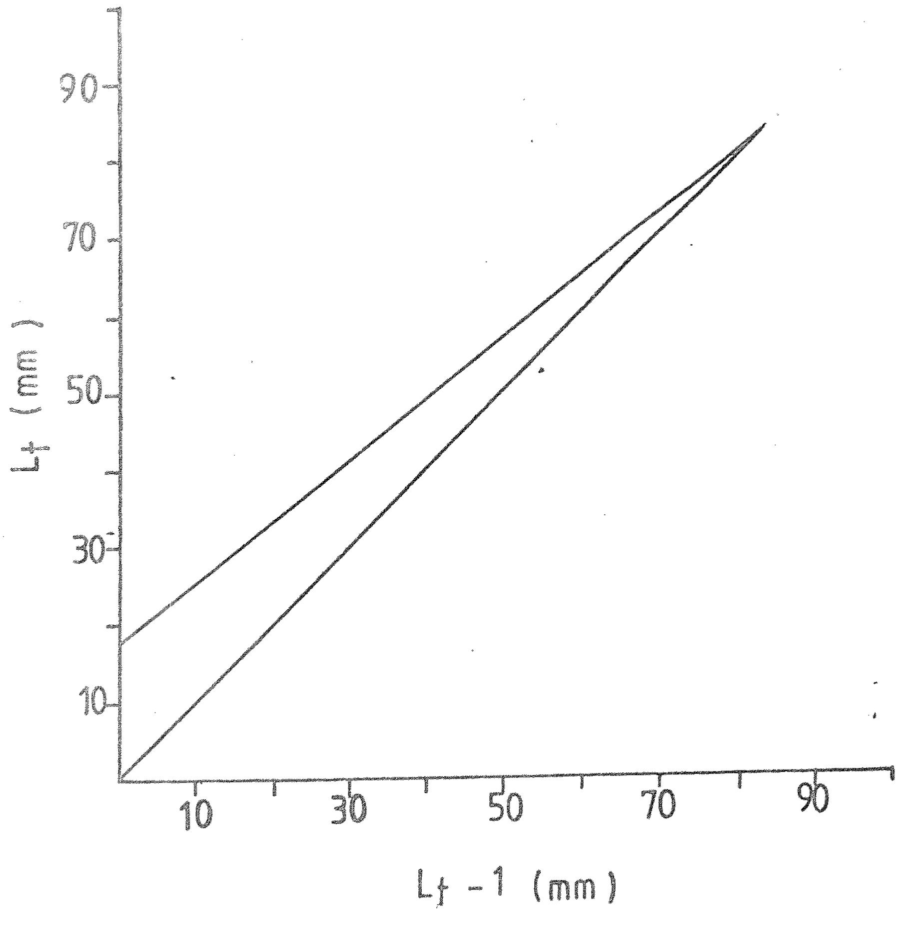


FIG. 4.13. FORD-WALFORD PLOT FOR M. mercenaria FROM 1979 SURVEY.

Table 4.2.

Mercenaria 1979 May (Grid) - Growth Ring Lengths — Age (Yr)

	No.	r11	r10	r9	r8	r7	r6	r5	r4	r3	r2	r1	Age (Yr)
	41	-	-	-	-	-	5.1	4.7	3.9	3.1	2.2	1.5	6
	42	-	-	-	-	-	-	-	3.2	2.4	1.7	1.0	4
	43	-	-	-	-	6.9	6.1	4.6	3.3	2.3	1.9	1.3	7
	44	-	-	-	6.8	6.0	5.2	3.9	2.9	2.5	1.7	1.1	8
	45	-	-	-	-	-	6.3	5.6	4.9	4.3	2.8	1.3	6
	46	-	-	-	6.6	6.3	5.5	5.1	4.2	3.3	2.3	1.2	8
	47	-	-	-	-	6.3	5.5	4.5	3.6	2.4	1.5	1.0	7
	48	-	-	-	-	6.3	5.4	4.4	3.3	2.7	2.0	1.3	7
	49	-	-	-	-	-	5.4	4.8	4.3	3.5	2.2	1.2	6
	410	-	-	-	-	-	-	4.9	4.2	3.0	2.0	1.1	5
	411	-	-	-	-	-	6.2	5.7	4.8	3.4	2.5	1.4	6
	412	-	-	-	-	-	-	6.3	5.2	3.6	2.2	1.6	5
(13)	413	-	-	-	-	-	-	6.3	5.1	3.6	1.9	1.2	5
	51	-	-	-	-	-	-	-	3.9	3.3	2.1	1.1	4
	52	-	-	-	-	-	-	6.3	5.3	3.8	2.3	1.3	5
	53	-	-	-	-	-	-	6.0	4.7	3.3	2.4	1.3	5
(4)	54	-	-	-	-	6.8	6.2	4.9	4.0	3.2	2.3	1.4	7
(1)	61	-	-	-	-	-	-	-	-	-	2.2	1.2	2
	121	-	-	-	-	-	-	5.0	4.1	3.0	1.9	1.3	5
	122	-	-	-	-	-	-	-	-	2.7	1.5	1.0	3
	123	-	-	-	-	-	-	-	-	2.4	1.6	1.0	3
	124	-	-	-	-	-	-	-	-	-	2.1	1.2	2
(5)	125	-	-	-	-	-	-	-	-	2.1	1.7	1.0	3
	161	-	-	-	-	-	-	-	-	3.4	2.0	0.9	3
	162	-	-	-	-	-	-	6.3	4.8	3.7	2.2	1.3	5
(3)	163	-	-	-	-	-	-	7.2	5.7	3.6	2.1	1.1	5
(1)	231	-	8.7	8.2	7.1	6.4	5.9	5.3	4.9	3.9	3.2	1.0	10
	241	-	-	-	-	6.8	5.8	5.1	4.1	2.7	1.9	1.2	7
	242	-	-	-	-	-	-	5.9	4.5	3.7	2.5	1.3	5
	243	-	-	-	-	5.9	5.4	4.7	3.7	2.4	1.8	1.0	7
	244	-	-	-	-	6.2	5.8	4.6	4.2	2.9	1.9	1.1	7
	245	-	-	-	-	-	5.9	5.0	3.8	2.9	2.1	1.1	6
	246	-	-	-	-	-	-	5.1	4.5	2.4	1.7	1.2	5
	247	-	-	-	-	-	-	-	-	3.2	1.8	0.8	3
(8)	248	-	-	-	-	-	-	-	-	2.4	1.5	1.0	3
($\bar{L}$)			8.7	8.2	6.8	0.4	5.7	5.3	4.3	3.1	1.7	1.2	

Lengths of Growth Rings of Mercenaria mercenaria recovered from 1979 Survey. The mean lengths are shown at the bottom of the table.

reduction in numbers of the larvae (Mitchell, 1974). Raymont and Carrie (1964) found that Pleurobrachia and Aurelia showed a marked increase in May-June and maintained high numbers throughout July and August in each year in Southampton Water, coinciding with the major spawning period of Mercenaria.

Carcinus maenas, a common crab in Southampton Water, appears to be the most important predator after Mercenaria has settled. Walne and Dean (1972) recorded a rate of predation equivalent to four small clams being eaten on average per day by each crab. Mitchell (1974, quoting Green) stated that shells of Mercenaria juveniles were found in the stomach of plaice and flounders caught in Southampton Water while plaice fed on the siphons of the buried adult clams.

Abra nitida

This equivalved bivalve occurs in large numbers in soft bottom deposits around the British Isles, e.g. off the coast of Northumberland (Buchanan and Warwick, 1974) in the Venus community of Bristol Channel (Warwick et al, 1978) in Southampton Water (Barnes et al, 1973; Soulsby, 1978; Levell, 1979). In spite of its wide distribution little is known about its reproductive biology. Tebble (1966) described the systematic position of A. nitida and stated that the bivalve occurs in a variety of bottoms around the British Isles, ranging from mud through sandy mud to gravel and from just offshore to about 190 metres deep. In Southampton Water, A. nitida is present as part of a Nephtys/Abra association (Barnes et al, 1973). Levell (1979) described the bivalve as patchily distributed and varying in its density, though at most sites in Southampton Water, it forms the principal bivalve component of the fauna.

In the present study, A. nitida was present in varying densities ($10 - 585 m^{-2}$), highest densities occurring near the mouth of the estuary.

The size frequency histograms of A. nitida at the four selected stations are shown in Figs. 4.14, 4.15 and 4.16. The life cycle of the population of Abra in the present study was based on the specimens present at Stations 5 and 20.

A single cohort was present at Station 5 in July and September 1978. Members of the cohort could not be sexed but on dissection females contained mature oocytes which measured between 60 and 80 μm in diameter. After spawning in November 1978, the cohort declined in abundance and disappeared from samples by March 1979. Juveniles recruited into the sieve between November 1978 and May 1979 and grew rapidly during summer. This cohort

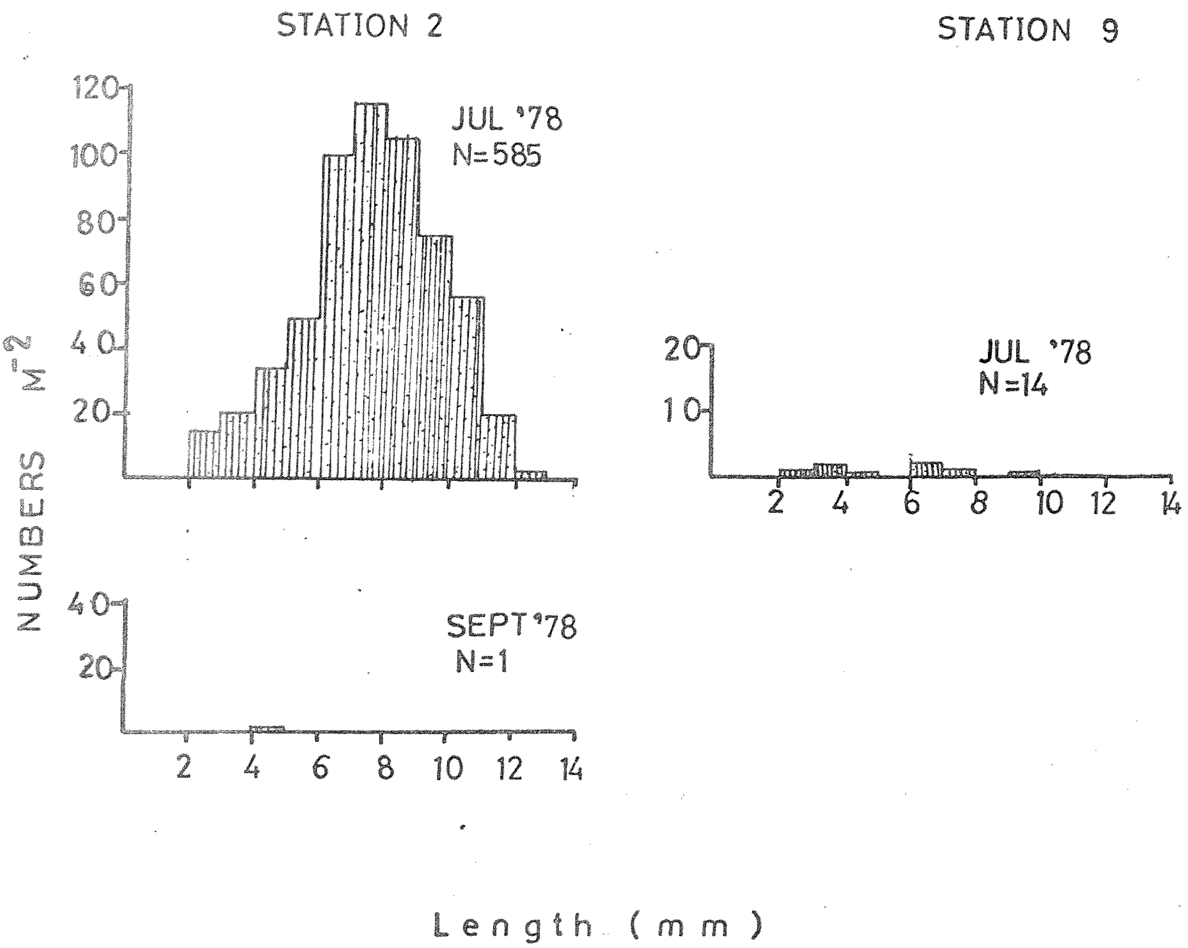


FIG. 4.14. ABRA NITIDA SIZE FREQUENCY HISTOGRAMS AT STATIONS 2 & 9

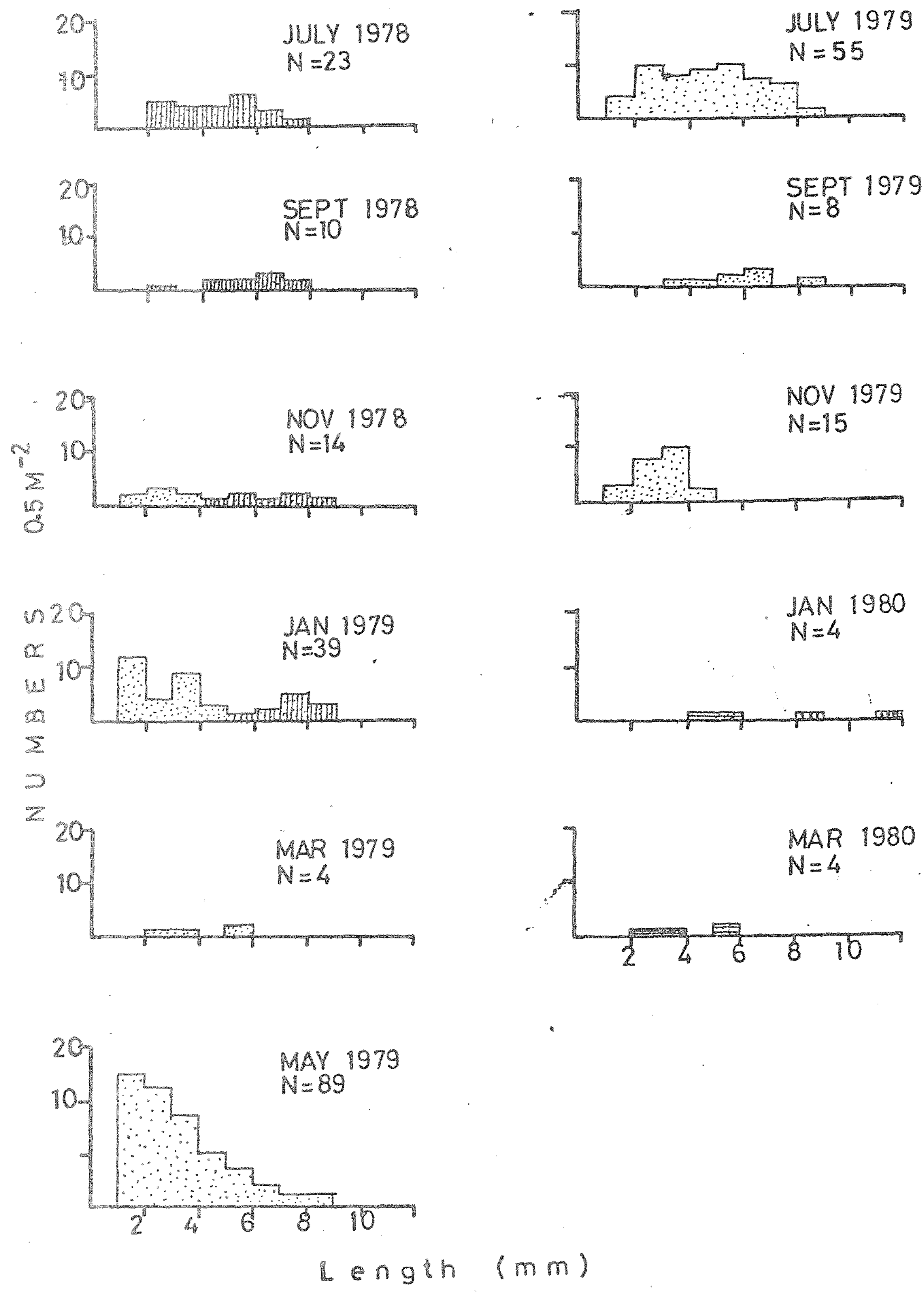
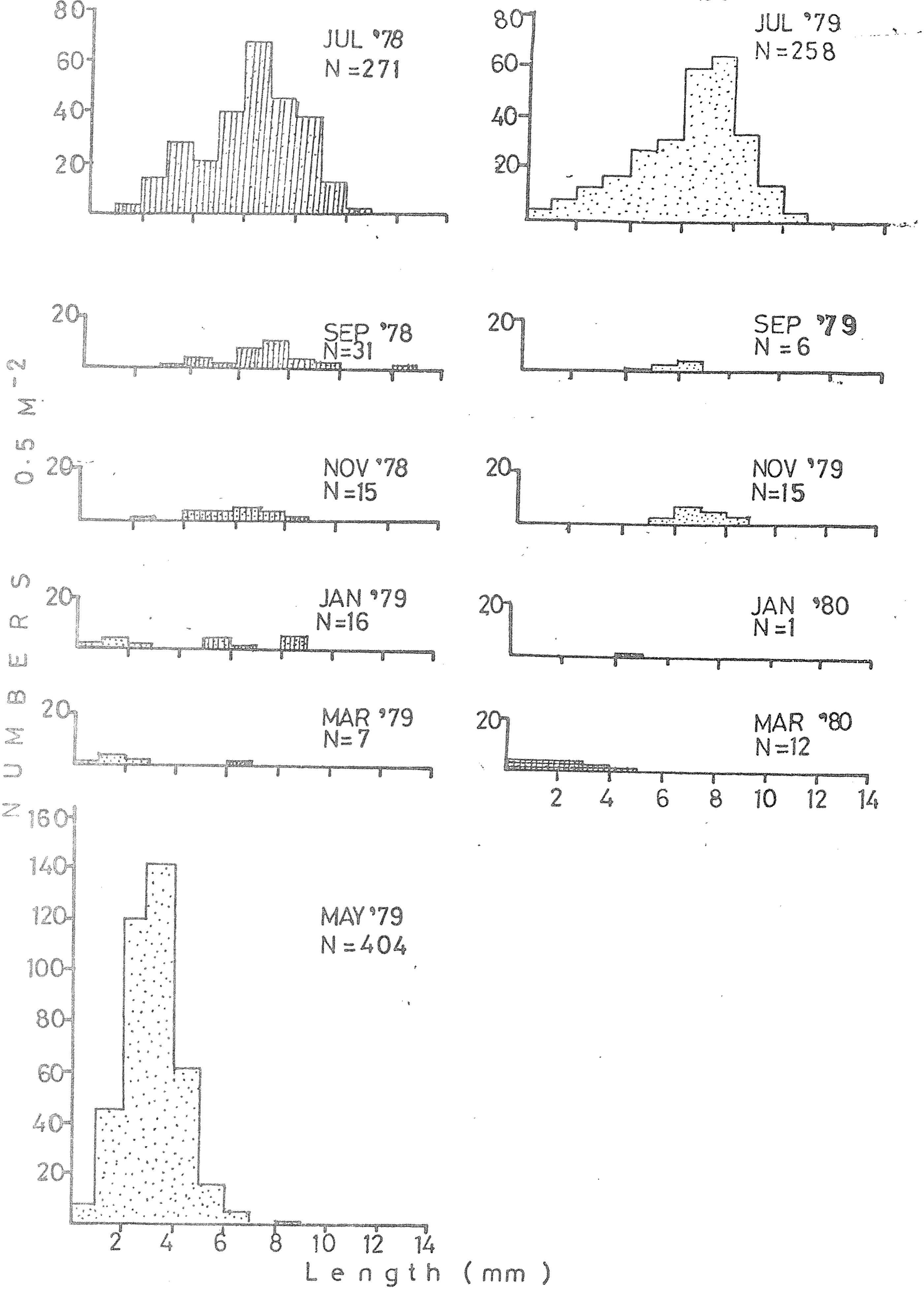


FIG.4.15. STATION 5 ABRA NITIDA SIZE FREQUENCY HISTOGRAMS



16. STATION 20 ABRA NITIDA SIZE FREQUENCY HISTOGRAMS

spawned between August and September 1979 with the few large individuals present in September 1979 containing no eggs. Young immature specimens appeared in the sieve from November 1979, spawned in winter and disappeared from samples by March 1980. The newly recruited juveniles in March 1980 remained sexually immature when sampling ceased.

At Station 20, the single cohort present in July 1978 comprised mature individuals which spawned between August and September 1978 and disappeared from samples by May 1979. Sieve recruitment of juveniles took place between November 1978 and May 1979, during which time growth was slow. Growth increased rapidly in the summer months and the cohort spawned between August and September 1979, followed by heavy post-spawning mortality, the density falling from $516m^{-2}$ to $12m^{-2}$ in September 1979. The cohort continued to decline and disappeared from samples by March 1980. A new recruitment had just begun when sampling ceased in March 1980.

4.4 Crustacea

Pariambus typicus

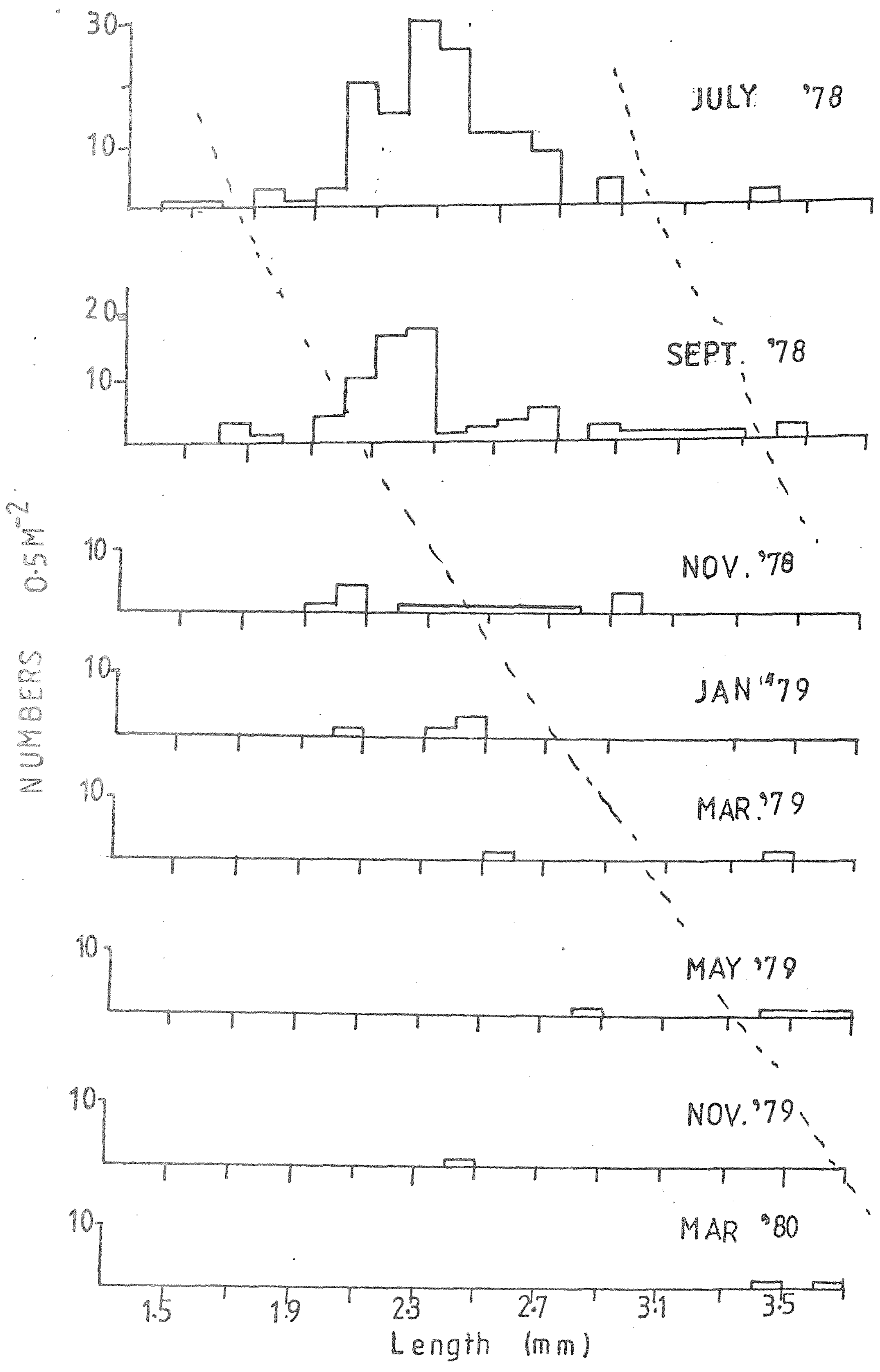
The size frequency histograms of *P. typicus* at Station 5 is shown in Fig. 4.17. Mature brooding females were present in samples taken throughout the study except in March and November 1979 and January 1980, though breeding reached a peak between July and November. Immature individuals were present in all samples between July 1978 and January 1979, but in low numbers. There were more adult females than males. The population suffered heavy post-breeding mortality and only a few females overwintered in January 1979, these disappearing from samples by March 1979.

Few juveniles entered the sieve in July 1978 and were sporadic in occurrence in successive samples until they reached sexual maturity in May 1979. The small size of juveniles present in the samples could have resulted in their loss from 0.5mm sieve and hence absence from most samples.

Eudorella truncatula

The size frequency histograms of this cumacean at Station 5 are shown in Fig. 4.18. Similar to the situation in *P. typicus*, mature brooding females of *E. truncatula* were present throughout the study. Breeding took place throughout the year with peaks in July to September and between January and March after which the breeding stock suffered heavy post-spawning mortality and disappeared from samples by May 1979. Juveniles did not recruit into the sieve until the summer months of 1979. The

FIG.4.17. STATION 5. *P. typicus* SIZE FREQUENCY HISTOGRAMS



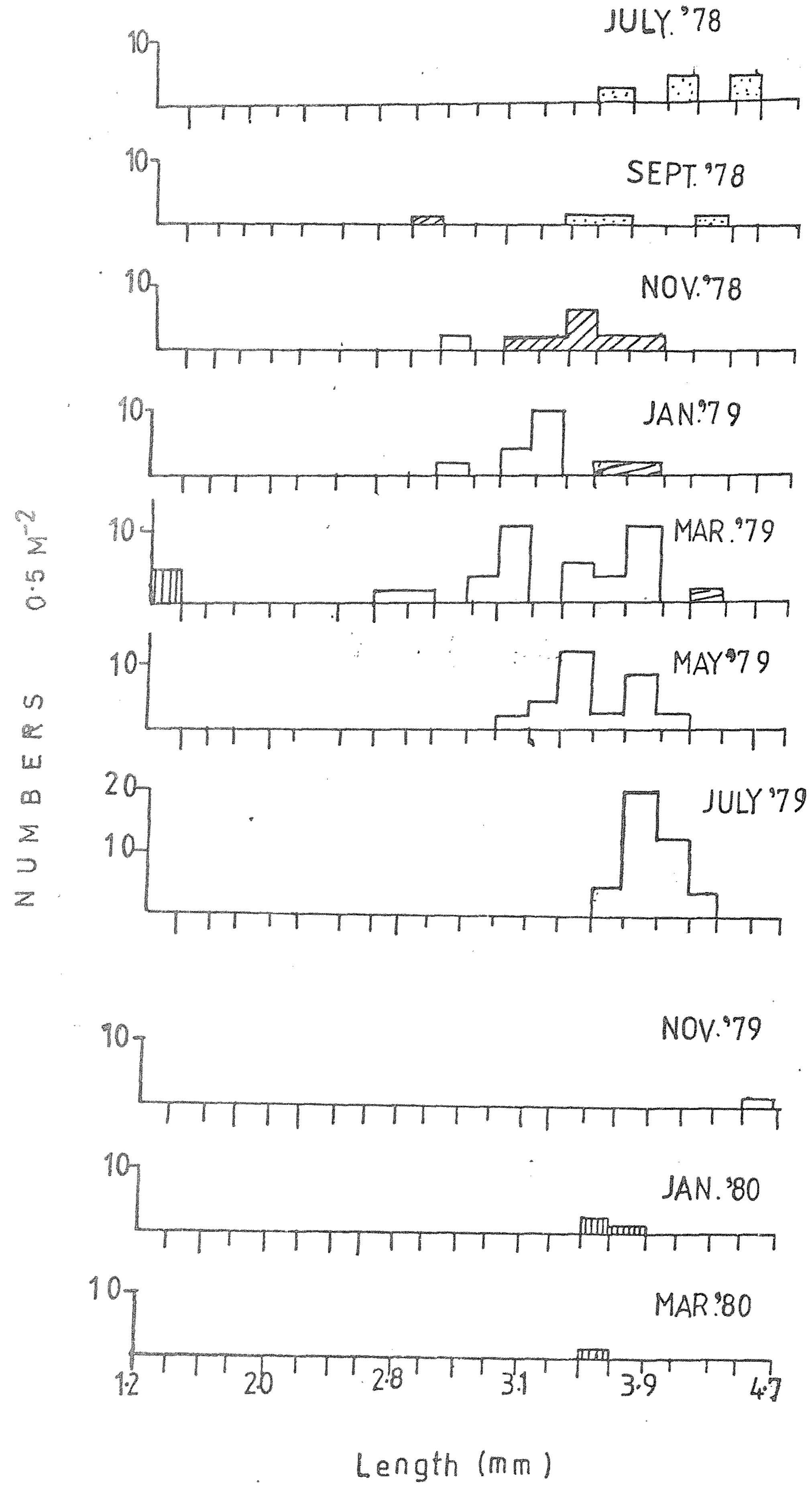


FIG. 4. 18. STATION 5. *E. truncatula* SIZE FREQUENCY HISTOGRAMS.

females contained mature oocytes and bred in June 1979. Post-spawning mortality occurred and only one specimen was present in Nov 1979. A new generation which had attained sexual maturity was present in November 1979 and March 1980.

Philomedes globosus

Fig. 4.19 shows the size frequency histograms of this ostracod at Station 5. Mature brooding females were present in all samples throughout the study but breeding was at its peak between July and November 1978 and also between January and March 1979. Juveniles recruited into the sieve between September and November 1978 and grew rapidly, containing mature oocytes or larvae in their broods by January 1979. No juveniles recruited into the sieve between May 1979 and March 1980 though adults containing mature ova or larvae in their broods were present.

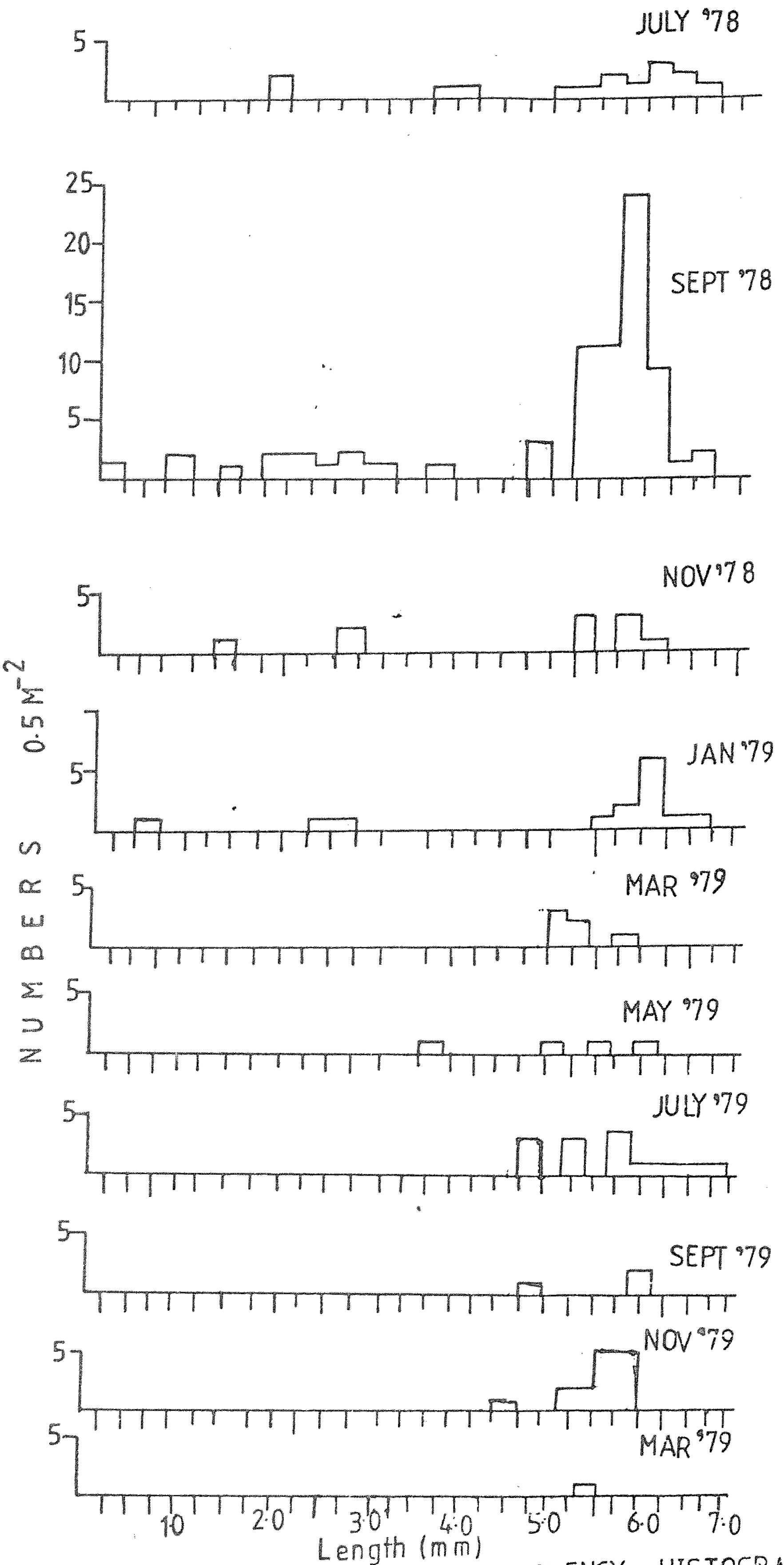


FIG.4.19. ST. 5. P. globosus SIZE FREQUENCY HISTOGRAMS.

4.5. DISCUSSION

Investigations into the life cycle of the polychaete populations in Southampton Water show a wide variation in the reproductive strategies by the animals. While a particular species may show one pattern of breeding, for example, almost continuously over an extended season, individual worms of the species may have a different reproductive strategy such as breeding once and dying. Some polychaetes are monotelic, that is, individuals breed only once and die. Others show a polytelic pattern of reproduction, releasing all their gametes in one or a few large batches and usually surviving to breed again in the following year.

Many polychaetes in Southampton Water show extended breeding seasons with peaks in the summer and the winter months. Melinna palmata breeds throughout the year with peaks in December and June while Nereis diversicolor, though breeding all the year has breeding peaks in April and August. Hutchings (1974) found that the related species of M. palmata, M. cristata population off the coast of Northumberland has a restricted breeding season of about two weeks between the end of December and the beginning of January. The life cycle of N. diversicolor tends to vary according to the area of study (Dales,1950, Muus,1967) Dales (1950) found that a population of N. diversicolor at Chalkwell had a spawning period towards the end of February which lasted for not more than three weeks. Herpin (1925) found that the population of N. diversicolor at Cherbourg spawned in every month of the year while Chambers and Milne (1975) found that the Ythan population of the worm spawned twice a year, between June and August and between January and March. Herpin (1925) attributed the continuous spawning at Cherbourg to the environmental gradients encountered throughout the habitat which caused various portions of the population to mature at different times of the year.

Though it is rather unusual for a polychaete to have a protracted breeding season, the tendency being for a short, fairly well defined spawning period, spawning in a population may vary between microhabitats in the same environemt. Chambers and Milne (1975) found that the populations of N. diversicolor from the upper and lower zones of the Ythan estuary did not spawn at exactly the same time, thereby protracting the spawning season. They found that the worms at Ythan mature and begin to carry eggs from a size about 2.5cm while the minimum size of mature females at Chalkwell (Dales,1950) was 7cm. The Ythan estuary population of N. diversicolor showed two peaks between June and August, coinciding with June's peak in the Southampton Water population and January-March coinciding with January's peak in the present study. Dales' (1950) account of a shorter spawning season at Chalkwell may have been due to the restricted area. The study of the dynamics of Nereis by Levis (1975) showed that similar populations of N. diversicolor could differ according to the local environment. Heip and Herman (1979) found that juveniles of N. diversicolor occurred in the Dievengat (Belgium) population throughout the year, a situation similar to that in the present study.

The population of N. diversicolor in Southampton Water occurs at moderate densities compared with other populations elsewhere. The numbers of N. diversicolor reported elsewhere ranged between 10 and $200m^{-2}$ in Tees estuary, (Gray, 1976); $50-300m^{-2}$ in Chalkwell, (Dales, 1950); and a maximum of $17,000m^{-2}$ in Dievengat (Heip and Herman, 1979). In Southampton Water (present study) the density of the worm ranged between $4m^{-2}$ at Station 5 (Netley) and $1029m^{-2}$ at Station 9 (Fawley). Chambers and Milne (1975) found variations in the densities of the Ythan population between the upper and lower zones of the estuary.

The population of Nephtys hombergi in Southampton Water showed a monotelic pattern of reproduction with individuals spawning twice a year in the June to August period and in January. The age at which they reach sexual maturity is variable, animals of two years or more spawned. Olive (1978) found that the population of N. hombergi at the Tyne estuary bred for the first time when two years old with a few individuals failing to spawn until three years old. In the offshore Northumberland waters, N. hombergi does not usually breed until three years old (Olive, quoting unpublished data of Buchanan) but in the Raunce estuary, N. hombergi reached sexual maturity in their first year (Retiere, 1976). The Southampton Water population of N. hombergi appears similar to the Tyne population in that they spawned when one year old but differ in that the population in Southampton Water suffered heavy post-spawning mortality while the Tyne population has a polytelic pattern of reproduction in which gametocytes are released annually for several years.

It is not known for certain what stimulates spawning in the Southampton Water population. Olive (1976) suggested that spawning in the Tyne population of N. hombergi may result from an unknown environmental stimulus which initiates the release of a 'spawning hormone' and that the level of success may in part depend upon the time of release of the hormone. It can be argued that the environmental conditions in Southampton Water and Tyne estuary could be similar, initiating the release of the 'spawning hormone' earlier in these populations than in the deeper sublittoral populations off the coast of Northumberland.

The _Capitella capitata_ population in Southampton Water shows a complex unsynchronized life cycle with a monotelic pattern of reproduction. Gametes are released almost throughout the year with peaks in August and late October. Grassle and Grassle (1974) found that the Massachussettes population bred all the year round. Blackstock and Pearson (per. comm) found that single individuals of _C. capitata_ were capable of producing several broods of eggs in rapid succession when detrital supplies are plentiful and observed breeding cycle of 35-43 days in conditions of maximum food supply. The population in Southampton Water produce large yolky ova in August. Such ova are brooded and probably develop into benthic larvae which settle quickly at the bottom. October spawning results in planktotrophic larvae which recruit into the sieve in spring. Grassle and Grassle (1974) found that _C. capitata_ is capable of producing larvae which may either be benthic or planktonic. The important characteristic of such animals as _C. capitata_ is that the planktonic larvae are responsible for colonising new areas while benthic larvae settle quickly in a restricted locality allowing selection of favourable genotypes to occur.

The cirratulid worm, _Caulleriella caputesocis_ in Southampton Water shows a well defined monotelic pattern of reproduction; the eggs are spawned only once a year. The individual animals spawn for the first time in their second year. The species shows an obvious synchronized reproductive cycle, the breeding stock releasing their gametes in March. Not all mature gametes are spawned, and those remaining are resorbed. Dales (1951a) found that in the _Tharyx marioni_ population at Chalkwell, spawning lasted for two or three days. The classic example of strict periodicity is, of course, that of _Eunice viridis_ of the Southern Pacific which spawns in great numbers at dawn on only one day in the year, the actual date of spawning showing some variation, being apparently associated with lunar phases (Korringa,1957).

The concept of protracted breeding seasons in polychaetes is, however, not new. Stephenson (1950a) found that _Cirratulus cirratus_ at Cullercoats, Northumberland, matured throughout the year. Olive (1970) found that _C. cirratus_ population off the coast of Northumberland bred several times at intervals with low level breeding in between. George (1962) found that the breeding season of _Cirriformia tentaculata_ in Southampton Water extended throughout the summer months from late March to September with peaks between April and August.

Several environmental factors probably play a key role in the timing of spawning in different polychaetes. George (1962) suggested that temperature might be an important factor in the breeding of C. tentaculata in the Hamble Spit, though Herpin (1925) suggested continuous breeding in N. diversicolor at Cherbourg to be influenced by environmental gradients. Orton (1920) had earlier suggested that most animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change. The relationship between temperature and the breeding season of some polychaetes in Southampton Water appears rather obscure. Melinna palmata and Nephtys hombergi, for example, breed in June and December when water temperatures are high and low respectively. The moderately high temperatures in spring and autumn though may appear to induce maturation of the gametes, the actual spawning, nevertheless, tends to be temperature independent.

Dales (1951a) found that a field population of Tharyx marioni at Chalkwell spawned after a rise in temperature of about 4°c over a period of 4-5 days. He then concluded that the rise probably induced spawning. Ansell (1963a) found that Mercenaria specimens collected from the Netley shore in May and kept in the laboratory first spawned when the ambient temperature rose from 16 to 18.6°c. George (1966) reported that Scolecolepis viridis was prevented from spawning by maintaining its population at low temperatures. Since no experiments on the temperature effects on the spawning of animals in the present study were carried out but many of the fauna spawned throughout the year, it may be assumed that temperature effect on their spawning is of negligible significance.

With regard to factors other than temperature that may bring about spawning, food availability, pollution tolerance and certain types of mechanical stimulation may play prominent roles. George (1962) found that mechanical stimulation induced slight shedding of genital products in C. tentaculata while Olive (1978) demonstrated spawning in N. hombergi to be induced by the release of a spawning hormone. Neither mechanical stimulation nor food availability has been established to stimulate spawning in the present study. Nevertheless it may be suggested that many factors rather than a single one may influence spawning in the Southampton Water polychaetes. Until a detailed work on the reproductive ecology of the animals is carried out, any review of the animals' breeding strategies will remain inconclusive.

The size of mature gametes of the polychaetes considered in the present study varies considerably. The M. palmata population in Southampton Water breeds in June and December when the diameter of their oocytes attains a size of about 240 μm. N. diversicolor spawns when the oocytes attain different sizes at several locations. At Chalkwell, spawning occurred when the oocytes measured 275 μm in diameter, but in Southampton Water and Ythan estuary, when the oocyte diameter reached 200 μm. In the population of N. hombergi off the coast of Northumberland spawning occurred when the oocyte diameter measured between 100 and 150 μm (Olive 1978) but in the present study only when the oocytes diameter reached about 200 μm. In this respect, The Southampton Water population spawns later than that of the Northumberland coast. The cirratulids appear to spawn their ova at a smaller size than other polychaetes.

An interesting aspect of the life cycle of the Southampton Water populations of polychaetes is that sieve recruitment appears to be dependent on size of larvae and settlement as well as the subsequent rate of growth.

Some polychaetes resorb their unshed mature gametes as in Ostrea lutaria, O. edulis and Crassostrea virginica (Loosanoff, 1962; Hollis, 1963). Loossanoff (1962) found that in Maine (U.S.A.) some individuals of O. edulis had full complement of gametes after the breeding season, and the gametes were resorbed. In the present study, . , N. diversicolor, N. hombergi and C. caputesocis resorbed their unspawned mature oocytes. Dales (1951a) also found that unspawned gametes of female N. diversicolor were resorbed. He noted that the female animal spawned only in the presence of males, and since the ratio of males to females was 1:10, some females failed to spawn. Such females resorbed their unshed gametes. In another study Dales (1951a) found that female Tharyx marioni failed to spawn, though the ratio of males to females in the animal population at Chalkwell was 1:1, resorbed their unshed gametes. Resorption of gametes in M. cristata has been reported by Nyholm (1951) and Hutchings (1974) and in N. hombergi by Olive (1978).

Several attempts have been made by many workers to explain the cause of this retention of gametes. The view expressed by some (Harvey,1956; Clark,1963) points to lack of food. It was suggested that individuals which failed to spawn could not obtain sufficient food at the time of spawning and therefore had to resorb their gametes to survive. It may be argued that if this is the case for those animals that show polytelic pattern of reproduction, the situation of those that suffer heavy post-spawning mortality remains unclear. Sastry (1970) suggested that reproductive physiological variation in the timing of spawning may have been favoured through selection, as an adaptive response to geographical differences in temperature and time of abundant food supply.

The type of larvae and the time taken to mature are interesting aspects of polychaete development. Except Capitella capitata which broods its summer lecithotrophic larvae and and spawns its planktotrophic larvae, other polychaetes investigated in the present study produce truly planktotrophic larvae. Thorson (1950) thought that the likely cause of change from the pelagic to non-pelagic type of larvae in polychaetes is a small increase in the yolk content. The wide distribution of Nephtys, Nereis and Capitella in the present study may be attributed to their ability to change their mode of reproduction in accordance with ecological conditions, an ability which many polychaetes share (Thorson, 1946).

Habitat selection and settlement of larvae are of great importance in the life cycle of any benthic animal. Wolff (1973) showed that C. capitata and Polydora ciliata were irresponsive to any substratum difference and both animals were found present in almost equal numbers in sand and muddy areas after an oil spill. Wass (1967) ranked C. capitata as an indicator of organic pollution and Rosenberg (1972) observed that the animal was the pioneering species that settled in formerly azoic areas. In the present study, C. capitata occurred in largest numbers on the western side of Southampton Water where the levels of sediment organic matter, hydrocarbon and metals were greatest, but only occasionally and in low numbers on the eastern side. The low numbers of C. capitata on the eastern side may be attributed to high species diversity and hence greater competition.

Though direct investigations on the growth of polychaetes have not been made in the present study, the data on the time of spawning and sieve recruitment on the taxon suggests that growth may be temperature dependent. Growth appeared to be retarded during the cold winter months. During the summer, the gametes of the polychaetes studied tend to mature with a general increase in the size of the individual polychaetes. Nevertheless, a decrease in the rate of growth in animals may not always be a direct result of low temperature; it may result from lack of food and/or reduction in the feeding activity though there may be plentiful food supply. Since feeding behaviour of animals investigated has not been studied in the present investigation, any conclusion on the effect of feeding or growth with season could only be speculative.

It is by no means an easy task to establish all possible causes of mortality in the polychaete populations. Since food is always plentiful in estuaries such as Southampton Water, it is unlikely that lack of food could be a major cause of mortality. Grassle and Grassle (1974) found large numbers of dead *C. capitata* in the sediment in a winter sample and suggested that the kill could have resulted from cold conditions rather than predation, since the decomposing animals would probably have been used as a source of food for the deposit-feeding *Capitella*, had the decline resulted from source depletion. Since many of the polychaetes suffered heavy mortality in the winter months in the present study, it may be suggested that prevailing climatic conditions are possible direct or indirect reasons for this mortality.

Often one of the main causes of mortality among marine organisms is predation. Besides *Nephtys hombergi*, commonly known as a selective omnivore, little literature exists on the feeding biology of the polychaetes investigated in the present study. *N. diversicolor* is known to be a predator on other organisms and a scavenger. It is commonly used as baits in fishing and serves as food for fishes and birds (Heip and Herman, 1979). Since little is known of the predators of the polychaetes in Southampton Water, it can only be assumed that reduction in the numbers of both young and adult invididuals of these polychaetes may be attributed to several species of benthic animals which are largely non-selective deposit feeders.

The crustaceans in the study area showed continuous breeding throughout the year. Females were, in general, more numerous than males. In the case of *Eudorella truncatula*, the males develop pleopods which aid them in swimming. The relatively small numbers of *Pariambus typicus* in the 1979 samples could be attributed to the higher silty conditions at the time. The absence of juveniles of *P. typicus* and *E. truncatula* in samples may be due to their small size resulting in their loss. This possibly indicates that the crustaceans are disappearing in the study area.

The present study reveals that the study area may not be comparable to offshore marine environments such as the silty mud situation off the coast of Northumberland (Buchanan et al,1974) where the communities were normally oversubscribed by larvae. In such situations, the numbers surviving is dependent on density dependent factors, that is, the number of animals settling and surviving is determined by the number of established animals already present. Such a condition may not be applicable to the physically controlled estuarine situation.

SECTION FIVE

BIOMASS AND SECONDARY PRODUCTION

5.1 Introduction

Many of the recent studies on the energy budget of estuaries have been confined to intertidal mud flats (Smidt, 1951; Chambers and Milne, 1975; Warwick and Price, 1975; 1980; Hibbert, 1976; Hiep and Herman, 1979). Smidt (1951) discussed the biomass per unit area of both meio and macrofauna from the Danish Wadden but failed to estimate their production. Production estimates in the sublittoral (Buchanan and Warwick, 1974; Buchanan et al, 1974; Cederwall, 1977; Warwick et al, 1977; Kirkegaard, 1978) and in the intertidal (Warwick and Price, 1975, 1980; Hibbert, 1976) allowed comparisons between several ecosystems. Such estimates of the community give better understanding of a particular ecosystem.

Though attempts to determine the production of benthic marine systems dates from the 1950s (Sanders, 1956; Knuenzler, 1961), much of the data has accumulated only within the last ten years. Many such studies on biomass and production of macrofaunal organisms were directed towards single species populations, for example: Nerita sp (Hughes, 1970); Venerupis pullastra (Johannessen, 1973); Arenicola marina (Longbottom, 1973); Ampelisca tenuicornis (Sheader, 1977); Nereis diversicolor (Chambers and Milne, 1975; Heip and Herman, 1979). Around the British Isles, some studies have been carried out on the total macrofaunal biomass (Moore, et al, 1968; McIntyre, 1970) and production (Buchanan and Warwick, 1974; Warwick and Price, 1975; Hibbert, 1976; Warwick, et al, 1978).

Comparisons of results of energy flow studies by different workers are made difficult because of different terminologies defining different purposes for which energy is used or conserved by organisms. Davis (1963) defined production as the actual rate of incorporation of organic matter or energy. Crisp (1971) defined biomass as the amount of living substance constituting the organisms which are being studied.

Many studies on the macrofaunal production have been limited to short periods (1-2 years), though Warwick and Price (1980) extended their studies beyond five years. Long term studies on population trends (Buchanan and Warwick, 1974; Buchanan, et al, 1974), however, showed considerable variation in species composition with overall production remaining stable. Hibbert (1976) suggested that studies of biomass and production could elucidate the ecological potential and relative contribution of the constituent species of the fauna in an area.

Previous sublittoral studies on the benthic macroinfauna of Southampton Water (Esser, 1972; Barnes, 1973; Mitchell, 1974; Soulsby, 1978; Levell, 1979) emphasised the distribution of the macrofauna in the estuary. The only production investigation hitherto carried out on the benthic macrofauna in Southampton Water was Hibbert's (1976) study of the bivalve population of the intertidal Hamble Spit. Hibbert (1976) extended his study to the polychaetes in the area and estimated a total macrofaunal production including the polychaetes (based on Esser's data) of 220g m^{-2} yr-1 ash free dry weight, a very high value of the same order as in high production Mytilus beds. Until now, the production of the sublittoral faunal assemblages in the estuary has been neglected. The aim of the present study is to estimate the biomass and secondary production of these benthic macrofaunal assemblages in terms of formalin-fixed ash free dry weight (gm^{-2} yr^{-1}) in the sublittoral region of the industrialized area of Southampton Water. It is aimed at identifying those animals, among the bulk of species which have the highest productive capability and rank them in order of productive importance. The intention is to provide a basis for future study on the temporal fluctuations in the biomass and annual production of the benthic macrofauna of the estuary.

5.2 MATERIALS AND METHODS

The animal species which were separated and identified according to the method outlined in Section II were divided into separate year classes using the measurement of linear dimension on the width or length as seemed appropriate to the particular species. The exact ageing techniques have already been described in the appropriate sub-sections in Section IV. Specimens were washed free of formalin, oven dried to constant weight at $90^{\circ}c$ for 8 hours. Molluscs were decalcified before drying. Estimates of biomass and secondary production were made following the method outlined by Crisp (1971). For production estimates, the product of mean number and change in mean weight was employed. The method involved measurement of mortality and residual biomass for stocks with recruitments which had their age classes separable. The estimates were made for a period of twenty months (July 1978 - March 1980) with bimonthly sampling.

RESULTS

5.3.1. BIOMASS

The total macrofaunal biomass expressed as ash free dry weight for each station is given in Table 5.1. The major animal taxa breakdown of the biomass is shown in Table 5.2. Highest values were recorded at Station 5 and lowest at Station 9. Except at Station 5 throughout the study, in July 1978 at Station 2 and in September 1978 at Station 20, polychaetes as a group emerged as biomass dominant and accounted for more than 60% of the total macrofaunal biomass. At Station 5, molluscs as a group dominated and accounted for over 90% of the total macrofaunal biomass throughout the study. Table 5.3 shows the mean annual biomass of the three biomass dominant species at each of the four stations.

Fig. 5.1. shows the seasonal variation in total macrofaunal biomass at Station 2. There was no obvious seasonality in biomass. During the study, the biomass fell between July 1978 and May 1979 and continued at a low level with a peak in November 1979.

Changes in the biomass of major animal taxa at this station are shown in Fig. 5.2. The biomass of polychaetes fell between November 1978 and January 1980 with a small peak in July-September 1979. Molluscs decreased in biomass between July and September 1978 but rose slightly in November 1978. The biomass of crustaceans rose slightly between July and November 1978 and fell gradually between January and July 1979.

The biomass ranking of the species at Station 2 is shown in Table 5.4. Except in July 1978, Nereis diversicolor remained the biomass dominant species throughout the study and accounted for more than 70% of the total macrofaunal biomass. The mean biomass of all macrofauna at the station amounted to 0.99gm^{-2}. On the basis of mean weights three species, N. diversicolor, Nephtys hombergi and Carcinus maenas had individual weight greater than 500mg; measured as ash free dry weight. The three species accounted for more than 80% of total macrofaunal biomass at the Station.

The variation in the biomass of the top ranked species at station 2 is shown in Fig. 5.3. The biomass of N. diversicolor fell between September 1978 and May 1979 and was followed by great fluctuations. C. capitata showed a seasonal trend in biomass with increase in the summer months with peaks in September but fell in the winter months. Eteone longa declined in biomass throughout the study with summer peaks between July and November.

Table 5.1.

VARIATION IN TOTAL MACROFAUNAL BIOMASS ($g.m^{-2}$)

JULY 1978- MARCH 1980

	STATION 2	STATION 5	STATION 9	STATION 20
1978 July	3.1888	89.3945	2.7456	3.3426
Sept	1.5842	120.6608	3.9266	8.8364
Nov	1.9747	138.7609	0.5265	2.0893
1979 Jan	1.1299	80.5572	0.2782	2.2098
March	0.6707	100.0813	0.2902	2.0973
May	0.2544	53.0930	2.2228	2.6443
July	0.8393	51.6104	0.2736	2.9642
Sept	0.4361	149.6768	0.3273	1.1988
Nov	2.2346	111.3371	0.2953	1.6756
1980 Jan	0.1418	43.2008	0.0928	1.5522
March	0.4476	56.3906	0.2067	2.0985
Mean biomass	0.9944g m^{-2}	90.5332g m^{-2}	0.8517g m^{-2}	2.5622g m^{-2}

Table 5.2. BIOMASS REPRESENTATION (per m^2 as % of total) OF MAJOR ANIMAL TAXA AT THE SELECTED STATIONS

	STATION 2				STATION 5				STATION 9				STATION 20			
	Polych.	Crust.	Moll.	Others	Polych.	Crust.	Moll.	Others	Polych.	Crust.	Moll.	Others	Polych.	Crust.	Moll.	Others
1978																
July	32.16	0.20	67.63	-	1.51	0.16	98.33	-	98.32	0.84	0.84	-	65.41	0.54	34.05	-
Sept	91.93	7.48	0.61	-	1.30	0.22	98.45	0.03	99.95	0.05	-	-	25.56	72.71	1.74	-
Nov	87.66	11.42	0.91	-	6.33	2.25	91.40	0.02	99.60	0.40	-	-	96.66	0.66	3.68	-
1979																
Jan	99.90	0.10	-	-	4.47	0.36	95.17	-	100.0	-	-	-	97.02	0.53	2.44	-
March	98.85	1.15	-	-	4.19	0.01	95.81	-	100.0	-	-	-	98.43	0.85	0.72	-
May	99.90	-	-	0.10	8.72	0.03	91.17	0.08	99.57	0.43	-	-	86.01	0.26	13.74	-
July	98.00	2.00	-	-	9.65	0.06	90.29	-	91.16	5.41	-	3.44	58.0	5.7	36.4	-
Sept	100.0	-	-	-	3.42	0.01	96.66	-	100.0	-	-	-	96.60	0.40	3.00	-
Nov	100.0	-	-	-	1.79	0.16	98.06	-	100.0	-	-	-	96.53	0.41	3.07	-
1980																
Jan	100.0	-	-	-	7.32	0.03	92.65	-	100.0	-	-	-	99.43	0.44	0.13	-
March	100.0	-	-	-	2.80	0.23	96.97	-	100.0	-	-	-	98.96	0.21	0.83	-

	Average Biomass $mg.m^{-2}$	% of total macrofaunal biomass
STATION 2		
Nereis diversicolor	899.0	76.8
Capitella capitata	33.0	2.8
Eteone longa	24.0	2.1
STATION 5		
Mercenaria mercenaria	80207	86.8
Nephtys hombergi	1496.0	1.62
Caulleriella caputesocis	1031.0	1.12
STATION 9		
Capitella capitata	496.0	48.8
Nereis diversicolor	313.0	30.8
Eteone longa	7.00	0.01
STATION 20		
Nephtys hombergi	1630.0	58.4
Caulleriella caputesocis	272.0	9.7
Abra nitida	264.0	9.5

Table 5.3. Mean biomass of three biomass dominant species at each of the four selected stations

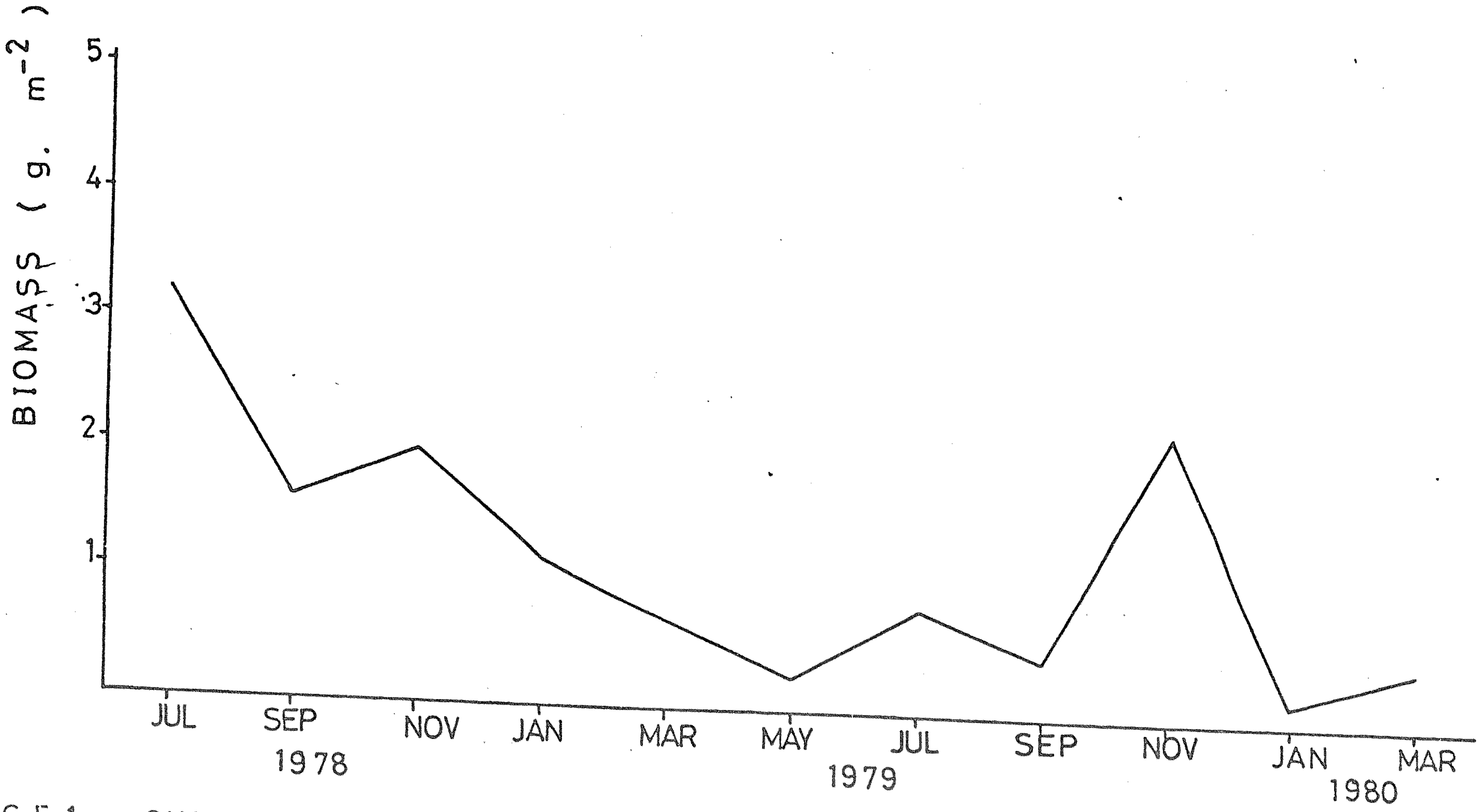


FIG. 5. 1. CHANGES IN TOTAL MACROFAUNAL BIOMASS AT STATION 2

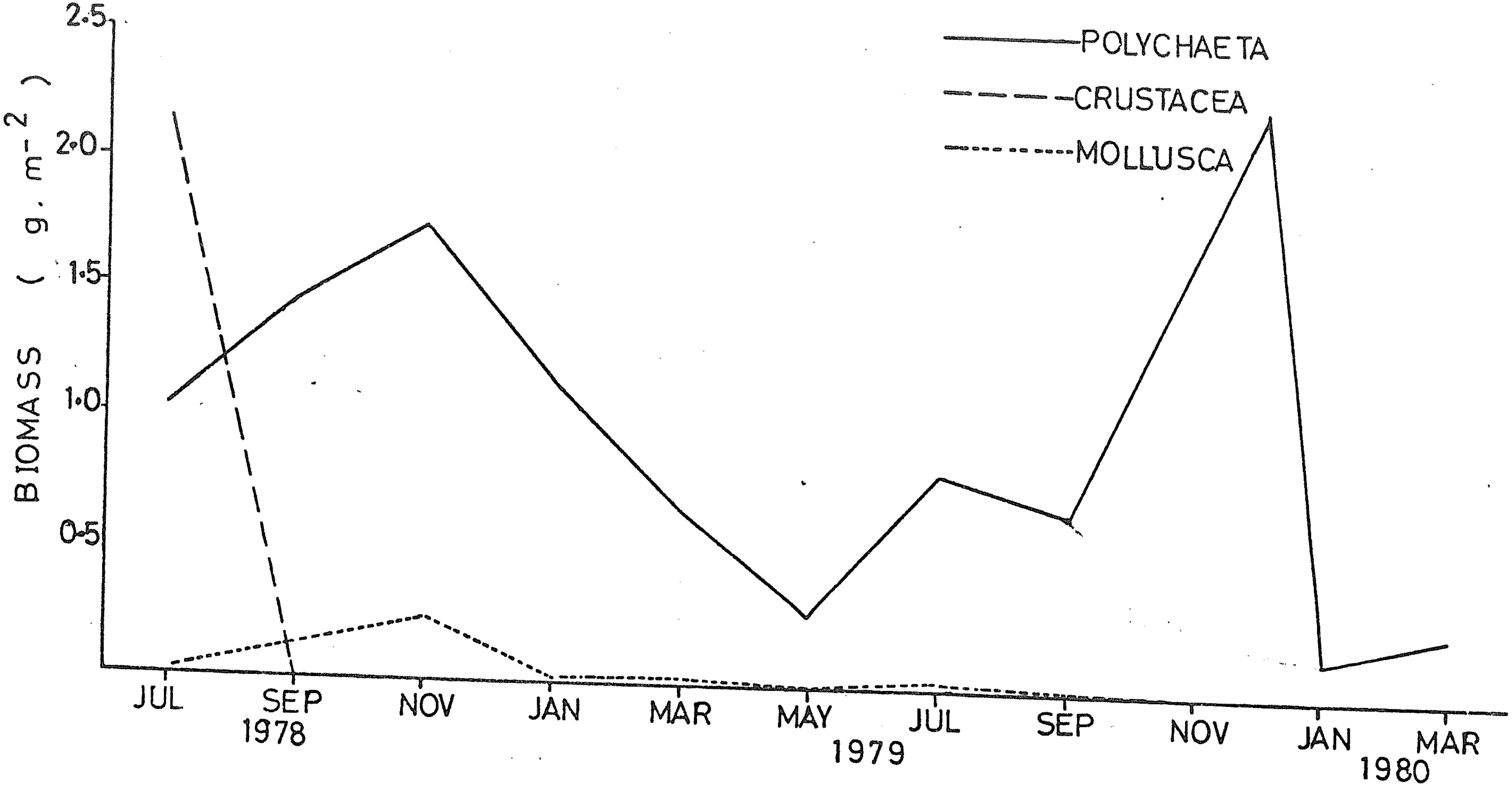


FIG.5.2. CHANGES IN BIOMASS OF MAJOR ANIMAL TAXA AT STATION 2

Table 5.4

STATION 2

BIOMASS RANKING OF TOP 7 SPECIES THROUGHOUT THE STUDY PERIOD (July 1978-March 1980)

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	March
Abra nitida	1	-	-	-	-	-	-	-	-	-	-
Nephtys hombergi	2	-	4	2	-	-	-	-	-	-	-
Cerastoderma edule	3	-	6	-	-	-	-	-	-	-	-
Caulleriella caputesocis	4	4	7	4	5	6	-	4	-	-	3
Crangon crangon	5	-	-	-	-	-	-	-	-	-	-
Mercenaria mercenaria	6	-	-	-	-	-	-	-	-	-	-
Eteone longa	7=	5	3	3	2	3	5	3	3	3	2
Philomedes globosus	7=	-	-	-	-	-	-	-	-	-	-
Nereis diversicolor	-	1	1	1	1	1	1	1	1	1	1
Carcinus maenas	-	2	2	-	-	-	-	-	-	-	-
Unidentified polychaete	-	3	-	-	-	-	-	-	-	-	-
Capitella capitata	-	6	-	6	3	2	2	2	2	2	4
Polydora ciliata	-	7	-	7=	-	4	4	-	-	-	-
Sabella pavonina	-	-	5	7=	-	-	-	-	-	-	-
Anaitides maculata	-	-	-	5	-	-	-	-	-	-	-
Idotea linearis	-	-	-	-	4	-	-	-	-	-	-
Unidentified mite	-	-	-	-	-	5	-	-	-	-	-
Praunus flexuosus	-	-	-	-	-	-	3	-	-	-	-
Corophium insidiosum	-	-	-	-	-	-	6	-	-	-	-

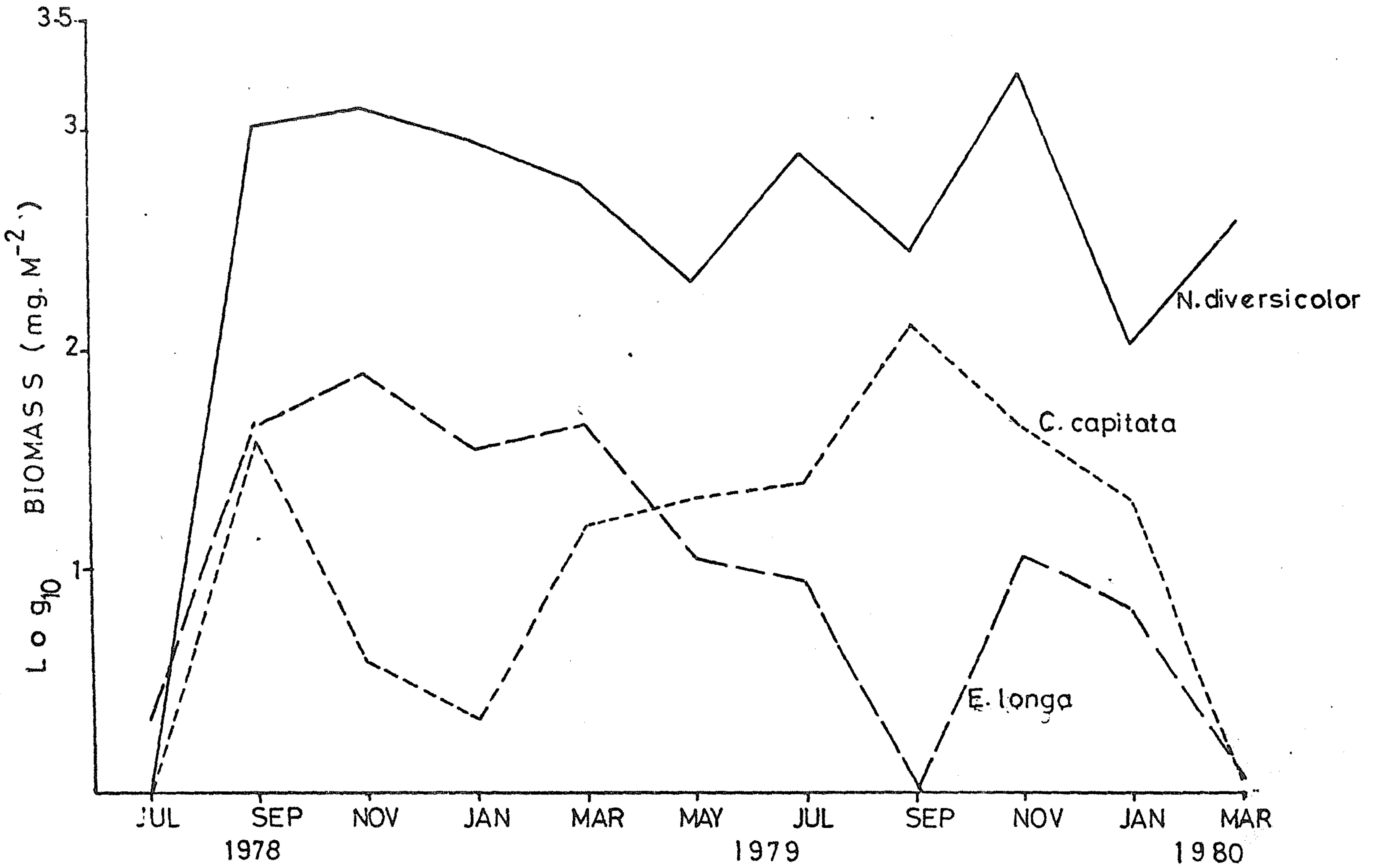


FIG.5.3. CHANGES IN BIOMASS OF DOMINANT SPECIES AT STATION 2

The total macrofaunal biomass at Station 5 is shown in Fig.5.4. The biomass increased in late summer and early autumn with peaks in September and November. There were drastic falls in the winter months particularly in January. The changes in the biomass of major animal taxa are presented in Fig. 5.5. Molluscs as a group were biomass dominant throughout the period of study. Their biomass remained high and constant with only small increases in November 1978 and September 1979. The biomass of polychaetes rose between July 1978 and September 1979 with peaks in November 1978 and September 1979. The biomass fell slightly from November 1979 onwards. The biomass of crustaceans remained low and fluctuated throughout the period of study. Increases in biomass occurred in November 1978, November 1979 and March 1980.

Based on biomass ranking, _Mercenaria_ _mercenaria_ was the biomass dominant species. Table 5.5. shows the biomass ranking of top ten species. Changes in the ranking position of other species were due to changes in their densities. _Mercenaria_ alone accounted for about 88% of the total macrofaunal biomass at this station. The mean biomass for all macrofaunal assemblage at this Station amounted to 90.53gm^{-2}.

The changes in biomass of the dominant species at this station are shown in Fig. 5.6. The biomass of _Mercenaria_ was high and stable throughout the study with peaks in September and November 1979. _N._ _hombergi_ and _Caulleriella_ _caputesocis_ showed a similar trend in biomass between July 1978 and January 1980. During the period, the biomass showed an obvious seasonality, increasing in the summer months with peaks in May-July 1979. At the end of sampling in March 1980, the biomass of _N._ _hombergi_ fell, but that of _C._ _caputesocis_ rose slightly.

The biomass of total macrofaunal assemblage at Station 9 is presented in Fig. 5.7. The biomass decreased between July 1978 and March 1980 and remained low except for a peak in September 1978 and May 1979. Polychaetes as a group were biomass dominant and their biomass amounted to more than 98% of the total macrofaunal biomass.

The biomass of major animal taxa at this station is shown in Fig. 5.8. The mollusca were represented only once in July 1978 and had a biomass of 0.84% of the total macrofaunal biomass. Crustaceans, as a group, showed variations in their biomass with time, and comprised between 0.05 and 0.84% of the total macrofaunal biomass at the station.

The biomass ranking of top five dominant species in terms of biomass at Station 9 is shown in Table 5.6. _Capitella_ _capitata_ was biomass dominant throughout except in July 1978 and March 1980. The

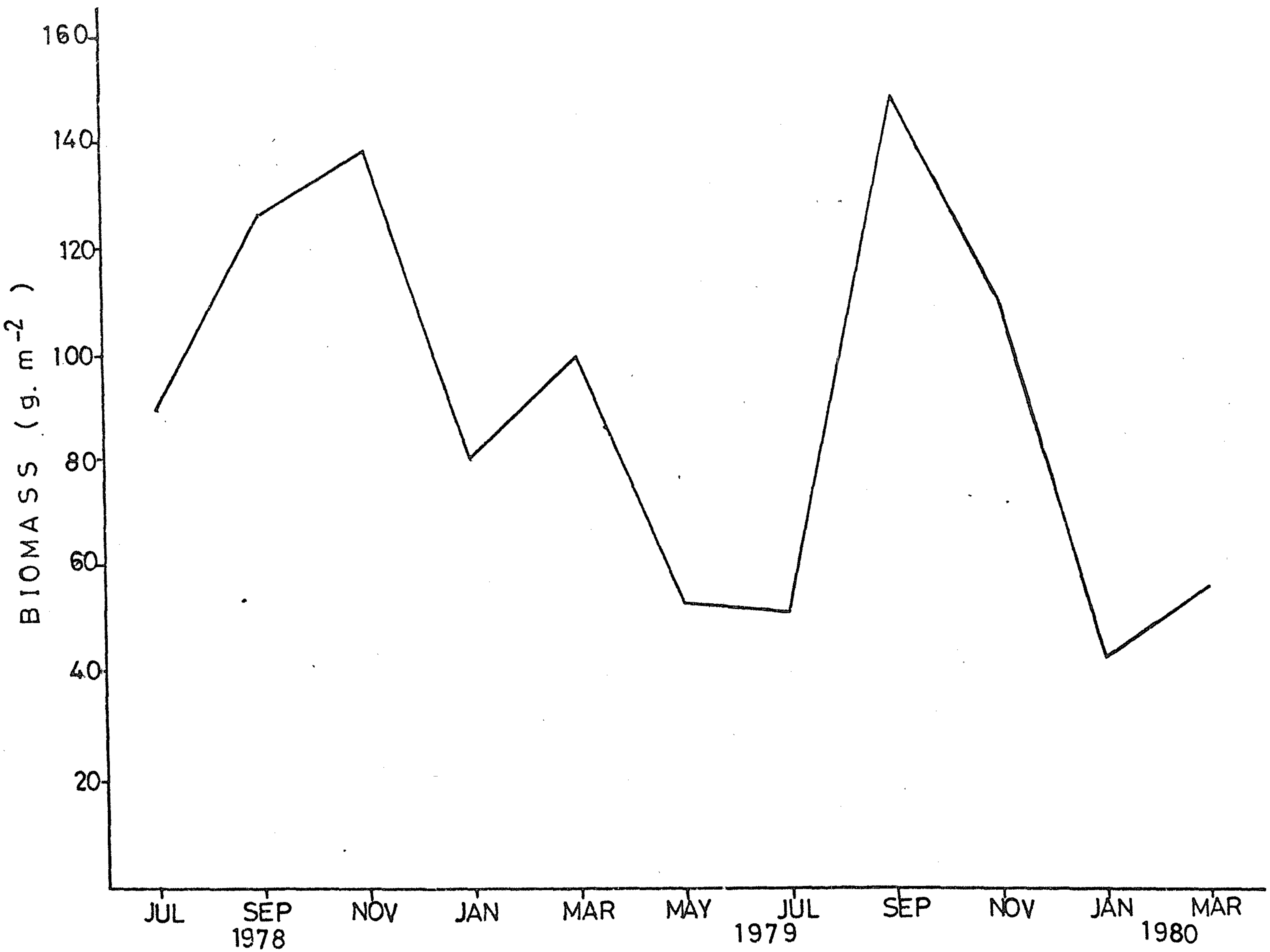


FIG.5.4. CHANGES IN TOTAL MACROFAUNAL BIOMASS AT STATION 5

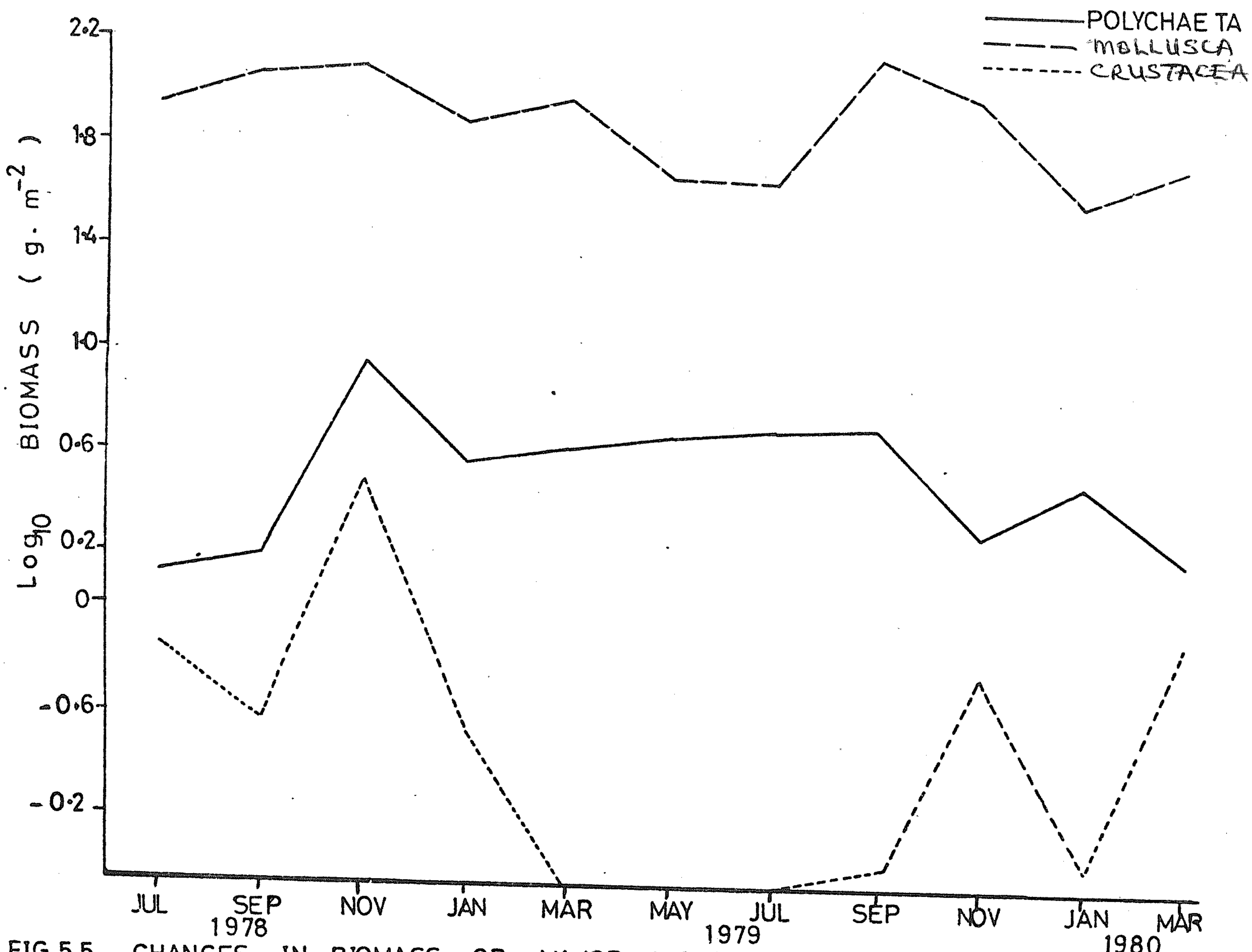


FIG.5.5. CHANGES IN BIOMASS OF MAJOR ANIMAL TAXA AT STATION 5

BIOMASS RANKING OF TOP 10 SPECIES THROUGHOUT STUDY PERIOD (July 1978-March 1980)

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Mercenaria mercenaria	1	1	1	1	1	1	1	1	1	1	1
Venerupis pullastra	2	2	-	4	-	-	-	2	-	-	-
Caulleriella caputesocis	3	5	3	3	3	3	3	4	5	5	3
Nephtys hombergi	4	6	4	2	4	2	2	3	2	2	2
Cirratulus cirratus	5	7	8	-	5	10	-	6	8	-	5
Melinna palmata	6	10	7	8	6	6	4	7	7	6	7
Carcinus maenas	7	10	2	6	-	-	-	-	6	-	6
Abra nitida	8	-	10	10	9	8	6	10	10	7	8
Nereis diversicolor	9	10	5	7	-	-	-	-	-	10	-
Cerastoderma edule	10	9	9	-	7	7	5	8	-	-	-
Crepidula fornicata	-	3	-	-	-	-	-	-	-	-	-
Nassarius reticulatus	-	4	6	5	-	4	-	5	3	4	4
Crangon vulgaris	-	8	-	-	-	-	-	-	-	-	-
Eteone longa	-	-	-	9	9	-	9	10	-	-	-
Nereis virens	-	-	-	-	2	5	7	8	4	3	-
Unidentified polychaete	-	-	-	-	7	-	-	-	-	-	-
Pycnogonum littorale	-	-	-	-	-	9	-	-	-	-	-
Philomedes globosus	-	-	-	-	-	-	8	10	-	8	10
Anaitides maculata	-	-	-	-	-	-	10	-	-	-	-
Lepidonotus squamata	-	-	-	-	-	-	-	-	9	-	-
Nucula turgida	-	-	-	-	-	-	-	-	-	8	-
Pariambus typicus	-	-	-	-	-	-	-	-	-	-	9

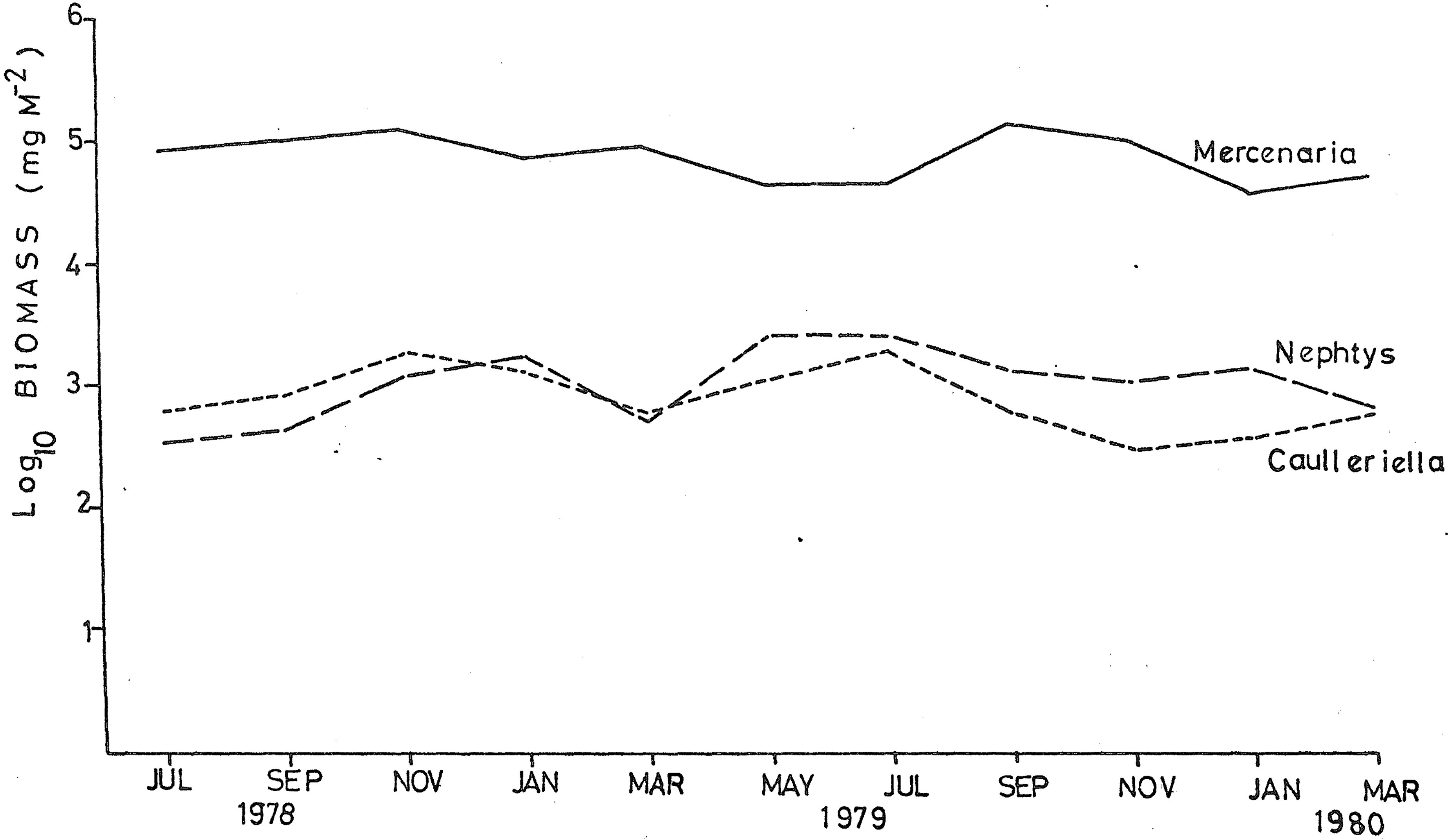


FIG.5.6. CHANGES IN BIOMASS OF DOMINANT SPECIES AT STATION 5

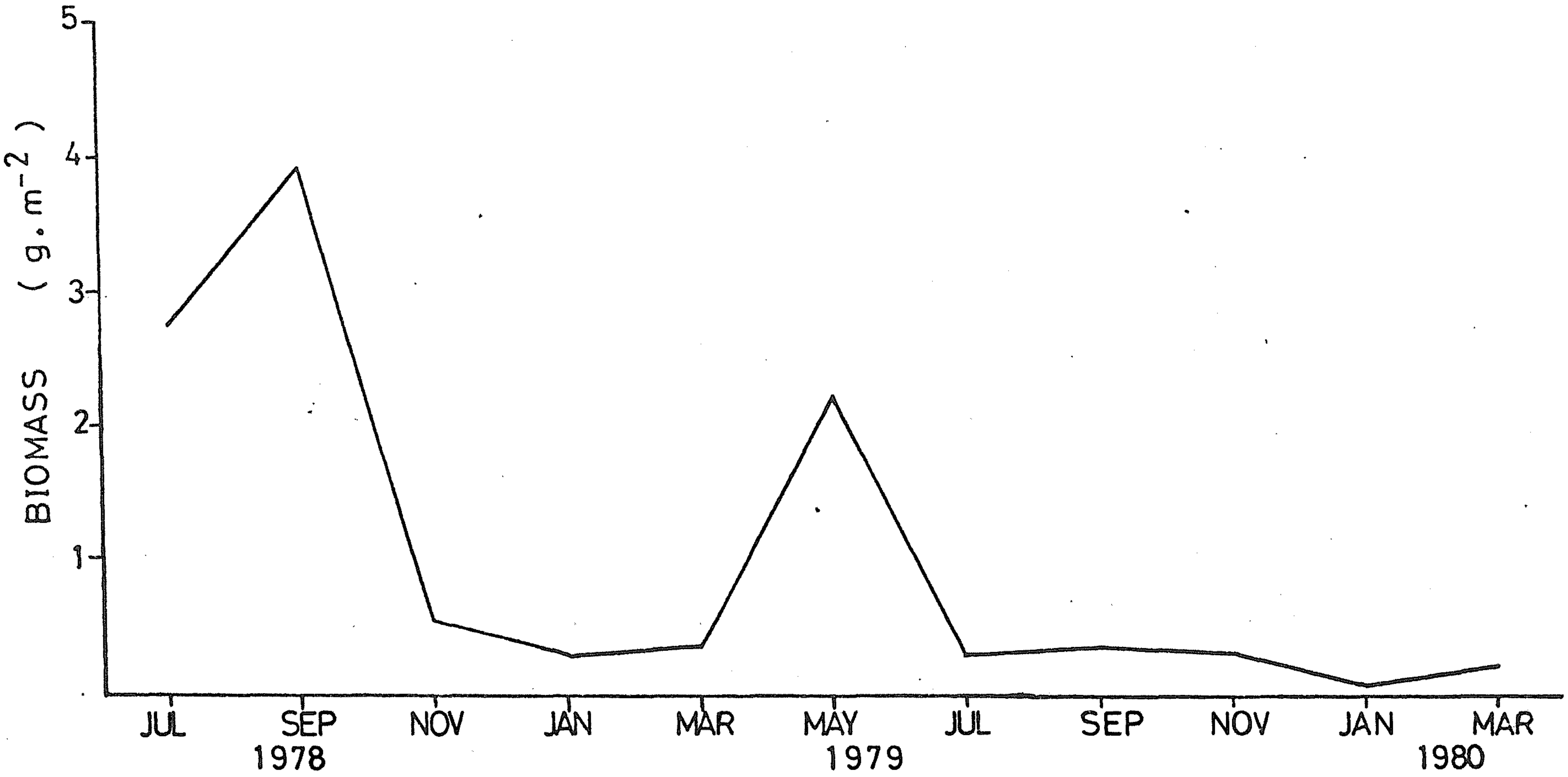


FIG.5.7. CHANGES IN TOTAL MACROFAUNAL BIOMASS AT STATION 9

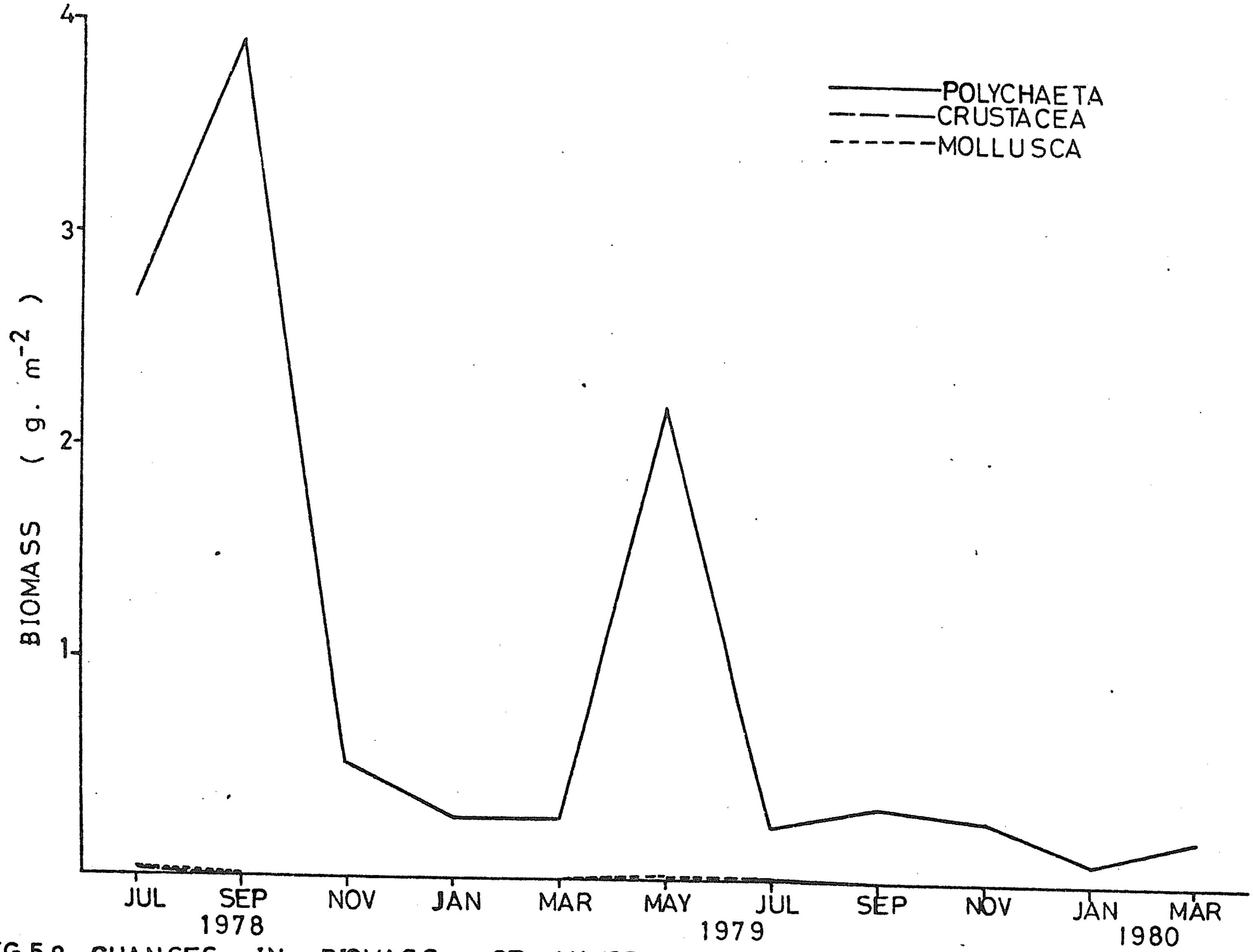


FIG.5.8. CHANGES IN BIOMASS OF MAJOR ANIMAL TAXA AT STATION 9

STATION 9

Table 5.6

BIOMASS RANKING OF TOP 5 SPECIES THROUGHOUT STUDY PERIOD (July 1978-March 1980

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Nereis diversicolor	1	3	2	2	4	2	2	2	2	3	1
Capitella capitata	2	1	1	1	1	1	1	1	1	1	2
Nephtys hombergi	3	-	4	-	-	-	-	-	-	2	-
Abra nitida	4	-	-	-	-	-	-	-	-	-	-
Caulleriella caputesocis	5	5	-	-	-	-	-	-	-	-	-
Sabella pavonina	-	2	3	4	-	-	-	-	-	-	-
Eteone longa	-	4	5	3	2	3	6	-	3	4	3
Cirratulus cirratus	-	-	-	-	3	-	-	-	-	-	-
Corophium insidiosum	-	-	-	-	-	4	-	-	-	-	-
Unidentified mysidae	-	-	-	-	-	5	-	-	-	-	-
Carcinus maenas	-	-	-	-	-	-	3	-	-	-	-
Gasterosteus aculeatus	-	-	-	-	-	-	4	-	-	-	-
Polydora ciliata	-	-	-	-	-	-	5	-	-	-	-

species accounted for 34-92% of total macrofaunal biomass at the station. Fluctuations in the ranking of N. diversicolor were due to the variation in recruitment of small individuals. In July 1978 and March 1980, when large numbers of small individuals of N. diversicolor were recruited into the sieve, the biomass was high and the animal was biomass dominant. Fluctuations in densities of other species probably accounted for their ranking positions. The total macrofaunal mean biomass amounted to $0.852gm^{-2}$.

Variations in the biomass of the dominant species at Station 9 are presented in Fig. 5.9. C. capitata showed great fluctuations in biomass, though ranked topmost at the station. N. diversicolor also decreased in biomass throughout the study with peaks in May 1979 and March 1980. E. longa fell in biomass throughout the study period except for peaks in July and November 1979.

The biomass of the total macrofaunal assemblage at Station 20 between July 1978 and March 1980 is shown in Fig. 5.10. The biomass remained stable throughout the study period with peaks in September 1978 and July 1979. The biomass of the major animal taxa is shown in Fig. 5.11. The first peak in the total macrofauna biomass in September 1978 was due to crustaceans reaching a biomass peak in that sample as evidenced from the graph. The second peak, however, was due to a peak in biomass by molluscs in July 1979. The high increase in the crustacean biomass in September 1978 was due to a large specimen of Carcinus (6.41g) which accounted for 72.5% of the macrofaunal biomass in the September 1978 sample at the station. When the biomass of Carcinus in September 1978 sample at the station is ignored, the biomass remained at a relatively high level between July 1978 and July 1979, but at a low level afterwards. The increase in the molluscan biomass in July 1979 was due to Abra nitida reaching its peak biomass. The polychaetes as a group had a steady biomass between July 1978 and May 1979 but fell between July and November 1979. The biomass of molluscs fell throughout the study except in May and July 1979.

The ranking of eight biomass dominant species is presented in Table 5.7. N. hombergi emerged as the top biomass dominant species except in September 1978, and accounted for more than 44% of the total macrofaunal biomass. Other species, except C. caputesocis and A. nitida showed wide fluctuations in their biomass ranking. The mean biomass of the macrofaunal assemblage at this station amounted to $2.562gm^{-2}$.

Changes in the biomass of three dominant species at the station

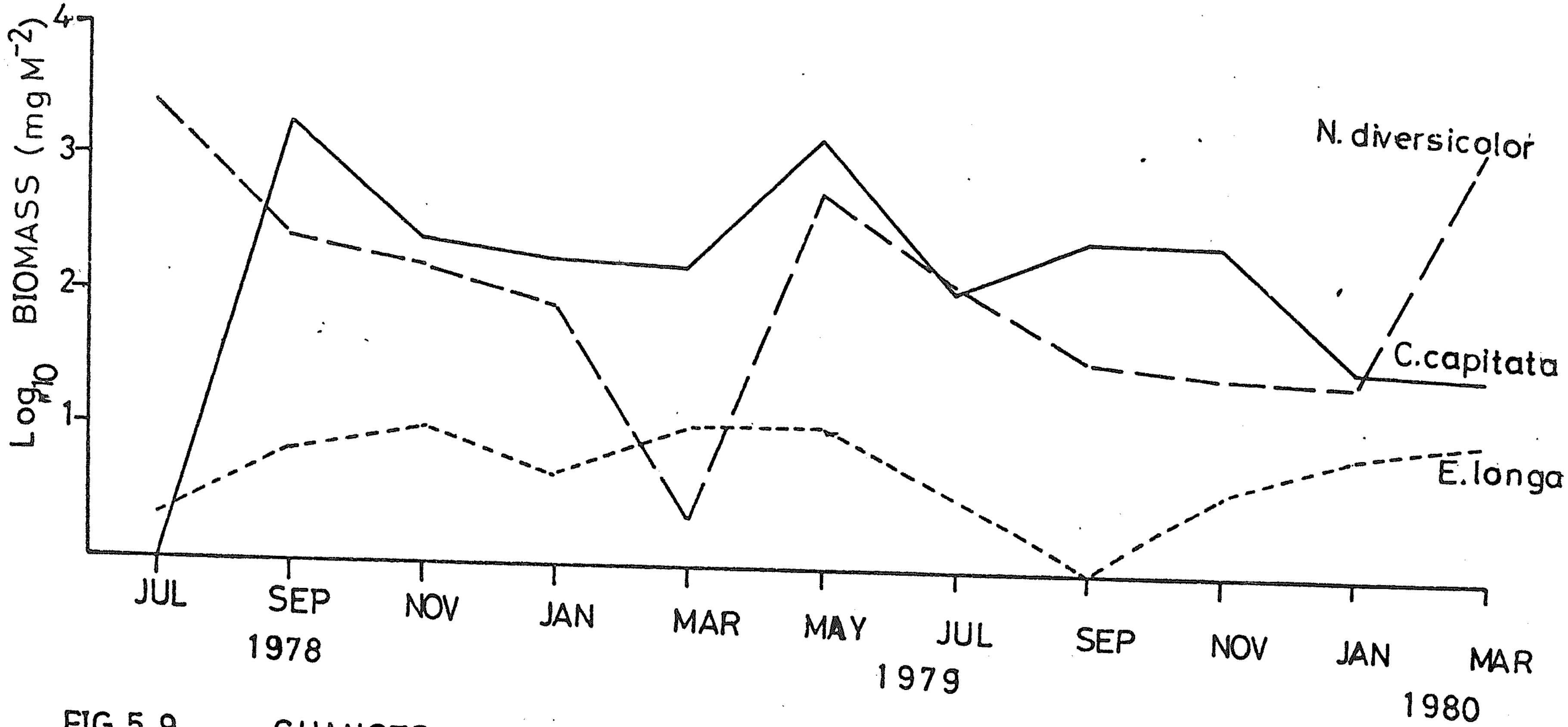


FIG. 5. 9. CHANGES IN BIOMASS OF DOMINANT SPECIES AT STATION 9

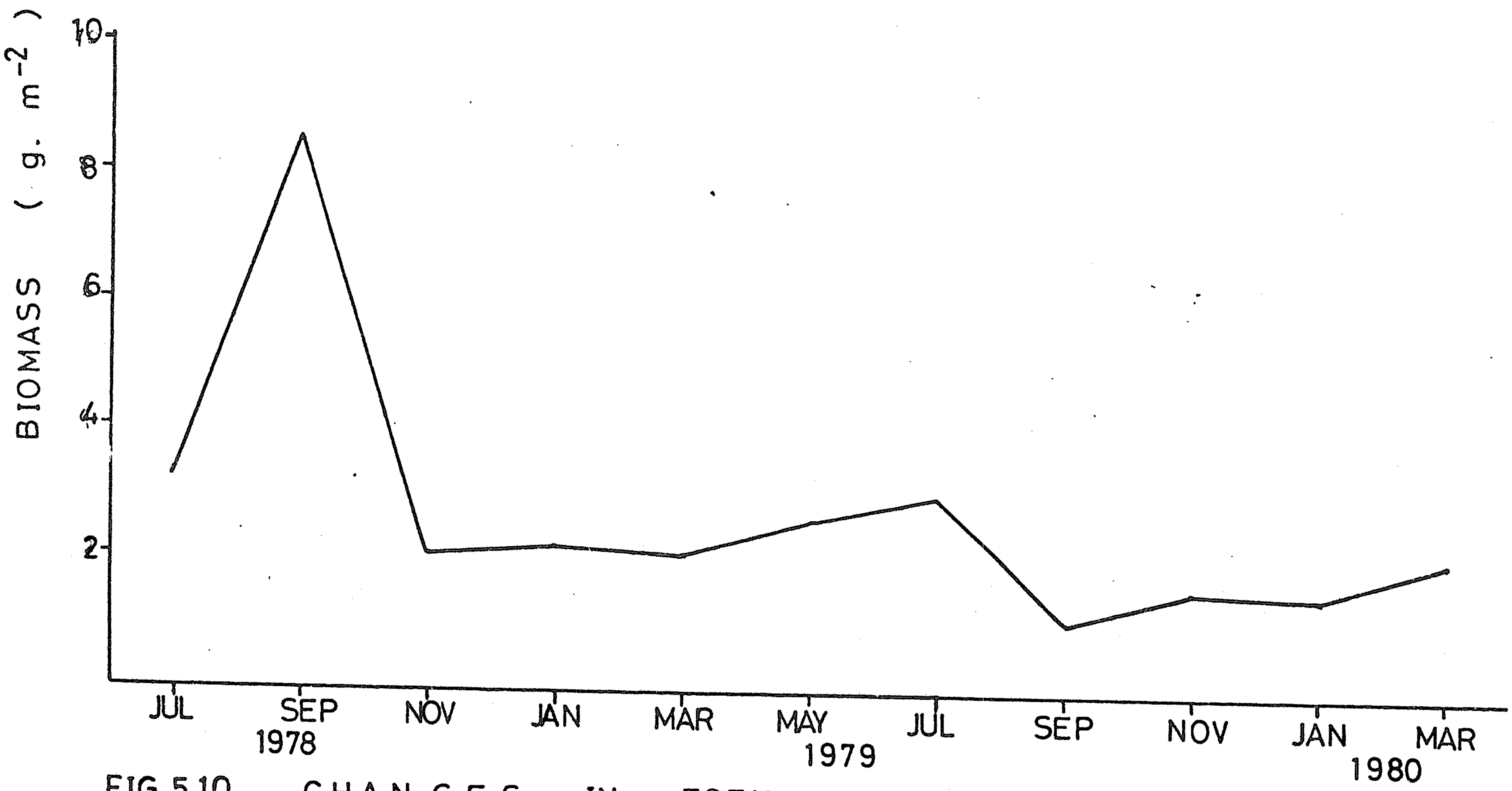


FIG. 5.10. CHANGES IN TOTAL MACROFAUNAL BIOMASS AT STATION 20

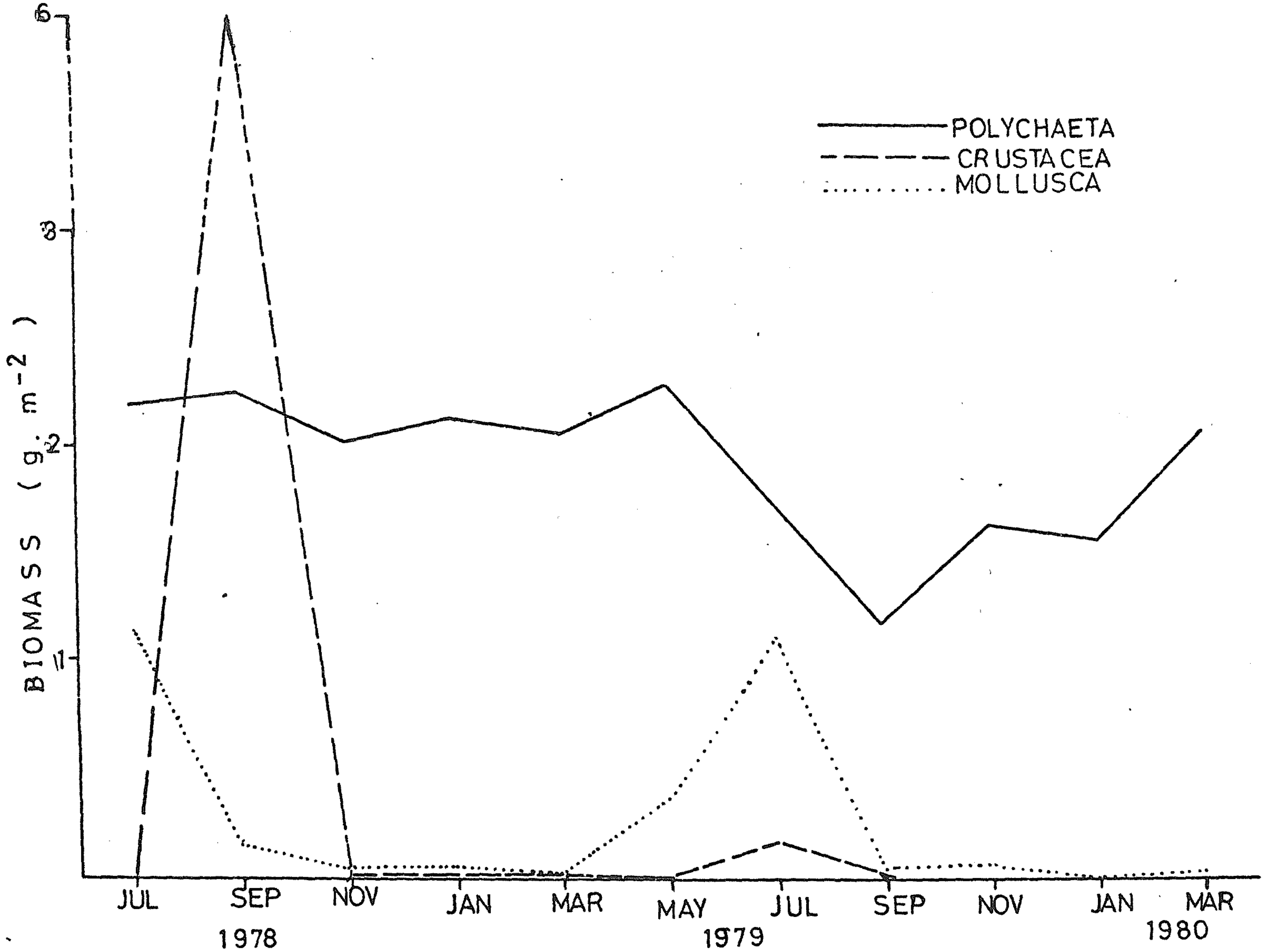


FIG.5.11. CHANGES IN BIOMASS OF MAJOR ANIMAL TAXA AT STATION 20

Table 5.7

STATION 20

BIOMASS RANKING OF TOP 8 SPECIES THROUGHOUT STUDY PERIOD (July 1978-March 1980)

	1978			1979						1980	
	July	Sept	Nov	Jan	Mar	May	July	Sept	Nov	Jan	Mar
Nephtys hombergi	1	2	1	1	1	1	1	1	1	1	1
Abra nitida	2	4	3	3	6	2	2	3	4	-	5
Caulleriella caputesocis	3	3	2	2	3	3	3	2	2	2	2
Nereis diversicolor	4	6	4	6	-	-	-	5	3	4	3
Eteone longa	5	5	-	4	4	4	6	-	7	3	4
Philomedes globosus	6	7	6	-	-	8	-	6	8	-	7
Polydora ciliata	7	8	-	7	-	6	-	-	-	5	7
Cerastoderma edule	8	-	5	-	-	-	-	-	-	-	-
Carcinus maenas	-	1	-	-	-	-	4	-	-	-	-
Cirratulus cirratus	-	-	7	-	-	-	-	-	-	-	-
Anaitides maculata	-	-	8	5	8	7	-	-	-	6	-
Eudorella truncatula	-	-	-	8	7	-	-	-	-	-	7
Nereis virens	-	-	-	-	2	-	-	-	-	-	-
Melinna palmata	-	-	-	-	5	-	-	-	-	-	-
Sabella pavonina	-	-	-	-	-	5	7	7	6	-	6
Abra alba	-	-	-	-	-	-	5	-	-	-	-
Capitella capitata	-	-	-	-	-	-	8	4	5	8	-
Corophium volutator	-	-	-	-	-	-	-	-	-	7	-

are shown in Fig. 5.12. The biomass of _N. hombergi_ was stable throughout the study. _C. caputesocis_ fell gradually in biomass between July 1978 and July 1979 with a peak in January 1980. _A. nitida_ showed seasonal trend in biomass at this station with peaks in July.

The mean biomass of some species whose production were estimated in the present study is shown in Table 5.8.

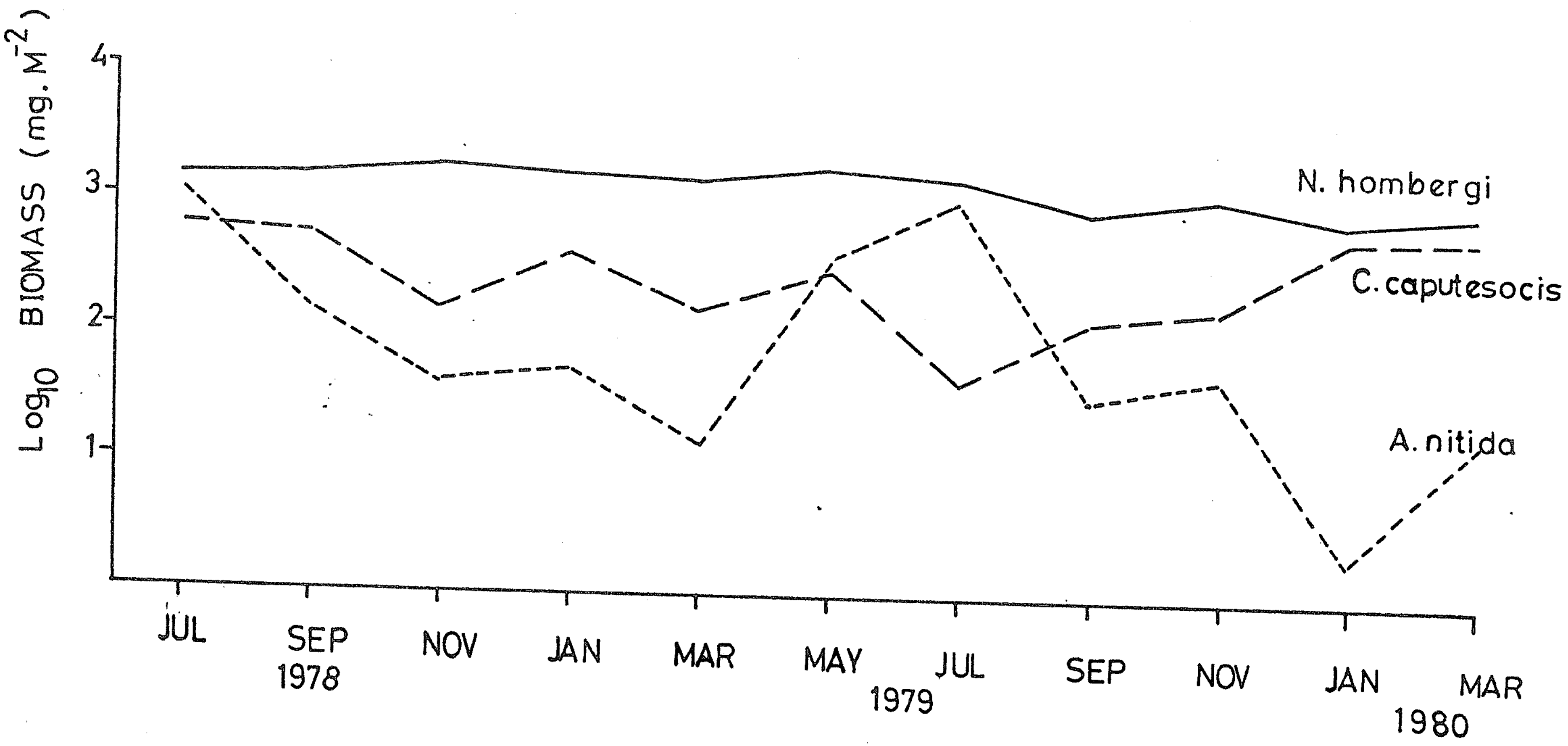


FIG. 5.12. CHANGES IN BIOMASS OF DOMINANT SPECIES AT STATION 20

SPECIES	STATION 2	STATION 5	STATION 9	STATION 20
Sabella pavonina	0.00359	0.00097	0.006734	0.00885
Melinna palmata	--	0.19279	-	0.00032
Capitella capitata	0.03289	0.00127	0.4963	0.00531
Caulleriella caputesocis	0.0117	1.0307	0.001305	0.2716
Nephtys hombergi	0.06377	1.4955	0.00304	1.5059
Nereis diversicolor	0.89916	0.1348	0.3128	0.03218
Eteone longa	0.0242	0.01376	0.00664	0.03178
Polydora ciliata	0.004	0.0012	0.00097	0.00414
Anaitides maculata	0.00106	0.00411	0.000	0.00597
Cirratulus cirratus	0.00021	0.09291	0.00149	0.00130
Abra nitida	0.11805	0.04514	0.00224	0.2639
Mercenaria mercenaria	--	80.207	--	--

Table 5.8 Mean biomass (gm^{-2}) of the benthic macrofaunal species used in estimating secondary production

5.3.2. SECONDARY PRODUCTION ESTIMATES

Two different approaches have been proposed by Crisp (1971) for estimating total secondary production of a population of animals in fundamental studies of an ecosystem. The first method sums up all growth increments of the members of the population as they occur during the period under consideration. The second approach ignores growth processes but considers the fate of the biomass that has been produced during a time interval. The latter approach assumes that the organic matter or energy produced will either remain as living matter at the end of study or have died or have been predated.

Most production estimates employ the second approach. Production can be estimated for stocks with no recruitment and for stocks with recruitment where age classes are either separable or not separable. In the present study, production was estimated for stocks with recruitment where age classes were separable. The number of species whose secondary production can be determined using this method of computation of mean number and weight increment is largely dictated by the presence of a sufficiently high population density allowing identification and separation of the year groups or cohorts. In this respect, production estimates were directed to only eighteen species listed below.

At sampling intervals of two months, the species were separated into cohorts. The mean number of individuals of each cohort was multiplied by the change in weight during the period of successive samples. The products from each sampling period were summed up and the annual production estimated.

5.3.2.1. Polychaetes

Sabella pavonina

At the start of study in July 1978, this species was absent at all four stations but was recorded in September 1978 at varying densities, viz. $1740m^{-2}$ at Station 2, $480m^{-2}$ at Station 20, but absent at Stations 5 and 9. The species occurred once in November 1978 at Station 9 and in March 1979 at Station 5. Peak recruitment at Stations 2 and 20 occurred in November 1978 and May 1979 respectively. The size frequency histograms of individuals of *S. pavonina* at each of the stations are shown in Figures 5.13 and 5.14.

Each of the specimens recovered during the study measured less than 4mm in length (less tentacular crown). The bulk of the population appeared to concentrate in a discrete group (1.7 - 3.0mm) and the mean

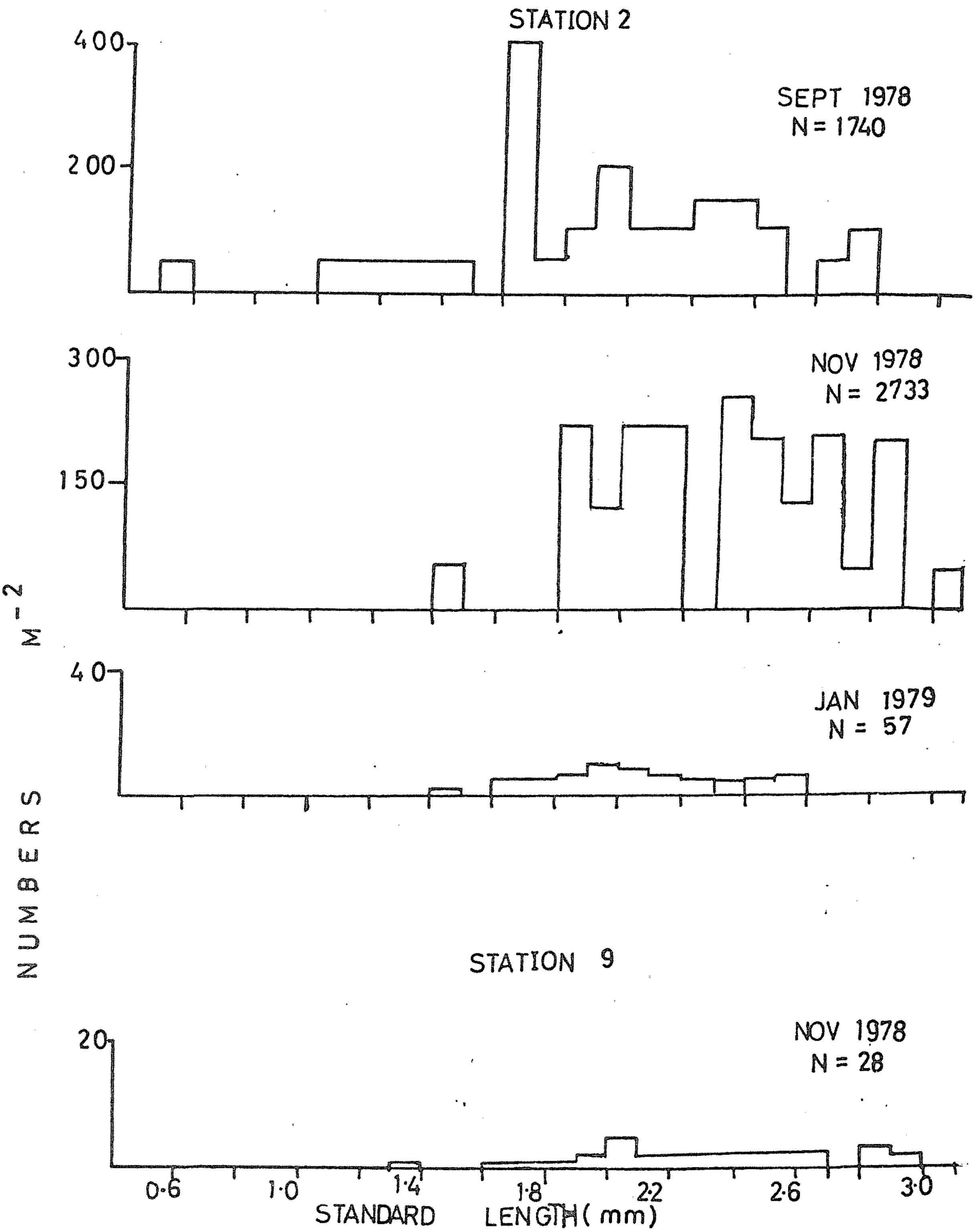


FIG. 5.13. SABELLA PAVONINA SIZE FREQUENCY HISTOGRAMS AT STATIONS 2 & 9

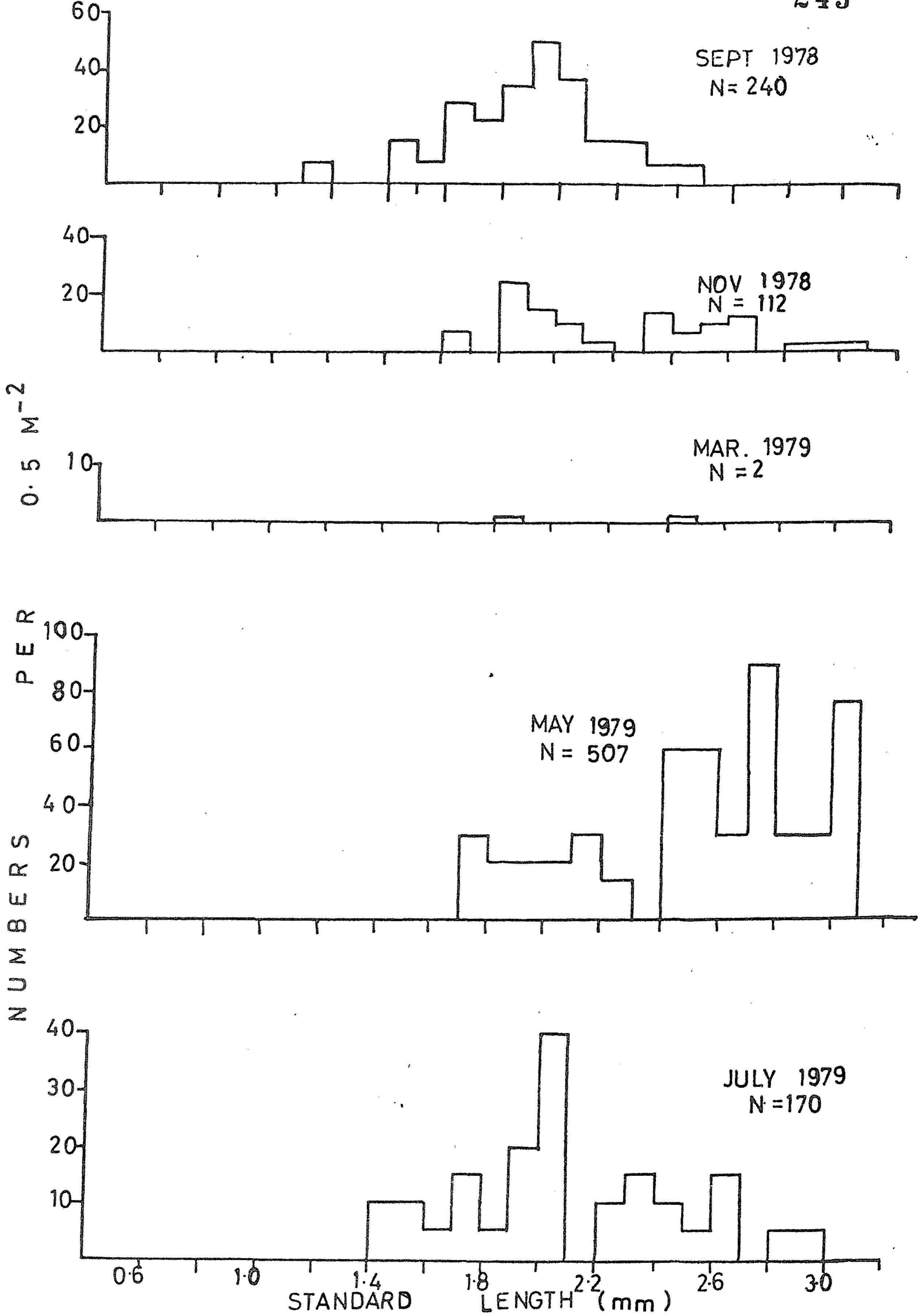


FIG. 5.14. SABELLA PAVONINA SIZE FREQUENCY HISTOGRAMS AT STATION 20

dry weight varied between 0.01 and 2mg. The individuals occurring in the same sample were regarded as belonging to the same year group since no coelomic gametes were apparent. It was assumed that spawning within the species took place outside the study area and that juveniles were recruited into the study areabut failed to mature.

At all stations the population declined in numbers during the winter months. At Station 20, a heavy recruitment occurred in May 1979 with heavy mortality in July, disappearing from samples by September 1979. A small recruitment also occurred in March 1980.

The annual and mean annual estimates of production for July 1978-March 1980 are shown in Table 5.9. Maximum annual production of $0.2747 gm^{-2} yr^{-1}$ was estimated at station 20 and the least estimate of $0.00837 gm^{-2} yr^{-1}$ at Station 2. The production increment computations for S. pavonina at all four stations are shown in Appendix V - VIII.

Melinna palmata

This ampharetid polychaete appeared as one of the dominant species in terms of abundance at Station 5 throughout the study, but only occasionally at Station 20. The July 1978 sample at Station 5 showed three distinct year classes which were designated '0', 'I' and 'II' year groups. The grouping was subsequently confirmed by further samples throughout the study period (Fig. 4.1 Section IV) The maximum width of the collar was measured and used in year group classification.

Observations on the presence and absence of the coelomic gametes revealed that M. palmata population in Southampton Water shed its ova twice a year, in June and December, in its second year. After breeding, the population suffered heavy post-spawning mortality. The '0' group individuals first recognised in July 1978 became the 'I' group in May 1979, recruiting throughout the year, with peak in May, when a new '0' group began to appear in the sieve.

The mean annual production estimate for M. palmata at Station 5 was $0.42 gm^{-2} yr^{-1}$. Production of M. palmata was at its peak during the 15 month period (July 1978-September 1979) when 83% of the total production for the 20-month period occurred, with 68% between July 1978 and July 1979 (Fig. 5.15).

The annual production estimates for each year class and cohort at Station 5 are presented in Table 5.10. The first cohort accounted for more than 98% of the total production. The production increments for M. palmata as computed are shown in Appendix IX.

	STATION 2	STATION 5	STATION 9	STATION 20
July 1978-July 1979	-	-	-	341.4144
Sept 1978-Sept 1979	0	-	-	342.574
Nov 1978-Nov 1979	0	-	139.139	342.574
Jan 1979-Jan 1980	41.85	-	-	342.574
March 1979-March 1980	0	-	-	4.3
Mean Annual Production	8.37	-	27.8287	274.6873
Mean Biomass (mg m^{-2})	3.59	0.97	6.73	8.85
$^{P}/_{B}$ ratio	2.35		4.13	31

Table 5.9 Annual and mean annual production of Sabella pavonina in mg m^{-2} yr^{-1} at four selected stations

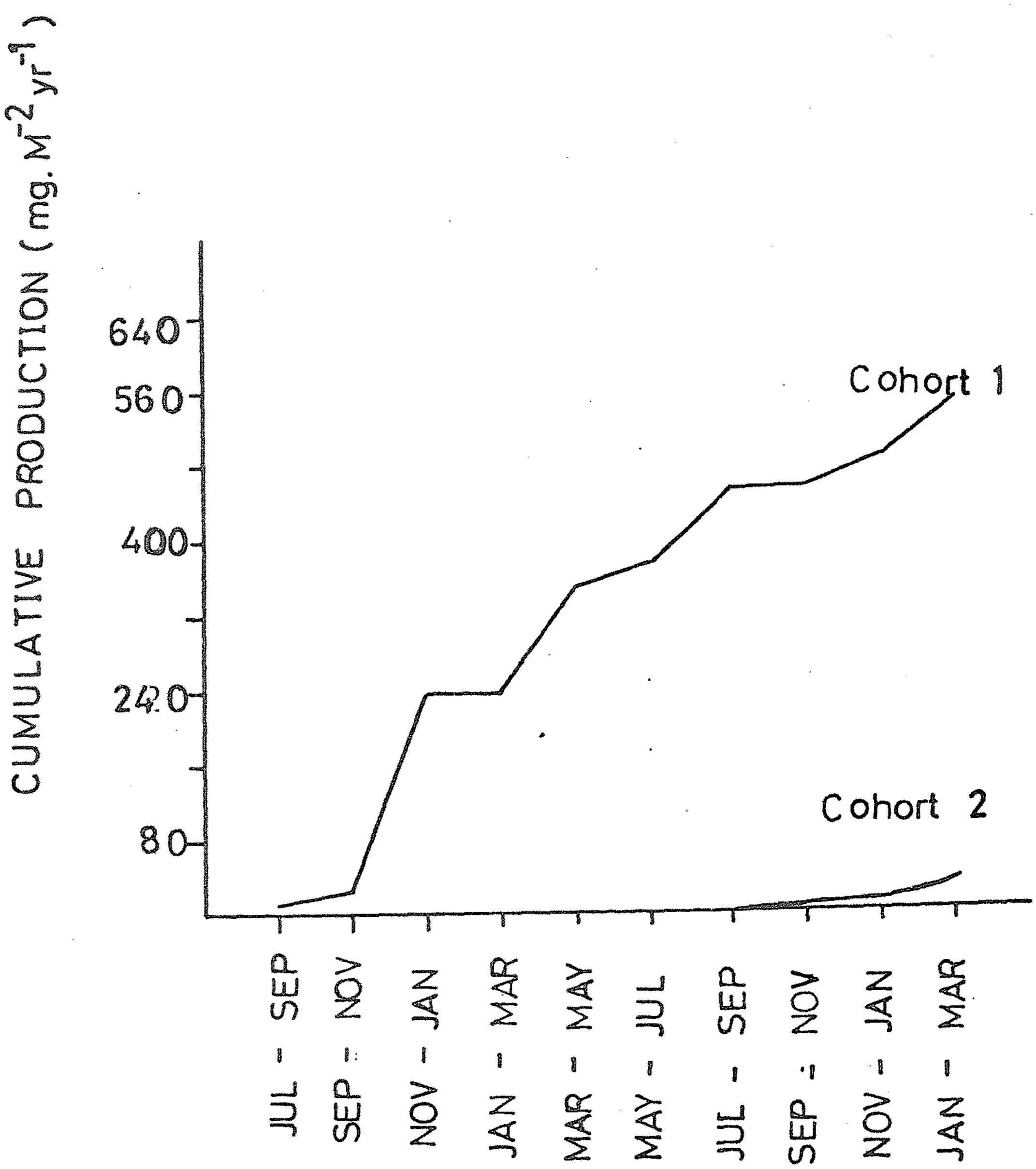


FIG.5.15. CUMULATIVE PRODUCTION FOR EACH COHORT OF M. PALMATA AT STATION 5 (JULY 1978 MARCH 1980)

	1st COHORT			2nd COHORT	Total Production
	0-1 Year Class	I-II Year Class	II-III Year Class		
July 1978-July 1979	109.040	254.270	9.00	3.480	375.790
Sept 1978-Sept 1979	187.730	254.270	9.00	3.480	454.480
Nov 1978-Nov 1979	187.730	244.000	9.00	8.990	486.730
Jan 1979-Jan 1980	224.740	238.420	0	8.990	472.150
March 1979-March 1980	281.940	28.460	0	8.990	319.390

Mean Annual Production = 421.708 mg m^{-2} yr^{-1}

Mean Biomass (gm^{-2}) = 0.193

$^{P}/_{B}$ ratio = 2.19

Table 5.10 Annual and Mean annual production of M. palmata in mg m^{-2} yr^{-1} at station 5 between July 1978 and March 1980

Capitella capitata

This capitellid polychaete proved to be numerically and biomass dominant at Station 9 and was important in terms of biomass at Station 2 throughout the study. At Station 5, three juveniles were recovered once in July 1978 and occurred at low densities ($< 10m^{-2}$) at Station 20. The September 1978 samples at Station 2 showed a single year group present but two year groups at Station 9.

Examination of the coelomic gametes proved that breeding in C. capitata in Southampton Water occurred throughout the year, with peaks in the late summer and the late winter months. Newly settled juveniles appeared in the sieved samples between September and March. Females produced benthic larvae in the summer months but planktonic larvae in the winter months. Small settlements resulting from the winter breeding extended over a period of months. The size requency histograms in Section IV suggest that the gonads could mature in less than six months especially during the summer. The population in Southampton Water bred at varying ages (usually less than a year) and suffered a heavy post breeding mortality.

The annual estimates of production for C. capitata in Southampton Water varied according to the sites. The annual and mean annual production estimates of C. capitata at all four stations are shown in Table 5.11. Production estimates were high at Station 9 ($1.62gm^{-2}\ yr^{-1}$) but low at Station 20 ($0.004gm^{-2}\ yr^{-1}$). The production increments for C. capitata at the stations as computed are shown in Appendix X.

Production for C. capitata at stations 2 and 9 was at its peak during the 12 month period, July 1978-July 1979 when 59.2% and 95.5% of the total production for the period of investigation occurred. At the stations, 48.6% and 45.7% respectively of the total production occurred between March and May 1979 (Fig. 5.16). Production of the animal remained low after March 1979 at Station 9 and low from September 1979 at Station 2.

Caulleriella caputesocis

This small cirratulid worm proved to be numerically dominant throughout the study at Stations 5 and 20 but occurred only occasionally at Station 2 and seldom at Station 9. Three distinct year classes were present between July and November 1978 at Station 5 and in July 1978 at Station 20 (see Section IV). The two smaller classes occurred in higher numbers but the group of largest animals in lower numbers.

	STATION 2				STATION 9				STATION 20
	COHORTS			Total annual Production	COHORTS			Total annual Production	
	1	2	3		1	2	3		
July 1978-July 1979	44.043	202.224	0	246.267	917.581	779.085	0	1696.666	0
Sept 1978-Sept 1979	44.043	202.224	169.498	629.305	917.581	854.216	0	1771.797	0
Nov 1978-Nov 1979	44.043	202.224	169.498	629.305	917.581	854.216	4559	1776.356	0.700
Jan 1979-Jan 1980	44.043	202.224	169.498	629.305	917.581	854.216	26.119	1797.936	0.700
March 1979-March 1980	0	202.224	169.498	371.722	176.118	854.216	26.119	1056.453	0.700
Mean annual Production		382mg m^{-2} yr^{-1}				1619.84mg m^{-2} yr^{-1}			0.42mg m^{-2} yr^{-1}
Mean Biomass (gm^{-2})		0.033				0.496			0.005
$^P/_B$ ratio		11.6				3.26			0.08

Table 5.11 Annual and mean annual production of C. *capitata* in mg m^{-2} yr^{-1} at selected stations

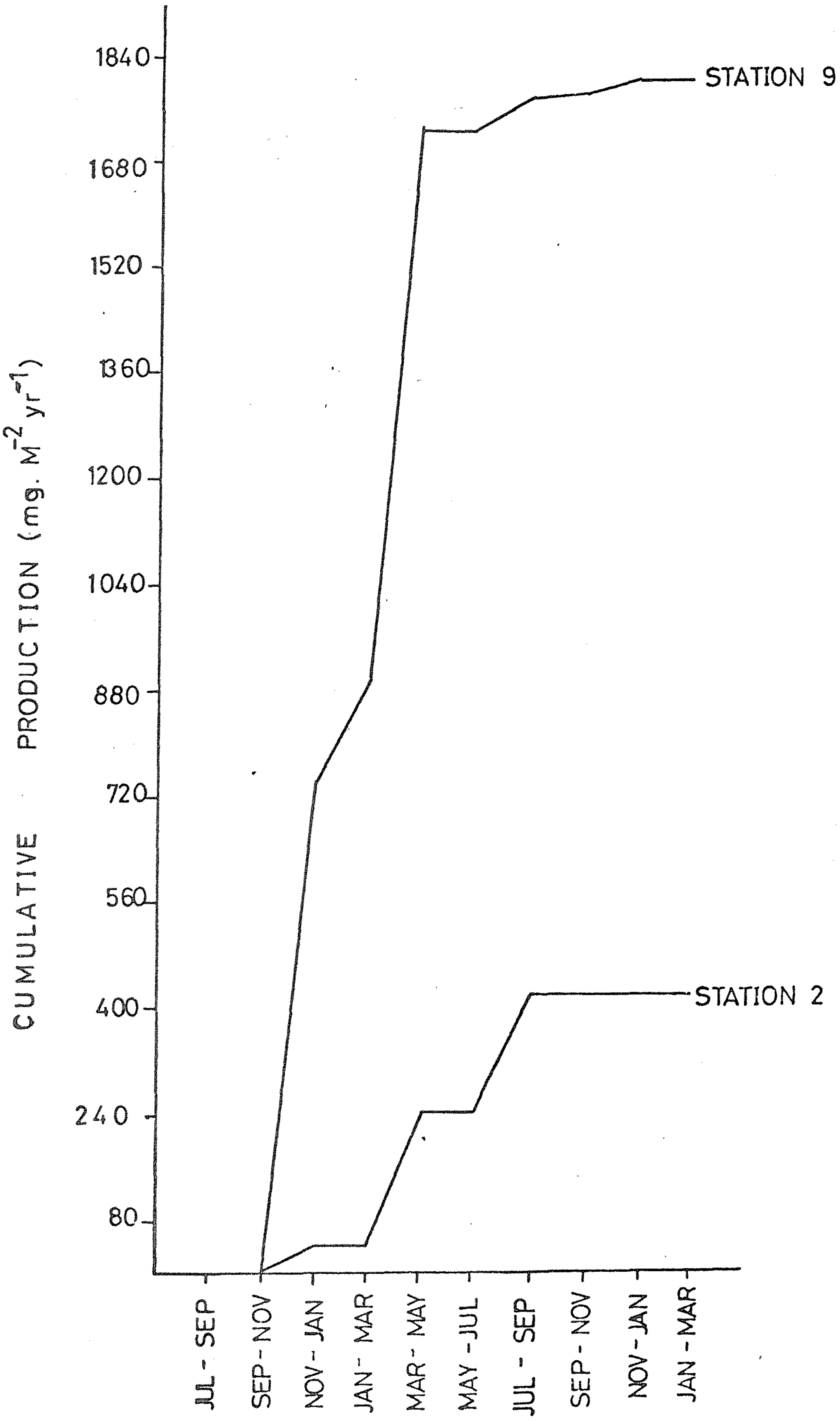


FIG.5.16. CUMULATIVE PRODUCTION FOR C. CAPITATA

No representatives of the third group were found after November 1978 until another sieve recruitment in May 1979 at Station 5, but the recruitment occurred subsequently in November 1978 at Station 20. The population at Station 2 comprised only two year classes.

Observations of the coelomic gametes showed that C. caputesocis spawned twice a year in Southampton Water, between June and October and between November and January. The prolonged breeding season in the summer months resulted in a series of small settlements. The species spawned when about a year old, and suffered heavy post spawning mortality. The unshed gametes were resorbed. Sieve recruitment of juveniles occurred over a period of months with peaks in October and May.

The estimates of annual production for C. caputesocis are presented in Table 5.12. The production varied between 0.00022gm^{-2} yr^{-1} at Station 9 to 5.81gm^{-2} yr^{-1} at Station 5. The computations of the annual production for C. caputesocis at each station are given in Appendix XI - XIV.

Nephtys hombergi

This nephtyid polychaete emerged as biomass dominant polychaete throughout the present study. The production of N. hombergi in various parts of Europe is well documented (Warwick and Price,1975; Warwick et al,1978; Kirkegaard,1978). Examination of the bimonthly samples in the present study showed that at least two year groups were present. As the animals in general tended to fragment, the year classes were separated by size frequency histograms based on the measurement of the body width of the third segment behind the head. Such method separated the year classes efficiently but whenever an overlap in the classes emerged, the use of probability paper was employed. The aging method using rings on the jaws was employed to confirm the ages of some individuals, though the rings in many cases were indistinct and produced less useful information compared with Kirkegaard's (1978) for North Sea specimens.

Examination of the coelomic gametes in the population of Southampton Water revealed that N. hombergi in the estuary spawned all the year with peaks between June and August and also in January, usually in its second year. The population suffered a post-spawning mortality with few 2-year old individuals surviving. Sieve recruitment reached its peak between September and March.

The annual and mean annual estimates of production for N. hombergi at each station are shown in Table 5.13. The cumulative percentage production at all three stations are shown in Fig. 5.17. Production was

	STATION 2			STATION 5			STN.9	STATION 20				
	COHORTS		Total Annual Production	COHORTS		Total Annual Production	Annual Production	COHORTS				Total Annual Production
	1	2		1	2			1	2	3	4	
July 1978-July 1979	12.354	0.268	12.602	5213.856	0	5213.856	0	1447.378	0	0	0	1447.378
Sept 1978-Sept 1979	12.354	0.268	12.602	5213.856	0	5213.856	1.080	1447.378	423.252	178.006	0	2048.637
Nov 1978-Nov 1979	12.354	0.268	12.602	7080.924	0	7080.924	0	1272.672	423.252	178.006	0	1873.931
Jan 1979-Jan 1980	12.354	0.268	12.602	5981.372	114.834	6096.206	0	1259.712	423.252	364.730	159.758	2207.452
Mar 1979-Mar 1980	0	0	0	5754.758	125.462	5580.220	0	1025.422	423.252	364.730	249.162	2062.565
Mean Annual Production	10.0816mg $m^{-2} yr^{-1}$			5806mg $m^{-2} yr^{-1}$			.216mg m^{-2} yr^{-1}	1928mg m^{-2} yr^{-1}				
Mean Biomass (gm^{-2})	0.012			1.031			0.001	0.272				
$^P/_B$ ratio	0.84			5.63			0.17	7.09				

Table 5.12 Annual and mean annual production estimates of <u>C. caputesocis</u> in mg m^{-2} yr^{-1} at selected stations (July 1978 - March 1980)

	STATION 2			STATION 5						STATION 20				
	COHORTS			COHORTS						COHORTS				
	1	2	Total	1	2	3	4	5	Total	1	2	3	4	Total
Jul 78-Jul 79	45.375	81.261	126.636	1142.179	1683.884	1303.294	65.754	0	4195.111	1564.655	706.837	51.814	0	2323.306
Sep 78-Sep 79	45.375	81.261	126.636	1142.179	1683.884	2108.974	65.754	0	5000.791	1564.655	706.837	69.766	0	2341.258
Nov 78-Nov 79	45.375	81.261	126.636	963.600	1683.884	2108.974	267.234	0	5023.692	1241.078	706.837	703.752	0	2651.667
Jan 79-Jan 80	0	80.201	80.201	963.600	1298.764	2108.974	520.662	50.720	3643.956	1241.078	576.987	703.752	5.750	2527.567
Mar 79-Mar 80	0	0	0	0	1033.366	1773.177	520.662	416.740	3743.945	811.958	569.907	766.266	291.125	2438.256
Mean Annual Production			92.022						4321.499					2456.4108
Mean Biomass (gm^{-2})		0.0510					1.4955					1.5059		
$^P/_B$ ratio		1.80					2.89					1.63		

Table 5.13. Annual and mean annual production of N. hombergi in mg m^{-2} yr^{-1} at the selected stations

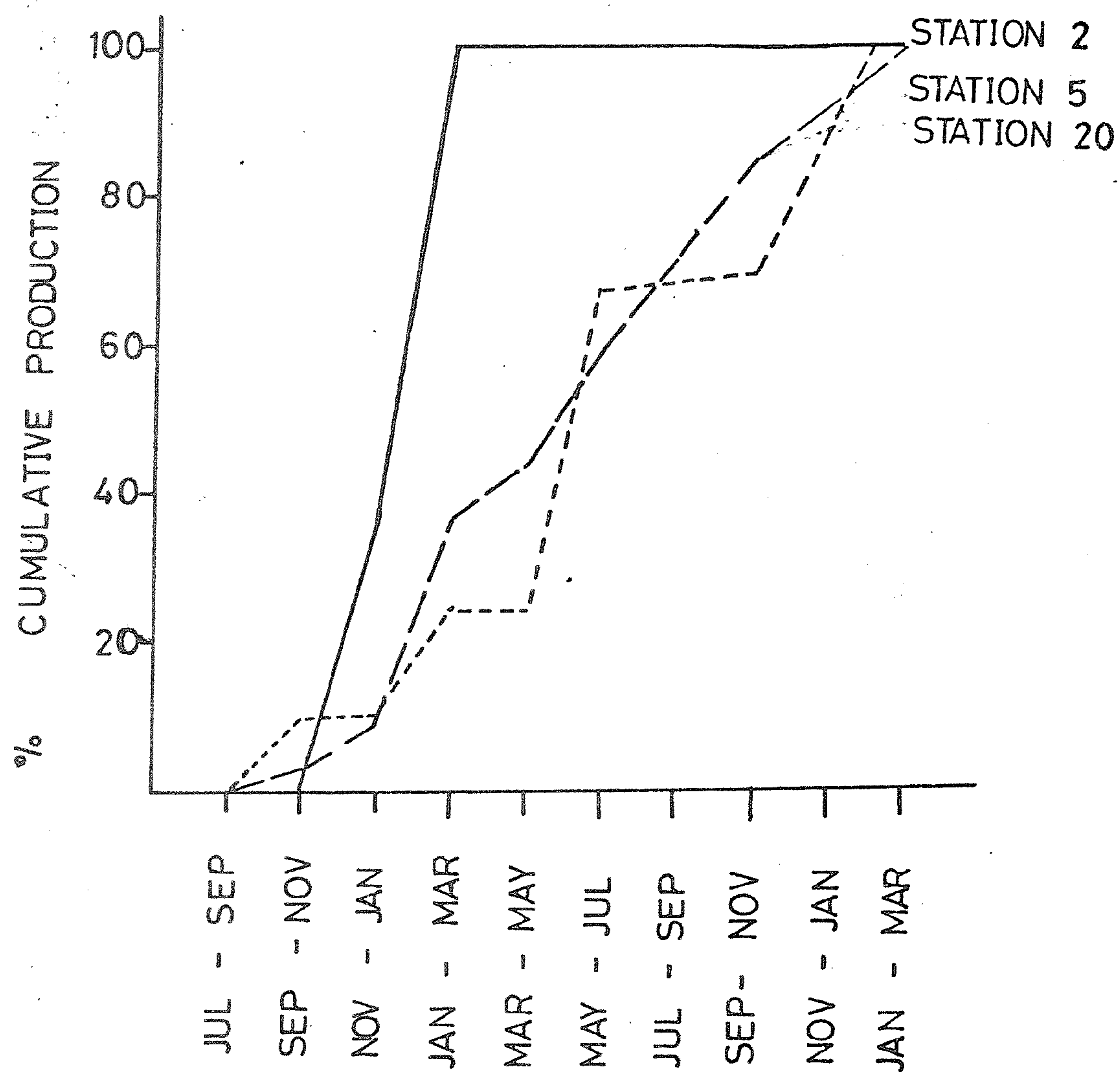


FIG.5.17. % CUMULATIVE PRODUCTION FOR N. HOMBERGI AT STATIONS 2, 5 & 20 (JULY 1978 MARCH 1980)

at its greatest during the three month period, November 1978 to January 1979 at Station 2, but between March and May 1979 at Station 20 when 63% and 43% respectively of the total annual production occurred. At Station 5, production was steady but peak production of 25% occurred between January and March 1979.

The annual production of N. hombergi ranged between 0.09gm^{-2} yr^{-1} at Station 2 and 4.32gm^{-2} yr^{-1} at station 5. The production increments as computed for N. hombergi at the four stations are shown in Appendix XV - XVII.

Nereis diversicolor

This species occurred in significant numbers at Stations 2 and 9 where it ranked dominant in terms of biomass throughout the study but showed less prominence at Stations 5 and 20. At stations 2 and 9, the species showed two or three year classes (Section IV) but the delicacy of the specimens often created some difficulty in obtaining intact specimens in large numbers. In this respect, the width of the first anterior segment behind the head was measured and used in classifying the year groups. Whenever an overlap occurred between the year groups, probability graph paper was used to separate them.

Spawning occurred throughout the year in the Nereis diversicolor population in Southampton Water, with peaks in April and August. The population suffered a rapid post-spawning mortality. Sieve recruitment took place throughout the year with peaks in November and March. The '0' group individuals first observed in November 1978 continued recruiting into the 0.5mm sieve until May 1979 when a peak in abundance was reached and the group became the 'I' group as the new '0' group started to make its appearance.

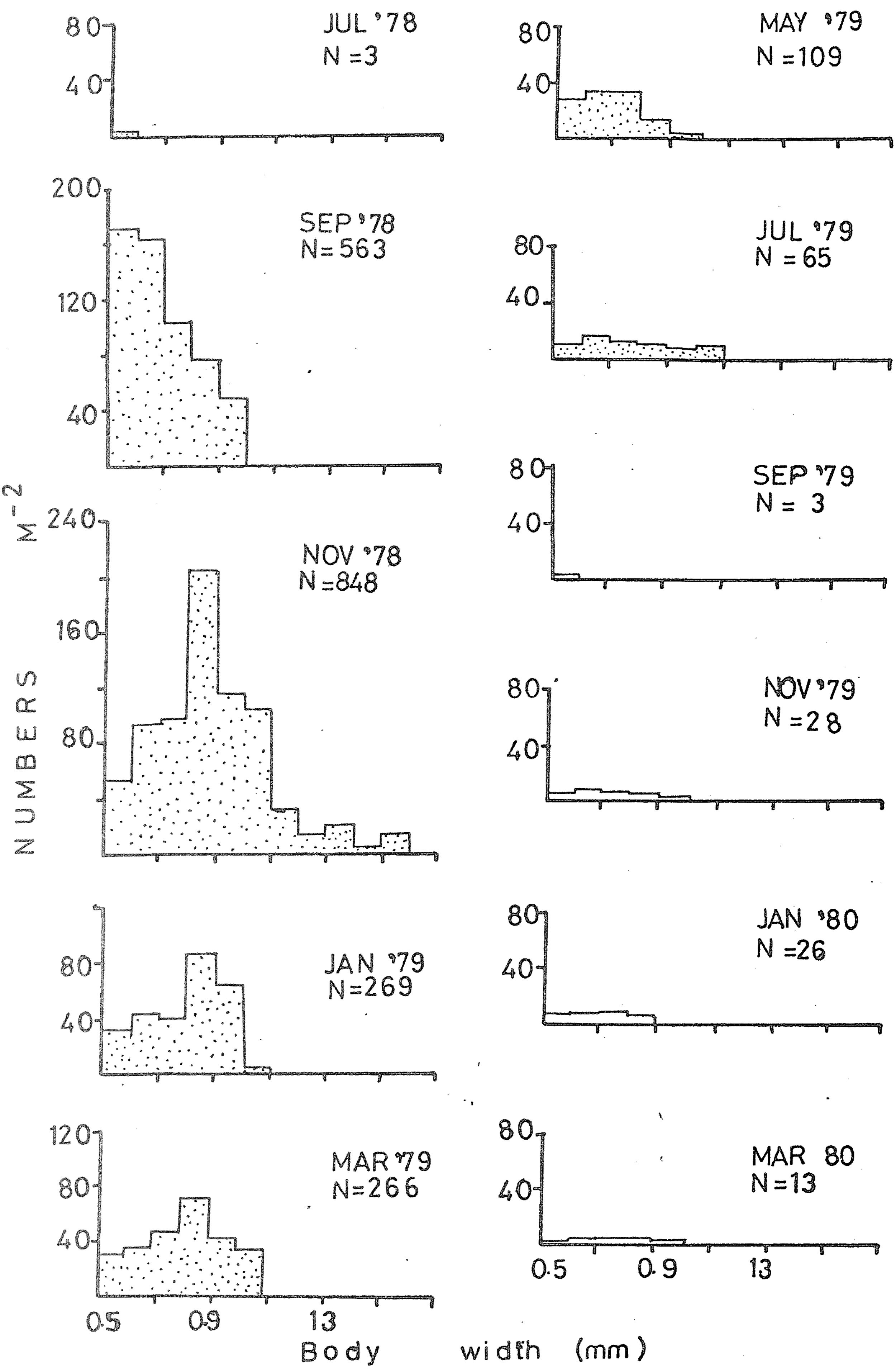
The annual and mean annual production for N. diversicolor at each of the stations are shown in Table 5.14. The annual production was highest at Station 2 with 4.36 gm^{-2} yr^{-1} and lowest at Station 5 with 0.08gm^{-2} yr^{-1}. The production increments for N. diversicolor at the stations as computed are shown in Appendix XVIII - XXI.

Eteone longa

This phyllodocid polychaete occurred in high numbers at Station 2 but in relatively lownumbers at the other stations. The size frequency histograms shown in Figs. 5.18 - 5.21 for the selected stations revealed that the polychaete was an annual in Southampton Water. Spawning took

	COHORTS					5	COHORTS					COHORTS			
	1	2	3	4	Total		1	2	3	4	Total	2	3	4	Total
Jul 78 to Jul 79	995.265	1071.467	0	0	2066.9120	0	500.692	600.627	4.175	0	1165.494	13.188	0	0	13.188
Sep 78 to Sep 79	995.265	1455.047	0	0	2450.312	82.800	500.692	660.627	12.950	0	1174.269	13.188	0	0	13.188
Nov 78 to Nov 79	4540.376	1455.047	874.08	0	6869.503	304.950	500.692	660.627	12.950	0	1174.269	13.188	96.46	0	109.64
Jan 79 to Jan 80	4025.245	1455.047	874.08	0	6354.3715	0	450.672	660.627	12.993	27.102	1154.394	13.188	96.46	0	109.64
Mar 79 to Mar 80	901.664	1455.047	1083.344	79.665	4421.3840	0	0	0	0	362.712	362.712	13.188	0	412.60	523.2
Mean Annual Production	4355.8164					77.550	1005.628					153.8			
Mean Biomass (gm^{-2})	0.8992					0.0809	0.3128					0.03218			
P/B ratio	4.84					0.96	3.22					4.78			

Table 5.14. Annual and mean annual production of N. *diversicolor* in mg m^{-2} yr^{-1} at the selected stations



IG.5.18. STATION 2 ETEONE LONGA SIZE FREQUENCY HISTOGRAMS

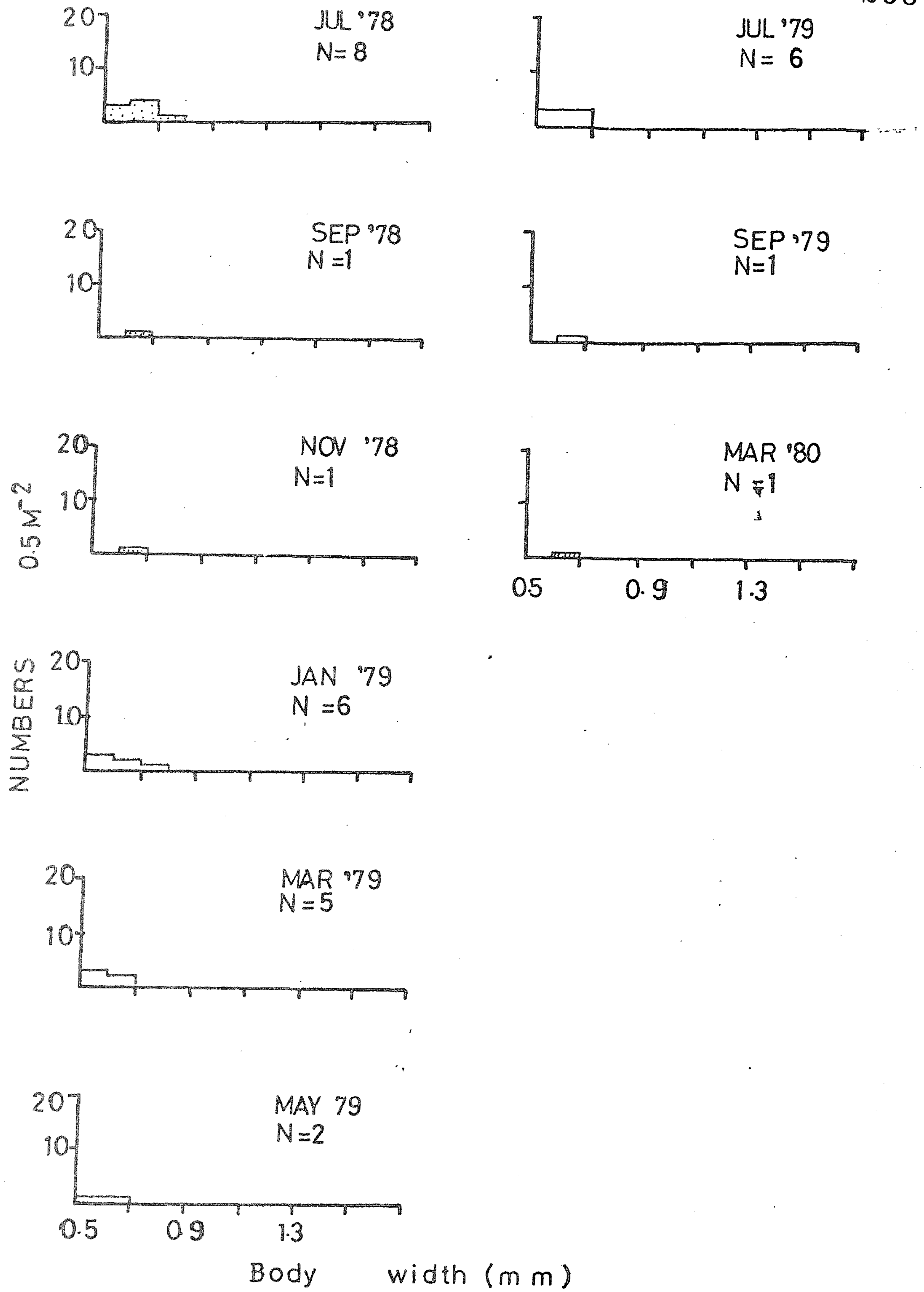


FIG.5.19. STATION 5 ETEONE LONGA SIZE FREQUENCY HISTOGRAMS

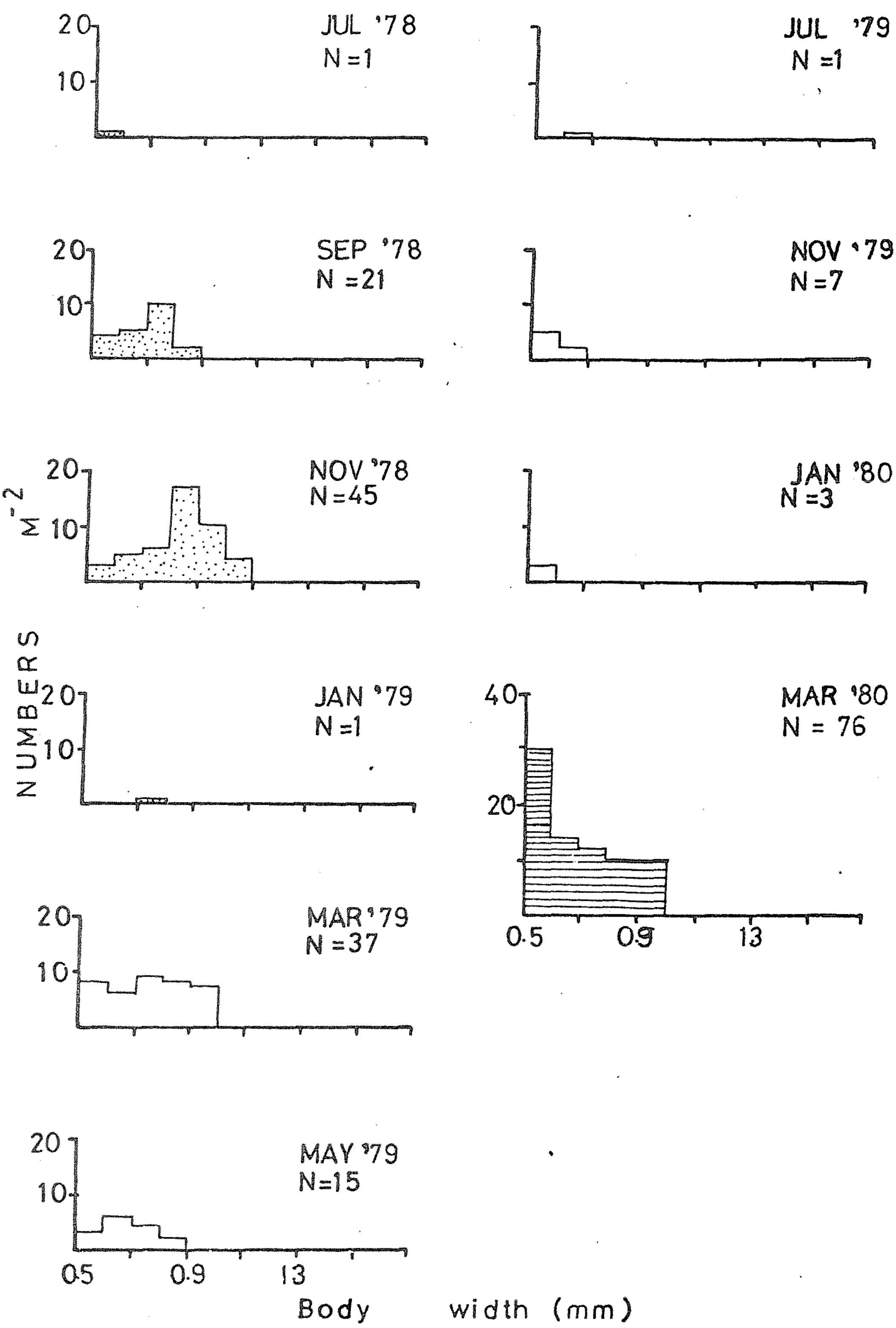


FIG.5.20. STATION 9 ETEONE LONGA SIZE FREQUENCY HISTOGRAMS

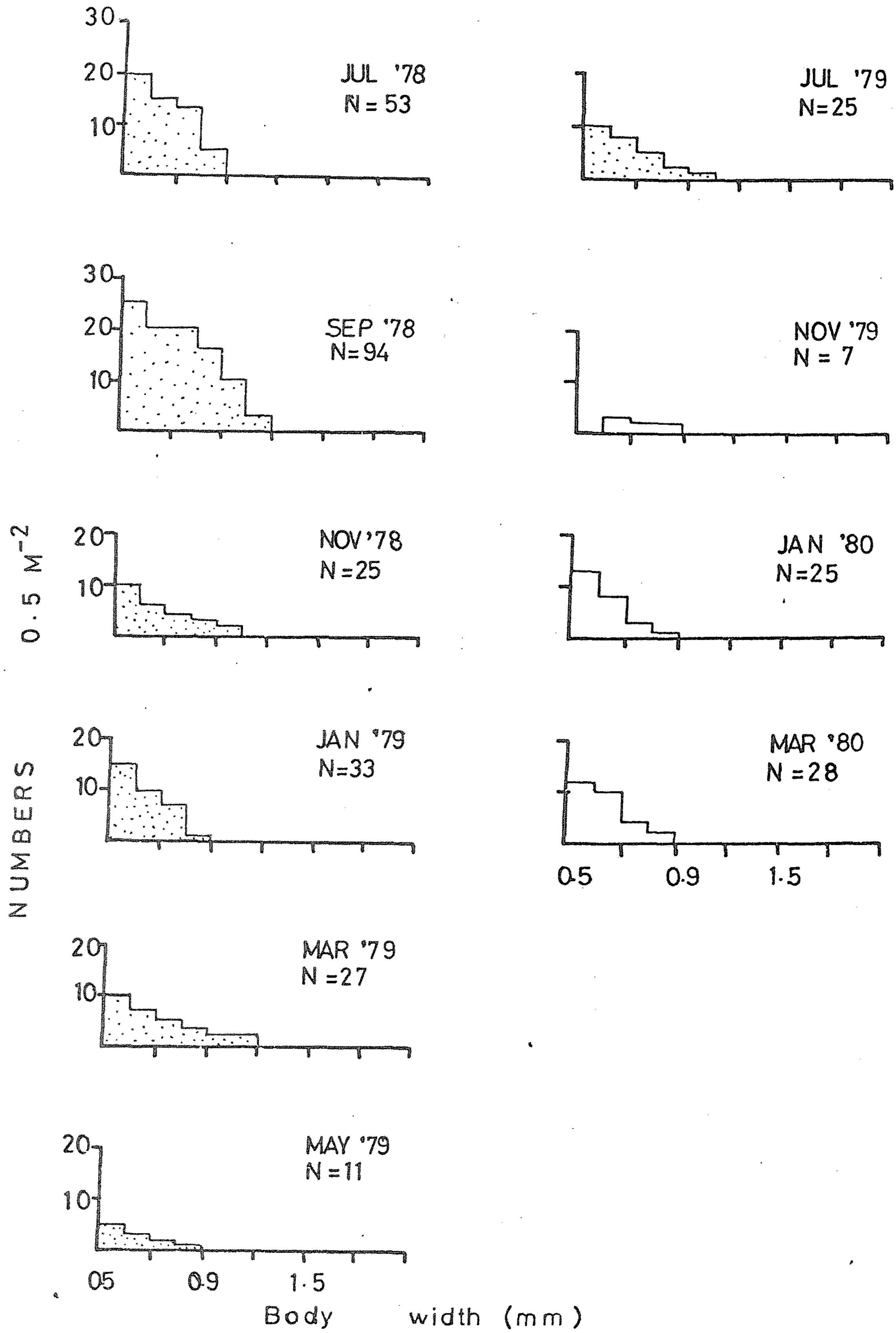


FIG.5.21. STATION 20 ETEONE LONGA SIZE FREQUENCY HISTOGRAMS

place some time between May and July at Station 2, between September and November at Stations 5 and 20 but between January and March at Station 9. The newly recruited juveniles entered the sieve between July and November at Station 2, 5 and 20, but not until March at Station 9.

The annual and mean annual production estimates for each cohort at the selected stations are shown in Table 5.15. The annual production ranged between $0.041gm^{-2}yr^{-1}$ at Station 2 and $0.13gm^{-2}yr^{-1}$ at Station 9. The production increments as computed at the four stations are presented in Appendix XXII - XXV.

Anaitides maculata

This phyllodocid worm occurred at low densities (less than $50m^{-2}$) at the selected stations. Apart from January and March 1979 samples at Station 20, where individual worms were easily grouped into '0' and 'I' year classes, all other individuals belonged to the '0' group (Figs. 5.22 - 5.23) After breeding between November and January, the population of A. maculata in Southampton Water suffered a gradual post-breeding mortality and disappeared from samples by March at Station 5, and by May at Station 20. The new '0' group appeared in the sieve in March 1979 at Station 5 and in January at Station 20. During the summer months in 1979, it was clear that the year class was poorly represented and the population as a whole fell in abundance.

The annual and mean annual production for A. maculata at the selected stations are shown in Table 5.16. Production was generally low in the study area, varying between $0.0007gm^{-2}yr^{-1}$ at Station 2 and $0.01gm^{-2}yr^{-1}$ at Station 20. The production increments computed for A. maculata at the four stations are presented in Appendix XXVI - XXVIII.

Cirratulus cirratus

The July 1978 samples of this cirratulid at all selected stations appeared to show only one year group. Subsequent samples at Station 5 revealed that this was not the case at the station as two year groups were distinct at the station between late summer and early autumn. At other stations the animal occurred at low densities making it difficult to follow its growth. Size frequency histograms of C. cirratus at the selected stations are presented in Figs. 5.24 - 5.26.

At Station 5, spawning of the animal occurred between August and September during the study. The '0' group first observed in November

	STATION 2			STATION 5			STATION 9			STATION 20		
	COHORTS			COHORTS			COHORTS			COHORTS		
	1	2	Total	1	2	Total	1	2	Total	1	2	Total
July 78 to July 79	46.243	0	46.243	59.176	4.130	63.306	98.187	32.283	130.470	85.370	0	85.370
Sept 78 to Sept 79	46.243	0	46.243	59.176	33.88	93.055	98.187	32.283	130.470	85.370	0	85.370
Nov 78 to Nov 79	46.243	0.357	46.600	0	33.88	33.88	98.187	34.133	132.320	85.370	0	85.370
Jan 79 to Jan 80	46.243	0.357	46.600	0	33.88	33.88	98.187	44.324	142.511	66.092	13.728	79.820
Mar 79 to Mar 80	19.423	0.357	19.779	0	33.88	33.88	0	0	0	54.318	15.424	69.742
Mean Annual Production	41.093			51.600			133.943			81.134		
Mean Biomass (gm^{-2})	0.0242			0.0138			0.0066			0.03178		
P:B ratio	1.70			3.74			20.17			2.55		

Table 5.15. Annual and mean annual production of E. longa in mg m^{-2} yr^{-1} at the selected stations

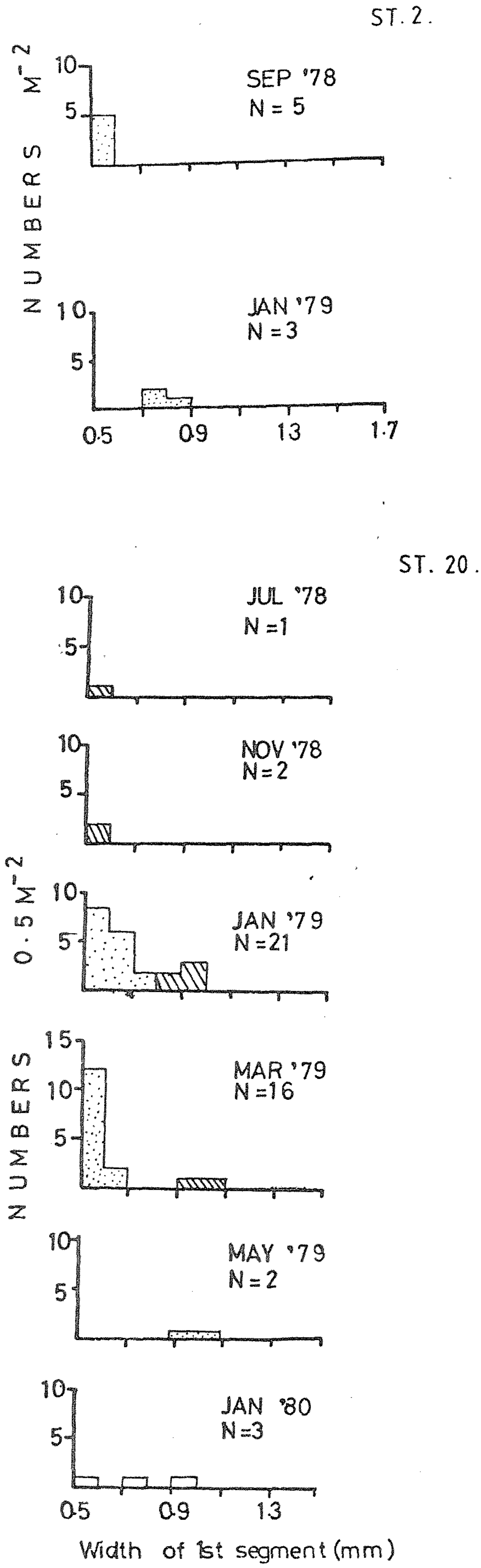


FIG. 5.22. STATIONS 2 & 20 ANAITIDES MACULATA
SIZE FREQUENCY HISTOGRAMS

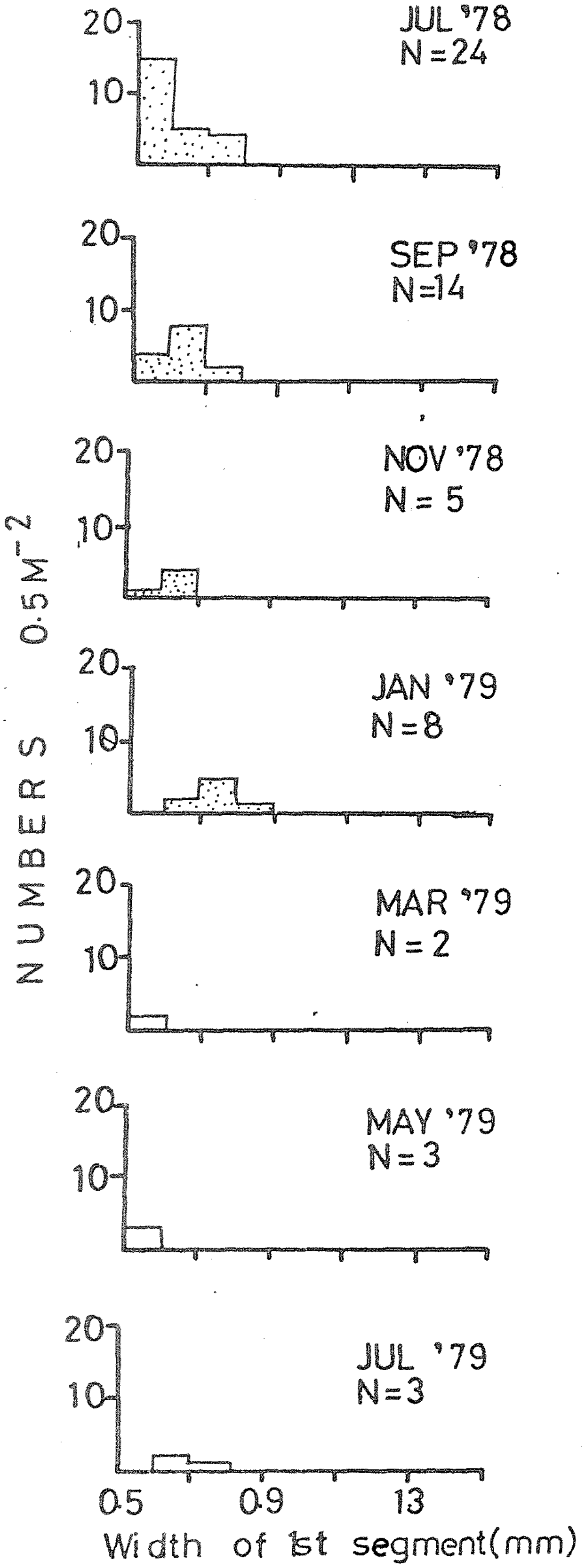


FIG.5.23. STATION 5 ANAITIDES MACULATA SIZE FREQUENCY HISTOGRAMS

	STATION 2	STATION 5	STATION 20
July 1978 - July 1979	0	3.838	11.232
Sept 1978 - Sept 1979	0	3.838	11.232
Nov 1978 - Nov 1979	0	3.838	11.232
Jan 1979 - Jan 1980	3.413	0	11.232
March 1979 - March 1980	0	0	11.232
Mean Annual Production	0.6826	2.3028	11.232
Mean biomass (gm^{-2})	0.00084	0.0041	0.00597
P:B ratio	0.81	0.56	1.88

Table 5.16. Annual and mean annual production of <u>A. maculata</u> in mg m^{-2} yr^{-1} at the selected stations

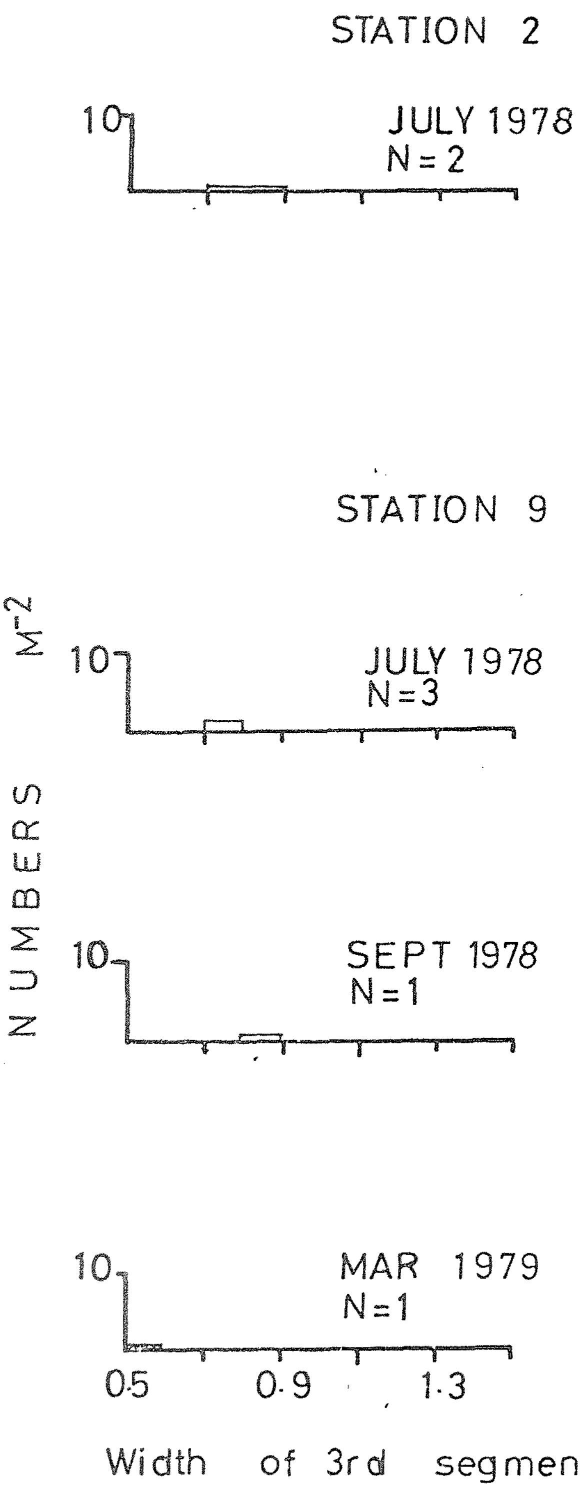
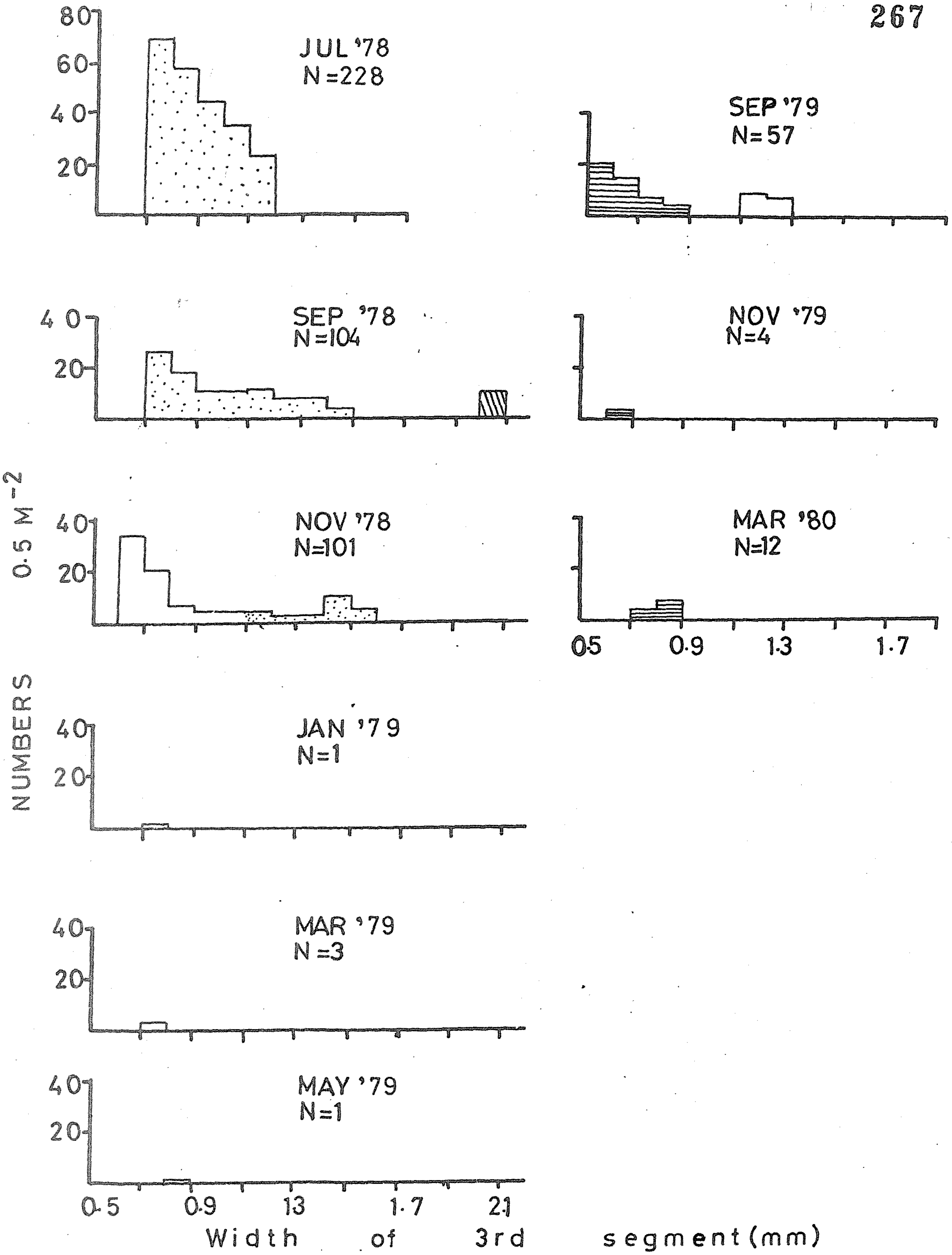


FIG.5.24. CIRRATULUS CIRRATUS SIZE FREQUENCY HISTOGRAMS AT STATIONS 2 & 9



5.25. CIRRATULUS CIRRATUS SIZE FREQUENCY HISTOGRAMS AT STATION 5

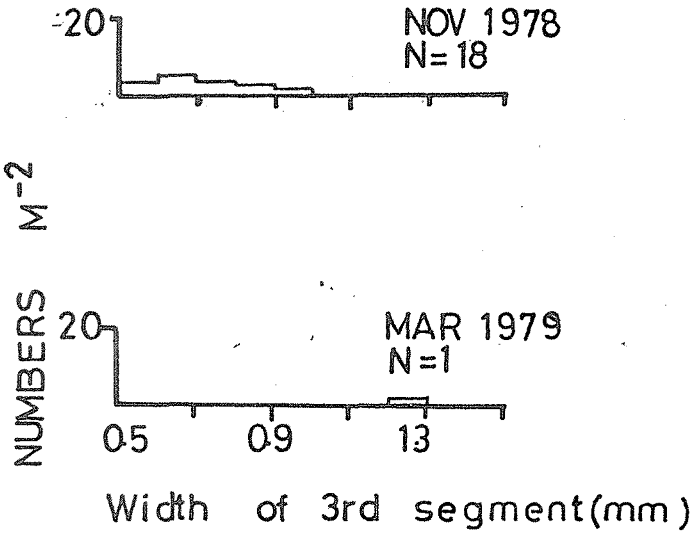


FIG.5.26. CIRRATULUS CIRRATUS SIZE FREQUENCY HISTOGRAMS AT STATION 20

1978 became the 'I' group in September 1979 when the new '0' group started to appear in the sieve. At other stations, the number of individuals in each sample was inadequate to determine the timing and age of breeding. Nevertheless the size frequency histograms at station 9 (Fig. 5.24) suggests that spawning of the animal at the station occurred some time between autumn and winter 1978/79, and sieve recruitment of juveniles in March 1979.

The production estimates for C. cirratus at the stations under investigation are shown in Table 5.17. The production estimates ranged between 0.006gm^{-2} yr^{-1} at Station 9 and 0.55gm^{-2} yr^{-1} at Station 5. Production increments computed for C. cirratus at each station are shown in Appendix XXIX - XXXI.

Polydora ciliata

This spionid polychaete occurred at fluctuating densities (1-1086m^{-2}) at the selected stations. No specimen of the worm recovered during the study was sexually mature. The association of the animal and C. capitata and the similarity in their reproductive strategies (Grassle and Grassle, 1974) demands further investigation, which is outside the scope of the present study.

The production estimates of the animal, based on the size frequency histograms at each of the four stations are presented in Table 5.18. The production at Station 2 was estimated at 0.04gm^{-2}yr^{-1}, at Station 5 at 0.005gm^{-2}yr^{-1}, at Station 9 at 0.01gm^{-2}yr^{-1} and at Station 20 at 0.02gm^{-2}yr^{-1}. The production increments computed for P. ciliata at the stations are shown in Appendix XXXII - XXXV.

5.3.2.2. Molluscs

Abra nitida

At Station 2, this shallow burrowing tellinid bivalve occurred only twice during the study. All the Abra individuals in July 1978 sample were assigned to the '0' group (Section IV). The group suffered heavy post-spawning mortality between July and September 1978, when the density fell from 585m^{-2} to 1m^{-2}, disappearing from samples by November 1978. The annual production for A. nitida at the station was estimated at 0.0004gm^{-2}yr^{-1}.

The bivalve occurred once, in July 1978 at Station 9 at a density of 14m^{-2}. No production was estimated at the station since no other individuals were obtained.

	STATION 5				STATION 9	STATION 20
	COHORTS					
	1	2	3	Total		
July 1978–July 1979	134.374	309.430	240.838	674.642	5.60	0
Sept 1978 – Sept 1979	134.374	309.430	240.838	674.642	5.60	0
Nov 1978 – Nov 1979	0	309.430	240.838	550.268	5.60	0
Jan 1979 – Jan 1980	0	309.430	240.838	550.268	5.60	0
March 1979 – March 1980	0	75.466	240.466	316.304	5.60	33.764
Mean Annual Production		553.225			5.6	6.753
Mean Biomass (gm^{-2})		0.0929			0.0015	0.00065
P:B ratio		5.9			0.67	6.8

Table 5.17 Annual and mean annual production of *C. cirratus* in mg m^{-2} yr^{-1} at the selected stations

	STATION 2	STATION 5	STATION 9	STATION 20			
				COHORTS			
				1	2	3	Total
July 1978 - July 1979	0	0	0	0	0	0	0
Sept 1978 - Sept 1979	0	8.138	1.370	0	0	0	0
Nov 1978 - Nov 1979	205.223	16.698	60.052	85.470	0	0	85.470
Jan 1979 - Jan 1980	0	0	0	0	0	0	0
March 1979 - March 1980	0	4.000	0	0	0	3.332	3.332
Mean Annual Production	41.0446	5.7672	12.2844			17.7604	
Mean Biomass (gm^{-2})	0.004	0.0001	0.0001			0.0041	
P:B ratio	10.26	5.77	12.28			4.29	

Table 5.18 Annual and mean annual production of _P. ciliata_ in mg $m^{-2}yr^{-1}$ at the selected stations

At Station 5, all the individuals in July and September 1978 were assigned to '0' group, and spawned between August and September 1978, after which the group suffered heavy post-spawning mortality. The group had disappeared from samples by the following March. A new '0' group appeared in the samples in November 1978 with recruitment reaching a peak in May 1979 (Section IV). The group spawned between July and August 1979 and suffered a heavy mortality afterwards, disappearing from samples by November 1979. The annual production of A. nitida at the station was estimated at $0.13 gm^{-2}yr^{-1}$.

At Station 20, all the July 1978 specimens were assigned to the '0' group which spawned between July and August 1978. The group, like others, suffered heavy post-breeding mortality and disappeared from samples by the following May. The new '0' group which appeared in samples in November 1978 was well represented and spawned between July and August 1979, disappearing from samples by March 1980.

The annual production estimate of A. nitida at this station was $1.06 gm^{-2}yr^{-1}$; and expressed with other stations' estimates in Table5.19. The production increments computed for A. nitida at the selected stations are shown in Appendix XXXVI - XXXVIII.

Mercenaria mercenaria

Mercenaria mercenaria proved to be biomass dominant at Station 5 throughout the study; though occurring at low densities ($40-66m^{-2}$). The annual and mean biomass of the species expressed as g ash free dry weight per metre^{-2} (excluding shell protein) is shown in Table 5.20. The mean biomass of Mercenaria accounted for 93.28% of total macrofaunal biomass at the station throughout the study period.

The annual production estimates for M. mercenaria at Station 5 are shown in Table 5.21. The production increments computed for the bivalve at Station 5 is shown in Appendix XXXIX. The P:B ratio calculated for M. mercenaria in the present study amounted to 1.09, about double that of the intertidal Hamble Spit population (Hibbert, 1976).

5.3.2.3. Crustaceans

Most of the crustaceans encountered in the present study bred continuously throughout the year. The exact time of breeding was difficult to delineate because samples were only taken at two monthly intervals. The production estimates of the crustacean species were made from the product of mean biomass of each species per sample and the overall annual

	STATION 2	STATION 5				STATION 20		
		COHORTS				COHORTS		
		1	2	3	Total	1	2	Total
July 1978 - July 1979	0	13.464	109.624	0	133.088	102.136	1049.008	1151.144
Sept 1978 - Sept 1979	2.067	13.464	109.624	0	133.088	102.136	129.040	321.176
Nov 1978 - Nov 1979	0	3.332	109.624	0	112.956	14.544	1290.040	1304.584
Jan 1979 - Jan 1980	0	0	109.624	20.102	129.726	14.544	1290.040	1304.584
March 1979 - March 1980	0	0	108.608	27.502	136.110	3.010	1290.040	1293.050
Mean annual production	0.4134		128.994				1056.9076	
Mean Biomass (gm^{-2})	0.0472		0.0451				0.2639	
P:B ratio	0.009		2.85				4.01	

Table 2.19 Annual and mean annual production of _A. nitida_ in mg $m^{-2}yr^{-1}$ at the selected stations

YEAR CLASSES

	1978	1977	1976	1975	1974	1973	1972	1971	1970
July 1978 - July 1979	0.0030	0.3388	0.948	1.370	5.484	21.896	22.839	20.060	5.294
Sept 1978 - Sept 1979	0.0030	0.3288	1.332	2.984	6.788	22.954	27.346	18.940	5.934
Nov 1978 - Nov 1979	0.0030	0.3288	1.250	4.070	10.040	24.440	21.924	17.254	4.866
Jan 1979 - Jan 1980	-	-	1.214	3.434	10.598	21.680	21.434	8.388	4.866
Mar 1979 - Mar 1980	-	-	1.330	3.900	13.194	29.280	22.026	7.072	3.548
Mean Biomass	0.0030	0.3288	1.216	3.152	9.221	24.050	23.114	14.342	4.781

Total Mean Biomass = 80.207g m^{-2}

Table 5.20 Table of Annual and mean annual biomass of *Mercenaria mercenaria* in gm^{-2} at Station 5.

YEAR CLASSES

	1978	1977	1976	1975	1974	1973	1972	1971	1970
July 1978 - July 1979	0	1413.8	3556.0	4404.0	12614.8	20878.6	16671.6	20791.2	1922.8
Sept 1978 - Sept 1979	0	1413.8	5187.4	4404.0	15274.2	25542.4	28625.4	25449.8	1922.8
Nov 1978 - Nov 1979	0	1413.8	5344.6	7607.8	13558.2	27608.2	28625.4	22445.0	1922.8
Jan 1979 - Jan 1980	11.0	1413.8	4144.6	4435.2	17271.6	10240.8	20789.2	4658.6	1922.8
March 1979 - March 1980	11.0	1682.4	6376.6	8976.2	15818.0	14701.0	20789.2	4658.6	380.0

Mean Annual Production = 87695.5 mg $m^{-2}yr^{-1}$

Mean Biomass (gm^{-2}) = 80.207

P:B ratio = 1.09

Table 5.21 Annual and mean annual production of M. mercenaria in mg $m^{-2}yr^{-1}$ at Station 5

P:B ratio at the station of occurrence.

Pariambus typicus

This amphipod was recorded only at Station 5 and at low densities (2-168m^{-2}) among the selected stations. Breeding took place throughout the year and separation of individuals into distinct cohorts was difficult because of short life-span. The mean biomass was calculated as 0.0028g m^{-2} and production for *P. typicus* at Station 5 estimated at 0.003gm^{-2}yr^{-1}.

Microdeutopus gryllotalpa

This amphipod was recorded at varying densities (2-140m^{-2}) at Stations 5 and 20. At Station 5, the mean biomass was calculated as 0.0020gm^{-2} and the annual production estimated for the period of study at 0.002gm^{-2}yr^{-1}. At station 20 during the same period, the mean biomass for *M. gryllotalpa* was 0.0004gm^{-2} and production estimated at 0.0001gm^{-2}yr^{-1}.

Aora gracilis

This amphipod occurred sporadically only at Station 5 but the life cycle could not be followed because of its low densities. The mean biomass was calculated as 0.002gm^{-2} and the production estimated at 0.003gm^{-2}yr^{-1}.

Corophium insidiosum

This crustacean occurred sporadically at Stations 2 and 5 at low densities. At Station 2, the mean biomass of *C. insidiosum* was calculated as 0.0001gm^{-2} and annual production estimated at 0.001gm^{-2}yr^{-1}. At Station 5, the biomass of this crustacean amounted to 0.001gm^{-2} and its annual production was estimated at 0.0001gm^{-2}yr^{-1}.

Philomedes globosus

The only ostracod crustacean recorded in the present study was recorded in all selected stations except Station 9. The animal bred at short intervals but continuously throughout the year, making separation of individuals into distinct cohorts difficult. At station 2, the mean biomass of *P. globosus* was calculated as 0.0007gm^{-2} and its production estimated at 0.003gm^{-2}yr^{-1}. At Station 5, the mean biomass of the ostracod amounted to 0.0078gm^{-2} and its annual production for the period of study was estimated at 0.0095gm^{-2}yr^{-1}. At Station 20, the mean biomass of the animal was 0.0051gm^{-2} and its production estimated at 0.011gm^{-2}yr^{-1}.

Eudorella truncatula

This cumacean crustacean was recorded only at Stations 5 and 20 and at low densities ($20m^{-2}$). The mean biomass of the animal at Station 5 was $0.004gm^{-2}$ and its production for the study period estimated at $0.0047gm^{-2}yr^{-1}$. At station 20, the mean biomass of the animal was $0.0028gm^{-2}$ and its production for the period estimated at $0.005gm^{-2}yr^{-1}$.

5.4 Production estimates and species ranking at the four selected Stations

The ranking of benthic macroinfaunal species in order of their productive importance at the selected stations in expressed in Tables 5.22 - 5.25. At Station 2, eight species accounted for more than 90% of the total macrofaunal production with N. diversicolor alone contributing more than 80% of the total production. The total macrofaunal production at the station was estimated at $5.3774gm^{-2}yr^{-1}$, the mean biomass as $1.170gm^{-2}$, giving a P:B ratio of 4.59.

At Station 5, ten species accounted for more than 88% of total macrofaunal production. M. mercenaria alone contributed almost 80% of the production. The total macrofaunal production at this station was estimated at $112.213gm^{-2}yr^{-1}$, the mean biomass as $92.433gm^{-2}$, with a P:B ratio of 1.215.

Six macrofaunal species were ranked in order of their productive importance at Station 9, and these accounted for about 99.2% of the total macrofaunal production in the station. C. capitata contributed more than 46% of the total production. The total macrofaunal production at the station was estimated at $3.4476gm^{-2}yr^{-1}$, the mean biomass being $1.017gm^{-2}$ and the P:B ratio was calculated as 3.39.

At Station 20, the annual production of the total macrofauna during the period of study (July 1978 - March 1980), was estimated at $5.7236gm^{-2}yr^{-1}$. Nine species (Table 5.24) accounted for 99.9% of the total macrofaunal production. N. hombergi, the most productive species at this station accounted for 42.9% of the total macrofaunal production. The mean biomass at the station was calculated as $2.792gm^{-2}$ and the P:B ratio was 2.05.

In general, production was high on the eastern side of Southampton Water and towards the mouth of the estuary but low on the western side around Cadland creek, especially at Station 9. The higher P:B ratio on the western side (Stations 2 and 9) probably explains the shorter life-span of animals in the area. Animals that are annuals usually process higher P:B ratio than those that are long-lived. The occurrence of short-lived animals on the western side of the study area probably serves as an indication of greater physical stress on the community.

Rank		Mean Biomass gm^{-2}	Production $gm^{-2}yr^{-1}$	P:B ratio	% of total macrofaunal production
1	Nereis diversicolor	0.899	4.3558	4.84	81.00
2	Capitella capitata	0.033	0.3820	11.6	7.10
3	Nephtys hombergi	0.051	0.0920	1.80	1.71
4	Polydora ciliata	0.004	0.0411	10.26	0.76
5	Eteone longa	0.024	0.0410	1.70	0.76
6	Caulleriella caputesocis	0.012	0.0101	0.84	0.19
7	Abra nitida	0.0472	0.0004	0.009	0.01
8	Anaitides maculata	0.001	0.006	0.081	0.01
	Total	1.071	4.923		91.54
	Others	0.099	0.4544		8.46
	Total macrofauna	1.170	5.3774	4.59	
	Polychaeta	0.93	4.27		79.41
	Crustacea	0.03	0.14		2.61
	Mollusca	0.20	0.92		17.11

Table 5.22 Mean Biomass, production and P:B ratios at Station 2

Rank	Species	Mean Biomass gm^{-2}	Production $gm^{-2}yr^{-1}$	P:B ratio	% of total macrofaunal production
1	*M. mercenaria*	80.207	87.6955	1.09	78.15
2	*C. caputesocis*	1.031	5.8060	5.63	5.17
3	*N. hombergi*	1.496	4.3215	2.89	3.85
4	*C. cirratus*	0.093	0.5532	5.9	0.49
5	*M. palmata*	0.193	0.4180	2.17	0.37
6	*A. nitida*	0.045	0.1230	2.85	0.11
7	*N. diversicolor*	0.0809	0.0776	0.96	0.07
8	*E. longa*	0.014	0.0516	3.74	0.05
9	*P. ciliata*	0.001	0.0058	5.77	0.01
10	*A. maculata*	0.004	0.0023	0.56	0.00
	Total	83.165	101.0545		88.27
	Others	9.268	11.1585		11.73
	Total macrofauna	92.433	112.2130	1.215	
	Polychaeta	3.21	3.90		3.48
	Crustacea	0.38	0.462		0.41
	Mollusca	86.32	104.769		93.37

Table 5.23. Mean biomass, production and P:B ratios at Station 5

Rank	Species	Mean Biomass gm^{-2}	Production $gm^{-2} yr^{-1}$	P:B ratio	% of total macrofaunal production
1	C. capitata	0.496	1.6198	3.26	46.98
2	N. diversicolor	0.313	1.0056	3.22	29.17
3	E. longa	0.007	0.1339	20.17	3.88
4	P. ciliata	0.001	0.0123	12.28	0.36
5	C. cirratus	0.002	0.0056	0.56	0.16
6	C. caputesocis	0.001	0.0002	0.17	0.01
	Total	0.820	2.7774		80.56
	Others	0.197	0.6702		19.44
	Total *macrofauna*	1.017	3.4476	3.39	
	Polychaeta	1.01	3.420		99.2
	Crustacea	0.005	0.016		0.46
	Mollusca	0.002	0.007		0.20

Table 5.24. Mean biomass, production and P:B ratios at Station 9

Rank	Species	Mean Biomass gm^{-2}	Production $gm^{-2}yr^{-1}$	P:B ratio	% of total macrofaunal production
1	*N. hombergi*	1.63	2.4564	1.63	42.92
2	*C. caputesocis*	0.272	1.9340	7.09	33.79
3	*A. nitida*	0.264	1.0569	4.01	18.47
4	*N. diversicolor*	0.032	0.1538	4.78	2.69
5	*E. longa*	0.032	0.0811	2.55	1.42
6	*P. ciliata*	0.004	0.0178	4.29	0.31
7	*A. maculata*	0.006	0.0112	1.88	0.20
8	*C. cirratus*	0.001	0.0068	6.8	0.12
9	*C. capitata*	0.005	0.0004	0.08	0.01
	Total	2.246	5.7184		99.93
	Others	0.546	0.0052		0.07
	Total macrofauna	2.792	5.7236	2.05	
	Polychaeta	1.92	3.936		68.76
	Crustacea	0.61	1.251		21.86
	Mollusca	0.27	0.554		9.68

Table 5.25. Mean biomass, production and P:B ratio at Station 20

Table 5.26 shows the annual production of total macrofaunal assemblage at each of the selected stations between July 1978 and March 1980.

	STATION 2	STATION 5	STATION 9	STATION 20
July 1978 - July 1979	2498.6602	93007.268	2998.2304	5384.2638
Sept 1978 - Sept 1979	2883.7662	119578.320	3083.5068	6245.6658
Nov 1978 - Nov 1979	7889.8697	122239.570	3287.7468	6475.7066
Jan 1979 - Jan 1980	6601.3432	75914.786	3096.8414	6594.1084
March 1979 - March 1980	4812.8852	85826.848	1424.765	6450.7200
Mean Annual Production ($mg\ m^{-2}yr^{-1}$)	4937.3048	99313.356	2778.218	6230.0926

Table 5.26. Annual production in $mg\ m^{-2}yr^{-1}$ for all selected Stations (July 1978 - March 1980)

5.5 DISCUSSION

One of the primary aims of the present study has been to obtain a reasonably accurate estimate of biomass and production of the major constituent species in the study area and to assess the total macrofaunal production. The methods employed in the present study have some short-comings. The time taken by some fauna before reaching a size large enough to be held by 0.5mm sieve could not be determined with great accuracy. Some under-estimations of production could arise from the inability of assessing early mortality. The results of the present study pointed to little evidence of severe mortality until the time of breeding as the population densities of many animals were high prior to breeding. Notwithstanding, many macrofauna recovered in the present study suffered heavy post-breeding mortality though high recruitments resulted from breeding. C. caputesocis, C. capitata and M. palmata, for example, occurred in high numbers throughout the study, but declined after breeding. A temporary high mortality rate soon after settlement could probably introduce an error in the production estimates.

It was assumed that those species occurring at low densities, where production could not be estimated, had the same P:B ratio as the overall P:B ratio for those species whose production could be determined. Since many of these species were small and short lived (e.g. Perioculodes longimanus) with probably higher P:B ratio than the mean, some under-estimation of production was probably made with regard to these rarer species. Being rare, such species accounted for a small proportion of the biomass and these errors probably have little effect on total production estimate at each station. Nevertheless, the production estimates of the macrofauna in the stations investigated were of significant value since production estimates themselves are approximate rather than exact values.

The mean biomass and annual production estimates of some top ranking species and the total macrofauna at the selected stations are comparable to those in other areas. The mean biomass of M. mercenaria, the biomass dominant species at Station 5 during the present study, was 82.2gm^{-2}, greater than that of the intertidal Hamble Spit population, 52gm^{-2} (Hibbert, 1976). The mean annual production of the bivalve in the present study (87.7gm^{-2}yr^{-1}) was almost six fold that of the Hamble Spit population, which Hibbert (1976) estimated at 14gm^{-2}yr^{-1}. The P:B ratio of Mercenaria in the present study is about twice that of the Hamble Spit population.

The most productive polychaete in the present study was N. diversicolor. The mean annual production estimates of the worm varied between 0.08 and 4.4gm^{-2}yr^{-1} at the selected stations. The mean annual production, mean biomass and P:B ratio of the animal in the present investigation are compared with results from other areas in Table 5.27a. The P:B ratio for N. diversicolor found in the present study, except at Station 5, was higher than those of previous studies though both mean biomass and production estimates were lower. The values in this study fit into a series of previously reported values for other polychaetes: for example, Ampharete acutifornis, P:B 5.5 (Warwick and Price,1975); A. acutifornis P:B 4.6 (Richards and Riley,1967); Glycera rouxi, P:B 0.4 (Buchanan and Warwick,1974). The lower P:B ratio obtained at station 5 in the present study is of particular interest as it shows that the P:B ratio does not necessarily decrease with increasing mean biomass.

The P:B ratios of some other polychaetes found in the present investigation are compared to other values in Table 5.27b. The limitations of the P:B ratios as a tool in estimating the production values have been discussed by Kay and Bradfield (1973), Chambers and Milne (1975) and Heip and Herman (1979). Chambers and Milne (1975) pointed out that the variations in the production estimates could be real and caused by the differing biotic and abiotic characteristics of the study area. The life-cycles of the animals could also influence the estimates as long-lived animals tend to have lower P:B values. Nevertheless, the inaccuracies in the measurements of the parameters necessary for the calculations of production and the mean biomass could lead to differences in the P:B ratios.

It may also be argued that migration of animals from place to place may affect the production estimates of an area. Though the majority of benthic animals are relatively immobile, some migrate and travel a considerable distance, as in the present study, aided either by currents or their own locomotory organs. Such migrations have considerable effect on the production estimates of both the particular species concerned and the entire macrofauna.

Many of the macrofauna recorded during the study are omnivorous (Nephtys and Nereis) or deposit feeders (Caulleriella caputesocis, Capitella capitata, Melinna palmata and Eteone longa). Though N. hombergi is generally regarded as a carnivore (Clay,1967) feeding on nematodes, ostracods and Carcinus, Sanders et al (1962) pointed out that carnivorous polychaetes in benthic populations could not be exclusive carnivores. Although Warwick and Price (1975) suggested that the animal

Biomass gm^{-2}	Production $gm^{-2}yr^{-1}$	P:B ratio	Depth m	Sediment type	Authority
4.22	12.78	3.1		Medium sand	Chambers & Milne (1975)
24.0	61.0	2.5	0.5		Heip and Herman (1979)
0.90	4.3558	4.8	1.5	Mud	Station 2, this study
0.08	0.0776	0.96	1.6	Mud	Station 5, this study
0.3128	1.0056	3.22	1.6	Mud	Station 9, this study
0.0322	0.1538	4.78	1.6	Sandy mud	Station 20, this study

Table 5.27a, Comparisons of mean biomass, production and P:B ratios of _N. diversicolor_ in recent studies

SPECIES	P:B ratios	Authority
Pectinaria hyperborea	4.6	Peer (1970)
Nephtys incisa	2.2	Sanders (1956)
Nephtys hombergi	1.2	Warwick & Price (1975)
N. hombergi	1.7	Kirkegaard (1978)
Anaitides groenlandica	1.0	
N. hombergi	1.66-3.06	Present study
Nereis virens	1.6	Kay & Bradfield (1973)
Lumbrinereis fragilis	1.3	Buchanan & Warwick (1974)
Heteromastus filiformis	1.0	
Anaitides maculata	0.8-3.8	Present study
Capitella capitata	0.08-11.6	
Caulleriella caputesocis	1.07-7.12	
Polydora ciliata	4.4-12.0	
Melinna palmata	2.17	
Eteone longa	1.69-20.2	

Table 5.27b P:B ratios for Polychaetes

is carnivorous because it lacks any trace of sediments in its gut, it is hard to believe that Nephtys, a dominant producer in the estuarine mudflat which contributed more than half of the total production in the area, would be an exclusive carnivore. If it is, and has an annual production of 7g $m^{-2}yr^{-1}$, with an ecological efficiency of 10%, it would require 70g $m^{-2}yr^{-1}$ of food which is greater than the production of other animals present in the area.

A similar argument could be made for the present study. Assuming that the ecological efficiency of N. hombergi was 10% (Slobodkin, 1964), an annual production of the animal of about 4.4 and 2.5$gm^{-2}yr^{-1}$ at Stations 5 and 20 respectively would require about 44 and 25$gm^{-2}yr^{-1}$ respectively. Since, except at Station 5, and when Mercenaria production is excluded, such requirement could not be met by other macrofaunal species, the animal could either feed on both Meiofauna and microfauna or on those animals migrating with the tide over the shore. The most likely prey would be juvenile Carcinus (Warwick and Price, 1975) which had high mean biomass. In view of the scarcity of information on the diets of N. hombergi, any conclusions on the animals contributing to the production of the polychaete at a lower trophic level could only be speculatory. A detailed study of the biology and ecology of the individual species is necessary to explain the P:B ratio.

Few attempts have previously been made to assess total bottom production and these have been carried out in areas of lower biomass and production (except at Hamble Spit) than found in the present study. Table 5.28 compares the results of previous studies to the present study. Sanders (1956) considered only those animals below 0.2g individual weight in biomass and production estimates. The larger animals added greatly to the biomass at most stations and could undoubtedly have lowered his overall P:B ratio. Few studies are strictly comparable to the present study. Several factors may be responsible for the variability in the production and P:B ratios. Buchanan and Warwick (1974) and Buchanan et al (1974) found that production of total macrofauna was markedly decreased with increasing depth. This was due to lower food supply at greater depths. Also Warwick and Price (1975) and Warwick et al (1978) found greater production in the Venus community than in the Macoma community of the Bristol Channel. They demonstrated that the sediment type and the hydrodynamics of the substrate have significant effect on the production of the benthic macrofauna. In the present study, production was highest at Station 5, on the eastern side of

	Biomass gm^{-2}	Production $gm^{-2}yr^{-1}$	P:B ratio	Depth in metres	Sediment type	Authority
Northumberland	3.98	1.74	0.44	80	Fine sandy silt	Buchanan & Warwick (1974)
"	5.80	2.90	0.5	60	Muddy sand	Buchan, et al (1974)
Long Island Sound U.S.A.	11.9	29.6	2.5			Sanders (1956)
Cornwall, England	13.2	13.3	1.0		Mud flat	Warwick & Price (1975)
Netherlands	25.7	41.3	1.6			Wolff & de Wolf (1977)
Hamble Spit (bivalves)	31-123	38-92	0.9		Mud flat	Hibbert (1976)
" " (bivalves + polychaetes)	220	190	0.9		"	" "
Bristol Channel	45.79	25.82	0.56	17.3	Fine sand	Warwick, et al (1978)
Baltic Sea proper	4.3	6.8	1.6	46		Cederwall (1977)
Southampton Water	1.0-92.4	3.4-112.2	1.6		Mud	This study

Table 5.28 Comparisons of biomass, production and P:B ratios for several studies

Southampton Water and lowest at Station 9, on the western side, though both sides were similar in depth and sediment type. The food availability and stability of the substrate may account for the differences in the production at both sides of the estuary. McIntyre (1970) assessed the proportion of meio and microfauna to the macrofauna and relates the proportions to food available to the macrofauna. On the western side of Southampton Water where greater sedimentation rate, higher hydrocarbon and sediment metals predominate, only few species are able to withstand the physical stress of the environment. Such paucity in the species number could account for lower biomass and production in the region compared with the eastern side.

Though the application of a P:B ratio to biomass estimates can make production estimates of a species easily assessed, it is not possible to deduce how much of the production is utilized by predators. A considerable portion of the production by some animals (e.g. Nereis diversicolor) is estimated to be in the form of gametes (Chambers and Milne,1975), and thus being unavailable to predators because of liberation of the gametes into the water during spawning. Some larger individuals of N. diversicolor live deep in the substratum (Muus,1967) and for much of the time will be unavailable to vertebrate predators. Notwithstanding, Peer (1970) estimated about 80% of mortality in Pectinaria hyperborea to be due to fish predation though less than 80% of the production would be utilized by predators if mortality was confined to the more abundant Pectinaria. In the present study, no evidence of remnants of any fauna recorded has been found in Flounder guts (Mitchell, 1974), making it impossible to assess their contribution to the flounder stock in Southampton Water.

SECTION SIX

GENERAL DISCUSSION AND CONCLUSION

Some detailed discussion of data for the main aspects of study has already been included in each section. The benthic macrofauna of the study area is numerically dominated by polychaetes, Capitella capitata being predominant on the western side and Caulleriella caputesocis on the eastern side and towards the mouth of Southampton Water. The biomass and production dominant species in the industrialized central region of Southampton Water is Mercenaria mercenaria, a hardshell clam introduced into the estuary in the 1920's, populations of which have now been introduced into other areas on the south coast of England (Mitchell, 1974). The benthic community of the study area is essentially similar to the Macoma community of Petersen (1913) and Thorson (1957) with Mercenaria and Crepidula fornicata, the introduced molluscan species replacing M. balthica. The species composition and distribution in the study area appeared to be influenced by the physico-chemical parameters.

The distribution of the benthic macroinfauna of Southampton Water was not examined until 1975 (Soulsby, 1978 and Levell, 1979). Differences in the number of species and numerical abundance between this study and others (Soulsby, 1978; Levell, 1979) were due to the area sampled, the season of sampling and the mesh size of the sieve used. The surveys in the present study were conducted in May 1978 and repeated in May 1979, using 0.5mm sieve, whereas those of the previous studies were conducted in September and used 1mm mesh. Buchanan et al (1974) demonstrated that in an offshore mud community, almost 75% of the individuals of three important producers which were retained by 0.5mm sieve were lost when sieves of 1mm were used.

Analysis of the results of the spatial distribution of the benthic macrofauna in Southampton Water points to the influence of sediment structure and stability as important factors in the faunal distribution. The study area, though predominantly mud, has a variable proportion of intermixed sand. On the western side of the study area, the sand content was low and the sedimentation rate was high. The high degree of sediment instability on the western side probably accounts for the low species diversity, the few species commonly found in the region being annuals. The sediment of the midchannel, the eastern side and the entrance of the estuary, was more heterogeneous, possibly providing a greater number of ecological riches for the fauna. The species diversity increased eastwards and towards the mouth of the estuary.

The distribution of the benthic macrofauna in the study area tends to be influenced by the degree of physical stress. The low diversity communities on the western side around Cadland creek were dominated by those species usually associated with high levels of organic pollution. Incidentally, the sediment hydrocarbon, copper and zinc were higher on the western side than on the eastern side or towards the mouth of the estuary. The dominant species on the western side, Capitella capitata, Nereis diversicolor, Polydora ciliata, have been ranked as 'opportunistic' species (Grassle and Grassle, 1974) because of their reproductive strategies. These species normally occur in low numbers, but increase in abundance in response to any environmental disturbance as other species decline. Those species occurring at low densities and sporadically on the western side were possibly washed into the area by tidal movements.

On the eastern side and towards the mouth of the estuary, the sediment heterogeneity probably resulted in a higher species diversity. Most of the fauna in the region were long-lived species probably due to the greater stability of the sediment. The region appeared similar to the typical Macoma community of Petersen (1913) with Mercenaria and Crepidula replacing M. balthica. The sediment hydrocarbon, copper and zinc on the eastern side were low but the water currents were stronger. The fauna in this region and at the mouth of the estuary are predominantly filter-feeders; the stronger water flow probably aids in the feeding. In contrast, most of the fauna on the western side are deposit feeders. The less stable sediment, weaker water currents and higher pollution load on the western side possibly limit the occurrence of the long-lived filter-feeding fauna to the eastern side. These extreme conditions appear suitable only to a few short lived deposit feeding opportunistic species.

Reclamation of part of the Southampton Water, especially the River Test estuary, has been in progress for some years. This involves a lot of dredging and has probably led to an increase and variation of the silt-load of the estuary. Such changes have possibly resulted in a decline in the number of macrofaunal species. Some animals which are better adapted to the instability in the environment appeared to extend their range. Cirratulus, Nephtys and Philomedes, almost exclusive in their distribution to the sandier high diversity region at the start of study, occasionally occurred at Cadland creek in 1979.

One interesting aspect of the distribution of benthic macrofauna in the present study is the absence of adult *Sabella pavonina* at all stations. All the specimens of the worm recovered were sexually immature though adult specimens were often dredged at the mouth of Southampton Water and occur infrequently in dredge hauls within the study area. *Mercenaria* also showed distinct restriction in distribution, usually absent on the western side of the midchannel in the study area. Mitchell (1974) found no specimens of *Mercenaria* below Hythe on the western side of Southampton Water. He showed that a large part of the estuary between Hythe and Calshot (which includes the western side of the present study area) was composed of very soft anoxic mud and that no invertebrate species were found to occur both littorally and sublittorally.

During the present study, there has been an overall decline in the species richness at all stations (see Figs. 3, 10; 3.13; 3.16 and 3.19). This type of change affecting all faunal elements is largely associated with toxic pollutants, whereas changes due to organic pollutants or to environmental factors such as climatic changes usually show a fall in the abundance of intolerant species and an increase in the abundance of tolerant species. Sediment copper levels have increased during the study period and this may be a possible contributing factor. However, other toxic wastes into the estuary might be involved.

The tendency of the short-lived species (e.g. *Polydora*, *Nereis*, *Capitella* and *Eteone*) to extend their range to the eastern side of the estuary may be attributed to the tidal mean velocities across the study area. Dyer (1973) showed that Southampton Water has a tendency for a stronger upward flow on the western side and a weaker downward flow on the eastern side. This bias probably promotes the transportation of some species from the western side to be deposited on the eastern side. The same may be argued for the differences in the sedimentation rate, hydrocarbon and sediment metals on both sides of the estuary.

The texture of the sediment may possibly contribute to the difference in numbers of individuals of species at a station. Coarser sediments and faster currents probably afford protection to smaller animals from predation. Mitchell (1974) reported that *Carcinus maenas* could not burrow successfully in coarse sediment (gravel) particularly in a swift current. He also quoted Carriker who showed the percentage survival of small *Mercenaria* from crab predation in soft sediments with negligible current to be 1% compared with 40% in coarse gravel with swifter currents.

The habitats in which many of the macrofauna recorded in the present study were found correspond to those of other studies. Carriker (1961) described the habitat of Mercenaria as 'the more saline coastal embayments and estuaries with only sporadic occurrence in the close vicinity of inlets of the ocean'. He found the salinities of Mercenaria habitats to range between 18 and 36‰. Dyer (1973) and Barnes (1973) recorded a salinity of around 32-34‰ for the eastern side of the study area where Mercenaria occurred at high densities. Even within the area of suitable salinity, the distribution of some animals was limited by the occurrence of unsuitable sediments. Mercenaria and Melinna palmata were found on the eastern side of the study area, in the sandy mud but were absent from the soft black mud smelling of hydrogen sulphide on the western side.

It is obvious from the investigation into the temporal changes in the fauna of the study area that seasonal fluctuations in the numerical abundance of the total macrofauna at the selected stations are influenced by a few dominant species. On the western side where C. capitata was dominant, the recruitment of new individuals entering the sieve after breeding increased the overall macrofaunal abundance and this fell when Capitella suffered mortality. On the eastern side and the mouth of the estuary, the recruitment and mortality of Caulleriella caputesocis altered the total macrofaunal abundance significantly. Only on few occasions did the two species occur together and even then, the presence of one in high numbers was accompanied by low numbers of the other. Although such variations in numbers could suggest competition between the two species, there was no evidence for such. The differences in abundance of the two species probably point to their response to the environmental disturbance; C. capitata usually occurring in high numbers in areas of great disturbance and C. caputesocis in high numbers in the relatively stable higher diversity region.

The seasonal fluctuation in the numerical abundance of the total macrofauna at the selected stations was primarily due to the influx of young animals into the populations of several species during the breeding periods. Most of the animals whose life-cycles were investigated (Melinna, Nereis, Nephtys, Caulleriella, Capitella, etc.) were annuals, breeding for the most part throughout the year with peaks in the summer months. The time of spawning of some polychaete populations in the present study compares well with those of other areas investigated by other workers. Table 4.1 shows that some polychaetes spawned at an early age in Southampton Water and this may possibly be due to the high levels of food available in the estuary. Heip and Hermann (1979) suggested that the dynamics of Nereis diversicolor populations appeared to show local characteristics.

The reproductive activity of the species could be limited to a short period in spring as in the Thames estuary, (Dales,1950) or could extend over the whole year (Herpin,1925; the present study). Though the general tendency of polychaetes is to have a short, fairly well defined spawning period as in N. diversicolor (Dales,1950), Tharyx marioni (Dales,1951), Melinna cristata (Hutchings,1974), some polychaetes have a protracted breeding season: Cirratulus cirratus (Stephenson,1950) (Olive 1970); Nephtys hombergi (Olive,1978), Cirriformia tentaculata (George,1962). Some factors have been suggested as important in determining the breeding season of polychaetes. Orton (1920) recognised the relationship between temperature and reproduction in marine organisms and concluded that 'Most animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species or at a definite temperature change'. Olive (1978) suggested that spawning in Nephtys could be the result of some unknown environmental stimulus which initiates the release of 'spawning hormone' which he suggested determined the time of spawning.

Though contrasting views have been expressed on the exact factors that determine the time of breeding in polychaetes, the immediate external stimulus for spawning has been attributed to a rise or fall in temperature. Dales (1951) found that ripe Tharyx marioni population in Chalkwell, Essex, spawned after a rise in water temperature of about 4^{o}c over a period of 4-5 days. He then concluded that the rise probably induced spawning. Although there is no evidence from the present study that the polychaete populations in Southampton Water shed their gametes in response to temperature changes of this nature, most of the polychaetes investigated spawned in the summer months when bottom water temperature was above 15^{o}c.

The influence of temperature on the spawning of Mercenaria in Southampton Water has been discussed by several workers (Ansell,1963a; Mitchell,1974; Hibbert,1976). The bivalve was reported to spawn in Southampton Water at temperatures between 18 and 20^{o}c with maximum spawning between mid July and mid August (Hibbert,1976). Mitchell (1974) pointed out that the influence of temperature in stimulating spawning in Mercenaria population was demonstrated by two spawning peaks in spring and summer in Marchwood where the influence of the warm water effluent was marked. He observed that outside the influence of the Marchwood outfall, the population of Mercenaria probably spawned only during peak summer temperatures in July and August.

Sheader (1977), working on the population of Ampelisca tenuicornis off the coast of Tyne and Wear, found no relationship between the abundance of *A. tenuicornis* in March and the winter temperatures of the same year. However, he found a corrrelation (significant at 1% level) between the number of *A. tenuicornis* in March and the mean winter temperature of two previous winters. He then suggested that a series of warm winters increased the abundance of *A. tenuicornis* and a series of cold winters resulted in a decrease. In the present study, the abundance of crustaceans in general appeared to increase in the summer months but fell in the winter months, suggesting that their lifecycle is sensitive to the seasonal change.

An interesting feature of the present investigation is the heavy post-breeding mortality and resorption of unspawned gametes by most of the macrofauna. Resorption of unspawned gametes among polychaetes is by no means a new phenomenon. Hutchings (1974) quoted Dales as noting that female *Nereis diversicolor* spawned only in the presence of males. Dales (1951) concluded that since the ratio of male to female in the Chalkwell population of *N. diversicolor* was 1:10, considerable numbers of females failed to spawn. In *Tharyx marioni*, the same author (Dales) found that unspawned gametes were resorbed. Resorption of unshed gametes were also reported in *Melinna cristata* (Nyholm,1951; Hutchings,1974) and in *Nephtys hombergi* (Olive,1978). Hutchings (1974) pointed out that the Northumberland population of *M. cristata* exhibited reduced reproductive capability since some mature worms failed to spawn, and those that spawned also showed reduced fecundity - the number of offspring produced by an individual per unit time.

It is not yet clear why some polychaetes fail to shed all mature gametes when breeding. Barnes and Barnes (1968) attributed the shedding of gametes to favourable environmental conditions while Barnes and Powell (1953) attributed the release of eggs to the amount of food material available for growth and development of the released gametes. It has been shown experimentally by Scott (1956) that in the trout *Salmo gairnerii kamloppe*, egg size is genetically controlled while fecundity varies with environmental and physiological conditions. The polychaetes of the study area reached sexual maturity at an early time, spawning their small sized oocytes earlier when compared with those in other areas studied. This may possibly be due to a high amount of food available in Southampton Water resulting in early growth and development of the gametes.

Many conflicting views have been expressed on the reduction of reproductive capability of some animals leading to a decrease in the length of their breeding season. Schroeder (1968) found that the breeding season in the central California populations of Nereis grubei was much shorter than those farther south but Reish (1954) found that in the latter, where more food was available, the worms bred throughout the year. Similar extension of breeding seasons have been reported for other invertebrates (Clark,1963). It may be suggested that some animals showed reduction in their reproductive capability because of suboptimal environmental conditions and maximise their capability when the optimum environmental conditions are available. It is not known for certain which conditions may be critical for the macrofaunal community in Southampton Water, but availability of food and temperature are likely to be important.

Though a limited study of growth and mortality of Mercenaria was made in the present investigation, the results obtained showed no successful settlement of Mercenaria since 1974. In recent years, there has been virtually no settlement of Mytilus edulis, once very common on the eastern shore of Southampton Water (Sheader, personal communication). Cockles have declined (Nossier, per. comm.) and Ostrea edulis (Key and Davidson, 1980) has shown poor settlement in recent years at the mouth of Southampton Water. As this covers a wide area (Southampton Water and part of the Solent at the mouth of Southampton Water) it is likely that the populations of these filter-feeding bivalves are responding to the same environmental parameters. These parameters may be affecting gonad development, spawning, fertilization, larval growth and settlement or the mortality of newly settled spat. The parametersmight possibly increase sedimentation due to dredging activity in the upper Test estuary though no evidence is available to support this.

Two phases of mortality have been associated with Mercenaria: the high mortality 'juvenile' phase and the low mortality 'adult' phase (Hibbert,1976). The juvenile mortality is caused mainly by Carcinus maenas and adult mortality by wading birds, gulls and fish, all of which prey on various sizes of clams. It is apparent that the commercial exploitation of the clams within the estuary has the effect of altering the population structure by reducing the numbers within exploited size classes. Some shells of large Mercenaria were found infested with the worm Polydora ciliata. The number of clams attacked by this worm is low and it is apparent that this pest does not increase mortality significantly. Mitchell (1974) suggested that the greatest mortality of the clam occurred at the larval stage in the plankton during the transportation of larvae into areas of unsuitable environmental conditions while others were possibly taken by carnivorous zooplankton and benthic filter feeders. He pointed out that during years when river flow and the time of spawning are high, settlement of larvae is generally low, with young larvae being flushed down Southampton Water into conditions of higher salinity and lower temperature, thus greatly reducing the probability of their survival to settlement. According to Mitchell, under low flow conditions, young larvae would be retained for longer periods in the Test arm of Southampton Water where salinity and temperature are optimal for the development of the larvae of this species. Though the flow of river is small compared with the tides, a year of low river flow would result in better settlement of Mercenaria in all parts of the estuary, increasing the chance of good recruitment.

Biomass and production studies on marine and estuarine invertebrates may be useful in understanding some aspects of their ecology. Production estimates have been suggested as requiring only the knowledge of growth and survivorship rates and nor relying on the behaviour of individuals under laboratory conditions (Hibbert,1976). Only a few production studies have been extended over periods of greater than one year (Price and Warwick,1980); nevertheless the production estimates for individual species appeared to be relatively unstable from one year to another. Price and Warwick (1980) found that the annual production of Nephtys hombergi in the Lynher estuary, Cornwall, declined from 6g $m^{-2}yr^{-1}$ in 1973 to 2.84g $m^{-2}yr^{-1}$ in 1977 and that of Ampharete acutifrons in the same area fluctuated between 0.12 and 12.5g $m^{-2}yr^{-1}$ in the same period. Buchanan et al (1974) found that the total production of macrofauna at a silty station off the coast of Northumberland remained stable over a period of four years though the relative abundance and production of individual species varied considerably. A direct comparison of the results obtained in the present study to other studies would be less useful, since this study lasted only twenty months. Nevertheless, most of the production of the macrofauna took place within the first year of the study. It is likely that if the study had been extended, a lower estimate of production would have been obtained in the second year than in the first.

The total macrofaunal biomass declined sharply during winter at all four stations. A major proportion of the biomass was contributed during the warmer summer months. On the western side of the study area, the biomass fell throughout the study with peaks in May and September. On the eastern side and mouth of the estuary, the decline in biomass was less marked. The lower biomass on the western side may be due to higher physical stress which resulted in a low species diversity and lower abundance except for occasional peaks in abundance of a few 'opportunistic' species such as Capitella capitata.

The production : biomass ratio (P:B) gives a measure of the rate of turnover of the biomass. The higher turnover on the western side of the study area was the result of a few 'opportunistic' species with typical r-strategist cycles. On the eastern side and near the mouth of the estuary, the smaller turnover resulted from domination by longer-lived species.

Several factors such as temperature and salinity have been suggested as imposing physiological stresses on organisms and thus influencing the degree of their tolerance on exposure to trace metals (Lockwood,1979). Any consideration of human impact on estuaries would take account of natural stresses, variations and the capacity of estuarine populations to respond to them. Lockwood (1979) categorized trace metals and hydrocarbons as naturally occurring potential pollutants. Many pollution studies have concentrated on the effects of trace metals and water soluble components of oil on organisms. Those species capable of withstanding physical and chemical variations in the environment have been suggested as being more susceptible to biological factors such as competition and predation (Kinne,1977). Jones (1975) stated that estuarine species are more likely to withstand additional metabolic stresses, as a result of exposure to toxicants than fully marine species. It may be assumed that the macrobenthic species on the western side of the study area have developed strategies to permit them to survive in regions of high industrial output such as the Cadland creek.

Several reports on the lethal effects of pollutants on macrofauna exist in the literature. The effect of oil on juveniles of Balanus (Mironov,1968) and of Gammarus oceanicus (Linder,1976) showed that they are killed at concentrations of about two orders of magnitude below that of the adult. Larvae of Crangon and Carcinus are 3 to 10 times more sensitive than adults to solvent emulsifiers (Portman and Cornor,1968). Jacobsen and Boylan (1973) showed that low concentration of water soluble extracts of kerosine disrupt orientation of food extracts by Nassarius obsoletus. Baker (1975) showed that treatment of Nereis diversicolor with refinery effluents caused the worm to vacate its burrow while Dicks (1976) observed that exposure of the worm to the refinery effluent in the field following an accident at Milford Haven caused the animal to escape from its burrows and thereby suffered predation from sea birds.

Though the effect of oil pollution on marine organisms resulting from oil spillage at sea has received a world wide interest, chronic pollution from the refinery effluents is always a more serious problem for it does not permit an early recovery from damage. The cumulative effect is the progressive impoverishment of the natural resources of an area, thus reducing the species diversity (Nelson-Smith,1970). Clark (1971) suggested that the exposure of some animals, particularly shell fish, to sublethal doses of toxic petroleum products may prevent the animals from breeding. In this regard, the reduced species diversity in the present study and the absence of echinoderms in the relatively marine environment of the study area may possibly be attributed to the effects of industrial discharges. Waste waters from the Esso petroleum refinery and the petrochemical industries contribute a large amount of oil to the estuary, particularly on the western side (Knap,1978).

Many studies on pollution suggest that contamination may be the most important effect of oil on shellfish. Small quantities of oil on a few shells of mussels, cockles or winkles usually taint the whole catch. Oil contaminated oysters (Ostrea) in the United States of America have been reported to take two months to loose their oily taste (Mackin and Sparks,1962). Mercenaria harvested in Southampton Water and which have been subject to low but chronic oil pollution have to be relaid in unpolluted water for a period before they are sold.

Results of the present study indicate that the benthic community of the area is physically controlled. The entire faunal community tends to be under severe physical stress with a high level of mortality in many species. A closer look at the dendrograms of size groups analysis of May samples based on abundance using Czekanowski's coefficient (Figs. 2.25 and 6.1.) showed interesting results. Figure 6.1 reveals that the entire community could be divided into two site groups at the 10% similarity level. A third site group with only station 10 is obtained at the 65% similarity level. Fig. 2.25 showed that two site groups are evident at the 23% similarity level. The two site groups at the 23% and 10% levels in the two surveys comprised a distinct 'low diversity' region (Group I) which is characterised by a high silt-clay content, high levels of sediment hydrocarbon and copper but a low species richness. The other site group (II) comprises the 'high diversity' region and is characterised by a low silt-clay, low sediment hydrocarbon and copper but a high species richness. A comparison of the two dendograms based on abundance in the two surveys showed an extension of the 'low diversity' region by 1979 to include some of the 'high diversity' stations (2, 7, 21) in 1978 (Fig.2.25). The similarity between the two site groups also increases by 1979.

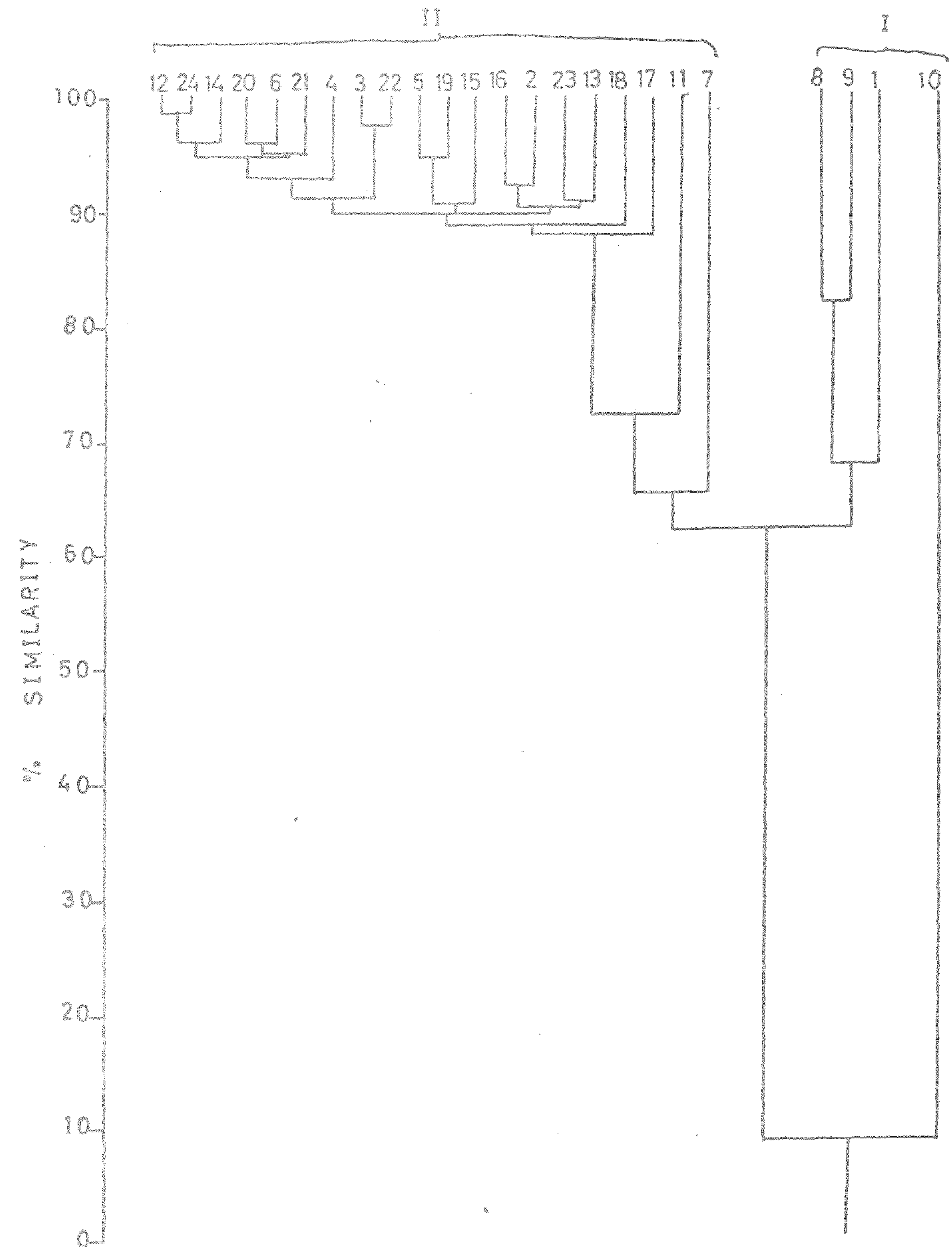


FIG. 6.1. DENDROGRAM OF SITE GROUPS ANALYSIS OF 1978 SURVEY ABUNDANCE (N) USING CZEKANOWSKI'S COEFFICIENT.

The dendrogram of site groups using May 1979 biomass showed two site groups at 45% similarity level but three site groups at 65% similarity level, (Fig. 6.2.) Group I corresponds to the 'low diversity' region in Fig. 6.1 (dendogram based on 1978 abundance). This region is dominated by Capitella capitata, Nereis diversicolor and Eteone longa. The best related stations (9 & 21) were dominated in terms of biomass by N. diversicolor and E. longa. Group II was dominated by Mercenaria and Caulleriella biomass. This site group comprised stations situated on the eastern side and the mouth of Southampton Water. The region is characterised by low silt/clay, high tidal currents and possibly low pollution load. Except for stations 3 and 20, all stations in this site group showed high degree of similarity. The low similarity between stations 3 and 20 with the rest of the group may be attributed to the absence of Mercenaria at these otherwise similar stations. The third site group (III) comprise stations where Nephtys hombergi, Crepidula fornicata and Caulleriella caputesocis dominated the biomass. Stations 18 and 22, dominated by C. fornicata tend to form a distinct sub-group.

The characteristic features of physico-chemical and biological parameters of the site groups are summarised in Table 6.1.

Ecological monitoring as in the present study is based on intensive studies of a few species and measures growth rates, fecundity and recruitment but need not necessarily be extremely costly. Though physiological and biochemical approaches predict effects on populations, ecological monitoring shows whether such predictions are correct. The importance of this particular study lies in the fact that it serves as a baseline for spatial and temporal distribution study of the benthic macrofauna and provides the first information of the production estimates of the benthic sublittoral fauna of the central industrialized region of Southampton Water. It is essential that further study on the problems looked into in the present study need be continued to assess the effects of pollutants on the fauna. It is by no means easy to predict a final conclusion on the work of this nature because of the effects of physical and chemical parameters on the benthic fauna of the physically controlled community as in the present study area. However, if the situation changes to one with a higher level of pollution, there could be a greater loss of fauna, an extension of the 'opportunistic' species and a possible decrease in the macrofaunal biomass and production. If on the other hand

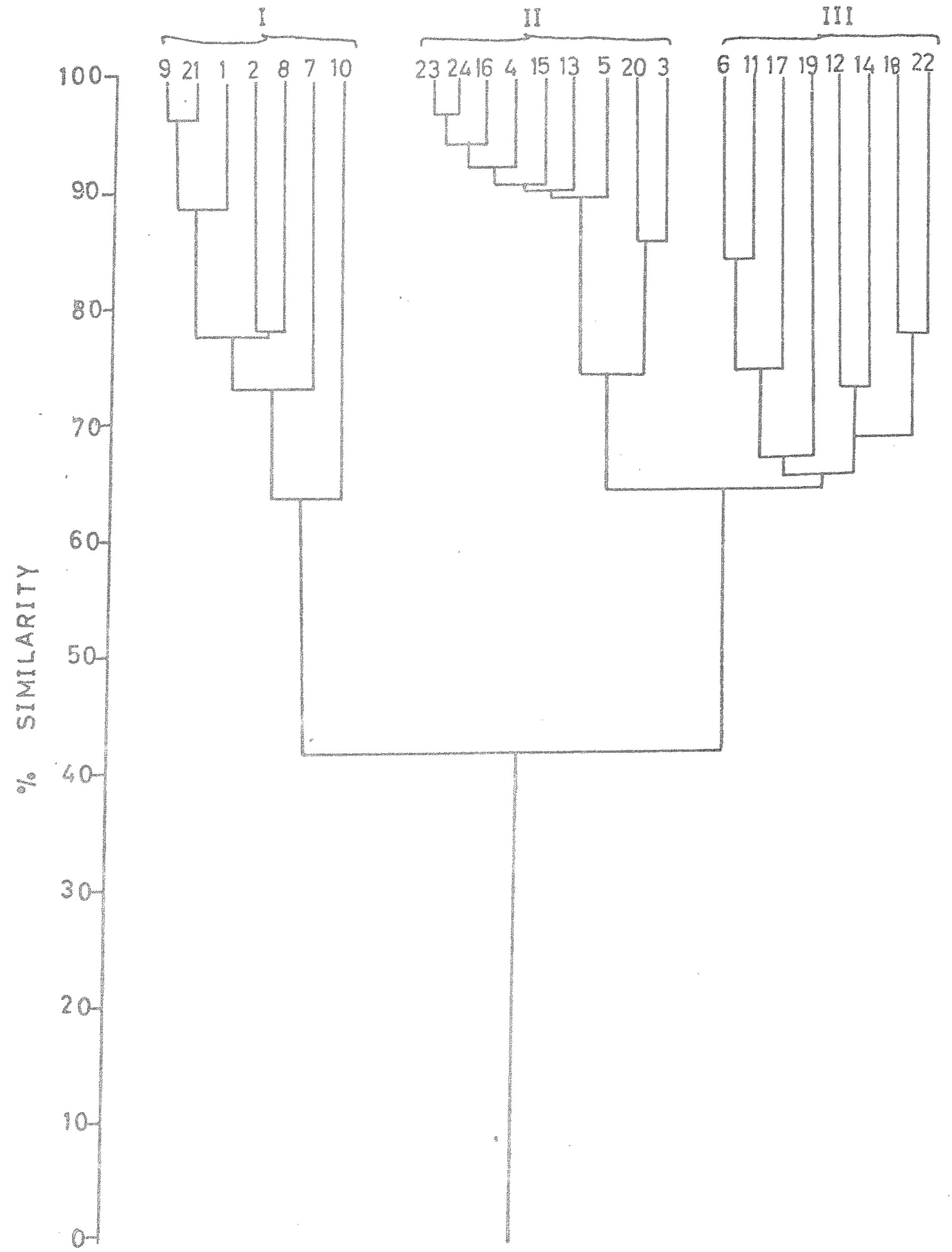


FIG. 6.2. DENDROGRAM OF SITE GROUPS ANALYSIS OF 1979 SURVEY BIOMASS USING CZEKANOWSKI'S COEFFICIENT.

STATIONS	GROUP I	GROUP II	GROUP III
	1, 2, 7, 8, 9, 10, 21	3, 4, 5, 13, 15, 16, 20, 23, 24	6, 11, 12, 14, 17, 18, 19, 22
Physico-chemical parameters			
% Silt/clay (1979	96-99	85-95	19-67
% Total Organic Matter (1979)	9-12	3-17	3-8
Tidal currents (knots)	1	1-2	2+
Copper (p.p.m.) (1979)	200-850	50-150	11-42
Zinc (p.p.m.) (1979)	100-200	50-100	60-80
Hydrocarbon (mg/g)	1-2.5	0.5-1	0.2-0.4
Biological parameters			
No. of species/0.3m^2 (1979)	2-5	6-9	10-13
No. of individuals/0.3m^2 (1979)	40-1000	1000-2000	2000-6000
Biomass mg/0.3m^2 (1979)	50-700	1000-3000	3000-6000
Diversity (Hs). (1979)	0.2-1.2	0.2-1.1	0.3-1.5

Table 6.1

the situation improves, more fauna may become established with a decrease in the 'opportunistic' species and an increase in the benthic macrofaunal biomass and production.

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APPENDIX I

DENSITY OF MACROFAUNA /0.3M² IN MAY 1978 SURVEY

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lepidonotus squamatus (L)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Aphrodita aculeata (Claparede)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Anaitides maculata (St Joseph)	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Eteone Longa Fabricius	16	-	2	1	15	6	13	41	22	-	-	6	3	3	6	5	-	-	14	8	8	9	-	5
Ophiodromus flexuosus Delle Chiaje	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syllidae	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Autolytus sp	-	-	1	-	-	2	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	-	-	-
Nereis diversicolor Muller	21	-	-	2	-	-	28	23	9	4	-	-	-	-	-	1	2	6	-	-	31	-	-	3
Cirriformia tentaculata (Montagu)	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-
Nephtys hombergi (Aud & Edin)	5	38	36	13	105	27	11	-	-	-	33	12	38	4	59	35	-	8	61	12	29	29	12	3
Caulleriella caputesocis (St Joseph)	6	281	1178	1334	779	878	46	-	-	220	39	1634	214	559	335	275	303	305	407	251	279	1146	57	1378
Scalibregma inflatum (Rathke)	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Capitella capitata (Fabricius)	3	2	1	1	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	3	1	-	-
Cirratulus cirratus (O.F.Muller)	-	-	-	2	-	-	-	-	-	-	-	-	-	-	16	-	28	-	-	-	-	-	1	-
Melinna palmata (Malmgren)	-	-	3	5	30	1	-	-	-	-	-	7	4	14	-	3	1	6	-	-	-	9	5	13
Polynoe sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Eulalia pusilla (St Joseph)	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoronidea	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
Pherusa plumosa (O.F.Muller)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Exogone sp	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crepidula fornicata L	-	-	-	6	-	-	-	-	-	-	-	-	-	3	-	17	-	6	-	-	-	-	-	-
Nassarius reticulatus L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-
Gibulla cineraria L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
Littorina littorea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-
Nucula turgida (Leckenby) (& Marshall)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule L	-	1	-	2	-	-	1	-	-	-	-	-	-	-	-	-	5	-	1	-	-	-	1	-
Abra Alba (Wood)	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Abra nitida (Muller)	-	12	180	26	95	28	1	-	-	-	4	4	13	1	78	-	-	-	61	5	13	147	2	4
Venerupis pullastra (Montagu)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mercenaria mercenaria L	-	-	-	9	-	3	-	-	-	-	-	3	1	1	-	-	-	6	-	-	-	6	1	-
Corophium insidiosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Microdeutopus gryllotalpa (crasta	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesopodopsis slabberi (van Beneden)	--	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Philomedes globosum Baird	-	2	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pariambus typicus (Kroyer)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eudorella truncatula (Bate)	-	-	3	1	6	9	-	-	-	-	-	7	10	2	3	-	-	-	-	-	-	-	-	-
Crangon vulgaris L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Corophium tuberculosum (Pallas)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Corophium volutator (Pallas)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Achelia echinata (Hodge)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ascidiacea	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S	5	9	8	25	8	8	7	2	3	2	3	7	7	10	7	7	11	11	7	4	7	[illegible]	7	9
N	51	342	1404	1489	1033	952	102	64	38	224	76	1628	283	589	498	338	347	356	556	276	364	134[illegible]	[illegible]	1411

APPENDIX II MAY 1978 BIOMASS (mg)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lepidonotus squamatus	-	-	-	-	-	-	-	-	-	-	-	-	-	7.4	-	-	-	-	-	-	-	-	-	62.6
Aphrodita aculeata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.6	-	-	-	-	-	-	-
Anaitides maculata	-	-	2.0	7.5	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-	-	-	-	-	-
Eteone longa	4.2	-	0.1	6.7	1.8	8.7	7.4	15.2	5.7	-	-	4.0	6.4	3.2	5.0	7.7	-	-	7.0	5.3	6.6	5.3	-	10.9
Ophiodromus flexuosus	-	-	-	11.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syllidae	-	-	-	66.4	-	-	-	-	-	-	-	-	-	-	-	-	-	98.9	-	-	-	-	-	-
Autolytus sp	-	-	-	3.3	-	-	222.4	-	-	-	-	-	-	601.7	3.3	-	-	-	-	-	7.5	-	-	3.4
Nereis diversicolor	68.8	31.5	-	178.3	-	-	188.7	100.0	20.9	68.4	-	-	-	-	-	6.6	8.3	58.1	-	-	37.9	-	-	99.0
Nephtys hombergii	13.7	83.5	259.3	73.4	646.3	182.0	23.8	-	-	-	230.9	115.7	99.6	39.5	318.5	543.8	-	41.2	333.5	119.9	109.3	251.6	120.1	63.4
Cirriformia tentaculata	-	-	-	5.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-
Caulleriella caputesocis	5.4	35.4	179.4	131.1	227.3	122.2	9.4	-	-	99.3	9.1	238.0	48.2	107.2	33.7	47.4	42.3	43.6	52.6	47.1	34.3	191.5	15.1	226.4
Scalibregma inflatum	-	-	-	-	3.2	-	-	-	-	-	-	-	-	-	-	-	3.1	-	-	-	-	-	-	-
Capitella capitata	1.0	8.9	1.1	1.0	-	-	-	-	7.4	-	-	-	-	-	-	-	-	-	-	-	3.3	6.6	-	-
Cirratulus cirratus	-	-	-	13.7	-	-	-	-	-	-	-	-	-	-	109.6	-	163.1	-	-	-	-	-	0.9	-
Polynoe sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.4	-	-	-	-	-	-
Eullalia pusilla	-	-	-	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoronidae	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	4.4	-	-
Phecusa plumosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exogone sp	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crepidula fornicata	-	-	-	1582.9	-	-	-	-	-	-	-	-	-	399.4	-	2747.2	-	1595.9	-	-	-	-	-	-
Melinna palmata	-	-	15.5	14.1	21.5	1.1	-	-	-	-	-	9.4	14.4	5.2	-	12.5	2.3	7.9	-	-	-	4.2	[illegible]	8.6
Nassarius reticulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	122.4	-	347.6	-	-	-	-	-	-
Gibulla cineraria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	38.5	-	-	-	-	-	-
Littorina littorea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	565.2	-	-	-	-	-	-
Cerastoderma edule	-	11.3	-	13.2	-	-	2.1	-	-	-	-	-	-	-	-	-	799.5	-	407.1	-	-	-	12.7	-
Abra alba	-	5.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Venerupis pullastra	-	-	-	794.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Abra nitida	-	2.8	277.0	5.7	26.3	19.3	9.0	-	-	-	2.0	8.0	9.4	6.5	79.0	-	-	-	133.7	5.2	17.2	181.1	9.0	7.2
Nucula turgida	-	3.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mercenaria mercenaria	-	-	-	14210.2	-	210.3	-	-	-	-	-	689.8	-	-	-	-	-	463.8	-	-	-	39779.2	6463.2	-
Corophium insidiosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	-
Microdeutopus gryllotalpa	-	-	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesopodopsis slabberi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.4	-	-
Philomedes globosus	-	2.2	-	0.8	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pariambus typicus	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eudorella truncatula	-	-	0.2	4.5	2.2	6.8	-	-	-	-	-	6.7	1.1	3.4	4.5	-	-	-	-	3.2	-	-	-	2.3
Crangon vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-
Corophium tuberculatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.2	-	-	-	-	-	-	-
Corophium volutator	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-
Achelia echinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2
Total	93.1	184.4	734.6	2925.1	930.9	340.1	462.8	115.2	34.0	167.7	242.0	381.8	179.1	1173.5	553.6	3487.6	1030.9	2807.3	935.7	180.7	216.1	6541	1676	2533.1

APPENDIX III

MAY 1979 DENSITY /0.3M^2

S	2	3	7	22	10	10	7	4	3	7	5	8	13	8	5	7	6	13	12	9	6	7	7	9
STATIONS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
pidonotus squamatus (L)	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
aitides maculata (St Joseph)	-	-	-	4	3	1	5	1	-	1	-	-	-	-	-	-	-	-	-	1	2	-	-	-
eone longa (Fabricius)	43	50	2	-	-	-	25	108	24	21	-	-	-	1	-	-	-	-	2	4	103	1	-	4
rmothoe impar (Johnston)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
pharete acutifrons (Grube)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
reis diversicolor .F.Muller)	1	69	-	1	-	-	11	42	230	1	-	-	-	-	-	-	-	-	-	-	228	-	-	-
ohtys hombergi udonia & M Edward)	-	-	56	6	57	32	-	-	-	6	25	7	22	10	24	5	1	13	12	20	-	24	28	19
rriformia tentaculata ontagu)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-
ulleriella caputesocis t Joseph)	-	-	318	5977	5161	1447	-	-	-	-	2877	5487	343	2785	339	1071	442	5959	1827	396	-	1870	1103	5356
alibregma inflatum (Rathke)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-
bella pavonina (Savigny)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	63	-	-	-	-
pitella capitata (Fabricius)	-	4	-	11	-	-	22	12	98	41	-	-	-	-	-	-	-	-	-	-	11	2	1	4
rratulus cirratus).F.Muller)	-	-	-	3	3	7	3	-	-	-	-	-	2	1	1	1	6	2	2	-	-	-	-	-
linna palmata (Malmgren)	-	-	-	2	40	-	-	-	-	-	-	-	5	-	-	1	1	1	-	-	-	-	2	3
lalia pusilla (St Joseph)	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
lydora ciliata (Johnston)	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
oronidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-
ucothoe spinicarpa bildgaard)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ilomedes globosus Baird	-	-	2	22	3	2	4	-	-	-	-	2	1	3	-	-	-	1	-	4	2	-	-	-
dorella truncatula (Bate	-	-	2	7	18	14	-	-	-	-	7	14	2	15	3	-	-	-	9	9	-	12	33	26
eucothoe spinicarpa Abildgaard)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
hilomedes globosus Baird	-	-	2	22	3	2	4	-	-	-	-	2	1	3	-	-	-	1	-	4	2	-	-	-
udorella truncatula (Bate	-	-	2	7	18	14	-	-	-	-	7	14	2	15	3	-	-	-	9	9	-	12	33	26
ariambus typicus (Kroyer)	-	-	-	5	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
rangon vulgaris L	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
assa marmorata	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
erioculodes longimanus	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
tylus vedlomensis Bate & Westwood)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
ammarus locusta L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
hierocrates intermedius ars	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
icrodeutopus gryllotalpa ousta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	1	-	-	-	-	-
ora gracilis (Kroyer)	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
dotea chelipes (Pallas)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-
arcinus maenas (L)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
orophium sextoni Crawford)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
chelia echinata (Hodge)	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
ycnogonum litterale (Strom)	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-
repidula fornicata (L)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	39	-	-	-	4	-	-
assarius reticulatus (L)	-	-	-	4	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-
uccinium undatum L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
bra nitida (Muller)	-	-	134	60	43	53	2	-	-	13	53	29	23	43	122	3	1	12	-	4	-	132	72	27
erastoderma edule (L)	-	-	-	3	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	4
ercenaria mercenaria (L)	-	-	-	13	4	1	-	-	-	-	-	5	2	-	-	3	-	-	1	-	-	-	1	9
enerupis pullastra Montagu)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total N	44	123	515	6159	5336	1559	67	217	352	84	2963	5547	405	2859	489	1089	459	6038	1864	502	347	2046	1240	5449

APPENDIX IV

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lepidonotus squamatum	-	-	-	3.2	-	-	-	-	-	-	-	-	0.9	4.2	-	-	-	-	-	-	-	-	-	-
Anaitides maculata	-	-	-	4.3	2.2	1.1	8.6	0.8	-	1.5	-	-	-	-	-	-	-	-	-	4.4	6.6	-	-	-
Eteone longa	2.7	9.5	5.6	-	-	-	52.4	38.4	965.0	185.1	-	-	-	120.3	-	-	-	-	1.1	36.7	696.4	4.3	-	5.4
Harmothoe impar	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	325.2	-	-	-	-	-
Nereis diversicolor	3.1	495.7	-	2.3	-	-	28.6	125.0	657.3	9.4	-	-	-	-	-	-	-	-	-	-	520.0	-	-	-
Amphafete acutifroms	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.5	-	-	-	-	-
Nephtys hombergii	-	-	533.6	164.1	666.1	295.4	-	-	-	30.0	258.8	255.6	238.8	128.1	142.7	11.6	73.4	234.3	201.5	323.6	-	60.8	115.2	119.6
Cirriformia tentaculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.1	-	-	-	-	-
Scalibregma inflatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.4	-	-	-	-	-	-
Sabella pavonina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.6	-	-	-	-
Caulleriella caputesocis	-	-	58.6	830.8	716.6	302.8	-	-	-	-	307.0	553.4	91.8	422.9	22.0	142.5	120.5	761.2	439.8	39.9	-	328.1	209.3	65[illegible].9
Capitella capitata	-	1.0	-	3.3	-	-	8.9	4.1	25.3	9.9	-	-	-	-	-	-	-	-	-	-	4.1	-	-	-
Cirratulus cirratus	-	-	-	16.3	24.6	36.8	6.5	-	-	-	-	-	2.2	5.0	8.2	4.3	55.5	12.7	24.1	-		-	-	-
Melinna palmata	-	-	-	4.0	59.3	-	-	-	-	-	-	-	16.3	-	-	6.2	4.4	3.9	-	-		-	4.3	12.5
Eulalia pusilla	-	-	-	4.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polydora ciliata	-	-	-	-	-	5.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoronidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-
Abra nitida	-	-	86.7	20.5	25.4	35.7	4.6	-	-	6.6	34.7	10.8	4.9	35.0	137.0	4.3	-	16.4	-	115.6	-	109.5	73.1	13.1
Mercenaria mercenaria	-	-	-	20525.8	7788.0	70.1	-	-	-	-	-	1149.6	-	-	-	4703.2	-	-	77.3	-	-	-	6463.2	11599.5
Nassarius reticulatus	-	-	-	583.6	-	-	-	-	-	-	-	-	28.7	-	-	241.6	-	-	-	-	-	-	-	-
Buccinum undatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4191.0	-	-	-	-	-	-
Cerastoderma edule	-	-	-	172.2	-	-	-	-	-	6.6	-	8.7	7.4	-	-	-	-	-	-	-	-	-	-	85.7
Venerupis pullastra	-	-	-	919.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crepidula fornicata	-	-	-	275.2	-	-	-	-	-	-	-	-	-	-	-	-	-	19681.6	-	-	-	1378.0	-	-
Carcinus maenas	-	-	-	107.4	-	-	-	-	-	-	-	-	-	-	-	-	-	736.8	-	-	-	-	-	-
Leucothoe spinicarpa	-	-	-	1.8	-	-	-	-	-	-	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-
Perioculodes longimanus	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-	-	-	-	-
Gammarus locusta	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-	-	-	-	-	-	-	-	-	-
Corophium sextoni	-	-	-	1.6	-	-	-	-	-	-	-	-	-	-	-	16.4	-	-	-	-	-	-	-	-
Crangon vulgaris	-	-	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jassa marmorata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.2	-	-	-
Atylus vedlomensis	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	1.1	-	-	-	-
Chierocrates intermedius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	8.5	-	-	-	-
Microdeutopus gryllotalpa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.8	-	-	-	-	-	-
Achelia echinata	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Pycnogonum littorale	-	-	-	-	-	-	-	-	-	-	-	3.6	-	6.2	-	-	-	-	-	-	-	-	-	-
Philomedes globosus	-	-	1.1	4.6	2.4	2.2	1.2	-	-	-	-	4.5	1.1	1.1	-	-	-	1.0	-	0.5	0.1	5.6	3.4	5.6
Aora gracilis	-	-	-	3.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Idotea chelipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-	-	-	-	-	-
Eudorella truncatula	-	-	2.2	5.5	6.6	3.2	-	-	-	-	3.3	1.0	1.1	2.1	3.3	2.2	3.3	-	1.0	3.2	-	4.4	3.1	[illegible].8
Pariambus typicus	-	-	-	6.6	1.0	2.3	-	-	-	-	-	-	1.2	-	-	-	-	-	-	-	-	-	-	3.4
Total	5.8	506.2	691.2	23660.2	9292.2	754.9	110.8	168.3	1647.6	249.1	608.	1988	397.5	742.9	313.2	5134.4	259.2	25662.1	1087.3	543.3	1230.4	1890.7	6931.6	12498.5

SECONDARY PRODUCTION COMPUTATIONS FOR EIGHTEEN BENTHIC MACRO-INFAUNA OF SOUTHAMPTON WATER

APPENDIX V

SABELLA PAVONINA STATION 2

Sampling Month		Year Class	No/M^2	Mean Wt $\overline{W}$ (mg)	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
1978	Sept.	0	1740	0.0129	–	–	–
1978	Nov.	0	2733	0.0086	–	2236.5	–
1979	Jan.	0	57	0.0386	0.03	1395	41.85
						P =	41.850 mg.

Net Production = 41.850 mg.

APPENDIX VI

SABELLA PAVONINA STATION 5.

Sampling Month		Year Class	$No/0.5M^2$	Mean Wt $\overline{W}$ (mg)	Wt Increment ΔW	Mean No. $\overline{N}$	Production $\overline{N} \Delta W$
1979	March	0	1	3.4	–	–	–

No Production for Sabella in Station 5.

APPENDIX VII

SABELLA PAVONINA STATION 9

Sampling Month		Year Class	No/M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
1978	Sept.	0	111	0.198	–	–	–
1978	Nov.	0	28	2.20	2.002	69.5	139.139
1979	Jan.	0	1	2.20	–	14.5	–
						P =	139.139

Net Production = 139.139 mg.

SABELLA PAVONINA STATION 20

	Sampling Month	Year Class	No/ 0.5M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No. $\overline{N}$	Production $\overline{N}\ \Delta W$
				1st Cohort			
1978	Sept.	0	240	0.0408	-	-	-
1978	Nov.	0	112	0.0188	-	176	-
1979	Jan.	0	-	-	-	-	-
1979	Mar.	0	2	2.15	2.15	1	2.150
						P =	2.150mg
				2nd Cohort			
1979	May	0	507	0.0219	-	-	-
	July	0	11	0.06727	0.6508	259	168.5572
	Sept	0	4	0.7500	0.0773	7.5	0.5798
	Nov.	0	-	-	-	-	-
1980	Jan	0	-	-	-	-	-
						P =	169.1370
				3rd Cohort			
1980	Mar	0	4	0.825	-	-	-

MELINNA PALMATA STATION 5

	Sampling Month	Year Class	No/ 0.5M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\ \Delta W$
1978	July	0	8	0.400	-	-	-
	Sept	0	8	0.360	-	8	-
	Nov	0	43	0.223	-	25.5	-
1979	Jan	0	47	0.236	0.013	45.0	0.585
	Mar	0	12	0.158	-	29.5	-
	May	1	87	1.370	1.212	44.5	53.935
	July	1	103	1.150	-	95	-
	Sept	1	80	1.580	0.430	91.5	39.345
	Nov	1	29	1.400	-	54.5	-
1980	Jan	1	54	1.860	0.460	41.5	19.09
	Mar	1	11	2.740	0.880	32.5	28.60
						P =	141.554
1978	July	1	48	0.87	-	-	-
	Sept	1	31	1.00	0.13	39.5	5.135
	Nov	1	62	1.06	0.06	46.5	2.790
1979	Jan	1	23	3.53	2.47	42.5	104.980
	Mar	1	21	1.67	-	22.0	-
	May	II	6	2.05	0.38	13.5	5.13
	July	II	20	2.75	0.70	13.0	9.10
						P =	127.135
1978	July	II	8	2.66	-	-	-
	Sept	II	2	1.75	-	5	-
	Nov	II	2	4.00	2.25	2	4.50
						P =	4.50

2nd Cohort

1979	May	0	7	0.11	-	-	-
	July	0	5	0.40	0.29	6	1.74
	Sept	0	17	0.24	-	11	-
	Nov	0	12	0.43	0.19	14.5	2.755
1980	Jan	0	10	0.28	-	11	-
	Mar	0	7	0.09	-	8.5	-
						P =	4.495

Net P = 277.684 mg.

PPENDIX X(a)

CAPITELLA CAPITATA STATION 2

	Sampling Month	Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
978	July	0	0	0	–	–	–
	Sept	0	608	0.065	–	–	–
	Nov	0	76	0.0063	–	342	–
979	Jan	0	2	1.15	1.144	39	44.043
						P =	44.043
				2nd Cohort			
979	Mar	0	362	0.039	–	–	–
	May	0	21	1.095	1.056	191.5	202.224
						P =	202.224
979	Mar	I	10	0.33	–	–	–
				3rd Cohort			
979	July	0	282	0.092	–	–	–
	Sept	0	167	0.847	0.755	224.5	169.498
	Nov	0	120	0.310	–	143.5	–
980	Jan	0	205	0.10	–	162.5	–
	Mar	0	25	0.0007	–	115.	–
						P =	169.498

Net P = 415.765 mg

PENDIX X(b)

CAPITELLA CAPITATA STATION 5

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
78	July	0	3	1.400	–	–	–

APPENDIX X(c)

CAPITELLA CAPITATA STATION 9

	Sampling Month	Year Class	No/M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
1978	July	0	0	-	-	-	-
	Sept	0	22736	0.075	-	-	-
	Nov	0	13362	0.0203	-	18049	-
1979	Jan	0	1582	0.1195	0.0992	7472	741.463
	Mar	I	750	0.2507	0.1312	1166	152.979
	May	I	107	0.3047	0.054	428.5	23.139
	July	I	150	0.268	-	128.5	-
						P =	917.581
1978	Sept	I	2500	0.067	-	-	-

2nd Cohort

	Sampling Month	Year Class	No/M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
1979	Mar	0	1537	0.05296	-	-	-
	May	0	5730	0.27270	0.2197	3633.5	799.085
	July	0	794	0.1037	-	3262	-
	Sept	I	1552	0.1507	0.047	1173	55.131
						P =	854.216

3rd Cohort

	Sampling Month	Year Class	No/M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
1979	Sept	0	6184	0.0378	-	-	-
	Nov	0	6841	0.0385	0.007	6512.5	4.559
1980	Jan	0	724	0.0442	0.0057	3782.5	21.560
	Mar	0	814	0.0386	-	769.0	-
						P =	26.119

Net P = 1797.916 mg

or 1.798g

APPENDIX X(d)

CAPITELLA CAPITATA STATION 20

	Sampling Month	Year Class	No/$0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta W$
1979	July	0	1	3.4	-	-	-
	Sept	0	3	2.2	-	2	-
	Nov	0	4	2.3	0.1	3.5	0.350
1980	Jan	0	I	2.0	-	2	-
	Mar	0	-	-	-	-	-
						P =	0.350

PPENDIX XI

CAULLERIELLA CAPUTESOCIS STATION 2

Sampling Month		Year Class	No/M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
978	July	0	2565	0.0582	–	–	–
	Sept	I	520	0.0385	–	1542.5	–
	Nov	I	35	0.0223	–	277.5	–
979	Jan	I	5	0.64	0.6177	20.0	12.354
						P =	12.354
978	July	I	860	0.0073	–	–	–
				2nd Cohort			
978	Sept	0	700	0.066	–	–	–
	Nov	0	216	0.0435	–	458	–
979	Jan	0	319	0.0445	0.001	267.5	0.268
	Mar	0	2	0.0028	–	160.5	
	May	0	1	0.0025	–	1.5	
	July	0	0	0.0023	–	–	
979	Sept	0	4	1.1	–	2.5	
						P =	0.268
				3rd Cohort			
980	Mar	0	1	1.1	–	–	–

Net P = 12.354 + 0.268 = 12.622 mg

PPENDIX XII

CAULLERIELLA CAPUTESOCIS STATION 9

Sampling Month		Year Class	No/M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
978	July	0	422	0.0334	–	–	–
	Sept	0	58	0.0379	0.0045	240	1.080
						P =	2.080 mg

APPENDIX XIII

CAULLERIELLA CAPUTESOCIS STATION 5

	Sampling Month	Year Class	No/0.5M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\ \Delta W$
1978	July	0	1400	0.073	–	–	–
	Sept	0	6420	0.029	–	3910	–
	Nov	0	6336	0.071	0.042	6378	267.876
1979	Jan	0	6400	0.075	0.004	6368	25.472
	Mar	0	2133	0.118	0.043	4266.5	183.460
	May	I	4835	0.0996	–	3484	–
	July	I	1000	0.176	0.076	2917.5	222.897
	Sept	I	638	0.134	–	819	–
	Nov	I	600	1.67	1.536	619	950.784
1980	Jan	I	200	0.071	–	400	–
	Mar	I	1621	0.0300	–	910.5	–
						P =	1650.489
1978	July	I	3544	0.041	–	–	–
	Sept	I	6440	0.028	–	4992	–
	Nov	I	6000	0.073	0.045	6220	279.900
1979	Jan	I	1985	0.095	0.022	3992.5	87.835
	Mar	I	400	0.130	0.035	1692.5	59.238
	May	III	200	5.00	4.870	300	1461.000
	July	II	200	0.196	–	200	–
						P =	1887.973
1978	July	II	500	0.114	–	–	–
	Sept	II	200	0.169	0.055	350	19.250
	Nov	II	400	0.158	–	300	–
						P =	19.250

2nd Cohort

	Sampling Month	Year Class	No/0.5M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\ \Delta W$
1979	May	0	700	0.10	–	–	–
	July	0	9363	0.078	–	5031.5	–
	Sept	0	3650	0.060	–	6506.5	–
	Nov	0	2225	0.051	–	2937.5	–
1980	Jan	0	2368	0.076	0.025	2296.5	57.413
	Mar	0	2950	0.078	0.002	2659	5.318
						P =	62.731

Net P = 3620.443 mg

APPENDIX XIV

CAULLERIELLA CAPUTESOCIS STATION 20

	Sampling Month	Year Class	No/ 0.5M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
1978	July	0	967	0.0598	-	-	-
	Sept	0	1684	0.0628	0.00297	1325.5	3.9367
	Nov	0	1000	0.0236	-	1342	-
1979	Jan	0	2300	0.0611	0.0375	1650	61.8750
	Mar	0	1722	0.0385	-	2011	-
	May	I	108	0.5833	0.5448	915	498.4920
						P =	564.3037
1978	July	I	3306	0.0488	-	-	-
	Sept	I	2200	0.0791	0.0303	2753	83.4159
	Nov	I	1656	0.0235	-	1928	-
1979	Jan	I	1060	0.0642	0.0407	1358	55.2706
	Mar	I	120	0.0883	0.0241	590	14.2190
						P =	152.9055
1978	July	II	480	0.1548	-	-	-
	Sept	II	0	-	-	-	-
	Nov	II	160	0.081	0.081	80	6.48
						P =	6.48
				2nd Cohort			
979	May	0	1300	0.0779	-	-	-
	July	I	1020	0.0081	-	1160	-
	Sept	I	60	0.4000	0.3919	540	211.626
						P =	211.626
				3rd Cohort			
979	July	0	1762	0.0057	-	-	-
	Sept	0	526	0.0835	0.0778	1144	89.0032
	Nov.	I	940	0.0400	-	733	-
980	Jan	I	1038	0.1344	0.0944	989	93.3616
	Mar	I	500	0.0282	-	769	-
						P =	182.3648
				4th Cohort			
979	Nov	0	1057	0.0483	-	-	-
	Jan	0	1574	0.1090	0.0607	1315.5	79.8793
	Mar	0	1570	0.1374	0.0284	1572	44.7016
						P =	124.5809

Net P = 1242.2609 mg

APPENDIX XV(a)

NEPHTYS HOMBERGII STATION 2

	Sampling Month	Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
1978	July	0	100	8.653	-	-	-
	Sept	I	2	8.350	-	51	-
	Nov	I	1	38.6	30.250	1.5	45.3750
						P =	45.3750
				2nd Cohort			
1978	Sept	0	1	1.7	-	-	-
	Nov	0	3	2.23	0.53	2	1.06
1979	Jan	I	19	9.521	7.291	11	80.201
						P =	81.261
				3rd Cohort			
1979	Jan	0	13	0.454	-	-	-

Net P = 126.636 mg

APPENDIX XVb

NEPHTYS HOMBERGII STATION 9

	Sampling Month	Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
1978	July	0	10	5.06	-	-	-
				2nd Cohort			
1980	Jan	0	4	7.00	-	-	-

Net P = -

PPENDIX XVI

NEPHTYS HOMBERGII STATION 5

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
978	July	0	29	4.983	-	-	-
	Sept	I	14	9.136	4.153	21.5	89.2895
	Nov	II	30	6.867	-	22	-
979	Jan	II	3	36.067	29.200	16.5	481.800
	Mar	II	1	35.700	-	2	-
						P =	571.0895
978	July	I	1	27.70	-	-	-
	Sept	I	6	14.217	-	3.5	-
						P =	0

2nd Cohort

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
978	Sept	0	3	0.267	-	-	-
	Nov	I	60	6.38	6.113	31.5	192.560
979	Jan	I	39	9.362	2.982	44.5	132.699
	Mar	I	11	18.709	9.347	25	233.675
	May	II	45	11.100	-	28	-
	July	II	21	19.696	8.576	33	283.008
						P =	841.942

3rd Cohort

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
978	Nov	0	6	1.483	-	-	-
979	Jan	0	71	5.844	4.361	38.5	167.8985
	Mar	0	30	1.223	-	50.5	-
	May	I	63	11.962	10.739	46.5	449.3635
	July	I	67	12.491	0.529	65	34.3850
	Sept	I	13	22.562	10.071	40	402.8400
						P =	1054.4870

4th Cohort

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
979	May	0	4	3.375	-	-	-
	July	0	9	8.433	5.058	6.5	32.8770
	Sept	0	57	6.172	-	33	-
	Nov	I	63	7.851	1.679	60	100.7400
980	Jan	I	35	10.437	2.586	49	126.7140
	Mar	I	-	-	-	-	-
						P =	260.3310

5th Cohort

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
979	Nov	0	7	7.514	-	-	-
980	Jan	0	33	8.782	1.268	20	25.3600
	Mar	0	22	15.450	6.668	27.5	183.370
						P =	208.7300

Net P = 2936.5795 mg

NEPHTYS HOMBERGII STATION 20

	Sampling Month	Year Class	No/ 0.5M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
1978	July	0	92	7.890	-	-	-
	Sept	I	65	9.951	2.061	78.5	161.7885
	Nov	I	100	8.528	-	82.5	-
1979	Jan	I	60	11.210	2.682	80	214.560
	Mar	I	57	9.488	-	58.5	-
	May	II	2	23.25	13.762	29.5	405.979
						P =	782.3275
				2nd Cohort			
1978	Sept	0	2	3.700	-	-	-
	Nov	0	8	6.200	2.500	5	12.500
1979	Jan	0	22	6.436	0.236	15	3.540
	Mar	0	36	6.225	-	29	-
	May	I	81	11.096	4.871	58.5	284.9535
	July	I	81	9.463	-	81	-
						P =	300.9935
1978	Sept	II	16	9.575	-	-	-
	Nov	II	2	15.400	5.825	9	52.4250
						P =	52.4250
				3rd Cohort			
1979	May	0	2	1.9	-	-	-
	July	0	7	7.657	5.757	4.5	25.9070
	Sept	I	61	7.921	0.264	34	8.9760
	Nov	I	45	13.902	5.981	53	316.9930
1980	Jan	I	42	9.691	-	43.5	-
	Mar	I	4	11.051	1.359	23	31.2570
						P =	383.1330
				4th Cohort			
1979	Sept	0	2	2.850	-	-	-
	Nov	0	-	-	-	-	-
1980	Jan	0	3	4.00	1.150	2.50	2.875
	Mar	0	52	9.275	5.275	27.5	145.0623
						P =	147.9373

Net P = 1666.8163 mg

NEREIS DIVERSICOLOR STATION 2

	Sampling Month	Year Clas	No/ M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
1978	Sept	0	202	1.051	–	–	–
	Nov	0	441	1.290	0.239	321.5	76.8385
1979	Jan	0	304	1.335	0.045	372.5	16.7625
	Mar	I	304	4.301	2.966	304	901.6640
	May	I	–	–	–	–	–
						P =	995.2650
1978	Sept	I	497	1.276	–	–	–
	Nov	I	400	1.826	0.550	443.5	243.9250
1979	Jan	I	29	16.310	14.484	214.5	3106.8180
						P =	3350.7430
1978	Sept	II	15	20.673	–	–	–
	Nov	II	7	38.343	17.670	11	194.3680
						P =	184.3680
				2nd Cohort			
1979	Mar	0	84	3.369	–	–	–
	May	0	10	26.170	22.801	47	1071.6470
	July	I	23	19.30	–	16.5	–
	Sept	I	4	48.90	28.40	13.5	383.4000
						P =	1455.0470
				3rd Cohort			
1979	July	0	126	2.598	–	–	–
	Sept	0	59	1.661	–	92.5	–
	Nov	I	85	13.801	12.140	72	874.0800
1980	Jan	I	14	4.271	–	44.5	–
	Mar	I	18	17.350	13.079	16	209.2640
						P =	1083.3440
				4th Cohort			
1979	Nov	0	357	2.501	–	–	–
1980	Jan	0	344	0.161	–	.5	–
	Mar	0	334	0.396	0.235	339	79.6650
						P =	79.6650

Net P = 7158.4320 mg

NEREIS DIVERSICOLOR STATION 9

	Sampling Month	Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
1978	July	0	16	2.5813	-	-	-
	Sept	0	107	1.870	-	61.5	-
	Nov	I	121	0.872	-	114	-
1979	Jan	I	2	8.200	7.328	61.5	450.672
						P =	450.672
1978	July	I	146	15.137	-	-	-
	Sept	I	60	11.070	-	103	-
	Nov	II	22	12.290	1.22	41	50.02
						P =	50.02
				2nd Cohort			
1978	Nov	0	20	0.095	-	-	-
1979	Jan	0	60	1.141	1.046	35	36.610
	Mar	0	-	-	-	-	-
	May	I	152	3.025	1.884	106	199.704
	July	I	5	8.500	5.475	77.5	424.313
						P =	660.627
				3rd Cohort			
1979	May	0	48	3.083	-	-	-
	July	0	2	3.250	0.167	25	4.175
	Sept	I	4	6.175	2.925	3	8.775
	Nov	I	3	5.233	-	3.5	-
1980	Jan	I	2	5.250	0.017	2.5	0.043
						P =	12.993
				4th Cohort			
1979	Sept	0	2	1.062	-	-	-
	Nov	0	53	0.234	-	27.5	-
1980	Jan	0	14	1.043	0.809	33.5	27.102
	Mar	I	99	6.983	5.940	56.5	335.610
						P =	362.712
				5th Cohort			
1980	Mar	0	930	0.973	-	-	-

Net P = 1537.024mg

PPENDIX XX

NEREIS DIVERSICOLOR STATION 5

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
978	July	0	2	9.100	-	-	-
	Sept	0	1	36.700	27.600	1.5	41.4000
	Nov	I	2	110.750	74.050	1.5	111.0750
						P =	152.4750
				2nd Cohort			
978	Nov	0	2	110.0	-	-	-
				3rd Cohort			
979	Jan	0	2	106.0	-	-	-
				4th Cohort			
980	Jan	0	1	1.0	-	-	-

Net P = 152.4750 mg

XXI

PPENDIX XXII

NEREIS DIVERSICOLOR STATION 20

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
978	July	0	2	17.45	-	-	-
	Sept	0	1	10.90	-	1.5	-
				2nd Cohort			
978	Nov	0	15	0.513	-	-	-
979	Jan	0	85	0.088	-	50	-
	Mar	0	21	0.105	0.017	53	0.901
	May	0	2	0.600	0.495	11.5	5.6925
						P =	6.5935
				3rd Cohort			
979	Sept	0	4	1.10	-	-	-
	Nov	0	10	7.99	6.89	7	48.2300
980	Jan	I	1	6.20	-	5.5	-
						P =	48.2300
				4th Cohort			
980	Jan	0	59	0.207	-	-	-
	Mar	0	29	4.907	4.700	44	P = 206.800

Net P = 261.6235 mg

APPENDIX XXII

ETEONE LONGA STATION 2

Sampling Month		Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
				1st Cohort			
1978	July	0	3	0.767	-	-	-
	Sept	0	563	0.091	-	283	-
	Nov	0	848	0.078	-	705.5	-
1979	Jan	0	269	0.126	0.048	558.5	26.8205
	Mar	0	266	0.187	0.061	266.5	16.3175
	May	0	109	0.112	-	137.5	-
	July	0	65	0.148	0.036	87	3.1052
						P =	46.2432
				2nd Cohort			
1979	Sept	0	3	0.3667	-	-	-
	Nov	0	28	0.3893	0.023	15.5	0.3565
1980	Jan	0	26	0.2423	-	27	-
	Mar	0	13	0.1462	-	19.5	-
						P =	0.3565

Net P = 46.5997 mg

APPENDIX XXIII

ETEONE LONGA STATION 5

Sampling Month		Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
				1st Cohort			
1978	July	0	8	1.225	-	-	-
	Sept	0	1	7.800	6.575	4.5	29.5875
	Nov	0	1	2.200	-	1	-
						P =	29.5875
				2nd Cohort			
1979	Jan	0	6	4.3833	-	-	-
	Mar	0	5	1.0600	-	5.5	-
	May	0	2	1.6500	0.5900	3.5	2.065
	July	0	6	1.2500	-	4	-
	Sept	0	1	5.5000	4.2500	3.5	14.875
						P =	16.940
				3rd Cohort			
1980	Mar	0	1	1.00	-	-	-

Net P = 46.5275 mg

ETEONE LONGA STATION 9

Sampling Month		Year Class	No/ M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
				1st Cohort			
978	July	0	1	2.300	-	-	-
	Sept	0	21	0.362	-	11	-
	Nov	0	45	0.231	-	33	-
979	Jan	0	1	4.500	4.269	23	98.187
						P =	98.187
				2nd Cohort			
979	Mar	0	37	0.2891	-	-	-
	May	0	15	0.7000	0.4109	26	10.6834
	July	0	1	3.4000	2.7000	8	21.6000
	Sept	0	0	-	-	-	-
	Nov	0	7	0.5285	0.5285	3.5	1.8500
980	Jan	0	3	2.5667	2.0382	5	10.1910
						P =	44.3244
				3rd Cohort			
980	Mar	0	76	0.2092	-	-	-

Net P = 142.5114 mg

PENDIX XXV

ETEONE LONGA STATION 20

Sampling Month		Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
				1st Cohort			
78	July	0	53	0.590	-	-	-
	Sept	0	94	0.226	-	73.5	-
	Nov	0	25	0.388	0.162	59.5	9.639
79	Jan	0	33	0.591	0.203	29.0	5.887
	Mar	0	27	1.496	0.905	30.0	27.159
	May	0	11	0.982	-	19	-
	July	0	25	0.408	-	18	-
	Sept	0	-	-	-	-	-
						P =	42.685
				2nd Cohort			
79	Nov	0	7	0.343	-	-	-
80	Jan	0	25	0.772	0.429	16	6.864
	Mar	0	28	0.804	0.032	26.5	0.848
						P =	7.712

Net P = 50.397 mg

'PENDIX XXVI

ANAITIDES MACULATA STATION 2

Sampling Month		Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
'78	July	-	-	-	-	-	-
	Sept	0	5	0.88	-	-	-
	Nov	0	-	-	-	-	-
'79	Jan	0	3	1.733	0.853	4	3.413
						P =	3.413

Net P = 3.413 mg

'PENDIX XXVII

ANAITIDES MACULATA STATION 5

Sampling Month		Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\,\Delta\,W$
				1st Cohort			
'78	July	0	24	0.208	-	-	-
	Sept	0	14	0.136	-	19	-
	Nov	0	5	0.54	0.404	9.5	3.838
'79	Jan	0	8	0.49	-	6.5	-
						P =	3.838
				2nd Cohort			
'79	Mar	0	2	1.30	-	-	-
	May	0	3	1.03	-	2.5	-
	July	0	3	0.73	-	3	-
						P =	0

Net P = 3.838 mg

APPENDIX XXVIII

ANAITIDES MACULATA STATION 20

Sampling Month		Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
				1st Cohort			
1978	July	0	1	2.100	-	-	-
	Sept	0	-	-	-	-	-
	Nov	0	2	1.60	-	1.5	-
						P =	-
				2nd Cohort			
1979	Jan	0	17	0.643	-	-	-
	Mar	0	14	0.121	-	15.5	-
	May	0	2	1.45	1.329	8	10.632
						P =	10.632
1979	Jan	I	4	1.7	-	-	-
	Mar	I	2	1.9	0.2	3	0.600
						P =	0.600
				3rd Cohort			
1980	Jan	0	3	2.43	-	-	-

Net P = 11.232 mg

APPENDIX XXIX

CIRRATULUS CIRRATUS STATION 2

Sampling Month		Year Class	No/ M^2	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
1978	July	0	2	0.75	-	-	-

Net P = 0

APPENDIX XXX

CIRRATULUS CIRRATUS STATION 9

Sampling Month		Year Class	No/ M^2	Wt Mean $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
1978	July	0	3	2.933	-	-	-
	Sept	0	1	2.2	-	2	-
	Nov	0	-	-	-	-	-
1979	Jan	0	0	-	-	-	-
	Mar	0	1	7.8	5.6	1	5.6
						P =	5.6

Net P = 5.6 mg

APPENDIX XXXI(a)

CIRRATULUS CIRRATUS STATION 5

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
				1st Cohort			
1978	July	0	228	0.318	-	-	-
	Sept	0	94	0.704	0.386	161	62.187
						P =	62.187
1978	Sept	I	10	1.46	-	-	-
				2nd Cohort			
1978	Nov	0	66	0.708	-	-	-
1979	Jan	0	1	4.2	3.492	33.5	116.982
	Mar	0	3	23.066	18.866	2	37.733
	May	0	1	6.10	-	2	-
						P =	154.715
1978	Nov	I	35	0.782	-	-	-
				3rd Cohort			
1979	Sept	0	43	2.372	-	-	-
	Nov	0	14	2.279	-	28.5	-
1980	Jan	0	-	-	-	-	-
	Mar	0	12	11.542	9.263	13	120.419
						P =	120.419
1979	Nov	I	4	8.5	-	-	-

Net P = 337.321 mg

APPENDIX XXXI(b)

CIRRATULUS CIRRATUS STATION 20

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N} \Delta W$
1978	Nov	0	18	0.233	-	-	-
1979	Jan	0	-	- -	-	-	-
	Mar	0	1	2.000	1.777	9.5	16.882
						P =	16.882

Net Production = 16.882 mg

APPENDIX XXXII

POLYDORA CILIATA STATION 2

Sampling Month		Year Class	No/ M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
				1st Cohort			
1978	July	0	9	0.122	-	-	-
	Sept	0	1086	0.022	-	547.5	-
	Nov	0	17	0.394	0.372	551.5	205.223
						P =	205.223
				2nd Cohort			
1979	Jan	0	42	0.0524	-	-	-
				3rd Cohort			
1979	May	0	1	2.4	-		-
	July	0	54	0.1796	-	27.5	-
						P =	-

Net P = 205.223 mg

APPENDIX XXXIII

POLYDORA CILIATA STATION 5

Sampling Month		Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
				1st Cohort			
1978	July	0	47	0.047	-	-	-
	Sept	0	18	0.172	0.125	32.5	4.0592
	Nov	0	2	0.600	0.428	10	4.2800
						P =	8.3492
				2nd Cohort			
1979	Jan	0	4	0.3	-	-	-
	Mar	0	1	1.1	0.8	2.5	2.00
						P =	2.00

Net P = 10.3492 mg

APPENDIX XXXIV

POLYDORA CILIATA STATION 9

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
				1st Cohort			
1978	July	0	50	0.016	-	-	-
	Sept	0	51	0.043	0.027	50.5	1.3704
	Nov	0	1	2.300	2.257	26	58.6820
						P =	60.0524
				2nd Cohort			
1979	July	0	1	4.5	-	-	-

Net P = 60.0524 mg

APPENDIX XXXV

POLYDORA CILIATA STATION 20

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
				1st Cohort			
1978	July	0	21	0.2095	-	-	-
	Sept	0	163	0.032	-	92	-
	Nov	0	2	0.550	0.518	82.5	42.7350
						P =	42.7350
				2nd Cohort			
1979	Jan	0	2	2.250	-	-	-
	Mar	0	2	1.700	-	2	-
	May	0	3	1.100	-	2.5	-
						P =	-
				3rd Cohort			
1980	Jan	0	3	0.2667	-	-	-
	Mar	0	1	1.1000	0.833	2	1.666
						P =	1.666

Net P = 44.4010 mg

APPENDIX XXXVI

ABRA NITIDA STATION 2

	Sampling Month	Year Class	No/ M^2	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
1978	July	0	585	2.816	-	-	-
	Sept	0	1	2.900	0.084	293	P = 2.067

Net P = 2.067 mg

ABRA NITIDA STATION 5

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
1978	July	0	23	1.083	-	-	-
	Sept	0	10	1.390	0.307	16.5	5.066
	Nov	I	7	1.586	0.196	8.5	1.666
1979	Jan	I	11	1.500	-	9.0	-
	Mar	-	-	-	-	-	-
						P =	6.732
				2nd Cohort			
1978	Nov	0	7	0.271	-	-	-
1979	Jan	0	28	0.300	0.029	17.5	0.508
	Mar	0	4	1.075	0.775	16	12.400
	May	0	89	0.485	-	46.5	-
	July	0	55	1.067	0.582	72	41.904
	Sept	0	8	0.588	-	31.5	-
						P =	54.812
				3rd Cohort			
1979	Nov	0	15	0.567	-	-	-
1980	Jan	0	4	1.625	1.058	9.5	10.051
	Mar	0	4	2.550	0.925	4	3.700
						P =	13.751

APPENDIX XXXVIII

ABRA NITIDA STATION 20

	Sampling Month	Year Class	No/ $0.5M^2$	Mean Wt $\bar{W}$	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
1978	July	0	271	2.007	-	-	-
	Sept	0	31	2.368	0.361	156.0	43.796
	Nov	I	14	1.343	-	22.5	-
1979	Jan	I	9	1.844	0.501	11.5	5.767
	Mar	I	1	2.100	0.256	5	1.280
	May	I	1	2.325	0.225	1	0.225
						P =	51.068
				2nd Cohort			
1978	Nov	0	1	3.300	-	-	-
1979	Jan	0	7	1.487	-	4	-
	Mar	0	6	0.917	-	6.5	-
	May	0	403	0.450	-	231.5	-
	July	0	258	2.037	1.587	330.5	524.504
	Sept	0	6	2.950	0.913	132	120.516
	Nov	0	15	1.713	-	10.5	-
						P =	645.020
				3rd Cohort			
1980	Jan	0	1	1.000	-	-	-
	Mar	0	12	0.725	-	-	-
						P =	-

Net P = 696.088 mg

APPENDIX XXXIX

MERCENARIA MERCENARIA STATION 5

1970 Year Class

	Sampling Month	Year Class	No/ 0.5M^2	Mean Wt (mg) $\overline{W}$	Wt Increment ΔW	Mean No $\overline{N}$	Production $\overline{N}\Delta W$
1978	July	8	1	5377.0	–	–	–
	Sept	8	1	3738.5	–	1	–
	Nov	9	–	–	–	–	–
1979	Jan	9	1	4609.9	871.4	1	877.4
	Mar	9	–	–	–	–	–
	May	9	1	4799.9	190.0	1	190.0
						P =	961.4

1971 Year Class

1978	July	7	4	2447.9	–	–	–
	Sept	7	2	2948.7	500.8	3	1502.4
	Nov	8	6	5172.0	2223.3	4	8893.2
1979	Jan	8	5	3988.6	–	5.5	–
	Mar	8	–	–	–	–	–
	May	8	–	–	–	–	–
	July	8	1	3543.3	–	3	–
	Sept	8	1	5872.6	2329.3	1	2329.3
						P =	12724.9

1972 Year Class

1978	July	6	5	2625.2	–	–	–
	Sept	6	11	2239.8	–	8	–
	Nov	7	3	3054.3	814.5	7	5701.5
1979	Jan	7	2	2434.4	–	2.5	–
	Mar	7	5	2024.0	–	3.5	–
	May	7	4	2609.4	585.4	4.5	2634.3
	July	7	3	2526.2	–	3.5	–
	Sept	7	8	3612.9	1086.7	5.5	5976.9
	Nov	8	2	2831.8	–	5	–
1980	Jan	8	2	3723.5	891.7	2	1783.4
						P =	16096.1

1973 Year Class

1978	July	5	8	1605.3	–	–	–
	Sept	5	11	1669.6	64.3	9.5	289.4
	Nov	6	7	2634.4	964.8	9	8683.2
1979	Jan	6	3	1782.6	–	5	–
	Mar	6	5	1861.5	80.9	4	323.6
	May	6	3	1873.0	11.5	4	46.0
	July	6	3	2238.7	365.7	3	1097.1
	Sept	6	6	2756.9	518.2	4.5	2331.9
	Nov	7	8	2945.8	188.9	7	1322.3
1980	Jan	7	4	2195.2	–	6	–
	Mar	7	13	2457.5	262.3	8.5	2229.6
						P =	16323.1

MERCENARIA MERCENARIA STATION 5

Sampling Year		Year Class	No/ $0.5M^2$	Mean Wt (mg)	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N}\Delta W$
1974 Year Class							
1978	July	4	1	458.9	–	–	–
	Sept	4	1	858.9	400.0	1	400.0
	Nov	5	–	–	–	–	–
1979	Jan	5	2	1430.0	571.1	1.5	856.7
	Mar	5	7	1271.0	–	4.5	–
	May	5	1	2419.3	1148.3	4	4593.2
	July	5	2	1848.0	–	1.5	–
	Sept	5	2	2512.6	664.6	2	1329.2
	Nov	6	8	1530.7	5	–	–
1980	Jan	6	1	1953.3	412.6	4.5	1856.7
	Mar	6	6	1990.4	37.1	3.5	129.9
						P =	9623.7
1975 Year Class							
1978	July	3	1	131.0	–	–	–
	Sept	3	1	746.7	615.7	1	615.7
	Nov	4	1	2333.0	1586.3	1	1586.3
1979	Jan	4	0	–	–	–	–
	Mar	4	0	–	–	–	–
	May	4	0	–	–	–	–
	July	4	1	1585.6	–	1	–
	Sept	4	4	1444.6	–	2.5	–
	Nov	5	4	1999.0	554.4	4	2217.6
1980	Jan	5	1	731.7	–	2.5	–
	Mar	5	4	1479.9	748.2	2.5	1870.5
						P =	6290.1
1976 Year Class							
1978	July	2	9	103.2	–	–	–
	Sept	2	4	72.7	–	–	–
	Nov	3	4	222.7	150.0	4	600.0
1979	Jan	3	2	106.4	–	3	–
	Mar	3	2	695.4	589.0	2	1178.0
	May	3	2	297.4	–	2	–
	July	3	0	–	–	–	–
	Sept	3	4	569.3	271.7	3	815.7
	Nov	4	8	582.4	13.1	6	78.6
1980	Jan	4	1	107.1	–	4.5	–
	Mar	4	2	815.1	744.0	1.5	1116.0
						P =	3788.3

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MERCENARIA MERCENARIA STATION 5

Sampling Month		Year Class	No/ 0.5M^2	Mean Wt (mg)	Wt Increment ΔW	Mean No $\bar{N}$	Production $\bar{N} \Delta W$
1977 Year Class							
1978	July	1	–	–	–	–	–
	Sept	1	1	79.7	–	–	–
	Nov	2	2	575.3	504.6	1.5	756.9
1979	Jan	2	0	–	–	–	–
	Mar	2	0	–	–	–	–
	May	2	0	–	–	–	–
	July	2	0	–	–	–	–
	Sept	2	0	–	–	–	–
	Sept	2	0	–	–	–	–
	Nov	3	0	–	–	–	–
1980	Jan	3	2	381.4	–	–	–
	Mar	3	3	851.1	433.7	2.5	1084.3
						P =	1841.2
1978 Year Class							
1978	Nov	1	1	7.6	–	–	–
1979	Jan	1	0	–	–	–	–
	Mar	1	0	–	–	–	–
	May	1	0	–	–	–	–
	July	1	0	–	–	–	–
	Sept	1	0	–	–	–	–
	Nov	2	0	–	–	–	–
1980	Jan	2	1	13.1	5.5	1	5.5
						P =	5.5
1979 Year Class							
1978	Nov	0	1	2.9	–	–	–
						P =	–