STUDIES ON THE PRODUCTION ECOLOGY OF SEVERAL MOLLUSC SPECIES IN THE ESTUARINE FIRTH OF FORTH.

VOL. I

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By
MICHAEL ELLIOTT

Department of Biology, University of Stirling.
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ABSTRACT.

The thesis, given in two volumes, deals with the population ecology of the macrofaunal mollusc species : *Macoma balthica* (L.), *Cerastoderma edule* (L.), *Mya arenaria* (L.), *Retusa obtusa* (Montagu) and *Hydrobia ulvae* (Pennant) studied at fourteen stations on Torry Bay, a large intertidal area in the estuarine Firth of Forth, over the period January, 1975 to February, 1977. These species occupy differing ecological niches within the estuarine ecosystem. The environmental factors at the stations, which represent the range of available habitats in the area, are described in Chapter 2. This chapter also outlines the statistical techniques used in ascertaining the relationships between the factors studied.

The population dynamics and magnitude of the growth, flesh condition, production and productivity of each species are given in Chapters 3 - 5. These chapters also discuss the environmental factors affecting the ecology of the species. Multivariate correlation and regression techniques have been used to describe the factors which influence the species' production ecology.

The anomalous production ecology of *M. balthica* found in the Forth Estuary (Chapter 3) was further studied by a field mark and recapture experiment and multivariate laboratory experiments (Chapter 6). Chapter 6 also discusses the mode of feeding of this bivalve in relation to its ecological preferences and describes a small study on heavy metal pollution within *M. balthica*.

The discussion in Chapter 7 gives general conclusions from the studies and their implications in estuarine productivity.

Features common to the population ecology of the five species are discussed and a food web detailing the role of the benthic macrofauna on Torry Bay is given.

Chapter 1. General Introduction.

The large intertidal areas, found within estuaries, have for many years interested biologists; that interest has been a result of the large animal populations and the interaction of the physical, chemical and biological factors that occur in those areas. Eltringham (1971), in considering those populations and factors, was prompted to suggest :

> "Physically, a mud flat is uninviting, if not repellant, but it has much to offer the intellect."

The biological and physical factors characterising an estuary have been previously studied in great detail (for reviews see Yonge, 1953; Lauff, 1967; Green, 1968; McLusky, 1971; Remane and Schlieper, 1971; Wolff, 1973; Perkins, 1974; Cronin, 1976); and although many authors have attempted to define an estuary (Caspers, 1967), the most widely accepted definition is that given by Pritchard (1967) :

> "An estuary is a semi-enclosed coastal body of water which has a free connection with the sea and within which seawater is measurably diluted with fresh water derived from land drainage."

Macrofaunal distribution has been studied in many British estuaries including the Tamar (Percival, 1929; Spooner and Moore, 1940); the Thames (Newell, 1954; Perkins, 1958); the Severn (Haderlie and Clark, 1959; Boyden and Little, 1973; Little and Boyden, 1976; Warwick and Davies, 1977); the Mersey (Fraser, 1932; Bassingdale, 1938); the Dovey (Beanland, 1940); the Dee (Stopford, 1951); the Towy (Howells, 1964); the Exe (Holme, 1949); the Medway (Wharfe, 1977) and the Clyde (Smyth et al, 1974); and in Danish estuaries (Muus, 1967) and Dutch estuaries (Wolff, 1973). Many of these authors emphasise the difficulty of colonising the estuarine environment because of the variability of its physico-chemical factors. These factors include widely fluctuating salinity levels; the conflict between tidal and river currents and the resultant high sedimentation levels which lead to the characteristic fine particulate shores; the relatively high temperature variation, and the frequent depletion of oxygen either in the sediment or the water column caused by abundant microorganism populations associated with effluent output. In addition to these problems, macrofauna living intertidally encounter problems associated with these areas, e.g. exposure, dessication, thermal stress and increased availability to predation (Newell, 1970).

However, for those species successfully colonising estuaries there is the advantage that food is at least equal to and usually more abundant than adjacent marine and freshwater areas. The enrichment of estuarine waters occurs by terrestrial erosion, agricultural drainage and the imput of organic and inorganic material via industrial and urban effluents. Unfortunately, the latter may result in pollution of the estuary. The rigorous conditions in estuaries result in successful colonisation by only a few species; however those successful species can occur in very high densities and in turn support large predator populations.

The present study in the Forth estuary, Scotland (see Section 2.1.1.) was commenced with many aims at several levels of importance. At the most fundamental level was the desire to gain information on the ecological energetics of the estuarine macro-infaunal molluscs and thus to describe and quantify the structure and dynamics of an intertidal ecosystem within a relatively polluted estuary. The primary aims were to study and quantify the variability in the macrofaunal production ecology within a small intertidal area (Torry Bay) and possibly to explain that variation by studying the interrelationships within and between the environmental factors and the macrofauna. This information was necessary in order to determine the size of macrofaunal population supported by a particular area and, furthermore, whether that support allowed for the growth and production by the macrofauna. It was further aimed to gain not only an insight into the interspecific and spatial intraspecific differences in the production ecology, but also into the ecological differences between the age groups within a population. The suggestions, first made by Kreger (1940) and Savilov (1953), that the ecology of different age groups may vary no less widely than the ecology of different species and that the importance of any factor may vary with age, are further considered in this study. The lesser aim of the study was to compare both the Torry Bay area and the Forth estuary with other polluted and non-polluted areas in order to comment on the effects of estuarine industrialisation on the macrofauna.

Many of the early estuarine studies were confined to estimating the macrofaunal densities in an attempt to evaluate their role in the estuarine food web (see above). Only recently has the emphasis been placed on quantifying that energy turnover in order to increase the understanding of the functioning of benthic communities; and then usually on either unpolluted estuaries (e.g. Milne and Dunnet, 1972; Warwick and Price, 1975; Wolff and De Wolf, 1977) or single species previously found important to predators (Hughes, 1970; Beukema, 1971; Chambers and

Milne, 1975a, b). There is the need, therefore, for a study on the production of many macrofaunal species within a polluted estuary so that comparisons with unpolluted areas could be made; the latter is necessary to assess the impact of pollution on the macrofauna which may ultimately affect the predator populations.

The present study was mainly restricted to the dominant intertidal molluscs which, although regarded as infauna, occupied differing ecological niches within the deposit :

Macoma balthica (Linne, 1758), a deposit-feeding lamellibranch, living at an intermediate depth in the sediment;

Cerastoderma edule (Linne, 1758), a shallow burrowing, filter-feeding lamellibranch;

Mya arenaria (Linne, 1758), a deep burrowing, filter-feeding lamellibranch;

Hydrobia ulvae (Pennant, 1777), a detritivorous prosobranch gastropod living at or just below the deposit surface;

Retusa obtusa (Montagu, 1803), a carnivorous opisthobranch gastropod, living at or just below the deposit surface.

These species were considered to occupy a central portion of the estuarine food web making energy available to predation by fish and large bird populations which inhabit the Forth estuary (McLusky et al, 1976). The aims of the present study were designed to integrate the role of the macrofauna into knowledge of the energy flow of the Forth estuary.

The term "production ecology" is used here to describe those aspects of the species' ecology primarily associated with the accumulation of material to the population and including the dynamics, production and productivity of the population and the growth and body weight changes of the individuals both seasonally and over the life span. The term production is used to describe the sum of organic material accumulated by a population or community in a given area per year, whilst the term productivity describes the relative production of an area as the amount of production per unit biomass. Previous studies have determined single aspects of the production ecology of estuarine macrofaunal species, e.g. growth (Pratt, 1953; Ohba, 1959; Lammens, 1967); flesh change over the year (Ansell and Trevallion, 1967); production and productivity (Hughes, 1970; Johannesson, 1973; Dame, 1976); whereas most of the major aspects of the production ecology within one species in one area have rarely been studied. The present study was designed to evaluate those parameters by using direct and indirect field techniques and by laboratory analyses and experiments.

Until recently, production ecology studies have only estimated the production by populations for single areas and then commented upon the geographical variability in the production estimates (e.g. Burke and Mann, 1974; Hibbert, 1976). The present study aimed to evaluate and explain the variability in those estimates within a small but environmentally heterogeneous area. The particular wide geographical and intertidal distribution of M. balthica, coupled with its presence in large densities and the wealth of data previously accumulated on the species, resulted in its dominant position within this study. The study was therefore designed to answer the fundamental questions : what biomass can a specific habitat type support, and can poor areas maintain populations of a certain size and still allow for individual growth and production ?

In considering the ecology of those macrofaunal species which utilize planktonic spawning (i.e. the bivalves), the assumption has been made that, over the area, each species is genotypically homogeneous. As the normal phenotype is the result of the continuous interaction between the genotype and the environment in which it develops (e.g. Needham, 1964), then any phenotypic differences observed spatially may be regarded as the result of environmental conditions. The relationships between the fauna and the environmental variables are therefore of the uppermost importance.

Chapter 2. The Study Area and Sampling, and the Monitoring of the Environmental Factors.

2.1. Introduction.

In considering the environmental factors affecting deposit- and suspension-feeding populations, it is necessary to quantify the major physical and biological environmental variables. Those variables are considered to be the sediment, which physically supports both types of population and provides food for the former type; the position inhabited within an intertidal environment which in turn would both be influenced by and influence other properties; the water column which provides oxygen for both populations and food for the latter; and the overriding factors of temperature and salinity.

Many workers have studied the inverse relationship between the substrate type (as characterised by the size of particles) and the quantity and quality of the organic matter in that sediment which is available food for deposit feeders (e.g. Morgans, 1956; Carriker, 1967; Pearson, 1970); such a relationship is linear on a double logarithmic basis (Longbottom, 1970; Wolff, 1973). Early research, outlining the importance of organic carbon content in relation to sediment type (Rees, 1940; Southward, 1953), was superseded by the suggestion that although deposit feeders ingest organic matter, their nourishment is derived from the microfloral populations on that organic matter (Newell, 1965). Greater importance is now attached, therefore, to the estimates of that microflora either as organic nitrogen determinations or as more critical measurements of living matter such as ATP. and proteins (Buchanan and Longbottom, 1970; Longbottom, 1970; Holm-Hansen and Paerl, 1972; Melchiorri-

Santolini and Hopton, 1972). As the organic carbon value of microorganisms is low (Newell, 1965) then sediment organic carbon values measure the organic debris component whereas an organic nitrogen measurement estimates the size of the microfloral population.

The importance of that microfloral population in the intertidal environment has been suggested by many authors (Zobell and Feltham, 1938, 1942; Perkins, 1957, 1974; Frankenberg and Smith, 1967; Hargrave, 1970a, b; Levinton, 1972; Meadows and Campbell, 1972; Rhoads, 1973; Johnson, 1974; also the work of Fenchel _et al_ (see Section 5.1)). Detritus and its associated bacteria are possibly one of the main energy sources for several estuarine species (Adams and Angelovic, 1970; Moriarty, 1976) and the amount of available organic detritus may determine the size of many inshore populations (Fox, 1950). It is therefore necessary to determine both sediment organic carbon and nitrogen in order to estimate the potential food available to the deposit-feeding fauna; this is especially so in estuarine sediments where there may be mineral organic and inorganic carbon compounds in the sediment (Southward, 1952, 1953; Morgans, 1956; Longbottom, 1970; Newell, 1970).

The sediment type that the deposit-feeding animals inhabit and ingest is associated with the amount of potential food available; that sediment type will both influence and be influenced by other factors (Webb, 1958, 1969; Newell, 1965, 1970; Longbottom, 1970; Wolff, 1973). It is therefore necessary, in a benthic study, to perform sedimentary analysis and ascertain the factors interrelated with the deposit type. Geological and sedimentological processes in sedimentary analysis have been used by most benthos workers (Morgans, 1956); these methods, however, may not always yield as much direct information to biological systems as other methods and may often lead to an underestimation of the biologically significant properties of a sediment (Johnson, 1974). Johnson (1974) therefore suggests that the quality, rather than the quantity, of sediment organic material is of greater importance. It is considered, however, that the further information gained by adopting his methods does not justify the use of the time-consuming procedures; it is necessary, however, to take his conclusions into account when studying the sediment/fauna relationships. An indication of the quality of the organic matter may be gained from the ratio of the sediment carbon to nitrogen levels as a rich microfloral population would lower such a ratio, while high levels of undecomposed organic debris would result in high C/N values (Newell, 1965).

The potential food available to the suspension-feeding benthos may be regarded as the level of particulate suspended organic material (P.S.O.M.) of various types in the water column (Jørgensen, 1962). The components of that material have been analysed by various workers; chlorophyll (Steele and Baird, 1961, 1962, 1965); carbohydrate and organic carbon (Marshall and Orr, 1962, 1964; Wangersky, 1974); organic nitrogen (Paerl, 1974, Heinle and Flemer, 1976); crude fibre (Rhoads _et al_, 1976); phaeopigments (Steele and Baird, 1972); bacteria (Hotchkiss and Waksman, 1936; Zobell and Feltham, 1942); and organic detritus in general (Teal, 1962; Darnell, 1967; Odum and De La Cruz, 1967). In addition to particulate matter other workers have measured dissolved organic matter, ATP. and nutrient levels

(Stephens et al, 1967; Paerl, 1974; Heinle and Flemer, 1976). Jørgensen (1966, 1975) and Riley (1970) review both the possible and potential food and its nutritional value to suspension feeders.

The most important limiting environmental factor in estuarine studies is the salinity of both the overlying and the interstitial water. The many studies regarding salinity are reviewed by Gunter (1956, 1961); Kinné (1963, 1964, 1966, 1967); Green (1968); McLusky (1971); Remane and Schlieper (1971) and Perkins (1974). Carriker (1967) categorised estuarine organisms by their salinity tolerances. The factors affecting that salinity may be summarised;

> "... superimposed upon the broad salinity gradient from mouth to head is a series of oscillations of varying duration and amplitude at any point along an estuary which are influenced by diurnal and linear tidal cycles, seasons, rainfall and melting snow and ice." (Yonge, 1949a).

The studies of Reid (1930, 1932); Alexander et al (1932); Smith (1956); Capstick (1957) and Wolff (1973) outline differences in external and interstitial salinity within both an estuary and a deposit.

The effects of temperature, the other major environmental factor, upon estuarine organisms has been reviewed by Kinné (1967) who suggests that water temperature in estuaries exhibit greater annual and diurnal fluctuations than in the sea; this is especially so where an estuary is shallow and when, during the flow tide, the water covers large areas of previously exposed sediment. With a progression along an estuary from the mouth the difference in water temperature from that of the sea increases. In addition to such large horizontal variations there are large vertical variations which are increased in areas where the fresh water flows over the more dense saline water (Kinné, 1967). Frolander (1964) further suggests that the shallowness of estuaries results in little heat storage from one season to the next; this in turn causes estuarine water to be colder in the winter and warmer in the summer than the open ocean. He also considers that the variation in water temperature increases with a progression along the estuary from its mouth.

Other physico-chemical parameters influencing the micro-environment such as pH, Eh., oxygen availability and sulphide and inorganic ion levels (e.g. phosphates and nitrates) have been reviewed by Biggs (1967); Carriker (1967); Green (1960); and Perkins (1974) and studies in depth in brackish-water sediments by Moore (1931); Fenchel and Jansson (1966); Jansson (1967, 1969); and Fenchel (1969). These lesser-important variables are of greater importance to the micro- or meiofauna and consequently are not considered in the present study.

2.1.1. The Forth Estuary.

This is the major industrialised estuary on the Scottish east coast and supports large petrochemical and power generating industries. The present state of knowledge regarding the area generally, the water movements and the effects of those industries have been extensively reviewed by Corlett, 1971; Craig, 1971; Collett, 1972; Stout, 1976; and McLusky, in press. Data concerning the abundance and distribution of macro-invertebrates and wading birds in the estuarine Firth of Forth are summarised by Bryant and McLusky, 1975-78; McLusky <u>et al</u>, 1976, 1978; and McLusky, in press. Goodier and Whyte, 1976, give information regarding other biological studies in the Firth of Forth while Anderson and Read (1974) and Read and Renshaw (1977) outline studies in the outer Forth.

In studying the water quality, Stout, 1976, concludes that although there is a higher concentration of pollutants in the industrialised region around Grangemouth (see Fig. 2.1a), the effects of that pollution decrease towards Queensferry and that there was no evidence of serious pollution at any location. However, the paucity of organisms in some intertidal areas has been related to the presence of industrial effluent outfalls (Bryant and McLusky, 1975-78; McLusky _et al_, 1976). Additionally, Collett (1972) describes the marked deoxygenation in the Upper Forth near Alloa (see Fig. 2.1a), however, the causes of this have been reduced since 1966 and its effects are not experienced in the lower, estuarine part of the Firth of Forth.

The study area, Torry Bay, is one of the three major mud-flats within the estuary (see Fig. 2.1a) and has a relatively heterogeneous intertidal area with respect to the diversity of habitats provided for the infauna (cf. the other major areas at Skinflats and Kinneil Bay on the south shore). The area was chosen partly because of that heterogeneity which was necessary in order to compare the macrofaunal productivity from differing areas, and partly because of a previous study on that area (McLusky and Allan, 1976). The intertidal area of Torry Bay, 3.50km^2, is 15.5% of the total intertidal regions in the area from the Forth bridges to Stirling (Fig. 2.1a).

Figure 2.1 The Study Area :

(a) The Forth Estuary Showing Extent of Intertidal Area.

(b) Torry Bay -

A, B, C - Transects with Stations;

U - Newmills Coal Mine Spillage Heap;

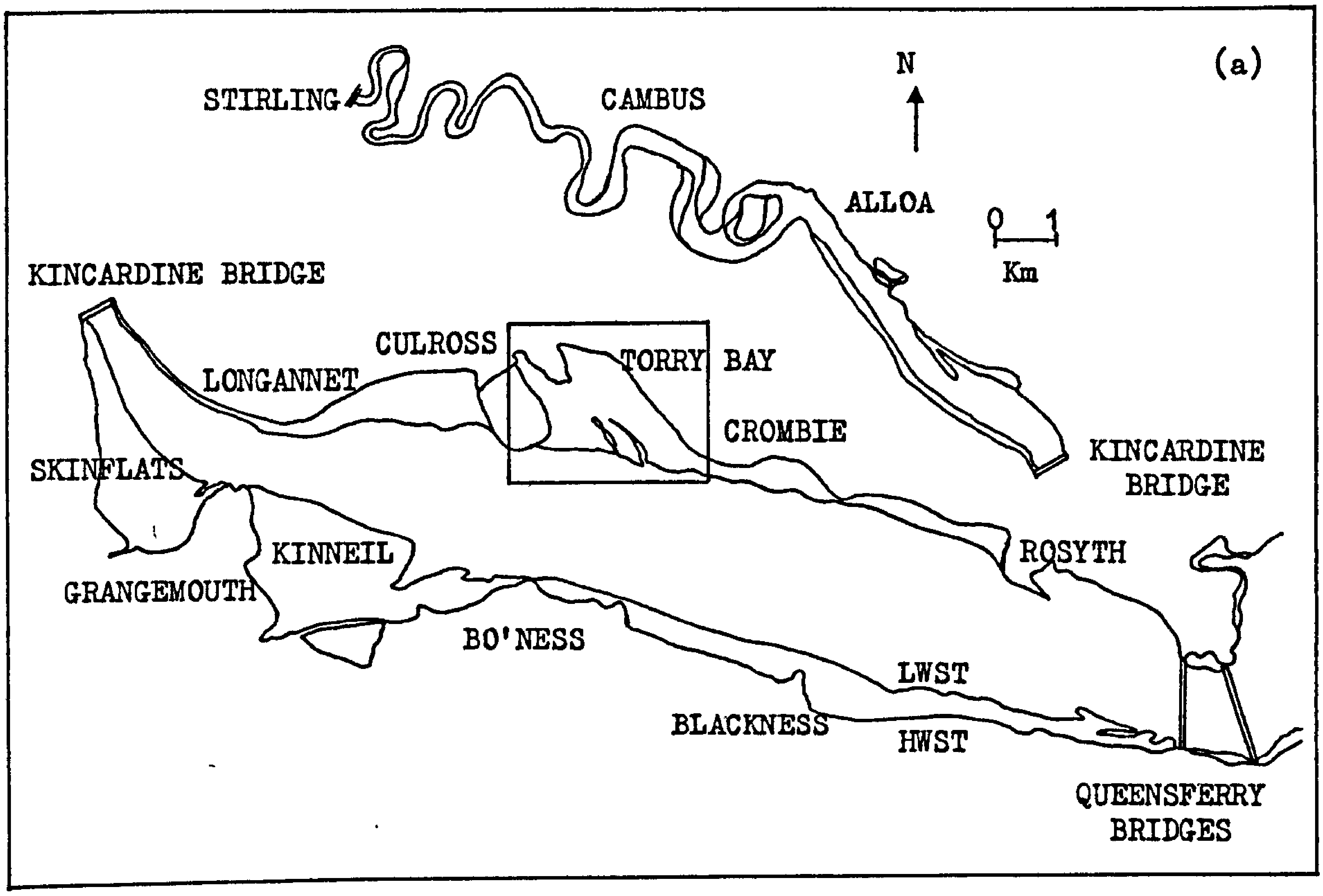
V - Reclaimed area for Ash from Longannet Power Station;

W - Torry Buoy;

X - Rock Outcrops;

Y - Oil Pipeline;

Z - Wall (Under Construction 1979) for Reclamation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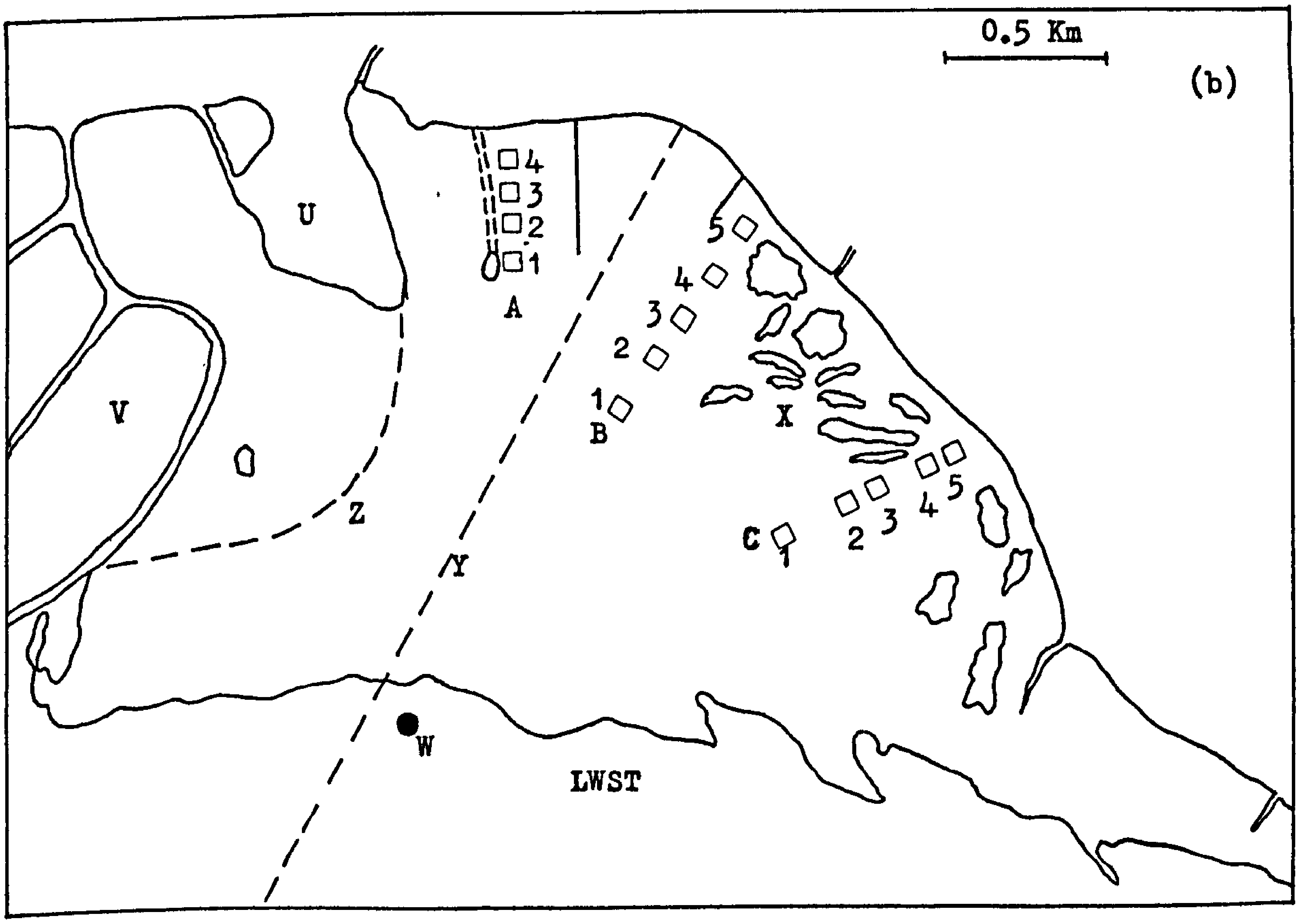
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2.2. Materials and Methods.

2.2.1. The Study Area.

Torry Bay is delimited by coal mine spillage heaps from Lower Valleyfield Mine to the west and by the disused Crombie pier to the east. It shows gradations from eastern clean sandy areas progressing to more muddy areas at comparable tidal heights at the west; and from muddy areas at the lower part of the shore to cleaner sandy areas with Zostera marina, stones and boulder cover on the surface of the sediment on the upper shore. There are large outcrops of weathered sedimentary rock in the upper central part of the Bay. The major fresh water outflows onto the Bay are the Bluther Burn to the west and the Torry Burn near the central part of the Bay. In addition, local domestic sewage effluent is discharged from both the villages and isolated houses and farms bordering the Bay.

In order to survey all areas of the Bay, three transects were chosen and positioned from fixed top-shore marks to the Torry Buoy at the edge of the deep water channel (Fig. 2.1b). The outer most points of the transects were fixed after a preliminary survey was carried out to determine the points at which the shore became more homogeneous and also at which sampling could be safely carried out. However, even with these limitations most of the widely differing habitats on the shore were sampled. The stations were positioned along the transects such that the range of major intertidal types and levels would be sampled. Therefore after the initial survey five stations were placed along Transects B (Torryburn) and C (Shoreside) and four along Transect A (Newmills) (Figs. 2.1b, 2.2; Table 2.1).

The shore profiles along each of the transects were

Figure 2.2 Diagrammatical Representation of Transect A.

Figure 2.2 Continued. Transect B (Key as given for Transect A).

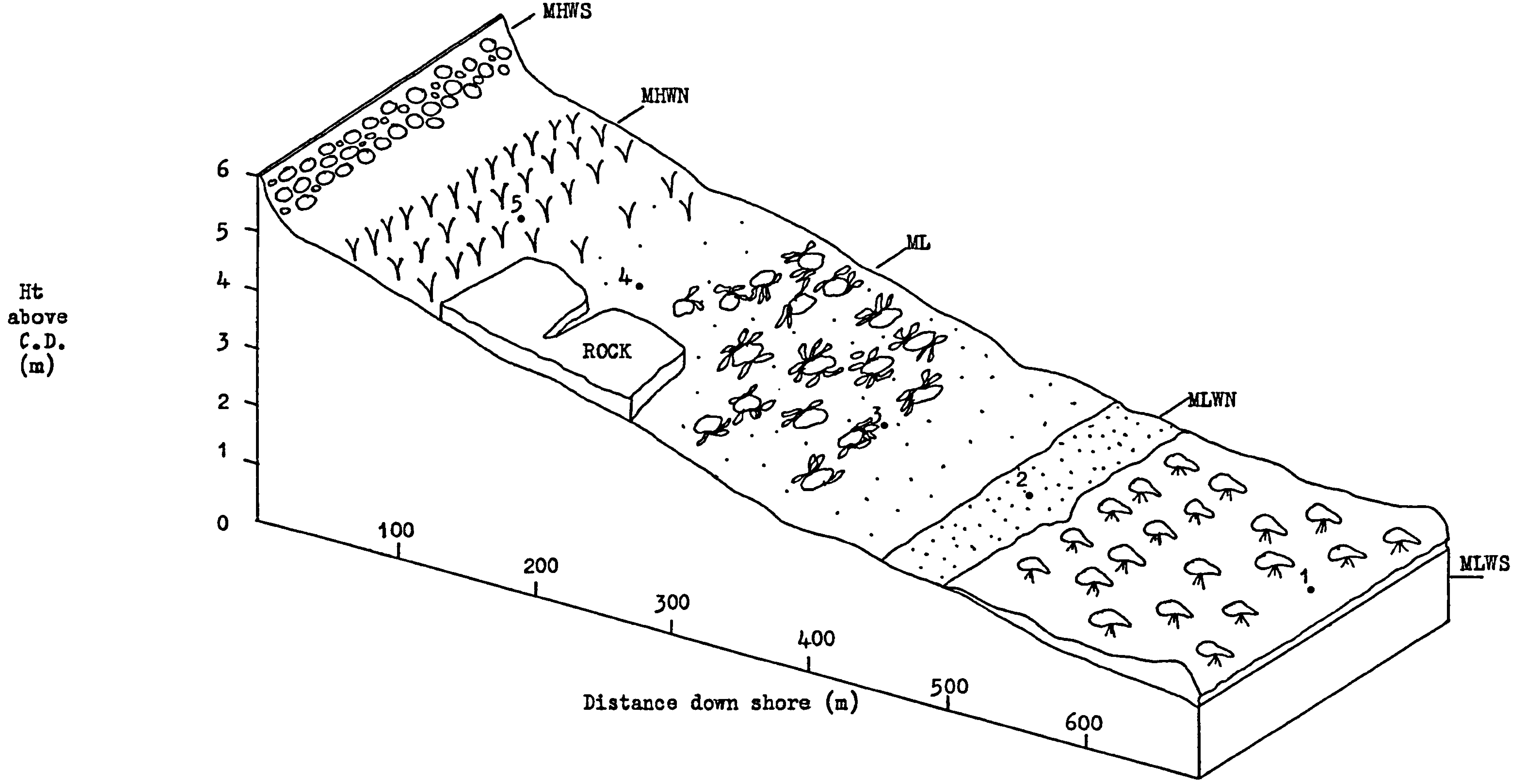


Figure 2.2 Continued. Transect C (Key as given for Transect A).

Table 2.1 The Surface Features at Each Station.

Station	Distance from top of shore (m)	Flora	Fauna	Additional Remarks
A1	430	No attached macroflora	Very few *A. marina*	Station subject to sediment transport. 20m seaward sediment becomes more fluid, impossible to walk on, area homogeneous and of very shallow slope.
A2	320	V. sparse *Enteromorpha*; sparse *Fucus vesiculosis*, *F. spiralis*, *Ascophyllum nodosum*, *Zostera marina*.	*A. marina*, *Corophium volutator* abundant.	V. few rocks, occasional boulders. 400m out shore rises steeply, sediment changes from soft-mud to coarse sandy-mud.
A3	220	Abundant *Enteromorpha*, *Zostera*, Fucoids.	*A. marina* abundant, no *C. volutator*.	Number of rocks increase.
A4	110	*Enteromorpha* abundant, sparse *Zostera*, Fucoids v. sparse.	Few *Mytilus* + barnacles on rocks, many *Littorina*.	Many rocks, large boulders.
B1	760	No attached macroflora.	Sparse *Mytilus* beds (5% of area), Littorinids.	
B2	580	Some *F. ceranoides*, *F. vesiculosis*.	Dense *Mytilus* beds (90-95% of area.	
B3	430	Some *F. vesiculosis* on rocks.	Sparse *Mytilus*, barnacles and *A. marina*.	Subject to sediment transport, very sparse rocks, *Mytilus* beds increasing in area.
B4	270	No attached macroflora.	Abundant *A. marina*.	320m out abrupt change of slope and sediment, no rocks.
B5	100	Abundant *Zostera*, *F. vesiculosis*, *F. spiralis*, and *A. nodosum*. Sparse Enteromorpha.	Sparse *A. marina*.	Many rocks and boulders.
C1	680	*F. vesiculosis* on rocks, *F. ceranoides*.	*Mytilus* beds (80% cover), barnacles, Littorinids.	Many rocks.
C2	470	Fucoids on sparse rocks.	Sparse *Mytilus*.	Soft-mud from 480m (where *Mytilus* bed stops) to 460m.
C3	370	Abundant Fucoids.	Many *A. marina*, *Lanice conchilega*, few *Mytilus*.	Bed of shale under sand surface. (Many rocks with all Fucoids + *Polysiphonia lanosa* on *A. nodosum* C3-C4).
C4	190	Abundant Fucoids.	Few *A. marina*.	Rocky outcrops, few boulders.
C5	110	Abundant *Zostera*, sparse Fucoids and *Enteromorpha*.	Few *A. marina*.	Few rocks.

determined from the tidal curves for Rosyth (S.E. Scotland) (Admiralty Tide Tables, Vol. I, 1975) and a knowledge of the times at which the flow tide reached marked points on the shore. In order to limit the effect of climatic factors on the tidal height, calm, dry, sunny days at or near the spring tides in November, 1975 were chosen in order to facilitate ease of computation of tidal heights. The immersion period and tidal height at each station were calculated from the appropriate Tide Tables (see Table 2.3). The immersion period was related to the tidal height (at this area) by :-

	n	r	p
$\text{M.I.P.} = 14.445 - 2.445 \pm 0.128\ \text{T.H.}$	14	-0.984	(<0.001)
$\text{S.I.P.} = 10.823 - 1.366 \pm 0.075\ \text{T.H.}$	14	-0.983	(<0.001)
$\text{N.I.P.} = 18.083 - 3.527 \pm 0.219\ \text{T.H.}$	14	-0.978	(<0.001)

where M.I.P. = Mean Immersion Period (hrs).
S.I.P. = Spring Immersion Period (hrs).
N.I.P. = Neap Immersion Period (hrs).
T.H. = Tidal Height.
n = Number of cases in equation.
r = Correlation coefficient.
p = Level of significance.

The angles of the shore slope at each station was calculated from the transect shore profiles (Fig. 2.2; Table 2.3).

2.2.2. Sampling and Sorting.

The sampling procedure was based partly upon the findings in other benthic macrofaunal studies (Holme, 1971; McGrorty, 1973; Wolff, 1973 and Beukema, 1974), but mainly on the findings of an initial study and on the practicability of the sampling. The intensity of sampling, as in most benthic studies, was a compromise between the desire for accuracy and the time available for the field work (see also Chambers and Milne, 1975b). In the sampling programme, the assumption that macrofaunal deposit feeders are randomly or uniformly distributed was made (Connell, 1963; Gilbert, 1968; Levinton, 1972). Macrofaunal suspension feeders may also be randomly distributed or they may be patchily distributed over large areas although uniformly or randomly distributed within those patches (Holme, 1950; Connell, 1955; Johnson, 1959).

One-tenth of a square metre was considered a suitable area for macrobenthos sampling (McIntyre, 1971; McGrorty, 1973; Beukema, 1974; Withers, 1977); this area was large enough to encompass any aggregation in the individuals distribution and yet produced a sample which could be easily processed. The time involved in sampling dictated that only one $0.1m^2$ quadrat per station was sampled as opposed to 10 x $0.001m^2$ cores which would have allowed limits to be placed on the faunal abundance at each station.

Each stations' sampling area was limited to a homogeneous area of 25m square around a central marker identifying the station; out-with that area the heterogeneity of the mudflat would have been encountered. Each monthly sampling site was determined by pacing random co-ordinates horizontally across and vertically down the beach from the centre marker. No part of the station was sampled more than once.

At each site, one large sample (Fig. 2.3; A) and five small cores (B - F) were taken, two (B, C) were placed in one bag and the others (D, E, F) combined in another. A sample of surface mud (to a depth of 0.5cm)(G) for the determination of water and

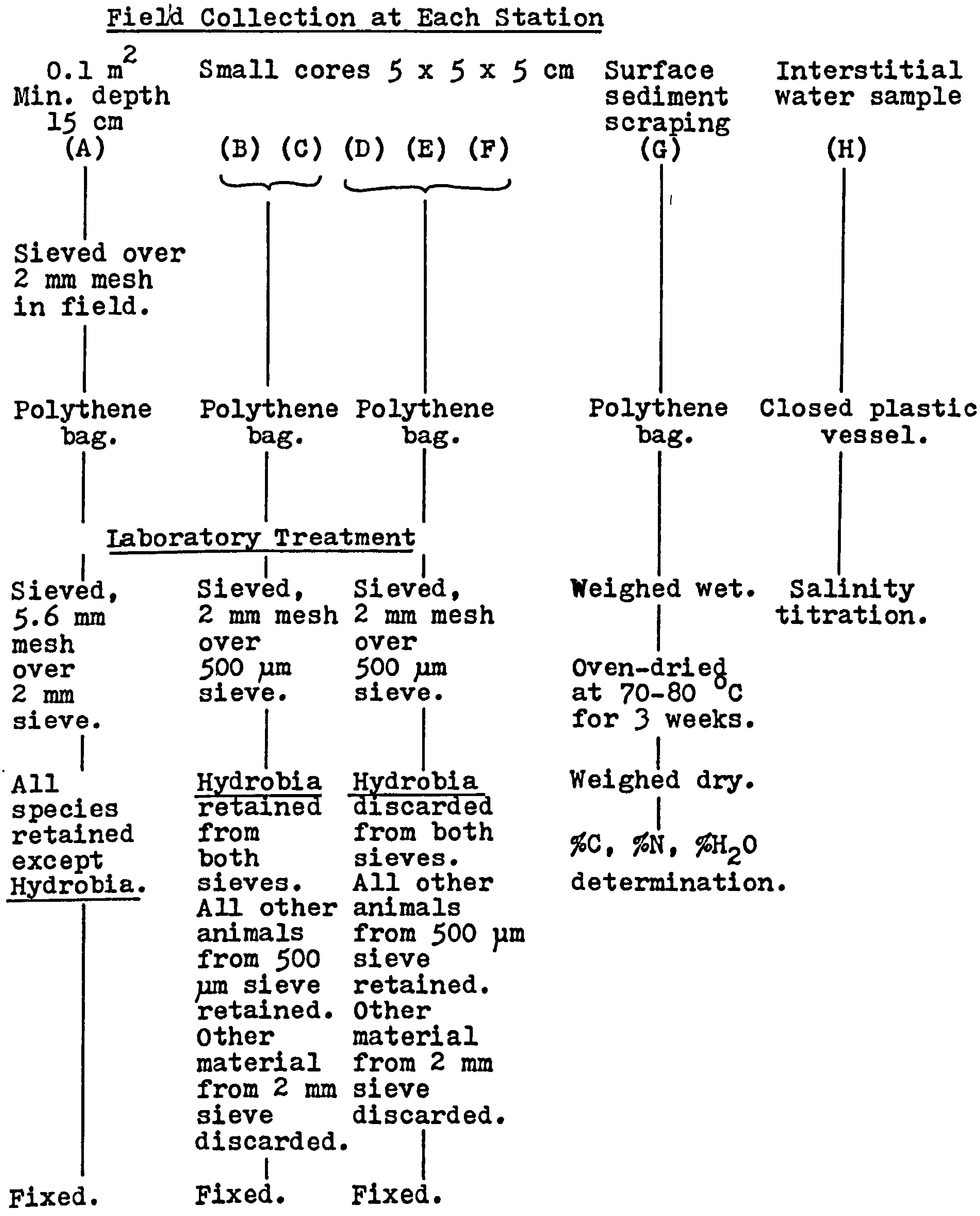


Figure 2.3 The Collection and Laboratory Analysis of the Field Samples.

organic matter content was collected. An interstitial water sample (H) for salinity determination was also taken by syringing water from the bottom of a hole dug to the water table. Care was taken to prevent dilution of the sample by surface water and rainwater and evaporation was reduced to a minimum.

The large faunal sample (A) was partially sieved in the field to remove as much of the sediment as possible. The remaining material was then returned to the laboratory and sieved through a 5.6mm sieve over a 2mm sieve using seawater. Large material and large members of the macrofauna could then be easily removed and the finer material (>2mm <5.6mm) sorted under water. The macrofauna removed were placed in filtered seawater for six hours to remove the sediment from their alimentary system before fixing and storing in a 4% saline formalin solution.

The small cores were not treated in any way in the field but sieved through a 2mm sieve over a 500µm sieve immediately on returning to the laboratory. The two core combined sample (B + C) was taken for the collection of H. ulvae individuals which were discarded from the other samples. Hydrobids were removed from the 2mm sieve after washing and placed with the material retained by the 500µm sieve which was then fixed and stored in a buffered formalin solution (see Fig. 2.3). To avoid an overlap between samples the remainder of the material on the 2mm sieve was discarded. Hence only members of the macrofauna (apart from H. ulvae) retained between the 2mm and 500µm sieves were taken in the small core samples. The material was subsequently sorted using a binocular microscope. The three core combined sample (D + E + F) was similarly sieved except that Hydrobids were not removed from the sample. The material retained between the 2mm and 500µm sieves was fixed and stored for subsequent sorting. Juvenile members of the macrofauna were removed from all five cores (B to F).

Initially a floatation technique was attempted for the separation of the fauna from the sediment which involved placing the sample in a solution with a specific gravity intermediate between that of the sediment and the organisms. Solutions of carbon tetrachloride, zinc chloride, sodium chloride and sucrose were tried but these proved unsuccessful. It appears that although floatation techniques are suitable for separating the meiofauna or the soft bodied macrofauna, they are unsuitable for shelled invertebrates (A. Ansell, J. Gage, pers. comm.). Decantation methods were also initially used but again proved unsuccessful as the sediment retained upto 40% of the fauna.

The surface sediment scraping (G on Fig. 2.3) was weighed on returning to the laboratory, then oven dried to a constant weight. It was then ground with a mortar and pestle and stored at 60°C for a few days before being stored in a dessicator until analysis.

Additionally, at each sampling occasion a 5 litre flow-tide water sample was taken by wading out at high tide to Station B4 and during July, 1976, an overlying water sample was obtained from each station at the flow tide.

Also during the January, 1976 sampling, two replicate cores were taken at each station for particle size analysis. The sediment was stored under distilled water until analysis.

2.2.3. Sediment Analysis.

2.2.3.1. Particle Size Analysis.

Many workers (e.g. Morgans, 1956; Buchanan, 1971) have outlined the basic problems in trying to quantify differences between sediments taken from different tidal or sublittoral areas. Although some workers (e.g. Boyden and Little, 1973; Warwick and Davies, 1977) have attempted to classify sediments subjectively the most widely accepted method of describing sediments is by particle size analysis in which a sediment is described in terms of the frequency distribution of grain size diameters. An initial problem is that as the sediment consists of particles of varying sizes which describe a continuous distribution, then in order to perform size frequency analysis the particles have to be placed within a discrete series of size classes. The most usual series adopted for the size class divisions is the Wentworth scale. This is a geometric scale in which the size of the divisions decrease with overall decrease in size of particles such that the minimum diameters of grades are halved successively from 4mm to 63µm. However, because it is easier to treat statistically an arithmetic scale than a geometric one, Krumbein (1939) logarithmically transformed the unequal class divisions of particles size (mm) of the Wentworth scale into equal divisions of the Phi (ϕ) scale, where

$$\phi \text{ units} = -\log_2 \text{ particle diameter (mm)}.$$

Morgans (1956), Newell (1970) and Buchanan (1971) discuss the advantages of the phi-scale over other notations.

The large size range of particles found in a sediment dictates that the same method of separation cannot be used for the whole sediment (Morgans, 1956; Buchanan, 1971; Beukema, 1976). Morgans (1956) advocates separation by sieving for the largest particles (>0.1mm), by elutriation for 0.2 - 0.02mm particles size and by sedimentation procedures for the smallest, while Buchanan (1971) considers that only sieving and sedimentation are necessary. Morgans (1956) and Folk (1966), conclude that sieving is the most accurate method of separating the middle size range of particles. Therefore, sieving coupled with a sedimentation analysis, either by the use of a hydrometer or pipette analysis, gives a relatively quick and precise means of analysing the whole sediment (Buchanan, 1971).

Some workers (Longbottom, 1970; Buchanan, 1971; Wolff, 1973) suggest drying the sediment before analysis. However, this results in the coherence of fine particles such that the sediment then had to be disaggregated. Longbottom (1970) overcame these problems to some extent by washing the fine deposits in alcohol and then drying in a dessicator with frequent stirring of the sediment. Buchanan (1971) advocates complete disaggregation of the sediment upon analysis such that any compaction and aggregation of the finer particles due to drying either in air or an oven would not have a marked affect on the final data. In the sediments encountered in the present study, any drying resulted in large aggregations of finer particles which could only be overcome with difficulty.

It was considered here that any pretreatment will lead to the final data presenting an "unnatural" picture of the sediment (see also Morgans, 1956; Barnett, 1968). As this latter consideration is important when analysing sediments in relation to their infauna, then any disaggregation of particles by deflocculating agents, e.g. sodium hexametaphosphate (Buchanan, 1971); by agents which destroy interstitial organic matter, e.g. hydrogen peroxide (Rees, 1940; Holme, 1953); or by air or oven drying and then dispersing the particles with alcohol or sodium carbonate (Southward, 1953; Howells, 1964; Newell, 1965; Longbottom, 1970), is unnecessary and may give misleading results. It is precisely these problems with the fine particles that lead sedimentologists to place little importance upon the 'fines' (A.T. Buller and J. McManus, pers. comm.). Therefore in order to minimise any change in the sediment due to collection the minimum amount of pretreatment was given to the sediment.

To remove salt from the sediment, which would otherwise interfere with the weights of the finer sediment fractions when they were finally dried, each sub-sample (half core) was placed in distilled water and gently stirred. After several days when the sediment had completely settled the water was decanted and discarded and the procedure repeated twice more. The sediment sub-samples were then wet sieved over a 63µm sieve to separate the sand fraction from the silt and clay fractions. Krumbein (in Morgans, 1956) considers that the sediment should be dry sieved as wet sieving of finer fractions results in errors when particles adhere to the water film on the sieve. However, this problem is overcome if wet sieving is performed with excess washing after the majority of small particles have passed through the sieve. (The sedimentary analysis procedure was performed on twentyeight preliminary sediment samples to ensure that consistent results were obtained. It was observed during these preliminary analyses that if there was an incomplete removal of the silt/clay fraction during the wet sieving, then the remaining sand fraction had a tendency to 'cake' during drying.)

Following the wet sieving, the 63µm sieve and the retained sand fraction was covered, attached to a receiving vessel and dried for 2 days at 105°C. This fraction was then dry sieved over a nest of Endecott (20cm) standard sieves of mesh 5.6mm, 2mm, 1mm, 500µm, 250µm, 125µm and 63µm placed on an Endecott model E.F.L.I. test sieve shaker; after 15 minutes shaking, no further material passed through the sieves. Each fraction was then weighed. Any further material that had passed through the 63µm sieve was added to the silt and clay fraction which was divided into its component fractions by pipette analysis; the method of sedimentation analysis used was essentially that described by Buchanan (1971).

Pipette analysis assumes that particles of a known size (x) will settle out of the uppermost part of a column of water in a known time. A pipette sample taken at the top of the column will, after that time, only contain the sediment fractions <x which will not have settled out of that part of the column. By difference, an estimate of the fraction that had settled through the column can be made. The procedure used differed from that given by Buchanan (1971) in two small details; (i) instead of standing the columns of suspended fine sediment in a constant temperature water bath, the settling rates for the particle sizes were calculated for a range of temperatures and the appropriate rate corresponding to the ambient temperature was used.

The settling velocities were calculated from Stoke's Law :

$V = Cr^2$

where V = settling velocity in cm $\sec^{-1}$

r = particle radius in cm

C = constant = $\frac{2(d_1 - d_2)g}{9z}$

where d_1 = density of particle = 2.65 (for quartz)

d_2 = density of water

g = acceleration due to gravity = 980cm $\sec^{-2}$

z = viscosity of water in dyne secs cm^{-2}

(Table F36 in Weast, 1970-71)

(the recalculated settling velocities are given in Appendix 2.1).

(ii) Additionally, in order to reduce errors when determining the total amount of the fraction in the sample which was originally made upto 1 litre, the sediment fraction weight obtained from drying the 20ml pipette sample was multiplied by 50 for the first fraction, 49 for the second and so on in order to take into account the removal of part of the sedimentary column with each pipette sample. This minor correction makes a small but noticeable difference to the results especially when the sediment contains a large proportion of silt and/or clay fractions.

The sedimentary analysis was carried out using distilled water which allows for ease of calculating the settling velocities of the various particle sizes. However, it is not known whether there are any adverse effects caused by placing the finer particles in distilled water; this may cause further aggregation or it may cause disaggregation of some of the fractions. For this reason, Morgans (1956) recommends that 'natural' water by used in the wet analysis of the finer fractions.

2.2.3.2. Carbon and Nitrogen Analysis of the Surface Sediment.

As a relative measure of the potential food available for deposit feeders various components of the sedimentary organic matter have been determined by different workers. Trask (1939) (in Morgans, 1956) suggested that the amount of organic matter is usually determined indirectly by measuring the quantity of carbon, nitrogen, phosphate or volatile substances and multiplying by an appropriate factor. Newell (1970) suggests that the organic component of intertidal deposits may be analysed in terms of either organic nitrogen, which comprises proteins, or as organic carbon. It is accepted that any measure of these constituents will give some indication of the availability of food for deposit-feeding organisms (Wakeel and Riley, 1956; Newell, 1965, 1970; Hughes, 1969a; Buchanan and Longbottom, 1970; Longbottom, 1970). However, one could be more precise if the particle size preference of the deposit feeder was known and one measured the amounts of organic matter within that fraction.

Organic carbon in the sediment is usually determined either by a loss on ignition method (Ball, 1964), or a wet oxidation method (Walkley and Black, 1934; Tinsley, 1950; Wakeel and Riley, 1956; Hughes, 1969a). Ball (1964) suggests that the loss on ignition method, i.e. where the weight of matter combusted at 850°C is determined, has many sources of error but these disadvantages are outweighed by the ease and speed of the method. Sources of error include loss of structural water from clay minerals and the breakdown at high temperatures of carbonates and other calcareous materials. These latter problems are not encountered when using the wet oxidation method; Wolff (1973) suggests that this method can be corrected for the loss of carbonates and constitutional water of soil colloids. He also found that the sources of error mentioned by Southward (1952) and Morgans (1956), such as the presence of ferrous materials and by the loss of sodium chloride, proved unimportant.

Additionally, the wet-oxidation methods, which are based upon the reduction of chromic acid by organic carbon, and the loss-on-ignition method do not differentiate between different forms of carbon such that cellulose and mineral carbon will affect the results. However, the first or both of these may be a substrate for microbial populations such that their inclusion would not be a source of error. A further source of error is the presence of ferrous sulphite in the deposits (Southward, 1952). It is likely that fine estuarine deposits will have ferrous minerals present due to their reducing characteristics.

Buchanan and Longbottom (1970) discuss the difficulties of measuring organic matter in sediments which may contain coal. They maintain that even nitrogen values are affected by the presence of coal and that coal nitrogen analyses gave a mean value of 0.89%. It is considered that the Torry Bay sediments contained less coal than those of Buchanan and Longbottom (1970). They ultimately suggest using a rather lengthy determination of protein in muds as a method of estimating nitrogen content as being more accurate than other determinations. While agreeing with their suggestions, it is necessary to consider whether the levels of coal in the sediment warrant such procedures.

Each of the methods for determining the amount of organic carbon, therefore, have sources of error in them, although the wet-oxidation methods are perhaps the most accurate. Initially, therefore, the Walkley and Black method outlined by Buchanan (1971) was used to determine the sediment organic carbon levels.

However, although organic carbon or organic matter can be accurately measured, the relationship between those levels and the food quantity available to the deposit feeders is unknown; the levels of organic matter, carbon or nitrogen will only give a relative indication of that food available (see also Hughes, 1969a; Wolff, 1973). Frankenberg and Smith (1967) and Levinton (1972) suggest that because of sediment reworking and coprophagy amongst deposit feeders then, over a period of time, all of the organic matter in the sediment is available to deposit feeders. Further, Turpaeva (1954)(in Levinton, 1972) found that in two deposit-feeding bivalves there was little qualitative difference between the stomach contents and the substrate.

Following the initial work of Newell (1965) it is considered that the sediment nitrogen levels may give a closer approximation of the amount of food available. Newell (1965) concludes that deposit feeders are more likely to absorb nitrogen (as proteins in microfloral populations) than carbon. He demonstrated that sediment carbon levels change little when passed through the animal but that nitrogen levels change markedly.

The micro-Kjeldahl method is widely used for nitrogen determinations (Newell, 1965; Longbottom, 1970) despite the disadvantage that the method requires lengthy digestion and titration procedures. The Williams (1963) method for nitrogen determination gives comparable results to the Kjeldahl method but has neither of those disadvantages. This method uses Nessler's reagent to measure liberated ammonia, has a short digestion period and a final determination by colorimetry. Therefore, initially, the Williams (1963) method was used for determining total nitrogen in the sediment.

The use of these methods for measuring carbon and nitrogen, however, was superseded by the aquisition of a Perkin-Elmer 240 model CHN. Elemental Analyser. This machine has recently been used by ecologists for the determination of carbon and nitrogen in sediments (Ansell, 1974; Oviatt and Nixon, 1975; Webster et al, 1975), in seawater suspended matter (Handa and Tominga, 1969; Ansell, 1974; Sharp, 1974) and in animals (Kerambrun, 1975; Salonen et al, 1976; Yingst, 1976). The machine determines the C., N. and H. content of organic material quickly and accurately by detecting and measuring their combustion products (i.e. CO_2, N_2 and H_2O respectively). Combustion occurs in pure oxygen and the products are then analysed in a "steady-state, self-integrating, thermal conductivity analyser". This eliminates conventional weighing of absorption traps as in other gas analysers.

The combustion products are carried through the machine in an equilibrium mixture of helium which passes, after combustion, through a system which reduces any oxides of nitrogen to nitrogen and removes any residual oxygen. The combustion products are detected in a series of three pairs of thermal conductivity cells. Platinum electrodes detect any differences in the two cells of each pair when the combustion product is removed between each pair of cells; these differences then being shown on a chart recorder. The sample results are then calculated against an acetaldehyde standard with a correction for the ambient levels of N., C., H. being made to both the standard and the sample.

Several authors (e.g. Ansell, 1974) have introduced a correction factor when using the machine to account for "non-organic" carbon and nitrogen present as carbonates and nitrates. This involves acid-treating the samples with either hydrochloric or sulphuric acid. In a preliminary set of analyses the sediment was analysed as both acid-treated and untreated subsamples (see Appendix 2.2). During acid treatment amounts of inorganic carbon and nitrogen are broken down thus the amount of C. and N. measured would be less. However, that treatment decreases the weight of the sample such that the remaining "organic" carbon and nitrogen would appear as a greater percentage by weight. This may explain why there was no consistent pattern between samples from different stations in the treated and untreated levels of C. and N. It was therefore considered that the little gain in information did not warrant the extra time being spent on the analyses. Bader (1954) whilst reviewing the use of conversion factors to obtain total organic matter levels from measuring C. or N., stresses that because detritus decomposition results in C. and N. being present in varying proportions, one conversion factor would not be adequate. It is therefore more accurate to report the elemental analyses and avoid the use of conversion factors.

Additionally, for two months' sediment samples, two sub-samples from each station were analysed. As the replicates were usually within 5% of the mean, subsequently only a single analysis was performed on each sample per stations per month. The closeness of replicate values was ensured by a detailed homogenising of the sample before analysis. During each analysis any material thought to be not included in the diet of deposit feeders was removed. This material included Hydrobids, bivalve spat, stones, large pieces of macroalgae or _Zostera marina_ leaves and roots where necessary. It was not possible, however, to remove any meiofaunal individuals (oligochaetes, nemerteans or nematodes), nor mollusc spat shortly after settling. At certain times of the year large numbers of the latter would therefore have been included in the sediment.

2.2.3.3. Sediment Water Content.

The sediment sample used for the organic matter analysis was weighed before and after drying to a constant weight at 60°C.

2.2.4. Interstitial and Overlying Water Salinities.

The salinity determination procedure given by Green (1968) and McLusky (1971) has long been regarded as adequate for estuarine work and was used in the present study for the measurement of interstitial water salinity. Silver nitrate solution (27.25g l^{-1}) was titrated against replicate 2ml sub-samples from each station each month using 8% potassium dichromate as an indicator. Each burette reading was then multiplied by the appropriate factor to give salinity as parts per thousand ($^{o}/oo$).

Estuarine water salinity data were obtained from the Forth River Purification Board (F.R.P.B.).

2.2.5. Estuarine Water and Air Temperatures.

Temperature recording during sampling proved both difficult and unreliable as sampling was not always carried out at the same time of day. Therefore water temperature data were obtained from the F.R.P.B. Both water temperature and samples for the salinity determination were taken at several places along the Firth of Forth at each spring tide in 2' of water at the same time of day on each occasion.

Air temperature data were obtained from the meteorological office at Pitreavie, Dumfermline, 7km from Torry Bay.

2.2.6. Analysis of Particulate Matter in the Overlying Flow-tidal Water.

Any determination of the food available to the herbivore/ suspension-feeding trophic level must include a measure of phytoplankton standing crop as well as detritus levels (Rhoads et al, 1976). Material present in and sinking throughout an open water column can originate from three main sources; (1) phytoplankton cells, (2) zooplankton and their waste products, and (3) material resuspended from the bottom (Steele and Baird, 1972). However, in the estuarine water column there is a fourth source of material - that brought into the system either from the marine areas, e.g. mineral material (Green, 1968), or from further up the estuary-freshwater system, e.g. detritic material and land erosion products. The latter two factors are probably more important than (1) and (2) above. In a shallow or intertidal area resuspension of bottom material may account for most of the material in the water column and will probably form an important food source for suspension feeders (Young, 1971; Levinton, 1972);

Rhoads et al (1976) however, suggest that an estimate of phytoplankton carbon levels as well as detritus carbon levels are necessary when considering the food of suspension feeders.

In water samples, measurements of total organic matter, fat or protein may be affected by zooplankton levels as well as phytoplankton levels whereas carbohydrate measurements will give a closer indication of the quantity of food provided by phytoplankton (Marshall and Orr, 1962, 1964). Raymont and Krishnaswamy (1960) and Raymont and Conover (1961) have shown that zooplankton are low in carbohydrate. Carbohydrate measurements also give closer estimates of the amount of phytoplankton available as food than do more conventional phytoplankton measurements such as levels of chlorophyll.

Suspended particulate organic carbon measurements include all plankton, detritus and resuspended organic matter. Leach (1971) concludes that organic carbon determination is a quantitative measure of the particulate organic matter in the water column. It will therefore provide a measure of the total food available in the water (Rhoads et al, 1976). Strickland and Parsons (1968) state that oxidizable carbon has long been accepted as a realistic measure of energy stored in a crop. Wangersky (1974) outlines problems encountered when measuring particulate organic carbon in open sea water due to its patchy distribution. However, as the levels encountered in estuaries and coastal regions are very much higher than in the open sea, these problems diminish.

Therefore to obtain an estimate of suspension feeders food levels, the levels of particulate organic carbon and carbohydrate in the overlying water column were measured. It must be emphasised, however, that it is impossible to state how much particulate matter in the water column is attractive or suitable to those animals and therefore that matter must only be regarded as potential available food.

Following sampling, the 5 litre water sample was constantly shaken and 8 x 250ml subsamples taken and filtered through Whatman G.F.C. filters (pore size 2µm). Particulate matter has been defined as that which is retained by these filters (Paerl, 1974; Heinle and Flemer, 1976). Four of the filters were then used for each of organic carbon and carbohydrate analysis. Carbohydrate was estimated by extraction from the particulate matter by a sulphuric acid digestion and then using 1.67% phenol solution as an indicator which produces a brown colour with an intensity directly proportional to the carbohydrate content (Marshall and Orr, 1962). The colour intensity was read at 490mµ in a Cecil Model CE272 spectrophotometer with a turbidity correction being made at 720mµ. The amount of particulate carbohydrate was determined using a glucose solution as a linear standard (Strickland and Parsons, 1968). Although different carbohydrates produce a slightly different colour on hydrolysis with phenol, Marshall and Orr (1962) suggest that as the main sugar formed on the hydrolysis of diatom cultures is glucose then this is an appropriate standard to use. Holm-Hansen (1972) suggests that this method is more sensitive than other methods used for CHO. determination.

The method used for estimating the amount of particulate organic carbon in a water sample was that given by Strickland and Parsons (1968) based on the chromic-acid wet-oxidation determination of carbon. This method was slightly modified from that used by Marshall and Orr (1964) in that the blank used by the latter had the dichromate sulphuric mixture reduced by sodium sulphite solution thus enabling a normal absorption reading to be taken. The method given by Strickland and Parsons (1968) does not involve reduction of the blank so that the absorbance of the samples is read as an optical density difference against a blank. The amount of organic carbon in the sample is then calculated using a linear glucose standard and employing the conversion :

$$750\mu g \text{ glucose} \equiv 300\mu g \text{ organic carbon}$$

(Russell-Hunter et al, 1968)

A correction reading for the turbidity of each sample was also made. Strickland and Parsons (1968) outline the advantages of using this method over more specialised and complex ones.

The water samples from each station, obtained in July, 1976, were similarly analysed for suspended particulate organic carbon and carbohydrate.

In addition, it would have been valuable to obtain a measure of the amount of this matter settling to become available to the deposit-feeding macrobenthos. However no practicable means of obtaining such measurements could be devised due to the large numbers of problems encountered. Steele and Baird (1972) suggested that in a sea loch system water movement by wind action was more important in resuspending bottom material than were tidal currents. In addition they attempted to determine the production in the water column available to the benthos but concluded that that production could not be separated from the benthic production because of resuspension. This problem would be even more acute in shallow, intertidal systems.

2.3. The Use of Statistical Analyses to Elucidate Biological and Physico-chemical Relationships.

In attempting to quantify the relationships : within the environmental variables; between the faunal parameters and environmental variables; and within the faunal parameters, a computer-assisted three-step analysis has been performed. The analysis was carried out both on spatial data, to elucidate the causes of the variation in any dependent variable with a change over the intertidal area; and, where necessary, on temporal data, to explain annual variability within a variable. The spatial analysis incorporated the environmental data for January-February 1976 (the time at which the sediment samples were obtained for analysis) and the mean annual faunal population data (of densities, biomasses, production, etc.). The temporal data analysis included those factors monitored monthly (e.g. %C., %N., %H_2O., temperature, salinity, faunal flesh condition, growth, etc.).

Firstly, in the analysis, a computer-plotted "scattergram" of each dependent variable against each independent variable was produced; this enabled meaningful relationships to be considered further and reproduced where necessary.

Secondly, a Pearson correlation matrix was produced which gives the linear correlation coefficient (r) and level of significance between pairs of variables. Any pair of variables that were curvilinearly related would, on a linear basis, produce a low r-value. In some such cases, therefore, a double logarithmic transformation was used which produced a more significant correlation. The following nomenclature has been used when discussing the relationships :-

Level of Significance	Name	Symbol
>5%	Not significant	n.s.
≤5>1%	Significant	*
≤1>0.1%	Very significant	**
<0.1%	Highly significant	***

Only significant relationships are further considered in the text; the relationships' positive or negative nature and significances (as its symbol) are given in the text (in parentheses following the relationship under discussion) and on the figures.

However, although correlation analysis indicates possible relationships or associations, it does not necessarily indicate causal relationships or the influence of more than one independent variable on a dependent variable.

The third step of the analysis was to construct a stepwise linear multiple regression of a dependent variable (e.g. sediment organic matter content, species' growth rate, etc.) against two or more independent variables (e.g. other environmental factors and/or other population variables) which are known, from the correlation analysis, to be associated with the dependent variable.

Multiple regression analysis was used to further quantify the relationships between the variables and to provide a mathematical representation of the causal factors which account for the major part of the variation of the dependent variable. At each step in the programme, the remaining independent variables were selected in a descending order of importance with regard to the amount of the remaining variance of the dependent variable attributable to each independent variable.

Two points, regarding the addition of an independent variable to the constructed regression equation against a dependent variable, are important when considering the regression. Firstly the % variation (i.e. the coefficient of variation, r^2 x 100) of the dependent variable accounted for by each of the independent variables in the presence of associated independent variables, and by the whole of the independent variables together; and secondly, the statistical significance of each of the independent variables when regressed against the dependent variable.

As some of the variables are related curvilinearly, a curvilinear multiple regression may be of greater accuracy than the linear multiple regression analysis employed. However as different independent variables are related to the dependent variable in different patterns of curvilinearity then the most appropriate multiple regression analysis would be difficult to construct.

Ideally, the independent variables should be uncorrelated with each other, i.e. truly independent. However, multiple regression analysis is still a perfectly valid technique when the independent variables are correlated (Mead, 1971). Intercorrelations between such variables, however, reduce the amount of variation accounted for by one of a pair of correlated independent variables (Mead, 1971; Yarranton, 1971). Therefore, because of the higher the correlation between two such variables then the more redundant one of them becomes and all but one of a group of intercorrelated variables have to be eliminated.

In many cases, two multiple regression equations were constructed for each dependent variable. Initially, all independent variables were regressed against each dependent variable in order to show which independent variables were of most importance and greatest significance in accounting for the variation within the dependent variable. In successive regressions the least important independent variables were omitted as were any that were highly intercorrelated with remaining independent variables. Therefore, although very few variables may be found to largely account for the variance of any dependent variable, it may be assumed that excluded independent variables, which are intercorrelated with the remaining independent variables, would also account for a large but lesser amount of the variation if substituted into the equation. In many cases, elimination of least important independent variables, results in the remaining variables producing a more significant equation.

Multiple regression analysis, therefore, may be used to construct a mathematical representation to account for the variability of one parameter from a detailed investigation and knowledge of the factors which affect that parameter. That mathematical representation may be valuable as a predictive model in certain situations where the same independent variables have been monitored in an identical manner.

Although the correlation and regression analysis has been used to explain and further quantify relationships between certain factors, it is necessary to consider constantly the biological relevance of those relationships and to discount any relationships which cannot be explained by past or experimental knowledge (Mead, 1971).

2.4. Results.

2.4.1. Sediment Analysis.

2.4.1.1. Particle Size Analysis.

As both the Wentworth-scale and the phi-scale have been used, the sediment nomenclature used for the Wentworth scale and subsequently by Wolff (1973) has been adopted in a slightly modified form :

M.P.D. between		Name
Ø units	µm	
0 - 1	500 - 1000	coarse sand
1 - 2	250 - 500	medium sand
2 - 3	125 - 250	fine sand
3 - 4	63 - 125	muddy sand
> 4	< 63	mud

The most widely used sediment characteristic is the median particle diameter (M.P.D.). Although the use of this alone reduces the sediment to a single parameter and hence leads to a considerable loss of information about the sediment as a whole, a parameter such as this is at least necessary initially if the relative effects of different sediments on the fauna are to be considered (Pearson, 1970). However, in order to consider the sediment in more detail and to obtain information about the way in which it was laid down and therefore about the water currents over that sediment, it is necessary to consider the sorting and skewness of the deposit.

A coefficient of sorting, and hence the degree of sorting, was obtained from the phi-curves by assuming that the sediment particles followed a normal size distribution. In such a distribution the distance where the phi-curve intercepts the 16 and 84% values is approximately twice the standard deviation (i.e. 2σ). Half of this value therefore, can be regarded as a coefficient of sorting for the sediment (Inman, 1952; Eisma, 1966; Folk, 1966). This is also a measure of the slope of the phi-curve about the central portion. This sorting coefficient is statistically more accurate than that proposed as the phi-quartile deviation (Morgans, 1956; Newell, 1970). Folk (1966) compares several sorting coefficients and describes others which are more representative of the degree of sorting of the deposit. However, these latter coefficients are also more difficult to calculate and it is considered that little would be gained in the present survey by using such coefficients.

The terms given by Folk (1966) have been used to convert the sorting coefficient into the relevant nomenclature to describe the degree of sorting :

Term	σ (ϕ units)
Very well sorted	< 0.35
Well sorted	0.35 - 0.05
Moderately well sorted	0.50 - 0.71
Moderately sorted	0.71 - 1.00
Poorly sorted	1.00 - 2.00
Very poorly sorted	2.00 - 4.00
Extremely poorly sorted	> 4.00

Another important parameter used to characterise the sediments is skewness, a measure of whether the phi-curve is straight or curved between the fine and coarse fractions. This parameter describes whether the coarse and fine fractions are equally or unequally sorted. Morgans (1956) and Newell (1970) suggest a measure of skewness based upon the quartile deviation of the curve, whereas sedimentologists (Folk, 1966) insist that a skewness measure based upon the phi-curves values at 84% and 16% is more accurate. For this reason, as well as the fact that the above sorting coefficient was used, the skewness factor used by Inman (1952) for the central part of the phi-curves has been used :

$$\text{Skewness } a_{\phi} = \frac{\phi 16 + \phi 84 - 2\phi 50}{\phi 84 - \phi 16}$$

(However, even more sensitive skewness measures are available which incorporate a skewness measure for the tails in the sediment size distribution (Folk, 1966).) A straight line between the 16 and 84% intercepts give a zero value for skewness. If the mean ϕ value of these intercepts lay to the left of the M.P.D. then a negative skewness will be obtained indicating that the finer particles are better sorted than are the coarse ones, and vice versa.

Folk (1966) also suggests that to measure the non-normality of a distribution it is necessary to measure both skewness (or asymmetry) and kurtosis (or peakedness). The latter is a measure of the ratio between the spread of the central part of the distribution and the spread of the tails. However, this parameter appears to have little known relevance to biological systems and may only be of importance when describing whether a sediment is made up of a mixture of two distributions of particles.

Over the intertidal area the sediment types range from mud to medium sand (Table 2.2; Fig. 2.4); with mud to muddy sand making up a larger proportion of Transect A than Transect B than Transect C. Most of the sediment types are poorly sorted except B4 and C3 which are moderately sorted. Stations B5 and C4 are marginally included in the poorly sorted class and A3 is only marginally excluded from the very poorly sorted class. The sediment types range from B1 being definitely positively skewed to B4 being definitely negatively skewed. The sediment types vary in the amount of silt and clay present (i.e. % <63µm), from those having 75 - 85% (B1, B2, A1) to those having <5% (C3, C4, C5, B4, B5). The general pattern of sediment type, which may be seen from the phi-curves (Fig. 2.4; Data in Appendix 2.3), becomes coarser with a progression from low to high water and from west to east across the beach.

From monthly field observations, it was expected that Stations C2 and B3 would have had a much finer M.P.D., however it has also been noticed that these stations, together with A1, were subject to covering by coarse material during stormy weather. Each of these stations, despite large amounts of coarse material, had relatively large silt and clay levels, and therefore had correspondingly high sorting coefficients. It was also noticed during the field work that the sediment at Station A3 was coarse and firm, characteristics not reflected by the sediment analysis data. However, this station had large clay deposits under the surface and it is probable that some of this material was included in the sediment samples for analysis.

2.4.1.2. Organic Matter Analysis.

The sediment %C. and N. levels are known to be influenced by many interacting variables such that very few patterns emerge

Table 2.2 The Sediment Characteristics at Each Station.

Station	M.P.D. ø	M.P.D. µm.	Quartiles ø units 84%	16%	Sorting Coef. ø units	Skewness	% S.& C.	Sediment Title
A1	4.607	41.2	6.43	3.46	1.49	0.228	79.29	Poorly sorted mud, positively skewed.
A2	3.020	123.0	4.84	2.03	1.40	0.297	31.88	Poorly sorted muddy-sand, positively skewed.
A3	4.173	55.0	5.80	1.94	1.93	-0.157	54.76	Poorly sorted mud, negatively skewed.
A4	2.213	216.0	3.57	1.07	1.25	0.083	13.97	Poorly sorted fine-sand, slightly positively skewed.
B1	4.687	38.7	6.88	4.01	1.44	0.527	84.35	Poorly sorted mud, definitely positively skewed.
B2	4.500	44.0	5.87	3.07	1.40	-0.024	76.37	Poorly sorted mud, slightly negatively skewed.
B3	2.527	176.0	4.68	1.53	1.57	0.368	29.78	Poorly sorted fine-sand, definitely positively skewed.
B4	2.267	210.0	2.81	1.05	0.88	-0.510	2.96	Moderately sorted fine-sand, definitely negatively skewed.
B5	2.480	180.0	3.40	1.28	1.06	-0.132	2.69	Poorly sorted fine-sand, negatively skewed.
C1	4.140	57.0	5.53	2.04	1.75	-0.202	54.12	Poorly sorted mud, negatively skewed.
C2	2.493	178.0	4.73	1.42	1.66	0.352	21.14	Poorly sorted fine-sand, positively skewed.
C3	2.100	234.0	2.79	1.30	0.75	-0.072	3.93	Moderately sorted fine-sand, slightly negatively skewed.
C4	1.533	350.0	2.39	0.26	1.07	-0.194	1.18	Poorly sorted medium-sand, negatively skewed.
C5	1.380	388.0	2.39	-0.68	1.53	-0.347	1.88	Poorly sorted medium-sand, negatively skewed.

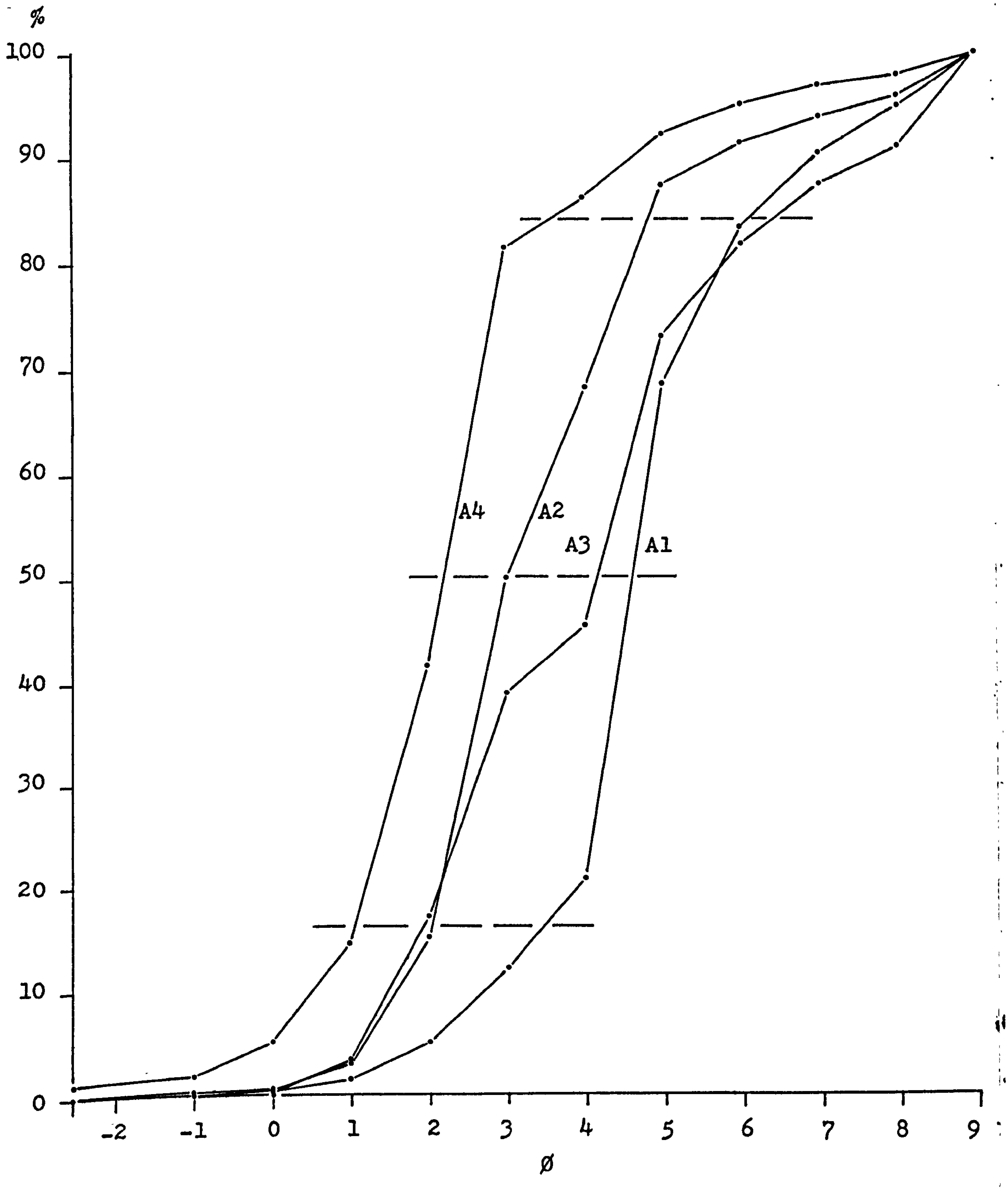


Figure 2.4 Sediment Particle Size Analysis : Cumulative Phi Curves. Transect A.

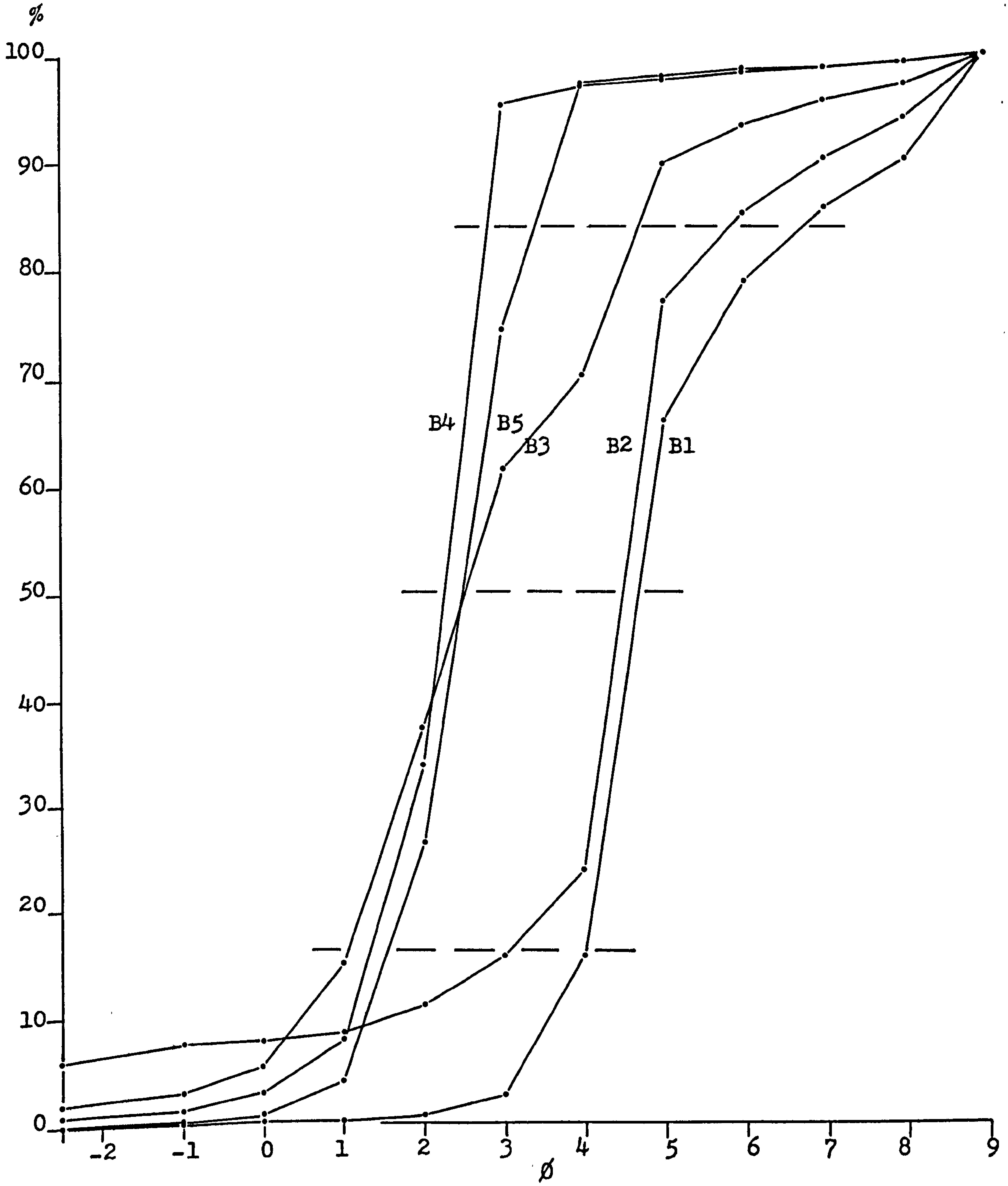


Figure 2.4 Continued. Transect B.

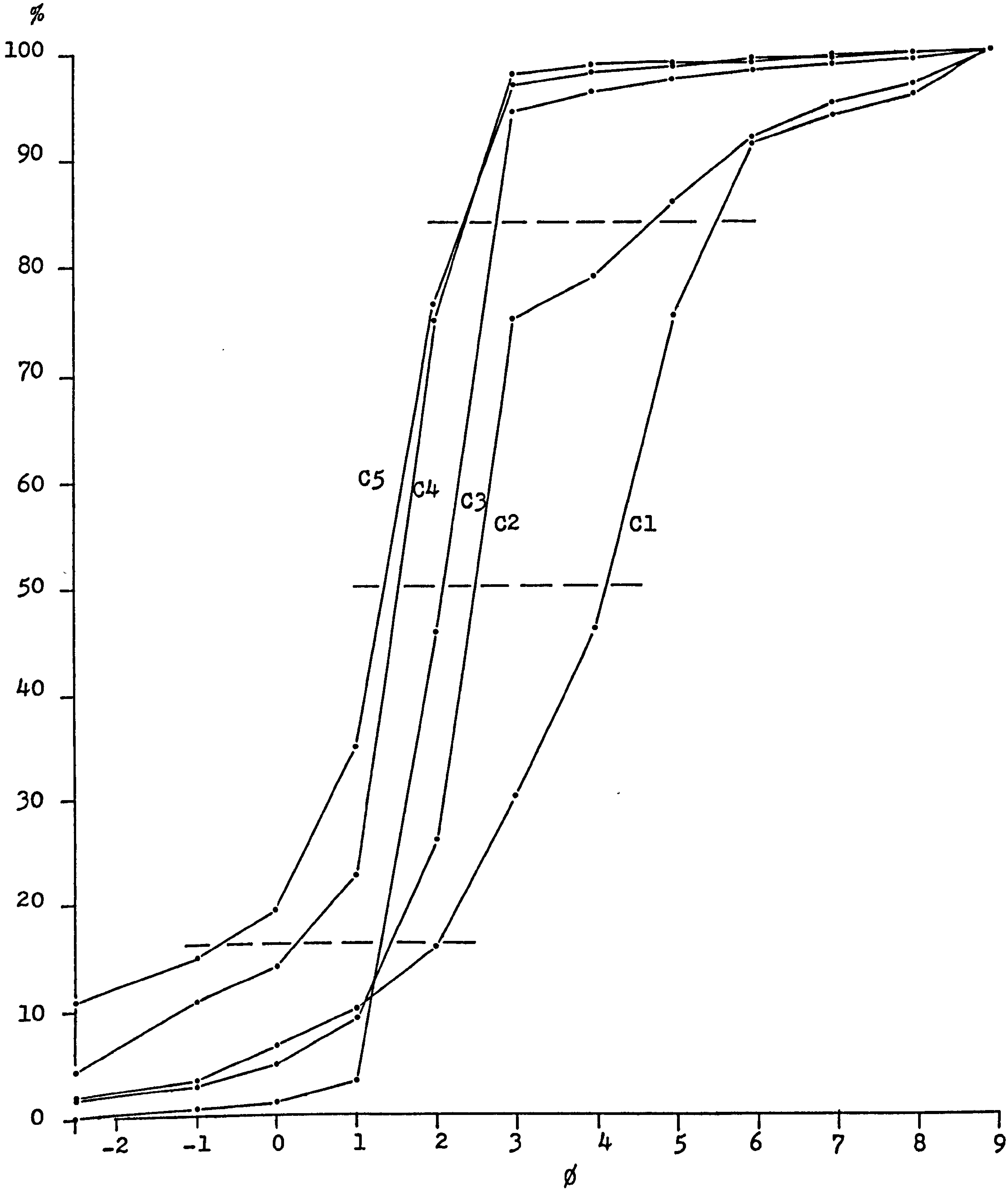


Figure 2.4 Continued. Transect C.

overall and only tentative explanations may be given to those patterns which do emerge (Figs. 2.5 and 2.6). The stations may be divided into two broad sub-areas, those lower down the shore (A1, B1, B2, B3, C1, C2) and those on the upper-shore. For the major part of the sampling period these two major areas were widely different in the %C. and N. content of the sediment.

An inverse correlation between the sediment particle size and the amount of organic matter present is indicated by the above data and is discussed in detail below (Section 2.4.1.4). However, the Station A3 was anomalous in this respect as it had a fine M.P.D. which was not reflected in the levels of %C. and %N. at the station. This suggests that the finer particles were not available to the large microfloral populations which colonise fine substrates and also that the finer particles do not appear to have retained large amounts of organic matter as do other fine sediments. This may again indicate that sub-surface clay was included in the sediment sample.

There appears to be some seasonality shown in the amounts of organic matter, particularly at the muddy, lower-shore stations, as the level of %N., and to a lesser extent %C., were lower during the winter months than other months.

The stations which had an abundant _Zostera marina_ cover (C5, B5 and to a lesser extent A2, A3, A4) showed a slight increase in the levels of %C., and to a lesser extent %N., in the autumn months. This was expected as the post-growing seasonal decomposition of _Zostera_ (and other macroflora) would cause the amount of sediment organic matter to increase. This added detritus would provide an additional substrate on which microflora could develop (Adams and Angelovic, 1970; Fenchel,

Figure 2.5 Sediment Analysis : Surface Percentage Carbon Levels.

Figure 2.6 Sediment Analysis : Surface Percentage Nitrogen Levels.

Figure 2.7 Sediment Analysis : Surface Carbon/Nitrogen Levels.

Figure 2.8 Sediment Analysis : Surface Percentage Water Levels.

Legend

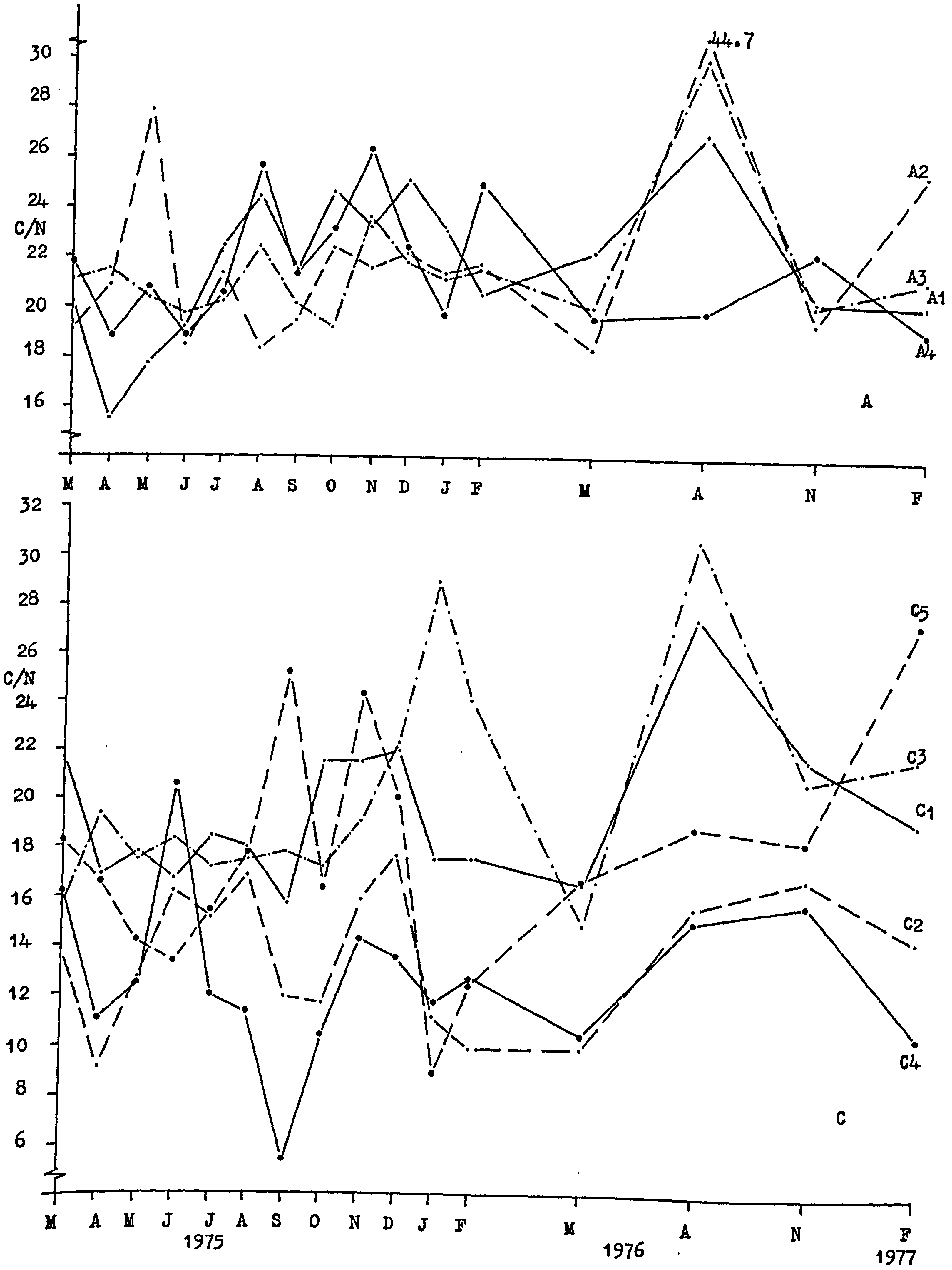
	Transect		
	A	B	C
—·—	1	1	1
– –·– –	2	2	2
—·—·—	3	3	3
—●—	4	4	4
– –●– –		5	5


A1
A2
A3
A4
A
B
B1
B2
B3
B4
B5
C
C1
C2
C3
C4
C5
%C
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
9.0
M A M J J A S O N D J F M A N F
1975
1976
1977

Figure 2.5


A
0.4
0.3
%N
0.2
0.1
0
A1
A2
A4
A3
M A M J J A S O N D J F M A N F
B
0.4
0.3
%N
0.2
0.1
0
B3
B2
B1
B5
B4
M M J J S O N D J F M A N F
C
0.3
%N
0.2
0.1
0
C1
C2
C5
C4
C3
M A M J J A S O N D J F M A N F
1975
1976
1977

Figure 2.6



44.7
30
28
26
24
C/N
22
20
18
16
A1
A2
A3
A4
A
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
32
30
28
26
C/N
24
22
20
18
16
14
12
10
8
6
C1
C2
C3
C4
C5
C
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

Figure 2.7

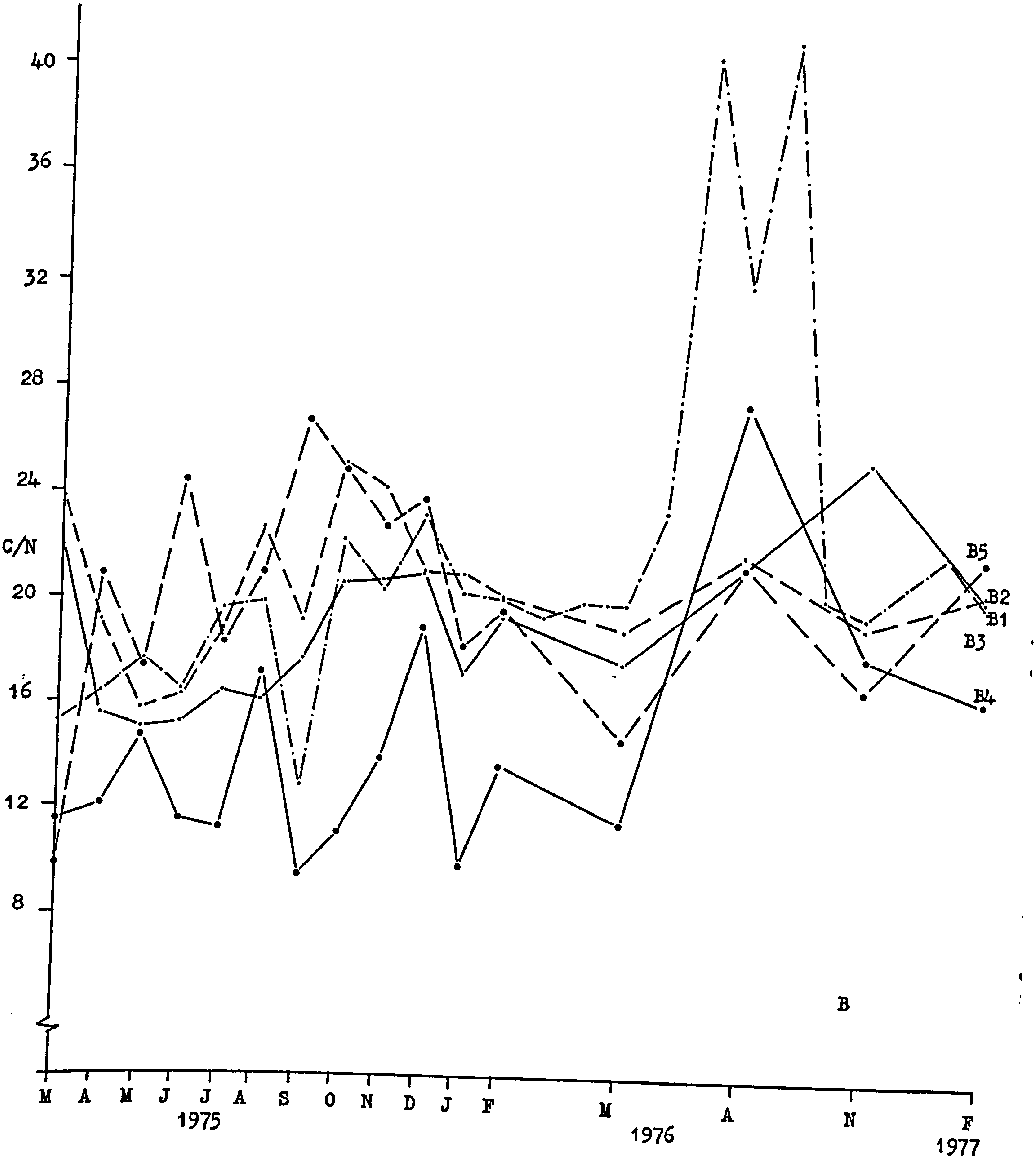


Figure 2.7 Continued.

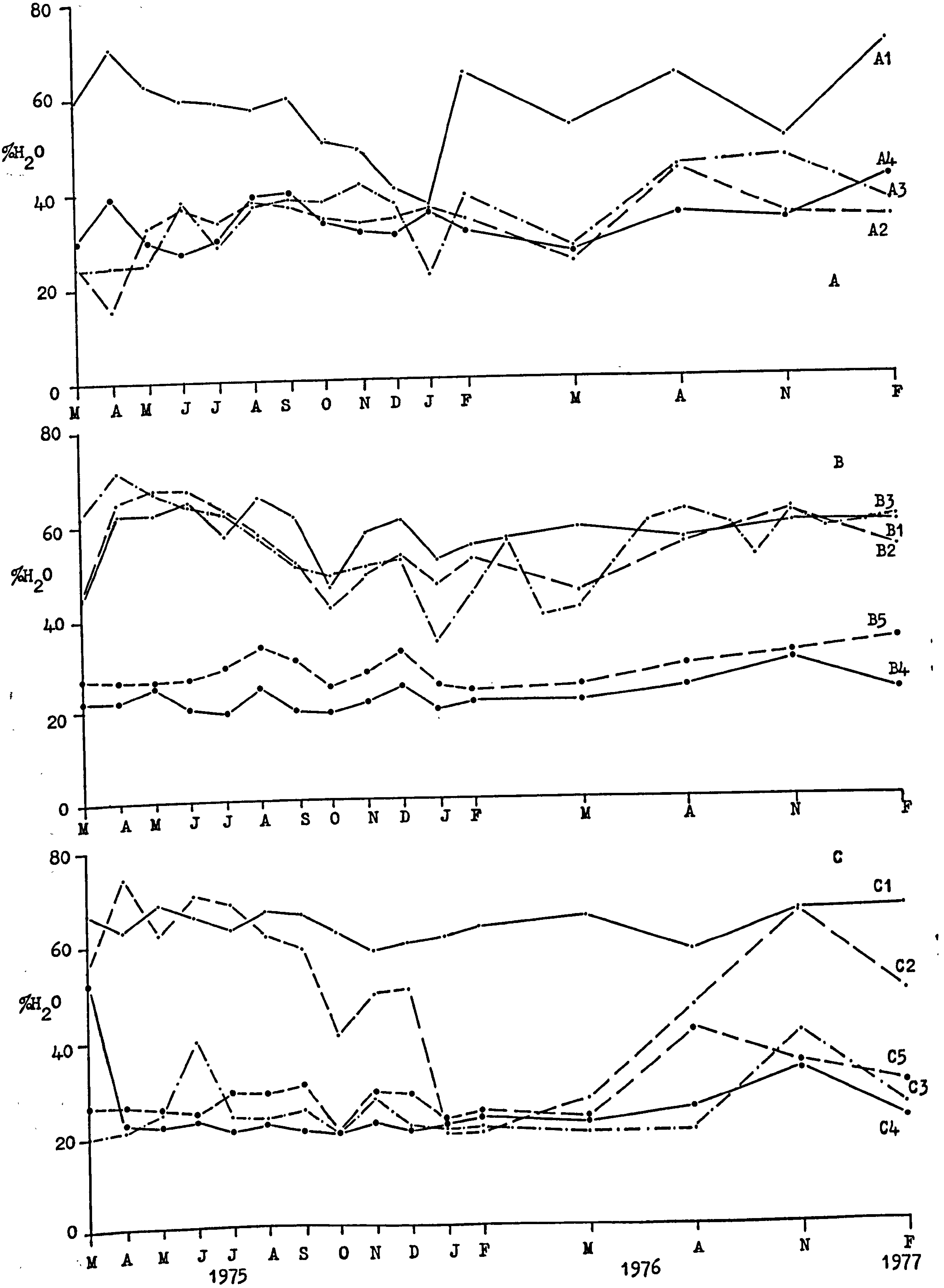

80
60
40
20
0
%H$_2$O
A1
A4
A3
A2
A
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
B
B3
B1
B2
B5
B4
C
C1
C2
C5
C3
C4
1975
1976
1977

Figure 2.8

1970; Levinton, 1972; Sand-Jensen, 1975.

Large reductions in %C. and %N. levels were observed at Stations A1 and C2 and to a lesser extent B3 from October 1975 onwards. This again may be attributed more to sediment transport effects than to seasonality in %C. and %N. levels. At C2 particularly, the sand influx had an influence on the sediment type for about a year (until November 1976) after which the station was covered by soft mud from lower down the shore and returned to a pre-October 1975 condition. Station A1 was influenced by coarser material from October 1975 to January 1976, although this station recovered its former state quickly because of the relatively fluid fine sediment further offshore from A1 which was easily transported by the tide. Station B3, as noticed from field observations, had coarse material mixed with the fine material such that the effect was smaller than at A1 and C2. However, %C. and %N. levels also decreased markedly at B1, B2 and C1 after autumn 1975 and recovered after the winter. As there was no sediment transport over these stations during this time, it is likely that those changes in organic matter levels were of a seasonal nature although only tentative explanations can be given for organic matter changes of this kind.

Stations C4 and B4 were of clean sand, had no Zostera cover and little seaweed cover and showed constantly low %C. and %N. levels. It is possible, however, that detritus from adjoining stations will be transported to them.

The differing levels of meiofaunal populations and newly settled mollusc spat will also have distorted the measured levels of %C. and %N. Stations B5, C1, B2 and B1 had large numbers of oligochaetes present as the first station was near to a local sewage outfall pipe and the latter three station were in or near mussel beds. Additionally, for example, from August 1975 onwards large numbers of newly settled Hydrobids were recorded at B2 and C4. These animals would have been included in the sediment analyses from June onwards and have influenced the results accordingly. (This would therefore lead to a predetermined result being achieved in any attempt to relate numbers of meiofauna or spat to the organic matter content in which they were found,)

The accumulation of pseudo- and normal-faeces in the sediments would also have affected the %C. and %N. levels depending on the size of the macrofaunal population and the age of the faeces (Newell, 1965). This factor would not therefore be constant throughout the year but as it presents a potential food source to the deposit-feeding fauna then it should be included.

An index of the nutritional value of material to its consumers is the C/N ratio (Mann, 1972). Most organic debris has a high C/N ratio as it contains little proteinaceous matter. However, on colonisation by microorganisms the carbon component will be utilised and the C/N will correspondingly decrease (Anderson, 1940), this will render the material more attractive to detritivores.

Rullier (1959)(in Longbottom, 1970) suggested that animal material normally has a C/N value of 10 or less while values of 20 or more indicate plant material. Holm-Hansen (1972) disagrees with this by suggesting that most phytoplankton have a ratio of 5 - 10 although the values range from 4 to 50. However, the senescence or death of phytoplankton cells would cause a measured C/N ratio to increase upto 60:1 (Russell-Hunter, 1970). Longbottom (1970) suggested that, as bacteria have a C/N value of 7, in deposits where the C/N is between 7 and 11 there are large bacterial populations.

Macrophytes have high C/N values, e.g. 14 - 27 in Laminaria and 40 - 80 in Kelp (Russell-Hunter, 1970; Mann, 1972); these ratios also increase at death until the material was colonised by microorganisms, i.e. Spartina detritus decreases from C/N 45 to 11 upon microorganism utilisation (Russell-Hunter, 1970). Russell-Hunter (1970) suggests that adult animals have a protein requirement corresponding to a ratio of less than 17, therefore the macrofloral detritus colonised by microorganisms is suitable for the deposit-feeding macrobenthos. Russell-Hunter (1970) also suggests that the C/N of detritus is likely to be high in the autumn and low in the spring. This is mainly because of the larger amount of non-living tissue following the growing season of the micro- and macroflora. The ratio would be likely to decrease from autumn to spring as the detritus is utilised by microorganisms.

Some workers have discussed the changes in the C/N ratio of sedimenting material. Holm-Hansen (1974) found that the ratio decreased as detritus passed down a water column as its micro-organism component increases. Suspended particulate matter in shallow embayments may usually have a C/N value of 6 - 10 (Stephens et al, 1967; Oviatt and Nixon, 1975), while that in a sea loch is higher and within the range 10 - 20 (occasionally upto 40)(Ansell, 1974); this suggests that the former areas' particulate matter was of a higher nutritional value.

The C/N ratios obtained in the present study on Transect A were usually within the range 18 - 28, 10 - 28 on Transect B, and 9 - 28 on Transect C (Fig. 2.7). The relatively high ratios measured may be attributed to one or both of the factors :
(i) Abundant organic detritus in an early state of microbial degradation. Russell-Hunter (1970) suggested that high C/N ratios in freshwater muds indicate an oligotrophic environment whereas low ratios would characterise eutrophic environments.
(ii) The presence of "non-organic" carbon either as carbonates or coal. Buchanan and Longbottom (1970) conclude that the C/N ratio for coal-free mud may be low between 8 and 12, and that for coal containing mud 15 - 40 suggesting that coal, as would be expected, influences the %C. levels much more than the %N. values. The C/N values for Torry Bay appear to be at the bottom part of the range of coal-containing muds. Coal dust was observed in the sediments but in small and possibly constant amounts. Additionally, carboniferous limestone is the bedrock on certain parts of the beach, e.g. C3, C4, C5; which, if present in the samples, would influence the %C. and %N. levels. Oviatt and Nixon (1975) suggest that the lack of acidification in bottom material analyses will result in high C/N ratios being obtained due to the presence of carbonates (although this was not reflected in the aforementioned untreated and acid-treated samples).

An analysis of the occurrance of the maximal ratios at each station shows that there were higher C/N ratios during the periods August - December 1975 and August - November 1976. The presence of large amounts of detritus following the growing season of macrophytes would account for this phenomenon.

There initially appears to be no pattern between the different stations' C/N ratios except that the clean sandy Stations C4 and B4 values were lower for most of the year than the other stations. However, B3 would also be expected to follow this pattern but does not (see Section 2.4.1.4.).

It may be seen, therefore, that many factors affect the quantity and quality of organic matter in a deposit and that the interactions between such factors result in the measurement of erratic levels (see Section 2.3.1.4.). However, underlying trends are still observed such that while there may be doubts about using %C. and %N. values per se for each station, this is still valid as a means of comparing stations.

2.4.1.3. Water Content of Deposit.

The sediment water content levels follow the same trends as the levels of %C. and N., i.e. the fine mud stations lower down the shore contain larger amounts of water in their deposits than the upper coarse stations (Fig. 2.8). This parameter varied both with season and with type of deposit. The levels of several stations show some seasonality although most stations appeared to have relatively constant levels.

The similarity between levels of %C., %N. and %H_2O. would be expected if these variables are characteristic of certain types of deposit and vary with the size of particles in that deposit (see Section 2.4.1.4.). It may be suggested that large changes in the water content of the substrate at a station reflect changes in substrate type. Such large changes were evident at the Stations A1, C2 and, to a lesser extent, B3. At stations where there was no evident sediment transport then any minor fluctuations in the water content may be attributed to seasonal differences.

2.4.1.4. Spatial Interactions Within the Environmental Variables.

The Pearson-correlation matrix (Fig. 2.9a from Table 2.3 data) shows intercorrelations (** or ***) between M.P.D., %H_2O., %S. & C., %N. and shore slope and also between tidal height, sorting coefficient and skewness and the other factors (*).

Tidal height was related to M.P.D. (-**), %H_2O (-*), %C. (-*) and %N. (-*); however it is likely that the latter three variables were only directly related to tidal height through particle size. Particle size (M.P.D.) was correlated with skewness (-*), water content (-**), organic matter content (-**), shore slope (+**) and the amount of silt and clay (-***); with the exception of the first of these the relationships between particle size and the other factors has been well documented. In all relationships except that with shore slope, particle size is considered to be the independent variable. The particle size was negatively and exponentially related to the sediment water, carbon and nitrogen contents (Fig. 2.10a, b, c) and indicate the importance of a particle size of 0.1mm, below which the %N., %C. and %H_2O. levels markedly increased.

The sorting of the sediments was correlated with sediment water content (+*), percentage fine material (+*), and shore slope (-*). Wolff (1973) found that the better sorted sediments occur outwith the rivers and estuaries and have a M.P.D. $\approx 2.50\ \phi$ (180µm); this is possibly because that grain size is most easily transported by sediments. It is expected therefore that the sorting coefficient and particle size would not be significantly correlated. Wolff (1973) further suggests that the degree of

	T.H.	M.P.D.	S.C.	SK.	$\%H_2O_F$	$\%H_2O_J$	%C.	%N.	%S. &C.	Slope	C/N.	Int. Sal.	Org. C.	CHO.
T.H.		+ *				- *	- *	- *				- ***		
M.P.D.				- *	- ***	- **	- **	- **	- ***	+ **	- **			
S.C.		- *			+ *				+ *	- *	+ *			
SK.					+ *	+ *	+ *	+ *	+ *					
$\%H_2O_F$		- ***	+ *			+ ***	+ ***	+ ***	+ ***	- **				
$\%H_2O_J$	- *	- **			+ ***		+ ***	+ ***	+ **	- *				
%C.		- **	+ **	+ *	+ ***	+ ***		+ ***	+ ***	- **				
%N.		- **	+ *		+ ***	+ ***	+ ***		+ **	- *				
%S. &C.		- ***	+ **		+ ***	+ **	+ ***	+ **		- **	+ *			
Slope		+ **	- *		- **	- *	- **	- *	- **		- **			- *
C/N.		- *	+ *		+ *		+ **		+ ***	- *			+ *	
Int. Sal.	- **													
Org. C.											+ *			
CHO.										- *				

Figure 2.9 Environmental Factors: Spatial Analysis - Pearson Correlation Matrices:- (a) Upper matrix linear correlations; (b) Lower matrix double-logarithmic correlations. (Only significant correlations are given.)

The direction and significance of the correlation between each pair of variables are given where:

*	= p 0.05	0.01	Significant correlation;
**	= p 0.01	0.002	Very significant correlation;
***	= p 0.001		Highly significant correlation.

Variables: T.H. = tidal height, m above C.D.; M.P.D. = sediment median particle diameter (μm); S.C. = sediment sorting coefficient (Ø units); SK. = sediment skewness (Ø units); $\%H_2O_J$, $\%H_2O_F$ = surface sediment percentage water Jan., Feb. 1976; %C., %N., %S. &C. = surface sediment percentage carbon, nitrogen and silt and clay at Jan. 1976; Slope = slope of shore (^{o}); C/N. = surface sediment carbon: nitrogen value Jan. 1976; Int. Sal. = Interstitial salinity (as a percentage of estuarine water salinity Jan. 1976; Org. C. = Overlying water suspended particulate organic carbon (mg l^{-1}); CHO. = overlying water suspended particulate carbohydrate (mg l^{-1}).

Table 2.3 Data Used in the Spatial Analysis of Environmental Factors.

Station	Tidal Ht. Above C.D. (m)	Slope of Shore Degrees	Salinity as % Estuarine Water	Immersion Period (Hrs./ Tide).		
				Mean	Springs	Neaps
A1	3.36	7.8	91.3	6.18	6.25	6.12
A2	3.97	8.2	91.0	5.09	5.87	4.31
A3	4.20	6.2	88.5	4.22	4.96	3.48
A4	4.50	11.0	85.2	3.44	4.46	2.42
B1	2.60	5.0	96.0	8.08	7.42	8.75
B2	2.97	1.9	94.3	7.07	6.92	7.23
B3	3.09	4.0	91.1	6.77	6.71	6.83
B4	3.50	9.0	87.2	5.71	6.02	5.40
B5	4.13	12.2	86.4	4.45	5.17	3.73
C1	1.27	5.9	96.3	10.64	8.58	12.70
C2	2.15	7.0	95.9	10.38	8.06	12.70
C3	2.71	18.2	96.3	7.67	7.32	8.07
C4	3.96	10.0	93.9	4.83	5.36	4.30
C5	4.56	18.0	90.8	2.84	4.25	1.43

Other variables used: M.P.D., sorting coefficient, skewness and % S.& C. (in Table 2.2); sediment %H_2O (Jan.'76), %H_2O (Feb.'76), %C., %N., C/N, (for Jan. 1976, given in Figs. 2.5-2.8.); and suspended particulate Organic Carbon and Carbohydrate (in Table 2.5).

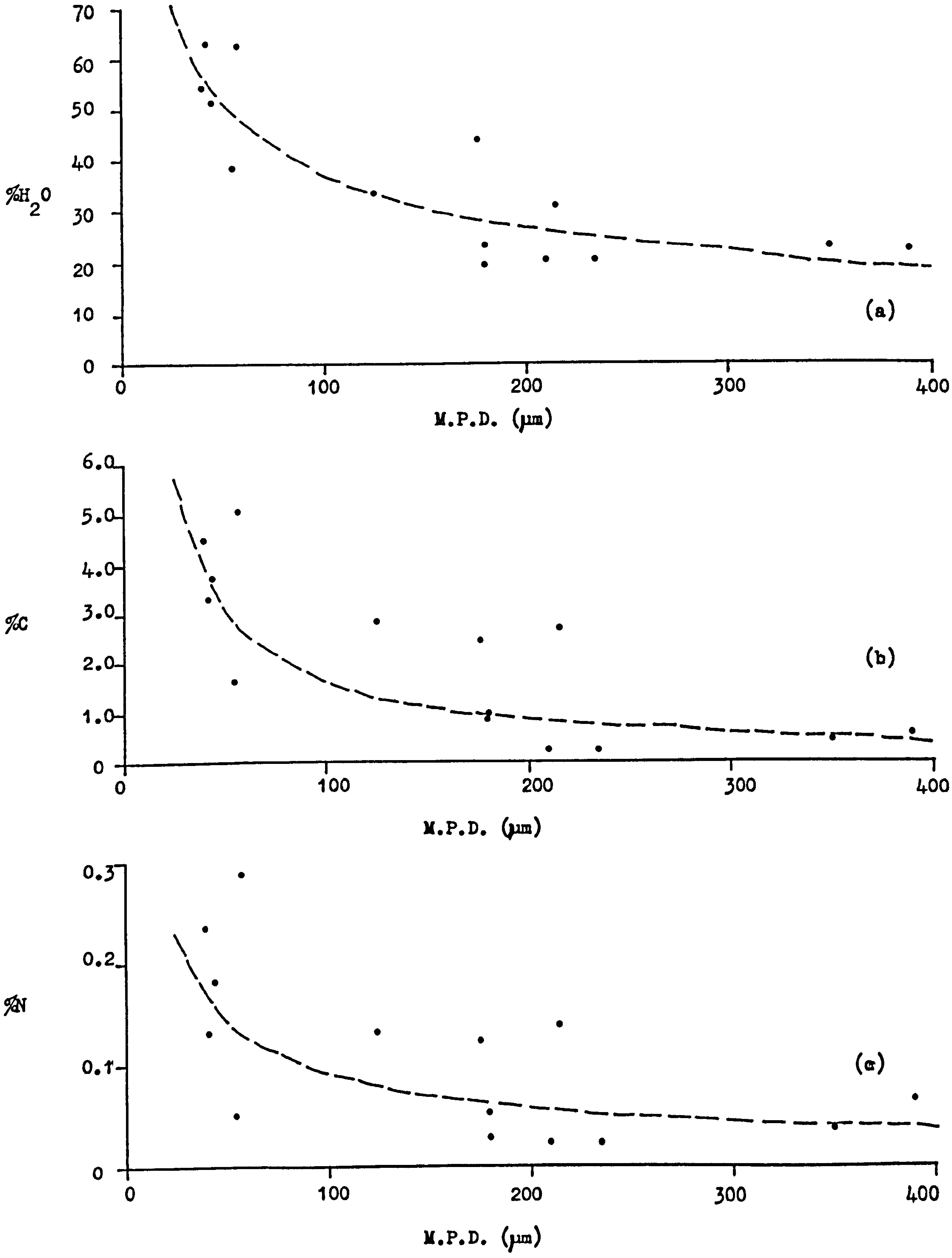
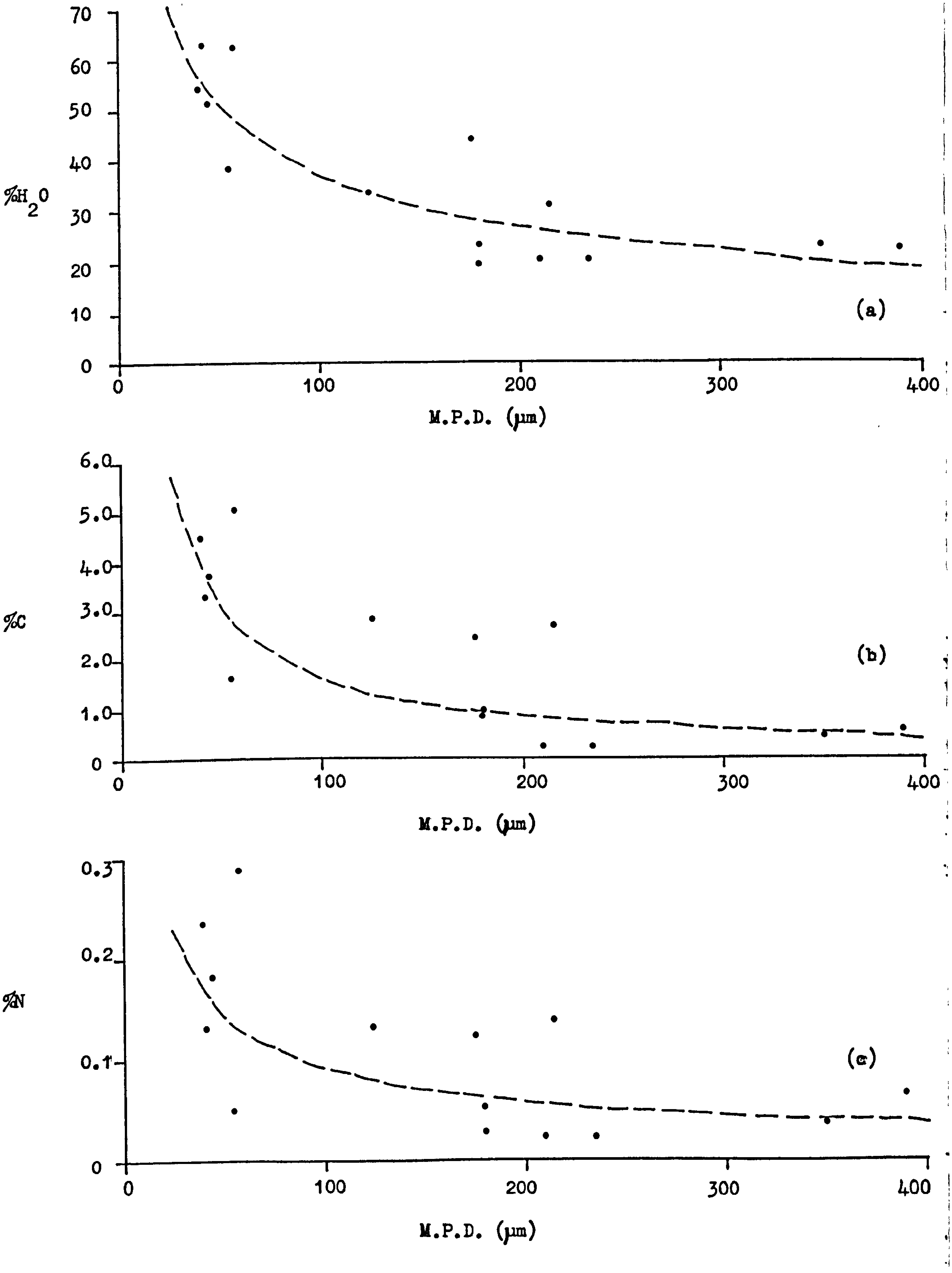

70
60
50
40
30
20
10
0
%H$_2$O
0
100
200
300
400
M.P.D. (µm)
(a)
6.0
5.0
4.0
3.0
2.0
1.0
0
%C
0
100
200
300
400
M.P.D. (µm)
(b)
0.3
0.2
0.1
0
%N
0
100
200
300
400
M.P.D. (µm)
(c)

Figure 2.10 Environmental Variables : Relationships Between Sediment Median Particle Size and Water, Carbon and Nitrogen Content.

Exponential Equations :-

	r	p
(a) $\%H_2O = \dfrac{308.96}{\text{M.P.D.}^{0.460 \pm 0.080}}$	-0.856	***
(b) $\%C = \dfrac{109.14}{\text{M.P.D.}^{0.913 \pm 0.258}}$	-0.714	**
(c) $\%N = \dfrac{1.972}{\text{M.P.D.}^{0.667 \pm 0.231}}$	-0.641	*

Dotted Lines Constructed From Above Exponential Equations.


%H$_2$O
70
60
50
40
30
20
10
0
0
100
200
300
400
M.P.D. (µm)
(a)
%C
6.0
5.0
4.0
3.0
2.0
1.0
0
0
100
200
300
400
M.P.D. (µm)
(b)
%N
0.3
0.2
0.1
0
0
100
200
300
400
M.P.D. (µm)
(c)

sorting influences the sediment permeability and is also a measure of the amount of fine particles, i.e. sediments with a high mud content have high sorting coefficient; this agrees with the above correlations. In the Torry Bay sediments the M.P.D. and sorting were negatively (but non-significantly) correlated although there was no minimal sorting coefficient at 180µm (see also McNulty _et al_, 1962). Brett (1963 in Carriker, 1967) found that as the current velocity increased there was a loss of fine sediments, and therefore with fewer sediment grades present the sorting coefficient became smaller.

The presence of _Zostera_ would lead to a reduction in water flow over an area thus allowing fine particles to be deposited in an otherwise coarse area. This would produce a larger sorting coefficient at the _Zostera_ stations (B5, C5) than would be expected from a comparison of them with adjacent clean sandy areas (B4, C4). In addition the presence of _Zostera_ would increase the stability of the sediment which is low in coarse deposits (Green, 1975). The amounts of _Z. marina_ at each station was determined in June, 1975, as the material (both aerial and root parts) that could easily be removed from the large samples :

Station	Standing Crop (g afdw m^{-2})
A2	9.84
A3	61.34
A4	20.18
B5	42.42
C5	110.88

(_Z. marina_ absent at all other stations.)

This gives an indication of, firstly, the amount of material fixed by this species during the growing season at different parts of the intertidal area, and secondly, the relative effect on stabilising coarse sediment in those areas.

The sediment water content was correlated with organic content (+***), percentage of fine material (+***) and shore slope (-***). It is likely, however, that the particle size and amount of fine material are the independent variables in this case, and that they determine the water holding capacity of the deposit, the available surface area for microorganism colonisation, and the sediments' facility for collecting detritus.

The sediment %C. and %N. were highly interrelated (+***) which may suggest that the coal dust in the deposits either affected all results equally or it did not have any effect upon the results; the latter is unlikely. However, this relationship may be indicative of the relationship between the capacity of the deposit for holding any detritus, which is likely to settle on fine substrates due to the reduced water flow over them, and the subsequent available area, both on the detritus and the particles, for colonisation by microorganisms. This is again demonstated by the %C./%S. & C. (+***) and %N./%S. & C. (+***) correlations. The relationships between %N. and %C. and the shore slope (-**) were also of a curvilinear nature but more importantly demonstrate indirect relationships in that the slope of the shore affected the particle size which influenced the organic matter levels.

Detritus accumulated in the fine sediments from the decomposition of local material as well as allochthonous material such as Zostera and saltmarsh debris. Additionally, faecal production by deposit feeders and the inclusion of meiofauna in the sediment samples will have also influenced the sediment organic matter data. Sanders (1956) and Pearson (1970), also found highly significant correlations between the organic content and %S. & C. of the sediment and suggest that this is because organic matter is associated with finer particles. However, they do not consider the accumulation of organic material in fine deposits. Newell (1965) further demonstrated that when a certain amount of organic matter is present in coarse and fine deposits there is a greater microfloral population associated with that organic matter in the fine sediments.

The C/N ratios were correlated with particle size (-**), %S. & C. (+*), shore slope (+**) and sorting coefficient (+*). The first two correlations suggest that organic matter deposited in fine sediments is not utilised as quickly by microorganisms as that deposited in coarse sediments. This may be the result of fine deposits having a lower permeability than coarse ones; this would lead to the development of anaerobic conditions and perhaps oligotrophic conditions (Russell-Hunter, 1970).

The shore slope was positively correlated with M.P.D. (**) and tidal height (n.s.) but negatively correlated with all other variables. The relationships between shore slope and the wave energy passing over it and between the particle size and wave energy are well documented (e.g. Newell, 1970). Many of the relationships found here are therefore indirect ones as the dependent variables (e.g. %N., %C.) were influenced by the particle size which in turn was a product of the shore slope and the wave energy over that deposit. The correlation between %S. & C. and shore slope (-***) was also a reflection upon that wave action.

The variables in the curvilinear relationships mentioned above were logarithmically transformed and recorrelated; this resulted in an increased correlation coefficient and significance level (Fig. 2.9b). Thus the slope of the shore was logarithmically, and significantly, related to water content (-), %C. (-), %N. (-) and %S. & C. (-). M.P.D. was related in the same way to %C. (-), %N. (-) and %H_2O. (-), and %S. & C. to %N. (+) and %C. (+).

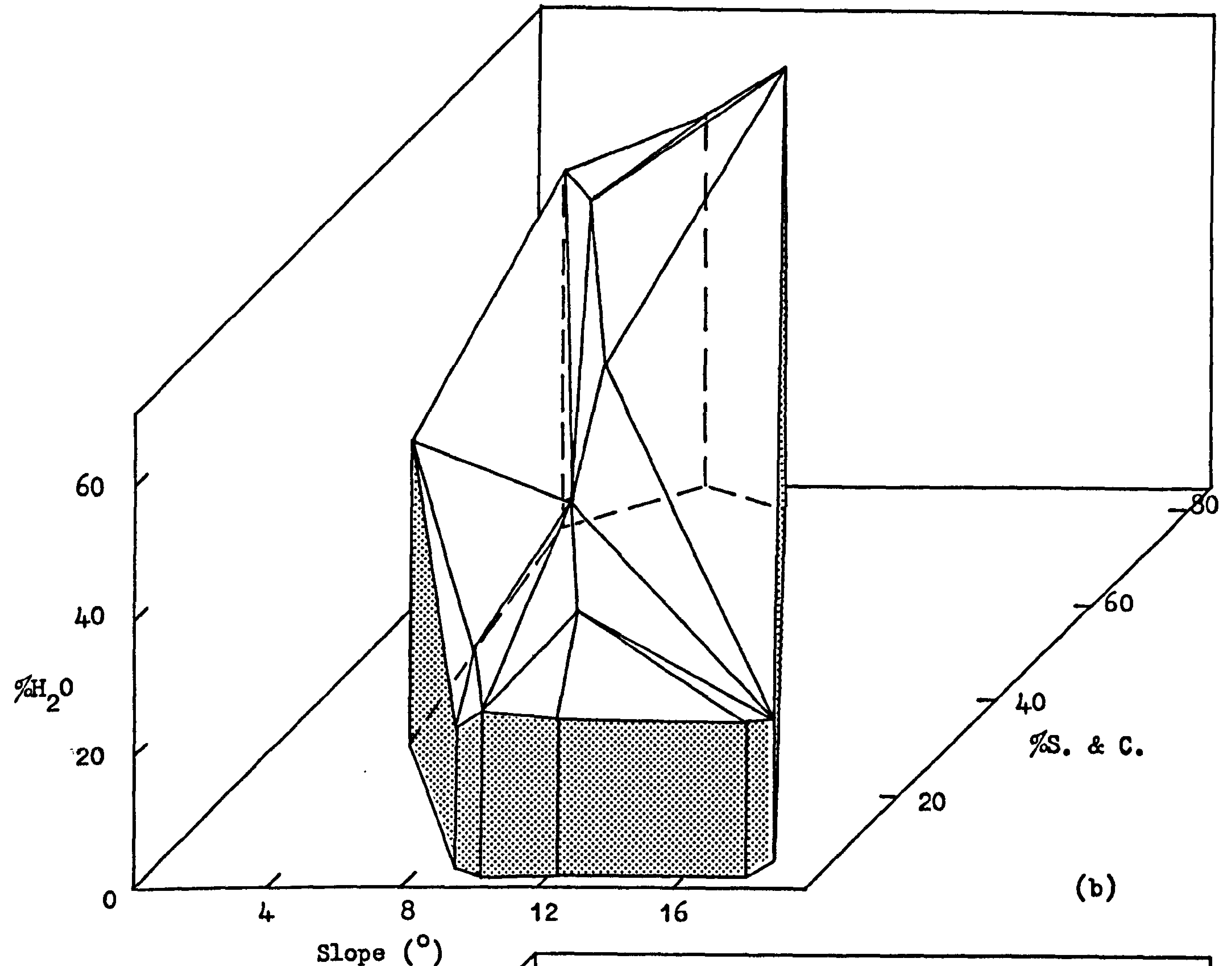
In order to explain the spatial variability of C/N, %H_2O., %C., %N. and interstitial salinity, multiple regressions of these dependent factors against all other environmental, independent factors were calculated (Table 2.4). Whereas the C/N ratio was mainly influenced by the tidal height and the sediment carbon content, the sediment carbon and nitrogen contents were wholly influenced by each other. The sediment water content was mainly influenced by the fine particle content of the sediments and by the tidal height to a lesser extent. The interstitial salinity, on the other hand, was mainly affected by the tidal height and, to a lesser extent, by the sediment silt and clay content.

Many of the relationships given above may be summarised (Fig. 2.11a, b) and show that with an increase in tidal height and shore slope,. an increasing particle size of deposit was found (Fig. 2.11a). Similarly, a decrease in the shore slope and the amount of fine material in a deposit resulted in the decrease of sediment water content (or carbon and nitrogen content since these sediment variables were highly intercorrelated with each other)(Fig. 2.11b).

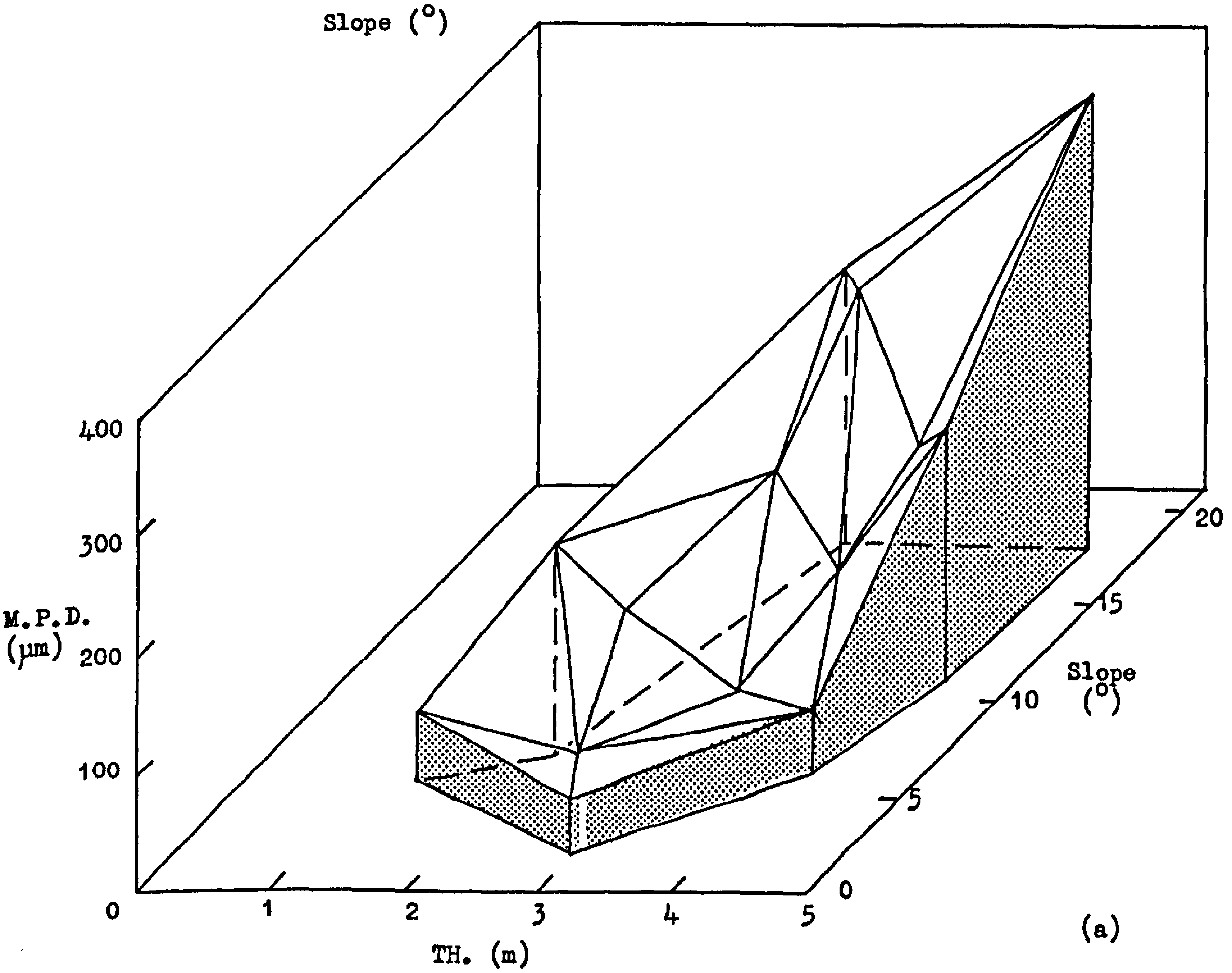
Table 2.4 Multiple Regressions of Selected Environmental Variables. (Abbreviations as Fig. 2.9.)

Dependent Variable	Incorporated Variables and Significant Equation	Excl. Variables	Total Variance Accounted For.	Main Variables
(1). C/N	TH.,M.P.D.,S.C.,SK.,%H_2O.,%C.,%N.,%S.& C.,Slope,Int. Salinity $12.\overset{*}{8}63_{\%C.} - 2.236$	-	88.9%	M.P.D.(37.8%), %C.(24.9%), S.C.(11.6%).
%N	TH.,M.P.D.,S.C.,SK.,%H_2O.,%C.,%S.& C.,Slope,C/N.,Int. Sal. All n.s. + 0.066	-	99.7%	%H_2O.(98.5%).
%C	TH.,M.P.D.,S.C.,SK.,%H_2O.,%N.,%S.& C.,Slope,C/N.,Int. Sal. All n.s. + 0.906	-	99.5%	%H_2O.(95.7%).
%H_2O	TH.,M.P.D.,S.C.,SK.,%C.,%N.,%S.& C.,Slope,C/N.,Int. Sal. All n.s. + 8.565	-	99.8%	%N.(98.5%).
Int. Sal.	TH.,M.P.D.,S.C.,SK.,%H_2O.,%S.& C.,Slope. $0.\overset{*}{0}31_{M.P.D.} + 0.\overset{*}{1}17_{\%S.\& C.} - 4.\overset{***}{0}10_{TH.} + 98.354$	-	83.7%	TH.(59.3%), %S.& C. (16.0%).
(2) C/N	TH.,M.P.D.,S.C.,SK.,%C.,%N.,%S.& C.,Slope. $8.\overset{**}{6}63_{S.C.} + 11.\overset{**}{0}51_{\%C.} - 210.\overset{***}{0}73_{\%N.} + 15.356$	Slope	87.6%	M.P.D.(37.8%), %C.(24.9%), S.C.(11.6%).
%N	TH.,M.P.D.,S.C.,SK.,%C.,%S.& C.,Slope. $0.\overset{***}{0}58_{\%C.} - 0.035$	-	97.4%	%C.(95.2%).
%C	TH.,M.P.D.,S.C.,SK.,%N.,%S.& C.,Slope. $16.\overset{***}{2}19_{\%N.} + 0.735$	-	98.0%	%N.(95.2%).
%H_2O	TH.,M.P.D.,S.C.,SK.,%S.& C.,Slope,C/N.,Int. Sal.	-	72.6%	%S.& C.(51.9%), TH.(7.0%).

Figure 2.11 Environmental Factors : Interrelationships Between (a) Shore Slope, Tidal Height and Median Particle Size and (b) Shore Slope, Sediment Percentage Silt and Clay and Sediment Water Content.


60
40
%H$_2$0
20
0
4
8
12
16
Slope (°)
80
60
40
%S. & C.
20

(b)


400
300
M.P.D. (μm)
200
100
0
1
2
3
4
5
TH. (m)
0
5
10
15
20
Slope (°)

(a)

A principle components analysis was performed incorporating all of the environmental variables; this indicates the similarities between the stations (the distance between stations on the figure is proportional to their similarity). The stations were then grouped together after all factors had been taken into account (see Fig. 2.12). The stations may be grouped into those at the low-shore, with fine mud, shallow slope and high organic matter contents; and stations at the upper-shore, with coarse sand, steep slope and low organic matter content. The similarity of the stations, however, will be shown to be modified in relation to each species under consideration.

2.4.2. Salinity.

2.4.2.1. Interstitial Salinity.

A seasonality pattern was observed in interstitial water salinity with the lower salinities being encountered during the late autumn-early winter period (Fig. 2.13). Transect C had overall interstitial salinity > Transect B > Transect A. The high-shore stations had lower winter salinities than the corresponding lower-shore ones as the former stations' salinities were more likely to be diluted by freshwater imputs. This pattern was reversed during the summer months because of increased evaporation. Therefore, the infauna at the higher stations, e.g. C4, C5, B4, B5, would experience larger salinity fluctuations than those at other stations.

The stations' salinity regimes may be summarised :

	Max. $^{o}/oo$	Min. $^{o}/oo$	Range
A1	33.75	28.10	5.60
A2	33.48	26.52	6.96
A3	33.15	28.00	5.15
A4	33.38	27.00	6.38
B1	33.80	25.62	8.18
B2	33.95	27.37	6.58
B3	32.75	25.00	7.75
B4	33.63	22.62	11.01
B5	34.53	27.37	7.16
C1	33.07	28.22	4.85
C2	34.00	22.47	11.53
C3	33.15	28.22	4.93
C4	34.65	22.32	12.33
C5	35.28	24.55	10.73
Transect A	33.80	27.00	6.8
Transect B	34.70	22.80	11.9
Transect C	35.40	22.30	13.1

showing that Transect C had larger seasonal fluctuations than Transect B than Transect A. This reflects the fact that Transect C had a greater covering of coarse sediments in which the interstitial salinity was easily influenced by external conditions. Also Transect C was closer to the mouth of the estuary and hence more susceptible to the larger fluctuations in the estuarine water.

Over the two years of sampling the interstitial salinity was lower during the autumn-winter months of 1976-77 than 1975-76.

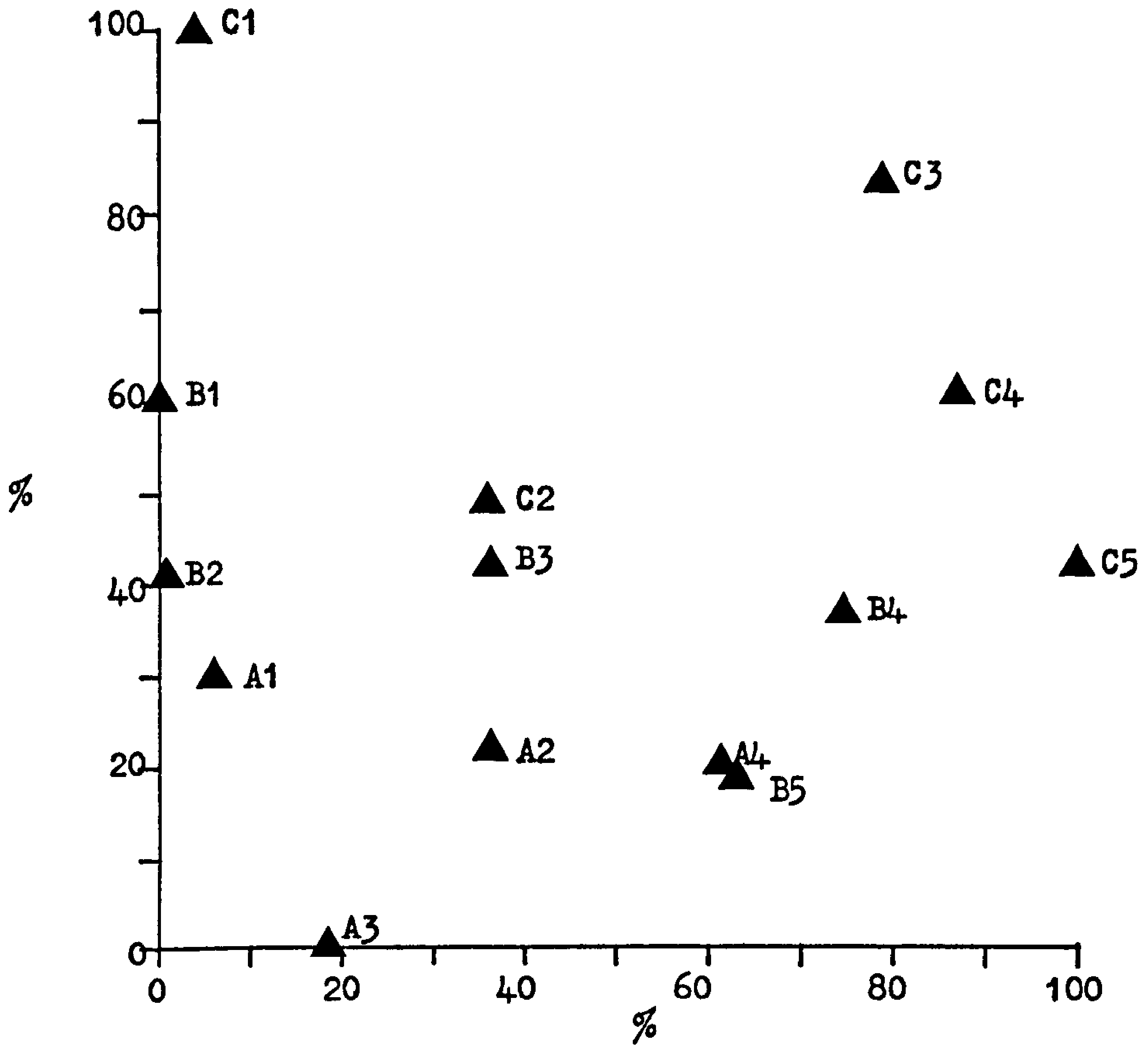


Figure 2.12 Environmental Factors : Plot of Values From Principle Components Analysis Indicating Levels of Similarity Between the Stations Based on the Environmental Variables Used in the Pearson Correlation Analysis.

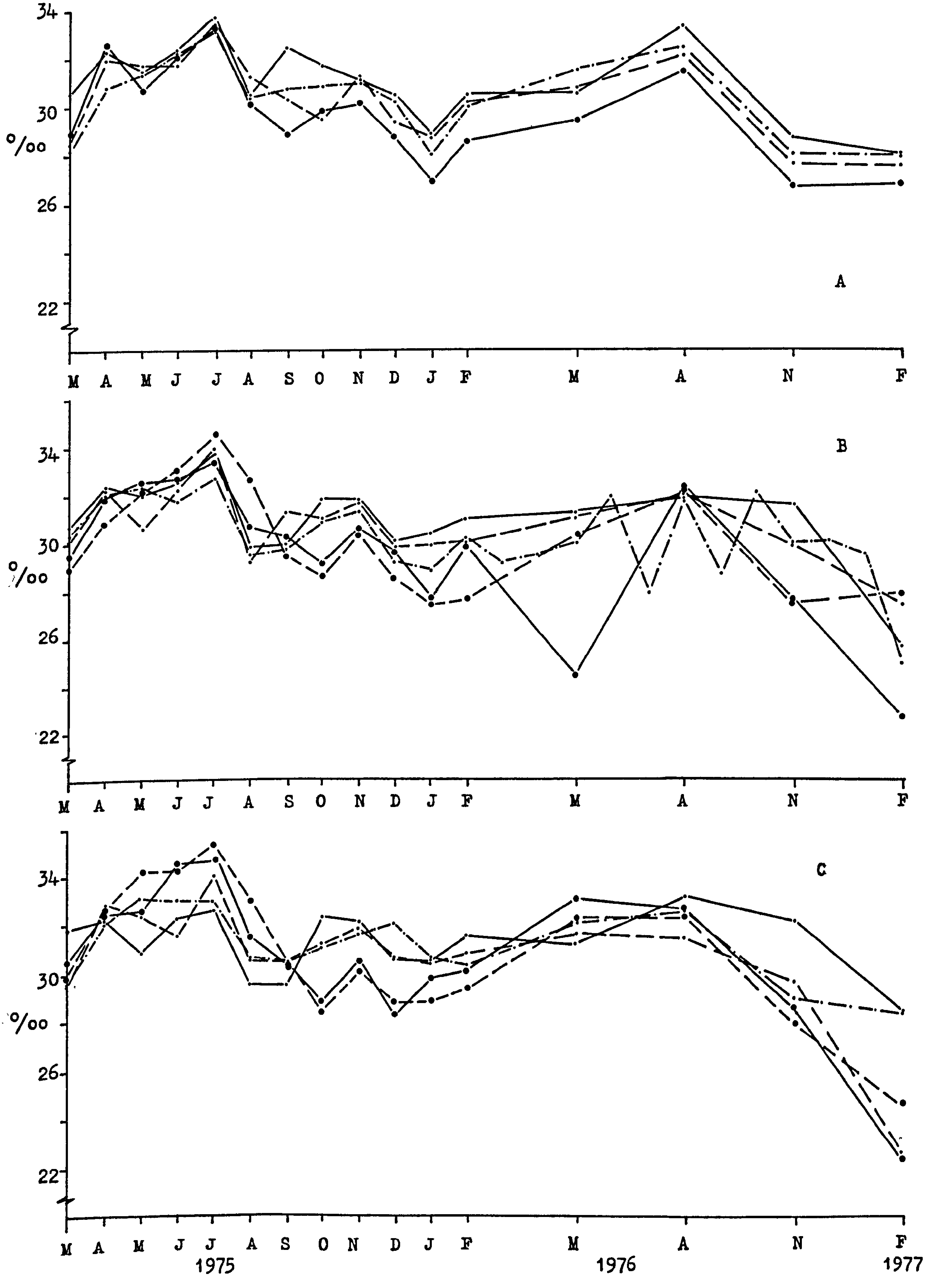


Figure 2.13 Environmental Factors : Interstitial Water Salinities (°/oo).

Legend as Figure 2.5.

2.4.2.2. Estuarine Water Salinity.

The estuarine water (at spring high tide) shows greater fluctuation in salinity than interstitial water but not normally a greater range of salinity (Fig. 2.14a). However, the water at high tide would have a higher salinity than at low tide due to the influences of marine inflow. Therefore it would be expected that, when compared to the tidal cycle of the overlying water salinity, the interstitial salinity would be relatively uniform (Reid, 1930, 1932; Alexander et al, 1932 and Capstick, 1957). When exposed, the interstitial salinity of the low-shore stations will be greater than that of the estuarine water. At high tide however, the upper-shore stations will have an interstitial salinity lower than the estuarine water (Alexander et al, 1932; McLusky, 1971).

The interstitial salinity for January 1976 (as a percentage of the overlying water salinity) was incorporated into the correlation matrix and only found to be correlated with the tidal height (-***)(and hence exposure time). Green (1968) states that the relationship between the overlying and interstitial salinities is influenced by the slope of the shore, i.e. the interstitial water will drain away more easily on a steep shore and be replaced by freshwater. It is considered, however, that this will be the result of coarse deposits being on a steep shore such that the relationship between the salinity and slope is an indirect one.

Smith (1956) and Capstick (1957) suggest that dessication (evaporation) during low tide periods would affect interstitial salinities to a lesser or greater degree. It is considered that

Figure 2.14 Environmental Factors:

(a) The Salinity of the Estuarine Water at HWS;

(b) The Temperature of the Estuarine Water at HWS;

(c) The Air Temperature at Each Sampling Occasion (mean, minimum and maximum).


36
34
32
30
°/oo
28
26
24
22
16.5
(a)
M A M J J A S O N D J F M A M J J A S O N D J F
20
18
16
14
°C
12
10
8
6
4
(b)
M A M J S O N D J F M A M J J S O N D J F
20
18
16
14
°C
12
10
8
6
4
2
0
(c)
M A M J J A S O N D J F M A M J J A S O N D J F
1975
1976
1977

evaporation would be far greater in coarse sediments. Capstick (1957) records that evaporation can be so great during summer periods of emersion that salt crystals are formed on the sediment surface. Southward (1952), however, suggests that evaporation at the surface of a marine deposit may only cause a slight increase, of not more than 1.0°/oo, above the sea value. The corresponding estuarine situation is unknown.

In the present study, the interstitial salinity followed loose negative relationships with shore slope and particle size (Fig. 2.15a, b) such that the salinity decreased as the latter variables increased. The differing positions of the transects within the estuary is reflected in the salinity/M.P.D. relationship and, to a lesser extent, in the salinity/shore slope relationship.

2.4.3. Temperature.

The data present a typical North Temperate seasonal cycle for both the air and water temperatures (Fig. 2.14b & c).

2.4.4. Water Analysis.

Although the monthly levels were rather erratic, some seasonality may be observed in that CHO. was higher in the summer than the winter and vice versa for Org. C. (Fig. 2.16 data in Appendix 2.4). These erratic patterns were expected as the levels of particulate matter were the product of the seasonal cycles of phytoplankton, zooplankton, macroflora and benthic macrofaunal activity together with climatic factors and wave action. Comparable studies also have obtained erratic patterns for particulate matter (Stephens et al, 1967; Leach, 1971; Steele and Baird, 1972; Heinle and Flemer, 1976). The

Figure 2.15 Environmental Factors : Spatial Analysis:- The Relationships Between Interstitial Salinity (as a Percentage of the Overlying Water Salinity) and (a) Median Particle Size and (b) Slope of Shore.

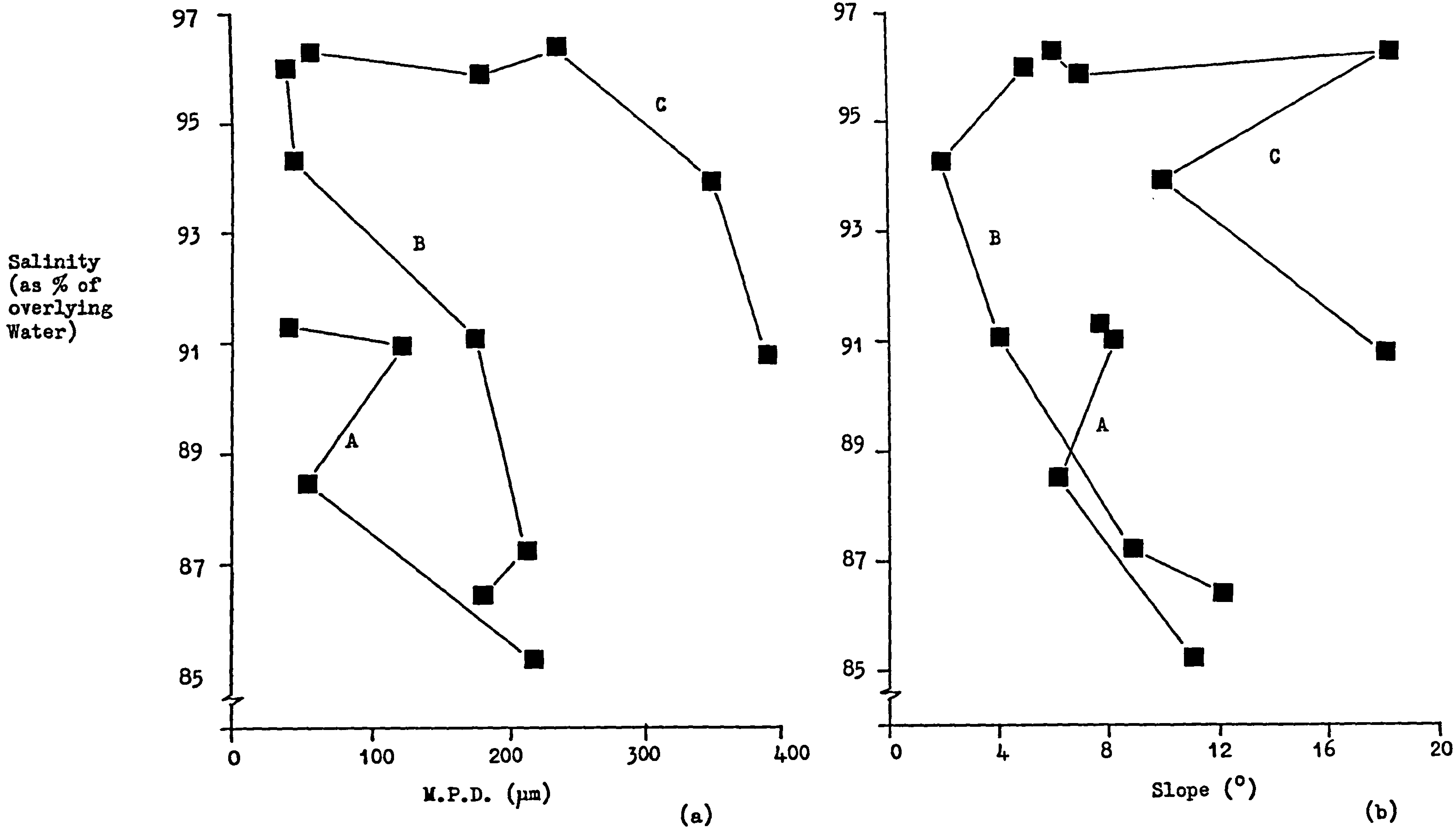

Salinity
(as % of
overlying
Water)
97
95
93
91
89
87
85
0
100
200
300
400
M.P.D. (μm)
(a)
A
B
C
97
95
93
91
89
87
85
0
4
8
12
16
20
Slope (°)
(b)
A
B
C

Figure 2.16 Environmental Factors : The Levels of Suspended Particulate Carbohydrate (C.H.O.) and Organic Carbon (Org. C.) in the Flow Tide at Each Sampling Occasion.


;. C.
l^{-1}
C.H.O.
mg l^{-1}
1.2
1.0
0.8
0.6
0.4
0.2
0
2.4
2.0
1.6
1.2
0.8
0.4
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

patterns observed appear to be more erratic when studying inshore, intertidal or estuarine areas than offshore open seas (Steele and Baird, 1965).

For much of the sampling period there was an inverse relationship between the Org. C. and CHO. levels. This is in contradiction to the results found by Marshall and Orr (1962, 1964) although they stressed that the effect of detritus on the levels was unknown. The large amounts of detritus present in estuarine water may distort any correlation between the levels. Marshall and Orr (1962), after working on diatom cultures, suggested that CHO. usually accounted for 20 - 30% of the organic matter available. However, in their later paper (1964) the carbohydrate levels during the spring diatom bloom greatly exceeded those of organic carbon. They suggest that although the increase in diatom numbers is accompanied by increases in both Org. C. and CHO., the relationship between the three varies greatly. In the case of the present study the only relationship between Org. C. and CHO. is a tentative inverse one. It may be suggested that the CHO. values reflect phytoplankton levels and Org. C. reflect detritus levels. The factors causing maxima in each of these levels do not occur together.

The carbohydrate values obtained were usually higher than the Org. C. ones which, as the CHO. method measured other matter in the water besides carbon, was to be expected. The organic carbon values however will also include the carbon in the CHO. If both values were expressed as glucose, then as 300µg Org. C $\equiv$ 750µg glucose, the Org. C. levels would always be greater than the CHO.

The spatial water analysis, on the flow tide samples obtained during July, 1976, show the magnitude of difference in CHO. and Org. C. with changes in station (Table 2.5). The Org. C. levels varied from 0.46 to >1.51 mg l^{-1}, while the CHO. levels varied from 0.88 to 11.85 mg l^{-1}. The date at which the samples were obtained was chosen randomly and the values encompass those encountered at Station B4 during the monthly sampling occasions. As the amounts of allochthonous material in the flow tide water may be uniform, the data give an indication of the amount of organic material resuspended by the flow tide.

When incorporated into the correlation matrix (Fig. 2.9) the CHO. levels were inversely related to shore slope; this may suggest that the incoming tide had resuspended material from the shallow slope (low-shore) areas at which large amounts of material had collected. Similarly, the areas of greatest sediment C/N levels (and sediment %C.) had the highest suspended organic carbon levels.

2.4.5. The Temporal Analysis of Environmental Factors.

In order to describe the temporal variation within the environmental factors at each station, those factors monitored monthly, i.e. interstitial and estuarine water salinity; mean temperature; sediment water, carbon and nitrogen contents; sediment C/N levels; and suspended particulate Org. C. and CHO., were incorporated into correlation matrices (Fig. 2.17). (The monthly data of mean temperature, estuarine water salinity, CHO. and Org. C. were assumed to be the same for all stations.) A matrix was created for each station together with a further matrix incorporating all stations' data.

Table 2.5 The Suspended Particulate Carbohydrate and Organic Carbon Levels (July, 1976).

Station	Organic Carbon mg l^{-1}		Carbohydrate mg l^{-1}	
	$\bar{x}$	S.D.	$\bar{x}$	S.D.
A1	0.986	0.113	1.801	0.035
A2	0.706	0.048	2.295	0.357
A3	1.024	0.005	1.599	0.293
A4	1.164	0.058	1.239	0.309
B1	1.515	0	4.926	0.164
B2	1.515	0	6.190	0.505
B3	1.433	0.142	11.851	0.560
B4	0.253	0.263	7.618	0.498
B5	1.515	0	5.921	0.220
C1	0.533	0.610	2.282	0.288
C2	1.515	0	2.933	0.774
C3	0.839	0.050	1.926	0.124
C4	0.460	0.109	3.712	0.754
C5	1.259	0.034	0.881	0.098

A1

	Water Sal.	Temp.	CHO.	Org.C.	C/N.	%N.	%C.	$\%H_2O$.
Int. Sal.	+	+++						
$\%H_2O$.					−	+++	+++	
%C.						+++		
%N.					−−−			
C/N.			+					
Org.C.								
CHO.								
Temp.	+							
Water Sal.								

A2

	Water Sal.	Temp.	CHO.	Org.C.	C/N.	%N.	%C.	$\%H_2O$.
Int. Sal.	+	+++						
$\%H_2O$.			++		+		+	
%C.				+	++	+		
%N.								
C/N.								
Org.C.								
CHO.								
Temp.	+							
Water Sal.								

A3

	Water Sal.	Temp.	CHO.	Org.C.	C/N.	%N.	%C.	$\%H_2O$.
Int. Sal.	+	+++						
$\%H_2O$.	+		++			+++	+++	
%C.	+				+++	+++		
%N.	+		+					
C/N.								
Org.C.								
CHO.								
Temp.	+							
Water Sal.								

A4

	Water Sal.	Temp.	CHO.	Org.C.	C/N.	%N.	%C.	$\%H_2O$.
Int. Sal.		+++						
$\%H_2O$.						+++	+++	
%C.						+++		
%N.								
C/N.								
Org.C.								
CHO.								
Temp.	+							
Water Sal.								

ALL STATIONS

	Water Sal.	Temp.	CHO.	Org.C.	C/N.	%N.	%C.	$\%H_2O$.
Int. Sal.	+++	+++				++	++	+
$\%H_2O$.					+++	+++	+++	
%C.		+			+++	+++		
%N.		+						
C/N.	+							
Org.C.		+	−−−					
CHO.	+++	+++						
Temp.	+++							
Water Sal.								

Figure 2.17 Environmental Factors: Temporal Data Analysis - Pearson Correlation Matrices for Each Station and for 'All Stations' Data Combined; Only Significant Correlations Given, (+ or − = significant; ++ or −− = very significant; +++ or −−− = highly significant, as figure 2.9).

Abbreviations: -

Int. Sal., Water Sal. = interstitial and estuarine water salinity (o/oo) respectively;

$\%H_2O$., C/N. = surface-sediment water content and carbon:nitrogen value respectively;

%C., %N. = surface-sediment carbon and nitrogen contents respectively;

Org.C., CHO. = suspended particulate organic carbon and corbohydrate values (mg l^{-1}) respectively;

Temp. = mean water and air temperature ($^{o}C.$). All monthly values used.

Figure 2.17 continued.

The intercorrelations shown on a spatial basis between sediment %H_2O., %C. and %N. were also found to occur at all stations over the year such that an increase in any one of these factors was related to increases in the others. The C/N levels at the low-shore stations decreased with increases in sediment %C., %H_2O., %N. content, whereas at the upper-shore stations that trend was reversed. This may possibly be attributable to the larger populations of decomposers at the lower-shore stations which would colonise debris at a faster rate than at the upper-shore.

At the majority of the stations, the interstitial salinity increased with temperature and at several stations on Transect A only the interstitial and overlying salinities were directly related. The pooled station data also show the direct relationship between temperature and overlying water salinity as expected. The mean temperature was also directly related to the overall levels of sediment %C. and %N. and the water particulate CHO. and Org. C. (but to a lesser extent with the latter than with the CHO. level). The correlation analysis again showed the inverse relationship between the particulate Org. C. and CHO. levels (see Section 2.4.4.).

2.5. Discussion.

In describing the environmental differences within an intertidal area, it is possible to consider the interrelationships between the environmental physico-chemical factors (e.g. substrate type, immersion period, shore slope, salinity) and the biological factors (quantity and quality of available organic material as potential food for macroinvertebrates).

Torry Bay has fine sediments at the low shore areas and coarse ones at the upper shore; with a progression away from the main deepwater channel within the estuary the sediments were less well-sorted and increasingly negatively skewed. These characteristics differ from a usual estuarine shore where the decreasing tidal currents, in areas away from the main water flow, increase the deposition of fine material which in turn increases the sorting and decreases the negative skewness (Green, 1968; Green, 1975; Perkins, 1974; Beukema pers. comm.). However, although the overall structure of the Bay differs from many estuarine areas, environmental factor interrelationships were observed which occur on all particulate shores.

The particle size of a deposit both influenced and was influenced by other factors. The current velocity, although not measured in the present survey, determines the size of particles settling out of suspension (Newell, 1970). The water content of a deposit was inversely related to the particle size; this was the combined result of the permeability and pore size, which are directly related to the grain size (Wolff, 1973), and the shore slope which was related to the water currents over an area (see also Newell, 1970). During periods of exposure, a low deposit water content would result in stress in the infauna in which water was necessary for gaseous exchange.

The particle size and water content of a substrate also influenced sediment stability. Fine deposits are usually more stable than coarse ones due to the larger interstitial spaces in the latter (Webb, 1958; Green, 1975); however, where a substrate was fine and had a very high water content (>70%) then the fluidity of the deposit facilitates sediment transport. Movement that covered a station with an abnormal type of deposit for any length of time, e.g. Station C2 and, to a lesser extent, B3, will affect the fauna. A covering of muddy areas by less-stable sand resulted in decreasing the amount of food available to support an existing deposit-feeding population. Similarly, suspension-feeding animals living in a coarse sand area and smothered by fine sediment would suffer stress or mortality. The effects on the infauna of such sediment movement will vary with season (Levinton, 1972) and increase with a decrease in the animals' physiological condition.

The particle size was also inversely related to the organic matter levels within a sediment. This is the result of two factors; firstly, fine particles have a large surface area/volume ratio (cf. large particles) which presents a large substrate area for microfloral colonisation and therefore results in high nitrogen values; secondly, a depositing environment receives large amounts of organic matter which then accumulates because of the anaerobic conditions and low flow rates through the fine sediments (Webb, 1958, 1969; Brafield 1964). The latter factor results in the presence of large amounts of sediment organic carbon.

While there is no doubt that fine sediments had more organic matter than coarse ones, those levels were distorted and the difference enlarged by the presence of increased meiofaunal and juvenile macrofaunal populations in fine sediments. These factors also reinforce the seasonality patterns on the organic matter levels. It is considered, therefore, that more of the measured organic matter in coarse sediments is available to deposit feeders than in fine sediments. However, all present methods of measuring deposit feeders' food would encounter these problems. In addition, if the C/N values estimate the nutritional value of that food (Russell-Hunter, 1970) then although more organic matter was available at the low shore, fine deposit stations, that material had a higher C/N value and was therefore less nutritious than the potential food for deposit feeders at the high shore, coarse sediment stations.

A further consideration when comparing fine and coarse deposit environments is the relationship between the sediment water and organic matter contents. This study, as all others, has determined the organic matter content as a percentage of the deposit dry weight and then considered the large differences between various sediment types. However, when the water content is incorporated into the calculation, as the water content increases with a decrease in particle size then, on a wet weight basis, the difference in organic matter levels between various sediment types is decreased;

e.g. considering a hypothetical coarse sediment (25%H_2O) and fine sediment (60%H_2O) ;

As dry weight:	Fine Sediment	Coarse Sediment	Ratio Coarse/Fine
%C.	5.5	0.5	11:1
%N.	0.25	0.04	6.25:1
As wet weight:			
%C.	2.2	0.38	5.8:1
%N.	0.10	0.03	3.33:1

so that the difference between coarse and fine sediments on a dry weight basis is approximately twice as large as on a wet weight basis. This has major implications when considering the amount of material that deposit feeders in different sediments have to ingest to obtain an amount of organic matter. However, because of the necessity to standardise the methods and results, only the dry sediment levels are used in the present study.

The amount of matter, accumulated by primary production in estuarine deposits, will be relatively small when compared to the material entering the sediment either as detritus from local macroflora (Z. marina or algae) or as allochthonous material from freshwater, saltmarsh or marine areas. The spatial and temporal variation in the levels of sediment organic matter was similar to that found in other areas (e.g. Longbottom, 1970; Newell, 1970). The sediment %N. and %C. on Torry Bay varied similarly and widely over the year whereas Longbottom (1968 in Newell, 1970) found that whilst the nitrogen content varied slightly over the year, the carbon content widely fluctuated. The time of the Torry Bay maximal carbon values varied with each station and was probably related more to the variation in rates of detritus falling onto the sediment and accumulating there from Z. marina and other sources, than to the phytoplankton bloom. Brown diatomaceous blooms were, however, evident on the fine sediments during the summer and would have contributed to the measured organic matter levels. Longbottom (1968) attributed the maximal sediment organic matter levels in May and September to the corresponding phytoplankton bloom.

Recent investigations emphasise the importance of macrophytes as detritus producers in estuaries (e.g. Teal, 1962; Fenchel , 1970, 1972; Mann, 1972). Detritus production, by the physical breakdown of macrophytes by detritivores or wave action and the subsequent colonisation by microorganisms, enables large deposit- and detritus-feeding populations to be supported in estuaries and coastal regions. Levinton (1972) and Sand-Jensen (1975) emphasise the importance of Z. marina in detritus production in supporting a large macrofaunal biomass. Although the main detritus production is at the end of the growing season, there is a continual export of detritus from Z. marina leaves which are discarded after becoming covered with a diatom crust. The large turnover of leaf material and the accumulation of root material over the growing season are indicative of the large productivity of Zostera beds (Sand-Jensen, 1975). Adams and Angelovic (1970) further suggest that as Z. marina beds contain at least four times as much dead as living plant material, then the detritus could provide most of the nourishment for the local infauna. They also conclude that some species obtained more nourishment from the detrital substrate than from the associated bacteria. This is contrary to the accepted conclusions of Newell (1965); Odum and De la Cruz (1967) and Fenchel (1970).

Detritus is also produced by saltmarshes, although the amount of saltmarsh production exported to the estuary is dependent upon the tidal flushing and tidal height of the marsh area (Heinle and Flemer, 1976). Teal (1962) found that 45% of the production was exported from a saltmarsh with a tidal amplitude of 2-3m and subjected to a large amount of flooding. However, the export from a less-well flooded marsh (where the tidal amplitude is less than 1m) can be as little as 1% (Heinle and Flemer, 1976), although that export will increase following ice-scouring and stormy weather. The saltmarshes on the upper-reaches of the Forth estuary also have a low tidal amplitude although an estimate of material from those areas cannot be made.

Heinle and Flemer (1976) found that while the growth of the marsh macroflora is greatest during the spring and early summer, decomposition is more evenly distributed although the amount of dead standing material in a saltmarsh decreases substantially in late summer. It is considered that these conclusions will apply to the Forth saltmarsh to estuary system and to the production of detritus by _Z. marina_ beds.

The water-borne detritus may be regarded as potential food for suspension feeders both before it initially settles out of the water column and during resuspension by water currents. The estimated monthly suspended particulate matter levels were assumed to be representative of those experienced over the whole intertidal area. The monthly samples were taken from a clean sand area (which supported a filter-feeding macrofaunal population intermediate in size for the Bay (see Chapter 4)), an area where water movement was relatively fast causing little of that suspended material to be deposited permanently. It is difficult to suggest what proportion of the material measured was allochthonous and what had been resuspended by the tide. The spatial analysis indicated that the major part had been resuspended and the greatest levels occurred over the fine deposit areas. All suspended material is available to the suspension feeders depending on the preference for different components of that material.

The amounts of suspended organic carbon measured both over the bay and over the year were similar to the levels encountered in other inshore or estuarine areas (see Table 2.6a). However, while the annual range of carbohydrate values was similar to that of other comparable areas, the range of values encountered in the bay encompassed other values and had a maximum value that was much higher than recorded for other areas (see Table 2.6b). The irregular annual cycles of suspended organic carbon and carbohydrate found in this study were similar to those found by Leach (1971) and Heinle and Flemer (1976) respectively. The estuary studied by the latter authors had many similarities with the Forth estuary and produced a seasonal pattern for carbohydrate which agrees with that obtained in the present study (Fig. 2.18). The annual pattern of suspended organic carbon found in the present study (i.e. a polymodal annual curve with maxima in May, August and November) was similar to that for a shallow bay in Canada which had seasonal maxima during May-July and October-December (Stephens et al, 1967). The erratic patterns observed in these studies could possibly be attributed to differences in wave action, precipitation, time in lunar cycle at sampling, flow rate and flushing rate of the estuary, and the degree of saltmarsh and Zostera bed flooding between sampling.

Table 2.6 Comparable Levels of Suspended Particulate Matter.

Location	Levels (mg l^{-1}).	Author
(a) Organic Carbon		
Forth Estuary	0.1-1.1 (up to 1.5 spatially)	This Study
Patuxent River Estuary	2.0-9.9	Heinle and Flemer (1976).
Arctic Surface Waters	0.008 maximum	Holm-Hansen (1972).
Californian Coast	0.05-0.3 Maximum in summer	" "
Ythan Estuary	1.0-3.0 Maximum in spring	Leach (1971).
Pacific Open Ocean	0.07 maximum	Handa and Tominga (1969).
Departure Bay, B.C.	0.2-0.7	Stephens <u>et al</u> (1967).
Loch Striven, W. Scot.	0.2-2.0	Marshall and Orr (1964).
English Channel	0.98-2.50	Corner (1961).
Aberdeen Bay	0.45-1.10	Steele and Baird (1961).
Long Is. Sound	1.0-3.0 Maximum in summer	Riley (1969).
Wadden Sea	4.0 maximum	Postma (1954).
(b) Carbohydrate		
Forth Estuary	0.2-3.0 (up to 11.85 spatially).	This Study.
Patuxent River Estuary	0.8-4.2	Heinle and Flemer (1976).
Pacific Open Ocean	0.002-0.005	Handa <u>et al</u> (1972).
Loch Striven, W.Scot.	0-1.83	Marshall and Orr (1964).

Figure 2.18 Environmental Factors : A Comparison of the Suspended Particulate Carbohydrate Levels Between the Forth Estuary (1975-76 Data) and the Patuxent Estuary (Heinle and Flemer, 1976, 1973-74 Data; See Text).


3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0.3
0
C.H.O.
mg l⁻¹
J
F
M
A
M
J
J
A
S
O
N
D
J
F
1973-74 Patuxent
1975-76 Forth

The lack of any consistent pattern between the Org.C. and CHO. levels encountered in the present study was also found by Heinle and Flemer (1976) and indicates that little further comment can be made on the type of detritus and phytoplankton suspended over the intertidal area. In addition, Heinle and Flemer (1976) found no consistent difference in the levels of Org.C. and CHO. between the ebb tide; it may therefore be confirmed that the measured levels are indicative of the potential levels of suspended food.

The amount of resuspended particulate matter is affected firstly by "bioturbation" (sediment reworking by the infauna), which is therefore directly proportional to the size of the infaunal population (Levinton, 1972; Rhoads et al, 1976), and secondly by the degree of compaction (or water content) of a deposit (hence large amounts of water-borne particulate material occurred over shallow sloping, fine sediment areas). As an indication of the level of bioturbation, Bubnova (1972) estimated that a population of 750 Macoma balthica m^{-2} would reprocess 1kg sediment per month; deposit-feeding populations occur at densities greater than this in the area studied (see Chapters 3 and 5). In addition to resuspension increasing the availability of detritus to suspension feeders, it also increases the breakdown of detritus by aerobic bacteria and wave action (Rhoads et al, 1976).

The salinity regime of an estuary also influences organic detritus production and its breakdown by microbial populations. Heinle and Flemer (1976) consider that the salinity of the saltmarsh may affect the level of material exported and suggest that their saltmarshes, as in the Forth estuary, were in the lower reaches of the estuary and were less productive than marshes in more saline areas (see also Teal, 1962). The number of bacteria attached to particles also declines with salinity (Meadows, 1965) and low salinity muds may therefore be less nutritive and have a correspondingly higher C/N value. This is possibly shown in Torry Bay deposits where Transect A had a higher average C/N value than Transect B or C. However, considering the small differences in salinity between the transects, it is more likely that the higher ratios were attributable to the large organic carbon levels caused by greater quantities of Enteromorpha, Zostera and finer sediments on the transect.

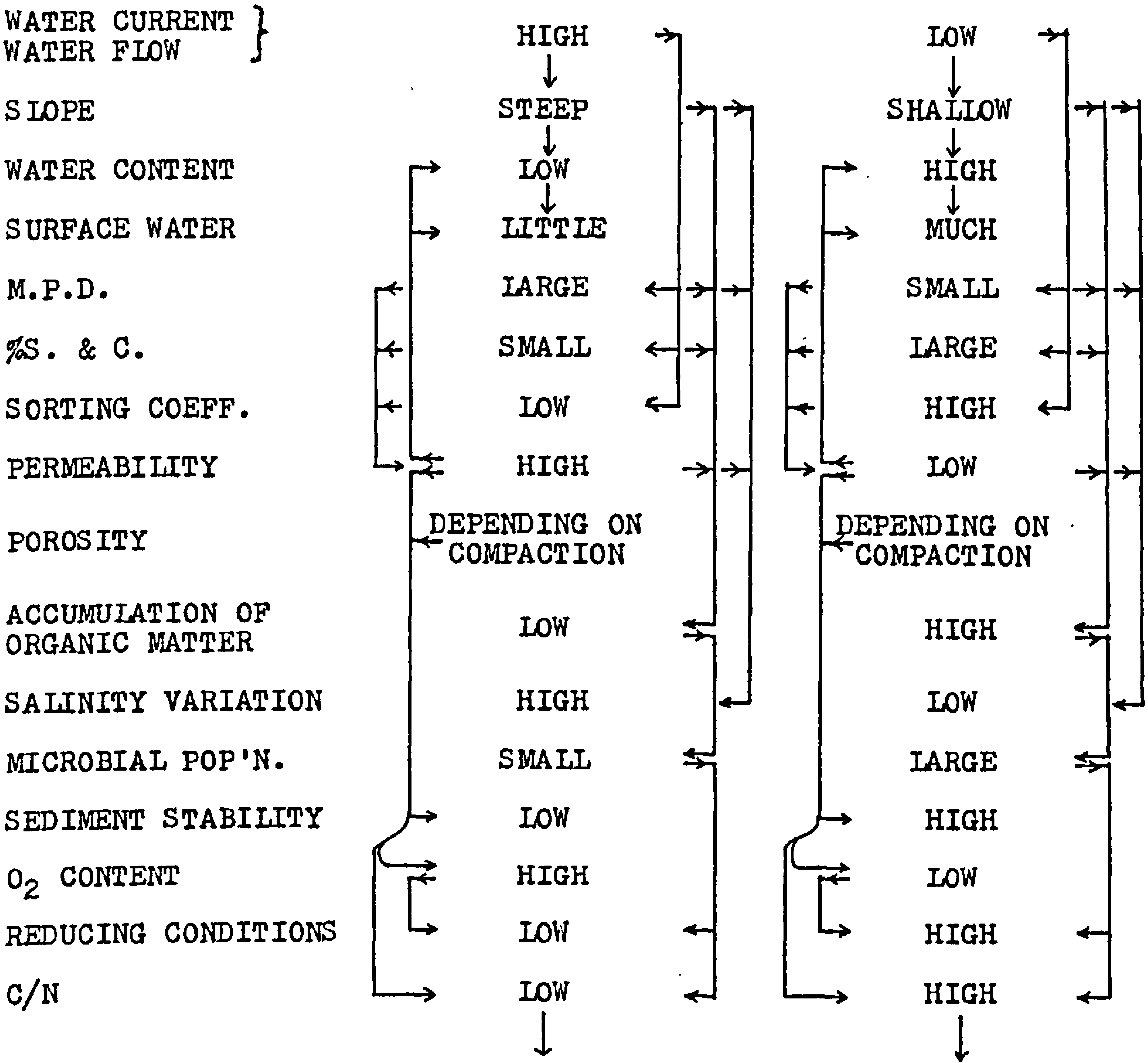
The interstitial salinity was influenced by, and was the result of, the overflowing water salinity and the immersion period (see also Smith, 1956). This, together with the fact that fresh water could be replaced in deposits easily by salt water but not vice versa, resulted in the interstitial salinities being greater than the average overlying water salinity for the majority of deposits and sampling occasions (see also Southward, 1953; Wolff, 1973). The interstitial salinity at deeper levels in the sediment was buffered from tidal and other large variations of the overlying salinity (see also Alexander et al, 1932; Reid, 1932; Smith, 1956; McLusky, 1971; Wolff, 1973). The infauna are therefore protected from any large or abrupt salinity changes.

The overall salinity pattern of an intertidal area also varies with its position within an estuary (Smith, 1956). Torry Bay has salinity characteristics intermediate between those for the lower and middle reaches of an estuary (given by Smith, 1956) as it (i) has relatively high salinities; (ii) has interstitial salinities which have marked variation with tidal height; and (iii) is slightly affected by fresh water flooding.

The interstitial salinity in the deposits studied here reflect annual fluctuations in the overlying salinity (see also Wolff, 1973). Wolff (1973) also showed that sandy sediments' interstitial salinity fluctuated more than that in fine sediments. This, together with the facts that the most saline water occurs at high tide and that on Torry Bay the coarse sediments occur at high-shore levels, result in the subjection of the upper-shore infauna to large salinity fluctuations. However, as bioturbation increases the mixing of interstitial and overlying water (Smith, 1956), then the infaunal populations in the fine sediments may be affected by some salinity fluctuations.

The differing salinity regimes of the various areas of the mud flat may not, however, have been large enough to influence the growth or ecology of the macrofauna (see also Savilov, 1953). The overall range of 28-34°/oo is narrow in relation to the salinity tolerances of estuarine macrofauna; at any one time the area may be regarded as being homogeneous with respect to salinity. Kinné (1967), however, suggests that differences of 1°/oo may be sufficient to account for physiological and ecological changes in estuarine populations.

In conclusion, although many seasonal and spatial changes in the environmental factors are discussed further in relation to the macrofauna (Chapters 3, 4, 5), the interrelationships discussed above between those factors may be summarised by simple flow diagrams (Fig. 2.19). While it is not usually a single environmental factor which influences the estuarine fauna



Sediment nutritious (quality not quantity of organic matter)

e.g. A2*, A3*, A4*, B4, B5*, C3, C4, C5*.

* = with Z. marina

ON TORRY BAY - ALL MID TO UPPER SHORE.

Sediment unnutritious (quantity not quality of organic matter)

e.g. A1, B1, B2, B3, C1, C2.

ON TORRY BAY - ALL LOW TO MID SHORE.

Fig. 2.19 Environmental Interactions.

but a combination of numerous factors counteracting, supporting and modifying each others' physical and physiological effects (Kinné, 1967), the above interrelationships indicate that the most important intertidal factor is the water speed over an area. This factor influences factors which in turn modify other factors. Southward (1953); Brawn et al (1968); Pearson (1970) and Wildish (1977), reach the same conclusion regarding the importance of water currents on the sediment properties and on the macrofauna.

Chapter 3. The Production Ecology of a Deposit-feeding Bivalve, Macoma balthica.

3.1. Introduction.

The deposit-feeding baltic-tellin, Macoma balthica L., is one of the most common and abundant estuarine and brackish water infaunal species in the Northern Hemisphere; it has been studied in areas ranging from California and Massachusettes on the western and eastern North American seaboards respectively to the Arctic Circle and from the West European and North African coast to the Baltic and Northern Soviet coastline (e.g. Segestråle, 1960; Clay, 1967b; Vassallo, 1969; Myren and Pella, 1977).

The bivalve occurs in densities upto 3000 adults m^{-2} (Fraser, 1932; Tunnicliffe and Risk, 1977) and therefore is an important member of the estuarine trophic web (e.g. Green, 1968; Chambers and Milne, 1975b). The success of the species within the depositing environment is due to its variable mode of feeding (see Section 6.2.) and its wide temperature and salinity tolerance ranges (e.g. McErlean, 1964; Gilbert, 1973). The various feeding methods employed by the species enable it to utilize the large resources of the decomposer part of the ecosytem (e.g. Newell, 1965; Tunnicliffe and Risk, 1977) thus returning energy to the predators at the higher trophic levels. The species therefore contributes greatly towards supporting large wading bird and fish populations inhabiting estuaries (e.g. Milne and Dunnet, 1972; Goss-Custard et al, 1977).

However, despite the importance of the species, many early studies were restricted to determining the abundance and zonation of the species within an intertidal area (Stephen, 1931; Brady, 1932). Following these studies, growth was quantified and growth variation within the geographical distribution was studied (Vogel, 1959; Segestråle, 1960; Gilbert, 1973); the species reproductive cycle determined (Caddy, 1967; Lammens, 1967); and the mode of feeding also studied (e.g. Brafield and Newell, 1961; Bubnova, 1972). The species energetic requirements, energy budget parameters, annual metabolic cycle and population dynamics, and role in the intertidal ecosystem have only recently been studied in further detail (Chambers and Milne, 1975b; Warwick and Price, 1975; De Wilde, 1975; Beukema _et al_, 1977).

While information regarding many aspects of the animals' ecology and physiology and single estimates for condition, growth and production have been obtained for different geographical areas, the variation in these parameters within an area attributable to small differences in habitat type had not previously been studied and quantified, with the exception of growth recently studied by Beukema _et al_ (1977).

Although, as an estuarine animal, the species may occur in areas subject to high effluent outfall, the effect on the species of living under polluted conditions has been little considered (Fraser, 1932; Shaw _et al_, 1976). As a result of the animals' dependence on the sediment during feeding, burrowing and respiration and because pollutants are adsorbed on to the high quantities of silt in the water column which subsequently settles and becomes available to the deposit feeders, then the biology of _M. balthica_ within an industrialised estuary may be adversely affected. The present study was partly initiated as the result of the unusual production ecology of _M. balthica_ in the estuarine Firth of Forth shown by the studies of Allan, 1973; Teare, 1975 and McLusky and Allan, 1976. However, before the anomalous growth and production found by these authors could be attributed to the industrialisation of the estuary, it is necessary to determine whether that anomalous growth, etc. persisted throughout the whole intertidal area and to identify the environmental causes of the variation in the production ecology of the species.

3.2. Materials and Methods.

Following the collection and treatment of the samples (see Section 2.2.2.), the growth, condition and production of the population was estimated. The linear shell measurements and weights of dried shell and flesh have been used throughout the survey as being the quickest method by which large numbers of animals could be analysed. Lammens (1967) suggested that as shell growth occurred in more than one direction the surface projection area of the shell should be used in preference to single measurements of height or length (as the dorso-ventral and anterio-posterior axes respectively). Lammens (1967), however, obtained a linear relationship between projection area and shell height; the additional analysis regarding the former therefore appears unnecessary. Fairbridge (1952) found a good correlation between the length, height and thickness of bivalve shells and suggested that proportional growth in all directions was characteristic of bivalve shells.

Whilst it is desirable to express production parameters in terms of energy units (Crisp, 1971), the calorific determination of the species studied was considered unnecessary as adequate calorific values exist for the species and also the majority of comparable data are given in gravimetric units. A calorific value of 4.55 K cal $g(flesh)^{-1}$ obtained as the mean of the available data for M. balthica is considered accurate, (Gilbert, 1973; Thayer et al, 1973; Chambers and Milne, 1975b; Cederwall, 1977; De Wilde and Berghuis, 1978) and can be used as a conversion index.

3.2.1. The Use of Flesh Condition and Standard Size and Weight Animals.

Several values have been used to describe fully the relative proportions of shell and flesh weight within an individual, namely: the condition factor, the flesh and shell weight of a standard-size animal, the flesh and shell weight of standard age animals.

The animals condition factor (CF) may be regarded as being an indication of their physiological state; it will reflect the variation in the amount of stored energy in the individuals and may be considered as the animals' "metabolic response to environmental conditions" (Peddicord, 1977). This index was initially used in fisheries biology to express "fatness" in fish but has been adopted, in molluscan studies, as a relative measure of the amount of flesh within a volume of shell. It was calculated as :-

$$CF_L = \frac{FDW}{L^3} \times 1000$$

$$CF_H = \frac{FDW}{H^3} \times 1000$$

where CF_L = condition factor by length.
CF_H = condition factor by height.
FDW = flesh dry weight (mg).
L = length (mm).
H = height (mm).

The change in length (or height) in bivalves with successive sampling occasions only indicates positive or no growth; therefore a measure of flesh change (as condition or flesh change within animals of a standard size or age) must be used as a measure of positive or negative growth, the latter being termed emaciation (De Wilde, 1975). In the majority of areas and sampling occasions the condition factor relationships with respect to length or height were not statistically significant such that the condition factor could therefore be expressed as a mean value. This is in agreement with Beukema and De Bruin (1977) who found flesh condition to be nearly independent of length in Macoma, and De Wilde (1975) who found very low regression coefficients (of -0.04) for this relationship although he does not state whether such a value was significant.

The condition factor, however, will also show disproportionate growth of an animals' shell and flesh, i.e. if energy is diverted into shell growth to the detriment of flesh growth then the condition would decrease and erroneously indicate emaciation. In order to overcome this problem the flesh and shell weights of standard size animals were calculated from the appropriate size/weight relationship.

The size/weight relationship was determined from the logarithmic equation:

$$\mathrm{Log}_{10} w = b\ \mathrm{Log}_{10} L - \mathrm{Log}_{10} a$$

$$\text{as} \quad w = \frac{L^b}{a}$$

where w = weight
L = size
b = regression coefficient
a = intercept

The use of standard-size animals minimises the complications attributable to size growth by keeping the size constant, although it does not entirely eliminate the results of differential growth between the size and body of the animals (Ansell and Trevallion, 1967). Therefore changes in the flesh and shell weights not attributable to size growth may be examined as in the case of flesh changes caused by maturation, spawning or emaciation. The flesh condition change will therefore be comparable to the flesh weight of a standard animal during that part of the year when the size remains constant, i.e. outwith the growing season (see also Beukema and De Bruin, 1977). In addition, the use of standard-size animals permits the use of many standard-sizes which cover the animals' size range such that the relative differences in flesh and shell weight attributable to spawning and emaciation between cohorts can be studied. The use of standard-size animals also permits the study of shell thickening processes which would not be evident if only cohort weight changes were studied.

As each of the parameters have advantages and disadvantages (see also Ansell and Trevallion, 1967), only by the use of both condition factors and standard-size animals can the annual cycle of body component changes be studied fully. The study of standard-aged animals was also necessary as the growth rate of the bivalves varied with habitat type, this resulted in the standard-sized animals being of differing age depending upon the environmental parameters. The sizes and weights of those standard-age animals were computed from the size/weight relationships and Bertalanffy equations for each station.

3.2.2. Age and Growth - Description and Estimation.

The age and growth of mollusc individuals may be estimated by three methods; (1) by the analysis of size frequency data,

(2) by the interpretation of shell-growth interruption lines, and (3) by the measurement of individuals in mark and recapture experiments. The methods (1) and (2) may give doubtful estimations such that either should be used in conjunction with one of the other methods (Haskin, 1954).

Where possible, the methods (1) and (2) have been used together in the present study for the bivalve species and in addition method (3) was used for M. balthica (see Chapter 6).

The following characteristics of mollusc populations; a life span of many years; an increasing overlap with age between cohorts; large differences in annual growth between years; variability in spawning between years and a long spawning season, all contribute to the difficulty in analysing size-frequency data. The polymodal histograms prepared from such data were studied with the knowledge gained from growth ring analysis (see below) and the cohorts' size distributions delimited for each sampling occasion. This delimitation was therefore only partly objective. The use of probability paper to separate the polymodal frequency distribution (Harding, 1949; Cassie, 1950, 1954) has been suggested as a means of eliminating any subjectivity in size-frequency analysis. This method was attempted but found to have few advantages above the method finally adopted; a subjective assessment of the point of inflexion within a cumulative percentage size-frequency curve is still required although a lengthy procedure for the determination of such inflexion points has been proposed (Cassie, 1950). In addition, Warwick and Price (1975) suggest that the probability paper method forces the data for each age class to conform to a normal size-frequency distribution but that size selective pressures, such as predation or differential rates of migration, would cause the distribution to be skewed and therefore render the method invalid.

The growth interruption lines on the bivalves' shells were used to estimate age and therefore to describe their growth. The height at each age was determined as the distance between the umbo and the ventral edge of the shell; allowance being made for the increasing curvature of the shell with age. In any study of growth it is necessary to adopt the convention that the age group (or cohort) corresponds to the number of growth cessation rings laid down, i.e. the 0+ group animals do not have any growth rings. It was necessary to take 1st. January as the arbitrary date when the growth rings were laid down. As the first years' growth, from spawning until the first ring is formed, therefore takes place over a shorter period than the growth of subsequent years, it was necessary to omit the first years' growth from the growth equation determination (see Section 3.2.2.1.).

The descriptions of the formation and appearance of growth cessation rings in M. balthica given by Segestråle (1960) and Lammens (1967) were used in the identification of such rings and any growth rings that did not conform to the regular pattern were regarded as disturbance and/or spawning growth interruption rings and discounted. However, the ease and accuracy of interpretation of shell growth rings decreases with age.

3.2.2.1. The Use of Ford-Walford Analysis and the Bertalanffy Equation in Growth Studies.

After obtaining data regarding the ages and sizes at those ages of individuals, it was necessary to quantify the growth pattern. The pattern of bivalve growth encountered indicated that the use of the Bertalanffy equation and the Ford-Walford growth analysis were applicable.

Bertalanffy (1938) developed an equation (I) to describe animal growth in species where the growth rate decreases with increasing age :

$$L_t = L_\infty \left(1-e^{-K(t-t_o)}\right) \qquad \text{(I)}$$

where t = time; L_t = size at that time; L_∞ = a constant, the maximum theoretical size; t_o = a constant, the theoretical time when L = 0; and K = also a constant.

The most important parameters are K and L_∞, the former being Bertalanffy's "coefficient of catabolism" which describes the rate at which the maximum or asymptotic size (L_∞) of the growth curve is reached (Beverton and Holt, 1957).

The Ford-Walford plot, a graphical representation of the above equation (I)(Walford, 1946; Crisp, 1971), has been used extensively in fisheries biology (Beverton and Holt, 1957), and more recently applied to lamellibranchs (Hancock, 1965; Munch-Petersen, 1973; Warwick and Price, 1975; Ralph and Maxwell, 1977). All methods of constructing such a plot involve consideration of the size of the whole or part of an animal before and after a time interval, usually one year (Hancock, 1965).

The parameters of equation (I) are obtained by a two part determination. Firstly, the length (or size) of an animal (L_t)

is plotted on the abscissa against the length one year later (L_{t+1}) at various times over the life span of the animal. If the growth is described by the equation (I), then a straight line will be produced which tends towards the 45^o intercept line from the origin. The point where the two lines meet, i.e. where $L_t = L_{t;1}$, gives the asymptotic size (L_∞).

As the plot will have the equation :

$$L_{t+1} = b.L_t + a \qquad \text{(II)}$$

where a = intercept on the ordinate.
b = regression coefficient.

then $$L_\infty = \frac{a}{1 - b} \qquad \text{(III)}$$

This equation (III) is idential to :

$$L_\infty = L_1/1 - k \qquad \text{(Walford, 1946)} \qquad \text{(IV)}$$

as a in (III) will equal the length at year 1 (L_1), i.e. when $L_t = 0$, then :

$$k \equiv b \text{ (in equation II) } \equiv e^{-K} \text{ (in equation I)}$$

The coefficient of catabolism can therefore be calculated using the transformation :

$$b = e^{-K} \equiv \mathrm{Log}_e b = -K$$

Therefore as the Ford-Walford line approaches the 45^o intercept then $b(\equiv e^{-K} \equiv k) < 1$, and the closer b is to unity the lower will be the parameter K.

The second part of the Ford-Walford analysis is the incorporation of L_∞ (obtained above) and the growth data into a graph of $\mathrm{Log}_e (L_\infty - L_t)$ against t. The straight line obtained :

$$\mathrm{Log}_e(L_\infty - L_t) = a_1 - b_1 t \qquad \text{(V)}$$

has a slope $b_1 = -K$, an intercept a_1, and the value of t_0 (equation I) is obtained from the point where the value of $\mathrm{Log}_e L_\infty$ meets the line. The parameters t_0, L_∞ and K are then incorporated into equation (I) to describe fully the animals' growth curve.

The Ford-Walford method can be applied either using data for the mean sizes of age cohorts at yearly intervals calculated from either size-frequency histograms or growth ring analysis, or by using consecutive annual measurements of individual animals. If a sufficient number of age classes or individuals are used then any variation in growth between years will not affect the final analysis (Hancock, 1965).

The most important aspect of, and possibly the greatest source of error in, the method is the type of growth curve exhibited by a population. Many species exhibit a sigmoid growth curve, i.e. the individuals show a period of slow initial growth. If data relating to this period are incorporated into the first stage of the Ford-Walford plot then the first points will lie away from the straight line indicated by the other points. This would result in a higher regression coefficient, a lower K value, and a higher L_∞ value, being obtained when compared to the line being fitted to only those points where the growth fits the Bertalanffy equation. (The resultant plot would also have a lower statistical significance.)

Where necessary, the Ford-Walford plots (first stage) employed in the present study have all been constructed with the omission of the first anomalous points. This is in agreement with Thiesen (1974) who suggests that the Ford-Walford plot is invalid over the first year or so of life of an animal. Some authors (e.g. Munch-Petersen, 1973; Warwick and Price, 1975) do not comment on this, although in other lamellibranch studies no inflexion point (indicating sigmoid growth) has been observed (Ralph and Maxwell, 1977).

A measure of accuracy of the method is given by the agreement between the L_∞ value obtained and the maximum size recorded for a population from field data, and also by the agreement between the two K values obtained (from the slopes of the first and second stages of the Ford-Walford plot).

The K parameter may be used to make inter- or intra-specific comparisons (Beverton and Holt, 1957; Ralph and Maxwell, 1977). Beverton and Holt (1957) suggest that K can be used as an index of the "intrinsic development rate" and that although it can be regarded as independent of the feeding level it might be expected to vary with certain environmental factors such as temperature. It is necessary, however, to exhibit caution when making inter- and intra-specific comparisons and to consider also the growth over any part of the animals' life cycle, the maximum (asymptotic) size attained (L_∞) and the longevity of a population. The longevity of a population has been arbitrarily taken as the time (in years) taken to reach 95% of that maximum size, since the time taken to reach the maximum size will, by virtue of the method, be infinite and cannot therefore be used as a measure of longevity. The measure of longevity (T_{95}) was therefore obtained from the second step of the Ford-Walford analysis (equation V) :

$$\text{Log}_e\,(L_\infty - L_{T_{95}}) = a_1 - b_1 t$$

$$\therefore \quad \frac{a_1 - \text{Log}_e(L_\infty - L_{T_{95}})}{b_1} = t = T_{95}$$

The growth of an animal can therefore only be fully described by the complete Bertalanffy growth equation and the graphically represented growth curve together with an estimate of the species' longevity and not by only part of the Ford-Walford analysis or by single growth parameters (Warwick and Price, 1975; Ralph and Maxwell, 1977). An advantage of the Bertalanffy equation is that it smooths out any variation in the population growth between different sampling years; it also enables growth to be extrapolated for years in which data were not available and to be quantitatively standardised such that the comparison between areas is possible.

Munch-Petersen (1973) further developed the Bertalanffy equation by incorporating the length/weight relationship for the population :

As $L_t = L_\infty(1 - e^{-K(t - t_o)})$

and $w = \frac{L^b}{a}$ where w = flesh weight

$$W_t = W_\infty(1 - e^{-K(t - t_o)})^b \quad \text{where } W_\infty = \frac{L_\infty{}^b}{a}$$

However, as the shell-size/weight relationship differs with sampling occasion and environment, it is impossible to present an 'average' size/weight equation for the population and so only size based Bertalanffy equations have been calculated.

3.2.3. The Estimation of Population Production.

Production (P) is considered the most important parameter within the energy budget as this reflects the net amount of organic material fixed by the population. It is the difference between the biomass gain by growth and recruitment and the biomass loss due to predation, senescence and unsuccessful settlement (see Crisp, 1971; Arntz and Brunswig, 1975). In the present study the term P is synonymous with the IBP term P_g (production attributable to growth) as distinct from total production which also includes P_r (production attributable to reproduction)(Hughes, 1970).

The annual population production attributable to somatic growth was calculated by the summation of the growth increments of each cohort for each sampling period for a population where recruitment occurs but where the age classes are separable (method 2 of Crisp, 1971; a derivation of Allen's growth/survivorship curve method). The production of each cohort over each sampling interval was therefore given by :

$$\Delta P = \tfrac{1}{2}(N_t + N_{t+\Delta t}).\Delta\overline{W}$$

where N = cohort density

$\overline{W}$ = mean cohort weight

t = time

As a comparison, the production of <u>M. balthica</u> was also calculated by the summation of the weight specific-growth rate as a function of size at each sampling occasion :

$$\text{Sampling interval production} = \sum_{t=0}^{t=1} \sum_{o}^{n} f_i\, G_i\, \overline{W}_i\, \Delta t$$

where G_i is the weight specific growth rate of size group i; $\overline{W}_i$ is the mean weight of the size group and f_i is the number of individuals of this size group existing in the population during the period Δt (Crisp, 1971).

The weight specific growth rates were obtained independently from the Bertalanffy parameters and the size/weight regressions :

$$G = bK(L_\infty - l)/l$$

where b = regression coefficient of size/weight relationship.

K, L_∞ = Bertalanffy parameters.

l = mean size of size class chosen.

It must be emphasised that the production methods used only give an indication of the addition to the population biomass attributable to somatic growth and recruitment. Material lost as spawned gametes, which may be upto 50% of the total energy flow (Hughes, 1970), and the loss and regeneration of material as predation of parts of the animals, e.g. siphons, which may also be a substantial proportion depending on the local predator populations (Wolff and De Wolf, 1977), will result in fluctuations in the flesh weight of cohorts and as such will be incorporated into the methods. However, the loss of material, by spawning for example, may result in negative production.

The mortality (M) as the yield to either predators or the decomposer food chain was also determined. The mortality was estimated as the product of the mean cohort weight and the change in density of that cohort, i.e.

$$\Delta M = \tfrac{1}{2}(\overline{W}_t + \overline{W}_{t+\Delta t})(-\Delta N) \qquad \text{(Crisp, 1971)}$$

Whilst absolute production and mortality values are important in assessing the productivity of an area, in order to compare areas either locally or geographically it was necessary to use the relative production indices $P/\overline{B}$ and $M/\overline{B}$, i.e. the production and mortality per unit biomass and unit time usually one year. The term $P/\overline{B}$ (productivity) is therefore used as the annual equivalent of the term diurnal specific production discussed at length by Zaika (1973) and the turnover ratio of Waters (1969). Several authors have discussed the importance of these ratios as a method of comparing populations, species, genera, trophic levels and ecosystems (e.g. Zaika, 1973; Warwick and Price, 1975; Hibbert, 1976). Waters (1969) and Peer (1970) discuss the importance of these ratios in predicting population production and mortality.

3.3. Population Results.

3.3.1. The Abundance and Biomass of M. balthica at Each Station.

3.3.1.1. The Abundance of "Large" Animals (> 2.5mm Height).

The occurrence of the maximal densities at each station were dependent upon the time of settling of the spat (see Section 3.3.1.2.) and their subsequent growth resulting in the appearance of the first years' animals in the larger sieve, and as such varied with area (Fig. 3.1; see also Table 3.7). Secondary spat transport also occurred resulting in the deposition of large 'spat' at several high-shore, coarse sand stations, e.g. A3-A4, C5, C4, B4 & B5.

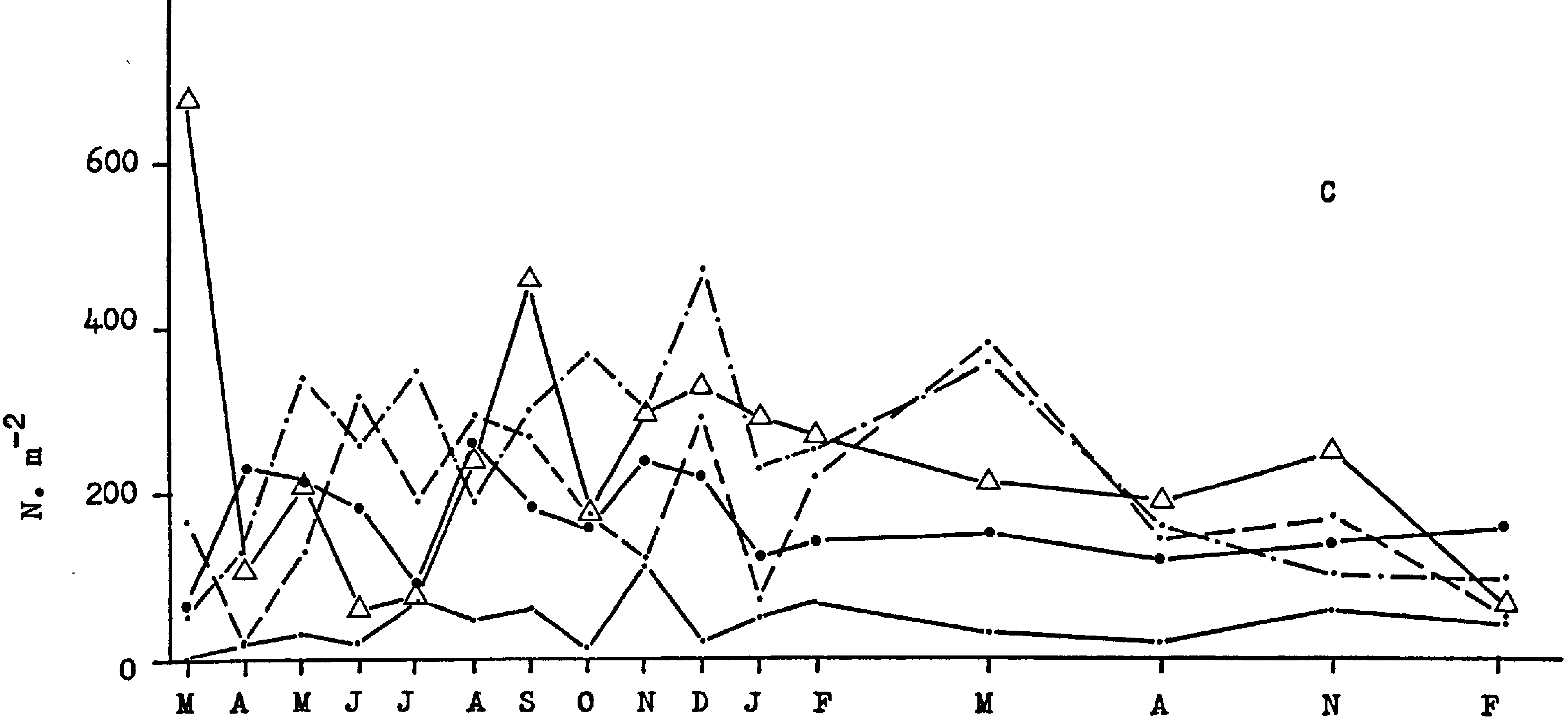
Transect A (Fig. 3.1): Whilst Stations A2-A4 had comparable densities of between 100 and 400 individuals throughout the sampling period, Station A1 had much greater densities with summer maxima exceeding 1000m^{-2}. Station A1 also showed the greatest mortality over the winter period. Station A2 had one summer peak in density which was possibly attributable to the settling of the previous years' spat, and a smaller one in November caused by the settling of the new spat. Stations A3 and A4 also showed bimodal density patterns over the year with peaks in June and September and July and October respectively. Station A1 however showed high numbers from June to September and, to a lesser extent, until December.

Transect B (Fig. 3.1): Station B1 supported relatively low densities in which the summer maxima reached 400m^{-2}. B2 had constantly higher densities which were relatively similar to B4 and B5. However, B3 was found to support the highest densities of upto 2000 individuals. Whilst all stations'

Figure 3.1 *M. balthica* : The Change in Density (N. m^{-2}) of 'Large' Animals (>2.5mm ht) at Each Station and Each Sampling Occasion.

Legend

	Transect		
	A	B	C
——·——	1	1	1
— —·— —	2	2	2
—·—·—·—	3	3	3
——△——	4	4	4
——●——		5	5


C
N. m^{-2}
600
400
200
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F

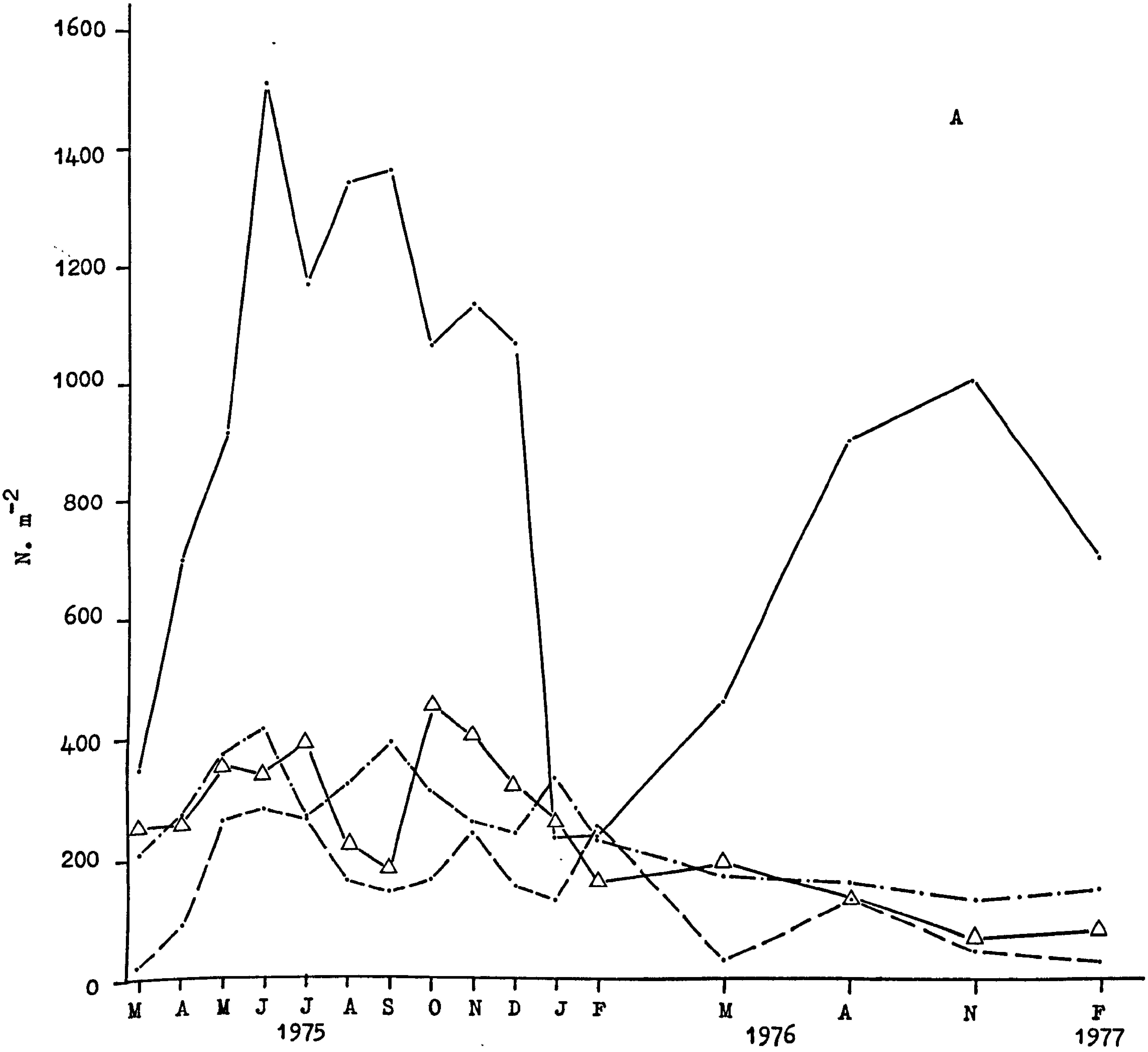

A
N. m^{-2}
1600
1400
1200
1000
800
600
400
200
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

Figure 3.1 M. balthica : The Change in Density (N. m^{-2}) of 'Large' Animals (>2.5mm ht) at Each Station and Each Sampling Occasion.

Legend

	Transect		
	A	B	C
—·—	1	1	1
– –·– –	2	2	2
–·–·–·–	3	3	3
—△—	4	4	4
—●—		5	5


C
N. m^{-2}
0
200
400
600
M A M J J A S O N D J F M A N F
A
N. m^{-2}
0
200
400
600
800
1000
1200
1400
1600
M A M J J A S O N D J F M A N F
1975
1976
1977

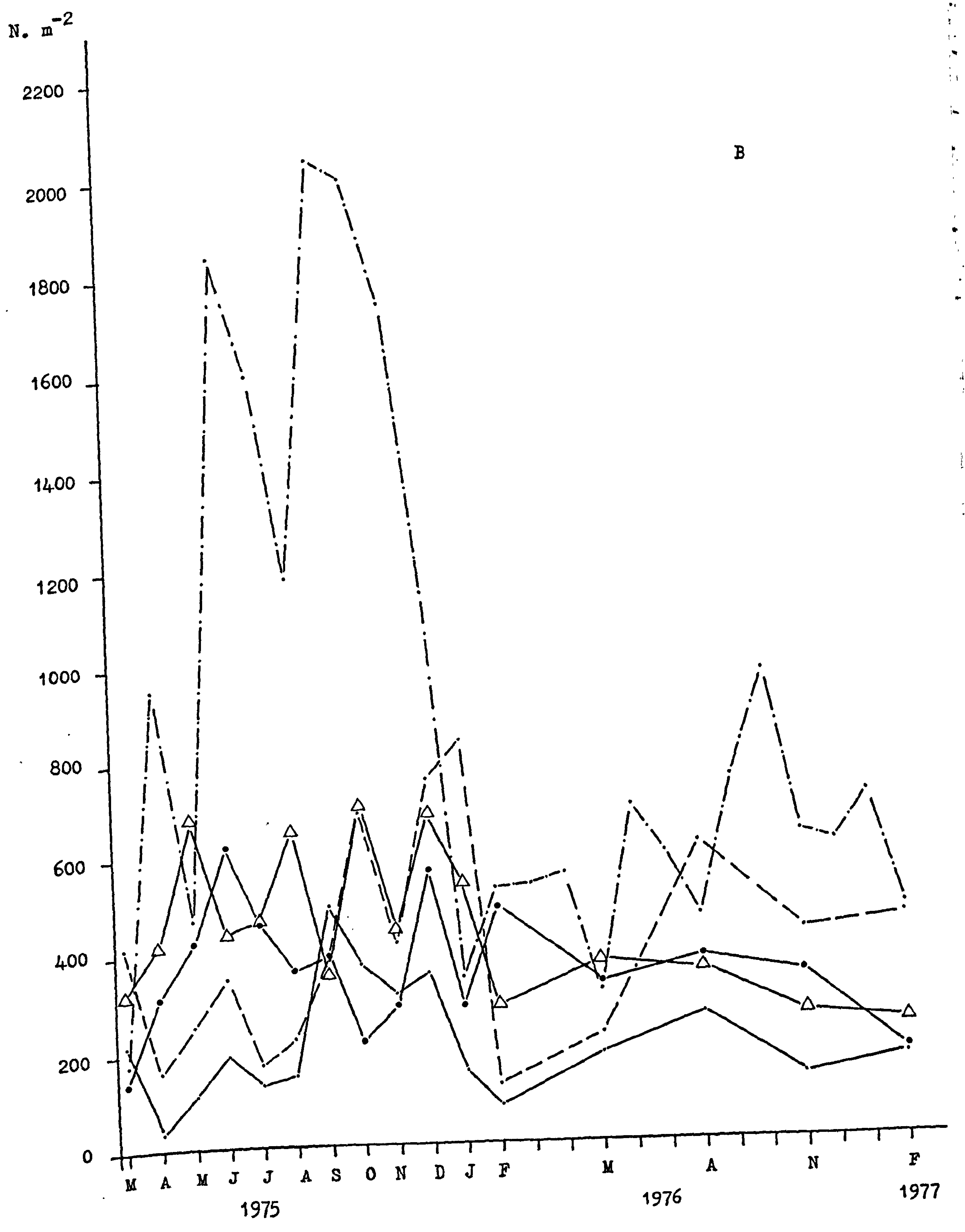


Figure 3.1 Continued.

populations suffered high mortality during the autumn and winter, that of B3, as with A1, declined by 80% between November and January.

Transect C (Fig. 3.1): All stations supported relatively low, erratic densities, although the mid-transect Stations, C2 and C3, had the highest densities. The high numbers recorded at C4 at the beginning of sampling in March was possibly the result of a high late settlement of the previous years' spat.

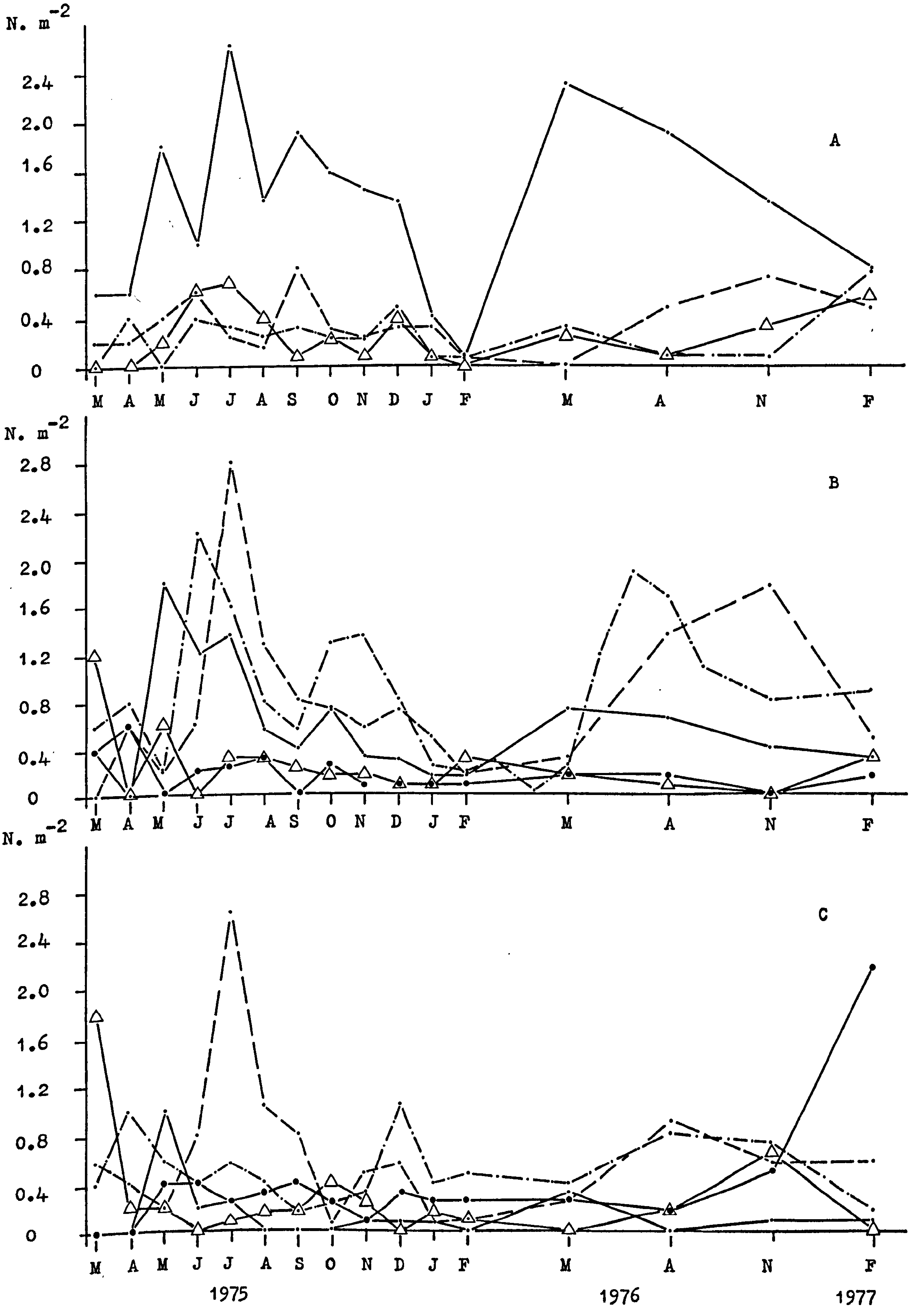
The main trend suggested here, of the highest densities being found in the mid-shore areas of each transect, is considered further in Section 3.4.1.1.

The majority of the stations showed comparable densities over the two years of sampling, i.e. 1975-76 and 1976-77. The density at the Transect A stations, however, all showed a slight decline over the period whilst Station B3 showed a large decrease in population density between the two years. The change in abundance at Stations B3 and C2 however did not appear to be associated with the change in sediment type observed at those stations (see Section 2.4.1.). The overall seasonal trends at each station were apparent to a lesser extent during the second year of sampling; this was possibly attributable to the extended sampling interval.

3.3.1.2. Station Spat Densities (Animals < 2.5mm Height).

All stations showed pronounced summer peaks in spat abundance which give an indication of the time of spat settling (Fig. 3.2) although the peaks vary in position depending on the amount of primary and secondary spat settlement. The main areas of settlement were found to be A1, B1, B2, B3, and C2 which were

Figure 3.2 M. balthica : The Change in Density (N. m^{-2}) of Spat at Each Station and Each Sampling Occasion. Legend as Figure 3.1.


N. m-2
2.4
2.0
1.6
1.2
0.8
0.4
0
A
M A M J J A S O N D J F M A N F
N. m-2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
B
M A M J J A S O N D J F M A N F
N. m-2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
C
M A M J J A S O N D J F M A N F
1975
1976
1977

all fine mud, mid- to low-shore areas (see Section 3.4.1.1.). These five stations showed two peaks of spat abundance, a summer maximum and a lesser peak during October, November or December. The Stations A2, A3, A4 and C4, although spat also settled over the summer, had spat densities which increased towards the end of the year suggesting secondary spat transport. The Stations B4, B5, C1 and C5 had low spat densities for most of the two year sampling period. The remaining station, C3, had a high spat density early in the year (April) which could only have been the previous years' spat, as well as peaks of spat abundance in the summer and late autumn.

The maxima of spat abundance present during the latter part of the year may be the result of either a second spawning period or secondary spat transport. These factors are further considered in Section 3.3.3. and are summarised in Table 3.7.

3.3.1.3. The Biomass of Large Animals and Spat at Each Station.

The mean total dry weight (tdw) and flesh dry weight (fdw) biomasses of each station are summarised in Table 3.1 from Appendix 3.2 and reflect, to a large extent, the trends shown by the mean population densities. As expected, however, where a station had a large complement of small animals in the large sample then the mean biomass would not necessarily reflect those large numbers. However, as a result of that, the biomass levels were more constant for each sampling occasion at each station.

During 1975-76 the mean biomasses of the stations' 'large' animals ranged from 5.74g tdw m^{-2} and 1.03g fdw m^{-2} at C2 to 53.4g tdw m^{-2} and 8.99g fdw m^{-2} at B3, whereas during the following year the majority of the stations supported lower

Table 3.1 **M. balthica:** The Mean Density (Nos. m^{-2}) and Total and Flesh Biomass (g m^{-2}) at Each Station (± S.E.).

Station	Sampling Year 1975/76						Sampling Year 1976/77					
	"Large"			"Spat"			"Large"			"Spat"		
	N.	Tdw	Fdw	N.	Tdw	Fdw	N.	Tdw	Fdw	N.	Tdw	Fdw
A1	919.2	41.699	7.459	1233.3	0.559	0.112	706.2	13.778	2.149	1510.0	0.493	0.099
	128.5	5.725	1.278	210.7	0.119	0.024	157.6	2.251	0.428	420.4	0.187	0.037
A2	178.3	11.135	1.393	323.3	0.112	0.022	87.5	4.539	0.496	370.0	0.060	0.012
	23.1	1.378	0.135	57.7	0.030	0.006	42.2	1.570	0.187	163.2	0.034	0.007
A3	300.0	13.488	2.081	233.3	0.102	0.020	162.5	6.068	0.700	230.0	0.052	0.010
	18.9	0.928	0.228	46.7	0.027	0.006	17.0	1.039	0.131	137.4	0.037	0.007
A4	298.3	11.604	1.741	226.7	0.064	0.013	127.5	7.632	0.944	230.0	0.022	0.004
	26.3	0.994	0.154	66.8	0.020	0.004	27.2	1.327	0.219	96.4	0.014	0.000
B1	215.8	7.321	1.214	616.7	0.222	0.044	173.7	18.113	2.207	500.0	0.175	0.035
	39.2	1.300	0.164	159.9	0.048	0.010	33.9	9.854	0.979	112.5	0.052	0.010
B2	395.8	38.582	5.173	743.3	0.348	0.069	386.2	40.611	5.912	940.0	0.252	0.050
	69.2	5.978	0.749	210.6	0.075	0.015	98.8	14.592	2.496	370.0	0.143	0.029
B3	1166.7	53.394	8.994	883.3	0.503	0.101	473.7	22.151	2.961	810.0	0.238	0.048
	195.3	7.855	1.441	179.3	0.104	0.021	66.1	1.346	0.164	328.5	0.107	0.021
B4	496.7	25.423	3.095	290.0	0.160	0.032	310.0	26.039	2.459	140.0	0.027	0.005
	43.2	1.934	0.317	96.1	0.065	0.013	29.7	5.387	0.455	68.3	0.014	0.000
B5	375.8	32.075	4.066	193.3	0.095	0.018	338.7	29.554	2.994	110.0	0.093	0.019
	40.8	3.234	0.536	51.8	0.029	0.006	46.1	5.239	0.441	39.5	0.054	0.010
C1	42.5	19.196	1.824	140.0	0.049	0.010	41.2	15.884	1.353	110.6	0.023	0.005
	9.1	4.974	0.457	81.7	0.041	0.008	10.6	6.882	0.434	72.8	0.030	0.005
C2	187.9	5.740	1.026	646.7	0.249	0.050	206.2	5.030	0.781	500.0	0.189	0.038
	27.1	1.049	0.166	202.9	0.063	0.013	63.4	1.875	0.292	159.6	0.086	0.017
C3	270.8	14.978	1.918	500.0	0.217	0.043	198.8	8.763	0.890	560.0	0.164	0.033
	32.0	2.308	0.280	78.4	0.039	0.008	60.2	3.599	0.313	126.5	0.063	0.012
C4	264.6	32.606	3.182	290.0	0.150	0.030	203.7	24.277	1.632	210.0	0.019	0.004
	49.9	6.750	0.694	140.8	0.097	0.019	35.2	4.819	0.382	147.8	0.017	0.000
C5	175.0	5.970	0.809	240.0	0.083	0.011	140.0	4.773	0.447	520.0	0.171	0.034
	18.4	0.795	0.103	41.8	0.026	0.004	7.6	0.657	0.053	364.4	0.102	0.021

biomasses which ranged from 4.54g tdw m^{-2} at A4 to 40.61g tdw m^{-2} at B2 and from 0.447g fdw m^{-2} at C5 to 5.912g fdw m^{-2} at B2.

The largest decreases in 'large' animal biomasses between the two years of sampling were at the Stations B3 and A1, which had the greatest biomasses during the first year of sampling, and were possibly the result of the increased mortality by predation (see Section 3.3.5.5.).

The stations' spat biomasses followed the same patterns as the spat densities as the weight range of the spat sizes sampled was relatively small. In 1975-76 the spat biomass ranged from 49mg tdw m^{-2} (10mg fdw m^{-2}) at Station C1 to 559mg tdw m^{-2} (112mg fdw m^{-2}) at Station A1. During 1976-77 the spat biomasses recorded were also much smaller with respect to the previous year and ranged from 22mg tdw m^{-2} (4mg fdw m^{-2}) at A4 and C4 to 493mg tdw m^{-2} (99mg fdw m^{-2}) at A1.

3.3.2. The Growth of M. balthica at Each Station.

The growth pattern of M. balthica at each station was determined by growth cessation ring analysis. The analysis was made upon the animals taken during 1976-77 at each station such that at those stations with low population densities (e.g. A2 and C1) fewer animals were incorporated in the analysis than at stations with high densities (e.g. A1 and B3). The Table 3.2 gives the mean heights of the year classes at each station from which the Bertalanffy growth equations were obtained using the two-step determination (Tables 3.3 and 3.4). The data for those year classes in which only one animal had been measured, e.g. at A1 for the 9+ cohort, were excluded from the analyses.

The equations were then plotted (Fig. 3.3) and show the

Table 3.2 *M. balthica*: Growth Ring Data for Each Station (Mean Height ± S.E.(mm) and Number of Observations).

Age Ring	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
	Station A1			Station A2			Station A3			Station A4					
1	2.84	0.08	158	3.31	0.35	7	2.63	0.18	31	3.17	0.20	23			
2	5.44	0.17	55	5.61	0.15	8	5.08	0.21	20	5.27	0.11	26			
3	7.14	0.32	19	7.36	0.16	7	6.66	0.18	14	6.78	0.12	21			
4	8.61	0.59	9	8.23	0.18	6	7.69	0.18	10	7.82	0.17	15			
5	11.27	1.14	3	8.67	0.24	6	8.22	0.26	8	8.30	0.24	8			
6	12.45	0.95	2	9.50	0.32	3	9.07	0.37	3	9.25	0.18	4			
7	12.90	0.70	2	9.85	0.55	2	9.45	0.55	2	9.90	-	-			
8	13.15	0.55	2				10.2	-	1						
9	13.00	-	1				10.4	-	1						
	Station B1			Station B2			Station B3			Station B4			Station B5		
1	3.06	0.11	43	2.96	0.13	69	3.19	0.10	122	2.45	0.10	73	2.63	0.12	71
2	5.45	0.30	18	6.16	0.15	52	6.09	0.13	67	5.09	0.12	65	5.19	0.12	62
3	7.16	0.36	14	8.37	0.15	41	7.97	0.15	40	6.56	0.12	50	6.91	0.16	43
4	8.61	0.34	13	9.47	0.26	26	9.09	0.23	24	7.70	0.16	40	8.24	0.14	37
5	9.80	0.31	12	10.31	0.31	20	10.55	0.28	13	8.63	0.20	30	9.05	0.17	26
6	10.73	0.36	12	10.86	0.42	12	11.08	0.35	9	9.44	0.20	26	9.88	0.22	17
7	11.57	0.34	12	11.68	0.51	9	11.72	0.55	6	9.98	0.20	19	10.36	0.22	10
8	12.07	0.39	10	12.70	0.80	5	12.10	0.72	4	10.69	0.28	11	10.63	0.33	6
9	13.11	0.26	8	13.45	1.25	2	12.6	-	1	11.19	0.37	7	11.02	0.41	5
10	13.78	0.37	6	12.4	-	1	13.1	-	1	10.4	-	1	11.33	0.48	3
11	14.23	0.34	6	12.6	-	1				10.6	-	1	12.00	0.20	2
12	14.75	0.47	4										12.0	-	1
13	15.23	0.67	3										12.0	-	1
14	16.3	-	1												
15	16.5	-	1												
	Station C1			Station C2			Station C3			Station C4			Station C5		
1	3.33	0.41	9	2.30	0.15	46	2.32	0.12	42	2.61	0.13	37	2.70	0.18	40
2	6.40	0.44	10	4.70	0.20	27	4.84	0.15	35	4.84	0.11	47	4.80	0.19	38
3	8.25	0.43	8	6.81	0.22	9	6.36	0.24	14	6.56	0.12	41	6.48	0.14	24
4	9.76	0.44	7	8.12	0.16	4	7.71	0.22	10	7.80	0.09	33	7.39	0.22	10
5	10.73	0.44	7	9.03	0.53	3	8.51	0.26	10	8.75	0.12	30	7.93	0.66	3
6	11.70	0.46	7	9.75	0.75	2	10.45	0.15	2	9.58	0.22	13	9.3	-	1
7	12.57	0.51	6	10.45	1.15	2	11.00	0.30	2	10.02	0.22	8			
8	13.28	0.50	6				11.50	0.40	2	10.38	0.21	6			
9	13.77	0.48	6				11.80	0.40	2	10.67	0.12	3			
10	14.08	0.63	5							10.95	0.25	2			
11	14.37	0.87	4							10.80	-	1			
12	15.15	1.25	2												
13	14.4	-	1												
14	14.9	-	1												
15	15.1	-	1												
16	15.3	-	1												
17	15.5	-	1												
18	15.6	-	1												
19	15.7	-	1												

Table 3.3 <u>M. balthica</u>: Stage 1 Ford-Walford Analysis.

$H_{t+1}(\mathrm{mm}) = b \pm \mathrm{S.E.}\ H_t(\mathrm{mm}) + a$

Station	b	S.E.	a	n	p	r	H_∞	K_1
A1	0.7992	0.0668	3.2132	7	***	0.983	16.002	0.224
A2	0.6735	0.0432	3.4121	6	***	0.992	10.450	0.395
A3	0.6820	0.0336	3.2227	6	***	0.995	10.134	0.383
A4	0.7238	0.0594	2.9471	5	**	0.990	10.670	0.323
B1	0.8466	0.0154	2.6032	12	***	0.998	16.970	0.166
B2	0.7353	0.0457	3.7111	8	***	0.989	14.020	0.307
B3	0.7143	0.0311	3.7088	7	***	0.995	12.981	0.336
B4	0.7557	0.0297	2.9410	8	***	0.995	12.038	0.280
B5	0.7498	0.0231	3.0699	10	***	0.996	12.270	0.288
C1	0.7627	0.0167	3.5686	10	***	0.998	15.038	0.271
C2	0.7442	0.0229	3.0945	6	***	0.998	12.097	0.295
C3	0.7911	0.0512	2.8219	8	***	0.988	13.508	0.234
C4	0.7505	0.0071	2.9008	9	***	1.000	11.626	0.287
C5	0.6628	0.0450	3.1089	4	**	0.995	9.220	0.411

Table 3.4 <u>M. balthica</u>: Stage 2 Ford-Walford Analysis.

$\mathrm{Log}_e(H_\infty - H_t) = b \pm \mathrm{S.E.}\ t(\mathrm{yrs}) + a$

Station	b	S.E.	a	n	p	r	t_0	K_2
A1	-0.2384	0.0154	2.8374	8	***	-0.988	0.271	0.238
A2	-0.4012	0.0192	2.3879	7	***	-0.994	0.103	0.401
A3	-0.3891	0.0163	2.4287	7	***	-0.996	0.290	0.389
A4	-0.3170	0.0172	2.3292	6	***	-0.994	-0.120	0.317
B1	-0.1659	0.0037	2.8092	13	***	-0.977	-0.134	0.166
B2	-0.3222	0.0320	2.8045	9	***	-0.967	0.509	0.322
B3	-0.3419	0.0075	2.6413	8	***	-0.999	0.228	0.342
B4	-0.2845	0.0128	2.5791	9	***	-0.993	0.320	0.284
B5	-0.2969	0.0262	2.6288	11	***	-0.967	0.410	0.270
C1	-0.2812	0.0067	2.7887	11	***	-0.997	0.278	0.281
C2	-0.2925	0.0051	2.5699	7	***	-0.999	0.263	0.292
C3	-0.2439	0.0101	2.6836	9	***	-0.994	0.329	0.244
C4	-0.2848	0.0029	2.4768	10	***	-1.000	0.083	0.285
C5	-0.4126	0.0116	2.2826	5	***	-0.999	0.148	0.413

Where K_1 (coefficient of catabolism from Stage 1), K_2 (same from Stage 2), t_0 and H_∞ are the derived Bertalanffy parameters.

"smoothed" growth curve for the animals at each station. On Transect A (Fig. 3.3), Station A1 animals showed very much higher growth at the greater ages (after the third year) than at the Stations A2-A4. On Transect B the animals at Stations B1 and B3 had constantly higher growth rates than those at B4 and B5 and at all ages animals at the former stations were larger than those at the latter stations. At their first winter the animals at B2, B4 and B5 were of the same size but from that point the growth of B2 animals was greater such that, at ages older than two years, Stations B1-B3 animals were larger than those at B4 and B5. The stations of Transect C could be placed in three groups based on the animals growth. At Stations C2-C4 the animals showed comparable growth whilst those at Station C1 showed much greater growth and at C5 much less.

The maximum theoretical heights (H_∞) were found to range from 9.22mm at C5 to 16.97mm at B1 and decrease with the progression along each transect towards the high tidal levels. Similarly, the rates at which those maximum sizes were reached, K, increased with the same progression.

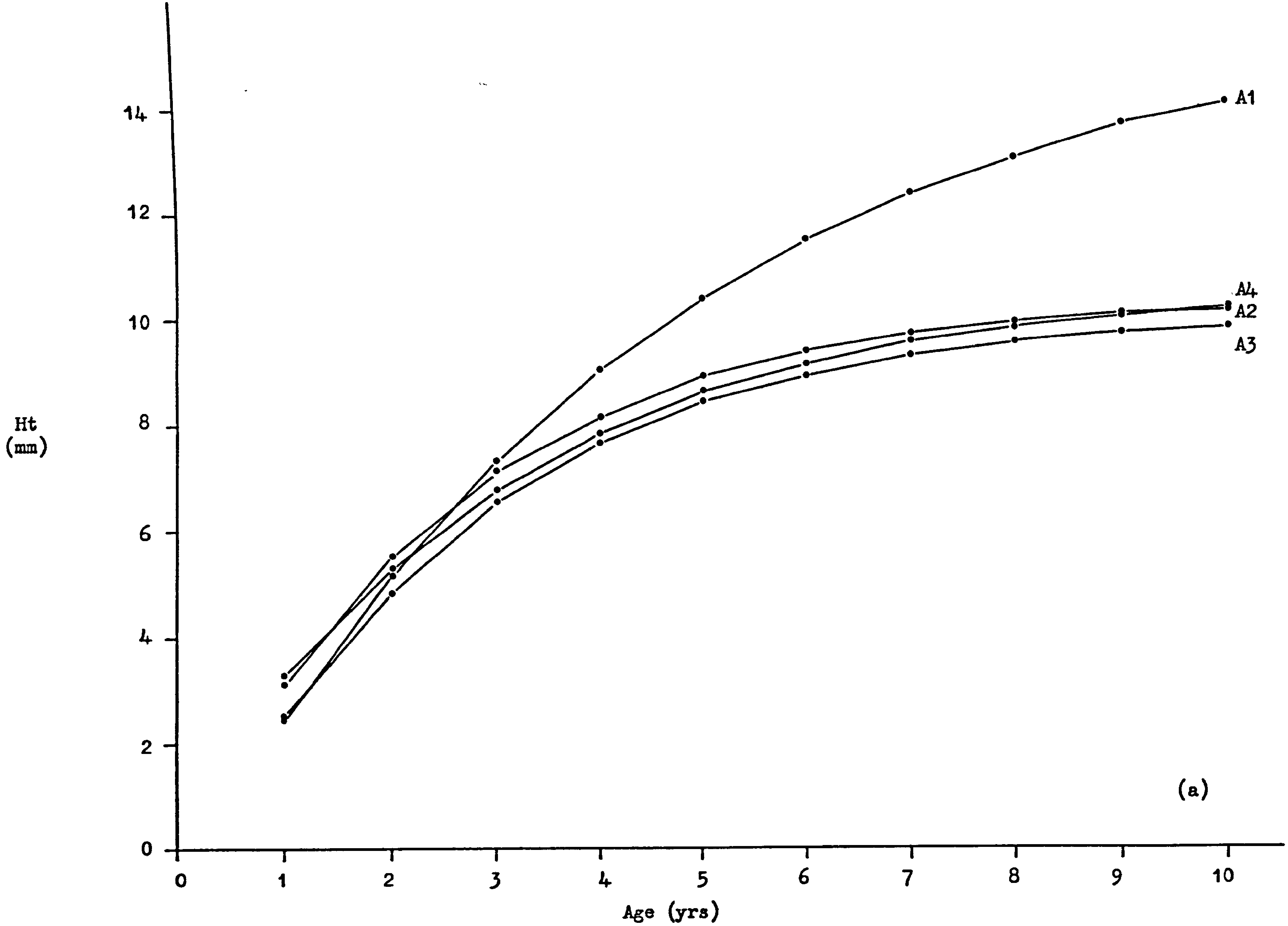
In order to check upon the accuracy of the Bertalanffy predicted maximal height, the maximal height of animals sampled is also given (Table 3.5) and shows good agreement with the former values. Only the animals at Stations A1, A4, B1 and C3 had maximal sizes less than the predicted H_∞, those at the remaining stations had a sampled maximum size greater than the H_∞ value. This suggests that the animals at the former stations were either not surviving long enough to attain a maximal size or were living below the depth of substrate sampled. The latter explanation is unlikely as the depth of substrate sampled was

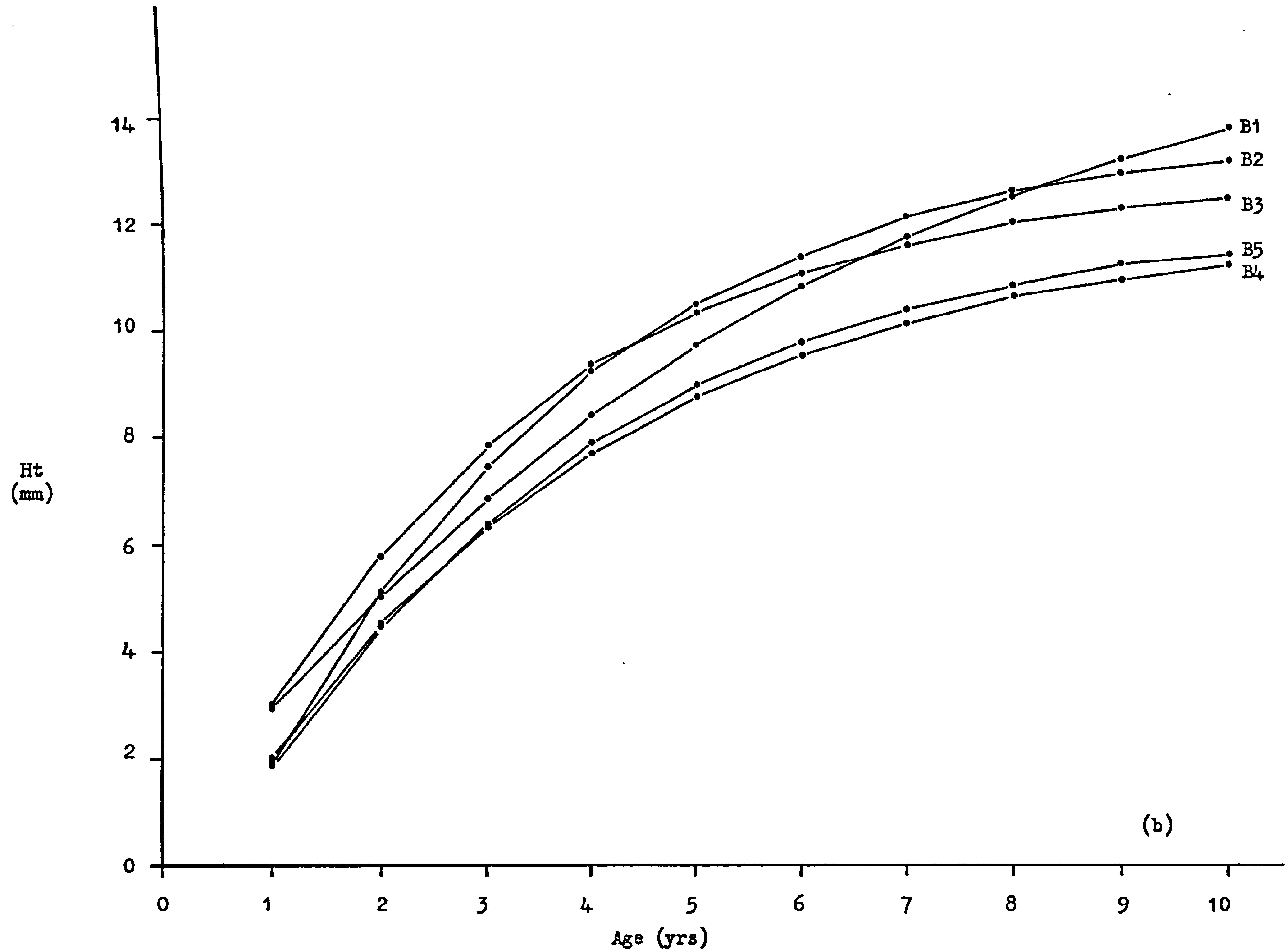
Figure 3.3 M. balthica : The Growth Rates at Each Station Derived From the Bertalanffy Growth Equations.

(a) Transect A;

(b) Transect B;

(c) Transect C.


Ht
(mm)
0
2
4
6
8
10
12
14
0
1
2
3
4
5
6
7
8
9
10
Age (yrs)
A1
A4
A2
A3
(a)


Ht
(mm)
14
12
10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
9
10
Age (yrs)
B1
B2
B3
B5
B4
(b)

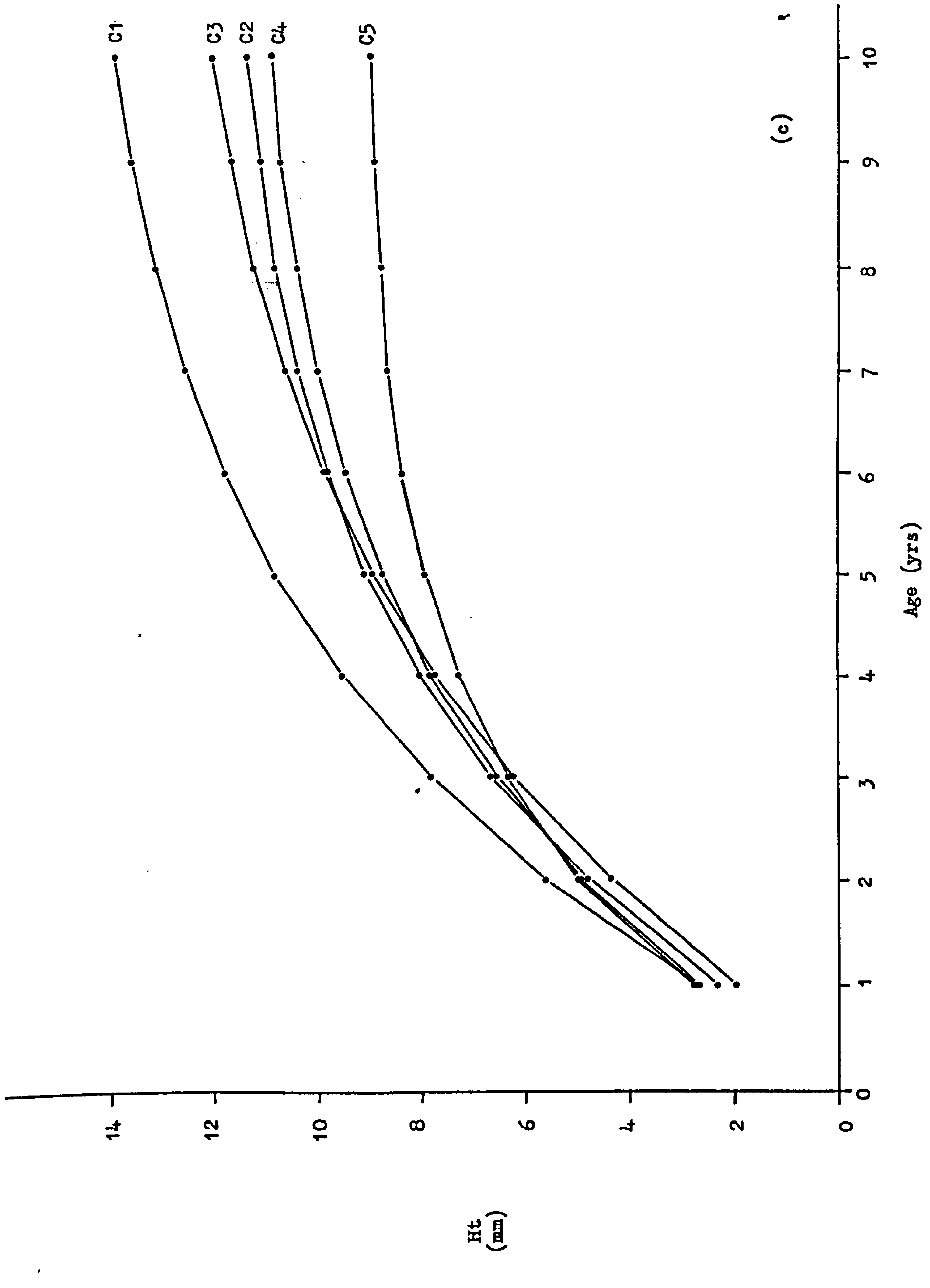

Ht (mm)
0
2
4
6
8
10
12
14
Age (yrs)
0
1
2
3
4
5
6
7
8
9
10
C1
C3
C2
C4
C5
(c)

Table 3.5 *M. balthica:* The Bertalanffy Growth Equations and the Parameters Derived from Those Equations.

Station	Equation	H_1 (mm)	H_2 (mm)	H_4 (mm)	H_6 (mm)	H_8 (mm)	T_{95} (yrs)	H_4 Tdw (mg)	H_4 Fdw (mg)	H_8 Tdw (mg)	H_8 Fdw (mg)	Max. Size Sampled (mm)
A1	$H_t = 16.002\ (1 - e^{-0.224(t - 0.271)})$	2.41	5.14	9.06	11.57	13.17	12.84	95.16	13.574	355.37	42.331	13.7
A2	$H_t = 10.450\ (1 - e^{-0.395(t - 0.103)})$	3.12	5.51	8.21	9.43	9.99	7.57	73.67	8.815	149.61	16.151	11.3
A3	$H_t = 10.134\ (1 - e^{-0.383(t - 0.290)})$	2.41	4.87	7.69	9.00	9.60	7.99	58.47	7.015	132.09	14.337	10.6
A4	$H_t = 10.670\ (1 - e^{-0.323(t + 0.120)})$	3.24	5.29	7.85	9.19	9.89	9.33	59.99	9.167	137.42	20.969	10.2
B1	$H_t = 16.970\ (1 - e^{-0.166(t + 0.134)})$	2.91	5.06	8.43	10.84	12.57	17.92	94.24	12.239	398.45	40.169	15.9
B2	$H_t = 14.020\ (1 - e^{-0.307(t - 0.509)})$	1.96	5.15	9.22	11.42	12.61	9.81	111.24	12.268	393.19	40.170	14.9
B3	$H_t = 12.981\ (1 - e^{-0.336(t - 0.228)})$	2.97	5.82	9.33	11.11	12.03	8.99	127.79	16.128	337.94	41.040	15.1
B4	$H_t = 12.038\ (1 - e^{-0.280(t - 0.320)})$	2.09	4.52	7.74	9.58	10.64	10.85	65.06	7.441	205.92	21.215	12.6
B5	$H_t = 12.270\ (1 - e^{-0.288(t - 0.410)})$	1.92	4.51	7.91	9.82	10.89	10.50	77.11	9.802	267.93	29.134	13.3
C1	$H_t = 15.038\ (1 - e^{-0.271(t - 0.278)})$	2.67	5.61	9.55	11.85	13.18	10.93	154.37	17.018	555.72	44.108	16.1
C2	$H_t = 12.097\ (1 - e^{-0.295(t - 0.263)})$	2.36	4.85	8.08	9.87	10.86	10.50	65.15	9.395	175.04	24.301	14.6
C3	$H_t = 13.508\ (1 - e^{-0.234(t - 0.329)})$	1.96	4.37	7.79	9.92	11.26	12.61	73.22	8.378	304.03	27.514	13.2
C4	$H_t = 11.626\ (1 - e^{-0.287(t - 0.083)})$	2.69	4.92	7.85	9.50	10.43	10.60	80.17	7.514	233.40	18.611	12.7
C5	$H_t = 9.220\ (1 - e^{-0.411(t - 0.148)})$	2.72	4.91	7.33	8.39	8.85	7.41	52.27	6.397	100.27	11.584	9.6

Where H_1, H_2, H_4, H_6 and H_8 = Heights at ages 1, 2, 4, 6 and 8 years respectively; T_{95} = age at which 95% of maximum size reached; H_4 Tdw, H_4 Fdw, H_8 Tdw, H_8 Fdw = total and flesh weight of 4 and 8 year animals, respectively.

much greater than the recorded depths at which the animals are known to occur. The mortality of M. balthica at these stations is discussed in Section 3.3.5.5.

The greatest maximum ages attained were calculated to occur at B1 (17.9 years) and A1 (12.8 years) and decreased to 7.4 years (at C5) and 7.6 years (at A2), (Table 3.5). The trends apparent on each transect with the variables H_∞ and K were not shown by this variable (T_{95}) although at Stations A3, B2, B3, B5, and C1 growth rings representing ages greater than this maximum age (T_{95}) were measured. Therefore, whilst T_{95} may accurately represent the maximum age attained by M. balthica at most stations it does not do so for all stations. However, because of a necessity for a standard method of estimating maximal ages attained this 95% convention has been used.

In order to compare the sizes of animals of certain ages at the stations, the sizes at standard ages were calculated from the Bertalanffy equations and are given as H_1 - H_8 where the age is denoted by the subscript. It may be seen that whilst the sizes of H_1 animals varied little between stations (Table 3.5; Fig. 3.3) the size at H_8 varied from 8.8 to 13.2mm in height suggesting that the environment exerts an increasing influence with age.

The sizes of each cohort at each station were also converted into mean flesh weights using the appropriate regression equations for January 1976, i.e. the time, arbitrarily taken, at which the annual growth ring was laid down (see $*_1$ and Table 3.6).

$*_1$ The regression equations, regarding the length, height, total dry weight, flesh dry weight, shell weight and condition factor for each station and sampling occasion used throughout this Chapter are given in Appendix 3.1.

The weight transformed Bertalanffy growth curves are given in Fig. 3.4. Similarly, for the comparison of stations' M. balthica growth patterns, the sizes of four and eight year old animals (H_4 and H_8 respectively) were converted to total as well as flesh dry weights. The total dry weight (tdw) of H_4 animals ranged from 52 to 154mg whilst the flesh dry weight (fdw) ranged from 6.4 to 17.0mg. The respective ranges in values for H_8 animals were from 100 to 555mg tdw and 11.6 to 44.1mg fdw. In each case the animals of Station C5 were of the least weight whereas those of Station C1 were of the greatest weight. As Transect C covered both the largest range of tidal height and particle size, this large difference between sizes and weights of certain cohorts may be explained (see Section 3.4.1.2.).

3.3.3. The Annual Change in Condition and in Flesh and Shell Weights of Standard Sized Animals.

The changes in mean body condition with respect to height (CF_H) of the animals at each station (Fig. 3.5) may be summarised by detailing the peaks (maxima) and troughs (minima) in the animals' condition (Table 3.7). While at most of the stations the animals reached a maximum condition in May, June or July, there were also smaller maxima at the majority of the stations during the period August to September. It is probable that the earliest condition maxima were attributable to the maturation of the animals prior to spawning. The decrease in condition following these were possibly due to spawning together with a decrease in condition caused by a period of rapid growth (see Section 3.3.5.3.). The second, smaller, rise and fall in condition during autumn could have been caused by a late maturation and spawning as has been reported for the species

Figure 3.4 M. balthica : Flesh-weight Transformed Growth Rates Derived From the Bertalanffy Equations. The Groups (1 to 5) Used in the Production Estimations (see Text) are Shown.


Flesh Weight (mg)
0
5
10
15
20
25
30
35
40
45
50
Age (yrs)
0
1
2
4
6
8
10
B1
A1
C1
1
2
B2
B3
B5
C3
C2
3
B4
A4
C4
4
A2
A3
C5
5

Table 3.7 M. balthica: The Months of Maximum and Minimum Values of Spat Density, Flesh Condition and Flesh Weight of 4mm and 8mm Standard-Size Animals, Summary of Figures 3.2,3.5-3.7.

MAY denotes month of maximum or minimum, May = other maxima or minima, sl. = other (slight) peaks or troughs.

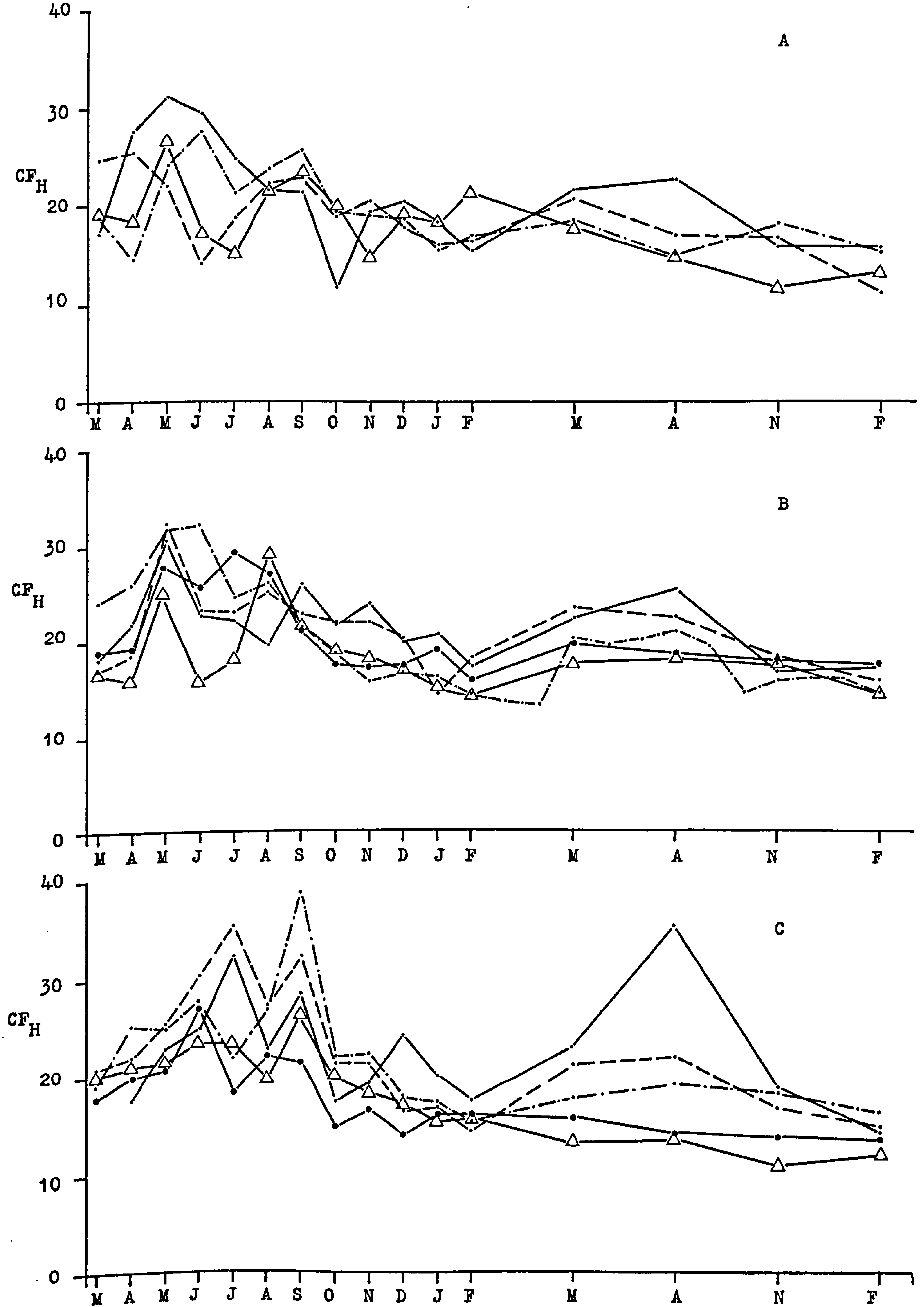
Station	Spat nos.	Flesh Condition		Fdw of 4mm Animal		Fdw of 8mm Animal	
	Maxima.	Maxima	Minima	Maxima	Minima	Maxima	Minima
A1	May,JULY, Sept.	MAY, (Apr. - July)	OCT.	JUNE, Jan.(sl.)	OCT., Feb.	MAY(Apr.-June), Nov. - Dec.(sl).	Oct., FEB.
A2	June, SEPT.	APR., Sept.	July, JAN.	MAY - Sept.	OCT., Feb.	APR., Nov.(sl.) Aug. - Sept.	July, Oct., JAN.
A3	JUNE(sl.)	JUNE, Sept.	Apr., July, JAN.	JUNE, Aug.(sl.)	July, FEB.	JUNE, SEPT., Nov.(sl.)	July - Aug., JAN.
A4	June - JULY, Dec.	MAY, Sept.	July, NOV.	MAY, Sept.(sl.)	NOV.	MAY, Dec.(sl.) AUG. - Sept.	June - JULY, NOV., Jan.
B1	MAY - July, Oct.	MAY, Sept.	Aug., FEB.	MAY, Sept.	AUG.	MAY, SEPT., Nov.	June, Oct., FEB.
B2	JULY, Dec.	MAY, Aug.	July, JAN.	MAY, Aug., Nov.(sl.)	July, JAN.	MAY, Aug.(sl.), Nov.(sl.)	June, Oct.(sl.) JAN.
B3	JUNE, Oct. - Nov.	MAY - June, Aug.	July, FEB.	JULY, Aug.	DEC.	May - JUNE, Dec.(sl.)	Nov., APRIL
B4	MAY, June - Oct.(sl.)	May, AUG.	June, FEB.	MAY, Aug.	June, FEB.	May, AUG.	JUNE, FEB.
B5	APR., June - Oct.(sl.)	May - JULY	FEB.	JULY, (May - Aug.)	NOV. - Dec.	MAY, JULY	June(sl.) DEC., FEB.
C1	MAY	JULY, Sept., Dec.	Aug., OCT., FEB.	July	SEPT.	JULY	FEB.
C2	JULY, Dec.	JULY, Sept.	Aug., FEB.	MAY, Sept.	June(sl.), FEB.	JULY, Sept.	Aug., FEB.
C3	APR., July, Dec.	June, SEPT.	July(sl.), FEB.	JUNE, Aug.(sl.)	July(sl.), FEB.	Apr., June, SEPT.	July, FEB.
C4	OCT. - Nov.	June - July, Sept.	Aug.(sl.), JAN.	JUNE (Apr. - Sept.)	JAN.	MAY	FEB.
C5	MAY - JUNE, SEPT., Dec.(sl.)	JUNE, Aug.	July, DEC.	JULY	NOV.	Apr., AUG.	June, FEB.

(Caddy, 1967) or have been attributable to the slowing and cessation of growth enabling the animals to slightly increase their condition before the main period of emaciation over the late autumn and winter. The main emaciation periods were found to be over the winter with the animals reaching minimal condition during January and February (Table 3.7). There were also lesser periods of emaciation between April and August for the majority of the stations (Fig. 3.5; Table 3.7) which possibly reflect the extent of the spawning.

The time of spawning in M. balthica can be inferred by noting the occurrence of the maximal spat densities sampled (see Fig. 3.2; Section 3.3.1.2. and Table 3.7). The maximum spat densities were usually recorded during the period May to July although as these densities included animals upto 2.5mm in height then these densities may include slower growing animals which were spawned the previous year. The majority of the spat, however, were only a few weeks old at the time of maximum abundance (see Fig. 3.10). Spat were not detected until they reached a height of 0.6mm and so will have settled a maximum of a month earlier. It is therefore concluded that in 1975 the majority of the spat were spawned between April and early July, as also shown by the flesh condition changes. The mean temperature during that spawning period ranged from 8.7 to 15.5°C (10.1 to 15.5°C air temperature; 7.3 to 15.5°C water temperature).

The Table 3.7 shows that at individual stations there was little connection between the maximum condition factor and the subsequent settling of spat. It would be erroneous to assume that planktonic larvae spawned at any particular station would necessarily settle there.

Figure 3.5 *M. balthica* : The Change in Mean Flesh Condition Factor (CF_H) at Each Station. Legend as Figure 3.1.


A
B
C
CF$_H$
40
30
20
10
0
M A M J J A S O N D J F M A N F
1975
1976
1977

The animals' condition at most stations decreased by similar amounts after spawning. Although the animals' condition at the lower-shore, finer mud stations, was still higher than at other stations, it is suggested from this data that spawning at certain stations was greater than at other stations. At Stations A3, B5, C3 and C4, the condition change attributable to spawning was small in comparison to that of the other stations.

The conclusions above are supported by the consideration of the flesh and shell weights of standard sized animals. Flesh condition values were affected by the growth of the animals but this problem is overcome by considering standard sized animals. However, in considering standard sizes from differing environments adjustment must be made for stations where the growth rate was slow so that the animals had a longer period at which to reach the status described by the standard size. The standard size animals considered were of heights 4mm and 8mm and had ages which ranged from 1.3 to 1.8 years for the former and 3 to 5 years for the latter (see Table 3.8). The 4mm animals may be immature (Caddy, 1967; Lammens, 1967) and so will only show trends in the flesh weight cycle associated with growth. The 8mm animals were mature and as such showed flesh changes associated with spawning. The patterns of flesh changes in 8mm animals (8 fdw)(Fig. 3.6) follow those of condition (CF_H) more closely than do those of the flesh weight of 4mm animals (4 fdw) (Fig. 3.7).

At half of the stations there is a similarity between the occurrence of peaks and troughs in the curves of 4mm and 8mm fdw with time (Figs. 3.6 & 3.7) however at other stations (A1, A2, B3, B5, C3, C4 and C5) the peak flesh weight of 8mm animals

Table 3.6 M. balthica: The Flesh-dry-weight (mg) of Animals of Standard Ages of 1, 2, 4, 6, and 8 Years (Calculated from the Bertalanffy Equations and the Regression Equations for January, 1976).

Station	H_1	H_2	H_4	H_6	H_8
A1	0.242	2.417	13.574	28.530	42.331
A2	0.445	2.578	8.815	13.540	16.151
A3	0.170	1.621	7.015	11.619	14.337
A4	0.387	2.237	9.167	16.114	20.969
B1	0.522	2.695	12.239	25.864	40.169
B2	0.035	1.355	12.268	27.594	40.170
B3	0.240	2.864	16.128	30.705	41.040
B4	0.098	1.258	7.441	15.046	21.215
B5	0.079	1.449	9.802	20.465	29.134
C1	0.393	3.523	17.018	32.167	44.108
C2	0.181	1.824	9.395	17.862	24.301
C3	0.099	1.306	8.378	18.305	27.514
C4	0.246	1.693	7.514	13.817	18.611
C5	0.287	1.826	6.397	9.777	11.584

Table 3.8 M. balthica: The Age of Standard-size Animals and the Shell-weight of 4 Year-old Animals (Calculated from the Bertalanffy Equations and the Regression Equations for January, 1976).

Station	Age (yrs.) at		H_4 Shell wt.
	Height 4 mm.	Height 8 mm.	(mg)
A1	1.48	3.18	81.59
A2	1.31	3.72	64.85
A3	1.58	4.29	51.73
A4	1.36	4.25	50.82
B1	1.49	3.71	82.00
B2	1.55	3.13	98.97
B3	1.30	3.03	111.66
B4	1.74	4.16	57.62
B5	1.74	3.96	67.31
C1	1.38	2.98	137.35
C2	1.64	3.96	55.75
C3	1.77	4.01	64.84
C4	1.56	4.17	72.65
C5	1.53	5.05	45.87

Figure 3.6 _M. balthica_ : The Change in Flesh Weight (mg) of an 8mm Standard Height Animal at Each Station. Legend as Figure 3.1.


A
B
C
mg
15
13
11
9
7
5
18
16
14
12
10
8
6
26
24
22
20
18
16
14
12
10
8
6
M A M J J A S O N D J F M A N F
1975
1976
1977

Figure 3.7 *M. balthica* : The Change in Flesh Weight (mg) of a 4mm Standard Height Animal at Each Station. Legend as Figure 3.1.


A
B
C
mg
2.5
2.0
1.5
1.0
0.5
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

occurred before that of the 4mm animals. This phenomenon reflects the earlier increase in weight of the larger animals during maturation and spawning before growth (as an increase in flesh) occurred while the smaller animals were predominantly concerned with growth. However, some 4mm animals, at Stations A1, A3, A4, B1-B4, C1 and C5, were sexually mature as indicated by the peak in the flesh weight during the May to June period which was followed by a rapid decrease (caused by spawning). At the remaining stations the 4mm animals gradually increased in weight over the summer period and then emaciated later in the year. The former group of stations includes those areas in which older M. balthica had the greatest growth rates: A1, B1-B3, C1. However, the ages of 4mm animals (Table 3.8) did not differ sufficiently to result in full sexual maturity at some areas but not at others.

The 8mm animals at most stations showed high peaks in flesh weight during the early summer which were followed by a large decline indicating spawning. The flesh weight and body condition of M. balthica therefore followed an annual cycle composed of two peaks (depending on the age of the animal) with each followed by a period of emaciation (Fig. 3.6 & Table 3.7). The animals' flesh weight, and condition, increased during the period May to June before spawning; spawning, together with a period of rapid growth, then resulted in a short period of emaciation in July. This in turn was succeeded by a condition rise associated with the slowing down of shell growth, an increase in flesh and a possible second smaller phase of maturity during the period August to September. The major period of emaciation occurred during the late autumn and winter when the body condition reached the annual minimum.

The shell weights of 4 and 8mm animals at each station were found to exhibit similar annual patterns (Figs. 3.8 & 3.9) in which, at the majority of stations, they decreased to minimal values in May and June; the period when the body-flesh condition was at a maximum. Following this minimum the shell weight then either increased upto the winter period or returned to the pre-May-June value and remained constant throughout the remainder of the year. This suggests that shell thickening occurred as the year progressed and certainly after the main growing season and reproduction had ended.

Generally, the elevation of the shell-weight curves decreased with a progression down each transect towards the low-shore areas (Figs. 3.8 & 3.9). This trend was more clearly defined for the larger (8mm) animals than the 4mm animals and the relative difference in shell weight between the different habitat types increased with age and size of the animals; both of which suggest that with age the environment exerted an increasing influence (see Sections 3.4.2.4. and 3.4.2.5.).

3.3.4. The Change in Shell Shape of M. balthica with Station.

The shell shape as characterised by the relationships between the length and height measurements of the shell was briefly investigated. At each station (except C1) the shell dimensions from 100 animals (62 in the case of Station C1) were regressed together (see Table 3.9). Using a modified t-test (Bailey, 1959) the differences between the regression coefficients of the stations within each transect was tested for significance (see Table 3.10A, B, C). On Transect A, the regression of Station A4 had a significantly lower slope than that of Stations A1 and

Figure 3.8 M. balthica : The Change in Shell Weight (mg) of a 4mm Standard Height Animal at Each Station. Legend as Figure 3.1.

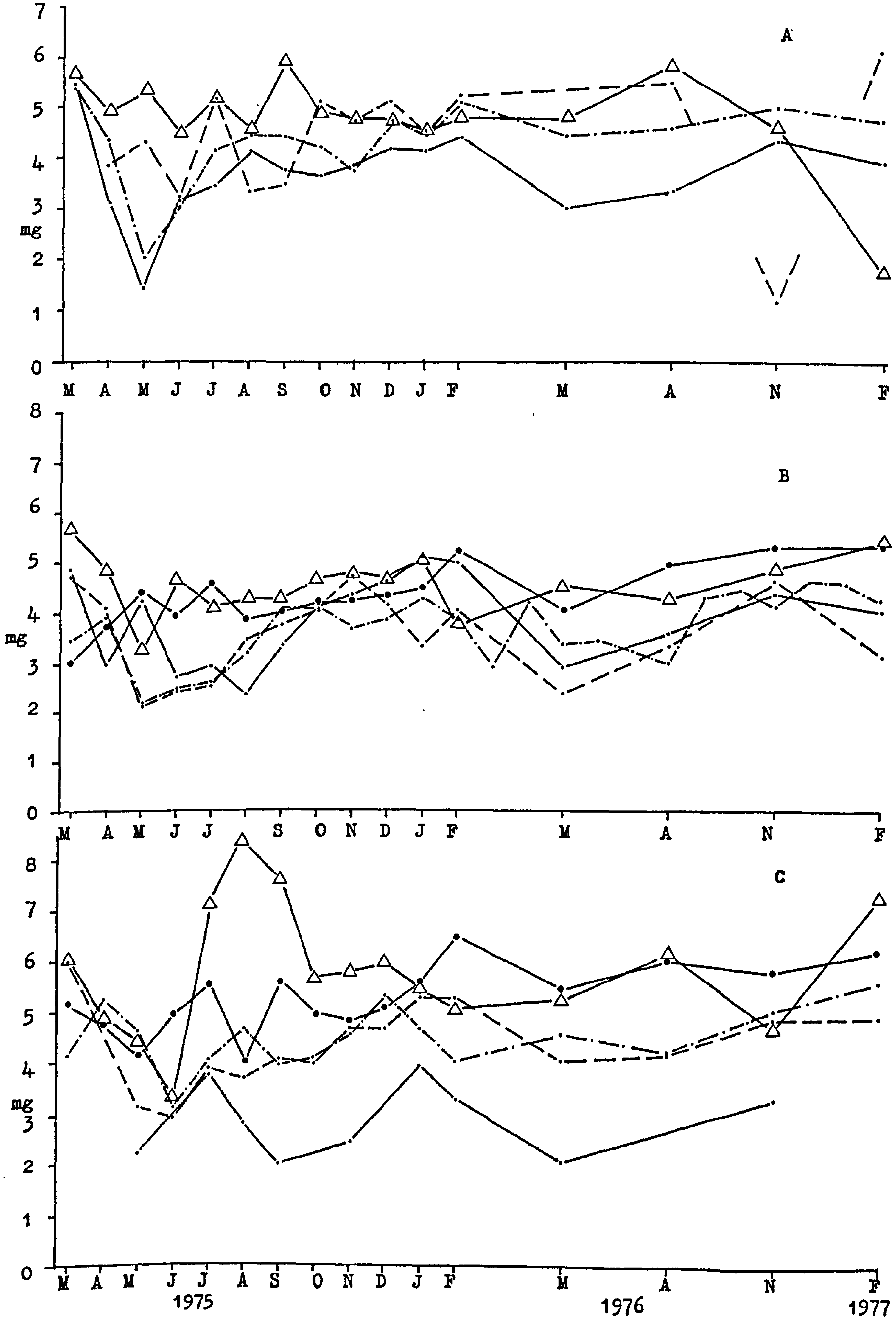

A
B
C
mg
0
1
2
3
4
5
6
7
8
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

Figure 3.9 M. balthica : The Change in Shell Weight (mg) of an 8mm Standard Height Animal at Each Station. Legend as Figure 3.1.

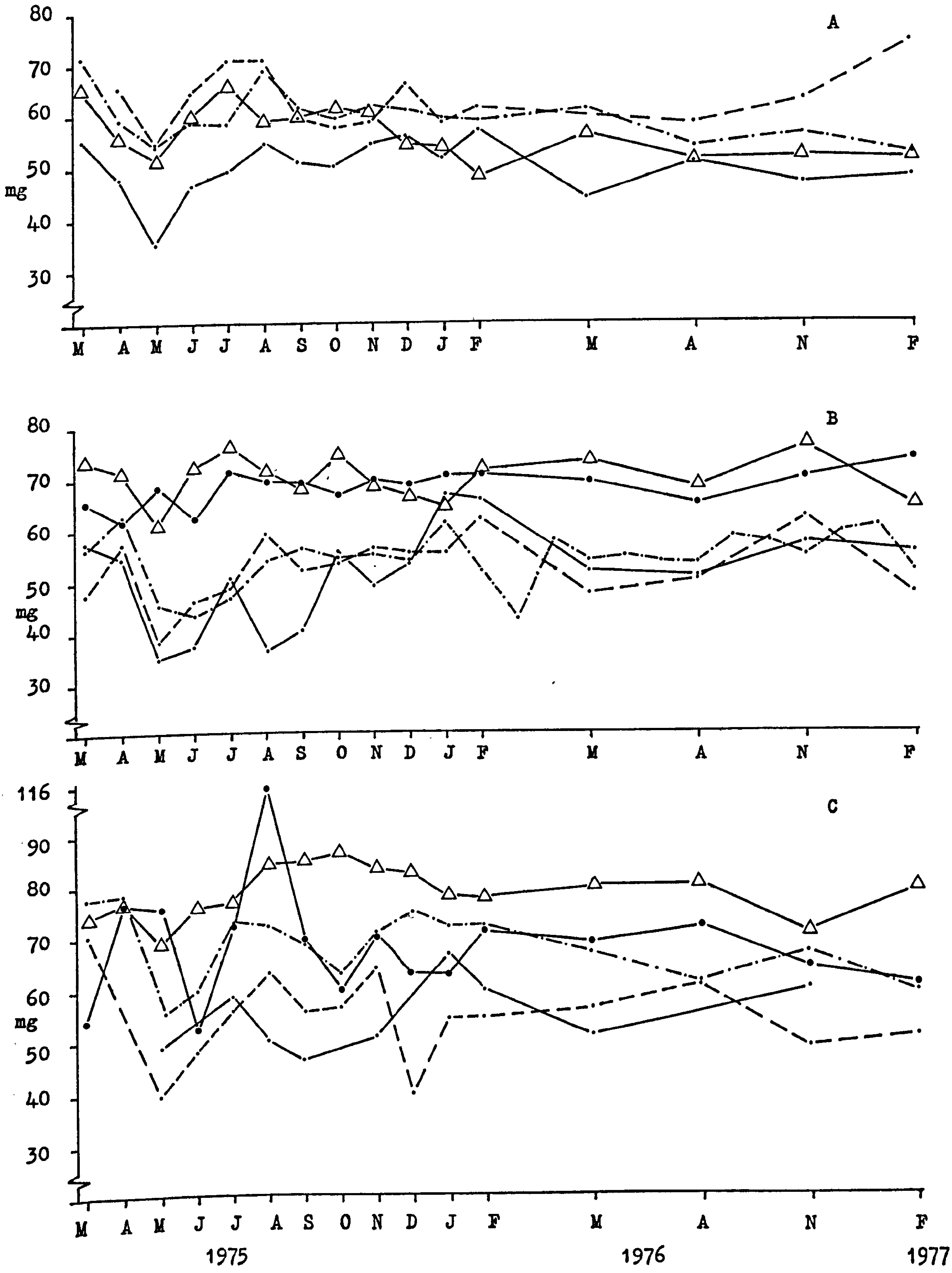

A
80
70
60
50
mg
40
30
M A M J J A S O N D J F M A N F
B
80
70
60
50
mg
40
30
M A M J J A S O N D J F M A N F
C
116
90
80
70
60
mg
50
40
30
M A M J J A S O N D J F M A N F
1975
1976
1977

Table 3.9 M. balthica: The Relationship Between Shell Length and Height.

$$\text{Ht.(mm)} = b \pm \text{S.E. L.(mm)} + a$$

Station	b	S.E.	a	r	n	p
A1	0.801	0.0060	0.0287	0.997	100	***
A2	0.796	0.0074	0.1179	0.996	100	***
A3	0.786	0.0069	0.2728	0.996	100	***
A4	0.768	0.0082	0.2674	0.994	100	***
B1	0.834	0.0057	-0.1337	0.998	100	***
B2	0.826	0.0064	-0.1968	0.997	100	***
B3	0.800	0.0061	-0.0486	0.997	100	***
B4	0.789	0.0077	0.1634	0.995	100	***
B5	0.806	0.0043	0.1099	0.998	100	***
C1	0.822	0.0136	0.0705	0.992	62	***
C2	0.805	0.0070	0.0019	0.996	100	***
C3	0.844	0.0075	-0.2016	0.996	100	***
C4	0.849	0.0220	-0.2950	0.967	100	***
C5	0.806	0.0117	0.1441	0.990	100	***

Table 3.10 The Use of Modified T-tests to Determine the Similarity Between the b-values of L./Ht. Regressions. (Level of significance and d-values given.)

(A)		A1	A2	A3
	A2	0.50 n.s.		
	A3	1.65 n.s.	1.02 n.s.	
	A4	3.20 **	2.51 *	1.62 n.s.

(B)		B1	B2	B3	B4
	B2	0.94 n.s.			
	B3	4.05 ***	2.91 **		
	B4	4.68 ***	3.66 ***	1.12 n.s.	
	B5	3.98 ***	2.63 **	0.72 n.s.	1.86 n.s.

(C)		C1	C2	C3	C5
	C2	1.06 n.s.			
	C3	1.42 n.s.	3.73 ***		
	C4	1.05 n.s.	1.87 n.s.	0.21 n.s.	
	C5	0.90 n.s.	0.01 n.s.	2.75 **	1.73 n.s.

Values of d less than 1.96 are produced when the regression coefficients are not significantly different at the 95% level.

A2; on Transect B, the Stations B3, B4 and B5 all had significantly lower regression coefficients than at Stations B1 and B2; on Transect C, the regression of Station C5 had a significantly lower slope than C3 whilst the latter station had a slope significantly greater than at Station C2. Therefore, the upper transect stations had significantly lower coefficients to the length/height regression equations than the lower stations showing that at the former areas the animals had a more pointed shell outline. Although this relationship was shown on Transects A and B, it was not evident to such a large extent on Transect C which had the largest variation in both tidal height and sediment particle size over the transect. Therefore while it is possible to suggest that the animals' change in shape between areas may be a result of living under different conditions this trend was not shown in all areas.

Mention may also be made of the shell appearance of M. balthica. At the fine mud, lower-shore stations the animals' shells had a glossy clean appearance with very little or no abrasion at the umbonal region. At the coarser stations however, the animals had shells with a much rougher surface with a white, "chalky" appearance and greatly eroded umbonal regions. At Stations A2 and A4 in particular the high degree of umbo erosion had resulted in the disintegration of that part of the shell during sieving. It was not possible, however, to quantify these observations.

3.3.5. Estimates of the Production and Mortality of M. balthica.

The biomass, growth and flesh status data discussed in the previous sections were incorporated together with size-frequency data into production (and mortality) estimates which were carried out in five stages: Sections 3.3.5.1. to 3.3.5.5.

3.3.5.1. The Creation of Groups of Stations to Facilitate the Estimation of Production.

On the basis of the constructed Bertalanffy growth curves with respect to both size and weight (Figs. 3.3 & 3.4) the stations which had similar growth rates of M. balthica were grouped together for the purposes of calculating production. This step was necessary in order to provide both a more accurate and time-saving estimation of production. The ease of interpretation of the size frequency data is dependent upon the number of individuals obtained at any one sampling occasion. As some stations had low densities then it was necessary to group these together with other stations. If, however, combined stations had differing growth rates then the separation of the cohorts in the size frequency histograms would prove difficult. It was therefore more accurate to group together stations with similar growth rates. A possible alternative to this method of increasing the accuracy of estimating the production would have been to combine stations with similar environmental factors. However, this latter method would predetermine the reaching of conclusions regarding the affect of environmental factors on the production of a species and would only be valid if all possible factors affecting the species were taken into consideration during grouping of the stations.

The stations were combined into five groups which, on a shell-size basis, were discrete (Fig. 3.3).

Group 1 - Stations A1, C1.
Group 2 - Stations B1, B2, B3.
Group 3 - Stations B4, B5, C2, C3, C4.

Group 4 - Stations A2, A3, A4.

Group 5 - Station C5.

At Station C5, the growth rate of M. balthica was sufficiently low to preclude the incorporation of the station into any of the other groups. As this station supported a low M. balthica population, the estimates of production and mortality may be subject to larger errors than those for the other groups.

3.3.5.2. The Size-Frequency Analysis of the Groups.

The size-frequency histograms were prepared for each group and sampling date and all demonstrate the continual presence, and usually dominance, of first year animals; 0+ to 1+ cohorts (Fig. 3.10; Groups 1 to 5). As with the size-frequency distribution of any species whose growth rate decreases with time, the tendency for the cohorts to merge together increased with age.

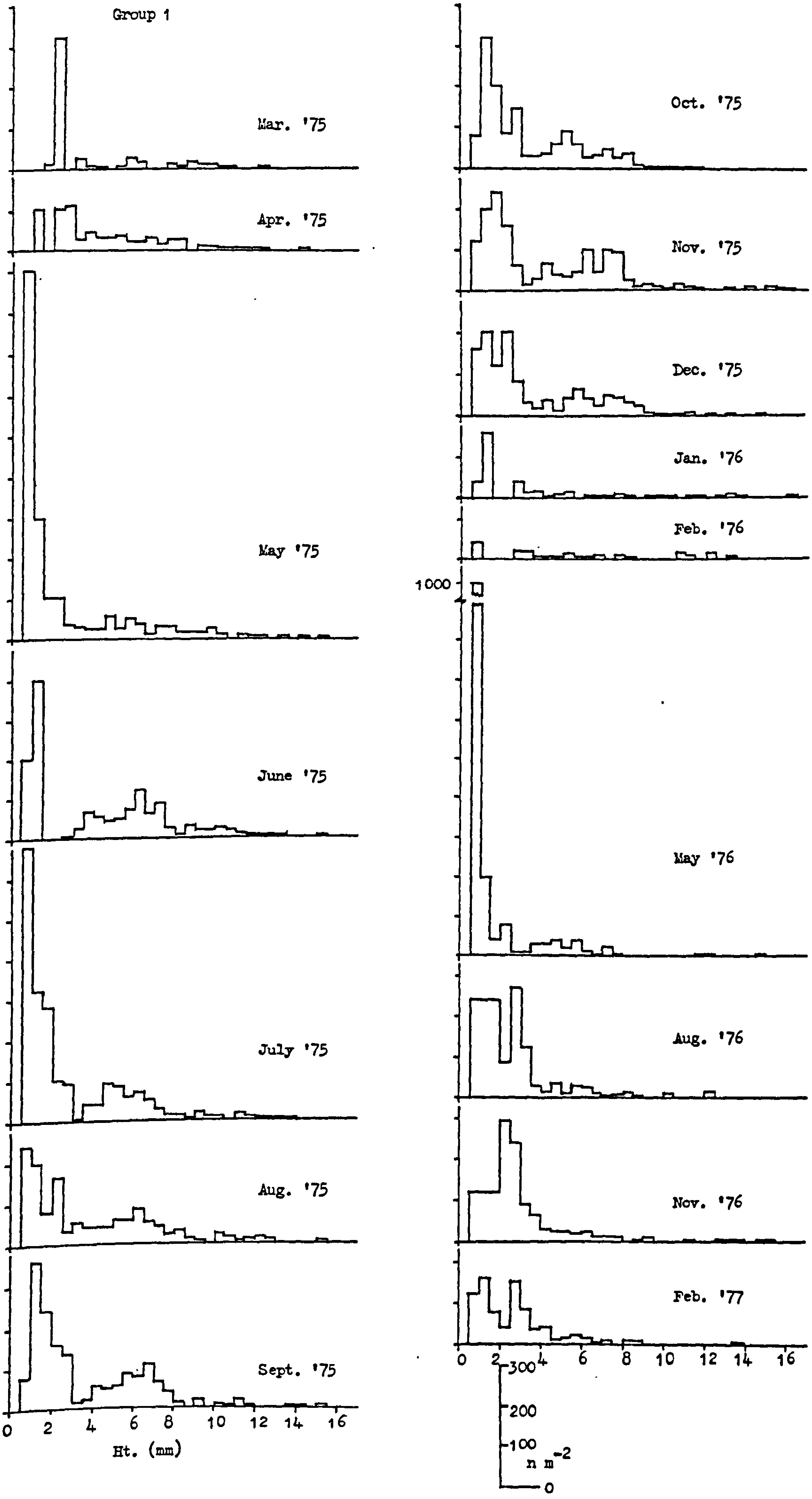
The range of sizes of M. balthica sampled decreased with the progression from Group 1 to Group 5 as did the growth rates, longevity and maximum sizes. In addition, the presence of the older cohorts at all stations in low numbers resulted in their being erratically sampled. This, together with the overlapping of older cohorts, resulted in the cohorts 6+ and older in Groups 1, 2 and 3, and cohorts 4+ and older in Groups 4 and 5, being analysed together.

3.3.5.3. The Change in Mean Size and Weight of Each Cohort With Time at Each Group of Stations.

The range of sizes in each cohort at each month were delimited utilising the winter sizes (i.e. the period of ring formation) of each cohort from the growth ring data and the

Figure 3.10 M. balthica : The Size-frequency Histograms for Each Group of Stations Used in the Production Calculations and at Each Sampling Occasion.

Group	Stations
1	A1, C1
2	B1, B2, B3
3	C2, C3, C4, B4, B5
4	A2, A3, A4
5	C5


Group 1
Mar. '75
Apr. '75
May '75
June '75
July '75
Aug. '75
Sept. '75
0 2 4 6 8 10 12 14 16
Ht. (mm)
Oct. '75
Nov. '75
Dec. '75
Jan. '76
Feb. '76
1000
May '76
Aug. '76
Nov. '76
Feb. '77
0 2 4 6 8 10 12 14 16
300
200
100
n m-2
0

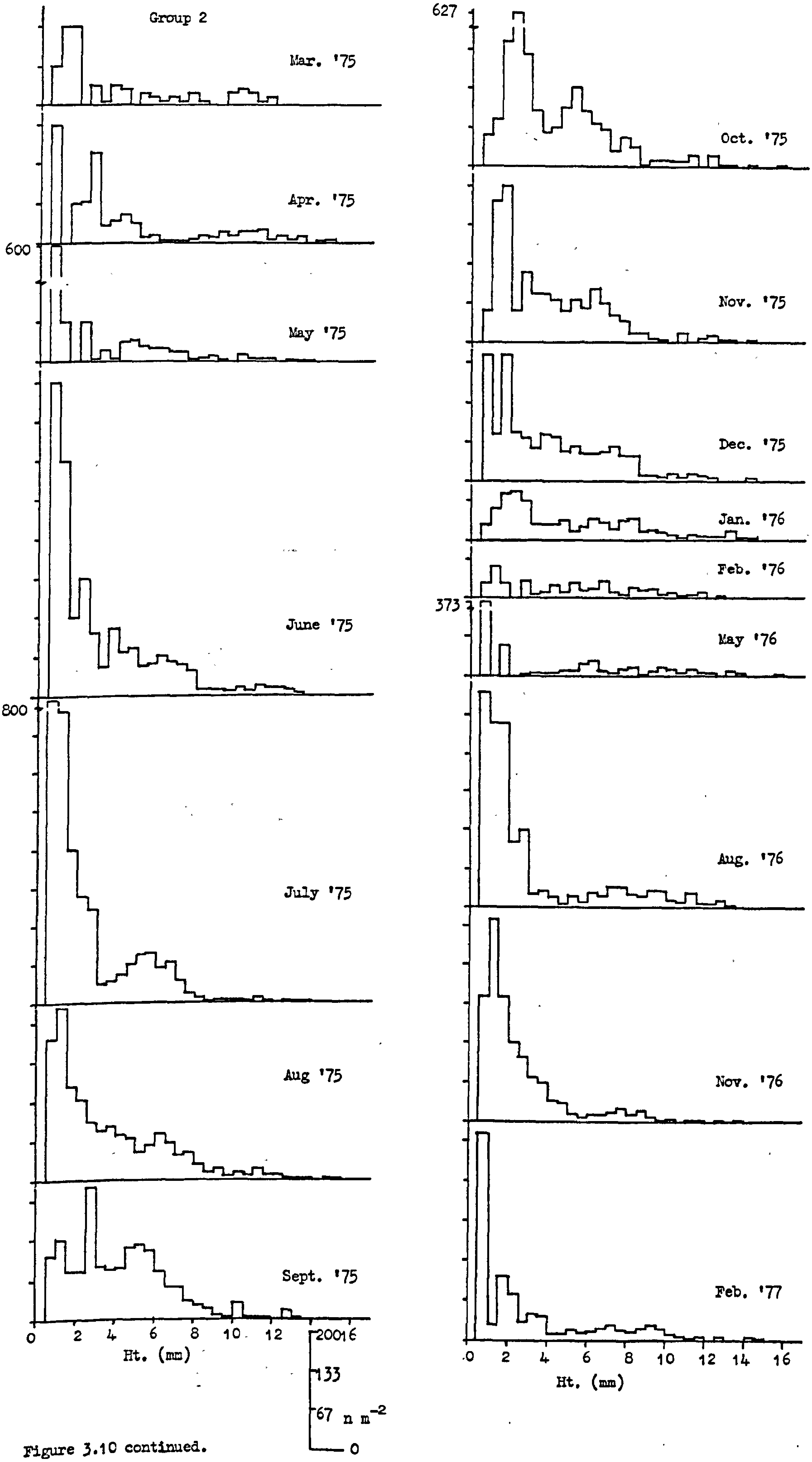


Figure 3.10 continued.

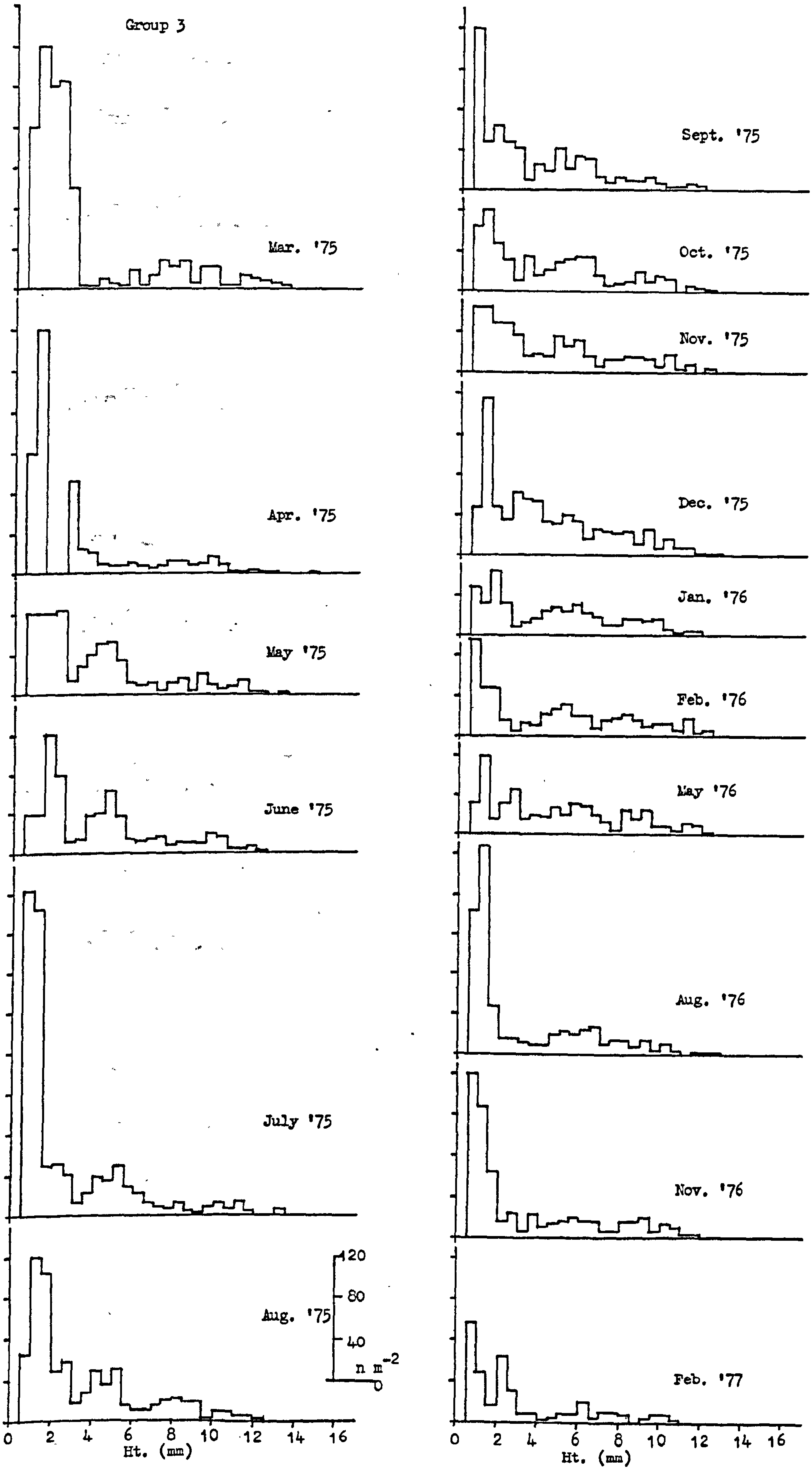


Figure 3.10 continued.

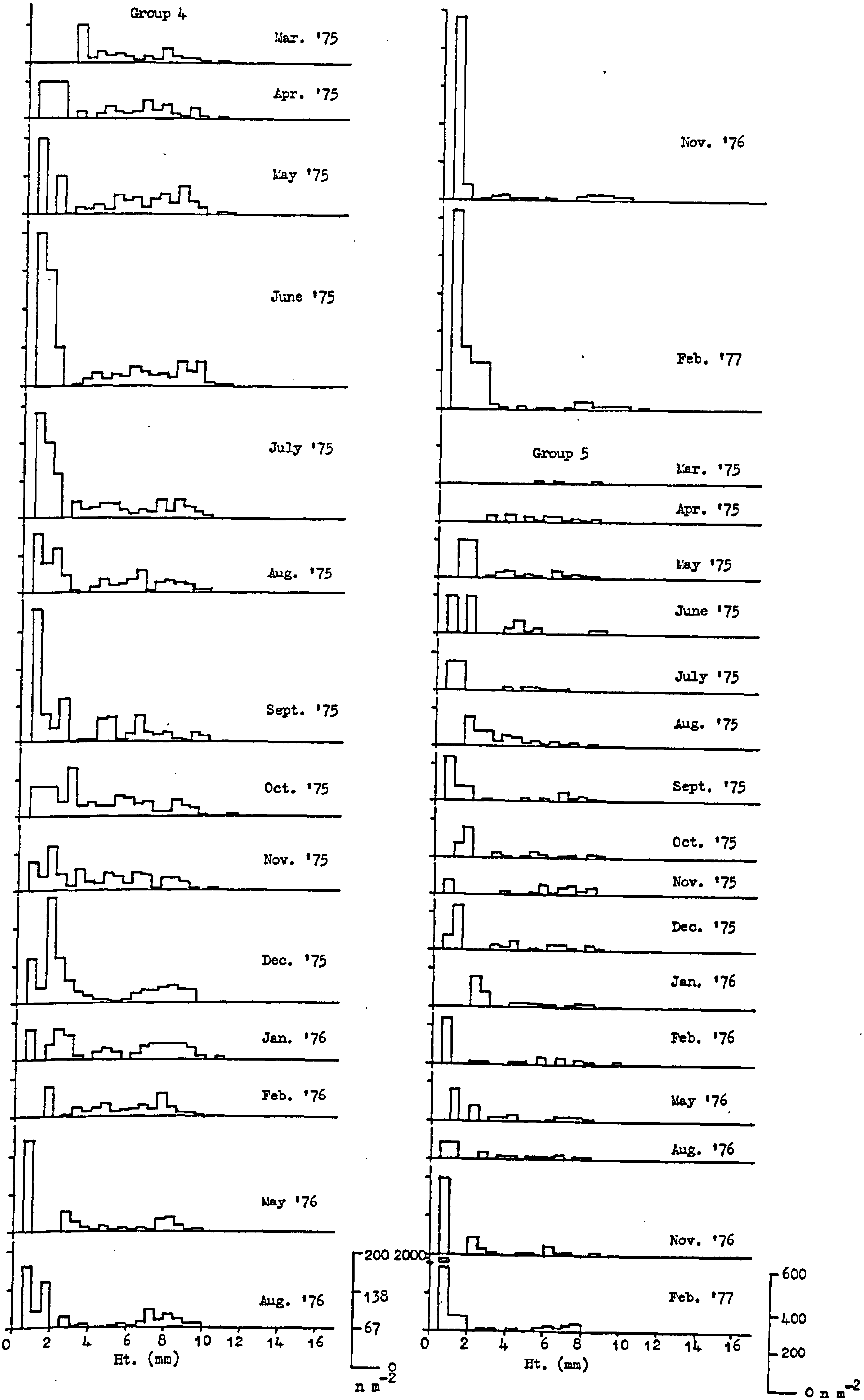


Figure 3.10 continued.

modes in the size-frequency histograms. The monthly mean size of each cohort in each group was then determined as were the cohort mean flesh weights using the appropriate height-fdw regression equations. The regression equations used for each group were those of the station which contributed the greatest amount to each group biomass; in Group 1, Station A1; in Group 2, Station B3; in Group 3, Station B4; in Group 4, Station A3; and in Group 5, Station C5. This assumption, that the stations within each group had similar regression equations, was considered valid on the basis of the data obtained.

The growth rate as mean sizes and weights of each group cohort at each sampling date are plotted in Figs. 3.11 to 3.15 and given in Appendix 3.3. All cohorts demonstrated sigmoid growth of both size and weight over the year although the period of most active growth changed both with cohort and group. In addition, the annual change in shell size and flesh weight decreased with increasing age of the cohorts and from Group 1 to Group 5.

Cohort Annual Growth.

Group 1.

Size Changes (Fig. 3.11a): the 0+ group showed an initial slow increase upto September and then ceased growing over the winter period. The major part of the following years' growth, as the 1+ cohort, was in the period April to July after which growth again slowed down over the winter period. The 2+ and older cohorts gradually increased in size over the period May to December which was followed by a period of little or no growth over the winter.

Figure 3.11 *M. balthica* : The Shell Height (a) and Flesh Dry Weight (b) Annual Growth Patterns of Each Cohort in Group 1 (Stations A1, C1).

(a)
(b)
Ht. (mm)
16
14
12
10
8
6
4
2
0
fdw (mg)
100
10.0
1
0.1
0.01
'69+
'70
'71
'72
'73
'74
'75
'76
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F

Figure 3.12 *M. balthica* : The Shell Height (a) and Flesh Dry Weight (b) Annual Growth Patterns of Each Cohort in Group 2 (Stations B1, B2, B3).


(a)
(b)
Ht. (mm)
16
14
12
10
8
6
4
2
0
fdw (mg)
100
10.0
1
0.1
0.01
'69+
'70
'71
'72
'73
'74
'75
'76
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F

Figure 3.13 M. balthica : The Shell Height (a) and Flesh Dry Weight (b) Annual Growth Patterns of Each Cohort in Group 3 (Stations C2, C3, C4, B4, B5).


(a)
(b)
Ht.
(mm)
0
2
4
6
8
10
12
14
16
fdw
(mg)
0.01
0.1
1
10.0
100
'69+
'70
'71
'72
'73
'74
'75
'76
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F

Figure 3.14 _M. balthica_ : The Shell Height (a) and Flesh Dry Weight (b) Annual Growth Patterns of Each Cohort in Group 4 (Stations A1, A2, A3).


(a)
(b)
Ht.
(mm)
16
14
12
10
8
6
4
2
0
'71+
'72
'73
'74
'75
'76
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F
fdw
(mg)
100
10.0
1
0.1
0.01

Figure 3.15 M. balthica : The Shell Height (a) and Flesh Dry Weight (b) Annual Growth Patterns of Each Cohort in Group 5 (Station C5).


(a)
(b)
Ht.
(mm)
16
14
12
10
8
6
4
2
0
'71+
'72
'73
'74
'75
'76
fdw
(mg)
100
10.0
1
0.10
0.01
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F

Weight Changes (Fig. 3.11b): in 1975 the 0+ cohort increased in weight upto September and, following a period of emaciation, increased more rapidly in weight from January to August as the 1+ cohort. The 1+ and 2+ cohorts, in 1975, increased in weight mainly during the period March to June and then emaciation occurred during the latter part of the year. The older cohorts showed very little change in weight over the year.

The 0+ cohort showed a mean weight loss during July and August which may be attributable to either emaciation or to an inflow of spat. The 1+ and 2+ groups showed emaciation in the period August to October whilst the 3+ and older cohorts showed emaciation from May to September and then again in October after a brief increase in flesh weight. All cohorts 1+ and older showed emaciation over the winter until the weight was at a minimum in February before the spring increase in flesh weight.

Group 2 (Fig. 3.12a & b).

In 1975 the 0+ and 1+ cohorts showed size growth upto September which was followed by a cessation of growth over the winter. The major part of the annual growth of the 2+ cohort occurred until August after which growth decreased and stopped in November. Whereas during the following year most of the growth of the 1975 spat (the 1+ cohort) occurred up to May, during that year and the previous year the year classes 2+ and older were shown to have the highest growth in the period May to August. This shows that animals 2+ and older diverted energy into reproduction at the expense of growth during the first part of the year and only after spawning did growth occur.

On a flesh weight basis, however, much of the annual weight increase occurred during the early part of the year from March to June, with most of the cohorts then showing emaciation during July. The weight subsequently increased during August and then after a period of little change the flesh weight decreased during October and November. The annual flesh weight minimum was preceeded by a slight weight increase during December and January.

Group 3 (Fig. 3.13a & b).

In 1975 the size of the 0+ cohort increased gradually from settlement up to August and, after a decrease in September possibly attributable to further settlement, further increased until December after which growth ceased during the winter. The mean size of the 1+ cohort increased from April to November and differed from the size increase by the older cohorts in which the size changed little until July, after which the annual size increment was achieved by November.

The largest relative weight changes were by the 1+ cohort in which the major part of the annual flesh increase occurred during the period April to August. The mean weight of all other cohorts increased to May, in some cases decreased over June and July, then a further increase in August was followed by a gradual emaciation which ended in February. The size and flesh weight of the 1967 and 1970 cohorts showed no overall change over the sampling period. This gradual emaciation and senility was not shown as markedly in Groups 1 and 2 where the corresponding cohorts continued to grow.

Group 4 (Fig. 3.14a & b).

In 1975 the greatest change in size was again by the 1+

cohort (1974 spat). The decrease in mean size and weight of this cohort in April 1975 was possibly due to the occurrence in the samples of spat which settled the previous year but were too small to be retained during sampling before the spring growth commenced.

The mean size of the 0+ cohorts increased until October when growth ceased over the winter period, whilst that of the 1+ and 3+ cohorts increased until November and that of the 2+ cohort increased until January. The 4+ cohort had only a short period of growth until the summer.

Each of the cohorts showed flesh weight increases until June and then, after a short period of emaciation, again increased slightly until September after which emaciation occurred over the winter period.

Group 5 (Fig. 3.15a & b).

The cohort size and weight changes in this group, which consisted only of Station C5, were erratic; much of which could be attributable to the low density of each cohort found at this station. All cohorts showed gradual size increases over the year although the 1+ cohort showed the greatest increase over the year. It is not possible, however, to comment with accuracy on the periods of the year when the major part of the annual growth occurred.

All cohorts reached a maximum flesh weight during the period August to September which was followed by emaciation over the late autumn and early winter period. This period was followed by a slight flesh weight increase during January and February.

3.3.5.4. The Computation of Production and Mortality.

The production and mortality of each cohort in each group for each sampling year were calculated using the data for survivorship and mean size of each cohort (see Appendix 3.3 and Summary Table 3.11).

In the sampling year 1975-76 the $P/\bar{B}$ and $M/\bar{B}$ values of the Group 1 animals decreased with increasing age of the cohorts and whereas the age classes 1+ and 2+ contributed most to the total production, the 1+ cohort also suffered the highest mortality (over 50%) of the group total. The following sampling year showed similar trends except that the 3+ cohort had the highest productivity and production. The $M/\bar{B}$ values also increased with age and the 5+ cohort suffered the greatest mortality.

In Group 2, during both sampling years the 1+ cohort had the greatest $P/\bar{B}$ value which then also decreased with increasing age of the cohorts. The older cohorts had the largest $M/\bar{B}$ values. The 1974 cohort (as the 1+ group in 1975-76, and 2+ in 1976-77) had the highest production while the older cohorts suffered the largest mortality.

In Group 3, again the 1+ had the highest productivity during both years, after which this value decreased with increasing age until the older cohorts had negative production and productivity as a result of the net annual emaciation. The 1974 cohort again had the largest production in both years, the highest $M/\bar{B}$ value in 1975-76, and, together with the 1+ and 7+ classes, had the highest $M/\bar{B}$ value in 1976-77. The annual total mortality in both years increased with increasing age. The 0+ class (the newly settled spat) had negative $M/\bar{B}$ and mortality values in 1976-77 which were attributable to the large

Table 3.11 *M. balthica:* The Production and Mortality of Each Group and Cohort, 1975-76 Data.

Cohort	$\bar{B}$ mg Fdw m^{-2}	S.D.	P_2 mg m^{-2} yr^{-1}	M_2 mg m^{-2} yr^{-1}	Annual $P/\bar{B}$	Annual $M/\bar{B}$
Group 1						
1975	27.728	21.216	69.666	58.447	2.512	2.108
1974	356.932	234.710	677.790	711.095	1.899	1.992
1973	995.962	691.951	786.902	110.566	0.790	0.110
1972	713.278	426.009	202.421	217.502	0.284	0.305
1971	976.552	654.581	161.139	202.905	0.165	0.208
1970	613.759	508.403	227.294	58.272	0.370	0.095
1969+	1196.749	943.653	-64.899	-52.818	-0.054	-0.044
Total	4880.960		2060.313	1305.969	0.422	0.268
Group 2						
1975	87.025	80.046	59.231	39.820	0.681	0.458
1974	837.597	528.013	1058.465	262.629	1.264	0.313
1973	864.546	576.388	206.686	143.871	0.239	0.166
1972	485.791	227.579	84.909	-18.338	0.175	-0.038
1971	501.917	248.259	111.772	-4.507	0.223	-0.009
1970	859.672	422.426	228.892	1233.604	0.266	1.435
1969+	1425.039	767.895	687.155	1673.332	0.482	1.174
Total	5061.587		2437.110	3330.411	0.481	0.658
Group 3						
1975	11.212	10.784	13.288	6.407	1.185	0.571
1974	147.168	65.893	375.862	253.088	2.554	1.720
1973	279.907	123.466	183.385	74.510	0.655	0.266
1972	252.907	98.536	23.009	54.442	0.091	0.215
1971	305.346	146.341	49.879	238.727	0.163	0.782
1970	400.835	128.111	-207.627	-59.613	-0.518	-0.149
1969+	1002.081	397.253	-64.291	902.713	-0.064	0.901
Total	2399.456		373.505	1470.274	0.156	0.613
Group 4						
1975	17.262	13.011	40.698	23.128	2.358	1.340
1974	97.560	61.154	96.764	37.591	0.992	0.385
1973	315.399	152.530	226.816	93.143	0.719	0.295
1972	321.266	146.156	206.225	-28.355	0.642	-0.088
1971+	1090.613	519.844	106.128	416.058	0.097	0.381
Total	1842.100		676.663	541.565	0.367	0.294
Group 5						
1975	20.176	33.824	17.252	14.111	0.855	0.699
1974	70.821	72.966	225.175	194.570	3.179	2.747
1973	184.188	95.842	111.877	-57.695	0.607	-0.313
1972	224.732	141.190	-55.805	-184.885	-0.248	-0.823
1971+	331.245	236.924	-606.946	-553.835	-1.832	-1.672
Total	831.162		-308.477	-587.734	-0.371	-0.707

Table 3.11 continued, 1976-77 Data.

Cohort	$\bar{B}$ mg Fdw m^{-2}	S.D.	P mg m^{-2} yr^{-1}	M mg m^{-2} yr^{-1}	Annual $P/\bar{B}$	Annual $M/\bar{B}$
Group 1						
1976	99.880	82.735	211.852	74.988	2.121	0.751
1975	154.463	63.656	289.181	140.757	1.872	0.911
1974	241.590	119.773	142.491	106.847	0.590	0.442
1973	286.968	107.087	703.180	82.730	2.450	0.288
1972	102.826	125.741	55.439	76.217	0.539	0.741
1971	289.291	326.501	47.483	523.415	0.164	1.809
1970	121.900	165.423	101.160	502.890	0.830	4.125
1969+	380.901	399.961	217.130	228.795	0.570	0.601
Total	4880.960		2060.313	1305.969	0.422	0.268
Group 2						
1976	49.033	40.901	36.410	-7.320	0.743	-0.149
1975	122.690	63.097	258.920	97.845	2.110	0.797
1974	510.286	283.178	307.170	236.376	0.602	0.463
1973	530.412	252.257	101.129	-352.667	0.191	-0.665
1972	513.990	357.722	219.183	-35.884	0.426	-0.070
1971	491.636	538.689	294.487	381.188	0.599	0.775
1970	365.932	233.779	115.588	444.972	0.316	1.216
1969+	635.364	346.429	36.945	-476.480	0.058	-0.750
Total	3219.343		1369.832	288.030	0.425	0.089
Group 3						
1976	10.888	9.162	20.467	-1.991	1.880	-0.183
1975	44.167	20.292	146.135	112.859	3.309	2.555
1974	239.070	63.771	210.785	240.214	0.882	1.005
1973	236.375	88.888	140.796	207.489	0.596	0.878
1972	232.170	80.751	58.512	230.118	0.252	0.991
1971	271.742	104.218	80.034	251.673	0.294	0.926
1970	250.378	101.285	20.584	249.583	0.082	0.997
1969+	539.461	389.801	-29.753	994.028	-0.055	1.843
Total	1824.251		647.560	2283.973	0.355	1.252
Group 4						
1976	8.658	8.811	8.640	-17.055	0.998	-1.970
1975	30.284	20.484	58.040	3.719	1.916	0.123
1974	58.594	28.300	61.009	113.704	1.041	1.940
1973	144.177	98.246	46.663	137.991	0.324	0.957
1972	229.129	131.243	39.788	296.927	0.174	1.296
1971+	221.080	56.805	39.885	149.700	0.180	0.677
Total	691.922		254.025	684.986	0.367	0.990
Group 5						
1976	8.969	14.758	-6.337	-45.577	-0.706	-5.082
1975	23.700	16.108	113.565	105.870	4.792	4.467
1974	85.084	65.820	60.530	-77.820	0.711	-0.915
1973	137.115	51.690	28.840	19.700	0.210	0.144
1972	208.256	116.273	-45.700	-63.540	-0.219	-0.305
1971+	16.382	50.049	-65.530	65.530	-4.000	4.000
Total	479.506		85.368	4.163	0.178	0.009

recruitment; the spatfall in 1976 in this group was greater than in 1975.

In 1975-76, the animals of Group 4 showed a decrease in both $P/\bar{B}$ and $M/\bar{B}$ with increasing age and although the 2+ and 3+ cohorts contributed most (60%) to the group total production, the 4+ and older cohorts suffered the greatest mortality. During 1976-77, the 1+ animals had the greatest $P/\bar{B}$ while the 2+ class had the highest $M/\bar{B}$ and again the spat showed negative mortality. In addition, while the 2+ and 1+ cohorts showed the greatest production which then decreased with age, the 4+ animals suffered the largest annual mortality.

In Group 5, the 1+ animals had the largest production and mortality during both years and also had the highest $P/\bar{B}$ and $M/\bar{B}$ values in 1975-76. The low and erratic densities of animals older than 1+ resulted in the estimation of negative mortality during 1975-76. The oldest classes suffered a high mortality during the second sampling year and, as a result of net emaciation and senility, also had both negative production and productivity.

The estimates for overall annual production for the first year of sampling were found to range from 2.4 to -0.3g fdw m^{-2} and the annual $P/\bar{B}$ from 0.481 to -0.371. It is of interest to note that while the first group had the highest growth rates, the second group had the highest productivity. In addition, the largest production and mortality estimates, as with the highest biomasses and densities, did not occur in those areas with the highest growth rate of M. balthica.

The trends described above and in the Fig. 3.16a & b, suggest that whilst the $P/\bar{B}$ declined with age after the first

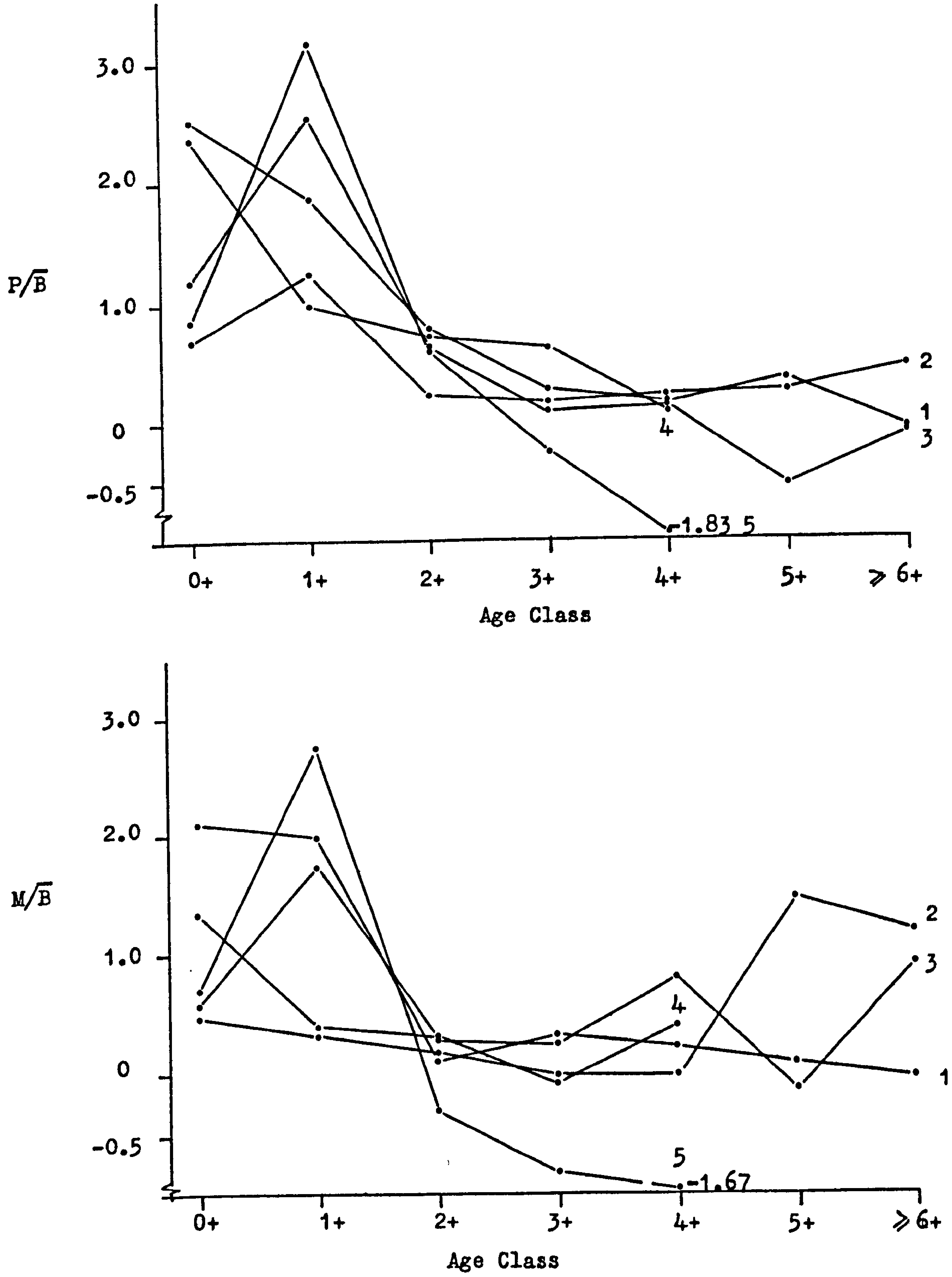


Figure 3.16 M. balthica : The Change in $P/\overline{B}$ and $M/\overline{B}$ Values With Age of Cohorts (1975-76 Data) and Groups 1-5 (see Text).

one or two years, the $M/\bar{B}$ was high during the first couple of years and in the older cohorts and relatively low during the ages 2+ to 4+. This may be interpreted as high mortality at the early stages, attributable to unsuccessful spat settlement and a high predation of the young (1 or 2 year old) animals, and to senility, overall emaciation and the increased influence of the environment in later life. In addition, the 1+ animals, which usually had the largest $P/\bar{B}$ (and growth rate), were possibly of a size and density conducive to high predation.

Additionally, while the greatest mortality occurred in the older cohorts, the 1+ and 2+ cohorts contributed the largest amounts to the population production. In most of the groups in which the 1+ cohort had the largest production during 1975-76, that cohort, as the 2+ cohort, also had the largest production during 1976-77. It is considered, therefore, that there was a large and successful spatfall in 1974 which largely influenced the population production ecology during the years studied.

In certain production and mortality estimates, negative values were calculated (Table 3.11). While negative production due to senility and negative mortality attributable to an increased recruitment period in very young animals was not unusual, the estimation of either negative production or mortality, in cohorts other than these, may be the result of sampling very low densities of certain cohorts at the constituent areas within a group of stations, i.e. those cohorts would not necessarily appear at each sampling occasion. In 1975-76, where many sampling occasions were incorporated into the production and mortality estimates, the errors caused by the presence or absence of such cohorts cancelled each other out to give more accurate estimates of annual production and mortality. In 1976-77, where fewer sampling occasions were used, the estimates obtained may be less accurate (see Section 3.3.5.6.1.).

3.3.5.5. The Application of Group $P/\bar{B}$ and $M/\bar{B}$ Values to the Stations.

The overall $P/\bar{B}$ and $M/\bar{B}$ values obtained for each group were then applied to the biomasses of the constituent stations within the groups to calculate the production and mortality at each station. In performing this step, the assumption was made that the station to which a ratio was applied had the same frequency of animals in each age class as the group that contained that station. This was necessary as the group overall $P/\bar{B}$ and $M/\bar{B}$ values were weighted according to the average biomass of each age class incorporated into the production and mortality estimates. In order to reduce possible errors in this assumption, separate $P/\bar{B}$ and $M/\bar{B}$ values were applied to the spat and large animal parts of the population (Tables 3.12, 3.13, 3.14). As the spat, although present in high numbers, contributed only a small proportion to the total biomass at each station, the overall $P/\bar{B}$ and $M/\bar{B}$ of each station was therefore, to a greater or lesser extent, dependent upon the group $P/\bar{B}$ and $M/\bar{B}$ for the "large" part of the population.

In 1975-76 the annual mean biomass ranged from 800mg m^{-2} to in excess of 9g m^{-2} fdw, the annual production ranged from -290mg to 4.4g m^{-2} although in both parameters the majority of the stations had values of less than 1g m^{-2} fdw (Table 3.13). In the following year the mean annual biomass values from 480mg to 6g fdw m^{-2} were estimated to produce between 55mg and 2.5g fdw m^{-2} yr^{-1}. However, whilst the majority of the stations (all but B1

Table 3.12 *M. balthica* : The $P/\bar{B}$ and $M/\bar{B}$ Values Used to Compute the Station Production and Mortality for Both Sampling Years and Small and Large Parts of the Populations.

Group	Stations	$P/\bar{B}$ Values				$M/\bar{B}$ Values			
		1975-76		1976-77		1975-76		1976-77	
		Spat	Large	Spat	Large	Spat	Large	Spat	Large
1	A1, C1.	2.512	0.422	2.121	1.054	2.108	0.268	0.751	1.035
2	B1, B2, B3.	0.681	0.481	0.743	0.425	0.458	0.658	-0.149	0.089
3	C2, C3, C4, B4, B5.	1.185	0.156	1.880	0.355	0.571	0.613	-0.183	1.252
4	A2, A3, A4.	2.358	0.367	0.998	0.367	1.340	0.294	-1.970	0.990
5	C5.	0.855	-0.371	-0.706	0.178	0.699	-0.707	-5.082	0.009

Table 3.13 *Macoma balthica*: The Production (g Fdw m^{-2} yr^{-1}), Mean Biomass (g Fdw m^{-2}) and Annual $P/\bar{B}$ Summary Data.

	1975-76							1976-77						
	Spat		Large Animals		Total			Spat		Large Animals		Total		
Station	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P	$P/\bar{B}$	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P	$P/\bar{B}$
A1	0.112	0.281	7.459	3.148	7.571	3.429	0.453	0.099	0.209	2.149	2.265	2.248	2.474	1.108
A2	0.022	0.053	1.393	0.511	1.415	0.564	0.398	0.012	0.012	0.496	0.182	0.508	0.194	0.382
A3	0.020	0.048	2.081	0.764	2.101	0.812	0.386	0.010	0.010	0.700	0.257	0.710	0.267	0.376
A4	0.013	0.030	1.741	0.639	1.869	0.669	0.358	0.004	0.004	0.944	0.346	0.948	0.350	0.369
B1	0.044	0.030	1.214	0.584	1.258	0.614	0.488	0.035	0.026	2.207	0.938	2.242	0.964	0.430
B2	0.069	0.066	5.173	2.488	5.242	2.554	0.487	0.050	0.037	5.912	2.513	5.692	2.550	0.428
B3	0.101	0.069	8.994	4.326	9.095	4.395	0.483	0.048	0.035	2.961	1.258	3.009	1.293	0.430
B4	0.032	0.038	3.095	0.483	3.127	0.521	0.167	0.005	0.010	2.459	0.873	2.464	0.883	0.358
B5	0.018	0.021	4.066	0.634	4.084	0.655	0.160	0.019	0.035	2.994	1.063	3.013	1.098	0.364
C1	0.010	0.025	1.824	0.770	1.834	0.795	0.433	0.005	0.010	1.353	1.426	1.358	1.436	1.058
C2	0.050	0.059	1.026	0.160	1.076	0.219	0.204	0.038	0.071	0.781	0.277	0.819	0.348	0.425
C3	0.043	0.051	1.918	0.299	1.961	0.350	0.179	0.033	0.062	0.890	0.316	0.923	0.378	0.409
C4	0.030	0.035	3.182	0.496	3.212	0.531	0.165	0.004	0.007	1.632	0.579	1.636	0.586	0.358
C5	0.011	0.010	0.809	-0.300	0.820	-0.290	-0.354	0.034	-0.024	0.447	0.080	0.481	0.056	0.116

Table 3.14 *Macoma balthica:* The Mortality (g Fdw m^{-2} yr^{-1}), Mean Biomass (g Fdw m^{-2}) and Annual M/$\bar{B}$ Summary Data.

	1975-76							1976-77						
	Spat		Large Animals		Total			Spat		Large Animals		Total		
Station	$\bar{B}$	M	$\bar{B}$	M	$\bar{B}$	M	M/$\bar{B}$	$\bar{B}$	M	$\bar{B}$	M	$\bar{B}$	M	M/$\bar{B}$
A1	0.112	0.236	7.459	1.999	7.571	2.235	0.295	0.099	0.074	2.149	2.224	2.248	2.298	1.022
A2	0.022	0.030	1.393	0.409	1.415	0.431	0.305	0.012	-0.023	0.496	0.491	0.508	0.476	0.921
A3	0.020	0.027	2.081	0.612	2.101	0.639	0.304	0.010	-0.020	0.700	0.693	0.710	0.672	0.947
A4	0.013	0.017	1.741	0.512	1.869	0.529	0.283	0.004	-0.009	0.944	0.935	0.948	0.926	0.977
B1	0.044	0.020	1.214	0.799	1.258	0.819	0.651	0.035	-0.005	2.207	0.196	2.242	0.191	0.085
B2	0.069	0.032	5.173	3.404	5.242	3.436	0.655	0.050	-0.007	5.912	0.526	5.962	0.518	0.087
B3	0.101	0.046	8.994	5.918	9.095	5.964	0.656	0.048	-0.007	2.961	0.263	3.009	0.256	0.085
B4	0.032	0.018	3.095	1.897	3.127	1.915	0.612	0.005	-0.001	2.459	3.079	2.464	3.078	1.249
B5	0.018	0.010	4.066	2.492	4.084	2.502	0.613	0.019	-0.003	2.994	3.748	3.013	3.745	1.243
C1	0.010	0.021	1.824	0.489	1.834	0.510	0.278	0.005	0.003	1.353	1.400	1.358	1.403	1.034
C2	0.050	0.028	1.026	0.629	1.076	0.657	0.611	0.038	-0.007	0.781	0.978	0.819	0.971	1.186
C3	0.043	0.025	1.918	1.176	1.961	1.201	0.612	0.033	-0.006	0.890	1.114	0.923	1.108	1.201
C4	0.030	0.017	3.182	1.951	3.212	1.968	0.613	0.004	-0.001	1.632	2.043	1.636	2.042	1.248
C5	0.011	0.008	0.809	-0.592	0.820	-0.584	-0.712	0.034	-0.174	0.447	0.004	0.481	-0.170	-0.353

and B2) had lower mean biomass estimates for the second year of sampling than for 1975-76, only five of the stations had lower production values (A1 to A4, B3). It is difficult to suggest what proportion of these differences was attributable to an increased sampling interval (see Section 3.3.5.6.1.).

The annual mortality values were found to be within the range -580mg fdw m^{-2} to 6g fdw m^{-2} in 1975-76 and from -170mg fdw m^{-2} to 3.7g fdw m^{-2} yr^{-1} the following year (Table 3.14). In addition, only five stations had lower mortalities during the second sampling year than in 1975-76.

The fact that in 1976-77 most stations had both higher production and mortality when compared to 1975-76 may be attributed to the high spatfalls over these two years. A high spatfall in 1975 would have resulted in a large proportion of highly producing individuals during the following year and similarly this age group would possibly have contributed to the high mortality. However, the even greater spatfall in 1976 would possibly have resulted in a greater population production during 1977.

The difference in production and mortality between the two years of sampling could not be attributed to changes in the physical environmental variables (see Chapter 2).

In addition, for purposes of comparison with other geographical area, the Torry Bay mean production, biomass, mortality, and annual $P/\bar{B}$ and $M/\bar{B}$ values were calculated for the two sampling years; (Table overleaf)

	1975-76	1976-77
$\bar{B}$ g m^{-2}	3.190	1.880
P g m^{-2} yr^{-1}	1.130	0.920
M g m^{-2} yr^{-1}	1.587	1.250
$P/\bar{B}$	0.354	0.489
$M/\bar{B}$	0.497	0.665

Although the mean biomass for the second year was considerably smaller than for 1975-76, the amount of material produced by that biomass was similar to the previous year. Similarly, both the mortality and the $M/\bar{B}$ values were higher during the second year of sampling.

While the mean areal values obtained reflect the levels of production, etc., for the part of Torry Bay which had been sampled, these values will not necessarily be accurate for the whole of the intertidal area. It is considered, however, that as that part of the intertidal area not sampled contains both areas similar to the low shore stations sampled and, because of the presence of coarse sand banks, to the coarse, upper-shore areas sampled, the areal mean values presented above were of the appropriate order for the whole intertidal area.

3.3.5.6. Alternative Production Estimates.

3.3.5.6.1. The Estimation of Production and Mortality at Station B3.

In order to identify any differences in the estimation of production and mortality between the two sampling years which were attributable to the sampling interval, the production and mortality of Station B3 for the year 1976-77 were calculated using the data collected for that station on a monthly basis (see Appendix 3.5 and Summary Table 3.15). Although the $P/\overline{B}$ values calculated on a quarterly and monthly sampling interval were similar (0.430 and 0.412 respectively) and together were in good agreement with that calculated for the previous year using a monthly sampling interval (0.483), the $M/\overline{B}$ values for the 1976-77 data estimates (0.085 quarterly and 0.599 monthly) were not in agreement. The $M/\overline{B}$ values from monthly estimates for the two years (0.656 for 1975-76 and 0.599 for 1976-77) however were of the same order. It is probable therefore that although the $P/\overline{B}$ estimates based on a quarterly sampling interval were as accurate as those based on a monthly interval, the $M/\overline{B}$ values were underestimated when a longer sampling interval was used. It has also been shown that the longer sampling period also underestimated the annual average biomass present at the stations (4.46g fdw m^{-2} cf. 3.01g fdw m^{-2}) and therefore also underestimated the values of total mortality and production obtained for those stations.

As the production and mortality estimates of many stations were higher during the second year of sampling, the values calculated on a monthly basis for 1976-77 could therefore have been even greater. The mean areal values for the production, biomass and mortality for the second year would also have been increased such that the estimates for both years would have been similar.

3.3.5.6.2. An Alternative Computation of Production.

The method used above for the computation of production (i.e. Crisp, 1971; Method 2) involved many problems, not the least of which was the suitability of the data in some cases to the method. It is considered necessary, therefore, to give an indication of the accuracy of the production estimates by the use

Table 3.15 M. balthica : Station B3, The Production Summary Data for 1976-77 Utilising Monthly Data.

Cohort	$\overline{B}$ mg fdw m^{-2}	S.D.	P mg fdw m^{-2} yr^{-1}	M mg fdw m^{-2} yr^{-1}	Annual $P/\overline{B}$	Annual $M/\overline{B}$
1976 0+	78.905 ±	78.582	12.789	2.003	0.162	0.025
1975 1+	306.309 ±	177.760	401.526	33.597	1.311	0.110
1974 2+	1086.315 ±	759.746	929.786	786.783	0.856	0.724
1973 3+	799.100 ±	450.614	469.402	612.447	0.587	0.766
1972 4+	505.012 ±	436.487	89.49	797.120	0.171	1.578
1971 5+	536.014 ±	305.925	272.01	559.010	0.507	1.043
>1970 6+	1150.989 ±	922.235	-336.165	-116.570	-0.292	-1.005
Σ Of Cohorts	4462.644		1838.838	2674.390	0.412	0.599
	(g m^{-2})		(g m^{-2} yr^{-1})	(g m^{-2} yr^{-1})		
Σ Cohorts 1976-77 on 4 monthly basis	3.0087		1.2934	0.2559	0.430	0.085
Σ Cohorts 1975-76 Monthly	9.0947		4.3946	5.9641	0.483	0.656

of an alternative method of production computation. The alternative method used corresponded to that given by Crisp (1971) as Method 3A (and also by Bergh, 1974) in which the population was separated into size classes and, using the Ford-Walford growth parameters, the sampling interval growth increment was calculated as the product of the weight-specific growth rate (G_i), the mean biomass of each size class and the time interval. The production was obtained by the summation of the sampling interval growth increments. (This alternative production estimate was quickly computed in the early stages of the data analysis and as such was subject to several assumptions.)

The stations were broadly grouped according to the major environmental characteristics:

Lower-shore/Fine Mud stations (LF) - A1, A3, B1-3, C1-2.
Upper-shore/Coarse Sand stations (UC) - A2, A4, B4-5, C3-5.

Three size classes for each group of stations for the field data 1975-76 were used:-

Size classes (Lengths mm)		0-5.0	5.1-10.0	> 10.1	
" " (Heights mm)	LF	0-3.9	4.0- 7.9	> 8.0	*^{1}
" " " "	UC	0-4.1	4.2- 8.2	> 8.3	*^{2}
" " Mean Length		2.5	7.5	12.5	
" " " Height	LF	1.95	5.95	9.95	*^{1}
" " " "	UC	2.12	6.15	10.18	*^{2}

*^{1} Obtained using the regression (for Station B3):
Ht. = 0,8003L - 0.0486

*^{2} Obtained using the regression (for Station B5):
Ht. = 0.8057L + 0.1099

where Ht. = shell height (mm)
L = shell length (mm)

The weight-specific growth rate (G_i) was then calculated:

$$G_i = bK\,(H_\infty - h)/h$$

where K, H_∞ = Bertalanffy Parameters.
b = Ht./fdw regression coefficient.
h = mean height of size class used.

∴ Parameters used

	LF	UC	
H_∞	12.981	12.038	*[3]
K	0.336	0.280	*[3]
b	3.499	3.192	*[4]

*[3] The H_∞ and K values were taken from the Bertanffy parameters of Stations B3 (for LF) and B5 (for UC) which were considered to be representative stations of the two groups of stations.

*[4] The b values were taken from the November Ht./fdw regression equations for B3 and B5. (This month was used as an 'average' month when the flesh weight was not affected by spawning or prolonged emaciation.)

∴ G_i values used :

Mean Size (mm)		G_i(LF)		G_i(UC)
L	Ht.		Ht.	
2.5	(1.95)	6.65	(2.12)	4.18
7.5	(5.95)	1.39	(6.15)	0.86
12.5	(9.95)	0.36	(10.18)	0.16

The values of G_i were then incorporated into the production computation (see Appendix 3.5 and Table 3.16) in which the monthly mean flesh weights of each size class were calculated using the mean size and the appropriate height/weight regression equations.

Table 3.16 *M. balthica* : The Production at Low Shore/Fine Mud Stations and Upper Shore/Coarse Stations Calculated by the Use of the Weight-Specific Growth Rate (see Appendix 3.5) 1975-76 Data.

Length Size-Class (mm)	LF STATIONS P mg fdw m^{-2} yr^{-1}	$\overline{B}$ mg fdw m^{-2}	Annual P/$\overline{B}$	UC STATIONS P mg fdw m^{-2} yr^{-1}	$\overline{B}$ mg fdw m^{-2}	Annual P/$\overline{B}$
0 - 5.0	470.6	77.5	6.071	130.3	34.1	3.816
5.1 - 10.0	1395.9	1100.0	1.269	659.7	585.5	0.785
> 10.1	543.0	1652.1	0.329	176.4	1207.5	0.146
	2409.6	2829.6	0.852	766.4	1827.1	0.419

Mean values for total area :

	P g m^{-2} yr^{-1}	$\overline{B}$ g m^{-2}	Annual P/$\overline{B}$
Using Above Data	1.588	2.328	0.682
Using Crisp's Method 1975-76	1.130	3.190	0.354
" " " 1976-77	0.920	1.880	0.489

As with the original production estimates (Table 3.15 cf. 3.16) the production and $P/\overline{B}$ estimates found by this alternative method also showed the large difference between the two distinct groups of stations. At the lower-shore/fine mud stations, while the biomass supported was only a factor of 1.5 times greater than at the upper-shore/coarse sand stations (2.83 cf. 1.83g flesh m^{-2}), the production was larger by a factor of three (2.41 cf. 0.77g flesh m^{-2} yr^{-1}) which resulted in the former group having an annual $P/\overline{B}$ value approximately double that of the latter group (0.85 cf. 0.42).

The mean P, $\overline{B}$ and $P/\overline{B}$ estimates for the whole area sampled were in good agreement when compared to those obtained by the original methods (Section 3.3.5.5.)(see Table 3.16). The mean biomass for the area obtained by the alternative estimate was relatively low compared to the original estimate, but the production was higher although of the same order of magnitude; resulting in the $P/\overline{B}$ value obtained for the former estimate being nearly twice the value of that obtained by the latter. In conclusion, the production, mean biomass and $P/\overline{B}$ estimates obtained by both methods and for the successive sampling years are considered to be in satisfactory agreement.

3.4. The Factors Causing Spatial and Temporal Variation in the Production Ecology.

3.4.1. Spatial Analysis.

In order to explain the spatial variation in the abundance, biomass, growth, condition, production and mortality of the population (determined in Section 3.3) in relation to the environmental factors (given in Chapter 2), correlation and regression analyses were conducted (see Section 2.3.). The data used in these analyses are given in Tables 2.3 and 3.18; the abbreviations used throughout this section are given in the legend to Fig. 3.17.

Each population variable is considered in turn with conclusions from, firstly, the Pearson correlation analysis and, secondly, the multiple regression analysis. Multiple regressions were initially constructed for the main population variables, as dependent ones, with all the environmental variables, as independent ones. Then, secondly, multiple regressions were constructed incorporating only selected environmental variables.

3.4.1.1. Factors Affecting the Density and Biomass of M. balthica.

3.4.1.1.1. Pearson Correlation Analysis (Fig. 3.17).

The parameters used are described in Section 3.3.1. The standard deviations of the large and spat animal densities were included as an estimate of the fluctuation in numbers over the year at each station and as such give an indication to the extent of settling and mortality within a station.

The mean station biomass was found only to increase with the CHO. in the water; it was not significantly correlated with any of the other environmental variables. The mean number of

Table 3.18 **M. balthica** : The Data Incorporated in the Spatial Analysis (Abbreviations as in Figure 3.17).

Variable \ Station	A1	A2	A3	A4	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
$\bar{B}$	7.571	1.415	2.101	1.869	1.258	5.242	9.095	3.127	4.084	1.834	1.076	1.961	3.212	0.820
P	3.429	0.564	0.812	0.669	0.614	2.554	4.395	0.521	0.655	0.795	0.219	0.350	0.531	-0.290
M	2.235	0.431	0.639	0.529	0.819	3.436	5.964	1.915	2.502	0.510	0.647	1.201	1.968	-0.584
$P/\bar{B}$	0.453	0.398	0.386	0.358	0.488	0.487	0.483	0.167	0.160	0.433	0.204	0.179	0.165	-0.354
$M/\bar{B}$	0.295	0.305	0.304	0.283	0.651	0.655	0.656	0.612	0.613	0.278	0.611	0.612	0.613	-0.712
$L\bar{N}$	919.2	178.3	300.0	298.3	215.8	395.8	1167.0	496.7	375.8	42.5	187.9	270.8	264.6	175.0
L SD	445.3	80.2	65.5	91.0	135.9	239.8	676.6	149.5	141.3	31.7	93.9	110.9	172.8	63.6
L $\overline{tdw}$	41.699	11.135	13.498	11.604	7.321	38.582	53.394	25.423	32.075	19.196	5.740	14.978	32.606	5.970
L $\overline{fdw}$	7.459	1.393	2.081	1.741	1.214	5.173	8.994	3.095	4.066	1.824	1.026	1.918	3.182	0.809
L%s.w.	82.11	87.49	84.57	85.00	83.42	86.59	83.16	87.83	87.32	90.50	82.13	87.19	90.24	86.45
$S\bar{N}$	1233.3	323.3	233.3	226.7	616.7	743.3	883.3	290.0	193.3	140.0	646.7	500.0	290.0	240.0
S SD	730.0	200.0	161.7	231.6	553.8	729.5	621.0	333.0	179.6	283.1	703.0	271.6	487.8	144.7
S $\overline{tdw}$	0.559	0.112	0.102	0.064	0.222	0.348	0.503	0.160	0.095	0.049	0.249	0.217	0.150	0.083
S $\overline{fdw}$	0.112	0.022	0.020	0.013	0.044	0.069	0.101	0.032	0.018	0.010	0.050	0.043	0.030	0.011
K	0.224	0.395	0.383	0.323	0.166	0.307	0.336	0.280	0.288	0.271	0.295	0.234	0.287	0.411
H_∞	16.002	10.450	10.134	10.670	16.970	14.020	12.981	12.038	12.270	15.038	12.097	13.508	11.626	9.220
H_1	2.411	3.118	2.413	3.239	2.912	1.962	2.966	2.087	1.917	2.672	2.364	1.963	2.690	2.724
H_2	5.138	5.510	4.870	5.290	5.062	5.149	5.824	4.517	4.508	5.608	4.850	4.372	4.920	4.913
H_4	9.061	8.208	7.687	7.850	8.426	9.219	9.326	7.742	7.907	9.553	8.080	7.786	7.848	7.327
H_6	11.567	9.433	8.996	9.192	10.840	11.422	11.114	9.584	9.817	11.848	9.870	9.925	9.498	8.388
H_8	13.169	9.988	9.605	9.895	12.572	12.614	12.028	10.636	10.891	13.183	10.863	11.264	10.427	8.854
T_{95}	12.84	7.57	7.99	9.33	17.92	9.81	8.99	10.85	10.50	10.93	10.50	12.61	10.60	7.41
H_4tdw	95.16	73.67	58.47	59.99	94.24	111.24	127.79	65.06	77.11	154.37	65.15	73.22	80.17	52.27
H_4fdw	13.574	8.815	7.015	9.167	12.239	12.268	16.128	7.441	9.802	17.018	9.395	8.378	7.514	6.397
H_4sw	85.74	88.03	88.00	84.72	87.01	88.97	87.38	88.56	87.29	88.98	85.58	88.56	90.63	87.76
H_8tdw	355.37	149.61	132.09	137.42	398.45	393.19	337.94	205.92	267.93	555.92	175.04	304.03	233.40	100.27
H_8fdw	42.331	16.151	14.337	20.969	40.169	40.170	41.040	21.215	29.134	44.108	24.301	27.514	18.611	11.584
H_8sw	88.09	89.20	89.15	84.74	89.92	89.78	87.86	89.70	89.13	92.06	86.12	90.95	92.03	88.45
CF_H Feb.	15.280	16.484	16.611	21.204	17.327	18.182	14.457	14.530	15.950	17.447	14.274	15.429	15.620	15.659
CF_H May	21.657	20.646	18.465	17.685	22.541	23.735	20.184	17.720	20.277	22.819	21.004	17.605	13.294	15.545
CF_H Aug.	22.685	16.935	14.852	14.817	25.613	22.618	21.083	18.265	18.462	35.185	21.878	19.198	13.652	14.229
CF_H Nov.	15.846	16.683	18.045	11.573	16.884	18.490	15.983	17.640	17.596	18.925	16.771	18.420	10.999	13.925

Figure 3.17 M. balthica: Spatial Data Analysis - Pearson Correlation Matrix of the Population Parameters with Each Other and the Environmental Variables.

Significance and direction of correlations are given as:
+ or - = p *
++ or -- = p **
+++ or --- = p ***

other correlations not significant.

Abbreviations:

$\bar{B}$ = Mean annual biomass, (g m^{-2}), as flesh dry-weight;
P = Annual flesh production, (g m^{-2} yr^{-1});
M = " " mortality, (g m^{-2} yr^{-1});
$P/\bar{B}$ = " production : mean biomass value;
$M/\bar{B}$ = " mortality : mean biomass value;
$L\bar{N}$ = 'Large' animal mean density, (N m^{-2}); L SD = Standard deviation of $L\bar{N}$;
L tdw = " " " total dry-weight biomass, (g m^{-2});
L fdw = " " " flesh " " , (g m^{-2});
L %s.w. = " " " % shell dry-weight of total dry-weight;
$S\bar{N}$ = Spat animal mean density, (N m^{-2}); S SD = Standard deviation of $S\bar{N}$;
S tdw = " " " total dry-weight biomass, (g m^{-2});
S fdw = " " " flesh " " , (g m^{-2});
K = Bertalanffy K value;
H_∞ = " H_∞ " , (mm);
H_1 = Size (height (mm)) at 1 year; H_2 = Size (height (mm)) at 2 years;
H_4 = " " " 4 years; H_6 = " " " 6 " ;
H_8 = " " " 8 " ;
T_{95} = Maximum age, (yrs);
H_4 tdw = Total weight of 4 yr animals, (mg);
H_4 fdw = Flesh " " " " " , (mg);
H_4 s.w. = % shell dry-weight of total dry-weight of 4 yr animals;
H_8 tdw = Total dry-weight of 8 yr animals, (mg);
H_8 fdw = Flesh " " " " " , (mg);
H_8 s.w. = % shell dry-weight of total dry-weight of 8 yr animals;
CF_H Feb. = Condition in Feb. '76;
CF_H May = " " May '76;
CF_H Aug. = " " Aug. '76;
CF_H Nov. = " " Nov. '76;

Environmental variables used as given in Fig. 2.9.

	$\bar{B}$	P	M	$P/\bar{B}$	$M/\bar{B}$	$L\bar{N}$	L SD	L tdw	L fdw	L %s.w.	$S\bar{N}$	S SD	S tdw	S fdw	K	H	H_1	H_2	H_4	H_6	H_8	T_{95}	H_4 tdw	H_4 fdw	H_4 sw	H_8 tdw	H_8 fdw	H_8 sw	CF_H Feb.	CF_H May	CF_H Aug.	CF_H Nov.
$\bar{B}$																																
P	+++																															
M	+++	+++																														
$P/\bar{B}$		+																														
$M/\bar{B}$			+	++																												
$L\bar{N}$	+++	+++	+++																													
L SD	+++	+++	+++			+++																										
L tdw	+++	+++	+++			+++	+++																									
L fdw	+++	+++	+++			+++	+++	+++																								
L %s.w.						-																										
$S\bar{N}$	++	+++	+			++	+++	+++	++	--																						
S SD	+	++	+		+	+	+	+	+	-	+++																					
S tdw	+++	+++	++			+++	+++	++	+++	-	+++	+++																				
S fdw	+++	+++	++			+++	+++	++	+++	-	+++	+++	+++																			
K					-							-																				
H				+	+						+	+	+	+	--																	
H_1																																
H_2		+		+													++															
H_4	+	+++	+	++			+	+	+		+	+	+	+		++		++														
H_6	+	++	+	++			+	+	+		+	++	+	++	-	+++			+++													
H_8	+	+		++	+		+	+	+		+	++	+	+	--	+++			+++	+++												
T_{95}															---	+++				+	++											
H_4 tdw	+	+	+	+				+	+							++		++	+++	+++	+++											
H_4 fdw	+	++	+	++			+	+	+		+	+	+	+		++		++	+++	+++	+++		+++									
H_4 sw																																
H_8 tdw				+											--	+++			+++	+++	+++	+	+++	+++								
H_8 fdw	+	++	+	++			+	+	+		+	++	+	+	--	+++			+++	+++	+++	+	+++	+++		+++						
H_8 sw																																
CF_H Feb.																																
CF_H May				++												++			+++	+++	++		+	++		++	+++					
CF_H Aug.				+											-	+++			+++	+++	+++	+	+++	+++		+++	+++			+++		
CF_H Nov.																	-													++	+	
TH.												-			+	--			--	---	---	-	--	--		---	--			-	---	-
M.P.D.				---												-			--	--	--		-	-		-	-			---	-	--
S.C.																		+														
SK.				+						--	++	+	+	+				+							-					+		
$\%H_2O$		+		++							+					++		++	+++	+++	+++		+++	+++		+++	+++			++	++	
%C				++												+		++	+++	+++	++		+++	+++		++	++		+	+++	++	
%N				+												+		++	+++	++	++		+++	+++		++	++		+	++	+++	
%S. & C.		+		++							+	+				++			++	++	++		+	+		+	++			+++	+	
Slope		-		---	-							-						-	--	--	-		-	-			-			--	-	
C/N				+						-		+													-			-		++		
Sal.												+				+				+	+		+			+		+			+	
CHO.	++	+	+++		+	++	++	++	+++					+																		
Org. C.										--															-			-				
$\bar{x}$ Imm. Per.												+			-	++			+	++	++	+	+	+		++	++			+	+++	+
S Imm. Per.				+	+							+			-	++			++	++	+++	+	++	++		+++	++			++	+++	+
N Imm. Per.												+			-	++			+	++	++		+	+		++	++			+	+++	+

'large' animals was also highest in areas of highest CHO, and of greatest abundance and biomass of spat. The $L_{S.D.}$ was highest at those areas which contained the larger sizes and flesh weight of the older cohorts, the highest CHO levels and also increased with $\bar{B}$, ΔP, ΔM and $L_{\bar{N}}$. This suggests that the highest fluctuations in animal densities were in the common areas (i.e. areas where large populations were found), and in the best areas for the bivalve which had both the greatest settlement and mortality. The L_{tdw} and L_{fdw} also showed the same trends as $L_{S.D.}$.

The spat $\bar{N}$ was greatest at those areas at which the older cohorts were larger and heavier (i.e. the spat settled at optimum areas for growth) and in areas of high SK, %H_2O, and %S & C (i.e. in the fine mud areas). The spat and larger animals were also found together in high numbers at the same site. The range of spat numbers ($S_{S.D.}$) was also greatest in the areas of highest $\bar{B}$, ΔP, ΔM, $M/\bar{B}$ and fdw and tdw of large and small animals; this again is a reflection of the large settlement and mortality in the common areas, areas also where to a large extent the highest growth occurred ($S_{S.D.}$ was -ve correlated with K but +ve with H_∞). The largest spat fluctuations were at the low tidal areas and at the areas of high sediment SK, %S & C, C/N, salinity and at the areas of shallow shore slope. The spat flesh and total biomasses were also greatest at the areas with high growth of the older cohorts and high SK and CHO levels.

The percentage shell weight of the large animals was negatively correlated with $L_{\bar{N}}$, all spat variables, C/N, SK and water organic carbon suggesting that in the common areas of the population less energy was put into producing the shell than in the coarser areas.

The numbers and flesh biomass of the large animals were shown to reach a maximum at the mid-shore area, 3 - 3.5m above C.D.; but with M.P.D. they showed a negative curvilinear relationship (Fig. 3.18a & b). However, Station B3, which had a "too-coarse substrate", and A3, which had "too-fine" a substrate, were exceptions to this general pattern. Stations C1, B1 and B2 also had lower numbers than would be suggested by the curvilinearity in the relationship; this was possibly attributable to the presence of mussel beds at each of these stations. An absence of mussels at these stations would possibly contribute to a positive curvilinear relationship with sediment, %C and %N and would enhance the negative curvilinear relationship with shore slope.

The numbers and flesh biomass were optimal at areas with 2.5% sediment carbon and 0.12% nitrogen (Fig. 3.19a, b, d & e) whereas with shore slope there was a curvilinear relationship with density and, to a lesser extent, with flesh biomass (Fig. 3.19 c & f). However, in all of these relationships, the stations B3 and A1 had biomass and density values which were much greater than all other stations such that they gave undue weighting to each curve. The nitrogen and carbon values show that the highest populations occurred at areas with a 20 - 23 C/N value and suggest that although the animals were found in relatively unnutritious muds, they were found in areas with a high sediment carbon content, which acted as a substrate for the microflora, together with substantial amounts of nitrogen.

The groups of stations constructed for the production analysis had separate distributions with respect to the environmental factors (Fig. 3.19a, b, c). The stations within the

Figure 3.18 *M. balthica* : Diagrammatical Relationships Between (a) Density and (b) Flesh Dry Weight Biomass of 'Large' Animals With Tidal Height and M.P.D.


Nos. m2 (x 10^2)
0
2.0
4.0
6.0
8.0
10.0
12.0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D. (µm)
(a)
Fdw (g m^{-2})
0
3.0
6.0
9.0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D. (µm)
(b)

Figure 3.19 *M. balthica* : The Relationships Between Density and Flesh Biomass of 'Large' Animals With Sediment %C (a, d), %N (b, e) and Shore Slope (c, f).

Legend

▲ Group 1 in Production Calculations.
△ Group 2 " " "
• Group 3 " " "
■ Group 4 " " "
□ Group 5 " " "


(a)
(b)
(c)
(d)
(e)
(f)
Nos. m2 (x 10^2)
12.0
8.0
4.0
0
Fdw (g m-2)
9.0
6.0
3.0
0
1
2
3
4
5
%C
0.01
0.02
0.03
%N
4
8
12
16
20
Slope (°)

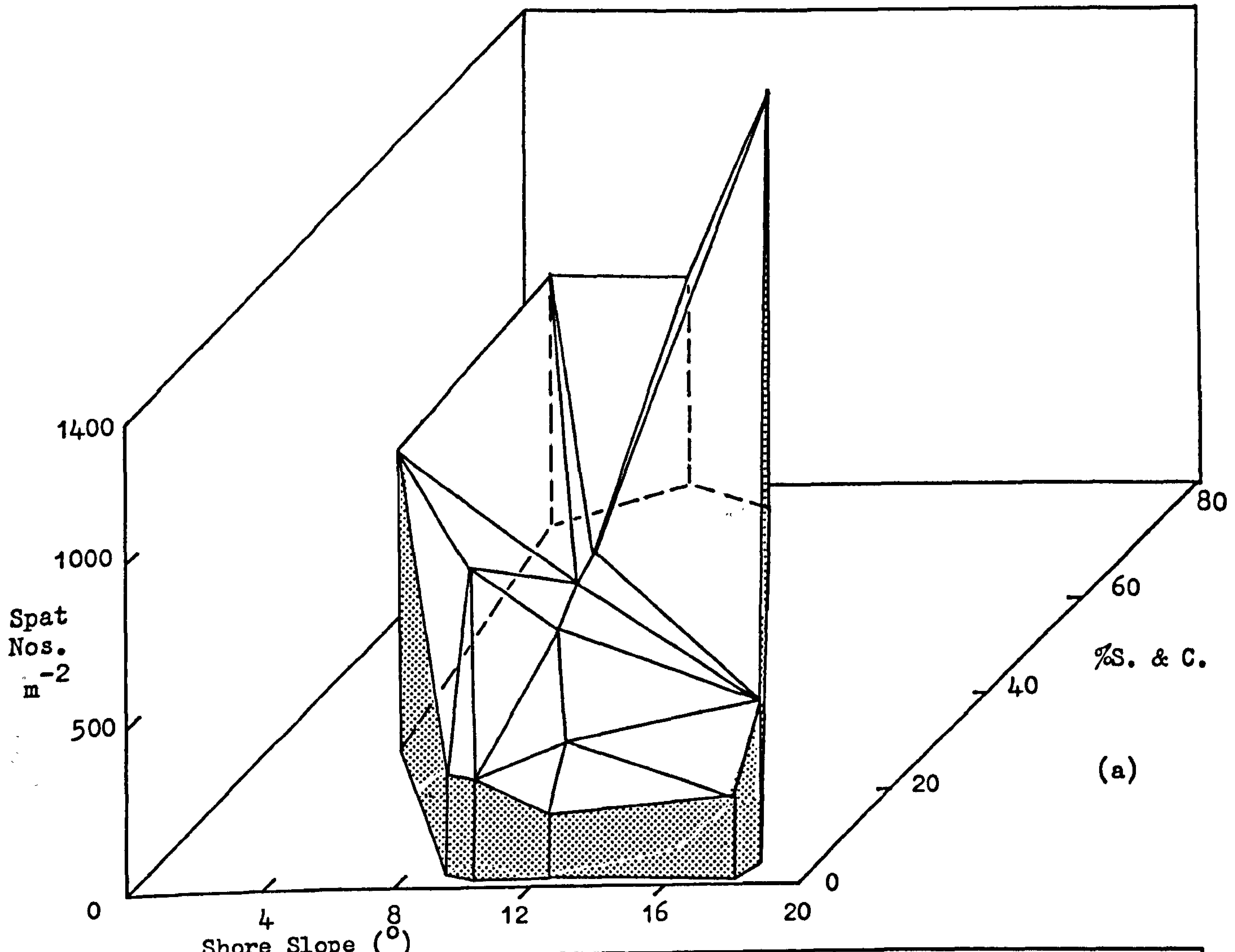
Groups 3 and 4 had relatively similar densities and biomasses although they occurred over a range of %C, %N and shore slope values. Stations of Groups 1 and 2, however, had large variations in biomass and density. It is therefore difficult, on the basis of correlation coefficients, to suggest the major factors which affected the animal populations (see Section 2.3).

The density of spat increased with an increase in sediment silt and clay and a decrease in shore slope (Fig. 3.20(a)) and that while the lowest densities were found at areas of high slope and low silt and clay, the highest values were found at areas both of high silt and clay and medium slope; and of low slope and medium silt and clay. This suggests either that both factors played a part in regulating spat density or that another factor which influenced one or both of these independent variables also influenced the spatfall. The highest spat density occurred at areas 3m above C.D. with M.P.D. < 200µm (Fig. 3.20 (b)). A mid tidal area of low shore slope covered by a fine sediment which includes a large proportion of silt and clay would appear to receive a large spatfall. The latter two factors may be dependent on the water currents passing over an area which in turn would be influenced by the shore slope and to a lesser extent the tidal height.

3.4.1.1.2. Multiple Regression Analysis (see Tables 3.19 & 3.20).

The first regression analysis, in which all the environmental factors were included as independent variables, showed that while the variation in the spatial range of numbers and flesh biomass of large M. balthica was highly significantly regressed to many factors, the major part of the variation was attributable to the water CHO levels and the sediment %N. In

Figure 3.20 *M. balthica* : Diagrammatical Relationships Between the Spat Density and (a) Shore Slope and Percentage Silt and Clay in Sediment, and (b) Tidal Height and M.P.D.


1400
1000
500
0
Spat Nos. m^{-2}
4
8
12
16
20
Shore Slope (°)
0
20
40
60
80
%S. & C.
(a)

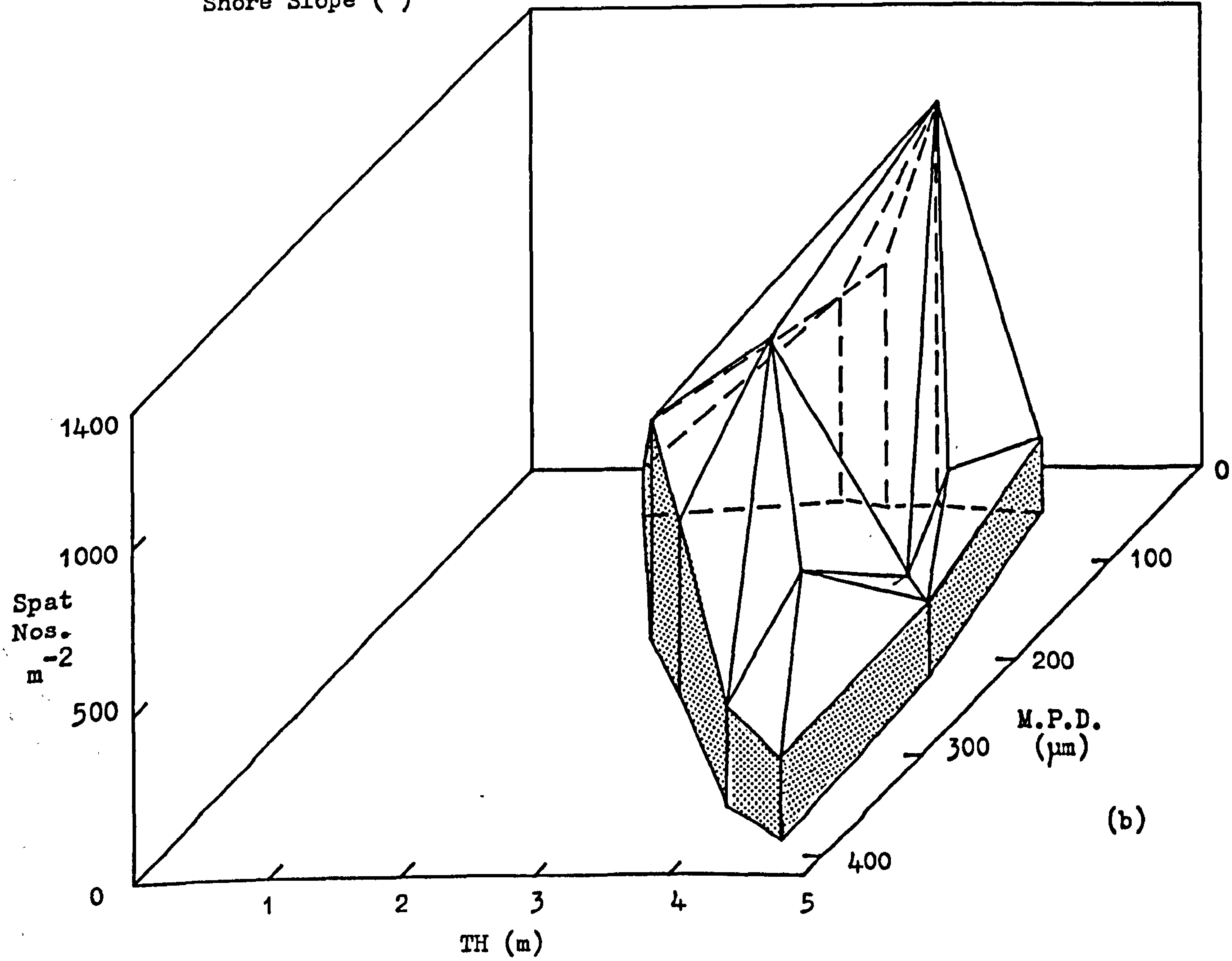

1400
1000
500
0
Spat Nos. m^{-2}
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D. (μm)
(b)

Table 3.19 <u>M. balthica</u> : Spatial Multiple Regression Analysis (1) of Population Variables With all Environmental Variables. (Abbreviations as given on Figure 3.17).

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
P	$\overset{***}{0.042}_{\%\text{H}_2\text{O}} + \overset{***}{0.178}_{\text{C.H.O.}} - \overset{***}{44.254}_{\%\text{N.}} + \overset{***}{1.813}_{\%\text{C.}} + \overset{***}{0.007}_{\text{M.P.D.}}$ $- \overset{***}{6.972}_{\text{TH.}} - \overset{***}{2.784}_{\bar{x}\ \text{Imm. Per.}} + \overset{**}{1.518}_{\text{SK.}} + \overset{*}{0.116}_{\text{C/N}} + 37.892$	Sal., Org. C.	All	$\%\text{H}_2\text{O}$ (35.2%), C.H.O. (29.4%), %N. (15.3%), M.P.D. (9.8%).
M	$\overset{***}{0.189}_{\%\text{H}_2\text{O}} - \overset{***}{0.053}_{\text{C.H.O.}} - \overset{***}{80.818}_{\%\text{N.}} + \overset{***}{3.396}_{\%\text{C.}} - \overset{***}{0.009}_{\text{M.P.D.}}$ $- \overset{***}{0.418}_{\text{Slope}} + \overset{***}{0.358}_{\text{Sal.}} - \overset{***}{1.513}_{\text{SK.}} + \overset{***}{3.162}_{\text{Org. C.}}$ $- \overset{***}{0.123}_{\%\text{S. \& C.}} - \overset{***}{0.414}_{\text{C/N}} - 0.150$	TH., $\bar{x}$ Imm. Per.	All	C.H.O. (74.6%).
P/$\bar{\text{B}}$	$\overset{***}{0.753}_{\text{SK.}} - \overset{***}{0.089}_{\text{Slope}} - \overset{***}{0.385}_{\text{S.C.}} - \overset{**}{0.002}_{\text{M.P.D.}}$ $- \overset{**}{0.011}_{\%\text{S. \& C.}} - \overset{*}{0.121}_{\%\text{C.}} - \overset{*}{0.577}_{\bar{x}\ \text{Imm. Per.}} + 10.016$	%N., C/N.	99.5%	M.P.D. (69.3%), Slope (7.7%), TH. (5.0%), S.C. (5.0%).
M/$\bar{\text{B}}$	$15.329 - \overset{***}{1.226}_{\text{S.C.}} - \overset{**}{0.168}_{\text{Slope}} + \overset{*}{0.992}_{\text{SK.}} - \overset{*}{0.002}_{\text{M.P.D.}}$ $- \overset{*}{0.018}_{\%\text{S. \& C.}}$	C/N, Sal.	98.4%	C.H.O. (29.5%), Slope (21.3%), $\bar{x}$ Imm. Per. (14.6%), S.C. (11.5%).

Table 3.19 (Continued)

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
$\overline{\text{LN}}$.	$\overset{***}{45.396}_{\text{C.H.O.}} + \overset{***}{14.950}_{\%\text{H}_2\text{O}} - \overset{***}{10034.597}_{\%\text{N.}} + \overset{***}{575.717}_{\text{SK.}}$ $- \overset{***}{366.546}_{\bar{x}\text{ Imm. Per.}} + \overset{***}{399.050}_{\%\text{C.}} + \overset{***}{2.128}_{\text{M.P.D.}} + \overset{**}{4.067}_{\%\text{S. \& C.}}$ $- \overset{**}{155.406}_{\text{Sal.}} - \overset{*}{1069.027}_{\text{TH.}} + 9918.2$	S.C., C/N.	All	C.H.O. (39.6%), %N. (29.8%).
L fdw	$\overset{***}{0.309}_{\text{C.H.O.}} + \overset{***}{0.303}_{\%\text{H}_2\text{O}} - \overset{***}{84.938}_{\%\text{N.}} - \overset{***}{0.077}_{\%\text{S. \& C.}}$ $+ \overset{***}{3.206}_{\%\text{C.}} + \overset{***}{1.697}_{\text{Org. C.}} + \overset{**}{0.004}_{\text{M.P.D.}} - \overset{*}{0.078}_{\text{Slope}}$ $- \overset{*}{0.103}_{\text{C/N}} - \overset{*}{0.987}_{\text{S.C.}} - 7.187$	SK., $\bar{x}$ Imm. Per.	All	C.H.O. (41.6%), %N. (23.9%), %H_2O (13.7%).
L%s.w.	$\overset{***}{0.660}_{\text{C.H.O.}} - \overset{***}{2.138}_{\text{SK.}} - \overset{***}{1.120}_{\text{Org. C.}} - \overset{***}{0.012}_{\overline{\text{LN}}.} + \overset{***}{2.618}_{\%\text{C.}}$ $- \overset{***}{0.146}_{\%\text{S. \& C.}} + \overset{***}{1.235}_{\text{Sal.}} - \overset{***}{0.768}_{\bar{x}\text{ Imm. Per.}} - \overset{***}{0.005}_{\text{M.P.D.}}$ $+ \overset{***}{0.351}_{\%\text{H}_2\text{O}} - \overset{***}{65.758}_{\%\text{N.}} - \overset{*}{1.573}_{\text{S.C.}} + 54.655$	Slope, C/N.	All	SK. (47.2%), Org. C. (10.9%).
$\overline{\text{SN}}$.	$\overset{***}{371.827}_{\text{SK.}} + \overset{***}{31.294}_{\%\text{H}_2\text{O}} - \overset{***}{26673.5}_{\%\text{N.}} + \overset{***}{393.508}_{\text{S.C.}}$ $+ \overset{***}{1.751}_{\text{M.P.D.}} + \overset{***}{842.10}_{\bar{x}\text{ Imm. Per.}} + \overset{***}{463.98}_{\text{Org. C.}}$ $+ \overset{***}{1313.67}_{\%\text{C.}} - \overset{***}{140.843}_{\text{C/N}} + \overset{**}{1674.41}_{\text{TH.}} - \overset{*}{179.0}_{\text{Sal.}} - 4862.1$	%S. & C., Slope.	All	SK. (38.4%), %N. (291.%).

Table 3.19 (Continued)

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
S fdw	$\overset{***}{0.036}_{SK.} + \overset{***}{0.001}_{C.H.O.} + \overset{***}{0.003}_{\%H_2O} - \overset{***}{2.312}_{\%N.} + \overset{***}{0.0002}_{M.P.D.}$ $+ \overset{***}{0.027}_{S.C.} + \overset{***}{0.047}_{\bar{x}\ Imm.\ Per.} + \overset{***}{0.109}_{\%C.} + \overset{***}{0.031}_{Org.\ C.}$ $- \overset{***}{0.010}_{C/N} - \overset{***}{0.012}_{Sal.} + \overset{*}{0.085}_{TH.} - 0.187$	%S. & C., Slope.	All	%N. (31.5%), SK. (27.9%), C.H.O. (15.9%).

In the regressions below, the variable 'Large' mean nos. was also included in the independent variable list.

K	$\overset{***}{0.341}_{S.C.} + \overset{***}{0.329}_{\%C.} - \overset{***}{5.377}_{\%N.} - \overset{**}{0.003}_{\%S.\ \&\ C.} - \overset{**}{0.027}_{C/N}$ $+ \overset{*}{0.018}_{Sal.} - \overset{*}{0.0005}_{M.P.D.} - 1.490$	Slope, C.H.O., $L\bar{N}$.	All	TH. (30.7%), S.C. (20.7%), %S. & C. (20.4%).
H_∞	$\overset{***}{0.230}_{\%H_2O} - \overset{***}{4.976}_{S.C.} + \overset{***}{2.577}_{\bar{x}\ Imm.\ Per.} + \overset{***}{1.056}_{Org.\ C.}$ $- \overset{***}{3.275}_{\%C.} + \overset{***}{48.261}_{\%N.} + \overset{***}{5.240}_{TH.} - \overset{***}{0.288}_{Sal.} + \overset{*}{0.349}_{SK.}$ $- 13.948$	%S. & C., C/N, C.H.O.	All	$\%H_2O$ (49.8%), S.C. (19.5%) $\bar{x}$ Imm. Per. (18.4%).
H_8	$\overset{***}{0.156}_{\%H_2O} + \overset{***}{2.851}_{TH.} - \overset{***}{2.023}_{S.C.} - \overset{***}{0.0005}_{L\bar{N}.} + \overset{***}{0.859}_{S.C.}$ $- \overset{***}{5.360}_{\%N.} - \overset{***}{0.023}_{\%S.\ \&\ C.} + \overset{***}{1.426}_{\bar{x}\ Imm.\ Per.} - \overset{***}{0.037}_{C/N}$ $- \overset{***}{0.788}_{SK.} - 9.188$	M.P.D., %C., Sal.	All	$\%H_2O$ (60.5%), TH. (20.2%), S.C. (11.3%).

Table 3.19 (Continued)

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
H_4 fdw	$\overset{***}{0.279}_{\%H_2O} + \overset{***}{0.243}_{C.H.O.} - \overset{***}{2.187}_{TH.} - \overset{***}{0.109}_{\%S.\ \&\ C.}$ $+ \overset{***}{1.273}_{Org.\ C.} + \overset{***}{0.118}_{C/N} + \overset{***}{0.819}_{SK.} - \overset{***}{0.510}_{S.C.} + \overset{**}{0.104}_{\%C.}$ $+ 0.142_{Sal.} - 0.482_{\bar{x}\ Imm.\ Per.} + 6.252$	%N., Slope, $\overline{LN}$.	All	$\%H_2O$ (63.8%), C.H.O. (12.3%), TH. (8.9%), %S. & C. (7.9%).
H_4 s.w.	$\overset{***}{2.055}_{Sal.} - \overset{***}{2.486}_{SK.} - \overset{***}{0.945}_{\bar{x}\ Imm.\ Per.} - \overset{***}{0.057}_{\%S.\ \&\ C.}$ $- 0.011_{M.P.D.} + 0.086_{\%H_2O} - 0.395_{\%C.} + 0.405_{C.H.O.} + 34.913$	S.C., %N.	All	C/N (32.3%), Slope (18.0%), SK. (11.8%), M.P.D. (13.0%).
H_8 fdw	$\overset{***}{1.105}_{\%H_2O} - \overset{***}{16.461}_{S.C.} + \overset{***}{11.179}_{Org.\ C.} - \overset{***}{0.224}_{\%S.\ \&\ C.}$ $+ \overset{**}{0.272}_{C.H.O.} - \overset{*}{0.259}_{Slope} - \overset{*}{0.488}_{Sal.} - \overset{*}{2.333}_{\%C.} - 14.238$	M.P.D., C/N, $\overline{LN}$.	All	$\%H_2O$ (59.5%), TH. (15.1%), C.H.O. (10.1%).
H_8 s.w.	$\overset{***}{3.303}_{SK.} - \overset{***}{0.341}_{C/N} + \overset{***}{0.751}_{C.H.O.} - \overset{***}{0.124}_{\%S.\ \&\ C.} + \overset{***}{0.497}_{\%H_2O}$ $- \overset{**}{0.014}_{\overline{LN}.} + \overset{*}{0.793}_{Sal.} - \overset{*}{0.007}_{M.P.D.} - \overset{*}{0.330}_{\bar{x}\ Imm.\ Per.}$ $- \overset{*}{103.600}_{\%N.} + 69.362$	S.C., Slope.	All	C/N (26.8%), Sal. (26.3%), M.P.D. (13.9%).
CF_H Feb.	$172.65 - \overset{**}{4.880}_{S.C.} + \overset{*}{3.655}_{Org.\ C.} - \overset{*}{1.026}_{C.H.O.} - \overset{*}{0.946}_{Slope}$	M.P.D., $\%H_2O$, C/N	97.2%	%N. (27.3%), TH. (23.6%) $\overline{LN}$. (10.8%).

Table 3.19 (Continued)

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
CF_H May	$\overset{**}{6.527}_{\text{Org. C.}} - \overset{**}{0.043}_{\text{M.P.D.}} + \overset{**}{37.625}_{\text{TH.}} + \overset{**}{11.578}_{\text{\%C.}}$ $- \overset{**}{0.199}_{\text{\%S. \& C.}} - \overset{**}{179.726}_{\text{\%N.}} - \overset{*}{1.629}_{\text{C/N}} - \overset{*}{6.029}_{\text{SK.}}$ $+ \overset{*}{15.826}_{\overline{x}\text{ Imm. Per.}} - 197.671$	Sal., C.H.O., $L\overline{N}$.	All	M.P.D. (75.5%), TH. (6.8%), Org. C. (6.3%).
CF_H Aug.	$\overset{***}{14.248}_{\text{TH.}} + \overset{***}{18.399}_{\text{\%N.}} - \overset{***}{1.073}_{\text{Sal.}} + \overset{***}{7.628}_{\overline{x}\text{ Imm. Per.}}$ $+ \overset{***}{0.399}_{\%H_2O} + \overset{***}{0.854}_{\text{Slope}} - \overset{***}{6.035}_{\text{SK.}} + \overset{***}{0.978}_{\text{C.H.O.}}$ $- \overset{***}{0.006}_{L\overline{N}.} + \overset{**}{1.459}_{\text{S.C.}} - 70.742$	M.P.D., %C., C/N.	All	TH. (80.0%), %N. (13.0%).
CF_H Nov.	$- \overset{**}{0.049}_{\text{M.P.D.}} + \overset{**}{3.894}_{\text{Org. C.}} - \overset{*}{0.116}_{\text{\%S. \& C.}} - \overset{*}{1.268}_{\text{C/N}}$ $- 46.510$	$\%H_2O$, C.H.O., $L\overline{N}$.	97.7%	M.P.D. (40.0%), %S. & C. (11.8%), Sal. (11.5%).
H_1	$\overset{***}{2.007}_{\text{SK.}} - \overset{***}{0.744}_{\text{Org. C.}} + \overset{*}{0.006}_{\text{M.P.D.}} - \overset{*}{0.239}_{\text{Sal.}} + 22.351$	%C., Slope, C.H.O., $L\overline{N}$.	All	$S\overline{N}$. (20.2%), SK. (18.4%), Org. C. (11.6%), %N. (11.4%), S.C. (10.2%).

Table 3.20 <u>M. balthica</u> : Spatial Multiple Regression Analysis (2) of Population Variables With Selected Environmental Variables.

(Legend as Figure 3.17).

Dependent Variable	Significant Equation and Other Included Independent Variables	Excl. Variables	Total Variance Accounted For	Main Variables
P	$0.\overset{*}{1}51_{\%H_2O} - 13.\overset{*}{6}77_{\%N.} - 1.620$ %S. & C., Slope, M.P.D., C/N, $\bar{x}$ Imm. Per. also included	-	72.2%	$\%H_2O$ (35.2%), %N. (17.7%), Slope (11.7%).
M	$0.1\overset{*}{3}2_{\%H_2O} - 0.\overset{*}{2}87_{Slope} + 3.\overset{*}{3}19_{S.\ Imm.\ Per.} - 1.\overset{*}{2}39_{N.\ Imm.\ Per.}$ $- 12.639$ %S. & C., %N., C/N, M.P.D. also included	-	75.3%	Slope (20.3%), N. Imm. Per. (18.5%), %N. (16.5%).
$P/\bar{B}$	All variables not significant + 0.618 M.P.D., Slope, $L\overline{N}$., %S. & C., %N., C/N, $\%H_2O$ included	$\bar{x}$ Imm. Per.	82.1%	M.P.D. (69.3%).
$M/\bar{B}$	All variables not significant + 1.777 Slope, $\%H_2O$, $\bar{x}$ Imm. Per., $L\overline{N}$., M.P.D., C/N, %S. & C., %N. included	-	65.6%	Slope (24.1%), $\%H_2O$ (10.9%), $\bar{x}$ Imm. Per. (10.5%).
$L\overline{N}$.	$0.\overset{***}{9}49_{S\overline{N}.} - 15.\overset{**}{4}64_{\%S.\ \&\ C.} - 53.\overset{**}{2}19_{\bar{x}\ Imm.\ Per.} - 31.\overset{**}{0}55_{Slope}$ $+ 17.\overset{*}{1}66_{\%H_2O} + 976.748$ M.P.D., C/N, %N. also included	-	93.8%	$S\overline{N}$. (51.0%), $\%H_2O$ (11.0%), $\bar{x}$ Imm. Per. (10.6%), Slope (10.3%).

Table 3.20 (Continued)

Dependent Variable	Significant Equation and Other Included Independent Variables	Excl. Variables	Total Variance Accounted For	Main Variables
L fdw	$\overset{***}{65.182}_{\text{S fdw}} - \overset{***}{0.096}_{\text{\%S. \& C.}} - \overset{*}{0.336}_{\bar{x}\text{ Imm. Per.}} - \overset{*}{0.183}_{\text{Slope}}$ $+ \overset{*}{0.135}_{\%H_2O} + 5.056$ M.P.D., C/N, %N. also included	-	94.9%	S fdw (68.6%), $\%H_2O$ (11.4%).
L%s.w.	$95.878 - \overset{**}{0.007}_{\text{L}\bar{\text{N}}\text{.}} - \overset{**}{0.152}_{\text{\%S. \& C.}} - \overset{*}{0.292}_{\text{C/N}} - \overset{*}{0.347}_{\text{Slope}}$ $+ \overset{*}{0.271}_{\%H_2O}$ %N., M.P.D., $\bar{x}$ Imm. Per. also included	-	85.2%	C/N (36.8%), L$\bar{\text{N}}$. (14.9%), $\%H_2O$ (14.6%).
S$\bar{\text{N}}$.	All variables not significant - 154.460 %S. & C., M.P.D., $\bar{x}$ Imm. Per. Slope included	-	34.6%	%S. & C. (28.9%).
S fdw	All variables not significant + 0.005 %S. & C., Slope, M.P.D., $\bar{x}$ Imm. Per. included	-	26.5%	%S. & C. (20.6%).
K	All variables not significant + 0.350 $\bar{x}$ Imm. Per., C/N, %S. & C., L$\bar{\text{N}}$., Slope, $\%H_2O$, M.P.D., %N. included	-	52.9%	$\bar{x}$ Imm. Per. (29.1%).
H_∞	$\overset{**}{0.578}_{\bar{x}\text{ Imm. Per.}} + 8.577$ $\%H_2O$, C/N, L$\bar{\text{N}}$., %S. & C., Slope, %N., M.P.D. also included	-	82.9%	$\%H_2O$ (49.8%), $\bar{x}$ Imm. Per. (18.0%).

Table 3.20 (Continued)

Dependent Variable	Significant Equation and Other Included Independent Variables	Excl. Variables	Total Variance Accounted For	Main Variables
H_1	All variables not significant + 0.484 %N., M.P.D., C/N, $\bar{x}$ Imm. Per., Slope, $\%H_2O$, $\overline{LN}$., $\overline{SN}$., %S. & C. included	-	60.4%	%N. (15.9%), M.P.D. (16.7%), C/N (13.6%), $\bar{x}$ Imm. Per. (10.8%).
H_8	$0.\overset{**}{336}_{\bar{x}\text{ Imm. Per.}} + 8.158$ $\bar{x}$ Imm. Per., $\overline{LN}$., C/N, M.P.D., Slope, %N., %S. & C. also included	-	88.9%	$\%H_2O$ (60.5%), $\bar{x}$ Imm. Per. (19.6%).
H_4 fdw	$0.540_{\bar{x}\text{ Imm. Per.}} + 0.004_{\overline{LN}.} - 0.067_{\%S.\ \&\ C.} + 21.622_{\%N.} - 0.444$ $\%H_2O$, C/N, M.P.D., Slope also included	-	97.5%	$\%H_2O$ (63.8%), $\bar{x}$ Imm. Per. (10.9%), %S. & C. (12.6%).
H_8 fdw	$\overset{**}{2.462}_{\bar{x}\text{ Imm. Per.}} + 0.\overset{*}{0}21_{\overline{LN}} + 0.468$ $\%H_2O$, %N., Slope, M.P.D., C/N, %S. & C. also included	-	88.7%	$\%H_2O$ (59.2%), $\bar{x}$ Imm. Per. (14.2%).
CF_H Feb.	$18.303 - 0.\overset{*}{4}74_{\bar{x}\text{ Imm. Per.}}$ %N., $\overline{LN}$., C/N, $\%H_2O$, M.P.D., Slope, %S. & C. also included	-	67.7%	%N. (27.3%), $\bar{x}$ Imm. Per. (21.3%), $\overline{LN}$.(11.2%).
CF_H May	$26.\overset{*}{8}07_{\%N.} + 18.121$ M.P.D., $\bar{x}$ Imm. Per., %N., $\%H_2O$, $\overline{LN}$., Slope, %S. & C. also included	-	90.4%	M.P.D. (75.5%)

Table 3.20 (Continued)

Dependent Variable	Significant Equation and Other Included Independent Variables	Excl. Variables	Total Variance Accounted For	Main Variables
CF_H Aug.	$\overset{***}{1.566}_{\bar{x}\text{ Imm. Per.}} + 7.856$ %N., %H_2O, %S. & C., M.P.D., C/N, Slope, L$\bar{N}$. also included	-	96.1%	$\bar{x}$ Imm. Per. (69.8%), %N. (20.4%).
CF_H Nov.	$24.171 - \overset{*}{0.032}_{\text{M.P.D.}}$ %S. & C., C/N, $\bar{x}$ Imm. Per., %N., Slope, %H_2O, L$\bar{N}$. also included	-	76.9%	M.P.D. (40.0%), %S. & C. (11.8%).

addition a relatively large proportion of variation in the station flesh biomass was attributable to the sediment water content.

The spat density and flesh biomass were also highly significantly regressed to many factors although most of the variation was attributable to sediment SK and %N. Both the Pearson correlation and multiple regression analysis suggested that the sediment skewness was important in determining the size of the spat populations and possibly that areas with a highly skewed sediment were favourable for settlement.

The percentage shell weight of the large animals was also highly significantly regressed to many environmental variables although SK and to a lesser extent water organic carbon were of the greatest importance. This is again a reflection of the fact that the animals towards the upper-shore, coarse areas had a larger proportion of their total weight as shell than at other areas.

In the second regression analysis (see Table 3.20), by far the major part of the spatial variation in numbers and flesh biomass of the large animals was accounted for by the spat density and flesh biomass respectively showing that both the large and small animals occur in large populations in common areas of the mud flat (c.f. C. edule spat distribution, Section 4.4.1.). The immersion period, sediment water content and shore slope also contributed towards accounting for this variation.

The percentage shell biomass was found to be influenced by sediment C/N, the 'large' animal density and the sediment water content, suggesting either that the percentage shell weight at each station was density dependent such that at high densities there was a relatively low percentage shell weight or that the highest percentage shell weights occurred as a result of unfavourable (i.e. too coarse) sediments which could not support large populations of bivalves and which resulted in the animals having a low body condition.

In the second regressions involving spat densities and flesh biomass only one third of the variation was accounted for by the variables presented although most of that variation was attributable to the sediment %S & C.

3.4.1.2. Factors Affecting the Growth of M. balthica.

3.4.1.2.1. Correlation Analysis (Fig. 3.17).

The maximum theoretical size (H_∞) was found to be greatest in the main population areas (i.e. was positively correlated with $P/\overline{B}$, $M/\overline{B}$, all spat parameters, the sizes of the older cohorts and the summer condition factors) and at areas of low K values. It decreased with increasing tidal height and M.P.D. and increased with sediment $\%H_2O$, %C, %N, %S & C, interstitial salinity and immersion period. The maximum theoretical size was therefore greatest at the low-shore, fine mud areas where the production and mortality rates were high and where the main spat settlement occurred. These areas, however, although supporting relatively high populations were not necessarily those areas supporting the greatest biomass and density of the population.

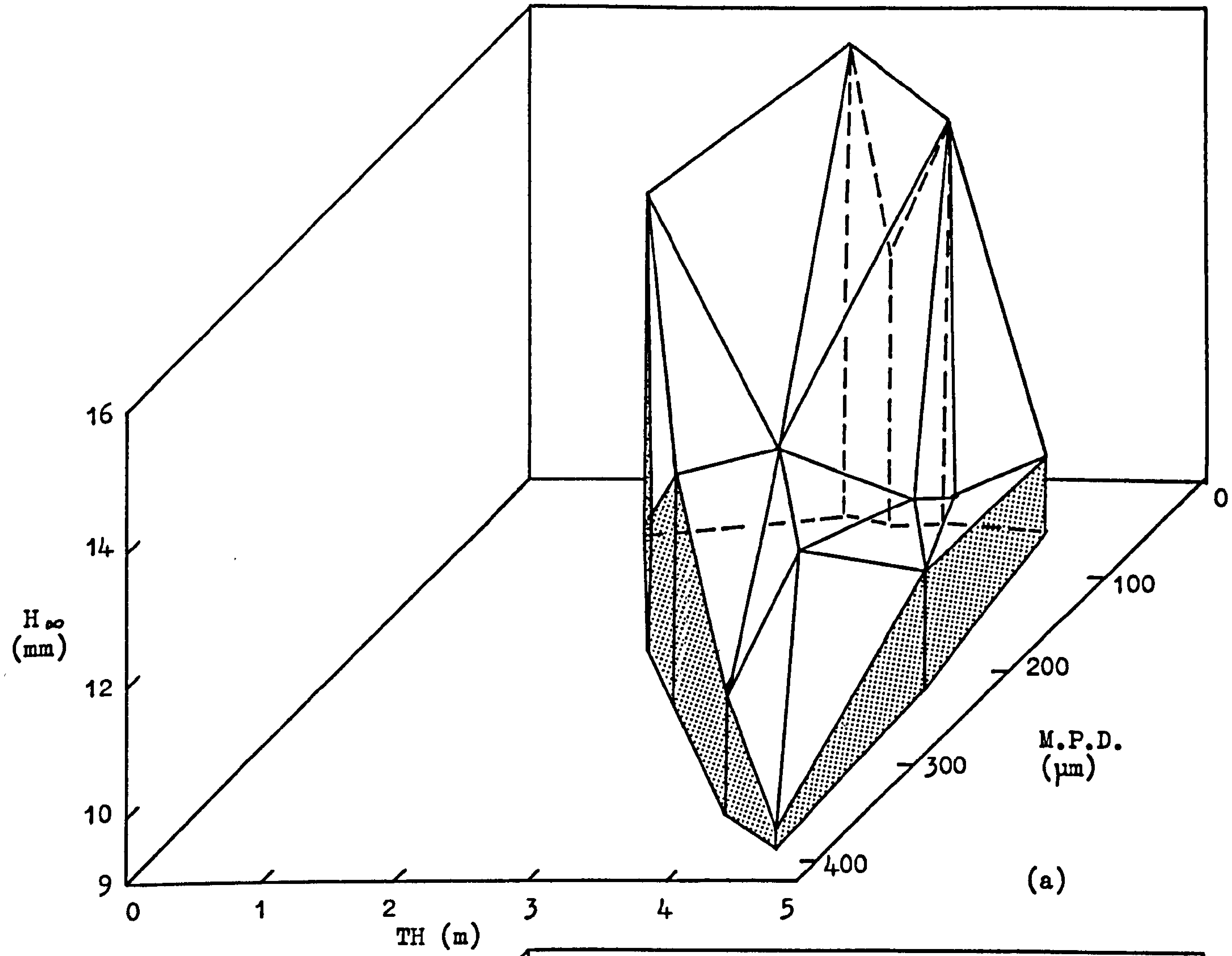
The parameter K, the rate at which the maximum size was reached, showed opposite trends to those shown by H_∞ and was greatest at the high intertidal areas. It decreased with increasing $M/\overline{B}$, spat number fluctuation ($S_{S.D.}$), H_∞, size and weight of the older cohorts and the maximum age attained (T_{95}).

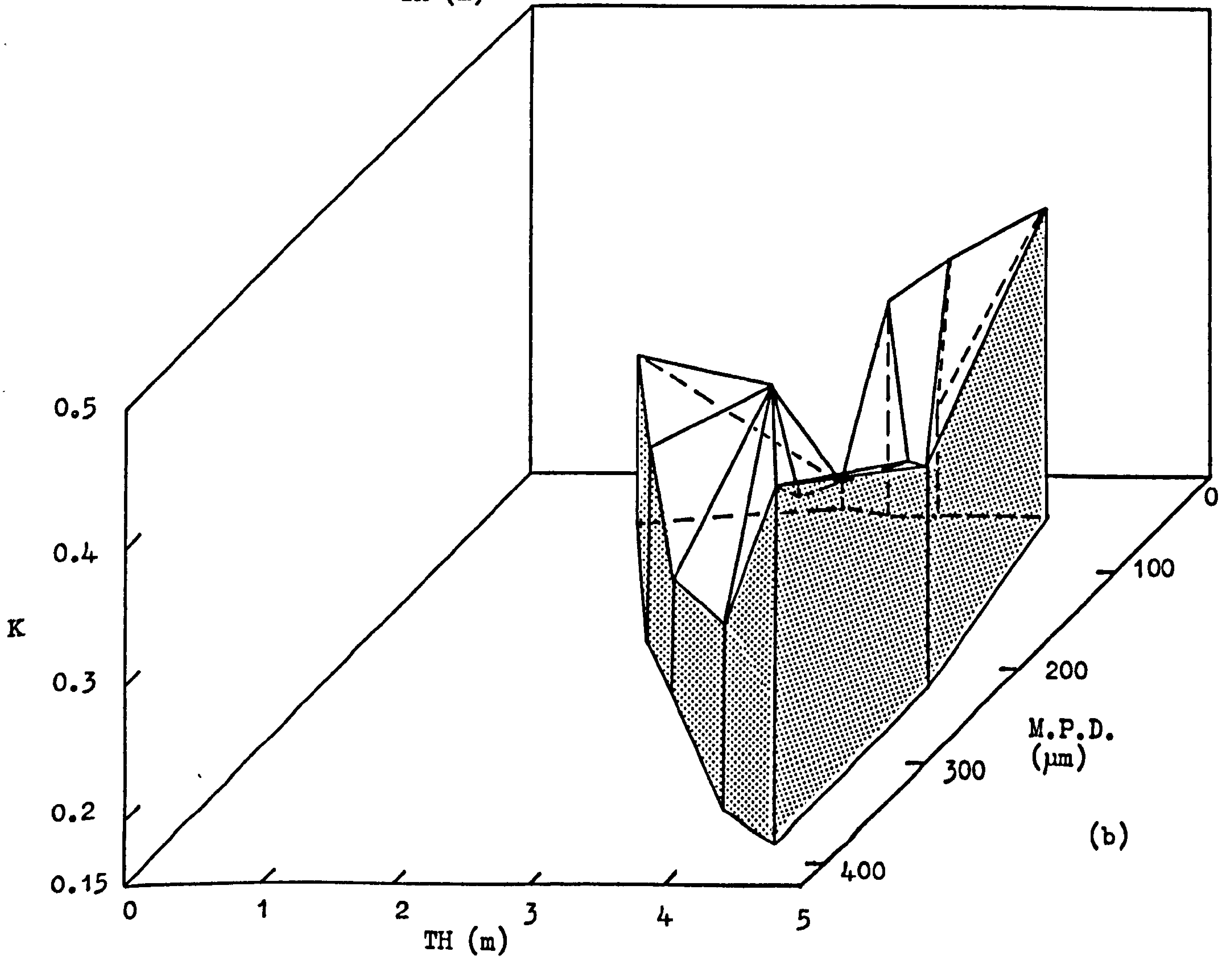
The diagram (Fig. 3.21a & b) illustrates many of these points and shows that whilst the highest H_∞ values were found in the mid- to low-shore fine mud areas, the greatest K values occurred mainly in the upper-shore areas in coarse substrate.

One of the most densely populated areas, A1, had a high H_∞ and a low K value whilst the other, B3, had a relatively low H_∞ value and high K value. It is considered therefore that although the areas supporting the largest populations may have been the most favourable for growth this was not always the case. Also, the H_∞ and K were respectively positively and negatively correlated with the size and weight of the older cohorts showing that the animals at the high-shore stations reached their maximum size in a shorter period than at the other areas but that maximum size and weight was always considerably smaller than at the other areas.

The size of H_1 animals was not correlated with any of the major environmental or population variables and only found to be larger at those areas with larger second year animals; this shows a similarity in the first two years growth of the animals at all stations. In turn, the H_2 animals were largest in the areas of high production and $P/\bar{B}$, H_4 size and weight, and sediment S.C., SK, $\%H_2O$, %C and %N and in areas of the lowest shore slope. The second year animals were apparently more influenced by the environment. At four years old (H_4) there was an increase in size, flesh weight and total weight with the parameters $\bar{B}$, P, M, $P/\bar{B}$, all parameters of large and spat animals (except large $\bar{N}$), H_∞, H_2, H_6, H_8, flesh and total weights of H_4 and H_8 and with the summer condition of the animals. They also increased with increases in sediment $\%H_2O$, %C, %N, %S & C and immersion period

Figure 3.21 *M. balthica* : Diagrammatical Relationships Between the Bertalanffy Parameters (a) H_∞ and (b) K of the Growth and the Tidal Height and M.P.D.


H ∞
(mm)
16
14
12
10
9
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D.
(μm)
(a)


K
0.5
0.4
0.3
0.2
0.15
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D.
(μm)
(b)

but decreased with increases in TH, M.P.D., and the slope of the shore.

Finally, the sizes of H_6 and H_8 and the flesh and total weights of H_8 were found to increase with increasing $\bar{B}$, ΔP, ΔM, $P/\bar{B}$ and the parameters of large and spat animals (except $I_{\overline{N}}$) the size of H_∞, H_4, H_8 (for H_6) and H_6 (for H_8), the T_{95}, H_4 and H_8 weights and the summer condition, and they decreased with increasing K values. The flesh weight and size of the older cohorts also increased with sediment %H_2O, %C, %N, %S & C, salinity and immersion period and decreased with increasing TH, M.P.D. and shore slope.

The percentage shell weight of H_4 animals was negatively correlated with sediment SK and C/N and water organic carbon whilst that of H_8 animals was negatively correlated with shore slope and winter organic carbon levels and positively with interstitial salinity. These trends show that although the animals of a certain age at the lower stations were usually larger than at the upper stations and therefore had heavier shells, the upper-shore animals were in a poorer body condition whereby the flesh-weight was a lower proportion of the total weight than at the other stations (Section 3.4.1.3.).

The number of environmental factors influencing the sizes of standard age animals increased with the age of the animals suggesting that the environment exerts a cummulative influence on the population with time. In summary, the growth of the youngest ages was not influenced by any of the environmental factors whereas the growth of the older cohorts was greatest in the low-shore, fine mud areas.

The maximal age of the animals (T_{95}) was found to decrease with an increasing K value and increased with the size and weight of H_∞, H_6 and H_8, and with the summer condition factor. It decreased with an increase in tidal height and therefore also exposure period.

3.4.1.2.2. Multiple Regression Analysis (Tables 3.19 & 3.20).

The first multiple regression analysis suggested that the most important factors influencing the Bertalanffy parameters were the sediment type (%S & C, S.C. and $\%H_2O$) and shore position (TH and immersion period) characteristics. In both regressions where K was the dependent variable, the major independent variable was tidal height (or immersion period), whereas the major variable in the H_∞ first regression was the sediment water content which accounted for nearly half of the variation in the dependent variable. In the second regression nearly all of the accounted-for variation was attributable to $\%H_2O$ and immersion period.

The conclusions reached in Section 3.4.1.2.1. regarding the size of H_1 animals were supported by the regressions which showed that although many factors accounted for relatively large proportions of the variance, no one factor was of paramount importance. In the first regression SK, spat number, water organic carbon, sediment S.C. and %N all contributed towards accounting for the variance; whereas in the second regression %N, M.P.D., C/N and immersion period influenced the size of the first year animals to a lesser extent.

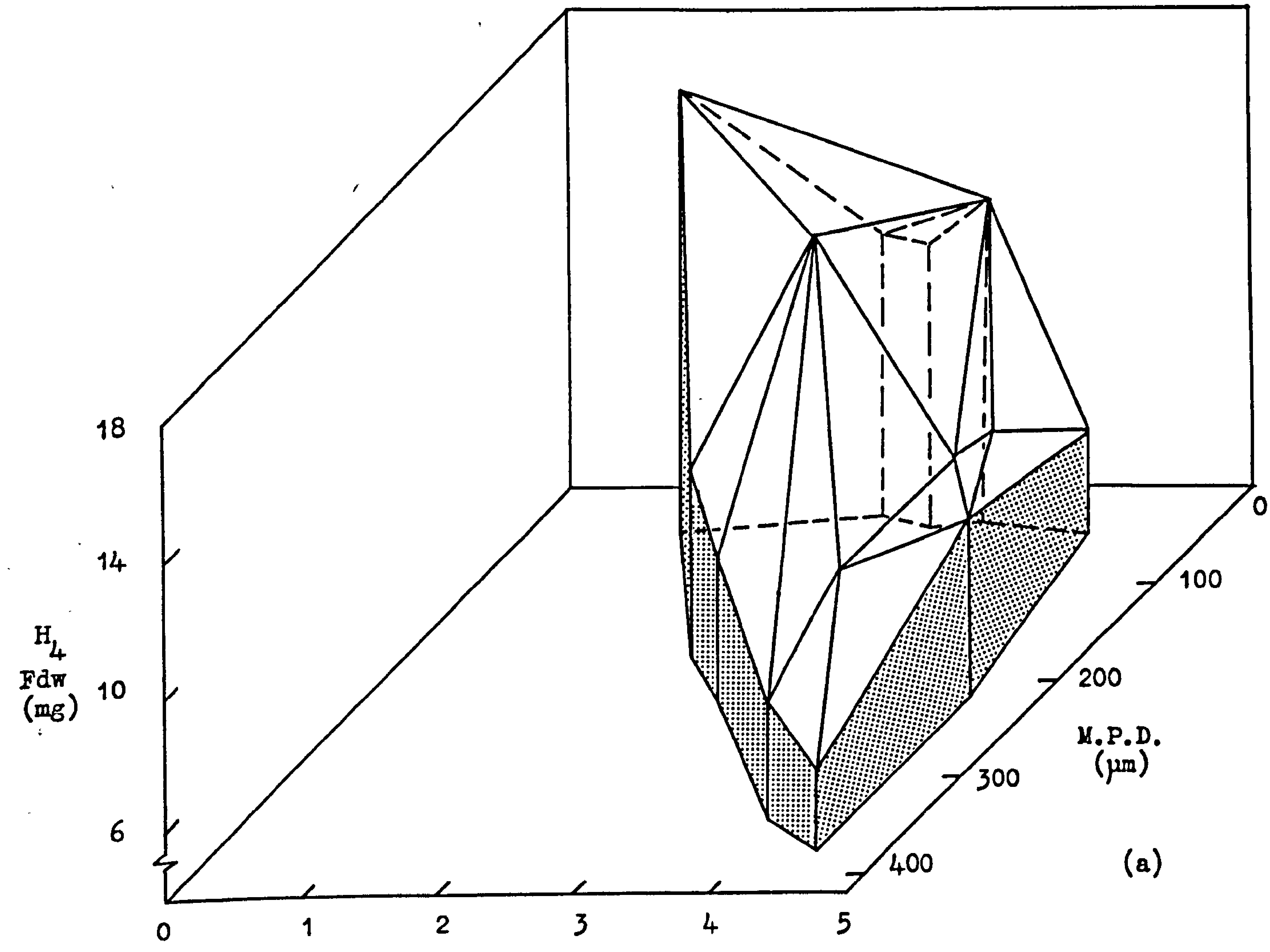
The size of H_8 was found to be largely influenced by the sediment water content and, to a lesser extent, by the sediment S.C. and immersion period. The weight of H_4 was also mainly influenced by the sediment water content which accounted for over half of the variation with immersion period and sediment %S & C further accounting for lesser amounts. The weight of H_8 animals was also mainly influenced by the sediment water content which again accounted for over half of the variation with immersion period (or tidal height) and water CHO levels accounting for a further 25% of the variation.

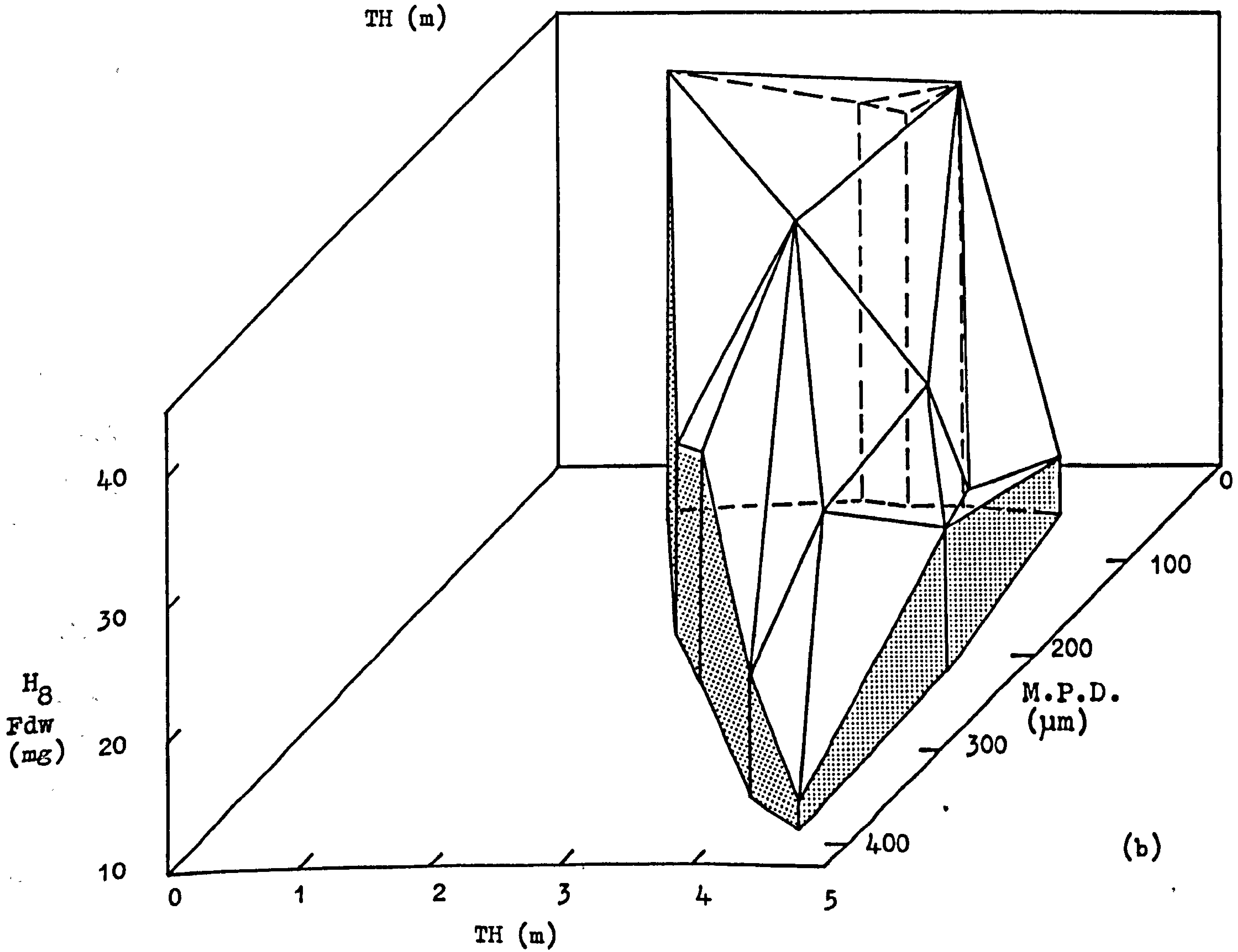
The variation in the percentage shell weight of H_4 animals was found to be mainly attributable to the sediment C/N value which, together with shore slope and sediment SK and M.P.D., accounted for 75% of the variation. Similarly the variation in the percentage shell weight of the H_8 animals was attributable to C/N, interstitial salinity and particle size.

The sizes of H_1 and H_2 animals were again intercorrelated as were those of H_2 and H_4 but not those of H_1 and H_4 animals. In turn, the H_4, H_6 and H_8 animal sizes were also intercorrelated. This suggests that the environmental effect on growth was gradual over the first few years resulting in the growth of the first and second year animals being similar; their requirements were met equally by all environments. However, after that period, the environmental influence was greater as the animals' requirements increased; however, the animals upto two years were not necessarily less susceptible to environmental changes than were older animals.

When depicted graphically (Fig. 3.22 (a), (b)) it is seen that with a decrease of both tidal height and particle size the flesh weights of four and eight year old animals increased. However, the H_4 animals' flesh weight increased towards the lowest levels of TH and M.P.D. encountered in the sampling whereas the flesh weight of H_8 animals was at a maximum in fine

Figure 3.22 M. balthica : Diagrammatical Relationships Between the Flesh Dry Weight of (a) H_4 Animals (Standard Four Year Old Animals) and (b) H_8 Animals (Standard Eight Year Old Animals) and Tidal Height and M.P.D.


18
14
10
6
H4
Fdw
(mg)
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D.
(μm)
(a)


40
30
20
10
H8
Fdw
(mg)
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D.
(μm)
(b)

sediments from the mid tidal level of 3.4m, downwards. In addition, with a change from a coarse, high-shore area to a low, fine mud area the flesh weight of H_4 animals increased by a factor of 2.7 whereas that of the H_8 animals increased by a factor of 3.8 showing that with an increase in age the relative difference between the areas also increases. This again suggests that with time the environment effects a greater influence on the size of the animal. It should be remembered that the weights of standard age animals used here were calculated according to January regression equations and that during the warmer months the difference between the extremes of environment were even greater (see Sections 3.4.1.3. and 3.4.2.1.).

3.4.1.3. Factors Affecting the Body Condition of M. balthica.

As the body condition was found to change markedly with temperature the four condition determinations in 1976 (February, May, August and November) were incorporated into the spatial analysis (see also Section 3.4.2.1.).

3.4.1.3.1. Correlation Analysis (Fig. 3.17).

The station mean condition factor for February was found to increase only with the sediment %C and %N. In May and August, however, the condition factor was greatest in areas of high $P/\overline{B}$, and large H_∞ and size and weight of the older cohorts. These condition factors also increased with increasing condition factor for the other summer and autumn months, the sediment SK and C/N (for May condition) and interstitial salinity (for August), with sediment $\%H_2O$, %C, %N and %S & C and also with the immersion period. The May and August condition decreased with increasing TH, M.P.D., and the shore slope. The November condition factor, however, apparently neither influenced nor was affected by many of these factors and only decreased with an increase in the size of H_1, the tidal height and the particle size. It similarly increased with the May and August animal body condition and with the period of immersion.

3.4.1.3.2. Multiple Regression Analysis (Tables 3.19 & 3.20).

The first regressions showed that whilst the sediment nitrogen content and the tidal height were the main factors influencing the February condition, by far the major part of the variation in May and August condition was attributable to particle size and tidal height respectively. In November the condition was mainly influenced by particle size, although to a much lesser extent than in May, and to a still lesser extent by sediment silt and clay content and interstitial salinity.

Only 68% of the variation in the February condition was attributable to the variables included in the second regression; much of that variation was accounted for by the sediment %N and by the immersion period. Particle size accounted for the major part of the variation in May condition whilst immersion period was the major factor in the August condition regression. Particle size also accounted for the major part of the variation in November condition although to a lesser extent than in May.

The Fig. 3.23 illustrates many of these trends and shows that whilst the condition values of the animals at the fine mud, low-shore stations increased to 25 - 35 as the year progresses and then decreased after the summer to about 15 over the winter, the condition of the animals at high-shore, coarse substrate areas remains relatively constant over the year at between 15 and 18. This pattern is also reflected in the change in the

Figure 3.23 *M. balthica* : The Change in Flesh Condition Factor With Tidal Height for Each Sampling Occasion, February, 1976 to February, 1977.

		r	p
Feb.'76	$CF_H = 15.221 + 0.327 \pm 0.545$ TH.	0.171	n.s.
May '76	$CF_H = 25.752 - 1.860 \pm 0.711$ TH.	-0.603	*
Aug.'76	$CF_H = 37.898 - 5.346 \pm 0.771$ TH.	-0.894	***
Nov.'76	$CF_H = 21.136 - 1.450 \pm 0.621$ TH.	-0.559	*
Feb.'77	$CF_H = 16.681 - 0.560 \pm 0.510$ TH.	-0.302	n.s.


20
10
0
Feb.'76
20
10
0
May '76
30
20
10
0
Aug.'76
20
10
0
Nov.'76
20
10
0
Feb.'77
0
1
2
3
4
5
TH. (m)
Condition Factor (CF_H)

statistics characterising the relationship for each month (Fig. 3.23).

The pattern of changes in animal condition with both position on the shore and time of year may be indicative of the fact that the lower-shore animals react in a greater manner to the annual environmental changes; that they increase in weight to a greater extent because of the larger amounts of food available; that they put more energy into spawning and also emaciate to a greater extent (see Section 3.4.2.1.).

3.4.1.4. Factors Affecting the Production, Mortality, $P/\bar{B}$ and $M/\bar{B}$ of M. balthica.

3.4.1.4.1. Correlation Analysis (Fig. 3.17).

The station M. balthica production was found to increase with the growth and flesh weight of the older cohorts and, as expected, was highest in those areas supporting high biomasses and densities. It was greatest in the areas of high sediment $\%H_2O$ and %S & C content and with high CHO levels in the water. Mortality was also greatest at areas with the largest size of the older animals, CHO levels and animal densities and biomasses.

The areas with the highest $P/\bar{B}$ and $M/\bar{B}$ values occurred together and the $P/\bar{B}$ also increased with the maximum size of the animals at each station, the mean size of the older cohorts and with the greatest summer condition. The $P/\bar{B}$ values, however, did not appear to be density dependent. The $P/\bar{B}$ was highest in areas of low M.P.D. and shore slope and at high levels of sediment $\%H_2O$, %C, %N, %S & C, C/N and SK and with a long spring-tide immersion period. Similarly, the $M/\bar{B}$ values decreased with an increasing K value and shore slope and increased with the size of H_∞ and older animals, at areas with high CHO levels and again a long spring-tide immersion period.

3.4.1.4.2. Multiple Regression Analysis (Tables 3.19 & 3.20).

The station annual production and mortality estimates both gave highly significant regressions, incorporating many environmental variables, which accounted for all of the variation in the dependent variables. The production was mainly influenced by the sediment $\%H_2O$, %N and M.P.D. and by the CHO levels in the water. The second multiple regression suggested that the slope of the shore also affected production.

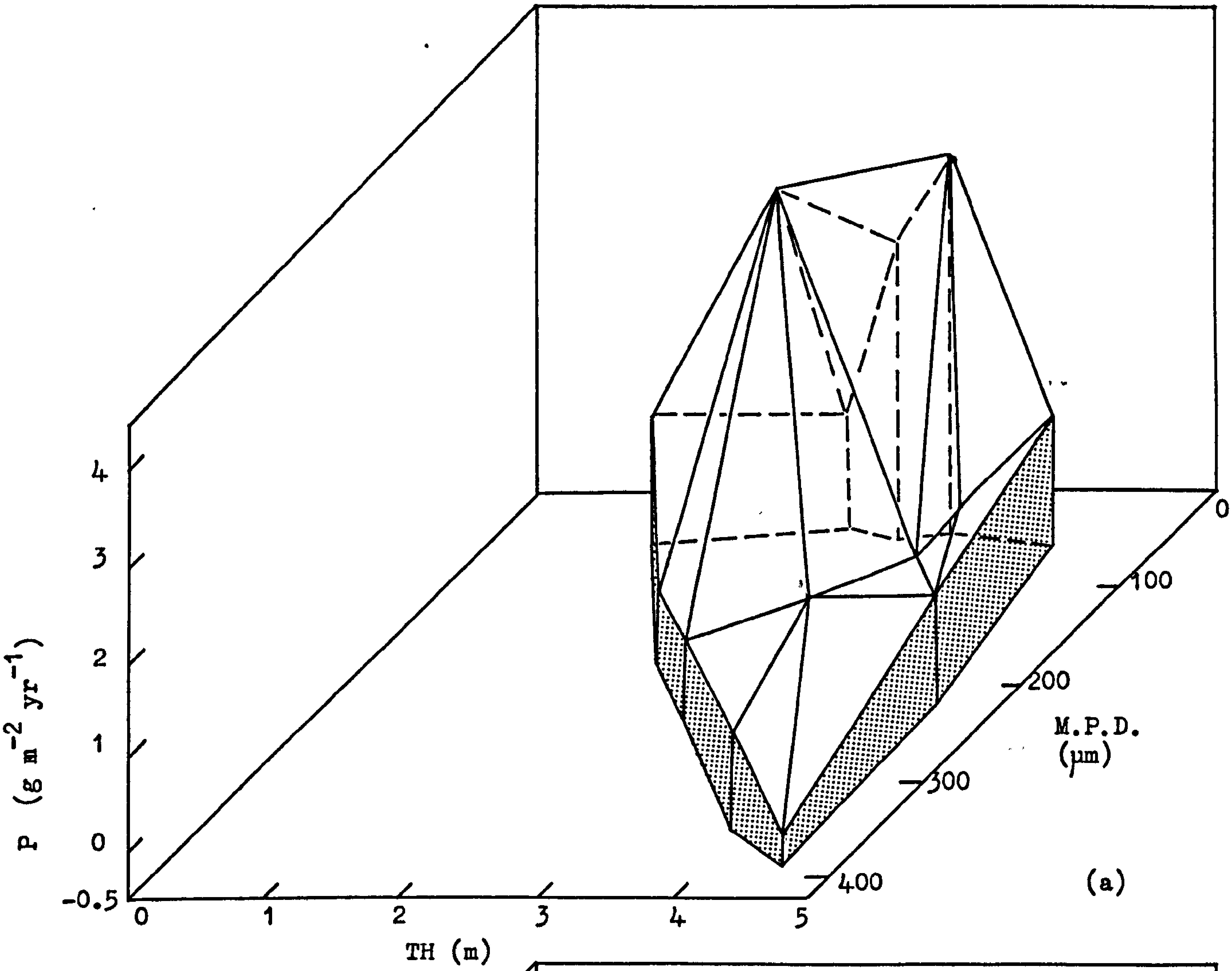
The multiple regression analysis suggested that 75% of the variation in the station mortality was attributable to the water CHO levels (in the correlation analysis CHO and mortality were highly correlated). It is unlikely, however, that too much water carbohydrate would lead to mortality; it is probable, however, that as mortality was highest in the common areas and those areas had the largest populations because of the sediment, tidal position and CHO levels in the water, then the regression result was of a spurious nature. In the second regression the shore slope, sediment %N and immersion period all accounted for large proportions of the variation in mortality: again suggesting that the greatest mortality occurred in the areas of densest population.

The main factor controlling $P/\bar{B}$ was found to be particle size which accounted for 70% of the variation in this dependent variable and although many factors (water CHO, shore slope, immersion period, sediment sorting coefficient) were found to influence the $M/\bar{B}$ values, none of the variables proved to be of greatest importance.

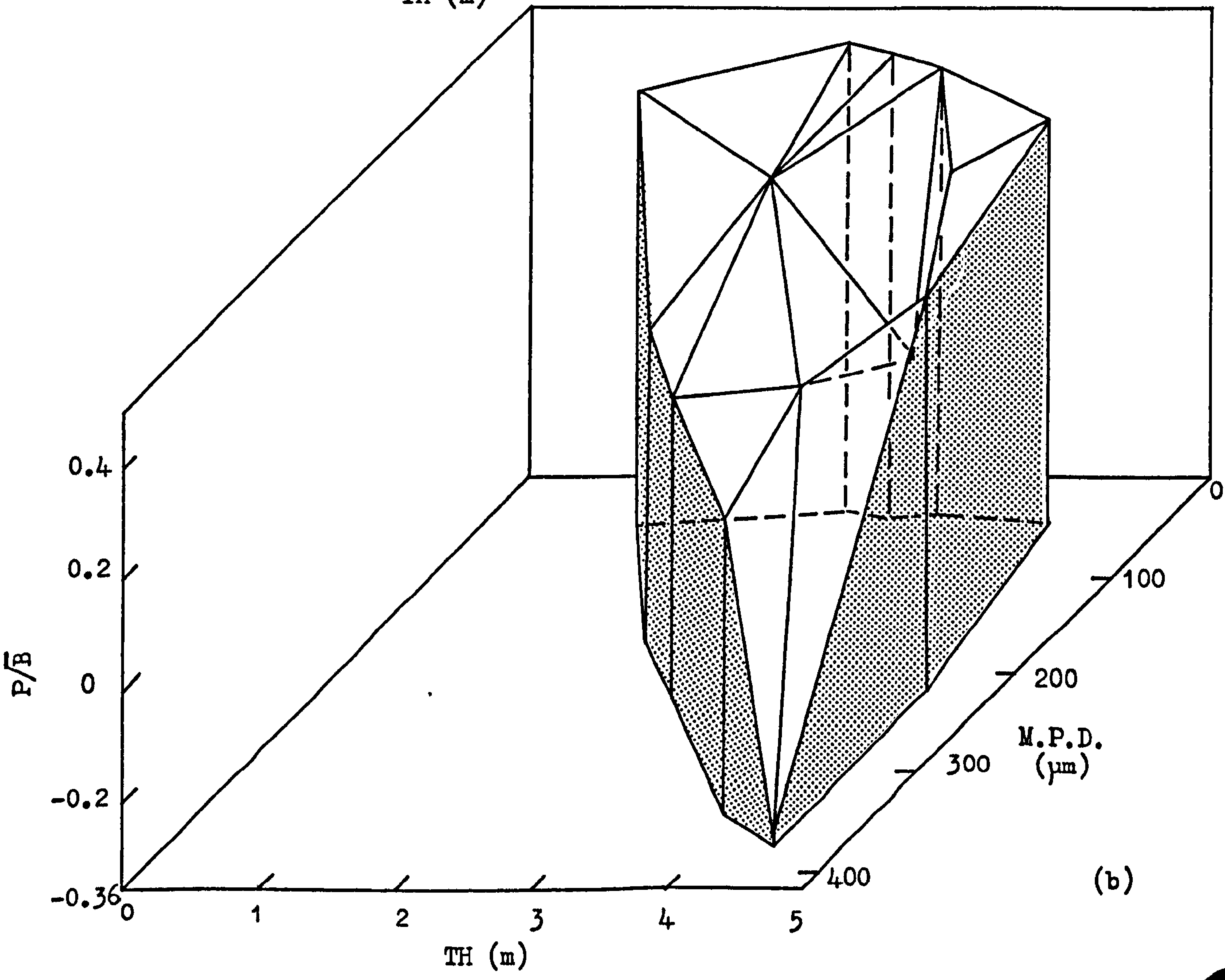
The highest production levels were therefore found in areas where a fine-sand to mud substrate occurred at mid tidal level (Fig. 3.24 (a)) and were directly related to the biomass levels (Fig. 3.24 (a) cf. Fig. 3.18 (b)). The $P/\overline{B}$ levels, however, increased with both a decrease in particle size and tidal height from a minimum at Station C5 (Fig. 3.24 (b)). The annual mortality was also found to show a maximum at the mid tidal levels (Fig. 3.25 (a)) and was directly related to the biomass and production available within an area. The $M/\overline{B}$ values however were shown to decrease with an increase in tidal height with the exception of C1 (Fig. 3.25 (b)).

The method used in calculating the individual station $P/\overline{B}$ and $M/\overline{B}$ values by the grouping of stations resulted in those stations with similar $P/\overline{B}$ and $M/\overline{B}$ values being plotted in groups which correspond to the original groups. Therefore any conclusions reached from the analysis performed between these values and the environmental factors were to some extent predetermined and based upon the major differences between the initial groups used. The only conclusions which can possibly be drawn is that the ratios increased towards the lower-shore, fine mud areas which supported the highest populations of the bivalve.

Figure 3.24 *M. balthica* : Diagrammatical Relationships Between (a) Production and (b) $P/\bar{B}$ Values and Tidal Height and M.P.D.


P (g m^{-2} yr^{-1})
4
3
2
1
0
-0.5
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D. (μm)

(a)


P/B̄
0.4
0.2
0
-0.2
-0.36
0
1
2
3
4
5
TH (m)
0
100
200
300
400
M.P.D. (μm)

(b)

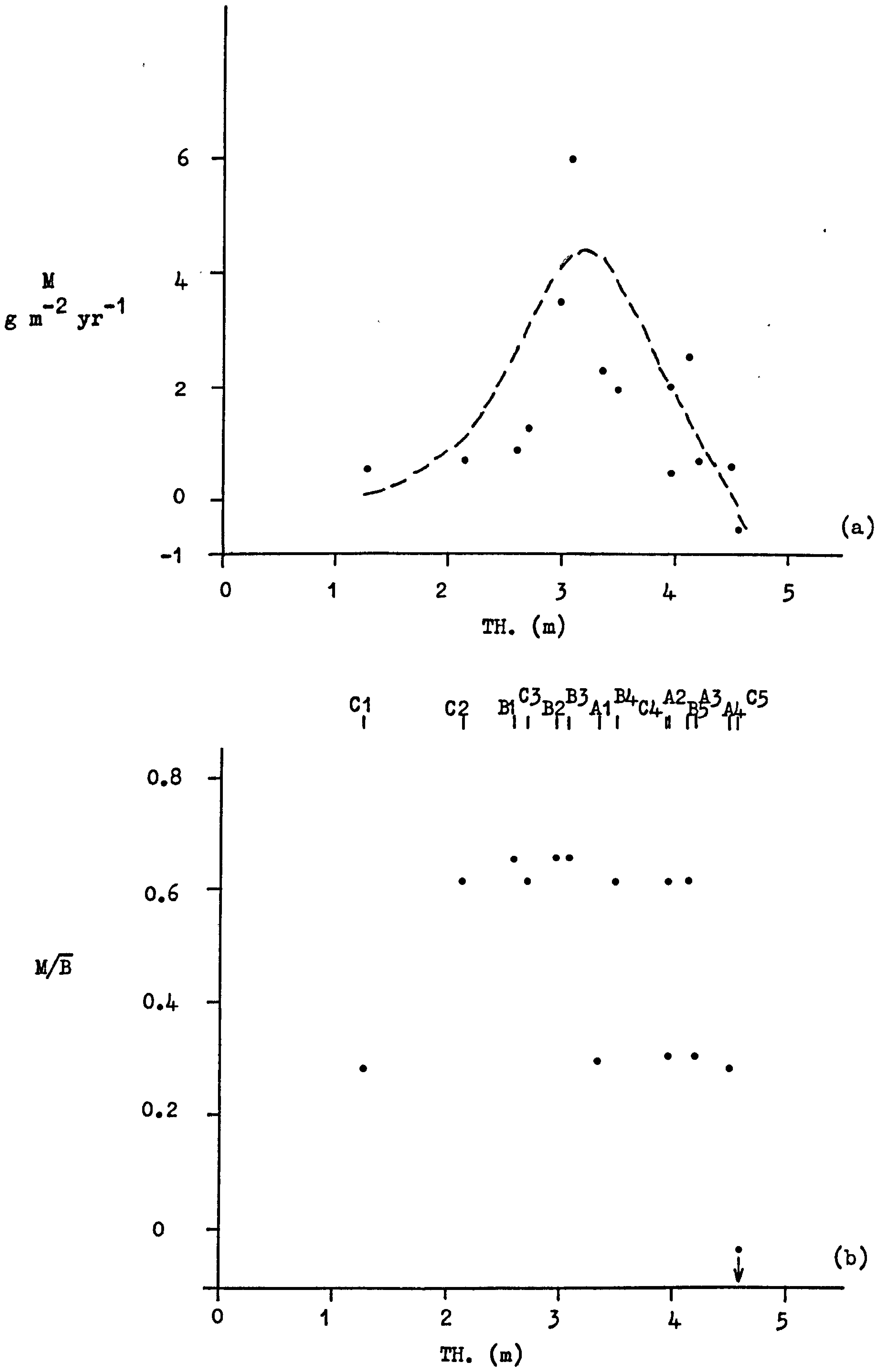


Figure 3.25 M. balthica : The Relationship Between Mortality and $M/\bar{B}$ With Tidal Height. Dotted Line Drawn by Eye.

3.4.2. Temporal Analysis.

In order to identify the causes of body weight fluctuations over the annual cycle, monthly body condition (CF_H), the flesh and shell dry weight of 4 and 8mm high standard sized animals (4mm fdw, 8mm fdw, 4mm s.w., 8mm s.w.) were analysed together with those environmental variables which had been monitored at each of the sixteen sampling dates (see Section 2.4.5.). The data are given in Figs. 3.5 to 3.9, and in Section 2.4. In order to identify whether any of the dependent variables were density dependent, the further variables of station monthly flesh and total biomass (of the 'large' animals) were also incorporated into the analysis.

The correlation and multiple regression analysis was performed on each station separately and on the total data in which all of the stations' data were combined (Fig. 3.26 (A1) to (C5), (ALL); Table 3.21).

3.4.2.1. The Monthly Condition Factor Analysis.

3.4.2.1.1. For Each Station. (See Fig. 3.26 (A1) to (C5); Table 3.21).

At the majority of the stations, the animals' condition was positively correlated with temperature (all stations except A2 and A4) and the monthly flesh biomass (all except A2, B1, B2, C1 and C4); at the Stations A1, A3, and B5 it was also correlated with the monthly total biomass. The condition was positively correlated with interstitial salinity at the mid- to upper-shore areas (A1, B3, B5, C2, C4 and C5) and with water salinity at the fine mud, mid- to low-shore areas (A1, B2 and C1).

With an increase in the sediment %N and %C the animals'

C4

	Int. Sal.	%H_2O.	%C.	%N.	C/N.	Tdw.	fdw.	Org.C.	CHO.	Temp.	Water Sal.
CF_H	+		+							+	
4_{fdw}	+									+++	
8_{fdw}	+									+	
4_{sw}											
8_{sw}											

C5

	Int. Sal.	%H_2O.	%C.	%N.	C/N.	Tdw.	fdw.	Org.C.	CHO.	Temp.	Water Sal.
CF_H	++						+			+	
4_{fdw}											
8_{fdw}	+						+			++	
4_{sw}	+						+			-	
8_{sw}								+		+	

ALL STATIONS

	Int. Sal.	%H_2O.	%C.	%N.	C/N.	Tdw.	fdw.	Org.C.	CHO.	Temp.	Water Sal.
CF_H	+++	+++	+++	+++		+	+++			+++	+++
4_{fdw}	+++	++	++	+++	--		+			+++	+++
8_{fdw}	+++	+++	+++	+++		+	+++			+++	+++
4_{sw}	---	---	---	---		---	---			---	-
8_{sw}		---	---	---	---		---				

Figure 3.26 M. balthica: Temporal Data Analysis - Pearson Correlation Matrices for Each Station and for 'All Stations' Data Combined; Only Significant Correlations are Given, (+ or - = significant; ++ or -- = very significant; +++ or --- = highly significant, as figure 2.9).

The abbreviations for the environmental factors are as given in figure 2.17.

Other abbreviations:

Tdw. = monthly total dry-weight biomass;
fdw. = monthly flesh dry-weight biomass;
4_{fdw} = flesh dry-weight of 4 mm standard-size animal; (monthly values);
8_{fdw} = " " " 8 mm " " " ; " " ;
4_{sw} = shell weight " 4 mm " " " ; " " ;
8_{sw} = " " " 8 mm " " " ; " " ;
CF_H = monthly condition factor.

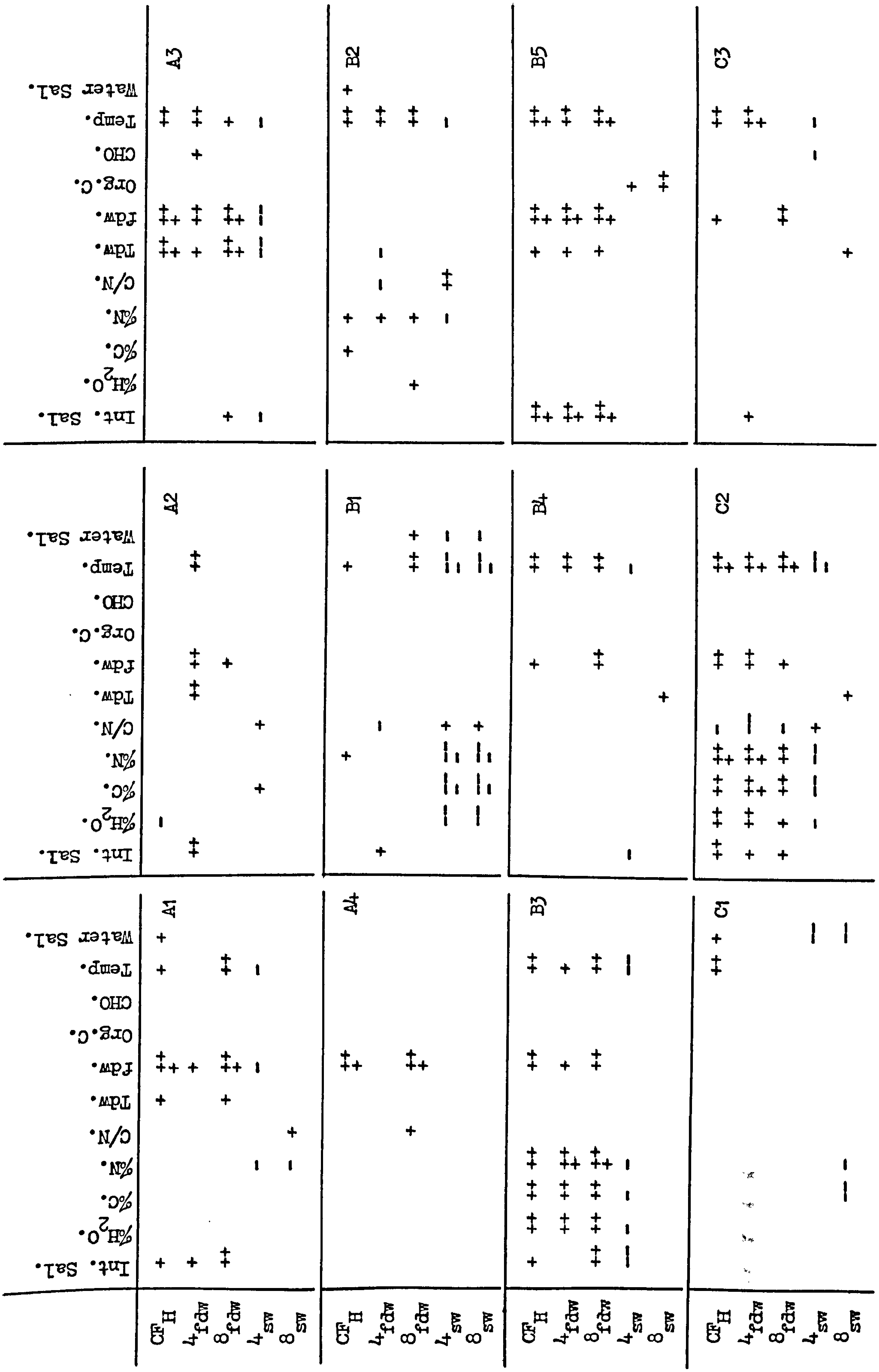


Figure 3.26 continued.

Table 3.21 M. balthica : Temporal Multiple Regression Analysis :- Flesh Condition and Shell- and Flesh-weight of Standard-size Animals Against all Monthly Environmental Variables and Monthly Biomass Data (Legend as Fig. 3.25).

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
A1	CF_H	$\overset{*}{1.887}_{Temp.} - \overset{*}{0.284}_{tdw} + 19.350$	Org. C.	90.1%	fdw (49.5%), tdw (19.0%) Int. Sal. (10.9%).
	4_{fdw}	$\overset{***}{0.144}_{fdw} - \overset{***}{0.028}_{tdw} + 0.665$	-	90.8%	fdw (32.0%), tdw (46.2%).
	8_{fdw}	$\overset{***}{0.765}_{fdw} - \overset{***}{0.126}_{tdw} + \overset{**}{0.323}_{Temp.} - \overset{**}{2.046}_{C.H.O.} + \overset{**}{0.252}_{Water\ Sal.} + 1.897$	-	98.4%	fdw (52.9%), tdw (14.4%), Temp. (10.5%).
	4_{sw}	$\overset{*}{0.145}_{\%H_2O} - \overset{*}{0.300}_{fdw} + 7.476$	-	88.7%	fdw (21.9%), tdw (23.9%), Org. C. (13.3%).
	8_{sw}	$\overset{**}{1.135}_{\%H_2O} - \overset{**}{17.035}_{\%C} - \overset{**}{2.379}_{fdw} + \overset{*}{6.238}_{C.H.O.} + \overset{*}{2.798}_{C/N} + \overset{*}{0.345}_{tdw} - 20.714$	-	92.9%	%N (27.8%), $\%H_2O$ (16.7%), tdw (18.5%).
A2	CF_H	$\overset{***}{7.262}_{fdw} - \overset{***}{0.980}_{tdw} + 7.471$	-	98.7%	fdw (34.3%), tdw (38.8%), C/N (10.3%).
	4_{fdw}	$\overset{***}{0.071}_{\%H_2O} - \overset{***}{22.121}_{\%N} + \overset{***}{1.089}_{\%C} - \overset{***}{0.132}_{C/N} - \overset{**}{0.814}_{Org.\ C.} - \overset{**}{0.761}_{C.H.O.} + \overset{*}{0.032}_{Temp.} + 0.032_{Water\ Sal.} - 0.763$	-	99.1%	fdw (49.3%), $\%H_2O$ (26.7%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
A2 (Cont.)	8_{fdw}	$\overset{***}{5.610}_{fdw} - \overset{***}{0.585}_{tdw} - \overset{*}{4.921}_{\%C} + 2.503$	-	98.9%	fdw (26.8%), tdw (51.0%).
	4_{sw}	All n.s. + 9.014	-	56.2%	%C (22.9%).
	8_{sw}	$\overset{*}{1.773}_{tdw} + \overset{*}{1.634}_{Temp.} + 174.528$	-	90.4%	fdw (12.3%), C/N (16.1%), Int. Sal. (13.4%).
A3	CF_H	$\overset{*}{1.001}_{Water\ Sal.} - \overset{*}{1.749}_{Int.\ Sal.} + 60.643$	-	95.9%	fdw (73.3%), tdw (10.8%).
	4_{fdw}	All n.s. + 4.262	-	78.1%	fdw (45.9%), %N (11.9%).
	8_{fdw}	$16.703 - \overset{*}{2.166}_{C.H.O.}$	-	96.0%	fdw (82.8%).
	4_{sw}	All n.s. + 1.785	-	79.9%	fdw (47.7%), Org. C. (14.5%).
	8_{sw}	$\overset{*}{4.562}_{tdw} - \overset{*}{22.126}_{fdw} + 115.097$	-	82.7%	%N (11.2%), $\%H_2O$ (31.4%).
A4	CF_H	$\overset{**}{10.702}_{fdw} - \overset{*}{1.421}_{tdw} + 26.066$	-	89.8%	fdw (48.6%), tdw (31.1%).
	4_{fdw}	$1.576 - \overset{***}{0.803}_{\%C} + \overset{**}{0.693}_{fdw} + \overset{**}{0.065}_{\%H_2O}$ $- 0.096_{tdw} + 0.405_{Org.\ C.}$	-	92.3%	C.H.O. (13.8%), C/N (12.7%) tdw (19.9%), Org. C. (10.6%), $\%H_2O$ (14.0%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
A4 (Cont.)	8_{fdw}	$\overset{*}{3.544}_{fdw} + 6.613$	-	91.5%	fdw (51.3%), tdw (28.4%).
	4_{sw}	$10.889 - \overset{**}{2.300}_{Org.\ C.}$	-	85.4%	Water Sal. (23.7%), Org. C. (14.5%), %C (10.9%).
	8_{sw}	$\overset{***}{1.889}_{C/N} - \overset{***}{14.967}_{Org.\ C.} - \overset{***}{1.612}_{Temp.} - \overset{***}{11.370}_{fdw}$ $- \overset{***}{11.068}_{C.H.O.} + \overset{**}{2.046}_{tdw} - \overset{*}{8.109}_{\%C} + 72.543$	-	93.5%	Int. Sal. (16.8%), Org. C. (14.0%), Water Sal. (11.4%), tdw (15.9%).
B1	CF_H	$\overset{***}{15.123}_{fdw} - \overset{***}{1.325}_{tdw} + \overset{**}{2.812}_{C/N} + \overset{**}{289.392}_{\%N}$ $- \overset{**}{13.446}_{\%C} - \overset{*}{1.123}_{Temp.} + \overset{*}{10.086}_{Org.\ C.}$ $- \overset{*}{0.671}_{\%H_2O} - 25.615$	-	95.0%	Temp. (28.7%), tdw (18.9%), fdw (12.7%), %H_2O (10.4%).
	4_{fdw}	$\overset{***}{0.873}_{fdw} - \overset{***}{0.124}_{Temp.} - \overset{***}{0.071}_{tdw} + \overset{**}{17.708}_{\%N}$ $+ \overset{**}{0.965}_{Org.\ C.} - \overset{**}{0.066}_{\%H_2O} - \overset{*}{0.678}_{\%C}$ $+ \overset{*}{0.553}_{C.H.O.} - 1.136$	-	92.6%	C/N (24.6%), fdw (16.4%), Int. Sal. (11.1%), tdw (11.1%).
	8_{fdw}	$\overset{***}{8.304}_{fdw} - \overset{***}{0.730}_{tdw} - \overset{**}{5.889}_{\%C} + \overset{*}{117.337}_{\%N}$ $+ \overset{*}{1.305}_{C/N} - 12.039$	-	95.7%	Temp. (39.6%), tdw (22.9%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
B1 (Cont.)	4_{sw}	All n.s. + 5.832	-	91.0%	Temp. (65.3%).
	8_{sw}	$\overset{***}{2.139}_{\%H_2O} + \overset{***}{1.956}_{tdw} - \overset{***}{19.801}_{fdw} + \overset{***}{3.504}_{Int.\ Sal.}$ $- \overset{***}{2.325}_{Water\ Sal.} - \overset{***}{553.316}_{\%N} + \overset{**}{2.290}_{Temp.}$ $+ \overset{**}{17.500}_{\%C} - \overset{**}{29.990}_{Org.\ C.} - \overset{**}{19.664}_{C.H.O.}$ $- \overset{*}{4.838}_{C/N} + 81.017$	-	97.8%	Temp. (54.7%), $\%H_2O$ (14.1%).
B2	CF_H	$\overset{*}{2.400}_{fdw} - \overset{*}{0.390}_{tdw} + \overset{*}{5.139}_{Org.\ C.} + 46.406$	-	94.0%	Temp. (45.7%), tdw (14.4%), fdw (13.8%).
	4_{fdw}	$\overset{***}{0.504}_{Org.\ C.} + \overset{***}{0.035}_{Temp.} - \overset{***}{0.070}_{Int.\ Sal.}$ $- \overset{***}{0.063}_{\%H_2O} + \overset{***}{11.639}_{\%N} - \overset{**}{0.356}_{\%C} + \overset{*}{0.054}_{Water\ Sal.}$ $+ 2.409$	-	99.0%	Water Sal. (34.4%), C/N (15.0%).
	8_{fdw}	$\overset{*}{1.806}_{fdw} - \overset{*}{0.280}_{tdw} + \overset{*}{4.212}_{Org.\ C.} + 28.692$	-	89.4%	Temp. (40.6%), tdw (11.8%), fdw (18.6%).
	4_{sw}	$- \overset{*}{0.107}_{Temp.} - \overset{*}{1.069}_{Org.\ C.} - 9.927$	-	95.4%	C/N (45.0%), Temp. (15.0%), Water Sal. (11.8%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
B2 (Cont.)	8_{sw}	$\overset{**}{7.828}_{\text{C.H.O.}} - \overset{**}{1.259}_{\text{Temp.}} - 15.476$	-	90.2%	C/N (16.5%), C.H.O. (14.%), tdw (10.4%), Water Sal. (17.8%).
B3	CF_H	$\overset{**}{0.640}_{\text{Temp.}} + \overset{*}{151.539}_{\%N} - \overset{*}{6.940}_{\%C} + \overset{*}{0.972}_{C/N}$ $- 6.814$	Int. Sal.	96.3%	%N (54.4%), Temp. (30.6%).
	4_{fdw}	$\overset{***}{28.594}_{\%N} - \overset{***}{1.319}_{\%C} + \overset{***}{0.210}_{C/N} - \overset{**}{0.099}_{\text{Int. Sal.}}$ $+ \overset{*}{0.051}_{\text{Temp.}} - 2.258$	-	96.4%	%N (54.1%), Temp. (15.7%), C/N (11.3%).
	8_{fdw}	$\overset{*}{0.247}_{\text{Temp.}} + 1.331$	-	95.6%	%N (48.3%), Temp. (31.4%).
	4_{sw}	$\overset{***}{0.031}_{tdw} - \overset{**}{0.111}_{\text{Int. Sal.}} - \overset{**}{0.158}_{fdw} + 8.386$	-	97.3%	Temp. (38.9%), %C (20.0%), tdw (13.6%).
	8_{sw}	$\overset{**}{0.370}_{tdw} - \overset{**}{2.098}_{fdw} + 71.361$	-	89.0%	Temp. (13.5%), tdw (18.4%), fdw (29.2%), Org. C. (11.0%).
B4	CF_H	$\overset{***}{2.997}_{fdw} - \overset{**}{0.269}_{tdw} + \overset{**}{0.853}_{\%H_2O} + \overset{*}{0.337}_{\text{Temp.}}$ $- 18.733$	-	96.7%	Temp. (40.0%), fdw (14.6%), tdw (20.0%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
B4 (Cont.)	4_{fdw}	$\overset{**}{0.040}_{\text{Temp.}} + \overset{**}{0.152}_{\text{fdw}} + \overset{*}{0.044}_{\%H_2O} - \overset{*}{0.015}_{\text{tdw}} - 1.017$	-	96.0	Temp. (38.8%), $\%H_2O$ (19.7%).
	8_{fdw}	$\overset{**}{1.771}_{\text{fdw}} - \overset{*}{0.161}_{\text{tdw}} - 10.496$	-	92.7%	fdw (40.0%), tdw (33.7%).
	4_{sw}	$14.994 - \overset{**}{1.882}_{\text{Org. C.}} - \overset{*}{0.152}_{\text{Int. Sal.}}$	-	83.3%	Int. Sal. (25.7%), Org. C. (22.4%).
	8_{sw}	All n.s. + 97.051	-	72.8%	tdw (32.5%), %N (12.0%).
B5	CF_H	$\overset{**}{0.651}_{\text{Temp.}} + \overset{*}{1.853}_{\text{fdw}} - \overset{*}{0.456}_{\text{Water Sal.}} + \overset{*}{0.312}_{\%H_2O} + 23.316$	-	98.3%	Int. Sal. (68.5%), fdw (12.3%).
	4_{fdw}	All n.s. - 2.004	-	88.8%	Int. Sal. (66.6%).
	8_{fdw}	$\overset{***}{1.384}_{\text{fdw}} + \overset{**}{0.314}_{\text{Temp.}} - \overset{*}{0.121}_{\text{tdw}} + 16.255$	-	98.0%	Int. Sal. (65.6%), fdw (10.4%), tdw (13.4%).
	4_{sw}	$\overset{**}{1.837}_{\text{Org. C.}} + 2.864$	-	81.7%	Org. C. (23.2%), Int. Sal. (17.1%), C.H.O. (18.8%), %C (10.7%).

Table 3.21 (Continued).

Station	Dependent Variable	Significant Equation	Ecl. Variables	Total Variance Accounted For	Main Variables
B5 (Cont.)	8_{sw}	$\overset{*}{8.396}_{\text{Org. C.}} + 86.149$	-	81.2%	Org. C. (33.5%), Int. Sal. (22.1%).
C1	CF_H	$\overset{**}{2.802}_{\text{Int. Sal.}} - \overset{**}{21.084}_{\text{Org. C.}} - 39.447$	$\%H_2O$, %N, tdw, fdw.	98.3%	Temp. (53.4%), Org. C. (11.6%), Int. Sal. (12.1%), C/N (15.0%).
	4_{fdw}	$\overset{***}{0.364}_{\text{Int. Sal.}} + \overset{**}{0.052}_{\%H_2O} - \overset{*}{0.349}_{\text{fdw}} - \overset{*}{0.092}_{\text{Temp.}}$ $- 10.148$	%C, C/N, Org.C., Water Sal.	99.4%	Int. Sal. (33.6%), $\%H_2O$ (29.9%), fdw (10.2%).
	8_{fdw}	$\overset{***}{0.485}_{\text{Temp.}} + \overset{***}{1.655}_{\text{Int. Sal.}} + \overset{***}{0.489}_{\%H_2O} - \overset{***}{3.371}_{\%C}$ $- \overset{***}{0.048}_{\text{Water Sal.}} + \overset{***}{0.156}_{\text{Temp.}} - \overset{*}{0.364}_{\text{C.H.O.}}$ $- 54.923$	%N, C/N, tdw, Org. C.	All	Temp. (29.9%), Int. Sal. (34.9%), $\%H_2O$ (14.9%), %C (19.4%).
	4_{sw}	$17.054 - \overset{***}{0.116}_{\text{Water Sal.}} - \overset{***}{0.117}_{\text{Int. Sal.}}$ $+ \overset{***}{0.183}_{\text{C.H.O.}} + \overset{***}{3.318}_{\text{Org. C.}} - \overset{***}{0.110}_{\text{tdw}}$ $+ \overset{***}{1.032}_{\text{fdw}} - \overset{*}{29.558}_{\%N}$	$\%H_2O$, %C, C/N, Temp.	All	Water Sal. (67.7%).

Table 3.21 (Continued).

Station	Dependent Variable	Significant Equation	Ecl. Variables	Total Variance Accounted For	Main Variables
C1 (Cont.)	8_{sw}	$217.546 - \overset{***}{1.196}_{\text{Water Sal.}} - \overset{***}{219.034}_{\%N} - \overset{***}{0.593}_{\text{tdw}}$ $- \overset{***}{1.261}_{\%H_2O} + \overset{***}{6.667}_{\%C} + \overset{***}{2.281}_{\text{fdw}} - \overset{**}{2.413}_{\text{C.H.O.}}$	Int. Sal., C/N, Org. C., Temp.	All	Water Sal. (69.1%), %N (14.6%).
C2	CF_H	All n.s. + 27.756	-	94.2%	Temp. (67.0%), %N (15.5%).
	4_{fdw}	$\overset{***}{10.845}_{\%N} + \overset{***}{0.085}_{\text{Temp.}} - \overset{***}{0.681}_{\text{fdw}} - \overset{***}{0.387}_{\text{C.H.O.}}$ $- \overset{**}{0.699}_{\%C} - \overset{**}{0.422}_{\text{Org. C.}} + 1.260$	-	99.4%	%N (67.2%), Temp. (12.5%).
	8_{fdw}	All n.s. + 8.971	-	86.9%	Temp. (56.7%), Org. C. (10.5%).
	4_{sw}	All n.s. + 2.934	-	87.7%	Temp. (64.8%), C/N (13.5%).
	8_{sw}	All n.s. - 3.914	fdw	67.3%	fdw (42.6%), C/N (16.1%).
C3	CF_H	$\overset{**}{6.148}_{\text{fdw}} + \overset{*}{0.662}_{\text{Temp.}} - \overset{*}{6.135}_{\text{C.H.O.}} - 14.934$	-	97.5%	Temp. (34.4%), fdw (15.0%), tdw (36.2%).
	4_{fdw}	$\overset{***}{0.088}_{\text{Temp.}} - \overset{***}{0.546}_{\text{C.H.O.}} + \overset{**}{0.142}_{\text{fdw}}$ $- \overset{*}{0.017}_{\text{Water Sal.}} - \overset{*}{0.052}_{\text{Int. Sal.}} + 4.640$	-	99.2%	Temp. (70.0%), C.H.O. (11.9%).

Table 3.21 (Continued).

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Varaince Accounted For	Main Variables
C3 (Cont.)	8_{fdw}	$\overset{***}{4.650}_{\text{fdw}} + \overset{**}{1.093}_{\%H_2O} - \overset{**}{5.137}_{\text{Org. C.}} - \overset{*}{3.709}_{\text{C.H.O.}}$ $- 17.910$	-	98.2%	fdw (41.4%), tdw (45.8%).
	4_{sw}	$\overset{**}{434.813}_{\%N} + \overset{*}{1.033}_{C/N} - \overset{*}{28.476}_{\%C} - 9.555$	-	81.0%	Temp. (23.3%), Org. C. (10.8%), %C (16.0%).
	8_{sw}	$\overset{*}{1.503}_{\text{tdw}} - \overset{*}{18.289}_{\text{C.H.O.}} - \overset{*}{23.595}_{\text{Org. C.}} + 141.899$	-	84.5%	tdw (19.3%), C.H.O. (15.9%), Org. C. (11.5%).
C4	CF_H	$\overset{**}{10.338}_{\text{fdw}} - \overset{**}{0.953}_{\text{tdw}} + \overset{*}{0.696}_{\text{Int. Sal.}} - 7.902$	-	97.0%	Int. Sal. (25.0%), %N (19.1%), fdw (11.4%).
	4_{fdw}	$\overset{*}{1.908}_{\text{fdw}} - \overset{*}{0.200}_{\text{tdw}} - 6.654$	-	85.9%	Temp. (54.3%), fdw (11.0%).
	8_{fdw}	$\overset{***}{3.819}_{\text{C.H.O.}} - \overset{***}{0.457}_{\text{Temp.}} + \overset{***}{4.106}_{\text{Org. C.}}$ $+ \overset{***}{9.895}_{\text{fdw}} - \overset{***}{0.768}_{\text{tdw}} + \overset{***}{0.608}_{\text{Int. Sal.}}$ $+ \overset{**}{0.516}_{\%H_2O} + \overset{**}{0.445}_{\text{Water Sal.}} - \overset{*}{97.707}_{\%N} - 23.794$	-	99.1%	Temp. (26.8%), Org. C. (12.8%), %C (15.2%), tdw (12.1%).
	4_{sw}	All n.s. + 26.934	-	49.0%	C/N (14.3%), Temp. (11.6%).
	8_{sw}	All n.s. + 264.380	-	59.6%	Temp. (17.9%), fdw (12.7%).

Table 3.21 (Continued)

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
C5	CF_H	$\overset{**}{24.795}_{\text{fdw}} - \overset{**}{3.551}_{\text{tdw}} + \overset{*}{19.505}_{\%\text{C}} - \overset{*}{342.956}_{\%\text{N}} + 5.896$	-	94.3%	Int. Sal. (43.6%), fdw (15.3%), tdw (21.7%).
	4_{fdw}	All n.s. - 0.717	-	65.9%	Int. Sal. (14.8%), Org. C. (10.4%).
	8_{fdw}	All n.s. + 10.688	-	85.3%	Temp. (37.7%), fdw (19.6%).
	4_{sw}	$\overset{**}{5.700}_{\%\text{C}} - \overset{**}{0.472}_{\text{C/N}} - \overset{**}{95.101}_{\%\text{N}} + 10.472$	-	89.8%	fdw (26.9%), tdw (29.8%), %N (11.4%).
	8_{sw}	All n.s. + 90.728	-	75.8%	Org. C. (26.6%), Temp. (20.4%).
All	CF_H	$\overset{***}{0.452}_{\text{Temp.}} + \overset{***}{40.872}_{\%\text{N}} - \overset{***}{2.317}_{\%\text{C}} + \overset{***}{1.171}_{\text{fdw}} - \overset{***}{0.151}_{\text{tdw}} - \overset{***}{1.887}_{\text{C.H.O.}} - \overset{***}{2.073}_{\text{Org. C.}} + \overset{*}{0.210}_{\text{Int. Sal.}} + \overset{*}{0.075}_{\%\text{H}_2\text{O}} + 9.275$	-	59.4%	Temp. (29.5%), %N (11.3%), tdw (6.0%).
	4_{fdw}	$\overset{***}{0.025}_{\text{Temp.}} + \overset{***}{0.035}_{\text{Int. Sal.}} - \overset{***}{0.006}_{\text{tdw}} + \overset{**}{2.901}_{\%\text{N}} - \overset{**}{0.162}_{\%\text{C}} + \overset{**}{0.032}_{\text{fdw}} - 0.206$	-	37.8%	Temp. (22.2%), %C (6.7%), %N (4.2%).

Table 3.21 (Continued).

Station	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
All (Cont.)	8_{fdw}	$\overset{***}{0.236}_{\text{Temp.}} - \overset{***}{1.069}_{\%\text{C}} + \overset{***}{0.661}_{\text{fdw}} - \overset{***}{0.090}_{\text{tdw}}$ $+ \overset{***}{0.065}_{\%\text{H}_2\text{O}} - \overset{***}{0.880}_{\text{C.H.O.}} - \overset{***}{1.270}_{\text{Org. C.}}$ $+ \overset{*}{15.361}_{\%\text{N}} + \overset{*}{0.131}_{\text{Int. Sal.}} + 4.054$	-	49.9%	Temp. (25.3%), %N (8.7%), tdw (6.3%).
	4_{sw}	$7.668 - \overset{*}{7.463}_{\%\text{N}} - \overset{*}{0.490}_{\text{Org. C.}}$	-	38.0%	%N (28.9%), Temp. (5.2%).
	8_{sw}	$\overset{***}{0.319}_{\text{tdw}} - \overset{***}{1.995}_{\text{fdw}} + 67.409$	-	47.3%	%C (41.0%), fdw (4.3%).

condition at B1, B2, B3, C2 and C4 increased; with an increase in sediment water content the condition at B3 and C2 increased but at Station A2 a decrease in the sediment water content was accompanied by an increase in the condition of the animals. Similarly, at Station C2 with a decrease in C/N value the condition increased.

The multiple regression analysis showed that each of the independent variables had varying amounts of influence which were dependent on the spatial characteristics of each station. On Transect A, the biomasses (mainly the flesh biomass but to a lesser extent also the total biomass) were found to be the most important factors influencing the condition. At Stations B1, B2 and B4 temperature, followed by flesh and total biomass, had the largest influence while at Stations C1, C2 and C3 temperature was again the most important factor together with water organic carbon, sediment content and flesh biomass respectively being of secondary importance. At Station B3, where changes of sediment type had occurred over the sampling period, the sediment nitrogen content and to a lesser extent temperature were the most important variables. At the coarse, high-shore stations on Transects B and C, however, the interstitial salinity variation accounted for the major part of the animals' condition variation although the secondarily important variables were flesh biomass (at B5 and C5) and the sediment nitrogen (at C4). It is difficult to say whether or not the interstitial salinity changes affected the condition. The top-shore animals would have been more susceptible to salinity changes caused by precipitation or evaporation which may have resulted in physiological stress and a lower condition. However, the salinity regime that <u>M. balthica</u>

is known to tolerate encompasses much of this salinity variation. This salinity/condition relationship may therefore be a result of the change in tidal height leading to areas of high evaporation where the animals were in poor condition due to a short immersion period, coarse sediment and low food availability.

3.4.2.1.2. For the Stations' Combined Data (Fig. 3.26; Table 3.21).

As a result of using a large amount of data, the majority of the environmental variables (interstitial and water salinity; sediment water, carbon and nitrogen content; total and flesh biomass and temperature) were positively and highly significantly correlated with the animals' condition. The scatter diagrams produced show that the body condition was positively and curvilinearly related to the sediment carbon and nitrogen content and to the interstitial salinity (Fig. 3.27a, b, f) and was optimal at a C/N value of about 17 (Fig. 3.27c). Condition also increased with temperature upto 12°C but then decreased slightly (Fig. 3.27 e)(see Section 3.4.2.1.3.). The condition also increased with the flesh biomass although the majority of the points lay within a narrow range and therefore weighted the relationship accordingly.

The multiple regression, however, showed that while temperature and sediment %N were the most important variables, the total variation accounted for by the independent variables was low, suggesting that many factors not included in the regression were responsible for influencing the body condition of the animals. It is evident that although, in these relationships on a station basis, the main factors such as tidal height (and immersion period) and particle size were kept relatively constant throughout the sampling period and therefore it was unnecessary to

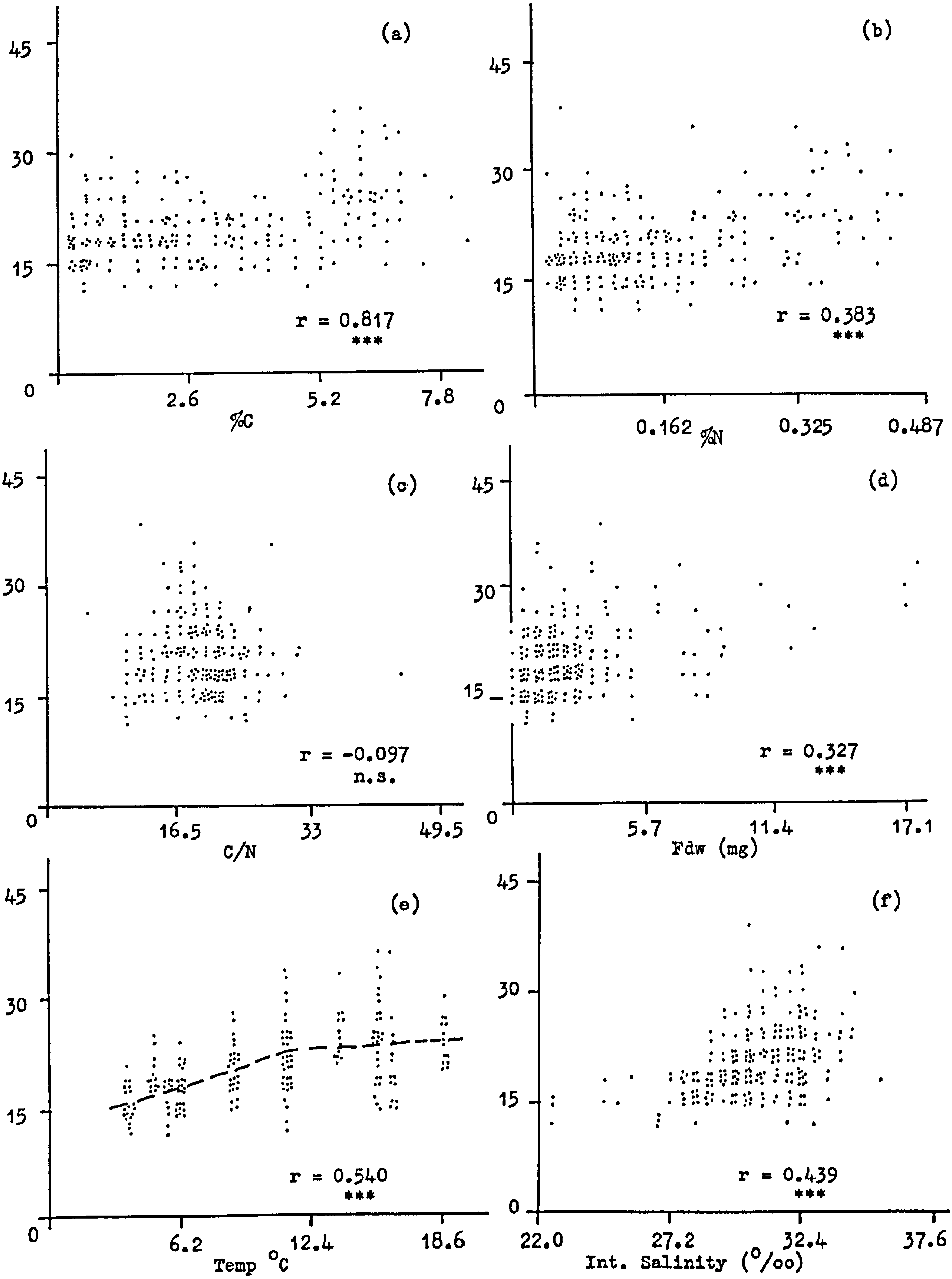


Figure 3.27 M. balthica : Temporal Data - Flesh Condition Factor :- With Environmental Variables. (Ordinate = CF_H.)

incorporate them into the relationships, on a whole area basis these main factors were not constant nor were they included in the regression. The inclusion of these variables would therefore have decreased the large proportion of unexplained variation in the relationship.

Finally, the magnitude of the flesh (or total) dry weight biomass was found not to have a deleterious effect on the animals but that the increased presence of the animals possibly increased the condition. Two possibilities may account for this phenomenon: either that the highest body condition was found in the best, common areas (this was true to a certain extent although the highest condition was found at the Stations C1 and B1 which supported relatively low biomasses), or that an increased biomass would lead to greater bioturbation which would improve the quality and possible quantity of the available food. Additionally, the body condition would be density dependent should food, space or oxygen be limiting; they were probably not limiting on the major part of Torry Bay (see Section 6.2.).

3.4.2.1.3. The Change in Condition with Temperature.

As temperature was found to be an important influence in the animals' condition at most stations, this association was further considered by constructing the diagram (Fig. 3.28 (b)) from the linear regression equations of these two variables (Table 3.22). Although the condition at all stations was similar and relatively low at low temperatures and with an increase in temperature the animals' condition increased, the condition at the lower-shore, fine substrate areas increased proportionately more than at the higher stations. This is also reflected in the range and standard deviation of the mean condition values plotted

Figure 3.28 _M. balthica_ : (a) The Relationship Between Flesh Condition Factor at Each Station (Standardised to $10^{o}C$ - see Figure 3.23) and Tidal Height and Particle Size.

(b) The Change in the Condition Factor at Each Station With Temperature and Tidal Height, Constructed From Linear Regression Equations.

CF$_H$
23
22
21
20
19
18
17
0
1
2
3
4
TH. (m)
100
200
300
400
M.P.D. (μm)
(a)
CF$_H$
25
20
15
0
4
8
12
16
20
Temp. (°C)
0
1
2
3
4
5
TH. (mm)
(b)

Table 3.22 M. balthica : The Linear Regression Equations of Flesh Condition Factor with Temperature (^{o}C).

$CF_H = b \pm S.E.\ t. + a$

Station	b	S.E.	a	n	r	p
A1	0.600	0.255	14.867	16	0.600	*
A2	0.279	0.207	15.641	14	0.363	n.s.
A3	0.494	0.181	14.471	16	0.590	*
A4	0.162	0.211	16.578	16	0.201	n.s.
B1	0.414	0.174	17.587	16	0.536	*
B2	0.601	0.175	15.200	16	0.676	**
B3	0.755	0.249	13.713	16	0.629	**
B4	0.529	0.173	13.132	16	0.632	**
B5	0.654	0.170	14.069	16	0.716	**
C1	0.704	0.249	15.420	9	0.730	*
C2	1.066	0.207	11.551	15	0.818	***
C3	0.716	0.264	14.663	16	0.586	*
C4	0.465	0.217	13.661	16	0.497	n.s.
C5	0.445	0.173	13.182	16	0.568	*
All	0.561	0.059	14.502	214	0.544	***

Table 3.23 M. balthica : The Change in Flesh Condition (Mean of all Stations) with Temperature (^{o}C).

Year	Month	Mean Temperature	Mean CF_H	S.D.
1975	March	4.9	19.41	2.54
	April	8.7	20.93	3.94
	May	11.3	26.21	3.98
	June	15.4	24.40	5.46
	July	15.7	25.53	5.57
	August	18.7	24.01	3.04
	September	13.4	25.33	4.96
	October	11.1	18.78	2.86
	November	8.7	19.16	2.65
	December	6.4	18.22	2.47
1976	January	5.9	17.11	2.00
	February	3.7	16.32	1.83
	May	11.3	19.51	2.94
	August	16.0	19.96	5.70
	November	5.5	14.27	2.48
1977	February	3.9	14.80	1.77

on Fig. 3.27 (e) which increased with increasing temperature (Table 3.23). However, although the diagram (Fig. 3.28 (b)) was constructed from the linear regressions it is unlikely that the condition would continually rise with temperature (see Fig. 3.27 (e)) and it is possible that high temperatures (>20°C) would either be directly limiting to the physiological condition of the animals or indirectly limiting by influencing the primary producers and decomposers and therefore affecting the bivalves' food supply.

Additionally, the condition at a standard temperature, 10°C, was found to increase with a decrease in both tidal height and particle size (Fig. 3.28a); this reflects both the effect of temperature upon the food supply of the animals, which was greater in the finer areas, and the amount of time available for feeding which was dependent on the immersion time and the water content of the sediment.

3.4.2.2. The 4mm Standard Animal Flesh Weight Analysis.

3.4.2.2.1. On a Station Basis (see Fig. 3.26 (A1) to (C5; Table 3.21).

The flesh weight of 4mm animals was positively correlated with temperature at all but the lowest, fine mud stations (A1, B1, C1) and the highest (C5, A4), with interstitial salinity at half the stations (A1, A2, B1, B5, C2, C3, C4) and with the sediment water, nitrogen and carbon content at Stations B2, B3 and C2; these were fine-mud, mid- to low-shore stations which, in the case of B3 and C2, were subject to sediment movement. It was negatively correlated with C/N at the fine, low-shore Stations C2, B1 and B2. In addition, the flesh weight of these animals was positively correlated with flesh biomass at A1, A2, A3, B3, B5 and C2 and with the total biomass at A2, A3 and B5 and surprisingly negatively correlated with total biomass at Station B2. This suggests that while in areas with much greater densities the flesh weight of these animals was relatively high, where the animals occurred under a mussel bed as at B2, they may be at a disadvantage.

In addition, only at Station A3 was the flesh weight of these animals positively correlated with water CHO, possibly suggesting that animals at this station utilized a water food source in the absence of sufficient sediment food, whilst at the Stations A4, C1 and C5 it was not correlated with any of the independent variables.

As with the body condition, the multiple regression analysis suggested that on Transect A the flesh biomass had the most influence on the 4mm fdw together with total biomass (at A1, A4), sediment %H_2O (at A2) and %N (at A3). At the clean bare-sand, upper-shore areas B4, C3 and C4 the most important factor was the temperature followed by the sediment %H_2O (at B4), water particulate CHO (at C3) and flesh biomass (at C4). At the highest and lowest Stations C5, B5 and C1, the interstitial salinity had the greatest influence followed by the water particulate Org.C. (at C5) and sediment %H_2O and flesh biomass (at C1). At Station B1, the 4mm fdw was most influenced by the sediment C/N followed by the flesh biomass, interstitial salinity and total biomass; at Station B2 by water salinity and then sediment C/N; and at Stations B3 and C2 by sediment %N and temperature followed by sediment C/N (at B3 only).

3.4.2.2.2. For the Stations' Data Combined (Fig. 3.26; Table 3.21).

As with the condition, the 4mm fdw increased with an increase in interstitial and water salinity; sediment %H_2O, %C and %N; flesh biomass and temperature and also with a decrease in sediment C/N values. The figures (Fig. 3.29 (a)-(f)) show the same trends as with condition although with sediment %C there was less of an upward pattern and more scatter (Fig. 3.29 (a)). The negative relationship with C/N (c) shows that in the more nutritious muds (with low C/N) there were higher 4mm fdw levels.

The multiple regression showed that temperature was again the most important factor, accounting for half of the 40% of the variation which was attributable to the factors presented in the regression. The sediment %C and %N accounted for a further 10% of the variation. This shows that within the mud flat the potential amounts of food regulated the flesh weight of these animals although over the year the temperature had an overlying effect.

3.4.2.3. The 8mm Standard Animal Flesh Weight Analysis.

3.4.2.3.1. On a Station Basis (see Fig. 3.26 (A1) to (C5); Table 3.21).

The flesh dry weight of 8mm animals was positively correlated with temperature at the majority of the stations (A3, B1-B5, C2, C4, C5), with interstitial salinity at A1, A3, B3, C2, C4 and C5 and with water salinity at B1. The 8mm fdw also increased with increasing flesh biomass at all stations except B1, B2, C1 and C4, and with the total biomass at Stations A1, A3 and B5. The sediment %H_2O, %C and %N were positively correlated

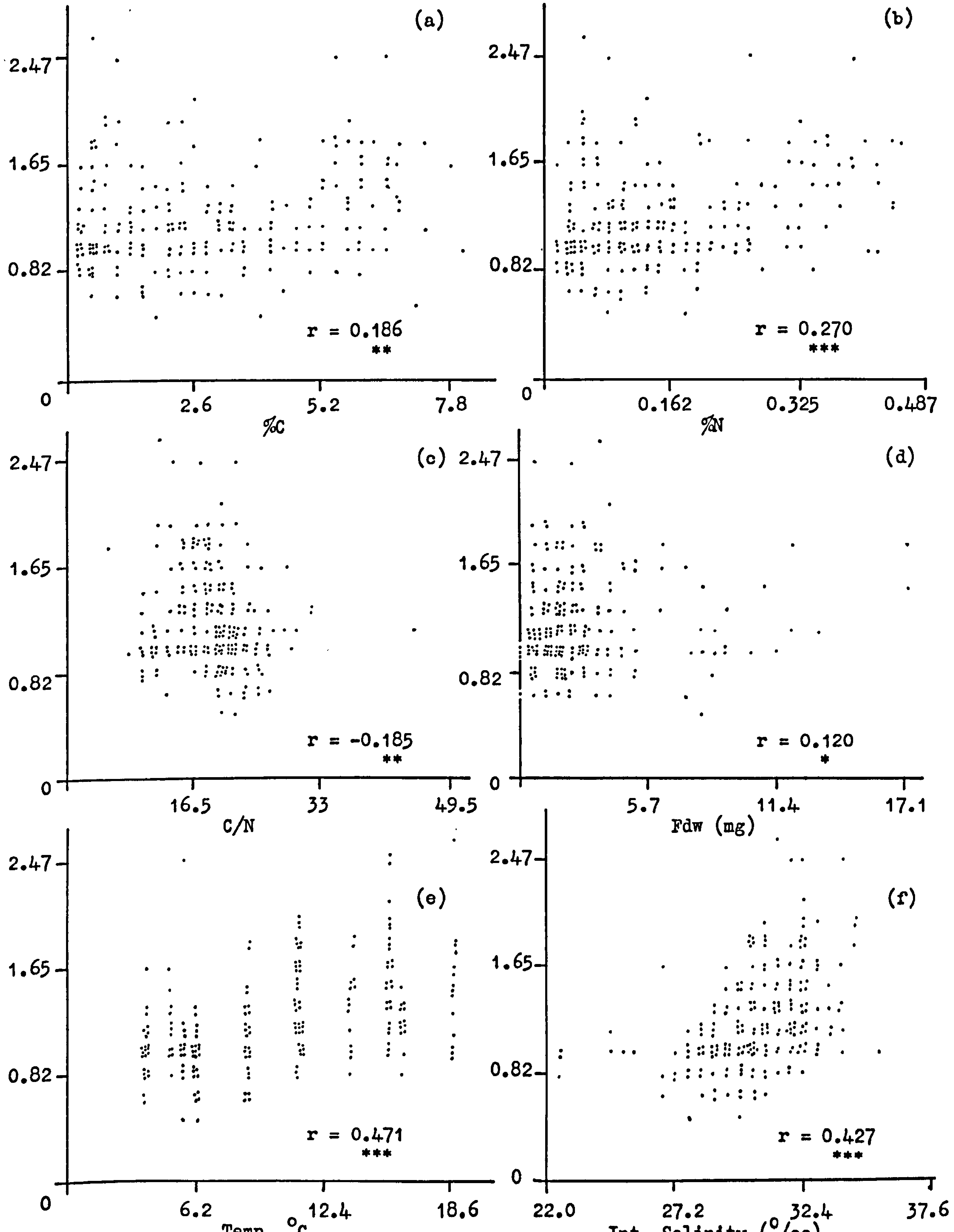


Figure 3.29 M. balthica : Temporal Data - Flesh Dry Weight of a Standard 4mm High Animal as Ordinate With Environmental Variables.

with the 8mm fdw at the low-shore, fine mud Stations B2, B3 and C2. In addition, a rise in 8mm fdw at Station C2 was accompanied by a decrease in C/N and at A4 by an increase in C/N. The change in 8mm fdw at Station C1 was not correlated with any of the independent variables; this was probably due to the paucity of data obtained for this station.

The multiple regression analysis showed that temperature, flesh biomass and total biomass were the most important variables influencing the 8mm fdw. At Stations A1, A2, A4, B4 and C3, the flesh biomass, followed by the total biomass (followed by temperature at A1), were the most important variables whereas at Station A3 the flesh biomass alone accounted for most of the variance. At the low-shore Transect B and C stations and the high-shore Transect C stations, the major part of the variance was attributable to temperature followed by total biomass (at B1), flesh and total biomass (at B2), flesh biomass (at C5), water organic carbon (at C2), water organic carbon, sediment %C, and total biomass (at C4), and interstitial salinity and sediment $\%H_2O$ and %C (at C1).

Of the remaining stations the most important variable at B3 was sediment %N followed by temperature and at B5 was interstitial salinity followed by flesh and total biomass.

3.4.2.3.2. For the Stations' Data Combined (see Fig. 3.26; Table 3.21).

The 8mm fdw again was found to increase with increases in interstitial water salinity; temperature; sediment water, carbon and nitrogen content and with total and flesh biomass. The figures (Fig. 3.30 (a) to (f)) again show similar trends with the environmental variables to those shown with the other dependent

Figure 3.30 *M. balthica* : Temporal Data - Flesh Dry Weight of a Standard 8mm High Animal as Ordinate With Environmental Variables.


(a)
20.6
13.7
6.9
0
2.6
5.2
7.8
%C
r = 0.297
***
(b)
20.6
13.7
6.9
0
0.162
0.325
0.487
%N
r = 0.364
***
(c)
20.6
13.7
6.9
0
16.5
33
49.5
C/N
r = -0.107
n.s.
(d)
20.6
13.7
6.9
0
5.7
11.4
17.1
Fdw (mg)
r = 0.315
***
(e)
20.6
13.7
6.9
0
6.2
12.4
18.6
Temp. °C
r = 0.503
***
(f)
20.6
13.7
6.9
0
22.0
27.2
32.4
37.6
Int. Salinity (°/oo)
r = 0.413
***

variables and although the correlation coefficients of sediment %C and %N and flesh and total biomass with 8mm fdw were lower than those obtained with the condition factor and these variables, they were greater for 8mm fdw than 4mm fdw. With interstitial salinity the condition factor r-value > 4mm fdw r-value > 8mm fdw r-value; but with the sediment C/N value, whilst the CF_H and 8mm fdw were not significantly correlated, the 4mm flesh weight was both significantly and negatively correlated.

In addition, as with both CF_H and 4mm fdw, in the multiple regression only half of the variation in the dependent variable was accounted for by the independent variables presented in the regression; of that 50%, 25% was attributable to temperature and another 15% jointly to sediment %C and %N.

3.4.2.4. The 4mm Standard-Size Animal Shell Weight Analysis.

3.4.2.4.1. On a Station Basis (see Fig. 3.26 (A1) to (C5); Table 3.21).

The correlation and multiple regression analysis showed that few conclusions could be reached regarding the factors affecting the 4mm animal shell weight although when compared to the three dependent variables above (CF_H, 4mm fdw, 8mm fdw) the water organic carbon level was found to play an important part at many stations. At Stations A1, A3 and C5 the most important variable was the flesh biomass followed by total biomass and water organic carbon (at A1), water organic carbon (at (A3) and total biomass and sediment nitrogen (at C5). At B1, B3, C2 and C3, temperature was the most important variable together with sediment carbon and total biomass (at B3), sediment C/N (at C2) and water organic carbon and sediment carbon (at C3). The 4mm s.w. at A4 and C1 was mainly influenced by the water salinity which at A4 was followed by the water Org. C. and the sediment %C; the sediment C/N followed by temperature were the major factors at B2 and C4 together with water salinity at B2. Of the remaining stations, the variation in 4mm s.w. at A3 was mainly attributable to sediment %C, at B4 to interstitial salinity followed by water Org. C. and at B5 to Org. C. followed by interstitial salinity.

3.4.2.4.2. For the Stations' Data Combined (Fig. 3.26; Table 3.21).

The 4mm s.w. was found to decrease with increases in interstitial and water salinity; temperature; sediment %H_2O, %C and %N and flesh and total biomass. It is of note that these factors increased together with an increasing flesh weight of 4mm animals.

The scatter diagrams (Fig. 3.31) show negative curvilinear relationships with sediment %C and %N (a, b) although with sediment C/N values there was no relationship evident (c). The negative linear relationship with flesh biomass (d) is again weighted by the large number of values at the lower end of the scale. In addition, although there was a negative linear relationship with temperature, the relationship is obscured by the large variability in the data (e). The multiple regression analysis showed that less than 40% of the total variation was accounted for and of that two-thirds was attributable to sediment nitrogen content.

3.4.2.5. The 8mm Standard-Size Animal Shell Weight Analysis.

3.4.2.5.1. On a Station Basis (see Fig. 3.26 (A1) to (C5); Table 3.21).

Unlike the other dependent variables (CF_H, 4mm fdw, 8mm fdw,

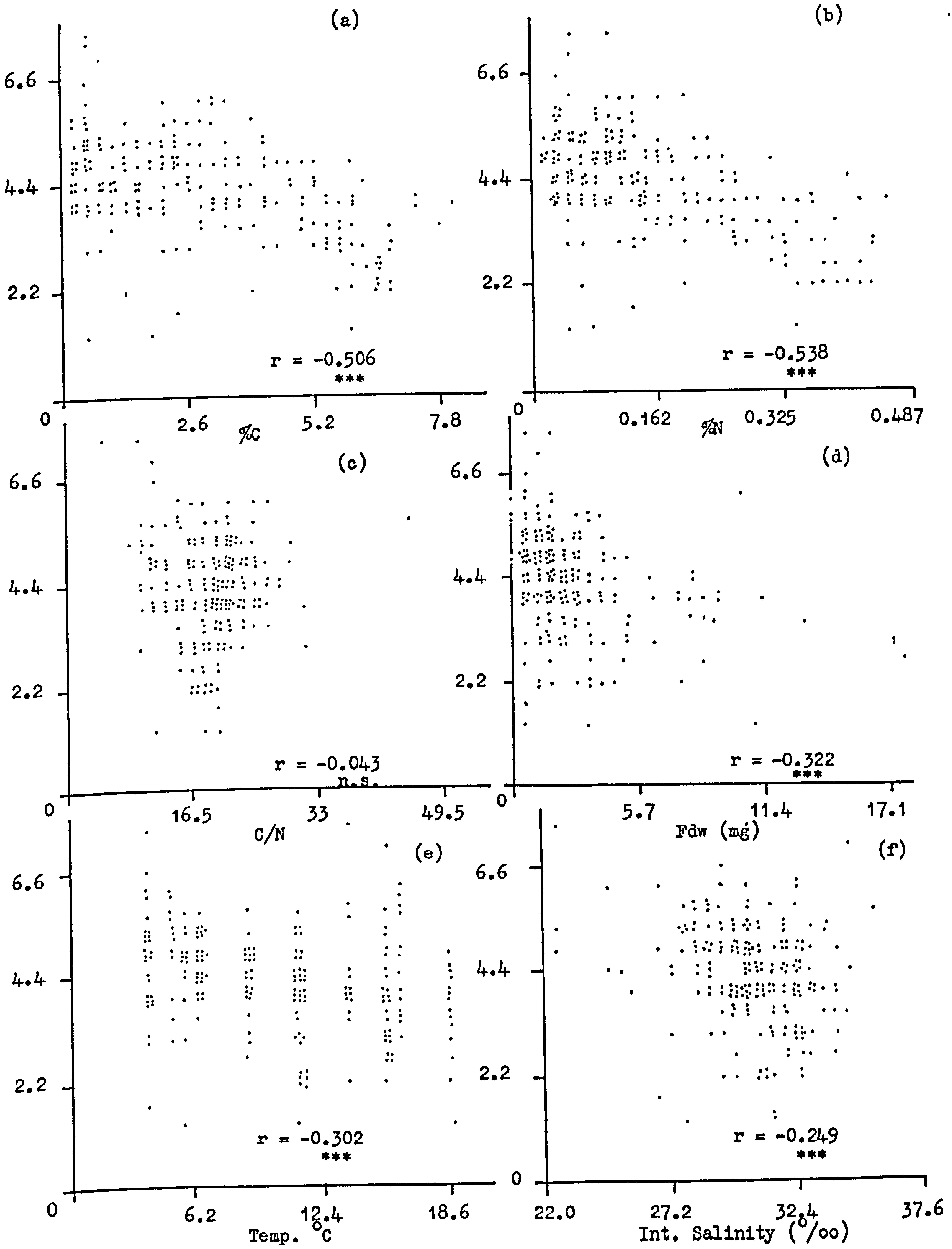


Figure 3.31 *M. balthica* : Temporal Data - Shell Dry Weight of a Standard 4mm High Animal as Ordinate With Environmental Variables.

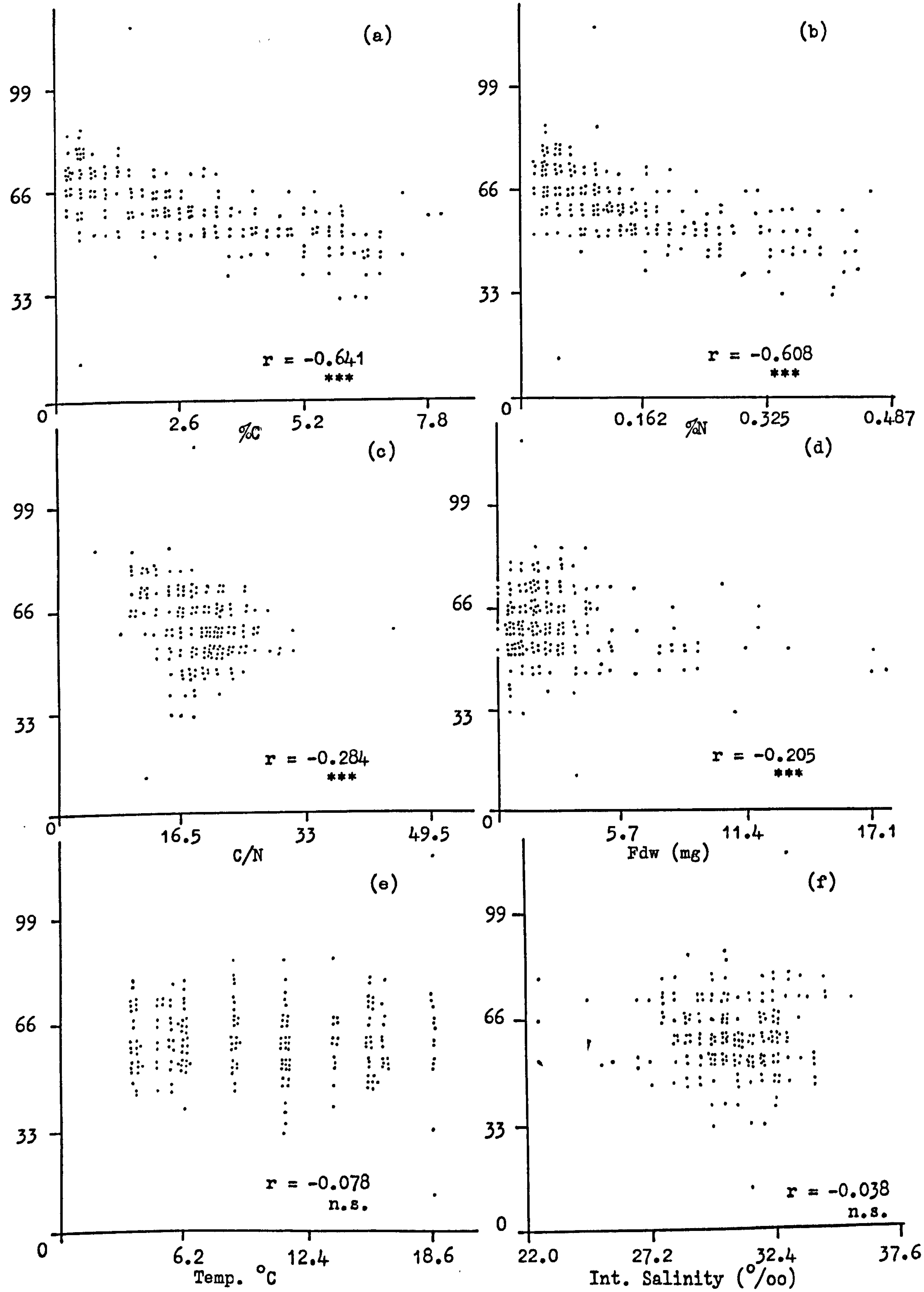
or 4mm s.w.), which were correlated with some independent variables such as flesh biomass or temperature at most of the stations, the 8mm s.w. was significantly correlated with few variables. Similarly, few overall patterns were suggested by the multiple regression analysis. At Stations A1 and A3 the sediment %N followed by the $\%H_2O$ were the most important variables, together with total biomass at A1. At Station A2 the flesh biomass followed by the C/N and interstitial salinity accounted for the most variation whilst at A4 the interstitial salinity followed by the water organic carbon, water salinity and total biomass were the major variables. Temperature changes at Stations B1, B3 and B5 accounted for the most variation in the 8mm s.w. together with sediment $\%H_2O$ (at B1), total and flesh biomass and water organic carbon (at B3) and flesh biomass (at C4). The variation in 8mm s.w. at B2 was attributed mainly to sediment C/N followed by water CHO, total biomass and water salinity, whilst at B4, C2 and C3 the total biomass was the most important factor followed by sediment %N (at B4), C/N (at C2) and water carbohydrate and organic carbon (at C3).

At the lowest station, C1, water salinity followed by sediment %N accounted for the major part of the variation whilst at the highest stations, B5 and C5, the water particulate organic carbon together with interstitial salinity (at B5) and temperature (at C5) accounted for most of the variance in the dependent variable.

3.4.2.5.2. For the Stations' Data Combined (Fig. 3.26; Table 3.21).

The shell weight of 8mm animals was negatively correlated with the sediment variables: $\%H_2O$, %C, %N and C/N and with the flesh biomass. The figures (Fig. 3.32 (a) to (f)) show that whilst there were negative relationships between 8mm s.w. and sediment %C and %N (a & b) and to a lesser extent with C/N and fdw (c & d), there were no significant relationships with temperature and interstitial salinity (e & f). In comparing the relationships between 8mm and 4mm s.w. and the independent variables (Figs. 3.31 and 3.32), it is seen that the former was more negatively correlated with sediment %C and %N than was the 4mm shell weight; also that whilst the 4mm s.w. was not significantly correlated with sediment C/N, that of the 8mm animals was highly significantly and negatively correlated with this variable. Conversely, the shell weight of 4mm animals showed a greater negative correlation with temperature, interstitial salinity and flesh biomass than did the other dependent variable. It appears, therefore, that although the shell weight of large animals was affected more by the large scale changes in sediment qualities over the beach than that of small animals, the smaller animals were affected by changes over the year in temperature and salinity as well as by the variation in flesh biomass encountered. This conclusion is a possible reflection of the fact that the shell weight of the small standard animals increases after the growing season (see Section 3.3.3.); that the 4mm animals at the stations were approximately of the same age and were growing at approximately the same rates (Section 3.3.2.) and that the 4mm animals were affected by the differences in spatial environmental changes to a lesser extent than were the 8mm animals (Section 3.4.1.2. in referring to H_1, H_2 and H_4 animals). The shell weight of the 8mm animals, however, was the cumulative result of living under differing conditions for a much longer period of time together with the additional problem that at the higher, coarser stations the animals had been subjected to those

Figure 3.32 *M. balthica* : Temporal Data - Shell Dry Weight of a Standard 8mm High Animal as Ordinate With Environmental Variables.


(a)
99
66
33
0
r = -0.641
***
2.6
5.2
7.8
%C
(b)
99
66
33
0
r = -0.608
***
0.162
0.325
0.487
%N
(c)
99
66
33
0
r = -0.284
***
16.5
33
49.5
C/N
(d)
99
66
33
0
r = -0.205
***
5.7
11.4
17.1
Fdw (mg)
(e)
99
66
33
0
r = -0.078
n.s.
6.2
12.4
18.6
Temp. °C
(f)
99
66
33
0
r = -0.038
n.s.
22.0
27.2
32.4
37.6
Int. Salinity (°/oo)

conditions for a longer period of time (5 years) than at the lower, finer stations (3 years)(Table 3.8).

The multiple regression analysis showed that although less than half of the variation in 8mm s.w. was accounted for by the variables presented, the major part of that was attributable to the sediment carbon content. This is a reflection of the low sediment %C levels at those areas of the shore at which the M. balthica growth rate was slow, i.e. the 8mm animals found there had thicker shells possibly as a result of their increased longevity. On an age basis, the 4 year old animals at the lower, coarser stations had heavier shells than those at the other stations as the former were larger (Table 3.18). With standard sizes, however, the animals of 8mm height at the high-shore areas had greater shell weights but were older than the animals at the lower areas by up to two years. It is therefore difficult to state definitely that the animals at the high-shore areas had thicker shells as a result of the environment; however, this is a possibility.

3.4.2.6. The Condition, Flesh and Shell Weight Changes at Station B3.

In order to further investigate the findings outlined above, the condition, body weight and shell weight data for Station B3, at which two years data were collected, were plotted against temperature (Fig. 3.33a, b, c). The points at which the condition or standard flesh weights reached plateaux with temperature were not evident although it appears that only at temperatures >9°C the flesh weight and condition increased with temperature. Upto 9°C there was no increase in condition. The values for body condition for the period March to June, 1975,

Figure 3.33 M. balthica : Temporal Data of Station B3 - The Change in (a) Condition Factor (■ March-June, 1975, • Other Months); (b) Shell Weight (•) and Flesh Dry Weight (▲) of 4mm Animals; (c) Shell Weight (•) and Flesh Dry Weight (▲) of 8mm Animals, With Temperature.


CF$_H$
32
30
28
26
24
22
20
18
16
14
0
4
8
12
16
20
Temp. °C
(a)
(mg)
5
4
3
2
1
0
0
4
8
12
16
20
Temp. °C
(b)
(mg)
65
60
55
50
45
40
20
15
10
5
0
4
8
12
16
20
Temp. °C
(c)

although also increasing with increasing temperature, appear to be much higher than for the other months at corresponding temperatures. It is probable that these elevated values were attributable to the increased condition of spawning animals. This phenomenon, however, did not occur during the second sampling year and may be the result of both lower levels of spawning and worse environmental conditions (see Sections 2.4.1. and 3.3.1.).

The shell weight of 4mm and 8mm animals also showed a greater decrease with temperatures greater than 9^oC than at temperatures less than 9^oC although there was a large amount of variability in the relationship with the shell weight of 8mm animals. The period of the year $<9^oC$ was from October to April and it appears therefore that M. balthica may increase in shell weight (i.e. shell thickness in a standard sized animal) in the period following the growing and spawning season.

3.5. Discussion.

3.5.1. The Status and Distribution of the Population.

Macoma balthica was found in habitats ranging from sandy to muddy sediment which, as found for M. nasuta (Hylleberg and Gallucci, 1975), suggested differences in conditions of food availability and for feeding behaviour, growth, flesh condition, and production.

The Torry Bay population was found to be comparatively large (see Table 3.24 for a review of recent literature and Clay, 1967b, p.3), with normally between 100-400 large (>2.5mm) animals m^{-2} but up to $2000m^{-2}$ in the preferred, common areas which supported high biomasses of large and small animals, had high mortalities and $M/\overline{B}$ values and produced the largest amounts of material. The mortality, as a decline in abundance, was as great as 80% between November and January at the common areas. The stations' mean biomass of large animals ranged from 5-50g tdw m^{-2} and 1-9g fdw m^{-2} during 1975-76 although it was lower the following year. The spat biomass ranged from 50-560 and 22-500mg fdw m^{-2} during the respective sampling years. Torry Bay therefore supports populations which encompass the range of populations reported elsewhere (Table 3.24); in the common areas the biomass was larger than has been reported for other areas although in studies in which very large populations were examined ($>3000m^{-2}$) the population biomasses were not given (Fraser, 1932; Tunnicliffe and Risk, 1977).

The largest populations occurred in areas of high water particulate carbohydrate content and with large spat populations, at 3 - 3.5m above C.D., an immersion period of 5.7 to 7.5 hours at neap tides and 6.0 to 6.7 at spring tides, and in the finer

Table 3.24. M. balthica: A Summary of Literature - (a) Abundance and Flesh Biomass, (b) Factors Affecting Population Distribution.

(a)

Density ($n\ m^{-2}$).	Flesh-dry-weight Biomass ($g\ m^{-2}$).	Author.
Mean 10 - 400 $>$ 2.5 mm (Upto 2000),	1 - 10 over area,	This Study;
52	0 - 25	Cederwall, (1977);
Max. 3500 adults, (mean 832)		Tunnicliffe & Risk, (1977);
Max. 3000, other areas 50,		Wolff & de Wolf, (1977);
	4.2	Ankar & Elmgren, (1976);
Max. 5500 spat, 2000 other cohorts,	Max. 5, mean 2.77,	Chambers & Milne, (1975b);
Max. 50,	0.337	Warwick & Price, (1975);
	2.6	Bergh, (1974);
184 - 492 depending on tidal height,		Gilbert, (1973);
	2.5 in March, 4.5 in June,	Beukema, (1971);
450 - 1200 $>$ 1.0 mm,		Lammens, (1967);
Max. 25,		Muus, (1967);
Max. 1500,		Newell, (1965);
302 - 1124 (Upto 2250 with spat),		Segestråle, (1960);
Max. 150,		Brady, (1932);
Max. 3071,		Fraser, (1932);
150 - 200.		Stephen, (1931).

(b)

Distribution.	Author.
(i) Studies Regarding Sediment Type, Tidal Height and Other Factors.	
Found in most sediments but prefers fine sediments at mid-tide height. Spatfall in fine, low-shore areas.	This Study;
Peak density found at mid-tide level; not found in sediments $<25\mu m$ or $>250\mu m$ M.P.D. Abundance related to bacterial numbers but not T.H. or %C.	Tunnicliffe & Risk, (1977);
Greatest spatfall at high areas (of 33% immersion period) found in very fine sediment.	Wolff & de Wolf, (1977);
Found in fine sand at LWS. to medium sand at HWN.	Chambers & Milne, (1975b);
Found just below mid-tide, 4.75 - 5.5 hours exposure, in soft fine sediments (97% 63um); 20 - $34\,^{o}/oo$ interstitial salinity, 12.2 - 13.7% Organic Carbon.	Warwick & Price, (1975);
Submergence period important but no definite pattern intertidally. High numbers in coarse sediment at top of shore.	Vassallo, (1969);
Found on soft or mixed bottom, mostly less than 3m sublittorally.	Muus, (1967);
Found in moist-sand to mud at mid-tide level.	Holme, (1949);
Food supply (as particle size) and immersion period regulate abundance, mid-tide mainly.	Beanland, (1940);

Table 3.24. continued.

(b) continued, Distribution.	Author.
(i) continued,	
Soil grade in itself not determining factor, abundant at mid-tide region.	Fraser, (1932); Rees, (1940);
Found at mid-tide to mid-upper shore, sediment determines distribution and density.	Stephen, (1932).
(ii) Studies Regarding Sediment Characteristics.	
Prefers particles ≈ 50 µm but will utilise food particles to 300 µm.	Ankar, (1977);
Sediment type important.	Boyden & Little, (1973);
Found on all types of sandy sediments but prefers sediments MPD. 3 - 4 ϕ.	Wolff, (1973);
Prefers sediments MPD. 2.25 - 2.75 ϕ with 0.5 - 10% mud.	Eisma, (1966);
Sediment %C and %N regulate distribution and density; more numerous in fine deposits but mainly young animals.	Newell, (1965);
Found in soft clayey-mud to muddy-sand.	McErlean, (1964);
Found in coarse sand to organic mud.	Segestråle, (1960);
Found in mud or muddy-sand; absent or sporadic in sandy-mud; shifting sand or high % S & C limit occurrence.	Allen, (1954);
Not found in unstable mud.	Brady, (1932).
(iii) Studies Regarding Tidal Exposure.	
Abundant in broad belt at or near mid-tide.	Myren & Pella, (1977); Brafield & Newell, (1961); Smidt, (1951); Brady, (1943); Spooner & Moore, (1940);
Found sublittorally down to 35m.	Ankar & Elmgren, (1976).

sediments. These findings agree with the majority of conclusions reached during other studies (see Table 3.24). In addition the population was optimal in sediments with 2.5%C, 0.12%N and C/N ratio values of 20-23. The latter factor suggesting that Macoma showed a preference for relatively unnutritious muds, i.e. those muds which contained a high proportion of undegraded carbon as well as a relatively high percentage of nitrogen (Newell, 1965; Tunnicliffe and Risk, 1977).

The relationship between the abundance and distribution of M. balthica and the type of sediment that it inhabits has been well documented (see Table 3.24), although as estuarine invertebrates are intimately associated with the sediments that they inhabit, then a general description of the animal-sediment relationship must be a prerequisite to understanding the ecology of such an organism (McNulty et al, 1962; Rhoads and Young, 1970; Young and Rhoads, 1971; Holland and Dean, 1977a; Tunnicliffe and Risk, 1977); furthermore, sediment type must be treated as a complex index of the environment which will reflect water movements, food supply, etc. (see Section 2.5.).

The importance of a fine substrate in providing food for M. balthica was first suggested by Beanland (1940) and demonstrated by Newell (1965), Ankar (1977) and Tunnicliffe and Risk (1977). As has been found in the present study, the latter authors found a correlation between the density of Macoma and the proportion of silt and clay in the sediments; however they found no overall correlation between the density and sediment size. The number of bacteria in the sediment was further correlated with the particle size of the sediment and their multiple regression analysis showed that M. balthica density may be accurately predicted by the bacterial density. Ankar (1977) and Tunnicliffe and Risk (1977) verified further the assumption made in this study (and by Newell, 1965, 1970) that the bacterial content of a sediment is directly related to the nitrogen and silt and clay content and that the carbon content is a direct measure of undecomposed detritus which acts as a substrate for the microflora. It is unknown whether the relationship between Macoma and bacteria density is one of cause and effect by the bivalve faecal production increasing the bacterial density (i.e. a "gardening strategy"); faecal pellets, however, do provide a good substrate for bacteria (Newell, 1965). It is likely that the bacteria were initially attracted by the high proportion of silt and clay and that the large microfloral biomass resulted from that high proportion. The importance of the proportion of silt and clay in a sediment has also been demonstrated as a factor influencing the distribution of the related, selectively deposit-feeding species M. tenta (Driscoll and Brandon, 1973). Beukema et al (1977) found that the primary production of the microphytobenthos was greatest in fine sediments (which therefore also had a high chlorophyll content) and that the sedimentation of allochthonous matter was also greatest in the fine mud areas. The microphytobenthos is considered to be the main food for Macoma (De Wilde, 1975; Beukema et al, 1977)(see Section 6.2.).

The ecology of the species cannot, however, be explained by one environmental variable, even one as important as substrate type. Particulate shores have zonation patterns as well defined as rocky shores (Eltringham, 1971) and it appears that although M. balthica is found throughout the whole intertidal area, and to large depths sublittorally (Ford, 1923; Thorson, 1957;

Segestråle, 1960; Ankar and Elmgrem, 1976; Ankar, 1977), it shows a preference for an area at or near the mid-tidal area with a 50% immersion period (see Table 3.24). Vassallo (1969) found the highest density of M. inconspicua (balthica) at the high tide area and concluded that the species had no definite intertidal preference. Reexamination of the literature does not support this conclusion. It should be repeated that the occurrence of favourable substrate at the mid/low tidal level on Torry Bay did influence the distribution. It is impossible to say whether the presence of favourable substrate at the upper-shore areas would have resulted in larger densities of the bivalve.

The analyses further show that the quantity of water particulate carbohydrate influenced the population size. It is not possible to suggest that this was a cause and effect relationship as the high CHO levels may have been the result of tidal currents resuspending bottom material. It has been shown elsewhere, however, that M. balthica may need to supplement its food intake by suspension feeding should the deposit food quantity or quality be insufficient to meet its needs (Brafield and Newell, 1961; Bubnova, 1972; Tunnicliffe and Risk, 1977; see also sections 6.1. and 6.2.). Tunnicliffe and Risk (1977), using the assimilation values obtained by Bubnova (1972), calculated that in an area with sediment carbon and nitrogen values of 0.13 - 0.98% and 0.02 - 0.05% respectively, M. balthica would have to supplement its diet by suspension feeding. In the present study, in which much higher values of sediment organic matter were measured and again using the same assumptions, it is considered unlikely that the animals in the fine, low-shore areas would have to resort to suspension-feeding although this is not the case with those animals in the less productive high-shore areas.

The densities of spat measured were similar for the two years of sampling, upto $2800m^{-2}$ in the first year and $2400m^{-2}$ in 1976-77, indicating a relatively steady-state condition of the population; however, over each of the sampling years there were large fluctuations in the population densities at each station. Hughes (1970) suggested that benthic invertebrates with planktonic larvae seldom maintain stable populations over periods of 2-3 years (often the time available for their study) whilst the periodic failure of spawning has been well documented for other tellinids (Stephen, 1929, 1932; Lammens, 1967; Hughes, 1970).

The spat mainly settled on the low-shore, fine mud areas of low shore slope and high sediment silt and clay content and at the optimal population areas. Areas which had highly skewed sediment containing a large amount of nitrogen were also favourable for settlement. It is possible that a highly skewed sediment is a reflection both of a fine particle distribution and a suitable water current pattern conducive to spat settlement (Newell, 1970; see also Section 2.5.). In addition, the analysis suggested that either the factors sediment silt and clay content and shore slope played a part in regulating spat density or another factor which influences these factors also influenced spat density. A mid-tidal area of low shore slope covered by a fine sediment which includes a large proportion of silt and clay would receive a large spatfall. The latter two factors may be dependent on the water currents passing over an area which in turn would be influenced by the shore slope and, to a lesser extent, the tidal height.

The role of water currents in determining the distribution of bivalve spat outlined above has been previously considered by many authors (Verwey, 1952; Baggerman, 1953; Posgay, 1953; Pratt, 1953; Turner, 1953; Turner and George, 1955; Kristensen, 1957; Segestråle, 1960; Wood and Hargis, 1971; Myren and Pella, 1977; Beukema, pers. comm.). Turner (1953) suggested that "hydrographic concentration" was important in determining the distribution of young sessile stages, although newly metamorphosed suspended larvae would also be affected by the same hydrographic forces. Segestråle (1960), Vassalo (1969) and Beukema (pers. comm.) also found that M. balthica larvae were restricted to sheltered silty areas and that the populations at more exposed coarse areas would receive a "secondary spatfall" of larger animals. The present study has indicated that spat settled at several coarse, sandy areas (e.g. A2, A4, C3, C4, C5) in the late autumn/winter months, long after the main settling period. In the Wadden Sea, large numbers of spat upto 5mm in length were transported 5-10km by tidal currents to arrive at coarse, clean sandy areas by their first winter (Beukema, pers. comm.; see also Chambers and Milne, 1975b and Wolff and De Wolf, 1977).

There is, however, very little direct evidence to show that larval settlement is influenced by water current patterns. Wood and Hargis (1971) suggested that bivalve larvae may be passively transported by currents although selective phases of swimming and resting associated with salinity changes would lead to the retention of larvae within an estuary and possibly their concentration in certain areas. Thorson (1966) suggests that larval selection is influenced firstly by the availability of food and the water temperature during pelagic life; secondly (and especially in estuaries where there is a stratification of the water mass), depending on the geo- and photo-tactic responses and salinity preferences of larvae, the larvae may select or avoid deep or shallow water sediments of one kind or another; thirdly, it is influenced by substrate selection as shown experimentally when larvae have discriminated between sediments, however whether such a discrimination occurs in nature is questionable (see also Sections 4.4.1. and 5.4.).

As Macoma spat have been found in high numbers on fine sediment, it is possible to suggest either that the larvae were attracted to the bacterial film and therefore the sediment size or that gregarious settlement had occurred (Wilson, 1955; Scheltema, 1961; Gray, 1966; Holland and Dean, 1977b; Tunnicliffe and Risk, 1977); it is not possible to say which of these had occurred. Other workers have found that, as a result of planktonic spawning, newly settled Macoma were uniformly distributed along the beach profile, and suggest that active transport by water movements together with migration and mortality then accounts for the change to graded distribution (Boyden and Little, 1973; Myren and Pella, 1977); such an initial uniform distribution was not found in the present study and may only be found on certain types of shore or immediately after settling. (Macoma larvae are 300µm at metamorphosis (Thorson, 1946) but were not sampled in the present study until twice that size.) In addition, the analyses showed that the spat and adult parts of the population occurred in high densities in the same areas (cf. C. edule Chapter 4). Brady (1932) also found that the same environmental factors affected both the large animal and spat parts of the population. It is therefore considered, in the case of this species, that its distributional pattern was established during or immediately following settlement and that the larval selectivity (either active or passive) is one of the mechanisms controlling the distribution of this benthic invertebrate (see also Meadows and Campbell, 1972; Holland and Dean, 1977a).

The large fluctuations in spat numbers at the most dense, low-shore areas were the result of many occurrences. The appearance of spat at an area was the result of several phenomena: the time between settlement and being sampled by a 500µm sieve was dependent on the animals' growth rate which varied with station (see Section 3.3.6.2.); the time and area of settlement depended upon the time of spawning, the water currents at metamorphosis and, probably of greatest importance, the water currents over the mud-flat leading to primary and secondary settlement. Similarly, the disappearance of spat from an area was the result of either mortality or the exclusion of animals from the small sample by growth. However, the time taken to reach the "exclusion-size" of 2.5mm was also dependent on the shore position.

The large mortality of spat shown in the common areas in the present study was possibly the result of either unsuccessful settlement or intra- or inter-specific competition for food and space. Initially spat are members of the meiofauna and as such are confronted by different physical and biotic factors from the adults (Thorson, 1966). Mortality resulting from the ingestion by suspension feeders before settlement and by unselective deposit feeders after settlement may be included in the term 'unsuccessful settlement' (see Sections 4.4. and 5.4.).

The large fluctuations in M. balthica abundance may be usual in an estuarine situation. Myren and Pella (1977) suggest that estuaries are characterised by simple food chains, and the presence of a few species each with a short life span and tolerant of wide physiological changes. They argue that as the estuarine ecosystem is held at immaturity by harsh environmental changes then the species have large temporal variation in abundance. Macoma, however, has features which suggest greater population stability: it may suspension or deposit feed therefore ensuring a more continuous food availability; it is comparatively long lived and is tolerant to relatively large scale changes in the physical environment. The large fluctuations in abundance may therefore be attributed to the success of its mode of reproduction and to the differences in food availability, physical characteristics and differential predation within the intertidal area.

At each station, the Macoma population was numerically dominated by the first year animals (0+ and 1+ groups), although these animals contributed only a small amount to each station biomass. This appears to be a normal population state for this bivalve (e.g. Segestråle, 1960; Gilbert, 1973; Chambers and Milne, 1975b; Wolff and De Wolf, 1977). That the large mortality of this class had little effect on the population biomass (or metabolism) is in agreement with Hughes (1970) who found that the population metabolism (and biomass) of the tellinid Scrobicularia plana was mostly influenced by the numbers of large animals in which the mortality (as numbers) was low. Similarly, Lammens (1967) found that at all sampling occasions the abundance of the cohorts ≥3+ were similar and that only the densities of younger animals fluctuated. Thorson (1966) suggested that the most heavy wastage per unit time during development of a macrofaunal species from a sediment bottom would occur during the pelagic life, although the loss after settlement is also large in that less than 1.4% of the young settling on the bottom will survive to be retained by a 2mm sieve.

3.5.2. The Growth and Longevity of the Species.

3.5.2.1. Spatial Growth Variation.

The bivalves at all areas exhibited sigmoid growth patterns which consisted of an initial slow growing phase, for only six months; a rapidly growing phase - the length of which varied with station - and a final slow growing phase during which the asymphotic size was reached in a total life span which also varied with area. This growth pattern may be considered characteristic of bivalves (e.g. Vogel, 1959; Segestråle, 1960; Gilbert, 1973; De Wilde, 1975; and Section 4.4.3.).

The maximum (theoretical) height of M. balthica, found to vary between 9 and 17mm, was dependent on the shore characteristics and decreased with the progression along each transect towards the high tidal areas. At some areas the maximum theoretical size was not attained, a factor possibly related to mortality at those areas (Gilbert, 1973). The value of K, the coefficient of catabolism, was found to increase with the same progression and the maximum age attained was calculated as ranging from 7.5 to 18 yrs, (the maximum number of growth rings found was 19). The population on Torry Bay therefore had low-shore individuals that were long living, had high growth rates and reached a larger size than the relatively short lived, slow growing, small animals found at the upper regions of the shore (see below).

The largest maximum theoretical sizes of Macoma were not only found in the 'common' population areas (at the mid tide, fine-sand/mud areas) but also at the low tidal fine mud areas which supported low population densities. The former areas also supported the largest production and mortality rates and received the main spat settlement. Therefore, although the areas which were most favourable for growth often supported the largest populations, this was not always the case. The Bertalanffy parameters were found to be influenced by sediment water content and immersion period suggesting that both an increased feeding period and the favourable feeding conditions of fine fluid sediment would result in a larger maximum size and lower coefficient of catabolism. These differences were further reflected when the sizes and weights of standard age animals were considered. Whilst the differences between the stations' first year animals were small, the size of eight-year old animals varied widely with position on the shore. After 2-3 years, the size and growth difference between the stations became apparent, i.e. although most habitats could support the 1 and 2 year old animals to the same extent, some conditions were more limiting to the older animals. The growth of the youngest animals was found to be not markedly influenced by any of the major environmental factors; after this age the number of factors influencing the size of standard age animals increased with the animals' age such that the growth of the older cohorts was greatest in the low-shore, fine mud areas. This suggests that the environment exerted cumulative influence on the animals which, with time, increased the difference in growth between the various areas. These differences were also found in relation to the weight of the standard age animals calculated according to the winter state of the animal. As shown by the annual changes in the animals' condition, the differences described would have been even greater had the summer state of the animals been taken into account.

It is considered that as the animals' requirements in terms of total food and O_2 increased with age, the higher-shore stations were increasingly ill-equipped to fulfill those requirements such that the growth of the bivalves decreased (see also Seed, 1969). However, although the animals total requirements increased, the animals upto 2 years old were not necessarily less susceptible to environmental change than were the older animals. In addition, after two years the animals would be contributing a proportion of their annual energy intake to reproduction (Caddy, 1967), this would also affect their growth although it is not possible to comment definitely on the amount of energy diverted to reproduction at each area (see also De Wilde, 1975).

The greater growth at the lower tidal levels is considered to reflect the abundance of food, the suitability of the substrate and the prolonged period of feeding at those areas. Macoma is known to feed mainly during tidal cover (Morton, 1970; Beukema et al, 1977) although in fine sediment with a high water content it has been observed to feed even when uncovered by the tide (see Section 6.2.). The spatial pattern of Macoma growth on Torry Bay was found to be similar to that found by Beukema et al (1977) on the Wadden Sea; however, the sediment and tidal characteristics of the area studied by these workers were such that at low tidal levels the animals growth was limited by a coarse substrate and therefore lack of food, whilst the abundant food on finer substrates at the higher-shore areas was not fully utilized because of the short immersion period and available time for feeding. Beukema et al (1977) found, in what they considered to be a food limiting situation, an optimal area for both growth and density in the mid-shore region and suggested that the competition for food in the central area was not harsh enough to limit growth. The Torry Bay growth/density relationship suggests the occurrence of one or more of the following: that the optimal area is more food limiting than the Wadden Sea, that there are larger populations or that there is more competition with other deposit feeders leading to slightly lower growth in the densest areas with respect to some low-shore areas. The area studied by Beukema et al (1977) supported smaller populations of the bivalve than the optimal areas in the present study (Beukema, 1971; see Table 3.24) which also supported large H. ulvae populations (see Section 5.3.4.). Segestråle (1960) found that growth deterioration in sublittoral populations of M. balthica could be attributed mainly to poor nutritive conditions and, to a lesser extent, temperature differences. He further found no indication of a decline in growth as a result of overcrowding but suggested that this may be the usual situation in bivalve populations (see Section 4.4.3.).

Other studies on Macoma growth variation within an area have found that the growth increases with increasing tidal elevation (Green, 1973; Myren and Pella, 1977) and attributed the increase to the longer exposure to high temperatures experienced by the high-shore animals. However, although De Wilde (1975) suggests that growth is dependent on the presence of temperatures below 15°C and of sufficient food, growth only increases with temperatures upto 10°C such that the generalisations proposed by Gilbert (1973) regarding temperature and growth are only valid at the lower end of the temperature range. Furthermore the North American populations (Green, 1973; and Myren and Pella, 1977) would have experienced much colder water temperatures than in the northern British Isles; this would have retarded growth in those animals covered for the longest periods. It is considered that the temperature regimes experienced by the various regions of Torry Bay were not of sufficient variation to explain growth differences. Similarly, growth variation in the species has also been explained by wide salinity variation (Vogel, 1959; Segestråle, 1960). In the present study the salinity variation over the area is considered to be relatively small with respect to the wide salinity tolerance of Macoma (see also Gilbert, 1973).

In addition, Macoma, like Scrobicularia (Hughes, 1970), is able to maintain respiration at low tide by utilizing the water film left over the surface of fine sediments with a high water content but not, therefore, in the well drained, coarse sediments at the upper-shore. Macoma can, however, obtain some O_2 by diffusion in the mantle if there is no water film left (De Wilde, 1973). The upper-shore animals will therefore be under a state of oxygen limitation which may lead to stress; however, as they were smaller at certain ages than the lower-shore ones, their O_2 demands would be similarly reduced.

The differences in growth over the area may therefore be attributable to the feeding condition variation both with respect to food availability, as sediment type, water content, organic content, etc., and time available for feeding, as immersion period, tidal height and, to a lesser extent, the sediment water content. It is probable that the temperature and salinity will only have an over-riding effect where there is a large spatial variation in these variables. Intra-specic competition also affects growth which, to some extent, may therefore be considered density-dependent. The inter-specific relationships are considered in further detail in Section 7.3.1.

In addition, the environment exerted an increasing influence on the size, weight and growth of the individuals with time resulting in the large differences between the older animals of a certain age with respect to their shore position. The size and growth of the high-shore animals was limited by the environment for all ages greater than two years when compared to the more favourable lower-shore conditions; they reached a limit imposed by the environment such that their growth ceased and mortality occurred at an earlier age. As the animals' total requirements (as, for example, oxygen and energy intake), increase certainly linearly and possibly exponentially, at least whilst actively growing and possibly throughout life generally (Needham, 1964; Duncan and Klekowski, 1975), then with increasing age the environment may not be able to meet those requirements.

In the present study, the increased longevity was associated with better growth, a larger maximal size and smaller coefficients of catabolism. This is the reverse of the situation encountered in other Macoma population studies (see below) and by Seed (1969) who found that whilst slow growth in mussels leads to increased longevity, rapid growth results in early mortality as the animals outgrow their environmental limits. Seed (loc. cit.) also suggested that senility was not the primary cause of reduced growth as the transplanting of old, slow-growing mussels to better conditions resulted in renewed rapid growth (see also Needham, 1964 pp. 279-81). It is considered therefore that the high-shore bivalves exist under a high physiological stress which is shown by their growth characteristics. The high K values reflect the excess of catabolic over anabolic processes in the upper-shore population; however, it is not possible to suggest whether this is reflected in a higher respiration rate by the animals living in coarse, high-shore areas. The population of the tellinid *Tagelus plebius* studied by Holland and Dean (1977b) also showed better growth, reached a larger final size and had lower K values at low intertidal areas when compared to high or sub-tidal areas. This led the authors to suggest that decreased stress results in increased longevity in bivalves (also suggested by Lammens, 1967) and that one of the causes of the increased stress was the decreased feeding time. This contradicts both Rubners' hypothesis (Allee *et al*, 1949), that longevity is related to the intensity of living, and the suggestion that a restriction of food may increase longevity (Comfort, 1964)(see p. 167 for further discussion).

3.5.2.2. Temporal Growth Variation.

All cohorts exhibited annual sigmoid growth patterns of both size and weight: slow growing periods at the beginning and later stages of each year were separated by the growth period (spring to early-autumn) in which the major part of the annual growth, condition increase and annual production increment was achieved (see Fig. 3.36 and Section 3.4.5.). The latter period differed with both cohort and group of stations. The annual change in the size of a cohort decreased with the age of the animals after the second year and the relative change in flesh weight over the year decreased with age; both of these decreased with the progression from Group 1 to Group 5. Other, more subtle, differences in the length of annual growing period, attributable to differences in environment, were obscured by the grouping together of stations i.e. whilst the animals of two areas may have the same growth patterns over their lives and grow by similar increments each year, it is not possible to state that those increments were attained in the same growing seasons. It is therefore only possible to comment generally on the annual growth periods of the population cohorts.

The annual growth in height ~~length~~ of the 0+ group occurred in the period from settlement until August-October and then either slowed down or stopped altogether over the winter. The annual weight increase occurred mainly in the period upto June or July after which emaciation proceeded. This pattern of spat growth agreed with that for a northern Scotland population (Chambers and Milne, 1975b; see Table 3.25) but not with that for a Dutch population (Wolff and De Wolf, 1977). However, as prolonged recruitment would decrease the mean size and weight of a year class then these differences in growth may be of a spurious nature.

The growth of the 1+ cohort varied with group (of stations) such that in some cases the size increase was over the period April to July whilst in others growth continued upto the September to November period. The weight, however, only increased up to June, or at the latest August, before emaciation proceeded. The growth of the cohorts 2+ and older commenced later in the year, in the period May to July, after spawning (see below); and ceased during the period August to December. The flesh weight of these cohorts mainly increased to June although they showed two peaks of condition and two troughs of emaciation over the year (see Fig. 3.36). Although the oldest animals (5+ and older cohorts) were found to increase slightly in size (upto 3mm) over the sampling period, they showed no net gain in flesh weight and in many cases showed a net emaciation. However, as some of these 'cohorts' were the result of combining all cohorts over 5 or 6 then any decrease in the mean weight could have been the result of mortality in the oldest cohorts. In addition, whereas most of the group cohorts showed definite periods of shell and weight growth, at C5 (Group 5) the cohorts showed a constantly slow size increase over most of the year while showing erratic weight changes. This was possibly a reflection of sampling such low densities although the animals at that station were probably under greater stress and subject to larger condition changes (see below).

The earlier initiation of growth by the first year (1+) animals over the older animals found here is in agreement with Lammens (1967). This phenomenon is considered attributable to the reproductive condition of the respective ages, i.e. whilst the mature individuals divert energy towards reproduction during the early part of the year before growth can occur (depending on the energy availablity), the sexually immature young animals can devote more energy to growth (Needham, 1964). This suggestion, however, does not explain why the older cohorts, in some areas, with larger total requirements than the younger animals, should continue to grow for a longer period and until later in the year. The answer to this latter problem may lie in the continual presence of available detrital food, the differential ability of the cohorts to utilize that food and the varying temperature tolerance of the different cohorts.

The cohort mean-weight increase apparently ceased earlier in the year than the cohort mean-size change. It is considered

Table 3.25 *M. balthica* : A Summary of Literature - Annual Growth Variation.

Area	Latitude	Author	Main Growth Period	Comments
Ythan Estuary, N.E. Scotland,	$57^{\circ}20'$	Chambers and Milne (1975b)	Until Oct. for 0+ cohort.	
			Mar. - late Oct. for 1+ cohort.	
			Mar. - Aug. for 2+ cohort.	
Forth Estuary,	56°	This Study	Until Aug./Oct. for 0+ cohort.	Ceases over Winter
			Apr./July - Sept./Nov. for 1+ cohort.	" " "
			May/July - Aug./Dec. for 2+ cohort.	" " "
Wadden Sea, N.W. Europe,	53°	Lammens (1967)	Mainly in Spring, Slows in Summer.	Stops in Winter
		De Wilde (1975)	Feb./Mar. - June/July.	
		Beukema (1971)	Mid Mar. - June/July.	
Grevelingen Estuary, Netherlands,	$51^{\circ}40'$	Wolff and De Wolf (1977)	0+ cohort grew little from settlement until Mar./Apr. following year.	
			1+ cohort had max. weight in Autumn.	
			>1+ cohort had max. weight June/July.	
St. Lawrence Estuary, Quebec,	48°	Lavoie *et al* (1968)	Apr. - Sept. Max. Aug.	Slows over Winter
Petpeswick Inlet, Nova Scotia,	$44^{\circ}45'$	Burke and Mann (1974)	Slowed markedly after July.	
Rand Harbour, Falmouth, Mass.,	$41^{\circ}30'$	Gilbert (1973)	May - Aug.	

the annual growth of Macoma was directly related to the length of the growing season whilst several other authors have related the growth of the species to temperature (e.g. Lammens, 1967; De Wilde, 1975). Beukema and De Bruin (1977), however, measured a high growth rate in a Wadden Sea population despite a short growing season (see Section 3.5.2.3. and Table 3.25). Several of these workers found that temperatures > 15°C limited annual growth and curtailed the growing season. Beukema and De Bruin (1977) however, suggested that temperature was not the sole factor as growth did not recommence during the autumn when the temperature decreased. De Wilde (1975) concluded that annual growth changes were dependent on temperature, food availability and, to a lesser extent, internal rhythm.

3.5.2.3. Intertidal and Geographical Variation in the Growth of M. balthica.

The Bertalanffy growth equation was calculated for the Torry Bay population as a whole by the combination of all data (see Table 3.2):-

Stage 1 : $H_{t+1} = 0.849 \pm 0.037H_t + 2.478$

$n = 11$, P = ***, $r = 0.991$.

Stage 2 : $\mathrm{Log}_e(H_\infty - H_t = 2.770 - 0.157 \pm 0.008t$

$n = 12$, P = ***, $r = -0.988$.

(See Section 3.2.1. for an explanation of the symbols.)

giving the complete growth equation as :-

$H_t = 16.41\ (1 - e^{-0.164(t + 0.178)})$ and $T_{95} = 18.9$ yrs.

The available growth data and Bertalanffy parameters for M. balthica are given in Fig. 3.34 and Table 3.26 respectively.

Table 3.26 Bertalanffy Parameters of M. balthica Populations.

Area	H_∞	K	t_0	T_{95}	Source
Torry Bay	16.41	0.164	-0.178	18.9	This study.
Wadden Sea	18.43	0.514	+0.500	6.2	From specimens obtained from J. J. Beukema (N.I.O.Z.).
Ythan	22.18	0.185	+0.492	16.2	Calculated from Chambers and Milne (1975b).
	L_∞				
Torry Bay	20.14	0.164	-0.189	18.9	This study.
North Sea *1	28.30	0.112	-0.577	25.2	Calculated from Vogel (1959).
Baltic Sea *2	23.97	0.304	+0.200	10.3	" " "
Lynher	12.89	0.823	+0.394	4.0	Calculated from Warwick and Price (1975).
Hudson Bay *2	37.3	0.086		34*4	Green (1973).
" " *3	21.1	0.309		10*4	" "

*1 = Sublittoral areas.

*2 = At MLW.

*3 = At 1m above MLW.

*4 = Maximum age.

The populations of Macoma can generally be grouped into two types according to their growth curves (see Fig. 3.34); those in which the animals have a high growth rate and reach a large maximum size but have a short life span (populations 1-11 on the figure), and those in which the animals have a lower growth rate, reach a smaller maximum size but yet have a much longer life span (populations 12-15). The first group include mainly temperate, intertidal or shallow water populations whilst the second is comprised of arctic or sublittoral populations. These

Figure 3.34 *M. balthica* : The Geographical Variation in Growth Rate.

Legend

▲ Torry Bay Population.

Other Curves:

1 Wadden Sea Population (Specimens obtained from N.I.O.Z.).

2 Rand Harbour, Massachusetts (Gilbert, 1973).

3 Wadden Sea (Lammens, 1967).

4 North Sea (Vogel, 1959).

5 Hudsons Bay (Green, 1973) - 1.1m above M.L.W.

6 Kiel Bay (Vogel, 1959).

7 Ythan Estuary (Chambers and Milne, 1975b).

8 Gulf of Finland (Vogel, 1959).

9 Hudsons Bay (Green, 1973) - at M.L.W.

10 Gulf of Finland, 3m (Segestråle, 1960).

11 Lynher Estuary (Warwick and Price, 1975).

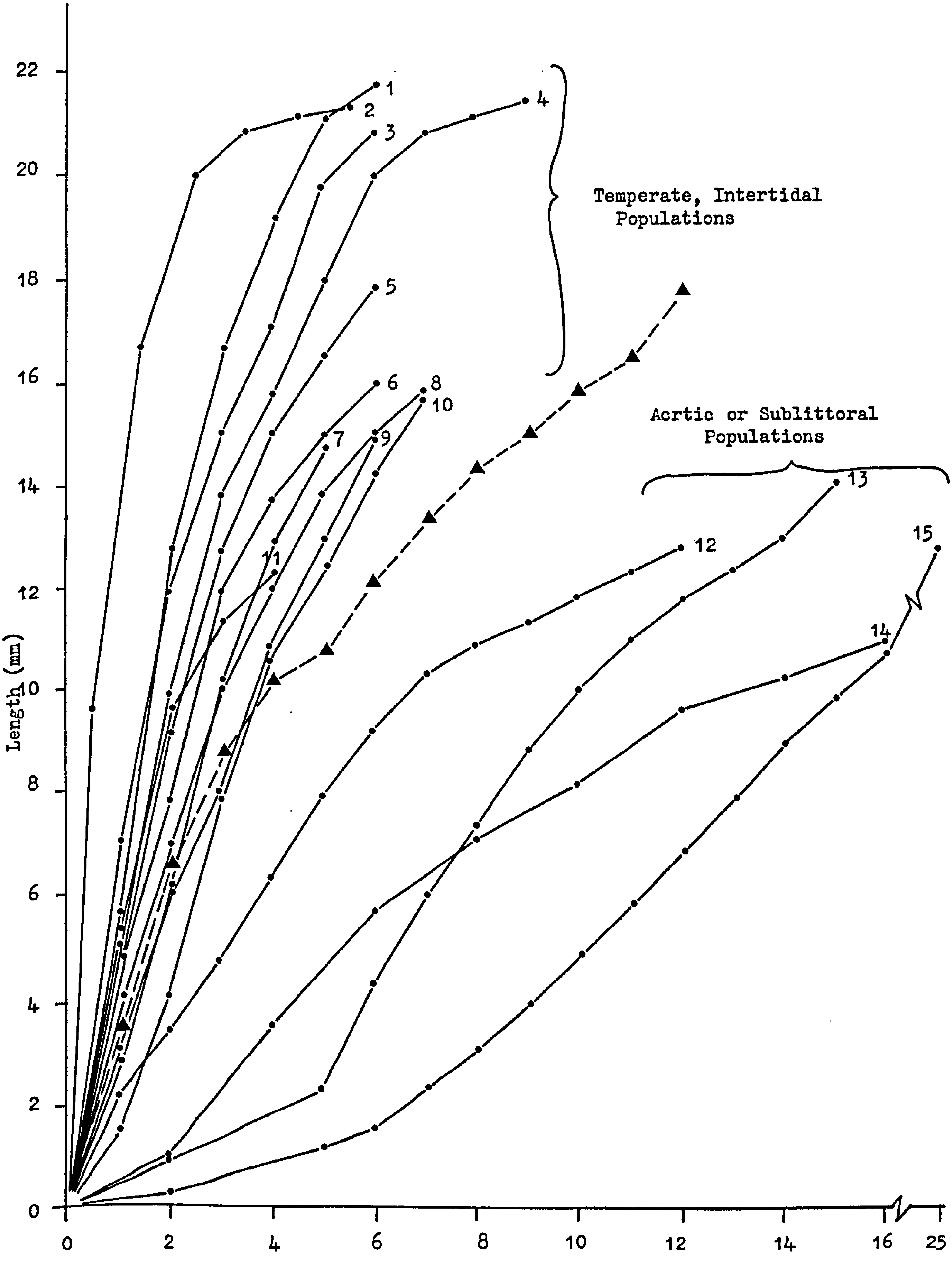
12 St. Lawrence Estuary (Lavoie *et al*, 1968).

13 Gulf of Finland, 20m (Segestråle, 1960).

14 Kandalski Bay, White Sea (Semenova, 1970 in Gilbert, 1973).

15 Gulf of Finland, 35m (Segestråle, 1960).

Nos. 2-6, 8-10, 12-15 inclusive - from Gilbert (1973).


Temperate, Intertidal Populations
Acrtic or Sublittoral Populations
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Length (mm)
Age (yrs)
0
2
4
6
8
10
12
14
16
18
20
22
0
2
4
6
8
10
12
14
16
25

differences have mainly been attributed to temperature (Dehnel, 1956; Gilbert, 1973; Green, 1973), although Segestråle (1960) and McErlean (1964) respectively attribute the slow growth in sublittoral Baltic and the large maximum size in sublittoral Maryland populations to the poor and optimal nutritive condition as well as temperature. However, the effect of temperature on this bivalve appears confusing;

> "... in cold the anabolic (synthetic) processes greatly exceed the obviously sluggish catabolic (breaking-down) ones, whereas in the heat the animals, stimulated to a fever pitch of activity, expend a greater part of their income, even in the presence of rich and abundant food, in catabolism. As a consequence the net balance available for growth is large in cold climates, small in hot ones." Segestråle (1960).

whilst Gilbert (1973) suggests that:

> "... measures of metabolic rate such as rate of heart beat and oxygen consumption, are higher in cold adapted animals (molluscs), i.e. those living at the northern of a species range or at the lower end of the intertidal. Cold adapted M. balthica may therefore be expending more energy on respiration and less on growth than warm adapted individuals."

Although the latter statement explains the Macoma growth patterns encountered, it is contrary to the accepted theory of Segestråle, 1960 (see also Needham, 1964) and to Rubners's hypothesis (Allee et al, 1949; also Comfort 1956 and 1964). The latter hypothesis suggests that within a given genetic combination (i.e. either within a species or between related species), the longevity is inversely proportional to the intensity of living, i.e. that a definite sum of living determines the physiological end of life; that at low temperatures poikilotherms live longer than at higher temperatures; that the total energy transformation is approximately the same regardless of the life span and therefore that animals with a higher metabolism tend to live for shorter periods than those with a lower metabolism. In addition, that lower-latitude animals expend a greater part of their income in catabolism would suggest that the value of K is higher at lower latitudes. Using limited evidence (Fig. 3.35) this appears to be the case. Segestråle (1960) further suggests that an extended life span and reduced growth rate is a normal occurrence in bivalves living at the northern limit of their geographical range when compared to southern populations; however, in many of these species and Macoma populations the increased life span produces a greater linear size. There is also evidence that a quantitatively poor ration will lead to both a decreased growth rate and increased longevity whilst an optimal diet will produce a short life span (Comfort, 1964; Needham, 1964).

When the Torry Bay M. balthica population is included in these considerations, the mean growth rate for the area lies between the two main types of growth rate (Fig. 3.34), and whilst showing a greater longevity, but smaller growth rate, than the normal temperate, intertidal populations (Nos. 1-11), it shows a greater growth than the arctic or sublittoral populations (Nos. 12-15). These considerations are taken further in the use of the Bertalanffy parameters (Fig. 3.35; Table 3.26). There is an inverse curvilinear relationship between the coefficient of catabolism, K, and both the maximum theoretical age, T_{95}, and size, l_∞, for the different geographical areas. Additionally, whilst the life span of Macoma is again shown to vary widely (upto 30 years), the final length of animals in the other populations generally appears to be within the

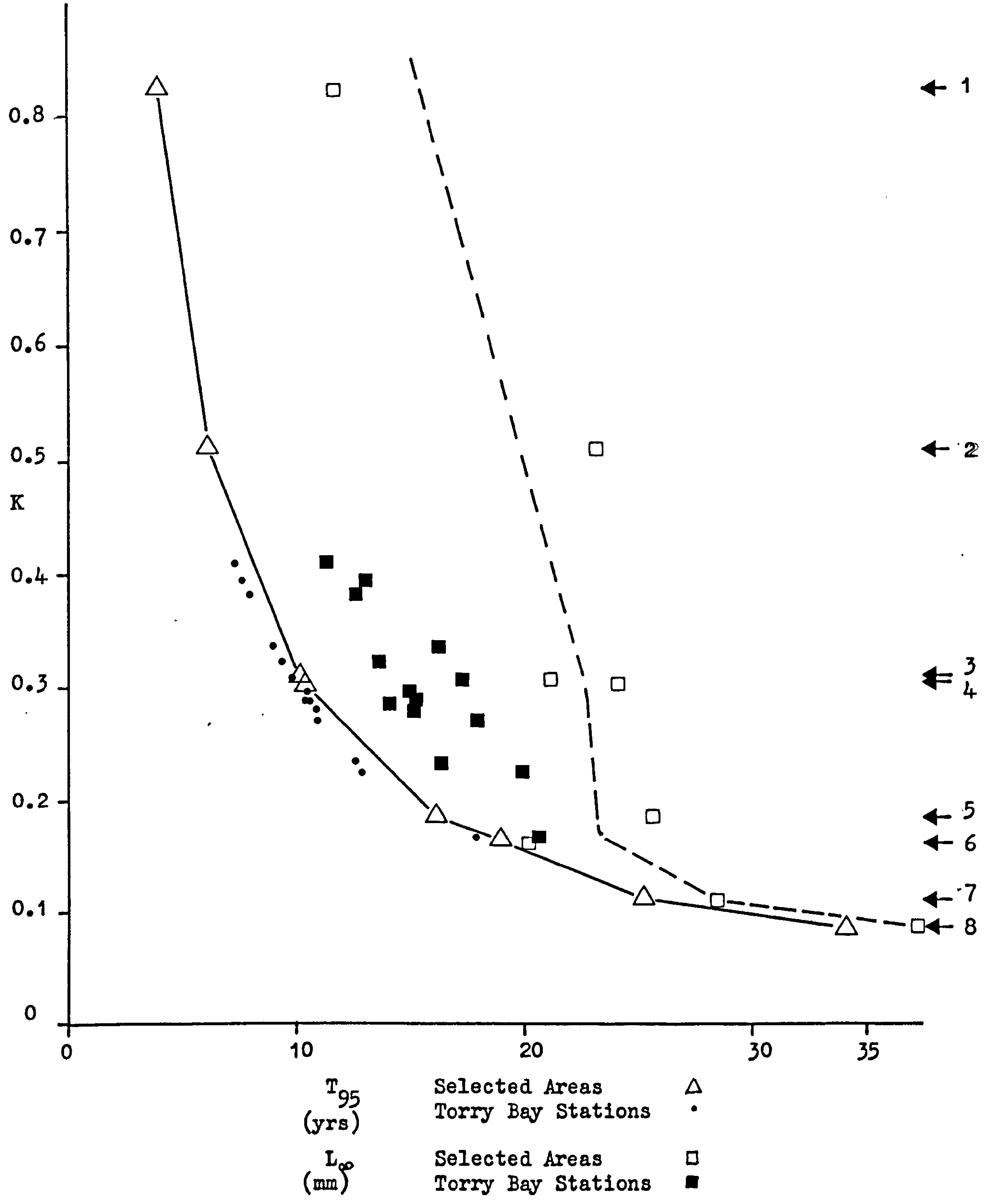


Figure 3.35 <u>M. balthica</u> : The Interrelationships Between the Bertalanffy Parameters K, T_{95} and L_∞. Selected Areas (For References see Table 3.26) :-

1 Lynher Estuary.
2 Wadden Sea.
3 Hudsons Bay, Upper.
4 Baltic Sea.
5 Ythan Estuary.
6 Torry Bay (Mean Values).
7 North Sea.
8 Hudsons Bay, Lower.

restricted range 21-29mm. The mean value for the Torry Bay population, however, is lower than this range. Needham (1964) stated that:

> "... the idea that animals are genetically determined to run a definite integral life program is supported by a good deal of evidence such as the relative constancy of the maximal size, regardless of the rate at which it is attained."

It is probable therefore that Macoma has a potential to reach a definite size (see Fig. 3.35) although this is not shown clearly in some populations (see Fig. 3.34).

The Torry Bay stations' data also approximate to the first trend described above and fit the predicted curve (K with T_{95}), i.e. the maximum age attained is dependent on the rate of catabolism (the rate at which the maximum size was attained). Although the relationship between K and L_∞ showed more variability, the Torry Bay overall value did not fit the predicted pattern, either the K value was too low for the maximum size reached or the L_∞ was too low for the K value calculated. The first pattern (K with T_{95}) suggests the latter alternative as a more likely one and that whilst the environment dictates a level of catabolism it cannot sustain growth over a certain size. The individual stations similarly conform to this pattern and appear to have lower maximal sizes than would be expected.

The phenomenon of a prolonged life span and lower growth rate for the Torry Bay population (cf. other geographical populations), may be attributable to environmental restrictions, possibly of food (Segestråle, 1960; Comfort, 1964; Needham, 1964; etc.) although many other factors could be responsible (see Sections 6.1.5.; 6.2.). It is unlikely that there is a virtue in growing slowly (Needham, 1964) or that the animals would have that ability to regulate their growth. The individuals will be living to the limits of their environment and their growth a reflection of the interaction between the animals and its environment (Needham, 1964).

The growth differences within Torry Bay may now be further considered. Whilst in Macoma populations as a whole, a larger growth rate decreases the life span (see above and Segestråle, 1960), this was not the case within the intertidal area studied in which the animals with the greatest growth rates attained the greatest ages. However, the phenomenon encountered in other populations, of a greater maximum size being reached in fast growing areas, was found on Torry Bay. It is apparent, therefore, that senescence commences both earlier and at a smaller size at those populations with both lower food and immersion period levels. This may be attributable to the upper-shore environment leading to greater stress in the species (as found for Tagelus plebius, Holland and Dean, 1977b). Needham (1964) states that the efficiency of the recovery process from stress, i.e. the ability of the animals to withstand stress, declines with age. This will therefore lead to premature senescence and gives one of the most evident relationships between senescence and the declining power of growth. It may therefore be stated that both senescence and the declining power of growth are "accelerated by environmental insults" (Needham, 1964) within the intertidal range of a M. balthica population, although this is not apparent within the geographical range of the species.

3.5.3. The Shell Shape of M. balthica in Relation to its Environment.

The animals' shell shape was also dependent upon the environment, such that the upper-shore animals generally had significantly more pointed shells than the low-shore ones. The sedimentary regime is regarded as the most important environmental factor controlling morphological adaptation in bivalves (Standley, 1970) and a wedge-shaped shell in bivalves in coarse unstable sand is necessary for quick burrowing as, for example, in Tellina tenuis and Donax spp. As Macoma has a much wider shell than either of these species and therefore requires more energy expenditure in burrowing in sand (Trueman et al, 1966), if it was not possible to reduce body width, although this was not measured, an adaptation such as a more pointed shell would assist in burrowing in unstable sands where there is a necessity to burrow quickly (Standley, 1970). It is therefore considered that water movements, in their effect on sediment type and stability, are a major influence on M. balthica shell shape (see also Standley, 1970).

In addition, Standley (1970) gave the length:height value as 1.28 for this species in North America, i.e. a regression coefficient of 0.781 of the height/length regression would be expected if the Forth animals were of the same shape. All of the stations except A4 had b values greater than this value showing that the Torry Bay animals were of a much rounder shape than the populations studied by this author. However, in the absence of further environmental data regarding the populations studied by Standley (1970) no further comment on the populations can be made.

The environment was also found to influence the shell appearance and thickness (see Section 3.4.4.) suggesting that shell maintenance was greater and thicker shells were necessary in coarser sediments where more abrasion occurred. Segestråle (1960) also found that at the shallow, fast growing areas, Macoma had a flattened shell which had a smoother surface and which was thinner with little abrasion when compared to the slow growing areas (which, in his case, were in deep sublittoral areas) where the animals had thicker shells. Standley (1970) considered that whilst deposit feeding bivalves often have thin shells which are useful in moving location (e.g. see Brafield and Newell, 1961), if a shell is too thin it would not withstand abrasion in coarse sand. In the latter environments therefore, it would be advantageous for the animals to have shells that are both thicker and more pointed. However the brittleness encountered in the shells of animals from some high-shore areas (see Section 3.4.4.) was probably a result of living in a harsh environment and could possibly even have been caused by a lack of calcium attributable to living under a short immersion period (see Section 4.4.4.). It is not possible to suggest whether the decreased growth rate of the upper-shore animals affected the shell condition or shape.

3.5.4. The Flesh Condition and Shell Weight Status of the Population.

At the majority of areas and sampling dates in the present survey there was no significant relationship between the flesh condition and the size of the species. This is basically in agreement with Beukema and De Bruin (1977) who found the animals' condition to be "nearly" independent of the size over the major part of the size range of their population although both very large and very small individuals had a consistently lower body condition. The overall pattern of a relatively constant relationship between the size and flesh content throughout the population size range may therefore by characteristic of the species. However the flesh condition and the shell weight as a proportion of the total weight were found to vary with both spatial and temporal variation in the environment.

3.5.4.1. The Spatial Variation in Flesh Condition and Shell Weight.

The body condition was regulated mainly by the particle size, immersion period and deposit food content. At the high-shore stations it remained relatively low over the year whilst at the low, fine mud stations the condition was correspondingly low in winter but increased as the year progressed. The lower-shore animals therefore reacted in a greater manner to the annual environmental changes, they increased in weight to a larger extent because of the larger amounts of food available; they put larger amounts of energy into spawning and emaciated to a larger extent (see below).

The percentage shell weight of the total weight was also generally greatest at the high-shore, coarse sediment areas where low populations existed. It is unlikely that this would be a density dependent phenomenon but more likely that the higher proportional shell weights occurred in unfavourable areas which supported low populations of animals having a low body condition. It is difficult to state definitely, however, that these unfavourable areas produced animals with heavier shells. The relative difference in shell weight between the habitat types increased with both age and size of the animals therefore suggesting that the environment exerted an increasing influence with age.

The findings may be summarised :-

At a certain age x : the faster growing animals, at the lower stations, had a higher shell weight than the slowing growing ones at the higher stations.

At a certain size y: the former animals had a lower shell weight than the latter which had a greater time to accumulate an amount of shell and therefore the environment had a longer time to influence the animals' morphology.

The coarse areas therefore sustained animals of low condition but probably with thicker shells. It is possible to ask : was the low condition the result of having to divert energy towards thickening the shell, which may be necessary in such deposits (and vice versa at the better areas), or is the body condition purely a result of the poor environmental conditions ? The latter is considered the more probable explanation as the body condition at the upper stations may be limited by the absence of potential food and adequate feeding time.

The flesh condition at a standard temperature increased with a decrease in particle size and tidal height and reflects both the effect of temperature upon the food supply of the animals (dependent on the fineness of the substrate) and the amount of time available for feeding (dependent on the immersion period and sediment water content). In addition, in some areas the flesh condition variation was the result of environmental differences indirectly associated with particle size and tidal height. The presence of Z. marina, and its detritus, increased the sediment water, carbon and nitrogen content at the coarse, higher-shore Stations C5 and B5; this resulted in the animals at these stations having lower shell weights and higher condition and flesh weights than animals at the clean sand areas C4 and B4 (see Section 6.2.). Similarly the animals' condition at Stations C2 and B3 fluctuated as the result of sediment transport due to winter tides and storms.

Other studies have been concerned more with temporal rather than spatial changes in flesh condition and shell weight. Lammens (1967), found that shell deposition resulting in shell thickening occurred in Macoma particularly in the third year; Fairbridge (1952) concluded that the shell thickness of Notovola meridionalis (a scallop) was more associated with age than shell length whilst Stephen (1932) found, somewhat surprisingly, a linear relationship between the length and weight of the shell of C. edule. In the related deposit-feeding Macoma nasuta, with a variation from a sandy, exposed to muddy, sheltered environment, no difference in the length/flesh weight relationship (as a reflection of condition) was found (Hylleberg and Gallucci, 1975). It is therefore impossible to generalize on this facet of bivalve ecology (see also Section 4.4.4.).

3.5.4.2. Temporal Variation.

The condition of Macoma varied largely with season depending on the amount of food reserves, state of maturation, spawning and emaciation and the occurrence of shell or flesh growth (see also Ankar, 1977). Many of these phenomena were further related to the food availability and environmental changes, in particular to temperature changes.

Within individual stations, the condition and flesh weight of large animals (8mm) was influenced by temperature and the flesh biomass at those stations, whilst the flesh weight of the small animals was influenced by the flesh biomass, sediment nitrogen, water content and C/N values and by the level of carbohydrate in the overlying water. At the majority of stations, therefore, the flesh status of most of the population increased upto the summer when temperatures increase and the largest flesh biomass was present. The increased condition would also have contributed to that increased biomass. In addition, the respective associations between the flesh condition at the upper and lower stations and the interstitial and estuarine water salinities reflect the length of time, and therefore effect upon, that the respective animals were subjected to these differing salinities. It is difficult to state whether the salinity had a direct effect on the flesh condition. The top-shore animals were subject to a large salinity variation, caused by precipitation and evaporation, which may have contributed to the physiological stress and lower flesh condition which were mainly attributable to the short immersion period, coarse sediment and low food quantities. However, the salinity regime known to be tolerated by <u>Macoma</u> encompasses much of this salinity variation which may therefore have had a limited effect.

In addition, although the flesh weight of the small standard animals was highest at areas of densest population, where those animals were under a mussel bed, e.g. at B2, their flesh status was low which, coupled with the slow initial growth rate at that area (cf. B1 and B3), suggests that young animals were at a disadvantage although once established their condition and growth improved with age (see p.186). Also, at Station A3, the water carbohydrate levels appeared important indicating than in some particularly harsh areas the young animals may be dependent on suspended matter (see Section 6.2.).

The total data showed that within the mud flat the potential amount of deposit food regulated the condition and standard flesh weights although over the year the temperature had an overlying affect. The condition was also directly and curvilinearly related to the interstitial salinity and was optimal at a C/N value of ≈ 17 reflecting the need for large amounts of sediment carbon as a substrate for the microflora.

The condition increased steeply with a temperature rise to 12°C and then increased only slightly with a further rise in temperature. At Station B3, the flesh weight and condition only increased after 9°C had been reached and upto which there was no increase, i.e. the latter period was during October to April when growth and reproduction had ceased. This again suggests that while temperature had an overall effect, within the mud flat other environmental factors influenced flesh condition. At all stations, the flesh condition increased with temperature although it increased relatively more at the lower-shore finer mud stations. Very high water temperatures (> 15°C), encountered only during July and August in the present study, would have been limiting either directly, by increasing the animals maintenance needs and lowering the food intake so reducing the condition (De Wilde, 1975), or indirectly by influencing the primary producers and decomposers and so affecting the food supply.

Although the flesh growth decreased both during and after these months of maximal water temperature, that decrease cannot solely be attributed to the temperature change. The higher-shore was exposed to the slightly higher temperatures for longer periods which may have resulted in condition being environmentally limited. In the finer sediments however, where there were greater quantities of decomposers and primary producers, high temperatures (up to a certain limit) for a shorter period may have increased the available food (Ankar, 1977) and led to an increase in condition.

The condition was not density-limited as generally the higher condition factors were encountered in the densest areas; the highest condition, however, was found at stations C1 and B1 which supported relatively low biomasses (see p. 186). The condition increases together with growth would lead to an increased biomass and thus produce the observed relationship. An increased biomass would, however, lead to greater bioturbation which would improve the food quantity and quality and also contribute to an increased condition (see Sections 2.5.; 6.1.5.).

In addition, when compared to the smaller standard animals, the larger standard animals were more affected by temperature and showed greater correlations with the environmental variables, i.e. their flesh weight was the result of the long term influence of the environmental factors such as particle size and tidal height.

The flesh weight of the older (4 year), larger standard animals was found to increase earlier in the year before growth occurred and these animals were found to mature such that spawning coincided with a minimum condition during the period April to early June (see also Chambers and Milne, 1975b). Unlike the Torry Bay population, however, the flesh weight and condition of a Wadden Sea population was not found to decrease with spawning (Beukema and De Bruin, 1977; De Wilde and Berghuis, 1978). The Torry Bay spawning period is in agreement with populations in the Thames estuary (April to early June spawning, Caddy, 1967); the Wadden Sea (April to late May, Lammens, 1967; De Wilde and Berghuis, 1978) and the Massachusettes coast (May spawning, Gilbert, 1973), although later than found for an Ythan estuary population (late February to early April, Chambers and Milne, 1975b) but earlier than in a Baltic population (May to June, Ankar, 1977). At the majority of stations, the animals of age 1-2 years (4mm size) were not mature although it is possible that at the stations with the fastest growing animals in highest condition, the species would mature earlier (see also Segestråle, 1960). The species is known to mature in the second year at length of 5 - 10mm and height > 3mm (Caddy, 1967; Lammens, 1967). The conclusion reached in the present study, that the animals 2+ and older diverted energy into reproduction at the expense of growth during the first part of the year and that growth only occurred after spawning, is in general agreement with these authors.

Several authors have described temperature as a major factor regulating spawning. The temperature range during spawning (8.7 - 15.5°C) was slightly higher than the range (7 - 14°C) estimated by Caddy (1967) whilst Lammens (1967) and De Wilde (1975) suggested that a critical water temperature threshold of 10°C would "trigger" spawning. Later, De Wilde and Berghuis (1978) showed that a thermal shock, as a large temperature increase over a short period, would cause the animals to spawn providing that the threshold level of 12°C had been attained. Such a thermal shock will be produced if low tides occur during the middle of the day. This leads to the further advantage that the gametes would be carried by the flood tide (De Wilde and Berghuis, 1978). Caddy (1967) similarly suggested that this was the reason why spawning mainly occurred during neap tides.

Temperature, however, may not be the only stimulus to spawning as a possible second, smaller spawning period occurred during the autumn in some areas (this study and Caddy, 1967) but not in others (Lammens, 1967; Warwick and Price, 1975). Ankar (1977) suggested that the spawning of Macoma was loosely related to the food abundance and to the spring phytoplankton bloom. The spawning of Macoma on Torry Bay was related to the potential food quantity (and the biomass) at each area, i.e. the condition fluctuations attributable to spawning were greater at the common, low-shore, fine mud areas. In addition gamete leakage was found to occur over most of the year in the population, i.e. whilst synchronous spawning did account for the major part of the annual spat settlement, some animals did mature at other times of the year; this may be a reflection on the constancy of the deposit food levels. Ansell and Trevallion (1967) suggested that whilst a minimal level of gonadal development throughout the year was normal, the extent of gonad proliferation in the tellinids may fluctuate widely from year to year thus leading to considerable fluctuation in spatfall between years.

The maximum spat numbers on Torry Bay were found during May to July, the same period as in the Llynher and Ythan estuaries

(Chambers and Milne, 1975b; Warwick and Price, 1975). Thorson (1946) stated that the larvae of this species was in the plankton mainly during April to May, although some larvae were present up to mid-August, and metamorphosed at 294µm. After an early settlement, therefore, the spat have the maximum time to reach as large an overwintering size as possible, a factor contributing to survival over the winter. Spat settling later in the year would therefore be at a selective disadvantage compared to older spat.

The annual growth commenced either during or after spawning (in young and old animals respectively), during early to mid summer depending on the age of the animals (see Section 3.5.2.2.). This was followed by a period of emaciation, the length and extent of which also being dependent on age. Emaciation was the result of two phenomena: a utilization of body reserves, either for growth or for the commencement of gametogenesis, due to poor food abundance; the diversion of energy into shell growth following a period of shell and flesh growth, i.e. the differential growth of shell and body. Some of the older cohorts were found either to emaciate for much of the year (see also Beukema and De Bruin, 1977) or to show net emaciation with little shell size increase over the two years of sampling; and while at the majority of stations the animals showed a dual cycle of condition increase and emaciation over the year (see below), all cohorts at the most environmentally harsh station (C5) had the largest emaciation and showed only a small net flesh weight change over the year. The increased emaciation with age and area of the shore indicates an increasing environmental limitation with age, particularly at the environmentally poor areas.

The flesh and shell weights of both standard animals were respectively directly and inversely correlated with the environmental factors, demonstrating the inverse relationship between the two components over the mud flat. The environment again exerted an increasing affect on shell weight with age. The areal shell weight changes may be summarised ;

1) The shell weight of small animals was affected more by temporal changes in temperature, salinity and flesh biomass than by spatial changes.

2) The standard size shell weight increased (i.e. thickened) during the period October to April following the cessation of both reproduction and growth.

3) The 4mm animals, which were approximately the same age and growing at the same rates, were affected by spatial environmental changes to a lesser extent than the large animals.

4) However, the differences encountered in large standard animals' shell weights were the result of large spatial changes in the sediment quality and were therefore the cumulative effect of the environmental conditions together with the age differences between areas, e.g. the shell weight of these animals was largely affected by the sediment carbon content but that carbon content was low in the coarse areas where the animals had thicker shells as a result of greater age.

It is therefore difficult to state that the high-shore animals had thicker shells and that shell weight differences between the animals over the shore increased with age, although these possibly explain the observed differences.

The seasonal cycle of shell thickening, as opposed to shell growth, has been studied little in tellinids although Lammens (1967) also found that the shell thickness increased after the growth period. The standard size shell weight of Tellina tenuis was also found to be low over the summer at the period of highest flesh weight and then increased until the original weight was regained in September (Ansell and Trevallion, 1967). It is considered that this cycle may be a result of the shell increasing in size either by the production of less calcified shell material than normal, i.e. the new shell then being less dense than normal (Ansell and Trevallion, 1967), or by the production of a thinner shell than normal (Lammens, 1967) during the growth period with the winter shell-density or thickness being restored after the growing season.

The annual cycle of flesh condition, shell weight and growth of Macoma on Torry Bay may therefore be summarised :

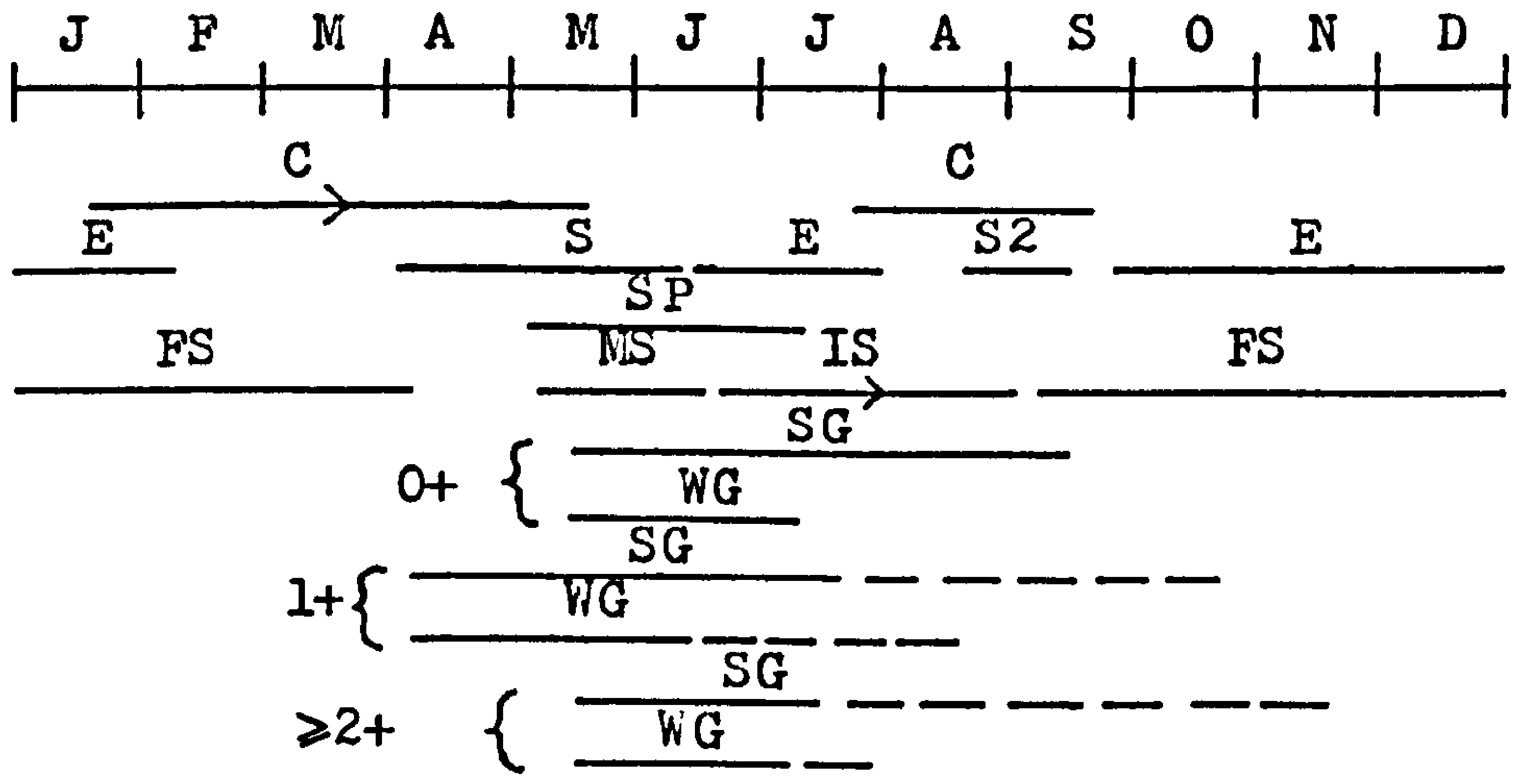


Fig. 3.36 The Annual Cycle of M. balthica where :
C = condition increase; E = emaciation; S = spawning;
S2 = possible second spawning; SP = main spat settlement;
FS = Full shell wt. of standard animal;
MS = Min. " " " " "
IS = Incr. " " " " "
SG = size growth & WG = flesh wt. growth for respective age classes.

This annual cycle differs from that found for the species by Lammens (1967), Chambers and Milne (1975b) and Beukema and De Bruin (1977) as two periods of condition rise were found over the year in the Torry Bay population. In the other populations, the single condition peak was attributable to maturation and growth. Spawning did not cause a 'check' in the condition increase in the Wadden Sea population and occurred before the condition increase in the Ythan population. It is possible therefore that food levels on Torry Bay were insufficient to support simultaneously both growth and spawning in mature animals, i.e. that physiological antagonism occurred with the available energy being ulitized in spawning with growth only occurring after spawning. Physiological antagonism has been found to occur in other bivalves (see Section 4.4.3.) and was found in Macoma by Lammens (1967) and De Wilde (1975) but not by Beukema and De Bruin (1977) nor in laboratory experiments by De Wilde (1975) nor by Ansell and Trevallion (1967) in Tellina tenuis where spawning coincided with the growth period. Physiological antagonism has been found between :

Spawning and shell growth in Ostrea edulis (Orton, 1928);

Gonad development (but not spawning) and growth in Venus striatula (Ansell, 1961);

Maturation and growth in Mercenaria mercenaria (Ansell et al, 1964a, b);

Spawning/maturation and growth in M. balthica (Lammens, 1967).

However, in another Wadden Sea population, the period of prolonged spawning coincided with that of most rapid growth (Beukema and De Bruin, 1977). This possibly suggests that the environment was not limiting and could support both processes.

Macoma has been found to commence maturation in some cases shortly after spawning (Chambers and Milne, 1975b), in late summer (Caddy, 1967) or in autumn (Lammens, 1967; De Wilde and Berghuis, 1978), i.e. in all but the Ythan population, maturation proceeds after growth has ceased. The utilisation of body reserves, usually glycogen (Ansell and Trevallion, 1967; Beukema and De Bruin, 1977) for maturation during food limitation is one of the causes of emaciation during the later part of the year. This probably occurs in the Torry Bay population although maturation was not examined.

A seasonal cycle for boreal bivalves has been suggested by Ansell and Trevallion (1967):

1) A winter period of inactivity when gametogenesis proceeds slowly and body reserves are used to supply reduced metabolic needs.

2) A short period following the renewal of activity in spring when the body reserves are renewed, growth recommences and rapid gonad proliferation and gametogenesis occurs.

3) A reproductive period occurs during the summer when the temperature rises above a certain limiting level and body growth, gonad growth and spawning proceed together.

This may therefore be more marked in suspension feeders (as T. tenuis), where food levels (as phytoplankton blooms) are much more seasonal, than in deposit feeders, in which detritus food levels are relatively constant over the year although microfloral activity levels change with temperature. The seasonal cycle may therefore be modified to include the occurrence of earlier maturation and the fact that spawning and growth may not coincide.

These differences are possibly the result of lower food levels over longer periods of the year for deposit feeders in contrast to the high food levels, during plankton blooms, for short periods available to suspension feeders (see also Lammens, 1967).

In M. balthica the large changes in condition were therefore more associated with temperature changes, spawning and growth than food availability. Its food intake is known to be reduced at low temperatures (e.g. Lammens, 1967; Hughes, 1969b), as a result of decreased metabolic processes, and at high temperatures, >15°C (De Wilde, 1975). The body condition increased because of an accumulation of reserves and gonad development and fluctuated as a result of changing balance between the growth of shell and gonad and the losses of material in spawning. The fall in condition represented a net deficit of food available over metabolic requirements. However, Macoma, unlike suspension feeders, does not appear to accumulate large food reserves because of the relatively constant food availability (Lammens, 1967).

In addition, while many authors have commented at length on the large temporal variation in body condition attributable to growth, spawning, maturation and emaciation in relation to temperature, food supply etc., as shown here, a similar variation can occur spatially within the intertidal, and possibly subtidal, area supporting this species. It is considered that the spatial differences encountered in this survey will also be found in other deposit-feeding populations which colonise a large number of habitats.

An additional consideration is the effect on M. balthica of living under the low-shore, fine mud mussel beds. These areas supported the largest growth rate, body condition, life span and more very large animals (>15mm ht.) than any other, but they unexpectedly supported low biomasses. It is considered that these factors were the result of living in a stable environment with protection from predators and from temperature extremes, and living in a fine mud, low-shore environment with its advantages together with a food supply enhanced by mussel faeces and pseudofaeces. Also, as much of the substrate surface was covered by pools of water for most of the period of exposure, the extent of feeding by the bivalves would be increased. However, these advantages were counteracted by the low densities that these areas supported. The presence of M. edulis resulted in the successful settlement by very few animals, larval mortality was caused by the high density of suspension feeders together with a possible smothering of spat once settled (Meikilovski, 1974); however, those animals which had settled successfully lived under conditions superior to any other area.

3.5.5. The Production and Mortality of M. balthica ; Spatial and Geographical Variation.

The large variation in mean biomass (0.8 to 9g fdw m^{-2} in 1975-76; 0.48 to 6.0 in 1976-77), production (-0.29 to 4.4g fdw m^{-2} yr^{-1}; 0.055 to 2.5) and $P/\overline{B}$ (-0.354 to 0.488, 0.116 to 1.108) encountered within the study area encompasses much of the geographical variation in these parameters in M. balthica populations see (Table 3.27 and below). Such a spatial variation has been considered by few authors although Wolff and De Wolf (1977) encountered M. balthica biomass, production and $P/\overline{B}$ variation of 0.0 to 2.93g m^{-2}, -0.74 to 3.4g m^{-2} yr^{-1} and 0.25 to 1.93yr^{-1}

respectively within the Grevelingen estuary which showed comparable environmental variation to that encountered in the present study.

The annual production was mainly influenced by fine sediment parameters, the shore slope and the water carbohydrate quantity, and was greatest in those areas supporting the largest biomasses and the largest growth rates, i.e. at mid tidal levels where fine sand/mud substrate occurred. These relationships indicate the dependence by Macoma not only on a suitable substrate, resulting in high carbon and nitrogen contents and being the result of suitable water currents and shore slope, but also on the availability of water particulate food. These findings suggest that although the sediment carbon and nitrogen levels were sufficient to meet the animals requirements (Bubnova, 1972; Tunnicliffe and Risk, 1977), Macoma does suspension feed to some extent (see Section 6.2.). It was also apparent that the sediment water content influenced the production by possibly partly determining the time available for feeding. The low levels of production in certain areas of Torry Bay were attributable to low sediment food levels, low sediment water contents and an insufficient immersion period for feeding. In addition the increase in $P/\bar{B}$ values with increasing C/N values and a decrease in tidal height again showed the relevance of the food quantity, rather than quality, as well as the time available for feeding in determining the relative productivity of an area.

The alternative method of estimating production also gave large differences in annual production and $P/\bar{B}$ values between the high-shore, coarse sediment stations and low, fine stations. The latter had a biomass 1.5 times greater than the former but produced three times the amount of somatic material from that biomass. This again demonstrates the large variation in the productivity of the areas within an intertidal mud flat. The comparisons of values between the two methods of calculating the production of a population (see Section 3.3.5.6.2. and Table 3.16) show the possible range of error in those calculations. The many errors and assumptions incorporated into each of these production estimates prevents confidence limits being attached to the final estimates. As all production estimates are subject to those errors then the final estimate should be taken as being of the appropriate order (see also Arntz and Brunswig, 1975).

Such variation in the macrofaunal production within an intertidal region has been studied by few workers. Chambers and Milne (1975b) intensively studied a small area which supported twice the biomass, therefore twice the production, of other areas within an estuary. Their assumption of a constant $P/\bar{B}$ value over the whole area, however, is considered to be erroneous and has resulted in the calculation of a high overall production estimate. The findings of Hughes (1970), regarding the smaller production of S. plana at higher tidal levels, are in agreement with the present survey. However, that high population was found to have a high $P/\bar{B}$ value (as calculated from his data) than the lower more successful population. Similarly, the Macoma areas studied by Wolff and De Wolf (1977) showed large changes in P, $\bar{B}$ and $P/\bar{B}$ with sediment and tidal height variation and whilst the area of highest mean biomass was similar to those in the present study, that area had a negative production. The area found to be the most productive, as having both a high production and $P/\bar{B}$, was a high-shore, very fine sandy area. It is therefore difficult to make generalisations regarding the most productive areas of deposit feeding tellinids.

The variation in the mortality and $M/\bar{B}$ estimates (-0.58 to 6g fdw m^{-2} yr^{-1} and -0.71 to 0.66 for 1975-76, -0.17 to 3.7 and -0.35 to 1.25 for 1976-77 respectively) between stations was also the result of many factors. The greatest mortality of this species occurred within the common areas and was possibly attributable to increased predation by wading birds, in favourable areas, or by fish as these areas had large immersion periods which would increase predation (see also Section 7.3.2.). In addition, the possible smothering of spat by sediment movement, the unsuccessful settlement by many of the large number of spat, and the mortality of a greater number of large, long lived animals of greater flesh weight would also increase the mortality in the favourable areas. The mortality was therefore related to the amount of somatic production at an area available to predation. Furthermore, the proportion of the biomass which died either by predation or as the result of senescence also increased with a progression down the shore.

The average Torry Bay production estimates obtained in this study are compared with other Macoma populations (see Table 3.27). While comparison of the absolute values of mean biomass and annual production is of little value, because of the large local spatial variation in these parameters, a comparison of the productivity of each area (i.e. $P/\bar{B}$ values) is of value. Although some areas of Torry Bay supported very small Macoma populations and other areas supported greater populations than found in other studies, the productivity of that biomass was lower than the other intertidal studies but in agreement with the sublittoral

Table 3.27 *M. balthica* : Comparable Studies of Mean Flesh Production and Productivity. (Range of Values in Parentheses.)

Situation	Location	Annual $\overline{B}$ (g fdw m^{-2})	Annual $\overline{P}$ (g fdw m^{-2})	Annual $P/\overline{B}$	Author
Intertidal	Firth of Forth	3.190 (0.8 - 9.0)	1.130 (-0.29 - 4.4)	0.354	This Study (1975/76 Data).
	Firth of Forth	1.880 (0.48 - 6.0)	0.920 (0.055 - 2.5)	0.489	This Study (1976/77 Data).
	Wadden Sea	3.5	2.5	0.7	Beukema (1971).
	Nova Scotia, Estuary	1.26	1.93	1.53	Burke and Mann (1974).
	Ythan Estuary	2.77	5.73 10.07	2.07	Chambers and Milne (1975b).
	Lynher Estuary	0.337	0.308	0.9	Warwick and Price (1975).
	Grevelingen Estuary	(0.01 - 2.93)	(-0.74 - 3.40)	0.96 (-0.25 - 1.93)	Wolff and De Wolf (1977).
Sublittoral	Gulf of Finland	8.97	4.22	0.47	Segestråle (1960) by Bergh (1974).
	S. Baltic Sea	2.60	1.01	0.388	Bergh (1974) *[1].
	N. Baltic Sea	4.2	1.7	0.45	Ankar and Elmgren (1976).
	N. Baltic Sea	0.27	0.1	0.37	Cederwall (1977).

*[1] Calculated from Bergh (1974) using conversion figures given by Ankar (1976).

studies. The majority of authors found a $P/\bar{B}$ value less than unity which may therefore be considered as the normal situation for such a long lived species (see also Zaika, 1973). This disagrees with Chambers and Milne (1975b), including the findings of Sanders (1956), Hughes (1970) and Burke and Mann (1974), who consider an annual $P/\bar{B}$ of between 1.5 and 2.5 usual for long lived North Temperate estuarine and marine bivalves. However, the comparable $P/\bar{B}$ calculated by Chambers and Milne (1975b) for Hughes (1970) data is too high; these authors have included the production due to reproduction as well as that due to growth. The $P/\bar{B}$ values for Hughes' (1970) S. plana populations should be 0.29 for lower-shore, 0.67 for upper-shore, with 0.33 as the average value.

Zaika (1973) and Burke and Mann (1974) suggest that macrofaunal species with a 2-3 year life span should have $P/\bar{B}$ values in the range 3-6 whilst longer lived (> 5 year) macrofaunal invertebrates should have a $P/\bar{B} < 1.0$. The population of Macoma studied by Burke and Mann was considered to only have 3 cohorts; it is probable that these authors combined too many older cohorts in their size-frequency analysis and therefore over estimated the productivity of their population. Chambers and Milne (1975b) may have also overestimated the $P/\bar{B}$ for their whole population by calculating the value for an intensively sampled area favoured by Macoma (and therefore having a relatively high value), and then using that value to estimate the production for other less populated areas.

Within the range of $P/\bar{B}$ values measured for the species, intertidal, temperate populations appear to have values 0.5 - 1.0 (exceptionally to 2.0) whilst sublittoral or arctic populations have values < 0.5. The mean P/$\bar{B}$ value for the Torry Bay population is of the same order as the latter populations; this is in agreement with the mean growth pattern for the population (see Section 3.5.2.3.). The present study has shown, however, that the range of P/$\bar{B}$ values encountered within an intertidal area was as large as the geographical range of P/$\bar{B}$ values for the species. Therefore while it may be possible to characterise either a species or a group of species by the P/$\bar{B}$ value (see e.g. Burke and Mann, 1974; Chambers and Milne, 1975b; Hibbert, 1976), more information is needed regarding both the local and geographical variability of this parameter.

Within an intertidal area, the highest P/$\bar{B}$ values were associated with areas supporting the largest number of juveniles, although this was not as marked as found by Wolff and De Wolf (1977) for the species, as on Torry Bay those areas also supported larger numbers of older cohorts. The P/$\bar{B}$ decreased with the increasing age of the cohort after the first year or two, At Torry Bay the spat was numerically dominant to a greater or lesser extent throughout the year, a situation different from other comparable populations where spat may only comprise 15% of the total numbers and other cohorts are more successful as the result of greater spatfalls (Burke and Mann, 1974). However, although the spat were both numerically dominant and had the highest productivity, they contributed little to the station biomass and production. This "productive dominance" of larger individuals, may be characteristic of populations of long lived species while small, metabolically more active individuals only become more important in short lived species (Hughes, 1970).

The 1+ and 2+ age classes produced the greatest amounts of material and the progress of the most successful cohort (the 1974 class) was evident throughout both years of sampling. This dominance, either numerically or as biomass, of one particular cohort is characteristic of planktonic spawning bivalves in which the extent of gonad proliferation may fluctuate widely from year to year (Ansell and Trevallion, 1967). Green (1957) studied a S. plana population in which the dominance of one cohort prevented the settlement of sufficient spat to replace it as the dominant cohort. The relatively large production and biomass of the 1+ cohort found on Torry Bay was also found in a Nova Scotia population (Burke and Mann, 1974). The success and dominance of certain age classes together with regular poor spat settlements may therefore also be characteristic of tellinids generally (e.g. see also Arntz and Brunswig, 1975).

In addition, the major part of the annual production in the population had occurred by July, i.e. during the period of flesh growth, after which elimination and emaciation were found to increase; these patterns were also found in other populations (Burke and Mann, 1974; Chambers and Milne, 1975b).

The areal mean production values for the Torry Bay population :

	$\bar{B}$ g fdw m^{-2}	P g fdw $m^{-2}yr^{-1}$	M g fdw $m^{-2}yr^{-1}$	$P/\bar{B}$ yr^{-1}	$M/\bar{B}$ yr^{-1}
1975-76	3.190	1.130	1.587	0.354	0.497
1976-77	1.880	0.920	1.250	0.489	0.665

show that in each year the mortality (elimination from the population) exceeded the production (net addition to the population); a situation also encountered for M. balthica by

Burke and Mann (1974) but not for other benthic invertebrates. This situation may represent an excessive predation of a population together with the large scale annual condition changes by an infaunal population. It is possible that the relationship $M/\bar{B} > P/\bar{B}$ suggests either that the population was in a state of decline or that the study measured a temporary decline in the normal fluctuation in the population trends. The oldest cohorts suffered the major part of the mortality whilst the main production was by the younger cohorts. It is generally evident therefore that the loss of lower numbers of larger animals from the population was greater than the production attributable mainly to larger densities of smaller animals. The $M/\bar{B}$ values were high during the first two years and in the older cohorts but low in the 2+ to 4+ cohorts. These trends were attributable to a high mortality of the available cohort biomass caused by unsuccessful spat settlement and by high selective predation in animals during the first one and a half years; and to senility, overall emaciation, the increasing influence of the environment and predation in later life. The increasing amount of material lost through mortality with age was also attributable to the latter factors. In addition the respective large recruitment and emaciation of young and old cohorts resulted in the calculation of negative mortality and production (see also Burke and Mann, 1974; Chambers and Milne, 1975b); whilst in all cohorts at all areas a greater or lesser amount of annual production was lost by emaciation (see also Beukema, 1971).

The population somatic production, as calculated here, does not allow for the predation of parts of animals e.g. siphons (Wolff and De Wolf, 1977) but, contrary to a suggestion by

Chambers and Milne (1975b), it does partially account for losses attributable to reproduction. McIntyre and Eleftheriou (1968), found that 0+ group plaice accounted for upto 0.04mg dry wt. siphon/day/Tellina during the summer; flat fish may therefore remove a substantial amount of material although no estimate for this loss from the Torry Bay population can be made owing to the paucity of data concerning estuarine fish populations. The losses of material from the standing crop by spawning contributes towards the elimination estimates and will therefore reduce the production estimates. Hughes (1970) found that up to 50% of the total annual production of S. plana was released as gametes, the remainder being the production attributable to growth (although the proportion was as low as 24% at an upper area where the animals possibly existed under stressful conditions). The total production of Macoma may therefore be up to twice the estimated value at each station on Torry Bay with lower values at the higher stations.

In conclusion, the field study has indicated that M. balthica on Torry Bay had an overall anomalous production ecology when compared to other areas. That abnormal productivity and growth cannot be explained by the environmental variables studied but may be attributed to environmental abiotic and biotic factors not monitored in the field survey. One such factor is the level of pollution within an industrialised estuary which, together with experimental studies regarding the production ecology of the species, is considered further in Sections 6.1., 6.2. and 6.3.

Chapter 4. The Production Ecology of Suspension-feeding Bivalves.

4.1. Introduction.

The suspension-feeding infaunal bivalves, Cerastoderma edule L., the edible cockle, and Mya arenaria L., the soft shelled clam, are among the most common species in estuaries around the British and north European coasts. The latter species is an immigrant species from the Eastern Seaboard of North America during the last century; a possible reason as to why the species is less-well established in northern Europe than in North America (Clay, 1967c).

The commercial importance of cockles in northern Europe and clams in North America has resulted in the accumulation of large amounts of information regarding their biology, (Clay, 1967c & d). The extensive cocklebeds of South Wales and the Wadden Sea have been studied in order to assess the growth, meat condition and reproduction of cockles in relation to environmental factors (e.g. Kreger, 1940; Verwey, 1952; Baggerman, 1953; Kristensen, 1957; Hancock, 1965; Farrow, 1971; Hancock and Franklin, 1972). Similarly, the clam-beds of the Eastern United States Seaboard have been studied with respect to commercial clam farming (e.g. Newcombe and Kessler, 1936; Glude, 1955; Ayers, 1956; Spear and Glude, 1957). As these areas are of economic importance, and therefore may be associated with high growth rates and yields, the biology of the bivalves thereon may reflect the optimal conditions for the species.

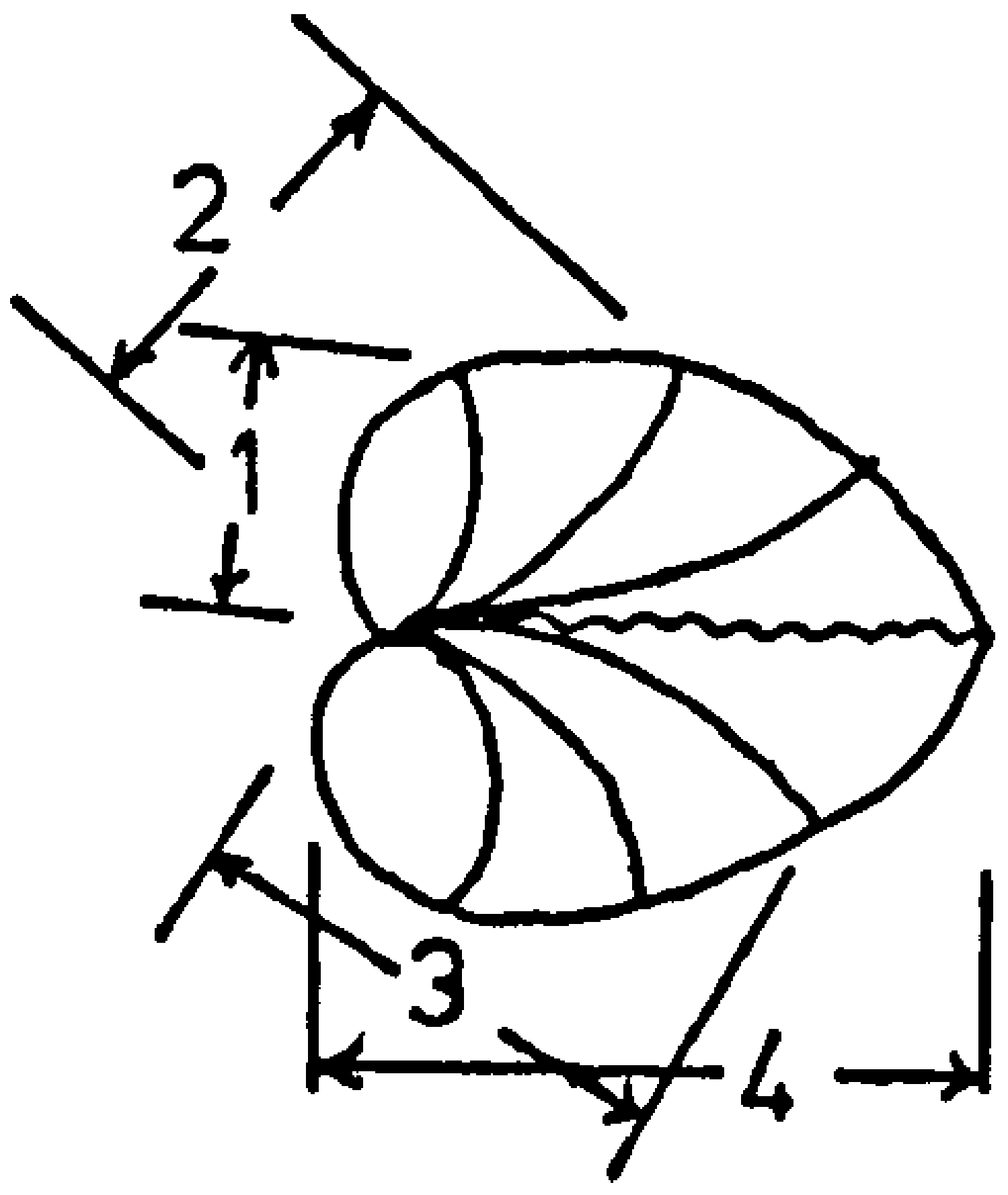
Other workers have studied clams and cockles from less commercially important areas and have found lower densities, biomasses and rates of growth (e.g. Jones, 1960; Munch-Petersen, 1973; Seed and Brown, 1975; Warwick and Price, 1975). However, the animals in these studies were taken from relatively unpolluted areas although recently cockle populations subjected to power-station cooling-water from Southampton Water have been studied (Barnes, 1972). In no case, however, have suspension-feeding bivalves been studied that were possibly affected by petrochemical effluent such as that encountered in the Forth Estuary. It is therefore of interest to consider the status of these bivalves within a polluted estuary.

These two species have been grouped together as they show similarities in the ecological niche that they occupy within an estuarine area as suspension-feeding, planktonic-spawning bivalves. These species may therefore be more susceptible to changes in water quality than the deposit-feeding macrofauna. The present study was designed to determine both the role of suspension-feeding bivalves within an industrialised estuary and the similarities between aspects of the production ecology of these species. A study of the population dynamics, growth, condition, reproduction and production in relation to environmental factors was necessary in order to quantify the species' presence and contribution to the energy flow within the estuarine area.

4.2. Materials and Methods.

The populations of C. edule and M. arenaria were sampled in the field and analysed in the laboratory, in an identical manner to that of M. balthica (Section 3.2.). Data were obtained regarding the species distribution and abundance at each station. The length (and height for C. edule), total dry weight and flesh dry weight of each individual were measured enabling the population dynamics of the species to be computed.

The growth of the bivalves was analysed in an identical manner to that of M. balthica (see Section 3.2.2.). The shell growth cessation rings of C. edule were measured as the distance from umbo to the ventral surface of the shells. Where necessary allowance was made for the curvature of the shell at the umbo although the shortest distance between the umbo and the ventral edge of growth was measured, e.g.



where 1, 2, 3, 4 indicate the height of the shell after that number of years.

This measurement of growth rings was considered to be more accurate than taking a measurement along the antero-posterior axis as the growth rings were less-clearly defined at the anterior or posterior edges than at the ventral edge. Growth cessation rings attributed to disturbance were ignored as were other rings that were not clearly delimited. Consequently only pairs of successive growth rings that were clearly defined were used in the growth ring analysis.

The measurement of the growth rings in the *M. arenaria* individuals proved difficult and unreliable as, although many rings were present on the shells, few could be accurately attributed to a winter cessation of growth. The problems of ageing *M. arenaria* by growth rings has confronted most workers studying the growth of this species (Newcombe, 1935; Munch-Petersen, 1973) and while growth ring identification is accurate in some areas it is not in others (Seed, 1969).

In the present study, methods (1) and (2) (Section 3.2.2.) were used to determine the age of *C. edule*. The age of *M. arenaria* was determined only by method (1); however, as only three age cohorts were separated and there were large size intervals between these ages, the size-frequency method was considered to give reliable results.

The population production due to somatic growth by *C. edule* and *M. arenaria* has been calculated using the weight increment method given by Crisp (1971) for each sampling period and age cohort and summed for each sampling year (see Section 3.2.3.). The flesh condition of the species was analysed as given in Section 3.2.1.

4.3. Results.

4.3.1. The Size of *M. arenaria* and *C. edule* populations on Torry Bay with Respect to Both Area and Station.

4.3.1.1. *C. edule* Total Population.

The total area supported relatively constant numbers and biomasses of each age cohort (Fig. 4.1 1975-76). After the first year of life, e.g. July to July, the cohort attained a relatively stable density and biomass with the population curves of density and biomass reaching plateaux against time. Although the numbers of spat present during 1975-76 had a maximum of 200m^{-2} as an average for the area, the first year (0+ group) contributed least to the areal cockle biomass. The overall maximum of cockle density was reached in September but mortality caused by predation and unsuccessful settlement reduced those numbers by 80% by December. The number of 0+ group cockles that had survived over the winter 1975-76 was much lower than the corresponding density during the early part of 1975. There was a decrease in cohort density with increasing age but further mortality was very slow after the first year of life. The cohort biomass increased with increasing age such that the gain to the population by the growth of surviving individuals was greater than any loss due to mortality.

The following year (1976-77) had a much more successful spatfall with a maximum average density of 640m^{-2} 0+ group animals (Table 4.1). This increase was accompanied by an increase in mortality such that the stability of the population was maintained. The older cohorts were present in similar densities and biomasses to the previous year (data given in Appendix 4.5).

Figure 4.1 C. edule : (a) The Density of and (b) Biomass of Each Cohort at Each Sampling Date (1975-76 Data).

Legend

— —▲— 1975 Cohort

——·—— 1974 "

—·—·—·— 1973 "

——■—— 1972 "

——•——> 1972 "

(a)
(b)
Density
(m^{-2})
198
150
140
120
100
80
60
40
20
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
100
100
10
1.0
Fdw
m^{-2}
(mg)

4.3.1.2. C. edule Numbers and Biomass per Station.

The 1975-76 data showed a range of mean spat densities per station from 0 to 170m^{-2} with a biomass of 16.40mg fdw m^{-2}. The spatfall was therefore poor when compared to the following year in which mean densities up to 680 spat m^{-2} with biomasses up to 68.05mg fdw m^{-2} were recorded (Table 4.2). The standard deviations attached to the means of the numbers and biomasses give an indication of the maximal sizes of population recorded at each station. In addition, the maximum numbers and biomasses of each station are given in Table 4.1.

The mean densities and biomasses of the large cockles (> 2.5mm height), provide an indication of the stable cockle population in the area by taking into account only successfully settled individuals and excluding the large fluctuations in numbers attributable to spat settlement and the resultant high mortality. The main cockle population was found in densities up to 100m^{-2} and biomasses up to 3500mg fdw m^{-2} in 1975-76 and up to 170m^{-2} and 2700mg fdw m^{-2} in 1976-77 (Table 4.2). The areas with the highest density of both cockle spat and the main population were not necessarily those with the greatest biomass.

4.3.1.3. M. arenaria Total Production.

In contrast to C. edule, the M. arenaria cohort numbers were found to decline until the end of the third year (Fig. 4.2a) although it is necessary to include provision for the greater depth of burrowing by the larger animals. It is considered likely that animals greater than 3+ were burrowed too deeply to be sampled.

The greatest numbers of spat were found during August and

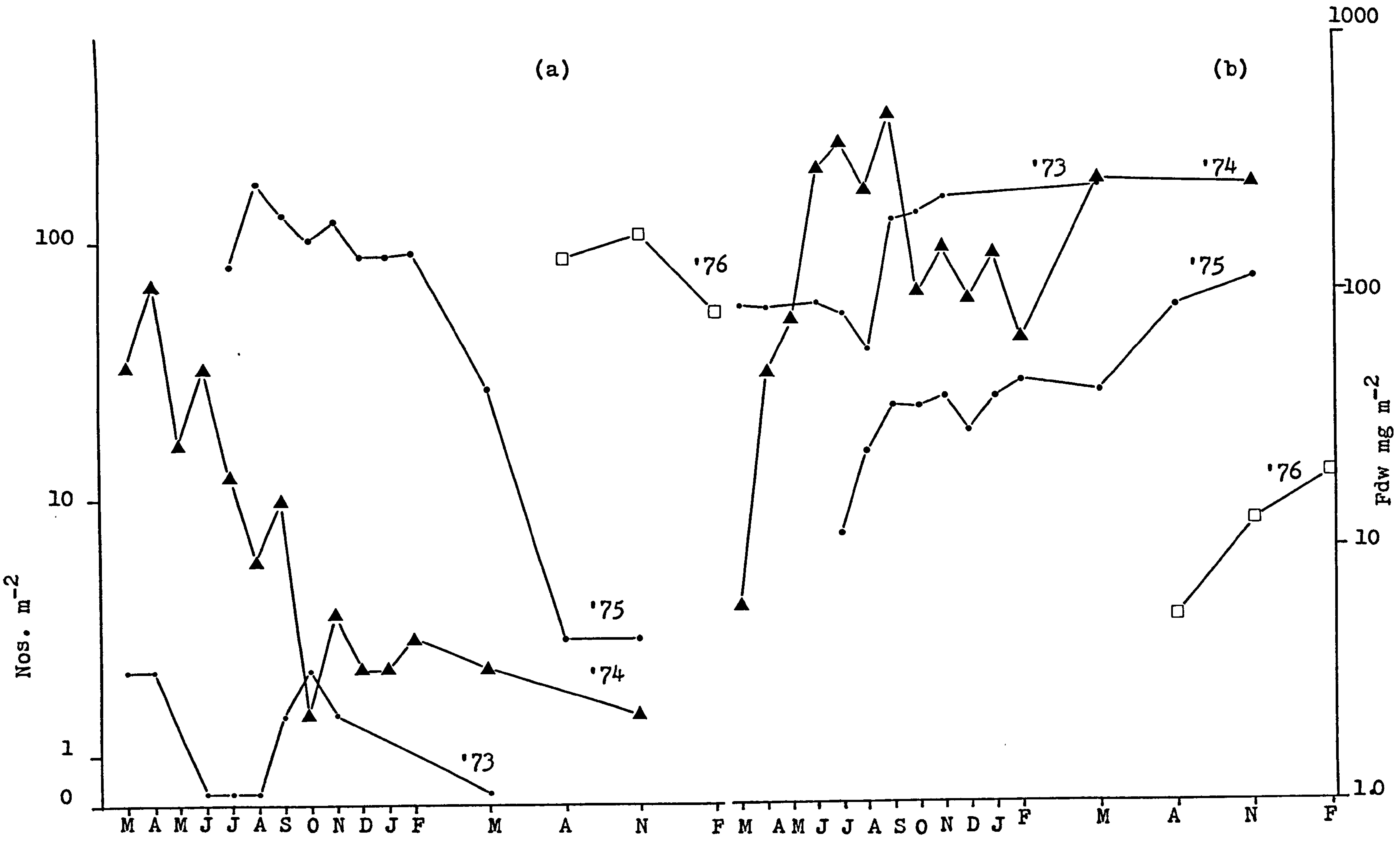
Table 4.1 *C. edule*, *M. arenaria*: The Maximum Abundance (n m^{-2}) and Flesh Biomass (mg m^{-2}) of 'Large' and Spat Animals at Each Station and in Each Sampling Year (1975-76 = (a), 1976-77 = (b)).

Station	*C. edule*								*M. arenaria*							
	Spat				'Large'				Spat				'Large'			
	$\bar{N}$. max.		$\bar{B}$. max.		$\bar{N}$. max.		$\bar{B}$. max.		$\bar{N}$. max.		$\bar{B}$. max.		$\bar{N}$. max.		$\bar{B}$. max.	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
A1	640	720	44.0	4.2	40	10	4842.7	1409.6	400	320	40.0	144.2	150	30	1529.1	68.9
A2	0	240	0	5.0	90	30	2792.0	2233.3	160	0	27.9	0	10	0	263.2	0
A3	80	240	0.8	10.1	70	80	2269.0	1075.7	200	160	56.4	56.4	80	40	6292.9	1156.3
A4	0	80	0	1.6	10	0	1352.2	0	240	0	126.7	0	20	10	194.9	13.9
B1	320	960	17.6	43.6	30	10	2652.2	27.4	640	640	156.0	53.4	60	20	1251.8	3902.5
B2	640	320	13.0	8.9	50	20	2479.0	37.8	800	320	113.9	84.3	90	20	14741.0	702.3
B3	240	2480	143.1	199.6	290	300	5435.6	3625.2	640	240	128.0	14.2	200	30	3086.6	536.7
B4	160	160	8.3	4.6	120	40	7474.0	3271.4	0	0	0	0	10	0	636.4	0
B5	80	0	6.6	0	70	130	2561.1	6380.5	0	0	0	0	10	20	1564.3	13533.0
C1	0	160	0	22.8	30	0	4097.0	0	80	160	2.2	29.2	10	0	26.6	0
C2	400	1920	89.9	47.6	33	30	1195.8	60.9	400	240	47.1	31.8	50	50	104.3	456.7
C3	400	960	17.9	64.7	70	70	4028.9	3784.0	240	80	67.0	42.3	20	20	60.8	60.8
C4	160	240	4.9	5.9	60	50	3362.0	1547.7	0	0	0	0	20	20	106.0	1966.4
C5	400	160	56.0	4.8	210	480	3923.4	3923.4	160	160	32.2	7.0	20	20	3216.0	172.7
$\bar{x}$	251	606	28.7	30.2	84	89	3461.8	1955.5	283	166	57.0	33.1	54	20	2362.4	1612.2

Table 4.2 C. edule: The Mean Biomass (mg Fdw m^{-2}) and Density (nos. m^{-2}) at Each Station.

	1975-76								1976-77							
	Spat (<2.5 mm Ht.)				Large Animals				Spat (<2.5 mm Ht.)				Large Animals			
Station	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.
A1	170.00	240.00	9.18	14.63	10.83	12.40	850.45	1477.65	220.00	338.62	1.50	1.60	6.00	6.32	439.39	695.58
A2	0	0	0	0	21.67	26.57	538.66	823.55	70.00	117.19	1.63	2.46	12.50	12.58	684.92	752.60
A3	6.67	23.09	0.07	0.23	32.50	22.61	1128.30	778.45	66.75	106.27	4.28	5.09	38.75	32.88	416.17	475.86
A4	0	0	0	0	1.67	3.89	113.35	390.14	20.00	40.00	0.41	0.82	0	0	0	0
B1	70.00	105.31	8.42	19.54	8.33	9.37	330.36	804.33	330.00	434.36	13.48	20.69	3.75	5.59	4.62	10.21
B2	73.33	181.98	1.37	3.69	12.50	17.12	533.31	934.44	120.00	153.19	2.50	4.29	8.75	9.01	8.99	13.51
B3	40.00	80.00	16.40	41.87	91.67	92.52	1354.60	1562.14	680.00	1201.8	68.05	93.17	172.50	130.86	2161.19	1248.63
B4	33.33	53.48	1.75	2.99	70.00	29.54	3531.94	2004.01	60.00	76.59	2.06	2.41	36.25	5.59	1821.54	1045.86
B5	13.33	31.14	0.82	2.05	28.33	22.90	1074.17	1059.43	0	0	0	0	60.00	53.23	2562.55	2675.08
C1	0	0	0	0	5.00	10.00	472.81	1225.54	40.00	80.00	5.71	11.41	0	0	0	0
C2	86.87	129.71	11.11	25.66	7.75	11.15	225.03	381.99	590.00	905.02	19.90	23.47	15.00	11.55	23.79	24.87
C3	80.00	127.64	4.67	6.85	15.83	20.65	433.46	1147.94	320.00	428.33	19.78	30.21	32.50	19.76	1471.75	2142.83
C4	20.00	49.73	0.56	1.46	22.50	19.60	960.77	1137.38	60.00	120.00	1.47	2.94	31.25	16.77	1181.92	397.95
C5	53.33	114.84	5.33	16.04	115.00	42.53	2007.24	1149.59	70.00	72.11	2.41	2.34	191.25	138.98	2695.07	855.14

Figure 4.2 *M. arenaria* : (a) The Density (N. m^{-2}) and (b) Flesh Biomass (mg m^{-2}) of Each Cohort at Each Sampling Occasion. Logarithmic Ordinate on Each Graph.


(a)
(b)
Nos. m^-2
100
10
1
0
Fdw mg m^-2
1000
100
10
1.0
'73
'74
'75
'76
'73
'74
'75
'76
M A M J J A S O N D J F M A N F
M A M J J A S O N D J F M A N F

September although the greatest spat mortality occurred mainly over the spring and early summer (c.f. C. edule). The biomasses of cohorts at ages greater than one year reached plateaux at around 200mg fdw m^{-2} which suggests that the bay could support only a limited clam population (Fig. 4.2b).

4.3.1.4. M. arenaria : Numbers and Biomass per Station.

The highest densities of spat during each sampling year were at or below mid tide on soft mud with up to a mean of $200m^{-2}$ and 40mg fdw m^{-2} during 1975-76 and up to a mean of $300m^{-2}$ the following year (Table 4.3). During the second year of sampling, however, there were more areas where no spat were recorded. This was a possible indication of a change in settlement areas between the two years and an overall reduced spatfall during the second year.

The average number of large animals sampled during 1975-76 was 30 - $40m^{-2}$, although Station B3 had a mean of $80m^{-2}$ (Table 4.3); a maximum average biomass of 1300mg fdw m^{-2} was encountered on the bay. During 1976-77 fewer large M. arenaria were sampled with $16m^{-2}$ being the maximum average density for the stations. The differences between sampling years could possibly have been attributed to a longer sampling period. However, as the main spatfall was sampled (in August) and regular samples taken at each season this was not considered to be the case.

4.3.2. The Factors Influencing Spatial Variation in the Population Size.

The statistical analysis described in Section 2.3. was performed on the mean number and biomass data for large and small C. edule and M. arenaria for 1975-76 i.e. any difference between

Table 4.3 <u>M. arenaria:</u> The Mean Biomass (mg Fdw m^{-2}) and Density (nos. m^{-2}) at Each Station.

	1975-76								1976-77							
	Spat (<2.5 mm Ht.)				Large Animals				Spat (<2.5 mm Ht.)				Large Animals			
Station	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.	$\bar{N}$.	S.D.	$\bar{B}$.	S.D.
A1	183.33	177.63	42.39	54.29	37.50	49.01	323.57	489.38	160.00	80.00	28.73	51.43	12.50	16.07	20.21	33.31
A2	26.67	52.11	2.40	8.04	1.67	3.89	22.50	75.82	0	0	0	0	0	0	0	0
A3	63.33	75.24	10.54	18.13	28.33	23.68	1316.56	1937.95	40.0	65.32	7.69	21.30	15.00	20.00	334.09	559.22
A4	20.00	69.28	10.56	36.58	7.50	7.54	50.26	74.30	0	0	0	0	2.50	5.00	3.49	6.97
B1	213.33	205.62	32.06	45.10	13.33	16.70	234.37	425.03	310.00	228.33	31.76	22.54	13.75	8.04	1047.47	1905.19
B2	161.67	238.85	24.69	38.42	30.83	29.37	1314.10	4229.96	190.00	172.43	18.57	30.75	8.75	6.92	207.63	332.43
B3	116.67	186.42	35.56	48.36	82.50	60.32	1201.17	1038.24	70.00	117.19	3.92	6.13	11.25	12.16	196.17	289.74
B4	0	0	0	0	1.67	3.89	53.60	183.55	0	0	0	0	0	0	0	0
B5	0	0	0	0	0.83	2.89	130.36	451.58	0	0	0	0	7.50	9.57	1233.57	1689.98
C1	6.67	23.09	0.19	0.65	0.83	2.89	2.22	7.68	50.00	79.16	3.85	11.06	0	0	0	0
C2	110.00	135.51	9.87	14.07	14.17	17.82	20.24	33.11	120.00	138.56	9.49	15.16	16.25	18.20	136.18	216.90
C3	80.00	83.56	15.36	21.73	7.50	8.66	12.92	19.36	10.00	30.55	5.29	16.17	5.00	8.16	8.96	22.77
C4	0	0	0	0	1.67	5.77	8.83	30.60	0	0	0	0	7.50	9.57	534.94	957.82
C5	33.33	53.48	4.48	9.46	5.83	6.69	411.94	906.89	20.00	61.10	0.88	2.69	7.50	9.57	82.08	95.04

sampling years was not considered. These population parameters were correlated with the environmental variables and with each other on a normal and logarithmically transformed basis and also incorporated into multiple regression analysis (Fig. 4.3; Tables 4.4, 4.5). The population parameters showed similar significance levels for both densities and their corresponding biomasses (see Section 4.3.3.).

The large cockles (i.e. the main part of the population) were shown to prefer areas with coarse sediments high on the shore with low amounts of organic matter and water in the sediment. The major part of the variation in numbers of large cockles was accounted for by M.P.D. together with water carbohydrate, sediment sorting coefficient and shore slope also contributing to the regression. The variation in the biomass of large cockles was mainly attributable to sediment C/N with salinity, water carbohydrate and sediment skewness also important. The importance of C/N may be a spurious conclusion; it is likely that this is the result of the sediment type affecting both C/N levels and the cockle population.

The _C. edule_ spat settled in downshore, fine mud areas with large amounts of sediment organic carbon. There were, however, very few significant correlations with the cockle spat parameters although the spat was very highly significantly related to the _M. arenaria_ spat which had many associations with the characteristics of downshore areas (see below and Section 4.3.3.). In the multiple regressions, cockle spat density variability was attributable to tidal height, the sediment type and its organic content and the shore slope. The spat biomass, however, appeared to be more determined by the amount of suspended potential food

	C. $\overline{SN}$.	C. $\overline{SB}$.	C. $\overline{LN}$.	C. $\overline{LB}$.	M. $\overline{SN}$.	M. $\overline{SB}$.	M. $\overline{LN}$.	M. $\overline{LB}$.
T.H.								+ (*)
M.P.D.			+ *		− (*)*	− *		
S.C.					− (*)			+ *
SK.				− (*)*	+ **	+ **	+ *	
%H_2O_F					+ (*)*	+ **		
%H_2O_J			− (*)					
%C.			− (*)	− *				
%N.								
%S. &C.					+ (**)***	+ (*)**	+ (*)	
Slope							− (*)*	− *
C/N.			− (*)*	− (*)*	+ (*)			
Int. Sal.								
Org. C.		+ *			+ (**)*	+ (**)*	+ (*)	+ (*)
CHO.							− *	
C. $\overline{SN}$.		+ (*)*			+ ***	+ (*)**	+ (*)	
C. $\overline{SB}$.					+ (*)**	+ (*)**	+ **	
C. $\overline{LN}$.				+ (***)***				
C. $\overline{LB}$.								
M. $\overline{SN}$.						+ (***)***	+ (***)*	+ (*)
M. $\overline{SB}$.							+ (***)***	+ (**)*
M. $\overline{LN}$.								+ (**)***

Figure 4.3 C. edule, M. arenaria: Spatial Data Analysis- Pearson Correlation Matrix of Density and Biomass of 'Large' and Spat Animals With Environmental Variables and Population Variables. (The significance of double-logarithmic correlations are given in parentheses.)

Environmental variables abbreviations as figure 2.9; symbols as given in figure 2.9. C. = C. edule parameters; M. = M. arenaria parameters; $\overline{SN}$ = mean annual spat density ($n\ m^{-2}$); $\overline{SB}$ = mean annual spat flesh biomass ($mg\ m^{-2}$); $\overline{LN}$ = 'large' animal mean annual density ($n\ m^{-2}$); $\overline{LB}$ = 'large' animal mean annual flesh biomass ($mg\ m^{-2}$).

Table 4.4 C. edule : Spatial Data Analysis - Multiple Regression Equations of 'Large' and Spat Mean Density and Biomass.

1) With All Environmental Variables : Variables $L\overline{N}$. and $L\overline{B}$ Also Used in (i) and (ii) Respectively.

(Legend as Fig. 4.3.)

	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(i)	$S\overline{N}$.	$\overset{***}{2.873}_{\%S.\ \&\ C.} - \overset{***}{38.870}_{TH.} + \overset{***}{0.508}_{M.P.D.} - \overset{***}{4.065}_{Salinity}$ $- \overset{**}{195.693}_{S.C.} - \overset{*}{0.008}_{C.H.O.} + \overset{*}{11.227}_{C/N} + 395.799$	SK., $\%H_2O_J$, Org. C.	99.8%	%N (21.4%), %S. & C. (16.1%), %C (12.7%), Slope (12.2%), TH. (10.7%).
(ii)	$S\overline{B}$	$\overset{***}{0.003}_{Org.\ C.} + \overset{***}{0.001}_{C.H.O.} + \overset{***}{1.296}_{Salinity} - \overset{***}{3.915}_{\%H_2O_J}$ $+ \overset{***}{509.518}_{\%N} + \overset{***}{0.543}_{\%H_2O_F} - \overset{***}{13.286}_{S.C.} + \overset{***}{0.520}_{C/N}$ $- \overset{***}{0.101}_{\%S.\ \&\ C.} + \overset{***}{2.219}_{\%C} - \overset{**}{1.493}_{SK.} - 62.512$	M.P.D., Slope, $L\overline{B}$.	All	Org. C. (23.0%), $\%H_2O_F$ (15.0%), C.H.O. (13.0%), %N (12.6%), C/N (12.4%).
(iii)	$L\overline{N}$.	$\overset{**}{0.015}_{C.H.O.} + \overset{**}{7.577}_{Slope} + \overset{*}{51.071}_{S.C.} - \overset{*}{15.473}_{\%H_2O_J}$ $+ \overset{*}{69.371}_{\%C} - 638.045$	$\%H_2O_F$, %S. & C.	99.2%	M.P.D. (28.3%), C.H.O. (17.7%), Slope (15.6%), S.C. (14.9%).
(iv)	$L\overline{B}$	$\overset{***}{202.902}_{C/N} + \overset{***}{120.244}_{Salinity} + \overset{***}{0.543}_{C.H.O.} - \overset{***}{3541.58}_{SK.}$ $+ \overset{***}{47.761}_{\%S.\ \&\ C.} - \overset{***}{376.579}_{\%H_2O_J} - \overset{***}{2.202}_{Org.\ C.} + \overset{***}{77615.96}_{\%N}$ $+ \overset{**}{292.362}_{Slope} - \overset{*}{827.523}_{\%C} + \overset{*}{1018.979}_{TH.} - 13944.668$	M.P.D., $\%H_2O_F$.	All	C/N (32.0%), Salinity (16.2%), C.H.O. (11.4%).

Table 4.5 <u>M. arenaria</u> : Spatial Data Analysis - Multiple Regression Equations of 'Large' and Spat Mean Density and Biomass.

1) With All Environmental Variables : Variables $L\bar{N}$. and $L\bar{B}$ Also Used in (i) and (ii) Respectively.

(Legend as Fig. 4.3.)

	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
(i)	$S\bar{N}$.	$3\overset{***}{.}151_{\%S.\ \&\ C.} + 0\overset{***}{.}043_{Org.\ C.} - 146\overset{***}{.}511_{S.C.} - 20\overset{***}{.}375_{\%H_2O_J}$ $+ 4\overset{***}{.}866_{Salinity} + 0\overset{***}{.}663_{L\bar{N}.} + 2402\overset{***}{.}742_{\%N} + 0\overset{**}{.}217_{M.P.D.}$ $- 15\overset{*}{.}902_{TH.} + 2.757$	SK., $\%H_2O_F$, Slope.	All	%S. & C. (58.2%), Org. C. (13.5%).
(ii)	$S\bar{B}$	$1\overset{***}{.}284_{\%H_2O_F} - 7\overset{***}{.}265_{\%H_2O_J} - 41\overset{***}{.}533_{S.C.} + 0\overset{**}{.}011_{Org.\ C.}$ $+ 711\overset{**}{.}381_{\%N} + 15\overset{*}{.}120_{\%C} + 0\overset{*}{.}007_{L\bar{B}} + 24.392$	%S. & C., C/N, C.H.O.	99.6%	SK. (50.7%), $L\bar{B}$ (10.9%), $\%H_2O_F$ (9.7%).
(iii)	$L\bar{N}$.	$65\overset{**}{.}733_{S.C.} - 1788\overset{**}{.}690_{\%N} + 60\overset{*}{.}903_{SK.} + 83\overset{*}{.}109_{\%C} + 626.116$	$\%H_2O_J$, %S. & C.	98.3%	C.H.O. (33.8%), S.C. (22.5%), %N (9.2%), $\%H_2O_F$ (8.2%), SK. (8.2%).
(iv)	$L\bar{B}$	$1\overset{***}{.}866_{Org.\ C.} - 219\overset{***}{.}354_{Slope} - 299\overset{***}{.}741_{TH.} - 331\overset{***}{.}964_{C/N}$ $+ 1831\overset{***}{.}10_{S.C.} - 53466\overset{***}{.}7_{\%N} + 2540\overset{***}{.}34_{\%C} - 5\overset{***}{.}021_{M.P.D.}$ $- 38\overset{***}{.}187_{\%S.\ \&\ C.} - 0\overset{**}{.}190_{C.H.O.} + 718\overset{*}{.}839_{SK.} + 7472.3$	$\%H_2O_J$, Salinity.	99.9%	Slope (23.9%), TH. (11.4%), %C (23.8%), Org. C. (9.5%).

(Org. C. and CHO.) as well as the fine sediment characteristics.

The large-clam part of the population occurred in fine mud areas of shallow slope and a high sorting coefficient together with large quantities of Org. C. and CHO. suspended in the water column. The larger biomasses were found at the higher tidal levels whilst the numbers of clam were optimal about the mid tide level (see below). This difference is probably attributable to the occurrence of large numbers of young clams > 2.5mm in length (0+, 1+ groups) around the mid tide level. The regression analysis suggests that the numbers of large M. arenaria were determined by the sediment characteristics of sorting, skewness and organic and water content although the most important variable was the water CHO. levels. The biomass of large clams was primarily determined by shore and sediment characteristics as well as suspended Org. C. in the water.

The clam spat settled in fine mud areas in which the sediment was positively skewed, with high water, silt and clay and organic matter content together with large amounts of detritus as Org. C. suspended in the water which was probably stirred-up from the soft bottom sediment. The major part of the variation in spat numbers was attributable to the amount of silt and clay in the deposit and the levels of water detritus, whereas the spat biomass variation was attributable to the sediment skewness and the presence of large M. arenaria.

As some of the environmental factors were considered to be of lesser biological significance to suspension-feeding bivalves they were omitted from a second series of regressions as were any highly intercorrelated independent variables. The population parameters were regressed against tidal height, M.P.D., %S. & C., shore slope, Org. C. and CHO. in the water and interstitial salinity (Table 4.6).

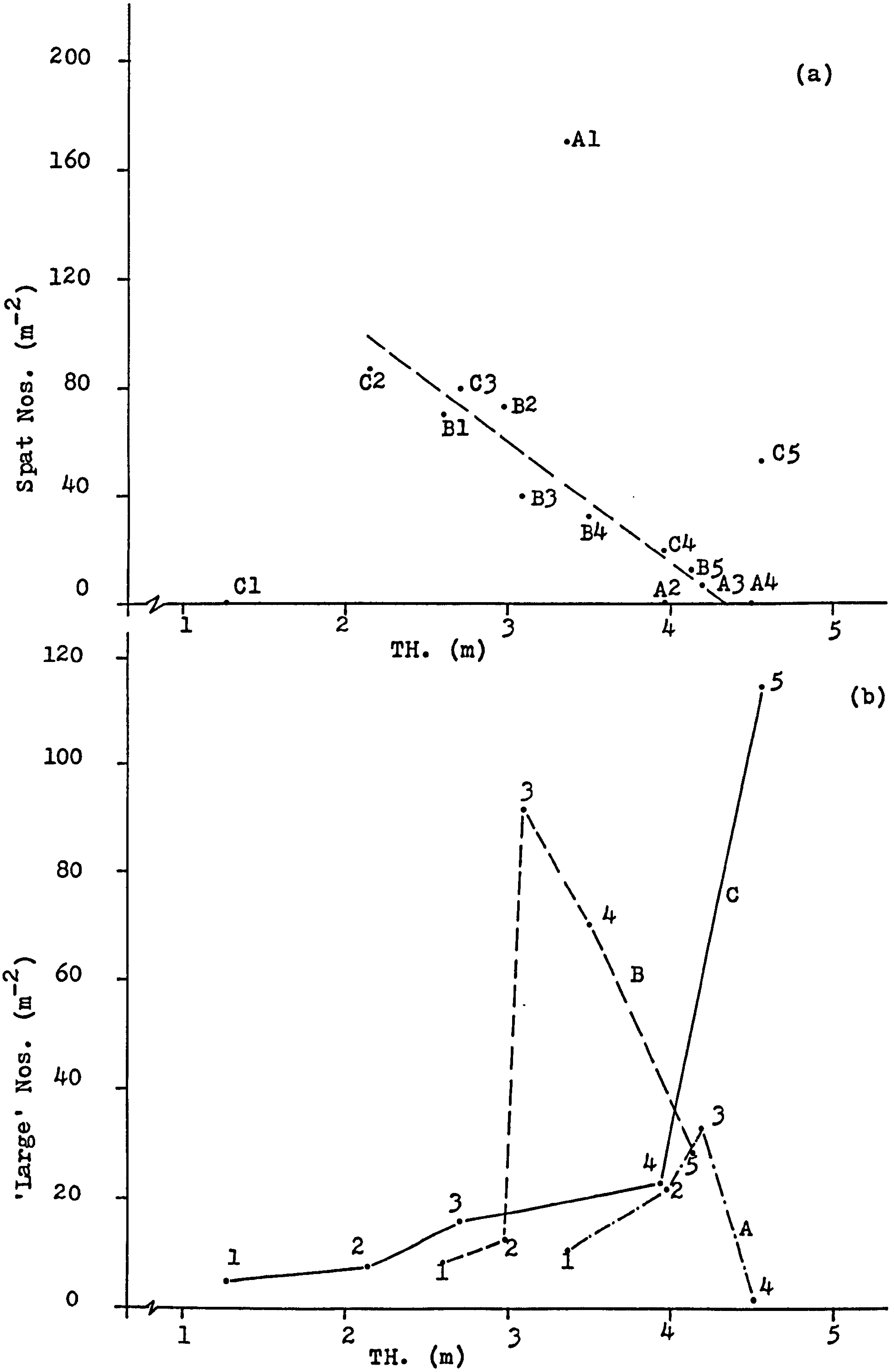
The variation in large and spat cockle densities was largely accounted for by the substrate and shore parameters, whereas the biomass variation was dependent upon the amount of detrital and phytoplankton material in the water and by the salinity. The variation in large and spat clam densities was mainly accounted for by the sediment %S. & C. and the Org. C. and CHO. levels in the water. The spat biomass was dependent upon the %S. & C. and the shore slope, whereas the variation in biomass of large clams appeared to be determined by shore slope, tidal height and water Org. C.

As possibly the most important variable for these bivalves was tidal height, the mean densities of large and spat cockles and clams were plotted against the tidal height of each station (Figs. 4.4a & b, 4.5a & b). Whilst the numbers of cockle spat generally decreased with an increase in tidal height (Fig. 4.4a), the opposite is seen for the large cockles (Fig. 4.4b). Certain stations were found to deviate from these patterns, e.g. A1 and C1 in the former figure and B3, B4 and A4 in the latter, again suggesting that the population dynamics of a species were the result of many interacting variables. The fine mud substrate at Station A1 contributed to the presence of high spat numbers whereas at C1 the dense mussel beds possibly resulted in a low spat settlement. However, as B2, a station also on a dense mussel bed, had high numbers of spat it is suggested that this was not the reason. As C1 was much lower it may be further suggested that tidal height played some part in spat settlement.

Table 4.6 a) *C. edule* and b) *M. arenaria* : Spatial Data Analysis - Multiple Regression Equations of 'Large' and Spat Mean Density and Biomass. 2) With Selected Environmental Variables :- TH., M.P.D., %S. & C., Slope, Salinity, Org. C., C.H.O. (Legend as Fig. 4.3.)

	Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
a) (i)	$S\bar{N}$.	All n.s. - 29.972	-	45.0%	%S. & C. (16.1%), Slope (14.4%).
(ii)	$S\bar{B}$	All n.s. + 17.513	-	56.0%	Org. C. (23.0%), C.H.O. (13.0%), Salinity (9.8%).
(iii)	$L\bar{N}$.	All n.s. + 304.83	-	61.7%	M.P.D. (28.3%), C.H.O. (17.7%).
(iv)	$L\bar{B}$	All n.s. + 14648.2	-	66.6%	Salinity (19.3%), C.H.O. (17.6%), Org. C. (14.9%).
b) (i)	$S\bar{N}$.	All n.s. - 701.36	-	83.7%	%S. & C. (58.2%), Org. C. (13.5%).
(ii)	$S\bar{B}$	All n.s. - 10.441	-	72.2%	%S. & C. (44.3%), Slope (11.1%), Org. C. (9.2%).
(iii)	$L\bar{N}$.	$0\overset{*}{.}004_{C.H.O.} + 25.610$	TH., Slope.	55.2%	C.H.O. (33.8%), %S. & C. (13.6%).
(iv)	$L\bar{B}$	All n.s. - 3720.2	-	53.4%	Slope (23.9%), TH. (11.4%), Org. C. (9.5%).

Figure 4.4 C. edule : The Relationships Between the Density of (a) Spat and (b) 'Large' Animals and Tidal Height (1975-76 Data). (Line in (a) Fitted by Eye.)

(a)
Spat Nos. (m^{-2})
200
160
120
80
40
0
A1
C2
C3
B2
B1
C5
B3
B4
C4
B5
A3
A4
A2
C1
1
2
3
4
5
TH. (m)
(b)
'Large' Nos. (m^{-2})
120
100
80
60
40
20
0
5
3
4
B
C
3
4
5
2
A
3
2
1
2
1
1
4
1
2
3
4
5
TH. (m)

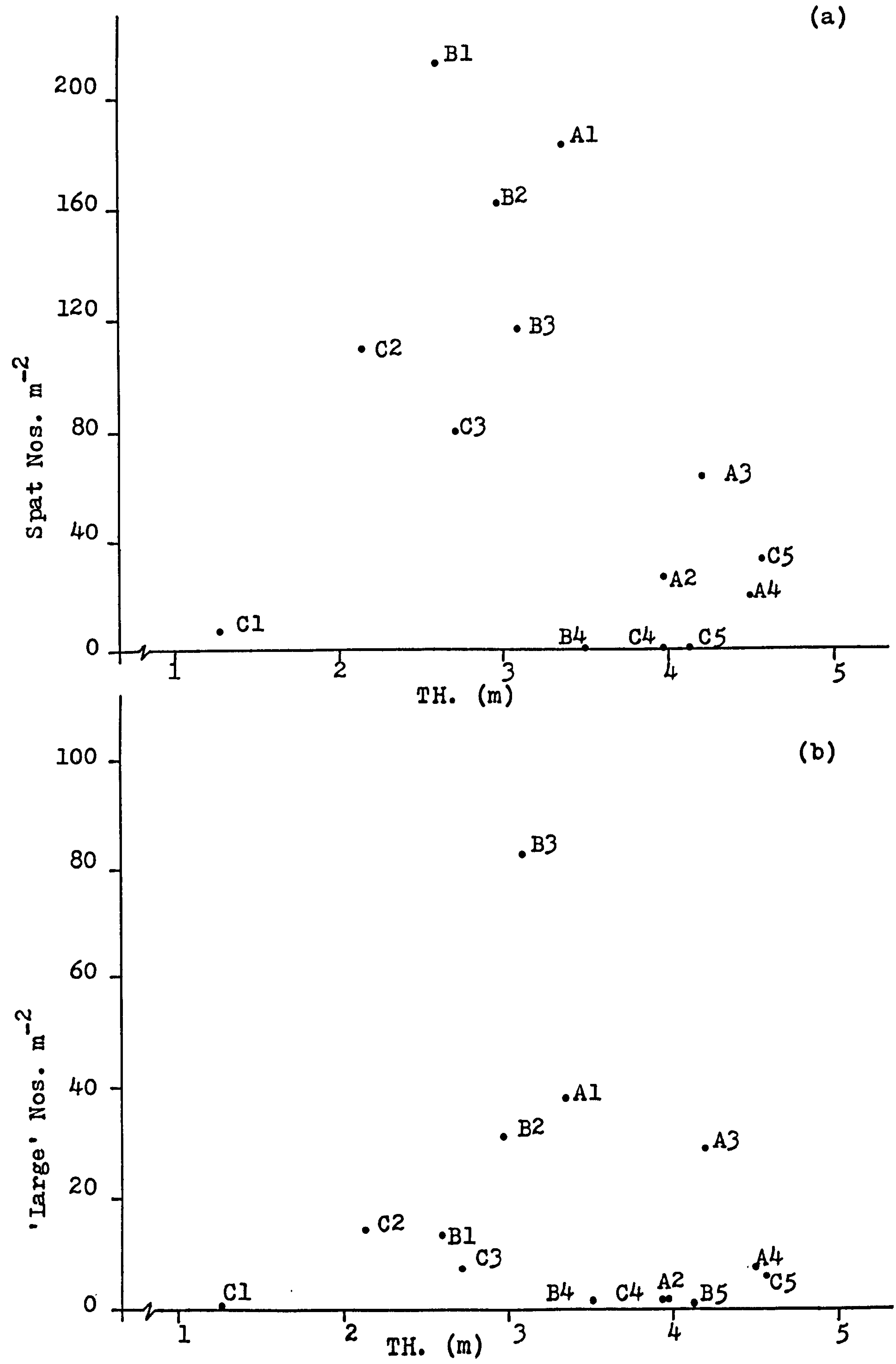


Figure 4.5 *M. arenaria* ; The Relationships Between the Density of (a) Spat and (b) 'Large' Animals and Tidal Height (1975-76 Data).

On a transect basis, A and B had highest values of large cockles between mid and high tide, e.g. B3, A3 and the density decreased with a further increase in tidal height. However, on C the density increased with tidal height with the upper limit of the transect supporting the greatest cockle density (Fig. 4.4b). There appears to be a high tidal level that in some areas will support high numbers of large cockles but in others very few, e.g. C5 and A4 respectively. This difference could have been attributable to local conditions such as the outflow of effluent near A4, differences in salinity or particle size or the abundance of food and/or silt and detritus in the water. The differences in water quality over these stations did not show major differences, although it is possible that the water over Transect A did contain a higher amount of suspended silt due to the soft sediments further downshore. Stations B3 and B4 showed elevated levels of large cockles which may have been the result of favourable substrates, tidal level, shore slope and/or food quantity.

The M. arenaria spat densities also showed an inverse linear relationship to tidal height (Fig. 4.5a) with C1 again being an exception. The relationship between adult M. arenaria and tidal height (Fig. 4.5b) suggests that the distribution has an optimum around mid tidal level where both immersion times and substrate types provide a suitable environment.

The relationships between clam and cockle spat density and particle size show that both decrease in a widely scattered curvilinear pattern with increasing particle size although in the case of the cockle spat this is a non-significant correlation (Fig. 4.6a & b). The analysis has shown however that spat density

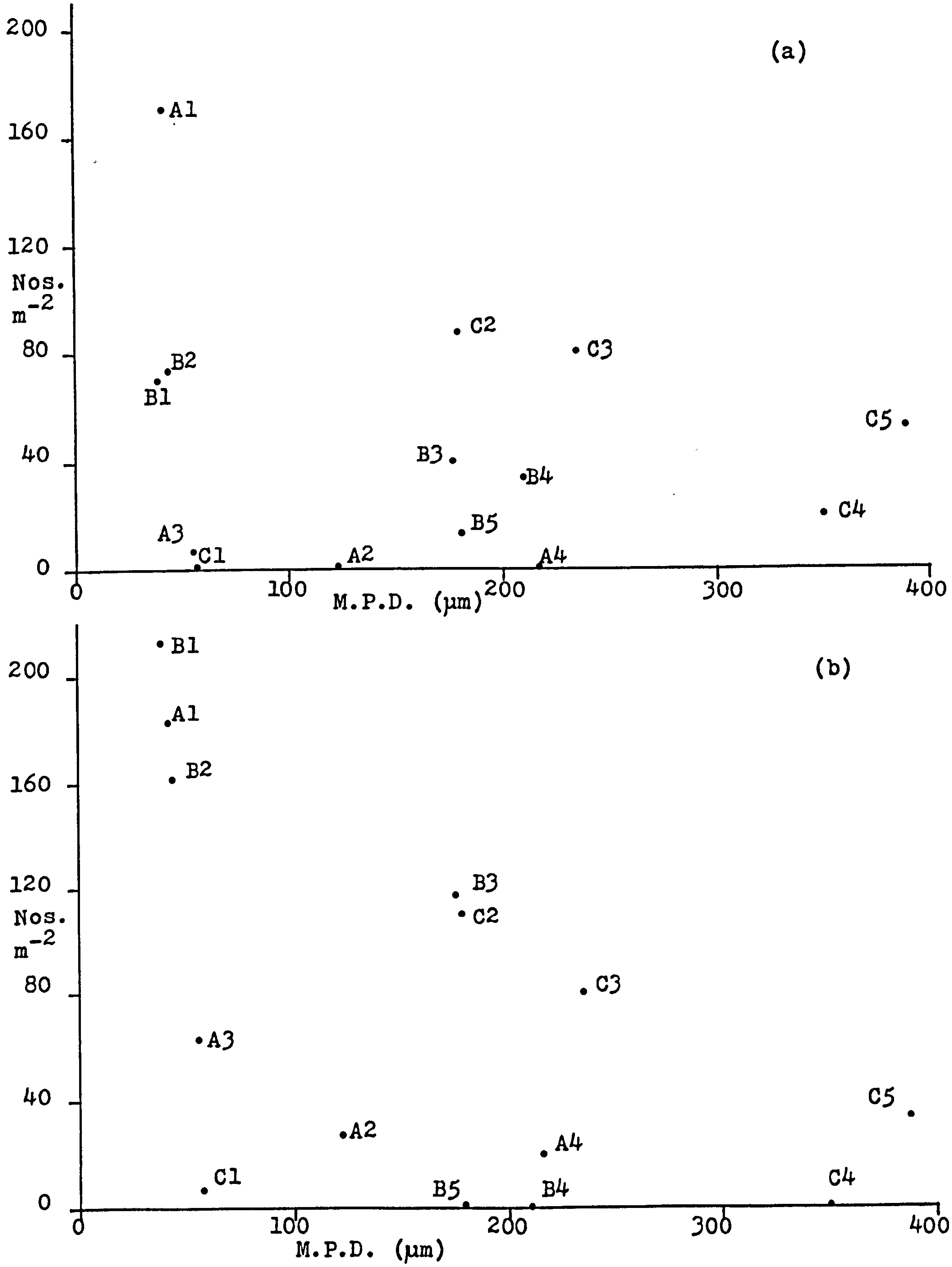


Figure 4.6 (a) C. edule and (b) M. arenaria : The Relationships Between Mean Spat Densities and Particle Size (1975-76 Data).

was related to particle size and %S. & C.

4.3.3. The Factors Affecting Spat Settlement and the Maintenance of the Main Populations, and Intercorrelations Between C. edule and M. arenaria Populations.

Highly positive intercorrelations were found between the densities and biomasses of cockle and clam spat, between clam spat and the main population and also between cockle spat and the main M. arenaria population (Fig. 4.7). The inter- and intra-specific correlations suggest that the M. arenaria and C. edule spat settled in similar soft mud, downshore areas, and that those areas were close to where the main M. arenaria population occurred in soft mud/fine sand on a shallow slope around the mid tidal level, but that the main cockle population was found at a higher level under different sediment and shore conditions. The diagram (Fig. 4.8a, b, c, d) demonstrates these relationships. Some stations which had low densities of large cockles had high spat densities and vice versa (Fig. 4.8a). There was however, a group of stations with a sparse population of any size. The figure (4.8b & c) shows the direct significant relationships between M. arenaria large and spat densities and between M. arenaria and C. edule spat densities, whereas there was no significant correlation between the numbers of large cockles and clams (Fig. 4.8d).

The diagramatic representation (Fig. 4.9) again demonstrates these relationships showing that although the cockle spat numbers decreased with distance along a transect, the numbers of large cockles increased. However, although the M. arenaria spat densities decreased with distance along a transect there were optimal numbers of large clams at various places along the

Figure 4.7 *C. edule* and *M. arenaria* : The Interrelationships Between the Mean Density and Flesh Biomass of 'Large' and Spat Animals. (*, **, *** Indicates Level of Significance on a Linear Basis.) (Legend as Fig. 4.3.)

Figure 4.9 (a) *C. edule* and (b) *M. arenaria* : The Change in Mean Density (Nos. m^{-2}) of 'Large' (Upper) and Spat (Lower) Animals With an Upshore Progression Along Each Transect.

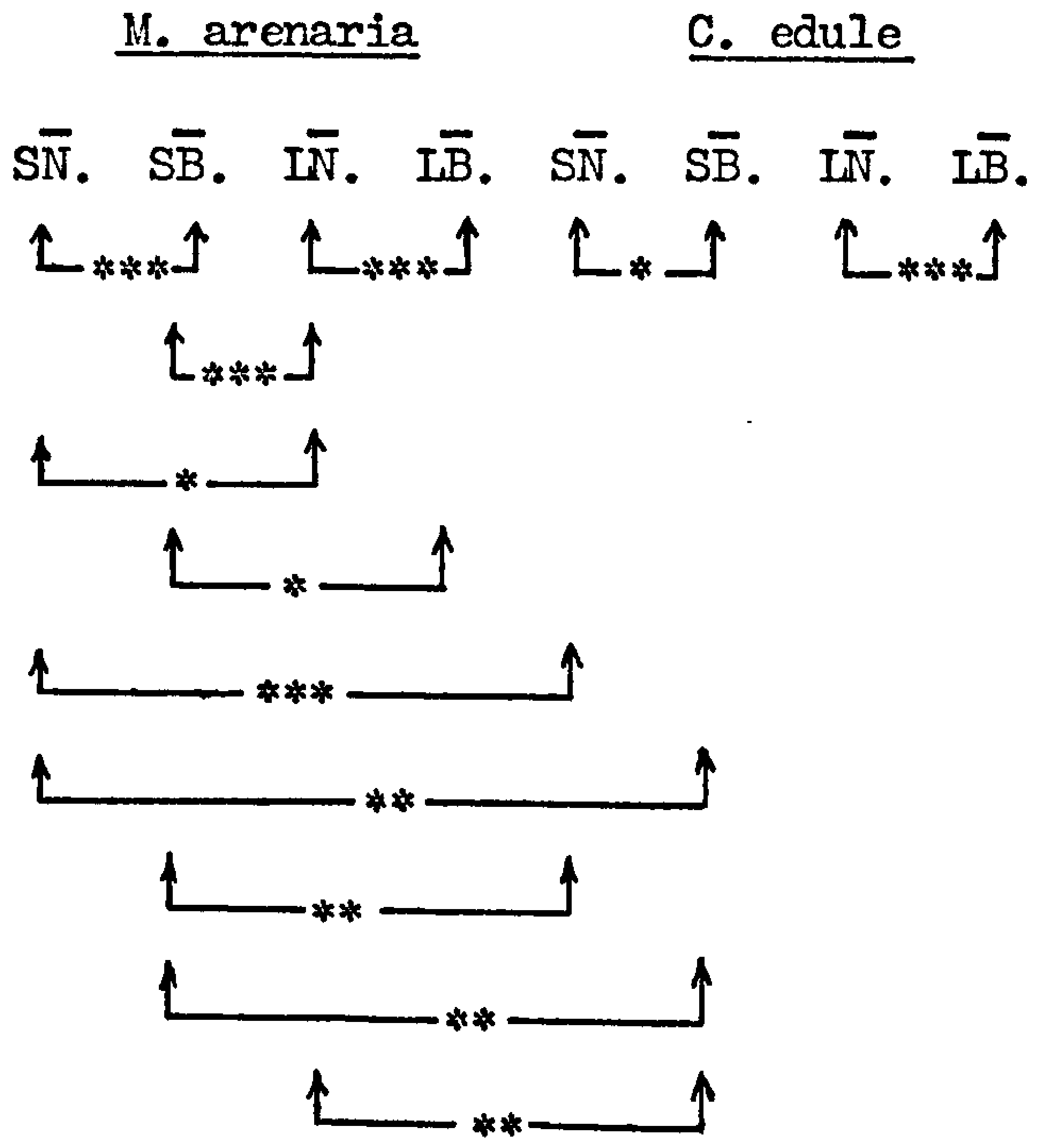


Figure 4.7

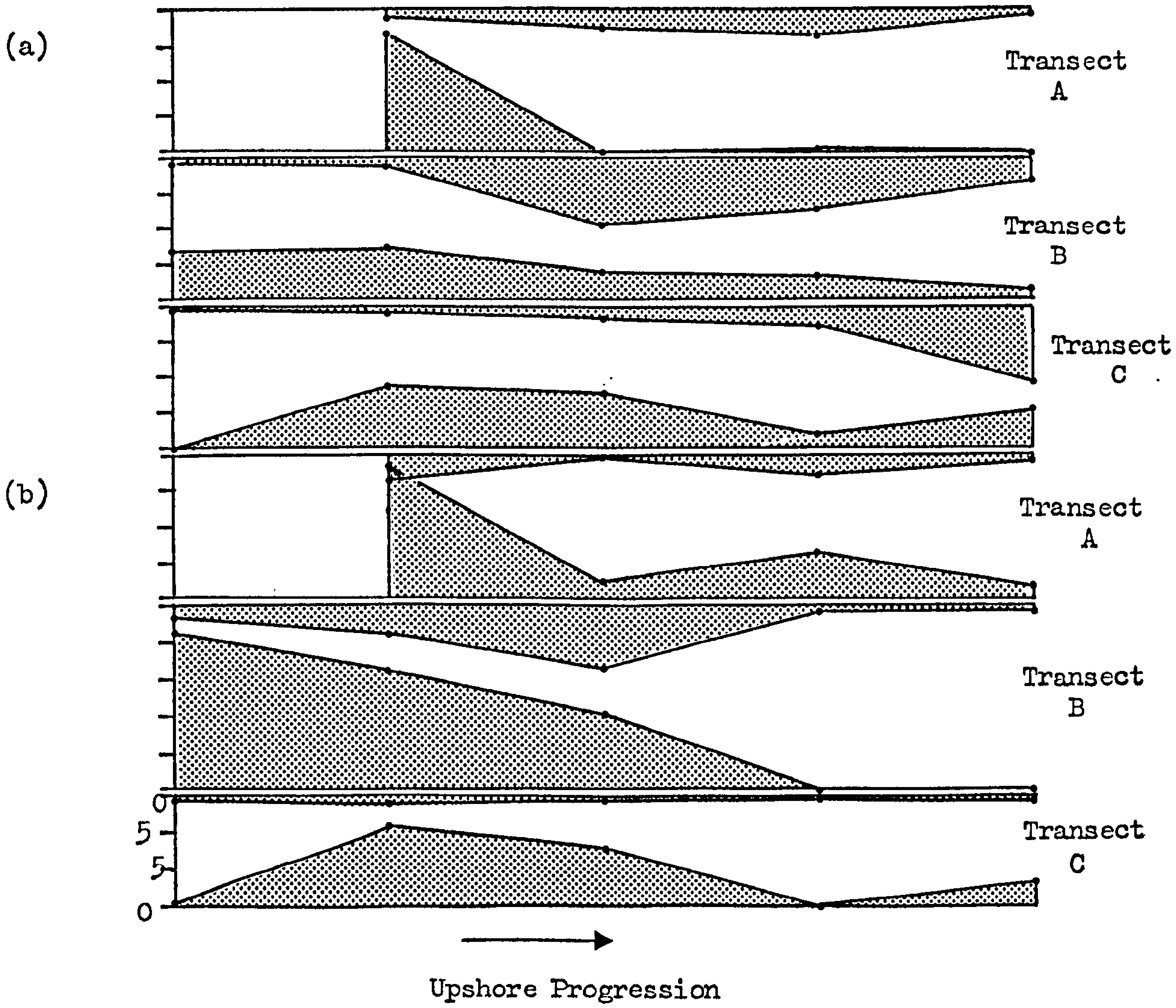


Figure 4.9

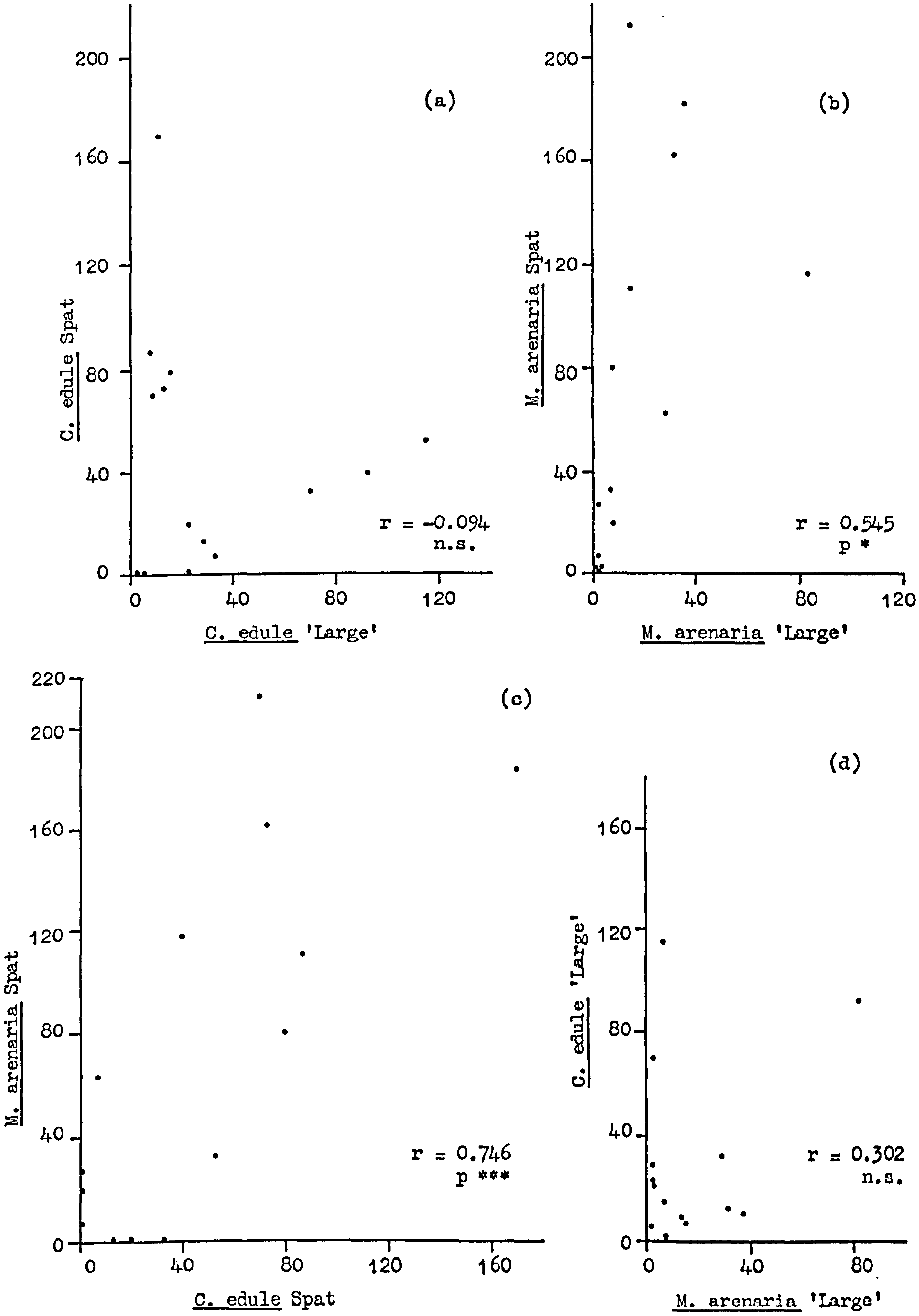


Figure 4.8 The Relationships Between the Spat and 'Large' Part (Nos. m^{-2}) of the C. edule and M. arenaria Populations. (1975-76 Data.)

transects.

The corresponding number and biomass data for large animals were incorporated into the multiple regressions for the numbers and biomass of C. edule or M. arenaria spat. Only in the equation for the M. arenaria spat biomass did the large M. arenaria biomass account for any large proportion (11%) of the variance of the dependent variable.

4.3.4. The Growth of C. edule and M. arenaria on an Areal, Station and Age-Cohort Basis.

4.3.4.1. The Size-frequency Histograms of the C. edule and M. arenaria Spat.

The large differences in the densities of large and spat individuals sampled dictated the use of separate size-frequency treatment for the two parts of the populations. The size-frequency analysis for the main part of the population is given below (Section 4.3.4.2.).

The histograms (Fig. 4.10a & b) demonstrates the presence of spat during the whole sampling period in lesser or greater quantities thus suggesting a limited gamete leakage during the months apart from the main spawning season. Even so, there were relatively well defined spawning seasons from July to September in both C. edule and M. arenaria. The end of the main settling period was less well-defined than the beginning; this was attributable to the low growth rate of those spat settling later in the season. The mean size of M. arenaria spat increased rapidly over the early part of the year but remained stationary over the winter months (Fig. 4.10b). This pattern reflected the seasonal growth curve shown by the older cohorts (see Section

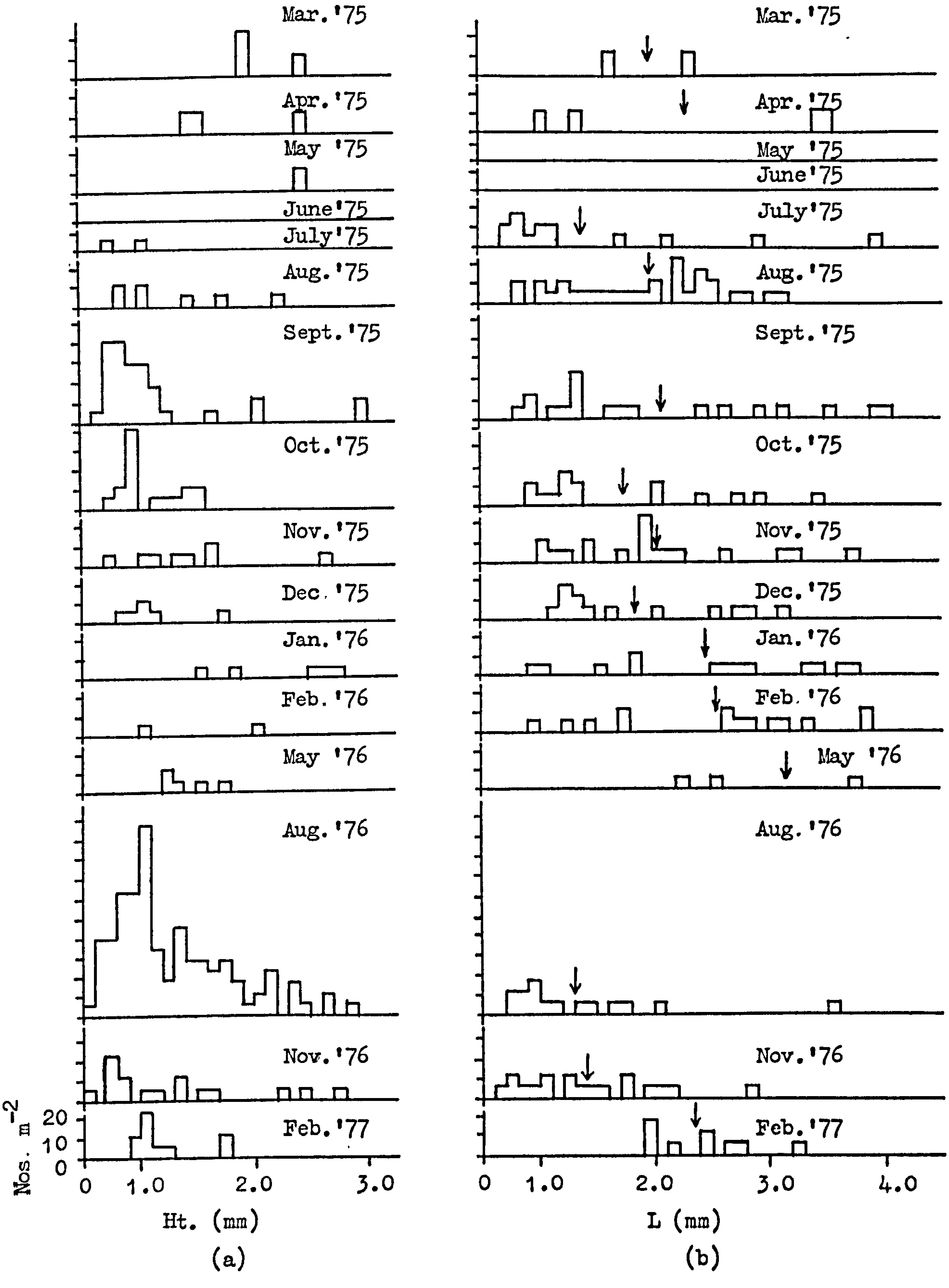


Figure 4.10 (a) C. edule and (b) M. arenaria : Size-frequency Histograms of Spat at Each Sampling Occasion. (Arrows on (b) Denote Mean Size.)

4.3.4.8.). The main settling period by M. arenaria was in July, after this the spat grew rapidly until they appeared in the large samples during August and September. There was possibly also a smaller settlement during the late summer months and it was these individuals which could not grow before the onset of winter and which therefore were not found in the large samples until the following spring (see Fig. 4.17).

The main cockle spatfall was during August to October and these cockles were found in the large samples from September onwards (Figs. 4.10a, 4.11) suggesting an initial period of rapid growth for the majority of the spat. However the spat growth rate then decreased overwinter. The Torry Bay population showed a much greater cockle spatfall during 1976 than 1975 and, although by November, 1976, the number had decreased by 80%, the number of 0+ group cockles overwintering 1976-77 was much greater than in the previous year. The spatfall of M. arenaria for each of the two years appeared similar but still in comparatively low numbers.

4.3.4.2. C. edule Main Population Size-frequency Analysis.

The size-frequency histograms (Fig. 4.11) show that the population was dominated by 0+, 1+ and 2+ group animals. As there are data from many stations and cohorts in the histograms then there is a correspondingly large overlap between cohorts. The small population size did not warrant a more detailed size-frequency analysis. However, some trends are still evident although the histograms were primarily studied in conjunction with the population growth rate calculated from the growth ring analysis (see Section 4.3.4.3.). The histograms for the period March to May 1975 include the 1+ and 2+ cohorts (i.e. 1974 and 1973 spat) within the range 3 to 12mm. The rapid growth of the

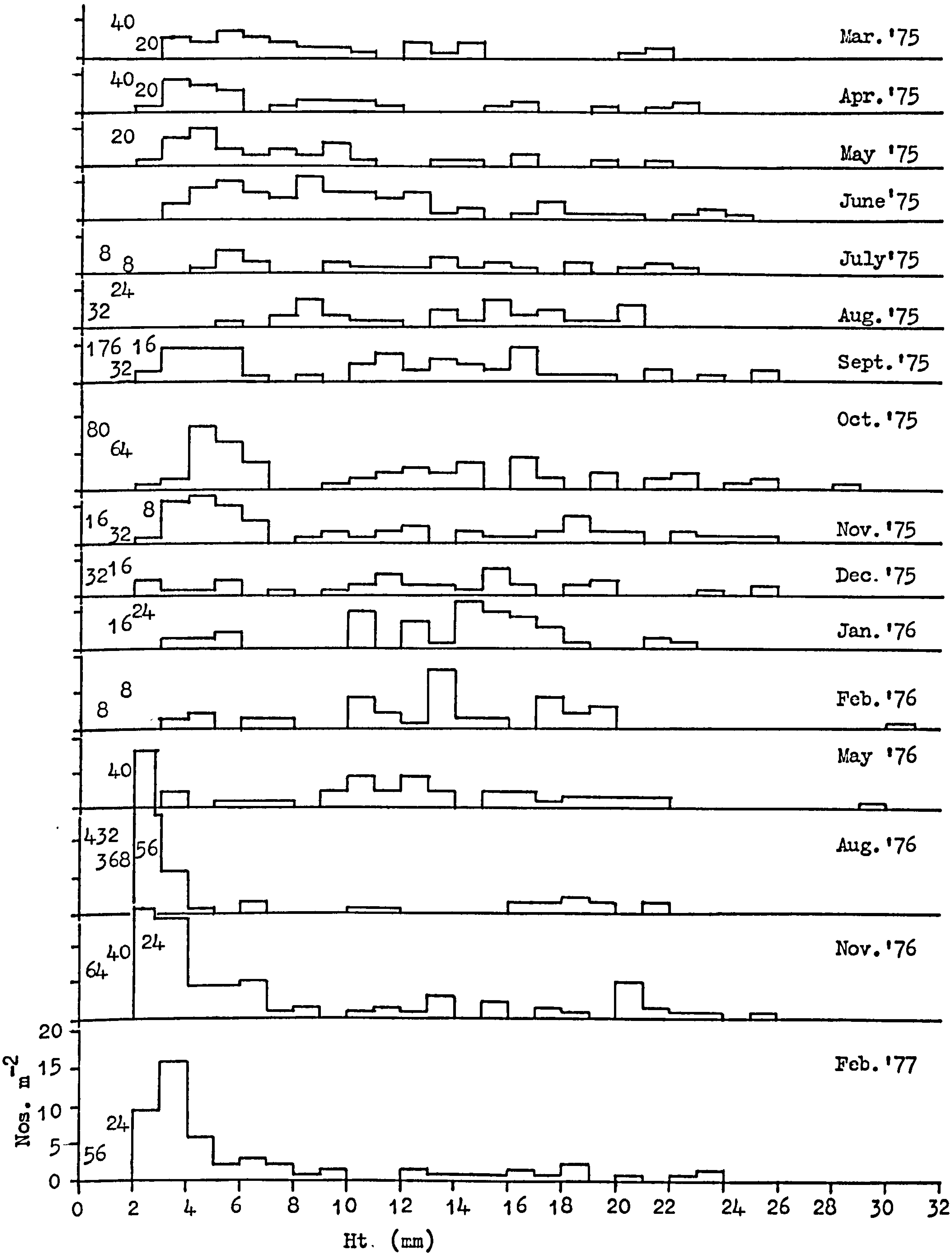


Figure 4.11 C. edule : Size-frequency Histograms of Animals in "Large" Samples. (Nos. Given = Density/m^2 of Spat.)

former and the slightly slower growth of the latter cohort results in both cohorts being within the 8 to 18mm range by the September with the years' spat (0+ cohort) then being present in the large samples. This latter cohort then remained less than 6mm in height until the following spring when the major part of its growth commenced. The 1976 spat were present in the large samples from August 1976 and again little growth occurred over the winter period.

The older cohorts can only be approximately identified with the use of the population growth curve (Fig. 4.12). The size-frequency histograms are therefore considered in greater detail below (Sections 4.3.4.3. and 4.3.4.4.).

4.3.4.3. The Growth Ring Analysis of C. edule on an Areal Basis.

Growth ring analysis was performed on individuals from each station and the station data then combined to give the areal growth rate as calculated by the back measurement of growth rings (Fig. 4.12), the areal growth rate therefore will show bias towards those stations which contributed the most animals towards its construction i.e. C5, B3, A3, B4 and C4. Rings formed during the eight year period ending February 1977 were used although occasionally older animals were found. It is apparent that the animals older than six years were approaching the asymptotic size, as growth intervals were small and there was increasing overlap between cohort sizes with age. The older an animal, therefore, the more difficult it was to identify the winter rings.

The cockle population growth curve shows the characteristic decreasing growth rate with increasing age; the population growth

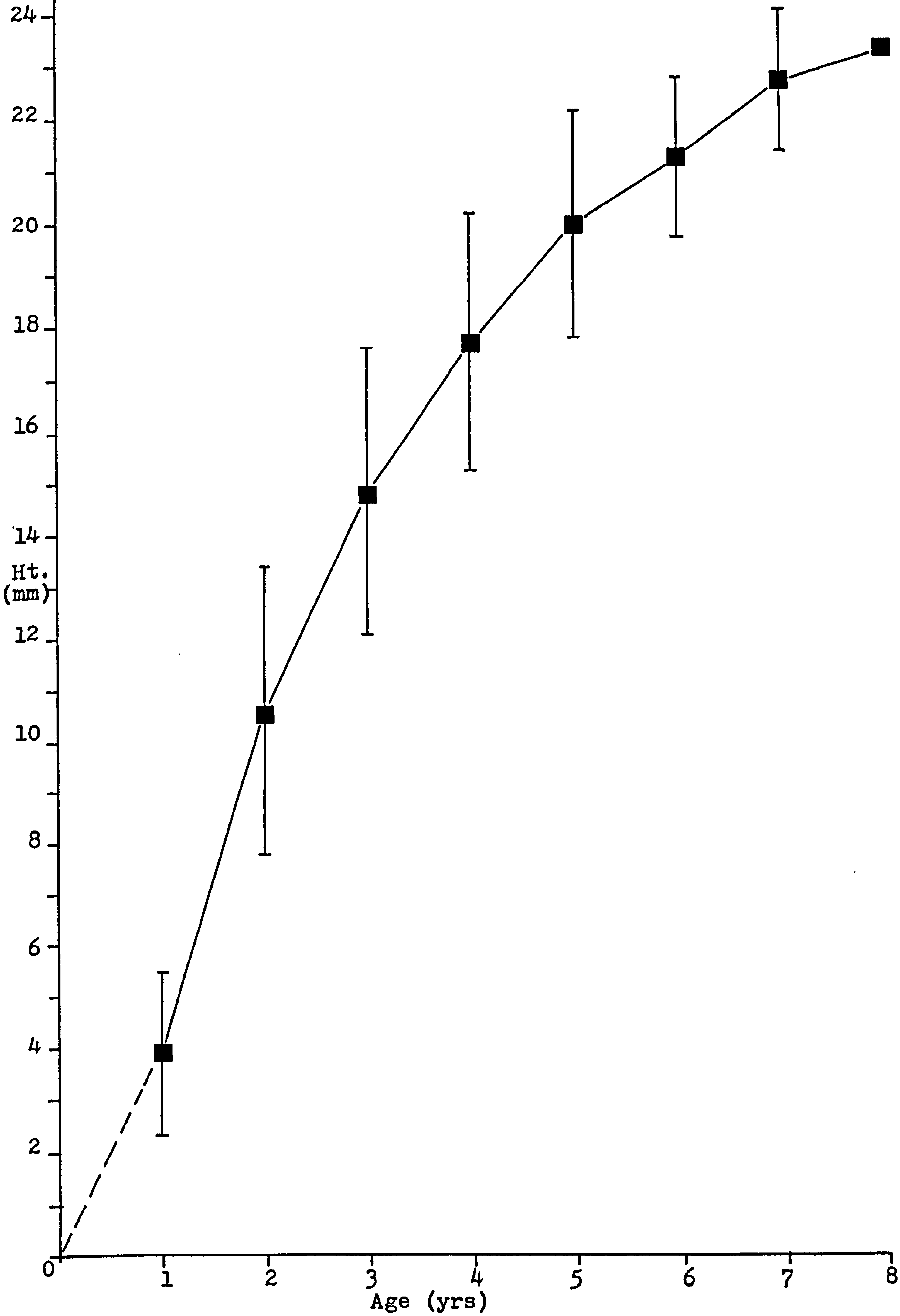


Figure 4.12 C. edule : The Mean Growth Curve For the Torry Bay Population (Mean ± 1 S.D. Given for Each Age).

rate could therefore be described by the Bertalanffy growth equation (Section 4.3.4.6.).

4.3.4.4. The Growth of C. edule Age Cohorts.

The size-frequency data was further interpreted using the population growth curve to delimit the sizes of the cohorts at each sampling period. The mean sizes and flesh weights of each cohort were then plotted for the sampling year 1975-76 (Figs. 4.13 a & b)(data given in Appendix 4.3). It is considered that the data for the following year would give comparable growth curves if plotted.

The 1+, 2+ and 3+ age cohorts showed the largest growth rates, as the change in size over the year, with the growth rates decreasing with increasing age. The major part of the annual growth of the cohorts occurred during the period April to September. The mean size of the spat however, appeared to increase little over the year and although the first spat which settled from July onwards would find favourable conditions for growth, the growth curve for this cohort was also affected by the spat settling later in the summer. The later spat would be unable to grow during the remainder of the year (Fig. 4.13a).

The sizes of each cohort at the beginning and the end of the year naturally correspond to the sizes per age shown on the growth curve (Fig. 4.12). However there is some indication of differences between years in that although the cockles in their first winter at the beginning or end of the year (1974 and 1975 spat respectively) were of a similar size, those in their second and third winters at the end of the year (1974 and 1973 cohorts respectively) were larger than those in their second or third

Figure 4.13 *C. edule* : The Annual Growth Rates of Each Cohort (a). Shell Height, (b) Flesh Dry Weight. (1975-76 Data.)

a 1975 Cohort
b 1974
c 1973
d 1972
e >1972

Inset : The Mean Annual Temperature Curves.

Fdw (mg)
1000
100
10
1.0
0.1
0.01
(b)
Mean Temp. °C
20
15
10
5
0
(a)
e
d
c
b
a
Ht. (mm)
28
24
20
16
12
8
4
0
M
A
M
J
J
A
S
O
N
D
J
F

winters at the beginning of the year (1973 and 1972 cohorts). The 1972 cohort entering their fourth winter 1975-76 were smaller than the >1972 cohort at the comparable time the previous year. However, as the latter cohort probably consisted of several year groups little importance can be attached to this difference. In addition, the cohort growth rate increased with an increase in temperature (Fig. 4.13a). Growth then ceased when the temperature started to decrease.

The changes in flesh weight over the year by the cohorts (Fig. 4.13b) show that the greatest change was by the spat in which the weight increased by nearly two orders of magnitude. The weight changes over the year for the other cohorts decreased proportionately with the increasing age and also the changes over the year reflect the emaciation by the animals from October to January. The net flesh weight change over the year between comparable cohorts was minimal.

4.3.4.5. The Growth Ring Analysis of C. edule per Station.

The mean sizes of each age cohort for each station from the back measurement of growth rings are given (Table 4.7 and Fig. 4.14). The station growth curves commence from the same place, i.e. the region of 3 - 4.5mm in height for the cockles at their first winter. There appears to be several groups of growth curve presented by the stations. Cockles at Stations A3 and C5 had a slightly slower growth rate after the second winter although after six winters the growth at these stations appeared to be declining less than at the other stations. The cockles at the majority of the stations, A2, B3, B5, C4, A1, B2, B4 and C3, all had similar growth rates up to the fourth winter. After this time the station growth rates decreased to a lesser or greater

Table 4.7 *C. edule* Growth Ring Data for Each Station (Mean Height ± S.E. mm and Number of Observations).

	Station	1			2			3			4			5		
Transect	Age Ring	$\bar{x}$	S.E.	N.	$\bar{x}$	S.E.	N.	$\bar{x}$	S.E.	N.	$\bar{x}$	S.E.	N.	$\bar{x}$	S.E.	N.
A	1	4.20	0.67	4	4.45	1.90	6	3.32	1.16	16						
	2	13.82	1.36	4	12.10	3.46	10	8.79	1.17	15	7.2	-	1			
	3	16.72	0.31	4	16.13	2.56	7	12.70	1.00	21	16.6	-	1			
	4	19.30	0.93	6	18.57	3.34	4	16.25	1.34	16	19.8	-	1			
	5	21.62	1.21	5	23.2	-	1	18.24	1.57	10	21.9	-	1			
	6	22.92	1.47	5				20.53	0.81	6	22.6	-	1			
	7	24.22	1.30	5				22.12	0.13	4						
	8	23.9	-	1				23.4	-	1						
	9	25.8	-	1				25.5	-	1						
	10							27.2	-	1						
B	1				3.80	1.51	4	4.67	1.63	67	3.86	1.73	44	3.02	1.26	25
	2				9.96	3.68	5	10.71	3.38	31	12.90	3.08	16	11.24	3.82	28
	3				17.30	3.53	2	15.70	2.96	25	17.15	2.71	15	16.01	2.82	18
	4				20.5	-	1	19.03	1.42	7	20.57	1.91	6	18.84	2.45	11
	5				22.6	-	1				23.40	0.85	4	20.45	2.37	6
	6				23.5	-	1				24.7	-	1	24.0	-	1
	7				23.8	-	1				25.7	-	1			
C	1				4.03	1.29	10	4.62	1.48	17	3.90	1.16	23	3.57	1.39	90
	2				5.45	2.76	2	10.27	3.94	6	11.17	1.85	18	10.04	2.14	87
	3				9.50	0.71	2	17.60	2.12	2	15.85	1.29	17	13.43	2.32	41
	4				15.45	0.21	2	19.65	1.77	2	18.53	1.52	10	16.00	2.44	15
	5							22.00	1.56	2	20.93	1.70	7	19.14	0.72	8
	6							24.45	0.92	2	21.97	1.84	4	20.72	0.51	4
	7							27.15	0.07	2	22.40	0.42	2	20.3	-	1
	8							28.25	0.35	2	23.20	-	1			
	9							29.60	0.14	2						
	10							30.2	-	1						

Figure 4.14 *C. edule* : The Growth Curves at Each Station Derived From the Growth-ring Analysis.

Observations For Each Curve:

A1 - 29
A2 - 27
A3 - 89
B2 - 15
B3 - 130
B4 - 87
B5 - 63
C3 - 33
C4 - 82
C5 - 245

C1, C2. A4, B1 - Insufficient Data to Produce Growth Curve.


27
24
21
18
15
12
9
6
3
0
Ht.
(mm)
0
1
2
3
4
5
6
7
8
C3
B4
A1
B2
A3
C4
C5
B5
B3
A2
B3
C3
A2
A1
C4
B2
B4
C5
A3
B5

extent. Stations B4 and C3 had the greatest growth rates with the latter stations' cockles apparently growing linearly after the fifth winter. However, this curve was produced by using very few animals and may be subject to large errors. As the curve for Station B4, which had a similarly clean sand, mid-to-uppershore environment to Station C3, was based upon a large number of measurements, it is considered to be a reliable representation of growth.

The standard deviations attached to the mean cohort sizes were in most cases large (Table 4.7) such that overlapping of the station cockle growth curves would be evident if confidence limits were attached to the curves.

4.3.4.6. C. edule Growth Patterns - The Ford-Walford Analysis on Both an Areal and Station Basis.

The Ford-Walford analysis of the whole cockle population further demonstrates the fact that the growth fits the Bertalanffy equation. However, when the sizes at successive ages were plotted the first point was found not to lie on the straight line given by the other points (Fig. 4.15(i), line b) such that the significance of the Ford-Walford regression equation was increased upon the ommission of the first point (line c). This is taken as an indication of sigmoid growth and erroneous Bertalanffy parameters would be obtained if the data for the cohort height at time zero and one were included. The regression line (c) was therefore used as being the more accurate Ford-Walford plot. The parameters of the Bertalanffy equation obtained from this plot were $K = 0.373$ and $H_\infty = 24.742$. When the second stage Ford-Walford plot was constructed (Fig. 4.15(ii)) then a value of $t_0 = 0.614$ was calculated. The slope of the second plot was

Figure 4.15 C. edule : Mean Growth Rate for Torry Bay - Ford-Walford Analysis Stages 1 & 2.

(i) Stage 1

(a) 45° Intercept

(b) $H_{t+1} = 0.797 \pm 0.050 H_t + 5.717$

(c) $H_{t+1} = 0.688 \pm 0.015 H_t + 7.708$

(with first point excluded)

$K = 0.373 \quad H_\infty = 24.74\text{mm}$

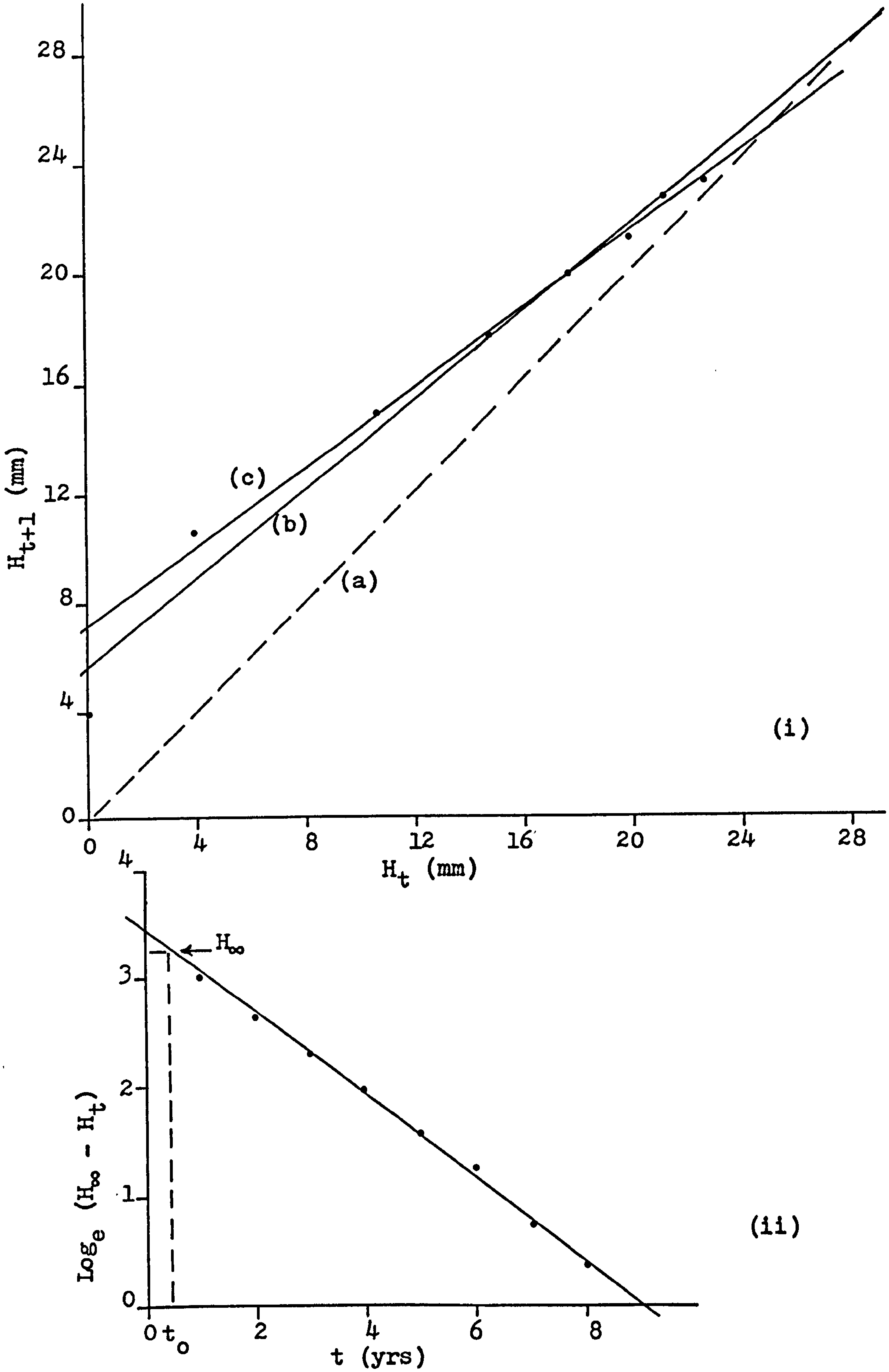
(ii) Stage 2

$\text{Log}_e (H_\infty - H_t) = 3.442 - 0.381 \pm 0.008 t$

$t_0 = 0.614$

Bertalanffy Equation :-

$H_t = 24.74 (1 - e^{-0.373(t - 0.614)})$


28
24
20
16
12
8
4
0
H_{t+1} (mm)
(c)
(b)
(a)
(i)
0
4
8
12
16
20
24
28
H_t (mm)
4
3
2
1
0
H_∞
$\log_e (H_\infty - H_t)$
(ii)
0
t_o
2
4
6
8
t (yrs)

0.3806 thus providing a check on the K-value obtained above.

The population Bertalanffy equation was therefore estimated as :-

$$H_t = 24.742\ (1 - e^{-0.373(t\ -\ 0.614)})$$

The maximum theoretical height of cockles appears to be slightly less than the maximum size encountered in the population. However, the growth rates at some of the stations produced higher H_∞ than calculated for the whole population. It must be emphasised therefore that the equation produced above is the result of the combined station data and will again show bias towards the stations that contributed the greatest number of growth ring determinations.

The Bertalanffy equations for each of the stations were calculated (Tables 4.8, 4.9a) together with the sizes of cockles at ages t = 1, 2, 4 and 6 years.

In order to determine which factors accounted for the differences in the growth rates, the values of the heights at each age and of the parameter K for each station were incorporated into Pearson correlation and multiple regression analyses against selected environmental factors and population parameters. The latter were included to ascertain the effects of population density on growth.

The significant relationships (Fig. 4.9b) show that the size at the greater ages decreased with an increase in tidal height; the first year animals grew better in areas of high silt and clay content, a low shore slope and a higher interstitial salinity. These factors usually occurred together at the low-shore areas. The young cockles also grew faster in areas with a low biomass of

Table 4.8 <u>C. edule:</u> Regression Equations of Stages 1 & 2 Ford-Walford Growth Analysis.

	Stage 1 : $H_{t+1}(mm) = b \pm S.E.H_t(mm) + a$								Stage 2: $Log_e(H_\infty - H_t) = b \pm S.E.t(yrs) + a$						
Station	b	S.E.	a	n	p	r	K	H_∞	b	S.E.	a	n	p	r	t_o
A1	0.5606	0.0695	10.5564	6	**	0.971	0.5787	24.025	-0.5487	0.0364	3.5583	6	***	-0.991	0.691
A2	0.5508	0.0204	9.6016	3	*	0.999	0.5964	21.375	-0.5967	0.0074	3.4275	4	***	-1.000	0.612
A3	0.8239	0.0252	5.6045	9	***	0.997	0.1937	31.826	-0.1886	0.0064	3.5368	10	***	-0.995	0.406
A4	0.4113	0.0383	13.4902	4	**	0.991	0.8884	22.915	-0.9648	0.0523	3.8132	5	***	-0.996	0.706
B1					Insufficient Data										
B2	0.6634	0.0697	8.8128	6	***	0.979	0.4104	26.182	-0.4009	0.0294	3.4531	7	***	-0.987	0.469
B3	0.7570	0.0446	7.3027	3	*	0.998	0.2784	30.052	-0.2800	0.0044	3.5150	4	***	-1.000	0.400
B4	0.6306	0.0345	9.9561	6	***	0.994	0.4611	26.952	-0.4792	0.0142	3.6630	7	***	-0.998	0.770
B5	0.5836	0.0026	9.4693	4	***	1.000	0.5385	22.741	-0.5389	0.0012	3.5209	5	***	-1.000	0.736
C1					Insufficient Data										
C2	1.7490	0.2850	-0.9323	3	n.s.	0.987		Inaccurate, insufficient Data							
C3	0.7679	0.0464	7.5772	9	***	0.987	0.2641	32.646	-0.2721	0.0076	3.6347	10	***	-0.997	0.547
C4	0.6391	0.0170	8.6738	7	***	0.998	0.4477	24.034	-0.4442	0.0129	3.4400	8	***	-0.997	0.586
C5	0.7123	0.0616	7.0108	5	**	0.989	0.3393	24.368	-0.3429	0.0150	3.3935	6	***	-0.996	0.584
Total	0.6884	0.0152	8.2836	7	***	0.999	0.3734	26.584	-0.3806	0.0084	3.4421	8	***	-0.998	0.614

Where K, H_∞, t_o are the derived Bertalanffy parameters (see text).

Table 4.9 C. edule: The Growth at Each Station.

(a) Bertalanffy Equations:

Station		Height (mm) at t years: t = 1	t = 2	t = 4	t = 6
A1	$H_t = 24.025 (1 - e^{-0.5787(t - 0.691)})$	3.934	12.761	20.484	22.912
A2	$H_t = 21.375 (1 - e^{-0.5964(t - 0.612)})$	4.416	12.034	18.541	20.515
A3	$H_t = 31.826 (1 - e^{-0.1937(t - 0.406)})$	3.459	8.454	15.961	21.056
A4*	$H_t = 22.915 (1 - e^{-0.8884(t - 0.706)})$	5.267	15.656	21.687	22.707
B1	Insufficient Data				
B2	$H_t = 26.182 (1 - e^{-0.4104(t - 0.469)})$	5.127	12.261	20.035	23.479
B3	$H_t = 30.052 (1 - e^{-0.2784(t - 0.400)})$	4.623	10.802	19.021	23.731
B4	$H_t = 26.952 (1 - e^{-0.4611(t - 0.770)})$	2.712	11.666	20.874	24.435
B5	$H_t = 22.741 (1 - e^{-0.5385(t - 0.736)})$	3.014	11.228	18.819	21.405
C1	Insufficient Data				
C2	" "				
C3	$H_t = 32.646 (1 - e^{-0.2641(t - 0.547)})$	3.681	10.404	19.531	24.912
C4	$H_t = 24.034 (1 - e^{-0.4477(t - 0.586)})$	4.066	11.273	18.822	21.095
C5	$H_t = 24.368 (1 - e^{-0.3393(t - 0.584)})$	3.208	9.296	16.722	20.489

(A4* excluded from spatial analysis as equation derived from one animal.)

(b) A Correlation Matrix: Height (mm) at 1,2,4 and 6 years and the K-values with the Spatial Environmental Data and the Mean Biomass and Abundance of Spat and 'Large' Parts of the C. edule Population.

t = 1	t = 2	t = 4	t = 6	K	
-n.s.	-n.s.	- *	- ***	+n.s.	T.H.
-n.s.	-n.s.	-n.s.	-n.s.	-n.s.	M.P.D.
+ *	+n.s.	+n.s.	+n.s.	+n.s.	%S. & C.
- *	-n.s.	-n.s.	-n.s.	-n.s.	Shore Slope
+ *	+n.s.	+n.s.	+n.s.	-n.s.	Int. Salinity
+n.s.	-n.s.	-n.s.	-n.s.	-n.s.	Water Partic. Org. C.
+n.s.	+n.s.	+n.s.	+n.s.	-n.s.	" " CHO.
+n.s.	+n.s.	+n.s.	+n.s.	+n.s.	Spat mean nos.
+n.s.	+n.s.	+n.s.	+n.s.	-n.s.	Spat mean biomass
-n.s.	-n.s.	-n.s.	-n.s.	-n.s.	'Large' mean nos.
- *	-n.s.	+n.s.	+n.s.	-n.s.	'Large' mean biomass

Direction and level of significance given for each correlation.
See text for further explanation of variable abbreviations.

large cockles.

The multiple regression analysis (Table 4.10) showed that the size of first and second year cockles was influenced mainly by the absence of adult cockles, the shore slope and the salinity. The tidal height and the levels of water Org. C. and CHO. were excluded from the regressions but sediment M.P.D. and %S. & C. did have an effect as well as the presence of small cockles. The young cockles therefore grew best in the area in which they were found in greatest abundance i.e. away from the main population of large cockles.

The size of the older cockles, aged 4 and 6 years, however, was influenced to a high degree by tidal height and, to a lesser extent, by the biomass of large cockles. These ages reached the larger sizes at areas around the mid tidal level, areas which did not support the greatest biomasses and numbers of large cockles.

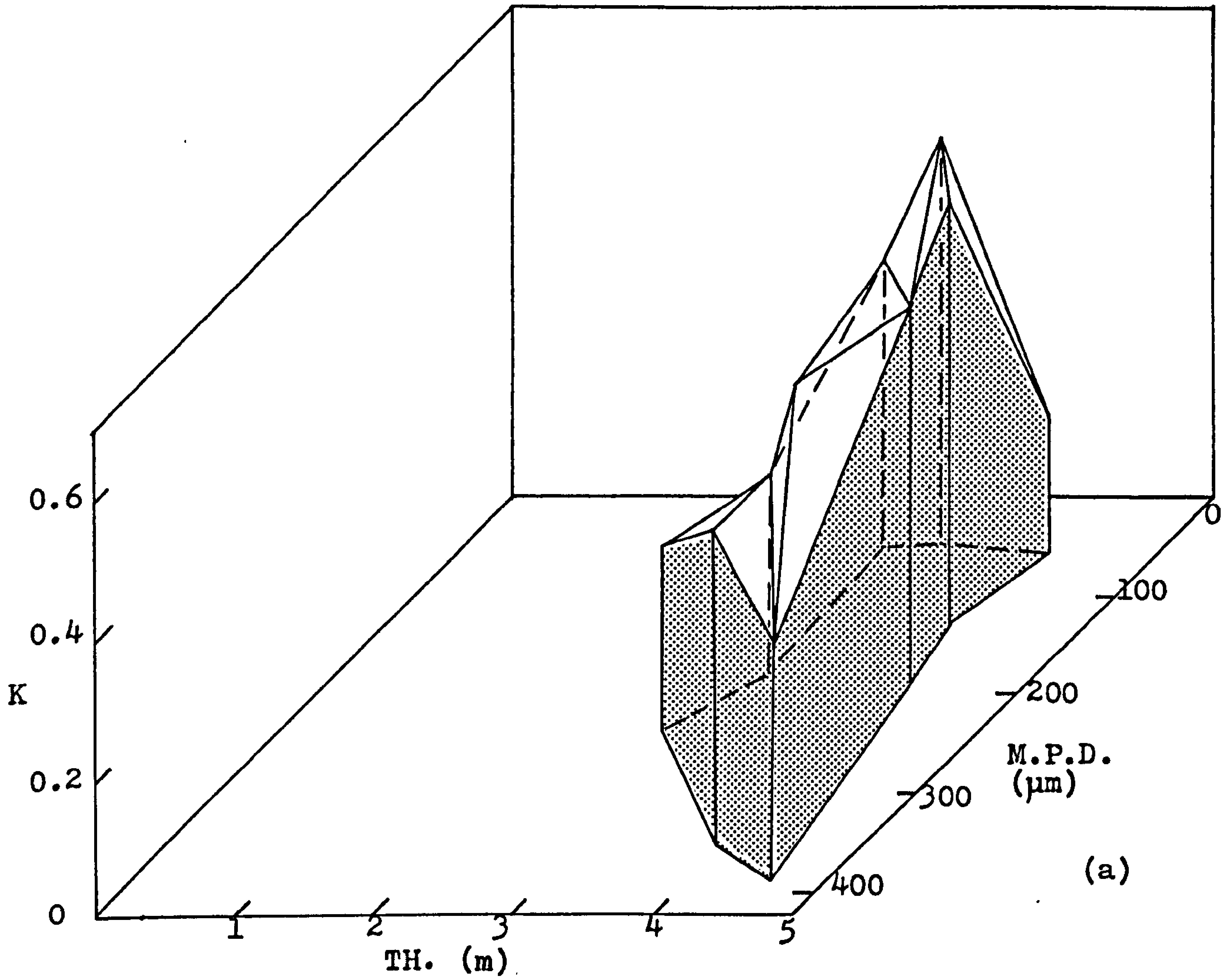
In the multiple regressions, nearly all of the variance in the dependent variables t = 1, 2, 4 and 6 years was accounted for by the independent variables. In the regression where K was the dependent variable, only 50.7% of its variance was accountable to the independent variables. The most important variables were the density of large cockles and the salinity but as such a small proportion of the variation was accounted for then few conclusions can be drawn from the regression.

The three-dimensional diagrams (Fig. 4.16) reflect some of the above trends and show that the K-values were highest at an area from the mid tidal level to the high-water neap tidal level and in the finer sediments (Fig. 4.16a). However, the maximum theoretical size, H_∞, occurred both in the lower-shore areas and,

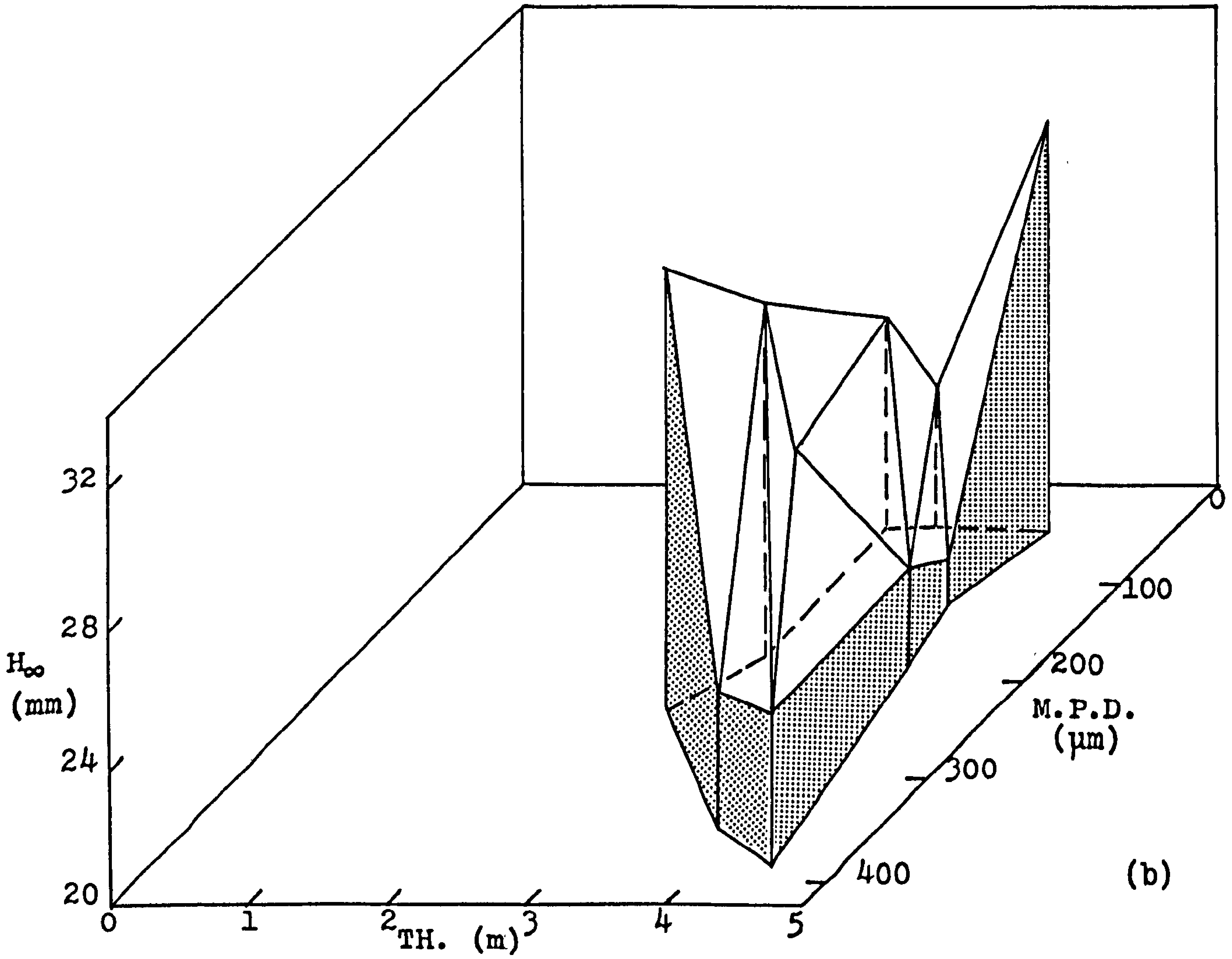
Table 4.10 *C. edule* : Spatial Data Analysis : Multiple Regression Analysis of Growth Variables with Environmental and Population Variables :- TH., M.P.D., %S. & C., Shore Slope, Interstitial Salinity, Suspended Particulate Org. C. and C.H.O. and Spat and 'Large' Animal Density and Biomass. (Legend as Fig. 4.9b.)

Dependent Variable	Significant Equation	Excl. Variables	Total Variance Accounted For	Main Variables
$H_t = 1$	All n.s. - 4.702	TH., Org. C., C.H.O.	96.9%	$\overline{LB}$ (41.5%), Slope (29.2%), Salinity (18.1%).
$H_t = 2$	$\overset{***}{0.158}_{\overline{LN}.} + \overset{***}{0.001}_{C.H.O.} + \overset{***}{0.093}_{\overline{SN}.} - \overset{***}{0.950}_{\overline{SB}} - \overset{***}{0.009}_{Org.\ C.} - \overset{**}{0.008}_{\overline{LB}} - \overset{*}{0.880}_{Salinity} + 100.316$	M.P.D., %S. & C., Slope.	99.5%	Salinity (29.6%), $\overline{LN}$. (19.9%), C.H.O. (17.6%), $\overline{SN}$. (14.9%).
$H_t = 4$	All n.s. + 18.450	M.P.D., Slope, Salinity.	92.7%	TH. (49.2%), $\overline{LB}$ (13.4%).
$H_t = 6$	$96.475 - \overset{**}{6.178}_{TH.}$	$\overline{SN}$., $\overline{SB}$, $\overline{LN}$.	99.7%	TH. (80.8%), $\overline{LB}$ (15.5%).
K	All n.s. + 4.609	TH., %S. & C., C.H.O.	50.7%	$\overline{LN}$. (12.0%), Salinity (11.7%).

Figure 4.16 C. edule : Spatial Analysis :- Diagrammatic Representation of Bertalanffy Parameters (a) K and (b) H_∞ with Tidal Height and Particle Size.


0.6
0.4
K
0.2
0
1
2
3
4
5
TH. (m)
0
100
200
300
400
M.P.D.
(µm)

(a)


32
28
H_∞
(mm)
24
20
0
1
2
3
4
5
TH. (m)
0
100
200
300
400
M.P.D.
(µm)

(b)

to a lesser extent, in the areas of fine sediment.

4.3.4.7. M. arenaria Main Population Size-frequency Analysis.

The low numbers of M. arenaria resulted in the size-frequency histograms being constructed from animals retained in the large samples of all stations (Fig. 4.17). Any variation in growth between stations is therefore masked by this treatment and, although the cohort distributions are visible to a lesser or greater extent, some variability between months is attributable to the sampling of low numbers. The cohort sizes were separated by eye as again the low numbers did not warrant more elaborate treatment of the polymodal frequency distributions. The mean sizes and their standard deviations of the cohorts are given in Appendix 4.6 and considered in Section 4.3.4.8.

The histograms show that usually only the first three age cohorts were sampled as the older animals were burrowed too deeply to be sampled. As there was no growth ring analysis to support the size-frequency analysis then the modal separation of the histograms was performed with a knowledge of the previous and successive months data. This was considered to be as accurate as possible as the cohorts were discrete; however, the analysis would have been easier had a larger population ~~have~~ existed.

The 0+ and 1+ age cohorts were predominant in the population and their annual growth patterns were determined (Fig. 4.18). Spat settlement was evident from June onwards although the 0+ cohort did not markedly grow until the following April when, as the 1+ cohort, a rapid period of growth occurred. These growth trends are further considered below.

Figure 4.17 M. arenaria : The Size-frequency Histograms for 'Large' Animals (>3mm Length). Number of Animals in Each Sample Also Given. The Ordinate For Each Histogram is as Oct.'75 Where the Percentage in Each Size Class is Given.


Mar.'75
(9)
Apr.'75
(19)
May '75
(23)
June '75
(48)
July '75
(19)
Aug.'75
(11)
Sept.'75
(29)
Oct.'75
(27)
30
20
10
0
0
10
20
30
Length (mm)
Nov.'75
(32)
Dec.'75
(22)
Jan.'76
(24)
Feb.'76
(19)
May '76
(15)
Aug.'76
(5)
Nov.'76
(11)
Feb.'77
(3)
0
10
20
30
40
Length (mm)

Figure 4.18 *M. arenaria* : The Annual Growth Rate of Each Cohort Over the Sampling Period.

The Curve of Mean Temperature (Mean of Air and Estuarine Water Temperatures) is Also Given (———■——).

Mean Temperature °C
20
15
10
5
0
F
1977
1976
N
A
1976
M
F
J
D
N
O
S
A
J
J
1975
M
A
M
1974
1975
1973
37.6
32
28
24
20
16
12
8
4
0
Length (mm)

4.3.4.8. The Growth of M. arenaria Cohorts.

Growth was greatest in the period from April to October in the cohorts older than nine months (1+ cohort and older)(Fig.4.18). The mean length of the 0+ group increased slightly over the period from settlement until the following spring but then increased from being 3mm at the first winter to approximately 20mm by the second winter. The growth in each cohort was reduced over the winter period and, although the growth curves contain variability attributable to the low numbers sampled and the depth of burrowing, it is considered that the animals upto 3+ exhibited the early part of a sigmoid growth curve and that growth in the population was linear after the very early part of the life span (Fig. 4.19). As with C. edule, the growth of M. arenaria increased with an increase in temperature (Fig. 4.18). However the growth continued shortly after the maximum temperature had been reached when the temperature started to decline. Growth then ceased after a further decline in temperature.

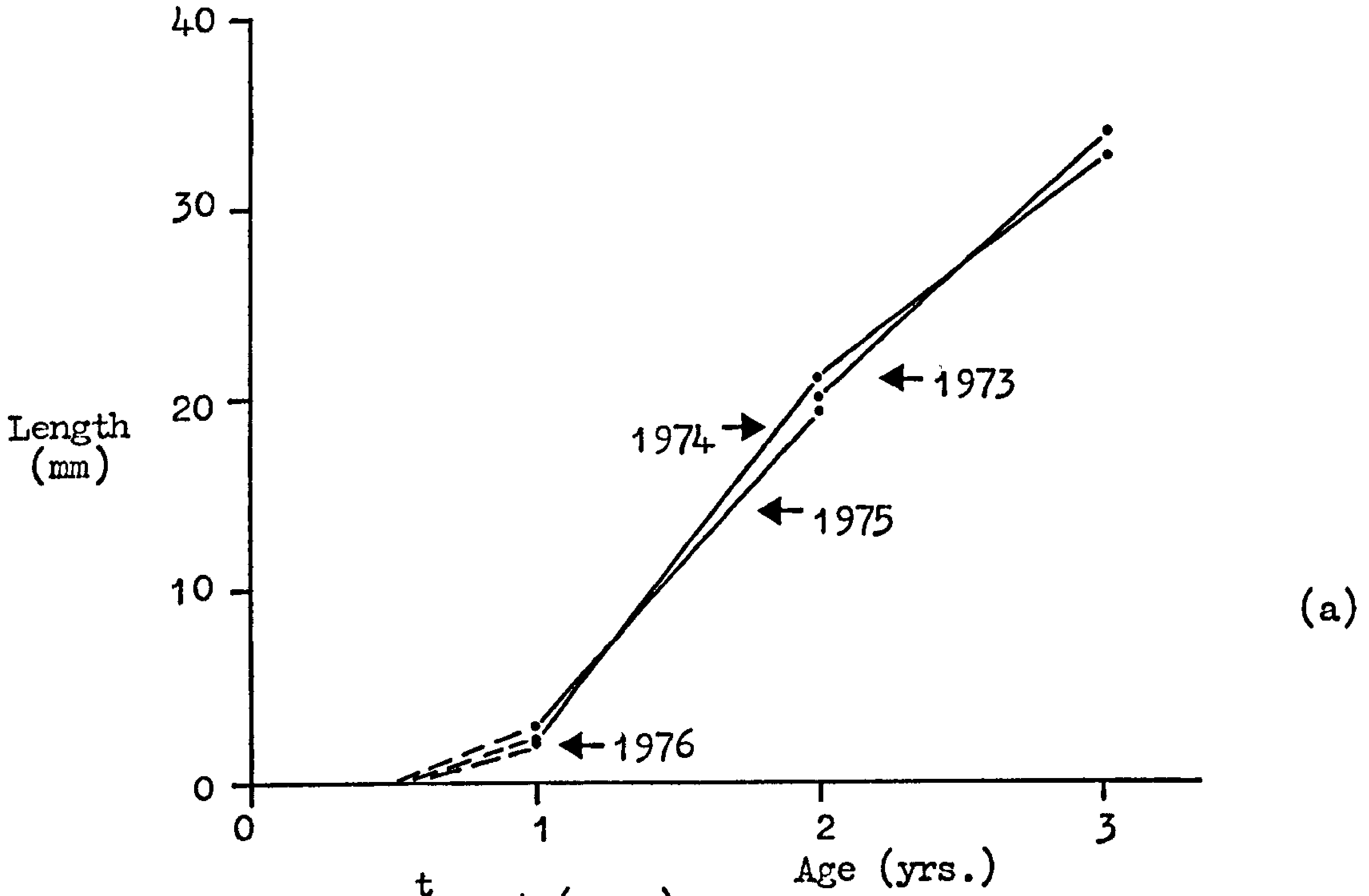
The paucity of specimens did not warrant growth curve treatment on a station basis.

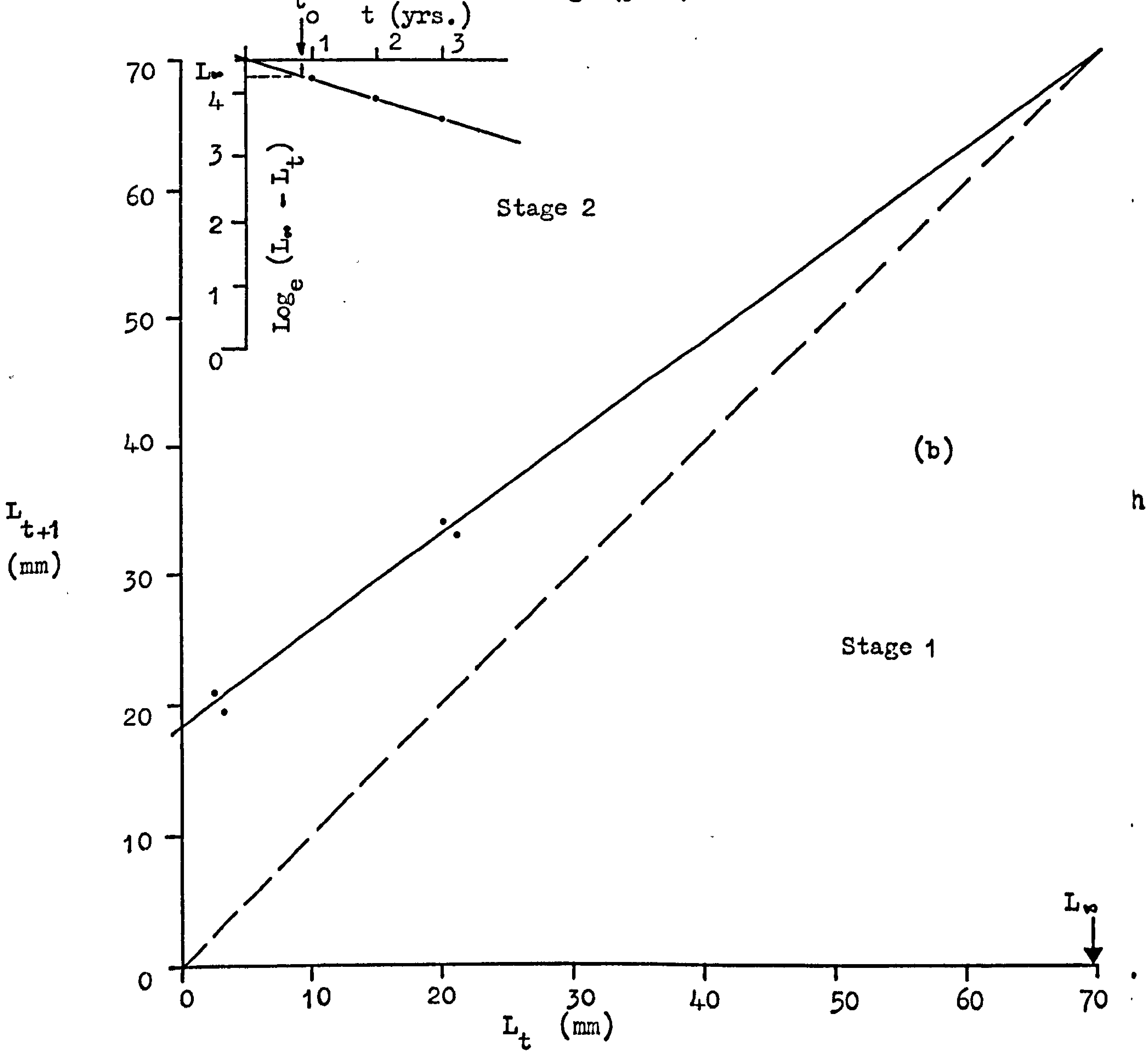
4.3.4.9. The Ford-Walford Analysis of the M. arenaria Population Growth Rate.

The size of each cohort at each winter was used in the two-step Ford-Walford analysis (Fig. 4.19b). The data used are given below :-

Cohort	1973	1974	1975	1976
Length (mm) at 1st winter	-	2.3	3.0	2.0
" 2nd "	20.0	21.0	19.5	-
" 3rd "	34.0	33.0	-	-

Figure 4.19 *M. arenaria* : The Population Growth Rate (a) and the Ford-Walford Analysis (b) :- Stage 1 and Stage 2 (Inset). The Bertalanffy Parameters, L_∞, t_o, are Given on (b). Equations are Given in Text.


Length (mm)
40
30
20
10
0
0
1
2
3
Age (yrs.)
1973
1974
1975
1976
(a)


t_o
t (yrs.)
1
2
3
L∞
4
3
2
1
0
Log_e (L∞ - L_t)
Stage 2
Stage 1
(b)
L_{t+1} (mm)
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
L_t (mm)
L∞

The first stage of the analysis of the length at one winter (L_n) plotted against the length the following winter (L_{n+1})(Fig. 4.19a) gave :

$$L_{n+1} = 0.737 \pm 0.074 L_n + 18.340$$

$n = 4$

$p < 0.05$

$r = 0.990$

$K = 0.305$, $L_\infty = 69.84$mm.

The second part of the analysis (Fig. 4.19b) gave :

$$\mathrm{Log}_e(L_\infty - L_t) = 4.520 - 0.309 \pm 0.005t$$

$n = 8$

$P < 0.001$

$r = 0.999$

$t_o = 0.889$

This gave the population Bertalanffy equation :

$$L_t \; 0 \; 69.84 \; (1 - e^{-0.305(t - 0.889)})$$

The largest specimen sampled in the area was 60.4mm in length (tdw = 10g and fdw = 1.5g) at Station B2, August 1975, which confirmed the accuracy of the predictive Bertalanffy equation maximum theoretical size (L_∞) of 69.8mm. The equation was then used to predict the following sizes of ages not sampled :

4 years = 43.0mm; 5 years = 50.2mm; 6 years = 55.5mm;
7 years = 59.5mm; 8 years = 62.7mm; 9 years = 65.0mm;

suggesting that the large specimen found may be approximately ten years old, an age within the life span calculated for the species.

4.3.5. The Changes in Body Condition of C. edule and M. arenaria Associated with Growth, Reproduction and Emaciation.

4.3.5.1. The Body Condition of C. edule and M. arenaria.

The condition of both M. arenaria and C. edule varied with season; the variability being caused firstly by changes in environmental factors which subsequently resulted in physiological changes of the animals associated with reproductive or nutritive changes (Fig. 4.20). The increase in condition to a maximum in May and June and its subsequent rapid decline was associated with maturation and spawning (as indicated by the first spat settlement during June and July), and the period of rapid growth until October (see Section 4.3.4.) together with poor nutritive conditions later in the year. The condition of both species was found to increase slightly following the cessation of growth and emaciation in October and then declined to a minimum in February. These latter changes may be attributable to minimal temperatures and food availability during the winter.

The condition changes of both species followed a similar pattern suggesting that these bivalves were affected by similar environmental factors; however, the magnitude of the condition was characteristic of each species. The monthly condition factor data were incorporated into regression and correlation analyses against mean interstitial salinity, mean air and water temperature, and the quantity of potential food as CHO. and Org. C. (Data given in Appendix 4.1). In all multiple regressions, over half of the variance was accounted for by the four variables although the most variation in the condition of C. edule was accounted for by salinity whereas with M. arenaria temperature was the most important variable (Table 4.11 Regressions (1)). The correlation

Figure 4.20 M. arenaria and C. edule : The Change in Mean Flesh Condition Factor Over the Sampling Period (± 1 S.E.).

Table 4.11 a) *C. edule* and b) *M. arenaria* : Monthly Data Analysis - Multiple Regression Analysis of Flesh Condition With Estuarine Water Salinity and Temperature, and Suspended Particulate Organic Carbon and Carbohydrate.

	Dependent Variable	Incorporated Variables and Significant Equation	Total Variance Accounted For	Main Variables
a)(1)	CF_H	Sal., Temp., Org. C., C.H.O. All n.s. - 6.004	60.6%	Sal. (57.6%).
(2)	CF_H	Temp., Org. C., C.H.O. All n.s. + 11.014	53.2%	Temp. (48.8%).
b)(1)	CF_L	Sal., Temp., Org. C., C.H.O. All n.s. - 1.765	66.8%	Temp. (60.2%).
(2)	CF_L	Temp., Org. C., C.H.O. $\overset{*}{0.147}_{Temp.} + 4.456$	62.8%	Temp. (60.2%).

	C. edule CF_H	*M. arenaria* CF_L	Salinity	Temperature	Org. C.	C.H.O.
C. edule CF_H		0.709 ***	0.576 **	0.488 *	0.116 n.s.	-0.006 n.s.
M. arenaria CF_L	0.724 ***		0.581 **	0.602 **	0.202 n.s.	0.076 n.s.
Salinity	0.572 **	0.543 *		0.691 **	-0.044 n.s.	0.080 n.s.
Temperature	0.572 **	0.594 **	0.734 ***		0.116 n.s.	0.383 n.s.
Org. C.	0.129 n.s.	0.256 n.s.	-0.020 n.s.	0.066 n.s.		-0.335 n.s.
C.H.O.	-0.063 n.s.	-0.021 n.s.	0.024 n.s.	0.343 n.s.	-0.106 n.s.	

Figure 4.21 *C. edule* and *M. arenaria* : Monthly Data Analysis - Pearson Correlation Matrix of Flesh Condition With Estuarine Water Salinity and Temperature, and Suspended Particulate Organic Carbon and Carbohydrate. (r and p values : Top R.H.S. Normal Data, Lower L.H.S. Log. Transformed Data.)

analysis (Fig. 4.21) shows that whilst there were significant intercorrelations between salinity, temperature and both species' condition, all correlations involving the water CHO. and Org. C. were not significant.

As salinity was found to be highly correlated with temperature, further regressions were constructed omitting salinity from the list of variables. These further regressions (Table 4.11 Regressions (2)) showed that temperature changes accounted for the major part of the variation in body condition of the species. It appears, therefore, that food availability as measured here did not limit the body condition. However, it is possible that, apart from the rapid decline of condition following spawning, the condition would be related to the large amount of particulate material over the summer. It must also be repeated that, as the estuarine water particulate material levels were influenced by many factors and as the particulate material measured in the present study may reflect levels of non-food material, then any influence of potential food levels on the bivalves' condition would not necessarily be apparent here.

It is also necessary to incorporate growth into these considerations. Rapid growth over the summer following reproduction would also result in the low condition measured if the increase in size of shell and body flesh were not proportional (see Section 4.3.5.2.).

Further study of the relationships between condition and water particulate matter (Fig. 4.22 a & b) showed that, with the exception of the data for the period April-May 1975, the condition of C. edule increased with CHO. levels; whilst the condition of M. arenaria possibly increased to a maximum between 1.1 - 1.4mg

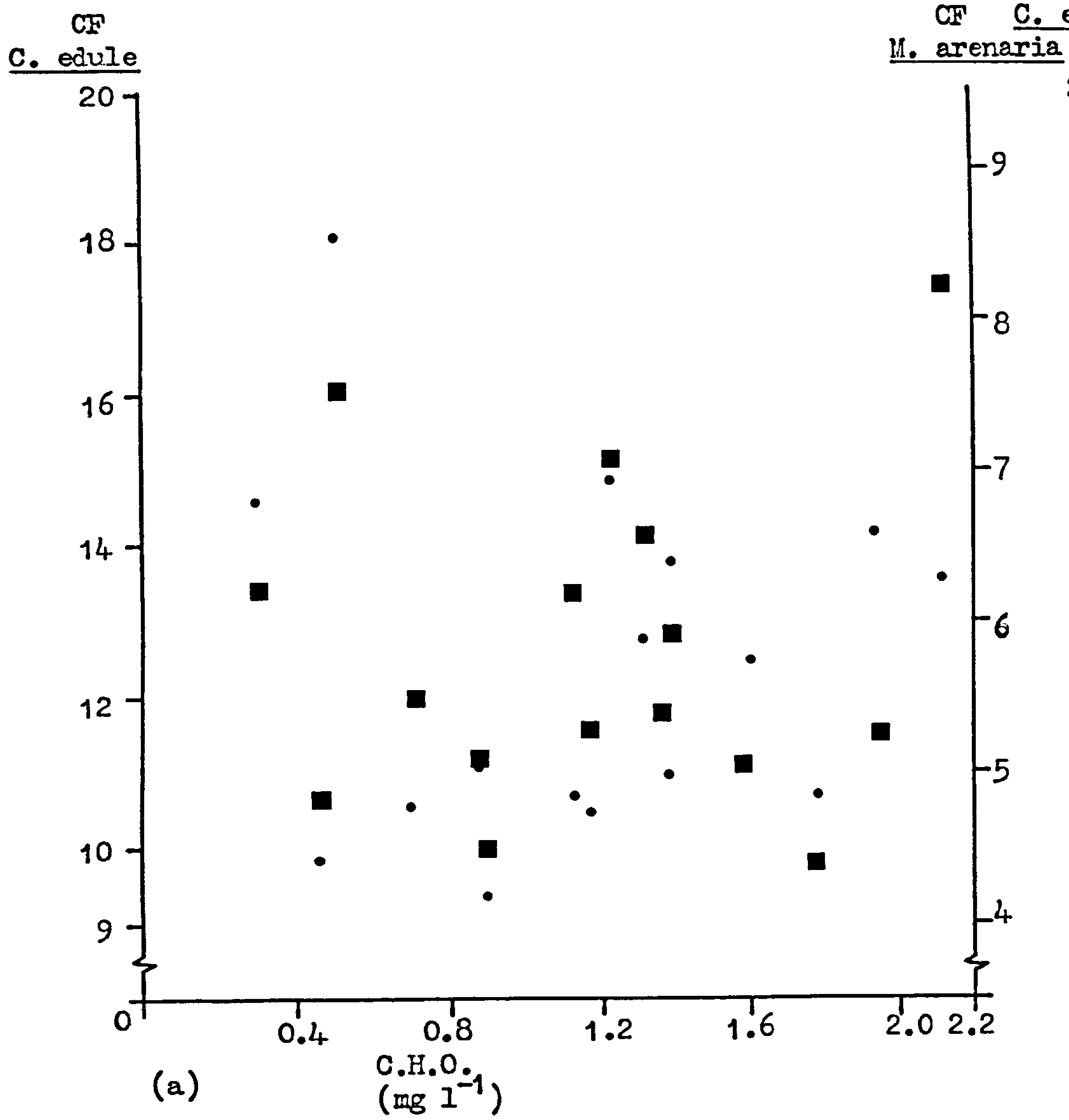
Figure 4.22 M. arenaria and C. edule : The Relationships Between Flesh Condition Factor and

(a) Suspended Particulate Carbohydrate, and

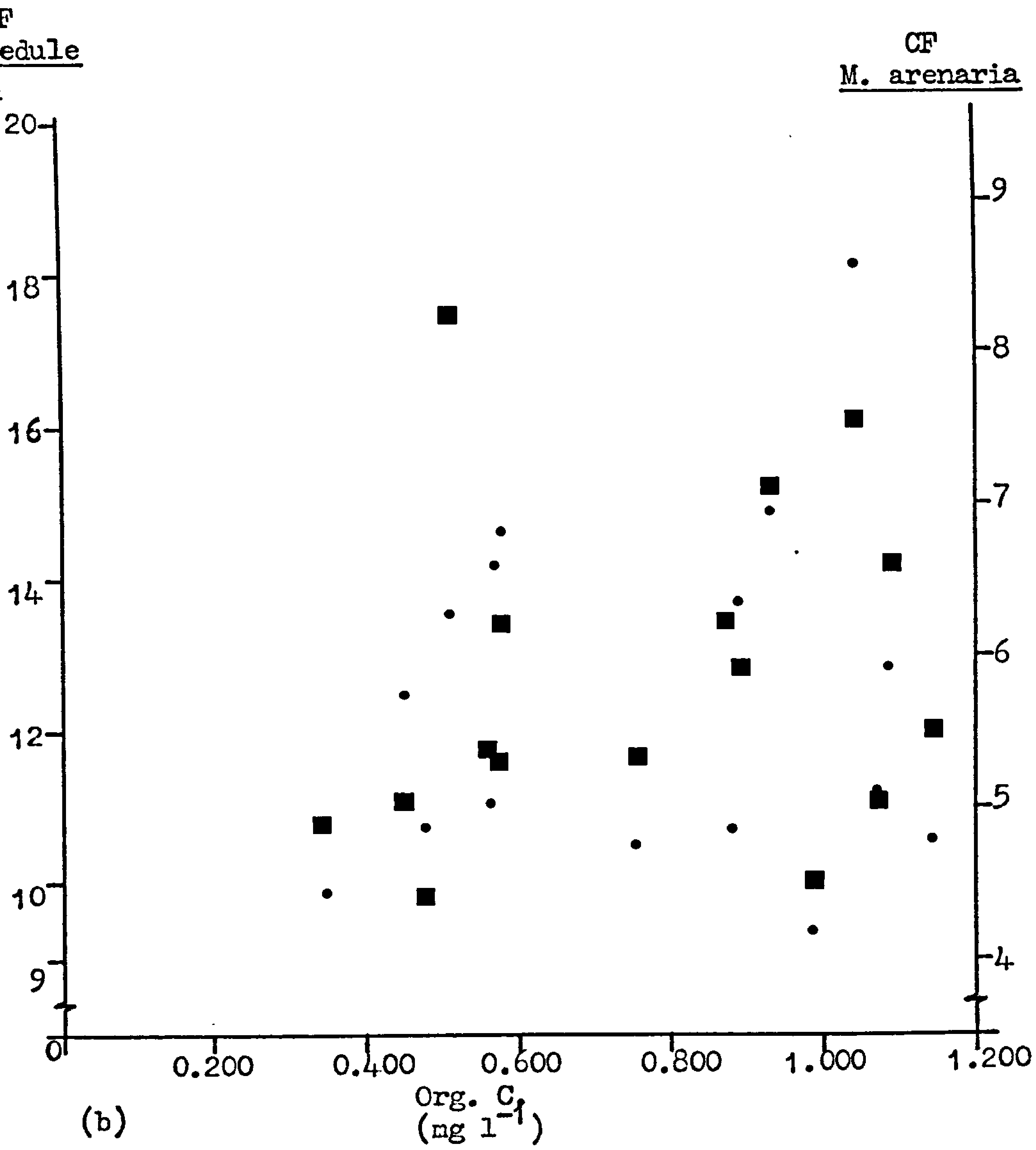
(b) Suspended Particulate Organic Carbon.

Key : M. arenaria CF_L ■

C. edule CF_H •


CF
C. edule
CF
M. arenaria
20
18
16
14
12
10
9
0
9
8
7
6
5
4
0.4
0.8
1.2
1.6
2.0
2.2
C.H.O.
(mg l^{-1})

(a)


CF
C. edule
CF
M. arenaria
20
18
16
14
12
10
9
0
9
8
7
6
5
4
0.200
0.400
0.600
0.800
1.000
1.200
Org. C.
(mg l^{-1})

(b)

CHO. 1^{-1} and then decreased with a further increase in CHO. levels. However, the April-June, 1975, condition of M. arenaria deviated from this general pattern and again reflected the reproductive status of the species (Fig. 4.22a).

The condition of M. arenaria increased linearly with the Org. C. levels with the exceptions of the high condition in July, 1975, again a possible spawning effect, and the low condition in November, 1975, February, 1976, and February, 1977, a reflection of winter emaciation (Fig. 4.20).

The condition of C. edule increased with Org. C. levels although there is a large amount of variability in the relationship (Fig. 4.22b). The levels of suspended organic carbon present during the winter were relatively high and possibly attributable to the flushing of detritus from the saltmarshes, Z. marina beds and agricultural areas. These levels, however, would not affect the condition if temperature was the primary limiting factor. The condition of both species was linearly and significantly related to temperature (Fig. 4.23a & b), although the simple relationships were again distorted by the spawning condition of the animals. In addition, the relationships between the levels of suspended Org. C. and CHO. and the condition of M. arenaria and C. edule were not significant.

4.3.5.2. The Changes in Total and Flesh Dry Weight of Standard Size Animals Over the Sampling Period.

In order to eliminate the changes in flesh weight and condition associated with the growth of the animals over the year, the flesh and total weights of standard sized animals (C. edule of height 5, 10, 15, 20 and 25mm; and M. arenaria of length 10 and

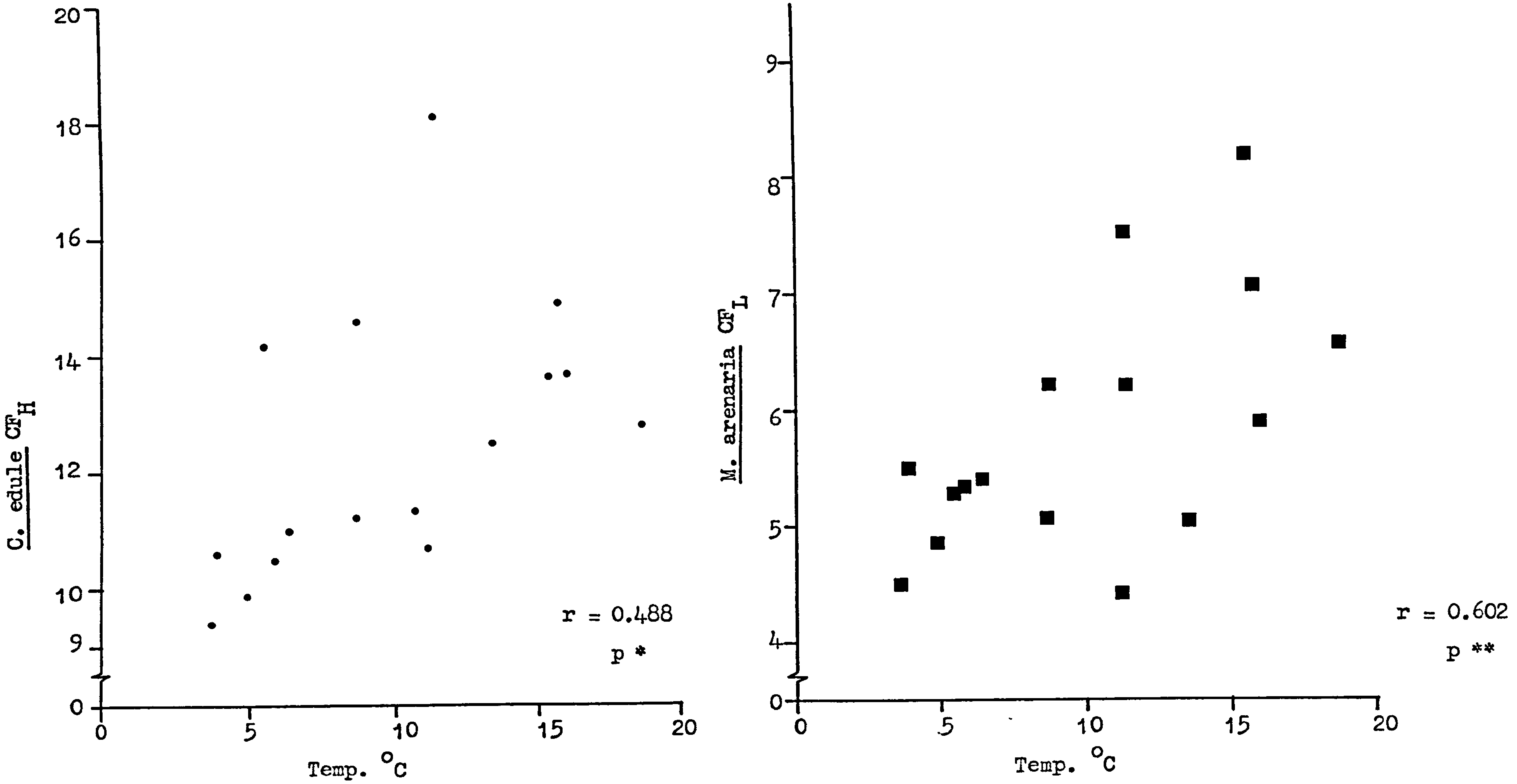


Figure 4.23 C. edule and M. arenaria : The Relationship Between Temperature and Flesh Condition Factor.

20mm) were calculated from the monthly size/weight relationships (Appendix 4.2). As the weight over the size range increased exponentially, the weight changes were plotted as the percentage change from the beginning of the sampling period (Figs. 4.24; 4.25; 4.27a & b).

(i) C. edule.

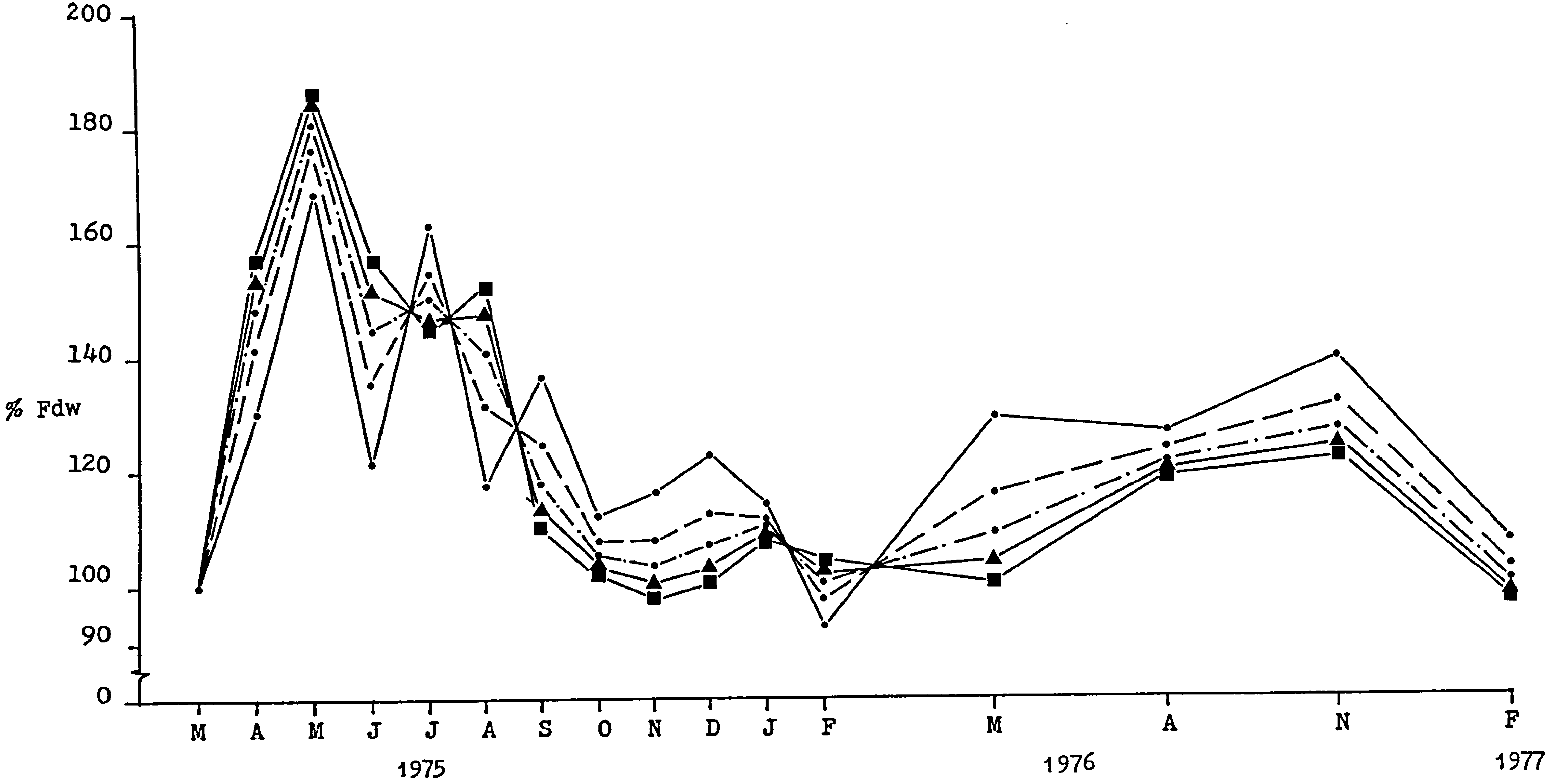
The change in the flesh weight over the early part of the year (March-May, 1975) was greatest in the larger animals. However, during the period May-August the change in flesh decreased with increasing age, suggesting that with increasing age a smaller proportion of the available energy was used for reproduction. During the autumn period the older animals showed greatest emaciation; a possible indication of the lower food levels present, such that whilst the younger animals could obtain a sufficient ration to maintain a certain flesh weight the older animals could not. The amount of change in flesh weight decreased with increasing age during the second sampling year (Fig. 4.24).

The changes in total weight are given for comparison (Fig. 4.25) and incorporated into which are the flesh weight changes mentioned above. It is considered, however, that the increase in total weight over the period July-December, when the flesh weight and condition were reduced, is attributable to a thickening of the shell following the period of rapid growth. The amount of fluctuation in the total weight of the standard sized animals over the two years decreased with increasing age such that the larger animals' total weight was relatively constant. This reflects the reduced reproductive activity and growth in the older animals.

The relationships between the flesh weight of the 10mm

Figure 4.24 *C. edule* : The Percentage Change in Flesh Dry Weight of Standard Size Animals (March 1975 = 100%).

Height 5mm —•—
10mm - - • - -
15mm —·—•—·—
20mm —▲—
25mm —■—


200
180
160
140
% Fdw
120
100
90
0
M
A
M
J
J
A
S
O
N
D
J
F
M
A
N
F
1975
1976
1977

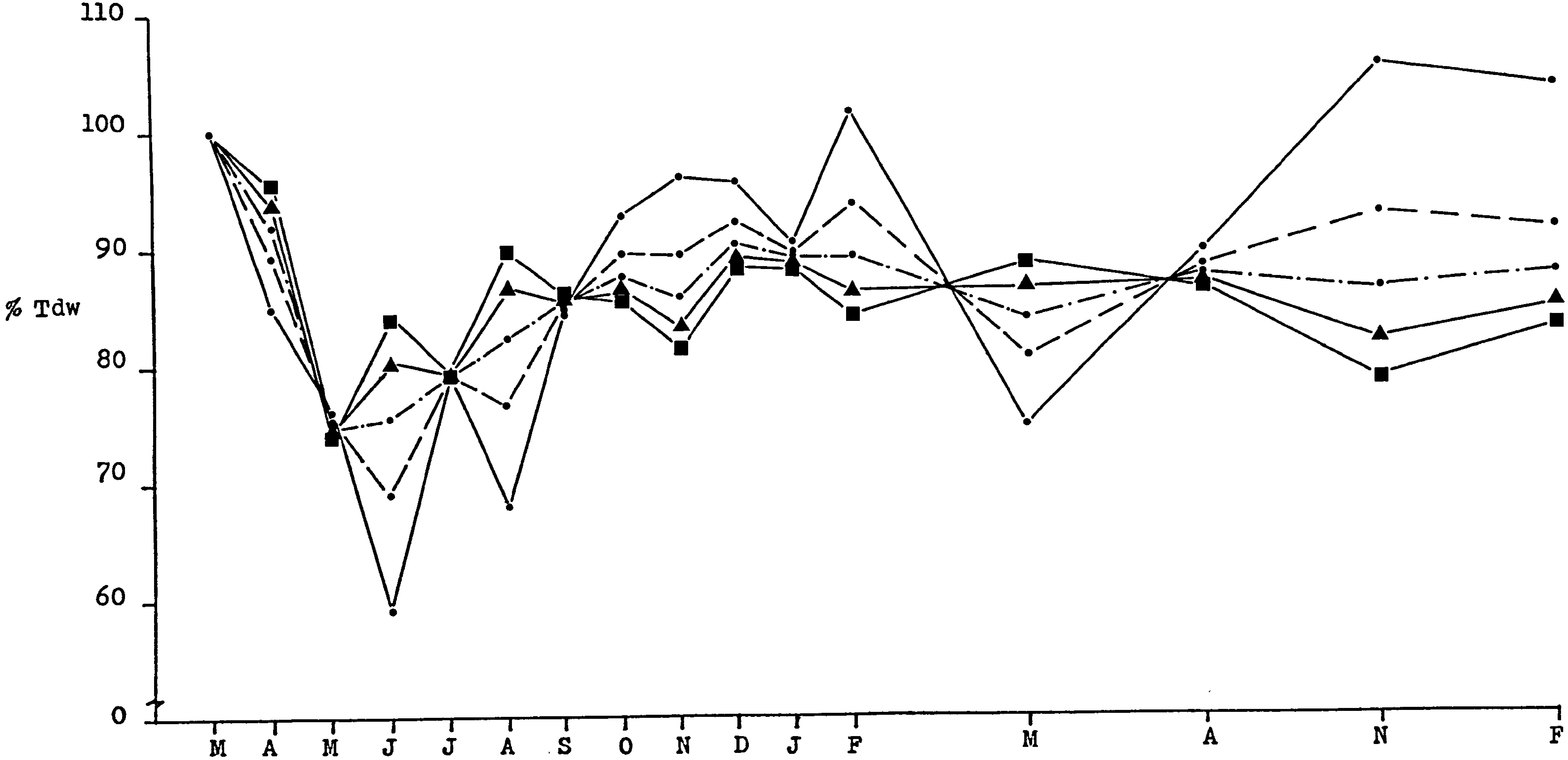


Figure 4.25 C. edule : The Percentage Change in Total Dry Weight of Standard Size Animals (March 1975 = 100%). (Legend as Fig. 4.24)

Figure 4.26 C. edule : The Relationship Between the Flesh Dry Weight of a 10mm Height Standard Size Animal and Suspended Particulate Organic Carbon and Carbohydrate, at Each Sampling Occasion.

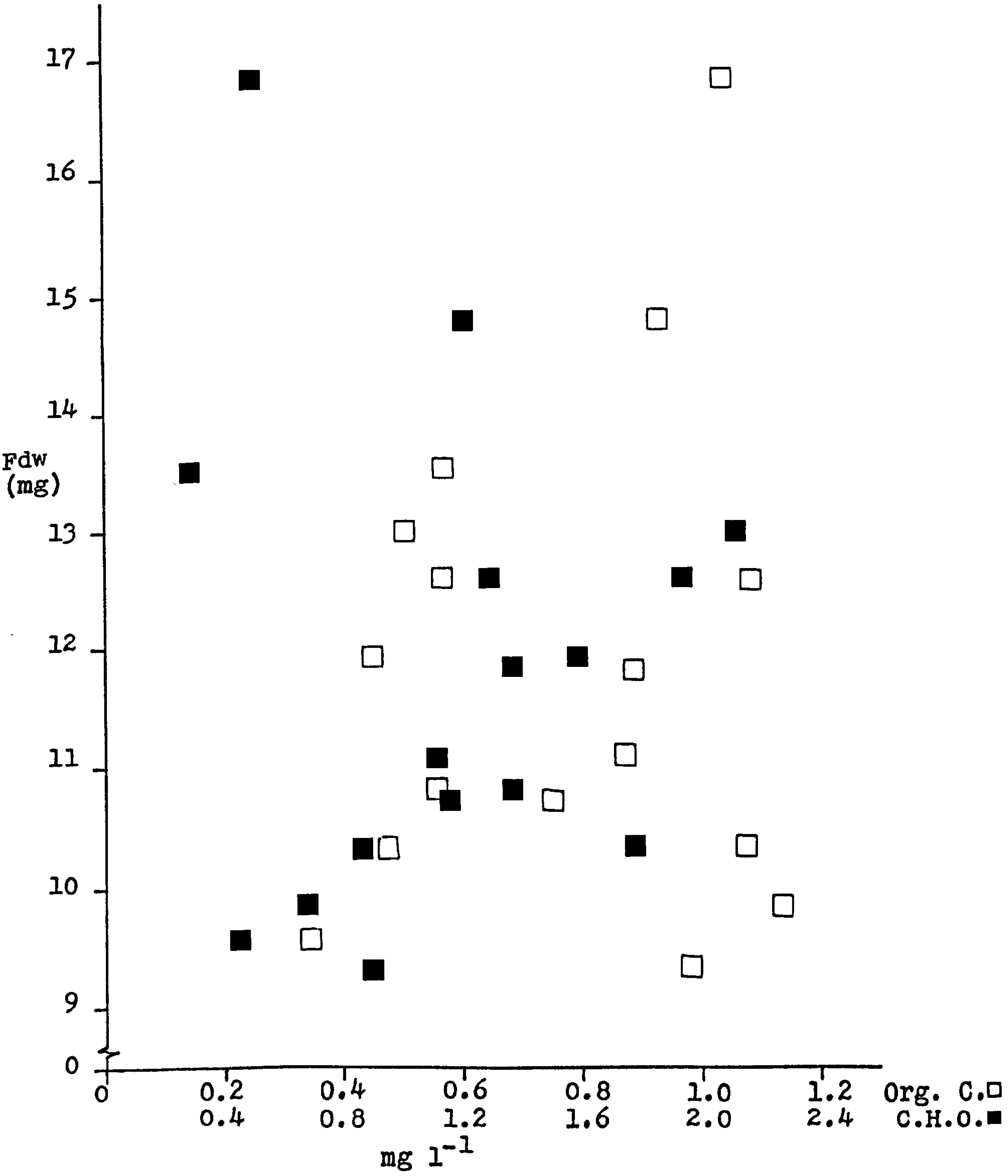

17
16
15
14
Fdw (mg)
13
12
11
10
9
0
0
0.2
0.4
0.6
0.8
1.0
1.2
Org. C.□
0.4
0.8
1.2
1.6
2.0
2.4
C.H.O.■
mg l^{-1}

Figure 4.27 *M. arenaria* : The Relative Change in (a) Flesh Dry Weight and (b) Total Dry Weight of Standard Size Animals (March 1975 = 100%) (Feb. '77 Insufficient Data).


Fdw
%
220
200
180
160
140
120
100
80
20mm
10mm
(a)
M A M J J A S O N D J F M A N F
Tdw
%
150
140
120
100
80
60
10mm
20mm
(b)
M A M J J A S O N D J F M A N F
1975
1976
1977

standard sized animal and the levels of Org. C. and CHO. (Fig. 4.26) show that while there was no significant relationship between the former and the Org. C. levels, most of the CHO. data described a positive linear relationship against the standard size flesh weight. The CHO. levels for April, May and July, 1975, however, deviated from that pattern, were indicative of the change in flesh weight prior to and during spawning, and contributed to the non-significance of the relationship.

(ii) M. arenaria (Fig. 4.27a & b).

The larger (20mm) animals' flesh weight increased over the spring period by greater amounts in comparison with the smaller animals. However, after the maxima in June, the flesh of both sizes declined by the same proportion until the minima were reached during the period September to October. This suggests that both sizes diverted a similar proportion of the available energy into reproduction although over the autumn period the smaller animals emaciated to a lower flesh value than at the beginning of the year. The flesh weight of the larger animals, although possibly increasing with the amount of Org. C. in the water, did not give significant relationships with either of the water column potential food levels (Fig. 4.28).

During the second year only, the shell weight increased during that part of the year when size-growth had stopped and when emaciation occurred. However, trends in these relationships may have been obscured by the inherent variation in the regression equations attributable to the analysis of a small population (see Appendix 4.2).

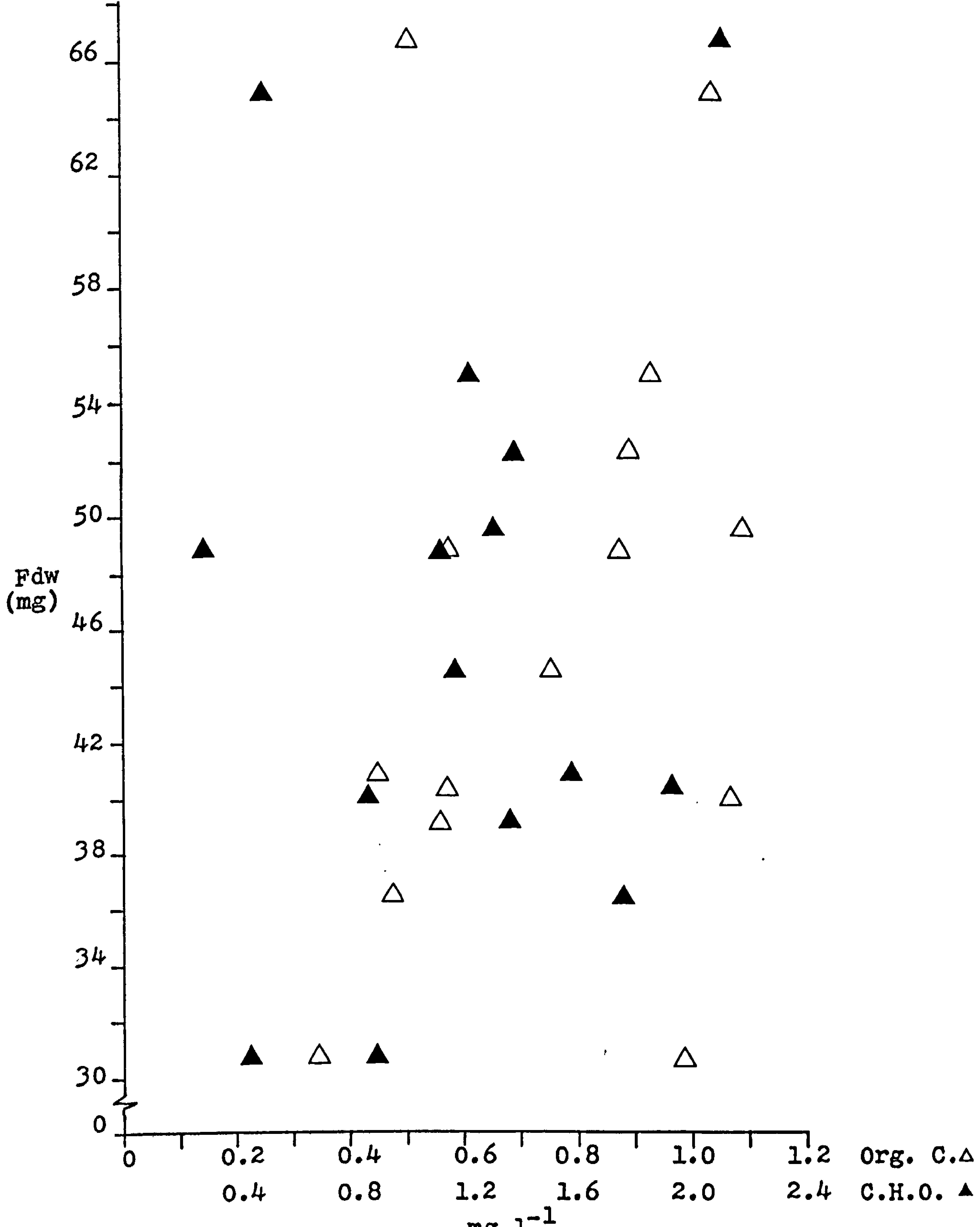


Figure 4.28 M. arenaria : The Relationship Between the Flesh Dry Weight of a 20mm Standard Length Animal, and Water Particulate Organic Carbon (r = 0.283 n.s.) and Carbohydrate (r = 0.131 n.s.) at Each Sampling Occasion.

4.3.5.3. The Difference in Condition and Flesh Weight in *M. arenaria* and *C. edule* with Large Changes in Environmental Factors.

Following the work of Newcombe (1935) and Swan (1952), showing morphological variation in clams from different areas, a brief analysis was performed to test for difference in the condition and flesh weight (as a percentage of total weight) of *M. arenaria* with environmental change. The data for the fine mud, low-shore stations (A1, B1-3, C1-2), were combined as were those for the coarse sand, upper-shore areas (A2-4, B4-5, C3-5). In order to eliminate the changes caused by spawning only the autumn/ winter data from October, 1975, to February, 1977, excluding May, 1976, were used.

The condition factor data gave :

	$\bar{x}$	S.D.	n	
Fine stations :	5.2872 ±	1.2850	28	t = 1.129 n.s.
Coarse stations :	4.8829 ±	0.9629	17	

The percentage flesh data gave :

	$\bar{x}$	S.D.	n	
Fine stations :	13.2257 ±	2.7335	28	t = 0.544 n.s.
Coarse stations :	12.8141 ±	1.9074	17	

Therefore, using a t-test where the variances were equal, the difference between the groups of stations were not significant ($P > 0.05$). In the absence of further data, there was found to be no difference either in the condition of the animals or in the amount of flesh with respect to shell, i.e. the animals from one type of area did not have thicker shells than those from the other area.

The corresponding monthly data for the condition of C. edule were similarly combined for the same sandy, upper-shore and muddy, low-shore stations.

The condition factor data gave :

	$\bar{x}$	S.D.	n	
Fine stations :	12.2488	± 4.0955	130	d = 3.5926
Coarse stations :	11.2942	± 3.2370	268	

Therefore, using a d-test, the difference between the groups of stations was statistically significant ($P < 0.001$). The animals from the low-shore areas therefore had a higher condition during the non-spawning period. This difference could possibly be attributed to the presence of younger animals at the lower-shore stations as the relationships between condition and height were negative for most of the months (see Appendix 4.2). However, as these relationships were not statistically significant, the differences in condition were probably attributable to the variation in environmental factors.

4.3.6. The Production Estimates for M. arenaria and C. edule.

4.3.6.1. On an Areal Whole Population Basis.

As there were few animals of each species present at each station, the mean numbers, biomasses and mean sizes for each cohort over the whole area and sampling period were used in the production calculations based upon the cohort growth increment method (Crisp, 1971). The production estimates (Appendix 4.3 to 4.7) were derived from the density, mean weight, mean size and biomass data of each cohort at each sampling date. The population production data ~~is~~ are summarised in Table 4.12 giving the production, mean biomass and $P/\bar{B}$ for each age cohort of C. edule and

Table 4.12 M. arenaria and C. edule: Summary of Cohort Production Values.

(a) M. arenaria:

Sampling Year 1975-76

Age Class	Mean Biomass mg Fdw m^{-2}	Production mg Fdw m^{-2}yr^{-1}	Annual P/$\bar{B}$
1975	21.562	47.971	2.225
1974	174.971	950.762	5.434
1973	87.010	31.318	0.360
Total	283.543	1030.051	3.633
Sampling Year 1976-77			
1976	6.991	27.599	3.948
1975	65.816	454.295	6.902
1974	140.674	125.758	0.894
Total	213.481	607.652	2.846
Mean of Both Years' Data	248.512	818.851	3.295

(b) C. edule:

Sampling Year 1975-76

Age Class	$\bar{B}$.	P.	P/$\bar{B}$
1975	19.608	51.081	2.605
1974	103.381	168.839	1.633
1973	263.812	369.703	1.401
1972	220.719	232.781	1.055
>1972	383.880	474.117	1.235
Total	991.400	1296.521	1.308
Sampling Year 1976-77			
1976	20.554	61.331	2.984
1975	32.777	187.098	5.708
1974	249.931	285.153	1.141
1973	338.357	199.730	0.590
1972	209.196	84.570	0.404
>1972	151.038	-98.715	-0.654
Total	1001.853	719.167	0.718
Mean of Both Years' Data	996.626	1007.844	1.011

M. arenaria for each year.

The M. arenaria population 1+ year class, in each year, had the greatest productivity with $P/\bar{B}$ values between 5 and 7 although during 1976-77 this year class did not have the greatest biomass (Table 4.12a). It is considered however, that inclusion of the age classes 3+ and older would have reduced the overall population $P/\bar{B}$ to a level comparable to other long living bivalves. The low $P/\bar{B}$ value of the spat in each year reflects the very slow growth of that cohort whose growth described the early part of a sigmoid growth curve. The 1974 age class was predominant during each sampling year suggesting that during 1974 there was an extremely successful spatfall.

The population production summary for C. edule (Table 4.12b) shows that with increasing age the $P/\bar{B}$ of each cohort decreased. However, unlike M. arenaria, in which the major part of the production was attributable to a single age cohort, each C. edule cohort between 1+ and 4+ contributed relatively equally to the total production although the most important were the 2+ and 3+ cohorts. As with the M. arenaria population, the C. edule population 1+ group had the highest $P/\bar{B}$ during 1976-77 although the previous year the spat had the greatest $P/\bar{B}$. In addition, whereas the spat were present in high densities, they were a relatively small part of the population biomass and contributed little towards the total production. It should also be noticed that the greater spatfalls of C. edule and, to a lesser extent, M. arenaria during 1976-77, were not reflected in the production of the respective 0+ groups.

The first sampling year, 1975-76, was more productive for both M. arenaria and C. edule in comparison to the following year.

The C. edule population produced over eighty per cent as much again during 1975-76 when compared to 1976-77 from a comparable population biomass. The M. arenaria population similarly produced 1.7 times as much from 1.25 times the population biomass.

4.3.6.2. On a Station Basis.

In order to make an approximation of the production on a station basis, the respective $P/\bar{B}$ values for both the whole population and the spat for each of the sampling years were used together with the data of the biomass of each of these parts of the population at each stations (Tables 4.13 and 4.14).

The $P/\bar{B}$ ratios used :

For M. arenaria

	1975-76	1976-77
Spat	2.255	3.948
Large	3.633	2.846

For C. edule

	1975-76	1976-77
Spat	2.605	2.984
Large	1.308	0.718

The M. arenaria station production (Table 4.14) for 1975-76 was generally greatest on the middle areas of the transects with upto 5g fdw m^{-2} yr^{-1}, e.g. A3, B2 and B3 although Stations A1 and C5 also had high production levels upto 1.5g fdw m^{-2} yr^{-1}. However, the following year the most productive areas were B1 and B5 (upto 3.5g fdw m^{-2} yr^{-1}) and C4 (1.5g fdw m^{-2} yr^{-1}), all areas that were relatively unproductive the previous year. Few generalisations can therefore be attached to the pattern of the

Table 4.13 <u>Cerastoderma edule</u>: The Production (mg Fdw m^{-2} yr^{-1}), Mean Biomass (mg Fdw m^{-2}) and Annual $P/\overline{B}$ Summary Data.

	1975-76							1976-77						
	Spat		Large Animals		Total			Spat		Large Animals		Total		
Station	$\overline{B}$	P	$\overline{B}$	P	$\overline{B}$	P	$P/\overline{B}$	$\overline{B}$	P	$\overline{B}$	P	$\overline{B}$	P	$P/\overline{B}$
A1	9.18	23.91	850.45	1112.39	859.63	1136.30	1.322	1.50	4.48	439.39	315.48	440.89	319.96	0.726
A2	0	0	538.66	704.57	538.66	704.57	1.308	1.63	4.86	684.92	491.77	686.55	496.63	0.723
A3	0.07	0.18	1128.30	1475.82	1128.37	1476.00	1.308	4.28	12.77	416.17	298.81	420.45	311.58	0.741
A4	0	0	113.35	148.26	113.35	148.26	1.308	0.41	1.22	0	0	0.41	1.22	2.984
B1	8.42	21.93	330.36	432.11	338.78	454.04	1.340	13.48	40.22	4.62	3.32	18.10	43.54	2.405
B2	1.37	3.57	533.31	697.57	534.68	701.14	1.311	2.50	7.46	8.99	6.45	11.49	13.91	1.211
B3	16.40	42.72	1354.60	1771.82	1371.00	1814.54	1.323	68.05	203.06	2161.19	1551.73	2229.24	1754.79	0.787
B4	1.75	4.48	3531.94	4619.78	3533.69	4624.26	1.309	2.06	6.15	1821.54	1307.87	1823.60	1314.02	0.721
B5	0.82	2.14	1074.17	1405.01	1074.99	1407.15	1.309	0	0	2562.55	1839.91	2562.55	1839.91	0.718
C1	0	0	472.81	618.43	472.81	618.43	1.308	5.71	17.04	0	0	5.71	17.04	2.984
C2	11.11	28.94	225.03	294.34	236.14	323.28	1.369	19.90	59.38	23.79	17.08	43.69	76.46	1.750
C3	4.67	12.16	433.46	566.97	438.13	579.13	1.322	19.78	59.02	147.75	106.08	167.53	165.10	0.985
C4	0.56	1.46	960.77	1256.69	961.33	1258.15	1.309	1.47	4.39	1181.92	848.62	1183.39	853.01	0.721
C5	5.33	13.88	2007.24	2625.47	2012.57	2639.35	1.311	2.41	7.19	2695.07	1935.06	2697.48	1942.25	0.720

Table 4.14 *Mya arenaria*: The Production (mg Fdw m^{-2} yr^{-1}), Mean Biomass (mg Fdw m^{-2}) and Annual $P/\bar{B}$ Summary Data.

	1975-76							1976-77						
	Spat		Large Animals		Total			Spat		Large Animals		Total		
Station	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P	$P/\bar{B}$	$\bar{B}$	P	$\bar{B}$	P	$\bar{B}$	P	$P/\bar{B}$
A1	42.39	95.59	323.57	1175.53	365.96	1271.12	3.473	28.73	113.43	20.21	57.52	48.94	170.94	3.493
A2	2.40	5.41	22.50	81.74	24.90	87.15	3.500	0	0	0	0	0	0	-
A3	10.54	23.77	1316.56	4783.06	1327.10	4806.83	3.622	7.69	30.36	334.09	950.82	341.78	981.18	2.871
A4	10.56	23.81	50.26	182.59	60.82	206.41	3.394	0	0	3.49	9.93	3.49	9.93	2.846
B1	32.06	72.29	234.37	851.47	266.43	923.76	3.467	31.76	125.39	1047.47	2981.10	1079.23	3106.49	2.878
B2	24.69	55.68	1314.10	4774.12	1338.79	4829.80	3.608	18.57	73.31	207.63	590.91	226.20	664.23	2.936
B3	35.56	80.19	1201.17	4363.85	1236.73	4444.04	3.593	3.92	15.48	196.17	558.30	200.09	573.78	2.868
B4	0	0	53.60	194.73	53.60	194.73	3.633	0	0	0	0	0	0	-
B5	0	0	130.36	473.60	130.36	473.60	3.633	0	0	1233.57	3510.74	1233.57	3510.74	2.846
C1	0.19	0.43	2.22	8.06	2.41	8.49	3.542	3.85	15.20	0	0	3.85	15.20	3.948
C2	9.87	22.26	20.24	73.53	30.11	95.79	3.181	9.49	37.47	136.18	387.57	145.67	425.03	2.918
C3	15.36	34.64	12.92	46.94	28.28	81.57	2.884	5.29	20.88	8.96	25.50	14.25	46.38	3.255
C4	0	0	8.83	32.08	8.83	32.08	3.633	0	0	534.94	1522.44	534.94	1522.44	2.846
C5	4.48	10.10	411.94	1496.58	416.42	1506.68	3.618	0.88	3.47	82.08	233.60	82.96	237.07	2.858

productive areas of M. arenaria. The production of the spat and large animals would show the same patterns as the comparable biomass (see Section 4.3.1.5.). However, as the spat usually contributed such a small biomass to each station biomass then the total station P/$\bar{B}$ value was almost wholly influenced by the large animals' biomass.

The most productive C. edule stations were the sandy, upper-shore areas B4 and C5; the latter station also supported Z. marina beds (Table 4.13). These areas had a production of up to 5g fdw m^{-2} yr^{-1} with the Stations A1, A4, B3, B5 and C4 also having relatively high values up to 1.5g fdw m^{-2} yr^{-1}. Similarly, the following year C5, B3, B4 and B5 were the most productive stations although the maximum levels of production were only half those of the preceeding year. The C. edule station P/$\bar{B}$ values during 1975-76 were relatively similar, a trend attributable to the similarity between the spat and whole animal P/$\bar{B}$ levels (2.605 and 1.308 respectively) and to the relatively low biomass of spat at the stations. In 1976-77 the stations P/$\bar{B}$ values showed a much wider variation which was attributable to the large difference in spat and large animal P/$\bar{B}$ values.

The 1976-77 C. edule P/$\bar{B}$ values also decreased with an increase in tidal height on Transects B and C; this was also a reflection of the larger, more successful spatfall during that year, and of the tendency, as also found the previous year, for the spat to settle in areas away from the main bulk of the population. Transect A, however, did not show these trends as at Station A4 no large cockles and only very few spat were found which resulted in a high P/$\bar{B}$ value.

The station P/B ratios for C. edule and M. arenaria therefore reflected the population densities and biomasses of both large and small animals to some extent. It must be realized however that the method employed to enable the station production to be calculated involves many assumptions which would only be verified further by using greater cockle and clam populations.

4.4. Discussion.

4.4.1. The Occurrence, Settling and Growth of Spat.

The spat of these suspension-feeding bivalves were found to show many inter-specific similarities regarding their occurrence, distribution and growth. Following a two-week weakly swimming larval phase (Baggerman, 1953; Ayers, 1956), the majority of the spat of both species settled within the period July-September; the small numbers of spat present during most of the year suggested that some gamete leakage had occurred. This latter phenomenon has been noted for other bivalve species and may be characteristic of this class (Caddy, 1967; Seed, 1969; Muus, 1973; Warwick and Price, 1975; and as shown for M. balthica, Chapter 3). The settling period (and spawning) was later than recorded for both M. arenaria and C. edule, in the Lynher estuary in S.W. England (Warwick and Price, 1975), but earlier than recorded for C. edule in Ireland where the main cockle recruitment was during October (Seed and Brown, 1975). However, the main settling period was in agreement with most cockle and clam studies (Kreger, 1940; Baggerman, 1953; Kristensen, 1957; Wolff, 1973; Burke and Mann, 1974). It is suggested that with a decreasing latitude the settlement of these boreal bivalves would occur both earlier and later in the year when temperatures are reduced (Pfitzenmeyer, 1962). In addition, both populations studied by Warwick and Price (1975) had a more well-defined spawning period than those in the Forth estuary.

The majority of both species' spat settled from July to August, a period within the growth season, and consequently found favourable conditions for some growth to occur. However, there were also smaller spatfalls later in the year, during late summer to early autumn, such that the spat settling then were not able to grow before the following spring. This secondary spatfall has also been recorded for both species in other areas (Baggerman, 1953; Kristensen, 1957; Pfitzenmeyer, 1962; and Warwick and Price, 1975). These late spat would have been at a competitive disadvantage to the early spat as they were smaller and more vulnerable over the winter. The long settling period, together with environmental and genetical variability, produced the large variation in size within an age class of the bivalves (see also Ansell, 1961).

The Torry Bay cockle spat reached a maximum density in August-September and declined by 80% by December. A larger spatfall in 1976 was accompanied by a larger spat mortality such that the stability of the population was maintained (see also Kristensen, 1957; Muus, 1973). Wolff and De Wolf (1977) recorded a greater mortality of 72% per month for cockle spat from a maximum density of $2400m^{-2}$. However, whereas the cockle spat showed the greatest mortality soon after settling, the clam spat, which were present in lower numbers, had the greatest mortality the following spring. Baggerman (1953), using a much finer sampling mesh and shorter sampling interval than in the present study, found that the mortality of M. arenaria spat was greatest immediately after settling. It is possible, therefore, that the low M. arenaria spat density found here was the result of early mortality not detected by the sampling methods employed. Using the calculations given by Ayers (1956), it is considered that the numbers of cockle and clam spat which survived to the first winter were large enough to ensure the stability of the population.

The cockle and clam spat predominantly settled in comparable areas of fine-mud above the mid- to low-shore level with a shallow slope, high amounts of silt and clay in the sediment, high interstitial salinity and with large amounts of detritus in the water column. These results indicate, by inference, that the spat were found in areas associated with the slow water currents found over the shallow sloping, low-shore, fine-mud areas. In addition the inverse relationship between spat density and tidal height was also a reflection, to some extent, on the fine sediments at the lower-shore. However, the absence of spat from the very low-shore may indicate that tidal height did contribute towards determining spat density.

The passive settlement of bivalve spat in "quiet areas" has been suggested by many authors (see Section 3.5.1.). Kreger (1940) suggested that the observed substrate preferences by cockle larvae were secondary and could be reduced to current influences. Baggerman (1953) and Kristensen (1957) found cockle spat on sediments of 50 - 176µm M.P.D. and stated that the spat did not have preference for a particular sediment type although both found spat mainly in areas of weak currents and wind action and fine sediments with large quantities of silt and clay and detritus. The avoidance of soft mud by spat >500µm found by Kristensen (1957) was not found here. Generally, therefore, large numbers of spat were found where fine sediments occur on the lower-shore area. If the spat were homogeneously distributed throughout the water column then, as the lower-shore had a greater amount of water passing over it, there was greater opportunity for settlement to occur (Kreger, 1940). If, however, a low-shore area has high currents flowing over it (it will have a coarse sediment) then spat will not successfully settle.

A low-shore, fine sediment area is therefore favourable for passive settlement by weakly swimming larvae. These fine areas, however, may be deleterious to spat after settlement as they are associated with a large silt inflow; this would lead to the smothering of the spat together with a low food (as living phytoplankton) and oxygen inflow and a slow removal of waste material. The opposite occurs in areas of high currents such that once settled there is a favourable environment for the spat; however, because of high currents few spat settle (Verwey, 1952; Baggerman, 1953; Pratt, 1953; Kristensen, 1957). On Torry Bay, the ripple marks on areas of clean sand, e.g. B4, C3 and C4, are indicative of strong currents and explain the lack of spat found at these stations attributable to either low rates of settling or to unsuccessful settlement. These factors contribute to explaining why the cockle spat and large animals occurred in different localities. It is therefore necessary to consider the adults and spat separately because of their ecological preferences, deposition and possibly differential mortality within an area (see Savilov, 1953; Kristensen, 1957).

Several authors have attempted to explain why cockle spat are not found in areas of greatest adult density at higher levels (Kreger, Verwey, Baggerman and Kristensen op. cit.). The sorting of larvae by current actions results in dense populations in restricted areas followed by large mortality in the low-shore settling areas by silt smothering (Newcombe, 1935).

Although cockle spat up to a size of 2mm (and clam spat up to 2.5mm) can be transported by water currents (spat of size 600 - 1800µm have a settling rate comparable to sand grains of 100 - 250µm), the adults can only inhale and kill transported spat up to 1mm in length (Baggerman, 1953; Kristensen, 1957) this would lead to the larger spat being successfully deposited in high-shore cockle areas of coarse sediment. Transported spat could also be deposited at high tidal levels during the period of slack water at high tide. In addition Mya spat have the ability to form a byssus on settling and may not be as susceptible as cockle spat to transport by currents (Yonge and Thompson, 1976). Also, as the clam adult population occurred in areas close to the settlement areas, transport of this spat is not as important as that of the cockle spat. The large numbers of spat found at Station B2, within the dense mussel beds, suggests that large filter-feeding populations do not totally decimate invertebrate larval populations; however, suspension-feeding macrobenthos may perceptibly influence spat mortality at certain sizes of spat and at certain times of the year (Thorson, 1946; Meikilovski, 1974). Meikilovsky (1974), however, suggests that shelled mollusc-spat may pass unharmed through the guts of unintentional predators such as suspension or deposit feeders, or that adults in a population may cease feeding during spatfall in order to reduce mortality. A combination of spat transport and differential mortality would therefore decrease the spat density on the low shore areas and populate the areas of adult cockle and clam occurrence.

Once settled, it was found that the first year cockles grew fastest in areas of high silt and clay content, low shore slope and high salinity (i.e. lower-shore areas) and where few adults were present. (The relationship between the latter factor and spat growth was a reflection of the different distributions of the spat and adults.) The greatest spat growth also occurred in areas of greatest spat density, a phenomenon not shown by the adult cockles, and the largest settlement occurred in areas that did not produce the greatest adult growth rate (see below). Verwey (1952) also found that settlement did not occur in the areas of greatest adult growth although he did not comment on the growth of the spat. Muus (1973), however, found that larvae of sublittoral bivalves can substrate-select and largely settle only where they can thrive as adults. It is possible that sublittoral spat do not have nor require the means of transport employed by littoral spat.

The growth of both species' spat described the first part of a sigmoid growth curve, with the spat size at the first winter being dependent upon the time of settling. The cockle spat showed a small amount of initial growth before growth ceased during the winter whereas the majority of the clam spat did not grow appreciably until the following spring. It is possible, therefore, that the late settling spat, which grew least until the first winter, were the most easily transported over the winter and led to the colonisation of the main population areas. The slow initial growth of the spat has also been found in other bivalves - M. balthica (see Chapter 3); Venus striatula (Ansell, 1961); Tapes japonica (Venerupis semidecessala)(Ohba, 1959) and may be common to most marine bivalves (Muus, 1973).

4.4.2. The Occurrence of Adult Clams and Cockles.

The adult cockles were found mainly in high-shore areas of steeply sloping coarse sediment with large amounts of carbohydrate in the water although they were encountered in all types of sediment and at all tidal heights. However, although the highest biomasses were found at high levels the greatest densities occurred in the mid- to upper-tide regions. This difference was attributable to the occurrence of large numbers of small 0+ - 1+

cockles (> 2.5mm in length) in some areas e.g. at Station B3. Overall, therefore, the main cockle population was not found in the areas which received the greatest spat settlement. Secondary spat transport did not occur evenly over the whole bay, as although the central areas of Transects A and B received the largest numbers of one year old animals, the upper-shore areas on Transect C were more populated with the young animals than the lower areas. Johannessen (1973), studying _Venerupis pullustra_, also found that the density and age distribution of the population changed with the increasing tidal depth on the shore. Similarly, the occurrence of high densities of small cockles and lower densities of large ones may be common in intertidal populations (Barnes, 1972).

Some previous studies suggest that although cockles prefer muddy sediments (of M.P.D. 2.75 - 3.30 ø and over 5% S. & C.) they have been found in a large range of substrates (e.g. Eisma, 1966) and in brackish areas (Barnes, 1972); other studies show that cockles are limited to sandy areas (for ease of burrowing) although the grain size may not be important (Verwey, 1952). Areas of coarse sediment (and therefore high currents) may be favourable for suspension feeders as these areas have a high exchange of food, oxygen and metabolites (Pratt, 1953) but have the disadvantage of high currents causing the removal of adults and resuspending large amounts of silt which is deleterious to the cockles (Kreger, 1940). However, fine mud areas may have little exchange of food, oxygen and metabolites due to the low currents; such that a large suspension-feeding population could exhaust the amount of food in the water (Kreger, 1940; Pratt, 1953). The reducing conditions in fine mud would also contribute to mortality

(Kristensen, 1957) and a high amount of resuspended silt in the water would be deleterious to growth (Barnes, 1972). It is widely accepted therefore that while coarse sand areas are beneficial to suspension feeders such as cockles the reason for this is unknown. This problem will be considered further below. In addition, it is also necessary, when comparing bivalve densities and sediment types to take into account the deposition of faeces which may lead to an alteration of the substrate type (Verwey, 1952; Baggerman, 1957).

Although in the present survey cockles were found throughout the tidal range, in other studies their vertical distribution has been found to be limited at the upper limit by exposure to extreme conditions, e.g. storms, high or low temperatures and salinities and an insufficient immersion period, and at the lower limit by poor light and food conditions (Kreger, 1940; Kristensen, 1957). Kristensen (1957) stated that a submersion period of less than four hours limits the feeding of cockles although, as they can obtain oxygen from the air to some extent, they can withstand periods of irregular immersion. The highest tidal station in the present survey, C5 at 4.56m, had a minimum submersion period of 4hr. 15mins. at the spring tides and 1hr. 25mins. at the neap tides. Therefore animals at this station were never uncovered for a period greater than one tidal cycle although for much of the time their feeding rate may have been limited by insufficient submersion.

The Torry Bay M. arenaria population had the greatest densities around the mid tide level on fine sediments with a shallow slope and rich water organic matter levels. The areas of greater biomass, however, were at the mid to upper-shore areas. This difference was attributable to the occurrence of large numbers of small clams >2.5mm (0+ - 1+ groups) around the mid tide levels. It is therefore possible that some transport of small clams was still occurring during the first year. The immersion times and substrate types around the mid tidal level appeared optimal for the M. arenaria populations within Torry Bay.

The distribution of adult clams was approximately the same as the spat for both species such that clam spat transport was minimal. The M. arenaria population was therefore found to favour muddy areas where the substrate was stable, i.e. not soft mud or clean sand as the animals were poor at reburrowing after excavation (Wolff, 1973); however the adult clams did also occur on all types of substrate and tidal height to a greater of lesser extent. These findings are in agreement with Jones (1960), Pfitzenmeyer and Drobeck (1963) and Wolff (1973). Newcombe (1935) further suggests that an excess of silt limits the distribution of M. arenaria as it leads to a reduction in feeding efficiency. This situation would occur in the fine mud low-shore areas within the bay. Munch-Petersen (1973) however, studying a population of comparable density and growth rate to that on Torry Bay, found the greatest clam population in a coarse substrate (240µm M.P.D.).

The vertical distribution of Mya has been recorded as being from the sublittoral to the high water area (Pfitzenmeyer, 1962) although the sublittoral distribution of both clams and cockles may be limited by the low levels of food available and obtainable by the slow feeding rates of the bivalves (Wolff, 1973). The salinities experienced by cockles and clams on Torry Bay were within the range of tolerance for the species (Savilov, Clay, Muus, Wolff, op. cit.) and was possibly a minor factor causing mortality. However, smothering by sediment transport may have been an important cause of mortality (see Section 2.4.1.).

Previous studies suggest that many environmental factors contribute to mortality. The younger cockles have been found to be more susceptible to extremes of salinity and temperature (Savilov, 1953; Kristensen, 1957; Farrow, 1971), although as the speed of reburrowing decreases with the age of the cockles, the older animals are more liable to be removed by storms (Kreger, 1940; Kristensen, 1957). Temperatures to -2°C have little effect on the mortality but below that mortality can be high unless the animals are buried sufficiently well.

In both species, the greatest mortality occurred during the first year of life after which the biomasses and densities of each cohort were relatively stable, although there was a slight decrease in density with increasing age. The biomasses of the M. arenaria cohorts greater than 1+ reached plateaux at ≈ 200mg fdw m^{-2} possibly indicating that the bay could support only a limited population with an average of 30-40 clams m^{-2} for the area. As the biomass of each cockle cohort increased with increasing age, the gain to the population by the growth of surviving individuals was greater than any loss due to mortality.

The mortality rates for older cockles of 4 - 25% per month given by Wolff and De Wolf (1977) are much higher than experienced in the present study. Many other studies describe the high mortality of second winter cockles attributable to oystercatchers and gulls (Kristensen, 1957; Hancock and Urquhart, 1965; Seed and Brown, 1975; Horwood and Goss-Custard, 1977) and the possible avoidance of young cockles by the main predators. That this selective mortality of older cockles has not been observed in the present study is probably attributable to the lower densities of both cockles and oystercatchers in the area. A proportion of the high mortality of very young cockles and clams may be attributable to predation by wading birds, although in other areas of the Forth both species have not been found to be prey items to any large extent (Bryant, Warnes, pers. comm.). Other predators such as flatfish and shore crabs also take small cockles (Kreger, 1940; Kristensen, 1957; Seed and Brown, 1975) although the extent to which this occurs on Torry Bay is unknown (see also Section 7.3.2.).

The major part of the cockles' mortality occurred during the late autumn and winter months, was attributable largely to extremes of temperature, wave action and associated sediment transport and, to a lesser extent, predation and mainly affected the very small cockles. Hancock and Urquhart (1965) also found that most of the mortality of cockles occurred during October to January although in their population it was mostly attributable to oystercatcher predation. The greatest mortality of M. arenaria occurred during the spring in 1+ age cohort animals. This period coincided with that of the greatest growth by these animals and may be indicative of greater mortality by predators attributable to the clams greater value as prey items. Burke and Mann (1974) recorded greatest mortality in their Mya population during the late summer but did not suggest the cause for this mortality.

The density of cockles found in Torry Bay, up to a maximum of $3000m^{-2}$ including a large number of spat, are in the central part of the range given by Clay (1967d) for northern European estuaries. The overall Torry Bay population was larger than as reported for many estuaries in Britain, e.g. Clyde, Tamar, Exe, Tees, Mersey, Dee, although the number of large cockles (up to $200m^{-2} > 2mm$) was less than for comparable areas. Comparable densities of cockles for muddy areas include :-

Mersey	up to $64m^{-2}$	Fraser (1932)
Dovey	up to $1600m^{-2}$	Beanland (1940)
Tamar	up to $383m^{-2}$ ($93m^{-2} > 10mm$)	Spooner and Moore (1940)
Exe	up to $288m^{-2}$ ($60m^{-2} > 10mm$)	Holme (1949)
Burry Inlet	up to $357m^{-2}$	Yonge (1949a)
Argyll (sandy areas)	up to $1000m^{-2}$	Raymont (1955)
Solent (central regions)	up to $485m^{-2}$ (> 4mm), generally $150 - 200m^{-2}$	Barnes (1972)

The maximum numbers of M. arenaria found on Torry Bay, up to an average of $220m^{-2}$ ($30 - 40m^{-2} > 2mm$), appear low to average when compared to other European areas (Clay, 1967c) although very little comparable data are available. However, the Eastern U.S. Seaboard, where clam farming occurs, has much greater densities of clams. Burke and Mann (1974) found similar densities in a Canadian population to those encountered here. Moreover, Jones (1960) suggested that 30 - 40 animals m^{-2} constituted a well-populated area. The Lynher estuary population studied by Warwick and Price (1975) had a maximum density of $184m^{-2}$ at settlement in April which was reduced to $12m^{-2}$ by the following June. Only 2 animals m^{-2} were found to survive the first year. It should be noted, however, that their "newly-settled" animals were 3 - 5mm in length in April; it is possible that these animals were the spatfall of the previous year and that these authors missed the very young animals and sampled the 1+ group during the period of rapid growth and high mortality found in the present study (see also Muus, 1973).

4.4.3. The Growth of the Animals.

The growth patterns found for these species showed many similarities to those found for many other suspension-feeding bivalves (see Table 4.15) regarding both the physical and biotic factors affecting growth and the extent and pattern of growth over both annual and life cycles.

The populations of both species were numerically dominated by the younger age classes (0+ and 1+ in M. arenaria and 0+, 1+ and 2+ in C. edule). The species exhibited sigmoid growth patterns both over the annual cycle (from winter to winter) and over the life span. Three phases of growth were observed over the life span of each species ; an initial period of slow growth lasting up to a maximum of nine months depending on the time of spawning of the individual, a period of linear growth, and a final period in which the growth decreased rapidly with increasing age as the asymptotic size was reached. The final stage was at ages > 6+ in both species. It should be realized that as growth occurs by volume and as large animals show a relatively greater increase in body mass over body length, in order to keep growth constant, large bivalves require either longer or more efficient periods of feeding (Seed, 1969). As these conditions were not fulfilled, growth declined with age.

The exclusion of the first part of the growth curve enabled Bertalanffy equations to be computed for each species ;

M. arenaria

$$L_t = 69.84\ (1 - e^{-0.305(t - 0.889)})$$

C. edule

$$H_t = 24.74\ (1 - e^{-0.373(t - 0.614)})$$

In order to facilitate easier comparison with other studies :

$$L_t = 26.58\ (1 - e^{-0.373(t - 0.583)})$$

$$\text{as } H_t = 0.942 \pm 0.006L_t - 0.289$$

The overall maximum theoretical size of C. edule was slightly lower than the actual maximum size found for the species on Torry Bay although some stations H_∞ values were more in agreement with the maximum size sampled. The maximum theoretical size of M. arenaria was in agreement with the size of the largest animal sampled of 61mm. The maximum theoretical sizes of both species indicate longevity of 9 or 10 years, which is within the range of the species' life spans (Clay, 1967c, d).

The Growth of M. arenaria.

The Forth population Bertalanffy equation is in agreement with that found for a Danish shallow sublittoral population :

$$L_t = 60.1\ (1 - e^{-0.297(t + 0.110)})$$

(Munch-Petersen, 1973) which reached a comparable size in a similar life span. The latter population, however, exhibited a faster growth rate during the first year than the Torry Bay population but decreased to a greater extent towards the end of the life span. Using data given in Newcombe (1935) a Bertalanffy equation for a Canadian intertidal population of M. arenaria was calculated :

$$L_t = 116.49\ (1 - e^{-0.124(t - 0.403)})$$

Table 4.15 The Growth of Suspension-feeding Bivalves.

Species, Author.	The Environmental Factors.	Growth over Annual Cycle.	Growth over Life Cycle.	Comments.
Mya arenaria,				
Newcombe, 1935	Growth best on lower shore, slow on large grained sediments, unstable sands, upper shore.	Seasonal variation not correspond to temp. variation. Max. growth spring - early Summer (to Dec. if good conditions,); depends on water food (diatoms) quality.	Best growth 1st. & 2nd. years; declines with age.	Up to 17 years age; max. size 98.4 mm.
Coe & Fox, 1942		Growth retarded by low temps. and during gametogenesis.	8-20 mm at spawning when 1 year old.	Max. size 143 mm.
Swan, 1952	Growth better in sand than mud or gravel. Suspended silt reduces growth.	23 mm at 1st. Winter.		Possibly missed 1st. yr. animals due to sampling.
Jones, 1960	No growth differences with substrate.		10, 20, 29, 34, 36 mm at successive years.	Cannot verify but probably missed 1st. year.
Munch-Petersen, 1973	Shallow water, salinity 14-19^{o}/oo, coarse sed. population studied.	Sigmoid growth.	Sigmoid, 0-17 mm at 1st. yr.; 17-27 mm at 2nd. yr.	Max. size 60.1 mm in 10 years.
Burke & Mann, 1974		Growth occurred until November.	35 mm at end of 3rd. yr. on sand flat.	
Warwick & Price, 1975	Popn. in v. fine muds, high %C.; 19-34^{o}/oo sal.; below MWL.			
Cerastoderma edule				
Orton, 1926		28 mm at Dec. after settling.	19-22, 28-32, 33-36, 35-39 mm at successive years.	
Stephen, 1930	Growth increased with submersion.		6, 18, 20.6, 20.9, 22.4, 23.0 mm at successive winters.	Author doubtful about 1st. 2 yrs.' rings as others follow Orton's work.
Kreger, 1940	Growth/density independent; limited by much detritus and decreasing submersion. Current flow and MPD. affects growth.		23.0 mm at 1st. winter.	Possibly missed spat due to sampling.

Table 4.15 continued.

Species, Author.	Environmental Factors.	Growth over Annual Cycle.	Growth over Life Cycle.	Comments.
Cerastoderma edule,				
Wernstedt, 1943		Most growth correlated with diatoms.		
Verwey, 1952	Growth best with submersion and fast currents.			
Kristensen, 1957	Detritus and 2000 m^{-2} 1st. yr. cockles decreases growth. Better growth with submersion and on coarser areas.	Growth in Spring- early Summer; v. little after August.	17, 27, 31, 34, 36 mm at successive years.	Max. age 8 yrs. May have missed early settlers.
Craig & Hallam, 1963			4.5, 10.5, 16.0 mm at successive ages.	Rings interpreted from Orton's work.
Farrow, 1971	Best growth in well sorted sand. Degree of tidal cover affects size only in 1st. yr. Cohort-size decreased with T.H.	Growth-season possibly shorter in dense popns. Shell growth not correl. with temp. but flesh growth may be.		
Barnes, 1972	Growth correlated with submergence.	Most growth May-July.	12 mm at 1st. winter, 20 mm at 2nd. winter.	Possibly missed spat (<4mm) due to sampling.
Hancock & Franklin, 1972		Growth mid-May to mid-Sept., but shell-thickening over rest of year.		
Seed & Brown, 1975		Main growth April-Sept.; little or no growth at remainder of year.	7mm at 1st. winter; 15 mm after 1 yr.; declines with age.	Reproduction in 2nd. yr. affects growth.
Warwick & Price, 1975	As for M. arenaria, (see above).			
Hibbert, 1976	Best growth on muddy, low-shore areas.			
Horwood & Goss-Custard, 1977	Inverse relationship between density & growth.			
Wolff & de Wolf, 1977		1+ group grew from Feb./Mar. to Aug./Sept.		
Mytilus edulis				
Baird & Drinnan, 1957	Growth decreases with increasing wave action and exposure.			

Table 4.15 continued.

Species, Author.	Environmental Factors.	Growth over Annual Cycle.	Growth over Life Cycle.	Comments.
Mytilus edulis,				
Seed, 1969	Immersion period, popn. density, temp., salinity, suspended silt, storms & genetic differences affect growth.	No growth in winter; 90% annual growth occurred Apr.-Sept. Food, not temp. limits growth.	Popn. growth relatively uniform. Inverse relationship between growth rate and longevity.	
Thiesen, 1975			Sigmoid growth.	
Dare & Edwards, 1975, 1976	Growth density dependent.	Max. growth Apr.-Sept. after spawning. Very little growth over winter.		
Mercenaria (Venus) mercenaria,				
Chestnut, 1952	Growth stunted in muddy areas.	Max. growth before and after hottest part of yr. in Feb., May, Oct.		
Pratt, 1953; Pratt & Campbell, 1956	Grows better in sand than muddy-sand; growth limited by detritus and suspended silt.	Grows mid-Apr.- mid-Nov. but max. growth occurred by mid-July. Temperature limits growth.		Areas of max. growth not best areas for density. Spawning occurred at time of max. growth.
Ansell, 1964a,b	Growth slightly better on sand than gravel or mud.	Growing season limited by temp., max. growth occurs June-Aug.		Most of growth occurs at same time as spawning.
Venerupis pullustra,				
Quayle, 1952,b		Growth increases with temp. to July then decreases while temp. still high.		
Tapes japonica (V. semidecussata),				
Ohba, 1956, 1959	Growth density dependent.	Sigmoid growth.	Sigmoid growth.	
Venus striatula,				
Ansell, 1961		Ditto as Quayle, 1952,b.		Max. growth occurs with spawning but not with gametogenesis.
Meretrix casta,				
Durve & George, 1973	Growth best in clean areas.			Areas of best growth not favourable for population.

Table 4.15 continued.

Species, Author.	Environmental Factors.	Growth over Annual Cycle.	Growth over Life Cycle.	Comments.
Mytilus californianus, Coe & Fox, 1942	Growth related to dinoflagellate density.	Growth inversely related to temperature.		
Patinopecten yessoensis, Fuiji & Hashizume, 1974		Max. growth period followed spawning.	Growth efficiency decreased with age.	
Tivela stultorum, Coe, 1947		Growth increased with temperature to July then decreased while temperature still high.		
Adamussium colbecki, Laternula elliptica, Ralph & Maxwell, 1977	Sublittoral, Antarctic species.		Probably showed sigmoid growth but no initial inflexion point found.	

Individuals in this population were found up to an age of 17 years, suggesting that the growth coefficient (K) was related to the longevity of the individuals. The growth constant (K) and maximum size of a comparable intertidal population in the Lynher estuary, South England (Warwick and Price, 1975) were respectively lower and greater than for the Forth population, although the linear growth over the first seven years in the Lynher population produced an exceptional maximum theoretical size :

$$L_t = 182.3\ (1 - e^{-0.093(t\ -\ ?)})$$

The isolation of the first year (spat) animals in the Lynher was questionable and may affect the final growth equation. The absolute growth of M. arenaria on Torry Bay was found to be in agreement with other intertidal populations :

Area \ Age (yrs.)	1	2	3	4	5	
Torry Bay	3	20	34	43	50	This study.
Bay of Fundy	16	21	33	45	54	Newcombe (1935).
Essex	10	23	37	46		Jones (1960).
Lancashire	19	33	45	55		" "

(all sizes in mm).

Ralph and Maxwell (1977) made inter-specific comparisons of the K-values of comparable temperate and antarctic lamellibranchs. The difference between M. arenaria ($K = 0.297$ $L_\infty = 60.1$ (Munch-Petersen, 1973); $K = 0.305$ $L_\infty = 69.8$ (This study)) and Laternula elliptica a convergent equivalent of M. arenaria (Yonge and Thompson, 1976)($K = 0.16$ $L_\infty = 105.4$ (Ralph and Maxwell, 1977)), reinforces the suggestion that "arctic" or sublittoral bivalves are slower growing and have a longer life span than their temperate or intertidal equivalents (see Section 3.5.2.3.). The growth of the Devon M. arenaria population ($K = 0.093$ $L_\infty = 182.3$ (Warwick and Price, 1975)) however, does not support these conclusions. It is possible that growth in the Lynher population decreased more rapidly in the ages greater than those measured than in other populations; the calculated maximum size would then have been within that found for the species generally (Newcombe, 1935; Swan, 1952; Tebble, 1966; McMillan, 1968).

The Growth of C. edule.

The growth parameters of the areal population agree with those for other populations and, although the overall K and L_∞ values appear lower than comparable populations, the range of values obtained for areas of Torry Bay encompass the values obtained for other areas :-

	K	L_∞	Author
Forth	0.373	26.6	This study.
Lynher (Fine mud)	0.460	42.3	Warwick and Price (1975).
Burry Inlet (Sand)	0.710	30.7	Hancock (1965).

		H_∞	
Forth	0.373 (0.194-0.596)	24.7 (21.4-32.6)	This study.
N. Ireland	0.463	30.4	Seed and Brown (1975).

The respective similarity and difference in the L_∞ and K values between the Forth and Burry Inlet populations suggest that the Forth population took longer to reach the asymptotic size, whereas a comparison between the Lynher and Forth populations indicates that the former grew faster over the first few years of life. It is necessary however to question the growth rate measured by these other bivalve studies as the spatfall and ages of the smallest animals encountered may have been misinterpreted (Muus, 1973; Yamaguchi, 1975).

The growth parameters estimated for the Irish cockle population were calculated from data given by Seed and Brown (1975) and show a similarity to the Forth population. The use of a 2mm sieve in sampling the former population would have missed the smallest animals and therefore overestimated the size of the first winter cockles. It is considered that had this bias been omitted then the growth parameters would be in greater agreement.

The absolute growth of Torry Bay C. edule showed similarities with that found by Stephen (1930) and Craig and Hallam (1963) for the outer Firths of Clyde and Forth respectively. These authors measured shell rings of 6, 18, 20.6, 20.9, 22.4 and 23.0mm and 4.5, 10.5 and 16.0mm respectively and then further suggested that the rings below 15mm in each population were not growth rings and that by omitting these rings, the cockles' growth was in agreement with that found by Orton (1926). The results of the present survey suggests that the ommission of the first rings as indicative of yearly growth was erroneous.

Other studies of growth estimated that the first year cockles (0+) grew to a size 17-23mm by the first winter (Orton, 1926; Kreger, 1940; Kristensen, 1957) and that after the very large growth during the first one or two years of life the growth rapidly decreased to 2-3mm per year. More recent studies suggest an initial period of slow growth is common to bivalve molluscs (Johannessen, 1973; Muus, 1973; Thiesen, 1974; Seed and Brown, 1975) followed by a period of rapid growth which then decreases with increasing age. It is possible, therefore, that the sampling and sorting methods employed by these early workers resulted in underestimates of the ages of the cockles in their respective populations. It is also possible, however, that many other areas produce much larger annual growth increments than encountered in the present survey.

The annual growth cycles of both C. edule and M. arenaria also described sigmoid growth patterns with little or no growth over the late-autumn to early-spring period and the major part of the annual growth occurring during the period April - October. Within both species, growth occurred as temperature increased until the maximum temperature in August; growth then continued slowly as the temperature decreased slightly until October. Growth in the majority of the cohorts commenced when the mean air and water temperature was 9°C in the spring but ceased at a temperature of 11°C in the autumn. It appears, therefore, that temperature or temperature-related effects regulate growth to some extent in both species. Most authors have identified temperature as being important in determining growth rates (Orton, 1926; Coe and Fox, 1942; Coe, 1947, 1948; Chestnut, 1952; Quayle, 1952b; Savilov, 1953; and Ansell, 1961), whilst Farrow (1961) suggested that internal growth, rather than shell growth, may be correlated with temperature. Pratt and Campbell (1956) found an upper and lower temperature limit between which growth in Venus mercenaria occurred. However both Newcombe (1935) and Seed (1969) suggested that the levels of food, e.g. detritus and diatoms, determined growth although these levels were to some extent dependent upon temperature. Many other authors do not identify temperature as a growth regulator but do show that, depending upon the geographical distribution of the species, most of the annual growth in bivalves occurred during the summer months (see Table 4.15 and Savilov, 1953).

Although growth commenced during April, the major part of the annual growth of the suspension-feeding bivalves occurred following spawning (May in C. edule, June in M. arenaria)(see following section) suggesting that while much of the available energy was used in spawning, less was available for flesh or shell growth. This is neither in strict agreement with Orton (1928) working on oysters nor Ansell (1961) studying Venus striatula, and demonstrates physiological antagonism (see Section 3.5.4.2.). Other workers, however, have also found that growth in suspension feeders either slows down or stops whilst spawning and the period of most vigorous growth occurs after spawning (Coe and Fox, 1942; Fuiji and Hashzumi, 1974; Dare and Edwards, 1976).

The growth of C. edule on Torry Bay varied spatially, was dependent on environmental conditions and may be summarised ;-

(i) the growth rate was greatest in clean sediments with little attached macroflora at the mid- to upper-shore area (e.g. Stations B4 and C3);

(ii) the growth curves diverged with time although the sizes of the first winter cockles were relatively similar at each station;

(iii) the growth of young cockles was greatest at the low-shore, muddy areas where few large cockles were present;

(iv) the growth later in the life span was greatest at the upper tidal areas supporting Z. marina and a relatively large cockle population (e.g. Stations A3 and C5). However the size of older animals decreased with increasing tidal height and they achieved the greatest size at mid tidal levels which did not support the greatest biomass of large cockles.

(v) The maximum size (H_∞) was greatest in the lower-shore fine sediment areas whereas the rate at which that size was attained (K) was greatest in the mid-shore, fine sediment areas.

The latter shows the inverse relationship between these two parameters and demonstrates the necessity to consider both the whole Bertalanffy equation and the growth curve when comparing populations (see also Section 3.5.2.3.).

These findings, of the large influence of tidal height on cockle growth, are partly in agreement with those of other workers who stress the importance of the submersion time as controlling feeding and growth in suspension feeders (see Table 4.15); a decrease in cockle size at a specific age with increasing tidal height was also, for example, found by Stephen (1930) and Farrow (1971), although the latter author found that the degree of tidal cover only affected growth in young cockles. The present study, however, suggests that tidal height should be considered together with the sediment type and its related characteristics, and the associated water movements. The deleterious effect of silt on suspension-feeding, whereby the filtration rate and feeding are decreased and the pseudofaeces production and energy expenditure are increased, has been well documented (Pratt, 1953; Johannessen, 1973). The greater growth shown by suspension-feeding bivalves in non-muddy areas is dependent on these factors as well as the increased water currents over coarser areas which increases food availability and oxygen exchange. The absence of adult C. edule from the very muddy, low tidal areas of Torry Bay may be attributable to those areas being unfavourable because of these factors.

The spatial growth of M. arenaria was not investigated although it is considered that it would be lesser affected by the factors affecting the growth of C. edule and other bivalves (see Table 4.15; Newcombe, 1935; Swan, 1952).

Growth of suspension-feeding bivalves therefore involves the interactions of many factors and that the correlations identified between growth and environmental factors can only suggest a possible explanation of the growth patterns. Ideally, controlled experiments would enable true correlations between biotic and physical factors and growth to be made.

4.4.4. The Condition of the Bivalves in Relation to Spawning and Growth.

The annual change in the condition of each species followed similar patterns and could, to some extent, be associated with environmental changes which resulted in physiological, reproductive or nutritional changes in the animals. The condition of individuals in both species increased to a maximum during May-June and then rapidly decreased with spawning before the period of rapid growth. The disproportionate shell and flesh growth also affected the condition, i.e. the period of growth involved an increase in shell dimensions at the expense of the flesh. The cessation of growth and its associated emaciation in October were followed by a slight increase in condition before a second period of emaciation during the winter. The latter was possibly attributable to a lower food uptake that was insufficient to either support growth or balance the requirements of normal metabolism. The low food uptake appeared to have been caused more by the low temperature leading to decrease in filtration than by low food availability. The changes in condition were therefore attributable to temperature and food availability (mainly suspended particulate carbohydrate but also organic carbon) with reproductive and growth activity having overlying effects. It is suggested that temperature was the main limiting factor on condition and that food availability would not effect the condition if the temperature was low. Furthermore there is little possibility that suspended food in an estuary was limiting as large amounts of organic matter were always found in the water column. However, further comment cannot be made as the proportion of that organic matter that is taken as food is unknown (see page 252).

Changes in condition, attributable to spawning, growth and winter emaciation, similar to those outlined above have been identified in various suspension-feeding bivalves, C. edule (Hancock and Franklin, 1972; Wolff and De Wolf, 1977); Venus (Mercenaria) mercenaria (Ansell et al, 1964a, b) and M. edulis (Baird, 1958; Dare and Edwards, 1975, 1976), and may be regarded as generally occurring in temperate, intertidal suspension-feeding bivalves.

The large decrease in condition following spawning in both species differs from the work of Kristensen (1957) and Hancock and Franklin (1972) who found that any loss of flesh weight due to spawning was compensated for by the rapid growth such that the flesh weight of C. edule was found to increase slightly up to the end of the shell growing period. This lack of compensation within the Forth populations may be an indication of greater spawning and/or poorer conditions leading to the cockles' slower growth. The conclusions reached in the section above suggest that the latter alternative may account for the differences.

It is considered that the spawning of C. edule and M. arenaria on Torry Bay commenced during May and June respectively when the mean temperature was 11° and 15°C, although, as indicated by the spat settlement, the majority of the spawning occurred from July to September. These patterns agree with those found in other studies (Jones, 1960; Pfitzenmeyer, 1962; Hancock and Franklin, 1972; Seed and Brown, 1975). Thorson (1946), Ansell (1961), Pfitzenmeyer (1962) and Ansell et al (1964a) suggested that temperature was the main factor controlling spawning and that in some species there may be a critical temperature range within which spawning occurs. Pfitzenmeyer (1962) found that M. arenaria spawns when the temperature is within the range 10-24°C, and suggested that colder temperatures were less critical than warmer ones in the spawning of boreal species.

It is considered that although the effect of potential food concentrations on the spawning of M. arenaria and C. edule was unclear, these concentrations were of secondary importance in determining spawning. Ansell (1961) found that an increase in temperature or phytoplankton density would cause an increase in the filtration rate of Venus striatula which would accelerate the rate of gonad proliferation. Furthermore, Thorson (1946) considered that whilst temperature controlled breeding, poor food conditions during warm temperatures will hamper both breeding and the development of the larvae.

The flesh weight of standard size cockles and clams showed a decrease following spawning similar to the corresponding change in condition, which decreased by one third because of spawning. This factor suggests that the decrease was attributable more to spawning than to growth and also gives an indication of the amount of energy diverted to spawning. Similarly, the cockles' flesh weight changes showed that although the larger animals increased in flesh weight proportionally more than the younger ones, a smaller proportion of the available energy was used in reproduction. Furthermore, the older cockles showed the greatest emaciation over the autumn and early winter. However, although the flesh weight of a standard size cockle was, except during spawning, linearly related to the suspended carbohydrate, the condition factor was not; this suggests that apart from changes attributable to growth and spawning, the animals' flesh weight was related to the amount of phytoplankton in the water. This factor further shows the need for the consideration of both condition factor and standard animals' flesh weight (see Section 3.2.1. and page 250). The flesh weight of a standard size clam was not related to the potential food within the water column.

The shell weight of both species increased during the latter part of the year, suggesting that a period of shell thickening occurred following the period of rapid growth when the animals were in a state of emaciation. This trend has also been shown to occur in other populations of <u>C. edule</u> (Hancock and Franklin, 1972), <u>Mercenaria mercenaria</u> (Hibbert, 1976) and <u>M. edulis</u> (Dare and Edwards, 1976). The latter authors found that shell and flesh weight changes fluctuated out of phase suggesting the occurrence of either shell thickening and/or a diversion of energy to shell growth during the summer which resulted in emaciation. The cockles' total and flesh weight fluctuations over the year decreased with increasing age which may be a reflection of the reduced reproductive activity, growth and metabolism in older animals (Wilbur and Owen, 1964; Seed, 1969). This was not shown in the clams as only a small age range was studied.

The condition and percentage flesh weight of standard size M. arenaria within broad areas of Torry Bay, did not significantly differ between low-shore, fine muddy areas and upper-shore, coarse sandy areas, i.e. animals from one area did not have thicker shells or more flesh with respect to another. The C. edule individuals from the low-shore fine areas however, were of higher condition than those from the upper-shore, coarse areas. These findings differ from those of studies on other suspension-feeding bivalves where excess silt either in the water or in the mud led to a decrease in condition which was attributable to the larger energy expenditure in obtaining food (Newcombe, 1935; Pratt, 1953; Durve and George, 1973; Peddicord, 1977). However, other authors have stressed the importance of the immersion period in determining the growth and condition of suspension-feeding bivalves (Newcombe, 1935; Baird and Drinnan, 1957). The latter authors suggest that as a result of exposure, mussels will not only obtain less food and calcium such that their shells are smaller, but because of the basal metabolic needs whilst exposed their condition will be lower than animals under greater submergence.

It is therefore considered that, for M. arenaria, any disadvantage of living in the low-shore, fine mud areas of Torry Bay and attributable to the high silt content, was overcome by the advantages of living under an increased immersion period. Similarly, the C. edule individuals suffered less from the deleterious effects of the fine sediments than from an increased exposure period.

4.4.5. The Production of Suspension-feeding Bivalves on Torry Bay.

The major part of the M. arenaria population production each year was attributable to the 1+ age cohort, i.e. during 1975-76, the 1974 cohort, and during 1976-77, the 1975 cohort. The 1974 cohort, as the remains of a very successful spatfall, was predominant in the population during each sampling year such that during 1976-77 this cohort was the most abundant, although the 1975 cohort was the most productive. The 1+ age group also had the largest $P/\overline{B}$ (in the range 5 - 7), in the population which was responsible for the relatively high population $P/\overline{B}$ of 3.29 (as an average for the two years sampled). This population $P/\overline{B}$ is in agreement with that found for a Canadian population of 2.54 but is much higher than values of 0.5 and 0.6 for south west England and Danish populations respectively (Munch-Petersen, 1973; Burke and Mann, 1974; Warwick and Price, 1975). The large difference between these two sets of estimates is attributable to the number of age classes included in the production estimates in each population. In this study and that of Burke and Mann (1974) only a depth of 15cm was sampled such that only the younger, more productive cohorts (< 3 yrs.) were sampled. Burke and Mann (1974), however, do not suggest this as the cause of their high estimate when compared to other long living populations. An indication of the declining $P/\overline{B}$ with increasing age was given by the decrease in $P/\overline{B}$ from the 2+ and 3+ age classes (see Table

4.12a); it is therefore considered that the inclusion of the older age classes would have reduced the population P/$\bar{B}$ value (see also Hibbert, 1976). The 1+ cohort studied by Burke and Mann (1974) also had the highest production although the 0+ cohort, unlike the corresponding cohort in the present study, had the highest P/$\bar{B}$.

Although the major part of the _M. arenaria_ production was attributable to a single age class, each _C. edule_ cohort between 1+ and 4+ contributed relatively equally to the total population production although the 2+ and 3+ were the most important age classes. As with the _M. arenaria_ population, the cohorts showing the greatest production were those whose growth rate described the linear part of the growth curve. The cockle population showed an inverse relationship between P/$\bar{B}$ and age although during 1975-76 the spat had the highest P/$\bar{B}$, whereas the following year the 1+ gave the highest value. This inverse relationship has also been noted for populations of _Mercenaria mercenaria_; _Venerupis aurea_ and _C. edule_ in Southampton Water (Hibbert, 1976, 1977a, b) and probably occurs in most animal populations (see Section 3.5.5. and Zaika, 1973).

The spat of both species, although present in high numbers, constituted a small part of the population biomasses and contributed relatively little to the annual production. The respective spat biomasses were of a similar size but while the _M. arenaria_ 0+ group had a low P/$\bar{B}$ value, possibly because of the slow growth of this cohort, the _C. edule_ spat had a relatively high P/$\bar{B}$ and therefore probably had a higher flesh growth rate. Similarly, the production of the 0+ groups of each species during 1976-77 did not reflect the greater spatfall of that year possibly because of the increased spat mortality together with the low biomasses present.

When compared to other North Temperate studies (see Table 4.16), the overall production and mean biomass estimates for both species of suspension-feeding bivalves on Torry Bay were at the lower part of the range. The cockle $P/\bar{B}$ estimate was within the range encountered for the species in other studies whilst the clam $P/\bar{B}$ was higher than encountered elsewhere; the reasons for this difference being given above. The $P/\bar{B}$ values for the intertidal and shallow sublittoral suspension-feeding bivalves all lie within the narrow range suggested for aquatic invertebrates generally (Boysen-Jensen, 1919 and Sanders, 1956, both in Munch-Petersen, 1973; Zaika, 1973). The table (4.16) also gives an indication of the inverse relationship, suggested by Zaika (1973), between the $P/\bar{B}$ and the number of age classes incorporated into the estimation although many more data are needed to quantify further the relationship.

It may be concluded, therefore, that while Torry Bay was found to support generally both a lower production and biomass of suspension-feeding bivalves than elsewhere the productivity was as great as that found in other studies. It may be suggested therefore that although the Torry Bay populations of <u>C. edule</u> and <u>M. arenaria</u> were not as well established as elsewhere, the animals present were in a comparable physiological condition.

The most productive stations for <u>C. edule</u> were similar for each year of sampling being B4 and C5, which were sandy, mid- to upper-shore regions producing ≈ 5g fdw m^{-2} yr^{-1} with A1, A3, B3, B5 and C4 also having the relatively high production of 1.5g fdw m^{-2} yr^{-1}. The productivity generally decreased with an increased

Table 4.16 The Production, Mean Biomass and Productivity of Suspension-feeding Bivalves. (Range of values in parentheses.)

Species	Production (* g f.d.w. others g afdw m^{-2} yr^{-1})	Mean Biomass (* g f.d.w. others g afdw m^{-2})	Productivity Annual P/B	No. of Cohorts Used.	Author
M. arenaria	0.819*	0.248*	3.295	3	This Study;
	(0 - 4.830)*	(0 - 1.339)*			" "
	2.66	5.54	0.5	8	Warwick & Price (1975);
	11.6*	4.6*	2.54	3	Burke & Mann (1974);
	100.1*	167.0*	0.6	10	Munch-Petersen (1973);
C. edule	1.008*	0.997*	1.011	6	This Study;
	(0.001 - 4.624)*	(0 - 3.533)*			" "
	0.205	0.847	0.2	-	Warwick & Price (1975);
	0.05 - 119.82	0.01 - 46.73	0.69 - 8.92 (1 - 2.5 norm.)	7	Wolfe & de Wolf (1977);
	29 - 71	18 - 65	1.1 - 2.6	7	Hibbert (1976);
Venerupis pullustra	20	13.5	0.15	-	Johannessen (1973);
V. aurea	1.25 - 0.70	1.14 - 0.63	1.1	5	Hibbert (1976);
Mercenaria mercenaria	4 - 14	8 - 50	0.2 - 0.5	10	" "
Mytilus edulis	4 - 20*	3 - 15*	1.3	-	Burke & Mann (1974);
	268*	240*	1.12	10	Milne & Dunnet (1972);
		(125 - 400)			" " "
Crassostrea virginica	815.6	405.8	2.01	-	Dame (1976).

tidal height again reflecting the settlement of the spat at areas away from the main bulk of the population. These findings are partly in agreement with those of Wolff and De Wolf (1977) who found the highest cockle $P/\overline{B}$ at stations with the greatest number of juveniles, although these authors estimated that the highest production of C. edule occurred low in the intertidal zone. The areas of highest M. arenaria production were generally at or near the mid to low tide, muddy/fine sand areas whilst the $P/\overline{B}$ values were relatively constant across the shore as both large and small animals occurred in similar areas. It is suggested therefore that the larger production of the M. arenaria population was attributable to greater growth at lower-shore, fine sand areas (as found by Savilov, 1953) as well as the occurrence of larger densities and biomasses of animals up to 3 years old.

The general distribution patterns displayed by the biomasses at each station were also evident with the station production estimates; however, as the spat contributed little to the total station biomass, the production and the $P/\overline{B}$ at the majority of the stations were mainly influenced by the biomass of large animals present.